AFRICAN PENGUIN (*SPHENISCUS DEMERSUS)* DISTRIBUTION DURING THE NON-BREEDING SEASON:
PREPARATION FOR, AND RECOVERY FROM, A MOULTING FAST

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Plagiarism declaration

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

ABSTRACT

Little is currently known about the spatial ecology of the endangered African penguin during the non-breeding season. As foraging success during this period is critical to adult survival, this project explores their dispersal patterns, as well as the degree of overlap with commercial purse-seine fisheries which target the same prey. African penguins from two colonies (Bird Island, Algoa Bay, south coast and Dassen Island, west coast) were tracked over 3 non-breeding seasons using Platform Terminal Transmitters and Global Positioning System devices to explore their pre- and post-moult dispersal patterns. Dispersal trips varied greatly between individuals, but there were still significant differences in the dispersal patterns found between islands and between life history-stages at Dassen Island. Bird Island penguins tended to make frequent, short trips, returning to their breeding colony in between, whereas Dassen Island penguins followed one of two strategies: either making few (up to 3) very long trips (up to 4000km), or adopting a central-place foraging pattern based at a point along the coast, distant from their breeding colony. At Dassen Island a clear spatial divide is evident with most pre-moulters dispersing south whereas most post-moult birds dispersed north, off the west coast. Bird Island penguins all moulted at their breeding colony and seldom visited either the adjacent coastline or other islands. During pre-moult, Dassen Island birds often spent nights close to shore along the coast or at other colonies and about a quarter of them moulted at another colony, most often at Stony Point, on the mainland east of Cape Point. Five dispersal patterns (defined in terms of the direction and distance of the furthest point reached) were identified for birds from Dassen Island and there is some indication that different dispersal patterns have distinct survival implications. Over 60% of PTT loss (a proxy for penguin mortality) occurred in a small area in the northern part of St Helena Bay, offshore from Lambert's Bay and Strandfontein and could be due to high levels of seal predation, which has been previously documented in the area.

Commercial small pelagic fishing data were analysed over three years (2012-2014). Average fishing effort decreased each month from September to December (when hardly any fishing occurred in any of the three years) and there was much greater fishing effort along the west coast than on the south coast. Commercial fishing effort was compared to penguin track data to assess the degree of potential overlap between these two pelagic predators. Firstly, the spatial overlap between core penguin non-breeding dispersal areas and core fishing areas was assessed on a broad temporal scale (three years). Bird Island penguins were found to be more spatially removed from fishing activity with no overlap in core fishing and dispersal areas on the south coast. Compared to the size of their dispersal area, Dassen Island penguins which stayed along the lower west coast showed the highest overlap with core fishing areas. The two most common dispersal patterns exhibited by Dassen Island penguins both involve journeying to areas outside the range of purse-seine fishing, indicating the possibility of avoidance behaviour once the pressures of breeding are lifted. Direct (daily) overlap between commercial fishing effort and penguin tracks was studied although the low frequency of the penguin position data restricted the analysis to a 20 km scale. The results were similar to those described above, with most direct overlap occurring between Dassen Island and Gansbaai.

Although the non-breeding range of these birds is too extensive and overlaps too much with important commercial fishing areas to be viably protected in its entirety, there are several small areas which are used repeatedly by non-breeding penguins and which could be considered for conservation measures (e.g. the area off-shore of Lambert's Bay).

CHAPTER 1: GENERAL INTRODUCTION

The importance of understanding marine systems

Historically, the ocean was perceived as a bountiful and unlimited resource for human use, but the possibility of negative repercussions have increasingly been acknowledged as the scale and efficiency of marine exploitation grows (Holm et al. 2010). The risk of over-fishing, for example, was recognised in the UK in the 1880s (Holm et al. 2010) . Unfortunately, preventative measures were slow to follow and, today, most marine ecosystems have been altered by anthropogenic activities. Those which are not targets for exploitation, habitat destruction and direct human disturbance are still affected by climate change, pollution and introduced species (Halpern et al. 2008).

In order to protect marine environments, mitigate anthropogenic impacts and facilitate sustainable harvesting of resources, the intricate functioning of these ecosystems must be understood as far as possible. Efforts in this direction are often hampered by the difficulty (and cost) of working at sea, as well as the short-term political and economic implications of restrictions on marine harvest. Satellite remote sensing, animal-borne data collecting equipment and sophisticated modelling have increased our understanding of ocean processes, but the details of ecosystem functioning and the effects of anthropogenic activities still need to be unravelled.

Studying seabirds as indicators

Seabirds (with some exceptions) can switch between land, air and sea at will. This requires physiological and behavioural adaptations and it is not surprising that <3% of bird species are marine (Croxall 1987). Seabirds have typical K-selection life histories with extended life-spans (up to 60 years) and delayed first breeding for several (up to 10-12) years. When they do breed they only lay a few eggs (one per season in some species) and spend a large amount of time and energy on chick-rearing (Croxall 1987; Schreiber & Burger 2001). This makes them especially vulnerable to adult mortality and slow to recover from population decline (Schreiber & Burger 2001). Like other marine species, many seabirds face a diversity of anthropogenic threats, making the introduction and enforcement of effective conservation measures a primary concern. Luckily some groups, such as the auks, albatrosses and penguins, have the charisma to excite public interest and draw funding into seabird research and conservation.

Seabirds are one of the best-studied groups of marine organisms. They spend a substantial amount of time on land, particularly when breeding, making them easier to observe and manipulate than most other marine organisms (Schreiber & Burger 2001). Consequently colonial seabirds are often used as indicators of ecosystem health or as a proxy for prey abundance (Furness & Camphuysen 1997). Cairns (1987) assessed the suitability of various seabird parameters as indicators of environmental conditions. He reported that breeding success, chick growth, colony attendance and activity budgets can all be used as indicators as they reflect short-term changes in food availability, but that adult survival remains fairly constant except in times of extreme prey shortage, e.g. during El Niño events.

Penguins: a unique order

Penguins (order Sphenisciformes) are well known for their extreme adaptation to a marine lifestyle. They are easily distinguishable, with a characteristic set of adaptations which have made them relatable and popular to the general public. At sea penguins reach speeds of 5 $m.s^{-1}$ (African penguins, Wilson 1985), dive to depths of over 500 m and stay below the surface for more than 20 minutes (emperor penguins, *Aptenodytes forster*, Wienecke et al. 2007). Their body is dense and streamlined and their wings flattened and fused into powerful propulsion devices with which they “fly” through the sea, steered by rudder-like tails and feet (Croxall & Lishman 1987; Schreiber & Burger 2001). Unlike most other birds, penguin bones are dense and non-pneumatic to assist deep diving and three layers of short, densely grown feathers provide exceptional insulation against the heat-sapping ocean water (Schreiber & Burger 2001). In spite of their novel adaptations, or in some cases because of them, penguins are as sensitive as any other specialist organisms to environmental change, habitat loss, human disturbance and changes in the abundance and behaviour of their prey. Of the 18 extant species, five penguins are classified as Endangered by the IUCN and only three as Least Concern (BirdLife International 2015).

Study species: the endangered African penguin

The African penguin is the only penguin which breeds in mainland Africa. The genus *Spheniscus* contains three other species: The Galapagos (*S. mendiculus*), Humboldt (*S. humboldti*) and Magellanic (*S. magellanicus*) penguins of South

America. The IUCN currently classifies two *Spheniscus* species as Endangered (the African and Galapagos penguins) while the Humboldt penguin is considered Vulnerable (Birdlife International 2015).

African penguins have been reported breeding from Hollamsbird Island off central Namibia to Bird Island in Algoa Bay, South Africa, although non-breeders occasionally wander to southern Angola and Mozambique (Shelton et al. 1984). Most breeding colonies are on islands which lack land predators and are subject to limited human disturbance. Historically, mainland colonies were confined to sea caves in remote desert areas along the Namibian coast, but since 1980, two colonies have formed in suburban areas around Cape Town where human activities largely exclude terrestrial predators. These sites at Boulders and Stony Point are now subject to formal protection and management.

African penguins first breed between the ages of two and six years, occasionally at a different colony from the one at which they fledged (Whittington et al. 2005) but adults show fidelity to their breeding colony once pair formation and breeding have occurred. Females lay one or two eggs (mean clutch size 1.86, Crawford et al. 1999) and parental care is shared. They often make more than one breeding attempt per season, at times even when chicks fledge successfully (Crawford et al.1999). Whittington et al. (2000) reported the death of a penguin which was at least 27 when it died. More recently a >29 year old was found near the Boulders colony.

The African penguin's population fell by about 90% during the 20th century (du Toit et al. 2004). After a brief respite in South Africa in the early 2000s the decline continued and the species was declared endangered in 2010 after collapsing by over 60% in eight years (Crawford et al. 2011). The decline was initiated by the collection of penguin eggs and guano. Sanctioned egg collecting ceased in 1968 (Shelton et al. 1984), but commercial guano scraping continued into the 1970s, causing disturbance as well as removing the ancient layers of guano in which penguins burrowed. Several massive oil spills between the Cape Peninsula and Cape Columbine, and increased predation by Cape fur seals (*Arctocephalus pusillus*), caused further losses (du Toit et al. 2004). However, these factors cannot account for the rapid collapse in penguin populations off the west coast of South Africa in the last few decades (Crawford et al. 2011). Breeding success has been linked to regional and local forage fish biomass (Crawford et al. 2006; Sherley et al. 2013a), indicating that competition with the pelagic fishing industry could be contributing to the decline but, although decreases in breeding success have been reported at several colonies, they cannot fully explain the rapid decrease in penguin numbers.

In a study on Robben Island, adult survival was found to have a much greater impact on the population and was correlated to prey abundance (Robinson et al. 2015). Annual adult survival at west coast colonies decreased between 2002 and 2006 (Dassen island: 0.70 to 0.46, Robben Island: 0.77 to 0.55, Crawford et al. 2011) and it seems to be during the non-breeding (moulting) season that most adults are lost (Sherley et al. 2013a; Wolfaardt et al. 2009). Adult mortality seems to have increased parallel to changes in prey availability (Crawford et al. 2011), although the role of commercial fishing in these changes is as yet unresolved (Pichegru et al. 2013; Robinson et al. 2015). Crawford et al. (2011) proposed that penguins in low body condition after a stressful breeding season might have difficulty in gaining moult condition and consequently be unable to forage efficiently as feather quality deteriorates, eventually leading to starvation.

Some background on moulting: a fundamental process for all things feathery

Once grown, feathers are dead structures that do not last indefinitely. As they become worn, e.g. by abrasion (Bonser 1995) or bacterial damage (Burtt & Ichida 1999; Gunderson 2008), their efficiency decreases. All birds therefore need to replace their feathers at regular intervals, but their strategies for doing so are many and varied, involving complicated time-budget trade-offs between breeding, moult and, in some species, migration (Barta et al. 2006; Bridge 2006; Langston & Rohwer 1996). Moult strategies differ in pattern, duration and timing with closely related species generally showing more similar strategies (Bridge 2006).

Most birds do not replace all their feathers at once but a few at a time. This takes longer to complete, but the energetic and nutritional costs are distributed over time and flight can continue throughout. As feather growth rate is relatively constant, short feathers are replaced faster and small passerines usually moult annually after breeding (Rohwer et al. 2009). In these species moult can be sped up if necessary (e.g. in late breeders) by replacing more feathers at once, although feather quality suffers (Dawson 2004; Griggio et al. 2009). Larger birds require more complicated strategies because replacing each feather takes longer and replacing more at once would impair flight (Edelstam 1984, Langston

& Rohwer 1996). Many large water birds drop all their flight feathers simultaneously and remain flightless until they regrow (Langston & Rohwer 1996).

Penguins have an even more extreme approach. With the exception of some juvenile African penguins which moult a small proportion of their head feathers at sea (Ryan et al. 1987), penguins typically moult all their feathers at the same time (Groscolas & Cherel 1992). This is a costly process as, apart from the energy required to grow a complete set of new feathers, the penguin is unable to forage at sea while its insulating plumage is compromised (Groscolas & Cherel 1992). Confined to land (or ice), moulting penguins rely solely on energy reserves built up in a pre-moult foraging period. Penguins are often underweight by the time they are ready to resume foraging and need to regain condition during a post-moult recovery period.

Except for the king penguin *Aptenodytes patagonicus*, which has an 18 month breeding-moult cycle, penguins moult annually (Borboroglu & Boersma 2013). This usually occurs after breeding and is initiated by non-breeders and failed breeders (Borboroglu & Boersma 2013). The length of moult is related to body (and hence feather) size, with the emperor penguin fasting for about five weeks (Groscolas & Cherel 1992), the smaller African penguin for about three weeks (Crawford et al. 2006) and the little penguin (*Eudyptula minor*) for two and a half weeks (Gales & Green 1990). Peak moult season also shows species-level differences with most species moulting after breeding towards the end of the austral summer, but king and African penguins have their peak moult in spring after a winter breeding season. Many southern species (such as the Adélie *Pygoscelis adeliae* and chinstrap *P. antarctica* penguins and most crested penguins *Eudyptes* spp.) undergo winter migrations during which they do not return to their breeding grounds for several months. Of these, most moult before embarking on this journey, but some undergo moult during this migration period at distant moult-locations (Borboroglu & Boersma 2013).

Because moulting is so costly for penguins, good foraging success before and after the starvation period is crucial for adult survival, as well as parent condition over the next breeding season (Sherley et al. 2013a; Wolfaardt et al. 2009). There is evidence of high variation in moult seasonality, duration and location within many species of penguin (Borboroglu & Boersma 2013) and even within colonies (Underhill & Crawford 1999). This could indicate that variability in moult strategy may have survival advantages.

A closer look at the moulting biology of the African penguin

Unlike many other penguins which undertake long winter migrations (including the closest relative of the African penguin, the Magellanic penguin, Pütz et al. 2000), adult African penguins usually moult at their breeding colony, sometimes even in the same nest in which they bred (Wolfaardt et al. 2009). However, some birds moult at colonies closer to their pre-moult foraging grounds (Harding 2013). As with all penguins, building up energy reserves prior to moult is essential as is a second bout of intense foraging which occurs after moult to regain condition before the onset of breeding (Wolfaardt et al. 2009). For African penguins the full moulting process, including pre- and post-moult foraging, lasts about 100 days each (Crawford et al. 2006) although substantial variation has been found in the length of both foraging periods (Wolfaardt et al. 2009).

The fasting African penguin loses about 40% of its pre-moult mass (Cooper 1978) and could easily starve if energy reserves are not sufficient. African penguins in pre-moult condition weigh about 30% more than breeders, with fat making up 20% of their body mass (Cooper 1978). Moult can be abandoned before it is complete (Cooper 1978), but this drastic measure is likely to result in the bird's death.

Figure 1.1 African Penguins swimming with just-moulted plumage (left) and un-moulted plumage (right)

Moult seasonality has been studied in various colonies by counts of African penguins in the feather-shedding stage of moult (Wolfaardt et al. 2009) and by re-sighting banded individuals (Kemper & Roux 2005; Kemper et al. 2008; Wolfaardt et al. 2009). The general understanding is that the African penguin's annual cycle revolves around the breeding season, which coincides with predictable prey available close to the colony (Kemper et al. 2008). This is supported by the differences in the timing of moult between the South African and Namibian populations. In South Africa, penguins breed mostly in autumn and winter and moult is synchronised with birds of all ages moulting in early summer, from September to January (Crawford et al. 2006; Kemper et al. 2008; Wolfaardt et al. 2009). But in Namibia, although juveniles and non-breeders moult during summer, the peak moulting season for adults is in autumn. This is because in Namibia, African penguins breed in summer and breeders must delay moulting until the demands of the breeding season are over (Kemper et al. 2008).

There is some indication that the onset of moult in African penguins is flexible, as cleaned-and-released oiled penguins moulted earlier than unaffected neighbours (Wolfaardt 2007). This suggests that penguins can adjust the timing of their moult to suit changing environmental conditions or if they were to move to new colonies (Crawford et al. 2006; Underhill & Crawford 1999). However, the timing of moult is more synchronous than that of breeding, leading Wolfaardt et al. (2009) to argue that moult is the central stage of the annual cycle because adult survival is at stake. Whether food shortages during pre-moult foraging can postpone moult, and if so for how long, is unclear, but there is a trade-off between the short term survival benefits of delaying moult and the costs of worn feathers. African penguins with newly-moulted plumage can swim significantly faster (18 km.h^{-1}) than other adults (13.5 km.h^{-1}), emphasizing the importance of plumage condition during foraging (Wilson 1985). Very worn plumage can initiate a vicious cycle where the bird is unable to moult because, with its old feathers, it cannot forage well enough to gain pre-moult condition (Kemper & Roux 2005). This is especially prevalent in immature birds, too young to moult in the first year, which must therefore wait for the next season before renewing their plumage (Kemper & Roux 2005). However, many juveniles do moult successfully after up to 18 months, showing that delayed moult does not necessarily have a large impact on performance. Good pre- and post-moult foraging success is critical and food scarcity during these periods could directly affect survival or reduce breeding success in the following season (Croxall & Davis 1999; Sherley et al. 2013a; Wolfaardt et al. 2009) but little is known about the African penguins' movements during the non-breeding season, making appropriate conservation efforts difficult.

Dissertation road-map: journey towards an optimistic goal

This project hopes to ultimately assist with the conservation of the African Penguin during the non-breeding season, when food availability is critical to adult survival. Chapter 2 identifies the marine areas used by African penguins from two colonies during pre- and post-moult dispersal. By comparing birds from the largest west coast colony, where numbers continue to collapse, with those from a relatively stable south coast colony, I hope to demonstrate the possible role of pre- and post-moult dispersal and foraging effort on recent population trends. This chapter also explores different individual dispersal patterns and their survival implications. Chapter 3 assesses the degree of overlap between penguin non-breeding dispersal areas and commercial purse-seine fishing using catch data and GPS positions of purse-seine sets.

CHAPTER 2: DISPERSAL PATTERNS OF AFRICAN PENGUINS BEFORE AND AFTER MOULT

INTRODUCTION

The African penguin is especially vulnerable to prey shortages during the pre- and post-moult foraging periods as foraging success during this time affects adult survival (Croxall & Davis 1999; Sherley et al. 2013a; Wolfaardt et al. 2009). This chapter reports the spatial distribution of African penguins during pre- and post-moult dispersal from two colonies with contrasting population trends to assess whether food shortages during the critical pre- and post-moult periods might explain the recent collapse in penguin populations particularly off the west coast of South Africa. This will hopefully help to direct conservation efforts to reduce the high levels of adult mortality sustained during these periods.

Previous tracking of non-breeding African Penguins

African penguin distribution at sea was first studied by Siegfried et al. (1975), who reported that penguins were generally seen within 15 km of the coast but could be substantially farther from the nearest penguin colony. Wilson et al. (1988) counted penguins at sea between Cape Agulhas and Lüderitz. They assumed that birds sighted >20 km from the nearest breeding colony were non-breeders, and reported that over 50% of these birds were found within 20 km of the mainland. The highest frequency of non-breeder sightings was in the area between Cape Agulhas and Dassen Island. Whittington et al. (2005) followed the movement of banded penguins over several years, showing that adults from the Western Cape visited other colonies more often than those banded in the Eastern Cape. They reported two sightings of breeders from Robben Island moulting at different colonies, one at Dyer Island, Western Cape, and another at Ichaboe Island in Namibia. Another bird captured at Dassen Island for rehabilitation was later seen moulting on Mercury Island in Namibia.

In 2000 about 19 500 African penguins from the west coast, which were threatened by the *Treasure* oil spill, were relocated to Algoa Bay (over 700 km away) to allow time for the oil to be cleaned up. Three of these birds were tracked on the return journey and, after they returned to their home islands, two of these devices continued to record what are arguably the first pre-moult tracks (Barham et al. 2006). Although the penguins' behaviour was undoubtedly affected by the preceding weeks, they foraged in areas outside the normal range of breeding birds (Crawford et al. 2006). One travelled south from Dassen Island onto the Agulhas bank and the second (a Robben Island bird) travelled north to an area offshore of Lambert's Bay. The only other direct tracking of non-breeding African penguins followed the post-fledging dispersal of five captive-reared juveniles released near Cape Town in 2013 (Sherley et al. 2013b). All five travelled northwards off the west coast, with three moving as far north as central Namibia.

Harding (2013) tracked 20 African Penguins, 10 from Dassen Island (off the west coast) and 10 from Bird Island (in Algoa Bay), during the 2012 pre-moult period. Birds from the two colonies displayed very different dispersal patterns; those from the west coast travelled to distant foraging grounds, while those from Algoa Bay remained close to their breeding colony, with 50% of evening satellite fixes within 20 km of Bird Island. Harding (2013) was limited to a single season of pre-moult dispersal. I continued this study in 2013, tracking both pre- and post-moult dispersal patterns. In this chapter I report pre-moult dispersal collected over three seasons (2012-14, including Harding's data) and post moult dispersal over two seasons (2013-14). I expected both pre-and post-moult penguins to exhibit similar behaviour to that described in Harding (2013) as his were the only data available on this key stage of the adult African penguin's annual cycle.

METHODS

Study colonies

Penguins from Dassen Island, west coast (33°25'S, 018°05'E) and Bird Island in Algoa Bay, south coast (33°50'S, 026°17'E, Figure 2.1) were tracked in three consecutive non-breeding seasons (2012-14). These colonies are representative of two very different systems in which African penguins breed. Dassen Island lies in the cold Benguela upwelling system in the South Atlantic while Bird Island is adjacent to the warm Agulhas current.

Dassen Island is the second largest island off South Africa (220 ha) and was once the largest African penguin colony, with more than 300 000 penguins in the early 1900s (estimated from egg collection counts, Frost et al. 1976). By the late 1970s it held an estimated 21 650 pairs but had decreased to just 4 600 by 1987 (Crawford et al. 1995, Figure 2.2). The population increased to almost 25 000 pairs following a period of strong pelagic fish recruitment in the late 1990s, but by 2010 there were again fewer than 5 000 breeding pairs, and only 2 100 pairs were recorded in 2014. The penguin population on Bird Island was historically much lower than that on Dassen, but has remained relatively stable with an average of 2 900 breeding pairs between 1991 and 2010 (Crawford et al. 2011) and 2 800 at the last count in 2014 (overtaking Dassen Island). Bird Island is only 19ha and home to the smaller of the two main penguin populations in Algoa Bay (St. Croix Island supporting over 7 000 breeding pairs, Crawford et al. 2011). The relative size of the three regional populations of African penguins (Namibia, West Coast and Algoa Bay) has changed over the last century, as first the Namibian population (in the 1970s) and then the west coast population (in the 2000s) were subject to massive decreases. Algoa Bay, which historically held about 10% of the population, was home to over half the world's population of African penguins by 2012 (Department of Environmental Affairs, unpublished data).

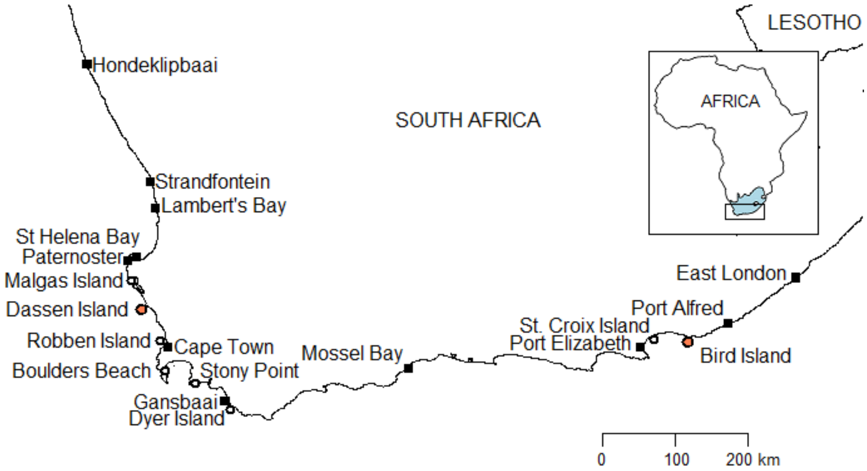


Figure 2.1. Map of South Africa showing the two study colonies (Dassen Island and Bird Island) and other important locations mentioned in the text. Study colonies are marked with orange circles, other penguin colonies with open circles and towns and cities with squares.

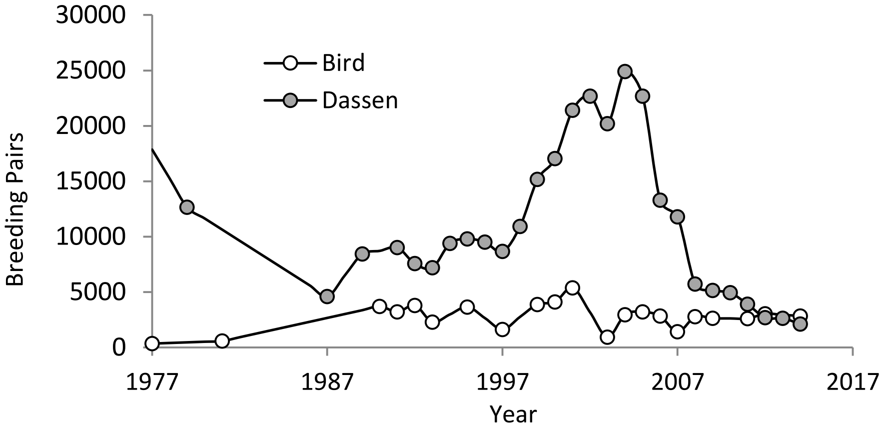


Figure 2.2. Estimated number of breeding pairs of African penguins at Dassen Island (grey points) and Bird Island (white points) from 1976 to 2014. Department of Environmental Affairs, unpublished data

On Dassen Island most penguins nest in burrows and under vegetation (Wolfaardt et al. 2009) and moulters are found either in these nests or along the shoreline where they shelter under large boulders. On Bird Island breeding takes place in surface nests and moulters typically congregate along the shore during the day, moving inland at night (personal observation).

Devices

Platform Terminal Transmitters (PTT; KiwiSat202, SirTrack, 58x28x18 mm with 180 mm antennae, 40 g) were initially used in this project. They were set to a duty cycle of 6 hours on (18:00 - 24:00 GMT) 18 hours off, to conserve battery life. Due to device loss and cost constraints I switched to using CatLog-S GPS loggers (catLogs) in addition to PTTs in 2014. CatLogs were set to record position every 20 minutes over a one-hour period each night (21:00-22:00 GMT). CatLogs were used on Bird Island for both pre- and post-moult while a mixture of catLogs and PTTs were used for

Dassen Island pre-moult. This saved PTTs for the Dassen post-moult tracking where they have the greatest advantage, as devices are more difficult to recover from this island. CatLogs were prepared for deployment by sealing into two layers of heat-shrink tubing (Fig 2.3), the inner tubing a clear plastic provided with the devices, the outer tubing a 2.5 mm thick black tubing with glue inside (EPS 24/8 mm 2.5 mm WALL). Between these a layer of foam was inserted as impact-protection. The completed catLogs (± SD) were 100±5 x 33±0.5 x 16±0.5 mm and weighed 35±5 g. VHF transmitters (SirTrack, V1G 112A, 2.4 g, 150 mm antenna) were added to four Dassen Island pre-moult catLogs, and three Bird Island post-moult catLogs to assist in re-locating them.

Figure 2.3. CatLogs at each stage of preparation (top left to bottom right) and a sealed catlog with a VHF device attached (inset, far right)

Deployment

Pre-moult

Devices were deployed on adult breeding penguins when their chicks were assessed as ready to fledge (no downy feathers left). The devices were attached to the feathers of the lower back with Tesa tape, superglue and a cable tie, following Harding (2013, Figure 2.4) and adapted from the attachment method described by Wilson et al. (1997). Devices were glued directly to the feathers as the impending moult obviated concerns regarding feather damage.

Before deployment, each bird was weighed to the nearest 5 g with an American Weigh Scales digital hanging scale, and the beak measured (length and depth) to the nearest 0.1 mm with Vernier callipers. The mass-to-bill-length ratio gives a rough estimate of body condition (Index = mass (g)/bill length (mm)) and bill length and bill depth can be used to infer sex with an accuracy of about 80% (Pichegru *et al.* 2013). Before release each bird was marked on the chest with a non-toxic animal marker (Porcimark pig marking spray, Kruuse) to facilitate recapture.

Figure 2.4. Device attachment; Left: Satellite PTT on a pre-moulter; Right: GPS logger on a post-moulter

Post-moult

After moulting penguins are often underweight and stressed, making the added stress of handling and of carrying a tracking device potentially dangerous. To avoid attaching loggers to particularly weak individuals, each penguin was assessed before post-moult deployment and only birds with a mass-to-bill-length ratio above 40 were used. As there are few data on post-moult body condition this limit was decided rather arbitrarily, but with the guidance of experienced penguin researchers and the South African Foundation for the Conservation of Coastal Birds (SANCCOB).

In order to ensure that the start of post-moult dispersal was recorded, adult birds still in the last stage of feather-shedding were targeted. Attachment was similar to the pre-moult procedure but no glue was used directly on the new feathers. Due to a combination of device loss during pre-moult tracking, and the difficulty of finding birds in the right moult stage and suitable condition, only ten post-moult deployments were made in 2013, and 11 in 2014.

Feasibility of post-moult tracking

To assess the feasibility of post-moult tracking, especially in relation to length of feathers (which continue to grow after the birds return to the sea) a PTT was attached to a captive post-moult bird in 2012. Based on this trial and measurements made by Dr Nola Parsons at SANCCOB, deployments were restricted to birds with new back feathers over 22mm long, to ensure secure attachment of devices. In addition, the first two PTT devices were deployed five days before more post-moult tracking was attempted, to check for any immediate adverse effects.

Data preparation

All analysis and data handling were done in R version 3.2.2 and earlier (R Core Team 2015) and Microsoft Office Excel 2007. PTT position data includes an estimated error radius for each position, which reflects the accuracy of that position. Because many fixes are too inaccurate to be informative the data must first be filtered to exclude these positions. The PTT tracks in this study were filtered to include only locations with a reported quality of 3, 2 or 1, the most accurate positions, corresponding to error radii of 250, 500 and 1500 m respectively, although the actual error could be larger (Boyd & Brightsmith 2013). The catlog points were then added and a second filter, this time excluding points associated with speeds of over 18 km.h^{-1} (the maximum recorded speed for an African Penguin, Wilson 1985) was applied (trip::speedfilter, Sumner 2015). In instances where gaps of more than a day occurred in the data and lower quality Argos points were available to fill the gap, the location with the lowest associated error radius was assessed for suitability. However, in several cases these low quality Argos points were rejected on the grounds of their turning angle (>150°). Where gaps occurred at the start or end of a trip a different process was followed, adding an artificial on-island point 24 hours before or after the first or last point, as the bird was most likely on the island. This is similar to the approach followed by Harding (2013) because signals from PTTs on land are often obstructed by rocks or burrows. When the straight line linking successive positions crossed land a minimum number of artificial fixes were added to allow the shortest-at-sea route around headlands. These additions were made using adehabitatLT::trajdyn (Calenge 2006). Where necessary, points were rediscretized (re-distributed along the track, adehabitatLT::redisltraj, Calenge 2006) to represent regular time intervals before analysis. This is especially necessary before conducting any density analysis. A frequency of six points per day was used to ensure the tracks remained at sea, although the actual sampling frequency is equivalent to a single point (or cluster of points) per night. All gaps were filled by simple linear interpolation during rediscretization, resulting in probable underestimates for both track distance and speed. Tracks with large gaps (>2 days) were categorized as 'incomplete' and treated with caution in further analyses. Albers equal-area conic projection (latitude of origin -32.233, first standard parallel -34.62, second standard parallel -29.85, central meridian 22.15) was used to reduce distance and area distortions.

Track parameters

A track was defined as the movement of an individual bird from the last point on the island to the first point recorded back at the island (or other moulting location) before the device was removed (or the last point recorded if the device was lost at sea). This included time spent on land. Tracks were divided into trips. Separate trips were distinguished if the penguin returned to its colony or to its central-place foraging base. A trip was measured from the last point on land before the trip to the first point on land after the trip. Points on land between trips were removed from the data set. After data preparation the following parameters were calculated for each track:

- Lag, defined as the length of time between device deployment and the start of dispersal.
- Duration, defined as the length of the track in days. This parameter includes time spent on land between trips. For Dassen Island pre-moult tracks, the start of the foraging period was taken as the start of the first trip which was longer than normal chick-rearing foraging (more than 3 days). For Bird Island it was more difficult as breeding and non-breeding tracks can be similar in length, but since no statistical difference was found in the lag period between the two islands (χ^2= 0.252, df= 1, p>0.1), all Bird Island tracks after deployment were

counted as pre-moult trips. For post-moult trips, the end of the foraging period was equally difficult to determine for Bird Island penguins and all trips prior to device retrieval were included.

- At-sea index, defined as the percentage of days in each track which were spent at sea (or the duration of all trips combined as a percentage of track duration)
- Number of trips
- Track Length, calculated as the sum of the shortest at-sea distance between consecutive points, giving a minimum estimate of distance travelled for the entire track
- Speed, defined as the average speed calculated from only the at-sea portions of each track.
- Maximum displacement, defined as the maximum distance travelled from the colony of each track, via the shortest at-sea route.

Data analysis

The non-breeding home range of adult African penguins from each colony was calculated using 100, 95, 75 and 50% minimum convex polygons (adehabitatHR::mcp, Calenge 2006). This involves drawing the smallest possible polygon around a given percentage of position fixes and is widely used to estimate home range (Calenge 2006). Simple linear models (stats::lm, R Core Team 2015) were used to assess differences in initial mass, body condition and track parameters in relation to island (Dassen or Bird), period (pre- or post- moult), season (named after the year in which the season started: 2012, 2013 or 2014) and sex (male or female). As sex was not a significant factor in any track parameter models it was dropped from these analyses. Type II ANOVAs (car::Anova, Fox & Weisberg 2011) were used to compare the significance of model factors.

Kernel density maps provided more detailed information about spatial use. An operation window (a geographic space to which all analysis are confined) was used to restrict Kernel density estimates (KDEs) to marine habitat (spatstat package, Baddeley & Turner 2005). The KDEs were made using the spatstat::density function (Baddeley & Turner 2005). This gives a fixed band-width Gaussian kernel estimate of the intensity function, and is expressed as the expected number of points per area. This figure in itself is biologically meaningless and depends highly on the selected smoothing bandwidth. The bandwidth controls the scale over which the density estimate is calculated. An extremely large bandwidth would give a single density estimate over the entire geographical area, whereas a very small bandwidth would show the exact vicinity of each recorded position as the highest possible density and areas between points as near zero estimates. A mid-ground is necessary in order to receive informative estimates of spatial use. Smoothing bandwidths were therefore calculated using spatstat::bw.ppl (Baddeley & Turner 2005) which selects an appropriate bandwidth by likelihood cross-validation. The bandwidths selected were relatively small, allowing good visualization of the activity of individual birds and, because the tracks were rediscretized (see data preparation, above) prior to calculating KDEs, the interpolated path between nightly fixes is taken into account. Any time spent on land between trips was not included as these points had been removed (see data preparation, above). First KDEs were plotted for each tracking session (2012 pre-moult, 2013 pre-moult, 2013 post-moult etc.) and then for each period (per island), combining data from different seasons. This allowed the overall 75% contour (a line around areas containing 75% of the rediscretized points) for pre- and post-moult tracks for each island to be found. Lastly, kernel density maps of points within 1.5km of land, excluding the colonies, were used to find important coastal areas.

Different dispersal patterns

Because the tracks collected show considerable individual variation, tracks with similar trajectories were grouped into dispersal ‘strategies’. For each island tracks were grouped using the shortest at-sea distance and the bearing of the furthest point reached (Figure 2.5). Each group was plotted, showing the 75% density contour, and the number of tracks from each tracking session in each group was calculated. Simple linear models for each Island were used to assess the relationship between the initial mass and body condition of the bird and the region to which it dispersed. The probability of survival for each strategy for birds from Dassen Island could only be estimated from PTT tracks, assuming that devices lost at sea were the result of mortality. This is not a fail-proof assumption as devices can simply stop working or detach from the bird, especially as time since deployment increases. The fact that no devices were lost at sea from Bird island penguins (although they were attached for a comparable length of time) and that those which were recovered from Dassen birds seemed well-attached, lends some credibility to the idea that mortality could be reflected in device loss, but this is more of an exploratory analysis and the results must be assessed critically with these limitations in mind. That no PTT devices were lost at sea after fitting to Bird Island penguins, seems to indicate high adult survival during the non-breeding season. One-sided Welch t-tests (stats::t.test, R Core Team 2015) were used to compare the initial mass and body condition and the latitude of the furthest point reached, between Dassen birds which survived and those which presumably died at sea. Maps were plotted of the furthest point reached by surviving and lost Dassen Island birds and, for lost devices, the last points recorded before loss.

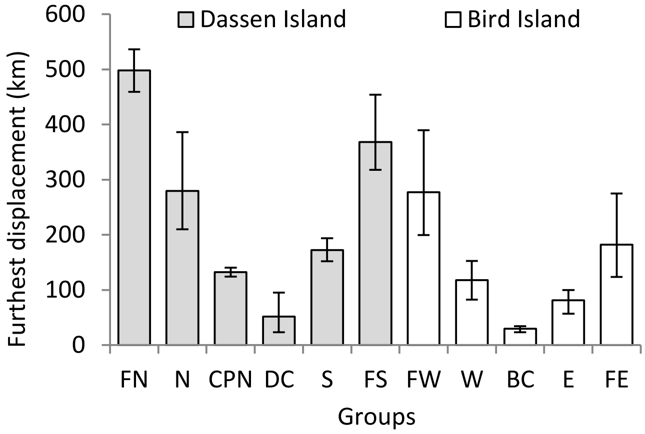


Figure 2.5. Average displacement of the furthest track point for each group of tracks, Error bars indicate the maximum and minimum furthest displacement in each dispersal pattern. Groups are named as follows: N, S, E, W = North, South, East, West; D, B = Dassen Island, Bird Island; F= Far, C=Central, CP= Central-place foraging

RESULTS

Tracking success

In total 57 tracking devices were deployed between September 2013 and December 2014. And, including Harding's (2013) pre-moult deployments, 77 devices were deployed on penguins for this research (Table 2.1). From these, 62 usable tracks were obtained, although 19 were partial: 15 because the device stopped while the bird was at sea and four because they contained large gaps (3-4 days).

Table 2.1. Number of devices deployed and number of full and partial tracks returned for each tracking session, partial tracks are those which end prematurely or contain continuous gaps of 3 or more days, Italics indicate the use of catLogs rather than PTTs

Island	Year	Period	Deployed	Full	Partial	Usable%
Bird	2012	Pre	10	9	1	100
Bird	2013	Pre	6	6	0	100
Bird	2014	Pre	*10*	*0*	*6*	60
Bird	2013	Post	5	3	2	100
Bird	2014	post	*6*	*1*	*0*	17
Dassen	2012	pre	10	8	1	90
Dassen	2013	pre	10	7	3	100
Dassen	2014	pre	4, *6*	2, *4*	1, *0*	70
Dassen	2013	post	5	3	1	80
Dassen	2014	post	5	0	4	80
TOTAL			**77**	**43**	**19**	**81**

Body condition

Simple linear models of initial mass and first-capture body condition of 75 of the tracked birds were designed, with island, period, season and sex as independent variables. Two birds could not be included due to missing measurements which made estimating sex impossible. Significant differences were found in mass between all four variables. There were significant differences in body condition between islands (Bird Island penguins 7.4 $g.mm^{-1}$ higher), periods (pre-moult 1.6 $g.mm^{-1}$ higher) and seasons (2014 birds 4.8 $g.mm^{-1}$ higher than the other two years), but there were no significant differences between sexes ($mean_{female}$= 48.9, n= 53; $mean_{male}$= 52.6, n= 22). The differences in period and season are probably driven by the exceptionally high body condition of the Bird Island pre-moulters in 2014 (Figure 2.6) but the difference between Islands seem consistent in all five tracking sessions. For test statistics see Appendix 1.

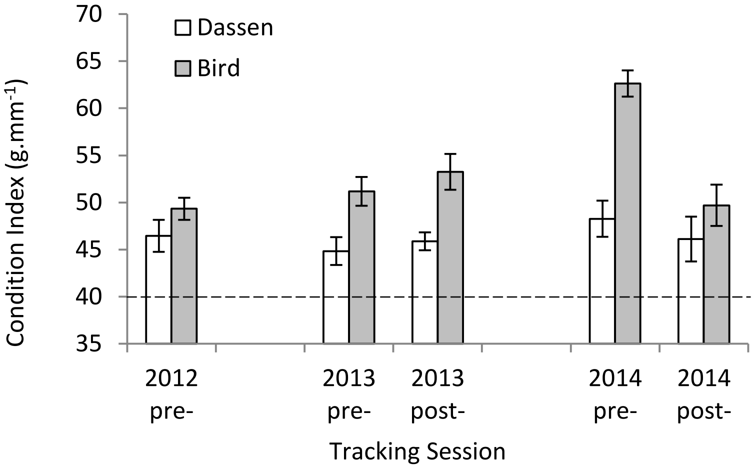


Figure 2.6. Average condition Index (mass/beak length) of penguins from two colonies (Dassen Island and Bird Island) off South Africa, on which tracking devices were deployed during pre- and post-moult periods 2012-2014. Error bars show standard error; dashed line shows 40 $g.mm^{-1}$ minimum deployment limit.

Tracking data

After filtering, the tracking dataset consisted of 4961 Argos points (2789 for penguins from Dassen Island and 2172 for Bird Island), 458 catLog points (329 for Dassen Island and 129 for Bird Island) and 114 points added to ensure tracks remained over the ocean (100 for Dassen Island and 14 for Bird Island, which lies adjacent to a more linear coastline). Of the Argos points 98.8% were of good quality (location qualities of 1, 2 or 3) with average reported error radii of 443±267 m (Dassen Island) and 474±519 m (Bird Island). The rest were lower quality points with much larger error radii (Dassen Island: 5105±6122 m, 50 points; Bird Island: 18800m±19086 m, 9 points). Of the final Dassen Island dataset (before rediscretization), 1.6 % were lower quality Argos points and 3% artificial points. Of the final Bird Island dataset 0.4% were lower quality Argos points and 0.6% artificial points. There were 45 one-day gaps, 5 two-day gaps, 3 three-day gaps and 2 four-day gaps in the final dataset (2.9% of Dassen Island track-days and 3.2 % of Bird Island track-days). Gaps longer than a day only occurred in post-moult tracks.

Non-breeding penguin distribution

The tracks of penguins from Dassen and Bird Islands did not overlap although they came within 40 km of doing so (Figure 2.7). All tracks stayed well within the boundaries of the continental shelf, venturing farthest off-shore over the Agulhas Bank (almost 100 km from land) and just south of the Namibian border (about 110 km off-shore). Penguins from Bird Island stayed particularly close to shore when heading eastward, where the shelf is narrow and bordered by the powerful Agulhas Current. Although several pre-moult Bird Island penguins journeyed a substantial distance westward (one nearly 400 km), Bird Island tracks were generally more concentrated around the colony than Dassen Island tracks, which extended both northwards (up to 540 km) and south-east around the Cape (up to 450 km). At both colonies, pre-moult birds ventured further afield than post-moulters. The north-south range of pre-moult points for penguins from Dassen Island (770 km), was nearly double that of post-moult points (425 km)and, for penguins from Bird Island, the trend is repeated along an east-west axis (615 km for pre-moult and 255 km for post-moult points).

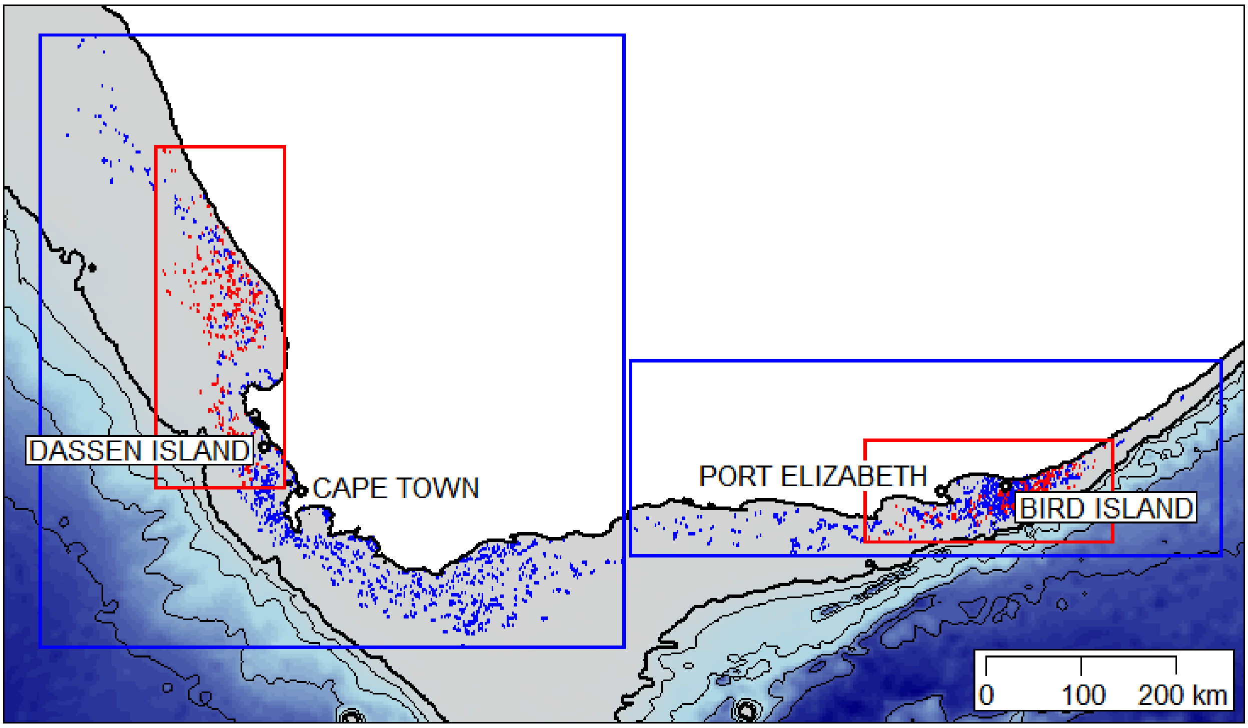


Figure 2.7. Recorded positions of African penguins from Dassen Island (left) and Bird Island (right) during pre-moult (blue) and post-moult (red) periods. Blue and red blocks show the range of tracks, bold black lines represent the shoreline and the edge of the continental shelf (500 m isobath).

During non-breeding dispersal the birds from the two study colonies used practically the entire continental shelf to depths of approximately 200 m (in some areas 400 m) from off the Orange River mouth to just beyond East London (Figure 2.8). The home ranges of penguins from Bird Island were much smaller than those from Dassen Island, and at both colonies there was a large difference in area when 5% of points were excluded (100% MCP$_{\text{Dassen}}$ = 160 000 km^2, 95% MCP$_{\text{Dassen}}$= 100 000 km^2; 100% MCP$_{\text{Bird}}$ = 49 000 km^2, 95% MCP$_{\text{birdn}}$= 24 000 km^2).

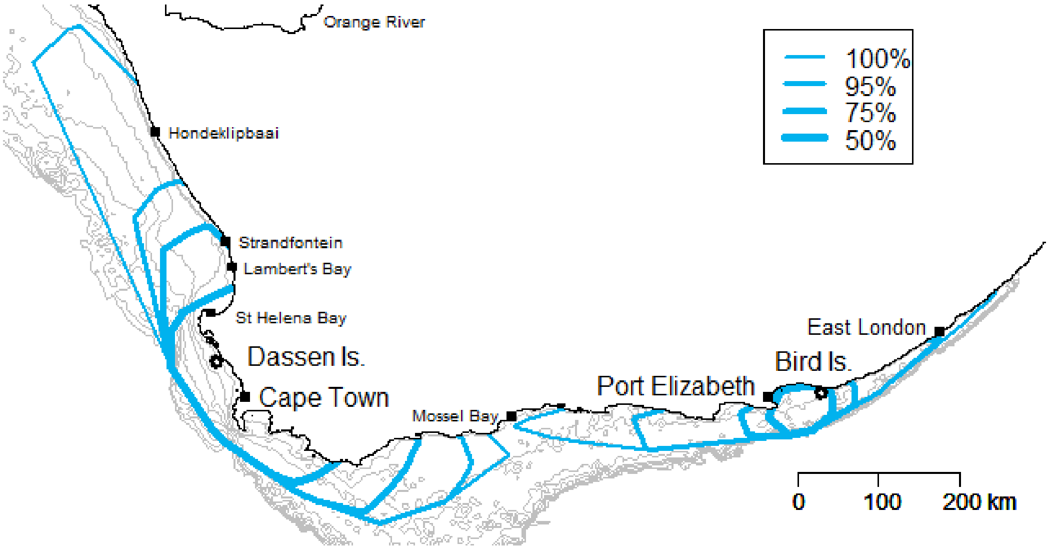


Figure 2.8. Minimum convex polygons showing home range estimates for adult African penguins from Dassen Island (left) and Bird Island (right) during the non-breeding season. Isobaths every 50 m to 400 m below sea level.

Pre and post-moult dispersal patterns

Bird Island penguins all moulted at their colony and predominantly stayed very close to it in all tracking sessions, although individual birds made trips both westward and eastward along the coast during pre-moult, especially in 2013 when one bird travelled as far as Mossel bay (Figure 2.9). Pre-moult tracks from 2014 were incomplete and throw little light on the bird’s movements but the lag period between device attachment and the first point off the Island was significantly longer than in other years, indicating that penguins were in no hurry to leave after breeding.

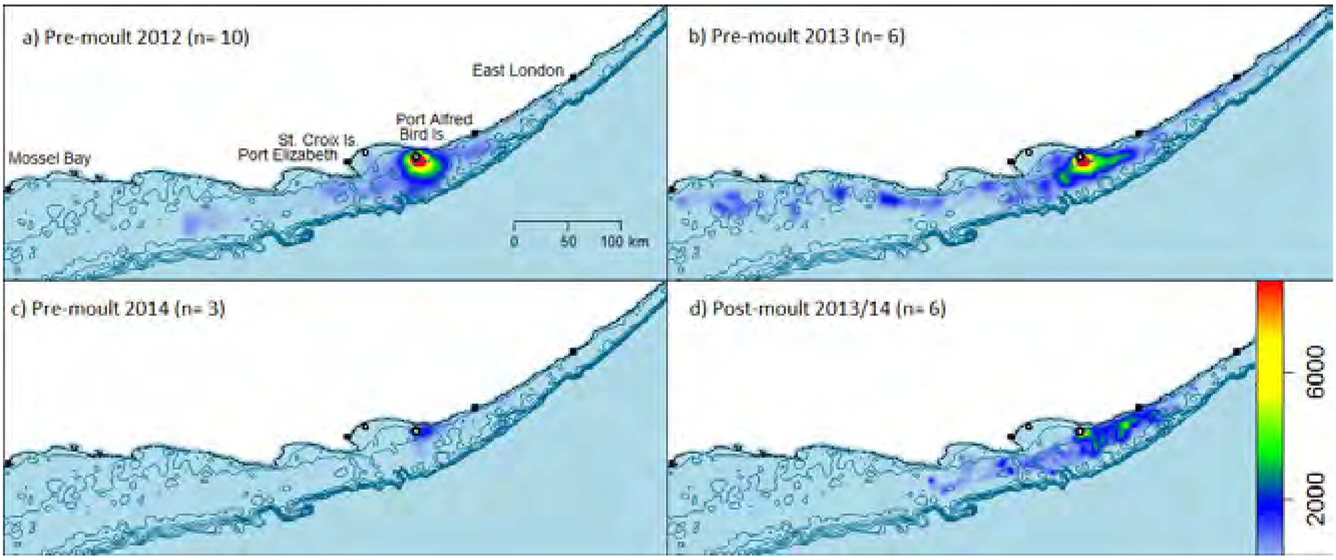


Figure 2.9. Kernel density plots for pre- and post-moult dispersal by penguins from Bird Island over three seasons (2012-2014); n= number of tracks used in density estimation; Bird Island Post-moult was combined due to a very small sample size in 2014.

Of the 21 pre-moult tracks of penguins from Dassen Island which did not end at sea, 13 (62%) of the birds returned to Dassen Island to moult, six (29%) moulted at Stony Point and two (9%) ended up at Dyer Island and St Helena Bay, where they may have moulted, although they were not observed doing so and the devices could have simply fallen off on shore. In 2012 and 2013 pre-moulters from Dassen showed very similar dispersal patterns (Figure 2.10), spending time just south of Dassen Island and offshore on the Agulhas Bank. However, in 2014, the areas of highest density were close inshore, between Dassen Island and Gansbaai. Only one bird went as far south as the Agulhas Bank and two birds spent time along the west coast north of Lambert’s Bay. This latter area was also used by post-moult birds in both years, which showed very similar dispersal patterns apart from the area of high density around the colony in 2013.

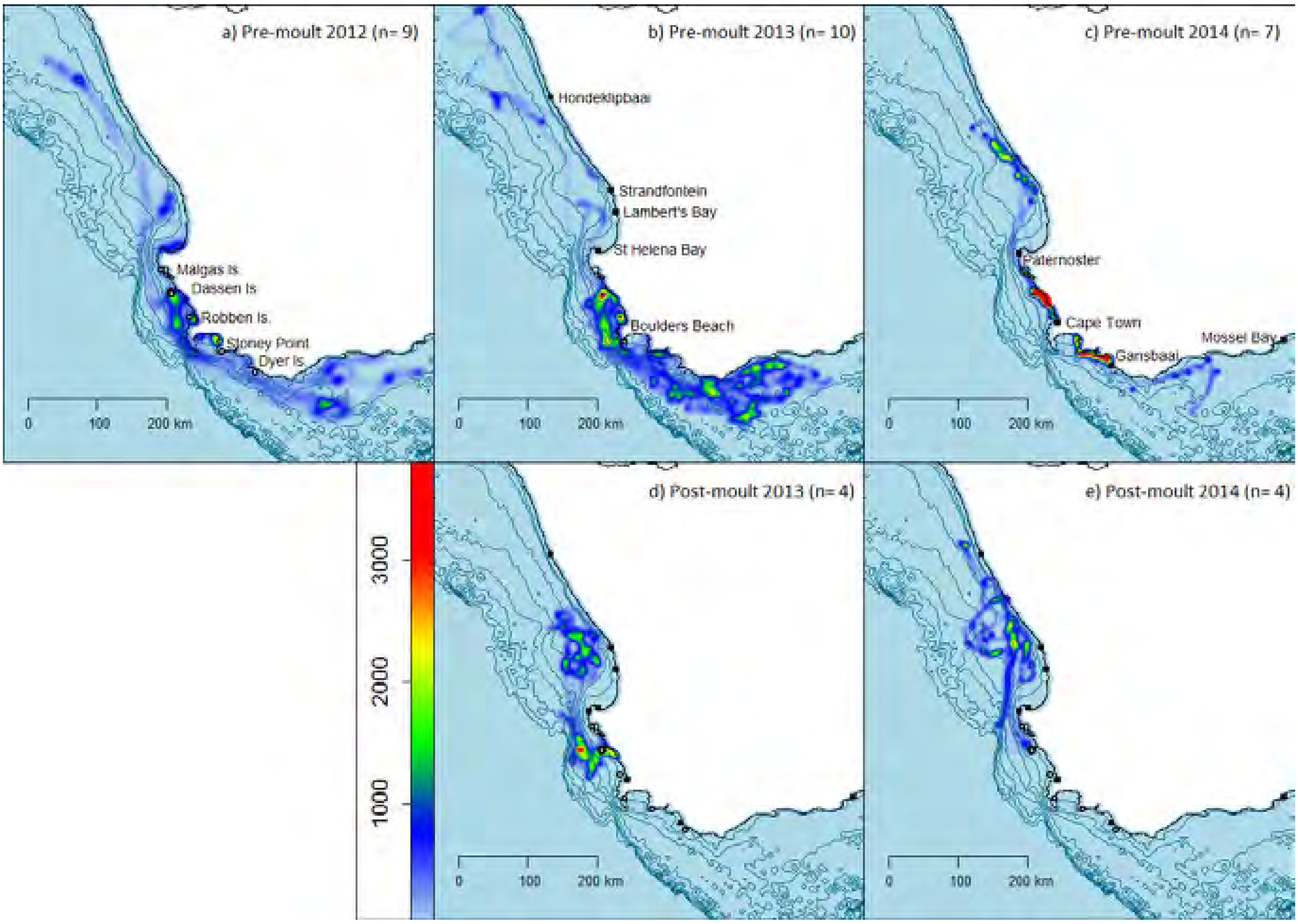


Figure 2.10. Kernel density plots for pre- and post-moult dispersal by Penguins from Dassen Island over three seasons (2012-2014); n = number of tracks used in density estimation. Isobaths every 50 m to 400 m below sea level.

The 75% density kernels (Figure 2.11) illustrate the large spatial divergence between pre- and post-moult dispersal areas used by penguins from Dassen Island. Among penguins from Bird Island, the area of overlap was more substantial, although there was more eastward movement post-moult. There was a large difference in the scale of core dispersal areas between the islands, with Dassen Island birds travelling much farther from their colony.

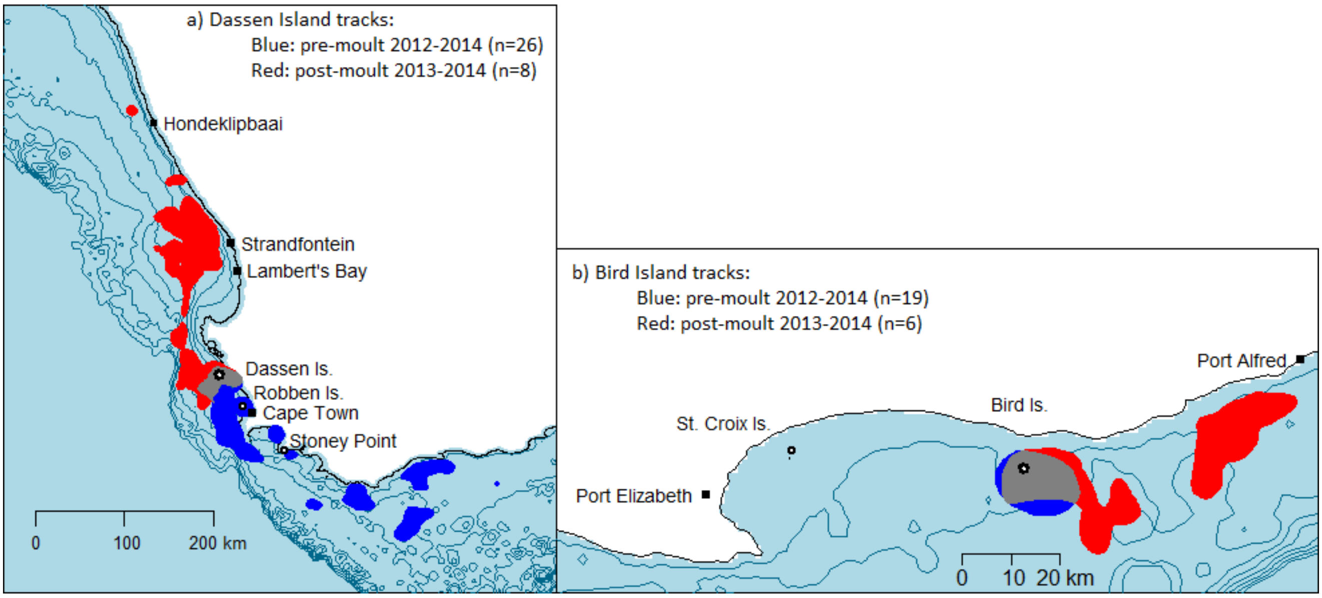


Figure 2.11. Map showing overall pre- and post-moult spatial use of African penguins from a) Dassen Island and b) Bird Island over three years (2012–2014). 75% density contours are shown. Isobaths every 50 m to 400 m below sea level.

Temporal and regional differences in penguin dispersal patterns

Linear models of parameters from complete tracks showed significant differences between islands, seasons and periods (Table 2.2). Bird Island penguins performed more individual trips per track and had slightly longer tracks, whereas Dassen Island penguins spent a higher percentage of time at sea and reached greater distances from the Island. Track length was low in 2012 compared to 2013 and speed was lower in 2014 than in both previous years. Pre-moult birds travelled significantly further from their colonies with most of the difference explained by Dassen Island birds (Dassen: pre-moult= 283(±27) km, post-moult= 126(±70) km; Bird: pre-moult= 128(±29) km, post-moult= 118(±15) km). Pre-moult penguins also seemed to travel faster (or less tortuously) than post-moulters, but this difference falls just short of statistical significance (p= 0.08). Several differences between seasons also fall just short of statistical significance (see Appendix 2 for test statistics, additional parameters, models including all tracks and models of parameters from only the furthest trip of each bird; the results are similar to those described above).

Table 2.2. Differences in track parameters between islands, seasons and periods (mean ±SE) and the significance of each variable; underlined p-values are significant and exact p-values are given for values between 0.01 and 0.1.

Parameter	Island			Season				Period		
	Bird n=19	Dassen n=24	*p*	2012 n=17	2013 n=19	2014 n=7	*p*	pre- n=36	post- n=7	*p*
Number of trips	5.1 ±0.4	2.5 ±0.5	<0.001	3.5 ±0.5	3.8 ±0.5	3.6 ±1.5	>0.1	3.6 ±0.4	3.7 ±0.6	>0.5
At-sea index (%)	58.8 ±5.7	83.6 ±5.2	<0.01	58.7 ±8.1	78.3 ±4.6	91.2 ±5.1	0.09	70.5 ±4.8	83.3 ±7.7	>0.1
Displacement (km)	126 ±23	264 ±27	<0.001	172 ±36	231 ±30	202 ±46	0.054	219 ±23	122 ±28	0.021
Duration (days)	47.9 ±4.1	37.7 ±3.5	0.045	37.2 ±3.7	46.9 ±4.8	41.3 ±5.0	>0.1	42.0 ±3.0	43.0 ±7.1	>0.1
Track length (km)	756 ±83	852 ±87	>0.5	617 ±78	984 ±92	801 ±144	0.011	811 ±69	803 ±122	>0.1
Speed (km.day^{-1})	27.7 ±1.0	29.5 ±2.1	<0.1	32.4 ±1.9	28.2 ±1.4	21.1 ±2.8	<0.01	29.8 ±1.3	22.8 ±1.6	0.082

Nearshore areas

Figure 2.12 highlights areas where Dassen Island penguins spent time on or within 1.5 km of the shore during the non-breeding season, excluding Dassen Island itself. Two areas, between Paternoster and St Helena Bay, were used by individual birds as land-bases for central-place foraging behaviour (large red points). A third high density point was at the Stony Point colony in Betty's Bay, where five penguins eventually moulted, some after visiting the colony on the way south and others after adopting it as a base for central-place foraging. Apart from these three areas Robben Island was a popular stop-over and inshore waters south-east of Dassen Island were important for birds which stayed close to their colony. Bird Island penguins were only found within 1,5 km of the shore on eight occasions. Many of these were east of Algoa Bay where penguins tended to stay close to shore as the shelf is narrow. One bird appeared to visit the neighbouring colony on St Croix Island, and two were tracked close to land at the eastern point of Algoa Bay.

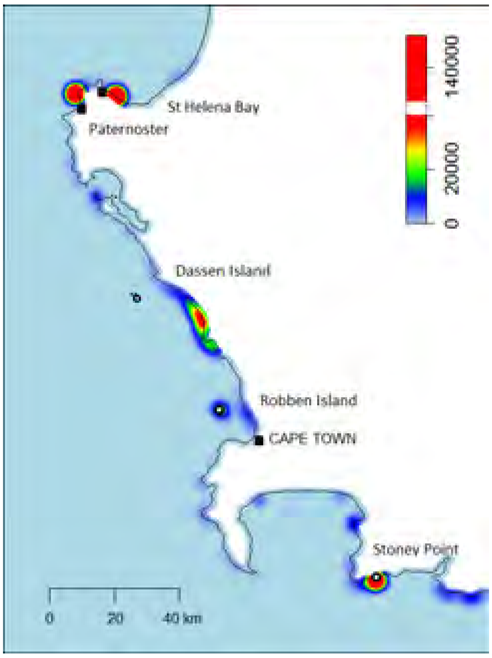


Figure 2.12. Kernel Density map of time spent within 1.5 km of land by non-breeding African penguins from Dassen Island. Points at the colony excluded.

Dassen Island dispersal patterns

Three main dispersal patterns (Figure 2.13 a-c) were used by most Dassen Island penguins: those that travelled south to the Agulhas Bank, those that travelled north to forage off the west coast north of St Helena Bay, and those that stayed close to Dassen Island for the entire tracking period. Three smaller groups were also identified (Figure 2.13 d-f): birds that travelled south to the Stony Point colony, birds that initially swam south before turning north and moving up the west coast further than any in the north-travelling group, and finally those that adopted central place foraging from land bases on Cape Columbine (probably roosting on offshore rocks). Post-moult tracks were present in only two groups ("North" and "Dassen Central") with the remaining four groups containing only pre-moult birds.

Far South (14 tracks): These birds travelled south around Cape Point and onto the Agulhas Bank, reaching distances of 300-450 km from Dassen Island. These were exclusively pre-moult birds and, with one exception, were all tracked in 2012 and 2013. Most returned to Dassen Island to moult but three moulted at Stony Point and one on Dyer Island. One 2013 penguin initially went northwards as far as Strandfontein, before going south to the Agulhas Bank.

North (8 tracks): These birds (six post-moulters and two pre-moulters) headed north from Dassen, remaining within about 400 km of the Island. They seem to concentrate in an area where the 150m isobath pushes westwards.

Dassen Central (5 tracks): These birds stayed within 100 km of Dassen Island throughout the tracking period. Four birds (three 2014 pre-moulters and a 2013 post-moulter) journeyed back and forth between the island and the coast, but the fifth bird (also 2013 post-moult) made five long, convoluted trips to the waters west of the island, staying at sea for between 3 and 34 days at a time.

South (3 tracks): These three pre-moult penguins headed south around Cape Point but stayed close to shore and didn't extend much further than the Stony Point colony (150-190 km). Two of these birds exhibited a central-place foraging pattern based at Stony Point before eventually moulting there, the third returned to Dassen Island to moult.

Far North (2 tracks): Single pre-moult birds in 2012 and 2013 swam more than 450 km up the west coast, one reaching the waters off the mouth of the Orange River, before turning back. Both made excursions southwards reaching the western Agulhas bank before going northwards.

Central-place foraging North (2 tracks): Two pre-moult penguins in 2012 initially went north, but stopped in St Helena Bay at most 125 and 140 km from Dassen Island, where they displayed a central-place foraging strategy. One returned to Dassen Island to moult but the other device remained on the shore where the bird had been based for weeks. Whether the bird moulted at this location is unknown but it was not included in the "lost-at sea" group (see below).

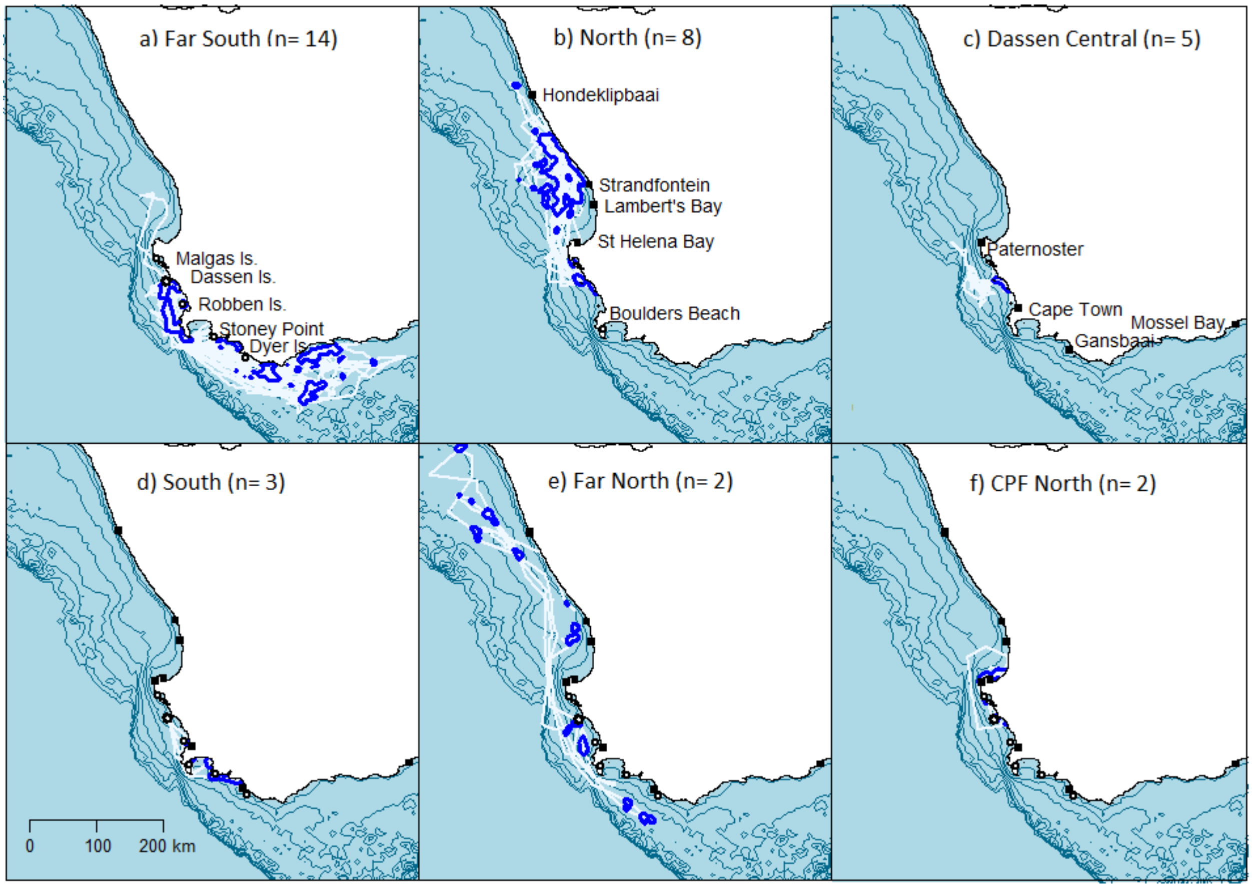


Figure 2.13 Penguin tracks for each Dassen Island dispersal group and the 75% density contours (dark blue). Isobaths every 50 m to 400 m below sea-level.

Bird Island dispersal patterns

The dispersal patterns of penguins from Bird Island were much more uniform with all groups spending over 75% of their time around, and to the east, of the island (Figure 2.14). The largest group was birds whose furthest point was east of Bird Island. The "Far West" and "Bird Central" groups were only recorded among pre-moult birds, while other groups contained both pre- and post-moult individuals (Figure 2.15). All the 2014 results were inadequate and are regarded as "incomplete tracks".

East (8 tracks): Penguins which headed east out of Algoa Bay, but turned back within 100 km. A mixed group with three pre-moult 2012 tracks, a pre-moult 2013 track, two (incomplete) pre-moult 2014 tracks and two post-moult 2013 tracks. Only two of these tracks extended west of Cape St Francis.

Bird Central (5 tracks): These birds stayed close to the island (within 40 km) throughout tracking. These are all pre-moulters with four 2012 tracks and one (incomplete) 2014 track. Three more 2014 penguins never left the island for 17-27 consecutive nights before the devices stopped recording, which is significantly longer than the normal lag-period for Bird Island tracks.

West (5 tracks): These birds travelled westwards, past Cape St. Francis, but turned back within 150 km. All four of these tracks also extended east of Algoa Bay. This group included two pre-moulters (2012 and 2013), two 2013 post-moulters and the only 2014 post-moult track.

Far West (4 tracks): Birds which traveled west for 200-390 km. The longest track turned back offshore from Mossel Bay. All four of these tracks were of pre-moult birds, three from 2013 and one from 2012. Their longest trips were undertaken towards the end of the tracking period.

Far East (3 tracks): These three penguins travelled between 120 and 280 km eastward, remaining close to the coast. They included two pre-moulters (2012 and 2013) and one post-moulter (2013). As with the long westward trips in the previous group, the longest eastward trips of pre-moulters were undertaken just before moulting.

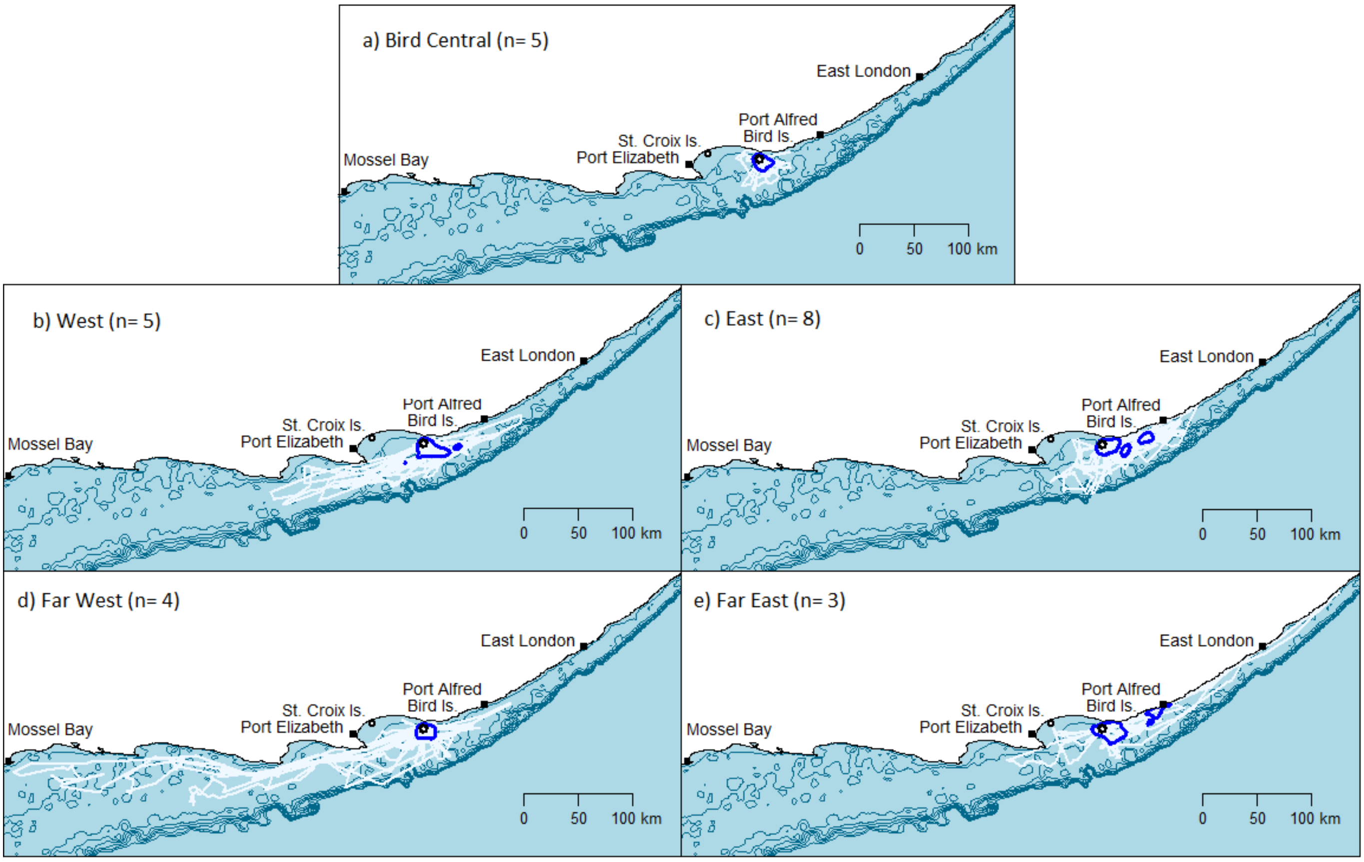


Figure 2.14 Penguin tracks for each Bird Island dispersal group and the 75% density contours (dark blue). Isobaths every 50 m to 400 m below sea-level.

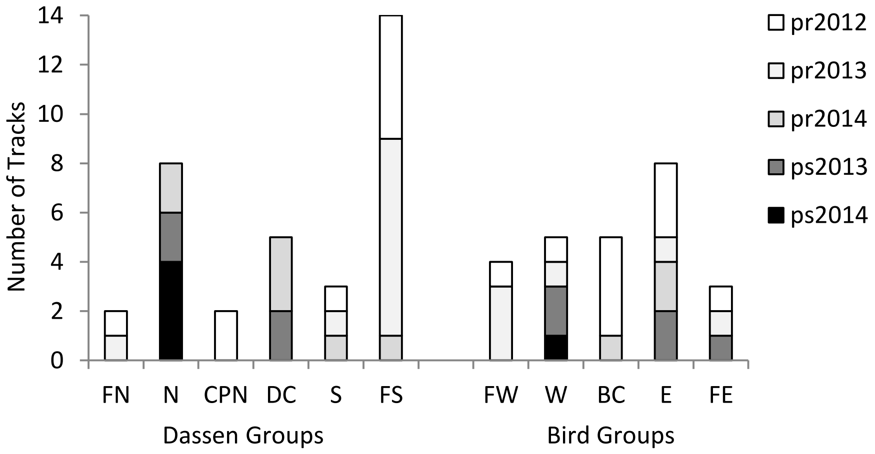


Figure 2.15 The number of African penguin tracks from each tracking session of pre- and post-moult birds from Dassen Island (left) and Bird Island (right) which displayed different dispersal patterns. Groups are named as follows: N, S, E, W = North, South, East, West; D, B = Dassen Island, Bird Island; F = Far, C = Central, CP = Central-place foraging; pr = pre-moult, ps = post-moult

Neither body index nor initial mass showed any relationship to group at either colony (see Appendix 3 for test statistics) and the observed distribution of sex between groups was no different to that expected by chance (Dassen: χ^2= 1.678, df= 5, p>0.5; Bird: χ^2= 5.507, df= 4, p>0.1).

Differential device loss between Dassen Island dispersal patterns

There was no significant difference in initial mass±SE ($\text{mean}_{\text{survived}}$= 2625±298 g, $\text{mean}_{\text{lost}}$= 2672±300 g; t= -0.3900, df= 12.40, p>0.5) or body condition ($\text{mean}_{\text{survived}}$= 45.7±4.4, $\text{mean}_{\text{lost}}$= 46.3±5.2; t= -0.263, df= 10.95, p>0.5) between Dassen Island birds whose PTT devices were recovered and those which were lost at sea, presumed dead. There was, however a significant difference in the latitude of the furthest point reached, with birds that lost devices travelling farther north on average ($\text{mean}_{\text{survived}}$= -33.79±1.52, $\text{mean}_{\text{lost}}$= -32.10±2.37; t= -1.8845, df= 9.1708, p= 0.046). This is visible when comparing the group-distribution of PTT-tracks which survived the tracking period to those which were lost at sea (Figure 2.16, 2.17). Five of eight lost devices stopped transmitting within a small area north of St Helena bay (Figure 2.17).

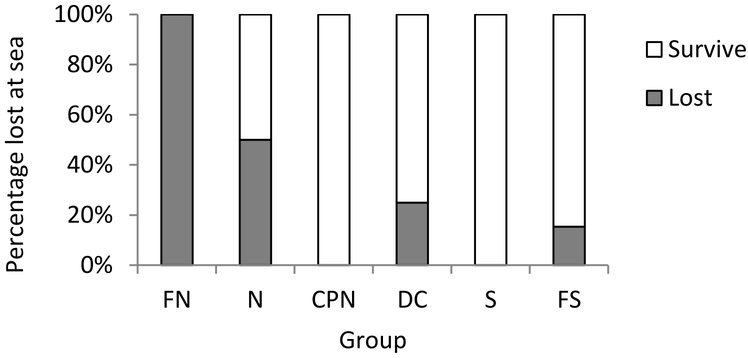


Figure 2.16. Proportion of PTT devices lost at sea in each Dassen Island group

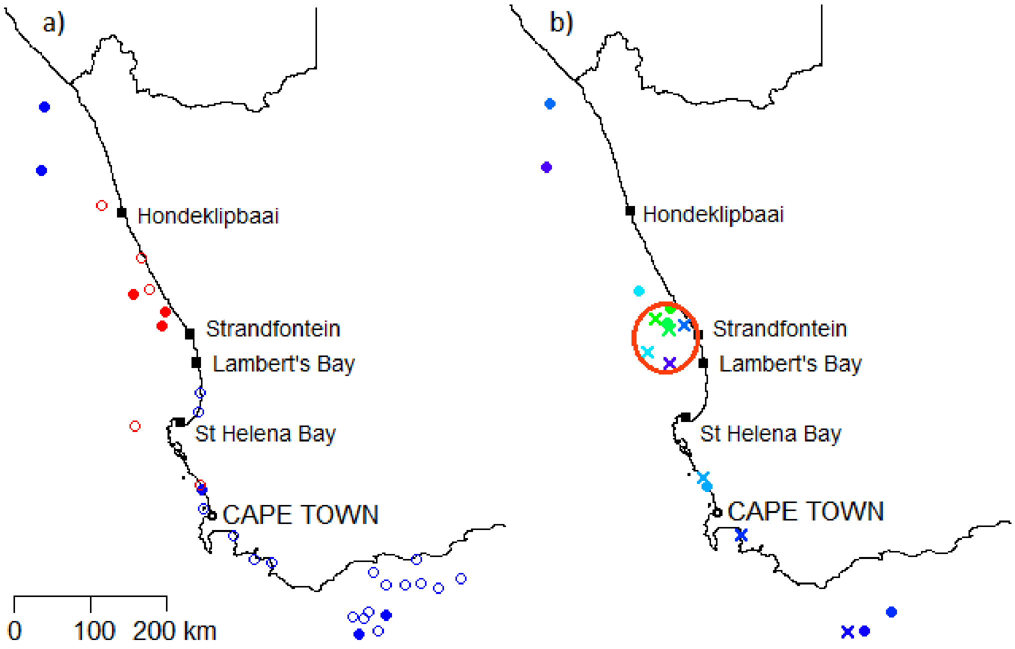


Figure 2.17 a) The farthest points reached by all PTT-tracked penguins from Dassen Island in pre- (blue) and post- (red) moult periods. Lost devices (presumed mortalities) are indicated by solid points and surviving birds by hollow points; b) The farthest point (solid circle) and last recorded point (cross) reached by eight lost PTT devices; five PTTs were lost within the red circle.

DISCUSSION

This is the first multi-seasonal study on the spatial ecology of non-breeding African penguins, providing valuable insight into a hitherto overlooked portion of their annual cycle. In spite of substantial individual variation in dispersal patterns, significant differences were found between colonies (with Dassen Island birds swimming further, spending more time at sea and visiting other colonies more often) and between life-history stages at Dassen Island (with pre-moult birds generally heading southwards towards the Agulhas Bank and post-moulters heading northwards into St Helena Bay and further up the west coast).

Body condition

The difference in body condition between the two colonies follows the general understanding that penguins from west coast colonies currently face greater stresses due to a lack, or displacement, of forage fish (Crawford 2007; Crawford et al. 2011). The differences in body condition of tracked birds from the two Islands, though already significant, is still an underestimate as, during post-moult on Dassen Island, only penguins in good enough condition were used for deployments. About half of the post-moult birds caught on Dassen were rejected due to very low body condition, while not a single underweight bird was caught on Bird Island. Although the chance to visually assess birds before capture is much higher on Bird Island, it did not seem necessary and was not consciously done. The difference in body condition between tracked pre- and post-moult birds was slight, and the fact that tracked birds with a lower initial body condition weren't more likely to die at sea shows that tracking was not a primary factor causing mortality of individuals with lesser body reserves. It is not certain whether this was due to the body condition limit imposed on post-moult tracking, but I would recommend keeping this limit in place should further tracking be conducted in the future.

Dispersal patterns: differences between islands, periods and seasons

The distinct dispersal patterns exhibited by pre-moult penguins from the two colonies, identified by Harding (2013), are supported in this study by tracks from subsequent years. The only real changes from the utilization distribution reported by Harding (2013) is the westward extension of the bird Island penguins' range and more weight given to the west coast north of St Helena Bay, mostly due to post-moult tracks. Over 150 of the penguins rescued from an oil-spill around Dyer Island in 1995 were later seen on Dassen Island, many of them breeding (Whittington et al. 2005). The birds were presumably foraging in these more productive waters before or after moult when the disaster occurred, supporting the idea that a large percentage of the Dassen Island population forages on the Agulhas bank. West coast penguins moulting at Namibian colonies (Whittington et al. 2005) was not observed in this study and is presumably a rare occurrence. The two tracks collected from *Treasure* oil-spill birds in 2000 after they had returned to their colonies (Barham et al. 2006) are similar to tracks collected in this study: one headed south from Dassen onto the Agulhas Bank, similar to most of 2013 pre-moulters, while the other (a Robben Island bird) headed north into St Helena Bay and offshore of Lambert's Bay, similar to post-moult tracks and two of the 2014 pre-moult tracks. Although those tracks were collected between July and September, after breeding was interrupted, they probably represent the pre-moult dispersal trips of early moulters. The high density of penguins spotted between Dassen Island and Cape Point by Wilson et al. (1988) is understandable given the relatively narrow shelf along the southern west coast which high numbers of birds traverse to reach foraging locations further south.

The South African Department of Agriculture, Forestry and Fisheries (DAFF) conducts biannual hydro-acoustic biomass surveys of pelagic fish (recruit biomass is surveyed in June and spawner biomass in November) in order to set the total allowable catch (TAC) of small pelagic fish for the following year (Barange et al. 1999, Prochazka 2014). November surveys for the three years of this study (Appendix 4) show high densities of both sardine *Sardinops sagax* and anchovy *Engraulis capensis* across the Agulhas Bank, supporting the idea that this area offers much better foraging than those closer to the Dassen colony. As Harding (2013) recognized, most Dassen Island penguins appear to have to work harder to attain moult condition than their Bird Island counterparts. They travel greater distances, presumably to find more productive foraging grounds, and are still unable to attain the same condition. This seems to indicate that the area around Bird Island is productive enough to allow penguins to remain there, even when breeding restrictions are lifted, and that, although travelling large distances is energetically costly, it is presumably more efficient than staying in the area around Dassen Island.

The longest trips undertaken by pre-moult penguins from Bird Island were equivalent in length to those of most Dassen Island penguins, and all occurred just before the start of moult. These could, by themselves, be seen as the pre-moult period and earlier trips could simply be those of loafing birds with time to spare between breeding and moult. The real difference between colonies would then be in the duration of these long trips and in the amount of "spare" time between the end of breeding and the start of pre-moult foraging. Unfortunately, with the loss of the 2014 devices the number of long trips recorded is too small to properly support this idea. These long trips were also almost all recorded in 2013, when there was particularly high anchovy density along the eastern Agulhas bank (Appendix 1.2) and could simply represent opportunistic use of these resources. It could also imply that, although Bird Island penguins can, and occasionally do, forage on the Agulhas bank, it is generally unnecessary as forage fish availability closer to their colony is sufficient. Wilson et al. (2005) also found differences in the length and distance of the incubation foraging trips of magellanic penguins from different colonies, and attributed this to differences in local prey availability.

A major difference between the non-breeding dispersal patterns of penguins from the two colonies is the fidelity of the Bird Island penguins to their own colony. Whittington et al. (2005) also noted that banded Eastern Cape penguins were hardly ever re-sighted at neighbouring colonies. Over a quarter of Dassen penguins in this study moulted elsewhere and even those that did moult at Dassen spent time at other colonies along their dispersal route. A recent study on Humboldt penguins (Wallace & Araya 2015) found groups of penguins moulting in areas unassociated with breeding. This has not been previously reported in African penguins and, although one bird might have moulted near St Helena Bay, it was not observed and the device could simply have dropped off. Moulting closer to good foraging areas would benefit birds both before and after moult by reducing the energy used to commute back to Dassen, but why spend time close to shore and at strange colonies? Most shoreline visits occurred on the way south from Dassen rather than on the return journey. The surface currents along the southern west coast move northwards and can become quite powerful at times, especially off the Cape Peninsular (Shillington et al. 2006). I speculate that southward travelling penguins tend to rest close inshore, where currents are less powerful, rather than risk being drifted back northwards.

An effect of surface currents could also explain the distinction in pre- and post-moult dispersal areas. After moulting, apart from having very low energy reserves, the birds' swimming muscles have atrophied and swim speeds are reduced (Wilson 1985). Fighting against a strong current in this weakened state would be difficult. By heading northwards these currents become an asset, naturally depositing the birds onto the relatively sheltered water in northern St Helena Bay, historically rich in forage fish (Coetzee et al. 2008). Following the decline of small pelagic fish along the west coast there has been very little biomass of forage fish reported in the area north of St Helena Bay (Appendix 4) and the preference shown for this area by post-moult birds could be contributing to the high levels of adult mortality. It is possible that post-moulters in this area have turned to an alternative food-source, as penguins on Possession Island did after the collapse of the Namibian sardine population in the early 1980s (Crawford et al. 1985). Fish larvae and cephalopods have been previously recorded in the diet of breeding Dassen Island penguins, though not in large quantities (Crawford et al. 2011). All penguins remained very close to shore in this area (within the 200 m isobath) and are probably targeting inshore prey. More recently, a single post-moult bird (one of three tracked in 2015, BirdLife SA, unpublished data) did travel south from Dassen Island, reaching De Hoop Nature Reserve before the signal was lost. Interestingly this bird stayed very close to shore along the way, and took longer to reach the Agulhas bank (over 10 days) than the pre-moult birds in this study. The similarity in core dispersal areas for pre- and post-moult penguins from Bird Island reflects the relative ease with which these birds can re-provision after moult. There are no strong currents to contend with in the shelter of the bay and enough fish close to the island that distant dispersal is unnecessary.

Why the Dassen Island pre-moult tracks were so different in 2014 is difficult to say. If the overall pattern is different, the actual tracks are similar to ones recorded in preceding years, although two of them more resemble post-moult tracks. Perhaps it is simply down to chance and the smaller sample size or perhaps oceanographic conditions pushed the forage fish inshore and the birds followed. The November fish survey (Appendix 4) shows a very similar prey distribution to preceding years, but with even fewer forage fish along the west coast. Dispersing to the Agulhas bank would seem a beneficial strategy under such conditions. It is possible that food scarcity during the breeding season could have left pre-moult birds too weak to make the journey south. The sardine and anchovy recruit biomass estimates for July 2014 are lower than preceding years, with sardine estimates substantially lower (Coetzee et al. 2014). However, body condition on Dassen Island was actually higher in 2014 than in other years, belying this conclusion.

Individual dispersal patterns

Investigating the drivers behind the different non-breeding dispersal patterns exhibited by Dassen Island birds could lead to a better understanding of the adaptability of individual penguins and the population as a whole. As different patterns were exhibited almost simultaneously it is unlikely that environmental drivers alone were influencing the birds' destinations and this implies that previous experience or innate drivers are leading to the differences observed. This could be explored further by tracking individuals over multiple seasons to test foraging site fidelity but would need to be ethically assessed as multiple deployments could lead to cumulative stress. There is growing evidence of forage patch fidelity in various seabird species (Hamer et al. 2001; Irons 1998; Kotzerka et al. 2011), including little penguins (Mattern et al. 2007), although generally associated with benthic foraging or persistent ocean features (Weimerstirch 2007). Although useful in defining conservation areas (Auge et al. 2014), high forage site fidelity in marine predators can have negative consequences when previously consistent ecosystem features shift (e.g. due to anthropogenic influences), both because previously high quality foraging areas could degrade over time, and because new, more productive or accessible areas may be overlooked. This could be the case with African penguins which disperse north of St Helena Bay. When compared to the consistency of Bird Island dispersal, the distinct dispersal patterns of Dassen Island birds seem to indicate penguins attempting, in different ways, to survive under less-than-favourable conditions.

Survival estimates

Although the analysis was compromised by the fact that devices could fall off or stop working for technical reasons, and that post-moult devices could be more likely to do so due to slight differences in attachment method, the fact that so many devices were lost in such close proximity to each other seems to indicate some sort of underlying process. The T*reasure* oil spill penguin from Robben Island foraged in this same high-risk area after returning to its colony in 2000 (Barham et al. 2006). This indicates that it is not only Dassen Island penguins which use this area and makes it even more important to explore any possible additional causes of mortality.

It is widely believed that the decline in forage fish density along the west coast is the major cause of adult penguin mortality which has driven the population collapse in this region over the last decade (Crawford et al. 2001, Crawford et al. 2008) but this would be expected to show a more widespread mortality pattern. Penguin predation by Cape fur seals has been observed in the area around Lamberts Bay (Crawford et al. 2001) and there are several seal colonies in the area (Griffiths et al. 2004). Seal numbers have increased significantly over the last century in response to conservation measures implemented in the 1890s when populations were severely over-exploited (Butterworth et al. 1995). Observations of seal predation on seabirds, in particular that of young male seals on juvenile gannets and breeding penguins, has increased over the last few decades (Makhado et al. 2006). Seal predation on penguins at Dyer Island is thought to have contributed, at least in part, to the population's decline (Marks et al. 1997; Ludynia et al. 2014) and Crawford et al. (2001) found that an 'unsustainable' number of juvenile and adult penguins were being predated from the tiny Lambert's bay colony, which has since been abandoned (Crawford et al. 2008).

I speculate that post-moult penguins which have not yet regained their strength could be easy targets for opportunistic seal attacks, especially in the non-breeding season when small pelagic fish have moved off the west coast to their spawning grounds, forcing seals to find alternative prey. A similar suggestion was made by Whittington (2002) to explain lower re-sighting rates (indicating lower survival) of banded juvenile penguins from Dassen Island, where juveniles tended to head northwards from the island, passing large land-based seal colonies. The stomach contents of over one and a half thousand seals collected at sea between 1970 and 1990 contained only two samples with seabird remains, leading David et al. (2003) to conclude that seal predation was only problematic around seabird breeding colonies. Many of these samples were collected across the area in question during the non-breeding season (Punt et al. 1995), indicating that if this is indeed a frequent cause of penguin mortality, it is a relatively new occurrence. The general management response to excessive seal predation in South Africa is the culling of problem animals when they are seen attacking birds (David et al. 2003). If substantial numbers of Dassen Island penguins are being killed by seals in their most frequented post-moult dispersal area, seal-control methods at nearby colonies could be required to slow the decrease in the penguins' adult breeding population. However, the majority of penguin predation seems to be carried out by particular "problem animals", generally young male seals with a predilection for attacking penguins (Makhado et al. 2006). Identifying these problem animals would be difficult in this situation where attacks occur out at sea, far from witnesses.

CHAPTER 3: AFRICAN PENGUIN PRE- AND POST-MOULT DISPERSAL IN RELATION TO COMMERCIAL PURSE-SEINE FISHERIES

INTRODUCTION

Fishing activities negatively affect seabirds through accidental by-catch, entanglement and disturbance. Some species are even collected for bait or culled as competitors (Tasker et al. 2000). The indirect effects of commercial fishing on forage fish availability are more difficult to predict as they are influenced by complex trophic interactions and environmental pressures. For example, fishing pressure on predators can buffer that on prey-fish (Furness & Camphuysen 1997); or intense exploitation of one fish species can upset the balance between competing stocks (Tasker et al. 2000). In extreme cases continued fishing pressure can cause a permanent regime shift to a system less hospitable to seabirds (Game et al. 2009). This occurred off the coast of Namibia when unsustainable fishing led to pelagic fish being largely replaced by jellyfish and salps (Lynam et al. 2006), leaving little for seabirds to eat.

In general, where fisheries and seabirds target the same fish there is the potential for competition. Cury et al. (2011) considered the effect of prey abundance on the breeding success of seabirds around the world and proposed that a third of the highest recorded abundance of forage fish is required to maintain seabird colonies. Further depletion of fish stocks by the fishing industry reduces the prey available for seabirds (Cury et al. 2011), necessitating more time and energy spent on foraging (Cairns 1987). Exploited fish populations also show higher variability (Hsieh et al. 2006) meaning lower predictability in food abundance and potentially more extreme food shortages for birds (Crawford 2004). Overlap between fishing industries and seabirds has been most often studied by comparing the diet composition of seabirds to local fishing catches (e.g. Karpouzi et al. 2007), recording seabird sightings and bycatch mortality from fishing vessels (e.g. Camphuysen & Garthe 1997) and comparing the at-sea distribution of seabirds with fishing location data (Pichegru et al. 2009; Reid et al. 2004; Tew Kai et al. 2013).

Most seabirds are adapted to cope with short-term changes in food availability (Furness 2007), but some species are more vulnerable to prey-shortages than others. Furness & Tasker (2000) identified six parameters to consider when estimating the sensitivity of a particular seabird species to reductions in food availability: the size of the bird, the cost of foraging, their foraging range, their ability to dive, the amount of spare time available for increased foraging effort, and plasticity in diet. Sensitivity also varies temporally, with age and with seasonal changes in energy use. It is assumed that breeding birds are especially vulnerable (Scott et al. 2006) as they must provide food for chicks as well as themselves, in spite of a restricted foraging range (Daunt et al. 2006). There have been recent studies directly linking local fishery catch to reduced foraging success in Peruvian boobies, *Sula variegate* (Bertrand et al. 2012) and African penguins (Pichegru et al. 2012) implying that implementing appropriate fishing restrictions could improve seabird breeding success.

In times of food shortage birds will either invest more time in foraging (Enstipp et al. 2007) or change their diet to a more easily available, but potentially lower-quality, food source (Gremillet et al. 2008; Österblom et al. 2008; Pichegru et al. 2007). Many birds also forego breeding entirely until conditions improve (Drent & Daan 1980). Being long-lived with relatively low fecundity, seabird populations are more sensitive to changes in adult survival than to changes in breeding success (Schreiber & Burger 2001) and food shortages are most often reflected in reduced breeding success or skipping breeding (Furness 2007; Sherley et al. 2013a; Wanless et al. 2005). For African penguins, however, food shortages in the foraging periods before and after moult directly impact adult survival (Wolfaardt et al. 2009), making food availability in the non-breeding season particularly important and competition with fisheries during these periods a potential conservation concern.

Small pelagic fisheries

Small pelagic fisheries are responsible for a third of global fish catches each year (Agenbag et al. 2003). Many seabirds rely almost exclusively on small pelagic fish, making competition between seabirds and fisheries inevitable (Furness & Camphuysen 1997). In South Africa, purse-seine fisheries target shoals of sardine, anchovy and red-eye round herring (*Etrumeus whiteheadi*) in what is the country's largest fishing industry by mass (Hara 2013). In upwelling systems such as the Benguela, a few small pelagic species are almost entirely responsible for energy flow through the system, making the system particularly sensitive to the exploitation of these species (Cury & Shannon 2004). But because pelagic fish populations fluctuate naturally (de Moor et al. 2011), fisheries-driven changes are difficult to detect (Tasker *et al*. 2003).

Small pelagic fishing in the Benguela began during the Second World War when the sardine population was high, but a decrease in catches in the 1960s led to the introduction of smaller net sizes to target anchovy (Fairweather et al. 2006). Fluctuations in sardine and anchovy biomass off the South African coast have been documented since the 1920s (Cury & Shannon 2004) and analyses of subfossil fish scales in bottom sediments indicate that similar switches have occurred for centuries (Shackleton 1987). Anchovy biomass increased in the late 1990s and early 2000s following several years of good recruitment (Cury & Shannon 2004). In spite of this, predators and fishermen on the west coast had to travel increasingly far to find prey as pelagic fish populations began to shift south and eastwards around the coast (Coetzee et al. 2008; Roy et al. 2007). As there are few suitable breeding islands along the south coast and many species show strong natal philopatry, seabirds cannot relocate to make better use of these resources (Okes et al. 2009).The fishing industry is similarly anchored by necessary infrastructure and facilities along the west coast and consequently fishing effort in this area remains high, targeting a declining resource (Coetzee et al. 2008). Sardine and anchovy are currently managed jointly under the same management procedure, with a biannually assessed Total Allowable Catch (TAC) for each species (de Moor et al. 2011). Recent evidence suggests that at least two sardine stocks exist along the South African coast (Coetzee et al. 2008; van der Lingen et al. 2013) and it seems likely that a multi- stock approach is needed to manage South African sardines effectively. Such measures will hopefully reduce pressure on west coast populations, with benefits to seabirds breeding in this region but will consequently increase pressure on south coast colonies.

South African seabirds which rely almost exclusively on sardine and anchovy include Cape gannets, Cape cormorants (*Phalacrocorax capensis*), and African penguins. The relationships between pelagic fish stocks and South African seabird populations have been studied since the mid-1950s, often in order to use seabird numbers as a proxy for fish biomass (Crawford et al. 1992). More recently, studies on the overlap between fisheries and seabird foraging have led to recommendations for no-take zones around breeding colonies and in important foraging areas (Okes et al. 2009; Pichegru et al. 2009; Pichegru et al. 2012).

Seabird conservation in South Africa

There has been some progress in fisheries-seabird relations in South Africa in recent years. DAFF has committed to an Ecosystems Approach to Fisheries Management which includes a stipend for seabirds and other marine predators in the Operational Management Procedure used to calculate the TAC for small pelagic species (Hara 2013). The iconic African penguin has received particular attention with the Department of Environmental Affairs (DEA) drafting a *Biodiversity Management Plan for African Penguins* in 2012, which included optimistic plans to ensure sufficient prey for them in the breeding and non-breeding seasons (DEA 2013). An extension to the no-take zone in Algoa Bay is being planned around the foraging ranges of African penguins breeding on St Croix Island (A. Oosthuizen, SANParks, pers. comm.) and the Pelagic Scientific Working Group at DAFF is conducting an extensive (and so far inconclusive) experiment to investigate the effects of closing areas around penguin colonies to fishing during the breeding season (DEA 2013).

Harding (2013) found substantial overlap between pre-moult penguin dispersal areas and the small pelagic fishing industry, showing the potential for competition over large areas. The fisheries data used in that analysis were on quite a course scale, with catches amalgamated on a 10x10 nautical mile grid over two months. In this chapter much finer-scale fishing data, with accurate dates are used to assess the overlap between fisheries and penguin non-breeding dispersal areas. This will still not shed any light on the effects of commercial fishing on either forage fish availability or penguin foraging success, but will simply highlight the spatial and temporal differences in the potential for competition and disturbance. Fishing vessels are logistically constrained throughout the year, whereas non-breeding penguins are able to range further afield. I hypothesize that penguins will preferentially forage in areas of lower fishing pressure when the restraints of the breeding season are lifted, indicating that either disturbance by fishing vessels or the local depletion of fish-stocks could negatively affect penguin foraging success in heavily fished areas.

METHODS

Fishing data

The GPS coordinates and times of national purse-seine nets set in the three years of tracking (2012 to 2014), along with corresponding catches of sardine, anchovy, red-eye round herring, juvenile horse mackerel (*Trachurus capensis*) and maasbanker (*Trachurus trachurus*) were supplied by DAFF. The data were cleaned by removing duplicates, entries without GPS coordinates, and points erroneously recorded, either on land, or obviously outside the range of the boats.

Vessels recorded both sardine caught as the target species as well as that caught as bycatch with anchovy in mixed schools. These values were combined to calculate total sardine catch for each set.

Data analysis

To identify temporal trends in catches, total catch per month of the three most abundant small pelagic species caught was plotted. KDEs (see methods in Chapter 2) of total sardine and anchovy catch during the three years were used to explore the spatial extent of the industry, weighting each point by catch so that those with larger catches counted more towards the density estimate than those which were less successful. Because fishing effort (number of sets) and combined anchovy and sardine catch were highly correlated (r^2=0.95, Figure 3.1) all further analysis was simplified by using only total sets.

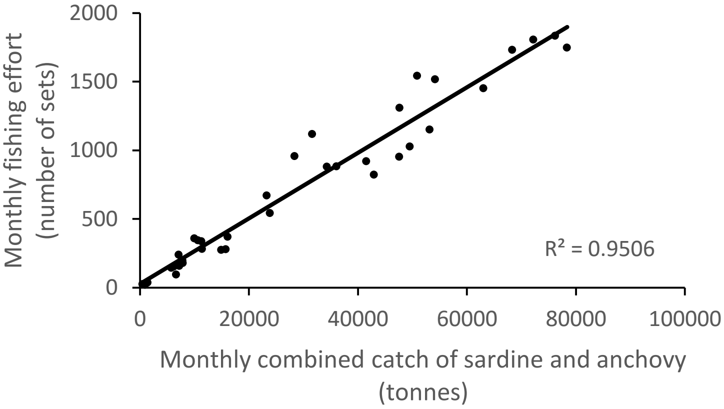


Figure 3.1. Correlation between monthly fishing effort and monthly combined sardine and anchovy catch of purse-seine fisheries in South Africa

Fishing data were split into west and south coast sections at 22.1°E as this was the midpoint between Dassen and Bird Island penguin tracks (Chapter 2). The 90% contours (see Chapter 2 methods) for all fishing effort over the three years, and for all nets set from August to January, were plotted for both sections of coast to identify any spatial differences in effort during the penguin non-breeding season. A smoothing bandwidth (see Chapter 2 methods) of 0.5 was used for all KDEs to make comparisons possible. This number was chosen visually to minimise the scatter of the 90% contour as the bandwidth methods in Chapter 2 were not appropriate for looking at broad scale overlap. The operation window (see Chapter 2 methods) was problematic when comparing contour polygons and had to be abandoned. This resulted in some overlap with land, but it was small enough to be negligible in this context. For each Island (or coast section), the areas of overlap were calculated between 90% pre- and post-moult penguin contours and 90% fishing effort contours for both overall fishing effort, and August to January fishing effort. The number of overlapping sets (as a percentage of total sets along that coastline), their combined anchovy and sardine catch (as a percentage of total anchovy and sardine catch along that coastline) and the average catch per unit effort (catch. number of sets^{-1}) was calculated within each penguin contour. Fishing pressure in the four main dispersal areas used by Dassen Island penguins (identified in Chapter 2) was similarly assessed. As in Chapter 2, an Albers equal-area conic projection was used throughout.

There are two possible mechanisms by which local fishing activity could influence penguin spatial use over a short period. Firstly, penguins might be directly disturbed by vessels and fishing activity. This was explored by assessing the frequency of encounter between tracked penguins and fishing boats. For each day on which both fishing and penguin data were available, the number of sets in close proximity to the penguin was counted. This was done by drawing a buffer around the day's penguin track and counting the number of fishing vessels within the buffer area. As tracks between nightly fixes were interpolated, the buffer size was necessarily quite large (calculated as half the third quartile value of daily distance travelled by penguins in this study: 38/2 ≈ 20km, Appendix 5). Overlap was reported as the number of sets within the buffer per penguin per day.

The coastline was divided into five zones following those used by DAFF to report their acoustic biomass survey results (e.g. Shabangu et al. 2012). Although DAFF's zones are divided by lines perpendicular to the coastline, I simplified the process by dividing along lines of latitude or longitude and believe the differences to be negligible in this context (see the zones in Figure 3.7 later in this Chapter, and DAFF's zones in the 2012 biomass results, Appendix 4). Zone A includes areas north of Paternoster, zone B between Paternoster and Cape Point, zone C between Cape Point and Cape Agulhas, zone D between Cape Agulhas and Mossel Bay and zone E east of Mossel Bay. For each zone the percentage of time spent in the area by tracked non-breeding penguins, the percentage of sets, the percentage of same-day overlap encounters and the percentage of combined anchovy and sardine spawner biomass from the November acoustic survey was calculated.

To test whether penguins were avoiding or associating with fishing boats at this scale, simulated Dassen Island tracks were made using adehabitatLT:: NMs.RandomCRW (Calenge 2006). This simulates random correlated walks from the parameters of input tracks. The start point was fixed as Dassen Island, and the coastline and the extent of collected tracks (following the 300 and 400m depth contours where appropriate) were set as boundaries. Because of the shape of the boundary, simulated tracks tended to head north from the island and this was corrected by maintaining the angles of the original track and only varying the track interval (within the parameters set by the original track). See Appendix 6 for examples of simulated datasets compared to Dassen Island tracks. Twenty datasets were created each containing 30 simulated tracks. The average number of sets encountered per penguin per day were compared between simulated and original data sets. As the simulated tracks are unaffected by the presence or absence of fishing sets, or the abundance of fish in the area, they provide a null model against which the actual tracks can be compared. If the number of encounters per penguin per day is found to be significantly lower in the real data than in the simulated data, this would suggest that penguins are preferentially avoiding fishing activity. If the reverse, it would indicate an association.

The second possible mechanism by which fishing activity could influence penguins over a short time period is by localized forage fish depletion after fishing. Penguins could be avoiding areas after fishing has occurred, due to a lack of prey. This was explored by extending the previous analysis to include nets set on preceding days (up to 30 days previously) to see if any decrease in the probability of penguin presence could be detected in the days following fishing activity. The results were once again calculated per zone.

RESULTS

Fishing data

The accuracy of the pelagic fishing dataset can be judged roughly by the percentage of the catch reportedly caught on land. This came to 9 579 tonnes of anchovy (1.5%) and 4 684 tonnes of sardine (1.6%). These points were removed from analysis except where total catch was calculated. There were also 449 entries without GPS coordinates (a further 1.7% of the data, 3.6% of sardine catch and 0.8% of anchovy catch) which were similarly removed. After filtering, the purse-seine data set included 25 528 recorded catch events, 24 431 of which reported catching either anchovy or sardine. Published annual catches for 2012 and 2013 (Prochazka 2014) matched those calculated from this dataset.

Purse-seine catch (2012 – 2014)

Over the three-year period the total recorded catch was 297 991 tonnes of sardine (8.1% of which was by-catch), 626 425 tonnes of anchovy and 133 945 tonnes of redeye round herring. The other two recorded species (maasbanker and mackerel) together made up just 6 485 tons (0.6% of the total catch). The penguin non-breeding season (August to January) coincides with a lull in small pelagic catches after September in all years, with very little fish caught in the last few months of the year (Figure 3.2). As this is associated with lower fishing effort, any direct interactions between fisheries and non-breeding penguins would therefore be expected to occur predominantly at the start of the non-breeding period (August to September) during pre-moult foraging. The noticeably lower anchovy catch in 2013 was reportedly the lowest catch for this species in 15 years (Prochazka 2014).

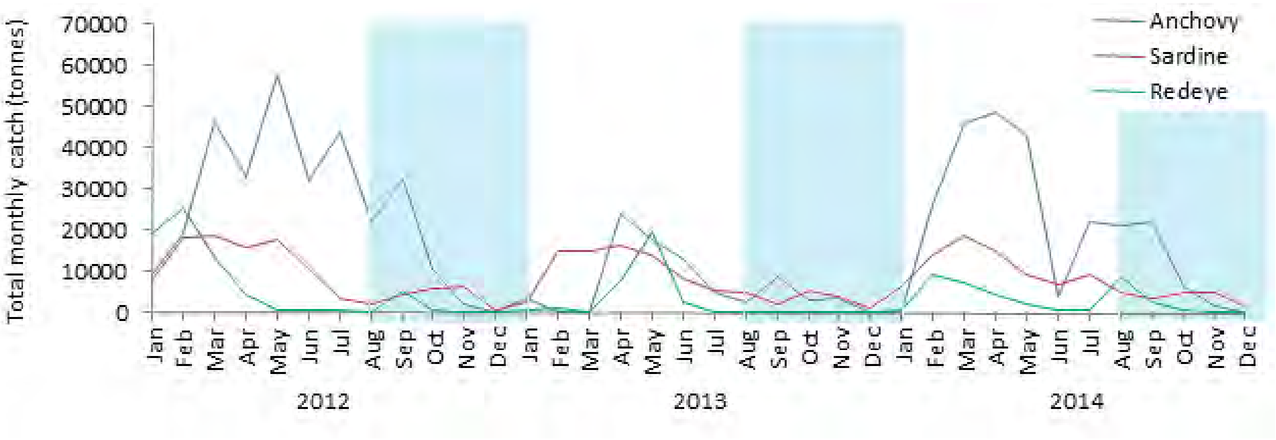


Figure 3.2. Monthly catch of three pelagic species over three years in relation to the peak African penguin moult season (shaded bars)

Anchovy were caught along the southern west coast, predominantly in St Helena Bay and off the Cape Peninsula. They were also heavily fished north-east of Dassen Island and around Gansbaai (Figure 3.3). Sardine catches were centred further south around Gansbaai and, to a lesser degree, on the south coast near Mossel Bay.

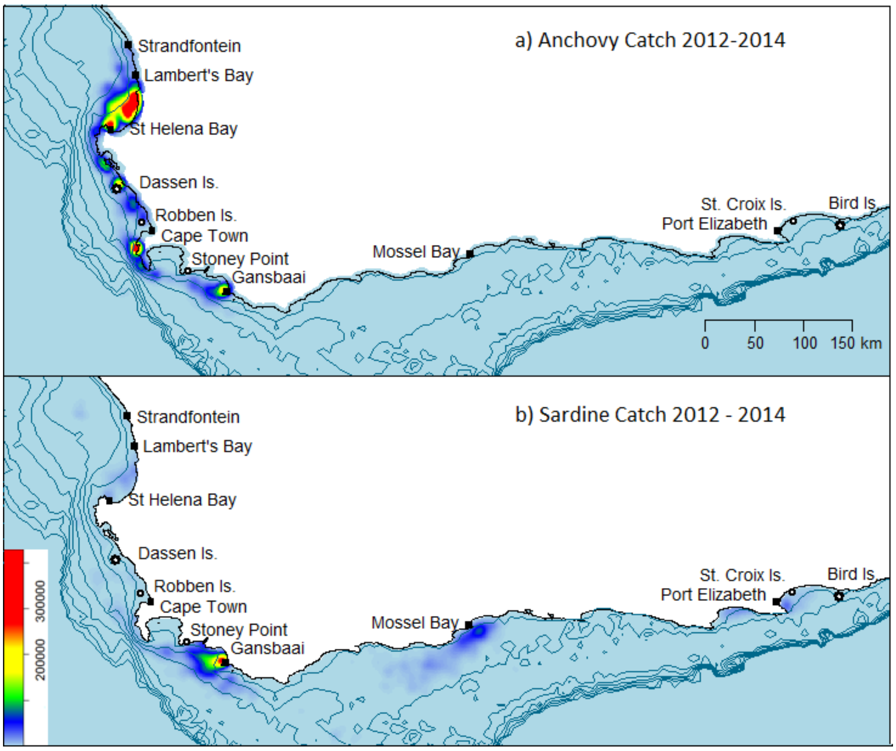
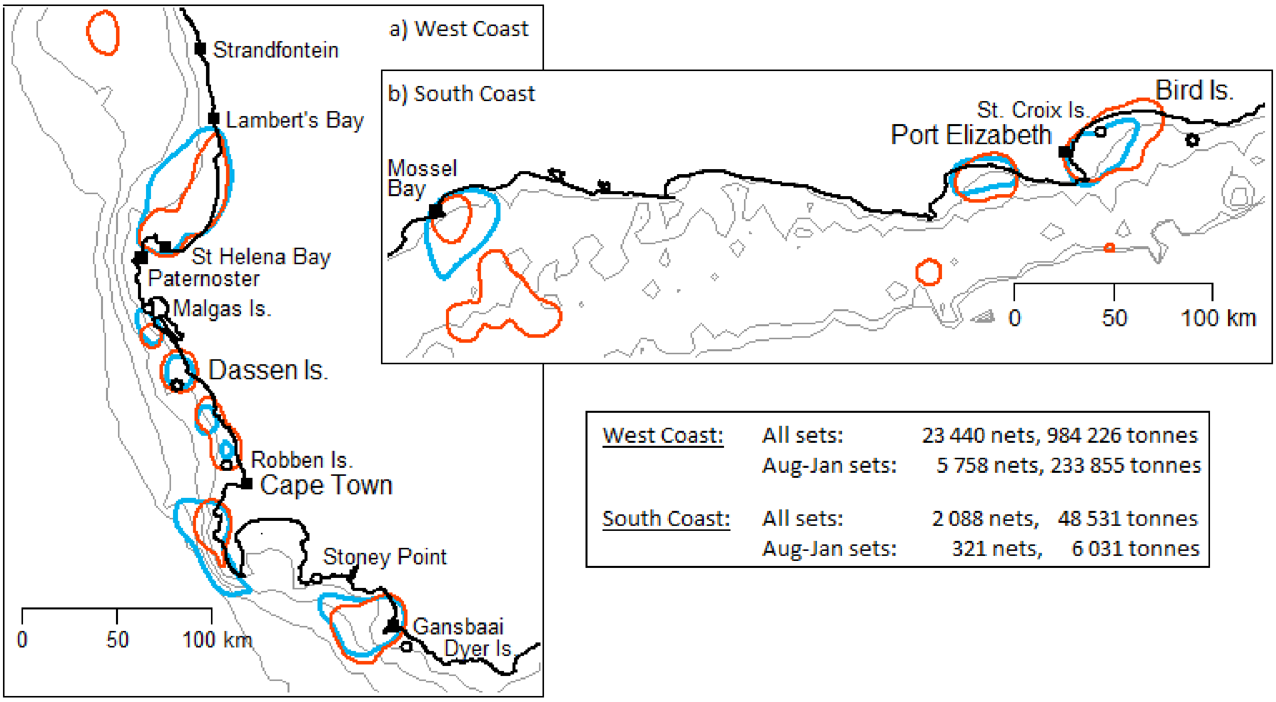


Figure 3.3. Kernel Density Maps of sardine and anchovy catches off the coast of South Africa 2012-2014. Isobaths every 50 m up to 400 m below sea-level.

Purse-seine fishing effort 2012-2014

Overall fishing effort was concentrated on the west coast, with the small amount of south-coast fishing restricted to the areas around Mossel Bay and Port Elizabeth. Fishing on the west coast was concentrated into several small, highly fished areas (Figure 3.4, from north to south: St Helena bay between Lambert’s Bay and Paternoster, near Langebaan, north and east of Dassen Island, along the coast north of Robben Island, off the Cape Peninsular, and near Gansbaai). These areas tend to be close to harbours and were similar between seasons, but with fewer areas used as heavily in 2013. South coast fishing was concentrated into two main areas: around Port Elizabeth (both in the western section of the bay and further west, outside the bay), and off Mossel Bay. Similar to on the west coast, fishing around Mossel Bay was very low in 2013. Average catch per set was significantly higher in the west coast section (Mean catch$_{west}$= 42.0 tonnes, Mean catch$_{south}$= 23.2 tonnes, t= 47.945, df= 4722.3, p<0.001) and in the breeding season months (February to July, t= -2.6313, df= 10397, p<0.01) although the difference was not as large (Mean catch$_{Feb\text{-}Jul}$= 40.8 tonnes, Mean catch$_{Aug\text{-}Jan}$= 39.5 tonnes). Areas of core fishing effort were similar whether the entire year or only the non-breeding season were mapped. The difference being in the number of sets (24.6 % of west coast sets occured from August to January and 15.4 % of south coast sets) and consequently the relative importance of each set within the 90% contour.



West Coast:	All sets:	23 440 nets,	984 226 tonnes
	Aug-Jan sets:	5 758 nets,	233 855 tonnes
South Coast:	All sets:	2 088 nets,	48 531 tonnes
	Aug-Jan sets:	321 nets,	6 031 tonnes

Figure 3.4. Purse-seine fishing effort off a) the west coast and b) the south coast of South Africa during 2012-2014. Blue: 90% contours of all sets; Red: 90% contours of sets in the non-breeding season (August to January); isobaths every 50m to 200m below sea level.

Broad scale overlap between purse-seine fishing and penguin non-breeding dispersal

Broad scale overlap with penguin tracks was assessed using all sets (Figures 3.5 -3.6) to include the carry-over effects from intense breeding-season fishing, but overlap statistics for only the non-breeding season are summarised in Appendix 7 and give similar results (see Figure 3.4, above). Dassen Island birds overlap more with fisheries than Bird Island Birds during both pre- and post-moult dispersal (Figure 3.5). Although a few sets were reported in core Bird Island penguin areas, there was no overlap in core areas along the south coast. Dassen pre-moult dispersal showed the most overlap, specifically in the fishing zones between Dassen and Robben Island, off the Cape Peninsula and close to Gansbaai.

Fishing effort in areas used by the four main Dassen dispersal patterns (Figure 3.6) shows substantial overlap with the core fishing areas between Dassen and Robben Islands. This makes the percentage of overlap in the core area of birds which stay close to Dassen especially high (13.1%, Table 3.1). The Far South group also shows substantial overlap off the Cape Peninsula and around Gansbaai, areas which they travel past to reach the Agulhas bank. The North dispersal pattern is similar to that of post-moult birds, overlapping fishing areas close to Dassen but appearing to avoid the heavily fished eastern section of St Helena bay. The South group overlaps with fishing out of Gansbaai, but this could also be interpreted as a pattern of avoidance, with penguins tending to stay north of the core fishing area. Of course the day-time activity of the birds is unknown and could show more overlap, but it seems unlikely that birds would journey back and forth in the way that that suggests. Similarly, the Agulhas bank seems to be divided between penguin tracks in the west and Mossel Bay fishing vessels in the east, but this could also be explained by the increasing distance from Dassen Island, rather than avoidance behaviour. Average catch per unit effort was low in nets overlapping Bird Island penguin areas and on the west coast north of Dassen Island (in the post-moult and north dispersal groups, table 3.1).

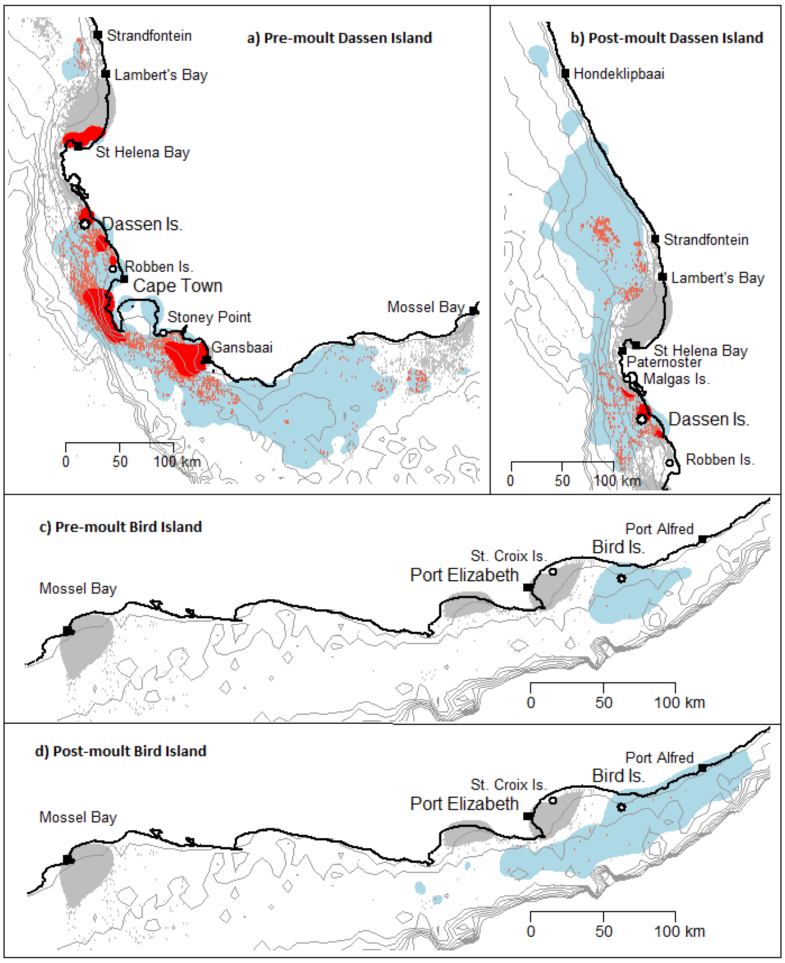
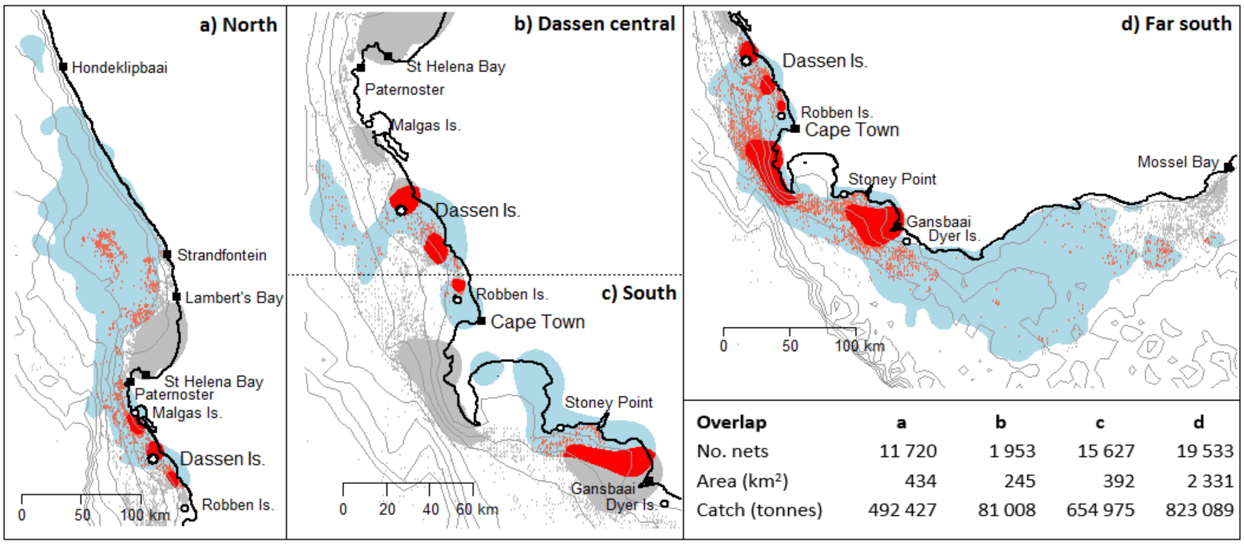


Figure 3.5. Overlap between core purse-seine fishing areas (90% kernel density contour) and the dispersal areas of pre- and post-moult African penguins from two island colonies off the coast of South Africa (Dassen Island and Bird Island, Algoa Bay); blue = 90% penguin track contour, grey= fishing sets and core fishing areas outside penguin contours, red= fishing sets (dull red) and core fishing areas (bright red) overlapping penguin contours. Isobaths every 50 m up to 400 m below sea level.



Overlap	a	b	c	d
No. nets	11 720	1 953	15 627	19 533
Area (km²)	434	245	392	2 331
Catch (tonnes)	492 427	81 008	654 975	823 089

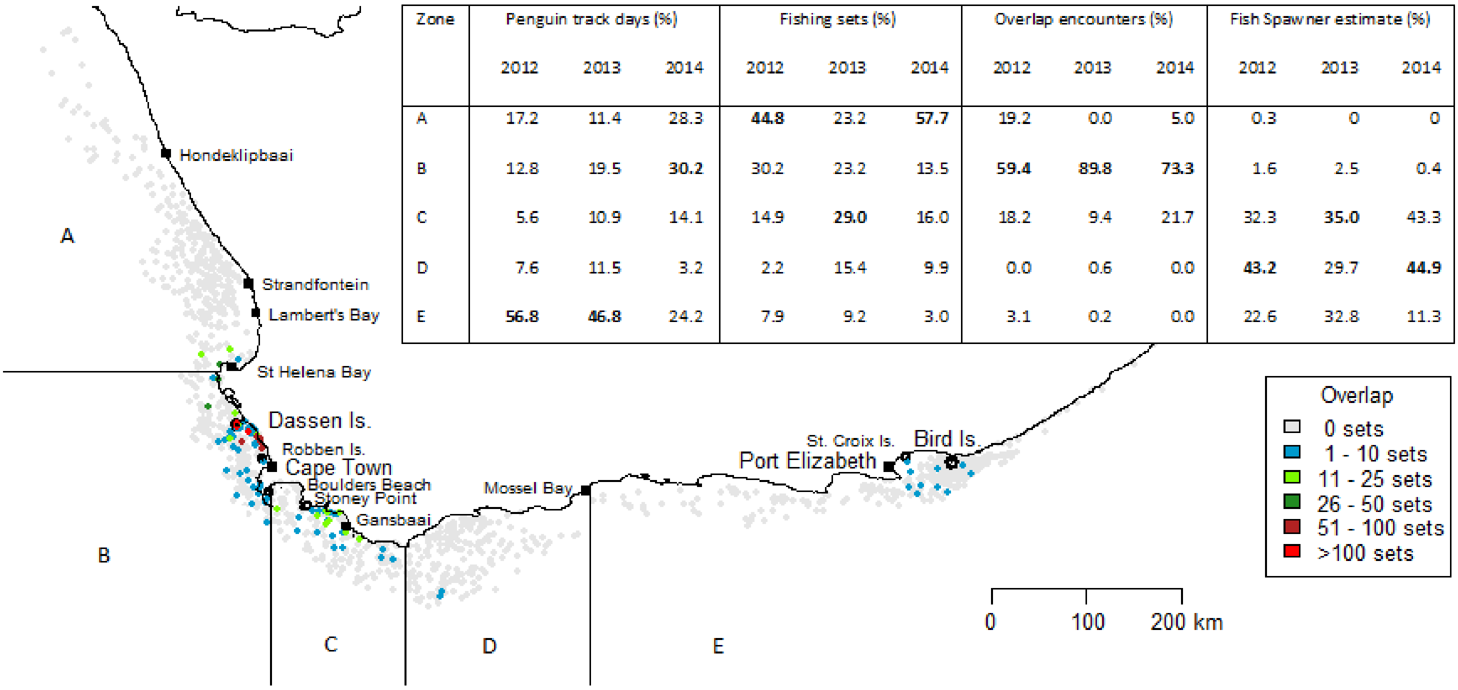
Figure 3.6 Maps of purse-seine fishing overlap with the four main Dassen Island groups; blue = 90% penguin track contour, grey= fishing sets and core fishing areas outside penguin contours, red= fishing sets and core fishing areas overlapping penguin contours. Isobaths every 50 m to 400 m below sea level.

Table 3.1. Overlap between core penguin non-breeding areas and purse-seine fishing (2012-2014). Catch = combined catch of sardine and anchovy; percentages are calculated from figures for the whole coast section (bold figures), % area overlap is the percentage of the core penguin area which overlaps with core fishing areas, ∆ CPUE is the difference in average catch per unit effort inside the penguin area, compared to that of the whole coast section.

Penguin Contour	Core penguin area (km^2)	Overlap with core fishing areas (km^2)	% area overlap	Number of sets in penguin area	% sets in penguin area	Total catch in penguin area	% catch in penguin area	∆ CPUE (±SE)
WEST COAST TOTALS		**4 793**	**100**	**23 440**	**100**	**847 085**	**100**	**36.138**
Pre-moult	24 918	2 694	10.8	11 552	49.3	45 8775	54.2	3.58 ±0.36
Post-moult	17 340	265	1.5	1 936	8.3	65 125	7.7	-2.50 ±0.93
North	17 614	434	2.5	2 515	10.7	101 602	12.0	4.26 ±0.81
Central	1 866	245	13.1	1 089	4.7	49 397	5.8	9.22 ±1.24
South	2 310	392	17.0	1 796	7.7	88 296	10.4	13.02 ±0.98
Far South	24 113	2 331	9.7	9 543	40.7	394 773	46.6	5.23 ±0.42
SOUTH COAST TOTALS		**2 310**	**100**	**2088**	**100**	**47 486**	**100**	**22.74**
Pre-moult	1 893	0	0	6	0.3	13	0.03	-20.51 ±2.21
Post-moult	5 374	0	0	20	0.9	88	0.2	-18.36 ±1.93

Direct overlap between purse-seine fishing and penguin non-breeding dispersal

Of the 728 daily penguin-tracks (not including time at land-bases), 86 % did not come within 20 km of purse-seine sets. Of the overlap instances which did occur, just under 75% were in zone B (between St Helena Bay and Cape Point) with some birds being within 20km of over 100 sets on a single day (Figure 3.7). This occurred around Dassen Island and between there and Robben Island. The percentage overlap in zone B was especially high in 2013. Zone C held most of the rest of the encounters. The highest percentages of sets were in zones A and C and the less frequent penguin overlap in these zones could indicate avoidance of high intensity fishing when possible. Fish spawner estimates for the five zones highlights the spatial mismatch between fishing effort and biomass (except in 2013), as well as the minimal forage fish available to birds which stay in zones A and B. A Kruskal-Wallis rank sum test showed no difference in daily encounter rates between the west coast penguin tracks and 20 individual null data sets simulated from them (χ^2=18.437, df=20, p>0.5, Figure 3.8), probably due to the large variation in encounters per day. However, comparing the actual data against all simulated data combined did show the real dataset to have a larger number of encounters (Wilcoxon rank sum test, W= 3398200, p<0.01) implying that penguins are frequenting the same areas as fishing boats more often than expected by chance.



Zone	Penguin track days (%)			Fishing sets (%)			Overlap encounters (%)			Fish Spawner estimate (%)		
	2012	2013	2014	2012	2013	2014	2012	2013	2014	2012	2013	2014
A	17.2	11.4	28.3	**44.8**	23.2	**57.7**	19.2	0.0	5.0	0.3	0	0
B	12.8	19.5	**30.2**	30.2	23.2	13.5	**59.4**	**89.8**	**73.3**	1.6	2.5	0.4
C	5.6	10.9	14.1	14.9	**29.0**	16.0	18.2	9.4	21.7	32.3	**35.0**	43.3
D	7.6	11.5	3.2	2.2	15.4	9.9	0.0	0.6	0.0	**43.2**	29.7	**44.9**
E	**56.8**	**46.8**	24.2	7.9	9.2	3.0	3.1	0.2	0.0	22.6	32.8	11.3

Figure 3.7. Map showing instances of direct overlap between penguins and purse-seine fishing activity over three years (2012-2014); Points show the mid-point of each daily penguin track, colours indicate the number of fishing sets within 20 km of the track on the same day. The table (inset) gives the percentage of penguin track days, fishing sets and direct overlap encounters in each of five zones around the coast (A-E) and the November combined anchovy and sardine spawner estimate for similar zones, from Shabangu et al. (2012), Mhlongo et al. (2013) and Mhlongo et al. (2014)

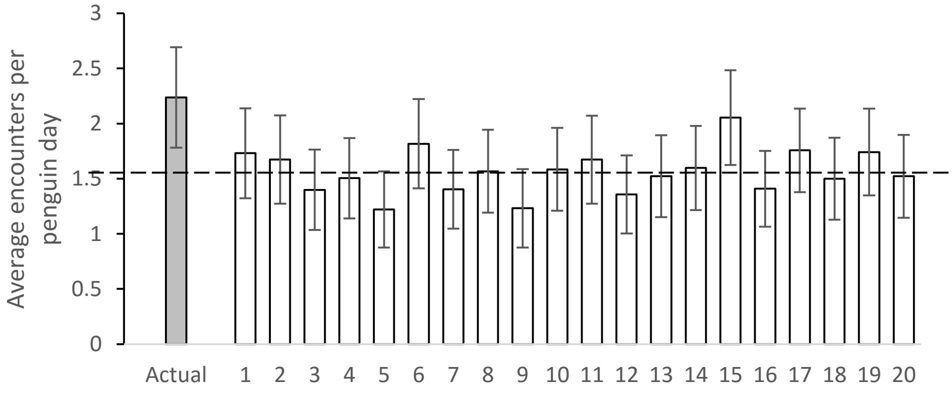


Figure 3.8. Average number of encounters between purse-seine fishing vessels and penguins per day on the west coast (2012-2014) for actual (grey bar) and simulated (white bars) penguin data sets; The average number of encounters for all simulated data is shown as a dashed line.

Overlap over time

There was no easily discernible pattern in the frequency of penguin presence in an area in the days following fishing activity (Figure 3.9), although, contrary to what I expected, there might be an increase in penguin presence in the first few days after fishing. Although there were slight overall decreases over time in the two coastal zones with the highest frequency of overlap, once again hinting that penguins could be targeting the same areas as fishing boats, the relationships were weak ($R^2<0.19$) and did not improve when the analysis was restricted to incidents with heavy fishing pressure (>20 sets).

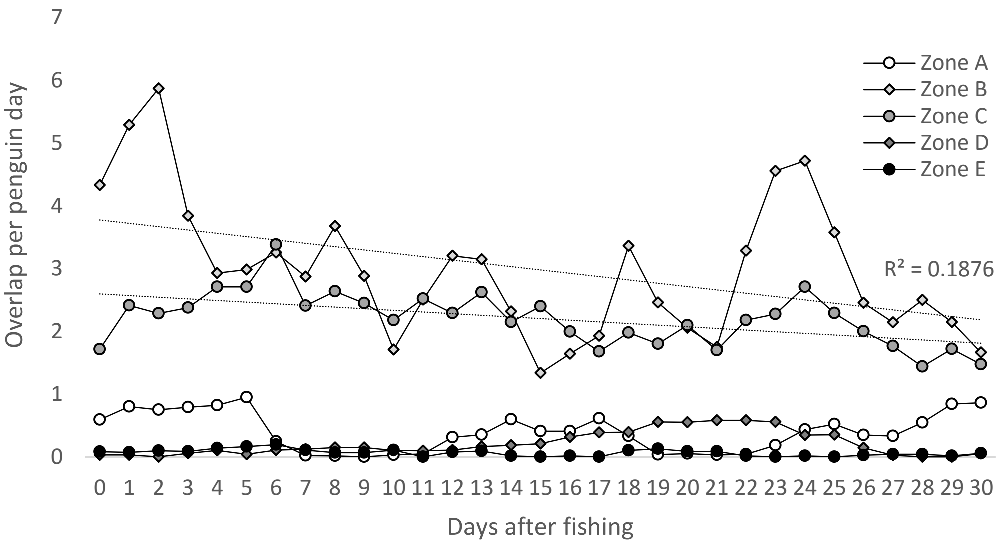


Figure 3.9. Overlap between pelagic fishing sets and African penguins at a 20 km scale for 0 to 30 days after fishing occurred.

DISCUSSION

Although the fishing data used in this study were reported at high temporal and spatial scales, it is the scale of the penguin data (effectively one position per night, with stretches of interpolated track in between) which limits the analysis of detailed penguin-fishery overlap. On a broad scale, however, core areas of potential fishery-penguin interaction across their non-breeding range were identified. There is some indication that areas of high fishing pressure are avoided once the restraints of breeding have been lifted, as the majority of Dassen penguins travelled to foraging grounds outside the normal range of purse-seine fishing. Most overlap was found close to Dassen colony, or along the coast (e.g. off the Cape Peninsula) en route to these foraging areas. This overlap is potentially unavoidable, at least at a large temporal scale. Particular instances where penguins appear to avoid high fishing density areas in the vicinity are in Algoa bay (penguins seem to forage further offshore in the eastern part of the bay where most fishing occurs but this could also be explained by resource partitioning with the St. Croix colony), St Helena Bay (where penguin tracks are found further north off-shore) and around Gansbaai (where penguins from Stony Point seem to keep close to the northern edge of the bay.) The latter would make a good study colony for detailed assessment of the small-scale interactions between penguins and boats. In contrast to Dassen Island, there is very little fishing around the Bird Island colony, presumably allowing birds to remain in the area year-round.

Although the amount of fish caught by the South African small pelagic fishery during the non-breeding season is low, the amount of fish in the area is also low (indicated by lower catch per unit effort compared to the rest of the year) and continued fishing on these stocks reduces them further, potentially influencing prey availability for other predators. Carry-over effects of forage-fish depletion during the breeding season are also likely to influence the availability of fish for pre- and post- moult foraging. Studies on sardine and anchovy behaviour show that these species pass through the southern Benguela system from their nursery grounds to their spawning grounds on the Agulhas bank (Barange et al. 1999). Because of this, the short-term local effects of intense fishing are buffered as new fish replace those which are caught. This neglects to consider the impacts on the ecosystem as a whole or the long-term depletion of any local fish stock. Although the TAC is designed to ensure a large enough spawning population at the end of each year, high levels of fishing pressure locally will reduce the small percentage of the population which remain in the area year-round. It is presumably these fish on which non-breeding penguins rely if they do not travel to the spawning grounds on the Agulhas bank.

Whittington (2002) suggested that differences in purse-seine fishing pressure could explain differences in survival found between west and south coast penguin colonies. The overlap between purse-seine fishing and the foraging ranges of breeding seabirds (African penguins and Cape gannets) in the southern Benguela and Algoa Bay was assessed by Pichegru et al. (2009). Overlap was found to be highest around west coast penguin colonies, similar to the results of this chapter. The breeding foraging range of gannets from Malgas Island, Bird Island (Lambert's Bay) and Bird Island

(Algoa Bay) reported by Pichegru et al. (2009) are similar to the dispersal ranges of pre-moult Dassen Island penguins, post-moult Dassen Island penguins and post-moult Bird Island penguins respectively and, although the two west coast gannet colonies were combined when overlap was analysed, the much higher overlap reported on the west, compared to the south, coast was similar to that found in this study.

Localized forage fish depletion and disturbance by fishing boats are two possible mechanisms by which fishing could be directly influencing penguins. It is thought that fishing vessel disturbance in the Benguela is augmented by the association of seals with fishing boats (with reports of over 200 seals attending purse-seine fishing sets in Namibian waters, Shaughnessy et al. 1981). Vessel disturbance would not be limited to fishing boats targeting the birds' prey, but to all vessels in the area, whereas the seal-boat interaction would occur around any boats with edible discards.

Direct overlap

The difference in the frequency of fishing overlap between simulated and real penguin tracks seems to show that penguins occasionally preferentially forage in areas close to (within 20 km of) active purse-seine fishing. This makes sense as they are both targeting the same prey. In 2013 the percentage of overlap in Zone B was especially high, as was the actual frequency of encounters (4.9 encounters per penguin day) compared to other years. This is interesting as the low anchovy catch that year was partially attributed to anchovy in this zone being collected into a small number of unusually dense shoals (Prochazka 2014). With forage fish aggregating in this way, penguins would be less able to avoid heavily fished areas. It is probable that more detailed penguin tracks could show a reversal in this pattern (see Reid et al. 2004's comments on the importance of scale in studies on fisheries - predator overlap) with penguins preferentially foraging close-to, but not alongside, fishing vessels.

It is probable that the impacts of fish depletion by individual fishing boats quickly disperses and is only noticeable over time at an ecosystem-level. However, the slightly higher frequency of overlap between penguins and fishing vessels which were in the area a few days previously could be tentatively explained by a combination of factors. Firstly, as using fish-finder equipment has become standard practise, sets are likely to occur where fish are present. Therefore, any fishing point can be considered a good foraging spot for penguins. However, if penguins are deterred from areas by the presence of fishing vessels (and possibly the seals which accompany them) then they might preferentially enter these areas only once fishing vessels have left. There would presumably still be forage fish in the area which were not caught. The presence of penguins in an area in the days preceding fishing activity was unfortunately not assessed, but theoretically would have shown high penguin presence (due to fish in the area) followed by a dip in frequency on the day of fishing (as penguins move away). However, the scale of the analysis might not be small enough for these interactions to be seen and the analysis is further complicated by the fact that individual fishing vessels move independently and often overlap. For example, a penguin foraging in any area could be three days after sets X and Y but, at the same time, five days after set Z. This could be corrected by treating each group of sets which are targeting the same area over the same time as a single event, with a certain duration and an intensity value which would reflect the amount of fishing pressure on the area. One could then assess penguin presence before, during and after these events to see whether penguins are displaced by the presence of boats. More detailed penguin location data would also be helpful to really answer these questions.

In summary, this chapter has found that non-breeding penguins and purse-seine fishing activity does overlap, both directly and over longer time frames, and that this overlap is highest for west coast birds between Paternoster and Gansbaai, where Dassen Island and four other important penguin colonies are situated. Most penguins (from both study colonies) seem to avoid core fishing areas during their pre- and post-moult dispersal, but this is much more difficult for Dassen Island penguins, that must pass through areas of heavy fishing on their way to distant foraging grounds, and is also costly, as the extended journey drains resources which are needed to prepare for or recover from moult.

CHAPTER 4: SYNTHESIS AND CONCLUSIONS

The decrease in the African penguin population over the last few decades has been attributed to high adult mortality during the non-breeding season (Wolfaardt et al. 2009). This study has extended the hitherto limited knowledge of the dispersal patterns of adult African penguins when they are not restrained by breeding, in order to shed light on possible causes of mortality away from the breeding colony, and direct conservation efforts to protect these birds in their non-breeding range.

The striking differences in dispersal patterns found between the fast-declining west coast colony (Dassen Island) and the relatively stable south coast colony (Bird Island) seem to indicate that changes in pre- and post-moult dispersal and foraging effort could play a role in population trends. Penguins from Dassen Island have lower body condition and display substantially more variation in dispersal patterns, many travelling to non-breeding foraging grounds far from their colony and often moulting at colonies closer to these areas. Unlike Bird Island penguins, their dispersal range overlaps extensively with purse-seine fishing, especially along the southern west coast between Dassen Island and Gansbaai, and they appear to avoid areas of high fishing pressure by travelling beyond the reach of the industry, onto the Agulhas bank and up the west coast. Higher supposed mortality was also observed for Dassen Island birds.

Small pelagic fisheries seem to be discouraging the majority of non-breeding penguins from using certain productive areas, e.g. within St Helena bay and around Gansbaai, either by depleting the resident stock earlier in the year, or by directly disturbing birds during pre-moult foraging. This seems to have necessitated an extension to the dispersal range of the majority of Dassen Island birds to areas beyond the reach of the fishery. Naturally the causal link between heavy purse-seine fishing on the west coast and this extended dispersal is arguable and will remain so until more detailed information about fish availability can be collected. It is also possible that west coast penguins historically foraged further south, even before the decrease in local stocks, but considering the minimal dispersal from Bird Island, it seems more likely that birds would remain close to their colonies if conditions were more favourable.

Even though African penguins (at least on a population level) seem quite flexible in their non-breeding dispersal patterns, this flexibility has not been enough to buffer population decline on the west coast. Although forage fish availability on the Agulhas bank, where most Dassen pre-moult penguins foraged, is high, west coast birds are in worse condition after moult than those on the south coast, implying that the extended journey could be counter-productive, depleting reserves before moult has begun. Wilson et al. 2005 describes a similar situation where incubating magellanic penguins face a trade-off between the benefits of distant more productive foraging areas and the energy used to reach them. The different dispersal patterns displayed by Dassen Island penguins can be seen as different solutions to this trade-off, with some birds staying in prey-depleted areas close to the colony, while others chase the fish. Those birds which moult at colonies further south after foraging on the productive Agulhas bank appear to have found a way around this problem and consequently should be in better condition after moult.

The preference of post-moult birds for the area north of St Helena Bay is understandable given the highly productive nature of this system, at least historically. However, unless these penguins have shifted to alternative food sources, they will find little prey to replenish their lost energy reserves in this area (November biomass surveys repeatedly find few adult forage fish north of Cape Columbine, Appendix 4). Heavy fishing pressure on anchovy within St Helena Bay continues into the beginning of the non-breeding season and some sets are found further north in the core area of post-moult birds, in spite of the low average CPUE of these sets. Although this fishing did not directly overlap the penguins tracked in this study it would presumably directly affect earlier moulters, as well as leaving the small pelagic fish population in this area diminished for later-moulting birds. Considering this area (the shelf off Lamberts bay where the 150 m isobath extends seawards) appears to be of higher relative importance to non-breeding penguins than to the purse-seine fishing industry, it might be considered as a potential marine protected area. And if seal predation is a major cause of mortality in this area, as seems to be suggested by the mortality pattern of tracked birds, excluding commercial fisheries would be futile without also initiating some form of seal population control.

As west coast colonies decrease, the south coast holds an increasing percentage of the world population of African penguins (over 50% in 2012). There is currently an ambitious initiative to set up new colonies along the south coast which, if successful, would help to stabilize the global population as long as conditions along the south coast remain favourable to penguins (C. Hagen, BirdLife SA, pers. comm.). As target fish populations move off the west coast the purse-seine fishing industry is slowly shifting its effort to follow (although apparent reversals of this trend have occurred in several years, Prochazka 2014). This will hopefully lift some of the stress on west coast penguins, but it will effectively transfer it to those on the south coast. Unless effective conservation measures are put in place to protect south coast colonies before these changes take effect, they could show similar decreases to those on the west coast as fishing pressure increases, with disastrous consequences for the population as a whole. This study has identified the areas used by non-breeding African penguins from the two study colonies, as well as exploring some of the threats faced by birds in these areas. Hopefully this information can be used by stakeholders and policy makers to extend African penguin conservation to protect these birds throughout their annual cycle.

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APPENDIX

Appendix 1. Table showing the F-statistic, adjusted R^2 and p-value of simple linear models of Initial Mass and Body Index of tracked African penguins, and F-statistics and p-values for each factor (Island, Period, Season and Sex) from type-II ANOVAs of the models. Underlined p-values are significant, exact p-values for values between 0.01 and 0.1 are given.

52 Deployed birds	linear model (Df=5,69)			Period (Df=1)		Island (Df=1)		Season (Df=2)		Sex (Df=1)	
Parameters	F	Adj R2	*p*	F	*p*	F	*p*	F	*p*	F	*p*
Start Mass	12.51	0.4375	<0.001	6.4374	0.013	27.9773	<0.001	5.1153	<0.01	10.0377	<0.01
Body Index	10.7	0.396	<0.001	5.7369	0.019	31.3983	<0.001	6.8428	<0.01	0.8699	>0.1

Appendix 2. Table showing the F-statistic, adjusted R^2 and p-value of simple linear models of African penguin track parameters, and F-statistics and p-values for each factor (Island, Period and Season) from type-II ANOVAs of the models. Underlined p-values are significant, exact p-values for values between 0.01 and 0.1 are given. Lag = the number of days between device deployment and dispersal, CPF (track)/CPF (Move): central place foraging index calculated from all track days and only moving days respectively.

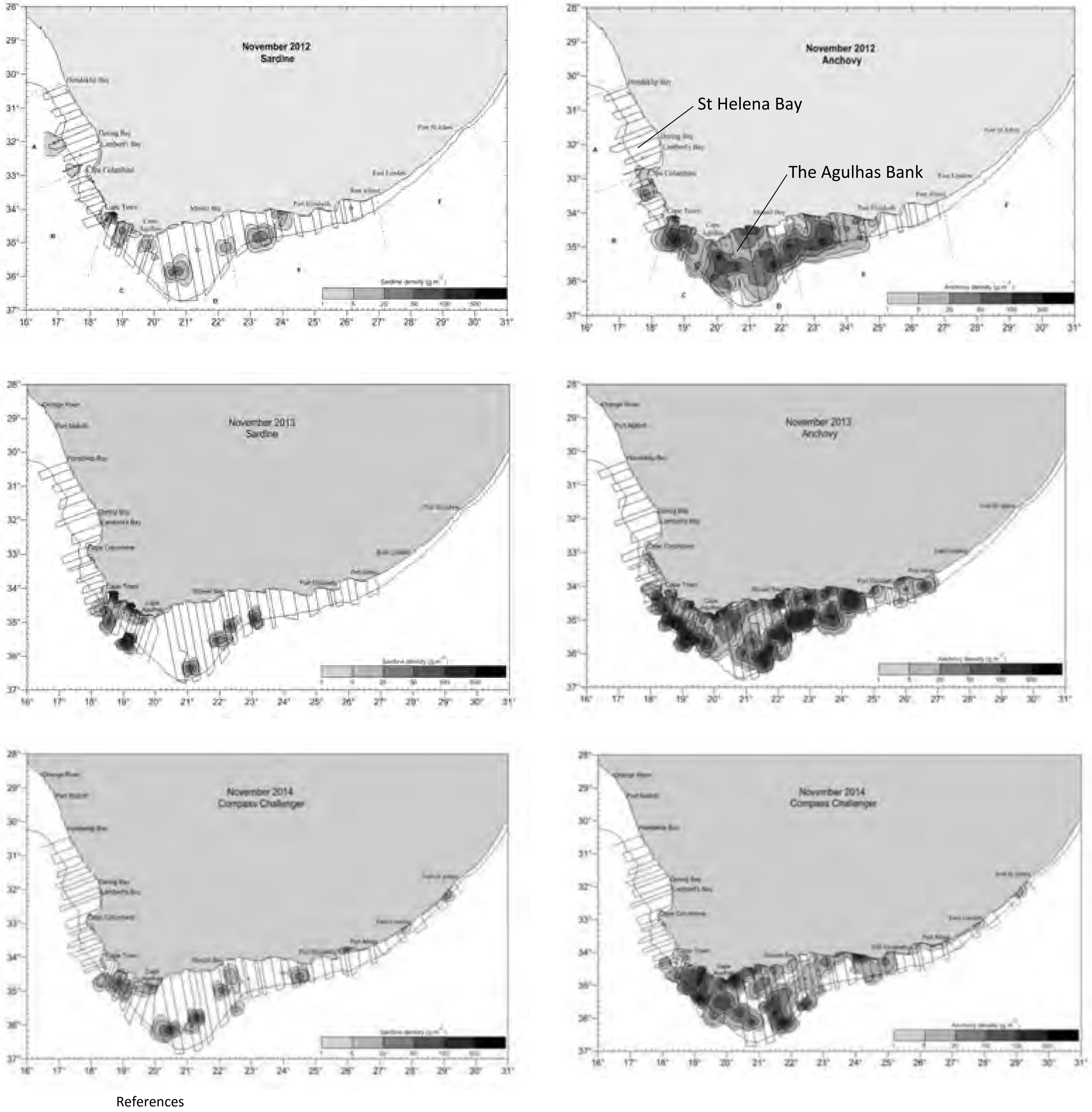
Complete Tracks	linear model (Df=4,38)			Period (Df=1)		Island (Df=1)		Season (Df=2)	
Parameters	F	Adj R2	*p*	F	*p*	F	*p*	F	*p*
log(Lag days)	2.913	0.1541	0.034	9.6664	<0.01	0.5401	>0.1	0.1680	>0.5
Track days	1.814	0.07197	>0.1	0.7250	>0.1	4.2815	0.045	1.9163	>0.1
Move days	7.143	0.3691	<0.001	0.0129	>0.5	0.0025	>0.1	12.1841	<0.001
At-Sea-Index (%)	4.897	0.2707	<0.01	0.7038	>0.1	8.2345	<0.01	2.5646	0.09
Trips	12.53	0.5233	<0.001	0.0739	>0.5	42.6076	<0.001	0.6490	>0.5
CPF (track)	9.528	0.4482	<0.001	0.0794	>0.5	33.4588	<0.001	0.4062	>0.5
CPF (Move)	5.048	0.2783	<0.01	0.0671	>0.5	16.3031	<0.001	1.1895	>0.1
Track Length (km)	2.752	0.1430	<0.042	1.5114	>0.1	0.3031	>0.5	5.1456	0.011
Speed (km/day)	5.253	0.2883	<0.01	3.1998	0.082	2.6096	>0.1	7.0954	<0.01
Displacement (km)	6.404	0.3398	<0.001	5.8373	0.021	14.0599	<0.001	3.1595	0.054
All tracks	linear model (Df=4,54)			Period (Df=1)		Island (Df=1)		Season (Df=2)	
Parameters	F	Adj R2	*p*	F	*p*	F	*p*	F	*p*
log of Lag days	5.074	0.2194	<0.01	15.8380	<0.001	0.0774	>0.5	0.1503	>0.5
Track days	1.251	0.0170	>0.1	0.5353	>0.1	0.1892	>0.5	1.9943	>0.1
Move days	3.554	0.1497	0.012	0.0448	>0.5	3.4749	0.068	4.4926	0.016
At-Sea-Index (%)	6.565	0.2774	<0.001	3.1948	0.079	12.1046	<0.01	2.1001	>0.1
Trips	11.71	0.4248	<0.001	0.6126	>0.1	34.6294	<0.001	2.0009	>0.1
CPF (track)	13.83	0.4695	<0.001	3.5203	0.067	47.9423	<0.001	1.6605	>0.1
CPF (Move)	10.51	0.3961	<0.001	2.2308	>0.1	34.6145	<0.001	3.1782	0.05
Track Length (km)	3.54	0.1491	0.012	0.9506	>0.1	5.1621	0.027	4.7626	0.012
Speed (km/day)	5.056	0.2186	<0.01	2.8935	0.095	4.2598	0.044	5.0645	<0.01
Displacement (km)	9.031	0.3564	<0.001	2.6343	>0.1	28.7277	<0.001	3.2041	0.048
Furthest Trip Only	linear model (Df=4,54)			Period (Df=1)		Island (Df=1)		Season (Df=2)	
Parameters	F	Adj R2	*p*	F	*p*	F	*p*	F	*p*
Move days	6.61	0.2790	<0.001	0.4466	>0.5	15.3750	<0.001	3.5108	0.037
Trip Length	5.924	0.2535	<0.001	0.2909	>0.5	15.4919	<0.001	4.5383	0.015
Speed	4.977	0.2152	<0.01	4.1918	0.046	0.1439	>0.5	4.5861	0.014

Appendix 3. Table showing the F-statistic, adjusted R^2 and p-value of simple linear models of Initial Mass and Body Index of tracked African penguins from Dassen and Bird Islands in relation to Group. No significance was found.

Dassen Island	linear model (Df= 5,28)		
Parameters	F	Adj R2	*p*
Start Mass	0.7316	0.04239	>0.5
Body Index	0.6441	-0.057	>0.5

Bird Island	linear model (Df= 4,20)		
Parameters	F	Adj R2	*p*
Start Mass	1.115	0.01878	>0.1
Body Index	0.7735	-0.0392	>0.5

Appendix 4. Sardine (left) and Anchovy (right) November acoustic surveys densities taken from Shabangu et al. (2012), Mhlongo et al. (2013) and Mhlongo et al. (2014)



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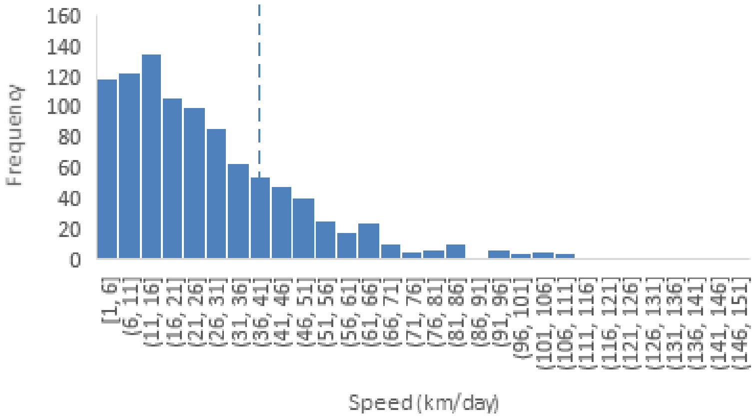
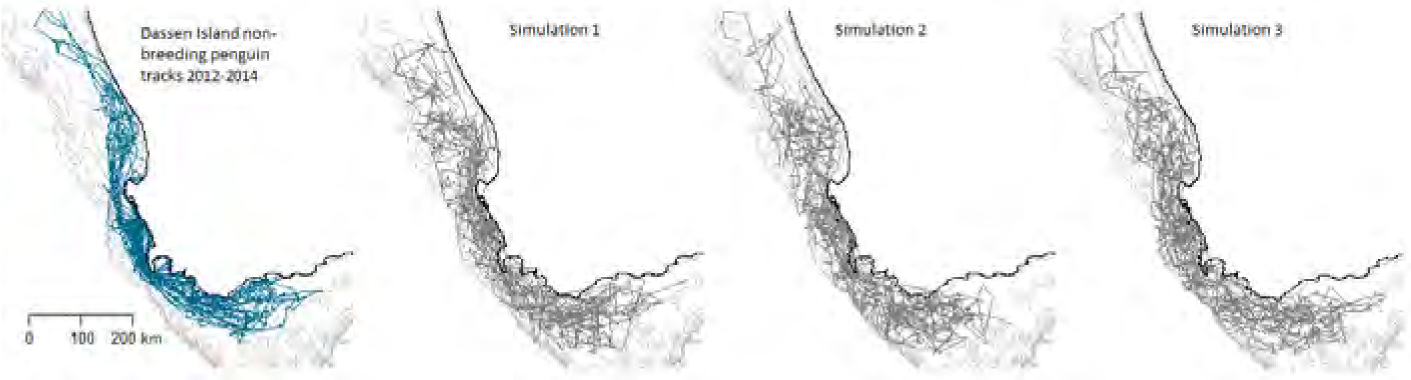
Mhlongo, N., J. Coetzee, F. Shabangu, D. Merkle, M. Hendricks and Y. Geja.2013. Results of the 2013 spawner biomass survey. Department of Agriculture, Forestry and Fisheries. Fisheries/2013/Dec/SWG-PEL/45.

Mhlongo, N., J. Coetzee, M. Phillips, D. Merkle, Y. Geja and C. Mtengwane. 2014. Results of the 2014 spawner biomass survey. Department of Agriculture, Forestry and Fisheries. Fisheries/2014/Dec/SWG-PEL/63.

Appendix 5. Histogram of speed (km per day) of all tracked penguins, showing the third quartile value (dashed line) used to estimate the buffer size around penguin tracks for overlap analysis.



Appendix 6. Maps of real (blue) and simulated (grey) Dassen Island penguin tracks 2012-2014. Isobaths every 50 m to 400 m below sea-level.



Appendix 7. Table summarising overlap between core penguin non-breeding areas and August – January purse-seine fishing (2012-2014). Catch = combined catch of sardine and anchovy; percentages are calculated from figures for the whole coast section (**bold**), % area overlap is the percentage of the core penguin area which overlaps with core fishing area, Δ CPUE is the difference in average catch per unit effort inside the penguin area, compared to that of the whole coast section.

Penguin Group	Core penguin area (km^2)	Overlap with core fishing areas (km^2)	% area overlap	Number of sets in penguin area	% sets in penguin area	Total catch in penguin area	% catch in penguin area	Δ CPUE (±SE)
WEST COAST TOTALS		**4 172**		**5 758**		**195 282**		**33.914**
Pre-moult	24 918	2 561	10.2	3 739	64.9	149 748	76.7	6.14 ±0.56
Post-moult	17 340	794	4.6	1 136	19.7	32 049	16.4	-5.70 ±1.08
North	17 614	932	5.3	1 265	22.0	36 868	18.9	-4.77 ±1.03
Central	1 866	484	25.9	642	11.1	29 751	15.2	12.43 ±1.52
South	2 310	407	17.6	607	10.5	20 611	10.5	0.04 ±1.18
Far South	24 113	2 239	9.3	3 154	54.8	133 303	68.3	8.35 ±0.63
SOUTH COAST TOTALS		**3785**		**321**		**5 873**		**18.30**
Pre-moult	1 893	0	0	1	0.3	13.3	0.2	-5.04 ±0
Post-moult	5 374	11.5	0.2	6	1.9	29	0.5	-13.55 ±2.00