The effect and conservation implications of the re-establishment of a Cape fur seal *Arctocephalus pusillus pusillus* breeding colony at Vondeling Island, Saldanha Bay

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Signed by candidate

S. Mduduzi Seakamela
January 2024

Dedicated to

Mom and Dad

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Abstract

The Benguela Current Large Marine Ecosystem (BCLME) has supported a substantial biomass of commercially important pelagic species such as sardines *Sardinops sagax*, anchovy *Engraulis encrasicolus* and West Coast rock lobster *Jasus lalandi*; which are important prey for seabirds and the only pinniped breeding in the BCLME, the Cape fur seal *Arctocephalus pusillus pusillus.* Environmental changes in the early 2000s have led to the collapse of these prey species off the west coast of South Africa, which in turn has impacted the population dynamics of dependent seabirds. Both faunal groups were historically exploited for their products: Cape fur seals for their fur and meat, and seabirds for their eggs and guano. The commercial importance influenced management regimes over time, such that when guano was more profitable than fur (i.e., during the guano rush), seals were excluded from breeding on guano islands for the exclusive use by seabirds.

Cape fur seals were decimated to less than 100 000 individuals but have since recovered to over two million animals after they were legislatively protected in the 1970s. Some seabird species (notably the African penguin *Spheniscus demersus*) have experienced long term effects of exploitation such as the loss of breeding habitat by removal of guano, in which they burrow to build their nests. The collapse of preferred prey off the west coast, where the majority of seabird and seal breeding colonies are located, has resulted in population declines of several dependent seabird species. African penguin, Cape cormorant *Phalacrocorax capensis* and Cape gannet *Morus capensis* are dependent on anchovy and sardine while bank cormorant *P. neglectus* is dependent on West Coast rock lobster. There were spatio-temporal changes in the distribution of breeding colonies of Cape fur seals which resulted in establishment of new colonies and recolonisation of previously occupied colonies. The recolonisation of Vondeling Island is one example of recolonisation. It is unique because it happened against the backdrop of established various seabird breeding colonies at the island.

This dissertation describes the recolonisation of Vondeling Island by Cape fur seals and possible impacts of seabirds breeding at the island. To achieve this, three datasets were scrutinised: 1) survey data, 2) island distribution maps and 3) telemetry data. Survey data on breeding performance of seabirds (i.e., number of breeding pairs) and Cape fur seals (i.e., pup production) was utilised to contrast the trends between the two faunal groups over the study period (1990 and 2018). For seabirds, ground surveys were conducted during an average of three visits per year over the study period. This allowed for surveys to align with different breeding timing of various seabirds that breed at Vondeling Island. Concurrently, a tally of the number of seals occupying the island was also recorded between 1993 and 2013. Systematic Cape fur seal surveys were conducted annually from 2003 by means of aerial photographic surveys during the peak of the pupping season (between 16 and 20 December). During each island visit for seabird surveys, areas occupied by Cape fur seals and the distribution of nests and roosting sites of seabirds were also mapped. These maps were used to visualise changes in areas utilised by seals in relation to seabirds' breeding and roosting sites, thus inferring competition for space. Telemetry data from individual Cape fur seals and African penguins that were instrumented with satellite-linked position transmitting tags were used to calculate home ranges, core areas and their overlaps.

The recolonisation of Vondeling Island was first observed in 1991 with 13 sub-adult males, followed by two adult females in 1999. Since then, the number of breeding individuals has gradually increased. The first 16 pups were born during the 2003 breeding season and pup production has since increased by 38.5% per year up to 2018. This annual rate of increase is attributed to immigration of females, probably from northern breeding colonies such as Kleinsee. Kleinsee experienced a 2.3% decrease in pup production over the study period. There was a reduction of more than 40,000 in pup production between the end and the beginning of the study period. Analysis of trends of African penguin and three cormorant species indicated an overall decline. African penguins had the lowest average annual rate of decline (–2.42%) while the Cape cormorants had the highest decline (–15.30%). In comparison to other breeding colonies, the trends of the four species indicated a divergent pattern. For instance, breeding performance of bank cormorants at other breeding localities was higher than that at Vondeling Island except for Malgas Island. Cape cormorant trends declined on all islands except at Dyer Island, Robben Island and Seal Island (Algoa Bay). The recorded declines, while partly influenced by seals for some species (African penguins and Cape cormorants), were chiefly driven by food shortages.

With regards competition for breeding space, Cape fur seals outcompeted African penguins and Cape cormorants. At the beginning of the study period, African penguins and Cape cormorants had bred in the interior of the island. An interior wall that was built for guano

retention had also kept seals out of the interior of the island. This area has suboptimal nesting habitat for penguins (ground nests), which made them vulnerable to destruction by the movement of seals. Bank and crowned (*Microcarbo coronatus*) cormorants were versatile at utilising island structures (houses and defunct jetty) for breeding which mitigated the potential impact of seal encroachment. The impact on African penguin was mitigated by installation of artificial nests in 2016 which resulted in a marginal increase in breeding pairs.

Cape fur seals and African penguins are central place foragers (during breeding) and their foraging distances from colony are restricted by the distribution of their prey. Their core areas were in the vicinity of the island, where the overall overlap was apparent (86%). These core areas extended north of the island for Cape fur seals but south of it for African penguins. These areas were also identified as important biodiversity areas. The high overlap suggests that they compete for forage resources, but the magnitude of competition or mitigation thereof is not clear. Both species likely compete with their conspecifics from other colonies whose published movements suggest an overlap. Home ranges and core areas of Cape fur seals were expectably larger than those of African penguins; 158,486 km^2 vs 40,495 km^2 and 25,682 km^2 vs 7,865 km^2 respectively. African penguins were limited to the west coast (southern limit in Cape Point) while Cape fur seals ranged eastwards up to Plettenberg Bay, where another core area was identified. Thus, Cape fur seals can traverse further from the breeding colony during times of poor feeding conditions in the vicinity of their breeding colony. By deduction, Cape fur seals will outcompete African penguins for a resource that has shifted in distribution away from breeding colonies.

Furthermore, this dissertation provides a detailed account of a recolonisation event by Cape fur seal at a locality already occupied by seabirds, some of which are endangered. It also demonstrates the importance of concurrent utilisation of long-term datasets in understanding dynamics of marine top predators in a changing environment. It further provides, for the first time, insights into potential at-sea competition for forage resources between sympatric pinniped and seabird species. The results of at-sea competition provide a coarse resolution of a critical question in species interaction within the BCLME. Further research efforts should be built around this foundation to better understand the magnitude of competition between Cape fur seals and African penguins. This could include diet studies that clarifies size and age classes of targeted prey by both species and a combination of horizontal and vertical movement studies to understand the depth at feeding around core areas. Consideration should also be given to the timing of deployment of instruments to capture data describing critical life stages (i.e., breeding, pre-moult, and post-moult periods).

Chapter 1: General Introduction

Overview of the Benguela Current Large Marine Ecosystem

The Benguela Current Large Marine Ecosystem (BCLME) is one of four Eastern Boundary Upwelling Systems (EBUS) in the world; the others are the California, Iberia/Canary and Humboldt Systems (Fréon et al. 2009). Upwelling is a short-term but sustained upward movement of water mass in the water column that lifts nutrients from the bottom (Kämpf & Chapman 2016). This results in nutrient-rich waters that support a high biodiversity and biomass of organisms, from primary producers (Verheye et al. 2016) to top predators (Cooper 1981). The four systems are associated with the subtropical gyres of the Atlantic and the Pacific Oceans (Chavez & Messié 2009). The BCLME is unique in that it is the only one of the four EBUS that is bounded by warm waters on both its northern (Angola Current system) and southern (Agulhas Current) limits (Shannon 2006; Pitcher & Louw 2021).

The BCLME spans three countries (Angola, Namibia and South Africa) with boundaries generally accepted to be between 5–37°S and 0–26°E (Shillington et al. 2006). The main upwelling cells (areas of enhanced upwelling) are Cunene (17–18°S), Northern Namibia/Palgrave Point (21°S), Central Namibia/Walvis Bay (23–24°S), Lüderitz (25.5–27°S), Namaqua(30°S), Columbine (32–33°S) and Cape Peninsula cells (34–34.5°S) (Santana-Casiano et al. 2009; Veitch et al. 2010). The Lüderitz cell is the most powerful (Lutjeharms & Meeuwis 2010) and separates the BCLME into two sub-systems, the Southern and Northern BCLME (sBCLME and nBCLME respectively), forming a partial barrier for several pelagic fish species (Hutchings et al. 2009).

An in-depth assessment of spatial variation in physical driving forces, primary and secondary production, trophic structures, and species richness further characterised four different subsystems: (i) north of the Angola-Benguela Front, (ii) from the Angola-Benguela Front to Lüderitz, (iii) from Lüderitz to Cape Agulhas and (iv) from Cape Agulhas to Port Alfred on the south-east coast of South Africa (Kirkman et al. 2016). The dynamics of these systems are detailed in Kirkman et al. (2016). This delineatory characterisation was in support of Marine

Spatial Planning processes and is relevant in the context of growing and sometimes conflicting oceanic economy activities in the BCLME (Kirkman et al. 2016). A simplified schematic map is provided as Fig. 1.1.

BCLME once supported a substantial biomass of commercially important pelagic species such as sardines *Sardinops sagax* and anchovy *Engraulis encrasicolus* which are important prey for seabirds and seals (Roux et al. 2013; Schwartzlose et al. 1999). Long-term environmental changes have resulted in an increase of phytoplankton biomass and zooplankton abundance (Verheye et al. 2016), changes in residency patterns and seasonal increases in abundance of humpback whales off west coast South Africa (subsystem iii) (Best et al. 1995; Barendse et al. 2010; Findlay et al. 2017), a shift in distribution of sardines and anchovy from the west coast of South Africa (subsystem iii) to its south coast (subsystem iv) in sBCLME (van der Lingen et al. 2006), a collapse of sardines in nBCLME (Erasmus et al. 2021), proliferation of jellyfish in the northern Benguela (Roux et al. 2013), declining populations of seabird species dependent on sardines and anchovy (Makhado et al. 2021) and spatio-temporal shifts in the distribution of Cape fur seal *Arctocephalus pusillus pusillus* colonies; resulting in formation of new colonies and recolonisation of previously occupied localities (Kirkman et al. 2013). The latter change has resulted in adverse interactions between Cape fur seals and established seabirds at recolonised coastal islands (Crawford et al. 1994; Chapter 2).

Seabirds

BCLME has a high abundance of seabird species but a low diversity (Vanstreels et al. 2023). The ecosystem supports 15 species of seabirds breeding at 369 localities along the coastal stretch of the ecosystem (Makhado et al. 2021; 2023). Seven of these species, including two sub-species are endemic to the BCLME (Crawford et al. 2022). Four species that breed at Vondeling Island are classified as "Endangered" (African penguin *Spheniscus demersus* (BirdLife International 2020), bank cormorant *Phalacrocorax neglectus* (BirdLife International 2018a), Cape cormorant *P. capensis* (BirdLife International 2018b), Cape gannet *Morus capensis* (BirdLife International 2018c)), and five as "Least Concern" (crowned cormorant *Microcarbo coronatus* (BirdLife International 2021a), Damara tern *Sternula balaenarum* (BirdLife International 2021b), Hartlaub's gull *Larus hartlaubii* (BirdLife International 2018d), kelp gull *L. dominicanus vetula* (BirdLife International 2018e) and greater crested (swift) tern *Thalasseus b. bergii* (BirdLife International 2018f)) in terms of criteria of the International Union for Conservation of Nature (IUCN). The general distribution of the mentioned endangered seabirds in the region is provided in Fig. 1.2.

Seabirds as top predators can be used to monitor the health and status of ecosystems (Durant et al. 2009). Changes in aspects of their ecology can be indicative of the status of prey biomass in the system (Crawford & Shelton 1978). For instance, the amount of guano deposits was reported to have fluctuated with the changes in the abundance of pelagic fish, which affected their breeding performance (Crawford & Jahncke 1999; Cury & Shannon 2004). In certain cases, seabirds have changed their breeding localities in response to a local decline or collapse of forage resources (Crawford et al. 2015). Monitoring their population dynamics (e.g. breeding success) can improve our understanding of their interactions with the environment (Crawford et al. 2008; Sabarros 2010). The populations' breeding performance of the four "Endangered" species in the BCLME is part of ongoing research and monitoring.

African penguins, Cape cormorants and bank cormorants have shown a considerable decline from the late 1970s/early 1980s to the late 2000s/late 2010s (Crawford et al. 2015). The African penguin bred at 32 island and mainland colonies forming three distinct clusters (Namibia, West Coast South Africa and East Coast South Africa) (Sherley et al. 2020). The overall population decreased by over 60% during the 30-year period from 1989 to 2019. In South Africa, numbers of African Penguins increased at the turn of the recent century, after an upsurge in the abundances of sardine and anchovy, their most important prey. Then, following a collapse of South Africa's sardine stock and a displacement of spawners of both prey species from South Africa's west coast to its south coast in the early- to mid-2000s, numbers of African Penguins breeding in South Africa fell rapidly (Crawford et al. 2011; 2015; Sherley et al. 2020).

Their main prey stocks in the nBCLME (sardine and anchovy) collapsed in the 1970s (Fairweather et al. 2006; Roy et al. 2007). Sardine and anchovy have relatively higher calorific values (6.59 kJ.g^{-1} and 6.03 kJ.g^{-1} respectively) compared to the pelagic goby *Sufflogobius bibarbatus* (3.69 kJ.g^{-1}) (Balmelli & Wickens 1994), which replaced these two preferred prey species in the diet of African penguins within the nBCLME (Erasmus et al. 2021). Thus, pelagic goby is a low-quality prey which may limit the prospects of recovery of the species in that subsystem; considering that top predators sometimes prefer quality over quantity (Mwaala 2022). In the sBCLME, the performance of individual colonies depends on their vicinity to optimal foraging grounds. During that time, colonies in subsystem iv (south/east coast) had outperformed those in subsystem iii (west coast) (Crawford et al. 2015), but have since experienced a 13 % annual rate of decline and an overall decline of 88.1% in the breeding population over the last 30 years (Sherley et al. in prep).

Their worrying decline has resulted to prohibition of fishing around six major breeding colonies, Dassen Island, Robben Island and Dyer Island (Sydeman et al. 2021). The Cape gannet breeds at six colonies within the BCLME (including the Namibian population) has declined by up to 98% (Crawford et al. 2007). This decline has contributed to an overall population decline of c 52% over three generations (Sherley et al. 2019). Sardine historically contributed 99% in numerical abundance to their diet in Namibia (Matthews & Berruti 1983). By the start of the 21st century, their diet was dominated by low-quality prey (i.e., trawler scavenged hakes *Merluccius* spp and naturally foraged saury *Scomberesox sarus,* juvenile horse mackerel *Trachurus trachurus capensis* and juvenile snoek *Thyrsites atun* (Dundee 2006). In South Africa, the eastward shift in distribution of sardines and anchovy led to a decrease of west coast (subsystem iii) colonies and a substantial increase in colonies on the east coast (subsystem iv) (Crawford et al. 2007). Currently, more than 70% of their population breeds at the eastern most colony in Algoa Bay (Sherley et al. 2019).

The Cape cormorant breeds at 69 localities in BCLME; at guano platforms off central Namibia, islands off southern Namibia and islands off South Africa's west coast (Crawford et al. 2007, Crawford 2015). The species lost 50% of their population over three generations between 1984 and 2014 due to food availability (Kemper & Simmons 2015, Crawford et al. 2016). Sardine and anchovy are typically a preferred prey in Namibia (Hampton 2003) and South Africa (Masiko et al. 2021). However the pelagic goby featured more in their Namibian diet since the 1980s (Crawford et al. 1985, Tom 2019). Off South Africa, colonies situated on the west coast have declined while those further south have fared well (Crawford et al. 2016). This discrepancy is attributed to the eastward shift in the distribution of their preferred prey.

The northern most breeding colony is situated at Ilha dos Tigres in southern Angola. It was first surveyed in 2005 when ca. 2600 breeding pairs were estimated (Dyer 2007). A survey conducted in 2020 yielded an estimate of 95,000 breeding pairs, which is more 50% of the global population and is attributed to the abundance of horse mackerel *Trachurus capensis* in that region (Makhado et al. 2024). The species was on a declining trend in the early decades of the 21st century (Birdlife International 2018). The increase in breeding pairs off southern Angola is significant enough to justify a down-listing at the next review.

The bank cormorant breeds at 52 localities within the BLCME between central Namibia and south coast of South Africa (Crawford et al. 1999). The Namibian population breeding at Mercury and Ichaboe islands accounts for up to 80% of the global population (Kemper et al. 2007). There was an overall population decline of 63% over three generations (Birdlife International 2018b). The Namibian population declined by 68% in the 1990s due to prey shortages and displacements by seals (Kemper et al. 2007, Crawford et al. 1989). In South Africa, the breeding trends at three colonies (Malgas, Dassen, Geyser islands) were decreasing and the colony at Lambert's Bay went extinct (Crawford et al. 2008). The magnitude of decline in South Africa is less than in Namibia. Their diet is dominated by pelagic goby in Namibia's northern colonies while the southern colonies are dominated by west coast rock lobster *Jasus lalandii* (Tom 2019). West coast rock lobster continues to dominate overall diet off South Africa in terms of frequency of occurrence (Dyer et al. 2019). Population trends were also directly correlated to their prey, west coast rock lobster landings adjacent to breeding colonies (Crawford et al. 2008).

1.1.3 *Cape fur seals*

The Cape fur seal is the only pinniped species breeding in the BCLME (David 1987). In 2009, there were 40 breeding colonies distributed along the coasts of southern Angola, Namibia and South Africa as far east as Algoa Bay (Kirkman et al. 2013). Breeding colonies have traditionally been regarded as localities where 100 or more pups are consistently born over time (Oosthuizen & David 1988). However, some recently colonised localities have limited breeding space and/or are too low-lying to accommodate 100 pups (Seakamela et al. 2024). Taking into consideration this limitation to the accepted definition, this study takes into account localities where some consistent production of pups has taken place. Thus, a total of 49 breeding localities are recognised: one extant breeding colony in Angola (Amaro 2024), 26 in Namibia (Mwaala et al. 2023) and 22 in South Africa (Seakamela et al. 2024) (Fig. 1.3 & 1.4).

Their diet is constituted by different prey species in different parts of the system. Stomach content analysis by David, (1987a) for years between 1974 and 1985 revealed diet constitution as follows: diet in Namibia (from Möwe Bay southward) was dominated by pelagic goby (52% of total diet) and horse mackerel (*Trachurus capensis*) (23%). Off South Africa's west coast, anchovy (23%) and Cape hake (*Merluccius capensis* and *M. paradoxus*) (23%) dominated the diet while the south coast was dominated by anchovy (17%), horse mackerel (14%), sardine (12%) and Cape hake (14%). A more recent scat-based study (1994 to 2018) at eight colonies spanning from northern to southern Namibia revealed that pelagic goby dominated the diet (Mwaala 2022). The same study further reported that pelagic goby was not necessarily preferred as Cape fur seals switched to Cape horse mackerel or Hector's lanternfish *Lampanyctodes hectoris* when they became available. A scat-based study in South Africa analysed diet data from 11 colonies covering the south and west coasts. The study compared two periods: 1974 to 1996 (stomach contents) and 2010 to 2019 (Gumede 2023). Overall, in the latter period, anchovy dominated the diet based on three metrics of importance: 88.3% Frequency of occurrence (FO),73.2% Numerical abundance (NA) and 69.4% Mass (M) (Gumede 2023). The contribution of seabirds to the diet increased to 9.2%FO from 0.2%FO in the first period. A 2014 scat-based study conducted in Angola revealed that horse mackerel *Trachurus* spp were important numerically (62.8%) and by weight (43.4%) (Winkler et al. 2019). Cape fur seals have flexible prey targeting and would switch prey based on availability (Mwaala 2022). This trait allows a lag in responding to environmental changes, including prey availability. Hence, the impact of east-ward shift in their preferred prey was not immediately pronounced in population trends or spatio-temporal dynamics of the population.

The impact of changes in the biomass of preferred prey seems to have been cushioned by establishment of new colonies in the direction of better foraging grounds. There was a northward expansion of breeding colonies in Namibia (Kirkman et al. 2013) and into Angola (Meÿer 2007). In South Africa, the establishment of new colonies such as Infanta Light House, Cape Point, Michell's Bay and Cape Donkin (Seakamela et al. 2024); and recolonisation of sites such as Robberg Peninsula (Huisamen 2012) and Vondeling Island (this study) appear to have balanced out numbers at colonies where reductions were recorded (Kirkman et al. 2013). Thus, the seal population has overall remained stable since the 1990's when their population was estimated at 1.5-2 million individuals (Butterworth et al. 1995). The increase in the number of colonies in the south of the west coast of South Africa will certainly increase interactions with humans and seabirds. Between 2021 and 2023, there had been at least 29 incidents of seals attacking humans in the general Cape Town area. There was also a recurrence of predation on seabirds South Africa (Strydom et al. 2022; A. Makhado pers. comm.).

1.1.3 *Threats to seabirds and the Cape fur seal*

Historical exploitation in the BCLME has had long lasting imbalance on the functioning of the ecosystem. The imbalance has had cascading effects across the trophic structure of the BCLME. Marine top predators (including predatory fish) are still recovering from extensive exploitation while others remain at low population levels (Griffiths et al. 2004). Cape fur seals and seabirds are no longer subjected to exploitation; but some species such as the African penguin are still reeling from the effects of human-induced system alterations (Griffiths et al. 2004; Sherley et al. 2020). Threats can cut across species at different magnitudes or can be species-specific. Some of the pressures that pose a threat to various species of seabirds and seals are fishing, climate change, pollution, ocean acidification and mining (Moloney et al. 2013), bycatch, diseases and oil spills. Except for climate change, some of these threats are reversible or can be avoided in future by introducing stringent policies and best practices.

Prey availability limitations due to overfishing of pelagic species led to decreased populations of seabirds targeting these resources (Crawford et al. 2022). This has led to a shift to low quality prey such as the pelagic goby (Crawford et al. 1985), which negatively impacts the dynamics of bird populations (Ludynia et al. 2010). Some species (e.g., Cape cormorants) may abandon their eggs and/or chicks during periods of food shortages. In 2021, approximately 2000 Cape cormorants were found abandoned at Robben and Jutten Islands (Phillips et al. 2023). A mismatch in breeding localities and areas of high preferred prey biomass has compounded impacts of prey limitations on seabirds (Crawford et al. 2015). This is primarily due to the limited foraging range of some of the species from their breeding colonies e.g., African penguin (20-30 km) (Pichegru et al. 2012). There have been at least 71 oil spill incidents in the BCLME from cargo vessels, tankers, ship-to-ship bunkering and unknown sources (Vanstreels et al. 2023). Although other species were impacted (Moloney et al. 2013), African penguin and Cape gannets were affected the most (Vanstreels et al. 2023). For both species, survival and breeding success of rehabilitated individuals seem to have been unfavourably affected (Altwegg et al. 2008, Vanstreels et al. 2023).

There has been several die-offs of seabirds and seals which were linked to diseases. In 2017, about 7,500 cases of High pathogenicity avian influenza (HPAI) of H5N8 strain were detected in South Africa, affecting mostly Swift terns (5363) but also African penguins (103), Cape cormorants (100) and Cape gannets (1627) (Roberts et al. 2023). In 2019, another HPAI- H5N8 outbreak was reported in Namibia, killing ~500 African penguins and an undetermined number of Swift terns (Molini et al. 2020). Also in Namibia, ~6500 Cape cormorants succumbed to HPAI (H5N1) in 2022 (Molini et al. 2023). Avian cholera (*Pasteurella multocida*) killed 14500 Cape cormorants off South Africa in 1991 affecting 8 island breeding sites (Crawford et al. 1992). Avian cholera further decimated a total of 29 750 individuals (adults and juveniles) at Dyer island between 2002 and 2005 (Waller and Underhill 2007). The latest HPAI (H5N1) outbreak was in 2021 and affected at least 11,700 Cape cormorants on the west and south coasts of South Africa (Roberts 2021). These outbreaks killed a significant number of seabirds in the BCLME, including endangered species. In 1994, about 10 000 Cape fur seal adults and 15 000 abortions were recorded in Namibia (Henton et al. 1999). Although these were largely linked to food shortages caused environmental anomalies (Roux et al. 2002), *Streptococcus phocae* was isolated and confirmed to be a secondary opportunist infection (Henton et al. 1999). In 2020, more than 7000 seals died off Pelican Point near the port of Walvis Bay in Namibia, which remain unexplained to date (SeaSearch and Conservation & Ocean Conservation Namibia unpublished data); no environmental anomalies were reported.

In 2021, an unprecedented mass-mortality affecting ~7000 individuals (mostly pups) were reported in South Africa. Laboratory test from 8 carcasses indicated protein energy malnutrition as a cause of death (Seakamela et al. 2021). Further analysis indicated that domoic acid (caused by *pseudo-nitzschia*) may have contributed to the mortalities (Gridley 2022). Cape fur seal as prey have few predators in the BCLME, such as brown hyena (Wiesel 2010), African lions (Stander 2019) and Great white sharks (Stewardson 1999). These predators have a negligible effect on their population. Seals as predators have increasingly included seabirds in their diet both in Namibia (du Toit et al. 2004) and South Africa (Makhado 2009). Predation on seabirds has been recorded for African penguin (Makhado et al. 2013), Cape gannet (Makhado et al. 2006; Strydom et al. 2022), Cape cormorant (Marks et al. 1997; Makhado et al. 2013), bank cormorant (du Toit et al. 2004) and crowned cormorant (David et al. 2003). In addition to predation, seals have outcompeted seabirds for breeding space in Namibia (Crawford et al. 1989) and South Africa (Chapter 2). The spatial shifts in breeding localities of Cape fur seals have raised concerns that they will increase interactions with birds at colonies. This may increase adverse interactions such as increased predation and competition for space. Although there are more threats to discuss, the above are considered most critical. The effects of these threats may be exaggerated if acting together in a multiple-stressors scenario. For instance, the African penguin lost ideal nesting habitat to the removal of guano at key islands (Sherley et al. 2012), then the collapse of their preferred prey (Crawford et al. 2001), then competition for space at breeding localities; and in 2021, the deaths of 65 individuals due to be being stung by the Cape honeybees *Apis mellifera capensis* (Tshuma 2021).

Overview of exploitation of seals and seabirds in South Africa

The history of exploitation of modern-day South Africa's marine resources predates colonial times (Griffiths et al. 2004). A more organised, and later, commercial exploitation history is intertwined with that of other countries, notably, those with historical links to economic exploitation of South Africa's resources. These linkages can be traced back to the arrival of European settlers in southern Africa. The modern-day Cape Town was the operational centre of exploitation (Ross 1989). Europeans of the time were initially concerned with subsistence-based exploitation, with the main objective being supply of ships with food and water. Although there was an initial strong agricultural focus, marine organisms such as seals, penguins and abalone were also strategically exploited (Pooley 2009).

Exploitation of marine resources was not conservation driven, at least in the modern-day sense that is typically backed up by scientific evidence. It is estimated that more than 50 million tonnes of biomass were extracted from the BCLME in the past two centuries (1800-2000) (Griffiths et al. 2004). This estimate covers periods for which data are available, before which it is difficult to ascertain how much was extracted from the marine system of the region. The prospect of running out of food supplies had forced earlier authorities to rethink extractive practices. The expansion of commercial activities of European settlers increased the intensity of extraction (Fourie 2012). Exploitation switched between species depending on demand and availability. As such, the impact of unsustainable practices was not always realised until it was too late. Moments of epiphany brought about by dwindling resources assisted with evolution of better regulations of extractive practices. However, the impact of earlier practices and administrative decisions would be long lasting.

Impacts of historical exploitation regimes and associated practices can be best demonstrated by modern-day's dynamics of top predators in the Benguela Ecosystem. Seabirds were exploited for their eggs, guano and feathers (Best et al. 1997), while the Cape fur seals were mainly exploited for their meat, pelts and blubber (David & van Sittert, 2008). The earliest record of systematic exploitation of seals is of 45,000 individuals killed around the then Cape of Good Hope in 1610 (Muller 1938). African penguins *Spheniscus demersus* were exploited for their eggs (Cott 1953). French and later Dutch sailors collected eggs in large quantities to service their crew and passing ships (Rand 1969) but not much information is available on quantities for period 1600 to 1800. Cape gannet and Cape cormorant *Phalacrocorax capensis* are guano producing species, a product which was harvested intensively in the 1800s (Watson 1930). Exploitation of these top predator species would later lead to unfavourable consequences for the BCLME; albeit various legislative interventions.

Seal Harvesting

Cape fur seals were important for their meat and fat (blubber) to precolonial communities and later ships passing through South Africa. Evidence of precolonial subsistence utilisation of seals is derived from archaeological records; for instance, the results of excavation of archaeological sites off the west coast of South Africa e.g. Vredenburg Peninsula (Klein & Cruz-Uribe 1989), Elands Bay (Woodborne et al. 1995) and Namaqualand (Dewar 2007). Further evidence is provided through records or notes of seafarers. For instance, a British Captain John Jourdain noted in 1608 that he saw locals in Saldanha Bay scavenging on seals that had been thrown overboard their vessel (Foster 1905). The utilisation of Cape fur seals along the west coast is thought to have been seasonal (Woodborne et al. 1995) and limited to <3-year age class for ease of transportation to the accommodation (Smith et al. 2006). Coastal communities used seal meat for food, blabber for skin-oil, skins for garments while bellies and bladders were used as water bags (Muller 1938).

Seafarers on passing ships harvested seals for food, oil and their skin (ref). The Dutch collected 100 seal skins in 1608, followed by 45,000 seal skins in 1610 (Muller 1938, Hart 1957 in David and van Sittert 2018). The intensity of harvests increased as more ships arrived in the region. Official commercial harvest records are available from 1900 to 1990 (Wickens et al. 1991). Quantities of seals taken prior to 1900 were reconstructed from oil and skin exports by David and van Sittert (2008). During the two periods, a combined 4,6 million seals were killed. The official commercial records account for 2 748 574 animals, 92% of which were pups. Pups were harvested for their fur that was used in production of clothes, bulls for their genitalia that were used as aphrodisiacs and the two age classes were also used in production of meat and oil (Campbell 2013). The relative importance of each sex- and age- class changed over time, for instance, harvesting focus shifted to bulls when the market for pup fur collapsed in the mid-1980s (Wickens et al. 1991). Cape fur seal harvesting ceased in 1990 through a moratorium by Anon (1990), and although Namibia continued to harvest, a new Seal Fisheries Management Plan is under review owing to the decline in demand of seal products (Boyer 2018).

Guano Harvesting

The fertiliser properties of guano were long known by the Inca people of Peru off the Humboldt Large Marine Ecosystem (HLME), which they used as a fertiliser for their crops (De La Vega 1961). The first known experimental trials of seabird guano as fertiliser were conducted at St Helena Island by an English Alexander Beatson in 1809 (Cushman 2013).

Commercial potential of guano was realised in Peru in the late 1830s, however, due to political instability, a global search for other sources was initiated. The explosion of guano as a commodity was as a result of scientific advancement in plant nutrition, accelerated by a demand transcontinental crop failures and famine (Snyders and Snyders 2016). Although the product was introduced to Europe by Baron von Humboldt in 1804 (Craig 1964), it was not until the 1840s during the European agricultural revolution brought about by global famine that guano was taken seriously.

Guano contains mineral nutrients, amongst others nitrogen (10–12%) and phosphorous (10–12%) which are essential for plant growth (Schnug et al. 2018). Johnson (1841) summarised chemical properties of guano in Farmer's Magazine and included earlier work by other Scientists. In that volume, successful accounts of farmers who had trialled the product were also published. This led to a global demand in the product. Schnug et al. (2018) further categorised guano as nitrogen or phosphate guano, depnding on which of the minerals dominated the deposits. In the BCLME, these were nitrogen guano.

The discovery of guano by an American Captain Morrell at Ichaboe Island in 1828 ignited a guano rush in in the BCLME (Craig 1964). It was not until 1843 that English Captain Farr scraped the first consignment of guano (Craig 1964). This discovery provided an alternative to the Peru market and led to a guano rush during the period 1843 to 1845 that led to the removal of 330,000 tons of guano from islands in the BCLME (van Sittert and Crawford 2003). Guano harvesting was only conducted in the HLME and BCLME owing to their large populations of guano producing seabirds at peak of the rush (Crawford & Jahncke 1999). As a result of commodification of guano, the Namibian islands became the epicentre of a tussle for control of southwest Africa by the British and Germans. In the 1860s, the British claimed Ichaboe Island and later claimed a further 11 island (Hollams Bird, Mercury, Seal, Penguin, Halifax, Long, Possession, Albatross, Pomona, Plumpudding and Sinclair islands) (Shaughnessy 1984).

Reliable data on quantities collected in the BCLME are available for periods 1895 onwards; before which the data were reconstructed by van Sittert and Crawford (2013). Rand (1952) published collection figures as follows (in metric tons): 182,000 (1895—1903, Namibia's islands); 34935 (1927—1950, Namibia’s islands) and 643,641 (1931—1947, Namibia’s platforms). Namibia’s first breeding platforms was built in 1930 to attract birds to breed and deposit guano (Best et al. 1997). Additional platforms were constructed following the initial success which led to an increase in a guano yield (Cooper et al. 1982). By the end of guano collections on record, a combined c. 458,000 metric tons were extracted from the BCLME (c. 292,000 metric tons from Namibia’s islands and c. 166,000 from South African islands (Tom et al. 2023).

Timeline of the legislative protection of seals and seabirds

Seals and seabirds have always utilised common breeding grounds. They feed at sea and breed on land, typically at coastal islands that are isolated from terrestrial predators (Crawford et al. 1989). The tendency to share breeding space has made one group collateral to regulatory framework for managing the other. For instance, during the peak of seal harvesting, seabird nests would be disturbed and/or destroyed. Similarly, at the peak of guano harvesting (termed guano-rush), seals were excluded from breeding at certain islands for exclusive use by guano producing seabirds. This issue and subsequent consequences are deliberated on in Chapter 2.

Prior to the first protective pieces of legislation for seals and seabirds, guano/penguin egg and seal harvesting were not tightly regulated (Snyders 2020, Wickens 1989). Driven largely by economic interests, the first formal protection of seabirds was promulgated in 1891 through the Proclamation 316 under the Game Act (Act 36 of 1886) that prohibited killing and disturbance of guano producing birds (gannets, cormorants) and source of meal eggs (penguins) (Snyders 2019). In 1893, the first legal protection for seals (Proclamation 499 of Game Act) prohibited capture, killing or harassment of seals and seabirds without a permit (Shaughnessy 1984). The Fish Protection Act (Act 15 of 1893) banned unauthorised landing on the islands for sealing and egg collecting, which afforded seals and seabirds some indirect protection (Snyders 2020).

In May 1973, the Sea Birds and Seals Protection Act was signed into law, repealing the Fish Protection Act. This Act however did not stop harvesting practices but stipulated (for seals) age classes, the time of the year they could be harvested and the mode of killing. In 2007, a Policy on the Management of Seals, Seabirds and Shorebirds was gazetted under the Seabirds and Seals Protection Act (DEA 2007). This policy banned the killing of seals and seabirds for profit. This was the time within the legal framework that issues affecting seals and seabirds were thoroughly focused upon. The scope of this policy included bycatch, breeding habitat degradation, and sustainable non-consumptive use. In 2017, additional protection was granted through the publication of Regulation Gazette No. 10722 (National Environmental Management: Biodiversity Act (10/2004): Threatened or Protected Marine Species Regulations).

The 2017 regulations were most stringent to date. It is noteworthy that not all practices around exploitation of seabirds and seals were in terms of law. Unwritten management policies/strategies were often implemented in favour of commercial interests. The most relevant to this thesis is the deliberate exclusion of seals from their breeding colonies for exclusive use by guano producing seabirds (Rand 1961). African penguin egg harvesting stopped in 1967 (Shelton et al. 1984a), guano harvesting stopped in 1991 (DFFE unpublished data) while seal harvesting was stopped in 1990 (Anonymous 1990).

System reset

Records of the Government Guano Islands indicate that at some islands, seal harvesting continued, albeit at small scale (Zeederberg 1920). The declining demand for seal products and the growing commercial importance of guano, guano-retaining walls and accommodation for island-minding officials were built at harvested islands (Crawford et al. 1989). When the market for guano collapsed around 1991, island headman left the islands. The absence of human disturbance at these islands afforded a natural system reset to take place. As such, seals began to return to these previously occupied islands. This process would later lead to undesirable inter-species interactions between seals and seabirds. Seals have since returned to Robberg Peninsula (Huisamen et al. 2011), Vondeling Island and more recently (2021) Dassen Island (Seakamela et al. 2024).

Species Interactions

Effective conservation management of natural resources depend on a good understanding of how species interact (Auster et al. 2013). Conservation proponents have now accepted that a species cannot be managed in isolation and consideration has to be given to other species that co-exist in time and space (Tylianakis et al. 2010). Understanding these interactions enables effective management towards a stable ecosystem and species level population viability (Heinen et al. 2020). The interactions can be trophic (e.g., predator-prey) (Arditi and Ginzburg 2012) and non-trophic (pollination or seed dispersal) (Abrol 2007). However, the non-trophic interactions can have an effect on trophic interactions. For instance, the presence of a species not directly linked to trophic interactions of the other two species that trophically interact, may affect those interactions (Hammil et al. 2015).

Ecosystem changes mediated by, amongst others, harvesting (e.g. fishing), habitat modification and climate change are altering conditions that species live under (Rahman and Candolin 2020). Thus, how species interact will drive how their populations respond to change (McCluney et al. 2012). However, resultant dynamics can favour some species and be detrimental to others, mainly due to the degree of behavioural plasticity of individual species (Wong and Candolin 2015). In both terrestrial and marine ecosystems, climate change driven changes have resulted in species redistribution leading to spatial mismatch of predators and their prey (Durant et al. 2007; Caroll et al. 2024). Disruption of predator-prey interactions due to these shifts can impact phenology of predators, depending on the dietary specialisation of the predator species (Bretagnolle and Terraube 2010). Further to predator-prey mismatches, predator species with high fidelity to a specific breeding habitat may be impacted by immigrating species that have shifted their ranges (Jones et al. 2013). A case in time is the perceived changes in the distribution of breeding colonies of Cape fur seals within their Southern African range (Kirkman et al. 2013). These changes may have led to negative impacts on endangered seabirds through displacement and predation (Kirkman 2009). This study will amongst others, investigate how the establishment of a Cape fur seal breeding colony at a locality with breeding colonies of seabirds (some endangered) has had an impact on their breeding performance. This dissertation describes the recolonisation process by Cape fur seals at Vondeling Island and utilised breeding performance trends data of both seals and seabirds to investigate impacts of seals on seabirds at the island. Subsequent interspecies interactions between seals and seabirds that were breeding at the colony prior to recolonisation (including endangered seabirds i.e. African penguins (BirdLife 2020), bank cormorant (BirdLife 2018a) and Cape cormorants (BirdLife 2018b) were also investigated using breeding habitat utilisation data. Lastly, telemetry data was used to investigate overlap in at-sea distribution of Cape fur seals and African penguins, thus inferring competition for forage resources.

Study animals

A single species of marine mammal (Cape fur seal) and 10 species of seabird (and one shorebird) have been recorded on Vondeling Island. Of the 10 seabird species, six are classified “Least Concern”, one “Near Threatened”, three “Endangered” (Makhado et al. 2021). Cape fur seal population was estimated at 1.5–2.0 million individuals in the 1990s (Butterworth et al. 1995). It has remained stable at these levels but there have been some changes at the colony level, including establishment of new colonies (Kirkman et al. 2013). Due to the stability of the population and little predation pressures, the species is classified as “Least Concern” (Kirkman et al. 2016).

Vondeling Island

In 1988, Vondeling Island (21 ha) was declared a Provincial Nature Reserve in terms of Section 6 the Nature Conservation Ordinance, 1974 (Official Gazette 4524, 1988). Prior to that, the island and other guano islands were managed by Department of Industries (Guano Islands division) (Siegfried and Crawford 1978). The island is located in the open ocean to the south of entrance to Saldanha Bay; it is considered part of the Saldanha Bay group of islands which includes Malgas, Marcus, Jutten, Meeuw and Schaapen Islands (Fig. 2.1). These other islands were transferred from Cape Nature to become part of the West Coast National Park (WCNP) in 1985 (Best et al. 1997). Cape Nature is a provincial conservation management agency responsible for biodiversity conservation in the Western Cape province of Suth Africa. Vondeling Island remained under the control of CapeNature to date, but negotiations are under way to transfer the island to WCNP (Johan Visagie pers. comm.).

The island is mostly rocky and low-lying (up to 8 m elevation above sea level) with its main beaches being on the south and west of the island. Historically, the island supported a few species of angiosperms such as *Urtica urens*, *Atriplex semibaccata*, *Prenia pallens*, *Malva parviflora* and *M. suffruticosa* (Brooke & Crowe 1982). The island has had no human occupation since 1963 and access is only allowed through a filming or research permit issued by CapeNature. The island is situated within an upwelling driven highly productive Benguela Upwelling System (Hutchings et al. 2009). Productivity of the ecosystem has supported enormous biomass of pelagic fish upon which top predators at the island prey. The ecosystem has historically maintained large populations of seabirds which gathered in their numbers to breed and deposit commercially viable quantities of guano (Crawford 1978). These seabirds historically bred on coastal islands, including Vondeling Island.

The island has a history of exploitation of both seals and seabirds. From known records, a total of 561,840 African penguin eggs were harvested between 1871 and 1916 (Shelton et al. 1984b). Records indicate that an average of 56.67 (range 3–224) metric tons of guano were harvested per year from Vondeling Island between 1897 and 1961 (DFFE data). There were unsuccessful attempts to catch seals between 1755 and 1764, but due to a lack of a proper landing place and the exposed nature of the island, several men died which discouraged further seal harvesting (Roux 1975). Since the last headman left the island around 1963 (Shelton et al. 1984b), the island has remained largely undisturbed by human activity. This has allowed the dynamics of the island to change organically, including the return of seals to the island. It is thus an ideal locality to investigate various aspects of a system resetting itself, including impacts thereof.

Thesis structure

This thesis contains two substantive chapters that attempt to describe both the recolonisation process by Cape fur seals at Vondeling Island and possible impacts thereof. The Chapters utilise breeding trends data for both Cape fur seals and seabird fauna. Aerial photographic survey data are used to provide context for the spatial utilisation by both faunal groups. Satellite telemetry data was used to examine the movements and possible overlap of seals and the endangered African penguin at sea.

Chapter 2 describes the recolonisation process by Cape fur seals since the first seals were observed hauling-out in 1991. Data from land-based surveys are presented together with aerial photographic survey data to describe the growth of the local Cape fur seal population. Seabird breeding trends data were also utilised to investigate their trends relative to Cape fur seal numbers. Statistical interrogation of these data will assist in determining if there are correlations between the increase in seal numbers and population trends of seabirds at the island. The seabird trends at Vondeling Island are then compared to trends of similar species breeding at other breeding localities. This assists in establishing if trends at Vondeling Island are uniquely affected by the presence seals or follow the trends at other colonies with similar species. To demonstrate changes in space utilisation by seals and seabirds over time, hand-drawn sketches of seal and seabird distribution (1990-2005) and later (2006 onwards) images from arial photographic surveys are utilised. The Chapter's objectives are therefore to 1) document the recolonisation of Vondeling Island by Cape fur seals using information obtained from land-based surveys and aerial photographic surveys; 2) investigate possible impacts of the recolonisation.

Chapter 3 utilises satellite-derived location data to investigate possible overlap in at-sea core feeding areas for Cape fur seals and seabirds. Due to resource limitations, only one species of bird was utilised for this investigation, the African penguin. These penguins have demonstrated the steepest decline in population trends compared to the other two endangered bird species (bank and Cape cormorants). Cape fur seals and African penguins were equipped with satellite-linked position transmitting tags in 2017 and allowed to transmit until they fell off or battery was exhausted. Comparing at-sea habitat utilisation of the two species will assist in inferring competition for prey resources. Various statistical approaches are utilised to understand their trip characteristics, movement behaviour and calculate percentage overlap in home ranges and core areas. Their core areas are further superimposed over spawner biomass density distribution maps and their overlap calculated. This Chapter's objective was therefore to implement the usage of satellite telemetry technique to investigate potential competition between seals and penguins that breed at Vondeling Island.

Chapter 4 provides a synthesis of the work and provides recommendations to policy makers. The Chapter further identifies future work that is needed based on the lessons learnt from this thesis.

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Figures and Tables

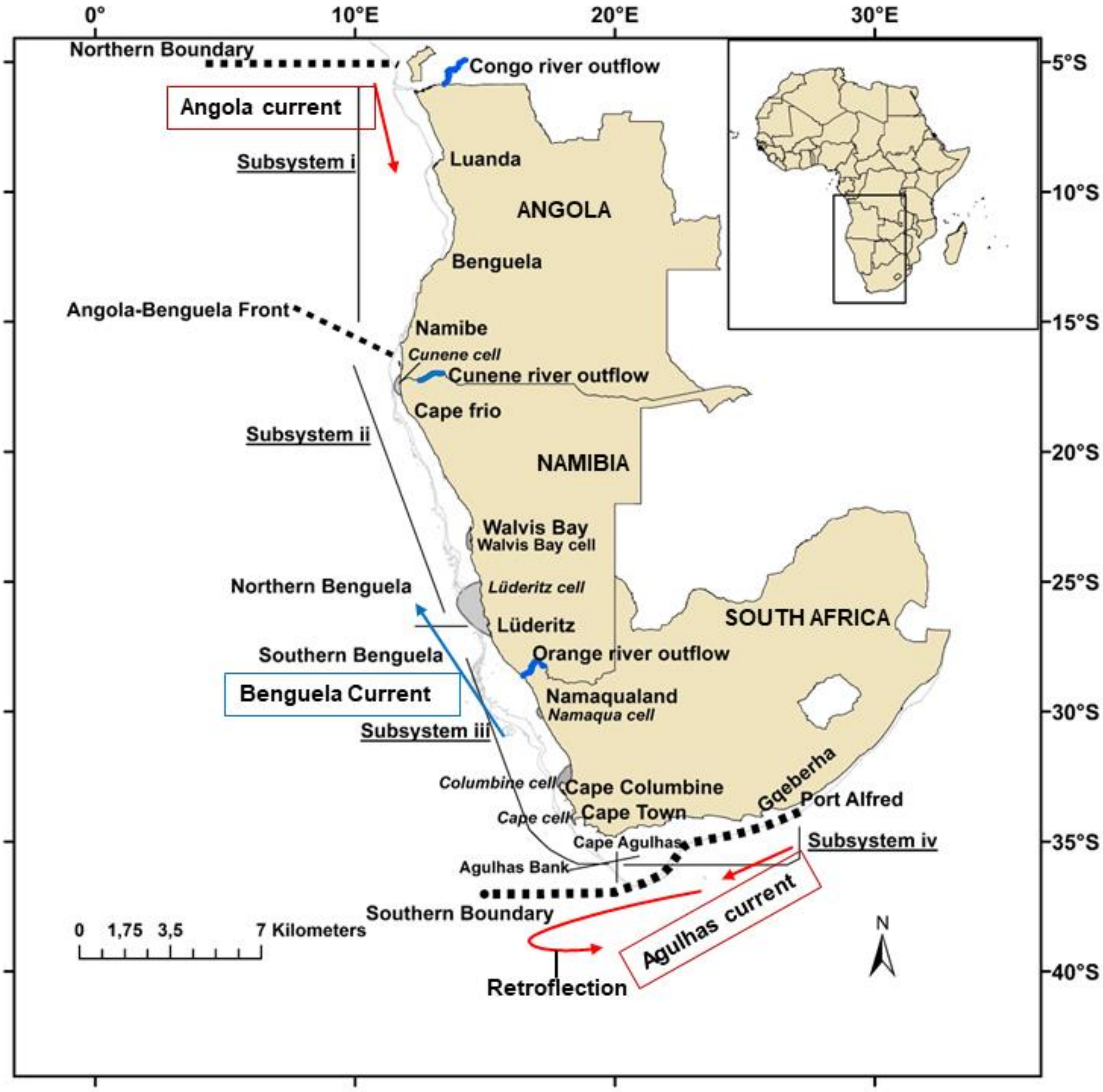

Figure 1.1 A simplified map of the Benguela Current Large Marine Ecosystem showing the northern and southern Benguela, major currents and their direction (red denotes warm and blue denotes cold, arrow denotes direction of flow). Locations of upwelling cells are also shown. Simplified from Hutchings et al (2009) and Kirkman et al. (2016).

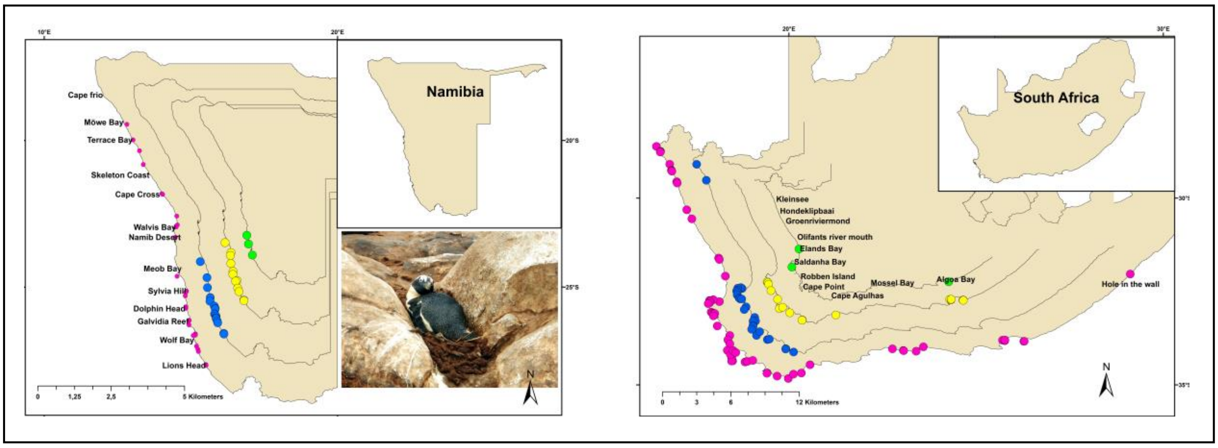

Figure 1.2 The distribution of 4 endangered seabirds mentioned in text. There is only one colony of Cape cormorants (not shown). Species are represented by the colour of filled dots as follows: Purple= Cape Cormorants; Blue= Bank Cormorants; Yellow = African penguin; Green = Cape gannet.

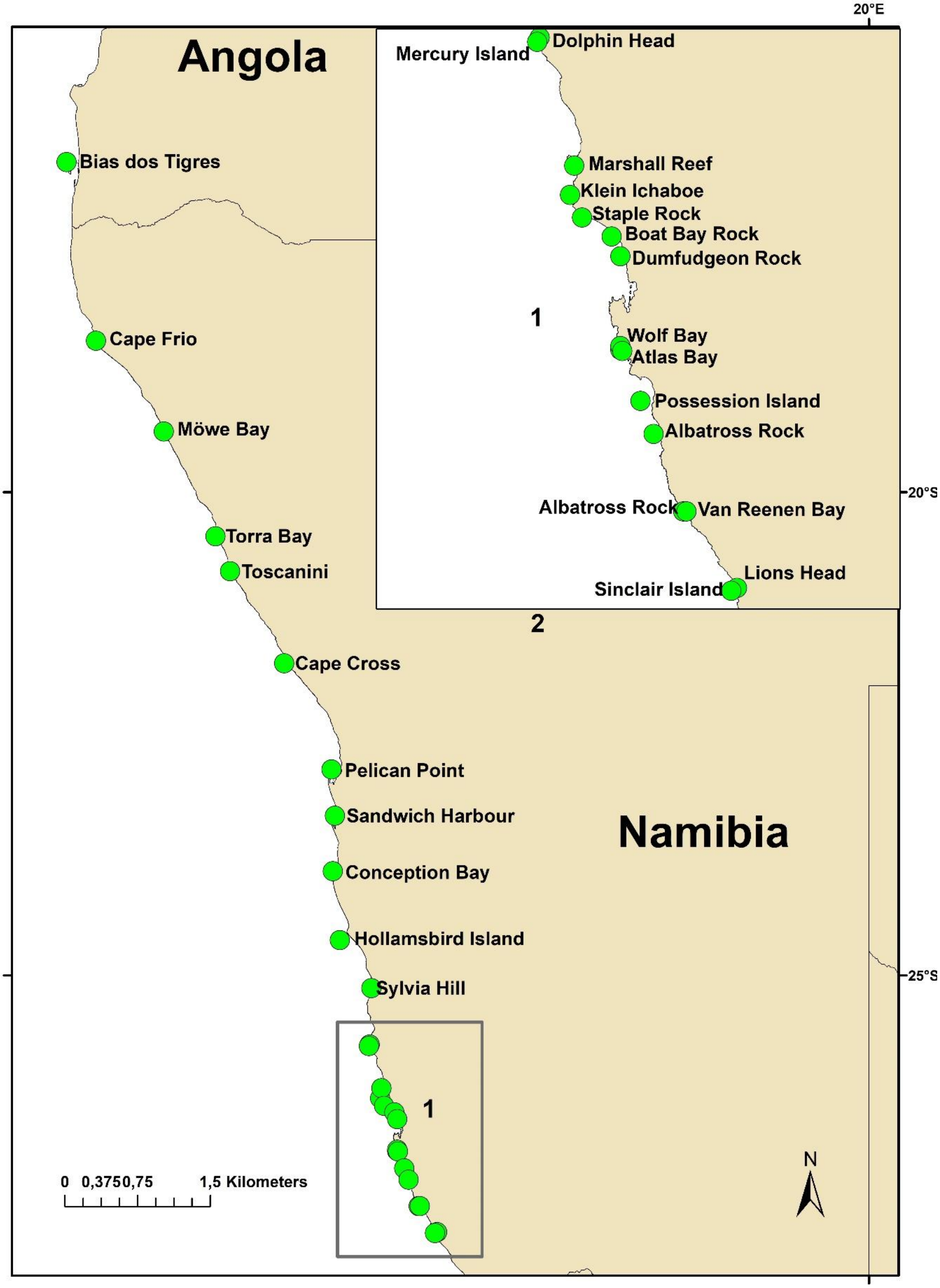

Figure 1.3 Localities of Cape fur seals colonies in Angola and Namibia.

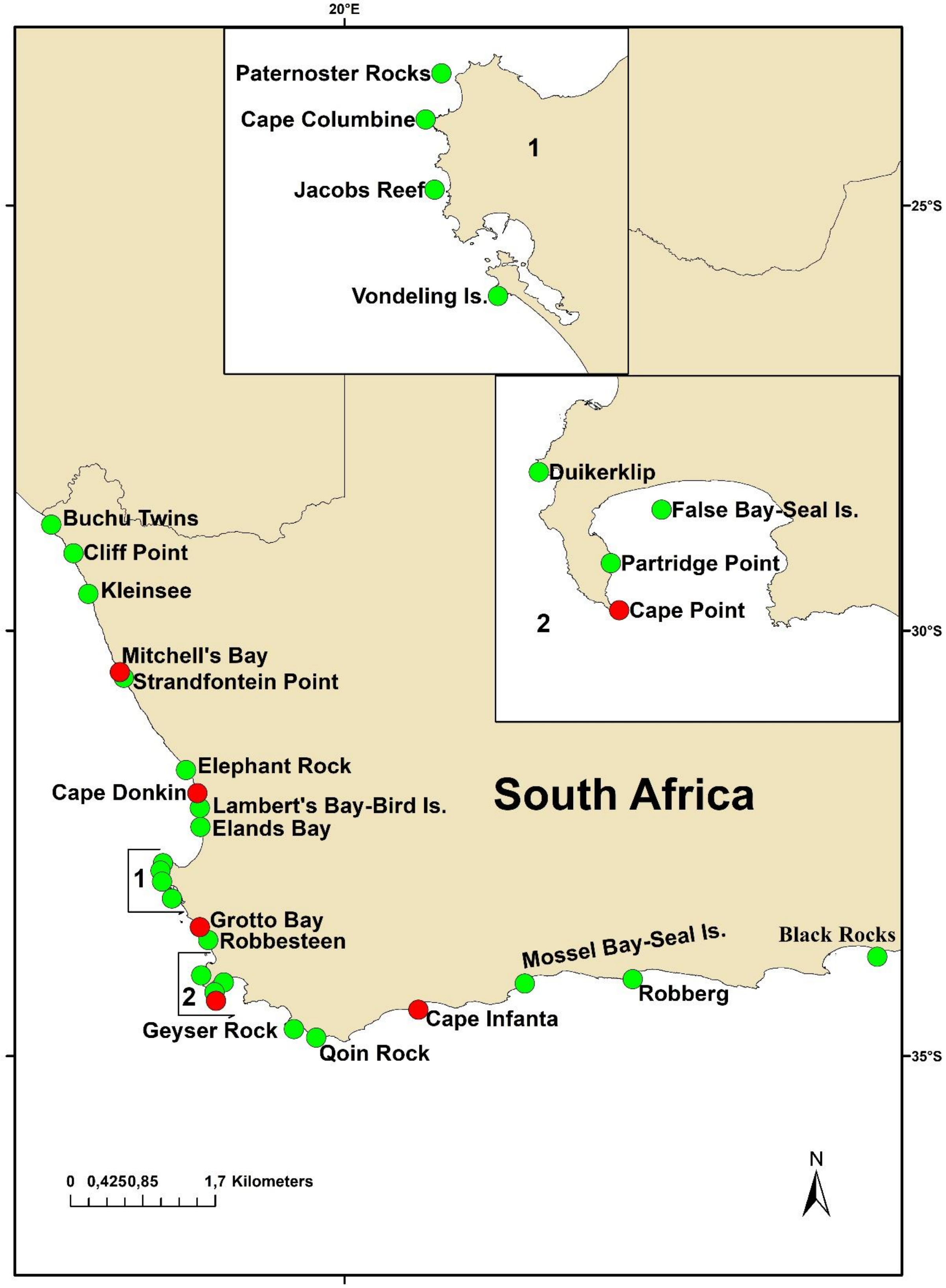

Figure 1.4. Localities of Cape fur seals colonies in South Africa. Red dots denote colonies that were established after Kirkman et al (2013).

Chapter 2: Recolonisation of Vondeling Island by Cape fur seals *Arctocephalus pusillus pusillus* and possible effects on avifauna

Abstract

The Cape fur seal *Arctocephalus pusillus pusillus* have recolonised islands from which they were previously excluded for exclusive use by guano producing seabirds. These include Mercury Island in Namibia, Robberg Peninsula on the south coast of South Africa and Vondeling Island on the west coast. This study reports on the recolonisation of Vondeling Island and the subsequent impacts on seabirds' population trends. The study utilised survey data (aerial and land-based) of Cape fur seals and seabirds breeding at the island. Survey data were collected between 1990 and 2018 (until 2008 for Cape fur seals) during land-based surveys. These surveys counted breeding pairs of seabirds and all age groups of seals present at the colony. In 2003, survey methods for Cape fur seals shifted to only counting pups from aerial photographic surveys. The study's analytical approach included 1) stratifying the time series into three periods: 1991–1998 (low seal numbers), 1999–2005 (intermediate numbers) and 2006–2018 (fully feldged seal breeding colony) and testing the differences in trends, 2) seal and seabird trends were compared to those of conspecifics breeding at other localities, and 3) the area occupied by both breeding and roosting seabirds species and seals were mapped to better elucidate possible competition for breeding space. The recolonisation was initiated for the first time by juvenile seal bulls in 1991 and the first cohort of pups ($n=16$) was born in 2003. The annual growth rate was 38.5% ($p < 0.003$) until 2018. Immigration was most likely the driver of this growth. Cape cormorants experienced the largest decline (-0.6734, $p < 0.005$) of all seabirds during the period of high seal abundance (2006–2018). African penguins experienced a slight but statistically insignificant decline (-0.1246; $p < 0.5$) in the same period, probably buffered by the installation of artificial nests in 2017. Trends of bank and crowned cormorants declined at study site and adjacent Saldanha Bay islands. The amount of space utilised by seals at the island increased substantially as the population increased. They encroached the interior of the island where African penguins and Cape cormorants predominantly bred. Bank and crowned cormorants' versatile utilisation of island structures (houses and defunct jetty) mitigated a potential impact. These results indicate that seals (re)colonising islands with established breeding colonies of seabirds can be detrimental to their breeding performance, largely by encroaching into their nesting areas.

2.1. Introduction

The Cape fur seal is the only pinniped that breeds in southern Africa. Its breeding range is from Algoa Bay in South Africa, through Namibia to Ilha dos Tigres in southern Angola (Chapter 1). Most breeding colonies are found in Namibia (Kirkman et al. 2011; Chapter 1). Adult fur seals have amphibious habits, feeding in the water and breeding on land (Chilvers 2018). The choice of breeding locality is determined *inter alia*, though not limited by, proximity to favourable foraging areas. Habitat should be suitable for pups, favourable for maternal attendance (i.e. easily accessible from the sea), exposed to cooling winds to avoid hyperthermia and provide protection from heavy seas, adverse weather and potential predators (Trites 1990; Stewardson et al. 2012). Cape fur seals therefore prefer near-shore rocky islands for breeding. When European sailors first arrived in southern Africa in the 1600s, Cape fur seals occupied more island breeding localities than in the first decades of the 21st century (Rand 1955).

Harvesting of Cape fur seals is one of the oldest industries based on marine living resources in southern Africa (David 1989; Stewardson 1999). It was conducted indiscriminately for three centuries and led to extinction of Cape fur seals at several islands (Rand 1952; 1972; Shaughnessy 1984). Cape fur seals were reduced to c. 100,000 animals at the start of the 20th century (Shaughnessy 1984). Large numbers of seal pups were harvested in South Africa and Namibia during the 1970s and early 1980s, but when the market for pup pelts collapsed in 1983, the emphasis shifted to exploitation of bulls (Wickens et al. 1991). Towards the end the 20th century, the seal population recovered rapidly, in response to management measures imposed (Shaughnessy and Butterworth 1981, Stewardson 1999). Exploitation of seals in South Africa terminated in 1990. The overall population of Cape fur seals was estimated in the mid-1990s to be about 1.5 to 2.0 million animals (Butterworth et al. 1995), and has stabilised at this level (Kirkman et al. 2013).

Seal harvesting at Vondeling Island started in 1755 out of desperation following a scarcity of seals at neighbouring and preferred harvesting islands, such as Marcus, Jutten and Malgas (David & van Sittert 2008). However, due to difficulty in accessing the island, harvesting operations were short lived. This island was therefore predominantly utilised for seabird guano harvesting. Island managers were deployed on this island and at the other guano islands to, amongst other tasks, keep seals away (Rand 1963a,b; Kirkman et al. 2013). When artificial fertilisers become widely available, the market for guano collapsed, and human occupation ceased as well as the active exclusion of seals (Shaughnessy 1984). The last guano collection at the Vondeling Island was in 1961 and humans abandoned the island in 1963. Structures erected to assist guano harvesting such as the interior guano retention wall (interior wall henceforth), jetties for transport and houses built for humans remain on the island. Lack of human disturbance allowed seals to haul-out at and they eventually recolonised the island (this study).

Seals have since recolonised Mercury Island in Namibia (Crawford et al. 1989), Robberg Peninsula on the south coast of South Africa (Huisamen et al. 2011) and Vondeling Island on the west coast (this study). Recolonisation of extinct colonies have been documented for other seal species that were previously subjected to over-exploitation. These include amongst others, Antarctic fur seal *Arctocephalus gazella* and Subantarctic fur seal *A. tropicalis* on the Crozet Islands (Jouventin et al. 1982), *A. topicalis* on Amsterdam Island (Roux 1987), grey seal *Halichoerus grypus* in the Wadden Sea (Reijnders et al. 1995), New Zealand fur seal *A. forsteri* off Otago Peninsula (Bradshaw et al. 2000) and Guadalupe fur seal *A. townsendi* at the San Benito Archipelago (Aurioles-Gamboa et al. 2017). In certain instances, recolonisation has been reported to affect vegetation positively through soil fertilisation (Haussmann et al. 2013) and negatively through trampling (Favero-Longo et al. 2011). The trampling of vegetation led to loss of breeding habitat for surface breeding birds in South Georgia (Bonner 1985).

In southern Africa, Cape fur seals have outcompeted seabirds for breeding space in Namibia (Crawford et al. 1989). There has also been an increase of seal predation on seabirds (Makhado 2009) which is partly attributed to spatio-temporal changes in the distribution of seal colonies and to subsequent local increase in seal abundance at or in the vicinity of seabird breeding colonies (Kirkman 2009). The changes have led to the establishment of colonies south of the west coast, where majority of seabird colonies are found (Crawford et al. 2015). Environmental changes which led to the eastward shifts in the distribution of their key prey, anchovy and sardine (van der Lingen et al. 2006), have contributed to these perceived changes. Thus, it is crucial to monitor and understand the colonisation process and its impact on the local ecosystems. This study therefore documents the recolonisation of Vondeling

Island by Cape fur seals using information obtained from land-based surveys and aerial photographic surveys. At least 10 species of seabird previously bred at the island. Information gathered from seabird censuses is utilised to investigate possible seal recolonisation impacts on their local populations.

2.2. Methods

2.2.1. Study site

Vondeling Island is one of six islands forming the Saldanha Bay group of islands, the others being Malgas, Marcus, Jutten, Meeuw and Schaapen Islands, all of which are important seabird breeding localities (Figure 2.1). It is situated on the west coast of South Africa (33°9'11"S, 17°58'57"E). Its surface area is c. 21°ha, mostly rocky and low-lying (up to 8 m elevation above sea level) with some sandy beaches on the south and east of the island. Historically, the island supported a few species of angiosperms such as *Urtica urens, Atriplex semibaccata, Prenia pallens, Malva parviflora* and *M. suffruticosa* (Brooke and Crowe 1982). The island lies within the southern section of the cold and nutrient rich Benguela Upwelling System, and c. 100 km north of Cape Town. It was declared a provincial nature reserve in 1988 in terms of section 6(1) of the then Cape of Good Hope Nature and Environmental Conservation Ordinance of 1974. Prior to that, the island and other guano islands were managed by Department of Industries (Guano Islands division) (Siegfried and Crawford 1978). The most notable fauna found on the island are various species of seabirds and the Cape fur seal, which are protected in terms of Threatened or Protected Species Regulations (TOPS) under the National Environmental Management: Biodiversity Act (NEMBA) of 2004 (DEA 2017). Since humans ceased occupation of the island in 1963, infrastructure such as the jetty were unmaintained and are now unusable, making access challenging for researchers.

2.2.2. Cape fur seal counts

Between 1990 and 2009, numbers of Cape fur seals at Vondeling Island were recorded by research technicians undertaking seabird surveys at the island. The technicians walked and covered the island’s coast and interior, counting and recording individual seals encountered. The number of technicians varied between one and four per visit depending on their availability; however, the entire island was covered independent of the number available. Seabird technicians attempted at least one island visit per year, each time recording the seals they encountered. These visits to the island did not always coincide with seals' breeding season. Counts of Cape fur seals recorded during regular seabird censuses were more accurate at low levels of abundance than when seals attained large densities. The sex of different animals was not always ascertained but bulls and females were sometimes distinguished and pups less than one year old were always separated from "other" seals. Pups were distinguished based on their size and the colour descriptions in Rand (1956). This provided information on the year when pups were first born at the island, following its recolonisation.

Since 1971, aerial surveys have been used to monitor the population of Cape fur seals across its entire breeding range. In 2003, these surveys were also introduced for the island as well. These surveys provide estimates of the pup production of Cape fur seals and have advantages over the traditional tag-recapture survey methods (Kirkman 2010). Firstly, they do not require capture of animals which minimises disturbance to breeding colonies; secondly, photographs provide a permanent and quantifiable record of the numbers and distribution of animals in the colony; thirdly, photographs reduce inter-observer variability (Erickson et al. 1993); and fourthly, improved photographic equipment and associated processing software technologies have increased the accuracy of counts by improving the ability to discriminate between objects on photographs.

Surveys focused on new-born pups as they provide a reliable proxy for population performance. They remain on the island during their first several months (8 to 11), whereas members of other age classes venture into the sea during daylight when surveys are conducted (Kirkman 2010). The small size of pups at birth and their charcoal black coat make this age group easily distinguishable on aerial photographs. Their numbers can be used in population growth models (e.g. Butterworth et al. 1995) and to model interactions with fisheries (Punt and Butterworth 1995).

Aerial photographic surveys were timed to coincide with the peak of the breeding season, between 16 and 20 December, a period when maximum numbers of pups are expected (David

1987; Shaughnessy 1987). Surveys were conducted interchangeably from a fixed wing aircraft (Pertenavia) or a helicopter (Jet Ranger). Near vertical, overlapping photographs were taken from the aircraft or helicopter, which flew parallel paths over the island at a height of c. 100 m. Photographs were later printed and laid out in frame sequence to form a mosaic of Vondeling Island. Boundaries between neighbouring, overlapping photographs were delineated on the photographs, using landmarks or seals shared by the photographs to prevent replicate counting. Technical details can be found in (Kirkman 2007).

2.2.3. Seabird and shorebird surveys

Attempts were made to visit Vondeling Island at least once each year to count numbers of seabirds breeding at the island. A total of 61 visits was undertaken to the colony, but due to difficulties with landing, the number of successful surveys conducted was 55. In the period 1990–2018, 10 seabird and one shorebird species bred at the island: African penguin *Spheniscus demersus*, great white pelican *Pelecanus onocrotalus*, Cape *Phalacrocorax capensis*, bank *P. neglectus*, white-breasted *P. lucidus* and crowned *Microcarbo coronatus* cormorants, kelp *Larus dominicanus* and Hartlaub's *Chroicocephalus hartlaubii* gulls, African oystercatcher *Haematopus moquini,* swift (greater crested) *Thalasseus bergii*, and Caspian *Sterna caspia* terns. From 1990–2018, Vondeling Island was visited 82 times, giving an average of three visits per year.

For each seabird species, numbers of active nests were counted on every visit to the island (Crawford et al. 1995). A nest was considered active if it contained fresh eggs or chicks, if it was defended by breeding adult bird(s) or if it showed recent signs of use, e.g. through the presence of substantial quantities of fresh guano or nesting material (Crawford et al. 2011). When unattended chicks were found in crèches away from nests, their number was divided by the approximate mean clutch or brood size of the species (one for great white pelican, two for bank cormorant, three for the other cormorants (Hockey et al. 2005), to estimate the number of nest sites they represented, because nests at which these chicks were reared would not have been counted. Remainders were taken to represent further sites. The maximum count of active nests recorded in any year was taken as an index of the breeding population at Vondeling Island of the seabird species concerned.

Counts of kelp gull nests were made from vantage points using binoculars after gulls had settled at nests, or by walking tightly spaced grids and marking nests (Crawford et al. 1982; Whittington et al. 2016). For Hartlaub's gulls, swift terns and Caspian terns' numbers of birds incubating eggs or with small chicks were counted with the aid of binoculars. Counts of chicks unattended by parents were divided by the mean clutch size; two for both gull species and one for swift terns (Hockey et al. 2005a) and added to those of breeding birds to estimate the number of pairs breeding.

On visits to Vondeling Island, the distributions of nests of pelicans, the four cormorant species, Hartlaub's gulls and the two terns were recorded on copies of a map of Vondeling Island. The original map was traced from an aerial photograph and indicated the locations of features such as houses, walls, the jetty, bays, promontories and prominent rocks, boulders and crevices (Fig. 2.2). This enabled distributions to be accurately mapped, except for large colonies of Cape cormorants. For seabirds that were mapped, their distributions in different years were aggregated to establish their overall use of the island for breeding. Numbers of African oystercatchers present at Vondeling Island were counted in all years between 1992 and 2018. The maximum count obtained in each year was taken as an index of the oystercatcher population at the island.

2.2.4. Statistical Analysis

Cape fur seal trends

Seal pups within each delineated boundary of each photograph were counted by two people, and the arithmetic mean of the counts was used. Counts were kept within 20% difference of each other. In the few instances where counts differed by more than 20%, additional counts were conducted until two counts were within 20% of each other. Typically, the means of counts (within 20% of each other) from all photographs of the island were added together to get the colony's total count for a year. In this study, computations were conducted in R Studio (R Core Team 2020) to calculate confidence limits on the estimated total number of pups from the results of the two counts. This was done for 2006-2018; breakdown of counts per area from 2003 were not found in archives. Each count per delineated boundary provided an independent estimate and their log mean was used to calculate standard deviations associated with the counts. To calculate the confidence intervals (CI), the counts (log) were resampled 1000 times (bootstrap) with a quantile range of 0.025 and 0.975. The resulting estimates were used for further analysis.

For years during which surveys were not conducted, a value was estimated using the mean of the count before and the count after:

Equation (1)

$$N_{y2} = (N_{y3} - N_{y1})/2 + N_{y1} = (N_{y3} + N_{y1})/2$$

Where y1 is the value of the year before, y2 is the year with missing value and y3 is the value of the year following the year of the missing value.

Combined trends analysis

Cape fur seal data were analysed using Analysis of Covariance (ANCOVA) test. The data were tested for normality (Dobson 2002) using the function *qqnorm* in package Stats and normalised using a square root transformation. The Vondeling Island Cape fur seal population growth rate and significance value (p-value) were calculated using function *lm* called from package *stats* in R. The rate was then contrasted with growth rates of other seals colonies in South African using a pairwise ANCOVA with logarithm of Counts and Year as explanatory variables. A further test of contrast was conducted using function *emtrends* called from package *emmean*s. While Vondeling Island was surveyed annually, other colonies are surveyed triennially. Therefore, this analysis was conducted utilising triennial survey data (1990–2018). The population trends of the African penguin and the three species of Cormorant (bank, Cape and crowned) were analysed against the growing population trends of the seals at the island.

Cape fur seal counts were conducted utilising two different method (land-based and aerial counts) (section 2.2.2). Initially, the numbers of seals at the island were small enough to count all age groups during surveys. This could be considered the population size. However, the introduction of aerial surveys of pups in 2003 meant these methods are incompatible to use in the same analysis. To estimate the seal population size, a pup: population ratio conversion factor was considered. This method provides a best alternative to estimating colony population size and the ratio was calculated for Cape fur seals as 1:5 (Wickens and Shelton 1992). In the absence of updated ratio for the species, this ratio was utilised to estimate the local population size. A Generalised Linear Model (GLM) was used to for the comparison using the function *glm* called from package *Stats.* Seal data containing land-based counts and aerial survey counts were combined and the periods stratified into three: No seals (N) -1990–1998; Land-based counts (LC) - 1998–2005; and Aerial surveys (AC): when aerial surveys were conducted (2006–2017); N was the intercept. An additional parameter named "Adjusted seals" was added, which included the total population estimate from land-based counts and estimated population size based on the population: pup ration conversion. Additionally, pelican presence data were included for testing. Thus, the response variables were: Year effect, Pelican presence effect, stratified period effect and Seal Presence/Absence effect (0 for absence and 1 for presence).

2.2.5. *Competition for space? Areas used by seals and seabirds at the island.*

A hand-drawn sketch of the island was traced from a 1961 aerial photograph in DFFE's archives. The sketch was further digitised into a map using Macromedia Freehand MX (Fig. 2.2). Final touches to the map and determination of scale were conducted in Adobe Photoshop (Version 22.2.0). For seabirds, areas utilised were marked for years 1999–2013. For seals, areas utilised were also marked during the same time for the years 1999–2013. However, from 2006 until 2018, distribution of seals at the island was plotted separately based on mosaics of photographs from photographic aerial surveys. Seabird distribution from hand drawn maps for years 2006–2013 were added to these distribution maps. Drawing of areas on the digital map was conducted using Adobe Photoshop (Version 22.2.0).

Whereas hand-drawn maps from land-based seabird surveys (1999–2005) did not allow for indication of where different densities of seals were observed; aerial photographs were used to determine areas of high and low densities. Areas at which seals were generally close together in large numbers were considered "High-density". Areas at which seals were loosely distributed in lower numbers were considered "Low-density". A planimeter was used to also measure these areas occupied by seals from these maps. Three building structures are still visible on aerial photographs; the longest of which was used to calculate the map scale. The length of this building was measured at 27.06 m and measured 5.5 mm on the map, yielding a scale ratio of 4920, so that 1 mm on the map yielded 4.92 m on the island. Squares of 22mm^2

were used to calculate total island area (excluding boulders at the periphery) and areas occupied by seals such that a square is 4.65 planimeter units (i.e., 4.65 units= 732,24m^2)

2.2.6. Predation

To determine whether Cape fur seals were feeding on seabirds at the island, searches were conducted for seabird carcasses with evidence of predation. Cape fur seals mainly target the soft abdominal tissues of a bird, perforating the peritoneum and tearing and stripping off the pelt (Marks et al. 1997). Observers therefore searched for carcasses and injuries consistent with seal predation. Opportunistic searches were conducted during seabird censuses and a dedicated search was undertaken along the 16 Mile beach (north of Yzerfontein, Western Cape) during August 2013. Any floating carcass originating from waters around the island is most likely to wash up on 16 Mile Beach, influenced by wave action. This is the mainland shoreline adjacent to Vondeling Island.

3. Results

3.1. Surveys

Cape fur seal counts

Land-based counts

Seals were first observed at Vondeling Island in March 1991 during a land-based seabird census, when 13 seals (Table 2.1) had hauled out on rocks at the north-eastern extremity of the island. No seals were encountered until in 1997 when four seals were seen at the same place. In February 1999, two bulls were spotted on the same rocks. In September of the same year, two bulls and two females (and one uncategorised individual) were observed. Since then, the number of seals (all age classes) occupying Vondeling Island were regularly recorded. Seal numbers increased from 13 to 8000 individuals between 1991 and 2009 (Table 2.1, Fig. 2.3). Pups were first observed in March 2004, when 10 were seen, indicating that the first recorded breeding/pupping took place during the 2003/04 breeding season. Between 2005 and 2009, counts ranged between 2500 and 8000 seals; as the colony expanded, it was difficult to get a good estimate (Huisamen et al. 2011). Land-based counts can be considered satisfactory up to 2004; subsequent counts should be considered to be a minimum population estimate.

Aerial survey counts

A total of 11 aerial photographic surveys were conducted between 2003 and 2018. Although the target was to conduct the surveys between 16 and 20 December, when the maximum numbers of pups are expected, this was not always logistically possible. Surveys were conducted between 12 and 23 December of each year (Table 2.2). There were 16 pups counted from the first aerial photographic survey of December 2003; 10 of these were visually confirmed during the land-based seabird census of March 2004. Since then, more than 100 pups were consistently produced (Table 2.3 & Fig. 2.3), which changed the island status from a haul-out to a breeding colony. Based on aerial survey counts, the annual growth rate of the colony was 38.5% until 2018 (Table 2.4).

Ten comprehensive aerial photographic surveys covering the entire breeding range of Cape fur seals were conducted between 1991 and 2017. Overall, there was a 4.35% ($p < 0.03$) increase in pup production at South African breeding colonies between 1991 and 2017. Vondeling Island recorded the largest growth rate (38.5%, $p < 0.003$) while Kleinsee recorded a decrease (–2.3% $p < 0.02$). Robberg Ledges, which was recolonised by seals between the late 1990s and early 2000s, recorded a rate of increase of 22.6%, $p < 0.13$. The two colonies at both extremities of the South African range, Buchu Twins (12.8%, $p < 0.11$) and Black Rocks (Algoa Bay) (17.3%, $p < 0.56$) recorded positive growth rates that were not statistically significant. Pairwise ANCOVA test revealed a statistically significant contrast in means of trends of all but one colony (Robberg Ledges). The biggest contrast with Vondeling Island was of Kleinsee at 9.8 % ($p< 0.0001$) (Table 2.5).

Seabird counts

Five of the 10 seabird species that bred at Vondeling Island between 1990 and 2018 were regular breeders there: African penguin, Cape, bank and crowned cormorants and kelp gull (Table 2.6). Additionally, African oystercatcher was regularly present and their counts at

Vondeling Island and Saldanha Bay islands are presented in Table 2.7. Cape cormorants were the most abundant seabirds during the study period (Table 2.6). An average of 2713 pairs were counted per year in the 29 years. By the end of the time series in 2018, only 0.06% (n=6) of the maximum breeding pairs counted during the study period were recorded (Table 2.8). Bank cormorants were the least abundant with an average of 24 breeding pairs counted during the study period (range: 1 – 65). No African oystercatchers were recorded at the colony after 2014; while no count of kelp gulls was available since 2015 (Table 2.6).

Hartlaub's gulls were only recorded breeding at the island in seven years: 1991, 1992, 1994, 1995, 1998, 2004, and 2014. Great white pelicans bred at Vondeling Island on two occasions during the period investigated: eight pairs in 2001 and nine pairs in 2005. Five pairs of white-breasted cormorant bred at the island in 1991, nine pairs in 1995 and three pairs in both 1996 and 1997; none were observed breeding in other years. Swift terns were only recorded breeding at the island in 1991 (80 pairs). One pair of Caspian terns was observed breeding at Vondeling Island in both 2006 and 2008. No breeding was observed in other years. These counts are presented in Table 2.9.

Results of GLM analysis indicated that for the Year effect, there was a statistically significant decline in trends of the three cormorant species (Table 2.10). African penguin trends declined by 2.4% per year, but this was not statistically significant ($p < 0.09$). There were no statistically significant changes for cormorants during the period of low seal abundance (1999 to 2005), however, there was a positive growth for African penguins (Table 2.11). For the period 2006 to 2008, there were statistically significant declines for cormorant species: bank (estimate -2.2; $p < 0.0000005$), Cape (estimate -2.4; $p < 0.0002$) and crowned (estimate -0.7; $p < 0.005$). Changes for African penguins were not statistically significant (estimate -0.1; $p < 0.5$). The presence of seals had no effect on the trends for African penguins and crowned cormorants but had a statistically significant effect on trends of the three cormorant species (Table 2.12). Adjusted seal numbers (total population) had no effect on trends of African penguins but had a significant effect on the three cormorant species (Table 2.11).

Bank cormorant declined at all localities with the exception of Stony Point (Table 2.13). Inter-colony contrast of mean of breeding trends indicates that, except for Malgas Island, trends were comparatively higher at other colonies than Vondeling Island (Table 2.14). Crowned cormorant trends declined at all but three breeding colonies (Dassen Island, Dyer Island and Lambert's Bay) (Table 2.15). There was a statistically significant positive contrast between trends at Vondeling Island and Lambert's Bay and Dassen Island (Table 2.16). Cape cormorant trends declined on all islands except Dyer Island, Robben Island and Seal Island (Algoa Bay) (Table 2.17). Statistically significant contrast was evident compared to trends at Dyer Island and Robben Island (Table 2.18). African penguins declined at all localities except at Boulders and Stony Point, with the highest rate of decline recorded at St Croix Island (Fig. 2.19). There was no statistically significant contrast in means of breeding pairs between penguins at Vondeling Island and other breeding localities except at St Croix Island (estimate -1.73, $p < 0.04$).

3.2. *Extent of areas utilised by seals and seabirds.*

An annotated map of Vondeling Island showing areas mentioned in this text is provided as Fig. 2.5. The distribution (i.e., areas utilised) of seals and seabirds determined from ground surveys for the years 1999–2005 are presented in Fig. 2.6A–I. The distribution of seals, determined from aerial photographs for the years 2006–2018 are presented in Fig. 2.7A–J. Mapping of the distribution of seabirds continued until 2013 and these were overlaid with the distribution of seals from aerial photographs of 2006–2013. Considering that seabirds breed at different times of the year, their distribution at the island was determined from all trips combined; this was also done for seals for the years 1999 to 2005 (land-based trips). To illustrate the impact of seals on the interior wall, the colour fill of the distribution shapes was reduced to 78% to allow for some transparency through which the wall outline (and other features) can be seen. An aerial image of Vondeling Island showing a correct orientation of the island and some of the features mentioned in this section is given in Fig. 2.2. For demonstration purposes and consistent with the orientation widely used, distribution maps were reorientated (Fig. 2.5, 2.6 & 2.7).

Cape fur seals

Seals initially occupied boulders on the north-east part of the island adjacent to a bank cormorant colony in 1991 (Fig. 2.6A). In 2002, the distribution of seals started overlapping with areas occupied by bank cormorants (Fig. 2.6F). Sixteen pups were born in the same area in 2013. The distribution had reached the interior walls by 2004 (Fig. 2.6H). By 2005, the areas covered by seals had extended inward of the island toward the storm walls built to keep water from reaching the interior wall (Fig. 2.6I).

Aerial photographs provided the true distribution of the colony during breeding seasons of 2006 to 2018 (Fig2.7A–J). This also assisted with calculating areas covered by seals at the colony; including the (degree of spatial property of being crowded together (i.e., density). The total area of the island was estimated at 19865 m^2. The area inside the wall was estimated at 5653 m^2. Details of annual distribution extent of seals during the breeding season are given in Table 2.21. Seals covered 29.2% of the island in 2006 covering the entire west and two-thirds of the east coasts of the island (Fig. 2.7A). High densities of seals were limited to coastal areas while a low density of seals (4% of the island) was limited to the south-western coast of the island. In 2008, high densities of seals covered the entire coast of the island, covering an area equivalent to 45% of the island's total surface area. Seals were then within the interior wall, albeit in low densities (Fig. 2.7B). At this stage, the integrity of the wall that was keeping them out of the interior was compromised enough for seals to break through.

In 2009, the number of seals within the interior wall remained small and occupied less area than in 2008. In the same year, the area occupied by seals had increased to 54.5% of the island's total surface area. Seals in lower densities were spread over a large area along the outside of the interior wall, including a cluster on the southern coast of the island. Seals evidently breached the wall in 2011; the areas inside of the interior wall were covered by seals, albeit in low densities. Between 2011 and 2018, seals were distributed throughout the island with a mix of low- and high-density areas. High densities of seals were consistently towards the outside areas of the colony towards the coast. Since 2011 when seals were distributed throughout the colony, the high densities covered more than 50% of the total island area except during the year 2012 (Table 2.21). The gradual degradation of the interior wall progressed until 2015 when the wall was effectively flattened (Fig. 2.7H). An aerial view of the section of the remainder of the wall is shown in Fig. 2.11.

Seabirds

The interior wall had had excluded seals from areas inside the wallwhich were mostly utilised by African penguins, bank cormorants and Cape gannets. The north-eastern area where seals first settled overlapped with the nesting area of bank cormorants. Distribution of African penguins was not always sketched during island visits, however, notes recorded by observers on data forms were used to infer distribution. For the three years that could be mapped, penguins preferred areas adjacent to the exterior of the interior wall (Fig. 2.7A & 2.6B, D). They were also recorded on the inside of the wall, associated with big boulders and rocks (Fig. 2.7A). Observer notes indicated that penguins were widely distributed inside the interior wall. Throughout the study period, penguins were observed nesting between boulders and in the open (Fig. 2.8).

Bank cormorant distribution was limited to the northern and north-eastern parts of the island. The areas are characterised by high boulders and man-made structures i.e., storm walls. Field notes from island visits indicate that bank cormorants have used the western stretch of the interior wall for breeding. Bank cormorants bred on these boulders for the entire study period, albeit at varying degrees. Cape cormorant distribution did not show any area preference by breeding birds. They were found in all areas of the island, including on houses and the interior wall and next to the old jetty (Fig. 2.6A–D and 11).

Crowned cormorants consistently bred on the old jetty and neighbouring boulders. In 2006, these birds bred in the north-west area of the island for the first time (Fig. 2.7A). Breeding was also recorded in the north-western, western, and southern areas of the island (Fig. 2.7B). In 2009, 2011 and 2012, small groups bred in the south (Fig. 2.7C, D, E). Great-white pelicans were recorded breeding at Vondeling Island for the first time in 2005. They nested in north-western areas inside the interior wall. Hartlaub's gull bred inconsistently at the island over the study period. They were mapped only twice, in 1991 inside the interior wall (Fig. 2.6A) and in 2006 outside the wall in the south-western areas of the island (Fig. 2.7A). African sacred ibis *Threskiornis aethiopicus* were consistently found on the roof of building structures (Fig 2.6 & 2.7). No birds were recorded for the years 1991 and 2012.

3.3. Evidence of predation

No seabird carcasses with evidence of seal predation were found. The only predation event by a Cape fur seal on a seabird involved a Cape cormorant in 1999. This event was observed and recorded during a visit to Vondeling Island for seabird censuses.

4. Discussion

4.1. Recolonisation

The dynamics of the recolonisation of Vondeling Island by Cape fur seals has taken place in the backdrop of a changing environment. Kirkman et al (2013) discussed expansion in the breeding range of Cape fur seals in the BCLME. In their paper, they discussed possible reasons for this expansion including space limitations, environmental perturbations and food shortages in the vicinity of potential source colonies. Most notably, directionality of expansion (i.e. northern expansion) corresponded with shifts in prey availability in the Northern BCLME. In the Southern BCLME, environmental changes led to a distributional shift and the collapse in the local abundance of prey resources off the west coast (van der Lingen et al. 2006; Blamey et al. 2012). These include anchovy and sardine which are targeted by Cape fur seals and Cape and crowned cormorants; and West Coast rock lobster *Jasus lalandii* which is targeted by bank cormorants (Wickens and Shelton 1992, Crawford 2007, Dyer et al. 2019).

The recolonisation of Vondeling Island is important to study because it has resulted in interactions with breeding seabirds, some of which are endangered. This island is in proximity to other Saldanha Bay islands some of which were historically seal colonies and which were harvested to extirpation by 1795 (Rand 1950; David and Van Sittert 2008). In contrast to other Saldanha Bay islands, which are situated inside the bay, Vondeling Island is situated outside. Seals are known to haul-out at other colonies during their foraging trips (Botha et al. 2020). Thus, the geographical position of Vondeling Island may have provided a convenient haul-out site for animals on their foraging trips. Seals have however consistently hauled-out on a rocky outcrop adjacent to Jutten Island. Between 52 and 850 individual seals have been reported at the site but little pupping has taken place (Seakamela et al. 2024). At Malgas Island, also within Saldanha Bay, seals were recorded preying on Cape gannet fledgelings in the surrounding waters and were subsequently culled (Makhado et al. 2006). Seals have since been observed attacking birds on the island itself and their landing is now being discouraged by humans (A. Makhado pers. comm.). These are almost exclusively sub-adult male seals (Makhado et al. 2009).

The first group of seals that were recorded hauling-out on Vondeling Island were mostly young bulls (B. Dyer pers. comm.). This age-sex class is known to disperse from their natal colony (Oosthuizen 1991), and has initiated a recolonisation process in Guadalupe fur seal (Elorriaga-Verplancken et al. 2020). The source colony for Vondeling Island seals is not obvious, neither is the initial dispersal trigger. Environmental changes that led to shifts in distribution of preferred prey remain plausible. According to Oosthuizen & David (1988), seals may disperse in response to prey availability, disturbance and overcrowding at the source colony. Similarly, Kirkman et al. (2013) proposed a hypothetical scenario for the formation of new colonies (Fig 2.8). In their scenario, dispersal to distant colonies is justified by improved feeding conditions in the proximity of the new locality. The transition to breeding colony will depend on births and recruitment.

Colonies north of Vondeling Island are protected in terms of law and/or by virtue of their location within private property (Seakamela et al. 2024). Disturbance is unlikely to have triggered the dispersal. During the study period, two additional colonies were formed between Kleinsee and Vondeling Island: Cape Donkin (31.913 S; 18.274 E) and Sammy's Bay (30.489 S; 17.363 E). Kleinsee is a mainland breeding colony stretching over 3 km of coastline (David & Wickens 2003). The extent of the colony has counter-intuitively remained stable in the presence of abundance of potential alternative breeding habitat. Although overcrowding seems implausible, the rest of the available space may not be ideal for pupping. Pup production trends have however declined at the rate of 2.3% per year during the study period. About 40,000 fewer pups were born in 2017 (36,876) than in 1990 (79,301). There were no records of mass abortions or mortality events at Kleinsee during the study period. The colony may have lost a significant quantity of breeding females to emigration/dispersal. There are six established breeding colonies (Strandfontein Point, Elephant Rock, Lambert's Bay, Paternoster Rocks, Cape Columbine, Jacob's Reef) and one haul-out colony (Elands Bay) between Kleinsee and Vondeling Island (Table 2.4). Of these, only Lambert's Bay had a statistically significant growth rate during the study period (11,30%, $p < 0.01$). However, only the maximum quantity of pups born in a breeding season at the colony was 738 pups in 2014. It is thus plausible that some females from Kleinsee may have dispersed and formed a breeding colony at Vondeling Island.

Cape fur seals give birth to an average litter of one (Wickens and York 1997), it is unlikely that the estimated population growth rate of 38.5% was a result of 16 females that first pupped at the island in 2003. Given the 1:1 cow-pup ratio, the estimated 1,253 pups born in 2006 translate to at least 1,253 actively breeding females at the island. Cape fur seals males and females sexually mature at about five and four years respectively (Wickens 1993; Oosthuizen and Miller 2000). The 2003 pup cohort would then only contribute to the local population growth from 2007/08. The observed population growth is therefore due to extrinsic factors, mainly immigration from other colonies such as Kleinsee. Vondeling Island is now South Africa's second largest breeding colony in terms of pup production. The maximum number of pups produced was 23,359 (2014), which remains the largest in the years up to 2018 (Table 2.3).

The recolonisation and establishment of new colonies in the Southern BCLME have corresponded with the directionality of the eastward shift in preferred prey abundance. Since Kirkman et al (2013), five Cape fur seal colonies have been established in southern Benguela (three North of the study site and two to the south) (Seakamela et al. 2024). Similarly, a distributional shift in breeding range of seabirds has been noted, such as the establishment of a new African penguin colony east of the Cape Agulhas (Crawford et al. 2008). The reported shifts in prey species distribution have resulted in a mismatch between the location of breeding colonies and food (Grémillet et al. 2008; 2015). Emigration or dispersal to establish new colonies or establish previously colonised colonies is one mechanism to correct the mismatch (Lewison et al. 2012).

4.2. Trends

Comparison of seal and seabird trends with their conspecifics at other breeding localities aids with a holistic perspective. Except for Elephant Rock, which is a small rocky island, there was a positive growth rate for Cape fur seal colonies located north of Vondeling Island but south of Kleinsee (Table 2.4). Lambert's Bay, Vondeling Island, Duikerklip, Roberg Ledges and Black Rocks are situated within protected areas and experienced double-digit growth rates. The colony localities are more suited for breeding because they experience little on-land human disturbance. Historically, coastal islands provided protection from land predators and humans. Mainland colonies were established on diamond mining properties, from which members of the public were totally excluded (Rand 1972b). The establishment of colonies south of the West Coast in areas of human footprint will restrict breeding site selection. Seals are already selecting sub-standard breeding habitat such as Grotto Bay and Cape Point. The former is low-lying, exposed to strong surf and the latter is on steep cliffs. This may increase pup mortality due to falls and being swept off the rocks (Stevens and Boness 2003).

Undisturbed or protected potential breeding sites have seen the establishment of breeding colonies of seabirds. Albeit recommendations against allowing seals to colonise these sites (du Toit et al. 2003), 2273 adults and 196 pups were counted from the 2022 aerial photographic survey at Dassen Island (33.432 S; 18.319 E). At Robben Island, seals have been reported since 2007 and sightings have since been regular (Underhill and Navarro 2023). Interspecies interactions resulting from such (re)colonisation by seals need better understanding. At the study site, trends of all four species of seabirds whose data were scrutinised declined over the study period. The largest decline was of Cape cormorant (Table 2.6 and 2.8) which had 0.06% (n=6) of the maximum number of breeding pairs (n=10,717) left at the end of the study period. The steepest decline was recorded during the period 2006–2018 (estimate –2.4%, p=0.0002) when seal abundance had increased (Table 2.11). Other west coast colonies (except Robben Island) also declined with most recorded at Schaapen Island (estimate=–0.85) and Jutten Island (estimate=–0.81), both in Saldanha Bay (Table 2.17). Poor performance of this species at west coast colonies is consistent with reported declines, largely driven by dispersal to southern parts of the west coast (e.g., Robben Island) and the south coast (e.g. Robberg, Stony Point) (Crawford et al. 2016). An outbreak of avian cholera *Pasteurella multocica* killed 3.8% of the Vondeling Island population in 1991 (Crawford et al. 1992). Their early age-at-breeding, larger clutch size and flexibility to move their breeding location (when required) allows them to recover more rapidly from population crashes (Hockey et al. 2005).

The African penguin had the smallest rate of decline (2%). The largest rate of decline of the species was recorded during the period of high seal abundance (2006–2018, estimate –0.1246). Breeding performance of penguins at Saldanha Bay colonies at which seals were absent also decreased during the study period. Although the study site population improved in the 2000s, the population markedly declined since 2010 (Crawford et al. 2011). However, between 2016 and 2018, there was a 26.1% increase in breeding pairs. This could be linked to 50 artificial nests that were installed at the colony in April 2016 (e.g. Fig. 2.9) (DFFE unpubl. data). These nests have proven successful in increasing reproductive output at Marcus Island, in Saldanha Bay (Kemper et al. 2007) and Robben Island (Sherley et al. 2012) in South Africa; and Halifax Island in Namibia (Wilson and Wilson 1989). Guano removal eliminated suitable breeding substrate (Frost et al. 1975). Open surface nests make penguins chicks and eggs vulnerable to gull predation (Pichegru 2013) and breeding failure due to heat stress (Seddon and Davis 1989). Although no gull predation events have been recorded at Vondeling Island, adults have been observed briefly leaving the nest to cool down by the author.

Of the three cormorant species that bred consistently at Vondeling Island, bank cormorant was the least abundant (max=65) (Table 2.6 & 2.8), with an average of 25 breeding pairs counted per year over the study period. The highest decline was also recorded during the 2006-2018 period when seals were abundant (Table 2.11). In the study region, the bank cormorant mainly relies on benthic fish and crustaceans (Rand, 1960) with the west coast rock lobster dominating preference (Dyer et al. 2019). An eastward shift in the distribution of West Coast rock lobster (Cockcroft et al. 2008), had an impact on bank cormorants (Botha 2014). Crowned cormorants feed on a variety of prey and are able to adjust their foraging and diet based on conditions around breeding sites (Crawford et al. 2012). Fidelity to breeding localities is low for this species (Crawford et al. 1994), thus breeding nomadism may have contributed to the declining trends at Vondeling Island.

Trends of kelp gulls remained fairly stable for the duration of the study, although no counts are available for the latter part of the study. Population trends at island colonies have decreased but offset by increases at mainland colonies (Whittington et al. 2016). Their ability to supplement their diet by targeting human croplands, dumpsites and fisheries discards (Steele 1992) makes the species resilient. African oystercatcher did not breed at the island.

They are known to roost where they do not breed (Hockey 1985) and can be assumed that these individuals are breeding at Saldanha Bay islands, a hotpots for the species (Underhill 2014). Their ideal performance within the bay is attributed to the abundance of the invasive *Mytilus galloprovincialis* which provided additional food source for the species (Loewenthal et al. 2015). Malgas Island continues to be an important site for the species (Table 2.20).

4.3. *Competition for space? Areas used by seals and seabirds on the island.*

The area inside the interior wall on Vondeling Island was important for the African penguin and the Cape cormorant (Fig. 2.6 & 2.8). Loss of guano as a suitable substrate forced penguins to build nests in the open or in crevices between the rocks and boulders (Fig. 2.10) (Shelton et al. 1984) which generally have high chick mortality (Seddon and van Heezik 1991). The area along the exterior of the wall was preferred by penguins which is closer to the water and cooler but is also a preferred environment for seals. Penguins nested amongst seals, especially on the eastern side of the island (Fig. 2.11). Seals tend to drag their bodies when they move and their repeated trips to sea would have caused disturbance to nesting penguins and could have led to displacement of penguins (Crawford et al. 1989), especially from the inside of the interior wall where most open-air nests were located. Destruction of nests and their contents was once recorded inside area of the interior wall (Bruce Dyer pers. comm.). Coastal access points used by penguins to venture to and from sea can potentially be blocked by seals, interfering with nest attendance patterns. The breakdown of the wall coincided with a decline in the number of breeding pairs of penguins from 361 in 2009 to 164 in 2010. The interior wall provided a much-needed barrier for the penguins. Seals therefore outcompeted penguins for breeding space.

Bank cormorants prefer a high vantage point near the sea on which to roost and breed, including man-made structures (du Toit et al. 2003). At Vondeling Island, bank cormorants used to roost and breed on high rocks at the northern eastern corner of the island. The area is located on the island's rocky shore exposed to wave action and storms; a typical nest habitat for bank cormorants (Sherley et al. 2012). Although some of the rocks are easy to climb for seals, no active displacement was recorded during the study. Cape cormorants were more widely distributed and more versatile than others. Elsewhere, they have been recorded breeding on cliffs, rocks, and man-made structures such as jetties, platforms, and moored fishing vessels/yachts (Brooke and Loutit 1984; Duffy and La Cock 1985). At Vondeling Island, active nests were found on houses, boulders, rocks, inside the houses and in the open on the inside of the interior wall. Although some areas were clearly encroached by seals (e.g. Fig. 2.12), no active displacement was recorded. But consistent with the African penguin, Cape cormorant breeding trends declined since seals breached the barrier around 2010/2011. This interior wall provided a buffer for this species as well. Seals thus outcompeted Cape cormorants for breeding space within the interior of the colony.

Similar to the Cape cormorants, crowned cormorants are known to breed on variety of habitats such as moored boats (Brooke & Loutit 1984), on ledges in caves (Bartlett et al. 2003), cliffs, jetties, trees, and shipwrecks (Kemper et al. 2007a). Utilisation of different areas during the study period is indicative of their ability to respond to encroaching seals. In 2017, 10 nests were built on artificial nesting platforms put up for flying birds at the colony (Fig. 2.13, DFFE unpubl. data). Due to their flexible utilisation of the colony, seals are unlikely to have impacted their population trends.

Other seabirds that were mapped whose distribution is considered less likely to be impacted by seals or not enough data is available to infer impact are: 1) African sacred ibis because they were only found on the rooftops of the three houses at the island (Fig. 2.6 & 2.7), 2) White-breasted cormorants which were associated with African sacred ibis and crowned cormorants on rooftops and the jetty, 3) Great white pelicans which utilised the inside and outside the south-western corner of the interior wall, 4) Swift terns which were mapped once in 1991 outside of the south-western corner of the interior wall and 5) Hartlaub's gulls which were mapped in 1991 inside the south-western corner of the interior wall; and in 2006 on the rocky shore in the south-western area of the island (Fig. 2.6A & 2.7A). Kelp gulls nesting areas overlapped with those of penguins in 2014; although penguins were not mapped but confirmed by observers that nests were observed in these areas. Gulls are known to grab chicks and eggs elsewhere (Pichegru 2013), however there is no evidence of this behaviour at Vondeling Island.

Seals have a poor physiological thermal stress regulation, and they use behavioural means such as frequenting the coastal zone to cool off (de Villiers & Roux, 1992), including lying on wet sand and swimming in the shallows. At Vondeling Island, houses (and now elevated nesting platforms) are the only available source of shade. Coastal areas are therefore cooler than the interior of the island. At daytime and especially during breeding and nursing periods, pups tend to form crèches along the coast for cooling. These areas are therefore prime spots at colonies. Penguins often moult along the coastline and their peak moulting season is in November (Randall et al. 1986); these preferred areas spatially coincide with preferred cool areas for seals and temporally with pupping season of seals. The preference of coastal areas by seals also influences different life stages of penguins. A high density of seals at these sites may interfere with nest attendance patterns (Crawford et al. 1989). Similarly, this hotspot area is utilised by African oyster catchers for feeding on intertidal mussels (Randall et al. 1986).

Conclusion

The recolonisation of Vondeling Island by Cape fur seals and the subsequent rapid increase is due to immigration. Vondeling Island provided an alternative habitat for the Cape fur seal in the southern part of the west coast population range. The other possible available islands to colonise are Robben Island and Dassen Island. At Robben Island, recolonisation has been hampered chiefly by human activity. There have been *ad hoc* deliberate disturbance attempts on Robben Island to discourage seals from settling (Bruce Dyer pers. comm.). Dassen Island had a seal disturbance programme that was interrupted by Covid-19 pandemic in 2020; by 2023 more than 1,000 seals had settled on the island and pupping had been recorded (Seakamela et al. 2024).

The declines that were recorded for various species of seabirds are consistent with other declines on the West Coast. Food shortages can be considered the main driving factor behind the declines. However, for African penguin and Cape cormorants, encroachment by seals seem to have exacerbated the food problem. There was no evidence of large-scale seal predation problem at Vondeling Island. However, seal predation on seabirds continues to be a problem at adjacent colonies within Saldanha Bay. Unravelling a problem arising from the occurrence and expansion of seals in an ecosystem under stress is not simple. Measures should be put in place to ensure a clear demarcation of breeding habitat for African penguin and Cape cormorants. This may include re-erecting the interior wall to block seals from accessing the area and adding more artificial nests within the new wall.

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Figures, Tables and Illustrations

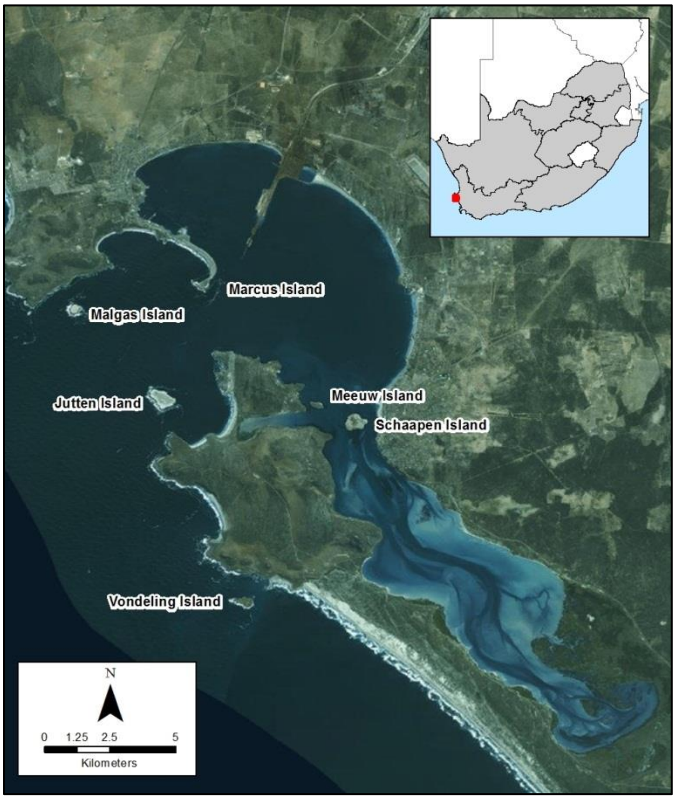


Figure 2.1. Map of Saldana Bay group of islands showing Vondeling, Malgas, Marcus, Jutten, Meeuw and Schaapen islands on the west coast of South Africa.

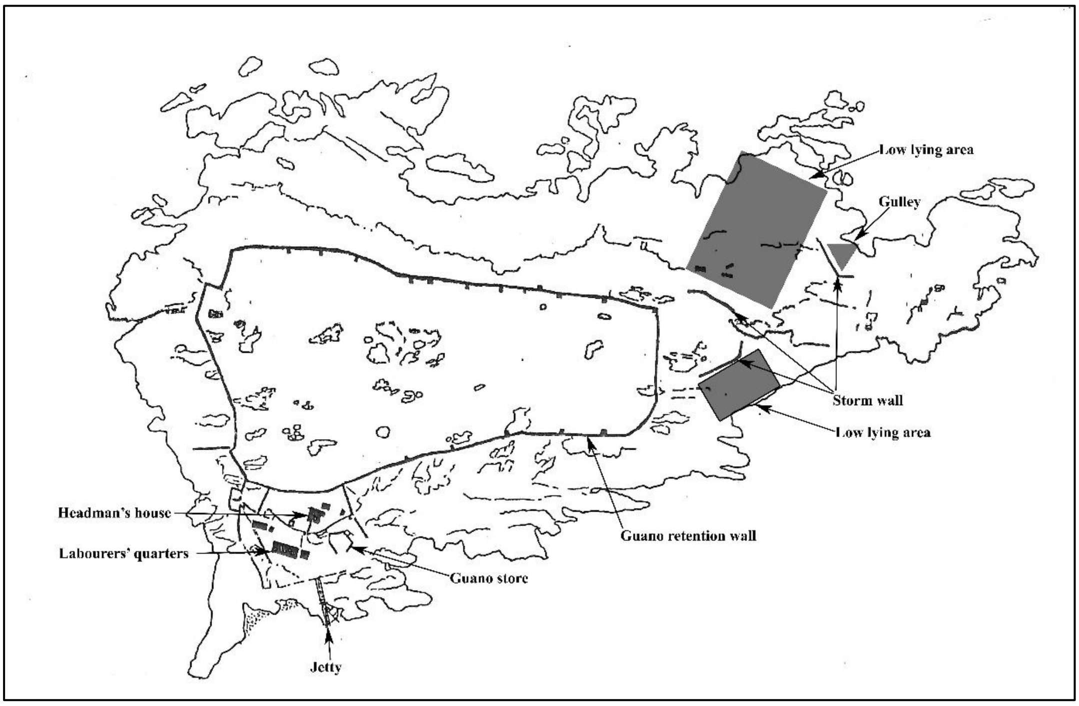


Figure 2.2. A reoriented annotated map of Vondeling Island showing some key features mentioned in text.

Table 2.1. Results of land-based counts of Cape fur seals at Vondeling Island during seabird surveys.

Date	Trip Number	Seals-Pups	Seals-Other
11/3/1991	1	0	13
21/3/1997	1	0	4
29/09/1999	2	0	5
28/11/2000	4	0	57
18/04/2001	3	0	50
19/02/2002	1	0	100
21/2/2003	1	0	1500
7/3/2004	1	10	3000
16/2/2005	1	0	2500
12/2/2006	1	0	4000
19/5/2006	2	500	3000
13/6/2007	2	0	6000
5/11/2008	2	0	5000
12/2/2009	1	0	8000

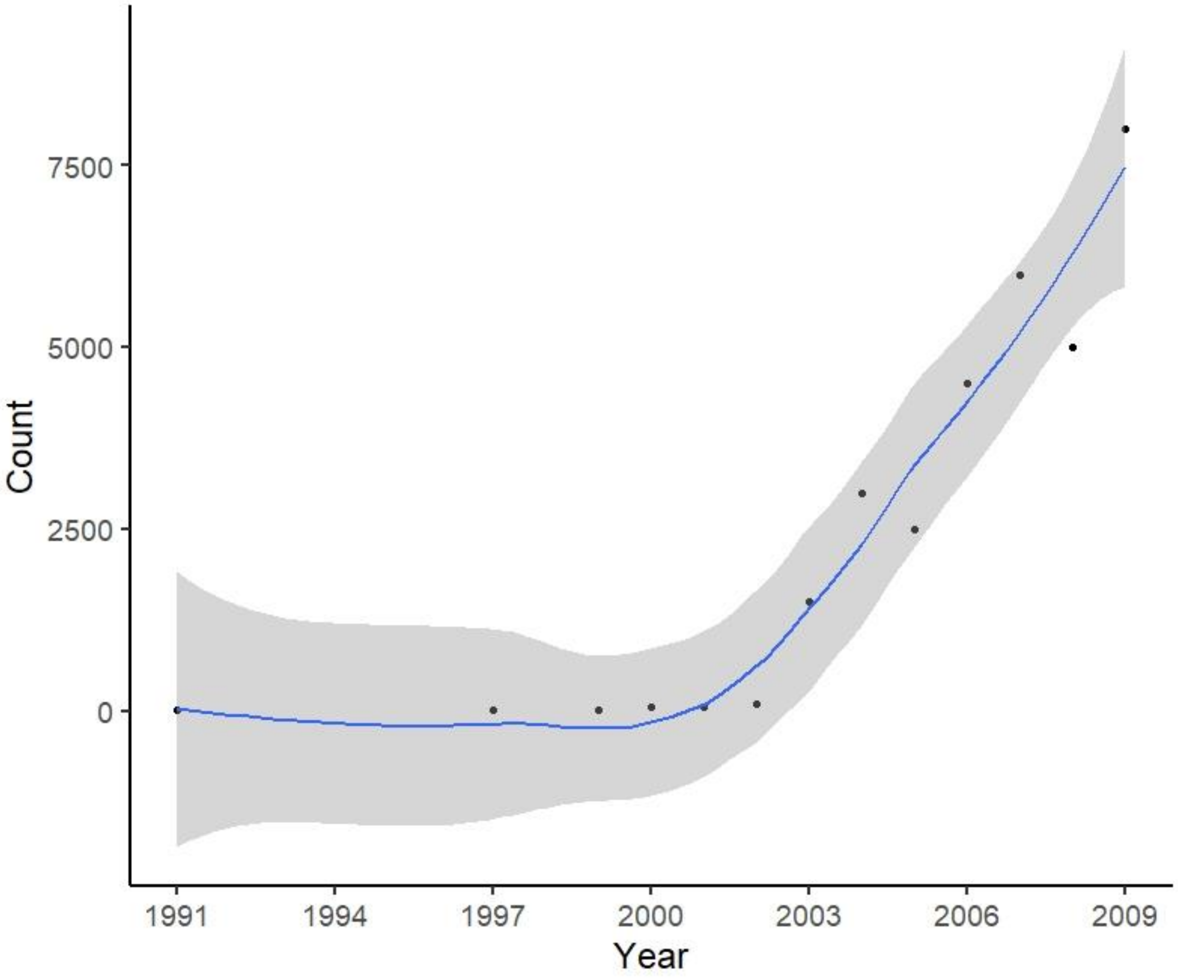


Figure 2.3. Estimated number of seals at Vondeling Island from land-based counts. Blue line is a trend line (smoothed) and grey shades the associated standard errors.

Table 2.2. Aerial photographic surveys of Cape fur seals conducted at Vondeling Island (2003-2018)

Date	Count
20-Dec-03	16
12-Dec-06	1253
23-Dec-08	8939
17-Dec-09	10959
20-Dec-11	16111
17-Dec-12	17699
18-Dec-13	18176
21-Dec-14	23359
17-Dec-15	17988
14-Dec-17	21578
14-Dec-18	16737

Table 2.3. Model output of Cape fur seal pups estimates with associated confidence intervals.

Year	Observed	y	Lower CI	Upper CI
2006	1253	1263	1202	1312
2008	8939	8946	8788	9129
2009	10959	10958	10800	11168
2010	15233	15922	15736	16177
2011	16111	16116	15886	16376
2012	17699	17984	17716	18309
2013	18176	18175	18007	18389
2014	23359	22714	21844	22336
2015	17988	17691	17538	17901
2017	21578	21579	21311	21865
2018	16737	16731	16558	16929

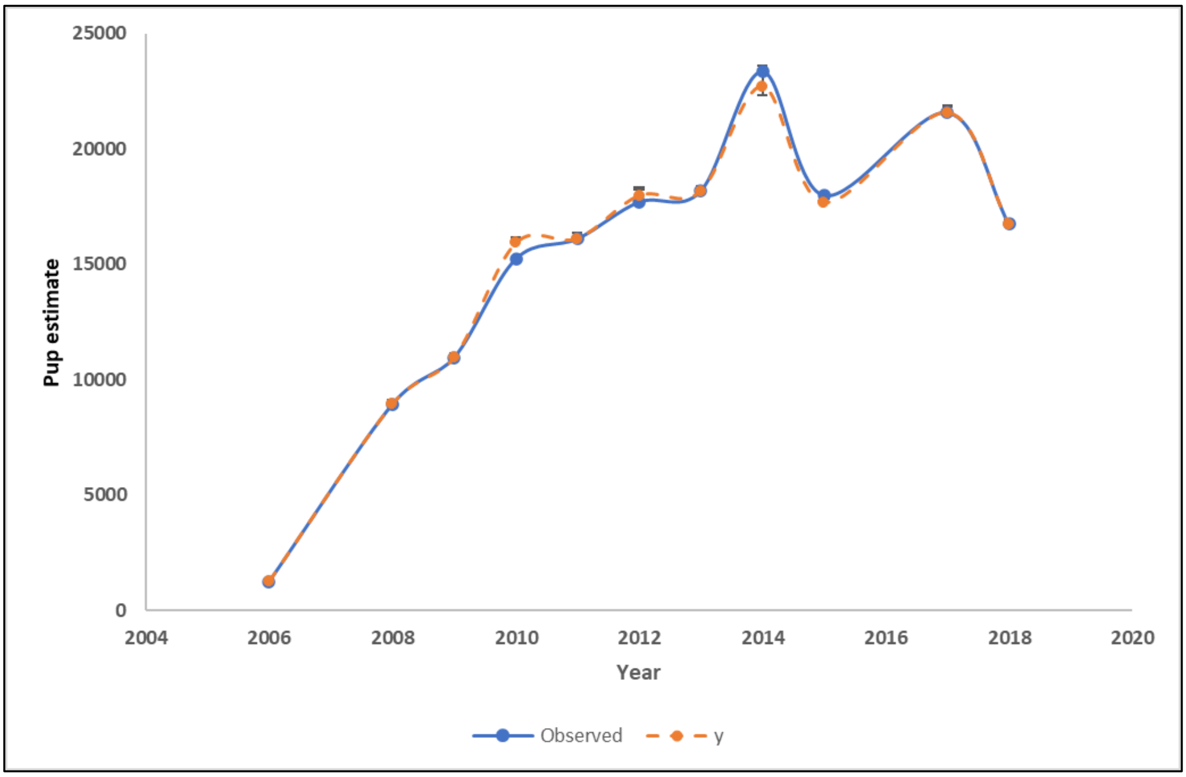


Figure 2.4. Estimates of number of seal pups at Vondeling Island obtained from aerial photographs. Blue line represents conventional pup production estimates. Orange dashed line represent modelled estimate.

Table 2.4. Average annual changes in pup production at Cape fur seal breeding localities in South Africa. Colonies are listed from northern most to the eastern most within their breeding range.

Colony	Zone	Colony Type	% Growth rate	P value
Buchu Twins	North	Mainland	12,83	0.11
Cliff Point	North	Mainland	-2,13	0.33
Kleinsee	North	Mainland	-2,34	0.02
Elephant Rock	North	Island	-0,19	0.89
Lambert's Bay	North	Mainland	11,30	0.01
Paternoster Rocks	North	Island	3,67	0.12
Cape Columbine	North	Island	4,634	0.08
Jacobs Reef	North	Island	0,39	0.98
Vondeling Island	**Study Site**	**Island**	**38,46**	**0.003**
Robbesteen	South	Island	1,95	0.20
Duikerklip (Hout Bay)	South	Island	18,28	0.0003
Seal Island (False Bay)	South	Island	-1,17	0.03
Geyser Rock	South	Island	-0,63	0.62
Quoin Rock	South	Island	1,21	0.25
Seal Island (Mossel Bay)	ECA	Island	1,787	0.21
Robberg Ledges (Plettenberg Bay)	ECA	Mainland	22,60	0.13
Black Rocks (Algoa Bay)	ECA	Island	17,32	0.56

Table 2.5. Contrast in annual rates of increase between Cape fur seals at Vondeling Island and other breeding colonies in South Africa.

	Estimate	SE	df	t.ratio	p.value
Buchu Twins - Vondeling Island	-5.2694	0.870	109	-6.055	<0.0001
Cliff Point - Vondeling Island	-7.9883	1.222	109	-6.535	<0.0001
Kleinsee - Vondeling Island	-9.7628	0.757	109	-12.902	<0.0001
Elephant Rock - Vondeling Island	-7.0147	0.789	109	-8.890	<0.0001
Lambert's Bay - Vondeling Island	-6.1525	0.822	109	-7.487	<0.0001
Paternoster Rocks - Vondeling Island	-6.0632	0.757	109	-8.013	<0.0001
Cape Columbine - Vondeling Island	-6.7187	0.760	109	-8.839	<0.0001
Jacobs Reef - Vondeling Island	-6.9798	0.757	109	-9.224	<0.0001
Robbesteen - Vondeling Island	-6.6225	0.760	109	-8.719	<0.0001
Duikerklip (Hout Bay) - Vondeling Island	-5.9324	0.772	109	-7.684	<0.0001
Seal Island (False Bay) - Vondeling Island	-7.6815	0.757	109	-10.151	<0.0001
Geyser Rock - Vondeling Island	-7.2887	0.757	109	- 9.629	<0.0001

Quoin Rock - Vondeling Island	-7.2072	0.757	109	-9.524	<0.0001
Seal Island (Mossel Bay) - Vondeling Island	-6.6795	0.757	109	-8.827	<0.0001
Robberg Ledges (Plettenberg Bay) - Vondeling Island	-4.1961	3.112	109	-1.348	0.9951
Black Rocks (Algoa Bay) - Vondeling Island	-6.7829	0.757	109	-8.964	<.0001

Table 2.6. Numbers of birds (counts of breeding pairs) recorded at Vondeling Island, 1990 to 2018. n/c denotes "No Count".

Year	African oystercatcher	African penguin	Bank cormorant	Cape cormorant	Crowned cormorant	Kelp gull
1990	0	n/c	25	1038	40	143
1991	0	229	57	4116	31	n/c
1992	4	133	42	6140	72	n/c
1993	60	141	33	8428	32	188
1994	84	169	65	10717	64	237
1995	0	205	40	2295	72	n/c
1996	0	258	44	3994	43	356
1997	0	361	31	4159	33	276
1998	63	157	20	2525	38	270
1999	90	333	24	3427	45	n/c
2000	101	528	36	945	66	363
2001	89	649	27	5018	40	114
2002	63	544	42	2126	34	377
2003	58	622	17	6314	57	366
2004	47	612	24	1486	35	219
2005	50	564	20	3182	83	259
2006	32	396	17	1449	47	234
2007	41	345	14	2005	59	163
2008	35	507	19	1670	44	225
2009	29	361	5	5017	39	178
2010	13	164	6	273	5	131
2011	23	158	3	1177	9	69
2012	25	175	3	350	6	n/c
2013	7	150	1	103	24	61
2014	12	116	5	228	11	61
2015	0	123	4	200	0	n/c
2016	0	82	0	172	24	n/c
2017	0	101	0	124	42	n/c
2018	0	111	0	6	20	n/c

Table 2.7. Counts of African oystercatcher at Saldanha Bay islands. The last column represents the sum of all 5 colonies within the bay. Vondeling Island counts are of individuals present.

Year	Vondeling Island	Jutten	Marcus	Malgas	Meeuw	Schaapen	Saldanha Bay
1990	0	0	3	60	0	0	63
1991	0	100	42	10	0	25	177
1992	4	0	0	7	0	0	7
1993	60	20	2	20	0	0	42
1994	84	192	0	60	1	20	273
1995	0	182	1	60	22	17	282
1996	0	239	0	135	2	34	410
1997	2	209	51	140	2	34	436
1998	63	200	61	119	17	30	427
1999	90	174	66	120	19	50	429
2000	101	162	66	232	23	22	505
2001	89	233	67	161	36	55	552
2002	63	149	71	138	19	36	413
2003	58	225	42	214	27	27	535
2004	47	279	29	137	15	37	497
2005	50	114	74	162	43	37	430
2006	32	117	78	224	23	37	479
2007	41	119	71	163	32	34	419
2008	35	119	40	345	19	25	548
2009	29	103	57	186	22	6	374
2010	13	132	66	140	20	25	383
2011	23	190	76	126	17	24	433
2012	25	141	76	118	24	25	384
2013	25	151	59	141	7	16	374
2014	12	87	20	181	11	24	323
2015	6	163	43	115	8	12	341
2016	9	139	20	159	28	29	375
2017	12	167	40	133	16	35	391
2018	18	130	0	142	12	13	297

Table 2.8. Summary of time series data (1990 to 2018) of 5 regular breeding seabird species at Vondeling Island.

	African black oystercatcher	African penguin	Bank cormorant	Cape cormorant	Crowned cormorant	Kelp gull
Average	46,3	296	24	2713	38	214
Min	4	82	1	6	0	61
Max	101	649	65	10717	83	377

% of max at 2018	11,9	17,1	6,2	0,06	24,1	16,2

Table 2.9. Counts of species that bred inconsistently at Vondeling Island during the study period.

Year	Great white pelican	White-breasted cormorant	Hartlaub's gull	Swift tern	Caspian tern
1990		3			
1991		5	350	80	
1992			4		
1993					
1994			58		
1995		9	17		
1996		3			
1997		3			
1998			21		
1999					
2000					
2001	8				
2002					
2003					
2004					
2005	9				
2006					1
2007					
2008					
2009					
2010					
2011					
2012					
2013					
2014					
2015					
2016					
2017					
2018					

Table 2.10. Results of glm analysis of endangered seabird trends at Vondeling Island with Year as a response variable.

Coefficients:					
		Estimate	Std. Error	t value	Pr(>|t|)
Cape Cormorant	Intercept	312.99076	48.34780	6.474	0.000000613
	Year	-0.15263	0.02413	-6.327	0.000000899
Crowned Cormorant	Intercept	84.13623	24.82550	3.389	0.00217
	Year	-0.04025	0.01239	-3.249	0.00309
Bank Cormorant	Intercept	268.32591	26.13489	10.27	0.0000000000804
	Year	-0.13260	0.01304	-10.17	0.0000000000993
African penguin	Intercept	54.01640	27.19728	1.986	0.06
	Year	-0.02421	0.01357	-1.784	0.09

Table 2.11. Results of glm analysis of seabird trends at Vondeling Island with Stratified periods as a response variable.

Coefficients:					
		Estimate	Std. Error	t value	Pr (>|t|)
Cape Cormorant	Intercept (N)	8.2786	0.4286	19.315	< 0.0000000000000002
	Period AS (2006-2018)	-2.3953	0.5576	-4.29	0.000215
	Period LC (1998-2005)	-0.3796	0.6480	-0.586	0.563073
Crowned Cormorant	Intercept	3.7079	0.1719	21.575	< 0.0000000000000002
	Period A (2006-2018)	-0.6734	0.2236	-3.012	0.00571
	Period C (1999-2005)	0.2711	0.2598	1.043	0.30643
Bank Cormorant	Intercept	3.6474	0.2531	14.413	0.0000000000000653
	Period A (2006-2018)	-2.1705	0.3292	-6.593	0.0000005422920151
	Period C (1999-2005)	-0.3147	0.3826	-0.823	0.418
African penguin	Intercept	5.3228	0.1525	34.910	< 0.0000000000000002

	Period A (2006-2018)	-0.1246	0.1983	-0.628	0.535497
	Period C (1999-2005)	0.9681	0.2305	4.200	0.000277

Table 2.12. Results of glm analysis of seabird trends at Vondeling Island with Presence/Absence of seals as a response variable.

		Estimate	Std. Error	t value	Pr(>|t|)
Cape Cormorants	Intercept	8.27	0.50	16.46	0.00000000000000133
	Presence (1)	-1.68	0.60	-2.79	0.00955
Crowned Cormorants	Intercept	3.70	0.21	17.45	0.000000000000000313
	Presence (1)	-0.34	0.25	-1.34	0.191
Bank Cormorants	Intercept	3.64	0.35	10.26	0.0000000000801
	Presence (1)	-1.52	0.42	-3.55	0.00141
African penguin	Intercept	5.322	0.21	25.16	<0.0000000000000002
	Presence (1)	0.25	0.25	1.01	0.32

Table 2.13. Annual growth trends of bank cormorants at their breeding localities.

Colony	Year.trend	SE	df	lower.CL	upper.CL
Dassen Island	-0.003	0.031	207	-0.103	0.096
Dyer Island	-0.15	0.031	207	-0.254	-0.055
Jutten Island	-0.22	0.031	207	-0.322	-0.123
Lambert's Bay	-0.13	0.031	207	-0.234	-0.035
Malgas Island	-0.30	0.031	207	-0.404	-0.205
Robben Island	-0.08	0.031	207	-0.177	0.022
Stony Point	0.22	0.046	207	0.071	0.371
Vondeling Island	-0.25	0.031	207	-0.346	-0.146

Table 2.14. Contrast of trends between bank cormorants breeding at Vondeling Island and other colonies

Contrast	Estimate	SE	df	t.ratio	p.value
Dassen Island - Dyer Island	0.1516	0.0436	207	3.481	0.0139
Dassen Island - Vondeling	0.2428	0.0436	207	5.574	<.0001

Dyer Island - Vondeling	0.0912	0.0436	207	2.093	0.4227
Jutten Island - Vondeling	0.0233	0.0436	207	0.534	0.9995
Lambert's Bay - Vondeling	0.1110	0.0436	207	2.548	0.1815
Malgas Island - Vondeling	-0.0586	0.0436	207	-1.345	0.8805
Robben Island - Vondeling	0.1682	0.0436	207	3.863	0.0037
Stony Point - Vondeling	0.4668	0.0556	207	8.390	<.0001

Table 2.15. Annual growth trends of crowned cormorants at their breeding localities.

Colony	**Year.trend**	**SE**	**df**	**lower.CL**	**upper.CL**
Dassen Island	0.33	0.06	242	0.12	0.54
Dyer Island	0.07	0.06	242	-0.15	0.27
Jutten Island	-0.08	0.06	242	-0.29	0.13
Lambert's Bay	0.18	0.06	242	-0.03	0.39
Malgas Island	-0.08	0.06	242	-0.29	0.14
Meeuw Island	-0.16	0.06	242	-0.37	0.07
Robben Island	-0.28	0.06	242	-0.49	-0.07
Schaapen Island	-0.17	0.07	242	-0.40	0.05
Vondeling Island	-0.10	0.06	242	-0.32	0.11

Table 2.16. Contrast of trends between crowned cormorants breeding at Vondeling Island and other colonies

contrast	**Estimate**	**SE**	**df**	**t.ratio**	**p.value**
Dassen Island - Vondeling Island	0.43150	0.0908	242	4.752	0.0001
Dyer Island - Vondeling Island	0.16310	0.0908	242	1.796	0.6849
Jutten Island - Vondeling Island	0.02184	0.0908	242	0.241	1.0000
Lambert's Bay - Vondeling Island	0.28537	0.0908	242	3.142	0.0483
Malgas Island - Vondeling Island	0.02755	0.0908	242	0.303	1.0000
Meeuw Island - Vondeling Island	-0.05147	0.0908	242	-0.567	0.9997
Robben Island - Vondeling Island	-0.17801	0.0908	242	-1.960	0.5726
Schaapen Island - Vondeling Island	-0.06820	0.0933	242	-0.731	0.9983

Table 2.17. Annual growth trends of Cape cormorants at their breeding localities.

Colony	**Year.trend**	**SE**	**df**	**lower.CL**	**upper.CL**
Dassen Island	-2.38	0.51	247	-4.08	-0.68
Dyer Island	1.33	0.51	247	-0.37	3.03
Jutten Island	-0.81	0.51	247	-2.51	0.89
Lambert's Bay	-1.61	0.51	247	-3.31	0.09
Malgas Island	-0.44	0.51	247	-2.14	1.26
Meeuw Island	-0.65	0.67	247	-2.89	1.59
Robben Island	1.74	0.51	247	0.03	3.45

Schaapen Island	-0.85	0.63	247	-2.98	1.28
Seal Is. Algoa Bay	0.29	0.70	247	-2.06	2.65
Vondeling Island	-2.34	0.51	247	-4.04	-0.64

Table 2.18. Contrast of trends between Cape cormorants breeding at Vondeling Island and other localities.

Contrast	**Estimate**	**SE**	**df**	**t.ratio**	**p.value**
Dassen Island - Vondeling Island	-0.0352	0.716	247	-0.049	1.0000
Dyer Island - Vondeling Island	3.6718	0.716	247	5.125	<.0001
Jutten Island - Vondeling Island	1.5350	0.716	247	2.143	0.4994
Lambert's Bay - Vondeling Island	0.7281	0.716	247	1.016	0.9911
Malgas Island - Vondeling Island	1.8992	0.716	247	2.651	0.2001
Meeuw Island - Vondeling Island	1.6926	0.839	247	2.018	0.5870
Robben Island - Vondeling Island	4.0797	0.718	247	5.683	<.0001
Schaapen Island - Vondeling Island	1.4890	0.812	247	1.833	0.7134
Seal Is. AB - Vondeling Island	2.6338	0.865	247	3.044	0.0762

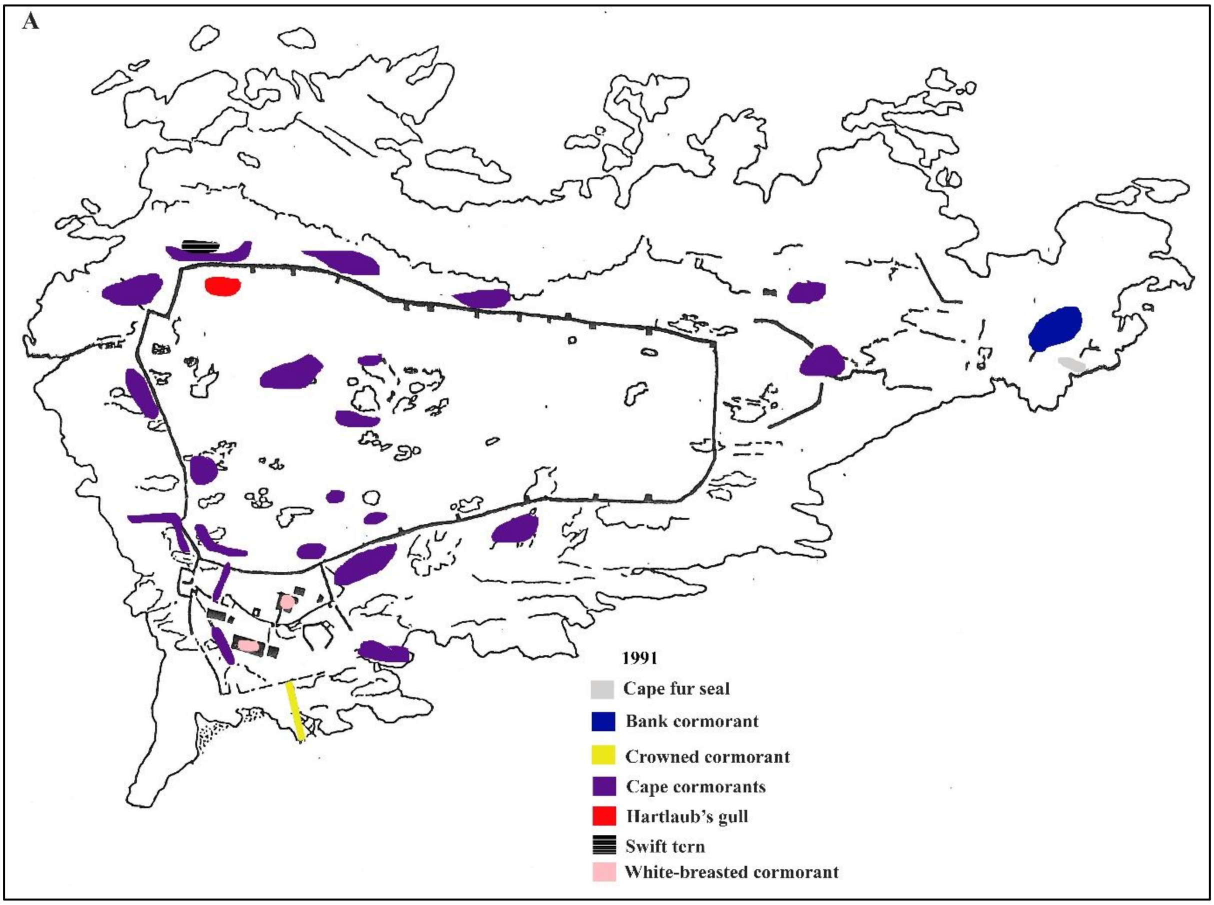
Table 2.19. Annual growth trends of African penguins at their breeding localities.

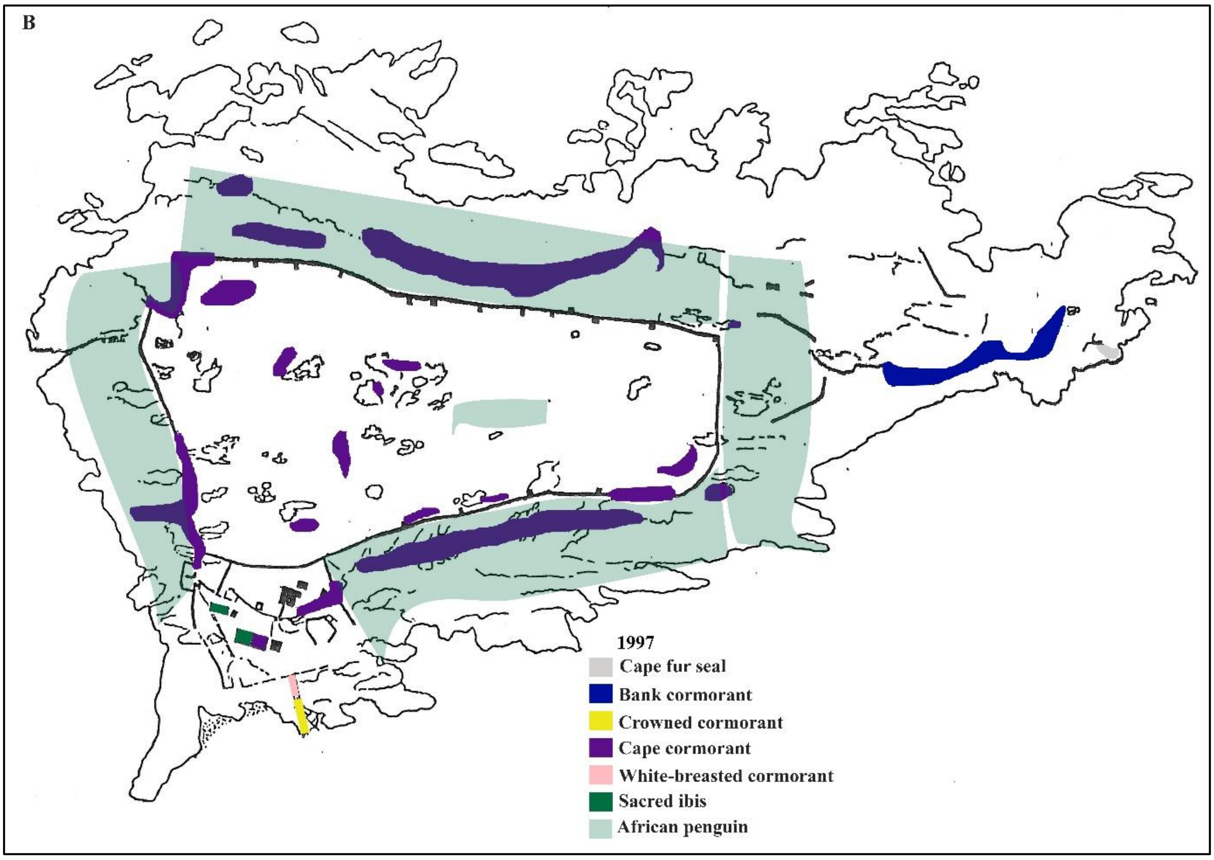
Colony	**Year.trend**	**SE**	**df**	**lower.CL**	**upper.CL**
Bird Is. Algoa Bay	-0.31	0.27	343	-1.30	0.68
Boulders	0.57	0.26	343	-0.36	1.51
Brenton	-0.14	0.39	343	-1.54	1.27
Dassen Island	-2.59	0.27	343	-3.58	-1.61
Dyer Island	-1.60	0.26	343	-2.53	-0.67
Jahleel	-0.36	0.39	343	-1.75	1.03
Jutten Island	-0.84	0.28	343	-1.82	0.14
Malgas Island	-0.22	0.26	343	-1.16	0.71
Marcus Island	-0.45	0.30	343	-1.53	0.63
Robben Island	-0.53	0.26	343	-1.46	0.40
Seal Island-Algoa Bay	-0.36	0.32	343	-1.51	0.78
St Croix	-1.90	0.38	343	-3.26	-0.53
Stag Island	-0.18	0.32	343	-1.33	0.96
Stony Point	1.56	0.28	343	0.56	2.56
Vondeling Island	-0.17	0.28	343	-1.16	0.81

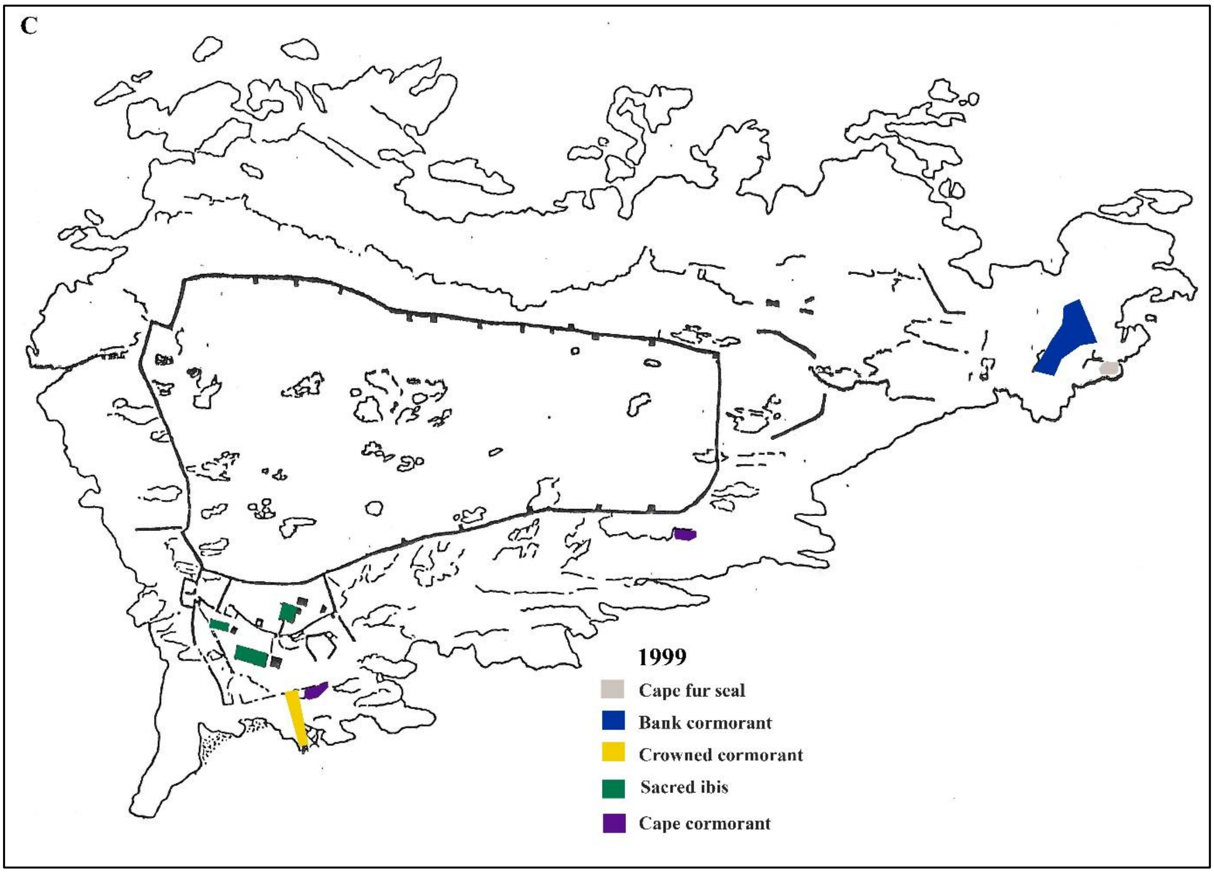
Table 2.20. Contrast of trends between African penguins breeding at Vondeling Island and other localities.

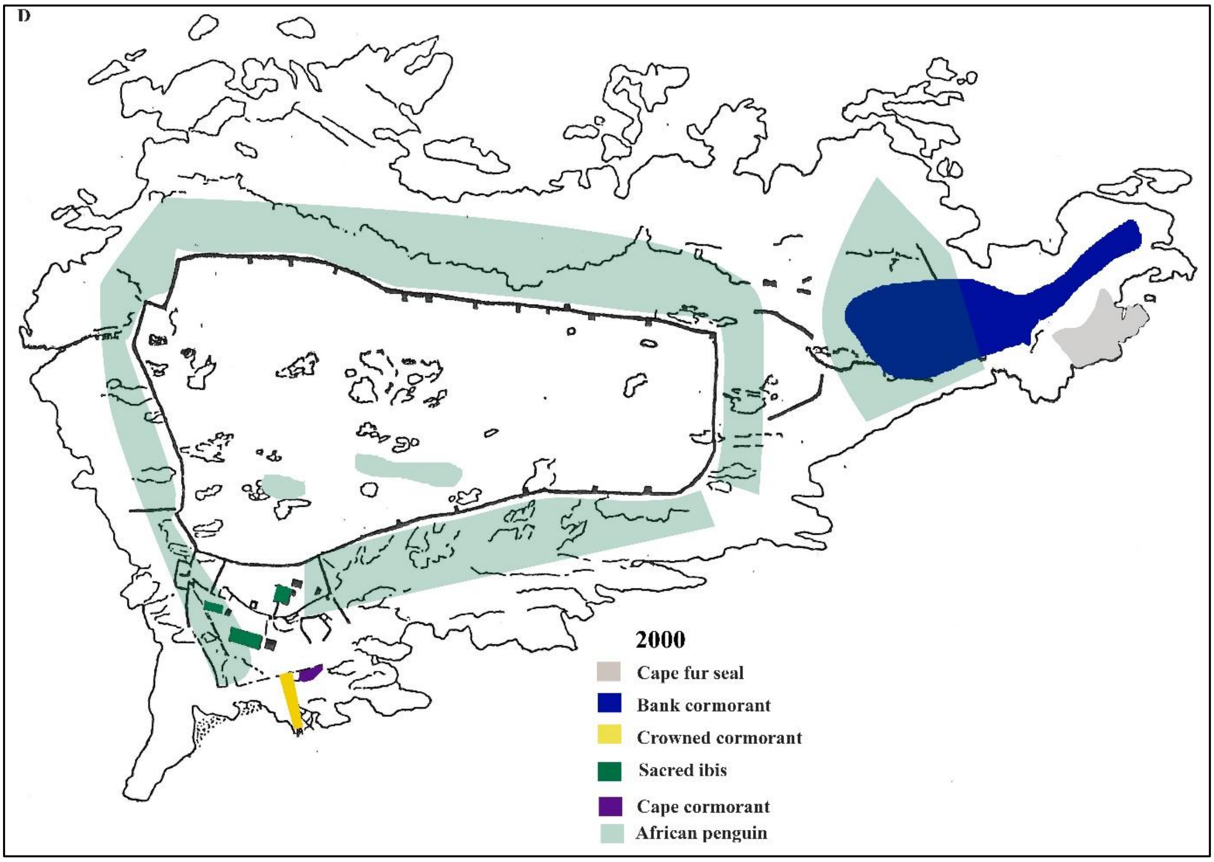
Contrast	**Estimate**	**SE**	**df**	**t.ratio**	**p.value**
Bird Is. AB - Vondeling Island	-0.14	0.39	343	-1.54	1.26

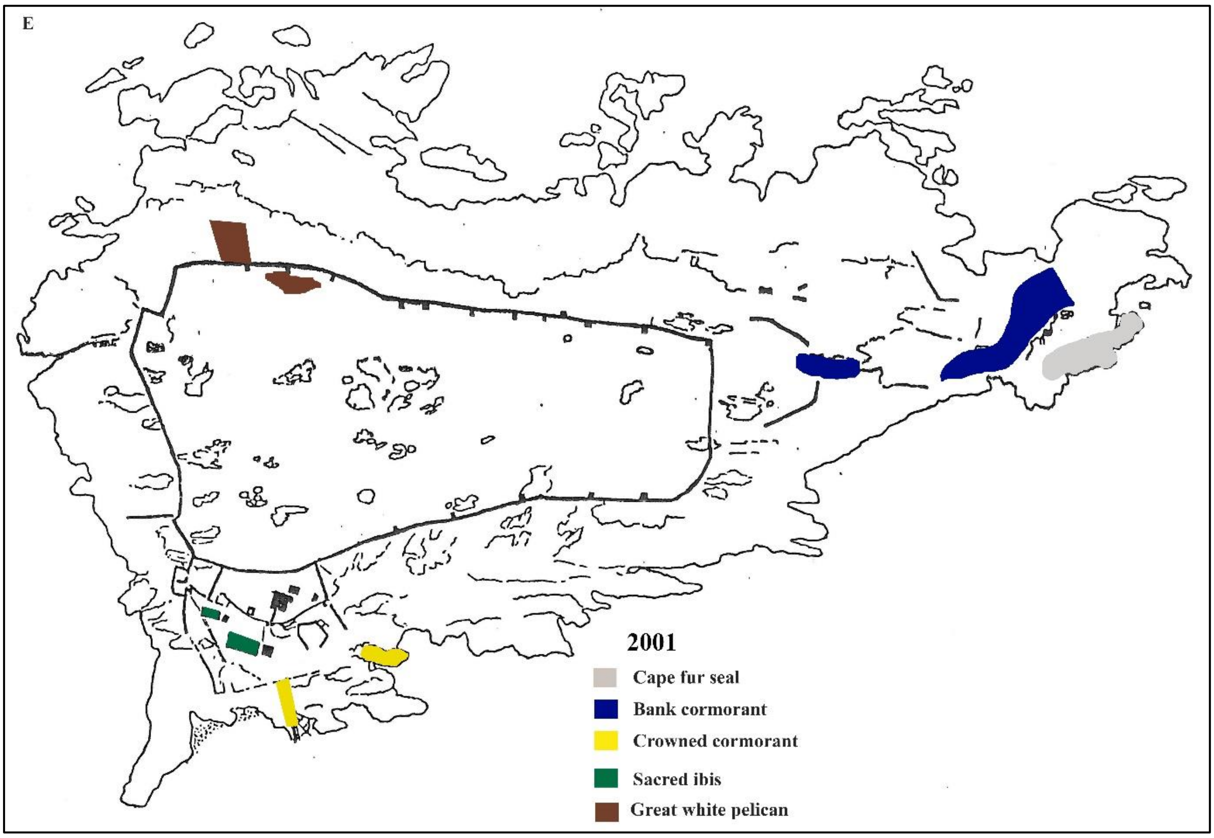
Boulders - Vondeling Island	0.75	0.38	343	-0.61	2.11
Brenton - Vondeling Island	0.04	0.48	343	-1.68	1.76
Dassen Island - Vondeling Island	-2.42	0.39	343	-3.81	-1.03
Dyer Island - Vondeling Island	-1.43	0.38	343	-2.78	-0.07
Jahleel - Vondeling Island	-0.19	0.48	343	-1.89	1.52
Jutten Island - Vondeling Island	-0.66	0.39	343	-2.06	0.73
Malgas Island - Vondeling Island	-0.05	0.38	343	-1.41	1.31
Marcus Island - Vondeling Island	-0.28	0.41	343	-1.74	1.19
Robben Island - Vondeling Island	-0.36	0.38	343	-1.72	1.00
Seal Island-AB - Vondeling Island	-0.19	0.42	343	-1.71	1.32
St Croix - Vondeling Island	-1.73	0.47	343	-3.41	-0.04
Stag Island - Vondeling Island	-0.01	0.424	343	-1.52	1.50
Stony Point - Vondeling Island	1.73	0.39	343	0.33	3.14

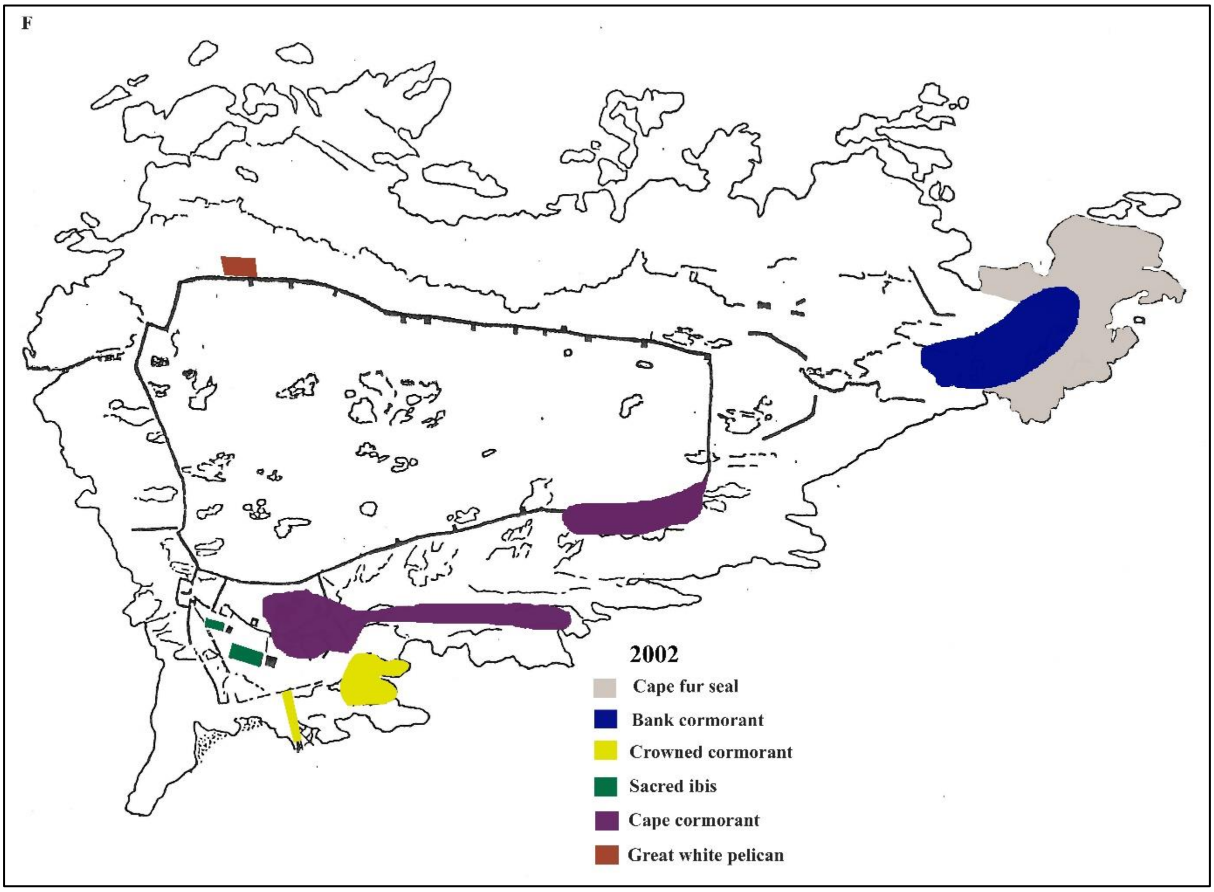


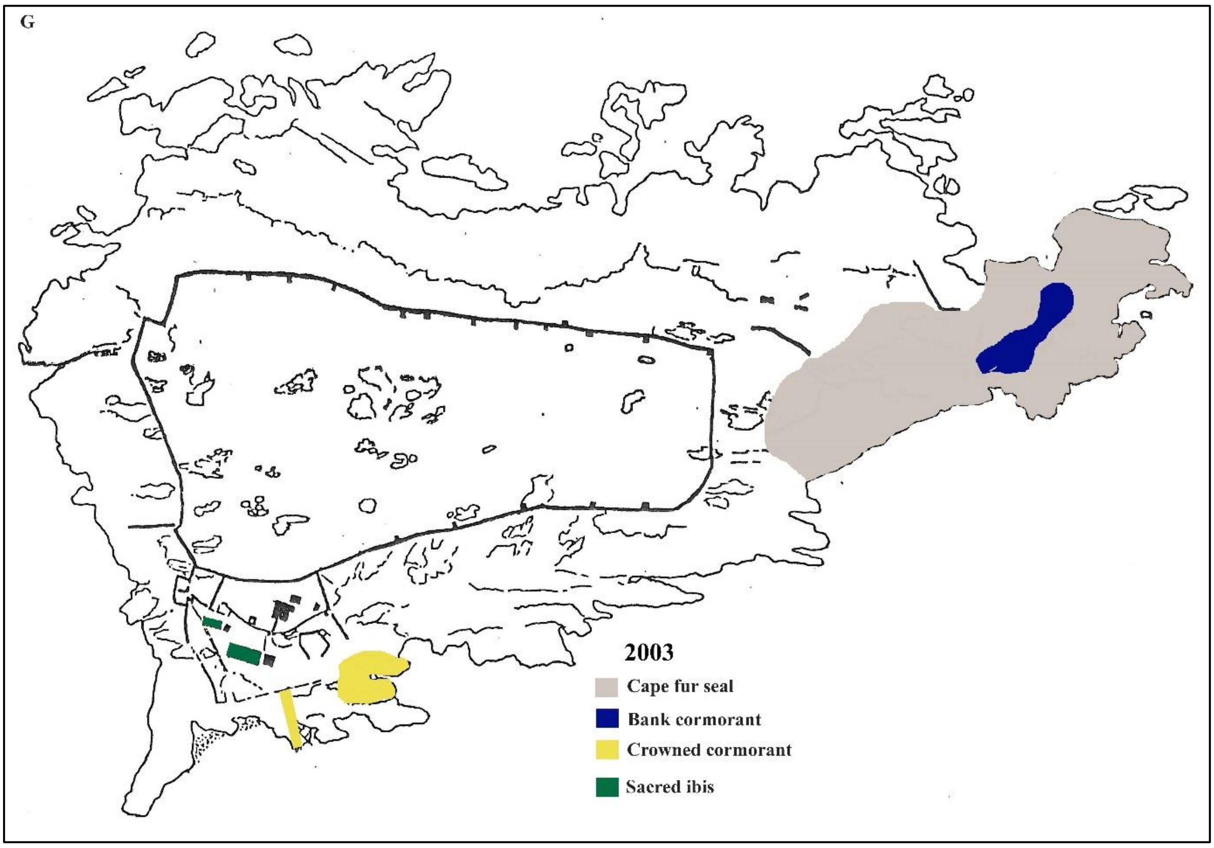

B
1997
Cape fur seal
Bank cormorant
Crowned cormorant
Cape cormorant
White-breasted cormorant
Sacred ibis
African penguin


C
1999
Cape fur seal
Bank cormorant
Crowned cormorant
Sacred ibis
Cape cormorant


D
2000
Cape fur seal
Bank cormorant
Crowned cormorant
Sacred ibis
Cape cormorant
African penguin


E
2001
Cape fur seal
Bank cormorant
Crowned cormorant
Sacred ibis
Great white pelican


F
2002
Cape fur seal
Bank cormorant
Crowned cormorant
Sacred ibis
Cape cormorant
Great white pelican


G
2003
Cape fur seal
Bank cormorant
Crowned cormorant
Sacred ibis

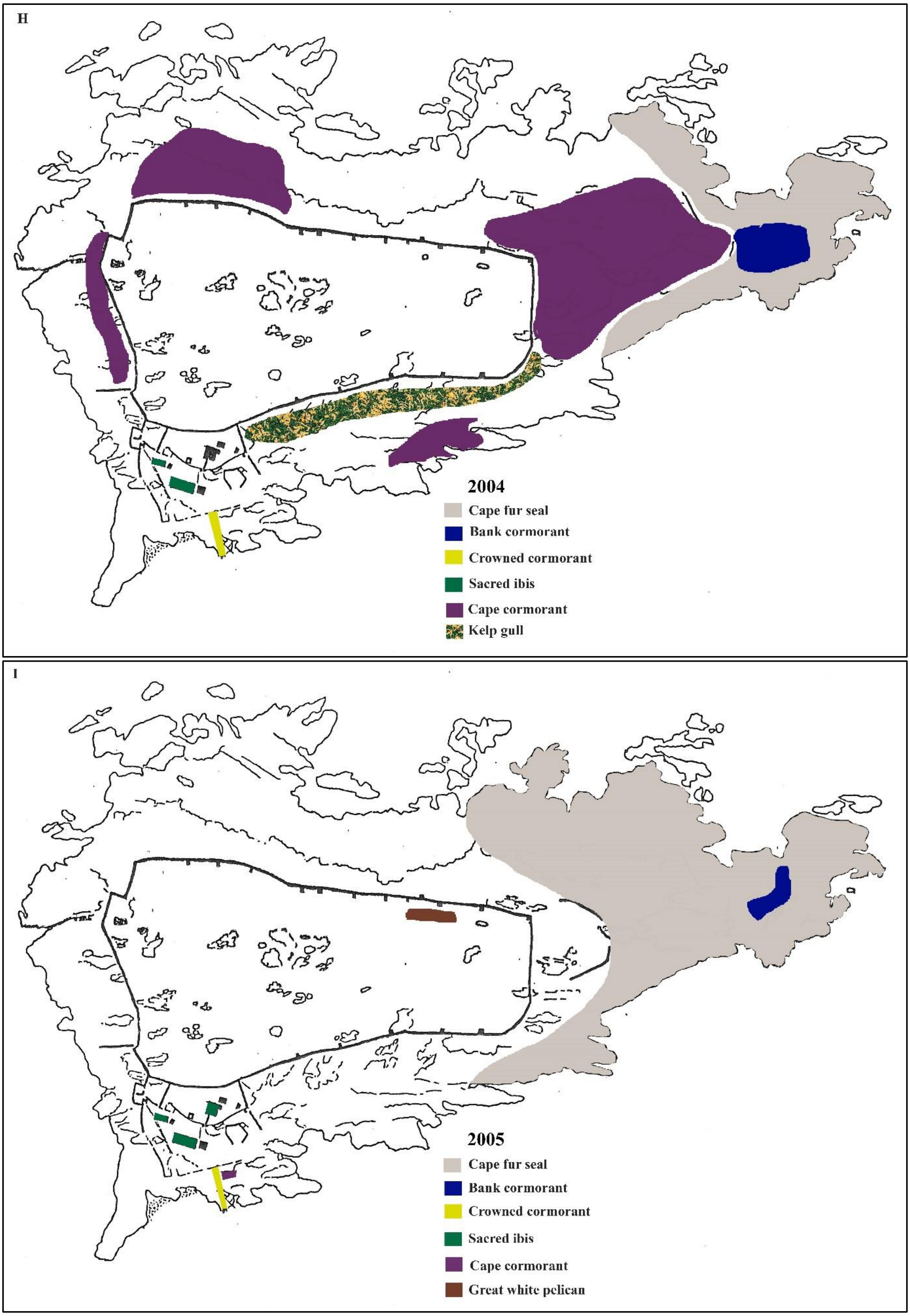
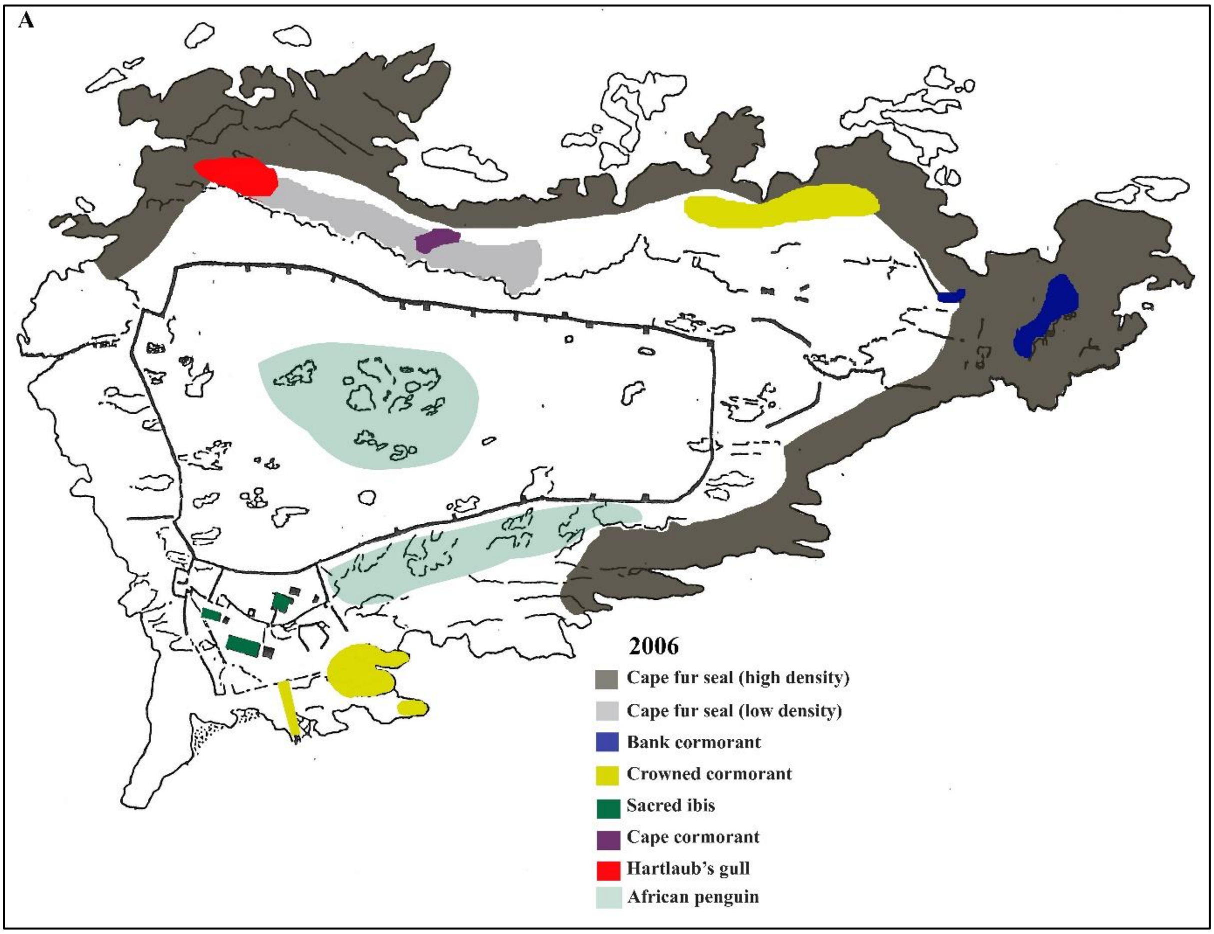
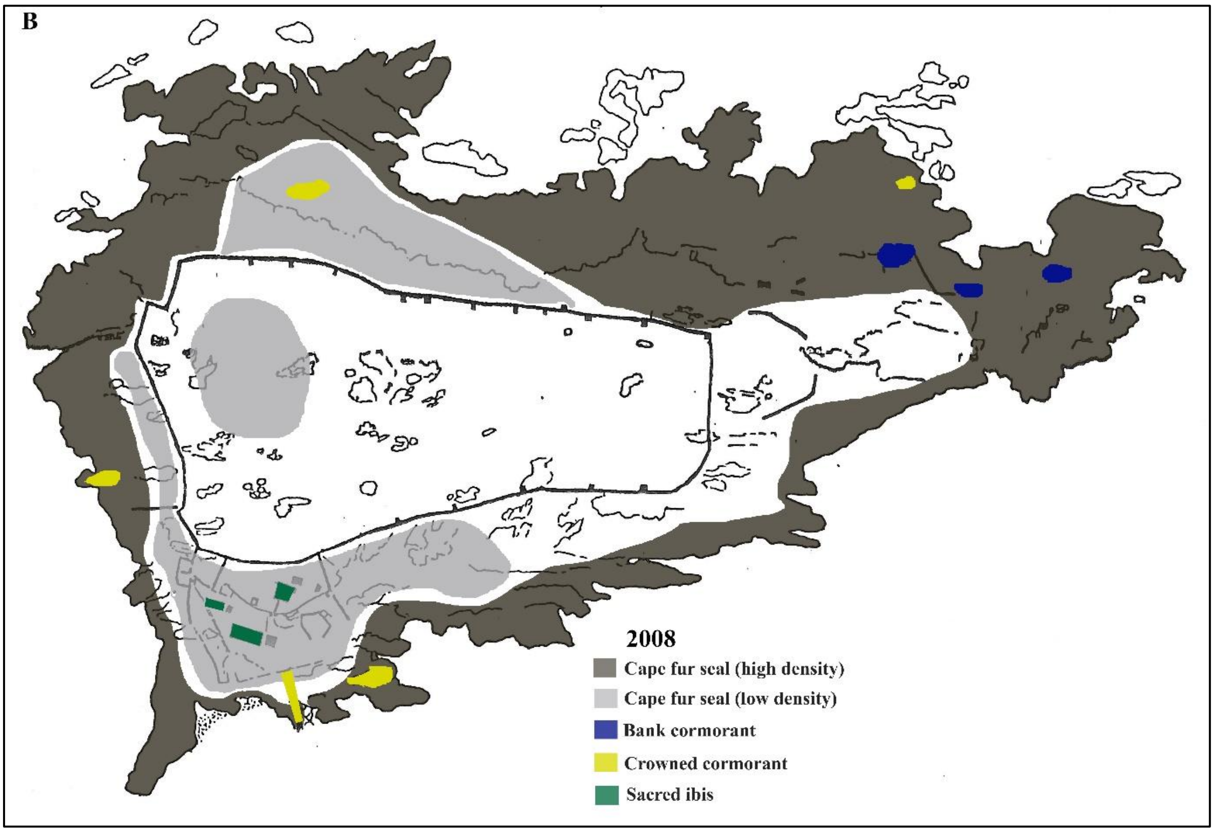
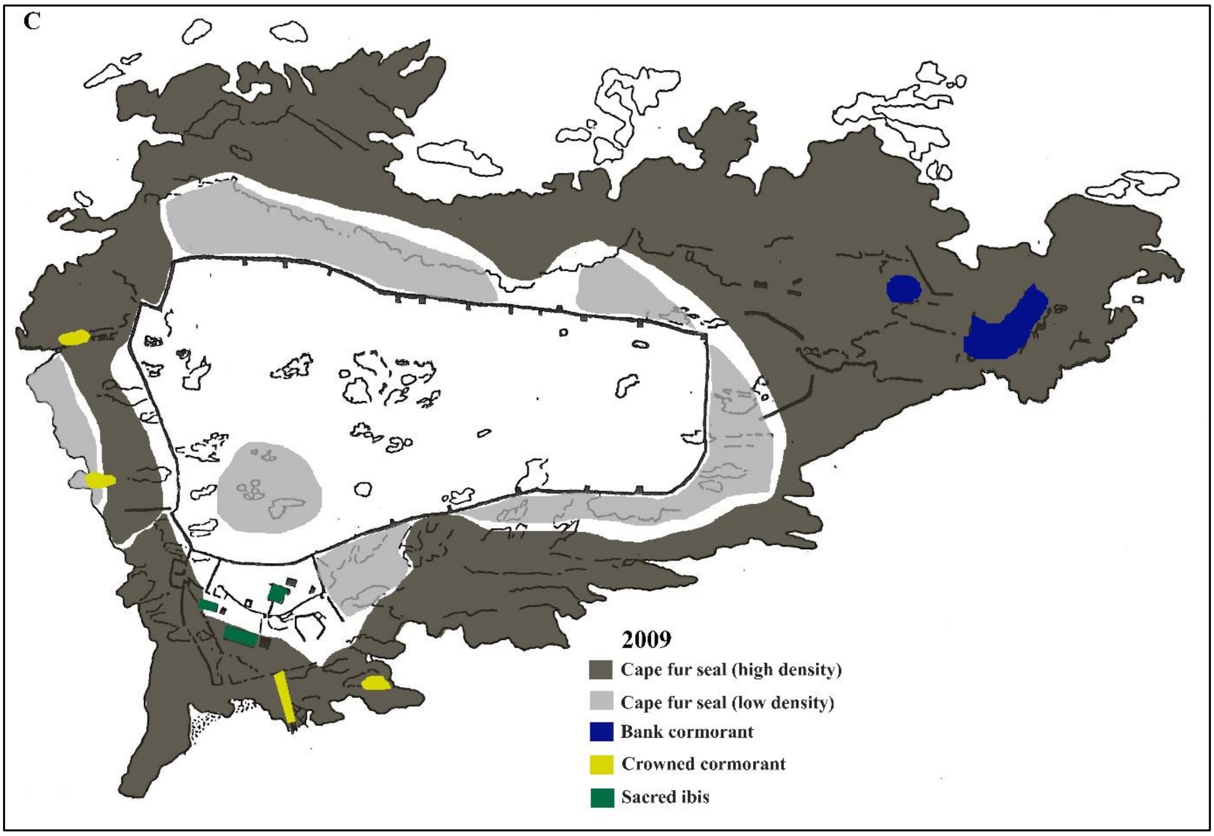
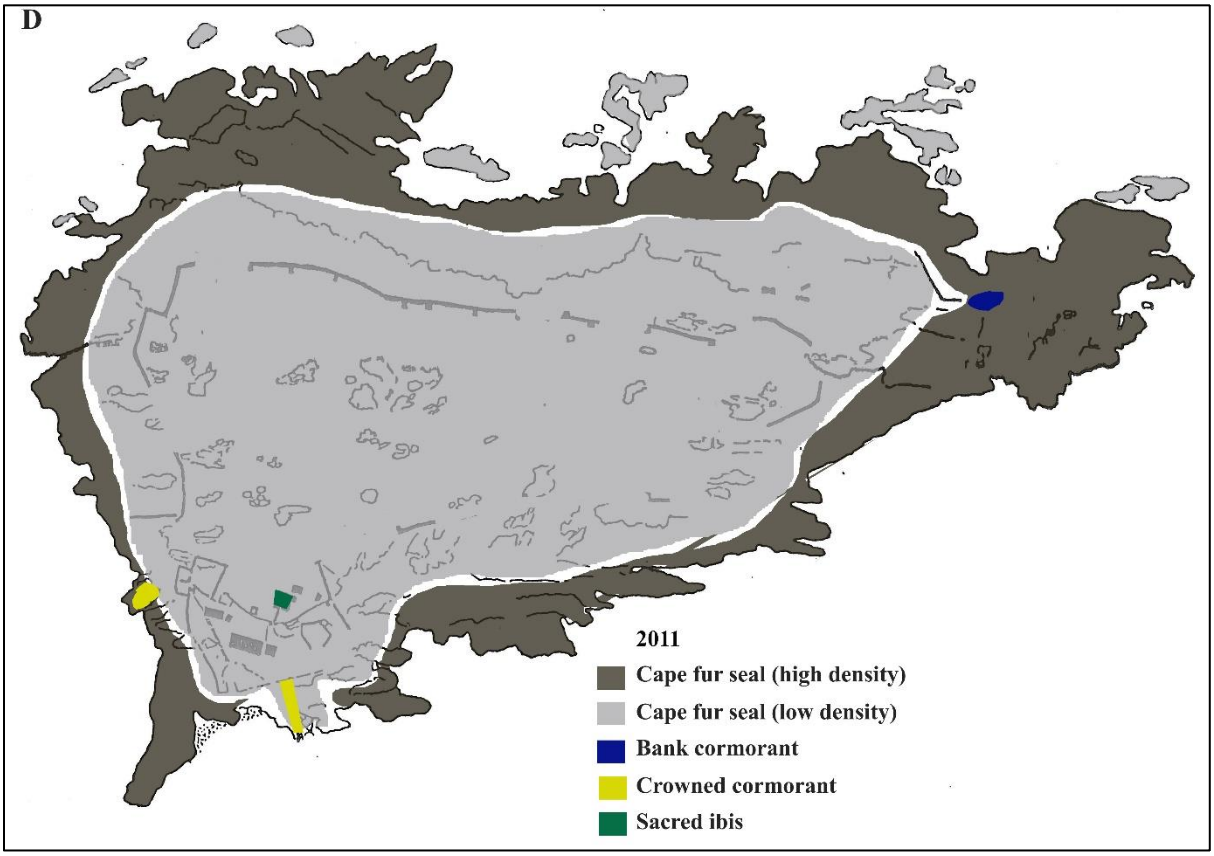


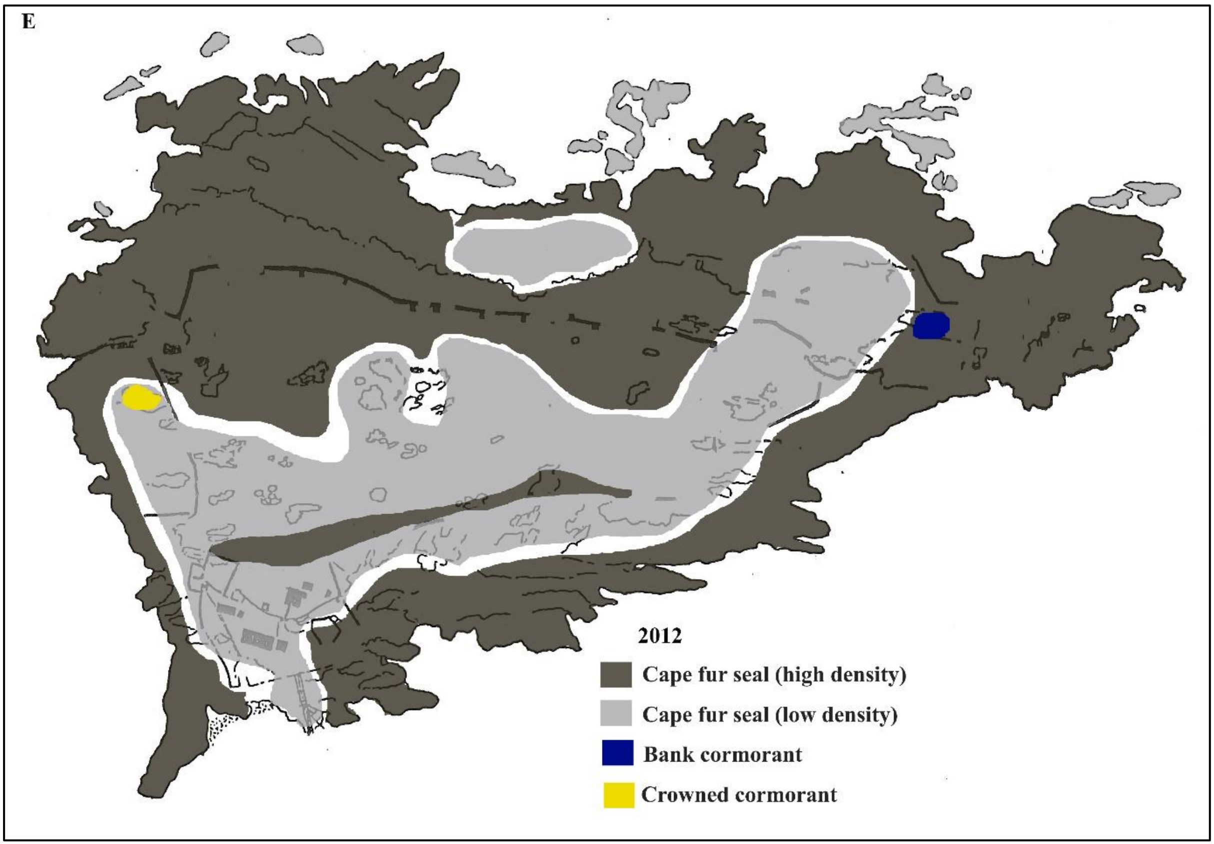
Figure 2.6 (A-I). The distribition ofseals and seabirds at Vondeling Islands from land-based seabird surveys (1999–2005).

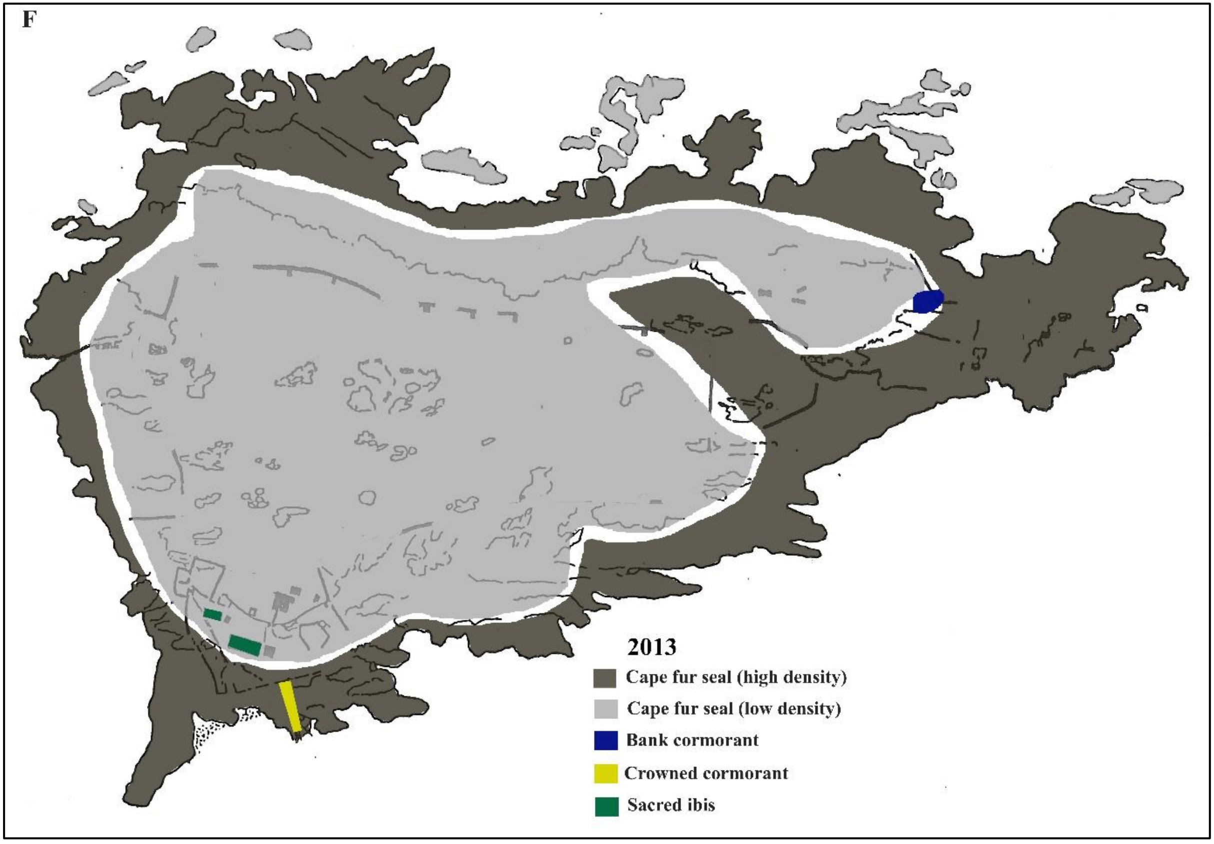

A
2006
Cape fur seal (high density)
Cape fur seal (low density)
Bank cormorant
Crowned cormorant
Sacred ibis
Cape cormorant
Hartlaub's gull
African penguin

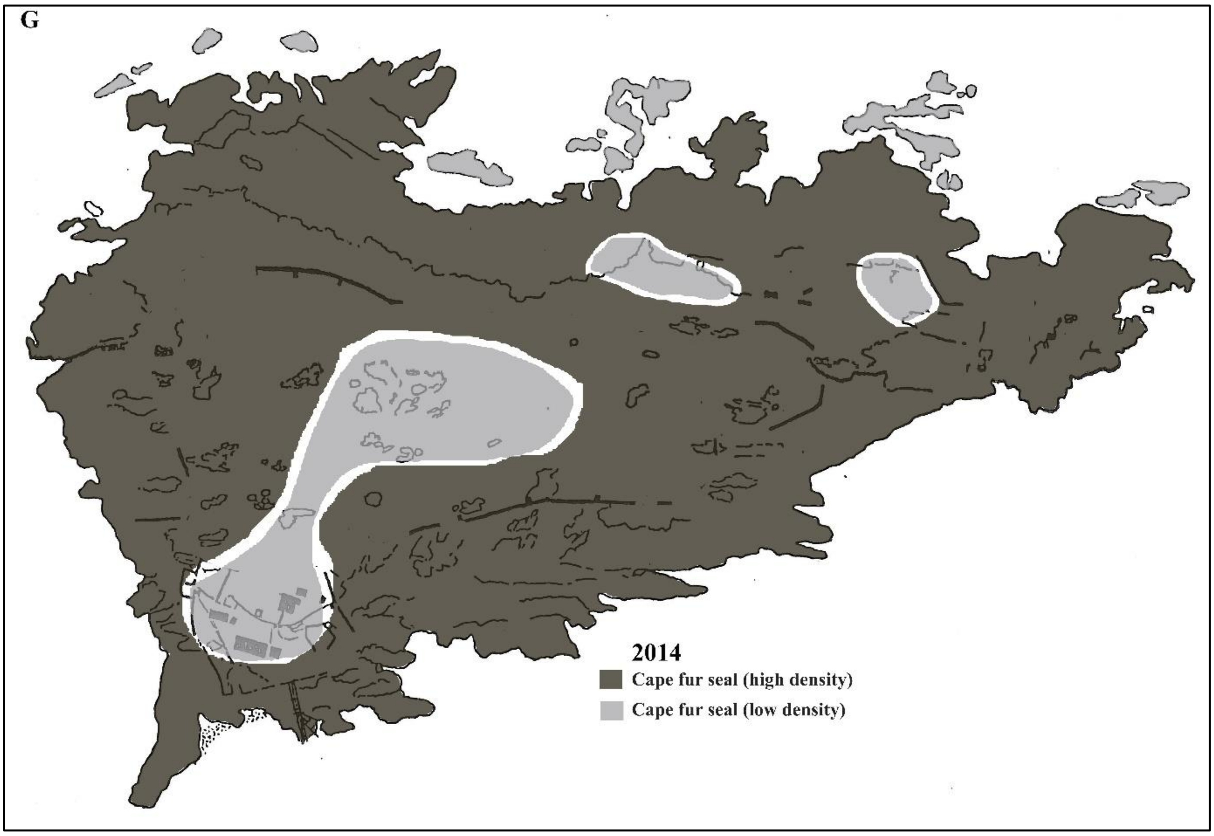

B
2008
Cape fur seal (high density)
Cape fur seal (low density)
Bank cormorant
Crowned cormorant
Sacred ibis

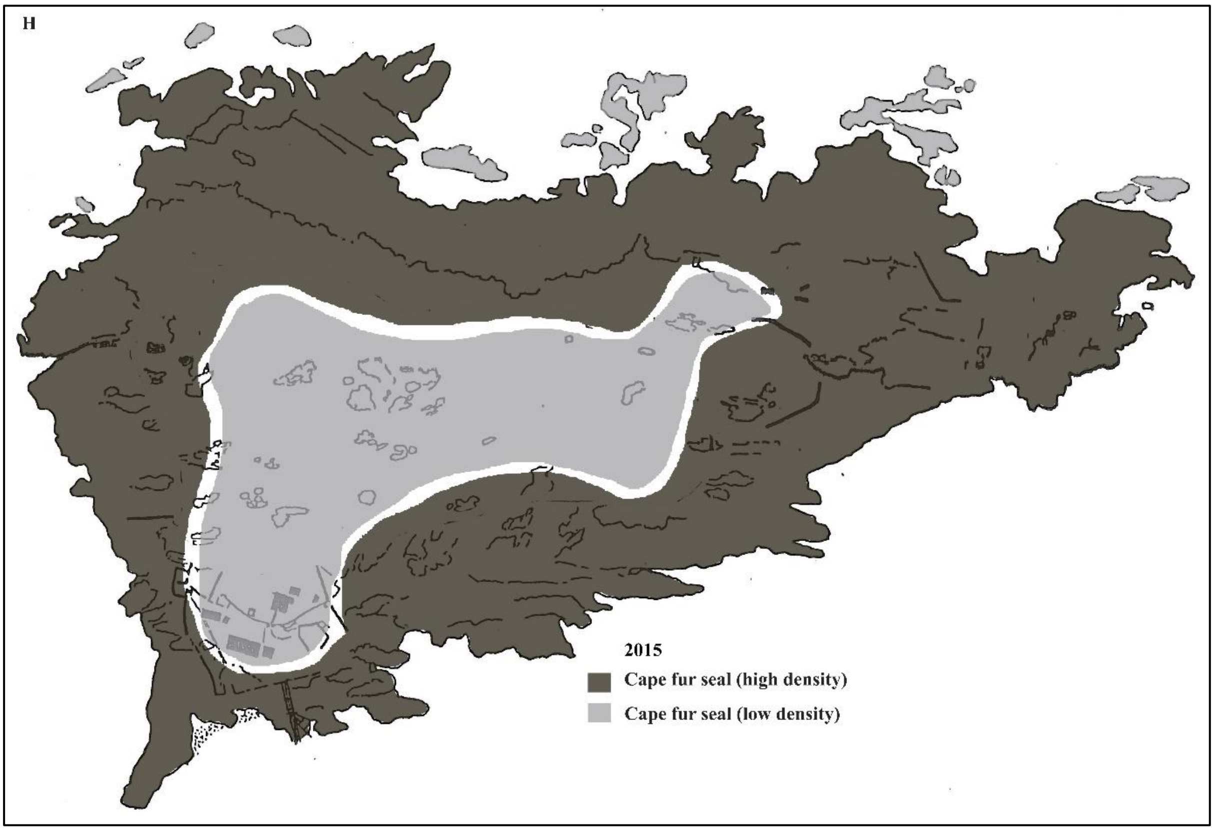

C
2009
Cape fur seal (high density)
Cape fur seal (low density)
Bank cormorant
Crowned cormorant
Sacred ibis


D
2011
Cape fur seal (high density)
Cape fur seal (low density)
Bank cormorant
Crowned cormorant
Sacred ibis


E
2012
Cape fur seal (high density)
Cape fur seal (low density)
Bank cormorant
Crowned cormorant


F
2013
Cape fur seal (high density)
Cape fur seal (low density)
Bank cormorant
Crowned cormorant
Sacred ibis


G
2014
Cape fur seal (high density)
Cape fur seal (low density)


H
2015
Cape fur seal (high density)
Cape fur seal (low density)

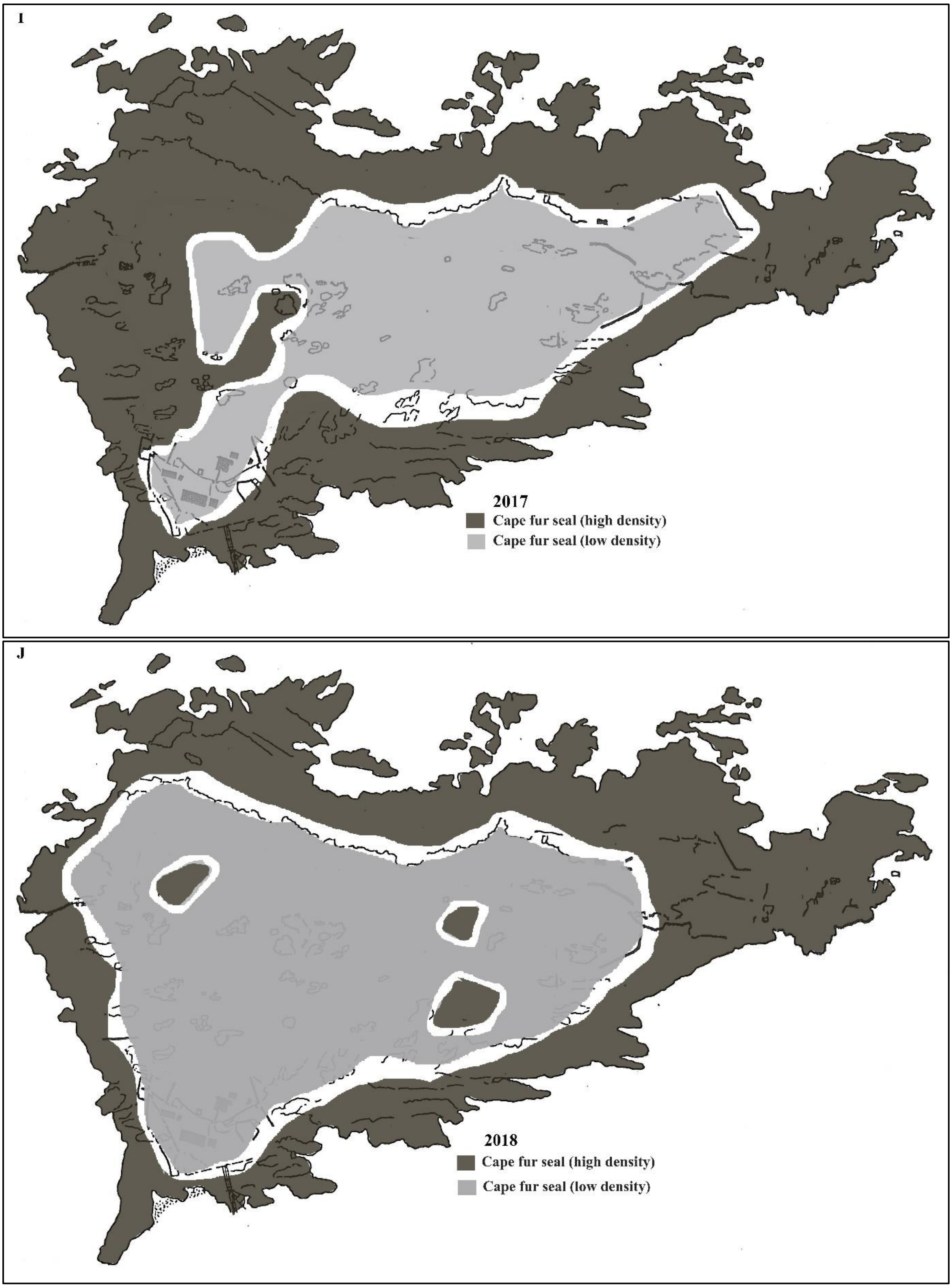


Figure 2.7(A-J). Areas occupied by seals obtained from aerial photographs (2006–2018) while the information for seabirds was obtained from island visits 2006–2013.

Table 2.21. Surface area of Vondeling Island covered by Cape fur seals during breeding season.

Year	**High Density (Units)**	**H.D. converted (m^2)**	**% of island surface area**	**Low Density (Units)**	**L.D. converted (m^2)**	**% of island surface area**	**% Total area covered**
2006	31,8	5008	25,1	5,0	787	4,0	29,1
2007	58,1	9146	45,9	21,7	3412	17,1	63,0
2008	69,1	10881	54,5	18,5	2905	14,6	69,1
2009	39,3	6189	31,0	20,2	3176	16,0	47,0
2010	44,8	7055	35,4	81,4	12810	64,3	99,7
2011	88,5	13943	69,9	37,6	5923	29,7	99,6
2012	56,4	8875	44,5	69,8	10990	55,1	99,6
2013	106,1	16713	83,8	20,0	3153	15,8	99,1
2014	90,6	14259	71,5	35,6	5606	28,1	99,6
2015	84,3	13272	66,5	41,9	6593	33,1	99,6
2016	66,1	10409	52,4	60,0	9448	47,6	100
2017	113,4	17857	89,5	12,8	2008	10,1	99,6

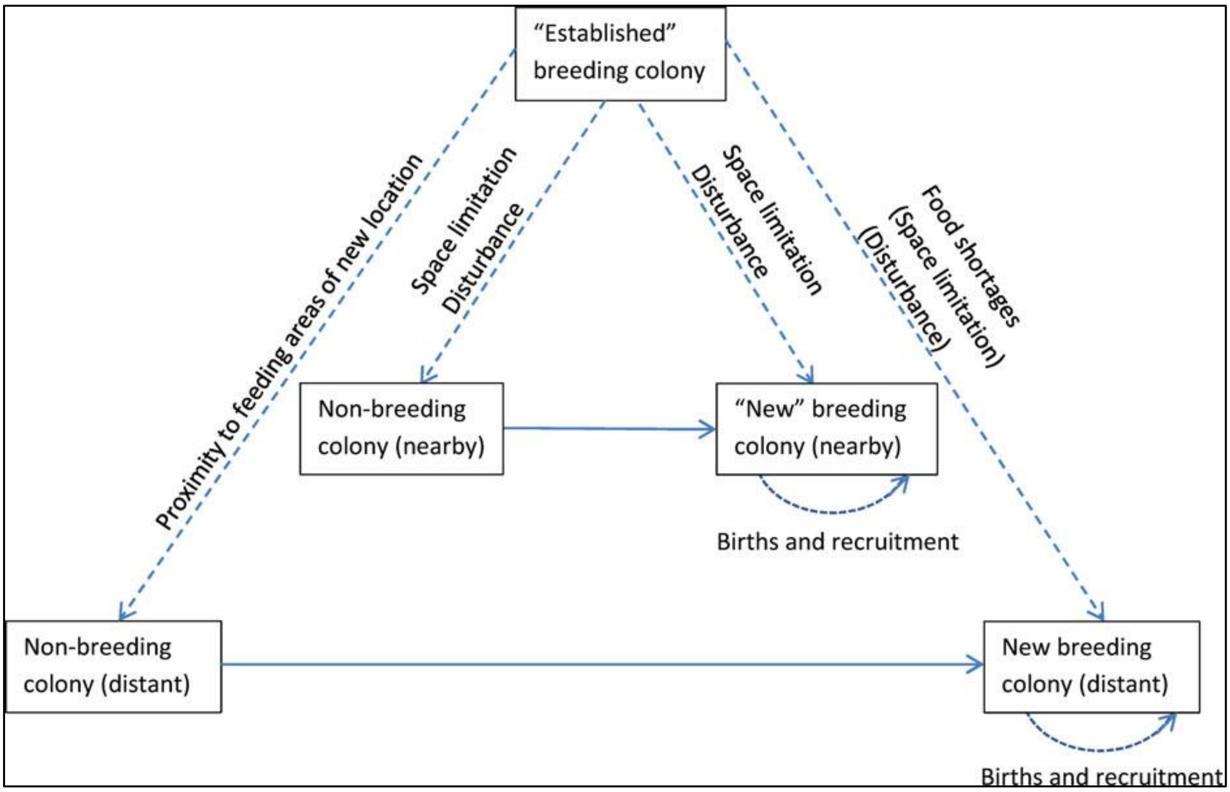


Figure 2.8. Hypothetical scenario of formation of new colonies (Kirkman et al. 2013)

Figure. 2.9. An example of artificial nests for African penguins that were installed at Vondeling Island.

Figure 2.10. African penguins nesting in the open (left) and in rock crevices (right)

Figure. 2.11. African penguin nesting amongst Cape fur seals

Figure 2.12. Cape cormorants nesting on man-made wall at Vondeling Island.

Figure 2.13. Crowned cormorants nesting on the edge of an artificial breeding platform at Vondeling Island (February 2017).

Chapter 3: Using satellite telemetry to infer at-sea foraging competition between Cape fur seal and African penguin breeding at Vondeling Island

Abstract

In a dynamic marine environment, the availability of resources may vary temporally. Among sympatric breeders, species may differ in biomass, morphology, physiology and experience, resulting in spatial segregation and specialisation in resource use. The Cape fur seal *Arctocephalus pusillus pusillus* and African penguin *Spheniscus demersus* are sympatric breeders at Vondeling Island and two other localities in South Africa. Knowledge around their interactions has focused on predation and displacement by seals. Their overlapping niche and breeding sympatry is predicted to trigger competition which must be mediated through partitioning of resources (i.e. habitat, diet). For examples, they have overlapping dietary niche; both species feed on anchovy and sardines as their main diet which have but collapsed on the west coast of South Africa since 2000s and have struggled to recover.

This Chapter utilised telemetry data to investigate potential at-sea competition. Platform Transmitter Terminal (PTT) tags were for the first time concurrently deployed on lactating female Cape fur seals and adult penguins to investigate their horizontal movement overlaps (home ranges and core feeding areas). Marine Important Bird/Biodiversity Areas (mIBAs) for both species were identified. Cape fur seals had a larger home range (158,486 km^2 vs 40,495 km^2 for penguins) and core area (25,682 km^2 vs 7,865 km^2 for penguins). Home ranges and core areas overlapped by 78% and 86% respectively. Core areas were around and in the vicinity of the colony for both species which were also identified as mIBAs. This is to be expected of central place foragers whose distances from the colony are restricted by the distribution of their prey during breeding. Although core areas overlapped in the vicinity of the Vondeling Island, seals' core areas extended north to coincide with waters associated with the Cape Columbine upwelling cell; while penguins' core areas extended south towards Yzerfontein. There was relatively less overlap at the individual level than there was at the population level; which is likely a mechanism to mitigate competition. Core areas and mIBAs

identified for Vondeling Island seals and penguins also overlapped with those of their conspecifics breeding at other localities such as Dassen Island and Robben Island. The mechanisms of mitigating impacts of competition by both species need better understanding but likely include targeting different prey sizes, feeding depths and diurnal/nocturnal patterns of feeding. Further research is recommended which should combine vertical and horizontal utilisation of water masses by both species.

3.1. Introduction

Large marine vertebrates such as seals and seabirds are upper trophic level consumers and as such have important top-down effects on marine ecosystems (Hazen et al. 2019). They exploit biophysical features and resources across various spatial and temporal scales, which can lead to unavoidable overlaps and competitions. While marine predators such as Cape fur seals may exhibit some plasticity in their response to environmental variability and forage prey species (e.g. Carpenter-Kling et al. 2020), competition with other predators, such as penguins, is tightly coupled and critical. This is especially important given the significant impact on this other species and the potential ecosystem role of these marine predators, which may have important ecological implications.

The population of Cape fur seal and African penguin have been on divergent trajectories in recent in the 20th century. The Cape fur seal population has a favourable conservation status of “Least Concern” with a stable outlook (Kirkman et al. 2016). In contrary, the African penguin has a conservation of status of “Endangered”, following decades of decline (BirdLife 2020; Sherley et al. 2020). Both species feed predominantly on pelagic teleost fish i.e., anchovy and sardines (Wickens et al. 1992; Crawford et al. 2011); and there is thus unavoidable competition between them for forage resources. Competition theory predicts that in nature, species that have similar niches and are sympatric cannot coexist (Hardin 1960). To reduce competition or the impact thereof, two or more species should partition resources through habitat, dietary, or temporal seclusion (Schoener 1974). Understanding how species manage competition is critical for their management.

Studies on seal-penguin interactions in the BCLME have largely focused on direct interactions such as predation and competition for space (Kirkman 2009). A more indirect or less observable form of interaction is competition for forage resources. Improved legislative protection for seals in South Africa (where ~40% of the global population occurs), has resulted in an increase in their population to over 1.5 million individuals in the 1990s (Butterworth et al. 1995), and has remained almost stable at that level since (Kirkman et al. 2013). Their population growth is limited chiefly by availability of ideal breeding habitat. These are islands that protect them from predators and human disturbance and mainland colonies with little human presence (Chapter 2). Predation has a negligible effect on the population; i.e. by African lions *Panthera leo* (Stander 2019), black-backed jackals *Canis mesomelas* (Oosthuizen et al. 1997), brown hyaenas *Hyaena brunnea* (Wiesel 2010), leopards *Panthera pardus* (Anonymous 2020) and white sharks *Carcharodon carcharias* (Martin et al. 2005). The increase in seal biomass in the BCLME has likely increased predation pressure on target forage fish species, thereby increasing competition with numerous other predators, such as the African penguin.

Concurrent studies on their diets at their shared breeding habitats are not available. Similarities in their dietary preferences can be drawn from independent studies e.g. David (1987), Gumede, (2023) for seals and Wilson (1985), Crawford et al. (2011) for penguins. Vondeling Island, Western Cape, South Africa, provides an opportunity to investigate aspects of seal-penguin interactions. Cape fur seals fully recolonised Vondeling Island, when between at which maximums of between 361 and 649 breeding pairs of African penguins were present in the 1990s and 2000s respectively (Chapter 2). In the absence of colony level concurrent dietary studies, competition for resources may be inferred from their at-sea distribution utilising a satellite telemetry technique. Satellite telemetry is the use of satellite-linked technology to remotely track the movements and habitats of individual animals (Hart and Hyrenbach 2009). This technique has been utilised to investigate potential at-sea competition between seals and penguins in the southern ocean (e.g. Barlow et al. 2002; Blanchet et al. 2013). This chapter therefore assesses their at-sea spatial distribution between the two species, investigates and infers potential competition between seals and penguins that breed at Vondeling Island, South Africa.

3.2. Materials and Methods

3.2.1. Study site and species

This study was conducted at Vondeling Island (33°9'11"S, 17°58'57"E), Western Cape, South Africa. The island is one of three breeding colonies in South Africa where Cape fur seals and African penguins co-existed in the last 20 years (Fig. 3.1 and 3.2). Cape fur seals recolonised the island in the late 1990s and started consistently breeding around 2003. Their local population at the island has grown to be the second largest in South Africa by pup production, after the mainland Kleinsee (Northern Cape); with an average of ~14634 pups produced between 2003 and 2018. Conversely, the number of breeding pairs of African penguins has declined from 622 to 111 in the same period (Chapter 2).

This breeding colony is situated in the nutrient rich southern Benguela Upwelling System (sBUS). Wind-driven upward movement of water mass (upwelling) lifts nutrients from the bottom to the surface (Kämpf and Chapman 2016) which supports high biodiversity and biomass of organisms in the trophic chain (Verheye et al. 2016). On the South African part of the sBUS, three upwelling cells are recognised: Namaqua(30°S), Columbine (32–33°S) and Cape Peninsula cells (34–34.5°S) (Santana-Casiano et al. 2009, Veitch et al. 2010). The three upwelling cells are located on the west coast of South Africa. However, upwelling has also been reported off Plettenberg Bay on the south coast (Schumann et al. 1982).

3.2.2. Satellite tag deployment

Deployment of Argos platform terminal transmitters (PTTs), henceforth tags, was conducted on 14 September 2017. Lactating female Cape fur seals observed suckling their pups were randomly selected for deployment. A long-handled hoop-net with a tapering PVC sleeve designed to conform to the body shape of a Cape fur seal, was used to catch and restrain each seal (David et al. 1990). The sleeve also doubled as a blind fold thereby minimising struggle during the capture and handling process (Gentry and Holt 1982). With the seal still in the hoop net, anaesthesia was induced using isoflurane gas delivered via a portable vaporizer (Stinger, Advanced Anaesthesia Specialists, Gladesville, New South Wales, Australia) (Gales and Mattlin 1998). A tag deployment summary report is provided in Table 3.1.

Each fur seal was weighed on a wooden platform by a suspension scale and measurements of standard length (SL) and auxiliary girth (AG) were taken using a plastic tape measure. A quick setting glue (Araldite AW2101, CIBAGEIGY Ltd) was used to attach each tag (SPOT6 Model-otariid series, Wildlife Computers, Redmond, WA, USA) directly on animal pelage along the dorsal midline, just posterior to the scapula (Kirkman et al. 2019). At the end of the attachment process, anaesthesia was reversed by introducing oxygen and tagged individuals were allowed to recover to normal behavioural state. The vaporiser was operated by a South African registered Veterinarian while tags were deployed by me under the guidance of an experienced tagger.

Adult African penguins provisioning chicks at their nests were selected for instrumenting. The number of chicks at each nest were recorded and their state of development classified into five categories (P0-4) (Barham et al. 2007; 2008) which factors in ontogeny described by Seddon and Van Heezik (1993). Tagging candidate penguins were caught by hand and moved away from the nest. A two-person team collaborated to manually keep the animal immobilised during the instrumentation process. One person put each penguin snugly on their lap with one hand gripping the head while covering the eyes and the head with cloth and the other towards the tail area. Once an individual was comfortably secured, tags (SPOT6 Model-penguin series, Wildlife Computers, Redmond, WA, USA) were attached by the second person. Tags were attached to the feathers of each bird with waterproof Tesa® tape, cyanoacrylate glue (Loctite® 401) and plastic cable ties, to the centre of the back, mid-body and in line with flippers following the guidelines of Wilson et al. (1997). Tagging was conducted by an experienced seabird tagger. A tag deployment summary report is provided in Table 3.2.

3.2.3. Data processing and analysis

Data processing and analysis were conducted in R-Studio version 1.3.1093 (R Core Team 2020) and maps produced in both R and ArcMap 10.6.1 (ESRI 2018). Daily data was downloaded online via Argos satellite systems. Observed locations were calculated by Argos from Doppler-shift data when multiple messages were received during a satellite's passage overhead. The system graded transmitted locations into location classes (LC) based on the quality of satellite reception (Nicholls et al. 2007). LC's are (in descending order of accuracy): 3, 2, 1, 0, A, B and

Z. Location classes A and B have no accuracy estimation and Z is an invalid location (Riekkola et al. 2018).

3.2.3.1. Trip characteristics

Analysis for trip characteristics from tracking data of African penguins and Cape fur seals was conducted in R using the package "t*rack2KBA*" (Beal et al. 2021). The package was developed to identify ecologically important areas for populations. Principles underlying "t*rack2KBA*" were based on the approach developed by Lascelles et al*.* (2016) for identifying marine Important Bird and Biodiversity Areas (MIBAs). Tracks were split into individual foraging trips (i.e., complete trips), henceforth "trips", using function *trip-Split.* For Cape fur seals data, a trip was defined as a period of ≥24 hr and a distance of ≥12 km away from the colony. Trips shorter than 24 hr and within 12 km of the colony are likely taken for thermoregulation (Skern-Mauritzen et al. 2009). For African penguin data, a trip was defined as periods of ≥2 hr and ≥2 km away from the colony. All locations points falling within these parameters were then excluded using argument 'rmNonTrip'. Characteristics of each trip were calculated using function *tripSummary*, which returns trip duration (total time between departure and return to the colony, hr), foraging range (distance from the colony, km), total distance travelled (calculated on a great circle, km) and directions of trips (measured from origin to furthest point of a track, °). Descriptive statistics were then calculated for *tripSummary* output.

Beal (2022) recommended a sample size of >10 for the data group to be utilised to identify mIBAs. However, in that publication, the author utilised global positioning system (GPS) data while this study utilises Argos data. Thus, identification of mIBAs was attempted for the two species to test if the package will satisfactorily identify the mIBAs at the population level (representativeness). Firstly, the function *estSpaceUse* was used to estimate utilisation distributions (UD) at level 50. UDs are calculated through the kernel density estimation (KDE) method, which is a non-parametric density estimator (Worton 1989). Smoothing parameter "*h*" was calculated using the function *findScale* for each dataset separately. The function *repAssess* was used to calculate the degree to which the data represents the space use of the wider population (Beal 2022). A minimum of 70% ʻrepresentativenessʼ is required to assume that the data were able to satisfactorily identify important areas of the population (Carpenter-Kling et al. 2022). Lastly, function *findSite* was used to delineate candidate mIBA, whose output is a scaled estimate of the proportion of the source population that predictably uses each grid cell in the study region (Beal et al. 2021).

3.2.3.2. Behavioural movement

Prior to conducting behavioural movement analysis from Argos data, raw data was filtered for unreliable or unlikely positions using a speed-distance-angle filter (Freitas et al. 2008), called from the *"foieGras"* package (Jonsen and Patterson 2020). A speed threshold of 5 m/s was used to exclude unlikely locations. Individual track data with transmission gaps of more than 3 days were split into segments and treated separately. In the model, the data were run through a continuous-random walk (CRW) state-space model (SSM) (Jonsen et al. 2019) with a 12-hour time step. This approach accounted for observation errors in tracking data, and also provided location estimates and standard errors at regular time steps along the track (Jonsen et al. 2013, Ropert-Coudert et al. 2020). SMM filtered location estimates (37% of raw data) were used to fit a random walk with time-varying move persistence model ($\boldsymbol{\gamma}_t$), using the *fit_mpm* function in "*foieGras*" package(Jonsen and Patterson 2020). The time-varying move persistence model can be used to objectively identify changes in horizontal movement patterns where $\boldsymbol{\gamma}_t$ forms a behavioural index on a continuous scale from 0 (low move persistence indicative of low speed and directionality [searching and foraging]) to 1 (high move persistence indicative of high speed and linear directionality [transit]) (Jonsen et al. 2019).

3.2.3.3. Home range sizes and distribution overlap

In order to test for and estimate possible distribution overlap, at-sea utilisation distribution (UD) of home ranges (95%) and core areas (50%) were calculated for African penguins and Cape fur seals by means of a kernel density estimation (KDE) approach (Worton 1989, Kenward et al. 2001). Overall home ranges and core areas were calculated in R using the package ''*adehabitatHR*'' v.0.4.18 (Calenge 2020) and some components of the script for visualisations were taken from Reisinger et al. (2020) . UD was estimated using the function KernelUD. The argument '*h*' controls the value of the smoothing parameter which was calculated using the reference parameter method (*href*). The resulting utilisation maps were exported as shapefiles and used in ArcMap Version 10 to double check the calculated utilisation total area in R and where necessary, for visualisation. Overlap indices (0-1) were calculated to determine the at-sea spatial interactions between Cape fur seals and African penguins. In essence, this is the proportion of animal *i*'s home/core range that is overlapped by animal *j*'s home/core range (Kernohan et al. 2001). The index of overlap values ranges from zero (no overlap) to 1 (identical UD).

3.2.3.4. Prey spawner biomass visualisation

To visualise at-sea movements of African penguins and Cape fur seals relative to densities of prey, spawner biomass density distribution maps were produced for sardine and anchovy in R. The surveys were conducted over the continental shelf between Hondeklip Bay on the West Coast and Port Alfred on the East Coast in 2017 (30 October to 13 November and 20 November to 18 December) (Coetzee et al. 2017). Data collection methods are detailed in Hampton (1987). Data were aggregated into density classes 1–25, 25–100 and >100 g per m^2 with a 0.16° resolution.

3.3. Results

Nine Argos PTTs were deployed on adult African penguin adults. However, only five transmitted and their data are utilised in this study. The seven tags deployed on lactating female Cape fur seals transmitted successfully. There was a varying duration and the number of transmissions across both species (Table 3.3). Argos location data for each species are presented in Fig. 3.3 and their individual tracks in Fig. 3.4 (a &b) for African penguins and Fig 3.5 (a & b) for Cape fur seals.

3.3.1 Trip characteristics

Details on each date, transmission duration, and number of transmissions per tag are provided in Table 3.3. A total of 1547 and 2653 speed filtered locations were utilised in the analysis of trip characteristics for African penguins and Cape fur seals respectively. Individual movement tracks are presented in Fig. 3.4 (a & b) and 3.5 (a & b). At the individual level, penguin AP151957 left the colony a few days after deployment and spent more than 30 days foraging north of the colony without returning to the island. AP151959 utilised waters within 50 km of the colony for first 49 days and thereafter spent more than 25 days north of the colony prior to returning to the colony (Figs. 3.4a, 3.4b, 3.6). All tagged penguins completed at least one foraging trip (Fig. 3.8). Three female seals (CFS151943, CFS151946 and CFS151948) travelled from the Vondeling Island to the south coast (Fig. 3.5a & b). CFS151943 undertook a complete trip to the south coast and managed to reach Gansbaai and hauled out at Geyser Rock breeding colony before the instrument died. CF151946 did not return to the colony (incomplete trip, Fig 3.9); but transmitted a considerable number of locations at and around Robberg Ledges breeding colony (Plettenberg Bay). CFS151948 undertook complete foraging trips off the west coast and one incomplete trip to the south coast. It reached Sebastian Bay before transmission stopped. A new colony, Cape Infanta is located within the bay in the vicinity of the lighthouse. Except for CFS151943 and CFS151947, all female Cape fur seals travelled further (>200km) from the colony after 25 days of tagging (Figs. 3.5a & b; Fig. 3.7).

Summary of descriptive statistics of trip characteristics are given in Tables 3.4 (penguins) and 3.5 (seals). There were 41 overall trips and 38 complete trips undertaken by tagged African penguins. Median direction of trips was in a south-south-easterly direction relative to the colony (148,1°; min: 23,9°, max: 345,5°) (Fig. 3.4). Trip duration had a median of 46,1 hr with a minimum of 3,3 hr and a maximum of 2004,6 (84 days). Median maximum distance from the colony was 18,6 km with minimum and maximum distances of 2,8 km and 368,9 km respectively. Total distances undertaken had a median of 49,1 km with a minimum of 6,9 km and a maximum of 2135,8 km. Distances from colony over the transmission period are presented in Figure 3.6.

For Cape fur seals, there were 37 overall trips and 32 complete trips undertaken. Visualisation of complete and incomplete trips is given in Fig. 3.3. Median direction of foraging trips was in a west-south-westerly direction (258,5°; min: 101,9°, max: 345,5°). The shortest trip was 25,5 hr (1 day) and the longest trip lasted 2105.8 hr (88 days) with a median duration of 124.4 hr. Minimum foraging distance from the colony was 14,9 km and the furthest was 429,8 km with a median of 86,9 km. The minimum total distance of trips conducted was 139,7 km and maximum 4214,5 km with a median of 256,7 km. Summary descriptive statistics are given in Table 3.5 and the distance from colony over the transition period is presented in Figure 3.7. With respect to mIBAs, tracked African penguins and Cape fur seals had representative scores of 92,7% and 87,9% respectively (Fig. 3.10 and 3.11). Thus, the Argos PTTs data was able to satisfactorily estimate the proportion (92,7%–penguins and 87,9%–seals) of the source populations that predictably uses each grid cell in the study region. The delineated candidate mIBAs for African penguins and Cape fur seals breeding at Vondeling Island are given in Figures 3.12 and 3.13 respectively. Candidate mIBAs for African penguins overlap with areas between Cape Columbine and Yzerfontein (Fig. 3.12). Candidate mIBAs for Cape fur seals overlaps with waters between Paternoster and 16 Miles beach but extends more offshore than does the candidate mIBAs for African penguins breeding at Vondeling Island.

Although one individual of each species went beyond the shelf break, both species' movements were mostly associated with the continental shelf (on the west coast) (Fig. 3.3). African penguins' movements were limited to the west coast and mostly close to the coast in waters of <500 m depth while Cape fur seals ventured into deeper waters along the shelf break (Fig 3.3). African penguins utilised waters associated with Namaqua (30°S) and Cape Peninsula (34°S) upwelling cells. Two main areas were evidently utilised: one between Namaqua and Lambert's Bay and another between Vondeling Island and Yzerfontein. Cape fur seals also intensively utilised waters between Saldanha Bay and St Helena Bay. The area is productive characterised by a narrow continental with a steep slope and the Cape Canyon cuts obliquely across it (Filander et al. 2022). Cape fur seals were more widely distributed, utilising waters of the southern BUS including the Agulhas Bank on the south coast.

3.3.2 Behavioural movement

The move persistence values for penguins, indicated that there were clumps of low move persistence values ($\boldsymbol{\gamma}_t < 0. 25$) along the coastal waters between the colony and Yzerfontein (including 16 miles beach) (Fig. 3.14). Other clumps of low move persistence values were in waters between Groenriviermond and Olifants river mouth and in offshore areas between Cape Town and Cape Point. For seals, a larger group of lower values ($\boldsymbol{\gamma}_t < 0. 25$) were between Saldanha Bay to Lambert's Bay (~32°S to 33.3 °S) and smaller values off Plettenberg Bay (Fig. 3.15). These values are indicative of searching or foraging. Higher move persistence values ($\boldsymbol{\gamma}_t < 0. 65$) were apparent for movement between the colony and the south coast, and the furthest movement north of the colony. The two extremes of the move persistence continuous index only account for searching/foraging and transit behaviours. Considering that seals and penguins do not behave in a binary fashion, there are intermediate values that represents movements that do not correspond to the two extremes (Vogel et al. 2021).

3.3.3 Home range sizes and distribution overlap

The total area (home range) utilised by Cape fur seals was four times greater than the home range for penguins. These were, based on the 95% kde of all individuals, 158,486 km^2 and

40,495 km^2 respectively (Table 3.6). The home range of the African penguin was limited to the west coast waters between south of Kleinsee (Northern Cape) and Cape Point (Western Cape) (Fig. 3.17). For Cape fur seals, their home range covered waters between Hondeklip Bay on the west coast and Plettenberg Bay (south coast) (Figs. 3.18). Core areas of Cape fur seals were in areas between Lamberts Bay and the Cape Peninsula with a small area identified around Plettenberg Bay (Fig. 3.18). Core areas of African penguins were between Cape Columbine and Ysterfontein on the west coast with a smaller core area identified to the north between Olifant River mouth and Groenriviermond (Fig. 3.17). The west coast waters of South Africa can be considered core feeding areas of both Cape fur seals and African penguins breeding at Vondeling Island. The total core areas were 7,865 km^2 and 25,682 km^2 for African penguins and Cape fur seals respectively (Table 3.6). Individual home ranges for penguins averaged 12,977 (range 587–31,86) km^2 while home ranges for individual seals averaged 42141 (range 4,38–84,54) km^2 (Tables 3.7 & 3.8). Individual core ranges (50% kde) for penguins averaged 3,015 (76–8443) km^2 while seals averaged 9,59 (range 559-22962) km^2 (Tables 3.7 & 3.8; Figs. 3.17 & 3.18). There were overall overlaps in at-sea distribution of Cape fur seals and African penguins. In terms of home range (95% kde), the Cape fur seals UD overlapped with African penguins UD by 78% (Table 3.9). For core areas (50% kde), Cape fur seals UD overlapped by 86% with African penguins UD (Table 3.10).

A matrix of home range and core areas overlap with their associated indices between individual seals and penguins are given in Table 3.11 and 3.12. The degree of overlap, expressed as an index of 0-1 (alternatively 0-100%), varied intra- and interspecifically. Higher overlap values (≥0.5) were common in matrix of home ranges than that of core areas. Intraspecifically, two individual African penguins had high overlaps in home ranges with their conspecifics while only one Cape fur seal female had high overlaps with all its conspecifics. CFS151945 overlapped with all other female Cape fur seals by between 0.98 and 1. AP151956 and AP151958 overlapped with their conspecifics by 0.51-1. Degree of overlap was less for core areas amongst penguins. Core areas of AP151956 completely overlapped with two conspecifics (AP151959 and AP151960) by index of 1. AP151958 core areas index was 0.5 with AP151959's core areas.

Interspecifically, all female Cape fur seals had high home range overlap indices (≥0.5) with at least one adult African penguin, but all had indices of ≥0.72 with AP151956. Two penguins had high home range overlap indices (≥0.78) with three seals: CFS151945, CFS151947 and CFS151949. AP151960 overlapped with the home range of CFS151945 by an index of 0.81. AP151956 and AP151958 overall had low indices (0.02-0.41) of home range overlap with all Cape fur seals. Similarly, Cape fur seals had high indices of core area overlap with penguins than did penguins with seals. Except for CFS151946, all female Cape fur seals had indices of (0.5-1) with AP151956. Two seals (CFS151944 and CFS151948) had a core area overlap index of 0.88 with AP151959. AP151959 overlapped with core areas of three seals (CFS151945, CFS151947, CFS151949) by indices between 0.5 and 1.

3.4. Discussion

Resource partitioning through habitat, dietary or temporal seclusion is crucial to reduce competition or limit the impact thereof (Schoener 1974). The mechanisms that sympatric marine top predator species adopt to reduce competition are critical to understand. If understood, they can be used to predict the possible functional response by the “loser” species (Breed et al. 2013). In central place foragers (i.e., those that return regularly to a common breeding location), competition for space is relatively easier to detect and/or quantify (Crawford et al. 1989; Somers et al. 2007; Quintana and Yorio 1998). The advent of telemetry has enabled investigations of potential at-sea competition for forage resources by studying vertical (in the water column) and horizontal (over the water) habitat utilisation which enables examination of overlap in home ranges, core areas and feeding depths (Planque et al. 2020).

This study was conducted in the backdrop of ongoing debates around measures needed to halt the decline of the African penguin and the number of hypotheses being advanced to explain (at least in part) the generally continuing decline in penguin numbers in South Africa and whether the local increases in Cape fur seals at shared breeding colonies in recent years may have contributed significantly to the decline. These measures include the installation of artificial breeding nests to address breeding-habitat degradation (Sherley et al. 2012), management of Cape fur seals predation and implementation of fishing limitations for the small pelagic fishery around selected breeding colonies, to mitigate apparent competition with fisheries (DFFE 2023). Perhaps due to the unavailability of studies around this topic, the debates have been silent on at-sea competition between seals and penguins occurring in sympatry at breeding colonies. Data utilised in this study has enabled, for the first time, a concurrent account of at-sea movements of seals and penguins. The two species are sympatric at Vondeling Island and have been demonstrated to compete for breeding space at the breeding colony (Chapter 2). Although the sample size is arguably small for large scale conclusions, some critical insights are drawn from these results.

Critical to conservation management of species is understanding their habitat requirements, particularly for important life stages (e.g., breeding). Quantifying home ranges of animals, defined as areas utilised by animals for normal activities i.e. foraging and mating (Burt 1943; Bjørge 2002), is the first step of understanding habitat utilisation. The relative frequency of utilisation of different parts of these home ranges can be calculated to identify core areas (Gitzen et al. 2006). In this study, utilisation distribution (UD) of African penguins and Cape fur seals breeding at Vondeling Island were calculated and their overlap quantified. Overall, there were overlaps in home ranges (78%) and core areas (86%) of African penguins and Cape fur seals at Vondeling Island (Fig. 3.16; Table 3.6). These overlaps are considered relative to African penguin due to their conservation status of "Endangered". The higher overlap in overall core areas is most likely during chick provisioning periods when penguins are limited in the distance that they can move to the waters away from the colony. Delineation of mIBAs further supports that waters in the vicinity of the breeding colony are critical to both species (Fig. 3.12 & 3.13). However, in terms of mIBA approach, penguins' areas are more to the south while seals' areas are to the north of the breeding colony. In terms if this metric, there is potentially minimal competition between the two species.

A relationship between body size of different species and home range size has been reported for fish (Nash et al. 2015), turtles (Hays et al. 2021) and ungulates (Ofstad et al. 2016). Thus, Cape fur seals' larger home ranges (158,486 km^2 vs 40,495 km^2 for penguins) and core areas (25,682 km^2 vs 7,865 km^2 for penguins) are consistent with this relationship. These areas sizes, combined with the ability of seals to traverse further than penguins from the breeding colony, suggest that in a compromised ecosystem, seals will out-perform penguins. A similar competitive advantage was reported for Antarctic fur seals over macaroni penguins *Eudyptes chrysolophus* (Barlow et al. 2002). Penguins reached distances of up to 368.9 km (median 18.6 km) while seals reached up to 585.8 km (median 868 km). However, the distances covered by penguins at Vondeling Island and may differ with other localities. For instance, penguins tagged at Dassen Island had larger home ranges (100,000 km^2) and core areas (21,129 km^2) (Roberts 2018).

Dynamics of individual tagged animals indicate varying levels of interactions within and between species (Figs. 3.17 & 3.18; Tables 3.11 & 3.12). This could be a strategy that mitigates competition at Vondeling Island, mostly intra-specific competition. Studies have shown that intra-specific niche partitioning is apparent in both penguins (Rosciano et al. 2016) and seals (Jones et al. 2020). This can be achieved by partitioning through sex (Pichegru et al. 2013) and depth (Kirkman et al. 2019). Interspecific competition may be mediated through reducing horizontal and vertical spatial overlap and targeting different-sized prey size. For instance, the African penguin mean foraging depths are 30 m although they can dive to 130 m (Wilson 1985). Differences may be habitat specific as different maximum and mean dive depths have been recorded elsewhere at 50–69m and 14–17m respectively (Petersen et al. 2006; Ryan et al. 2007). Cape fur seals feed at depths of <100 m but reach maximum of 400 m (Kirkman et al. 2019). As in penguins, these depths may differ according to feeding habitat; e.g. seals breeding at False Bay: 29−202 m (mean depths) (Botha et al. 2020). Thus, concurrent investigations of vertical movements of both species maybe better elucidate how they mediate competition.

Penguins are limited by ambient light levels and thus forage during the day (Wilson and Wilson 1990); in contrast, seals can forage at night (Kirkman et al. 2019; Botha et al. 2020). It is not clear to what degree this difference mitigates competition, but would sure be more favourable for seals in the context of competition. Furthermore, competition may occur with conspecifics from other breeding sites. Comparing these results with published accounts (i.e., Carpenter-Kling et al. 2022), it appears that core areas of penguins at Vondeling Island overlap with those from Dassen Island, albeit at different life stages (pre vs post-moult). Similarly, seals from Vondeling Island are potentially competing with seals from False Bay (Botha et al. 2020) and colonies within their home range on the west and south coast.

Horizontal movement behaviour of both species in terms of move persistence coincided with location of core areas in the vicinity of the breeding colony and supports mIBAs delineation

(Figs. 3.12, 3.13, 3.14, & 3.15). Lower move persistence values ($\gamma_t < 0.25$) which are consistent with feeding or Area Restricted Searches (ARS), were along coastal areas south of the colony as far as Yzerfontein for penguins. These include the 16 Miles Beach Marine Protected Area (MPA) which may also be utilised by penguins from the nearest southern colony on Dassen Island (off Yzerfontein). South of Dassen Island, small values were offshore than inshore and up to Cape Point. Purse-seine fisheries sector targeting forage species (anchovies and sardines) is known to have a considerable fishing effort in these waters (Gumede 2023). The Cape Peninsula upwelling cell is located at ~34 °S and drives productivity in these waters (Griffiths 1981). Lower values in move persistence north of the colony between Olifants river and Groenrivier mouths were in areas historically utilised as nursery and spawning grounds for anchovies and sardines (Hutchings et al. 2002; Mhlongo et al. 2015). These areas were also utilised by juveniles tracked from Dassen Island in what is considered an ecological trap (Sherley et al. 2017). Post-moult adults from Dassen Island also utilised these waters intensively (Carpenter-Kling et al. 2022). Considering that penguins from the latter study and those from Vondeling Island were adults, it is likely that these waters are not totally void of prey but could be in lower quantities or of inferior quality. For seals, only the core area associated with the Cape Columbine Upwelling Cell was considered a mIBA. Another core area was identified associated with upwelling waters of Plettenberg Bay but not a mIBA (Fig. 3.15 & 3.16). This may be an artefact of sample size (n=1) for the only seal that ventured that far east. Vondeling Island and Robberg Ledges (Plettenberg Bay) are recolonised localities (Huisamen et al. 2011). This suggests that amongst other reasons, availability of prey resources in the vicinity of available habitat may drive selection of breeding locality in seals. This has been shown for Antarctic fur seal *Arctocephalus gazella* in Antarctica where their breeding colonies are close to areas of high krill abundance (Hunt Jr et al. 1992). This is particularly important for understanding why Cape fur seals colonise certain localities.

During the study period, penguins likely fed on anchovy than sardine; while both forage species would have been available to seals. Higher biomass (25–100 g per m^2) of sardines were east of Cape Point whereas similar biomass of anchovy was off the west coast (Fig. 3.19). Scats collected in 2017 at Vondeling Island were dominated by anchovy with no sardine hard parts present (DFFE unpublished data). A detailed dietary examination off the west coast revealed a sardine dominated diet in northern breeding colonies and anchovy dominated diet at Vondeling Island, Jutten Island and colonies to the south (Gumede 2023). Penguin diet was not available for comparison but a previous study (Crawford et al. 2011) reported an anchovy dominated diet at Robben Island and Dassen which are situated south of Vondeling Island. Considering that the foraging ranges of penguins at the three colonies overlap (Campbell 2016; Carpenter-Kling et al. 2022), it is fair to infer that anchovy may have been at the core of competition between seals and penguins at Vondeling Island.

Comparison of our results with those of other studies ought to be interpreted cautiously, especially with regards penguins. Previous studies were particular in differentiating breeding vs non-breeding, pre-moult vs post-moult. In this study, their status was inferred from chicks' developmental stages. Adults whose chicks were at advanced developmental stage-P4 (AP151957, AP151960), undertook longer trips with higher net distances from the colony within the first 10 days of tagging (Fig. 3.6). Logistical difficulties with accessing the colony prevented independent verification of cessation of provisioning. Thus, it fair to assume that these adults had stopped provisioning and had entered the pre-moult activity (fattening up). A concurrent tag deployment timed with breeding, pre-moult and post-moult period of Vondeling Island penguins would improve understanding of movements during these periods.

3.4.1. Conclusions and recommendations

African penguins forage close to their colonies during breeding (Pichegru et al. 2010) as do female Cape fur seals (Botha et al. 2020). It is thus expected that there is overlap in their core feeding areas and competition, though this competition may be more pronounced within the foraging range of penguins, particularly during breeding times. However, it is worth noting that central-place foragers may travel even longer distances when availability of foraging resources around the breeding colony is low (Staniland et al. 2010). In a compromised ecosystem, seals would out-perform penguins due to their biological and physiological "superiority". This includes ability to forage further than penguins, foraging at night and their more flexible dietary preferences.

Guided by these results, the following recommendations are made:

1. Conduct a concurrent investigation into dietary habits of both species.

2. Investigate vertical utilisation of the water column by both species through the deployment of Time-Depth-Recorders.
3. Deploy more position loggers (Argos or GPS) to increase sample size and spread the effort to cover critical life stages of penguins (breeding, pre-moult, post-moult); where possible, also deploy during early lactation stages of seals (i.e., earliest January).

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Figures and Tables

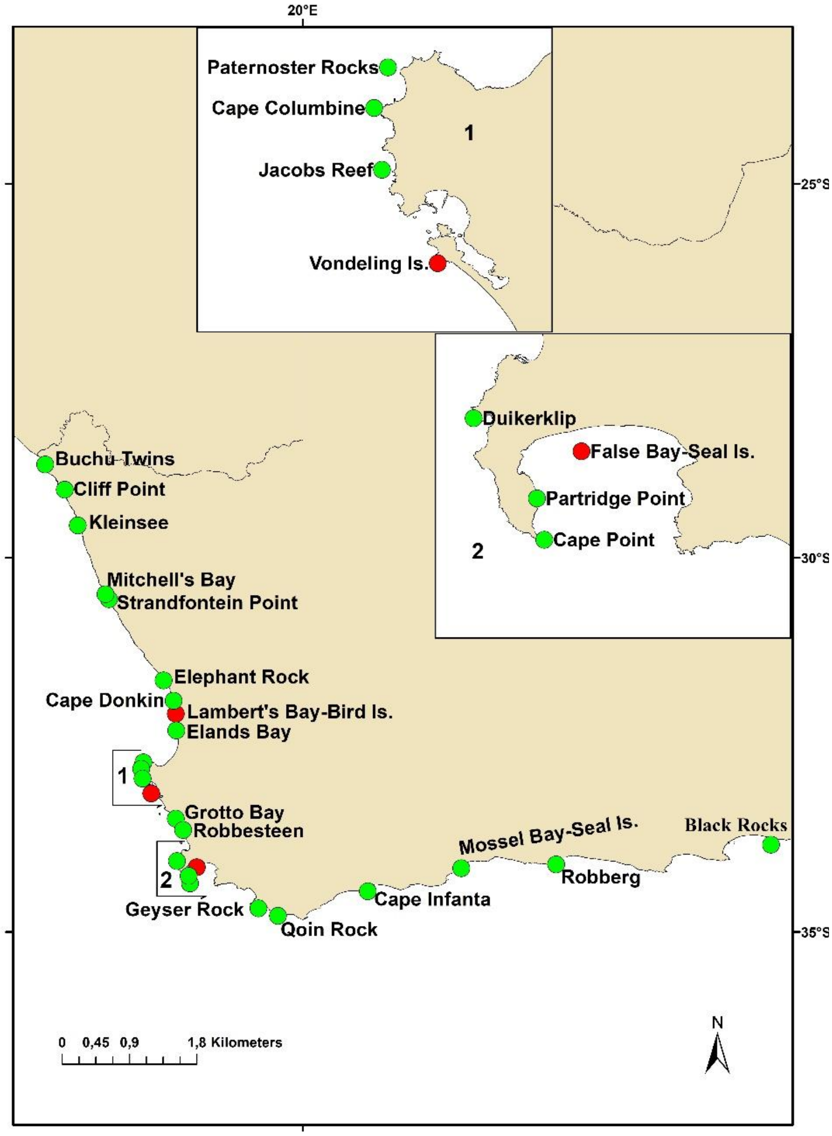

Figure 3.1. Distribution of Cape fur seal colonies where >0 pups were born until 2020. Red dots indicate co-breeding with the African penguin.

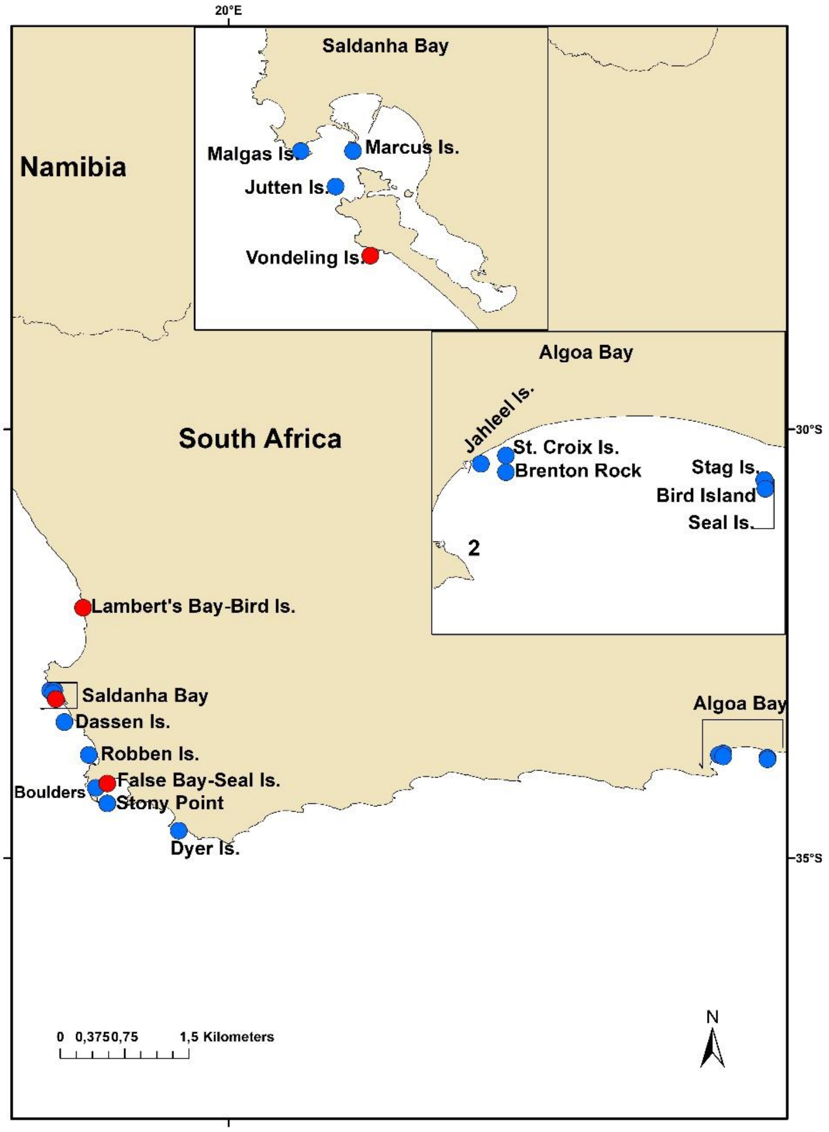

Figure 3.2. Distribution of African penguin colonies in South Africa. Red dots indicate co-breeding with Cape fur seal.

Table 3.1. Cape fur seal tag deployment summary report. PTT: Platform Transmitters Terminals, SL: Standard Length, AG: Auxiliary Girth, ISF: Isoflurane.

PTT ID	Time Captured	SL (cm)	AG (cm)	ISF on	Induction time	ISF off	Wake up	Sit up	Flipper Tag (Right)	Flipper Tag (Left)
151943	10h00	143.2	95.8	10h05	10h11	10h20	10h32	10h32	U7213	U7204
151944	10h56	150.0	98.6	11h00	11h04	11h16	11h24	11h24	U7215	U7214
151945	11h40	148.2	99.0	11h43	11h49	11h58	12h14	12h14	U7217	U7216
151946	12h37	133.2	89.8	12h39	12h42	12h51	13h14	13h14	U7219	U7218
151947	13h33	138.4	86.0	13h36	13h39	13h59	13h59	14h00	U7221	U7220
151948	14h16	144.9	86.9	14h19	14h23	14h32	14h37	14h37	U7223	U7222
151949	14h53	135.0	91.0	14h56	14h57	15h06	15h14	15h14	U7225	U7224

Table 3.2. African penguin tag deployment summary report

PTT ID	Time deployed	Sex	Nest contents	Development Stage
170443	12h16	F	Mate and chick	P4
170444	13h05	M	Mate and chick	P4
170445	13h35	F	Two chicks	P4
170446	13h45	F	One chick	P3
151956	13h51	F	One chick	P3
151957	14h20	F	One chick	P4
151958	14h28	F	One chick	P3
151959	14h35	F	Mate and Two chicks	P3
151960	14h45	F	Mate and chick	P4

Table 3.3. Tag information from 12 animals instrumented at Vondeling Island. Start and end dates refer to the date of first location transmitted.

Species	Tag ID	Start Date	End Date	Number of Days	Total Transmissions
African penguin	151956	2017/09/15	2017/09/26	11	100
African penguin	151957	2017/09/15	2017/12/09	85	328
African penguin	151958	2017/09/15	2017/10/24	39	268
African penguin	151959	2017/09/15	2017/12/18	94	671
African penguin	151960	2017/09/15	2017/10/20	35	227
Cape fur seal	151943	2017/12/25	2018/03/04	69	264
Cape fur seal	151944	2017/09/17	2017/11/17	61	349
Cape fur seal	151945	2017/10/23	2017/11/21	29	196
Cape fur seal	151946	2017/09/18	2018/01/12	116	627
Cape fur seal	151947	2017/09/16	2018/03/03	168	944
Cape fur seal	151948	2017/09/14	2017/10/24	40	167
Cape fur seal	151949	2017/09/15	2017/11/09	55	223

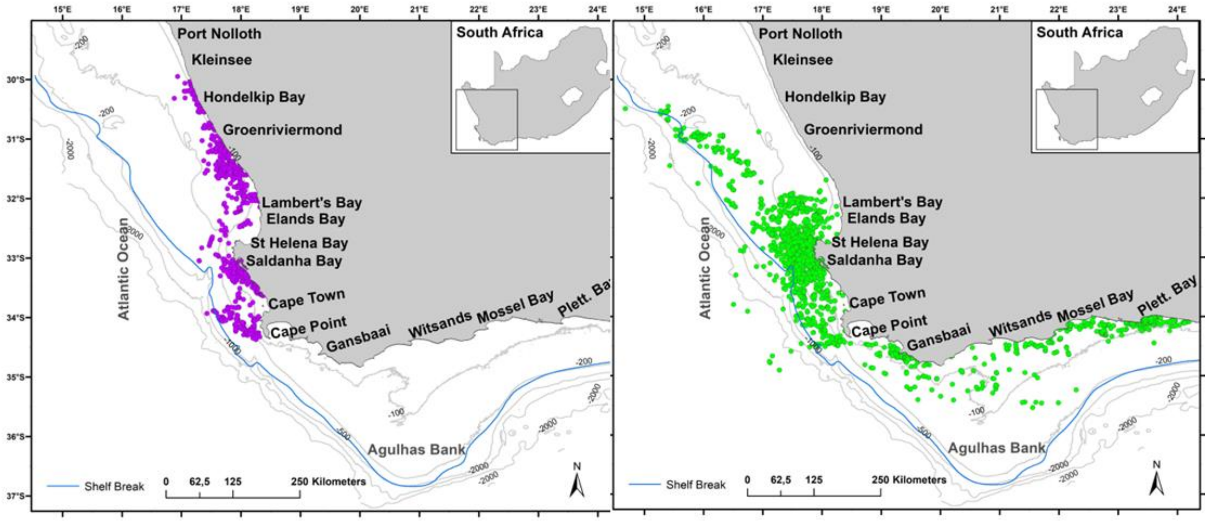

Figure 3.3. Transmitted Argos locations of African penguins (left panel, purple dots) and Cape fur seals (right panel, green dots).

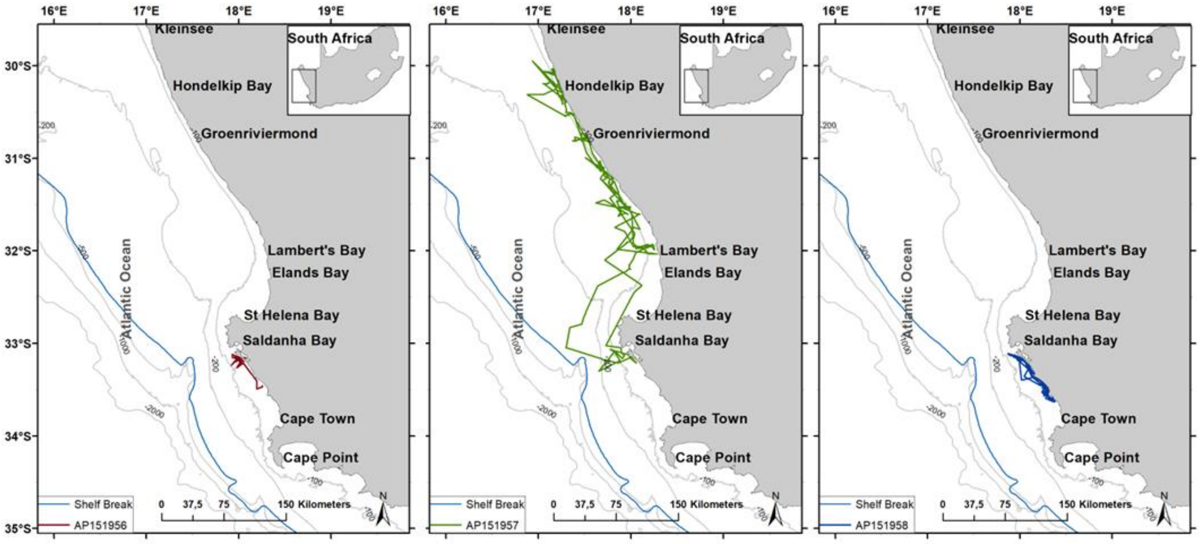

Figure 3.4a. Individual movements of adult African penguins tagged at Vondeling Island.

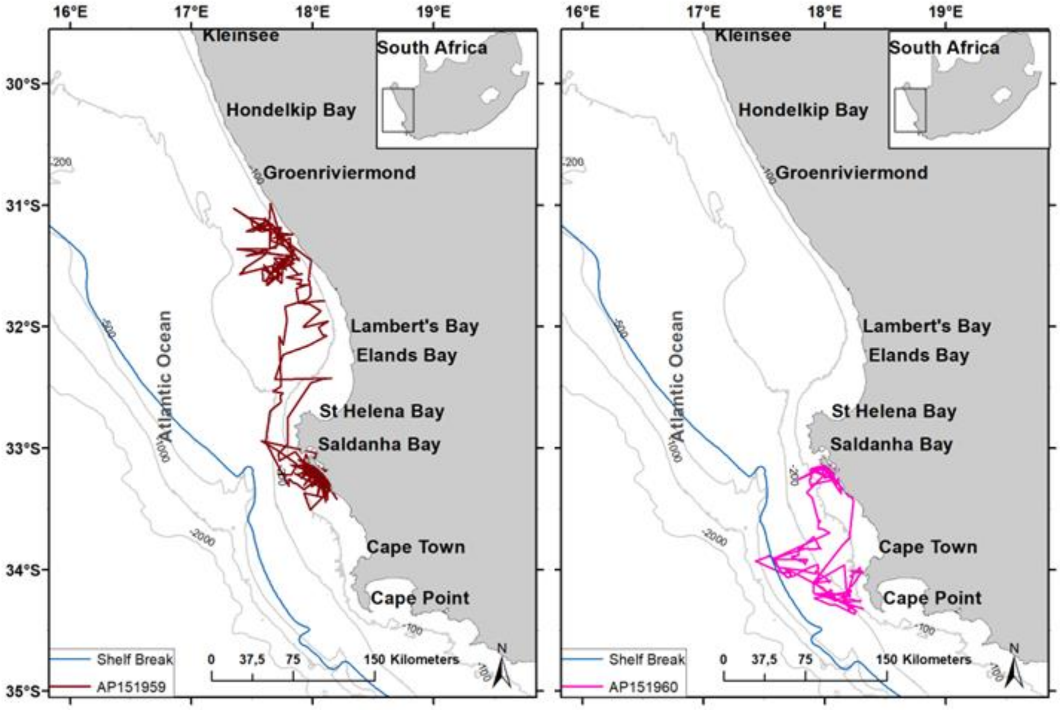

Figure 3.4a. Individual movements of adult African penguins tagged at Vondeling Island

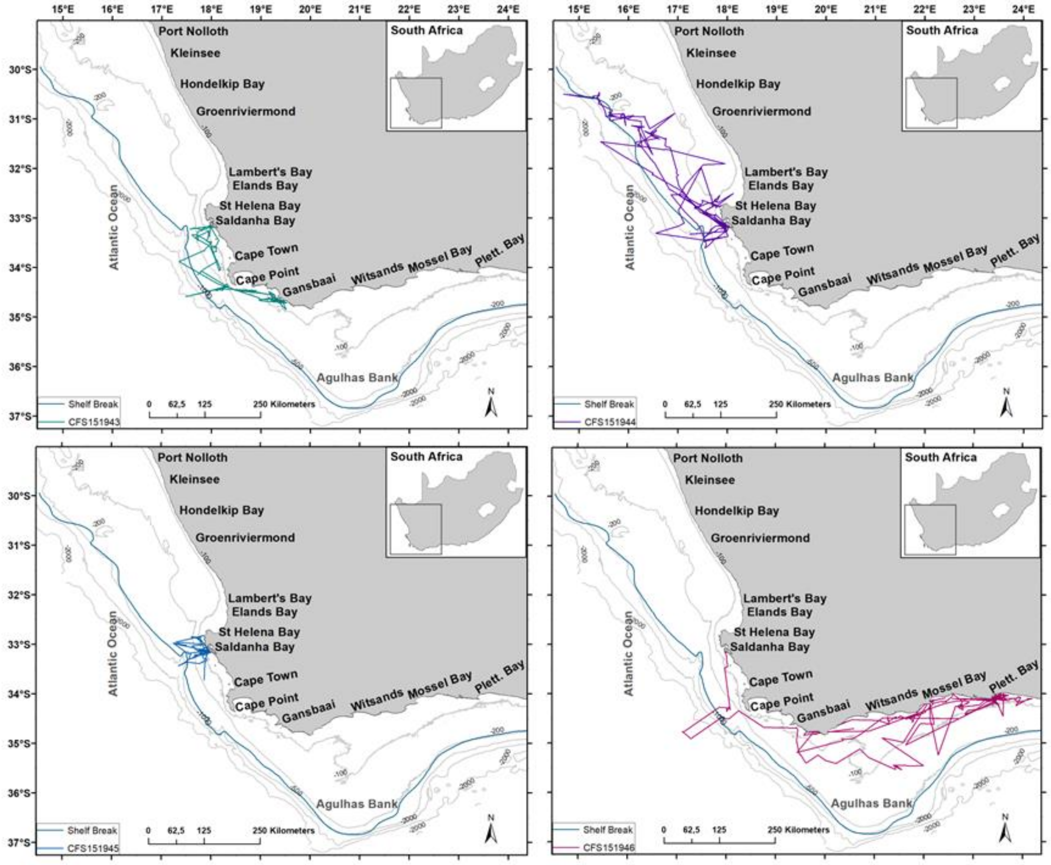

Figure 3.5a. Individual movements of female Cape fur seals tagged at Vondeling Island

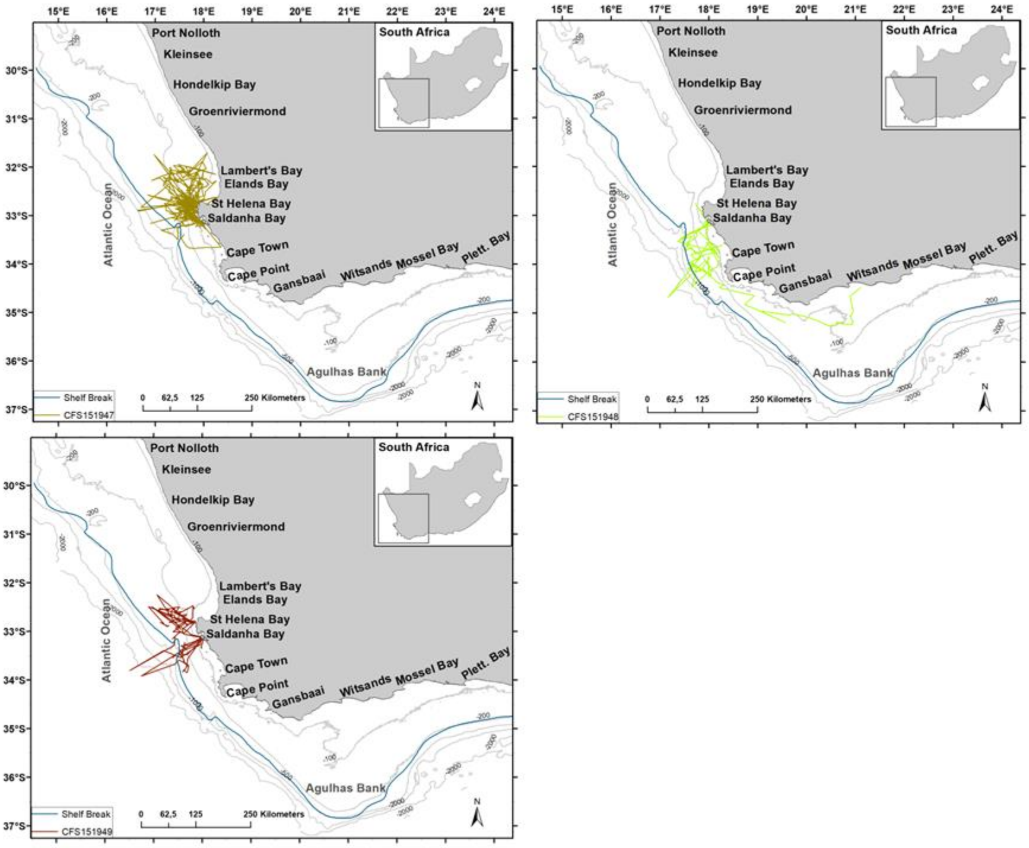

Figure 3.5b. Individual movements of female Cape fur seals tagged at Vondeling Island

Table 3.4. Summary statistics of African penguin trip characteristics for all trips undertaken.

Variable	min	max	median	q1	q3
Direction (°)	23.9	345.5	148.1	140.9	177.2
Duration (hr)	3.3	2004.6	46.1	19.0	82.8
Max distance (km)	2.8	368.9	18.6	9.1	28.8
Total distance (km)	6.9	2135.8	49.1	23.3	114.8

Table 3.5. Summary statistics of Cape fur seal trip characteristics.

variable	min	max	median	q1	q3
Direction (°)	101.9	354.2	258.5	204.1	309.7
Duration (hr)	25.5	2105.8	124.4	77.9	213.3
Max distance (km)	14.9	585.8	86.9	52.4	142.9
Total distance (km)	42.8	4708.5	256.7	139.1	762.6

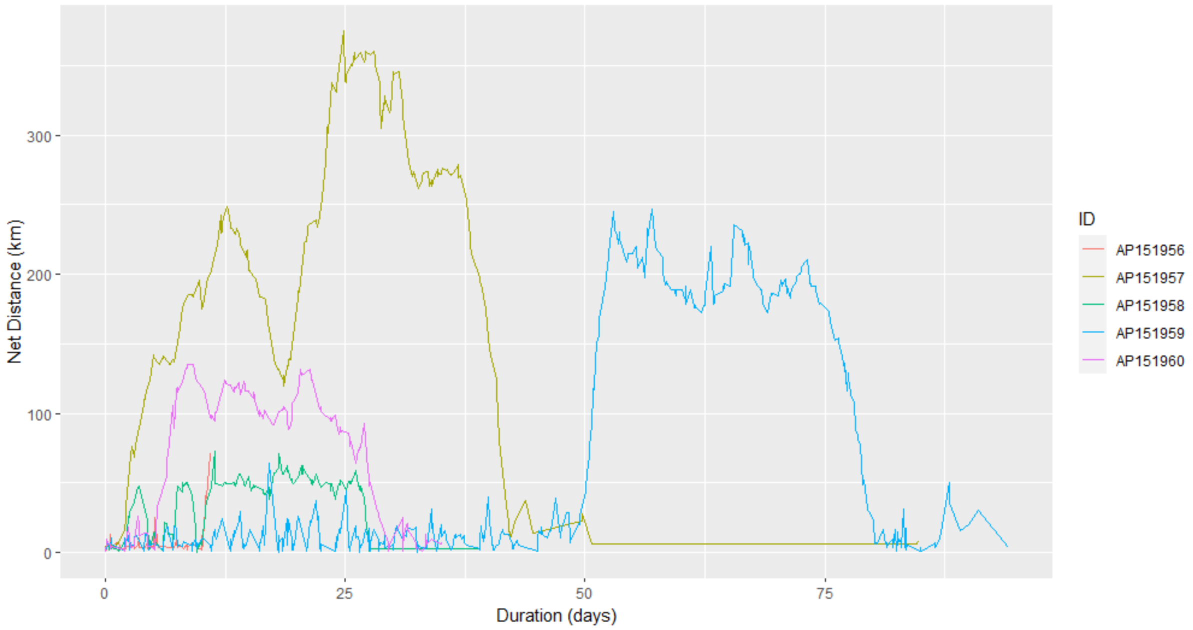

Figure 3.6. Net distances from the Vondeling Island covered by individual African penguins.

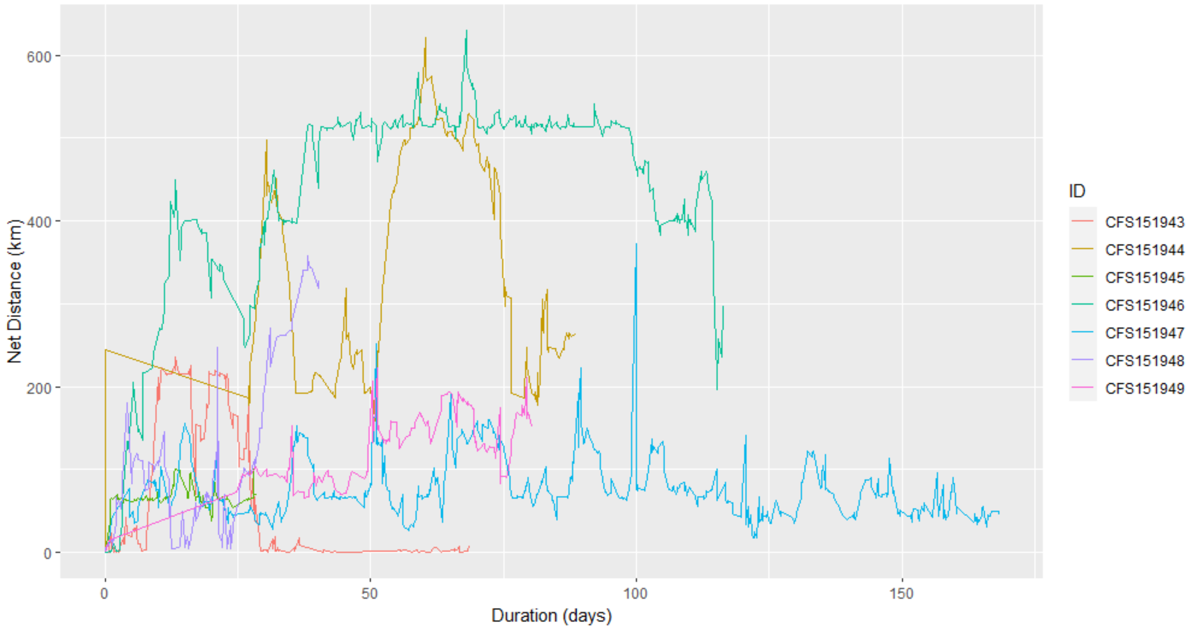

Figure 3.7. Net distances from the Vondeling Island covered by individual African penguins.

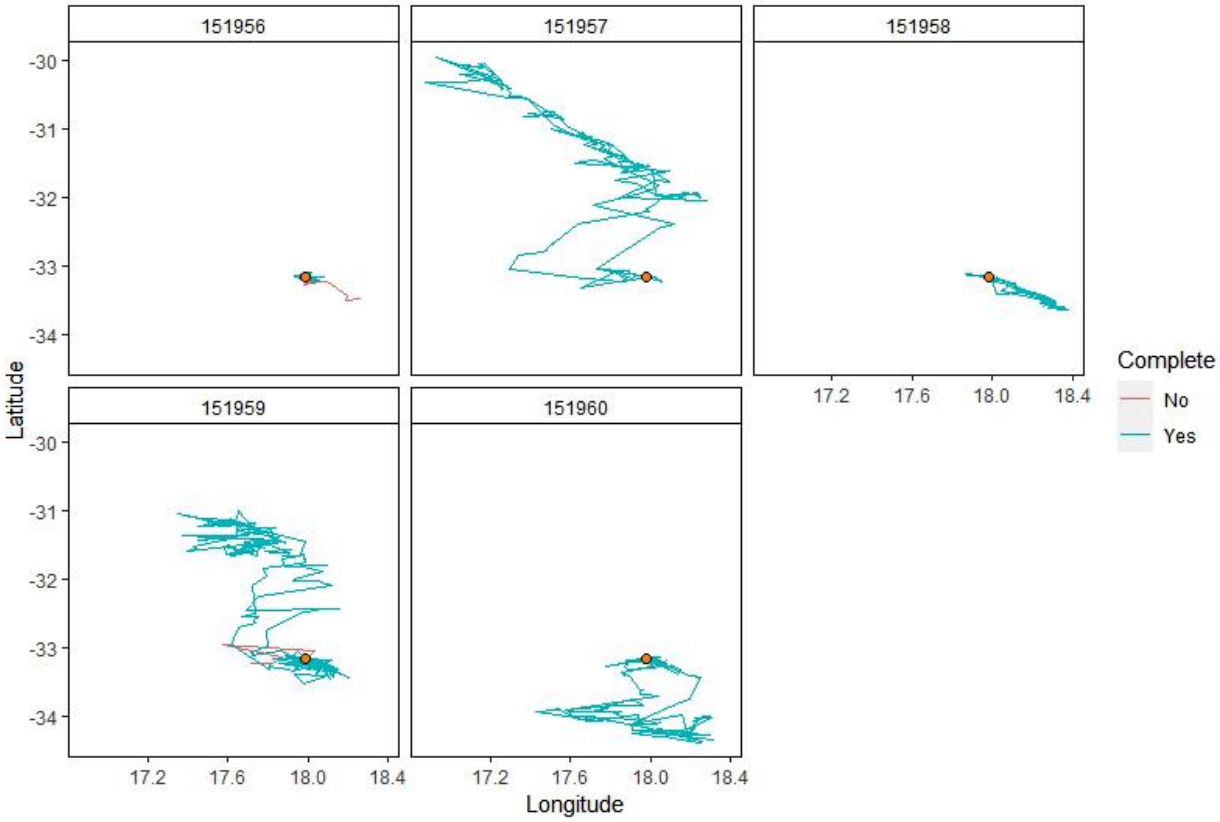

Figure 3.8. The output of function "*tripSplit*" after splitting data into individual trips showing both complete and incomplete trips undertaken by tagged African penguins. General direction of trips is also illustrated.

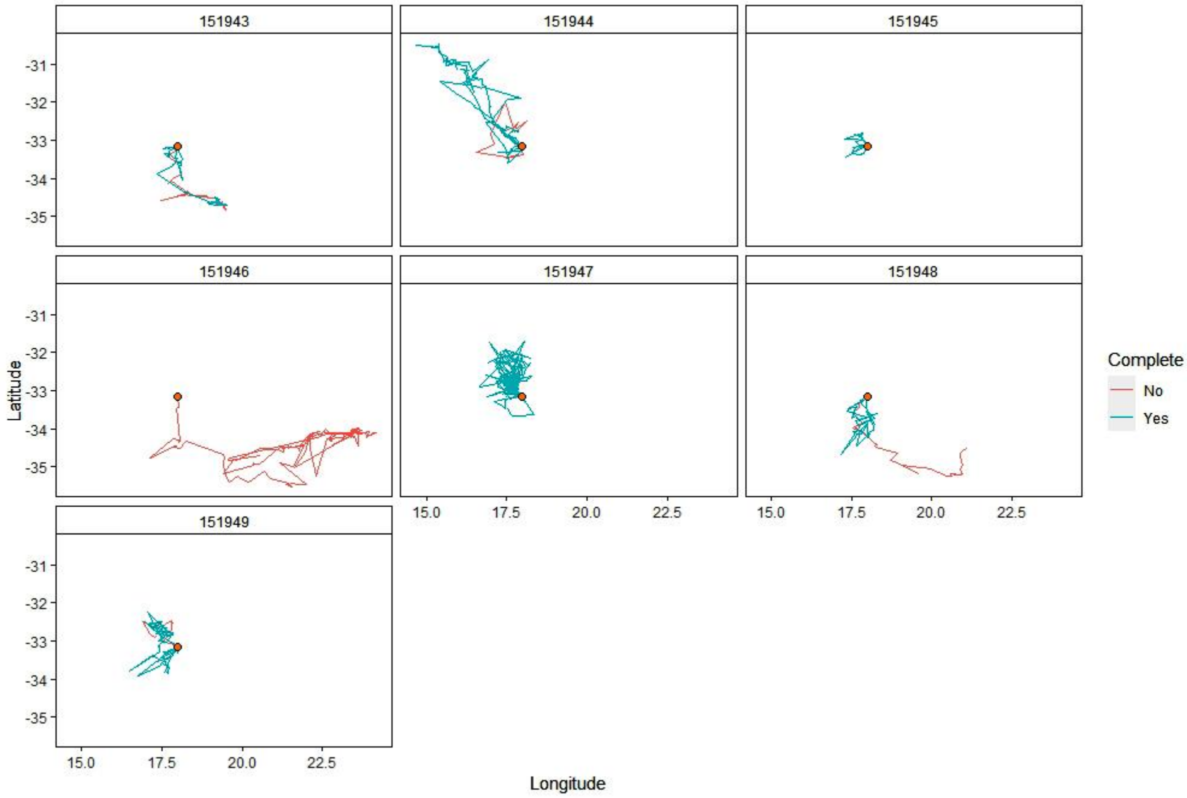

Figure 3.9. The output of function "*tripSplit*" after splitting data into individual trips showing

both complete and incomplete trips undertaken by tagged Cape fur seals. General direction of trips is also illustrated.

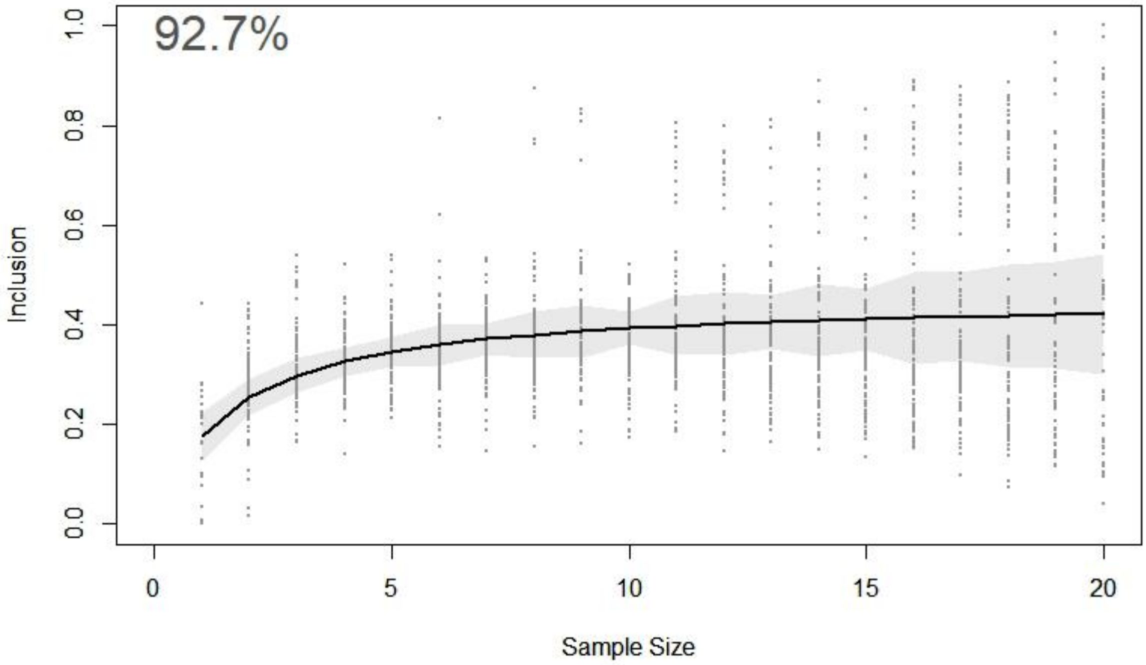

Figure 3.10. Representativeness of the data (n=5) for the source population of African penguins at Vondeling Island.

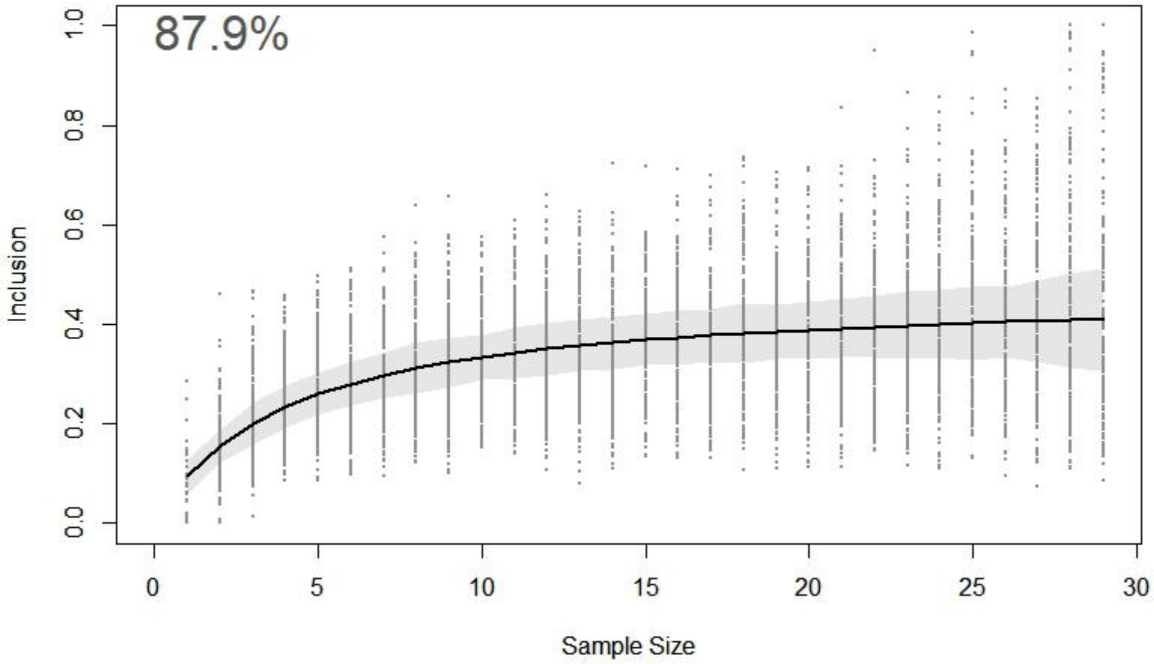

Figure 3.11. Representativeness of the data (n=7) for the source population of Cape fur seals at Vondeling Island.

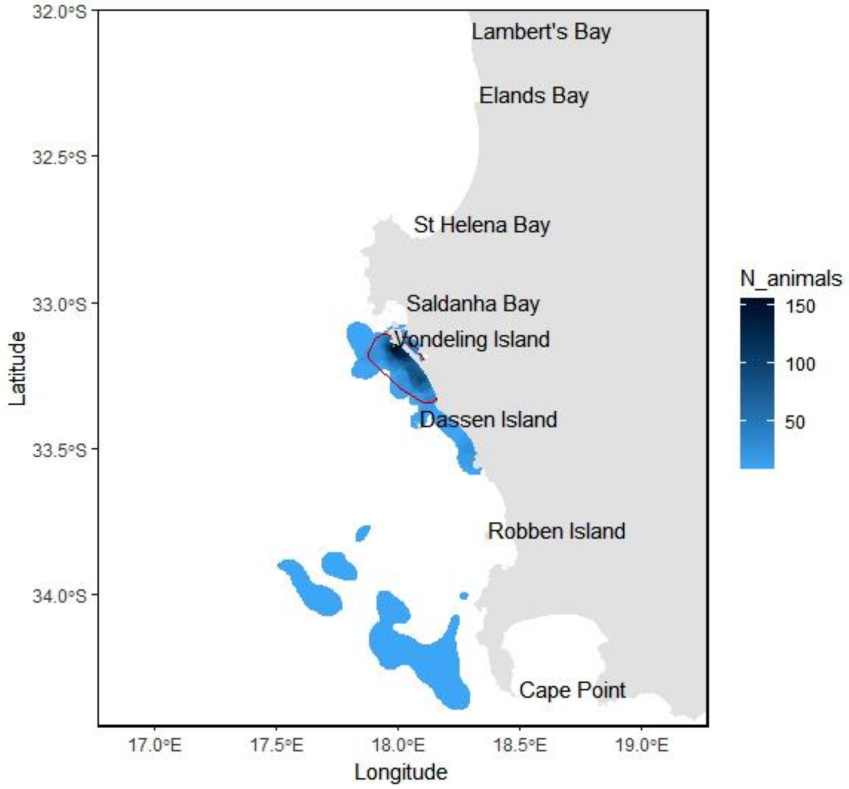

Figure 3.12. Marine Important Bird Area (mIBA) for African penguin delineated by red border.

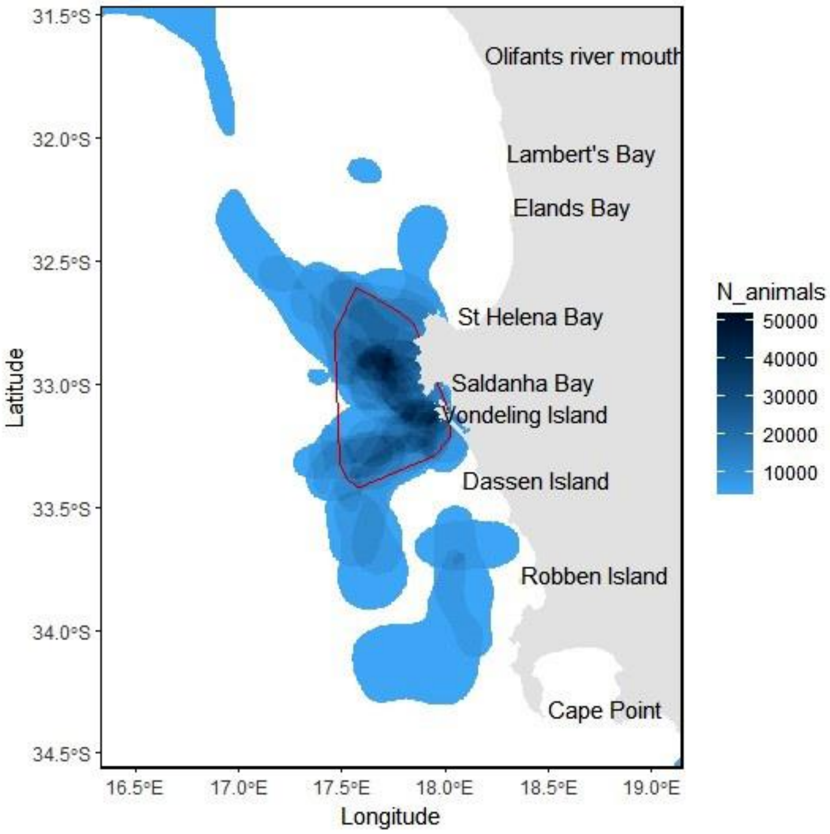

Figure 3.13. Marine Important Biodiversity Area (mIBAs) for Cape fur seals delineated by red border.

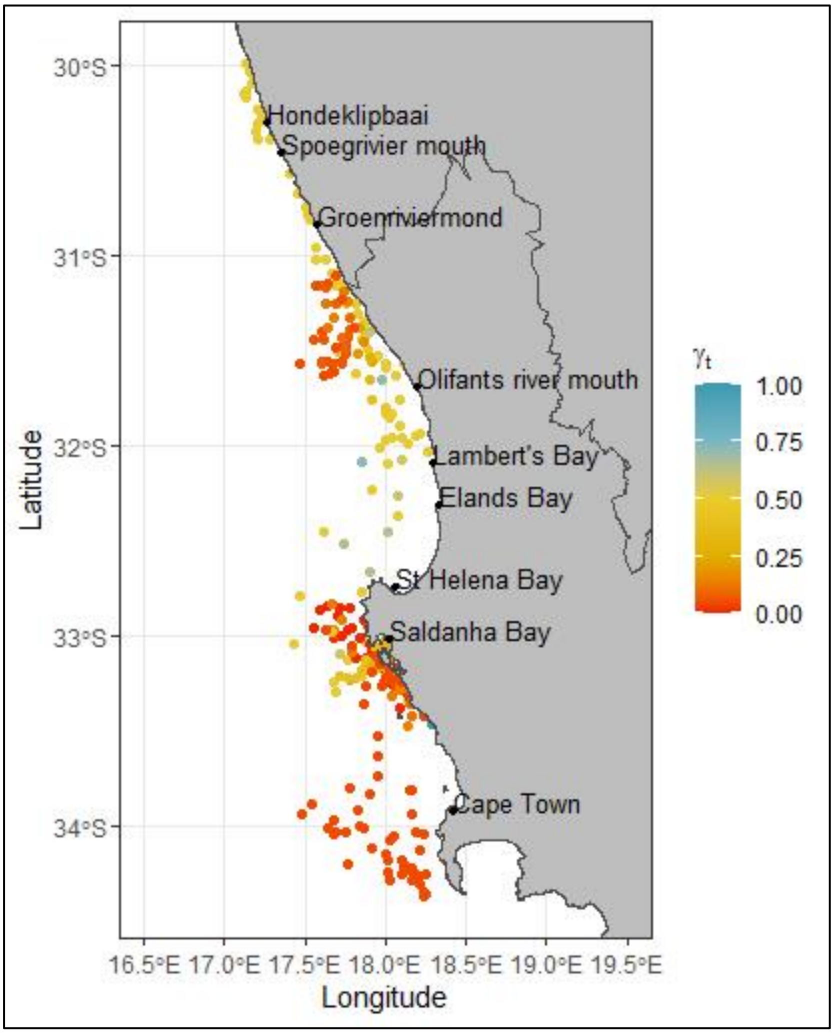

Figure 3.14. Map of SSM-filtered African penguin tracks tagged at Vondeling Island. Each position is colour coded according to its move persistence value ($\boldsymbol{\gamma}_t$) calculated from move persistence model.

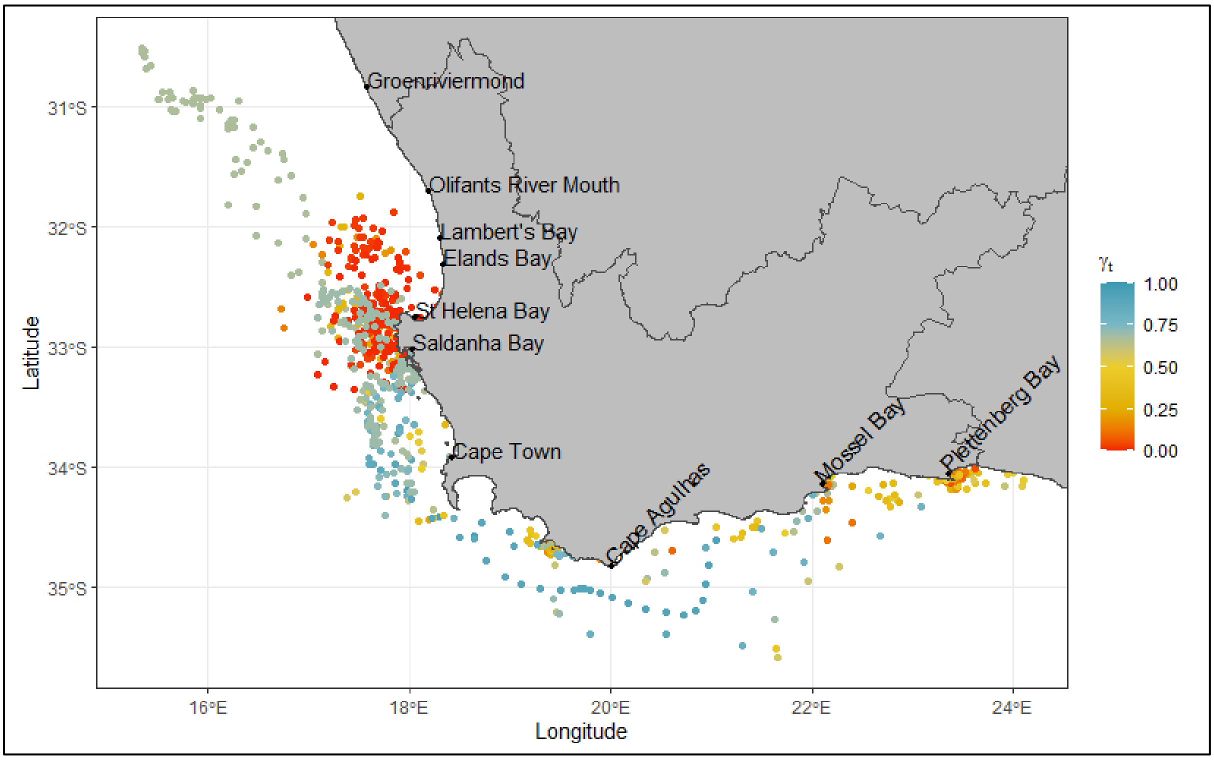

Figure 3.15. Map of SSM-filtered Cape fur seal tracks tagged at Vondeling Island. Each position is colour coded according to its move persistence value ($\boldsymbol{\gamma}_t$) calculated from move persistence model.

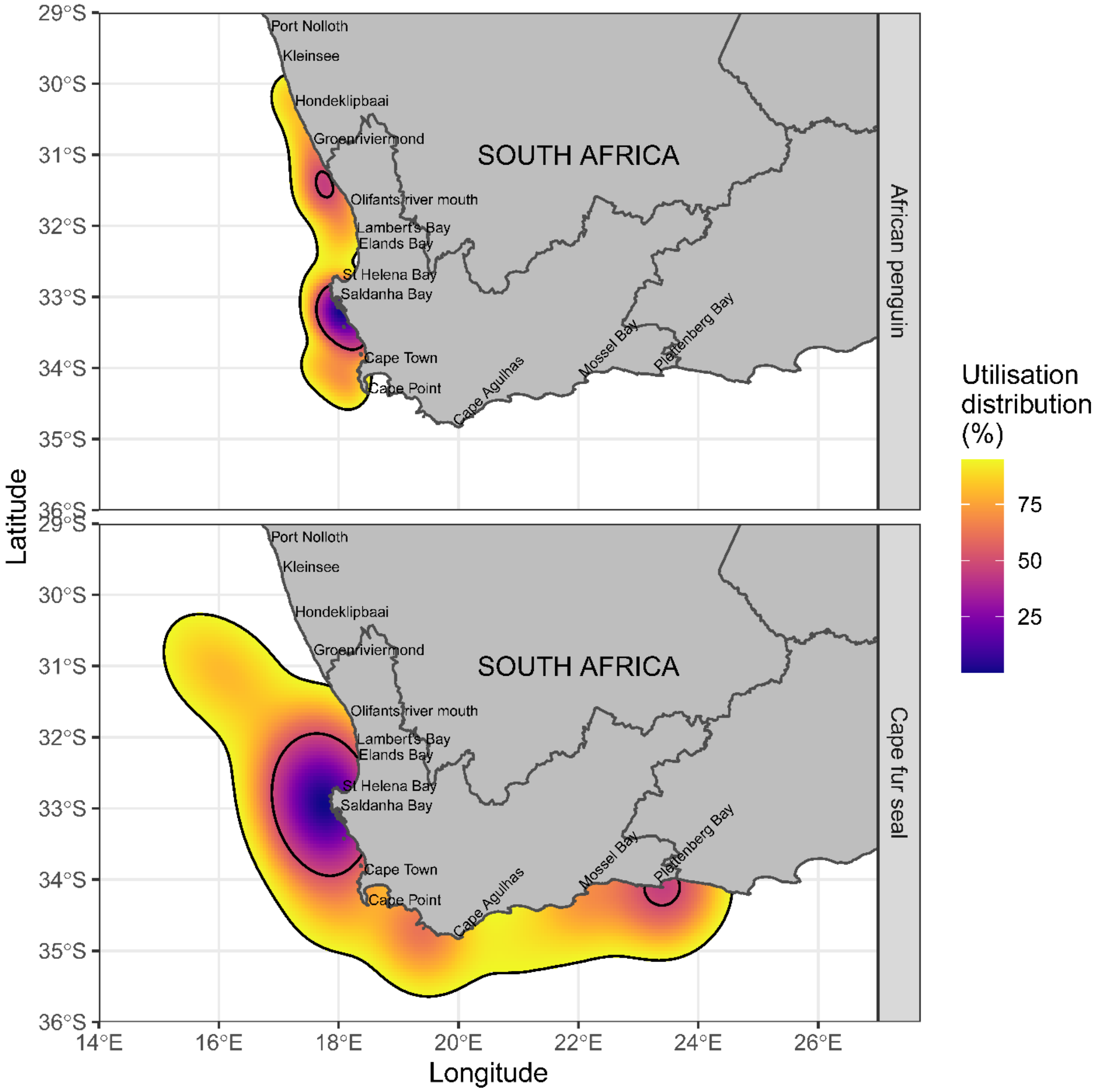

Figure 3.16. Overall kernel utilization distributions (0-95%) of African penguin (top panel) and Cape fur seal (bottom panel). Outside black contours represent 95% (home ranges) and inside black contours 50% (core areas).

Table 3.6. Overall kernel distribution estimations (50% and 95% KDE) of African penguins and Cape fur seals tagged at Vondeling Island

Species	**50% UD Area (km^2)**	**95% UD Area (km2)**
African Penguins	7,865	40,495
Cape fur seals	25,682	158,486

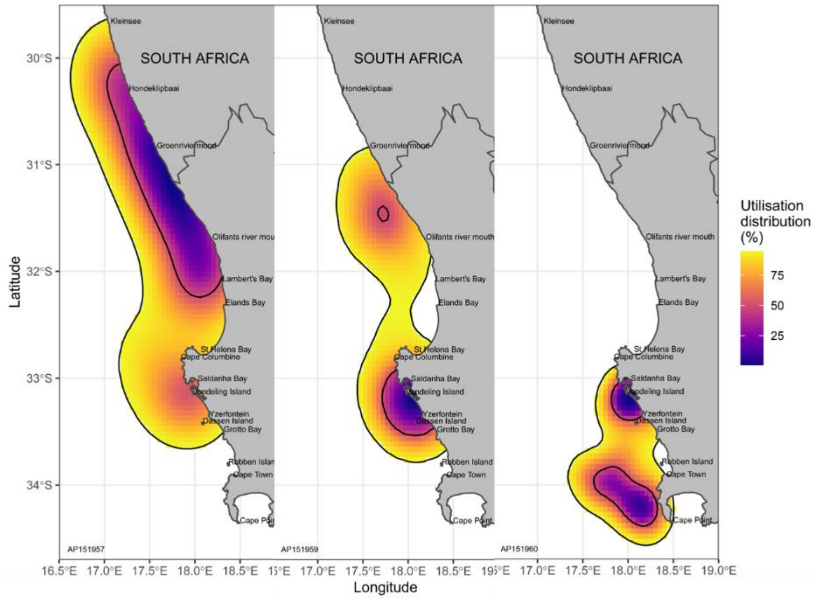

Figure 3.17a. African penguin kernel utilization distributions (UD's 0-95%) with outside black contours representing 95% (home ranges) and inside black contours 50% (core areas). UD's maps are given in descending size (Table 7). Left: AP151957, middle: A151959, right: AP151960.

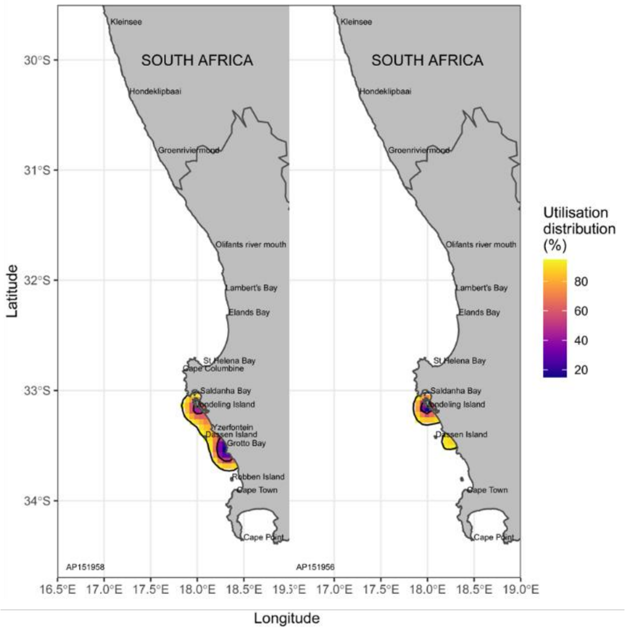

Figure 3.17b. African penguin kernel utilization distributions (0-95%) with outside black contours representing 95% (home ranges) and inside black contours 50% (core areas). UD's

maps are given in descending size (Table 7). Left: AP151958, Right: AP151956.

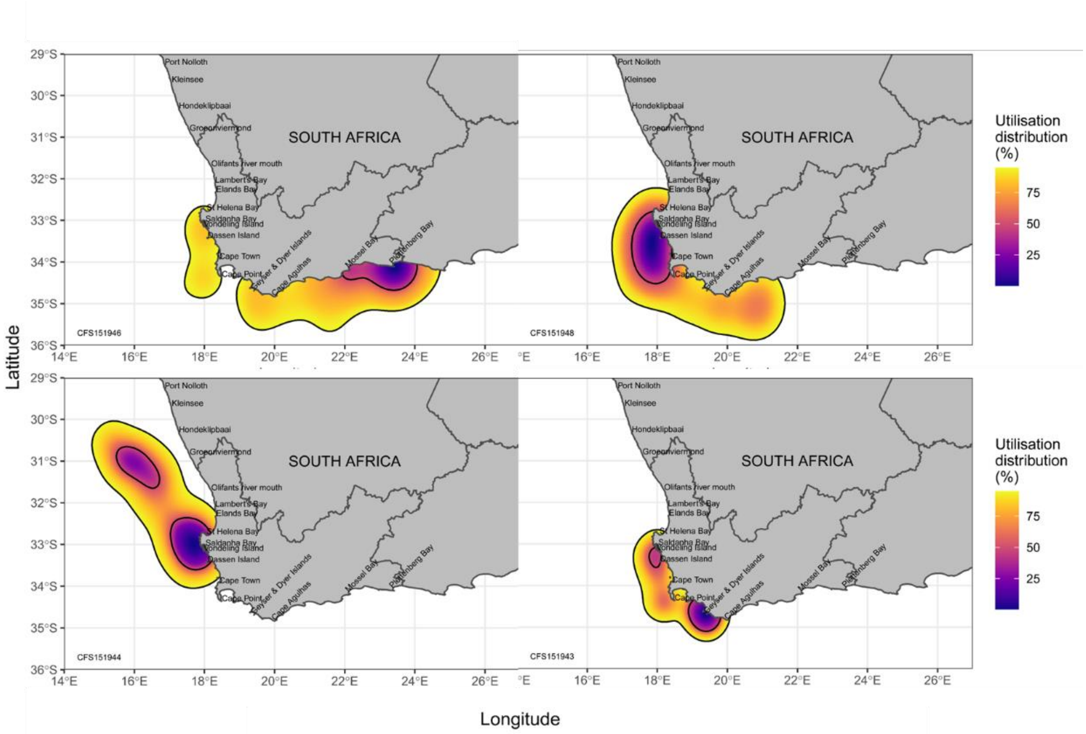

Figure 3.18a. Cape fur seal kernel utilization distributions (0-95%) with outside black contours representing 95% (home ranges) and inside black contours 50% (core areas). UD's maps are given in descending size (Table 7). Top left: CFS151946, top right:CFS151948, bottom left:CFS151944, bottom right:CFS151943.

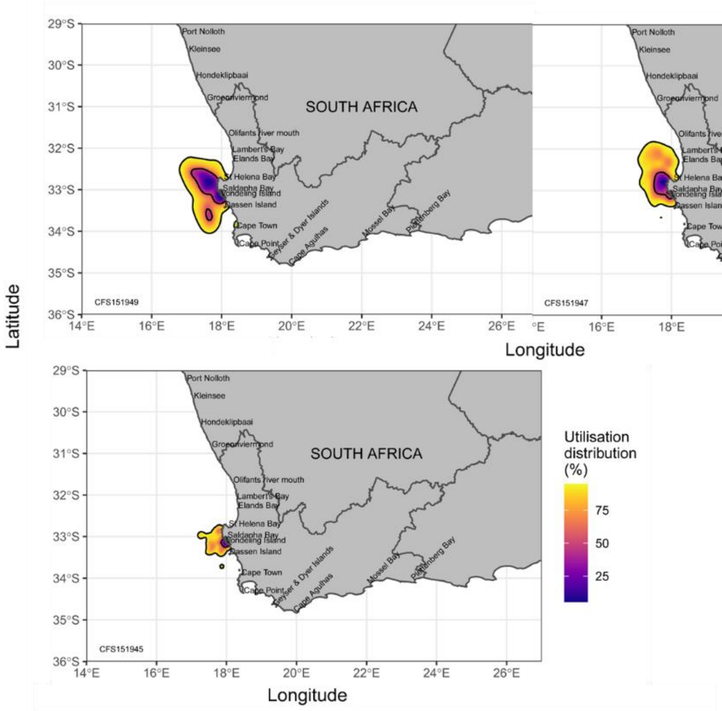

Figure 3.18b. Cape fur seal kernel utilization distributions (0-95%) with outside black contours representing 95% (home ranges) and inside black contours 50% (core areas). UD's maps are given in descending size (Table 7). Top left:CFS151949, Top right:CFS151947, Bottom Left:CFS151945.

Table 3.7. Estimated individual sizes of home ranges (95% UD) and core areas (50% UD) for African penguins. UD denotes Utilisation Distribution.

Animal ID	**50% UD Area (km^2)**	**95% UD Area (km2)**
151957	8443	31,866
151959	3036	19,954
151960	3215	11,042
151958	305	1,439
151956	76	587

Table 3.8. Estimated individual sizes of home ranges (95% UD) and core areas (50% UD) for Cape fur seal. UD denotes Utilisation Distribution.

Animal ID	**50% UD Area (km^2)**	**95% UD Area (km2)**
151946	13476	84549,3
151948	16856	74915,0
151944	22962	73451,3
151943	5710	28670,0
151949	4763	15634,0
151947	2819	13383,8
151945	559	4383,1

Table 3.9. Index of overlap (0-1) for home ranges (95% kde) of African penguins and Cape fur seals tagged at Vondeling Island. Kde denotes kernel density estimator.

	Penguins	**Seals**
Penguins	1	0.78
Seals	0.20	1

Table 10. Index of overlap (0-1) for core areas (50% kde) of African penguins and Cape fur seals tagged at Vondeling Island. Kde denotes kernel density estimator.

	Penguins	**Seals**
Penguins	1	0.86
Seals	0.27	1

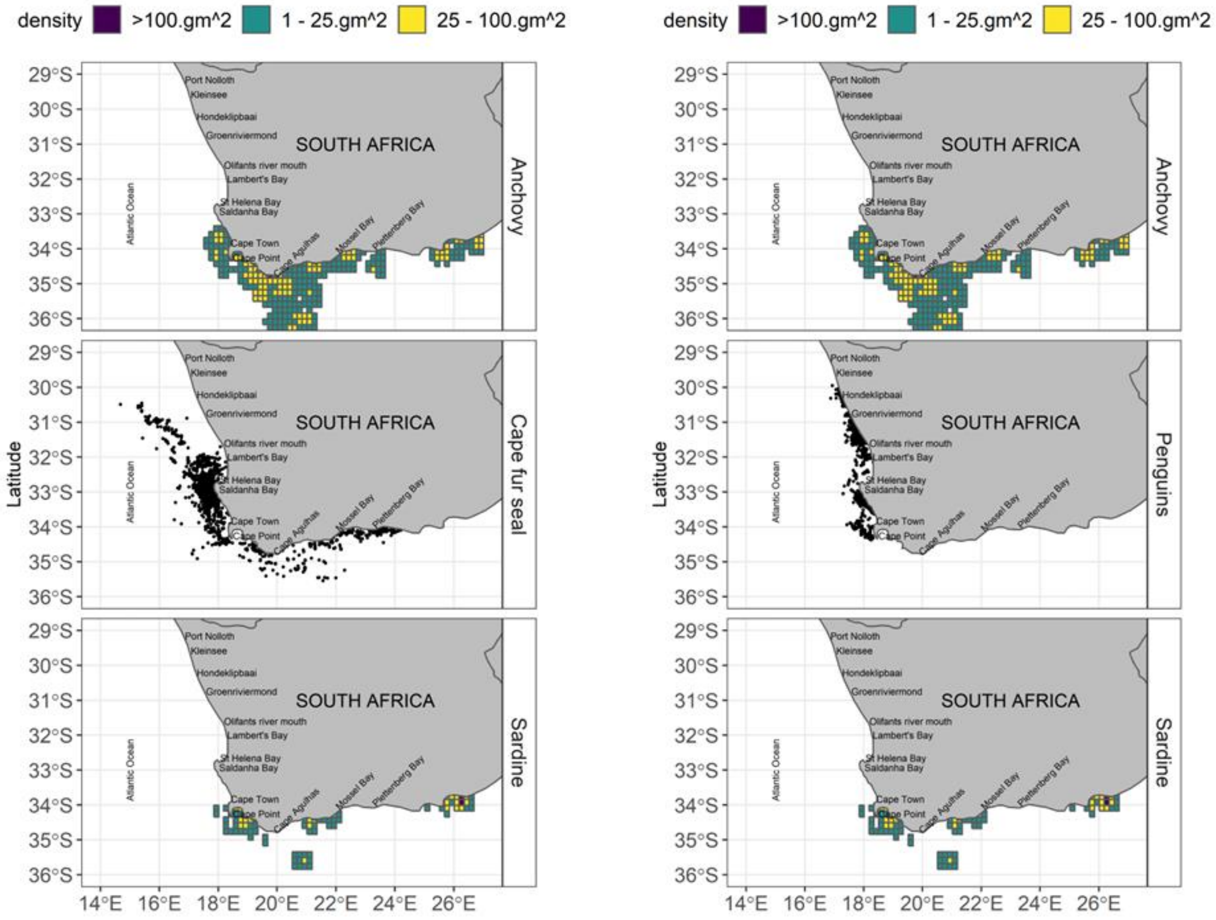

Figure 3.19. Distribution of anchovy and sardine densities relative to movements of African penguins and Cape fur seals.

Table 3.11. Overlap matrix of home ranges (95% kde) of African penguins and Cape fur seals breeding at Vondeling Island

	CFS 151943	**CFS 151944**	**CFS 151945**	**CFS 151946**	**CFS 151947**	**CFS 151948**	**CFS 151949**	**AP 151956**	**AP 151957**	**AP 151958**	**AP 151959**	**AP 151960**
CFS 151943	1	0,4	0,13	0,94	0,21	0,96	0,26	0,06	0,31	0,09	0,3	0,39
CFS 151944	0,19	1	0,06	0,2	0,21	0,36	0,19	0,03	0,35	0,04	0,23	0,14
CFS 151945	1	1	1	1	0,94	1	1	0,41	0,97	0,28	0,97	0,81
CFS 151946	0,26	0,12	0,04	1	0,06	0,45	0,07	0,02	0,08	0,03	0,09	0,11
CFS 151947	0,46	1	0,26	0,45	1	0,74	0,63	0,11	0,92	0,09	0,72	0,29
CFS 151948	0,41	0,03	0,05	0,69	0,15	1	0,15	0,03	0,21	0,04	0,17	0,17
CFS 151949	0,64	1	0,31	0,64	0,71	0,9	1	0,13	0,78	0,13	0,65	0,49
AP 151956	0,88	1	0,72	0,89	0,72	1	0,72	1	0,89	0,67	0,89	0,89
AP 151957	0,2	0,5	0,08	0,21	0,28	0,32	0,22	0,04	1	0,06	0,45	0,15
AP 151958	1	1	0,38	1	0,46	1	0,54	0.5	0,92	1	1	0,96
AP 151959	0,44	0,73	0,18	0,45	0,48	0,56	0,38	0,09	0,97	0,14	1	0,31
AP 151960	0,94	0.75	0.25	1	0,33	1	0,48	0,15	0,52	0,22	0,51	1

Table 3.12. Overlap matrix of core areas (50% kde) of African penguins and Cape fur seals breeding at Vondeling Island

	CFS 151943	**CFS 151944**	**CFS 151945**	**CFS 151946**	**CFS 151947**	**CFS 151948**	**CFS 151949**	**AP 151956**	**AP 151957**	**AP 151958**	**AP 151959**	**AP 151960**
CFS 151943	1	0,14	0,08	0	0,06	0,14	0,14	0,04	0	0	0,14	0,14
CFS 151944	0,05	1	0,03	0	0,12	0,32	0,19	0,13	0	0,01	0,21	0,08
CFS 151945	1	1	1	0	0,25	1	1	0,5	0	0	1	1
CFS 151946	0	0	0	1	0	0	0	0	0	0	0	0
CFS 151947	0,17	1	0,06	0	1	0,56	0,83	0,05	0	0	0,5	0,17
CFS 151948	0,06	0,4	0,04	0	0,09	1	0,15	0,01	0	0,04	0,26	0,25
CFS 151949	0,25	1	0,14	0	0,54	0,64	1	0,07	0	0	0,54	0,29
AP 151956	1	1	1	0	0,5	1	1	1	0	0	1	1
AP 151957	0	0	0	0	0	0	0	0	1	0	0,04	0
AP 151958	0	0,5	0	0	0	1	0	0	0	1	0,5	0
AP 151959	0,21	0,88	0,12	0	0,26	0,88	0,44	0,06	0,12	0,06	1	0,35
AP 151960	0,25	0,42	0,14	0	0,11	1	0,28	0,07	0	0	0,43	1

Chapter 4: Synthesis and Conclusions

The aim of this study was to describe the recolonisation of Vondeling Island by the Cape fur seal *Arctocephalus pusillus pusillus* and investigate potential impacts on endangered seabirds that were breeding at the island when the recolonisation took place. The endangered seabirds, African penguin *Spheniscus demersus*, Cape gannet *Morus capensis* and Cape cormorant *Phalacrocorax capensis* and Cape fur seals target commercially important anchovy *Engraulis encrasicolus* and sardine *Sardinops sagax* (Crawford et al. 2022; Gumede 2023). Bank cormorant *P. neglectus* targets fisheries overexploited West Coast rock lobster *Jasus lalandii* (Dyer et al. 2019). Abundance of these prey have drastically reduced off the west coast (van der Lingen et al. 2006, Cockcroft et al. 2008) negatively affecting the breeding performance of west coast seabird colonies (Makhado et al. 2021). Spatio-temporal changes in the distribution of breeding colonies of Cape fur seals were also noted (Kirkman et al. 2013), leading to recolonisation of previously held colonies such as Robberg peninsula (Huisamen et al. 2011), Vondeling Island (this study) and establishment of new colonies (Seakamela et al. 2024).

Chapter 2 reported on the recolonisation by scrutinising survey data of Cape fur seals and seabirds at the island (1990 to 2018). For Cape fur seals, data from land-based surveys and aerial photographic surveys focusing on pups were utilised. For seabirds, data from land-based surveys of breeding pairs and active nests of African penguins and cormorants were utilised. Presence data of African oystercatcher were also scrutinised. These data were used to investigate changes in population trends of the two faunal groups (seals and birds) and compare them with the state of their conspecifics breeding at other colonies in South Africa. Distribution of nests and roosting localities of different seabirds and seals were mapped to better elucidate possible competition for breeding space between seals and seabirds.

Juvenile Cape fur seal bulls were first recorded at Vondeling Island in 1993 followed by females which were recorded six years later. The first cohort of 16 pups was recorded in 2003 and 1253 were born in 2006. Based on pup survey data, the population grew by 38.5% per year between 2006 and 2018 (see Table 2.4 of Chapter 2). This growth is attributed to immigration from other breeding colonies. As central place foragers, female fur seals forage within a limited area during period of maternal care (Pomeroy et al. 2018). The locality of their breeding colonies tend to be in the vicinity of available prey resources (Hunt Jr et al. 1992). There was a decline in pup production at Kleinsee, the largest breeding colony in South Africa by size and pup production. At the end of the study period, pup production had reduced from 79,301 to 36,876, a decline of 42,425 pups. New colonies were established south of Kleinsee (and south of the West Coast). In the backdrop of reduced abundance of their preferred prey on the west coast, the shift in distribution of colonies may be in response to the shift in the distribution of prey. These factors lend credence to the deduction that initial female breeders were from the Kleinsee breeding colony.

Cape cormorants experienced the highest decline of all seabirds. Their decline was most pronounced during the period in which seals were well established and abundant. Trends of African penguins, bank, crowned and Cape cormorants declined at study site and adjacent Saldanha Bay islands, albeit at different proportions to Vondeling Island. There was a marginal increase in African penguin breeding pairs at Vondeling Island following installation of artificial nests in 2016. Cape fur seal utilisation of space at the island increased as rapidly the population increased. The effect was more pronounced for African penguins and Cape cormorants. Due to the loss of guano as a breeding substrate, penguins nest in the open and between boulders. This has left them vulnerable to the destruction of nests by the movement of seals while they traverse between the colony and the sea. A guano retaining wall had been built during the guano harvesting period. This wall had prevented seals from extending into the centre of the island where African penguins and Cape cormorants had nested. Seals breached this wall and extended into this area. Penguins in this area now have artificial nests to offer protection but Cape cormorants have not been seen nesting therein since. Although Cape fur seals have encroached into bank and crowned cormorants nesting areas, the versatile utilisation of island structures (houses and defunct jetty) by the cormorants mitigated a potential impact. These results indicate that seals (re)colonising islands with established breeding colonies of seabirds can be detrimental to their breeding performance, largely by encroaching into their nesting areas. This is especially true for seabird breeding on the ground and low-lying rocks.

Chapter 3 utilised telemetry data to investigate potential competition for forage resources between Cape fur seal and the African penguin. The two species are sympatric and share similar dietary niche. Competition theory predicts that in nature, species that have similar niches and are sympatric cannot coexist (Hardin 1960). To better understand their at-sea movements and possible horizontal overlaps, Platform Transmitter Terminal (PTTs) tags were for the first time concurrently deployed on lactating female Cape fur seals and adult penguins with chicks and their movements tracked. Their home ranges, core areas and overlap were calculated at individual and population level. Further, marine Important Bird/Biodiversity Areas (mIBAs) for both species were determined. The African penguin was selected for this study due to their relatively dire conservation outlook (Sherley et al. 2020) and ongoing debates on various approaches to help halt their decline. These include installation of artificial nests (Sherley et al. 2012), predation management (Makhado et al. 2009) and implementation of fishing limitations for the small pelagic fishery around selected breeding colonies, to mitigate apparent competition with fisheries (DFFE 2023).

At the population level, Cape fur seals had a larger home range (158,486 km^2 vs 40,495 km^2 for penguins) and core area (25,682 km^2 vs 7,865 km^2 for penguins). Home ranges and core areas overlapped by 78% and 86% respectively. The core areas were around and in the vicinity of the colony for both species, where the overall overlap was apparent. The species are central place foragers (CPF) (during breeding) and their distances from colony are restricted by the distribution of their prey (Massardier-Galatà et al. 2017). Seals' core areas extended north to coincide with waters associated with the Cape Columbine upwelling cell; while penguins' core areas extended south towards Yzerfontein. The importance of these waters for both species was further supported by determination of mIBAs and low move persistence values (which coincide with Area Restricted Searchers or Feeding).

At the individual level, there were dissimilar intra and inter-specific core areas. There was relatively less overlap at the individual level than there was at the population level (i.e., pooled data). This could be one mechanism with which intra- and inter-specific competition is mitigated. Such niche partitioning has been reported for both penguins (Rosciano et al. 2016) and seals (Jones et al. 2020). Dedicated studies are required to better understand how the two species limit competition. However, insights can be drawn from their known attributes. Cape fur seals generally feed at depths of <100 m (Kirkman et al. 2019) while African penguins feed at ~30 m (Wilson, 1985), although these can change based on feeding habitat and the depths at which their target prey is found. African penguins conduct diurnal foraging (Wilson & Wilson 1990) while Cape fur seals can forage diurnally and nocturnally (Kirkman et al. 2019; Botha et al. 2020). In terms of prey size, African penguins feed on anchovy of length range 50–120 mm (Wilson 1985b) and Cape fur seals of 17.1–249.8 mm (Gumede 2023).

Both African penguins and Cape fur seals at Vondeling Island are likely competing with conspecifics from other colonies. Core areas of Vondeling Island penguins appear to overlap with those from Dassen Island reported in Carpenter-Kling et al. (2022). Similar distribution patterns were apparent between Cape fur seals from Vondeling Island and those from False Bay, reported in Botha et al. (2020). The results in this chapter provide a baseline from which to develop further research. The reported overlap is a basis on which competition can be inferred, though may not fully explain how this is mitigated, if at all. In a compromised ecosystem, Central place forager species may be forced to travel further from the colony due to low availability of foraging resources around the breeding colony (Staniland et al. 2010). This will inevitably increase travel and foraging cost to the individuals (Massardier-Galatà et al. 2017). The demonstrated ability of Cape fur seals to travel further than African penguins suggest that in a compromised ecosystem, seals would out-perform penguins.

Recommendations for future research

This study has demonstrated the importance of concurrent investigations on sympatric marine top predators. However, this is a tip of the iceberg and requires in depth investigations of parameters such as diet, energetics, and vertical movements of these species. The diet of Cape fur seal in South Africa is subject of dedicated and opportunistic monitoring (Gumede 2023). Although diet studies have been conducted on African penguins (Wilson 1985a, Crawford et al. 2011), crucial metrics such as length frequencies would assist in determining overlap if prey size targeted. This effort should be undertaken at Vondeling Island to ensure that the effort is colony specific, and conclusions are not inferred.

This study utilised horizontal movement data from which inferences could be made about importance of areas frequented by the two top predators. This is based on the inclination of marine predators to restrict their foraging effort in areas of high prey abundance i.e. Area Restricted Search (Kareiva & Odell 1987). There has been some evidence that these horizontal movements correspond with vertical movement (feeding dives) (Planque et al. 2020). However other studies have demonstrated that this is oversimplification of a complex behaviour where a one-dimensional approach is used for a multi-dimensional issue (Bestley et al. 2019). It is this recommended that future studies should incorporate both a vertical and horizontal dimension to fully understand at-sea behaviour of these two species (see Riaz et al. 2021).

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