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**Tracking African penguins (*Spheniscus demersus*) outside
of the breeding season: Regional effects and fishing
pressure during the pre-moult period**



by

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Submitted in partial fulfilment for the degree of
Master of Science in Conservation Biology

February 11th, 2013

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Table of Contents

Plagiarism Declaration	ii
Abstract	iii
Acknowledgements	iv
Chapter 1: Population declines of the African penguin (<i>Spheniscus demersus</i>) in relation to historical exploitation, fishing pressure, and a lack of understanding regarding foraging ranges outside of the breeding season	- 1 -
Global trends in seabird populations	- 1 -
Penguin biology	- 2 -
Population status of the African penguin: pattern of decline, and threats	- 7 -
Management of fisheries in a South African context	- 11 -
Current understanding of spatial habitat use of the African penguin	- 12 -
Aims and objectives	- 13 -
Chapter 2: Pre-moult foraging of the African penguin: Areas of importance, regional differences, and fishing pressure	- 15 -
Introduction	- 15 -
Methods	- 17 -
Results	- 24 -
Discussion	- 33 -
Chapter 3: Synthesis and Evidence for a disturbance hypothesis	- 40 -
Conclusions and implications for conservation of the African penguin	- 40 -
Study limitations	- 41 -
Anecdotal evidence for a disturbance hypothesis	- 42 -
Future research	- 47 -
Synthesis	- 49 -
References	- 51 -
Appendices	- 61 -

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Abstract

African penguins (*Spheniscus demersus*) have experienced a 60% population decline in the past 30 years due to an eastward shift in the relative abundance of their main food source, anchovy (*Engraulis encrasicolus*) and sardine (*Sardinops sagax*). This shift may be exacerbated by pressure from the small-pelagic fishery targeting these species. A lack of knowledge regarding foraging areas when not breeding has been identified as a deficiency in management planning for African penguins. Satellite transmitters were deployed on 20 adults during the pre-moult foraging period from colonies on the west coast (Dassen Island, n=10) and south coast (Bird Island, Algoa Bay, n=10) of South Africa. Kernel density analyses were produced using nightly locations to create foraging range maps, which were compared to catches made by the small-pelagic fishery during September-December 2012. Birds from the two colonies differed in their foraging strategies. Compared to penguins from Bird Island, those from Dassen Island spent more than six times the number of nights beyond the foraging range used during the breeding season (40 km from their colony). Birds from Dassen Island typically made long, looping trips more than 300 km away from the colony, and travelled further and at higher daily rates to foraging areas than individuals from Bird Island, feeding outside areas where fishing activity was highest. Kernel density analysis showed the foraging range of Dassen Island penguins was between Cape Columbine and the central Agulhas Bank. Individuals from Bird Island continued to central place forage, typically staying within 35 km of the colony. Penguins from Dassen Island that remained on the west coast had to compete with higher levels of fishing pressure than penguins from Bird Island. More than 70% of the fleet-wide, 2012 purse-seine catch occurred within the area where Dassen Island penguins spent 50% of their time. These colony-specific characteristics suggest that management plans for African penguins need to be regionally targeted and incorporate larger foraging ranges during the pre-moult period for birds from western colonies. The larger foraging ranges and effort demonstrated by birds from the west coast suggest that a combination of the low relative fish abundance and higher commercial fishing pressure may force pre-moulting birds to seek food sources farther from the colony, putting them at higher risk of not surviving the annual moult. This project requires more years of data to ensure these foraging patterns are representative, and to more accurately provide management suggestions directed to alleviate stress on African penguins for long-term protection of this endangered seabird.

Acknowledgements

I would like to thank the Percy FitzPatrick Institute, BirdLife South Africa, and the Charl van der Merwe Trust for funding this research and giving me the opportunity to take on this project. I want to express my gratitude to my supervisors for their support throughout this project; Ross Wanless for his unwavering enthusiasm and allowing me make my own mistakes, your approach has let me grow as a scientist, Peter Ryan for his guidance and knowledge in the world of seabirds, Christina Moseley for her dedication to this project (be it her holidays or weekends), and Lorien Pichegru for help with field techniques and her vast knowledge of African penguins.

I would like to extend a special thank you to Marlene van Onselen, for going above and beyond the call of duty, and to the SANParks staff and Addo Elephant Park rangers on Bird Island who aided in device retrieval and monitoring. I am grateful to CapeNature and SANParks for transport and ensuring we had a place to stay during device deployments and retrievals on Dassen Island and Bird Island respectively.

I would like to thank the staff of the Two Oceans Aquarium, especially Ana-Alicia Marais, Hayley McLellan, Michael Farquhar, Claire Taylor, and Maresia Haasbrook for their assistance with post moulting trial deployments. I would also like to thank those who provided information critical to this project; Janet Coetzee, and Carl van der Lingen of the Department of Agriculture, Forestry, and Fisheries for data on fish abundance and small-pelagic fisheries catch, and Rob Crawford of the Department of Environmental Affairs for current data on population trends.

Katherine Forsythe gave up precious office time to aid with field work on Dassen Island, and for this I am grateful. I'm glad I had someone to help find and follow the trail of feathers and to search for (very expensive!) needles in a haystack. Special thanks go out to the 2012/13 CB class for their friendship, late-night discussions, and for being a bouncing board for ideas. The skill set contained within the lab is like a book of knowledge waiting to be tapped into. My family has always been there to challenge me and has instilled within me the aspirations to reach for the stars. I thank you for this, as without your guidance and support, this adventure would have never been possible. I would also like to thank Laura, I hope that one day I will be able to show you how much I appreciate all of the things you have done for me over this past year. You are a rock to lean on when I need support and your contribution to this thesis goes far beyond the words on the pages.

Chapter 1: Population declines of the African penguin (*Spheniscus demersus*) in relation to historical exploitation, fishing pressure, and a lack of understanding regarding foraging ranges outside of the breeding season

Global trends in seabird populations

Many seabird populations are declining, with 42% of the 346 extant seabird species listed as Near Threatened (NT), Vulnerable (VU), Endangered (EN), or Critically Endangered (CR); (Croxall et al. 2012). Over 60 species of seabird are undergoing rapid population declines, 40 have small populations or ranges, and more than 70 have either; small and declining populations, or ranges. Croxall et al. (2012) reported that 50% of listed species are being affected either directly or indirectly by the fishing industry (i.e. from by-catch, overfishing, or inadequate spatial management of fisheries). Direct impacts can be as severe as death to albatrosses, petrels, penguins and other seabirds due to interactions with fishing gear (e.g. BirdLife International 2004; Wagner & Boersma 2011). Indirect effects also stress marine systems through altering the trophic landscape (Myers & Worm 2003; Coll et al. 2008). An increase in fishing effort world-wide has been driven by a growing demand for coastal pelagic fish and their products (i.e. fish oil, Naylor et al. 2009), leading to increased potential for direct interactions and indirect effects described above.

A lack of spatial management of fisheries is one issue that indirectly affects seabirds by potentially altering the availability of their prey. Cury et al. (2011) suggested that the management of fisheries will continue to be controversial until the explicit relationships between what fisheries remove from specific locations, and how this affects seabird foraging and food availability are better understood. Bertrand et al. (2012) demonstrated that estimates of national fish abundance are not precise enough to set fishing legislation that will properly safeguard food availability for seabirds, due to issues of temporal variability and local abundance of fish. The idea of “one third for the birds” in low trophic level fisheries was suggested as a necessary threshold below which seabird breeding success declines rapidly (Cury et al. 2011). This value represents one third of the maximum observed long-term biomass of the species for which the fishing industry and seabirds compete (Cury et al. 2011). Bertrand et al. (2012) discussed the importance of the spatial understanding of movements of the Peruvian booby (*Sula variegata*) in relation to fisheries. Daily foraging tracks demonstrated that these birds avoided areas that are fished for a few days. Once schooling fish are removed locally, birds may move farther from the colony as foraging

efficiency decreases in areas where fishing has taken place (Bertrand et al. 2012). The decrease in foraging could result from either a decrease in fish abundance, or changes in fish behaviour such as school dynamics or altered depth of fish.

Most seabirds are K-selected species, with high adult survival, low fecundity, and delayed onset of reproduction, choosing survival over reproduction (Furness 2003). If local food abundance is low over a prolonged period, seabird species are likely to have compromised long-term breeding success, thereby increasing potential for negative population trajectories (Cury et al. 2011). Due to adult seabirds' longevity and preservation of self over current reproduction, there is expected to be a lag of about five years between the cause of the decline and the measurable population decline (Furness 2003).

The most globally threatened seabirds are Sphenisciformes and Procellariiformes, with over 50% of the species in each of these orders listed as threatened on the IUCN Red List (Croxall et al. 2012). Ten of 17 penguin species are threatened, and another four species are NT (IUCN 2012). Penguins have been described as “marine sentinels”; they are spread over the southern oceans and respond to changes in the environmental variables of the ocean and on land, as well as anthropogenic changes that occur due to pollution, land development, and over-fishing (Boersma 2008).

Penguin biology

1.1 General biology

Penguins are flightless, colonial seabirds of the southern hemisphere, using the marine environment to forage, and land or frozen pack-ice to breed and raise young (Müller-Schwarze 1984). Breeding and moulting are typically annual cycles, with variability between species (Payne 1972, Stonehouse 1975, Müller-Schwarze 1984). Larger foraging ranges are used outside the breeding season, when not feeding offspring at nesting sites (Table 1).

1.2 Foraging patterns of penguins

Fishing actions have altered the spatial use of marine environments by some seabirds (Bertrand et al. 2012). This relationship is not very well understood from an annual-temporal perspective. Most studies are conducted on breeding adults, during the breeding season, when they are constrained to visit their nests regularly (e.g. Hull et al. 1997; Culik et al. 1998; Stokes et al. 1998;; Boersma et al. 2007; Pichegru et al. 2009). As a result, foraging patterns of penguins are well established during breeding seasons, and less information is available for

penguins when not breeding (Table 1). Foraging studies investigate both diving parameters (i.e. depth, number of dives, length of dive, speed) and surface movements during foraging trips to better understand foraging strategies. Some studies apply these parameters to species conservation issues that include oil spills (Boersma 2012), fishing overlaps (Pichegru et al. 2009; Bertrand et al. 2012), and competition with other species (Lynnes et al. 2002).

The imbalance in literature available for the breeding and non-breeding seasons stems from the fact that during the breeding season penguins are known to return to their nests to swap with partners (incubation), and to provide food for chicks (chick rearing). This increases the probability of device retrieval, an important issue to consider if data must be retrieved from the device or to re-use devices for future deployments, as the cost of devices is a significant portion of research budgets. Within existing research on non-breeding penguins, sample sizes are very small (Table 1), and some studies occur because devices have not been retrieved after breeding season monitoring, continuing to transmit information during the pre-moulting migration. Understanding the entire season of spatial foraging areas will be imperative to help protect African penguins (*Spheniscus demersus*) in the future, and to appropriately provide information to help with marine management programs.

Table 1 demonstrates that foraging ranges used by penguins are generally larger outside of the breeding season, and during the breeding season there can be differences between studies, years, or even between colonies. Humboldt penguins (*Spheniscus humboldti*) at land based colonies forage within 95 km of the coast during the breeding season, spending most of their time within 35 km of their colony (Culik & Luna-Jorquera 1997; Culik 2001; Boersma et al. 2007). At a nearby island colony, Culik et al. (1998) established that the same species spent most of their time within 20 km of the colony and over 75% of location data was from within 5 km of the colony, indicating a much tighter affinity to their colony at this location. Humboldt penguins at two colonies in the same upwelling system, at the same life-history stage used the waters around their colonies differently. These results could possibly be due to differences in local food availability, local environmental conditions, or different levels of competition. Similar patterns have also been demonstrated in Magellanic penguins in Argentina at different colonies (Boersma 2007).

Penguins from lower latitudes tend to have smaller foraging ranges within the breeding period, with variation among breeding stages (Table 1). The lack of information collected on pre- and post-moulting penguins is an important research void that must be filled to develop a better understanding of the annual spatial use of the southern oceans by penguins. Only for the most abundant *Spheniscus* species, the Magellanic penguin

(*Spheniscus magellanicus*), has spatially explicit research investigating foraging movements when not breeding been conducted (Table 1). Considering that all four species in this genus are currently undergoing population declines (IUCN 2012), spatial patterns must be collected, mapped, and analyzed to better understand these declines.

1.3 The African penguin: An endangered seabird of southern Africa

The African penguin is endemic to southern Africa and can be found breeding from Hollamsbird Island (Namibia) in the north, to Bird Island (Algoa Bay, South Africa) in the southeast (Shelton et al. 1984). The breeding localities in South Africa are in two distinct regions, separated by >800 km (as the penguin swims). There are eight island colonies and two mainland colonies between Saldanha Bay and Dyer Island in the Western Cape, and two colonies on island groups in Algoa Bay near Port Elizabeth in the Eastern Cape (Crawford et al. 2011).

The African penguin averages 55-65 cm in height, weighs 2.9-3.5 kg, and has a flipper length of 15-18 cm (Hockey et al. 2005). Males are typically larger than females in body size (Hockey et al. 2005) and bill measurements (Cooper 1977), but both show the same feather colouration. African penguins breed in a range of nest types including; excavated sand or guano burrows, under boulders and shrubs, on the surface, and in manmade structures (e.g. buildings, shipwrecks, and artificial burrows) (Shelton et al. 1984; Wolfaardt et al. 2008, personal observations). Breeding pairs usually lay two eggs (Hockey et al. 2005), each hatching about 38 days after the laying date (Randall 1989). Chicks fledge between 64 and 105 days for two chick broods, whereas single chick broods fledge at the lower end of this range (Cooper 1980). Annual diet is composed mainly of anchovy (*Engraulis encrasicolus*) and sardine (*Sardinops sagax*) (Crawford et al. 2011).

1.3.1 Annual cycle of African penguins, with a focus on the moulting period

The breeding season of African penguins usually runs from February-September and January-July at colonies to the west (Crawford et al. 1995b) and east of Cape Agulhas (Randall & Randall 1981) respectively. Outside of the breeding season, African penguins go through the pre-moult, moult, and post-moult phases. This moulting period typically occurs between September and January (Wolfaardt et al. 2009).

Moulting is defined as the periodic replacement of feathers, with new feathers pushing out the old and worn feathers (Payne 1972). The moulting phase for African penguins is a crucial time for the survival of the adult population, and includes the pre-moult,

moult, and post-moult periods. The pre-moult period spans *ca* 35 days (Hockey et al. 2005) during which penguins gain 30% extra body weight compared to their breeding mass (Cooper 1976). This weight gain prepares African penguins for the annual moult (Randall & Randall 1981; Crawford et al. 2006b), during which they must fast while they shed their old feathers and re-grow an entirely new set (Cooper 1976). During the moulting fast, penguins do not enter the water to fish due to lack of waterproofing (Payne 1972), and can lose >40% of their body weight (Cooper 1976). If they fail to accumulate sufficient energy and nutrient reserves during the pre-moult, they will not survive the fasting period of *ca* 21 days (Randall & Randall 1981). Too much atrophy of the breast muscles can occur and they cannot swim fast enough to catch food once they have their new set of feathers (Cooper 1976). Feather shedding takes 12.7 (\pm 1.4) days (Hockey et al. 2005), during which they will renew the insulating ability and waterproofing of old feathers that have become worn over the year (Payne 1972). After completing their moult, African penguins must regain their body mass to prepare for the breeding season. Moulting is necessary as feathers are not capable of regeneration/repair when damaged throughout the year, they must be fully shed and new feathers must take their place (Cooper 1976). If moulting is delayed, additional energy may need to be used for maintenance costs due to poor insulation of old feathers (Crawford et al. 2011). In South Africa, the moult is roughly synchronous within each colony, but the timing of moult varies between colonies (Underhill & Crawford 1999; Crawford et al. 2006b). The moulting period at each colony may be different between years, and generally occurs when food is least available in proximity to colonies, following the breeding season (Crawford et al. 2006b).

1.3.2 Commitment to a breeding colony

African penguins seldom relocate to a different colony to breed once established (mostly returning to their natal colonies) and demonstrate very high levels of nest site fidelity, ranging from 89% in males to 79% in females (Randall 1983). They are monogamous, generally retaining the same mate in subsequent breeding attempt, with mate fidelity rates reported at over 80% (Randall 1983; Hockey et al. 2005). After the *Treasure* oil spill in 2000, which occurred on South Africa's west coast in Table Bay between Dassen Island and Robben Island, un-oiled birds that were relocated to Port Elizabeth returned to Dassen and Robben Island within 17 days, swimming a distance of over 800 km (Hockey et al. 2005).

Table 1: A summary of foraging ranges of various penguin species during the breeding and non-breeding seasons. Male (♂) and female (♀) are denoted where information was available, A and B show where different studies found different results for the same species. Information that is not available in current literature is denoted by NA.

Species Name	Breeding Range (km)	Sample Size	Location	Non-Breeding Range (km)	Sample Size	Location	Source
Macaroni penguin <i>Eudyptes chrysolophus</i>	<500, <300	A) 7 ♂ and 6 ♀ B) 95	A and B) South Georgia Islands	2000-3000	2	Marion Island	(Brown 1987; Barlow & Croxall 2002)
Southern rockhopper penguin <i>E. chrysocome</i>	A)<160 B)<10	A) 7 B) 119	A) Marion Island B) French Islands	NA	NA	NA	(Brown 1987; Tremblay & Cherel 2003)
Adelie penguin <i>Pygoscelis adeliae</i>	<165	19	South Orkney Island	>1500	2	Ross Island, Antarctica	(Davis et al. 1996; Lynnes et al. 2002)
Chinstrap penguin <i>P. antarcticus</i>	A)20-115 B)<10	A) 24 B) 6	A) South Orkney Island B) Bouveøya Island	A) 300-400 B) >3000	A) 6 B) 1	Bouvetøya	(Lynnes et al. 2002; Biuw et al. 2009)
Gentoo penguin <i>P. papua</i>	10-50	7	French Islands	30	5	South Georgia	(Tanton et al. 2004; Lescroël & Bost 2005; Weiss et al. 2009)
Yellow-eyed penguin <i>Megadyptes antipodes</i>	10-20	14	New Zealand	NA	NA	NA	(Moore 1999)
Emperor penguin <i>Aptenodytes forsteri</i>	100	2♀	Auster Glacier	A) >500 B) >1000	A) 9 B) 12	A) Taylor Glacier B) Ross Ice Shelf	(Kirkwood & Robertson 1997; Kooyman et al. 2000; Wienecke et al. 2004)
King penguin <i>A. patagonicus</i>	140-1500	18	Crozet Islands	A) 30-3000 B) 350	A) 1 B) 1	Crozet Islands	(Jouventin et al. 1994; Culik et al. 1996)
Humboldt penguin <i>Spheniscus humboldti</i>	A)<35 B)<5	A) 2♀, 9, 4 B) 8	A) Peru, Chile (mainland, Pan de Azucar Island) B) Pan de Azucar Island	NA	NA	NA	(Culik & Luna-Jorquera 1997; Culik et al. 1998; Culik 2001; Boersma et al. 2007)
Galapagos penguin <i>S. mendiculus</i>	<25	23	Galapagos Islands	NA	NA	NA	(Steinfurth et al. 2008)
Magellanic penguin <i>S. magellanicus</i>	A) 60-330 B) <450	A) 44 B) 148♂, 57 ♀	A) Punta San Juan, Peru B) Punta Tombo Argentina	750	4	Punta Tombo, Argentina	(Stokes et al. 1998; Boersma et al. 2007, Boersma and Rebstock 2009)
African penguin <i>S. demersus</i>	<40	25, 48, 91	Eastern and Western Cape, South Africa	NA	NA	NA	(Heath and Randall 1989, Petersen et al. 2006; Pichegru et al. 2010)

Population status of the African penguin: pattern of decline, and threats

1.4 Population decline

The African penguin was up-listed to endangered (EN, IUCN 2012) in 2010 due to a 60% population decline between 1979 and 2009 (BirdLife International 2012) and an 80% decline over the past 50 years (Crawford et al. 2008). The first global African penguin census was undertaken in 1956 by Rand (1963). After this survey, there were no further counts until the mid-1970s, when relatively regular counts were initiated at most breeding locations. The estimated population size decreased between 1976-1994 from >220,000 to <180,000 (Crawford et al. 1995b). This downward trend has continued in recent history to a mere 26,000 breeding pairs in 2009 (Crawford et al. 2011). During this recent decline, adult survival rates dropped by 20% at both Dassen and Robben Island (Crawford et al. 2011). Since 1991, these two colonies have supported over 70% of the Western Cape population of African penguins. However, both colonies peaked in the early 2000s, correlating with higher than usual spawner biomass levels, and have been in severe decline ever since (Crawford et al. 1995b, 2011). After 2009, the decline continued, with 2012 seeing the lowest estimate of breeding pairs to date, and the South African breeding population falling below 20,000 pairs for the first time (unpubl. data from CapeNature, Department of Environmental Affairs, Percy FitzPatrick Institute of African Ornithology and South African National Parks). This illustrates the continuing severity of the decline of African penguins, and the need for increased protection.

The success of African penguins has been tightly associated with the availability of sardine and anchovy during the breeding and moulting seasons (Crawford et al. 2006a; Wolfaardt et al. 2009). National fish stocks of over two million tonnes were tightly correlated with increases in breeding success, younger age of first reproduction, and fewer adults abstaining from reproduction during the early 2000s (Crawford et al. 2006a). However, no such value has been estimated as a threshold for maximizing survival of African penguins through the moulting season. Understanding why penguins choose to forage in certain locations with respect to fish abundance and fishing pressure is imperative to better manage this species for the long-term survival of African penguins.

1.5 Historical threats to African penguins

Utilizing both terrestrial and aquatic settings exposes African penguins to pressures found in both environments, systems that have been exploited heavily by humans. The following history of exploitation explains how the African Penguin population has been under stress in the past, and how these stresses have played a role in the current state of the population.

1.5.1 Consumption and use of African penguins

Records of penguin consumption go as far back as the 1600s, when they were killed for provisions, used for oil, and burned for fuel in boilers (Rand 1949; Randall 1989). When the Cape settlement was created in 1652, excursions to the nearby island colonies increased (Randall 1989). The feathers of penguins were used for pillows and bedding, but carried with them a fishy stench, as did the meat (Rand 1949).

1.5.2 Guano scraping

The 17th century saw the first recorded guano removal from islands in South Africa, for use as an agricultural fertilizer. The guano industry re-emerged and intensified from the late 1800s through the early 1900s after the depletion of the Namibian guano stocks (Snyders 2011). Guano is important to the penguins for digging nest burrows, which provide protection from avian predators and the elements (Shelton et al. 1984). The constant disturbance to the guano colonies and the removal of material used for burrowing had a lasting influence on population trends (Shelton et al. 1984).

1.5.3 Egg collection

Historically, egg collecting was a major stress on African penguin populations in southern Africa. Shelton et al. (1984) reported the harvest rates from the islands around Cape Town from 1871 through the cessation of commercial egg harvesting in 1968. These records show that between 1897 and 1930, more than 400,000 eggs were harvested annually, and as many as 800,000 eggs were harvested in a single year. During this period, a wall was built around Dassen Island to force the penguins to breed in a smaller area, facilitating egg collection (Rand 1963). It has been estimated that the rate of harvest was as high as 48% of egg production, and that even a harvest of 1% of natural egg production would have led to a decline in the African penguin population (Shannon & Crawford 1999). The effects of long-term egg collection are not fully understood, but Shannon & Crawford (1999) show how unsustainable it was and discuss the impacts the collection had on the population trends of African penguins.

There were an estimated 1.5 million penguins living on Dassen Island in the early 1900s, which collapsed to roughly 180,000 birds in the 1970s (Crawford et al. 1995b). Crawford et al. (1995) estimated that 70% of the decline in penguin numbers can be attributed to egg harvesting.

1.5.4 Overfishing

Overfishing has been identified as a threat to African penguin populations in southern Africa (Crawford et al. 2001, Pichegru et al. 2009). The African penguin population in Namibia decreased from over 40,000 birds to about 1,000 individuals between 1956 and 2000. This trend followed the collapse of the Namibian small-pelagic fishery due to overfishing (Crawford et al. 2001), and has never recovered.

1.6 Current threats and processes

1.6.1 Oil spills

Westphal & Rowan (1970) discussed the effects of the *Esso Essen* oil spill in 1968 that lost 4,000 litres of oil near Cape Point, South Africa. This disaster is suspected to have oiled *ca* 2,000 birds. The *Apollo Sea* (1994) and the *Treasure* (2000) oil spills both occurred in Table Bay near Dassen and Robben Island, and killed an estimated 5,000 and 6,350 birds respectively from west coast colonies (Underhill et al. 1999; Crawford et al. 2000). Effects of oiling go beyond decreasing a penguin's ability to forage, also leading to higher divorce rates, decreased fledging success, and slower chick growth rates (Wolfaardt et al. 2008), all affecting the population into the future. Overall, it is estimated that 30,000 birds have been lost to the oil spills of the 1990s and 2000s (BirdLife International 2012).

1.6.2 Natural predation and competition for nesting sites

The removal of guano has not only led to more competition for nesting sites with Cape gannets (*Morus capensis*; Crawford & Whittington 1997) and Cape fur seals (*Arctocephalus pusillus*) who share some of the island breeding sites, but has also exposed eggs and chicks to predation by kelp gulls (*Larus dominicanus*) (Shelton et al. 1984). Some penguin colonies have seen population declines as Cape fur seal numbers increase, with reports of islands being cleared of penguins entirely (e.g. Seal Island, Mossel Bay; Shelton et al. 1984). Mainland penguin colonies have seen predation from leopards (*Panthera pardus*), caracals (*Caracal caracal*), and other land based predators (Whittington et al. 1996; Crawford et al. 2001). Predation by land-based mammals is the reason for the failure of the De Hoop colony (Crawford et al. 2008),

established in 2003 (Underhill et al. 2006). Marine predators known to eat African penguins include Cape fur seals (Marks et al. 1997; Crawford et al. 2001), great white sharks (*Carcharodon carcharias*; Randall et al. 1988), and possibly killer whales (*Orcinus orca*; Randall & Randall 1990).

1.6.3 Food availability: A natural shift in prey species and overfishing

Overexploitation of anchovy and sardine in South African waters in the 1960s and 1970s heavily affected African penguins (Crawford & Shelton 1981; Pichegru et al. 2009). The targeted species in the purse-seine fishery, anchovy and sardine, are also the main food sources of African penguins (Hockey et al. 2005). On average these two species have contributed more than 70% by mass to their diet annually between 1989 and 2009, with squid, goby, round herring (*Etrumeus whiteheadi*), and horse mackerel (*Trachurus* spp.) as minor dietary items (Crawford et al. 2011). Competition between the purse-seine fishery and penguins could be an important driver of the current penguin population decline (Crawford et al. 2001; Pichegru et al. 2009) in conjunction with the apparently natural eastward shift in anchovy and sardine stocks (Roy et al. 2007). There is economic pressure on the purse-seine fishery to harvest near to their processing plants to reduce fuel and labour costs (Coetzee et al. 2008). Due to the historic concentration of fish off the west coast, processing plants are near major penguin and other seabird colonies on the west coast, making it likely that conflicts will occur. Fishing intensity in these areas has continued even with the shift of the sardine and anchovy biomass east of Cape Agulhas (Pichegru et al. 2009).

Sardine stocks frequently alter their spawning grounds, but historically, there have been higher levels of adult biomass along the west coast. This pattern started to change in 1995, and adult sardine biomass has been higher east of Cape Agulhas since 1999 (Coetzee et al. 2008). Anchovy have shown a similar pattern, with the relative biomass shifting slowly eastward between 1990 and 1998. An abrupt shift in the stocks in 1996 is thought to have occurred as a result of higher winds causing an increase in cold water upwelling leading to a sustained temperature decrease of 0.5°C (Roy et al. 2007).

This has led to a spatial disparity between fish availability and fishing pressure. Through 2004, higher proportions of the Total Allowable Catch (TAC) were taken from the west coast, even though more fish were available east of Cape Agulhas after 1999 than in previous years (Coetzee et al. 2008). In 10 out of 20 years between 1987 and 2007, >20% of the estimated adult

sardine biomass on the west coast was harvested. In three of those years the west coast harvest was >30%, and in 2006 this spatial bias peaked when 44% of the estimated adult biomass was removed. Due to the spatially disproportionate extraction of fish biomass following the shift, fisheries are thought to have altered the local fish stock availability (Pichegru et al. 2011). Currently, the TAC is given to the industry as a number in tonnes, but aside from a few designated no-take marine protected areas (MPAs), there is no spatial component to the TAC (De Oliveira & Butterworth 2004).

Spawning grounds for sardine and anchovy are located to the south and east of Cape Agulhas, and the main nursery grounds for these fish are north of Table Bay up the west coast towards Namibia (Hutchings et al. 2002) (Figure 1). A decrease in adult fish populations during the fishery collapse of the 1960s continued and resulted in fewer adults on the west coast after the fish population recovered (Coetzee et al. 2008). Poor recruitment on the west coast since 2004 was not accounted for when setting TAC levels (Coetzee et al. 2008), however, spatial management is being discussed for future management of the small-pelagic fishery in South Africa (Coetzee and Merkle 2012).

Management of fisheries in a South African context

Understanding long-term trends and dynamics in both the fisheries and seabird populations is critical to implementing an Ecosystem Approach to Fisheries (EAF). Shannon and Moloney (2004) proposed a management strategy for fisheries that was designed to model the outcome of fish species' harvest rates, and the effects they would have on other species utilizing these resources in South African waters. The idea of an EAF is also supported by the Benguela Current Commission (BCC), looking to aid in sustainably managing the Benguela region, crossing the borders of South Africa, Namibia, and Angola (BCC 2008). South Africa is bounded by the warm Agulhas current flowing from the Indian Ocean on the east coast along the south coast, and the Benguela current moving northward along the west coast. Cold upwelling water, driven by wind from the south-east, creates a highly productive system (Hutchings et al. 2009), making the Benguela Current one of the most productive systems in the world (BCC 2008).

The small-pelagic fishery, targeting primarily sardine and anchovy, is South Africa's largest fishery by catch volume, and second largest in terms of economic production (Nielsen &

Hara 2006). Sardine catches peaked in 1962 with a haul of 400,000 tonnes in that year, leading to the fishery's collapse. In an attempt to rebuild the fisheries through more conservative harvest levels, management strategies were implemented (Coetzee et al. 2008). The fishery landed more than 200,000 tonnes of anchovy in most years between 1972 and 2005, peaking in 1987 and 1988 with over 580,000 tonnes of anchovy caught each year (Fairweather et al. 2006). After the recovery of the sardine population through the 1980s and 1990s, the population was mostly found east of Cape Agulhas, instead of the west coast where it was centred prior to the collapse (Coetzee et al. 2008). In the early 2000s, the fishery caught an average of 200,000 tonnes of sardine per annum, but catches decreased sharply after 2005 following a period of poor recruitment (Coetzee et al. 2008). Over the past 50 years, the small-pelagic fishery in South Africa has averaged about 375,000 tonnes of sardine and anchovy combined annually (Fairweather et al. 2006). The fishery provides employment for 10,000 people as a combination of full-time, part-time, and seasonal contracts (Nielsen & Hara 2006).

Currently, South Africa's TAC in the small-pelagic fishery is based on the national abundance of sardine and anchovy (De Oliveira & Butterworth 2004). The TAC lacks a spatial management strategy (van der Lingen 2005; Pichegru et al. 2009) for areas not protected as MPAs or with other legislation preventing fishing activities. Recently, evidence has been put forth to consider spatial management of the South African small-pelagic fish stocks, and Cape Agulhas has been suggested as a potential dividing line based on historical sardine abundance data (van der Lingen 2011; Coetzee & Merkle 2012). This division point at Cape Agulhas will be used throughout this thesis when referring to the south and west regions in terms of fish stocks and penguin colonies.

Current understanding of spatial habitat use of the African penguin

African penguins demonstrate central place foraging during the breeding season, typically feeding within 40 km of their colony while provisioning small chicks on the south coast (Heath and Randall 1989, Petersen et al. 2006; Pichegru et al. 2010, Table 1), and within 15 km for colonies on the west coast (Hockey et al. 2005; Petersen et al. 2006). A central place forager continues to return to the colony or nesting site between foraging trips. Foraging close to their nesting site during the breeding season is necessary so that adults can return to the colony to feed their young and relieve their partner of nesting duties. When not breeding, African penguins can

move well beyond this range (Randall et al. 1987; Whittington et al. 2005a), however the route taken is unknown and therefore does not identify the potential interactions that may occur along the path they travel. Between 1970 and 1998, Whittington et al. (2005b) demonstrated that 35% of birds banded as juveniles, and only 9% of birds banded as adults were seen in locations that were not their natal colony. Such observations have been made through banding and re-sighting exercises, and are therefore very coarse and lack an understanding of where the penguins travel in between the periods when they were re-trapped on land. Owing to the abundance of spawning anchovy on the Agulhas Bank, Whittington et al. (2005a) and Wolfaardt et al. (2009) both hypothesized that African penguins migrate there during the pre-moult phase. Understanding the complex spatial dynamics of habitat use is necessary to help properly manage a species, especially when a population is in severe decline. Until now, there have been no studies undertaken to investigate the spatial use of the African penguin in marine environments around the South African coast outside the breeding season. Without an understanding of how and where African penguins are using the ocean throughout the year, potential threats cannot be assessed nor remedial actions implemented to aid with the conservation of this species.

Aims and objectives

This project provides the first insights into the movements of African penguins in the pre-moult phase. It compares the movements of birds from two South African colonies, one on the west coast (Dassen Island), and the other on the south coast (Bird Island, Algoa Bay) (Figure 1). Where penguins forage from these two colonies is of interest due to the recent shifts of relative abundance of forage fish from the west to the south coast, with an understanding that the penguin populations are decreasing in both regions. In recent years, the number of birds in the western colonies has fallen below the number of birds in the south-eastern colonies for the first time (Crawford et al. 2011), suggesting that the areas east of Cape Agulhas may be more productive and could become the future stronghold for African penguins if the shift in sardine and anchovy continues.

This study gives the opportunity to compare the foraging effort at two colonies in different localities, acting as models for colonies found within the western and south-eastern colony groupings (Figure 1). It also incorporates fishery catch data to assess where African penguins forage in relation to fishery catches during the pre-moulting season. Uncovering differences in

foraging patterns between sites could enhance the current understanding of how these birds are using their marine environment to gain weight before their annual moult. Investigating the spatial overlap between the areas targeted by the small-pelagic fishery and those used by pre-moult African penguins allows the first assessment of the extent of this overlap and provides important guidance for future spatial management of the South African small-pelagic fishery.

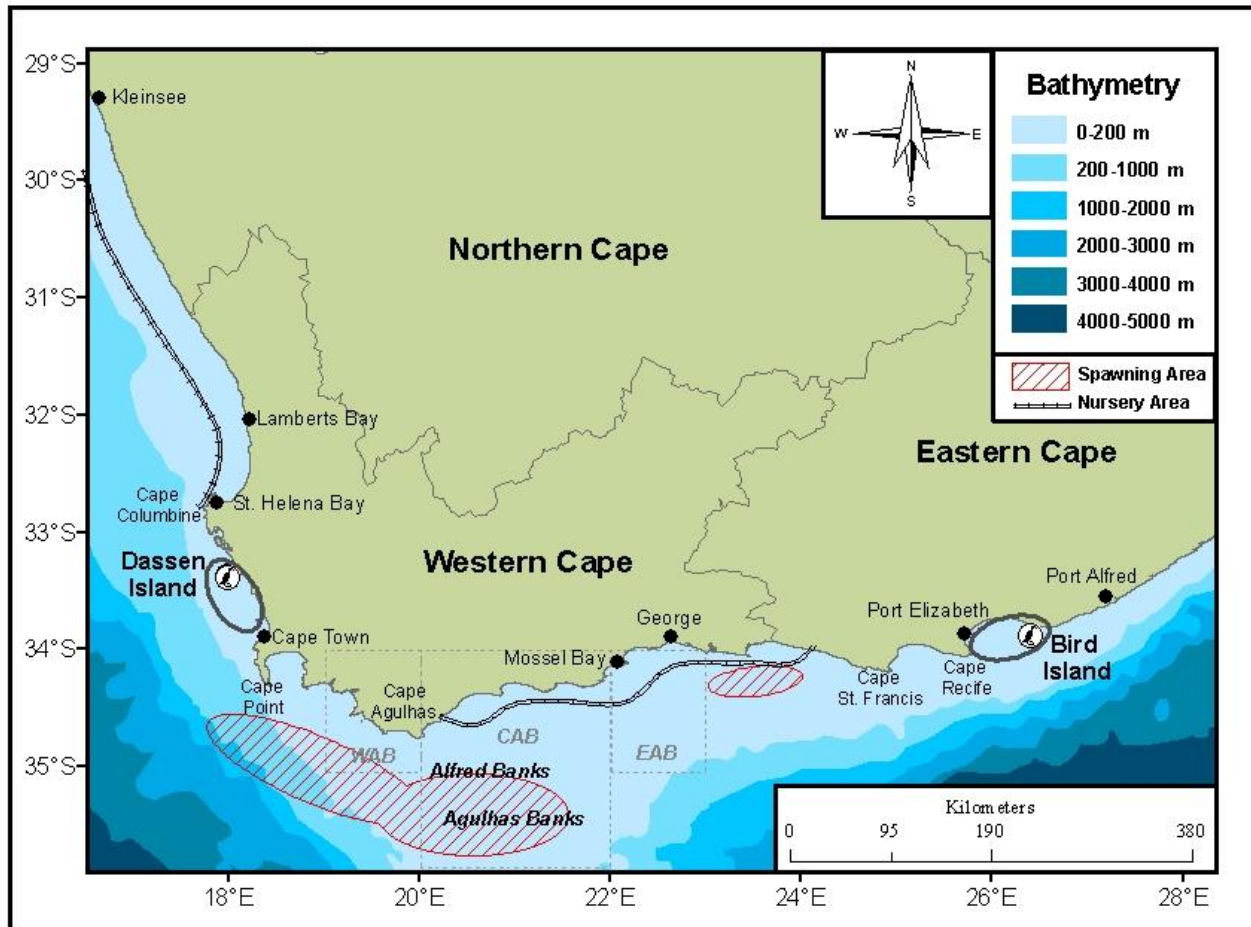


Figure 1: Map of study sites, Dassen Island and Bird Island, and other places on the South African coast for reference to places mentioned in this thesis. West and south-eastern coast African penguin (*Spheniscus demersus*) colony groupings are circled in grey. The Agulhas Bank is divided into three sections; the Western Agulhas Bank (WAB), Central Agulhas Bank (CAB), and the Eastern Agulhas Bank (EAB) (Roy et al. 2007), designated by grey hashed lines. Spawning regions and nursery grounds of anchovy (*Engraulis encrasicolus*) and sardine (*Sardinops sagax*) are also identified (altered from Hutchings et al. 2002).

Chapter 2: Pre-moult foraging of the African penguin: Areas of importance, regional differences, and fishing pressure

Introduction

Following a 60% population decline over the last 30 years (BirdLife International 2012), African penguin colonies are continuing to decrease across their range, with the largest declines occurring in the Western Cape (Crawford et al. 2011, unpublished information of CapeNature, Department of Environmental Affairs, Percy FitzPatrick Institute of African Ornithology and South African National Parks). The decreases since 2005 have been ascribed to a combination of competition with the small-pelagic fishing industry (Pichegru et al. 2009), and an eastward shift of anchovy and sardine relative abundance (van der Lingen 2005; Roy et al. 2007). Surveys have shown that the relative abundance of both sardine and anchovy have shifted eastward, from the west to the south coast, where higher fish densities have been recorded since 1999 and 1996, respectively (Roy et al. 2007; Coetzee et al. 2008). The centre of gravity (CoG) of catches of sardine moved from near Saldanha Bay (less than 50 km north of Dassen Island) towards Cape Agulhas between 1997 and 2005 (Fairweather et al. 2006). The CoG of the anchovy-directed catches, however, remained between Lambert's Bay and Hout Bay over the same period (Fairweather et al. 2006).. The region east of Agulhas is thought to be utilized by adult penguins out of the breeding season (Randall et al. 1987; Whittington et al. 2005a; Wolfaardt et al. 2009). The shift of the anchovy stock suggests that anchovy directed fishing also should move east to follow the fish stocks, as the sardine fishery has started to do (Fairweather et al. 2006). The eastward shift of the relative abundance of sardine and anchovy has led to a reduction in food availability for African penguins on the west coast, which has been correlated with a decline in penguin populations there since 2002 (Crawford et al. 2006a, 2008, 2011). If fishing intensity stays high, it will further reduce the availability of fish in this region, potentially forcing penguins to relocate, something that few active breeders are likely to do (Randall 1983).

The survival of adults is a key factor in the long-term survival of African penguins. Life history theory predicts that penguins, like other seabirds, should favour their own survival over reproduction and abandon their nests if circumstances are not conducive to successful breeding, allowing adults to stay healthy for future breeding attempts (Crawford et al. 1995a; Hemming 2001). Understanding adult survival outside of the breeding season is crucial. During this

portion of the year, they must gain weight before the moulting fast, when they lose up to 47% of their body weight (Cooper 1976), and then must have sufficient reserves to return to the water to forage and regain their body condition for the next breeding season (Randall 1989).

The moult of African penguins in South Africa occurs mainly between September and January, with the synchrony of moult varying annually and among colonies (Underhill & Crawford 1999; Crawford et al. 2006b). Peaks in moulting seasons occur in December at west coast colonies (Wolfaardt et al. 2009) and November on the south coast (Crawford et al. 1995b). In South Africa, the earliest moulting is initiated at Bird Island, Algoa Bay, and the latest moult occurs at Robben and Dassen islands on the west coast (Crawford et al. 2006b). Of the western colonies, the moult on Dassen Island is spread over five months, as breeders on Dassen Island delay their moult until after their final breeding attempt for the year is complete (Wolfaardt et al. 2009), instead of abandoning chicks to initiate moult as has been seen on Robben Island (Underhill et al. 2006).

Research on spatial foraging patterns of African penguins has been conducted by tracking the movements of adults provisioning small chicks (Heath & Randall 1989; Ryan et al. 2004; Petersen et al. 2006; Pichegru et al. 2009, 2011; Waller 2011), of juveniles that have just fledged (Sherley et al. 2013), and inferred from transects from vessels at sea (Wilson et al. 1998a, 1988b). These studies demonstrate that African penguins are central place foragers during the breeding season, with a foraging range of 15-40 km from their colony.

African penguins breeding at Dyer Island were shown to have larger foraging ranges (11-52 km, Waller 2011) than penguins from other colonies in South Africa (typically <30 km, Petersen et al. 2006; Pichegru et al. 2010). During the breeding season, penguins from colonies off the west coast of South Africa typically forage closer to their colonies than do those from colonies off the south coast (Heath & Randall 1989; Hockey et al. 2005; Petersen et al. 2006; Pichegru et al. 2010). These different strategies suggest that local factors (predation, competition, fish abundance, environmental conditions, etc.) may influence foraging strategies, which allow penguins to deal with local variation in food availability.

This thesis investigates foraging movements during the pre-moulting season and compares how African penguins from west and south-eastern colonies use the ocean during this period. Spawning aggregations of sardine and anchovy occur on the Agulhas Bank between September and February (Crawford et al. 2006b), and it has been suggested that African

penguins forage in this area when they are not breeding (Whittington et al. 2005a; Barham et al. 2006). I hypothesize that African penguins target areas of high fish abundance during the pre-moult phase to maximize their rate of mass increase, even if this means moving outside of the 15-40 km zones used in the breeding season. I also expect that due to the eastward shift of the relative abundance of sardine and anchovy biomass that birds on the west coast will travel farther from their colonies than birds from the south coast. I therefore predict that birds from Dassen Island will have a larger foraging range than those from Bird Island. The third aspect of this thesis is to explore the potential overlap of areas targeted by the small-pelagic fishing industry and those used by the African penguin during the pre-moult phase. Based on historical fishing trends (typically higher catches on the west coast despite the distribution of the relative abundance of sardine and anchovy), I expect that a higher proportion of anchovy will be caught on the west coast, despite the distribution of spawner biomass.

Methods

2.1 Study sites

Dassen Island (33°25'S, 18°05'E) is situated in the Western Cape, South Africa (Figure 1) covering an area of 2.73 km². Dassen Island is located in the Benguela current, a highly productive system (Heilman & O'Toole 2006) with environmental and climatic variability leading to biomass turnover (Shannon et al. 2006). Gremillet et al. (2008) demonstrated that in the Benguela system, low trophic levels of productivity were not good predictors of intermediate productivity (small-pelagic fish), as seabirds foraging in areas of high phytoplankton productivity were not finding an abundance of small-pelagic fish. Sea surface temperatures in the Benguela are variable, and changes are thought to be driven by local upwelling events and advection flowing from the Agulhas current (Heilman & O'Toole 2008). Bird Island (33°50'S, 26°17'E) is located in Algoa Bay, Eastern Cape, South Africa, and is the easternmost breeding colony of African penguins (Figure 1). At 0.19 km², it is the largest of a three-island archipelago and has supported about 2,500 pairs of breeding African penguins since 1999 (Crawford et al. 2011). Addo Elephant Park expanded in 2004 to incorporate the Bird Island Group as an MPA, with a radius approximately 8 km from the island. This MPA is much smaller than the 20 km radius experimental fishery closures implemented around breeding colonies as reported by Pichegru et al. (2010), and does not cover the foraging range of breeding African penguins

(Pichegru et al. 2010). Bird Island is located in the Agulhas current, a moderately productive system (Lutjeharms 2006) with intense but intermittent primary productivity (Heilman et al. 2010). This current has seen a warming trend over the last 60 years (Belkin 2009), and sees warm circular currents form on shoreward side as it passes the southern coast of South Africa (Lutjeharms 2007).

Experimental closures were implemented near important breeding colonies in South Africa. Alternating closures annually between island pairs of Dassen and Robben Island, and Bird and St. Croix Island, researchers investigated the effects of fishing in close proximity to the penguin colonies on foraging efficiency, travelling distance, and breeding success (Pichegru et al. 2013).

2.2 Platform Terminal Transmitter deployment

To follow African penguins during the pre-moult phase, Platform Terminal Transmitters (PTT; KiwiSat202, SirTrack) were attached following an altered method of Wilson et al. (1997). By transmitting signals to satellites, PTTs allow movements of individuals to be followed remotely over the duration of the pre-moult period. The PTTs weigh 40 g, measure 6 x 2.7 x 1.7 cm, and cover a surface area of 16.2 cm² with an antenna extending 18 cm from the back of the device (Figure 2). The waterproof protective coating has a rounded front edge and tapered sides to reduce drag. All PTTs were on a duty cycle of 6 hours on, 18 hours off, with saltwater switches to prevent unnecessary battery use when birds were underwater during the active portion of the duty cycle. The active period was 18:00 to 24:00 hours (GMT +2), as this corresponds to the period when African penguins rest on the surface (Petersen et al. 2006), aimed to maximize the chance of receiving high quality signals as the antennae is less likely to be submerged. Battery life was approximately 100 days, more than 2.5 times the expected duration of at sea foraging prior to moulting, estimated at 35 days (Randall 1983; Hockey et al. 2005). Daily satellite positions were accessed online through the ARGOS satellite online system and were downloaded three times a week for as long as devices were active.

Twenty individuals were fitted with PTTs, 10 from each of the two study sites (Figure 1). Deployments occurred between 12-16 September 2012. Before attaching PTTs, study colonies were monitored to identify birds that had successfully reared chicks, and had late stage “blues”, chicks that were ready to fledge and leave the nest. Using adults in the late stage of parenthood

decreased the likelihood of recording tracks that are associated with feeding young. Instead, monitored individuals were expected to self-feed and recover from the breeding season to gain weight prior to the annual moult. All PTTs were deployed on adults with large “blues”, except for B5 which had a large downy chick.

Individuals were caught in their burrows/nesting sites and PTTs were attached to the lower back above the uropygial gland and centred to maximize balance. In addition to Wilson et al.’s (1997) methods using Tesa® tape woven into the back feathers, Loctite 401 superglue (Henkel Ltd.) was applied to hold the device firmly within the tape. The PTT was placed onto the glue-covered feathers, and the tape was then folded over the device, alternating sides to create a tightly woven matrix around the PTT. Superglue was then applied liberally over the tape and smoothed to fill the joins between layers of tape. A cable tie was inserted under the tape/feather layers of the glued on PTT and wrapped around the entire unit near the front of the device to hold it firmly in place (Figure 2). This additional hold-fast mechanism was used to prevent the front of the device lifting away from the feathers, which would create substantially more drag. Although applying glue directly to the feathers is known to cause feather damage (Wilson & Wilson 1989), in this case, devices were to be removed from individuals moulting their old feathers, making any damage irrelevant. Once the PTT was attached, individuals were returned to the nesting site from which they were caught. Attachment of PTTs took an average of 11 ± 3 minutes with a range of 8-20 minutes. Nesting sites were visited for at least five consecutive nights after PTT attachment to monitor nest behaviour.

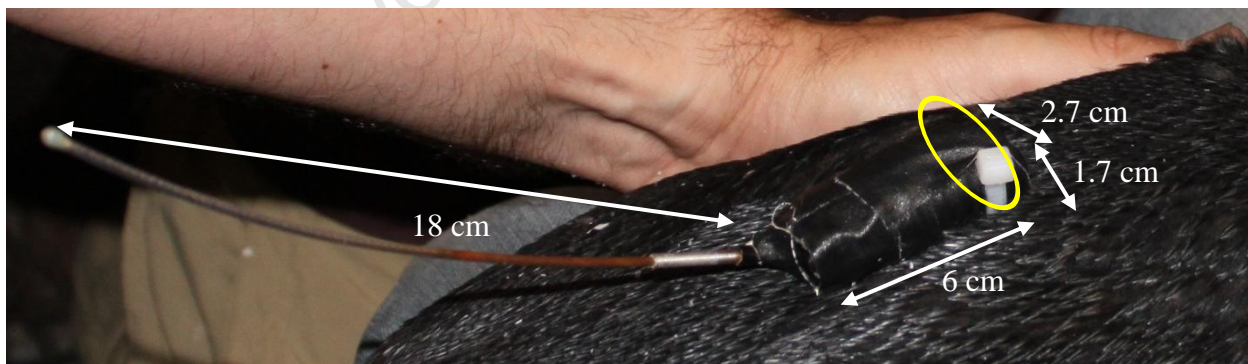


Figure 2: Platform Terminal Transmitter (PTT) attached to an African penguin (*Spheniscus demersus*) with Tesa® tape and Loctite superglue (Henkel Ltd). The yellow circle identifies the cable tie used to help hold the front of the PTT.

2.3 Chick feeding foraging trips vs. pre-moult foraging

All tracked individuals from Dassen Island left the island on trips of more than three days within eight days of deployment, and were therefore considered to have ceased parental duties. However, study birds from Bird Island may have continued provisioning chicks after deployments occurred based on observation of study birds staying close to the island. Possible bias arising from this was tested by ignoring the first 5, 10 and 15 days of the tracking record and comparing the results against the entire data set (for relevant parameters) to establish if more trips and larger distances were being used in later periods after deployment. Larger distances and more trips later in the monitoring period would suggest a change in foraging behaviour, spending less time alternating with partners and returning food to chicks. Possible differences were tested using ANOVAs and Tukey's post-hoc tests, where necessary, to establish if foraging behaviours differed sufficiently between time frames to justify truncating the Bird Island datasets. Analysis did not reveal a significant increase in the frequency of trips from the colony or the distance within which birds were foraging, therefore the entire dataset was used in analyses.

2.4 ARGOS data interpretation

Location fixes of PTTs were only used if accompanied by error radius measurements from ARGOS. These levels range in accuracy from <250 m, 250-500 m, and 500-1500 m for location quality Class 3, 2, and 1, respectively (CLS 2011). The most accurate position (lowest error radius) from each active device per night was used for analysis, and is referred to as point-per-night (PPN) data. Overall, 80% of all PPN were accurate within 500 m (Class 2 or 3). Straight line paths were created between nightly fixes, producing a minimum estimate for daily distance travelled. It is unlikely that birds followed straight lines between points, therefore reported distances are conservative estimates.

If there were no usable data points for a device-night, a location was interpolated. If the points before and after a missing device-night were both in the ocean, the midpoint was assigned. If a point before or after a missing night was on land, I assumed that the missing night was also on land. Only 13 PPN were interpolated, eight land based points and five ocean points, out of 896 device-nights (1.5% of the total data).

2.5 Statistical analysis

Of the seven parameters used to describe foraging ranges, two were standardized as a proportion of time monitored (X/days monitored by PTT) to account for variable tracking effort between individuals.

2.5.1 Average distance travelled per day was calculated using the distance between points that were not consecutively <1.5 km apart, corresponding with the lowest PTT accuracy (ARGOS Class 1) used in analysis. PTTs only collected data for six hours at night, allowing for the possibility that an individual could leave the colony and return without this being detected by the PTT. The value estimates the average daily distance each individual travelled, leaving out consecutive fixes within a buffer of the maximum error radius and compensating for potential missed foraging trips.

2.5.2 Maximum distance from colony was defined as the farthest distance an individual travelled from the colony. When sequential points straddled areas of land, the shortest distance around the land was interpolated.

2.5.3 Standardized trips were defined as the number of times an individual spent at least one night off of the island and then returned, during the period it was monitored. This value was standardized to account for different monitoring periods and reported as the percentage of days monitored. Higher values suggest greater affinity to the colony during the pre-moult season.

2.5.4 Standardized T40 was the proportion of nights each individual spent more than 40 km from the colony. This value indicated the percentage of nights that each individual spent outside of the main foraging range during the breeding season (Heath & Randall 1989; Petersen et al. 2006; Pichegru et al. 2010). Typical foraging ranges from island colonies on the west coast are smaller than this (Petersen et al. 2006), so movements beyond 40 km were assumed to represent foraging outside the breeding range for both colonies.

2.5.5 Minimum duration of pre-moult period was defined as the number of days between the first time an individual spent at least three consecutive nights away from the colony until it returned to land and did not leave again prior to moulting, or until the device stopped transmitting. Three days away from the colony was used based on the upper limit of time spent away by African penguins during the breeding season (Ryan et al. 2004). This parameter measured differences in time taken to achieve moulting condition. It is expected that if fish are

less abundant, more distant from the colony, or commercial fishing pressure is higher in an area, the duration of the pre-moult foraging period should be longer. Birds that did not spend three consecutive nights away from the island within the first week of monitoring were removed from this analysis to remove any bias from birds that continued to make short trips after chicks fledged.

2.5.6 Distance travelled to foraging locations was defined as the total distance an individual travelled away from the colony in search of foraging grounds. The travelling phase is defined as consecutive days in which an individual moved $>25 \text{ km.d}^{-1}$ in the same direction, more than the average foraging range during the breeding season (*ca* 20 km, Petersen et al. 2006; Pichegru et al. 2010; Waller 2011). A travelling phase ended when more than one night was spent within 25 km of the preceding PPN. This parameter investigates how far individuals swam before encountering adequate foraging grounds and can be considered a measure of effort.

2.5.7 Daily rate of travel was calculated as the minimum distance swam per day during travelling phases to provide another measure of relative effort required to reach adequate foraging sites.

Differences in mean foraging parameters between colonies were investigated using Mann-Whitney rank sum tests, as there was an uneven sample size, and the data were not normally distributed for both standardized variables (T40 or Trips) and descriptive statistics of foraging parameters. Generalized Linear Models (GLMs) were used to examine how the two variables describing movements to and from foraging grounds (distance travelled and daily rate of travel) responded to the effects of colony (Bird or Dassen) and directionality (moving to foraging grounds or to the colony). Each response variable was analyzed separately with a Gaussian distribution and an identity link. Non-significant variables were removed sequentially to yield the model with the lowest Akaike's Information Criterion (AIC) value. Inter-colony differences in the minimum duration of the pre-moult were tested using a t-test.

2.6 Kernel Density Analysis

Kernel Density Analysis (KDA) was performed with the program Home Range Tools (Rodgers et al. 2007) in ArcGIS 9.3.1, using the adaptive kernel method with smoothing parameters selected based on least-squares-cross-validation. Estimates were created for foraging ranges based on 25, 50, 75, and 90% spatial use estimates (utility distributions) from PPN data as

time spent in a given area. Some individuals continued to use central-place foraging patterns during their pre-moult period. I investigated the potential overestimate this created by performing KDA after removing all points on land, eliminating the bias of consecutive land based points from daily trips that were not captured due to the timing of active PTT duty cycles. These analyses were carried out based on 1 km x 1 km grid cells. KDA was performed to establish areas of importance for birds from both colonies within the pre-moult foraging period and to compare these areas of use with small-pelagic fishery catch data over the monitoring period.

2.7 Small-pelagic fishery catch data

Small-pelagic fishery catch data were obtained for September-November 2012 (unpubl. data, Department of Agriculture, Forestry and Fisheries) to determine the tonnage of sardine and anchovy caught in each of the pelagic fishing blocks (PFB) around South Africa's coastline between Hondeklip Bay and Port Alfred. The annual PFB data collection area encompassed all but one foraging trip by tracked penguins, as one individual swam north of Hondeklip Bay during monitoring, further north than the annual surveys are done. Each PFB designates a 10 x 10 nautical mile grid cell (18.5 x 18.5 km). These data were analyzed using ArcGIS 9.3.1 to evaluate the overlap between the fishing industry and areas used by African penguins during the pre-moult foraging period. ANOVA was used to compare the amount of fish (anchovy, sardine, and total catch) caught in each marine use range, calculated above using KDA. All catch data were standardized as tonnes km⁻².

All statistical analyses were conducted in R 2.15.1 (R Core Team 2012) unless otherwise stated. When ArcGIS 9.3.1 was used for spatial analysis or distance measures, the datum WGS1984 was used, and analysis performed on Dassen Island and Bird Island were completed in projections of UTM34S and UTM35S, respectively, to accurately calculate distance measures. A summary of all individual values used to analyze foraging parameters described above are listed in Appendix 1. Individuals that failed to leave the island or had devices removed before entering into moult were excluded from analyses where appropriate. Sex could not be determined in the field for all individuals, and was therefore left out of all analyses.

Results

2.8 PTT deployments and retrievals

Ten PTTs were successfully deployed at each study site. Average mass of adults deployed on was $2,714 \pm 288$ g, and PTTs weighed less than 1.8% of adult body mass for all deployments (Table 2). Bill length averaged 56.7 ± 2.7 mm, and bill width at gonys was 21.9 ± 1.3 mm (Table 2). D10 was the only bird to never leave a colony for more than a single day, and stopped transmitting after 26 days. The device may have fallen off, or been removed by the bird (Wilson et al. 1997), causing the signal to no longer transmit. However, the device was not recovered nor was the individual resighted, despite extensive searches. The nest was monitored by the island manager over the duration of the 26 days it was tracked, and the chicks were still present after the signal was lost. As this individual never entered the pre-moult period and was caring for chicks for the duration of the time it was monitored, it was removed from all analyses; thus the effective sample size for all Dassen Island analyses was nine. All other individuals were successfully monitored during the pre-moult period and used in all analyses unless otherwise stated.

Sixteen devices were recovered from individuals that returned to a breeding colony. Nine individuals from Bird Island were recaptured either moulting or in early-moulting condition (indicated by swollen wings and ruffled feathers). One bird had its PTT retrieved without confirmation of its moulting status (B4), and was therefore removed from the analysis on minimum duration of pre-moult. On Dassen Island, six individuals were identified as moulting or in early pre-moulting condition upon their return to the colony. D3 moulted at the Stony Point penguin colony, Betty's Bay, Western Cape. D2 was monitored for 61 days, when the signal was lost while the bird was in the vicinity of the Paternoster Rock islands, near Cape Columbine, Western Cape. D7 returned to Dassen Island for 10 days and was observed on the beach near its nesting site. It then left the island without undergoing moult, and signal was lost 150 km north of Dassen Island after 88 days of signal transmission.

2.9 Satellite tracking

Individuals from Bird Island seldom made long trips (Figure 3), whereas Dassen Island birds made one long foraging trip or a few medium to long trips (Figure 4). Penguins monitored from Bird and Dassen Island typically stayed within 50 km and 60 km of the coastline

respectively, which falls within the 200 m depth zone around the South African coast (Figure 3, Figure 4). However, over the Agulhas Bank, individuals moved up to 100 km offshore, still within the 200 m depth zone (Figure 4). Maximum distances of single day travel were higher for birds from Dassen Island, seven of them travelling >100 km in a day (Appendix 1).

Penguins from Dassen Island travelled significantly farther from the colony than those from Bird Island ($W=5$, $p<0.001$, $n_1=9$, $n_2=10$, Figure 5), with six birds from Dassen Island travelling more than 300 km (Appendix 1). The average daily distance showed a similar pattern with penguins from Dassen Island swimming farther on a daily basis, seven individuals moving 30 km or more per day ($W=15$, $p=0.014$, $n_1=9$, $n_2=10$, Appendix 1).

Table 2: Summary of deployment details and morphometrics for African penguins (*Spheniscus demersus*) monitored with Platform Terminal Transmitters (PTTs) during the 2012 pre-moult period. Bird ID identifies the breeding colony from which each individual was deployed (B=Bird Island, D=Dassen Island) and identification number.

Bird ID	Mass (g)	PTT % of mass	Bill length (mm)	Bill depth at gonys (mm)
B1	2650	1.51	52.5	20.4
B2	3000	1.33	61.3	24.0
B3	2650	1.51	55.7	20.3
B4	2925	1.37	60.2	24.3
B5	2750	1.45	56.5	20.7
B6	2425	1.65	57.0	21.0
B7	3000	1.33	56.0	21.7
B8	2750	1.45	55.0	21.8
B9	2500	1.60	53.7	20.1
B10	3150	1.27	56.0	23.6
D1	2260	1.78	54.6	21.4
D2	2290	1.75	57.4	22.7
D3	2540	1.57	56.7	22.8
D4	3290	1.22	58.2	23.5
D5	2470	1.62	53.7	20.9
D6	2900	1.38	54.0	21.7
D7	2800	1.43	58.4	20.9
D8	2370	1.69	54.6	20.7
D9	2960	1.35	60.5	23.4
D10	2600	1.54	61.8	22.3

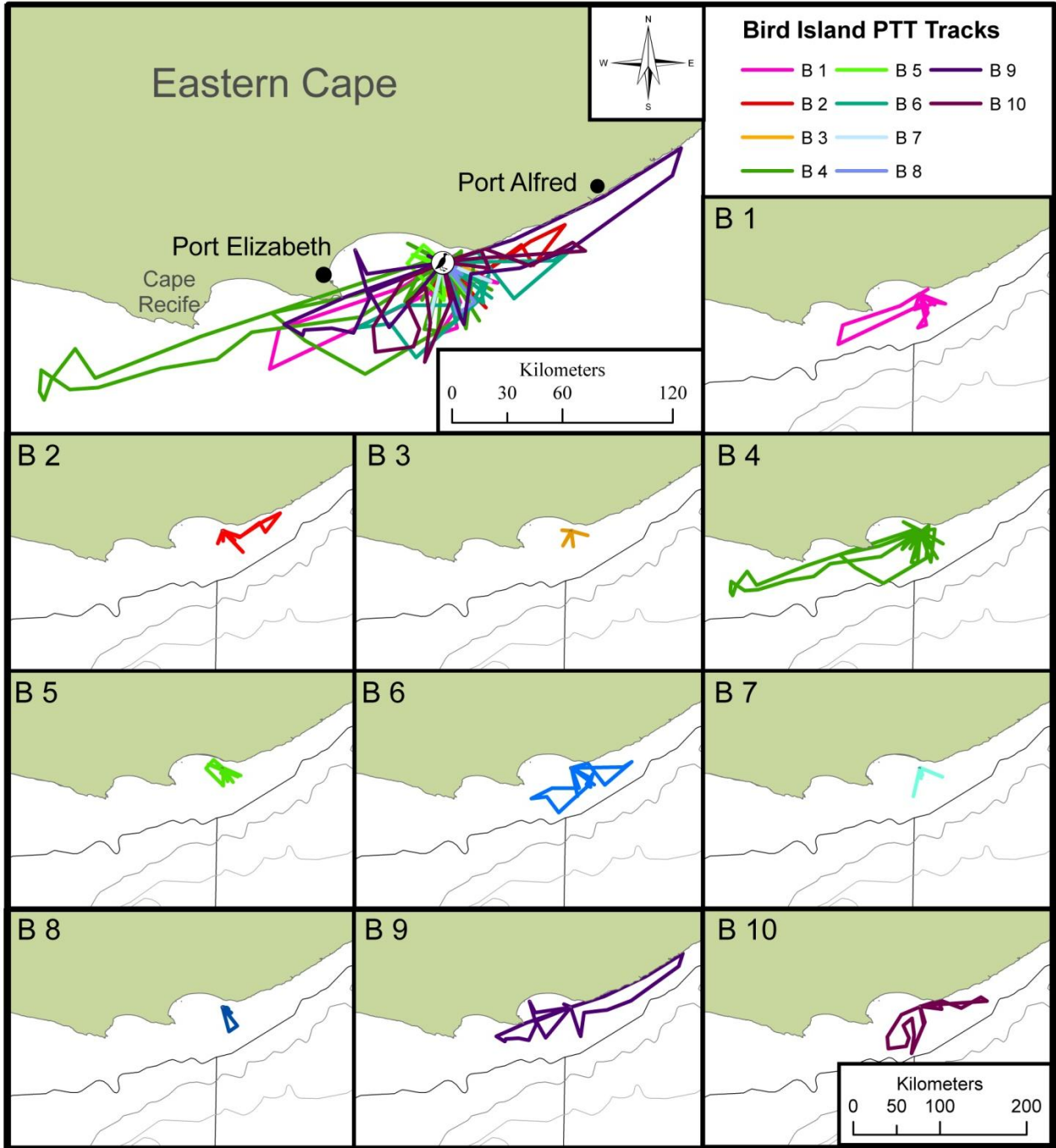


Figure 3: Pre-molt foraging tracks for individual African penguins (*Spheniscus demersus*) monitored from Bird Island, Eastern Cape, South Africa during the pre-molt foraging period of 2012. Bathymetry lines represent 200 m (black), 2,000 m (grey), and 4,000 m (light grey) depth zones.

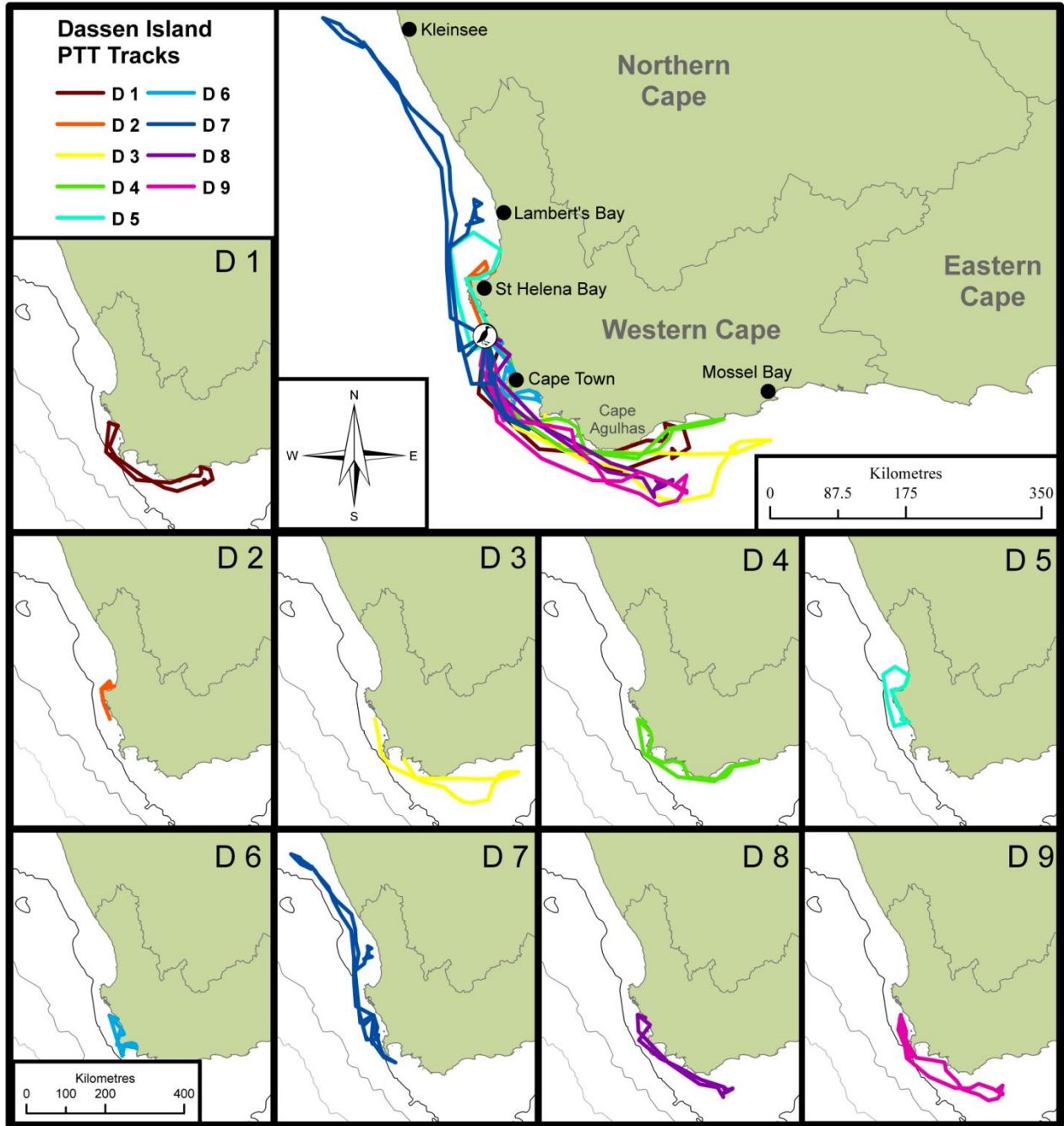


Figure 4: Pre-moult foraging tracks for individual African penguins (*Spheniscus demersus*) monitored from Dassen Island, Western Cape, South Africa during the pre-moult foraging period of 2012. Bathymetry lines represent 200 m (black), 2,000 m (grey), and 4,000 m (light grey) depth zones.

2.9.1 Standardized parameters

Dassen Island birds spent less time within 40 km of their colony ($W=5.5$, $p=0.001$, $n_1=9$, $n_2=10$), spending more than six times as many days outside the 40 km range than penguins from Bird Island (Figure 6). Similarly, individuals from Dassen Island had proportionately fewer trips from the island ($W=79$, $p=0.006$, $n_1=9$, $n_2=10$, Figure 6). Along with PTT tracks in Figure 4, this provides evidence that Dassen Island birds were not using the colony as a home base while foraging.

2.9.2 Minimum duration of pre-moult

The overall mean duration of pre-moult observed in this study (37 ± 20 days, Appendix 1) is similar to the estimate previously reported (34.5 ± 6.2 days, Randall 1983). Although it took individuals from Dassen Island an average of six more days than those from Bird Island to begin moult (39 ± 24 days and 33 ± 10 days, respectively), there was no significant difference between colonies ($t_{12}=-0.54$, $p=0.6$). The lack of statistical significance is likely due to small sample size and the apparently large variation among individuals in this parameter.

2.9.3 Travelling to foraging grounds

Dassen Island penguins travelled more than twice as far as those from Bird Island ($F_{1,30}=10.82$, $p=0.003$, Figure 5). Individuals from Dassen Island travelled at an average rate of 48 ± 13 km.d⁻¹ from the island and 63 ± 9 km.d⁻¹ when returning to the island. Penguins from Bird Island travelled 37 ± 9 km.d⁻¹ when leaving and 50 ± 11 km.d⁻¹ when returning. The differences in daily rate of travel were significant for both directionality ($F_{1,29}=12.48$, $p=0.001$) and colony ($F_{1,30}=8.24$, $p=0.008$, Figure 5). There was no interaction effect between the two explanatory variables. All values for individual travelling periods are listed in Appendix 2. When combined with the time taken to achieve moult, this provides convincing evidence that Dassen Island birds worked harder than Bird Island penguins to accumulate sufficient body reserves to commence moulting.

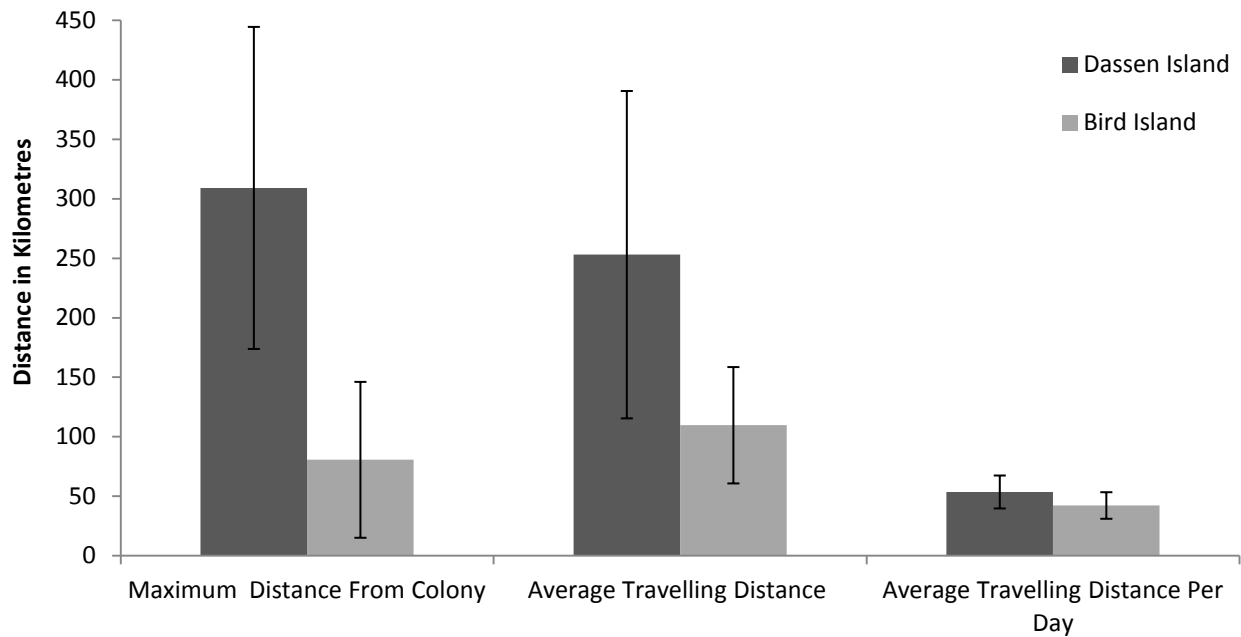


Figure 5: Distance related variables of African penguins (*Spheniscus demersus*) tracked during the 2012 pre-moult period for both Bird Island and Dassen Island. Error bars represent 1 standard deviation. All three measures above demonstrated significant differences between colonies.

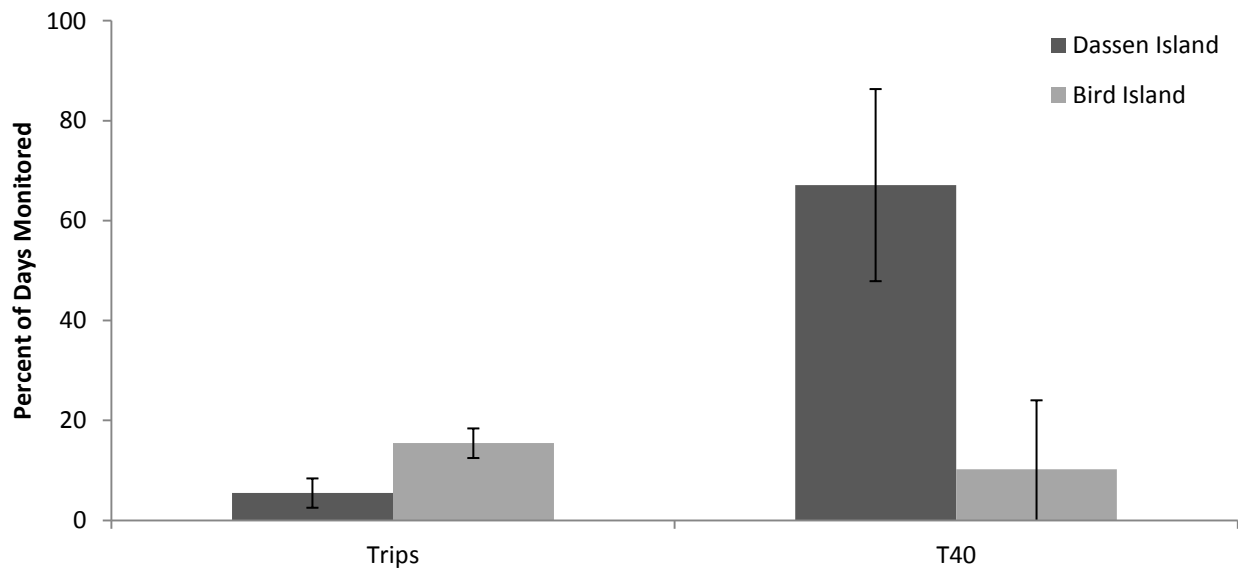


Figure 6: Standardized foraging parameters of African penguins (*Spheniscus demersus*) tracked during the 2012 pre-moult period for both Bird and Dassen Island. Both parameters were significantly different between colonies, error bars represent 1 standard deviation. Both measures above showed significant differences between colonies. T40 refers to the percent of time individuals were monitored that they spent more than 40 km from the colony.

2.10 Kernel Density Analysis

In the first week of monitoring (tracking via AGROS satellite) birds from Dassen Island, four individuals made at least two trips to Grotto Bay, a private nature reserve on the west coast located *ca* 20 km east of Dassen Island, suggesting this is an area frequented by birds from local colonies before they leave the island to commence pre-moult foraging. The area denoting 50% use for birds from Dassen Island stretches from Lambert's Bay to the west of False Bay, with an area of importance (75% use) including the Agulhas Bank (Figure 7A). The area near St Helena Bay was heavily influenced by D2 and D5, which demonstrated central place foraging based on the Paternoster Rocks and St Helena Bay, respectively. Figure 7B displays the results of KDA when these two individuals were removed from the analysis, and reveals that the area of importance shifts to the south and east. The 50% kernel includes the area between Saldanha Bay and the central Agulhas Bank. Penguins from Dassen Island not foraging from their colony or other fixed sites during the pre-moult phase, have areas of importance to the south and east of the colony, centred between Cape Point and Cape Agulhas. By comparing Figure 7A and 7B, the presence of D2 and D5 causes a change in the centre of the utility distribution by 150 km for 25, 50, and 75% distributions. The majority of time was spent between St Helena Bay and Cape Agulhas, spanning the 50-75% use areas of both Figure 7A and 7B.

As expected, KDA illustrated that individuals from Bird Island were far more constrained compared to those from Dassen Island. Their 25, 50, 75, and 90% utility distributions were within 10, 15, 25-30, and 50-70 km of Bird Island, respectively (Figure 8). Even with the removal of all land-based points for this analysis, monitored birds were located within 20 km of the colony 50% of the time.

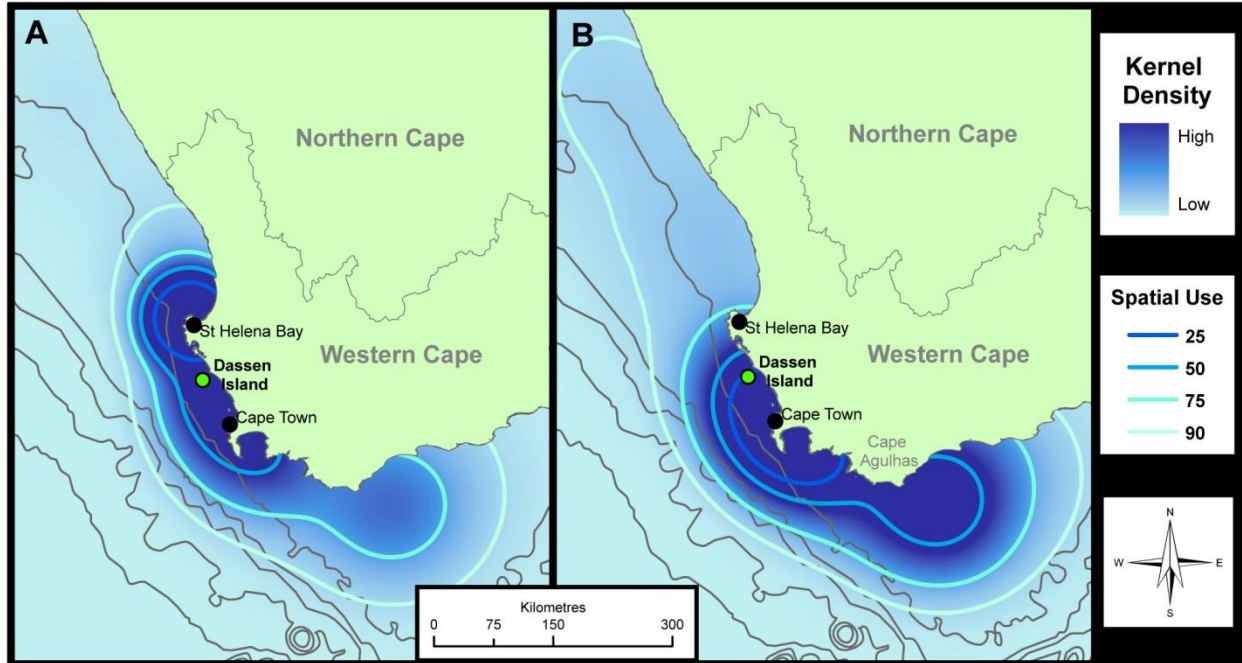


Figure 7: Kernel density analysis (KDA) of spatial use by nine African penguins (*Spheniscus demersus*) from Dassen Island with isolines representing percent area use in 2012. Maps represent A) all Dassen Island penguins, and B) the removal of birds demonstrating central place foraging (D2 and D5) from the KDA. Dassen Island is identified by a green dot.

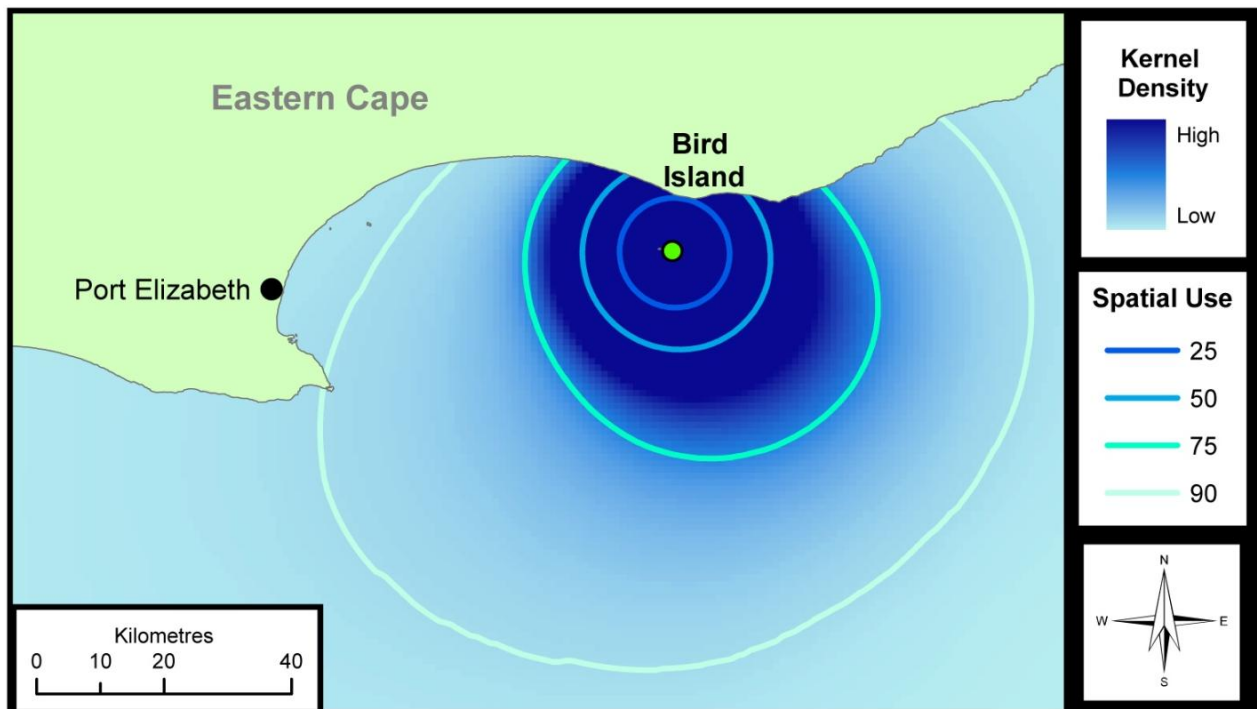


Figure 8: Kernel density analysis of spatial use by 10 African penguins (*Spheniscus demersus*) monitored from Bird Island with isolines representing percent area use in 2012. Bird Island is identified with a green dot.

2.11 Small-pelagic fishery catch data

Sardine, anchovy, and total catches were significantly greater in all kernel areas for birds from Dassen Island (all birds, Fig. 6A) than for those from Bird Island (anchovy: $F_{2,9}=11.25$, $p=0.004$, sardine: $F_{2,9}=7.86$, $p=0.01$, total: $F_{2,9}=10.45$, $p=0.005$, Table 3). The majority of fishing occurred west of Cape Agulhas, with no anchovy and only small quantities of sardine caught east of Cape Agulhas (Figure 9). Most anchovy were caught between Cape Point and Lambert's Bay, whereas sardines were mainly caught between Cape Point and Cape Agulhas (Figure 9). The largest catch in a single PFB (18.5 x 18.5 km designated fishing area) occurred adjacent to Dassen Island (PFB centred at 18°08'E, 33°42'S), with a total catch of 8,832 tonnes of anchovy and sardine combined. All fishing in this PFB occurred between 7-30 September, when PTT deployments were made and adults began foraging to gain mass. The two PFBs with the next highest catches were located in St Helena Bay and off Paternoster Rocks, 80 km north of Dassen Island (4,400 and 3,882 tonnes, respectively). Most of the catches in these three PFBs were anchovy, with less than 140 tonnes of sardine caught in each PFB.

A total catch of only 150 tonnes was taken within the 90% use area around Bird Island, and none of that was caught within the 25 or 50% use areas. The total catch between Cape Agulhas and Cape Recife during this study was only 1,030 tonnes of sardine, compared to 57,210 tonnes off the west coast. Almost all fishing activity occurred within 75-90% use areas of Dassen Island birds, and over 70% of fish extraction occurred within the 50% use area of monitored birds from this colony (Table 3).

Table 3: Catches of anchovy (*Engraulis encrasicolus*) and sardine (*Sardinops sagax*) from September-December 2012, the pre-moult period for African penguins (*Spheniscus demersus*), in each of the four utility distributions identified for penguins from Dassen Island and Bird Island.

Colony	Percent use area	Anchovy (tonnes)	Sardine (tonnes)	Combined catch as a % of the total catch
Bird Island	90	0	185	<1
	75	0	32	<1
	50	0	0	0
	25	0	0	0
Dassen Island	90	43,975	13,257	98
	75	43,975	13,179	98
	50	36,018	5,200	71
	25	12,576	1,053	23

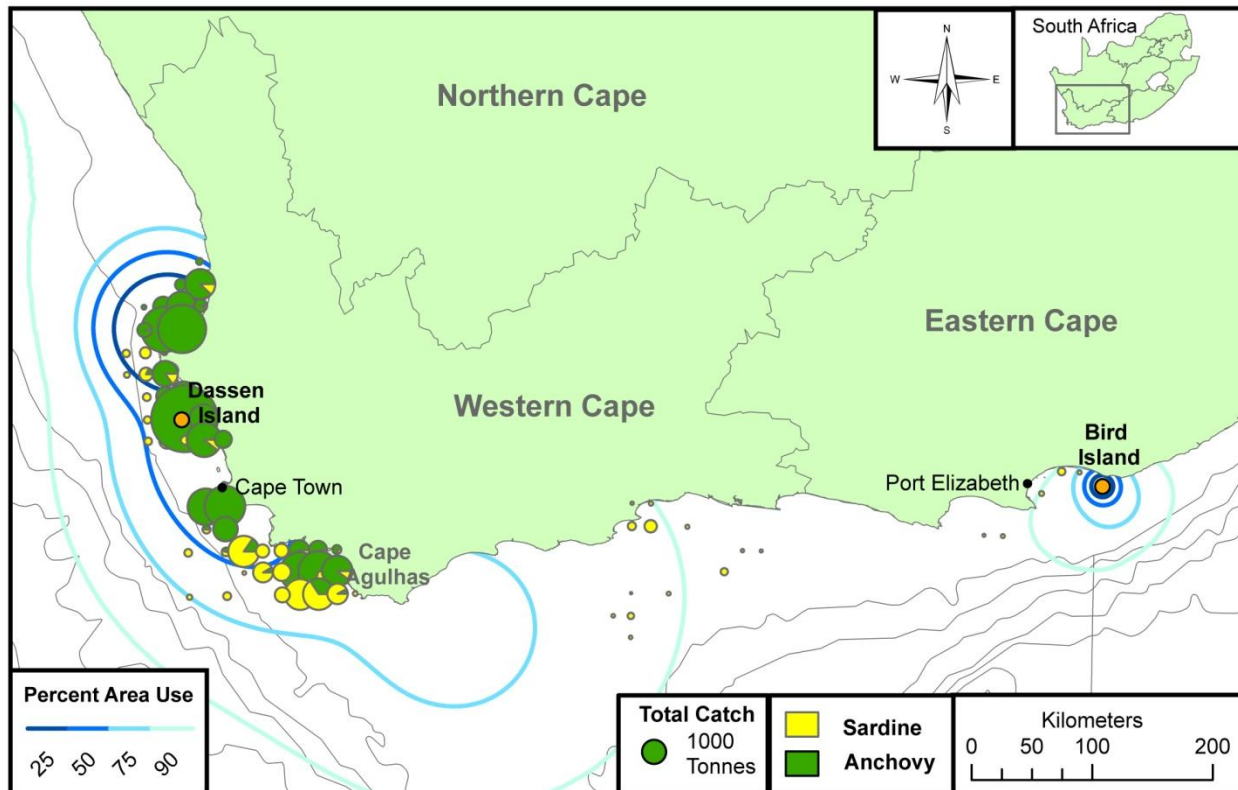


Figure 9: South African catch data (September-December) for sardine and anchovy with utility distributions of Africa penguins (*Spheniscus demersus*) during the pre-moult foraging period of September through November 2012. Circle size is proportionate to the amount of fish caught in each pelagic fishing block. Dassen and Bird Islands are identified by orange dots. Fishery catch data is compliments of Carl van der Lingen at the Department of Agriculture, Forestry and Fisheries.

Discussion

This study provides the first map-based data representing foraging strategies and movement patterns of African penguins when not breeding, adding to our understanding of year-round spatial use by this species. The results show that pre-moult adults from a west coast colony have significantly larger foraging ranges than conspecifics from the south coast. Unlike the penguins from Bird Island, they do not rely on the area around their breeding colony for food, typically foraging over 300 km from their colony. They also demonstrated greater foraging effort through higher daily rate of movement when travelling to foraging areas. With significant differences between colonies in all foraging parameters investigated (refer to section 2.9), including the size of kernel use areas, it is clear that penguins from the two islands employ different foraging behaviours during the pre-moult phase. Such differences in foraging strategies

demonstrate the importance of a regional understanding of spatial use of the marine environment by African penguins at various life history stages for proper management of the species.

In 2012, the draft Biodiversity Management Plan for the African penguin was released for public comment (Shaw et al. 2012). This document reiterates the importance of adult survival throughout the year, and emphasizes a lack of understanding in spatial use by African penguins when not breeding. Tracking African penguins from Dassen and Bird islands during the pre-moult stage has revealed significant colony-specific differences in foraging strategies, identified areas of importance for penguins from these colonies, and allowed for a preliminary assessment of relative fishing pressures faced by south and west coast birds. Waller (2011) described the importance of understanding colony-specific foraging parameters, as African penguins use different foraging strategies based on local conditions such as food, predation, competition, and effects of environmental variables during the breeding season. Access to local resources during the pre-moult season is essential to African penguin survival due to the fasting requirement of the annual moult (Wolfaardt et al. 2008, 2009; Waller 2011; Shaw et al. 2012). The importance of local food availability, rather than national abundance levels, is also a consideration when creating an EAF (Shannon & Moloney 2004; Crawford et al. 2011) and is supported by the BCC (BCC 2008).

2.12 Foraging strategies and inter-colony differences

Three foraging strategies were identified during the pre-moult period; 1) a continuation of central place foraging from the breeding colony, 2) central place foraging from a location that was not the breeding colony, and 3) long looping trips away from the colony. A continuation of central-place foraging from the colony was the dominant strategy utilized at Bird Island. A surprising result was that foraging ranges of Bird Island penguins did not change substantially between breeding (Pichegru et al. 2010) and pre-moult stages (this thesis). Despite being freed from the obligation to return to the colony to feed chicks, adults continued to use the colony as a base, suggesting that optimal foraging was consistently close to Bird Island.

By comparison, no penguins from Dassen Island stayed at the colony to forage. This suggests that there is significant disturbance or competition, or insufficient resources necessary to achieve moulting condition in the vicinity of the colony. Crawford et al. (2006b) demonstrated that the pre-moult period occurs during a three-month window when abundance of

sardine is at an annual low, and suggested that this may force African penguins to forage in locations farther from the colony. This period of lower food availability from September-November is mirrored by catch rates of the small-pelagic fishery, which are also lowest during this period (Agenbag et al. 2003).

It has been hypothesized that individual penguins may range farther from their colony when not breeding and may moult at colonies other than the one at which they breed (Randall et al. 1987; Whittington et al. 2005a, 2005b). Wolfaardt et al. (2009) suspected that birds from Dassen Island may forage near the Agulhas Bank and then stop at Stony Point or Boulders Beach (two colonies located between Cape Point and Cape Agulhas) to moult, skewing the ratios of moulting birds to breeders in the following season. The foraging track of D3 confirms this pattern, as this individual left Dassen Island, spent 15 days foraging near the Agulhas Bank, then moulted at Stony Point.

2.13 Travelling variables

The importance of local fish abundance has been demonstrated for Magellanic penguins during the breeding season, as distance travelled to foraging grounds is negatively correlated to breeding success due to increased energy use (Boersma & Rebstock 2009). Energy expenditure of African penguins when foraging and swimming is estimated to be 6.6-9.8 times the standard metabolic rate when resting on land (Nagy et al. 1984), suggesting that individuals travelling farther to feed and spending more time at sea use much more energy than those using a land-based central location travelling shorter distances. Birds that make long looping trips must either catch more prey, be more efficient in their foraging activities and energy use, or are adversely affected by higher energy costs associated with longer travel distances and higher rates of travel.

Since 2002, there has been a continuous decrease in both the number of breeding pairs and the number of penguins moulting at colonies on the west coast (Crawford et al. 2011). An increase in foraging effort during the pre-moult season presumably has life-time reproductive fitness consequences, and could contribute to the low, decreasing survival observed from Dassen Island penguins since 2002 (Crawford et al. 2011). Alternatively, a lengthy delay before birds enter moult could contribute to fewer adults reaching breeding condition and therefore lower levels of breeding participation and increased divorce rates leading to forgone reproductive opportunities (Wolfaardt et al. 2009). Considering the importance of the pair bond (mate

fidelity) in African penguins during the breeding season (Randall 1983; Crawford et al. 1995a; Wolfaardt et al. 2008), lower survival through the moulting period could have serious implications for the following breeding season, and therefore the future of African penguin populations.

2.14 Important areas identified

Once moving away on longer journeys, no individuals returned to Grotto Bay, suggesting that this could be an area of importance during the chick rearing season when they must forage close enough to return to the colony to care for young. Once penguins left Dassen Island, half visited the Agulhas Bank. This location had previously been recorded as an area visited by non-breeding African penguins, when 'Pamela' (one of three tracked birds) travelled there after the *Treasure* oil spill in 2000 (Barham et al. 2006).

Areas important for foraging by pre-moult penguins from Dassen Island are much larger than those of birds from Bird Island, and are not centred on the colony, making it harder to manage the threats to this population. Despite the areas of high use being smaller for Bird Island penguins than those from Dassen Island, the 75% use areas (ranging 35 km from the colony) suggest that fishing closures would need to be greater than 20 km around colonies to contain the majority of foraging during the pre-moult season. This supports the conclusion that the current experimental fishery closures around selected breeding islands (20 km radius) are too small to aid breeding populations of African penguins (Pichegru et al. 2011). The situation is even worse at Dassen Island, where the large range suggests the need for a different management strategy to reduce fishing pressure on west coast penguins.

The 90% use area of penguins monitored from Dassen Island, from north of Lambert's Bay to east of Cape Agulhas, covers the same region of use reported for breeding Cape gannets from Saldanha Bay (Pichegru et al. 2009). In both studies, all individuals foraging east of Cape Agulhas returned west between 20-22°E, suggesting that this is as far east as colonial seabirds from the west coast forage. This apparent limit may be due to an environmental barrier caused by a lack of food in this area. Estimated densities of both sardine and anchovy are, and have historically been, low in this 2° region immediately east of Cape Agulhas (Agenbag et al. 2003; Roy et al. 2007; Coetzee et al. 2008).

2.15 Overlap of penguin foraging areas, fish catches, and fish abundance

The rate of fish extraction around Dassen Island is currently much higher than around Bird Island (Table 3). Fishing pressure potentially has negative impacts on penguins using the area around the island as a result of depletion of local fish stocks, an aversion to fishing boats, or a combination of these factors. Peruvian boobies also avoid areas of active fishing (Bertrand et al. 2012). Fishery impacts provide one explanation for the larger foraging ranges of penguins from Dassen Island, but more evidence is necessary to test this hypothesis. Comparing individual tracks from Dassen Island with catch data from September-December it is evident that six birds travelled to foraging grounds outside of the area where high levels of fishing occurred (St Helena Bay to the western Agulhas Bank). Those that did not follow this pattern were D2 and D5 which demonstrated a different foraging strategy than other birds from Dassen Island, and D3 who foraged in an area of False Bay (Gordon's Bay) with a high density of anchovy and sardine (Figure 10 and 11) where fishing has been banned. This theme is explored more fully in Chapter 3.

Low fish abundance and local overfishing could also explain why two individuals did not return to Dassen Island (D2 and D7) before losing signal from their PTTs. D2 may have moulted on the Paternoster Rocks where it was last recorded, but its PTT was not recovered and no observations were made of penguins moulting at this site. Signal from D7 stopped transmitting over 50 km from the coastline after 88 days of monitoring due to either a depleted battery, loss of the device, or the individual dying at sea.

Values of estimated spawner biomass must be taken as estimates only, as they are derived from static snapshots of dynamic, mobile species that move during the duration of these surveys. The results of the 2012 spawner biomass surveys of sardine and anchovy (Shabangu et al. 2012) illustrate that the highest densities of both species were found east of Cape Agulhas, with a region of high density between Cape Point and Cape Agulhas for both species (Figure 10 and Figure 11). The abundance of sardine was also lower than it has been for the last four years and below the 29-year average (Shabangu et al. 2012). However, the region of highest anchovy extraction (*ca* 80% of total) was on the west coast between Cape Point and Hondeklip Bay (Figure 9) where less than 3% of the estimated anchovy abundance occurred (Shabangu et al. 2012). The higher density of sardine between Cape Point and Cape Agulhas (51% of estimated sardine biomass, Figure 11) corresponds with higher levels of sardine extraction (70% of total) in

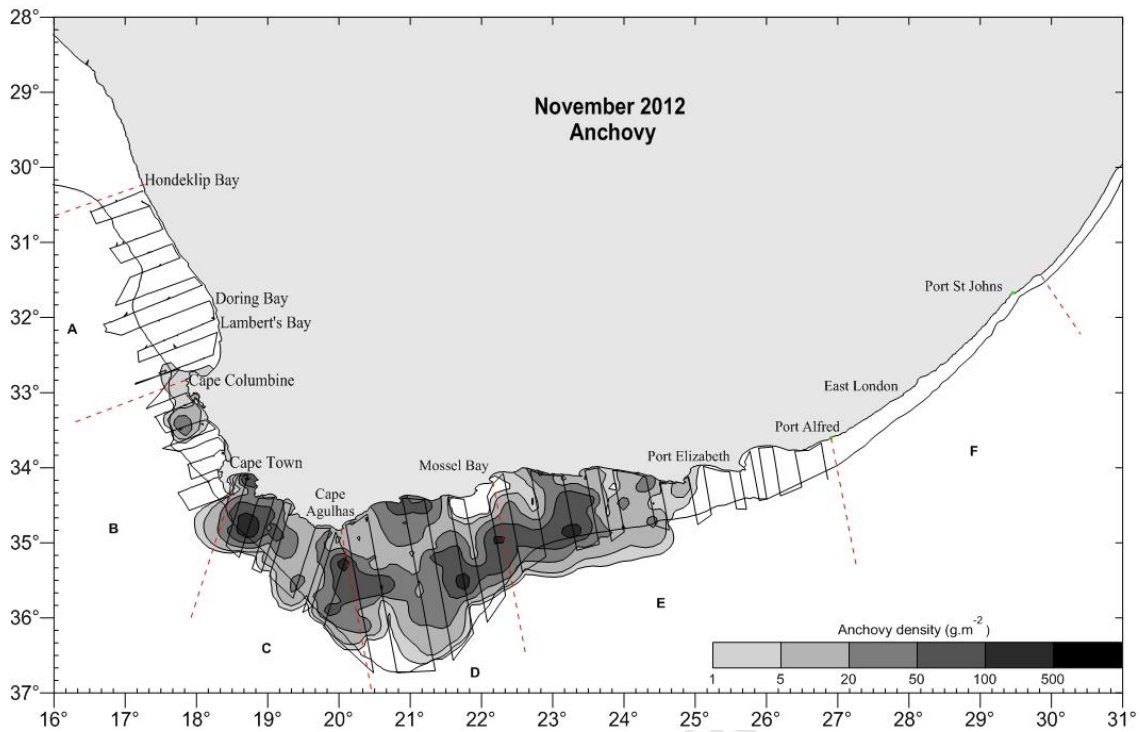


Figure 10: Distribution and relative density of anchovy (*Engraulis encrasicolus*) during the November-December 2012 surveys (from the Department of Environmental Affairs; Shabangu et al. 2012).

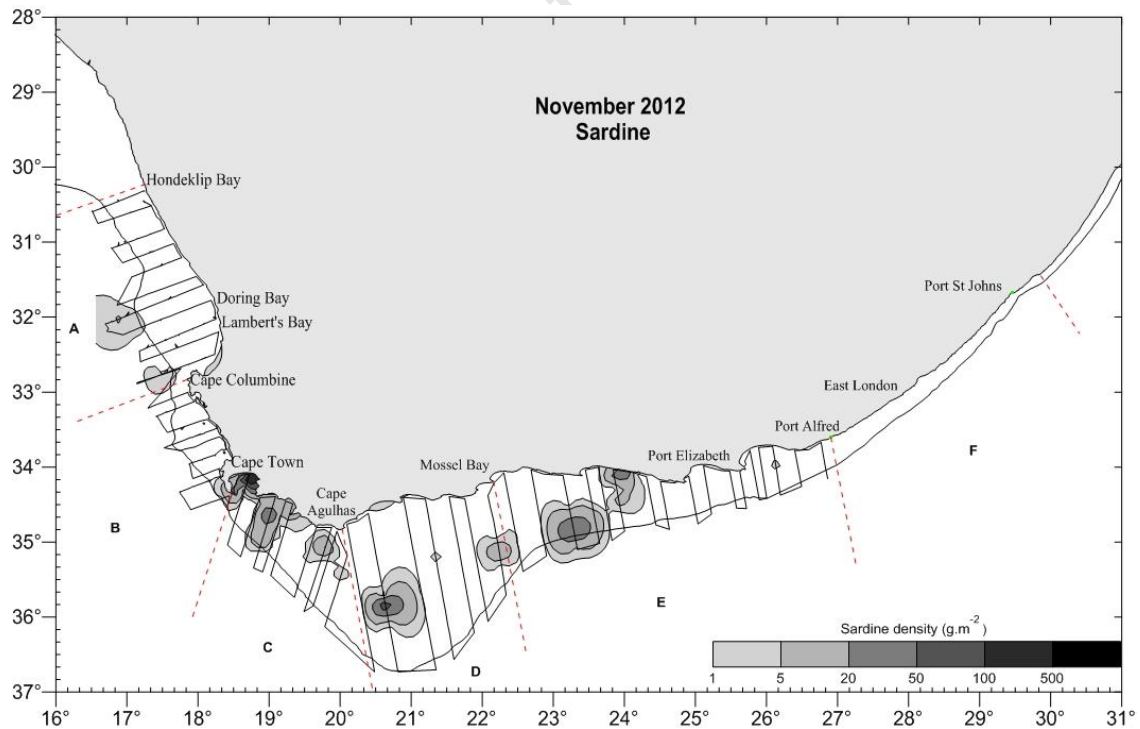


Figure 11: Distribution and relative density of sardine (*Sardinops sagax*) during the November-December 2012 surveys (from the Department of Environmental Affairs; Shabangu et al. 2012).

this region (Figure 9). Seven of the nine penguins from Dassen Island chose to forage between Cape Point and the central Agulhas Bank (Figure 4) in areas of high fish abundance, away from the low density of anchovy and sardine near Dassen Island (Figure 10, Figure 11).

2.16 Duration of pre-moult foraging

Despite the duration of moult being similar between the colonies and to Randall's (1983) estimate, the extended pre-moult foraging trips by some birds from Dassen Island are of concern when considered with the lower return rate of loggers and observations of moulting study birds. Two of the three birds that were monitored for more than 40 days without moulting did not return to the island before signal from the PTT was lost (D2 and D7), suggesting they either died or the battery of the PTT was depleted. Both birds foraged north of the island, one in St Helena Bay and the other towards the Namibian border between Lambert's Bay and Kleinsee. By comparison, six individuals taking less than 40 days to return to the island were observed moulting or preparing to moult. These observations suggest that birds taking longer in the pre-moult phase are at a higher risk of death, as moult cannot be partial or abandoned without consequences to future survival (Cooper 1976). Further decreases in adult survival will be detrimental to the future survival of African penguins through both immediate population declines due to adult mortality, and the loss of long-term contribution to future breeding seasons. Developing management strategies that take into account inter-colony differences and annual variation may be difficult, but will be necessary to properly aid in halting the population decline of African penguins.

Chapter 3: Synthesis and evidence for a disturbance hypothesis

Conclusions and implications for conservation of the African penguin

Management strategies can be simplified to cover large areas based on generalized trends and averages, including multiple populations under one strategy. For example, the way in which the current sardine TAC in South Africa is managed does not take into account evidence for multiple fish stocks that could be managed separately, despite this is being considered for future management plans (Coetzee & Merkle 2012). In the case of the African penguin, strategies involving adaptive management techniques incorporating regional (or colony-specific) differences would be necessary to properly manage the population while minimizing impacts on the fishery. Future management should consider variation in important areas of use at different times of the annual cycle of African penguins (Petersen et al. 2006; Waller 2011; this study), and annual fluctuation in the distribution and abundance of fish stocks (Hutchings et al. 1998; Roy et al. 2007a; Coetzee et al. 2008). Incorporating all of these aspects into a management plan is seeded within the goals of an EAF, highly regarded by the BCC as the type of management necessary within the Benguela system (BCC 2008).

Comparing small-pelagic catch rates between Cape Point and Hondeklip Bay to the estimated abundance of fish, illustrates the continued imbalance of catch locations of the small-pelagic fishery (Coetzee et al. 2008, Shabangu et al. 2012, Figure 10 and 11). This emphasizes the need for spatial management within the small-pelagic fishery, either in the form of closures (year round, or portions of the year), or through a form of regional management based on annual fish abundance per region.

The addition of spatial information from the pre-moult foraging period to the current understanding of how African penguins are using South African waters is another step towards understanding the potential threats causing their current population declines. Although it is hard to draw robust conclusions from a single year of monitoring, the results of this study demonstrate the potential for misguided management if a single-solution plan is used to manage the African penguin population. The incorporation of inter-colony differences must be highlighted to prevent implementation of management strategies that would further impact African penguin populations. The goal of African penguin conservation is to help prevent the extinction of a species, a 'marine sentinel' that responds to the health of the South African coastal systems

(Boersma 2008), a species that is currently in decline, and showing no signs of altering this trend.

Study limitations

This study was limited by the single year data set, the relatively coarse resolution of the data (both temporally and spatially), and the small sample size. Contributing multiple years of data would allow for long-term comparisons to the changing distribution of fish availability and fishing effort (van der Lingen 2005; Roy et al. 2007; Coetzee et al. 2008), and therefore add more thorough analyses to management procedures. Another factor limiting the understanding of foraging patterns is the ‘snapshot’ like views of the location of anchovy and sardine around the coast used for fish density estimates. Densities of spawner biomass are estimated based on transects that are only visited once over the annual data collection period (usually Oct-Nov, but November-December in 2012). As both fish species are mobile schooling fish, these estimates represent a very static version of reality (Hutchings et al. 1998, 2002; Barange et al. 1999), and must be used as rough estimates only. The small sample size of African penguins is only a representation of the entire population, and continued monitoring would help to see if areas targeted by the individuals from this study are similar to areas targeted in future pre-moult deployments. The density of sardine and anchovy around west coast colonies has been investigated to demonstrate the availability of fish to birds at Robben and Dassen Island within 20 km of their colonies. Collecting a higher resolution (both temporal and spatial) of abundance data than the bi-annual spawner biomass surveys, these hydro-acoustic surveys aim for monthly sampling around both colonies (Merkle et al. 2012). This year’s surveys stopped in September, however in subsequent years of study, this information could be invaluable to understanding movements of non-breeding birds if such surveys can be conducted during the period of pre- and post-moult foraging.

Estimates of the duration of pre-moult foraging are less specific than they could have been if more intensive monitoring occurred as birds returned to moult. In future pre-moult monitoring, I suggest that observations similar to those made by Randall (1983) on St Croix Island are made to more accurately divide the pre-moult period between i) the duration of at sea self-foraging, ii) days between returning to land and moulting, and iii) the duration of moult. This would require more time in the colonies, or increased monitoring by island staff. Increased

monitoring would allow for more accurate comparison between colonies to further investigate the observed differences between Bird and Dassen Island in this study. This would also provide a better comparison to the historical data collected by Randall (1983) to investigate potential changes in the time needed to complete these phases. The division of pre-moult phases would produce a more accurate understanding of which phases were changing over time, and if they could be contributing to fewer individuals entering or surviving the moulting phase.

Anecdotal evidence for a disturbance hypothesis

Analyzing fish catch data and seabird movement patterns in sequential time periods at fine temporal and spatial scales allows for a better understanding of how seabirds move in relation to fish removal than comparing large areas where overlaps occur (Torres et al. 2013). In this section I summarize the evidence for a disturbance hypothesis suggesting that penguins may move away from areas where fishing occurs (R.M. Wanless, pers.comm.), similar to that described by Bertrand et al. (2012) for the Peruvian booby. Movements of satellite-tagged African penguins from Dassen Island that provide preliminary evidence for this hypothesis are described below. A chi-squared test was performed to determine if the distribution of penguins in relation to fishing boats followed the expected level of overlap. Figures illustrate weekly movement of penguins and weekly catch totals, but catch data and penguin movements were available daily, and therefore finer-scale interactions are reported in the text. Only in weeks where both a spatial (within the same PFB) and temporal (on the same day) overlap occurs are figures and descriptions reported. There was no overlap during Week 4-5, or after Week 7, therefore these weeks are left out of figures and descriptions.

Penguins spent the night in a PFB where fishing occurred on the same day only 2.7% of the time, with 75% of these observations from the same individual (D2). There were only six events of overlap, and half of these occurrences resulted in a penguin leaving the PFB. On two occasions when penguins left, more than 2,900 tonnes of fish were caught in the PFB, the annual fish requirement of approximately 20,000 African penguins (Nagy et al. 1984). These events lasted no more than three days, and each event had one day where more than 2,000 tonnes were removed. These two events occurred in the PFB around Dassen Island and the Paternoster Rocks, with D7 and D2 leaving these areas, respectively.

On the three occasions that birds stayed, they were individuals that were central place foraging from a location that was not their colony (D2 and D5). Less than 400 tonnes of fish were caught over 2-3 days on two occasions, and in the third instance, fishing was spread over five days with a maximum of 600 tonnes removed in a single day. The few occasions of overlap that occurred between penguin foraging and fishing activity demonstrated that there were fewer days when both penguins and fishing boats were present in the same PFB than expected ($\chi^2=281$, $df=1$, $p<0.001$), suggesting that penguins may avoid fishing boats. This could relate to the amount of time boats are spending in the area, the number of boats present, the amount of fish being removed, stress boats cause penguins, or the alteration of fish schooling behaviour when fishing occurs. More observations of overlap are necessary to investigate this hypothesis further. The presence of successful fishing days suggests that there are fish available in the vicinity of penguins while they are relocating in search of other foraging grounds.

Weeks 0-1: 2-8 and 9-15 September

A total of 8,750 tonnes of sardine and anchovy was caught in the PFBs between Saldanha Bay and Robben Island during Week 0. The PFB surrounding Dassen Island contributed 54% of the catch, and over 90% of the total catch for the week was removed from PFBs within 20 km of Dassen Island (Figure 12). All catches occurred from 4-7 September, the week before deployments took place on Dassen Island (11-12 September). Following deployments, three penguins moved south (D3, D7, and D9) towards Cape Point, one (D2) swam north towards Saldanha Bay, while the other five spent their nights in Grotto Bay, >20 km from Dassen Island, where minimal fishing occurred in the previous week (Figure 12, Week 1).

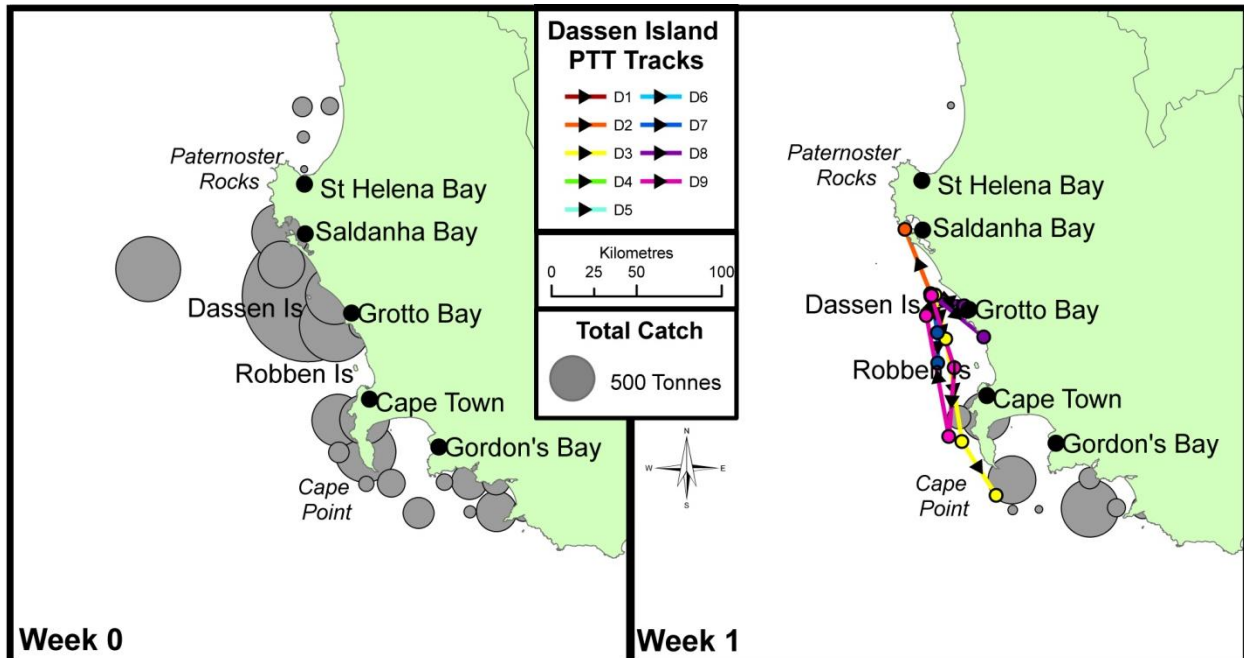


Figure 12: Fish catch data in Week 0 (September 2-8) and Week 1 (September 9-15), with associated penguin movements in Week 1. Fish catches are represented by grey circles, proportional to the amount of fish caught in tonnes within a Pelagic Fishing Block. Arrows represent the direction of travel for each penguin.

Week 2: 16-22 September

Both D2 and D5 arrived off Cape Columbine while high levels of fish extraction were occurring in St Helena Bay. A total of 6,600 tonnes of anchovy and sardine were caught from 16-20 September in St Helena Bay. D5 swam north of fishing areas in St Helena Bay, and did not enter these PFBs until the day after fishing ceased. D2 remained on the Paternoster Rocks, west of St Helena Bay, where only a few hundred tonnes of fish were extracted. Fishing continued in six PFBs around Dassen Island between the 17-20 September, and three penguins moved south of Dassen Island during this period. D4 and D6 continued to overnight in Grotto Bay, and then moved south to Table Bay (Figure 13). All penguins had left the island at this time.

Week 3: 23-29 September

D7 returned to Dassen Island on the 22 September and left again three days later, coinciding with the second largest catch in a PFB, taking place around Dassen Island, the same day fishing activity started in two PFBs off Hout Bay (between Cape Town and Cape Point). D7 again moved south of Dassen Island and spent five nights between these areas without entering PFBs where fishing took place. D6 swam around Cape Point and into False Bay, where

commercial purse-seining has been banned since the 1980s, overnighing off Gordon's Bay (Figure 13).

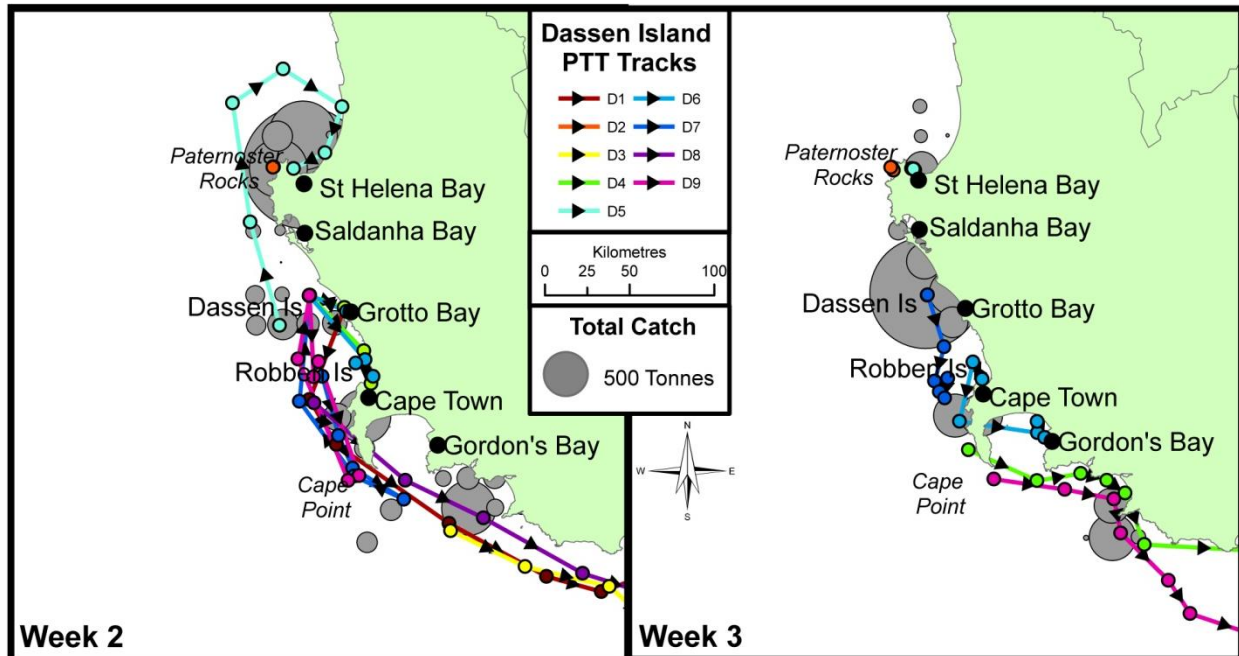


Figure 13: Penguin paths and fish catch data from Week 2 (September 16-22) and Week 3 (September 23-29); conventions as Figure 12.

Weeks 6 and 7: 14-20 and 21-27 October

D2 spent the entire pre-moult period based at Paternoster Rock in St Helena Bay. The only time it left this site was for three days, on 18 October, which coincided with the timing of heavy fishing pressure. Most fishing occurred around Cape Columbine and the southern part of St Helena Bay in Week 6 (mainly from 16-18 October), removing 4,228 tonnes of anchovy and sardine. More than 60% of this total was caught on 17 October in the PFB surrounding the Paternoster Rocks. This behaviour suggests that despite an abundance of fish (evidenced by successful fishing), D2 chose to leave its preferred foraging area during the period of high fishing pressure. In Week 7, no fishing occurred around Paternoster Rocks, and D2 returned on October 21, three days after fishing stopped (Figure 14).

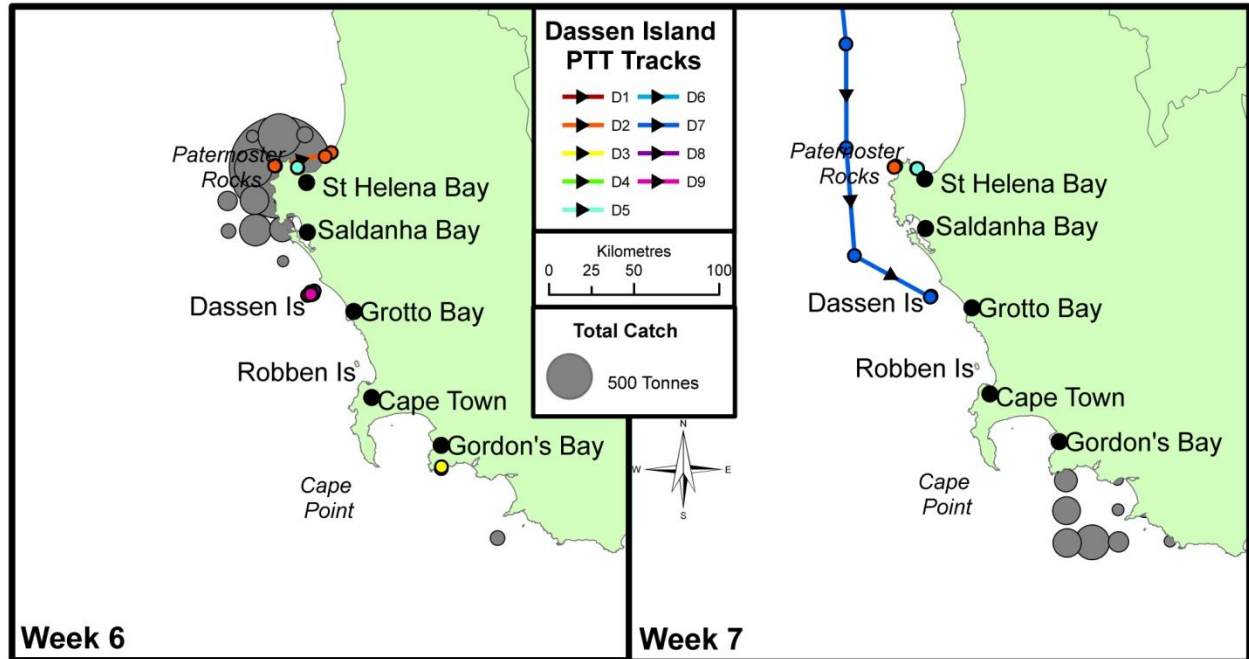


Figure 14: Penguin paths and fish catch data for Week 6 (October 14-20) and Week 7 (October 21-27); conventions as Figure 12.

More accurate spatial data on the location of boats are necessary to pursue this hypothesis in more detail, as locations of fish catches are only given to the nearest 10 nautical miles (PFBs). Vessel monitoring systems (VMS) have been used to better position fishing vessels temporally and spatially in relation to foraging seabirds (i.e. Votier et al. 2010; Granadeiro et al. 2011; Torres et al. 2011). Fishing may occur on one side of the PFB while the bird is close to 20 km away. In future studies, this hypothesis could be tested by investigating the likelihood of penguins leaving a PFB they occupy when fishing is initiated. If the likelihood of leaving a PFB once fishing starts is higher than expected, this would suggest displacement of penguins due to disturbance by fishing activity. Results from this research would better quantify the direct relationship between fishing activities and the decision by penguins to forage in specific locations. Locations of penguins were collected at night, a period of rest for African penguins (Petersen et al. 2006), and therefore movements are coarsely estimated from the next nights location, using only the next PPN. To properly investigate direct interactions between African penguins and fishing vessels, a finer spatial and temporal scale of penguin movement would be necessary. Such analysis would require hourly GPS points (instead of daily), which typically have accuracy greater than the minimum of 250 m accuracy given from PTTs using ARGOS satellite positioning.

Future research

3.1 Allee effects

One potential hypothesis for the African penguin's declining population is that group foraging efficiency has decreased due to small or declining local numbers of birds. Foraging behaviour of African penguins was previously thought to be a solitary activity, or to include only a few individuals, with <5 birds foraging at a time on average and a maximum of 15 birds foraging synchronously (Wilson et al. 1988a, 1988b). When >20 individuals are foraging, it has been suggested that synchronous foraging is not possible to co-ordinate between penguins, however >20 birds may be seen in travelling groups (Wilson et al. 1998a). New evidence shows hundreds of birds involved in "herding" behaviour with some on the surface and up to 75% of the group beneath the water (Ryan et al. 2012). Group foraging tactics may increase fishing efficiency on a 'bait ball' (Ryan et al. 2012). In some cases however, colony-specific population decreases would preclude group foraging, as their entire colony may not be large enough for the observed large group tactics (Ryan et al. 2012). The impact of Allee effects at the local population level will depend on the extent to which African penguins rely on this foraging strategy. Historical observations of group foraging have shown no temporal changes in group size (Wilson et al. 1988b), suggesting that additional data are needed to investigate possible changes over time (Ryan et al. 2012), if this behaviour has simply gone unnoticed, or if it is a learned behaviour from a specific colony/region. Theoretically, group coordinated fishing tactics should be more efficient when fish schools are small and less dense, bringing the school tighter together, making the prey easier to catch than if they were spread apart, if birds involved are co-operating synchronously. My results suggest that penguins from the west coast may use the Agulhas Bank to feed in the pre-moult phase, as half of the monitored penguins from Dassen Island foraged in this area. More evidence during this phase of the annual cycle is necessary to investigate the potential benefits of group foraging tactics during the pre-moult foraging trips, or if this type of behaviour occurs by individuals from different colonies who meet at sea. As populations continue to decrease, Allee effects could become more prevalent, highlighting the importance of research targeting group dynamics and group foraging strategies in relation to local population sizes.

3.2 Post-moult foraging

To fully understand how African penguins utilize the oceans throughout their annual cycle, we also need to monitor post-moult foraging movements. This period is important as individuals must regain the body mass they have lost during the moulting season (Cooper 1976, described in Chapter 1). Added stress during this period could be detrimental to their survival, and therefore understanding where they are foraging and potential interactions is imperative to proper management of this species. During this study, I worked with the Two Oceans Aquarium (Cape Town, South Africa) to test the deployment of a PTT on a post-moult captive bird. The attachment, following Wilson et al. (1997) with the addition of a cable-tie, was successful. The deployment was carried out after the newly-grown back feathers were >22 mm in length (*ca* 85% of final length), as suggested by Dr Nola Parsons (SANCCOB Vet). This feather length was reached 5-7 days after the last old feathers were dropped. Glue was only applied lightly to the top of the device to cover joints between the layers of tape, ensuring it did not get onto the new feathers. Upon removal of the device, small amounts of residue were present on the new feathers where tape was attached, but this was preened off within a week of removal. Similar deployments have been conducted on closely related Magellanic penguins (Stokes et al. 1998), and this trial demonstrates the feasibility of post-moulting deployments on African penguins.

3.3 Monitoring duration, annual variation, and altered foraging behaviour

Multiple years of movement data are required to draw robust conclusions about the pre-moulting movements of African penguins, and their relationships to fishing activity. A single year of data may not be representative of the typical ranges used by penguins, especially given the high natural variability in the Benguela ecosystem (Cury et al. 2000). With long-term data available, analysis of foraging ranges with respect to fish abundance and fishing pressure would allow the relationship to be better understood. This is necessary for both management strategies and legislation to the fishing industries in an attempt to alleviate the pressure on affected species where appropriate (Cury et al. 2011).

Based on the different foraging strategies observed in this study, birds that remained in (or went to) areas of low food availability may have been more successful by continuing to central place forage. By commuting shorter distances to food sources, they are expected to have a lower foraging effort (Nagy et al. 1984; Boersma & Rebstock 2009), potentially compensating

for the lower densities of fish available. If African penguins are going to travel large distances, these results suggest that it is typically to areas of high fish density. Regions of low fish abundance used by African penguins at this time may also represent areas of high historic fish abundance, suggesting an affinity to foraging grounds at certain times of the year as a “learned” behaviour. This would suggest that as these individuals die out of the population, targeting areas of historically high fish abundance should become less common. To investigate this, multiple years of data collected on the same individuals could be used to see if they target the same areas annually. Knowing the age of birds may also help to see if the older members of the population are targeting areas of historic fish abundance and vice versa.

Based on anecdotal evidence presented in this chapter, it is also clear that that a new direction in African penguin research must target both the direct and indirect interactions of penguins and the fisheries through fine scale analysis. Mechanisms that may be driving movement of penguins away from areas where fishing activities are taking place should be investigated, such as a threshold of fish extraction or simply the presence of fishing vessels. This research would be directly related to conservation and management of African penguin populations to understand more about the relationship between African penguin foraging patterns and the small-pelagic fishing industry.

Synthesis

Despite interventions to alleviate pressure on African penguins through creating artificial nests, chick bolstering programs, and rotating fishing closures around penguin colony islands, the African penguin population continues to decline (Crawford et al. 2011). The need for continued collection of spatial data is evident, as South African coastal waters are in a state of change that is causing small-pelagic fish stocks to move eastward (van der Lingen 2005; Roy et al. 2007). We must understand how penguins react to these changes, in light of added pressure from the fishing industry, to properly quantify overlaps and infer the true relationship between foraging patterns, fishing pressure, and fish abundance. Teasing apart these relationships is a prerequisite to implementing appropriate conservation management strategies for African penguins. Simultaneously, it is important to ensure that management implications for fisheries are not disproportionate relative to the benefits to African penguins.

Comparing fishery catches to key areas used by foraging penguins (and other seabirds) is thought to overestimate interactions, causing misleading conclusions, if interpretations assume that overlap is equivalent to interaction (Torres et al. 2013). Torres et al. (2013) demonstrated the value of fine-scale analysis of data sets (on both temporal and spatial scales), but also described the importance of large (>100 km) and meso-scale (10-100 km) studies to lead future research in the direction appropriate to the fishery, the species in question, and the interactions that may exist. The outcomes of my study on pre-moult foraging in African penguins do not suggest that the areas identified as overlaps are equal to interactions, but simply illustrate areas where the likelihood of interactions and indirect impacts are higher. The results also demonstrate that despite the large overlap between fisheries and penguin foraging grounds (Chapter 2), there appears to be very few occasions of direct interactions on a temporal scale (this chapter). Such interactions must be investigated further, and should be considered as the direct impacts of overlaps between fishing and penguin foraging. However, Torres et al. (2013) failed to discuss how disturbance by fishing might affect seabirds and that avoidance of fishing activities needs to be considered (Bertrand et al. 2012). If fishing vessels catch fish close to seabird colonies causing seabirds to forage elsewhere, the alteration of foraging grounds due to ongoing disturbance could result in an increase in foraging effort. Building on this need for a more spatially explicit analysis, anecdotal evidence presented in this chapter describes a hypothesis for disturbance on a finer scale, derived from a broader scale preliminary analysis. This thesis is presented as a first step in understanding and exposing these patterns and highlighting areas where more detailed analysis is necessary.

Such analysis should be carried out from multiple colonies in different regions due to the large differences in foraging strategies identified for birds from different colonies both in this thesis and other studies (Petersen et al. 2006; Pichegru et al. 2010, 2011; Waller 2011). A time series of spatial foraging data is required for comparison with fishery catch data and fish abundance estimates to more accurately identify and quantify interactions (Pichegru et al. 2011). This will allow for better implementation of management strategies (such as island closures) that may help to minimize competition without advocating unnecessary restrictions to the fishing industry.

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Appendices

Appendix 1: Summary of the data collected on foraging parameters from individuals tracked using Platform Terminal Transmitters during the 2012 pre-moult phase. Values of NA for minimum duration of pre-moult represent individuals that did not leave the island for more than three days during monitoring. Average is reported for each island with 1 standard deviation. Letters B and D in Bird ID refer to Bird Island and Dassen Island respectively.

Bird ID	Data collection (days)	Path length (km)	Max. distance from colony (km)	Mean distance per day (km)	Max. distance in one day (km)	Trips as % of monitoring duration	T40	Minimum Duration of Moult
B1	44	561.4	110.3	24.1	95.5	13.6	4.6	43
B2	40	336.1	69.0	19.2	33.8	17.5	10.0	NA
B3	41	168.7	20.5	12.1	20.2	19.5	0.0	NA
B4	72	1369.5	229.0	27.3	73.4	18.1	25.0	NA
B5	44	309.1	22.9	18.7	37.4	15.9	0.0	43
B6	68	595.0	70.0	25.3	59.3	16.2	10.3	19
B7	41	176.6	34.6	20.4	33.8	17.1	0.0	NA
B8	40	141.0	30.2	11.1	29.1	15.0	0.0	28
B9	40	715.3	142.5	28.5	67.5	10.0	42.5	31
B10	69	505.4	77.4	22.2	57.2	11.6	10.1	NA
Average	32±12	487±368	81±66	21±6	51±24	15±3	10±14	33±10
D1	39	843.1	350.2	35.9	105.6	5.1	46.2	23
D2	64	238.3	117.6	19.1	42.6	1.6	95.3	23
D3	35	887.1	455.2	35.6	103.8	2.9	94.3	21
D4	39	932.8	403.7	37.3	104.1	10.3	51.3	60
D5	69	436.5	142.8	32.7	71.8	2.9	81.2	24
D6	36	464.6	157.01	17.9	108.2	8.3	58.3	86
D7	88	1845.4	462.1	32.8	132.6	4.6	50.0	23
D8	38	805.2	335.9	30.0	111.6	5.3	55.3	28
D9	36	1237.6	361.8	39.9	110.5	8.3	72.2	63
Average	39±24	855±480	310±135	31±8	99±26	6±3	67±19	39±24

Appendix 2: Summary of individual travelling values derived from individual track analysis in ArcGIS 9.1.3 for pre-moult foraging tracks collected during between September-December 2012. Letters B and D in Bird ID refer to Bird Island and Dassen Island respectively.

Bird ID	Date travel initiated	Distance travelled (km)	Days spent travelling	Minimum average distance travelled per day (km)	Directionality
B2	2012/10/23	53.1	2	26.5	Foraging Grounds
B4	2012/10/27	203.8	5	40.8	Foraging Grounds
B4	2012/11/08	196.2	3	65.4	Colony
B4	2012/10/12	94.9	2	47.5	Foraging Grounds
B4	2012/10/14	60.9	2	30.4	Foraging Grounds
B4	2012/10/16	97.3	2	48.6	Colony
B9	2012/09/21	124.0	3	41.3	Foraging Grounds
B9	2012/09/25	143.5	3	47.8	Colony
B9	2012/10/17	92.4	2	46.2	Foraging Grounds
B10	2012/11/03	76.1	3	25.4	Foraging Grounds
B10	2012/11/07	77.4	2	38.7	Colony
D1	2012/09/16	345.4	7	49.3	Foraging Grounds
D1	2012/10/02	227.1	4	56.8	Colony
D2	2012/09/14	79.5	2	39.8	Foraging Grounds
D3	2012/09/12	467.5	12	39.0	Foraging Grounds
D3	2012/09/30	311.2	5	62.2	Colony
D4	2012/09/20	178.2	5	35.6	Foraging Grounds
D4	2012/09/27	104.2	2	52.1	Foraging Grounds
D4	2012/10/06	385.3	5	77.1	Colony
D5	2012/09/16	240.6	5	48.1	Foraging Grounds
D6	2012/09/26	111.0	2	55.5	Foraging Grounds
D6	2012/10/12	137.2	2	68.6	Colony
D7	2012/09/24	53.5	2	26.8	Foraging Grounds
D7	2012/09/30	496.2	10	49.6	Foraging Grounds
D7	2012/10/19	414.1	8	51.8	Colony
D7	2012/11/29	162.3	2	81.1	Foraging Grounds
D8	2012/09/14	318.7	6	53.1	Foraging Grounds
D8	2012/10/13	294.6	4	73.7	Colony
D9	2012/09/15	110.8	2	55.4	Foraging Grounds
D9	2012/09/18	115.5	2	57.7	Colony
D9	2012/09/21	373.6	10	37.4	Foraging Grounds
D9	2012/10/06	386.8	7	55.3	Colony

Appendix 3: Summarized Statistics of ANOVA for catch per area of anchovy (*Engraulis encrasicolus*), sardine (*Sardinops sagax*), and total catch of small-pelagic fishing vessels in foraging ranges of African penguins (*Spheniscus demersus*) during the 2012 pre-moult season.

		Df	Sum of Squares	Mean Square	F Statistic	P Value	Sig
Anchovy Catch per Area	Between	2	42.978	21.4892	11.251	0.004	**
	Within	9	17.189	1.9099			
	Total	11	60.167				
Sardine Catch per Area	Between	2	3.8452	1.92262	7.86	0.01	*
	Within	9	2.2015	0.24461			
	Total	11	6.0467				
Total Catch per Area	Between	2	71.272	35.636	10.45	0.005	**
	Within	9	30.693	3.41			
	Total	11	101.965				

Appendix 4: Summarized statistics of General Linear Models for travelling variables for African penguin (*Spheniscus demersus*) comparing Dassen Island, west coast, and Bird Island, Algoa Bay, South Africa during the 2012 pre-moult season.

		Df	Deviance	Residual Df	Residual Deviance	F Statistic	P value
Distance Travelled	Null	31	550337				
	Colony	1	145849	30	404488	10.817	0.002572
Rate of Travel	Null	31	6188.6				
	Colony	1	1025.2	30	5163.4	8.2359	0.007589
	End	1	1553.6	29	3609.8	12.4814	0.001398

Appendix 5: Summarized statistics of Mann-Whitney rank sum test for foraging parameters of pre-moult variable for African penguin (*Spheniscus demersus*) comparing Dassen Island, west coast, and Bird Island, Algoa Bay, South Africa. T40 represents the proportion of time penguins spent outside of the average foraging range during the 2012 breeding season.

Parameter	W Statistic	P Value	n1	n2
Maximum distance from colony	5	0.000411	9	10
Average distance travelled per day when moving	15	0.01327	9	10
Trips	79	0.00621	9	10
T40	5.5	0.001375	9	10

Appendix 6: Summarized statistics for T-test of minimum duration of pre-moult for African penguins (*Spheniscus demersus*) comparing Dassen Island, west coast, and Bird Island, Algoa Bay, South Africa between September and December 2012.

Parameter	DF	T Statistic	P Value
Minimum Duration of moult	12	-0.5398	0.5992