SPATIAL, SEASONAL, INTERANNUAL VARIABILITY AND LONG-TERM TRENDS IN THE DIET OF CAPE FUR SEALS ALONG THE NAMIBIAN COAST (1994 – 2018)

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Abstract

To fully understand how the Cape fur seal population responds to changing ecological and environmental conditions, and be able to comprehend their functional roles in the ecosystem, a thorough understanding of their diet composition, seasonality, interannual variation and long-term trends, is necessary. The diet of the Namibian Cape fur seal population was studied from prey remnants recovered across a 25-year time-series (1994 – 2018) of monthly scat samples (n = 1270) collected at various colonies situated along the entire Namibian coastline. Colonies in close proximity had similar prey matrices, and all colony samples were grouped into four geographical regions, namely the Far North (FN), Central North (CN), Central South (CS) and Far South (FS) regions. The study found that bearded goby *Sufflogobius bibarbatus* was the most abundant prey species at all four regions. This was followed by Cape horse mackerel *Trachurus capensis* in northern Namibia (CN and FN) and the lanternfish *Lampanyctodes hectoris* in southern Namibia (CS and FS). Cape hake *Merluccius capensis* was the third most abundant prey species in three regions, but negligible in the Far North. All the other prey species combined contributed less than 7 % of the total numerical diet composition.

The monthly contribution of the three main prey species varied in all regions, but, bearded goby was dominant during all months in the Far North and Far South regions. The study indicated that the bearded goby abundances were less variable in relation to other species in all the regions. However, the bearded goby seemed to be the least preferred prey. This is because when Cape horse mackerel or lanternfish were available, the Cape fur seals readily switched and fed more on those than the more abundant bearded goby. There were significant interannual variations in the contribution of the first two most important prey species in each region, being negatively correlated to each other ($r = -0.84$, $n = 10$, $P < 0.002$; $r = -0.62$, $n = 25$, $P < 0.001$) for bearded goby and Cape horse mackerel in the FN and CN respectively, ($r = -0.52$, $n = 25$, $P < 0.007$; $r = -0.63$, $n = 22$, $P < 0.002$) for bearded goby and lanternfish in the CS and FS regions, respectively. The spatial, seasonal and long-term variations in the contributions of the main prey species were related to the geographical distribution, abundances as well as the calorific values of each prey species (the bearded goby has the least calorific content of the considered species). There was a

long-term increase in the proportion of the bearded goby in the diet of the Cape fur seals in the Central North and Far South regions ($t = 3.21$, $n = 10$, $p < 0.001$; $t = 4.06$, $n = 22$, $P = 0.001$), an increase in Cape horse mackerel in the Far North region ($t = -5.01$, $n = 10$, $P < 0.001$) and a decline in lanternfish ($t = -2.19$, $n = 22$, $P = 0.04$) in the Far South region.

Lanternfish and bearded goby are currently not exploited in Namibia. With minimal pressure from fishing, their variability in the diet is thus likely related to their natural variability in abundance, with possible alterations due to changing environmental conditions affecting their abundance directly or their availability to the fur seals through depth distribution. The study indicated that the abundance of the lanternfish declined whereas that of the bearded goby increased in southern Namibia (CS and FS). Therefore, to understand the decline in lanternfish abundance in the Cape fur seal diet in southern Namibia, the study further investigated the link between its discrete monthly and long-term diet contribution and to the coastal upwelling index and sea surface temperature recorded across the same timeframe in the same area. There was a significant positive correlation between the discrete monthly lanternfish abundance and coastal upwelling in the Central South region ($r = 0.41$, $n = 90$, $P < 0.001$) and a significant negative correlation between the discrete monthly lanternfish abundance and *in situ* SSTs in both the Central South ($r = -0.27$, $n = 300$, $P < 0.001$) and Far South region ($r = -0.27$, $n = 300$, $P < 0.001$). The long-term monthly lanternfish abundances showed significant correlations with the SSTs in the Far South region ($r = -0.60$, $n = 12$, $P = 0.04$). This was the first attempt to relate the abundance of the lanternfish in the diet of the Cape fur seal to fluctuations in the coastal upwelling and sea surface temperature in Namibia. These correlations provided a view of how climate variability affected the diet of higher trophic levels. Furthermore, they revealed that the diet composition of Cape fur seals inferred from scat sampling do not only help us understand their dietary composition and variations over time, but also contribute to better understanding the underlying causes of abundance fluctuations - especially for species that are currently commercially unexploited (and thus not actively assessed and/or monitored in Namibia). The knowledge assimilated by this study therefore helps in better understanding the relative importance of prey species, especially the non-commercially important species to the diet of a top predator in a functional ecosystem, as well as insights into the relationships that these species have with environmental variables such as coastal upwelling and sea surface temperature.

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List of Abbreviations and/or Acronyms

BCLME	-	Benguela Current Large Marine Environment
CN	-	Central North region
CS	-	Central South region
FN	-	Far North region
FS	-	Far South region
GOBY	-	Bearded Gobies *Sufflogobius Bibarbatus*
HAKES	-	Cape hake *Merluccius capensis*
HMACK	-	Horse Mackerel *Trachurus capensis*
LANTERN	-	Lanternfish *Lampanyctodes hectoris*
MFMR	-	Ministry of Fisheries and Marine Resources
NIMPA		Namibian Islands Marine Protected Area
OTHERS	-	Aggregate species that sporadically contributes to the diet of the seal
PELAG	-	"Pelagics"
SQUID	-	Squids

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Dedication

I dedicate this work to my wonderful and deeply missed late mother, Ms. Magano Naambo Malakia and my hero, late grandfather Tatekulu Malakia Shiwalo Momala. I know you both are proud of me up in heaven. I also would like to dedicate this work to my prayer warriors, my aunt and namesake, Meme Diina Momala and my loving grandmother Kuku Johanna Mbala Iitsinkila. I love you lots and I speak blessings and protection upon your lives.

Declaration

I, Diina Nuugwanga Mwaala, hereby declare that this study is my own work and is a true reflection of my research, and that this work, or any part thereof has not been submitted for a degree at any other institution.

Diina N. Mwaala		01 October 2022
Name of Student	Signature	Date

Chapter 1: Introduction

1.1. General introduction

Cape fur seals *Arctocephalus pusillus pusillus* (Schreber, 1776) are considered an important component of the marine ecology, mostly as an apex predator, although they also fall prey to killer whales *Orcinus orca*, great white sharks *Carcharodon carcharias* and other predatory sharks (Hammerschlag et al., 2006; Fallows et al., 2016) as well as coastal and land based predators such as black backed jackals *Canis mesomelas*, brown hyenas *Parahyaena brunnea* (Kuhn et al., 2008; Wiesel, 2006, 2010) and desert lions *Panthera leo* (Stander, 2019). The diet of the Cape fur seal has been studied from the identification of fish otoliths, cephalopod beaks and other prey remains recovered from fecal samples collected at several mainland and island colonies along the Namibian coast in the South-East Atlantic (David, 1987; de Bruyn et al., 2005; Mecenero et al., 2006b). These studies showed that the Cape fur seals are generalists, and prey on a variety of species over the continental shelf (David, 1987; de Bruyn et al., 2005; Mecenero et al., 2006b). The bulk of the Cape fur seal diet is made up of pelagic and bentho-pelagic shoaling fish species, some of which are commercially important such as Cape horse mackerel *Trachurus capensis*, anchovy *Engraulis capensis* and juvenile hake *Merluccius capensis* (David, 1987; David, 1995; Mecenero et al., 2006b). The bearded goby *Sufflogobius bibarbatus* and lanternfish *Lampanyctodes hectoris*, are two non-exploited species that have been reported as prominent prey items in the diet of the Cape fur seal along the Namibian coast (Mecenero et al., 2006b). Cephalopods and crustaceans such as Chokka squid, mostly *Loligo vulgaris reynaudii* and West coast rock lobster *Jasus lalandii* also feature in the diet of the Cape fur seal, especially in southern Namibia (de Bruyn et al., 2003, 2005).

Like most Otariidae (fur seals and sea lions), Cape fur seal are central place foragers, particularly during the breeding season and the long period of lactation to the pups. They are known to feed on seasonally and locally abundant and aggregating prey, sometimes consuming several species at the same time. While fur seals can remain at sea for extended periods of time, considerable foraging selection occurs within close range of the haul-out locations (Harcourt et al., 2002). This suggests that, the composition of the diet is a representation of the prey availability and abundance surrounding the haul-out locations (and colonies) at different times, explaining the observed spatial and temporal variations in the diet (de Bruyn et al., 2003; Mecenero et al., 2006a,b, 2007). Dietary differences between locations can reflect local variations in the abundance of the prey species, or variations due to differences in oceanographic conditions. Variations in diet between seasons may reflect the short time changes, such as changes in spawning, growth, migration and prey density, whereas, variations between years can be caused by long-term changes in the prey species composition or prolonged fluctuations in environmental conditions.

The lanternfish, family Myctophidae *Lampanyctodes hectoris* and bearded goby *Sufflogobius bibarbatus* are two of the most abundant non-commercial meso-pelagic fishes in Namibian waters, playing an integral role in the trophic dynamics and ecology of the northern Benguela ecosystem. Previous studies have shown that, numerically, they constitute the bulk of the diet of the Cape fur seal off the Namibian coast (Mercenero *et al*., 2006b), as well as of predatory fishes (Roel & Macpherson, 1988; Traut, 1996) and seabirds (Crawford et al., 1985; Ludynia et al., 2010; Tom, 2020). However, despite the visible ecological role of lanternfish in the northern Benguela ecosystem, their abundance and migration patterns are not well understood. Also, the influences of the environmental conditions, such as the coastal upwelling intensity and sea surface temperature on their abundances, hence their availability to the predators have not been studied.

In the light of direct and indirect pressures on marine ecosystems, effective conservation of species and their habitat requires an understanding of the trophic interactions that drive the functioning of an ecosystem (Mecenero et al., 2007). Detailed information on the diet of Cape fur seals from different geographical areas and over a protracted time period, can provide insights into their most important and preferred prey, including prey distributions, availability and variability, and how this is influenced by environmental factors (e.g. seasonal coastal upwelling intensities and sea surface temperatures). Additionally, it can help to fully explore the seasonal, interannual and long-term changes, in the contributions of the major prey species to the diet of the Cape fur seal. Exploring some factors influencing what is being consumed, such as location and effects of the seasonal coastal upwelling intensities and sea surface temperatures on the contribution of some of the prey species will be an additional advantage.

1.2. Problem statement

Traditionally, many of the fisheries research and surveys have been driven by the need to fully understand the population dynamics of commercially targeted species, as they will consequently help to manage those stocks (Boyer & Hampton, 2001). Additionally, many studies have focused on the interactions between Cape fur seals and commercially important species (e.g. Wickens, 1994; Wickens et al., 1992; Mecenero et al., 2007). Thus, there is still a poor understanding of many forage fish species that are of little or no commercial importance, yet have a prominent role in the ecological functioning of the ecosystem. Ultimately, there is little information on population sizes, distributions, fluctuations and their responses to changing environmental conditions of species such as the bearded goby *Sufflogobius bibarbatus* and the lanternfish *Lampanyctodes hectoris*.

The spatial and temporal description of the Cape fur seal diet in Namibia (Mecenero et al., 2006a, 2006b) was limited to just three of the seal colonies on the Namibian coast and just 8 years of data collection, so long term trends of important prey items in the diet could not be described. Also, the previous studies only compared three distinct fur seal colonies along the entire Namibian coast and did not describe the long-term trends of some of the important prey species (i.e. those contributing over 50 % or more of the total diet). Furthermore, no studies have yet explored the effects of environmental variability and change on the contribution of important prey species to the diet. To fully understand how the Cape fur seal population responds to changing ecological and environmental conditions, and be able to comprehend their functional roles in the ecosystem, a thorough understanding of their diet composition, seasonality, interannual variations and long-term trends, is necessary. Therefore, this study aims to fill some of these gaps in knowledge.

1.3. Objectives of the study

The objectives of this study were:

1. To determine the numerical contribution of all prey species to the diet of the Cape fur seals at multiple locations along the Namibian coast from 1994 to 2018.
2. To determine the monthly numerical contributions of commercially important (hake, horse mackerel) and unimportant fish species (bearded goby, lanternfish) to the diet of the Cape fur seal along the Namibian Coast from 1994 to 2018.
3. To determine the interannual variability of the bearded goby, horse mackerel and lanternfish as relative contribution to the diet of the Cape fur seal from 1994 to 2018.
4. To describe the long-term trend of annual numerical contributions of the bearded goby and lanternfish to the diet of the Cape fur seal from 1994 to 2018.
5. To test the relationship between the monthly numerical contributions of lanternfish to the diet of the Cape fur seals and environmental factors, specifically Sea Surface Temperature anomalies and upwelling index.

1.4. Significance of the study

Diet studies of a top predator, such as the Cape fur seal, are crucial in analyzing the relationship and interactions between the predator and its prey. This study will contribute to a considerable better understanding of the relative importance of the key forage species in the dietary needs of the Cape fur seal. Additionally, the seasonal and annual numerical contributions of key prey species to the diet of the Cape fur seal will provide knowledge on their abundances, and insights to their availability to other predatory species as food items in the ecosystem. This study will contribute to previous literature highlighting the importance of non-commercial species (the bearded goby and lanternfish *L. hectoris*), as well as other species such as the Cape horse mackerel and Cape hake (Mecenero, 2005; Mecenero et al., 2006a,b) that plays an integral role in the diet of the Cape fur seal along the Namibian coast. The results of this study will be of importance when analyzing the potential impacts that the Cape fur seal may have on the prey population sizes. Additionally, it will help in fully understanding the impacts that the shifts in the prey composition and structure have on the growth and population sizes of the Cape fur seal. Cape fur seals in Namibia are regarded as an exploitable marine resource and the management policy is to guarantee a sustainable harvest of this resource. Also, the fishing industry has always been concerned of the possible impacts that seals consumption might have on fish stocks and fisheries. Therefore, the knowledge emanating from this study, is valuable in constructing management policies for populations (be it for the top predator itself or for its prey species), for managing fisheries-predator conflicts over prey consumption, as well as in identifying prey populations that may need to be supported for conservation purposes. Finally, variability in the prevalence of particular prey species in the diet, such as the lanternfish, can assist understanding of the influence of environmental variables (e.g. coastal upwelling or sea surface temperatures) on their abundance or distribution.

1.5. Ethics statement

Collection of scat samples for diet analysis is a non-invasive method of monitoring feeding habits and was conducted with minimum disturbance to the fur seals, and as such did not cause any ethical issues. The research was permitted (Appendix 2) and an ethical clearance certificate was issued by the University of Namibia's Research Ethics Policy and Guidelines, reference number: REC/001/2021 (Appendix 1).

1.6. Literature review

1.6.1. Cape fur seal *Arctocephalus pusillus pusillus*

Fur seals are marine carnivores in the family Otarridae (eared seals) and subfamily *Arctocephalinae*. The otariids family is comprised of two major groups, namely the fur seals and the sea lions. The two groups are differentiable from the layer of under-fur, which acts as a trap for air and provision of waterproof (Bonner, 1982; Nowak, 2003). Fur seals have a shorter and denser layer of hair whereas the sea lions have a sparse layer of shorter hair, which is ineffective in keeping the skin dry (Nowak, 2003). The sub-family *Arctocephalinae* comprises the northern fur seals *Callorhinus ursinus* (consisting of only one species) and the southern fur seals, the *Arctocephalus* species (consisting of 8 species) (Bonner, 1982). The *Arctocephalus pusillus* is classified into two sub-species, namely the Cape fur seals (*Arctocephalus pusillus pusillus*) and the Australian fur seals (*Arctocephalus pusillus doriferus*). The sub-specificity status was based on a cranial character and their divergent geographical ranges (Warneke and Shaughnessy, 1985, as cited in Hofmeyer, 2015). The Cape fur seal *Arctocephalus pusillus pusillus* (Figure 1.1), are the only resident pinnipeds off the southern-west coast of Southern Africa (Wickens, 1997). Namibia hosts about two thirds of the total population, with the remainder being found along the South African and Angolan coasts (David, 1995, Robertson, 2012). The Cape fur seal is the largest member of the fur seal group (Bonner, 1982). They are highly sexually dimorphic, with females being much smaller in size and lighter in colour than males (Warneke & Shaughnessy, 1985).

Figure 1.1: Cape fur seals in a southern Namibian breeding colony, showing the size dimorphism between males and females. Also visible is a new born pup. Photo: M. Lemerle (used with permission).

1.6.2. Distribution and abundance of fur seals in Namibia

The population of Cape fur seals is made up of around 23 breeding and non-breeding colonies, extending from the Baia dos Tigres (16°36′S 11°41′E) in southern Angola, along the Namibian coast to the South East, at Algoa Bay (34̊ S, 26 ̊ E) in South Africa (Kirkman et al., 2013) (Figure 1.2). In Namibia, the fur seal stock assessment for 2020 estimated the total population size to be at 1.365 million individuals which had increased by 36 % as compared to the 1994 stock reference point (MFMR, 2020). Historically, the majority of the Namibian fur seal population inhabited southern colonies. However, since the mid-1990s there has been an observable northward shift, which resulted in a reduced population size in southern Namibia and an increased population size in northern Namibia (Kirkman et al., 2016). Currently, a large proportion of the Cape fur seal population is found in northern Namibia, at mainland colonies such as Cape Cross, Torra Bay and Cape Frio (see Figure 1.2). This population shift has been related to changes in environmental conditions, which has restructured the overall composition and abundances of their prey species in the ecosystem (Kirkman et al., 2013).

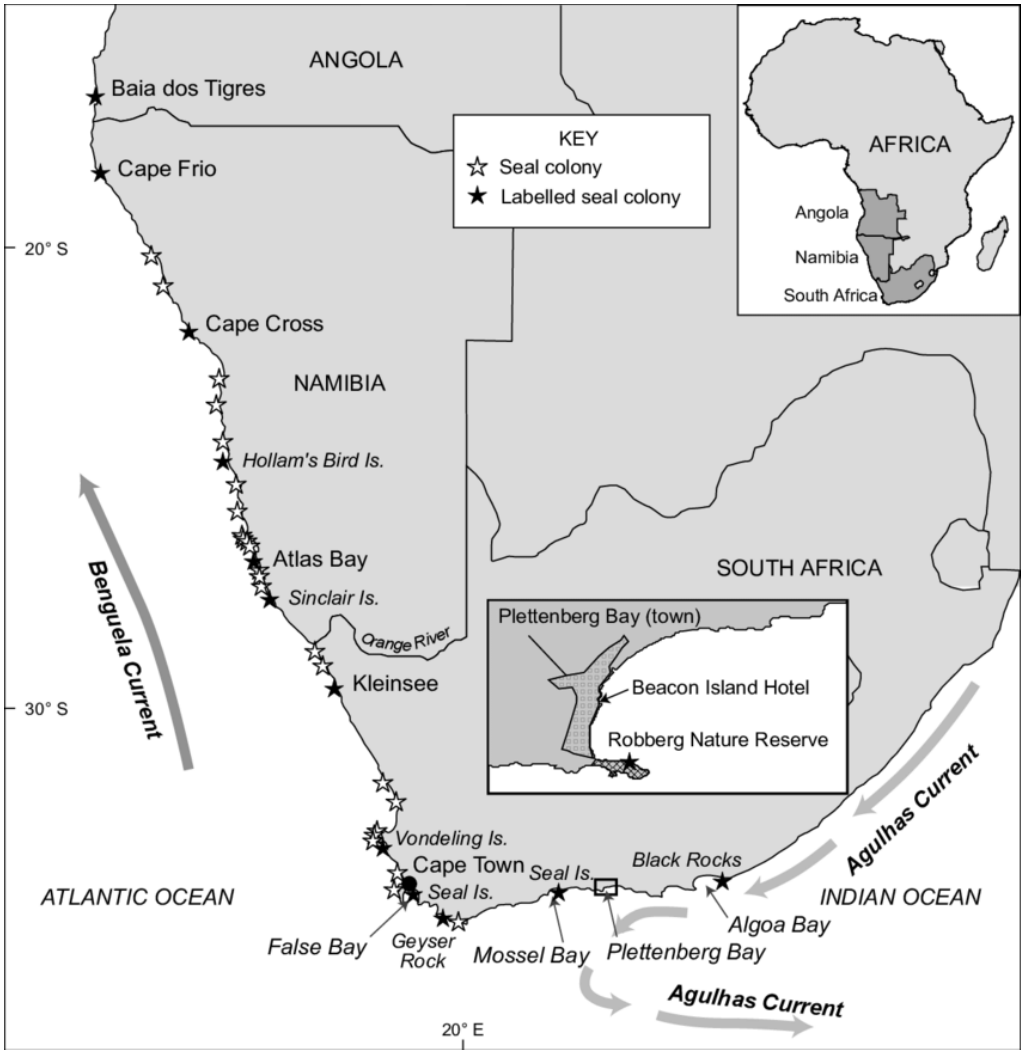

Figure 1.2: Distribution range of Cape fur seal breeding colonies from Baia dos Tigres, southern Angola, through Namibia to Algoa Bay, South Africa. Source: Huisamen et al. (2012).

1.6.3. Benguela Environment

Situated off the west coast of Africa, at 5 – 37 ºS, 0 – 26 ºE, spanning three countries (Angola, Namibia and South Africa), the Benguela Upwelling system is one of the four major eastern boundary upwelling systems of the world (Bakun, 1996; Molloy & Reinikainen, 2003; Shillington et al., 2006). The Benguela upwelling system is characterized by predominantly southerly winds together with the relatively narrow and deep continental shelf, allowing deep, nutrient rich and cooler waters to upwell along the coast (e.g. Branch & Griffiths, 1988; Bakun, 1996; Hutchings et al., 2009). Where nutrients are high, light is abundant and a stable water column exists, rapid development of phytoplankton blooms occur, thence, very high primary production (Shannon & Field, 1985; Verheye et al., 2016). The high primary productivity of the Benguela promotes and supports large population abundances of pelagic and demersal fish stocks (e.g. Cury et al., 2000; Moloney et al., 2004). Apex predators, such as fur seals and seabirds exist at the top of the food chain, enhancing healthy functioning and balancing the Benguela ecosystem (Crawford et al., 1992).

Many drivers, such as over-fishing and major environmental perturbations have led to dramatic and significant changes in the Benguela ecosystem (Shannon et al., 1992; Hall et al., 1998; Hampton & Willemse, 2012). A phenomenon known as a regime shift might have occurred in the northern Benguela in the 1980s (Boyer et al., 2001; Cury & Shannon, 2004; van der Lingen et al., 2006; Roux et al., 2013). The regime shift has led to significant changes in the ecosystem, such as the reduction in species biomass and alterations in trophic levels (Shannon et al., 1992; Boyer et al., 2001; Cury & Shannon, 2004; Heymans et al., 2004; van der Lingen et al., 2006; Travers et al., 2010; Watermeyer et al., 2016). For instance, sardine *Sardinops sagax* was the most important component of the northern Benguela mid trophic level forage fish stock. However, during the 1990s, its biomass decreased significantly (Lluch-Belda et al., 1992; Boyer et al., 2001). Its collapse has led to a switch in the diets of many top predators in the Benguela, including seabirds (Ludynia et al., 2010; 2012) and fur seals (Mecenero, 2005; Roux et al., 2013) from sardine towards a dominance of bearded goby (Crawford et al., 1985; Tom, 2020). Because the bearded goby is a poor quality prey compared to sardine, many populations of seabirds have suffered major declines due to the sudden decrease in sardine abundances (Ludynia et al., 2010; Sherley et al., 2017) and similar changes may be currently playing a role in the reduction of the fur seal population abundance in southern Namibia.

1.6.4. The usage of scats for spatial and temporal description of the Cape fur seal diet

Several methods have been used in studying the diets of marine mammals. Of these are; the analysis tissue samples using the stable isotopes of carbon and nitrogen (Hobson et al., 1996; Burns et al., 1998; Hall-Aspland et al., 2005; Newsome et al., 2010); the usage of fatty acid signatures (Brown et al., 1999; Iverson et al., 1997; Arnould et al., 2005; Tucker et al., 2009; Bromaghin et al., 2013), as well as the analysis of DNA from the guts and feces (Deagle et al., 2005; Deagle & Tollit, 2007; Dunshea, 2009). To a lesser extent, some studies have quantified the diets of marine mammals from regurgitates (spews) (Gales & Pemberton, 1994; Kiyota et al., 1999; Hume et al., 2004), and from airborne video. The most common and oldest method of identification and quantification of the prey species in marine mammals has been through recovery of the prey remains/structures from the guts and feces which are mostly resistant to digestion (Mecenero, 2005; Trites & Joy, 2005). The common prey remains used for identifications are the sagittal otoliths of bony fishes, beaks of cephalopods, bones, scales and lenses of the preyed fish. These structures are mostly collected from the gut (stomach and intestines) (Murie & Lavigne, 1985; Castley et al., 1991), and from scats (Kiyota et al., 1999; Browne et al., 2002; Trites & Joy, 2005; Laake et al., 2012). Scats have been extensively used, because they are easy and relatively in-expensive to collect and process, and therefore have a high chance of collecting larger sample sizes than from the gut. Also, they are the least intrusive and non-lethal methods of collecting diet data. Because scat analysis is an indirect method, studies have indicated that the results could be associated with biases. For example, 1) prey needs to have species specific hard remains (such as otoliths or beaks) to be used in identification; 2) some prey's hard remains may be less likely retained in scats than of the others (i.e. large squid beaks that get vomited (regurgitated) or the otoliths of large fish because the heads are not ingested, hence biasing the otoliths of smaller sized prey); 3) some hard parts may be not resist digestion (e.g. the smaller, more fragile otoliths (e.g. those of anchovies, sardines and round herring) and may be more prone to digestion and disintegration than larger ones, hence very few will be recovered from the remains; 4) it is possible that some secondarily ingested prey contaminate samples; and 5) if seals fragment their prey, they may discard of portions with the identifiable structures, such as the heads of the fish and may result in underrepresenting the prey groups. This may result in misidentification of prey remains and improper quantification of the diet composition. However, the use of correction factors (derived from feeding experiments), which accounts for the otoliths lost during digestion or erosion, have filled many of the gaps in the interpretation of these data (Murie & Lavigne, 1985; Dellinger & Trillmich, 1988; Tollit et al., 1997; Bowen, 2000; Deagle & Tollit, 2007). Studies on several *Arctocephalus* spp. have shown that although there is always a high diversity of prey species that can be recovered from scats, only few of those prey species relatively dominate their diet (David, 1987; Tollit & Thompson, 1996; Mecenero et al., 2006a). The relative abundance of these prey species also varies seasonally and interannually (Dellinger & Trillmich, 1988; Castley et al., 1991; Klages & Bester, 1998; Harcourt et al., 2002; Hume et al., 2004; Mecenero, 2005). Therefore, information from scats can provide important insights on spatial and temporal changes in the diet of the Cape fur seals.

1.6.5. Prey species of the Cape fur seals

At least 28 species of teleost fishes have been identified in the diet of Cape fur seals (mainly females) (Mecenero et al., 2006b; Huisamen et al., 2012). Some of these teleost fishes are of economic importance, such as Cape hake, Cape horse mackerel, sardine, anchovy and round herring, whereas, some are infrequently or not harvested, such as the bearded goby and the lanternfish (David, 1987a; 1987b; Mecenero, 2005). Some crustaceans and cephalopods such as shrimps, rock lobster and squid also form part of the Cape fur seal diet (female) in some regions (de Bruyn et al., 2005; Huisamen et al., 2012). Some fur seal males have been reported to prey on seabirds, including the African penguin (*Spheniscus demersus*), Cape cormorants *Phalacrocorax capensis*, bank cormorants *Phalacrocorax neglectus*, crowned cormorants *Phalacrocorax coronatus* and the Cape gannet (*Morus capensis*), all of which are of conservation concern (Crawford et al. 1989; David et al., 2003; Makhado et al., 2006).

1.6.5.1. Bearded goby *Sufflogobius bibarbatus*

Six goby species are indigenous to the Benguela ecosystem (Staby & Krakstad, 2005), but the bearded goby is the most abundant between Walvis Bay and South of Lüderitz (Prosch et al.,1989). Formerly known as the pelagic goby, the bearded goby *Sufflogobius bibarbatus* (Figure 1.3), in the subfamily Gobiinae, are small shoaling fish that occur only in the Benguela ecosystem (Prosch et al.,1989; Hoese, 1991; Bianchi et al., 1999). Although their occurrence in South African waters has been known since 1923, they were only first recorded off the Namibian waters in 1956 (Prosch et al.,1989). In their acoustic surveys in the northern Benguela, Salvanes et al. (2011) found out that the bearded goby spends much of the day on the seabed (which is associated with hypoxic and sulfidic mud) and makes vertical diel migration to spend the nights in the more oxygenated water layers.

The ecological significance of the bearded goby in the northern Benguela came to light after the collapse of its trophic level competitor, the sardine *Sardinops sagax* (Prosch et al., 1989, Moloney, 2010; Utne-Palm et al., 2010). They play a key role in the ecosystem, as phytoplankton and occasionally zooplankton feeders, and as prey to many commercially important fishes, seabirds and Cape fur seals (Staby & Krakstad, 2005; van der Lingen et al., 2006; Mecenero et al., 2006c; Ludynia et al., 2010). In the diet of the < 35 cm total length shallow-water hake *Merluccius capensis*, the bearded goby is the highest contributor by number (Wilhelm et al., 2015a). In the deep-water hake *M. paradoxus*, bearded goby form the highest percentage component by numbers in the diet of fish size < 26 cm total lengths (Wilhelm et al., 2015a).

Figure 1.3: The bearded goby *Sufflogobius bibarbatus*. Photo: D. Mwaala.

1.6.5.2. Lanternfish *Lampanyctodes hectoris*

Lanternfishes (family Myctophidae), are abundant fishes in the entire world oceans (Prosch, 1991; Prosch et al.,1989). Approximately 49 species of lanternfishes can be found in Namibian waters (Rubies, 1985; Bianchi et al., 1999). Out of this speciose family, the species *Lampanyctodes hectoris* (Figure 1.4) is a relatively small fish (maximum of 13 cm total length, Bianchi et al., 1999), that is abundant in Namibian waters (Rubies, 1985; Cruickshank, 1985; Sabates & Olivar, 1989; Hulley, 1991; Bianchi et al., 1999). They occur in the oceanic midwaters and are well known for their diurnal vertical migration from depths of between 200 m and 1000 m below the surface during daytime and generally to the upper 50 m of the surface at night (Cruickshank, 1985; Bianchi et al., 1999; Staby & Krakstad, 2005), hence they are termed nyctoepipelagic (Hulley, 1991; Prosch et al.,1989).

The diurnal migrations of lanternfishes play a key role in the ecosystem by transporting food energy from the upper, richer photic water zones (acquired during feeding) to deeper less productive aphotic waters (during excretion) (Staby & Krakstad, 2005; de Castro et al., 2010). Lanternfishes also play an influential role in the pseudo-oceanic fauna, acting as both predator and prey in the marine food web (Hewitson & Cruickshank, 1993). As predator, lanternfishes are opportunistic feeders on copepods, ostracods, amphipods, chaetognaths, euphasiids, fish eggs and fish larvae. Lanternfishes form prey of large predatory fishes such as tuna, Cape horse mackerel, hakes, kinglip and snoek (Prosch et al.,1989). Diet studies of the hakes in the Benguela (Roel & Macpherson, 1988; Durholtz et al., 2015; Wilhelm et al., 2015a) showed that lanternfishes, particularly *Lampanyctodes hectoris* are an important dietary component of both the shallow-water hake (*Merluccius capensis*) at < 30 cm total length and deep-water hake (*Merluccius paradoxus*) at < 40 cm total length. In wet mass, *L. hectoris* are the second highest contributor to the diet of *M. paradoxus* (Wilhelm et al., 2015a). In addition, several cetaceans and pinnipeds also prey on lanternfish (Rubies, 1985). Several Namibian endemic seabirds (with the exception of African penguins (*Spheniscus demersus*) do not consume large quantities of lanternfishes, probably because in daylight, they are too deep to be available to the birds. However, there are records of some migrant birds in the region, such as the white chinned petrel *Procellaria aequinoctialis* and sooty shearwater *Ardenna* grisea, that prey on *L. hectoris* (Crawford et al., 1985).

Although uncommon, commercial harvesting of *Lampanyctodes hectoris* was considered as a potentially alternative exploitable resource (Prosch, 1991; Cruickshank, 1985; Staby & Krakstad, 2005) for fish oil and fish meal (Prosch et al., 1989; Bianchi et al., 1999; Hulley, 1991).

Figure 1.4: Lanternfish *Lampanyctodes hectoris* (which lost most of their scales during trawling operations). Photo: D. Mwaala.

1.6.5.3. Cape horse mackerel *Trachurus capensis*

Cape horse mackerel *Trachurus capensis* (Figure 1.5) is a benthopelagic teleost fish species in the south eastern Atlantic Ocean from the Gulf of Guinea to eastern South Africa (Froese & Pauly, 2010). Its distribution is largely restricted to the Benguela current, with the main concentration of fish found in the north from around 17°00'S - 20°00'S (Bianchi et al., 1999; Boyer & Hampton, 2001; Uanivi et al., 2019). Juvenile horse mackerel usually occupy shallower waters (~20 – 100 m) and adults are found mainly offshore in deeper waters up to the shelf edge at a depth of about 500 m (Van Zyl, 2001; Boyer & Hampton, 2001; Uanivi et al., 2019). In Namibia, the size of Cape horse mackerel increases southwards with the largest fish (>35 cm total length) caught south of the Lüderitz upwelling cell at about 27ºS (Bauleth-D'Almeida et al., 2001). Cape horse mackerel are known to undergo diel vertical migration, the shoals rising to feed in surface waters at night and are found close to the oceanic bottom during the day. Juvenile horse mackerel mainly feed on copepods, while adults feed on mainly smaller fish species such sardines, anchovy, round herring as well as on crustaceans (such as euphasiids) and cephalopods (Boyer & Hampton, 2001; Kadila et al., 2020).

In Namibia, Cape horse mackerel form the largest commercial catch by volume and are targeted by the mid-water trawlers, and are utilized as fresh, frozen, salted and dried or smoked and canned (Hampton et al., 1999; Boyer & Hampton, 2001). Additionally, they play an important role in the diet of the many predatory fishes such as hakes (*Merluccius* spp.) (Roel & Macpherson, 1988) and tuna (*Thunnus* spp.) (Boyer & Hampton, 2001), as well as marine mammals (David, 1987; Mecenero et al., 2006b) and seabirds (Mecenero et al., 2007).

Figure 1.5: Cape horse mackerel *Trachurus capensis*. Photo: D. Mwaala

1.6.5.4. Cape hake *Merluccius capensis*

Cape hake *Merluccius capensis* (Figure 1.6) is an important component of the diet of the Cape fur seals (David, 1987; Mecenero, 2005; Mecenero et al., 2006a,b). The deep-water hake *M. paradoxus*, the other important hake species in the Benguela, occurs at depths > 300 m, which does not overlap with the feeding ranges of the Cape fur seal population, hence, this species is not represented in the diet of the Cape fur seal and not further discussed. Cape hake is distributed in the southeast Atlantic, from Angola, through Namibia to South Africa and is most abundant north of 27ºS (Payne & Punt, 1995; Wilhelm et al., 2015a). They are mostly found over the continental shelf and slope at depths as shallow as < 100 m to 450 m (Wilhelm et al., 2015a). Juveniles (to about 29 cm) usually feed on small crustaceans (particularly euphausiids) and small deep-sea fishes such as lanternfish, whereas ≥ 30 cm $^{+}$ individuals feed mainly on small hakes, bearded goby and horse mackerel (Roel & Macpherson, 1988; Traut, 1996; Wilhelm et al., 2015a). Cape hake is an important source of food for humans (Wilhelm et al., 2015a). The juveniles in particular, play a major role in the diets of top predators such as seabirds (Tom, 2020), seals (David, 1987b; Mecenero et al., 2006b), tuna, Cape hake and deep-water hake (Roel & Macpherson, 1988; Traut, 1996; Wilhelm et al., 2015a).

Figure 1.6: Cape hake *Merluccius capensis*. Photo: D. Mwaala.

1.6.5.5. Clupeiformes

The sardine *Sardinops sagax*, round herring *Etrumeus whiteheadi* and the Cape anchovy *Engraulis capensis* (Figure 1.7) are the major species of small pelagic fish occupying the rich waters of the Benguela current. Sardine and anchovy are distributed from KwaZulu-Natal in South Africa to southern Angola (Beckley & Van der Lingen, 1999; Boyd, 1983). The greatest part of the total sardine catch of the region has previously come from the northern stock, which is situated in Namibian waters (Boyer et al., 2001). However, there has been dramatic changes in the sardine and anchovy populations, dating back to the 1960s and 1970s (Lluch-Belda et al., 1992; Beckley & Van der Lingen, 1999; Boyer et al., 2001). The regime shift occurring in the early 1980s, where bearded goby have replaced sardine in the diet of many predators in the northern Benguela, is thought to have led to the decline in their population sizes, survival rates and sizes of breeding colonies (Boyer et al., 2001; Van der Lingen et al., 2001, 2006; Coetzee et al., 2008; Mhlongo et al., 2015). In Namibia, the sardine stock has been placed under a fishing moratorium since 2018.

Round herring *Etrumeus whiteheadi* is currently not commercially important and a poorly known species in Namibian waters, which is occasionally caught as bycatch in the purse seine fisheries (Boyer & Hampton, 2001). These fish could be an important food source to other top predators such as large pelagic fish (Shannon & Jarre-Teichmann, 1999), seals and seabirds (Crawford et al. 1991).

A

B

C

Figure 1.7: Small pelagic species, A) sardine *Sardinops sagax*, B) anchovy *Engraulis capensis* and C) round herring *Etrumeus whiteheadi*. Photos: N. Ekandjo (used with permission).

1.6.6. The calorific content of the main teleost fish species in the diet of the Cape fur seals

Calorific content can be defined as the amount of nutrition value or energy density in any fish as food to its predators (Anthony et al., 2000). Studies have shown that the energy density of fish as food varies widely within and between species (Balmelli & Wickens, 1994; Anthony et al., 2000). Therefore, piscivorous predators such as Cape fur seals and seabirds, may experience differences in energy intake from the various prey species they are consuming at any given time (Benoit-Bird, 2004). For instance, many forage fishes (such as sardines, anchovies and round herring) are known to contain high energy values, and others with low, such as the bearded goby (Balmelli & Wickens, 1994; Ludynia et al., 2010). High nutritious food are important to top predators, especially during their high energy demanding life cycles, such as mating, gestation, lactation and post natal care of the young ones (Pierotti & Annett, 1990; Ludynia et al., 2010; Mecenero, et al., 2006c). Often, predators would rely on prey availability to satisfy nutritional and energy requirements (David, 1987; Mecenero et al., 2006), however, they may compensate to some extent through adjustments in selection for prey quality (Martin, 2014). Central place foragers, such as lactating female Cape fur seals may optimize their energy delivery rate to their pup by increasing meal size or energy content (Mecenero, et al., 2006a,c). Therefore, as prey resource values vary, Cape fur seals would be expected to select prey based on energy density, in addition to availability. Few studies have investigated the energy content and nutritional value of forage fishes, despite their importance as food for many marine predators. The calorific values of the main prey in the diet of the Cape fur seals as cited in Balmelli & Wickens (1994) were used for comparisons in this study; Cape horse mackerel 5.65 $kJ.g^{-1}$, lanternfish 4.90 $kJ.g^{-1}$, hake 4.47 $kJ.g^{-1}$ and bearded goby 3.69 $kJ.g^{-1}$.

Chapter 2: Materials and Methods

2.1. Study sites and geographical locations

Initially, feacal samples (commonly referred to as scats) were collected at five mainland colonies (i.e. breeding sites) along the Namibian coast starting in January 1994 to December 2018. In an attempt to cover a wider foraging range of the Cape fur seals along the Namibian coast, additional scat collection programs were initiated at Pelican Point in 2005 and at Lion’s Head in 2017 (Figure 2.1). These 12 colonies were grouped into four geographical regions, Far North situated in the Skeleton coast National Park (Cape Frio, 18° 25’ S, 12° 00’ E; Mowe Bay, 19° 22’ S, 12° 42’ E, Torra Bay 20° 18’ S, 13° 14’ E and a few samples from Toscanini 20º 50´ S, 13º25´ E), Central North (Cape Cross; 21° 47’ S, 13° 57’ E and Pelican Point, 22° 53’ S, 14° 26’ E), Central South (Atlas Bay, 26° 49’ S, 15° 08’ E ; Wolf Bay, 26° 48’ S, 15° 07’ E, and a few samples from Ichaboe Island, 26º 9´S, 14º 33´ E and Spencer Bay 25° 44' S, 14° 50' E) in the immediate vicinity of the Lüderitz upwelling cell, and Far South (Van Reenen Bay 27° 23’ S, 15° 21’ E; and a few samples from Lion’s Head 27° 41’S, 15° 31’E and Albatross Rock 27°7’ S 15°13' E) (Figure 2.1). The colonies were allocated to these specific regions, because colonies in close proximity had similar prey matrices (i.e. the same prey species occurring at similar frequencies). Because the Atlas and Wolf Bay colonies are so close to each other (i.e. merely one kilometer apart), these two sites were considered as a single colony for the purpose of this study. This study focused on all scat samples collected from January 1994 to December 2018 (25 years) from all sampled fur seal colonies and dates. All of these colonies are active breeding sites of Cape fur seal population in Namibia.

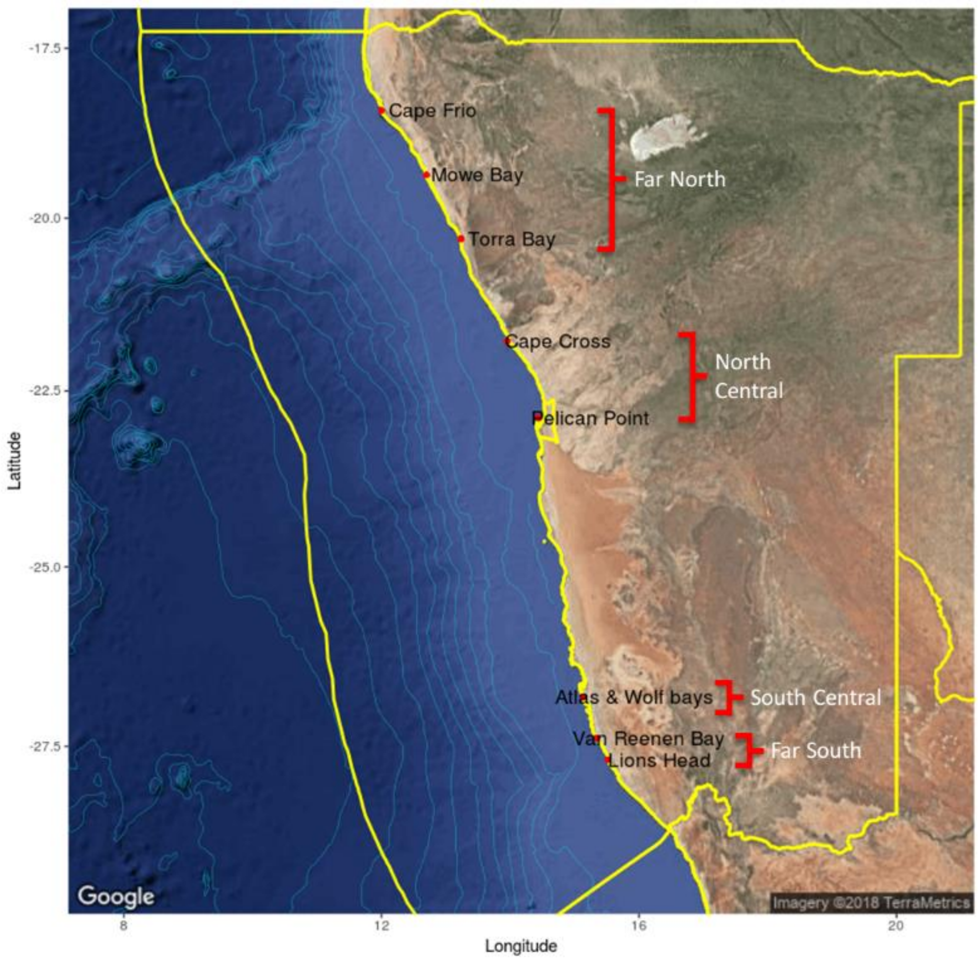

Figure 2.1: The Cape fur seal colonies along the Namibian coast sampled for feacal samples in this study, grouped into four geographical regions: Far North (FN), Central North (CN), Central South (CS) and Far South (FS). The yellow line marks Namibia's EEZ (Source: Google Earth Imagery 2018, TerraMetrics).

2.2. Collection and processing of the feacal samples

All samples for this study were collected and processed by the staff of the Ministry of Fisheries and Marine Resources (MFMR), Namibia. The scat samples (Figure 2.2) were collected on a monthly basis, but not all sites were visited during each sampling month due to logistics and other constraints (e.g. bad weather, transportation, etc.). Typically, ~ 30 – 60 fresh scats, less than five days old were pooled in 215 X 315 × 315mm (40µm) zipper storage bags (Figure 2.2b). Each collected bag was treated as a single sample (bag sample) in further processing and data analysis thereof. Where a colony was visited more than once within a given month, all samples were pooled to represent that specific sampling month.

The quality and freshness of the scat sample was determined by the colour and moisture content to ensure that only fresh (i.e. dark and moist) scats were collected (Figure 2.2a). In the Laboratory, the scat samples were then soaked in cold water for 24 - 48 hours to soften and facilitate the washing process. During washing, scat samples were rinsed through nested stainless-steel sieves with mesh apertures of 2.0, 1.0, 0.425 and 0.212 mm, sequentially. After a full day of draining, the samples were dried in an oven at not more than 50 ºC. The samples were then sieved and kept in plastic zipper storage bags for further processing. The soaking and washing processes are always done in the shortest amount of time possible (after sampling), to prevent further decomposition of any calciferous remnants (e.g. fish otoliths and other carbonate-based hard parts) in the feacal samples that may be used for prey species identification. (see scat collection and processing detailed in Kirkman et al., 2007).

Subsequent to the washing and drying processes, the dried material was placed on a hard, smooth, even-surfaced sorting board (Figure 2.2c). With sufficient light, tweezers were then used to separate prey structures from the waste materials. Identifiable prey structures such as the sagittal otoliths of teleost fishes as well as beaks of cephalopods were identified per species and grouped together to ease the counting process (Figure 2.3). Where possible, the otoliths were classified to the species level with the help of keys by Smale et al. (1995). All sagittal otoliths and beaks per species were counted to make up a total of 3.52 million prey species items from the colonies over two decades (1994 – 2018, Table 2.1).

Figure 2.2: Scat collection and processing. A) A fresh scat at the fur seal colony, B) a collected bag sample and C) a washed and dried sample which is ready for sorting.

The number of bag samples collected depended on the haul-out accessibility, the commencing date of scat collection at certain sites within the region and logistical constraints. As a result, there was a variation in the number of scats collected across the regions over the years. A total of 1270 bag samples were collected from 1994 – 2018 over the entire Namibian coast (Appendix 3). Most bag samples were collected from the

Central South (n = 438), followed by Central North (n = 379), Far South (n = 260), and Far North (n = 194) (Table 2.1; Appendix 3).

Figure 2.3: Some of the sagittal otoliths and beaks of the prey species frequently identified in the scats of the Cape fur seals along the Namibian coast. **A** - Cape hake *Merluccius capensis*, **B** - Bearded goby *Sufflogobius bibarbatus*, **C** - Lanternfish *Lampanyctodes hectoris*, **D** – Horse mackerel *Trachurus capensis*, **E** – Pelagics *Engraulis capensis*, *Etrumeus whiteheadi*, *Sardinops sagax*, and **F** – Squid beaks.

2.3. Analytical techniques used for describing the seal diet composition from scat samples

Many indices have been used in numerous studies to indicate the composition and importance of prey recovered from scat samples. Each index is used depending on the specific questions to be answered. The most common used methods are; the Frequency of Occurrence index (FO); the average numerical abundance; index of split-sample frequency of occurrence and index of relative importance (Lance et al., 2001). Each index has its strengths and weaknesses, as well as data requirements in using any of them. In this study, the relative numerical abundance of the prey species was used for analysis. This index expresses the numerical proportion of a prey species group with respect to the other groups, in percentages. Pooled scat samples collection and analyses allowed to establish the relative numerical importance of prey species to all fur seals in the regions, without necessarily focusing on individual seals diets.

2.4. Data handling and analysis

All sample collection dates were adjusted (retrospectively) by four days to determine the date of consumption at a higher degree of certainty. As such, a sample that was collected on the 1st of a month logically was considered to have been consumed the previous month and thus was assigned to (i.e. pooled with other samples of) the previous month. This was based on the assertion that a fresh scat sample collected on any specific date was consumed by a seal at most four days before it was deposited at the colony, 2 days for digestion and 2 days for collection (Wilhelm et al., 2013). For this reason, all sample dates used in the statistical analyses indicate the assigned (back-calculated) sample dates and not the collection dates.

Table 2.1: The total number of samples collected as well as the total and corrected number of prey items (in millions) per region from January 1994 to December 2018.

Region	Colonies (see Figure 2)	Total no. of bag samples collected	Total no. of prey items (in millions)	Corrected total no. of prey items (in millions)
Far North (FN)	Cape Frio Mowe Bay Torra Bay Toscanini	194	0.34	0.61
Central North (CN)	Cape Cross Pelican Point*	379	1.09	1.91
Central South (CS)	Wolf Bay Atlas Bay Ichaboe Island Spencer Bay	438	1.59	2.80
Far South (FS)	Van Reenen Bay Lion's Head*	260	0.50	0.88
	Total	**1270**	**3.52**	**6.20**

Raw otolith counts were corrected for numbers lost through digestion using species-specific correction factors in Table 2.2 using Equation 2.1. These species-specific correction factors were adapted from Mecenero et al., (2006b). For fish otoliths, whose correction factors are unknown, their numbers were corrected with the correction factors of species known to have similar otolith size, shape and thickness. In addition, a unified correction factor for a group of "Others" (which constitutes a variety of unidentified species that occasionally contributes to the diet) was developed.

$$\text{Corrected count} = \text{Raw otolith count} \times \text{species specific correction factor} \quad (2.1)$$

The corrected counts were then converted into the numerical proportion of each prey group as with respect to all the other prey groups, using equation 2.2.

$$\%\, N = n_i/n_T \times 100 \quad (2.2)$$

where,

N = are the numbers of individuals of the different prey groups in the corrected count

n_i = is the number of individuals of prey group *i* in the sample and

n_T = is the number of individuals of all prey groups in a sample.

Table 2.2: The correction factors to correct for numbers of teleost fish otoliths lost during digestion for Cape horse mackerel (*Trachurus capensis*), Cape hake (*Merluccius capensis*), lanternfish (*Lampanyctodes hectoris*), bearded goby (*Sufflogobius bibarbatus*), "pelagics" (sardine *Sardinops sagax*, anchovy *Engraulis capensis* and round herring *Etrumeus whiteheadi*), squid and others. The "others" group consists of species that infrequently exist in the diet of the Cape fur seal.

Species	Cape horse mackerel	Hake	Lanternfish	Goby	Pelagics	Others	Squid
Corr. factors	1.754	1.515	1.786	1.786	2.125	1.800	1.910

Prior to data analysis, all samples with a count of < 500 total corrected number of prey items were considered insufficient, hence, of the 1270 samples collected, only 1228 samples (97 %) were considered as good samples and were used in data analysis. The remaining 42 samples contained < 500 total corrected prey items, and were excluded from further analysis. Appendix 4 shows the samples that were deemed insufficient for data analysis.

The numerical proportions (% N) of prey groups in the samples were binomially distributed. Therefore, in an attempt to achieve a normal distribution, the arcsine data transformation was employed on the square root of all the numerical proportions (percentages) (Equation 2.3). However, after the transformation, some monthly, seasonal and annual contributions were still non-normally distributed. Also, the variances were typically heterogeneous. Therefore, Kruskal-Wallis test was considered as an appropriate test as it was not sensitive to unequal variances data or non-normal data. The Kruskal-Wallis test was used to test for spatial, monthly and seasonal differences in the contribution of the prey species to the diet of the Cape fur seal. If the Kruskal-Wallis test showed differences, the Nemenyi post hoc test was used as a follow up test to pinpoint the differences. The Bonferroni correction was kept at 1 (the default) with a set statistical significance at $P < 0.05$. All the statistical tests were performed on the arcsine transformed data. For visual clarity, all the plots and their standard deviations were developed from back-transformed data (in percentages) using Equation 2.4.

$$P' = \arcsin(\sqrt{p}) \tag{2.3}$$

$$P = (\sin p')^2 \tag{2.4}$$

Where P´ is the transformed values of the data and P is the back-transformed values.

The data analysis and graphs for this study were generated using the Microsoft Excel™ (2013) and Real Statistics Resource Pack software (Release 6.8) Copyright (2013 - 2021) Charles Zaiontz. www.real-statistics.com.

Chapter 3: The spatial and monthly variation in the numerical contribution of the bearded goby, Cape hake, horse mackerel and lanternfish to the diet of Cape fur seals along the Namibian coast over 25 years

3.1. Introduction

Determining the diets of marine mammals is crucial in understanding how individuals and populations respond to ecological and environmental variability (Bowen, 1997; Bowen & Iverson, 2012; Boyd 2012). Diet estimation of Cape fur seals has been central to many studies exploring predator-prey relationships (Roux, 2004; de Bruyn et al., 2005; Mecenero et al., 2005; Makhado et al., 2006; Roux, 2007), seal interactions with fisheries (David, 1987; Wickens et al., 1992; Wickens, 1994; Punt & Butterworth, 1995; Mecenero et al., 2007) and conservation measures (David et al., 2003; Kemper et al., 2007).

Pinniped diets are well known to vary geographically and seasonally (Sinclair & Zeppelin, 2002; Hume et al., 2004; Ciaputa & Sicinski, 2006; McKenzie & Wynne, 2008; Meynier, 2009) and the Cape fur seal is no exception (Mecenero et al., 2006a,b). The data on seasonal and spatial variability of prey species in the Cape fur seal diet can serve various advantages from an ecological standpoint: it can provide data on the distribution and availability of different prey species in various regions within the Benguela ecosystem; it can provide indications to the effects of environmental changes on the prey species at different times of the year (Cury et al., 2000; van der Lingen et al., 2006), and it can also assist with the identification of incoming prey-species cohorts, growth rates and age validation (Wilhelm et al., 2013, 2015c).

Previous studies have indicated that the Cape fur seal diet is dominated by teleost fish (David, 1987; Castley et al., 1991; Mecenero et al., 2006; Huisamen et al., 2012). Building on the previous study by Mecenero et al. (2006a,b), the present study refined the seasonal and regional variations in the Cape fur seal diet. Because it made use of consistent regional scat collections, with larger sample sizes, and a wider coverage of the distribution of the Cape fur seals along the Namibian coast, as well as a longer sampling timeframe than used in Mecenero et al (2006a,b). This Chapter aimed to determine the seasonal and spatial numerical contribution of the main prey species, the bearded goby *Sufflogobius bibarbatus,* Cape horse mackerel *Trachurus capensis,* Cape hake *Merluccius capensis* and lanternfish *Lampanyctodes hectoris* to the diet of the Cape fur seal in Namibia, from scat samples collected consistently in the four regions defined in Chapter 2 over the period from 1993 to 2018. Specifically, the objectives of this chapter were;

1. To describe the overall diet of the Cape fur seals in each of four regions along the Namibian coast, in terms of the relative abundance of different taxa as determined from identifiable prey hard parts retrieved from scats.
2. To assess monthly trends in the relative abundance of the four main prey items in the diet of the Cape fur seals in Namibia, namely the bearded goby, hake, lanternfish and horse mackerel in each region.

3.2. Methods

3.2.1. Data analysis for spatial, and monthly contributions

The overall percentage abundance of each prey species at a region was calculated using Equation 3.1.

$$\%\ abundance\ of species\ A\ (in\ area) = \frac{Total\ number\ of\ items\ of\ species\ A}{Total\ number\ of\ items\ of\ all\ prey\ species\ pooled\ for\ the\ study\ period} \times 100 \quad (3.1)$$

The monthly percentage abundance of each prey group were calculated using equation 3.2, but summed all bag samples for all years for each month in each region (for example the January contributions would be January 1994 – January 2018).

$$\%\ monthly\ abundance\ of\ species\ A\ (in\ area) = \frac{Total\ monthly\ number\ of\ items\ of\ species\ A}{Total\ number\ of\ items\ of\ all\ prey\ species\ pooled\ for\ that\ month} \times 100 \quad (3.2)$$

Standard deviation of the monthly contribution of a prey species to the Cape fur seal diet was calculated as follows:

$$S = \sqrt{\frac{1}{n-1}\sum_{i=1}^{n}(x_i - \overline{x})^2} \qquad (3.3)$$

Where;

S = standard deviation of a monthly contribution of a prey species to the Cape fur seal diet

x_i = arcsine-transformed value of sample *i* collected within a given sampling month,

$\overline{x}$ = mean (arcsine-transformed) of all the samples collected in a sampling month, and

n = total number of samples collected within a sampling month.

The coefficient of variation is a statistical measure of the relative dispersion of the prey group's contributions in a region around the overall mean contribution of a prey group from all regions. The coefficient of variation of each prey group was calculated using equation 3.4:

$$\text{CV} = \frac{Stadard\ deviation}{Mean} \times 100 \qquad (3.4)$$

where,

CV = is the coefficient variation of each prey group contribution in a region

Standard deviation = sample standard deviation as calculated in equation 3.3

Mean = is the overall mean contribution of each group from all the regions. The coefficient of variation was expressed in percentages.

To achieve a normal distribution and equality of variances, the arcsine data transformation was employed on the square root of all the proportions (Equation 2.3, Chapter 2). Even after the data transformations, the Shapiro-Wilk test for normality showed that data in some months and in some regions were not normally distributed.

Also, the data was highly variable between months. Therefore, analyses were performed using the Kruskal-Wallis tests in the Real Statistics Resource Pack software (Release 6.8). The percentage of the monthly contribution of each prey species was calculated using Equation 3.2. The standard deviations (Equation 3.3) were calculated from the arcsine transformed data for each prey species. All the graphical illustrations were plotted using the back-transformed data (in percentages), using equation 2.4, Chapter 2.

3.3. Results

3.3.1. Spatial variation in the numerical contribution of the prey items in the Cape fur seal diet along the Namibian coast.

Overall, the most frequently occurring of the 6.2 million prey items consumed by the Namibian Cape fur seals over 25 years were four main groups of teleost fish, in order of frequency: bearded goby *Sufflogobius bibarbatus* (51.9 %), lanternfish *Lampanyctodes hectoris* (18.4 %), Cape horse mackerel *Trachurus capensis* (13.9 %), Cape hake *Merluccius capensis* (9.3 %) and the three most common pelagic species pooled together; sardine *Sardinops sagax*, round herring *Etrumeus whiteheadi* and anchovy *Engraulis capensis* (3.3 %) (Table 3.1). The "other" teleosts group merely contributed 1% across the regions. Cephalopods (squids), were among the least common groups in the diet of the Cape fur seal in all the regions as determined from scats, with an overall contribution of 2.1 % (Table 3.1).

Based on the calculated coefficient of variation, it is evident that there was a high variability in the contribution of all prey species in the diet of the Cape fur seals between the regions (Table 3.1). The species that showed the highest variation were; the lanternfish (115.4 %), horse mackerel (110.0 %) and squid (118.5 %). The Cape hake, pelagics and others groups had 53.5 %, 64.1 % and 71.9 %, respectively. The bearded goby showed the least variation of 22.5 %.

Table 3.1: The percentage regional numerical contribution, variance, standard deviation and coefficient of variation of each prey group (Goby = bearded goby *Sufflogobius bibarbatus,* Lantern = lanternfish *Lampanyctodes hectoris,* Hmack = Cape horse mackerel *Trachurus capensis*, Hake = Cape hake *Merluccius capensis*, Pelagics = sardine *Sardinops sagax,* anchovy *Engraulis capensis* and round herring *Etrumeus whiteheadi* pooled, Squid = six species of cephalopods pooled, Other = all other fish species pooled) and the overall mean of each prey species across the regions (FN = Far North, CN = Central North, CS = Central South and FS = Far South).

	FN	**CN**	**CS**	**FS**	Overall mean %	Overall variance ($\%^2$)	Standard Deviation	Coefficient of variation
Goby	61.94	55.82	54.97	35	**51.93**	**137.1**	**11.7**	**22.5**
Lantern	0.26	0.1	33.1	40.23	**18.42**	**452.2**	**21.3**	**115.4**
Hmack	30.91	22.8	0.46	1.5	**13.92**	**234.3**	**15.3**	**110.0**
Hake	2.67	14.6	9.16	10.75	**9.29**	**24.7**	**5.0**	**53.5**
Pelagics	1.92	5.21	1.08	5.04	**3.31**	**4.5**	**2.1**	**64.1**
Squid	0.66	1.11	0.86	5.96	**2.15**	**6.5**	**2.5**	**118.5**
"Other"	1.63	0.37	0.37	1.52	**0.97**	**0.5**	**0.7**	**71.9**

In terms of the overall numerical composition of all the prey species in the diet of the Cape fur seal from January 1994 to December 2018, in all regions under study (Figure 3.1), the bearded goby and Cape hake were consumed in sizeable amounts across all the regions, whereas the Cape horse mackerel was only consumed in high amounts in the two northern regions (Far North (FN) and Central North (CN)) and the lanternfish in the two southern regions (Central South (CS) and Far South (FS)). The pelagic species occurred in relatively low numbers in all the regions. Comparing all the regions, squid contributed highest in the Far South region (6 %), whereas, it only contributed 0.7 %, 1.1 % and 0.9 % in the Far North, Central North and Central South regions, respectively (Figure 3.1). In descending order, the overall contribution of the bearded goby to the diet of the Cape fur seal in the different regions were; 61.8 % (FN), 55.8 % (CN), 55.0 % (CS) and 35.0 % (FS). The Cape hake contributions were; 14.6 % (CN), 10.7 % (FS), 9.16 (CS) and 2.66 % (FN). The horse mackerel contributions were; 30.9 % (FN), 22.8 % (CN), 1.5 % (FS) and 0.5 % (CS). The lanternfish contributions were; 40.2 % (FS), 33.1 % (CS), 0.3

% (FN), 0.1 % (CS). The pelagics contributions were; 5. 2 % (CN), 5.0 % (FS), 1.9 % (FN) and 1.1 % (CS) (Table 3.1).

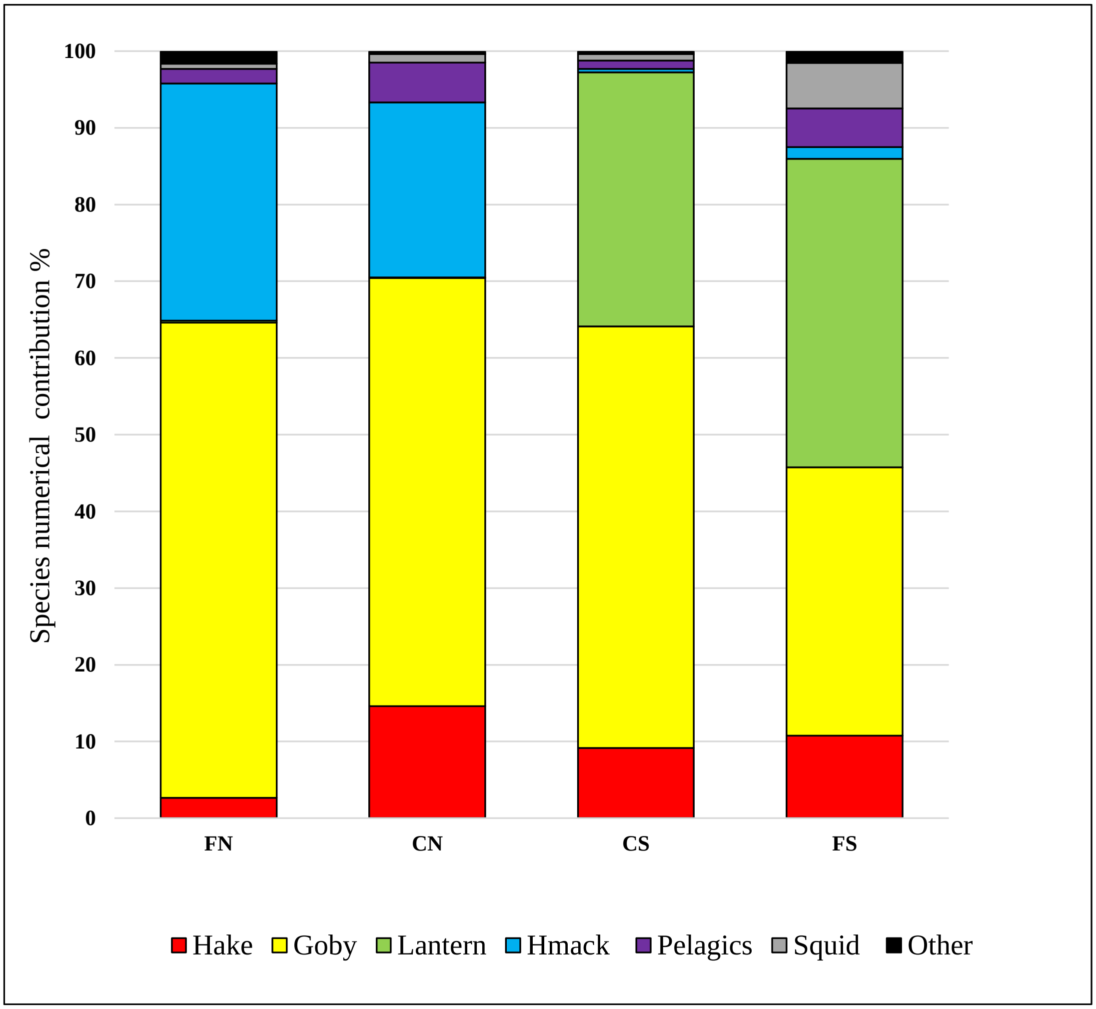

Figure 3.1: The overall numerical composition of all the prey species in the diet of the Cape fur seal from January 1994 to December 2018, in all regions in Namibia. FN = Far North, CN = Central North, CS = Central South, FS = Far South (Figure 2.1). Hake = Cape hake *Merluccius capensis*, Goby = bearded goby *Sufflogobius bibarbatus*, Lantern = lanternfish *Lampanyctodes hectoris*, Hmack = Cape horse mackerel *Trachurus capensis*, Pelagics = (sardine *Sardinops sagax*, anchovy *Engraulis capensis*, round herring *Etrumeus whiteheadi*) pooled, Squid = six species of cephalopods pooled and Other = other fish species pooled.

The Kruskal-Wallis test indicated that there were highly significant differences in the numerical contribution of each prey species, bearded goby (H (3) = 68.91, P < 0.001), hake (H (3) = 179.95, P < 0.001), lanternfish (H (3) = 734.26, P < 0.001) and horse mackerel (H (3) = 664.10, P < 0.001) to the diet of the Cape fur seal between the regions. The post hoc test (Nemenyi test) indicated that the contribution of the bearded goby in the Far North region was not different from that in the Central South region (P = 0.99) as well as that in the Central North region and in the Far South region (P = 0.17), but was significantly different between all other regions (P < 0.001) (Appendix 5). Similarly, the contribution of the Cape hake was significantly different between all the regions (P < 0.001) (Appendix 5). The contribution of the lanternfish in the Far North region was not different from that in the Central North region (P = 0.99), and that of the Central South region was not different from that in the Far South region (P = 0.99), but all others were significantly different from one another (P < 0.001). The contribution of the Cape horse mackerel was significantly different between all the regions (P < 0.001) (Appendix 5).

3.3.2. Monthly variation in the numerical contribution of four major prey items in the Cape fur seal diet along the Namibian coast.

Monthly differences in the contribution of the four most important prey species in the diet of the Cape fur seals along the Namibian coast were clearly observable in each region. The contributions are as follows;

3.3.2.1. Bearded goby

The highest and lowest monthly contributions of the bearded goby to the diet of the Cape fur seal were recorded as follows: FN: highest in February, September and November (> 60 %) and lowest in May (36 %); CN: highest between June and October, with a peak in August (80 %) and lowest in April (4.6 %); CS: highest between January and May, with a peak in March (82 %) and lowest in December (35 %); FS: highest between February and April, with a peak in March (47 %) and lowest in October (18 %) (Figure 3.2). The monthly numerical contribution of the bearded goby to the diet of the Cape fur seal was below 30 % only in the Central North region between January to April and December as well as in May, July, September and October in the Far South region. There were significant monthly variations in the numerical contribution of the bearded goby to the diet of the Cape fur seals in the Central North and Central South region (H (11) = 104.98, P = 0.001; H (11) = 91.82, P = 0.001, respectively) and non-significant in the Far North and Far South region (H (11) = 12.41, P = 0.33; H (11) = 104.98, P = 0.14, respectively) (Appendix 6).

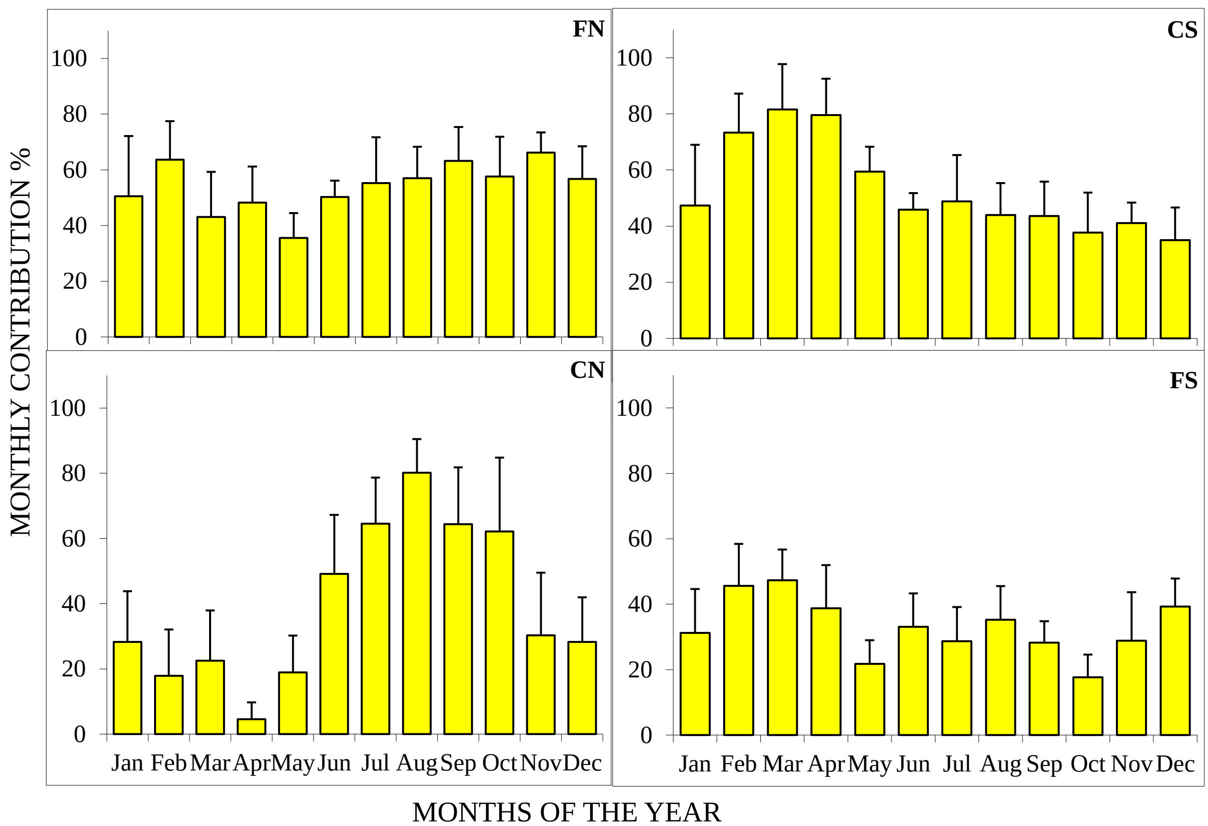

Figure 3.2: The monthly mean (+ SD) contribution (in percentages) of the bearded goby *Sufflogobius bibarbatus* to the diet of the Cape fur seals in the four regions. FN: Far North, CN: Central North, CS: Central South and FS: Far South regions. The error bars represent the standard deviations from the means.

3.3.2.2. Cape Hake

The highest contribution of the Cape hake in the Far North region did not exceed 5 %, and the lowest was merely 0.2 % (Figure 3.3). In the other regions, the highest and lowest contributions were recorded as follows: CN: highest in November (46 %) and December (47 %), lowest in March and April (1.5 %); CS: highest in June (22 %) and July (21 %) and lowest in October (4.5 %); FS: highest in March (24 %) and April (27 %) and lowest in November (5.4 %) (Figure 3.3). There was a clear monthly shifting pattern in the peaks of the hake contribution with the regions. The peaks were observed from November to January in the Central North region, then peaked between February to September in the two southern regions (CS and FS). The numerical contribution of the Cape hake to the Cape fur seal's diet varied significantly between the months in the Central North, Central South and Far South regions (*H* (11) = 110.37, *P* < 0.001; *H* (11) = 51.55, *P* < 0.001, *H* (11) = 38.50, *P* < 0.001, respectively) except in the Far North region (*H* (11) = 14.57, *P* < 0.20) (Appendix 6).

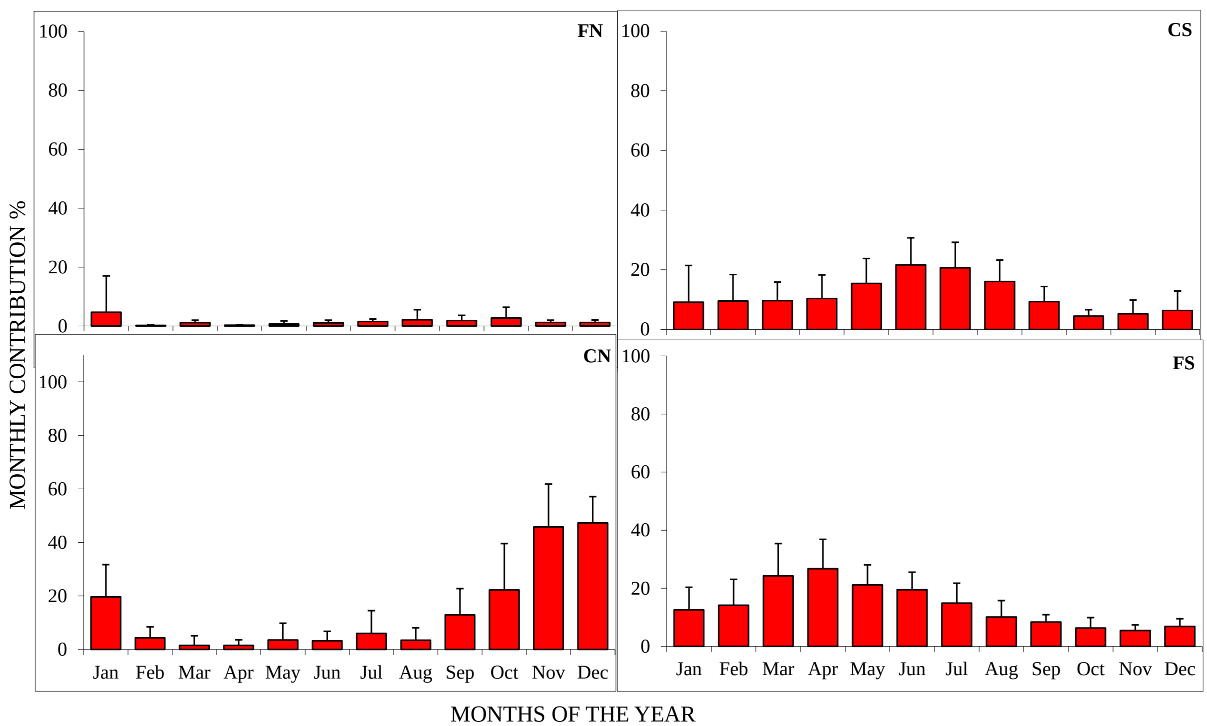

Figure 3.3: The monthly mean (+ SD) contribution (in percentages) of the Cape hake *Merluccius capensis* to the diet of the Cape fur seal in the four regions. FN: Far North, CN: Central North, CS: Central South and FS: Far South regions. The error bars represent the standard deviations from the means.

3.3.2.3. Horse mackerel

The monthly numerical contribution of horse mackerel to the diet of the Cape fur seal was negligible in the Central South and Far South regions with the overall monthly contributions being 0.25 % and 0.9 %, respectively (Figure 3.4). The highest contribution of the Cape horse mackerel to the diet of the Cape fur seal in the Far North and Central North regions were in the autumn months, with the highest contributions recorded in May (60 %) and April (77 %), respectively (Figure 3.4). The Cape horse mackerel contribution remained relatively high in all months in the Far North region, however, there were low contribution recorded between August to December in the Central North region (ranging between 2.8 % and 6.0 %) (Figure 3.4), during which time the Cape hake contribution peaked in the same region (Figure 3.3). The numerical contribution of the Cape horse mackerel to the diet of the Cape fur seals varied significantly between months in the Central North: H (11) = 174.60, $P < 0.001$; Central South: H (11) = 18.62, $P < 0.050$ and Far South H (11) = 23.81, $P < 0.01$ regions, except in the Far North region H (11) = 19.17, $P < 0.058$ (Appendix 6).

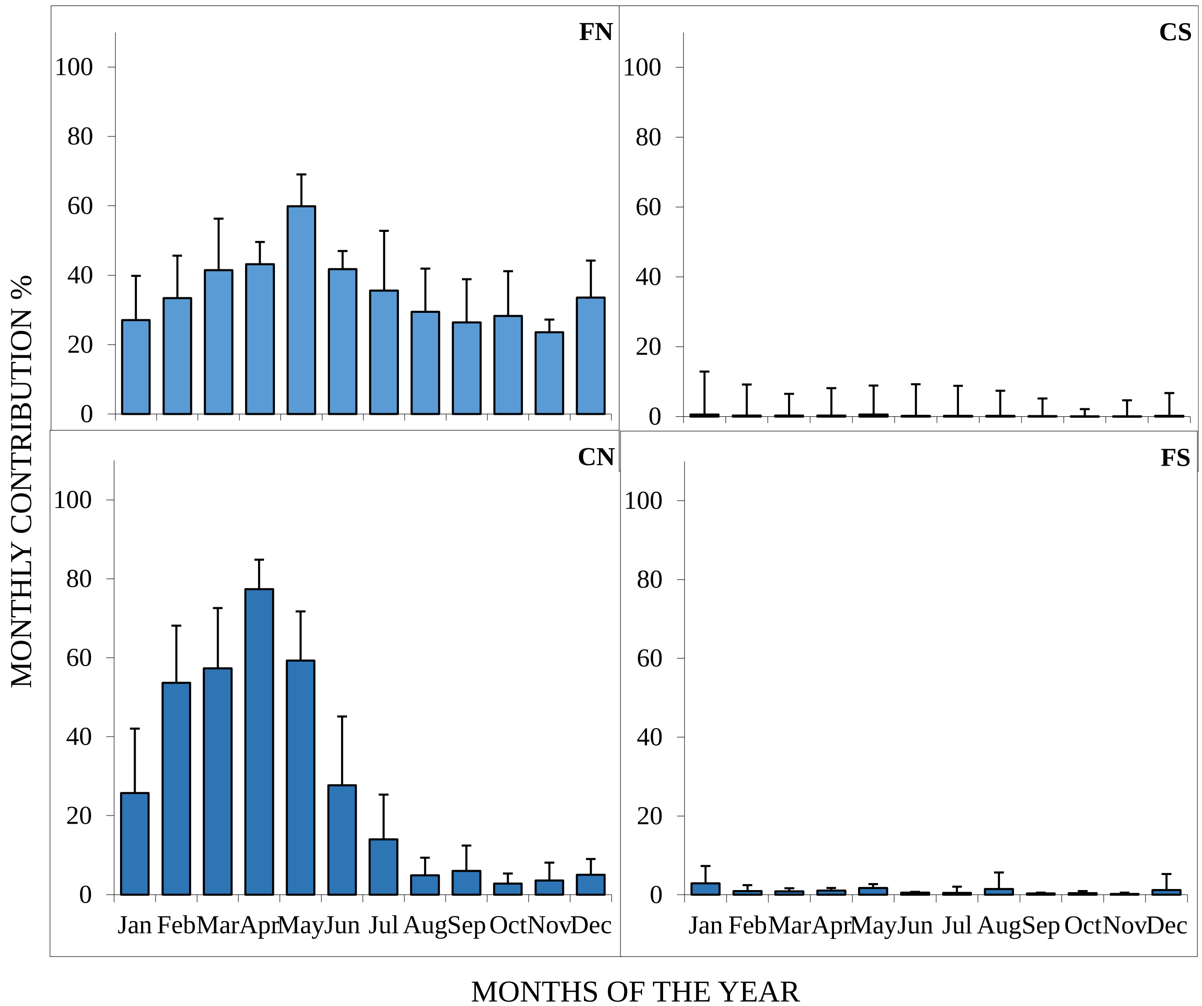

Figure 3.4: The monthly mean (+ SD) contribution (in percentages) of the Cape horse mackerel *Trachurus capensis* to the diet of the Cape fur seal in the four regions. FN: Far North, CN: Central North, CS: Central South and FS: Far South regions. The error bars represent the standard deviations from the means.

3.3.2.4. Lanternfish

The monthly contribution of the lanternfish to the diet of the Cape fur seal was negligible in the Far North and Central North regions, with overall monthly contribution in these regions being, 0.01 % and 0.008 %, respectively (Figure 3.5). The highest and lowest monthly contribution of the lanternfish were recorded as follows: CS: highest between September and January, with a peak in October (51 %) and lowest in April (3.0 %); FS:

highest between September and November, with a peak in October (62 %) and lowest in March (4.1 %) (Figure 3.5). The monthly contribution pattern was very similar between the Central South and Far South regions, with low contribution between February and April and peaks from May to January (during which time the bearded goby and Cape hake contributions were lowest in the same regions, see Figures 3.2 and 3.3). The numerical contribution of the lanternfish to the Cape fur seal diet varied significantly between months in the Central South and Far South region (Appendix 6).

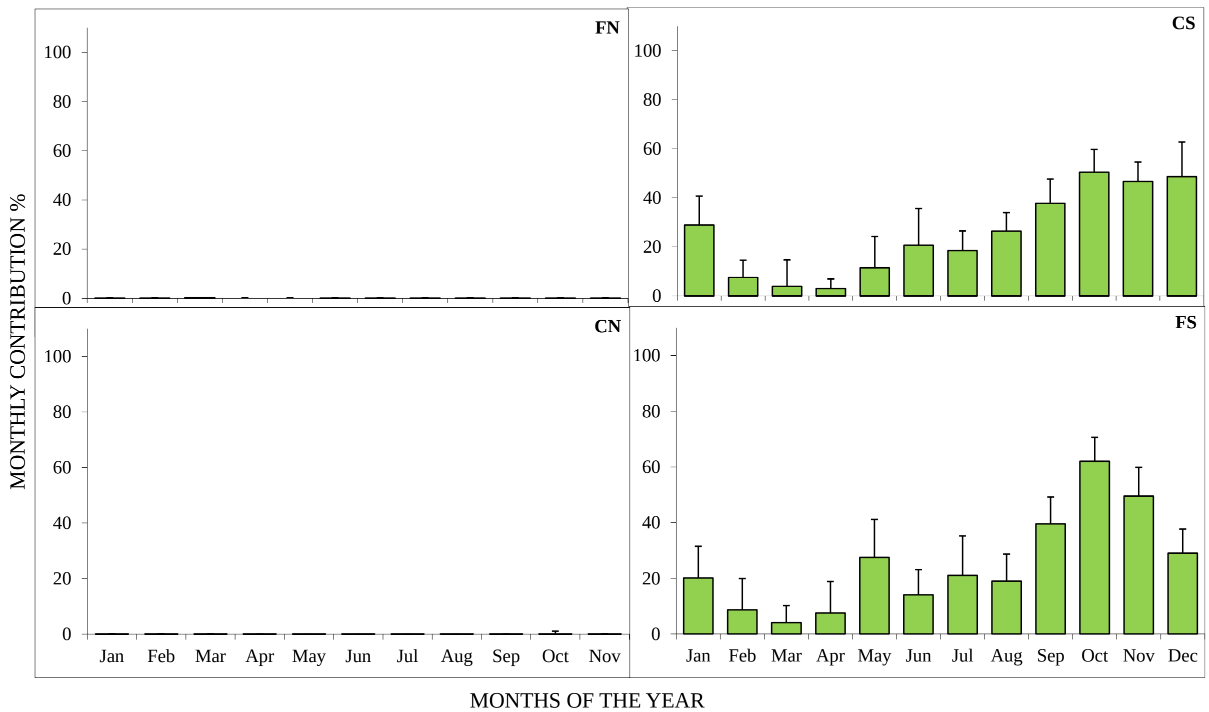

Figure 3.5: The monthly mean (+ SD) contribution (in percentages) of the lanternfish *Lampanyctodes hectoris* to the diet of the Cape fur seal in the four regions. FN: Far North, CN: Central North, CS: Central South and FS: Far South regions. The error bars represent the standard deviations from the means.

3.4. Discussion

The regional variations in the diet of the Cape fur seal in Namibia, could be strongly defined by seasonal prey species contribution. Numerically, the bearded goby *Sufflogobius bibarbatus*, Cape hake *Merluccius capensis*, lanternfish *Lampanyctodes hectoris* and horse mackerel *Trachurus capensis*, were the dominant prey species in the diet of the Cape fur seal along the Namibian coast for over three decades from 1994 to 2018. The bearded goby were consumed in relatively high amounts across all the regions, whereas the horse mackerel was consumed in high amounts only in the Far North and Central North regions. The lanternfish was consumed in minor amounts in the two northern regions, but, was very important in the Central South and Far South regions. Cape hake was the third most important prey species in all the regions except in the Far North.

Cape fur seals are opportunists, and feed on a variety of prey species encountered (David, 1987; de Bruyn et al., 2005; Mecenero et al., 2006a). To date, a total of at least 62 species have been recovered from the diet of the Cape fur seals (Mecenero et al., 2006a), however, the majority of prey groups were composed of two to three species and others infrequently features in the diet. The numerical contribution of the pelagics, squids and "others" groups were fairly minimal (ranging between 0.4 % and 5.9 % per group in a region). The "pelagics" group is composed of three main forage species and clupeiformes of the Benguela ecosystem, the sardine *Sardinops sagax*, anchovy *Engraulis capensis* and round herring *Etrumeus whiteheadi*. These have in the past been the major constituents of top predator diets, however, after changes in the Benguela ecosystem, these have become low. A study by de Bruyn et al. (2003) which assessed the cephalopod component and its diversity in the diet of the Cape fur seal at Atlas and Wolf bay colonies, found out that there were six main species being preyed upon by the fur seals, with *Todarodes angolensis* being the dominant species. This study did not categorize the consumed cephalopods to species level, hence were all pooled and called as "squids" in this study. All the species that rarely contributed to the diet of the Cape fur seals were grouped under the "others" category.

The seasonal contribution of the three main prey species to the diet of the Cape fur seal varied notably in each region with similarities between the Far North and Central North regions as well as between the Central South and Far South regions. In the Far North region, the Cape fur seals fed almost exclusively on horse mackerel and bearded goby, with high amounts of goby in winter, spring and summer, switching to more of horse mackerel in autumn. In the Central North region, the fur seals fed more on the horse mackerel in summer and autumn, switching to goby in winter and spring with an additional contribution of the Cape hake in spring and summer. In the Central South and Far South regions, the fur seals fed more on bearded goby in summer, autumn and winter, then switching to lanternfish in spring with an additional contribution of the Cape hake in autumn and winter.

Different aspects such as, prey distribution, abundance, and environmental fluctuations as well as the calorific contents of the prey species should be looked into in order to explain the possible causes of the spatial, monthly and seasonal variations in the contributions of each prey species to the diet of the Cape fur seal in the respective regions. Ideally, an abundant and largely distributed prey species provides a large amount of foods to the predators. However, marine ecosystems are dynamic, varying in time and space (Hutchings et al., 2009; Kirkman et al., 2016), and these variations could possibly have consequences in changing the prey species abundances over time (Boyer et al., 2001; Shannon et al., 2020). Also, it is understood that predators sometimes select quality over quantity (Balmelli & Wickens, 1994; Bowen et al, 2002; Ludynia et al., 2010), hence, recognition of the calorific value of the prey species will also be important in explaining the spatial and seasonal variations in the diet of the Cape fur seal. According to a calorific content of prey species of the Cape fur seal in Balmelli and Wickens (1994), the horse mackerel contains 5.65 $kJ.g^{-1}$, lanternfish 4.90 $kJ.g^{-1}$, hake 4.47 $kJ.g^{-1}$ and bearded goby with the least of 3.69 $kJ.g^{-1}$.

3.4.1. The bearded goby

The bearded goby *S. bibarbatus* was the most dominant prey species in almost all the regions and in almost all the seasons except in the Far South region where it was the second highest after the lanternfish in the 25 years of the study. In the Far South, it contributed 35.0 %, making it the second highest after lanternfish, which contributed 40.2 %. David (1987) and Mecenero et al. (2006b) also found that bearded goby was dominant in the diet of the Cape fur seal in colonies such as Cape Cross (CN), Atlas-Wolf Bay (CS) and Van Reenen Bay (FS).

It was speculated that the highest contribution of the bearded goby to the diet of the Cape fur seal is a phenomenon that resulted from the collapse of the vital forage fish in the Benguela ecosystem, the sardine *Sardinops sagax*. In fact, studies by Crawford et al. (1985) and Crawford et al. (1987) indicated that following the decline of the sardine population in the late 1960s and a subsequent collapse in the 1980s, many marine predators (teleost fishes, mammals and marine birds) off Namibia have been feeding steadily on the bearded goby as prey. Cury & Shannon (2004) and van der Lingen et al. (2006) stated that the increase in the biomass of the bearded goby is considered to be the most visible consequence of an overfished ecosystem, such as the Benguela Current ecosystem, and was suspected to be detrimental to its functioning, and possibly could be irreversible. Studies by Lynam et al. (2006) and Roux et al. (2013) at the same time observed a dramatic increase and widespread distribution of the two species of jellyfishes, *Aequorea forskalea and Chrysaora fulgida*, most especially after the collapse of the Namibian sardine fishery. These jellyfishes are known to contribute 17 - 60 % to the diets of the bearded goby (Moloney, 2010; Utne-Palm et al., 2010). Therefore, the increase in food (which is jellyfishes) for the bearded goby cascaded into an increase in the bearded goby population in the Benguela, consequently becoming available to the predators, such as the Cape fur seals along the entire Namibian coast all year-round (present study).

Staby & Krakstand (2005) as well as Salvanes et al. (2015) found that bearded goby possess unusual characteristics, giving them high chances of surviving and thriving through the low-oxygen conditions along the Namibian coast that are hostile to many other fishes. Therefore, this gives them resilience to thrive and multiply in the face of harsh environmental anomalies, which could be an additional reason why they are highly abundant in the Benguela and therefore in the diet of the Cape fur seal. Ludynia et al. (2010) noted that, although the bearded goby were highly abundant, and of importance to the diet of many top predators in the Benguela ecosystem, they are of low nutritional value, compared to other common prey species such as the Cape horse mackerel, lanternfish and Cape hake; hence they have been associated with poor breeding success, specifically in seabirds. To date, no studies have been conducted to relate the breeding success of the Cape fur seals to the quality of their dietary rations. However, future studies should address this question, since bearded goby is currently playing an important role in the diet of the Cape fur seal in Namibia, and may have some possible effects on the growth successes.

3.4.2. The Cape hake

Hake was the third most important prey species in the diet of the Cape fur seal in all the regions. The contribution of Cape hake to the diet of the Cape fur seal increased southwards, with the lowest contribution calculated in the Far North region and highest in the Central North region. Its contribution was significantly different seasonally in the Central North, Central South and Far South regions, first appearing in the Central North in spring to early summer, followed by the Central South and Far South regions in autumn to winter.

A study by Jansen et al. (2015) on the spawning patterns of the Cape hake in the Benguela indicated that there was a strong seasonality in the spawning, with the peak occurring in austral winter (from July to September, peaking in August) in the northern Benguela (20 – 25ºS). Wilhelm et al. (2015b) observed nursery aggregations of the Cape hake in the central (22 - 25ºS) and southern (26 - 29ºS) regions of Namibia, with peaks in winter in the central region and later in the year in the southern region. This information corresponds with the high contribution of the juvenile Cape hake (Wilhelm et al., 2013) to the diet of the Cape fur seal in the Central North, Central South and Far South region in the present study. Cape hakes are widespread over the continental shelf, as shallow as 17 m out to 400 – 500 m (Botha, 1985; Badenhorst & Smale, 1991; Burmeister, 2001; Sundby et al., 2001) and very abundant in the shelf waters of the entire Benguela region (Olivar & Shelton, 1993; Hamukuaya et al., 1998). The distribution ranges of the juvenile Cape hake along the Namibian coast overlaps with the foraging and diving ranges of the Cape fur seal, which is 150 - 200 km from the shoreline to bathymetric depths of <500 m

(Skern-Mauritzen et al., 2009; Kirkman et al., 2019). This makes them available to the Cape fur seal as from 4 cm – 23 cm in total length (2 – 21 months old), which is when they occur more close inshore (Wilhelm et al., 2013, 2015b).

3.4.3. The lanternfish

Lanternfish were very important in the diet of the Cape fur seal in the Central South and Far South regions and non-significant in the Far North and Central north regions. In the Far South region, the lanternfish had the highest overall contribution to the diet of the Cape fur seal compared to all the other prey species. Likewise, Mecenero (2005) found that the lanternfish *L. hectoris* was numerically most abundant in the diet of the Cape fur seal at Atlas-Wolf Bay (CS) and Van Reenen's Bay (FS), and very low in contribution at Cape Cross (CN). Mecenero (2005) further detailed that although the lanternfish were abundant in these two regions, their contribution to mass consumed by the fur seal was relatively low due to their small sizes. However, lanternfish are well known to aggregate in extensive shoals and so even with their smaller sizes, they are highly desirable as prey to fur seals because of their high content of fine quality oil (ranging between 23.2 to 28. 9 kJ at 20 % by oil) and a mean calorific content 4.90 $kJ.g^{-1}$ (Ahlstrom et al., 1976; Prosch, 1986; Balmelli & Wickens, 1994), which is higher than that of the Cape hake and bearded goby but lower than that of the Cape horse mackerel. Therefore, Cape fur seals may prefer preying on lanternfish over other available prey species that are available in the area as they will benefit them energy-wise.

Lanternfish populations occur in the coldest regions such as the Benguela upwelling cells, and are well-known for their diel-vertical migration from deeper colder waters to the surface zones (Rubies, 1985; Prosch, 1991). In terms of distribution and abundance, the northern Benguela ecosystem supports several mesopelagic species of lanternfishes and *L. hectoris* is by far the most abundant lanternfish in the region (Ahlstrom et al., 1976; Cruickshank, 1985; Sabates & Olivar, 1989). In the southern Benguela, *L. hectoris* is the only lanternfish found inshore of the 300 m isobaths (Hulley & Prosch, 1987; Prosch, 1991). A larval study by Ahlstrom et al. (1976) found that *L. hectoris* was widely distributed between latitudes 19º and 25º, at a distance of 8 to 112 km from the coast but were most abundant in offshore waters between Mowe Point (20º20´S) and Cape Cross (22ºS) as well as between Walvis Bay (23ºS) and Hollams Bird Island (25ºS) (Hewitson & Cruickshank, 1993). Cruickshank (1982) reported that *L. hectoris* were found on the outer shelf edge more than 50 kilometers offshore in the northern Benguela but only 9 kilometers offshore near Lüderitz (27ºS). Cruickshank (1985) confirmed that mesopelagic lanternfish were found farther offshore along the whole coast of Namibia, especially around Walvis Bay. Hence, a high abundance of lanternfish in the diet of the Cape fur seals in southern Namibia than in the North. Hulley (1992) found that depth, regional temperature structure of the water column and upper slope can affect the distribution of oceanic lanternfishes. Some authors have found that the shallowing of the continental slope to the shelf-break is the major factor in determining the shoreward distribution of vertically-migrating oceanic mesopelagic fishes (e.g. Ahlstrom et al., 1976; Rubies, 1985; Prosch et al., 1989; Hewitson & Cruickshank, 1993; Alexander Hulley, 1992; Hulley & Lutjeharms, 1995). The two study regions in which lanternfish were most abundant in the Cape fur seal population's diet, Far South and Central South lie at the centre of the Lüderitz upwelling cell, the largest and coldest upwelling cell in the world (Bakun, 1996). Therefore, the two regions are situated within the lanternfishes favourable habitat and distribution, and hence their largest contribution to the diet of the Cape fur seals foraging within this area. The negligible amounts of lanternfish in the diet of the Cape fur seal at regions located within the northern part of the northern Benguela (Far North and Central North regions) could be explained from the bathymetry zonation, width of the shelf edge, and the distance from the shoreline as well as temperature conditions. In the northern Benguela, the shelf edge is extended much further offshore and little upwelling activities occurring in the region, hence, making the lanternfish not readily available to the seals. In southern Namibia, the shelf edge is narrower and allows the intrusion of lanternfish into depths and spaces that easily overlaps with the foraging ranges of the Cape fur seal population, resulting in a maximal contribution to their diet in the Far South and Central South regions. Also, in the northern region, Cape horse mackerel are more abundant and are preferred because of their highest calorific value.

3.4.4. The Cape horse mackerel

Cape horse mackerel *Trachurus capensis* played an important role in the diet of the Cape fur seal in the regions located within northern Namibia, the Far North and Central North regions, with negligible amounts to the regions within southern Namibia, the Far South and Central South region. The Cape horse mackerel is an abundant benthopelagic species in northern Namibia, with a wide latitudinal distribution with hotspots between 17º30´S and 22º00´S and least abundant in southern Namibia (Hecht, 1990; Bianchi et al., 1999; Shannon & Jarre-Teichmann, 1999; Geist et al., 2014; Uanivi et al., 2019). Therefore, their higher distribution and greater abundance in northern Namibia defines the uppermost contribution of horse mackerel to the diet of the Cape fur seal population in the Far North and Central North regions and very low in the Central South and Far South regions. According to Balmelli and Wickens (1994), Cape horse mackerel has a mean calorific content of 5.65 $kJ.g^{-1}$ wet mass which is higher than that of the bearded goby, lanternfish and hake. Therefore, it is possible that the fur seals in Namibia would prefer to feed on the horse mackerel whenever they are available due to their high quality. In the Far North region, Cape fur seals fed on Cape horse mackerel in high amounts all months, whereas in the Central North region, they switched to bearded goby and Cape in summer.

Chapter 4: Interannual variability and long-term trends of prey species in the diet of the Cape fur seals in Namibia, with focus on the three main prey items

4.1. Introduction

Studies of the diets of several pinniped species have recorded seasonal, annual and geographical differences in their diet composition (Bowen et al., 1993; Tollit & Thompson, 1996; Sinclair & Zeppelin, 2002; de Bruyn et al., 2003; Garcia-Rodriguez & Aurioles-Gamboa, 2004; Hume et al., 2004; Mecenero et al., 2006a, 2006b; McKenzie & Wynne, 2008; Ciaputa & Sicinski, 2006; Bowen & Harrison, 2007). However, most of these investigations were recorded over slightly short timeframes (i.e. < a decade), which presents a concern when trying to assess the extent to which these patterns remain consistent over time.

In Chapter 3 it was shown that the diet of the Cape fur seals along the Namibian coast was dominated by four species of teleost fish, making up to > 80 % of the total diet composition in each region. Three species of the teleost fish, i.e. the bearded goby (*Sufflogobius bibarbatus*), lanternfish (*Lampanyctodes hectoris*) and Cape horse mackerel (*Trachurus capensis*), in particular played an integral role in the diet of Cape fur seals along the Namibian coast (Chapter 3, present study). Their importance in the diet of top predators came to light after the collapse of another important pelagic fish species, the sardine *Sardinops sagax* in the 1980s (Staby & Krakstand, 2005; Ludynia et al., 2010; Cedras et al., 2011; Boyer et al., 2001; Roux et al., 2013) and recorded in the present study since 1994 (Chapter 3).

The Cape fur seal distribution is endemic to the cold, nutrient rich Benguela ecosystem (Shillington, 2003). Being a highly dynamic environment, it is subject to variable temporal and spatial environmental fluctuations (Summerhayes et al., 1995). These environmental fluctuations, in turn, can greatly influence the primary productivity of the system and can lead to cascading effects throughout the food web, which is directly linked to shifts in prey distribution and availability over time (Cury et al., 2000; Cury &

Shannon, 2004; van der Lingen et al., 2006) and will therefore influence the abundance and therefore availability of certain prey items to Cape fur seals. Considering that Cape fur seal females, resident at the colonies, forage in close proximity to their breeding sites, they tend to consume locally abundant species and as such research on their diet can be used to examine the temporal variability in their prey base.

This chapter aims to assess the extent of interannual variability and long-term changes in the relative contribution of the bearded goby, lanternfish and horse mackerel to the diet of the Cape fur seals in the four regions (as defined in Chapter 2) along the Namibian coast over a period of 25 years. Specifically, the objectives of this study were;

1. To determine the annual numerical contribution of all prey species in the diet of the Cape fur seals in all the regions.
2. To determine the interannual variations of the bearded goby and horse mackerel in the Far North and Central North regions as well as that of the bearded goby and lanternfish in the Central South and Far South regions.
3. To determine the long-term changes of the bearded goby, horse mackerel and lanternfish in the fur seal diet in each region from 1994 to 2018.

4.2. Methods

4.2.1. Data analysis for interannual variation and long-term trends.

For the annual analysis, years that had fewer than five sampling months of scat collection were not included in the data analysis (see Appendix 4). Very few or no samples were collected at the Far North sites during the period 1994 – 2005 and 2011 – 2013. Hence, no annual averages were calculated for those years. The Central North and Central South regions had a full representation of annual samples for the entire period of the study, 1994 to 2018. The Far South region had a full representation of samples with the exception of 3 years (1996, 1997 and 1998) that had fewer than the minimum number of samples required for the calculation of averages (see Appendix 4).

Linear regression analyses were performed on the arcsine transformed annual numerical contribution of each species in each region against year to investigate the long-term changes over time. The Pearson's correlation was used to test the correlations between the annual contributions of the Cape horse mackerel and bearded goby in the FN and CN regions and between the bearded goby and lanternfish in the CS and FS as the principal prey species to the Cape fur seal diet.

To achieve a normal distribution and equality of variances, the arcsine data transformation was employed on the square root of all the proportions (Equation 2.2, Chapter 2). Even after the data transformations, the Shapiro-Wilk test for normality showed that data in some years and in some regions were not normally distributed. Also, the data was highly variable between years. The analyses were performed in the Real Statistics Resource Pack software (Release 6.8). The percentage of the annual contribution of each prey species was calculated using Equation 4.1. The standard deviations (Equation 4.2) were calculated from the arcsine transformed data for each prey species. Graphical illustrations were plotted using the back-transformed data (in percentages), using equation 2.3, Chapter 2.

$$\%\ Annual\ abundance\ of species\ A\ (in\ area) = \frac{Total\ annual\ number\ of\ items\ of\ prey\ species\ A}{Total\ number\ of\ items\ of\ all\ prey\ species\ pooled\ for\ that\ year} \times 100 \quad (4.1)$$

Standard deviation of the annual abundance of a prey species to the Cape fur seal diet was calculated as follows:

$$S = \sqrt{\frac{1}{n-1}\sum_{i=1}^{n}(x_i - \overline{x})^2} \quad (4.2)$$

Where;

S = standard deviation of an annual contribution of a prey species to the Cape fur seal diet

x*i* = arcsine-transformed value of sample *i* collected within a given sampling year,

$\overline{x}$ = mean (arcsine-transformed) of all the samples collected in a sampling year, and n = total number of samples collected within a sampling year.

4.3. Results

4.3.1. General description of the annual contributions of the two major prey species in each region

In the Far North region (Figure 4.1a), the bearded goby and Cape horse mackerel contributed in the highest amounts to the diet of the Cape fur seal in all the years. The yearly contribution of the Cape hake, pelagics, squid and others were minimal in all the years and their combined annual contribution did not exceed 7 % in any year (Figure 4.1a). Similarly, in the Central North the bearded goby and Cape horse mackerel were the most important prey species in all the years and unlike in the Far North region, the Cape hake played a role too, with particularly high contributions in the years 1994 (50 %), 2001 (47 %), 2005 (45 %) and 2015 (32 %), and the lowest contributions recorded in 2007 (2.1 %), 2014 (0.9 %), 2017 (1.6 %) and 2018 (0.9 %) (Figure 4.1b). The contribution of the pelagics was also evident in this region, with the highest contribution in the year 2002 (23.5 %), and decreasing for all the other years before and after 2002 (Figure 4.1b).

In the Central South region (Figure 4.1c), the annual contributions to the diet of the Cape fur seal were mostly bearded goby, lanternfish and Cape hake. Cape hake was the third highest prey species, with particularly high contributions recorded in years 1994 (27 %), 1997 (41 %), 2003 (39 %), 2009 (39 %) and 2013 (27 %) and with lowest records in 1995 (4 %), 1998 (2.7 %), 2002 (0.9 %), 2014 (3 %) and 2018 (1.3 %) (Figure 4.1c). Similarly, in the Far South region (Figure 4.1d), the bearded goby, lanternfish and Cape hake were also the most frequently consumed prey species in all the years. Pelagics contributed to the diet in a considerable amount in 2004 (26 %), with years contributing more than 10 % being 2000 (12.3 %), 2002 (11.3 %), 2005 (12.4 %), 2006 (10.1 %) and 2007 (11.0 %) after which the percentage decreased while squid and "other" species increased. The Cape horse mackerel contributions were only clearly visible, in 2004 (17 %). Unlike all the other regions, the Far South region had also considerable contributions of the squid and "other" species in most of the years (Figure 4.1d).

a) FN

b) CN

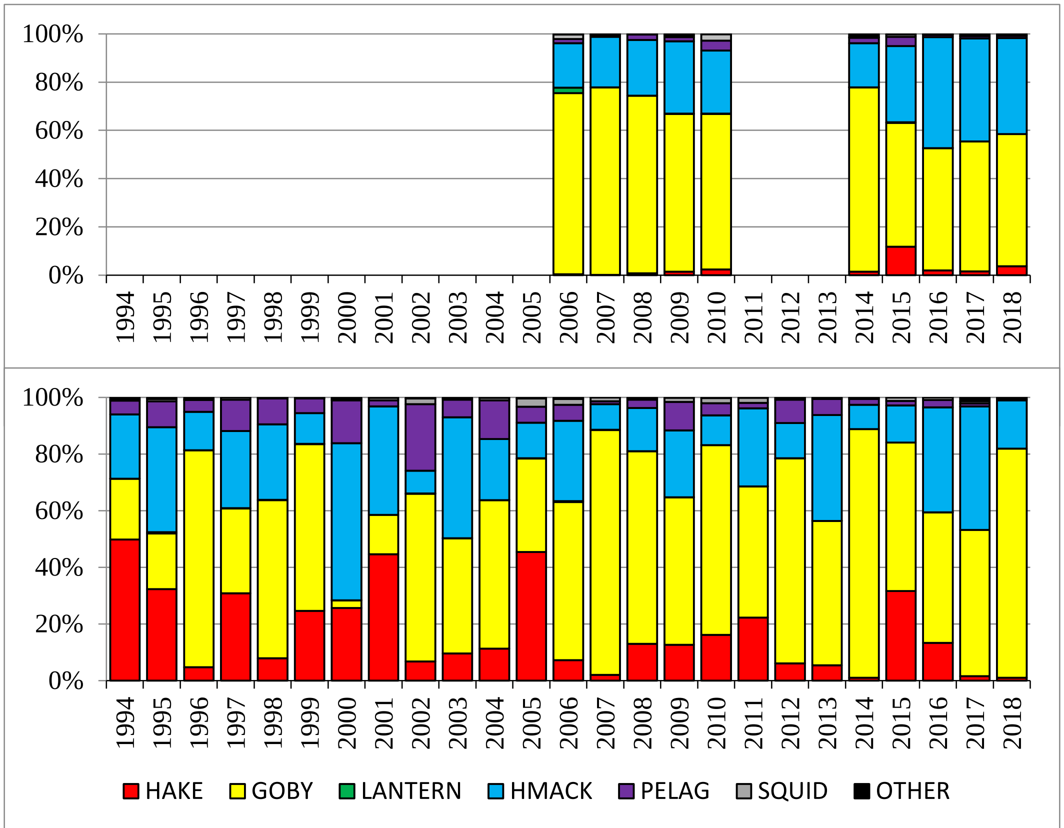

Fig.4.1.continued

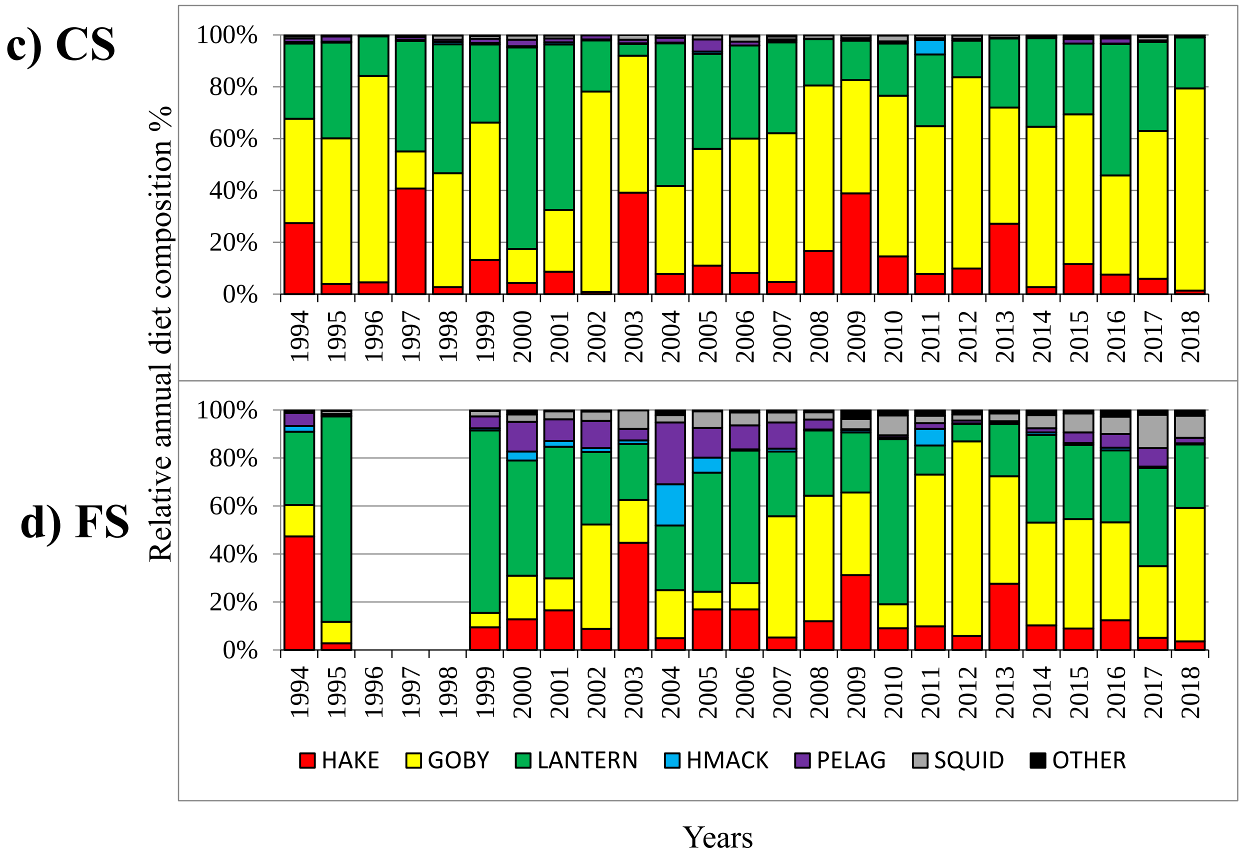

Figure 4.1: The relative annual composition of all prey species to the Cape fur seal diet in the four study regions. a) Far North (FN), b) Central North (CN), c) Central South (CS) and d) Far South (FS). PELAG = sardines *Sardinops sagax*, anchovy *Engraulis capensis* and round herring *Etrumeus whiteheadi*, GOBY = bearded goby *Sufflogobius Bibarbatus*, LANTERN = Lanternfish *Lampanyctodes hectoris*, HAKE = Cape hake *Merluccius capensis*, HMACK = Cape horse mackerel *Trachurus capensis*, SQUID = 6 cephalopod species, OTHER = All other fish species.

4.3.2. Interannual variations in the contribution of the bearded goby, Cape horse mackerel and lanternfish to the diet of the Cape fur seal

Figure 4.2 shows the individual contribution of the two most important prey species in each region in all the years of the study. In the Far North region, the annual contribution of the bearded goby to the diet of the Cape fur seal was higher than 50 % from 2006 to 2014 and was overtaken by Cape horse mackerel between 2016 and 2018 (Figure 4.2a). The highest contribution of the bearded goby to the diet of the Cape fur seal in this region was recorded in 2007 with a contribution of 76 ±6 %. In the same year, the horse mackerel contribution to the diet was the lowest (22 %) when compared to all the years in the study period and switched around for 2016 to 2018, resulting in a significant negative correlation between the annual contribution of the bearded goby and horse mackerel to the diet of the Cape fur seal in the Far North region ($r = -0.84$, $n = 10$, $P < 0.002$) (see Appendix 7).

The highest (> 50 %) annual contribution of bearded goby to the Cape fur seal diet in the Central North region were recorded in 1998 (55 %), 2007 (77 %), 2008 (60 %), 2014 (68 %) and 2018 (72 %) (Figure 4.2b). In contrast to this, the highest horse mackerel contributions to the seal diet were only recorded in 2000 (56.3 %) and 2003 (52.1 %), years in which the bearded goby abundance was low (Figure 4.2b), showing highly significant negative correlation between the annual contribution of the bearded goby and the horse mackerel in the Central North region ($r = -0.62$, $n = 25$, $P < 0.001$) (see Appendix 7). The lowest annual diet contributions of bearded goby were recorded in 1995 (10.5 %), 2000 (2.2 %) and 2001 (9.3 %); whereas for horse mackerel, this occurred in 2002 (8.6 %) and 2007 (8.9 %) (Figure 4.2b).

In the Central South region (Figure 4.2c), the annual contribution of lanternfish to the Cape fur seal diet only exceeded 50 % in two years, 2000 (67 %) and 2004 (52 %) (Figure 4.2c). Bearded goby abundance was above 50 % often when the lanternfish abundance was low (Figure 4.2c), showing highly significant negative correlation between the annual contribution of the bearded goby and the lanternfish in the Central South region($r = -0.52$, $n = 25$, $P < 0.007$) (Appendix 7).

In the Far South region, the bearded goby's annual diet contribution exceeded 50 % in very few years, namely, 2011 (62.3 %); 2012 (80.2 %) and 2018 (56.2 %) (Figure 4.2d) when the lanternfish abundance was very low (< 20 %) showing highly significant negative correlation between the annual contribution of the bearded goby and lanternfish to the diet of the Cape fur seal in the Far South region, r = -0.63, n = 22, $P < 0.002$) (see Appendix 7).

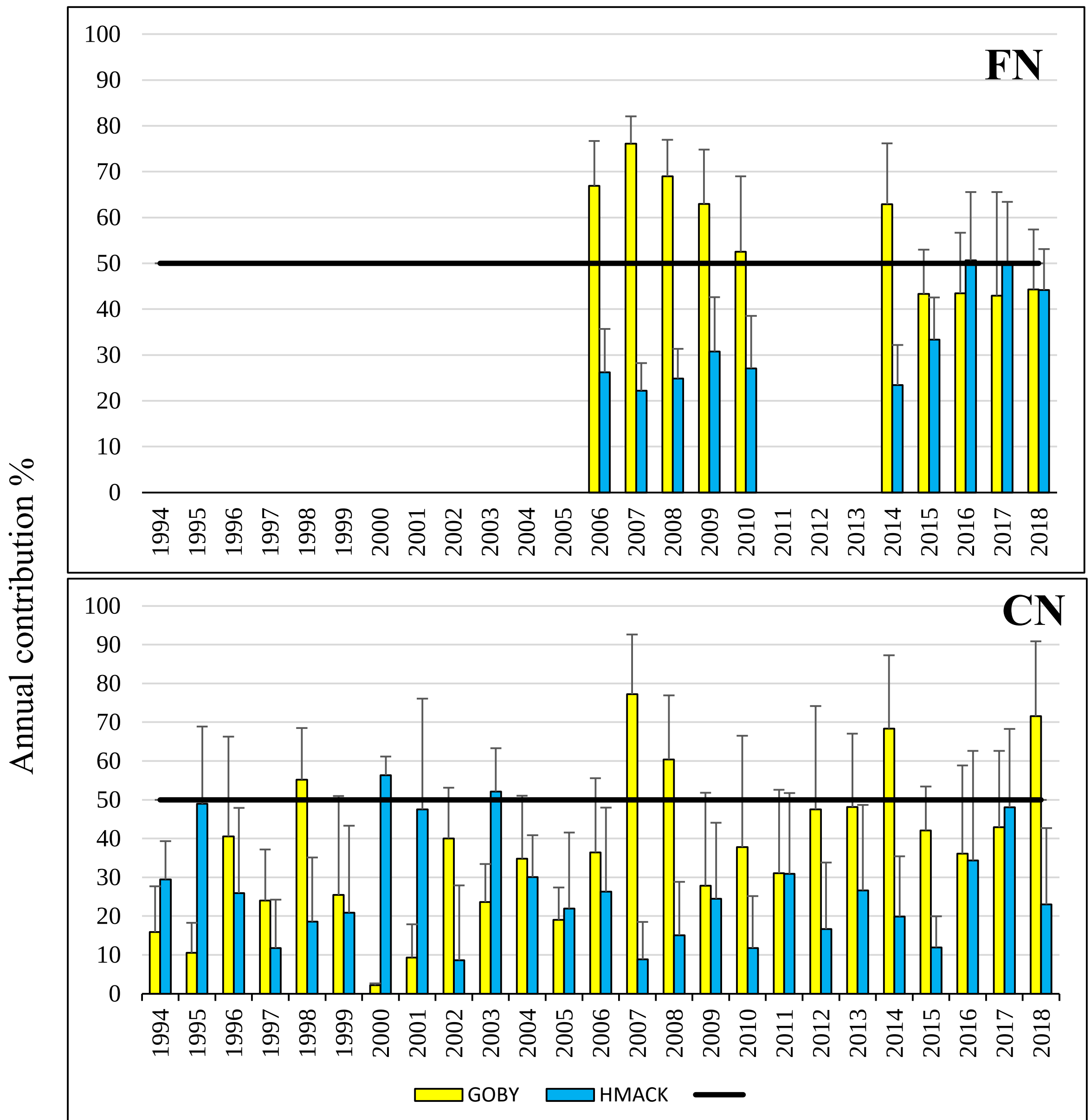

Fig. 4.2. Continued

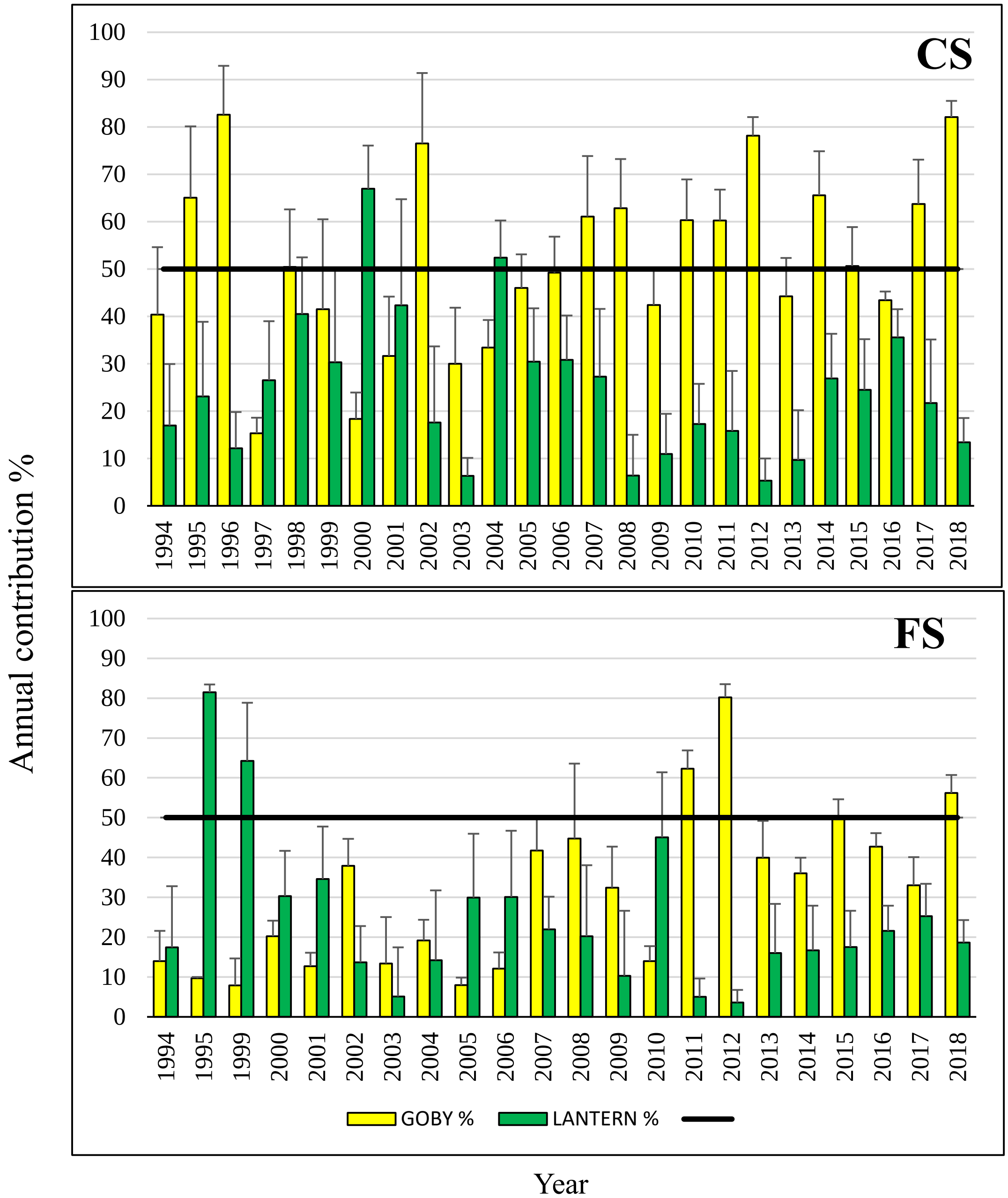

Figure 4.2: The mean annual contribution (in percentages) of the bearded goby (GOBY, yellow), horse mackerel (HMACK, blue) and lanternfish (LANTERN, green) to the diet of the Cape fur seal in the four study regions. a) Far North, b) Central North, c) Central South and d) Far South

4.3.3. The long-term trends in the contribution of the bearded goby, Cape horse mackerel and lanternfish to the diet of the Cape fur seal in each region.

In the Far North region, the bearded goby abundance decreased significantly by -2.5 % per year (t = -5.01, n = 10, $P < 0.001$) and horse mackerel abundance increased significantly by 1.9 % per year in the Cape fur seal diet (t = 3.69, n = 10, $P < 0.006$) (Figure 4.3; Appendix 8). In the Central North region, the annual contribution of the bearded goby significantly increased by 1.5 % per year (t = 3.21, n = 25, $P < 0.004$), with no significant change in the annual contribution of the Cape horse mackerel, (t = -0.70, n = 25, $P = 0.49$) (Figure 4.4; Appendix 8). There were no significant changes over time in the annual contribution of the bearded goby or lanternfish to the diet of the Cape fur seal in the Central South region, t = 1.71, n = 25, $P = 0.10$ and t = -1.26, n = 25, $P = 0.22$, respectively (see Figure 4.5; Appendix 8). In the Far South region, the annual contribution of the bearded goby significantly increased by 1.9 % per year (t = 4.06, n = 22, $P = 0.0001$) and that of the lanternfish significantly decreased by -1.2 % (t = -2.19, n = 22, $P = 0.04$) in the diet of the Cape fur seal (Figure 4.6; Appendix 8).

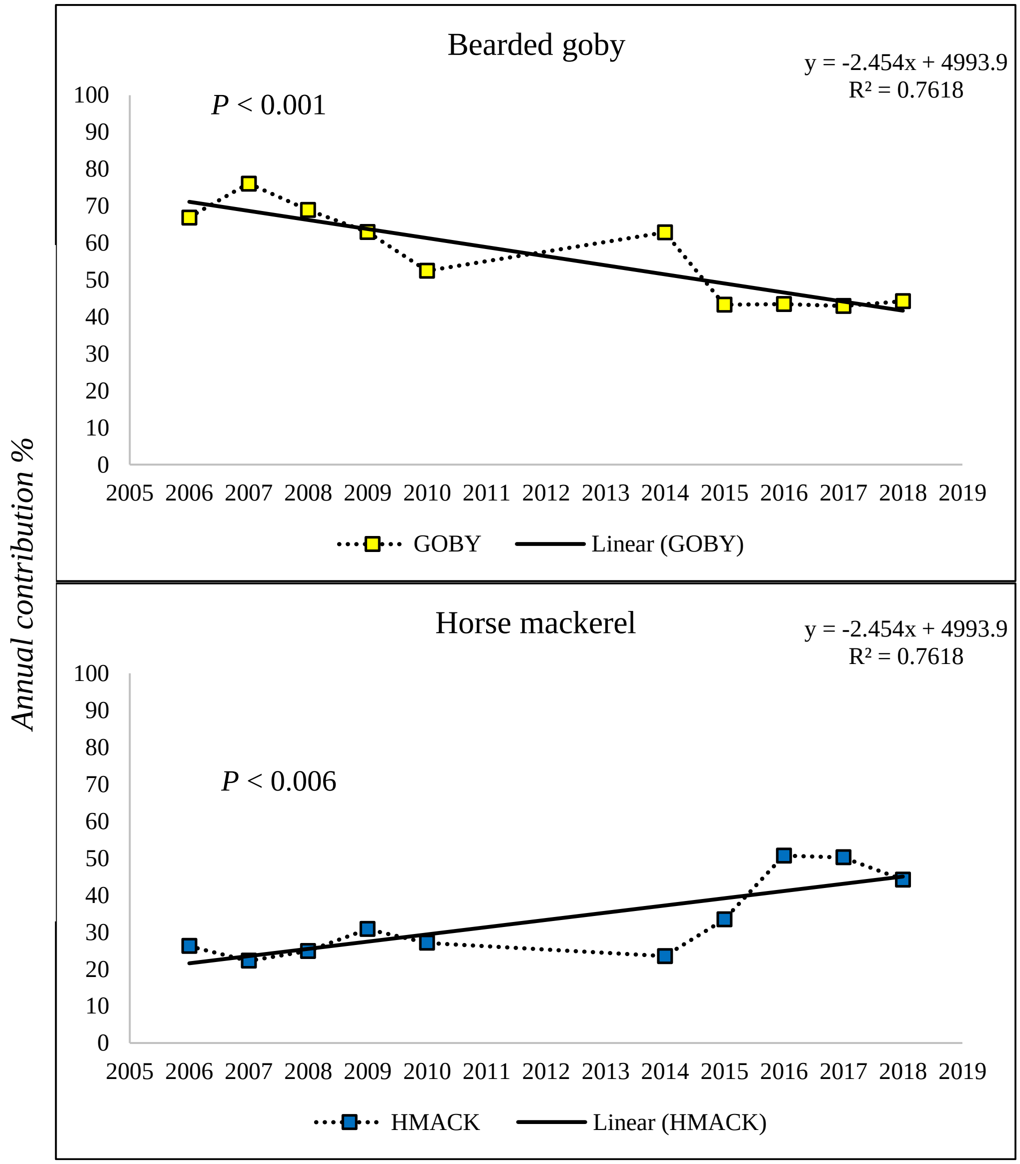

Figure 4.3: The long-term changes of the mean contribution of a) bearded goby and b) Cape horse mackerel to the diet of the Cape fur seal in the Far North region over the years. The backslash in the graphs are indicating the gap in sample collection.

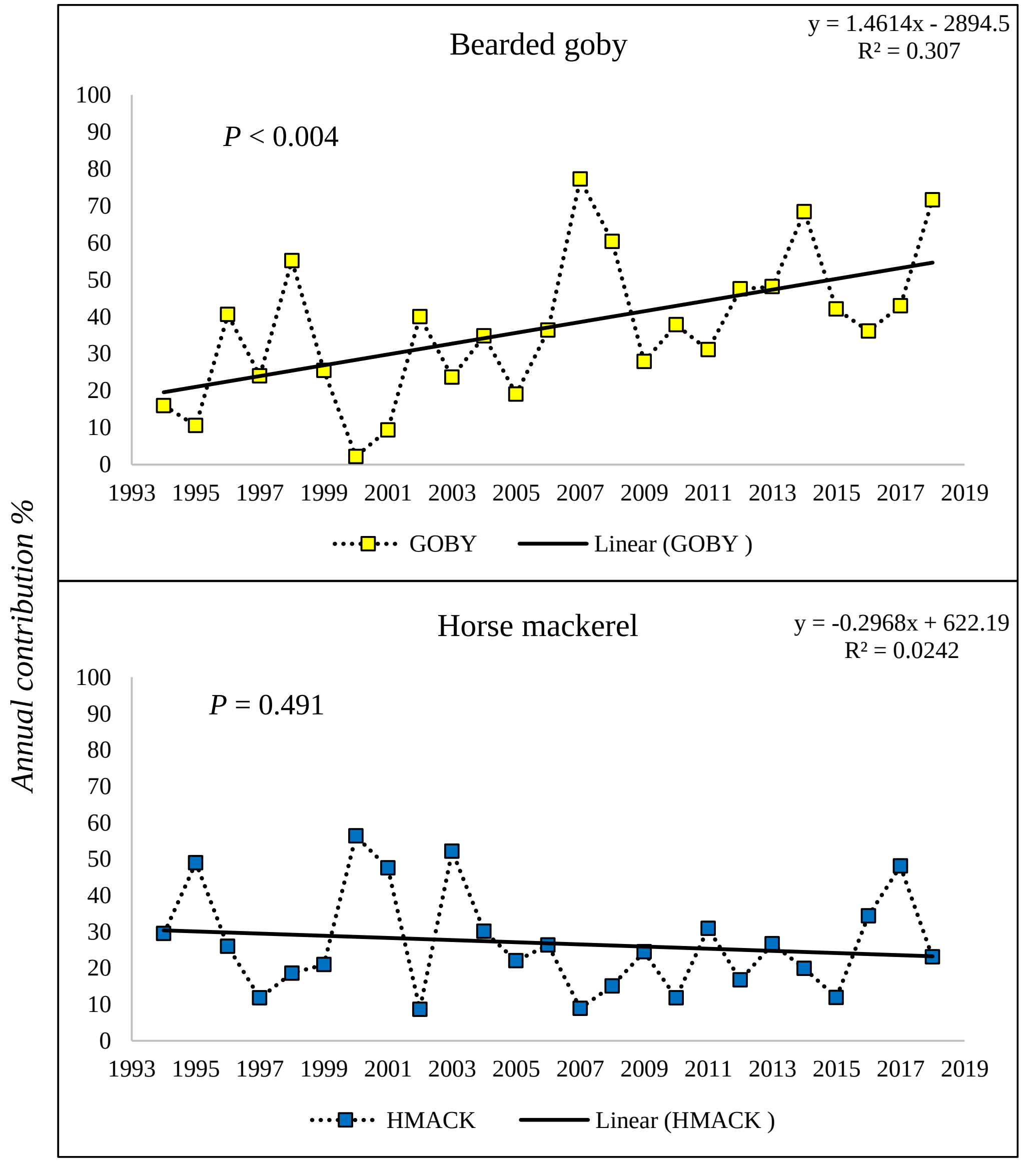

Figure 4.4: The long-term changes of the mean contribution of a) bearded goby and b) Cape horse mackerel to the diet of the Cape fur seal in the Central North region over the years.

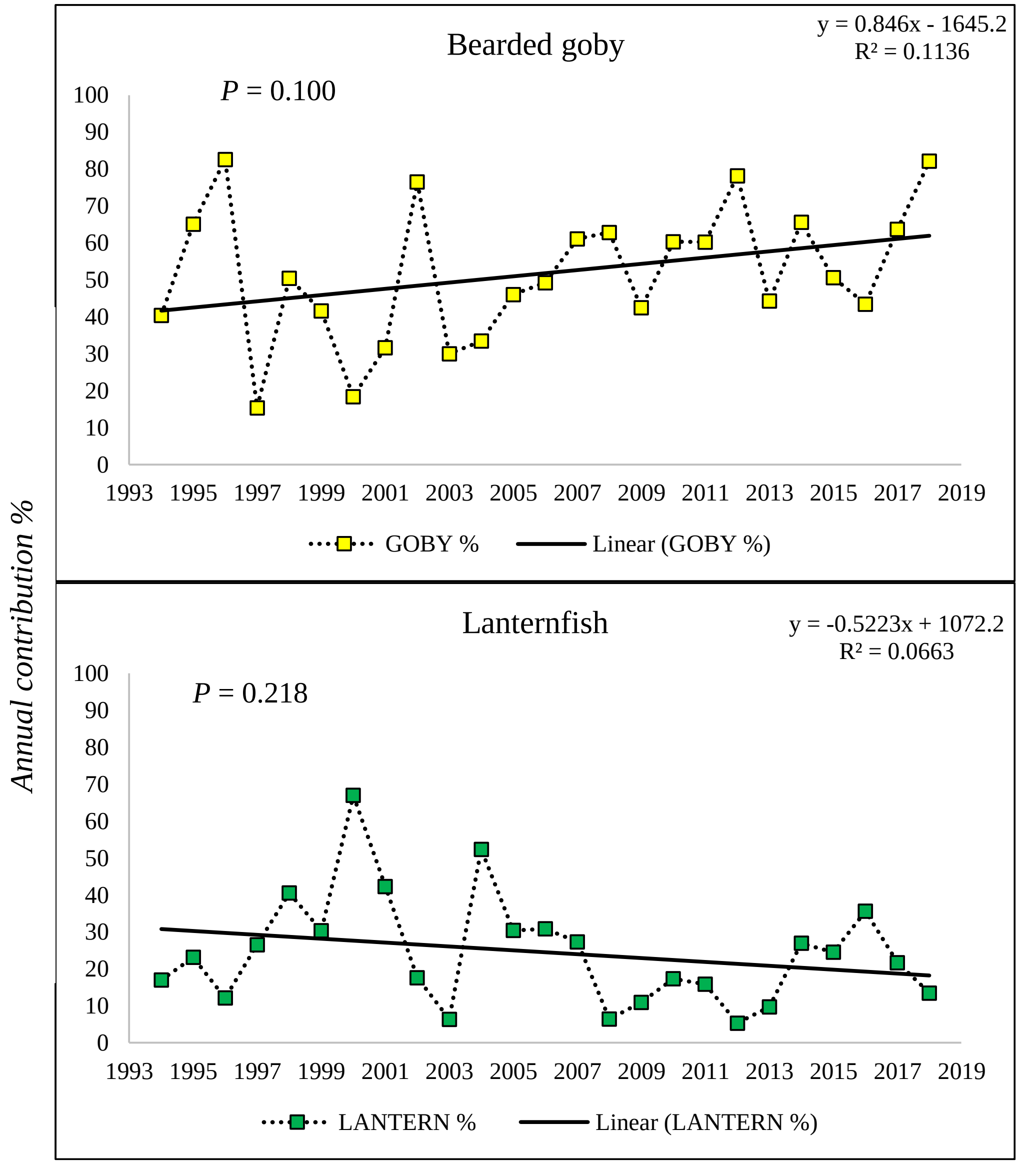

Figure 4.5: The long-term changes of the mean contribution of a) bearded goby and b) lanternfish to the diet of the Cape fur seal in the Central South region over the years.

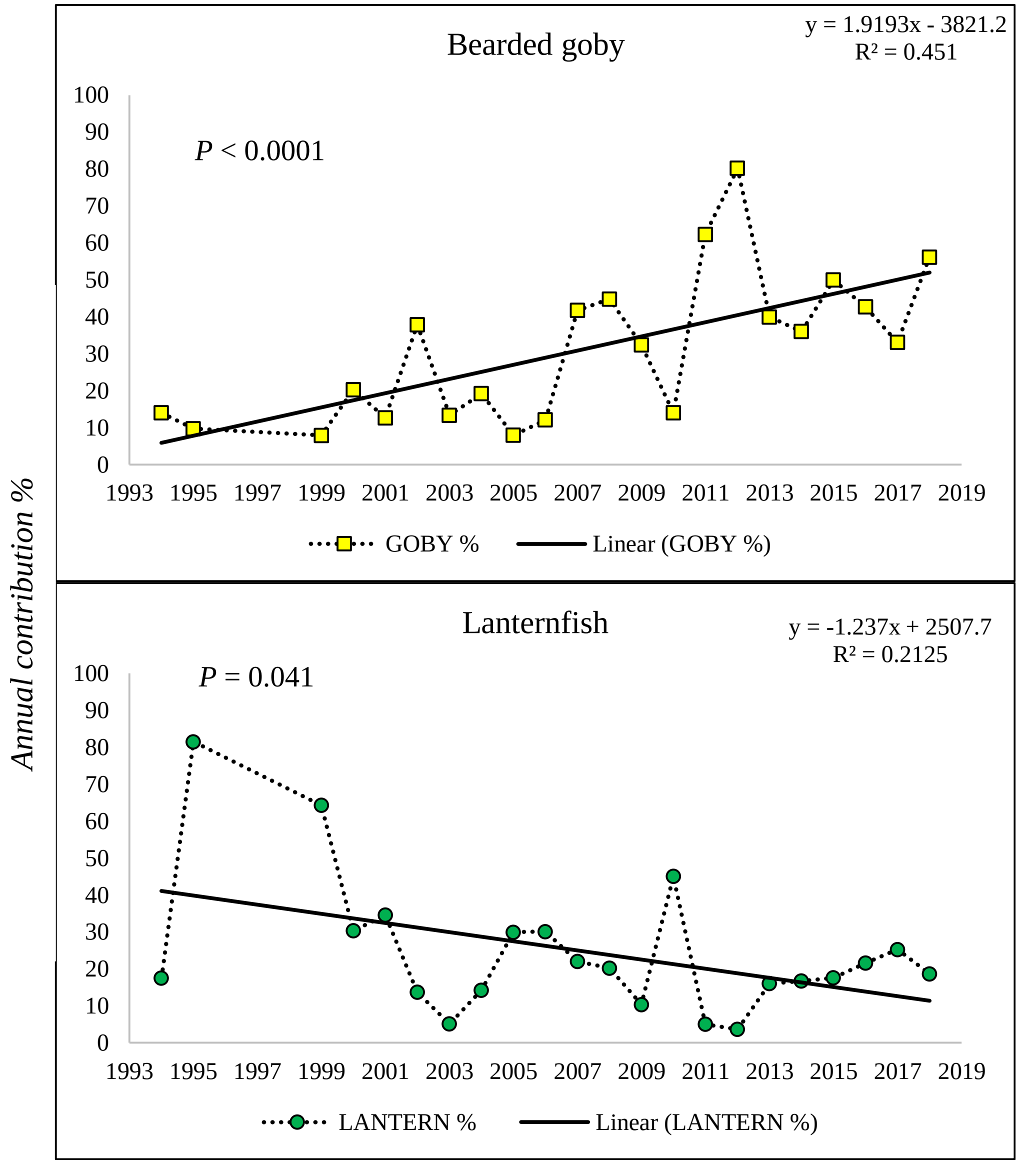

Figure 4.6: The long-term changes of the mean contribution of a) bearded goby and b) lanternfish to the diet of the Cape fur seal in the Far South region over the years.

4.4. Discussion

This study covered an extensive temporal scale (25 years of almost continuous sampling); and is by far the longest time series of diet data available for this species – as well as being one of the longest-running studies for any pinniped species at the time of this write-up. It is therefore a good basis for assessing the interannual variability and long-term trends of three important prey species in the diet of the Cape fur seal population in different regions along the Namibian coast.

Like most pinnipeds, Cape fur seals are generalists, so they typically prefer to feed on highly abundant species and prey found in close vicinity of their territories, aggregating and schooling fishes as well as nutritious species. They use this foraging behaviour in order for them to maximize on energy at feeding (Bowen et al., 2002). The observed consistency in the total contribution of the two major prey species at each region may reflect the availability of those prey species in their local areas (Chapter 3). Similarly, the higher annual contribution of the bearded goby than all the other prey species in the regions may reflect that this species is highly abundant and probably available almost all the time along the entire inshore part of the Namibian coast, hence taken by fur seals in larger amounts compared to other species. The bearded goby is a non-shoaling species, with low nutritional value and also spends much of its time at demersal layers (Cedras et al., 2011; Salvanes et al., 2011; Salvanes & Gibbons, 2018). A fur seal dive study by Kirkman et al. (2019) showed that Cape fur seals are mainly epipelagic foragers. They further found that many of the dives were at night to much shallower depths than during the day, which they presented was consistent with the diel vertical migration of the prey species such as horse mackerel, juvenile hake, anchovies, sardine and round herring. Although they associated the bearded goby consumption with the benthic dives, the bearded goby and lanternfishes are known to undertake diel vertical migrations as well (Staby & Krakstand, 2005). This then overlaps with the vertical foraging distribution of the Cape fur seal population and they currently depend on them as food.

The contribution of the bearded goby in the Central North and Far South regions increased 7-fold from the 1990s to the 2010s, and in the Central South region by two times. The pooled annual contribution of the bearded goby and the lanternfish varied between years, only in the Central South region. The results revealed that it was mainly due to the high effect of the Cape hake contribution in the Central South region. It is unclear how the Cape hakes contributed in higher amounts to the diet of the Cape fur seal population in 1994 due to massive reduced stock sizes as a result of the Benguela Niňo event that was experienced from the winter of 1994 (Boyer et al., 2001; Hampton & Willemse, 2012). However, the high contribution of hakes in year 2003 and 2005 corresponded to high relative hake recruitment from the winter of the previous year, 2002 and 2004 that were recorded in those years (Wilhelm et al., 2015a). In particular, it was indicated that the hake cohort spawned in the winter of 2002 was the highest to date, hence, corresponding to the higher contribution to the diet of the Cape fur seal throughout 2003 in the Central North and Far South region (Wilhelm et al. in review). Due to low catch rates of the small pelagics and Cape horse mackerel in the South of Namibia, substantial studies and abundance estimates from research surveys of these species are conducted only in northern Namibia and hardly at all in southern Namibia (Hamre et al., 1997; Uanivi et al., 2019). Therefore, it is difficult to correspond the high contribution of the pelagics and horse mackerel to the Cape fur seal diet in 2004 in the Far South region without biomass data.

According to strata divisions in the annual horse mackerel research surveys in northern Namibia (e.g. Uanivi et al., 2019), the inshore Stratum IV (17°15’S - 21°00’ S) and Stratum V (21°00’S - 23°00’S), is in the immediate vicinity of the two regions, Far North and Central North, and corresponds with the foraging ranges of the Cape fur seals in these two regions, which is in the range of 150 km – 300 km from shoreline, at bathymetric depths of < 500 m (Skern-Mauritzen et al., 2009). From the horse mackerel survey reports, it was evident that Stratum IV usually has the second highest biomass of horse mackerel after the offshore Stratum II (22°00’S - 19°00’S), and biomass in this stratum appeared to be increasing, whereas Stratum V carried the second lowest biomass after Stratum I (25°00’S - 22°00’S) (Uanivi et al., 2019; Uanivi & Van der Plas, 2014). Also, the surveys of the *RV* Dr. Fridtjof Nansen (Krakstad et al., 2017) found very high densities of Cape horse mackerel north of Cape Frio (18°25’S), up to Mowe point (19°22’S), with most fish captured between 20 and 200 m depth. The increase in the biomass of the horse mackerel in that region, corresponds to the significant increase in its annual contribution to the diet of the Cape fur seal in the Far North region from 2014 to 2018. It is possible that the continued increase of the Cape horse mackerel off the FN region reflected in the diet of the Cape fur seals, takes place at the expense of bearded goby which are of lower nutritional quality and have been declining in the diet in this region (see Chapter 3). Therefore, the long-term decline of the bearded goby in the diet of the Cape fur seals in that region.

According to *RV* Dr. Fridtjof Nansen (Krakstad et al., 2017) horse mackerel survey report, there was a small patch of low density distribution of Cape horse mackerel parallel to the Cape cross fur seal colony and relatively low densities South of Walvis Bay (southwards of the CN region), with most of fish caught beyond the 200 m depth contour in this area. This could explain the decrease in the contribution of the horse mackerel to the diet of the Cape fur seal in the Central North region. Little information is available on the abundance of the bearded goby in both regions, hence making it very difficult to relate it to their decreased contribution to the fur seal diet in the Far North region.

Under ideal circumstances, an individual predator will encounter high-quality food items on a regular basis. These preferred foods provide the most nutritional benefit with the fewest costs. In the case of the Cape fur seal, the costs of hunting would be handling time (e.g., time required to catch prey or distance travelled for hunting) or presence of chemicals that may reduce the nutritional quality of the food item. However, when the preferred foods are scarce, the predators are then forced to switch to other, less-desirable alternatives. This choice is also dependent of many other factors such as the relative abundance of each of the foods and the potential costs associated with acquiring each food item. Due to this low calorific value, the bearded goby is most probably a less preferred prey species of the Cape fur seal, but, less seasonal and with a very high abundance in all years and seasons (see Chapter 3). It appears then that as soon as the abundance of the highly favored foods (in this case the Cape horse mackerel in the North or the lanternfish in the South) increases, then the Cape fur seals consume more of those, and switches back to the bearded goby when there is less of the Cape horse mackerel or the lanternfish.

Fishing exploitation intensities of the prey species that overlaps with the diet of the Cape fur seals may also result in interannual variations in their diet. The scenario, was explained in Chapter 3, which showed that bearded goby (as an indigenous prey species) only increased in abundance after the collapse of the previous most important prey species, i.e. sardine (*Sardinops sagax*). During the early 1960s when the sardines were highly abundant in the ecosystem (Boyer et al., 2001), they probably contributed significantly to the Cape fur seal's diet – most certainly more than any other species. As the decline in sardine abundance ensued post-1960 (in lieu of excessive fishing pressure) fur seals were forced to adapt their diets to other available species. This scenario also caused major collapses in populations of specialist predators such as seabirds (Crawford, 2007; Sherley et al., 2017). Therefore, a collapse of a common forage fish species in a heavily exploited ecosystem (such as the sardines *Sardinops sagax* in northern Benguela (Boyer & Hampton, 2001)), as a result of the predators demand coupled with fishing concentrations, may create gaps in the predator's consumption needs, forcing them to partially or fully switch to other available prey species.

In the South, the long-term contribution of the lanternfish is decreasing and that of the bearded goby increasing. In his study, Asseburg (2006) found out that the energy intake of a generalist predator does not depend on the density of any single species as it can be affected by the availability of an alternative prey species. In this scenario, the intake of the lanternfish in the South could be affected by the availability of all the other prey species at any given time. Lanternfish and bearded goby are currently not being commercially harvested, hence it is suspected that the fluctuations in the contribution of the lanternfish to the diet of the Cape fur seals in southern Namibia would be related to environmental conditions such as sea surface temperature and coastal upwelling. Much of the relationship between the abundance of lanternfish in the diet of the Cape fur seals in southern Namibia and the effects from fluctuations in in-situ SSTs and upwelling index will be investigated in Chapter 5.

Chapter 5: Assessing the relationship between the abundance of lanternfish in the Cape fur seal's diet and the Lüderitz coastal upwelling index and Sea Surface Temperature

5.1. Introduction

Marine top predators forage within highly variable environments and therefore must adapt to changing environmental conditions that can potentially influence prey availability at both the temporal and spatial scales (Trathan et al., 2007; Hunsicker et al., 2011). In the Benguela Current Large Marine Ecosystem (BCLME), coastal upwelling is one of the major drivers of ecosystem productivity (Bakun, 1996; Hutchings et al., 2009). It plays an important role by delivering cold, nutrient-rich waters from the bathypelagic depths to the meso- and epipelagic areas of the ocean (Bakun, 1996; Cury et al., 2000; Lamont et al., 2018; Shannon et al., 2020). This consequently influences the chemical and biological systems of the ocean, inducing high productivity which helps in supporting the high density pelagic fishes/ forage fish of the Benguela Current (Cury et al., 2000; Mecenero et al., 2006; Moloney et al., 2004). These high densities of small pelagic fishes then in turn sustain top predators, such as the Cape fur seals and vast colonies of seabirds along the Namibian coast (Cury et al., 2000; Roux et al., 2013; Ekau et al., 2018; Peck et al., 2021). Environmental conditions have impacts on marine species either directly by affecting meiotic and mitotic growth rates (as indicated by physiological and chemical processes related to the variable permeability of cell membranes across temperature profiles, and mineralization effects as regulated by temperature and pH, respectively); or indirectly through alterations in prey species habitats (Wingfield et al., 2011). In Cape fur seal breeding colonies, nursing females predominantly exhibit central place foraging behaviour – which means they forage on any available and abundant prey species found within a narrow spatial range of the breeding colonies (Mecenero, 2005; Skern-Mauritzen et al., 2009; Kirkman et al., 2019). For this reason, nursing female fur seals are more susceptible to changes in localized prey availability than male seals that are able to track migratory or other highly abundant prey species at greater distances from the colonies.

The lanternfish *Lampanyctodes hectoris*, is a prominent species from the speciose family Myctophidae (Prosch et al., 1989; Hulley, 1991; 1992), and the second most consumed prey species by Cape fur seals, specifically in the Central South (CS) and Far South regions (FS) however, decreasing in the diet (Chapters 3 and 4, present study).

Hulley (1992), showed that lanternfish occur in high abundances in cold water systems, and the present study confirmed that lanternfish recorded the highest abundances at the CS and FS regions during the summer months (November to January, Chapter 3). These two regions, (CS and FS) are located within the Lüderitz Upwelling Cell, a well-defined ecological feature characterized by the prevalent south-westerly wind which are the strongest during the summer months (Peard, 2007). The upwelling events are associated with cold, nutrient-rich waters that are driven up from deeper layers of the ocean to the surface and result in high primary productivity that supports large communities of fish species (Bakun, 1996; Cury et al., 2000; Lamont et al., 2018; Shannon et al., 2020). Because of the link between the upwelling and the sea surface temperature, it will be interesting to contrast both variables with the abundance of the lanternfish in the regions.

Fisheries acoustic research surveys in the BCLME traditionally, have focused on attempts to fully understand the distribution and density variability of commercially important species, such as the sardine, anchovy, horse mackerel and round herring (Barange et al., 1994; Boyer & Hampton, 2001). As a result of this, very little effort has been directed towards trying to understand the distribution and abundances of commercially non-important species, such as the lanternfish *L. hectoris*. At the time of conducting this study, there existed only sparse information on the abundance of the lanternfish and its correlation to important environmental factors such as coastal upwelling and sea surface temperature variability. In this chapter, an attempt was made to formulate a link between the observations of the lanternfish *L. hectoris* abundance in the Cape fur seal diet (in the Central South and Far South regions) and the Coastal Upwelling and Sea Surface Temperature. Specifically, the objective of this chapter was:

To test the relationship between the discrete monthly and overall monthly abundance trends of lanternfish *L. hectoris* in the Cape fur seal diet in the Central and Far South regions and the corresponding coastal upwelling index and sea surface temperature index in the same periods.

5.2. Methods

5.2.1. Environmental data

To evaluate the potential link between lanternfish abundance in the Cape fur seal diet and environmental variability at the aforementioned study sites; two meso-scale environmental indices were used, i.e., the Coastal Upwelling Index (CUI) and the monthly sea surface temperature (SST) index spanning the temporal scale of the current Cape fur seal diet study.

For the assessment of the Coastal Upwelling Index, a dataset (containing a total of 65448 hourly wind stress data points) was sourced from the Environment Section of the Ministry of Fisheries and Marine Resources, Namibia (Appendix ***9***9). Within this dataset, two variables i.e. wind speed and the South-North component of the wind direction (as recorded from a Campbell automatic weather station housed at the Dias Point Lighthouse, situated close to Lüderitz at 26° 38’ S, 15° 05' E) were considered as key variables in approximating the upwelling index and thus were the only two variables used during this assessment. The wind data series from this weather station covers a period starting in the mid-1960s. However, for the purpose of this study, only data from 15 July 2011 to 31 December 2018 were used. The January 1994 – 14 July 2011 wind data were excluded from this assessment for the reason that this data subset fell within a period when technical difficulties were experienced with the weather station and the wind measurements are considered to be inaccurate or, by the most conservative judgments, unreliable.

The hourly upwelling data points were aggregated into discrete monthly averages (e.g. 01 – 31 January pooled for each year), and into long-term monthly averages (e.g. January 2012 – January 2018 pooled as January as an overall monthly signal). The proxy for coastal upwelling intensity was calculated from the wind stress component of the Ekman Transport equation;

$$M_E = r * Cd * v^2 / 2 * \Omega * \sin(\varphi) \tag{8}$$

where:

M_E = Ekman Transport measured in kg.m.s^{-1}.

r = air density (1.22 kg m^{-3});

Cd = drag coefficient (0.0013);

v = speed of the wind component parallel to the coast (m.s-1) (at Dias Point this is the South-North component);

Ω = angular rotation of earth (7.292 s^{-1}); and

Φ = Latitude (26° 38'S at Dias Point).

(Johnson & Nelson, 1999; Mann & Lazier, 2013, data updated from Peard, 2007).

A dataset containing 2727 of daily *in situ* SST values (in degrees Celsius - ºC), recorded from the Lüderitz harbour were obtained from the Environment section of the Ministry of Fisheries & Marine Resource (MFMR). To fit the fur seal diet dataset used in this study, all in situ SST data from January 1994 to December 2018 were used. The discrete mean monthly and long-term monthly *in situ* SST averages were then calculated from the smoothed values in the same way as the upwelling index. Smoothing of the data was applied by taking 11-day moving averages over the period.

5.2.2. Data analysis

To test the relationship between the Coastal Upwelling Index and lanternfish abundance, the lanternfish data set was adjusted to match the coastal upwelling index cycle data (which started in July 2011). The relationship between the *in situ* SST and the lanternfish abundance was tested using all data collected between January 1994 and December 2018.

The discrete and long-term monthly abundances of lanternfish in the Central South and Far South regions were calculated in the same way as described for the upwelling index (all abundance data averaged by month separately for CS and FS as outlined in Chapter 3). In cases where two or more fur seal scat samples were collected per month, a pooled percentage of the two samples was considered to represent that specific month.

The Pearson's Product-Moment Correlation Coefficient or "Pearson's r" was used to measure the correlation between the discrete and long-term monthly abundances of the lanternfish (arcsine transformed) and each of the two environmental indices (i.e. coastal upwelling and sea surface temperature, untransformed). A multiple linear regression was used to determine the extent of the variation in the abundance of lanternfish in the diet of the Cape fur seals as a result of the changes in coastal upwelling and sea surface temperature in the regions.

5.3. Results

5.3.1. Relationship between the Coastal Upwelling Index and lanternfish abundance in the Cape fur seal diet in the Central South and Far South regions.

In general, the contribution of the lanternfish *L. hectoris* in the Central South region followed a similar monthly pattern as that of the coastal upwelling index (Figure 5.1, Figure 5.2). The months with peak coastal upwelling (November to February) were associated with high abundances of the lanternfish in the fur seal diet and the months with the lowest coastal upwelling index (May to July) corresponded to the lowest abundances (Figure 5.2). This pattern had a highly significant positive correlation between the discrete monthly abundance of the lanternfish to the Cape fur seal diet in the Central South region, and the mean monthly Coastal Upwelling Index ($r = 0.41$, $n = 90$, $P < 0.001$). Seasons with the highest upwelling values in the time series were recorded for 2012 – 2015. The outliers in the data series was July 2014 in which the contribution of the lanternfish was relatively high and the Coastal Upwelling Index was relatively low and 2012 that showed the highest upwelling index but lowest lanternfish abundance and thus showed no synchronicity (Figure 5.1a). In the Far South region, the discrete monthly lanternfish abundance did not match the pattern of the Coastal Upwelling Index, with a non-significant positive correlation between the discrete monthly abundances of lanternfish in the Cape fur seal diet and the Coastal Upwelling Index, ($r = 0.13$, $n = 90$, $P = 0.22$, Figure 5.1b).

There was a non-significant positive correlation between the long-term monthly Coastal Upwelling Index and the abundances of lanternfish in the Cape fur seal diet in the Central South region ($r = 0.39$, $n = 12$, $P = 0.21$, Figure 5.2a). Also, there was a positive but non-significant correlation between the long-term monthly abundances of the lanternfish in the fur seal diet and the long-term Coastal Upwelling Index in the Far South region, ($r = 0.53$, $n = 12$, $P = 0.08$, Figure 5.2b). The multiple linear regression showed that for every 1 % increase in coastal upwelling, there was 0.26 % ± 0.05 ($P < 0.001$) and 0.38 % ± 0.06 ($P < 0.001$) increase in the abundance of lanternfish in the diet of the Cape fur seals in the Central South and Far South regions, respectively (Appendix 15).

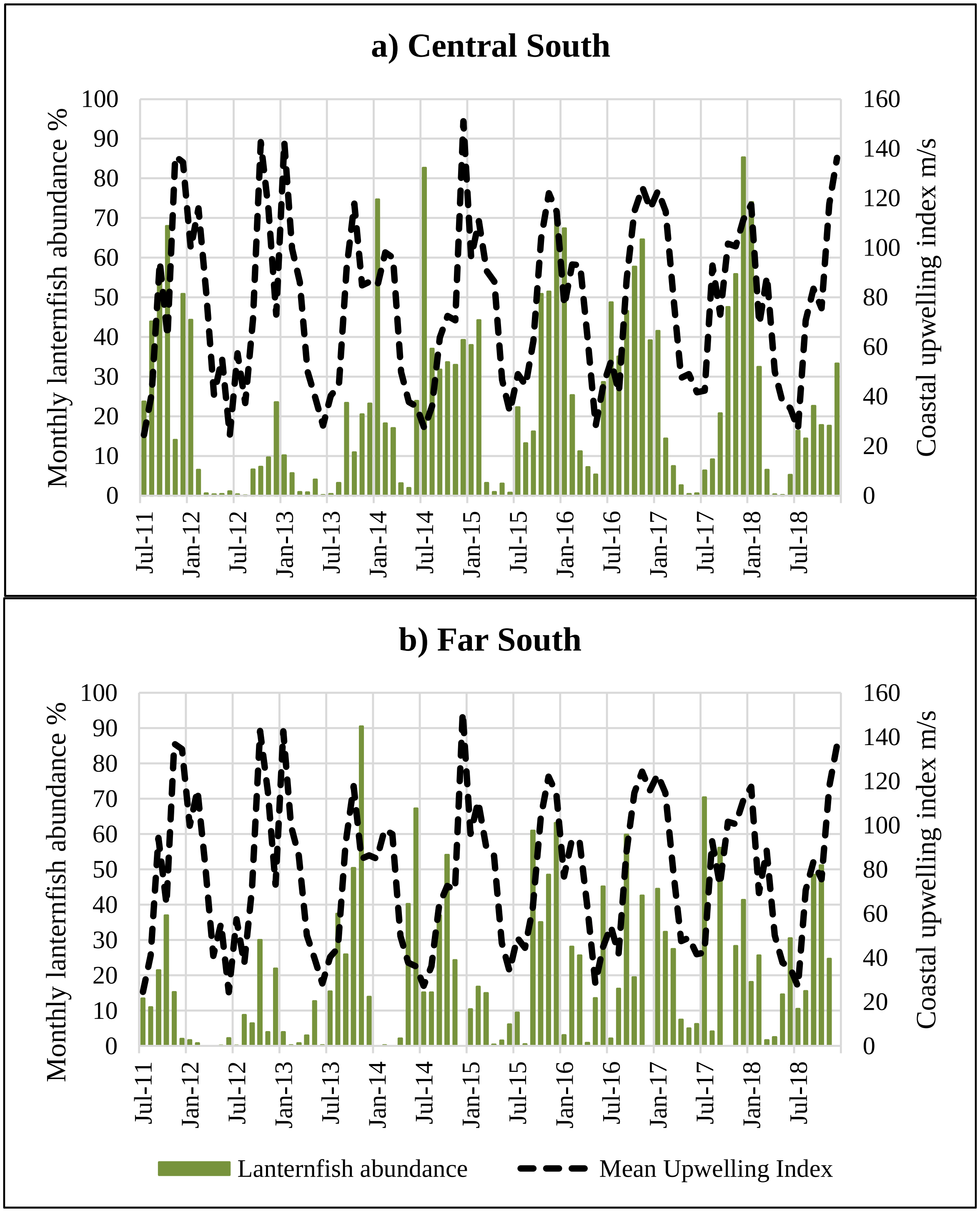

Figure 5.1: The discrete mean monthly Coastal Upwelling Index and the monthly abundances of the lanternfish *L. hectoris* in the diet of the Cape fur seal in the a) Central South and b) Far South regions plotted against month (July 2011 – December 2018).

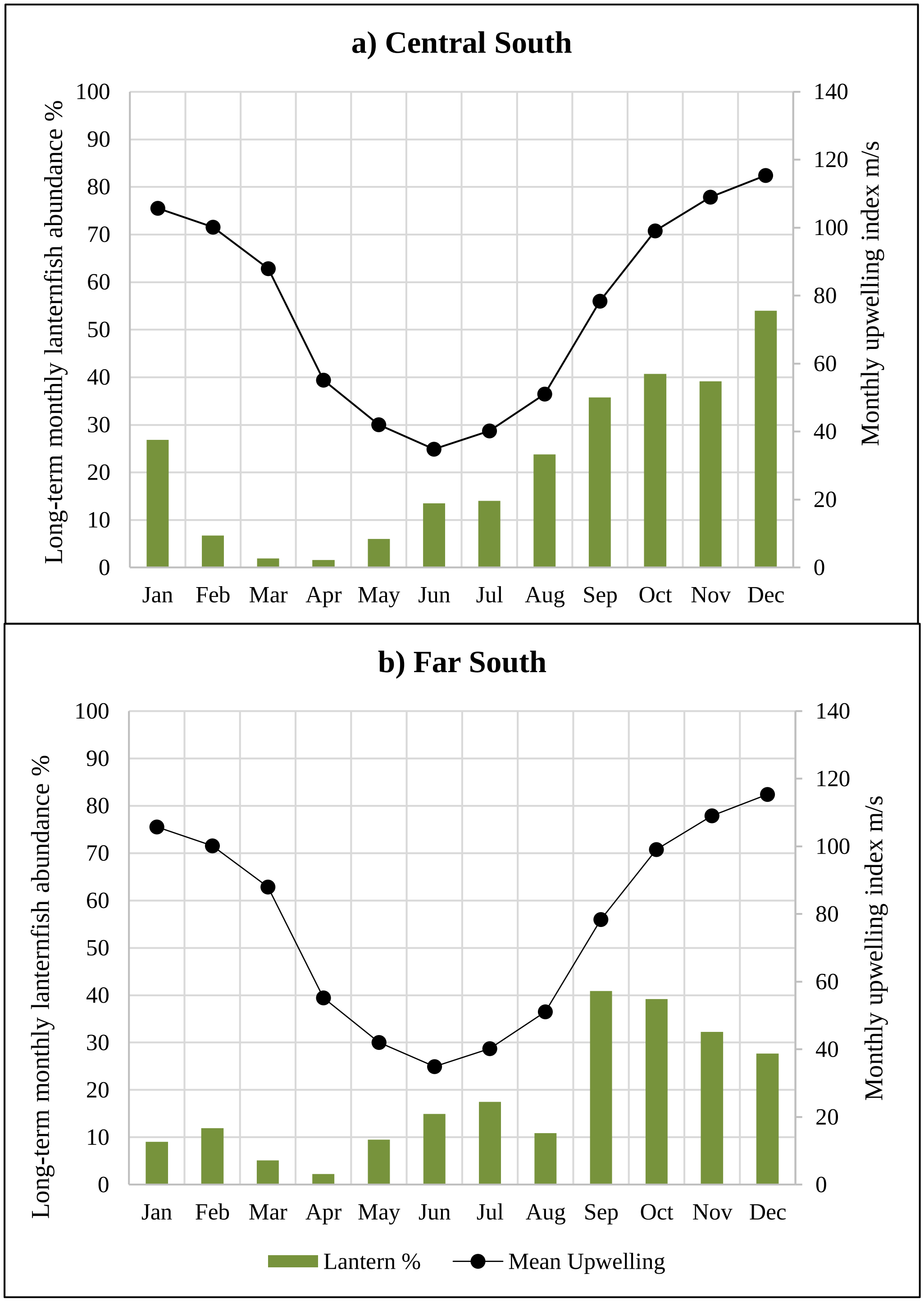

Figure 5.2: The long-term (2011 – 2018) monthly abundances of lanternfish in the Cape fur seal diet and the mean monthly upwelling index in the a) Central South and b) Far South region plotted against month.

5.3.2. Relationship between *in situ* Sea Surface Temperatures and lanternfish abundance in the Cape fur seal diet in the Central South and Far South regions.

There was a well-defined seasonal pattern (lagged) between the long-term monthly upwelling index and long-term monthly Sea Surface Temperatures, with the SST showing a delayed temporal response to changes in the coastal upwelling values (Figure 5.3). The SST seasonality showed that the warmest sea surface temperatures in southern Namibia are usually recorded between January and April - with peaks in February and March, (summer) and the coldest SSTs were generally recorded between August and September (spring).

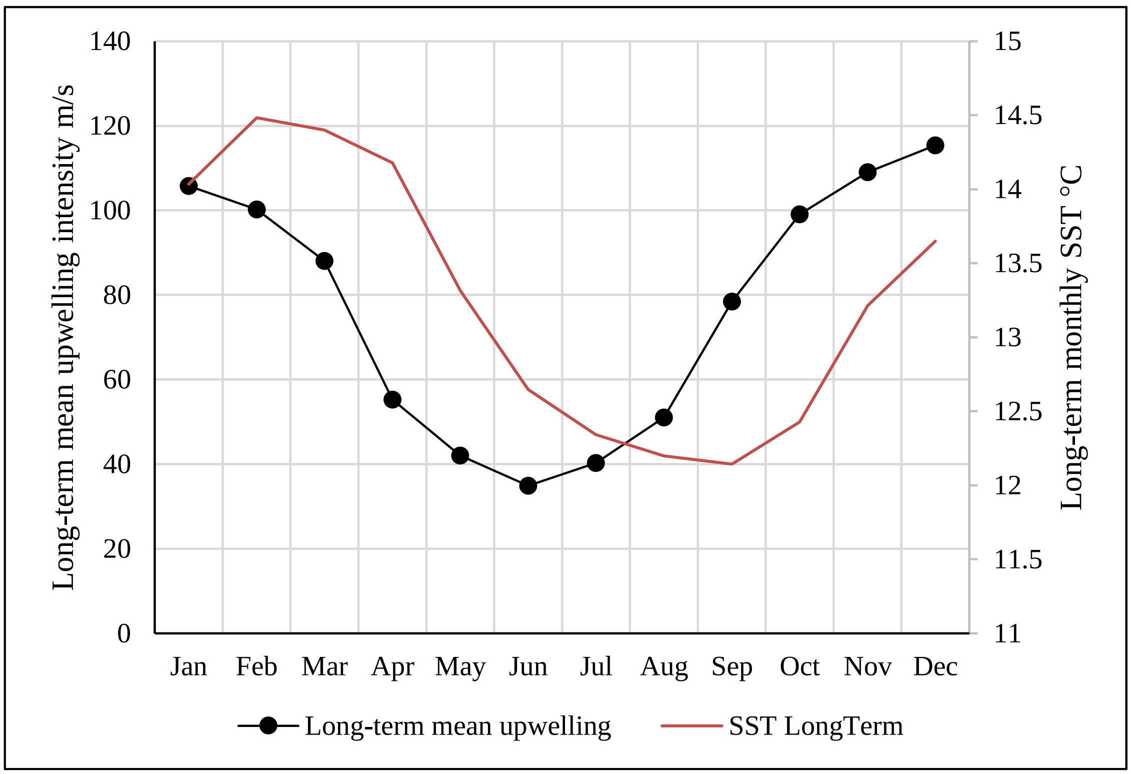

Figure 5.3. The seasonal pattern between the Coastal Upwelling Index and the Sea Surface Temperature (July 2011 - Dec 2018).

In both regions, the highest discrete monthly abundance of the lanternfish *L. hectoris* in the Cape fur seal diet were recorded during months with the lowest mean monthly SST values (Figure 5.4). The discrete mean monthly SST and SST anomalies showed that the summer months of 1997, 1998, 2003 and 2004 were cooler than other summers, and were associated with high contributions of lanternfish to the diet of the Cape fur seals, especially in the Central South region (Figure 5.4, Appendix 10). The winter months of 1999, 2000, 2008, 2009, 2010, 2011 and 2014 were warmer than winters in the other years, and were associated with comparatively lower abundances of lanternfish (Figure 5.4, Appendix 10)There were highly significant negative correlations between the monthly lanternfish abundance and the monthly SST, for both the Central South (r = -0.23, n = 300, $P = 0.001$, Figure 5.4a) and Far South (r = -0.27, n = 300, $P < 0.001$, Figure 5.4b) regions.

On the long-term averages, the highest SSTs were recorded between January and April (at a level of 14.3 ºC, on average); and were associated with the lowest abundances of the lanternfish in the Cape fur seal diet for both regions. There was a delayed and gradual decrease in the SSTs recorded between May (13.3 ºC) and July (12.3 ºC), reaching the lowest temperatures in August and September (12.1 ºC) and after which a gradual increase from October (12.4 ºC) to December (13.6 ºC) was recorded. There were significant negative correlations between the long-term SST and lanternfish abundance in the Far South region (r = -0.60, n = 12, $P = 0.04$, Figure 5.5b), but non-significant in the Central South region (r = -0.47, n = 12, $P = 0.13$, Figure 5.5a).

The multiple linear regression showed that for every 1 % increase in SST, there was 12.31 % ± 2.14 ($P < 0.001$) and 10.36 % ± 1.64 ($P < 0.001$) decline in the abundance of the lanternfish in the diet of the Cape fur seals in the Central South and Far South regions, respectively (Appendix 15).

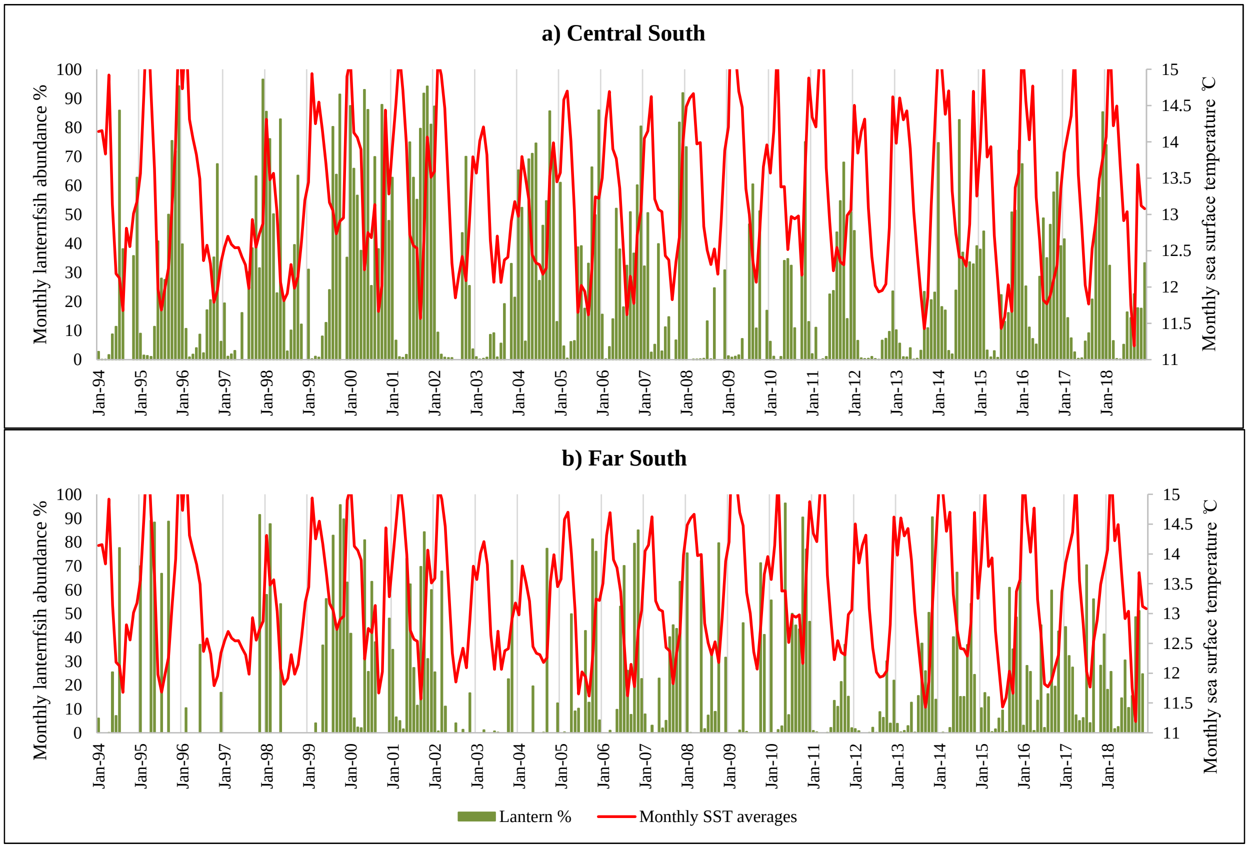

Figure 5.4: The discrete mean monthly Sea Surface Temperature and the monthly abundances of the lanternfish *L. hectoris* in the diet of the Cape fur seal in the a) Central South and b) Far South region plotted against month (Jan 1994 – December 2018).

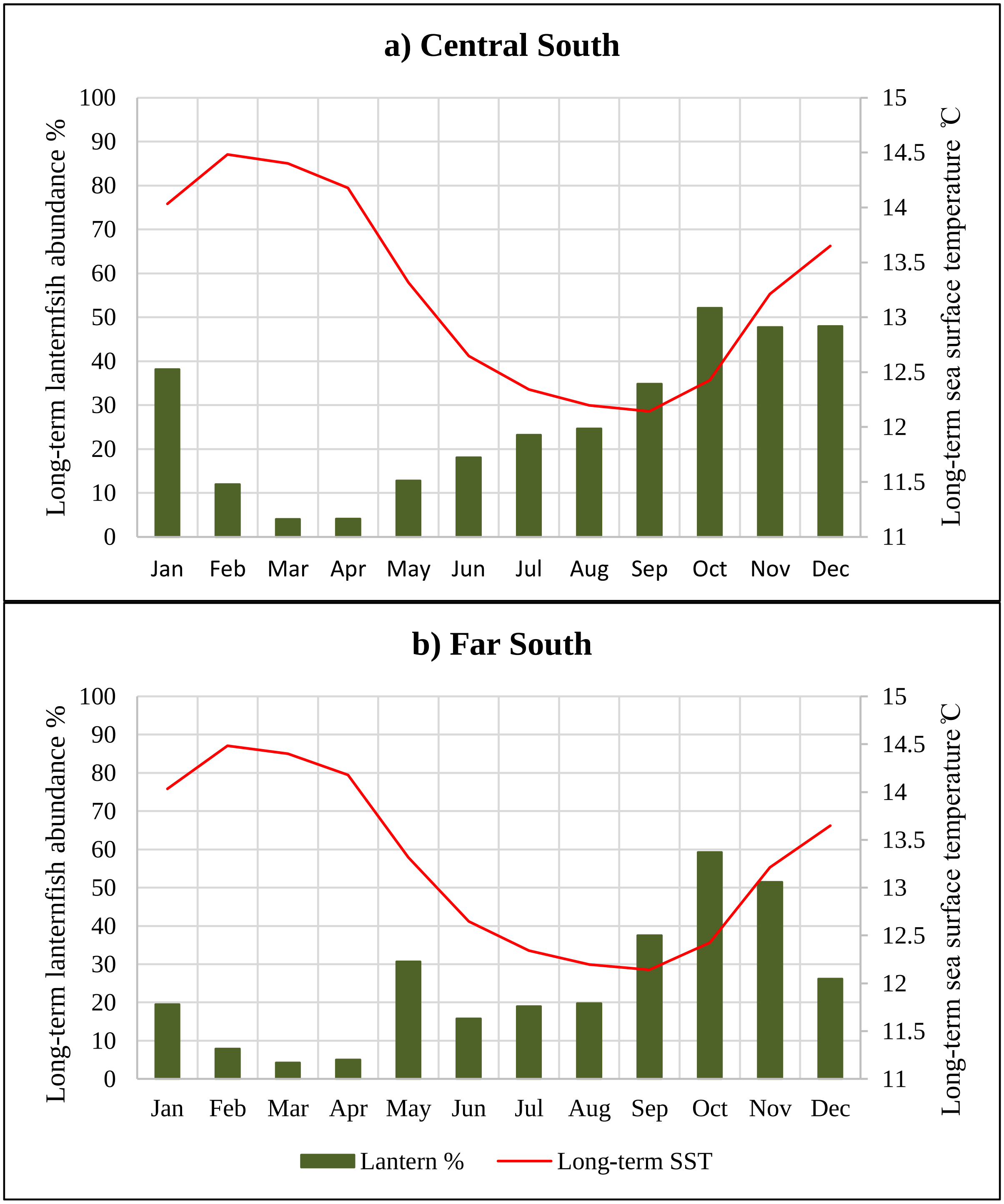

Figure 5.5: The long-term (1994 – 2018) monthly abundances of lanternfish in the Cape fur seal diet and the long-term monthly sea surface temperatures in the a) Central South and b) Far South region plotted against month.

5.4. Discussion

This study was the first of its kind to relate the discrete monthly and long-term variability in the coastal upwelling intensity and Sea Surface Temperatures to the abundance of one of the most important prey species of the Cape fur seal in southern Namibia. There was clear seasonality in the upwelling index, with a peak during the austral summer (November to February) months and a trough during the winter (May to August) months. The Sea Surface Temperature dataset also showed a clear seasonal pattern, with the highest values recorded in mid-summer to early autumn (January to April), and the lowest SSTs in August and September. This seasonality corresponds with the upwelling off Lüderitz being perennial on average, with a marked maximum in summer and minimum in winter (Shannon, 1985; Roux, 2003; Peard, 2007).

The abundance of the lanternfish *L. hectoris* in the diet of the Cape fur seal in the Central South and Far South regions clearly followed the pattern of the coastal upwelling and *in situ* SSTs. The highest coastal upwelling was associated with the highest abundance of lanternfish, with a significant positive correlation in the Central South region. The lowest *in situ* SSTs were associated with the highest abundances of *L. hectoris* in both regions. There was a significant negative correlation between the highest lanternfish abundance and the SST index (a later peak than the upwelling index) in the Far South region. This indicates that there is an indirect effect of the coastal upwelling to the diet of the Cape fur seals in southern Namibia through SST.

Chapter 4 indicated that the numerical contribution of the lanternfish in the Central South and Far South regions are declining, despite that they are not targeted for commercial harvesting. Coastal upwelling regions are said to have experienced changes in timings, durations and intensity due to climate change over the past century, with even more changes projected to happen towards the end of the 21st century (Lima et al., 2019). Evidence suggests that these changes have resulted in marked ecological changes including species distribution and abundances (Boyer et al., 2001) as well as patterns in population (Shannon et al., 1988) and seasonal breeding in some of the top predators (Crawford, 1999; Crawford et al., 2007; Crawford et al., 2011). There has been records of declines in the intensity of upwelling favourable winds off Lüderitz as well as increasing SST trends off Namibia (Blamey et al., 2012; Jarre et al., 2015). The results of this study clearly indicate that the changes in environmental variables (such as coastal upwelling and SST) have been playing a role in defining the distribution of the lanternfish off southern Namibia, with SST being the best predictor of the changes thereof. This would mean, in weak upwelling periods (which will be associated with high SST), the distribution of the lanternfish may be unavailable to the seals. Therefore, the seals will be forced to then switch to a less desirable diet i.e. bearded goby. The long-term decrease in the abundance of the lanternfish in southern Namibia, a highly nutritious prey species compared to the bearded goby, could be linked to the ongoing decrease in the overall population of the Cape fur seals in southern Namibia offset by an increase in population and formation of new colonies in northern Namibia which is sustained by a higher nutritious food prey in that region (i.e. Cape horse mackerel) (Chapter 3).

Despite the extensive amount of studies that have been done on the abundance and egg larval distribution of the lanternfish *Lampanyctodes hectoris* in the northern Benguela (Ahlstrom et al., 1976; Sabates & Olivar, 1989; Olivar et al., 1992; Olivar & Shelton, 1993), very few studies have focused on understanding the population dynamics of this species and its relationships to hydrographical variables such as Sea Surface Temperature. Only two research surveys conducted by the *RV* Dr. Fridtjof Nansen, one in 2006 (23 August – 12 September 2006) and another one in 2017 (03 – 12 December 2017), have captured the biomass records of *L. hectoris* along the Namibian coast as well as the records of hydrographic variables from the specific sampling stations. Since these surveys were conducted over a much shorter period of time (2 – 4 weeks maximum) and were spaced 11 years apart (Coetzee et al., 2006; Krakstad et al., 2017), these datasets could not be used in assessing the monthly or long-term abundances of the lanternfish *L. hectoris* in relation to the monthly and long-term fluctuations of coastal upwelling and sea surface temperatures over the aforementioned period of time.

The Luderitz upwelling cell has been in a slackened phase since around 2004, as deduced from reduced wind velocity anomalies during this period (Appendix 11; Appendix 12). The upwelling index calculated using southerly wind speed and direction data from an automatic weather station at Dias Point (Lüderitz) during 2011 - 2018, thus fall entirely within this slackened upwelling phase. However, if lanternfish abundance is considered in comparison with the long-term southerly wind velocities at Lüderitz since 1994 (unpublished data of annual standardised wind speed anomalies) the lowest abundance of lanternfish (2008 – 2013, CS, 2009 – 2012, FS) occurred during years (2009 - 2014) of lowest wind speed anomalies (indicative of low upwelling strength), with moderate abundance (2004 - 2007 CS, 2005 - 2008 FS and 2014 - 2018 CS, 2013 - 2018 FS) during the years immediately prior (2003 - 2007) and post (2015 - 2020) to this period of lowest wind speeds (Appendix 11, Appendix 13).

The outlier in lanternfish abundance of 2010 during the period 2011 - 2018 in the Far South could be due to increased food supplies, as unpublished data from MFMR oceanographic surveys indicated a significant increase in abundance of meso-zoopankton in inshore waters off Lüderitz during late 2010 (Nov - Dec) (Appendix 14). A similar increase in abundance of lanternfish was however, not detected in 2010 in the CS region, which is closer to the Lüderitz region. The very low values of 2002 - 2003/2004 in lanternfish abundance in the seal diet is possibly due to increased abundance of Cape hake (2003), and other, as yet, unknown factors (e.g. 2002).

When comparing annual lanternfish abundance versus 11-year running average of wind speeds (Appendix 13), after excluding the outliers, the trend of lanternfish abundance follows the same trend as wind speeds during the slackened upwelling phase (2000 onwards when wind speeds were well below the long-term average) for both FS & CS. Prior to 2000, when upwelling was stronger (i.e. annual wind speed anomalies were near the long-term average), this positive relationship still seems present between wind speeds and fish abundance in the Far South, but not in the Central South, where an inverse relationship is seen. Is it possible that a) increased turbulence under increased upwelling conditions changes the distribution and/or behaviour of lanternfish, and b) populations at FS is more affected (being closer to the upwelling centre) than those at CS?

The statistical non-significance in the linkages between the long-term variability of the lanternfish abundance and coastal upwelling (in both regions) and with the Sea Surface Temperature (in the Central South region) could be a result of multiple factors that influence the availability of lanternfish *L. hectoris* against the backdrop of the environmental variability, such as the temporal delays (i.e. time lags) in the effect of favorable conditions brought on by upwelling events. Lagged or time delayed relationships are well documented for certain ecological systems, considering that certain species may have biologically delayed responses to changes in the environment, one particular example being coastal upwelling (Martin, 2014; Moraes et al., 2012). This study showed that there was a synchronized, but temporally delayed relationship between SST and the Coastal Upwelling Index. Therefore, the proper calculation of these time lags and their correlations to the abundance of the lanternfish in the Cape fur seals diet could potentially yield significant relationships. Additionally, significant long-term correlations might be influenced by the masking effect linked to the presence of other important prey species in the Cape fur seal diet (for example the third highest prey species, Cape hake). As such, a multi-factorial analysis may be required to give adequate insight into how these additional factors affect the abundance of the lanternfish across time.

Even though this chapter was only restricted to eight years of coastal upwelling data, the results look promising and should be extended in the future. Most importantly, Cape fur seals are generalist top predators – and their diets are likely to be dominated by the most abundant prey species at any given time (Mecenero, 2005). Changes in environmental conditions may therefore affect the relative abundance and therefore signify the importance of the main prey species, which further emphasizes the need to understand the relationship between the abundance of the prey species and the environmental conditions over longer periods of time. Compared to acoustic research surveys, monitoring the diet of Cape fur seals is exceptionally cheap and the results may complement most of the long-term environmental data sets in the region which in turn may help in defining linkages between ecologically viable species and some of the recorded environmental conditions.

Overall, the abundance of the lanternfish *L. hectoris* in the Cape fur seal diet in southern Namibia can easily be linked to corresponding environmental data recorded in the area for better understanding of the prey species population variability.

Chapter 6: Conclusions and Recommendations

6.1. Summary of the study findings

This is the first diet study of the Cape fur seal (*A. pusillus pusillus*) population in Namibia that spans a period of 25 years (1994 to 2018). The study revealed that the diet of the Cape fur seal was distinctively different between the northern and southern colonies in Namibia with the numerical contribution of prey species varying spatially and temporally. The bearded goby *Sufflogobius bibarbatus* was the most commonly consumed prey by Cape fur seals at all colonies along the Namibian coast (Chapter 3). The Cape horse mackerel *Trachurus capensis* was the second-most important prey species for the northern seal colonies, while the lanternfish *Lampanyctodes hectoris* was the second most important prey species for the southern colonies. The Cape hake *Merluccius capensis* recorded the third highest diet composition figures for the regions (except in the Far North region), with distinctive abundance peaks correlated with the hake high abundances and nursery aggregation periods in the Central North region (in tandem with its migration pattern) and the hake no longer were accessible to the Cape fur seals in the southern region of the study.

The study also showed that the abundance of the bearded goby in the diet of the studied Cape fur seal population was negatively correlated with the availability of the second and third highest prey species in the northern and southern colonies, respectively (Chapter 4). Furthermore, its contribution to the Cape fur seal's diet less varied and did not follow any distinct seasonal pattern in any region. This suggests that even though bearded goby are highly abundant along the entire Namibian coast, they are only consumed by fur seals in large quantities when the more preferred prey species, i.e. Cape horse mackerel and hake (North) and lanternfish (South) are less frequently encountered and available in lower densities – which essentially bridges the gaps in the Cape fur seal's diet during "lean times". The abundance of lanternfish in the southern colonies was linked to upwelling intensities (and therefore *in situ* SSTs) in the area.

This study also revealed that there was a long-term increase in the numerical contribution of the bearded goby to the fur seal diet in the Central North and Far South regions; while there was a decreasing trend of bearded goby in the Far North region correlated with a significant increase in Cape horse mackerel over the 25-year study period. The contribution of lanternfish decreased in both of the southern regions from 1994 to 2018, clearly linked to the fluctuations in the coastal upwelling index calculated between July 2011 and 2018 as well as with the *in situ* SSTs measured between 1994 and 2018 (Chapter 5). The decrease in lanternfish abundance could be why the fur seals were forced to switch to bearded goby, the least desirable prey, in this region.

6.2. Conclusion and significance of study

The single species approach for the management of commercially important living marine resources in Namibia (Boyer et al., 2001; Van der Westhuizen, 2001), as was the case at the time of this study, does not take into consideration the complexity of environmental perturbations and the influence they have on the abundances of the different stocks. Efforts of moving into an ecosystem based management of fisheries (e.g. Roux & Shannon, 2004; Garcia & Cochrane, 2005; Petersen et al., 2007) will be essential in understanding the ecosystem at large, and how all of its various components are inextricably linked. In the Namibian marine environment, such information may also be important in the maintenance of a functional marine protected area, such as the Namibian Islands Marine Protected Area (NIMPA), considering that the Cape fur seal colonies in southern Namibia are located within this Marine protected area. This study could be useful as a first step towards the application and standard implementation of such assessments.

Studying the relationships between the abundance of the prey species and environmental factors is essential in creating a baseline for monitoring the shifts in marine community structure, which may arise as a result of climate change, as was indicated in this study, anthropogenic activities and natural predatory-prey interactions. Additionally, the usage of data from fishery-independent surveys (such as the fur seal scat surveys) provide unique opportunities to obtain region-wide, unbiased datasets covering several months and years, which ultimately may be useful for stock assessments and management of commercially important as well as ecologically important species such as the lanternfish and bearded goby. Thus, information from the Namibian Cape fur seal diet is also valuable, in the sense that it sheds light on the importance of the non-commercially important species, and most importantly on their relationships with the upwelling and SST variability. In fact, it is these "non-commercial species" that are often ignored by surveys supporting single-species fisheries management that clearly are of great ecological importance in the proper functioning of ecosystems. The Cape fur seal population, as a proxy sampler, through a well-maintained scat monitoring program provides undeniably insightful information on the changes in the ecology of unexploited species and climate related variability of species abundances. Therefore, to avoid any detrimental effects, such information can be considered, especially if any attempts of harvesting lanternfish and bearded goby is to be considered. Because many predators now depend on these species as prey in the near-absence of the sardine in the system.

The knowledge assimilated by this study therefore helps in better understanding the functionality of the ecosystem, most especially the roles that non-commercially important species have in ecosystem health of an important marine system such as the Benguela Current.

6.3. Recommendations

Because Cape fur seals, as one of the top predators in the Benguela ecosystem have been shown to be excellent samplers of small fish and fish species that may be difficult to sample adequately by traditional fishery management survey methods, studies on the diet of a top predator, such as the Cape fur seal, is a good (near real-time) indicator of ecosystem trophic variability, and provide useful information that are well suited for incorporation in existing and new ecosystem-based fisheries management approaches. It is therefore recommended to continue the long-term monitoring of the Cape fur seal diet by means of scat sampling in Namibia (housed under MFMR), and to possibly enhance this monitoring program with external inputs (i.e. getting help in scat collections from other organizations that frequently visit the fur seal colonies) to minimize gaps in the spatial and temporal contexts of this important data series.

The logistical constraints in the scat sampling program led to noticeable gaps in the 25-year data series used in this study, especially for the Far North region. Accurate, timely and standardized data collection protocols for future Cape fur seal diet studies will certainly improve the qualitative value that of the data collected, and may help to further extend its use in marine ecology research, fisheries research, as well as in more distal biological and physical oceanography spheres. Therefore, it is recommended to adhere to a monthly sampling schedule as much as possible for all accessible fur seal colonies in Namibia.

It is recommended to possibly extend the Cape fur seal diet monitoring further South (i.e. to the Cape fur seal colonies in South Africa) and further North to newly emerging colonies in southern Angola, which would provide similar data to the southern Benguela and to tip of the northern Benguela. This would help in comparing the diversity in prey species composition, as well as the spatial and temporal variability, between northern and southern components of the BCLME.

Prey biomass is also an important indicator of different prey items in terms of wet and dry weights. Together with the numerical abundance described in this study, it may be of help to fully understand the complete roles of the different prey species in the diet of Cape fur seals in Namibia. Therefore, it is recommended that a follow up study be conducted using the recovered otoliths and necessary conversion factors to fish length in order to determine the relative biomass contributions across time.

In this study, correlations were performed between the contributions of a highly variable prey species in the Cape fur seal's diet in southern Namibia (the lanternfish *L. hectoris*) with selected environmental conditions, such as the coastal upwelling indices and sea surface temperature. However, a number of other co-variate environmental and biological factors may also be at play. Some of these covariates include the modes of the upwelling (i.e. winter or summer upwelling, (Wilhelm et al., 2020), the concentrations of chlorophyll-a in the water as well as meso-zooplankton abundance which forms basis of prey species diets. Therefore, there is a need to acquire all the relevant environmental and biological parameters that may help in fully understanding the patterns of the lanternfish contributions to the Cape fur seal's diet in southern Namibia, to some extent also exploring the indirect effects (using path analysis) and combinations of effects from all these different variables. This would help to identify the underlying causes for the continued decline in the abundance of *L. hectoris* as a prey species of the Cape fur seal and possibly in the diet of the other predatory fishes in the Benguela ecosystem. Essentially, there is a need to fully understand the effect of the time-lag in some of the environmental variables and its consequent effects on the changes in abundances and contributions of the lanternfish to the Cape fur seal diet. It is therefore recommended that a follow up multi-factorial test is conducted, using various environmental parameters, and considering possible time lags between the parameters.

Finally, it is recommended that a study using, GPS trackers, Time-Depth Recorders (TDRs) and accelerometers mounted on fur seals should be used in conjunction with the diet samples to determine the frequency of prey captures. This will also help to record some of the environmental variables such as SST and other physical parameters; associated with those prey species at specific feeding locations.

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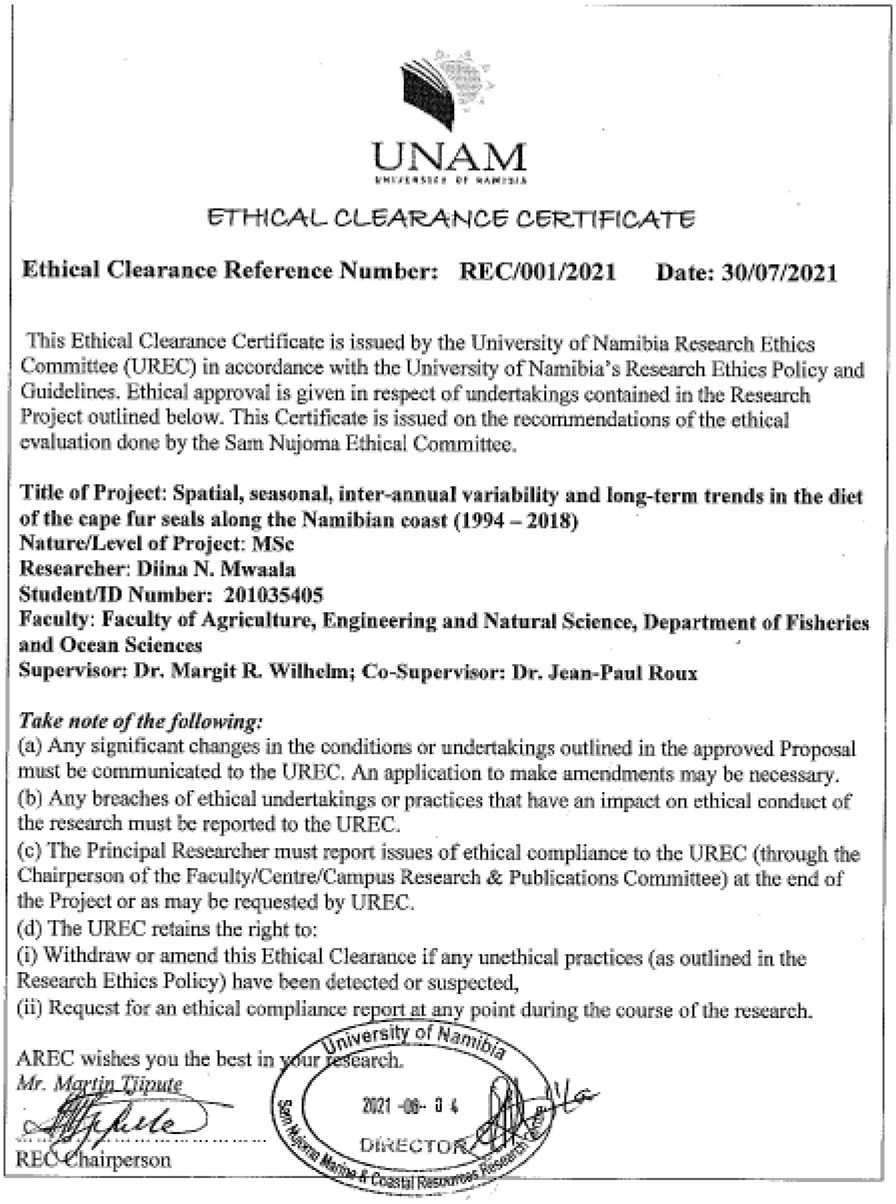
Appendices

Appendix 1: Ethical clearance certificate.



UNAM

UNIVERSITY OF NAMIBIA

ETHICAL CLEARANCE CERTIFICATE

Ethical Clearance Reference Number: REC/001/2021 Date: 30/07/2021

This Ethical Clearance Certificate is issued by the University of Namibia Research Ethics Committee (UREC) in accordance with the University of Namibia's Research Ethics Policy and Guidelines. Ethical approval is given in respect of undertakings contained in the Research Project outlined below. This Certificate is issued on the recommendations of the ethical evaluation done by the Sam Nujoma Ethical Committee.

Title of Project: Spatial, seasonal, inter-annual variability and long-term trends in the diet of the cape fur seals along the Namibian coast (1994 – 2018)
Nature/Level of Project: MSc
Researcher: Diina N. Mwaala
Student/ID Number: 201035405
Faculty: Faculty of Agriculture, Engineering and Natural Science, Department of Fisheries and Ocean Sciences
Supervisor: Dr. Margit R. Wilhelm; Co-Supervisor: Dr. Jean-Paul Roux

Take note of the following:
(a) Any significant changes in the conditions or undertakings outlined in the approved Proposal must be communicated to the UREC. An application to make amendments may be necessary.
(b) Any breaches of ethical undertakings or practices that have an impact on ethical conduct of the research must be reported to the UREC.
(c) The Principal Researcher must report issues of ethical compliance to the UREC (through the Chairperson of the Faculty/Centre/Campus Research & Publications Committee) at the end of the Project or as may be requested by UREC.
(d) The UREC retains the right to:
(i) Withdraw or amend this Ethical Clearance if any unethical practices (as outlined in the Research Ethics Policy) have been detected or suspected,
(ii) Request for an ethical compliance report at any point during the course of the research.

AREC wishes you the best in your research.

Mr. Martin Tjipute

……………………………

REC Chairperson

University of Namibia
2021 -08- 0 4
DIRECTOR
Sam Nujoma Marine & Coastal Resources Research Centre

Appendix 2: Research permission letter.

CENTRE FOR RESEARCH SERVICES
Office of the Pro-Vice Chancellor: Research Innovation and Development
UNIVERSITY OF NAMIBIA, Private Bag, 13301 Windhoek, Namibia
340 Mandume Ndemufayo Avenue, Pioneers Park, Office F224

UNAM

RESEARCH PERMISSION LETTER

Date: 15/09/2021

Student Name: Diina N Mwaala

Student Number: 201035405

Programme: MASTER OF SCIENCE (FISHERIES)

Approved Research Title: SPATIAL, SEASONAL AND ANNUAL VARIABILITY AND LONG TERM TRENDS IN THE DIET OF THE CAPE FUR SEAL ALONG THE NAMIBIAN COAST (1994-2018)

TO WHOM IT MAY CONCERN

I hereby confirm that the above mentioned student is registered at the University of Namibia for the programme indicated. The proposed study met all the requirements as stipulated in the University guidelines and has been approved by the relevant committees.

The proposal adheres to ethical principles as per attached Ethical Clearance Certificate. Permission is hereby granted to carry out the research as described in the approved proposal.

Best Regards

CENTRE FOR RESEARCH SERVICES
Office of the Director
2021 -09- 15
University of Namibia
UNAM

Dr. AEE Shikongo
Head: Postgraduate Support Services
Tel: +264 61 206 3129
E-mail: aeshikongo@unam.na

Appendix 3: The breakdown of the scat (bag sample) sampling effort. Number of months represented (total number of bag samples collected). Only bag samples with a total corrected count of ≥ 500 prey items were considered. Below the table is the total number of samples collected (Total collected) and the total number of samples that were used in the data analysis (Total used). The asterisks identify the years where no samples were collected or where years were let out because < 5 months were represented.

Year	**FN**	**CN**	**CS**	**FS**	Total
1994	*	9(14)	10(16)	5(5)	35
1995	2(2)*	12(14)	12(21)	5(5)	42
1996	1(1)*	12(13)	12(17)	3(3)*	34
1997	*	11(12)	11(14)	1(1)*	27
1998	*	10(11)	11(11)	3(3)*	25
1999	*	7(7)	11(13)	9(16)	36
2000	2(2)*	5(5)	12(15)	9(9)	31
2001	*	10(10)	12(13)	12(16)	39
2002	1(1)*	9(9)	10(10)	7(8)	28
2003	*	11(11)	11(13)	7(8)	32
2004	*	9(10)	12(12)	5(5)	27
2005	4(3)*	9(14)	12(12)	9(14)	43
2006	5(14)	12(40)	12(13)	10(10)	77
2007	7(15)	12(21)	11(11)	10(10)	57
2008	10(27)	11(21)	11(20)	11(11)	79
2009	9(21)	11(23)	11(18)	11(11)	73
2010	6(13)	10(18)	10(20)	11(11)	62
2011	*	10(18)	12(23)	12(12)	53
2012	1(4)*	12(25)	12(24)	12(14)	67
2013	3(5)*	10(17)	12(23)	12(12)	57

2014	7(8)	8(11)	12(21)	11(11)	51
2015	10(19)	9(13)	12(23)	12(12)	67
2016	12(23)	11(18)	12(27)	11(12)	80
2017	11(20)	9(14)	12(24)	11(19)	77
2018	9(14)	7(10)	11(23)	11(22)	69
Total samples collected	**193**	**379**	**438**	**260**	1270
Total sample used	**186**	**364**	**428**	**250**	1228
Years represented	**10**	**25**	**25**	**22**	

Appendix 4: The distribution of all samples that had a total corrected prey count of < 500 and were not included in the data analysis. FN: Far North, CN: Central North, CS: Central South and FS: Far South.

	FN	CN	CS	FS
January	**2010**	**2006, 2012, 2014**		**1999, 2001, 2009**
February		**2002**		**2002, 2009**
March		**2002, 2011**	**2012**	
April	**2009, 2016**	**2010, 2011**	**1994, 2012**	**2005**
May		**2012**		
June	**2005**		**2009**	**1999**
July		**2011, 2012**	**1997**	
August		**2009**	**2008**	**1999, 2009**
September		**1997, 2010**	**2009**	
October	**2008, 2009**	**2010**	**2009**	
November	**2007**		**2008(2)**	
December				**2007**

Appendix 5: The Kruskal-Wallis test and post hoc (Nemenyi test) test results showing the H-statistic, degrees of freedom (df) the mean difference (Mean D) and *P*-value on the spatial contribution of the bearded goby, hake, lanternfish and horse mackerel in the four regions; Far North (FN), Central North (CN), Central South (CS) and Far South (FS). The *** indicates the significance.

	Kruskal-Wallis test (alpha 0.05)		
	H stat	df	*P*-value
Goby	68.91	3	<0.001***
Hake	179.95	3	<0.001***
Lanternfish	734.26	3	<0.001***
Horse Mackerel	664.10	3	<0.001***

Nemenyi tests (alpha 0.05)

Bearded goby				**Cape horse mackerel**			
group 1	group 2	MeanD	*P*-value	group 1	group 2	meanD	*P*-value
FN	CN	9.101	<0.001***	FN	CN	5.875	0.001**
FN	CS	0.077	0.99	FN	CS	32.924	<0.001***
FN	FS	12.689	<0.001***	FN	FS	30.225	<0.001***
CN	CS	9.024	<0.001***	CN	CS	27.049	<0.001***
CN	FS	3.588	<0.001***	CN	FS	24.350	<0.001***
CS	FS	12.612	0.17	CS	FS	2.699	<0.001***
Cape hake				**Lanternfish**			
group 1	group 2	meanD	*P*-value	group 1	group 2	meanD	*P*-value
FN	CN	11.687	<0.001***	FN	CN	0.207	0.99
FN	CS	12.323	<0.001***	FN	CS	26.634	<0.001***
FN	FS	14.554	<0.001***	FN	FS	28.132	<0.001***

CN	CS	0.636	0.001	CN	CS	26.840	<0.001***
CN	FS	2.867	0.001***	CN	FS	28.339	<0.001***
CS	FS	2.231	0.02	CS	FS	1.499	0.99

Appendix 6: The Kruskal-Wallis test for the monthly contribution of the bearded goby, hake, lanternfish and horse mackerel to the diet of the Cape fur seal at the four regions. The test could not be performed on the contributions of the lanternfish in the Far North and Central North regions, also, that of the horse mackerel to the Central South and Far South regions.

	Kruskal-Wallis test (alpha 0.05)			
		H stat	df1	*P*-value
FN	Goby	12.41	11	0.33
	Hake	14.57	11	0.06
	Horse Mackerel	19.17	11	0.050
	Lanternfish	4.12	11	0.28
CN	Goby	104.98	11	<0.001***
	Hake	110.37	11	<0.001***
	Horse Mackerel	174.60	11	<0.001***
	Lanternfish	2.94	11	0.823
CS	Goby	91.82	11	<0.001***
	Hake	51.55	11	<0.001***
	Horse Mackerel	18.62	11	<0.050***
	Lanternfish	157.72	11	<0.001***
FS	Goby	15.96	11	0.142
	Hake	38.50	11	<0.001***
	Horse Mackerel	23.81	11	0.01

Lanternfish	69.34	11	<0.001***

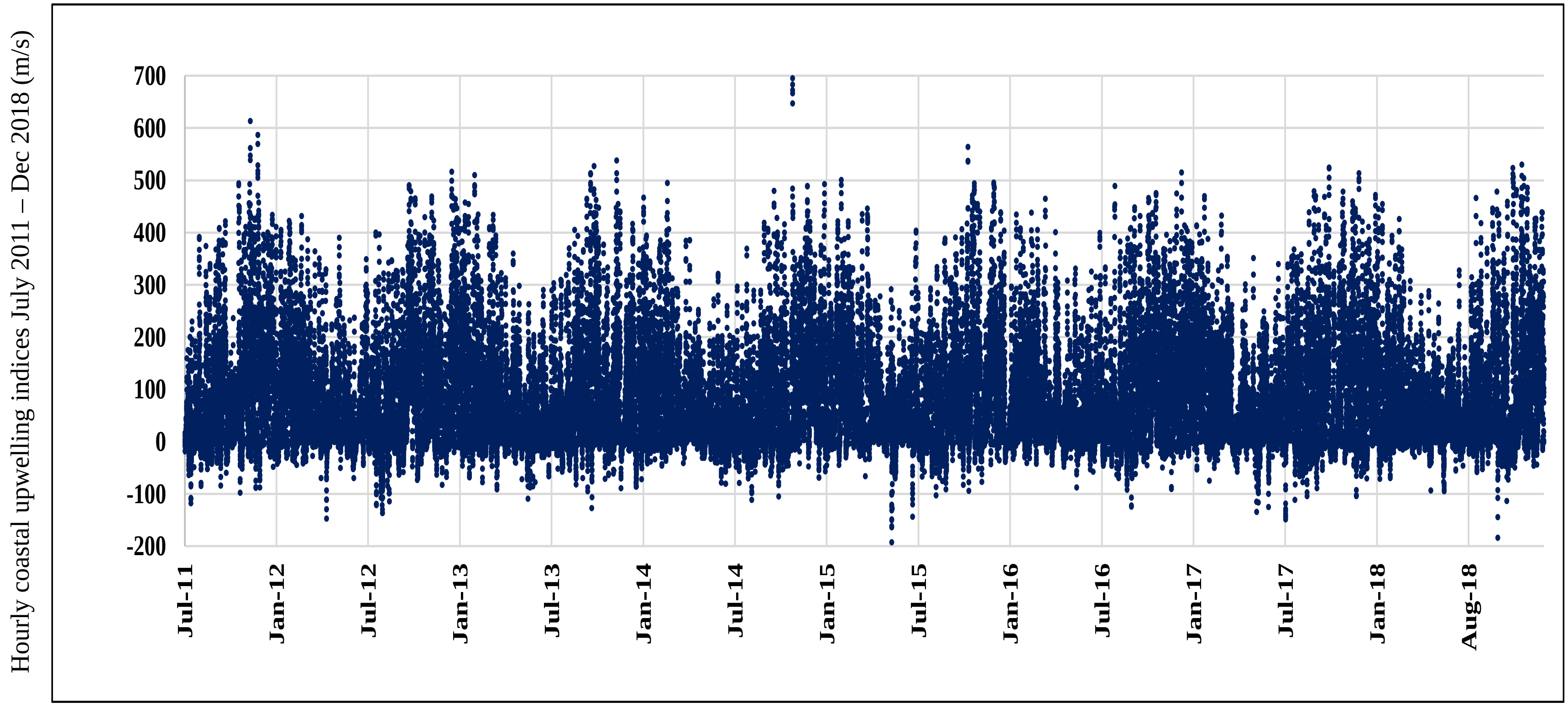
Appendix 7: The results of the Pearson's correlation (two-tailed) between the first two important prey species in the diet of the Cape fur seal in each region. The *** indicates the significance.

	Pearson's Correlation	
	r	*P*-value
FN	-0.837	0.002**
CN	-0.615	0.001***
CS	-0.523	0.007**
FS	-0.63	0.002**

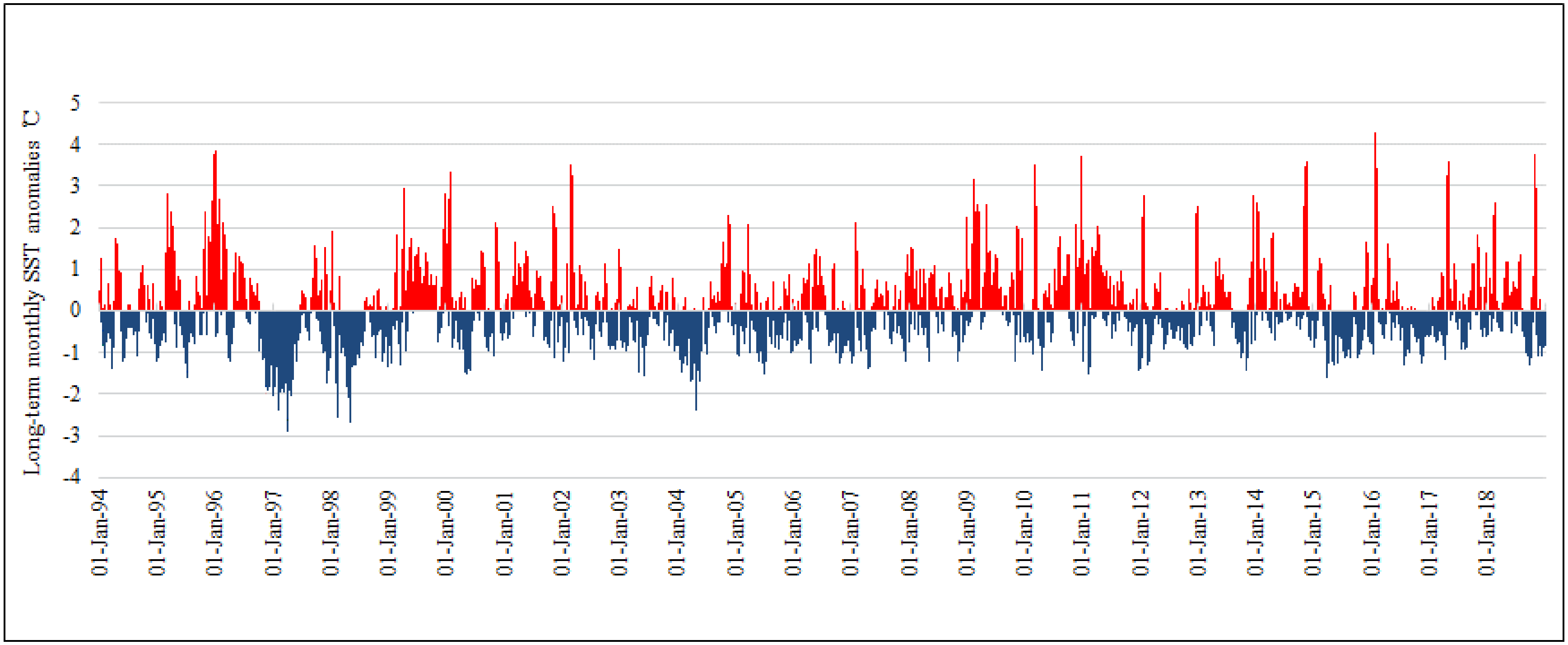
Appendix 8: The linear regression outputs on the contribution of the bearded goby, horse mackerel and lanternfish (performed on in arcsine transformed values) to the diet of the Cape fur seal in all four regions of the study against the year. R2 is the coefficient of determination and the p is the level of marginal significance from the test as well as the slope/gradient. The *** indicates the significance.

	Linear regression				
Region	**Species**	**t stat**	**Slope**	**R^2**	***P***
FAR NORTH	Goby	-5.01	-2.454	0.762	<0.001***
	Horse mackerel	3.69	1.953	0.629	0.006**
CENTRAL NORTH	Goby	3.21	1.461	0.307	0.004**
	Horse mackerel	-0.70	-0.297	0.024	0.491
CENTRAL SOUTH	Goby	1.71	0.846	0.114	0.100
	Lanternfish	-1.26	-0.522	0.066	0.218
FAR SOUTH	Goby	4.06	1.919	0.451	<0.0001***
	Lanternfish	-2.19	-1.237	0.213	0.041*

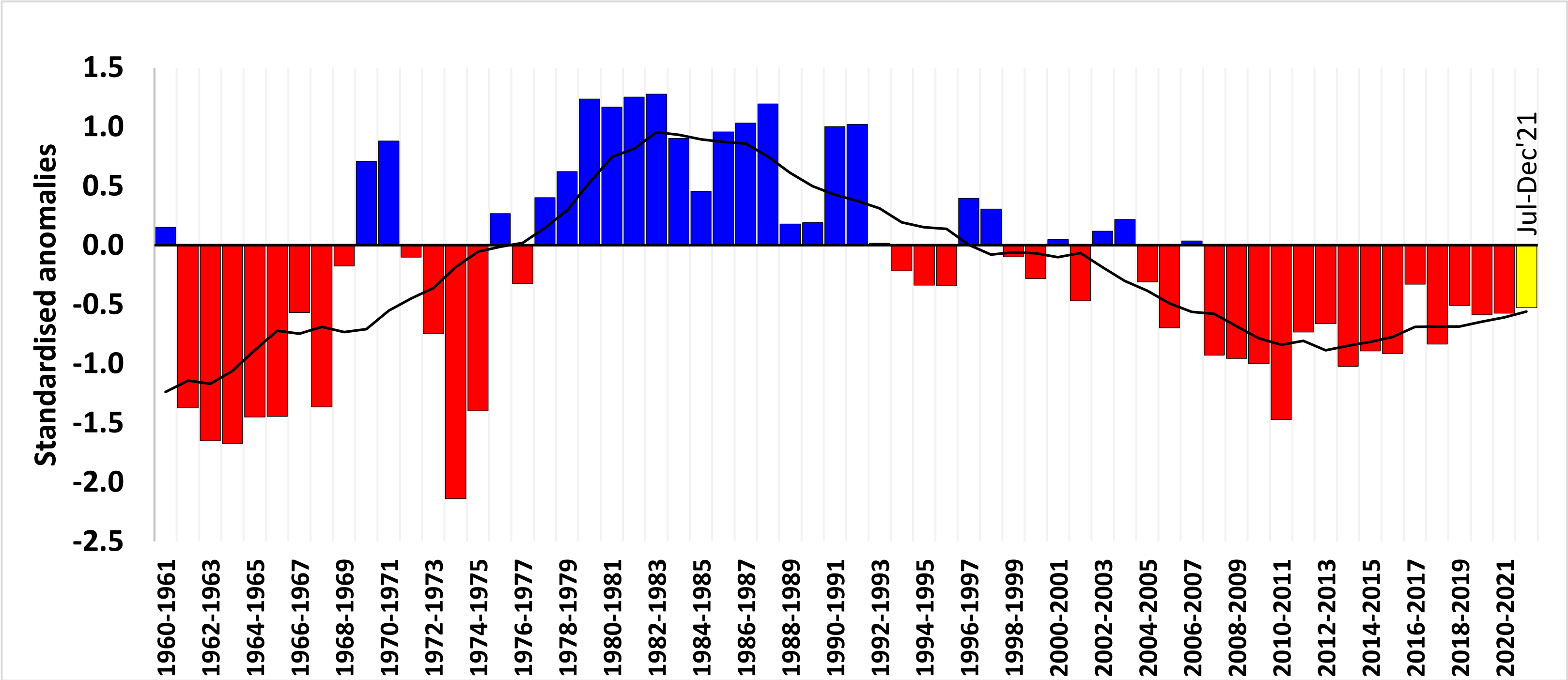
Appendix 9: Hourly coastal upwelling indices from July 2011 to Dec 2018 (n = 65448).



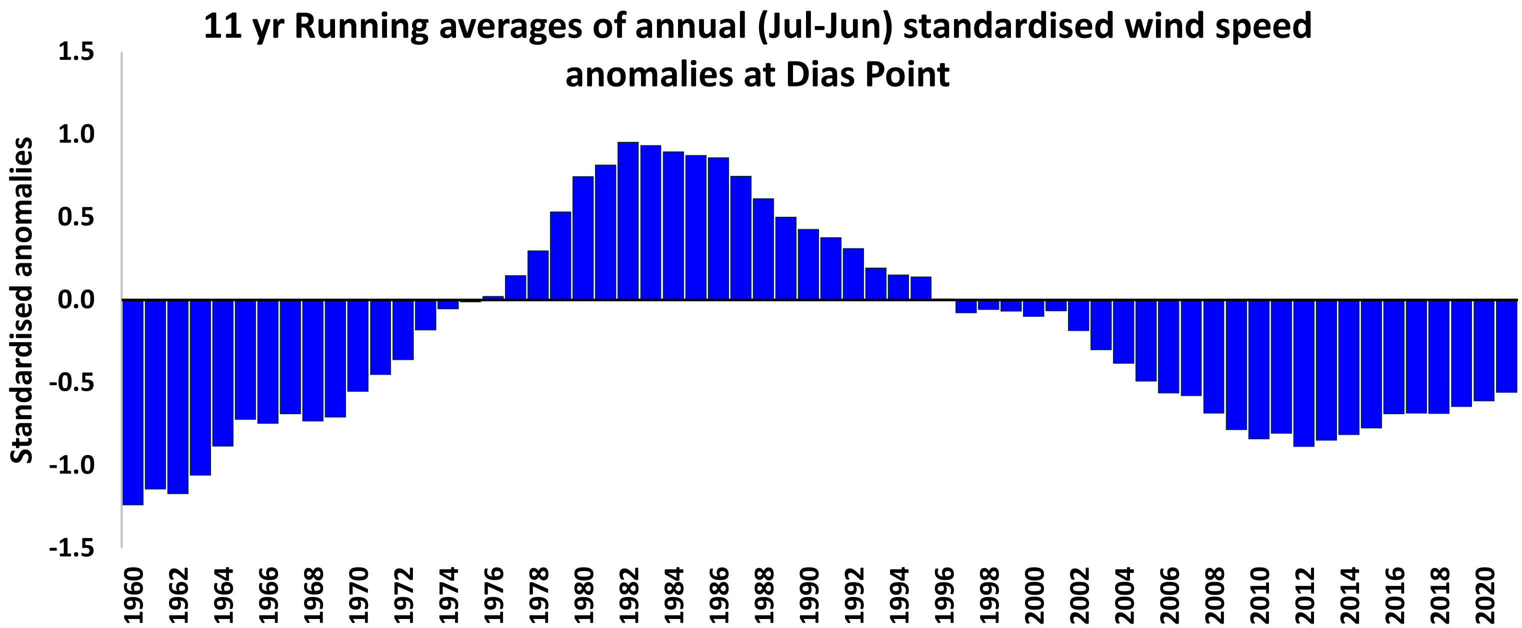
Appendix 10: The long-term monthly sea surface temperature (ºC) anomalies (value minus long-term average) recorded in the Lüderitz harbour between Jan 1994 and December 2018.



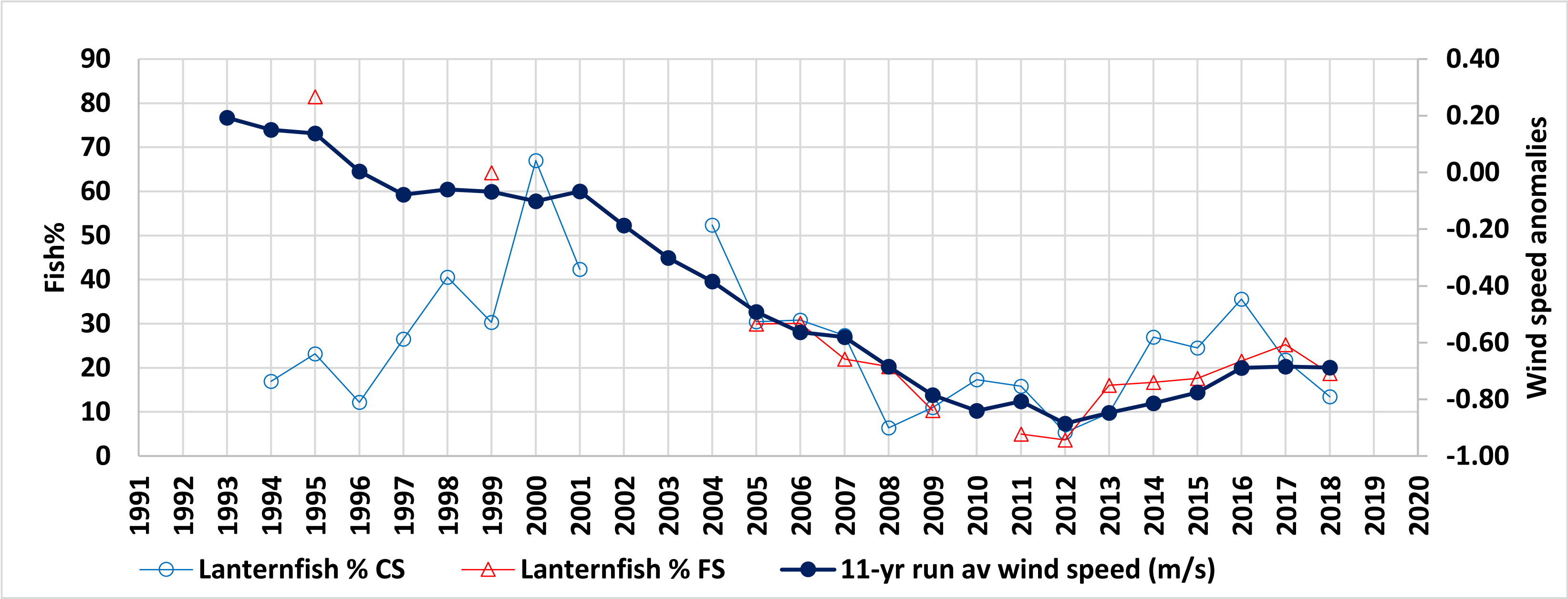
Appendix 11: Standardized wind speed anomalies recorded from an automatic weather station at Dias Point in Lüderitz. The red bars represents the years of lowest wind velocities (and indication of the slackened upwelling) and the blue bars represents years with the highest wind velocities (an indication of strong upwelling). The line graph represents the 11-year running averages of standardized wind speed anomalies at Diaz point (a year defined as Jul – June).



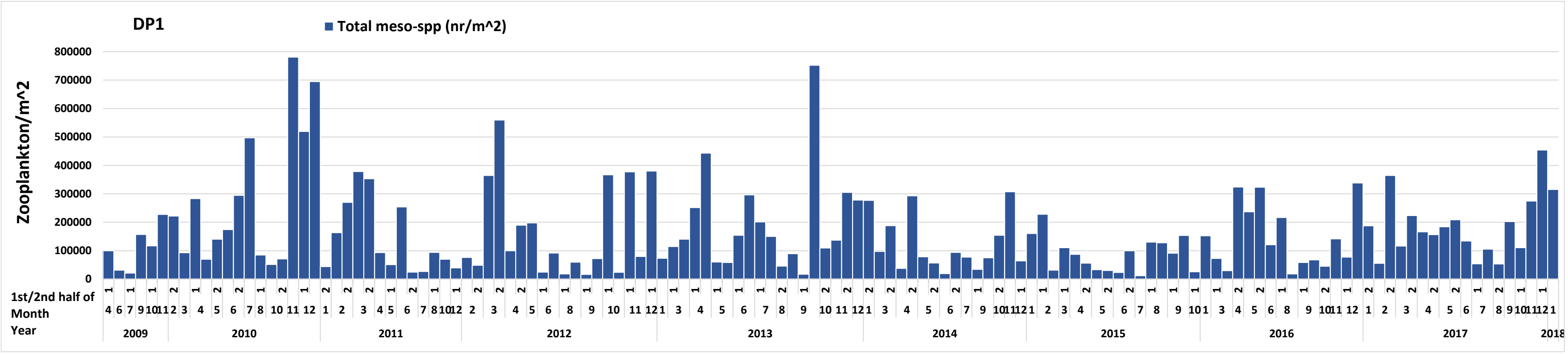
Appendix 12: The 11-year running averages of annual standardized wind speed anomalies at Dias Point. This graph is similar to the line graph in Appendix 11 (Unpublished data, K. Grobler, MFMR).



Appendix 13: The 11-year running wind-speed anomalies average of (dark blue) vs. the annual lanternfish abundance in the diet of the Cape fur seals in the Central South (light blue) and Far South region (red) (Unpublished data, K. Grobler, MFMR).



Appendix 14: Meso-zooplankton abundance inshore of Lüderitz (Unpublished data, K. Grobler, MFMR).



Appendix 15: The multiple linear regression results on the relationship between the lanternfish abundance in the Central South and Far South regions with the environmental conditions (i.e. coastal upwelling and Sea Surface Temperature).

	Multiple linear regression (alpha 0.05)			
		Slope	t-stat	*P*-value
CN	Coastal upwelling	0.38	6.05	0.001**
	SST	-12.31	-5.76	0.001**
FS	Coastal upwelling	0.26	5.29	0.001**
	SST	-10.36	-6.33	0.001**

Appendix 16: List of publication(s)/Conference(s) proceedings

1. **What do we eat and when? Diet of Cape fur seal in the southern region**

Authors: Mwaala DN; Roux J-P; Wilhelm MR

Conference: Annual Research Meeting (6 – 8 August 2019).

Conference, at Ministry of Fisheries and Marine Resources, NatMIRC, Swakopmund

2. **What do we eat and When? Seasonal, interannual variability and long-term trends in the Diet of Cape fur seal along the Namibian coast (1994 – 2018)**

Authors: Mwaala DN; Wilhelm MR; Roux J-P.

Conference: 5th Annual Research Conference (06 November 2020).

Virtual Conference, At University of Namibia, Sam Nujoma Campus, Henties Bay, Namibia.

3. **Assessing the relationship between the abundance of lanternfish in the Cape fur seal diet and the Lüderitz coastal upwelling index and Sea Surface Temperature**

a) Authors: Mwaala DN; Wilhelm MR; Roux J-P.

   Conference: 6th Annual Research Conference (19 - 20 October 2021).

   Virtual Conference, At University of Namibia, Sam Nujoma Campus, Henties Bay, Namibia.

b) Authors: Mwaala DN; Wilhelm MR; Roux J-P.

   Forum: BCC's Science and Governance Forum (03 – 05 November 2021), Virtual Conference.

c) Authors: Mwaala DN; Wilhelm MR; Roux J-P.

Conference: 17th Southern African Marine Science Symposium (SAMSS) (20 – 24 June 2022), Elangeni Hotel, Durban, South Africa.