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**THE DIET OF THE CAPE FUR SEAL
ARCTOCEPHALUS PUSILLUS PUSILLUS IN NAMIBIA:
VARIABILITY AND FISHERY INTERACTIONS**

by

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For Dune



In darkness ... your eyes shall be opened to the beauty of God
(7 July 2001)

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Abstract

Author: Silvia Mecenero

Title: The diet of the Cape fur seal *Arctocephalus pusillus pusillus* in Namibia: variability and fishery interactions.

Date: February 2005

This study investigated spatial and temporal variability of the teleost portion of the diet of Cape fur seals *Arctocephalus pusillus pusillus* at three mainland breeding colonies in Namibia (Cape Cross, Atlas-Wolf Bay and Van Reenen Bay) over a period of eight years. Diet data was obtained from monthly scat samples, from which fish otoliths were processed. The diet reflected mainly that of lactating seals. The monthly percentage abundance and mass of the six prey groups identified was estimated, and compared between the three colonies and at annual, seasonal and monthly scales. This information was used to estimate the total consumption of lactating seals in Namibia by developing a more dynamic model of consumption. Also investigated was the degree to which seals and the purse-seine fishery overlapped in the utilization of the Cape horse mackerel *Trachurus trachurus capensis* resource, an important commercial fish of Namibia. The concept of using horse mackerel information from seal scats to predict future fish stocks was explored. Due to the controversy surrounding the consumption of endangered seabirds by Cape fur seals, the occurrence of seabirds in the samples was investigated. Lastly, the methods of scat collection and analysis were examined (sample size and sampling unit), mainly using randomisation and bootstrap procedures, and recommendations made for the future analysis of seal diets using scats.

Six main teleost prey groups were identified. The diet of Cape fur seals in Namibia varied between colonies. The main prey at Cape Cross, the northerly colony, constituted Cape horse mackerel, Cape hakes *Merluccius capensis* and *M. paradoxus* and pelagic goby *Sufflogobius bibarbatus*. At Atlas-Wolf Bay and Van Reenen Bay, the southerly colonies, the main prey were Cape hakes, pelagic goby and lanternfish *Lampanyctodes hectoris*. The diet displayed annual, seasonal and monthly variation. Seal diets did not display strong annual patterns, and was therefore not predictable on a seasonal basis. The total annual consumption of commercial teleost prey (Cape hakes and Cape horse mackerel) by lactating seals in

Namibia was less than the amount taken by fisheries. The consumption of commercial prey at Cape Cross was greater than at Atlas-Wolf Bay and Van Reenen Bay, where non-commercial prey were mainly consumed. The model estimated that a female of average mass 56 kg ingested 13% of her body mass per day.

Seals at Cape Cross and the purse-seine fishery in northern Namibia overlapped in their utilization of age-2 horse mackerel when overlap was high. When overlap was low, seals consumed mainly age-0 horse mackerel while the fishery caught age-2 horse mackerel. Both unadjusted and adjusted overlap measures showed that overlap between seals and the fishery in their utilization of juvenile horse mackerel was high only at times when horse mackerel abundance was high, and was low when abundance was small. The annual mean percentage mass of horse mackerel in the seal diet was strongly correlated to the annual purse-seine total catch lagged by two years. It was concluded that seal scat analysis could be used to complement fishery and survey data to improve models for the management of the horse mackerel resource.

Seabirds were negligible in the diet of lactating female seals at the study colonies, confirming the current belief that it is a minority of sub-adult males which are responsible for the overwhelming majority of the predation on seabirds.

Scat analysis has biases, especially due to the partial or complete erosion of otoliths during digestion, and consequently correction factors for numbers of otoliths lost and erosion of otolith diameters were used in this study. The sample size required depends on the degree of precision required; the widths of the 95% confidence intervals decreased as sample size increased. Individual scat sampling is preferred to bag (pooled) sampling. The study confirmed that monthly sampling is the appropriate frequency to obtain insight in trends in seal diets within the complexities of the Benguela System. Sampling should be extended to the entire range of the Cape fur seal, thus including South Africa.

Layout and contributions of co-authors

This thesis consists of seven main chapters, each written as papers for submission to a journal. As a result, some repetition, particularly of methods, was inevitable; I tried to keep this to a minimum by, for example, describing the scat processing method in full in one chapter and referring to this chapter elsewhere in the thesis. Tables and figures follow the text for each chapter, as would be done in a paper submitted for publication. The references for all the chapters are gathered together at the end of the thesis. I was responsible for the analysis and writing of each chapter. I was also responsible for collecting most of the individual scats and for all of their processing, as well as for validating bag sample data (checking counts and prey identification) and measuring most otoliths. The contribution of co-authors is stated below, and their comments were incorporated into the chapters.

CHAPTER 2: MECENERO, S., ROUX, J-P., UNDERHILL, L. G., and M. N. BESTER Submitted — Spatial variation in the diet of Cape fur seals *Arctocephalus pusillus pusillus* in Namibia. *Afr. J. mar. Sci.*

CHAPTER 3: S. MECENERO, J-P. ROUX, L. G. UNDERHILL and S. P. KIRKMAN In prep. — Temporal variation in the diet of Cape fur seals *Arctocephalus pusillus pusillus* at three mainland breeding colonies in Namibia. *Afr. J. mar. Sci.*

CHAPTER 4: S. MECENERO, S. P. KIRKMAN and J-P. ROUX In prep. — Fish consumption estimates of lactating Cape fur seals *Arctocephalus pusillus pusillus* in Namibia based on scat analyses.

CHAPTER 5: S. MECENERO, J-O. KRAKSTAD, L. G. UNDERHILL and J-P. ROUX In prep. — Overlap in the utilization of juvenile Cape horse mackerel by Cape fur seals and the purse-seine fishery in Namibia.

CHAPTER 6: MECENERO, S., KRAKSTAD, J-O., ROUX, J-P. and L. G. UNDERHILL Submitted — Can seal diet predict future catches of commercial prey? *J. Appl. Ecol.*

CHAPTER 7: MECENERO, S., KIRKMAN, S. P. and J-P. ROUX 2005 — Occurrence of seabirds in the diet of Cape fur seals *Arctocephalus pusillus pusillus* at three mainland breeding colonies in Namibia. *Afr. J. mar. Sci.*, in press.

CHAPTER 8: S. MECENERO and L. G. UNDERHILL In prep. — Investigating fur seal diet using scats: recommendations for sampling and analysis.

LGU commented on drafts and suggested methods of data analysis. JPR provided data and fundamental ideas for this thesis. JOK commented on drafts and methods of analysis. SPK provided ideas, commented on drafts and on methods of data analysis. MNB commented on a draft.

University of Cape Town

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I am most grateful to my supervisor Professor Les Underhill for having had the vision to accept me as a PhD student conducting a study on nothing other than a mammal within the Avian Demography Unit (ADU). I am most indebted to Les for his continued support, encouragement, advice and trust throughout the period of my study. Without this, I would not have grown as much both mentally and emotionally. His statistical expertise was also most appreciated.

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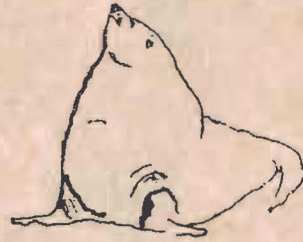
mackerel. Dr Graham Avery of the Iziko Museums (Cape Town) identified feathers found in scats. Dr Tony Williams (Cape Nature) commented on a draft of Chapter 7. Referees of submitted chapters (Chapters 2 and 7) provided constructive recommendations. The sealers at MCM, Dr Herman Oosthuizen, Dr Jeremy David, Mr Mike Meyer and Mr Stefan Swanson are also thanked for their help with queries and for their friendship.

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CHAPTER 1



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Introduction

Cape fur seals in relation to other pinnipeds

The Cape fur seal *Arctocephalus pusillus pusillus* (also known as the South African fur seal) belongs to the family Otariidae (Bonner 1994). Fur seals are characterised by having fur, comprising of stiff guard hairs and shorter, denser under-fur fibres, as well as external ears (Bonner 1994). Two other pinniped families exist, namely the Odobenidae (walruses *Odobenus rosmarus*) and the Phocidae (true seals). Otariids are “dramatically” sexually dimorphic; males are larger than females (Bonner 1994). For example, the mass of adult male Cape fur seals ranges from 200-360 kg and length from 230-272 cm, whereas adult female mass ranges from 40-110 kg and length from 120-160 cm (Bonner 1994).

The family Otariidae consists of two sub-families, the fur seals (*Arctocephalinae*) and the sea lions (*Otariinae*) (Bonner 1994). The sub-family of fur seals comprises the northern fur seal *Callorhinus ursinus* and the southern fur seals (*Arctocephalus* spp.). The genus *Arctocephalus*, meaning “bear-headed”, consists of eight species of fur seals mainly found in the southern hemisphere (Bonner 1994). The Cape fur seal and the Australian fur seal *A. p. doriferus* share sub-species status. The remaining seven species of fur seal are the South American *A. australis*, Juan Fernandez *A. philippi*, Galapagos *A. galapagoensis*, Guadalupe *A. townsendi*, New Zealand *A. forsteri*, Subantarctic *A. tropicalis* and Antarctic *A. gazella*. Most southern fur seal species were heavily exploited during the 19th century, mainly for their pelts. Population size estimates range from about 7 000 (Guadalupe fur seal) and 18 000 (Juan Fernandez fur seal) seals to about 1.6-1.7 million seals (Antarctic and Cape fur seals) (Wickens and York 1997). All southern fur seal species are listed under Appendix II of the Convention on International Trade in endangered Species (UNEP-WCMC 2003).

The volume of research related to the diet of the Antarctic fur seal (e.g. diet composition, foraging and diving behaviour, foraging energetics, food consumption, competition and overlap) far surpasses that on the diet of any other of the southern fur seal species (e.g. Costa *et al.* 1989,

Boyd and Croxall 1992, Daneri and Coria 1992, Boyd *et al.* 1994, Casaux *et al.* 1998, Kirkman *et al.* 2000, Guinet *et al.* 2001).

Few diet-related studies of the other southern fur seal species have been conducted, of which most mainly concentrate on diet composition (e.g. Juan Fernandez fur seal, Acuña and Francis 1995; Subantarctic fur seal, Klages and Bester 1998; New Zealand fur seal, Fea *et al.* 1999; South American fur seal, Naya *et al.* 2002; Australian fur seal, Hume *et al.* 2004). For the Cape fur seal, studies have been conducted on diet composition (Rand 1959, Shaughnessy 1985, David 1987a, Lipinski and David 1990, Castley *et al.* 1991, Punt *et al.* 1995, De Bruyn *et al.* 2003, De Bruyn *et al.* in press), energy requirements (Balmelli and Wickens 1994), food consumption (Shaughnessy 1985, David 1987a, Butterworth *et al.* 1988, Wickens *et al.* 1992b, Smale *et al.* 1994, Butterworth *et al.* 1995) and interactions with fisheries (Shaughnessy 1985, Wickens *et al.* 1992a).

Distribution and habitat

The Cape fur seal occurs in south-western Africa, from southern Angola (about 17°S) to Algoa Bay (34°S, 26°E) in the south (Fig. 1). Most Cape fur seals (93%) occur along the west coast of southern Africa (Shaughnessy 1985, David 1989), and 65-70% of the total population is found along the Namibian coast (Wickens *et al.* 1991, David 1987a). Colonies typically occur on rocky outcrops of islands, but the largest colonies are found on the mainland (Bonner 1994). In Namibia, about 187 000 individuals occur on the mainland at Cape Cross (21°47'S, 13°57'E; Marine and Coastal Management (MCM), unpublished data), and about 167 000 individuals at Wolf Bay (26°48'S, 15°07'E) and Atlas Bay (26°49'S, 15°08'E; MCM, unpublished data) together. In South Africa, there are about 81 000 individuals at the mainland colony at Kleinsee (29°40'S, 17°04'E; MCM, unpublished data).

The west coast of southern Africa is characterised by the cold, nutrient-rich Benguela System (Currie 1953). The Benguela is one of the four major upwelling systems in the world, exhibiting high biological productivity (Shannon and Jarre-Teichmann 1999) and experiencing highly variable environmental conditions (Shannon *et al.* 1992). The degree of upwelling is dependent on the prevailing wind conditions, the angle of the coast to the prevailing wind direction, and the depth and width of the continental shelf (Shannon 1989). Prevailing winds in the Benguela System are determined by the high-pressure system in the South Atlantic, atmospheric pressure over the

mainland, and low-pressure systems related to westerly winds south of South Africa (Shannon 1989). Upwelling centres occur where the wind is strongest and the continental shelf deepest and narrowest (e.g. Lüderitz and Cape Frio in Namibia; Fig. 1) (Shannon 1989). The upwelling centre around Lüderitz is the coldest, dividing the Benguela System into the northern and southern Benguela; it has been suggested that it forms a barrier to the movement of marine species (Shannon 1985).

Population trends

Cape fur seals have been harvested since the early 17th century (David 1989), mainly for pelts and male genitalia, with meat and oil as by-products (Wickens *et al.* 1991). Intense and unregulated harvesting during the 18th and 19th centuries resulted in a large reduction in seal numbers throughout its range. Consequently, harvesting management was introduced during the late 19th century and a quota system was introduced in 1974 for further regulation (Shaughnessy 1985, David 1989). Harvesting was terminated in South Africa in 1990 (Wickens *et al.* 1991), where the Cape fur seal is protected by the Sea Birds and Seal Protection Act of 1973 (Wickens *et al.* 1991). It continues to take place in Namibia at three mainland colonies, namely Wolf Bay, Atlas Bay and Cape Cross.

Despite continued harvesting, the annual growth rate of the overall Cape fur seal population from 1971 to 1989 was estimated as 3% (Wickens *et al.* 1991). The increase in population size during the 20th century may be largely attributable to the control of sealing since 1893 (Bonner 1994), which allowed the species to recover from over-exploitation. In 1997, the total population was estimated to be 1.5 to 2 million seals (Best *et al.* 1997), 65% of which occurred in Namibia (David 1987a). The fur seal population in Namibia peaked in 1994 at about 1.1 million individuals, but decreased by as much as 40% following a warm water event in 1994, and a Benguela Niño phenomenon in 1995 (Roux 1998). The seal population size in Namibia was estimated at just over half a million individuals in December 2001 (MCM, unpublished data). Population estimates in Namibia were derived from aerial surveys of pup numbers carried out in December of some years (censuses in 1994 to 1997 and 2001 coincide with this study), by converting these pup numbers to population estimates using a population:pup ratio of 5:1. This ratio was determined by Wickens and Shelton (1992), taking into consideration the harvesting history of the species. It is unknown whether current population sizes exceed pre-exploitation

levels. Prior to the extermination of large terrestrial predators, mainland breeding colonies would not have been established (David 1989). The largest colonies are now on the mainland, established since about 1940 (David 1989), which are not space-limited in the way that the island colonies are.

Life cycle

Male Cape fur seals attain puberty at three to four years (Stewardson and Bester 1998), but are rarely capable of securing territories before about age ten (David 1989). Females attain sexual maturity at about the age of three or four years, giving birth for the first time at four to five years of age (Shaughnessy 1985, David 1989). Like all Otariids, Cape fur seals are polygynous. Females give birth in harems of seven to 66 females (mean of 28; Rand 1967), that are aggressively defended by territorial males for about six weeks during summer (Rand 1955). Adult males (bulls) begin to arrive at the breeding colonies in October to establish their territories, and adult females (cows) start arriving towards the end of October (Rand 1955, Shaughnessy 1985). Each cow gives birth to a single pup soon after hauling out at the breeding colonies, and is mated about six days later by the harem's bull (Rand 1955). Once females are mated, bulls return to the sea. From February to June bulls are non-reproductive, and spermatogenesis commences during July in preparation for the following breeding season (Stewardson and Bester 1998).

The gestation period is almost 12 months, including a four-month period of delayed implantation (Rand 1955, Bonner 1994). Most pups are born from early December to early January (David 1987b). After mating, cows return to sea for the first time to feed (Rand 1955). They feed for three to six days, before returning to suckle their pups for about three days (Rand 1955). This pattern is repeated throughout the following months; the mothers gradually increase their periods of absence until the pups are weaned eight to 10 months later (August to October) (Rand 1955, David 1989). Cows then return to sea for a long and intensive foraging period before hauling out to give birth again (Rand 1955, David 1989).

Unlike cows, which spend about 39% (Gentry *et al.* 1986) of their time on land at their breeding colony between the times of birth and weaning of their pups, immature animals of either sex and (except during the breeding season) bulls are not bound to land (Rand 1959). These animals are not restricted in their range by the proximity of the breeding colony and the requirements of pups. While bulls and immatures may haul out sporadically at breeding colonies

outside of the breeding season, mothers and pups form the majority of seals found in breeding colonies at any time.

Foraging ecology

Cape fur seals are carnivorous and a top predator in the local marine ecosystem, although they do fall prey to great white sharks *Carcharodon carcharias* (Compagno *et al.* 1989). They feed mainly over the continental shelf (David 1987a), but foraging also takes place farther offshore, as far as 220 km (Shaughnessy 1985), as they grow older (Oosthuizen 1991). Results of a study on the diving behaviour of Cape fur seals, based on a sample size of just two individuals, showed that Cape fur seals can dive to depths of 200 m, although 66% of the registered dives were shallower than 50 m and dives to greater depths than 150 m were rare (Kooyman and Gentry 1986). Half of the dives occurred at night; they became shallower as the night progressed, possibly in response to prey migrating to the surface during the night (David 1989). Daytime dives were mostly shallow to pursue shoaling fish (David 1989). In contrast, the closely related Australian fur seal dives mainly during daylight hours and does not display diel variation in dive depths (Arnould and Hindell 2001). However, dive depths are also shallow (most less than 90 m) and occur over the continental shelf (Arnould and Hindell 2001). Subantarctic fur seals showed some similarities in diving behaviour to Cape fur seals; their diving behaviour displayed diel variations, and dives were shallow (mean dive depth less than 50 m), although 99% of their dives occurred at night (Georges *et al.* 2000b). Their diving behaviour changed seasonally and dive depths increased through winter.

Lactating Cape fur seals are central place foragers, therefore the foraging distance from the colony is an important factor (Guinet *et al.* 2001) determined by the physiological limits of the mothers and requirements of pups (Beauplet *et al.* 2004). Gamel *et al.* (2005) found that trip lengths of lactating Cape fur seal females increased during the first four months of lactation. No information is available for the latter months of the lactation period, but Arnould and Hindell (2001) found that foraging trips by lactating females of the closely related Australian fur seal increased in duration right up to weaning. It is unknown whether increases in foraging trip lengths are caused by reduced prey availability, or increasing independence on the part of the pups. In the case of subantarctic (Georges *et al.* 2000a, 2000b, Beauplet *et al.* 2004) and Antarctic (Bonadonna *et al.* 2000, Staniland and Boyd 2003) fur seals, increases in trip duration by lactating females are apparently associated with longer distances traveled to foraging

locations, suggesting the former. Thus the duration of foraging trips are probably determined mainly by changes in prey availability, and mothers adjust their foraging behaviour to maximize the energy needs of their pups (Boyd 1998). A Lactating mother's trip duration is determined by the time taken to regain the energy lost during suckling and traveling (Costa *et al.* 1989). Longer trips seem to indicate that seals are searching for food along more distant routes as apposed to spending more time in one feeding location (Bonadonna *et al.* 2000). When food availability is low, mothers may stay away for longer to provide energy for themselves at the risk of their pup starving (Trillmich and Kooyman 2001).

The diet of Cape fur seals consists mainly of teleost fish (David 1987a, Punt *et al.* 1995), with cephalopods (David 1987a, Lipinski and David 1990, Punt *et al.* 1995, De Bruyn *et al.* 2003, De Bruyn *et al.* in press), crustaceans (David 1989) and rock lobster (Punt *et al.* 1995) contributing to the rest of the diet. Cape fur seals have also been observed to prey on seabirds (e.g. Marks *et al.* 1997, Crawford *et al.* 2001, David *et al.* 2003, Du Toit *et al.* 2004). Being generalist feeders in a highly variable ecosystem, Cape fur seals can be expected to feed on locally abundant prey species (Shaughnessy 1985, Oosthuizen 1991). This is particularly true for lactating females that are restricted in terms of the range that they can forage from their breeding colony. For instance, it has been shown that consumption of pelagic goby *Sufflogobius bibarbatus* and Cape horse mackerel *Trachurus trachurus capensis* by Cape fur seals is correlated with the distribution of these species (Cram 1977, Cruickshank *et al.* 1980, Shaughnessy 1985, David 1987a). The diet of Cape fur seals therefore varies geographically.

David (1987a) found that along the South African west coast seals consumed mainly Cape anchovy *Engraulis capensis* and shallow- and deep-water Cape hakes *Merluccius capensis* and *M. paradoxus*, respectively. Along the South African south coast anchovy, sardine *Sardinops ocellatus*, hake and horse mackerel were important prey, and in Namibia goby and horse mackerel were most prevalent (David 1987a). The main commercial fish species found in stomach contents of Cape fur seals in southern Africa are anchovy, sardine, hake, horse mackerel, Cape round herring *Etrumeus whiteheadi* and snoek *Thyrsites atun* (Shaughnessy 1985, David 1987a, Punt *et al.* 1995).

Cephalopods are minor prey items of seals in Namibian waters, increasing in importance southwards along the coast towards the western and southern waters of South Africa (David 1987a), and displaying spatial variation (Lipinski and David 1990, Castley *et al.* 1991, De Bruyn *et*

al. in press). Crustaceans do not contribute significantly to the diet of seals from Namibia and the south coast of South Africa, but are more prominent in the diet of seals from the west coast of South Africa (David 1987a).

Daily food consumption by Cape fur seals has been estimated as 8% of average body mass (Shaughnessy 1985, David 1987a) and 10% of the average body mass of lactating females (Wickens *et al.* 1992b). Balmelli and Wickens (1994) estimated that a Cape fur seal of average size (72 kg) consumes 3.8 kg per day or 1.4 tonnes per year. In the 1980s, the population of 1.1 million fur seals was estimated to consume 1.05 million tonnes of fish, in comparison with fisheries which removed 700 000 tonnes (David 1989). However, almost half of the diet of seals consisted of non-commercial gobies (David 1989). In Namibia, the estimated total annual consumption of hake, anchovy and pilchard by seals in the 1970s was 30 000, 31 500 and 23 000 tonnes respectively, compared to the total catch of these prey by commercial fisheries in 1979 of 300 000, 270 000 and 41 000 tonnes respectively (David 1987a).

Nevertheless, the Cape fur seal is regarded by fishers as a serious competitor for commercial fish (Wickens *et al.* 1992a). The situation is exacerbated by the fact that Cape fur seals frequently interfere directly with fishing operations, resulting in losses from the catch and damage to equipment (Shaughnessy 1985, Wickens 1994, Wickens and Sims 1994, Wickens 1996). Although a reduction in the seal population would be welcomed by most fishers, other natural predators of commercial fish may replace seals and have a larger impact on commercial fish stocks (Shaughnessy 1985, Punt and Butterworth 1995). For example, deep-water hake preys on shallow-water hake, and depending on the degree to which seals consume deep-water hake, a reduction in seal numbers may negatively affect shallow-water hake fisheries (Punt and Butterworth 1995).

Aspects of this study

The marine ecosystem is a complex system influenced by a variety of interactions between constituent species and the fluctuating environment. Apart from seasonal and spatial variation in the abundance and distribution of marine species, there are also large-scale processes (e.g. decadal phenomena) which may further influence the long-term dynamics in the marine ecosystem (Crawford and Payne 1989). The Benguela System experiences a large degree of variability in environmental conditions (Shannon *et al.* 1992). By investigating the diet of Cape fur seals in this

system, using the cheap and non-intrusive method of scat analysis (Pierce and Boyle 1991), important information is gained on the complex interactions between seal populations, their prey and fisheries.

Until 1990, all diet studies of Cape fur seals were conducted by examining the stomach contents of seals mainly shot at sea (Rand 1959, David 1987a, Lipinski and David 1990, Castley *et al.* 1991, Punt *et al.* 1995). Besides being expensive and lethal, stomach content analysis is also prone to biases such as those associated with the degree of digestion of prey which affects prey identification and diet quantification (Pierce and Boyle 1991). Moreover, stomachs can be empty (David 1987a). This thesis is part of a global trend to study diet by non-destructive sampling methods. Other examples of this trend in diet sampling are the collection of regurgitations from gannets (Klages *et al.* 1992), stomach pumping of penguins (Randall and Davidson 1981), collection of faecal samples of waders (Dekinga and Piersma 1993) and foxes (Elmhagen *et al.* 2002), and regurgitated pellets of cormorants (Duffy *et al.* 1987, Härkönen 1988).

This study focuses on the teleost portion of the diet of Cape fur seals from three mainland breeding colonies in Namibia, as determined from the analysis of scats collected from these colonies over a period of eight years. Prey hard parts resistant to digestion are found in scats, and it was therefore possible to investigate the spatial (**Chapter 2**) and temporal (**Chapter 3**) variation of the diet of these seals in Namibia. Spatio-temporal variations in seal diets have been related to the availability and abundance of prey in different areas, as well as to variability in oceanographic conditions which is the most important factor controlling patterns of prey abundance and distribution (e.g. Acuña and Francis 1995, Bowen and Harrison 1996, Lake *et al.* 2003).

Refining knowledge of changes in the seal diet in relation to space and time is a step in the direction of unraveling the complexities that influence prey consumption by seals. It also permits the improvement of estimates of prey consumption by the seals (**Chapter 4**), which are useful for assessing levels of competitive interactions between seals and fisheries or other predators, or impacts of seals on prey species. Previous prey consumption estimates for Cape fur seals have mostly been based on static rather than dynamic diet composition models (e.g. Wickens *et al.* 1992b, Butterworth *et al.* 1995).

Cape fur seals feed on a number of commercially important fish, such as the Cape horse mackerel (Shaughnessy 1985), Namibia's most valuable commercial fish (Axelson *et al.* 2004). In order to contribute to the management of the horse mackerel stock, an understanding of the

interactions between Cape fur seals and the horse mackerel fishery is necessary. The age classes of horse mackerel consumed by seals can be reconstituted from the otoliths found in the scats. Therefore, it was possible to investigate the level of overlap in the utilization of this fish stock between seals and the horse mackerel purse-seine fishery (**Chapter 5**).

Stock assessments of horse mackerel are subject to errors, and improvements to these models will allow for more reliable management decisions. It was also possible, by comparing the proportion of horse mackerel mass reconstituted from otoliths found in scats with horse mackerel biomass estimates from acoustic surveys and landed catches, to investigate whether seal dietary information could be used to complement fishery and survey data in management models (**Chapter 6**).

A current issue of concern is the predation of red data book seabird species by Cape fur seals (Marks *et al.* 1997, Crawford *et al.* 2001, David *et al.* 2003, Du Toit *et al.* 2004). However, this predatory behaviour has been linked to a few rogue individuals, mostly sub-adult males (Du Toit *et al.* 2004). In the interests of seabird conservation, individual seals displaying this behaviour are selectively culled from the population on the west coast of South Africa (David *et al.* 2003), while in Namibia seals are prevented from permanently residing on some islands where seabirds breed (e.g. Mercury Island, Crawford *et al.* 1994; J. Kemper, Avian Demography Unit, pers. comm.). Because feathers that enter the gut of seals are not digested but pass through the gut, the frequency of occurrence of seabird remains in seal scats can easily be determined. Therefore, this study investigated the degree of seabird consumption by Cape fur seals in Namibia (**Chapter 7**).

This entire study is based on the method of scat analysis, which is associated with a number of biases (Pierce and Boyle 1991). However, scat analysis provides valuable information on the diet composition, and changes therein, of seals (Tollit and Thompson 1996). Recommendations are made to improve the reliability of this method (**Chapter 8**).

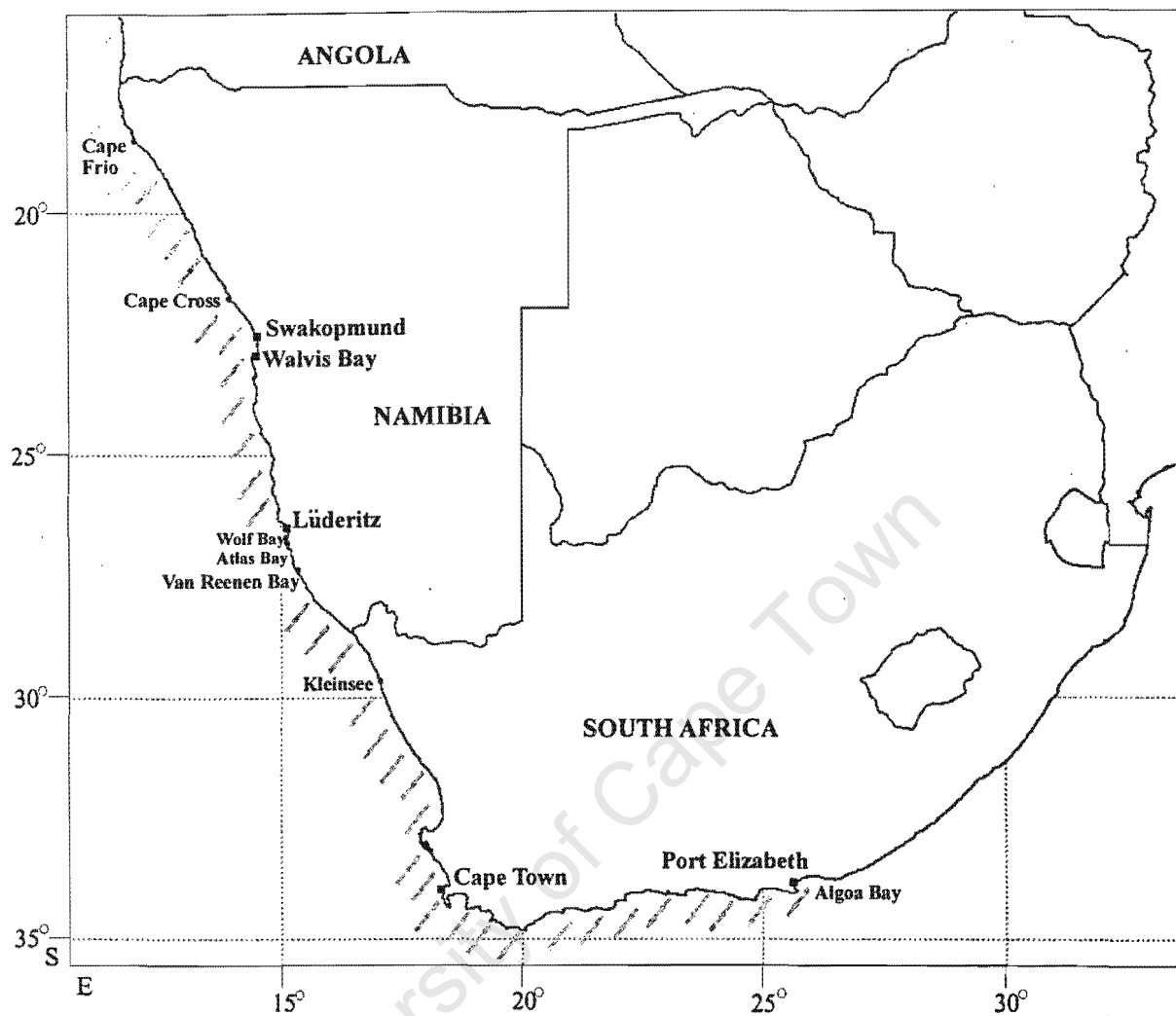
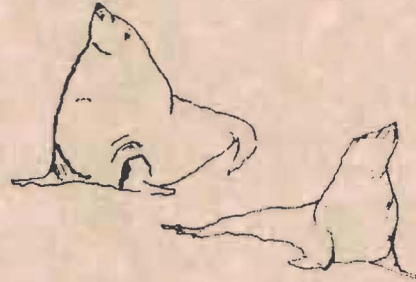


Figure 1. Map of southern Africa showing the extent of the Cape fur seal *Arctocephalus pusillus pusillus* population and the location of the four largest mainland breeding colonies (Cape Cross, Wolf and Atlas Bays, and Kleinsee).

CHAPTER 2



University of Cape Town

Spatial variation in the diet of mainland Cape fur seals

Arctocephalus pusillus pusillus in Namibia

INTRODUCTION

Following a survey in December 2001, the Cape fur seal *Arctocephalus pusillus pusillus* population in Namibia was estimated at just over half a million individuals (Marine and Coastal Management (MCM), unpublished data). Here they breed on several offshore islands as well as on the mainland. The Namibian coast is characterized by the northern part of the cold, nutrient-rich Benguela current ecosystem (Currie 1953), which is one of four major upwelling zones on the eastern boundaries of the world's oceans (Shannon and Jarre-Teichmann 1999). Owing to the high productivity associated with this ecosystem, several substantial commercial fisheries operate in Namibian waters, e.g. Cape hakes *Merluccius* spp. (Van der Westhuizen 2001) and Cape horse mackerel *Trachurus trachurus capensis* (Krakstad and Kanandjembo 2001).

Cape fur seals are carnivorous and top predators in the Benguela System. Previous diet studies have shown that they feed mainly on teleost fish (Rand 1959, Shaughnessy 1985, David 1987a, Castley *et al.* 1991, Punt *et al.* 1995). Some of these are commercially important species, and thus competitive interactions between seals and fisheries exist (David 1987a, Wickens *et al.* 1992a). An improved understanding of the Cape fur seals' diet is therefore timely for the management of Namibia's marine resources: firstly, the seal population is large; secondly, its prey species overlap with target species of commercial fisheries; and thirdly, some of these fisheries have recently experienced reduced catches (e.g. the sardine *Sardinops sagax* fishery, Boyer *et al.* 2001).

In some species of pinnipeds, diet composition varies spatially and this variation seems to be related to the availability and abundance of prey in different areas (Payne and Selzer 1989, Hammond *et al.* 1994, Bowen and Harrison 1996, Mikkelsen *et al.* 2002, Lake *et al.* 2003). Spatial differences in prey communities may reflect different oceanographic or topographical characteristics between regions (Payne and Selzer 1989, Hammond *et al.* 1994). Previous diet studies of the

Cape fur seal in southern Africa have been based on irregular sampling of shot or drowned seals whose stomach contents were analysed. Sporadic sampling events cannot reliably reflect spatial differences in the diet considering that pinniped diets also vary temporally (Pierce *et al.* 1991, Bowen and Harrison 1996, Casaux *et al.* 1998).

The analysis of scats has become a standard method for investigating pinniped diet composition, despite the biases associated with it (Pierce and Boyle 1991; see chapter 8, Discussion). This method is cheap and non-intrusive (Pierce and Boyle 1991), and is also well suited for the analysis of teleost prey which contribute hard parts to scats. This study describes and compares the diets of Cape fur seals at three mainland colonies in Namibia, concentrating on the teleost prey. Together these three colonies, on average, constitute 65% of Namibia's seal population.

MATERIAL AND METHODS

Study sites

Seal diets were studied at three mainland breeding colonies along the coast of Namibia: Van Reenen Bay (27°23'S, 15°21'E; VRB), Atlas and Wolf Bays (26°49'S, 15°08'E and 26°48'S, 15°07'E, respectively) and Cape Cross (21°47'S, 13°57'E; CC) (Fig. 1). The Atlas and Wolf Bay (AWB) colonies were considered as one because they are approximately 1 km apart. The distance between AWB and VRB is ~70 km, and between AWB and CC ~600 km. The population size in December 2001 was estimated at VRB to be just under 15 000 individuals, at AWB close to 167 000 individuals, and at CC approximately 187 000 individuals (MCM, unpublished data).

Collection and processing of Cape fur seal scats

Scat collection

Scat samples were collected between January 1994 and April 2002, at monthly intervals when possible. Only fresh scats, less than approximately two days old, were collected. Sampling was most regular at AWB (nine months missed out of 100) and less regular at CC and VRB (22 and 59 months missed, respectively). The temporal distribution of sample collections is shown in Figure 2 of Chapter 3. At AWB, the nine missing samples occurred during 1994 and 1997-2000. At CC, most of the missing samples ($n = 16$) were found in years 1999-2001 during the summer

(December to February) and winter (June to August) months. At VRB, nearly 60% of the months from the onset of the study until the end of 2000, were not represented, due to poor sampling effort.

Prior to May 2001, an unknown number of scats (usually 30 to 60), as well as pieces of broken up scats in the dense colonies, were pooled to form “bag” samples. These bag samples were collected any time during a month. From May 2001 to April 2002 bag samples consisted of 30 pooled whole scats, collected on the same date each month. Samples were stored at -10°C until processed. When samples were collected on more than one occasion within a month, samples were pooled to represent that month. This only occurred at AWB, in 27 of the 100 months of the study period.

Additionally, from May 2001 to April 2002, 30 individual whole scats were collected each month from the three colonies concurrent to collections of bag samples. Individual scats were not pooled but placed into separate plastic sampling bags and stored at -10°C until processed.

Extraction and sorting of hard parts of prey from scats

Undigested prey items included fish otoliths, cephalopod beaks, crustacean hard parts and bird feathers. After thawing, individual scats were washed in plastic jars under running water and the mixture passed through a stainless steel laboratory test sieve of mesh aperture 0.212 mm (only one sieve was necessary because of the small amount of material in one scat). Bag samples were rinsed in a bucket with running water and the material was passed through nested stainless steel laboratory test sieves with mesh apertures of 2.0, 1.0, 0.425 and 0.212 mm. The material containing prey items was thoroughly rinsed and dried overnight in an oven at 50°C.

Sagittal otoliths were sorted from the dried matter, identified to the lowest possible taxon (usually species level), and counted. Identification followed Smale *et al.* (1995), and also made use of the otolith reference catalogue at the Ministry of Fisheries and Marine Resources in Namibia (MFMR). Cephalopod beaks were sorted from the dried matter, their presence or absence in the sample noted, and investigated further as part of a separate study (De Bruyn *et al.* 2003, De Bruyn *et al.* in press). Crustacean hard parts and bird feathers were only noted from individual and bag samples taken during May 2001 to April 2002. Crustacean hard parts were sorted from the dried matter, but were unidentifiable, and therefore only their presence or absence in each sample was noted. The percentage frequency of occurrence (%FO) of cephalopod beaks

and crustacean hard parts was calculated as the number of scats containing these items expressed as a percentage of the total number of scats containing items of any prey species.

Measurement of otoliths

Otolith diameter (OD) is defined as the greatest diameter of the otolith (Smale *et al.* 1995), which in most cases is the distance parallel to the sulcus from the anterior to the posterior margins. ODs of whole otoliths except those heavily eroded were measured with a vernier caliper to 0.05 mm. Six teleost prey groups were identified. The number of otoliths measured in each group depended on the degree of variability in otolith diameters (Table I). The following procedures were used: (1) **Horse mackerel group.** ODs of at least 200 otoliths per sample were measured due to the high variability in ODs observed for this species. If a monthly sample consisted of less than 200 otoliths, the whole sample was measured. (2) **Hake group.** As for horse mackerel. (3) **Lanternfish group.** OD variability was small and thus a total of 200 otoliths was measured from various samples and the mean OD was used in all further analyses. (4) **Goby group.** ODs of c. 30 otoliths per sample were measured, because OD variation was small. If less than 30 otoliths constituted the sample then all otoliths were measured. (5) **Pelagics group.** As for goby. (6) **Others group.** Around 10 otoliths or less (where sample size was <10) were measured per species per sample from each colony, and the mean OD per species per colony was used in further analyses.

The “Hake” group consisted of juvenile *Merluccius capensis* and *M. paradoxus*. Otoliths of juveniles of these species are not easily distinguishable (Punt *et al.* 1995). The “Lanternfish” group consisted mainly of *Lampanyctodes hectoris* and possibly one or two Myctophidae species whose otoliths were indistinguishable from those of *L. hectoris* (see Smale *et al.* 1995). Other lanternfish species in the samples, which were distinguishable from *L. hectoris*, were placed in the “Others” group. The “Goby” group was represented by the species *Sufflogobius bibarbatus*. The “Pelagics” group consisted of sardine, anchovy *Engraulis capensis* and round herring *Etrumeus whiteheadi*.

Correction and conversion factors for otoliths

Correction for otolith numbers lost through digestion

Otolith counts were corrected for numbers lost through digestion. Such correction factors exist for horse mackerel, hake, goby and sardine (D. L. Millar *et al.*, MCM, unpublished data; Appendix I). Otoliths of species (including unidentified species) for which such correction factors do not exist were compared to the otoliths of these four species to determine which corresponded most in size, shape and thickness (column 2 of Appendix I), and the respective correction factors were used (column 3 of Appendix I). Once otolith numbers were corrected in this way, the monthly percentage numerical abundance (%N) of teleost prey of seals at each colony was determined. %N is defined as the number of individuals per prey species expressed as a percentage of the total number of individuals of all prey species. Despite the fact that each fish has two otoliths, the number of otoliths was not divided by two because the proportions of each prey would remain the same and therefore %N would not be affected.

Correction for erosion of otolith diameters

Erosion of otoliths occurs during digestion and results in a decrease in OD. Individual ODs of horse mackerel, hake, goby, sardine, anchovy and round herring were corrected for erosion, whereas the mean OD for lanternfish and the mean OD per colony of each species in the “Others” category were corrected for erosion. These correction factors exist for horse mackerel, hake, goby and sardine (D. L. Millar *et al.*, MCM, unpublished data), and the same procedure as above was used to assign OD correction factors to all other species (column 4 of Appendix I).

Conversion of corrected otolith diameters to fish total length and mass

For horse mackerel, sardine, anchovy and round herring, existing relationships between otolith diameter and fish total length relationships (Appendix I; Smale *et al.* 1995) were used to convert each corrected OD to fish total length (length from the tip of the snout to the tip of the longest caudal ray). Fish length was then converted to fish mass using relationships between fish total length and fish mass determined by the MFMR (Appendix I). This procedure was used because conversions should preferably be based on relationships obtained from fish populations as close as possible to the study sites (Staniland 2002). For some of the remaining species, relationships

between otolith diameter and fish mass given by Smale *et al.* (1995), mainly based on data obtained from South African waters, were used to convert each corrected OD to fish mass (Appendix I). For those species for which these relationships have not yet been derived, the corresponding relationships of closely related species were assigned (column 5 of Appendix I). For otoliths which could not be identified to a species, relationships were assigned on the basis of similarity in otolith size, shape and thickness (column 5 of Appendix I).

The importance of large prey is underestimated when expressed as numerical abundance because small prey are usually more abundant (Fea *et al.* 1999). Therefore, diet composition expressed also as mass may give a better indication of important prey. For each sample at each colony, the mean fish masses for horse mackerel, hake, goby, sardine, anchovy and round herring were determined, and multiplied by that species' corrected otolith counts for that month, to estimate the total mass of each species in a sample. For lanternfish, the mean corrected OD (1.68 mm) was converted to fish mass (0.669 g) and this value was used to convert monthly counts at each colony to mass. For species in the "Others" category, the mean corrected OD per species at each colony was converted to fish mass and this value was used to convert monthly corrected otolith counts to monthly mass. For each species, the percentage mass (%M) was calculated as the total mass of that species in a sample expressed as a percentage of the total mass of all teleost prey species in the sample. As for %N, the %M was based on all otoliths.

Secondary prey

Secondary prey are prey which were ingested by larger predatory fish such as hake and horse mackerel, which were subsequently eaten by seals. The bias in numbers associated with secondary prey was investigated by examining whether otoliths in a scat that reflected large predatory prey (horse mackerel > 200 mm and hake > 300 mm in length) were associated with those of smaller prey such as lanternfish and goby, which are consumed by these large predators.

Sampling year

The sampling year, defined as beginning on 1 August and ending on 31 July of the following year, corresponded approximately to sea surface temperature, wind and upwelling cycles (Cole and McGlade 1998, Cole and Villacastin 2000, K. Peard and J-P. Roux, Namibian Ministry of Fisheries and Marine Resources (MFMR), unpublished data).

Statistical analyses

Means are followed by one standard deviation (SD) or 95% confidence intervals. Medians are given for fish total lengths and mass at each colony for the horse mackerel, hake, lanternfish, goby and pelagics prey groups. The median is a robust statistic and is advantageous in representing the typical size of the fish consumed in cases where there are outliers (Samuels 1991). The non-parametric Kruskal-Wallis test was used to test for differences in fish length and mass between colonies, because the data were not normally distributed.

RESULTS

Six main groups of teleost prey were identified, which consisted of at least 48 species and 19 families (Appendix I). The "Others" group consisted of 41 species, of which five species could only be identified to the genus level and 21 species remained unidentified (not in identification guide or reference catalogue). In most bag samples, the majority of prey remains (>85% by abundance and/or mass) were composed of two to three species, and the number of species in each sample ranged from four to 17.

The mean number of otoliths per scat (Table II) was used to estimate the approximate number of scats constituting bag samples collected up to and including December 2000 at each colony. Bag samples at VRB, AWB and CC were estimated to constitute 54, 47 and 56 scats, respectively.

Of the total number of individual scats collected, 15.0% contained goby otoliths not associated with hake nor horse mackerel. Of these scats, 39.1% contained >100 goby otoliths (maximum = 2 152 otoliths). Similarly, 8.6% of the individual scats contained lanternfish otoliths not associated with hake nor horse mackerel. Of these, 37.1% contained >100 lanternfish otoliths (maximum = 1 354 otoliths). Moreover, of all individual scats containing hake together with goby and/or lanternfish, only 3.4 % contained large hake. Scats with large hake and scats with small hake contained similar amounts of lanternfish otoliths (mean $\pm$ SD, 167 ± 246 and 153 ± 263 otoliths, respectively), and fewer goby otoliths (41 ± 105 otoliths and 70 ± 177 otoliths, respectively). Of all scats containing horse mackerel together with goby, 16.0% contained large

horse mackerel. Scats with large horse mackerel contained fewer goby otoliths (43 ± 66 otoliths) than scats containing small horse mackerel (140 ± 186 otoliths).

Inter-colony variation in diet composition

Prey ranged in size from 8.7 to 1 123.4 mm (Appendix II). However, disregarding the “Others” prey group, which contained prey that were negligible in the seal diet (Figs 2a and 2b), the range in size of prey consumed was 8.7 mm (round herring) to 490.4 mm (hake, Fig. 3a, Appendix II), and the mass of prey consumed ranged from 0.003 g (round herring) to 905.3 g (hake) (Fig. 3b, Appendix III). The largest prey in terms of median length was round herring at both VRB and AWB colonies, and sardine at CC (Fig. 3a, Appendix II). The largest prey in terms of median mass at both CC and VRB was sardine, and round herring at AWB (Fig. 3b, Appendix III). Lanternfish were the smallest fish consumed at all three colonies in terms of length and mass (Appendices II and III). There were large discrepancies between medians and means for the length and mass of some prey groups at some colonies (Appendices II and III), and the large variances were a result of the data not being normally distributed.

Few horse mackerel were consumed by Cape fur seals at both VRB and AWB, whereas this prey was the most important in both %N and %M in the diet of seals at CC (Figs 2a and 2b). The %FO of horse mackerel in scats was also highest at CC (Fig. 2c). The size of horse mackerel represented by otoliths in seal scats was significantly larger at CC (median 116.4 mm) and significantly smaller at AWB (median 82.8 mm; Fig. 3a, Appendix II).

Hake were an important prey group at all three colonies, especially in terms of %M contribution at VRB and AWB colonies (Figs 2a and 2b). %FO of hake was also highest at VRB and AWB (Fig. 2c). The sizes of hake taken showed a significant southward increase from CC (median 69.4 mm) to VRB (median 171.0 mm; Fig. 3a, Appendix II).

Lanternfish formed a small part of the diet of seals at CC and were only important at VRB and AWB in terms of %N (Figs 2a and 2b). %FO was highest (71%) at AWB (Fig. 2c). Goby were important prey to seals, especially at AWB (Figs 2a and 2b), where %FO was greater than 80% (Fig. 2c). Significantly smaller gobies (median 56.5 mm) were consumed in the north at CC and significantly larger gobies (median 87.7 mm) in the south at VRB (Fig. 3a, Appendix II). The “Others” prey group was negligible in the diet at all three colonies (Figs 2a and 2b), and %FO exceeded 20% only at VRB (Fig. 2c).

Pelagic fish occurred in low numbers in seal scats but contributed more in terms of %M (Figs 2a and 2b). %FO ranged from 20% to 33% (Fig. 2c). Round herring predominated at VRB in both %N and %M, whereas sardine and anchovy predominated at CC (Fig. 4). Round herring showed a similar trend to hake and goby of a significant southward increase in size from CC (median 156.5 mm) to VRB (median 208.6 mm) (Fig. 3a, Appendix II). Sardine sizes in seal diets did not differ between the CC and VRB colonies, where they were significantly larger than at AWB (Fig. 3a, Appendix II). However, anchovy in seal diets at VRB and AWB colonies were similar in size but were significantly smaller than those at CC (Fig. 3a, Appendix II).

Hard part remains of cephalopods (beaks) and crustaceans were most prevalent in scats from VRB and AWB (Fig. 5). Crustacean remains were found in less than 5% of scats at CC (Fig. 5). The evidence and extent of bird predation resulting from feathers in the scats was small (Chapter 7).

DISCUSSION

During this study scat collections took place at breeding colonies, where adult males are present mainly during the breeding season (October to January), when they mainly fast (Rand 1959). Therefore, the overwhelming majority of the scat samples represented the diet of lactating adult females, which regularly alternate shore visits to feed their pups with foraging trips at sea (David and Rand 1986). Lactating females forage close to their colonies on locally abundant prey (Shaughnessy 1985, Oosthuizen 1991). Cape Cross also serves as a haulout site for non-breeding males throughout the year, and although some scats collected here may have been deposited by males, most of the scats from CC would represent the diet of lactating females which are by far the majority at this colony (S. P. Kirkman, pers. comm.). That prey availability affects the dissimilarity in diet between CC and AWB is supported, e.g. by the fact that the scats of seals at CC reflect the high abundance of horse mackerel in that region (Krakstad and Kanandjembo 2001), whereas this prey species, which is much less abundant and accessible to seals in the south, is practically absent from scats at AWB and VRB.

Data were collected over a relatively long time period, therefore this study provides a reliable estimate of the diet of this species in Namibia. Scat analysis indicated that Cape fur seals consumed a wide range of prey, corroborating results from other studies on Cape fur seal diets

(Rand 1959, Shaughnessy 1985, David 1987a, Castley *et al.* 1991, Punt *et al.* 1995), and this could indicate that they feed opportunistically (Green *et al.* 1989). Cephalopods were also taken but their relative overall importance within the diet remains unknown for this study period (De Bruyn *et al.* 2003, De Bruyn *et al.* in press). However, David (1987a) and Lipinski and David (1990) found that cephalopods constituted 3 to 8% by mass of Cape fur seal diets in Namibia. Crustacean hard parts occurred more frequently in scats of seals from the southern part of the Namibian coast. However, it was impossible to identify and quantify these prey. No rock lobster *Jasus lalandii* hard parts were observed in scats from the study colonies. Seabirds were negligible in the diet of fur seals from the three mainland colonies (Chapter 7). As in the other diet studies (Rand 1959, Shaughnessy 1985, David 1987a, David 1991, Castley *et al.* 1991, Punt *et al.* 1995), teleosts constituted the greatest proportion of prey species, and this discussion will concentrate on these prey.

Some otoliths may be of secondary origin, which would overestimate the abundance and mass of some fish species consumed by seals. It is difficult to determine when the presence of otoliths of smaller prey in seal scats is of primary or secondary origin, especially in bag samples when individual scats are lumped together. Consequently, primary prey status applied to small prey must be considered carefully (Fea *et al.* 1999). Lanternfish are preyed on by other teleost predators, including hake and horse mackerel (Krzeptowski 1982, Prosch 1986) and are thought to be of secondary origin when found in Cape fur seal diets (Punt *et al.* 1995). Goby is also consumed by both horse mackerel (Andronov 1985) and hake (Krzeptowski 1982, Andronov 1983, Punt and Leslie 1995), and hake preys on a number of other prey species of seals, such as anchovy and round herring (Punt and Leslie 1995). Hake are also cannibalistic and *M. capensis* feeds on juveniles of *M. paradoxus* (Assorov and Kalinina 1979, Payne *et al.* 1987, Punt and Leslie 1995).

The present study showed that goby and lanternfish otoliths were seldom associated with large hake and horse mackerel in scats. Individual scats contained large numbers of otoliths of these smaller prey which were not associated with large predatory fish. Moreover, scats containing large hake or horse mackerel did not contain more goby and/or lanternfish otoliths than scats containing small hake and horse mackerel. Lanternfish and goby are both abundant in Namibian waters (Cruickshank 1982). It is therefore likely that these species are primary prey to seals. Lanternfish were found to be an important component of the diet of Antarctic and New Zealand fur seals (Green *et al.* 1989, Daneri and Coria 1992, Cherel *et al.* 1997, Klages and Bester 1998, Fea *et al.*

1999, Casaux *et al.* 2003). Fur seals are able to feed on lanternfish at night when this prey migrates towards the sea surface (Acuña and Francis 1995, Cherel *et al.* 1997, Fea *et al.* 1999). For the purposes of this study, it was assumed that all prey were primary prey of seals.

Spatial variability in the diet composition of Cape fur seals

Of the six teleost prey groups identified in this study, four predominated in terms of abundance and/or mass in the diet of Cape fur seals: juvenile horse mackerel (mean mass 19.0 g), juvenile hake (mean mass 26.5 g), pelagic goby (mean mass 4.6 g) and lanternfish (*L. hectoris*; mean mass 0.8 g). Two of these prey, horse mackerel and hake, are commercially important. Horse mackerel were negligible at VRB and AWB, and lanternfish were negligible at CC. This suggests that the diet of seals varied spatially, those at VRB and AWB, the two most southerly and closest colonies, being most similar (this study). David (1987a), Green *et al.* (1990) and Childerhouse *et al.* (2001) attributed spatially variable diets to differences in prey abundances and distributions between areas. The availability of fish to seals is also determined by the foraging and diving ranges of Cape fur seals: within 220 km from the colony (Shaughnessy 1985), and 66% of dives of two individuals were found to be shallower than 50 m (Kooyman and Gentry 1986).

Juvenile horse mackerel are found in large concentrations in northern Namibian waters (O'Toole 1977, Hatanaka and Kawahara 1985, Krakstad and Kanandjembo 2001), from 20°S to the border with Angola (~17°S) (Krakstad in press). The CC colony is situated on the coast of northern Namibia (21°47'S), accounting for the prevalence of horse mackerel in the diet of seals from this colony. Shaughnessy (1985) also found that horse mackerel predominated in the seal diet between CC and 19°S. Smaller concentrations of horse mackerel are found south of Walvis Bay (Axelsen *et al.* 2004), and this is reflected by the low proportion of horse mackerel in scats from VRB and AWB. Juvenile horse mackerel remain in the northern part of the region to feed, while adults migrate southwards into South Africa, increasing in size southwards (Krakstad in press, Axelsen *et al.* 2004).

The fact that both VRB and AWB seals consumed smaller horse mackerel than seals from CC may be due to the fact that horse mackerel juveniles from South Africa migrate into the southern part of Namibia to just south of the Lüderitz upwelling cell (Axelsen *et al.* 2004). Juvenile horse mackerel are found inshore (Axelsen *et al.* 2004) in shallower waters, explaining

the preponderance of juveniles consumed at all three colonies where median lengths consumed were less than 120 mm (Appendix II).

Adult horse mackerel are found in deep water (Krakstad in press) and may therefore be less accessible than juvenile horse mackerel to seals. However, large horse mackerel, from 300 to 350 mm, were consumed by seals. This may be possible because horse mackerel migrate upwards at sunset to within the upper 50 m (Pillar and Barange 1998, Krakstad in press) where they are vulnerable to seal predation. Half of the dives by Cape fur seals occur nocturnally, and become shallower as the night progresses, possibly a response by the fur seals to prey migrating to the surface during the night (David 1989).

Hake (*M. capensis* and *M. paradoxus*) are dominant fish predators in Namibian waters (Huse *et al.* 1998). Hake was numerically important in the diet of seals from all three colonies. The smaller contribution of hake mass to the seal diet at CC than at VRB and AWB is due to the smaller size of hake that were consumed there. This may be a result of juveniles remaining in the area of the spawning grounds, which are situated in northern waters between 22°S and 24°S (O'Toole 1977), in the vicinity of CC. The larger hake (> 300 mm) in the diet may have been scavenged from trawlers (Wickens and Sims 1994) because hake of this size occur at depths greater than 200 m (Burmeister 2001) and may therefore be inaccessible to the seals.

M. capensis is abundant over the entire Namibian shelf (Hamukuaya *et al.* 1998) with a minimum abundance at 19-21°S (Burmeister 2001), while *M. paradoxus* is found mainly south of 24°S (Burmeister 2001) in deep waters. *M. capensis* occurs in shallower water than *M. paradoxus* (Botha 1973), and is thus more accessible to seals. Small *M. paradoxus* (300 - 400 mm in length) are abundant at five to 50 m from the bottom at depths generally greater than 300 m (Huse *et al.* 1998, Burmeister 2001) which may be out of the diving range of most Cape fur seals. Around CC, the hake stock is comprised mainly of *M. capensis* (Chłapowski 1975). Thus, it is likely that the hake otoliths in seal scats in this study mainly represented juvenile *M. capensis*. David (1987a) found that seals from the South African west coast mainly consumed *M. paradoxus*.

Pelagic goby were numerically most abundant in the diet of seals at AWB. The foraging range of lactating seals (~200 km from the shore) at AWB overlaps with the area of highest goby concentrations, found between Lüderitz and Walvis Bay (Cruickshank *et al.* 1980, Crawford *et al.* 1985, Hewitson and Cruickshank 1993). Further north, between Walvis Bay and 18°S and including the area in which CC is situated, gobies have a patchy distribution (Cruickshank *et al.*

1980), explaining the presence of goby in seal diets there albeit at lower levels. Shaughnessy (1985) also found that goby were important seal prey between Lüderitz and Walvis Bay, with a lower occurrence observed in diets of seals north of Walvis Bay. The foraging range of seals at VRB conceivably overlaps with that of seals at AWB and therefore seals at VRB also consume gobies but to a smaller extent. This is likely because seals from different colonies can share the same feeding grounds (Oosthuizen 1991).

Gobies are found up to about 60 km offshore (Cruickshank *et al.* 1980), with highest concentrations at 10 – 15 m depths (O'Toole 1977). They thus occur within the foraging and diving range of the fur seals. Gobies usually do not form shoals (Hewitson and Cruickshank 1993) but are poor swimmers (O'Toole 1977), making them easy prey for seals. Moreover, small gobies are pelagic compared to larger gobies, which are mainly bottom dwellers and found offshore (Crawford *et al.* 1985). However, gobies have a low fat content (1.5% by mass; Cruickshank 1982) and are energetically less rewarding compared to other pelagic fish (Crawford *et al.* 1985). The fur seals probably prefer more energy-rich prey when it is available. Cape gannets consumed gobies with a mode at 50 – 55 mm (Crawford *et al.* 1985). According to scat analysis, Cape fur seals ingested gobies which included lengths of over 100 mm (Fig. 3a). There is some evidence that gobies migrate to the surface at night (O'Toole 1977), and the seals may therefore consume these larger goby then. Seals also dive deeper than gannets, thus large gobies would be more accessible to seals.

L. hectoris is the most abundant lanternfish off Namibia (Cruickshank 1982), preferring waters of 300 to 1000 m in depth (Prosch 1986). It displays vertical migration to within 200 m of the surface at sunset and descends to the midwater region at sunrise (Cruickshank 1983a, Prosch 1986). These vertical migrations may make it available to predation by Cape fur seals. Although *L. hectoris* has been found along the edge of the continental shelf as far north as the Cunene River (Cruickshank 1982), it is mainly concentrated from Walvis Bay to the Orange River (Cruickshank 1983a). Usually it is found 30 km from the shore (Cruickshank 1983a); south of Lüderitz it has been recorded as close as 9 km from the shore (Cruickshank 1982).

In the upwelling cell in the Lüderitz area (Currie 1953), *L. hectoris* is numerically abundant during the upwelling season when southerly winds prevail. Upwelling brings cold water to the surface, eliminating the thermocline and thus enabling lanternfish to come closer to the surface. Moreover, Klages and Bester (1998) attributed the high prevalence of lanternfish in the diet of

Antarctic *Arctocephalus gazella* and Subantarctic fur seals *A. tropicalis* to the absence of an extensive shelf area at Marion Island. The area around Lüderitz presents a narrowing of the shelf (Nelson and Hutchings 1983), and this may also contribute to lanternfish being more accessible to seals. Because the shelf is wide in the region of CC (Bianchi *et al.* 1993) and CC is not an upwelling region, *L. hectoris* is not readily available to seals, which explains the negligible amount of lanternfish consumed by seals from this colony.

Although *L. hectoris* was numerically abundant in the diet of seals at AWB and VRB, it contributed minimally to the mass consumed by seals due to its small size (Fig. 2, Appendices II and III). *L. hectoris* has a high oil content (Ahlstrom *et al.* 1976, Cruickshank 1982, Prosch 1991), equating to a high energy content, and seals may prefer this prey to others when it is available, even though it contributes minimally in mass to the overall diet.

The pelagics prey group formed a small proportion of the diet of the seals at the three study colonies. Anchovy has been found to be more common than sardine in the diet of seals in Namibia (Shaughnessy 1985, David 1987a). The low sardine stocks in Namibia (Cram 1977, Boyer *et al.* 2001) may be responsible for this. Sardine and anchovy are mainly found in the northern half of Namibian waters (Hewitson and Cruickshank 1993), although anchovy migrate as far south as Lüderitz before returning to Walvis Bay (Cruickshank 1983a). Round herring occur in southern Namibia (Roel and Armstrong 1991). This would explain sardine and anchovy being most prevalent in the diet of the fur seals at the northernmost colony, CC, whereas round herring was mainly consumed by seals at VRB in the south. The Lüderitz upwelling cell is thought to constitute a barrier to the migration of small pelagic fish (Shannon 1985).

Overall, Cape fur seals mainly consumed small prey that display shoaling behaviour and are found in shallow water. Prey median lengths ranged from 47 mm (lanternfish) to 209 mm (round herring). Sardine, anchovy and round herring often shoal together (Roel and Armstrong 1991, Hewitson and Cruickshank 1993) and may be joined by juvenile horse mackerel (Cruickshank 1983b). *L. hectoris* also occurs in shoals (Crawford 1980), as do juvenile hake (Iilende *et al.* 2001). Day dives by Cape fur seals are shallow to follow shoaling fish (David 1989). Abundant shoaling fish maximise the energy gain for seals because they are more frequently encountered, have higher capture rates than dispersed species, can be ingested whole resulting in a reduced handling time, and have high energy levels during certain times of the year (Bowen and Harrison 1996).

Some prey species in the Others prey group are demersal trawl indicator species (Punt *et al.* 1995), such as *Genypterus capensis*, *Helicolenus dactylopterus*, *Austroglossus microlepis*, and *Chelidonichthys capensis*, as well as *Cynoglossus*, *Lophius* and *Caelorinchus* species. Most of these fish found in seal scats had average lengths greater than 200 mm. While some of these species occur at depths greater than 400 m (Bianchi *et al.* 1993), most also occur at shallower depths (less than 100 m) easily accessible to seals, which may explain their presence in the diet. Castley *et al.* (1991) suggested that seals forage on the sea floor to obtain demersal species, and this cannot be discounted due to the paucity of data on the diving depths of Cape fur seals. However, it also cannot be discounted that these demersal species were scavenged when the nets of bottom trawlers were brought to the surface or from discards of trawlers (Wickens and Sims 1994, Punt *et al.* 1995).

The reliability of using scats for seal diet analyses

Analyses of scats have been used extensively in studies of the diet composition of pinnipeds. The main assumption of this method is that the relative abundance and mass of prey consumed is reflected by that estimated from hard part remains in scats (Tollit *et al.* 1997). The biases associated with this method were reviewed by Pierce and Boyle (1991) (see Chapter 8, Discussion). The main bias when quantifying the numerical abundance of prey from scats is that only a fraction of the otoliths ingested are recovered in scats (Da Silva and Neilson 1985, Murie and Lavigne 1985, Jobling 1987, Dellinger and Trillmich 1988, Harvey 1989, Gales and Cheal 1992, Harvey and Antonelis 1994, Tollit *et al.* 1997, Orr and Harvey 2001, Staniland 2002).

Although scat analysis does not accurately quantify the abundance and mass of prey consumed by seals (Tirasin and Jørgensen 1999), it is nevertheless able to provide information on spatial and temporal trends in the main prey consumed by seals (Tollit and Thompson 1996). This is well represented by the relative proportion of prey in the diet in terms of numerical abundance and mass. Furthermore, if large samples are collected, then the estimate of prey abundance using scats will be reliable (Dellinger and Trillmich 1988). Scat analysis also remains the most affordable, least destructive and least intrusive method for determining the composition of seal diets, although some disruption of animals at haul-out sites may occur (Pierce and Boyle 1991). For the purposes of this study, it was assumed that errors or biases in determining diet composition were consistent between samples.

Implications of this study

Diet composition of Cape fur seals in Namibia varied between colonies, even between two colonies only 70 km apart. If the diets of top predators reflect the distribution and abundance of prey (Payne and Selzer 1989, Hammond *et al.* 1994, Bowen and Harrison 1996), the results of this study suggest that prey abundances and distributions vary in space. They are also expected to vary in time (Acuña and Francis 1995, Bowen and Harrison 1996, Reid and Arnould 1996, Daneri and Carlini 1999, Naya *et al.* 2002), and it is anticipated that the diet of seals will vary between years, seasons and months (Chapter 3). Such variation highlights the fact that the Benguela is a complex system, influenced by a large number of factors.

Possibly the most important factors controlling patterns of prey abundance and distribution are environmental conditions (Acuña and Francis 1995). Understanding the relationship between the environment and seal diet composition may shed light on the factors determining prey abundance and distribution. This information will be valuable to fisheries management. With life history information of prey obtained from scats, there will be a better understanding of commercial fish stocks. Overexploitation of commercial stocks has resulted in attention being focused on stocks of non-utilized fish species (Prosch 1991) and seal diet analysis may contribute towards understanding the dynamics of fish which are currently non-commercial.

Table I. The mean $\pm$ standard deviation (SD), coefficient of variation (CV) and range of measurements of otolith diameters for five prey groups in the diet of Cape fur seals *Arctocephalus pusillus pusillus* in Namibia. The number of otoliths measured is given by n .

Prey Group	Otolith diameter lengths			
	Mean $\pm$ SD (mm)	CV	Range (mm)	n
Horse mackerel	3.69 $\pm$ 1.27	34.42%	1.00 – 10.30	17 759
Hake	5.74 $\pm$ 2.49	43.38%	0.80 – 18.10	34 512
Lanternfish	1.60 $\pm$ 0.28	17.50%	0.95 – 2.50	201
Goby	1.92 $\pm$ 0.60	31.25%	0.35 – 4.50	6 453
Pelagics				
Sardine	2.80 $\pm$ 0.72	25.71%	1.10 – 5.70	831
Anchovy	2.45 $\pm$ 0.53	21.63%	1.00 – 4.10	2 828
Round herring	2.98 $\pm$ 0.71	23.82%	0.20 – 4.95	1 933

Table II. The mean number of otoliths recovered from bag samples of scats of Cape fur seals *Arctocephalus pusillus pusillus* at three colonies in Namibia, from January 1994 to April 2002, as well as the mean number of otoliths per individual scat and the proportion of individual scats containing no otoliths for each colony. The number of bags is given by N and the number of individual scats is represented by n .

Colony	Number of otoliths per bag sample		Number of otoliths per individual scat sample		% Individual scats containing no otoliths
	Mean $\pm$ SD	Range	Mean $\pm$ SD	Range	
Van Reenen Bay ($N = 41$, $n = 423$)	4 904 $\pm$ 6 199	350 – 31 536	91 $\pm$ 173	1 – 1 448	4.7%
Atlas-Wolf Bay ($N = 91$, $n = 416$)	10 624 $\pm$ 8 639	1 503 – 44 660	227 $\pm$ 292	1 – 2 152	1.2%
Cape Cross ($N = 78$, $n = 385$)	6 990 $\pm$ 8 375	274 – 42 220	126 $\pm$ 293	1 – 2 928	4.4%

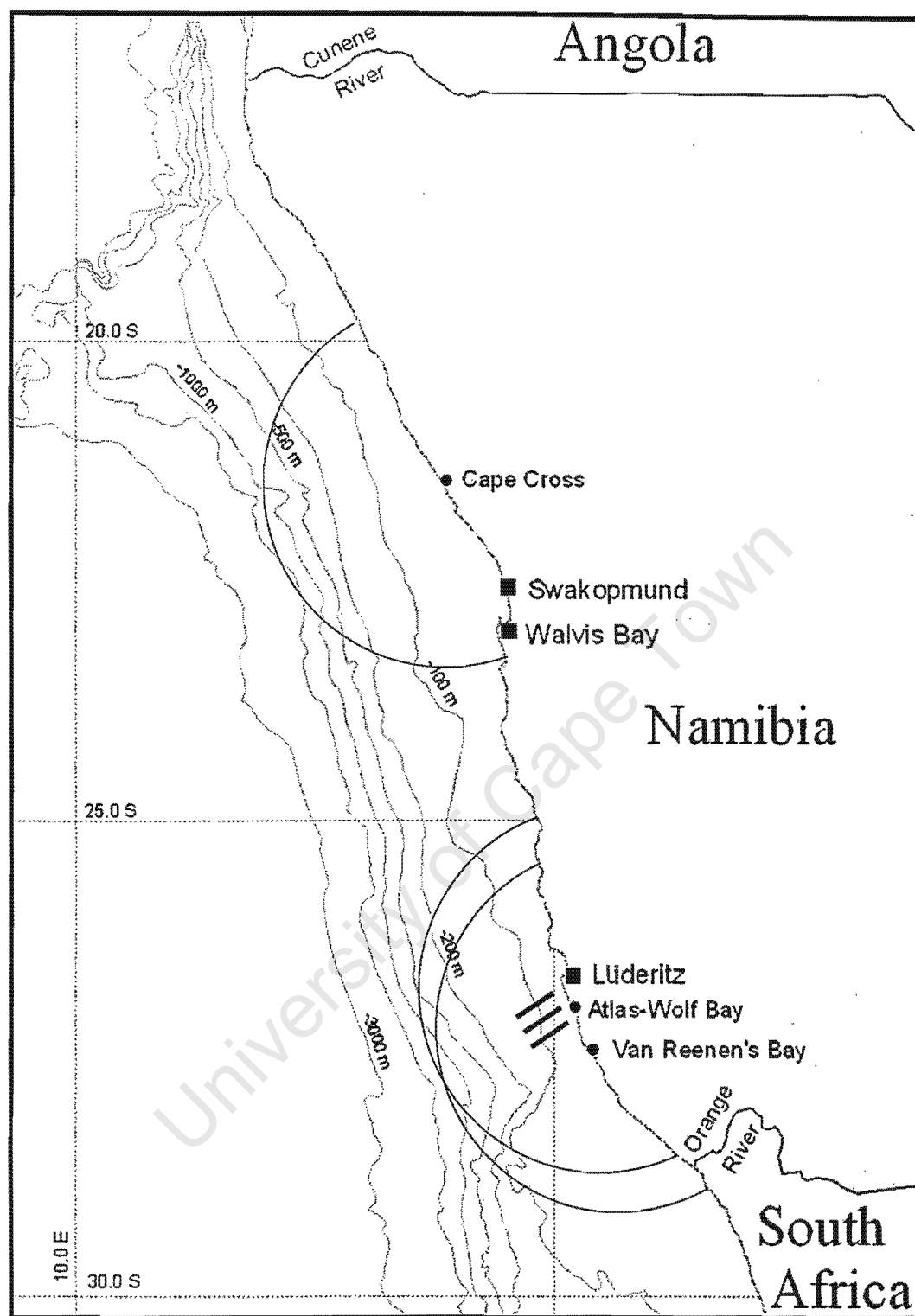


Figure 1. The location of the three Cape fur seal *Arctocephalus pusillus pusillus* study colonies on the Namibian mainland, with the 200 km foraging ranges shown. The approximate position of the Lüderitz upwelling cell is shown by the short diagonal lines.

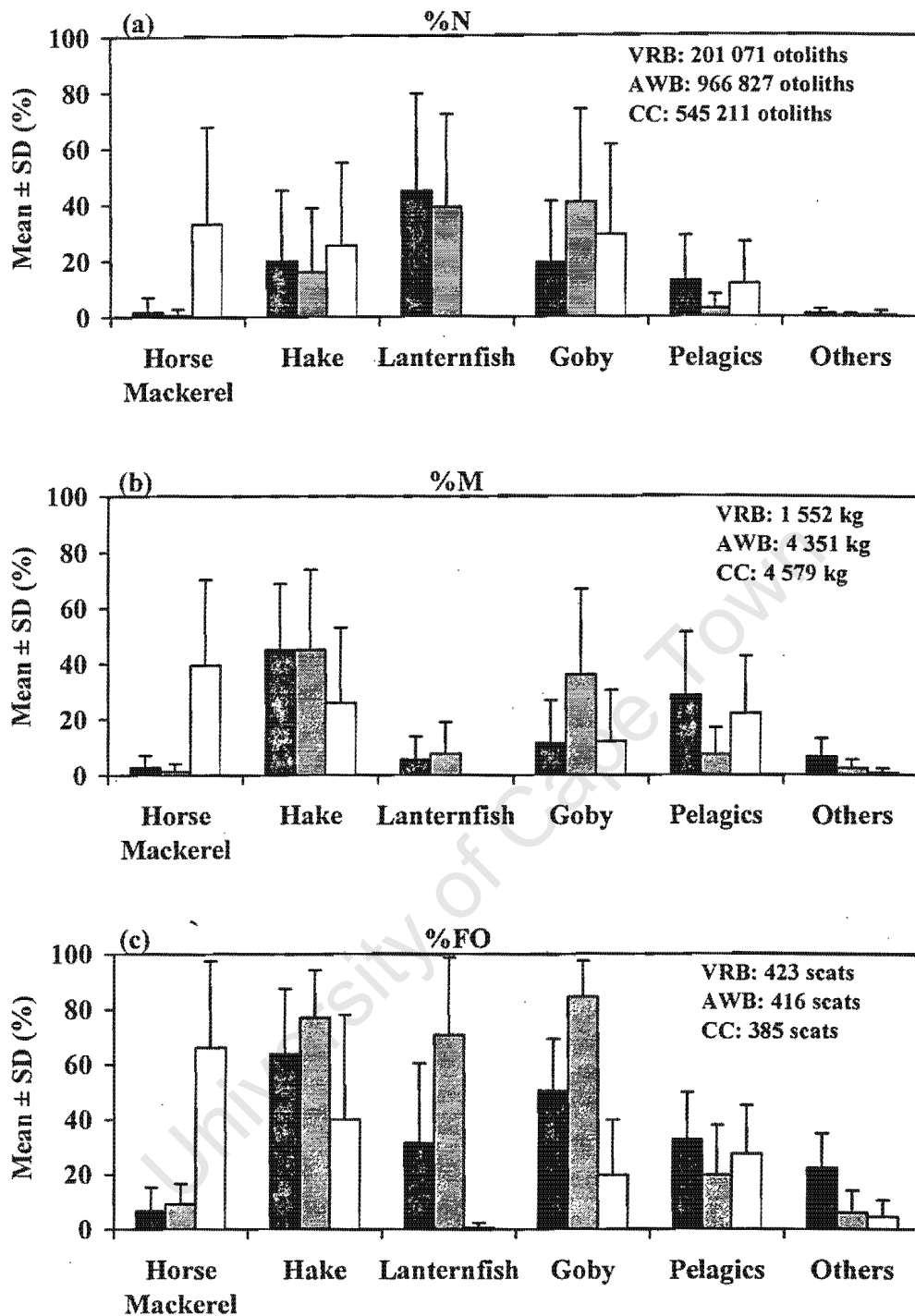


Figure 2. The mean $\pm$ standard deviation (SD) of (a) percentage abundance (%N) and (b) percentage mass (%M) of the six prey groups (Cape horse mackerel *Trachurus trachurus capensis*, Cape hake *Merluccius* spp., lanternfish, pelagic goby *Sufflogobius bibarbatus*, pelagics and others) in the diet of Cape fur seals *Arctocephalus pusillus pusillus*, from January 1994 to April 2002 at each colony (■ = Van Reenen Bay (VRB), $N = 41$ months; ▨ = Atlas-Wolf Bay (AWB), $N = 91$ months; and □ = Cape Cross (CC), $N = 78$ months). Also, (c) the mean $\pm$ SD of the percentage frequency of occurrence (%FO) of the six prey groups in individual seats of the Cape fur seal collected from February 2001 to April 2002 at each colony (VRB, $N = 14$ months; AWB, $N = 15$ months; and CC, $N = 14$ months).

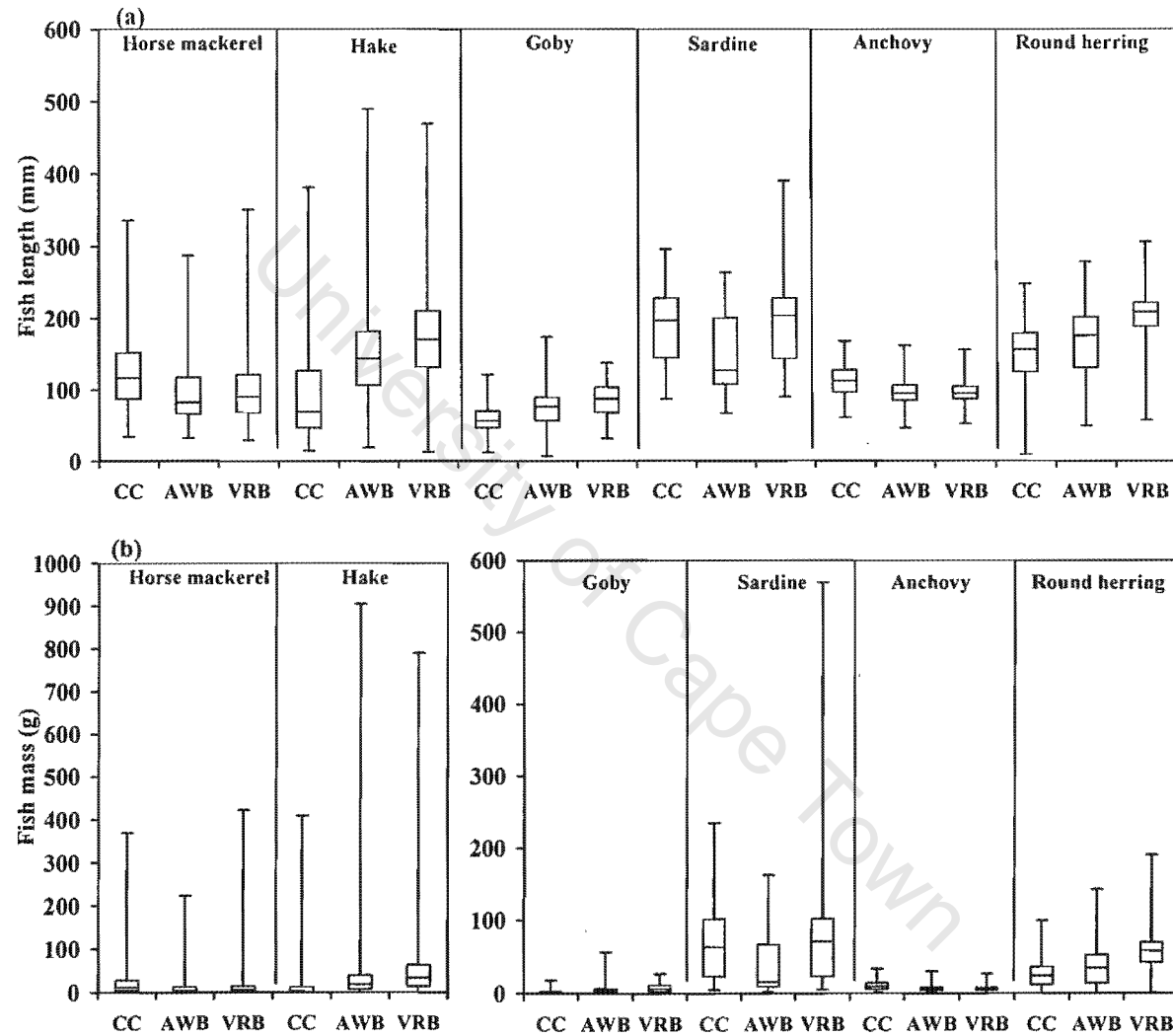


Figure 3. Box-and-whisker plots of (a) length and (b) mass of fish prey consumed by Cape fur seals *Arctocephalus pusillus pusillus* at Cape Cross (CC), Atlas-Wolf Bay (AWB) and Van Reenen Bay (VRB) during the period January 1994 to April 2002. The upper and lower ends of the box represent the quartiles, the horizontal line through the box is the median, and the endpoints of the whiskers represent the minimum and maximum values. Sample sizes are given in Appendices II and III.

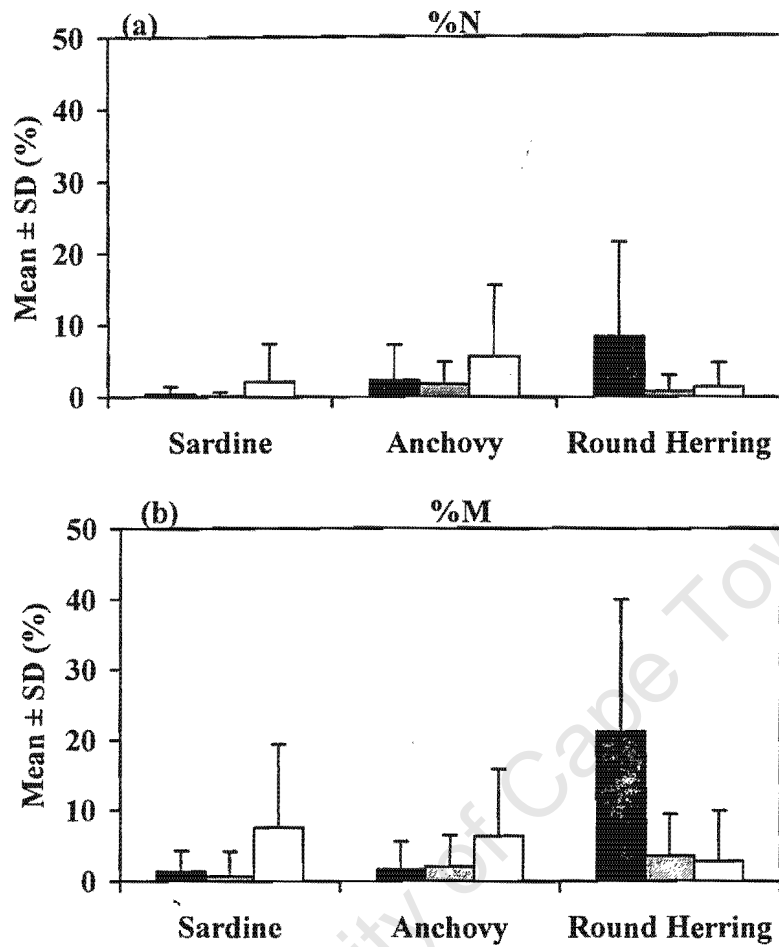


Figure 4. The mean $\pm$ standard deviation (SD) of (a) percentage abundance (%N) and (b) percentage mass (%M) of the pelagics prey group (sardine *Sardinops sagax*, anchovy *Engraulis capensis* and round herring *Etrumeus whiteheadi*) in the diet of Cape fur seals *Arctocephalus pusillus pusillus* from January 1994 to April 2002, at three mainland colonies (■ = Van Reenen Bay, $N = 41$ months; ▨ = Atlas-Wolf Bay $N = 91$ months; □ = Cape Cross, $N = 78$ months).

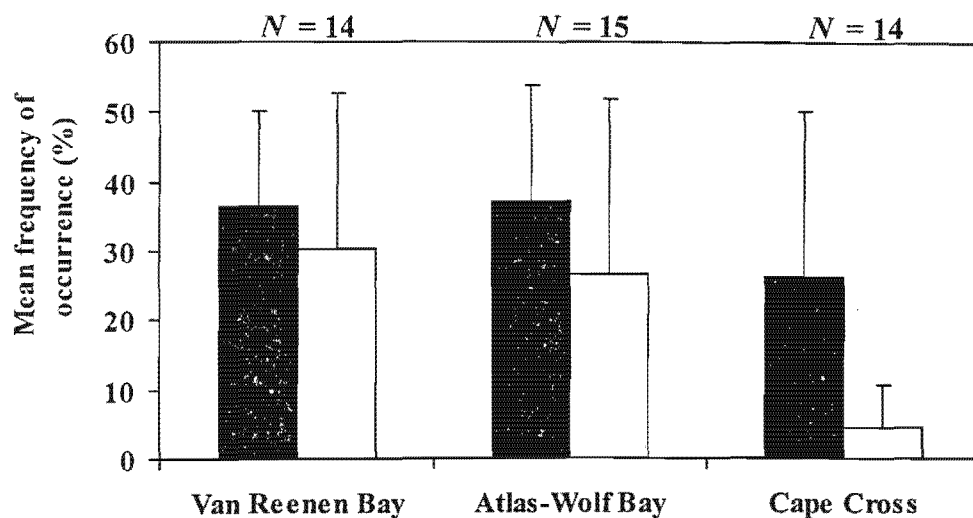


Figure 5. The mean $\pm$ standard deviation (SD) of the percentage frequency of occurrence (%FO) of cephalopod (■) and crustacean (□) hard part remains in individual scats of the Cape fur seal *Arctocephalus pusillus pusillus* collected from February 2001 to April 2002 at three mainland colonies. The number of monthly samples collected is represented by *N*.

Appendix I. Correction factors to correct for numbers of otoliths lost and erosion of otolith diameters during digestion, as well as equations for converting corrected otolith diameter to fish total length and mass, for teleost species in each of the six prey groups of the Cape fur seal *Arctocephalus pusillus pusillus*. Family, species and common names are given. Otoliths of species for which there are no correction factors or for which relationships between otolith diameter and fish length or mass were unknown, were allocated the correction factors or relationship equation of either horse mackerel (HM), hake (H), goby (G) or sardine (S) (D. L. Millar *et al.*, MCM, unpublished data) depending on otolith similarities (shape, size and thickness; see column two and five, respectively). "Unid" refers to unidentified species, A to anchovy and RH to round herring.

Prey Group Family Species (common name)	Correction factors			Equation values for relationships between otolith diameter and fish total length or mass				
	Prey species correction factor used	Numbers lost ^a	Otolith diameter erosion ^a	Prey species relationship used	Fish total length		Fish mass	
					a ^b	b ^b	a ^b	b ^b
1) Horse mackerel (juvenile) Carangidae <i>Trachurus trachurus capensis</i> (Cape horse mackerel)	HM	1.754	1.025	HM	3.3550	1.0627	0.0042 ^c	3.2384 ^c
2) Hake (juvenile) Merlucciidae <i>Merluccius capensis</i> and <i>M. paradoxus</i> (Shallow and deep water Cape hake, respectively)	H	1.515	1.073	H	2.7273 ^d	1.1691 ^d	-4.1569 ^d	3.6965 ^d
3) Lanternfish Myctophidae <i>Lampanyctodes hectoris</i>	G	1.786	1.050	<i>L. hectoris</i>	3.1988	1.2676	-2.5907	4.2197
4) Goby Gobiidae <i>Sufflogobius bibarbatus</i> (Pelagic goby)	G	1.786	1.050	G	3.5201	1.0564	-1.1459	3.3309
5) Pelagics Clupeidae <i>Sardinops sagax</i> (South African sardine)	S	3.125	1.150	S	3.9583	1.0689	0.0045 ^c	3.2049 ^c
<i>Engraulis capensis</i> (Cape anchovy)	S	3.125	1.150	A	3.7039	0.9137	0.0041 ^c	3.1951 ^c

Appendix I. (cont.)

<i>Etrumeus whiteheadi</i> (Cape round herring)	S	3.125	1.150	RH	3.7965	1.1088	0.0047 ^c	3.1002 ^c
6) Others								
Albulidae								
<i>Pterothrissus belloci</i> (Longfin bonefish)	H	1.515	1.073	H	2.7273	1.1691	-4.1569	3.6965
Ariidae								
<i>Galeichthys feliceps</i> (White barbel)	H	1.515	1.073	<i>G. feliceps</i>	2.3402	1.4017	-4.6236	4.2773
Cynoglossidae								
<i>Cynoglossus</i> sp. (Sole sp.)	G	1.786	1.050	<i>Cynoglossus capensis</i>	3.3518	1.3272	-2.1634	4.1337
Gempylidae								
<i>Thyrssites atun</i> (Snoek)	HM/H ^e	1.635	1.049	<i>T. atun</i>	3.9602	1.1198	-1.7389	3.9189
Lophiidae								
<i>Lophius</i> sp. (Monkfish sp.)	G	1.786	1.050	<i>Lophius vomerinus</i>	3.6028	1.2790	-0.3543	3.8554
Macrouridae								
<i>Coelorinchus quadricristatus</i>	H	1.515	1.073	<i>Coelorinchus simorhynchus</i>	2.9046	1.1803	-4.7557	3.9875
<i>Coelorinchus</i> sp.	H	1.515	1.073	<i>C. simorhynchus</i>	2.9046	1.1803	-4.7557	3.9875
Mugilidae								
<i>Liza</i> sp. (Mullet sp.)	HM/H ^e	1.635	1.049	<i>Liza richardsonii</i>	2.8651	1.3398	-2.7832	3.9285
Myctophidae								
<i>Gymnoscopelus piabilis</i>	G	1.786	1.050	<i>G. piabilis</i>	3.2514	0.9420	-2.7910	3.1981
<i>Lampadena luminosa</i>	G	1.786	1.050	G	3.5201	1.0564	-1.1459	3.3309
<i>Lampichthys procerus</i>	G	1.786	1.050	<i>L. hectoris</i>	3.1988	1.2676	-2.5907	4.2197
<i>Symbolophorus</i> sp.	G	1.786	1.050	<i>Symbolophorus boops</i>	3.6919	0.7005	-0.8470	2.1726

Appendix I. (cont.)

Ophidiidae								
<i>Genypterus capensis</i> (Kingklip)	H	1.515	1.073	<i>G. capensis</i>	2.3930	1.5630	-6.4094	5.2076
Sciaenidae								
<i>Atractoscion aequidens</i> (Cape salmon)	H	1.515	1.073	<i>A. aequidens</i>	2.2440	1.4816	-4.4887	4.2412
Scorpaenidae								
<i>Helicolenus dactylopterus</i> (Jacopever)	H	1.515	1.073	<i>H. dactylopterus</i>	2.6947	1.2357	-3.2748	3.8463
Soleidae								
<i>Austroglossus microlepis</i> (West coast sole)	G	1.786	1.050	<i>A. microlepis</i>	4.1534	1.1042	-0.0803	3.7411
Stromateidae								
<i>Centrolophus niger</i> (Black fish)	H	1.515	1.073	H	2.7273	1.1691	-4.1569	3.6965
Trichiuridae								
<i>Lepidopus caudatus</i> (Buttersnoek)	S/HM ^e	2.440	1.088	<i>L. caudatus</i>	4.2069	1.4239	-1.9230	4.5316
Triglidae								
<i>Chelidonichthys capensis</i> (Cape gurnard)	G	1.786	1.050	<i>C. capensis</i>	3.6942	1.3392	-0.6257	4.1191
Unidentified								
Unid 1	HM	1.754	1.025	HM	3.3550	1.0627	-1.5889	3.1973
Unid 2	HM/H ^e	1.635	1.049	HM	3.3550	1.0627	-1.5889	3.1973
Unid 3	S/HM ^e	2.440	1.088	HM	3.3550	1.0627	-1.5889	3.1973
Unid 4	S	3.125	1.150	A	3.7039	0.9137	-1.0158	2.8541
Unid 5	S	3.125	1.150	A	3.7039	0.9137	-1.0158	2.8541
Unid 6	HM	1.754	1.025	HM	3.3550	1.0627	-1.5889	3.1973
Unid 7	H	1.515	1.073	H	2.7273	1.1691	-4.1569	3.6965
Unid 8	G	1.786	1.050	G	3.5201	1.0564	-1.1459	3.3309
Unid 9	HM	1.754	1.025	HM	3.3550	1.0627	-1.5889	3.1973
Unid 10	H	1.515	1.073	H	2.7273	1.1691	-4.1569	3.6965

Appendix I. (cont.)

Unid 11	G	1.786	1.050	G	3.5201	1.0564	-1.1459	3.3309
Unid 12	S	3.125	1.150	A	3.7039	0.9137	-1.0158	2.8541
Unid 13	HM/H ^e	1.635	1.049	HM	3.3550	1.0627	-1.5889	3.1973
Unid 14	H	1.515	1.073	<i>C. simorhynchus</i>	2.9046	1.1803	-4.7557	3.9875
Unid 15	G	1.786	1.050	<i>L. hectoris</i>	3.1988	1.2676	-2.5907	4.2197
Unid 16	HM	1.754	1.025	HM	3.3550	1.0627	-1.5889	3.1973
Unid 17	S	3.125	1.150	A	3.7039	0.9137	-1.0158	2.8541
Unid 18	HM/H ^e	1.635	1.049	H	2.7273	1.1691	-4.1569	3.6965
Unid 19	HM	1.754	1.025	HM	3.3550	1.0627	-1.5889	3.1973
Unid 20	G	1.786	1.050	G	3.5201	1.0564	-1.1459	3.3309
Unid 21	HM/H ^e	1.635	1.049	<i>C. simorhynchus</i>	2.9046	1.1803	-4.7557	3.9875

^a Millar *et al.* 1999.

^b $\ln y = a + b \ln x$, where y = fish total length (mm) or mass (g) and x = corrected otolith diameter (mm) (Smale *et al.* 1995).

^c $y = ax^b$, where y = mass (g) and x = total length of fish (cm); Horse mackerel: equation based on length-mass measurements made during 2000 and 2001 by MFMR (horse mackerel section), $r = 0.99$, $n = 1027$; Sardine, anchovy and round herring: equations determined by MFMR (pelagics section).

^d Mean of *M. paradoxus* and *M. capensis*.

^e Mean correction factor of the two species was used.

Appendix II. The mean $\pm$ SD, median (in parentheses, where given) and range of fish total length (mm) per species in each prey group of the Cape fur seal *Arctocephalus pusillus pusillus* at each colony for the period January 1994 to April 2002. Sample size is given by *n*. Kruskal-Wallis was used to compare fish lengths between colonies for the first five prey groups.

Prey Group Species	Van Reenen Bay (VRB)			Atlas-Wolf Bay (AWB)			Cape Cross (CC)		
	Mean $\pm$ SD (median) (mm)	Range (mm)	<i>n</i>	Mean $\pm$ SD (median) (mm)	Range (mm)	<i>n</i>	Mean $\pm$ SD (median) (mm)	Range (mm)	<i>n</i>
1) Horse mackerel ^a	104.41 $\pm$ 55.57 (90.33)	29.41 - 350.59	924	96.86 $\pm$ 45.46 (82.84)	32.54 - 287.64	1 445	120.86 $\pm$ 41.20 (116.41)	34.12 - 336.14	15 390
2) Hake ^a	172.27 $\pm$ 58.33 (170.99)	12.79 - 469.88	5 095	147.39 $\pm$ 56.20 (144.12)	18.96 - 490.41	16 884	90.74 $\pm$ 57.27 (69.43)	14.68 - 381.46	12 533
3) Lanternfish	47.38 $\pm$ 10.53 (47.30)	24.43 - 83.27	201	(For all three colonies combined)					
4) Goby ^a	85.27 $\pm$ 23.28 (87.73)	31.83 - 137.66	1 173	74.34 $\pm$ 22.57 (75.94)	22.57 - 174.26	3 055	58.67 $\pm$ 17.96 (56.52)	11.74 - 121.56	2 225
5) Pelagics									
Sardine ^b	190.96 $\pm$ 56.49 (203.78)	90.46 - 390.75	64	147.24 $\pm$ 54.72 (127.56)	67.33 - 264.03	94	187.72 $\pm$ 46.45 (196.76)	87.13 - 296.30	673
Anchovy ^c	95.63 $\pm$ 16.54 (94.82)	52.42 - 156.24	378	96.99 $\pm$ 17.84 (94.82)	46.14 - 161.87	1 041	112.18 $\pm$ 20.27 (112.40)	60.69 - 167.47	1 407
Round herring ^a	201.21 $\pm$ 35.89 (208.62)	57.81 - 306.39	729	167.28 $\pm$ 47.55 (175.85)	49.14 - 279.06	563	152.47 $\pm$ 37.67 (156.46)	8.73 - 248.63	641
6) Others ^d									
<i>Pterothrissus belloci</i>	-	-	-	207.34 $\pm$ 6.45	199.89 - 211.07	3	167.49 $\pm$ 34.43	103.91 - 239.37	21
<i>Galeichthys feliceps</i>	-	-	-	-	-	-	211.89 $\pm$ 54.18	137.95 - 268.97	6
<i>Cynoglossus</i> sp.	131.76 $\pm$ 35.39	56.85 - 207.87	30	86.75	-	1	128.04	-	1
<i>Thyrsites atun</i>	308.86 $\pm$ 63.81	196.51 - 419.34	12	283.22 $\pm$ 53.36	182.37 - 419.34	24	262.27 $\pm$ 87.68	144.11 - 419.34	12
<i>Lophius</i> sp.	-	-	-	342.10 $\pm$ 51.02	306.03 - 378.18	2	196.76 $\pm$ 35.90	169.48 - 237.43	3
<i>Coelorinchus</i>									
<i>quadricristatus</i>	216.41 $\pm$ 68.95	172.56 - 318.33	4	168.93 $\pm$ 31.66	107.94 - 213.99	12	-	-	-
<i>Coelorinchus</i> sp.	227.89 $\pm$ 69.83	78.31 - 469.74	46	214.19 $\pm$ 75.28	44.96 - 439.51	217	219.26 $\pm$ 63.14	101.90 - 341.72	47
<i>Liza</i> sp.	-	-	-	235.85 $\pm$ 27.36	174.79 - 258.61	10	211.02	-	1
<i>Gymnoscopelus piabilis</i>	-	-	-	-	-	-	67.41 $\pm$ 11.37	40.86 - 95.10	33
<i>Lampadena luminosa</i>	-	-	-	-	-	-	77.90	-	1
<i>Lampichthys procerus</i>	76.75 $\pm$ 9.48	62.76 - 89.66	6	-	-	-	-	-	-
<i>Symbolophorus</i> sp.	102.23 $\pm$ 13.68	74.41 - 131.76	37	95.17 $\pm$ 13.93	62.67 - 129.98	159	97.40 $\pm$ 15.26	69.81 - 129.98	23

Appendix II. (cont.)

<i>Genypterus capensis</i>	356.09 ± 117.58	80.86 - 722.46	129	390.20 ± 94.74	241.71 - 617.47	36	-	-	-
<i>Atractoscion aequidens</i>	-	-	-	-	-	-	171.45	-	1
<i>Helicolenus dactylopterus</i>	317.59 ± 70.02	206.01 - 443.50	11	185.45 ± 61.74	120.91 - 243.93	3	-	-	-
<i>Austroglossus microlepis</i>	249.39 ± 45.00	156.41 - 362.25	52	271.32 ± 65.04	132.50 - 467.92	67	446.77 ± 120.09	349.23 - 621.50	4
<i>Centrolophus niger</i>	-	-	-	-	-	-	111.54	-	1
<i>Lepidopus caudatus</i>	355.50 ± 218.35	141.23 - 1123.36	28	292.85 ± 69.71	147.76 - 478.14	65	456.05 ± 207.75	327.80 - 695.74	3
<i>Chelidonichthys capensis</i>	172.91 ± 97.83	83.95 - 331.37	15	137.18 ± 80.02	61.00 - 395.53	39	134.06 ± 75.31	54.80 - 467.71	78
Unid 1	-	-	-	-	-	-	128.31	-	1
Unid 2	-	-	-	135.00	-	1	-	-	-
Unid 3	-	-	-	173.21	-	1	-	-	-
Unid 4	133.54	-	1	-	-	-	76.93	-	1
Unid 5	-	-	-	110.46	-	1	-	-	-
Unid 6	94.51	-	1	-	-	-	-	-	-
Unid 7	137.52	-	1	117.96	-	1	-	-	-
Unid 8	114.56 ± 8.87	103.58 - 123.57	4	123.18 ± 10.50	117.55 - 141.71	5	-	-	-
Unid 9	-	-	-	60.92 ± 10.51	53.30 - 72.91	3	59.33 ± 6.29	50.07 - 69.62	10
Unid 10	-	-	-	86.42	-	1	-	-	-
Unid 11	-	-	-	-	-	-	114.09 ± 15.15	93.65 - 129.60	4
Unid 12	-	-	-	-	-	-	88.90	-	1
Unid 13	-	-	-	93.44	-	1	-	-	-
Unid 14	-	-	-	-	-	-	170.93	-	1
Unid 15	-	-	-	55.71 ± 9.61	43.58 - 74.92	9	54.95 ± 16.53	32.84 - 100.51	32
Unid 16	-	-	-	-	-	-	147.14	-	1
Unid 17	-	-	-	-	-	-	78.94	-	1
Unid 18	-	-	-	-	-	-	161.25	-	1
Unid 19	152.30	-	1	-	-	-	-	-	-
Unid 20	123.57 ± 8.52	117.55 - 129.60	2	101.38 ± 28.38	35.57 - 127.59	9	101.59	-	1
Unid 21	-	-	-	214.11 ± 1.16	213.28 - 214.93	2	-	-	-

^a Lengths significantly different between all three colonies: Horse mackerel ($H_2 = 767.52$, $p < 0.001$, $n = 17\ 759$), hake ($H_2 = 8547.43$, $p < 0.001$, $n = 34\ 512$), goby ($H_2 = 1107.48$, $p < 0.001$, $n = 6\ 434$) and round herring ($H_2 = 519.36$, $p < 0.001$, $n = 1\ 933$).

^b Lengths significantly smaller at Atlas-Wolf Bay ($H_2 = 50.62$, $p < 0.001$, $n = 831$).

^c Lengths significantly larger at Cape Cross ($H_2 = 412.93$, $p < 0.001$, $n = 2\ 825$).

^d See Appendix I for common names.

Appendix III. The mean $\pm$ SD, median (in parentheses, where given) and range of fish mass (g) per species in each of the main prey groups of the Cape fur seal *Arctocephalus pusillus pusillus* at each colony for the period January 1994 to April 2002. Sample size is given by *n*. Kruskal-Wallis tests for differences in fish mass between colonies yielded the same results as for fish lengths in Appendix II because these are ranks tests.

Prey Group Species	Van Reenen Bay (VRB)			Atlas-Wolf Bay (AWB)			Cape Cross (CC)		
	Mean $\pm$ SD (median) (g)	Range (g)	<i>n</i>	Mean $\pm$ SD (median) (g)	Range (g)	<i>n</i>	Mean $\pm$ SD (median) (g)	Range (g)	<i>n</i>
1) Horse mackerel	20.57 $\pm$ 48.48 (5.23)	0.14 – 422.59	924	13.52 $\pm$ 27.52 (3.95)	0.19 – 222.64	1 445	19.47 $\pm$ 21.18 (11.90)	0.22 – 368.74	15 390
2) Hake	46.41 $\pm$ 47.69 (32.36)	0.01 – 790.84	5 095	31.04 $\pm$ 38.93 (18.85)	0.03 – 905.32	16 884	12.14 $\pm$ 25.97 (1.87)	0.01 – 409.09	12 533
3) Lanternfish	0.80 $\pm$ 0.56 (0.67)	0.07 – 4.40	201	(For all three colonies combined)					
4) Goby	7.35 $\pm$ 5.39 (6.44)	0.26 – 26.66	1 173	5.04 $\pm$ 4.50 (4.09)	0.09 – 56.07	3 055	2.43 $\pm$ 2.45 (1.61)	0.01 – 18.01	2 225
5) Pelagics									
Sardine	75.38 $\pm$ 76.89 (70.70)	5.23 – 568.98	64	38.23 $\pm$ 43.38 (15.74)	2.03 – 161.98	94	65.90 $\pm$ 44.98 (63.12)	4.64 – 234.41	673
Anchovy	6.17 $\pm$ 3.61 (5.42)	0.82 – 26.73	378	6.55 $\pm$ 4.08 (5.42)	0.54 – 29.93	1 041	10.33 $\pm$ 5.58 (9.33)	1.30 – 33.37	1 407
Round herring	56.52 $\pm$ 23.49 (57.86)	1.08 – 190.48	729	36.53 $\pm$ 25.82 (34.06)	0.65 – 142.58	563	26.11 $\pm$ 17.24 (23.71)	0.003 – 99.68	641

CHAPTER 3



University of Cape Town

Temporal variation in the diet of Cape fur seals

***Arctocephalus pusillus pusillus* at three**

mainland breeding colonies in Namibia

INTRODUCTION

Understanding the diet composition of seals and its variability has significance for the management of fisheries, as well as for understanding ecosystem function. For example, fishers view Cape fur seals *Arctocephalus pusillus pusillus* as competitors for marine resources (Wickens *et al.* 1992a). Indices of competition between seals and fisheries (Harwood and Croxall 1988) and models investigating the biological interactions between seals and their fish prey (Punt and Butterworth 1995) both require estimates of consumption by seals. The accuracy of such estimates would be improved by taking temporal variability in diet composition into consideration. Monitoring the diet of seals over time has other potential advantages: temporal changes in seal diet may give early warnings or confirmation of changes in environmental conditions or ecosystem health (Reid and Arnould 1996) and can give an indication of changes in the availability of prey species (e.g. Lowry *et al.* 1991, Acuña and Francis 1995). The importance of considering temporal variation when studying dynamic food webs has been highlighted by Tavares-Cromar and Williams (1996).

Cape fur seals are top predators in the cold and nutrient-rich upwelling Benguela System (Currie 1953). In Namibia, six teleost prey groups dominate in their diet: Cape horse mackerel *Trachurus trachurus capensis*, Cape hake *Merluccius capensis* and *M. paradoxus*, lanternfish *Lampanyctodes hectoris*, pelagic goby *Sufflogobius bibarbatus*, pelagics (sardine *Sardinops sagax*, anchovy *Engraulis capensis* and round herring *Etrumeus whiteheadi*) and others (Chapter 2). The Benguela System is subject to considerable temporal variability in environmental conditions and marine resources (Shannon *et al.* 1992). Local distributions of fish species preyed upon by seals are influenced by the availability of food resources, such as plankton (e.g. Bowen and Harrison 1996), which are affected by variable environmental conditions. The diet composition of

the Cape fur seal population inhabiting the Benguela System can therefore also be expected to vary with time. Indeed, the cephalopod component of the diet of seals from the Atlas and Wolf Bay colonies in Namibia, as determined from analysis of scats, show both annual and seasonal variation (De Bruyn *et al.* 2003).

A number of studies have revealed the occurrence of temporal differences in the diet composition of various pinniped species (e.g. Payne and Selzer 1989, Lowry *et al.* 1991, Pierce *et al.* 1991, Hammond *et al.* 1994, Acuña and Francis 1995, Bowen and Harrison 1996, Reid and Arnould 1996, Tollit and Thompson 1996, Casaux *et al.* 1997, Brown and Pierce 1998, Casaux *et al.* 1998, Naya *et al.* 2002, Lake *et al.* 2003, Pierce and Santos 2003, Hume *et al.* 2004). Pinniped diet composition may change both within and between years, as has been demonstrated for Juan Fernández fur seals *Arctocephalus philippii* (Acuña and Francis 1995), California sea lions *Zalophus californianus* (Lowry *et al.* 1991) and harbour seals *Phoca vitulina* (Tollit and Thompson 1996). Such changes have been attributed to variable oceanographic conditions which in turn affect prey availability (Acuña and Francis 1995), and possibly to changes in the sex-age structure of the onshore pinniped populations (Green *et al.* 1989).

Previous diet studies of the Cape fur seal in southern Africa have been based on irregular sampling events (Rand 1959, Shaughnessy 1985, David 1987a, Castley *et al.* 1991, Punt *et al.* 1995) and are thus inadequate for investigating temporal shifts in diet composition. In the present study, scats were collected at three Namibian breeding colonies over a period of eight years. Analysis of this data set enables the assessment of the diet composition of Cape fur seals at varying time scales, namely annual, seasonal and monthly. An understanding of temporal (inter- and intra-annual) patterns in the composition of the seal diet, combined with existing knowledge of spatial variation (Chapter 2) and population size and structure (Wickens *et al.* 1991, Butterworth *et al.* 1995), allows the refinement of prey consumption estimates, and improves their usefulness for management decisions regarding the seal population in relation to commercial fish resources.

MATERIAL AND METHODS

Study sites

Samples were collected at three mainland breeding colonies along the coast of Namibia: Cape Cross (21°47'S, 13°57'E; denoted CC), Atlas and Wolf Bays (26°49'S, 15°08'E and 26°48'S, 15°07'E, respectively; AWB) and Van Reenen Bay (27°23'S, 15°21'E; VRB) (Fig. 1). The Atlas and Wolf Bay colonies were considered as one because they are only 1 km apart. The population size at VRB is just under 15 000 individuals, at AWB close to 167 000 individuals, and at CC approximately 187 000 individuals (Marine and Coastal Management, (MCM), unpublished data). Together, these three colonies comprise about 65% of Namibia's seal population, estimated at just over half a million individuals in December 2001 (MCM, unpublished data).

Collection and processing of Cape fur seal scats

Adult lactating Cape fur seal cows forage close to their breeding colonies, on locally abundant prey (Oosthuizen 1991, Shaughnessy 1985). Bulls are present at colonies mainly during the breeding season, during which time they fast (Rand 1959). Thus, scats at breeding colonies can be assumed to have been largely deposited by lactating females, and to reflect their diet.

The scat collection and processing protocol has been described in Chapter 2. Scat samples were collected monthly from January 1994 to April 2002 (100 months). Prior to May 2001, samples consisted of an unknown number of scats collected at any time during a month and pooled together to form a "bag" sample. From May 2001 to April 2002, bag samples consisted of 30 pooled whole scats which were collected on the same date each month. Bag samples were collected regularly on a monthly basis at AWB (nine months missed), but less regularly at CC (22 months missed) and VRB (59 months missed). When more than one bag sample was collected in a month, these were combined to represent that month. Furthermore, 30 individual whole scats were collected from the three colonies on a monthly basis, from May 2001 to April 2002, coinciding with collections of bag samples.

Sagittal otoliths were sorted from processed scat samples, identified, counted and measured. Only teleost prey species were examined in this study; teleosts form a major portion of the diet of Cape fur seals (Rand 1959, Shaughnessy 1985, David 1987a, Castley *et al.* 1991, Punt *et al.* 1995). Cephalopods, which constitute a far smaller component of the diet of Cape fur seals

(16.7%, David 1987a), were the subject of a separate study (De Bruyn *et al.* 2003, De Bruyn *et al.* in press). Teleost prey were divided into six prey groups (hake, horse mackerel, goby, lanternfish, pelagics and others), and the percentage contribution of each prey group to total teleost abundance (%N) and mass (%M) was determined (Chapter 2). Mass of prey was determined from relationships between otolith diameters and fish length and mass (Chapter 2). For individual scat samples, the percentage frequency of occurrence (%FO) was also determined (Chapter 2).

Statistical analyses

Variation in the diet was investigated at an annual scale at each colony, where a year was defined as beginning in August and ending in July of the following year ("upwelling year"), corresponding approximately to sea surface temperature, wind and upwelling cycles (Cole and McGlade 1998, Cole and Villacastin 2000, K. Peard and J-P. Roux, Ministry of Fisheries and Marine Resources (MFMR), unpublished data). Monthly variation in diet was also investigated at each colony. The relative importance of between-year and within-year effects were then compared only for AWB and CC, VRB was omitted due to the paucity of data. Analysis of variance (ANOVA; General Regression Models, Statistica 6.1) was used to determine the effect of year (one-way ANOVA with an effect for each year), month (one-way ANOVA with an effect for each month), and year-month (two-way ANOVA with effects for both month and year) on prey abundance and mass. The coefficient of determination (r^2) indicated the percentage of the variation which was attributable to each of these effects. Additionally, seasonal variation was investigated by dividing the year into two six-month periods, namely a warming period (August to January the following year) and a cooling period (February to July), starting from February 1994 and ending at January 2002.

RESULTS

The total numbers of otoliths processed at CC, AWB and VRB during the study period were 545 211, 966 826 and 201 070, respectively. The number of otoliths in a bag sample ranged from 274 to 42 220 at CC, 1 503 to 44 660 at AWB and 350 to 31 536 at VRB.

The four most important prey groups, in terms of %N and %M, were horse mackerel, hake, lanternfish and goby. However, the importance of these varied between colonies: horse mackerel

were negligible at both AWB and VRB, whereas lanternfish were negligible at CC (Fig. 2). Visual inspection showed no clear seasonal patterns over the eight-year study period, nor any apparent long-term trends (Fig. 2).

Relative importance of annual and monthly variation

Nearly 50% of the variation in both %N and %M of hake in the diet of seals at CC could be explained by the interactive effect of year and month (Table I). In the case of %N, the effect of year on its own was insignificant, with monthly differences accounting for most of the explainable variation. The converse was true for %M. At AWB, around 40% and 25% of the variation in %N and %M, respectively, were explained by the effect of year and month together (Table I). In both cases, monthly differences were insignificant and annual differences explained most of the variation.

For goby, 40% and 55% of the variation in %N and %M in the seal diets at CC were explained by the interactive effect of year and month (Table I). In both cases, annual differences significantly explained most of the variation. At AWB, around 50% and 40% of the variation in %N and %M, respectively, of goby in the seal diet were explained by both year and month effects together (Table I). Monthly differences accounted for most of the variation in %N, although annual differences were also found to be important. For %M, annual differences explained most of the variation.

For lanternfish at AWB, both monthly and annual differences significantly accounted for the variation in %N in the seal diet (Table I). Month and year effects together explained 56% of the variation. Of the 43% variation in %M of lanternfish in the diet of seals at AWB explained by the interactive effect of year and month, most of this variation was accounted for by monthly differences (Table I).

Almost 70% of the variation in both %N and %M of horse mackerel in the diet of seals at CC could be explained by the year-month interaction (Table I). In both cases, both annual and monthly differences contributed significantly towards this variation.

For the main prey groups at CC and AWB, a large proportion of the temporal variation in the diet, considered both from the perspective of %N and %M, was unexplained, ranging from 31% (horse mackerel abundance at CC) to 74% (hake mass at AWB) (Table I). Therefore,

temporal variation in the diet was considered and described at each site at annual, seasonal and monthly scales.

Annual variation in diet composition

Cape fur seal diet composition, represented both as %N and %M, varied between years at VRB, AWB and CC (Fig. 2). At CC, horse mackerel, hake and goby were the dominant prey groups of seals according to scat analyses. The relative abundance and mass of horse mackerel in the scats from this colony were highest in 1994/95, 1995/96 and 2000/01 (Fig. 2). Horse mackerels were on average longer in 1998/99 (mean 13.5 cm) than in other years, and shorter in 1999/2000 (mean 10.5 cm; Fig. 3a). In terms of relative abundance, hake predominated from 1994/95 to 1996/97 and 2001/02, and the relative mass contribution of hake was of significance during 1996/97 and 2001/02. The longest mean hake length was in 1996/97 and 1997/98 (mean 11.6 and 13.7 cm, respectively; Fig. 3b). Goby featured strongly in the diet at Cape Cross in terms of both abundance and mass during 1996/97 (Fig. 2).

Three of the six prey groups dominated the diet of seals at AWB, namely hake, goby and lanternfish. At AWB, hake abundance in scats was high during the year 1996/97 (Fig. 2a), when the reconstituted mean fish length of this species was lowest over all the years of study (mean 12.5 cm; Fig. 3c). Reconstituted mass of hake was high at this colony during all upwelling years except for 1995/96 (Fig. 2b). The length of hake in the diet fluctuated between years, but on average was longest in 1995/96 and 1997/98 (mean 18.8 cm; Fig. 3c). Gobies were abundant in the diet during all years except for 1999/2000, when their relative mass contribution was lowest (Fig. 2). Lanternfish abundance in the diet of seals at AWB was high for most years except for 1996/97 and 1998/99, and their mass contribution to the diet was insignificant for all years.

Trends in prey abundance and mass at VRB were not clear due to missing data. Hake lengths estimated from scats differed between years; mean fish length was greatest during 1997/98 (mean 22.6 cm) and lowest in 1998/99 (mean 15.5 cm; Fig. 3d).

Seasonal variation in diet composition

At each of the seal study colonies, diet composition expressed as %N and %M of the teleost component of prey species as adjudged from scat analysis, showed variation between seasons

within years, and between matching seasons of different years (Fig. 4; Appendix I). Despite this, some general patterns did emerge.

Hake %N in the diet of seals at CC was generally highest during the August to January season, whereas hake %M was greater than 50% for the seasonal periods February to July 1997, August 1997 to January 1998, and August 2001 to January 2002 (Fig. 4a). At CC, reconstituted mean hake length was greater during the February to July period (mean 12.4 cm) than during the August to January period (mean 7.4 cm; Fig. 5a). At AWB, hake %N in the diet was low during all seasons throughout the study period except for February to July 1997 (66%; Fig. 4b). Hake %M in the diet was greater than 40% for almost all seasons; %M peaked (greater than 70%) only during two seasonal periods, February to July 1997 and August 1997 to January 1998 (Fig. 4b). The mean length of hake at AWB was also similar between seasons (~15.0 cm; Fig. 5a). At VRB, hake %N in the seal diet was generally low throughout the study period, reaching its highest levels during three of the eight February to July seasons, coinciding with the highest (greater than 60%) hake %M in the diet (Fig. 4c). The mean length of hake at VRB was similar between seasons (~17.0 cm; Fig. 5a).

At CC, both goby %N and %M in the seal diet tended to be highest during the August to January season (Fig. 4a), but mean goby length was similar between seasons (~6.0 cm; Fig. 5b). At AWB goby %N in the diet of seals was typically highest (greater than 50%) during five of the eight February to July seasons (Fig. 4b). Goby %M did not show any seasonal differences except for a peak in February to July 1996 (Fig. 4b). At VRB, goby %N and %M in the diet were low in all seasons except for the season February to July 1996 (Fig. 4c). At both VRB and AWB, reconstituted mean goby length was greater during the August to January period (mean 9.4 cm and 8.3 cm, respectively; Fig. 5b) than during the February to July period (mean 7.8 cm and 6.7 cm, respectively).

At CC, horse mackerel %N and %M in the seal diet were generally greater than 50% during five of the eight February to July seasons (Fig. 4a). Horse mackerel length was similar between seasons (~12.0 cm; Fig. 5c).

At both AWB and VRB, lanternfish %N in the diet of seals was generally greater than 50% during the August to January season, whereas %M was low during all seasons (Figs 4b and 4c).

Monthly variation in diet composition

The diet of seals, as determined from scat analysis, displayed monthly variation in prey group importance (Figs 2, 6 and 7). At CC, hake %N peaked in November and December (greater than 50%), which coincided with a slight increase in %M (Figs 6a and 7a). At CC, hake length was smallest from September to December and longest from February to April (Fig. 8a). At AWB, hake %N in the diet was less than 25% throughout the year (Fig. 6d), while hake %M was greater than 50% from June to August (Fig. 7d). Hake length was smallest in December, increasing gradually until August (Fig. 8b). At VRB, hake %N in the diet was highest during March and April (greater than 40%) (Fig. 6g), when the reconstituted hake length was at a minimum (Fig. 8c). The %M of hake in the diet was lowest in December (18%), after which it increased until April (Fig. 7g).

At CC, both goby %N and %M peaked in August (68% and 32%, respectively) and were low from February to May (less than 20% and 5%, respectively; Figs 6b and 7b). However, mean goby length during these two periods did not differ (Fig. 8d). At AWB, both goby %N and %M in the seal diet were highest from February to May (greater than 50% and 40%, respectively; Figs 6e and 7e). This period was characterized by small goby (Fig. 8e). At VRB, goby %N in the diet was highest (greater than 30%) in December and from February to April (Fig. 6h), while %M peaked in December (30%; Fig. 7h). This coincided with a peak in goby length around December, after which length decreased steadily to a minimum in May (Fig. 8f).

At AWB, lanternfish %N in the diet of seals was high from September to January (greater than 50%; Fig. 6f). Lanternfish %N in the seal diet was highest from May to November at VRB, with a peak in October (94%; Fig. 6i). Lanternfish %M in the diet was low throughout the year at both colonies (less than 30%; Figs 7i and 7f).

At CC, horse mackerel abundance and mass were highest from February to June and February to July, respectively (greater than 40%; Figs 6c and 7c). Mean horse mackerel length reached a peak in March and in November (Fig. 8g).

Monthly variation in diet composition in relation to frequency of occurrence

Hake %N, %M and %FO were highest (>51%) from September to December at CC (Fig. 9a). At AWB, hake %FO was highest from May to September (93-97%), within which period the highest

values of %N and %M were found (Fig. 9d). Hake %FO at VRB was highest from May to July (79-97%) during which period the highest levels of %N and %M were also reached (Fig. 9g).

At CC, %N, %M and %FO peaked in January to March, with a smaller peak in August (Fig. 9h). At AWB, goby %N and %M showed similar trends and peaked February to May (Fig. 9e). Goby %N and %M was low from June to January, although %FO was high during this time. At VRB, goby %FO, %N and %M reached two minimums, one in June and one in October (Fig. 9h), and generally, %FO was positively related to %N and %M.

Horse mackerel %N, %M and %FO were highest from May to July and April (>70%) with a smaller second peak in December (Fig. 9c). The %N, %M and %FO were similar to each other and followed the same trend in values over the time period.

At AWB, lanternfish %N was highest from August to January with similar high levels of %FO, but levels of %M were lower during this period (Fig. 9f). Lanternfish %N, %M, and %FO peaked in October at VRB (Fig. 9i).

DISCUSSION

The reliability of using scats for determining the diet of Cape fur seals is discussed in Chapters 2 and 8. Scat analysis can provide information on temporal trends in the main prey consumed by seals (Tollit and Thompson 1996). It is also a cost effective and non-destructive way to determine the diet of seals based on large samples (Pierce and Boyle 1991). For this study, errors or biases in determining diet composition were assumed to be consistent between samples. The problem that some prey may be of secondary origin (Pierce and Boyle 1991) was addressed in Chapter 2, where it was argued that goby and lanternfish are presumably primary prey of Cape fur seals. Thus, all prey were assumed to be primary prey.

Temporal variation of diet composition

The results of this study have indicated that the diet of Cape fur seals in Namibia is not predictable, but that considerable inter- and intra-annual variation in diet composition exists. The diet may reflect the availability of prey (Lowry *et al.* 1991, Brown *et al.* 2001, Naya *et al.* 2002). Stomach content analyses of Cape fur seals showed that they feed on locally abundant prey (Shaughnessy 1985). Thus it is probable that Cape fur seals in Namibia feed opportunistically and

proportionally on prey that are locally abundant. Variable oceanographic conditions likely impact the availability of prey to marine top predators such as seals (Acuña and Francis 1995, Reid and Arnould 1996, Hedd *et al.* 2002, Lea *et al.* 2002). Thus the variability in abundance and mass of prey in the diet of Cape fur seals is most probably attributable to the variable oceanographic conditions inherent to the Benguela System (Crawford *et al.* 1990).

Variation of prey in the diet may also be related to changes in the foraging strategies of seals (Casaux *et al.* 1998), their reproductive cycle (Naya *et al.* 2002) and their population structure (Green *et al.* 1989). The foraging behaviour of Cape fur seals is largely unknown (Kooyman and Gentry 1986), but Harcourt *et al.* (2002) suggested that the diving behaviour of New Zealand fur seals *Arctocephalus forsteri* changes according to seasonal changes in prey abundance and availability. The seals collected during this study mainly represent the diet of a single component of the population, adult lactating female seals at breeding colonies (see Methods), therefore the temporal changes in the diet found during this study can be assumed to be unrelated to changes in seal population structure.

Some seasonality was observed with respect to the abundance of horse mackerel, hake and goby at CC, goby at AWB and lanternfish at AWB and VRB in the seal diet. This may reflect the life histories of the prey, as has been suggested for the seasonal variation of lanternfish in the diet of Antarctic fur seals *Arctocephalus gazella* (Klages and Bester 1998), and is discussed in the following section.

Prey variability in relation to life histories

Hake abundance, length and mass in the diet of seals from each of the three study colonies varied inter-annually. Although hake abundance in the diet of seals at VRB and AWB was generally low throughout the study period, the large size of hake (15 – 17 cm) consumed at these colonies nevertheless resulted in this prey group accounting for a large proportion of the prey mass, as reconstituted from otoliths. At AWB, the frequency of occurrence of hake was always higher than the abundance, suggesting that hake is possibly always available here, albeit at low numbers. This may indicate that other preferred prey are available, e.g. lanternfish which have a higher energy content (Prosch 1991). Hake abundance in the seal diet was most seasonal at CC, where small hake (7 cm) mainly contributed to the high abundance in the August-January season. This was corroborated by the frequency of occurrence being high only during this period. Hake spawn

mainly from October to December (O'Toole 1977), and the small size of hake consumed by seals at CC during this period suggests that spawning occurs offshore of northern Namibia. The increase in length of hake consumed from September to November at CC possibly reflects the growth of juveniles.

Lanternfish abundance in the seal diet at AWB varied inter-annually. This was probably also the case at VRB, though there were insufficient data from there to detect such a pattern (see Fig. 2a). This variability may be due to the inter-annual variability in recruitment strength of *L. hectoris* (Young *et al.* 1988), the main species constituting the lanternfish prey group of Cape fur seals. The high abundance of lanternfish during the August-January season at VRB and AWB, as well as the corresponding high frequency of occurrence during this season, may be attributable to the intense upwelling which occurs within this season (Bailey 1979). At the upwelling area at Cape Columbine (32°48'S, 17°51'E), South Africa, in the southern Benguela, *L. hectoris* are more available to purse-seine fisheries during spring and autumn when south-easterly winds are strongest (Crawford 1980). Therefore, during the upwelling season in the northern Benguela, when strong southerly winds prevail, lanternfish are probably transported to the surface and closer inshore, making them more accessible to seals. Reid and Arnould (1996) attributed the seasonal consumption of lanternfish by Antarctic fur seals to the appearance of large shoals in their foraging area resulting from oceanographic changes.

The mass of individual lanternfish consumed by seals was negligible due to the small size of fish consumed (mean of 4.7 cm, Chapter 2). The lanternfish consumed were mainly juveniles because sexually mature *L. hectoris* are greater than 6.5 cm in length (Cruickshank 1983a). In the southern Benguela, the peak spawning season of *L. hectoris* is during late winter and spring (Prosch 1991) and juveniles start to recruit in August (Prosch 1986). Because the period when lanternfish (juveniles) were abundant in the seal diet was August-January in Namibia, this suggests that the spawning season in the northern Benguela is similar.

Goby abundance in seal diets varied inter-annually at each colony, probably due to variable environmental conditions (O'Toole 1977). Goby abundance in the diet of seals at AWB was generally highest during the February to July season, when upwelling is at a minimum (February to April; Bailey 1979). However, the high frequency of occurrence of goby throughout the year, especially when abundance was very low, seems to indicate that although it is always available it is not also the preferred prey. In contrast, goby abundance peaked within the August to January

season at CC. Goby spawn continuously from July to February, with most of the spawning taking place from September to December (O'Toole 1977). Spawning is greatest south of Walvis Bay between 24 and 25°S, although the spawning area probably extends further south (O'Toole 1977). Seals mainly consumed smaller gobies at CC than at AWB and VRB (Chapter 2). Apparently then, juvenile goby are available to CC seals during the August to January season, and to the more southerly colonies once they migrate southwards and increase in size during the February to July season. However, no information on the movement of goby in relation to oceanographic conditions is available to corroborate this hypothesis.

Lanternfish abundance in seal scats at AWB was higher during the time of year when the abundance of gobies was low, and vice versa. Lanternfish have a high oil content (Prosch 1991), therefore it is likely that they are preferred prey over gobies, which are energetically unrewarding (Crawford *et al.* 1985). Once the degree of upwelling diminishes, the scarcity of lanternfish might cause seals to switch to preying on goby.

Horse mackerel abundance and mass in seal scats from CC generally predominated during the February to July season, and mainly juveniles were consumed (Chapter 2). Juveniles recruit into the pelagic stock as 0-year-olds during January to March (Barange *et al.* 1998). This period is within the season that juvenile horse mackerel predominated in the seal diet (February to July). High levels of frequency of occurrence were only found during this period, supporting the suggestion that the availability of horse mackerel may be seasonal. The mean length of horse mackerel, as reconstituted from the otoliths, showed two peaks (March and November), which probably reflect biannual spawning, a characteristic of this species (Kerstan and Leslie 1994, Kerstan 1995). However, this bimodality may also be caused by varying growth rates within cohorts as a result of size-dependent food availability (Kerstan 1995).

The management of Namibia's marine resources

This study serves to highlight the complexity of the relationship between predators and their prey. Not only do Cape fur seals feed on a large variety of teleost prey, but the prey type and amount consumed varies between seasons and between years. Moreover, this study has hinted at life-history strategies that are not well known, such as the southward migration of goby. Furthering our understanding of these relationships will provide insight into the complexities of the dynamic food web within the northern Benguela. Including temporal variation into food webs

improves knowledge of the trophic structure, and also allows the association of trophic structure with life histories (Tavares-Cromar and Williams 1996).

Ecosystem modelling of the northern Benguela (e.g. the Ecopath model) aims at contributing towards fisheries management at an ecosystem level (Shannon and Jarre-Teichmann 1999). Ecopath models the trophic functioning of the northern Benguela by considering various states of the ecosystem. One of the input data requirements for Ecopath is diet composition of organisms in the ecosystem, which has a large influence on the model outputs depending on how diet composition is assigned (Shannon and Jarre-Teichmann 1999). Results from this study suggest that the northern Benguela ecosystem is subject to varying states over time, and thus models such as Ecopath should incorporate variability in seal diet composition to better understand trophic function and to improve fisheries management in the region.

It is important to include temporal variation into prey consumption models for fisheries management (Tollit and Thompson 1996), because it refines the resolution of prey consumption estimates. All previous Cape fur seal prey consumption models are based on a static diet composition (e.g. Shaughnessy 1985, David 1987a, Wickens *et al.* 1992b), thus falsely assuming that there is no variation in diet composition. The results of this study allow for improved consumption estimates for Cape fur seals, by breaking the year down into seasons or months (Chapter 4).

Large-scale processes, such as decadal phenomena, may influence the long-term dynamics of the marine ecosystem (Crawford and Payne 1989). For instance, regional changes in the marine environment that affect fish abundance and distribution may only be evident at decadal scales (Crawford and Payne 1989). The data of this study are part of a time series that is too short to investigate variability at time scales larger than a year. It is therefore recommended that monthly data collection continue into the future to lengthen the data series, so that long-term changes may be studied.

Table I. The coefficient of determination (r^2 ; one-way and two-way ANOVA, General Regression Models) for year, month and year-month effects on the percentage abundance and mass of Cape horse mackerel *Trachurus trachurus capensis*, Cape hakes *Merluccius* spp., lanternfish (*Lampanyctodes hectoris*) and pelagic goby *Sufflogobius bibarbatus* determined from scats of Cape fur seals *Arctocephalus pusillus pusillus* at Atlas-Wolf Bay (AWB) and Cape Cross (CC). The asterisk (*) represents significance at $p < 0.05$.

Colony	Effect	Percentage r^2							
		Horse Mackerel ^a		Hake		Lanternfish ^a		Goby	
		Abundance	Mass	Abundance	Mass	Abundance	Mass	Abundance	Mass
CC	Year	31*	39*	12	34*	-	-	22*	30*
	Month	41*	32*	36*	14	-	-	20	24
	Year-Month	69*	65*	48*	46*	-	-	39*	54*
	Unexplained variation	31	35	52	54			61	46
AWB	Year	-	-	39*	19*	23*	11	18*	23*
	Month	-	-	5	8	37*	34*	35*	14
	Year-Month	-	-	42*	26	56*	43*	51*	37*
	Unexplained variation			58	74	44	57	49	63

^a Lanternfish formed a minor component of the seal diet at CC, and horse mackerel at AWB.

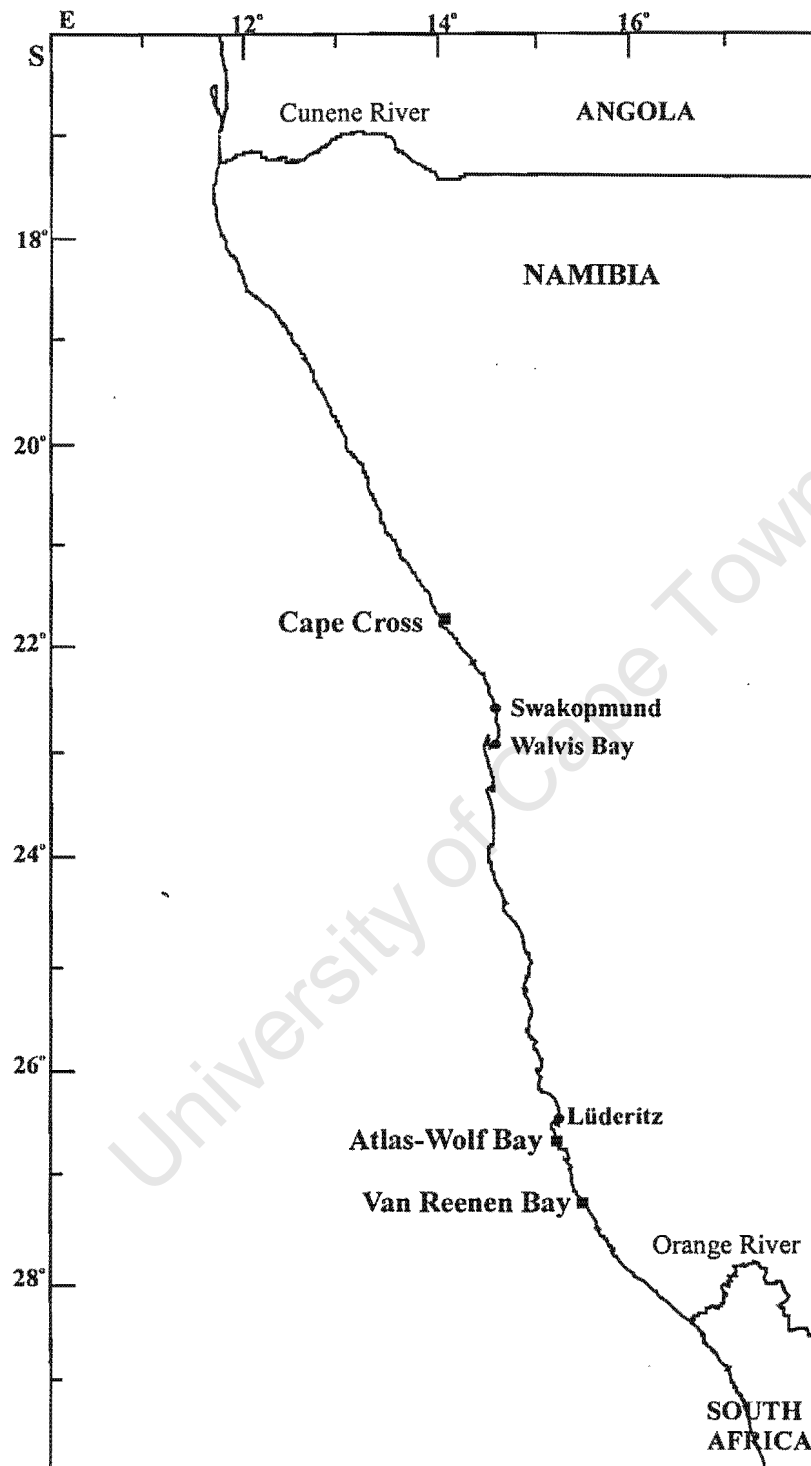


Figure 1. The location of the three Cape fur seal *Arctocephalus pusillus pusillus* study colonies (Cape Cross, Atlas-Wolf Bay and Van Reenen Bay) in Namibia.

Cape Cross

n: 49 905 73 774 145 153 107 052 34 872 22 668 34 758 32 146 44 883
Upwelling year: 1994/95 1995/96 1996/97 1997/98 1998/99 1999/2000 2000/01

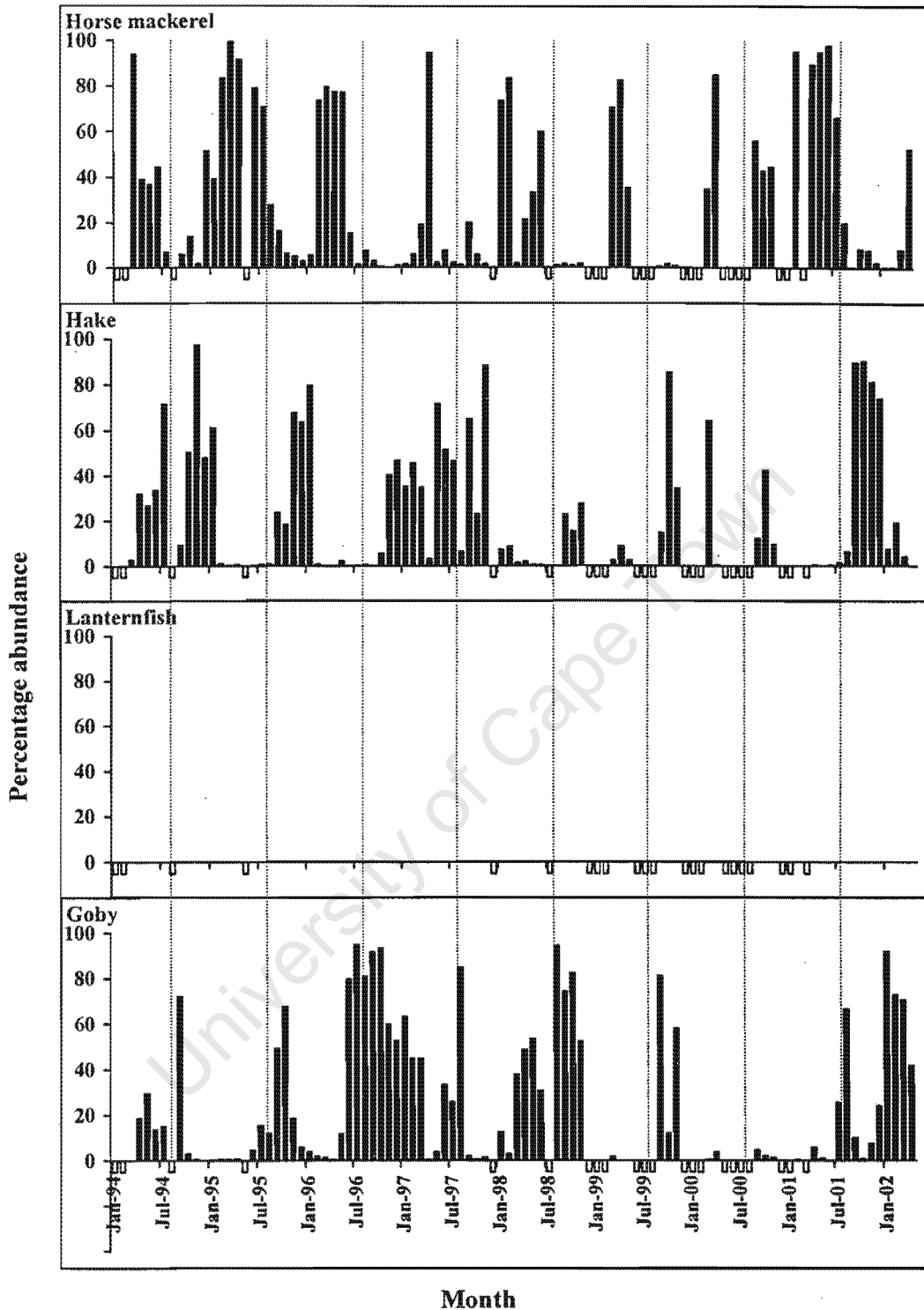


Figure 2a. The monthly percentage abundance of Cape horse mackerel *Trachurus trachurus capensis*, Cape hakes *Merluccius* spp., lanternfish *Lampanyctodes hectoris* and pelagic goby *Sufflogobius bibarbatatus* determined from scats of Cape fur seals *Arctocephalus pusillus pusillus* at Cape Cross, Atlas-Wolf Bay and Van Reenen Bay for the period January 1994 to April 2002. Vertical lines delineate the upwelling years (August to July the following year), and months where data were missing are represented as short open bars extending below the x-axis. The total number of otoliths of all prey is given by *n*.

Atlas-Wolf Bay

n: 34 879 138 863 257 214 118 116 94 989 39 956 59 891 87 543 135 376
 Upwelling year: 1994/95 1995/96 1996/97 1997/98 1998/99 1999/00 2000/01

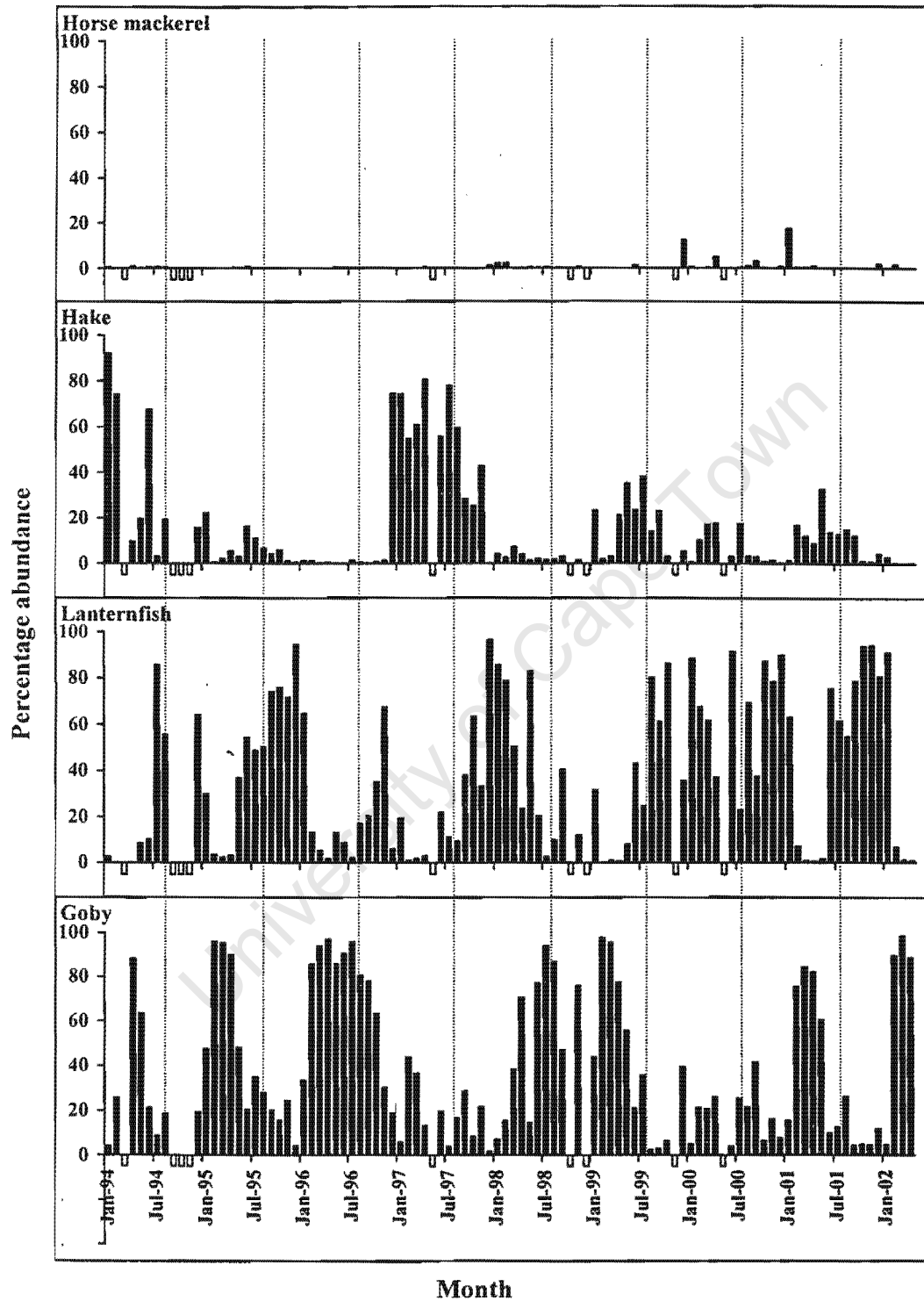


Figure 2a. (cont.)

Van Reenen Bay

n: 12 031 42 837 37 211 0 18 301 3 783 18 873 15 535 52 499
 Upwelling year: 1994/95 1995/96 1996/97 1997/98 1998/99 1999/2000 2000/01

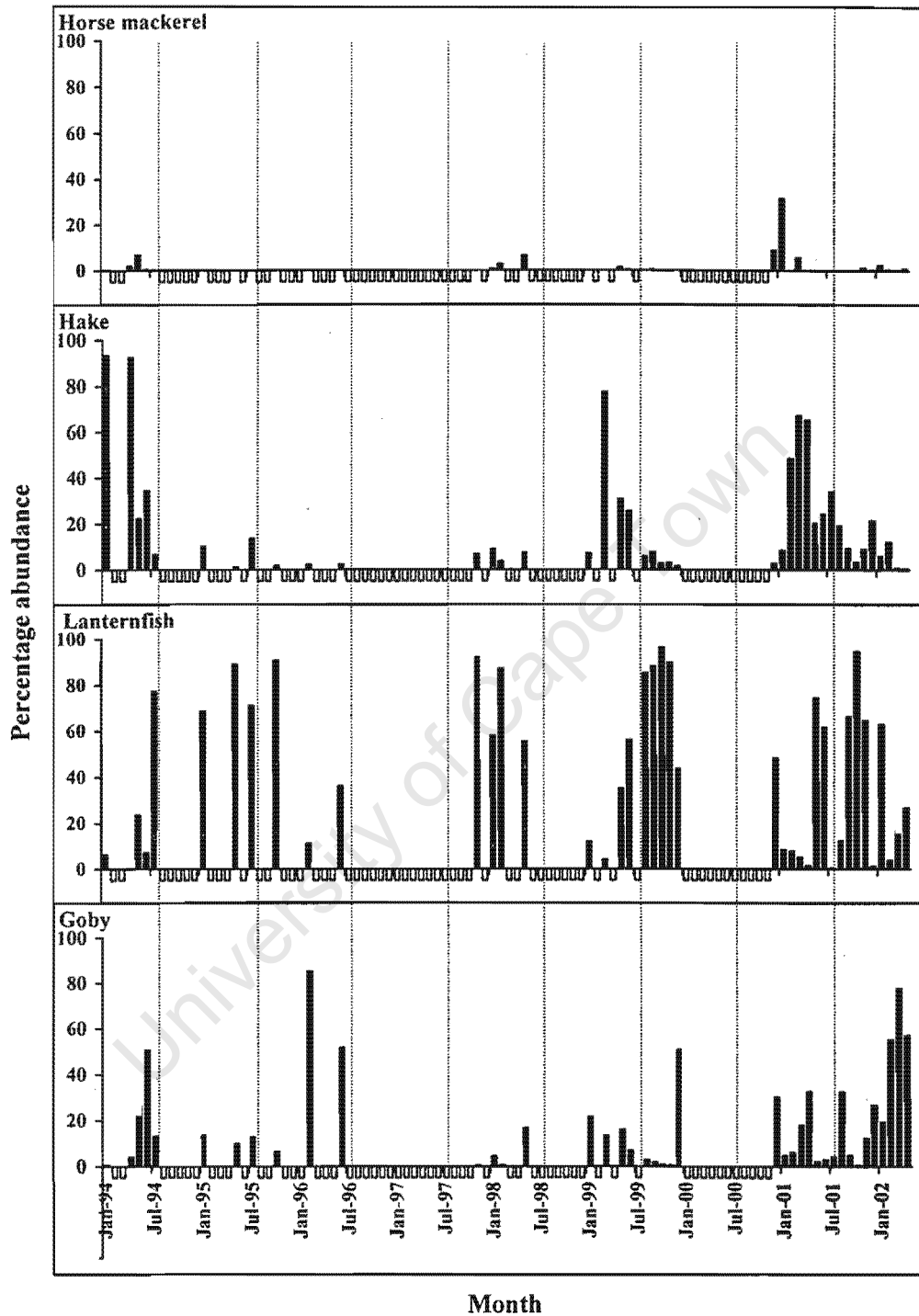


Figure 2a. (cont.)

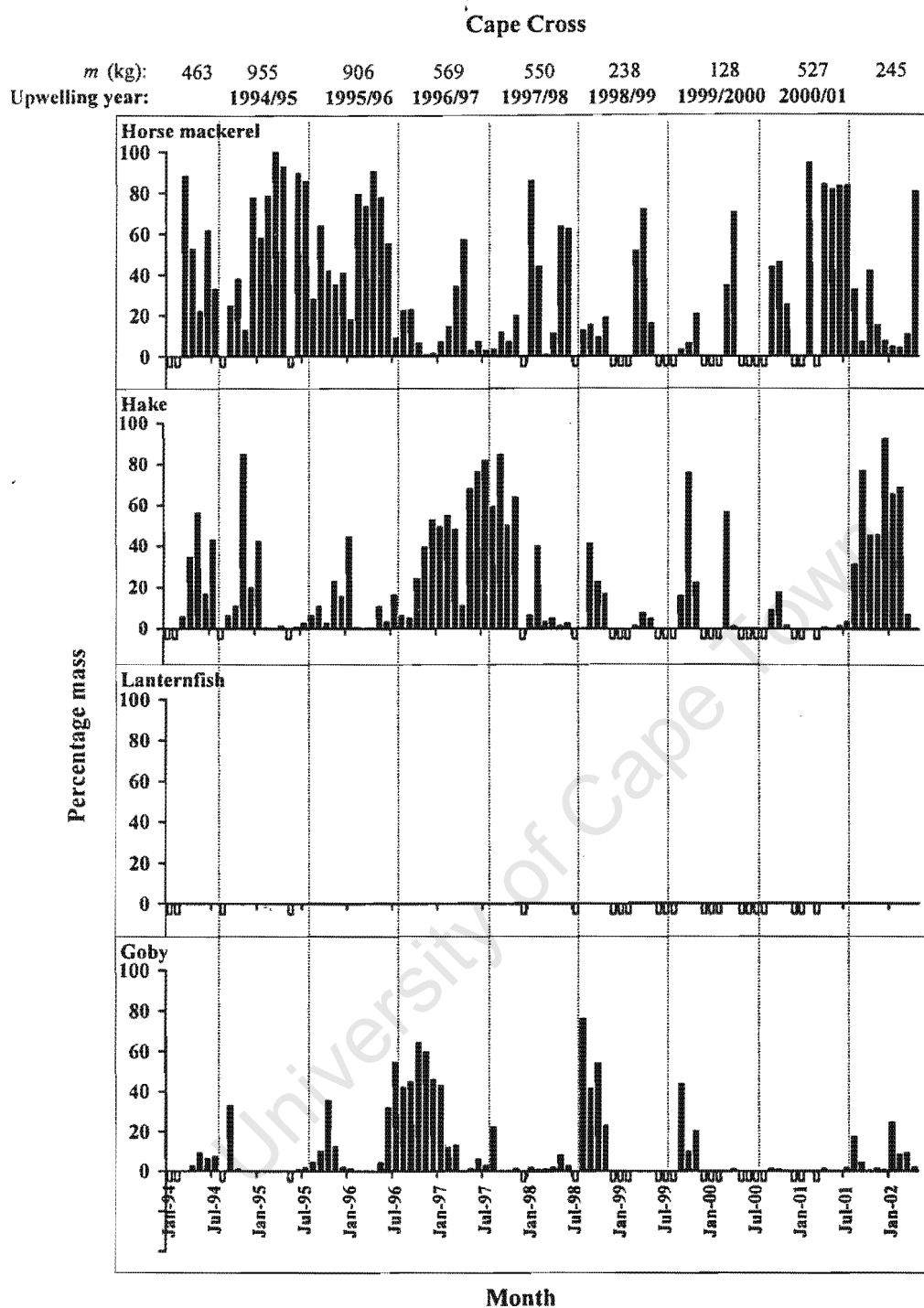


Figure 2b. The monthly percentage mass of Cape horse mackerel *Trachurus trachurus capensis*, Cape hakes *Merluccius* spp., lanternfish *Lampanyctodes hectoris* and pelagic goby *Sufflogobius bibarbatus* determined from scats of Cape fur seals *Arctocephalus pusillus pusillus* at Cape Cross, Atlas-Wolf Bay and Van Reenen Bay for the period January 1994 to April 2002. Vertical lines delineate the upwelling years (August to July the following year), and months where data were missing are represented as short open bars extending below the x-axis. The total mass of all prey (kg) is given by *m*.

Atlas-Wolf Bay

m (kg): 232 525 864 759 555 310 276 522 309
Upwelling year: 1994/95 1995/96 1996/97 1997/98 1998/99 1999/2000 2000/01

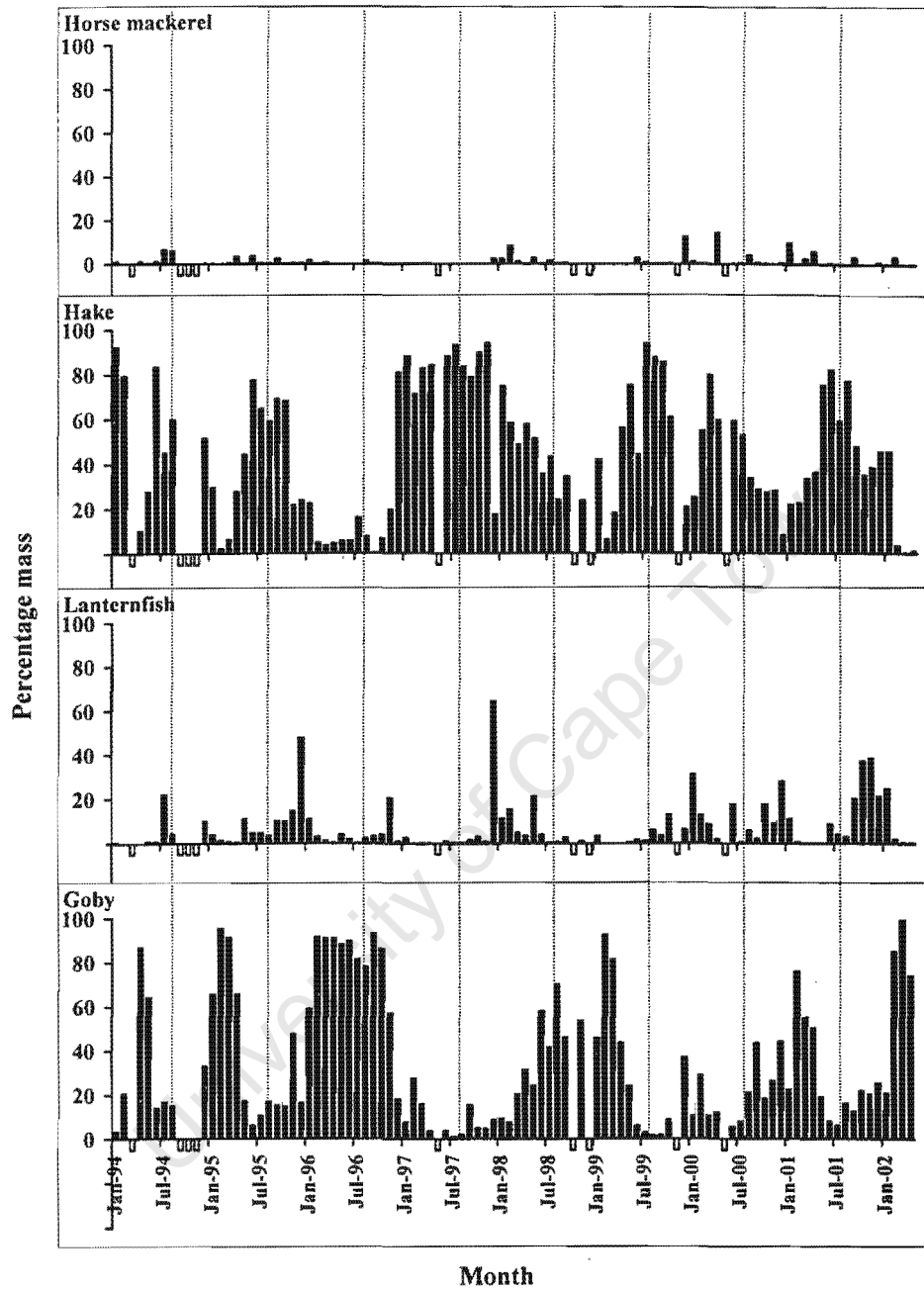


Figure 2b. (cont.)

Van Reenen Bay

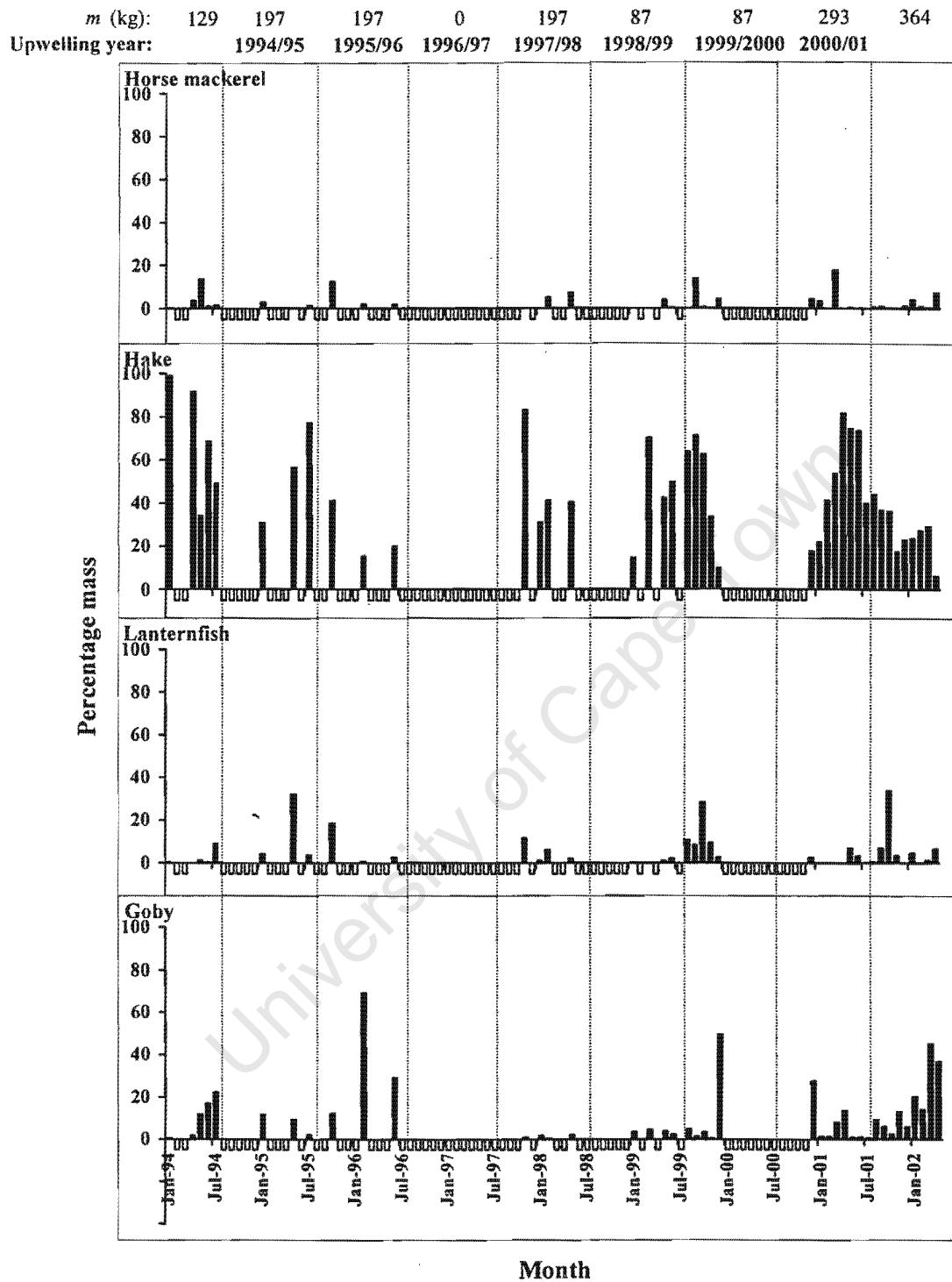


Figure 2b. (cont.)

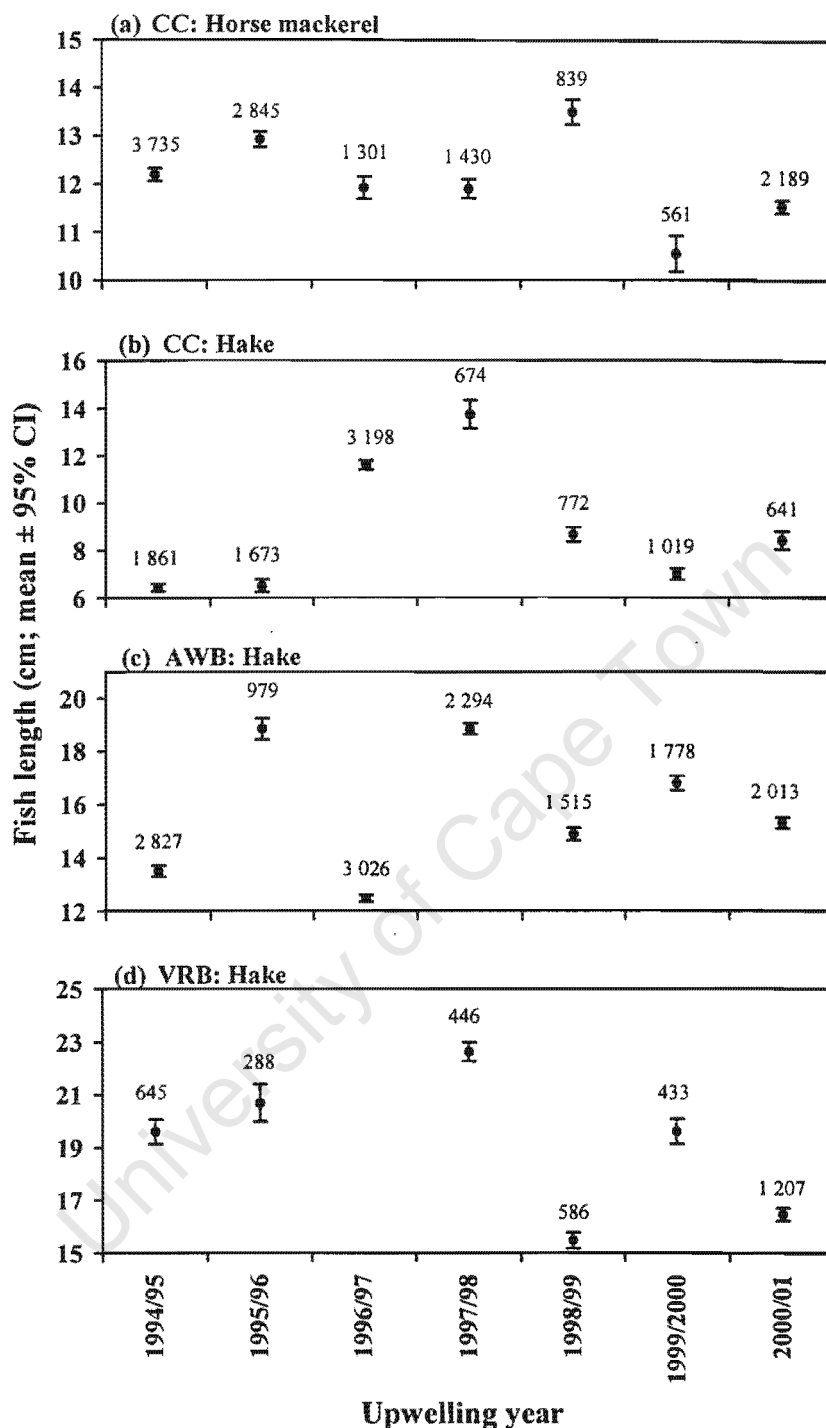


Figure 3. The mean $\pm$ 95% confidence interval (CI) length (cm) of (a) Cape horse mackerel *Trachurus trachurus capensis* and (b-d) Cape hakes *Merluccius* spp. estimated from otoliths in scats of Cape fur seals *Arctocephalus pusillus pusillus* at the three mainland breeding colonies in Namibia (Cape Cross, CC; Atlas-Wolf Bay, AWB; Van Reenen Bay, VRB), for the upwelling year (August to July). Horse mackerel was negligible in the diet at AWB and VRB. The number of fish measured is given above the mean.

(a) Cape Cross

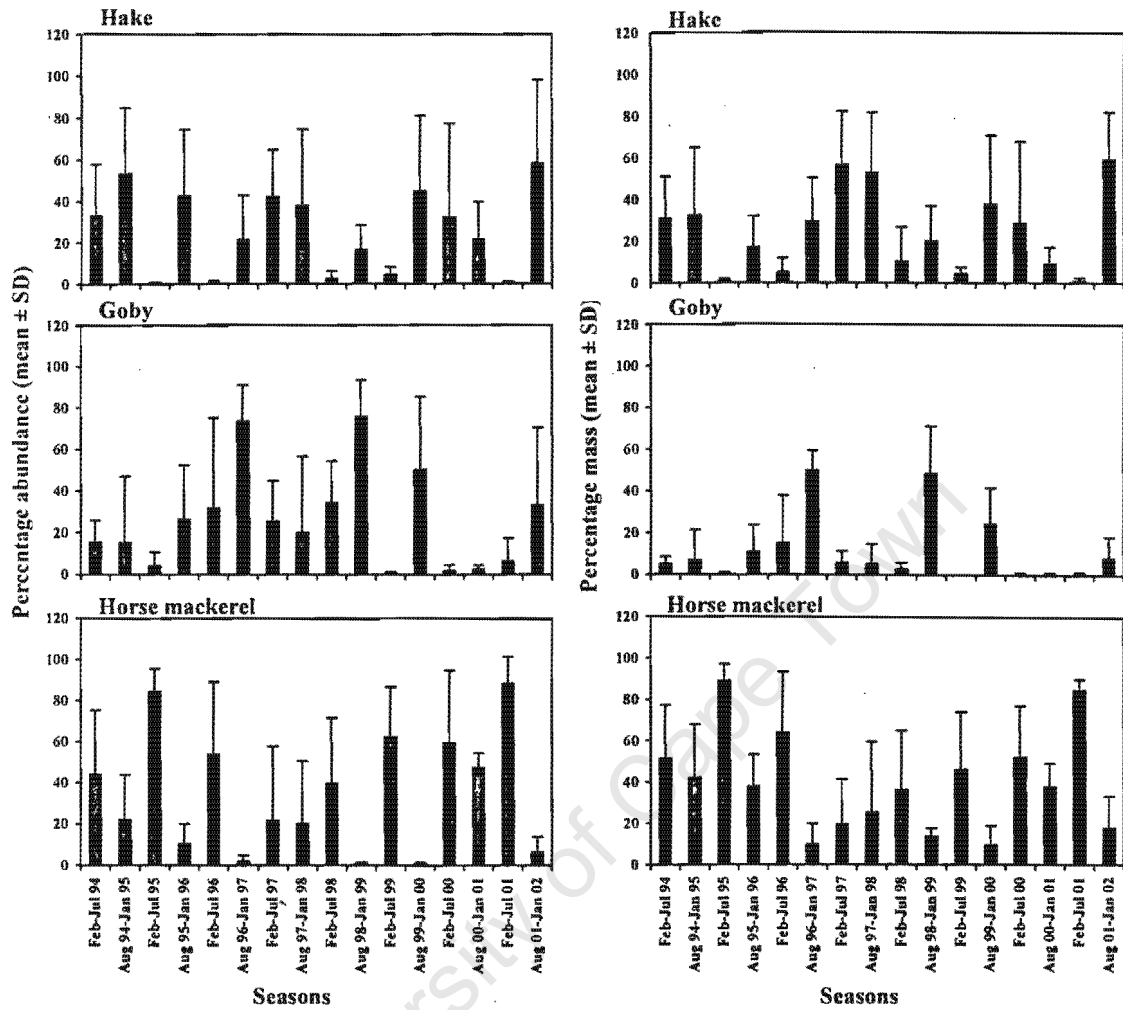


Figure 4: The percentage abundance and mass (mean $\pm$ SD) of main prey in the diet of Cape fur seals *Arctocephalus pusillus pusillus* at (a) Cape Cross, (b) Atlas-Wolf Bay and (c) Van Reenen Bay, for the six-month seasonal periods (February to July and August to January) over the study period January 1994 to April 2002. The number of months, otoliths and prey mass contributing towards each season's estimate are given in Appendix I.

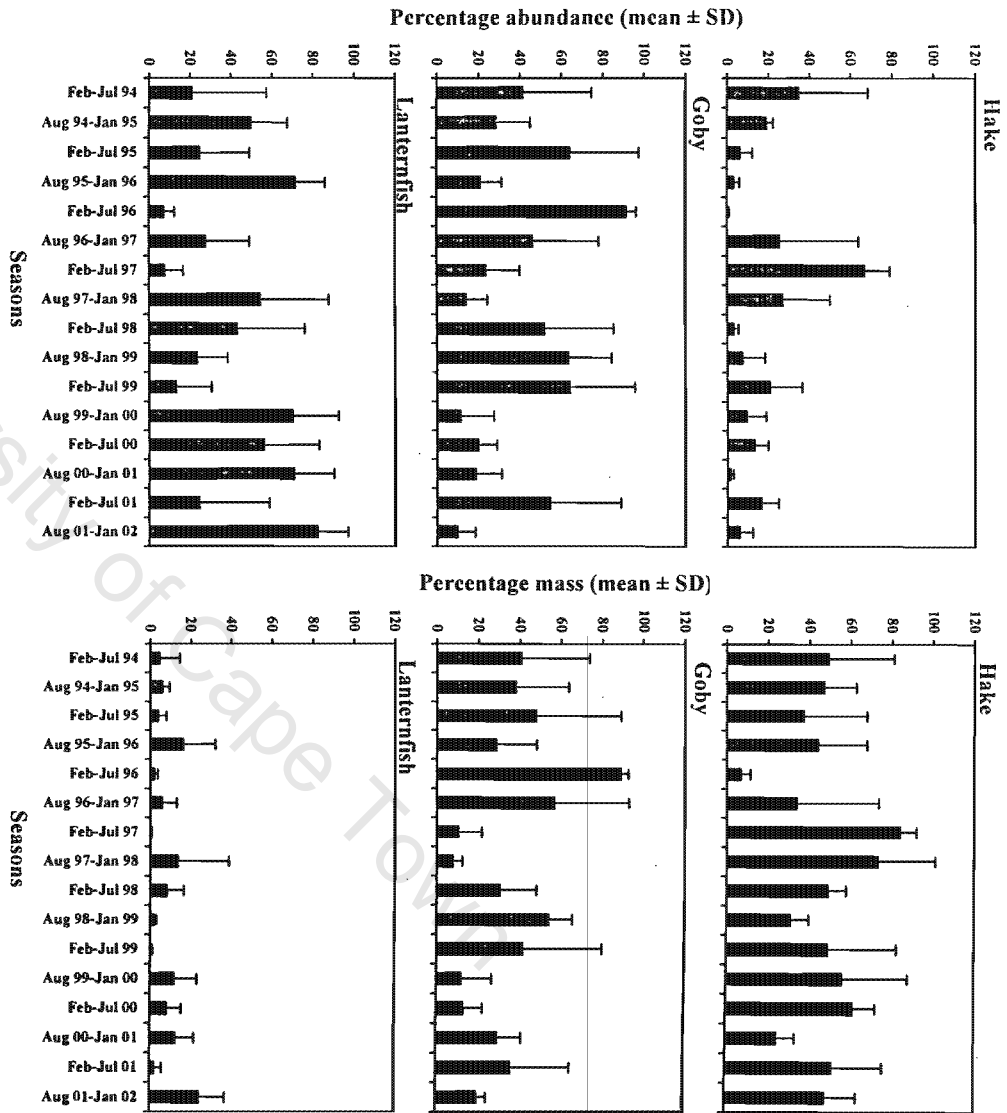


Figure 4: (cont.)

(c) Van Reenen Bay

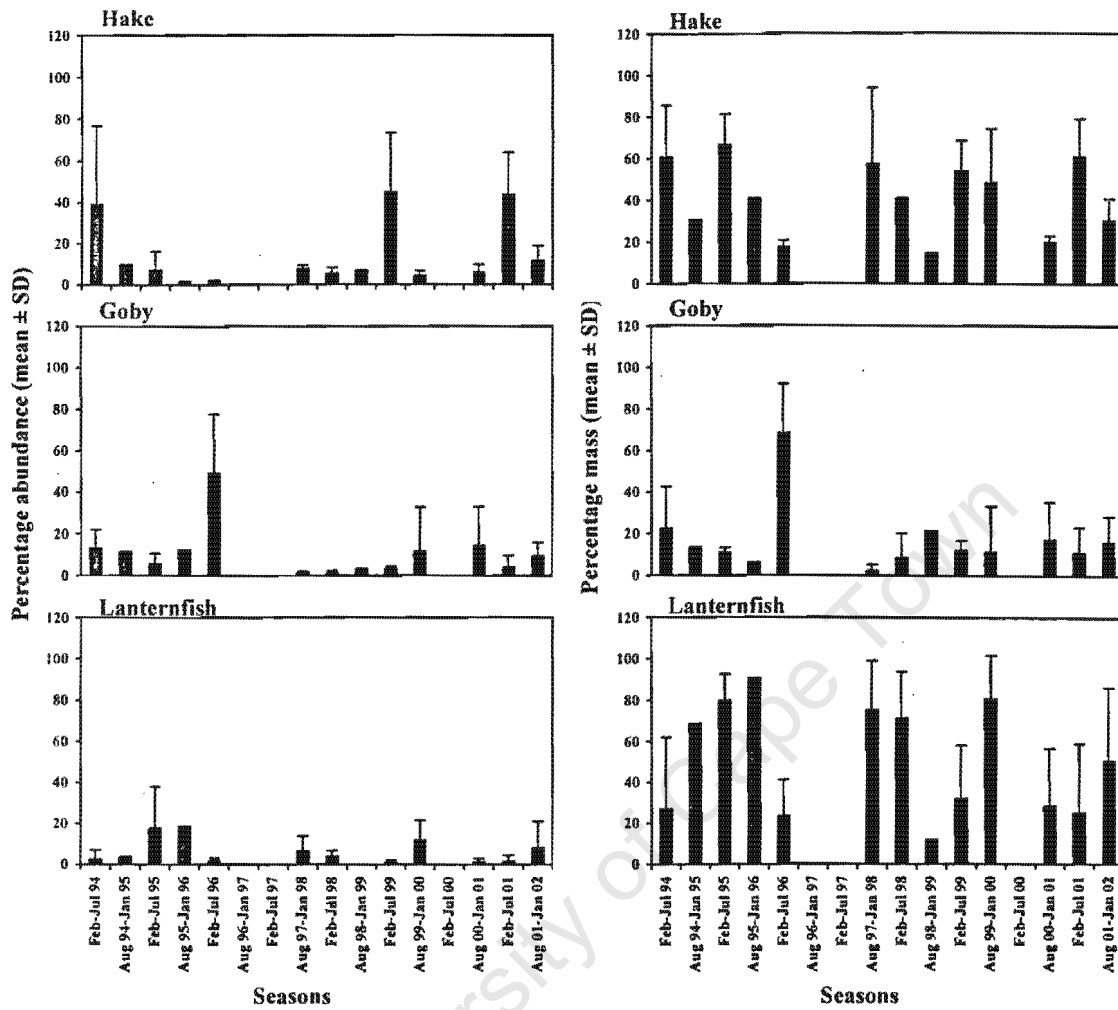


Figure 4: (cont.)

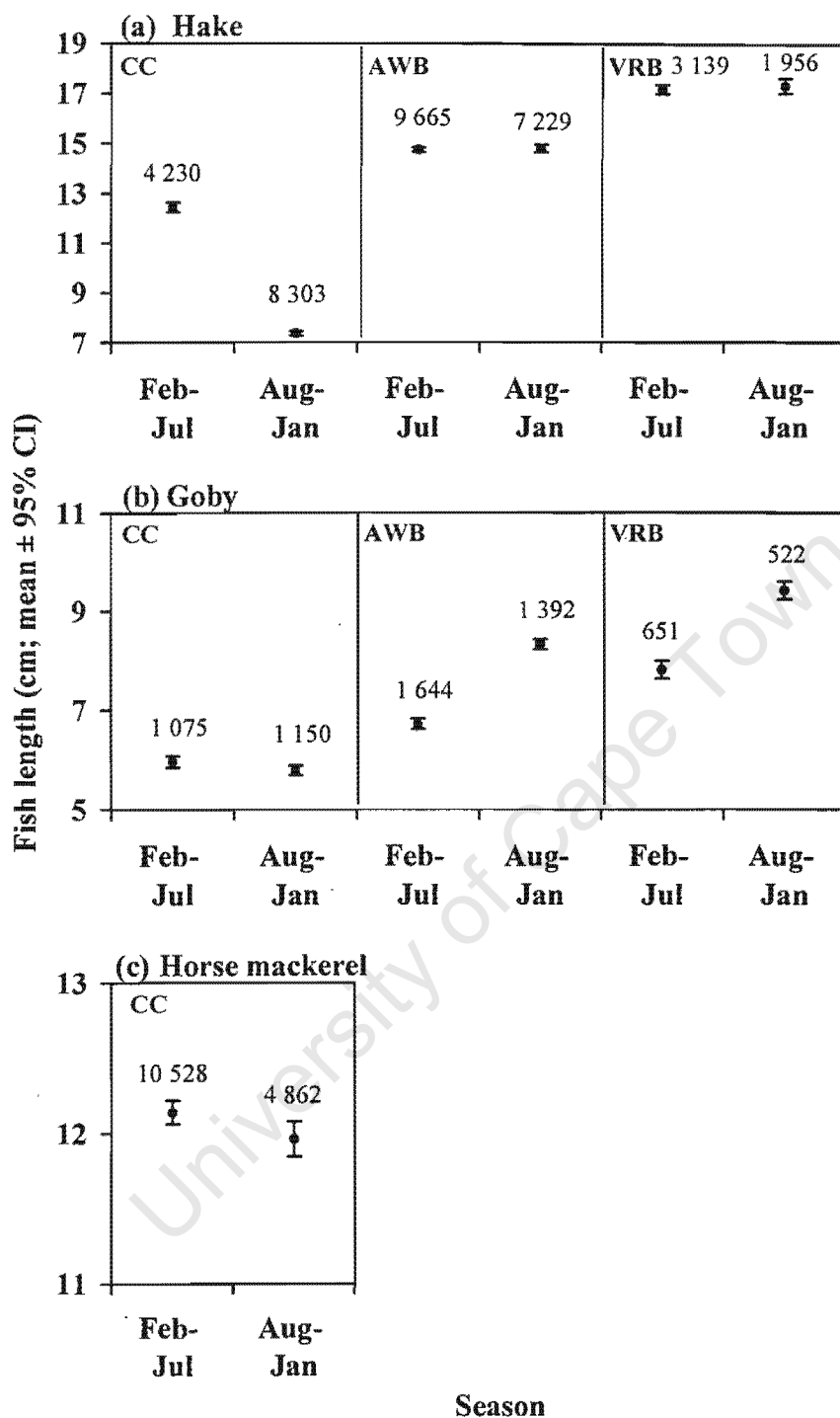


Figure 5. The seasonal mean $\pm$ 95% confidence interval (CI) length (cm) of (a) Cape hakes *Merluccius* spp., (b) pelagic goby *Sufflogobius bibarbaratus* and (c) Cape horse mackerel *Trachurus trachurus capensis* estimated from otoliths in scats of Cape fur seals *Arctocephalus pusillus pusillus* at the three mainland breeding colonies in Namibia (Cape Cross, CC; Atlas-Wolf Bay, AWB; Van Reenen Bay, VRB). Horse mackerel was negligible in the seal diet at AWB and VRB. The number of fish measured is given above the mean.

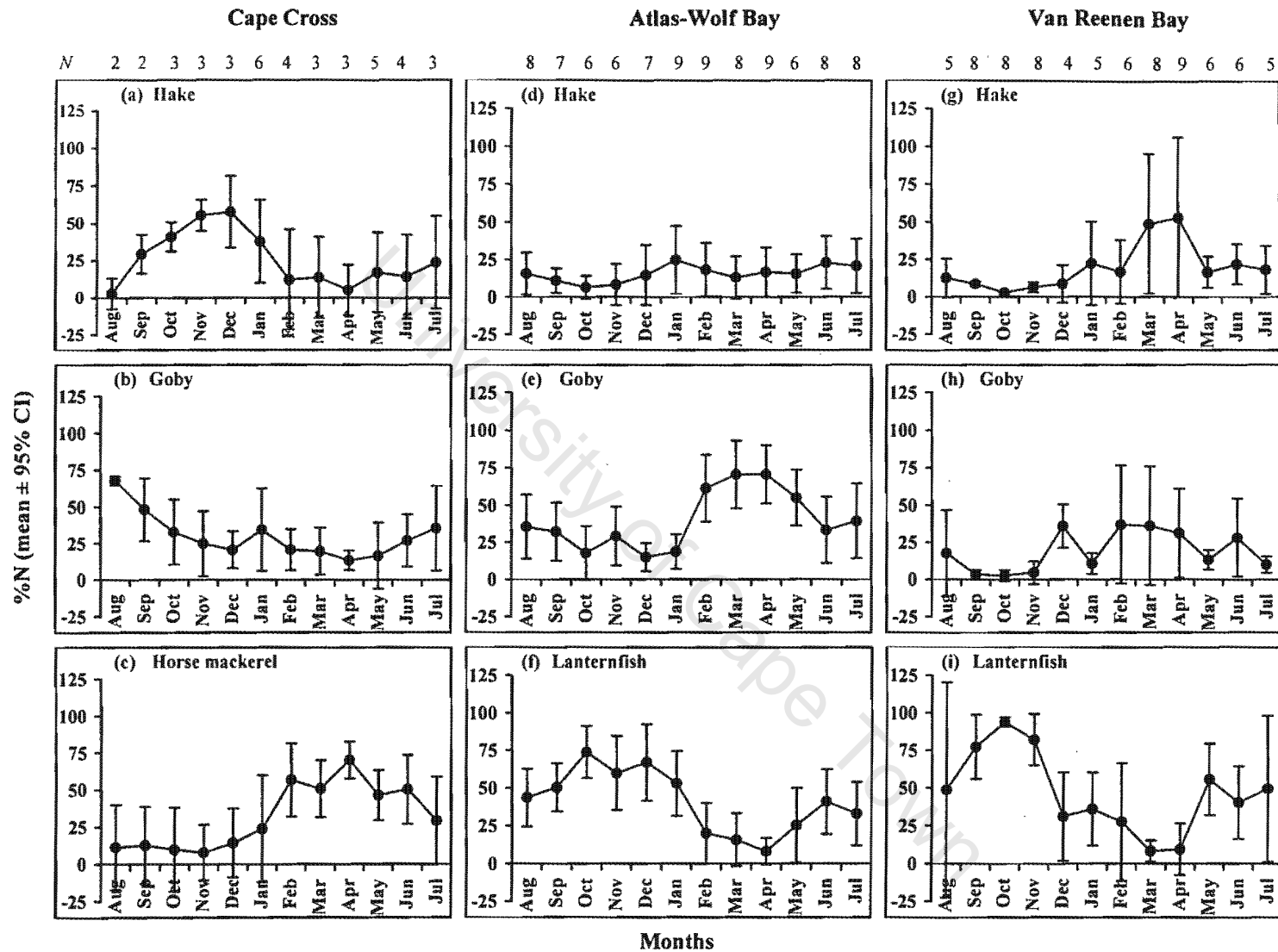


Figure 6. Mean percentage abundance (%N; $\pm$ 95% confidence intervals, CI) of main prey groups from scats of Cape fur seals *Arctocephalus pusillus pusillus* at (a-c) Cape Cross, (d-f) Atlas-Wolf Bay, and (g-i) Van Reenen Bay, for the period January 1994 to April 2002. Months are from August-July, the upwelling year, and the number of month samples is given by *N*.

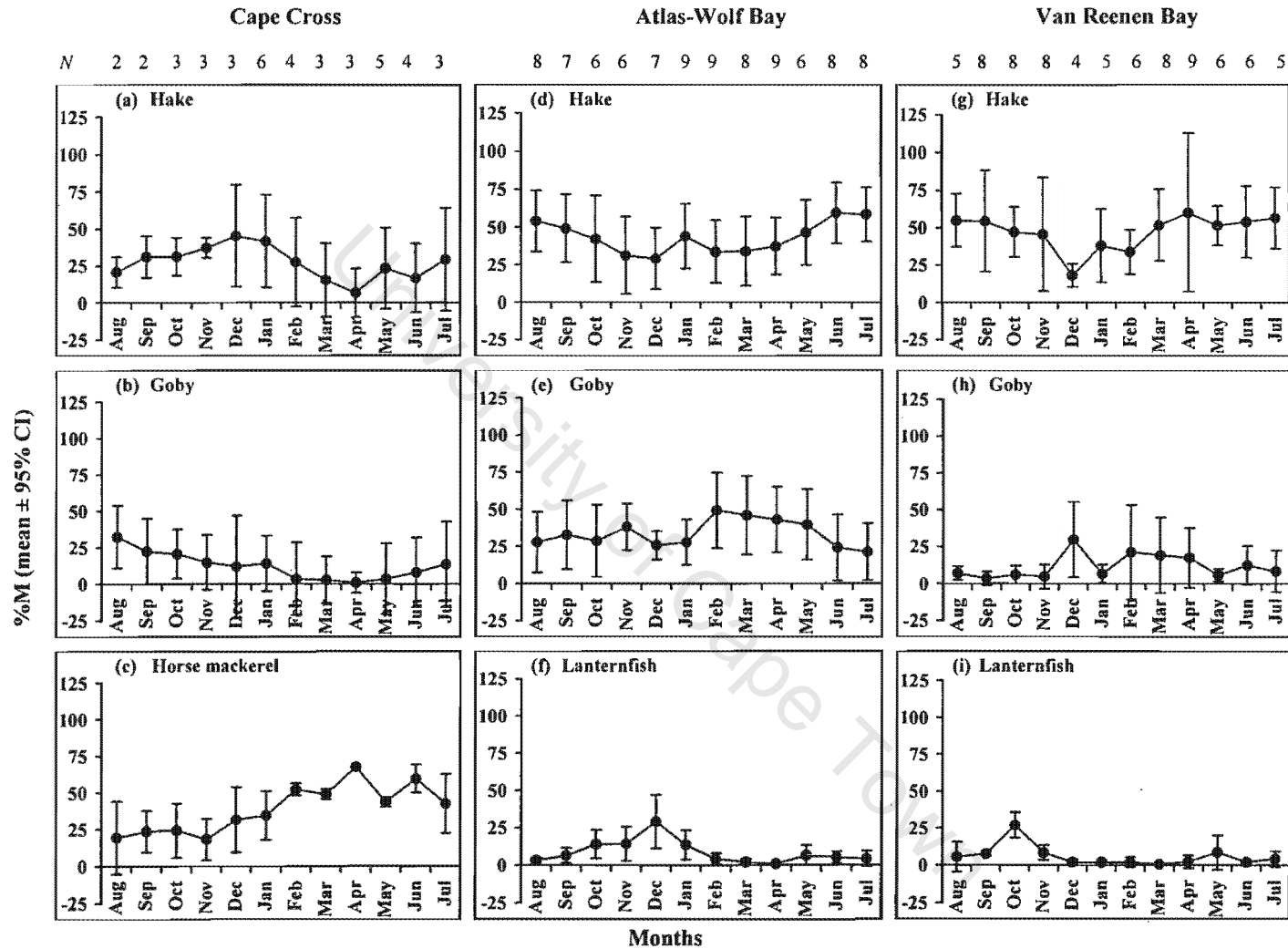


Figure 7. Mean percentage mass (%M; $\pm$ 95% confidence intervals, CI) of main prey groups from scats of Cape fur seals *Arctocephalus pusillus pusillus* at (a-c) Cape Cross, (d-f) Atlas-Wolf Bay, and (g-i) Van Reenen Bay, for the period January 1994 to April 2002. Months are from August-July, the upwelling year, and the number of month samples is given by *N*.

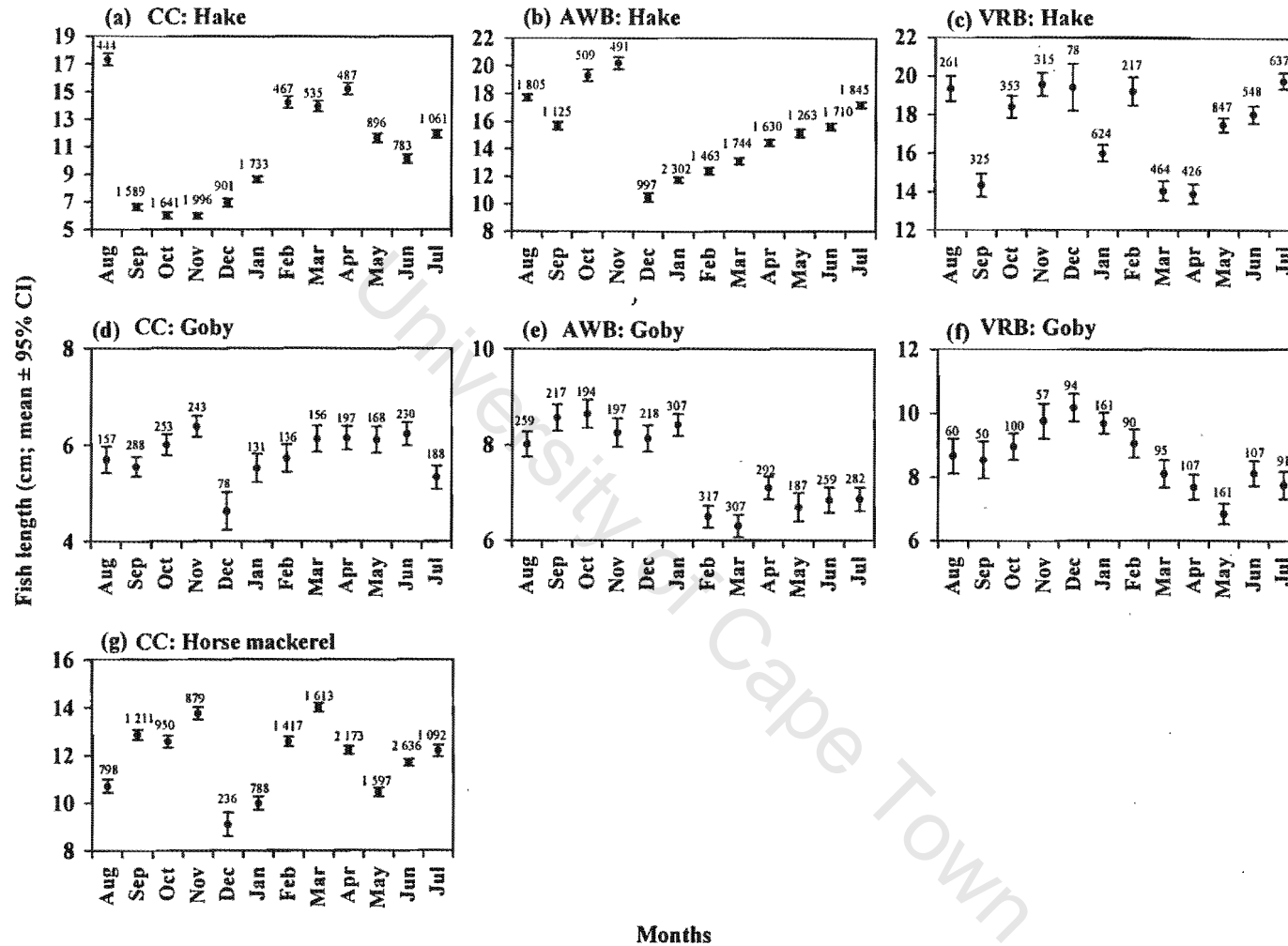


Figure 8. The monthly mean $\pm$ 95% confidence interval (CI) length (cm) of (a-c) Cape hakes *Merluccius* spp., (d-f) pelagic goby *Sufflogobius bibarbatatus* and (g) Cape horse mackerel *Trachurus trachurus capensis* estimated from otoliths in scats of Cape fur seals *Arctocephalus pusillus pusillus* at the three mainland breeding colonies in Namibia (Cape Cross, CC; Atlas-Wolf Bay, AWB; Van Reenen Bay, VRB). Horse mackerel was negligible at AWB and VRB. The number of fish measured is given above the mean.

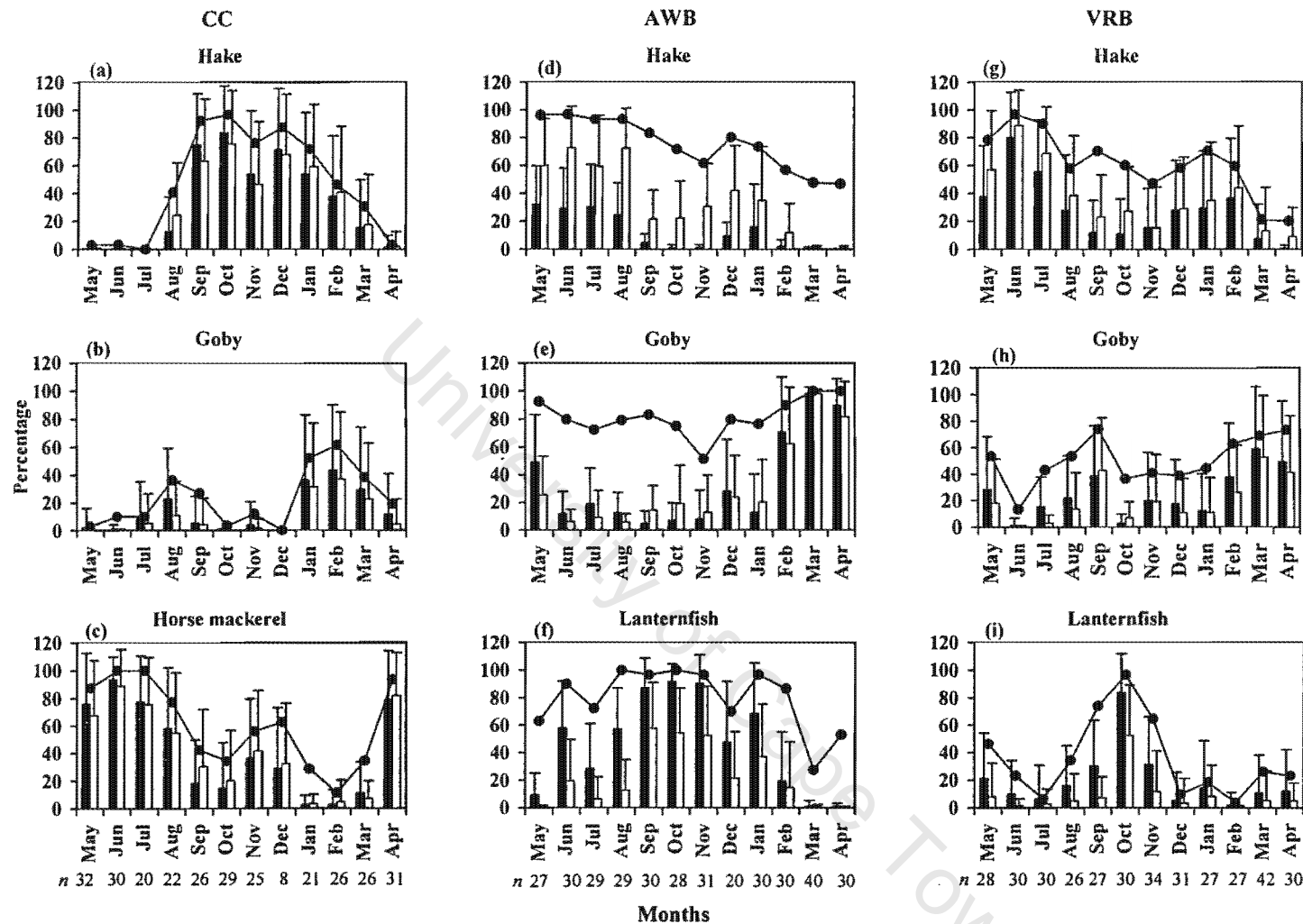


Figure 9. The percentage numerical abundance (N_{is}) (black bar) and mass (M_{is}) (white bar) of main prey groups consumed by Cape fur seals *Arctocephalus pusillus pusillus* in Namibia at (a-c) Cape Cross (CC), (d-f) Atlas-Wolf Bay (AWB) and (g-i) Van Reenen Bay (VRB), as determined from monthly individual scat samples collected from May 2001 to April 2002. The FO_{is} of the main prey groups in individual scat samples is represented by (●). Sample size is given by n and error bars denote one standard deviation.

Appendix I. The mean ($\pm$ standard deviation, SD) percentage numerical abundance and percentage mass (in parentheses) of the six prey groups of the Cape fur seal *Arctocephalus pusillus pusillus* at the Cape Cross, Atlas-Wolf Bay and Van Reenen Bay colonies in Namibia, for the period January 1994 to April 2002. The study period has been divided into six-month periods (February to July of one year, and August of that year to January the following year). The number of months in each period is indicated by N , and the total number of otoliths and mass of prey (kg) in each period are represented by n and m , respectively.

Six-month periods	Mean $\pm$ SD percentage abundance of prey group (mean $\pm$ SD percentage mass of prey group)					
	Horse mackerel	Hake	Lanternfish	Goby	Pelagics	Others
Cape Cross colony						
January 1994 ($N = 0$)	-	-	-	-	-	-
February 1994 – July 1994 ($N = 5$, $n = 49\ 905$, $m = 462.53$)	44.04 $\pm$ 31.39 (51.36 $\pm$ 25.82)	33.37 $\pm$ 24.58 (31.19 $\pm$ 20.06)	0.02 $\pm$ 0.03 (0.001 $\pm$ 0.002)	15.43 $\pm$ 10.50 (4.97 $\pm$ 3.61)	6.32 $\pm$ 2.90 (10.48 $\pm$ 3.65)	0.83 $\pm$ 1.06 (2.00 $\pm$ 2.22)
August 1994 – January 1995 ($N = 5$, $n = 34\ 722$, $m = 160.93$)	22.26 $\pm$ 21.58 (42.03 $\pm$ 25.90)	53.11 $\pm$ 31.49 (32.74 $\pm$ 32.14)	0.06 $\pm$ 0.08 (0.01 $\pm$ 0.01)	15.12 $\pm$ 31.91 (6.80 $\pm$ 14.55)	9.39 $\pm$ 14.15 (16.98 $\pm$ 21.48)	0.06 $\pm$ 0.11 (1.44 $\pm$ 2.01)
February 1995 – July 1995 ($N = 5$, $n = 39\ 052$, $m = 794.15$)	84.47 $\pm$ 11.12 (89.10 $\pm$ 7.98)	0.54 $\pm$ 0.34 (1.03 $\pm$ 1.08)	0.09 $\pm$ 0.09 (0.003 $\pm$ 0.004)	4.27 $\pm$ 6.38 (0.55 $\pm$ 0.71)	10.55 $\pm$ 6.84 (9.19 $\pm$ 7.84)	0.08 $\pm$ 0.11 (0.13 $\pm$ 0.26)
August 1995 – January 1996 ($N = 6$, $n = 70\ 213$, $m = 395.08$)	10.54 $\pm$ 9.59 (37.70 $\pm$ 15.44)	42.22 $\pm$ 31.93 (17.13 $\pm$ 15.05)	0.04 $\pm$ 0.07 (0.003 $\pm$ 0.004)	26.33 $\pm$ 26.17 (10.87 $\pm$ 12.93)	19.91 $\pm$ 21.08 (32.68 $\pm$ 18.04)	0.97 $\pm$ 1.92 (1.62 $\pm$ 2.08)
February 1996 – July 1996 ($N = 6$, $n = 74\ 940$, $m = 511.18$)	53.71 $\pm$ 35.51 (64.01 $\pm$ 29.39)	0.57 $\pm$ 0.85 (5.09 $\pm$ 6.80)	0 (0)	31.66 $\pm$ 43.56 (15.10 $\pm$ 22.86)	11.12 $\pm$ 8.99 (15.39 $\pm$ 8.00)	2.94 $\pm$ 4.65 (0.42 $\pm$ 0.40)
August 1996 – January 1997 ($N = 6$, $n = 80\ 799$, $m = 238.34$)	2.17 $\pm$ 2.70 (9.91 $\pm$ 9.89)	21.28 $\pm$ 21.47 (29.60 $\pm$ 20.90)	0.01 $\pm$ 0.01 (0.001 $\pm$ 0.002)	73.62 $\pm$ 17.34 (49.98 $\pm$ 9.47)	2.76 $\pm$ 4.19 (9.85 $\pm$ 13.19)	0.16 $\pm$ 0.35 (0.65 $\pm$ 1.13)
February 1997 – July 1997 ($N = 6$, $n = 26\ 253$, $m = 330.63$)	21.73 $\pm$ 35.95 (19.51 $\pm$ 21.71)	42.00 $\pm$ 22.43 (56.59 $\pm$ 25.63)	0.04 $\pm$ 0.06 (0.002 $\pm$ 0.002)	25.52 $\pm$ 19.53 (5.83 $\pm$ 5.49)	10.67 $\pm$ 10.65 (17.97 $\pm$ 10.55)	0.04 $\pm$ 0.05 (0.09 $\pm$ 0.11)
August 1997 – January 1998 ($N = 5$, $n = 11\ 521$, $m = 126.26$)	20.23 $\pm$ 30.49 (25.25 $\pm$ 34.20)	37.80 $\pm$ 36.58 (52.72 $\pm$ 28.75)	0.05 $\pm$ 0.11 (0.002 $\pm$ 0.004)	20.16 $\pm$ 36.45 (5.07 $\pm$ 9.46)	21.74 $\pm$ 27.75 (16.46 $\pm$ 15.51)	0.02 $\pm$ 0.04 (0.49 $\pm$ 1.10)

Appendix I. (cont.)

February 1998 – July 1998 (<i>N</i> = 5, <i>n</i> = 23 351, <i>m</i> = 423.70)	39.72 ± 31.90 (36.05 ± 28.97)	2.58 ± 3.41 (10.34 ± 16.55)	0.01 ± 0.02 (0.001 ± 0.001)	34.64 ± 19.84 (2.78 ± 2.94)	23.04 ± 21.64 (50.81 ± 35.53)	0.01 ± 0.02 (0.02 ± 0.05)
August 1998 – January 1999 (<i>N</i> = 4, <i>n</i> = 17 243, <i>m</i> = 56.39)	1.30 ± 0.40 (13.72 ± 3.88)	16.39 ± 11.92 (20.05 ± 16.82)	0.08 ± 0.15 (0.02 ± 0.03)	75.79 ± 17.66 (48.55 ± 22.48)	6.44 ± 8.29 (17.67 ± 17.17)	0 (0)
February 1999 – July 1999 (<i>N</i> = 3, <i>n</i> = 5 425, <i>m</i> = 181.20)	62.45 ± 24.42 (46.03 ± 28.15)	4.49 ± 3.52 (4.45 ± 3.03)	0 (0)	0.56 ± 0.88 (0.04 ± 0.06)	32.18 ± 27.37 (49.28 ± 29.23)	0.31 ± 0.54 (0.20 ± 0.34)
August 1999 – January 2000 (<i>N</i> = 3, <i>n</i> = 30 781, <i>m</i> = 53.02)	1.06 ± 0.56 (9.69 ± 9.18)	44.68 ± 36.30 (37.77 ± 32.87)	0.02 ± 0.02 (0.01 ± 0.01)	50.32 ± 35.01 (24.42 ± 17.34)	3.91 ± 2.80 (28.07 ± 16.84)	0.003 ± 0.005 (0.03 ± 0.05)
February 2000 – July 2000 (<i>N</i> = 2, <i>n</i> = 3 977, <i>m</i> = 74.53)	59.49 ± 35.31 (52.03 ± 25.09)	32.23 ± 44.87 (28.70 ± 39.07)	0.03 ± 0.05 (0.001 ± 0.001)	2.05 ± 2.50 (0.43 ± 0.57)	6.20 ± 7.01 (18.83 ± 13.41)	0 (0)
August 2000 – January 2001 (<i>N</i> = 3, <i>n</i> = 10 740, <i>m</i> = 198.68)	47.52 ± 7.04 (37.72 ± 11.31)	21.25 ± 18.11 (9.21 ± 7.92)	0.03 ± 0.03 (0.001 ± 0.001)	2.56 ± 1.77 (0.73 ± 0.41)	28.34 ± 15.98 (51.46 ± 19.84)	0.30 ± 0.16 (0.89 ± 0.91)
February 2001 – July 2001 (<i>N</i> = 5, <i>n</i> = 21 406, <i>m</i> = 328.03)	88.50 ± 12.96 (84.87 ± 5.17)	0.47 ± 0.62 (1.05 ± 1.41)	0 (0)	6.51 ± 10.88 (0.60 ± 0.76)	4.52 ± 1.81 (13.48 ± 4.82)	0.005 ± 0.010 (0.01 ± 0.01)
August 2001 – January 2002 (<i>N</i> = 6, <i>n</i> = 37 588, <i>m</i> = 159.14)	6.54 ± 7.43 (17.79 ± 15.35)	57.96 ± 39.97 (59.54 ± 22.73)	0 (0)	33.44 ± 37.02 (8.01 ± 10.20)	1.91 ± 2.88 (12.77 ± 13.63)	0.15 ± 0.20 (1.89 ± 2.31)
February 2002 – April 2002 (<i>N</i> = 3, <i>n</i> = 7 295, <i>m</i> = 85.66)	20.33 ± 28.07 (31.44 ± 42.20)	7.71 ± 9.93 (25.32 ± 37.82)	0 (0)	61.74 ± 17.29 (6.55 ± 3.85)	8.62 ± 7.18 (33.58 ± 32.83)	1.60 ± 2.51 (3.11 ± 3.66)
Total (<i>N</i> = 78, <i>n</i> = 545 211, <i>m</i> = 4579.45)	33.11 ± 34.52 (39.36 ± 31.00)	25.49 ± 29.44 (25.91 ± 27.17)	0.03 ± 0.06 (0 ± 0.01)	29.19 ± 31.98 (11.96 ± 18.51)	11.71 ± 14.95 (21.98 ± 20.70)	0.48 ± 1.60 (0.78 ± 1.53)
Atlas-Wolf Bay colony						
January 1994 (<i>N</i> = 1, <i>n</i> = 7 414, <i>m</i> = 49.65)	0.50 (1.17)	92.14 (92.09)	2.79 (0.28)	4.14 (3.44)	0.25 (2.64)	0.18 (0.38)
February 1994 – July 1994 (<i>N</i> = 5, <i>n</i> = 27 465, <i>m</i> = 182.08)	0.39 ± 0.31 (1.91 ± 2.73)	34.88 ± 33.37 (49.11 ± 31.90)	20.96 ± 36.52 (4.74 ± 9.71)	41.55 ± 33.07 (40.57 ± 33.07)	1.87 ± 2.99 (1.86 ± 2.14)	0.34 ± 0.30 (1.82 ± 1.98)

Appendix I. (cont.)

August 1994 – January 1995 (<i>N</i> = 3, <i>n</i> = 24 770, <i>m</i> = 136.83)	0.19 ± 0.23 (2.18 ± 3.36)	19.13 ± 3.22 (46.92 ± 15.63)	49.96 ± 17.77 (6.05 ± 3.38)	28.61 ± 16.54 (37.90 ± 25.57)	1.74 ± 2.74 (4.92 ± 5.80)	0.37 ± 0.40 (2.02 ± 1.28)
February 1995 – July 1995 (<i>N</i> = 6, <i>n</i> = 114 093, <i>m</i> = 388.16)	0.23 ± 0.26 (1.42 ± 1.71)	6.39 ± 6.04 (37.05 ± 30.60)	24.92 ± 24.52 (3.82 ± 3.99)	64.22 ± 33.55 (47.85 ± 41.24)	3.65 ± 4.46 (8.15 ± 10.69)	0.58 ± 1.17 (1.70 ± 1.46)
August 1995 – January 1996 (<i>N</i> = 6, <i>n</i> = 92 865, <i>m</i> = 343.13)	0.13 ± 0.07 (0.97 ± 1.00)	3.30 ± 2.75 (44.02 ± 23.75)	71.86 ± 14.48 (16.28 ± 15.76)	21.15 ± 10.17 (28.42 ± 19.66)	3.04 ± 5.57 (7.14 ± 7.19)	0.52 ± 0.70 (3.17 ± 2.08)
February 1996 – July 1996 (<i>N</i> = 6, <i>n</i> = 164 349, <i>m</i> = 520.77)	0.06 ± 0.06 (0.18 ± 0.26)	0.63 ± 0.48 (6.79 ± 4.69)	7.48 ± 5.07 (1.89 ± 1.56)	91.50 ± 4.93 (88.90 ± 3.73)	0.25 ± 0.19 (1.86 ± 1.48)	0.09 ± 0.13 (0.39 ± 0.48)
August 1996 – January 1997 (<i>N</i> = 6, <i>n</i> = 92 251, <i>m</i> = 411.99)	0.12 ± 0.14 (0.49 ± 0.50)	25.33 ± 37.99 (33.82 ± 39.68)	27.70 ± 21.61 (5.71 ± 7.26)	46.27 ± 31.93 (56.75 ± 36.25)	0.24 ± 0.46 (1.07 ± 1.94)	0.35 ± 0.44 (2.17 ± 1.63)
February 1997 – July 1997 (<i>N</i> = 5, <i>n</i> = 25 865, <i>m</i> = 347.36)	0.10 ± 0.11 (0.05 ± 0.04)	66.04 ± 12.36 (83.86 ± 8.06)	7.85 ± 8.85 (0.34 ± 0.40)	23.60 ± 16.47 (10.42 ± 11.20)	1.93 ± 1.87 (4.10 ± 5.24)	0.49 ± 0.92 (1.24 ± 1.80)
August 1997 – January 1998 (<i>N</i> = 6, <i>n</i> = 50 372, <i>m</i> = 384.80)	0.58 ± 0.95 (0.83 ± 1.29)	26.84 ± 22.60 (72.93 ± 28.06)	54.55 ± 33.32 (13.61 ± 25.20)	14.16 ± 10.09 (7.54 ± 4.66)	3.46 ± 5.36 (3.39 ± 5.34)	0.42 ± 0.65 (1.69 ± 2.41)
February 1998 – July 1998 (<i>N</i> = 6, <i>n</i> = 44 617, <i>m</i> = 169.88)	0.51 ± 0.82 (2.37 ± 3.13)	3.22 ± 2.21 (48.92 ± 8.67)	43.25 ± 32.95 (8.33 ± 8.11)	51.78 ± 33.52 (30.50 ± 17.62)	0.97 ± 1.24 (8.57 ± 8.77)	0.27 ± 0.46 (1.30 ± 1.36)
August 1998 – January 1999 (<i>N</i> = 4, <i>n</i> = 17 042, <i>m</i> = 142.75)	0.16 ± 0.25 (0.27 ± 0.29)	7.50 ± 10.58 (30.84 ± 8.77)	23.59 ± 14.90 (1.95 ± 1.24)	63.37 ± 21.08 (53.97 ± 11.44)	3.90 ± 3.61 (4.83 ± 1.18)	1.47 ± 2.08 (8.14 ± 7.95)
February 1999 – July 1999 (<i>N</i> = 6, <i>n</i> = 22 914, <i>m</i> = 167.38)	0.24 ± 0.48 (0.62 ± 1.14)	20.63 ± 15.41 (48.75 ± 33.27)	13.11 ± 17.57 (0.59 ± 0.65)	63.95 ± 31.67 (41.76 ± 38.06)	1.66 ± 3.86 (7.36 ± 16.88)	0.40 ± 0.41 (0.92 ± 1.27)
August 1999 – January 2000 (<i>N</i> = 5, <i>n</i> = 27 951, <i>m</i> = 110.63)	2.59 ± 5.40 (2.77 ± 5.43)	9.36 ± 9.27 (55.69 ± 31.81)	70.42 ± 22.04 (11.95 ± 11.13)	11.34 ± 15.88 (11.98 ± 14.60)	5.58 ± 4.49 (11.85 ± 10.95)	0.72 ± 1.12 (5.77 ± 4.79)
February 2000 – July 2000 (<i>N</i> = 5, <i>n</i> = 31 940, <i>m</i> = 164.91)	1.15 ± 2.13 (3.13 ± 6.33)	13.14 ± 6.41 (61.07 ± 10.77)	56.21 ± 26.77 (8.35 ± 7.09)	19.56 ± 8.97 (13.07 ± 9.19)	9.72 ± 14.20 (13.43 ± 14.56)	0.23 ± 0.26 (0.95 ± 0.91)
August 2000 – January 2001 (<i>N</i> = 6, <i>n</i> = 39 979, <i>m</i> = 186.53)	3.73 ± 6.72 (2.59 ± 3.75)	1.72 ± 1.18 (24.55 ± 8.87)	70.94 ± 19.27 (12.48 ± 9.18)	18.34 ± 12.71 (29.43 ± 11.56)	4.67 ± 4.73 (23.99 ± 5.77)	0.60 ± 0.58 (6.96 ± 3.38)

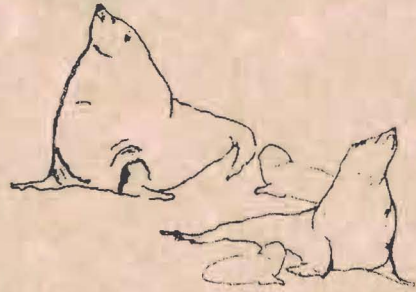
Appendix I. (cont.)

February 2001 – July 2001 (<i>N</i> = 6, <i>n</i> = 47 564, <i>m</i> = 335.20)	0.24 ± 0.27 (1.53 ± 2.34)	16.31 ± 8.54 (51.29 ± 24.24)	24.57 ± 34.34 (2.39 ± 3.53)	54.29 ± 34.21 (35.88 ± 28.69)	4.44 ± 4.61 (8.45 ± 10.34)	0.15 ± 0.20 (0.46 ± 0.69)
August 2001 – January 2002 (<i>N</i> = 6, <i>n</i> = 77 768, <i>m</i> = 189.16)	0.35 ± 0.72 (0.76 ± 1.28)	6.17 ± 6.12 (48.21 ± 14.82)	82.19 ± 14.93 (24.25 ± 12.91)	9.57 ± 8.67 (19.62 ± 4.51)	1.60 ± 1.85 (5.06 ± 5.76)	0.12 ± 0.10 (2.09 ± 1.90)
February 2002 – April 2002 (<i>N</i> = 3, <i>n</i> = 57 608, <i>m</i> = 119.64)	0.50 ± 0.85 (1.28 ± 2.04)	0.24 ± 0.09 (1.67 ± 1.76)	3.06 ± 3.32 (0.91 ± 0.92)	92.21 ± 5.51 (86.15 ± 12.56)	3.92 ± 5.31 (9.62 ± 12.49)	0.07 ± 0.10 (0.37 ± 0.32)
Total (<i>N</i> = 91, <i>n</i> = 966 827, <i>m</i> = 4350.85)	0.68 ± 2.27 (1.35 ± 2.60)	16.05 ± 22.66 (45.14 ± 28.88)	39.09 ± 32.93 (7.60 ± 11.30)	40.79 ± 32.91 (36.17 ± 30.81)	2.99 ± 4.97 (7.38 ± 9.61)	0.41 ± 0.72 (2.35 ± 3.19)
Van Reenen Bay colony						
January 1994 (<i>N</i> = 1, <i>n</i> = 3 009, <i>m</i> = 23.35)	0.29 (0.24)	93.18 (98.82)	6.17 (0.53)	0.36 (0.41)	0 (0)	0 (0)
February 1994 – July 1994 (<i>N</i> = 4, <i>n</i> = 9 022, <i>m</i> = 105.91)	2.45 ± 3.06 (4.97 ± 5.94)	39.05 ± 37.41 (60.76 ± 24.74)	27.08 ± 34.88 (2.57 ± 4.26)	22.32 ± 20.22 (13.29 ± 8.67)	8.57 ± 11.22 (15.59 ± 15.85)	0.52 ± 0.53 (2.82 ± 3.53)
August 1994 – January 1995 (<i>N</i> = 1, <i>n</i> = 6 541, <i>m</i> = 75.67)	0.19 (2.91)	10.03 (30.75)	68.67 (3.97)	13.46 (11.58)	7.31 (47.63)	0.34 (3.16)
February 1995 – July 1995 (<i>N</i> = 2, <i>n</i> = 36 296, <i>m</i> = 120.97)	0.12 ± 0.15 (0.83 ± 0.59)	7.34 ± 8.84 (66.66 ± 14.51)	80.03 ± 12.70 (17.79 ± 20.01)	11.22 ± 2.07 (5.73 ± 5.07)	0.76 ± 1.05 (5.17 ± 6.07)	0.53 ± 0.59 (3.81 ± 3.91)
August 1995 – January 1996 (<i>N</i> = 1, <i>n</i> = 23 460, <i>m</i> = 77.09)	0.22 (12.43)	1.70 (41.03)	90.73 (18.48)	6.29 (12.19)	0.45 (6.42)	0.61 (9.46)
February 1996 – July 1996 (<i>N</i> = 2, <i>n</i> = 13 751, <i>m</i> = 120.01)	0.25 ± 0.16 (1.85 ± 0.17)	2.26 ± 0.06 (17.68 ± 3.11)	23.61 ± 17.58 (1.81 ± 1.32)	68.51 ± 23.60 (49.18 ± 28.46)	4.19 ± 5.93 (16.44 ± 23.25)	1.19 ± 0.13 (13.04 ± 0.94)
August 1996 – January 1997 (<i>N</i> = 0)	-	-	-	-	-	-
February 1997 – July 1997 (<i>N</i> = 0)	-	-	-	-	-	-

Appendix I. (cont.)

August 1997 – January 1998 ($N = 2, n = 12\ 056, m = 112.91$)	0.34 ± 0.46 (0.04 ± 0.05)	7.77 ± 1.54 (57.03 ± 36.60)	75.06 ± 23.90 (6.52 ± 7.29)	2.44 ± 2.74 (1.35 ± 0.71)	12.58 ± 16.77 (28.00 ± 36.26)	1.81 ± 2.39 (7.06 ± 6.88)
February 1998 – July 1998 ($N = 2, n = 6\ 245, m = 83.97$)	4.64 ± 2.60 (6.08 ± 1.48)	5.43 ± 2.58 (40.72 ± 0.44)	71.21 ± 22.37 (4.04 ± 2.74)	8.58 ± 11.45 (1.20 ± 1.23)	9.22 ± 4.79 (45.45 ± 0.82)	0.93 ± 0.96 (2.51 ± 0.36)
August 1998 – January 1999 ($N = 1, n = 350, m = 19.09$)	0 (0)	6.93 (14.52)	11.74 (0.14)	21.44 (3.38)	58.95 (79.75)	0.94 (2.20)
February 1999 – July 1999 ($N = 3, n = 3\ 433, m = 68.31$)	0.47 ± 0.64 (1.31 ± 2.16)	44.41 ± 28.48 (53.98 ± 14.29)	31.83 ± 26.20 (1.10 ± 1.03)	12.09 ± 4.72 (3.57 ± 1.09)	9.79 ± 7.43 (32.41 ± 23.58)	1.42 ± 1.87 (7.63 ± 11.00)
August 1999 – January 2000 ($N = 5, n = 18\ 873, m = 87.15$)	0.17 ± 0.19 (3.74 ± 5.93)	4.19 ± 2.48 (48.30 ± 25.82)	80.57 ± 20.98 (11.91 ± 9.65)	11.29 ± 22.05 (11.83 ± 21.03)	3.41 ± 2.66 (18.14 ± 21.07)	0.37 ± 0.36 (6.09 ± 6.14)
February 2000 – July 2000 ($N = 0$)	-	-	-	-	-	-
August 2000 – January 2001 ($N = 2, n = 4\ 262, m = 111.09$)	20.42 ± 16.11 (3.86 ± 0.82)	5.64 ± 4.05 (19.90 ± 2.95)	28.34 ± 28.12 (1.36 ± 1.69)	17.43 ± 17.82 (14.43 ± 18.57)	27.73 ± 25.82 (58.39 ± 19.51)	0.44 ± 0.04 (2.06 ± 1.38)
February 2001 – July 2001 ($N = 6, n = 11\ 273, m = 182.23$)	0.97 ± 2.36 (2.99 ± 7.15)	43.16 ± 20.15 (60.92 ± 18.10)	25.17 ± 33.67 (1.71 ± 2.73)	11.05 ± 12.03 (4.17 ± 5.35)	18.18 ± 24.44 (22.94 ± 23.54)	1.47 ± 1.45 (7.27 ± 5.74)
August 2001 – January 2002 ($N = 6, n = 27\ 309, m = 218.59$)	0.77 ± 1.00 (1.17 ± 1.50)	11.39 ± 7.18 (30.46 ± 10.26)	50.44 ± 35.87 (8.15 ± 12.69)	16.04 ± 12.43 (9.49 ± 6.33)	19.54 ± 15.71 (43.63 ± 10.81)	1.82 ± 3.26 (7.10 ± 8.63)
February 2002 – April 2002 ($N = 3, n = 25\ 190, m = 145.22$)	0.49 ± 0.43 (2.80 ± 3.68)	4.39 ± 6.59 (21.02 ± 12.77)	15.41 ± 11.41 (2.69 ± 3.46)	63.26 ± 12.33 (32.13 ± 16.03)	14.55 ± 9.23 (27.37 ± 17.15)	1.89 ± 2.26 (13.99 ± 9.33)
Total ($N = 41, n = 201\ 070, m = 1722.56$)	1.86 ± 5.24 (2.85 ± 4.34)	19.99 ± 25.13 (45.05 ± 23.89)	44.89 ± 34.33 (5.53 ± 8.37)	19.32 ± 21.89 (11.53 ± 15.32)	12.84 ± 16.04 (28.60 ± 22.75)	1.10 ± 1.61 (6.45 ± 6.50)

CHAPTER 4



University of Cape Town

Fish consumption estimates of lactating Cape fur seals

Arctocephalus pusillus pusillus in Namibia

based on scat analyses

INTRODUCTION

Both in South Africa and Namibia, the Cape fur seal *Arctocephalus pusillus pusillus* population is perceived by some as a competitive threat to the success of commercial fisheries (Wickens *et al.* 1992a). Subscribers to this point of view believe that increases in the size of the seal population negatively affect the catches of the fisheries. Their concerns have intensified in recent decades because the Cape fur seal population has increased at about three per cent per annum since 1971 (Wickens *et al.* 1991), despite substantial annual harvests in Namibia (suspended in South Africa after 1990) (Wickens and York 1997). The Cape fur seals' total population size in Namibia was estimated at just over half a million individuals during a survey in December 2001 (Marine and Coastal Management (MCM), unpublished data). Commercially important fish species in Namibia include Cape horse mackerel *Trachurus trachurus capensis*, Cape hakes *Merluccius capensis* and *M. paradoxus*, sardine *Sardinops sagax*, anchovy *Engraulis capensis* and round herring *Etrumeus whiteheadi* (Shaughnessy 1985). All these species are consumed by Cape fur seals (Chapter 2).

In order to determine levels of competition for a prey resource between two or more groups of predators, it is necessary first to estimate levels of consumption by each group (Harwood and Croxall 1988). Previous studies have estimated prey consumption of the Cape fur seal population. They estimated consumption as the product of population size and the daily prey requirement of an average-sized individual, the latter assumed to be a set percentage of body weight in some cases (Shaughnessy 1985, Butterworth *et al.* 1988, Wickens *et al.* 1992b) or estimated from an allometric equation for growing marine mammals (Wickens *et al.* 1992b, Balmelli and Wickens 1994, Smale *et al.* 1994, Butterworth *et al.* 1995). The more refined of these studies incorporated information on the population age structure (Butterworth *et al.* 1995) or apportioned the total consumption into

prey groups using information on diet composition obtained from analyses of stomach contents (David 1987a). However, none of these studies took into account the varying calorific content (or energy density) and the digestive efficiency (also known as the assimilation efficiency) of prey of different species, or variation in the diet composition between locations and over time as found for Namibia's seal population (Chapters 2 and 3).

In this study a model was developed that considers all these factors (except digestive efficiency, assumed to be the same for all prey species) and is based upon analyses of scat samples collected at three mainland colonies in Namibia, over a period of eight years. The model is limited to the teleost portion of the seals' diet, as this is the only component that can be quantified from scats. The model only applies to lactating females, which were assumed to have deposited almost all the scats found at the colonies during the lactation period (Rand 1959), which comprises the greater part of the year.

Female Cape fur seals of this species attain sexual maturity at three to four years of age (Shaughnessy 1985, David 1989). Pregnant females start arriving at breeding colonies towards the end of October or early November and give birth to one pup soon afterwards (Rand 1955, Shaughnessy 1985). The bulk of pup production occurs in December (median pupping date 3 to 10 December, De Villiers and Roux 1992). After giving birth, females alternate foraging trips to sea with suckling periods on land until the pup is weaned eight to ten months later (Rand 1955, David 1989).

The model takes account of temporal variation in prey consumption that is related to variation in both diet composition (detected in scat analyses) and seal population numbers, making this model dynamic compared to previous models. This is appropriate considering the environmental variability that characterises the northern Benguela System (Shannon *et al.* 1992).

MATERIAL AND METHODS

Data collection and preparation

Scat samples were collected at three mainland breeding colonies of Cape fur seals in Namibia from January 1994 to April 2002: Cape Cross (21°47'S, 13°57'E; CC), Atlas Bay and Wolf Bay (26°49'S, 15°08'E and 26°48'S, 15°07'E, respectively; AWB) and Van Reenen Bay (27°23'S, 15°21'E; VRB) (Fig. 1). Because of the close proximity of the Atlas and Wolf Bay colonies,

which are about 1 km apart, they were considered to be a single colony for the purposes of this study. Together the above colonies constitute about 65% of Namibia's seal population.

The lactation period was assumed to be from December (the peak of the breeding season) to July of the following year. This is because after July pups start being weaned (Rand 1955) and, at CC and AWB, the onset of commercial seal harvesting at this time results in lactation being terminated for a substantial number of the mother-pup pairs. The annual pup harvests at CC and AWB were as high as 25 000 and 19 000 pups, respectively, during the study period (Ministry of Fisheries and Marine Resources (MFMR), unpublished data). It was intended that scats be collected on a monthly basis during the lactation period, but logistical constraints meant that none of the colonies could be visited every month. Of the 72 months constituting the nine lactation periods over the entire study period, CC was sampled during 49, AWB during 64 and VRB during 31 months, therefore sampling effort varied between colonies.

The scat processing procedure is detailed in Chapter 2. A month's sample of scats constituted a bag of 30 to 60 scats. Each sample was washed through a 0.212 mm sieve, and the remaining material dried overnight in an oven. Sagittal otoliths were sorted from the dried material, identified and counted. Six prey groups were identified: Cape horse mackerel, Cape hakes, lanternfish (mainly *Lampanyctodes hectoris*), pelagic goby *Sufflogobius bibarbatus*, pelagics (sardine, anchovy and round herring) and other species.

Otolith counts were corrected for loss during digestion using correction factors (Chapter 2). The otolith diameters of monthly sub-samples of otoliths from each prey group were measured to the nearest 0.05 mm for each month. Otolith diameters were corrected for erosion using correction factors, and then converted to fish mass using species-specific relationships between otolith diameters and fish total length and mass (Chapter 2).

Prey consumption model

The model used to estimate the daily consumption of teleost prey by lactating Cape fur seals at each study colony follows that of Winship *et al.* (2002) and Goldsworthy *et al.* (2001), and includes correction factors for the efficiency of converting prey energy to digestible energy (Doidge and Croxall 1985, Goldsworthy *et al.* 2001):

$$BR_{im} = \left(\frac{prop_{im} \times T}{(ED_i)(DE_i)} \times \sum_y [ER_y \times w_y \times N_{ym}] \right) \quad (\text{Eqn 1})$$

where BR_{im} is the daily mass requirement of prey group i (g.day^{-1}) by lactating females in month m , which for this study are the eight months December to July (the lactation period; see above), $prop_{im}$ is the proportion of teleost fish in the diet made up of prey group i in month m , T is the total proportion of teleost fish in the diet, ED_i is the energetic density of prey group i (kJ.g^{-1}), DE_i is the digestive efficiency of prey group i by seals which is the efficiency of converting prey energy to digestible energy, y is the female age class, ER_y is the daily energy requirement of a female in age class y (kJ.kg^{-1}), w_y is the mean mass of a female (kg) in age class y , and N_{ym} is the number of females in age class y in month m . The input values are discussed below. The model assumes that the daily prey requirements of seals are fulfilled, and therefore does not take into account years of high mortality due to starvation or other causes. The model can be adapted for use for each sex-age class of the seal population.

The annual mass requirement for prey group i (MR_i ; tonnes) by lactating Cape fur seals over the eight-month lactation period was estimated as follows:

$$MR_i = \frac{\sum_m (BR_{im} \times D_m)}{1 \times 10^6} \quad (\text{Eqn 2})$$

where D_m is the number of days in month m , taken as 28 days for February.

For months between December and July for which no diet data were collected at one of the colonies, $prop_{im}$ was estimated from the average relative weight contribution of species i in the months with data, within the same lactation period. For the lactation period of 1996/97 at VRB, no diet data were available for any months and therefore the $prop_{im}$ values for each month were estimated as the average of the $prop_{im}$ values for this month in the lactation periods of 1995/96 and 1997/98.

Prey consumption for lactating females was estimated for eight of the nine years of the study period. The exception was 1994 (December 1993 to July 1994) because this year was characterised by mass mortality of pups (~95% mortality) and a high mortality of adults (~300 000 seals) as a result of a warm water event which is characterised by an incursion of warm water into the Benguela System from the north (Roux 1998). In the years when pups were counted by aerial survey, the numbers of lactating females at each of the colonies was estimated from the pup counts (see following section). In the years without an aerial survey, the average of the pup counts from the rest of the years was used.

Because the three study colonies occur in regions that are distinct from each other in the northern Benguela System (Fig. 1), estimates of prey consumption for lactating females at these colonies were extrapolated to the entire sub-populations of lactating females falling within those regions. Thereby, an estimate of prey consumption was obtained for this portion of the Namibian Cape fur seal population during the eight-month lactation period. Region 1 extended from the border with Angola (17°S) to Conception Bay (24°17'S), Region 2 from Conception Bay to just north of VRB (27°15'S), and Region 3 from just north of VRB to the border with South Africa (28°30'S) (Fig. 1). Conception Bay divided Regions 1 and 2 because seals from AWB swim as far north as this bay (W. H. Oosthuizen, MCM, pers. comm.). The division between Regions 2 and 3 was placed just north of VRB because the upwelling cell around 27°S (near Lüderitz) acts as a barrier to movement of small pelagic fish (Shannon 1985), which are the main constituents of the seal diet.

Estimates of the annual total consumption of commercial prey (hake, horse mackerel and pelagics) by lactating females during the lactation period in Namibia was compared with total Namibian fishery landings of these groups in the same years.

Numbers and age structure of lactating females

Pup production at each study colony, as determined from aerial surveys conducted in the third week of December of five of the eight lactation periods (1994/95, 1995/96, 1996/97, 1997/98 and 2001/02) (Johnston *et al.* 2004), was assumed to represent the number of females lactating at that colony in December of that year (Table I); females give birth to one pup only (Rand 1955). Adjustments were made for pup mortality over the December to July period; in January pup mortality was assumed to be 30% of the pup production and for February to July 35% of the pup production (MFMR, unpublished data). The age distribution of lactating Cape fur seals from age-four onwards was taken from Butterworth *et al.* (1995) (see Table II).

Diet composition

Teleosts have previously been reported to comprise between 92% and 97% of the diet of seals in Namibia (David 1987a, Lipinski and David 1990), therefore for this study it was assumed that they accounted for 95% (*T*) of the diet, on average. The relative percentage mass of each teleost prey group at each study locality for the period December to the following July is given in Table III.

This was based on the sorting, counting and measurements of otoliths from the scat samples, and the conversion of abundance of respective prey items in the samples to mass, as reported in Chapter 2.

Energy requirement of lactating females

The at-sea energy requirement (ER_{at-sea}) of Cape fur seals was previously estimated to be 7.0 W.kg^{-1} for a female of mass 68 kg (Gentry *et al.* 1986). However, the equation that was used (Gentry *et al.* 1986) was based on the northern fur seal, a sub-polar species that is somewhat smaller (Females, 30-50 kg) than the Cape fur seal (Females, 40-110 kg). In the absence of any relationship specific to Cape fur seals, a relationship supplied by Goldsworthy *et al.* (2003) was considered an improvement on the Gentry *et al.* (1986) relationship, in that it was based studies of seven otariid species, ranging in size and geography:

$$ER_{at-sea} = 2.234(w_{av})^{0.665} \quad (\text{Eqn 3})$$

where ER_{at-sea} is MJ.day^{-1} and w_{av} is the average mass of lactating Cape fur seals. The average mass of lactating Cape fur seals was assumed to be 56 kg, based on the average mass of lactating females from age-four onwards as given in Butterworth *et al.* (1995). From this, it was determined that lactating Cape fur seals have an average ER_{at-sea} of 6.7 W.kg^{-1} .

The ER_{at-sea} for lactating northern fur seals *Callorhinus ursinus* (Costa and Gentry 1986) and for Antarctic fur seals *Arctocephalus gazella* (Costa *et al.* 1989) were found to be 1.8 and 1.9 times greater, respectively, than their on-shore energy requirements ($ER_{on-shore}$). Both the Antarctic and northern fur seals inhabit cold waters of the sub-polar regions (Bonner 1994). Krill is the main prey of Antarctic fur seals (Reid and Arnould 1996, Kirkman *et al.* 2000, Casaux *et al.* 2003), although myctophids are also known to form a substantial component of their diet (Cherel *et al.* 1997, Klages and Bester 1998, Lea *et al.* 2002). Like Cape fur seals, northern fur seals feed mainly on schooling fish (Perez and Bigg 1986). Accordingly, the ratio between at-sea and on-shore ER for northern fur seals was assumed to apply to Cape fur seals. Thus, $ER_{on-shore}$ for lactating Cape fur seals was taken to be 3.7 W.kg^{-1} .

According to Costa and Gales (2000) and Winship *et al.* (2002), the total energy requirement (ER) of lactating female seals is determined as:

$$ER = (ER_{on-shore})(\text{proportion time on shore}) + (ER_{at-sea})(1 - \text{proportion time on shore}) \quad (\text{Eqn 4})$$

Lactating Cape fur seals spend 39% of their time on shore during the lactation period (Gentry *et al.* 1986). Therefore, ER for lactating Cape fur seals is estimated to be 5.5 W.kg^{-1} , which is equivalent to $475.2 \text{ kJ.day}^{-1}.\text{kg}^{-1}$. The mean mass of each age class of adult female Cape fur seals was taken from Butterworth *et al.* (1995) (Table II) to determine ER , in equation 1.

Digestive efficiency

The digestive efficiency (DE) of fish consumed by fur seals has previously been documented as 93% by Miller (1978), while that of fish fed to captive juvenile Steller sea lions *Eumetopias jubatus* was reported to range from 93.9-95.4% (Rosen and Trites 2000). For this study a DE of 93% (i.e. 0.93) was assumed for all prey. Although DE is known to increase with the energy density of prey (e.g. 92-96%; Rosen and Trites 2000), and may vary with predator age (Harper 1998), this variation has not been quantified for Cape fur seals and their prey and therefore was not considered in the model.

Energetic density of prey

The mean calorific content (wet mass, kJ.g^{-1}), or energetic density (ED), of Cape fur seal prey items as presented by Balmelli and Wickens (1994) was used, which averaged the calorific content measured by Jackson (1990), Prosch (1986), Batchelor and Ross (1984), Cruickshank *et al.* (1980) and Balmelli and Wickens (1994): Cape horse mackerel (5.65 kJ.g^{-1}), Cape hakes (4.47 kJ.g^{-1}), lanternfish (4.90 kJ.g^{-1}), pelagic goby (3.69 kJ.g^{-1}), pelagics (6.18 kJ.g^{-1} ; the average of sardine 6.59 kJ.g^{-1} , anchovy 6.03 kJ.g^{-1} and round herring 5.91 kJ.g^{-1}) and others (4.98 kJ.g^{-1} ; average of the previous five prey groups). The ED of prey species varies seasonally (Balmelli and Wickens 1994, Rosen and Trites 2000), with geographic location and with prey age class (Rosen and Trites 2000). This variation in calorific content was disregarded in the model because it is currently unknown, but can be included in future revisions.

Sensitivity test for the prey consumption model

Some of the input values for the model are founded on assumptions. Three such parameters were chosen to be included in sensitivity tests to assess the affects of their expresssion on the outcome of the model. Two of these parameters are unknown for the Cape fur seal and values determined for other otariids were used in the base case, while there is some uncertainty surrounding the

estimation of the third parameter. The first of these parameters, the digestive efficiency (*DE*) of fish was based on a value determined for fur seals as a group (93%, Miller 1978). For the sensitivity test, a higher (96%) and lower (92%) value for the *DE* was used, based on values obtained for Stellar sea lions (Rosen and Trites 2000). The second parameter, namely the energy requirement of lactating females was based on an equation for the field metabolic rate of seven other otariid species (Goldsworthy *et al.* 2003). For the sensitivity test, the field metabolic rates determined from equations of two other studies (Gentry *et al.* 1986, Winship *et al.* 2002) were used, which produced a higher (6.1 W.kg^{-1}) and lower (4.1 W.kg^{-1}) energy requirement. The numbers of lactating females at a colony were based on the assumption that the numbers of pups, determined by aerial surveys, represented the same number of lactating females. However, it is possible that the pup counts may have been underestimated as a result of pups been hidden by shadows or rocks in the photographs (Butterworth *et al.* 1991). Effects of pup count underestimates of ten and twenty percent (following Butterworth *et al.* 1991) on the model outcomes, were investigated.

RESULTS

At each colony, the estimated intake of teleosts by lactating fur seals during the lactation period varied between years (Table IV). Over the eight years of the study, estimated annual prey consumption by lactating females during the December-July period ranged between 25 921 and 41 377 tonnes at CC, 27 398 and 89 185 tonnes at AWB, and 2 926 and 5 254 tonnes at VRB. At all three colonies, annual consumption was highest in the lactation period of 1997/98. Combining estimates for the three colonies, teleost prey consumption ranged from 59 455 (1994/95) to 135 816 tonnes (1997/98) (Table IV).

The annual total consumption of teleost prey by lactating seals in the whole of Namibia was estimated to range between 91 000 and 187 000 tonnes (Table V). On average, lactating seals in Region 2 consumed 53% of all teleosts consumed, whereas seals in Regions 1 and 3 consumed 32% and 15%, respectively.

The proportional representation of the different teleost prey groups in the estimates of consumption, varied between years at each colony. Non-commercial prey accounted for 0-22% of the total teleost mass consumed at CC, whereas at AWB and VRB non-commercial prey constituted 15-87% and 11-74% of total prey consumed, respectively (Table IV). The annual

consumption of hake in Namibia by lactating females, during the lactation period, was between one and 10 times less than the total annual fishery landings of this species; for horse mackerel, the equivalent seal consumption was seven to 45 times less than the fishery landings; for the pelagics group, seals consumed two to 28 times less than the total annual fishery landings (Table VI).

Assuming an average mass of 56 kg for lactating seals, and estimating the daily mass ingested per individual seal for every month of each lactation period at the study colonies, then each individual lactating seal ingested between 8% and 14% (mean of 11%, $n = 184$) of its body mass per day, according to the model.

The sensitivity tests showed that adjustments to the digestive efficiency value had little affect on consumption estimates of teleost fish by seals (Table I). The model outcomes were more profoundly affected by adjustments to the values representing energy requirements of lactating females and estimates of pup production (Table I).

DISCUSSION

Previous models of consumption by Cape fur seals have been wholly static, based on a single population size and a single diet composition (Shaughnessy 1985, David 1987a). This is the first dynamic model of Cape fur seal consumption that takes into account spatial and temporal variation in the diet and which provides an estimate in the variability in consumption. However, data gaps necessitated the use of average values on occasion. These components and an understanding of this variability are important when using models for fisheries management (Tollit and Thompson 1996).

Of necessity, the model was limited to a single component of the Cape fur seal population, namely lactating females, because most scats at breeding colonies are deposited by these animals. The model was therefore also limited to the lactation period. The teleost prey consumption estimates thus obtained were not extrapolated to the entire population in Namibia because diet composition of seals have been shown to vary within species, according to sex, age and reproductive stage (e.g. Lowry *et al.* 1980, Acuña and Francis 1995, Lawson *et al.* 1995, Casaux *et al.* 1998, Mikkelsen *et al.* 2002). Specifically, gender differences in dietary composition of

Cape fur seals have been shown (Castley *et al.* 1991) and are probably a consequence of gender differences in both energy requirements and ranging behaviour (Pierce and Boyle 1991).

The consumption model in this study is based on the assumption that the daily mass requirements of a seal are fulfilled. Therefore, the annual total consumption of teleosts would be overestimated for years of high mortality due to starvation or other reasons, for which reason the lactation period of 1993/94 was excluded from the model. In at least two other years, there were observations of high pup mortality and poor body condition among adults, though not on the scale of 1994 (J-P. Roux, MFMR, pers. obs). These were 1995, a Benguela Niño year, and 1999, a warm water event (Hardman-Mountford *et al.* 2003) similar to that of 1994 (Roux 1998). The model may therefore over-estimate teleost consumption in these years.

The model also assumes that estimates of pup numbers were unbiased. However, pup counts from aerial photographs may be biased downwards (Butterworth *et al.* 1991), resulting in numbers of lactating females being underestimated if inferred directly from the pup counts. The sensitivity analyses indicated that pup count underestimates of up to 20% down-scaled prey consumption estimates by as much as up to 22 000 tonnes. Therefore, the accuracy of pup counts is essential in providing reliable consumption estimates for lactating females.

The model uses information retrieved from scat samples to estimate consumption and is therefore subject to the many weaknesses inherent to the use of scats for diet studies (Pierce and Boyle 1991; see Chapter 8, Discussion). For example, small otoliths can be completely eroded during digestion, and otoliths that are retrieved have undergone a degree of erosion during digestion, affecting estimates of fish length from otolith diameter. The effects of erosion on otolith numbers and size were corrected for in this study using conversion factors determined during captive feeding trials on Cape fur seals (D. L. Millar *et al.*, MCM, unpublished data). These contributed to a more reliable estimate of fish mass in the diet (Harvey 1989, Staniland 2002). Also, while the relative importance of different teleost prey species can be estimated from the information contained in scats, it is impossible to estimate the relative importance of teleosts to other prey groups such as cephalopods, crustaceans and birds.

Bird and crustacean remains found in scats comprise mainly feathers and crushed carapace, respectively (S. M., pers. obs.), allowing for little more than detection of their occurrence, while differences in retention rates of otoliths and cephalopod beaks means that information obtained from these two types of prey remains are not directly comparable (Pierce and Boyle 1991, Gales

and Cheal 1992). Based upon previous analyses of stomach contents (David 1987a, Lipinski and David 1990), it was assumed for the model that teleosts comprise 95% of the diet of seals in Namibia. It is probable, however, that the intake of teleosts relative to other prey groups changes with time and location. For example, scats found at a non-breeding locality north of AWB (Sylvia Hill, 25°08'S 14°50'E) comprised almost 100% crustaceans (S. M., pers. obs.).

Information on the efficiency of digestion of prey by different sex-age classes of Cape fur seals is lacking, therefore an assumption had to be made in this regard for lactating females, based on other studies. Digestive efficiency may vary with sex and age of the seal, and with prey type and calorific content (Rosen and Trites 2000). However, it may not have that great an impact on the consumption estimates. Moreover, the calorific content of prey may vary seasonally, geographically and with age (Rosen and Trites 2000). Captive feeding trials including variation in prey type and the sex-age class of seals may allow for a more informed estimate in this regard.

This study's model would be further improved if the actual energetic requirements of lactating Cape fur seals were determined, for instance by conducting energetic studies on free-ranging seals using doubly-labelled water methods (e.g. Costa and Gentry 1986, Costa and Gales 2000, Trillmich and Kooyman 2001). This is important because the energetic requirements of lactating females can alter the outcome of consumption estimates to a large extent. The energetic requirements of Cape fur seals should take into account the energy required and the amount of time spent both at sea and on shore (Costa *et al.* 1989, Costa and Gales 2000, Goldsworthy *et al.* 2001). In this study, the at-sea energy requirements of lactating Cape fur seals were based on a scaling equation (Goldsworthy *et al.* 2003). Following this, the on-shore energy requirements were determined by using the factor of difference between the at-sea and on-shore energy requirements of northern fur seals. However, there are differences in lactating, diving and foraging behaviour, as well as in average body size, between Cape and northern fur seals. Such variation would likely influence the difference between at-sea and on-shore energy requirements (Doidge and Croxall 1985, Innes *et al.* 1987, Costa *et al.* 1989). The energy requirements of seals vary by sex, age and reproductive status (Laake *et al.* 2002) and these factors should also be taken into account in consumption models.

This study determined that, on average, lactating females ingested 11% of their body mass per day. This figure becomes 12% after correction for the non-teleost proportion of the diet (assumed to be 5%). That is, an average size lactating female (56 kg) consumed on average

6 kg.day⁻¹ (range 5 to 8 kg.day⁻¹, $n = 192$). This value falls within the daily energy requirements for other otariids, which range from 5% (Stellar sea lion; Winship *et al.* 2002) to 23% (Antarctic fur seal; Doidge and Croxall 1985) of body mass. When foraging, lactating seals would consume a higher percentage of their body mass (Winship *et al.* 2002), because 39% of their time is spent on land (Gentry *et al.* 1986). The consumption models of Wickens *et al.* (1992b) and David (1987a) assumed that the daily prey requirement of lactating Cape fur seals was 10% and 8% of the body mass, respectively, which are 2% and 4% below the value estimated in this study. Consumption estimates for lactating Cape fur seals based on the allometric equations for growing marine mammals (Innes *et al.* 1987) or eutherians (Nagy 1987) are also low in relation to the estimate produced by this study. Using the former equation, Balmelli and Wickens (1994) and Smale *et al.* (1994) estimated that an individual Cape fur seal consumed 4 kg.day⁻¹, making no distinction between seal age-sex classes. According to Nagy's (1987) equation, a lactating Cape fur seal of average mass 56 kg would need 2 kg.day⁻¹. Lactating females require more energy due to the energetic demands of raising a pup. For example, lactating Steller sea lions require 70% more daily energy than similarly-aged non-lactating females (Winship *et al.* 2002). Therefore, the consumption rate estimated in this study conforms with the higher energy required by lactating females.

The estimated consumption of commercial prey was greatest at CC. This was due to the abundance of hake and juvenile horse mackerel remains in scats collected from there (Chapter 2). Juvenile horse mackerel are mainly found along the northern coast of Namibia in the vicinity of CC (Krakstad and Kanandjembo 2001). At AWB and VRB, the two colonies on the southern coast of Namibia, consumption of horse mackerel was low due to its limited abundance in the region (Axelsen *et al.* 2004). For seals from these colonies, non-commercial species such as goby and lanternfish were more common in the diet (Chapter 2).

Although this study only regards a part of the seal population (lactating females) and a fraction of the year (lactation period), the annual consumption of the commercial species, hake and especially horse mackerel, were on average much lower than the annual fishery landings of these species. Differences in amounts of commercial species caught by fisheries and consumed by seals can be affected by the distribution of the stock, which in turn is influenced by changes in environmental conditions and food availability (Shannon *et al.* 1992). For example, although the biomass of the horse mackerel stock during 2001 and 2002 were similar (~850 000 tonnes; Bauleth-D'Almeida *et al.* 2001a, Krakstad *et al.* 2002), the 2001 stock was more widely distributed

in the northern waters of Namibia, encompassing CC, and consisted of smaller fish (less than 17 cm in length), than the 2002 stock which consisted of larger fish (greater than 17 cm in length) and was concentrated in the north near Cape Frio (18°30'S) (Bauleth-D'Almeida *et al.* 2001a, Krakstad *et al.* 2002). Consequently, the 2002 horse mackerel stock was largely inaccessible to lactating seals at CC, as it was largely outside of their foraging range, and this was reflected in the lower consumption of horse mackerel in 2002 compared to the fishery.

The model developed in this study provides an improved estimate of prey consumption by Cape fur seals, more specifically for lactating individuals. By improving estimates of prey consumption, a better understanding can be obtained regarding competition between consumers of a common resource (Harwood and Croxall 1988), in this case seals and fisheries competing for commercial fish stocks. Using well planned captive feeding trials, better estimates of some of the model parameters will be obtained, which will make the model more accurate and thus provide a better understanding of the interactions between seals, their prey and fisheries.

Table I. Counts of Cape fur seal *Arctocephalus pusillus pusillus* pups at each study colony determined by aerial surveys during December of five years (Johnston *et al.* 2004). These counts were assumed to represent the number of lactating females. The contribution of the three study colonies to the total pup count for Namibia is also given.

Colony	Pup counts				
	1994	1995	1996	1997	2001
CC	30 000	35 498	38 564	48 993	37 394
AWB	26 673	22 739	52 832	82 925	33 377
VRB	3 011	3 317	3 989	5 783	2 953
Proportion of all pups in Namibia (%)					
CC+AWB+VRB	66.9	66.5	72.2	73.0	65.2

Table II. The mass and proportional contribution to the population of adult female Cape fur seal *Arctocephalus pusillus pusillus* age classes (from Butterworth *et al.* 1995).

Female age class	Mass (kg)	Age distribution (%)
4-year-old	41	18
5-year-old	47	9
6-year-old	51	8
7-year-old	54	9
8-year-old	57	7
9-year-old	60	7
10-year-old	63	5
11-year-old	66	4
12+-year-old	69	35

Table III. The mean percentage mass of prey (range in parentheses) in the diet of Cape fur seals *Arctocephalus pusillus pusillus* at Cape Cross (CC), Atlas-Wolf Bay (AWB) and Van Reenen Bay (VRB), for each annual lactation period (December to July). *N* is the number of months in each lactation period for which diet data were available.

Colony	Lactation period ^a	<i>N</i>	Mean percentage prey composition (mass)					
			Horse mackerel	Hake	Lanternfish	Goby	Pelagics	Others
CC	1994/95	7	82.96 (57.79-99.72)	9.58 (0.15-42.07)	0.01 (0-0.03)	0.41 (0-1.73)	6.95 (0-21.42)	0.09 (0-0.59)
	1995/96	8	55.29 (8.82-90.26)	11.31 (0-44.29)	0	11.67 (0.03-54.33)	21.36 (7.11-42.03)	0.37 (0-0.93)
	1996/97	8	15.65 (1.36-56.74)	55.20 (11.08-81.64)	0.001 (0-0.005)	15.47 (0.18-45.96)	13.60 (0-31.80)	0.07 (0-0.25)
	1997/98	6	44.29 (0.68-85.48)	9.70 (1.23-39.85)	0.002 (0-0.008)	2.61 (0.59-7.79)	43.39 (6.29-95.19)	0.02 (0-0.11)
	1998/99	3	46.03 (15.67-71.26)	4.45 (1.32-7.37)	0	0.04 (0-0.10)	49.28 (21.36-79.67)	0.20 (0-0.60)
	1999/2000	2	52.03 (34.30-69.77)	28.70 (1.07-56.32)	0	0.43 (0.03-0.84)	18.83 (9.35-28.32)	0
	2000/01	5	84.87 (81.19-93.99)	1.05 (0-3.39)	0	0.60 (0-1.66)	13.48 (6.00-18.65)	0.01 (0-0.03)
	2001/02	5	21.20 (3.90-80.02)	46.75 (0.14-92.25)	0	8.90 (0.54-24.31)	20.21 (0-71.32)	2.93 (0-7.15)
AWB	1994/95	8	1.12 (0.02-3.64)	37.91 (2.09-77.22)	4.60 (0.43-10.86)	48.21 (6.42-95.42)	6.55 (0-25.11)	1.61 (0.67-4.50)
	1995/96	8	0.40 (0-1.58)	10.85 (3.63-23.63)	8.75 (0.33-47.62)	76.13 (16.56-91.50)	2.89 (0.08-9.96)	0.98 (0-3.82)
	1996/97	7	0.06 (0.02-0.14)	83.99 (71.38-93.16)	0.76 (0.09-2.57)	11.11 (1.07-27.64)	2.98 (0-12.02)	1.09 (0-4.39)
	1997/98	8	2.40 (0.07-8.41)	48.21 (17.45-74.69)	15.73 (0.44-64.35)	25.09 (7.57-57.99)	6.81 (0.24-23.73)	1.76 (0-6.26)
	1998/99	7	0.53 (0-2.86)	47.74 (6.23-93.73)	0.97 (0.04-3.23)	42.33 (2.81-92.42)	7.13 (0-41.79)	1.29 (0.20-3.52)
	1999/2000	7	4.17 (0.15-14.43)	50.14 (20.66-79.63)	11.28 (0.68-30.91)	16.15 (5.58-37.08)	15.52 (0.41-37.15)	2.73 (0-12.20)

Table III. (cont.)

VRB	2000/01	8	2.45 (0-9.66)	42.20 (8.23-81.84)	6.70 (0.07-27.98)	35.27 (6.41-76.13)	11.68 (0-28.35)	1.70 (0-6.52)
	2001/02	5	1.03 (0-3.64)	19.19 (0.28-45.51)	9.75 (0.30-24.60)	60.99 (21.04-99.18)	8.45 (0.07-23.75)	0.58 (0-1.80)
	1994/95	3	1.53 (0.41-2.91)	54.69 (30.75-76.92)	13.19 (3.64-31.94)	7.68 (2.14-11.58)	19.32 (0.88-47.63)	3.60 (1.05-6.58)
	1995/96	2	1.85 (1.73-1.97)	17.68 (15.48-19.88)	1.81 (0.87-2.74)	49.18 (29.06-69.30)	16.44 (0-32.88)	13.04 (12.38-13.70)
	1996/97	0	-	-	-	-	-	-
	1997/98	3	4.08 (0.07-7.13)	37.53 (31.14-41.03)	3.15 (1.36-5.98)	1.42 (0.33-2.07)	48.18 (44.87-53.64)	5.65 (2.26-11.93)
	1998/99	4	0.99 (0-3.81)	44.11 (14.52-69.95)	0.86 (0.14-2.19)	3.52 (2.35-4.47)	44.24 (5.18-79.75)	6.27 (0-20.24)
	1999/2000	1	4.40	9.90	2.70	49.32	18.87	14.82
	2000/01	8	3.21 (0-17.58)	50.67 (17.82-81.59)	1.62 (0-6.64)	6.73 (0.48-27.56)	31.80 (1.02-72.18)	5.97 (1.09-18.42)
	2001/02	5	2.75 (0.41-7.04)	22.03 (6.31-29.32)	2.56 (0.02-6.61)	24.55 (6.11-45.25)	34.55 (7.73-45.42)	13.57 (1.91-24.00)

^a The lactation period 1993/94 was not included because of mass mortality of pups during that time (see Methods).

Table IV. The estimated consumption (tonnes) of teleost prey groups by lactating Cape fur seals *Arctocephalus pusillus pusillus* at each study colony for each lactation period (December to July), as well as the estimated proportion of commercial and non-commercial prey consumed.

Colony	Lactation period ^a	Estimated total teleost prey consumed (tonnes)	Estimated teleost prey consumption (tonnes)						Estimated % commercial prey consumed			Estimated % non-commercial prey consumed
			Horse mackerel	Hakes	Lantern-fish	Goby	Pelagics	Others	Horse mackerel	Hakes	Pelagics	
CC	1994/95	25 921	20 832	3 420	3	149	1 493	24	80.37	13.20	5.76	0.68
	1995/96	32 066	16 040	4 574	0	5 061	6 274	117	50.02	14.27	19.57	16.15
	1996/97	39 968	4 730	22 635	0	8 860	3 718	24	11.83	56.63	9.30	22.23
	1997/98	41 377	18 476	4 890	1	1 659	16 343	9	44.65	11.82	39.50	4.03
	1998/99	31 150	14 751	1 803	0	18	14 506	73	47.35	5.79	46.57	0.29
	1999/2000	34 111	16 687	11 689	0	213	5 521	0	48.92	34.27	16.19	0.63
	2000/01	31 933	27 222	431	0	298	3 980	2	85.25	1.35	12.46	0.94
	2001/02	36 704	6 347	19 821	0	4 123	5 436	977	17.29	54.00	14.81	13.90
	Mean	34 154	15 635	8 658	1	2 548	7 159	153	48.21	23.92	20.52	7.36
	SD	5 051	7 335	8 470	1	3 209	5 329	335	25.92	21.63	14.64	8.73
AWB	1994/95	30 506	239	11 084	1 292	16 163	1 315	413	0.78	36.33	4.31	58.57
	1995/96	27 398	81	2 879	2 513	21 103	590	232	0.30	10.51	2.15	87.04
	1996/97	57 115	30	47 259	413	7 767	1 123	524	0.05	82.74	1.97	15.24
	1997/98	89 185	1 646	40 994	15 225	25 621	4 106	1 594	1.85	45.96	4.60	47.59
	1998/99	49 637	193	22 425	426	23 654	2 387	551	0.39	45.18	4.81	49.62
	1999/2000	45 211	1 730	22 318	4 730	9 787	5 239	1 408	3.83	49.36	11.59	35.22
	2000/01	47 818	895	18 602	3 477	19 921	4 113	810	1.87	38.90	8.60	50.62
	2001/02	38 682	281	7 594	3 490	25 003	2 136	178	0.73	19.63	5.52	74.12
	Mean	48 194	637	21 645	3 946	18 627	2 626	714	1.23	41.08	5.44	52.25
	SD	19 298	701	15 593	4 814	6 812	1 676	526	1.25	21.60	3.23	22.10
VRB	1994/95	3 028	39	1 748	383	300	455	103	1.29	57.71	15.01	25.98
	1995/96	3 673	52	626	59	2 099	424	414	1.41	17.03	11.54	70.02
	1996/97	4 021	99	1 172	95	1 299	997	359	2.46	29.14	24.80	43.60
	1997/98	5 254	197	2 306	174	107	2 152	318	3.74	43.89	40.97	11.40
	1998/99	3 554	31	1 779	32	173	1 309	228	0.89	50.08	36.85	12.19
	1999/2000	4 164	141	402	100	2 426	554	540	3.40	9.65	13.31	73.64
	2000/01	3 702	108	1 958	62	397	969	209	2.91	52.89	26.16	18.04
	2001/02	2 926	66	696	70	892	804	398	2.27	23.79	27.48	46.46
	Mean	3 790	92	1 336	122	962	958	321	2.30	35.52	24.52	37.67
	SD	731	57	708	114	900	570	138	1.03	17.99	10.81	24.83

Table IV. (cont.)

Total	1994/95	59 455	21 109	16 252	1 679	16 612	3 262	541	35.50	27.34	5.49	31.67
	1995/96	63 136	16 172	8 079	2 572	28 263	7 287	763	25.62	12.80	11.54	50.05
	1996/97	101 104	4 858	71 066	509	17 926	5 838	907	4.81	70.29	5.77	19.13
	1997/98	135 816	20 318	48 190	15 400	27 387	22 601	1 921	14.96	35.48	16.64	32.92
	1998/99	84 340	14 975	26 007	458	23 846	18 202	852	17.76	30.84	21.58	29.83
	1999/2000	83 486	18 558	34 409	4 831	12 426	11 315	1 948	22.23	41.22	13.55	23.00
	2000/01	83 453	28 224	20 991	3 539	20 616	9 062	1 021	33.82	25.15	10.86	30.17
	2001/02	78 312	6 694	28 112	3 560	30 018	8 376	1 552	8.55	35.90	10.70	44.86
	Mean	86 138	16 364	31 638	4 068	22 137	10 743	1 188	20.41	34.88	12.02	32.70
	SD	23 939	7 667	19 948	4 828	6 268	6 513	543	11.08	16.69	5.35	10.30

^a The lactation period 1993/94 was not included because of mass mortality of pups during that time (see Methods).

Table V. The percentage of Cape fur seal *Arctocephalus pusillus pusillus* pups in each study colony relative to the total number of pups within the respective region, and the estimated total consumption of teleost prey by lactating Cape fur seals for each region and Namibia as a whole, for each annual lactation period.

Lactation period	Estimated % pups at colony within respective region			Estimated total teleost prey consumption (tonnes)			
	CC (Region 1)	AWB (Region 2)	VRB (Region 3)	Region 1	Region 2	Region 3	All regions
1994/95	90.79	64.40	20.41	29 000	47 000	15 000	91 000
1995/96	89.11	62.10	20.58	36 000	44 000	18 000	98 000
1996/97	89.72	73.07	23.74	45 000	78 000	17 000	140 000
1997/98	87.20	77.20	23.07	48 000	116 000	23 000	187 000
1998/99	86.44	71.44	21.31	36 000	70 000	17 000	123 000
1999/2000	86.44	71.44	21.31	40 000	63 000	20 000	123 000
2000/01	86.44	71.44	21.31	37 000	67 000	17 000	121 000
2001/02	77.46	69.31	17.71	47 000	56 000	17 000	120 000

Table VI. The total annual fishery landings of Cape hakes *Merluccius* spp., Cape horse mackerel *Trachurus trachurus capensis* and pelagics (sardine *Sardinops sagax*, anchovy *Engraulis capensis* and round herring *Etrumeus whiteheadi*) (tonnes) in Namibia, and the total amount of hake, horse mackerel and pelagics consumed by lactating Cape fur seals *Arctocephalus pusillus pusillus* during the lactation period in Namibia (December to July). The ratio between fishery landings and seal consumption for these prey groups is given.

Year	Total fishery landings (tonnes)			Total consumption by seals (tonnes)			Ratio of fishery catch to seal consumption		
	Hake ^a	Horse mackerel ^b	Pelagics ^c	Hake	Horse mackerel	Pelagics	Hake	Horse mackerel	Pelagics
1994	112 206	364 000	142 000						
1995	130 362	310 000	141 000	24 875	32 310	4 993	5.2	9.6	28.2
1996	129 102	320 000	17 000	12 541	25 103	11 311	10.3	12.7	1.5
1997	116 593	300 000	38 000	98 407	6 727	8 084	1.2	44.6	4.7
1998	150 825	311 000	70 000	66 351	27 975	31 118	2.3	11.1	2.2
1999	160 690	321 000	43 259	37 928	21 839	26 546	4.2	14.7	1.6
2000	162 821	327 000	27 896	50 695	27 342	16 670	3.2	12.0	1.7
2001	157 000	279 000	20 427	30 435	40 922	13 139	5.2	6.8	1.6
2002	165 000	308 000	53 797	43 077	10 258	12 835	3.8	30.0	4.2

^a Rademeyer and Butterworth (2004).

^b Axelsen *et al.* (2004).

^c H. J. Boyer, National Marine Information and Research Centre, Ministry of Fisheries and Marine Resources, Namibia, pers. comm.

Table VII. The mean total teleost prey consumed (standard deviation in parentheses, SD) by Cape fur seals *Arctocephalus pusillus pusillus* at each study colony, as well as the mean percentage body mass consumed by a lactating seal of average mass 56 kg, under different scenarios of some of the model parameters; digestive efficiency (*DE*) of prey, the energy requirement of lactating females (*ER*) and the underestimate of pup counts from aerial surveys.

Colony	Mean (SD) total teleost prey consumed (tonnes)						
	Original model ^a	<i>DE</i> (92%)	<i>DE</i> (96%)	<i>ER</i> (5.0 W.kg ⁻¹)	<i>ER</i> (7.4 W.kg ⁻¹)	Pup count underestimate (10%)	Pup count underestimate (20%)
CC	34 154 (5 051)	34 525 (5 106)	33 086 (4 893)	24 932 (3 687)	37 880 (5 602)	37 948 (5 612)	42 692 (6 313)
AWB	48 194 (19 298)	48 718 (19 507)	46 688 (18 695)	35 182 (14 087)	53 452 (21 403)	53 549 (21 442)	60 243 (24 122)
VRB	3 790 (731)	3 831 (739)	3 672 (708)	2 767 (534)	4 204 (811)	4 211 (812)	4 738 (914)
CC+AWB+VR	86 138	87 074	83 446	62 881	95 535	95 709	107 672
B	(23 939)	(24 200)	(23 191)	(17 476)	(26 551)	(26 599)	(29 924)
Mean (range) body mass consumed (%)							
CC+AWB+VR	11	11	10	8	12	11	11
B	(8-14)	(8-14)	(8-13)	(6-10)	(9-15)	(8-14)	(8-14)

^a The original model parameters are: *DE* (93%), *ER* (6.7 W.kg⁻¹) and no pup count underestimate.

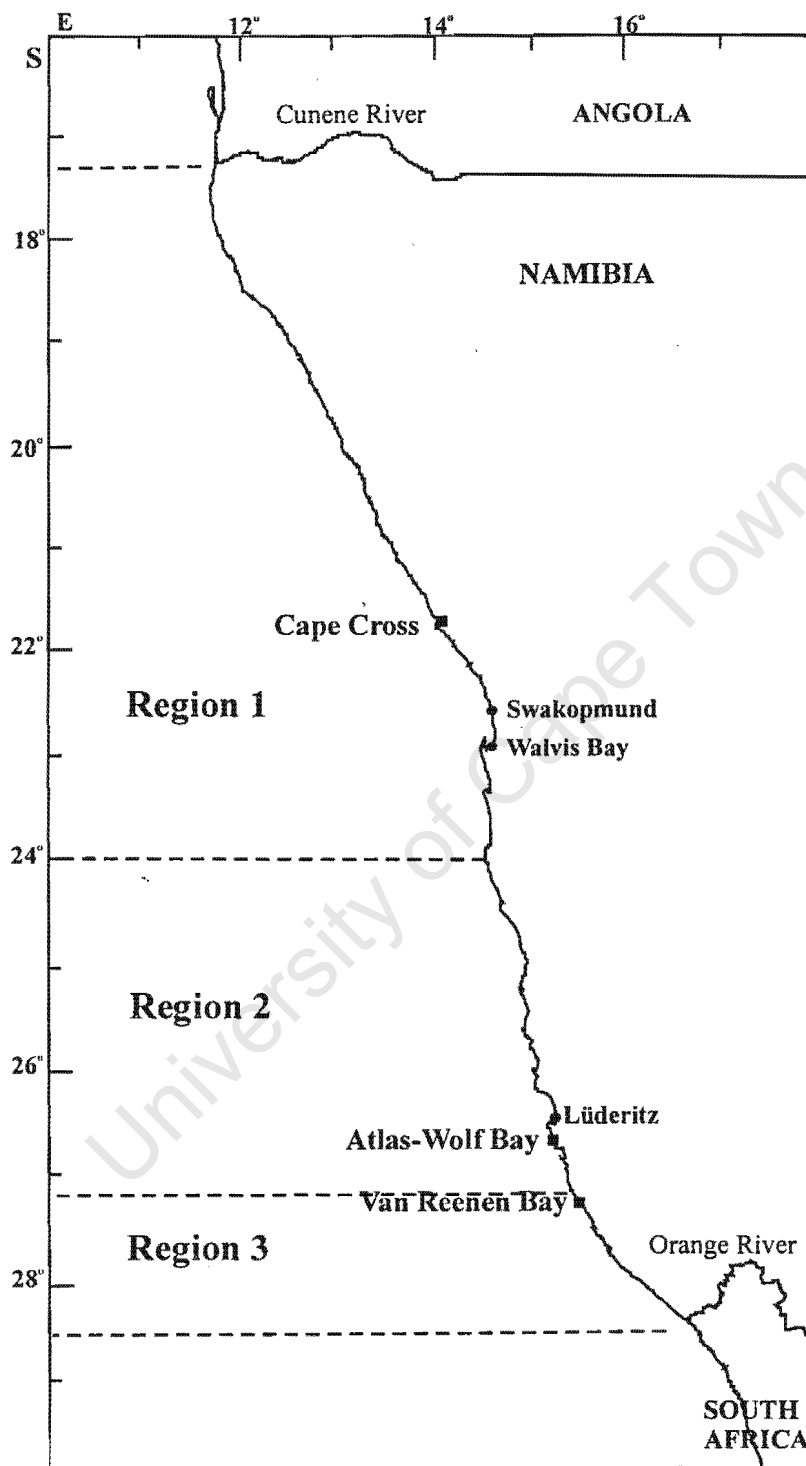


Figure 1. The location of the three mainland Cape fur seal *Arctocephalus pusillus pusillus* study colonies (Cape Cross, Atlas-Wolf Bay and Van Reenen Bay) in Namibia, as well as the three regions in the northern Benguela System.

CHAPTER 5



University of Cape Town

Overlap in the utilization of juvenile Cape horse mackerel by Cape fur seals and the purse-seine fishery in Namibia

INTRODUCTION

The northern Benguela along the coast of Namibia is a highly productive ecosystem (Currie 1953), comprising part of one of the four major eastern boundary upwelling centres in the world (Shannon and Jarre-Teichmann 1999). It sustains prey required by top predators such as marine birds and mammals, and its resources are exploited by Namibian fishing industries (Boyer and Hampton 2001). Some commercial fish resources are shared between marine top predators and fisheries. For example, the Cape fur seal *Arctocephalus pusillus pusillus* consumes commercially important fish such as Cape hakes *Merluccius* spp., Cape horse mackerel *Trachurus trachurus capensis*, sardine *Sardinops sagax* and anchovy *Engraulis capensis* (Chapter 2). For this reason, and the fact that seals are amongst the most visible of the top predators in the system, fishers consider Cape fur seals to be their main competitors for fish stocks (Wickens *et al.* 1992a).

The Cape horse mackerel is the most abundant commercially exploited fish resource in Namibian waters (Axelsen *et al.* 2004). This resource has been exploited by the purse-seine fishery since 1971 (Boyer and Hampton 2001). The fishery targets juveniles (12.5-20 cm in length) inshore of the 200 m isobath (Bauleth-D'Almeida *et al.* 2001b) and focuses its attention off the northern coast of Namibia (Krakstad and Kanandjembo 2001, Axelsen *et al.* 2004) where large concentrations of juvenile horse mackerel are found (O'Toole 1977, Krakstad and Kanandjembo 2001). Horse mackerel purse-seiners operate mostly during the first half of the year when the fish occur in dense schools, making them easier to catch.

Stomach contents of seals collected along the entire Namibian coastline between 1975 and 1979 showed that juvenile horse mackerel were the prey item most frequently consumed by seals in northern Namibia, which includes the foraging area of seals from the Cape Cross colony (Shaughnessy 1985). The Cape Cross colony is one of the largest mainland seal breeding colonies in Namibia, comprising about 187 000 individuals, which is about 30% of the Namibian

Cape fur seal population (Marine and Coastal Management (MCM), unpublished data). Prey hard parts retrieved from seal scats collected at Cape Cross two decades later showed that horse mackerel are an important part of the diet of seals from this colony, particularly during the first half of the year (Chapter 3). The possibility therefore exists that the purse-seine fisheries and seals at the Cape Cross colony share the horse mackerel resource. Indeed, Plarre (1996) found that Cape fur seals and the purse-seine fishery in Namibia overlapped in their utilization of the juvenile horse mackerel resource for some months in a year (up to 72% overlap). However, the overlap measure used, Schoener's Index (Schoener 1970), is biased (Hurlbert 1978, Smith and Zaret 1982), mainly in that it ignores the variation in abundance of the horse mackerel resource states (length classes) by assuming all classes are equally abundant. A number of other overlap measures have been proposed in recent decades (e.g. Lloyd 1967, Schoener 1970, Pianka 1973, Hurlbert 1978, Petraitis 1979), each with its own limitations (Hurlbert 1978, Petraitis 1979, Abrams 1980, Ricklefs and Lau 1980, Smith and Zaret 1982).

The aim of this study was to measure the overlap between seals and the purse-seine fishery with regard to their utilization of juvenile horse mackerel offshore of northern Namibia, using seal scats collected at the Cape Cross colony and records of fishery catches. The scats from this breeding colony mainly represent those of lactating female fur seals. Although scat analysis has biases (see Chapter 8, Discussion), it can provide valuable information on the prey consumed (Pierce and Boyle 1991). This study expands on the work of Plarre (1996) because it is based on eight years of diet and catch data as opposed to two. Moreover, this study compares the findings of two overlap measures, and includes confidence intervals and significance testing derived from randomization and bootstrapping methods (Manly 1991). Investigating overlap in the utilization of a fish resource by seals and a fishery can provide important information on the interactions between seals and fisheries for fish stock management decisions.

MATERIAL AND METHODS

Seal scat collection and processing

The collection and processing of scats is described in Chapter 2. Briefly, fresh seal scat samples were collected at the Cape Cross breeding colony (21°47'S, 13°57'E) in northern Namibia, on a monthly basis from January 1994 to December 2001, with no samples collected for 22 out of 96

months. Prior to May 2001, samples consisted of 30 to 60 scats pooled together to form a “bag” sample; from May 2001 bag samples consisted of 30 scats. Where more than one sample was collected in a month, they were pooled to represent that month. Samples were rinsed with running water and passed through nested stainless steel laboratory test sieves with apertures of 2.0, 1.0, 0.425 and 0.212 mm. The rinsed material was dried overnight in an oven (50°C). Saggital otoliths were sorted from the dried matter of each sample. Horse mackerel otoliths were identified following Smale *et al.* (1995), removed and counted. Otolith counts were corrected for numbers lost during digestion using the correction factor of 1.754 (D. L. Millar *et al.*, MCM, unpublished data).

Otolith diameters (distance parallel to the sulcus from the anterior to the posterior margins of the otolith) of c. 200 whole otoliths per sample, displaying little or no erosion, were measured with a vernier caliper to 0.05 mm. If a monthly sample consisted of less than 200 otoliths, the entire sample was measured. Each measured otolith diameter was corrected for erosion, which occurred during the process of digestion, using the correction factor of 1.025 (D. L. Millar *et al.*, MCM, unpublished data). Each corrected otolith diameter was converted to total fish length (length from the tip of the snout to the tip of the longest caudal ray) using the equation

$$\ln(y) = 3.3550 + 1.0627\ln(x) \quad (\text{Eqn 1})$$

where y is fish total length (mm) and x is corrected otolith diameter (mm) (Smale *et al.* 1995).

Length-frequencies of horse mackerel in the seal diet were determined at 0.5 cm class intervals ranging from 0 to 33.0 cm. Fish lengths were converted to mass using the equation

$$y = 0.0042x^{3.2384} \quad (r = 0.99, n = 1\,027) \quad (\text{Eqn 2})$$

where y is mass (g) and x is fish total length (cm). This equation is based on length-mass measurements made by the Ministry of Fisheries and Marine Resources (MFMR) in Namibia during 2000 and 2001. The mean mass of fish in each sample was multiplied by that sample's corrected otolith count to estimate the overall mass of horse mackerel in that sample. The relative contribution of horse mackerel compared to other teleost prey in each sample was estimated (Chapter 2).

Purse-seine catches

The purse-seine fishery for horse mackerel was most active between February and April of each year and no fishing occurred from August to December or mid-January. Random samples of 50

fish were taken from landed purse-seine catches and the total length of each fish was measured to the nearest 0.5 cm (Bauleth-D'Almeida *et al.* 2001b). Data for the years 1994 to 2001 were used in this study.

Seals are able to forage as far as 220 km from their colony (Shaughnessy 1985). Therefore, only purse-seine catches made within a radius of approximately 200 km from the Cape Cross colony were used in the analyses. For catches made in the years 1994 to 1998 only latitude positions of each catch were available, whereas for catches made during 1999 to 2001 both latitude and longitude positions were available. For 1994 to 1998, catches made within the latitudes 20-24°S were used; 477 out of 669 catches fell within this area. For 1999 to 2001 catches made within the latitudes 20-24°S and between the coastline and 12°E were used; 70 out of 99 catches were within this area and 2 catches were within 20-24°S but outside of 12°E. When more than one catch was landed during a month, measurements from each were pooled to represent that month. Length-frequencies of horse mackerel caught were determined at 0.5 cm class intervals ranging from 0.25 to 32.75 cm.

Measurement of overlap

Schoener's and Morisita's measures were used to examine overlap in the utilization of juvenile horse mackerel by Cape fur seals and the purse-seine fishery in northern Namibia. Morisita's measure of overlap was employed in this study as it was shown by Smith and Zaret (1982), in a comparative study of seven overlap measures, to be the least biased by sample size and the number of resource states. Schoener's overlap measure was also included as it had been used during the only previous investigation of overlap in horse mackerel utilization by Cape fur seals and the purse-seine fishery (Plarre 1996).

Schoener's (1970) index (S)

$$S = 1 - \frac{1}{2} \left(\sum_{i=1}^r |p_{si} - p_{fi}| \right) \quad (\text{Eqn 3})$$

where $i = 1, \dots, r$ is the number of resource states, in this case the number of 0.5 cm length classes of horse mackerel from 0 to 33.0 cm, thus $r = 66$; $p_{si} = \frac{n_{si}}{N_s}$ and is the proportion of the

resource in state i taken by seals and $p_{fi} = \frac{n_{fi}}{N_f}$ and is the proportion of the resource in state i taken by the fishery; n_{si} and n_{fi} are the numbers of horse mackerel in resource state i taken by seals and the fishery, respectively; $N_s = \sum_{i=1}^r n_{si}$ and $N_f = \sum_{i=1}^r n_{fi}$. S ranges in value from zero (no overlap) to one (complete overlap).

Morisita's (1959) unadjusted index (M)

$$M = \frac{2 \sum_{i=1}^r p_{si} p_{fi}}{\sum_{i=1}^r p_{si} \frac{n_{si} - 1}{N_s - 1} + \sum_{i=1}^r p_{fi} \frac{n_{fi} - 1}{N_f - 1}} \quad (\text{Eqn 4})$$

where the variables are defined as for Schoener's index. M ranges in value from zero (no overlap) to one (complete overlap).

Adjustments to Schoener's and Morisita's indices

Some studies have shown that the proportion of a prey species or its length classes in the diet of a predator reflects the abundance of that prey species or its length classes (Crawford *et al.* 1992, Klages *et al.* 1992, Montevecchi and Myers 1995, Hunt *et al.* 1996, Reid *et al.* 1999). Accordingly, in order to integrate prey abundance into overlap measures, which is one of the requirements for understanding competitive interactions between predators (Harwood and Croxall 1988), Schoener's and Morisita's overlap measures were multiplied by the proportion of horse mackerel abundance in the diet of Cape fur seals during each month when purse-seine catches occurred. Thus, $S^* = S \times (\text{proportion of horse mackerel in the seal diet})$, and $M^* = M \times (\text{proportion of horse mackerel in the seal diet})$.

Confidence intervals and randomization tests for overlap indices

Confidence intervals for Schoener's and Morisita's indices were determined using the bootstrap procedure (Ricklefs and Lau 1980, Manly 1991). Bootstrap samples ($n = 10\,000$, sampling with replacement) were taken from the original samples of horse mackerel in the seal diet and purse-seine fishery, for each month where both sets of data existed. From these, 10 000 estimates of the

overlap index were determined for each month. The 10 000 estimates were arranged in increasing order, and the 95% confidence intervals were determined by taking the 250th and the 9750th values. To obtain confidence intervals for the adjusted Schoener's and Morisita's indices, the confidence intervals for unadjusted Schoener's and Morisita's indices were multiplied by the proportion of horse mackerel abundance in the diet of Cape fur seals for the corresponding months.

In the absence of appropriate precedents in the literature, 0.25 (and less) and 0.75 (and more) were arbitrarily adopted as low and high levels of overlap, respectively, between seals and the purse-seine fishery for the utilization of horse mackerel. Therefore, months for which the upper limit of the 95% confidence interval was below 0.25 were considered to have a high probability of small overlap, and months for which the lower limit of the 95% confidence interval was above 0.75 were taken as months with a high probability of large overlap.

In order to test the null hypothesis that the observed overlap index could have originated from a distribution of fish lengths that was the same for both seals and fisheries, randomization methods were used (Manly 1991). In randomization tests (as in all statistical hypothesis testing), the null hypothesis states that some feature of interest is absent from the observed data. A test statistic is devised which measures the extent to which the data departs from this feature. The test statistic is computed first for the observed data. Thereafter, the test statistic is computed for many thousands of random permutations of the observed data, and the distribution of the test statistic is obtained. If the value of the test statistic obtained from the observed data lies in the tails of this distribution, the null hypothesis is rejected.

In this case, the overlap index (Schoener's and Morisita's) was used as the test statistic. The overlap index for the observed data was denoted S_1 or M_1 , respectively. For each of the 34 months for which both seal diet data and purse-seine fishery data were available, the lengths of the horse mackerel sub-samples of seal diet and fishery data were pooled. The observed data for month m ($n_{sl} + n_{fl}$ observations) were randomly permuted 10 000 times. The first n_{sl} observations were assigned to the seals and the remaining n_{fl} to the fishery. The overlap indices S and M were computed for each randomization of the data. A count was kept of the number of times the values of S and M were greater than or equal to S_1 and M_1 , respectively. This count, divided by 10 000, estimates the significance level of the test. If it is less than 0.05, the null hypothesis is rejected at

the 5% significance level. Manly (1991) has provided a philosophical discussion of randomization tests, and their applicability to these kinds of data.

RESULTS

Over the eight-year study period (1994 to 2001) the percentage mass of horse mackerel in the Cape fur seal diet, as determined using scat analysis, varied between years, with a minimum of 15.0% in 1997 and a maximum of 64.7% in 1995 (Fig. 1). The total catch of horse mackerel by the purse-seine fishery appeared to lag the proportion consumed by seals by one to two years (Fig. 1); there was a peak in the catch in 1997 (93 500 tonnes) and the catch decreased by 72.1% the following year to 26 000 tonnes, and remained at this level until the end of the study period.

Except for 1998, the resource utilization curve of the purse-seine fishery fell within that of the seals (Fig. 2). Seals consumed smaller length classes more frequently than those caught by the purse-seine fishery. For both seals and fishery, there were annual differences in the lengths of horse mackerel consumed or caught (Fig. 2). Five main modes (age classes) of horse mackerel length were observed, and the length values of these main modes varied between years. Age-0 was represented by the mode 5.25 to 7.75 cm, age-1 by the mode 8.75 to 11.75 cm, age-2 by the mode 14.75 to 16.75 cm, age-3 by the mode 20.25 to 22.25 cm, and age-4 by the mode 24.75 cm.

Schoener's overlap measures for each of the months were similar to those of Morisita's ($r = 0.98$; Table I). The degree of overlap varied between months; overlap measures (Schoener's and Morisita's indices) greater than 0.75 were found within the period February to June (Table I), and overlap measures less than 0.25 were found in January and during the period March to September (Schoener's index) or during January, within the period April to July, and during September (Morisita's index) (Table I). None of the lower confidence limits for Schoener's measures were above 0.75, whereas for Morisita's index three of the months had lower confidence limits greater than 0.75 (June 1995, March 1996 and February 1997) (Table I). Seven and five months had upper confidence limits less than 0.25 for Schoener's and Morisita's indices, respectively, the months shared by both being May 1994, September 1994, January 1997, April 1997 and July 1997 (Table I).

Where overlap measures were greater than 0.75, seals and fisheries mainly overlapped in the utilization of age-2 horse mackerel (e.g. Fig. 3). In the instances where overlap was less than

0.25, seals were consuming age-0 horse mackerel whereas the fishery was catching mainly age-2 horse mackerel (e.g. Fig. 4). There was no correlation between the proportion of horse mackerel in the seal diet and Schoener's and Morisita's measures of overlap ($r = 0.21$ and 0.13 , respectively, n.s., $n = 34$). However, for seven of the nine Schoener's overlap values, and 11 of the 17 Morisita's values, where overlap was greater than 0.50, the proportion of horse mackerel in the diet was 70% or more (Table I). Schoener's and Morisita's overlap values less than 0.50 were related to proportions of horse mackerel in the diet ranging from 0-100% (Table I). Six of the eight Schoener's overlap values, and five of the six Morisita's values, that were less than 0.20 were associated with horse mackerel proportions less than 37% (Table I).

When Schoener's and Morisita's measures were adjusted by the proportion of horse mackerel in the seal diet, none of the Schoener's adjusted values were greater than 0.75, whereas those of Morisita which meet this criterion were confined to the period March to May (Table I). None of the lower confidence limits for Schoener's and Morisita's adjusted measures were above 0.75 (Table I). Adjusted overlap measures (Schoener and Morisita) less than 0.25 were found in months throughout the entire period January to September (Table I). The number of months with upper confidence limits less than 0.25 were 21 and 19 for Schoener's and Morisita's indices, respectively (Table I). When both Schoener's and Morisita's adjusted values were greater than 0.50, then the proportions of horse mackerel in the teleost portion of the seal diet were greater than 77% and 70%, respectively (Table I). For overlap values less than 0.50, the proportion of horse mackerel in the seal diet ranged from 0-100%; a proportion of 44% or less of horse mackerel in the seal diet always had overlap values less than 0.20 for both indices (Table I).

The relationships between the width of the confidence intervals for both Schoener's and Morisita's indices (unadjusted and adjusted) and the sample size of horse mackerel taken by seals and the fishery are given in Figure 5. The widths of the confidence intervals were less than 0.20 for catch sample sizes greater than 450 and for seal sample sizes greater than 390 (Figure 5). Confidence interval widths for sample sizes in the range of 2 000 to 4 000 for the fishery and 500 to 1 300 for the seals were not available and therefore did not allow for determining the minimum sample size for confidence interval widths of less than 0.1 (Figure 5). The widths of the confidence intervals for Schoener's and Morisita's indices were negatively related to the logarithm of seal sample size (Schoener's index: $r = -0.40$, $p = 0.02$, $n = 34$; Morisita's index:

$r = -0.41$, $p = 0.02$, $n = 34$) and fishery sample size (Schoener's index: $r = -0.31$, n.s., $n = 34$; Morisita's index: $r = -0.41$, $p < 0.001$, $n = 34$).

Only two months (February 1997 and May 2001) displayed the possibility that the observed overlap indices (Schoener and Morisita) could have originated from a distribution of fish lengths that was the same for both seals and fisheries (Table I).

DISCUSSION

Niche overlap is the shared use of a resource by two or more species (Colwell and Futuyma 1971). The intensity of overlap between marine predators and fisheries is strongest if the fishery exploits the principal prey species of a marine predator which is at carrying capacity (Lowry and Frost 1985). The status of the Cape fur seal population in relation to its carrying capacity is unknown. However, the highest levels of overlap between seals at the Cape Cross breeding colony, which are mainly lactating females, and the fishery occurred from March to May (Morisita's index), coinciding with the period when horse mackerel abundance in the seal diet was highest (Chapter 3).

Schoener's and Morisita's indices of overlap, both unadjusted and adjusted, yielded similar results. Lactating females forage on locally abundant prey (Shaughnessy 1985, Oosthuizen 1991). Therefore, assuming that the proportion of horse mackerel in the diet of seals at Cape Cross reflects the abundance of juvenile horse mackerel in the coastal waters of Cape Cross, then overlap values (both unadjusted and adjusted) suggest that overlap between seals and the fishery in their utilization of juvenile horse mackerel was high only at times when horse mackerel abundance was high. At this time, either seals were targeting horse mackerel as their preferred prey due to their high availability, or the abundance of other prey species was low. When horse mackerel abundance was low, overlap was small. As horse mackerel mature they move into deeper water (Krakstad in press) and become unavailable to seals which dive to an average depth of 50 m (Kooyman and Gentry 1986). Seals therefore switch to other more accessible prey such as hake and goby (Chapter 2), thus reducing the degree of overlap with the horse mackerel fishery. This pattern is similar to that found by Croxall *et al.* (1999), who showed that when krill biomass decreased over a period of years, predators reduced their consumption of krill, increased their diversity of prey, and overlap between them was reduced.

My research might help to discover whether this is the case.

The degree of overlap between marine predators and fisheries varies according to the accessibility of resource classes. A dietary overlap study between harbour seals *Phoca vitulina* and great cormorants *Phalacrocorax carbo* in Sweden and Denmark showed that overlap is higher when the prey resource is most accessible to both predators with regards to foraging habitat type (Härkönen 1988). Juvenile horse mackerel occur in shallow inshore waters (Axelsen *et al.* 2004), and are thus accessible to seals. On the other hand, the purse-seine fishery mainly targets juveniles that are 12.5 to 20.0 cm in length (Bauleth-D'Almeida *et al.* 2001b), the minimum size of which is determined by the mesh size of the net used, although fish smaller than the mesh size may still be caught. Moreover, the purse-seine industry is required by regulation to stop fishing in an area if more than 5% of the catch, by weight, consists of fish less than 12.5 cm in length (MFMR 2002). Accordingly, fish smaller than 12.5 cm would be less accessible to the fishery than to seals. This difference in accessibility of seals and the fishery to horse mackerel reduces overlap between them. It may also explain why seals mainly consumed age-0 (5-8 cm) horse mackerel whereas the purse-seiners targeted mainly age-2 (15-17 cm) horse mackerel in this study.

Selection of specific prey length classes by a predator, as well as capture avoidance by certain age classes of the prey targeted by a fishery, may also lead to differences between predators and fisheries in the utilization of prey resource classes (Hill *et al.* 1996, Reid *et al.* 1996). It is unknown whether Cape fur seals select smaller horse mackerel than the fishery. Seals usually consume small fish that shoal (Chapter 2), and because juvenile horse mackerel up to about 10 cm in length occur within shoals (Cruickshank 1983b, Boyer and Hampton 2001), small juveniles may be easy targets for seals. Large horse mackerel, greater than 25 cm, may display net avoidance and thus bias purse-seine catches towards smaller fish (Bauleth-D'Almeida *et al.* 2001b). However, large horse mackerel were caught by purse-seining on the west coast of South Africa in the 1950s and 1960s (Geldenhuys 1973) and if present off the Namibian coast, should be accessible to the purse-seiners there.

Differences in techniques and timing of foraging by predators may also explain differences in prey species or classes of a prey resource taken by predators (Reid *et al.* 1996, Dellinger and Trillmich 1999, Wathne *et al.* 2000, Goldsworthy *et al.* 2001). Cape fur seals have been seen to forage throughout the day, but the extent to which they forage at night is unknown (Rand 1959, Punt *et al.* 1995). Purse-seiners operate throughout the day and night. Only purse-seine catches

made within the foraging range of seals were used in this study. The depths targeted by the pure-seine fishery were within the diving range of seals; 86% of the catches were made within the first 50 m of depth and 12% of catches were made at a depth of 50 to 100 m.

The present study used two overlap indices (Schoener's and Morisita's indices). Smith and Zaret (1982) investigated seven overlap indices, including Morisita's but excluding Schoener's, and considered that Morisita's index (Morisita 1959) was least biased by sample size and the number of resource states. However, Morisita's and Schoener's indices are biased because they ignore the variation in abundance of the resource states or classes (Hurlbert 1978, Petraitis 1979). In order to reduce this bias, it was assumed that the relative abundance of horse mackerel in the seal diet reflects the relative abundance of this fish in the water. Therefore, both Schoener's and Morisita's indices were adjusted by the percentage abundance of horse mackerel in the seal diet. Lloyd's adjusted index (Hurlbert 1978) takes into account the abundance of resource classes, but this overlap measure could not be used because the actual monthly abundance of horse mackerel over the study period is unknown.

One of the main pitfalls of overlap measures is that they do not include confidence limits. Monte Carlo simulations have been used in this regard for some overlap measures (Ricklefs and Lau 1980). Confidence intervals can allow for further interpretation of overlap measures and provide information regarding their limitations. For this study, confidence intervals determined by bootstrapping showed that a high degree of overlap (greater than 0.75) between seals and fisheries in their use of the horse mackerel resource was rare, whereas a low degree of overlap (less than 0.25) was more common. The smaller the confidence interval around the overlap measure, the more reliable the overlap measure (Sokal and Rohlf 1995). This study showed that smaller confidence intervals (less than 0.20) resulted when seal diet and fishery catch sample sizes of measured horse mackerel were large (greater than 390 and 450, respectively). Sample sizes for both the fishery and seals for some months in this study were small (less than 50). The reliability of overlap measures would be improved by sampling larger amounts of the horse mackerel taken by seals and the fisheries.

Another drawback of overlap measures is that most do not provide a means of determining whether the degree of overlap is significant (Ricklefs and Lau 1980, Zaret and Smith 1984). In this study, significance levels determined by bootstrapping were useful in highlighting that, in

most cases, seals and fisheries were exploiting different size classes of the horse mackerel resource.

Overlap indices fail to measure competition because overlap is not linearly related to competition (Colwell and Futuyma 1971, Hurlbert 1978), i.e. large values for the overlap index do not automatically represent direct competition, they may in fact imply reduced competition due to an abundance of the prey resource (Pianka 1974). The study by Plarre (1996), which investigated the overlap in utilization of horse mackerel by Cape fur seals and the purse-seine fisheries, concluded that there was "competition" between the seals and the purse-seine fishery for this prey. Plarre's (1996) study was based on Schoener's index, which is not a measure of competition because it does not include information on the static and dynamic properties of competition (Harwood and Croxall 1988, Green *et al.* 1998). Static properties include fish distribution and abundance, as well as feeding effort, amount of fish utilized and size classes utilized by seals and fisheries in time and space. Dynamic properties include the response of fish to changes in predation rate, the response of seals, fisheries and other predators to changes in fish abundance, and the response of the market to fish supply. Unless all this information is incorporated into a competition index, then competition, defined as occurring when the concurrent presence of two competitors is mutually disadvantageous (Harwood and Croxall 1988), between seals and fisheries cannot be determined. Usually it is impossible to provide all this information because it is either not available or difficult to obtain.

In conclusion, the results of this study showed that Cape fur seals and the horse mackerel purse-seine fisheries mostly take different resource classes of the horse mackerel stock, resulting in little overlap between them. However, because seals generally consumed smaller size classes than the fisheries, the fisheries may be affected by the proportion of small fish consumed by seals which would have become available to the fishery in the future. On the other hand, by taking bigger fish, the fishery may have an effect on the future recruitment of horse mackerel and therefore ultimately on what will become available to seals in the future. This study provides important insights into the interactions between Cape fur seals and the purse-seine fishery, which should be considered in the management of the horse mackerel stock.

Table I. Overlap measures of Schoener (S) and Morisita (M) for the utilization of the Cape horse mackerel *Trachurus trachurus capensis* resource by Cape fur seals *Arctocephalus pusillus pusillus* at Cape Cross and the purse-seine fishery (between 20 and 24°S) in Namibia. These measures were determined for months where resource utilization data for both seals and the fishery existed, between 1994 and 2001. S^* and M^* are Schoener's and Morisita's measures, respectively, adjusted by the proportion of horse mackerel (numerical abundance, NA) in the diet of the seals at Cape Cross. Approximate 95% confidence intervals, determined by bootstrapping, are in parentheses. The number of horse mackerel in the seal and fishery samples are represented by n_s and n_f , respectively. Overlap indices for which H_0 (observed overlap index could have originated from a distribution of fish lengths that was the same for both seals and fisheries) was accepted are indicated by an "a".

Date	n_s	n_f	S	M	NA	S^*	M^*
Mar-94	211	250	0.45 (0.38-0.52)	0.49 (0.38-0.60)	0.94	0.42 (0.35-0.49)	0.46 (0.36-0.56)
Apr-94	210	323	0.40 (0.33-0.47)	0.46 (0.36-0.56)	0.39	0.15 (0.13-0.18)	0.18 (0.14-0.22)
May-94	474	434	0.10 (0.08-0.13)	0.09 (0.06-0.13)	0.37	0.04 (0.03-0.05)	0.03 (0.02-0.05)
Jun-94	520	453	0.26 (0.22-0.30)	0.21 (0.16-0.26)	0.44	0.11 (0.10-0.13)	0.09 (0.07-0.11)
Jul-94	394	281	0.48 (0.42-0.54)	0.60 (0.52-0.69)	0.07	0.03 (0.03-0.04)	0.04 (0.04-0.05)
Sep-94	277	359	0.14 (0.10-0.18)	0.11 (0.07-0.17)	0.06	0.01 (0.01-0.01)	0.01 (0-0.01)
Mar-95	340	12	0.13 (0.08-0.19)	0.22 (0.11-0.35)	0.99	0.13 (0.08-0.18)	0.21 (0.10-0.34)
Apr-95	308	695	0.65 (0.59-0.70)	0.79 (0.72-0.86)	0.91	0.59 (0.54-0.64)	0.72 (0.65-0.79)
Jun-95	1 363	1 419	0.75 (0.72-0.78)	0.89 (0.86-0.92)	0.79	0.59 (0.57-0.62)	0.70 (0.68-0.72)
Jul-95	223	40	0.39 (0.27-0.51)	0.52 (0.32-0.73)	0.70	0.27 (0.19-0.36)	0.37 (0.22-0.51)
Aug-95	314	86	0.21 (0.15-0.27)	0.23 (0.15-0.32)	0.28	0.06 (0.04-0.08)	0.06 (0.04-0.09)
Feb-96	465	1 228	0.52 (0.47-0.56)	0.65 (0.59-0.72)	0.73	0.38 (0.34-0.41)	0.48 (0.43-0.52)
Mar-96	310	3 967	0.79 (0.74-0.84)	0.95 (0.90-0.98)	0.79	0.62 (0.59-0.66)	0.75 (0.71-0.77)
Apr-96	211	1 679	0.67 (0.61-0.73)	0.83 (0.75-0.90)	0.77	0.52 (0.47-0.56)	0.64 (0.58-0.69)
May-96	205	1 985	0.45 (0.39-0.51)	0.56 (0.47-0.66)	0.77	0.35 (0.30-0.39)	0.43 (0.36-0.50)
Jun-96	223	52	0.43 (0.33-0.53)	0.55 (0.39-0.71)	0.15	0.06 (0.05-0.08)	0.08 (0.06-0.11)
Jul-96	200	50	0.44 (0.35-0.53)	0.59 (0.44-0.74)	0.01	0 (0-0.01)	0.01 (0-0.01)

Table I. (cont.)

Aug-96	199	52	0.43 (0.35-0.51)	0.61 (0.47-0.74)	0.07	0.03 (0.02-0.04)	0.04 (0.03-0.05)
Jan-97	23	1 988	0.04 (0-0.08)	0.04 (0-0.13)	0.02	0.001 (0-0.002)	0.001 (0-0.003)
Feb-97	112	660	0.72 ^a (0.64-0.79)	0.93 ^a (0.84-0.99)	0.06	0.04 (0.04-0.05)	0.06 (0.05-0.06)
Mar-97	200	449	0.59 (0.52-0.66)	0.80 (0.71-0.88)	0.19	0.11 (0.10-0.13)	0.15 (0.13-0.17)
Apr-97	201	27	0	0	0.94	0	0
May-97	47	37	0.25 (0.13-0.37)	0.29 (0.11-0.54)	0.02	0.01 (0-0.01)	0.01 (0-0.01)
Jul-97	44	25	0.07 (0-0.16)	0.07 (0-0.22)	0.02	0.001 (0-0.003)	0.001 (0-0.004)
Jan-98	198	1 518	0.27 (0.21-0.33)	0.23 (0.16-0.31)	0.73	0.20 (0.16-0.24)	0.17 (0.11-0.23)
Feb-98	230	160	0.26 (0.20-0.31)	0.28 (0.19-0.38)	0.83	0.21 (0.16-0.26)	0.23 (0.16-0.31)
Mar-98	22	199	0.19 (0.11-0.27)	0.25 (0.12-0.41)	0.02	0.004 (0-0.01)	0.01 (0-0.01)
Apr-98	210	4	0.07 (0.02-0.11)	0.16 (0.05-0.38)	0.21	0.01 (0.01-0.02)	0.03 (0.01-0.08)
Mar-99	232	350	0.66 (0.59-0.73)	0.81 (0.71-0.89)	0.70	0.46 (0.41-0.51)	0.56 (0.49-0.62)
Apr-99	301	200	0.47 (0.41-0.54)	0.61 (0.51-0.70)	0.82	0.39 (0.34-0.44)	0.50 (0.41-0.58)
Mar-00	240	300	0.31 (0.25-0.36)	0.34 (0.26-0.43)	0.35	0.11 (0.09-0.13)	0.12 (0.09-0.15)
Feb-01	383	282	0.47 (0.41-0.52)	0.52 (0.43-0.61)	0.95	0.44 (0.39-0.50)	0.50 (0.41-0.58)
Apr-01	475	986	0.24 (0.20-0.28)	0.23 (0.19-0.28)	0.89	0.21 (0.18-0.25)	0.20 (0.16-0.25)
May-01	230	100	0.65 ^a (0.56-0.73)	0.86 ^a (0.73-0.95)	0.95	0.62 (0.54-0.69)	0.81 (0.69-0.91)

^a p is non-significant, therefore the null hypothesis of complete overlap is accepted.

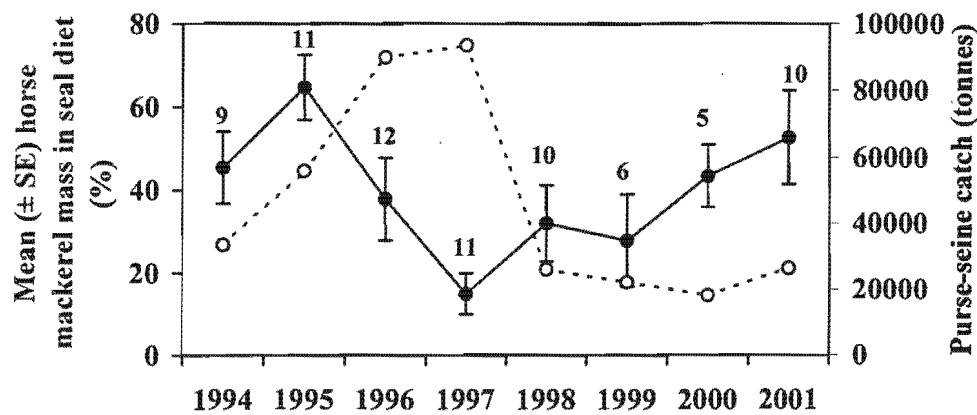


Figure 1. The mean $\pm$ standard error (SE) percentage mass (the number of months that each mean is based on is given above the error bar) of Cape horse mackerel *Trachurus trachurus capensis* in the diet of Cape fur seals *Arctocephalus pusillus pusillus* at the Cape Cross colony ($\bullet$), and the total catch of horse mackerel (tonnes) by the purse-seine fishery ($\circ$) in northern Namibia, for the period 1994 to 2001.

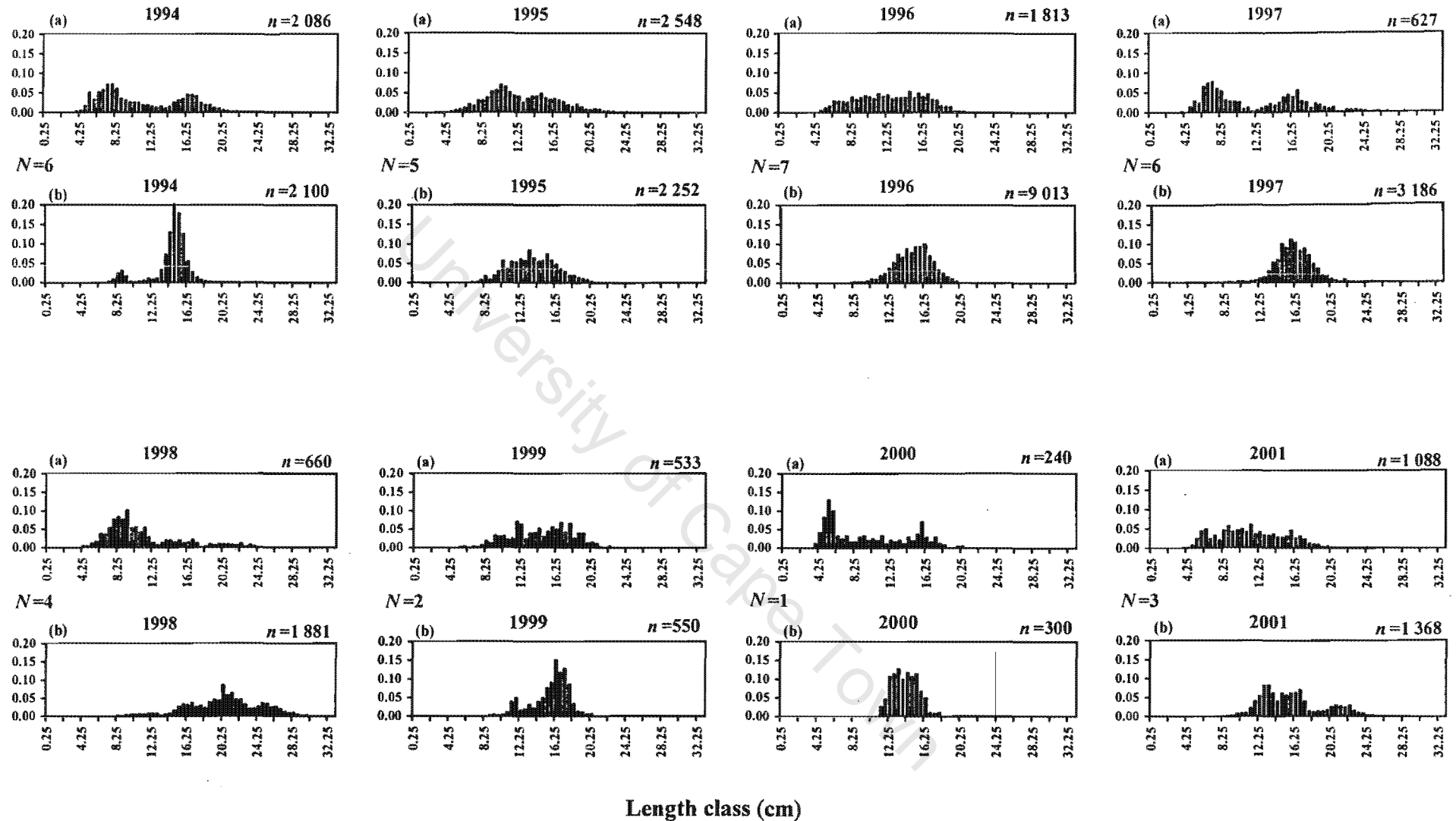


Figure 2. Length-frequencies of Cape horse mackerel *Trachurus trachurus capensis* in (a) the diet of Cape fur seals *Arctocephalus pusillus pusillus* at Cape Cross and (b) the purse-seine catches between 20 to 24°S, for the period 1994 to 2001, in northern Namibia. The number of otoliths or fish measured is given by n , and the number of months for which both seal and fishery resource utilization data was available is given by N .

Proportion horse mackerel in seal diet or fishery catch

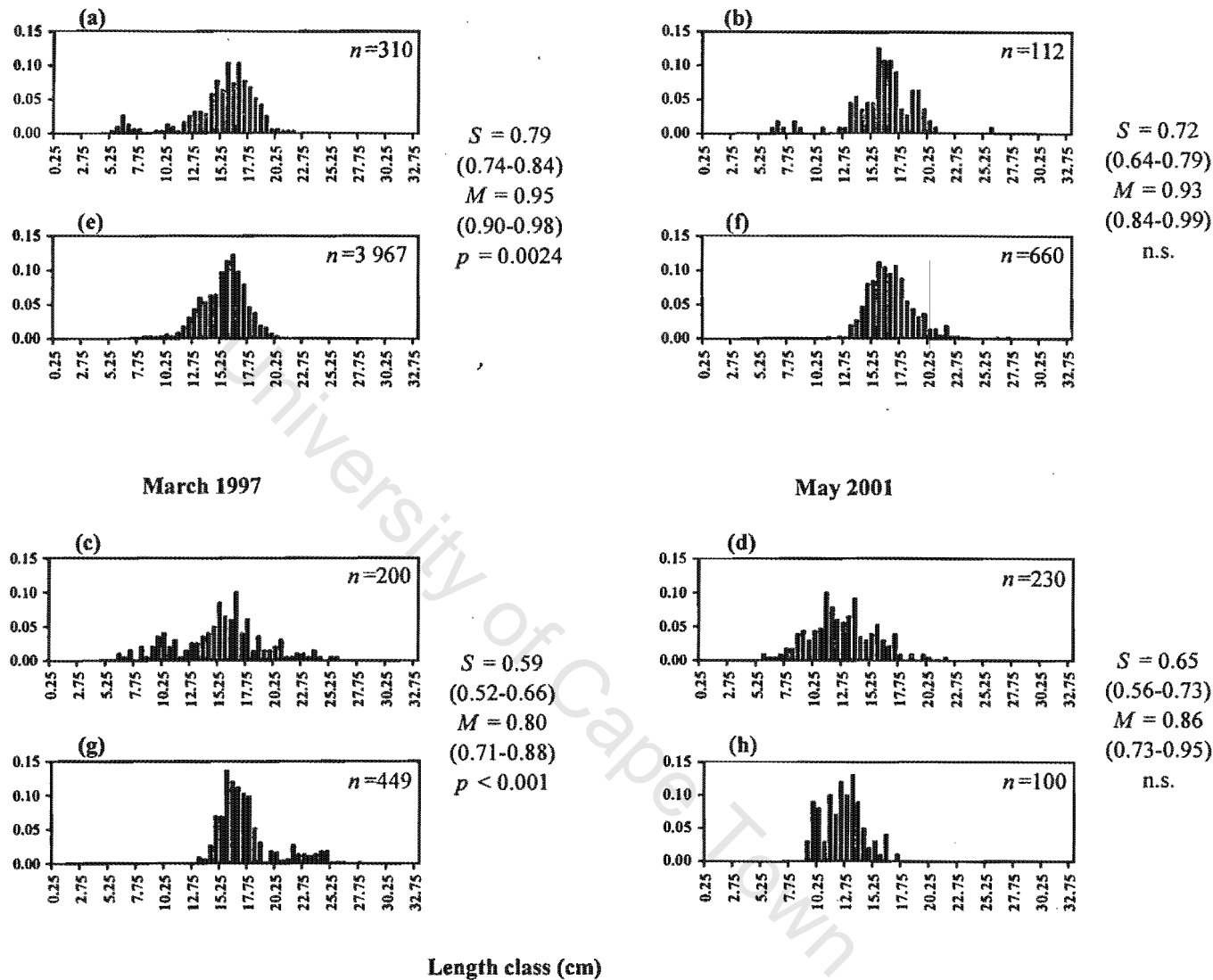


Figure 3. Length-frequency distributions for Cape horse mackerel *Trachurus trachurus capensis* (a-d) consumed by Cape fur seals *Arctocephalus pusillus pusillus* at Cape Cross and (e-h) caught by the purse-seine fishery in Namibia (20 to 24°S), for months when Morisita's overlap measure (M) was greater than 0.75. The seal and fishery sample sizes are given by n . Also presented for each month are Schoener's (S) and Morisita's (M) measures, each followed by their confidence interval in parenthesis, as well as the p -value for H_0 (observed overlap index could have originated from a distribution of fish lengths that was the same for both seals and fisheries).

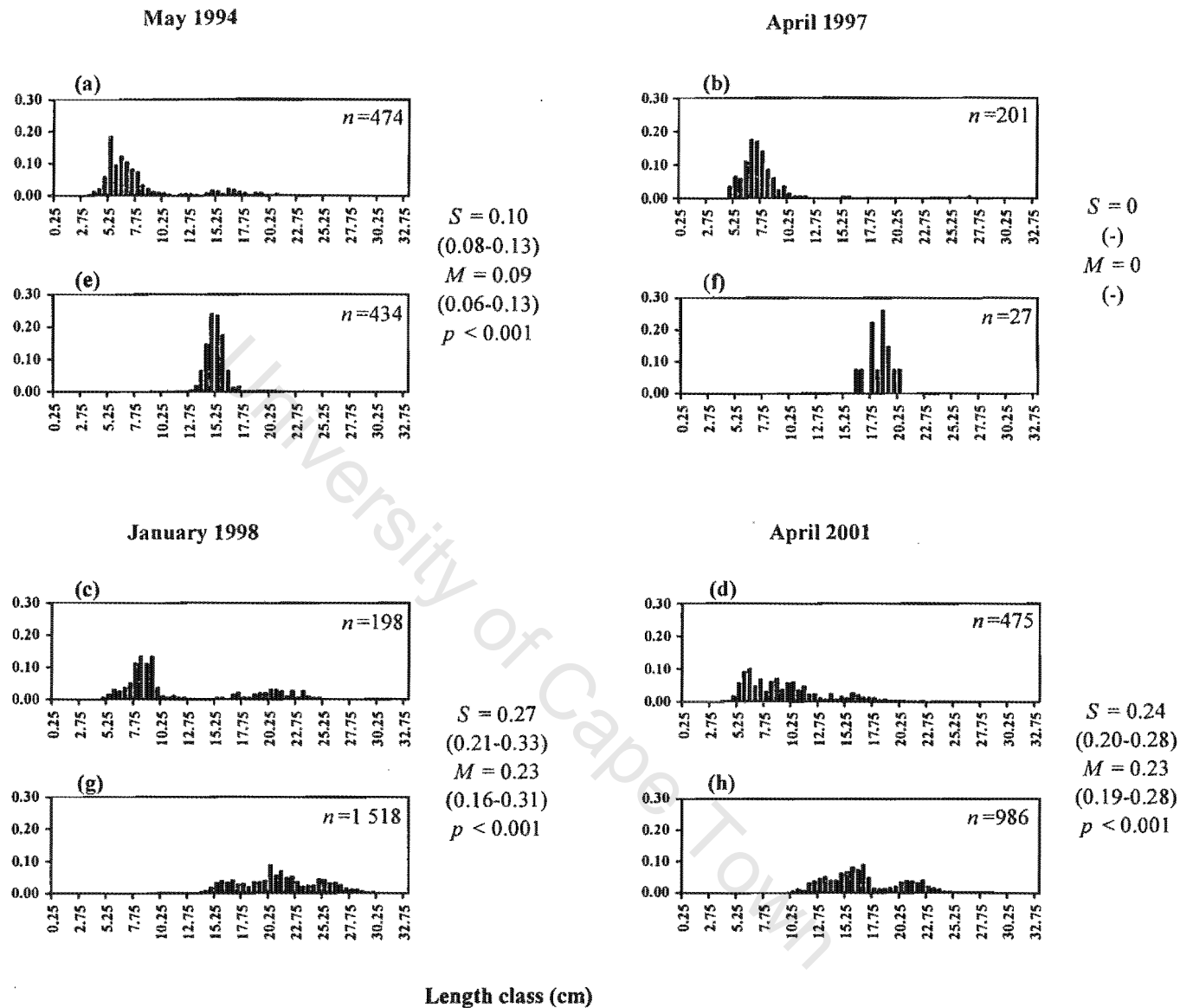


Figure 4. Length-frequency distributions for Cape horse mackerel *Trachurus trachurus capensis* (a-d) consumed by Cape fur seals *Arctocephalus pusillus pusillus* at Cape Cross and (e-h) caught by the purse-seine fishery in Namibia (20 to 24°S), for months when Morisita's overlap measure (M) was less than 0.25. The seal and fishery sample sizes are given by n . Also presented for each month are Schoener's (S) and Morisita's (M) measures, each followed by their confidence interval in parenthesis, as well as the p -value for H_0 (observed overlap index could have originated from a distribution of fish lengths that was the same for both seals and fisheries).

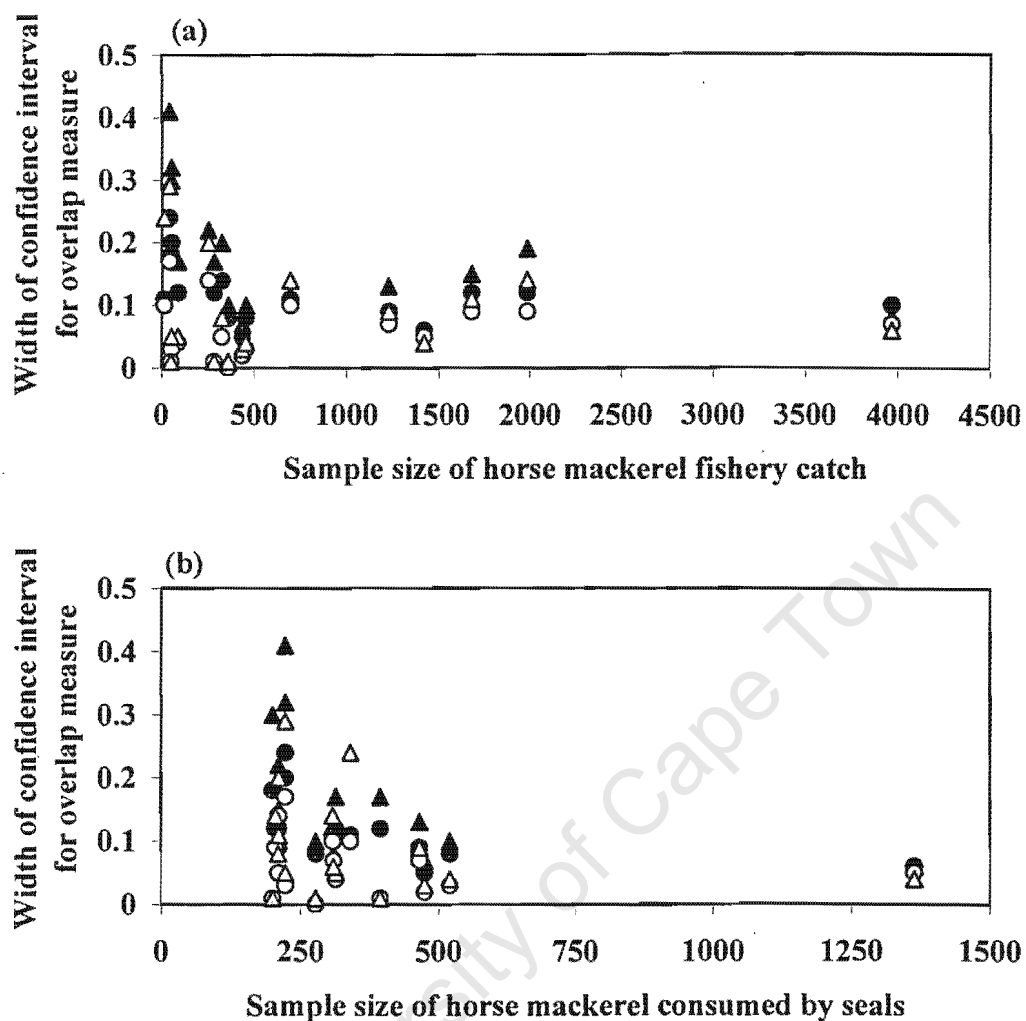


Figure 5. The relationship between the width of the confidence interval for each overlap measure (● Schoener's measure, ○ Schoener's adjusted measure, ▲ Morisita's measure, △ Morisita's adjusted measure) and the sample size of Cape horse mackerel *Trachurus trachurus capensis* measured from the (a) fishery catch and (b) from those consumed by Cape fur seals *Arctocephalus pusillus pusillus* at Cape Cross.

CHAPTER 6



University of Cape Town

Can seal diet predict future catches of commercial prey?

INTRODUCTION

The Cape horse mackerel *Trachurus trachurus capensis* is the most abundant harvested fish in the northern Benguela System (Axelsen *et al.* 2004) and has been exploited by purse-seine fisheries since 1971 (Boyer and Hampton 2001). Due to its commercial importance, the sound management of horse mackerel is important to ensure its sustainable utilization. Such management procedures depend on accurate estimates of stock size and information on fish age and growth. However, although Axelsen *et al.* (2004) argued that the errors involved in the hydro-acoustic abundance surveys of horse mackerel in the northern Benguela are well accounted for, the estimates are subject to several sources of bias (Barange *et al.* 1998, Bauleth-D'Almeida *et al.* 2001b, Boyer and Hampton 2001, Coetzee *et al.* 2001, Axelsen *et al.* 2003, Anon. 2003). Age and growth estimates for Namibia's horse mackerel stock are also inaccurate (Bauleth-D'Almeida *et al.* 2001b), thus stock assessments need to be treated with caution.

During hydro-acoustic surveys, which have taken place annually since 1990 in Namibia, trawls are conducted to estimate horse mackerel targets recorded by the hydro-acoustic system and to allow conversion of these recordings to numbers and biomass of fish per size group (length group). Biases introduced during the trawling operation include the fact that fish less than 10 cm in length are not caught representatively because they can escape through the mesh of the sample trawl. Number and biomass are thereby underestimated for this size group. At the opposite end of the size range, net avoidance by large horse mackerel biases the samples in favour of smaller fish (Bauleth-D'Almeida *et al.* 2001b). Consequently, length-frequency samples may not give a true reflection of the underlying population and no attempts have been made to produce a fishery-independent recruitment index from the hydro-acoustic surveys. All means of providing more accurate or reliable estimates of fish biomass or recruitment are valued by fishery management and the fishing industry.

Top predators in the marine environment, such as seals and seabirds, have been found to be reliable indicators of fish abundance (Sunada *et al.* 1981, Berruti and Colclough 1987, Montevecchi and Myers 1995, Reid 1995, Hunt *et al.* 1996, North 1996, Crawford 1998, Thompson *et al.* 1998, Brown *et al.* 2001, Barlow *et al.* 2002). The Namibian horse mackerel purse-seine fishery is operational mainly off northern Namibia (Axelsen *et al.* 2004), where the main concentration of juvenile horse mackerel is found (20°S to the southern border of Angola; Assorov *et al.* 1988, Krakstad and Kanandjembo 2001). A large Cape fur seal *Arctocephalus pusillus pusillus* colony exists in this area, at Cape Cross (21°47'S, 13°57'E; Fig. 1). Horse mackerel is an important prey item of seals at Cape Cross, usually comprising more than 50% of their diet during the period February to July (Chapters 2 and 3). Other important prey of seals at Cape Cross include hake *Merluccius capensis* and pelagic goby *Sufflogobius bibarbatus* (Chapter 2).

The aim of this study was to investigate the relationship between acoustic survey and purse-seine fishery biomass estimates of horse mackerel in the northern Benguela, and the proportion of this species in the diet of Cape fur seals, (a) to determine whether horse mackerel biomass consumed by seals reflects trends in the biomass of its stock, and (b) to investigate the development of a recruitment index of horse mackerel for the purse-seine fishery in Namibia using information from seal diets. Investigating these aims will assist in evaluating whether information from the diet of top predators, which is obtained inexpensively, can be used to complement fishery and survey data to improve models for the management of the horse mackerel resource.

MATERIAL AND METHODS

Comparisons between the proportion of horse mackerel in the seal diet, horse mackerel biomass estimates through acoustic surveys and horse mackerel catches by the purse-seine fishery were made for the period 1994-2002. A horse mackerel age-length key was used to age the fish in the seal diet (Anon. 2000; Table I). The year classes age-0, age-1 and age-2 refer to juvenile horse mackerel in their first, second and third years of life, respectively.

Seal diet

Seal scat samples were collected at Cape Cross (Fig. 1) between January 1994 and April 2002, at monthly intervals as far as possible (22 out of 100 months were missed). The scat processing protocol was described in detail in Chapter 2. Briefly, horse mackerel otoliths were removed from processed scats and counted. Otolith numbers were corrected for numbers lost during digestion, and otolith diameters were corrected for erosion (D. L. Millar *et al.*, Marine and Coastal Management (MCM), unpublished data). The diameters of at least 200 otoliths from each sample, or the entire sample when fewer than 200 otoliths were present, were measured to the closest 0.05 mm. Corrected otolith diameters were converted to fish lengths using the relationship of otolith diameter to fish total length for horse mackerel (Smale *et al.* 1995). The relative mass of horse mackerel in the seal diet was determined per monthly sample. The annual mean ($\pm$ standard deviation, SD) of the percentage mass of horse mackerel in the diet was used for comparisons.

The annual mean percentage mass of horse mackerel in the diet was divided into age-class proportions and these proportions were also used for comparisons. However, this assumes that horse mackerel is the preferred prey of Cape fur seals (Berruti and Colclough 1987). Such an assumption cannot be made because seals not only consume horse mackerel, but other prey as well, such as hake and goby, which were also important components of the diet of Cape fur seals at Cape Cross (Chapter 2). Thus the annual proportion of each age class of horse mackerel was corrected by the annual mean percentage horse mackerel mass in the diet. Length measurements were pooled per year, and annual length-frequency distributions were determined.

Hydro-acoustic surveys

The acoustic survey procedure was described by Bauleth-D'Almeida *et al.* (2001b). Surveys were carried out annually; in May or June from 1994 to 1998, and in January or February from 1999 onwards. Data collected within Namibian waters ($17^{\circ}15' - 26^{\circ}00'S$) were used to estimate annual horse mackerel biomass. Transects were placed parallel to lines of latitude and the spacing between transects was dictated by the density of Cape horse mackerel in the survey area during previous surveys. A Simrad 38 kHz 38B splitbeam transducer connected to a Simrad EK 500 echosounder was used during the surveys to collect acoustic data. The data were further analysed using the BEI (Bergen Echo Integrator, Foote *et al.* 1991) System, aboard the Norwegian *R.V.*

Dr. Fridtjof Nansen, or Sonardata Echoview[®], aboard the Namibian *R.V. Welwitschia*. Targeted trawling with a pelagic, or especially in shallow waters, a bottom trawl, identified acoustic targets. Length-frequencies and biological samples of the target species in the catch were sampled to convert the recorded backscattered energy from the echosounder to numbers of fish per length group and biomass per length group. The annual biomass of horse mackerel determined by acoustic surveys was compared to the annual mean percentage mass of horse mackerel in the seal diet.

Purse-seine catches

The purse-seine fisheries were most active in Namibian waters from February to April each year (Fig. 2a). This period overlapped with the time of year when seals consumed the largest proportions of horse mackerel (Fig. 2b). No fishing occurred from around October to December. During this period horse mackerel consumption by seals was low. Fishery activities were mainly concentrated in northern Namibian waters from 18°S to 24°S (Fig. 1) (Namibian Ministry of Fisheries and Marine Resources (MFMR), unpublished data). Random sub-samples of 50 fish were taken from purse-seine catches once they were landed. The total lengths of these fish were measured to the nearest 0.5 cm and they were weighed to the nearest 0.1 g (Bauleth-D'Almeida *et al.* 2001b). The length-frequencies obtained from these samples were pooled for each month and converted to the total number of fish in the monthly catch from the purse-seine fleet, using the total weight of all landings for that month divided by the weight of the samples as conversion factor, as follows:

$$N_{l_j} = \sum_{i=1}^x n_{(s_i, l_j)} \times \frac{W_T}{\sum_{i=1}^x W_{s_i}} \quad (\text{Eqn 1})$$

where N_{l_j} is the total number of fish caught in length group j in a particular month, s_i is sample i from the purse-seine fleet ($i = 1, 2, \dots, x$), l_j is length group j ($j = 1, 2, \dots, y$), $n_{(s_i, l_j)}$ is the number of fish in sample i for length group j , W_T is the total weight of all landed fish in a month, and W_{s_i} is the weight of each sample s_i .

The annual catch of horse mackerel by the purse-seine fleet, lagged by zero to three years, was compared to the annual mean percentage mass of horse mackerel in the seal diet at Cape Cross, as well as to the proportion of age-0, age-1 and age-2 horse mackerel in the horse

mackerel portion of the seal diet. The annual purse-seine catch, lagged by zero to four years, was compared to the annual proportion of age-0 and age-1 horse mackerel in the seal diet corrected by the annual percentage mass of horse mackerel in the diet.

RESULTS

The size of fish from acoustic surveys ranged from 2 - 44 cm, but most fish surveyed were juveniles less than 20 cm in length (Fig. 3a; Bauleth-D'Almeida *et al.* 2001b). Purse-seine fisheries caught fish within the range of 5 - 32 cm and most fish caught had a modal length of 14 - 16 cm (Fig. 3b), corresponding with age-2 fish (Table I). The estimated size of horse mackerel consumed by seals ranged from 3 - 33 cm, but most fish consumed had modal lengths at 5 - 7 cm (age-0), 8 - 11 cm (age-1), and 14 - 16 cm (age-2) (Fig. 3c; Table I).

Horse mackerel biomass in relation to seal diet

From 1994 to 1997, the annual biomass of horse mackerel determined by acoustic surveys and the annual mean percentage mass of horse mackerel in the seal diet followed similar trends (Pearson's product-moment correlation $r = 0.87$, $p = 0.13$, $n = 4$; Fig. 4a). From 1997 to 2002, the relationship between the two was poor ($r = 0.08$, $p = 0.88$, $n = 6$). For the entire period the correlation between horse mackerel biomass from acoustic surveys and horse mackerel percentage mass in the diet was weak ($r = 0.14$, $p = 0.73$, $n = 9$). The correlation between annual acoustic biomass estimates and the mean percentage mass of horse mackerel during the months when the surveys took place, May and June (1994 to 1998) and January and February (2001 and 2002; no scats were collected during these months for 1999 and 2000), was stronger ($r = 0.35$, $p = 0.44$, $n = 7$; Fig. 4b).

Purse-seine fishery catches versus seal diet

The annual catch of horse mackerel by the purse-seine fisheries lagged the annual mean percentage of horse mackerel mass in the seal diet by one to two years (Fig. 5). The correlation between the annual purse-seine fishery catch, lagged by one and two years, and the annual mean percentage mass in the diet was strong (Table II). When the horse mackerel component of the seal diet was broken down into age classes (0, 1 and 2), there was little correlation between

annual proportions of these age classes in the diet and the annual total catch by the purse-seine fisheries lagged by zero to three years (Table II). However, once the annual proportions of each of these age classes in the seal diet were corrected by the annual mean percentage mass of horse mackerel in the diet, relationships became evident. The corrected proportion of age-0 horse mackerel in the seal diet was strongly correlated with the purse-seine catch lagged by two years ($r = 0.88$, $p = 0.009$, $n = 7$; Figs 6a and 6b), and the corrected annual proportion of age-1 horse mackerel in the diet was strongly correlated with the purse-seine catches lagged by one and two years ($r = 0.54$, $p = 0.17$, $n = 8$, and $r = 0.70$, $p = 0.08$, $n = 7$, respectively; Fig. 7).

DISCUSSION

Horse mackerel in the seal diet versus survey estimates

The relationship between the annual mean percentage horse mackerel mass in the diet of seals from Cape Cross and the acoustic survey biomass estimates was weak, and could be due to several factors. Firstly, a proportion of horse mackerel detected by the surveys could have been beyond the foraging range of seals and thus unavailable as prey. Cape fur seals forage within 220 km from the colony (Shaughnessy 1985; Fig. 1) and dive to a mean depth of 50 m (Kooyman and Gentry 1986), and fish outside this range would be of reduced accessibility.

Secondly, inconsistent scat sampling in some of the latter years may have contributed to the poor correlation observed. For instance, in 1999 and 2000, scat samples were not collected during the summer (December to February) and winter (June to August) periods. The availability of horse mackerel to seals is greatest in summer when they aggregate in dense patches over the continental shelf (Krakstad and Kanandjembo 2001), as opposed to winter when they are more dispersed and juvenile fish probably move further from the coast (Assorov *et al.* 1988). This is because fish that occur in dense groups are encountered and captured more easily by seals than are dispersed fish (Bowen and Harrison 1996). It should be noted that scats were not collected in January 2001. Because the proportion of horse mackerel in the seal diet usually increases from January to February at Cape Cross (Fig. 2b), this may have contributed to the disproportionately high percentage of horse mackerel in the seal diet for 2001 relative to the acoustic survey estimate (Fig. 4b).

Thirdly, the timing of the acoustic survey period was shifted after 1998, from May/June (winter) to January/February (summer). At the same time, the survey vessel was replaced by another with different gear dimensions (Bauleth D'Almeida *et al.* 2001b). Additionally, the mesh size of the trawl net used biased the survey to fish greater than 10 cm in length. Moreover, juvenile horse mackerel occupy the upper part of the water column within very shallow waters making identification on the echosounder a problem (Axelsen *et al.* 2004).

Alternatively, the poor correlation may be a result of the surveys taking place only once a year (Bauleth D'Almeida *et al.* 2001b). Seal diets were sampled on a monthly basis throughout the year, and were therefore more sensitive to seasonal changes in horse mackerel abundance. The stronger relationship between acoustic survey estimates of horse mackerel biomass and the average percentage mass of horse mackerel in the seal diet during the months when the acoustic surveys were carried out (Fig. 4b) suggests that diet sampling can reflect trends in acoustic estimates for comparable time periods. However, further data is required to determine if this relationship holds over a longer time period.

Finally, the acoustic estimate or the scat analysis may have been erroneous. Because of the errors embedded in acoustic surveys (Anon. 2003, Axelsen *et al.* 2004), the method arguably renders a poor absolute estimate of population biomass. However, most errors are well accounted for (see Axelsen *et al.* 2004). Results of acoustic surveys are therefore inferred to reflect trends in population biomass. Scat analysis is also not without its own set of biases (see Chapter 8, Discussion), which is based on the assumption that the relative abundance and mass of prey consumed is reflected by that estimated from hard part remains in scats (Tollit *et al.* 1997). Otoliths that are recovered are partially eroded in length and width due to their exposure to gastric fluids (Da Silva and Neilson 1985, Dellinger and Trillmich 1988). Above all, only some of the ingested otoliths are recovered in scats (Pierce and Boyle 1991); small otoliths are especially prone to being eroded completely during digestion. For this study, the loss and erosion of horse mackerel otoliths during digestion were corrected for using correction factors determined during Cape fur seal captive feeding trials (D. L. Millar *et al.*, MCM, unpublished data). This improves the accuracy of horse mackerel abundance and mass estimates from seal scats (Tollit *et al.* 1997, Cottrell and Trites 2002).

Recruitment index for horse mackerel from the seal diet

Cape fur seals consume juvenile horse mackerel from age-0 to age-2 (Chapter 5). The fact that horse mackerel begin recruiting into the fishery at age-1 (Hecht 1990) explains the correlation of horse mackerel in the diet to the catch lagged by one year. However, purse-seiners mainly target juveniles 12.5 to 20.0 cm in length (Bauleth-D'Almeida *et al.* 2001b), which corresponds mostly with age-2 juveniles, resulting in the stronger correlation observed between horse mackerel in the diet and the catch lagged by two years.

Once the proportion of horse mackerel in the seals' diet was broken down into age classes and corrected by the annual mean percentage contribution of horse mackerel to the diet, the strongest relationship found was between the age-0 cohort of horse mackerel in the seal diet and the purse-seine catch two years later. The age-0 cohort of horse mackerel in the diet explained about 88% of the variation in the purse-seine catch lagged by two years. This is of applied importance considering all the uncertainties in the methods discussed above, and including the reliability of purse-seine catch estimates and sampling of the catch composition. The purse-seine fishery acts under a catch restriction, which requires that an area should be vacated or closed if the percentage of horse mackerel smaller than 12.5 cm in total length exceeds 5% per set by weight (MFMR 2002). This is to prevent the excessive removal of growing individuals from the population.

Mecenero and Roux (2002) suggested that studying the diet of a predator can provide quantitative information which can be used in managing the hake stock. They showed that the numerical abundance of juvenile hake in the Cape fur seal diet reliably predicts the cohort strength measured a year later by demersal surveys, and that hake growth during their pelagic phase is well estimated by hake length-frequency distributions over time for each cohort in the seal diet.

Although this study was based on a short time series of scat sampling and catch statistics, the findings are promising enough to warrant further investigation, because scat sampling is an inexpensive method and provides information which can be used in management models for the horse mackerel resource.

Implications for the management of the horse mackerel resource

Although scat analysis has biases, it does provide information on the temporal trends in the main prey consumed by seals (Tollit and Thompson 1996). Studies of the diets of top predators in the marine environment, such as seabirds, have produced useful indices of prey abundance and availability (Montevecchi 1993). For instance, the proportion of anchovy *Engraulis capensis* and sardine *Sardinops sagax* in the diet of Cape gannets *Morus capensis* proved to be a reliable indicator of abundance estimates of these fish as determined by surveys (Crawford 1998), and the proportion of Antarctic krill *Euphausia superba* in Macaroni penguin *Eudyptes chrysolophus* diets was positively correlated to acoustic survey estimates of krill density (Barlow *et al.* 2002). Berruti and Colclough (1987) found a significant correlation between the annual mean percentage of sardine in the Cape gannet diet and total catches of sardine. The diet of common murre *Uria aalge* chicks indicated a shift in capelin *Mallotus villosus* size to smaller fish, which was supported by fisheries data (Davoren and Montevecchi 2003). The diet of Atlantic puffin *Fratercula arctica* chicks proved to be a good indicator of fish availability for three species of fish prey (Barrett 2002). Diet data of top predators can therefore be used to complement data obtained by surveys in stock assessments (Montevecchi 1993).

Despite some known flaws in the acoustic method (Axelsen *et al.* 2004), the methodological challenges involved in surveying Cape horse mackerel in Namibia are reasonably well understood. The method has so far been effective in Namibia, by providing management with the only fishery-independent index of horse mackerel abundance and, together with commercial catches, providing sound advice on the level of fishing pressure. In addition, this method has provided information on the behaviour and ecology of the horse mackerel stock.

Being able to predict the recruitment of horse mackerel into the fishery two years earlier than is possible using conventional acoustic survey strategies or by monitoring purse-seine catches, has obvious benefits for fisheries science and management. Biomass estimates from various survey methods should be combined to obtain a more accurate indication of horse mackerel abundance (Barange *et al.* 1998). Thus in Namibia, once the accuracy of these results have been established over a longer time series, information gained from seal diets could supplement the acoustic data in the stock assessment models to improve their reliability. However, as this study has shown, care should be taken that data covering similar time periods within a year be used, because this seems to improve the value of the data.

Table I. The age classes for modal lengths observed in Cape fur seal *Arctocephalus pusillus pusillus* diets compared with those determined during a Cape horse mackerel *Trachurus trachurus capensis* ageing workshop based on otolith readings (Anon. 2000).

Age Class	Modal lengths (cm)	
	Ageing workshop	Seal diet
0	-	5.25 – 7.75
1	11.0	8.75 – 11.75
2	17.6	14.75 – 16.75
3	23.3	20.25 – 22.25
4	27.2	24.75

Table II. The correlation (r , Pearson's product-moment correlation) between the annual total catch of Cape horse mackerel *Trachurus trachurus capensis* by purse-seine fisheries, lagged by zero to three years, and the annual percentage mass of horse mackerel in the diet of Cape fur seals *Arctocephalus pusillus pusillus*, as well as to the proportion of age-0, age-1 and age-2 horse mackerel in the horse mackerel portion of the diet. Significant correlations at $p < 0.05$ are indicated by an asterisk.

Lag of annual purse-seine fishery catch (years)	r			
	Annual percentage horse mackerel in the diet	Annual proportion age-0 horse mackerel	Annual proportion age-1 horse mackerel	Annual proportion age-2 horse mackerel
0	-0.35	0.22	-0.66	0.46
1	0.67	-0.16	0.00	0.26
2	0.84*	0.32	-0.03	-0.48
3	0.15	0.48	-0.17	-0.58

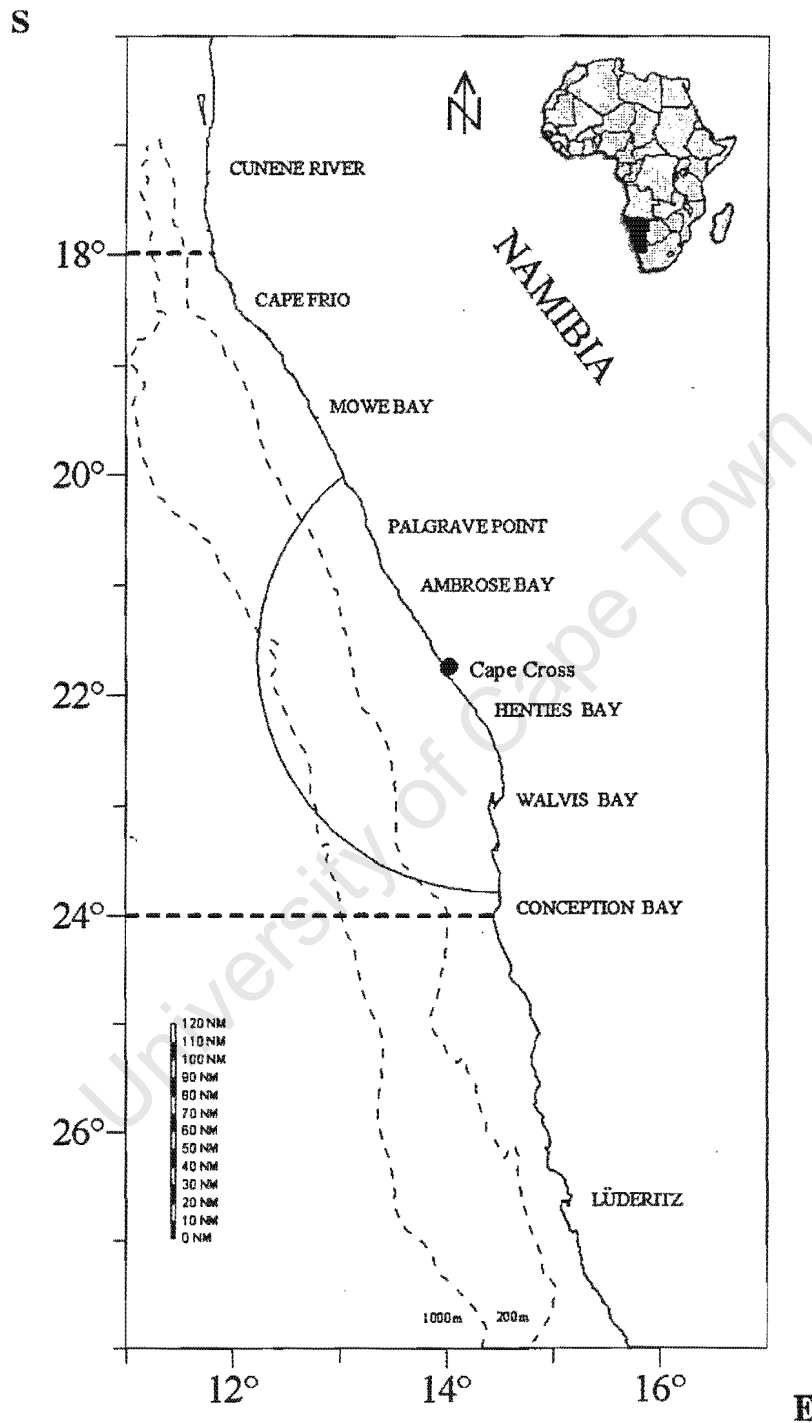


Figure 1. A map of the Namibian coast showing the location of the Cape Cross colony and the approximate foraging range of Cape fur seals *Arctocephalus pusillus pusillus*. The purse-seine fishery operated within the horizontal dashed lines. The 200 m and 1 000 m depth lines are shown.

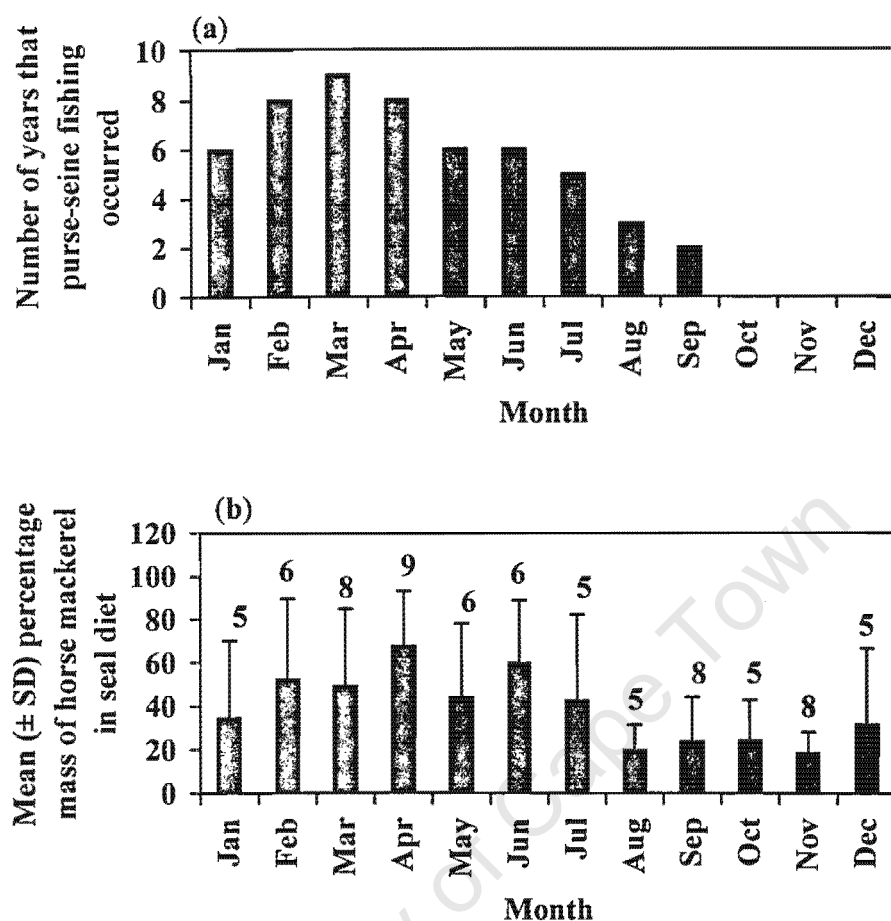


Figure 2. Monthly distribution from 1994 to 2002 of (a) the occurrence of the Cape horsed mackerel *Trachurus trachurus capensis* purse-seine fishing industry in Namibia and (b) the mean ($\pm$ standard deviation, SD) percentage mass of horse mackerel in the diet of Cape fur seals *Arctocephalus pusillus pusillus* at Cape Cross as determined from scat analysis. The number of years is given above the error bars.

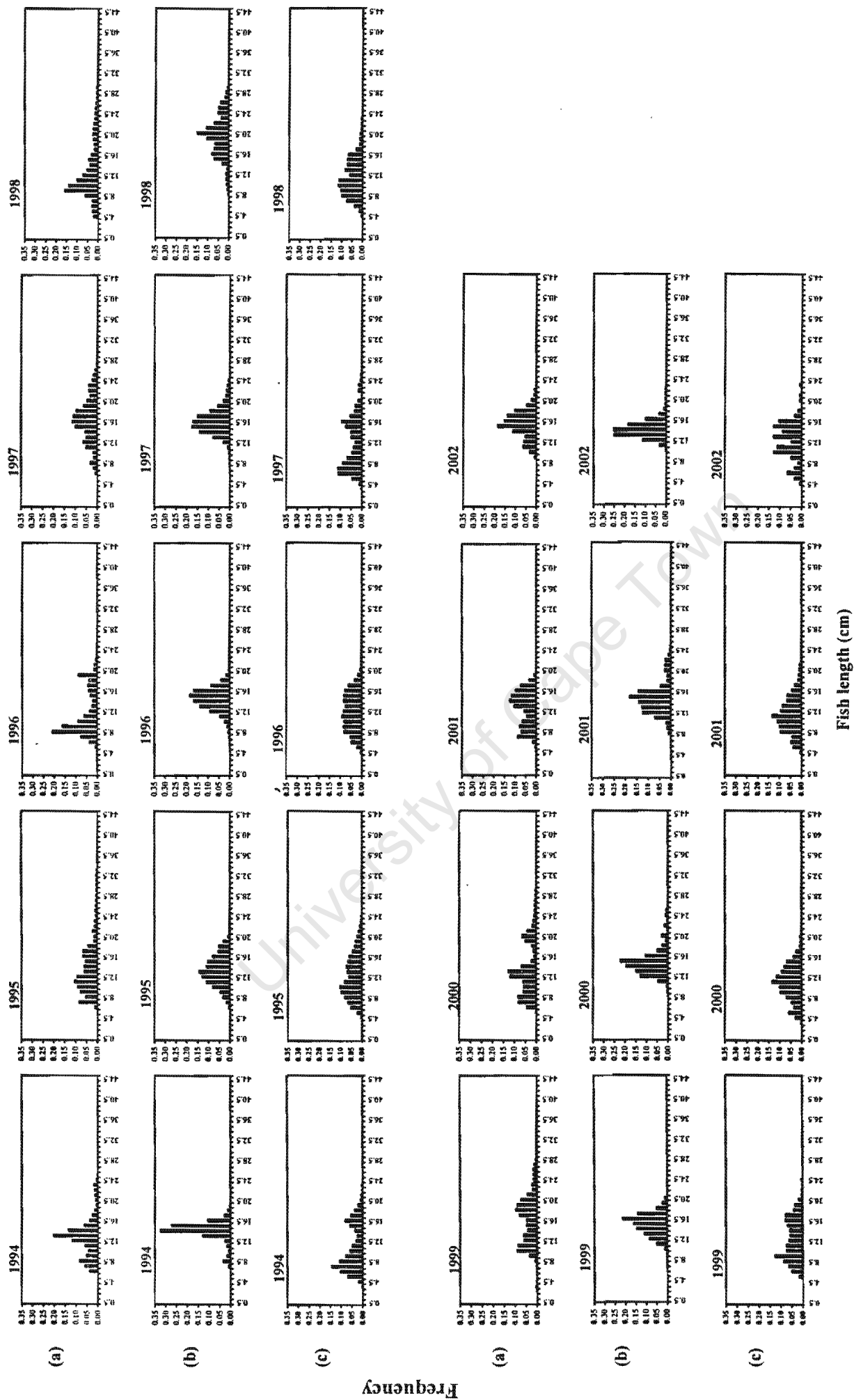


Figure 3. Annual length-frequency distributions of Cape horse mackerel *Trachurus trachurus capensis* in Namibia from (a) acoustic surveys, (b) purse-seine fisheries, and (c) the diet of Cape fur seals *Arctocephalus pusillus pusillus* from Cape Cross colony, from 1994 to 2002.

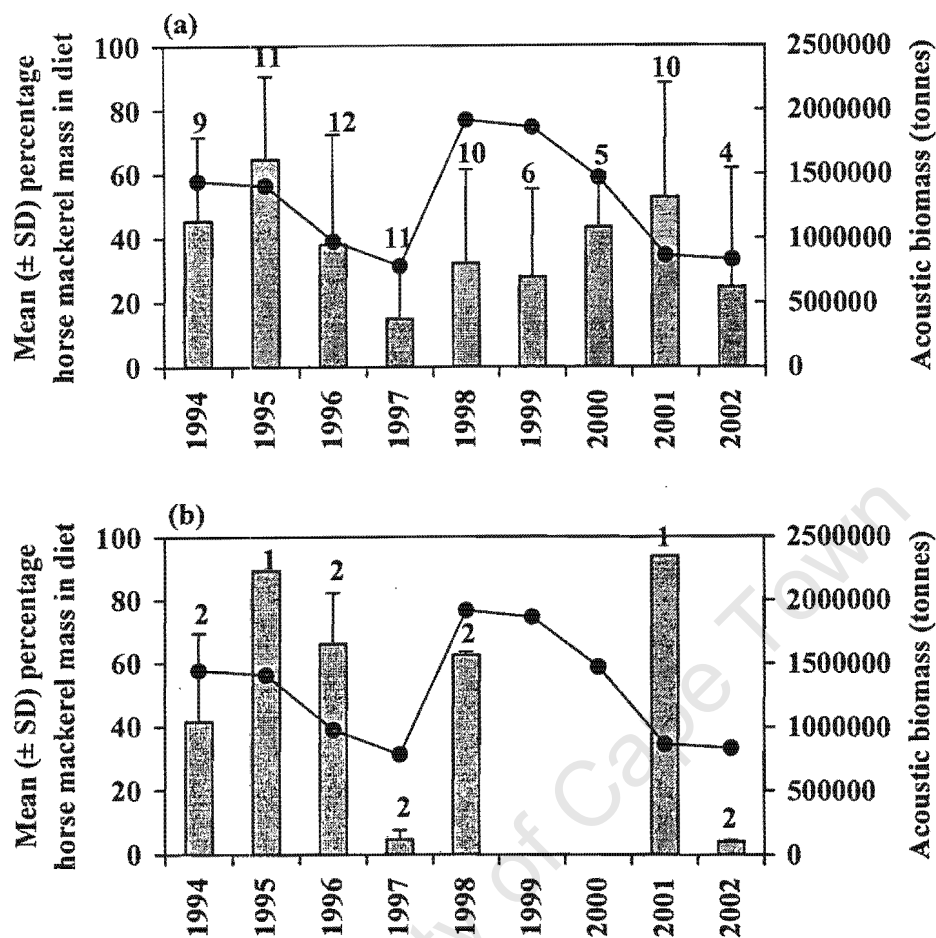


Figure 4. The annual biomass of Cape horse mackerel *Trachurus trachurus capensis* determined by acoustic surveys (line) in Namibia and the mean ($\pm$ standard deviation, SD) percentage mass of horse mackerel in the Cape fur seal *Arctocephalus pusillus pusillus* diet (bars) at Cape Cross for (a) the percentage mass of horse mackerel in the seal diet over all months within years and (b) the percentage mass of horse mackerel in the seal diet for May and June (1994 to 1998) and January and February (1999 to 2002), the months when acoustic surveys took place. Exceptions are 1995 and 2001 where the contribution of horse mackerel to the seal diet was only known for June and February, respectively. No seal diet samples were collected in January and February of 1999 and 2000. The number of months are given above the error bars.

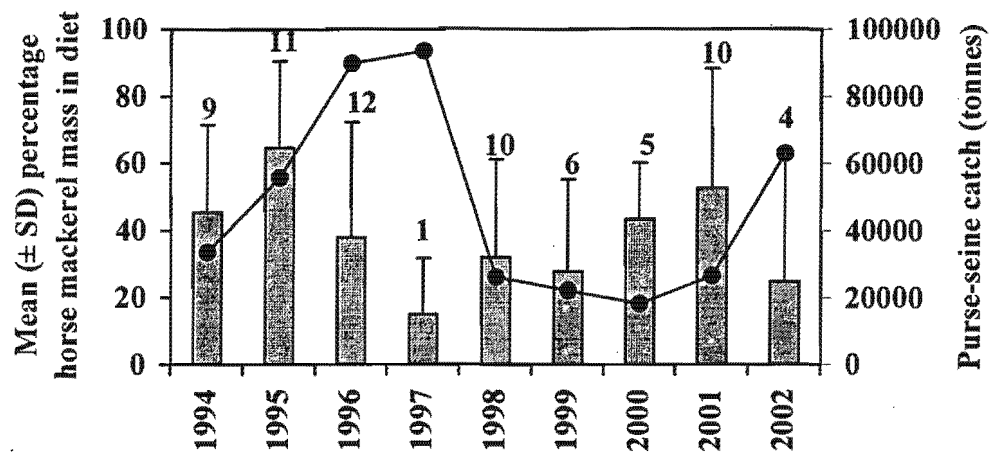


Figure 5. The annual catch of Cape horse mackerel *Trachurus trachurus capensis* by the Namibian purse-seine fisheries (line) and the mean ($\pm$ standard deviation, SD) annual percentage mass of horse mackerel in the Cape fur seal *Arctocephalus pusillus pusillus* diet (bars) at Cape Cross, with the number of months above the error bars.

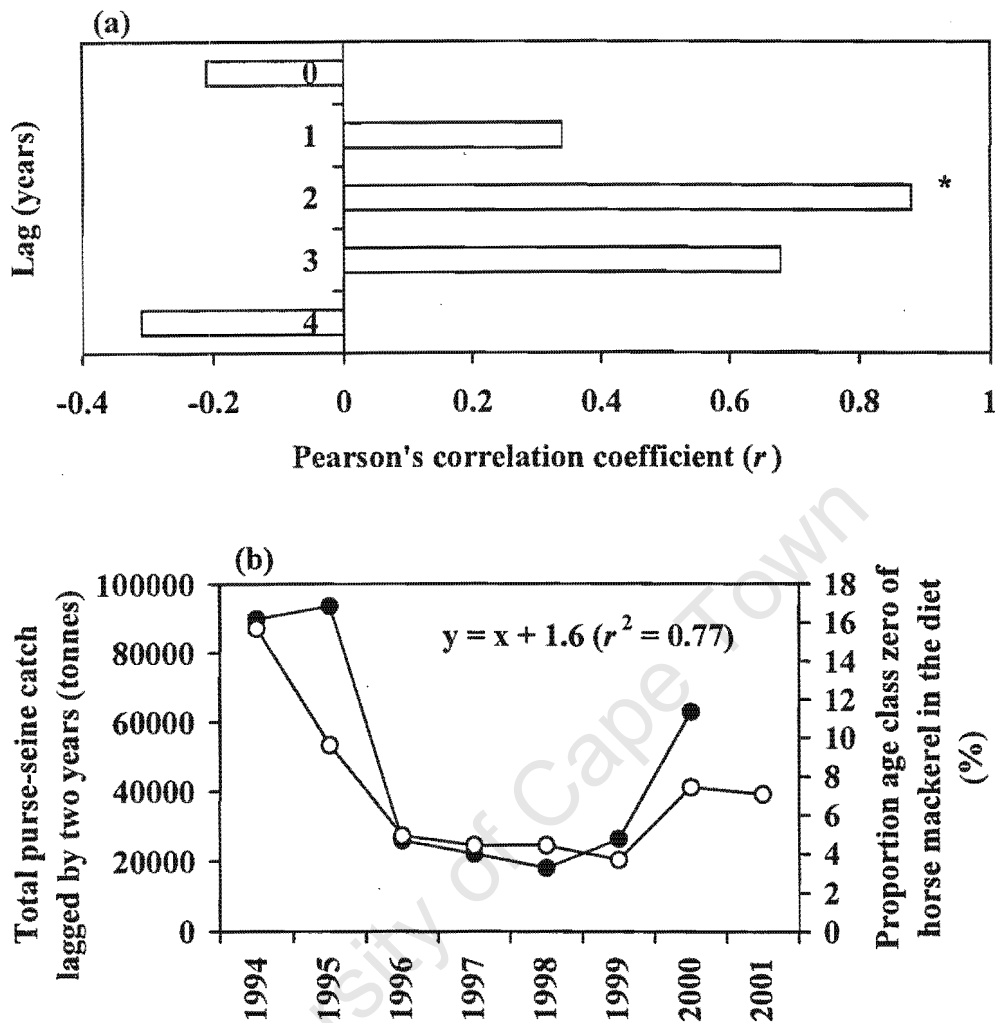


Figure 6. (a) Correlogram of Pearson's correlation coefficient for the relationship between the annual total catch of Cape horse mackerel *Trachurus trachurus capensis* by the purse-seine fishery, lagged by zero to four years, and the annual corrected proportion of age-0 horse mackerel in the Cape fur seal *Arctocephalus pusillus pusillus* diet. Correlations significant at $p < 0.05$ are marked by an asterisk. (b) The annual catch of horse mackerel by the purse-seine fisheries (●) lagged by two years, compared to the annual proportion of age-0 horse mackerel in the seal diet corrected by the percentage mass contribution of horse mackerel to the diet (○). The straight line equation for the correlation between the two lines is given.

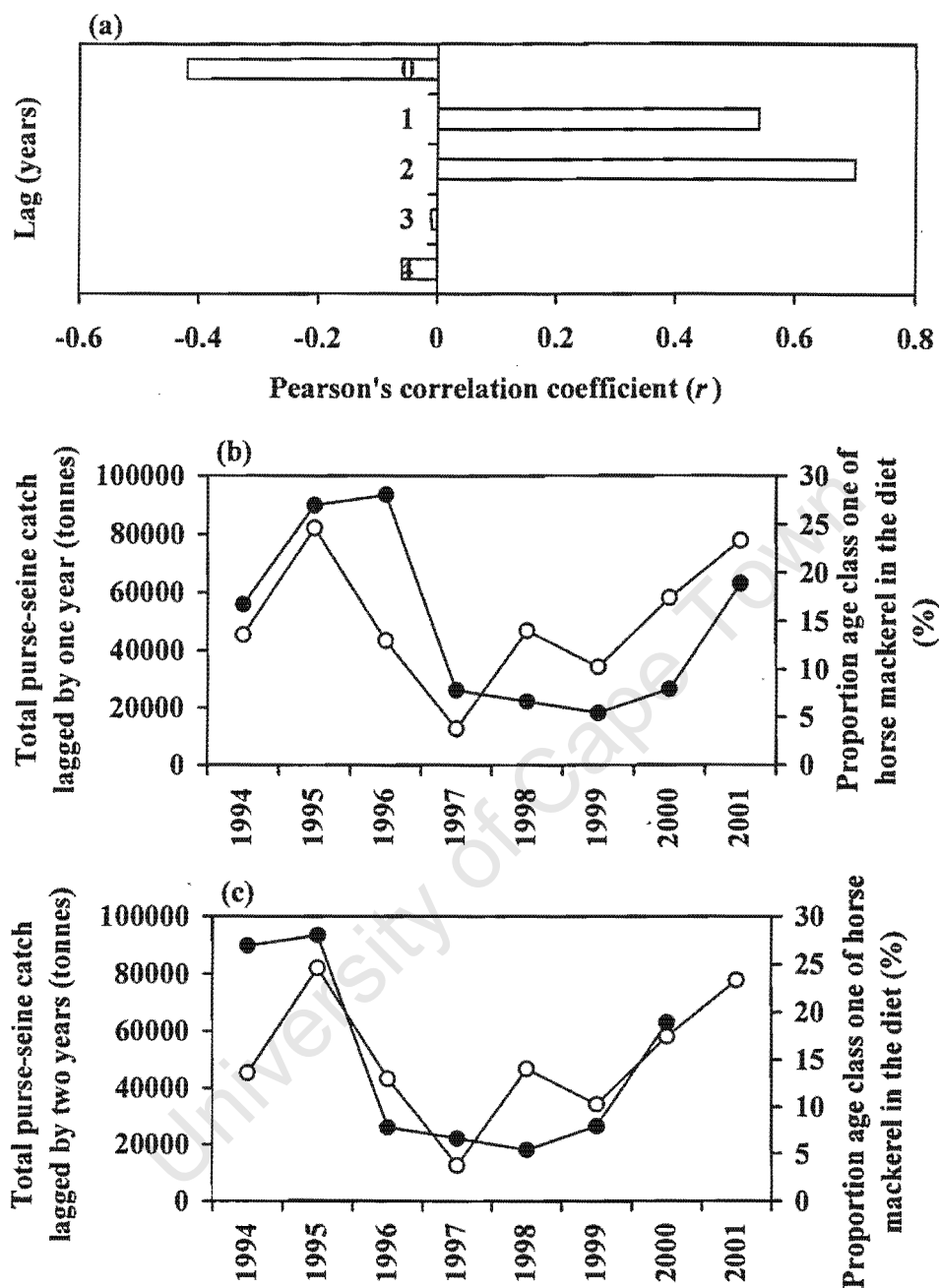


Figure 7. (a) Correlogram of Pearson's correlation coefficient for the relationship between the annual total catch of Cape horse mackerel *Trachurus trachurus capensis* by the purse-seine fishery, lagged by zero to four years, and the annual corrected proportion of age-1 horse mackerel in the Cape fur seal *Arctocephalus pusillus pusillus* diet. None of the correlations were significant at $p < 0.05$. The annual catch of horse mackerel by purse-seine fisheries (●) lagged by (b) one and (c) two years, and compared to the annual proportion of age-1 horse mackerel in the seal diet corrected by the annual mean percentage mass of horse mackerel in the diet (○).

CHAPTER 7



University of Cape Town

Occurrence of seabirds in the diet of Cape fur seals *Arctocephalus pusillus pusillus* at three mainland breeding colonies in Namibia

INTRODUCTION

Cape fur seals *Arctocephalus pusillus pusillus* are known to prey upon seabirds such as African penguins *Spheniscus demersus*, Cape gannets *Morus capensis*, Cape cormorants *Phalacrocorax capensis*, crowned cormorants *P. coronatus* and bank cormorants *P. neglectus* (Cooper 1974, Shaughnessy 1978, Rebelo 1984, Marks *et al.* 1997, Navarro 2000, Crawford *et al.* 2001, David *et al.* 2003, Du Toit *et al.* 2004). Predation of seabirds (mainly penguins) by other otariids (Hofmeyr and Bester 1993, Thompson *et al.* 1998, McMahon *et al.* 1999, Childerhouse *et al.* 2001), and less commonly by phocids (Lawson *et al.* 1995, Rogers and Bryden 1995, Copley and Bell 1998), has also been documented. In the case of otariids (fur seals and sea lions), it is generally believed that a few individuals (usually males) within populations are responsible for the bulk of attacks on seabirds, and that seabirds feature negligibly in the overall diet of these populations (Bonner and Hunter 1982, McMahon *et al.* 1999, Childerhouse *et al.* 2001, Du Toit *et al.* 2004).

The populations of three of the seabird species taken by Cape fur seals, namely the African penguin, Cape gannet and bank cormorant, have been classified as Vulnerable (Barnes 2000). Seal predation of African penguins could lead to the extinction of small penguin colonies in the near future (Crawford *et al.* 2001). In Namibia, important seabird colonies are located within the foraging ranges of three large Cape fur seal breeding colonies (Fig. 1). This study investigates whether seabirds are included in the diet of fur seals from these colonies, by analyzing scats found at the colonies.

MATERIAL AND METHODS

Scat samples were collected monthly at three breeding colonies on the Namibian mainland: Van Reenen Bay (27°23'S, 15°21'E), Atlas and Wolf Bay (26°49'S, 15°08'E and 26°48'S,

15°07'E, respectively) and Cape Cross (21°47'S, 13°57'E; Fig. 1), from February 2001 to April 2002. The Atlas and Wolf Bay colonies were considered as one colony because they are only one kilometer apart. At each colony, approximately 60 fresh, whole scats were collected each month. No loose feathers adhered to the scats as they were collected. The scat samples were washed in containers under running water. The rinsed material was passed through nested stainless steel laboratory test sieves (apertures of 2.0, 1.0, 0.425 and 0.212 mm), and the remaining material was dried overnight in an oven (~ 50°C). The presence or absence of feathers in the dried matter of a sample was noted, and the monthly percentage frequency of occurrence of feathers determined. Percentage frequency of occurrence is defined as the percentage of scats in a month that contained feathers. Feathers were identified by comparison with the seabird reference collection at the Natural History Division of the Iziko Museums (Cape Town, South Africa).

RESULTS AND DISCUSSION

Over the entire study period, approximately 900 scats were collected at each study colony. No feathers were found in scat samples from the Van Reenen Bay and Atlas-Wolf Bay colonies. Only two individual scats from Cape Cross, one collected during July 2001 and the other during August 2001, contained feathers, each with a frequency of occurrence of less than two percent. The feathers were identified as belonging to an African penguin of unidentified age and a juvenile cormorant (either *P. capensis* or *P. neglectus*), respectively. Over the entire study period, therefore, the occurrence of seabird feathers found in the scats was negligible (Table I).

Feathers are known to pass through the gut of seals, as a number of previous studies have documented predatory interactions between seals and seabirds based on the presence of feathers in scats (Bonner and Hunter 1982, Green *et al.* 1989, Daneri and Coria 1992, Rogers and Bryden 1995, Casaux *et al.* 1998, Thompson *et al.* 1998, Childerhouse *et al.* 2001). However, if seals regurgitate indigestible prey items, the occurrence of seabird remains in the scats will be underestimated (Pierce and Boyle 1991). Antarctic fur seals *Arctocephalus gazella*, for instance, have been seen to regurgitate penguin feathers (Bonner and Hunter 1982, Kirkman *et al.* 2000) as well as skin (Bonner and Hunter 1982). In this study, only one regurgitate, containing only cephalopod beaks, was found in any of the colonies, and no seals were observed regurgitating (S. M., pers. obs). This is in contrast to Rand's (1959) regular observations of Cape fur seals regurgitating along the South African west coast. Most likely

then, the paucity of feathers found in scats during this study reflects that seabirds featured negligibly in the diet of the seals defecating at the study colonies.

The determination of seal diet from scat analysis is potentially subject to biases (see Chapter 8, Discussion), including that the scats found on land may represent only the last meals eaten by seals before hauling out (Dellinger and Trillmich 1999). Furthermore, adult male seals are only found in large numbers at breeding colonies from October until January (Rand 1959). During this period males spend much of their time fasting (Rand 1959). Scat samples from breeding colonies therefore largely reflect the diet of adult females, the majority of which regularly alternate foraging trips to sea with shore visits throughout most of the year. This may contribute to the rarity of scats containing feathers found in this study, because most records of predation on seabirds by fur seals and sea lions implicate males (Bonner and Hunter 1982, McMahon *et al.* 1999, Childerhouse *et al.* 2001). Du Toit *et al.* (2004) found that subadult male Cape fur seals were responsible for the bulk of seabird predations at Ichaboe Island off Namibia (Fig. 1). Individual seals culled around Malgas Island (South Africa), which were responsible for the mortality of a large number of Cape gannet fledglings, were all juvenile, subadult or adult males (David *et al.* 2003). Males have also been implicated in other observations of Cape fur seal–seabird interactions (Shaughnessy 1978, Rebelo 1984, Navarro 2000). Unlike the other two colonies, Cape Cross is not merely a breeding colony but also serves as a haulout site for non-breeding males throughout the year (S. P. Kirkman, pers. obs.). It is therefore possible that male seals deposited the scats containing feathers which were found in July and August. The age or sex class of individuals of other seal species predating on seabirds (Table I) are mainly unknown, except for two Antarctic fur seal studies (Casaux *et al.* 1998, Daneri and Coria 1992) where non-breeding males were found to be responsible for the behaviour.

The three Namibian colonies that were investigated together comprise about 65% of Namibia's Cape fur seal population, estimated at just over half a million individuals in December 2001 (Marine and Coastal Management (MCM), unpublished data). The occurrence of seabird remains in diet samples from these colonies combined is lower than found in any other study involving pinnipeds (Table I).

Cape fur seals forage up to 220 km from their colony (Shaughnessy 1985), and therefore most of the important seabird colonies in Namibia are within foraging distance of the study colonies (Fig. 1). The proximity of these large seabird colonies to the study colonies, and the negligible occurrence of seabird remains in the seal diet, indicates that seabirds are not an important food source, at least for female seals. Cape Cross Lagoon

(Fig. 1), situated to the south of the Cape Cross seal colony, supports up to 14% of the total Cape cormorant population (Simmons *et al.* 1998). Non-breeding bank cormorants may occur as far north as Cape Cross, although sightings further north than Swakopmund are rare (Crawford 1997). The main breeding sites of bank cormorants are on Ichaboe and Mercury Islands (Fig. 1) and these islands account for more than 70% of the population (Crawford 1997). The cormorant feather remains found in the August scat sample therefore most likely belonged to a Cape cormorant. Juvenile cormorants are particularly vulnerable to seal predation because of their inexperience of predators (Marks *et al.* 1997). Although the most northerly breeding site of the African penguin is Hollams Bird Island (24°38'S, 14°32'E), individuals have been observed along the entire Namibian coast as well as along the Angolan coast (Collar and Stuart 1985). The occurrence of penguins in northern Namibian waters would explain the penguin feather remains in the July scat sample.

Most observations of Cape fur seal predations on seabirds have been made in the immediate vicinity of bird colonies (Cooper 1974, Shaughnessy 1978, Rebelo 1984, Marks *et al.* 1997, Navarro 2000, Crawford *et al.* 2001, David *et al.* 2003, Du Toit *et al.* 2004). While this study found a negligible quantity of seabird remains from scats found in seal colonies, indicating that predation on seabirds is not widespread and is most probably insignificant away from the bird colonies, one cannot rule out the possibility of seals defaecating and/or regurgitating at sea prior to haulout, resulting in a loss of data. In those populations of fur seals and sea lions where predation on seabirds occurs, predatory behaviour on seabirds seems to be restricted to a few individuals (Bonner and Hunter 1982, Marks *et al.* 1997, McMahon *et al.* 1999, Childerhouse *et al.* 2001, Du Toit *et al.* 2004). Some attacks have been likened to surplus killings observed in other carnivores, because not all carcasses were utilized (Marks *et al.* 1997). Moreover, such attacks may be an extension of play behaviour (Bonner and Hunter 1982, Hofmeyr and Bester 1993, Du Toit *et al.* 2004). Although seabirds may feature negligibly in the overall diet of Cape fur seals, the few individuals responsible can detrimentally affect endangered seabird populations (Crawford *et al.* 2001, David *et al.* 2003). The removal of individual seals known to specialize in preying upon seabirds has been shown to be effective in increasing the survival of gannet fledglings at Malgas Island (David *et al.* 2003). The results of the present study suggest that decreasing the number of breeding females of the Cape fur seal population through culling in order to reduce the incidence of seabird predation is not likely to be effective due to the very low overall incidence of seabirds in female fur seal diets.

Table I. The frequency of occurrence (%) of seabird remains in scat samples (diet samples other than scats are indicated) of pinniped species, including that for the Cape fur seal *Arctocephalus pusillus pusillus* during the present study. The range of frequency of occurrence is given in parentheses.

Pinniped species	Frequency of occurrence of bird remains in diet samples	Reference
Cape fur seal (<i>Arctocephalus pusillus pusillus</i>)	0.2% (0 - 1.7%) 0.1% (0 - 1.7%) 0.8% (stomachs)	This study (Cape Cross) This study (all three study colonies combined) Rand 1959
Antarctic fur seal (<i>A. gazella</i>)	45.1% (27.8 - 54.6%) 15.2% (0 - 22.7%) 4.8% (0 - 14.3%) 2.3% (0 - 8.3%)	Casaux <i>et al.</i> 1998 Daneri and Coria 1992 Green <i>et al.</i> 1989 Green <i>et al.</i> 1990 (<i>A. gazella</i> and <i>A. tropicalis</i> together)
New Zealand fur seal (<i>A. forsteri</i>)	37.6% (10.3 - 65.2%)	Green <i>et al.</i> 1990
New Zealand sea lion (<i>Phocarctos hookeri</i>)	3.0% 2.0% (regurgitates)	Childerhouse <i>et al.</i> 2001 Childerhouse <i>et al.</i> 2001
Southern sea lion (<i>Otaria flavescens</i>)	9.5%	Thompson <i>et al.</i> 1998
Leopard seal (<i>Hydrurga leptonyx</i>)	85.7% 9.8% (0.6 - 28.0%)	Rogers and Bryden 1995 Walker <i>et al.</i> 1998
Harp seal (<i>Phoca groenlandica</i>)	0.3% (stomachs)	Lawson <i>et al.</i> 1995

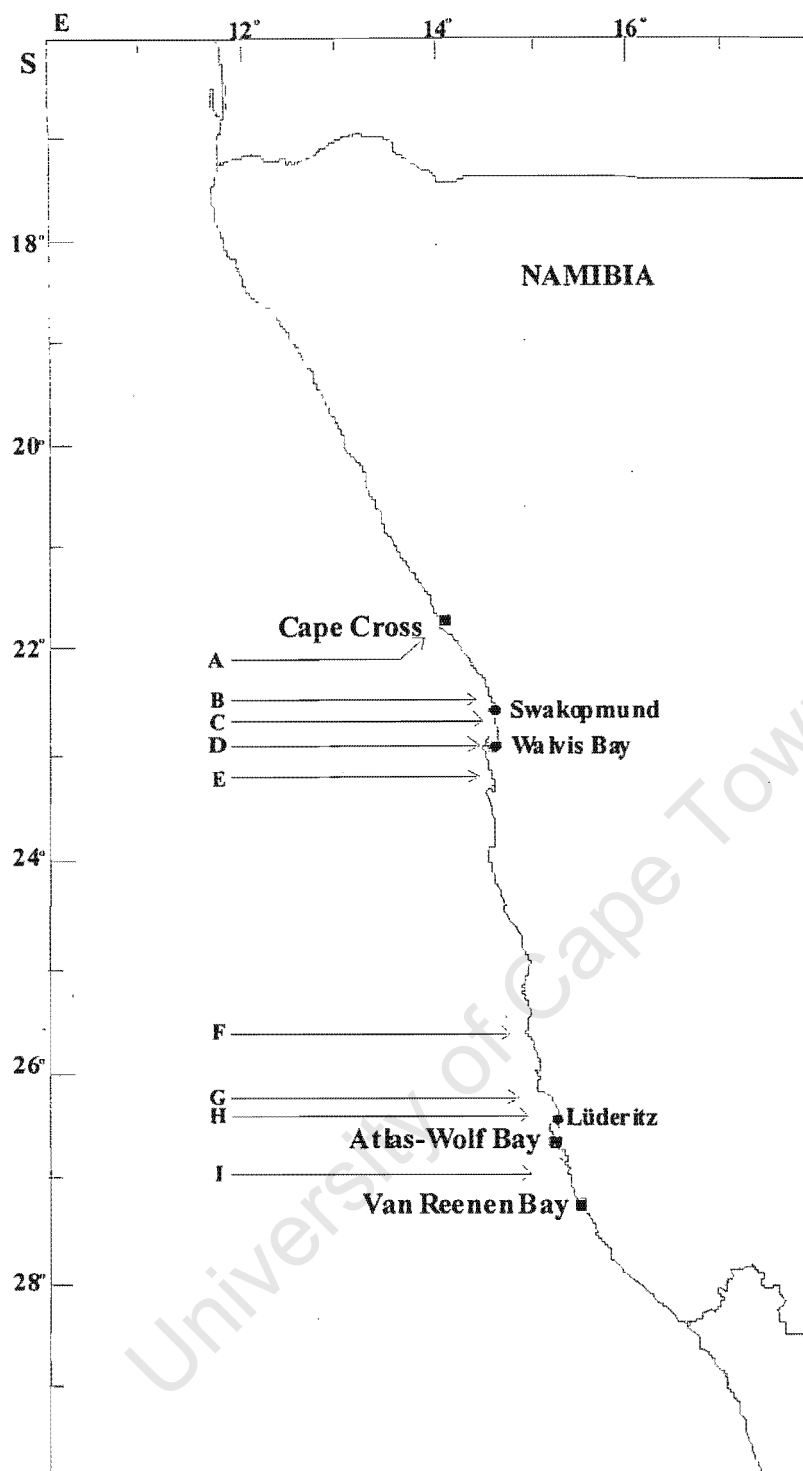


Figure 1. Map of the Namibian coastline showing the position of the three study mainland breeding colonies of the Cape fur seal *Arctocephalus pusillus pusillus*, and their proximity to the important Namibian coastal bird areas (Simmons *et al.* 1998): A = Cape Cross Lagoon (21°45'S, 13°50'E), B = Mile 4 Saltworks (22°39'S, 14°33'E), C = 30 Km Beach, between Walvis Bay and Swakopmund (22°42'-22°56'S, 14°31'-14°31'E), D = Walvis Bay (22°59'S, 14°31'E), E = Sandwich Harbour (23°20'S, 14°30'E), F = Mercury Island (25°43'S, 14°50'E), G = Ichaboe Island (26°17'S, 14°56'E), H = Halifax, Seal and Penguin Islands, Lüderitz Bay (26°37'S, 15°07'E), and I = Possession Island (27°01'S, 15°12'E).

CHAPTER 8



University of Cape Town

Investigating fur seal diet using scats: recommendations for sampling and analysis

INTRODUCTION

The majority of diet studies of pinnipeds make use of scat analysis (e.g. Härkönen 1987, Green *et al.* 1989, Hammond *et al.* 1994, Acuña and Francis 1995, Casaux *et al.* 1998, Childerhouse *et al.* 2001, Naya *et al.* 2002, Casaux *et al.* 2003), whereas stomach content analysis is being used to an increasingly lesser extent (e.g. Lowry *et al.* 1980, Green and Burton 1987, Hjelset *et al.* 1999, Holst *et al.* 2001). Scat analysis is the preferred method because it is cheap, non-intrusive and non-destructive (Pierce and Boyle 1991), and a large number of samples can be collected (Laake *et al.* 2002). It can also be carried out concurrently with telemetric studies which collect data on movement patterns (Guinet *et al.* 2001), especially for lactating female otariids which make regular, relatively short foraging trips before returning to their pups at the breeding colony (Rand 1955, Antonelis *et al.* 1990, Bonner 1994, Harcourt *et al.* 1994).

In most diet studies of pinnipeds where scat analysis is used, each scat deposit is assumed to be independent of others (Pierce and Santos 2003), and sampled scats are stored, processed and analyzed discretely. Analysis is based on the assumption that prey hard part remains in scats reflect the relative abundance and mass of prey consumed (Tollit *et al.* 1997). However, there are a number of biases associated with the method (Pierce and Boyle 1991). With respect to teleost fish in the diet, probably the most important bias is that otoliths are partially or even completely eroded during the digestion process, affecting abundance and mass estimates of teleost prey from the scats (Da Silva and Neilson 1985, Murie and Lavigne 1985, Jobling 1987, Dellinger and Trillmich 1988, Harvey 1989, Gales and Cheal 1992, Harvey and Antonelis 1994, Tollit *et al.* 1997, Orr and Harvey 2001, Staniland 2002).

Other important limitations of the method with respect to investigations of otariid diet, are that the sex and age distribution of the individuals responsible for scat deposits at any time of the year may be skewed towards one or more classes, and that it is unknown whether the contents of

a scat represent food taken at the primary foraging location. Despite these biases, scat analysis can provide valuable information on prey consumption including temporal and spatial changes (Tollit and Thompson 1996) and is therefore a useful indicator of prey distribution and availability.

To obtain the most reliable information possible from scat analysis, the sampling protocols should aim to reduce sources of error wherever possible. For instance, the effect of sample size on the precision and interpretation of results should always be considered (Hammond and Rothery 1996, Trites and Joy 2005). Also, the frequency of sampling should be such that switches in diet are detected. Considering that the diet of Cape fur seals varies temporally (Chapter 3), the frequency of sampling is an important consideration for analysis of seal diet using scats.

The objective of this chapter was to evaluate sampling protocols used throughout thesis, with a view to recommending standards for future studies. To this end, information obtained by two sampling techniques employed during the study period, namely 'bag' sampling (where the scats collected are pooled together and analysed as a single unit) and 'individual scat' sampling (where each scat collected is stored, processed and analysed separately from each other scat) are compared. Also examined were the amount of scats required to provide adequate information in the case of each technique, and the frequency with which sampling should occur. Biases inherent to scat analysis are reviewed with regard to the diet composition of Cape fur seals in Namibia determined from scats during the study.

MATERIAL AND METHODS

Study sites

Cape fur seal scat samples were collected from three mainland breeding colonies along the Namibian coast: Cape Cross (21°47'S, 13°57'E; CC), Atlas and Wolf Bays (26°49'S, 15°08'E and 26°48'S, 15°07'E, respectively), which for this study were considered as one because they are approximately 1 km apart (AWB), and Van Reenen Bay (27°23'S, 15°21'E; VRB). These three colonies comprise 65% of the total seal population of Namibia, estimated at just over half a million individuals in December 2001 (Marine and Coastal Management (MCM), unpublished data).

Scat collection and processing

From May 2001 to April 2002, fresh scats were collected at monthly intervals at each colony, on the same date each month. For this study, two types of sample units were collected: individual scat samples and bag samples. Where possible, 30 individual whole scats were collected and kept discrete by placing each scat into a separate plastic sampling bag, and 30 more scats were collected and pooled into one bag. Two scats lying close to each other were considered as separate.

The processing method of Cape fur seal scats for this study is described in detail in Chapter 2. Individual scats were washed in plastic jars under running water and the mixture was passed through a stainless steel laboratory test sieve of mesh aperture 0.212 mm. Bag samples were rinsed in a bucket with running water and the material was passed through nested stainless steel laboratory test sieves with mesh apertures of 2.0, 1.0, 0.425 and 0.212 mm. The material containing prey items was thoroughly rinsed and dried overnight in an oven at 50°C.

Sagittal otoliths were sorted from the dried material, identified and counted. Six main prey groups were identified: Cape horse mackerel *Trachurus trachurus capensis*, Cape hakes *Merluccius capensis* and *M. paradoxus*, lanternfish (mainly *Lampanyctodes hectoris*), pelagic goby *Sufflogobius bibarbatus*, pelagics (sardine *Sardinops sagax*, anchovy *Engraulis capensis* and round herring *Etrumeus whiteheadi*) and others (Chapter 2). Otolith counts were adjusted for numbers lost during digestion using correction factors (D. L. Millar *et al.*, MCM, unpublished data; Chapter 2). The scope of these correction factors is detailed in the Discussion. The following statistics were calculated for the samples:

The percentage numerical abundance (N_{is}) of each prey group i in a month's sample of k individual scats (s) was determined as follows:

$$N_{is} = \frac{\sum_{j=1}^k \frac{n_{ij}}{n_j}}{k} \times 100 \quad (\text{Eqn 1})$$

where n_{ij} is the number of otoliths of prey group i in scat j ($j = 1, 2, \dots, k$), and n_j is the number of otoliths of all prey groups in scat j . The percentage numerical abundance (N_{ib}) of prey group i in a month's bag sample (b) was determined as:

$$N_{ib} = \frac{n_i}{n_T} \times 100 \quad (\text{Eqn 2})$$

where n_i is the number of otoliths of prey group i in the bag sample and n_T is the number of otoliths of all prey groups in the bag sample. In the results this is referred to as $N_{ib}(\text{bag})$. Furthermore, for each month's sample of individual scats, the abundance data from all the scats were pooled together to reproduce a bag sample; the percentage numerical abundance of the prey groups were determined as above (Eqn 2), but were referred to as $N_{ib}(\text{indiv})$.

For each sample, otolith diameters of sub-samples of otoliths were measured to the nearest 0.05 mm. Otolith diameters were corrected for erosion during digestion (D. L. Millar *et al.*, MCM, unpublished data), and converted to fish mass using relationships between otolith diameter and fish length and mass (Smale *et al.* 1995; Chapter 2). The mean of the reconstituted masses of each prey type, per monthly sample from each colony, was used to convert otolith counts to mass. The percentage mass (M_{is}) of each prey group i in a month's sample of k individual scats (s) was determined as follows:

$$M_{is} = \frac{\sum_{j=1}^k \frac{m_{ij}}{m_j}}{k} \times 100 \quad (\text{Eqn 3})$$

where m_{ij} is the mass of prey group i in scat j ($j = 1, 2, \dots, k$), and m_j is the mass of all prey groups in scat j . The percentage mass (M_{ib}) of prey group i in a month's bag sample (b) was determined as:

$$M_{ib} = \frac{m_i}{m_T} \times 100 \quad (\text{Eqn 4})$$

where m_i is the mass of prey group i in the bag sample and m_T is the mass of all prey groups in the bag sample (in results indicated as $M_{ib}(\text{bag})$). As with abundance, for each month's sample of individual scats the mass data from all the scats were pooled together to reproduce a bag sample; the percentage mass of the prey groups were determined as above (Eqn 4), but were referred to as $M_{ib}(\text{indiv})$.

The percentage frequency of occurrence (FO_{is}) of each prey group i in the monthly samples of individual scats (s) was expressed as:

$$FO_{is} = \frac{\sum_{j=1}^k p_{ij}}{k} \times 100 \quad (\text{Eqn 5})$$

where $p_{ij} = 1$ if scat j contained prey group i , $p_{ij} = 0$ otherwise.

At each colony, the standard deviations (SD) of N_{is} and M_{is} for each of the main prey groups were related to the corresponding N_{is} and M_{is} values, to determine the pattern of variability of these estimates over a scale ranging from 0 to 100%. For the same reason, N_{is} and M_{is} values were also related to the corresponding FO_{is} values.

Definitions of the abbreviations for the expressions above are contained in Box I for perusal throughout this chapter.

Recommended sample sizes

To determine how many scats are required to provide information that will adequately describe diet composition, randomization and bootstrap methods were used (Manly 1991, Efron and Tibshirani 1993).

Individual scat data (otolith counts and fish mass per prey group) collected from the three study colonies from May 2001 to April 2002 ($n = 1\,012$ scats) were placed together into one dataset and assumed to represent the diet of the population of seals. From this dataset, five sets of 200 scats were randomly selected without replacement. From each set of 200 scats, the first 10, 20, 30, ..., 200 scats were resampled with replacement 5 000 times, and the size of the bootstrapped samples equaled the size of the original sample (i.e. 10, 20, 30, ..., 200, respectively). Resampling with replacement ensures independence of samples (Efron and Tibshirani 1993). For each of the 5 000 replications, and for each prey group, N_{is} , M_{is} and FO_{is} were determined. The 5 000 values of N_{is} , M_{is} and FO_{is} for each prey group were ordered and the 95% confidence intervals (CI) determined by taking the 2.5th and 97.5th percentiles (Manly 1991, Tirasin and Jørgensen 1999). Coefficients of variation (CV) for each of the 5 000 values were also determined. The samples were bootstrapped 5 000 times because Tirasin and Jørgensen (1999) found that 3 000 to 5 000 bootstrap samples gave stable estimates of 95% confidence intervals for diet estimates. Moreover, to obtain reliable estimates of 95% confidence intervals, the number of bootstrap samples needs to be large (usually greater than 1 000) so that the variance of the percentiles is low (Efron and Tibshirani 1993).

For the purposes of this section, eight prey group bootstrapped resample sets (10, 20, 30, ..., 200 scats) were selected (irrespective of the prey group identity), so that N_{is} , M_{is} and FO_{is} values for 200 scats covered the range from 0 to 100%. This was to enable testing of sample size effects along a scale of small to large values of N_{is} , M_{is} and FO_{is} . The widths of the CIs were

determined, and related to the corresponding N_{is} , M_{is} and FO_{is} values. The CVs were also related to the corresponding N_{is} , M_{is} and FO_{is} values.

Individual scat samples versus bag samples

To determine if individual scat sampling and bag sampling gave the same results regarding diet composition in terms of abundance and mass, the monthly differences between $N_{ib}(\text{indiv})$ and N_{is} , and $M_{ib}(\text{indiv})$ and M_{is} , for prey groups in the diet of seals at each study colony from May 2001 to April 2002 were determined. Also, results obtained from pooling the data of individual scat samples to represent a bag sample were compared to results obtained from actual bag samples that were collected at the same time as the individual scat samples, to determine if bag samples gave similar results. Therefore, monthly differences between $N_{ib}(\text{indiv})$ and $N_{ib}(\text{bag})$, and $M_{ib}(\text{indiv})$ and $M_{ib}(\text{bag})$, were assessed. Also, differences between $N_{ib}(\text{indiv})$ and N_{is} , and between $M_{ib}(\text{indiv})$ and M_{is} , were determined for sample sizes of 10, 20, 30, ..., 200 scats for each of the eight bootstrapped resample sets, in order to assess the relationship between sample size and abundance and mass data achieved from the two techniques.

Frequency of sample collection

To assess if monthly scat sampling is adequate for tracking changes in the diet of seals, scats were collected on a more frequent basis (every 3-7 days) at AWB during two separate sampling periods of two months each (4 June to 26 July 2001 and 18 January to 13 March 2002). Each sample was a bag sample consisting of 30 scats. The main prey groups that dominated in the scats during these sampling periods, namely lanternfish and goby, were used to detect whether shifts in the diet within a month, if any, occurred gradually or suddenly, and if the latter how frequently such changes occurred within a month period. Differences between the $N_{ib}(\text{bag})$ values of the two prey groups were determined for each sample, and for each of the two prey groups between consecutive samples.

RESULTS

The total number of otoliths in single scats ranged from 2 to 4 436 (mean $\pm$ SD, 282 ± 479 otoliths, $n = 1\,012$ scats), whilst the estimated total mass of teleost prey represented by

a scat ranged from 0.001 to 9.0 kg (0.7 ± 0.9 kg, $n = 1\,012$ scats). The percentage abundance (N_{is}), mass (M_{is}) and frequency of occurrence (FO_{is}) of the prey groups in the seal diet, per month, at each study colony varied between 0% and 100% (Fig. 1). For reference, the information for the main prey types are tabulated in Appendices I (abundance), II (mass) and III (frequency of occurrence), together with the same information for the less important prey groups at each colony. The SDs of N_{is} and M_{is} of the main prey of seals in individual scat samples from the three study colonies, ranged from 0 to 48% (Fig. 1). SDs were less than 10% when N_{is} and M_{is} values were less than 10% and close to 100% (Fig. 2a), but exceeded 30% when N_{is} and M_{is} values were in the range of 40 to 80% (Fig. 2a). When below 10%, both N_{is} and M_{is} values were associated with a wide range of FO_{is} values (0 to 100%), but when exceeding 80%, each was associated with high FO_{is} values (greater than 93%) (Fig. 2b). Therefore, with increases in N_{is} and M_{is} of a prey group, variation in FO_{is} for the prey group decreased and the FO_{is} approached 100% (Fig. 2b).

Individual scat samples versus bag samples

The percentage numerical abundance and mass of prey groups from pooled data of individual scat samples, to represent bag samples ($N_{ib}(\text{indiv})$ and $M_{ib}(\text{indiv})$), and from individual scat samples (N_{is} and M_{is}) are given in Appendices I and II. Absolute differences between $N_{ib}(\text{indiv})$ and N_{is} , and $M_{ib}(\text{indiv})$ and M_{is} , ranged from 0 to 55% and 0 to 29%, respectively (Tables I and II).

The percentage numerical abundance and mass of prey groups from bag samples ($N_{ib}(\text{bag})$ and $M_{ib}(\text{bag})$) are given in Appendix IV. Absolute differences between $N_{ib}(\text{indiv})$ and $N_{ib}(\text{bag})$, and $M_{ib}(\text{indiv})$ and $M_{ib}(\text{bag})$, ranged from 0 to 37% and 0 to 46%, respectively (Tables III and IV).

Differences between $N_{ib}(\text{indiv})$ and N_{is} , and $M_{ib}(\text{indiv})$ and M_{is} , for the eight bootstrapped resample sets of 10, 20, 30, ..., 200 scats are given in Appendices V and VI, respectively. Absolute differences did not decrease as sample size increased, and in some situations (resample sets six and seven in Appendix V, and resample set seven in Appendix VI) the absolute differences remained high even for sample sizes of 200 scats.

The time required to process 30 scats ranged from 18 to 85 hours, depending on the number of otoliths in a scat. It took approximately 15 min to wash each scat, 20 min to two hours to sort

and count otoliths per scat, and one to 34 min to measure sub-samples of otoliths per scat. The time required to process a bag sample of 30 scats was less (minimum of 10 hours); one to three hours for washing the sample (the density of the large sample determined how fast water drained through the nested sieves), a minimum of eight hours for sorting and counting otoliths, and about 30 min to measure sub-samples of otoliths.

Sample size

Results of the eight bootstrapped resample sets of 10, 20, 30, ..., 200 scats, covering the range of 0 to 100% each for N_{is} , M_{is} and FO_{is} , are given in Appendices V (abundance), VI (mass) and VII (frequency of occurrence), respectively, together with their CVs and confidence intervals. CVs decreased as N_{is} , M_{is} and FO_{is} values increased, and CVs decreased as sample size increased (Figs 3a-c). CVs were similar for sample sizes of 50, 100, 150 and 200 scats (Figs 3a-c).

The widths of the 95% CIs tended to be smallest for values of N_{is} , M_{is} and FO_{is} close to 0% and 100% (Figs 3d-f). The 95% CI widths decreased as sample size increased, but were similar for samples of 50, 100, 150 and 200 scats (Figs 3d-f). For values of N_{is} at 200 scats ranging between 15% and 85% (resample sets 4 to 7 in Appendix V), the widths of the CIs were less than 15% for sample sizes ranging from 90 to 120 scats, and less than 20% for sample sizes of 50 to 80 scats. For values of M_{is} at 200 scats ranging between 15% and 50% (resample sets 4 to 8 in Appendix VI), the widths of the CIs were less than 15% for sample sizes ranging from 70 to 110 scats, and less than 20% for sample sizes of 40 to 50 scats. For values of FO_{is} at 200 scats ranging between 20% and 80% (resample sets 3 to 6 in Appendix VII), the widths of the CIs were less than 15% for sample sizes ranging from 120 to 170 scats, and less than 20% for sample sizes of 50 to 100 scats.

Frequency of sample collection

The difference between the $N_{ib}(\text{bag})$ of lanternfish and that of goby ranged between 24% and 85% for the sampling period of 4 June to 26 July 2001 (Fig. 4a). During this period lanternfish dominated in the diet. For the sampling period of 18 January to 19 March 2002, the difference between the $N_{ib}(\text{bag})$ of lanternfish and that of goby ranged from -99% to 86% (Fig. 4b). The difference was greater than zero for the first half of the sampling period when lanternfish dominated in the diet, and less than zero in the last half of the sampling period when goby

dominated in the diet. There was no switch in diet during the 4 June to 26 July 2001 sampling period, and the differences between the consecutive $N_{ib}(\text{bag})$ of lanternfish and of goby during this period were less than 23% (Fig. 4c). The switch in the diet from lanternfish to goby during the 18 January to 19 March 2002 sampling period occurred within six days (between 13 and 20 February 2002; Fig. 4b), and was characterized by a sudden large difference between the consecutive $N_{ib}(\text{bag})$ of lanternfish and of goby, 56% and -53%, respectively (8th consecutive sample in Fig. 4d). The consecutive differences for all other sample days within this period were less than 15% (Fig. 4d).

DISCUSSION

Individual scats versus bag sampling

The discrepancies between $N_{ib}(\text{indiv})$ and $N_{ib}(\text{bag})$, and between $M_{ib}(\text{indiv})$ and $M_{ib}(\text{bag})$, were sometimes large. This could be for a number of reasons. Scats collected for either or both sample types may not always have been collected at random and independent of one another. If two or more scats found close to each other were included in one of the samples, they may not have been independent of each other because they may have been deposited by the same individual. Although scats for this study did not tend to be clustered, some were close together (within a few metres) but were treated as separate scats. Moreover, if sampling was restricted to certain areas of the colony, for instance because of the density of seals or to avoid disturbing sensitive breeding season activities, sampling may have been skewed towards scats deposited by a certain group of individuals not necessarily representative of the on-shore population. Another possibility is that the size of the samples (~ 30 scats) may not have been large enough to reliably represent the diet composition of the seal population.

Differences between $N_{ib}(\text{indiv})$ and N_{is} , and between M_{is} and $M_{ib}(\text{indiv})$, were also large at times. Equivalence between the two methods (i.e. between individual scats versus pooling of the data of these individual scats to represent a bag sample), for abundance and mass estimates, would mathematically only arise if each of the scats had an equal number of otoliths or prey mass. In reality there are unequal numbers of otoliths and prey mass between scats. Therefore, abundance and mass estimates between the two methods would never be equivalent. Increasing

the number of scats sampled would therefore also not result in smaller differences between the two methods, as found in this study.

The key distinction between individual scat sampling and bag sampling is that the former effectively treats each scat as a sampling unit, whereas the latter treats each otolith as a sampling unit. The N_{is} and M_{is} measures, based on the individual scat sampling method, assign equal importance to each discrete scat by giving equal weight to each scat, and treat it independently to other scats in the sample. With bag sampling, all otoliths within a sample are assigned equal importance and are thus seen as independent of every other otolith.

A disadvantage with the bag sampling method is that it may consider the wrong paradigm with respect to the foraging behaviour of seals. Marine predators generally focus their foraging effort upon locally abundant prey such as shoals of fish (Tirasin and Jørgensen 1999). Shoaling fish maximise the energy gain of the predators as they are more frequently encountered and have higher capture rates than dispersed fish species (Bowen and Harrison 1996). Seals in this study mainly consumed prey that display shoaling behaviour (Chapter 2). From the perspective that fish within shoals are not independent of each other, they (viz. their otoliths) are inappropriate sampling units for the study of seal diet.

Bag sampling can be used for qualitative purposes, such as for determining which prey species contribute to the diet. But to obtain reliable estimates of diet composition, the sampling of individual scats is preferable because it is relevant to the foraging behaviour of seals. Individual scat sampling also allows for determining the frequency of occurrence of prey in the diet. This gives an indication of what proportion of the seal population is consuming a specific prey group or species. Together with information on the abundance and mass of prey consumed, frequency of occurrence may provide important insights into the foraging behaviour of seals (Cortés 1997), and therefore also on the dispersal of prey. For example, this study showed that high values of percentage numerical abundance and mass of a prey species or group in the diet were associated with high values of percentage frequency of occurrence for the same species or group. This may indicate that the particular prey species or groups were easily accessible to the entire population of seals at a colony by occurring in a shoal close to the shore.

Alternatively, low values of percentage numerical abundance and mass of prey in the diet were associated with values of percentage frequency of occurrence that ranged from low to high (0 to 100%). The high values may have been indicative of prey that were evenly dispersed within

the foraging range of the population of seals, but could not be consumed as copiously as shoaling fish. Low values suggest that the prey were widely dispersed and low in abundance, thus seldom encountered by the seals.

Individual scat samples also provide a means of determining variability (e.g. standard deviations and coefficients of variation) and precision (e.g. 95% confidence intervals) of diet estimates. Many diet studies have been criticised for ignoring these (Ferry and Cailliet 1996, Tirasin and Jørgensen 1999), and seal diet studies using scat analysis have generally lacked precision estimates, despite the scope for error inherent to the method. Discrete samples, such as individual scats, are necessary for generating confidence intervals using randomization and bootstrapping methods, as some studies have shown, e.g. grey seals *Halichoerus grypus* (Hammond and Rothery 1996), minke whales *Balaenoptera acutorostrata* (Harbitz and Lindstrøm 2001, Haug *et al.* 2002), fish (Tirasin and Jørgensen 1999, Daly *et al.* 2001) and small terrestrial carnivores (Mukherjee *et al.* 2004). The randomization and bootstrap methods employed in this study have shown that the sample size of 30 scats, which was collected monthly for both individual scat samples and bag samples, was not adequate for achieving 95% confidence interval widths of less than 15% and 20%.

The decision to use either of the two sampling methods (individual scat sampling versus bag sampling) will ultimately depend on the level of reliability or precision required and on logistical constraints. It may not be feasible to collect and process a large number of scats individually because the cost in time could be too great to justify more accurate results than those achieved from bag samples composed of the same number of scats. Studies constrained by time or cost must understand the limitations of their data and make appropriate conclusions relative to the reliability of confidence of the data (Ferry and Cailliet 1996).

Sample size

This study showed that variability (SDs) was highest when a prey group had a percentage numerical abundance or mass value that was in the middle of the range (between about 40 and 80%) of the possible values. This suggests that sample size in terms of scats numbers would have a greater influence on these quantifying statistics of prey groups in a sample than for prey groups with high or low values for the corresponding statistics. Indeed, bootstrapping showed that confidence intervals were greatest for mid-range values, and that confidence intervals became

smaller if sample size was increased. Theoretically then, for a specific level of confidence in the statistics quantifying a prey group relative to other prey groups in a sample, fewer scats would be required for prey groups with values close to 0 or 100% than for prey groups with intermediate values. The latter should therefore be considered if sample size, in terms of the numbers of scats, is to be determined from a specific level of confidence required in the quantifying statistics. Generally, the less confidence one requires, the fewer scats need to be collected.

This study showed that for confidence interval widths less than 15%, 170 scats are needed, while for widths less than 20% only 100 scats are required. Hammond and Rothery (1996) suggested that a minimum of 100 scats should be collected for each sampling occasion that distinguishes locations and seasons. Trites and Joy (2005) showed that close to 100 scats were necessary for comparing diets between locations and over time when the diet was composed of a minimum of six prey species, and fewer were needed to identify the main prey. Because diet data were pooled across colonies and months, this dataset is probably broader than the diet of the population at any one time and colony. This has the effect of increasing the errors for each bootstrapped monthly sample.

Sample size is important for obtaining data to describe the diet adequately, so that reliable comparisons can be made between locations and over time (Ferry and Cailliet 1996, Trites and Joy 2005). If sample sizes are too small, bootstrapping can give unreliable estimates, therefore an adequate number of samples is needed in the first place to obtain reliable estimates of precision (Tirasin and Jørgensen 1999). Sample sizes should also be large enough so that sampling errors which result from differences in diet composition between scats do not become too large (Hammond and Rothery 1996). However, the choice of sample size is also affected by logistical constraints such as processing time, as discussed above.

Frequency of sample collection

Apart from the sudden change from lanternfish to goby during the sampling period at the beginning of 2002, the diet was relatively constant between samples in both sampling periods. For the samples prior to the switch in this sampling period, the diet composition in terms of the two main prey items was very similar to that of the normal monthly sample collected just before the onset of the sampling period, and the diet composition of the samples collected just after the switch were very similar to that of the monthly sample collected soon after the sampling period.

Therefore in this experiment, the information in the once-monthly samples sufficiently described the variation in the relative abundance and mass of the main prey groups in the scats.

The fact that the only change was sudden and gradual shifts in the main prey groups were not apparent is noteworthy, as this attributes to the suitability of once monthly sampling of scats. However, gradual shifts in diet composition, and sudden changes that occur with such frequency that the resolution of once monthly sampling is too coarse to detect them, cannot be ruled out though they were not apparent in the two month sampling periods of this experiment. Samples at more regular intervals, one weekly for example, would probably be sufficient to capture such variation, but in the case of the three study colonies would probably be impractical considering logistical constraints (e.g. regular accessibility to a colony may be unfeasible if the distance that needs to be travelled to reach it is large).

Other factors affecting the reliability of using scats for seal diet analyses

Of the main biases related to scat analysis, the partial or complete erosion of otoliths are the most important. In order to improve the reliability of scat analysis, correction factors should be used to correct for the number of otoliths that have been completely digested (Harvey 1989, Bowen 2000, Orr and Harvey 2001, Cottrell and Trites 2002, Staniland 2002) and to correct for the erosion of otolith diameters (Dellinger and Trillmich 1988, Harvey 1989, Orr and Harvey 2001, Staniland 2002, Tollit *et al.* 2004). Few pinniped diet studies using scat analyses have used otolith correction factors, especially for numbers of otoliths lost during digestion.

The correction factors used in this study to correct for the partial and complete erosion of otoliths were determined during captive feeding experiments on Cape fur seals (D. L. Millar *et al.*, MCM, unpublished data). These experiments showed that the recovery of otoliths in scats of four teleost prey species fell within the range of 32% to 74%. These recovery rates are relatively high compared to studies of other otariid species, where recovery rates ranged from less than 2% up to 72% (Dellinger and Trillmich 1988, Gales and Cheal 1992, Orr and Harvey 2001, Cottrell and Trites 2002, Staniland 2002). The lowest recovery rate during the Cape fur seal feeding experiments was for sardine otoliths (32%) (D. L. Millar *et al.*, MCM, unpublished data). Sardine otoliths are small and fragile and, together with small, fragile otoliths of other teleost prey in this study (anchovy, round herring, goby, lanternfish, and very small hake and horse mackerel), their probability of being completely digested is high, probably resulting in underestimates of these

species in the diet. The recovery of otoliths is also affected by meal size, and Marcus *et al.* (1998) found that a lower proportion of otoliths were recovered from small meals.

Otoliths that are recovered are partially eroded in length and width due to their exposure to gastric fluids (Da Silva and Neilson 1985, Dellinger and Trillmich 1988). During captive feeding trials, otoliths passing through the digestive tract of Cape fur seals were eroded by 5% (goby) to 40% (hake) (D. L. Millar *et al.*, MCM, unpublished data). In other otariids the degree of otolith erosion ranged from 12% to 40% (Dellinger and Trillmich 1988, Gales and Cheal 1992, Orr and Harvey 2001). Correcting for the partial erosion of otoliths ensures that fish sizes and mass, determined from species-specific relationships between otolith length and fish length and mass, are not underestimated (Da Silva and Neilson 1985, Murie and Lavigne 1985, Jobling and Breiby 1986, Dellinger and Trillmich 1988, Harvey 1989, Hammond and Rothery 1996, Tollit *et al.* 1997, Orr and Harvey 2001, Staniland 2002).

The use of correction factors increases errors in estimates of abundance and mass of prey in the diet. Hammond and Rothery (1996) found that most of the digestion and measurement errors were due to correcting for the complete and total erosion of otoliths during digestion. Little of the digestion error was due to the random variation of digestion coefficients, and little of the measurement error was due to determining fish length or mass from their relationships to otolith size (Hammond and Rothery 1996). They suggested that these correction factors should be improved in order to reduce the variability in abundance and mass estimates of prey in the diet. This could be achieved by carrying out carefully planned feeding experiments.

Tollit *et al.* (1997) found a high degree of intra-specific variation in the digestion of otoliths, and suggested using a grading scale for the degree of otolith erosion which improved the estimates of fish mass. Applying a species-specific correction factor to all otoliths of one prey species usually overestimated the mean mass of fish (Tollit *et al.* 1997). Correction factors for the partial and complete erosion of otoliths of different prey species and of varying sizes of a prey species is largely lacking for Cape fur seals, and therefore standardised and well-planned feeding trials on Cape fur seals need to be undertaken to enable more accurate interpretations of scat prey remains.

Otolith recovery and erosion are dependant on the passage rate of otoliths through the digestive tract, which determines the amount of exposure of otoliths to the gastric fluids. Passage rates are affected by a number of factors, including the degree of activity and physiology of the

individual seal, meal size, feeding frequency, otolith size, prey size and prey species (Bigg and Fawcett 1985, Da Silva and Neilson 1985, Dellinger and Trillmich 1988, Goodman-Lowe *et al.* 1997, Bodley *et al.* 1999, Bowen 2000, Staniland 2002).

Captive feeding studies on Cape fur seals showed that 84% of the otoliths were recovered within 24 hours after ingestion and that no otoliths were recovered later than 48 hours after ingestion (D. L. Millar *et al.*, MCM, unpublished data). Similar passage rates have been found for other pinniped species (Da Silva and Neilson 1985, Dellinger and Trillmich 1988, Harvey 1989, Goodman-Lowe *et al.* 1997, Bodley *et al.* 1999, Orr and Harvey 2001). However, seals held in captivity can become constipated due to inactivity, prolonging the passage rate of otoliths and thus increasing the erosion of otoliths (Dellinger and Trillmich 1988). The size of the experimental facility for the feeding trials on Cape fur seals was small (105 m³ water, 36 m² haulout, D. L. Millar *et al.*, MCM, unpublished data), limiting seal activity, and as a result otolith erosion may be lower for individuals in wild populations. Moreover, passage rates are probably higher in wild animals, so that food consumed may be defaecated in a shorter time than 24 hours. Scats would mostly represent the diet of seals feeding closer to the shore than those feeding offshore which defaecate in the sea. If some scats are produced in the sea before the seal hauls out, then scats would not represent the overall prey species consumed during the entire foraging trip (Gales and Cheal 1992, Staniland 2002). Lactating female Cape fur seals forage close to their colonies (Oosthuizen 1991), and thus scats collected at the breeding colonies during this study would be a good representation of the prey consumed by these individuals.

Some authors have suggested that other fish hard parts (e.g. vertebrae, eye lenses, scales) be identified from scats to improve diet estimates (Bigg and Fawcett 1985, Pierce *et al.* 1991, Cottrell and Trites 2002). This, however, would require many years of training to identify all fish hard parts from scats (Cottrell and Trites 2002), as well as captive feeding trials to determine rates of bone loss and erosion (Tollit *et al.* 2004). The fact that these structures are not always unique to a species makes species identification difficult (Laake *et al.* 2002). Moreover, such structures only provide evidence of the presence or absence of a prey, and thus the number of prey consumed cannot be determined (Laake *et al.* 2002). During the present study, it was noted on a few occasions that some scats contained many sardine scales but no sardine otoliths (S. M., pers. obs). Although scales cannot be used to estimate fish abundance and mass consumed, it may be worthwhile to investigate whether skeletal structures other than otoliths can be used to improve

the representation in the diet of prey species, such as sardine, whose otoliths are prone to complete digestion.

Other factors which may reduce the amount of information obtained from scat analysis include the incorrect or non-identification of otoliths, as well as not knowing the age and sex of the seal which produced the scat (Pierce and Boyle 1991). Scats collected during this study were mostly defaecated by adult, lactating female seals. All otoliths were identified or classed by SM, thus decreasing the bias associated with using more than one person for otolith identification. Broken pieces of otoliths were unidentifiable and were not included in the analyses.

Part of the food consumed may be regurgitated and thus would not be represented in scats (Pierce and Boyle 1991). Although Rand (1959) stated that Cape fur seals were seen frequently to regurgitate on South Africa's West coast, between February 2001 and April 2002 only one regurgitation (containing a few cephalopod beaks and some stones) was found at the study sites in Namibia. No seals were observed regurgitating (S.M., pers. obs). It was assumed that Cape fur seals at these Namibian colonies mainly defaecate prey remains and the study concentrated on prey remains found in scats.

Some otoliths may be of secondary origin, which means that some prey found in seal diets are ingested by larger predatory prey found in the diet and not directly by the seal (Pierce and Boyle 1991). The secondary origin of small prey of Cape fur seals was discussed in Chapter 2, and it was subsequently assumed that all prey were primary prey.

Recommendations for seal scat analysis

Although scat analysis has a number of biases (Pierce and Boyle 1991) and does not give an indication of the proportion of fish in the overall diet (Reid & Arnould 1996), this method nevertheless provides important information on spatial and temporal trends in the relative consumption of main prey by seals (Tollit and Thompson 1996). The following recommendations are made for the sampling and analysis of seal scats to determine diet composition, based on the results of this study:

- 1) To improve the randomness and independence of scat collection, scats should be collected that are at least 10 m apart, which would increase the probability that they were deposited by different individuals.

- 2) Scat collection at different locations and at regular time intervals over a year is encouraged, due to the spatio-temporal variation of diet composition. To reduce variability between diet samples on a temporal and spatial scale, samples should be collected on the same date each month at different locations. Sampling at a monthly scale seems to be adequate.
- 3) Individual scats is the preferred method of sampling. However, logistical constraints need to be taken into account together with the degree of confidence required, in order to decide what sample size would be adequate. If time and money is constrained, bag sampling can provide a reasonable idea of diet composition, although at a cost of precision and loss of information on the foraging behaviour of seals and distribution of fish.
- 4) Captive feeding trials of age-sex classes of Cape fur seals, and with different species and ages of prey, need to be carefully planned and carried out, so that correction factors for the erosion of otoliths during digestion are accurate.
- 5) Little is known about the foraging behaviour of Cape fur seal. Therefore, telemetry studies conducted concurrently with diet studies could provide this information (Prime and Hammond 1990).

Box I. Compendium of abbreviations used in this chapter.

N_{is}	Percentage numerical abundance of prey group i in a month's sample of individual scats.
$N_{ib} = N_{ib}(\text{bag})$	Percentage numerical abundance of prey group i in a month's bag sample of scats.
$N_{ib}(\text{indiv})$	Percentage numerical abundance of prey group i in a month's sample of pooled individual scats to represent a bag sample.
M_{is}	Percentage mass of prey group i in a month's sample of individual scats.
$M_{ib} = M_{ib}(\text{bag})$	Percentage mass of prey group i in a month's bag sample of scats.
$M_{ib}(\text{indiv})$.	Percentage mass of prey group i in a month's sample of pooled individual scats to represent a bag sample.
FO_{is}	Percentage frequency of occurrence of each prey group i in a month's sample of individual scats.

Table I. Differences in the percentage numerical abundance of the main prey groups in the diet of Cape fur seals *Arctocephalus pusillus pusillus* achieved from samples of individual scats when analysed separately (N_{is}), and together ($N_{ib}(\text{indiv})$), per month from May 2001 to April 2002 for each study colony.

Month	$N_{ib}(\text{indiv}) - N_{is}$								
	Cape Cross			Atlas-Wolf Bay			Van Reenen Bay		
	Horse mackerel	Hake	Goby	Hake	Lantern-fish	Goby	Hake	Lantern-fish	Goby
May 2001	9.0	0	3.7	-15.5	-5.1	24.5	-22.9	33.0	-0.5
June 2001	2.1	0	-0.2	-19.2	28.4	-8.5	-28.8	32.2	1.2
July 2001	-10.6	0	17.1	-13.1	9.9	-2.9	-24.9	30.9	-2.4
August 2001	-11.8	-6.8	18.9	-12.5	17.6	-5.2	-22.6	-5.0	-13.2
September 2001	-16.4	18.1	-0.2	-1.5	7.0	-2.9	-3.3	10.8	2.0
October 2001	-9.2	9.6	-0.1	-0.1	2.0	-1.9	-7.6	10.8	-2.1
November 2001	-17.7	25.6	-3.5	-0.4	3.8	-3.3	-6.2	33.3	-7.7
December 2001	3.2	-3.2	0	-5.1	32.8	-16.5	-6.3	-4.1	9.0
January 2002	-2.3	-46.2	55.0	-13.1	22.5	-8.0	-23.0	48.7	7.1
February 2002	-2.4	-18.7	29.1	-1.8	-12.7	18.7	-24.4	2.2	17.3
March 2002	-3.1	-11.6	40.9	-0.4	0.3	0.1	-6.8	4.5	18.2
April 2002	-26.3	-1.4	30.1	0	-0.1	-1.1	-0.3	14.6	7.5

Table II. Differences in the percentage mass of main prey groups in the diet of Cape fur seals *Arctocephalus pusillus pusillus* achieved from samples of individual scats when analysed separately (M_{is}), and together ($M_{ib}(\text{indiv})$), per month from May 2001 to April 2002 for each study colony.

Month	$M_{ib}(\text{indiv}) - M_{is}$								
	Cape Cross			Atlas-Wolf Bay			Van Reenen Bay		
	Horse mackerel	Hake	Goby	Hake	Lantern-fish	Goby	Hake	Lantern-fish	Goby
May 2001	2.7	0	0.3	-12.4	-0.3	3.8	8.7	-1.9	-4.0
June 2001	-4.6	0.1	0	8.9	-5.9	-2.4	-1.0	0	0.3
July 2001	8.9	0	-3.6	-1.5	-4.3	-3.1	-4.8	-1.5	-0.5
August 2001	1.1	-2.1	-3.1	9.8	-6.5	0.3	-18.1	-4.4	-9.5
September 2001	-5.7	9.1	-2.3	4.9	-6.0	-1.5	-0.9	-4.5	-10.9
October 2001	15.6	-16.0	-0.1	13.4	-16.7	2.8	9.0	-19.0	-4.4
November 2001	-1.4	3.5	-1.5	6.9	-15.1	7.1	3.4	-8.0	-5.6
December 2001	20.6	-20.6	0	3.5	-0.1	1.6	-3.8	-3.3	-4.3
January 2002	1.5	8.8	-6.2	11.1	-12.3	0.9	-10.0	-3.3	9.8
February 2002	-1.2	22.5	-29.3	-8.3	-12.8	23.0	-11.1	-0.1	-9.2
March 2002	3.5	-10.5	-13.4	-0.6	0.1	0.6	-0.5	-3.9	-11.3
April 2002	-2.1	-1.8	-2.4	-0.1	-0.1	-10.8	-3.2	1.2	-7.0

Table III. Differences in the percentage numerical abundance of main prey groups in the diet of Cape fur seals *Arctocephalus pusillus pusillus* from samples of individual scats that were analysed together ($N_{ib}(\text{indiv})$), and bag samples that were collected at the same time as the individual scats ($N_{ib}(\text{bag})$), per month from May 2001 to April 2002 for each study colony.

Month	$N_{ib}(\text{indiv}) - N_{ib}(\text{bag})$								
	Cape Cross			Atlas-Wolf Bay			Van Reenen Bay		
	Horse mackerel	Hake	Goby	Hake	Lantern-fish	Goby	Hake	Lantern-fish	Goby
May 2001	-9.8	0.1	5.2	-16.6	2.5	12.9	-5.4	-20.0	25.9
June 2001	-2.1	-0.3	0.7	-3.8	11.0	-6.7	27.2	-19.7	-0.5
July 2001	0.9	-1.5	0.1	4.3	-23.0	3.4	-3.2	37.0	8.7
August 2001	26.5	-0.3	-24.8	-3.0	20.2	-19.0	-13.7	-1.2	-23.4
September 2001	1.3	3.6	-4.7	-9.2	15.4	-2.3	-0.5	-25.1	36.2
October 2001	-2.6	3.0	-0.9	0	0	0	0	0	0
November 2001	11.2	-1.4	-7.1	0	0	0	0	0	0
December 2001	29.5	-5.5	-24.0	0	0	0	0	0	0
January 2002	0	0	0	0	0	0	0	0	0
February 2002	0	0	0	0	0	0	0	0	0
March 2002	0	0	0	0	0	0	0	0	-0.1
April 2002	0	0	0	0	0	0	0	0	0

Table IV. Differences in the percentage mass of main prey groups in the diet of Cape fur seals *Arctocephalus pusillus pusillus* from samples of individual scats that were analysed together ($M_{ib}(\text{indiv})$), and bag samples that were collected at the same time as the individual scats ($M_{ib}(\text{bag})$), per month from May 2001 to April 2002 for each study colony.

Month	$M_{ib}(\text{indiv}) - M_{ib}(\text{bag})$								
	Cape Cross			Atlas-Wolf Bay			Van Reenen Bay		
	Horse mackerel	Hake	Goby	Hake	Lantern-fish	Goby	Hake	Lantern-fish	Goby
May 2001	-10.9	0.1	0.8	-27.5	0.2	10.3	-9.0	-0.8	13.2
June 2001	1.4	-1.1	0.1	-0.3	5.1	-4.4	13.9	-2.0	-0.5
July 2001	1.2	-3.4	0	-1.2	-2.4	-0.4	23.6	1.1	2.1
August 2001	23.4	-9.1	-9.1	5.0	2.7	-10.2	-24.0	0.2	-4.9
September 2001	17.8	-4.5	-2.3	-21.4	31.5	0.3	-14.9	-4.2	26.2
October 2001	-5.5	13.8	-0.3	0.4	0.5	0.3	0	0	0
November 2001	25.4	3.7	-1.4	-1.2	-1.1	-0.6	0.8	0.2	0.6
December 2001	45.8	-45.2	-0.5	0	0	0	1.8	0	0.5
January 2002	0.2	2.4	0.9	0.3	0.2	0.1	0.7	0.1	0.6
February 2002	-0.3	-5.6	-0.7	0	0	0.2	5.2	0	2.7
March 2002	0.2	0.1	0.1	0	0	0	-16.7	-0.1	-3.8
April 2002	-0.2	0.0	0	0	0	-3.2	-0.4	-0.4	-2.5

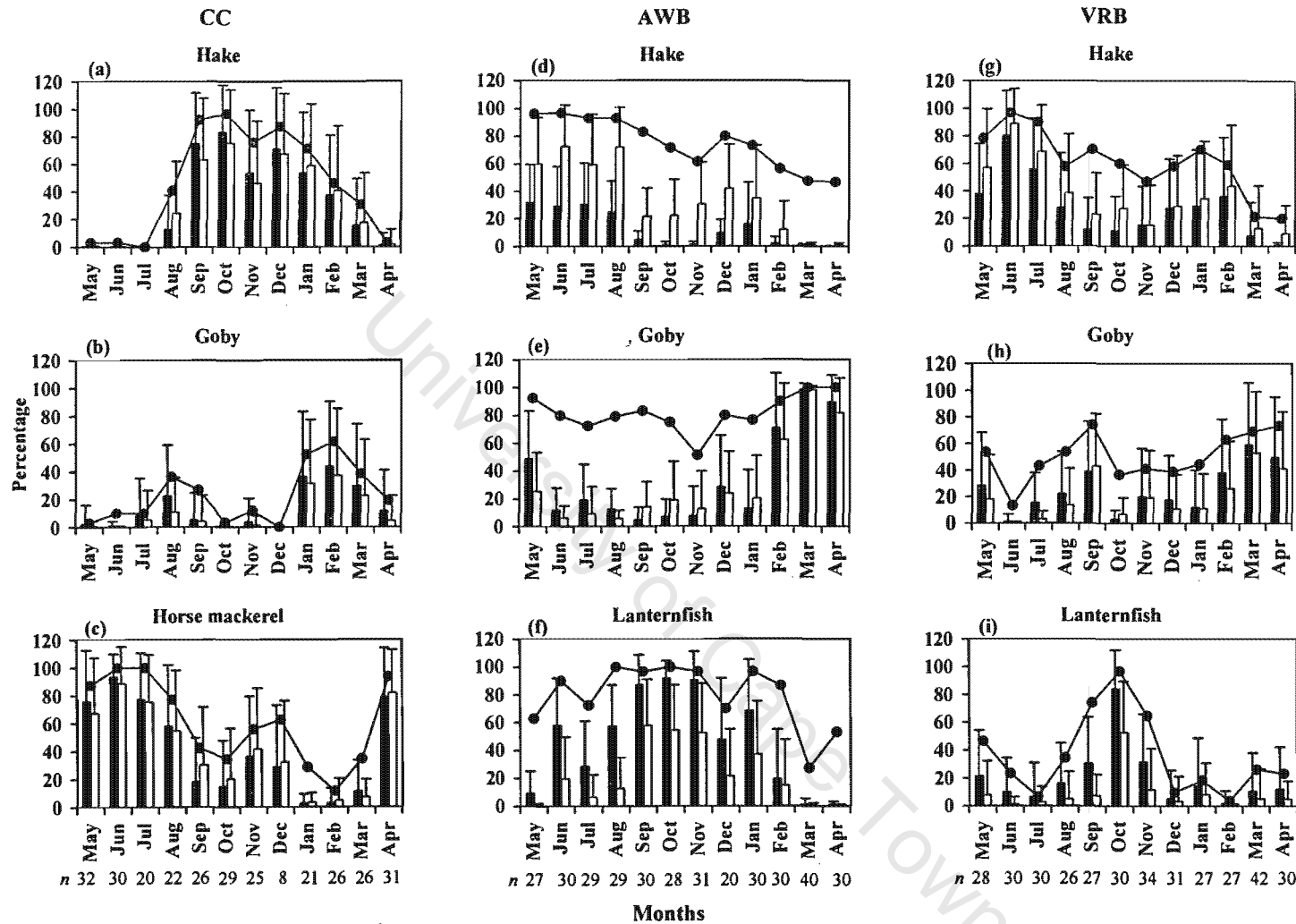


Figure 1. The percentage numerical abundance (N_{is}) (black bar) and mass (M_{is}) (white bar) of main prey groups consumed by Cape fur seals *Arctocephalus pusillus pusillus* in Namibia at (a-c) Cape Cross (CC), (d-f) Atlas-Wolf Bay (AWB) and (g-i) Van Reenen Bay (VRB), as determined from monthly individual scat samples collected from May 2001 to April 2002. The FO_{is} of the main prey groups in individual scat samples is represented by (●). Sample size is given by n and error bars denote one standard deviation.

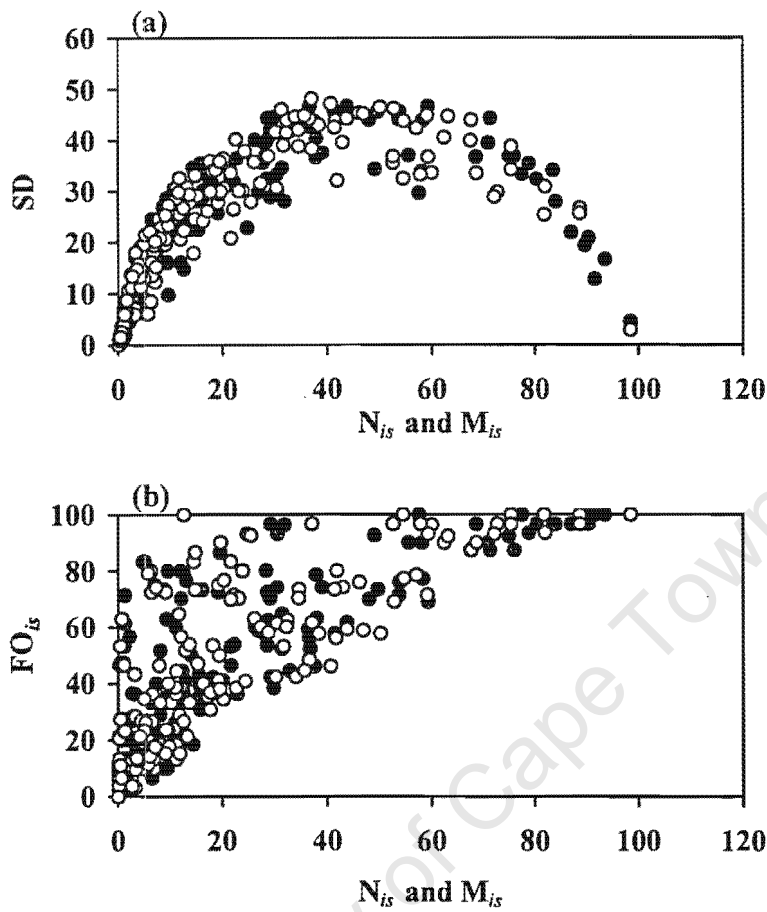


Figure 2. The relationship of N_{is} ($\bullet$) and M_{is} ($\circ$) of prey groups to (a) the standard deviations (SD) of these values, and to (b) the FO_{is} of the respective prey groups, as determined for monthly individual scat samples of Cape fur seals *Arctocephalus pusillus pusillus* collected at the three study colonies in Namibia from May 2001 to April 2002.

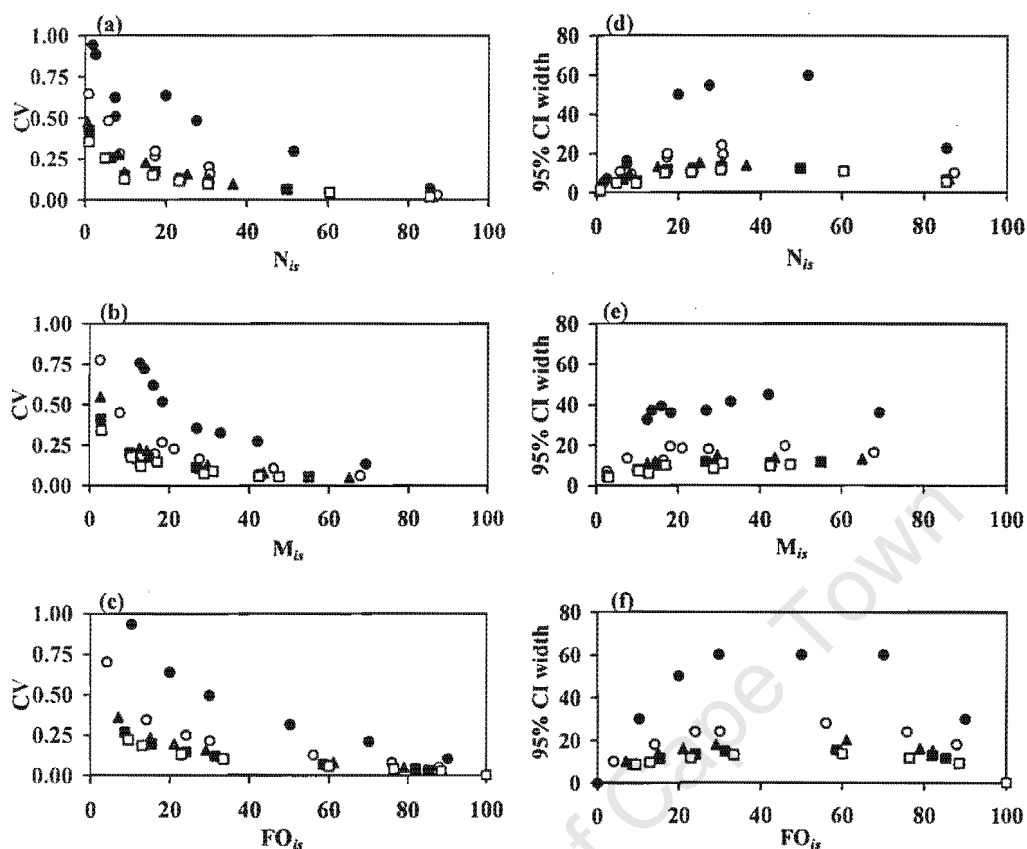


Figure 3. The relationship of N_{is} , M_{is} , and mean FO_{is} to (a-c) the coefficients of variation (CV), and (d-f) the widths of the 95% confidence intervals (CI), for bootstrap resamples ($n = 5\,000$) of 10 (●), 50 (○), 100 (▲), 150 (■) and 200 (□) scats.

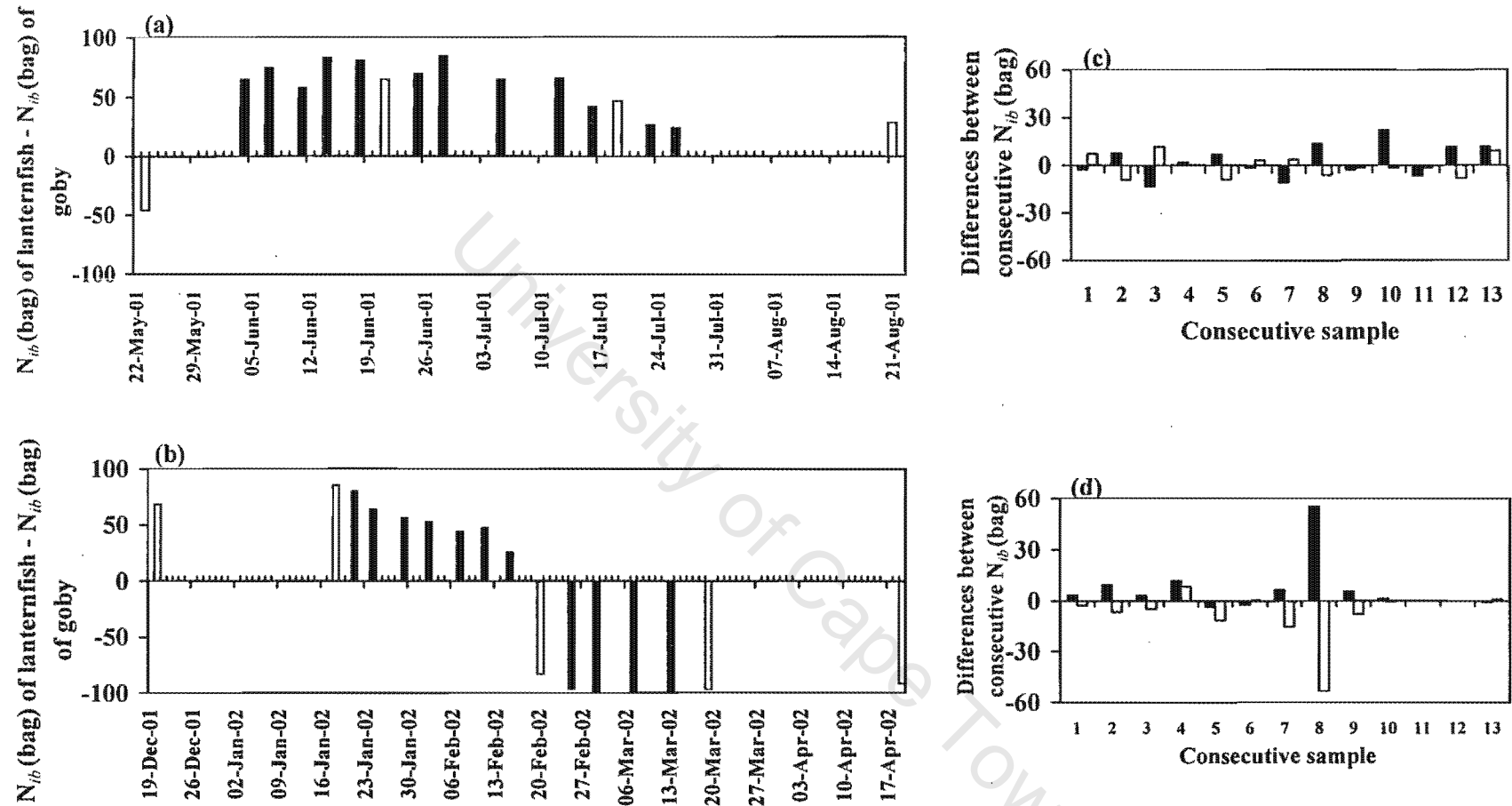


Figure 4. The differences between the $N_{lb}(\text{bag})$ of lanternfish *Lampanyctodes hectoris* and that of pelagic goby *Sufflogobius bibarbatatus* from bag samples of Cape fur seal scats *Arctocephalus pusillus pusillus* collected approximately biweekly during (a) 4 June to 26 July 2001 and (b) 18 January to 19 March 2002. Differences for monthly bag samples taken just prior to, after and within these periods are shown as white bars. The differences between consecutive $N_{lb}(\text{bag})$ of lanternfish (black bars) and of goby (white bars) from approximately biweekly bag samples collected during (c) 4 June to 26 July 2001 and (d) 18 January to 19 March 2002.

Appendix I. The percentage numerical abundance of the six prey groups in the diet of Cape fur seals *Arctocephalus pusillus pusillus*, from individual scats pooled to represent a bag sample ($N_{ib}(\text{indiv})$) and from individual scat samples ($N_{is} \pm \text{SD}$), per month from May 2001 to April 2002 at each study colony. The number of individual samples collected is given by n .

Colony	Month	n	$N_{ib}(\text{indiv})$						$N_{is} (\pm \text{SD})$					
			Horse mackerel	Hake	Lantern-fish	Goby	Pelagics	Others	Horse mackerel	Hake	Lantern-fish	Goby	Pelagics	Others
CC	May 2001	32	85.00	0.08	0	6.12	8.80	0	75.97 (± 36.84)	0.08 (± 0.44)	0	2.43 (± 13.73)	21.52 (± 34.16)	0
	June 2001	30	95.61	0.03	0	0.71	3.64	0	93.52 (± 16.57)	0.01 (± 0.08)	0	0.91 (± 3.44)	5.56 (± 15.69)	0
	July 2001	20	66.86	0	0	25.66	7.48	0	77.44 (± 33.28)	0	0	8.61 (± 26.88)	13.95 (± 22.51)	0
	August 2001	22	46.49	6.14	0.04	41.70	5.24	0.39	58.25 (± 43.86)	12.91 (± 24.56)	0.03 (± 0.15)	22.78 (± 36.44)	3.12 (± 7.32)	2.91 (± 11.92)
	September 2001	26	1.67	92.95	0	5.25	0.12	0.01	18.03 (± 31.60)	74.89 (± 36.80)	0	5.44 (± 19.37)	1.22 (± 3.39)	0.42 (± 2.17)
	October 2001	29	5.75	93.07	0	0.02	1.17	0	14.92 (± 32.96)	83.50 (± 34.12)	0	0.15 (± 0.83)	1.43 (± 4.94)	0
	November 2001	25	18.86	79.46	0	0.43	1.21	0.05	36.54 (± 42.99)	53.83 (± 45.52)	0	3.94 (± 16.76)	5.56 (± 20.08)	0.13 (± 0.67)
	December 2001	8	31.93	68.07	0	0	0	0	28.72 (± 44.29)	71.28 (± 44.29)	0	0	0	0
	January 2002	21	0.47	7.51	0	91.68	0.05	0.30	2.75 (± 6.52)	53.71 (± 44.11)	0	36.69 (± 46.57)	0.39 (± 1.78)	6.46 (± 22.36)
	February 2002	26	0.45	18.94	0	72.75	3.37	4.50	2.82 (± 10.71)	37.61 (± 43.59)	0	43.70 (± 46.57)	4.18 (± 18.99)	11.69 (± 32.53)
	March 2002	26	8.09	4.14	0	70.66	16.80	0.30	11.19 (± 22.54)	15.74 (± 33.76)	0	29.76 (± 44.43)	41.40 (± 45.50)	1.91 (± 9.72)
	April 2002	31	52.44	0.06	0	41.81	5.70	0	78.77 (± 35.41)	1.49 (± 8.32)	0	11.75 (± 29.31)	7.99 (± 22.07)	0
AWB	May 2001	27	0.04	16.38	4.19	73.53	5.85	0	0.02 (± 0.12)	31.84 (± 27.90)	9.25 (± 15.96)	49.05 (± 34.24)	9.84 (± 26.13)	0
	June 2001	30	0.03	9.97	86.45	3.42	0.12	0	0.11 (± 0.42)	29.19 (± 28.75)	58.09 (± 33.91)	11.95 (± 16.05)	0.67 (± 2.44)	0
	July 2001	29	0.28	17.41	38.47	16.22	26.99	0.63	0.76 (± 2.15)	30.53 (± 30.04)	28.62 (± 32.54)	19.12 (± 25.60)	17.53 (± 32.21)	3.44 (± 11.16)
	August 2001	29	0.04	12.23	75.11	7.32	4.92	0.39	0.04 (± 0.22)	24.70 (± 22.71)	57.51 (± 29.57)	12.54 (± 14.82)	3.03 (± 7.21)	2.18 (± 5.93)

Appendix I. (cont.)

VRB	September 2001	30	0	3.22	94.00	2.13	0.60	0.06	0	4.74 (± 6.29)	87.02 (± 21.75)	4.99 (± 8.88)	3.22 (± 16.99)	0.04 (± 0.16)
	October 2001	28	0	1.08	93.68	5.08	0.01	0.14	0	1.18 (± 2.24)	91.64 (± 12.71)	6.97 (± 12.63)	0.01 (± 0.03)	0.20 (± 0.64)
	November 2001	31	0.05	0.83	94.16	4.73	0.01	0.21	0.04 (± 0.15)	1.26 (± 2.07)	90.36 (± 20.75)	8.01 (± 20.80)	0.04 (± 0.24)	0.28 (± 1.43)
	December 2001	20	1.81	4.43	80.74	11.86	1.15	0	9.29 (± 28.60)	9.48 (± 9.70)	47.93 (± 43.91)	28.37 (± 36.99)	4.93 (± 19.87)	0
	January 2002	30	0.14	3.06	91.04	4.99	0.67	0.10	0.12 (± 0.52)	16.15 (± 30.10)	68.51 (± 36.70)	13.02 (± 27.67)	2.08 (± 5.91)	0.12 (± 0.46)
	February 2002	30	1.49	0.33	6.89	89.51	1.76	0.02	1.96 (± 6.62)	2.09 (± 4.66)	19.56 (± 35.54)	70.84 (± 39.48)	5.52 (± 19.18)	0.02 (± 0.13)
	March 2002	40	0	0.15	1.28	98.55	0.02	0	0	0.50 (± 1.05)	0.97 (± 4.32)	98.49 (± 4.46)	0.04 (± 0.24)	0
	April 2002	30	0.02	0.24	1.01	88.58	9.97	0.18	0.05 (± 0.20)	0.23 (± 0.30)	1.12 (± 2.01)	89.65 (± 19.40)	8.80 (± 19.50)	0.16 (± 0.85)
	May 2001	28	0.11	15.02	54.60	28.08	1.61	0.57	0.20 (± 0.82)	37.89 (± 36.55)	21.59 (± 32.62)	28.53 (± 39.80)	4.30 (± 14.57)	7.48 (± 22.73)
	June 2001	30	0.06	51.50	42.14	2.55	3.43	0.32	0.03 (± 0.18)	80.29 (± 32.30)	9.98 (± 24.45)	1.36 (± 5.25)	8.08 (± 23.48)	0.25 (± 0.83)
	July 2001	30	0	30.69	37.28	12.99	14.51	4.53	0	55.57 (± 36.92)	6.42 (± 24.45)	15.39 (± 22.48)	15.44 (± 23.19)	7.18 (± 17.58)
	August 2001	26	0	5.33	11.27	9.01	73.47	0.93	0	27.96 (± 39.42)	16.29 (± 28.81)	22.23 (± 31.83)	29.21 (± 42.10)	4.31 (± 13.64)
	September 2001	27	0.07	8.75	41.24	41.04	8.06	0.84	0.15 (± 0.56)	12.00 (± 22.99)	30.45 (± 33.25)	39.01 (± 37.47)	12.18 (± 27.74)	6.21 (± 19.72)
	October 2001	30	0.06	3.44	94.76	0.57	1.11	0.05	0.11 (± 0.60)	10.99 (± 24.91)	83.95 (± 27.84)	2.67 (± 7.07)	2.24 (± 7.02)	0.04 (± 0.18)
	November 2001	34	1.39	9.08	64.69	12.38	12.03	0.43	1.14 (± 4.73)	15.31 (± 28.03)	31.40 (± 34.50)	20.04 (± 36.32)	26.84 (± 29.72)	5.28 (± 15.85)
	December 2001	31	0.22	21.33	1.34	26.71	42.05	8.36	3.23 (± 17.96)	27.67 (± 35.62)	5.48 (± 20.14)	17.74 (± 33.31)	36.55 (± 44.36)	9.33 (± 16.16)
	January 2002	27	2.54	6.17	63.01	19.32	8.82	0.14	11.35 (± 26.75)	29.12 (± 40.83)	14.31 (± 34.54)	12.25 (± 27.94)	32.87 (± 41.66)	0.09 (± 0.39)
	February 2002	27	0.56	12.00	4.01	55.24	23.74	4.45	0.37 (± 1.93)	36.41 (± 42.68)	1.77 (± 9.19)	37.96 (± 40.34)	11.00 (± 28.49)	12.49 (± 27.79)
	March 2002	42	0.03	0.74	15.38	77.41	5.28	1.16	0.07 (± 0.41)	7.58 (± 24.22)	10.84 (± 27.31)	59.20 (± 46.54)	6.54 (± 21.27)	15.77 (± 35.45)
	April 2002	30	0.88	0.44	26.82	57.09	14.63	0.13	10.84 (± 30.57)	0.74 (± 1.98)	12.22 (± 30.02)	49.59 (± 45.51)	26.28 (± 40.07)	0.32 (± 1.68)

Appendix II. The monthly percentage mass of the six prey groups in the diet of Cape fur seals *Arctocephalus pusillus pusillus*, from individual scats pooled to represent a bag sample ($M_{ib}(\text{indiv})$) and from individual scat samples ($M_{is} \pm \text{SD}$), from May 2001 to April 2002 at each study colony. The number of individual samples collected is given by n .

Colony	Month	n	$M_{ib}(\text{indiv})$						$M_{is} (\pm \text{SD})$					
			Horse mackerel	Hake	Lantern-fish	Goby	Pelagics	Others	Horse mackerel	Hake	Lantern-fish	Goby	Pelagics	Others
CC	May 2001	32	70.26	0.14	0	1.00	28.59	0	67.51 (± 39.93)	0.14 (± 0.79)	0	0.66 (± 3.76)	31.69 (± 38.95)	0
	June 2001	30	84.14	0.12	0	0.14	15.60	0	88.70 (± 26.56)	0.06 (± 0.33)	0	0.17 (± 0.63)	11.07 (± 26.48)	0
	July 2001	20	84.18	0	0	1.67	14.15	0	75.30 (± 34.21)	0	0	5.29 (± 21.29)	19.41 (± 29.42)	0
	August 2001	22	55.67	22.26	0	7.95	13.29	0.83	54.57 (± 43.73)	24.34 (± 37.84)	0	11.05 (± 24.66)	6.48 (± 13.54)	3.56 (± 14.72)
	September 2001	26	24.51	72.24	0	2.05	1.08	0.12	30.19 (± 41.59)	63.13 (± 44.71)	0	4.31 (± 19.06)	1.19 (± 2.79)	1.18 (± 6.00)
	October 2001	29	35.79	59.29	0	0.01	4.92	0	20.15 (± 36.42)	75.29 (± 38.80)	0	0.07 (± 0.40)	4.48 (± 15.51)	0
	November 2001	25	40.16	49.54	0	0.09	10.10	0.11	41.60 (± 43.79)	46.09 (± 45.25)	0	1.55 (± 6.76)	10.63 (± 24.76)	0.13 (± 0.66)
	December 2001	8	53.00	47.00	0	0	0	0	32.40 (± 43.86)	67.60 (± 43.86)	0	0	0	0
	January 2002	21	4.66	67.88	0	25.19	0.34	1.94	3.16 (± 7.03)	59.08 (± 44.82)	0	31.38 (± 45.95)	0.30 (± 1.37)	6.07 (± 22.09)
	February 2002	26	3.58	63.18	0	7.76	9.17	16.32	4.79 (± 15.63)	40.69 (± 47.09)	0	37.09 (± 48.00)	5.69 (± 20.92)	11.75 (± 32.52)
	March 2002	26	10.55	7.12	0	9.22	72.40	0.72	7.03 (± 12.76)	17.64 (± 35.90)	0	22.60 (± 40.21)	50.10 (± 46.37)	2.63 (± 13.40)
	April 2002	31	79.84	0.14	0	2.11	17.91	0	81.92 (± 30.81)	1.92 (± 10.71)	0	4.50 (± 18.23)	11.65 (± 25.45)	0
AWB	May 2001	27	0.38	47.59	0.35	29.28	22.41	0	0.23 (± 1.20)	60.01 (± 33.57)	0.66 (± 1.27)	25.45 (± 27.86)	13.65 (± 29.32)	0
	June 2001	30	0.60	81.54	13.75	3.84	0.26	0	0.37 (± 1.39)	72.66 (± 29.71)	19.70 (± 29.88)	6.27 (± 8.50)	1.00 (± 3.99)	0
	July 2001	29	0.18	57.77	2.06	5.98	31.93	2.08	0.20 (± 0.54)	59.25 (± 36.69)	6.34 (± 16.08)	9.08 (± 19.63)	18.11 (± 33.93)	7.02 (± 21.41)
	August 2001	29	0.19	81.86	6.07	5.99	3.51	2.38	0.11 (± 0.61)	72.05 (± 28.82)	12.59 (± 22.29)	5.73 (± 6.11)	5.23 (± 15.96)	4.29 (± 11.26)
	September 2001	30	0	26.46	51.85	12.92	6.05	2.72	0 (± 20.66)	21.60 (± 33.21)	57.84 (± 33.21)	14.44 (± 17.84)	4.59 (± 18.04)	1.54 (± 6.54)

Appendix II. (cont.)

VRB	October 2001	28	0	35.58	37.73	22.07	0.26	4.37	0	22.14 (± 26.43)	54.46 (± 32.43)	19.22 (± 27.69)	0.04 (± 0.21)	4.13 (± 13.27)
	November 2001	31	0.02	37.36	37.40	19.95	0.30	4.97	0.02 (± 0.06)	30.41 (± 30.58)	52.52 (± 35.51)	12.81 (± 26.91)	0.41 (± 2.27)	3.82 (± 15.70)
	December 2001	20	1.03	45.50	21.45	25.44	6.58	0	6.77 (± 20.94)	41.96 (± 32.08)	21.60 (± 33.57)	23.87 (± 30.03)	5.80 (± 19.56)	0
	January 2002	30	0.29	45.71	24.77	21.16	6.54	1.54	0.21 (± 0.70)	34.60 (± 38.75)	37.10 (± 38.27)	20.31 (± 30.52)	6.75 (± 18.09)	1.03 (± 3.98)
	February 2002	30	3.65	3.66	1.97	85.38	5.05	0.28	4.19 (± 14.11)	11.92 (± 20.61)	14.75 (± 33.15)	62.41 (± 40.57)	6.43 (± 20.51)	0.31 (± 1.68)
	March 2002	40	0	0.28	0.47	99.14	0.11	0	0	0.90 (± 1.85)	0.40 (± 1.88)	98.52 (± 2.88)	0.18 (± 1.12)	0
	April 2002	30	0.20	1.03	0.29	70.97	24.36	3.15	0.51 (± 1.95)	1.09 (± 1.54)	0.36 (± 0.68)	81.75 (± 25.24)	14.69 (± 24.54)	1.59 (± 8.72)
	May 2001	28	1.23	65.65	5.86	14.07	10.06	3.14	0.68 (± 2.53)	56.99 (± 42.41)	7.77 (± 24.60)	18.10 (± 33.57)	6.82 (± 19.41)	9.63 (± 27.22)
	June 2001	30	0.23	87.63	1.24	0.46	9.85	0.60	0.07 (± 0.41)	88.65 (± 25.57)	1.25 (± 5.11)	0.20 (± 0.72)	9.54 (± 25.58)	0.27 (± 0.89)
	July 2001	30	0	63.79	1.08	2.57	24.45	8.11	0	68.55 (± 33.53)	2.54 (± 11.17)	3.06 (± 5.99)	16.28 (± 24.17)	9.56 (± 23.31)
	August 2001	26	0	20.31	0.52	4.13	71.62	3.42	0	38.42 (± 42.96)	4.90 (± 19.66)	13.64 (± 27.68)	34.02 (± 44.50)	9.02 (± 25.29)
	September 2001	27	0.12	22.19	2.71	32.11	41.14	1.73	0.07 (± 0.26)	23.10 (± 29.96)	7.22 (± 15.21)	42.96 (± 39.50)	18.66 (± 34.10)	8.00 (± 20.73)
	October 2001	30	0.19	36.36	33.51	2.58	26.93	0.43	0.03 (± 0.18)	27.32 (± 31.53)	52.54 (± 36.76)	7.00 (± 12.22)	12.48 (± 26.64)	0.62 (± 2.58)
	November 2001	34	0.07	18.60	3.66	13.57	62.86	1.24	0.02 (± 0.08)	15.20 (± 29.13)	11.61 (± 29.72)	19.20 (± 35.60)	46.93 (± 45.17)	7.04 (± 20.21)
	December 2001	31	1.30	25.05	0.02	6.58	48.72	18.34	3.23 (± 17.96)	28.82 (± 36.83)	3.29 (± 17.95)	10.86 (± 25.97)	36.61 (± 44.14)	17.19 (± 26.07)
	January 2002	27	4.23	24.57	4.82	20.84	45.06	0.49	10.10 (± 26.44)	34.54 (± 41.94)	8.11 (± 22.81)	11.08 (± 26.27)	35.73 (± 44.80)	0.44 (± 1.57)
	February 2002	27	1.14	32.63	0.09	16.98	41.28	7.89	1.09 (± 5.69)	43.75 (± 44.18)	0.24 (± 1.26)	26.15 (± 35.71)	11.04 (± 28.52)	17.73 (± 29.90)
	March 2002	42	0.38	12.64	1.26	41.48	28.94	15.31	0.31 (± 1.68)	13.17 (± 30.82)	5.17 (± 21.49)	52.76 (± 46.12)	9.09 (± 23.97)	19.50 (± 35.81)
	April 2002	30	6.57	5.89	6.18	34.37	46.15	0.84	11.17 (± 30.79)	9.05 (± 20.60)	4.93 (± 12.95)	41.36 (± 42.52)	32.24 (± 41.38)	1.25 (± 5.53)

Appendix III. The monthly percentage frequency of occurrence (FO_{is}) of the six prey groups in the diet of Cape fur seals *Arctocephalus pusillus pusillus*, from individual scats collected from May 2001 to April 2002 at each study colony. The number of individual samples collected is given by n .

Colony	Month	n	FO_{is}					
			Horse mackerel	Hake	Lantern-fish	Goby	Pelagics	Others
CC	May 2001	32	87.50	3.13	0	3.13	53.13	0
	June 2001	30	100.00	3.33	0	10.00	23.33	0
	July 2001	20	100.00	0	0	10.00	50.00	0
	August 2001	22	77.27	40.91	4.55	36.36	36.36	13.64
	September 2001	26	42.31	92.31	0	26.92	23.08	3.85
	October 2001	29	34.48	96.55	0	3.45	13.79	0
	November 2001	25	56.00	76.00	0	12.00	24.00	4.00
	December 2001	8	62.50	87.50	0	0	0	0
	January 2002	21	28.57	71.43	0	52.38	4.76	14.29
	February 2002	26	11.54	46.15	0	61.54	11.54	15.38
	March 2002	26	34.62	30.77	0	38.46	57.69	3.85
	April 2002	31	93.55	3.23	0	19.35	29.03	0
AWB	May 2001	27	3.70	96.30	62.96	92.59	33.33	0
	June 2001	30	6.67	96.67	90.00	80.00	10.00	0
	July 2001	29	20.69	93.10	72.41	72.41	37.93	17.24
	August 2001	29	3.45	93.10	100.00	79.31	20.69	20.69
	September 2001	30	0	83.33	96.67	83.33	10.00	6.67
	October 2001	28	0	71.43	100.00	75.00	3.57	21.43
	November 2001	31	9.68	61.29	96.77	51.61	3.23	12.90
	December 2001	20	10.00	80.00	70.00	80.00	20.00	0
	January 2002	30	10.00	73.33	96.67	76.67	13.33	6.67
	February 2002	30	20.00	56.67	86.67	90.00	26.67	3.33
	March 2002	40	0	47.50	27.50	100.00	2.50	0
	April 2002	30	6.67	46.67	53.33	100.00	73.33	3.33
VRB	May 2001	28	7.14	78.57	46.43	53.57	17.86	17.86
	June 2001	30	3.33	96.67	23.33	13.33	23.33	10.00
	July 2001	30	0	90.00	6.67	43.33	40.00	40.00
	August 2001	26	0	57.69	34.62	53.85	42.31	15.38
	September 2001	27	7.41	70.37	74.07	74.07	37.04	33.33
	October 2001	30	3.33	60.00	96.67	36.67	26.67	6.67
	November 2001	34	5.88	47.06	64.71	41.18	58.82	17.65
	December 2001	31	3.23	58.06	9.68	38.71	48.39	35.48
	January 2002	27	33.33	70.37	18.52	44.44	44.44	11.11
	February 2002	27	3.70	59.26	3.70	62.96	18.52	37.04
	March 2002	42	4.76	21.43	26.19	69.05	23.81	38.10
	April 2002	30	13.33	20.00	23.33	73.33	60.00	6.67

Appendix IV. The percentage numerical abundance and mass of the six prey groups in the diet of Cape fur seals *Arctocephalus pusillus pusillus*, from bag samples ($N_{ib}(\text{bag})$ and $M_{ib}(\text{bag})$, respectively) collected concurrently to individual scat samples, per month from May 2001 to April 2002 at each study colony.

Colony	Month	$N_{ib}(\text{bag})$						$M_{ib}(\text{bag})$					
		Horse mackerel	Hake	Lantern-fish	Goby	Pelagics	Others	Horse mackerel	Hake	Lantern-fish	Goby	Pelagics	Others
CC	May 2001	94.79	0	0	0.95	4.26	0	81.19	0	0	0.16	18.65	0
	June 2001	97.73	0.36	0	0	1.91	0	82.70	1.24	0	0	16.06	0
	July 2001	65.97	1.52	0	25.53	6.99	0	82.95	3.39	0	1.66	12.00	0
	August 2001	19.96	6.41	0	66.50	7.14	0	32.23	31.34	0	17.10	19.34	0
	September 2001	0.42	89.37	0	9.97	0.17	0.08	6.76	76.78	0	4.30	8.08	4.09
	October 2001	8.35	90.05	0	0.93	0.64	0.03	41.25	45.52	0	0.31	12.73	0.19
	November 2001	7.65	80.87	0	7.54	3.46	0.48	14.80	45.84	0	1.46	36.14	1.75
	December 2001	2.39	73.57	0	24.04	0	0	7.21	92.25	0	0.54	0	0
	January 2002	0.47	7.51	0	91.68	0.05	0.30	4.50	65.53	0	24.31	0.32	5.33
	February 2002	0.45	18.94	0	72.75	3.37	4.50	3.90	68.81	0	8.45	11.69	7.15
	March 2002	8.09	4.14	0	70.66	16.80	0.30	10.40	7.02	0	9.09	71.32	2.18
	April 2002	52.44	0.06	0	41.81	5.70	0	80.02	0.14	0	2.12	17.72	0
AWB	May 2001	0	32.93	1.70	60.67	4.67	0.03	0	75.07	0.11	19.00	5.78	0.04
	June 2001	0.03	13.78	75.41	10.14	0.62	0.03	0.40	81.84	8.70	8.26	0.68	0.11
	July 2001	0.13	13.08	61.43	12.80	12.04	0.52	0.11	58.93	4.47	6.41	28.28	1.80
	August 2001	0	15.22	54.87	26.29	3.34	0.27	0	76.82	3.34	16.21	1.30	2.33
	September 2001	0.11	12.37	78.64	4.43	4.42	0.03	3.25	47.82	20.39	12.65	15.09	0.80
	October 2001	0	1.08	93.68	5.08	0.01	0.14	0	35.15	37.24	21.81	0.25	5.55
	November 2001	0.05	0.83	94.16	4.73	0.01	0.21	0.02	38.53	38.53	20.57	0.31	2.04
	December 2001	1.81	4.43	80.74	11.86	1.15	0	1.03	45.51	21.43	25.45	6.58	0
	January 2002	0.14	3.06	91.04	4.99	0.67	0.10	0.29	45.44	24.60	21.04	6.84	1.80
	February 2002	1.49	0.33	6.89	89.51	1.76	0.02	3.64	3.65	1.97	85.14	5.02	0.58
	March 2002	0	0.15	1.28	98.55	0.02	0	0	0.28	0.47	99.18	0.07	0
	April 2002	0.02	0.24	1.01	88.58	9.97	0.18	0.21	1.08	0.30	74.12	23.75	0.54
VRB	May 2001	0.04	20.44	74.56	2.19	2.45	0.32	0.36	74.64	6.64	0.91	12.78	4.67
	June 2001	0	24.33	61.83	3.08	10.24	0.52	0	73.78	3.27	0.99	17.57	4.39
	July 2001	0	33.91	0.29	4.28	60.65	0.88	0	40.20	0	0.48	55.50	3.81
	August 2001	0.13	19.04	12.45	32.43	34.24	1.70	0.65	44.33	0.35	9.07	38.43	7.16

Appendix IV. (cont.)

September 2001	0.28	9.28	66.38	4.81	19.00	0.26	0.83	37.07	6.86	5.93	45.74	3.57
October 2001	0.06	3.44	94.76	0.57	1.11	0.05	0.19	36.39	33.51	2.58	26.95	0.38
November 2001	1.39	9.08	64.69	12.38	12.03	0.43	0.06	17.83	3.50	13.01	60.02	5.57
December 2001	0.22	21.33	1.34	26.71	42.05	8.36	1.20	23.25	0.02	6.11	45.42	24.00
January 2002	2.54	6.17	63.01	19.32	8.82	0.14	4.11	23.86	4.67	20.24	45.20	1.91
February 2002	0.56	12.00	4.01	55.24	23.75	4.44	0.95	27.42	0.08	14.27	35.07	22.21
March 2002	0.03	0.74	15.39	77.46	5.28	1.10	0.41	29.32	1.39	45.25	7.73	15.90
April 2002	0.88	0.44	26.82	57.09	14.63	0.13	7.04	6.31	6.61	36.86	39.33	3.85

Appendix V. The true N_{is} compared to the bootstrapped N_{is} , for eight different bootstrap resampling sets of 10, 20, 30, ..., 200 scats. The coefficients of variation (CV) are given, as well as the lower, upper and the width of the 95% confidence intervals (CI). The eight resampled sets are arranged in increasing order of N_{is} values at 200 scats. Also given are the differences between $N_{ib}(\text{indiv})$ and N_{is} .

Bootstrapped resample set	Number of scats bootstrapped	True N_{is}	Bootstrapped N_{is}	CV	Lower 95% CI	Upper 95% CI	Width of 95% CI	$N_{ib}(\text{indiv})$ - N_{is}
1	10	2.56	2.52	0.89	0	7.28	7.28	0.23
	20	1.28	1.28	0.90	0	3.74	3.74	-0.04
	30	0.86	0.88	0.89	0	2.50	2.50	-0.07
	40	0.71	0.71	0.81	0.01	1.95	1.94	-0.09
	50	0.78	0.78	0.65	0.05	1.93	1.89	-0.22
	60	0.76	0.76	0.57	0.12	1.74	1.62	-0.18
	70	0.66	0.67	0.55	0.10	1.49	1.38	-0.12
	80	0.61	0.61	0.53	0.11	1.32	1.21	-0.13
	90	0.59	0.58	0.50	0.14	1.24	1.10	-0.13
	100	0.55	0.55	0.48	0.15	1.14	0.99	-0.15
	110	0.55	0.55	0.44	0.17	1.10	0.93	-0.13
	120	0.98	0.99	0.50	0.24	2.08	1.85	-0.47
	130	0.97	0.98	0.47	0.27	2.05	1.78	-0.46
	140	1.01	1.02	0.44	0.34	2.03	1.70	-0.44
	150	0.95	0.96	0.43	0.32	1.90	1.58	-0.43
	160	0.92	0.92	0.42	0.32	1.80	1.48	-0.41
	170	0.87	0.87	0.42	0.31	1.68	1.37	-0.39
	180	0.86	0.85	0.40	0.32	1.63	1.31	-0.37
	190	0.95	0.94	0.37	0.37	1.71	1.34	-0.44
	200	0.96	0.96	0.36	0.41	1.72	1.32	-0.43
2	10	1.76	1.77	0.94	0	5.28	5.28	1.95
	20	13.03	13.12	0.48	2.15	26.63	24.48	-2.51
	30	8.85	8.95	0.50	1.34	18.78	17.43	-3.89
	40	6.64	6.62	0.52	0.94	14.07	13.13	-3.96
	50	5.71	5.75	0.48	1.17	11.88	10.71	-3.42
	60	4.99	4.96	0.47	1.11	10.05	8.94	-3.18
	70	5.46	5.50	0.42	1.64	10.55	8.91	-3.64
	80	7.63	7.58	0.32	3.33	12.77	9.44	-0.78
	90	9.11	9.12	0.28	4.57	14.60	10.03	-1.86
	100	8.34	8.29	0.28	4.17	13.20	9.03	-1.47
	110	8.02	8.00	0.26	4.23	12.53	8.31	-1.00
	120	7.35	7.36	0.26	3.89	11.44	7.55	-1.30
	130	7.52	7.55	0.26	3.99	11.51	7.52	-1.77
	140	6.99	7.01	0.26	3.69	10.76	7.07	-2.21
	150	6.52	6.53	0.26	3.51	10.14	6.63	-2.63
	160	6.11	6.11	0.26	3.24	9.42	6.18	-2.59
	170	5.76	5.79	0.26	3.04	8.83	5.79	-2.96
	180	5.44	5.38	0.26	2.90	8.41	5.51	-3.03
	190	5.15	5.17	0.26	2.74	8.02	5.28	-2.90
	200	4.90	4.92	0.25	2.65	7.54	4.89	-2.87
3	10	7.30	7.40	0.63	0.73	17.28	16.55	-1.62
	20	7.59	7.58	0.43	1.81	14.83	13.02	1.12
	30	7.86	7.83	0.34	3.15	13.44	10.29	1.84
	40	8.20	8.25	0.32	3.64	13.94	10.30	1.04
	50	8.48	8.51	0.28	4.16	13.61	9.45	0

Appendix V. (cont.)

	60	9.74	9.67	0.24	5.53	14.53	9.00	0.30
	70	9.54	9.50	0.21	5.69	13.69	8.00	1.04
	80	9.53	9.47	0.20	6.12	13.31	7.19	0.04
	90	9.64	9.65	0.19	6.25	13.37	7.12	-0.46
	100	9.68	9.65	0.17	6.63	12.94	6.30	-0.76
	110	10.11	10.10	0.16	7.10	13.32	6.22	-1.16
	120	9.54	9.57	0.16	6.78	12.61	5.83	-1.19
	130	9.43	9.39	0.15	6.73	12.24	5.52	-1.54
	140	10.45	10.47	0.15	7.61	13.63	6.02	-1.07
	150	9.87	9.84	0.15	7.07	12.83	5.76	-1.23
	160	9.84	9.82	0.14	7.20	12.62	5.41	-1.36
	170	9.57	9.56	0.14	7.07	12.12	5.05	-1.37
	180	9.48	9.42	0.13	7.12	12.05	4.93	-1.53
	190	9.80	9.76	0.13	7.44	12.32	4.88	-1.68
	200	9.68	9.70	0.12	7.48	12.16	4.68	-1.50
4	10	20.00	19.95	0.64	0	50.00	50.00	-15.00
	20	19.92	19.72	0.44	5.00	39.38	34.38	-8.14
	30	19.95	19.89	0.36	6.67	33.43	26.76	-14.30
	40	17.41	17.33	0.34	7.39	29.79	22.40	-11.30
	50	17.33	17.31	0.30	7.91	27.63	19.72	-10.50
	60	14.45	14.34	0.31	6.27	23.81	17.54	-9.40
	70	16.48	16.49	0.26	8.42	25.44	17.02	-9.58
	80	15.90	15.99	0.25	8.66	24.11	15.45	-5.94
	90	16.03	16.01	0.24	8.91	23.78	14.87	-6.44
	100	14.95	14.97	0.23	8.79	21.92	13.13	-6.09
	110	16.49	16.54	0.21	9.96	23.57	13.61	-7.81
	120	15.95	15.97	0.20	9.83	22.54	12.72	-7.53
	130	16.89	16.94	0.19	11.06	23.50	12.44	-8.17
	140	16.40	16.49	0.18	11.02	22.79	11.78	-8.62
	150	17.29	17.37	0.17	11.65	23.40	11.75	-9.39
	160	17.77	17.91	0.16	12.50	23.78	11.28	-10.50
	170	17.31	17.26	0.16	12.10	23.05	10.96	-9.33
	180	16.91	16.93	0.16	11.96	22.28	10.32	-9.09
	190	16.68	16.67	0.16	11.64	21.78	10.14	-8.65
	200	16.85	16.77	0.15	12.07	21.88	9.81	-8.38
5	10	27.55	27.55	0.48	0.46	55.11	54.65	30.70
	20	16.96	17.09	0.44	3.94	33.53	29.59	11.50
	30	18.28	18.25	0.35	6.37	31.80	25.43	11.40
	40	17.02	17.07	0.31	7.47	28.17	20.70	11.50
	50	17.25	17.27	0.27	8.69	26.68	17.99	20.20
	60	18.44	18.33	0.24	10.24	27.47	17.24	9.23
	70	20.04	20.02	0.21	12.10	28.31	16.21	7.92
	80	23.61	23.66	0.18	15.57	32.40	16.83	13.80
	90	24.51	24.46	0.16	16.72	32.67	15.95	10.60
	100	25.24	25.18	0.16	17.58	32.95	15.37	12.40
	110	23.26	23.25	0.15	16.37	30.13	13.76	12.20
	120	24.49	24.39	0.14	17.77	31.42	13.65	12.20
	130	22.98	22.89	0.15	16.40	29.56	13.16	12.30
	140	24.02	24.01	0.14	17.83	30.70	12.87	10.00
	150	23.68	23.65	0.13	17.73	29.84	12.11	9.69
	160	23.46	23.50	0.13	17.83	29.33	11.50	7.66
	170	22.79	22.76	0.12	17.23	28.25	11.02	7.40

Appendix V. (cont.)

6	180	22.60	22.54	0.12	17.37	28.15	10.79	6.88
	190	23.93	23.98	0.11	18.67	29.39	10.72	6.49
	200	23.24	23.23	0.11	18.16	28.39	10.23	6.98
	10	51.52	51.56	0.30	21.60	81.29	59.68	-18.70
	20	36.07	36.37	0.29	16.28	56.24	39.96	-8.24
	30	36.82	37.00	0.23	20.61	54.12	33.51	11.80
	40	34.92	34.95	0.21	20.82	49.19	28.37	6.77
	50	30.66	30.59	0.20	18.79	42.93	24.14	9.99
	60	33.92	33.97	0.17	22.59	45.07	22.48	16.70
	70	31.25	31.27	0.16	21.33	41.66	20.32	16.40
	80	31.60	31.57	0.15	22.41	41.25	18.84	14.90
	90	31.75	31.72	0.14	23.25	40.48	17.23	13.70
	100	30.51	30.59	0.13	22.71	38.73	16.02	12.90
	110	29.53	29.54	0.13	22.09	37.33	15.24	11.20
	120	29.79	29.72	0.12	22.75	37.00	14.25	11.20
	130	30.45	30.31	0.12	23.71	37.60	13.89	11.30
	140	30.13	30.08	0.11	23.44	37.00	13.56	11.10
	150	30.55	30.55	0.11	24.16	37.09	12.94	11.80
	160	29.41	29.37	0.11	23.17	35.70	12.52	12.60
	170	29.17	29.17	0.11	23.16	35.41	12.25	13.10
	180	29.58	29.56	0.10	23.82	35.50	11.68	13.70
7	190	30.69	30.67	0.10	25.01	36.63	11.62	12.80
	200	30.37	30.39	0.09	24.81	36.01	11.21	12.70
	10	7.51	7.44	0.51	0.92	15.52	14.60	-1.15
	20	9.12	9.20	0.34	3.60	15.80	12.21	-5.72
	30	12.80	12.76	0.32	5.79	21.46	15.68	3.53
	40	24.88	24.91	0.21	14.89	35.55	20.67	24.40
	50	30.92	30.87	0.16	21.55	41.02	19.47	22.60
	60	34.98	35.08	0.13	26.23	44.34	18.11	27.80
	70	32.68	32.68	0.13	24.54	41.05	16.52	27.90
	80	32.93	32.96	0.12	25.25	41.04	15.79	24.20
	90	34.66	34.69	0.11	27.36	42.04	14.67	24.00
	100	36.56	36.60	0.10	29.76	43.50	13.75	22.70
	110	38.45	38.37	0.09	31.85	45.18	13.34	21.90
	120	41.33	41.39	0.08	35.05	47.93	12.88	22.40
	130	43.98	43.95	0.07	37.68	50.45	12.77	22.10
	140	47.39	47.36	0.07	41.09	53.58	12.49	23.80
	150	49.95	49.90	0.06	43.85	55.93	12.08	25.10
	160	52.87	52.88	0.06	46.99	58.90	11.91	24.20
	170	55.11	55.08	0.05	49.23	60.70	11.47	25.20
	180	57.51	57.20	0.05	51.41	62.85	11.43	25.40
	190	58.89	58.96	0.05	53.44	64.47	11.02	24.30
	200	60.52	60.48	0.04	55.19	65.81	10.63	23.90
8	10	85.38	85.36	0.07	73.05	95.54	22.49	3.65
	20	87.66	87.70	0.04	79.73	94.66	14.93	0.34
	30	88.27	88.30	0.03	82.35	93.60	11.24	-0.50
	40	87.48	87.43	0.03	81.55	92.52	10.97	0.72
	50	87.27	87.24	0.03	81.86	91.90	10.04	1.69
	60	86.01	86.08	0.03	80.97	90.53	9.56	1.34
	70	86.29	86.34	0.03	81.92	90.37	8.46	0.55
	80	86.38	86.44	0.02	82.24	90.21	7.97	1.66
	90	86.31	86.31	0.02	82.37	90.05	7.68	1.94

Appendix V. (cont.)

	100	85.92	85.94	0.02	82.29	89.36	7.07	2.63
	110	85.65	85.68	0.02	82.15	89.01	6.87	2.88
	120	85.53	85.51	0.02	82.03	88.70	6.67	3.08
	130	85.78	85.82	0.02	82.58	88.80	6.23	3.43
	140	84.63	84.60	0.02	81.15	87.85	6.70	2.85
	150	85.36	85.39	0.02	82.17	88.54	6.37	2.99
	160	85.49	85.52	0.02	82.43	88.46	6.04	3.09
	170	85.89	85.90	0.02	82.99	88.64	5.65	2.96
	180	85.69	85.78	0.02	82.84	88.48	5.64	3.41
	190	85.30	85.35	0.02	82.49	88.05	5.56	3.64
	200	85.45	85.41	0.02	82.67	87.97	5.30	3.39

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Appendix VI. The true M_{is} compared to the bootstrapped M_{is} , for eight different bootstrap resampling sets of 10, 20, 30, ..., 200 scats. The coefficients of variation (CV) are given, as well as the lower, upper and the width of the 95% confidence intervals (CI). The eight resampled sets are arranged in increasing order of M_{is} values at 200 scats. Also given are the differences between $M_{ib}(\text{indiv})$ and M_{is} .

Bootstrapped resample set	Number of scats bootstrapped	True M_{is}	Bootstrapped M_{is}	CV	Lower 95% CI	Upper 95% CI	Width of 95% CI	$M_{ib}(\text{indiv})$ - M_{is}
1	10	12.64	12.54	0.76	0	32.64	32.64	-9.98
	20	6.32	6.24	0.80	0	17.64	17.64	-4.95
	30	4.21	4.23	0.81	0	11.76	11.76	-3.23
	40	3.16	3.11	0.81	0	8.82	8.82	-2.33
	50	2.64	2.63	0.78	0	7.16	7.16	-1.87
	60	2.20	2.16	0.78	0	5.97	5.97	-1.49
	70	2.00	1.98	0.74	0.08	5.36	5.28	-1.15
	80	1.99	1.97	0.66	0.17	4.94	4.77	-0.58
	90	2.88	2.86	0.56	0.31	6.48	6.17	-1.32
	100	2.60	2.60	0.55	0.30	5.76	5.46	-1.18
	110	2.66	2.65	0.50	0.48	5.57	5.09	-1.24
	120	2.44	2.43	0.51	0.44	5.09	4.65	-1.17
	130	2.44	2.46	0.46	0.55	4.95	4.40	-1.03
	140	2.27	2.28	0.47	0.53	4.63	4.10	-0.95
	150	2.82	2.82	0.41	0.82	5.33	4.51	-1.47
	160	2.64	2.65	0.42	0.77	5.08	4.30	-1.36
	170	3.46	3.44	0.36	1.27	6.05	4.78	-1.61
	180	3.27	3.27	0.35	1.27	5.77	4.50	-1.48
	190	3.24	3.25	0.34	1.34	5.63	4.28	-1.48
	200	3.08	3.08	0.34	1.24	5.31	4.07	-1.38
2	10	15.92	15.93	0.62	0.01	39.18	39.17	-13.50
	20	8.08	8.13	0.65	0.18	20.24	20.06	-6.78
	30	8.95	8.99	0.54	0.69	19.31	18.62	-7.63
	40	7.03	7.05	0.51	0.93	15.07	14.14	-5.77
	50	7.66	7.65	0.45	1.73	15.32	13.59	-6.09
	60	9.20	9.11	0.37	3.22	16.40	13.17	-7.58
	70	9.43	9.44	0.33	3.94	15.99	12.06	-7.79
	80	11.43	11.46	0.26	5.92	17.59	11.67	-8.97
	90	11.42	11.36	0.25	6.07	17.33	11.26	-8.86
	100	12.61	12.53	0.23	7.10	18.40	11.30	-9.51
	110	11.48	11.49	0.23	6.44	16.89	10.45	-8.61
	120	11.97	11.89	0.21	7.21	17.04	9.83	-9.16
	130	11.05	11.03	0.22	6.52	15.97	9.45	-8.56
	140	10.76	10.79	0.21	6.61	15.51	8.90	-8.31
	150	10.24	10.21	0.20	6.52	14.46	7.94	-7.96
	160	9.87	9.89	0.20	6.31	13.95	7.64	-7.55
	170	9.79	9.77	0.19	6.24	13.70	7.46	-7.52
	180	9.83	9.81	0.19	6.26	13.66	7.41	-7.54
	190	11.00	11.02	0.17	7.47	14.95	7.47	-8.63
	200	10.50	10.50	0.18	7.08	14.38	7.29	-8.16
3	10	26.81	26.96	0.35	9.37	46.50	37.12	-11.30
	20	22.05	21.95	0.27	10.93	34.28	23.35	-1.35
	30	22.61	22.58	0.21	13.75	32.47	18.72	3.21
	40	18.09	18.04	0.22	10.89	26.12	15.23	-0.37
	50	16.45	16.44	0.20	10.48	23.17	12.69	-1.01

Appendix VI. (cont.)

	60	14.28	14.24	0.19	9.13	19.75	10.62	-0.60
	70	14.74	14.78	0.18	9.84	20.41	10.57	-0.97
	80	13.57	13.58	0.18	9.13	18.71	9.58	-2.75
	90	12.57	12.56	0.17	8.63	17.18	8.55	-2.32
	100	11.85	11.84	0.17	8.15	15.98	7.83	-2.01
	110	11.04	11.06	0.17	7.65	15.00	7.35	-1.69
	120	11.10	11.09	0.15	7.99	14.62	6.64	-1.88
	130	11.63	11.62	0.14	8.60	15.07	6.47	-2.16
	140	11.50	11.52	0.14	8.67	14.75	6.08	-2.16
	150	12.82	12.82	0.13	9.73	16.16	6.43	-2.07
	160	12.44	12.44	0.12	9.45	15.57	6.12	-1.94
	170	12.99	13.02	0.12	10.15	16.28	6.13	-1.31
	180	12.53	13.02	0.12	10.08	16.13	6.05	-1.21
	190	12.97	12.94	0.12	10.07	16.11	6.04	-0.35
	200	12.92	12.96	0.12	10.03	15.96	5.93	-0.19
4	10	13.52	13.66	0.72	0	37.04	37.04	-5.83
	20	9.98	9.98	0.58	0.54	23.23	22.68	-3.64
	30	16.10	16.20	0.38	5.29	29.08	23.79	5.86
	40	19.01	18.91	0.30	8.35	30.71	22.36	1.02
	50	18.33	18.23	0.27	9.02	28.58	19.55	1.75
	60	17.05	16.97	0.26	8.96	25.97	17.01	-3.80
	70	15.52	15.49	0.25	8.26	23.14	14.88	-5.52
	80	15.19	15.14	0.23	8.74	22.23	13.48	-5.09
	90	13.79	13.87	0.23	7.92	20.55	12.63	-4.42
	100	14.44	14.42	0.22	8.61	20.57	11.95	-4.62
	110	14.93	14.98	0.21	9.15	21.24	12.08	-4.40
	120	14.58	14.56	0.19	9.28	20.33	11.05	-3.82
	130	15.02	14.96	0.19	9.72	20.54	10.83	-6.99
	140	15.27	15.25	0.18	10.02	20.77	10.75	-6.45
	150	14.92	14.90	0.18	9.93	20.11	10.18	-7.47
	160	15.22	15.22	0.17	10.40	20.32	9.91	-6.97
	170	15.45	15.43	0.16	10.73	20.39	9.66	-6.71
	180	16.26	16.28	0.16	11.58	21.48	9.90	-7.22
	190	17.09	17.05	0.15	12.23	22.25	10.02	-7.69
	200	17.13	17.10	0.15	12.28	22.17	9.89	-7.18
5	10	33.10	32.88	0.32	12.89	54.30	41.41	-21.80
	20	26.73	26.54	0.25	14.08	39.92	25.84	-8.92
	30	25.82	25.76	0.21	15.71	36.56	20.85	-8.21
	40	26.35	26.36	0.19	17.23	36.43	19.20	-11.70
	50	27.67	27.60	0.17	18.87	36.79	17.92	-12.10
	60	29.48	29.49	0.13	22.01	37.38	15.38	-16.90
	70	29.12	29.12	0.13	22.04	36.43	14.40	-17.10
	80	27.92	27.91	0.13	21.03	34.93	13.90	-15.70
	90	26.94	26.92	0.12	20.77	33.21	12.45	-15.00
	100	27.48	27.54	0.11	21.65	33.49	11.83	-14.20
	110	27.47	27.45	0.10	22.12	33.16	11.04	-13.50
	120	29.40	29.43	0.10	24.00	35.22	11.22	-11.50
	130	28.97	28.94	0.10	23.54	34.34	10.80	-11.30
	140	28.17	28.20	0.09	23.21	33.35	10.14	-10.40
	150	28.74	28.71	0.09	23.96	33.74	9.79	-10.10
	160	28.07	28.04	0.09	23.22	32.81	9.59	-9.56
	170	27.92	27.87	0.08	23.36	32.36	9.00	-8.26
	180	28.78	28.62	0.08	24.10	33.23	9.13	-8.60

Appendix VI. (cont.)

	190	28.59	28.60	0.08	24.22	32.81	8.60	-8.53
	200	28.82	28.81	0.07	24.70	33.09	8.38	-8.59
6	10	18.11	18.28	0.52	3.93	39.74	35.81	-15.30
	20	14.31	14.29	0.44	3.58	27.97	24.39	-9.42
	30	20.27	20.23	0.30	9.02	32.81	23.78	-11.00
	40	23.81	23.92	0.23	13.54	35.19	21.65	-12.60
	50	21.09	21.21	0.23	12.28	30.89	18.62	-12.20
	60	26.72	26.71	0.18	17.47	36.42	18.94	-11.80
	70	29.37	29.42	0.16	20.52	38.53	18.01	-10.70
	80	30.49	30.50	0.14	22.21	39.17	16.96	-10.80
	90	28.18	28.27	0.14	20.70	36.32	15.62	-8.42
	100	29.51	29.58	0.13	22.23	37.29	15.05	-8.79
	110	28.43	28.30	0.13	21.29	35.43	14.14	-8.06
	120	28.60	28.64	0.12	21.80	35.81	14.01	-9.03
	130	28.09	28.09	0.12	21.64	34.73	13.09	-9.75
	140	27.33	27.42	0.12	21.16	33.62	12.46	-9.76
	150	26.84	26.91	0.11	21.10	32.82	11.72	-9.56
	160	27.61	27.63	0.11	21.60	33.42	11.82	-7.26
	170	29.22	29.19	0.10	23.55	35.15	11.60	-8.24
	180	30.37	30.33	0.10	24.75	36.11	11.36	-9.12
	190	30.13	30.17	0.09	24.91	35.68	10.77	-9.32
	200	30.98	31.03	0.09	25.71	36.53	10.82	-9.04
7	10	41.95	42.07	0.27	19.99	65.01	45.02	-32.00
	20	51.12	51.29	0.17	34.74	67.81	33.07	-36.00
	30	48.47	48.48	0.13	36.29	61.26	24.97	-32.00
	40	48.25	48.15	0.12	37.11	59.08	21.97	-35.50
	50	46.15	46.16	0.11	36.70	56.34	19.65	-34.20
	60	42.86	42.98	0.10	34.16	51.88	17.72	-33.30
	70	43.45	43.53	0.10	35.37	51.69	16.32	-34.20
	80	45.13	45.18	0.09	37.36	53.12	15.76	-35.00
	90	44.63	44.68	0.08	37.41	52.24	14.83	-34.50
	100	43.68	43.65	0.08	36.61	50.56	13.95	-32.50
	110	43.10	43.14	0.08	36.76	49.82	13.06	-31.40
	120	42.43	42.35	0.08	36.03	48.70	12.67	-30.80
	130	42.68	42.79	0.07	36.66	48.99	12.33	-30.80
	140	42.44	42.33	0.07	36.54	48.15	11.62	-30.70
	150	42.80	42.81	0.07	37.30	48.48	11.18	-30.20
	160	42.68	42.73	0.06	37.34	48.21	10.87	-29.70
	170	43.56	43.60	0.06	38.39	48.70	10.31	-30.00
	180	43.64	43.93	0.06	38.78	49.04	10.25	-29.60
	190	43.07	43.12	0.06	38.14	48.21	10.07	-29.30
	200	42.59	42.54	0.06	37.77	47.42	9.65	-28.70
8	10	69.44	69.26	0.13	50.39	86.39	36.00	5.75
	20	60.67	60.64	0.12	45.72	74.53	28.81	-10.30
	30	62.28	62.24	0.09	50.46	73.25	22.79	-7.91
	40	65.33	65.33	0.08	54.91	74.68	19.77	-0.81
	50	67.93	67.91	0.06	59.61	75.85	16.25	0.60
	60	67.29	67.32	0.06	59.11	74.82	15.71	2.08
	70	67.54	67.44	0.06	60.08	74.76	14.68	3.32
	80	66.45	66.49	0.05	59.37	73.15	13.78	-4.92
	90	62.88	62.88	0.06	55.85	70.07	14.22	-3.77
	100	65.05	65.11	0.05	58.62	71.48	12.86	-3.28

Appendix VI. (cont.)

	110	65.08	65.16	0.05	58.88	71.16	12.28	-3.76
	120	63.46	63.43	0.05	57.35	69.49	12.13	-0.81
	130	59.92	59.91	0.05	53.80	65.88	12.09	0.89
	140	57.19	57.10	0.05	51.22	62.80	11.58	2.44
	150	54.94	54.98	0.05	49.26	60.72	11.46	2.56
	160	52.84	52.83	0.05	47.33	58.34	11.01	3.77
	170	50.98	50.99	0.05	45.67	56.29	10.63	4.27
	180	49.65	49.44	0.05	44.01	54.69	10.68	4.70
	190	48.25	48.16	0.06	42.97	53.37	10.40	4.85
	200	47.61	47.52	0.05	42.44	52.56	10.12	4.88

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Appendix VII. The true FO_{is} compared to the bootstrapped FO_{is} , for eight different bootstrap resampling sets of 10, 20, 30, ..., 200 scats. The coefficients of variation (CV) are given, as well as the lower, upper and the width of the 95% confidence intervals (CI). The eight resampled sets are arranged in increasing order of FO_{is} values at 200 scats.

Bootstrapped resample set	Number of scats bootstrapped	True FO_{is}	Bootstrapped FO_{is}	CV	Lower 95% CI	Upper 95% CI	Width of 95% CI
1	10	0	0		0	0	0
	20	0	0		0	0	0
	30	0	0		0	0	0
	40	0	0		0	0	0
	50	4.00	4.00	0.70	0	10.00	10.00
	60	3.33	3.36	0.69	0	8.33	8.33
	70	5.71	5.68	0.48	1.43	11.43	10.00
	80	5.00	5.00	0.49	1.25	10.00	8.75
	90	5.56	5.55	0.44	1.11	11.11	10.00
	100	7.00	7.01	0.36	2.00	12.00	10.00
	110	6.36	6.33	0.37	1.82	10.91	9.09
	120	5.83	5.82	0.38	1.67	10.83	9.17
	130	6.92	6.91	0.33	3.08	11.54	8.46
	140	8.57	8.55	0.27	4.29	13.57	9.29
	150	8.67	8.70	0.27	4.67	13.33	8.67
	160	8.75	8.73	0.25	4.38	13.13	8.75
	170	9.41	9.48	0.24	5.29	14.12	8.82
	180	9.44	9.45	0.23	5.56	13.89	8.33
	190	8.95	8.91	0.23	5.26	13.16	7.89
	200	9.50	9.56	0.22	5.50	14.00	8.50
2	10	10.00	10.28	0.94	0	30.00	30.00
	20	15.00	15.14	0.52	0	30.00	30.00
	30	13.33	13.25	0.47	3.33	26.67	23.33
	40	15.00	14.99	0.38	5.00	27.50	22.50
	50	14.00	14.03	0.35	6.00	24.00	18.00
	60	13.33	13.34	0.33	5.00	21.67	16.67
	70	12.86	12.83	0.31	5.71	21.43	15.71
	80	12.50	12.49	0.30	6.25	20.00	13.75
	90	13.33	13.34	0.26	6.67	21.11	14.44
	100	15.00	14.97	0.24	8.00	22.00	14.00
	110	14.55	14.60	0.23	8.18	21.82	13.64
	120	14.17	14.11	0.22	8.33	20.83	12.50
	130	14.62	14.60	0.21	8.46	20.77	12.31
	140	15.00	15.04	0.20	9.29	21.43	12.14
	150	15.33	15.34	0.19	10.00	21.33	11.33
	160	15.00	15.01	0.19	10.00	20.63	10.63
	170	14.12	14.16	0.19	9.41	19.41	10.00
	180	13.33	13.32	0.19	8.33	18.33	10.00
	190	13.16	13.18	0.19	8.42	18.42	10.00
	200	13.00	12.98	0.18	8.50	18.00	9.50
3	10	20.00	19.95	0.64	0	50.00	50.00
	20	25.00	24.75	0.39	5.00	45.00	40.00
	30	23.33	23.27	0.33	10.00	40.00	30.00
	40	25.00	24.79	0.28	12.50	37.50	25.00
	50	24.00	24.02	0.25	12.00	36.00	24.00
	60	21.67	21.58	0.24	11.67	31.67	20.00

Appendix VII. (cont.)

	70	22.86	22.88	0.22	12.86	32.86	20.00
	80	22.50	22.58	0.20	13.75	31.25	17.50
	90	22.22	22.22	0.20	13.33	31.11	17.78
	100	21.00	21.00	0.19	13.00	29.00	16.00
	110	22.73	22.78	0.18	15.45	30.91	15.45
	120	22.50	22.49	0.17	15.83	30.00	14.17
	130	23.85	23.90	0.16	16.92	31.54	14.62
	140	22.86	23.00	0.15	16.43	30.00	13.57
	150	24.00	24.05	0.14	17.33	30.67	13.33
	160	24.38	24.53	0.14	18.13	31.25	13.13
	170	23.53	23.46	0.14	17.06	30.00	12.94
	180	22.78	22.81	0.14	16.67	29.44	12.78
	190	23.16	23.15	0.13	17.37	28.95	11.58
	200	23.00	22.92	0.13	17.50	29.00	11.50
4	10	30.00	29.84	0.49	0	60.00	60.00
	20	35.00	35.22	0.30	15.00	55.00	40.00
	30	33.33	33.12	0.26	16.67	50.00	33.33
	40	30.00	30.12	0.24	17.50	45.00	27.50
	50	30.00	30.03	0.21	18.00	42.00	24.00
	60	31.67	31.78	0.19	20.00	43.33	23.33
	70	31.43	31.62	0.17	21.43	42.86	21.43
	80	31.25	31.45	0.16	21.25	41.25	20.00
	90	30.00	29.90	0.16	21.11	40.00	18.89
	100	29.00	29.06	0.16	20.00	38.00	18.00
	110	30.91	30.88	0.14	22.73	39.09	16.36
	120	30.00	29.96	0.14	22.50	38.33	15.83
	130	30.00	30.00	0.13	22.31	37.69	15.38
	140	31.43	31.47	0.13	23.57	39.29	15.71
	150	31.33	31.34	0.12	24.00	38.67	14.67
	160	31.88	31.89	0.12	25.00	39.38	14.38
	170	33.53	33.55	0.11	26.47	40.59	14.12
	180	33.33	33.39	0.11	26.67	40.56	13.89
	190	33.68	33.71	0.10	27.37	40.53	13.16
	200	33.50	33.48	0.10	27.00	40.00	13.00
5	10	70.00	70.10	0.21	40.00	100.00	60.00
	20	50.00	50.19	0.22	30.00	70.00	40.00
	30	56.67	56.83	0.16	40.00	73.33	33.33
	40	62.50	62.45	0.12	47.50	77.50	30.00
	50	56.00	56.03	0.13	42.00	70.00	28.00
	60	61.67	61.65	0.10	48.33	73.33	25.00
	70	61.43	61.36	0.10	50.00	72.86	22.86
	80	61.25	61.20	0.09	50.00	72.50	22.50
	90	62.22	62.16	0.08	52.22	72.22	20.00
	100	61.00	61.10	0.08	51.00	71.00	20.00
	110	57.27	57.27	0.08	48.18	66.36	18.18
	120	58.33	58.22	0.08	49.17	66.67	17.50
	130	58.46	58.38	0.07	50.00	66.92	16.92
	140	57.86	57.77	0.07	49.29	65.71	16.43
	150	58.67	58.67	0.07	51.33	66.67	15.33
	160	58.13	57.98	0.07	50.00	65.63	15.63
	170	58.82	58.83	0.06	51.18	65.88	14.71
	180	59.44	59.45	0.06	52.22	66.67	14.44
	190	60.53	60.56	0.06	53.68	67.37	13.68

Appendix VII. (cont.)

	200	60.00	60.06	0.06	53.50	67.00	13.50
6	10	90.00	90.07	0.10	70.00	100.00	30.00
	20	90.00	89.84	0.08	75.00	100.00	25.00
	30	93.33	93.42	0.05	83.33	100.00	16.67
	40	87.50	87.38	0.06	77.50	97.50	20.00
	50	88.00	87.94	0.05	78.00	96.00	18.00
	60	85.00	85.06	0.05	75.00	93.33	18.33
	70	84.29	84.35	0.05	75.71	92.86	17.14
	80	81.25	81.22	0.05	72.50	88.75	16.25
	90	82.22	82.19	0.05	73.33	90.00	16.67
	100	82.00	82.03	0.05	74.00	89.00	15.00
	110	80.91	80.86	0.05	72.73	88.18	15.45
	120	80.83	80.91	0.04	73.33	87.50	14.17
	130	80.00	79.98	0.04	73.08	86.15	13.08
	140	80.71	80.71	0.04	74.29	87.14	12.86
	150	82.00	81.99	0.04	75.33	88.00	12.67
	160	80.63	80.62	0.04	74.38	86.25	11.88
	170	81.18	81.16	0.04	75.29	87.06	11.76
	180	79.44	79.65	0.04	73.89	85.56	11.67
	190	77.37	77.38	0.04	71.05	83.16	12.11
	200	76.50	76.49	0.04	70.50	82.00	11.50
7	10	50.00	50.04	0.31	20.00	80.00	60.00
	20	65.00	65.10	0.16	45.00	85.00	40.00
	30	66.67	66.82	0.13	50.00	83.33	33.33
	40	70.00	69.99	0.10	55.00	82.50	27.50
	50	76.00	75.94	0.08	64.00	88.00	24.00
	60	76.67	76.65	0.07	65.00	86.67	21.67
	70	72.86	72.94	0.07	62.86	82.86	20.00
	80	75.00	75.00	0.07	65.00	83.75	18.75
	90	76.67	76.70	0.06	67.78	85.56	17.78
	100	79.00	79.01	0.05	71.00	87.00	16.00
	110	80.91	80.86	0.05	73.64	88.18	14.55
	120	82.50	82.54	0.04	75.83	89.17	13.33
	130	83.08	83.07	0.04	76.15	89.23	13.08
	140	84.29	84.22	0.04	77.86	90.00	12.14
	150	85.33	85.31	0.03	79.33	90.67	11.33
	160	86.25	86.26	0.03	81.25	91.25	10.00
	170	87.06	87.00	0.03	81.76	91.76	10.00
	180	87.78	87.34	0.03	82.22	91.67	9.44
	190	87.89	87.93	0.03	83.16	92.11	8.95
	200	88.50	88.46	0.03	84.00	93.00	9.00
8	10	100.00	100.00	0	100.00	100.00	0
	20	100.00	100.00	0	100.00	100.00	0
	30	100.00	100.00	0	100.00	100.00	0
	40	100.00	100.00	0	100.00	100.00	0
	50	100.00	100.00	0	100.00	100.00	0
	60	100.00	100.00	0	100.00	100.00	0
	70	100.00	100.00	0	100.00	100.00	0
	80	100.00	100.00	0	100.00	100.00	0
	90	100.00	100.00	0	100.00	100.00	0
	100	100.00	100.00	0	100.00	100.00	0
	110	100.00	100.00	0	100.00	100.00	0

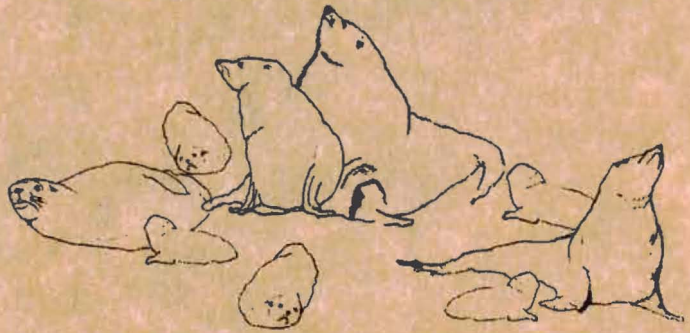
Appendix VII. (cont.)

	120	100.00	100.00	0	100.00	100.00	0
	130	100.00	100.00	0	100.00	100.00	0
	140	100.00	100.00	0	100.00	100.00	0
	150	100.00	100.00	0	100.00	100.00	0
	160	100.00	100.00	0	100.00	100.00	0
	170	100.00	100.00	0	100.00	100.00	0
	180	100.00	100.00	0	100.00	100.00	0
	190	100.00	100.00	0	100.00	100.00	0
	200	100.00	100.00	0	100.00	100.00	0

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CHAPTER 9



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Synthesis

Summary

Cape fur seals *Arctocephalus pusillus pusillus* are one of the top predators in the Benguela System along the west coast of southern Africa (Crawford *et al.* 1992). They consume mainly teleost fish including some of commercial importance (David 1987a), and therefore are perceived by many as a competitive threat to the success of commercial fisheries. Cape fur seals also compete with other top predators for prey resources, e.g. they consume pelagic gobies *Sufflogobius bibarbatus* in the northern Benguela which are also an important prey item of Cape gannets *Morus capensis*, the African penguin *Spheniscus demersus*, Cape cormorants *Phalacrocorax capensis* and bank cormorants *P. neglectus* (Crawford *et al.* 1985). Moreover, the seals are known to prey directly upon some of these species, which are listed in the Red Data Book (Barnes 2000), and is currently an important conservation topic (David *et al.* 2003).

Knowledge of the diet and foraging ecology of the Cape fur seal are required to assess the direct or indirect impacts of this species on their prey, other predators, and fisheries. Despite this, there have been very few studies of diet for this species and none that have taken into account dietary fluxes that one might expect of a population foraging within the Benguela System, which is subject to considerable variability in environmental conditions and marine resources (Shannon *et al.* 1992). Knowledge of the diet composition of seals will lead to a greater understanding of the complexities within this ecosystem.

The relative accessibility of three mainland Cape fur seal breeding colonies in Namibia, comprising about two thirds of that country's Cape fur seal population (Marine and Coastal Management, (MCM), unpublished data), permitted a study of the diet and spatio-temporal comparisons therein of this species in the northern Benguela system. The colonies were at Cape Cross (CC), Atlas Bay and Wolf Bay (AWB) and Van Reenen's Bay (VRB). The method used was the analysis of prey hard parts found in scats deposited by the seals at these colonies over a period of eight years. Scat analysis is known to be the most affordable, least destructive and least intrusive method for determining the diet of fur seals (Pierce and Boyle 1991) and although it is subject to a number of limitations, it nonetheless provides valuable information on the prey

consumed (Tollit and Thompson 1996). Scats at these breeding colonies were mainly deposited by adult, lactating females which alternate shore visits to feed their pups with foraging trips at sea (David and Rand 1986). Males are only present at breeding colonies during the breeding season when they mainly fast (Rand 1959).

Data from January 1994 to August 2002 were available for this study. It was intended that each colony be sampled every month. However, due to logistical constraints this was not possible, and of the 100 months comprising the study period, sampling was conducted during 91 at AWB, 78 at CC and 41 at VRB. The sampling procedure simply entailed pooling a number of scats into a bag. After collection, samples were washed and rinsed with water and then dried overnight. Prey hard part remains (sagittal otoliths of teleosts and cephalopod beaks) were removed from the dried material. Sagittal otoliths were identified and counted.

Otolith numbers were adjusted for those lost during digestion using correction factors developed by D. L. Millar *et al.* (MCM, unpublished data) before determining the percentage numerical abundance of prey in each sample. Otolith diameters of sub-samples of otoliths from each of the teleost prey types were measured to the closest 0.05 mm. These were corrected for erosion during digestion (D. L. Millar *et al.*, MCM, unpublished data) and were then converted to fish length and mass using relationships between otolith diameter lengths and fish length and mass (Smale *et al.* 1995), to determine the percentage mass of prey in samples.

From May 2001 to April 2002, in addition to collecting monthly bags of scats at colonies, samples of individual scats (about 30 scats) were collected concurrently and kept separate from each other. Each of the individual scats of a month's sample were processed in the same fashion as the bag sample. Crustacean hard parts and bird feathers were additionally sorted from the dried material. The aim of this was to be able to compare the bag sampling method to the individual scat sampling method, which has been used in most other seal diet studies involving scat analysis (e.g. Hammond *et al.* 1994, Acuña and Francis 1995, Reid 1995, Tollit and Thompson 1996, Brown and Pierce 1998, Casaux *et al.* 1998, Kirkman *et al.* 2000).

The cephalopod component of the diet was investigated further in a separate study (De Bruyn *et al.* 2003, De Bruyn *et al.* in press), in which it was found that the abundance and mass of cephalopods consumed by the seals varied between colonies and over time. Crustacean remains were unidentifiable and therefore only their presence or absence could be noted. They

were mostly encountered in scats collected from the southerly colonies, AWB and VRB, and hardly occurred in scats from CC.

Teleosts constitute between 92% and 97% of the diet of seals in Namibia (David 1987a, Lipinski and David 1990), and therefore this study focused on this component of the diet. Generally, Cape fur seals mainly consumed small pelagic prey that display shoaling behaviour. In all, six teleost prey groups were identified, consisting of at least 19 families and 48 species. The prey groups were Cape horse mackerel *Trachurus trachurus capensis*, Cape hakes *Merluccius capensis* and *M. paradoxus*, lanternfish (mainly *Lampanyctodes hectoris*), pelagic goby, pelagics (sardine *Sardinops sagax*, anchovy *Engraulis capensis* and round herring *Etrumeus whiteheadi*) and others. The horse mackerel, hake and pelagics groups are of commercial importance in Namibia (Bauleth-D'Almeida *et al.* 2001b, Boyer *et al.* 2001, Van der Westhuizen 2001).

Scat analysis showed that the diet of Cape fur seals varied between colonies, even between the two southerly colonies which are only 70 km apart. At CC, seals mainly consumed horse mackerel and lanternfish were negligible. At VRB and AWB, the two southerly colonies, lanternfish were numerically prevalent in scats but were not important in terms of mass, and horse mackerel were negligible. Hake and goby featured in scats from all three colonies. The species in the pelagics prey group were not important; among these species round herring was most prevalent in the south at VRB and anchovy and sardine were most prevalent in scats from CC. Species in the others prey group were negligible in the seal diet.

The diet of Cape fur seals varied temporally. Scat analysis showed that there was considerable inter- and intra-annual variation in diet composition. The diet was not predictable on an annual pattern, and little consistent seasonality was apparent. However, some prey species tended to be most abundant in scats during certain times of the year (e.g. lanternfish tended to be most abundant in scats from AWB and VRB during the August to January season). Such seasonality as could be detected was probably influenced by life-history patterns of the prey species, but it could also be affected by the biology of the predator (Green *et al.* 1989, Casaux *et al.* 1998, Naya *et al.* 2002). For example, the foraging range of lactating females may shift as the ability of pups to fast for longer periods increases with the progression of the lactation period.

Generally though, Cape fur seals feed on prey that are locally abundant (Shaughnessy 1985, Oosthuizen 1991), so that shifts in their diet are likely to reflect shifts in the distribution and abundance of prey types (e.g. Hammond *et al.* 1994, Bowen and Harrison 1996). Thus the

variability in the diet between colonies and between years emphasises the complexity of a system like the Benguela, where patterns of prey distribution and abundance are probably influenced by fluxes in oceanographic conditions (Acuña and Francis 1995, Reid and Arnould 1996, Hedd *et al.* 2002, Lea *et al.* 2002).

Improving our understanding of spatio-temporal variation in the seal diet could be seen as a step in the direction of unraveling the complexities that influence prey consumption by the seals. Moreover, this understanding would contribute towards refining estimates of prey consumption by the seals, useful for assessing levels of competitive interactions between seals and fisheries (Tollit and Thompson 1996) or other predators, or impacts of seals on prey species. Therefore, a dynamic prey consumption model for lactating Cape fur seals during the eight-month lactation period, that allowed for changes in diet with space and time, was developed. This model is easily applied to other age-sex classes of the seal population.

The model relied on assumptions for a few of its input variables (daily energy requirements of lactating females and digestive efficiencies of prey), and missing data were estimated from the rest of the data series. The model showed that, during the eight-month lactation period, lactating Cape fur seals in Namibia consumed up to 10 times less hake and 45 times less horse mackerel than the amount caught by fisheries. The consumption of commercial prey (hake and horse mackerel) was greatest at CC, whereas at VRB and AWB non-commercial prey were mainly consumed. The model also estimated that a female of average mass 56 kg ingested, on average, 11% of her body mass per day, which is 2-4% higher than estimates from previous models (David 1987a, Wickens *et al.* 1992b).

One of the Cape fur seal's prey items, the Cape horse mackerel, is one of Namibia's most valuable fish stocks (Axelsen *et al.* 2004). The age classes of horse mackerel consumed by seals can be reconstituted from the otoliths found in the scats. Therefore, it was possible to investigate the level of overlap in the utilization of this resource between seals at CC and the purse-seine fishery in northern Namibia. Two overlap measures were employed, Schoener's and Morisita's indices, and bootstrap methods were used to estimate confidence intervals for the measures. The total catch of horse mackerel by the purse-seine fishery lagged the proportion consumed by seals by one to two years.

Seals consumed smaller length classes compared to the catches of the purse-seine fishery. Both overlap indices gave similar results. For overlap measures greater than 0.75, seals and the

purse-seine fishery utilized age-2 (14.75 to 16.75 cm length) horse mackerel. For overlap measures less than 0.25, seals mainly consumed age-0 fish (5.25 to 7.75 cm) while the fishery caught age-2 fish.

Both indices were adjusted by the proportion of horse mackerel in the diet of seals at CC, with the assumption that the proportion consumed by the seals reflected the abundance of juvenile horse mackerel in the coastal waters of CC. Both unadjusted and adjusted overlap measures showed that overlap between seals and the fishery in their utilization of juvenile horse mackerel was high only at times when horse mackerel abundance was high, and low when abundance was small. Overlap is not directly related to competition; to determine competition between two utilizers of a common resource, information on the dynamic and static properties of competition is needed (Harwood and Croxall 1988, Green *et al.* 1998), which usually is impossible or difficult to obtain.

Due to the commercial importance of horse mackerel in Namibia, the sound management of this resource is important to ensure its sustainable utilization. The consumption of horse mackerel by Cape fur seals at CC provided the opportunity of investigating whether trends in horse mackerel biomass were reflected by the Cape fur seals' diet, and whether this information can be used in the development of an inexpensive recruitment index for the Namibian purse-seine fishery. The relationship between annual mean percentage horse mackerel mass in the diet of seals and the acoustic survey biomass estimates was weak. The annual mean percentage mass of horse mackerel in the seal diet was strongly correlated to the annual purse-seine total catch lagged by two years. The corrected proportion of age-0 horse mackerel in the seal diet was significantly correlated to the purse-seine catch lagged by two years. It was concluded that seal scat analysis could be used to complement catch and survey data to improve models for the management of the horse mackerel resource.

Cape fur seal predation on endangered seabirds is currently a controversial issue (Marks *et al.* 1997, Crawford *et al.* 2001, David *et al.* 2003, Du Toit *et al.* 2004). Therefore, individual scats from the three study colonies were examined for bird remains such as feathers during 2001 and 2002. Only two scats, both from CC, contained feather remains, with an overall frequency of occurrence of 0.1%. Feathers from each sample were identified as African penguin *Spheniscus demersus* and a species of cormorant (*Phalacrocorax* sp.). Therefore, according to the scat analysis method, the occurrence of seabirds in the diet of fur seals at breeding colonies was

negligible, despite that important seabird colonies in Namibia are within the foraging range of seals from these colonies. Seabird predation by seals has been attributed to a few individuals, mainly males (Du Toit *et al.* 2004), which may explain why birds were negligible in the diet of seals at the breeding colonies, the seals being mainly adult females.

Although scat analysis is associated with a number of biases (Pierce and Boyle 1991), this method provides valuable information on trends in diet composition, and prey consumption. However, sample size is important for attaining reliable values of prey abundance and mass consumed by seals (Hammond and Rothery 1996, Trites and Joy 2005). Also, the type of sampling method used (individual scat sampling versus bag sampling) and the frequency of sampling can affect the reliability of prey abundance and mass estimates obtained from the samples.

Comparisons were made between individual scat sampling and bag sampling with regards to abundance and mass estimates obtained, to determine whether the different sampling methods provided the same results. It was determined that sometimes differences were large, and that individual scat sampling was preferred. The frequency of sampling was examined using data from scats collected three to seven days over two months and for two different sampling periods, and this showed that sampling once a month was adequate to pick up shifts in the diet. The effect of sample size was examined using randomization and bootstrap methods, which showed that at least 100 scats were necessary for 95% confidence interval widths of less than 20%. The decision on what sample size to use will be determined by the degree of precision that is required and by logistical constraints. The biases associated with scat sampling were discussed in relation to using scat analysis for determining the diet of Cape fur seals, and it was recommended that well planned captive feeding trials of Cape fur seals are needed to obtain more accurate correction factors for the erosion of otoliths during digestion.

Overall, this study served to highlight the complexity of the relationship between predators and their prey. Furthering our understanding of these relationships would provide insight into the complexities of the dynamic food web within the northern Benguela. Moreover, this study showed that valuable information can be obtained from seal scat analysis which can contribute to fisheries management.

Implications of the study

Generally, the diet of lactating Cape fur seal females was found to be composed mainly of locally abundant fish species, including many small schooling fish. Capture rates and handling times of small schooling fishes are likely to be higher and lower, respectively, compared to dispersed fish species (except perhaps the abundant, sluggish goby). Such a feeding strategy is what can be expected by central place foragers such as lactating fur seals, which have to balance the length of foraging trips with the energetic requirements of their pups.

This study has also highlighted the usefulness of scat analysis on a long-term basis for monitoring changes in prey availability and abundance, which may reflect life-history strategies of the prey. Such information provides important insight into species of non-commercial importance for which little is known, e.g. pelagic goby.

Up until now, management considerations regarding the Cape fur seal have revolved mainly around sustainable seal harvesting, interactions between seals and commercial fisheries, and impacts of seals on declining seabird populations. This study has emphasized that seals *per se* can serve as useful management tools. Dietary information obtained from scats, while subject to numerous biases, provided information on spatial and temporal trends in the relative consumption of the main prey species. A relationship between relative consumption rates by seals of an important commercial fish species, and commercial catches of the same species, indicated that scat analysis can potentially be employed to forecast future catches of the species. Quantitative information obtained from seal scats may therefore be used to complement fishery and survey data that are used as input by fisheries scientists towards the management of stocks. Further advantages of including spatio-temporal effects in this study was that they permitted more dynamic approaches, both to estimating prey consumption by the seals, and to measuring overlap in utilization between the seals and a commercial fishery, than were previously possible.

In short, the utility of seal scats as sources of information relevant to the management of the highly productive, highly variable and highly utilized Benguela ecosystem, has been demonstrated in this study. Such information is applicable to the objective of the BCLME (Benguela Current Large Marine Ecosystem) programme, which is the facilitation of integrated management, sustainable development and protection of that ecosystem (Anon 2002). It is of particular relevance to BCLME's project "Top predators as biological indicators of ecosystem

change in the BCLME” which aims to assess the effectiveness of land-breeding top predators as biological indicators of change in the Benguela ecosystem.

Recommendations for future research

(a) Although scat analysis may not accurately quantify the abundance and mass of prey consumed by seals (Tirasin and Jorgenson 1999), it provides a cheap, non-intrusive and relatively un-disruptive means of detecting changes in the seal diet in space or time (Chapters 2 and 3). As such, it is preferable to the shooting of seals for their stomach contents, or stomach lavaging, both of which are disruptive and/or destructive and are also associated with numerous sources of bias. Sampling of stomach contents is expensive because shooting requires weapons and ammunition and lavaging requires equipment and drugs (Pierce and Boyle 1991). Moreover, stomachs are often empty (Pierce and Boyle 1991).

(b) Cape fur seals feed on locally abundant prey (Shaughnessy 1985), so that changes in their diet reflect prey availability, which in turn may be influenced by a number of factors operating at a range of spatio-temporal scales. Relatively fine scale effects may include life history characteristics of prey reflected in seasonal shifts in diet composition, or anomalous environmental conditions (Cury *et al.* 2000, Boyer and Hampton 2001). Large scale phenomena may include shifts in climatic and or oceanographic conditions that only become evident over many years, e.g. decades or longer time intervals (Crawford and Payne 1989).

As a cheap and relatively easy means of monitoring prey availability in relation to such effects, the scale of scat sampling needs to be adequate to be able to separate short from long term effects. It is recommended that it be continued in the long-term, with sampling conducted at a fine enough scale (e.g. monthly) to detect responses to short term changes; after eight years of data collection, it is apparent that each year differs from all others. Gaps in the data at colonies diminish the strength of results and deter spatio-temporal comparisons, therefore all attempts should be made to ensure that sampling takes place at regular intervals. Also, the current spatial component to sampling should be adhered to considering the shifts in oceanographic conditions, productivity and prey availability that occur between regions in the Benguela System. To this end, analogous sampling should take place throughout the range of the Cape fur seal and include sites in South Africa.

(c) Scat sampling protocols are important considerations for obtaining reliable estimates of dietary statistics for seals (Chapter 8). Individual scats are the preferred method of sampling. Sample size, i.e. the number of scats constituting a sample, is determined by the degree of precision required for estimates of dietary statistics, and a minimum of 100 scats per sample provide reasonably small widths of 95% confidence intervals (widths less than 20%). However, a higher degree of precision would require a larger sample size. Sampling at a monthly scale can capture changes in diet composition. However, more studies are needed to investigate the frequency of shifts in the diet of Cape fur seals. Sample size, the sampling method used (individual scat samples versus bag samples of pooled scats) and the frequency of sampling are ultimately determined by logistical constraints, and the interpretation of results must take these factors into account.

(d) It is well documented that scat analysis has a number of biases (Pierce and Boyle 1991). This study used correction factors to correct for the partial or complete erosion of otoliths. However, correction factors exist only for four prey species (horse mackerel, hake, goby and sardine; D. L. Millar *et al.*, MCM, unpublished data) of the Cape fur seal, and correction factors for other prey species were estimated from these. Also, the study by D. L. Millar *et al.* (MCM, unpublished data) was based on small sample sizes. It is therefore recommended that well-planned captive feeding trials be conducted for a greater variety of species, and for larger sample sizes of species, also investigating the erosion of otoliths from different sizes of fish within a species. The more accurate the correction factors, the less the errors in estimates of abundance and mass of prey in the diet (Hammond and Rothery 1996).

(e) Dietary information from scat analysis can be complemented by other monitoring studies. These include pup mortality and growth studies and telemetric (VHF) studies on lactating females, to determine the lengths of foraging trips. Thus affects of prey availability on the reproductive success of seals may be investigated, towards understanding trends in seal population size.

(f) It was shown in this study (Chapter 6) that the annual mean numerical abundance of juvenile horse mackerel found in seal scats at Cape Cross could potentially be used to forecast fisheries catches of this commercially important stock. However, for scat analysis to be a useful tool for

fisheries scientists, the data collection should be as refined as possible. Inconsistency between years in allotment of months used to estimate the annual mean juvenile horse mackerel abundance in the scats should be prevented by sampling in each month of each year, i.e., by preventing gaps in the data series within any year. Also, more years of data are required before the predictive power of the relationship between juvenile horse mackerel in the seal scats and future catches by the fishery can be assessed.

(g) Spatio-temporal data on diet composition from seal scats, together with information on the seal population size and structure, and assumptions on daily energy requirements of seals and the efficiency with which their prey is digested, allowed for an estimate of prey consumption by the component of the population that were sensibly assumed to have deposited the bulk of the scats collected, namely lactating females. The prey consumption model developed in this study is based on assumptions for some of its input variables; information is lacking for the digestive efficiency of prey and the daily energy requirements of Cape fur seals. To obtain the digestive efficiency of prey, captive feeding trials need to be carried out for seal sex-age classes with different prey species and varying prey age classes. This is because the digestive efficiency of prey varies according to prey species and prey calorific content, as well as with seal age and sex (Rosen and Trites 2000). Doubly-labelled water methods should be employed in the field on free-ranging seals, to obtain energetic requirements of seals, both on-shore and at-sea (Costa and Gentry 1986, Costa and Gales 2000, Trillmich and Kooyman 2001).

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