The effects of prey availability on the endangered bank cormorant *Phalacrocorax neglectus*

Philna Botha

BTHPHI008

Thesis presented for the Degree of Master of Science in Zoology,
Department of Biological Sciences, University of Cape Town,
South Africa

April 2014

Supervisors: Prof Les Underhill, Prof Peter Ryan,
Dr Richard Sherley & Dr Timothée Cook

Plagiarism declaration

I know the meaning of plagiarism and declare that all of the work in this thesis, save for that which is properly acknowledged, is my own.

Signature: ________________________

Date: _____________________________

Abstract

The bank cormorant *Phalacrocorax neglectus* is a seabird endemic to the south-western coast of southern Africa and the Benguela Upwelling System and has suffered a decline of more than 50% over three generations. Main threats include displacement by Cape fur seals *Arctocephalus pusillus,* direct human disturbance, pollution, climate change and food shortage. This thesis focuses on the bank cormorant's response to food shortage, both directly and indirectly. Four colonies (Jutten Island, Dassen Island, Robben Island and Stony Point) were studied in terms of responses on population level in relation to the spatial distribution of prey surrounding the various colonies, foraging behaviour and breeding success.

First, I tested the response of the bank cormorant's population dynamics in relation to the availability of West Coast rock lobster *Jasus lalandii* in different spatial scales around three colonies (Jutten Island, Dassen Island and Stony Point) over a subset of years. I found that birds at Dassen Island showed the strongest response to the availability of rock lobster. Birds also showed strongest response to the availability of rock lobster in an accumulative distance around colonies, and their largest response was to rock lobster within 30 km distance from the colony. Various aspects including the life-history traits and moulting stages of this particular rock lobster species may be the reason to this response.

Second, I present foraging effort data of bank cormorants in localities known to be situated in areas with different prey availability. I found that at Jutten Island, situated in an area where West Coast rock lobster have dramatically decreased, bank cormorants spent significantly longer time at sea than at Robben Island and Stony Point, which were situated in areas where rock lobster were known to be abundant at the time of the study.

Third, I tested the effect of food availability on the breeding success of bank cormorants at Jutten Island, Robben Island and Stony Point. There was no significant relationship between food availability and the survival probability of the birds. The number of chicks fledged per successful nest, however was significantly related to the availability of rock lobster during the relevant breeding season, as well as during the relevant month of hatching.

Acknowledgements

Firstly I would like to thank my four supervisors, Les Underhill, Peter Ryan, Richard Sherley and Timothée Cook. Thank you for your guidance throughout the past two years, for your help in the field and in the office, and for teaching me so much.

The Animal Demography Unit and National Research Foundation funded the project.

Sue Kuyper went beyond the call of duty in sorting our admin throughout the past two years, and always provided a warm welcome in her office no matter how busy she was.

Danie van Zyl and Andy Cockroft at Department of Agriculture, Forestry and Fisheries (DAFF), helped and provided me with valuable rock lobster data. Rob Crawford and Bruce Dyer at Department of Environmental Affairs (DEA) provided me with bird count data as well as valuable insights.

Pierre Nel and the SANParks team enabled us to conduct research in the West Coast National Park.

Cuan McGeorge, Cape Nature, and the staff at Stony Point, thank you so much for all your help, coffee, chats and making it so much fun working there.

Thank you to Brian Hodgson who got us safely on and off Jutten Island every time, even in rough weather, mist and rain. He was truly a lifesaver, and I am so grateful for his service.

A special thanks to the friends upstairs in the 5th floor lab, especially Mark Burnman, who shared his R expertise and helped me with my stats. Thanks also to Emilee Sparks and Jenni Roberts for their help and company in the field in 2012.

Thank you to Corlia Meyer for being my colleague, partner in crime, and most of all, friend. I would not have been able to do this without her.

Thank you to Michiel de Villiers for helping me in the field, carrying equipment, assisting me in nest checks, and sometimes being there to share the beautiful Stony Point sunrises with. This would not have been possible without my family, especially my parents Judene and Philip- thank you so much for your endless support and interest in this project. And lastly I would like to thank my heavenly Father, what an amazing experience!

Contents

CHAPTER 1

Introduction:

Background information on marine biodiversity, seabirds, exploitative competition, the Benguela Upwelling System and the bank cormorant

Marine Biodiversity

Biodiversity is under severe pressure from anthropogenic influences. The areas richest in biodiversity are being destroyed at the fastest rate, driving reliant species into extinction. We are facing a loss of up to 50% of species within the next 50 years (Pimm & Raven, 2000).

Some of the most vulnerable ecosystems to human interference are coastal and marine areas, where oil spills (Gundlach & Hayes, 1987), human induced climate change (Harley *et al.,* 2006), and pollution (Derraik, 2002) pose important threats to marine life. Since human industrial development and the increase of fishing over the past century, native species of marine ecosystems have undergone rapid decline (Worm *et al.,* 2006). As a result of climate change (Tasker *et al.,* 2000), pollution (Votier *et al.,* 2008) and overfishing, numerous marine ecosystems have furthermore been altered through reduced diversity and rapid decline of vulnerable but important species (Dayton *et al.,* 1995; Worm *et al.,* 2006). Most ecosystems are dependent on high species and genetic diversity to maintain a state of relative stability in order to survive negative impacts such as the influences of overfishing (Worm *et al.,* 2006). Diversity in an ecosystem is important to maintain the ability to buffer against a certain level of disturbance.

Overfishing may disrupt links in the chain providing important ecosystem services to humanity. It potentially alters species diversity, resulting in ineffective ecosystem functioning and lower provisioning of food services for a growing human population (Worm *et al.,* 2006). Fisheries primarily focus on a certain size structure of species to exploit, which often result in an alteration of genetic composition in populations (Gray, 1997).

Coastal zones are more vulnerable to human influence than offshore areas, as are benthic ecosystems more genetically diverse than pelagic systems (Gray, 1997). With the most diverse coastal areas being more exposed to the growing human population, it becomes more feasible to focus on the conservation of these inshore areas.

The impact of fishing causes changes in the composition and density of prey distribution, influencing predator foraging behaviour (Dayton *et al.,* 1995). Some predators are dependent on high aggregations of prey for optimum foraging. These indirect effects result in the removal of important predators crucial for optimum trophic structure functioning (Dayton *et al.,* 1995), ultimately disrupting ecosystems.

Seabirds

Seabirds are a distinct group that differ significantly from terrestrial birds in many life history traits including their extended longevity, delayed sexual maturity, smaller clutch sizes, and protracted chick rearing periods (Schreiber & Burger, 2002). Seabirds generally breed in large colonies, often consisting of thousands of individuals (Schreiber & Burger, 2002). They tend to show strong fidelity to their colony of origin, even though most have high levels of mobility in terms of foraging behaviour (Milot *et al.,* 2008). By inhabiting all environments in and around marine areas, seabirds can be important indicators of ecosystem health (Lewison *et al.,* 2012). They provide a glimpse into a combination of terrestrial and marine systems, relying on the land for breeding habitat and the ocean for food (Grémillet & Charmantier, 2010).

Seabirds fulfil important roles in marine ecosystems. They are top predators in many ecosystems, but also often act as scavengers. This places them in a vulnerable position, where they can both influence, and be influenced by different trophic levels (Tasker & Reid, 1997). Seabirds are also affected by numerous abiotic factors including water temperature, salinity, distance from shore and water depth (Baird, 1990). They are exposed to extreme weather conditions and storms (Wolfaardt *et al.,* 2012), which often result in high rates of breeding failure (Schreiber & Burger 2002).

Seabirds are considered important indicators of the state of marine ecosystems due to their mobile, but accessible nature, being forced to come ashore to breed and thus providing insight that few other organisms can (Furness & Camphuysen, 1997; Piatt *et al.,* 2007). They tend to migrate to and from seasonally productive areas, as well as practice central place foraging while breeding, greatly aiding observations and studies of their behaviour.

Many seabirds have undergone dramatic changes in abundance in recent years (Butchart *et al.,* 2004; Lewison *et al.,* 2012). Though some species have shown increases, declines have occurred on a much larger scale. These declines are consistent with patterns occurring on a global scale, and include overall biodiversity loss with up to 50% of species currently facing high risks of extinction (Croxall *et al.,* 2012; Lewison *et al.,* 2012;). Seabirds are thus considered more vulnerable to extinction than passerines or other groups of terrestrial birds.

The threats seabirds face can be classified into both direct and indirect factors. Direct effects on seabirds involve predation and displacement by larger organisms like seals (Jones *et al.,* 2007), as well as by-catch causing mortality from drifting nets and other fishing gear (Dayton *et al.,* 1995). Pursuit divers such as cormorants and penguins are especially affected by entanglement in nets (Žydelis *et al.,* 2013). Indirect factors include pollution (Votier *et al.,* 2008) and competition with humans for the same resources (Croxall *et al.,* 2012). Changes in prey abundance are one of the most important factors in seabird population declines. Most marine fish stocks are currently overexploited (Hilborn *et al.,* 2003). One of the groups most influenced by this, are pelagic foragers (Croxall *et al.,* 2012), but benthic foragers may also fall victim to overfishing when benthic prey such as rock lobster are exploited commercially (Ling *et al.,* 2009).

Seabirds foraging on benthic prey typically have relatively smaller foraging ranges and benthic prey species such as crustaceans tend to be less agile than pelagic prey (Cairns, 1988). A smaller foraging range is a result of benthic prey having specific areas of abundance, causing benthic predators to be more vulnerable to localised low prey availability. Depending on water depth, benthic foragers have to invest most cost into reaching the ocean floor, after which searching commences (Costa & Gales, 2003).

The exact relationship between fish stocks and seabird survival are not fully understood as there are many factors to be explored. Overall environmental changes and anomalies, particularly in combination with direct and indirect anthropogenic influences may have large and prolonged effects on seabird population dynamics (Lewison *et al.,* 2012).

Exploitative competition

Seabirds are in continuous competition with conspecifics or humans when resources are limited (Oro *et al.,* 2009). When dominant species vulnerable to food shortage rely on the same resource, depending on foraging mode, interference competition occurs where one group is forced to be subordinate (Oro *et al.,* 2009).

Though competition between different seabird species is an important factor, the most important exploitative competition is that between seabirds and fisheries (Tasker *et al.,* 2000; Brooke, 2004). The competition between top predators and fisheries is one of the main problems our marine ecosystems face (Karpouzi *et al.,* 2007). Globally, seabirds consume roughly the same amount of fish stocks as fisheries, just below 100 million tons annually (Croxall *et al.,* 2012) and numerous studies have linked the impact of overfishing to seabird population dynamics (e.g. Oro *et al.,* 2009; Cury *et al.,* 2011), both directly and indirectly.

It is, however an important issue to take all social and economic aspects of conservation into account. The conflict arises when different economic societies do not prioritize ecosystem conservation on the same level. When looking at impoverished communities who are in critical need for the jobs and food security fisheries provide, most do not see the plight of key predators in an ecosystem as of any importance (Gasalla, 2011). Nevertheless, exploitative competition remains one of the most important factors influencing seabirds, whether it is in combination with climate change (Tasker *et al.,* 2000), or with ecosystem regime shifts– a process whereby marine ecosystems undergo dynamic changes over a period of 10–30 years, influencing marine life (Cury & Shannon, 2004; Blamey *et al.,* 2012) altering prey distributions (Watermeyer *et al.,* 2008).

Measures of exploitative competition

Prey availability

Benthic fisheries are important in the commercial fisheries industry (Thrush *et al.,* 1998). One of the most important benthic prey exploited by fisheries along the West Coast of southern Africa, is the West Coast rock lobster *Jasus lalandii* (Cockroft & Payne, 1999).

Being an important predator, rock lobsters fulfil a key role in marine ecosystems (Blamey & Branch, 2012; Eddy *et al.,* 2014). As in all ecosystems, intricate relationships occur in the kelp forest ecosystems (Blamey & Branch, 2012), being an exclusive habitat for West Coast rock lobster. Kelp forests along the southern African coastline are dependent on the cool-temperate and shallow waters consistent with in-shore regions of the Benguela Upwelling

System (Blamey & Branch, 2012). They are dominated by bull kelp *Ecklonia maxima* and split-fan kelp *Laminaria pallida* and provide an important shelter for West Coast rock lobster and their prey.

Intricate relationships are responsible for optimum functioning of kelp forest ecosystems in the Benguela Upwelling System. Sea urchin species such as *Parechinus angulosus*, are responsible for important functioning and transformations of kelp forests by means of their grazing abilities (Lang & Mann, 1976) by which they are able to prevent kelp regeneration and expansion. This intense grazing pressure is in turn controlled by predators including rock lobsters (Tarr *et al.,* 1996) and other crustaceans. Kelp forest ecosystems are therefore dependent on these important trophic relationships (Blamey & Branch, 2012) in order to survive.

Most ecosystems are dependent on relationships in which top predators serve as important structuring agents controlling prey abundance (Pace *et al.,* 1999). Any removal of an agent in this trophic chain causes a shift in dominance and impacts lower tropic levels (Pace *et al.,* 1999). Overfishing can act as a driver of trophic cascades following the removal of important predators in marine ecosystems (Pace *et al.,* 1999). Natural, as well as human induced impacts causing exploitation of important predators (fish and rock lobster) are key factors contributing as drivers of a marine shift (Blamey *et al.,* 2013).

Rock lobster abundance experienced a shift in distribution from South Africa's West Coast to southern areas between the late 1980s and 2007 (Cockroft *et al.,* 2008; Crawford *et al.,* 2008). This was seen in a decline from approximately 600- to less than 100 tons rock lobster landings per year occurring on the West Coast, whereas landings increased from less than 50 to approximately 200 tons per year in the south-western area of the species' range (Cockroft *et al.,* 2008). This phenomenon is classified as a regime shift. The main drivers of regime shifts are thought to be abiotic (atmosphere climatic changes in the ocean); however, other drivers can include biotic changes such as fishing (Blamey *et al.,* 2012).

The reason for this shift in rock lobster abundance is not completely understood, and it is unclear whether the shift was driven by adult migration or an increase in larval settlement (Blamey *et al.,* 2013). Several species of lobster are however known to travel or migrate over hundreds of kilometres (Groeneveld & Branch, 2002). Many *Jasus* species migrate between inshore and off-shore habitats during reproduction or moult, and may move up to 300 km along the shore (McKoy 1983; Annala and Bycroft, 1993).

Possible natural causes of regime shifts were assessed in terms of weather anomalies which took place in the late 1980s (Pollock *et al.,* 1997). Numerous accumulative environmental disturbances resulted in severe pressure on rock lobster productivity in the Benguela. There was a clear decline in growth rates during male moulting which led on to a severe decrease in productivity in the following seasons (Pollock *et al.,* 1997).

Between 1988 and 1993, the *El Niño*-Southern Oscillation (ENSO) lead to dramatic inconsistencies in environmental conditions influencing not only rock lobster yield but also other marine resources including anchovy *Engraulis capensis* and sardine *Sardinops sagax* (Pollock *et al.,* 1997). Environmental pressures included unusually low water temperatures, causing a delay in female incubation, and red tides dramatically reducing oxygen levels in the water and serving as a detrimental poisoning agent. Rock lobsters resorted to foraging in deeper, more oxygenated water, which increased pressure on overall productivity (Pollock *et al.,* 1997).

During this detrimental period between 1988 and 1993, the food source of rock lobster was strongly influenced, causing an indirect effect on rock lobster productivity (Pollock *et al.,* 1997). An overall decline in productivity during the ENSO event caused dietary deficiencies for rock lobster (Pollock *et al.,* 1997). This indicates the importance of large scale productivity as a factor influencing keystone species such as the rock lobster (Eddy *et al.,* 2014).

Seabird responses to prey availability

Seabird foraging behaviour and breeding success

Seabirds have physiological adaptations enabling them to make use of various methods to forage at sea. They are diversely developed and can be found at almost all trophic levels of marine ecosystems (Schreiber & Burger, 2002). This includes feeding on pelagic- and or benthic prey, as well as scavenging on dead animal remains (Schreiber & Burger, 2002). Seabirds are adapted to survive even though environmental factors may result in patchy prey distributions or low availability of food. They often make use of aggregations with conspecifics or heterospecifics, relying on cooperative methods to locate and catch prey (Schreiber & Burger, 2002). Not all seabirds are exclusive inshore or offshore foragers and may alter their feeding areas or preferred prey in order to find sufficient food for themselves and/or their offspring (Burger & Piatt, 1990).

All seabirds are central place foragers– foraging in a certain radius around their breeding sites during incubation and subsequently, to deliver food to offspring (Davoren & Montevecchi, 2003; Burke & Montevecchi, 2009). Several factors influence optimum foraging by adult seabirds, including distribution and abundance, as well as the quality or type of prey (Pyke, 1984). Seabirds may change their preferred prey depending on availability (Pyke, 1984; Ludynia *et al.,* 2010b) even though their nutrient requirements exceed that of the available food source.

Foraging efficiency decreases as the cost to obtain food increases. When food is abundant, seabirds have the ability to maintain high productivity in terms of foraging success and offspring rearing (Burger & Piatt, 1990). When food is scarce, birds spend more time foraging, and decrease the time spent ashore, often with negative effects on offspring and themselves (Burger & Piatt, 1990; Zador and Piatt, 1999). At high prey abundances, seabirds increase their time spent on courtship (Harding *et al.,* 2007), resting and nest maintenance, especially when nesting density is high (Davoren & Montevecchi, 2003). Adult birds allocate their time to ensure reproductive success as a result of effective provisioning rates, and providing chicks the minimum quantity of food in order for them to survive (Harding *et al.,* 2007). Pressure increases as offspring grow from hatchlings to larger chicks and require more food, thus demanding greater energy expenditure from foraging adults (Nagy *et al.,* 1984; Bertram *et al.,* 1996).

Depending on the marine habitat type and spatial scale of foraging (Weimerskirch, 2007), seabirds generally have flexible time-budgets to account for patchy or scarce food distribution (Burger & Piatt, 1990; Litzow & Piatt, 2003; Chivers *et al.,* 2012), which allows them sufficient time to forage without negatively influencing offspring growth or survival. Flexible time-budgets can be seen as an adaptive feature for maintaining breeding success despite possible food scarcities (Litzow & Piatt, 2003). Most seabirds are able to buffer against low food availability to some extent by including spare time, usually used for preening or resting, in their foraging time. This allows for constant chick provisioning even though food availability is unpredictable (Burger & Piatt, 1990; Smout *et al*., 2013).

Although seabirds usually compensate for longer foraging trips by decreasing time spent with their partner and offspring, some birds may spend the same amount of time at the nest even though food availability is scarce, decreasing trip length and frequency, resulting in a decline in chick provisioning and thus influencing fledging conditions (Davoren &

Montevecchi, 2003). Food shortages can be seen in several breeding characteristics including brood size and chick growth where adults have to compromise the amount of food given to offspring, as well as altering their own body reserves (Gaston & Hipfner, 2006).

The ability to buffer against low prey abundance varies among species. Some are able to maintain successful chick rearing despite low food availability while others show breeding failures and low success rates when increased foraging effort is required (Zador & Piatt, 1999; Litzow & Piatt, 2003; Piatt *et al.,* 2007). Inter-specific variations in the ability to account for low food scarcities can be due to biological features such as methods of foraging, body size, clutch size and life history traits (Litzow & Piatt, 2003).

In all seabird species, feeding behaviour is limited by physiological parameters as well as environmental factors (Sapoznikow & Quintana, 2003). Food stress can be assessed by looking at different behavioural aspects representing a lack of sufficient resources. Nest or offspring neglect are one of the most commonly used proxies to assess food availability (Lewis *et al.,* 2006).

When the pressures of low resource availability become too high, the trade-off between maintaining self- versus maintaining offspring provisioning becomes an important aspect affecting the life-history of seabirds. The life-history theory dictates that in a long-lived species, individuals would focus on future reproduction as optimum survival strategy to insure overall lifetime fitness, and would thus compromise current reproduction by maintaining self- rather than offspring survival if resources are limited below a certain threshold (Williams, 1966). A fixed limit of available resources therefore permits an individual to provision current offspring, without compromising own fitness and in turn future reproduction, after which it would abandon current reproduction if resource availability is too low. Seabirds have developed foraging strategies allowing them to provision their offspring even in an exploited environment (Burger & Piatt, 1990), but with a decline in marine resources due to overfishing and environmental changes, the pressure increases toward a possible effect on population level. Depleted prey stocks may therefore not only affect a species directly through breeding failures, but also indirectly when the pressures of an increased cost to find sufficient food on adult seabirds risk offspring survival (Ponchon *et al.,* 2014).

The Benguela Upwelling System

The Benguela Upwelling System is located off the south-western coast of Southern Africa, between the warm Agulhas Current of the south-eastern coast of Africa, and the subtropical Angolan Current to the north (Veitch *et al.,* 2009; Roux *et al.,* 2013). The Benguela can be divided into northern and southern subsystems. The northern subsystem is bordered from the Angola-Benguela front extending south towards Lüderitz, and the southern subsystem extends from Lüderitz south towards the Agulhas bank off the south coast of South Africa (van der Lingen *et al.,* 2006). The southern subsystem off the South African coast can be further divided into a more productive wind-driven upwelling off the west coast, and a more temperate shelf system towards the southern part of the Benguela (Roux *et al.,* 2013). The west coast of Southern Africa is subject to continuous upwelling and therefore high productivity, but is also prone to high levels of oxygen depletion (Roux *et al.,* 2013). The upwelling system's high productivity, derived from wind-driven coastal upwelling, forms part of one of the world's most important eastern boundary current ecosystems (Roux *et al.,* 2013).

The high productivity and abundance of food sources in the Benguela Upwelling System (Shannon *et al.,* 2003) result in great seabird species diversity. Eleven seabird species breed in the region, seven of which are endemic to southern Africa (Kemper *et al.*, 2007). Nine of these seabird species breeding in the Benguela ecosystem are listed in the Red Data Book of South Africa as regionally threatened (du Toit *et al.,* 2003) and four are considered globally threatened by the World Conservation Union (IUCN, 2013).

The risks seabirds face in the region include food shortages caused by commercial fisheries (Okes *et al.,* 2009; Bertrand *et al.,* 2012), by-catch caused by fishing nets and hooks (Dayton *et al.,* 1995; Tasker *et al.,* 2000; Peterson *et al.,* 2008), oil pollution (Wolfaardt *et al.,* 2009), habitat displacement and predation by Cape fur seals *Arctocephalus pusillus* (Mecenero *et al.,* 2005; Makhado *et al.,* 2006), and human disturbance (du Toit *et al.,* 2003). These factors have placed many of the seabird species in the Benguela Upwelling System under great pressure.

The bank cormorant

The bank cormorant is endemic to the Benguela Upwelling System (Crawford & Cooper 2005), and breeding has been reported between Hollamsbird Island (24° 38' S; 14° 32' E) in central Namibia and Quoin Rock (34° 46' S; 19° 38' E) in South Africa (du Toit *et al.,* 2003). Despite the high productivity and historically large seabird abundance in the Benguela Upwelling System, there is concern regarding the rate at which bank cormorant numbers have decreased from the 1980s to the 2000s. Within the Western Cape of South Africa, there has been a decrease from more than 500 pairs during the late 1970s to the late 80s, to approximately 350 pairs from 1995 to 2006 (Crawford *et al.,* 1999). In Namibia, where the majority of the bank cormorant population occurs, their numbers decreased from 8700 to approximately 3600 pairs over the same period (du Toit *et al.,* 2003; Kemper *et al.,* 2007). Bank cormorants were classified as Endangered in 2006 when the overall population decline over three generations was 53% (Kemper *et al.,* 2007).

The reason for the bank cormorant decline is not completely understood, although numerous factors must be considered. Bank cormorant colony distribution and breeding success are often influenced by breeding site availability and breeding habitat loss (e.g. Sherley *et al.,* 2012). Human disturbance (David *et al.,* 2003), displacement and predation by Cape fur seals (Mecenero *et al.,* 2005; Makhado *et al.,* 2006) and food shortage (Crawford *et al.,* 1999) are some reasons suggested to explain the bank cormorant's decline. Many of these negative impacts can be traced back to anthropogenic influences.

An important food source of bank cormorants in South Africa is West Coast rock lobster, while Namibian colonies primarily feed on bearded goby *Sufflogobius bibarbatus* (Ludinya *et al.,* 2010a). By making use of rock lobster as food source, bank cormorants are in competition with commercial fisheries along the West Coast of South Africa.

Within the southern part of their range, bank cormorants are primarily benthic feeders, where they practice an 'investigative' foraging method, searching for food among crevices on the sea bed (Cooper, 1985). Like all southern African marine cormorants, bank cormorants forage inshore, and they rarely disperse more than 10 km from their colonies (Cooper, 1985; 1981). Within the southern part of their range, their foraging habitat is consistent with the distribution of kelp beds (Cooper, 1981). The exact relationship between prey quality and availability versus population trends are not yet fully understood and more data on population parameters for bank cormorants are needed (Crawford *et al.,* 2008; Ludynia *et al.,* 2010a).

The shift of West Coast rock lobster along the West Coast of South Africa has impacted the population dynamics of bank cormorants (Crawford *et al.,* 2008). Rock lobster landings increased in the southern part of the Western Cape, along with a major decrease in landings in the northern West Coast region, where landings were previously abundant. The increase in rock lobster abundance in the southern region has contributed to the establishment and growth of the Stony Point bank cormorant colony (Crawford *et al.,* 2008). The Stony Point colony was only established in the late 1980s, after the colonization of African penguins *Spheniscus demersus* in the area (Cooper, 1988). An explanation for the decrease in bank cormorant colony size in the northern regions of South Africa's West Coast can be drawn from the shift of rock lobster towards southern regions (Crawford *et al.,* 2008; Blamey *et al.,* 2012).

Dissertation goal and structure

The bank cormorant is poorly studied and there is great need for more information on specific reasons for the species' decline. This thesis aims to build on the information we have on bank cormorant population dynamics, behaviour in response to food availability and breeding success, and focuses on the hypothesis that food availability may be one of the most important causes for the species' decline. The main focus of the thesis is the relationship between bank cormorants and an important prey species surrounding selected colonies along the West Coast of South Africa. The thesis is divided into three separate research papers, and completed by a concluding chapter.

In the following chapter (Chapter 2), the response of bank cormorants in relation to the distribution of West Coast rock lobster on a population level is studied in different spatial scales around three colonies along South Africa's West Coast. Rock lobster data was obtained from the Department of Agriculture, Forestry and Fisheries (DAFF), and provides rock lobster abundance as well as proportional data for different distances around each colony. The response is tested over a period of 18 years (1993–2011). Taking into account the foraging range of bank cormorants during the breeding season, their population dynamics are related to the spatial distribution of prey surrounding the colonies.

The next chapter (Chapter 3) focuses on the foraging behaviour in terms of foraging trip duration, number of trips per day and total time spent at sea per day by bank cormorants during breeding. The study was carried out at three bank cormorant colonies along the West Coast of South Africa, known to be situated in areas with different levels of surrounding prey availability. By comparing foraging behaviour in terms of energy requirements and costs of offspring provisioning in these areas, the bank cormorant's behavioural responses can be coupled to the hypothesis that prey availability may be a crucial factor directly influencing the bank cormorant.

Chapter 4 focuses on the breeding success of bank cormorants at the same colonies tested in the previous study. The effect of food abundance in terms of West Coast rock lobster catch per unit effort (CPUE) data obtained from DAFF is tested on the survival probabilities and number of chicks fledged per successful bank cormorant nest.

Lastly, the concluding chapter encapsulates all findings in the three studies, and provides suggestions for future research in order to broaden the scope of information on the endangered bank cormorant.

CHAPTER 2

Bank cormorant population numbers in response to West Coast rock lobster abundance off the West Coast of South Africa

Abstract

Seabird population dynamics are greatly influenced by resource availability. In combination with climate change, direct and indirect anthropogenic influences including overfishing are important drivers of ecosystem functioning and potentially regime shifts. West Coast rock lobster *Jasus lalandii* abundance experienced a drastic distributional shift between the late 1980s and early 1990s, after which it stabilized around the turn of the century. Abundance shifted to significantly lower levels in the northern part of South Africa's West Coast to higher levels in the South Coast, east of Cape Point. The bank cormorant *Phalacrocorax neglectus*, an endemic seabird to the Benguela Upwelling System along the West Coast of southern Africa, makes use of West Coast rock lobster as an important prey item in its diet. With the distributional shift of rock lobster abundance, the population numbers of bank cormorants have responded by decreasing in numbers in the West Coast, and dramatic growth in colony size in the southern area, east of Cape Point. By making use of rock lobster survey data between 1993 and 2011, the response of bank cormorant population dynamics in the form of annual counts are tested to see how dynamics change in response to rock lobster distribution in accumulative distances around three colonies along the West Coast of South Africa having different rock lobster availability. Bank cormorants, having a breeding foraging range of 9 km, responded significantly to the proportion of traps containing lobsters in 5, 10, 20 and 30 km radiuses around colonies. Their greatest response, however, was to rock lobster abundance in a 30 km radius around their colonies. A combination of factors including the importance of prey availability before the onset of the breeding season, as well as the moulting processes of rock lobsters may play a role in the response of bank cormorants to rock lobster abundance in accumulative distances around their breeding sites.

Introduction

Resource availability influences the population dynamics of seabirds (Oro *et al.,* 2004). Overall environmental change and anomalies (Pollock *et al.,* 1997), particularly in combination with direct and indirect anthropogenic influences, may have large and prolonged effects on resource distribution and availability, and in turn have negative effects on seabird population dynamics (Lewison *et al.,* 2012). Climate change may impact marine resources, influencing almost all trophic levels in different ways within an ecosystem (Durant *et al.,* 2007). It is also one of the most significant drivers behind ecosystem shifts, impacting marine ecosystems through extreme weather events and sea temperature changes (Visser & Both, 2005). Climate change-induced fluctuations in atmospheric and oceanic circulation patterns are altering nutrient availability, resulting in changes in species composition and distribution, seasonality and production (Brander, 2010). One of the most important direct human impacts influencing marine life is overfishing (Dayton *et al.,* 1995; Watermeyer *et al.,* 2008), but its impact can be exacerbated by climate change (Bustnes *et al.,* 2013).

The West Coast rock lobster *Jasus lalandii* is one of the most valuable species targeted by commercial fisheries in South Africa. The species has been exploited commercially since the late 1800s, and is South Africa's third most valuable marine resource (Johnston & Butterworth, 2005). Lobsters initially were harvested mainly with hoop nets, after which large traps came into use with the commercial growth of the fishery. Catches peaked in the 1950s in both South Africa and Namibia and then declined as a result of overfishing (Pollock *et al.,* 2000; van der Lingen *et al.*, 2006). In South Africa the annual yield decreased from 16 000 t around the 1950s, to less than 5 000 t after 1960 (van der Lingen *et al*., 2006). Total allowable catch (TAC) regulations and other restrictions were enforced to stabilize lobster yields (Cockroft & Payne, 1999) but the West Coast rock lobster population has not recovered to its initial size (van der Lingen *et al.,* 2006). An explanation which has been suggested is that there was a decrease in growth rate along with the drop in abundance after the 1960s (Pollock *et al.,* 2000).

The decline in rock lobster growth rates coincided with a shift in its distribution along the West Coast of South Africa (Cockroft *et al.,* 2008). This is classified as a 'regime shift', a process whereby marine ecosystems undergo dynamic changes in structure and function over a period of 10–30 years, influencing all dependent marine life (Cury & Shannon, 2004; Blamey *et al*., 2012). The distributional shift of rock lobster resulted in the percentage of rock lobster landings on the West Coast (north and west of Cape Town, Fig. 2.1) declining from ca 60% to less than 10% between the late 1980s and 2000, while the opposite was seen in the Cape Point area (south and east of Cape Town, Fig. 2.1), with an increase from 18% to ca 60% (Cockroft *et al.,* 2008).

The bank cormorant *Phalacrocorax neglectus*, a seabird endemic to the Benguela Ecosystem of southern Africa, has experienced a major decline since the 1980s. The global population size decreased from ca 9 000 breeding pairs in the late 1970s to ca 5 000 pairs 20 years later. The population subsequently decreased to fewer than 3 000 breeding pairs in 2006 (Kemper *et al.,* 2007). The bank cormorant's IUCN classification is Endangered based on a population decline of more than 50% in three generations (Kemper *et al.,* 2007; IUCN, 2013). The reasons for the decrease in bank cormorant numbers are not completely understood, but important factors include human disturbance, displacement and predation by Cape fur seals *Arctocephalus pusillus* (David *et al.,* 2003), as well as competition with fisheries for food (Tasker *et al.,* 2000; Crawford *et al.,* 2008; Blamey *et al.,* 2012). Crawford *et al.* (1999; 2008) suggested that food shortage was the key factor.

Bank cormorants are inshore benthic foragers and target a wide variety of prey, with marked regional and local differences among colonies (Cooper, 1985). Within South Africa, they predate mainly on species associated with kelp beds including crustaceans, octopus and clinid fish (Cooper, 1985), with West Coast rock lobster forming an important component of their diet (Crawford *et al*., 2008). However in Namibia, they feed on the superabundant bearded goby *Sufflogobius bibarbatus*, a mesopelagic species with low energy content (Ludynia *et al*., 2010a; b).

Crawford *et al.* (2008) found important correlations between rock lobster abundance and bank cormorant numbers, where the birds responded to the shift of prey, showing increases in areas where rock lobster increased in abundance and vice versa. For example, the extinction of the Lambert's Bay bank cormorant colony followed a significant decline of rock lobster off the West Coast of South Africa (Cockroft *et al.,* 2008). In contrast, the increase in rock lobster abundance east of Cape Point was followed by an increase in bank cormorants breeding at Stony Point (Crawford *et al.,* 2008; Blamey *et al.,* 2012).

Bank cormorants rarely forage more than 10 km from their colonies when breeding (Cooper, 1985; Ludynia *et al*., 2010). As a result, their conservation status may benefit from protecting their main prey close to breeding colonies. The marine environment around Robben Island, Table Bay, was designated a rock lobster reserve in 1960 (Pollock, 1987), and despite being affected by oil spills, Robben Island supports the largest and most stable bank cormorant colony in South Africa (Crawford *et al.,* 2008). Studies have shown positive effects of dependent species recovery following the establishment of marine protected areas to conserve target prey (Gell & Roberts, 2003; Russ *et al.,* 2004). With the absence of commercial rock lobster fishing in the area, the growth of the Robben Island colony may be limited by the availability of breeding space rather than prey availability (Sherley *et al.,* 2012).

This study examines the relationship between the number of breeding pairs of bank cormorants at three colonies, and the abundance of West Coast rock lobster at increasing distances from these colonies, to determine the spatial scale of lobster abundance most influential to bird numbers. The goal is to recommend management strategies that could be implemented through fishing closures to best induce a positive response of bank cormorants to prey levels within their foraging grounds.

Materials and methods

Bank cormorant count data

Annual counts of bank cormorant breeding pairs from 1993 to 2011 were provided by the Department of Environmental Affairs (DEA) for three colonies: Jutten Island in Saldanha Bay (33˚ 05' S; 17˚ 57' E); Dassen Island (33˚ 25' S; 18˚ 05' E) and Stony Point (34˚ 22' S; 18˚ 53' E) (Fig. 2.1). Counts were conducted between one and three times each breeding season, and the largest number of active nests was taken as the number of breeding pairs for a given year (Crawford *et al.,* 2008).

Rock lobster data

The west coast of South Africa is divided into commercial fishing zones for rock lobster (Fig. 2.2). These areas are divided into subareas providing a smaller scale to rock lobster abundance.

Fisheries Independent Monitoring Survey (FIMS) data were collected by the Department of Agriculture, Forestry and Fisheries (DAFF). The survey was conducted annually at the major rock lobster fishing areas to obtain an index of relative abundance and information on movements, sex ratios and size structures of West Coast rock lobsters. This was done independently of commercial fisheries with the goal to perform management practices on the species (D. van Zyl, unpubl. data).

Between 110 and 160 sampling points were allocated randomly to each respective area around Lambert's Bay (Area 3), Saldanha Bay (Area 6), Dassen Island (Area 7) and Cape

Point (Area 8; Fig. 2.2). Each sampling point consisted of five rock lobster traps and was visited twice in a two week interval between January and May annually. At each visit, the traps were set, left for a standard time of 15–20 min, and recovered after which the number of lobsters present in each trap was recorded.

The Rock Lobster FIMS data were used to test the impact of food availability at different distances to the island on the adjacent bank cormorant colonies: Areas 5 and 6 (Fig. 2.2) were used for the Saldanha Bay islands and Area 7 for Dassen Island. Jutten Island supports the largest and most central colony within Saldanha Bay (Crawford *et al.,* 2008), and thus was used as proxy for the other Saldanha Bay islands (Malgas, Marcus and Vondeling), due to the close proximity of these islands to each other, and to avoid overlapping stations when calculating different distances from colonies. FIMS data from Cape Point were used as a proxy for rock lobster abundance around the Stony Point bank cormorant colony, because the FIMS survey was not conducted east of False Bay.

Data Analysis

All FIMS station GPS coordinates were plotted in Google Maps (e.g. Fig. 2.3). Stations were sorted into distance intervals of 5, 10, 20 and 30 km radius around each bank cormorant colony using distance measurements in Google Maps. Rock lobster abundance was then calculated annually in distance bands around each colony: 0–5 km; 0–10 km; 0–20 km; and 0–30 km. Catch per unit effort (CPUE) was calculated by dividing the total number of lobsters caught by the number of traps set across the two week sampling period for each station. The proportions of traps containing lobsters (propTCL) in relation to number of traps set, as well as CPUE were used as predictors to provide the best indication of rock lobster abundance and spatial distribution. The mean CPUE and proportion of traps containing lobsters were calculated for each area per year.

Explanatory variables were sorted into the CPUE and propTCL for each distance, e.g. for 5 km: the CPUE within a 5 km radius around colonies, and propTCL 5 km: the proportion of traps containing lobsters within a 5 km radius around each colony. The effects of overall CPUE and proportion of traps containing lobsters, including the entire FIMS survey area, were also investigated. Area was included as explanatory variable indicating rock lobster availability around each colony: Jutten Island, Dassen Island and Cape Point (Stony Point).

To control for first order correlation between years in the number of breeding birds, an autocorrelation analysis was carried out on each variable using the acf function in R v. 3.0.1 (R Core Team 2012). When first order autocorrelation was present the studentised prewhitened residuals of the counts were obtained from the AR–1 autocorrelation model in R.

Linear models were used to test cross-correlations between bank cormorant numbers and rock lobster abundance using the lm function in R. The explanatory variables included area, catch per unit effort (CPUE) for any given distance around the colonies as well as the proportion of traps containing lobsters (propTCL). Models were run for each distance category. Model fits were assessed using Akaike's Information Criterion adjusted for small samples sizes (AICc) to select the best supported model in each case (Zuur *et al.,* 2009).

Results

Bank cormorant population dynamics

At Jutten Island, bank cormorant numbers were relatively stable between 1993 and 2000, with an average (±SD) of 51 ± 7 pairs (Fig. 2.4). Numbers declined to 41 ± 5 pairs between 2001 and 2005 and to 24 pairs by 2011 (25 ± 5). At Dassen Island, numbers fluctuated with a decrease from 70 pairs in 1993, to 32 ± 9 pairs between 1994 and 2000. Numbers then increased to 51 ± 9 pairs between 2001 and 2009, followed by a decrease to 20 pairs in 2011 (Fig. 2.4). At Stony Point, bank cormorant numbers increased from 11 ± 3 pairs between 1993 and 2002, to 28 ± 7 pairs between 2003 and 2011 (Fig. 2.4; Table 2.1).

West Coast rock lobster abundance

The FIMS data showed that rock lobster CPUE fluctuated in abundance between Cape Point and the other two areas (Fig. 2.5). The overall average (±SD) CPUE between 1993 and 2011 was 1.6 ± 1.7 for Saldanha Bay, 19.0 ± 16.3 for Dassen Island, and 124.7 ± 24.1 for Cape Point. It was consistently low in the Saldanha Bay region during the study period, decreasing from an average of 6.7 lobsters per trap in 1993 to 1.3 ± 1.1 lobsters per trap up to 2011. The CPUE off Dassen Island fluctuated from 21.5 ± 3.7 lobsters per trap between 1993 and 1994, to 7.0 ± 3.5 lobsters in the late 1990s, then increased in both magnitude and variability to 33.8 ± 18.3 between 1999 and 2005, before again decreasing to 11.5 ± 5.8

lobsters per trap from 2006 to 2011. Rock lobster abundance around Cape Point averaged 124.7 ± 23.4 lobsters per trap; it showed no trend during the study period and was much larger than in the other two areas (Fig. 2.5).

The proportion of traps containing lobsters was less variable than the CPUE, with high proportions in Cape Point compared to Saldanha Bay and Dassen Island (Fig. 2.6). The overall average (±SD) proportions of traps containing lobsters between 1993 and 2011 were 0.13 ± 0.05 for Saldanha Bay, 0.29 ± 0.10 for Dassen Island, and 0.82 ± 0.05 for Cape Point. Off Saldanha Bay, the mean proportion of traps containing lobsters was 0.20 ± 0.06 from 1993 to 1995, after which it decreased to an average of 0.12 ± 0.03 from 1996–2011. Around Dassen Island, the proportion of traps containing lobsters decreased from 0.37 in 1993 to 0.22 ± 0.05 between 1994 and 2001, increased to 0.40 ± 0.03 from 2002–2006, and then decreased to 0.27 ± 0.10 from 2007–2011. The proportion of traps containing lobsters at Cape Point remained relatively stable with an average of 0.82 ± 0.03 between 1993 and 2005, after which it decreased to an average of 0.77 ± 0.05 towards 2011. During the 18 years, it was only below 0.80 on five occasions (Fig. 2.6).

Correlations between bank cormorant and rock lobster abundance

For all distances, the changes in the bank cormorant populations showed the strongest relationship with the proportion of traps containing lobsters (Table 2.2; Table 2.3), but the relationship to the overall proportion of traps containing lobsters only bordered on significant ($t = 1.81$; $df = 50$; $p = 0.08$). The proportion of traps containing lobsters within 5 km ($t = 2.07$; $df = 48$; $p = 0.04$; Fig. 2.7) and 10 km ($t = 2.10$; $df = 48$; $p = 0.04$; Fig.2.8) of the colonies were significantly related to bank cormorant population numbers for models including Area as a covariate. The proportion of traps containing lobsters in a 20 km radius were significantly related to bird numbers for the three colonies ($t = 2.37$; $df = 48$; $p = 0.02$; Fig. 2.9). The best model according to the AICc criteria had proportion of traps containing lobster in a 30 km distance around each colony, which were significantly related to bank cormorant numbers ($t = 2.51$; $df = 48$; $p = 0.02$; Fig. 2.10; Table 2.4) in the model including Area as covariate.

Bank cormorant numbers were not significantly related to the overall CPUE for all three areas ($t = 1.09$; $df = 50$; $p = 0.29$), nor with the CPUE within a 5 km ($t = 0.72$; $df = 50$; $p = 0.48$) or 10 km ($t = 1.12$; $df = 50$; $p = 0.27$) radius around the three colonies. The interaction between Dassen Island and the CPUE of lobsters in a 20 km radius were significantly related to bird numbers (t = 2.09; df = 46; p = 0.04), but for all three colonies, CPUE in a 20 km radius had no significant effect (t = 1.05; df = 50; p = 0.30). The CPUE within a 30 km radius of the three colonies was not significant (t = 1.15; df = 50; p = 0.25), but the interaction between Dassen Island and the CPUE was significantly related to the prewhitened residuals of the number of birds breeding there (t = 2.01; df = 46; p = 0.04).

Overall, the relationship between the bank cormorant population and the availability of their prey increased with increasing distance from the colony. The highest response was at 30 km for which the model explained 9% of the variance in the number of breeding pairs (Fig. 2.11; Table 2.2).

Bank cormorants at Dassen Island showed the strongest response to rock lobster abundance (Table 2.3). No significant relationship was found for the CPUE of lobsters within a 5 km radius around the island (t = 0.57; df = 16; p = 0.58), but the proportion of traps containing lobsters showed a significant positive relationship with bird numbers (t = 2.58; df = 16; p = 0.02). The model explained 25% of the variance. The response of birds at Dassen Island increased with the proportion of traps containing lobsters at increasing distances around the colony. Cormorant numbers had a significant positive relationship with proportion of traps containing lobsters within 10 km (t = 2.61; df = 16; p = 0.02; adj $R^2 = 0.26$); 20 km (t = 3.14; df = 16; p = 0.006; adj $R^2 = 0.34$) and 30 km (t = 3.38; df = 16; p = 0.004; adj $R^2 = 0.38$) of the colony (Fig. 2.12; Table 2.3).

Discussion

Bank cormorant breeding participation responded stronger to the proportion of traps containing lobsters around their colonies than to the CPUE index based on lobster abundance within the traps. This may be due to the proportion representing the spatial distribution of rock lobsters within a given area, and not necessarily the density. CPUE may overestimate spatial distribution, often staying stable even though actual abundance decreases (Harley *et al.,* 2001). Although the proportion of traps containing lobsters is also not a direct way of indicating biomass, it may provide a better indication of the spatial distribution of rock lobster in the foraging areas of bank cormorants as it is not influenced by extreme results (e.g. many lobsters in one or two traps) in the same way as CPUE.

Most seabirds show foraging site fidelity, returning to the same area to forage especially when prey availability is reliable (Hamer *et al.,* 2001; Cook *et al.,* 2006). Ludynia *et al.* (2010a) observed this behaviour in bank cormorants in Namibia, even though they are not exclusive benthic feeders in this part of their range. The proportion of traps containing lobsters likely indicates the spatial distribution of lobsters and represents the approximate presence of areas containing prey. With bank cormorants along the West Coast of South Africa also showing foraging site fidelity, this may be the reason why their population dynamics responded to the proportion of traps containing lobsters when used as an index of prey availability.

The population trends of bank cormorants at Dassen Island showed the strongest relationship to rock lobster abundance. Their greatest response was to lobster presence/absence data in traps within 30 km of the colony, which explained 38% of the variance in population counts. By the time regular counts of bank cormorant breeding pairs began in 1993, West Coast rock lobster abundance was already low in Saldanha Bay and the northern parts of the West Coast. Rapid decreases in lobster growth somatic rates occurred between the late 1980s and early 1990s (Cockroft *et al.,* 2008; Blamey *et al.,* 2012). Given that rock lobster landings peaked in South Africa in the 1950s (van der Lingen *et al.,* 2006), bank cormorants probably had already started to respond to the altered availability of their prey prior to 1993 (Crawford *et al.,* 2008), hence the limited amount of variance explained in this study. The number of pairs counted at Dassen Island decreased from ca 211 in 1978 to 70 by 1993 and the population at Malgas Island declined from around 120 pairs in the 1980s to fewer than 60 during the 1990s (Crawford *et al.,* 2008). The extinction of the Lambert's Bay bank cormorant colony in 1998 is most likely attributable to the disappearance of rock lobsters in that area (Crawford *et al.,* 2008). However, we were unable to examine the relationship with prey availability around colonies prior to 1993 because the FIMS data were not collected prior to that time (Cockroft *et al.,* 2010).

By 1990, large numbers of West Coast rock lobster had 'invaded' the southern coast, east of Cape Point (Cockroft *et al.,* 2008; Blamey *et al.,* 2013). Bank cormorants first colonized Stony Point around 1987, after the establishment of the African penguin colony there in 1984 (Cooper, 1988; Whittington *et al.,* 1996). Seabirds often show lagged responses to environmental changes (e.g. Thompson & Ollason, 2001; Zador *et al.*, 2013). Deferred maturity may play a role, as bank cormorants only start breeding at three years of age

(Crawford *et al.,* 2001, Vincenzi *et al.,* 2013). Food shortages during the breeding season usually have the greatest effect on breeding success or juvenile survival (Thompson & Ollason, 2001), which would result in a delayed response to a decline or increase of food resources. This was seen in the growth of the Stony Point bank cormorant colony, currently still responding to the already high abundance of rock lobster around Cape Point. It is likely that the bank cormorant population at Dassen Island was responding to the decrease of rock lobster in that area during the 18 years of study, hence the strong correlation in that area. These observations are in keeping with the progressive shifts to the south and east of several marine resources off South Africa in this period (e.g. Crawford *et al.,* 2008; Blamey *et al*., 2012).

Although the West Coast rock lobster is one of the most important food sources for bank cormorants and a keystone species in the kelp bed ecosystem (Paine, 1969; Barkai and Branch, 1988; Eddy *et al.,* 2014), these birds feed on other organisms as well. Bank cormorants at Jutten Island did not respond to rock lobster availability as rapidly as the other the other colonies during the 18 years of study, probably because they resorted to alternative prey items. Rock lobster remains are seldom found in the pellets of bank cormorants in Saldanha Bay (B. M. Dyer, pers. comm.). By the time this study started there were already low levels of rock lobster availability in the Saldanha Bay region (Crawford *et al.,* 2008; Blamey *et al.,* 2012). At Jutten Island, the prey items most often found in their pellets were Cape mantis shrimp *Pterygosquilla capensis* and West Coast sole *Austroglossus microlepis* (B. M. Dyer, pers. comm.). Availability of prey other than rock lobster can enable a small colony to persist (Crawford *et al.,* 2008). Barkai and Branch (1988) showed that benthic environments may differ extensively even between adjacent islands, which may result in different levels of prey availability around colonies.

Like all seabirds, bank cormorants are central place foragers and they seldom forage farther than 10 km from their breeding colonies (Cooper, 1985; Ludynia *et al*., 2010a). Bank cormorant numbers were related to rock lobster presence within 5−10 km of their colonies, which may be as a result of these distances being their main foraging grounds during the breeding season. Breeding bank cormorants undertake short foraging trips that rarely last more than two hours during chick rearing, depending on food availability, and make up to nine trips per day (see Chapter 3). This suggests that they may not be able to forage farther than 10 km from their colonies without compromising chick provisioning rates and thus survival (Burger & Piatt, 1990; Harding *et al.*, 2007).

The reason for the bank cormorant's highest response to rock lobster availability being at 30 km may be coupled to the life history traits of palinurid lobsters. The larval stage of these lobsters lasts approximately two years, and undergoes 11 moulting stages, after which they reach their post larval stage and return to shallower inshore waters by settling on inshore reefs. The post larval stage lasts up to three years, after which lobsters move to slightly deeper waters as they reach adulthood (George, 2005; Melville-Smith, 2011). Bank cormorants generally feed on small lobsters, often swallowing their prey underwater to avoid kleptoparatism by kelp gulls *Larus dominicanus* (Cooper, 1985). The majority of lobsters caught in the FIMS survey was between the size class of 60–90 mm carapace length (D. van Zyl, unpubl. data), which indicates that lobsters of smaller size are not caught by the fishing equipment used by the study. Rock lobster abundance documented by fisheries and the FIMS study between 10 and 20 km from shore, may be an important indication of the abundance of smaller juvenile lobsters closer to shore, on which bank cormorants generally feed.

Adult seabirds' body condition has major influences on their reproductive effort and breeding success (Monaghan *et al.,* 1989; Chastell *et al.,* 1995). Food availability before or during the start of the breeding season critically affect breeding investment in adult seabirds. Poor body condition when the breeding season approaches, causes an inability to engage in breeding, delayed onset of breeding (Robinson *et al.* 2005), or desertion of laid eggs (Chastell *et al.,* 1995) or chicks (Erikstad *et al.,* 1997). Adult birds often lose a large proportion of their body mass during incubating and chick rearing (e.g. Chaurand & Weimerskirch, 1994; Ballard *et al*., 2010). The assumption can therefore be made that adult birds need to be in good body condition at the start of the breeding season, indicating that food availability is not only important during incubating and chick rearing, but also outside of the breeding season over a larger spatial scale (e.g. Sherley *et al*., 2013).

Although the foraging range of breeding bank cormorants is limited, the distance they range outside of the breeding season is likely larger. Bank cormorants are generally inshore foragers, owing to the distribution of kelp beds. They are rarely seen farther than 20 km (Cooper, 1985), although on one occasion an immature bird was collected 93 km from shore (Rand 1960). The significant response of birds to the proportion of traps containing lobsters within 20 and 30 km from shore may be linked to food availability outside of the breeding season. When taking into account that the bank cormorant counts are done annually within the peak breeding season with the highest number of active nests (Crawford *et al.,* 2008), combined with the fact that the correlation between numbers and prey availability is the highest at 30 km, indicates that food availability during the nonbreeding seasons may be an important factor concerning bank cormorant population dynamics.

When making use of prewhitening, any possible trend in a data set is removed (Yue & Wang, 2002; Bayazit & Önöz, 2007) to control for first order autocorrelation. However, the fact that we still found significance for proportion of traps containing lobsters around colonies is of crucial importance. This suggests that bank cormorants are significantly affected by rock lobster abundance surrounding their colonies, both inside and outside of their breeding season. Future research recommendations include intensive foraging behaviour studies by making use of data loggers, to both breeding and non-breeding birds. Intensive diet data will be of great importance, especially to draw comparisons of the foraging preferences between the different localities of the remaining colonies.

Table 2.1 Number of bank cormorant pairs breeding at Jutten Island, Dassen Island and Stony Point from 1993 to 2011.

Year	**Jutten Island**	**Dassen Island**	**Stony Point**
1993	54	70	6
1994	52	16	6
1995	45	36	7
1996	42	31	9
1997	47	25	12
1998	49	29	14
1999	61	46	15
2000	61	41	14
2001	43	54	13
2002	40	51	13
2003	34	50	18
2004	50	47	22
2005	41	52	26
2006	30	30	26
2007	24	55	24
2008	29	66	37
2009	16	56	41
2010	27	42	28
2011	24	20	31

Table 2.2 Explanatory variables associated with population numbers of bank cormorants at three colonies in the Western Cape, South Africa. Catch per unit effort (CPUE) and the proportion of traps containing lobsters (propTCL) were used to explain the response of prewhitened studentized residuals of bank cormorant counts over 18 years of study.

Distance	Covariate	Coefficient estimate	AICc	t	p	adj R^2	Significance
5 km	CPUE	0.001	152.2	0.72	0.48	0.01	NS
	propTCL	2.41	148.4	2.08	0.04	0.05	*
10 km	CPUE	0.002	151.4	1.12	0.27	0.005	NS
	propTCL	3.62	149.4	2.10	0.04	0.06	*
20 km	CPUE	0.002	152.9	1.05	0.30	0.002	NS
	propTCL	4.37	150.01	2.441	0.02	0.08	*
30 km	CPUE	0.003	151.3	1.16	0.25	0.006	NS
	propTCL	4.71	149.4	2.51	0.02	0.09	*
Overall	CPUE	0.003	151.5	1.09	0.28	0.004	NS
	propTCL	0.82	149.4	1.81	0.08	0.04	NS

Table 2.3 Simple linear regression of the relationship between the prewhitened residuals of bank cormorant breeding pairs and West Coast rock lobster abundance around Dassen Island.

Distance	Catch per unit effort			Proportion traps containing lobsters		
	Relationship	P value	Adj R^2	Relationship	P value	Adj R^2
5 km	NS	0.58	–0.04	+ve	0.02	0.25
10 km	NS	0.26	0.02	+ve	0.02	0.26
20 km	NS	0.15	0.07	+ve	0.01	0.34
30 km	NS	0.13	0.08	+ve	0.004	0.38

Table 2.4 Explanatory variables in relation to the studentised prewhitened residuals of bank cormorant numbers, to see the effect of West Coast rock lobster in given distances (5, 10, 20 and 30 km) around colonies. Variables are chategorized by proportion (propTCL) of traps containing lobsters in given distance, and the catch per unit effort (CPUE) in given distance. K represents the number of parameters in each model, and AICc values indicate model fit. ΔAICc shows the difference from the preferred model, and AICc weight indicates the support given for each model.

Model	Explanatory variable	K	AICc value	ΔAICc	AICc weight
1	propTCL 5km	3	148.4	0	0.68
2	Area + propTCL 5km	5	151.6	3.2	0.14
3	5km CPUE	3	152.2	3.7	0.10
4	Area * propTCL 5km	7	153.9	5.5	0.04
5	Area + 5km CPUE	5	155.1	6.7	0.02
6	Area * 5km CPUE	7	157.5	9.1	0.01
1	propTCL 10km	3	149.4	0	0.53
2	Area + propTCL 10km	5	151.2	1.8	0.21
3	10km CPUE	3	151.4	2.0	0.19
4	Area * propTCL 10km	7	154.4	5.0	0.04
5	Area + 10km CPUE	5	155.8	6.4	0.02
6	Area * 10km CPUE	7	158.1	8.7	0.01
1	propTCL 20km	3	149.4	0	0.43
2	Area + propTCL 20km	5	150.0	0.6	0.32
3	20km CPUE	3	151.6	2.2	0.14
4	Area * propTCL 20km	7	153.5	4.1	0.06
5	Area*20km CPUE	7	154.7	5.3	0.03
6	Area + 20km CPUE	5	155.6	6.2	0.02
1	propTCL 30km	3	149.3	0	0.38
2	Area + propTCL 30km	5	149.4	0.1	0.36
3	30km CPUE	3	151.3	2.1	0.13
4	Area * propTCL 30km	7	152.6	3.3	0.07
5	Area*30km CPUE	7	154.1	4.8	0.03
6	Area + 30km CPUE	5	155.8	6.5	0.01

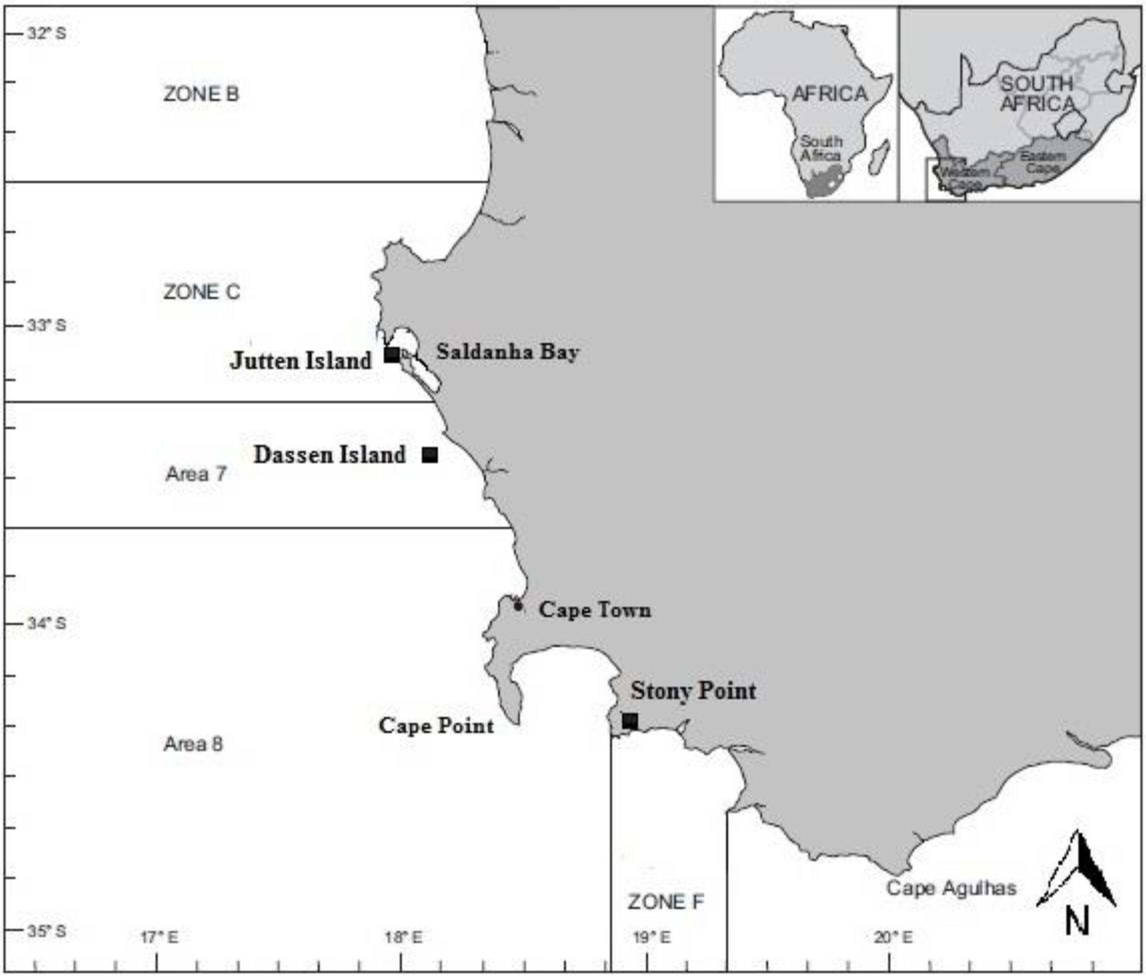

Figure 2.1 The Western Cape of South Africa with the three bank cormorant colonies (Jutten Island, Dassen Island and Stony Point) used in this study to test response of bird numbers in relation to West Coast rock lobster abundance between 1993 and 2011. Map from Crawford *et al.* (2008).

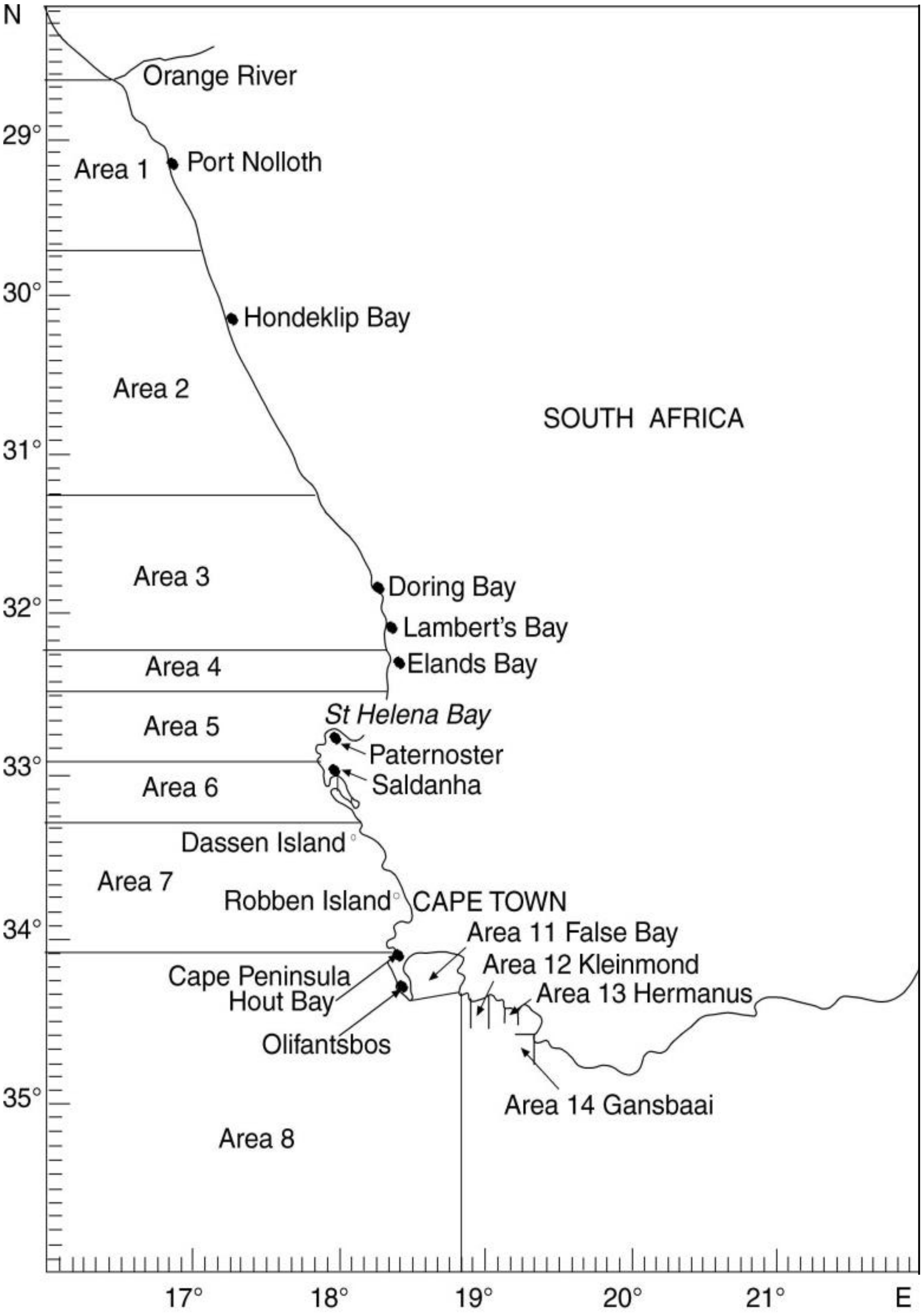

Figure 2.2 Commercial fishing zones, defined by Department of Agriculture, Forestry and Fisheries (DAFF), for West Coast rock lobster along the west and southwest coast of South Africa. Map from DAFF.

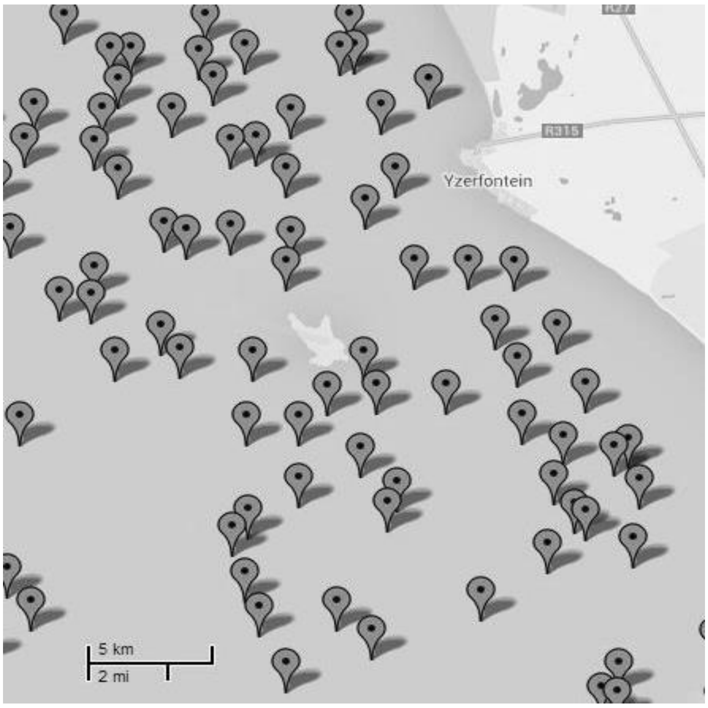

Figure 2.3 An example of the Fisheries Independent Monitoring Survey (FIMS) stations plotted around Dassen Island in the Western Cape of South Africa using Google Maps.

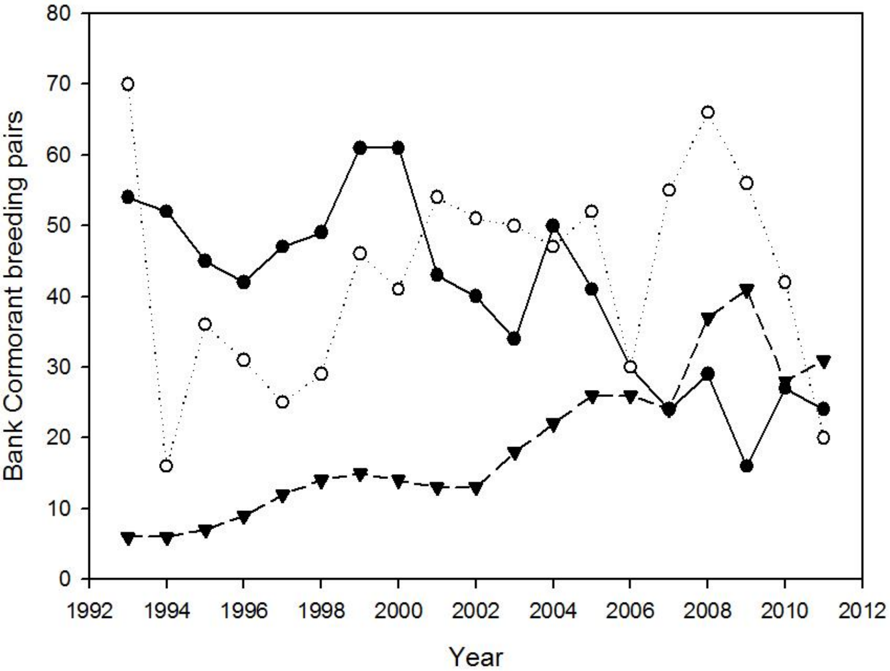

Figure 2.4. The number of breeding pairs of bank cormorants at Jutten Island (closed circles), Dassen Island (open circles) and Stony Point (black triangles) between 1993 and 2011.

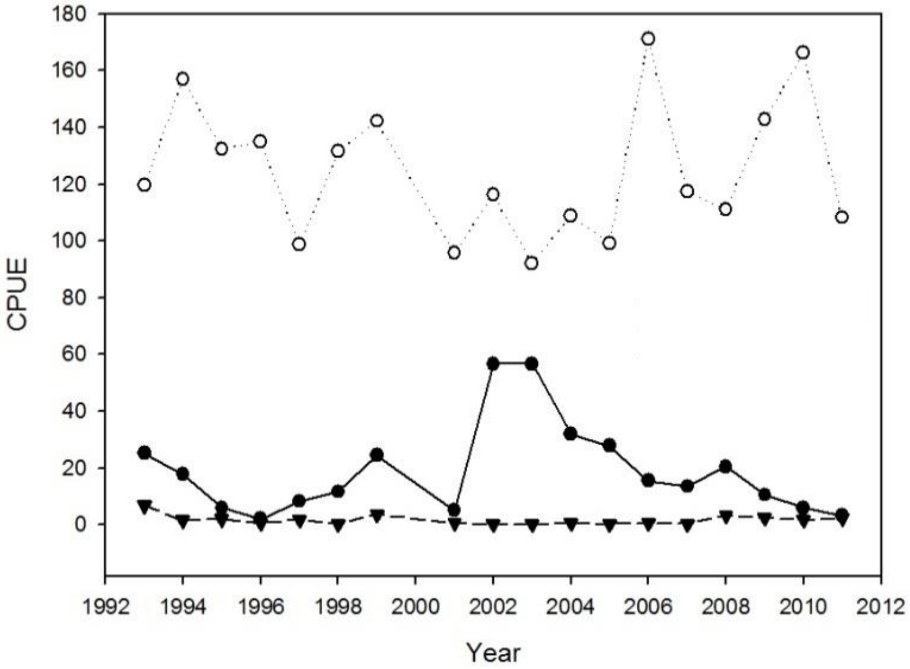

Figure 2.5 West Coast rock lobster catch per unit effort CPUE dynamics for Jutten Island (black triangles); Dassen Island (closed circles) and Cape Point (open circles) between 1993 and 2011.

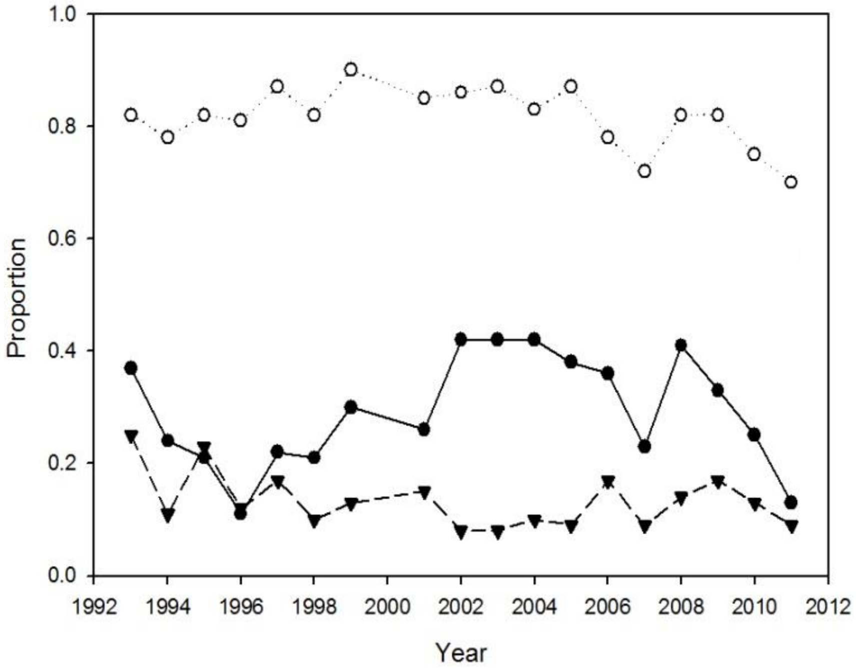

Figure 2.6 The proportion of traps containing West Coast rock lobsters for Jutten Island (black triangles); Dassen Island (closed circles) and Cape Point (open circles) between 1993 and 2011.

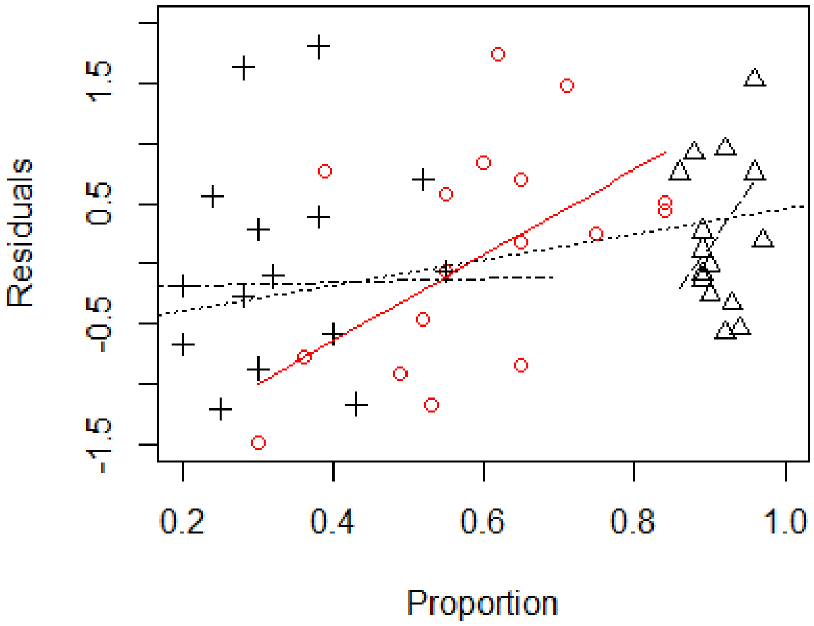

Figure 2.7 Response of the prewhitened studentized residuals of bank cormorant counts to the proportion of traps containing lobsters within 5 km distance of each colony. + = Saldanha Bay; ○ = Dassen Island and Δ = Cape Point. Trendlines indicate each area.

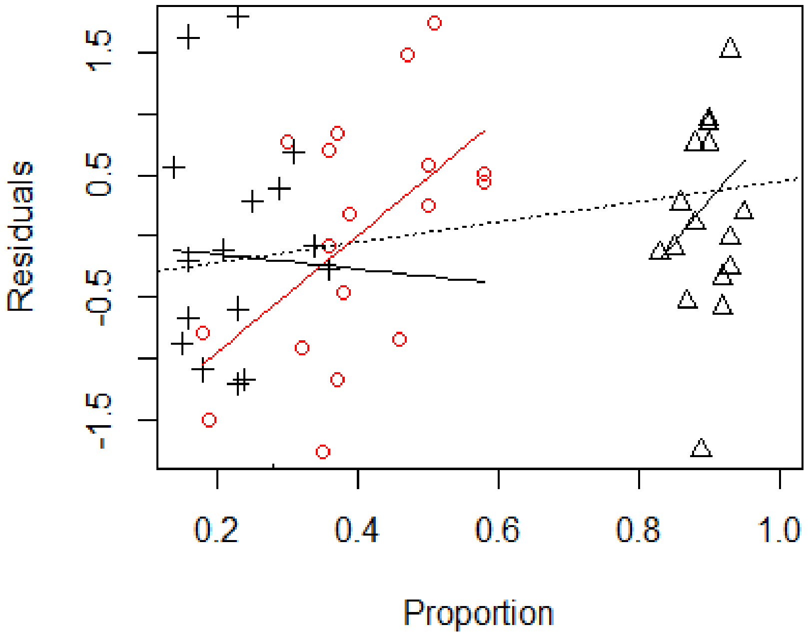

Figure 2.8 Response of the prewhitened studentized residuals of bank cormorant counts to the proportion of traps containing lobsters within 10 km distance of each colony. + = Saldanha Bay; ○ = Dassen Island and Δ = Cape Point. Trendlines indicate each area.

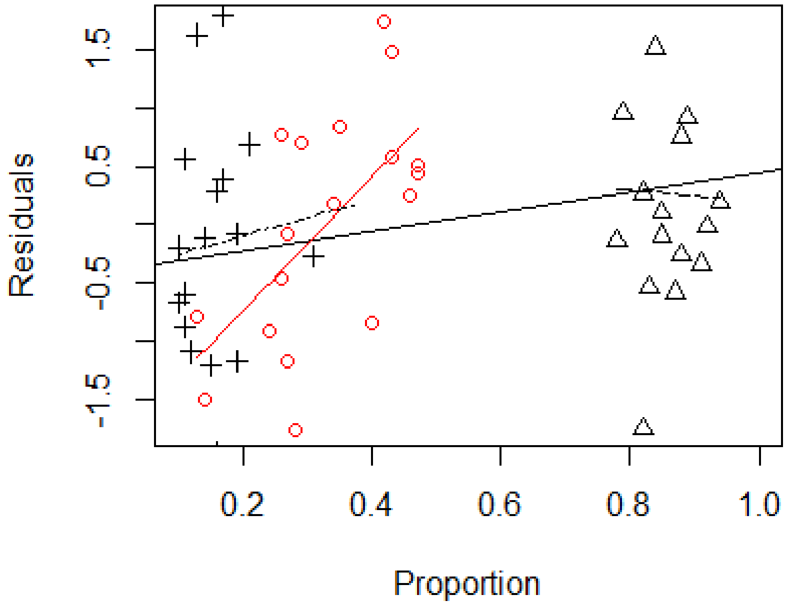

Figure 2.9 Response of the prewhitened studentized residuals of bank cormorant counts to the proportion of traps containing lobsters within 20 km distance of each colony. + = Saldanha Bay; ○ = Dassen Island and Δ = Cape Point. Trendlines indicate each area.

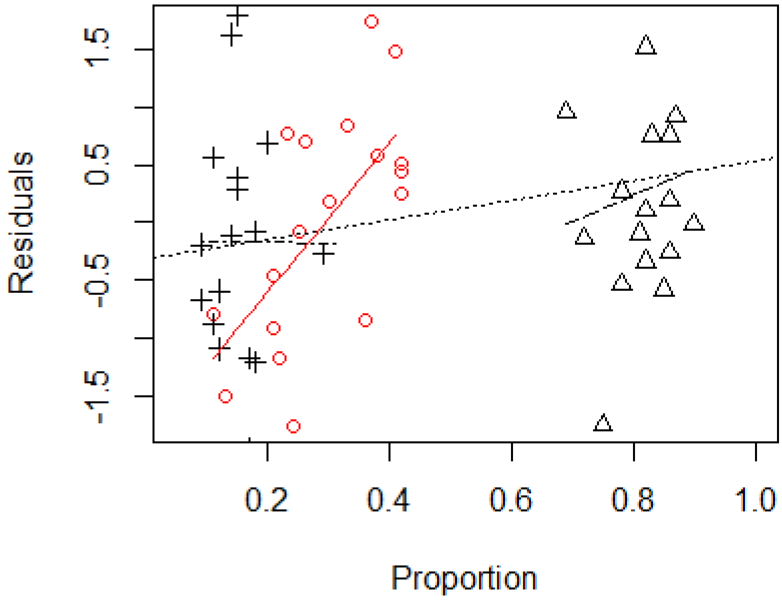

Figure 2.10 Response of the prewhitened studentized residuals of bank cormorant counts to the proportion of traps containing lobsters within 30 km distance of each colony. + = Saldanha Bay; ○ = Dassen Island and Δ = Cape Point. Trendlines indicate each area.

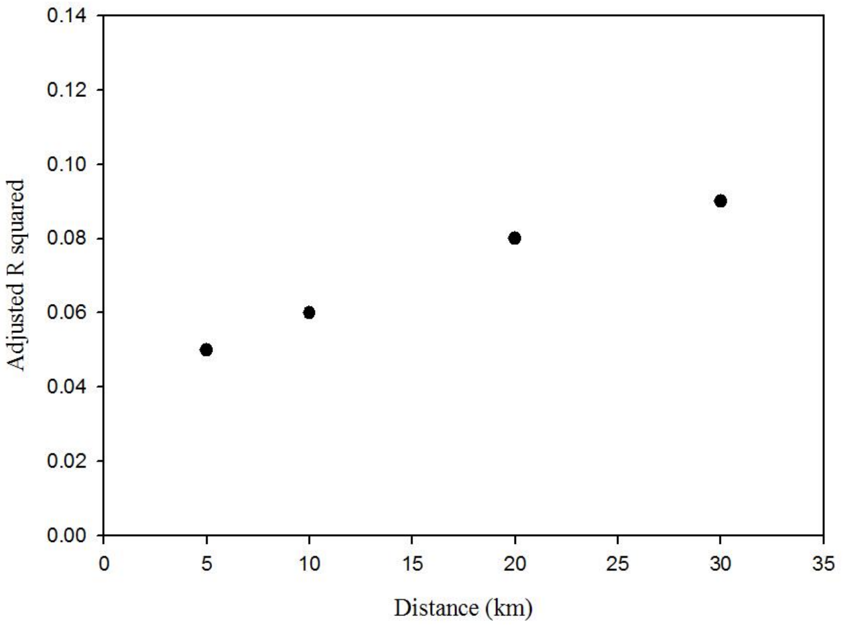

Figure 2.11 The correlation of studentised prewhitened residuals of bank cormorant numbers to rock lobster abundance at a range of distances (km) around colonies. The effect increases with distance, with the strongest response at 30 km (adjusted R^2= 0.09).

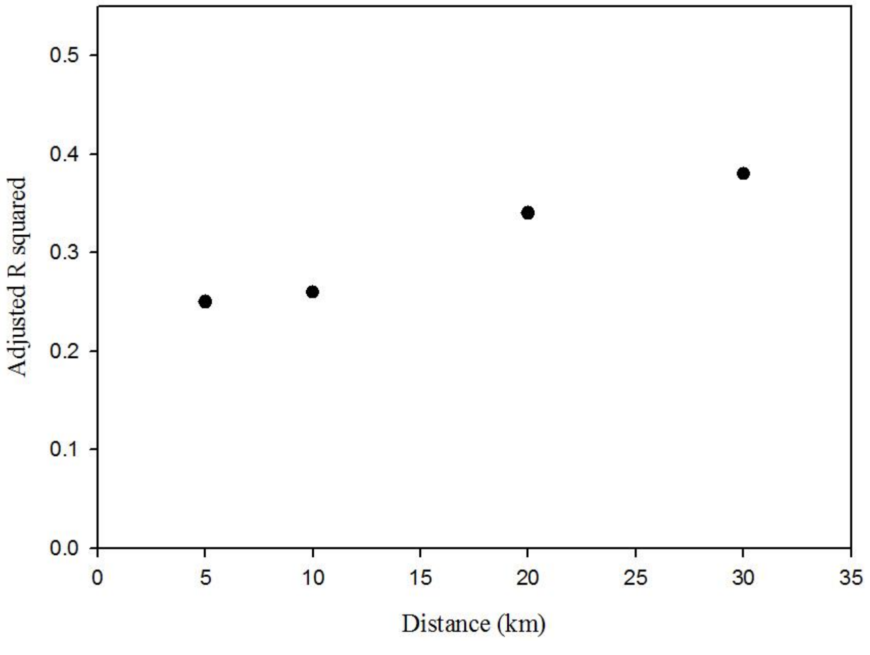

Figure 2.12 Adjusted R^2 showing the response of studentised prewhitened residuals of bank cormorant numbers to rock lobster abundance in an accumulative distance (km) around Dassen Island. The effect increases with distance, with the strongest response seen at 30 km (adjusted R^2= 0.38).

CHAPTER 3

Foraging behaviour of the endangered bank cormorant along the West Coast of South Africa

Abstract

The bank cormorant *Phalacrocorax neglectus*, a seabird endemic to the Benguela Upwelling System, is an inshore benthic forager currently listed as Endangered by the IUCN. Although the reason for the species' decline is not well understood, food shortage may be one of the most important factors. The West Coast rock lobster *Jasus lalandii*, an important prey species for bank cormorants in South Africa, experienced a south- and eastward shift in distribution from the northern part of South Africa's West Coast towards the south coast during the 1990s. This study compares the foraging behaviour of breeding bank cormorants obtained by filming nests at three different localities along the West Coast during 2012 and 2013. The waters around Jutten Island, Robben Island and Stony Point have different levels of rock lobster abundance. Foraging trip lengths at Jutten Island, the northernmost colony studied, were significantly longer than at Robben Island and Stony Point, where rock lobster are more abundant. There was a difference between the two years of study, with shorter trips at Jutten Island in 2013 than in 2012, possibly as a result of better feeding conditions or different prey items of lower quality consumed in 2013. Feeding on lower quality prey result in shorter, but more frequent foraging trips to maintain sufficient energy provision to offspring. Recommendations for future research include direct sampling of the cormorant's diet at each colony, as well as validation of their foraging ranges by deployment of GPS loggers, in order to better understand the information of the bank cormorant's response to an exploited environment.

Introduction

Seabird foraging efficiency is strongly influenced by food availability (Burger & Piatt, 1990). When food is abundant, seabirds can maintain high levels of chick production through efficient foraging. When food is scarce, birds need more time to forage, resulting in less time spent ashore, with often negative effects on offspring and themselves (Burger & Piatt, 1990; Zador and Piatt, 1999). At high prey abundance, time spent resting increases allowing time for courtship (Harding *et al.,* 2007) and nest maintenance (Davoren & Montevecchi, 2003). Adults have a minimum provisioning rate threshold to ensure reproductive success, determined at least in part by the minimum quantity of food required for chick growth and survival (Harding *et al.,* 2007). Provisioning pressure increases as offspring grow from hatchlings to larger chicks and require more food, thus demanding greater energy expenditure from foraging adults (Nagy *et al.,* 1984; Bertram *et al.,* 1996).

Seabirds generally have some degree of flexibility in their time-budgets to account for patchy or scarce food availability (Burger & Piatt, 1990; Litzow & Piatt, 2003). Flexibility in time-budgets is an adaptive feature for maintaining breeding success despite possible food scarcities (Litzow & Piatt, 2003). Depending on their life-history traits (Piatt *et al.,* 2007), they can however only maintain constant provisioning rates above a certain limit of food availability.

The success of a seabird breeding colony may be influenced indirectly by the ability of adults to maintain constant provisioning rates despite unreliable prey availability (Davoren & Montevecchi, 2003). In areas with low prey availability, adults may spend significantly more time at sea, undertaking longer foraging trips (Zador & Piatt, 1999; Davoren & Montevecchi, 2003). This is often seen in declining colonies, whereas adults in increasing colonies typically have more time to spend at their nests, and spend a significantly shorter time at sea (Zador & Piatt, 1999).

The West Coast rock lobster *Jasus lalandii* is an important food source for bank cormorants *Phalacrocorax neglectus* in South Africa (Crawford *et al.,* 2008; Ludinya *et al.,* 2010a). Rock lobsters have experienced a southward shift in distribution from South Africa's West Coast to southern areas in the last three decades (Cockroft *et al.,* 2008; Blamey *et al.,* 2012). This has resulted in a significant decrease in rock lobster landings along the West Coast and an increase in catches east of Cape Point (Cockroft *et al.,* 2008).

The West Coast rock lobster is the target of one of the most commercially important fisheries in South Africa, comprising the country's third most valuable marine resource (Johnston & Butterworth, 2005). The shift in rock lobster distribution has been inferred to have caused regional changes in the population dynamics of bank cormorants (Crawford *et al.,* 2008; Chapter 2), contributing to their decline and even extinction in the northern part of the Western Cape, and promoting colony establishment and growth in the south of their range (Crawford *et al.,* 2008). However, the direct effects of changes in food availability on the foraging and breeding behaviour of bank cormorants have not been demonstrated.

This study compares the foraging behaviour of bank cormorants in three different areas, along the south-west coast of South Africa where there have been contrasting trends in rock lobster abundance. By comparing the average foraging trip duration and number of trips made per day by bank cormorants during different breeding stages in areas inferred to have different levels of rock lobster availability, I test whether the reduction in rock lobster abundance has influenced bank cormorant behaviour and indirectly, colony success.

Materials and methods

Study sites

Three bank cormorant colonies in the Western Cape of South Africa were used to obtain foraging trip duration data: Jutten Island (33˚ 05' S; 17˚ 57' E) located in Saldanha Bay, approximately 100 km north of Cape Town; Robben Island (33˚ 48' S; 18˚ 22' E) in Table Bay, 13 km north of Cape Town; and Stony Point (34˚ 22' S; 18˚ 53' E), a mainland colony approximately 90 km south east of Cape Town (Fig. 3.1). Bank cormorants in South Africa breed between March and September (Crawford *et al.,* 1999). This study was conducted during the 2012 and 2013 breeding seasons.

The Jutten Island bank cormorant colony declined by almost 60% between 2000 and 2011 (Crawford *et al.,* 2011b). The Robben Island colony, which is situated in a rock lobster reserve, is the largest bank cormorant colony in South Africa and has been relatively stable, despite being affected by two large oil spills in the last 20 years (Crawford *et al.,* 2008). The Stony Point colony has been increasing since it formed in 1987 (Cooper, 1988; Crawford *et al.,* 2008).

Data collection

Bank cormorants on Robben Island breed on the eastern side of the island, on man-made structures on the harbour wall. On Jutten Island and Stony Point they breed on elevated rocks very close to the water. At each colony, vantage points were chosen approximately 30–50 m from the breeding birds to minimize disturbance. Photo maps were made on which each nest was numbered (e.g. Fig. 3.2). Nests were monitored throughout incubation and chick rearing. Filming took place from April–August in 2012, and from March–August in 2013. Colonies were visited in two week intervals and were filmed every 7–14 days to ensure sufficient sample sizes of different breeding stages and to document nest contents and/or new or lost nests.

On each visit, video cameras were set up for full days (07h00–18h00) to record foraging trip durations (time away from nest), as well as the number of trips made by each breeding pair per day. Nests of bank cormorants are generally under the constant care of at least one parent (Crawford & Cooper, 2005), so offspring are almost never left alone at nests. On one occasion adults left their two large chicks to both go out foraging at Jutten Island, but that was not included in the analysis as it was impossible to distinguish the duration of an individual trip. Due to the distance of the vantage points from the colony, it was not possible to distinguish between the different sexes of birds, but nest contents were documented at all times using a spotting scope and binoculars. During observations, nests were categorized into six stages: incubating; hatchlings; small downy chicks (still sheltered by parent); medium downy chicks (sitting next to adult on the nest); large downy chicks (taller than half the size of adult) and 'woolly necks' (starting to show primary feathers) (Sherley *et al.,* 2012).

For analysis, breeding stages were grouped into three categories: incubating, early chick rearing and late chick rearing (Table 3.1), to control for chick size and the impact of thermal emancipation of chicks on foraging trip lengths. Early rearing included stages where chicks were still sheltered by parents (i.e. hatchlings and small chicks starting to present with down). The late rearing stage included chicks that were no longer sheltered by adults (i.e. medium downy chicks to chicks already having primary feathers). Within the late stage, chicks are no longer dependent on shelter, but they require more nutrients, and therefore require more food from the adults (Nagy *et al.,* 1984; Bertram *et al.,* 1996).

At all three study sites, three or four cameras were used to film 5–10 nests at each visit. On Jutten Island and Stony Point where no electricity was available, video cameras were powered via a portable system containing two deep cycle 12V batteries and an AC/DC power inverter (Fig. 3.3). Batteries were charged by generator overnight.

Video data were investigated afterwards to distinguish between foraging and those to collect nest material. The latter almost never exceed 10 minutes (Ludynia *et al.,* 2010a), thus trips that were shorter than 10 minutes, or when a bird was seen returning with nest material, were excluded from the analysis. Each trip made by monitored birds was recorded, as well as the number of trips per day. A trip was measured from the moment a bird left the nest, until its arrival back at the nest. Members of pairs would generally switch, after which the next trip would commence by the partner that had been relieved at the nest. If birds had already left the nest by the start of filming at dawn, civil twilight was used as proxy for that departure time. Civil twilight is when the centre of the sun is 6° below the earth's horizon

(Hull *et al.,* 2001). The time of twilight on a given date at each colony was determined by a sunrise/sunset calculator on https://www.timeanddate.com.

Data Analysis

Linear mixed models were used to compare foraging trip durations and total time spent at sea between the three colonies, using the nlme library in R v. 3.0.1 (R Core Team 2013). Breeding stage (incubating, early- and late rearing), colony and year were used as predictors of trip duration. To control for the same breeding pairs being monitored several times, nest and bird were used as random factors in the models. For foraging trip duration, log transformation was used to obtain normally distributed residuals. I used restricted maximum likelihood estimation and Akaike's Information Criterion (AIC) to select the random component, followed by a stepwise backward selection using AIC and maximum likelihood estimation to select the preferred fixed structure from the model containing all possible interactions (Zuur *et al.,* 2009).

To compare number of foraging trips per day, generalized linear models with Poisson distribution were used (glm function in R). The number of trips was the response variable with colony, breeding stage and year as covariates. The best fitting models were selected using AIC.

Results

Foraging trip duration and number of trips per day were calculated from a total of 87 nests at Jutten Island, 89 at Robben Island, and 84 at Stony Point. During the 2012 breeding season, 46, 49 and 43 nests were observed for Jutten Island, Robben Island and Stony Point respectively. For the 2013 season, 41, 40 and 41 nests were observed for the three colonies respectively.

According to AIC model selection the best model included nest as random factor and an interaction between colony and year as the fixed effects (Table 3.2). Trips at Jutten Island were significantly longer than at Robben Island ($t = -3.44$; $df = 1280$; $P < 0.001$) and Stony Point ($t = -6.96$; $df = 1280$; $P < 0.001$), and Robben Island trips also were significantly longer than those at Stony Point ($t = -2.73$; $df = 1280$; $P = 0.007$). For all three colonies, trips were longest when the birds were incubating and shortest when chicks were in the late rearing stage (Fig. 3.4). Trips differed significantly between the two years of study ($t = -4.87$; $df = 1280$; $P < 0.001$) with shorter trips in 2013 at Jutten Island and Robben Island but not at Stony Point (Fig. 3.5).

Mean number of trips per day was greater at Robben Island than at Jutten Island ($t = 2.07$; $df = 252$; $P = 0.04$), but there were no significant differences between Stony Point and Jutten Island ($t = 1.6$; $df = 252$; $P = 0.11$) or Robben Island ($t = -0.35$; $df = 252$; $P = 0.72$). Year was a significant effect in the model ($t = 2.38$; $df = 252$; $P = 0.02$), indicating increases in the number of foraging trips per day at all colonies from 2012 to 2013 (Fig. 3.6). Birds made significantly fewer foraging trips when incubating than when chick rearing (Fig. 3.7).

Birds spent significantly more time at sea per day at Jutten Island than at Robben Island ($t = -2.63$; $df = 224$; $P = 0.01$) and Stony Point ($t = -3.98$; $df = 224$; $P < 0.001$). Stony Point birds averaged less time at sea than birds from Robben Island, but the difference was not significant ($t = -1.09$; $df = 224$; $P = 0.28$; Fig. 3.8). Year did not affect the total time spent at sea per day ($t = -0.49$; $df = 224$; $P = 0.62$).

Discussion

Bank cormorants at Jutten Island, the northernmost colony in this study, spent significantly more time foraging than birds at the other two colonies. This is what would be expected based on the distributional shift of West Coast rock lobster from northern areas of the West Coast towards Cape Point over the last two decades (Cockroft *et al.,* 2008; Crawford *et al.,* 2008; Blamey *et al.,* 2012). Rock lobster catches are significantly higher around Cape Point and Stony Point than in Saldanha Bay on the West Coast (Chapter 2). At Jutten Island, the significantly longer trips probably indicate lower prey availability around that island.

Seabird colonies differ not only in surrounding prey availability, but also in distance of feeding grounds from colonies. Breeding seabirds are central place foragers, and typically show fidelity to their feeding grounds (Irons, 1998; Cook *et al.,* 2006; Ludynia *et al.,* 2010a), especially benthic feeders like the bank cormorant, as benthic prey are often more static in their location (Birt *et al.,* 1987; Cairns, 1988; Takahashi *et al.,* 2003a). If prey availability becomes more unpredictable, foraging trip lengths increase causing a decrease in offspring provisioning, indirectly resulting in lower levels of reproductive success (Jakubas *et al.,* 2013). Davoren & Montevecchi (2003) compared two common murre *Uria* *aalge* colonies located at different distances from their foraging grounds and found that while the colony close to food was increasing in size, the farther colony was stable. This may be a result from the colony being at carrying capacity, or from reduced chick provisioning rates (Davoren & Montevecchi, 2003).

Foraging effort is an important indicator of environmental conditions and prey availability (Piatt *et al.,* 2007). Depending on the species, seabirds provide inportant insights by their behavioural responses like duration of foraging trips in relation to food abundance. Monaghan (1996) found significantly longer foraging trips for three different seabird species in years when food was scarce. Low prey availability does not only influence the amount of searching time as soon as birds leave their nests, but also the energetics in terms of diving frequency and rest time at sea (Monaghan *et al.,* 1994).

Seabird activity budgets tend to be influenced more by prey availability than by weather conditions such as wind, visibility or rain (Burger & Piatt, 1990). Seabirds compensate for low prey availability by working harder, spending less time ashore and more time searching for food, and also compensate by switching prey items in order to maintain delivery of the required energy levels to offspring (Burger & Piatt, 1990; Uttley *et al.,* 1994; Bryant *et al.,* 1999; Litzow & Piatt, 2003, Schrimpf *et al.,* 2012; Smout *et al.,* 2013). Another indication of food availability is seen in the frequency of trips made per day. Large numbers of trips often indicate high food availability whereas fewer, longer trips tend to indicate that food is scarce (Uttley *et al.,* 1994). The ability to practise flexible time budgets in systems having unpredictable food availability is an adaptive feature, and enables seabirds to maintain constant provisioning and therefore maintain chick growth and in turn breeding success (Litzow & Piatt, 2003).

Overall, birds at Jutten Island made fewer foraging trips per day, as a result of longer trip lengths. There was, however no significant difference between the number of trips per day between Jutten Island and Stony Point. This may be due to the fact that birds at Stony Point were not under any food constraints, and managed to provide chicks with high quality food, so that they have more time to spend on rest and self-maintenance (Davoren & Montevecchi, 2003; Harding *et al.,* 2007). Birds at Jutten Island had to maintain constant food provisioning rates, though not as frequent due to possible low levels of surrounding prey, and therefore spent more time foraging. Number of trips per day is also positively correlated with chick age and size, due to an increase in chick size requiring more energy, and higher frequency provisioning (Bertram *et al.,* 1996).

Seabirds can adjust the amount of food given to offspring in response to chick age and size (Bertram *et al.,* 1996). While chicks grow, the frequency of food provisioning increases to meet increasing energy demands (Bertram *et al.,* 1996; Takahashi *et al.,* 2003b). During incubation, adult birds can spend extensive periods of time at sea, and include time for resting and 'loafing' away from their nests (Ojowski *et al.,* 2001). This is represented in the significantly longer time away from the nest while birds were in the incubating stage of breeding.

Bank cormorant chicks fledge after 55–60 days, prior to which time they stay on the nest and are under almost constant attendance by at least one parent (Crawford & Cooper, 2005). It is during these late rearing stages that chicks require high frequency provisioning, which is a constraining period for the adult birds (Weimerskirch *et al.,* 2003). After fledging, chicks are often left alone or form crèches (Crawford, 2007; Crawford *et al.,* 2008), during which time both adults can go out foraging, and thus spend more time at sea. On Jutten Island, two 'woolly necked' chicks, which generally are still under constant attendance of parents, were once left alone for periods of time during the day (pers. obs.). This behaviour likely indicates an urgent need for both parents to be out foraging due to low food availability and high energy requirements of the two large chicks (e.g. Piatt *et al.,* 2007).

The differences in trip duration between 2012 and 2013 may be due to better feeding conditions and higher prey availability in 2013. This difference was mainly due to a significant difference in trip duration at Jutten Island, with longer trips in the first year of the study than the second. When preferred prey is scarce, seabirds may switch to different prey often of lower quality (Montevecchi, 2002; Baduini & Hyrenbach, 2003; Grémillet *et al.,* 2008; Ludynia *et al.,* 2010b). Lower quality food can often be obtained with less effort by the parents, and therefore in some cases its abundance may be beneficial for maintaining adult seabird condition and survival (Tasker *et al.,* 2000; Montevecchi, 2002). This however is not generally beneficial to offspring, which often require the high energy which preferred prey provide (Grémillet *et al.,* 2008). Birds at Jutten Island may have resorted to food of lower quality in 2013, hence the reduced duration of trips in that year. (B. M. Dyer, pers. comm.) indicated that few pellets recovered from bank cormorants on Jutten Island contained rock lobster remains in recent years, with Cape mantis shrimp *Pterygosquilla* *capensis* and West Coast sole *Austroglossus microlepis* dominating the diet. Although these observations were based on small sample sizes, they indicate that bank cormorants in the area around Jutten Island are sometimes unable to find rock lobster in many years, so feed on alternative prey species. However, diet information is limited, making conclusions difficult to draw.

Bank cormorants and African penguins *Spheniscus demersus* in Namibia feed primarily on bearded goby *Sufflogobius bibarbatus* (Ludynia *et al.,* 2010a), a prey species of relative low energy value (Ludynia *et al.,* 2010b), but more predictable in its distribution than the two species' known preferred prey items off South Africa (West Coast rock lobster and sardine *Sardinops sagax*, respectively). Compared to foraging trip lengths in Namibia (seldom > 60 min; Ludynia *et al.,* 2010a), bank cormorants in South Africa made longer foraging trips (60–120 min). The low quality and spatial predictability of goby (Ludynia *et al.,* 2010b) may result in shorter, but more frequent trips. These differences may reflect different methods used; the Namibian study was conducted by means of GPS loggers attached to individual birds to test trip lengths, in contrast to the use of filming in this study. Some information may have been missed by using cameras, where a foraging trip was only considered completed once the bird arrived back at its nest. The time spent 'loafing' or resting away from the nest have been included in foraging trip time.

Although foraging trip duration provides some important aspects of the effort bank cormorants undertake in order to find food in an exploited environment, more in depth information on distances travelled, depth of the water column exploited and prey items delivered to the chicks would be of importance. Filming provides a non-invasive method of obtaining behavioural information, but it would be informative to validate this with information obtained through GPS loggers in order to implement effective conservation planning for the species. In order to fulfil conservation management practices for the species, a data set of leading indicators concerning bank cormorants would be crucial to assess the impact of conservation strategies. This would include foraging behaviour, breeding success and population dynamics data over several years to emphasize the need for management practices including fishing closures around colonies and nest site development in areas where breeding space is limited.

Table 3.1 Breeding state and approximate brood mass (g) allocated to bank cormorant nests from observation towards analysis. Incubation indicates eggs; hatchling indicates newly hatched chicks; small, medium, large downy chick indicates chicks with down, and downy neck indicates chicks with primary feathers.

Breeding state	**Stage for analysis**	**Approximate brood mass (grams)**
Incubating	Incubation	50
Hatchling	Early	50–70
Small downy chick	Early	200
Medium downy chick	Late	500
Large downy chick	Late	1 000
Downy neck	Late	1 500

Table 3.2 Linear mixed-effects models relating foraging trip lengths of bank cormorants to colony, breeding season (year) and breeding stage. Variables are categorized by breeding stage (incubating, early, late), colony (Jutten Island, Robben Island and Stony Point) and year (2012 and 2013). K is the number of parameters in each model, and AIC values indicate model fit. ΔAIC shows the difference from the preferred model, and AIC weight indicates the support for each model.

Model	**Predictors**	**K**	**AIC value**	**ΔAIC**	**AIC Weight**
4	Colony * Year + Colony + Year + Breeding stage	10	2081.4	0	0.74
3	Colony * Year + Year * Breeding stage + Colony + Year + Breeding stage	12	2083.7	2.4	0.23
2	Colony * Breeding state + Colony * Year + Year * Breeding stage	16	2087.6	6.3	0.03
1	Colony * Breeding stage * Year	20	2092.3	10.9	0

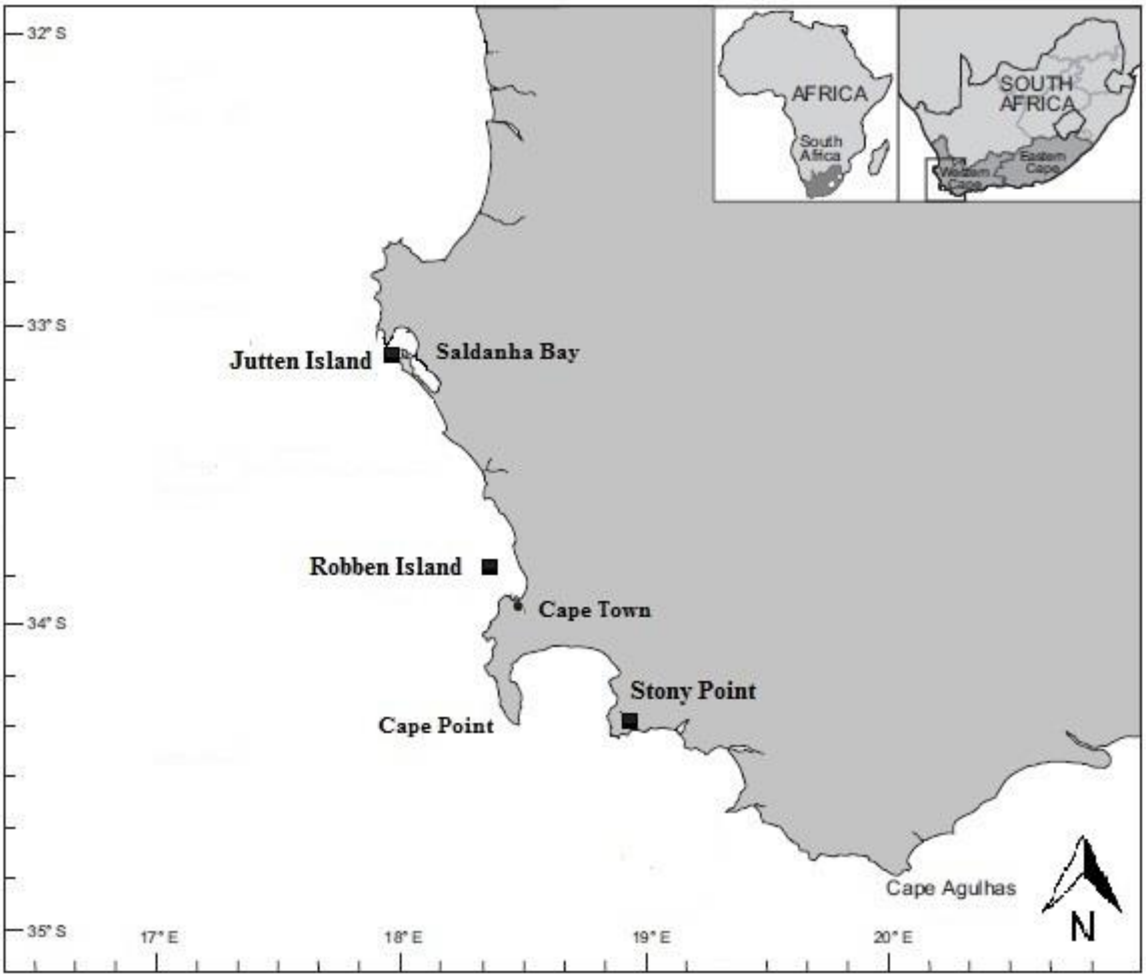

Figure 3.1 The three bank cormorant colonies (Jutten Island, Robben Island and Stony Point) in the Western Cape of South Africa where foraging parameters were collected in this study. Map by Crawford *et al.* (2008).

Figure 3.2 Photo map of bank cormorants breeding at Robben Island.

Figure 3.3 Portable box system containing two deep cycle 12V batteries and an inverter supplying power to the video cameras to film bank cormorant foraging behaviour at Jutten Island.

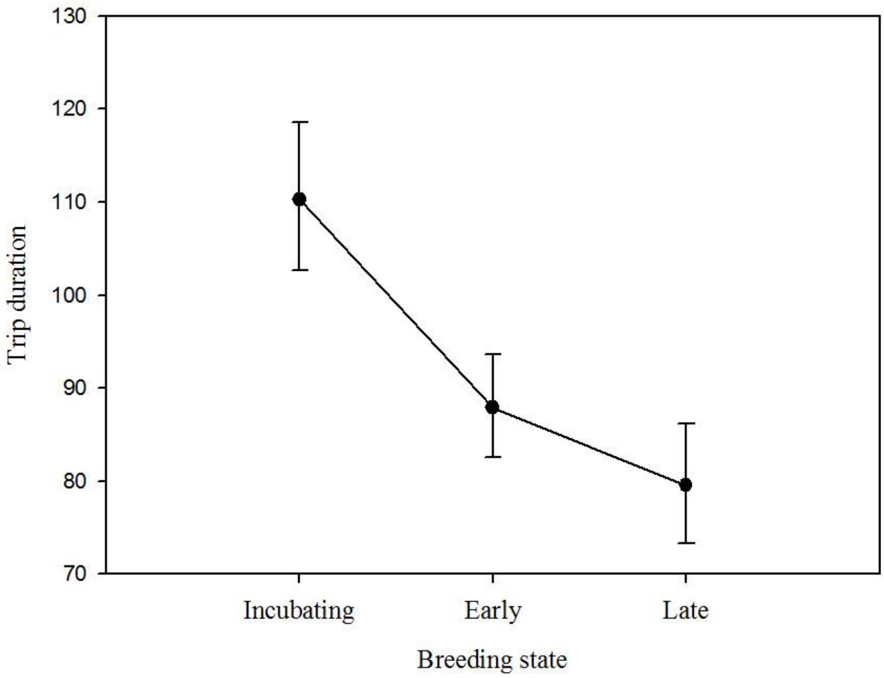

Figure 3.4 Foraging trip duration (minutes) related to overall breeding state (incubating, early chick rearing and late chick rearing) for bank cormorants at Jutten Island, Robben Island and Stony Point. Bars represent the 95% confidence intervals

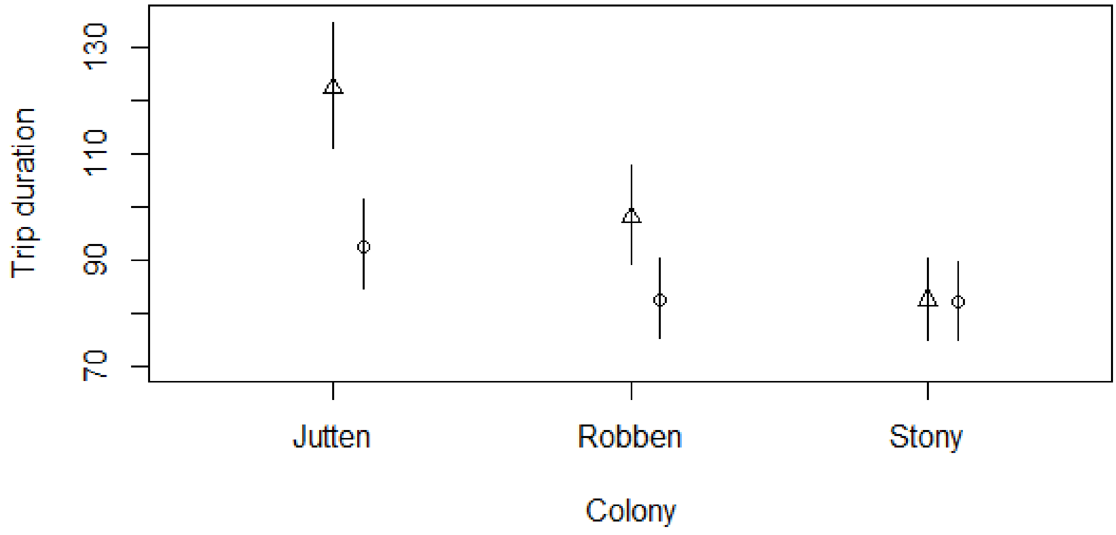

Figure 3.5 Mean trip duration (minutes) at the three bank cormorant colonies (Jutten Island, Robben Island and Stony Point) for 2012 (triangles) and 2013 (circles). Bars represent the 95% confidence intervals.

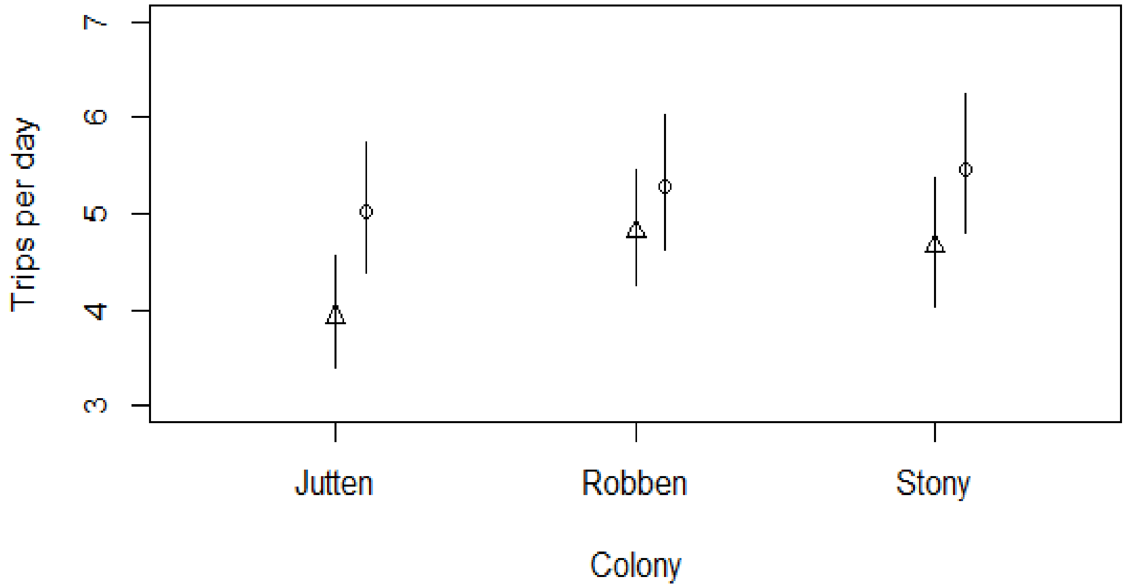

Figure 3.6 Mean number of foraging trips per day at three bank cormorant colonies (Jutten Island, Robben Island and Stony Point) for 2012 (triangles) and 2013 (circles). Bars respresent the 95% confidence intervals.

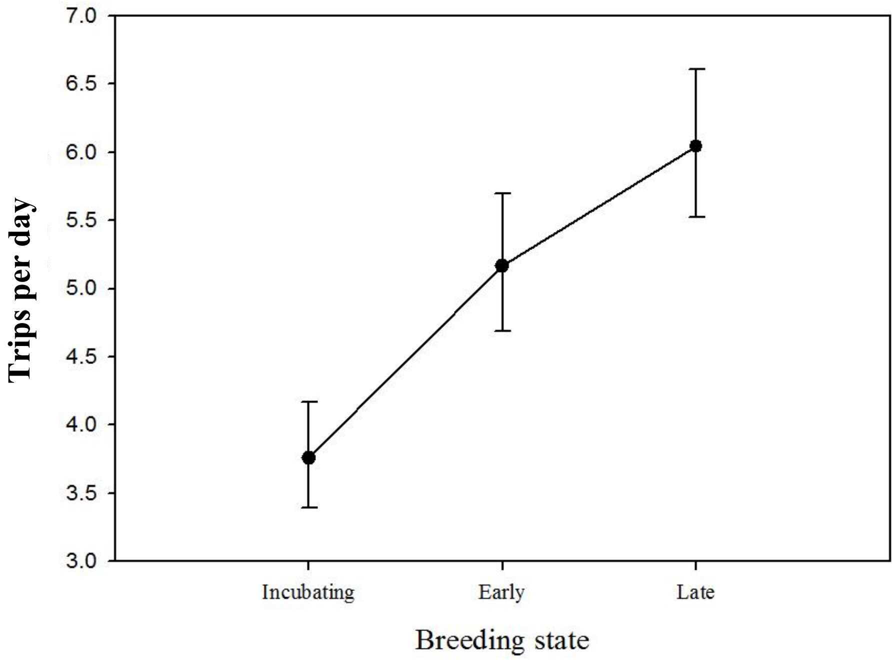

Figure 3.7 Mean number of foraging trips per day for bank cormorants breeding at Jutten Island, Robben Island and Stony Point in relation to breeding state: incubating, early chick rearing and late chick rearing. Bars represent 95% confidence intervals.

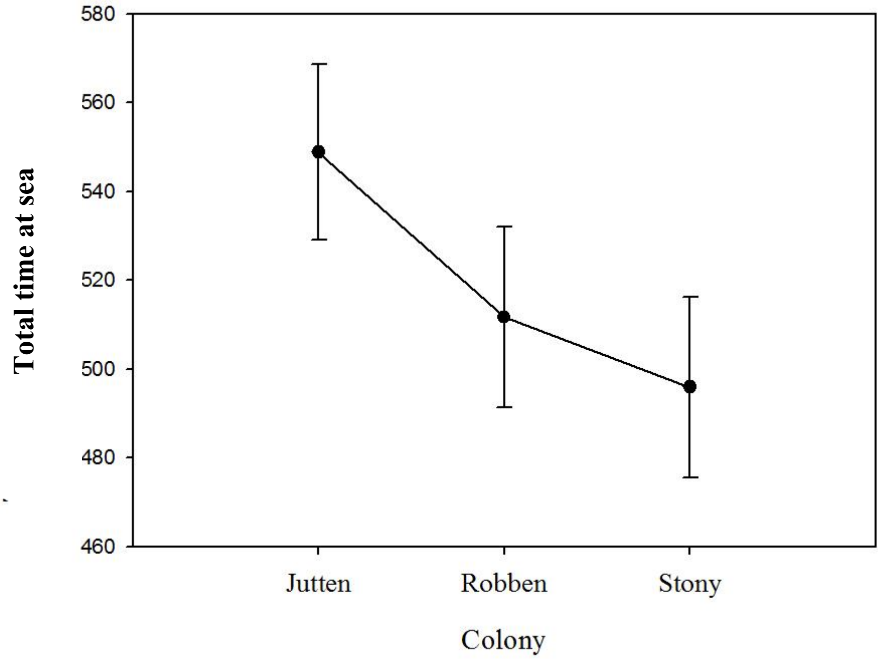

Figure 3.8 Total time spent at sea per day in minutes for bank cormorants breeding at Jutten Island, Robben Island and Stony Point. Bars represent 95% confidence intervals.

CHAPTER 4

The effect of food availability on the breeding success of the endangered bank cormorant along the West Coast of South Africa

Abstract

Bank cormorants *Phalacrocorax neglectus,* an endemic seabird in the Benguela Upwelling System, breed during the austral winter in South Africa. Numerous factors including weather conditions and prey availability play a role in influencing breeding success of long-lived seabirds. West Coast rock lobster *Jasus lalandii*, an important prey species for bank cormorants in South Africa, has experienced a southward shift in abundance along the West Coast in the last 30 years. The breeding success of three bank cormorant colonies known to be located in areas with different levels of food availability was compared and tested in relation to seasonal catch per unit effort (CPUE) data for rock lobster. Breeding success was variable between years, and did not reflect the influence of prey availability. However, rock lobster CPUE was significantly related to the number of chicks fledged per successful nest. It is apparent that bank cormorant nests that failed were more likely influenced by storms, while successful nests were influenced by food availability in the number of chicks fledged. A larger dataset including chick condition parameters and diet data is needed to obtain a better understanding of the influence of exploited resources on this endangered seabird.

Introduction

Seabird- nest or offspring neglect are among two of the most commonly used proxies to assess food availability (Lewis *et al.,* 2006). In several seabird species, feeding behaviour is limited by physiological parameters as well as environmental factors (Sapoznikow & Quintana, 2003). Food stress can be assessed by looking at different behavioural- or population-level parameters which reflect a lack of sufficient resources.

Clutch and brood sizes, together with foraging biology are life-history traits of seabirds (Anderson & Ricklefs, 1992). Birds that travel far from land to feed on pelagic resources generally lay only one to two eggs per clutch, while inshore foragers including several cormorant species, can lay up to six eggs (Hamer *et al.,* 2002). The energetic cost to form and produce eggs is lowest among Pelecaniformes, and among seabirds, cormorants produce the smallest eggs in relation to their body size (Whittow, 2002), hence the often large clutch sizes found in some Phalacrocoracidae species. Bank cormorants, however have a modal clutch size of two eggs (Cooper, 1987), indicating that the loss of a brood may have greater impact on the population than in other species. Breeding success in terms of the number of chicks fledged per pair per year is a parameter often affected by food availability (Crawford *et al.,* 2006).

Long-lived seabirds' ability to buffer against low prey abundance varies among species. Some are able to maintain successful chick rearing despite low food availability, while others show breeding failures and low success rates when increased foraging effort is required (Zador & Piatt, 1999; Litzow & Piatt, 2003). Inter-specific variations in the ability to account for food scarcity can be due to biological features such as methods of foraging and life history traits including body size and clutch size (Litzow & Piatt, 2003).

Low food availability requires higher foraging effort, which indicates that food scarcity does not necessarily affect breeding success directly, but rather indirectly through the physiological threshold at which adult seabirds can maintain both self- and offspring survival (Ponchon *et al.,* 2014). Food shortages can be seen in several breeding characteristics including brood size and chick growth where adults have to compromise the amount of food given to offspring, as well as often altering their own body reserves (Gaston & Hipfner, 2006; Ballard *et al.,* 2010).

The trade-off between breeding investment and favouring the adult's own survival provides interesting insights into the life-history traits of long-lived seabirds. When greater feeding effort is required and prey availability (or quality) falls below a critical threshold, birds often favour their own body condition and survival above that of their offspring and tend to invest more in their future ability to reproduce than in current chick provisioning (Sæther *et al.,* 1993; Weimerskirch *et al.,* 2001). In some species, the adult's adjustment of provisioning rates to match offspring energy requirements (Bertram *et al.,* 1996) is only possible in favourable environmental conditions, when food availability is high (Weimerskirch *et al.,* 2001).

In southern Africa, studies have shown significant influences of food availability on the breeding success of African penguins *Spheniscus demersus* (e.g. Crawford *et al.,* 2006; Sherley *et al.,* 2013), while bank cormorants *Phalacrocorax neglectus* exhibited relatively low breeding success in Namibia (Sherley *et al*., 2012) where they feed predominately on low quality prey (Ludynia *et al.,* 2010b).

West Coast rock lobster *Jasus lallandii* is an important food source for bank cormorants in South Africa (Crawford *et al.,* 2008; Ludinya *et al.,* 2010a), and has experienced a shift in distribution from South Africa's West Coast to areas east of Cape Point (Fig. 4.1) between 1980 and 2000 (Cockroft *et al.,* 2008; Crawford *et al.,* 2008; Blamey *et al.,* 2012). Of the total lobster catches in South Africa, landings decreased from 60% to less than 10% in the West Coast, and increased from less than 10% to approximately 60% in the south-western area of the species' range (Cockroft *et al.,* 2008) towards the Cape Point area. The population dynamics of bank cormorants have been influenced by this shift in the relative abundance of rock lobster (Crawford *et al.,* 2008; Chapter 2), but the level at which these changes act upon the population remain to be examined.

This study focuses on the breeding success of three bank cormorant colonies over a subset of years, in relation to the food availability in terms of West Coast rock lobster in those areas. The hypothesis is that breeding success is a function of food availability. The prediction for this study is that bank cormorant breeding success will have been negatively affected by a reduced availability of rock lobster in the northern part of the species' range within South Africa. Further comparisons of the nest survival probabilities of this endangered seabird are also calculated by including data from a previous study.

Materials and methods

Bank cormorant breeding success was studied at three colonies in the Western Cape, South Africa. Jutten Island lies in Saldanha Bay in the West Coast National Park (33˚ 5' S, 17˚ 57' E) approximately 100 km north of Cape Town, Robben Island is in Table Bay, approximately 13 km north of Cape Town (33˚ 48' S; 18˚ 21' E) and Stony Point is a mainland colony approximately 90 km southeast of Cape Town (34˚ 22' S; 18˚ 53' E) (Fig. 4.1). An average of 17 breeding pairs were present at Jutten Island during the two years of study, 100–110 pairs at Robben Island, and 40 pairs at Stony Point. The latter is a fairly new bank cormorant colony, established in 1988 following the colonization of African penguins (Whittington *et al.,* 1996).

Bank cormorants in South Africa breed between March and September (Crawford *et al.,* 1999) and this study was conducted during the breeding seasons of 2012 and 2013.

Breeding success data for Robben Island from 2007 to 2011 were obtained from Sherley *et al.* (2012). Data for Mercury Island were included in the breeding success analysis (obtained from Sherley *et al.,* (2012). Mercury Island is one of the largest (Cooper, 1981) and northern-most bank cormorant colonies and located off the coast of Namibia. Food availability data for Namibia were not available, so Mercury was excluded from regression analysis with food as an explanatory variable.

Nest observations

Bank cormorants at Robben Island breed on man-made structures on the harbour wall on the eastern coast of the island. At Stony Point and Jutten Island they breed on elevated rocks close to the water. Nests were monitored at all three colonies during the breeding seasons of 2012 and 2013 (Table 4.1).

At each locality, maps of the colonies were made by means of photos on which each nest was numbered (Fig. 4.2). Suitable vantage points were chosen at each colony ca 10–30 metres from the breeding birds so that any disturbance was avoided. The colonies were visited at 7–14 day intervals and by making use of scopes and binoculars, breeding state and nest contents were documented where possible. Due to distance from colony, it was not possible to determine number of eggs in an incubating nest.

Following Sherley *et al.* (2012), chicks were classified into 5 breeding stages: hatchling (smallest size of observed chick, no down yet), small downy chick (smaller than half the size of the adult bird, sheltered by parent), medium downy chick (half the size of adult), large downy chick (larger than half the size of the adult) and ‘woolly neck’ where the down only persists on the head and neck. Chicks were classified as fledged when they were no longer at the nest or when the down on the head and neck had been lost. On occasions that nests failed due to extreme weather conditions, observations continued on those nests until the end of the observation period.

Rock lobster data

Inshore West Coast rock lobster data were obtained from the Department of Agriculture, Forestry and Fisheries (DAFF) of South Africa. The west coast of South Africa has been divided into zones and areas to record rock lobster catches and abundance (Fig. 4.3). Areas

5 and 6 are close to Jutten Island, area 8 abuts Robben Island (Table Bay in this area has been declared a West Coast rock lobster reserve since the 1960s, Pollock, 1987), and Areas 11 and 12 area close to Stony Point. For these areas data on commercial catches of rock lobster and associated effort were available from 2007–2013.

Catch per unit effort (CPUE) were calculated by dividing the total mass landed by number of traps set:

$$\mathrm{CPUE} = \frac{\text{Lobsters (kg)}}{\text{Number of traps}} \tag{4.1}$$

CPUE data were sorted into monthly as well as seasonal catches. The average CPUE was calculated for each month in which bank cormorant chicks hatched as well as for each breeding season.

Data analysis

Breeding success was determined using a combination of parametric survival models and the Mayfield method (Mayfield, 1961). Because laying, hatching and fledging can rarely be seen the laying date was estimated as the mid-point between the date the bird was last seen without eggs and the first date the bird was seen incubating. For the hatching date, the mid-point was taken between the last date the bird was seen on eggs and the first date hatchlings were seen. To estimate the fledging date, the mid-date was taken between the last date large chicks were seen on a nest and the first date such chicks were absent.

A binary code to record failure (1) or survival (0) and the exposure time (nest days) at each nest were the two response variables used to calculating breeding success, by making use of the survreg function in the survival library in R v. 3.0.1 (R Core Team 2013).

For failure, the following equation was used:

$$\mathrm{F} = \exp(-\alpha - \beta x) \tag{4.2}$$

Where α and β indicate the parameters including the intercept and coefficients. The nest survival equation is:

$$S(t) = \exp(-\exp(-\alpha - \beta x)t) \tag{4.3}$$

where α and β again indicate the intercept and coefficients, x the value of the explanatory variable (equal to 1 for factorial variables), and t time. The average number of days eggs are incubated before hatching is 30 (Cooper, 1987), and the average fledging period in bank cormorants is 55–70 days (Crawford & Cooper, 2005). Upper and lower 95% confidence intervals were calculated as follows: $\exp[-t(F - 1.96\, F/\sqrt{n})]$ and $\exp[-t(F + 1.96\, F/\sqrt{n})]$ respectively, where F indicates the failure probability and n the number of failures that occurred during incubating or brooding.

For the model calculating survival of chicks during the chick-rearing period, CPUE of rock lobster was used as an explanatory variable. The CPUE of the month in which each clutch hatched, the CPUE for the relevant breeding season were both tested separately. Generalized linear mixed models with binomial distribution, using the glmer function within the lme4 library in R v. 3.0.1, were used to test the effect of rock lobster CPUE during the breeding season, as well as within the month of hatching on the birds fledging 1 or more than 1 chicks (only 1 nest fledged 3 chicks in all years of the study). CPUE, year and colony were used as predictors of number of chicks fledged. To control for pseudo replication at the level of the explanatory variable in some months, month was used as random factor in the model. Akaike's Information Criterion adjusted for small samples sizes (AICc) was used to select the best model fit for all tests (Burnham & Anderson, 2002) and to select the mixed model with the preferred fixed structure (Zuur *et al.,* 2009).

Results

For the survival analysis, a total of 508 nests was observed and monitored over the period of eight years (Table 4.2). Data for Robben Island and Mercury Island for the years before 2012 and 2013 were included in the study.

The incubation period survival probabilities for Stony Point for 2012 and 2013 were 0.82 and 0.90, respectively. For Jutten Island, the survival probabilities during incubation for

2012 and 2013 were 0.86 and 0.81, and for Robben Island 0.89 and 0.90, respectively. For brooding, the survival probabilities were lower, with 0.64 and 0.68 for Stony Point, 0.82 and 0.73 for Jutten Island, and 0.78 and 0.79 for Robben Island for 2012 and 2013, respectively.

There were no significant differences for Stony Point between 2012 and 2013 in survival of nests during incubation (coefficient estimate: 0.64; z = 0.84; P = 0.40), or between Stony Point (2012) and Jutten Island (2012: coefficient estimate: 0.30; z = 0.34; P = 0.73; 2013: coefficient estimate: –0.04; z = –0.05; P = 0.95) or Robben Island (2012: coefficient estimate: 0. 54; z = 0.81; P = 0.42; 2013: coefficient estimate: 0.63; z = –0.01; P = 0.99) (Fig. 4.4).

For the chick survival analysis, the model with only year as an explanatory variable best fitted the data (Table 4.3). For all the colonies combined, there were significant differences between 2008 and 2005 (coefficient estimate: –1.39; z = –2.20; P = 0.03); 2009 (coefficient estimate: –2.20; z = –3.11; P = 0.002) and 2013 (coefficient estimate: –1.37; z = –2.19; P = 0.03). To investigate the differences between colonies and years, the model with ColonyYear as a combined covariate was fitted. There were no significant differences between Stony Point for 2012 and 2013 (coefficient estimate: 0.15; z = 0.27; P = 0.78) or between Stony Point (2012) and Jutten Island (2012: coefficient estimate: 0.79; z = 0.99; P = 0.32; 2013: coefficient estimate: 0.36; z = 0.52; P = 0.61) or Robben Island (2012: coefficient estimate: 0.55; z = 1.03; P = 0.30; 2013: coefficient estimate: 0.60; z = 1.16; P = 0.25) (Fig. 4.4).

The CPUE of lobsters during the breeding season (March–September) for the years 2007 to 2013 are indicated in Figure 4.5 for three localities. High fluctuations are visible at Stony Point, with a clear decline from a CPUE of 10.03 in 2011 to 6.21 in 2013. CPUE at Jutten Island also declined from 5.55 in 2011 to 3.06 in 2013. The CPUE at Robben Island experienced a 34% increase from 6.47 in 2009 to 8.67 in 2013.

The CPUE of lobsters within the relevant breeding season (coefficient estimate: 0.05; z = 0.74; P = 0.46), or within the relevant month of hatching (coefficient estimate:–0.02; z = –0.3; P = 0.76) were not significantly related to the breeding success at any of the colonies from 2007–2013. According to the AICc selection criteria, the best model contained only the intercept, with the next best model having a ΔAICc = 2.0.

The rock lobster CPUE had a positive significant relationship with the proportion of nests fledging more than one chick from successful nests for the relevant breeding season ($z = 2.13$; $df = 152$; $P = 0.03$), as well as with the CPUE within the relevant month of hatching ($z = 2.73$; $df = 152$; $P < 0.001$). The best model included CPUE during month of hatching (Table 4.3).

Discussion

No significant differences in breeding success (survival of the nest contents) were found between Jutten Island, Robben Island and Stony Point for either incubation or brooding. Stony Point, however, had a lower, though not significant, survival probability during chick rearing than the other two colonies. This result is counter to the hypothesis that due to known low food availability on the West Coast, lower reproductive success was expected at Jutten Island.

Nest location is an important factor contributing to breeding success (Stokes & Boersma, 1998). Both Jutten Island's and Robben Island's bank cormorant colonies are on the eastern side of the island, not exposed to direct wave action. The Stony Point colony is in direct contact with wind and waves being situated in a south eastern orientation relative to the coastline, which may have an impact on the breeding success of bank cormorants. On more than one occasion, bank cormorant chicks in their late rearing stage were seen to have disappeared from their nests after the occurrence of high storms at Stony Point. This was especially the case where there were two large chicks on the nests, after which one or both were not present after the storm (pers. obs.). During large swells caused by storms, some nests at the Stony Point colony often got completely submerged by water. Nest survival was affected by storms during this study period at Jutten Island, Robben Island and Stony Point (Meyer, 2014).

Although in severe weather conditions adult seabirds are often directly influenced by strong winds and storms (Wolfaart *et al.,* 2012), most negative effects occur in the form of chick and egg mortality (Hennicke & Flachsbarth, 2009). Chicks often die as a result of hypothermia if too large to be sheltered by adults, or if directly blown or flushed off nests by heavy rains and storms (Wolfaart *et al.,* 2012). Storms may also indirectly influence seabird offspring by their effect on prey distribution as well as foraging difficulty. Adult seabirds may be unable to leave the colony if feeding conditions are unfeasible (Finnley *et al.,* 1999;

Hennicke & Flachsbarth, 2009). Chicks are often then affected by the lack of energy from sufficient food provisioning, affecting thermoregulatory processes.

Food availability during the breeding season as well as during the month of hatching had a significant effect on the number of chicks fledged per successful nest in this study. Fledging success in relation to initial clutch size is an important proxy to assess food stress on a breeding seabird (Oro *et al.,* 1995). Some seabird species show clear impacts of food shortage through unsuccessful offspring fledging, while others are able to maintain sufficient provisioning so that breeding success is not negatively influenced (Piatt *et al.,* 2007). With high prey abundance, adults can often maintain higher chick provisioning, resulting in chicks being less vulnerable to starvation (Davis *et al.,* 2005). This study shows a strong relationship between number of chicks fledged per successful nest and rock lobster availability during the month of hatching, which may suggest that food availability in the early chick rearing stages is crucial for chick survival.

The parametric survival models used in this study were not sensitive to changes in food availability. The survival models did not account for partial failures, therefore do not distinguish between adults raising one or two chicks to fledging. As we could not reliably determine how many eggs were present within a nest, the survival models were not sensitive to brood size and percentage of chicks fledged relative to the initial clutch size. By using logistic regression we could, however, consider partial failure by considering nests that fledged more than one bank cormorant chick as successful, and one chick as a partial failure of the brood. Information on juvenile birds in the post-fledging stage will provide an informative index into the influence of prey availability on the entire life cycle of a long-lived seabird (Oro *et al.,* 2004). If chicks fledged successfully by altering their own growth processes (Barrett & Rikardsen, 1992), the effect of food availability may directly influence them as juveniles if they are not fit enough to survive in an exploited environment. Though adult survival appears less likely to be directly influenced by food shortages, some species may be negatively influenced by drastic resource decreases (Oro & Furness, 2002). In southern Africa, Cape gannets *Morus capensis* have been able to maintain high adult survival rates at colonies on the west coast, despite declines in the availability of their main prey (Distiller *et al*., 2012). In contrast, adult survival of African penguins, which exploit the same resources, has declined markedly after the turn of the century (Crawford *et al*., 2011a).

It is apparent that bank cormorant breeding success may often be affected by weather, after which if a nest is successful, food availability's influence becomes important to determine if a bird can successfully raise more than one chick. Bank cormorants' most common clutch size is two eggs (Cooper, 1987), but clutches of three, the maximum size known for the species, are also possible. When energy requirements increase with chick size (Bertram *et al.,* 1996), higher provisioning frequency is needed (Chapter 3), and thus greater energy expenditure by parents.

Within-nest competition between broods of more than one chick may be the reason for chick losses caused by low food availability. Brood conflicts between two or more chicks within a nest do not affect adult provisioning rates (Anderson & Ricklefs, 1992). The dominant, most likely older of the two chicks generally receives more food, resulting in a size and strength difference within a brood. When food is scarce, the weaker chick would most likely suffer mortality. High regional density of resources surrounding particularly Robben Island and Stony Point (Chapter 2), should also contribute to higher post-fledging survival and in turn higher recruitment within the local population (Davis *et al.,* 2005). This is most likely the cause of the growth in the Stony Point bank cormorant colony over the last 20 years (Crawford *et al.,* 2008).

It would be highly informative if chick condition parameters of bank cormorants at these colonies could be examined, for this would provide further insights into their response to food availability. It will however be difficult to obtain data which requires direct contact with chicks, as bank cormorants are easily disturbed (Crawford & Cooper 2005) and may abandon nests in response to human interference. With a greater breeding success dataset for especially Jutten Island and Stony Point, a larger time series might provide better correlations of the relationship between prey availability and reproductive output in bank cormorants. A study combining the exact foraging behaviour of bank cormorants by means of GPS loggers during the breeding season, as well as diet data in the form of prey items delivered to offspring in areas with different food availability would provide important information regarding the response of the bank cormorant to exploited food resources.

Table 4.1 Nest observations were carried out between the dates shown below at Jutten Island, Robben Island and Stony Point for the 2012 and 2013 bank cormorant breeding seasons.

Year	Colony	Start	End
2012	Jutten Island	23 May 2012	12 September 2012
	Robben Island	11 April 2012	2 September 2012
	Stony Point	09 May 2012	9 September 2012
2013	Jutten Island	15 April 2013	26 August 2013
	Robben Island	25 March 2013	5 September 2013
	Stony Spoint	04 April 2013	23 August 2013

Table 4.2 The number of nests used to compare bank cormorant breeding success, for different years of study at Mercury Island, Jutten Island, Robben Island and Stony Point.

Year	Island	Number of nests
2005	Mercury Island	95
2007	Robben Island	35
2008	Mercury Island	46
	Robben Island	34
2009	Robben Island	44
2010	Mercury Island	83
2011	Robben Island	13
2012	Jutten Island	16
	Robben Island	38
	Stony Point	24
2013	Jutten Island	16
	Robben Island	41
	Stony Point	23
Total		**508**

Table 4.3 Results from generalized linear mixed models with binomial distribution relating number of bank cormorant chicks fledged per successful nest to West Coast rock lobster CPUE during the relevant month of hatching, for three colonies (Jutten Island, Robben Island and Stony Point) along the West Coast of South Africa. Explanatory variables are categorized by rock lobster catch per unit effort (CPUE) during month of hatching, CPUE during the entire breeding season, Colony (Jutten Island, Robben Island and Stony Point) and Year (2007–2013).

Model	**Predictors**	**K**	**AICc value**	**ΔAICc**	**AICc weight**
2	CPUE_month_hatching	3	184.4	0	0.8
1	CPUE_breeding_season	3	187.7	3.3	0.2
3	CPUE_month_hatching + Colony + Year	10	188.6	4.2	0.1
4	CPUE_breeding_season + Colony + Year	10	192.5	8.1	0.01

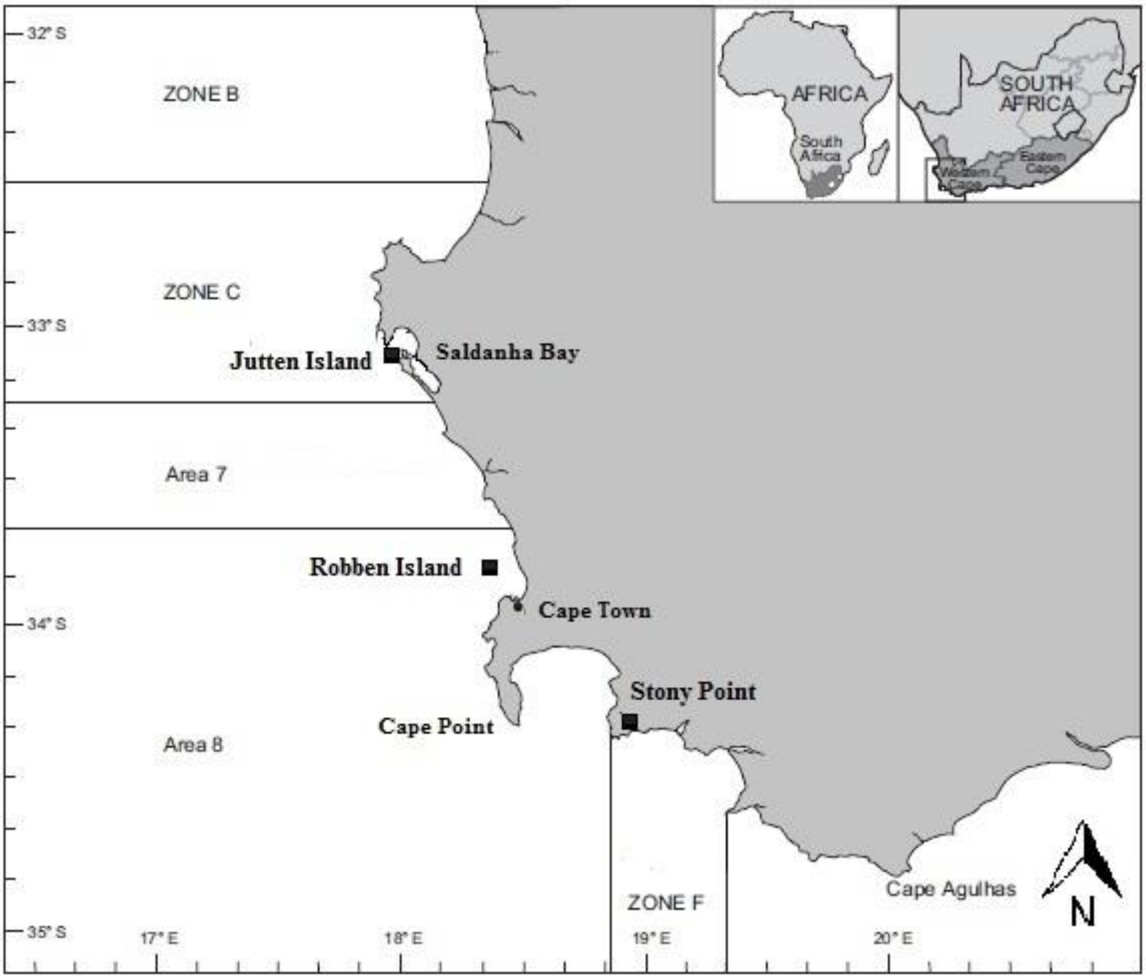

Figure 4.1 The three bank cormorant colonies (Jutten Island, Robben Island and Stony Point) in the Western Cape of South Africa used in this study to test the effect of West Coast rock lobster CPUE on the breeding success of these birds. Map by Crawford *et al.* (2008).

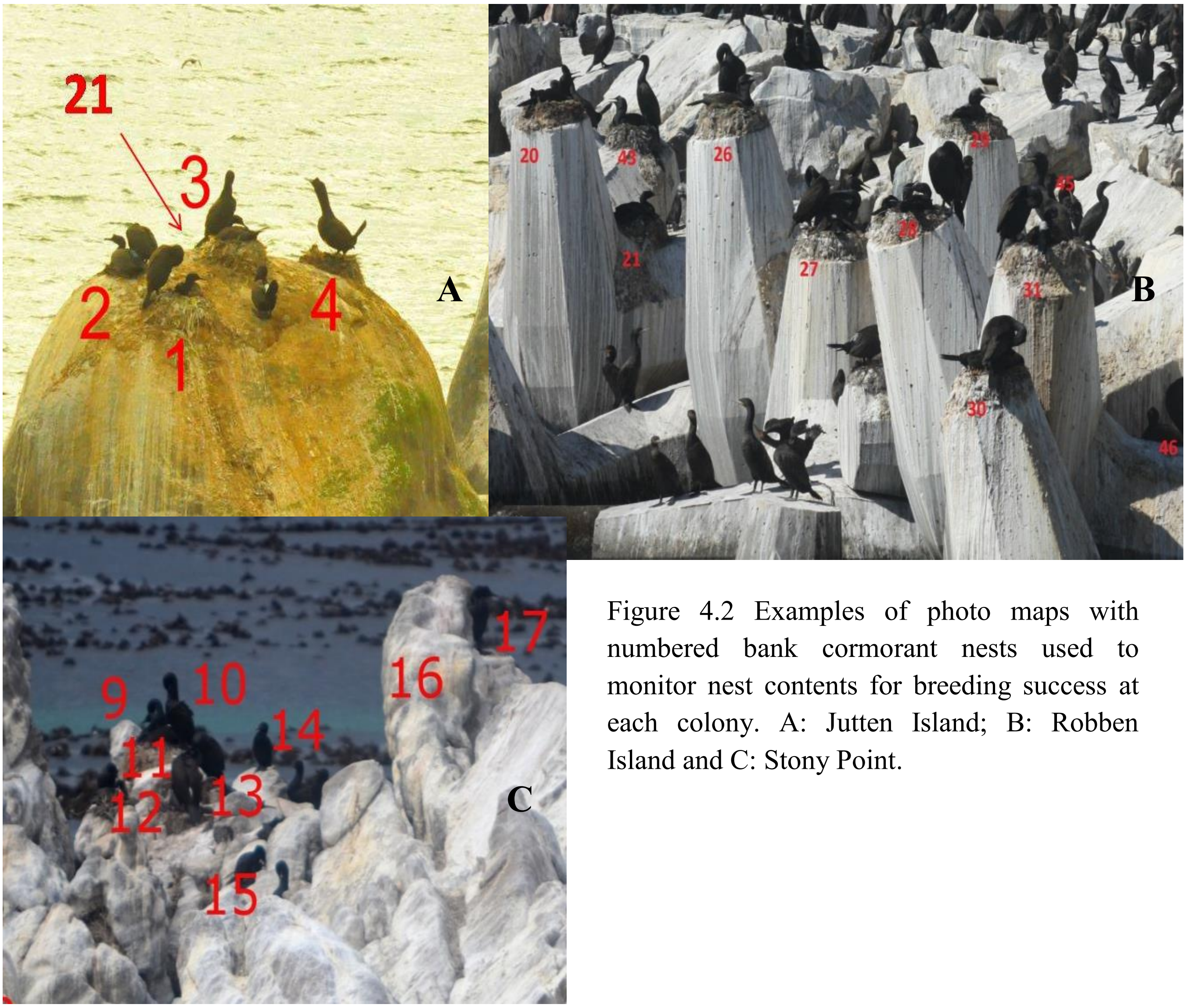

Figure 4.2 Examples of photo maps with numbered bank cormorant nests used to monitor nest contents for breeding success at each colony. A: Jutten Island; B: Robben Island and C: Stony Point.

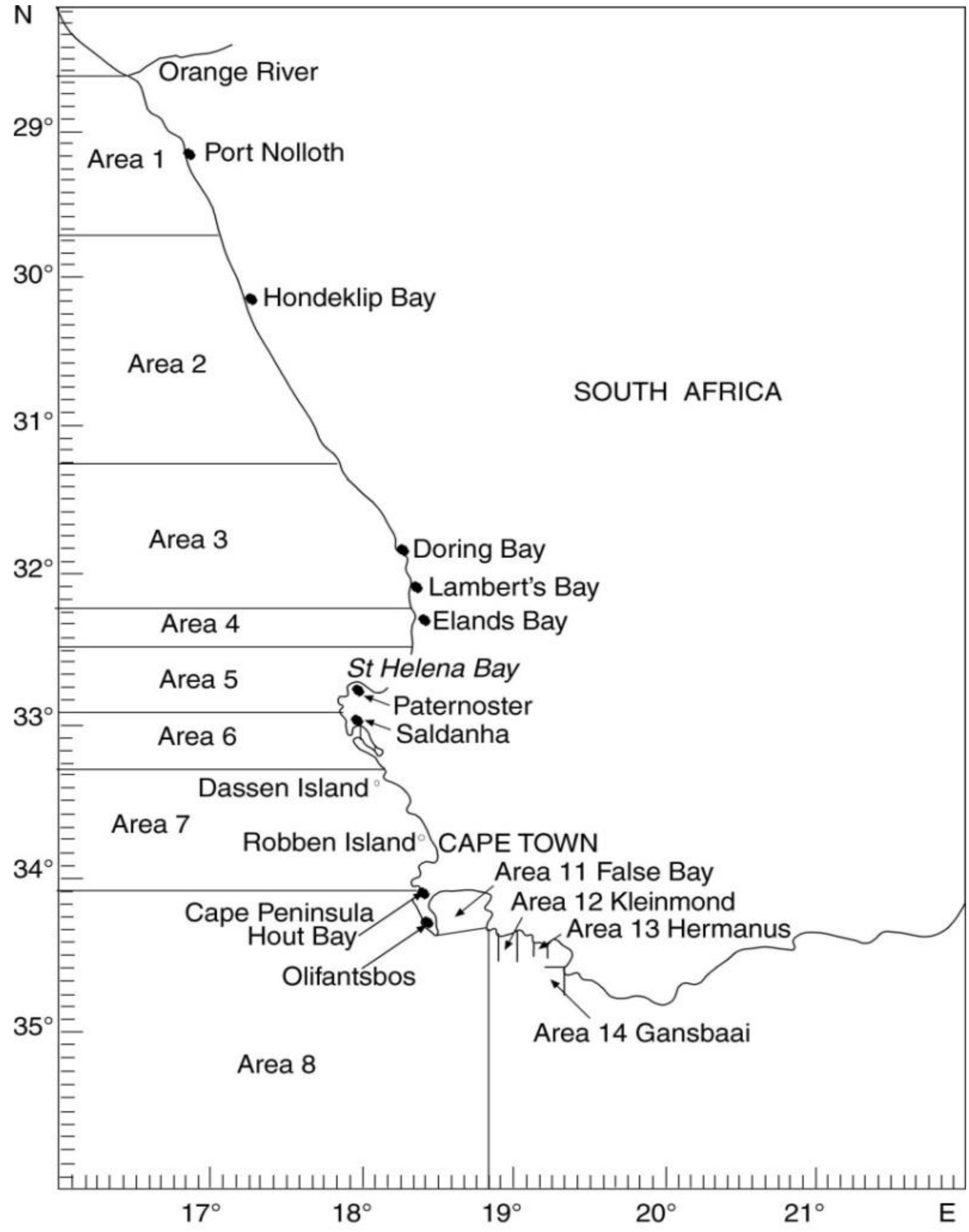

Figure 4.3 The commercial West Coast rock lobster fishing zones defined by Department of Forestry and Fisheries in the west and southwest coast of South Africa. Map from DAFF.

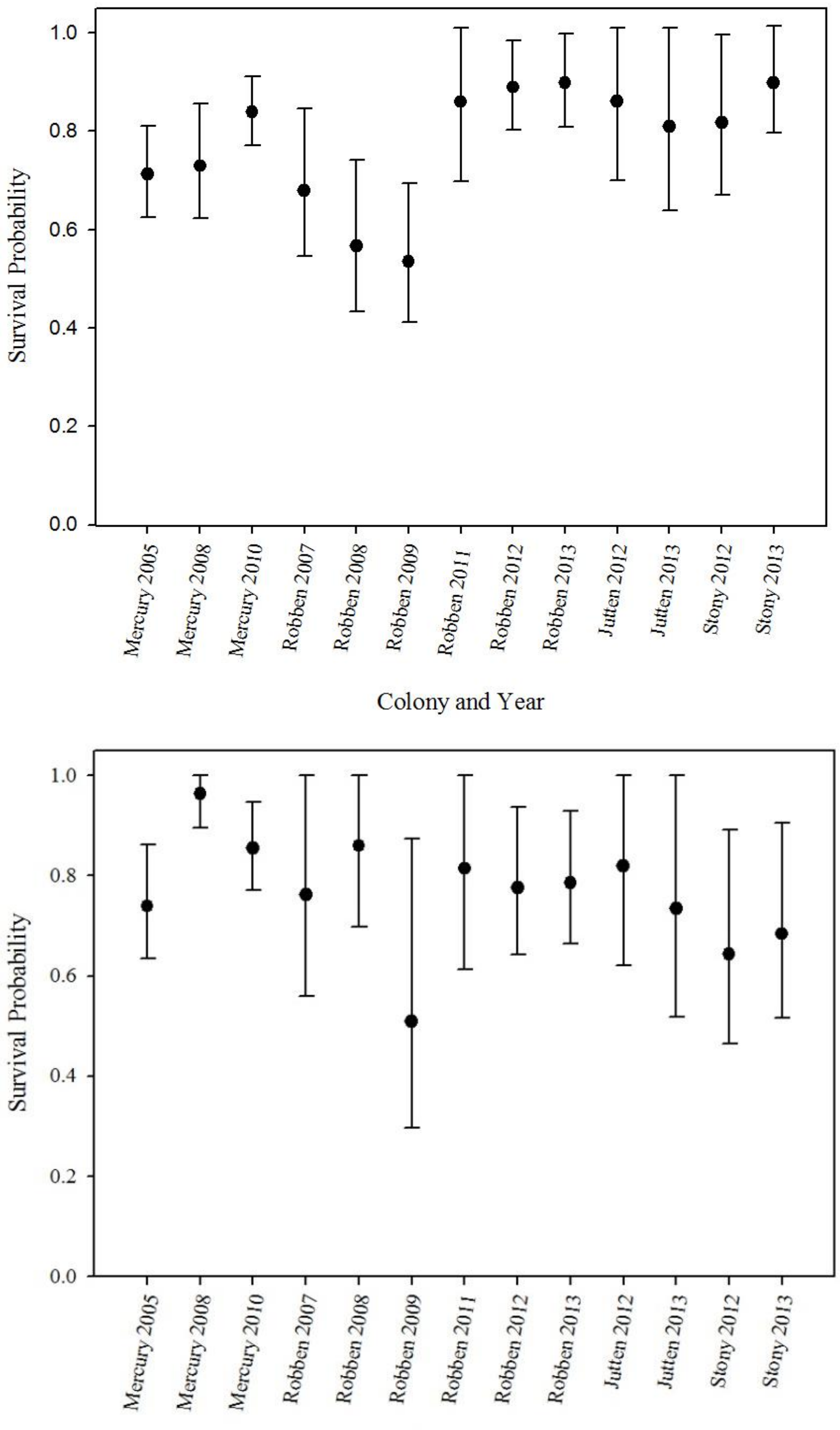

Figure 4.4 Incubating (top) and chick rearing (bottom) survival probabilities for different bank cormorant colonies and years. Mercury Island (2005, 2009, 2010); Robben Island (2007–2009, 2011–2013); Jutten Island (2012, 2013) and Stony Point (2012, 2013). Bars represent 95% confidence intervals.

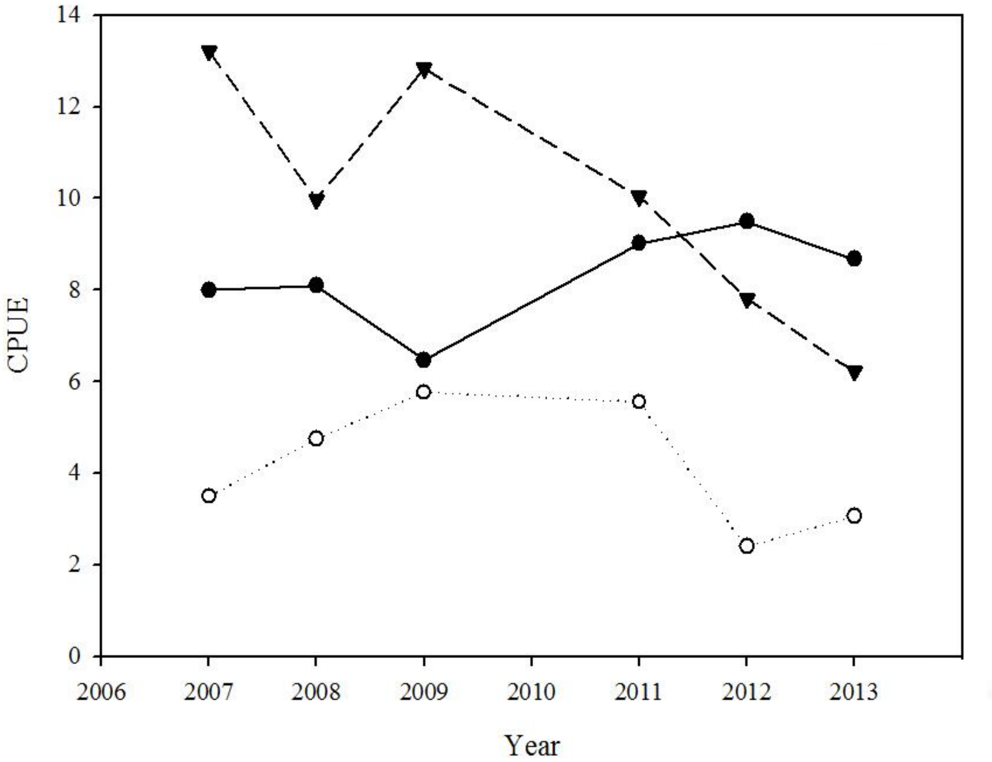

Figure 4.5 The change in CPUE (kg) of West Coast rock lobster near Jutten Island (open circles), Robben Island (closed circles) and Stony Point (black triangles) during the bank cormorant breeding seasons of 2007–2013.

CHAPTER 5

Key findings and conclusion

Bank cormorants are significantly affected by food availability, both directly and indirectly. The abundance of rock lobster around the bank cormorant colonies in the Western Cape of South Africa is driving the population dynamics of these birds to a large extent (Chapter 2). Annual bird counts were overall significantly related to prey availability indexed by the proportion of traps containing lobsters within 5, 10, 20 and 30 km of Jutten Island, Dassen Island and Stony Point. Because the bank cormorant's foraging range during breeding is seldom greater than 10 km (Cooper, 1985), one would expect the strongest response to prey to be within 10 km distance from colonies. However, the greatest response was found to rock lobster within 20 to 30 km radius surrounding colonies.

Several factors may contribute to this phenomenon, including the life-history traits of palinurid lobsters, as well as the nature of the FIMS survey. Bank cormorants would primarily feed on smaller, juvenile lobsters which are found inshore in shallower waters, whereas larger lobsters that occur further offshore are mostly recorded by the FIMS survey. The lobsters caught in a 30 km distance from shore, therefore provide a key insight in the availability of bank cormorant prey found inshore. Fitness before onset of breeding (Robinson *et al.*, 2005) is also an important aspect affecting the population dynamics of seabirds. Food availability outside of the breeding season, when the bank cormorants' foraging range is much greater than 10 km (Cooper, 1985), may be the reason for the increased response to prey at greater distances from colonies.

The greatest response of population numbers to rock lobster availability was shown by birds at Dassen Island. This was not surprising because the study period coincided with the time frame during which rock lobster abundance around this breeding colony decreased most strongly (Blamey *et al.,* 2012). At the colonies immediately to the north, in Saldana Bay, the bank cormorant colony size had already responded to the decrease in rock lobster abundance prior to the study period. At Stony Point, to the south of Dassen Island, the increase in rock lobster abundance had already occurred prior to the study period, and the bank cormorants were responding to the already high levels of rock lobster availability in this area (Blamey et al. 2012). These findings show an expected response to the distributional shift West Coast rock lobster experienced along South Africa's West Coast (Blamey *et al.,* 2012).

Bank cormorants' foraging effort also showed responses to the shift in prey availability between the different colonies (Chapter 3). At Jutten Island, which is situated in an area where rock lobster availability is low (Crawford *et al.,* 2008; Chapter 2), foraging trip duration was significantly higher than at Robben Island and Stony Point, which are near Cape Point where rock lobster abundance is high. Birds at Jutten Island need to work harder to find food, and therefore spent more time at sea per day, with lower a frequency of trips. Birds at Stony Point are not as constrained by food availability, and spent significantly shorter time at sea per day.

At Jutten Island, foraging trips were significantly shorter in 2013 than in 2012, though still significantly longer than at the other two colonies. Marine ecosystems generally undergo inter-annual fluctuations causing differences in resource availability even on a small temporal scale (Montevecchi, 2007). Feeding conditions may have been better in 2013, or bank cormorants at Jutten Island may have resorted to prey of different quality, causing shorter and more trips per day.

Bank cormorant breeding success showed interesting responses to food availability (Chapter 4). The probability of nest survival was not significantly influenced by rock lobster CPUE during the breeding season or month of hatching at Jutten Island, Robben Island or Stony Point. However, limited sample sizes at especially Jutten Island and Stony Point, where only two years of data were available, may have played a role in the low level of sensitivity of the survival models. Survival models tested the probability of a nest to fledge at least one chick. The bank cormorant's modal brood size is two chicks (Cooper, 1987), and broods of three chicks have also been observed. Rock lobster CPUE influenced the number of chicks fledged per successful nest, i.e. if more than one chick fledged, it was considered as a 100% fledging rate, whereas if only one chick fledged, a nest was considered to have failed partially.

It is apparent that food availability does not influence bank cormorants while incubating as much as it does successful brood fledging rates. With increasing brood size, energy demands place increasing pressure on adult birds (Bertram *et al.,* 1996), and therefore if food availability is unpredictable, it may cause within-brood conflicts (Anderson & Ricklefs, 1992), where the dominant chick would survive whereas the second chick would suffer mortality. Storms and weather can largely influence survival probability of a nest

(Meyer, 2014), after which food availability becomes a factor in the successful fledging of number of chicks in relation to initial clutch size.

Future recommendations for research and conservation

In order to build on the baseline information we have on the bank cormorant, crucial aspects of this endangered species are yet to be studied. Firstly, a greater data set on the breeding success and time budget data is needed for Jutten Island, Robben Island and Stony Point in order to build a stronger time-series in relation to prey availability.

Insights on the diet of the species could be used to further examine the prey items bank cormorants consume in relation to their environment. We have no detailed information on the foraging ecology of bank cormorants in South Africa, which need to be obtained through GPS loggers to acquire diving depth and foraging range. Additionally, diet samples as well as data during the non-breeding seasons would provide more information. Management practices to conserve the species would be made feasible by a leading set of indicators including a time series of breeding success, foraging behaviour and population numbers.

Some management goals include attempting to solve the problem of breeding site availability in areas like Robben Island and Stony Point, where food is not a limiting factor, but rather breeding space (Sherley *et al.,* 2012; Chapter 2). Also, with knowledge of the significant response of bank cormorant population dynamics to surrounding prey, rock lobster fishing closures would be a feasible option to limit the effect of commercial exploitation of prey of these seabirds. The colony at Robben Island, which has been situated in a rock lobster reserve since the 1960s (Pollock, 1987), supports the largest bank cormorant colony in South Africa and has been stable since the 1980s (Crawford *et al.,* 2008), indicating that the surrounding fishing reserve may play a role in the success of that colony. A rock lobster reserve surrounding Dassen Island may be a feasible action to control the current declining rate of the bank cormorant colony on the island. However, if rock lobsters continue to decline in the area around Dassen Island, the effectiveness of a reserve might be limited by the distributional shift of bank cormorant prey.

The bank cormorant colony at Stony Point was initiated soon after the establishment of the African penguin *Spheniscus demersus* colony in the area. The presence of penguins resulted in a reduction of human disturbance at Stony Point, due to the construction of a fence to control predation and interference to the area in 1987 (Whittington *et al.,* 1996). This enabled other seabird species including bank cormorants to start breeding there. The bank cormorant colony on Dyer Island to the east of Stony Point, is in a declining state due to high levels of Cape fur seal *Arctocephalus pusillus* predation in the area. Seals have significantly influenced the breeding productivity of Cape cormorants *Phalacrocorax capensis* on Dyer Island (Voorbergen *et al.,* 2012) and are likely to have the same influence on bank cormorants breeding on the island. The bank cormorant colony is therefore unlikely to grow at the current rate of predation by seals. Breeding to the east of Stony Point, may thus be constrained by high levels of human disturbance as well as predation. Consideration could therefore be given to the construction of breeding platforms or sheltered bays providing protected areas for bank cormorants to establish breeding east of Stony Point.

References

Anderson, D. J. and Ricklefs, R. E. 1992. Brood size and food provisioning in masked and blue-footed boobies (*Sula* spp.). *Ecology,* 73: 1363–1374.

Annala, J. H. and Bycroft, B. L. 1993. Movements of rock lobsters *Jasus edwardsii* tagged in Fiordland, New Zealand. *New Zealand Journal of Marine and Freshwater Research,* 27: 183–190.

Baduini, C. L., and Hyrenbach, K. D. 2003. Biogeography of procellariiform foraging strategies: does ocean productivity influence provisioning. *Marine Ornithology*, 31: 101–112.

Baird, P. H. 1990. Influence of abiotic factors and prey distribution on diet and reproductive success of three seabird species in Alaska. *Ornis Scandinavica,* 21:224–235.

Ballard, G., Dugger, K. M., Nur, N., and Ainley, D. G. 2010. Foraging strategies of Adélie penguins: adjusting body condition to cope with environmental variability. *Marine Ecology Progress Series,* 405: 287–302.

Barkai, A., and Branch, G. M. 1988. Contrasts between the benthic communities of subtidal hard substrata at Marcus and Malgas islands: a case of alternative stable states? *South African Journal of Marine Science*, 7: 117–137.

Barrett, R. T. and Rikardsen, F. 1992. Chick growth, fledging periods and adult mass loss of Atlantic puffins *Fratercula arctica* during years of prolonged food stress. *Colonial Waterbirds,* 15: 24–32.

Bayazit, M and Önöz, B. 2007. To prewhiten or not to prewhiten in trend analysis? *Hydrological Sciences,* 52: 611–624.

Bertram, D. F., Welham, C. V. J. and Ydenberg, R. C. 1996. Flexible effort in breeding seabirds: adjustment of provisioning according to nestling age and mass. *Canadian Journal of Zoology,* 74: 1876–1881.

Bertrand, S., Joo, R., Smet, C. A., Tremblay, Y., Barbraud, C. and Weimerskirch, H. 2012. Local depletion by a fishery can affect seabird foraging. *Journal of Applied Ecology,* 49: 1168–1177.

Birt, V. L., Birt, T. P., Goulet, D., Cairns, D. K., and Montevecchi, W. A. 1987. Ashmole's halo: direct evidence for prey depletion by a seabird. *Marine Ecology Progress Series,* 40: 205–208.

Blamey, L. K. and Branch, G. M. 2012. Regime shift of a kelp-forest benthic community induced by an 'invasion' of the rock lobster *Jasus lalandii*. *Journal of Experimental Marine Ecology*, 420: 33–47.

Blamey, L. K., Howard, J. A., Agenbag, J., and Jarre, A. 2012. Regime-shifts in the southern Benguela shelf and inshore region. *Progress in Oceanography*, 106: 80–95.

Blamey, L. K., Plagányi, E. E. and Branch, G. M. 2013. Modelling a regime shift in a kelp forest ecosystem caused by a lobster range expansion. *Bulletin of Marine Science,* 89: 347–375.

Brander, K. 2010. Impacts of climate change on fisheries. *Journal of Marine Systems*, 79: 389–402.

Brooke, M. 2004. The food consumption of the world's seabirds. *Proceedings of the Royal Society of London, Series B: Biological Sciences,* 271: 246–248.

Bryant, R., Jones, I. L., and Hipfner, J. M. 1999. Responses to changes in prey availability by common murres and thick-billed murres at the Gannet Islands, Labrador. *Canadian Journal of Zoology,* 77: 1278–1287.

Burger, A. E. and Piatt, J. F. 1990. Flexible time budgets in breeding common murres: buffers against variable prey abundance. *Studies in Avian Biology,* 14: 71–83.

Burke, C. M. and Montevecchi, W. A. 2009. The foraging decisions of a central place foraging seabird in response to fluctuations in local prey conditions. *Journal of Zoology,* 278: 354–361.

Burnham, K. P., and Anderson, D. R. 2002. *Model Selection and Multimodel Inference: a Practical Information-Theoretic Approach, 2nd edition*. Springer-Verlag, New York.

Bustnes, J. O., Anker-Nilssen, T., Erikstad, K. E., Lorentsen, S. H., and Systad, G. H. 2013. Changes in the Norwegian breeding population of European shag correlate with forage fish and climate. *Marine Ecology Progress Series,* 489: 235–244.

Butchart, S. H. M., Stattersfield, A. J., Bennun, L. A., Shutes, S. M. and Akçakaya, H. R. 2004. Measuring global trends in the status of biodiversity: Red List Indices for birds. *PLOS Biology,* 2: 2294–2304.

Cairns, D. K. 1988. Seabirds as indicators of marine food supplies. *Biological Oceanography,* 5: 261–271.

Chastell, O., Wirmerskirch, H. and Jouventin, P. 1995. Body condition and seabird reproductive performance: a study of three petrel species. *Ecology*, 76: 2240–2246.

Chaurand, T., and Weimerskirch, H. 1994. Incubation routine, body mass regulation and egg neglect in the blue petrel *Halobaena caerulea*. *Ibis*, 136: 285–290.

Chivers, L. S., Lundy, M. G., Colhoun, K., Newton, S. F., Houghton, J. D. R. and Reid, N. 2012. Foraging trip time-activity budgets and reproductive success in the black-legged kittiwake. *Marine Ecology Progress Series,* 456: 269–277.

Cockroft, A. C. and Payne, A. I. L. 1999. A cautious fisheries management policy in South Africa: the fisheries of rock lobster. *Marine Policy*, 23: 587–600.

Cockroft, A. C., van Zyl, D. and Hutchings, L. 2008. Large-scale changes in the spatial distribution of South African West Coast rock lobsters: an overview. *African Journal of Marine Science,* 30: 149–159.

Cook, T. R., Cherel, Y., and Tremblay, Y. 2006. Foraging tactics of chick-rearing Crozet shags: individuals display repetitive activity and diving patterns over time. *Polar Biology*, 29: 562–569.

Cooper, J. 1981. Biology of the Bank cormorant, Part 1: Distribution, population size, movements and conservation. *Ostrich,* 52: 208–215.

Cooper, J. 1985. Biology of the bank cormorant, part 3: Foraging Behaviour. *Ostrich,* 56: 86–95.

Cooper, J. 1987. Biology of the Bank cormorant, part 5: clutch size, eggs and incubation. *Ostrich,* 58: 1–8.

Cooper, J. 1988. Marine cormorants breeding on the mainland at Stony Point, southern Cape, South Africa. *Cormorant*, 16:55.

Costa, D. P. and Gales, N. J. 2003. Energetics of a benthic diver: Seasonal foraging ecology of the Australian Sea Lion, *Neophoca cinerea. Ecological Monographs,* 73: 27–43.

Crawford, R. J. M. and Cooper, J. 2005. Bank cormorant *Phalacrocorax neglectus*. In: Hockey, P. A. R., Dean, W. R. J., and Ryan, P. G., editors, *Roberts – Birds of Southern Africa*, pages 577–578. Trustees of the John Voelcker Bird Book Fund, Cape Town.

Crawford, R. J. M. 2007. Trends in numbers of three cormorants *Phalacrocorax* spp. breeding in South Africa's Western Cape province. In: Kirkman, S. P., editor, *Final Report of BCLME (Benguela Current Large Marine Ecosystem) Project on Top Predators as Biological Indicators of Ecosystem Change in the BCLME,* pages 173–178. Avian Demography Unit, Cape Town.

Crawford, R. J. M., Cockroft, A. C., Dyer, B. M. and Upfold, L. 2008. Divergent trends in bank cormorants *Phalacrocorax neglectus* breeding in South Africa's Western Cape consistent with a distributional shift of rock lobsters *Jasus lalandii. African Journal of Marine Science,* 30: 161–166.

Crawford, R. J. M., Dyer, B. M., Cordes, I. and Williams, A. J. 1999. Seasonal pattern of breeding, populaion trend and conservation status of bank cormorants *Phalacrocorax neglectus* off south western Africa. *Biological Conservation,* 87: 49–58.

Crawford, R. J. M., Altwegg, R., Barham, B. J., and Barham, P. J. 2011a. Collapse of South Africa's penguins in the early 21st century. *African Journal of Marine Sciences*, 33: 139–156.

Crawford, R. J. M., Dyer, B. M., Kotze, P. G. H., Meÿer, M. A., Upfold, L. and Makhado, A. B. 2011b. Status of seabirds breeding in South Africa. Unpubl. report. Branch Oceans & Coasts. Department of Environmental Affairs, Cape Town.

Crawford, R. J. M., Dyer, B. M., Upfold, L. and Word, Y. L. 2001. Age at first breeding of bank cormorants, *Phalacrocorax neglectus,* and Cape cormorants, *P.capensis. Ostrich,* 72: 145–148.

Crawford, R. J., Barham, P. J., Underhill, L. G., Shannon, L. J., Coetzee, J. C., Dyer, B. M. and Upfold, L. 2006. The influence of food availability on breeding success of African penguins *Spheniscus demersus* at Robben Island, South Africa. *Biological Conservation*, 132: 119–125.

Croxall, J. P., Butchart, S. H. M., Lascelles, B., Stattersfield, A. J., Sullivan, B., Symes, A. and Taylor, P. 2012. Seabird conservation status, threats and priority actions: a global assessment. *Bird Conservation International,* 22: 1–34.

Cury, P, and Shannon, L. 2004. Regime shifts in upwelling ecosystems: observed changes and possible mechanisms in the northern and southern Benguela. *Progress in Oceanography,* 60: 223–243.

Cury, P.M, Boyd, I.L., Bonhommeau, S., Anker-Nilssen, T., Crawford, R.J.M., Furness, R.W., Mills, J.A., Murphy, E.J., Österblom, H., Paleczny, M., Piatt, J.F., Roux, J., Shannon, L., Sydeman, W.J. 2011. Global seabird response to forage fish depletion-one-third for the birds. *Science,* 334: 1703–1706.

David, J. H. M., Cury, P., Crawford, R. J. M., Randall, R. M., Underhill, L. G. and Meÿer, M. A. 2003. Assessing conservation priorities in the Benguela ecosystem, South Africa: analysing predation by seals on threatened seabirds. *Biological Conservation,* 114: 289–292.

Davis, S. E., Nager, R. G. and Furness, R. W. 2005. Food availability affects adult survival as well as breeding success of parasitic jaegers. *Ecology,* 86: 1047–1056.

Davoren, G. K. and Montevecchi, W. A. 2003. Consequences of foraging trip duration on provisioning behaviour and fledging condition of common murres *Uria aalge*. *Journal of Avian Biology*, 34: 44–53.

Dayton, P. K., Thrush, S. F., Agardy, M. T. and Hofman, R. J. 1995. Environmental effects of marine fishing. *Aquatic Conservation Marine and Freshwater Ecosystems,* 5: 205–232.

Derraik, J. G. 2002. The pollution of the marine environment by plastic debris: a review. *Marine Pollution Bulletin*, 44: 842–852.

Distiller, G., Altwegg, R., Crawford, R. J., Klages, N. T., and Barham, B. 2012. Factors affecting adult survival and inter-colony movement at the three South African colonies of Cape gannet. *Marine Ecology Progress Series*, 461: 245–255.

du Toit, M., Boere, G. C., Cooper, J., de Villiers, M. S., Kemper, J., Lenten, B., Petersen, S. L., Simmons, R. E., Underhill, L. G., Whittington, P. A., and Byers, O. P. 2003. *Conservation Assessment and Management Plan for Southern African Coastal Seabirds*, Avian Demography Unit, New York and Conservation Breeding Specialist Group, Apple Valley.

Durant, J. M., Hjermann, D. O., Ottersen, G., and Stenseth, N. C. 2007. Climate and the match or mismatch between predator requirements and resource availability. *Climate Research*, 33: 271–283.

Eddy, T. D., Pitcher, T. J., MacDiarmid, A. B., Byfield, T. T., Tam, J. C., Jones, T. T., and Gardner, J. 2014. Lobsters as keystone: only in unfished ecosystems? *Ecological Modelling*, 275: 48–72.

Erikstad, K. E., Asheim, M., Fauchald, P., Dahlhaug, L., Tveraa, T., and Dahlhaug, P. 1997. Adjustment of parental effort in the puffin; the roles of adult body condition and chick size. *Behavioral Ecology and Sociobiology,* 40: 95–100.

Finnley, S. K., Wanless, S. and Harris, M. P. 1999. The effect of weather conditions on the feeding behaviour of a diving bird, the common guillemot *Uria aalge*. *Journal of Avian Biology,* 30: 23–30.

Furness, R. W. and Camphuysen, C. J. 1997. Seabirds as monitors of the marine environment. *ICES Journal of Marine Science,* 54: 726–737.

Gasalla, M. A. 2011. Do all answers lie within (the community?) Fishing rights and marine conservation. In: Chuengpagdee, R., editor, *World Small-Scale Fisheries Contemporary visions,* pages 185–203. Eburon Academic Publishers, Delft.

Gaston, A. J. and Hipfner, J. M. 2006. Adult Brunninch's Guillemots *Uria lomvia* balance body condition and investment in chick growth. *Ibis*, 148: 106–113.

Gell, F. R., and Roberts, C. M. 2003. Benefits beyond boundaries: the fishery effects of marine reserves. *Trends in Ecology and Evolution*, 18: 448–455.

George, R. W. 2005. Evolution of life cycles, including migration in spiny lobsters (Palinuridae). *New Zealand Journal of Marine and Freshwater Research,* 39: 503–514.

Gray, J. S. 1997. Marine biodiversity: patterns, threats and conservation needs. *Biodiversity and Conservation,* 6: 153–175.

Grémillet, D. and Charmantier, A. 2010. Shifts in phenotypic plasticity constrain the value of seabirds as ecological indicators of marine ecosystems. *Ecological Applications*, 20: 1498–1503.

Grémillet, D., Pichegru, L., Kuntz, G., Woakes, A. G., Wilkinson, S., Crawford, R. J., and Ryan, P. G. 2008. A junk-food hypothesis for gannets feeding on fishery waste. *Proceedings of the Royal Society B: Biological Sciences*, 275: 1149–1156.

Groeneveld, J. C. and Branch, G. M. 2002. Long-distance migration of South African deep-water rock lobster *Palinurus gilchristi. Marine Ecology Progress Series,* 232: 225–238.

Gundlach, E. R., and Hayes, M. O. 1978. Vulnerability of coastal environments to oil spill impacts. *Marine Technology Society Journal,* 12: 18–27.

Hamer, K. C., Phillips, R. A., Hill, J. K., Wanless, S. and Wood, A. G. 2001. Contrasting foraging strategies of gannets *Morus bassanus* at two North Atlantic colonies:

foraging trip duration and foraging area fidelity. *Marine Ecology Progress Series,* 224: 283–290.

Hamer, K. C., Schreiber, E. A. and Burger, J. 2002. Breeding biology, life histories, and life history-environment interactions in seabirds. In: Schreiber, E. A. and Burger, J., editors, *Biology of Marine Birds*, pages 217–305. CRC Press, Boca Raton.

Harding, A. M. A, Piatt, J. F., Schmutz, J. A., Schultz, M. T., Van Pelt, T. I., Kettle, A. B. and Speckman, S. G. 2007. Prey density and the behavioral flexibility of a marine predator: the common murre *Uria Aalge*. *Ecology,* 88: 2024–2033.

Harley, C. D., Randall Hughes, A., Hultgren, K. M., Miner, B. G., Sorte, C. J., Thornber, C. S., and Williams, S. L. 2006. The impacts of climate change in coastal marine systems. *Ecology Letters,* 9: 228–241.

Harley, S. J., Myers, R. A. and Dunn, A. 2001. Is catch-per-unit-effort proportional to abundance? *Canadian Journal of Fisheries and Aquatic Sciences,* 58: 1760–1772.

Hennicke, J. C. and Flachsbarth, K. 2009. Effects of cyclone Rosie on breeding red-tailed tropicbirds *Phaethon runricauda* on Christmas Island, Indian Ocean. *Marine Ornithology,* 37: 175–178.

Hilborn, R., Branch, T. A., Ernst, B., Magnusson, A., Minte-Vera, C. V., Scheuerell, M. D. and Valero, J. L. 2003. State of the world's fisheries. *Annual Reviews of Environmental Resou*rces, 28: 359–99.

Hull, C. L., Kaiser, G. W., Lougheed, C., Lougheed, L., Boyd, S., and Cooke, F. 2001. Intraspecific variation in commuting distance of marbled murrelets *Brachyramphus marmoratus*: ecological and energetic consequences of nesting further inland. *Auk*, 118: 1036–1046.

Irons, D. B. 1998. Foraging area fidelity of individual seabirds in relation to tidal cycles and flock feeding. *Ecology*, 79: 647–655.

IUCN, 2013. *The IUCN Red List of Threatened Species, Version 2013.2.* http://www.iucnredlist.org.

Jakubas, D., Trudnowska, E., Wojczulanis-Jakubas, K., Iliszko, L., Kidawa, D., Darecki, M., and Stempniewicz, L. 2013. Foraging closer to the colony leads to faster growth in little auks. *Marine Ecology Progress Series*, 489: 263–278.

Johnston, S. J., and Butterworth, D. S. 2005. Evolution of operational management procedures for the South AfricanWest Coast rock lobster *Jasus lalandii* fishery. *New Zealand Journal of Marine and Freshwater Research*, 39: 687–702.

Jones, H. P., Tershy, B. R., Zavaleta, E. S., Croll, D. A., Keitt, B. S., Finkelstein, M. E and Howald, G. R. 2007. Severity of the effects of invasive rats on seabirds: A global review. *Conservation Biology,* 22: 16–26.

Karpouzi, V. S., Watson, R. and Pauly, D. 2007. Modelling and mapping resource overlap between seabirds and fisheries on a global scale: a preliminary assessment. *Marine Ecology Progress Series,* 343: 87–99.

Kemper, J., Underhill, L. G., Crawford, R. J., and Kirkman, S. P. 2007. Revision of the conservation status of seabirds and seals breeding in the Benguela Ecosystem. In: Kirkman, S. P. *Final report of the BCLME (Benguela Current Large Marine Ecosystem) project on top predators as biological indicators of ecosystem change in the BCLME,* pages 697–704. Avian Demography Unit, Cape Town.

Lang, C. and Mann, K. H. 1976. Changes in sea urchin populations after the destruction of kelp beds. *Marine Biology*, 36: 321–326.

Lewis, S., Grémillet, D., Daunt, F., Ryan, P. G., Crawford, J. M. and Wanless, S. 2006. Using behavioural and state variables to identify proximate causes of population change in a seabird. *Oecologia,* 147: 606–614.

Lewison, R. , Oro, D., Godley, B. J., Underhill, L., Bearhop, S., Wilson, R. P., Ainley, D., Arcos, J. M., Boersma, P. D., Borboroglu, P. G., Boulinier, T., Frederiksen, M., Genovart, M., González-Solís, J., Green, J. A., Grémillet, D., Hamer, K. C, Hilton, G. M., Hyrenbach, K. D., Martínez-Abraín, A., Montevecchi, W. A., Phillips, R. A., Ryan, P. G., Sagar, P., Sydeman, W. J., Wanless, S., Watanuki, Y., Weimerskirch, H. and Yorio, P. 2012. Research priorities for seabirds: improving conservation and management in the 21st century. *Endangered Species Research,* 17: 93–121.

Ling, S. D., Johnson, C. R., Frusher, S. D. and Ridgmay, K. R. 2009. Overfishing reduces resilience of kelp beds to climate-driven catastrophic phase shift. *Proceedings of the National Academy of Sciences,* 106: 22341–22345.

Linn, I. J., Campbell, K. L. I. 1992. Interactions between white-breasted cormorants *Phalacrocorax carbo* (Aves: Phalacrocoracidae) and the fisheries of Lake Malawi. *Journal of Applied Ecology,* 29: 619–634.

Litzow, M. A. and Piatt, J. F. 2003. Variance in prey abundance influences time budgets of breeding seabirds: evidence from pigeon guillemots *Cepphus columba*. *Journal of Avian Biology,* 34: 54–64.

Ludynia, K., Jones, R., Kemper, J., Garthe, S. and Underhill, L. G. 2010a. Foraging behaviour of bank cormorants in Namibia: implications for conservation. *Endangered Species Research,* 12: 31–40.

Ludynia, K., Roux, J. P., Jones, R., Kemper, J., and Underhill, L. G. 2010b. Surviving off junk: low-energy prey dominates the diet of African penguins *Spheniscus demersus* at Mercury Island, Namibia, between 1996 and 2009. *African Journal of Marine Science*, 32: 563–572.

Makhado, A. B., Crawford, R. J. M. and Underhill, L. G. 2006. Impact of predation by Cape fur seals *Arctocephalus pusillus pusillus* on Cape gannets *Morus capensis* at Malgas Island, Western Cape, South Africa. *African Journal of Marine Science,* 28: 681–687.

Mayfield, H. 1961. Nesting success calculated from exposure. *Wilson Bulletin,* 73: 255–261.

McKoy, J. L. 1983. Movements of rock lobsters*, Jasus edwardsii* (Decapoda: Palinuridae), tagged near Stewart Island, New Zealand. *New Zealand Journal of Marine and Freshwater Research*, 17: 357–366.

Mecenero, S., Kirkman, S. P. and Roux, J. 2005. Seabirds in the diet of Cape fur seals *Arctocephalus pusillus pusillus* at three mainland breeding colonies in Namibia. *African Journal of Marine Science,* 27: 509–512.

Melville-Smith R. 2011. Factors potentially affecting the resilience of temperate marine populations. *Report prepared for the Australian Government Department of Sustainability, Environment, Water, Population and Communities on behalf of the State of the Environment 2011 Committee*. DSEWPaC, Canberra.

Meyer, C. 2014. MSc Thesis. University of Cape Town, South Africa.

Milot, E., Weimerskirch, H. and Bernatchez, L. 2008. The seabird paradox: dispersal, genetic structure and population dynamics in a highly mobile, but philopatric albatross species. *Molecular Ecology*, 17: 1658–1673.

Monaghan, P. 1996. Relevance of the behaviour of seabirds to the conservation of marine environments. *Oikos,* 77: 227–237.

Monaghan, P., Uttley, J. D., Burns, M. D., Thaine, C. and Blackwood, J. 1989. The relationship between food supply, reproductive effort and breeding success in Arctic terns *Sterna paradisaea. Journal of Animal Ecology,* 58: 261–274.

Monaghan, P., Walton, P., Wanless, S., Uttley, J. D., and Bljrns, M. D. 1994. Effects of prey abundance on the foraging behaviour, diving efficiency and time allocation of breeding guillemots *Uria aalge. Ibis*, 136: 214–222.

Montevecchi, W. A. 2002. Interactions between fisheries and seabirds. In: Schreiber, E.A. and Burger, J., editors, *Biology of Marine Birds*, pages 527–557. CRC Press, Boca Raton.

Montevecchi, W. A. 2007. Binary dietary responses of northern gannets *Sula bassana* indicate canging food web and oceanographic conditions. *Marine Ecology Progress Series,* 352: 213–220.

Nagy, K. A., Siegfried, W. R. and Wilson, R. P. 1984. Energy Utilization by free-ranging jackass penguins, *Sphenicus demersus*. *Ecology,* 65: 1648–1655.

Ojowski, U., Eidtmann, C., Furness, R., and Garthe, S. 2001. Diet and nest attendance of incubating and chick-rearing northern fulmars *Fulmarus glacialis* in Shetland. *Marine Biology*, 139: 1193–1200.

Okes, N. C., Hockey, P. A., Pichegru, L., Lingen, C. D., Crawford, R. J., and Grémillet, D. 2009. Competition for shifting resources in the southern Benguela upwelling: seabirds versus purse-seine fisheries. *Biological Conservation*, 142: 2361–2368.

Oro, D. and Furness, R. W. 2002. Influences of food availability and predation on survival of kittiwakes. *Ecology,* 83: 2516–2528.

Oro, D., Bosch, M., and Ruiz, X. 1995. Effects of a trawling moratorium on the breeding success of the yellow-legged gull *Larus cachinnans*. *Ibis*, 137: 547–549.

Oro, D., Cam, E., Pradel, R. and Martínez-Abraín, A. 2004. Influence of food availability on demography and local population dynamics in a long-lived seabird. *Proceedings of the Royal Society B. Biological Sciences,* 271: 387–396.

Oro, D., Pérez-Rodríguez, A., Martínez-Vilalta, A., Bertolero, A., Vidal, F. and Genovart, M. 2009. Interference competition in a threatened seabird community: A paradox for a successful conservation. *Biological Conservation,* 142: 1830–1835.

Pace, M. L., Cole, J. J., Carpenter, S. R. and Kirchell, J. F. 1999. Trophic cascades revealed in diverse ecosystems. *Trends in Ecology and Evolution*, 14: 483–488.

Paine, R. T. 1969. A note on trophic complexity and community stability. *American naturalist*, 103: 91–93.

Petersen, S. L., Honig, M., and Nel, D. C. 2008. The impact of longline fisheries on seabirds in the Benguela current large marine ecosystem. *Collective Volume of Scientific Papers,* 62: 1739–1756.

Piatt, J. F., Harding, A. M. A., Schultz, M., Speckman, S. G., van Pelt, T. I., Drew, G. S. and Kettle, A. B. 2007. Seabirds as indicators of marine food supplies: Cairns revisited. *Marine Ecology Progress Series,* 352: 221–234.

Pimm, S. L. and Raven, P. 2000. Extinction by numbers. *Nature,* 403: 843–845.

Pollock, D. E, Cockroft, A. C., Groeneveld, J. C and Schoeman, D. S. 2000. The commercial fisheries for *Jasus* and *Palinurus* species in the south-east Atlantic and south-west Indian Oceans. *Spiny Lobsters Fisheries and Culture,* 5: 105–120.

Pollock, D. E. 1987. Simulation models of rock-lobster populations from areas of widely divergent yields on the Cape west coast. *South African Journal of Marine Science*, 5: 531–545.

Pollock, D. E., Cockroft, A. C. and Goosen, P. C. 1997. A note on reduced rock lobster growth rates and related environmental anomalies in the southern Benguela, 1988–1995. *South African Journal of Marine Science,* 18: 287–293.

Ponchon, A., Grémillet, D, Christensen-Dalsgaard, S., Erikstad, K. E., Barrett, R. T., Reiertsen, T. K., McCoy, K. D., Tveraa, T. and Boulinier, T. 2014. When things go wrong: intra-season dynamics of breeding failure in a seabird. *Ecosphere,* 5: 1–19.

Pyke, G. H. 1984. Optimal foraging theory: a critical review. *Annual Reviews Ecological Systems*, 15: 523–75.

R Development Core Team 2009. *R: A Language and Environment for Statistical Computing.* R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0. http://www.R-project.org.

Rand, R. W. 1960. The biology of guano-producing seabirds 3. The distribution, abundance andfeeding habits of the cormorants Phalacrocoracidae off the south-western coast of the *Cape Province.Investigational Report*, *Division of Sea Fisheries South Africa*, 42: 1–32.

Robinson, S., Chiaradia, A., and Hindell, M. A. 2005. The effect of body condition on the timing and success of breeding in little penguins *Eudyptula minor*. *Ibis,* 147: 483–489.

Roux, J., van der Lingen, C. D., Gibbons, M. J., Moroff, N. E., Shannon, L. J, Smith, A. D. M. and Cury, P. M. 2013. Jellyfication of marine cosystems as a likely consequence of overfishing small pleagic fishes: Lessons from the Benguela. *Bulletin of Marine Science,* 89: 249–284.

Russ, G. R., Alcala, A. C., Maypa, A. P., Calumpong, H. P., and White, A. T. 2004. Marine reserve benefits local fisheries. *Ecological applications*, 14: 597–606.

Sæther, B., Andersen, R. and Pedersen, H. C. 1993. Regulation of parental effort in a long-lived seabird: an experimental manipulation of the cost of reproduction in the Antarctic petrel, *Thalassoica antarctica. Behavioural Ecology and Sociobiology,* 33: 147–150.

Sapoznikow, A. and Quintana, F. 2003. Foraging behavior and feeding locations of imperial cormorants and rock shags breeding sympatrically in Patagonia, Argentina. *Waterbirds: The International Journal of Waterbird Biology,* 26: 184–191.

Schreiber, E. A. and Burger, J. 2002. Seabirds in the marine environment. In: Schreiber, E.A. and Burger, J., editors, *Biology of Marine Birds*, pages 1–15. CRC Press, Boca Raton.

Schrimpf, M. B., Parrish, J. K., and Pearson, S. F. 2012. Trade-offs in prey quality and quantity revealed through the behavioural compensation of breeding seabirds. *Marine Ecology Progress Series*, 460: 247–259.

Shannon, L. J., Moloney, C. L., Jarre, A. and Field, J. G. 2003. Trophic flows in the southern Benguela during the 1980s and 1990s. *Journal of Marine Systems,* 39: 83–116.

Sherley, R. B., Ludynia, K., Underhill, L. G., Jones, R. and Kemper, J. 2012. Storms and heat limit the nest success of bank cormorants: implications of future climate change for a surface-nesting seabird in southern Africa. *Journal of Ornithology,* 153: 441–455.

Sherley, R. B., Underhill, L. G., Barham, B. J., Barham, P. J., Coetzee, J. C., Crawford, R. J., and Upfold, L. 2013. Influence of local and regional prey availability on breeding performance of African penguins *Spheniscus demersus*. *Marine Ecology Progress Series*, 473: 291–301.

Smout, S., Rindorf, A., Wanless, S., Daunt, F., Harris, M. P. and Matthiopoulos, J. 2013. Seabirds maintain offspring provisioning rate despite fluctuations in prey abundance: a multi-species functional response for guillemots in the North Sea. *Journal of Applied Ecology,* 50: 1071–1079.

Stokes, D. L. and Boersma, P. D. 1998. Nest-site characteristics and reproductive success in Magellanic penguins (*Spheniscus magellanicus*). *Auk,* 115: 34–49.

Takahashi, A., Dunn, M. J., Trathan, P. N., Sato, K., Naito, Y. and Croxall, J. P. 2003a. Foraging strategies of chinstrap penguins at Signy Island, Antarctica: importance of benthic feeding on Antarctic krill. *Marine Ecology Progress Series,* 250: 279–289.

Takahashi, A., Watanuki, Y., Sato, K., Kato, A., Arai, N., Nishikawa, J., and Naito, Y. 2003b. Parental foraging effort and offspring growth in Adélie penguins: does working hard improve reproductive success? *Functional Ecology,* 17: 590–597.

Tarr, R. J. Q., Williams, P. V. G. and Mackenzine, A. J. 1996. Abalone, sea urchins, and rock lobster: a possible ecological shift that may affect traditional fisheries. *South African Journal of Marine Science,* 17: 319–323.

Tasker, M. L. and Reid, J. B. 1997. Seabirds in the marine environment. *ICES Journal of Marine Science,* 54: 505–506.

Tasker, M. L., Camphuysen, C. J., Cooper, J., Garthe, S., Montevecchi, W. A., and Blaber, S. J. M. 2000. The impacts of fishing on marine birds. *ICES Journal of Marine Science,* 57: 531–547.

Thompson, P. M. and Ollason, J. C. 2001. Lagged effects of ocean climate change on fulmar population dynamics. *Nature,* 413: 417–420.

Thrush, S. F., Hewitt, J. E., Cummings, V. J., Dayton, P. K., Cryer, M., Turner, S. J., Funnel, G. A., Budd, R. G., Milburn, C. J. and Wilkinson, M. R. 1998. Disturbance of the marine benthic habitat by commercial fishing: Impacts at the scale of the fishery. *Ecological Applications,* 8: 866–879.

Uttley, J. D., Walton, P., Monaghan, P., and Austin, G. 1994. The effects of food abundance on breeding performance and adult time budgets of guillemots *Uria aalge*. *Ibis*, 136: 205–213.

van der Lingen, C. D., Shannon, L. J., Cury, P., Kreiner, A., Moloney, C. L., Roux, J. P., and Vaz-Velho, F. 2006. Resource and ecosystem variability, including regime shifts, in the Benguela Current System. *Large Marine Ecosystems*, 14: 147–184.

Veitch, J., Penven, P. and Shillington, F. 2009. The Benguela: a laboratory for comparative modelling studies. *Progress in Oceanography,* 83: 296–302.

Vincenzi, S., Hatch, S., Mangel, M., and Kitaysky, A. 2013. Food availability affects onset of reproduction in a long-lived seabird. *Proceedings of the Royal Society B: Biological Sciences*, 280: 1471–2954.

Visser, M. E., and Both, C. 2005. Shifts in phenology due to global climate change: the need for a yardstick. *Proceedings of the Royal Society B: Biological Sciences*, 272: 2561–2569.

Voorbergen, A., De Boer, W. F., and Underhill, L. G. 2012. Natural and human-induced predation on Cape cormorants at Dyer Island. *Bird Conservation International*, 22: 82–93.

Votier, S. C., Hatchwell, B. L., Beckerman, A., McCleery, R. H., Hunter, F. M., Pellatt, J., Trinder, M. and Birkhead, T. R. 2008. Oil pollution and climate have wide-scale impacts on seabird demographics. *Ecology Letters,* 8: 1157–1164.

Watermeyer, K. E., Shannon, L. J., Roux, J. P., and Griffiths, C. L. 2008. Changes in the trophic structure of the northern Benguela before and after the onset of industrial fishing. *African Journal of Marine Science*, 30: 383–403.

Weimerskirch, H. 2007. Are seabirds foraging for unpredictable resources? *Deep-Sea Research,* 54: 211–223.

Weimerskirch, H., Ancel, A., Caloin, M., Zahariev, A., Spagiari, J., Kersten, M., and Chastel, O. 2003. Foraging efficiency and adjustment of energy expenditure in a pelagic seabird provisioning its chick. *Journal of Animal Ecology,* 72: 500–508.

Weimerskirch, H., Zimmermann, L and Prince, P. A. 2001. Influence of environmental variability on breeding effort in a long-lived seabird, the yellow-nosed albatross *Behavioural Ecology,* 12: 22–30.

Whittington, P. A., Hofmeyr, J. H., and Cooper, J. 1996. Establishment, growth and conservation of a mainland colony of Jackass Penguins *Spheniscus demersus* at Stony Point, Betty's Bay, South Africa. *Ostrich*, 67: 144–150.

Whittow, G. C. 2002. Seabird reproductive physiology and energetics. In: Schreiber, E.A. and Burger, J., editors, *Biology of Marine Birds*, pages 409–437. CRC Press, Boca Raton.

Williams, G. C. 1966. Natural selection, the cost of reproduction and a refinement of Lack's principle. *Journal of American Naturalist,* 100: 687–690.

Wolfaardt, A. C., Williams, A. J., Underhill, L. G., Crawford, R. J. M. and Whittington, P. A. 2009. Review of the rescue, rehabilitation and restoration of oiled seabirds in South Africa, especially African penguins *Spheniscus demersus* and Cape gannets *Morus capensis*, 1983–2005. *African Journal of Marine Science*, 31: 31–54.

Wolfaardt, A. C., Coerfts, S. and Maylis, A. M. M. 2012. Effects of a storm on colonies of seabirds breeding at the Falkland Islands. *Marine Ornithology,* 40: 129–133.

Worm , B., Barbier, E., B., Beaumont, N., Duffy, J. E., Folke, C., Halpern, B. S., Jackson, J. B. C., Lotze, H. K., Micheli, F., Palumbi, S. R., Sala, E., Selkoe, K. A., Starchowicz, J, J, and Watson, R. 2006. Impacts of biodiversity loss on ocean ecosystem services. *Science,* 314: 787–790.

Yue, S. and Wang, C. Y. 2002. Applicability of prewhitening to eliminate the influence of serial correlation on the Mann-Kendall test. *Water Resources Research,* 38: 4–6.

Zador, S. G. and Piatt, J. F. 1999. Time-budgets of common murres at a declining and increasing colony in Alaska. *Condor,* 101: 149–152.

Zador, S., Hunt, G. L., TenBrink, T., and Aydin, K. 2013. Combined seabird indices show lagged relationships between environmental conditions and breeding activity. *Marine Ecology Progress Series*, 485: 245–258.

Zuur, A. F., Ieno, E. N., Walker, N. J., Saveliev, A. A. and Smith, G. M. 2009. Mixed Effect Models and Extensions in Ecology with R. Springer, New York.

Žydelis, R., Small, C. and French, G. 2013. The incidental catch of seabirds in gillnet fisheries: A global review. *Biological Conservation,* 162: 76–88.