Foraging ecology of the African Penguin *Spheniscus demersus* in relation to ocean physical processes

Rowen Brandon van Eeden

Dissertation presented for the degree of Master of Science
Percy FitzPatrick Institute of African Ornithology, DST~~TS~~/NRF Centre of Excellence
Zoology Department, Faculty of Science,
University of Cape Town

September 2012

Foraging ecology of the African Penguin *Spheniscus demersus* in relation to ocean physical processes

CONTENTS

Plagiarism declaration

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

____

Abstract

Marine top predators play a pivotal role in stabilizing marine food webs. Their presence and behaviour can be used as a bio-indicator of the state of our oceans, making them invaluable tools for detecting changes in the marine environment. However, it is important to understand how predators integrate with their environment if we are to fully interpret the link between top predators and lower trophic levels. Seabirds are top predators facing substantial threats from fisheries and climate change, thus understanding their ecology is of growing importance. Their life histories characterized by long life spans and late maturation, have evolved as a means to cope with the heterogeneous ocean landscape, low prey availability and often long commutes between foraging and breeding areas. These birds have also evolved a suite of strategies to increase the probability of locating these scarce and patchy prey distributions. For instance, many seabirds, especially long-range foragers such as albatrosses and the larger penguins, are known to utilize temperature gradients to locate meso-scale (100-1000 km) ocean physical features such as eddies, fronts and upwelling zones where nutrients are advected to the euphotic zone from deeper cool bottom waters. This nutrient injection drives productivity, making these features predictable feeding grounds for top predators. Some seabirds are also capable of using olfactory cues and currents to locate these features. However on a fine (> 1 km) to coarse scale (1-100 km) it is less well understood how these predators ~~locate~~ find patchy prey ~~distributions~~ locations where physical cues such as temperature may be more ephemeral.

Breeding African Penguins *Spheniscus demersus* have short foraging ranges (10-50 km), and forage in dynamic coastal environments making them an ideal model for understanding how short-range top predators locate their prey. By modeling the sea-surface thermal habitat preferences and the dive behaviour in relation to thermoclines of African Penguins, I assess how these short-range foragers use ocean physical processes to increase the probability of locating their small pelagic prey. African Penguins breeding on Bird Island, Algoa Bay, were capable of utilizing temperature as a potential cue to foraging in three-dimensions. Penguins mainly commuted east and south of their colony, likely predicting the occurrence of cool nutrient rich waters

from a periodic upwelling cell. Penguins departed in the early morning before dawn travelling towards these areas, maximizing the time they foraged during the day in cooler waters with a higher probability of containing prey patches. Penguins used a correlated random search strategy during foraging, suggesting that they searched continuously for prey, and it is therefore likely that penguins are limited by the patchy distribution of prey rather than an abiotic heterogeneous marine environment. When diving, penguins utilized thermoclines that fronted cool waters (14.1 ± 2.2 °C) as a potential cue to prey. However, their dive depths may also reflect the distribution of their prey, which may aggregate around thermoclines due to increased productivity. Penguins dived deeper, foraging below the thermocline, when the thermocline depth increased and also responded in their dive behaviour under different thermocline structures. For instance, when thermoclines were a diffuse barrier to nutrients and less likely to concentrate prey, birds dived deeper towards the benthos. Warm water intrusions into Algoa Bay from the Agulhas Current resulted in birds diving deeper in search of cooler bottom waters.

This research demonstrated the dual utility of bio-loggers as a method for generating accurate, high-resolution oceanographic data. These data can be used in future studies, generating a cross disciplinary platform for research. The thesis augments our knowledge base of the African Penguins foraging ecology. African Penguins show flexibility in their foraging behaviour by adjusting their dive behaviour to subsurface thermal structures. Penguins also demonstrated foraging optimization by using temperature cues and behavioral switching to maximize the probability of locating prey patches on a fine temporal and spatial scale. The distribution of primary production and small pelagic prey fishes in relation to temperatures require further investigation, as the behaviour of African Penguins suggests that these fishes occupy specific thermal habitats. By knowing the distribution of these fishes we can determine if African Penguins are utilizing temperatures as a cue or the temperatures used by African Penguins simply reflect the distribution of their prey.

Acknowledgments

Firstly and most importantly I would like to extend my utmost gratitude to my supervisors, Dr Lorien Pichegru and Assoc. Prof. Peter G. Ryan. I would like to thank Lorien for conceiving this project and teaching me both invaluable life and academic skills. Peter and Lorien critically assessed my work, devoting their time and skills to this project. Peter has helped me develop a strong analytical approach to science and has aided in helping me discover my written voice. I struggle to imagine how one could have a better balance of supervision and I truly have little idea how I would have made it this far without their support.

My acknowledgements extend to my parents, Albert and Karen, and my sister Jocelyn, for their support through my studies. They continued to encourage and guide me through the hardest parts of this thesis. Thank you for housing and feeding me as well as for financial support.

I would like to thank the team at the South African Environmental Observation Network (SAEON) for their help with this project. Angus Paterson (Manager of the Elwandle node at the time of data collection), Shaun Deyzel, Sean Bailey and Bruce Donovan assisted in transport to and from Bird Island. Thank you for the time and effort you put into managing your research vessel *Ukwabelana* as well as risking the sharks when installing temperature and current recorders at the bottom of the freezing Algoa Bay. I would like to make a special thank you to Wayne Goschen for disseminating data and guiding me in analysis.

I would like to thank Lloyd Edwards of Raggy Charters, his dogs, his family and his friends for their support in and out of the field. Lloyd opened up his home to me in Port Elizabeth for which I will be forever grateful. I would like to thank you for the invaluable times we spent at sea and helping me find my sea legs.

From SANParks I would like to thank the Marine Rangers: Roget Fox, Henvik Visser, Guy Padayachee and your team for transport to Bird Island, accommodation and

security. The laughs and stories on Bird Island made it a memorable time not many are fortunate enough to experience.

I would like to thank Assoc. Prof. Akinori Takahashi and Dr Cedric Cotté for help with analytical advice and for help with circular statistics, respectively. Furthermore, I would like to thank Dr Sean O'Donoghue for assistance with SST data acquisition.

I would like to thank everyone involved at the FitzPatrick Institute especially Dr Tim Reid and Prof. Graeme Cumming~~s~~ for statistical advice and Dr Timothée Cook for constructive discussion. Alistair McInnes assisted with GIS mapping. A special thank you needs to be extended to the cogs of the Fitz: Chris Tobler who aided in technical computer related issues, Anthea Links, Tania Jansen and Hilary Buchanan for ~~your~~ help with administrative processes, and Margaret Koopman who runs one of the most pristine ornithological libraries. I would also like to thank Dr Rob Little our Manager and especially Prof. Phil Hockey, our Director.

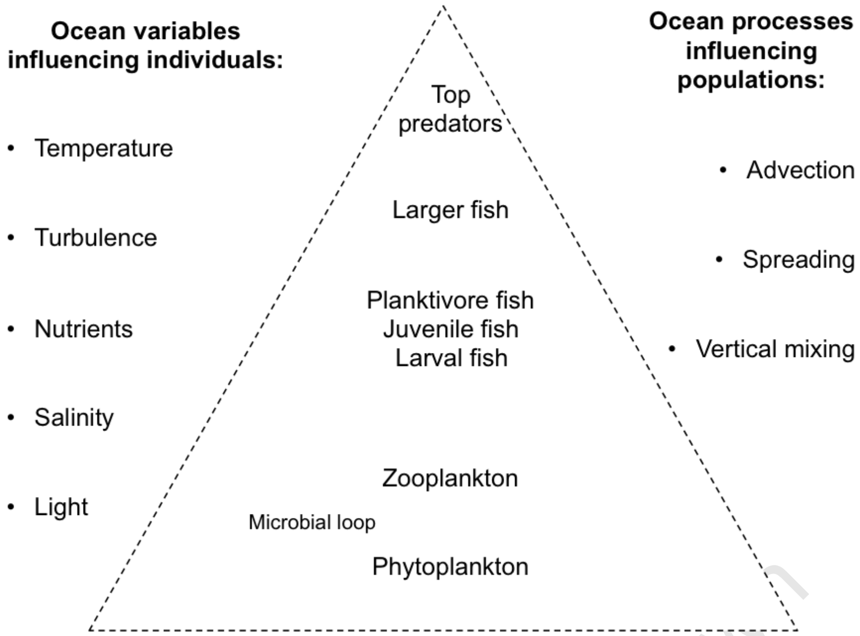
Finally, I am ever indebted to my close friends for all your support.

Chapter 1

-General Introduction

Marine top predators are positioned at the pinnacle of food webs and are ultimately affected by the stability of lower trophic levels (Moloney et al. 2011). However, the abiotic conditions of the oceans govern primary production as a function of nutrient availability, light availability, salinity and to a lesser extent temperature. Ocean physical processes such as eddies, upwelling zones and fronts bring nutrient rich bottom waters into the euphotic zone allowing phytoplankton to bloom, thus stimulating the food chain that leads to top predators (Figure 1.1; Moloney et al. 2011). We therefore expect top predators to be associated with these processes that drive ocean productivity due to enhanced primary production (Bost et al. 2009). Seabirds are top predators that are highly associated with such features. For example, King Penguins *Aptenodytes patagonicus* travel hundreds of kilometres towards oceanic fronts or meso-scale (100–1000 km) eddies using currents and temperature gradients to locate these features (Charrassin and Bost 2001; Cotté et al. 2007; Trathan et al. 2008). Top predators such as the African Penguin *Spheniscus demersus* forage on a much finer scale (10-50 km; Wilson 1985), where processes are more ephemeral than meso-scale features. Answering questions regarding predator association with physical features on a meso-scale is already complex (Bost et al. 2009). At finer scales this complexity is magnified. Thus it is no surprise we lack fundamental ideas on how short-range foragers structure their foraging trips to locate areas that may increase the chances of locating prey.

In order to effectively~~properly~~ conserve African Penguins, it is necessary to gain a better understanding of their habitat use and behaviour in relation to the processes that govern local productivity and prey distribution. If foraging behaviour and the areas African Penguins forage in are linked to local physical processes we can aid~~better~~ the survival of these birds by implementing protected areas and appropriate fisheries management measures. Each chapter of this thesis is written as a stand-alone paper. Although this results in some



repetition, it has been done to facilitate dissemination of results through publication.

Figure 1.1: Trophic pyramid in the oceans showing the environmental forces governing the abundance and occurrence of individuals and populations within an ecosystem. Adapted from Moloney et al. (2011).

Conservation importance of, and challenges faced by seabirds

Direct and indirect exploitation, habitat degradation, fishing, pollutants and climate change continue to threaten marine species and their habitats (Burger and Gochfeld 2001; Brothers 1991; Myers and Worm 2003; Shannon and Crawford 1999, Walther et al. 2002). In the modern industrial era, fisheries have had perhaps the most substantial negative effects, reducing species biomass by up to 16% per annum (Myers and Worm 2003). In the context of marine birds, fisheries also contribute to the significant decrease in seabird populations either directly through by-catch (e.g. Brothers 1991) or indirectly through competition for shared prey items (e.g. Furness and~~&~~ Ainley 1984; Pichegru et al. 2009; Croxall et al. 2012).

~~Due to the considerable amount of prey s~~Seabirds consume much greater quantities of prey in comparison to other marine species, such as mammals and predatory fish~~, they are considered predators~~ (Furness 1990). For instance, seabirds on the west coast of South Africa consumed about 5 000 t of Anchovy *Engraulis encrasicolus* per year in the 1980s (Crawford et al. 1991). Top predators are often charismatic species and can facilitate the conservation and management of entire ecosystems (Simberloff 1998; Sergio et al. 2006). Their pivotal role as flagship species can aid the conservation of other species that share their habitat, generate economic revenue and encourage public conservation appeal (Simberloff 1998). In addition, their presence and behaviour is indicative of the functioning of lower trophic levels making them ideal candidates for understanding ecosystem functioning (Cury et al. 2003). Seabirds can thus act as indicators for environmental change such as climate related or fisheries related changes, that are often difficult to measure (Furness and Camphuysen 1997). Finally, top predators are important for the top down control of~~stability of~~ marine ecosystems, therefore it is imperative that large losses of seabirds are mitigated if we are to maintain an evolved balance in the oceans and avoid trophic cascades (Cury et al. 2003).

Seabird life history traits such as long life spans, ~~reduced~~ small clutch sizes, slow growth rate, and late maturation are traits that have been largely driven by the temporal and spatial inability to provide sufficient food for their chicks in successive breeding seasons (Lack 1968; Ricklefs 1990). Indeed, such traits buffer them against some short-term environmental variability. Seabirds also demonstrate behavioural plasticity, such as prey switching or altering foraging behaviours, which helps them cope with environmental unpredictability (Deagle et al. 2008; Pichegru et al. 2010; Crawford et al. 2011). However, long-term shifts beyond the inter-annual fluctuations in prey, with which seabirds have adapted to cope, may have drastic effects on many species (Kappes et al. 2010). Species that are more flexible may be able to adapt to change faster, but the costs of adapting to a changed environment may resonate in future generations, through e.g. decreased reproduction associated with prey changes (Pierotti and Annett 1990). Environmental perturbations can rapidly change marine habitats and their species composition, therefore it is important to understand as many connections in the marine food web as possible if we aim to predict the down stream effects of on-going global change (Moloney et al. 2011). Furthermore, we need to understand the behavioural links between seabirds and their prey.

Seabird foraging adaptations to locate prey

The energetics and life histories of seabirds forces them to locate prey in as short a time or as small an area as possible (Weimerskirch 2007). This is especially pertinent to flightless species such as penguins that expend a large amount of time travelling to locate prey (Froget et al. 2004). All breeding seabirds are central place foragers; they must return to their nests to relieve partners from incubation or brooding duties and must gather enough food to feed their chicks as well as sustain their own energy needs. Thus, they are under substantial energetic constraints during the breeding season and maximising energy intake during this period is of utmost importance (Stearns 1992).

Seabirds forage in an environment that is largely heterogeneous, often highly variable, and unpredictable (Cury et al. 2003; Weimerskirch 2007). Marine top predators utilize sophisticated search strategies and cues to aid in dealing with this environmental heterogeneity and to reduce the energy required when locating areas with greater food availability (Bailleul et al. 2007; Trathan et al. 2008). Physical oceanographic features such as eddies, fronts, currents, upwelling cells and thermoclines all have the ability to increase productivity or concentrate prey, creating a heterogeneous landscape

(Pakhomov et al. 1994; Hunt et al. 1999; Polard et al. 2002). It is not surprising then that top predators are strongly associated with these features (Charrassin and Bost 2001; Nel et al. 2001; Hyrenbach et al. 2006; Cotté et al. 2007; Bost et al. 2009). Temperature gradients, circulation patterns, scent trails and ocean colour have been hypothesised to be important indicators of oceanographic processes for marine predators (Nevitt 2000; Bailleul et al. 2007; Cotté et al. 2007; Weimerskirch 2007; Cunningham et al. 2008). Furthermore, cues such as nearest neighbour, or social cues, can be used by predators to locate prey patches (e.g. Silverman et al. 2004). In some instances social cues may still be dependant on sensory cues, for instance when olfactory cues are used by one species, the behaviour of that species acts as a social cue for others (Verheyden and Jouventin 1994). However, one could expand the hypothesis by Verheyden and Jouventin (1994) to any cue such as the use of temperatures, thereby creating predator aggregations at the fronts of currents or eddies These aggregations may be comprised of species that used temperature as a cue and also those that relied on the resulting local enhancement.

Sea temperature as a cue for locating frontal zones

Sea temperature has been hypothesised to act as an important physical cue for predators that forage at frontal zones, upwelling cells or meso-scale eddies. King Penguins are perhaps the most well studied flightless seabird species with regards to their use of physical processes (Charrassin and Bost 2001; Cotté et al. 2007; Trathan et al. 2008). On a large- (>1000 km) to meso-scale (100 – 1000 km), King Penguins follow linear paths along temperature gradients until they reach the polar frontal zone (Trathan et al. 2008) and associated meso-scale eddies (Cotté et al. 2007). When sea-surface temperatures associated with these physical features are met, they reduce their swimming speed and increase their turning rate, increasing the amount of time spent in these areas (Trathan et al. 2008). Similarly, Sooty *Onychoprion fuscatus* and Bridled Terns *O. anaethetus* as well as Wedge-tailed Shearwaters *Puffinus pacificus* show a strong association with small-scale convergence zones at the fronts of meso-scale eddies in the sub-tropical Indian Ocean (Hyrenbach et al. 2006). These birds probably use sea-surface temperature as a cue to locate eddy fronts (Hyrenbach et al. 2006). Off northern Chile, the dive durations of Humboldt Penguins *Spheniscus humboldti* are correlated with sea-surface temperature anomalies, further supporting the hypothesis that sea-surface temperature could be an important foraging cue for seabirds (Culik and Luna-Jorquera 1997). Laysan *Phoebastria immutabilis* and Black-footed *P. nigripes* Albatrosses increase their foraging effort when sea-surface temperatures decrease, preferentially foraging at the front formed along the North Pacific Transition Zone (Kappes et al. 2010), which is bounded by Subtropical and Subartic Gyres (Roden 1991). Sea temperature variation can also act as an important cue for breeding in Little Penguins *Eudyptula minor*, as positive heat fluxes increase prey availability and lengthen the breeding season (Cullen et al. 2009). ~~But temperature~~ However, sea temperature cues are not exclusive to horizontal space as the ocean is three-dimensional. Temperature gradients over the vertical depth of the water column can also be as important in concentrating prey and may also act as a foraging cue for diving seabirds.

The importance of thermoclines as a foraging cue

Thermoclines are rapid changes in water temperature with depth due to stratification of surface waters. Seabird prey may be concentrated around thermoclines (Hansen et al. 2001). Thermoclines typically form the boundary between the surface mixed layer and deeper layers, creating distinct fronts between these water masses. Nutrient advection from more nutrient rich, deeper waters is limited across the thermocline because of different water densities (Fielder 2010). King Penguins forage preferentially within and below the thermocline where prey is concentrated by the cold surface mixed layer (Charrassin and Bost 2001). Inter annual differences in the foraging behaviour of Thick-billed Murres *Uria lomvia* are attributed to the position and structure of the thermocline and in the overall thermal structure of the water column (Takahashi et al 2008; Kokubun et al. 2010). Southern Elephant Seals *Mirounga leonina* also forage preferentially along temperature gradients (thermoclines) beneath pack ice where their prey is likely to be aggregated (Biuw et al. 2007). Thermoclines, which are created by deep upwelling associated with the Antarctic Circumpolar Current, are also preferred hunting grounds for Southern Elephant Seals (Biuw et al. 2007).

The use of ~~C~~currents use as a foraging strategy to reduce energy costs

In order to reduce their travel costs, penguins may use currents in transit (e.g. Cotté et al. 2007; Raya Rey et al. 2010). These currents can be driven by a number of processes such as tidal influences (Raya Rey et al. 2010) or currents associated with fronts of meso-scale eddies (Cotté et al. 2007). Tidal currents provide the best possible situation for a marine predator as both the ebb and flow currents could be used while unidirectional currents require an animal to return against the current (Raya Rey et al. 2010). Looping routes may avoid return costs, for instance when the main current is avoided and areas with only tidal influence are encountered (Putz et al. 2002). For slow currents, the return may not be impeded, but the benefits of passive drift may be beneficial to the overall energy budget of the animal. Currents may also be linked directly to processes that increase productivity, e.g. eddies, making currents a potential cue for locating areas that have an increased probability of containing prey patches (Cotté et al. 2007).

Biological foraging cues

Top predator abundance is often associated with a combination of physical and biological cues. In the northern Pacific, Short-tailed Albatrosses *Phoebastria albatrus* spend more time in areas with high chlorophyll α concentrations and only respond to temperature cues on large spatial scales (Suryan et al. 2006). A multi-level approach is required to deduce the suite of cues used, as often the obvious cues,~~-~~which could be utilised by some predators are irrelevant for others. For example, a study exploring the relationship between 12 seabird species and their habitat found the densities of some birds were better correlated with chlorophyll α and salinity than sea temperature (Ainley et al. 2005). This suggests that marine birds may be capable of detecting changes in primary production. Procellariiforms such as albatrosses have highly evolved scent organs and may be able to forage along odour trails that are generated when phytoplankton is grazed by zooplankton (Nevitt 2000; Nevitt et al. 2004, 2008). Humboldt Penguins are also capable of locating high incidences of chlorophyll α, which is associated with high primary production, a cue they use on a coarse (1-100 km) to fine scale (>1 km) (Culik 2001). Often potential cues such as temperature, currents and chlorophyll production are all correlated, which can make identifying the actual cue being used by a predator difficult (Ainley et al. 2005). ~~–~~Further more, ~~C~~cues may~~ also~~ ~~-~~exist at various scales, such that the scale of detection needs to be considered when linking potential cues and foraging ecology of top predators.

Scales of detection

The foraging cues used by seabirds are all temporally and/or spatially scale dependant (Weimerskirch 2007). ~~Not only should t~~The predictability of locating prey should increase with the time and spatial scale searched by an individual predator (Weimerskirch 2007)~~,~~. Furthermore, with regards to ~~but with regards to~~ the use of oceanographic features, ~~the~~ larger ~~a given~~ foraging areas are likely to include~~, the~~ more persistent ~~a~~ features ~~is likely to be and thus the more likely it is to~~that are ~~be utilised as a~~more reliable indicators of productivity ~~–~~(Weimerskirch 2007). At fine-scales there can be considerable lags between physical processes, their associated increase in primary production and the proceeding response by intermediate prey species according to the match/mismatch hypothesis (Durant et al. 2007). It is also important to highlight the differences in cue sensitivity on a spatial and temporal scale for different species given their different ranges and modes of locomotion (Weimerskirch 2007). Long distance flying birds may rely more on sight e.g. actively spotting prey patches, ocean colour or nearest neighbour cues (Ainley et al. 2005, Silverman et al. 2004), ~~where as~~compared to species such as penguins which are in constant contact with the water and may rely more heavily on cues such as temperature or currents (e.g. Cotté et al. 2007).~~.~~ Regardless of the cues available, seabirds should adopt a movement pattern that helps them cope with varying levels of environmental patchiness (Weimerskirch 2007).

The African Penguin as a top predator and conservation icon

The African Penguin is a marine top predator endemic to southern Africa. African Penguins breed from Hollams Bird Island, Namibia to Bird Island, Algoa Bay on the south coast of South Africa (Figure 1.2; Crawford et al. 2011). The western colonies around the Western Cape of South Africa and the south eastern colonies are separated by ca 600 km (Crawford et al. 2011). Penguins are limited by the availability of island habitats and mainland habitats that are free from predators resulting in three distinct populations: Namibia; Western Cape and Algoa Bay (Randall 1989). African Penguins have experienced severe population decreases over the last century with the most rapid decrease occurring over the last decade. A 50% decrease in the number of breeding birds since 2004 has resulted in the species being up-listed from Vulnerable to Endangered (Crawford et al. 2011; IUCN 2012) and has attracted powerful conservation efforts (e.g. Pichegru et al. 2010).

Penguins are charismatic animals that provide substantial revenue through tourism, branding and marketing (Lewis et al. 2012). Cape Gannets *Morus capensis* and Cape Cormorants *Phalacrocorax capensis* share similar prey and population decreases with African Penguins, but are arguably less appreciated by the public, although they are equally important and vulnerable to environmental changes (Crawford 2008). These and many other species stand to gain considerably from African Penguin conservation efforts either as a direct result of habitat protection or through funding achieved as a by product of African Penguin conservation, for instance from money generated via tourism. In order to properly conserve a species we need to understand its ecology. African Penguins utilise diverse island habitats that are shared by a multitude of sensitive and near threatened species, which makes this species a potential conservation icon for its ecosystem. It is thus imperative that we understand how this species locates areas in the open ocean where prey is likely to be encountered.

African Penguins depend largely on pelagic fish stocks, with Anchovies and Sardines *Sardinops sagax* making up the majority of their present day diet (Petersen et al. 2006). On the west coast of southern Africa, African Penguins consumed ca 2 600 t of Anchovies in the 1980s (Crawford et al. 2001). Penguin diet has shown considerable variation since the first studies examining their diet in the 1950s and 1960s. For instance diet samples recorded by Rand (1960) contained 26 different species of prey.

Anchovies and Sardines made up ca 21% and 31%, respectively. In the 1980s penguin diets from the Western Cape contained upwards of 80% Anchovy showing a large shift in diet composition (Crawford et al. 1991). Diets of African Penguins from Algoa Bay are still predominantly Anchovy (>97%, Pichegru et al. 2012) although cephalopods occasionally dominate stomach samples (L. Pichegru unpublished data). It is suggested that penguins switch to cephalopods, the main species being *Loligo reynauldii*, when Anchovy are scarce (Crawford et al. 2011).

When foraging, African Penguins can attain speeds up to ca 5 $m.s^{-1}$ but they travel at surface speeds of 0.8 $m.s^{-1}$ (Petersen et al. 2006). Birds forage to a mean depth of 10-25 m and maximum depths of ca 50 m in the Western Cape (e.g. Dassen Island; Petersen et al. 2006). African Penguins from Algoa Bay (Bird and St Croix Island) have deeper dive depths with a mean depth of 20–30 m and maximum depths recorded of ca 90 m (Pichegru et al. 2012). Penguins hunt by diving below their prey and then capturing prey by rapid surface ascents (Wilson and Duffy 1986; Simeone and Wilson 2003; Wilson et al. 2010). The breeding success of African Penguins is closely dependant on the availability of prey within 20-30 km of their breeding location (Crawford 1998; Pichegru et al. 2009).

African Penguin breeding success and the number of breeders is correlated with fluctuations in the abundance of small pelagic fish (Crawford et al. 2008, 2011). Years with low pelagic fish recruitment decrease reproductive output in the following year, most likely as a result of skipped breeding by adults and delays in the time that immature penguins first breed (Crawford et al. 2008). Penguins breed throughout much of the year except when moulting, which occurs during October – December (Randall and Randall 1981). Penguins lay eggs when prey availability is suitable with the first peak in egg laying occurring in January, followed by further peaks in March/April and May/June (Randall and Randall 1981). Parents co-operate in brooding chicks and incubating eggs. Birds rotate roughly once every 24 hours. Birds in Algoa Bay have trip times ranging from 5–48 h (Pichegru et al. 2012). During this time birds can travel up to ca 18 km away from their colony on the west coast and ca 44 km on the south coast in search for prey. The distances birds travel are likely driven by the availability of prey around their colonies (Pichegru et al. 2010).

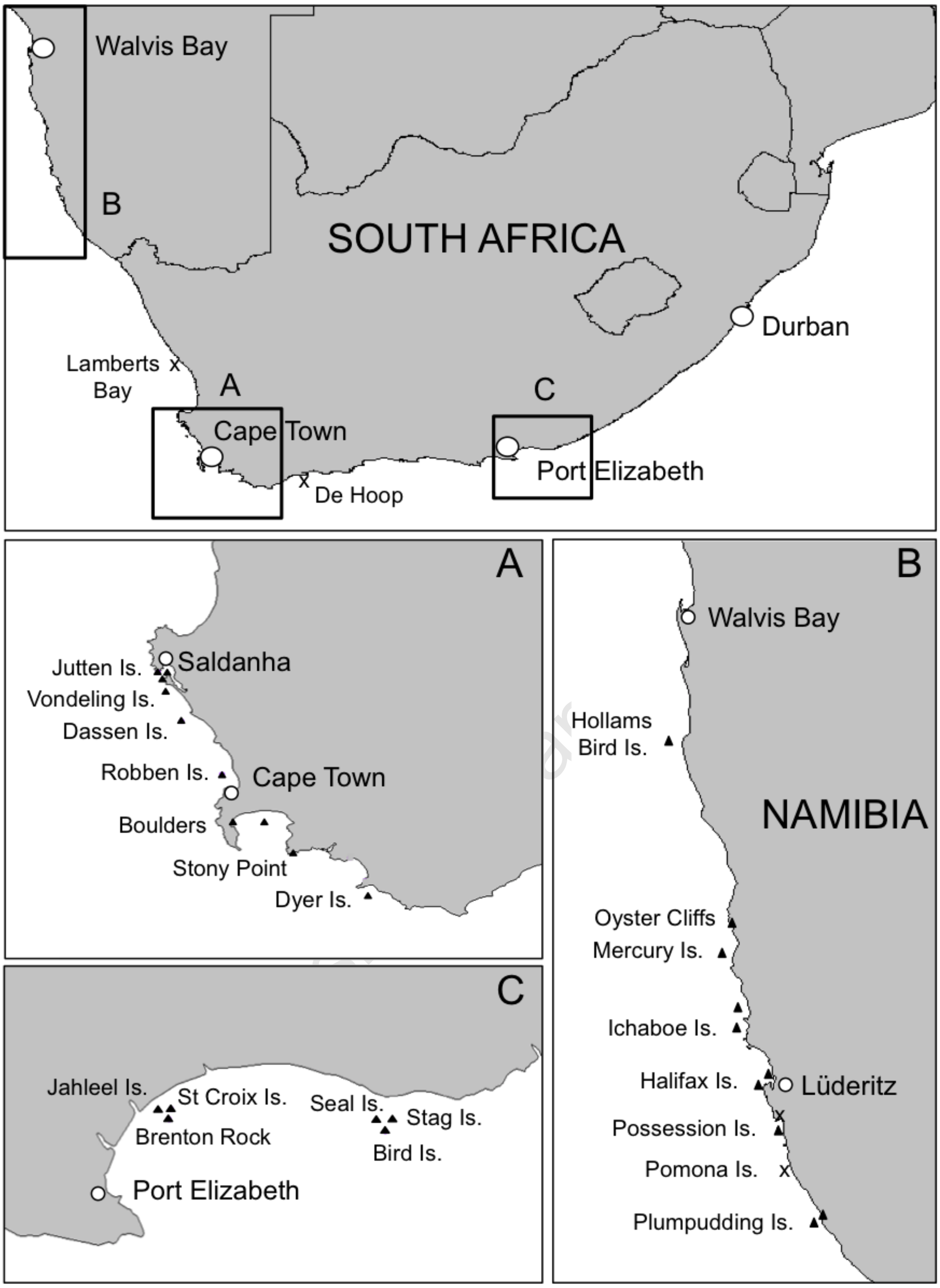


Figure 1.2. The breeding locations of African Penguins on the south (A), west (B) and southeast (C) coasts of southern Africa. The locations are marked with a triangle if the colonies are extant circa 2011, and are marked with an x if the location no longer hosts breeding penguins. Adapted from Crawford et al. (1998, 2011).

Using physical cues to cope with variability

The distribution of African Penguins span two large and different marine ecosystems: the Benguela ecosystem on the west coast of southern Africa and the Agulhas ecosystem on the southern coast of South Africa. The potential cues that could be used by each population of birds are likely to differ in accordance with what cues are actually available. For the purpose of gaining a ~~broad~~ general view of the foraging ecology of African Penguins, this research thesis focuses on the southern population of African Penguins, which are found on island habitats in Algoa Bay. A recent eastward shift in the southern African distribution of Sardines (Fairweather et al. 2006; van der Lingen et al. 2006) has resulted in most of this stock being situated beyond the foraging range of African Penguins breeding on islands off the Western Cape of South Africa (Crawford et al. 2008). Farther east on the south coast, where penguins breed on islands in Algoa Bay, this displacement has not benefitted African Penguins, because the stock movement has not extended this far east and there has been an increase in fishing effort east of Cape St Francis from 10 000 t in 2002 to 30 000 t in 2006 (Crawford et al. 2009). Historically, the availability of food for African Penguins breeding on the south east coast has been less than their counterparts on the west coast of South Africa (Coetzee et al. 2008). However, the importance of prey availability for Algoa Bay colonies is more important than ever; the region supported only ca 12 500 pairs of penguins (6% of all penguins) in the 1950s (Rand 1960), ca 19 600 pairs (50%) in the early 1990s but currently (ca 2010) supports ca 10 400 pairs, 58% of the global population (Crawford et al. 2011). Fluctuations in abundance and changes in the spatial temporal distribution of prey, which in part govern African Penguin populations, are compounded by the unpredictability in environmental conditions e.g. upwelling timing, intensity and location. Fluctuations in pelagic fish stocks are largely driven by environmental inter annual cycles (Cury et al. 2003).

Algoa Bay is known for its high degree of environmental variability, with conditions changing on spatial-temporal scales of kilometres or days (Schumann et al. 2005). The bay experiences frequent low-pressure storms from the west in winter (Hunter 1982) and extensive easterly winds in summer (e.g. Goschen and Schumann 1988). Warm waters from the Agulhas Current intrude over the narrow continental shelf north east of the Agulhas Bank and cool waters enter the bay from the Port Alfred upwelling cell (Goschen and Schumann 1990; Roberts 2010; Figure 1.3). Together with meteorological influences, they create a heterogeneous marine environment that is almost always in flux (Schumann et al. 2005). Much of the oceanographic foundations of Algoa Bay have been established while long-term monitoring programmes continue to deliver high resolution and uninterrupted data on temperatures, salinity, currents and productivity in the bay. Thus it is possible to hypothesize certain cues that are likely to be used by these birds to locate prey. Currents in the bay are mostly wind driven (Goschen and Schumann 1988) but are also influenced by the Agulhas Current which exhibits periodic intrusions into the bay as warm water plumes that shear off the shoreward side of the current (Roberts 2010). ~~African Penguins might use long-shore eastward currents to passively drift when travelling at night, which is when most birds depart from their colonies, in order to reach distant cool waters associated with the Port Alfred upwelling cell and upwelling along the bays eastward cape.~~

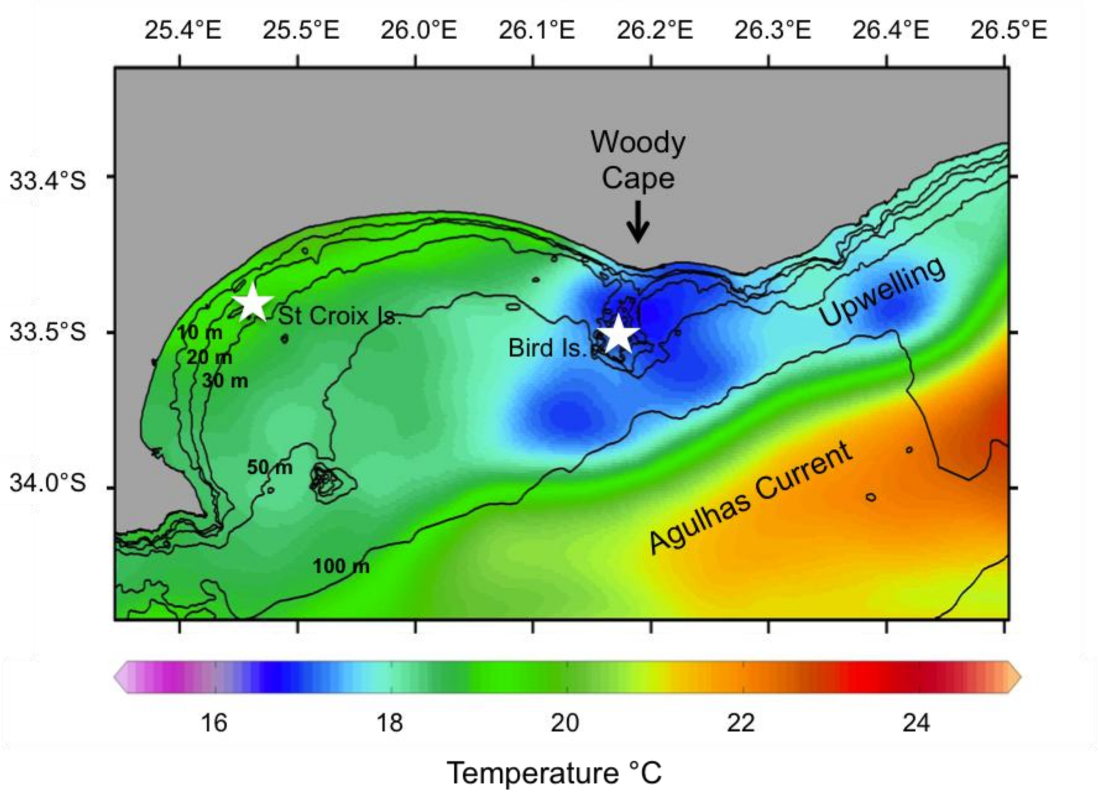


Figure 1.3. Map showing the typical sea-surface temperature patterns in Algoa Bay, South Africa. The south-east flowing Agulhas Current and periodic

upwelling cell which originates near Woody Cape are shown in relation to Bird Island, nearby St Croix Island, and bathymetry. 1 x 1 km SST data supplied by the Marine Remote Sensing Unit , UCT, via the NASA MODIS platform.

African Penguins might use long-shore eastward currents to passively drift when travelling at night, which is when most birds depart from their colonies, in order to reach distant cool waters associated with the Port Alfred upwelling cell and upwelling along the bays eastward cape.

Currents can also be used to travel southwest when upwelled water is blown into the bay from the east. This would allow birds to reduce their net travel costs, allowing them to spend more time downstream of the current during daytime and aid in locating prey concentrated by the currents in cool waters.

Sea-surface temperatures could be used to direct foraging effort towards upwelling cells. Upwelling is a common occurrence within Algoa Bay (Figure 1.3), either around the bays two headlands or "capes" where wind forcing results in upwelling on the western side of the headlands (Schumann et al.1982; Beckley 1983, 1988; Schumann et al. 1988) or over the continental shelf as a result of interactions between the Agulhas Current and the continental shelf (Schumann 1987). Thermoclines are often formed in waters deeper than 50 m within the bay and are known to be capable of concentrating nutrients in the cooler waters below the thermocline (Goschen and Schumann 1988). African Penguins should therefore adopt a foraging dive behaviour that allows them to exploit the thermocline as a cue for locating prey, as their prey may be associated with the possible primary production concentrated by the thermoclines nutrient gradient (Sverdrup 1953).~~.~~

Objectives and aims

The location of pelagic seabirds is dependent on the location of their prey, a pattern that is enhanced when they are not constrained by breeding (Ainley et al. 2005). However, it is sometimes poorly understood how predators know where their prey resides. Miniature data loggers attached to marine organisms that can record location and abiotic variables simultaneously, allow us to understand how many top predators use ocean physical processes to locate prey (e.g. Wilson et al. 2002; Takahashi et al. 2008). African Penguins present an ideal ~~framework~~ model species for understanding how short-range, flightless seabirds successfully locate prey, in the context of search strategy and in relation to temperature and current patterns. African Penguins from Bird Island, South

Africa, have been equipped with GPS data loggers since 2008 (Pichegru et al. 2010). Tracking these birds during their breeding season has been performed in an attempt to understand their foraging ecology in relation to fishing activities with regards to declining penguin populations (Pichegru et al. 2010, 2012).

This research thesis examines how African Penguins interact with ocean physical processes such as currents and sea-surface temperature (Chapter 2), as well as thermoclines (Chapter 3) to locate their scarce and patchily distributed prey. In Chapter 2, I evaluate three core ideas that could determine the foraging behaviour of African Penguins: 1) foraging on the presumption of spatially predictable prey distributions, 2) the use of temperature gradients as a cue to locate potentially profitable foraging areas and 3) the use of currents to minimize energy expenditure during transit. I hypothesize firstly that African Penguins that anticipate the spatial and temporal location of their prey should undertake near linear commuting paths to reach foraging areas with a higher probability of containing patches of their prey. Secondly I hypothesize that birds should forage in cool, nutrient rich waters to maximize the probability of locating prey, avoiding warmer Agulhas Current waters that are inherently nutrient poor (Lutjeharms et al. 2000). If this were possible, penguins would follow temperature gradients to reach cooler waters. Lastly, African Penguins tend to show possible commuting when performing over night trips, traveling substantial distances with no diving activity (tested empirically in hypothesis 1 above; Petersen et al. 2006). I therefore hypothesize that birds might use currents to minimize travel costs. The use of temperatures and currents are presented as mutually exclusive hypotheses as no clear linear relationship between current direction and temperature has been empirically reported; currents are largely wind driven. However, temperatures and currents could be used either together or separately in the decision making process when leaving the island, or on the premise of predictability of prey, ignored entirely.

In Chapter 3, I develop the habitat use and behaviour of African Penguins in relation to the vertical thermal structure of the water column. I hypothesize that penguins should dive towards cool nutrient rich bottom waters fronted by the thermocline. Nutrient rich waters within the euphotic zone increase primary and secondary production and thus provide the base for higher trophic levels. Small pelagic fish, the prey of African Penguins, may in turn be associated with the thermocline as a result of this nutrient concentration and potential concentration of primary production. I hypothesize that the structure of the thermocline should determine how strong of a cue the thermocline is for foraging. A weak thermocline i.e. one that has a small temperature change with depth, or low intensity (small difference between temperatures above and below the thermocline) will act as a weaker barrier to nutrients and be a weaker cue to foraging, while a thermocline with a more steep slope and stronger intensity will act as a stronger barrier for nutrient flux and thus a stronger cue for foraging African Penguins.

It has also become increasingly evident that not only can we begin to understand the behaviour at sea of species through the ~~GPS devices~~data loggers used in this study, but an interdisciplinary convergence has resulted whereby animal borne loggers can inform us about the oceanography in the areas where they forage (Fedak 2004). This thesis provides further understanding of how animal-~~-~~borne loggers can provide a dual function in terms of informing researchers on both animal behaviour and oceanography (Chapter 4). The thesis also shows how animal- borne devices can augment the understanding of the physical environment, especially where traditional oceanographic studies are challenging, for instance in areas that are largely inaccessible on a long temporal or frequent basis, or when large scale oceanographic studies are limited by financial constraints (Fedak 2004). In the context of global change and the current lack of understanding of how African Penguins locate patchily-~~-~~distributed prey, this work aims to broaden our understanding of the foraging ecology of this e~~E~~ndangered species.

Chapter 2

Foraging in a dynamic ecosystem: Do African Penguins use temperature gradients ~~or currents~~ as a cue~~s~~ for locating prey patches and currents to minimize energetic costs?

ABSTRACT

Physical process such as upwelling, eddies and frontal zones bring nutrient rich waters to the euphotic zone, driving marine food chains from the bottom up. The currents and temperatures associated with these features can be used as cues by top predators, often over meso-scales (100–1000 km), to locate areas where the chances of encountering prey is enhanced, reducing energy costs of locating prey. On a fine scale (<1 km), processes are ephemeral and highly variable, which poses the question: how do short-range, central place foragers locate prey in these unpredictable landscapes? By implementing habitat preference models using mixed-effects generalized additive mixed models (GAMM) and by analyzing foraging trip structure in relation to currents, this chapter demonstrates that African Penguins from Bird Island, South Africa, have evolved a suite of behaviours to efficiently locate areas with a greater likelihood of containing prey patches. Birds that departed earlier from their colony than conspecifics traveled farther distances in a commuting type fashion towards areas of cooler waters associated with upwelling and with the preferred temperature range of their prey species. No difference was detected in temperatures between areas foraged in and the rest of the home range of the birds, which may be due to the large homogeneity in temperatures of the birds' small home range. Nevertheless, when a cold patch was encountered, birds seemed to preferentially forage in it. Wind driven currents were generally slow and aided little in transport, however birds increased their swim speed when foraging against currents, which would potentially increase energetic costs of foraging. When foraging, birds switched from a commuting search strategy to a correlated random search strategy to maximize encounters with their patchy distributed prey. This research demonstrates the flexibility of bird foraging behaviour under a highly variable environment but also highlights the positive feedback of possible learnt behaviour to travel towards areas

that may increase success as detected through previous experience, a topic for future research.

INTRODUCTION

Small pelagic prey fishes such as Anchovy and Sardine are distributed heterogeneously across the continental shelf of South Africa (Barange et al. 2005)~~The~~. The patchy distribution of prey species and their presumed unpredictability in the open ocean has been implicated as a primary explanation for shaping the life history traits of predatory seabirds, e.g. late onset of first breeding and slow maturation (Lack 1968; Ashmole 1971). However, the ways in which seabirds potentially predict and detect prey on a variety of spatial and temporal scales have been, until recently, poorly studied. This has led many authors to reiterate four-decade-old theories that seabirds rely on inherently 'unreliable' resources (Weimerskirch 2007). The advent of miniature data loggers that track marine predators in three dimensions in relation to abiotic variables has provided new knowledge on the foraging ecology of seabirds, at the individual level and on extremely fine spatio-temporal scales (e.g. metres and seconds; Wilson et al. 2002, 2008; Ryan et al. 2004). Such loggers provide insight into the ability of seabirds to implement search strategies to locate prey patches by assessing their movements in relation to ocean physical structures at varying scales (Weimerskirch 2007).

The simplest search pattern employed by foragers is a random walk, but when patches are detectable, movement patterns should align themselves with these patches along a landscape detectable by the forager (Hawkes 2009). Although the ocean might appear relatively "featureless" to human observers (Nevitt 1999), the oceanic environment is in fact heterogeneous in terms of physical processes such as upwelling zones, currents and eddies. Such processes create localised nutrient concentrations, shaping the distribution of productivity in the oceans. The movement pattern of central place foragers, such as breeding seabirds, is characterized by either commuting or looping type trips (Weimerskirch 1997). Commuting birds travel rapidly along a nearly linear path to and from their foraging grounds (Weimerskirch 1997, 2007; Pettex et al. 2010), which presupposes they have some predefined idea of where to locate prey. This might be based on previous experience or on the use of cues such as temperature gradients, currents or scent trails (Nevitt 2000, Cotté et al. 2007; Weimerskirch 2007). Physical forcing mechanisms may thus act as cues for top predators that undertake commuting trips, which can follow currents and temperature gradients towards productive areas such as the edges of eddies (Cotté et al. 2007), or upwelling zones (Biuw et al. 2007). By comparison, looping foraging trips (or sometimes figures of eight) are undertaken by birds that search continuously for prey, feeding whenever prey is encountered (Weimerskirch 1997, 2007). The fact that more than 90% of seabird populations studied to date undertake commuting trips suggest that the location of most seabirds prey is fairly predictable at the scale of their trips (Weimerskirch 2007).

The strategy and cues used on an individual level are likely to be determined by the scale at which an individual forages, the nature of the physical forces within their environment, and the abundance and distribution of prey (Weimerskirch 2007). For example, in upwelling ecosystems considerable lags exist between the physical process and actual response by primary producers, grazers, etc. (Moloney et al. 1991), generating a spatial and temporal discontinuity between predators and available physical structures and furthermore their prey (Cushing 1975). For instance, pelagic prey fishes such as Anchovy form high-density schools that are patchily distributed but are also sensitive to a narrow range of temperatures (Barange and Hampton 1997). This pattern decreases the predictability of prey location compared to prey that is regularly distributed through space in a homogenous environment.

Although it is evident that seabirds are capable of implementing specific search strategies and may use diverse cues to locate their prey, most results stem from research on species that travel long distances to forage at persistent meso-scale features (e.g. Nel et al. 2001, Cotté et al. 2007, Trathan et al. 2008). It is less clear how species that travel shorter distances (1-100 km) are capable of detecting patchily distributed and scarce prey in variable habitats where potential environmental cues may be short-lived.

African Penguins breeding on Bird Island have been found to forage predominantly east or south of the island (Pichegru et al. 2010). The clear directionality in where these birds forage is likely to be driven by the local environment. The currents and temperature regimes around Bird Island have recently been given increased attention in light of a proposed marine protected area (Pattrick and Strydom 2008). The local processes are governed by periodic upwelling, influences on the local oceanography by the adjacent Agulhas Current and wind driven movements of shelf waters (Schumann et al. 1988; Goschen and Schumann 1990, 1994; Roberts 2010). I hypothesize that birds should perform commuting trips if they can predict the spatial and temporal occurrence of their prey. I further hypothesize that birds should forage preferentially in cool, nutrient rich water associated with upwelling rather than warmer waters associated with the Agulhas Current, which are inherently nutrient poor. Finally, I hypothesize that birds should use currents to reduce energy costs of locating prey, especially for birds that depart in the late evening or early morning travelling at night. African Penguins seldom forage at night and it is proposed that they partially drift with the current during this time, but may also use the current to maximize the distance they travel away from the colony in order to have the greatest chance of finding prey on the return to the colony.

METHODS

African Penguins provisioning small chicks were tracked during three successive austral autumns (2009–2011) using GPS-TD loggers (a GPS recorder combined with a time-depth recorder; 96 mm x 39 mm x 26.5 mm; earth&OCEAN Technologies, Germany) that were attached to the lower dorsal section of the bird using waterproof tesa® tape (for attachment details see Pichegru et al. 2010). GPS-TD loggers recorded latitude and longitude (to 0.001 minutes of latitude and longitude) every 1 min to an accuracy of less than 10 m (Ryan et al. 2004). The GPS-TD loggers carried a pressure sensor, which recorded depth at 1 s intervals to the nearest 0.1 m (Ryan et al. 2007), and a temperature sensor, which recorded temperature at 1 s intervals. The GPS-TD temperature probe has a resolution of ca 0.03 K and can detect a 90% change in temperature in ca 2 s, confirmed by a calibration certificate that the loggers are provided with.

Dive analyses were conducted in MT Dive software, with a dive defined as a descent to depths >3 m to distinguish between diving and porpoising (Pichegru 2010). Tracks were visualized in Arcview 3.2 (ESRI) and only complete tracks (i.e. no substantial gaps in GPS data) were selected for analysis. GPS signals are lost underwater, resulting in tracking gaps when the logger is submerged for extended periods, for instance when birds make frequent short dives (e.g. porpoising). GPS locations of dives were inferred by linear extrapolation based on time between GPS records from the loggers. Only inferred dive locations that were within 1000 m and 30 min of a GPS fix were then retained for spatial analysis.

Habitat selection and search strategy

To define the area used by penguins rearing chicks on Bird Island, all the GPS positions associated with a dive were plotted in Arcview 3.2. The extreme locations defined the edges of a hypothetical box that described the potential foraging range. The bearing of birds from the island to the farthest point of their trip was calculated. These bearings were then binned into those that travelled north (315°-45°), east (45°-135°), south (135°-225°) and west (225°-315°) based on the direction from the colony to the farthest point of a trip. This was used to determine preferences in area usage and to group birds foraging in different areas for behavioral comparisons. Foraging behaviours (maximum distance from colony, path lengths, trip duration, and number of dives) were compared using ANOVA between birds returning from the four different sectors.

To determine whether birds used search loops or commuting search strategies, I separated birds according to whether they searched for prey continuously along their path (looping) or travelled (commuting) towards foraging areas (Weimerskirch 2007). Foraging paths were separated into four sections: transit (leaving colony to first dive), foraging out (between first dive and farthest point), foraging in (from farthest point to last dive) and return (last dive back to colony) sections. Sinuosity was calculated along the paths of birds following Grémillet et al. (2004).

Habitat use and search strategy in relation to SST

Temperatures from the GPS-TD logger were averaged into 1 m depth bins using both the bird's ascent and descent temperature profiles, thus accounting for temperature lags experienced due to the response time of loggers. The 1-2 m temperatures from the loggers were then compared to the spatially nearest (>1 km) SST recorded by the MODIS satellite platform (www.afro-sea.org.za), which records daily averages at a 1 x 1 km scale. The mean, maximum, and minimum SST recorded by the loggers and satellite were calculated along each birds foraging track, as well as for SST recorded in the entire home range of the birds by satellite. Temperature data was obtained from 28/36 loggers. SST from satellite telemetry was available for 25/36 deployments. Cloud cover often prevented SST recordings to be made by the satellite platform. Surface scatter plots of satellite telemetry were graphed in Ocean Data View 4 (http://odv.awi.de) and allowed for the visual identification of thermal fronts and thermally related physical processes such as upwelling which aided in the dissemination of results.

In order to determine if penguins demonstrated habitat preference for cooler patches of water, I used binomial generalized additive mixed models (GAMMs) to compare the SST of locations where birds foraged to where birds were absent (Aarts et al. 2008; Wakefield et al. 2011). A set of 10 000 pseudo-absence locations (long, lat) within the home range of the birds was generated. Pseudo-absences came from a normal distribution of possible locations within the potential home range with the mean centered at the colony. A normal distribution was selected as penguins are likely to travel as far from the island as is required to locate prey, or until a point where a number of constraints are imposed due to the nature of breeding central place foragers (e.g. time constraints imposed by the necessity to relieve a partner incubating eggs or brooding chicks). I quasi randomly selected three points from the pseudo random data set for each bird GPS location. To each pseudo random GPS location and real bird GPS location, I assigned the nearest remotely sensed (<1 km) SST. The depth of the water column (bathymetry) and distance from the colony were assigned as additional covariables to the GPS locations and the pseudo-absence locations, which further aided in explanation of habitat use. The spatial distributions of SST within the foraging range of African Penguins were modeled using GAMMs as a function of distance from the colony, bearing from the colony and sea depth. I then correlated average water column depth where birds foraged with the average as well as maximum SST of the calculated home range for each bird to determine whether birds foraged closer in shore in response to Agulhas Current intrusions over the continental shelf.

Swimming behavior in relation to current direction and speed

Current data were recorded during the 2009 and 2010 African Penguin breeding season using a Teledyne RDI Workhorse Sentinel Express 43.03 Acoustic Doppler Current Profiler (ADCP) stationed south of Bird Island in 30 m of water. The ADCP was set to a frequency of 600 Hz with a ping rate of 121 pings per ensemble with 7 pings/s. Data were averaged internally. Current direction and speed were recorded every 20 min every 50 cm starting at 4.8 m deep. Current directions were binned into 8° bins to determine general flow directions. Using these data, I compared the bird's speed and direction to the current speed and direction at 4.8 m deep. Bird bearing along its path was calculated between each GPS fix and a ten point running average was used to smooth the bearing over these points. The smoothed bearing of the GPS fix was matched to the temporally closest (<20 min) current bearing. The difference in current direction and bird bearing was then calculated. Angular differences of 0–60° and 300–360° (positive rheotaxis) indicated that birds travelled in a similar direction as the current, while angles of 120-240° (negative rheotaxis) indicated that birds travelled against the current.

For assessing the swim speed of the bird it was necessary to account for the fact that bird speed over ground as recorded by the GPS loggers is influenced by current speed. Swim speed was estimated by defining the bird's speed over ground (travel speed) and movement vectors as the parameters $\bar{u}_N$ (east – west) and $_N$ (north – south) (Cotté et al. 2007). Current speed and direction were defined by $\bar{u}_C$ (east – west) and $_C$ (north – south). Net bird speed (swim speed) and direction was then estimated as the resultant of current and bird speed over ground, as $\bar{u}_P = \bar{u}_N - \bar{u}_C$ and $_P = {}_N - {}_C$ and the resultant vectors for birds (swim speed) was estimated as $\overline{\qquad\qquad}$. Circular statistics were carried out using the package CircStats in R (Rao Jammalamadaka and SenGupta 2001) to determine the mean speed of current and swim speed vectors as well as the bootstrap confidence intervals for direction. The speeds and differences between swim angle and current angle were also compared between each of the four sections of the trip i.e. transit, foraging away from and back to the colony, and return phases. Swim speeds and speed over ground were compared traveling with (330-0°

and 0-60°) and against (120-240°) the current. Means and standard deviations are reported, unless stated otherwise.

RESULTS

Habitat use and trip patterns

Birds tended to reach the farthest point of their trip in two main locations, either east or south of Bird Island in waters 50-100 m deep (Figure 2.1; Table 2.1). Birds headed towards the farthest point of their trip predominantly east during 2009, but the proportion of trips that were in a southerly direction increased during 2010 and 2011. Between years, birds did not show significant differences in their foraging effort (Table 2.2), although there were differences in behaviour between the different directions where birds foraged. Birds that foraged east travelled farther from the colony than birds that travelled south (TukeyHSD: 14.9 ± 4.0 km vs. 9.0 ± 3.0 km, $p = 0.002$) and also performed significantly more foraging dives (TukeyHSD: 349 ± 96 vs. 227 ± 56, $p = 0.004$). There were no differences in the path lengths (ANOVA: $F_{3,32} = 2.13$, $p = 0.115$) or the trip duration (ANOVA: $F_{3,32} = 1.07$, $p = 0.375$) of birds foraging in different directions from the colony. Most birds (92%) departed before sunrise, thus performing a trip that began with a night component. Birds seldom dived between sunset and sunrise (Figure 2.2).

Table 2.1. The number and proportion of birds that reached their farthest point north, east, south or west of Bird Island in each year which birds were tracked with GPS loggers, showing spatial habitat preferences.

Bearing	2009	2010	2011
N (315° - 45°)	1 (10%)	0 (0%)	0 (0%)
E (45° - 135°)	8 (80%)	7 (47%)	4 (36%)
S (135° - 225°)	0 (0%)	5 (33%)	6 (55%)
W (225° - 315°)	1 (10%)	3 (20%)	1 (9%)

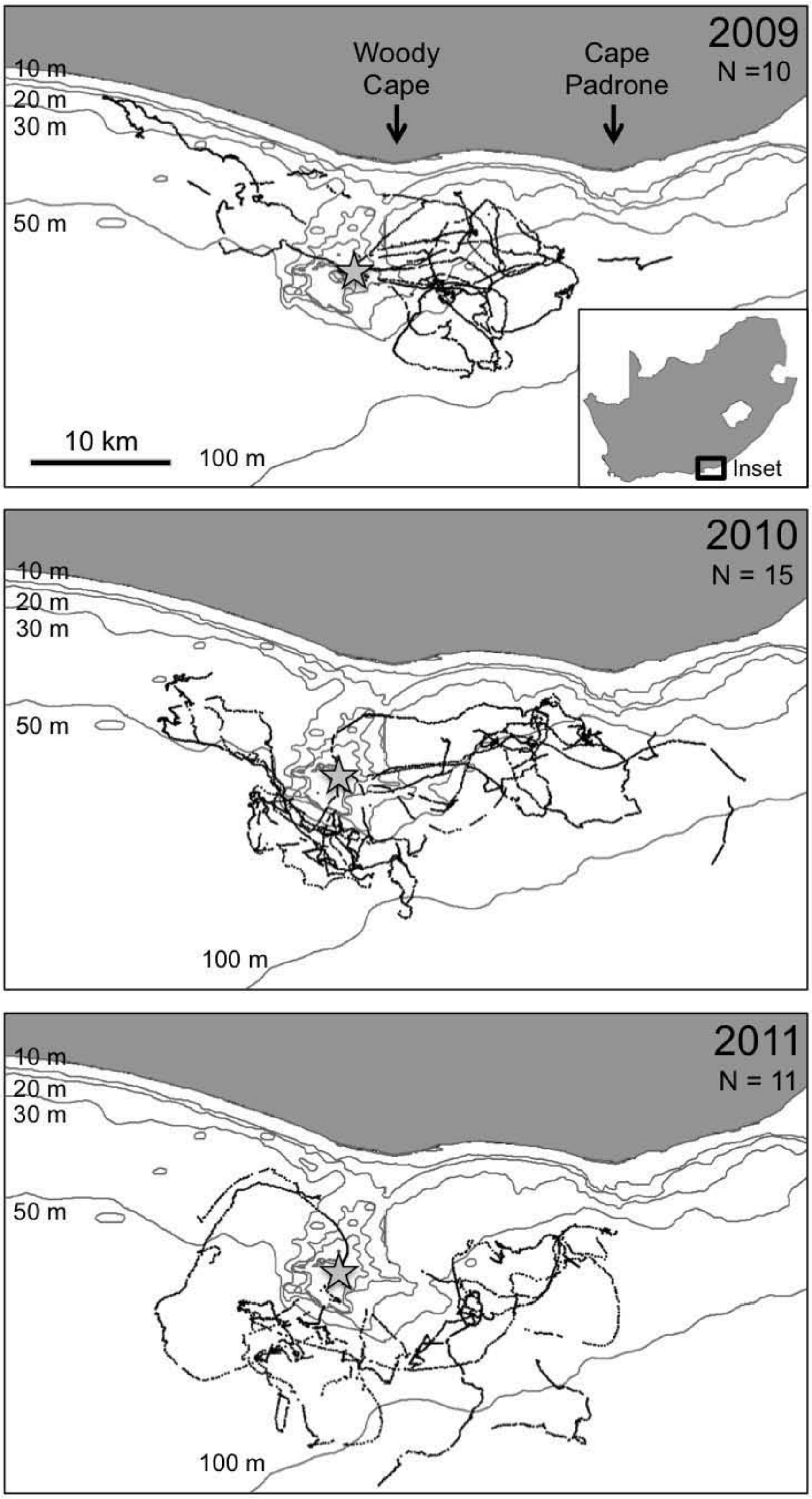

2009
N =10
Woody Cape
Cape Padrone
10 m
20 m
30 m
50 m
10 km
100 m
Inset
2010
N = 15
10 m
20 m
30 m
50 m
100 m
2011
N = 11
10 m
20 m
30 m
50 m
100 m

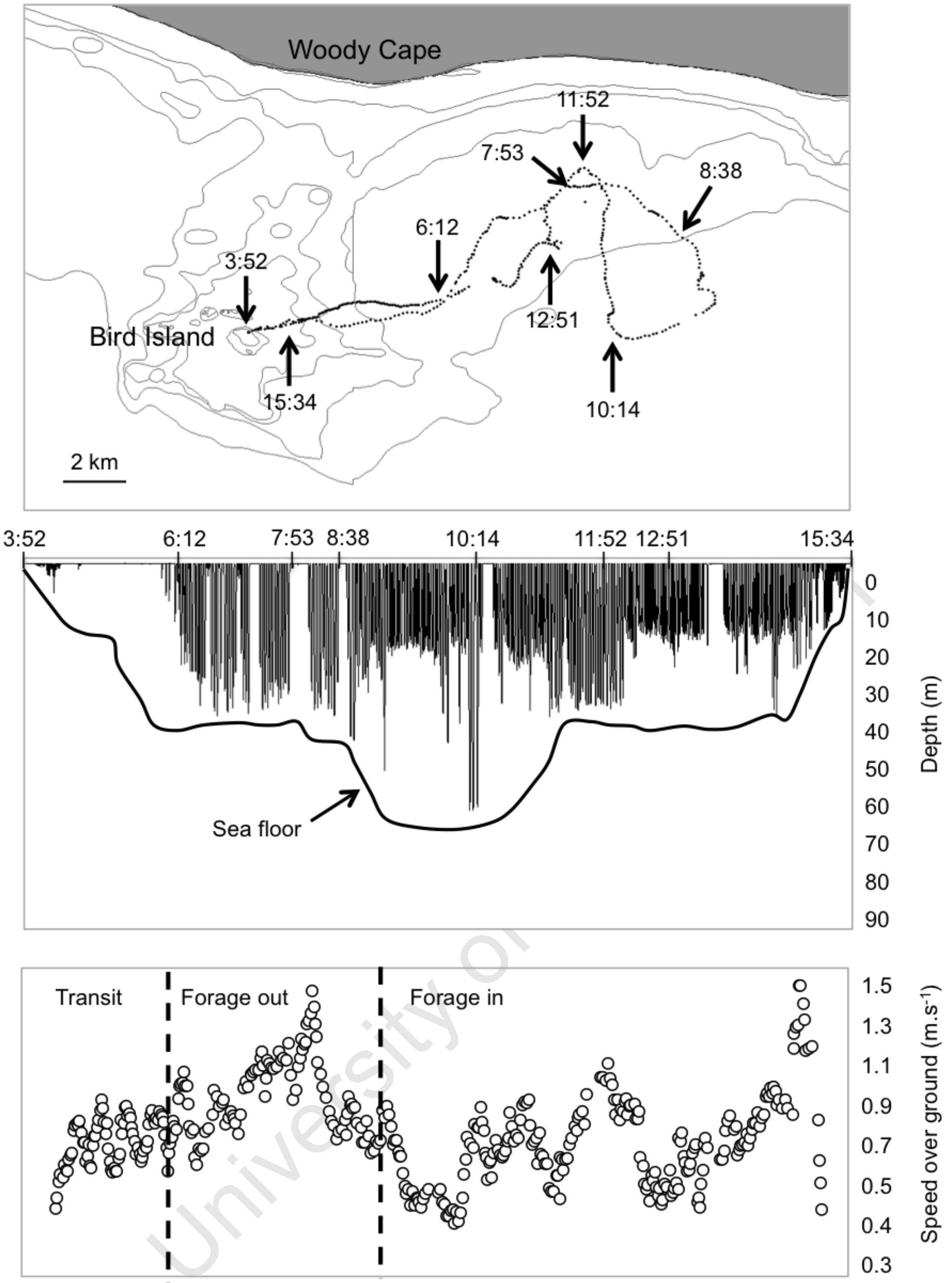
Figure 2.1. Maps showing foraging tracks of breeding African Penguins from Bird Island (grey star) during 2009, 2010 and 2011 in relation to bathymetry.

The 3/36 birds that departed after sunrise began diving to depths >3 m soon after departing from the colony (>53 min and >2.7 km). Two of these birds foraged east and the third foraged south of the colony. The amount of time that birds departed before sunrise was strongly correlated with the distance they travelled away from the colony before sunrise, thus birds were likely to use the time they spend at night to travel (Figure 2.3). The direction birds travelled was not influenced by how early before sunrise they departed. However, there was a tendency for birds that foraged east to depart earlier than birds that forged south (TukeyHSD: 8.0 ± 4.7 h vs. 3.7 ± 3.8 h, $p = 0.083$).

During the travelling component, paths had low sinuosity indices (mean: 0.73, range: 0.01-22.7), typical of commuting (Figure 2.2). The paths became significantly more sinuous when foraging (mean: 0.93, range; 0.01-39.58; Mann-Whitney U-test: W = 3420, $p < 0.001$; $\log_{10}$ transformed). During foraging, birds performed wide looping paths, changing direction and diving almost continuously along the path; a trip structure characteristic of a continuous correlated random search strategy (Figure 2.2). All birds that departed for a foraging trip at night showed this characteristic commuting component before switching to a correlated random search during daylight.

Table 2.2. Inter annual comparison (ANOVA) of foraging behaviour of African Penguins provisioning small chicks from Bird Island, Algoa Bay, with sample sizes and averages ± SD.

	2009	2010	2011	$F_{2, 35}$	p
Number of birds	10	15	11		



Number of dives/trip	316 ± 98	318 ± 91	315 ± 127	0.003	0.997
Trip duration (h)	17.4 ± 7.7	18.2 ± 6.5	22.4 ± 11.9	1.04	0.362
Foraging duration (h)	6.2 ± 1.6	6.8 ± 1.6	7.2 ± 3.4	0.50	0.609
Max. distance (km)	12.9 ± 4.4	12.5 ± 4.9	12.6 ± 4.3	0.22	0.978
Path length (km)	40.7 ± 6.9	49.1 ± 17.3	57.4 ± 21.3	2.63	0.087

Figure 2.2. An example of a penguin foraging track (top panel). The trip shows the characteristic commuting pattern (3:52 – 6:12) used before the bird begins diving, when it switches to a more sinuous search pattern. The corresponding dive profile (center panel) shows the dives over the time of the trip in relation to the seafloor. Each vertical line represents one dive, highlighting the high dive rate of African Penguins and the absence of dives before sunrise (ca 6:30). The bird showed little variation in speed during transit, but increased its speed during the beginning and end of its dive activity (bottom panel).

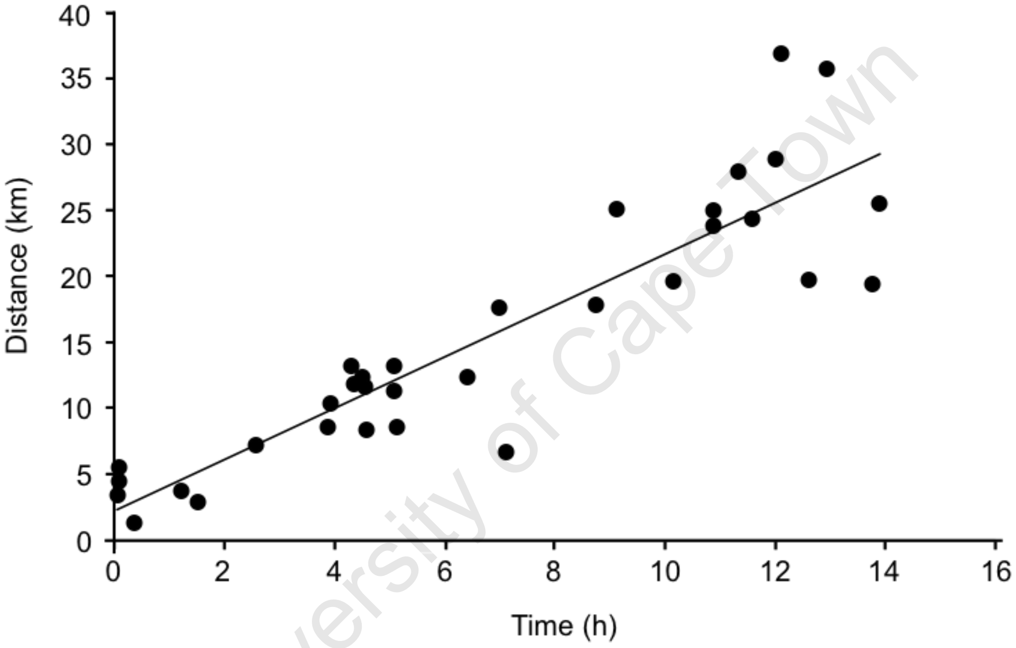


Figure 2.3. The relationship ($r_{31} = 0.9$, $p < 0.001$) between the time (h) birds traveled from departure between sunset and sunrise to their first dive and the beeline distance (km) they covered from the colony to their first dive.

Temperature use

Average SST over the three years collected by loggers attached to penguins was 18.3 ± 0.4 °C (range: 14.2-20.7 °C). SST recorded by satellite remote sensing within the potential home range of penguins from Bird Island averaged 19.1 ± 1.4 °C (range: 13.0-24.5 °C). There was no difference (paired t-test: $t_{413} = 1.8$, $p = 0.07$) in the temperatures recorded by the loggers on the ascent and those recorded on the descent of the dive in the 1-2 m bin, suggesting that there is very little temperature lag recorded by these loggers. SST measured by the loggers attached to penguins was on average 0.4 ± 0.8 °C cooler than the closest (<1 km) satellite measurements (paired t-test: $t_{15377} = 58.76$, $p < 0.001$). These differences may be due to three influences. Firstly SST recorded by the satellite platform is a daily average, while devices are recording in situ data to the nearest second thus the diurnal warming and cooling of the sea surface is recorded. Secondly, SST recorded by devices are taken in the 1–2 m bin to mitigate lags experienced when the device enters from air to water and are

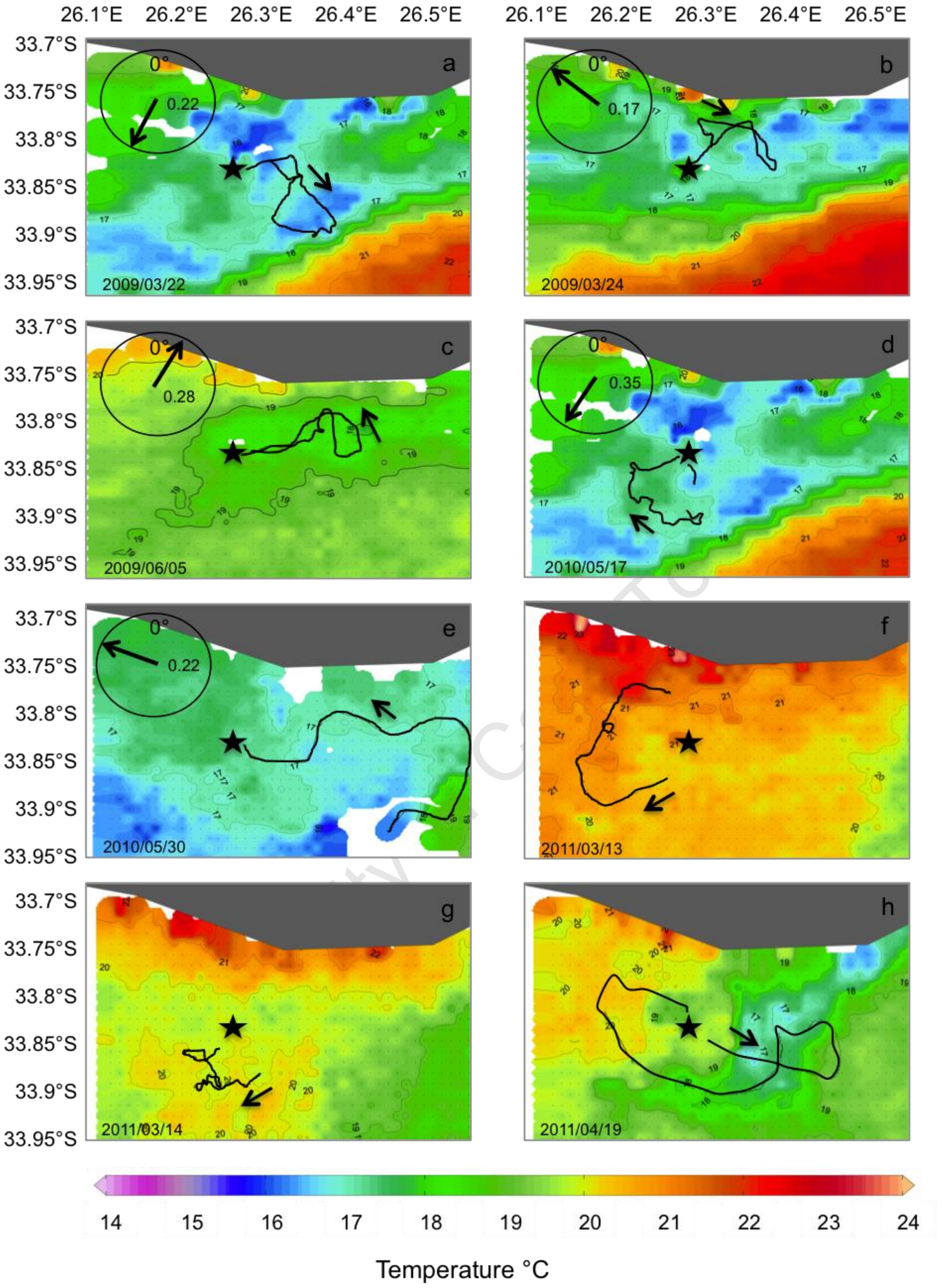


Figure 2.4. SST plots showing the variation in temperatures within the foraging area of breeding African Penguins from Bird Island (black star). Each panel (a-h) is representative of one bird, with its track superimposed on SST on the day of its foraging trip. Arrows represent trip direction. The circle in the top left of panels a – e show the mean current direction and speed ($m.s^{-1}$).

therefore only proxies for true SST, and lastly divergences may be a result of calibration differences in the two instruments. Penguins experienced average differences (max-min) in SST as recorded by the loggers along their tracks of 1.6 ± 1.1 °C (range: 0.3–4.6 °C) which highlights the often largely homogenous thermal structure along birds tracks. However, when differences associated with encounters with cool waters were observed, birds actively tracked these cooler waters (Figure 2.4a, #4b, #4e and #4h). The modeled SST (GAMMs) around Bird Island highlight how temperatures differ between directions from the colony, with varying distances and in different depths of water (Figure 2.5). SST increased with increasing distance from the island. SST was lowest north of the colony (330-30°) and increased south. SST was coolest in water 40-80 m deep, with SST generally increasing rapidly in water depths >80 m. Contextualizing these patterns using SST images informs on the processes that govern these temperature patterns (Figure 2.4). Cold, upwelled water from the northeast was often channeled by the 50 m contour south of Bird Island (e.g. Figure 2.4a, #4b, #4d, #4h). The Agulhas Current warmed waters south and east of the island as the current intruded over the continental shelf (e.g. Figure 2.4b, #4d). From the GAMM analysis predicting how birds use the thermal landscape, birds preferred areas >15 km from the colony and waters <80 m deep (Figure 2.6). Birds did not have any preference for specific temperatures, exploiting all temperatures available equally. There was also no relationship between the depth of the water column where birds foraged and the maximum SST within their foraging range (Pearson correlation: $r = 0.08$, $t = 0.39$, $p = 0.659$). Thus, birds were statistically unlikely to move shoreward when SST in their foraging range increased. Further inspection of SST images highlights that birds never forage beyond the shoreward edge of the Agulhas Current when it is in its most northerly position over the continental shelf (e.g. Figure 2.4b), however, when warm waters completely engulfed the area around the colony birds had little option than to forage in warm waters (e.g. Figure 2.4f).

Current use

In 2009-2010, currents recorded by the ADCP flowed in all directions (0-360°), at generally slow speeds (0.2 ± 0.1 $m.s^{-1}$) although maximum speeds of up to 0.9 $m.s^{-1}$ were recorded during westerly winds (Figure 2.7a and 2.7b). The fastest current flows were eastward flowing currents. The highest frequencies of current direction flowed between 80-102° (ca 14%) and 216-248° (ca 21%) in both 2009 and 2010. Currents were largely uniform in both direction and speed through the water column. Slack waters (speeds = <0.1 $m.s^{-1}$) occurred rarely. Current flow direction was related to the temperature regime experienced at the ADCP (Figure 2.7a and 2.7b). Temperatures generally increased during eastward flow and were lowest during southward flows.

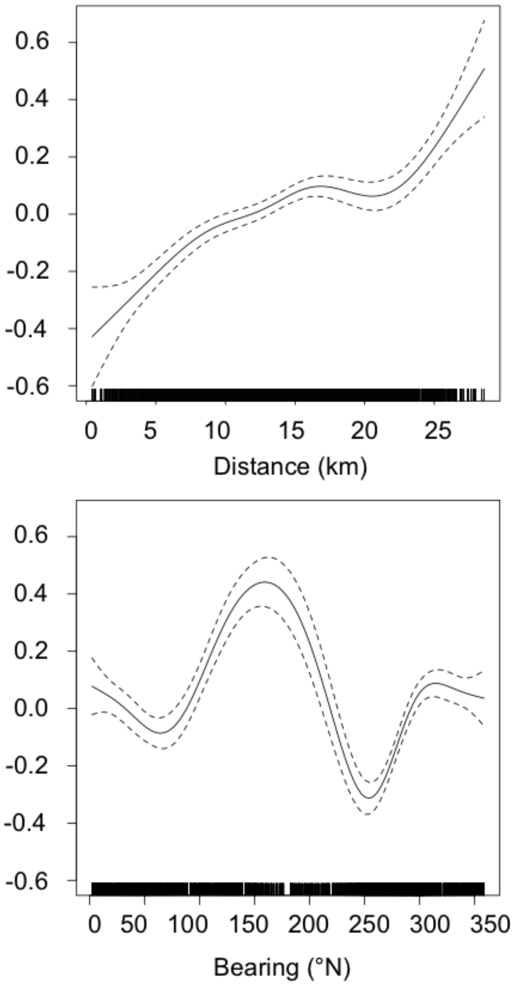


Figure 2.5. Fixed-effects covariates of GAMMs describing the patterns of SST distributions around Bird Island and within the potential foraging range of breeding African Penguins from Bird Island. The y-axes show the relationship of the effect and dashed lines represent 95% confidence intervals. The vertical lines on the x-axes show the distribution of data points used in the models.

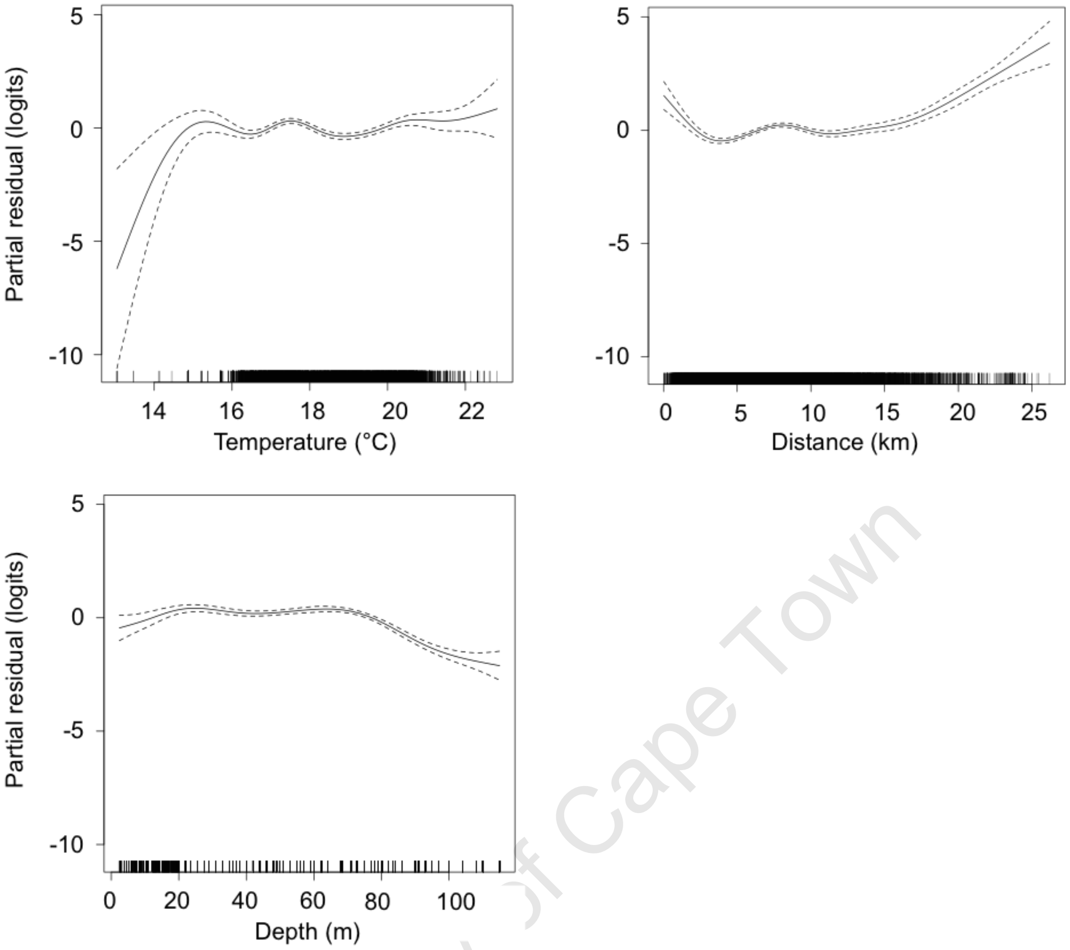


Figure 2.6. Fixed-effects covariates of GAMMs describing the habitat preference (absence/presence models) of African Penguins in relation to SST (°C), distance from the colony (km), and depth of the seafloor (m); (Aarts et al 2008; Wakefield et al. 2011). The y-axes show partial residuals, thus the effect once all other covariates are removed. Dashed lines represent 95 % confidence intervals. The vertical lines on the x-axes show the distribution of data points used in the models.

The direction of bird travel and the direction of current flow showed higher congruence during the transit phase at the beginning of trips than during the foraging and return phases of the trips (Table 2.3; Figure 2.8). Nevertheless, during the transit phase more than half of observations (58%) were not aligned with the direction of the current flow and the distribution of observations were not significantly different from a random distribution ($X^2_{17} = 11.11$, $p > 0.05$). Following the transit phase, birds began diving (foraging) and the number of observations where birds travelled in a similar direction to the current decreased to an average congruence of 40% from the first dive to the furthest point away from the colony. When birds were foraging on the return to the colony birds aligned themselves on average 30% of observations and 47% during the return phase.

Table 2.3. Congruence (difference between current direction and bird travel direction) between bird travel direction and the direction of the underlying current, the average (± SD) bird travel speed and the average speed of the underlying current and the bootstrap direction confidence intervals (CI) for travel and current directions in each of the four phases of the trip (see Methods for details).

Trip phase	Congruence (%)	Penguin CI (°)	Travel speed ($m.s^{-1}$)	Swim speed ($m.s^{-1}$)	Current CI (°)	Current speed ($m.s^{-1}$)
Transit	44	80-99	0.7 ± 0.3	0.7 ± 0.3	136–164	0.2 ± 0.1
Foraging out	34	97–131	0.8 ± 0.3	0.7 ± 0.3	296–343	0.2 ± 0.1
Foraging in	30	263-289	0.8 ± 0.3	0.8 ± 0.4	200–250	0.2 ± 0.2
Return	31	287-64	0.8 ± 0.4	0.8 ± 0.4	205–230	0.3 ± 0.1

The travel speeds of birds were not significantly different in the different phases of the trip (ANOVA: $F_3 = 2.27$, $p = 0.07$). However, birds had higher travel speeds around sunrise and sunset (Figure 2.2). The travel speeds of birds were significantly greater when travelling with the underlying current compared to traveling in the opposite direction to the current (with: 0.79 ± 0.3 $m.s^{-1}$ vs against: 0.72 ± 0.3 $m.s^{-1}$;

Students t-test: t_{694} = 2.72, $p < 0.001$). Swim speeds, which account for current speed, were significantly greater when traveling against the current than with the current (with: 0.6 ± 0.3 $m.s^{-1}$ vs against: 0.9 ± 0.4 $m.s^{-1}$; Students t-test: t_{694} = 10.48, $p < 0.001$). There was a weak but significant positive correlation between the speed of birds travelling in the same direction as the current and the underlying current speed (Pearson correlation coefficient r = 0.35, t = 7.13, $p < 0.001$). However, the swim speeds of birds travelling in the same direction as the underlying current showed almost no correlation to the current speed (Pearson correlation coefficient r = 0.04, t = 0.85, p = 0.39). There was also no correlation between the congruence in trip direction and current direction, and the speed of the underlying current (Pearson correlation coefficient r = 0.01, t = 0.47, p = 0.63).

DISCUSSION

Ocean physical processes create a heterogeneous landscape of currents and temperatures that top predators can use to locate profitable foraging grounds such as fronts, eddies, currents or upwelling zones. Much work has been done using species which remain at sea for long periods of time or that travel over vast distances, enabling them to use predictable meso- to large-scale features to locate their prey (Nel et al. 2001, Cotté et al. 2007). It is less understood how top predators locate prey at finer scales, where such processes are more ephemeral. African Penguins could potentially use thermal gradients to locate nutrient rich upwelling cells where prey is likely to be concentrated but this has not been previously tested. Several studies have shown that seabirds structure their trips to minimize their energy expenditure during trips by taking advantage of prevailing winds and or currents, yet African Penguin foraging path structure in relation to current strength and direction is poorly understood. Some penguin species could potentially align themselves with currents to minimize energy expenditure (Cotté et al. 2007), especially during the night where they may drift passively with the current for many kilometers before they are able to start foraging after sunrise (Petersen et al. 2006), however slow current speeds may have a negligible influence on bird foraging trips.

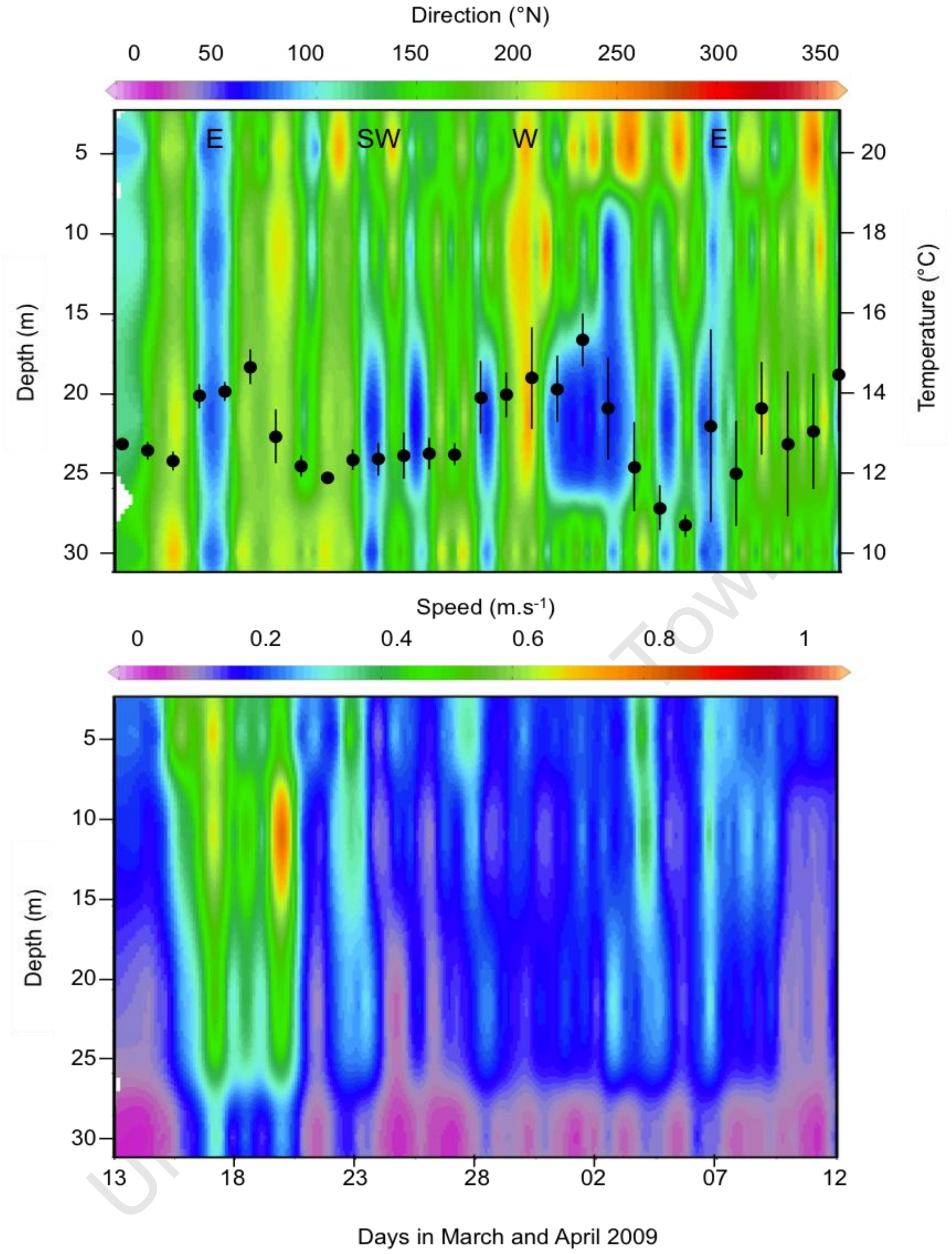


Figure 2.7a. Current and temperature regimes in Algoa Bay during and one week before African Penguins were deployed with data loggers. ~~-~~Direction (top panel) and speed (bottom panel) of currents recorded by an ADCP stationed in 30 m water depth, south of Bird Island during 2009. ~~The plots show the current conditions one week before and during African Penguin deployments.~~ The daily (mean ± SD) temperature recorded by the ADCP at 30 m is superimposed on the top panel in order to demonstrate temperature regimes with current direction. For instance, temperatures

increase following quick eastward currents and decrease under slow southwestward currents.

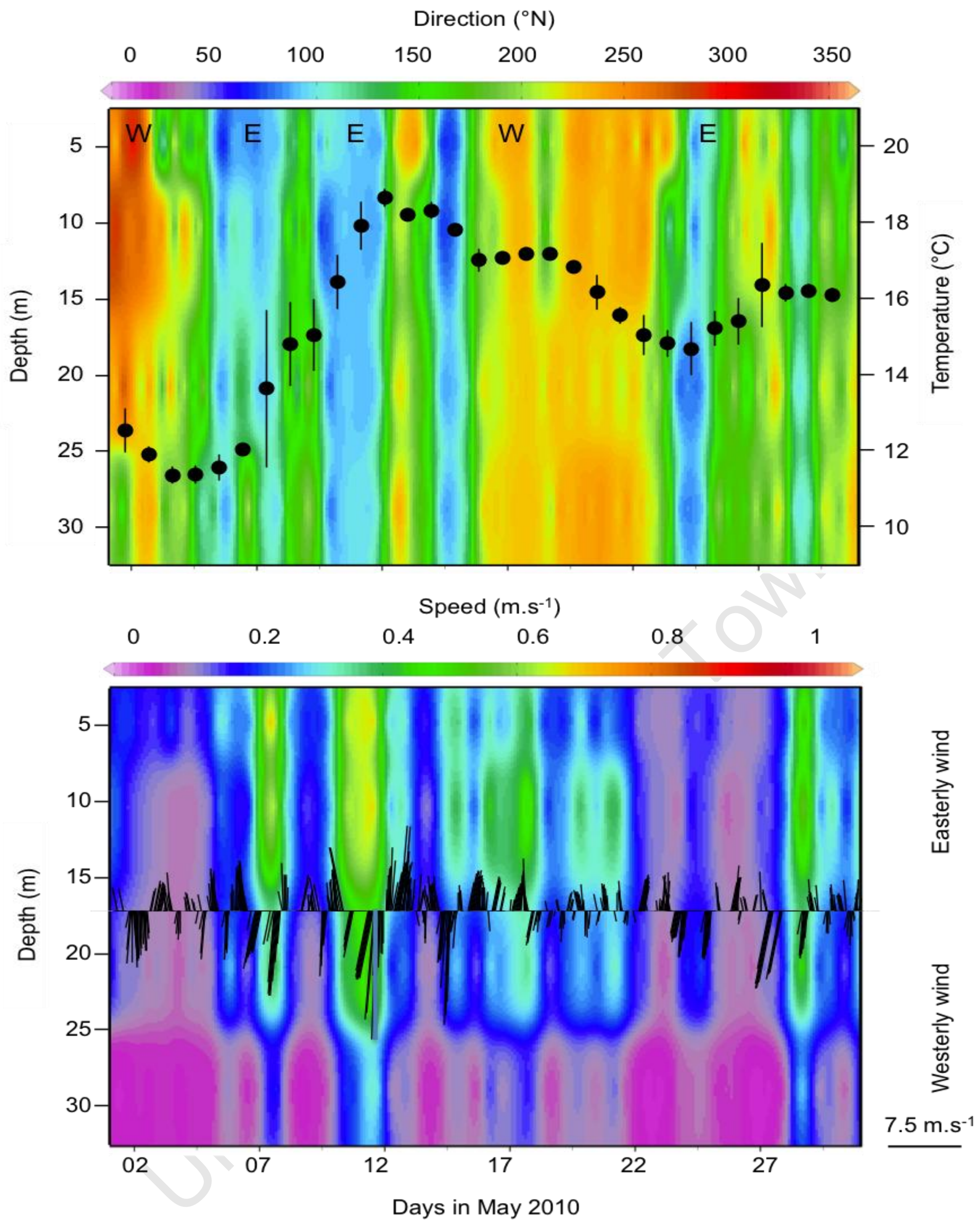


Figure 2.7b. Current and temperature regimes in Algoa Bay during and one week before African Penguins were deployed with data loggers. Direction (top panel) and speed (bottom panel) of currents recorded by an ADCP stationed in 30 m water depth, south of Bird Island during 2010. ~~The plots show the current conditions one week before and during African Penguin deployments.~~ The temperature (mean ± SD) recorded by the ADCP at 30 m is superimposed on the top panel in order to demonstrate temperature regimes with current direction. The hourly wind direction and speeds recorded at Bird Island are superimposed on the current speed plot to show the influence of wind on current speed and direction. Currents are mostly wind driven

except for warm eastward flowing intrusions apposed by strong easterly winds, e.g. 13 May 2010.

Foraging behaviour: random searches vs. orientated commutes

Bird Island penguins foraged in two main areas, utilizing areas southwest and east of the island more so than other directions of travel. It is likely that penguins use these areas in response to knowledge of higher probability of prey abundance. Birds that forage towards areas where prey is predictable should adopt a foraging strategy that maximizes their efficiency at sea in order to locate prey in as short a time and space as possible, similarly birds that forage in an unpredictable environment adopt a search strategy that maximizes prey encounter (Weimerskirch 2007; Trathan et al. 2008). African Penguins typically depart at night despite their inability to forage during this time, being visual hunters (Wilson 1985, Petersen et al. 2006, Ryan et al. 2007). In this study, birds departing on foraging trips at night traveled longer distances, suggesting that birds leave earlier to reach more distant prey patches or to maximize the area that they can search during the day when returning to the colony. Furthermore, early departure times that were correlated to distance travelled shows that birds may be anticipating the spatial occurrence of their prey. Indeed, penguins from Bird Island spent longer periods of time at sea compared to birds from west coast colonies (Bird Island: ca 17 h vs. Robben and Dassen Island: ca 10 h; Petersen et al. 2006), which may result from the earlier departure times of Bird Island penguins. Historically pelagic stock densities have been higher off the west coast where Dassen and Robben Island are located (Coetzee et al. 2008). However, we need to test whether departure times are independent of the return time of their partners to validate this influence.

The low sinuosity indices during the transit and return phases of their trips associated with commuting further support the hypothesis that African Penguins may anticipate the spatial occurrence of their prey. Penguins (e.g. Wilson 1995, Petersen et al. 2006, Cotté et al. 2007, Ryan et al. 2007, Trathan et al. 2008) as well as flying seabirds such as gannets (e.g. Grémillet et al. 2004, Pettex et al. 2010) and murres (e.g. Benvenuti et al. 1998) often begin their trips with a linear component before performing more complicated and erratic search behaviour. In the case of King Penguins, these linear paths can be explained by linear travel in currents or along temperature gradients (Cotté et al. 2007, Trathan et al. 2008), while gannets may have liner paths as a result of wind use to reduce travel costs (Grémillet et al. 2004; Pettex et al. 2010). African Penguins adopted a more random search strategy during foraging phases, which was described by paths that had a high degree of sinuosity and were looping in shape, similar to other short-range penguin species (e.g. Magellanic Penguins: Pütz et al. 2002). African Penguins on the west coast often display looping type trips (Petersen et al. 2006), which could be associated with a correlated random search strategy (Weimerskirch 2007). Small, randomly dispersed shoals of fish are likely to be encountered more often under a random looping search than linear paths that effectively cover less area (Wilson 1985). African Penguins from Bird Island likely anticipate the spatial occurrence of their prey before performing a finer scale search strategy.

Temperature as a cue for locating prey patches

In this study, the waters encountered by African Penguins showed little variation in temperature on a daily scale. Top predators such as King Penguins travel down thermal slopes towards fronts or eddies suggesting that these birds use thermal slopes to locate preferable foraging grounds (Cotté et al. 2007, Trathan et al. 2008). However, King Penguins travel hundreds of kilometers and thus anticipate meso-scale features that are largely persistent and therefore predictable. It seemed that rather than actively searching for SST associated with cool upwelled waters along some gradient, birds were predicting areas of potential cool, nutrient rich waters. Although the daily variability of SST within the foraging range of African Penguins was small and there was no apparent SST habitat preference, the models of SST distributions highlight the higher occurrence of cool waters east and south of the island, similar to where birds foraged (Figure 2.5). The areas south and east and farther than 15 km from the colony preferentially used by African Penguins (Figure 2.6) are linked to the enhanced occurrence of nutrient rich, cool waters. For instance, cool nutrient rich water from the Port Alfred upwelling cell enters the bay from the east and flows southwest around Bird Island (Lutjeharms et al. 2000). Upwelling in the Bird Island region is observed ca 45% of the time (Lutjeharms et al. 2000). Furthermore, small pelagic fish surveys revealed that the biomass of Anchovies was highest east and south of Bird Island in 2001 (Barange et al. 2005).

Nevertheless, when one individual encountered cool waters, that bird actively tracked these waters to the end of the upwelling plume southwest, after which the track shape can be described as a correlated random search when the bird travels back towards the colony through warmer waters (Figure 2.4h). This individual demonstrated temperature restricted area use similar to Leatherback Turtles *Dermochelys coriacea*, which remain in waters that are likely to contain their main prey items (Fossette et al. 2009). The apparent lack of habitat preference for cooler SST despite foraging in areas associated with cooler water may be due to a time lag between cool SST and associated production; as the waters with a low SST reach the preferential foraging range of the African Penguins, SST has warmed as it mixes with bay waters and productivity has begun. Cool waters associated with upwelling contain higher traces of nutrients for primary production, but mismatch between upwelling and where seabirds forage can be experienced due to time lag effects in productivity and shifts in prey distributions (e.g. Simmons and Cordes 2000; Grémillet et al. 2008).

The main prey of African Penguins in Algoa Bay is the Anchovy which has a habitat preference for waters with SST of 15-20 °C and are largely absent in waters with SST above 20 °C (Barange and Hampton 1997). Interestingly though, African Penguin habitat preference increased for warmer SST (>20 °C). These warm waters were often at greater distances from the colony (Figure 2.5) and are probably encountered as a result of intrusions of the shoreward edge of the Agulhas Current, a process which may drive pelagic fishes inshore (O'Donoghue et al. 2010). Warmer average SST did not result in birds using shallower waters, contrary to O'Donoghue et al. (2010) hypothesis. When warm Agulhas waters intrude into the bay, the intrusion occurs as a warm water wedge that engulfs the eastern bay and cools as the intrusion mixes with bay waters (Goschen and Schumann 1990; Goschen and Schumann 1994). Birds may not move shoreward as the thermal regime is unlikely to change closer to the shore during a full intrusion of waters associated with the Agulhas Current. The dilution of Agulhas waters with bay waters may also result in a less severe thermal stress for prey, unlike on the narrow shelf northeast of Algoa Bay. Lastly, penguins may remain in deeper waters as they can dive below the surface wedge to cooler bottom waters where prey may be concentrated, a concept that is covered later in Chapter 3.

The influence of currents on foraging paths

The bearings of the farthest point of penguins' foraging paths were generally similar to the dominant current bearings in Algoa Bay, southwest and east (Roberts 2010). The currents measured during the days penguins were deployed with GPS loggers

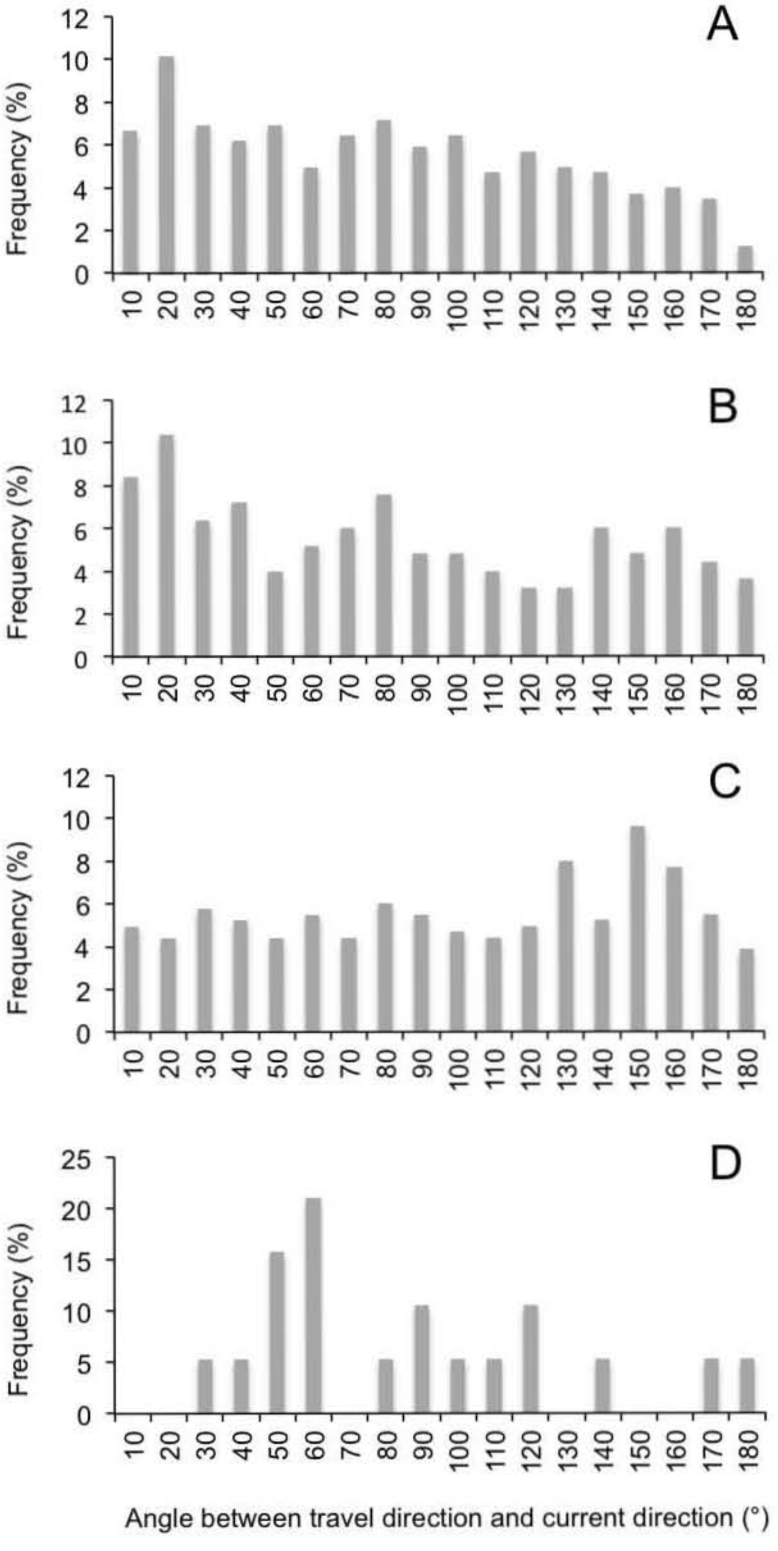


Figure 2.8. Graphs showing the binned distribution of differences between bird travel direction and the temporally closest current direction. Differences are shown for the four trip phases: transit phase from departing the colony and the first dive (a), foraging away from the colony (b), foraging towards the colony (c), and the return phase from the last dive to returning to the colony (d).

were dominantly southwest and east, similar to the current directions recorded by Roberts (2010); (Figure 2.7a and 2.7b). Although penguin departure directions and dominant current directions were similar, the directions of travel along trips were only weakly associated with current direction during the transit phase and the two were largely independent during foraging and return phases of each trip. Currents around Bird Island are largely wind driven with some deflection around the island itself and are generally weak (Goschen and Schumann 1988; Roberts 2010). Many top predators are inferred to use currents over a variation of scales to reduce their energy demands. For example Magellanic Penguins use tidal forces to depart from and return to their colony (Raya Rey et al. 2010) and strong coastal currents to increase their speed away from the colony (Pütz et al. 2002). Northern Fur Seals *Callorhinus ursinus* utilize the geostrophic flow associated with eddies (Ream et al. 2005), similarly to King Penguins (Cotté et al. 2007) to reduce energy costs. Current use is analogous to wind forces on flying species, e.g. Wandering Albatrosses *Diomedea exulans*, which circulate the oceans using tail winds to increase flight speed and reduce energy costs of flight (Weimerskirch et al. 2000). Even though not significant, African Penguin swim speeds were slower with tail currents than with head on currents, suggesting birds reduced energy inputs when traveling in the same direction as the current or swam faster against the current to overcome the force of the current. The swim speeds of penguins and currents in this study indicate that birds swam at almost three times the underlying current speed and thus use energy to propel themselves along with the current. The average speeds of currents are much slower than African Penguin swimming speeds, suggesting that currents do not impede bird movement. However, the increase in speed of birds when swimming against the current may suggest increased energy expenditure. Therefore, this study supports~~aids in~~ work by Gasper et al. (2006) ~~in~~ by demonstrating how important it is to consider currents (and winds for flying birds) when calculating the energy budgets of species.

Conclusions

African Penguins exhibit rapid changes in behaviour in response to changes in their habitat, e.g. adjusting trip duration and the distance they travel away from the colony in relation to prey availability (Pichegru et al. 2010). These birds are likely to have evolved flexibility in their foraging behaviour due to the stochastic nature of their environment. By using a combined strategy of linear commutes towards areas associated with upwelling zones before switching to a correlated random search penguins maximize their chances of encountering small patchily~~randomly~~ distributed prey~~ patches~~. Currents were likely too slow to be used in transport, however the importance of current speed and direction should be taken into consideration when calculating energy budgets. Birds likely achieve an understanding of their habitat over time, probably utilizing a combination of physical and biological cues, as well as memory as to where to forage. In the context of Ashmole (1971) and Lack (1968), birds are likely limited by a patchy and scarce prey resource, while behavioral adaptations such as the use of cues ~~use~~ to allow them to increase the probability of locating these patches.

Chapter 3

African Penguin dive behaviour in relation to variable and ephemeral thermoclines

ABSTRACT

Temperature and nutrient gradients exist subsurface as frontal zones which are formed at thermoclines, typically where warmer, nutrient poor surface waters meet cooler, nutrient rich deeper waters. Thermoclines are known to be important foraging zones for top predators, as their prey tend to aggregate below the thermocline. In high energy environments, such as near-shore ecosystems, the structure of the water column is less stable and is vulnerable to mixing through processes such as wind shear and influences from local currents. But how top predators cope with a thermocline that frequently changes in depth and strength, thus its ability to concentrate nutrients~~, remains poorly understood~~is a topic that warrents further investigation. African Penguins forage in shallow and dynamic coastal waters where perturbations in the thermocline are frequent. By implementing general linear mixed models (GLMMs), I determine how penguins' foraging effort (dive depth, dive bottom time and ascent and descent rates) is related to the depth and structure of the thermocline, such as its gradient and strength. Penguins increased the depth of their foraging dives in response to deeper thermoclines. The bottom of foraging dives was associated with a narrow range of temperatures, suggesting penguins foraged to and below the thermocline, i.e. where cooler waters are found. Penguins dived deeper and faster when the thermocline had a less steep gradient and the thermocline acted as a diffuse thermal barrier, suggesting that prey was not concentrated by these thermoclines. Birds also decreased their dive descent rates when the thermocline was shallow and a strong barrier to nutrients. Thermoclines with steep gradients could be important cues as the probability of a dive occuring near these thermoclines was greater compared to diffuse thermoclines with a shallow gradient. This research shows the importance of thermoclines as a potential cue for foraging in a marine predator and the flexibility of African Penguins foraging in a dynamic thermal habitat, or that prey is associated with cooler waters fronted by a thermocline.

INTRODUCTION

Thermoclines occur where horizontally stratified water masses with different temperatures meet. They generally form at depths where wind forces reach zero, marking the lower limit of surface mixing. Strong thermoclines are characterized by rapid temperature changes with depth and form an ecological and physical barrier that can limit the upward advection of nutrients from deeper waters due to the different densities of the two water masses separated by the thermocline (Fielder 2010). Thermoclines vary in terms of depth, thickness, gradient and strength. Thermoclines may also be permanent or seasonal features or a combination of both (González-Pola et al. 2007). Strong thermoclines (large temperature differences across the thermocline) and thermoclines with steep gradients (rapid temperature change with depth) represent systems with highly stratified water columns. Nutrient fluxes across strong thermoclines are reduced relative to those across weaker and more diffuse thermoclines.

Persistent and strong thermoclines can concentrate nutrients and prey (Gray and Kingsford 2003) and their ecological importance for many top predators has been well documented (e.g. Northern Fur Seals: Kuhn 2011; Thick-billed Murres: Takahashi et al. 2008, Kokubun et al. 2010; King Penguins: Charrassin and Bost 2001; Southern Elephant Seals: Biuw et al. 2007). The foraging depth of top predators is often dependent on the depth of the thermocline (e.g. Takahashi et al. 2008). For example, the foraging depths of Thick-billed Murres are associated with stronger thermoclines more so than weak thermoclines as prey distribution probably shifts in the absence of a strong thermocline (Kokubun et al. 2010). In well-mixed water columns prey may also have a more diffuse distribution within the water column as opposed to concentration of prey around a stronger thermocline (Ropert-Coudert et al. 2009). In shallow coastal waters, perturbations in the depth and intensity of thermoclines are frequent and thermoclines typically are less important in determining the vertical distribution of species such as mesozooplankton and fish larvae (Gray and Kingsford 2004). ~~As a result, the use of thermoclines by top predators in these dynamic ecosystems is less apparent in the literature.~~

On the southern coast of South Africa, Algoa Bay is the eastern most of a series of crescent-shaped bays where thermoclines often form in waters deeper than 50 m (Goschen and Schumann 1988). Summer thermoclines tend to be stronger, and result from upwelling driven by extended easterly winds (Schumann et al. 1982, Beckley 1983) as well as interactions of the Agulhas Current with a widening continental shelf (Largier and Swart 1987; Schumann et al. 1988). Cold, nutrient rich waters originating from Indian Ocean Central Waters rise over the continental shelf via Ekman veering, a process that is common with western boundary currents (see Hsueh and O'Brien 1971). However in winter, frequent storms associated with winter cold fronts, as well as warm water intrusions from the Agulhas Current, often dissipate thermoclines, resulting in a thermally homogenous water column (Goschen and Schumann 1988). Recent oceanographic findings based on data from an array of under water temperature recorders around Bird Island have highlighted how variable temperature structures in the shallow coastal waters are on a fine temporal scale (Figure 3.1; SAEON unpublished data).

Since ca 2010, the islands in Algoa Bay have supported >50% of the global population of African Penguins (Figure 1.1; Crawford et al. 2011). In this chapter, I compare the foraging behaviour of African Penguins in waters with different vertical thermal structures, i.e. in the presence or absence of thermoclines, and under different thermocline characteristics. I assess how African Penguins dive in relation to the weak winter thermocline and how they react to changes in the thermocline at fine temporal and spatial scales. The thermocline concentrates nutrients necessary for increased phyto/zooplankton production and therefore is likely to attract small pelagic fish that feed on small zooplankton (James 1987). I predict that penguins will use the temperature changes felt at the thermocline when diving as a cue for likely prey encounter. Penguins are likely to show a stronger association with the thermocline when the strength of the thermocline is greater and/or when the thermocline has a smaller gradient (a strongly stratified water column where temperature changes rapidly with depth). Strong thermoclines may be either more detectable by a top predator and act as a thermal cue or establish prey aggregations due to nutrient concentrations. Therefore, correlations between dive depth and thermocline depth may merely represent prey distribution and not cue use by penguins.

Higher sea surface temperatures associated with Agulhas Current intrusions (Goschen and Schumann 1994) are also likely to result in deeper dives as birds aim to reach deeper cooler nutrient rich waters. Warm water Agulhas intrusions have been described to enter Algoa Bay as a warm surface wedge approximately 20–50 m deep (Goschen and Schumann 1990; Goschen and Schumann 1994). I hypothesize that birds dive deeper in warmer mixed waters than cooler waters, as nutrients, and therefore productivity and prey fishes, are dispersed over the entirety of the water column in cooler waters~~,~~. Warmer waters are associated with the Agulhas Current whose waters are nutrient poor. ~~which in turn distributes the productivity and prey fishes throughout the water column warmer mixed waters are likely to be nutrient scarce due to the nature of warmer waters being associated with the Agulhas Current.~~

Finally, I assess how the foraging effort of African Penguins is related to thermocline structure and the conditions of waters with no thermocline. I use bottom time and descent and ascent rates to describe how birds structure their dive in relation to the different thermocline structure and mixed water thermal composition~~s~~. Birds are likely to increase their bottom times, ascent and descent rates in water columns with intense, steep gradient thermoclines that act as strong cues and strong barriers for nutrient flux as birds may try to maximize their time in a narrow area of increased production. Birds may also increase their bottom times in cool mixed water columns that are nutrient rich from upwelling, when compared to mixed warmer waters resulting from an intrusion of the Agulhas Current.

METHODS

Data collection

Birds were fitted with GPS-TD loggers following methods described in Chapter 2. Temperature and pressure data with known GPS fixes allowed me to determine the structure of the water column where birds dived (see “vertical thermal structure” below). Dive and GPS data were collected from 33 birds from Bird Island in May - June 2010, and a further 24 in March - April 2011. The differences between 2010 and 2011 in the depth of dives, the descent rate and ascent rates and the bottom times of penguins (Table 3.1) are unlikely to be biologically meaningful, given low magnitude of the differences observed and the large sample sizes of dives in both years. Therefore, the data from 2010 and 2011 were pooled for the analyses.

Penguin dive data analysis

To exclude commuting dives from the analyses, I excluded dives <3 m following Wilson and~~&~~ Wilson (1990). A GPS position was inferred for each dive by linear extrapolation between the two closest GPS positions based on the start time of each dive. Only dives with an inferred position within 500 m of a GPS fix were considered for analysis. Dive data were analyzed with MultiTrace-dive (Jensen Software Systems). For each dive, the maximum depth, the duration of the dive and the bottom time (calculated as the time between the first inflection in the descent phase of the dive and the last inflection on the ascent phase of each dive) were calculated, as well as the ascent and descent rates ($m.s^{-1}$). Dives were separated into foraging and search dives. Foraging dives were characterized by undulations in the bottom phase of the dive. These undulations are thought to be a result of prey pursuit, as the number of undulations in the bottom phase of the dive are correlated with beak opening events in other penguin species (Simeone and Wilson 2003; Hanuise et al. 2010). An undulation in the bottom phase was defined as three consecutive points where vertical velocity was zero and the vertical displacement between these three points was >1 m (Halsey et al. 2007).

Vertical thermal structure

The depth of the water column where birds dived was inferred from bathymetric charts. The thermal structure of the water column was determined from dives that sampled at least 80% of the water column depth. Temperature data for these dives were averaged into 1 m bins using data from both the ascent and descent of penguins dive. Sea-surface temperature (SST) was taken as the 1–2 m bin as the response time of the loggers temperature probe stabilizes in the first 1 m of the water column when the logger moves from air to water. A thermocline was recognised if the temperature difference (ΔT) between the near bottom waters and the SST differed by >2 °C and ΔT with depth was >0.25 °C/m (following Takahashi et al. 2008; Kuhn 2011). The start and end depths of the thermocline, giving its thickness, were taken as the depths at which the rate of ΔT with depth first and last exceeded 0.25 °C/m. From these, I calculated the midpoint depth of the thermocline, its intensity (TI) as the ΔT from the top to the bottom of the thermocline (following Takahashi et al. 2008; Kokubun et al. 2010), and its gradient (TCg), as ΔT between the start and end depths of the thermocline divided by the thickness of the thermocline. Thermocline intensity and gradient define the strength of the thermocline. Thermoclines that are more intense have a greater difference in temperature across the thermocline, while gradient characterises how vertically compressed the thermocline is. Hence a thermocline with a high intensity and a steep gradient forms a strong front between different water masses.

In dives where the vertical ΔT was too gradual to be recognised as a thermocline, i.e. in mixed waters, a stratification index was calculated as the ΔT from the SST to the bottom of dives that covered >80 % of the water column. Data describing the thermal profile of the water column for representative dives were assigned to all other dives that occurred within 750 m or 30 min of the representative dive. In addition to temperature records provided by GPS-TD loggers, hourly measurements of temperatures obtained from a string of under water temperature recorders (Onset Hobo Pro v2 Water Temperature Loggers) spaced vertically 10 m apart ca 7.4 km south of Bird Island. Data for t~~T~~emperature-~~-~~depth plots ~~from the data~~were obtained from ~~the ~~UTRs and were plotted in Ocean Data View 4 (http://odv.awi.de).

Table 3.1. Comparison (Students t-test) of foraging and dive parameters (average ± SD) of breeding African Penguins from Bird Island in 2010 (33 individuals) and 2011 (24 individuals).

	2010	2011	n1,n2	t	p-value
Path length (km)	52.9 ± 25.3	52.5 ± 20.3	33, 24	0.06	0.94
Max distance (km)	15.0 ± 8.3	14.6 ± 5.4	33, 24	0.2	0.83
Trip duration(h)	20.7 ± 7.1	21.9 ± 8.5	33,24	-0.47	0.64
Dive rate (dives/h)	16.6 ± 4.7	15.6 ± 3.5	33,24	0.75	0.45
Dive duration (s)	75 ± 28	82 ± 35	11807, 8085	-13.77	<0.001

Dive depth (m)	20.0 ± 19.3	21.9 ± 23.8	11807, 8085	-6.88	<0.001
Bottom time (s)	40.1 ± 16	40.5 ± 17	11807, 8085	-1.76	0.07
Descent rate (m.s^{-1})	1.3 ± 0.4	1.3 ± 0.4	11807, 8085	4.94	<0.001
Ascent rate (m.s^{-1})	0.8 ± 0.4	0.8 ± 0.4	11807, 8085	-1.88	0.05

Statistical analysis

General linear mixed models (R package nlme; Pinheiro et al. 2011) were used to assess the relationships between penguin foraging parameters and the water structure in which birds dived. In waters presenting a thermocline, the distance within the water column a bird dived from the midpoint of the thermocline as well as bottom times, maximum dive depths and ascent and descent rates were each modelled as a function of the thermocline midpoint depth, TI and TCg, as well as SST. Binomial models were implemented to determine whether a dive was more likely to be above or below the thermocline midpoint. In mixed waters where thermoclines were absent, maximum dive depths, bottom times, and ascent and descent rates were modelled as a function of average water column temperature, stratification index and SST. In addition, bathymetry, time of day, time of day as a quadratic (time^2) and types of dives (foraging or searching) were included as co-variables in all models, as these variables are likely to influence the response variables. Bathymetry naturally constrains dive depth and furthermore, daylight (i.e. time of day) is likely to explain some of the variation of the response variables as penguins are visual hunters (Wilson et al. 1993). Time was fitted as a quadratic as birds are expected to dive shallower during the early morning and evening, and deeper at midday because of the constraints of light availability. Search dives are shallow dives with shorter bottom times and slower ascent and descent rates compared to foraging dives (Table 3.2). Bird ID was included as a random effect in all models, to take into account the pseudo-replication effect due to repeated dives by single individuals. No co-linearity was observed between fixed effects. Residuals and random effects were normally distributed. Models with the lowest AIC were chosen and non significant variables dropped from the model unless they contributed to a lower AIC score or patterns appeared in the residual vs fitted plots performed during model validation. Fixed variance structures were fitted to variables that indicated heteroscedacity. Means and standard deviations are reported, unless stated otherwise.

RESULTS

Water temperature structure during the study periods

The formation of thermoclines was largely a result of cold bottom waters advancing towards the surface forming a thermal discontinuity with warm well mixed surface waters (e.g. Figure 3.1a). During deployments in March 2011, the thermocline maintained a stable position in the water column (TC depth: 21.3 ± 5.0 m; Figure 3.1b) for 11 days. The thermocline during this period had, on average, a steep TCg (0.58 ± 0.56 °C.m^{-1}) and had a high TI (5.3 ± 1.8 °C). Warm water intrusions from the Agulhas Current were observed during deployments between 12-13 May 2010 and 22 April 2011 – 02 May 2011, resulting in a homogenous warm water column (column temperature: 17.0 ± 1.6 °C; Figure 3.1a; #3.1d). However, renewed upwelling re-established a thermocline, quickly advancing the thermocline towards the surface as upwelling intensified (e.g. 2010/05/16–2010/05/26; Figure 3.1a). When upwelling commenced thermoclines were deep (TC depth: 48.8 ± 4.3 m) with steeper TCg (TCg: 0.5 ± 0.3 °C.m^{-1}) and high TI (TI: 4.2 ± 1.7 °C), generating a highly stratified water column (e.g. 2010/05/17; Figure 3.1d). When complete upwelling occurred towards the near surface a cool mixed water column was observed (Fig 3.1c). Wind mixing of the water column occurred once during a storm event on 28 May 2010, which resulted in the thermocline position deepening before the thermocline waters were incorporated into the surface mixed waters resulting in a moderately warm, mixed water column (column temperature: 16.6 ± 0.2 °C; Figure 3.1d).

Table 3.2. Characteristics of two different African Penguin dive types: searching/traveling dives and foraging dives i.e. those that had undulations in the bottom phase of the dive.

	Search dive (13679 dives)	Foraging dive (6113 dives)	t - value	p - value
Dive depth	24.0 ± 19.6	39.2 ± 21.1	47.7	<0.001

Bottom time	36 ± 16.1	50 ± 14.0	61.6	<0.001
Descent rate	0.9 ± 0.4	1.2 ± 0.3	66.9	<0.001
Ascent rate	0.9 ± 0.4	1.3 ± 0.4	59.81	<0.001

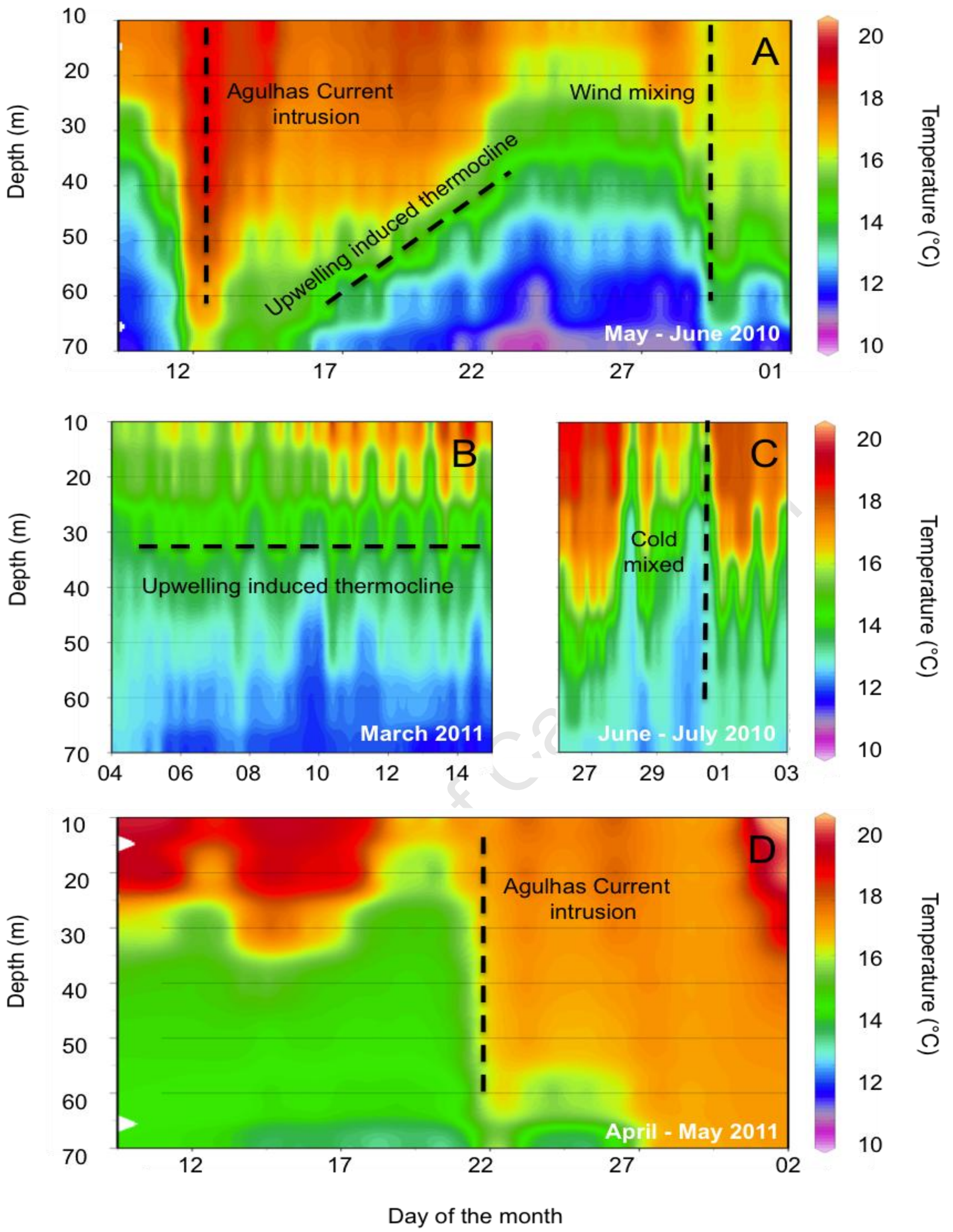


Figure 3.1. Temperature depth plots from a string of under water temperature recorders situated ca 7.4 km south of Bird Island. The plots show the variability of the vertical thermal structure of the water column over the periods of time when African Penguins were deployed with GPS-TD loggers. Dashed lines highlight the labeled process or feature.

Thermocline midpoint depths were on average 31.5 ± 14.1 m, and TI and TCg were 5.9 ± 1.8 °C and 0.38 ± 0.3 °C.m^{-1}, respectively. The average temperature at the thermocline midpoint was 15.9 ± 1.1 °C. Thermoclines were on average 12.8 ± 7.6 m thick, which accounted for ca 20% of the water column depth where they occurred. Sea-surface temperatures where birds dived averaged 18.6 ± 1.1 °C over both years. Mixed waters above thermoclines were on average 18.4 ± 11.9 m thick, accounting for ca 30 % of the water column structure. Mixed waters presented a high variability in their average temperatures, ranging from 13.8 °C to 18.9 °C, with an average stratification index of 1.9 ± 1.3 °C. The average temperature of mixed waters during complete upwelling was 13.4 ± 1.8 °C and 17.4 ± 0.7 °C during wind mixing events (. During Agulhas Current intrusions the average water column temperature was 16.1 ± 1.9 °C. The distribution of water depths containing mixed waters did not differ from the distribution of water depths where birds dived (= 0.03, p >0.05). Similarly the distribution of water depths presenting thermoclines did not differ to the distribution of water depths where birds dived (= 0.11, p >0.05), therefore the spatial distribution of waters presenting thermoclines and those that were mixed were not a consequence of bottom depth.

Dive behaviour in relation to thermoclines

The average temperature at the bottom of foraging dives in stratified water columns was 14.1 ± 2.2 °C. When a thermocline was present, penguin diving behaviour was influenced by its characteristics (Table 3.2). Penguins increased their dive depths with the depth of the thermocline and decreased their dive depth when TCg was steeper (Figure 3.2). Penguins maximum dive depths were farther from the thermocline mid point depth when the thermocline increased in intensity or in depth. Although there was no significant difference between search and foraging dives in their distance to the thermocline depth, foraging dives had a higher probability of occurring below the thermocline than above it (Table 3.3; Figure 3.3). Search dives showed greater central tendency around the thermocline, with more dives occurring above the thermocline compared to foraging dives (Figure 3.3). However, search dives were largely surface dives that may be associated with travelling (e.g. Figure 3.2 and Figure 3.4). In 2010, 51% of dives were foraging dives while in 2011 this decreased to 35%.

Table 3.3. Results of the general linear mixed models (GLMMs) testing how dependant variables such as the depth birds dived in relation to the thermocline depth (|dive depth – TC depth|), their maximum dive depths, their bottom time, and descent and ascent rates are influenced by the thermocline midpoint depth, intensity and gradient, as well as bathymetry, time of day, type of dives (foraging or searching), and SST in stratified waters.

Response	Fixed effect	Estimate	Std. Error	t - value	p - value
|Dive depth - TC depth|	Intercept	-9.190	7.842	-1.172	0.241
	Bathymetry	0.205	0.013	15.318	<0.001
	Time	5.013	0.432	11.593	<0.001
	Time^2	-0.211	0.018	-11.404	<0.001
	Foraging (True)	0.584	0.346	1.688	0.091
	SST	-0.943	0.417	-2.261	0.024
	Thermocline depth	0.078	0.029	2.744	0.006
	Thermocline intensity	0.688	0.184	3.746	<0.001
Max dive depth	Intercept	-71.842	10.169	-7.065	<0.001
	Bathymetry	0.325	0.020	16.056	<0.001
	Time	4.752	0.621	7.650	<0.001
	Time^2	-0.190	0.027	-7.133	<0.001
	Foraging (True)	16.299	0.493	33.050	<0.001
	SST	2.730	0.516	5.295	<0.001
	Thermocline depth	0.078	0.036	2.139	0.033
	Thermocline gradient	-2.469	1.182	-2.089	0.037
Bottom time	Intercept	-15.981	7.784	-2.053	0.040
	Bathymetry	0.052	0.015	3.449	<0.001
	Time	2.240	0.463	4.843	<0.001
	Time^2	-0.115	0.020	-5.797	<0.001
	Foraging (True)	12.457	0.365	34.119	<0.001
	SST	2.162	0.398	5.427	<0.001
Descent rate	Intercept	0.581	0.066	8.823	<0.001
	Bathymetry	0.002	0.0003	6.239	<0.001
	Time	0.050	0.011	4.742	<0.001
	Time^2	-0.001	0.0004	-3.286	0.001
	Foraging (True)	0.320	0.008	38.276	<0.001
	Thermocline depth	-0.003	0.0006	-5.439	<0.001
	Thermocline gradient	-0.149	0.020	-7.327	<0.001

Table 3.3 Continued

Ascent rate	Intercept	-0.340	0.072	-4.715	<0.001
	Bathymetry	-0.004	0.0004	-9.611	<0.001
	Time	-0.044	0.012	-3.704	<0.001
	Time^2	0.001	0.0005	2.347	0.019
	Foraging (True)	-0.414	0.009	-44.119	<0.001
	Thermocline gradient	0.163	0.023	7.193	<0.001

Table 3.4. General linear mixed model (GLMM) results showing the response variables predicting the probability of African Penguin dives occurring below the thermocline midpoint depth.

Response	Fixed effect	Estimate	Std. Error	z- value	Pr (>|z|)
Presence below the thermocline	Intercept	-6.328	1.236	-5.118	<0.001
	Bathymetry	0.019	0.002	7.679	<0.001
	Time	0.153	0.074	2.060	0.0394
	Time^2	-0.006	0.003	-1.991	0.0464
	Foraging (True)	1.652	0.066	25.015	<0.001
	SST	0.321	0.062	5.174	<0.001
	Thermocline depth	-0.049	0.005	-11.112	<0.001
	Thermocline gradient	-0.910	0.154	-5.925	<0.001

Penguins were more likely to dive below the thermocline midpoint when the thermocline midpoint was deeper, but they concentrated their dives above the thermocline when TCg was steep (Table 3.3; Figure 3.2). TI had no effect on whether a dive was above or below the thermocline, even though dives occurred farther away from the midpoint as TI increased. When birds foraged in waters with higher SST values, the depth of their dive in relation to the thermocline had a higher probability of being below the thermocline midpoint (Table 3.3). Penguin dive depth was also influenced by SST in waters with a thermocline, with birds diving deeper with a longer bottom time when SST increased, as well as diving closer to the thermocline. Penguins decreased their descent rates when the thermocline was shallow and when

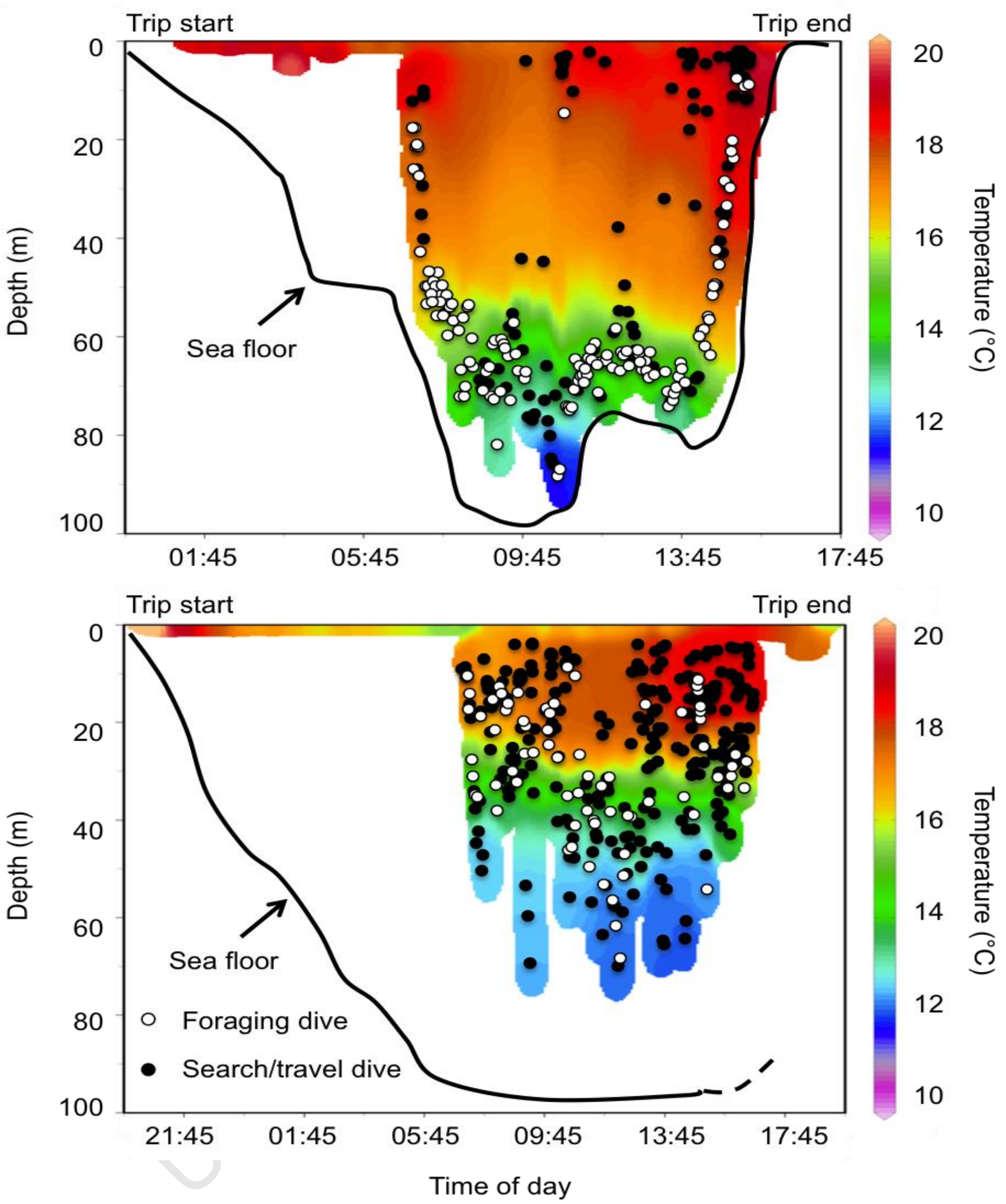


Figure 3.2. Temperature depth profiles along the trips of two African Penguins that foraged in waters with a deep (top panel) and shallow thermocline (bottom) on the 15 May 2010 and 30 June 2010, respectively, showing the distribution of foraging and searching/travelling dives in relation to the thermocline (14–16 °C) and sea floor. The deeper thermocline has a shallower gradient with dives concentrated near the seafloor where as the bottom panel shows a thermocline that is steeper with dives dispersed around the thermoclines midpoint. The dashed sea floor line represents the start of insufficient data to determine sea floor depth.

the TCg was steep. Similarly, birds' ascent rates decreased when TCg was steep, although TI did not seem to influence penguin diving behaviour.

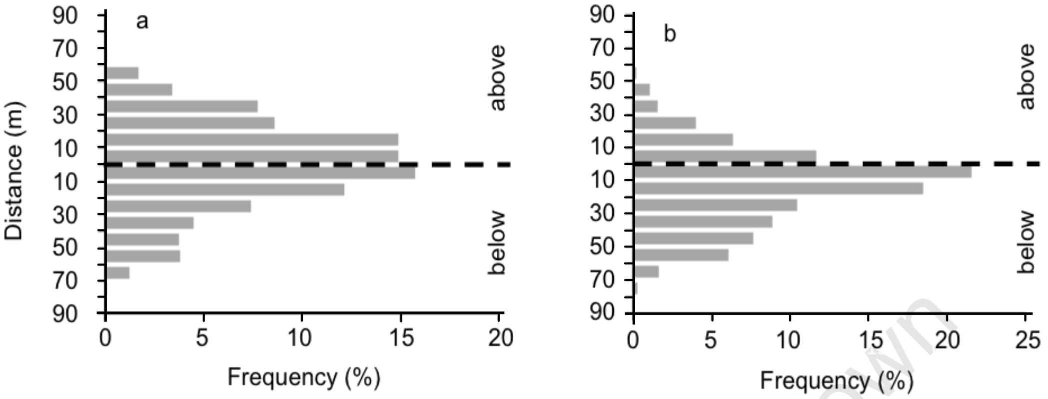


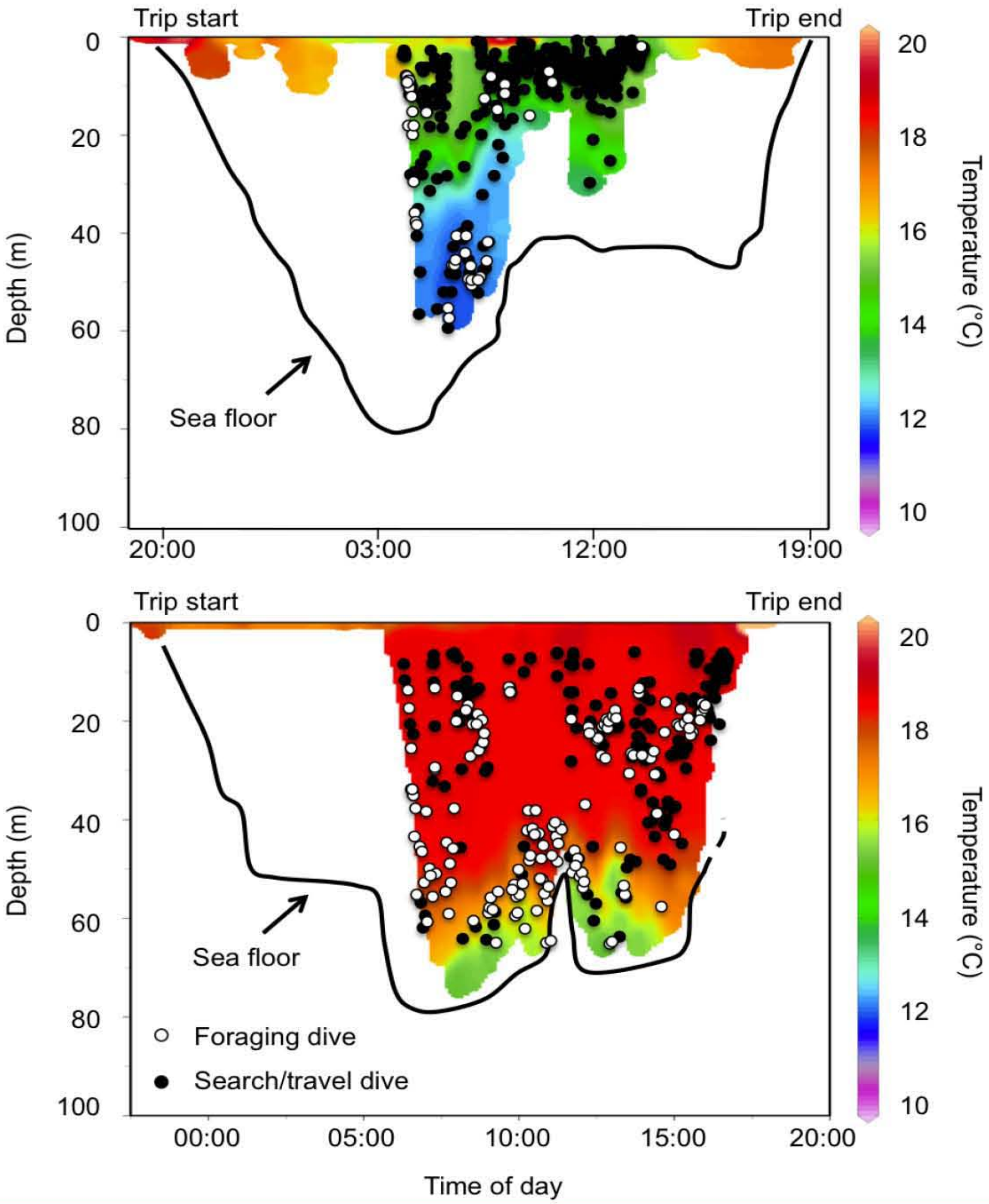
Figure 3.3. Distributions of (a) searching/travelling dives and (b) foraging dives in relation to the thermocline (dashed lines = thermocline midpoint depth).

Dive behaviour in mixed water columns

The average temperature at the bottom of foraging dives when there was no identifiable thermocline was 16.8 ± 1.4 °C. In the absence of thermoclines, bird dive depths were influenced by the average water column temperature, increasing their dive depth when waters were on average warmer, as well as when the stratification index increased (Table 3.5; Figure 3.4). However, when SST was higher in mixed water columns, birds performed shallower dives with a slower descent rate (Table 3.5). Neither bottom times of dives nor ascent rates were correlated with any of the thermal properties of the water column, i.e. average column temperature, SST and stratification index.

Table 3.5. General linear mixed model (GLMM) results describing penguin diving behaviour (search or foraging dive) in mixed waters (with no apparent thermocline) as a function of the average temperature of the water column, the water stratification index, bathymetry, time of the day, type of dives, and SST.

Response	Fixed effect	Estimate	Std. Error	t - value	p - value
Max dive depth	Intercept	-55.075	26.756	-2.058	0.040
	Bathymetry	0.662	0.043	15.558	<0.001
	Time	1.031	0.246	4.199	<0.001
	Foraging (True)	14.806	1.013	14.620	<0.001
	SST	-3.598	2.081	-1.729	0.040
	Column temperature	5.079	2.178	2.332	0.020
	Stratification index	2.679	1.061	2.527	0.012
Bottom time	Intercept	7.004	6.773	1.034	0.301
	Bathymetry	0.166	0.040	4.203	<0.001
	Time	3.531	1.387	2.546	0.011
	Time^2	-0.145	0.065	-2.246	0.025
	Foraging (True)	13.932	0.849	16.416	< 0.001
Decent rate	Intercept	1.235	0.376	3.289	0.001
	Bathymetry	0.007	0.0008	9.318	<0.001
	Foraging (True)	0.294	0.018	16.094	<0.001
	SST	-0.045	0.021	-2.174	0.030
Ascent rate	Intercept	-0.303	0.061	-4.996	<0.001
	Bathymetry	-0.009	0.0008	-10.380	<0.001
	Foraging (True)	-0.364	0.021	-17.635	<0.001


Trip start
Trip end
Depth (m)
0
20
40
60
80
100
20:00
03:00
12:00
19:00
Sea floor
Temperature (°C)
20
18
16
14
12
10
Trip start
Trip end
Depth (m)
00:00
05:00
10:00
15:00
20:00
Sea floor
○ Foraging dive
● Search/travel dive
Time of day

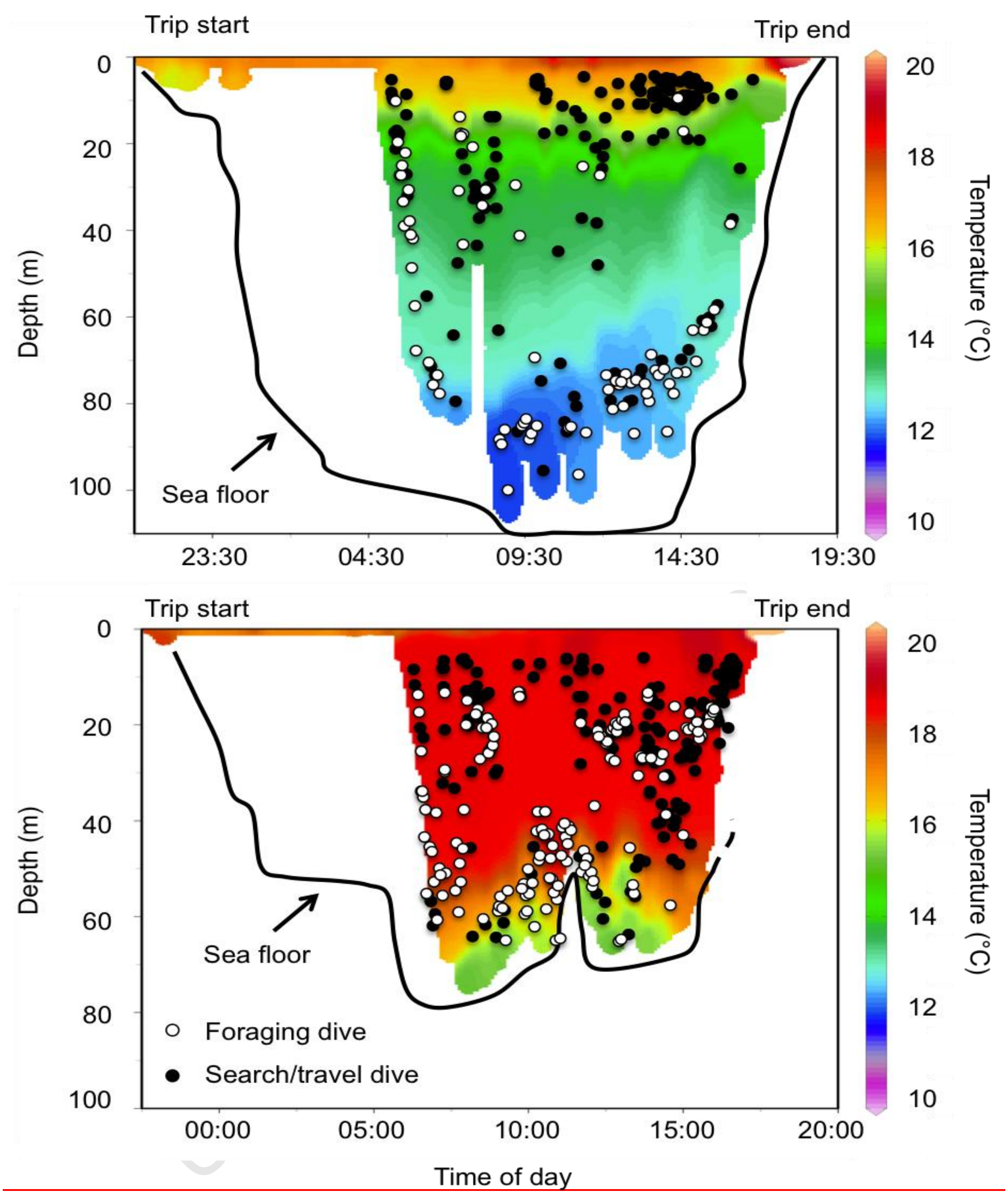


Figure 3.4. Temperature depth profiles along the trips of two African Penguins that foraged in waters that were classed as mixed (no thermocline was detected) on the ~~4~~ 30 ~~March~~ June ~~2011~~ 2010 and 14 May 2010, respectively, showing the distribution of foraging and search dives. In the top panel showing cooler waters, search dives were the most frequent between 0-30 m. Both cool (top panel) and warm (bottom panel) waters were observed which influenced the depth of dives and foraging behaviour. The dashed sea floor line represents the start of insufficient data to determine sea floor depth.

DISCUSSION

Top predators are known to associate with persistent physical features such as fronts, meso-scale eddies and upwelling cells (e.g. Charrassin and Bost 2001). How these predators cope within~~in~~ highly variable ecosystems where physical features are ephemeral remains a challenging topic. One way of dealing with variability is to adopt a comparative approach on a small scale (Lescroël and Bost 2005), but when variation occurs over a continuum (such as a heteroscedastic distribution of data) it is often unclear where to draw the line for most comparisons. African Penguins on the south coast of South Africa mainly forage in shallow coastal waters (<80 m, Chapter 2) that are prone to rapid changes, in particular changes in the vertical thermal structure of the water column (Figure 3.1). Therefore, I take a modelling approach in dealing with the question: How do African Penguins forage in relation to thermoclines that show a high degree of variability over a short temporal scale? Weak winter thermoclines in these shallow waters are driven by the advection of cool bottom waters i.e. upwelling (Figure 3.1), a similar process to the formation of thermoclines over the greater Agulhas Bank (Largier and Swart 1987). Penguins adjusted their dive depth in response to changes in the thermocline position in the water column and its structure on a daily scale; these changes were likely due to the advection of cool bottom waters advancing the thermocline upwards (Figure 3.1). The thermal structure of the water column can also be influenced by large storm events and interactions between shallow coastal waters and the adjacent Agulhas Current (Goschen and Schumann 1988), phenomena that were also observed in my data (Figure 3.1). These influences independently result in drastic changes in the thermal properties and structure of the thermocline in waters where African Penguins foraged.

Foraging in stratified waters

Primary production layers fluctuate in response to forcing factors such as nutrient and light availability, thermal stratification of the water column or phytoplankton interspecific competition for nutrients and light (Sverdrup 1953; Ryabov et al. 2010). Thermoclines are likely to concentrate nutrients and prey in the waters below the thermocline, because of the different densities of water masses that are separated by the thermocline. However, prey may aggregate above the thermocline as nutrients can trickle across the thermocline into the mixed layer, further more, primary production is a complex interaction between light availability and nutrient availability, thus if the critical depth for light is above the thermocline, primary production will be dependant on nutrients trickling across the thermocline into the mixed and luminated layer above (Sverdrup 1953). Predators have been shown to increase their foraging effort, diving efficiency and foraging success when diving within proximity of thermoclines (e.g. Spear et al. 2001;Takahashi et al. 2008; Ropert-Coudert et al. 2009; Kuhn 2011) suggesting that maximum production occurs at the interface of the thermocline. African Penguin search dives occurred slightly above the thermocline, while foraging dives were mostly below the thermocline (Figure 3.3), associated with a narrow range of temperatures. The distribution of African Penguin prey is likely to ~~occur~~ be concentrated below the thermocline in cooler more nutrient rich waters and penguins tend to dive below their prey, foraging upwards in quick bursts aided by their own buoyancy (Wilson 2010). African Penguins utilize the weak winter thermocline by diving to and foraging below the thermocline (Figure 3.3), and adjusting their behaviour with the thermocline structure (Table 3.3). Similarly, other piscivorous predators, such as King Penguins (Charrassin and Bost 2001) and Northern Fur Seals (Kuhn 2011) are known to dive either to or within close proximity of thermoclines.

The thermocline could act as a cue for foraging but associations between penguin dives and thermoclines may merely reflect the distribution of their prey. Anchovies can make up to 98% of African Penguin diets from the Bird Island colony (Crawford et al. 2011) and since the 1980s make up the majority (80–98%) of the prey items consumed by penguins at other colonies (Furness and Cooper 1982, Petersen et al. 2006). Elsewhere, Anchovies are often associated with the thermocline, showing highest abundance just above the thermocline (Hansen et al. 2001). Anchovies are also predominant in habitats that are more susceptible to changes in the thermal structure of the water column compared to other small pelagic fishes such as S~~s~~ardines, which prefer more stable environments (van der Lingen et al. 2010). African Penguins seemed to actively track thermoclines; not only their foraging dives increased in depth as the thermocline increased in depth, but also penguins modified their descent and ascent rates with TCg (Table 3.3), increasing their speed when the gradient was less steep. Faster descent and ascent rates are associated to dives with foraging, compared to commuting or search dives in many air-breathing marine predators (Bodkin et al. 2004; Mattern et al. 2007; Scott and Chivers 2009). Thus the faster decent and ascent dives observed in this study is likely a result of birds diving deeper in less stratified water. It is important to highlight that a correlation has been found between dive depths, bottom times and descent and ascent rates in African Penguins and thus presumptions on faster descents in less stratified waters are likely a result of deeper dives targeting prey concentrated near the benthos (Ryan et al. 2007; Wilson et al. 2010).

Thermoclines with a steeper gradient probably concentrate prey below the thermocline because these thermoclines are formed as a result of a more pronounced two layer system of warm surface waters fronted by cooler bottom waters compared to a thermocline that is more diffuse which occurs when there is mixing of waters above and below the thermocline. Penguins did not react to the actual intensity of the thermocline (i.e. the temperature change across the thermocline), but only TCg, unlike Northern Fur Seals (Kuhn 2011) and Thick-billed Murres (Kokubun et al. 2010). These latter species increase their use of the thermocline when the intensity of the thermocline increases. For instance in the Bearing Sea where these species were studied, the intensity of the thermocline is known to be associated with higher productivity, which in turn influences upper trophic levels (Stabeno et al. 2001; Hunt et al. 2008; Kuhn 2011). Thus African Penguins' prey are likely to be driven by the temperatures associated with the cold upwelling that forms the thermocline. A steeper TCg could also provide a greater cue of potential prey occurrence, given a rapid change in temperature associated with a steeper gradient.

Interestingly, bottom times did not differ with regards to the structure of the thermocline nor its depth, suggesting that foraging effort was unaffected by the thermal structure of the water column. Birds also dived closer to the thermocline when SST was higher, which can be expected as thermoclines are reinforced by positive heat fluxes (Largier and Swart 1987) and birds are likely associating with cooler waters below the warmer surface mixed waters.

Foraging in mixed waters

African Penguins also responded as expected to the temperatures of mixed waters, diving deeper in warm mixed waters than cooler mixed waters (Table 3.4). Agulhas Current waters which cause warm mixed waters within the bay are nutrient poor

(Goschen and Schumann 1988) and are likely to force prey to deeper depths in search of cooler, more nutrient rich bottom waters. African Penguins increased their dive depth (Table 3.4) in more ~~mixed~~ stratified waters, like Little Penguins (Pelletier et al. 2012). Wing beats revealed an increase in Little Penguin foraging effort in mixed waters with lower prey encounter rates, suggesting that prey were distributed over a greater depth range making foraging more challenging. Even though African Penguins had to dive deeper in more stratified and in warmer water columns, neither the stratification nor the mixed temperature of these water columns had an effect on the bottom times of African Penguins. This result suggests that foraging effort is similar between warm and cool mixed waters and in less mixed waters and those that are better mixed. Because penguins dived deeper in warmer mixed waters, it can be assumed that prey may be concentrated ~~against~~ near the benthos, ~~at depth~~ thus making foraging as efficient as when prey is distributed closer to the surface. In stratified water columns, birds similarly target cooler deeper waters near the benthos where prey may be concentrated ~~with the sea floor~~ (Figure 3.4).

Descent rates were slower and dive depths decreased (and were thus more likely to incorporate some travel dives) in warmer mixed waters and in the presence of increasing SST. The shallower dive depths of birds in warm mixed water columns with higher SST may be understood by assessing the actual depths of water where birds foraged during these regimes. ~~A relationship dependant between dive depth and temperature may be linked to the water depths where these higher SST occurred.~~ ~~Re~~Recent aerial surveys from the northern Eastern Cape to the Natal Bight have shown that with increasing SST, greater foraging activity of top predators, such as Bottlenosed Dolphins *Tursiops aduncus*, Common Dolphins *Delphinus capensis* and Cape Gannets is observed inshore (O'Donoghue et al. 2010). ~~; s~~Small pelagic prey fish of such as Sardines and Anchovies are assumed to move inshore as the Agulhas Current moves closer to the coast (O'Donoghue et al. 2010). Anchovies are typically associated with SST from 14-20 °C (Barange and Hampton 1997). Agulhas Current waters are ca 20 °C at the current's boundary (Goschen and Schumann 1994). However, there was no habitat preference with regards to SST (see Chapter 2). Nevertheless, bathymetric depth is still a likely explanation for shallower dive depths and slower descent rates in African Penguins in the presence of higher SST, warmer mixed water columns. In Chapter 2, SST decreased from shallow waters towards waters that were ca 80 m deep. This is also observed in Figure 3.2 where SST are clearly higher at the end of the trip where the water column is shallower and dives are less deep.

Conclusions

This study highlights how African Penguins adjust their behaviour in response to~~with~~ the thermal structure of the water column they feed in. African Penguins ~~to maximise~~ foraged~~ing intake~~ in cool nutrient rich waters by~~,~~ adjusting their dive depth to the depth of the thermocline ~~depth~~which fronts these cooler waters. Penguins~~,~~ ~~as well as~~also responded to the temperature of mixed waters by diving deeper in warmer mixed waters to search for cooler waters near the benthos. Thermoclines in shallow near-shore waters often exhibit frequent perturbations, or completely dissipate, resulting in frequent nutrient injection into near surface waters. The thermocline is usually hypothesised to determine the depth of primary production as it is the front between cool nutrient rich waters below and nutrient poor waters above. African Penguins association with the variable thermocline in this study suggests that their prey occurs near the thermocline, even though the thermocline undergoes perturbations, making the winter thermocline an important biological feature. Therefore we can assume that in future research we will locate the highest density of prey fishes and their food, mesozooplankton (James 1987), within close proximity to the thermocline. However, further investigation is required to link the weak winter thermocline with nutrient availability, primary production and small pelagic fish distributions in the water column.

~~Thermoclines in the shallow near shore waters off south-eastern Australia exhibit frequent shifts in position and intensity while fish larvae and mesozooplankton remain in the upper reaches of the water column, unaffected by perturbations to the thermocline (Gray and Kingsford 2003).Although the main prey of African Penguins feed predominantly on mesozooplankton (James 1987), the movement of African Penguins suggest that the behaviour of small pelagic fishes on which they prey is likely linked to the thermocline and thus the actual production layer is linked to the thermocline. In summary, the thermocline is likely to be important as it is formed as a front between nutrient rich bottom waters advancing upwards against warmer nutrient poor surface mixed waters. Therefore it can be assumed that the relatively~~

~~weak winter compared to summer, and highly variable wonter thermocline plays an important role in the biotic relationships in Algoa Bay as it is inherently linked to nutrient rich waters below.~~

Chapter 4

Synthesis and conclusions of thesis

In this chapter, I provide an overview of the motivation for the research within this thesis, summarise the key findings and appraise the research. The chapter also discusses the implications of the findings, and combines the ideas presented in the thesis to generate a novel model of the foraging ecology of African Penguins as a typical short-range seabird. The chapter concludes with suggestions for future research.

Purpose of the study

This thesis investigated the foraging ecology of breeding African Penguins in relation to ocean physical processes. The primary motivation for the study was based on the premise that we have only limited understanding for how African Penguins feeding small chicks make decisions on where to forage. The research was also carried out to understand the broader behavioural aspects of how short-range breeding seabirds structure their foraging trips and the cues they may use to locate areas with a higher probability of containing prey patches. ~~For example, odours~~For instance, odours ~~are likely to be used as cues by some seabird species such as Procellariiformes which have highly developed sense organs~~ (e.g. Nevitt 2000; Nevitt et al. 2008; Wright et al. 2011), and thermal gradients (e.g. Charrassin and Bost 2001; Cotté et al. 2007; Trathan et al. 2008) are used by some seabirds to locate foraging grounds many hundreds of kilometres away from their colonies. Furthermore, ocean processes such as ~~). Odours also have been suggested to be used by African Penguins for fine-scale foraging (Wright et al. 2011). C~~currents are used ~~by related penguin species, e.g. Magellanic Penguins,~~ to minimize energy expenditure when foraging (Pütz et al. 2001; Raya Rey et al. 2010). ~~Thermal gradients and currents are also used by other penguin species, e.g. King Penguins that are capable of long-range foraging to locate foraging grounds many hundreds of kilometres away from their colonies at the edges of eddies or frontal zones (Charrassin and Bost 2001; Cotté et al. 2007; Trathan et al. 2008).~~ These research papers, and others cited in Chapters 1 and 2 provide further insight into the sophisticated foraging strategies used by seabirds, and other marine predators. However, how short-range breeding seabirds locate prey patches is still open for investigation. On fine-scales, ocean physical processes are often ephemeral or habitats are homogenous because the scale of foraging is often smaller than the physical process. Here I assessed the association of African Penguins with water temperature patterns (at the surface and below) and the potential use of currents by African Penguins to reach distant prey patches, thereby minimizing travel costs.

The foraging behaviour of top predators in relation to vertical thermal structure such as the presence and structure of thermoclines (rapid temperature changes with depth) is also a widely studied theme in top predator behavioural ecology (e.g. Charrassin and Bost 2001; Biuw et al. 2007; Takahashi et al. 2008; Kokubun et al. 2010; ~~Ropert-Coudert~~Pelletier et al. 2012). Thermoclines form a barrier for advection of nutrients due to the different densities of water masses separated by the thermocline and thus productivity is likely to be largely concentrated around and below the thermocline (Fielder 2010). Although most predators studied to date utilize the thermocline, changing their behaviour in relation to the depth and structure of the thermocline, little is known as to how birds respond to changes in the thermocline structure. This is due in part to most studies taking a comparative approach between thermoclines with different structures, and in part to the stability in thermoclines in the areas studied. Therefore, in this thesis I quantifie~~y~~d the usage of thermoclines and examined how birds reacted to a thermocline changing in structure and position over a fine temporal scale.

Summary of the findings

African Penguins in this study performed foraging trips that were distributed non randomly, with penguins showing an increased probability to travel south and east. Birds trips were constrained in part by the coast, such as birds from Boulders, False Bay (Petersen et al. 2006). Birds thus have a net decrease in the foraging area around their colony. African Penguins from Boulders increased their foraging range in response to a decrease in available foraging area, when compared to nearby island colonies. However, penguins in this study largely ignored foraging west of the colony, where there is substantial space for foraging, which may be linked to the perceived distribution of their prey occuring predominantly towards the south and east. Furthermore, African Penguins from Bird Island, Algoa Bay, travel shorter distances than their counterparts from St Croix Island, Algoa Bay (Pichegru et al. 2010). St

Croix birds are also constrained by their colonies near proximity to the coast and thus differences are likely to be a result of the proximity of the two colonies to biologically productive areas. A second hypothesis for the increased foraging range for Boulders penguins was a decrease in prey availability (Petersen et al. 2006). This hypothesis may also apply to the differences between St Croix and Bird Island. However, this study focused on Bird Island and the cues they could potentially use to locate prey.

In this study, African Penguins from Bird Island began their trips with a long night commute away from the island travelling for an average time of 8.0 ± 3.6 h at night covering distances of 17.5 ± 8.7 km towards areas that showed trends of cooler waters associated with upwelling. Birds travelled slowly at night (0.7 ± 0.3 $m.s^{-1}$) in near linear paths that can be classified as commuting (sinuosity index: 0.73). Birds that commute are thought to have some predefined idea of areas where prey is likely to be encountered (Weimerskirch 2007) or in animals that have the ability to predict the location of their prey, possibly utilising the landscape of their environment as a cue (Hawkes 2009). There was a strong correlation between the time birds spent at sea at night and the distance they covered during this time (Figure 2.3), suggesting birds that left earlier increase the distance they travel away from the colony and thus maximize the area they can search returning to the colony during daylight when African Penguins forage. By maximizing the area and time they search, birds can increase their probability of locating prey (Weimerskirch 2007). Around sunrise, birds increased their speed of travel before they began diving (e.g Figure 2.2). At this time birds may change the cues they use. For instance birds may reach an area likely to contain prey by commuting at night but then use finer scale cues such as visual or olfactory cues during daylight. Foraging activity of conspecifics and heterospecifics is likely to act as a strong cue to prey presence (Silverman et al. 2004). When birds began foraging they dived frequently (19 ± 5 $dives.h^{-1}$) along the day time portions of their trips performing foraging trips that looped and became more sinuous (sinuosity index: 0.93), a search strategy that may be classified as a correlated random search strategy. Given a high dive rate and more looping type behaviour, birds increase their search effort, probably enhancing their chances of encounter with patchily distributed prey (Weimerskirch 2007; Hawkes 2009).

Sea-surface temperatures within the foraging range of African Penguins in Algoa Bay were largely homogenous, with an average difference between maximum and minimum waters encountered of 1.6 ± 1.1 °C. Thus there was little evidence of habitat preference based on SST (Figure 2.6). The scale at which penguins foraged generally was smaller than the scale of physical processes within their foraging range. It is likely that birds are constrained by the patchiness of their prey rather than the variability of their environment. However the directions penguins travelled were associated to the directions in which cool upwelled waters arise. Therefore it is likely birds from Bird Island anticipate the distribution of cooler waters from previous experience and thus increase the likelihood of encountering a prey patch during their random searches.

African Penguins largely ignored the direction of currents, although the congruence between travel direction and current direction was higher during the transit phase (44%) of their trip compared to the foraging phases (32%) and return phase of their trips (30%). Birds thus commute independently of the current, but utilize the currents more during transit than other parts of their trips, suggesting that the underlying current might be used to minimize travel costs. When birds travelled in a similar direction to the current, their swimming speed was slower than when birds travelled against the current, suggesting that either penguins decreased their swimming speed when travelling with the current or increased their speed when travelling against the current (Table 2.3). Birds achieved higher net travel speeds when travelling in a similar direction to the current than against it. The cues associated with subsurface temperatures or foraging site fidelity may over ride the necessity to minimize energetic costs. The currents recorded were largely wind driven and closely associated with the thermal regime in the bay, with eastward currents often bringing warm waters and westward currents bringing cooler waters from upwelling cells north east of Bird Island. Birds are thus likely to utilize currents by association with water temperature rather than as a means to reduce costs of foraging, especially given that the currents recorded were four times slower than the mean travel speed of African Penguins.

Dive depths of birds were influenced by the subsurface vertical thermal structure of the water column (Table 3.3). Thermoclines in this study were largely a result of the advection of cool bottom waters rising to meet warmer well-mixed surface waters. When a thermocline was present penguins increased their dive depth with increasing depth of the thermocline, mostly targeting cooler waters below the midpoint of the thermocline. The thermocline is therefore an important foraging cue for African Penguins similar to other seabirds (e.g. Takahashi et al. 2008; Kokubun et al. 2010; Pelletier et al. 2012). However, the gradient of the thermocline probably plays an important role in the use of the thermocline by the birds. When the thermocline gradient was less steep, penguins increased their dive depth, mostly diving below the thermocline depth suggesting that thermoclines with shallow gradients were a weak cue for foraging (Table 3.4). Birds are thus likely to have a higher foraging efficiency when the thermocline has a strong structure in terms of its gradient and intensity as the thermocline will either act as a stronger cue for foraging or act as a better barrier to nutrients and thus create a productivity layer that potentially attracts small pelagic fishes. Interestingly the thermocline during winter is less stable than the strong summer thermocline in Algoa Bay (Goschen and Schumann 1988). Birds breed predominantly in winter (Randall and Randall 1981). During breeding birds are under substantial energetic constraints, which are evidently exacerbated by the variability in their environment. The bottom times of penguin dives were not influenced by the depth or structure of the thermocline, suggesting that the actual prey capture ability was not influenced by the thermocline structure, however penguins had longer bottom times when SST was higher. Agulhas Current waters are inherently nutrient poor and thus intrusions of these waters into Algoa Bay may decrease primary productivity. Even though penguins did not adjust the spatial use of their foraging range during Agulhas Current intrusions into the bay, penguins increased their dive depth, foraging below the warm waters associated with Agulhas Current intrusions (Table 3.5). In the absence of a thermocline, penguins increased their dive depth in warm mixed water columns in search of cooler bottom waters. Therefore Agulhas Current intrusions are likely to impact negatively on the energetics of African Penguins breeding on Bird Island.

Expanding traditional oceanography using African Penguins

Traditionally, oceanographers have relied on ship-based surveys to collect data, using sophisticated equipment to understand subsurface abiotic and biotic characteristics of the ocean structure. These methods are expensive and in some areas unfeasible or inaccessible (Fedak 2004). They also only provide a snap shot of the environment at the time of the study. Other methods such as floats or gliders, which descend and ascend collecting data such as thermal properties and then relay the data back to researchers via satellite, have been largely successful and provide longer periods of study (Fedak 2004). However, currents passively carry these instruments and thus the data collected on them is to some extent randomly distributed. On the other hand top predators, which are capable of carrying recording devices, associate themselves with dynamic features such as eddies and fronts to locate their prey. These areas also happen to be of interest to oceanographers (Fedak 2004). Thus attaching devices to top predators provides insight into animal behaviour but also has the dual benefit for investigating and describing marine habitats (Hart and Hyrenbach 2009).

Bio-logging has provided unique insights into understanding some of the most difficult to observe species on earth. Bio-logging is the practice of attaching recording devices to free-living animals that record multiple variables such as position (GPS), pressure, temperature and consumption (Ropert-Coudert and Wilson 2005). In the marine environment the abiotic variables collected by animal-borne loggers can aid in the understanding of the environment in which the studied species forage (e.g. Charrassin et al. 2004). Researchers deploying such devices on marine mammals, which are larger and are thus capable of carrying larger devices, with more sensors and larger batteries, have proved the effectiveness of bio-logging in understanding oceanographic processes in the areas they inhabit (e.g. Meredith et al. 2011). In this thesis, the loggers that were used had exceptional performance and were able to record temperatures in three dimensions at 1 s sample intervals. The data were comparable to remote sensed SST data and almost no lag was recorded on the descent and ascent of the loggers, despite the high swimming speed of penguins. Data from these loggers could be used to calibrate or validate remote sensing techniques (Weimerskirch et al. 1995). However, even in loggers with inferior performance, methodology that corrects for temperature at specific depth have been developed especially for loggers with slow response times thus taking lag effects into account (Daunt et al. 2003, Charrassin et al. 2004). For data to be accepted by oceanographers it is vital to demonstrate the utility of animal borne devices and how they can augment traditional methodologies (Fedak 2004). The data collected in this study should be implemented in secondary studies in order to increase our knowledge of the area in question and to act as an ethical framework in which data are shared and a convergence of different disciplines can be achieved.

~~**Summary of the findings**~~

~~African Penguins in this study performed foraging trips that were distributed non randomly, with penguins showing an increased probability to travel south and east. Evidently, birds' trips were constrained in part by the coast, such as birds from Boulders, False Bay (Petersen et al. 2006). African Penguins from Boulders increased their foraging range in response to a decrease in available foraging area, amongst other hypothesis such as limited prey availability, when compared to nearby island colonies. However, penguins in this study largely ignored foraging west of the colony, which may be linked to the perceived distribution of their prey. Furthermore, African Penguins from Bird Island, Algoa Bay, travel shorter distances than their counterparts from St Croix Island, Algoa Bay (Pichegru et al. 2010). St Croix birds are also constrained by their colonies near proximity to the coast and thus differences are likely to be a result of the proximity of the two colonies to biologically productive areas. This study focused on Bird Island and the cues they could potentially use to locate prey.~~

~~In this study, African Penguins from Bird Island began their trips with a long night commute away from the island travelling for an average time of 8.0 ± 3.6 h at night covering distances of 17.5 ± 8.7 km towards areas that showed trends of cooler waters associated with upwelling. Birds travelled slowly at night (0.7 ± 0.3 m.s^{-1}) in near linear paths that can be classified as commuting (sinuosity index: 0.73). Birds that commute are thought to have some predefined idea of areas where prey is likely to be encountered (Weimerskirch 2007) or in animals that have the ability to predict the location of their prey, possibly utilising the landscape of their environment as a cue (Hawkes 2009). There was a strong correlation between the time birds spent at sea at night and the distance they covered during this time (Figure 2.3), suggesting birds that left earlier increase the distance they travel away from the colony and thus maximize the area they can search returning to the colony during daylight when African Penguins forage. By maximizing the area and time they search, birds can increase~~

~~their probability of locating prey (Weimerskirch 2007). Around sunrise, birds increased their speed of travel before they began diving (e.g Figure 2.2). At this time birds may change the cues they use. For instance birds may reach an area likely to contain prey by commuting at night but then use finer scale cues such as visual or olfactory cues during daylight. Foraging activity of conspecifics and heterospecifics is likely to act as a strong cue to prey presence (Silverman et al. 2004). When birds began foraging they dived frequently (19 ± 5 dives.h^{-1}) along the day time portions of their trips performing foraging trips that looped and became more sinuous (sinuosity index: 0.93), a search strategy that may be classified as a correlated random search strategy. Given a high dive rate and more looping type behaviour, birds increase their search effort, probably enhancing their chances of encounter with patchily distributed prey (Weimerskirch 2007; Hawkes 2009).~~

~~Sea surface temperatures within the foraging range of African Penguins in Algoa Bay were largely homogenous, with an average difference between maximum and minimum waters encountered of 1.6 ± 1.1 °C. Thus there was little evidence of habitat preference for the SST they exploited (Figure 2.6). The scale at which penguins foraged generally was smaller than the scale of physical processes within their foraging range. It is likely that the constraint on foraging for these birds is the patchiness of their prey rather than the variability of their environment. However the directions penguins travelled were associated to the directions in which cool upwelled waters arise. Therefore it is likely birds from Bird Island anticipate the distribution of cooler waters from previous experience and thus increase the likelihood of encountering a prey patch during their random searches.~~

~~African Penguins largely ignored the direction of currents, although the congruence between travel direction and current direction was higher during the transit phase (44%) of their trip compared to the foraging phases (32%) and return phase of their trips (30%). Birds thus commute independently of the current, but utilize the currents more during transit than other parts of their trips, suggesting that the underlying current might be used to minimize travel costs. When birds travelled in a similar direction to the current, their swimming speed was slower than when birds travelled against the current, suggesting that either penguins decreased their swimming speed when travelling with the current or increased their speed when travelling against the~~

~~current (Table 2.3). Birds achieved higher net travel speeds when travelling in a similar direction to the current than against it. The cues associated with subsurface temperatures or foraging site fidelity may over ride the necessity to minimize energetic costs. The currents recorded were largely wind driven and closely associated with the thermal regime in the bay, with eastward currents often bringing warm waters and westward currents bringing cooler waters from upwelling cells north east of Bird Island. Birds are thus likely to utilize currents by association with water temperature rather than as a means to reduce costs of foraging, especially given that the currents recorded were four times slower than the mean travel speed of African Penguins.~~

~~Dive depths of birds were influenced by the subsurface vertical thermal structure of the water column (Table 3.3). Thermoclines in this study were largely a result of the advection of cool bottom waters rising to meet warmer well mixed surface waters. When a thermocline was present penguins increased their dive depth with increasing depth of the thermocline, mostly targeting cooler waters below the midpoint of the thermocline. The thermocline is therefore an important foraging cue for African Penguins similar to other seabirds (e.g. Takahashi et al. 2008; Kokubun et al. 2010; Ropert-Coudert et al. 2012). However, the gradient of the thermocline probably plays an important role in the use of the thermocline by the birds. When the thermocline gradient was less steep, penguins increased their dive depth, mostly diving below the thermocline depth suggesting that thermoclines with shallow gradients were a weak cue for foraging (Table 3.4). Birds are thus likely to have a higher foraging efficiency when the thermocline has a strong structure in terms of its gradient and intensity as the thermocline will either act as a stronger cue for foraging or act as a better barrier to nutrients and thus create a productivity layer that potentially attracts small pelagic fishes. Interestingly the thermocline during winter is less stable than the strong summer thermocline in Algoa Bay (Goschen and Schumann 1988). Birds breed predominantly in winter (Randall and Randall 1981). During breeding birds are under substantial energetic constraints, which are evidently exacerbated by the variability in their environment. The bottom times of penguin dives were not influenced by the depth or structure of the thermocline, suggesting that the actual prey capture ability was not influenced by the thermocline structure, however penguins had longer bottom times when SST was higher. Agulhas Current waters are inherently nutrient poor and~~

~~thus intrusions of these waters into Algoa Bay may decrease primary productivity. Even though penguins did not adjust the spatial use of their foraging range during Agulhas Current intrusions into the bay, penguins increased their dive depth, foraging below the warm waters associated with Agulhas Current intrusions (Table 3.5). In the absence of a thermocline, penguins increased their dive depth in warm mixed water columns in search of cooler bottom waters. Therefore Agulhas Current intrusions are likely to impact negatively on the energetics of African Penguins breeding on Bird Island.~~

Implications of the findings and suggestions for future research

African Penguins have evolved a suite of behaviours to cope with the variability of their environment. Birds are thus likely to show foraging behaviour plasticity under a changing environment, but large-scale regime shifts may result in birds having to adapt to a new environment that could carry substantial energetic and evolutionary costs (Kappes et al. 2010). The decline of African Penguin numbers in recent years has been attributed to a number of processes such as mortalities related to oil spills (Wolfaardt et al. 2009), and local decrease in the availability of prey (Crawford et al. 2007; 2011). Seabirds have been studied extensively and our ecological understanding of these birds has lent them to being prime bio-indicators of fish stocks and pollution (Furness and Camphuysen 1997). By analyzing the foraging behaviour of African Penguins we can begin to make assumptions on productivity, the ecology of the prey and the environment (e.g. Charrassin et al. 2002).

Climate change could prove to be an important variable driving changes in the distribution of prey species, further impacting African Penguin survival and their breeding success (Crawford et al. 2006; Crawford et al. 2008; Pichegru et al. 2010). On the south coast of South Africa upwelling is largely driven by two modes: Ekman veering as a result of the Agulhas Current interacting with the continental shelf and wind driven upwelling (Schumann 1988). Predictions based on an altered wind stress over the South Indian Ocean could result in more frequent Natal pulses which would influence the location of the Agulhas Currents axis moving it further south (Lutjeharms and de Ruijter 1996). The biological implications of such a shift is largely unknown, although the important role the Agulhas Current plays in determining the oceanography in Algoa Bay is likely to have implications on the species occurring in this region (Lutjeharms and de Ruijter 1996; Roberts 2010). Continued monitoring of the environment is needed in order to contextualize behavioural changes in African Penguins.

This study was limited by the lack of information regarding pelagic prey distribution in relation to thermal structures in Algoa Bay. The scope for potential research in Algoa Bay with regards to pelagic fish movements and distributions in relation to oceanographic forcing remains open. It is imperative that a multi-disciplinary approach is undertaken when pursuing studies of this nature. Rarely is contemporaneous data on prey distributions recorded with animal tracking (Bost et al. 2009). So far, it has been difficult in this thesis to determine whether temperature is a potential cue for foraging in African Penguins. It is likely that many of the correlations reported are auto correlated with the presence of prey which may be showing thermal habitat preferences, setting up a classic paradox as to which comes first: prey encounter or temperature as a cue. Understanding the underlying oceanographic conditions that result in the biotic and abiotic conditions favourable for productivity also need to be accounted for as well as understanding the behaviour of prey species in relation to physical forcing before a real understanding of how top predators 'use' thermal structures can be achieved. Hence, an ecosystem approach is needed that is likely to cross disciplines and require a strong collaborative effort. The system in Algoa Bay could potentially set up a world class experiment demonstrating the links from nutrients up the trophic ladder to top predator behaviour. The small scale at which birds foraged in relation to physical processes is also likely to reduce our ability to determine if African Penguins use oceanographic processes to locate their prey.~~compound any real results.~~ Future research may benefit from comparing the behaviour of penguins from St Croix Island, as these penguins forage over a greater distance and may forage at a scale that allows us to analyse their behaviour with respect to the local oceanography (Pichegru et al. 2010). It may be worth considering that~~is likely that~~ inter-colony differences are driven by the local oceanography. ~~This is an important concept given that the colony at St Croix is ca three times larger than the African Penguin colony at Bird Island, despite the colonies being separated by >50 km.~~

The work contained in this thesis focused on breeding birds which are constrained in space by the necessity to return to their nests to provide for small chicks. Birds that are not constrained by breeding may show different associations with fronts and other physical features (Weimerskirch et al. 1994; Nel et al. 2001). It would also be interesting to record repeated trips by the same individuals to assess how individuals respond to environmental variability. The inherent randomness in animal tracks is likely to be a result of population heterogeneity and other factors such as landscape features, in this case changing over time (Hawkes 2009). Inclusion of individual variation is likely to increase our ability in making sound conclusions on animal movement (Hawkes 2009). The loggers used in this study, although achieving high resolution data, are limited by battery life. In order to achieve a goal of tracking individuals for longer time series, we would need loggers with better battery life or increase the ‘coarseness’ at which we collect data (Ryan et al. 2004). Data loggers are mostly constrained by the size of the battery, which remains the bulkiest component of most loggers. Considerations need to be ~~made with regards~~given to the effects device attachment have on animals. Although the size of loggers has been suggested to be no more than 3% of the mass of flying species (Phillips et al. 2003) and can be slightly more for swimming species given the differences in cross sectional area, the real effect of loggers is often difficult to quantify and attempts to understand the effects of attaching loggers to animals has been poor (Wilson and McMahon 2006). Ultimately the negative effects of attaching loggers to animals, such as the physical and psychological stress endured during capture and handling (Wilson et al. 1986, Hawkins 2004, McMahon et al. 2005) requires a real quantifiable approach such as the development of a “detriment index” (Wilson and McMahon 2006). Improvements in technology may allow for long term device attachment. In the future we may see an increase in the use of devices that charge themselves using perhaps solar energy or a small turbine that generates power when the bird dives, providing almost unlimited power supply and thereby providing us with an unprecedented diary of the life at sea of the African Penguin. By showing how African Penguins from Bird Island, Algoa Bay, associate with specific three dimensional thermal habitats, research into African Penguin foraging behaviour is likely to continue, while incorporating the latest technology. A framework for an ecosystem approach to understanding predator behaviour is also likely to occur by taking an inter-disciplinary approach.

References

Aarts, G., MacKenzie, M., McConnell, B., Fedak, M. and Matthiopoulos, J. 2008. Estimating space-use and habitat preference from wildlife telemetry data. *Ecography* 31: 140–160.

Ainley, D.G., Spear, L.B., Tynan, C.T., Barth, J.A., Pierce, S.D., Ford, R.G. and Cowles, T.J. 2005. Physical and biological variables affecting seabird distributions during the upwelling season of the northern California Current. *Deep-Sea Research Part II* 52: 123–143.

Ashmole, N.P. 1971. Seabird ecology and the marine environment. In: Farner, D.S., King, J.S. and Parkes, K.C. (Eds.). *Avian Biology Vol. I.* New York: Academic Press pp. 224–286.

Bailleul, F., Charrassin, J., Monestiez, P., Roquet, F., Biuw, M. and Guinet, C. 2007. Successful foraging zones of southern elephant seals from the Kerguelen Islands in relation to oceanographic conditions. *Philosophical Transactions of the Royal Society B* 362: 2169–2181.

Barange, M. and Hampton, I. 1997. Spatial structure of co-occuring Anchovy and Sardine populations from acoustic data: implications for survey design. *Fisheries Oceanography* 6: 94–108.

Barange, M., Coetzee, J.C. and Twatwa, N.M. 2005. Strategies of space occupation by anchovy and sardine in the southern Benguela: the role of stock size and intra-species competition. *ICES Journal of Marine Science* 62: 645–654.

Beckley, L.E. 1983. Sea-surface temperature variability around Cape Recife, South Africa. *South African Journal of Science* 79: 436–438.

Beckley, L.E. 1988. Spatial and temporal variability in sea temperatures in Algoa Bay, South Africa. *South African Journal of Science* 84: 67–69.

Benvenuti, S., Bonadonna, F., Dall'Antonia, L. and Gudmundsoson, G.A. 1998. Foraging flights of Thick-billed Murres (*Uria lomvia*) as revealed by bird-borne direction recorders. *Auk* 115: 57–66.

Biuw, M., Boehme, L., Guinet, C., Hindell, M., Costa, D., Charrassin, J.-B., Roquet, F., Bailleul, F., Meredith, M., Thorpe, S., Tremblay, Y., McDonald, B., Park, Y.-H., Rintoul, S.R., Bindoff, N., Goebel, M., Crocker, D., Lovell, P., Nicholson, J., Monks, F. and Fedak, M.A. 2007. Variations in behaviour and condition of a Southern Ocean top predator in relation to in situ oceanographic conditions. *Proceedings of the National Academy of Sciences of the USA* 104: 13705–13710.

Bodkin, J.L., Esslinger, G.G. and Monson, D.H. 2004. Foraging depths of sea otters and implications to coastal marine communities. *Marine Mammal Science* 20: 305–321.

BirdLife International 2012. *Spheniscus demersus*. In: IUCN 2012. IUCN Red List of Threatened Species. Version 2012.1. www.iucnredlist.org.

Bost, C.-A., Cotté C., Bailleul, F., Cherel, Y., Charrassin, J.B., Guinet, C., Ainley, D.G. and Weimerskirch, H. 2009. The importance of oceanographic fronts to marine birds and mammals of the southern oceans. *Journal of Marine Science* 78: 363–376.

Brothers, N. 1991. Albatross mortality and associated bait loss in the Japanese longline fishery in the Southern Ocean. *Biological Conservation* 55: 255–268.

Burger, J. and Gochfeld, M. 2001. Effects of chemicals and pollution on seabirds. In: Schreiber, E.A. and Burger, J. (Eds.). *Biology of Marine Birds*. Boca Raton: CRC Press pp. 485–426.

Charrassin, J. and Bost, C.-A. 2001. Utilisation of the oceanic habitat by King Penguins over the annual cycle. *Marine Ecology Progress Series* 221: 285–297.

Charrassin, J.-B., Park, Y.-H., Le Maho, Y. and Bost, C.-A. 2002. Penguins as oceanographers unravel hidden mechanisms of marine productivity. *Ecology Letters* 5: 317-319.

Charrassin, J.-B., Park, Y.-H., Le Maho, Y. and Bost, C.-A. 2004. Fine resolution 3D temperature fields off Kerguelen from instrumented penguins. *Deep-Sea Research Part I* 51: 2091-2103.

Coetzee, J.C., van der Lingen, C.D., Hutchings, L., Fairweather, T.P. 2008. Has the fishery contributed to a major shift in the distribution of the South African sardine? *ICES Journal of Marine Science* 65: 1676–1688.

Cotté C., Park, Y.-H., Guinet, C. and Bost, C.-A. 2007. Movements of foraging King Penguins through mesoscale eddies. *Proceedings of the Royal Society B* 274: 2385-2391.

Crawford, R.J.M. 1998. Responses of African Penguins to regime changes of sardine and anchovy in the Benguela system. *South African Journal of Marine Science* 19: 355–364.

Crawford, R.J.M., Ryan, P.G. and Williams, A.J. 1991. Seabird consumption and production in the Benguela and Western Agulhas ecosystems. *South African Journal of Marine Science* 11: 357-375.

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

Crawford, R.J.M., Underhill, L.G., Coetzee, J.C., Fairweather, T. Shannon, L.J. and Wolfaardt, A.C. 2008. Influences of the abundance and distribution of prey on African Penguins *Spheniscus demersus* off western South Africa. *African Journal of Marine Science* 30: 167–175.

Crawford, R.J.M., Whittington, P.A., Martin, A.P., Tree, A.J. and Makhado, A.B. 2009. Population trends of seabirds breeding in South Africa's Eastern Cape and the possible influence of anthropogenic and environmental change. *Marine Ornithology* 37: 159–174.

Crawford, R.J.M., Altwegg, R., Barham, B.J., Barham, P.J., Durant, J.M., Dyer, B.M., Geldenhuys, D., Makhado, A.B., Pichegru, L., Ryan, P.G., Underhill, L.G., Upfold, L., Visage, J., Waller, J.L. and Whittington, P.A. 2011. Collapse of South Africa's penguins in the early 21st century. *African Journal of Marine Science* 33: 139–156.

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

Culik, B.M. 2001. Finding food in the open ocean: foraging strategies in Humboldt Penguins. *Zoology* 104: 327–338.

Culik, B.M. and Luna-Jorquera, G. 1997. Satellite tracking of Humboldt Penguins (*Spheniscus humboldti*) in northern Chile. *Marine Biology* 128: 547–556.

Cullen, J.M., Chambers, L.E., Coutin, P.C. and Dann, P. 2009. Predicting onset and success of breeding in little penguins *Eudyptula minor* from ocean temperatures. *Marine Ecology Progress Series* 378: 269-278.

Cunningham, G.B., Strauss, V. and Ryan, P.G. 2008. African Penguins (*Spheniscus demersus)* can detect dimethyl sulphide, a prey-related odour. *Journal of Experimental Biology* 211: 3123–3132.

Cury, P., Shannon, L. and Shin, Y.J. 2003. The functioning of marine ecosystems: a fisheries perspective. In: Sinclair, M. and Valdimarsson, G. (Eds.). *Responsible Fisheries in the Marine Ecosystem*. Rome: FAO and Wallingford: CABI Publishing pp. 103–123.

Cushing, D.H. 1975. *Marine Ecology and Fisheries*. London: Cambridge University Press.

Daunt, F., Peters, G., Scott, B., Grémillet, D. and Wanless, S. 2003. Rapid-response recorders reveal interplay between marine physics and seabird behaviour. *Marine Ecology Progress Series* 255: 283-288.

Deagle, B.E., Gales, N.J., Hindell, M.A. 2008. Variability in foraging behaviour of chick-rearing Macaroni Penguins *Eudyptes chrysolophus* and its relation to diet. *Marine Ecology Progress Series* 359: 295–309.

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

Fairweather, T.P., van der Lingen C.D., Booth, A.J., Drapeau, L. and van der Westhuizen, J.J. 2006. Indicators of sustainable fishing for South African Sardine *Sardinops sagax* and Anchovy *Engraulis encrasicolus*. *African Journal of Marine Science* 28: 661–680.

Fedak, M. 2004. Marine animals as platforms for oceanographic sampling: a "win/win" situation for biology and operational oceanography. *Memoirs of the National Institute of Polar Research* 58: 133–147.

Fielder, P.C. 2010. Comparison of objective descriptions of the thermocline. *Limnology and Oceanography: Methods* 8: 313–325.

Fossette, S., Girard, C., Bastian, T. Calmettes, B., Ferraroli, S., Vendeville, P., Blanchard, F. and Georges, J.-Y. 2009. Thermal and trophic habitats of the Leatherback Turtle during the nesting season in French Guiana. *Journal of Experimental Marine Biology and Ecology* 378: 8–14.

Froget, G., Butler, P.J., Woakes, A.J., Fahlman, A., Kuntz, G., Le Maho, Y. and Handrich, Y. 2004. Heart rate and energetics of free-ranging King Penguins (*Aptenodytes patagonicus*). *Journal of Experimental Biology* 207: 3917–3926.

Furness, R.W. 1990. A preliminary assessment of the quantities of Shetland Sandeels taken by seabirds, seals, predatory fish and the industrial fishery in 1981–1983. *Ibis* 132: 205–217.

Furness, R.W. and Ainley, D.G. 1984. Threats to seabirds presented by commercial fisheries. *ICBP Technical Report* 2: 701–708.

Furness, R.W. and Cooper, J. 1982. Interactions between breeding seabird and pelagic fish populations in the southern Benguela region. *Marine Ecology Progress Series* 8: 243-250.

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

Gasper, P., Georges, J.-Y., Fossette, S., Lenoble, A., Ferraroli, S. and Le Maho, Y. 2006. Marine animal behaviour: neglecting ocean currents can lead us up the wrong track. *Proceedings of the Royal Society B* 273: 2697–2702.

González-Pola, C., Fenández-Díaz, J.M. and Lavín, A. 2007. Vertical structure of the upper ocean from profiles fitted to physically consistent functional forms. *Deep-Sea Research Part I* 54: 1985-2004.

Goschen, W.S. and Schumann, E.H. 1988. Ocean current and temperature structures in Algoa Bay and beyond in November 1986. *South African Journal of Marine Science* 7: 101–116.

Goschen, W.S. and Schumann, E.H. 1990. Agulhas Current variability and inshore structures off the Cape Province, South Africa. *Journal of Geophysical Research* 95: 667–678.

Goschen, W.S. and Schumann, E.H. 1994. An Agulhas Current intrusion into Algoa Bay during August 1988. *South African Journal of Marine Science* 14: 47–57.

Gray, C.A. and Kingsford, M.J. 2003. Variability in thermocline depth and strength, and relationships with vertical distributions of fish larvae and mesozooplankton in dynamic coastal waters. *Marine Ecology Progress Series* 247: 211-224.

Grémillet, D., Dell'Omo, G., Ryan, P.G., Peters, G., Ropert-Coudert, Y. and Weeks, S.J. 2004. Offshore diplomacy, or how seabirds mitigate intra-specific competition: a case study based on GPS tracking of Cape Gannets from neighbouring colonies. *Marine Ecology Progress Series* 268: 265-279.

Grémillet, D, Lewis, S., Drapeau, L., van der Lingen, C.D., Hugget, J.A., Coetzee, J.C., Verheye, H.M., Daunt, F., Wanless, S. and Ryan, P.G 2008. Spatial match-mismatch in the Benguala upwelling zone: should we expect chlorophyll and sea-surface temperature to predict marine predator distributions? *Journal of Applied Ecology* 45: 610 – 621.

Halsey, L.G., Bost, C.-A. and Handrich, Y. 2007. A thorough and quantified method for classifying seabird dive behaviour. *Polar Biology* 30: 991-1004.

Hanuise, N., Bost, C.-A., Huin, W., Auber, A., Halsey, L.G. and Handrich, Y. 2010. Measuring foraging activity in a deep-diving bird: comparing wiggles, oesophageal temperatures and beak-opening angles as proxies for feeding. *The Journal of Experimental Biology* 213: 3874–3880.

Hansen, J. E., Martos, P. and Madirolas, A. 2001. Relationship between spatial distribution of the Patagonian stock of Argentine Anchovy, *Engraulis anchoita*, and sea temperatures during late spring to early summer. *Fisheries Oceanography* 10: 193–206.

Hart, K.M. and Hyrenbach, K.D. 2009. Satellite telemetry of marine megavertebrates: the coming of age of an experimental science. *Endangered Species Research* 10: 9-20.

Hawkes, C. 2009. Linking movement behaviour, dispersal and population processes: is individual variation a key? *Journal of Animal Ecology* 78: 894-906.

Hawkins, P. 2004. Bio-logging and animal welfare: practical refinements. *Memoirs of the National Institute for Polar Research* 58: 58–68.
Hsueh, Y. and O'Brien, J.J. 1971. Steady coastal upwelling induced by an along-shore current. *Journal of Physical Oceanography* 1: 180-186.

Hunt, G.L. Jr., Mehlum, F., Russell, R.W., Irons, D., Decker, M.B. and Becker, P.H. 1999. Physical processes, prey abundance, and the foraging ecology of seabirds. *Proceedings of the International Ornithological Congress* 22: 2040–2056.

Hunt, G.L. Jr., Stabeno, P.J., Strom, S. and Napp, J.M. 2008. Patterns of spatial and temporal variation in the marine ecosystem of the south-eastern Bering Sea, with special reference to the Pribilof Domain. *Deep-Sea Research Part II* 55:1919–1944.

Hunter, I.T. 1982. The coastal wind field off the southern Cape. In: Edge, B. L. (Ed.). *Proceedings of the Eighteenth Coastal Engineering Conference*, *Cape Town*. New York: American Society of Civil Engineers pp. 25.51-25.61.

Hyrenbach, K.D., Veit, R.R., Weimerskirch, H. and Hunt, J.L. Jr. 2006. Seabird associations with mesoscale eddies: the subtropical Indian Ocean. *Marine Ecology Progress Series* 324: 271–279.

James, A.G. 1987. Feeding ecology, diet and field-based studies on feeding selectivity of the Cape anchovy *Engraulis capensis* Gilchrist. In: Payne, A.I.L., Gulland, J.A. and Brink, K.H. (Eds). *The Benguela and Comparable Ecosystems*. *South African Journal of Marine Science* 5: 673 – 692.

Kappes, M.A., Shaffer, S.A., Tremblay, Y., Foley, D.G., Palacios, D.M., Robinson, P. W., Bograd, S.J. and Costa, D.P. 2010. Hawaiian albatrosses track interannual variability of marine habitats in the North Pacific. *Progress in Oceanography* 86: 246–260.

Kokubun, N., Takahashi, A., Ito, M., Matsumoto, K., Kitaysky, A.S. and Watanuki, Y. 2010. Annual variation in the foraging behaviour of Thick-billed Murres in relation to upper-ocean thermal structure around St. George Island, Bering Sea. *Aquatic Biology* 8: 289–298.

Kuhn, C.E. 2011. The influence of subsurface thermal structure on the diving behavior of Northern Fur Seals (*Callorhinus ursinus*) during the breeding season. *Marine Biology* 158: 649–663.

Lack, D. 1968*. Ecological adaptations for Breeding in Birds*. London: Methuen.

Largier, J.L. and Swart, V.P. 1987. East-west variation in thermocline breakdown on the Agulhas Bank. *South African Journal of Marine Science* 5: 263-272.

Lewis, S.F.F., Turpie, J.K. and Ryan, P.G. 2012. Are African Penguins worth saving? The ecotourism value of the Boulders Beach colony. *African Journal of Marine Science* In Press.

Loscroël, A. and Bost, C.-A. 2005. Foraging under contrasting oceanographic conditions: the Gentoo Penguin at Kerguelen Archipelago. *Marine Ecology Progress Series* 302: 245–261.

Lutjeharms, J.R.E. and de Ruijter, W.P.M. 1996. The influence of the Agulhas Current on the adjacent coastal ocean: possible impacts of climate change. *Journal of Marine Science* 7: 321-336.

Lutjeharms, J.R.E., Cooper, J. and Roberts, M. 2000. Upwelling at the inshore edge of the Agulhas Current. *Continental Shelf Research* 20: 737–761.

Mattern, T., Ellenberg, U., Houston, D.M. and Davis, L.S. 2007. Consistent foraging routes and benthic foraging behaviour in Yellow-eyed Penguins. *Marine Ecology Progress Series* 343: 295–306.

McMahon, C.R., van den Hoff, J. and Burton, H.R. 2005. Repeated handling and invasive research methods in wildlife research: impacts at the population level. *AMBIO* 34: 426–29.

Meredith, M.P., Nicholls, K.W., Renfrew, I.A., Boehme, L., Biuw, M. and Fedak, M. 2011. Seasonal evolution of the upper-ocean adjacent to the South Orkney Islands, Southern Ocean: Results from a "lazy biological mooring". *Deep-Sea Research Part II* 58: 1569-1579.

Moloney, C.L., Field, J.G. and Lucas, M.I. 1991. The size-based dynamics of plankton food webs. II. Simulations of three contrasting southern Benguela food webs. *Journal of Plankton Research* 13: 1039-1092.

Moloney, C.L., St John, M.A., Denman, K.L., Karl, D.M., Köster, F.W., Sundby, S. and Wilson, R.P. 2011. Weaving marine food webs from end to end under global change. *Journal of Marine Sciences* 84: 106–116.

Myers, R.A and Worm, B. 2003. Rapid worldwide depletion of predatory fish communities. *Nature* 423: 280–283.

Nel, D.C., Lutjeharms, J.R.E., Pakhamov, E.A., Ansorge, I.J., Ryan, P.G. and Klages, N.T.W. 2001. Exploitation of mesoscale oceanographic features by Grey-headed Albatrosses *Thalassarche chrystostoma* in the southern Indian Ocean. *Marine Ecology Progress Series* 217: 15-26.

Nevitt, G.A. 2000. Olfactory foraging by Antarctic procellariiform seabirds: life at high Reynolds numbers. *Biological Bulletin* 198: 245–253.

Nevitt, G.A., Reid, K. and Trathan, P. 2004. Testing the olfactory foraging strategies in an Antarctic seabird assemblage. *Journal of Experimental Biology* 207: 3537–3544.

Nevitt, G.A., Losekoot, M. and Weimerskirch, H. 2008. Evidence for olfactory search in Wandering Albatross, *Diomedea exulans*. *Proceedings of the National Academy of Sciences of the USA* 105: 4576–4581.

O'Donoghue, S.H., Drapeau, L. and Peddemors, V.M. 2010. Broad-scale distribution patterns of Sardine and their predators in relation to remotely sensed environmental conditions during the Kwazulu-Natal Sardine run. *African Journal of Marine Science* 32: 279–291.

Pakhomov, E.A., Perissinotto, R. and McQuaid, C.D. 1994. Comparative structure of the macro-zooplankton/micronecton communities of the Subtropical and Antarctic Polar Fronts. *Marine Ecology Progress Series* 111: 155–169.

Pattrick, P. and Strydom, N.A. 2008. Composition, abundance, distribution and seasonality of larval fishes in the shallow nearshore of the proposed Greater Addo Marine Reserve, Algoa Bay, South Africa. *Estuarine, Coastal and Shelf Science* 79: 251-262.

Pelletier, L., Kato, A., Chiaradia, A. and Ropert-Coudert, Y. 2012. Can thermoclines be a cue to prey distribution for marine top predators? A case study with Little Penguins. *PLoS ONE* 7: e31768. doi:10.1371/journal.pone.0031768.

Petersen, S.L., Ryan, P.G. and Grémillet, D. 2006. Is food availability limiting African Penguin Spheniscus demersus at Boulders? A comparison of foraging effort at mainland and island colonies. *Ibis* 148: 14–26.

Pettex, E., Bonadonna, F., Enstipp, M.R., Siorat, F. and Grémillet, D. 2010. Northern Gannets anticipate the spatio-temporal occurrence of their prey. *Journal of Experimental Biology* 213: 2365-2371.

Phillips, R.A., Xavier, J.C. and Croxall, J.P. 2003. Effects of satellite transmitters on albatrosses and petrels. *Auk* 120: 1082–90.

Pichegru, L., Ryan P.G., Le Bohec C., van der Lingen C.D., Navarro R., Petersen S., Lewis S., van der Westhuizen J. and Grémillet D. 2009. Overlap between vulnerable top predators and fisheries in the Benguela upwelling system: implications for marine protected areas. *Marine and Ecological Progress Series* 391: 199-208.

Pichegru, L., Grémillet, D., Crawford, R.J.M. and Ryan, P.G. 2010. Marine no-take zone rapidly benefits endangered penguin. *Biology Letters* 6: 498–501.

Pichegru, L., Ryan, P.G., van Eeden, R., Reid, T., Grémillet, D. and ~~&~~ Wanless, R. 2012. Industrial fishing, no-take zones and endangered penguins. *Biological Conservation* In Press.

Pierotti, R. and Annett, C.A. 1990. Diet and reproductive output in seabirds. *BioScience* 40: 568–574.

Pinheiro, J., Bates, D., DebRoy, S. and Sarkar, D. 2011. Linear and nonlinear mixed effects models ver. 3.1-102.

Pollard, R.T., Bathmann, U., Dubischar, C., Read, J.F. and Lucas, M.I. 2002. Zooplankton distribution and behaviour in the Southern Ocean from surveys with a towed optical plankton counter. *Deep-Sea Research Part II* 49: 3889–3915.

Pütz, K., Ingham, R.J. and Smith, J.G. 2002. Foraging movements of Magellanic Penguins *Spheniscus magellanicus* during the breeding season in the Falklands Islands. *Aquatic Conservation: Marine and Freshwater Ecosystems* 12: 75–87.

Rand, R.W. 1960. The biology of guano-producing seabirds. 2. The distribution, abundance and feeding habits of the Cape penguin, *Spheniscus demersus*, off the southwestern coast of the Cape Province. *Investigational Report Sea Fisheries Research Institute South Africa* 41 pp. 1-28.

Randall, R.M. 1989. Jackass Penguins. In: Payne, A.I.L., Crawford, R.J.M. and van Dalsen, A.P. (Eds.). *Oceans of Life of Southern Africa*. Cape Town: Vlaeburg Publishing.

Randall, R.M. and Randall, B.M. 1981. The annual cycle of the Jackass Penguin *Spheniscus demersus* at St Croix Island, South Africa. In: Cooper, J. (Ed.) *Proceedings of the Symposium on Birds of the Sea and Shore, 1979*. Cape Town: African Seabird Group pp. 427–450.

Rao Jammalamadaka, S. and SenGupta, A. 2001. Circular Statistics. In: *Topics in Circular Statistics*. Singapore: World Scientific Publishing.

Raya Rey, A.R., Bost, C.-A., Schiavini, A. and Pütz, K. 2010. Foraging movements of Magellanic Penguins *Spheniscus magellanicus* in the Beagle Channel, Argentina, related to tide and tidal currents. *Journal of Ornithology* 151: 933–943.

Ricklefs, R.W. 1990. Seabird life histories and the marine environment: some speculations. *Colonial Waterbirds* 13: 1–6.

Roberts, M.J. 2010. Coastal current and temperatures along the eastern region of Algoa Bay, South Africa, with implications for transport and shelf-bay water exchange. *African Journal of Marine Science* 32: 145-161.

Roden, G.I., 1991. Subarctic-subtropical transition zone of the North Pacific: large- scale aspects and mesoscale structure. In: Wetherall, J.A. (Ed.), *Biology, Oceanography, and Fisheries of the North Pacific Transition Zone and Subarctic Frontal Zone. NOAA Technical Report NMFS* 105 pp. 1–38.

Ropert-Coudert, Y. and Wilson, R.P. 2005. Trends and perspectives in animal-attached remote sensing. *Frontiers in Ecology and the Environment* 3: 437-444.

Ropert-Coudert, Y., Kato, A. and Chiaradia, A. 2009. Impact of small scale perturbations on local marine food resources: a case study of a predator, the Little Penguin. *Proceedings of the Royal Society B*: doi:10.1098/rspb.2009.1399.

Ryabov, A.B., Rudolf, L. and Blasius, B. 2010. Vertical distribution and composition of phytoplankton under the influence of an upper mixed layer. *Journal of Theoretical Biology* 263: 120–133.

Ryan, P.G., Keith, D.G. and Kroese, M. 2002. Seabird bycatch by tuna longline fisheries off southern Africa, 1998–2000. *South African Journal of Marine Science* 24: 103-110

Ryan, P.G., Petersen, S.L., Peters, G. and Grémillet, D. 2004. GPS tracking a marine predator: the effects of resolution, precision and sampling rate on foraging tracks of African Penguins. *Marine Biology* 145: 215–223.

Ryan, P.G., Petersen, S.L., Simeone, A. and Grémillet, D. 2007. Diving behaviour of African Penguins: do they differ from other *Spheniscus* penguins? *African Journal of Marine Science* 29: 153–160.

Schumann, E.H. 1987. The coastal ocean off the east coast of South Africa. *Transactions of the Royal Society of South Africa* 46: 215–229.

Shumann, E.H., Perrins, L.-A. and Hunter, I.T. 1982. Upwelling along the South Coast of the Cape Province, South Africa. *South African Journal of Science* 78: 238–242.

Schumann, E.H., Ross, G.J.B and Goschen, W.S. 1988. Cold water events in Algoa Bay and along the Cape south coast, South Africa, in March/April 1987. *South African Journal of Science* 84: 579–584.

Schumann, E.H., Churchill, J.R.S. and Zaayman, H.J. 2005. Oceanic variability in the western sector of Algoa Bay, South Africa. *African Journal of Marine Science* 27: 65-80.

Scott. M.D. and Chivers, S.J. 2009. Movements and diving behaviour of pelagic Spotted Dolphins. *Marine Mammal Science* 25: 137–160.

Shannon, L.G. and Crawford, R.J.M. 1999. Management of the African Penguin *Spheniscus demersus* – insights from modelling. *Marine Ornithology* 27: 119–128.

Silverman, E.D., Veit, R.R. and Nevitt, G.A. 2004. Nearest neighbours as foraging cues: information transfer in a patchy environment. *Marine Ecology Progress Series* 277: 25–35.

Simberloff, D. 1998. Flagships, umbrellas, and keystones: Is single-species management passé in the landscape era? *Biological Conservation* 83: 247–257.

Simeone, A. and Wilson, R.P. 2003. In-depth studies of Magellanic Penguins (*Spheniscus magellanicus*) foraging: can we estimate prey consumption by perturbations in the dive profile? *Marine Biology* 143: 825–831.

Simmons, R.E. and Cordes, I. 2000. Why is shorebird density so high in Walvis Bay? Delayed blooming and Benguela upwellings. *African Journal of Aquatic Science* 25: 229.

Stabeno, P.J., Bond, N.A., Kachel, N.B., Salo, S.A. and Schumacher, J.D. 2001. On the temporal variability of the physical environment over the south-eastern Bering Sea. *Fisheries Oceanography* 10: 81–98.

Stearns, S.C. 1992. *The Evolution of Life Histories*. Oxford: Oxford University Press.

Suryan, R.M., Sato, F., Balogh, G.R., Hyrenbach, K.D., Sievert, P.R. and Ozaki, K. 2006. Foraging destinations and marine habitat use of short-tailed albatrosses: A multiscale approach using first-passage time analysis. *Deep-Sea Research Part II* 53: 370–386.

Takahashi, A., Matsumoto, K., Hunt, J.L Jr., Shultz, M.T., Kitaysky, A.S., Sato, K., Iida, K., Watanuki, Y. 2008. Thick-billed Murres use different diving behaviours in mixed and stratified waters. *Deep-Sea Research II* 55: 1837–1845.

Trathan, P.N., Bishop, C., Maclean, G., Brown, P., Fleming, A. and Collins, M.A. 2008. Linear tracks and restricted temperature ranges characterise penguin foraging pathways. *Marine Ecology Progress Series* 370: 285–294.

van der Lingen, C.D., Shannon, L.J., Cury, P., Kreiner, A., Moloney, C.L., Roux, J-P. and Vaz-Velho, F. 2006. Resource and ecosystem variability, including regime shifts, in the Benguela Current system. In: Shannon, V., Hempel, G., Malanotte-Rizzoli, P., Moloney, C.L. and Woods, J. (Eds.). *Benguela: Predicting a Large Marine Ecosystem.* Amsterdam: Elsevier pp. 147–184.

van der Lingen, C.D., Hutchings, L. and Field, J.G. 2010. Comparative trophodynamics of Anchovy *Engraulis encrasicolus* and Sardine *Sardinops sagax* in the southern Benguela: are species alternations between small pelagic fish trophodynamically mediated? *African Journal of Marine Science* 28: 465–477.

Verheyden, C. and Jouventin, P. 1994. Olfactory behaviour of foraging Procellariiforms. *The Auk* 111: 285-291.

Wakefield, E.D., Phillips, R.A., Trathan, P.N., Arata, J., Gales, R., Huin, N., Robertson, G., Waugh, S.M., Wemierskirch, H. and Matthiopoulos, J. 2011. Habitat preference, accessibility, and competition limit the global distribution of breeding Black-browed Albatrosses. *Ecological Monographs* 81: 141-167.

Walther, R.G., Post, E., Convey, P., Menzel, A., Parmesan, C., Beebee, T.J.C., Fromentin, J., Hoegh-Guldberg, O. and Bairlein, F. 2002. Ecological responses to recent climate change. *Nature* 416: 389–395.

Weimerskirch, H., Wilson, R.P., Guinet C. and Koudil, M. 1995. Use of seabirds to monitor sea-surface temperatures and to validate remote-sensing measurements in the Southern Ocean. *Marine Ecology Progress Series* 126: 299-303.

Weimerskirch, H., 1997. Foraging strategies of southern albatrosses and their relationship with fisheries. In: Robertson, G., Gales, R. (Eds.), *Albatross Biology and Conservation*. Sydney: Surrey Beatty and Sons pp. 168–179.

Weimerskirch, H., Guionnet, T., Martin, J., Schaffer, S.A. and Costa, D.P. 2000. Fast and fuel efficient? Optimal use of wind by flying albatrosses. *Proceedings of the Royal Society of London B* 267: 1869–1874.

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

Wilson, R.P. 1985. The Jackass Penguin (*Spheniscus demersus*) as a pelagic predator. *Marine Ecology Progress Series* 25: 219–227.

Wilson, R.P. and Duffy, D.C. 1986. Prey seizing in African Penguins *Spheniscus demersus*. *Ardea* 74: 211–214.

Wilson, R.P., Grant, W.S. and Duffy, D.C. 1986. Recording devices on free-ranging marine animals: does measurement affect foraging performance. *Ecology* 67: 1091–93.

Wilson, R.P. and~~&~~ Wilson, M.P.T. 1990 Foraging ecology of breeding *Spheniscus* penguins. In: L.S. Davis and J.T. Darby (Eds.). *Penguin Biology*. San Diego: Academic Press pp. 244–265.

Wilson, R.P., Puetz, K., Bost, C.-A., Culik, B.M., Bannasch, R., Reins, T. and Adelung, D. 1993. Diel dive depth in penguins in relation to diel vertical migration of prey: whose dinner by candle light? *Marine Ecology Progress Series* 94: 101–104.

Wilson, R.P., Grémillet, D., Syder, J., Kierspel, M.A.M., Garthe, S., Weimerskirch, H., Schäfer-Neth, C., Scolaro, J.A., Bost, C.-A., Plötz, J. and Nel, D. 2002. Remote-sensing systems and seabirds: their use, abuse and potential for measuring marine environmental variables. *Marine Ecology Progress Series* 228: 241–261.

Wilson, R.P. and McMahon, C.R. 2006. Measuring devices on wild animals: what constitutes acceptable practice? *Frontiers in Ecology and the Environment* 4: 147-154.

Wilson, R.P., Shepard, E.L.C. and Liebsch, N. 2008. Prying into the intimate details of animals lives: use of a daily diary on animals. *Endangered Species Research* 4: 123-137.

Wilson, R.P., Shepard, E.L.C., Gómez Laich, A. Frere, E. and Quintana, F. 2010. Pedalling downhill and freewheeling up; a penguin perspective on foraging. *Aquatic Biology* 8: 193–202.

Wolfaardt, A.C., Underhill, L.G., Altwegg, R. and Visagie, J. 2008. Restoration of oiled African Penguins *Spheniscus demersus* a decade after the *Apollo Sea* oil spill. *African Journal of Marine Science* 30: 421- 436.

Wright, K.L.B., Pichegru, L. and Ryan, P.G. 2011. Penguins are attracted to dimethyl sulphide at sea. *The Journal of Experimental Biology* 214: 2509-2511.