SPATIO-TEMPORAL VARIABILITY ASSESSMENT OF CAPE CORMORANT (*PHALACROCORAX CAPENSIS*) AND BANK CORMORANT (*PHALACROCORAX NEGLECTUS*) DIETS AT FOUR NAMIBIAN ISLANDS

By

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DECLARATION

I, Desmond Bosco Tom, declare that the contents of this dissertation represent my own unaided work, and that the dissertation has not previously been submitted for academic examination towards any qualification. Furthermore, it represents my own opinions and not necessarily those of the Cape Peninsula University of Technology.

Signed **Date: 21/08/2019**

ABSTRACT

Seabirds form a fundamental component of the marine ecosystem and are excellent indicators of the health of marine environments. This study examined temporal, spatial and inter-annual variability of bank cormorant and Cape cormorant diets on four islands in Namibia from 2003 to 2017. Data from 2003 to 2014 was regarded as old data and data from 2015 to 2017 as recent data. Seabirds are declining drastically owing to scarcity of food and competition from commercial fisheries for prey species previously exploited. The seabird species under study feed on fish that are commercially as well as ecologically important such as sardines and bearded gobies. Both seabird species are listed as endangered owing to the decline of key colonies in Namibia and South Africa as a result of various threats such as diseases, lack of food, overfishing and commercial fisheries, among other factors. Diet regimes of the bank and Cape cormorants need to be properly understood in order to understand the functionality of the Benguela Current Large Marine Ecosystem (BCLME) as these seabirds are endemic to the BCLME. The research findings from the study can assist fisheries managers and scientists to better manage fisheries resources and make informed decisions as well as providing recommendations on marine protected areas, closure of fishing areas and nursery grounds (sanctuaries) for juvenile fish. The results of the study will provide information on recruitment areas of some prey items that are commercially important such as rock lobsters, as bank cormorants feed on juvenile rock lobsters both in Namibia and South Africa. Fresh regurgitated pellets were collected in their natural setting at seabird colonies on the four study islands. The pellets were then dried, hand-crushed and sorted, and prey items were identified with the aid of identification manuals. The main prey species for bank cormorants on Ichaboe and Mercury Islands were gobies, while for the southern islands the main prey species were rock lobsters and other crustaceans in terms of frequency of occurrence. The main prey species for Cape cormorants on all islands were gobies. Possession Island had the fewest number of gobies and Mercury Island had the highest number of gobies in terms of prey species per pellet for Cape cormorants. The Independent Samples *t*-test was used to test for significant differences in the diet of both species between the seasons (summer and winter). The null hypothesis was rejected and the significant level was less than 0.001 for both bank and Cape cormorant diets between the seasons. To test for significant differences between the islands and between

years, one-way analysis of variance (one-way ANOVA) was used. The mean squares between the groups were 18.663 and 0.229 within the groups, giving a significant difference at 0.05 level. There was a spatial variation of both cormorant species on the different islands as well as inter-annual variation and temporal/seasonal variation in the diets of the bank and Cape cormorants on the different islands in Namibia. Economically important species such as rock lobster form the main part of prey species off Lüderitz (Penguin Island) and south of Lüderitz (Possession Island) for bank cormorants. To ensure the conservation of bank and Cape cormorants to avoid extinction, interventions from fisheries managers are needed such as a multi-species management approach and the introduction and promotion of MPAs and EBSAs. It is recommended that Marine Protected Areas within the seabirds' feeding range need to be protected and monitored for illegal fishing and susceptible overfishing of recruitment stock.

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GLOSSARY

Terms

Abundance: The number of a species in a given area (Mathews & Berruti, 1983).

Bearded goby: A relatively small fish (less than 10cm) from the family Gobiidae and abundant in Namibian waters (Bianchi et al., 1999).

Otolith: A structure composed of calcium carbonate found in the saccule of the inner ear of bony fish.

Pellets: Regurgitated casts containing indigestible material such as fish bones, scales and eye lenses.

Sardine: The species *Sardinops sagax*, previously known as *Sardinops ocellatus* (Bianchi et al., 1999).

Small pelagic fish: Fish of the Clupeidae family that live in the pelagic zone of the ocean.

Upwelling ecosystem: An oceanographic process by which cold, nutrient-rich water is brought to the surface by currents as a result of Ekman transport, prevailing winds and the earth's rotation (Bakun, 1996).

Abbreviations and Acronyms

BCLME	Benguela Current Large Marine Ecosystem
BENEFIT	Benguela Environment Fisheries Interaction and Training
CBD	Convention on Biological Diversity
DVM	Diel Vertical Migration
EBSA	Ecologically or Biologically Significant Marine Area
EEZ	Exclusive Economic Zone
FAO	Food and Agriculture Organization
GDP	Gross Domestic Product
IBA	Important Bird Areas
MFMR	Ministry of Fisheries and Marine Resources
MPA	Marine Protected Areas
MSY	Maximum Sustainable Yield
NB	Northern Benguela
NIMPA	Namibian Islands' Marine Protected Area
SB	Southern Benguela
SEAFO	South-Eastern Atlantic Fisheries Organisation
SST	Sea Surface Temperature

CHAPTER ONE: INTRODUCTION

1.1 Introduction

Seabirds, as top predators, form a fundamental component of the marine ecosystem and are excellent indicators of changes in the marine environment and good indicators of the health status of the environment. Namibia has many offshore islands, islets and rocks (all are within the Namibian Islands' Marine Protected Area: NIMPA) that are inhabited by different species of seabirds such as bank cormorants, Cape cormorants, crowned cormorants, white-breasted cormorants, African penguins, Cape gannets, kelp gulls, swift terns, and African black oystercatchers among others. Access to the islands is very strict and is managed by the Ministry of Fisheries and Marine Resources. Therefore there is no feeding and disturbance of seabirds from the general public and tourists.

The offshore islands provide breeding and roosting grounds for different seabird species of high economic and conservation importance. However, seabirds face some serious threats such as competing with commercial fisheries for prey which has already experienced over exploitation in the past and these cormorants are no exception (Kemper, 2007). Other factors threatening seabirds are diseases, predation, natural disasters, unsustainable harvesting practices and human activities such as pollution and disturbance. However, terrestrial predators such as brown hyenas, lions and jackals cannot access the islands.

This study focused on the diets of bank cormorants and Cape cormorants. The two cormorant species are endemic to the Benguela Current Large Marine Ecosystem (BCLME) region and are both listed as endangered species. The BCLME is one of the most productive upwelling systems in the world with upwelling centres that differ spatially and temporally and that are dependent on strong prevailing winds (Shannon, 1985). All the islands are located in the range of the Lüderitz upwelling cell which is the strongest within the BCLME. Between the two cormorant species, Cape cormorants are more abundant in Namibia. Bank and Cape cormorant diets can give a clear indication of what is happening in our marine ecosystem, particularly around the islands and further offshore as these two seabird species inhabit offshore islands and have different feeding niches. Cape cormorants feed in the pelagic layer of the marine environment and are pursuit divers (Crawford et al., 2007) while the bank cormorants are benthic feeders (Ludynia et al., 2010). Bank Cormorants feed mostly on the benthic zone between the kelp beds and can also forage on other substrates such as coarse or shingle sand (Cooper, 1985). Cape cormorants feed by pursuit-diving in large flocks, often with other seabirds species (Kemper & Simmons, 2015). Diet studies of these two species are of paramount importance as these cormorant species feed on some fish species that are of economic importance as well as other species that are ecologically important for the functioning of the marine ecosystem. For example, seabird diet data can give early indications of fluctuations in fish stocks, fish distribution and relative abundance of fish stocks. Seabirds are sampling the oceans and reduction in fish stocks can be detected in their diets. Seabirds feed on different prey species such as sardines, anchovies, mullet, myctophids, horse mackerel, hake, bearded goby and crustaceans as well planktonic species. The bearded goby is an ecologically important species in the BCLME as most of the predators such as seabirds, seals and other fish species feed on it (Crawford et al., 1985). Both the seabird species under study feed on the bearded goby but they feed on it at different life stages. Cape cormorants feed on the juvenile bearded goby because they are pelagic and bank cormorants feed on the adult bearded goby that is more of a demersal/benthic fish (Crawford et al., 1985).

The diets of the two cormorant species were studied through the analysis of prey remains in fresh regurgitated pellets by the researcher. Diet studies can also be used to assess pelagic fish distribution. The results from this study can also be used to assist fisheries managers to manage small pelagic fish as they play a crucial role in the lower and higher trophic levels in the food web of the marine ecosystem. The results can also be used to protect spawning and nursery grounds of the prey species to increase prey species abundance, maintain marine biodiversity and genetic diversity, as well as protect essential ecological processes. Eventually this will lead to an ecosystem approach to fisheries where the conservation of the endangered cormorant species is considered as well as other species, habitats and the entire marine ecosystem. The study aims to investigate the diets of bank and Cape cormorants on four Namibian offshore islands as well as the temporal, spatial and inter-annual variability of their diets on these four islands.

1.2 Location of the study area

The study area includes the islands inhabited by Cape cormorants and bank cormorants along the southern coastline of Namibia. These islands and their co-ordinates are: Mercury Island (S 25°43'02'', E14°49'59''; S 25°43'04'', E14°49'56'' S 25°43'10'', E14°49'54''; S 25°43'20'', E14°49'54''; S 25°43'11'', E14°50'00''; S 25°43'03'', E14°50'01'') and the island is less than 3 ha, Ichaboe Island (S 26°17'13'', E 14°56'13''; S 26°17'21'', E 14°56'07''; S 26°17'23'', E 14°56'07''; S 26°17'26'', E 14°56'09''; S 26°17'26'', E 14°56'11''; S 26°17'24'', E 14°56'14''; S 26°17'16'', E 14°56'16''), Penguin Island (S 26°36'38'', E 15°09'16''; S 26°37'02'', E 15°09'03''; S 26°37'18'', E 15°09'10''; S 26°37'21'', E 15°09'19''; S 26°37'17'', E 15°09'23''; S 26°36'43'', E 15°09'21'') and Possession Island (S 27°59'18'', E 15°11'16''; S 27°01'22'', E 15°12'13''; S 27°01'04'', E 15°12'16''; S 27°01'54'', E 15°12'01''; S 27°00'36'', E 15°11'15''; S 27°00'05'', E 15°11'07'') (Kahle & Wickham, 2013). These islands are within the BCLME region, the Northern Benguela region to be specific and falls under the Namibian Islands and Marine Protected Area known as NIMPA (Figure 1.1 and Figure 1.2). The highest island among the four islands under study is Penguin island while Possession island is the largest island with a surface area of 90 ha and Mercury is the smallest island. Ichaboe Island is 6.5 ha in size and 1.4km from the shore. There is strict controlled access to all Namibian islands. The Marine Resources Act (Act 27 of 2000) controls access to the islands, conservation of marine resources, fisheries, seabirds and marine mammals in the territorial sea and the Exclusive Economic Zone that covers an area of 504 000km^2.

Figure 1.1: Namibia and its MPAs known as NIMPA (A), NIMPA and its offshore islands (B), the four islands where data was collected (C) (Ministry of Fisheries and Marine Resources, 2009)

Figure 1.2: Locations of the four islands under study. The northern islands (Mercury & Ichaboe) and the southern Islands (Penguin & Possession)

1.3 Climate and vegetation

The coast of Namibia is predominantly straight with sandy and rocky beaches. The coastline is 1570km in length and has three major bays at Walvis Bay, Sandwich harbour and Lüderitz Bay (Molloy, 2003b). Sandwich harbour is a natural fish nursery and foraging area, as well as a fish recruitment site. Sandy beaches constitute 60% of Namibia's coast, a mixture of sandy and rocky shores 28%, and rocky shores 10%, with the remaining 2% the lagoons along the coast (Maartens, 2003). All Namibian islands are regarded as true desert islands and are adjacent to the Namib desert which is regarded as one of the oldest deserts on earth and is around 65–70 million years of age (Molloy, 2003b). The entire Namibian coast is within conservation areas such as the Skeleton Coast National Park, Namib-Naukluft National Park and the Tsau /Khaeb (Sperrgebiet) National Park. According to Maartens (2003), the Namibian coast consists of two biogeographic zones which are the South Temperate Zone (Namaqua) and the North Temperate Zone (northern Namib). These temperate zones are divided by the Lüderitz upwelling centre. All four islands share the same climatic conditions and are in the Namaqua temperate zone. The sea surface temperatures on the islands ranges from 12 °C to 14 °C while the air temperature ranges from 9 °C to 25 °C but can reach 38 °C with east winds (more often on Mercury Island). The southern part of the Atlantic Ocean off Namibia is governed by the South Atlantic High Pressure system, therefore all offshore islands are characterised by low rainfall of less than 20mm per year and during periods of good inland rain (Molloy, 2003b). Hence the coastal areas between Lüderitz and Cape Cross contain higher organic carbon matter in the form of subsurface sediments. Another form of precipitation on the islands is fog. There is hardly any vegetation cover on the islands, as they are rocky. The islands are covered with guano and because of this they have rich inter-tidal zones supporting kelp-bed communities. Penguin and Possession Islands support a few *Lycium* bushes/shrubs, but Mercury and Ichaboe Islands lack any terrestrial vegetation (Ministry of Fisheries and Marine Resources, 2009). Off the Namibian shelf, the most dominant sediment is biogenic diatomaceous mud.

1.4 Statement of the research problem

There is a paucity of knowledge/research in Namibia regarding the diets of some seabird species such as the Cape cormorant, *Phalacrocorax capensis*, and bank cormorant, *Phalacrocorax neglectus*. However, many studies have been done regarding other endangered species such as the African penguin, *Spheniscus demersus.* The Cape and bank cormorant species face extinction if the current decline in their populations continues. The decline of seabirds result from many factors, but the main one is the lack of prey availability. This lack of food is caused by many anthropogenic activities as well as natural activities. Diet studies of seabirds can give insight into what type of fish are available and which fisheries have the greatest effect on the declining number of seabirds. This study therefore aims at giving insights into the main prey species for the seabirds, spatial and temporal variation in diet, and how diet has changed over the years.

1.5 Research questions

- What are the main prey species of both the bank and Cape cormorants?
- Is there any significant spatial variation in the diet of the same species (intraspecific variation) among the islands under study?
- How does the diet of the Cape and bank cormorants change inter-annually over different breeding seasons? (What is the inter-annual temporal variation of prey items of both cormorant species?)

1.6 Aims and objectives of the study

The study aims to assess temporal, spatial and inter-annual variability of Cape cormorant (*Phalacrocorax capensis*) and bank cormorant (*Phalacrocorax neglectus*) diets on four Namibian islands. For this purpose, the specific objectives of the study are to:

- identify and assess the main prey species within the diet of both Cape and bank cormorants of some colonies in Namibia;
- assess how the diet of both the Cape and bank cormorants changes over the years and different seasons; and
- determine the variation in prey species of the same cormorant species on different islands in Namibia (compare prey species between the northern and southern islands).

1.7 Justification of the study

It is vital to know what is happening in the diets of these endangered species as this can provide invaluable information pertaining to the factors leading to the decline of the cormorant population. How the Cape and bank cormorants fit in the marine ecosystem also needs to be understood. By studying their diets, more insight into how to improve the species conservation status can be obtained. Foraging needs of these birds under study can be incorporated in fishery management plans such as commercial fish quota limitations.

1.8 Outline of the dissertation

The dissertation is divided into six chapters. Chapter 1 presents an introduction to the main research study and includes the location, climate and vegetation of the study area, statement of the research problem, research questions and their objectives, significance of the study, delineation of the study, and outline of the dissertation. Chapter 2 describes the background to the study and provides a literature review. In the literature review all aspects relating to the study are covered and these aspects include topics such as the Benguela current ecosystem and NIMPA, a protected MPA within the Benguela ecosystem. This chapter examines previous studies regarding the two cormorants' diet. Chapter 3 covers all the methodologies and tools used as well as providing an analysis of the collected diet data and the distribution of the two seabird species on the islands that they inhabit. Chapter 4 notes the findings of the entire study. Chapter 5 provides an in-depth discussion of the findings of the study. This chapter attempted to substantiate the results of the study with existing facts to support the results. In addition, major findings of the study are restated in the conclusions while proposing recommendations and future studies in this chapter.

CHAPTER TWO: BACKGROUND AND LITERATURE REVIEW

2.1 Background

This study examines the diet of two sympatric cormorant species relative to temporal, spatial and inter-annual variability over a period of 14 years from 2003 to 2017. Resources have been heavily exploited in marine ecosystems and as a result, the marine ecosystems are facing major environmental problems. Seabirds are included in this dilemma. It is evident that the overall seabird populations are declining in Namibia (MFMR, unpublished data). These seabird populations include our endangered seabirds such as bank cormorants and Cape cormorants, endemic to the Benguela current ecosystem. It is therefore important to study these seabird populations. The aspect covered in this study is the diet of the seabirds. With fishing pressure from the industry, it is important to ascertain what proportion of fish is left for top predators such as seabirds in the ecosystem. The Benguela ecosystem is highly variable owing to processes such as upwelling, sulphide eruptions and intrusions of warmer waters from tropical areas (Shillington, 2003). This variability has negative ultimate effects on the fish stocks, and these stocks are prey species of seabirds such as bank and Cape cormorants. Sardines and anchovies are preferred prey species, but owing to overfishing, the low-energy prey species (the bearded goby) are available to top predators. The bearded goby thus is now an important prey species in the Benguela ecosystem (De Bruyn et al., 2003; Heymans et al., 2004; Ludynia et al., 2010; Salvanes et al., 2011; Roux et al., 2013).

2.2 Literature review

2.2.1 The Benguela Current Large Marine Ecosystem

The Benguela Current Large Marine Ecosystem (BCLME) is situated along the south-western African coast and spans three countries: southern Angola, across Namibia, up to the Cape of Good Hope in South Africa (Shannon, 2006; Van der Lingen et al., 2006). The Benguela current upwelling system is among the four main eastern boundary upwelling systems in the world and is highly productive (Shillington, 2003). The other four upwelling systems in the world are: the California current (off Oregon and California), the Peruvian current (also known as the Humboldt current), the Canary current (off northwest Africa) and the Somali current (in the western Indian Ocean). The Benguela ecosystem is second to the Humboldt ecosystem in terms of fish stock biomass (Boyer & Hampton, 2001). According to Shillington (2003), the Benguela current is a cold productive current due to the south and south-westerly prevailing winds, the Coriolis Effect and Ekman transport. The Coriolis effect is when shore winds blow surface waters and movement of water is deflected to the left in the southern hemisphere because of the rotation of the earth. The layers of water are blown in slightly different directions until in the opposite direction to the prevailing winds (Shillington, 2003). This water movement of surface water offshore (moving 90° from the wind direction) and replaced by cooler water from the ocean bottom caused by prevailing wind is known as the Ekman transport.

The Benguela current is productive, with highly productive upwelling cells that vary spatially and temporally owing to prevailing wind conditions, depth, width of the continental shelf and the angle of the coastal line (Shillington, 2003). The Benguela current has a strong wind-driven coastal upwelling and the area around Lüderitz has an intense upwelling compared with other eastern boundary systems in the world (Bakun, 1996). The upwelling cells in the Benguela current ecosystem are the Lüderitz upwelling cell, Cunene upwelling cell, northern and central Namibian upwelling cell, Namaqua upwelling cell, Columbine upwelling cell and Cape Peninsula upwelling cell. The perfect wind speed for optimal upwelling is 5–6m/sec, otherwise too much wind can result in the surface being too turbulent and this removes phytoplankton from the surface back to the bottom (Molloy, 2003a).

The northern boundary of the Benguela is formed by the Angolan–Benguela front, the southern boundary of the Benguela region is formed by the Agulhas retroflection and the ocean–coastal boundary of the Benguela current is where warm oceanic waters form convoluted boundaries (cross-frontal mixing) with cold upwelled waters (Shillington, 2003). The Lüderitz upwelling cell divides the BCLME into the Northern Benguela (NB) and the Southern Benguela (SB) (Van der Lingen et al., 2006). However, the Orange River conventionally is regarded as the border between the southern and northern Benguela ecosystems (van der Lingen et al., 2006). The entire BCLME has three main environmental boundaries: the area between the Angolan frontal zone and the Benguela, the Lüderitz upwelling centre, and the intrusions at the

Agulhas waters. The Lüderitz upwelling centre can obstruct the movement of organisms between the SB and the NB due to the differences in prevailing winds and the temperatures of the water (Heymans et al., 2004). The upwelling in the Benguela region ranges from northwards at 15°S along the south-western coast of Africa and eastwards to 20°E at 35°S (Duffy et al., 1987). The upwelling process in the NB region is considered to be perennial and upwelling is at its maximum in summer around the Lüderitz area (Shilington, 2003). Hence the region experiences environmental variability on a large scale. According to Duffy et al. (1987), variability in seabird diet can occur spatially and temporally.

The NB ecosystem is mostly characterised by widespread oxygen depletion as well as hydrogen sulphide eruptions. However, the *Thiomargarita namibiensis*, together with *Beggiatoa* species as well as *Thioploca* species are the bacteria responsible for oxidising sulphur and returning sulphur and nitrogen to their natural environments. Without these bacteria our ocean would be smelling of sulphur. Anoxic conditions and Benguela *Niño* (warm water events) cause poor recruitment of fish stocks which results in the decline of commercially important fish stocks and ultimately causes changes in the species distribution of fish stocks (Roux et al., 2002; Hardman-Mountford et al., 2003). It is evident that the 1994–1995 environmental anomalies affected top predators because their prey, non-commercial meso-pelagic or epi-pelagic species such as the bearded goby were also affected (Roux et al., 2002). According to Heymans et al. (2004), the NB upwelling system covers an area range of 179000km². The BCLME, like other eastern boundary upwelling systems, is known to have large populations of small pelagic fish which are prey species of top predators such as seabirds and marine mammals, and also support commercial fishing industries (Roux et al., 2013). Main prey species in the BCLME include pelagic fish like anchovy, sardines, horse mackerel, bearded goby, squid, mantis shrimp, *euphausiids* and other crustaceans. However, their proportions or biomass contributions differ greatly temporally and spatially. The distribution of oceanic and pseudo-oceanic species is associated with the 800m isobath line in the southern and central Benguela region (Sutton et al., 2017). According to Bakun (1996), upwelling ecosystems are known to have large populations of sardines and anchovies, and this result in supporting large populations of seabirds. In total, 65 seabird species have been recorded within the Benguela region, of which 14 are rare species. Of the remaining 51, only 16 breed in the Benguela region and 11 are migratory visitors from the northern hemisphere and 24 are migratory seabirds from the Southern Ocean (Duffy et al., 1987). In the BCLME, the Cape cormorant and bank cormorant are sympatric (occur or found in the same or overlapping geographical locations). The islands that the seabirds inhabit are within the BCLME and are around the Lüderitz area. Two islands are north of Lüderitz, one is in Lüderitz Bay, and one is south of Lüderitz.

Historical events, such as industrialised fishing activities since the 1960s, and warm water events such as the Benguela *Niño* in 1995, affected the abundance of fish stocks such as anchovies and sardines by affecting their spawning (egg production), resulting in very low recruitment in the Northern Benguela region (Gammelsrød et al., 1998). Warm water events (Benguela *Niño*) in the NB cause diminution of the upwelling intensity in the region resulting in a lack of food for fish stocks and other marine organisms (Daskalov et al., 2003). A reduction in fish stocks and other factors such as disease outbreaks, pollution and predation affect populations of seabird species, not excluding the cormorant species. According to Heymans et al. (2004), some secondary consumers such as seabirds and large pelagic species tend to feed at lower trophic levels in the food web than in previous years owing to diet shifting. This is caused by lack of prey availability.

Purse seine fishing for anchovy is also responsible for a reduction in Cape cormorants in South Africa (Crawford et al., 1992). This is due to uncontrolled fishing practices in the 1900s. The Northern Benguela within the BCLME has undergone major changes (Heymans et al., 2004; Watermeyer et al., 2008; Roux et al., 2013). The NB ecosystem hosted large numbers of planktivorous fish such as anchovy and sardines (Heymans et al., 2004). Exploitation of small pelagic fish in the Northern Benguela ecosystem has impacted the structure and function of the ecosystem (Roux et al., 2013). However, the decline of sardine fish stocks reduced competition between zooplankton and sardines, which resulted in an increase in the number of the bearded goby, anchovies and juvenile horse mackerel as a result of more zooplankton available to these species (Hampton, 2003). When the huge masses of sardines were overfished, they created more food availability for other species that feed on zooplankton. The jellyfish and bearded goby dominate in the NB region since the decline of small pelagic fishes and the bearded goby became an important prey species regardless of its low energy content when compared with sardines and anchovies (Roux et al., 2013). Human-induced changes to the Northern Benguela, such as overfishing, affected all trophic levels in the food web of the region and more predators have been forced to switch/change diet to low-energy prey species such as the bearded goby. The bearded goby was first observed as a bycatch in purse seine fishing in the early 1970s and was not seen as a commercial fishery resource.

Furthermore, with a conservative approach, management of small pelagic fish needs to be given attention to avoid such huge changes in ecosystem functioning in similar ecosystems such as the Southern Benguela region (Roux et al., 2013). However, fisheries managers should not only look at pelagic fish in isolation. Fisheries managers need to consider and study interactions between species and not only between pelagic fish and the environment (Cury et al., 2000). This is because other species also have an effect on population dynamics of pelagic fish. For example, the overfishing of baleen whales resulted in a phenomenal increase of euphausiids. According to May et al. (1979), prey species have many predators; hence a multi-species management of fisheries is more ideal than an MSY (Maximum Sustainable Yield) of individual species. Having knowledge of the degree of overlap between cormorant diets and commercially important species in the fishing industry may be of paramount importance in the structuring of management and conservation plans (Punta et al., 1993). This will give insight into how much fish stock goes to cormorant species, especially Cape cormorants that are prolific in Namibia.

Sardines (*Sardinops sagax*) have been an important component of the Benguela upwelling ecosystem. Since the depletion of pelagic fish stocks in the 1970s in Namibia, seabirds mostly have fed on the bearded goby which is a low-energy prey (Ludynia et al., 2010). Population dynamics of marine top predators in Namibia is also influenced by low-quality prey, among other factors (Ludynia et al., 2010). The bearded goby is relatively abundant in the southern parts of Namibia’s coast (Ludynia et al., 2010). Food resources for seabirds are better in the north of Mercury Island than south of the island (Ludynia et al., 2010). Studies of seabird diet are mainly focused on teleost fish components. Cephalopods are important food sources for seabirds, especially in the productive cooler oceanic waters like the Southern Ocean and cold currents such as the Benguela current (De Bruyn et al., 2003). According to Van der Lingen et al. (2006), all these ecosystem changes and the changes in the marine resources in the entire Benguela region result from various factors, including environmental variability as well as overfishing.

2.2.2 The Namibian Islands' Marine Protected Area (NIMPA)

Marine protected areas (MPAs) have been introduced as a fisheries tool to protect marine habitats and conserve marine biodiversity. In addition, MPAs have been established in recognition of human-induced conservation crises, degradation of coastal areas and overexploitation of marine resources (Castilla, 2000). These MPAs are showing an increasing trend worldwide as many countries continue to proclaim vast marine areas as MPAs. Namibia declared its first and only MPA in February 2009. It is known as the Namibian Islands' Marine Protected Area (NIMPA) and covers a marine area of 9555.25km² and is 400km offshore, along the southern coastline of Namibia. The main objectives of NIMPA are to protect marine resources by protecting habitats of threatened or endangered species and commercially important resources, and to restore overexploited fish stocks, spawning and nursery areas of marine organisms, sensitive marine ecosystems, breeding areas of marine organisms such as southern right whales and Heaviside's dolphins as well as seabirds (Ministry of Fisheries and Marine Resources, 2009; Ludynia et al., 2012). According to Ludynia et al. (2012), another objective is to protect foraging areas and breeding sites of three threatened seabirds (bank cormorant, African penguin and Cape gannet). In addition, these foraging sites need to include the pelagic fishery EEZ for a holistic ecosystem approach to fisheries (Ludynia et al., 2012). NIMPA includes three rock lobster sanctuaries. Threats to coastal and marine environments including NIMPA are offshore diamond mining (dredging), oil and gas exploration (drilling and seismic activity), guano harvesting on islands, kelp harvesting, marine oil pollution and littering, mariculture and aquaculture activities, tourism and coastal development (Tarr, 2003). According to Ludynia et al. (2012), seabirds with low dispersal and high fidelity characteristics benefit more from small MPAs than seabirds with high dispersal and low fidelity. Therefore, Cape cormorants and bank cormorants will benefit more, especially during the breeding season, because they will be protected at their breeding sites as well as at their foraging sites compared with organisms that change breeding sites. Namibia's proclamation of NIMPA does not only serve the protection of marine environments but also assures Namibia of meeting other legal requirements on conventions where the country is a signatory state, such as the Convention on Biological Diversity, Ramsar Convention, and World Summit on Sustainable Development.

2.2.3 Ecologically and biologically significant marine areas (EBSAs)

Ecologically and biologically significant marine areas (EBSAs) are oceanographically distinct areas providing important services to species/populations of an ecosystem as a whole (Johnson et al., 2018). These important services may include essential habitats, breeding areas or food sources for given species. The main objective of EBSAs is to prevent the rapid loss of biodiversity in the marine environment, both in the pelagic and benthic habitats (Johnson et al., 2018). EBSAs can include any area of the water column from the surface up to the abyssal plain or from coastlines to deep ocean trenches (Johnson et al., 2018). International agreements are important tools in the conservation of marine areas beyond national jurisdiction (Clark et al., 2014). In addition, there are different criteria used to identify marine areas as EBSAs: uniqueness and rarity, special importance for life-history stages of species, importance for threatened, endangered or declining species and habitats, vulnerability, sensitivity, fragility and slow recovery, biological productivity, biological diversity and naturalness of the EBSAs (Clark et al., 2014). EBSAs were supported and motivated by the Convention on Biological Diversity (CBD). Under the auspices of the CBD there are 11 targets to be met by the year 2020. These include identifying priority areas beyond national jurisdiction of countries that need protection measures and improved conservation efforts. According to Sutton et al. (2017), EBSAs play important roles globally such as carbon cycling. They can be vulnerable to issues that affect the entire globe such as ocean acidification, global warming and deoxygenation. EBSAs profoundly support MPAs as management tools. There are 279 EBSAs on earth, including marine areas within and beyond national jurisdiction (Johnson et al., 2018). At the moment, Namibia has two EBSAs: the Namibian islands and the Namib Flyway.

There are organisations such as South-Eastern Atlantic Fisheries Organisation (SEAFO) that function on an ecosystem approach to fisheries and the precautionary principle in protecting and promoting conservation of distinct/rare species that are of great economic and ecological importance (Skagestad, 2013). According to Skagestad (2013), SEAFO is known for closing off 10 sensitive areas for fisheries activities in 2007, reducing seabird bycatch and combating illegal unregulated and unreported fishing. This organisation aims at making sure marine resources are used sustainably and there is long-term conservation of marine resources (Skagestad, 2013).

2.2.3.1 The Namib Flyway

This EBSA is a coastal area off central Namibia that draws large seabird populations as well as other marine organisms. The Namib Flyway is an important habitat for migratory, foraging and breeding seabirds and consists of two main bays (Walvis Bay and Sandwich harbour), one cape, four lagoons, two Ramsar sites and four Important Bird Areas (IBAs). Within this EBSA there are two newly proposed IBAs. The Namib Flyway has nursery and spawning areas for some fish species that are of economic and ecological importance such as sardine and anchovy. The EBSA spans 380km of the coastline and lies between the 21° S and 24° S latitudes. Furthermore, 17 seabird species are found within this EBSA and both the bank and Cape cormorants forage within this marine area (Simmons et al., 2015). The area was declared an EBSA because it is important to other marine organisms such as marine mammals that use the area for calving as well as foraging. However, there are activities that threaten the existence of marine life within the EBSA such as purse seine fisheries, development of coastal establishments and offshore mining and exploration.

2.2.3.2 The Namibian islands

The second EBSA in Namibia is the offshore islands within NIMPA. NIMPA was declared an EBSA because of the life history stages of threatened seabird species that occur on the islands and surrounding waters. The waters adjacent to the islands are foraging areas for seabirds breeding and roosting on the islands. NIMPA boundaries were primarily demarcated based on the foraging ecology of threatened seabirds such as the bank cormorant, Cape cormorant, Cape gannet and African penguin. The waters adjacent to these offshore islands are also nursery areas for other commercially important marine organisms such as the rock lobster (*Jasus lalandii*). The rock lobster is predominantly found in the diet of the bank cormorant and it plays a paramount role in the economy of the coastal town of Lüderitz and the entire Namibia. The area was declared an EBSA due to other ecologically important, iconic and threatened species found in the area such the critically endangered leatherback turtle. There 11 seabirds breeding on the islands and 8 seabird species that are endemic to the Benguela region within the EBSA. In addition, six of the offshore islands are declared as Important Bird Areas (IBAs).

2.2.4 Cape Cormorants

Cape cormorants (*Phalacrocorax capensis*) are endemic to the southwestern coasts of Africa and breed in southern Angola, Namibia and South Africa only (Boyer & Hampton, 2001; Crawford et al., 2007). About 60% of Cape cormorants breed in Namibia and the remaining 40% of the species breed in South Africa (Crawford et al., 1992). However, the South African population was greatly affected by the avian cholera caused by *Pasteurella multocida* in 1991 (Crawford et al., 1992). Cape cormorants have been up-listed to endangered species status because key colonies in Namibia and South Africa are known to have undergone rapid population declines in recent decades (Ministry of Fisheries and Marine Resources, 2009; Kemper & Simmons, 2015). Cape cormorants have about 60 000 to 70 000 breeding pairs in Namibia (Kemper, 2007). The breeding season of Cape cormorants in Namibia is from August to May and peaks between October and February (Kemper & Simmons, 2015). During the breeding season, large numbers of Cape cormorant are seen covering almost the entire island of Ichaboe.

Ichaboe Island and artificial platforms north of Swakopmund have more than 10 000 pairs of Cape cormorants in Namibia (Crawford et al., 2007). However, Cape cormorants have shown flexibility in selecting breeding localities prior to their breeding seasons or in occupying new breeding sites such as guano platforms (Crawford et al., 2008). Compared with other cormorants, Cape cormorants are more mobile and their breeding range changes in concert with fish stocks (Crawford et al., 2007). It is very difficult to have accurate population estimates of Cape cormorants because of the lack of breeding site fidelity and poor breeding seasonality (Kemper & Simmons, 2015). If conditions are not favourable, these birds do not breed. Thus it makes it difficult to study these seabird species. Lack of prey availability and periodic food scarcity are among the threats to Cape cormorants in Namibia, especially southern Namibia. These threats can cause nest abandonment as well as mass mortality of chicks (Crawford et al., 2007). According to Hampton (2003), the decline in the sardine as a resource resulted in a decline in the number of Cape cormorant as their preferred preys are sardine and anchovy. Food resources and Cape cormorant populations are directly proportional to each other.

Cape cormorants are the most abundant cormorant species in Namibia and are major guano producers on islands and platforms (Bianchi et al., 1999). According to Hampton (2003), guano harvesting on offshore islands also contributed greatly to the decline of seabirds (cormorants included) in the 1840s as the guano scrappers used to eat seabird meat and eggs, especially when their food rations were low. Cape cormorants are known to take pelagic prey (Wilson & Wilson, 1988). According to Bianchi et al. (1999), Cape cormorants feed mostly on anchovy, sardine and bearded goby (these are mainly juvenile gobies that are pelagic). According to Kemper and Simmons (2015), sardine and anchovies are more likely to be found in the diet of the birds feeding in central and northern Namibia. However, according to a study that was done on Mercury Island and Ichaboe Island, off southern Namibia, anchovies were hardly present in the diet of Cape cormorants (Duffy et al., 1987). Anchovies and sardines are pelagic fish that occur over depths of less than 350m while bearded gobies can be demersal and pelagic, depending on the stages in their life cycles. When sardine is limited, the pelagic goby is important in the diet of Cape cormorants (Boyer & Hampton, 2001). According to Kemper and Simmons (2015), Cape cormorants forage in distances of about 50km to 70km off the coast and they forage in large flocks by pursuit diving. Along with being pursuit divers, Cape cormorants are largely dependent on populations of shoaling fish (Hampton, 2003). The favourite prey of Cape cormorants are sardines and anchovies, while gobies are their important prey when their favoured prey is limited (Hampton, 2003).

2.2.5 Bank cormorants

The bank cormorant (*Phalacrocorax neglectus*) is an endangered species and is also endemic to Namibia and South Africa. Of all the cormorant species, bank cormorants are the most threatened species (Roux & Kemper, 2015) . Adults are sedentary as they feed few kilometres from their habitats. According to Crawford et al. (1999), the population of bank cormorants has declined by 60% in three recent generations; therefore they are classified as "endangered" according to International Union for Conservation of Nature (IUCN) criteria. In Namibia, Mercury, Ichaboe and Penguin islands support 90% of the breeding population (Ministry of Fisheries and Marine Resources, 2009). Threats to the bank cormorant populations include scarcity of food, oiling, disturbance, natural disasters, mining and competition with commercial fisheries. According to Monteiro and Van der Plas (2006), low oxygen and warm water events are endemic to the BCLME and they result in major losses of marine organisms. Low oxygen levels in 1994 decreased marine organisms, including the bank cormorant population. The bank cormorant population in Namibia experienced drastic declines from 5000 breeding pairs to 300 breeding pairs due to the Benguela *Niño* that occurred in 1994 and oceanic anomalies such as low oxygen events (Roux & Kemper, 2015). Bank cormorants breed between central, southern Namibia and Quoin Rock in the Western Cape Province of South Africa (Crawford et al., 2008). This species consists of about 2196 breeding pairs in Namibia according to recent data and this is 87% of the world population (Kemper, 2007). The breeding season of bank cormorants in Namibia ranges from November to April (Crawford et al., 1999). There is movement of breeding adult bank cormorants between the Ichaboe and Mercury islands as this was seen by colour bands on birds that were banded/ringed at either island during collection of pellets. There are seasonal trends in breeding adults and these affect the counts of the breeding pairs (Crawford et al., 1999). According to Crawford et al. (2008), bank cormorant distribution follows a similar trend to that of kelp beds. Kelp beds are known to be habitats of rock lobsters and the bank cormorant species prey on rock lobsters.

According to Wilson and Wilson (1988), foraging behaviour in cormorants mostly depends on various aspects such as the environment, bottom topography, depth and water turbidity. Breeding bank cormorants can travel 9km from their colony for feeding and can dive up to 30m depth (Crawford et al., 2008). Bank cormorants are generalised bottom feeders that dive up to 45 seconds when feeding (Crawford et al., 1985). The seabirds feed mostly on or near the sea floor. Bank cormorants feed mainly on benthic fish such as bearded goby, *Sufflogobius bibarbatus*, and their distribution is restricted to the Benguela Current Large Marine Ecosystem (Wilson & Wilson, 1988; Bianchi et al., 1999; Ludynia et al., 2010). Bank cormorants feed mainly on bearded gobies that are between 45mm and 70mm in length (Crawford et al., 1985). Other prey species include sole, clinids, cuttlefish, klipfish and octopus (Ministry of Fisheries and Marine Resources, *unpublished data).* These birds also feed on crustaceans such as the West Coast rock lobster, *Jasus lalandii* (Crawford et al., 2008). Bank cormorants also feed on other crustaceans like the mantis shrimp and mud prawns. Bank cormorants were heavily affected by the crash of the rock lobsters in the late 1950s.

2.2.6 Seasonal breeding patterns and trends on the islands

Most seabirds in Namibia are found in the southern parts owing to the geographical location of offshore islands that the seabirds use for roosting and breeding. However, the preferred food of seabirds is sardine and anchovy, mostly found off northern and central Namibia (Boyer & Hampton, 2001). The seasonal patterns of breeding of bank and Cape cormorants have an effect on the counts of breeding pairs at different localities. To determine breeding patterns, long-term information from aerial surveys and seabird counts on different islands are needed. Aerial surveys and censuses have shown that Cape cormorants have declined from more than a million individuals in the 1970s to 120 000 breeding pairs in the 1980s (Boyer & Hampton, 2001). According to Boyer and Hampton (2001), the abundance and distribution of Cape cormorants have changed over the past 30 years in response to the changes in sardine and anchovy abundance and distribution. The numbers of guano-producing seabirds such as the Cape cormorant in the Benguela upwelling system and Guanay cormorant (*Phalacrocorax bougainvillii*) in the Humboldt upwelling system showed a positive correlation with anchovy biomass from 1954 to 1996 (Crawford & Jahncke, 1999). According to Crawford and Jahncke (1999), Cape cormorants and anchovies were abundant in the 1920s in the BCLME. When Cape cormorant numbers decreased, so did the anchovy biomass and guano production was also proportional to anchovy biomass.

Possession Island had the greatest decline in seabird numbers over the years (Boyer & Hampton, 2001). The island of Ichaboe, on the other hand, supports the largest number (50 000) of seabirds compared with the other three islands and includes seabird species such as African penguins, Cape cormorants, bank cormorants, Cape gannets, kelp gulls, African black oystercatchers and crowned cormorants. Mercury Island and Penguin Island however have shown an increase in the number of bank cormorants over the past decade (Boyer & Hampton, 2001).

2.2.7 History of fisheries (prey species) in Namibia

In the 1960s, before Namibia's independence, fishing activities were not properly regulated and monitored; many catches and landings went unrecorded, while other catches were either over-reported or under-reported (Boyer & Hampton, 2001; Maartens, 2003). In other studies, Boyer and Hampton (2001) noted that in the 1970s and 1980s catches were controlled by the International Commission for the Southeast Atlantic Fisheries, and these catches were questionable owing to political as well as management considerations, while other catches were inaccurately recorded. Furthermore, these catches were not recorded within the sovereign or environmental boundaries but in five degree latitude bands (20–25°S and 25–30°S), a method introduced by the Food and Agriculture Organization (FAO) in the 1970s (Boyer & Hampton, 2001). In addition, foreign fishing fleets harvested marine resources outside the exclusion zones off Namibia and Angola (Van der Lingen et al., 2006). However, the catches and landings after independence (1990) were controlled and monitored by fisheries inspectors from the Inspectorate Directorate under the Ministry of Fisheries and Marine Resources. The fisheries inspectors are advised by fisheries researchers and scientists from the Lüderitz Research Centre and the National Marine Information and Research Centre in Swakopmund. The fishing sector is the third-largest sector in terms of Gross Domestic Product (GDP) in Namibia (Boyer & Hampton, 2001). After independence, measures were put in place such as exploitation rights, introduction of close seasons for some fish resources, vessel restrictions, quota allocation and restrictions on Total Allowable Catch (TACs) for the sustainable use of marine resources (Boyer & Hampton, 2001). Acoustic surveys are used in Namibian waters to estimate pelagic fish abundance and biomass. In addition, landings can also be used to estimate relative abundance of fish abundance. In summary, most of all catches from the different fishery types have decreased substantially since the 1960s (Van der Lingen et al., 2006). The different types of fisheries are trawl fisheries, purse seine fisheries, line and pole fisheries, as well as trap fisheries. Hake fishery is the most important fishery in Namibia in terms of monetary value as it contributes N$3.9 billion in exports (Maartens, 2003). According to Maartens (2003), some of the notable declines in some fisheries, particularly the hake fisheries, was due to reduction in fishing effort because after independence most of the fishing fleet were foreign vessels and were not allowed to fish in the Namibian Exclusive Economic Zone. Hake catches prior to independence were about 500 000–600 000 tons per year on average; however the catches dropped to 55 000–200 000 tons annually (Maartens, 2003). Most of the catches are exported, notably to Spain and European Union countries. According to biomass surveys and hake landings, there was a slight increase of hake in Namibian waters and a decline again in the 2000s due to poor recruitment within the Namibian hake population (Maartens, 2003). In the purse seine fisheries, catches were 200 000 tons in the 1950s and rose to 1.4 million tons in 1968. Since then there has been a general declining trend caused mainly by overfishing and environmental perturbations (Boyer & Hampton, 2001). Other fish stocks such as horse mackerel fluctuated between 50 000 tons and 500 000 tons in the 1980s. Since Namibia took control of the entire fisheries they decreased to 200 000 tons per year (Boyer & Hampton, 2001). According to Boyer and Hampton (2001), the horse mackerel market was mostly in the Soviet Union. Catches of rock lobster declined drastically from 9000 tons prior to independence to a few 100 tons in the 1990s (Van der Lingen et al., 2006) and this resource was mainly exported to Japan (Boyer & Hampton, 2001).

Furthermore, the decomposition of excessive phytoplankton depletes oxygen levels over the continental shelf and these low oxygen levels affect most fish species and result in major shifts in population dynamics of fish such as fish distribution (Maartens, 2003). In summary, Namibian fisheries are still in a transitional phase after exploitation of marine resources by foreign fleets, hence the introduction of research programmes such as the Benguela Environment Fisheries Interaction and Training (BENEFIT) programme and the BCLME programme to promote extensive research, monitoring and surveillance of the resources within the BCLME.

2.2.8 Prey species

Breeding seabirds are central place foragers, meaning they are restricted to their colonies in order to feed their chicks; hence they need a sufficient food supply in a reasonable foraging distance from breeding localities. Change in the distribution of prey may have detrimental effects on the breeding success on seabirds, such as skipping reproduction if conditions are unfavourable for breeding. For example, if seabirds have to travel longer distances to their feeding grounds, they spend more energy in travelling and return to their breeding colonies in poor condition, which has a negative effect on fledglings and reproductive success (Crawford et al., 2008). It is ideal for prey species to be distributed in close proximity to the breeding localities of seabirds. Another study by Crawford et al. (2008), showed that the reduction in the abundance of anchovy in 1989 and 1990 led to the poor breeding of Cape cormorants in the Southern Benguela region. The Cape cormorants were heavily affected by the decline of small pelagic fish compared with the bank cormorants, as they are known to be sardine and anchovy specialists (Duffy et al., 1987). There is cannibalism among some fish prey species such as in hake species. The larger fish in the marine environment such as hake feed on planktonic crustaceans, lantern fish (Myctophidae), pelagic goby, squid, as well as juvenile hake (Maartens, 2003).

The area north of Lüderitz, also known as the central shelf area, is dominated by hake, pelagic goby, Cape monk, flying squid, myctophids and jacopever (Maartens, 2003). The central shelf area has a low species diversity due to the occurrence of hypoxic events. The area south of Lüderitz has higher species diversity and species found in this area include hake species (Cape hake and deep-water hake), silver bardfish, Cape John Dory, Cape gurnard, kingklip, snoek, Cape bonnet-mouth and Cape elephant fish (Maartens, 2003). As in many cormorant diet studies, fish dominates as prey items such as in the pellets of imperial cormorants (Casaux et al., 1997). Fish could also be the main prey in the diet of the cormorants under study. Adult cormorants (*P. aristotelis)* in Scotland eat 16% to 17% (mean of 288g and 267g fish/day) of their body weight per day (Johnstone et al., 1990). Cephalopod beaks and other hard prey items are also found in undigested faecal remains or pellets and are used for seabird diet studies as prey species are hardly found intact. Squid beaks can persist in seabird stomachs longer than most of the other prey hard parts (Furness et al., 1984).

There is however a fluctuation of prey species in the marine environment depending on various factors. The effects of these fluctuations or variations of prey species can be seen in changes in prey abundance, prey distribution, seabird diet and breeding success of seabirds (Boyer & Hampton, 2001). Therefore, studies of these two seabird species over longer periods can give insight into the foraging range of the seabirds. The diet studies data and analysis can also be used as a guideline to show good nursery areas for other prey species that form part of their diet but are also commercially important, such as lobsters. Such studies can be used in the management of sanctuaries and marine protected areas.

2.2.8.1 The bearded goby

The bearded goby is a very important component (prey item) of the BCLME, particularly the Northern Benguela (Salvanes et al., 2011). The bearded goby *Sufflogobius bibarbatus* is more abundant south of Cape Cross in Namibia. According to Salvanes et al. (2011), the bearded goby is a major prey species for large populations of seals (*Arctocephalus pusillus pusillus*), horse mackerel (*Trachurus trachurus*), hake (*Merluccius capensis*) and the African penguin (*Spheniscus demersus*). Bearded gobies were important prey numerically in the diet of seabirds on islands north of Lüderitz from 1978 to 1982, but less prominent in the seabird diet south of Lüderitz (Crawford et al., 1985; Kemper & Simmons, 2015). The bearded goby is a demersal fish that occurs up to 90m depths (Figure B.1A). The larval assemblages of the bearded goby are available throughout the year but more so during the strongest upwelling periods (Olivar & Shelton, 1993). The juvenile and adult bearded gobies do not occur in the same habitats. The juveniles, which are 3 to 7cm in length, occur in the pelagic layer, while the adults that grow to 7 to 15cm are more demersal as they prefer cooler waters (Bianchi et al, 1999). Cape cormorants feed on a wide range of length classes of bearded gobies but bearded gobies of 35mm and less in length dominate and these juvenile bearded gobies are typically pelagic as they show characteristics of pelagic fish such as lighter colouration compared with benthic species (Crawford et al., 1985). The bearded gobies have a diel vertical migration (DVM); this is when the fish stays on the sea bed during the day and migrates to waters above the seafloor at night (Salvanes et al., 2011). According to studies done by Cooper (1978), it was observed that bank cormorants fed on significantly larger bearded gobies on average compared with Cape cormorants at the same time of year (Cooper, 1978).

2.2.8.2 Rock lobster

Another important prey species in the diet of cormorant species in the BCLME is the rock lobster (*Jasus lalandii*) (Figure B.1F and Figure B.1H). The rock lobster is a commercially important species on the western coast of southern African (Heydorn, 1969; Newman & Pollock, 1971). Mostly, bank cormorants feed on juvenile rock lobsters. Lobsters are linked to cool waters and they range around the 25°S latitude up to Cape Point in South Africa but in Namibia they are predominantly off Lüderitz close to rocky shore areas (Boyer & Hampton, 2001; Hampton, 2003). According to Newman and Pollock (1971), during calm conditions the lobsters are seen feeding and moving, but not during unfavourable conditions. Lobsters have a range of 135m depth up to the low-water mark (Heydorn, 1969) and they have onshore and offshore migrations caused by environmental as well as physiological processes and only move for small distances less than 8km (Newman & Pollock, 1971). In addition, their depth range is also affected by or limited to oxygen levels (Hampton, 2003; Maartens, 2003). The eggs of rock lobsters hatch between October and November and their larval stage is planktonic for some months until they can actively swim on their own and reach their sexual maturity at 4 to 5 years (Hampton, 2003). Rock lobsters are slow growing and long-lived species (Maartens, 2003). Furthermore, adults are found offshore although juveniles are closer to shore (Hampton, 2003). Kelp beds form shelters for adult and juvenile lobsters and are food sources for various other marine organisms (Heydorn, 1969). According to Maartens (2003), there are two lobster sanctuaries in Namibia: the Ichaboe Island sanctuary and the Lüderitz sanctuary between Diaz Point and north-east point (26°34’S). However, there is a third sancuary south of Possession Island known as the southern lobster sanctuary (Ministry of Fisheries and Marine Resources, 2009). The southern lobster sanctuary is located between Chamais Bay and Prince of Wales Bay and covers a marine area of 478.07km² (Ministry of Fisheries and Marine Resources, 2009).

2.2.8.3 Cluepeiform species

Cluepeiform species are also prey species for the seabird species under study. The clupeiform species group includes anchovy, sardine and round herring. Sardine and anchovy exist together in temperate waters from KwaZulu-Natal (South Africa) to southern Angola, although they spawn in different areas divided by the Lüderitz upwelling cell (Boyer & Hampton, 2001; Hampton, 2003). Mostly, cluepeiform species spawn when the upwelling is less intense or quiescent around the Lüderitz upwelling centre (Olivar & Shelton, 1993). Sardines spawn 60km offshore central Namibia and further north at the Angolan front and Benguela current boundary relatively late in summer at 200m depths and around temperatures of 19 °C to 20 °C; on the other hand spawning of the same species in southern Namibia occurs in summer in cooler waters close to upwelling cells (Hampton, 2003). Off the Namibian coast, larval assemblages that dominate during strong upwelling periods are the bearded goby, *Lampanyctodes hectoris*, *Maurolicus muelleri* and Cape hake (*Merluccius capensis)* and during periods of less or no upwelling, *Sardinops ocellatus, Trachurus trachurus capensis* and *Engraulis capensis* dominate (Olivar & Shelton, 1993). Spawning of cluepeiform species such as anchovy occurs in clearly defined areas apart from the distributional range as a species, and for their succesfull recruitment, there are various factors that play paramount roles such as food availability, wind and temperature (Mullon et al., 2002). According to Hampton (2003), anchovy spawns offshore north of Walvis Bay in a vicinity of 100km from the coast. Furthermore, when the Lüderitz upwelling is less intense or weak, the anchovy spawned in the Western Cape can move past this environmental barrier (Lüderitz upwelling cell) and enter Namibian waters. However, according to Maartens (2003), sardines, anchovy, round herring and mullet occur together within 50km from the shore and they are widely distributed across the shelf. All these cluepeiform species: anchovy, sardine, round herring, mullet and horse mackerel are found around 100m depth (Boyer & Hampton, 2001). Round herring found in Namibia is predominantly juvenile and is caught as a bycatch in purse seine fisheries (Boyer & Hampton, 2001). According to Mullon et al. (2002), wind and temperature have many ecological and biological implications that affect the survival of larval assemblages of anchovies. Wind on its own affect the intensity of currents and the level of offshore transport. Anchovies spawn between September and December on the Agulhas Bank and the larvae and eggs are carried by jet currents to the nursery areas northwards on the southern west coast of Africa (Mullon et al., 2002). However according to Hampton (2003), acoustic surveys indicate that anchovy spawn late summer. Less anchovy was landed in Namibia prior to 1966, but catches improved after the downward plunge of the sardine fishery. The shift from sardine fishery to anchovy fishery could be due to overfishing of sardine fish stocks or the change in mesh size which prevented high catches of anchovy previously. According to Hampton (2003), the Benguela *Niño* of 1963 and 1974 caused the sardines to accumulate off Walvis Bay. In addition, Benguela *Niños* and overfishing resulted in the reduction of sardine biomass in Namibian waters. Before the 1980s, sardines used to spawn off Walvis Bay, but owing to the change in the population structure, migration partterns, and distribution due to overfishing, they now spawn in less convenient spawning grounds north of Walvis Bay (Daskalov et al., 2003). According to Hampton (2003) and Boyer and Hampton (2001), there has been a northward movement in the distribution of sardines since the downward plunge of the fishery due to overexploitation of the populations spawning in the Southern Benguela region. This in the end resulted in poor recruitment and therefore less prominence in the diet of seabirds feeding in the Northern Benguela region. According to Daskalov et al. (2003), sardines in Namibia have their spawning peak between January and March.

Before the collapse of the sardine fishery, the Cape cormorant diet consisted mainly of sardines (*Sardinops sagax*) (Mathews & Berruti, 1983). The study that was done in 1958–1959 by Mathews and Berruti (1983), shows that most of the sardines found in the diet belonged to the class of 3 to 6 years old (with length ranging from 14.5cm to 24.7cm). According to Mathews and Berruti (1983), the fall in this fishery resulted in variations in the diet of Cape cormorants; changes in populations caused diet switching of various seabirds. The sardines had a 71% frequency of occurrence, 90% by mass and 76% by abundance in the diet of Cape cormorants (Mathews & Berruti, 1983; Crawford et al., 1992). It is suggested that anchovy only became abundant after the sardine collapse (early 1970s). After the anchovy fishery collapsed, the Cape cormorants switched to bearded goby (*Sufflogobius bibarbatus*) (Mathews & Berruti, 1983). It is also believed that anchovy became abundant due to the change in mesh size regulations that allowed more anchovy to be caught than previously.

2.2.8.4 Horse mackerel

Horse mackerel as a prey species is found almost over the entire continental shelf and spawn off northern Namibia and southern Angola. They are divided from South African stock by the Lüderitz upwelling centre; however there is little connection between the stocks from the two countries (Boyer & Hampton, 2001; Hampton, 2003). The cormorants under study feed on juvenile horse mackerel that takes up the epipelagic zone in the ocean. According to Maartens (2003), Cape horse mackerel are common off southern Angola as well as northen Namibia. Another species of horse mackerel, the Kunene horse mackerel (juveniles), is mostly found in southern Angola and at times off northern Namibia (Boyer & Hampton, 2001). Horse mackerel favour warmer waters for spawning and they spawn mid-October to March in the mixing frontal zone between cool coastal upwelled waters and warmer oceanic waters. Juvenile horse mackerel are notably found off northern Namibia at depths of 200m and are also generally found inshore (Hampton, 2003). In winter, the larger individuals of Cape horse mackerel move southwards (Walvis Bay), while mature adults move from Walvis Bay towards the north to spawn mostly north of the 21°S line (Boyer & Hampton, 2001).

2.2.8.5 Hake

The seabirds under study, especially bank cormorants, feed on demersal fish species such as hake. However, it is mostly juvenile fish that are found in the diet of cormorants, although most of the juveniles are more prevalent in the pelagic zone of the ocean. Hake species spawn off Walvis Bay around 200m depths (mesopelagic zone) through the entire year and their spawning peak is between mid-spring and early summer (Hampton, 2003; Maartens, 2003). However, the distribution of hake in Namibia is affected by temperaure and low oxygen events such as the 1993 and 1994 hypoxic events (Boyer & Hampton, 2001; Hampton, 2003; Maartens, 2003). According to Boyer and Hampton (2001) and Maartens (2003), juvenile hake species have a diel feeding pattern similar to the bearded goby where the fish feed in the demersal zone during the day and at night they migrate to the pelagic zone. Bottom-trawl surveys do not necessarily determine juvenile hake growth rates and when the fish are hatched, as they are only done once per annum during summer (Wilhelm et al., 2013). Furthermore, hake species tend to move to deeper waters as they grow old (Boyer & Hampton, 2001; Wilhelm et al., 2013). Therefore only juvenile hake is found in the diet of seabirds as they do not forage more than 200km offshore. There are three hake species in the BCLME, *Merluccius capensis* (Cape hake), *M. paradoxus* (deepwater Cape hake) and *M poli*. However it is only the Cape hake and the deepwater Cape hake that are found in Namibia. The Cape hake occurs in the depth range of 0–380m at water temperatures between 4 and 8 °C, while the deepwater Cape hake is found at a depth range of 150–800m and at water temperatures between 4 and 12 °C. In addition, the former is more common in Namibian waters (off central Namibia) and its nursery areas are off south of Cape Columbine, close to Walvis Bay and off the Orange River.

2.2.8.6 Kingklip and West Coast sole

Other demersal fish such as kingklip and sole are prey species of seabirds but only in their juvenile phases. Kingklip is found on rocky bottoms at around 250m–400m depth and is mostly found north of Lüderitz and tends to differ from the South African stocks, while the West Coast sole in Namibian waters is found on soft botoms at depths of 75m–300m around the 20°S and 25°S lattitudes (Hampton, 2003). These two species are demersal fish but their larvae assemblages are found in the pelagic or meso-pelagic oceanic zones. In addition, demersal species larval assemblages are more abundant when upwelling is strong/intense (Olivar & Shelton, 1993).

2.2.8.7 Snoek

Seabirds only feed on juvenile snoek. Juvenile snoek are also found in the diet of seabirds in the BCLME. Snoek spawn around the edge of the continental shelf in winter and spring and their distribution ranges from Cape Agulhas to southern Angola (Boyer & Hampton, 2001; Hampton, 2003). According to Hampton (2003), there are two snoek fish stocks in Namibia and one population is found in the Northern Benguela while the other is found in the Southern Benguela; however, both populations spawn around the same time. The environmental barrier between these two populations is the Lüderitz upwelling cell.

2.2.8.8 Other prey species

Mussels constitute a very minor (incidental) part of seabird diet, including cormorant species. According to Maartens (2003), mussels are most dominant along the coast around the Langstrand area (83%) and the Cape Cross area where they constitute 75% of the inter-tidal zone. Other large populations of mussels are found between Walvis Bay and Sandwich harbour (Maartens, 2003). Most mussels are found within the intertidal zone along the entire coast. Nektonic organisms also form part of seabird diet. Nektonic organisms are free-swimming organisms in the marine environment. According to Maartens (2003), these organisms include African mud shrimps, *Solenocera Africana*, and are distributed off northern Namibia between Walvis Bay and the Kunene River. Other nektonic species that dominate in this same area include the thinlip splitfin, longfin bonefish and the large *dentex* (Maartens, 2003).

Planktonic species are not prey species for seabirds but they are food sources for many fish species that are in turn eaten by seabirds. The planktonic species forms the basis of food webs. Planktonic organisms include phytoplankton and zooplankton. Furthermore, phytoplankton are also good indicators of the health state of the marine environment and can indicate if there is an environmental change in the marine environment (Maartens, 2003).

2.2.9 Predations on seabirds

Seabirds are among the top predators in the BCLME but they are also regarded as prey species by other top predators. Marine mammals such as seals can negatively affect seabirds that have threatened conservation statuses (David et al., 2003). According to David et al. (2003), it was thought that only few lazy individual seals fed on seabirds until the number of seals increased due to the halt of indiscriminate killing of seals in the late nineteenth century and this problem of a few individual seals was magnified. However, this type of predation has dangerous effects on seabirds such as bank cormorants, Cape cormorants, African penguins, Cape gannets and crowned cormorants in the Benguela ecosystem (David et al., 2003). This phenomenon was observed on Dassen Island, South Africa. In addition, the seal–seabird predation was also reported in Namibia. The Cape fur seal that is also endemic to the region is known to feed on bank cormorants and Cape cormorants in Namibia on Ichaboe Island (Du Toit et al., 2004). In Namibia, seal–seabird predation was also seen as a rare incidental event until the rapid decline of seabird numbers on Ichaboe Island and in Namibia at large. The seals preying on seabirds are predominantly sub-adult males. Furthermore, other recent studies have indicated that seabirds do not only have marine predators but also terrestrial predators such as lions (*Panthera leo*) that feed on seabirds (Stander, 2019). One incident was in April 2017 when a lioness was observed feeding on four Cape cormorants and six white-breasted cormorants at Torra Bay, Namibia. Another incident was in March 2017 when young lionesses killed cormorants and other seabirds such as flamingos and red-billed teals (Stander, 2019). Other seabirds such as kelp gulls also prey on eggs and chicks of Cape cormorants on Dyer island, South Africa (Voorbergen et al., 2012). In addition, Cape fur seals on Dyer island predate on Cape cormorant fledglings on the water surface around the island. Furthermore, Voorbergen et al. (2012) concluded that this kelp gull predation is natural and also human induced in the sense that people that do research and bird counts on the island trigger cormorants to fly off their nests when disturbed. Kelp gulls thus can prey on the eggs and chicks of the Cape cormorants. Predation on seabirds together with other factors has drastic effects on seabird populations globally.

CHAPTER THREE: RESEARCH DESIGN AND METHODOLOGY

The chapter will cover different topics under research design and methodology. Firstly the chapter will look at the research design. The research design will explain the type of procedures and methods used in collecting and analysing data for the different variables like spatial, temporal, inter-annual and prey species abundance in the diet of bank and Cape cormorants. The study used two types of research design and it was field experiment survey and laboratory based analysis. The chapter further will discuss the literature review of different methods to study seabird diet as well as a desktop study of the methodology. This will basically review other methods and explain why some methods were used over others. There is a section of data collection explaining how the diet data for bank and Cape cormorants were collected. Furthermore, chapter three has a field sampling section that deals with the sampling techniques used as well as procedures on how to work with seabirds and to avoid disturbance of seabirds in their natural environment. The chapter will explain data analysis and the different statistics used to analyse the data of the study. Lastly, the chapter will look at the distribution of bank and Cape cormorants on the different islands and the techniques and software used to determine the distribution as well as the counting techniques for the seabirds on the islands.

3.1 Research design

The collection of pellets was done as part of a larger monitoring programme involving technical staff based on the islands. The study used two types of research designs: field experimental survey and laboratory-based analysis. For the field experimental survey, the islands were visited from 2003 to 2017 on various occasions throughout the years and the species under study were observed in their natural setting. The distribution of both bank and Cape cormorants was observed and recorded on the four maps of the islands. The Google Earth software package was used to digitize the distribution of cormorants on the different islands. Fresh regurgitated pellets were opportunistically collected in their natural environment (Plate 3.1A). The population of the study was all the bank and Cape cormorants breeding and roosting on the four islands and the sample was only the seabirds whose pellets were collected. The pellets with their prey items are found at the breeding and roosting sites of the seabirds. The pellets were opportunistically collected throughout the year but with little or no disturbance to the seabirds. The pellets were then taken to the laboratory for analysis. This constituted the second part of the research design. In the laboratory, the collected pellets were air dried and crushed, and identifiable prey remains were identified (Plate 3.1D). Quantitative methods were used to analyse the data collected numerically.

3.2 Methodology

3.2.1 Literature review and desktop study

Various methods are used to study seabird diet, depending on the research questions and the objective of a study. The methods include making observations of birds feeding at sea, looking at stomach contents (either by killing the bird or inducing vomit), and by analysing pellets for undigested prey items (Johnstone et al., 1990; Grémillet & Plös, 1994; Derby & Lovvorn, 1997). Another method of studying seabird diet is through stomach temperature variations caused by intake of food by homeotherms (Grémillet & Plös, 1994). Killing of seabirds for diet studies should be avoided or kept minimal. Observation of birds feeding reveals more of foraging behavour of seabirds than diet. Comparing diet composition, fish availability and fish abundance in piscivorious seabirds is very difficult because of technical problems in fish sampling, recording predator–prey interactions under water as well as assessing bio-energetics involved in prey selection by seabirds (Suter, 1997).

Several seabird species regurgitate pellets of indigestible material and these pellets are very important in studying seabird diet as this method causes little disturbance to the birds and large samples can be collected (Duffy & Laurenson, 1983). Samples of pellets can be used to study diet regimes of these seabirds. Marine cormorant species such as Cape cormorant, bank cormorant and crowned cormorant can also use mainland breeding habitats like cliff ledges, caves, stacks on rocky shores, boulders, guano platforms, shipwrecks, jetties and piers, and moored boats, as these habitats are naturally not accessible to land-based predators (Bartlett et al., 2003). The pellets are collected on islands at the nesting or roosting sites of both seabird species under study. Fresh regurgitated pellets of bank cormorants are covered in clear mucous and are much bigger than pellets of Cape cormorants (Kemper et al., 2007). Cape cormorants' regurgitated pellets are covered in yellowish mucous. Otoliths and other items in the pellets were used to determine diet composition of both Cape and bank cormorants. The use of cormorant pellets for diet is good for long-term studies showing changes in the marine environment. Diet samples should be processed and analysed as soon as possible as preservation of samples changes certain characteristics that aid in identification of prey items such as colour, smell, size and mass (Duffy & Jackson, 1986) and pellets need to be collected as soon as possible to avoid losing pellets to scavenging Hartlaub's gulls, *Larus hartlaubi* (Duffy et al., 1987). Frequency of occurence of prey species can be used to express diet from pellet analysis (Punta et al., 1993). Here, the percentage of prey species in the pellets collected can be used by examining the presence and absence of prey species in the pellets collected.

However, as with any method used for diet studies, there are some advantages and disadvantages. According to Kemper et al. (2007), the advantage of using pellets in diet studies is that pellets are easy to sample and a more humane method, while the method is least destructive. Another advantage of using pellets is that a large sample size can be collected with less effort and time (Derby & Lovvorn, 1997). The advantages of using pellets are: they are a cheap or less expensive method and there is fewer disturbances as pellets are collected when the birds are out feeding (Kemper et al., 2007). The disadvantage of using pellets is that certain biases are associated with this method and there is an inability to assess the retention time of some prey species/elements in the stomach of the predator (Kemper et al., 2007). The digestive acids may completely or partly dissolve some of the otoliths in the digestive track of the seabirds (Derby & Lovvorn, 1997). Like most methods in diet studies, the method of using pellets has its limitations, for example, otoliths are reduced in size (at least by 25% in length from digestion and production of pellet), otoliths are broken, making identification difficult, etc. Another major drawback of using pellets is that small fish or fish with small otoliths are under-represented as the small otoliths are completely digested or pass through the digestive track (Duffy & Jackson, 1986; Johnstone et al., 1990; Suter & Morel, 1996). In addition, otoliths and other bony remains from regurgitated pellets are affected to different degrees by gastric fluids in the digestive tracts of birds (Suter & Morel, 1996). Despite the setbacks, regurgitated pellets and the otolith method in diet analysis are still widely used (Derby & Lovvorn, 1997).

3.2.2 Data collection

In this study, a field research design was used because this method studies the subject in its natural environment and the results have a higher probability of reflecting reality as the seabirds are unware that they are being studied. Another method used was the laboratory research design: this was the analysis of regurgitated pellets in the laboratory to uncover the diet composition of the bank cormorant and Cape cormorant. The laboratory research design was chosen because it gives quantitative information and the researcher could not have an effect on the results (Zar, 1999). The sampling method was random sampling, to give the seabirds in the colonies an equal chance of being studied or selected. The advantages of random sampling are that costs are reduced by not studying the entire population, and data can be analysed more quickly.

In Namibia, bank and Cape cormorants are resident breeding seabirds that can be seen on Namibian islands throughout the year but are more frequent in the summer season. Numbers reach their peak between October and February on average. Regurgitated pellets were used to determine the diet of the cormorant species. The three islands (Mercury, Ichaboe, and Possession) under study have been inhabited since 1990 by MFMR researchers and they have collected regurgitated pellets on the islands since 1990. Collection is still continuing and many collected pellets have not been analysed. In total, 1957 regurgitated pellets were collected from 12 January 2003 to 24 August 2017 for this study. Of the 1957 pellets, 834 were collected from 2 January 2015 to 24 August 2017 from all four islands. The pellets were collected in different months within the different years and not all the months within the years were sampled.

However, in some years regurgitated pellets for both cormorant species were not collected owing to various reasons and research interests such as the inaccessibility of some colonies (indicated by the shaded area in Table 3.1), seabirds not breeding on some islands in some years, pellets not collected because of poor sea conditions for the research vessel, pellets being preyed on by predators, and pellets being degraded by elements such as water. Bank cormorant pellets were not collected on Penguin Island in 2008 and 2009. On Ichaboe Island, to avoid disturbance, the bank cormorant colonies were not accessible for pellet collection as the cormorants would fly away and leave the nests vulnerable to other predatory seabirds that prey on their eggs and chicks. On Possession Island, the nests of breeding bank cormorants were inaccessible and pellets were collected only from roosting sites. For the purpose of this study, pellets of both bank cormorants and Cape cormorants were collected from 2015 to 2017 on all four islands. Collection of pellets was more erratic before 2003, hence data from 2003 to 2014 was regarded as old data and data from 2015 to 2017 as recent data. The table below (Table 3.1) shows the years in which regurgitated pellets from bank and Cape Cormorants were collected on all four islands.

Table 3.1: The years in which regurgitated pellets from bank cormorants (BCs) and Cape cormorants (CCs) were collected, indicated by * on all four islands.

Island	Mercury		Ichaboe		Penguin		Possession	
Year	BC	CC	BC	CC	BC	CC	BC	CC
2003	*	*	*	*				
2004	*	*	*	*				
2005								
2006								
2007	*	*		*				
2008	*	*	*	*		*		
2009	*	*	*			*		
2010	*	*						
2011	*							
2012	*			*				
2013	*		*	*				
2014		*		*				
2015	*	*	No	*	*	*	*	*
2016	*	*	Access	*	*	*	*	*
2017	*	*	to colony	*	*	*	*	*

3.2.3 Field sampling

During field sampling, procedures on how to work with seabirds were followed. According to Kemper et al. (2007), special care should be taken when working with cormorant species to avoid disturbances and nest abandonment as these seabirds are gregarious. The pellets were collected when available and accessible using a research vessel (RV *Anichab*) to visit the islands (Plate 3.1C). On all the islands, fresh regurgitated and complete pellets were collected individually at accessible nest sites of Cape and bank cormorants. The pellets of the bank cormorant differ from those of the Cape cormorant in colour and size (Kemper et al., 2007). The pellets were collected by hand and put in zip-lock bags and labelled with date of collection, locality and bird species. A total of 1957 pellets were collected at known roost sites for Cape and bank cormorants and only 1920 were analysed due to quality. The sampling method of pellets was opportunistic sampling. Opportunity sampling is a convenient method of getting pellets in a natural setting. The pellets were air dried on a tray in the laboratory. Once the pellets were dry, each individual pellet was rolled up in tissue paper and taped with masking tape. Masking tape was used to prevent the pellet from unravelling and moulding. The masking tape was marked with information such as date, locality, seabird species, pellet number and place of collection. The pellets then were packed in a set of samples ready for the next step, pellet analysis.

The retrieved pellets from the rolled-up tissue papers were then crushed individually by hand while wearing latex gloves and identifiable indigestible prey remains such as shells, squid beaks and fish otoliths were separated and counted with the aid of a binocular microscope for smaller prey remains (Plate 3.1). Pellets can also consist of carapaces of crustaceans, mandibles and other hard parts such eye lenses. Otoliths found in the pellets can be used to determine the type of fish eaten and can also be used to determine the size of the fish consumed with correction factor of each individual prey species (Duffy & Laurenson, 1983). The recovered indigestible prey remains were identified up to order, family, genus or species level. Different fish otoliths were identified using identification manuals (Smale et al., 1995). Prey species were identified according to standard procedures as indicated by Derby and Lovvorn (1997). Reference collections were also used to identify fish otoliths. Identified parts from each individual pellet were packed into smaller zip-lock bags with labels inside. All identified prey remains were separately placed in each bag (40mm x 60mm) and all these bags from one individual pellet placed in one bigger zip-lock bag (60mm x120mm). The identified prey remains from the pellets were stored per colony and collection date for reference and future studies. From the 1957 collected pellets, only 1920 contained prey species after pellet analysis and 37 pellets contained only stones, glass pieces and seagrass.

Plate 3.1: Searching and collecting of fresh regurgitated pellets of both bank cormorants and Cape cormorants (A), collecting and wrapping of pellets in tissue paper (B), the RV *Anichab* used to access the islands (A), sorting of prey items such as otoliths from the pellets (D).

3.2.4 Data analysis

To express diet composition from the pellets, frequency of occurence of prey species was used as well as abundance in numbers for prey remains that could be quantifiable. From the entire data set, it was prey remains from crustaceans and molluscs that could not be quantified. Therefore, frequency of occurrence was used because not all prey remains could be quantified. It was assumed that all pellets of the same seabird species are of equal sizes. For relative comparison between samples with different sizes, the number of prey individuals was expressed per pellet for different species on different islands. For all statistical analysis, IBM statistical software was used.

To test for temporal variability with statistical analysis, an Independent Samples *t*-Test (Levene's Test for Equality of Variances) was used to test whether there was a significant difference for bank cormorant diet between the summer and winter season. To test for significant differences in the diet of Cape cormorants between summer and winter, an Independent Samples Test (Levene's Test for Equality of Variances) was used. To test statistically for spatial variability between the diets of bank cormorants on the different islands from 2003 to 2017, the one-way analysis of variance (ANOVA) was used. To test for spatial variability between Cape cormorant diets on different islands, a one-way ANOVA was used. The one-way analysis of variance (ANOVA) was further used to test for inter-annual variability in the diet of bank cormorants from 2003 to 2017 and the same one-way ANOVA was used to test for significant differences in inter-annual variability of Cape cormorant diet from 2003 to 2017.

3.2.5 Distribution of cormorants on the islands

To determine seabird distribution and abundance on the islands, head counts of breeding and non-breeding seabirds are done every month. Known breeding and roosting areas are counted using binoculars and tally counters. There is a map of each island on which seabird distribution or the size of cormorant colonies are indicated with the use of the Google Earth software package. Seabird monitoring and counting techniques are used as described by Veldkamp (1995) and Kemper et al. (2007). Mostly annual peak counts of active nests are used for the population of breeding pairs (Kemper et al., 2007). However, the annual peaks may differ from species, years and sites.

CHAPTER FOUR: RESULTS

4.1 Distribution of cormorants on the islands

The figures below, Figure 4.1 to Figure 4.4, show the distribution of the breeding pairs of bank and Cape cormorant colonies on the islands. Cape cormorants are more abundant on three islands (Ichaboe, Penguin, and Possession) than bank cormorants and they are also widely distributed. Mercury Island is the only island where bank cormorants are more abundant and more widely distributed than Cape cormorants.

Figure 4.1: The distribution of bank cormorants and Cape cormorants on Possession Island

Figure 4.2: The distribution of bank cormorants and Cape cormorants on Penguin Island

Figure 4.3: The distribution of bank cormorants and Cape cormorants on Ichaboe Island

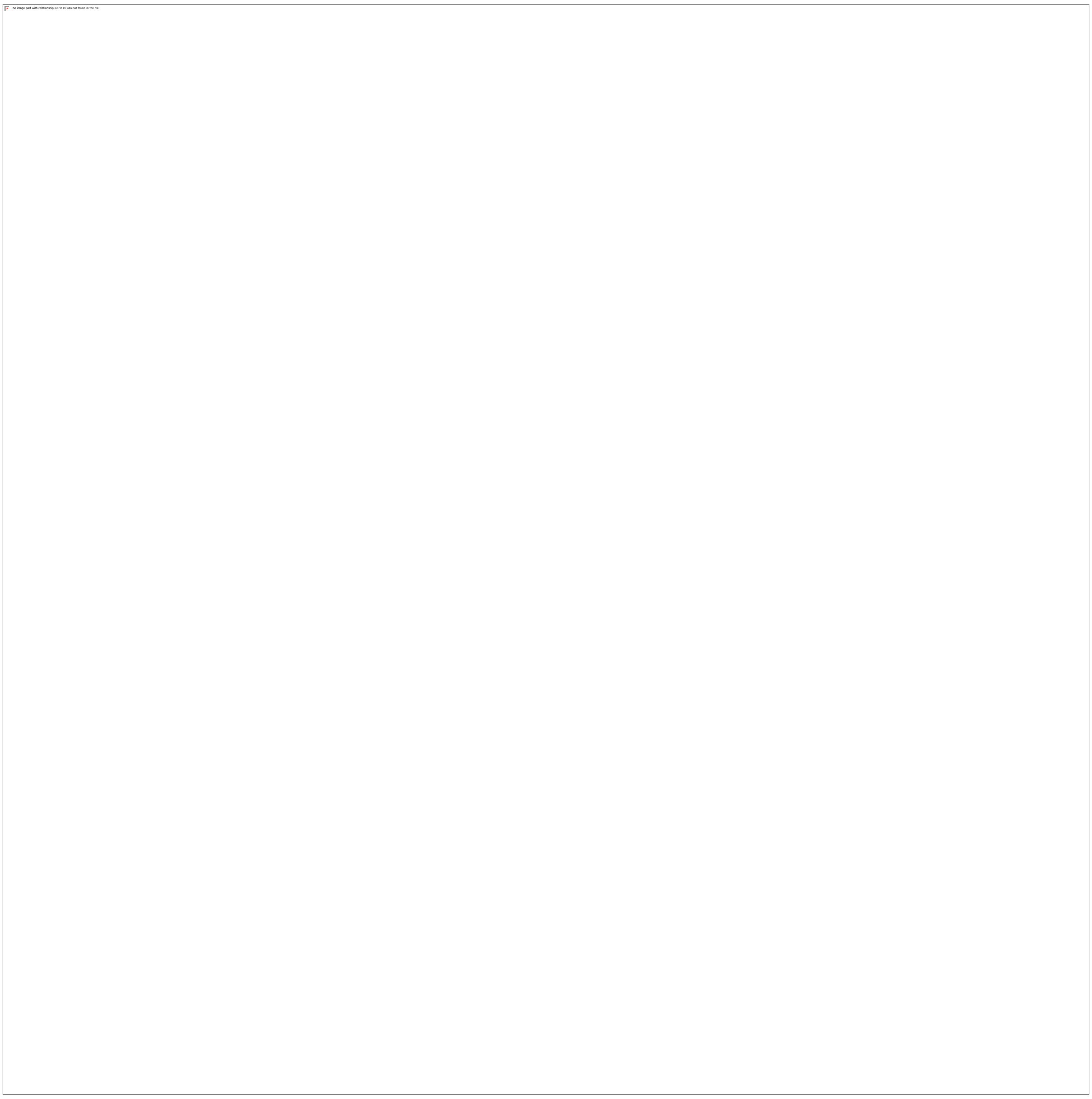

Figure 4.4: The distribution of bank cormorants and Cape cormorants on Mercury Island

4.2 Sampling populations

Table 4.1 overleaf shows the sampling populations of both the bank and Cape cormorants on the islands, the number of sampling years, as well as the number of pellets collected on each island, which is the sample size from each island of each seabird species. The population size in Table 4.1 is the number of breeding pairs. In total, 1048 Cape cormorant pellets and 873 bank cormorant pellets were collected and sorted from the four islands from 2003 to 2017. The number of pellets depended on the breeding population sizes of the cormorant species on each island as well as the accessibility of colonies. There was an unequal sample size, therefore the number of prey per pellet was calculated to have relative comparison between the different species at different islands.

Table 4.1: Different islands with the population sizes (individuals) of both cormorant species and their corresponding numbers of samples from 2003–2017.

Islands	Possession		Penguin		Ichaboe		Mercury	
Seabird species	Bank Corm	Cape Corm	Bank Corm	Cape Corm	Bank Corm	Cape Corm	Bank Corm	Cape Corm
Population size	15	500	200	500	138	35000	2500	800
No. of sampling years	3	3	3	5	5	10	12	10
No. of pellets	46	53	76	105	73	394	678	495
No. of prey species	1065	2684	261	6997	6116	27330	80179	53001
No. of prey/pellets	23.2	50.6	3.4	66.6	83.8	69.4	118.3	107.1

The plate overleaf shows the roosting of Cape cormorants (Plate:4.2a) and the roosting of bank cormorants (Plate: 4.2c). Plate 4.2b shows a large coverage of mostly Cape cormorants and Cape gannets during the breeding season on Ichaboe Island. On Ichaboe Island, the number of breeding Cape cormorants is the highest in Namibia. The breeding pairs of bank cormorants can be seen in Plate 4.2d on Mercury Island.

Plate 4.2: Roosting Cape cormorants (A), breeding cormorants and Cape gannets on Ichaboe island (B), roosting Bank Cormorants (C), and breeding bank cormorants on Mercury Island (D).

Table 4.2 overleaf shows the various prey species found in the entire study; these are prey species found in the diet of both bank cormorants and Cape cormorants on all four islands. It can be seen that Cape cormorants have a wide range of prey species compared with bank cormorants. The diet of bank cormorants does not contain prey species such as worms, unknown species B, and unknown species D.

Table 4.2: The presence and absence of prey species found in the pellets of both bank and Cape cormorant species.

Number	Prey Species	Bank Cormorant	Cape Cormorant
1	Goby	√	√
2	Hake	√	√
3	Pelagic species	√	√
4	Horse mackerel	√	√
5	Myctophidae	√	√
6	Squid	√	√
7	Mullet	√	√
8	Crustaceans	√	√
9	Molluscs	√	√
10	Sole	√	√
11	Gurnard	√	√
12	Worm	none	√
13	Unknown A	√	√
14	Unknown B	none	√
15	Unknown C	√	√
16	Unknown D	none	√

4.3 Spatial variation

One-way ANOVA was used to test for spatial variability between the diets of bank cormorants on the islands from 2003 to 2017. It was found that there were statistically significant differences in the diets of bank cormorants from 2003 to 2017 among the islands ($p < 0.001$). From Figure 4.5, it can be seen that the frequency of occurrence of crustaceans was higher at Possession Island and Penguin Island with 58% and 77% respectively, while the bearded goby as a prey species was higher at Ichaboe Island and Mercury Island with 56% and 73% respectively. No pelagic species, hake, horse mackerel, myctophids and mullet prey species were found on Penguin Island. Pelagic species and molluscs were prevalent on the northern islands.

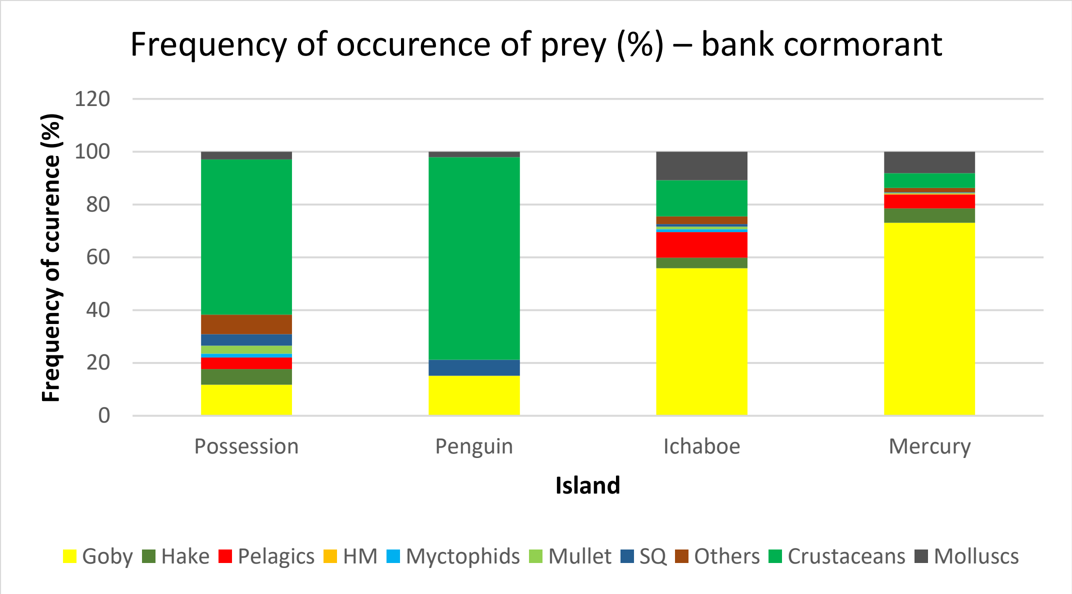

Figure 4.5: Frequency of occurrence (%) of prey species found in bank cormorant pellets on the four islands in Namibia

The results of the one-way ANOVA test were used to test for spatial variance between the diets of Cape cormorants from the year 2003 to the year 2017. It was found that there were statistically significant differences in the diets of Cape cormorants from 2003 to 2017 among the islands (sites) (p<0.001). Figure 4.6 shows the frequency of occurrence of goby was the highest on Mercury Island with 70%, followed by 66% on Ichaboe Island, Penguin Island with 46%, while Possession Island had the lowest frequency of goby with 24%. The frequency of occurrence for pelagic species was the highest on Possession Island with 21%, followed by Penguin Island with 13%. Possession Island and Penguin Island also had a higher frequency of occurrence of crustaceans compared with the northern islands (Ichaboe and Mercury). The frequency of occurrence for crustaceans on Possession Island was 16% and 6% on Penguin Island.

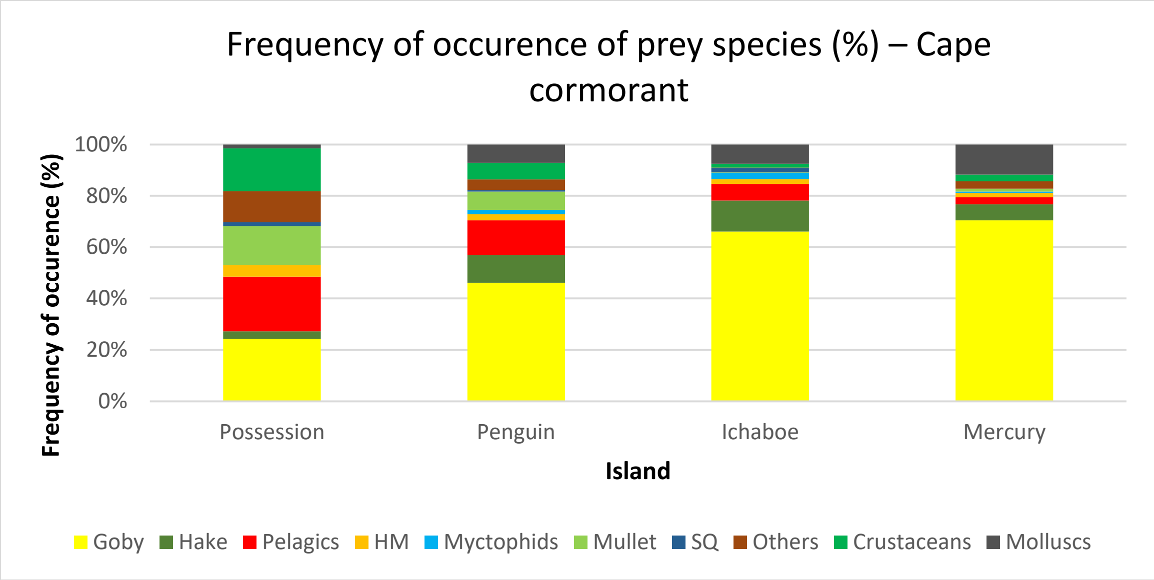

Figure 4.6: Frequency of occurrence (%) of prey species found in Cape cormorant pellets on the four islands in Namibia.

4.4 Prey species in numbers

Figure 4.7 overleaf shows the quantifiable prey species of bank cormorants, excluding crustaceans and mollusc, as they could not be quantified. It can be seen clearly that the goby dominated in abundance on Mercury Island. Mercury Island had the highest number of gobies per pellet (118.26) and Penguin Island had the least number of gobies per pellet (3.43). On Ichaboe Island, myctophids were secondly the most abundant after gobies, with 2.7 myctophids per pellet.

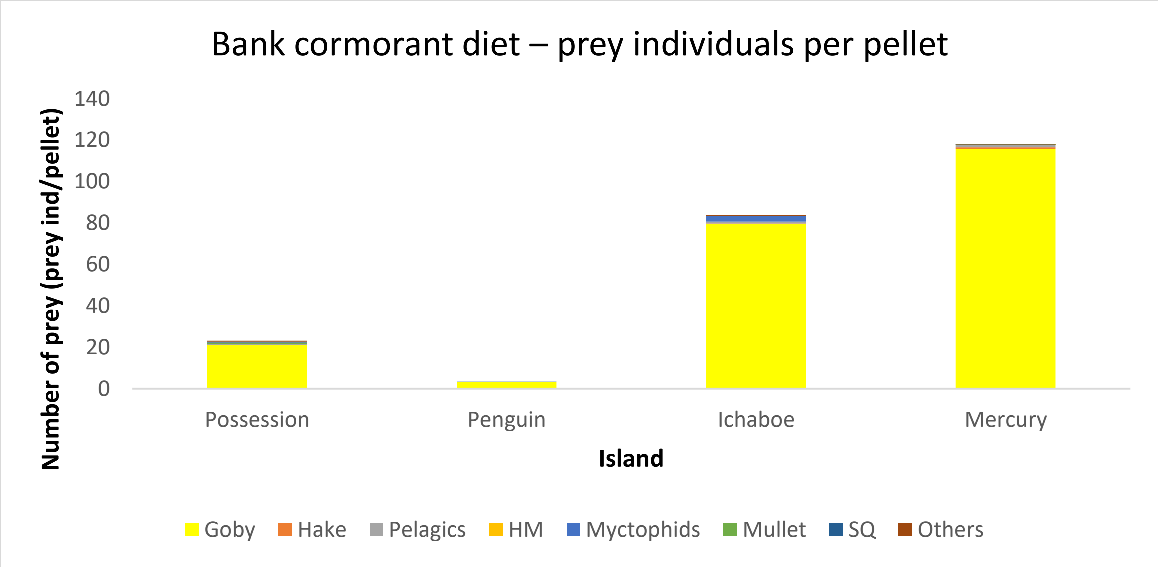

Figure 4.7: Quantifiable prey items per pellet of bank cormorants on the four islands in Namibia

Figure 4.8 shows quantifiable prey species of Cape cormorants on the islands. Mercury Island had the highest number of gobies (107) per pellet and Ichaboe Island had the second highest number of gobies (69.4) per pellet, followed by Penguin Island with 66.6 gobies per pellet. Possession Island had the lowest number of 50.6 gobies per pellet. Possession Island was, however, dominated by pelagic prey items rather than gobies compared with the other three islands, with 27.9 pelagic species per pellet.

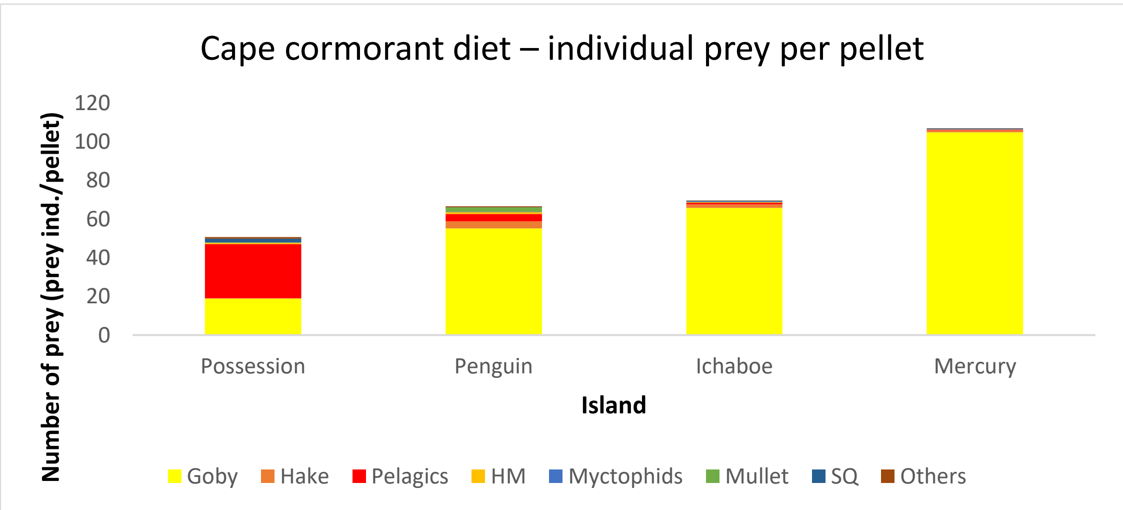

Figure 4.8: Quantifiable prey items per pellet of Cape cormorants on the four islands in Namibia

4.5 Temporal/seasonal variation

Results from the Independent Samples Test (Levene's Test for Equality of Variances) indicate that there were statistically significant differences for bank cormorant diets between the summer and winter season ($p < 0.001$) (Figure 4.9). Gobies dominated the diet of bank cormorants during the summer season as well as in early winter, while during late winter crustaceans dominated the diet of bank cormorants on all islands (Figure 4.10). Pelagic species were more prevalent in the diet of bank cormorants during the summer season compared with the winter season. Hake species only occurred in the diet of bank cormorants during the summer, while mollusc species occurred in the diet of bank cormorants in both winter and summer, but were more dominant in the summer season. No sample was collected in September, as most bird species start breeding in October. The samples collected in winter were mostly from roosting birds.

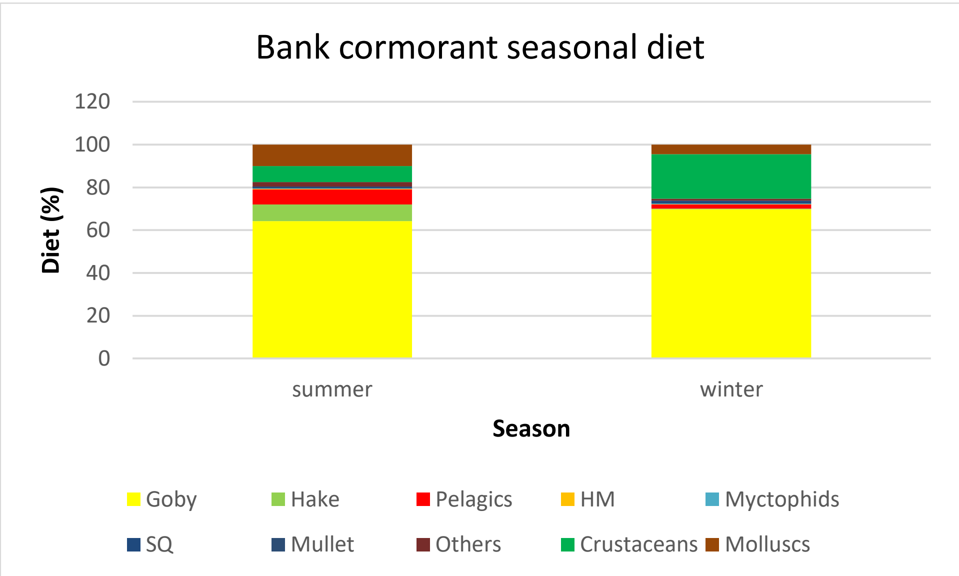

Figure 4.9: Bank cormorant prey species between winter and summer on all islands from 2003 to 2017

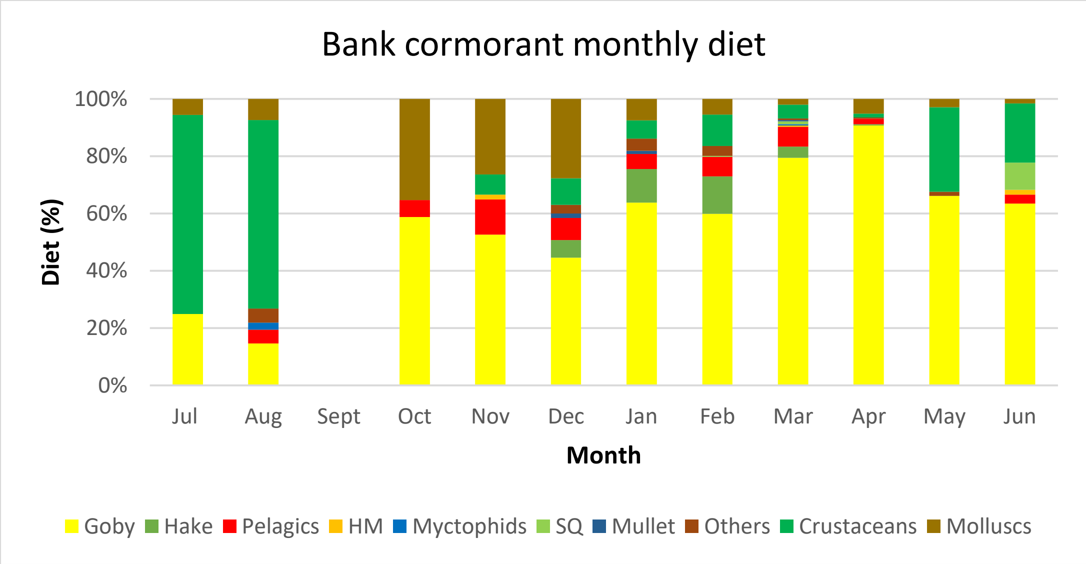

Figure 4.10: Bank cormorant monthly diet (prey species) on all islands from 2003 to 2017. Summer is from October to March and winter is from April to September.

The results from the Independent Samples Test (Levene's Test for Equality of Variances) show that there were statistically significant differences in the diets of Cape cormorants between summer and winter seasons ($p < 0.001$) (Figure 4.11). The null hypothesis was rejected. According to Figure 4.12, gobies dominated the diet of Cape cormorants, with pelagic species being more dominant in the summer than in winter. In mid-summer (December), pelagic species were more dominant as opposed to other months where gobies were dominant. Hake as a prey species was more dominant in summer than in winter in the diet of Cape cormorants. Overall, there are seasonal (temporal) differences in the diet of both cormorant species on the four islands.

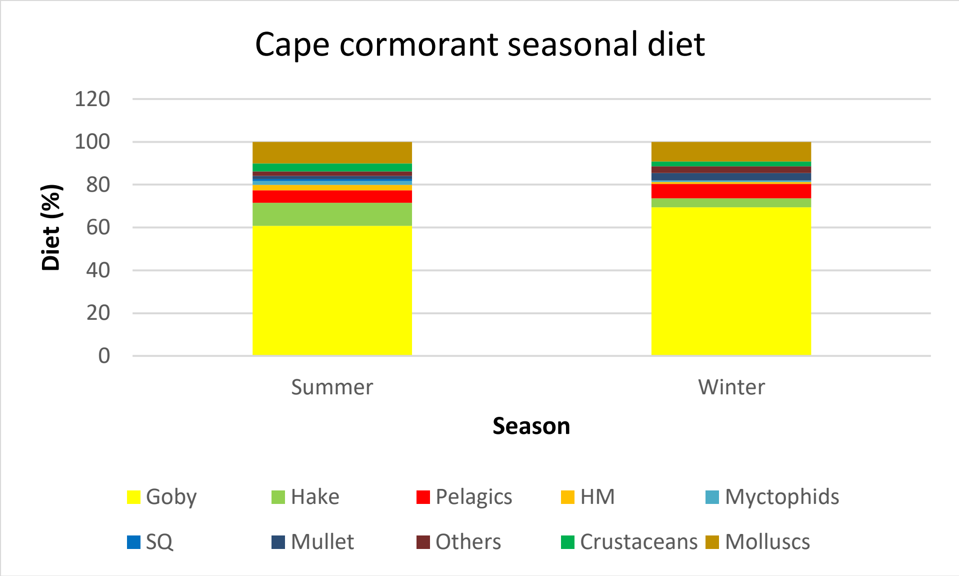

Figure 4.11: Cape cormorant prey species between winter and summer on all islands from 2003 to 2017

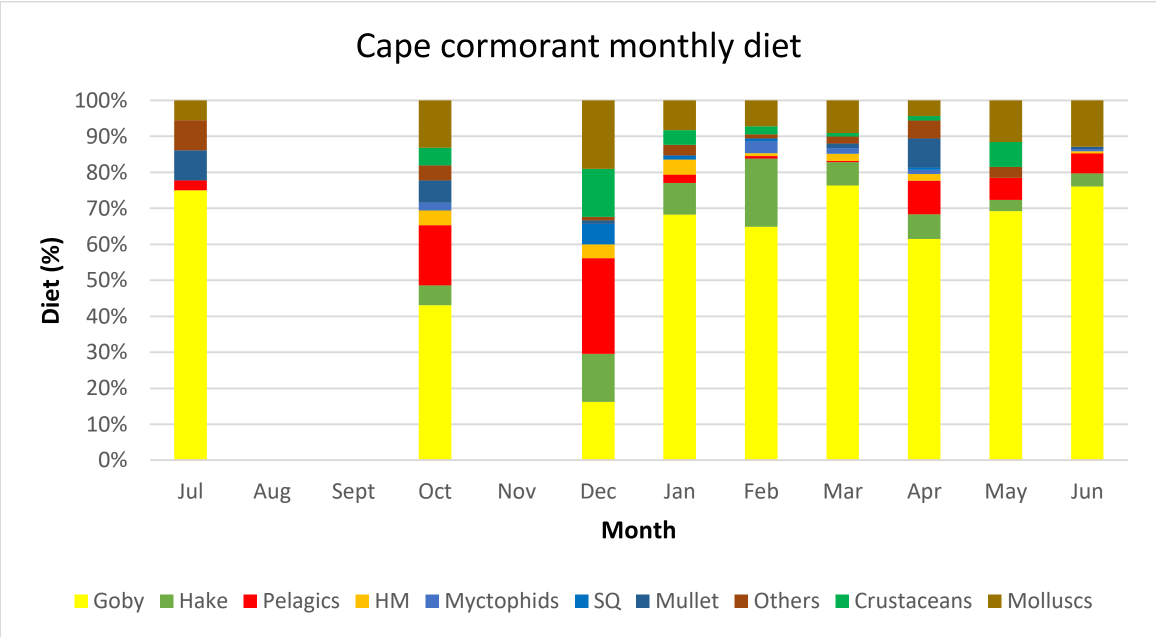

Figure 4.12: Cape cormorant monthly diet (prey species) on all islands from 2003 to 2017. Summer is from October to March and winter is from April to September.

4.6 Inter-annual variation

One-way analysis of variance (ANOVA) was used to test for significant differences in the diet of bank cormorants from 2003 to 2017. It was found that there were statistically significant differences in the diet of bank cormorants from 2003 to 2017 (p<0.001).

ANOVA was also used to test for significant differences in the diet of Cape cormorants from 2003 to 2017. It was also found that there were statistically significant differences in the diet of Cape cormorants from 2003 to 2017 (p<0.001). Figure 4.13 shows that from 2003 to 2017, the goby as prey species dominated the diet of both bank cormorants and Cape cormorants on Ichaboe Island, interchanging with crustaceans and molluscs (Figure 4.13A and Figure 4.13B), while on Mercury Island the goby as a prey species dominated all the samples from 2003 to 2017. Hake and molluscs showed a declining contribution to the seabird species (Figure 4.13C and Figure 4.13D). In Figure 4.13E and Figure 4.13F it can be seen that crustaceans were in the diet of bank cormorants from 2015 to 2017, while the goby dominated in the diet of Cape cormorants, with declining hake and pelagic species as prey species. Figure 4.13G shows that the diet of bank cormorants on Possession Island was dominated by crustaceans from 2015 to 2017 with a decreasing overall trend for both crustaceans and gobies, while there was an increasing trend for the other species. Figure 4.13H shows that the diet of Cape cormorants demonstrated an increasing trend for pelagic species and crustaceans, and a declining trend for gobies.

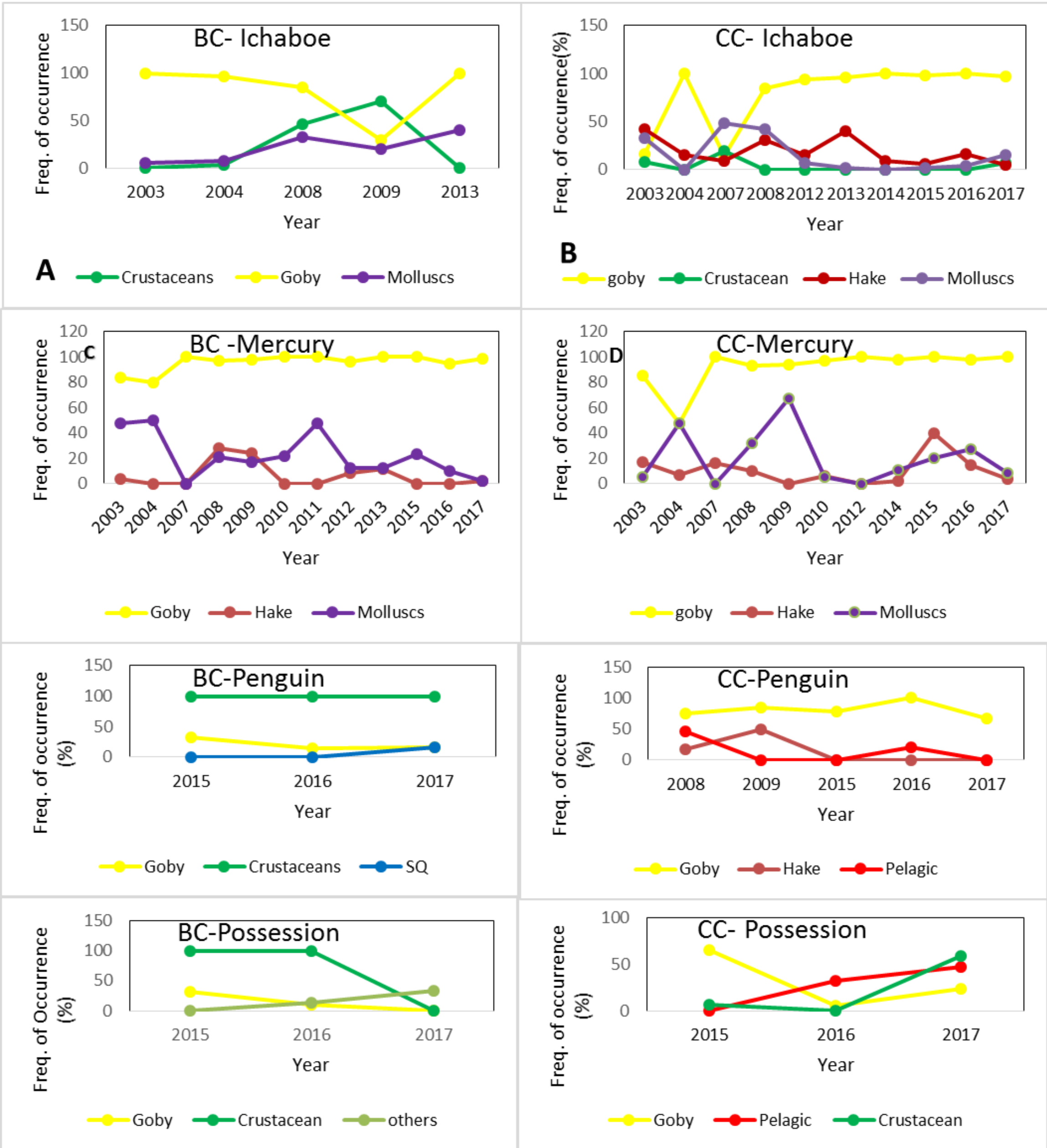

Figure 4.13: Frequency of occurrence (in %) of the most frequent prey species of bank cormorants (BC) and Cape cormorants (CC) on all four islands in Namibia from 2003 to 2017. (*Freq. of occurrence is frequency of occurrence).

The results of the study indicated that there was variability between the diets of both cormorant species spatially, temporally and inter-annually, and the bearded goby dominated the diet in numbers. In general, there was a declining trend in the number of prey species in the diet of bank cormorants and Cape cormorants over the years.

CHAPTER FIVE: DISCUSSION AND CONCLUSION/SYNTHESIS

This chapter is going to discuss the results of the study and use existing facts to support the findings of the study. The chapter will address different aspects of the results such as spatial variability, differences in the number of prey species, temporal/seasonal variability and inter-annual variability in the diet of bank and Cape cormorants on the four different islands in Namibia. From the results, there was spatial variability and this could be due to various factors such as prey distribution and foraging behaviour of the different seabirds under study. Furthermore, the chapter will have an in depth discussion on the differences in prey species observed as well to potential answers why there was temporal and inter-annual variation in the diets of the bank and Cape cormorants. Possible answers include the physiological adaptations of an important prey species, the upwelling and the variability of the Northern Benguela. The chapter also have a concluding summery as well as recommendations from the study. The recommendations include the direction for future studies as well as the limitations of the study.

5.1 Spatial variation

The results indicated that there was spatial variability in the diet of both bank cormorants and Cape cormorants, implying a difference in the diet of cormorants on the four islands studied. This is an indication that the prey species are not evenly distributed or the seabirds from the four islands have different fishing/feeding areas, hence the variability in diet due to various locations. The availability of prey species is also dependent on the foraging range of the seabirds. Prey species abundance and the quality of prey species are also important factors in influencing foraging behaviour of top predators. Bank cormorants are known to feed in the benthic zone inshore (shallow waters), while Cape cormorants feed far offshore in the pelagic zone. The two species feed in different oceanic zones, which is another reason why there was spatial variability in their diets at the different sites. If the two seabirds showed similarity in their diets it would mean the prey species were evenly distributed around the four islands. The abundance and distribution of Cape cormorants changes owing to changes in the distribution and abundance of sardines and anchovies. This means that prey species greatly affect the population dynamics of Cape cormorants in the Benguela ecosystem.

In the diet of bank cormorants, the main prey species was crustaceans on Possession Island and Penguin Island, but on Mercury Island and Ichaboe Island the main prey species was the bearded goby (Figure 4.5). The presence of crustaceans (mainly rock lobsters) in the diet of the bank cormorant can be associated with kelp beds. The area between Elizabeth Bay and Possession Island consists of a large kelp bed area which is important to marine organisms and most importantly for the recruitment and habitat of rock lobsters (Ministry of Fisheries and Marine Resources, 2009). It is understood that the areas surrounding the Possession and Penguin islands have more kelp beds compared with the northern islands, Mercury and Ichaboe. Bank cormorants are more abundant on Mercury Island, but feed more on gobies on this island. This behaviour indicates that there are fewer rock lobster habitats (kelp beds), or gobies are more abundant, compared with the southern islands of Possession and Ichaboe. Rock lobsters tend to follow the distribution of kelp beds off the Western Cape, South Africa (Crawford et al., 2008). This is the same scenario in Namibia, as southern Namibia is dominated by kelp beds and this is the same area where rock lobsters are found compared with central and northern Namibia. The substrate of the seafloor where the different seabirds feed can have an influence on the diet of seabirds. For example, seaweeds are more prevalent on rocky ocean floors than on sandy ocean floors. Seaweeds can be habitats of many prey species such as small fish and invertebrates that foraging seabirds can feed on. In addition, rock lobsters are associated with cooler waters. Possession Island is dominated by lobsters as prey species because the waters around Possession Island are cooler compared with the other northern islands (Ichaboe and Mercury). The island of Possession is closer to the southern oceans of colder water compared with the other islands that are closer to the equator. Hence, the lobsters are only found in southern Namibia and not in central or northern Namibia. Oxygen levels in the ocean have a spatial effect on fish stocks also. Low oxygen levels occur off central and northern Namibia and are associated with sulphur eruptions. Rock lobsters are found mainly in southern Namibia as they are very sensitive to changes in oxygen levels.

Reefs are known to have higher species diversity, and if the seabirds feed in the reefs, they are likely to have a higher diversity of prey species than seabirds that feed in non-reef areas. According to Maartens (2003), the central shelf area (north of Lüderitz) is dominated by hake, myctophids, pelagic goby squid and jacopever, and has low species diversity, while the area south of Lüderitz has higher species diversity. Possession Island had the highest prey species diversity in the diet of bank cormorants. Possession Island is near a reef area, while Mercury Island has no reef area in its proximity. Ichaboe Island is near a small reef, while Penguin Island is in a bay near reefs and shallow lagoons known to have a high diversity of fish species. The different topographic conditions around the various islands can contribute to the variations in diet of the two seabird species.

From the results it can be noted that the main prey species of the Cape cormorants differs spatially (Figure 4.6. On Mercury, Ichaboe and Penguin islands, the main prey species were gobies; however on Possession Island the main prey species of Cape cormorants were gobies and other pelagic species, with the 'other' prey species category also fairly represented but not dominant, such as mullet and crustaceans. Oceanographic parameters could be the reason why bearded gobies are dominant on all other islands but not on Possession Island (the most southern island). The upwelling varies spatially and temporally, depending on the depth, width and coastline angle. These properties of the upwelling can result in differences in availability of prey species because they occupy different habitats in the marine environment. Some species might be found in deeper or shallower waters, and others might inhabit slightly warmer waters than others. The islands are not located in close proximity to one another. The direct distance from Penguin Island to Possession Island is about 40km and the direct distance between the furthest islands is 148km. The Lüderitz upwelling cell can form an environmental barrier to species. In another study done by Heymans et al. (2004), it was argued that the upwelling core around Lüderitz was an environmental barrier to the movement of organisms between the southern and northern systems. The same upwelling also forms a barrier to horse mackerel that favour warmer water in northern Namibia. Horse mackerel were not common in the diets of bank and Cape cormorants on the four islands because the water is cooler, and they prefer warmer waters for spawning in the northern part of Namibia. The prevailing winds around the Lüderitz upwelling cell are the strongest, the shelf is the deepest and narrowest, and the cell acts as a physical barrier to small pelagic prey species. This includes pelagic bearded goby. The southern system has stronger prevailing winds and colder water. The Lüderitz upwelling cell can form a barrier to the movement of prey species, especially pelagic species that are more affected by the physicality of the upwelling. For example, the most northern island (Mercury) was dominated by gobies, while the most southern island (Possession) was dominated by crustaceans with regard to the diet of bank cormorants. The gobies are more abundant south of Cape Cross (Crawford et al., 1985; Salvanes et al., 2011; Kemper & Simmons, 2015). This is why Mercury and Ichaboe islands are dominated by gobies while Possession Island is not. The upwelling cell could be a barrier to the movement of gobies, especially juvenile bearded gobies that are pelagic.

5.2 Prey species in numbers

From the results of the study, the bearded goby dominated the diet of both seabird species. The bearded goby dominated the prey species in numbers of prey species per pellet as well as in the frequency of occurrence of prey species. Therefore, the bearded goby is a very important prey species in the northern Benguela (NB). The NB has been severely altered at all trophic levels since the overexploitation of small pelagic fish like sardine and anchovy, therefore most seabirds have switched their diets to a less preferred prey which is the bearded goby. The bearded goby currently dominates the diet of seabirds. It is not the preferred diet, but it is a readily available prey species in the NB as it is not commercially exploited. The bearded goby is a low-energy prey (Ludynia et al., 2010). For the seabirds to get maximum energy from feeding on gobies, they have to consume a lot of gobies, hence its dominance in the diet of the seabirds in terms of individual prey species per pellet. The bearded goby is a very small pelagic fish of about 3cm to 15cm. A prey species that provides high energy doesn’t need to be taken in abundance to satisfy the predator. Another reason why the bearded goby could dominate the diet of seabirds is that sardine and anchovy fish stocks have not yet recovered their expected levels prior to their exploitation. Sardines and anchovies are found more off central and northern Namibia. Anchovies are hardly found off Ichaboe Island and Mercury Island (Kemper & Simmons, 2015). Hence the dominance of the bearded goby, as all the islands are considered to be off southern Namibia where the data from the study was collected. If the sardines, anchovies and gobies were evenly distributed, sardines would dominate the diet of the seabirds as they are shoaling fish and easier catches, especially for Cape cormorants.

For the quantifiable prey categories, the bearded goby dominated other prey categories on all islands for bank cormorant diet (Figure 4.7). This was mainly due to the fact that crustacean and mollusc prey categories were removed since their undigested remains could not be quantified. For the Cape cormorants, the bearded goby dominated the diet on all islands except Possession Island (Figure 4.8). Possession Island was dominated by the pelagic species category in numbers per pellet. This could be supported by the discussion above that argues that there could be an environmental barrier or oceanographic barrier that limits the bearded goby around Possession Island. The environment around the island could be favourable to pelagic species and not gobies. The bearded goby is present but not in abundance as around the other three islands, or there are other prey species that are in abundance or preferred. In addition to the bearded goby being less dominant around Possession Island, there could be other more nutritious species that are not dominant or are taken in low numbers. This other species could be preferred over the gobies. Most of the other prey species such as snoek, kingklip, and longfin bonefish were under-represented as their otoliths are unknown and they are were not common in the diet of the seabirds.

The distribution of seabirds depends on various factors and one important factor is an adequate stock of sufficient prey species (Hunt, 1991). The seabirds on the different islands are not evenly distributed and food availability can be a contributing factor together with other factors such as habitat availability and prey accessibility. Prey availability plays an important role in the abundance of prey species for seabirds. Some prey species could be readily available while others are less in abundance, hence less likely to be encountered by foraging seabirds. Localised oceanographic conditions on the various islands can affect prey species for seabirds as well.

5.3 Temporal/seasonal variation

There was temporal/seasonal variation in the diet of both bank cormorants and Cape cormorants on the four Namibian islands. In the diet of bank cormorants, bearded gobies were more prominent in summer while crustaceans were more prominent in winter; pelagic species and molluscs also were relatively more prominent in summer (Figure 4.9). This seasonal variation can be attributed to the life histories of the prey species. This is because different prey species have different spawning periods as well as different favourable spawning conditions. For example, the bearded goby in Namibian waters spawns from July through to February with peaks from September to December (Olivar & Shelton, 1993). This means from May to June there will be fewer gobies and other prey species that have a different spawning cycle compared with the gobies might be more prevalent. The larvae of the bearded goby are more abundant during the strongest upwelling periods. The strongest upwelling in Namibia is around Lüderitz, hence the dominance of gobies in the diet of the seabirds in terms of numbers. The upwelling cells have periods when they are stronger, as in summer, while the upwelling activity is calmer in winter. This means gobies will be more dominant in summer compared with in winter. This is shown in our results. Sardines and anchovies on the other hand prefer calm upwelling periods for spawning. However, sardines and anchovies were few in the diet because they spawn off northern Namibia as they prefer warmer waters and also away from the strong Lüderitz upwelling cell in southern Namibia where the islands are situated.

In the diet of the Cape cormorants, the bearded gobies were prominent both in the summer and winter, but in the peak of summer (December) the bearded goby did not dominate (Figure 4.10). Pelagic species dominated during December, followed by molluscs and then gobies. During the month of December most of the prey categories were fairly represented in the diet compared with the other months. In the northern Benguela region, sardines spawn between September and April over the Namibian continental shelf (Kreiner et al., 2001). This can explain the prominence of pelagic species (including sardines) in the diet of the Cape cormorant in summer. Only when the eggs develop into larval assemblages can they swim and start foraging. However, upwelling conditions (strong or weak) affect the retention of eggs, and the concentration and recruitment of fish stocks. For succcesfull larval development these three characteristics must be met. However, for different species these characteristics differ greatly. During larval stages, the species are drifted by ocean currents because they cannot actively swim, especially against the current, and more so when the upwelling is at its strongest. This will result in seasonal changes in prey species. According to Ettahiri et al. (2003), the distribution of pelagic fish eggs and larvae is affected by marine conditions that have an effect on the geographical concentration of reproducing adult pelagic fish. It is believed that if the marine conditions are seasonal, differences in prey species distribution over the different seasons can be observed. Larval assemblages of some prey species will be more affected by currents than others. For example, pelagic eggs or larvae might be more affected than demersal larvae or eggs. Some organisms, such as the rock lobster, tend to spawn in calmer waters.

Prevailing winds over the BCLME are known to be seasonal, with strongest winds blowing in summer and less intense winds in winter. For example, rock lobsters are more mobile in calm conditions and tend to hide in the kelp beds in rough conditions. Therefore, in reality, rock lobsters will be more available to predators in winter than in summer and this can be seen clearly in Figure 4.9 in the diet of bank cormorants as they are known to be benthic feeders. Rock lobsters were more prominent in the diet of bank cormorants from May to August (dominant during July and August). This observation coincided with prevailing seasonal wind conditions (Figure A4 in Appendix A).

5.4 Inter-annual variation

Generally, the diets of both bank and Cape cormorants varied greatly over the years with the bearded goby dominating the diet for both seabird species. Furthermore, pelagic species and hake were more prominent over the years in the diet of Cape cormorants, while crustaceans and squid were more prominent in the diet of bank cormorants (Figure 4.13). The bearded goby was present on all islands over the years but dominant on the northern islands (Mercury and Ichaboe) in the diet of both Cape cormorants and bank cormorants. On Penguin Island the bearded goby also dominated the diet over the years for Cape cormorants. Furthermore, rock lobsters and pelagic species dominated the diets of Cape and bank cormorants on Penguin Island and Possession Island. The bearded goby dominated among other prey species over the years in the diet of both cormorant species. The bearded goby is well adapted to the environmental marine conditions of the northern Benguela region (Salvanes et al., 2011). The bearded goby is known to exist in areas of sulphide eruptions and hypoxic conditions in the northern Benguela, while other organisms, including all vertebrates, are killed by such conditions. The adaptation of the bearded goby in surviving low oxygenated waters is the best compared with other teleost fish. In addition to this survival characteristic, the bearded goby’s natural predators cannot prey on it while in this extreme environment. This is because gobies' predators cannot survive environments with low oxygen and high levels of sulphides. The bearded goby performs a Diel Vertical Migration (DVM) from anoxic seabed to more oxygenated waters 40m to 60m above the seabed. With this migration technique they move to less hypoxic and oxygen-saturated waters but at the same time associate themselves with jellyfish. Jellyfish are normally avoided by their natural predators like horse mackerel. These adaptation techniques in the highly variable and extreme northern Benguela can explain why the bearded goby dominated the diet of Cape and bank cormorants over the years. The decline of one species could increase the food availability for another species, as the overexploitation of the sardine resulted in the increase of other fish species. Other fish species might increase because it means more zooplankton is available for them. The bearded goby could be dominating the diet of seabirds owing to the decline of sardines.

Molluscs were found in the diet of both seabird species over the years but only in the northern islands (Mercury and Ichaboe). The study by Mullon et al. (2002) indicated that cluepeiform species such as anchovies do not spawn in Namibian but in South African waters on the Agulhas Bank and the larvae and eggs are transported by advection currents northwards to nursery areas. It is believed that some of these larvae and eggs could cross over into Namibian waters, hence the dominance of pelagic species in the diet of Cape cormorants. The pelagic species (anchovy included) are only dominant on the southern islands compared with the northern islands. However, there is a higher loss of anchovy larvae and eggs in the southern Benguela owing to coastal upwelling, stronger currents and stronger southerly winds. The losses even could be more due to the BCLME having the strongest upwelling cell around the Lüderitz area and Possession Island is few kilometres south of Lüderitz.

The upwelling process in the NB region is known to be perennial. This means this upwelling process changes yearly, therefore the prey species within this ecosystem are susceptible to change as well. The inter-annual variability of the diets of the bank cormorant and Cape cormorant was caused by the upwelling being a perennial process. Oceanographic conditions, such as sea surface temperatures (SSTs), may vary from year to year. By using the Kohonen self-organising map, SSTs over a long period were studied and showed that the 1990s were warmer than the 1980s (Stachlewska et al., 2002). Some years tended to be warmer than average while other years were cooler than average. Sea surface temperatures do have an effect on the distribution and availability of prey species for predators, hence the oscillations of prey species between 2003 and 2017 (Figure 4.13). According to Mecenaro and Roux (2002), the Lüderitz upwelling cell and the Angolan front are main oceanographic characteristics that affect the migration and distribution of pelagic fish stocks in the northern Benguela (NB) region. These characteristics are caused by wind, temperature, nutrients and the intensity of the upwelling waters. The NB region is characterised by variable oceanic conditions that can cause annual differences in the diet of one of the top predators, the cape fur seal. The diet of seabirds in the NB region can also be affected by the same oceanographic conditions as they are also top predators in the ecosystem.

It can be seen that over the years, gobies dominated the diet of both bank cormorants and Cape cormorants on Mercury Island and Ichaboe Island (Figure 4.13). There were no real trends/patterns, however; these up and down oscillations between the years could be as a result of natural events that affect the availability of prey due to the variability of the BCLME. Several natural events occurred in the BCLME that drastically affected marine life such as whales, seals and seabirds. These natural disasters include the 1984 Benguela *Niño*, 1994 low oxygen water event, and the 1995 Benguela *Niño*. There were also several natural disasters that occurred between 2003 and 2017 as the BCLME is known to have large-scale environmental variability such as widespread oxygen depletions and Benguela *Niño* or warm-water intrusion events. According to the SSTs of the islands, it can be seen in Figure A.1, Figure A.2 and Figure A.3, that on average the SST of Mercury Island is higher than that of Ichaboe Island and Ichaboe's SST is higher than that of Possession Island (Ministry of Fisheries and Marine Resources, *unpublished data*). The average SST is dropping from north to south with the increase in latitude. This phenomenon can explain the distribution of prey items on different Namibian islands. The Angolan front pushes warmer water down to Namibian waters. Hence, the higher SST of Mercury Island (northernmost) and lower SST of Possession Island. Warmer water is known to have higher salinity content than colder water, therefore salinity can affect the distribution of prey species. On Mercury Island both the diet of Cape and bank cormorants over the years was dominated by the bearded goby, followed by hake and molluscs. Gobies had a decline in 2004 as a prey species for both seabird species. From the SST of

Mercury Island, the results show that the SST in 2004 was higher than average, which can explain why the decline in gobies occurred. It could be that the bearded goby as a species did not tolerate warmer waters and moved to cooler, more favourable waters. The decline of the bearded gobies only occurred on Mercury, meaning this event was localised on Mercury or islands south of Mercury were not affected during 2004. On Mercury Island, heat waves are common and many juveniles and chicks used to die owing to heat stress caused by heat waves.

5.5 Conclusions

In conclusion, there was variability in the diet of both the bank and Cape cormorants spatially and temporally, as well as inter-annually. This can be attributed to the variable nature of the BCLME. The diet of the bank cormorant is different from that of the Cape cormorant on the studied islands. The bearded goby as a prey species plays a prominent role in their diet with its physiological and behavioural adaptation techniques. Although the two cormorant species have different feeding niches, the bearded goby is the dominant prey species in numbers between the two cormorant species. The bearded goby is an important prey species because it is available to both seabird species at different stages of its life cycle. The goby is available in its adult (benthic phase) for the bank cormorants and available in its juvenile (pelagic phase) for the Cape cormorants.

The differences in the diet can be explained by the strong Lüderitz upwelling cell and the Angolan front in the northern Benguela within the BCLME as they form environmental barriers for prey species of the seabirds under study. Sea surface temperatures and prevailing winds also have a strong effect on the availability of prey species as different prey species tolerate different climatic conditions. The timing and location of spawning prey species play a very important role in the diet of the seabirds in terms of temporal and spatial diet variability. In some cases, rough oceanographic conditions are needed for some fish larvae to survive, while other larval assemblages need calm oceanographic conditions for survival. Different prey species have different spawning conditions. Physical oceanographic conditions such as bays, lagoons and seafloor topography can also affect the distribution of prey species. The substrate of the ocean at any given area can have an effect on the prey species abundance and diversity of a given area. For example, kelp bed distribution is associated with rock lobsters.

Inter-annual variability in the diet of the two cormorant species is mainly due to natural events that occur in the BCLME such as low oxygen events caused by sulphide eruptions, upwelling and warm water intrusions (Benguela *Niños*). The effects of these natural disasters can persist for years. The BCLME is a very productive marine ecosystem; however overexploitation has negative effects on the biomass of fish stocks directly or indirectly. Overexploitation of sardines and anchovies by humans has greatly affected the diet of seabirds, especially Cape cormorants, as they are known to prefer sardines as their ideal prey species. However, owing to the unavailability of sardines and anchovies, seabirds had to switch their diet to the bearded goby. This is evident from the results of the study. The temporal, spatial and inter-annual variability observed is a clear indication that the Benguela region is in fact a complex ecosystem affected by various factors.

5.6 Recommendations

To ensure the conservation of these endemic and endangered seabird species, government officials and fisheries research scientists should work with small-scale fisheries sectors that are impacting the food of cormorant species, especially bank cormorants. There is a large lobster industry in the Lüderitz area and lobsters tend to feed considerably on juvenile lobsters too. All the stakeholders should integrate their management plans for long-term conservation of these endangered seabird species. Therefore, a holistic approach to fisheries management is needed. One method that will aid in the conservation of marine species is to place moratoriums on certain fish stocks. In that way, fish stocks will be given some time to recover. Placing moratoriums on certain fish stocks for some years can help recover some commercially and ecologically important fish stocks such as sardines and anchovies overexploited during the first Industrial Revolution. This moratorium can recover the biomass of other important prey species in the ecosystem too, especially species that feed on the prey species under the moratorium. Generally, there is a decline of prey species over the years. To prevent a further decline of prey species of globally endangered seabirds, considerable intervention is needed. Interaction between species needs to be studied, and not only interaction between the species and environment. This is because species do not live in isolation but in a complex ecosystem, and prey species have many predators. Therefore, a multi-species management approach is better than the MSY approach that only focuses on a single species. Another area of research regarding the diet of the seabirds, is to investigate whether the decline of sardines might have affected their foraging behaviour.

With regard to the pellet collection, the sample sizes were not the same on the different islands as Mercury Island had the greatest number of pellets collected while Possession Island had the fewest number. Unequal sample sizes might have affected the outcome of the results. However, sometimes this phenomenon is inevitable as the number of pellets depends on the number of birds breeding and roosting in a given location or on a specific island. However, further studies are needed to locate the feeding areas of these seabirds using data loggers/transmitters to ascertain which areas need to be protected and to protect the foraging areas of seabirds from overexploitation of marine resources by humans. The Marine Protected Areas aid in protecting food sources for seabirds and these areas must be monitored closely. To mitigate the problem of food availability for seabirds, MPAs need to be increased, fishing activities need to be reduced, especially around the habitats (islands) and foraging ranges of seabirds, and industrial activities such as offshore mining and oil exploration need to stop within the marine protected areas. New MPAs need to be identified in Namibia especially off central and northern Namibia because these areas have better food for seabirds than southern Namibia. This is mainly because of a predominance of sheltered bays, lagoons and capes. In April 2019 the Department of Environmental Affairs of South Africa added Robben Island to the list of their existing MPAs mainly to conserve marine biodiversity. MPAs are globally used as tools for marine protection and conservation. In addition, further studies are needed to see if there is any way of quantifying the number of crustaceans (lobsters) eaten by bank cormorants or seabirds in general. Indigestible lobster parts that can indicate the number of individuals eaten need to be identified. This can help the lobster sector also, as the sector will have an estimate of how much of the recruitment stock is taken by seabirds per day or per annum. The only MPA in Namibia, namely NIMPA, needs to be monitored; however this is done inadequately owing to its vastness and a lack of resources. Better monitoring or surveillance is needed within NIMPA because poaching in the proclaimed lobster sanctuaries still occurs as vessels are not monitored by any fisheries patrolling vessels. However, patrolling vessels do not monitor often, because of budgetary constraints.

NIMPA boundaries were initially demarcated according to the foraging ecology of the seabirds on the islands. Therefore it is of paramount importance to protect the foraging grounds of seabirds as commercially and ecologically important species will be protected simultaneously. In addition, the number of EBSAs need to be increased and human activities within these EBSAs need to be reduced, such as fishing (especially purse seine), mining, oil and gas exploration, coastal development, and guano harvesting. By introducing more EBSAs, more marine habitats and greater biodiversity will be protected. In addition, EBSAs will also create awareness of the significant areas in general. International organisations such as SEAFO can assist in monitoring and surveillance of NIMPA to help protect the foraging areas of seabirds as well as assist the fisheries inspectors. SEAFO can help with capacity building of monitoring and surveillance officials. Capacity building can be in the form of training, workshops and symposia for better surveillance and will create awareness of the effects that the fisheries industry has on the ecosystem.

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APPENDIX A

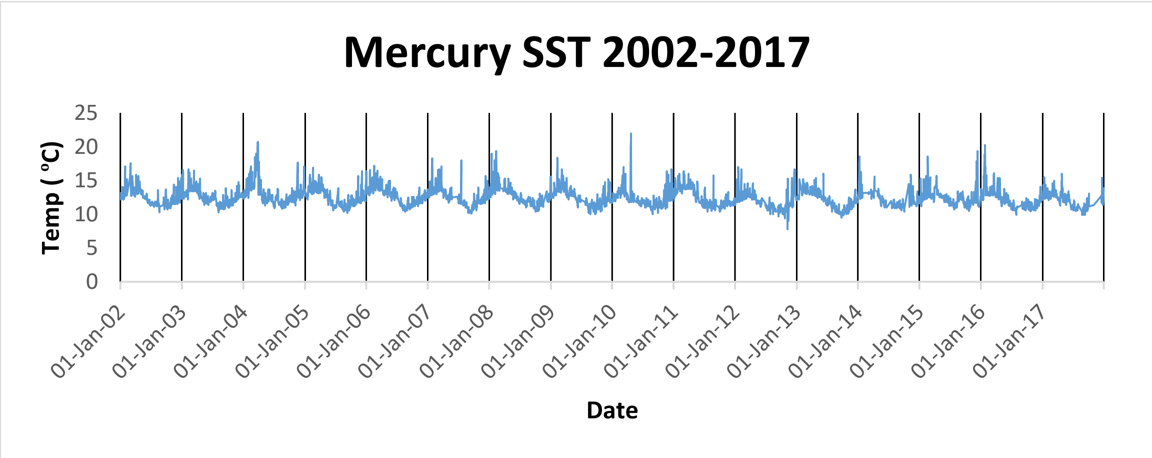

Figure A.1 Sea Surface Temperatures (SSTs) at Mercury Island from 2002 until 2017 (unpublished data)

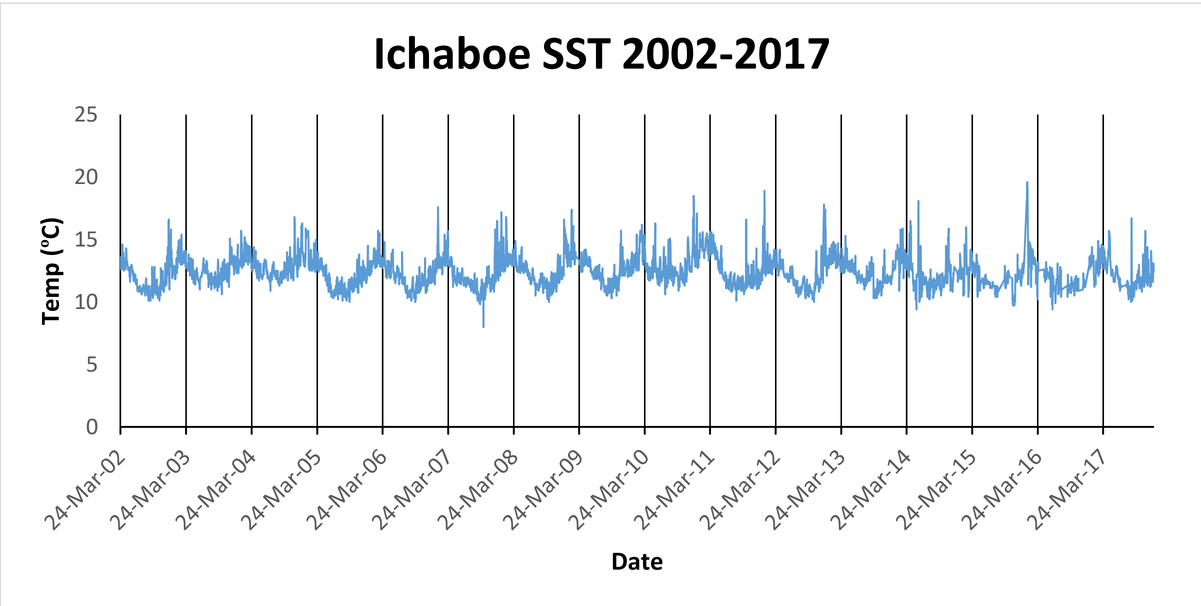

Figure A.2 Sea Surface Temperatures (SSTs) at Ichaboe Island from 2002 until 2017 (unpublished data)

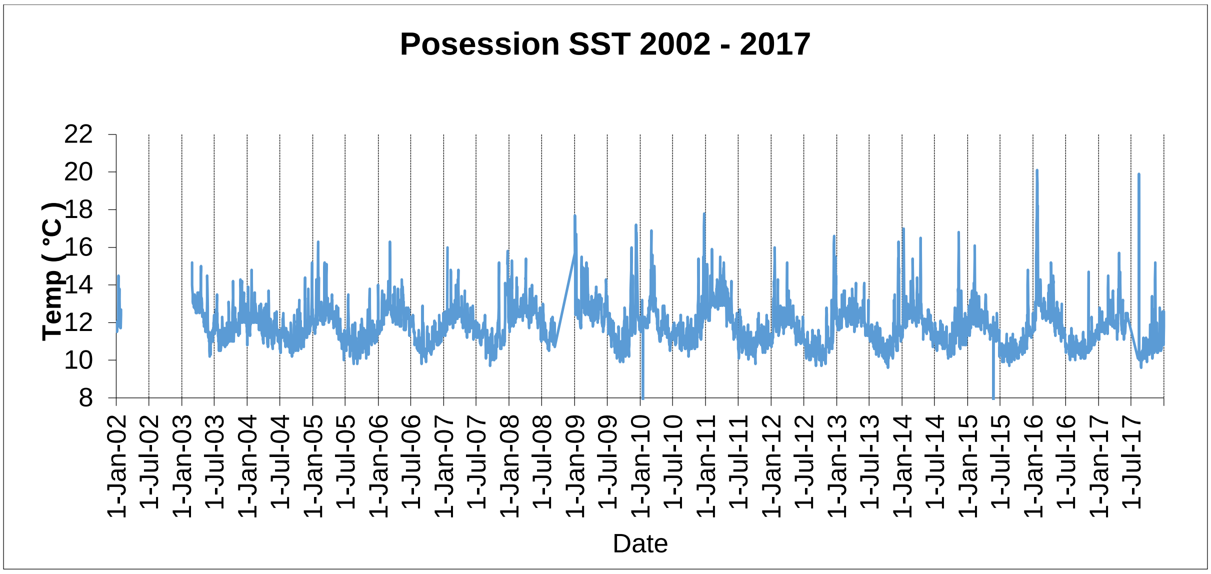

Figure A.3 Sea Surface Temperatures (SSTs) at Possession Island from 2002 until 2017 (unpublished data)

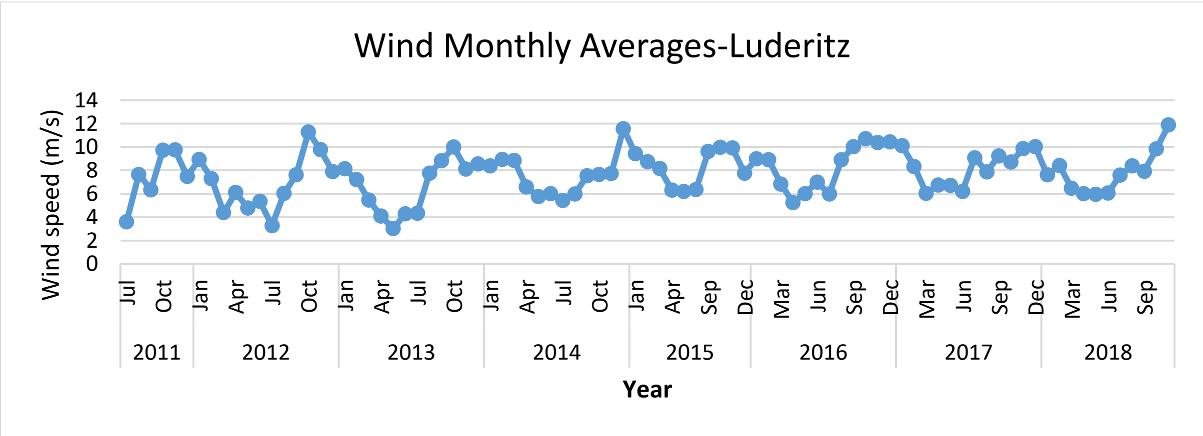

Figure A.4 Monthly wind speed (m/s) averages from 2011 to 2018 at the Diaz Point Lüderitz peninsula (unpublished data)

APPENDIX B

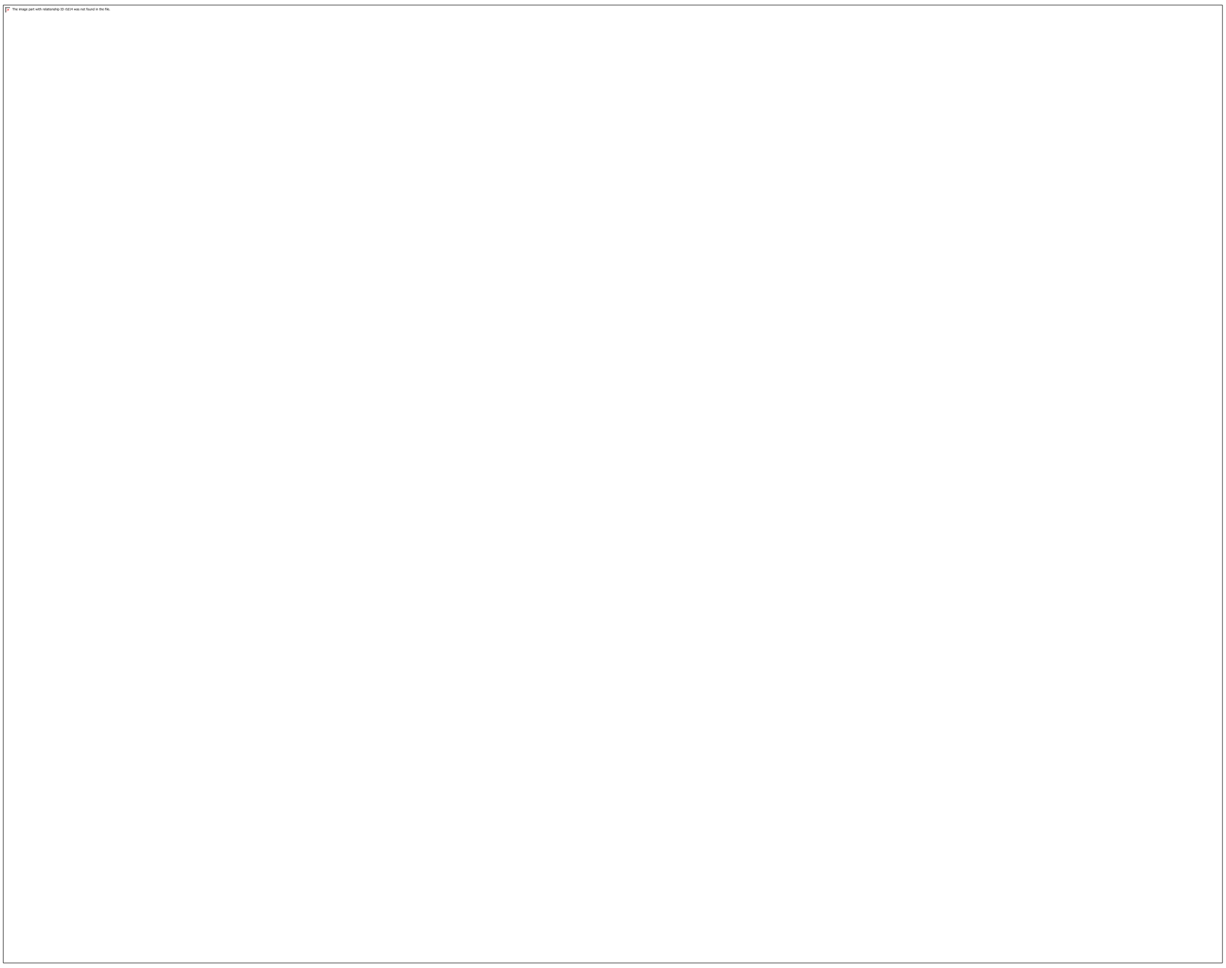

Plate B.1: Some of the prey species of the bank and Cape cormorants. (A) The bearded goby. (B) Mullet. (C) Sardines are ideal prey species for Cape cormorants. (D) Squid. (E) Pelagic fish species. Crustaceans such as rock lobsters (*Jasus lalandii*) (F), shrimps (G) and juvenile lobsters (H) are also found in the diet of the seabirds.