

**Are Cape Cormorants (*Phalacrocorax capensis*) losing the competition? Dietary overlap
with commercial fisheries**



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Submitted in partial fulfilment of the requirements for the degree of
Master of Science in Conservation Biology in coursework and dissertation

March 2018

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ACKNOWLEDGEMENTS

First and foremost I would like to offer my sincerest gratitude to my supervisors, Drs A.B. Makhado and Robert Crawford as well as Prof Peter Ryan, who supported me throughout my thesis with their patience and knowledge whilst allowing me the room to work in my own way. Their invaluable support has had great contribution towards my growth as a scientist and without them, this thesis would have never been completed.

A number of people have provided resources, moral support, constructive criticism on this thesis when I needed it the most. Amongst them, I would like to give special thanks to the FitzPatrick Institute of African Ornithology team, specifically, Dr. Susie Cunningham and Hilary Buchanan. I will forever be grateful for their advice and all the time they put into helping me navigate through the UCT systems. To my fellow Conservation Biology classmates, whose support has been firm and unwavering and from which I drew most of the energy I needed to continue my research, I give very special thanks to each and every last one of you.

I thank Sobahle Somhlaba and Yonela Geja for their statistical genius. Thank you for always pointing me in the right direction every time I had an idea that seemed slightly out of reach or scientifically nonsensical. I am also thankful to Dr. Carl van den Lingen who also provided and allowed access of the use of the data used in assessing the extent of overlap.

Last but definitely not least, I must express my very profound gratitude to my family for providing me with unfailing support and continuous encouragement throughout my years of study and through the process of researching and writing this thesis. This accomplishment would not have been possible without them. Thank you.

1 ABSTRACT

Characterisation of the diet of pelagic feeders can be regarded as key to development of ecosystem-based management plans, conservation of predators as well as understanding of ecological and trophic interactions. Therefore, long term studies on dietary changes provide insights into the nature of competition and overlap between seabirds and fisheries. The Cape Cormorant *Phalacrocorax capensis* breeds in the Benguela upwelling region of southern Africa. Its population has decreased by over 50% in the three most recent generations resulting in the species being listed as Endangered in the IUCN Red Data List. Its decline has previously been postulated to result from reduced prey availability. In this thesis, I examined and reported on the spatio-temporal distribution of Cape cormorant diet obtained from different colonies over two decades (1988 – 1997 and 1998 – 2007). I further investigated the extent of overlap between the diet composition and sizes of fish eaten by Cape Cormorants and those caught by the purse-seine fishery.

Epipelagic fish (Anchovy, Sardine, Horse Mackerel and Redeye) dominated the diet of Cape cormorants at all sites. Anchovy was the most important in the diet in all years except in 1992 and 1993, when Sardine dominated the diet, and in 2007 when 'other' fish species (mainly Cape Silverside *Atherina breviceps* and Southern Mullet *Chelon richardsonii*) became the most frequently eaten fish.

There were decadal variations in the relative numerical abundance of different prey species. Over both decades investigated, the diet was largely dominated by Anchovy and Sardine, with Horse Mackerel contributing more in the second than first decade. There was, however, an increase in the contribution of Anchovy relative to Sardine from the first decade to the second. At all colonies, Cape Cormorants mostly preyed on Anchovies of sizes between 5 and 11cm. Sardines eaten were larger than Anchovies (mostly 11 – 23 cm), with a

bimodal distribution in the first decade. However, the few Sardine eaten in the second decade were smaller (4 – 7 cm) perhaps reflecting the length of fish available. There was an overlap in the distribution of fish sizes caught by the fishery and those found in the diet of Cape Cormorants especially in the first decade. However, increased sampling of Cape Cormorant diet is required to more fully understand the extent of competition and overlap with fisheries.



2 INTRODUCTION

2.1 *Top-predators and fisheries*

Marine ecosystems contribute approximately half of global primary production (Myers and Worm, 2003) and for years humanity has depended on their resources for survival (Crain *et al.*, 2009). However, as the global human population increases, these ecosystems continue to be negatively impacted by human activities, such as the overexploitation of fish resources through overfishing (Pauly *et al.*, 1998) In recent years, this has resulted in changes within food web relationships that have altered ecosystem functioning within the marine environment (Worm *et al.*, 2006; Halpern *et al.*, 2008). Top predators such as sharks, cetaceans, pinnipeds and seabirds play a pivotal role in the maintenance of these ecosystems, specifically their structure and function (Myers and Worm, 2003). Seabirds, in particular, can potentially reflect ecosystem shifts (e.g. declining prey resources) through several aspects of their demography such as survival, breeding success and ultimately population size (Cairns, 1987; 1992; Weimerskirch, 2001). Their sensitivity to variations in both the quantity and quality of prey has been well studied, making them effective indicators of environmental change in marine ecosystems (Monaghan, 1996; Diamond and Devlin 2003; Wanless *et al.*, 2005; Breton *et al.*, 2008).

Fishing is one of the oldest human activities that alters marine ecosystems but commercial fishing in particular has resulted in massive changes in biodiversity globally (Worm *et al.*, 2006). Fisheries not only affect the target species but also the ecology and population dynamics of the marine predators (such as seabirds) that feed on those fish species targeted by fisheries (DeMaster *et al.*, 2001; Roux and Shannon, 2004; Crowder *et al.*, 2008). Many seabird populations are rapidly decreasing globally, with their overall

conservation status having deteriorated faster than most comparable groups of birds (Croxall *et al.*, 2012; Paleczny *et al.*, 2015). Their declines have been attributed to a number of interacting factors that impact them both at sea and at their breeding colonies, including introduced and natural predators, diseases, pollution, incidental fishing mortality, reduced prey availability and the effects of climate change (Burger and Cooper, 1984; Adams *et al.*, 1992; Crawford *et al.*, 1992a; 2015; Crawford, 1999; Crowder *et al.*, 2008; Hamann *et al.*, 2012; Grémillet *et al.*, 2015).

Fisheries can be detrimental to seabirds by reducing prey availability to below thresholds necessary for survival and reproduction (Cury *et al.*, 2011; Robinson *et al.*, 2015; Sugishita *et al.*, 2015; Sydeman *et al.*, 2017). However, there has been a fundamental challenge in trying to find a relationship between the impacts of fisheries on seabirds using prey-related studies (particularly focusing on resource competition), which is the fact that the prey species themselves tend to vary naturally (Sydeman *et al.*, 2017). Prey species differ in abundance in relation to oceanographic factors that can affect their spatial organization and distribution, recruitment and stock size (Baumgartner *et al.*, 1992; Chavez *et al.*, 2003; Trivelpiece *et al.*, 2011; Checkley *et al.*, 2017).

Interactions between fisheries and top predators, specifically seabirds, vary globally depending on the extent and nature of the interaction (Arcos and Oro, 2002). Such interactions have the ability to alter the dynamics of seabird populations and communities (Tasker *et al.*, 2000). For instance, a large proportion of seabirds is impacted by fisheries both directly (e.g. reduction of prey availability, see Cury *et al.*, 2011; Sydeman *et al.*, 2017) and indirectly (e.g. incidental mortalities from bycatch, see Crawford and Cooper, 2003; Croxall *et al.*, 2012; Phillips *et al.*, 2015). Generally seabird-fishery interactions are

considered negative with a few positive effects on certain seabird populations (Tasker *et al.*, 2000). Some fisheries generate food for scavenging seabirds that have limited diving abilities. For example, in the Benguela ecosystem, albatrosses benefit from scavenging at benthic trawlers that provide access to discarded offal from deep-water prey such as hakes (*Merluccius* spp.) that would normally be inaccessible to these birds (Petersen *et al.*, 2008). However, with some of these fisheries, scavenging can also be associated with high mortality and is currently the leading cause of population declines in albatross and petrel species (Crawford and Cooper, 2003; Croxall *et al.*, 2012; Phillips *et al.*, 2015).

Seabirds can be used as indicators of the relative abundance of their prey species, many of which are also targeted by commercial fisheries. Studies have shown that the proportions of different prey species in seabird diets are often correlated to the general abundance of those prey species and for seabirds that exhibit strong diet selectivity, changes in their diet often reflect a change in the prey base (Montevecchi *et al.*, 1988; Crawford *et al.*, 1992a; Barrett *et al.*, 2007; Velarde *et al.*, 2013; Green *et al.*, 2015). Most seabirds have to compete with fisheries to satisfy their dietary requirements (Crawford *et al.*, 2015). Commercial fisheries remove large amounts of biomass from different trophic levels within ecosystems. Increasing fishing pressure, coupled with improved technology to locate and catch fish results in biomass reduction, and often, fishing down food webs (i.e. trophic downgrading; Pauly *et al.*, 1998, Hilborn *et al.*, 2017). This alters habitats and forces impacted species to adapt to the rapidly changing environments (Crowder *et al.*, 2008; Hilborn *et al.*, 2017).

Direct competition between seabirds and fisheries may be shown by the similarity between the proportion of a prey species in the diet of the bird and that of the fishery's

yield (e.g. with Cape Gannets *Morus capensis*; Berruti and Colclough, 1987). Such overlaps also occur when both the fishery and the seabird exploit prey of the same length (Pichegru *et al.*, 2009) as well as at the same depth (Ropert-Coudert *et al.*, 2004). In such instances, seabirds may resort to targeting fish of smaller sizes than those caught by the fishery in order to reduce competition (Pichegru *et al.*, 2009).

2.2 The Benguela Current Large Marine Ecosystem (BCLME)

The Benguela Current Large Marine Ecosystem (BCLME) is renowned for being highly productive through coastal upwelling (Bakun, 1996; van der Lingen *et al.*, 2006). Off the west coast of South Africa, this nutrient-rich region creates one of the four most productive upwelling marine ecosystems in the world (Bakun, 1996; Kemper *et al.*, 2007a; Hutchings *et al.*, 2009). The Benguela ecosystem is highly dependent on a few species of small pelagic fish for the regulation/transfer of energy between lower and upper trophic levels (Cury *et al.*, 2000). This species-poor, intermediate trophic level is dominated by Sardine (*Sardinops sagax*) and Anchovy (*Engraulis encrasicolus*; Shannon *et al.*, 2009; Pichegru *et al.*, 2009). These two fish species are ecologically important throughout southern Africa as a source of food for many piscivorous fish, marine mammals and seabirds (Roy *et al.*, 2007; Coetzee *et al.*, 2008). The relative abundance of many top predators within the Benguela ecosystem therefore relies on the availability/abundance of these small pelagic fish species (Pichegru *et al.*, 2009).

Sardine and Anchovy are also of great economic importance as they are the main target species for the purse-seine fishery off the west coast of South Africa, constituting over 80% of small pelagic fish catches, which average approximately 400 000 tons per annum in the southern Benguela (Barange *et al.*, 1999; Roy *et al.*, 2007). Their relative

abundance varies at both temporal and spatial scales (Pichegru *et al.*, 2009), with some historically observed fluctuations in dominance between the two species also influenced by climatic and oceanographic factors (Shackleton, 1987). Top predators evolved to cope with these climatic and oceanographic variations, but as a consequence of overexploitation, Sardine catches still collapsed during the mid-1960s. Prior to this collapse, Sardines dominated the Benguela ecosystem but thereafter, numbers decreased to extremely low levels (Fossen *et al.*, 2001; Griffiths *et al.*, 2005; Hutchings *et al.*, 2009). As an attempt to remedy this whilst simultaneously decreasing the pressure on Sardines, heavy fishing of Anchovy was encouraged. However, the increased fishing pressure on Anchovy merely led to a decline in Anchovy biomass, with limited recovery of the Sardine fish stocks. This resulted in an overall crash in small pelagic fish catches within the Benguela ecosystem, particularly off Namibia (Hutchings *et al.*, 2009). During this time, the northern Benguela ecosystem in particular, became dominated by gelatinous zooplankton, which according to Roux *et al.* (2013) tend to increase when small pelagic fish numbers decrease. The Namibian fishery, thereafter, had a partial recovery in Sardine during the 1990s, however, the recovery was followed by massive declines in Sardine biomass during the early 2000s (Kreiner *et al.*, 2001; Roux and Shannon, 2004; Ludynia *et al.*, 2010).

In South Africa, during the late 1990s, there was a shift in the biomass distribution of Sardine and Anchovy from the west coast towards the south coast (van der Lingen *et al.*, 2005; Roy *et al.*, 2007). The reason behind the altered distribution is still debated (see van der Lingen *et al.*, 2005; Roy *et al.*, 2007; Coetzee *et al.*, 2008). However, the eastward shift affected the South African fishery, which is traditionally centered along the west coast, and has failed to catch its Total Allowable Catch (TAC) of Anchovy in most years since 1990

(Fairweather *et al.*, 2006; Roy *et al.*, 2007; Prochazka, 2014). Over the last few decades, catches of Sardine have fluctuated between 16 000 and 375 000 tonnes annually and of Anchovy between 41 000 and 596 000 tonnes (de Moor *et al.*, 2016; Appendix 1).

The biomass estimates and numbers of recruits of Sardine and Anchovy have also been fluctuating since the early 1990s, due to altered environmental conditions as well as fishing pressure during years of poor recruitment and poor biomass (Hutchings *et al.*, 2009; Prochazka, 2014). These fluctuations are regularly monitored, along with other issues that possibly impact the sustainability of the small pelagic fish stocks (Prochazka, 2014) such as spatial mismatch between stock estimates and fishing efforts (Cury and Shannon, 2004; Coetzee *et al.*, 2008). Their management and monitoring depends largely on acoustic surveys (see Methods) which are used to estimate the overall spawner biomass and recruitment numbers annually and are used to set the annual TAC (Barange and Hampton, 1997; de Moor *et al.*, 2008; although in the last decade the purse-seine fishery has struggled to catch even half the TAC each year – see Prochazka, 2014).

2.3 Resource competition on the west coast of southern Africa

In South Africa, four breeding seabird species rely on Sardine and Anchovy, the species targeted by the purse-seine fishery. Amongst the most abundant of these is the Cape Cormorant (*Phalacrocorax capensis*), which feeds on various fish species but mainly Sardines and Anchovy. The remaining three species are the Greater Crested or Swift Tern (*Thalasseus bergii*; see Crawford, 2003,2009; Gaglio *et al.*, 2018), Cape Gannet (see Crawford *et al.*, 2007b, Green *et al.*, 2015) and African Penguin (*Spheniscus demersus*; see Crawford *et al.*, 2006; Pichegru *et al.*, 2010; Sherley *et al.*, 2013). Of these four species, all except the tern are endemic to the Benguela region (Crawford, 2004). Another endemic seabird species, the

Bank Cormorant (*Phalacrocorax neglectus*), competes with the West Coast Rock Lobster (*Jasus lalandii*) fishery for food (Crawford *et al.*, 2015). The four endemic species, namely the Cape Cormorant, Bank Cormorant, Cape Gannet and African Penguin, are listed as globally Endangered (IUCN, 2017a,b,c,d).

The extent of the impact of prey availability and competition with fisheries is well-studied for Cape Gannets (see Berruti, 1987, Berruti *et al.*, 1993; Pillay, 2002; Crawford, 1999, 2004; Cohen, 2014) and African Penguins (Kemper *et al.*, 2001; Whittington, 2002; Crawford, 1998, 2004; Crawford *et al.*, 2001; Pichegru *et al.*, 2009, 2010). Some research has also been focused on Swift Terns, which did not seem to be negatively impacted by the purse-seine fishery as their overall population in the region seemed to have increased (Crawford, 2004, 2009).

As a result of the Sardine-Anchovy eastward shift, the Cape Gannet population collapsed in the Western Cape Province but increased at the easternmost breeding colony, at Bird Island Algoa Bay, in the Eastern Cape (Crawford *et al.*, 2008, 2015). By comparison, African Penguins have experienced a decrease over three generations of 56% (Crawford *et al.*, 2011), which can be attributed mostly to a lack of quality prey and generally low prey abundance (Kemper *et al.*, 2007a). Cape Cormorants have also experienced the same fate as the African Penguins, with a decrease of c. 3% annually since the late 1970s (Kemper *et al.*, 2007a). However, little is known about the mechanisms driving the decline in Cape Cormorants. Threats to the species include disease outbreaks (Crawford *et al.*, 1992b; Waller and Underhill, 2007) and disturbance at breeding sites (Marks *et al.*, 1997), but the main driver of their decline also is assumed to be reduced availability of the small pelagic fish that form the bulk of their diet (Matthews and Berruti, 1983; Cooper, 1985; Crawford *et*

al., 1992a; Hockey *et al.*, 2005; Kemper *et al.*, 2007a; Okes *et al.*, 2009; Kemper and Simmons, 2015). Little has been published on the diet of Cape Cormorants since the 1980s. Here, I report how their diet overlaps with purse-seine fishery operations off South Africa.

2.4 *Ecosystem approach to managing South African fisheries*

The Cape Cormorant is just one among a suite of predators that rely on Anchovy and Sardine fish stocks as a source of food (Coetzee *et al.*, 2008). Given that both fish species are short-lived and commercially important, adopting an ecosystem approach to the management of the fisheries is necessary (Cochrane *et al.*, 2004). Essentially, such an approach is aimed at planning, developing and managing fisheries in such a way that socio-economic needs and desires are met without depleting marine resources or risking the benefits to future generations arising from these resources (Shannon *et al.*, 2004).

An ecosystem-based approach to managing fisheries is not a new concept and many researchers have investigated the feasibility of such approaches, specifically relative to South African fisheries (e.g. Cochrane *et al.*, 2004; Shannon *et al.*, 2004, 2010). Internationally, the importance of using such an approach to fisheries management has also been recognized by at least 47 countries (Cochrane *et al.*, 2004). Using this kind of approach to managing the purse-seine fishery off the west coast of South Africa, could improve not only the status, growth and development of the target species but also that of the predators that depend on them for survival (Cochrane *et al.*, 2004; Shannon *et al.*, 2004; Roy *et al.*, 2007).

2.5 *Investigating prey overlap between the purse-seine fishery and Cape Cormorants*

Seabird diet has been used historically to assess the population dynamics of a number of prey species as well as to assess the foraging ecology of different seabird species in the

Benguela upwelling ecosystem (see Duffy *et al.*, 1987; Montevecchi *et al.*, 1988; Crawford *et al.*, 1992a; Barrett *et al.*, 2007; Velarde *et al.*, 2013; Green *et al.*, 2015). Using Cape Cormorant regurgitates as well as length frequency distributions and biomass estimates of Sardine and Anchovy caught by the purse-seine fishery, I investigated the extent of target forage fish overlap between the purse-seine fishery off the west coast of South Africa and Cape Cormorant diet. This was done to create better understanding of the influence the purse-seine fishery has on Cape Cormorant populations throughout the west coast. The extent of overlap is investigated by conducting a direct comparison of the sizes of fish species, specifically Sardine and Anchovy, caught by the fishery and those caught by Cape Cormorants. The study had two objectives: (i) to determine the diet composition of Cape Cormorant in relation to regional variations in Sardine and Anchovy biomass; and (ii) to compare the sizes of Sardine and Anchovy eaten by Cape Cormorants with those caught by the purse-seine fishery.



We hypothesized that colonies located within the Saldanha Bay area will have a wider variety of prey within their diet as they have a much broader range of forage species to feed on at this locality which includes the sheltered waters of Saldanha Bay and Langebaan Lagoon. We also assumed that regional Anchovy and Sardine biomass estimates, as estimated by acoustic surveys conducted by the Department of Agriculture, Forestry and Fisheries (DAFF), might reflect the relative contributions of each species to Cape Cormorant diet at colonies situated within the respective sampling strata. Considering that Anchovy and Sardine spawning typically occurred farther south of the west coast, we expected Cape Cormorant diet from colonies such as Bird Island at Lambert's Bay to comprise mostly smaller fish (i.e. recruits) whereas those farther south to be predominantly spawners.

Providing strong evidence of intensive competition between this seabird species and the fishery should influence management policies for the purse-seine fishery, if an ecosystem approach to the fishery is implemented.



3 METHODS

3.1 *Study species*

Cape Cormorants have a non-breeding distribution that stretches from Lobito in central Angola to Maputo Bay, southern Mozambique, with vagrants recorded as far north as Gabon (Payne *et al.*, 1989; Crawford, 2007a; Cook, 2015; Crawford *et al.*, 2016). The species' breeding range lies within the nutrient-rich Benguela upwelling ecosystem, from Ilha dos Tigres off southern Angola to Bird Island group, Algoa Bay (Figure 1; Roux and Shannon, 2004; Kemper *et al.*, 2007a; Ryan *et al.*, 2009; Cook *et al.*, 2012; Cook, 2015; Kemper and Simmons, 2015). One historical record exists of the species breeding outside this range between 1925 and 1926 at the Hole-in-the-Wall, south of Coffee Bay in the Eastern Cape Province of South Africa (Crawford *et al.*, 2016).

Historically, Cape Cormorants were the most numerous seabird species breeding in southern Africa (Berry, 1976). However, between 1985 and 2011, the population decreased by over 50% at its main breeding colonies (Cook, 2015). This decrease resulted in a global estimate of Cape Cormorant breeding pairs being 100 000 in 2005–2006 as opposed to the estimate of 277 000 pairs in 1977–1981 (of which 107 000 pairs bred in South Africa; Kemper *et al.*, 2007a; Crawford *et al.*, 2007a, 2015, 2016). Consequently, in 2013, the species was listed as Endangered by the International Union for Conservation of Nature (IUCN) both regionally (Taylor *et al.*, 2014) and globally (Birdlife International, 2017).

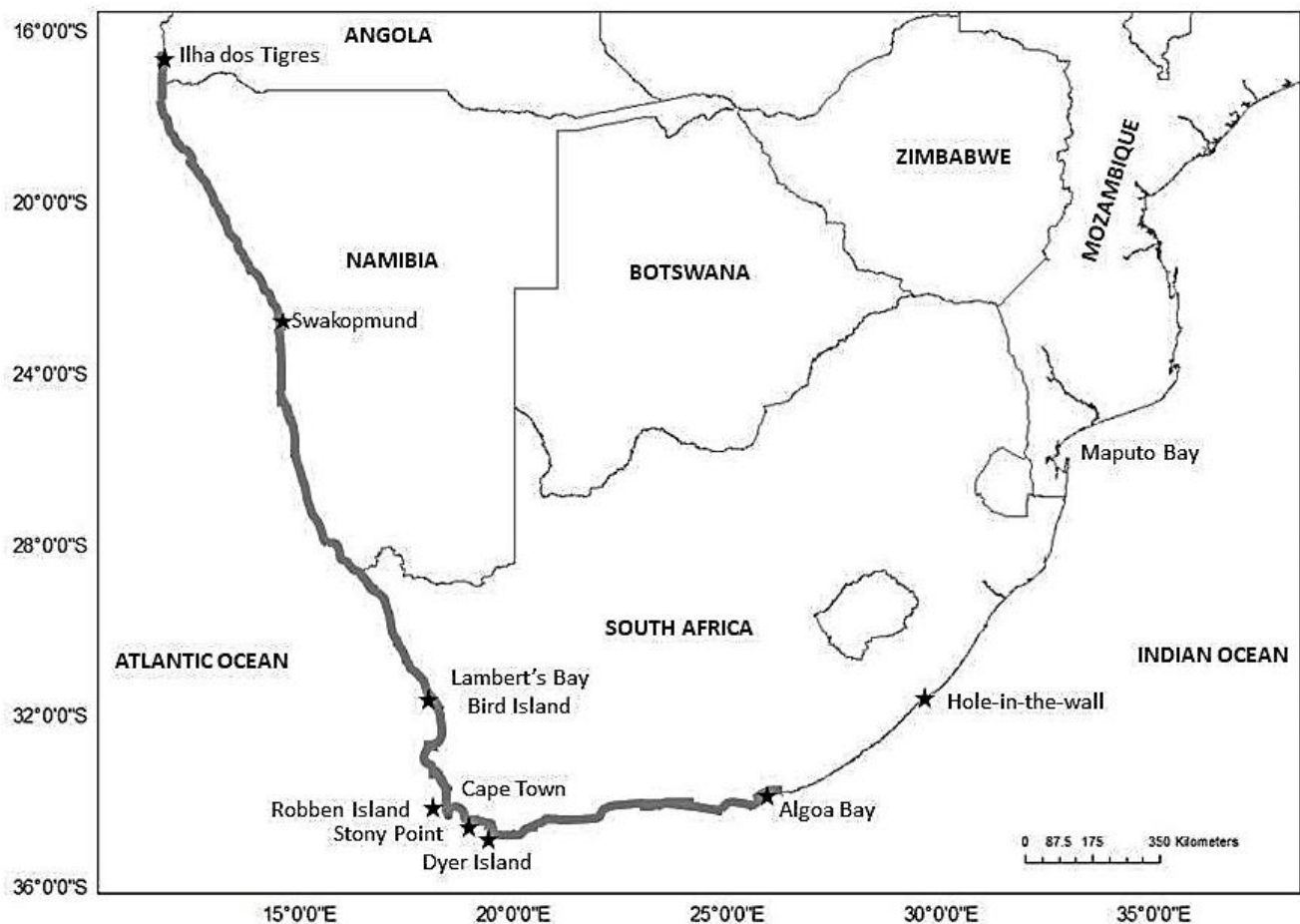


Figure 1: Southern Africa, showing the current breeding range of Cape Cormorants (grey shading along the coast) and other localities mentioned in the text.

By 2013, the number of breeding pairs in South Africa had decreased to an even lower estimate of 68 000 pairs, from the previous estimate of 107 000 breeding pairs between 1977 and 1981 (Crawford *et al.*, 2016). These declines were mostly attributed to prey depletion by the purse-seine fishery (Cook, 2015), although other drivers included outbreaks of avian cholera (Williams and Ward 2002; Waller and Underhill, 2007), human disturbance, predation, pollution and climatic variations (Kemper *et al.*, 2007a; Cook, 2015). The decreases were coupled with a shift in the breeding distribution of Cape Cormorants towards the south and east, mirroring a shift in their preferred prey (Crawford *et al.*, 2016). Of particular interest were the increases in numbers of breeding pairs at colonies such as Robben and Dyer Islands as well as Algoa Bay, and the formation of new colonies along the

south coast of Stony Point and between Knysna and Tsitsikamma. The inter-annual variations in prey distribution and abundance appear to have driven changes in the Cape Cormorant's distribution in South Africa (Crawford *et al.*, 2016).

Environment and prey

Cape Cormorants feed predominantly in marine waters, from estuaries and shallow tidal pools up to 80 km offshore (Crawford *et al.*, 2007a; Ryan *et al.*, 2009). However, during breeding periods, most Cape Cormorants forage within 20 km of their colony (Hamann *et al.*, 2012). They forage by pursuit-diving, usually in large flocks but sometimes solitarily (Hockey *et al.*, 2005). At sea, they often feed with African Penguins, Cape Gannets and other marine predators including dolphins and fur seals (e.g. Cape Fur Seal *Arctocephalus pusillus pusillus*), and are often accompanied by terns and gulls, occasionally losing their prey to the latter (Hockey *et al.*, 2005). Foraging flocks primarily target pelagic schooling fish as well as crustaceans, with the main components of their diet including Anchovy, Sardine, Horse Mackerel (*Trachurus trachurus capensis*) and Pelagic Goby (*Sufflogobius bibarbatus*; Cooper, 1985; Hockey *et al.*, 2005; Crawford *et al.*, 2007a; Cook, 2015). Typically, their prey is caught in mid-water near the water surface, but some benthic fish are caught at or near the sea bottom (Cook *et al.*, 2012).

3.2 *Study sites*

Stomach contents were collected at 11 Cape Cormorant breeding colonies off the Western Cape Province, South Africa: Elephant Rock (-31.644, 18.1430), Bird Island at Lambert's Bay (-32.0872, 18.299), Malgas Island (-33.0528, 17.925), Jutten Island (-33.0833, 17.9550), Schaapen Island (-33.091, 18.0211), Meeuw Island (-33.085, 18.0082), Vondeling Island (-33.15283, 17.9839), Dassen Island (-33.4233, 18.0872), Robben Island (-33.8044, 18.3678),

Seal Island in False Bay (-34.1376, 18.583) and Dyer Island (-34.6836, 19.4153; Figure 2). During the study period, these colonies were known to be the most important Cape Cormorant breeding sites in South Africa and supported over 30% of the global population (Crawford *et al.*, 2007a).

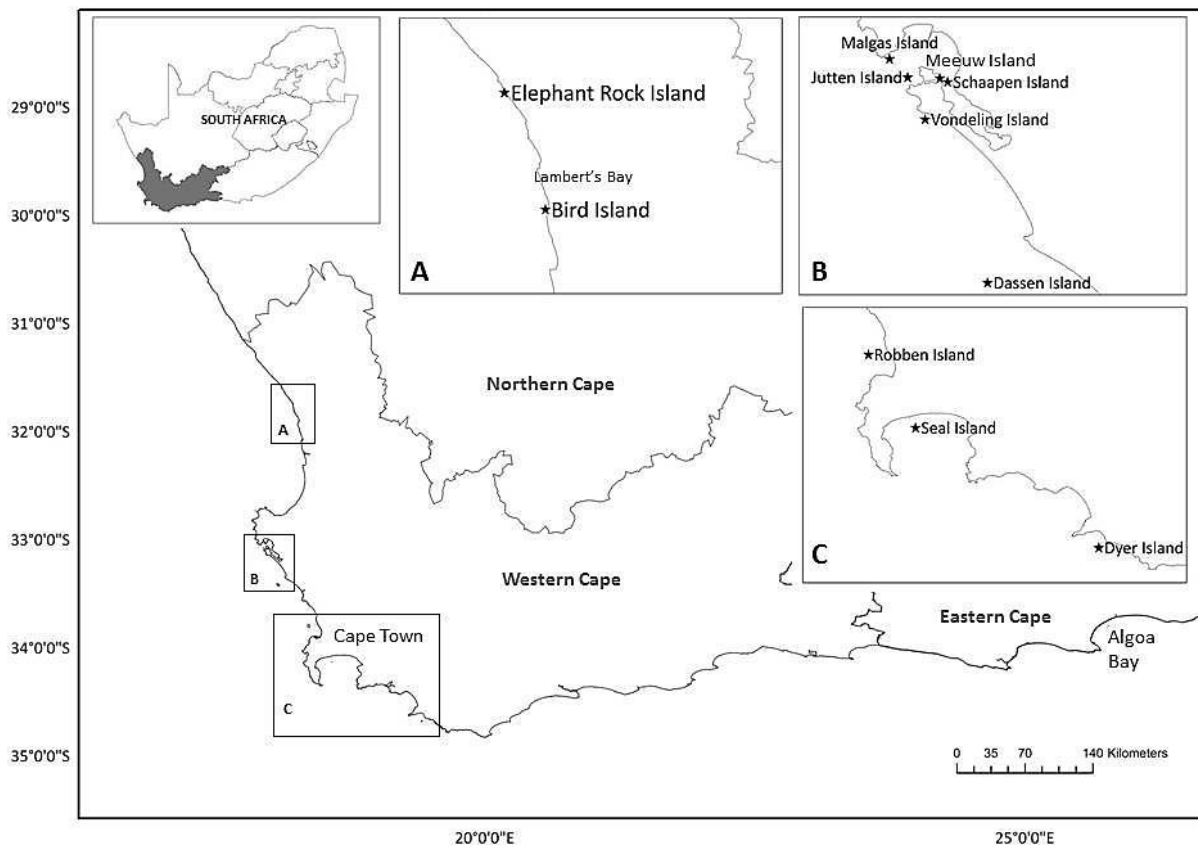


Figure 2: Map of South Africa showing the Cape Cormorant breeding localities along the west and south coasts where cormorant regurgitations were collected.

3.3 Diet composition and variability

Regurgitations were collected between 1978–2016 when banding chicks and/or breeding or roosting adults. However, with the increased threat status to the species, any disturbance of breeding birds was minimized substantially, therefore much less regurgitate samples were obtained in the last decade. Banding was usually done before midday when the weather was still cool to minimize heat stress and energy loss (cf. Smith *et al.*, 1999; Whitworth *et al.*, 2007). Cape Cormorants are susceptible to human disturbance and may regurgitate

when handled or even if approached too closely (see Cook *et al.*, 2012). Therefore, since regurgitation is a stress response, adult regurgitates were collected opportunistically and not as part of a standard procedure (Kemper *et al.*, 2007b).

Diet samples were collected in plastic bags which were labeled with a marker pen specifying the species, location, age class of individual as well the date of sample collection. Samples that were not processed immediately after collection were preserved (by freezing or fixing in formalin) until samples could be processed (Kemper *et al.*, 2007a; Cook *et al.*, 2012). Each sample was sorted into prey components e.g. fish, cephalopod, crustacean or other. Prey types were then identified to species level where possible, using techniques described by Smith and Heemstra (1991) and Smale *et al.* (1995). Prey items were weighed, counted and measured (Bruce M. Dyer pers. comm., December 2017). The caudal lengths of only fresh whole fish, mantles of cephalopods and carapaces of crustaceans were measured to the nearest millimeters (e.g. Cooper, 1985; Klages *et al.*, 1992).

3.4 Population trend estimates

Annual Cape Cormorant breeding population estimates for the different colonies sampled in this study were obtained from the literature (Crawford *et al.*, 2007a, 2016) and unpublished data of the Department of Environmental Affairs (DEA). Counts were made of the numbers of breeding pairs as close to the peak of the breeding season as possible (Crawford *et al.*, 2007a). Different strategies were used to obtain these estimates, depending on the size and accessibility of each colony. Ground counts were made on most of the easily accessible colonies (Kemper *et al.*, 2007a), whereas photographic surveys were used for large or cliff-side colonies (Crawford *et al.*, 2007a). Because of regional variations in breeding seasonality,

the peak breeding periods differed among colonies (Crawford *et al.*, 2007a; Kemper and Simmons, 2015).

3.5 *Fish distribution patterns and size frequencies*

The purse-seine fishery has great economic and biological significance to South Africa and is therefore closely monitored (Roy *et al.*, 2007). Fish biomass and size frequency distribution data were obtained from long-term acoustic surveys and commercial catch landings respectively (Fairweather *et al.*, 2006; de Moor *et al.*, 2008; Barange *et al.*, 1999).

Acoustic survey data

Acoustic surveys of pelagic forage fish species off South Africa have been conducted since 1984 (Fairweather *et al.*, 2006; Coetzee *et al.*, 2008) by DAFF. They indicate inter-annual variation in the abundance and distribution of Anchovy, Sardine and Redeye Round Herring *Etrumeus whiteheadi*, which account for over 80% of South Africa's purse-seine catches by mass (Barange *et al.*, 1999; Roy *et al.*, 2007; Coetzee *et al.*, 2008). The surveys are timed to coincide with the migratory patterns and life cycles of these fishes (Barange and Hampton, 1997). Recruit surveys are conducted between the Orange River and Cape St Francis typically around May (Figure 3a), whereas spawner biomass surveys are conducted between Hondeklip Bay and Port Alfred typically in November (Figure 3b; DAFF, 2016). Since historically, the recruitment of pelagic fish species was predominantly off the west coast, greater surveying effort was directed towards areas around that region. However, the eastward shift in Sardine and Anchovy spawners over the last two decades has resulted in survey efforts increasingly moving towards the east coast (Roy *et al.*, 2007; Coetzee *et al.*, 2008).

For the acoustic surveys, the continental shelf is grouped into different strata based on the expected fish distribution patterns from previous surveys (Coetzee *et al.*, 2008). Each survey was a series of predetermined parallel transects that were randomly-spaced within each pre-defined stratum (see Figure 3b; Barange, *et al.*, 1999; Roy *et al.*, 2007; Coetzee *et al.*, 2008). Along each transect, back-scattering intensity was estimated using a SIMRAD echo-sounder, pre-calibrated using the standard sphere gap technique (Barange and Hampton, 1997; Barange, *et al.*, 1999; Ungureanu and Nemțoi, 2014) and processed using echo-integration software (DAFF, 2016). Mid-water trawl samples were conducted to determine the size (caudal length) distributions of surveyed populations. The length distributions were weighted by the estimated biomass near each trawl as per echo-sounder to obtain overall length frequency distributions (Coetzee *et al.*, 2008).

Commercial catch data

Samples collected from commercial landings by DAFF personnel based at harbours located near fish factories along the west coast were used to obtain information on the size composition of catches (Fairweather *et al.*, 2006). These samples can be linked to the catch area because for every trip made, the skipper records the estimated catch biomass per 10' by 10' block position. The landings are weighed and the species composition assessed at port. Random samples from landings are used to estimate species composition and length frequency data. Ports sampled regularly include Lambert's Bay, Laaiplek, St. Helena Bay, Saldanha Bay, Cape Town, Hout Bay, Kalk Bay, Hermanus, Gansbaai, Mossel Bay and Port Elizabeth (de Moor *et al.*, 2016). Other biological data collected includes sex, length of fish, mass (both whole fish and gonad mass) as well as the maturity stage of the gonads using guidelines from Davies (1956).

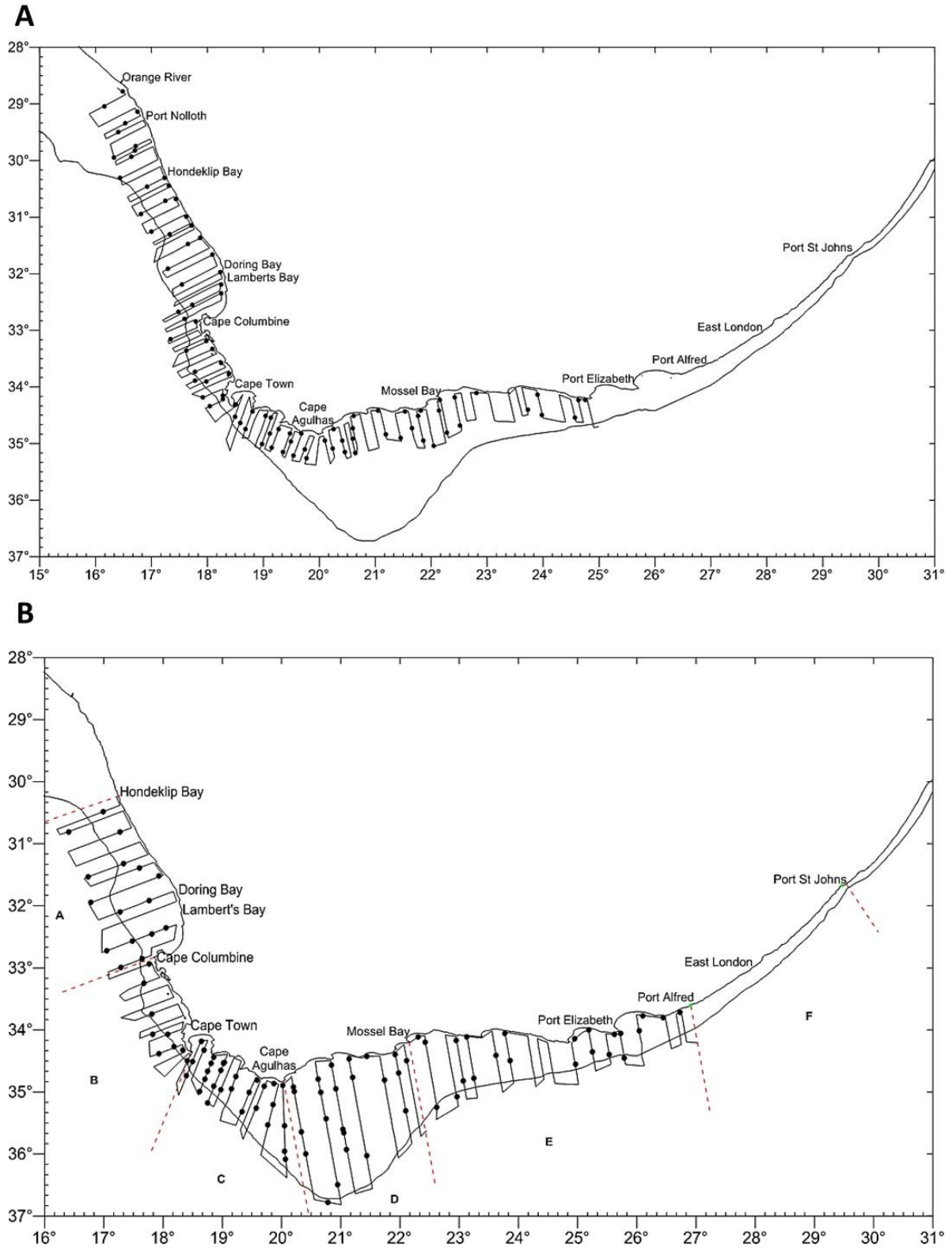


Figure 3: Typical tracks used for hydro-acoustic surveys for (A) recruits in winter (May-June) and (B) spawners in summer (November-December). The dotted lines indicate different strata for which predetermined, randomly-spaced parallel transects were used to estimate fish abundance (DAFF, 2016).

3.6 Data processing and analysis

The data were analyzed using the R statistical environment (R Development Core Team, 2011) as well as the Data Analysis add-in in Microsoft Excel (2013 version). Diet composition was determined using mass, frequency of occurrence as well as numerical abundance. Relative proportional contributions of species by mass to the diet of Cape Cormorants (F_p) for a sampling period were calculated, using the formula:

$$F_p = \frac{X_{p'}}{\sum X_p}$$

where $X_{p'}$ is the mass of a specific prey species and $\sum X_p$ is the summed mass of all the prey species contributing to the diet (see Punt *et al.*, 1995). The average mass per year was estimated from the total mass of all specimens per sampling period. These were then computed to get the average mass per annum and thereafter summed for each decade between three regions (west coast, Saldanha Bay region and south coast). These regions were grouped in such a way that Bird Island and Elephant Rock were regarded as part of the west coast region; Malgas, Meeuw, Schaapen, Jutten and Vondeling Islands formed part of the Saldanha Bay region and Dassen, Robben, Seal and Dyer Islands made up the south coast region. Since some colonies had quite patchy data, they were excluded for some analyses (see text for details). A weakness of this method is that the mass of all well-digested prey items is underestimated because no reconstruction of original mass was undertaken. Each year was weighted equally to allow for a comparative analysis.

During the analysis, prey species that were only recorded infrequently in the diet were combined and considered as 'other' prey. Diet data were grouped into the aforementioned three regions in order to test for spatial variations in the diet. The Saldanha Bay islands are

nested geographically among the west coast colonies, but were kept separate in the analysis because the cormorants breeding there also had access to the bay-lagoon system, and thus could exploit a wider array of prey than birds from other colonies. Years with sample sizes below the 5th percentile (i.e. years with less than 20 samples recorded and assessed for all regions; see Appendix 6 for yearly sample sizes per region) were identified using the Percentile.inc function in Excel and were excluded from the analysis.

Length frequency distributions of Sardine and Anchovy in the diet of Cape Cormorants and in catches by the purse-seine fishery were compared. Acoustic biomass estimates, specifically of Anchovy, were used to compare with the overall contribution of Anchovy to the diet of Cape Cormorants (see Appendix 3). However, due to the patchy coverage among years, the diet data were consolidated into decadal scales i.e. (1988–1997) and (1998–2007) for Anchovy and (1988–1997) for Sardine. The absence of Sardine data during the second decade is assumed to be owed to the massive declines in Sardine biomass experienced in the early 2000s (Ludynia *et al.*, 2010; see Introduction).

Post 2007, as a result of the changed conservation status of the species, very few samples were collected within colonies in order to minimize disturbance and therefore there was little data to compare across years and across regions. These data were not included in the analysis as they had sample sizes below the 5th percentile. Variations in the length frequencies between years and between study colonies were tested using the Kolmogorov-Smirnov statistical test (Klugman *et al.*, 2008). It was not assumed that the error distribution of the data was from any particular distribution or that variances were equal. Results were considered to be significant where $P < 0.05$.

For years when data were available, the average and median size of Anchovy within Cape Cormorant diet were plotted to compare with those of fish caught by the fishery during the same months. This analysis was only conducted for Anchovy because it was the most abundant species in Cape Cormorant diet. Colonies were grouped and linked with the stratum to which they were classified according to Figure 3 in order to compare the diet at each colony with the catch data. On account of limited data, a minimum sample size of 20 Anchovy in the Cape Cormorant diet for each site was considered adequate for monthly comparisons. Recruit Strata A, B and C were used for this analysis: Stratum A stretches from Hondeklip Bay to Cape Columbine, Stratum B lies between Cape Columbine and Cape Point, and stratum C from Cape Point to Cape Agulhas (Figure 3). A relationship was also investigated between the years where both the Cape Cormorants and the fishery caught spawners. The cut off sizes for recruit and spawner lengths were determined using Coetzee *et al.* (2008), where <11 cm and <15 cm were considered recruits for Anchovy and Sardine respectively and anything above that a spawner. Linear regression models were used to compare, separately, the proportion of recruits and that of spawners caught by the cormorants to those caught by the fisheries the same year.

4 RESULTS

4.1 Diet composition

Overall, 2460 prey items were recorded from at least 29 different species collected across 11 Cape Cormorant colonies (Appendix 2). Most (80%) of prey items were identified to species level. As expected, epipelagic fish dominated prey consumed at all sites. The species recorded most frequently and that contributed most to the diet were Anchovy, Sardine, Horse Mackerel and Redeye. Anchovy dominated in all years except in 1992 and 1993 when Sardine dominated diet samples, and 2007 when 'other' fish (mainly Cape Silverside *Atherina breviceps* and Southern Mullet *Chelon richardsonii*) were the most frequently eaten fish (refer to Figure 4a). Anchovy increased in importance from 70% of prey in 1988-1997 to 85% in 1998-2007, with a corresponding decrease in Sardine ($F_{19} = 8.9$, $p < 0.01$; Figure 4b). According to the Cape Cormorant diet data and Anchovy biomass estimate data used from 1984 – 2015, the mean numerical abundance of Anchovy in the cormorant diet strongly correlates to the annual biomass estimates obtained from acoustic surveys throughout the years ($R^2 = 0.72$, $p < 0.001$; Appendix 3).

Spatial variation in diet

Anchovy and Redeye were the only two prey species recorded in the diet in all three regions (west coast, Saldanha Bay and south coast) in both decades. Pelagic Goby was recorded in two regions (west and south coast regions), but only during the second decade. At Lambert's Bay and the Saldanha Bay region, the northernmost colonies in this study, the contribution of Anchovy decreased from the first to the second decade, although the change at Saldanha Bay was not statistically significant ($t_{30} = 2.19$, $p = 0.26$). By comparison,

Anchovy mass at the southeasternmost colonies, Dyer and Seal Islands, increased from the first to the second decade while Sardine mass decreased (Figure 5).

Despite these spatio-temporal changes, Anchovy was more important at Lambert’s Bay than at Dyer Island in both decades ($t_{30} = 2.19, p = 0.04$). Sardine contribution to the diet, on the other hand, varied significantly between all three regions, with a strong difference between Lambert’s Bay and Dyer Island ($F = 2.26, df = 30, p = 0.01$). At Lambert’s Bay, the proportion of Sardine in the diet increased from the first to the second decade, whereas at Dyer Island, it decreased over this period. Sample sizes for Dassen, Robben and Seal Islands did not allow for a spatio-temporal comparison between colonies.

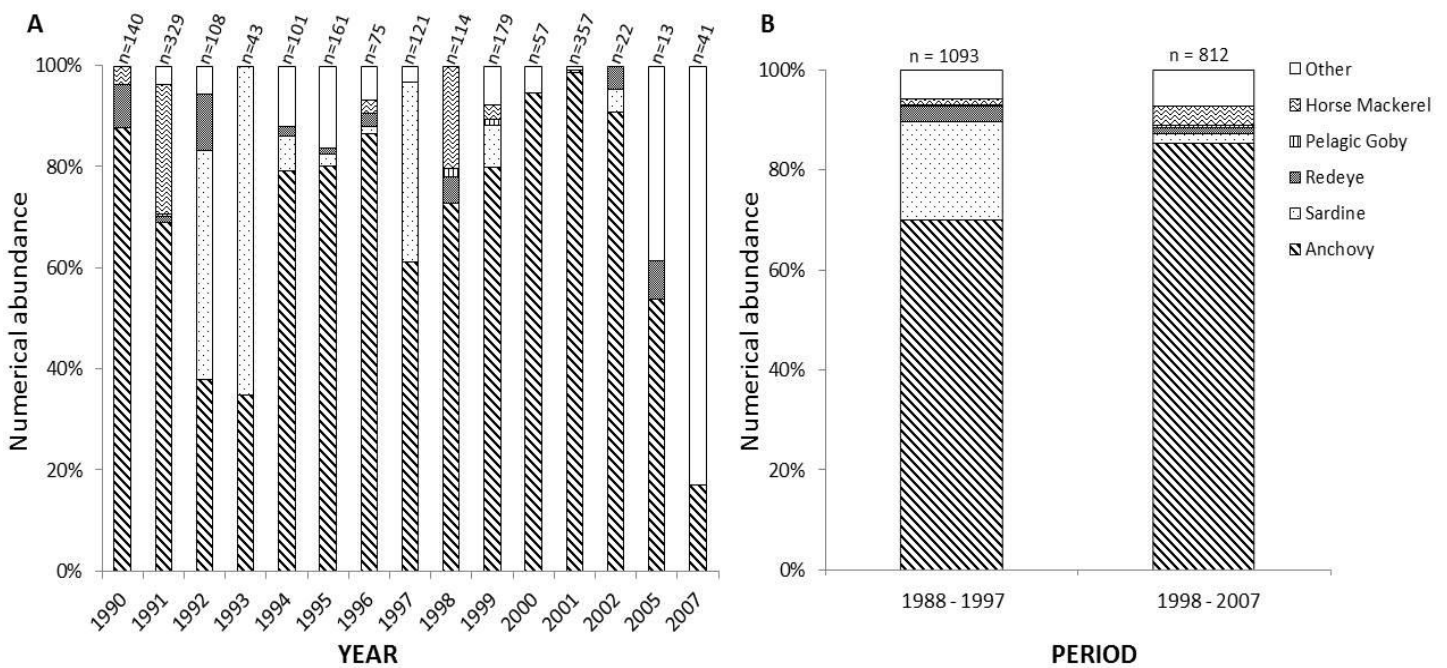


Figure 4: Contributions of each of the dominant prey groups to Cape Cormorant diet throughout the study period (excl. 1988, 1989, 2003, 2004 and 2006 where no regurgitate samples were collected) based on (A) annual numerical abundance and (B) relative numerical abundance per decade for each prey species.

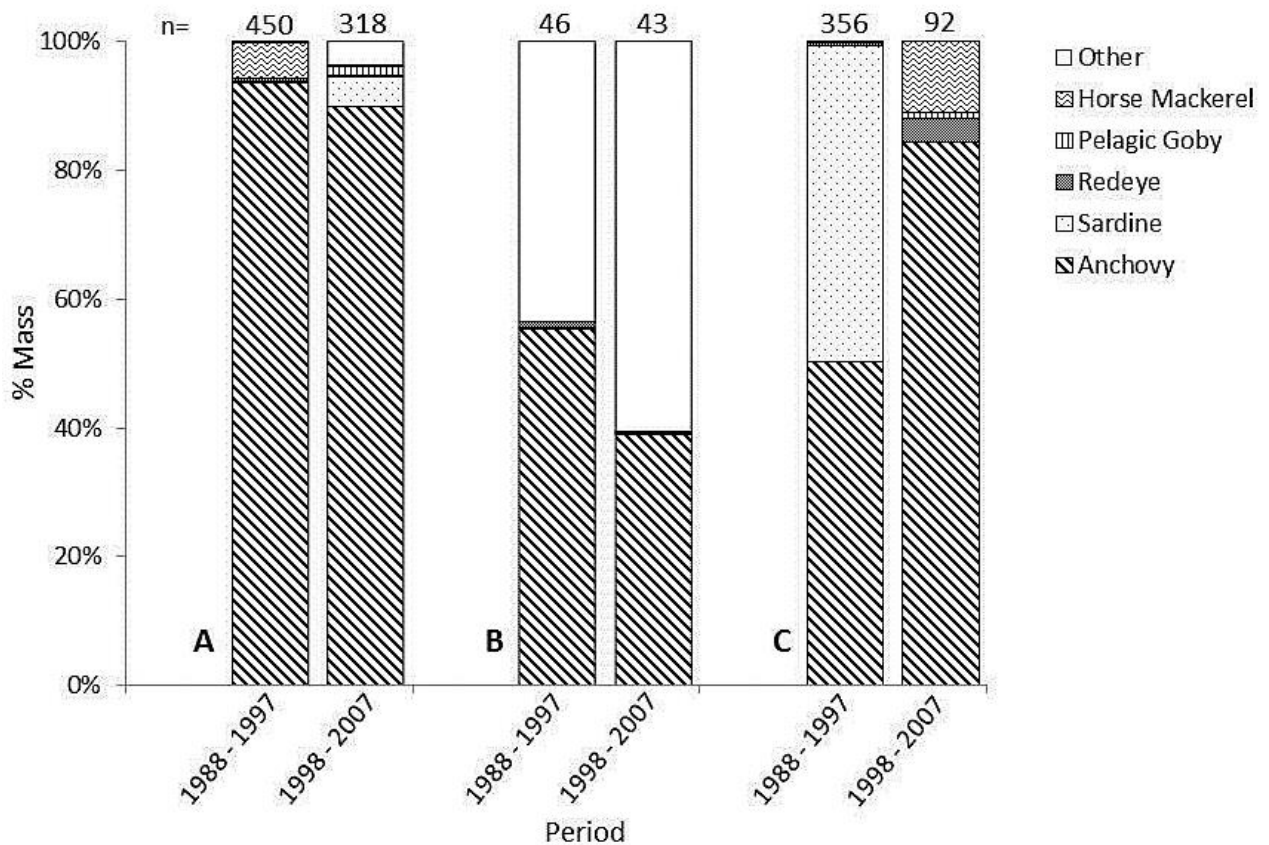


Figure 5: Proportion of the diet contribution (by mass) for each prey species during the first and second decade at different localities: (A) Lambert's Bay on the west coast, (B) the Saldanha Bay region (Malgas, Schaapen and Meeuw Islands) and (C) Dyer and Seal Islands on the south coast. n = overall number of prey items assessed.

4.2 Spatial and Temporal variations in fish size frequencies

Anchovies eaten by Cape Cormorants at all colonies were predominantly fish between 5 and 11 cm throughout the study period (Figure 6a). Sardine were larger than Anchovies (mostly 11 – 23 cm), with a bimodal distribution in the first decade (Figure 6b). During the second decade, Sardine contribution to the overall Cape Cormorant diet was < 2% across all colonies, with their lengths much smaller (between 4 and 7 cm) than that found in the diet during the first decade.

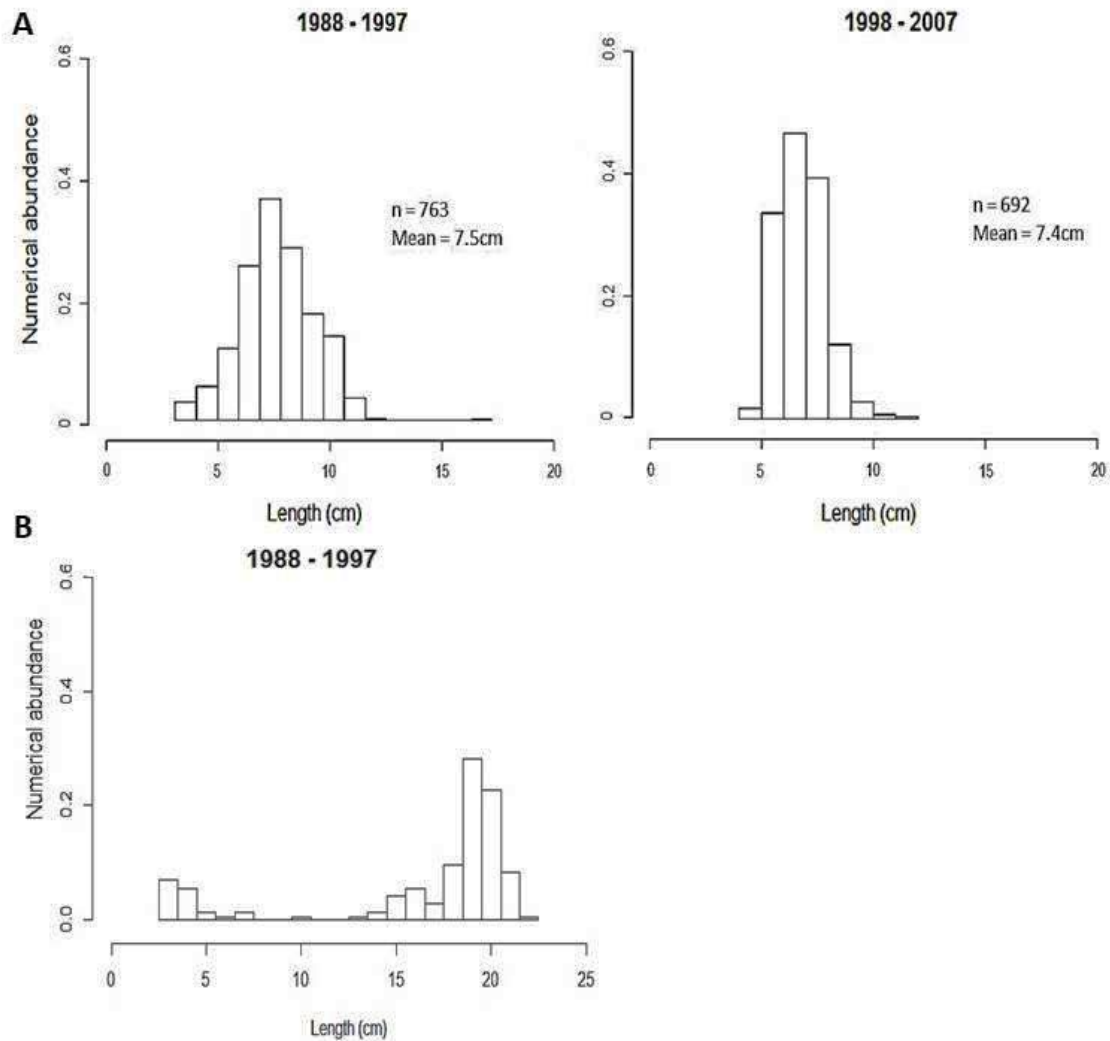


Figure 6: Proportional numerical abundance in the size distribution of (A) Anchovy in 1988 – 1997 and 1998 – 2007 and (B) Sardine in 1988 - 1997 in the diet of Cape Cormorants during two study decades

There was an overlap in the distribution of fish sizes caught by the fishery and those found in the diet of Cape Cormorants during the first decade. The size distribution of the Cape Cormorant diet displayed a similar trend to that of the commercial catch data for both Anchovy ($r_{29} = 0.91$, $p < 0.001$) and Sardine ($r_{40} = 0.53$, $p < 0.001$). Where it was possible to compare cormorant prey with fishery catches in the same month and location, the Anchovies caught by Cape Cormorants averaged slightly smaller than those caught by the fishery, with the exception (although trivial) of Vondeling Island in March 1990 ($F = 5.79$; df

= 17; $p < 0.05$), but the difference in median length was only marginally significant ($p < 0.1$; Table 1).

Table 1: Differences between mean and median sizes (cm) of Anchovy in the diet of Cape Cormorants and in fisheries catches from the same region. Mean diff. (cormorant diet; fishery catch) and Median diff. (cormorant diet; fishery catch).

Year	Month	Locality	$\bar{x}_{\text{corm}} - \bar{x}_{\text{catch}}$	$\text{med}_{\text{corm}} - \text{med}_{\text{catch}}$
1990	March	Vondeling Island	0.22 (7.68; 7.46)	1.25 (8.00; 6.75)
1991	May	Vondeling + Dassen Islands	-2.03 (6.85; 8.88)	-1.75 (7.00; 8.75)
	July	Seal Island	-1.74 (6.49; 8.22)	-1.75 (6.00; 7.75)
1994	March	Dyer Island	-1.27 (9.17; 10.44)	-1.25 (9.00; 10.25)
1996	April	Jutten Island	-2.05 (5.94; 7.99)	-1.75 (6.00; 7.75)
1997	May	Lambert's Bay (Bird Island)	-1.43 (6.89; 8.32)	-1.25 (7.00; 8.25)
1999	September	Vondeling Island	-0.05 (7.56; 7.61)	0.25 (7.50; 7.25)
2000	September	Lambert's Bay (Bird Island)	-0.44 (6.48; 6.93)	-0.25 (6.50; 6.75)
2001	October	Lambert's Bay (Bird Island)	-1.31 (6.46; 7.77)	-0.75 (6.50; 7.25)

Throughout the study period, the mean lengths of Anchovy eaten by Cape Cormorant predominantly averaged between 6.5 and 11 cm, meaning the birds were mostly targeting recruits. The size distribution of Anchovy was similar in cormorant diet and the fishery catches during the first decade. However, during the second decade, cormorant diet was less varied, mainly comprising fish with caudal lengths between 7 and 8 cm with a mode of 7.5 cm (Figure 7).

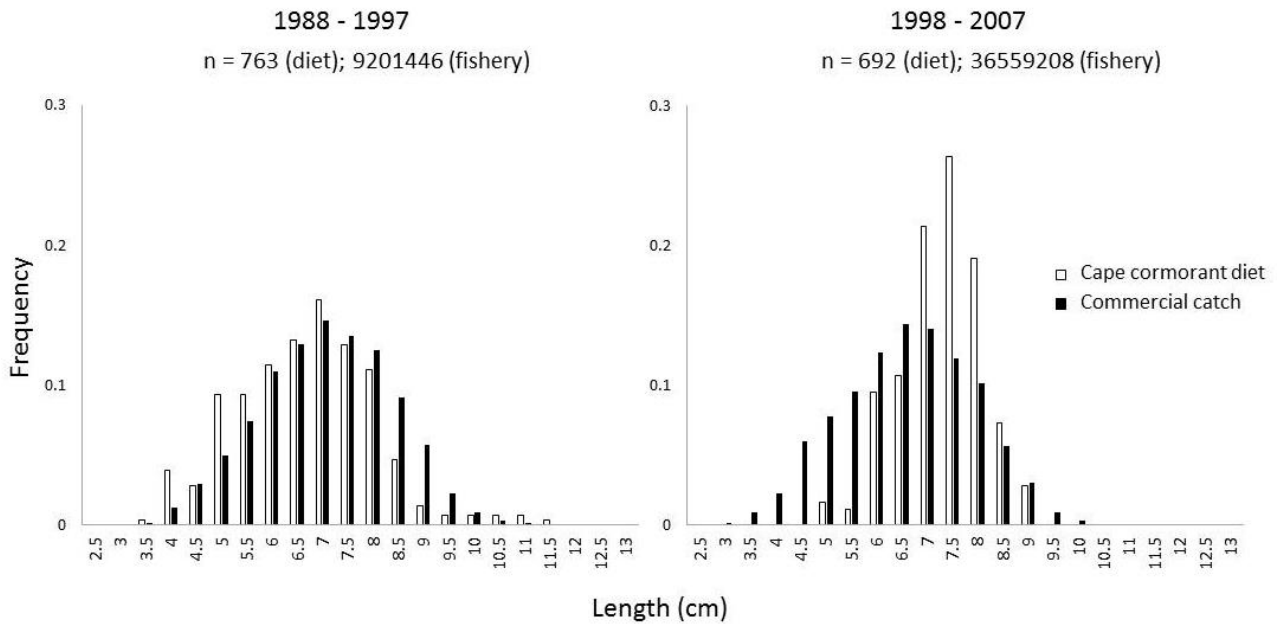


Figure 7: Size distribution of Anchovy in the diet of Cape Cormorants and the purse-seine catch during the two decadal periods

Interestingly, during some years (1991 – 1994 and 1997; Appendix 5), the birds targeted spawners (i.e. > 11 cm for Anchovy and > 15 cm for Sardine). For the years with sufficient data to compare the proportions of spawning Sardine and Anchovy in the diet of Cape Cormorants to those caught by the fishery, there was no significant relationship for Anchovy ($R^2 = 0.334$, $p = 0.17$). On the other hand, the proportion of Sardine spawners found in the diet was positively correlated to that found in the fishery. However this showed a non-significant trend ($R^2 = 0.712$, $p = 0.07$; Figure 8), possibly as a result of the relatively small sample size (i.e. only 5 years had sufficient data to compare).

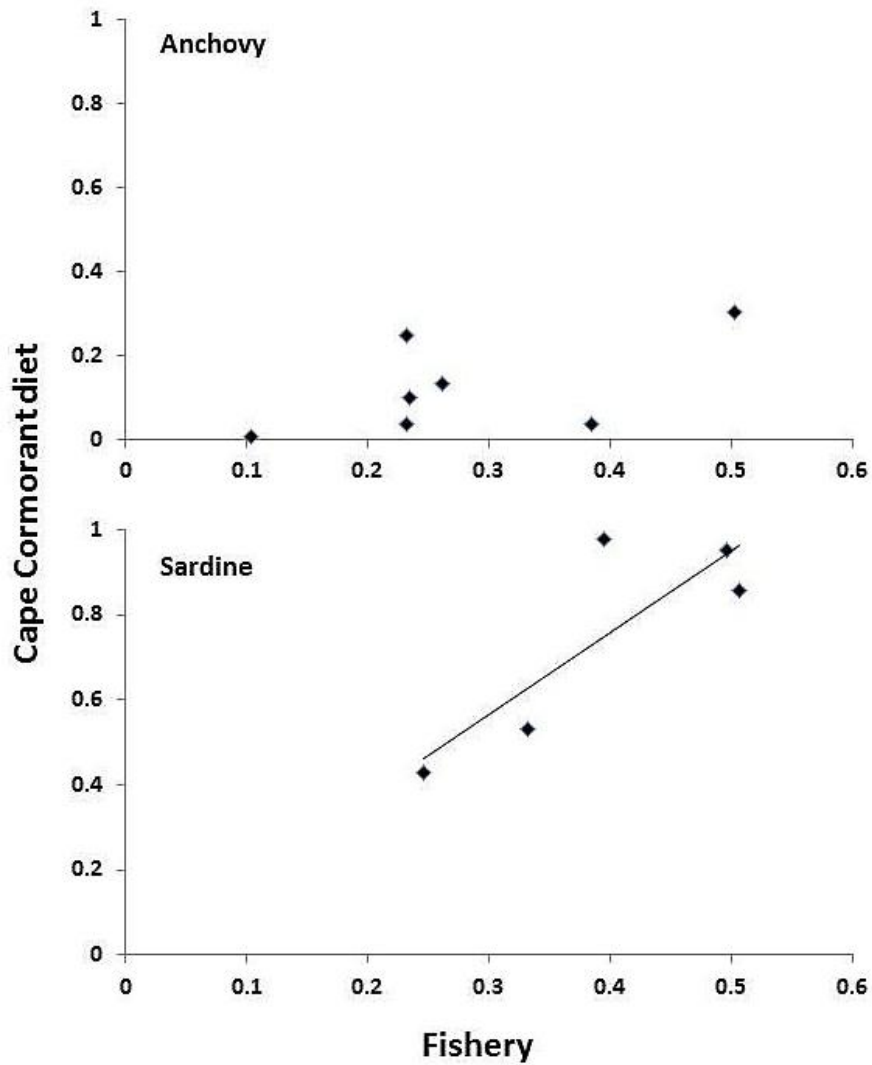


Figure 8: Relationship between the proportions of Anchovy and Sardine spawners caught by Cape Cormorants and by the commercial purse-seine fishery during the first decade.

5 DISCUSSION

Diet studies have previously been used to understand prey selection by predators, specifically looking at prey composition in relation to its distribution and temporal availability (Barrett *et al.*, 2007; Pichegru *et al.*, 2009; Hilborn *et al.*, 2017). Trends in Cape Cormorant populations, focusing on the number of breeding pairs at localities, have been attributed to an altered availability of dominant prey species (e.g. Crawford, 2007a; Crawford, *et al.* 2007a; 2016), but hitherto there has been little information on the sizes of prey eaten by Cape Cormorants. It is important to have more detailed information on long-term trends in the composition of their diet, as well as the sizes of prey selected by Cape Cormorants, in order to more fully understand the influence fishing has on their prey and on their population trends.

5.1 *Diet composition*

Cape Cormorants eat a wide variety of prey species (Appendix 2) that range from epi- to bathy-pelagic species (Rand, 1960; Klages *et al.*, 1992). Their feeding grounds range from offshore waters to shallow tidal pools and estuaries (Ryan *et al.*, 2009). Throughout my study period, only a few species contributed the bulk of their diet: Anchovy, Sardine, Redeye, Pelagic Goby and Horse Mackerel, with Anchovy being the dominant species by far. These fish species are also the main targets of South Africa's purse-seine fishery (Burger and Cooper, 1984; Coetzee *et al.*, 2008), which could lead to competition between Cape Cormorants and the fishery for these prey species. Cape Cormorants require a substantial consumption of these prey species, most commonly the high-energy Sardine and Anchovy, for optimal survival (Kemper and Simmons, 2015) and breeding (Furness and Cooper, 1982).

Like Cape Cormorants, other locally-breeding seabird species such as Cape Gannets and African Penguins that also rely on Anchovy and Sardine as a food source have decreased in numbers, and/or in the importance of these prey species to their diet (Crawford *et al.*, 2008; Okes *et al.*, 2009). Cape Gannets, which only breed at three localities in South Africa (i.e. Algoa Bay, Bird Island at Lambert's Bay and Malgas Island; Crawford, 1999), show a declining trend at both west coast localities (Bird and Malgas Islands). Prior to the Sardine collapse, Sardine comprised most of Cape Gannet diet. However, the collapse in Sardine resulted in fluctuations in the overall diet contributions (Green *et al.*, 2015). Subsequently, considerable dietary changes have been noted such an increased contribution of trawl fishery discards to their diet, specifically off the west coast. These dietary changes resulted in marked decreases of population numbers off the west coast of South Africa over time (Crawford *et al.*, 2008) which can be attributed to competition with the purse-seine fishery for food.



African Penguins are less flexible foragers than Gannets, and as a consequence of their high energetic demands and restricted foraging ranges, they are particularly sensitive to changes in forage fish availability off the west coast of South Africa (Coetzee *et al.*, 2008; Hutching *et al.*, 2009). Historically, Sardine used to comprise most of African Penguin diet, however, like the Cape Gannet and Cape Cormorant, Anchovy became more dominant in the diet with Pelagic Goby also contributing a significant amount after the 1970s (Crawford and Dyer, 1995; Crawford, 1999). A number of studies have demonstrated that African Penguin numbers are strongly correlated to prey availability and therefore their recent decreases can be linked to competition with the purse-seine fishery (see Crawford, 1998, 1999; Crawford *et al.*, 2001, 2006; Kemper *et al.*, 2001; Pichegru *et al.*, 2010; Sherley *et al.*,

2013). Their population numbers have also been further declining since mid-1990s as a result of limited prey (Crawford, 1999; Pichegru *et al.*, 2009).

Temporal variation

Although Cape Cormorant diet samples were collected opportunistically, they showed a similar trend of Anchovy dominance as also presented by Crawford and Dyer (1995) as well as Hockey *et al.* (2005). In all years between 1990 and 2007, except 1992, 1993 and 2007, Anchovy contributed at least half the diet of Cape Cormorants in South Africa and up to 99% by mass of the overall food eaten. Sardine was more abundant in 1992, 1993 and 1997, which coincides with the period when the Sardine stocks recovered somewhat from previous exploitation (Crawford, 2007b). This does not necessarily reflect that the birds only targeted these two species but that the other prey species were overshadowed by their abundance.

The abundance of other fish species in the diet of Cape Cormorant increased substantially from 2005–2007. The cormorants could have been compelled to broaden their diet as a result of a decreased Anchovy abundance, although diet sample sizes were small in these years. This altered abundance and distribution of prey was assumed to have been a result of prior large-scale environmental irregularities caused by the Pacific El Niño weather pattern (Roux and Shannon, 2004; NOAA, 2005). According to Nicholson (2010), a low-level atmospheric jet links Pacific El Niño events to parts of southern Africa, which affects ecosystem functioning and leads to reduced productivity and altered distributions of fish. In years of low Anchovy abundance, Cape Cormorants, like many other top predators such as sharks and seals (Crowder *et al.*, 2008), likely face reduced participation in breeding and breeding success (Crawford *et al.*, 1992a). During this same period (2005 – 2007), the total

number of Cape Cormorant breeding pairs decreased by c. 9 000 pairs, going from an estimate of 43 900 breeding pairs to 35 100 pairs (DEA unpublished data; as demonstrated in Appendix 4). Similarly, during the same period, the number of Cape fur seal successful breeders at the largest colony in Kleinsee in the Northern Cape decreased by c. 50%. Two more colonies, Seal Island in False Bay and Elephant Rock, also on the west coast of South Africa displayed similar declines (Kirkman, 2010).

Throughout the Western Cape, the numerical contribution of four (Anchovy, Pelagic Goby, Horse Mackerel and 'other') out of the six dominant prey groups in the diet of Cape Cormorants increased during the second decade investigated compared to the first, while Sardine and Redeye decreased (Figure 4b). An eastward shift in the distribution of both Sardine and Anchovy occurred during this period (van der Lingen *et al.*, 2006), resulting in decreased Sardine populations off the west coast (Pichegru *et al.*, 2009). Historically, Cape Cormorants subsisted almost exclusively on this species, especially at the northern colonies off the west coast (Hockey *et al.*, 2005).

The eastward shift in forage fish resulted in the populations of Cape Gannets and African Penguins decreasing (see above). Swift Terns, however, were unusual in having increased during this period, despite the impact of the purse-seine fishery (Crawford, 2004, 2009). This is partly because this species is nomadic and can adapt to changed prey distributions (Crawford *et al.*, 2015; Gaglio *et al.*, 2017, 2018), and partly because of marked declines in the numbers of Palearctic migrant terns wintering in South Africa which, to a certain extent, limits competition for resources (Ryan, 2013).

Large fluctuations in the abundance and distribution of Cape Cormorant prey species in the Benguela ecosystem, particularly Anchovy, Sardine and Horse Mackerel, have been

attributed to a number of factors but are still not fully understood (e.g. Crawford *et al.*, 1987; Coetzee *et al.*, 2008; Blamey *et al.*, 2015). It does, however, seem that increased exploitation by the purse-seine fishery has amplified these fluctuations to a level that makes it hard for many top predators to accommodate the changes, particularly off the west coast where the bulk of fishing effort still is concentrated (Pichegru *et al.*, 2009). The overexploitation of prey species has contributed to population decreases of a number of top predators off the west coast of South Africa (see David, 1987; Crawford *et al.*, 1992a, 2011; Wickens *et al.*, 1992; Crawford, 2004; Pichegru *et al.*, 2009).

Spatial variation

Cape Cormorant diet primarily comprises pelagic schooling fish (Payne *et al.*, 1989; Hockey *et al.*, 2005; Kemper and Simmons, 2015). However, within this category of forage species, the present study demonstrates flexibility in their diet based on the regional availability of prey species. Birds from the Saldanha Bay region had the highest proportional contributions by mass of 'other' fish in both decades investigated. As expected, given the greater diversity of foraging habitats available to them, cormorants within this area had the most diverse diet, with large contributions from 'other' fish (mainly Cape Silverside, White Stumpnose *Rhabdosargus globiceps* and Knysna Goby *Psammogobius knysnaensis*). The colonies in this region are located near the mouth of Langebaan Lagoon (Hanekon *et al.*, 2009), which serves as a nursery ground for a wide variety of fish species (BirdLife International, 2012).

Foraging effort differs regionally, with cormorants breeding at west coast colonies having to invest more effort into foraging while provisioning small chicks than birds breeding at Dyer Island off the south coast (Hamann *et al.*, 2012), probably as a result of the

lower abundance of prey off the west coast. When there is a particular shortage of prey, Cape Cormorant populations experience reduced breeding success as a result of either abandoning their breeding attempts, or skipping breeding entirely (Crawford *et al.*, 2016). The differences in prey composition support the proposition that variations in seabird diet indicate local variations in prey availability (Berruti and Colclough, 1987; Barrett *et al.*, 2007), but may not accurately reflect differences in absolute abundance of prey items (see Klages *et al.*, 1992).

5.2 *Distribution patterns and size frequencies*

Previous research has demonstrated extensive overlap between purse-seine fishery catches and diets of seabirds such as Cape Gannets and African Penguins, which has been inferred as evidence of competition between the fishery and these predators (Berruti, 1987; Pillay, 2002; Crawford *et al.*, 2007b; Green *et al.*, 2015). This thesis also revealed spatio-temporal correlation between Cape Cormorant diets and fishery catches. During years when the birds targeted much larger fish (i.e. 1991 – 1994 and 1997), the Anchovy size distribution reflected a bimodal pattern (Appendix 5), which was only apparent during 1992 and 1997 for Sardine. This shows that although Cape Cormorants predominantly catch juvenile Sardine and Anchovy, they can eat Sardine and Anchovy spawners when these larger fish are available.

Cape Cormorants and the fishery target similar-sized fish; both mainly catch Anchovy recruits (<11 cm, Figure 7). As expected, the largest Anchovy caught by both Cape Cormorants and the fishery was in the south-west region, at Dyer Island, which lies within the Anchovy spawning grounds (Richardson *et al.*, 1997; Hutchings *et al.*, 1998; Barange *et al.* 1999). The decrease in the size of Anchovy eaten by Cape Cormorants between 1988–

1997 and 1998–2007 (Figure 6a) may have resulted from the eastward shift of Sardine and Anchovy (Roy *et al.*, 2007; Coetzee *et al.*, 2008; Watermeyer *et al.*, 2016). The overall mass contribution of the different prey group to Cape Cormorant diet has changed compared to prior early 1960s where Sardine was more dominant in the diet than other prey (see Hockey *et al.*, 2005). Anchovy only began to dominate the diet, both by number and by mass, in the 1970s (Cooper, 1984; Dufft *et al.*, 1987; Hockey *et al.*, 2005) following Sardine stock collapse during the mid-1960s (Fossen *et al.*, 2001; Griffiths *et al.*, 2005; Hutchings *et al.*, 2009). The apparent increased abundance of Sardine spawners within the Cape Cormorant diet during the first decade of the study (1988 – 1997) coincides with information provided by Coetzee *et al.* (2008), who state that during this period Sardine stocks had recovered to levels that were similar to those estimated prior their earlier collapse (Coetzee *et al.*, 2008). According to Barange *et al.* (2009), Sardine does not necessarily depend on a single year's strong recruitment in order to maintain its stock size but nonetheless, successive years of high spawner mortality can negatively affect species biomass (Coetzee *et al.*, 2008). Such high mortalities may result in poor recruitment (Hutchings *et al.*, 1998), which leads to poor breeding by Cape Cormorants and results in decreased population abundance (Crawford *et al.*, 1992a). During the decade (1988 – 1997), despite the partial recovery of the Sardine stocks, the Cape Cormorant population decreased by over 70% in South Africa from c. 96 000 breeding pairs in 1988 to c. 25 000 pairs in 1997. A displacement of sardine to the southeast in this period substantially reduced its availability to formerly large Cape cormorant colonies in northwest South Africa's, e.g. Lambert's Bay, Jutten Island, Dassen Island (Crawford *et al.*, 2016).

6 CONCLUSION

Seabirds have been used as ecological indicators for many years (Grémillet *et al.*, 2016) ranging from simple tools to detect presence of different fish species (Barrett *et al.*, 2007) to indicators of change in stock size (e.g. Crawford *et al.*, 1983). The impacts of reduced pelagic fish availability on Cape Cormorants likely had far-reaching consequences, resulting in reduced population size of this top predator. Such impacts may result in trophic downgrading that alters the overall structure and dynamics of their ecosystem (Sugishita *et al.*, 2015). However, Cape Cormorants have seldom been used to inform or support management decisions when it comes to fisheries. This study therefore has the potential to provide crucial information towards a better understanding of the influence of the purse-seine fishery on the population of Cape Cormorants in South Africa. Only when these influences are fully understood can areas of environmental importance be identified and managed.



Although this study used fine-scale assessments of the prey contribution to the diet of Cape Cormorants, owing to their changed conservation status, the collection of consistent data from regurgitates proved to be problematic. Diet regurgitates are a stress response to human disturbance and cannot be regarded as a standard procedure for sampling the diet of threatened species (Kemper *et al.*, 2007a). The regular collection of pellets could, however, be explored more as a non-invasive alternative in order to obtain diet data at a finer scale. This could be done during routine patrols around colonies where Cape Cormorants breed and roost, or while conducting various other monitoring or research activities. Sampling kits, together with a well-defined sampling protocol, could be supplied to the managing authorities of the various Cape Cormorant colonies to assist with collection

of regurgitate samples when the opportunities arise. The pellets can then be used for investigating future spatial or temporal variations in the diet (Carss *et al.*, 1997). After collection, the samples would be preserved in ethanol for later assessment by trained professionals for quality control purposes.

Cape Cormorants exist within a highly dynamic ecosystem and play a significant role in the stability and resilience of marine ecosystems. They have a narrow prey base, with only a few species contributing to the bulk of their diet (Hockey *et al.*, 2005). However, they have demonstrated flexibility in their diet based on the regional availability of the species within their prey base. Looking at the range of prey sizes caught by cormorants and the purse-seine fishery, specifically Sardine and Anchovy, one would conclude that there is substantial overlap in their target sizes. Therefore there is considerable potential for competition for food between Cape Cormorants and the fishery. Other top predators such as the Cape Gannets (Green *et al.*, 2015), Cape fur seals (Pillay, 2002; Kirkman, 2010) and African Penguins (Crawford *et al.*, 2006; Pichegru *et al.*, 2010) also compete for the same resources and have shown similar trends to those presented in this study relative to competition with the purse-seine fishery (Crawford *et al.*, 1992a; Pichegru *et al.*, 2009). This needs to be accounted for in an ecosystem-approach to management of the fishery (e.g. Ainley *et al.*, 2018).

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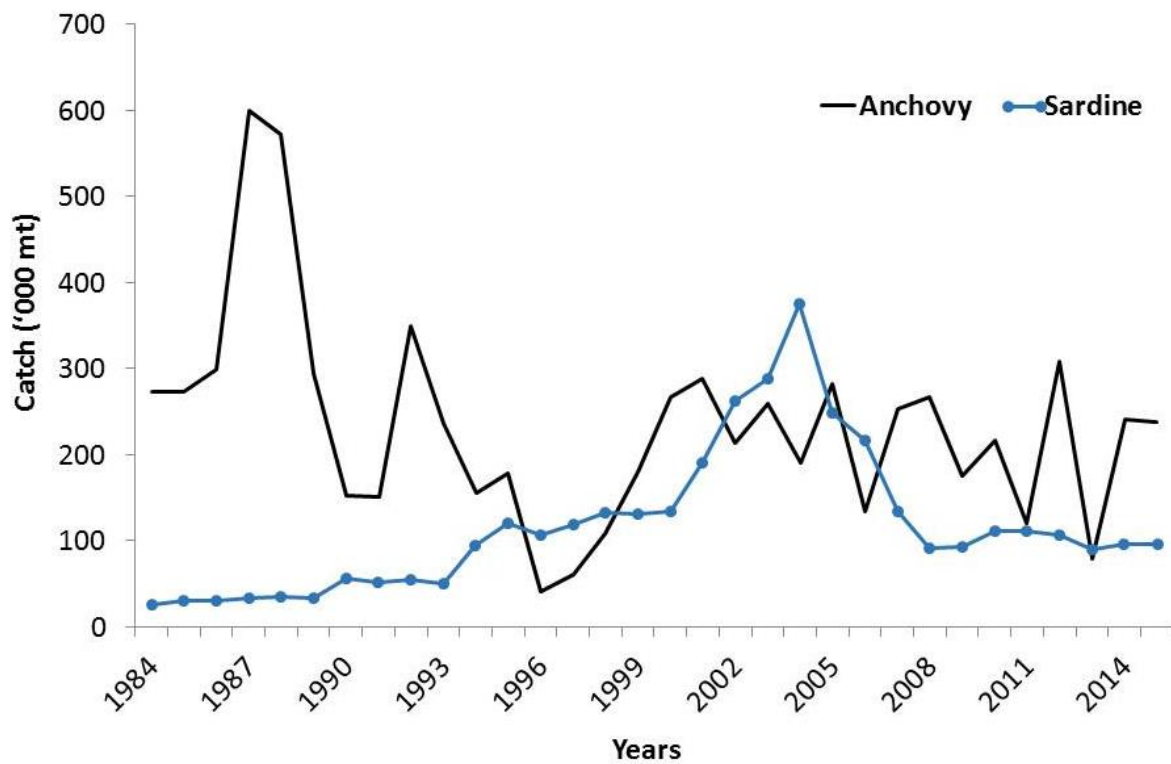
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8 APPENDICES – supplementary material

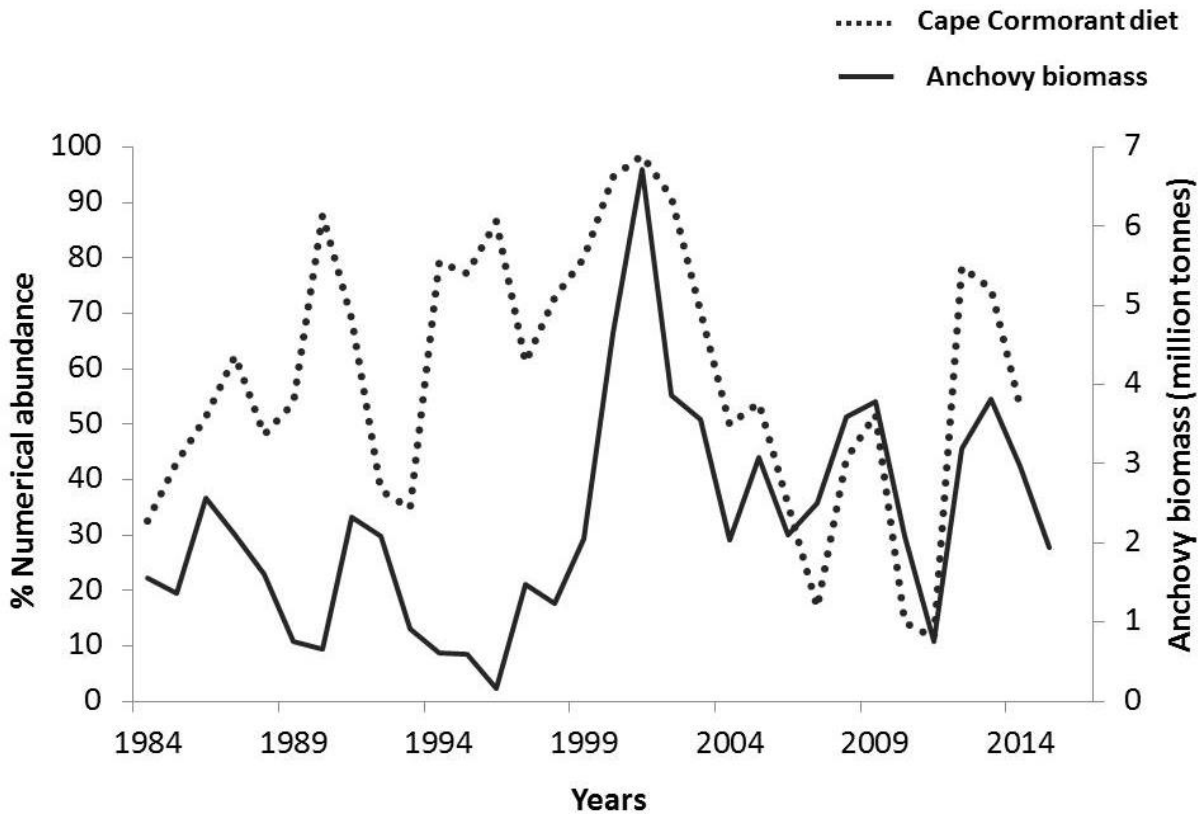


Appendix 1: Trends in commercial catches of Sardine and Anchovy off the west coast South Africa, 1984 – 2015 (adapted from de Moor *et al.*, 2016).

Appendix 2: Summary of all prey species found in Cape Cormorant diet during study period at all the colonies.

Species	Common Name
<i>Engraulis encrasicolus</i>	Cape Anchovy*
<i>Sardinops sagax</i>	Sardine*
<i>Sufflogobius bibarbatu</i> s;	Pelagic Goby*
<i>Trachurus trachurus capensis</i>	Horse Mackerel*
<i>Etrumeus whiteheadi</i>	Redeye*
OTHER	
<i>Atherina breviceps</i>	Cape Silverside*
<i>Austroglossus pectoralis</i>	Sole
<i>Blennidae</i> sp.	Unid Blenny
<i>Caffrogobius saldanha</i>	Commafin Goby
<i>Champsodon capensis</i>	Gaper
<i>Chelidonichthys capensis</i>	Cape Gurnard
<i>Chelon richardsonii</i>	Southern Mullet
<i>Clinidae</i> sp.	Unid. Klipfish
<i>Clinoporus biporosus</i>	Ladder Klipfish
<i>Conger wilsoni</i>	Eel
<i>Gonorynchus gonorynchus</i>	Beaked Sandfish
<i>Lampanyctodes hectoris</i>	Lantern Fish
<i>Loligo vulgaris reynaudi</i>	Chokka Squid*
<i>Lolliguncula mercatoris</i>	Thumbstall Squid
<i>Merluccius</i> sp.	Hake*
<i>Muraenesox bagio</i>	Pike
<i>Pomatomus saltrix</i>	Elf
<i>Psammogobius knysnaensis</i>	Knysna Goby
<i>Rhabdosargus globiceps</i>	White Stumpnose
<i>Syngnathus acus</i>	Longnout Pipefish*
<i>Thyrsites atun</i>	Snoek
Unid. Squid	
Unid. Prawn	

*Also recorded in Cape Cormorant diet by Cooper, 1985; Duffy *et al.*, 1987 and Hockey *et al.*, 2005.



Appendix 3: Anchovy numerical abundance in Cape Cormorant diet (DEA unpublished data) relative to Anchovy biomass estimates from DAFF acoustic surveys conducted on the West Coast (west of 20°E, DAFF unpublished data).

Population trend estimates

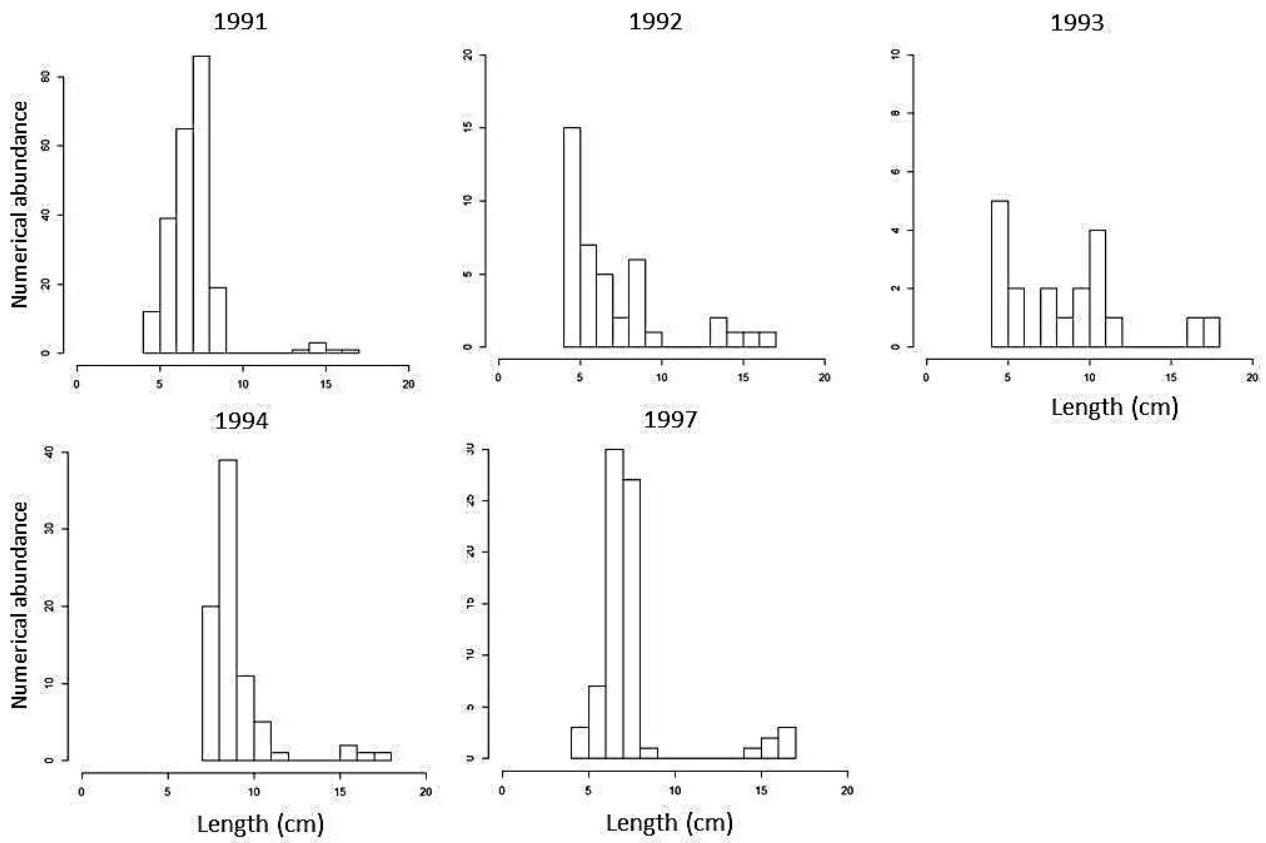
Population trend estimates (derived from the number of successful breeding pairs each year) were available for 10 colonies: Lambert’s Bay (Bird Island), Malgas, Jutten, Meeuw, Schaapen, Vondeling, Dassen, Robben, Seal and Dyer Islands. These population estimates represent the minimum estimates of the overall South African population, considering that some birds may skip or abandon breeding during certain years (maybe as a result of limited food sources). Also, depending on the time the count is conducted, not all breeding birds might be present (Crawford et al., 2007a).

Appendix 4: Number (thousands of pairs) of Cape Cormorants breeding at 10 selected colonies in the Western Cape, South Africa, between 1956 and 2016.

	Lambert's Bay	Malgas Island	Jutten Island	Meeuw Island	Schaapen Island	Vondeling Island	Dassen Island	Robben Island	Dyer Island	Seal Island	Total
1956	30.98	14.55	27.76			0.80			3.19		77.28
1963				0.04	0.14						0.18
1967	9.70	1.86				0.10					11.66
1969		5.54									5.54
1970	30										30
1977										0.04	0.04
1978	13.52	8.71	24.28	0.06	0.14	7.89	13.77		35.58		104.0
1979	9.60	0.45		0.03	0.21						10.29
1985		0.02	0.22			0	11.14		48.29		59.67
1988	4.41	3.07	16.47			0.25	48.18		23.34		95.72
1989	2.44		2.55			0.20	0		3.26		8.45
1990	2.88	0.57	1.86			1.04	3.08		8.60		18.03
1991	4.77	5.36	13.47			4.12	29.61		32.96		90.29
1992	2.15	1.20	8.11			6.14	36.49		18.42		72.51
1993	0.88	0.78	0.01			0			18.35		20.02
1994		0.05	0.21			10.72			14.56		25.54
1995	1.62	1.68	2.74			2.30	7.15		14.77		30.26
1996	0.64	0.85	6.62	0.33	1.16	3.99	1.08		13.83		28.5
1997	0.96	3.03	5.06			4.16	0.67		11.04		24.92
1998	0.52	0.73	0.35			2.53	0.08		17.94		22.15
1999	1.62	2.61	5.41	0.71	0.79	3.43	5.26		15.62		35.45
2000	2.09	0.47	0.93	0.50	1.00	0.95	3.19		18.11		27.24
2001	3.38	3.93	7.25	1.41	1.58	5.02	2.06	0	18.44		43.07
2002	1.15	0.51	1.71	0.44	1.49	2.13	0.28		9.21		16.92
2003	0.54	1.18	2.88	0.80	1.17	6.31	1.36		15.00		29.24

2004	0.27	0.78	0.66	1.06	2.07	1.49	0.21	0.17	33.02		39.73
2005	0.29	2.56	9.04	0.34	2.14	3.18	3.15	0.38	22.77	0.05	43.9
2006	0.06	2.26	2.74	0.33	0.56	1.45	0.17	0.62	25.96		34.15
2007	0.06	0.60	4.28	0.13	0.01	2.01	1.32	1.66	24.97	0.06	35.1
2008	0.14	0.31	3.04	0.36	0.19	1.67	1.40		5.23	0.09	12.43
2009	0.04	0.30	5.74	0.49	2.11	5.02	0.17	1.74	36.28	0.01	51.9
2010	0.02	0.92	7.33	0.05	0.23	0.27	5.65	1.93	23.70	0.12	40.22
2011	0.03	0.01	2.19	0.25	0.90		9.03	0.98	24.00		37.39
2012	0.01	1.91	3.50	1.58	0.05	0.35	0.77	2.17	20.02	0.03	30.39
2013	0.12	0.62	0.50	0.04	0.01	0.10	0.15	0.92	12.21	0.09	14.76
2014	0.04	1.84	6.38	0.14	0.03	0.23	0.80	0.74	30.52	0.10	40.82
2015	0.07	1.03	4.41	0.01	0.14	0.00	0.18	1.18	37.08	0.39	44.49
2016	0.10	4.51	4.41	0.14	0.05	0.17	1.26	1.40	21.08	0.38	33.5





Appendix 5: Anchovy size distribution for years that demonstrated bimodal distributions in Cape Cormorant diet.



Appendix 6: Summary of the sample size per region during each year throughout the study period (1988 – 2007).

Year	Region		
	West Coast	Saldanha Bay	South Coast
1988	9	-	-
1989	-	-	-
1990	31	87	22
1991	-	63	266
1992	23	15	70
1993	-	5	38
1994	20	12	69
1995	133	33	1
1996	33	36	6
1997	75	5	41
1998	57	35	22
1999	55	124	-
2000	34	-	23
2001	302	18	37
2002	-	14	8
2003	2	12	-
2004	-	-	2
2005	-	5	8
2006	-	11	-
2007	-	41	-