Variability in the diet of Cape fur seals and their interaction with fisheries off the South African coast, 2010-2019

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Table of Contents

List of Figures

List of Tables

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Abstract

Cape fur seals (*Arctocephalus pusillus pusillus*) are sentinel marine top predators in southern African coastal waters due to their generalist diet and wide breeding range from southern Angola (Baia dos Tigres) to Algoa Bay, South Africa. Their long-life span makes them good indicators of ecosystem health by providing insights on ecological interactions in the food webs of the South African marine ecosystem, and on the variation in the availability of prey resources. This dissertation describes the diet of Cape fur seals off the South African coast between 2010 and 2019 based on the analysis of scats collected at 11 South African colonies from Kleinsee (29°39' S, 17°04' E) to Robberg Ledges (34º03' S, 23º22' E). The colonies were divided into three geographical regions: St Helena Bay, Saldanha Bay to Cape Agulhas, and east of Cape Agulhas. Potential competition for prey fish between the Cape fur seal and fishery catches was also investigated. Catches by the purse-seine fishery landed at Lambert's Bay, Saldanha Bay and Gansbaai were compared with the diet of fur seals at nearby colonies (Lambert's Bay, Jutten Island and Geyser Rock, respectively). The importance of small pelagic fish in the Cape fur seal diet also was compared to acoustic biomass estimates of these key fish species.

A total of 4165 scat samples were used to infer spatial and temporal variation in the Cape fur seal diet. Fish otoliths, cephalopod beaks and seabird feathers were used to identify prey to the lowest taxonomic level possible, and the mass and length of fish prey were estimated from otolith lengths using regression equations. Fifty-three prey taxa (43 fish, 6 cephalopods, 4 seabirds) were identified from scats, and indices of relative importance (%IRI), mass contribution (%M), numerical abundance (%NA), and frequency of occurrence (%FO) were used to determine the importance of each prey taxon to the diet. Fish dominated the diet (88.0%FO) followed by seabirds (9.1%FO), cephalopods (5.5%FO) and crustaceans (0.4%FO). In decreasing order of importance and in terms of %NA, the most important prey species were anchovy (*Engraulis encrasicolus capensis*), horse mackerel (*Trachurus trachurus capensis*), sardine (*Sardinops sagax*) and hake (*Merluccius capensis* and *M. paradoxus*). Anchovy dominated the diet across all study areas and years, while other species varied in importance over the study years. There was seasonal variation in the diet across all three regions, with anchovy being consumed more during winter (non-upwelling season) than summer. Almost all other fish taxa were consumed more during summer in all the three study regions. Larger prey such as hake and horse mackerel contributed less to the diet; in terms of mass contribution (10.9%M and 10.3%M, respectively) than the smaller anchovies and sardines (combined 68.8%M).

Scat samples were compared with stomach content samples obtained from 1974 to 1996. There were no changes in diet composition (fish, cephalopods, crustaceans, seabirds) between the different study

periods or the different diet analysis methods. However, there were changes in proportions of prey type consumed; seabirds were consumed less during 1974 - 1996 compared with 2010 to 2019. Pelagic goby (*Sufflogobius bibarbatus*) (55.0%NA) dominated the diet in 1974 – 1996, while anchovy (67.6%NA) predominated in 2010 – 2019. Only 30 prey taxa (22 fish, 5 cephalopods, 2 crustaceans, 1 seabird) were identified from 2 336 stomach content samples, compared with 53 from scats. Although there is some uncertainty due to the different methods, it seems that prey proportions have changed between the two periods.

Among the commercial targeted pelagic species (i.e. sardine and horse mackerel), Cape fur seals and purse-seine fisheries mainly targeted juvenile to adult fish, except for anchovy, where fisheries caught much smaller fish. There was an overlap in fish size distribution (50 – 200 mm) of sardine and red-eye (*Etrumeus whiteheadi)* found in seal scats and commercial landings records. A positive correlation was found between spawner acoustic biomass estimates and the importance (%NA) of anchovy and sardine in the Cape fur seal diet. The importance of sardine decreased in contribution when biomass estimates were low. Similarly, anchovy importance in the diet was positively correlated with biomass estimates. However, the overall consumption of anchovy did not correlate with the estimated biomass, but there was correlation between sardine consumption and the biomass estimate. Cape fur seals seemingly could switch between prey depending on the available biomass. This was evident in the study colonies and during the study periods.

This study demonstrates that the diet of Cape fur seal has remained relatively unchanged since 1974. They have largely increased the proportions of species they consume based on abundance. The consistent presence of anchovy in the diet of Cape fur seals over time suggests that this fish species constitutes an important food item for fur seals. In general, there was no competition between the purse-seine fishery and Cape fur seals. The difference in anchovy sizes caught by the fishery (45 – 130 mm) and seals (17 – 250 mm) indicate that there may be less competition than previously thought. However, purse-seine fishery and seals both target similar sizes (21.9 – 250 mm) of red eye and sardine. Increases in the presence of seabirds in the diet since 1974 have implications for three species of Endangered seabirds: African Penguins (*Spheniscus demersus*), Cape Gannets (*Morus capensis*) and Cape Cormorants (*Phalacrocorax capensis*). Overall, the study demonstrated some long-term changes in the diet of Cape fur seals over the past 40 years despite the use of two different sampling methods and the spatially patchy data.

Chapter 1: General Introduction

1.1 Marine top predators

The wide diversity of marine top predators (i.e. sharks, marine mammals, seabirds) may be used as ecological indicators to provide essential information on the health and stability of marine ecosystems (Cury *et al.,* 2000; 2011; Cury and Shannon, 2004; Sergio *et al.,* 2008; Botha, 2022; Strydom *et al.,* 2022). As top predators, they are drivers of natural selection, evolution (Reid *et al.,* 2005; Creel and Christianson, 2008; Hammerschlag and Trussell, 2011; Heithaus *et al.,* 2008), and play a critical role in influencing ecosystem structure and function through the effects of prey populations (Estes *et al.,* 2016; Roman *et al.,* 2014). Knowledge of the spatial distribution and population trends of these marine predators forms an essential foundation for understanding ecosystem structuring and functioning, as it is driven by prey availability, which varies over space and time (Russell *et al.,* 1992; Botha, 2022). Therefore, long-term monitoring of various parameters of top predators' ecology, therefore aids in understanding of their role in ecosystem functioning and can provide signals of ecosystem change (Boen, 1996; Botha, 2022; Strydom *et al.,* 2022).

Marine predators impact their prey's dynamics through top-down cascades but also may be impacted by prey dynamics through bottom-up effects. Top-down effects imply control through predation, whereas bottom-up effects imply control through prey abundance, which is often driven by biophysical conditions such as climate and nutrient loads (Frederiksen *et al.,* 2006). Top-down controls can also modify prey behaviour through risk effects (Fallows *et al.,* 2014). For instance, Great white sharks (*Carcharodon carcharias*) changed their distribution in South Africa in response to the presence of killer whales (*Orcinus orca*) in their preferred habitat (Towner *et al.,* 2022). An example of bottom-up controls was evident in the steep decline of the African penguin (*Spheniscus demersus*) population following the collapse of their preferred prey, anchovy (*Engraulis encrasicolus capensis)* and sardine (*Sardinops sagax*) in South Africa (Crawford, 2009; Crawford *et al.,* 2011; 2014; Robinson *et al.,* 2015, Sydeman *et al.,* 2021). The sensitivity of top predator biology (e.g. breeding success, phenology) to bottom-up effects makes them good indicators of ecosystem health and identifies potential changes in the ecosystem (Hindell *et al.,* 2003; Piatt *et al.,* 2007; Hazen *et al.,* 2019; Botha, 2022).

Selecting the most appropriate sentinel species of ecosystem health requires detailed information, knowledge, and understanding of species relevance in tracking changes in a particular ecosystem (Hazen *et al.,* 2019). This dissertation considered Cape fur seal as a sentinel species, because the species is the most abundant in terms of biomass along its range (Angola-South Africa), has adaptive capabilities to

environmental perturbations, is long-lived, and provides insight into trophic dynamics across multitude spatio-temporal scales (Sydeman *et al.,* 2015; Fleming *et al.,* 2016, Hazen *et al.,* 2019). Marine top predators such as whales, dolphins, and sharks spend all their life stages in the water, which complicates access to researchers. Research costs generally limit the scope of research; these include costs associated with gear, boats, and equipment (Heithaus *et al*., 2008).

Seals and seabirds are relatively easier to study as they return to land to breed and, in some cases, to moult (Makhado *et al.,* 2006; Mecenero *et al.,* 2006a; Hofmeyr, 2015; Dakwa *et al.,* 2021; Masiko *et al.,* 2021). Accessibility to these sentinel predators affords researchers an opportunity to investigate their breeding trends, deploy biologging devices, conduct population surveys, and monitor dietary trends over time (Frederiksen *et al*., 2006; Hazen *et al.,* 2019; Strydom *et al*., 2022). Dietary information is critical in explaining population dynamics, when food is a limiting factor, density-dependent factors such as intra-species competition may be evident (Wakefield *et al.,* 2013). Such competition might influence spatial differences in foraging ecology within and across breeding localities (Newsome *et al.,* 2015; Botha, 2022). This might result from spatial variation in the diet (Drago *et al.,* 2016; Handley *et al.,* 2017), distribution (Robson *et al.,* 2004b; Baylis *et al.,* 2018), and behaviour (Staniland *et al.,* 2010; Huckstadt *et al.,* 2016), which have been increasingly identified within marine predator species. Furthermore, functions and dynamics of the marine environment are induced by the availability of resources (i.e. food/prey), which may vary over time and space (Forero *et al.,* 2002; Hume *et al.,* 2004; Danckwerts *et al.,* 2016; Handley *et al.,* 2017). Long-term studies of the diet of sentinel species can help track changes in their environment (Bossart, 2011; Fossi *et al.,* 2014; Moore, 2008; Nelms *et al.,* 2019; Botha, 2022). Fur seal diets have been investigated through stomach contents (David, 1989; Arim and Naya, 2003), scat analysis (Arim and Naya, 2003; Makhado *et al.,* 2006; Mecenero *et al.,* 2005; 2006a; Huisamen *et al.,* 2013; Botha, 2022), indirect markers such as stable isotopes (Conna *et al.,* 2014), and more recently through eDNA (Kirkman *et al.,* 2010; du Doit *et al.,* 2017). Scat analysis is a cost-effective and least intrusive method for investigating fur seal diet (Pierce *et al.,* 1991).

1.2 Cape fur seals

In southern Africa, the only breeding pinniped species is the Cape fur seal (David, 1989). Its breeding distribution extends from Baia dos Tigres in southwest Angola (16°34' S, 11°41' E) to islands in Algoa Bay, southeast of South Africa (33°50' S, 26°17' E) (Kirkman *et al*., 2007; Hofmeyr, 2015). Cape fur seals are members of the eared seal family, Otariidae (Warnecke and Shaughnessy, 1985; Hofmeyr and Bester, 2018) and are the largest fur seal species with marked sexual dimorphism (Kirkman *et al*., 2016).

Adult males (218 - 360 kg) are significantly larger than adult females (41 - 113 kg) (Shaughnessy, 1979). Breeding is synchronous and occurs between October and January each year. Each female gives birth to one pup with lactation of approximately 7 – 8 months (David, 1989, Kirkman, 2010; Kirkman *et al.,* 2013; 2016a; Hofmeyr *et al.,* 2015). During lactation, females make short foraging trips of approximately 3 to 4 days and return to the colony to nurse their pups. Their foraging duration and distance from the colony likely indicate the variability in local foraging conditions and food availability (Rand, 1955; Warnecke and Shaughnessy, 1985). Pup weaning and independent foraging occurs from 7 to 12 months, although occasional breastfeeding may occur up to 2 or even 3 years (Warnecke and Shaughnessy, 1985; David and Rand, 1986).

The population of Cape fur seals was last estimated to be 1.7 –2 million individuals in the early 1990s (Butterworth *et al*., 1995). Historically, and similar to most other seal species, the Cape fur seal experienced high levels of exploitation through uncontrolled harvesting between the 17th and 19th centuries for their fur, meat, and oil (David and van Sittert, 2008; Botha, 2022). A harvesting moratorium was put in place in South Africa in 1990 (Wickens *et al.,* 1991; Kirkman 2010, Kirkman *et al.,* 2013), however, it continued in Namibia albeit at low levels in recent years. Angola does not have a history of harvesting seals. The species was protected under the Seals and Seabirds Protection Act, and the Marine Living Resources Act (MLRA 18 of 1998) (Cochrane *et al.,* 2004) and additional protection was granted through the National Environmental Management: Biodiversity Act (10/2004): Threatened or Protected Marine Species Regulations of 2017. The Cape fur seal population showed considerable recovery throughout the 20th century (Butterworth *et al.,* 1995; Kirkman *et al.,* 2007b; 2013; Hofmeyr, 2015), and majority of the Cape fur seal population (>60%) is found along the Namibia coast, owing to the country's three large mainland colonies (David, 1989; Kirkman *et al.,* 2007b, 2013).

Associated with this recovery, the number of colonies has increased from 23 in the 1970s to approximately 40 in 2012 (Kirkman *et al.,* 2013). At least 18 breeding colonies are found in South Africa plus 12 haul-out sites (DFFE, unpublished data). Despite the increase in post-commercial harvesting population levels, the population increase has slowed down to < 1.0 annually (Kirkman *et al*., 2013; 2016a; 2016b). The population has experienced occasional mortality events on the west coast recently (Kirkman *et al*., 2016a), with the last mass die-off recorded off South Africa in 2021 (Seakamela *et al.,* 2021). Since the early 1990s, changes in the Benguela include an increase in water temperature of the west coast of South Africa and interannual upwelling variability (Jarre *et al.,* 2015; Kirkman *et al.,* 2019). Coincident with these changes were noticeable adjustments in the distribution and abundance of diverse forage species of importance to Cape fur seals (i.e. sardine and anchovy) in the southern Benguela (Roy

et al., 2007; Blamey *et al.,* 2012; 2015), which coincides with the west coast of South Africa and the southern portion of Namibia's waters south of Lüderitz (Kirkman *et al.,* 2016b; Botha, 2022). These changes have led to a shift in the distribution of colonies, with new breeding colonies established and former colonies re-colonised (Coetzee *et al*., 2008; Huisamen *et al.,* 2012; Jarre *et al.,* 2015).

The Cape fur seal population does not have top-down controls but faces other threats such as lack of food due to low prey biomass; entanglement in fishing gear and other marine debris (Rand, 1955; Oosthuizen *et al.,* 1997; Martin *et al*., 2005; Wiesel, 2006; Jefferson *et al*., 2015), bycatch in fisheries operations (trawls, purse-seines, long-liners) (Wickens *et al.,* 1992; David and Wickens, 2003). In the Northern Cape and Namibia, brown hyenas (*Hyaena brunnea*), black-backed jackals (*Canis mesomelas*), and African lions (*Panthera leo*) feed on seals in some mainland colonies (Shaughnessy and Butterworth, 1981; Oosthuizen *et al.,* 1997; Wiesel, 2006; Kirkman *et al.,* 2019; Stander, 2019). There are no major known epidemic diseases that affect Cape fur seals; however, evidence is emerging of potential domoic acid poisoning, which is linked to a harmful algal bloom causing species of the genus Pseudo-nitzschia (SeaSearch, unpublished data). Seals are also vulnerable to disease transmission from domestic/wild dogs and other terrestrial carnivores (Kennedy *et al.,* 2000; Hofmeyr, 2015; Kirkman *et al*., 2016a). Unfavourable environmental conditions associated with climate change would impact the fur seal population by inducing increases in sea level, air temperature, extreme weather events (i.e. storms), and as such might result in habitat loss (in this case colonies) (Gerber and Hillborn, 2001; Stewardson *et al.,* 2012; Kirkman *et al*., 2016a).

Other threats include oil spills, which decrease the insulation characteristics of their fur, which might result in hypothermia, and other toxins such as persistent organochlorines that can potentially damage the immune, endocrine, or nervous systems of animals, disrupting growth, and resistance to disease (Kirkwood and Goldsworthy, 2013). In addition, human activities, including tourism and mining activities close to mainland colonies such as Kleinsee, which are easily accessible through human intrusion, could potentially alter the seals' behavioural patterns (seals flee from humans, stampeding might result in injury/death, especially to pups) (Boren and Barton, 2002). The movement of fur seals from their preferred areas due to human intrusion can disrupt mother-pup bonds, which might lead to neglect of pups/offspring (Boren and Barton, 2002; Gales *et al.,* 2003; Boren, 2010). Despite all these threats to the Cape fur seal population, the global population is stable and the species is listed as Least Concern by the IUCN (Hofmeyr, 2015).

Cape fur seal diet and interactions with fisheries

Cape fur seals are generalist feeders that consume a wide range of prey species (David, 1987a; Mecenero *et al.,* 2006; Huisamen *et al.,* 2012), and tracking/monitoring their diet make fur seals good indicator of change in the marine ecosystem (Botha, 2022). Geographic and individual specialisation has been recently reported (Botha *et al.,* 2023). Their diet comprises of pelagic and demersal prey species such as teleost fish, cephalopods, crustaceans, and occasional seabirds (Shaughnessy, 1985; David, 1987a; Crawford *et al.,* 1989; de Bruyn *et al.,* 2003; Hume *et al.,* 2004; Page *et al.,* 2005; Mecenero *et al.,* 2006a; Makhado *et al.,* 2006; Kirkwood *et al.,* 2008; Huisamen *et al.,* 2012; Hlati, 2015; Botha, 2022; Mwaala, 2022). Although the diet consists of diverse prey sources, fish is the dominant prey item. Cape fur seals consumed approximately 2 million tons of fish annually between 1973 and 1993 in southern Africa, with 600 000 tons consumed off the west coast of South Africa (Butterworth *et al.,* 1995; Coetzee *et al.,* 2008).

Despite the wide variety of known prey taxa that constitute fur seals diet, they are species known to be key/preferred prey species (i.e. anchovy; hake (*Merluccius capensis* and *M. paradoxus)*; horse mackerel (*Trachurus trachurus capensis)*, sardine) in the diet, which are also targeted by fisheries (David 1987b; Castley *et al.* 1991; Mecenero *et al.,* 2006; Huisamen *et al.,* 2012; Hlati, 2015). Previous studies have reported that the Cape fur seal diet constituted 80% of commercially targeted fish species off the South African coast (Punt and Butterorth 1995; Huisamen *et al.,* 2012). Thus, the Cape fur seal is not viewed favourably by the fisheries sector and fishing communities alike (David, 1987b; Huisamen *et al*., 2012). Direct competition by way of loss of fishing gear and depredation has been reported in west coast fisheries (David, 1987; Wickens *et al*., 1992; Kirkman *et al.,* 2013). More recently, there have been numerous deaths of malnourished Cape fur seals in Namibia and South Africa, where preferred prey fish stocks are known to be exhausted (Hofmeyr, 2015; Kirkman *et al.,* 2016a; 2006b; DFFE, unpublished data). The reduced biomass of preferred prey fish along the majority of their breeding colonies (west coast) will exacerbate competition with fisheries (Coetzee *et al.,* 2008)

1.3 Study Region

South African coastal waters are rich in biodiversity and high productivity because of the three co-occurring oceans (Atlantic Ocean, Indian Ocean, and Southern Ocean), and two associated current systems (Benguela and Agulhas current system) (Griffiths *et al.,* 2010; Sink *et al.,* 2019; Wepener and Degger, 2019). These current systems support commercial fisheries for a range of species including sardine, anchovy, horse mackerel, and tuna (*Thunnus* and *Katsuwonus* species) (Sink and Attwood,

2008; Wepener and Degger, 2019). They are also home to a diverse array of top predators, including marine mammals (Cape fur seal, dolphins, whales), seabirds, and sharks (Sink *et al.,* 2019).

Benguela Current Ecosystem

The Benguela Current system is one of four eastern boundary upwelling systems in the South Atlantic Ocean (Sink *et al.,* 2019; Wepener and Degger, 2019). The northern Benguela ecosystem is situated off Angola/Namibia, whereas the southern Benguela ecosystem is located off the west and south coasts of South Africa (Mecenero *et al.,* 2006a; Kirkman *et al.,* 2013; Blamey *et al.,* 2016). These waters are highly productive because of the wind-driven upwelling, which brings nutrient-rich bottom waters to the surface (Mecenero *et al.,* 2005; van der Lingen *et al,* 2006; Sink *et al.,* 2019). Upwelling depends on the strength and duration of southerly winds, as well as the depth and width of the continental shelf (Shannon, 1989). Nutrient-rich waters support the abundance of primary producers, which maintains fish stocks that serve as food resources for top predators (van der Lingen *et al,* 2006). Benguela Current Ecosystem is defined by the above characteristics, as the ecosystem supports a large number of land-breeding top predators such as seabirds and marine mammals (e.g. seals) (Kirkman, 2010). Approximately 30 islands that provide protection from terrestrial predators are used as breeding habitats for seals and seabirds (Shaughnessy, 1984; Williams *et al.,* 2000). Most Cape fur seal breeding colonies are found in the southern Benguela ecosystem in South Africa.

Agulhas Current ecosystem

The Agulhas Current Ecosystem is found in the western boundary section of the southwest Indian Ocean gyre, transporting warm tropical and sub-tropical water southward along the east African coast (Lamont *et al*., 2016; Russo *et al.,* 2020; Shannon *et al.,* 2020). This part of coastline extends from the Cape Agulhas in South Africa (partial Eastern Cape, South Africa) to the north end of Somalia (Sink *et al.,* 2019; Wepener and Degger, 2019). Agulhas Current is the world's fastest and largest western boundary current, and influences climate and weather the African continent (Reason, 2002; Rouault *et al.,* 2002; Beal *et al.,* 2011; Lamont *et al.,* 2016). This might be due to the dominant oceanographic characteristics (i.e. warm water current, warm weather and the subtropical biogeographic) of the region (Reason, 2002; Rouault *et al.,* 2002; Beal *et al.,* 2011; Lamont *et al.,* 2016). The ecosystem is characterised by thermally stratified surface waters with generally low-chlorophyll concentrations (i.e. nutrient poor). However, it is an important region for larval distribution processes, and the chokka squid (*Loligo vulgaris reynaudii)* fishery (Lamont *et al.,* 2016; Sink *et al*. 2012a; 2019). Few land-breeding marine predators occur in this

area because of the paucity of offshore islands for breeding and unsatisfactory environmental conditions (low/lack nutrients) at sea (Stewardson, 1999; Kirkman *et al.,* 2007b).

Research sites

There are 18 Cape fur seal breeding colonies and 12 non-breeding colonies (haul-out sites) in South Africa (Figure 1.1). Cape fur seal scat samples were collected from 11 accessible South African colonies, whcih were divided into three geographical regions in this study: those north of St Helena Bay (Kleinsee (29°39' S, 17°04' E), Strandfontein Point (30º58' S, 17º39' E), and Lambert's Bay (32º05' S, 18º18' E)); those situated between Saldanha Bay and Cape Agulhas (Jutten Island (33º05' S, 17º57' E), Vondeling Island (33º09' S, 17º58' E), Robbesteen Rock (33º38' S, 18º24' E), Duikerklip Rock (34º16' S, 18º22' E), Seal Island, False Bay (34º08' S, 18º34' E), and Geyser Rock (34º41' S, 19º24' E)) and those to the east of Cape Agulhas (Mossel Bay (34º10' S, 22º05' E), Robberg Ledges (34º03' S, 23º22' E) and Black Rock (33°50' S, 26°17' E)) (Figure 1.1). Details of each study colony are provided in Table 2.1

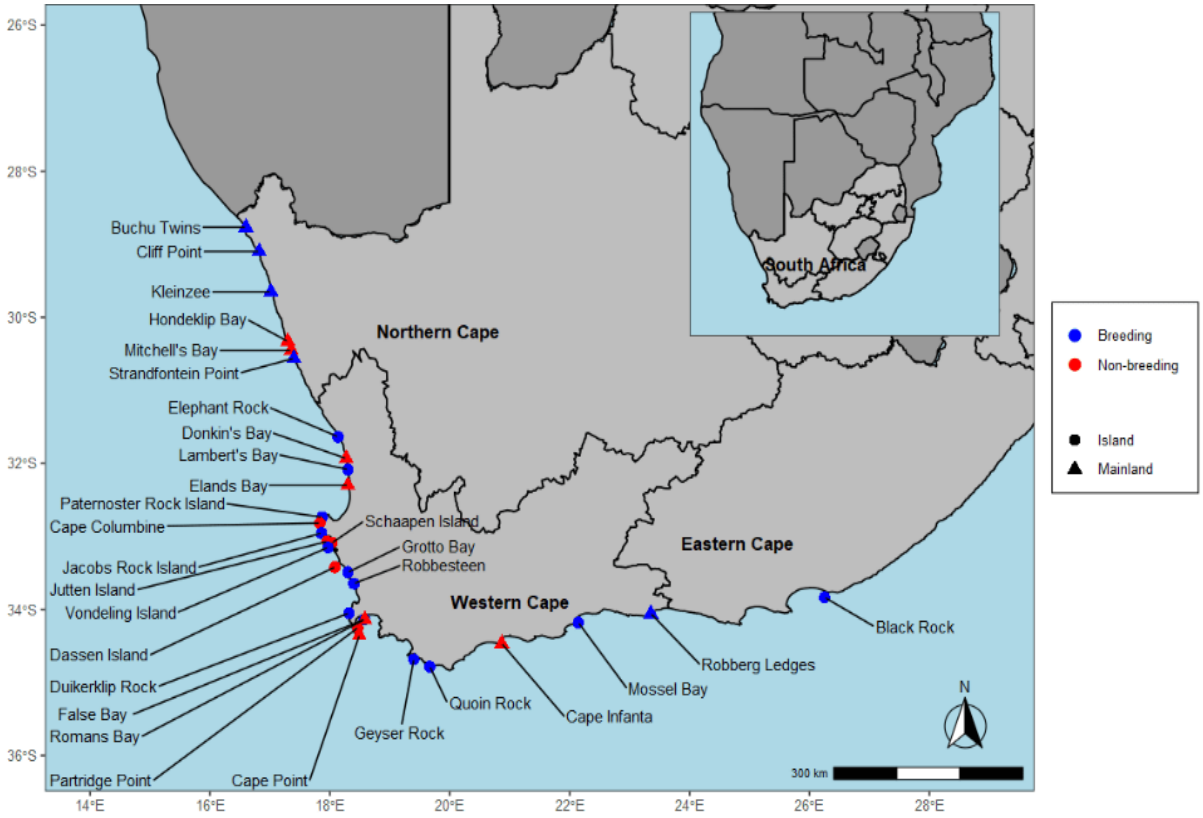

Figure 1.1: Map of the 18 breeding and 12 non-breeding colonies of Cape fur seals along the South African coast (18 on offshore Islands and 12 on the mainland), which includes the 11 accessible colonies used in this study as research sites.

1.4 Dissertation structure

This dissertation is divided into two main chapters. Chapter 2 summarises the diet of Cape fur seals off the South African coast between 2010 and 2019 based on analyses of scats collected at the 11 accessible colonies and compares these with historical diet information to check for possible long-term changes. Chapter 3 infers potential competition for food between Cape fur seals and commercial fisheries at three fur seal colonies (Lambert's Bay, Jutten Island, Geyser Rock) situated near three fishing harbours (Lambert's Bay harbour, Saldanha Bay harbour, Gansbaai harbour) of South Africa, utilising Cape fur seal diet data, commercial catches by the purse-seine fishery and acoustic biomass estimates for small pelagic fish, which make up the bulk of fur seals' diet. Each chapter is written as a stand-alone chapter to facilitate publication with some duplication and linkages across the chapters.

Chapter 2 describes variability in the diet of Cape fur seals off the South African coast between 2010 and 2019, on a spatio-temporal scale based on scat analysis. Important key prey species are identified, quantified, and ranked in terms of importance using four main descriptors. The scat-derived diet information is compared with the stomach sample diet information that was collected between 1974 – 1996. This chapter thus gives a 10-year account of changes in the diet of Cape fur seals at 11 localities spread along the south and west coasts of South Africa. The comparison between two period sheds light on possible changes that may have occurred in the intervening period. The aim of this chapter was to:

1. Characterise the prey species composition of Cape fur seals off the South African coast from 2010 to 2019.
2. Investigate spatial-temporal variation of the presence of prey species in Cape fur seals diet at annual, seasonal, and periodic scales.
3. Explore fish size variation within prey species and across study regions and colonies.
4. Compare the diet composition of Cape fur seals between stomach content samples (1974 – 1996) and scat samples (2010 – 2019).

Chapter 3 assesses potential competition for food between Cape fur seals and commercial fisheries at three colonies (Lambert's Bay, Jutten Island, Geyser Rock) near the fishing harbours from 2010 to 2019. The three harbours receive landings from fisheries targeting anchovy, sardine, horse mackerel and red-eye (*Etrumeus whiteheadi)*. The Cape fur seal as a generalist forager and marine predator provides an opportunity to investigate potential competition for forage species resources. Until recently, the Cape fur seal's population has been increasing but the growth rate has slowed down to <0.9 per annum (Kirkman *et al.,* 2013; 2016a).

The shift in the distribution of preferred prey that led to a mismatch between key foraging areas and their breeding sites on the west coast may lead to increased competition for limited prey species within the range of their breeding colonies. This is crucial for breeding females during the nursing period. The further the females travel from the colony for foraging, the more energy they expend. This may not be ideal for their reproductive success or survival of their pups. Thus, a better understanding of competition between seals and fisheries is critical in terms of prey fish stock management (i.e. Total Allowable Catch (TAC) process). This Chapter therefore aims to:

1. Explore the fish size eaten by Cape fur seals and reported in fishery landings.
2. Investigate potential competition or overlap for food between purse-seine fishery catches and Cape fur seal consumption (diet).
3. Compare geographical and temporal variations between acoustic biomass estimates and consumption by Cape fur seals.

Chapter 4 summarises the findings of the dissertation, identifies colonies that require more sampling, and makes recommendations for future studies.

Chapter 2: Spatio-temporal variation in the dietary composition of Cape fur seals off the South African coast

2.1 Abstract

Cape fur seals breed from southern Angola to Algoa Bay on the southeast coast of South Africa and are the greatest marine predator species within the Benguela Current Ecosystem. Their diet has been well studied in Namibia and on the west coast of South Africa using both stomach contents and scat analysis, and the results have been used to implement conservation measures, environmental management, and to determine potential changes in the ecosystem. This study reports the spatio-temporal variation in the diet of Cape fur seals off the South African coast based on the analysis of scat samples from 2010 to 2019. Scats were collected from 11 Cape fur seal accessible colonies, which were divided into three regions: St Helena Bay, Saldanha Bay to Cape Agulhas, and East of Cape Agulhas. Fish otoliths, cephalopod beaks and, seabird feathers were used to identify prey to the lowest taxonomic level possible, and the occurrence of crustacean remains was also recorded. Fifty-six prey species (46 fish, 6 cephalopods, 4 seabirds) were identified from 4165 scats. In order to determine the importance of each prey taxon to the diet, an index of relative importance (%IRI), mass contribution (%M), numerical abundance (%NA), and frequency of occurrence (%FO) were calculated. Fish occurred most often (88.0%FO), followed by seabirds (9.1%FO), cephalopods (5.5%FO), and crustaceans (0.4%FO). Anchovy (*Engraulis encrasicolus capensis*), horse mackerel (*Trachurus trachurus capensis*), sardine (*Sardinops sagax*), and hake (*Merluccius capensis* and *M. paradoxus*) were key prey species in the diet in terms of %IRI. The diet varied seasonally; there was more consumption of anchovy and "other" species during the non-upwelling season (autumn-winter) compared to the upwelling season (spring-summer) (Figure 2.6; Table 2.6). Hake and horse mackerel were the largest fish species in size consumed but contributed less mass to the diet (10.9%M and 10.3%M, respectively) than the smaller but much more abundant anchovy and sardine (combined 68.8%M). Comparing the diet based on scat samples with stomach content samples collected from 1974 –1996, there were changes in the proportions of prey consumed. Seabirds were less consumed during 1974 –1996 compared to 2010 – 2019, and pelagic goby (*Sufflogobius bibarbatus*) (55.0%NA) dominated in 1974 –1996 while anchovy (67.6%NA) dominated in 2010 – 2019. Thirty prey species (22 fish, 5 cephalopods, 2 crustaceans, 1 seabird) were identified from 2 336 stomach content samples. These results show variability in the diet of Cape fur seals from the 1974 to 2019, and how the predominant prey species (i.e. decrease sardine, increase anchovy) changed in the diet and in relation with fish stock sizes in the region over the last 40 years.

2.2 Introduction

Global changes in climate and fishing pressure have induced shifts in trophic interactions in marine ecosystems (Trathan *et al.,* 2012; Gutt *et al.,* 2015). These changes are assumed to occur most through bottom-up processes, whereby climate changes are influenced by oceanographic conditions directly impacting species at low trophic levels, eventually impacting marine predators (Barbraud *et al.,* 2012; Bond & Lavers, 2014; Bost *et al.,* 2015). These marine predators (seabirds, marine mammals, sharks) merge with changes in food webs at levels below them, thus making them good indicators of the state of marine trophic webs (Weimerskirch *et al.,* 2003; Kirkman *et al.,* 2013). Particular marine predators, such as land-breeding seabirds and fur seals, are central place foragers that can easily be sampled when they return to the land to nurse their young at their breeding colonies and thus facilitate dietary studies that can stretch over long periods (Tarroux *et al.,* 2016). These predators' distribution and abundance are interlinked to their habitat whciht determines prey availability (Fadool, 2020; Benoit-Bird *et al.,* 2013). Recently, in the southern Benguela ecosystem off South Africa, there have been eastward shifts in the distributions of anchovy (*Engraulis encrasicolus capensis*) and sardine (*Sardinops sagax*), which were probably influenced by environmental changes, although fishing pressure might have played a part (Crawford *et al.,* 2016).

The Cape fur seal (*Arctocephalus pusillus pusillus*) is a marine apex predator confined to southern Africa and the only pinniped species that breeds regularly in the region. It is widely distributed, with at least 40 breeding colonies (Kirkman *et al.,* 2013) from Baia dos Tigres in southwest Angola to Algoa Bay in southeast South Africa (Hofmeyr, 2015; Kirkman *et al.,* 2016a; 2016b; DFFE, unpublished data). In South Africa, Cape fur seals breed at 18 offshore islands and 12 mainland sites from the west coast (Benguela Current) to the southeast coast (Agulhas Current) ecosystems (Kirkman *et al.,* 2013; Hofmeyr, 2015; DFFE, unpublished data; Figure 1.1). Historically, most seals were associated with the higher productivity of the cold, nutrient-rich Benguela upwelling ecosystem (David, 1987), but shifts in the distribution of their prey have resulted in the formation of new colonies mostly along the south coast (Kirkman *et al.,* 2013). Food availability in waters adjacent to breeding colonies is the most likely factor behind these shifts (Kirkman *et al.,* 2011; 2013; Wcisel, 2013; Poloczanska *et al.,* 2016).

Cape fur seals are generalist feeders that consume approximately two million tons of fish annually in South Africa and Namibia (Wickens *et al.,* 1992). Analysis of stomach contents of seals collected at sea indicated that they mainly feed on teleost fish such as anchovy, sardine, hake *(Merluccius capensis* and *M. paradoxus*), horse mackerel (*Trachurus trachurus capensis*), lanternfish (*Lampanyctodes hectoris*), round herring (*Etrumeus whiteheadi*), and pelagic goby (*Sufflogobius bibarbatus*) (Shaughnessy, 1985; David, 1987a; de Bruyn *et al.,* 2003; Hume *et al.,* 2004; Page *et al.,* 2005; Mecenero *et al.,* 2006a;

Kirkwood *et al.,* 2007a; Huisamen *et al.,* 2012). More recently, analysis of hard prey remaining in scats has confirmed the dominance of these fish species (Trites and Joy, 2005; Bowen and Iverson, 2012; du-Dot *et al*., 2017). Anchovy, sardine, hake, and horse mackerel are also of commercial importance, and thus the seals compete for these resources with fisheries (David and Rand, 1986; Wickens, 1989; Wickens *et al.,* 1992; David and Wickens, 2003). Although the diet of Cape fur seal is dominated by fish, they also feed on crustaceans (including rock lobster (*Jasus lalandii*), shrimp (Caridea), prawns (Dendrobranchiata) and amphipods (Amphipoda)) (David, 1987; de Bruyn *et al.,* 2003; 2005; Mecenero *et al.* 2006a), as well as cephalopods (squid (Teuthida) and octopus (Octopoda)), and seabirds, including endangered species such as the African Penguin (*Spheniscus demersus*), Cape Cormorant (*Phalacrocorax capensis*), and Cape Gannet (*Morus capensis)* (Crawford *et al.,* 1989; 2007; 2011; 2014; 2015; Makhado *et al.,* 2006; 2013; Marks *et al*., 1997; Mecenero *et al.,* 2006a).

Variability in the Cape fur seal diet probably results, at least in part, from local variations in prey availability (Reid et al., 2005; Boyd *et al.,* 2006). Their diet is influenced by both the biological and physical oceanographic features of a region (Rice, 2000; Swain and Sinclair, 2000; Zwanenburg *et al*., 2002). As a result, long-term studies of their diet can indicate changes in trophic structure and functioning, providing information about prey species diversity, distribution, and abundance in the ecosystem at local and regional scales (Diamond and Devlin, 2003; Reid *et al.,* 2005). Dietary studies also allow an understanding of predator-prey relationships as they provide information on Cape fur seal foraging behaviour (Kirkman*,* 2010), and they are also a critical addition to a suite of parameters that are considered in the ecosystem approach to fisheries management (Mecenero *et al.,* 2006a; 2006b; Kirkman*,* 2010; Huisamen *et al.,* 2012). While considerable effort has been invested in studying the diet of Cape fur seals (David, 1987; Mecenero *et al.,* 2006a; 2006b; Connan *et al.,* 2014; Kirkman *et al.,* 2019), these efforts have been limited to easily accessible colonies. To date, the only recent diet studies of Cape fur seals in South Africa have been conducted at Robberg Ledges from 2003 to 2008 (Huisamen *et al*., 2012); at Lambert's Bay and Geyser Rock between 2010 and 2014 (Hlati, 2015); and at Lambert's Bay between 2015 and 2018 (Gumede, 2019).

This chapter describes the diet of Cape fur seals off South Africa utilising the scat analysis method based on samples collected from 2010 to 2019. These data were compared with to historic stomach content samples collected from 1974 to 1996. Spatio-temporal dietary composition, relative importance of each prey taxon (species/group), fish size frequency distribution of targeted prey, and long-term changes in the dietary proportion of key species were investigated.

2.3 Methods

Study area

Scat samples were collected from 11 accessible colonies between Kleinsee (29°39' S, 17°04' E) in the Northern Cape and Robberg Ledges (34°03' S, 23°22' E) in the Western Cape (Table 2.1, Figure 2.1). These colonies coincide with the Benguela Current ecosystem and the east of Cape Agulhas in South Africa (Figure 1.1; 2.1). Based on distribution of the Cape fur seal breeding colonies in South Africa, the study area was divided into three regions: St Helena Bay (southern Benguela Current), Saldanha Bay to Cape Agulhas (southern Benguela Current), and east of Cape Agulhas (south-east Benguela Current), (Figures 1.1 and 2.1).

Cape fur seal stomach contents were collected opportunistically at sea during various research cruises conducted from 1974 to 1996 between the Northern Cape (29°2' S, 21°51' E) and Eastern Cape (32°17' S, 26°25' E) of South Africa (DFFE, unpublished data; Figure 2.1).

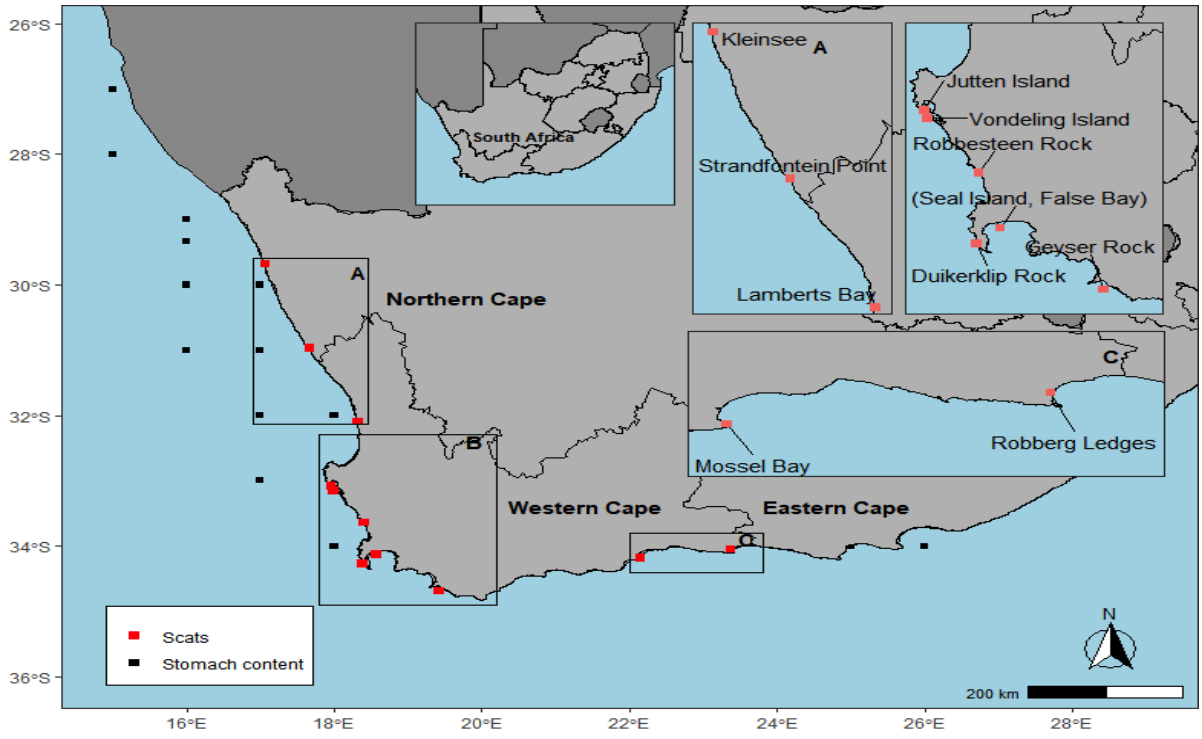

Figure 2.1: The 11 accessible sites (red squares) of Cape fur seals in South Africa from which scat samples were collected. Locations of at-sea stomach contents collection operations are marked in black squares. Study regions were divided into three, St Helena Bay (A), Saldanha Bay to Cape Agulhas (B), and East of Cape Agulhas (C).

Table 2.1: Description of 11 accessible Cape fur seal colonies, where scat samples collected were used for this study.

Colonies	Location	Size	Characteristics
Kleinsee	29°09' S, 17°04' E	9.2 km^2	- Diamond coast (mineral mining)
		~80 000 pups since 2000-2005 (Kirkman *et al.,* 2019)	-Kleinsee Nature Reserve
Strandfontein Point	30°58' S, 17°39' E	8.2 km^2	-Bird Island Nature Reserve
		Seal population size unknown	-Olifants River Estuary
Lambert's Bay	32°05' S, 18°18' E	45.73 km^2	-Cape Gannet colony
		Seal population size unknown	
Jutten Island	33°05' S, 17°57' E	0.46 km^2	-Also, a breeding island for seabirds such as Kelp Gull (*Larus dominicanus*), Hartlaub's Gull (*Chroicocephalus hartlaubii),* Swift Tern (*Thalasseus bergii),* Crowned (*Microcarbo coronatus*), Cape, Bank Cormorants (*Phalacrocorax neglectus*), and African Black Oystercatcher (*Haematopus moquini)*
		Seal population size unknown	
Vondeling Island	33°09' S, 17°58' E	0.21 km^2	-Bank Cormorant colony
Robbesteen Rock	33°38' S, 18°24' E	Seal population ~316 (Kirkman *et al.,* 2007a)	-
Duikerklip Rock	34°16' S, 18°22' E	Seal population size unknown	-
Seal Island (False Bay)	34°08' S, 18°34' E	Seal population ~3138 (Kirkman *et al.,* 2007)	-African Penguins, Kelp Gull, and cormorants
Geyser Rock	34°41' S, 19°24' E	0.03 km^2	-

		Seal population ~2137 (Kirkman *et al.,* 2007a)	
Mossel Bay	34°10' S, 22°05' E	36.8 km^2	- Santos Beach
		Seal population ~262 (Kirkman *et al.,* 2007a)	
Robberg Ledges	34°03' S, 23°22' E	Seal population ~3100 (Huiseman *et al.,* 2012)	-Game fish angling (Huiseman *et al.,* 2012)

Sampling methods

Scat analysis

Scat analysis has been widely used to understand the diet of fur seals (Livaitis, 2000; Mecenero *et al.,* 2006a; Casper *et al.,* 2007; Valentini *et al.,* 2009; Mumma *et al.,* 2016). Seal scats contain hard parts of prey such as otoliths, bones, teeth, and feathers that remain undigested (Livaitis, 2000; Casper *et al.,* 2007; Mumma *et al.,* 2016), and which can be used to identify prey species and estimate prey size. Scat analysis is a non-invasive technique that allows large sample size collection, enable long-term diet studies, and enable diet studies over a wide spatial range (Table 2.1). The technique is also time and cost effective, but it is difficult to identify secondary prey (indirect consumption) using scat analysis, because some prey species leave no trace in the scats.

Up to 30 fresh scat samples were collected per month at colonies from February 2010 to October 2019, but the target at times was not achieved. However, no scats were collected during the peak breeding months (November – January), when the seals have small pups, to avoid undue disturbance and mortality. Even outside this period, not all 11 colonies were visited each month (Table 2.2). Scat samples were kept in individual ziplock bags, allocated a sample number and stored in a freezer. The samples were thawed overnight, and prior to processing, the wet weight was recorded. Samples were then soaked in tap water prior to extraction of hard prey remains (fish otoliths, cephalopod beaks, seabird feathers, and crustacean exoskeletons). Hard prey remains were extracted by gradually washing each scat through a 0.5 mm mesh sieve. Care was taken to limit any damage caused by handling the samples during processing. Fish otoliths were stored in tap water, and cephalopod beaks, seabird feathers, and crustacean exoskeletons were stored in 75% ethanol.

Stomach content samples

Stomach content samples have been used to study the diet of Cape fur seals in South Africa and Namibia from the 1950s to 1996 (Rand, 1959; David, 1987; Lipinski and David, 1990; DFFE, unpublished data). These data were retrieved from the DFFE marine mammal archives. Cape fur seals were collected opportunistically at sea during various research cruises (David, 1987; Green *et al.,* 1989; Castley *et al.,* 1991; Punt *et al*., 1995; Figure 2.1) by shooting them with a 12-bore shotgun and retrieving the body for processing (David, 1987; Lipinski and David, 1990). Once on board the research vessel, each seal's sex and age were determined, the carcass was weighed, and the teeth and stomach were removed. Stomach samples were frozen for later processing. In the laboratory, stomachs were defrosted, weighed, and the contents were removed by rinsing. The technique is invasive as it requires a seal to be dead or shot (at sea/mainland), although it allows identification of primary (direct consumption by seals) and secondary (indirect consumption by seals) prey species (Table 2.2)

Table 2.2: Advantages and disadvantages of stomach contents and scat analysis methods used to study the diet of Cape fur seals.

	Advantages	Disadvantages
Stomach contents analysis	Allows confirmation and identification of primary prey species (direct consumption) and secondary prey species (indirect consumption) of prey species (Boren, 2010; Horswill *et al.,* 2018; Nielsen *et al*., 2019; McCluskey *et al.,* 2021) Allows determination of the sex and age of the seal (David, 1987; Lipinski and David, 1990; Trites and Joy, 2005)	Lethal Expensive (Research vessel, gear and equipment used costs), (David, 1987; Lipinski and David, 1990; Boren, 2010; Horswill *et al*., 2018).
Scat analysis	Nonlethal (seal scats collected) Allows large sample sizes Can be used to assess spatial and temporal variation in diet (De Bruyn *et al*., 2003; Trites and Joy, 2005) Cost and time effective	Difficult to identify secondary prey species (indirect consumption) Issues with differential retention of prey species (over-estimate/under-estimate prey consumed)

Prey identification and measurements

Undigested prey hard parts found in stomach contents and scat samples, such as fish otoliths, cephalopod beaks, crustacean remains, and seabird feathers, were used to identify the species consumed. Fish otolith identification, count, and measurement were based on Smale *et al.* (1995) and otolith reference specimens housed at the DFFE. Identification was made using a dissecting microscope fitted with a graticule to measure the length of intact otoliths. Broken otoliths were identified, where possible, and counted but not measured. For stomach contents, otoliths were identified to fish species, separated into left and right sides, paired according to size to determine the number of fish eaten, and measured to estimate fish total length and mass (David, 1987; DFFE, unpublished data). For cephalopod beaks (also damaged beaks), the upper and lower beaks were counted and identified to species level where possible, for both stomach contents and scat samples (David, 1987, Smale *et al.,* 1993, Xavier *et al*. 2011, Xue *et al.* 2013; DFFE research personnel). Seabird feathers were identified from reference feathers curated at DFFE (B. Dyer pers. Comm). Crustaceans found in stomach contents samples were identified at the species level, but only the occurrence of crustacean remains was recorded in scat samples.

Scats data processing and analysis of diet composition

Correcting otolith diameter for erosion (fish total length (TL) and mass (M))

During digestion, erosion reduces the size of some otoliths (Mecenero *et al.,* 2006b). Consequently, otolith diameters (OD) were corrected for erosion using conversion factors per prey species and regression equation (Mecenero *et al.* 2006b). The corrected ODs were used to estimate total length and mass fish from species-specific regressions using Allometric relationships in Smale *et al*. (1995).

Diet composition

To assess the differential contribution of each prey taxon to the Cape fur seal diet, four measures were calculated. Frequency of occurrence (%FO) is the percentage of scat or stomach content samples collected in which each taxonomic group was represented. Numerical abundance (%NA) is the proportion of each prey taxon out of all prey items. Mass contribution (%M_{fish}) is the proportion of mass contributed by an individual fish prey species using the estimated total mass from otolith diameters (OD). The %FO, %NA, and %M_{fish} of each taxonomic group in the diet were determined for each month, each year, per study region, and during the study period (2010–2019). The index of relative importance (IRI) was originally not expressed in percentages values; however, more recently and for easier interpretation, it has been expressed on a percentage basis (Pinkas *et al.,* 1971; Corte, 1997). The percentage index of

relative importance (%IRIfish), which indicates the importance of an individual prey species in the diet (Pinkas *et al.,* 1971), was calculated as:

$$\%IRIfish = \frac{(\%NAi+\%Mi)x\ \%FOi}{\sum_{i=1}^{n}\ (\%NAi+\%Mi)x\ \%FOi}\ x\ 100$$

where $\%NA_i$ is the numerical abundance of the i^{th} prey species, $\%M_i$ is the mass contribution of the i^{th} species, %FO is the frequency of occurrence of the i^{th} prey species, and *n* is the total number of prey species.

To assess spatial variation in the Cape fur seal diet, %FO and %NA were used to identify important prey species in the three study regions. Seasonal variation was compared between the spring-summer upwelling season (September – March) and the autumn-winter non-upwelling season (April – August).

Only %FO and %NA were used for the analysis of stomach contents.

Statistical analyses

Trites and Joy (2005) suggested that a minimum size of 59 scats is necessary to identify principal prey remains occurring in 0.5% of scats. However, 94 samples are required when comparing diets to distinguish moderate effect sizes over time or between areas. Our study had more than 59 scats per area, which fulfilled the required sample size (Table 2.3).

All data analyses were conducted using R-Studio statistical software, version 3.6.1 (R Core Team, 2019). The data were checked for normality using the Shapiro-Wilks test and histograms as a visual method, and when the data were not normal, non-parametric tests (Kruskal-Wallis test, Mann-Kendall test) were used. To test for inter-annual variation in the diet, %NA of predominant prey taxon (species or group) between the years and the Kruskal-Wallis test were used, as well as to test for a trend in %NA over the years. For spatial variation, %FO and %NA were used to determine the importance of each prey species in the study regions. Kruskal-Wallis tests were used to test for differences in fish size among the four important prey species, while chi-squared goodness-of-fit tests were used to test for differences between the four most important prey species and the study regions. Analysis of similarities (ANOSIM) using function Anosim in the vegan package was used to determine differences in prey composition between regions and for the two dietary sample methods (Warton *et al.,* 2012). This test was used because it does not assume equal group variances, accommodates groups with different sample sizes, and can distinguish within group dispersion (low R^2 value) and between group dispersion (high R^2 value) (Oksanen *et al.,* 2020).

Permutational multivariate analysis of variance (PERMANOVA) was used to test for significance in seasonal differences in the numerical abundance (%NA) of the four most important prey species between upwelling and non-upwelling seasons across the study regions. Each time series was tested for autocorrelation and partial autocorrelation using acf () and pacf (), and if autocorrelation and partial autocorrelation were detected, a modified Mann-Kendall test was applied using the modified mk package (Yue and Wang, 2004; Patakamuri and O'Brien, 2020). To test for long-term changes in %NA of the dominant prey in the Cape fur seal diet, a Mann-Kendall test was implemented with function 'mkttest' if no autocorrelation was detected or 'mmkh' when autocorrelation was detected in package 'modifiedmk'.

2.4 Results

The diet of Cape fur seals was determined from 4165 scat samples collected from 11 breeding colonies along the South African coast between February 2010 and October 2019 (Table 2.3; Figure 2.1). Sampling of seal scats was extremely patchy at most colonies, while Lambert's Bay (n= 2241), Geyser Rock (n= 794) and Jutten Island (n= 452) had the most scat samples (Table 2.3). Fish predominated in the diet, occurring in 88.0%FO of scats. Other prey species were recorded infrequently: seabirds (9.1%FO), cephalopods (5.5%FO), and crustaceans (0.4%FO) (Figure 2.2, Table 2.4). Anchovy, horse mackerel, sardine, and hake were the most abundant prey species, with small pelagic fish (anchovy, sardine, red eye) accounting for 69.4%M, hake 10.9%M and horse mackerel 10.3%M. There were 28 prey species (21 fish, 4 cephalopods, 3 seabirds) identified in scat samples (n= 2269) in the St Helena Bay region. Species richness was greatest in the Saldanha Bay to Cape Agulhas region with 51 prey species (41 fish, 6 cephalopods, and 4 seabirds) identified from 1643 scat samples, and the east of Cape Agulhas region had the lowest richness with only 15 prey species (13 fish, 1 cephalopod, 1 seabird) identified from 253 scats examined (Table 2.3).

Table 2.3: Sample sizes of Cape fur seal scats collected at 11 accessible colonies along the South African coast from February 2010 to October 2019.

Colony	Year										
	2010	**2011**	**2012**	**2013**	**2014**	**2015**	**2016**	**2017**	**2018**	**2019**	**Total**
St Helena Bay (HB)											**2269**
Kleinsee	-	-	-	-	-	16	6	-	-	-	22
Strandfontein Point	-	-	-	-	-	-	6	-	-	-	6
Lambert's Bay	192	204	261	283	241	210	146	178	263	263	2241
Saldanha Bay to Cape Agulhas (SB-CA)											**1643**
Jutten Island	4	-	-	119	58	45	65	108	23	30	452
Vondeling Island	-	-	-	-	8	31	84	11	-	-	134
Robbesteen Rock	-	-	-	-	16	19	15	-	-	-	50
Duikerklip	-	-	-	-	6	-	10	-	-	-	16
Seal Island, False Bay	-	-	-	-	42	43	50	40	-	22	197
Geyser Rock	120	161	79	179	71	31	90	33	-	30	794
East of Cape Agulhas (ECA)											**253**
Mossel Bay	68	90	-	-	44	18	-	-	-	-	220
Robberg Ledges	-	-	-	-	15	-	18	-	-	-	33
Total	384	455	340	581	501	413	490	370	286	345	**4165**

Diet composition and inter-annual variation 2010 – 2019

Fish

The scat analysis indicated that the Cape fur seal diet was dominated numerically by small pelagic fish Clupeidae (anchovy, red-eye and sardine) (73.2%NA), Carangidae (horse mackerel and Atlantic mackerel) (11.9%NA), Myctophidae (lanternfish) (4.2%NA), Gobiidae (pelagic goby) (3.6%NA), Merluccidae (hake) (3.3%NA)and other fish taxon (31 species in 28 families, Table 2.4) for 3.8%NA. Four species together accounted for 96.2%NA of all fish prey (Table 2.4). Anchovy was the most important fish prey (%FO, %NA, %M, %IRI), followed by horse mackerel, sardine, and hake (Table 2.4).

Anchovy contributed >75.0%NA of the diet in all years except 2010 and 2011, when it was <50%NA (Figures 2.3), with a significant inter-annual difference (Kruskal-Wallis $H = 282.2$, $df = 9$, $p < 0.001$, Figure 2.3*)*. Horse mackerel contributed <25%NA of the diet in all years except 2011, when it comprised 64.2%NA with a significant inter-annual difference (Kruskal-Wallis $H = 185.3$, $df = 9$, $p < 0.001$, Figure 2.3. There were also significant inter-annual differences in sardine (Kruskal-Wallis $H = 76.7$, $df = 9$, $p < 0.001$, Figure 2.3) and hake (Kruskal-Wallis $H = 23.5$, $df = 9$, $p = 0.01$, Figure 2.4).

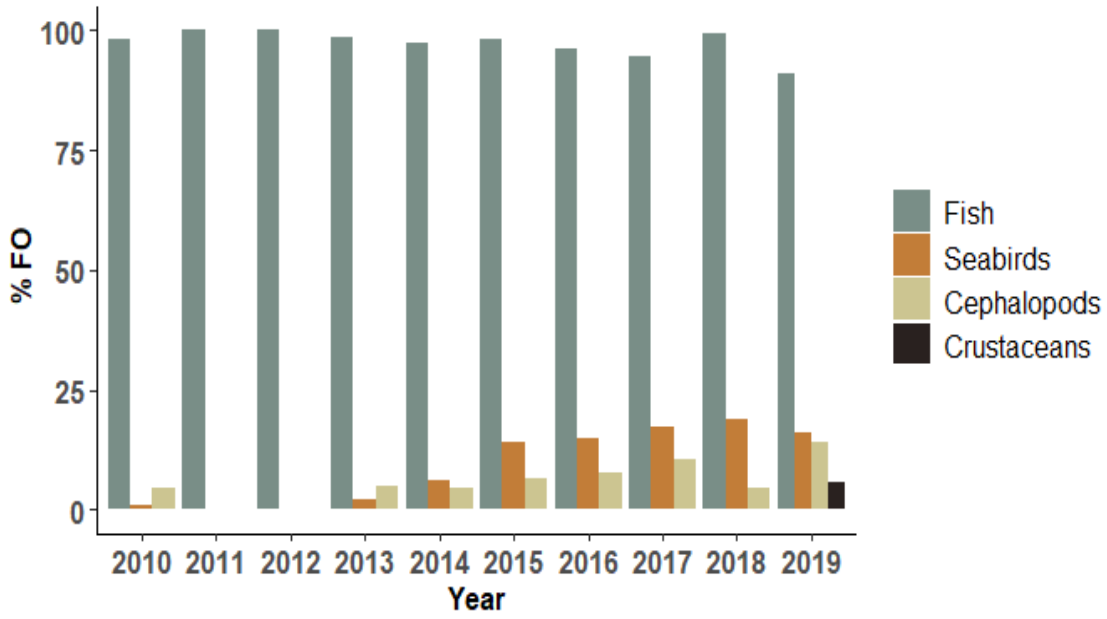

Figure 2.2: Inter-annual variability (frequency of occurrence (%FO)) for each main prey taxon: fish, seabirds, cephalopods, and crustaceans) identified in the diet of Cape fur seals based on the analysis of scat samples collected at 11 colonies around the coast of South Africa from 2010 to 2019.

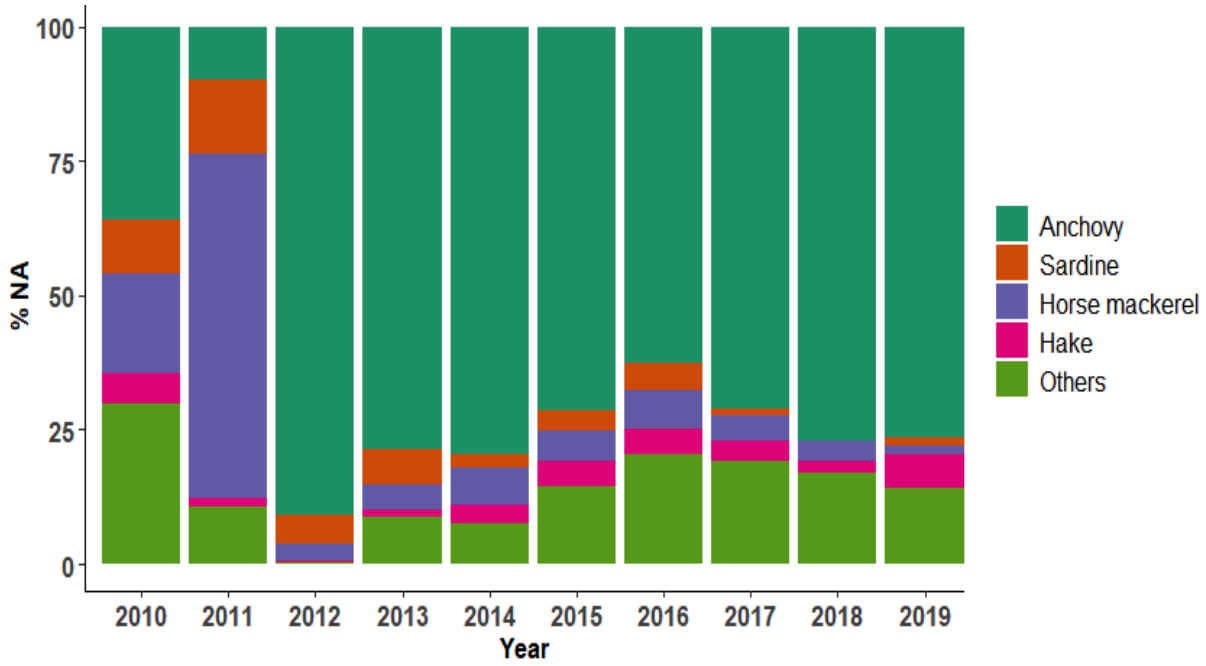

Figure 2.3: Numerical abundance (%NA) of the main fish prey species in the diet of Cape fur seals based on scat samples collected from 2010 to 2019.

Seabirds

Four seabird taxa were identified from 377 scat samples (9.1%FO) (Table 2.4, Figure 2.4). There was an increase in the occurrence of seabirds in scat samples from 2010 to 2019 (linear model; $F_{(1, 6)} = 30.9$, *t*-

value = 5.57, *p* = 0.001, R^2 = 0.84, Figure 2.2, 2.4). Cormorants (Phalacrocoracidae, Microcarbo) were the most common (*n* = 324, 7.8%FO), followed by Cape Gannets (*n* = 29, 0.7%FO), Kelp Gulls (*Larus dominicanus*) (*n* = 16, 0.4%FO) and African Penguins (*n* = 9, 0.2%FO). The highest seabird occurrence was recorded in 2018, whereas there was no record of occurrence in 2011 or 2012 (Figure 2.2, 2.4).

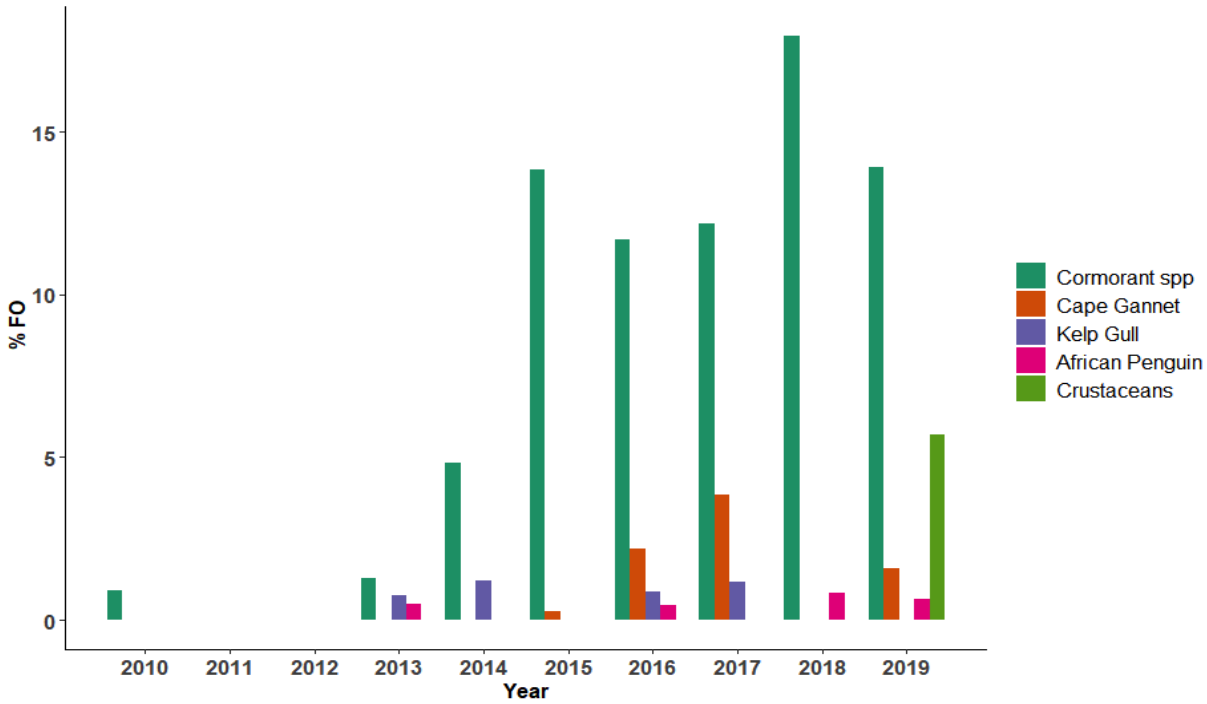

Figure 2.4: The frequency of occurrence (%FO) of seabird and crustacean remains in Cape fur seal scats collected at 11 breeding colonies along the South African coast from 2010 to 2019.

Cephalopods

Cephalopods were infrequent (Figure 2.2, Table 2.4) in the scat samples, comprising 657 beaks. Cephalopods were most often recorded in 2019 (12.8%FO), with no records in 2011 or 2012 (Figure 2.2, 2.5). Six species of cephalopods were identifiable from the beaks found in 204 scat samples (4.9%FO; Figure 2.5). Chokka squid (*Loligo reynaudi*) was the cephalopod most frequently consumed (70.0%NA, Figure 2.5, Table 2.4), followed by the common octopus (*Octopus vulgaris)* (13.3%NA) and cuttlefish (Sepiidae) (4.9%NA, Figure 2.5, Table 2.4).

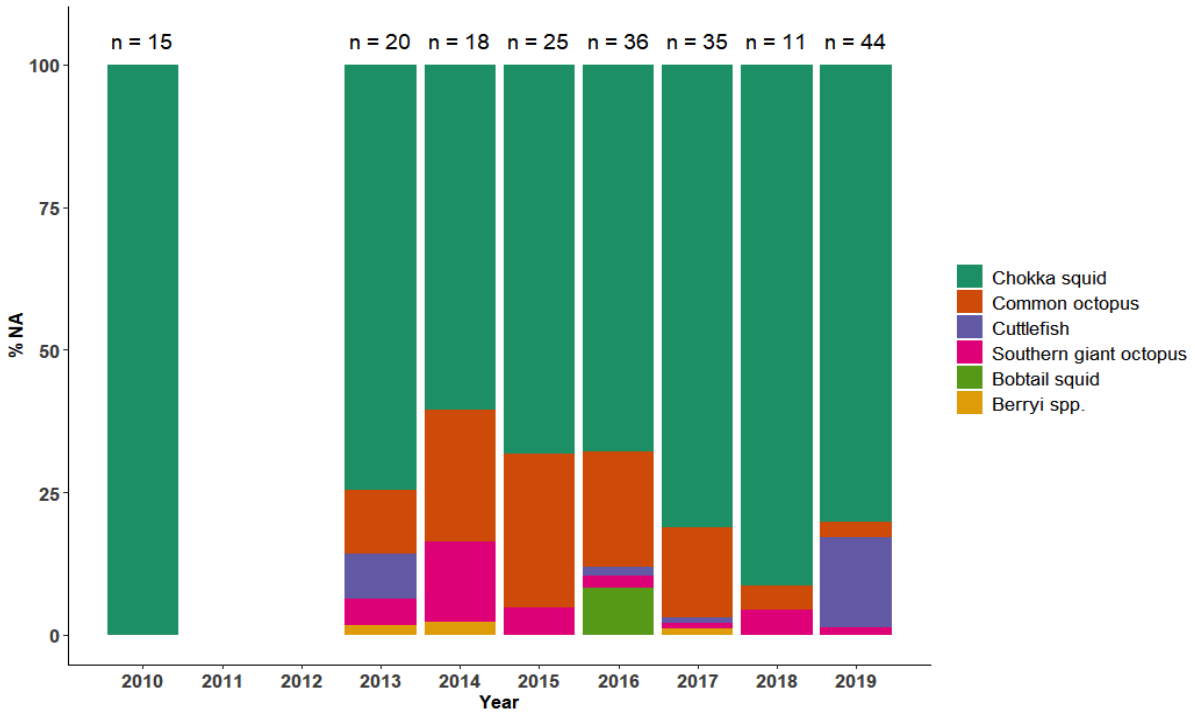

Figure 2.5: Numerical abundance (%NA) of cephalopods in Cape fur seal scats collected around the South African coast from 2010 to 2019. The number of samples (*n*) in which cephalopods were found is shown above each bar.

Crustaceans

Crustaceans were found in only 18 scat samples, all from 2019. Overall, the occurrence of crustaceans in the diet was 0.4%FO (Table 2.4, Figure 2.2, 2.4). The crustacean remains could not be identified to the taxonomic level (Figure 2.2, 2.4).

Table 2.4: Each prey taxon (species/group) identified in Cape fur seal scats collected at 11 colonies around the South African coast from 2010 to 2019 and stomach contents collected between 1979 and 1996. Prey taxa are grouped according to habitat, and contribution of each prey taxon to the diet is expressed from highest to lowest as frequency of occurrence (%FO), numerical abundance (%NA), mass contribution (%M), and index of relative importance (%IRI). Cephalopods, crustaceans, and seabirds' %M and %IRI were not calculated as size measurements were not taken.

			Scats (2010 – 2019)				Stomach contents (1974 – 1996)	
Scientific name	**Common name**	**Habitat**	**%FO**	**%NA**	**%M**	**%IRI**	**%FO**	**%NA**
Fish prey species by family								
Clupeidae			**88.3**	**73.2**	**69.4**	**91.2**	**48.8**	**22.7**
Engraulis encrasicolus capensis	Anchovy	Pelagic	70.4	67.6	46.2	86.1	32.5	18.6
Sardinops sagax	Sardine	Pelagic	15.9	5.1	22.6	5.0	11.9	3.4
Etrumeus whiteheadi	Red eye	Pelagic	2.0	0.5	0.6	-	4.4	0.7
Carangidae			**23.0**	**11.9**	**10.4**	**5.5**	**14.9**	**7.3**
Trachurus treacherous capensis	Horse mackerel	Pelagic	21.9	11.8	10.3	5.5	14.6	7.2
Scomber scombrus	Atlantic mackerel	Pelagic	1.1	0.1	0.1	-	0.3	<0.1
Merluccidae			11.3	3.3	10.9	1.9	12.5	2.9
Merluccius capensis & M. paradoxus	Hake	Demersal	11.3	3.3	10.9	1.9	12.5	2.9
Myctophidae			**10.2**	**4.2**	**3.5**	**0.5**	**14.6**	**9.7**
Lampanyctodes hectoris	Lanternfish	Mesopelagic	6.7	3.6	2.6	0.5	14.6	9.7
Lampanyctus ater	Dusky lanternfish	Mesopelagic	2.5	0.5	0.7	-	-	-
Lampanyctus alatus	Winged lanternfish	Mesopelagic	0.9	0.1	0.1	-	-	-
Ceratoscopelus warmingii	Warmings lanternfish	Mesopelagic	<0.1	<0.1	-	-	-	-
Kreffichthys anderssoni	Rhombic lanternfish	Mesopelagic	<0.1	<0.1	0.1	-	-	-
Gobiidae			**9.0**	**3.6**	**4.1**	**0.8**	**13.0**	**55.0**
Sufflogobius bibarbatus	Pelagic goby	Demersal	9.0	3.6	4.1	0.8	13.0	55.0
Fish in other families			**32.7**	**3.8**	**1.7**	**0.1**	**39.6**	**1.8**
Cynoglossus capensis	Sandtongue-fish	Demersal	8.3	1.8	-	-	-	-
Clinus superciliosus	Super-klipfish	Demersal	2.2	0.6	-	-	0.4	<0.1
Eptatretus hexatrema	Hagfish	Demersal	-	-	-	-	1.3	0.2
Maurolicus muelleri	Light fish	Demersal	1.1	0.2	-	-	1.0	0.1
Liza richardsonii	South African mullet	Demersal	0.5	0.1	-	-	-	-
Austroglossus microlepsi	West-coast sole	Demersal	0.1	<0.1	-	-	1.5	0.2
Lophius vomerinus	Devil anglerfish	Demersal	0.3	0.1	0.1	-	<0.1	<0.1
Gonorynchus gonorynchids	Beaked sandfish	Demersal	0.3	<0.1	0.1	-	-	-
**Coccotropsis Gymnoderma*	Smooth-skin scorpionfish	Demersal	0.3	<0.1	-	-	-	-
Sebastes capensis	False jacopever	Demersal	0.1	<0.1	-	-	2.4	0.4
**Halosaurus ovenii*	Oven's halosaur	Demersal	0.1	<0.1	-	-	-	-
Cheilodactylus fasciatus	Red fingers	Demersal	0.1	<01	-	-	-	-
Cremnochorites capensis	Cape triplefin	Demersal	0.1	<0.1	0.1	-	-	-
Chelidonichthys capensis	Cape gurnard	Demersal	0.1	<0.1	-	-	1.0	<0.1
**Galeichthys ater*	Black sea-catfish	Demersal	0.1	<0.1	-	-	-	-

**Galeichthys feliceps*	White sea-catfish	Demersal	-	-	-	-	0.1	<0.1
**Physiculus capensis*	Bigeye rockling	Demersal	0.1	<0.1	-	-	-	-
**Pomadasys olivaceum*	Pinky grunter	Demersal	0.1	<0.1	-	-	-	-
**Bassanago albescens*	Hairy conger	Demersal	<0.1	<0.1	-	-	-	-
**Uroconger lepturus*	Long-tail conger	Demersal	<0.1	<0.1	0.1	-	-	-
Heteromycteris capensis	Cape sole	Demersal	<01	<0.1	-	-	1.3	0.1
Genypterus capensis	Kingklip	Demersal	<0.1	<0.1	-	-	0.5	<0.1
**Callorhinchus capensis*	Cape elephant-fish	Demersal	-	-	-	-	0.3	<0.1
Thyrsites atun	Snoek	Pelagic	-	-	-	-	1.1	<0.1
Spicara axillaris	Windtoy	Pelagic	0.5	0.1	0.1	-	-	-
**Lepidopus caudatus*	Robbon fish	Pelagic	-	-	-	-	0.4	<0.1
Diplodus sargus capensis	Blacktail	Pelagic	0.3	<0.1	0.3	-	-	-
Pseudomyxus capensis	Freshwater-mullet	Pelagic	0.2	<0.1	0.1	-	-	-
**Atherina breviceps*	Cape silverside	Pelagic	<0.1	<0.1	<0.1	-	-	-
**Pomatomus saltatrix*	Bluefish	Pelagic	<0.1	<0.1	<0.1	-	-	-
**Amoglossus capensis*	Cape scaldfish	Pelagic	<0.1	<0.1	<0.1	-	-	-
Cynoglossus zanzibarensis	Redspotted tonguefish	Pelagic	-	-	-	-	<0.1	<0.1
**Alectis ciliaris*	African pompano	Pelagic	<0.1	<0.1	<0.1	-	-	-
**Coracinus capensis*	Galjoen	Pelagic	<0.1	<0.1	<0.1	-	-	-
**Lycodes agulhensis*	Lycodid fish	Pelagic	<0.1	<0.1	<0.1	-	-	-
**Chirodactylus jessicalenorum*	Natal finger-fin	Pelagic	<0.1	<0.1	<0.1	-	-	-
**Pterogymus laniarius*	Panga	Pelagic	<0.1	<0.1	<0.1	-	-	-
Unidentified fish	-	-	17.2	0.9	0.9	0.1	28.2	0.8
Cephalopods			**5.5**	**100**			**24.1**	**100**
Loligo vulgaris reynaudii	Chokka squid	Pelagic	1.1	70.0	-	-	1.9	8.8
Sepiidae	Cuttle fish	Pelagic	0.3	4.9	-	-	8.7	22.8
Argonauta spp.	Paper nautilis squid	Pelagic	-	-	-	-	2.3	5.8
Afrololigo mercatoris	Guinean thumbstall squid	Pelagic	-	-	-	-	0.1	0.1
Lycoteuthis diadema	Oceanic squid	Pelagic	-	-	-	-	0.1	0.1
Octopus vulgaris	Common octopus	Demersal	0.6	13.3	-	-	-	-
Enteroctopus magnificus	Southern giant octopus	Demersal	0.4	3.2	-	-	-	-
Benthoctopus berryi	Berryi spp.	Demersal	0.1	0.5	-	-	-	-
Austrossia enigmatica	Bobtail squid	Demersal	<0.1	1.7	-	-	-	-
Unidentified cephalopods	-	-	3.0	6.4	-	-	11.0	62.4
Seabirds			**9.2**	**-**	**-**	**-**	**0.2**	**-**
Phalacrocorax spp. *Microcarbo* sp.	Cormorant spp.	Pelagic	7.8	-	-	-	-	-
Morus capensis	Cape Gannet	Pelagic	0.7	-	-	-	-	-
Larus dominicanus	Kelp Gull	Pelagic	0.4	-	-	-	-	-
Spheniscus demersus	African Penguin	Pelagic	0.2	-	-	-	<0.1	-
Unidentified seabirds	-	-	-	-	-	-	0.2	-
Crustaceans			**0.4**	**-**	**-**	**-**	**17.7**	**100**
Stomatopoda	Mantis shrimp (Squilla)	Demersal	-	-	-	-	3.5	55.7
Jasus lalandii	West-coast rock lobster	Demersal	-	-	-	-	2.9	1.9

Unidentified crustaceans	-	-	0.4	-	-	-	11.3	42.4

*These species were identified as the closest relative species possible

Spatial variation

There was an overall numerical abundance composition (88.1%NA) of the top four prey species (anchovy, sardine, horse mackerel, hake) in the Cape fur seal diet under the three study regions, but there were slight differences in their ranking. Here, anchovy (67.6%NA) was the most consumed prey species, followed by horse mackerel (11.8%NA), sardine (5.1%NA) and hake (3.3%NA). There were 28 prey species (21 fish, 4 cephalopods, 3 seabirds) identified in 2269 scat samples in the St Helena Bay region, with horse mackerel (13.7%NA) being the most consumed, followed by anchovy (9.0%NA), hake (3.0%NA), and sardine (0.9%NA). Species diversity was greatest between Saldanha Bay and the Cape Agulhas region, with 51 prey species (41 fish, 6 cephalopods, and 4 seabirds) identified from 1643 scat samples. The East of Cape Agulhas region had the lowest diversity with only 15 prey species (13 fish, 1 cephalopod, 1 seabird) identified, but sampling effort was much less in this region, with only a total of 253 scat samples examined (Table 2.3). There was a significant difference in prey composition across the different regions (ANOSIM, $R = 0.094$, $p = 0.01$). However, the low R value indicates that there was as much difference in prey composition within the respective regions as there was between the regions.

Seasonal variation in the regions

There were significant seasonal differences in the diet of Cape fur seals between the upwelling and non-upwelling seasons in St Helena Bay (PERMANOVA, $F = 44.8$, $df = 1$, $p = 0.002$, Figure 2.6) and from Saldanha Bay to Cape Agulhas (PERMANOVA, $F = 3.83$, $df = 1$, $p = 0.01$, Figure 2.6), while there was no significant seasonal difference in the region east of Cape Agulhas (PERMANOVA, $F = 1.02$, $df = 1$, $p = 0.39$, Figure 2.6) as the sample size was too small to detect a difference. There was more anchovy in the diet of seals in the non-upwelling season, while “other” species were higher in proportion during the upwelling season in all three regions (Figure 2.6).

In the upwelling season, consumption of anchovy decreased in dominance across all three regions (Figure 2.6). Sardine consumption remained constant in St Helena Bay and from Saldanha Bay to Cape Agulhas in both seasons but decreased in the region east of Cape Agulhas (Figure 2.6).

Horse mackerel consumption was greater during the upwelling season at St Helena Bay colonies (Figure 2.6), but not during the non-upwelling season farther south or east (Figure 2.6). Hake consumption increased during the upwelling season and across all study regions (Figure 2.6). The “other fish” prey species that were infrequent in the diet of Cape fur seals, were consumed more during the upwelling

season in all three study regions: St Helena Bay from 12.0%NA to 18.0%NA, Saldanha Bay to Cape Agulhas from 14.0%NA to 19.0%NA, and east of Cape Agulhas 26.0%NA to 52.0%NA. There was also an increase in the consumption of "other fish species" east of Cape Agulhas during the upwelling season, when the consumption of anchovy and sardine was low.

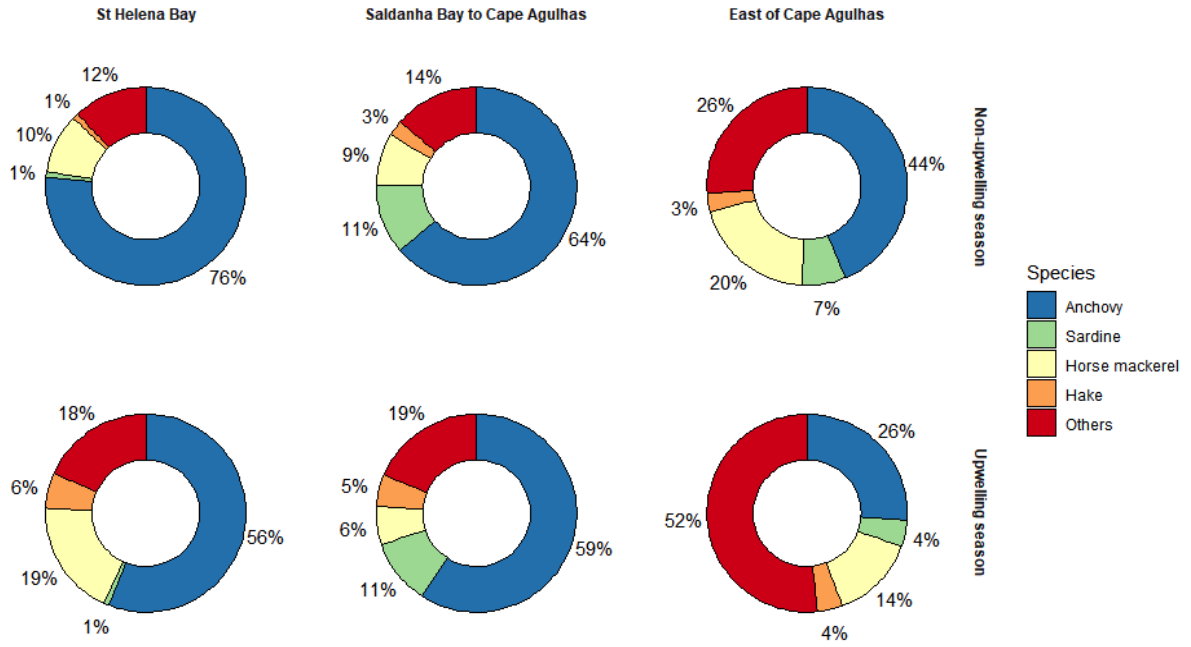

Figure 2.6: Seasonal differences in the numerical abundance (%NA) of the four key prey species of Cape fur seals from scats during the upwelling and non-upwelling seasons and across the three study regions from 2010 to 2019.

Fish size and mass distribution

Of the four key fish prey species in the Cape fur seal diet, anchovy and sardine were the smallest, whereas hake and horse mackerel were the largest (Table 2.5, Figure 2.7). The size distribution of anchovy, horse mackerel, hake, and sardine consumed by fur seals differed significantly among the three regions ($p<0.05$, Table 2.5; 2.6). Cape fur seals in St Helena Bay consumed larger amounts of anchovy and hake compared to anchovy and hake in the Saldanha Bay to Cape Agulhas and east of Cape Agulhas regions (Table 2.6). The Cape fur seals in the Saldanha Bay to Cape Agulhas region consumed larger sardine (165.9 ± 60.7 mm) and horse mackerel (112.8 ± 63.2 mm) compared with sardine (64.9 ± 31.3 mm) and horse mackerel (70.3 ± 39.9 mm) at the east of Cape Agulhas region and St Helena Bay (Table 2.6).

At the most sampled colonies (Lambert's Bay, Jutten Island and Geyser Rock, Table 2.3), larger anchovy and hake were consumed by fur seals at Lambert's Bay and Geyser Rock (Table 2.7), compared with

Jutten Island (anchovy 88.3 ± 18.5 mm; hake 141.9 ± 68.6 mm), while seals consumed larger sardine and horse mackerel at Geyser Rock and Jutten Island (Table 2.7), compared with Lambert's Bay (sardine 100.5 ± 63.6 mm; horse mackerel 74.0 ± 41.4 mm).

Table 2.5: Sizes of the four key fish prey species in the diet of Cape fur seals off South Africa from 2010 to 2019 based on extrapolation from the otolith sizes in their scats.

Fish species	Total length (mm)		Mass (g)	
	Mean ± SD	Range	Mean ± SD	Range
Anchovy	105.3 ± 33.2	17.1 – 249.8	10.5 ± 12.2	0.1 – 163.0
Sardine	146.4 ± 68.5	21.9 – 250.0	43.2 ± 42.5	0.4 – 135.6
Horse mackerel	82.8 ± 48.7	6.7 – 296.6	10.9 ± 24.9	0.1 – 245.9
Hake	143.1 ± 85.3	9.1 – 393.7	45.9 ± 79.3	1.2 – 452.1

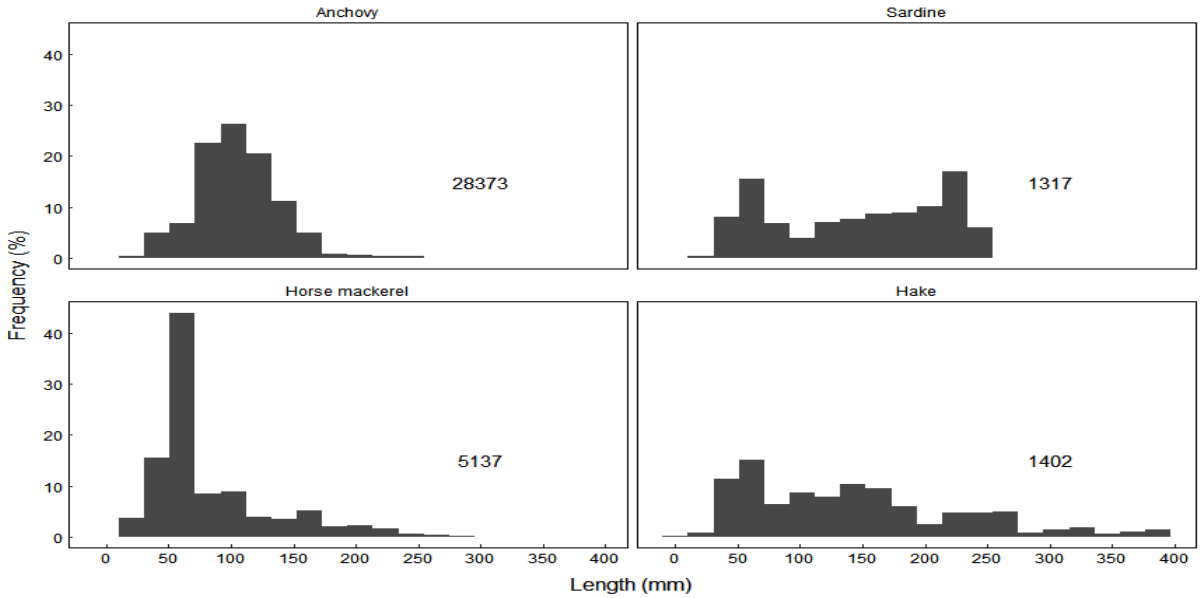

Figure 2.7: Fish total length-frequency (mm) distribution of four key prey fish species consumed by Cape fur seals off South Africa from February 2010 to October 2019.

Table 2.6: Regional differences in the sizes of the four main fish species in Cape fur seal scats.

Species	St Helena Bay	Saldanha Bay to Cape Agulhas	East of Cape Agulhas	X^2-value+
	Mean ± SD	Mean ± SD	Mean ± SD	
Anchovy	108.1 ± 31.6	100.9 ± 32.8	101.9 ± 60.6	571.3***
Sardine	104.9 ± 64.1	165.9 ± 60.7	64.9 ± 31.3	425.6***
Horse mackerel	73.9 ± 41.4	112.8 ± 63.2	70.3 ± 39.9	623.9***
Hake	157.9 ± 90.6	136.2 ± 82.9	58.6 ± 26.6	132.5***

Significance based on the Kruskal-Wallis test was used for significant difference between the four prey species. **p<0.05, **p<0.01 and ***p<0.001* indicate significant difference.

Table 2.7: Differences in the sizes of the four main fish species in Cape fur seal scats from the most regularly sampled breeding colonies (see Table 2.2).

Species	Lambert's Bay	Geyser Rock	Jutten Island	X^2-value+
	Mean ± SD	Mean ± SD	Mean ± SD	
Anchovy	108.09 ± 31.57	116.06 ± 35.51	88.29 ± 18.49	2258.4***
Sardine	100.45 ± 63.61	174.88 ± 61.59	137.54 ± 36.99	185.93***
Horse mackerel	73.98 ± 41.41	137.55 ± 61.76	83.66 ± 46.44	533.76***
Hake	157.33 ± 90.66	224.08 ± 128.51	141.89 ± 68.55	13.74**

Significance based on the Kruskal-Wallis test was used for significant difference between the four prey species. **p<0.05, **p<0.01 and ***p<0.001* indicate significant difference

Diet of Cape fur seals from stomach content samples (1974-1996)

The species composition based on stomach samples was largely similar, but scats recorded more species (at least in part because of larger number of scat samples collected). Stomach content samples total species richness was lower than that of scats, 22 fish, 5 cephalopods, 2 crustaceans, and 1 seabird (Table 2.4) were only recorded in the 2 336 stomach samples collected between 1974 and 1996. Only 1888 stomach samples contained fish species, with pelagic goby being the overall dominant species (55.0%NA), followed by anchovy (18.6%NA), lanternfish (9.7%NA), horse mackerel (7.2%NA), sardine (3.4%NA) and hake (2.9%NA; Table 2.4). Among non-fish prey, seabirds were consumed less often than cephalopods and crustaceans.

Proportions of key species in stomach and scat samples

Sardines showed a significant decreasing trend in %NA in stomach content samples from 1974 to 1989 but increased in 1990 – 1996, then decreased again in 2010 to 2019 (Mann-Kendall test, τ = 0.52, n = 16, p = 0.01, Figure 2.8). There was a consistent pattern in the consumption of hake (Mann-Kendall test, τ = -0.03, n = 19, p = 0.89, Figure 2.8), with most consumption of pelagic goby recorded between 1974 and 1989 (Mann-Kendall test, τ = -0.23, n = 17, p = 0.22, Figure 2.8), while consumption of anchovy (Mann-Kendall test, τ = 0.05, n = 18, p = 0.82, Figure 2.8) was also relatively important during 1981 – 1989 and mostly consumed from 1990 to 2019. Horse mackerel (Mann-Kendall test, τ = 0.05, n= 15, p= 0.84, Figure 2.8) and lanternfish (Mann-Kendall test, τ = 0.18, n= 13, p= 0.43, Figure 2.8) consumption was consistent since the 1981 – 2019 period.

The 2010 to 2019 scat samples showed no significant trend in the consumption of hake (Mann-Kendall test, τ = 0.33, n = 10, p = 0.21, Figure 2.8), anchovy (Mann-Kendall test, τ = 0.07, n = 10, p = 0.86, Figure 2.8), pelagic goby (Mann-Kendall test, τ = 0.11, n = 9, p = 0.75, Figure 2.8, excluding 2012 when no

pelagic goby was recorded) or horse mackerel (Mann-Kendall test, τ = -0.47, n = 10, p = 0.07, Figure 2.8). A decrease was observed in the number of sardines consumed (Mann-Kendall test, τ = -0.7, n = 10, p = 0.07, Figure 2.8), offset to some extent by an increase in lanternfish (Mann-Kendall test, τ = 0.51, n = 10, p = 0.05, Figure 2.8), and this increasing trend lasted up to 2016 and then decreased. A significant difference (r = 0.19, p = 0.01) in terms of species diversity was observed in the diet of Cape fur seals between the two sampling methods (Tables 2.3, 2.4, Figure 2.8). The low R value shows that there is much difference between the sample methods as there are differences within the diet samples groups, suggesting that stomach and scat samples were different from each other. Although there were no differences in species composition in the diet of Cape fur seals, there was a difference in the proportion of prey species consumed (Table 2.4, Figure 2.8).

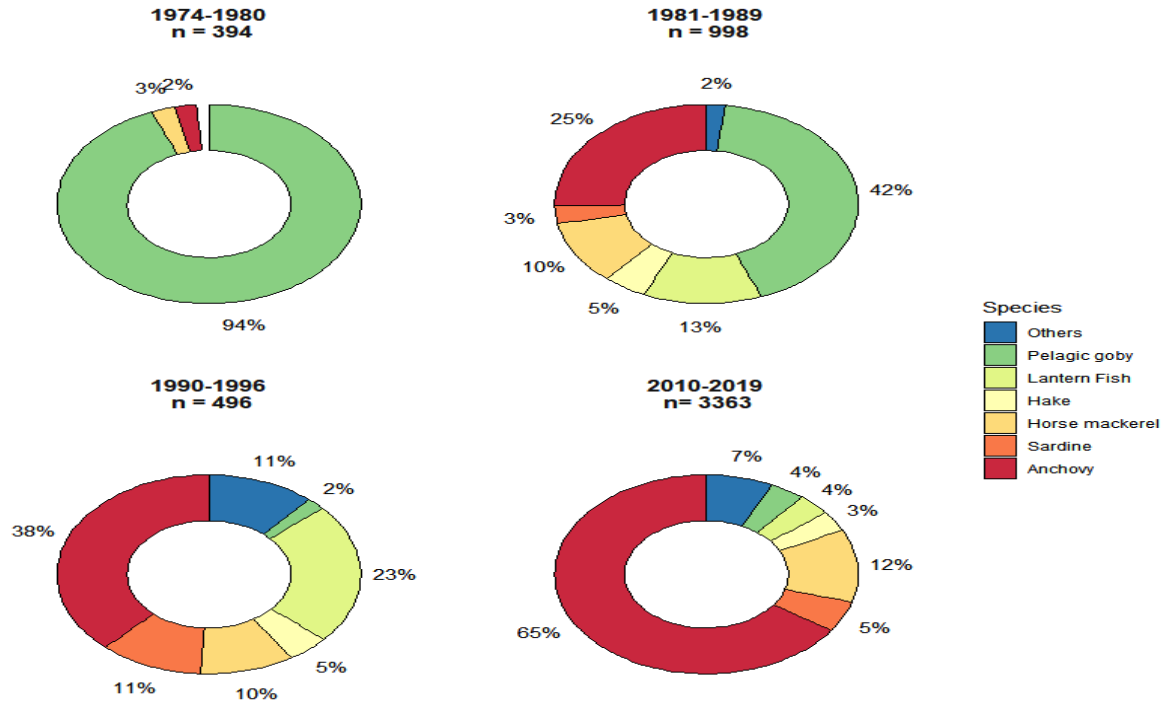

Figure 2.8: Numerical abundance (%NA) of the six key fish prey species identified from the diet of Cape fur seals based on stomach content samples collected from 1974 to 1996 and scats from 2010 to 2019. The (*n)* represents the number of samples collected that had the key species and others.

2.5 Discussion

The Cape fur seal has the largest marine top predator biomass in the southern Benguela region (Shannon *et al.,* 2003; Kirkman *et al.,* 2019). Fur seal diet provides information about fish stocks and overall marine ecosystem variability in the region (Montevecchi *et al.,* 1998; Furness, 2002; Iverson *et al.,* 2007; Fossi

et al., 2012; Chiaradia *et al.*, 2014; Gosch *et al*., 2019). As these predators' shape food-chain, survival and reproductive success are mainly dependent on prey abundance (Kirkman *et al.,* 2016; Masiko *et al.,* 2021). The availability for energy transfer provides feedback on the presence of species in the ecosystem and their distribution, bringing ecological stability (Breed *et al.,* 2009; Gosch *et al*., 2019; Kirkman *et al.,* 2019; Masiko *et al.,* 2021). Thus, this is a first study to investigate the diet of Cape fur seals across different breeding colonies off the coast of South Africa and is the first to utilise the two methods (stomach contents and scats analyses) to try to infer long-term changes in the fur seal's diet.

Stomach contents versus scat analysis

Both techniques used to infer diet mainly rely on the identification of hard part remains of prey items (Goldsworthy *et al*., 1997; Klages and Bester, 1998; Robinson *et al.,* 2002). Historically, only stomach content sampling was used to study the diet of fur seals (David, 1987; Punt and Butterworth, 1995; Mecenero *et al.,* 2006; Huisamen *et al.,* 2012), although, this study tried to compare the non-invasive scat analysis method with past stomach content sampling (David and Rand, 1986; Oosthuizen, 1991; Mecenero *et al.,* 2006a; Barnet *et al.,* 2010; Huisamen *et al.,* 2012). Scat analysis has mostly been used in South Africa and Namibia to study the diet of Cape fur seals, since they are the main countries where they breed (Mecenero *et al.,* 2006a, Huisamen *et al.,* 2012; Hlati, 2015; Gumede, 2019), because the method allows the collection of large sample sizes, is inexpensive, and can be used to compare diet across and within spatio-temporal variation (de Bruyn *et al*., 2003; Trites and Joy, 2005). The method underestimates the presence of crustaceans and cephalopods in the diet and can result in inaccurate estimates of fish size due to erosion of otoliths (David, 1987; Gales *et al.,* 1993; Yonezaki *et al.,* 2003; Mecenero *et al.,* 2010). In this study, erosion conversion factors were used to correct for partial or total erosion of the otolith beauset of digestion (Mecenero *et al*., 2006a; Huisamen *et al.,* 2012). Crustaceans and cephalopods are particularly under-represented in scats, because their carapaces are often regurgitated (Lake *et al.,* 2003; Mecenero *et al.,* 2006a; Kirkwood *et al.,* 2008; Huisamen *et al.,* 2012). On the other hand, stomach content analysis allows the identification of mainly fresh prey in reasonably good condition and the identification of secondary prey species (Trites and Joy, 2005). Regardless of biases associated with both the scat and stomach content analyses, prey species identified in scat samples, such as teleost fish, remain represented in a similar proportion to when they were consumed (Harwood and Croxall, 1988).

Diet composition and inter-annual variation in scat contents (2010 – 2019)

Cape fur seals forage on a wide diversity of prey species, from pelagic, demersal to benthic species; including fish, cephalopods, seabirds, and crustaceans (Payne and Selzer, 1989; Bowen and Harrison,

1996; Mecenero *et al.,* 2006a, Huisamen *et al.,* 2012). This study was conducted against the backdrop of the changing southern Benguela system. Anthropogenic changes in the system were first reported in 1960s, when the suspected collapse of fish stocks first became apparent, they were actually changes in line fish dating back much earlier 1960s. Subsequent changes in environmental conditions in the early 2000s resulted in further alterations to the southern Benguela system (Howard *et al.,* 2007; Hutchings *et al.,* 2012; Jarre *et al.*, 2013). Various studies have investigated aspects of these climate-driven changes, including plankton (Verheye *et al*., 2016), coelenterates (Wright *et al.,* 2021), and seabirds (Crawford *et al.,* 2015). These changes have resulted in a shift in fur seal breeding localities, with new colonies being established (Kirkman *et al.,* 2013; 2016; 2019). As a result, their diet was also expected to have changed due to prey shift (Kirkman *et al.,* 2019).

Cape fur seals can dive to depths of up to 450 m, which enables them to feed on pelagic and demersal fish species, including species that undergo a diel vertical migration (Kirkman *et al.,* 2019). As most fur seal dives are shallower than 50 m, fish species are found closer to the surface, while half of the dives occur at night, which reduces foraging energy expenditure by Cape fur seals (James, 1987; Roel and Armstrong, 1991; Pillar and Barange, 1995; Beckley *et al.,* 1999; Misund *et al.,* 2003; Axelsen *et al.,* 2004, Kirkman *et al.,* 2019; Botha *et al*., 2020). This indeed suggests that half of the feeding occurs at night (Castley *et al*., 1991; Kirkman *et al.,* 2019) in response to fish (pelagic, mesopelagic, demersal) migrating to the surface during the night (Thomas and Schulein, 1988; David, 1989; Bacheler *et al.,* 2019; Christiansen *et al.,* 2019; Kirkman *et al.,* 2019). Cape fur seals are generalist feeders that can switch prey based on availability and can travel at least 220 km from their colonies to forage (Kirkman, 2016a; Botha *et al*., 2020). Hence, the importance of small pelagic fish species (i.e. anchovy, sardine, pelagic goby) in this study is consistent with the findings of previous fur seal diet studies in southern Africa (Stewardson, 2001; Mecenero *et al.,* 2006; Huisamen *et al.,* 2012; Connan *et al.,* 2014; Kirkman *et al.,* 2019), and they are the most abundant pelagic species in South African coastal waters (van der Lingen *et al*., 2006; Hutchings *et al.,* 2009; Kirkman *et al*., 2016), which explains their dominance in the diet.

Cape fur seal diet varied among years (Figures 2.2, 2.3, 2.4, 2.5), which might be due to variation in local prey availability (de Bruyn *et al*., 2003; Mecenero *et al.,* 2006b; Reisinger *et al.,* 2018; Kirkman *et al.,* 2019), but could also be due to patchy scat sampling (Table 2.2). Inter-annual variability in fish prey species could be linked to variability in upwelling (Lamont *et al*., 2016), sea surface temperature, and chlorophyll concentration (Dunstan *et al*., 2018). Furthermore, the timing, distribution and availability of prey resources to predators in marine ecosystems are influenced by various oceanographic factors (Dorman *et al.*, 2015), which induce generalist feeder behaviour of Cape fur seals, as there is diversity of prey species to feed on. In the current study, horse mackerel dominated fur seal diets in 2011, while

the contribution of hake remained more or less constant over time. Anchovy increased in the scat samples throughout the study period, whereas sardines decreased in importance (Figure 2.3, 2.4). The low consumption of sardine by Cape fur seals and the large amounts of anchovy found in the diet were similar to the findings at Robberg Ledges by Huisamen *et al.* (2012); at Lamberts Bay and Geyser Rock (2010-2014) by Hlati (2015); and at Lambert's Bay (2015-2018) by Gumede (2019), taking into consideration that Hlati (2015) and Gumede (2019) diet studies data were incorporated in this study. Similar trends in anchovy and sardine consumption have been recorded in the diets of other marine predators in southern Benguela, such as Cape Cormorants (Masiko *et al*., 2021). The results could be due to changes in the availability of anchovy and sardine*,* as both species are observed mostly as a shoal inshore compared with any other fish pelagic species, which are more accessible to marine predators such as seabirds and Cape fur seals (Roy *et al*., 2007; Coetzee *et al.,* 2008).

Spatial variation in the regions

Anchovy were largely consumed from St Helena Bay to Cape Agulhas (Figure 2.6); this might be due to the western and eastern Agulhas Bank spawner population and the apparent increase in anchovy biomass west of Cape Agulhas (Cape Columbine) (Shabangu *et al.,* 2012; van der Sleen *et al.,* 2018). Sardine were more often recorded in the diet from Saldanha Bay to the south coast (Figure 2.7), following overexploitation of sardine stocks off the west coast (Coetzee *et al.,* 2008; 2019), and changes in environmental and oceanographic conditions (Fairweather *et al.,* 2006a; Coetzee *et al*., 2008; Hutching *et al*., 2012; Jarre *et al.,* 2013). Sardine biomass is affected by variability in recruitment, as environmental changes may affect the transporting of eggs and larvae, and feeding conditions, especially off the west coast (de Moor *et al*. 2011; de Moor, 2020; Coetzee *et al.,* 2019). The prevalence of sardine in seal diets off the south coast and north of Saldanha Bay is due to the sardines' spawning grounds off the west and south coasts before migrating to the east coast (Beckley and van der Lingen, 1999; Connell, 2010; de Moor, 2018; Freon *et al*., 2010; McGrath *et al.,* 2020; van der Lingen *et al*., 2010a; 2010b; van der Sleen *et al*., 2018).

Horse mackerel were mostly present in the scat samples collected from west coast seal colonies, as this fish species is mainly found along the continental shelf edge and upper slope of the west coast from Namibia south to the Agulhas Bank (Kerstan and Leslie, 1994; Axelsen *et al*., 2004; Mecenero *et al.,* 2006a; McLaverty, 2012; Johnston and Butterworth, 2019). According to Figure 2.6, horse mackerel is also important in terms of %NA in the east of Cape Agulhas colonies, which is in correlation with the occurrence of the species in this region. Hake, however, were consumed across all study regions due to the large distribution of the species around the South African coast (Payne and Punt, 1995; Payne *et al.,*

2001; Kirkman *et al.,* 2013). *Merluccius paradoxus* occurs from northern Namibia to southern Mozambique and *M. capensis* from southern Angola to northern KwaZulu-Natal (Rademeyer *et al*., 2008a; Pillar and Wilkinson, 2015). In this study, hake consumed by fur seals could not be identified to species, but previous diet studies have found that both species are consumed (Mecenoro *et al*. 2005; 2006a; 2006b; Huisamen *et al.* 2012; Hofmeyr 2015; Mwaala 2022).

Seasonal variation

Seasonal fluctuations were observed in the diet composition (Figure 2.6). During the spring-summer upwelling season, there was a decrease in the consumption of sardine and anchovy across all the study regions, while hake and "other species" consumption increased, and horse mackerel only increased in two regions (Figure 2.6). The seasonal fluctuations among key fish species in the Cape fur seal diet are related to factors including the fishes' life stages (spawning, recruits), environmental conditions (oceanographic conditions as drivers of prey species availability and distribution), and abundance of seals in a certain region (de Bruyn *et al*., 2003; Schwarz *et al.*, 2013; Jarre *et al.,* 2015). Figure 2.6 shows that when dominant species (i.e., anchovy, horse mackerel, sardine, hake) were scarce in the diet, seals consumed mostly "other species" which speaks to the Cape fur seal's opportunistic foraging behaviour. The changes in prey composition during the upwelling season are based on fish availability and abundance, for example, anchovy and sardine spawn during the upwelling season (Pillar *et al*., 1998; Beckley and van der Lingen, 1999; van der Lingen and Hugget, 2003; Miller *et al.,* 2006), and hence they are less consumed during the upwelling season by seals. Anchovy spawn from the western Agulhas Bank to the west coast (Pillar *et al.,* 1998), and after spawning they, migrate east to the central and eastern bank (Hampton, 1992). This eastward migration decreases the abundance, and hence the availability of these species to fur seals.

The study found that anchovy was largely consumed across all study regions during the non-upwelling season (Figure 2.6). On the other hand, sardines spawn on the west and south coasts and migrate to the east coast after spawning (Beckley and van der Lingen, 1999; Connell, 2010; Freon *et al*., 2010; van der Lingen *et al*., 2010a; 2010b). A similar trend was observed in this study east of Cape Agulhas (Figure 2.6), were sardine consumption by Cape fur seals was higher during the non-upwelling season (7%NA) than in the upwelling season (4%NA). The large sardine consumption during the non-upwelling season east of Cape Agulhas might be due to the "sardine run" that normally occurs off the east-coast after the sardine spawning season (van der Lingen *et al*., 2010a, 2010b). Horse mackerel was consumed more in the St Helena Bay region during the upwelling season, and mostly consumed at the Saldanha Bay to east of Cape Agulhas during the non-upwelling season. This benthopelagic species is abundant in the

west and southeast coast of South Africa (Hecht, 1990; Kirkman *et al.,* 2013), and its vertical migrations decrease during winter with the spawning peak between June and November (ICES, 2005). This explains the results from this study, as there was a slight difference in horse mackerel consumption between the seasons. Hake was mostly important in the fur seals' diet during the upwelling season (Figure 2.6). Hake are serial spawners in autumn-winter (Jansen *et al.,* 2015), which is when they were consumed least by fur seals, presumably due to a lack of availability.

Fluctuations in prey distribution, abundance, and perhaps calorific value may help to explain spatio-temporal variation in prey species in the diet of Cape fur seals. Marine ecosystems are diverse and vary over time and across regions (Hutchings *et al.,* 2009; Kirkman *et al.,* 2016b), inducing changes in prey availability (Boyer *et al.,* 2001; Shannon *et al.,* 2020) and affecting predator preferences (Balmelli & Wickens, 1994; Bowen *et al.,* 2002; Ludynia *et al.,* 2010).

Fish size and mass distribution

Small, immature sardine were eaten in all regions but mature sardine was only eaten in the central region between Saldanha Bay and Cape Agulhas (Table 2.6; 2.7), which is the spawning ground for the western sardine stock (Coetzee *et al*., 2020). Mature anchovy was mostly eaten in St Helena Bay and east of Cape Agulhas (Table 2.6; 2.7), which are the spawning grounds for the western and eastern anchovy stocks, respectively (Coetzee *et al*., 2020; Richardson *et al*., 1997). Mature horse mackerel were mostly eaten between Saldanha Bay and Cape Agulhas (Table 2.6; 2.7). This might involve both stocks of horse mackerel spawners found in southern Africa: one spawning on the Agulhas Bank and one off the west coast (Williamson and Norman, 2020). Maturing juveniles migrate northward towards Angola (west coast) and south toward the Agulhas Bank (south-east) (Williamson and Norman, 2020). Mature hake were eaten from St Helena Bay to Cape Agulhas (Table 2.6; 2.7), where most benthic trawl fishing occurs. This suggests that Cape fur seals scavenge on mature fish from commercial fishing vessels (Payne and Punt, 1995; Payne *et al.,* 2001; Rademeyer *et al.,* 2008a; Kirkman *et al.,* 2013; Durholtz *et al.,* 2015).

Cape fur seals consumed large numbers of small pelagic fish (anchovy, sardine). These species serve as a primary food source, which might result from their shoaling behaviour, small size, availability and accessibility (Thomas and Schulein, 1988; Roel and Armstrong, 1991; Hewitson and Cruickshank, 1993; Kirkman *et al.,* 2013; Huisamen *et al.,* 2012). The length frequency distribution of both anchovy and sardine in the diet suggests that mostly juveniles to adults (<250 mm) are targeted by seals (Figure 2.7). On the other hand, horse mackerel (shoal) and hake (not as a shoal) can only be consumed individually due to their larger sizes (Burmeister, 2001; Mecenero *et al*., 2006a), as these species are hard to catch individually but rather scavenge from trawlers, longlines, and handlines (which is not easy to catch)

(Kirkman *et al.,* 2013). Horse mackerel and hake, mainly juveniles to young adults >250 mm was targeted (Table 2.4, 2.4, Figure 2.7)

A similar size target was observed by Mecenero *et al.* (2006a), who reported that juvenile horse mackerel migrate from southern Namibia to the South African coast and increase in size (Axelsen *et al.,* 2004; Williamson and Norman, 2020), which explains why juvenile horse mackerel are found in the Cape fur seal diet. Overall, juveniles of the key fish species were targeted more in the region from St Helena Bay to Cape Agulhas than east of Cape Agulhas (Table 2.6). This is because the Agulhas Bank east of Cape Agulhas is a spawning ground for many fish species (mostly pelagic fish), as spawners move to the nursing grounds on the west coast and recruits migrate down to the west coast closer to the Agulhas Bank (Hutchings *et al.,* 1998; Roy *et al.,* 2007). The movement of recruits allows Cape fur seals on the south coast to have access to both juvenile fish and spawner populations that reside on the Agulhas Bank (Barange *et al.,* 1999; Huisamen *et al.,* 2012).

Comparison of diet from stomach contents and scat samples

The diet composition of the Cape fur seal has not shown substantial changes between 1974 – 1996 and 2010 – 2019, based on comparison of stomach contents and scat samples. Similarly, the fur seal diet study conducted by David (1987) and unpublished DFFE data based on stomach content analysis and a recent study by Huisamen *et al.* (2012) based on scat analysis show the same diet composition (fish, cephalopods, crustaceans, seabirds) with fish predominating the diet. Although there were no substantial changes in the diet composition, there were changes in the proportions and occurrence of prey species in the fur seal diet. For example, high proportions of pelagic goby were observed between 1974 and 1996, whilst its occurrence in the diet was trivial from 2010 to 2019, when anchovy dominated the diet (Table 2.4, Figure 2.8). From 1974 to 2019, there has been an increase in the consumption of seabirds and in the diversity of fish species consumed by Cape fur seals (Table 2.4). The results might be influenced by fishing pressure, as the preferred prey species (i.e. sardine and anchovy) biomass has decreased, and fur seals switch the prey species based on prey available as they are generalist feeders. Another diet study based on scat analysis of Antarctic (*Arctocephalus gazella*) and Subantarctic (*A. tropicalis*) fur seals at Marion Island showed no long-term changes in their diet, but the fur seal diet varied seasonally and annually as a result of oceanographic conditions and prey availability (Reisinger *et al.,* 2018).

Although there is diet variability, the infer of stomach and scat analysis based on %NA identified anchovy, sardine, horse mackerel, and hake, lantern fish and pelagic goby as the most important prey species (Table 2.4, Figure 2.8). The same prey species were of great significance in the diet of Cape fur seals in

South Africa (David 1987) and unpublished DFFE data (based on stomach content analysis) and Huisamen *et al.* (2012) (based on scats samples); and in Namibia by Mecenero *et al.* (2006; 2006a; 2006b). The opportunistic foraging behaviour of Cape fur seals explains the considerable variation in their diet, which might result from environmental variability and species scarcity that cause spatio-temporal fluctuations in prey species (Dorman *et al*., 2015; Kirkman *et al.,* 2019). It is worth noting that changes in prey proportions and abundance are influenced by sampling methods and sampling period (de Bruyn *et al.,* 2003; Huisamen *et al.,* 2012; Wcisel, 2013; Reisinger *et al*., 2018). These differences likely result from differences in sample size (more scat samples taken = more prey species), and differences in the proportions of major groups likely reflect differences in prey retention in gut vs. scats. For example, pelagic goby was the dominant prey species in 1974 – 1989, whereas anchovy dominated from 1990 in stomach samples and 2010 to 2019 in the scat samples collected (Table 2.4, Figure 2.8). In addition, the region of occurrence influenced the availability of species such as anchovy, which are commercially important species for the South African fishing industry (Huisamen *et al.,* 2012; Kirkman *et al*., 2013; 2019; Hlati, 2015), whereas pelagic goby is not.

2.6 Conclusions

This study provided useful insights into variability in the diet of Cape fur seals on the South African coast; identified prey species, occurrence, abundance, and preferred species based on a spatio-temporal context; and how species proportions in the diet have changed over time from the stomach content sampling method was used (1974 1996) to the current method of scat sampling (2010 2019). Further studies are essential for understanding Cape fur seal diet variability in the southeast coast (Eastern Cape), as there has not been enough information to conclude what fur seals are foraging in this region of South Africa. Therefore, continuous monitoring of seal diet using the scat analysis technique is recommended to track the seals' responses to ecosystem changes (which might be a potential indicator of environmental changes on a large-scale), track long-term changes in prey species abundance (Huisamen *et al.,* 2012), and complement other monitoring data, including temporal and spatial trends in numbers. Additional, using data from scat analysis is essential to obtain information about the dominance of teleost prey species in the diet of fur seals, which in turn may be used to infer interactions between commercial fishery activities and fur seal predation on teleost species (Huisamen *et al.,* 2012). Hence, the next chapter deals with the assessment of potential competition between Cape fur seal and commercial fisheries, based on seal consumption and fisheries catches.

Chapter 3: Potential competition and overlap between Cape fur seal diet and commercial fisheries catches off the South African coast (2010 – 2019)

3.1 Abstract

In the Benguela Current Ecosystem, Cape fur seals and fisheries are important predators and potential competitors for harvested fish species. The increase in fur seals during the 20th century could have reduced catches and catch rates for commercial fisheries off southern Africa, whilst overexploitation of prey species could impact the seal's population and other marine predators. Ecosystem changes are also associated with global changes that influence fisheries, which might affect the diet of top predators such as Cape fur seals due to changes in prey availability. Decreases in food availability have a bottom-up effect on fur seal populations, and seal survival is dependent on their foraging success. This chapter assesses potential competition and overlap for food between Cape fur seals and commercial fisheries at three South African colonies (Lambert's Bay, Jutten Island and Geyser Rock) from 2010 to 2019 using data derived from fur seal scats (Chapter 2), purse-seine fishery landings, and acoustic biomass estimates of small pelagic fish from the Department of Forestry, Fisheries and the Environment (DFFE) annual surveys. Among commercially targeted fish pelagic species (anchovy, sardine, horse mackerel), Cape fur seals mainly consumed juveniles to early adult fish, whereas commercial landings mostly targeted juveniles. There was an overlap in prey size caught by fur seals and commercial landings for anchovy and horse mackerel, as well as potential competition for sardine. Significant positive relationships were found between anchovy, sardine and horse mackerel consumed by seals and purse-seine fishery catches, but no relationship for red-eye. The mass proportion of anchovy and sardine consumed by fur seals had no significant relationship with the estimated acoustic biomasses of these species across the three study colonies (2010 – 2019). Sardine and anchovy consumed had no significant correlation with the recruit biomass estimates, but anchovy consumed in the upwelling season was positively correlated with spawner biomass estimates. However, the fur seal diet in spring-summer is not well characterised given the lack of scat data during the mid-summer pupping season. Overall consumption of anchovy increased in the Cape fur seal diet, and there was no significant correlation with the overall anchovy acoustic biomass estimate. In contrast, overall sardine consumption decreased in the fur seal diet and was correlated with a decrease in acoustic biomass estimates. These results provide evidence of competition for sardine between Cape fur seals and fisheries between 2010 and 2019, as there was an overlap. In addition, the purse-seine fishery catches correlated with anchovy, sardine, and horse mackerel found in the diet of Cape fur seals.

3.1 Introduction

The last century has been marked by a rapid decline in the health of many marine ecosystems due to exploitation, invasive species, climate change, pollution, and eutrophication (Smith, 2003; Halpern *et al*., 2008). South Africa has one of the most diverse, dynamic, and highly productive marine environments in the world because of the merging of three oceans: the Atlantic Ocean (upwelling in the Benguela Current along the west coast), the Indian Ocean (warm Agulhas Current on the east coast), and the Southern Ocean (west-east flowing Antarctic Circumpolar Current) (Griffiths *et al.,* 2010; Sink *et al.,* 2019; Wepener and Degger, 2019). These diverse environments support over 12 000 marine species in South African waters (Sink *et al.,* 2019; Wepener and Degger, 2019). The marine environment plays a crucial role for both humans and marine top predators, as it serves as a source of food that contains important nutrients (Allison, 2011; Thilsted, 2012; Beveridge *et al.,* 2013; FAO, 2018), and also serve as sole source of energy as well as nutrients for marine top predators (Williams *et al.,* 2018; Machovsky-Capuska and Raubenheimer, 2020; Martin *et al*., 2021). As for humans, fisheries are estimated to contribute at least 0.5% of the South African Gross Domestic Product (DAFF GDP sector draft, 2010a; FAO, 2018) and create employment for an estimated 27 700 people (FAO, 2018). Hence, there has been a going conflict for food resources such as fish between humans and marine top predators.

The wasp-waist ecosystem paradigm has been noticed within marine top predators on the South African coast, as the predators mostly feed on species targeted by commercial fisheries, increasing competition and overlap with commercial fisheries and are susceptible to impact from commercial fishing for food (fish) (Crawford *et al.,* 1992; Huisamen *et al.,* 2012; Masiko *et al.,* 2021). Increasing competition and conflict between commercial fisheries and marine predators such as seabirds and Cape fur seals have also been noted in South Africa (David, 1987; FAO, 2018; Sink *et al.,* 2019). As competition increases, we would expect competing species populations to decrease as well. However, in South Africa this is not the case for some marine predators (i.e. Cape fur seal) and target commercial fisheries (fish prey) populations to keep decreasing. Cape fur seals can switch diet/species due to their generalist character, which allows the species to maintain their population, but specialist predators (i.e. seabirds) and commercially targeted fisheries (i.e. anchovy, sardine) populations decrease due to food competition. The southeast and west coast of South Africa has seen, for a long time, an ongoing competition between commercial fisheries and marine predators (mainly seabirds and Cape fur seals) for small pelagic fish species (i.e. sardine, anchovy), whose stock size has decreased drastically (David, 1987; Kirkman *et al.,* 2013; FAO, 2018; Sink *et al.,* 2019).

Pelagic fish species such as anchovy, sardine, red-eye, horse mackerel, and demersal hake (*Merluccius capensis* and *M. paradoxus*) are of commercial importance in South Africa (see Chapter 2; David, 1987;

Kirkman *et al.,* 2013; FAO, 2018; Sink *et al.,* 2019), and they are also key species in the diet of Cape fur seals (David, 1987; Mecenero *et al.,* 2006a; Kirkwood *et al.,* 2008; Huisamen *et al.,* 2012; Chapter 2). At least 80%NA of the Cape fur seal diet is comprised of these commercially valuable fish (Punt and Butterworth*,* 1995; Huisamen *et al.,* 2012, Hlati, 2015; Chapter 2). However, changes in the South African coastal ecosystems (Benguela and Agulhas Current), linked to perturbation, climate changes, and exploitation of commercially valuable fish, which might have had an effect on the dietary composition of the Cape fur seal due to reduced prey abundance, availability, and distribution across the region (Watermeyer *et al*., 2016). Decreases in food availability (top-down effect) for such marine predators have led to a bottom-up effect on their populations. Post after the commercial harvesting, the Cape fur seals population increased showing recovery, and then it was stable late in 1990s to early 2000s (Hofmeyr, 2015; Kirkman *et al.,* 2016a; 2016), as off recently it seems stable or slowly declining based on the high pup's mortality rate (Botha, 2022). However, the fur seal's current population status remains unclear.

Cape fur seals can be used to predict the distribution, occurrence, and estimate abundance of pelagic fish species, as seals distribution and movement facilitate ecological processes (David, 1987; Wickens *et al.,* 1992; 1997; Balmelli and Wickens, 1994; Mecenero *et al.,* 2006a). Therefore, utilising data derived from Cape fur seal scats data (Chapter 2), fisheries and scientific fish surveys (DFFE) may give a clearer insight into fish stocks (prey in this study) in the region and the extent of the competition between fisheries and Cape fur seals, similar to the case studies of David (1987) and Wickens *et al.* (1992) who used stomach contents instead of scats, then Mecenerol *et al.,* (2006a) and Huisamen *et al.,* (2012) who utilised scats data. Previous studies by Wickens *et al.* (1992) also utilised fisheries data and seal predation to determine the seal and fisheries competition and conflict in South Africa. Therefore, this study used the scat analysis technique to identify the prey species consumed by Cape fur seals (Chapter 2). Commercial landings, purse-seine fishery, and acoustic biomass estimates of small pelagic fish species were used to assess potential competition, overlap in fish size frequency distribution between fish consumed by Cape fur seals and those caught by commercial fisheries (David, 1987; Mecenerol *et al.,* (2006a); Huisamen *et al.,* 2012). Fish stock estimates were based on acoustic surveys data, which provides relative abundance of the target species in a region, this study, small pelagic fish were targeted. Acoustic surveys consist of two data sets, recruits (autumn-winter, non-upwelling season) and spawner (spring-summer, upwelling season) data. These techniques were previously used by Huisamen *et al.* (2012) to investigate potential competition between Cape fur seals and fisheries at the Robberg Ledges colony, and Masiko *et al*. (2021) investigated Cape Cormorants dietary overlap with commercial fisheries.

This study reports on potential dietary competition and overlap for pelagic fish species between Cape fur seals and commercial fisheries in the three fur seal breeding colonies from chapter 2 that are adjacent to fishing harbours (Lambert's Bay, Jutten Island and Geyser Rock) (see Table 2.3; Chapter 2). Here the sampling focused on these colonies as they are adjacent to fishing harbours (Lambert's Bay, Saldanha Bay and Gansbaai) where fishery catches could be sampled with the exception at Lambert's Bay as there are no more landings at this site. The study investigated (1) overlap in fish size frequency distribution between Cape fur seal prey and commercial landings, (2) the relationship between the %NA of anchovy and sardine consumed by Cape fur seals and catches by the purse-seine fishery, and (3) compared spatial, temporal, and seasonal variation of anchovy and sardine mass contribution in fur seal diet with acoustic biomass estimates of pelagic fish for each study colony (spatial variation), over the study period of 10 years (temporal variation), and across the two seasons (upwelling and non-upwelling).

3.3 Methods

Study area

In this study, Cape fur seal breeding colonies adjacent to fishing harbours (Figure 2.1, Table 2.3) were Lambert's Bay (in the St Helena Bay region, Figure 2.1, Table 2.3), Jutten Island and Geyser Rock (in the Saldanha Bay to Cape Agulhas region, Figure 2.1, Table 2.3). These regions and colonies were grouped according to the Cape fur seal distributional range and breeding colonies (Chapter 2, Figure 2.1, Table 2.3). Strata and the three breeding colonies adjacent to fishing harbours were categorised, grouped and associated according to Figure 3.1; to compare the Cape fur seal diet of each colony with the fisheries catch data and the acoustic stock estimates data (spawners and recruits) (Figure 3.1). Fur seals within the St Helena Bay region (Lambert's Bay) were assumed to forage within Stratum A, and Saldanha Bay to Cape Agulhas region (Jutten Island and Geyser Rock) were assumed to forage in Stratum B and C in this study (Table 2.3, Figure 2.1, Figure 3.1).

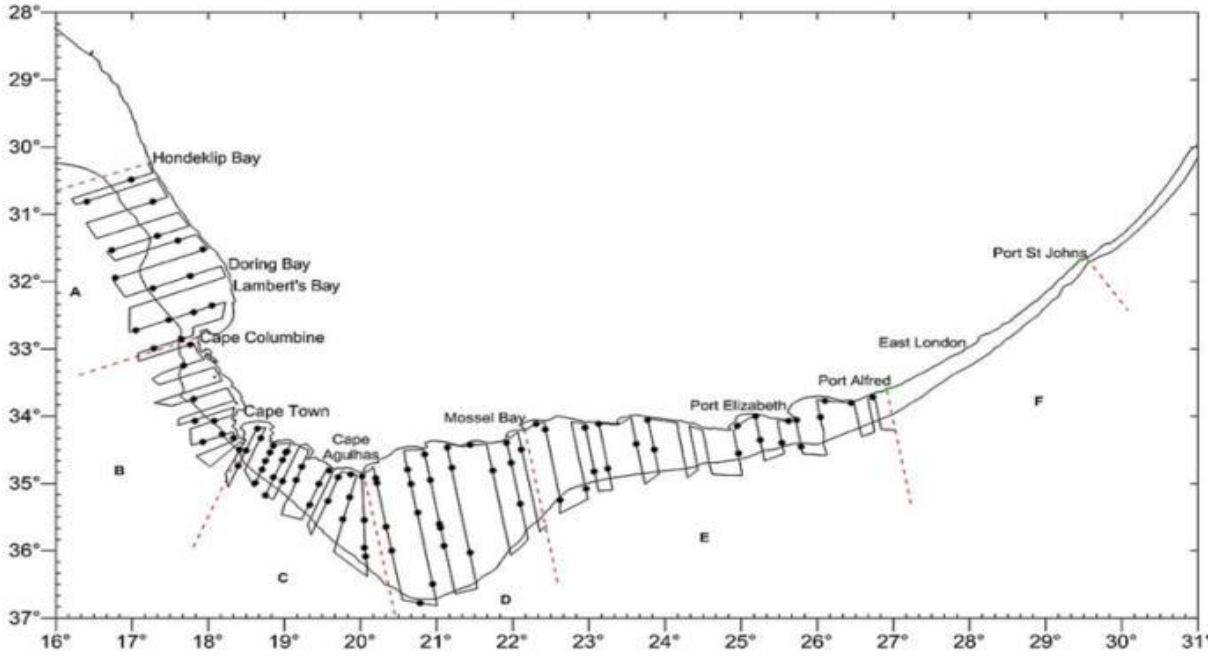

Figure 3.1: Track-line used by the Department of Forestry, Fisheries and the Environment (DFFE) for the acoustic biomass survey. The dotted lines indicate boundaries of the stratum (A, B, C, D, E, and F) for which predetermined transects were used to obtain acoustic biomass estimates of anchovy and sardine (Shabangu *et al.,* 2012).

Data collection

Cape fur seal diet data

The diet of Cape fur seal from scat samples (Table 2.1, 2.3, 2.4) was described in detail in Chapter 2, with all the methods and analysis.

Size of pelagic fish eaten by seals and caught by the fishery.

Samples of commercial fishery landings were obtained from DFFE fishery observers based at harbours where fish are landed (Fairweather *et al.,* 2006a). These samples were used to obtain information on the fish size distribution of catches (Fairweather *et al*., 2006a) (see study area in Figure 3.1). The samples were grouped according to the fishing blocks (10 x 10 nautical mile (nm)) close to the fisheries harbours (such as Lambert's Bay harbour, Saldanha Bay harbour, Gansbaai harbour) (Fairweather *et al*., 2006a) and colonies where seal scats were collected. Skippers recorded the weight of the landing samples collected from every trip made. Then a designated fisheries inspector/monitor would collect biological data such as fish length, mass, and sex from the opportunistic landing samples (David, 1987). The opportunistic samples from landings were then used to determine species constitution and fish length frequency (Fairweather *et al.,* 2006a), and these were compared with species in the diet of fur seals and

fish size consumed by Cape fur seals (Chapter 2). Harbours near the study colonies were Lambert's Bay harbour (close to Lambert's Bay), Saldanha Bay harbour (close to Jutten Island) and Kleinbaai & Gansbaai harbour (close to Geyser Rock).

Potential purse-seine fishery catches and the Cape fur seal's diet.

Pelagic purse-seine fishing is conducted almost every month in a 10 x 10 nautical mile (nm) fishing block area (Fairweather *et al.,* 2006a). The vessel skipper records the locations of each catch in a 10 x 10 fishing block and estimates the tonnage of each species caught (Fairweather *et al.,* 2006a; Huisamen *et al.,* 2012; Hlati, 2015). Pelagic purse-seine fishery data were used to investigate the correlation between the number of small pelagic species found in the diet of Cape fur seals and purse-seine fishery catches for each relevant block area. Purse-seine fishery block data near the colonies were considered noting that Cape fur seals can travel a distance of at least 220 km from their colonies and mainly forage over the continental shelf (David, 1987; Shaughnessy, 1985; Mecenero *et al.,* 2006; Kirkman *et al.,* 2013; 2019;). The total tonnage of each species caught in the relevant blocks per month, was compared with proportion of the equivalent species in terms of %NA of each key species obtained from the Cape fur seal scat samples in the same months (Chapter 2).

Geographical and temporal variation of prey estimated biomass and consumption by Cape fur seals.

Anchovy and sardine biomass estimates were obtained from acoustic surveys conducted by DFFE annually in May (recruit data) and November (spawner data). This study compared recruit and spawner data with Cape fur seal diet data collected from 2010 to 2019. The annual anchovy and sardine biomass estimates were compared with similar species consumed by the Cape fur seal. The fish biomass per stratum was linked to the %M prey eaten in the colonies in close proximity to the stratum. This was assumed to be the fish availability at that stratum. Diet collected at various breeding localities in close proximate consumption were Lambert's Bay (Stratum A; St Helena Bay); Jutten Island (Stratum B; Saldanha Bay to Cape Agulhas); and Geyser Rock (Stratum C).

Statistical analysis

All data analysis was conducted using R-Studio statistical software, version 3.6.1 (R Core Team, 2019). The data were checked for normality using the Shapiro-Wilks test. To compare the size of fish eaten by Cape fur seals per month with the commercial landings for that month at the commercial landings' harbours, the significance of any differences and identification of any patterns were tested using Pearson's product moment correlations for normal data, and Kendall's rank correlations if the data were

not normally distributed. Pearson's product moment correlations were used to investigate relationships between the average %NA of small pelagic fish species consumed by Cape fur seals and catches by the purse-seine fishery. %NA was used for fur seals because it provided an average contribution of each small pelagic fish species in the diet, as the purse-seine fishery provided an average of fish caught per trip. Correlation tests were also used for comparisons between seal consumption and acoustic biomass estimation of anchovy and sardine across the study years (2010 -2019), three study colonies (Lambert's Bay, Jutten Island, Geyser Rock), and seasons (Non-upwelling, Upwelling). The seasons are explained in detail in chapter 2, although there was a big gap in scats sampling over the pupping season, and the acoustic estimate surveys were only done twice per year (May (Non-upwelling) and November (Upwelling)). Cape fur seal recruit diet data which includes autumn-winter months (April -August) were used as the non-upwelling season and compared with the annual acoustic estimate surveys of recruit data (May). The diet data for spring-summer months (September-March excluding November, December and January due to pupping season) were compared with the annual acoustic estimate surveys of spawner data (November).

3.4 Results

Size of pelagic fish eaten by seals and caught by the fishery.

Both anchovy and sardine constituted the greatest proportion of small pelagic fisheries catches; and were also found in a greater proportion of Cape fur seal scats (Table 2.4, Chapter 2, Figure 3.2). Cape fur seals targeted/fed mostly on juvenile to adult anchovy, sardine, red-eye, and horse mackerel, whereas commercial landings were mostly dominated by both juvenile and adult fish for both sardine and red eye with bimodal distribution (Figure 3.2). Individuals caught by fisheries were smaller for anchovy than those consumed by the Cape fur seals, whereas there was a slight overlap in fish size distribution for horse mackerel juveniles by both fisheries and seals (Figure 3.2).

There was a considerable overlap in fish size distribution for sardine (Pearson's r= -0.045, df= 9, p= 0.782, Figure 3.2) and red eye (Pearson's r= 0.045, df= 9, p= 0.790, Figure 3.2) for both commercial landings and Cape fur seal catches. Between commercial landings and fur seal consumption for horse mackerel (Pearson's r= 0.104, df= 9, p= 0.523, Figure 3.2), there was no significant relationship. Anchovy on the other hand, showed a strong positive correlation (Pearson's r= 0.766, df= 9, p< 0.04, Figure 3.2) with fish size distribution between commercial landings and Cape fur seal diet.

Overall, commercial catches were mainly juvenile anchovy < 115 mm and horse mackerel < 150 mm (Figure 3.2). A combination of both juvenile and adult sardine and red eye caught by seals and fishery catches displays a similar bimodal distribution (Figure 3.2). Interestingly, when fisheries caught juvenile

sardine, seals would catch young or adult fish and vice-versa, and the sardine average catches were slightly less than the commercial landings. Red eye consumed by seals and caught by fisheries were within the same size range; when commercial landings were juvenile or early adults, seals consumed either young fish or adults (Figure 3.2). In addition, anchovy showed a right-skewed distribution, which suggests that commercial landings average catches (%f) were more compared to seals. For horse mackerel, the average catches of commercial landings were slightly more than those of fur seals (Figure 3.2).

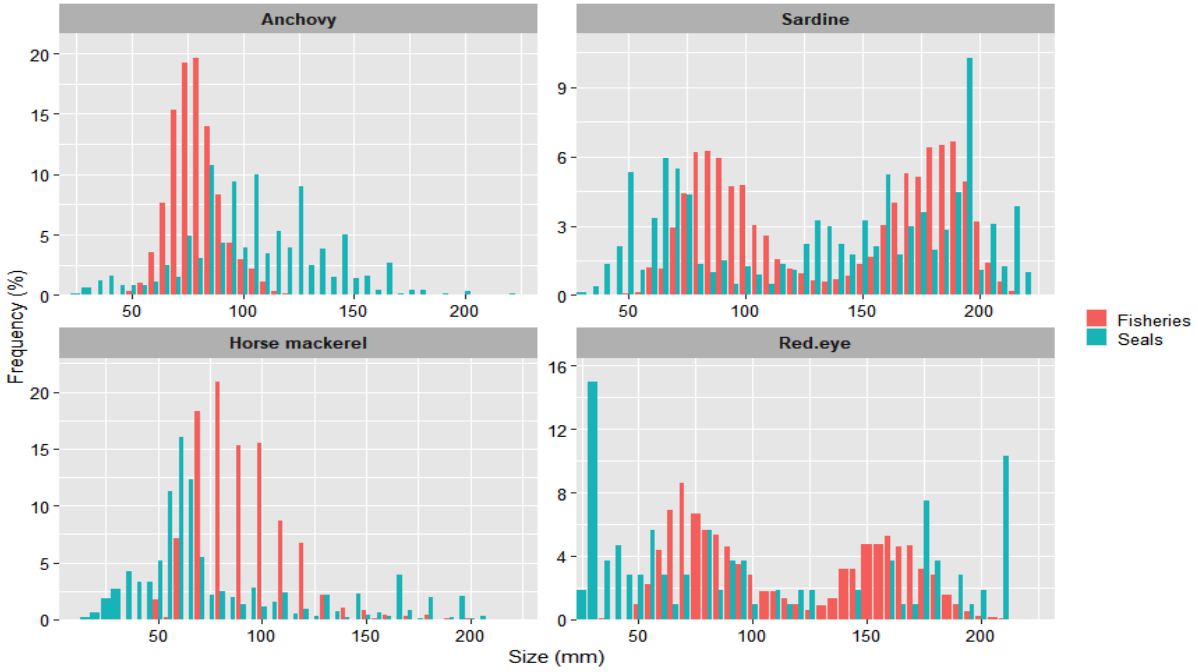

Figure 3.2: Size (mm) distribution of anchovy, sardine, horse mackerel, and red eye in the diet of Cape fur seals and commercial fishery landings between February 2010 and October 2019 off the South African coast.

Potential purse-seine fishery catches and the Cape fur seal's diet.

There was an overall positive but weak significant relationship (Pearson's $r < 0.3$, $df = 9$, $p < 0.05$, Figure 3.3) between Cape fur seal consumption and purse-seine fishery catches for anchovy (Pearson's $r = 0.19$, $df = 9$, $p = 0.011$, Figure 3.3), sardine (Pearson's $r = 0.23$, $df = 9$, $p = 0.012$, Figure 3.3), and horse mackerel (Pearson's $r = 0.15$, $df = 9$, $p = 0.046$, Figure 3.3). However, for the red-eye consumed by fur seals and caught by the purse-seine fishery, there was no significant relationship (Pearson's $r = 0.058$, $df = 9$, $p = 0.74$, Figure 3.3).

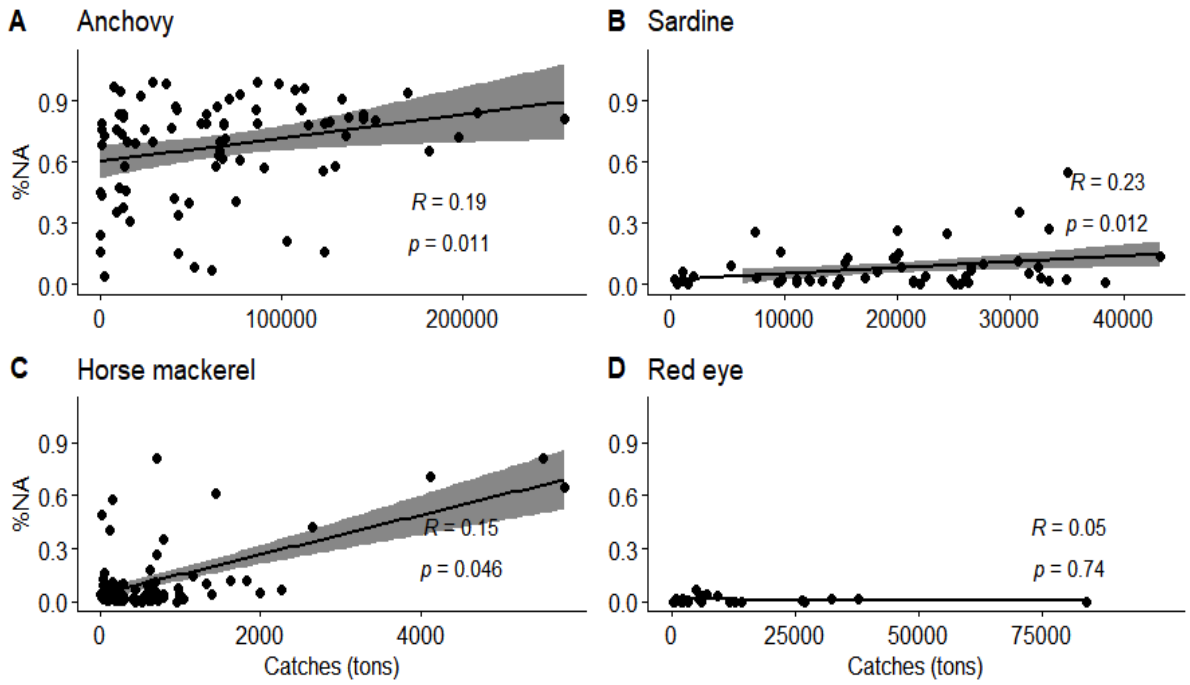

Figure 3.3: Relationship between purse-seine fishery catches (tons) and average numerical abundance (%NA) of Anchovy (A), Sardine (B), Horse mackerel (C) and Red-eye (D) eaten by Cape fur seals from 2010 to 2019.

Geographical and temporal variation of prey estimated biomass and consumption by Cape fur seals.

The consumption of anchovy and sardine by Cape fur seals was not correlated with the acoustic biomass estimate in the area around each of the three colonies (Figure 3.4). Anchovy consumed by fur seals had no significant relationship with the overall estimated acoustic biomass at Lambert's Bay (Kendall's τ = -0.11, *df*= 7, *p*= 0.65, Figure 3.4), Jutten Island (Pearson's *r*= 0.01, *df*= 7, *p*= 0.98, Figure 3.4), or Geyser Rock from 2010 to 2019 (Pearson's *r*= 0.61, *df*= 7, *p*= 0.08, Figure 3.4). However, there was a significant relationship between 2010 and 2017 (Pearson's *r*= 0.93, *df*= 6, *p*< 0.01, Figure 3.4) at Geyser Rock. It is worth noting that there was no acoustic biomass survey conducted for anchovy and sardine at Lambert's Bay and Jutten Island in 2018, and sardine was also not recorded/detected in the fur seal diet in these two colonies in 2018 (Figure 3.4). Sardine consumption by Cape fur seals and estimated acoustic biomass showed no significant relationship at Lambert's Bay (Pearson's *r*= -0.37, *df*= 3, *p*= 0.53, Figure 3.4), Jutten Island (Kendall's τ = 0.45, *df*= 4, *p*= 0.19, Figure 3.4), or Geyser Rock (Pearson's *r*= 0.15, *df*= 7, *p*= 0.69, Figure 3.4). Noting that acoustic biomass estimate found no evidence of sardine at Lambert's Bay in 2013, 2014, 2015, and 2019, and at Jutten Island in 2013, 2014 and 2019 (Figure 3.4)

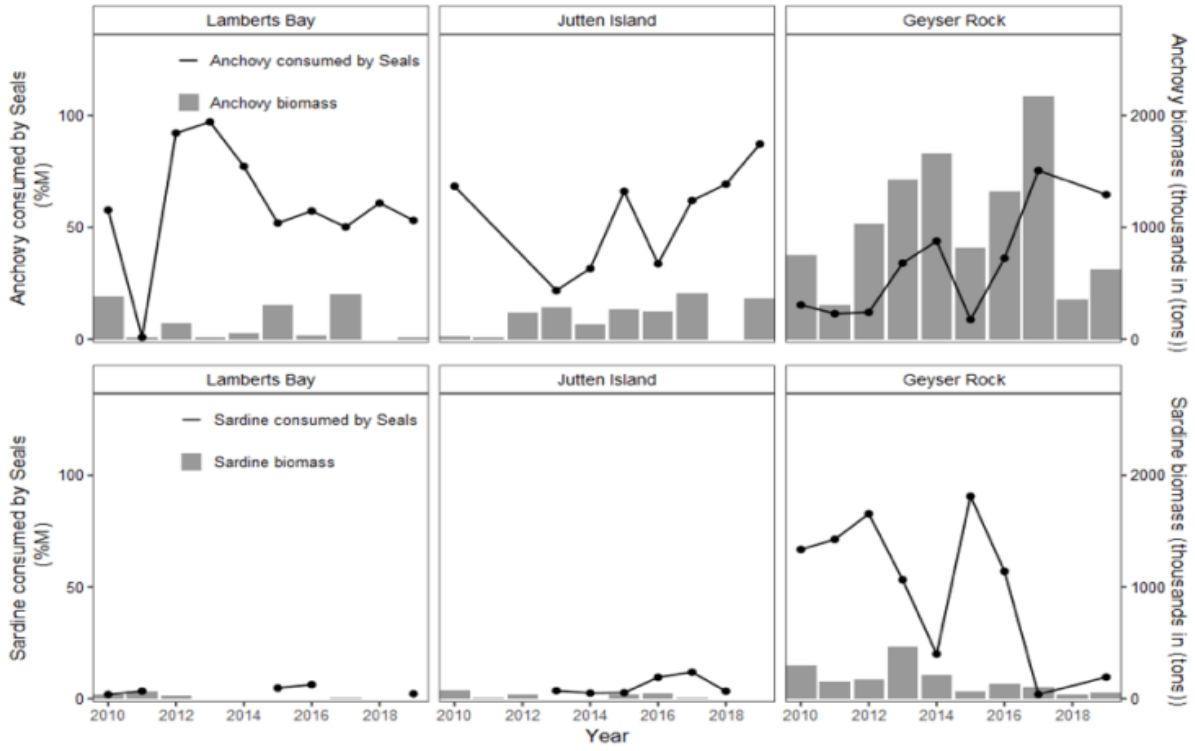

Figure 3.4: Trends in the mass proportions (%M) of anchovy and sardine in the diet of Cape fur seals at three study colonies in relation to acoustic biomass estimate based on the Department of Forestry, Fisheries and the Environment (DFFE) survey strata (Lambert's Bay = stratum A, Jutten Island = stratum B ,and Geyser Rock = stratum D) off the coast of South Africa from 2010 to 2019.

During the non-upwelling season, anchovy consumed by fur seals had no significant relationship with the recruit biomass estimate (Kendall's τ = -0.33, *df*= 7, *p*= 0.21, Figure 3.5). However, anchovy consumption by Cape fur seals in the upwelling season was positively related to the November spawner biomass estimate (Pearson's *r*= 0.74, *df*= 8, *p*= 0.025, Figure 3.5). By comparison, there was no relationship between sardine consumed by fur seals and acoustic biomass estimates in either the non-upwelling season (Kendall's τ = -0.22, *df*= 7, *p*= 0.40) or the upwelling season (Kendall's τ = 0.39, *df*= 7, *p*= 0.14; Figure 3.5). Very little sardine was estimated during the non-upwelling season in 2013, 2015, and 2016. Furthermore, there was no acoustic biomass survey in 2018 (Figure 3.5). However, and interestingly, sardine was recorded in the Cape fur seal diet throughout the study years (2010-2019).

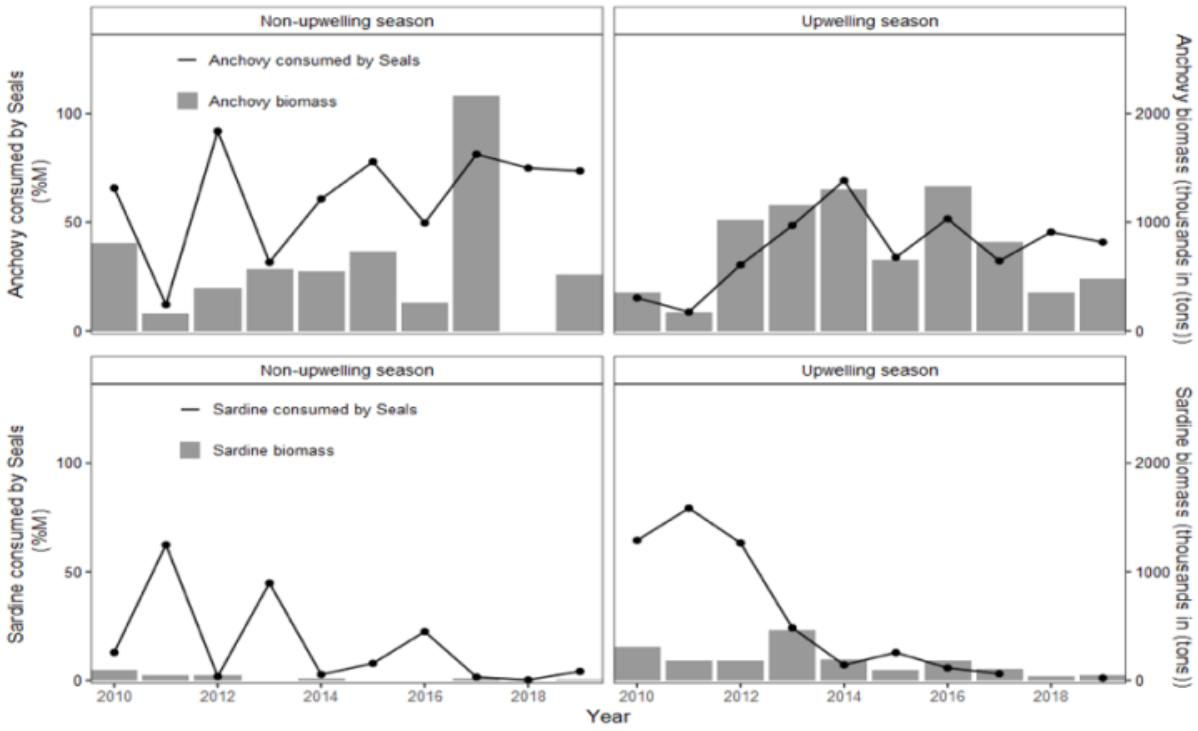

Figure 3.5: Trends in anchovy and sardine mass proportions (%M) in the diet of Cape fur seals and acoustic biomass estimates based on recruit (May) and spawner (November) surveys off the coast of South Africa from 2010 to 2019.

There was, however, an overall increase of anchovy consumed by the fur seals throughout the study period and across the three study colonies (Pearson's r= 0.77, df= 8, p= 0.01, Figure 3.6, 3.7, 3.8), with no significant relationship to the overall acoustic biomass estimate of anchovy (Pearson's r= 0.35, df= 8, p= 0.31, Figure 3.6, 3.8). In addition, there was no trend in anchovy biomass estimate (Pearson's r= 0.13, df= 8, p= 0.71, Figure 3.6, 3.7). As shown in Figure 3.8, anchovy was largely distributed between St Helena Bay and Cape Agulhas.

However, a strong significant relationship was found between the overall sardine consumed (total %M contribution) by fur seals across the three study colonies and the overall acoustic biomass estimate of sardine (Pearson's r= 0.69, df= 8, p= 0.03, Figure 3.6, 3.7, 3.9), with sardine consumption decreasing over the study period (Pearson's r= -0.90, df= 8, p< 0.01, Figure 3.6, 3.9). Concomitantly, there was a significant decrease in sardine biomass estimates (Pearson's r= -0.78, df= 8, p= 0.01, Figure 3.6, 3.7), and sardine were largely distributed in the south and east of Saldanha Bay (Figure 3.9).

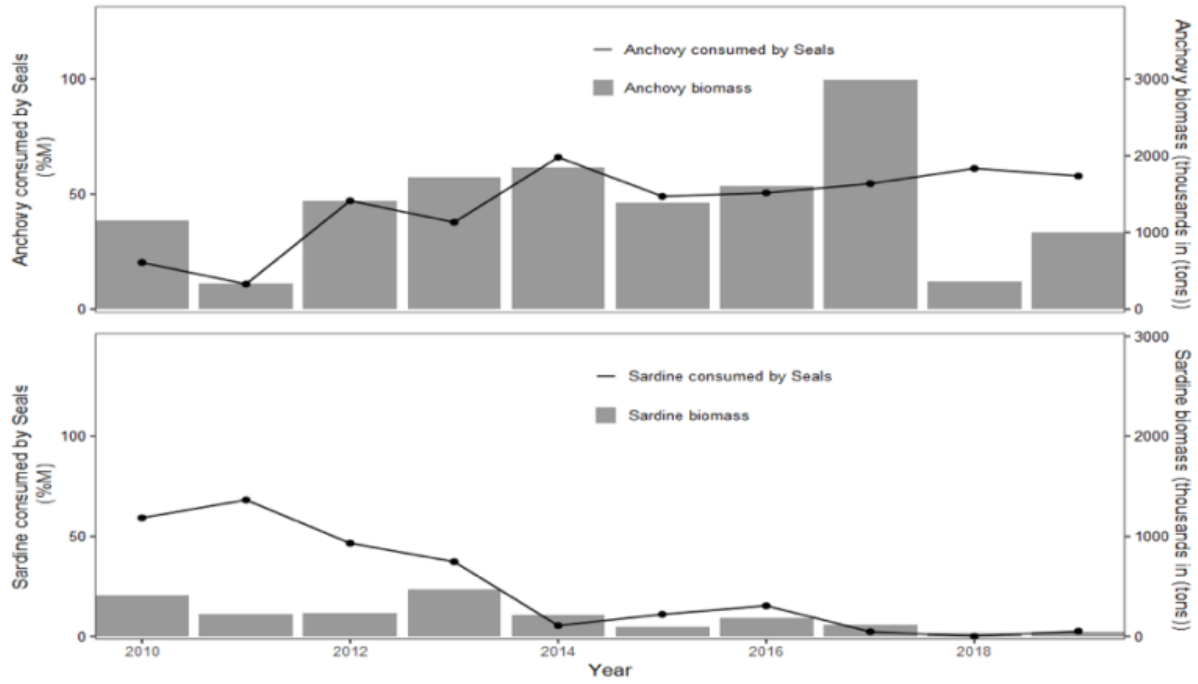

Figure 3.6: Overall fish consumption of anchovy and sardine by Cape fur seals and acoustic biomass estimate by the Department of Forestry, Fisheries and the Environment (DFFE) every May and November (2010 to 2019) off the South African coast.

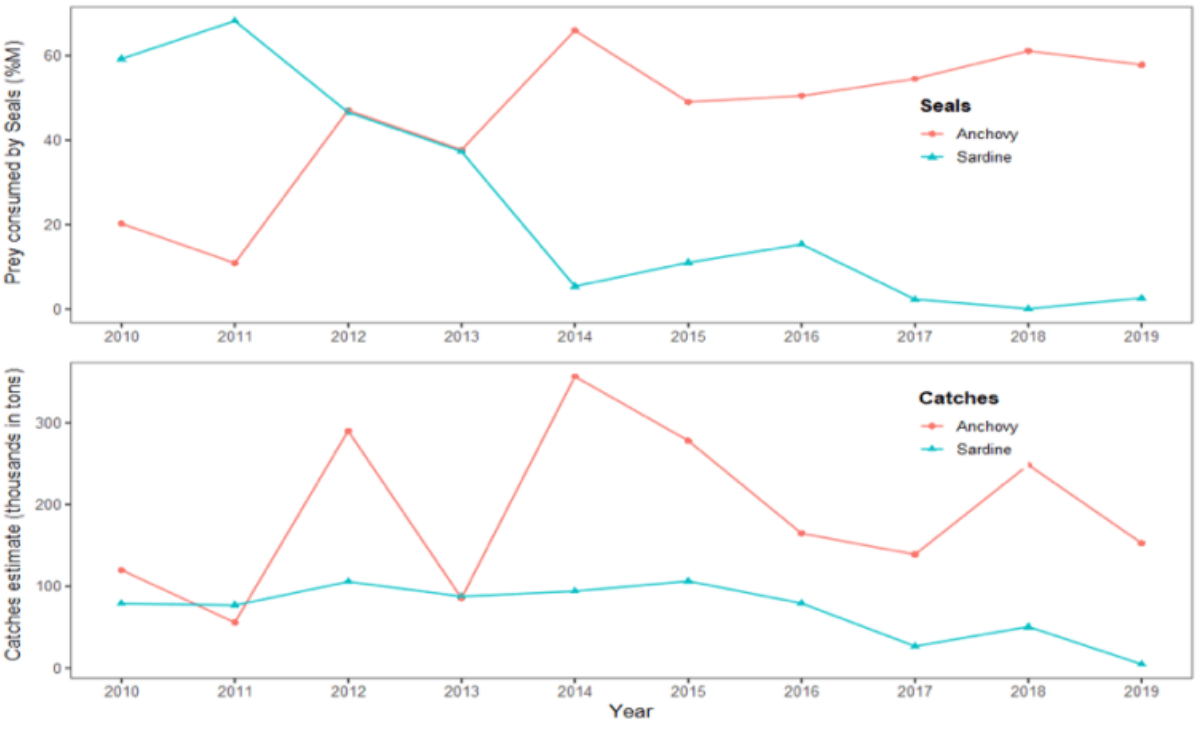

Figure 3.7: Overall proportion of anchovy and sardine consumed by Cape fur seals at the three study colonies and commercial fish catches from 2010 to 2019.

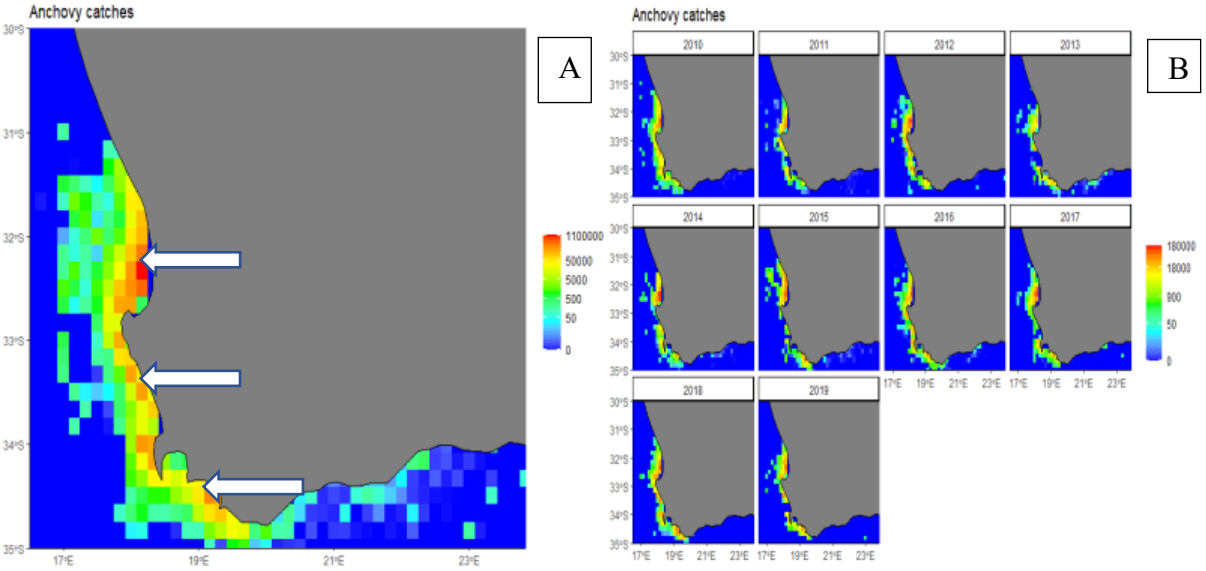

Figure 3.8: Anchovy overall purse-seine fishery catches, (A) across the South African coast, and (B) in each study year (2010-2019). The white arrows representing the Cape fur seal colonies near fishery blocks.

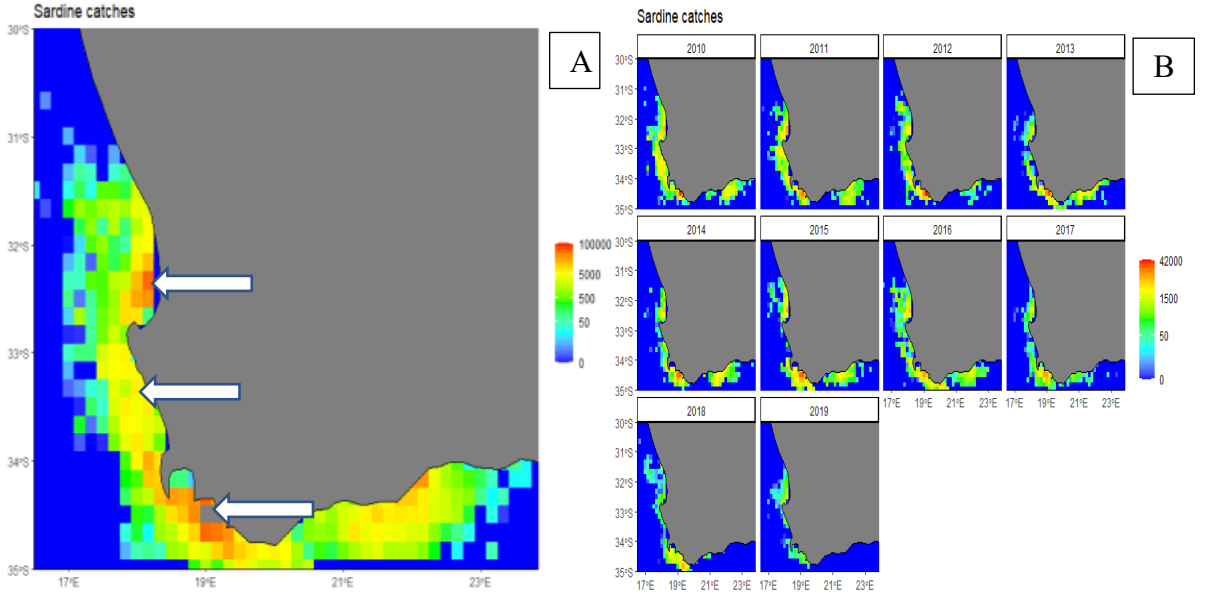

Figure 3.9: Sardine overall purse-seine fishery catches, (A) across the South African coast, and (B) in each study year (2010-2019). The white arrows representing the Cape fur seal colonies near fishery blocks.

3.5 Discussion

Land-breeding marine predators (i. e. seabirds and fur seals) can be used as sentinel species because of their accessible. These species feed within restricted areas when nursing their offspring and thus are

responsive to any local environmental changes or disruption (Fretwell and Trathan, 2019). As a result, marine predators such as the Cape fur seals could be used as environmental indicators for any possible changes in the environment. Long-term studies conducted on the Cape fur seal diet serve as a good representation of prey species availability, abundance, and diversity in a region and over time (David, 1987; Wickens *et al.,* 1992; 1997; Balmelli and Wickens, 1994; Mecenero *et al.,* 2006a; Kirkman *et al.,* 2011). The pattern of fish consumption however might reflect the fish availability within the seals' foraging areas at different localities (Casaux *et al.,* 2003). Pelagic species such as anchovy and sardine predominate the Cape fur seal diet (see Chapter 2); and are also important species for commercial fisheries. These species play a vital role in the diet composition of marine top predators (such as Cape fur sea and seabirds) and in the human diet as essential nutrients (Fairweather *et al*., 2016a; FAO, 2018; Sink *et al.,* 2019; Speakman *et al.,* 2020). Therefore, understanding pelagic species availability in along South African coastline allows full comprehension of predator and prey population status as well as trends in the marine environment, and enables environmental suitability measures (Sink *et al.,* 2019; Coetzee *et al.,* 2019; Masiko *et al.,* 2021). In addition, Cape fur seal diet can be used to regulate and establish management policies for seal population, particularly in regions where there is potential for interaction with fisheries (Castley *et al.,* 1991). Hence, this study used commercial landings catch, purse-seine fishery catches, acoustic biomass estimate survey, and Cape fur seal diet data (see Chapter 2) to assess potential competition and overlap between fur seal consumption and commercial fisheries catch on important pelagic fish species.

Size of pelagic fish eaten by seals and caught by the fishery.

Small pelagic fish species (anchovy, sardine, horse mackerel) are important in the diet of Cape fur seals (Chapter 2) and commercial fisheries (Coetzee *et al*., 2018). In this study, commercial landings were found to catch smaller size fish (mostly juveniles), whereas fur seals caught a wide-range of fish in size (mostly juveniles to early adults) (Figure 3.2). Of which, there was an overlap for horse mackerel and anchovy between the commercial landings and Cape fur seal consumption as they both caught young to juvenile sizes of these fish species. Fisheries midwater trawls are known to catch juvenile horse mackerel while other fish size distributions are caught as bycatch during the process (McLaverty, 2012; Smith and Cochrane, 2016; Johnston and Butterworth, 2019). On the other hand, Cape fur seals mostly targeted young and juvenile horse mackerel (Chapter 2; Figure 3.2). A previous Cape fur seal diet study by Huisamen *et al.* (2012) also reported that seals prey on young to juvenile horse mackerel. A negative relationship was found in this study between sardine consumed by Cape fur seals and that caught by commercial landings, indicating competition for fish species of the same size. A noticeable potential

competition is reflected by the similar size of horse mackerel and anchovy eaten by fur seals and caught in commercial fishery landings.

Potential purse-seine fishery catches and the Cape fur seal's diet.

The biomass of anchovy, sardine, horse mackerel, and red-eye consumed by the Cape fur seal and catches by purse-seine fishery were used to determine their interaction and the most targeted species. This study found a significant correlation between anchovy, sardine, and horse mackerel consumed by fur seals with the purse-seine fishery catches, but red-eye had no significant correlation (Figure 3.3). The lower occurrence of red-eye in the fur seal diet and catches in the purse-seine fishery resulting from this species should be precautionary managed by the DFFE, as only 100 000 tons are allocated to the fishery; the species is mostly found in deeper depths and offshore; this makes it difficult to catch, especially for fisheries as it will require big ships for their catches (Smith and Johnson, 2012; DFFE, unpublished data). Unlike anchovy and sardine, which are reported to constitute more than 80.0% of the total pelagic purse-seine catches, red-eye and juvenile horse mackerel are target species of lesser relevance for this fishery (Coetzee *et al.*, 2018). However, sardine is considered the main target for the South African purse-seine fishery on the west and south coasts because approximately 85.0% of sardine caught is canned and used for bait markets (Louw, 2014; Coetzee *et al.*, 2018, FAO, 2018). Following the rapid decline of sardine biomass, the purse-seine fishery targeted juvenile anchovy to keep the industry active (van der Lingen *et al.,* 2006; Coetzee *et al.*, 2008; Louw, 2014; 2018; FAO, 2018)

Geographical and temporal variation of prey estimated biomass and consumption by Cape fur seals.

Anchovy and sardine consumed by Cape fur seals did not correlate with the acoustic biomass estimate across the three study regions (Figure 3.4, 3.5), except for anchovy at Geyser Rock between (2010 and 2017). The negative correlation between anchovy and sardine consumed at Lambert's Bay; and the acoustic biomass estimate shows that when seals consumed more, there was less in the acoustic biomass estimate, as when one decreases the other increases and vice-versa. This describes the interactions between prey availability and how much is taken/caught from what is estimated to be available. In addition, this study reported that anchovy catches were largely distributed in the St Helena Bay and Saldanha Bay to Cape Agulhas regions (Figure 3.8), while sardine catches were largely distributed in the Saldanha Bay to eastern Agulhas region (Figure 3.9). The study also showed a potential interaction with the vessels, meaning that when the catches goes down so as the prey availability in Cape fur seals diet (Figure 3.7, 3.8, 3.9). This is supported by various studies conducted on the west-coast of South Africa on the availability of anchovy and sardine, and the southward to eastward distributional shift

of sardine (Lluch-Belda *et al.,* 1989; Beckley and van der Lingen,1999; Coetzee *et al.,* 2018). More recent reports state that there is only a single stock of sardine reported to occur in the South African coastline and distributed into three: (1) in St Helena Bay (distributed off the west-coast to the west of Cape Agulhas), (2) east of Cape Agulhas to Kwa-Zulu Natal (distributed off the south coast in spring/summer), and (3) KwaZulu-Natal (east coast in autumn/winter when they undertake the annual sardine run) (Coetzee *et al.,* 2008; van der Lingen *et al.,* 2010a; van der Lingen *et al.,* 2015; Weston *et al.,* 2015; Coetzee *et al.,* 2019). Sardine stock occurrence was evident in the Cape fur seal diet, as the sardine biomass estimate and catches (Figure 3.5, 3.7, 3.9) show similar occurrences of sardine in the seals diet at Saldanha Bay and are most dominant in the east of Cape Agulhas regions. An increase in the estimated biomass from the Saldanha Bay to Cape Agulhas and Cape Agulhas regions correspond with a decrease in the estimated biomass off St Helena Bay (van der Lingen *et al*., 2005; Fairweather *et al.,* 2006a). This explains the strong significant correlation between the overall sardine consumed by fur seals and the acoustic biomass estimate, unlike anchovy, there was no correlation over the years and across regions (Figure 3.5, 3.7, 3.8). Although sardine showed a strong correlation, there was a decrease in consumption of sardine and spawner biomass estimate across the study years and an increase in anchovy consumption by the Cape fur seals in this study (Figure 3.5, 3.8, 3.9). Previous Cape fur seal diet studies conducted on the west coast and south east coasts by Huisamen *et al.* (2012) and Hlati (2015) have also shown a similar trend.

3.6 Conclusions

There is evidence that Cape fur seals compete for sardine with commercial fisheries, and there is overlap for anchovy and horse mackerel between seals and fisheries. Strong evidence is still required to support whether or not there is indeed competition for other pelagic and demersal fish species between seals and fisheries, and how it impacts the fur seal and pelagic fish biomass in South Africa. Despite the patchy data, this study was able to provide insight into the fish size-frequency distribution and overlaps for anchovy and horse mackerel consumed by seals and caught in commercial landings, and the competition for the same size distribution for sardine. A significant correlation existed for anchovy, sardine, and horse mackerel consumed by Cape fur seals and purse-seine fishery catches. No significant seasonal correlation was found for sardine consumed and the acoustic biomass estimated but there was a significant correlation for anchovy consumed in the upwelling season. Finally, the overall decrease of sardine in the diet of fur seals correlated with the decrease of sardine in the acoustic biomass estimate, while the overall increase of anchovy in the diet had no significant correlation with the estimated biomass but showed that there is more anchovy in both the diet and acoustic biomass estimate compare with that of sardine. Therefore, these results suggest and support that sardine is the most preferred prey species

of Cape fur seals (Huisamen *et al*., 2012), based on the sardine fish size-frequency distribution preyed on by seals and commercial landings; significant correlation between sardine consumed and purse-seine fishery (interaction with fishing vessels); and the decrease of sardine acoustic biomass estimate correlated with the decrease of sardine in Cape fur seals' diet. In addition, in the absence of or low numbers of sardine, consumption was based on prey availability. Furthermore, there is a need to measure or determine the biomass of fish prey consumption by Cape fur seals, which could not be determined in this study; only the mass contribution of fish prey was estimated.

Chapter 4: Synthesis and Conclusions

4.1 Synthesis and Conclusions

The Cape fur seal is the only pinniped that breeds in the southern African region. Their distribution ranges across three countries (Angola, Namibia, South Africa) and two oceanic currents, the Benguela Current and Agulhas Current systems (Hofmeyr, 2015). They are dependent on the marine environment for feeding and the terrestrial environment for breeding. Their position on the upper trophic levels makes them sensitive to changes at lower tropic levels (i.e., prey dynamics). Cape fur seals mainly feed on teleost fish but have generalist feeding habits, which permits them to adapt to changes in the availability of preferred prey. Dietary changes likely reflect a broad change in the prey community within a region or ecosystem, compared with more specialised predators (Horn and Witcombe, 2015; Fleming *et al.,* 2016; Strydom *et al*., 2022). This makes Cape fur seal species an ideal ecosystem sentinel (Kirkman *et al*., 2013; Hofmeyr, 2015; Sydeman *et al*., 2015; Hazen *et al.,* 2019; Strydom *et al*., 2022). Fur seal terrestrial habits such as to breed or rest at predictable sites enable researchers to investigate their diet, amongst others, scat analysis. Long-term investigations into the Cape fur seals diet facilitates tracking of changes in the ecosystem (Sergio *et al.,* 2008; Hazen *et al.,* 2019; Dakwa *et al.,* 2021; Masiko *et al.,* 2021; Strydom *et al*., 2022). Against this backdrop, the aim of this study was to describe spatio-temporal variation in the dietary composition of Cape fur seal off the South African coast, and to further investigate potential competition or overlap between Cape fur seals consumption and commercial fisheries' catches in South Africa from 2010-2019.

The results showed both inter- and intra -annual trends in species across the study colonies, which may be linked to the availability of prey distributions. This study also reported variations in prey occurrences and abundance in the diet of fur seals between 2010 and 2019, indicating changes in fish availability and biomass in the study region (South Africa). Despite substantial variation in the diet of Cape fur seals over the past 10 years, there were no consistent changes in the diet (2010 - 2019). These results and the lack of significant differences in species composition between 1974 - 1996 and 2010 - 2019 signifies that seals are robust species that adapts well.

A similar study was conducted at eight study sites along the Namibian coast between 1994 and 2018 (Mwaala, 2022). In South Africa, this is the first study to account for Cape fur seal diet at this spatio-temporal scale. Previous crucial Cape fur seal diet studies have been limited to either temporal or geographical scales. These include those conducted at the only Cape fur seal colony in Angola (Winkler *et al.,* 2019), three mainland breeding colonies in Namibia (Mecenero *et al.,* 2005; 2006a; 2006b), and

two colonies in South Africa (Robberg Peninsula and Algoa Bay) (Huisamen *et al.,* 2012; Connan *et al*., 2014).

Chapter 2 reported that Cape fur seals fed on a diverse range of prey species off South Africa from 2010 to 2019, but mainly consumed small pelagic and mesopelagic prey (anchovy, sardine, horse mackerel) that display shoaling behaviour and some demersal species such as hake. Anchovy and hake dominated the diet across all regions during the study period. These species (anchovy, sardine, horse mackerel) are all of commercial fisheries importance in South Africa and form part of major catches for fisheries and other predators such as seabirds. Cape Cormorants (*Phalacrocorax capensis*) were frequently recorded in the diet of fur seals, which is worrying given that their population has decreased by over 50% in the last three decades and is listed as Endangered in the IUCN Red Data List (Birdlife International, 2019; Masiko *et al*., 2021).

Potential competition between Cape fur seals and commercial fisheries was investigated in Chapter 3, with special focus on colonies that were easily accessible and reside near the fishing harbours (i.e Lambert's Bay, Jutten Island and Geyser Rock). Only prey species that were most important and predominated the Cape fur seal diet were considered (i.e. anchovy, horse mackerel, sardine and red-eye) for reporting. Cape fur seals fed on various fish sizes, including both juvenile and adult fish, of similar size to commercial fisheries. A considerable overlap in fish size distribution between commercial landings catch and Cape fur seal diet was found for sardine and red eye., However between fur seal diet and purse-seine fishery catches, there was a significant correlation for anchovy, horse mackerel, and sardine but not with the red-eye. For the acoustic biomass estimate data, there was no significant relationship with the Cape fur seal diet. However, the overall decrease in sardine biomass estimates correlated with the decrease of sardine in the fur seal diet. Similarly, with the increase of anchovy in seal diet, there was also an increase in the biomass estimate of anchovy compared with that of sardine. Similar trends were observed in seabirds and other fur seal diet studies conducted by Mecenero *et al.* (2006b), Huisamen *et al.* (2012), Hlanti, (2015, Reisinger *et al*. (2018), Masiko *et al.* (2021), and Strydom *et al.* 2022, showing that acoustic fish biomass overlaps largely between marine top predators and fisheries, and the overall biomass estimate correlated with the consumption of prey.

4.2 Recommendations for future research

This being the first diet study of the Cape fur seal population in South Africa that spans a period of 10 years (2010 to 2019), investigating geographical and temporal changes in the diet at various breeding colonies range in South Africa. There were limited scat samples at colonies, especially on the southeast coast

restricted geographical analysis. The results however, provided adequate information to scrutinise the dietary composition and spatio-temporal trends. Dedicated sampling efforts should be maintained at currently regularly sampled colonies (i.e. Lambert's Bay) and increase consistency in sampling is required for the southeast coast. Research and monitoring efforts must be extended to Namaqualand colonies (e.g., Strandfontein Point or Kleinsee) that are adjacent to the Namaqua upwelling cell. A multi-institutional approach is also required to coordinate efforts such that the national diet database is created and maintained. The points raised above will ensure proper coverage of the distribution extent in South Africa and improve the understanding of Cape fur seal diet in the next review.

Thus, analysis should be preceded by a study design that aims to address potential competition between seals and fisheries and other top predators such as the African Penguin. Furthermore, these results may assist in better prediction of the population performance of seals under different environmental scenarios. Satellite-derived movement data should be used to augment the information generated in this dissertation. Understanding Cape fur seal core areas by studying their movements may improve our understanding of trends observed in this dissertation. Breeding success (pup survival index) should be measured at colonies where diet is monitored. If analysed together, these data (diet, movement, breeding success) may provide a better picture of the short-term implications of variability in prey abundance.

Several areas of interest for future research have been identified in the present study, such as building or strengthening relationships between the DFFE (government of South Africa) and other relevant stakeholders (i.e. research institutions, NGOs, NPC, Cape Nature, SANParks) across various Cape fur seal colonies for consistent scat collection. Also, regular commercial fisheries data are crucial for understanding potential competition between fisheries and fur seals. It would be useful to definitively differentiate between the two hake species from otoliths in scats to determine whether seals mainly feed on shallow (*M. capensis*) or deep-water hake (*M. paradoxus*). Telemetry data will surely provide empirical evidence using known hake's core areas by Cape fur seals. Multi-sensor instruments such as those measure oceanographic data must be considered. Thus, it may provide data on feeding habitat preference and its characteristics. These recommendations will contribute toward building insight into information on population and individual level effects about foraging dynamics on the Cape fur seal. The resulting information for cross-cutting applicability; these could include the management of fisheries species (e.g., population models), managing competition, and mitigating potential impacts of seals on endangered seabirds. In a nutshell, the ultimate aim is to manage the coexistence of different species of top predators with one another and with human activities towards sustainable management of South Africa's resources.

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