

FORAGING DYNAMICS OF LITTLE PENGUINS IN A HOTSPOT OF OCEAN WARMING



by Gemma Carroll (BSc.)

Marine Predator Research Group
Department of Biological Sciences
Faculty of Science and Engineering
Macquarie University

A thesis submitted to Macquarie University in fulfilment of the requirements of

Doctor of Philosophy

April 2017

Abstract

In an era of rapid environmental change, predators can act as sentinels of shifts in ecosystem structure. By studying when, where and how much prey predators find under different foraging conditions, we can gain insight into how environmental changes affect food webs. Advances in bio logging technology have opened a window into animal lives, and it is increasingly possible to identify feeding behaviour by cryptic predators under natural conditions. By linking feeding events to key physical and biological parameters, we can improve our understanding of the factors underpinning prey availability and predator ecology in complex and changing systems.

In this thesis, I explored factors that influence prey capture by little penguins (*Eudyptula minor*) off the southern east coast of Australia. This region is a hotspot of global ocean warming, owing to the intensification of the warm, nutrient poor East Australian Current. The pelagic food web in this area remains poorly characterised, and it is unknown how the system will respond to increasing oceanographic change. Understanding interactions among predators, prey availability and the physical environment can therefore provide a lens through which to explore changes in the East Australian Current ecosystem.

I developed a prey capture signature from accelerometry to identify feeding events by wild penguins. Using this index, I showed that prey capture was related to sea surface temperature at multiple spatial and temporal scales. Penguins usually caught prey in foraging habitat associated with the coolest available temperatures, and high offshore temperatures ($> 21^{\circ}\text{C}$) were related to low prey capture rates. I showed that patterns of prey capture by penguins matched independent estimates of the distribution of prey at nested spatial scales. I also found that penguins exhibited a flexible foraging strategy in this dynamic environment, incorporating information on prior foraging success and *in situ* conditions. These findings present new perspectives on predator prey interactions and resource availability in the pelagic ecosystem off eastern Australia, providing a foundation for future examination of this food web as the East Australian Current intensifies.

Author's Declaration

I, Gemma Carroll, certify that this thesis entitled “Foraging dynamics of little penguins in a hotspot of ocean warming” is an original piece of work and has not been submitted in whole or in part for a higher degree at any institution other than Macquarie University. This work was undertaken in the Marine Predator Research Group in the Department of Biological Sciences at Macquarie University under the supervision of Distinguished Professor Lesley Hughes (Macquarie University), Dr Ian Jonsen (Macquarie University) and Dr David Slip (Taronga Conservation Society Australia). Funding was provided by a Macquarie University Research Excellence Scholarship, and by an Australian Research Council Linkage grant (LP110200603).

This thesis was prepared and written by me. All assistance in the preparation of this thesis has been acknowledged and all references and sources of information used in this thesis are listed within. Animal ethics approval was granted for the work presented in this thesis by the Macquarie University Animal Ethics Committee, under animal research authorities 2011/054 and 2014/057, and by the Taronga Animal Ethics Committee, under animal research authority 3b/04/13.

Gemma Carroll

April 2017

Statement of Contributions

Chapter Two: ‘Supervised accelerometry analysis can identify prey capture by penguins at sea’.

This chapter presents the development and validation of a prey capture signature from accelerometry to identify feeding events by wild little penguins. I designed and carried out captive experiments at Taronga Zoo, and tracked penguins from Montague Island with assistance from Dr David Slip and Prof Rob Harcourt. I processed the video and accelerometry data, and designed and conducted the analyses with statistical advice from Dr Ian Jonsen. I prepared the manuscript, which was published in the *Journal of Experimental Biology* in 2014. Dr David Slip, Dr Ian Jonsen and Prof Rob Harcourt contributed critically to the final version of the manuscript and are listed as coauthors on the paper.

Chapter Three: ‘High sea surface temperatures driven by a strengthening current reduce foraging success by penguins’.

This chapter presents an analysis of the influence of the East Australian Current on prey capture success by little penguins. I tracked penguins from Montague Island with assistance from Dr David Slip, Prof Rob Harcourt and Dr Ian Jonsen. I analysed accelerometry and tracking data in relation to oceanographic variables, with feedback on selection and interpretation of oceanographic parameters from Dr Jason Everett, and statistical guidance from Dr Ian Jonsen. I prepared the manuscript, which was published in the journal *Scientific Reports* in 2016. Dr Jason Everett, Dr David Slip, Dr Ian Jonsen and Prof Rob Harcourt contributed critically to the final version of the manuscript and are listed as coauthors on the paper.

Chapter Four: 'Hierarchical influences of prey distribution on patterns of prey capture by a marine predator'.

This chapter presents a spatial analysis of prey captures by penguins in relation to the distribution of potential prey aggregations around Montague Island. I tracked penguins from Montague Island with assistance from Dr Ben Pitcher and Dr Ian Jonsen. Dr Martin Cox and Prof Rob Harcourt mapped the distribution of prey aggregations using boat based active acoustics. Dr Martin Cox processed the acoustic data to identify aggregations, and I processed and analysed the tracking data, then designed and performed statistical analyses with feedback from Dr Ian Jonsen and Dr Martin Cox. I prepared the manuscript, which will be published in the journal *Functional Ecology* in 2017. Dr Ben Pitcher, Dr Martin Cox, Dr David Slip, Dr Ian Jonsen and Prof Rob Harcourt contributed critically to the final version of the manuscript and are listed as coauthors on the paper.

Chapter Five: 'Flexible foraging for a dynamic environment: relationships among site fidelity, foraging success and the environment in a marine predator'.

This chapter describes short term behavioural flexibility of little penguins in relation to the foraging environment. I tracked penguins from Montague Island with assistance from Dr Ben Pitcher, Dr Ian Jonsen and Dr David Slip. I designed and performed statistical analyses, and prepared the manuscript. Dr Ben Pitcher, Dr David Slip, Dr Ian Jonsen and Prof Rob Harcourt contributed critically to the final version of the manuscript and will be listed as coauthors on the paper.

Conference Presentations, Awards

Conference Presentations:

Carroll, G., Everett, J., Harcourt, R., Slip, D., Jonsen, I. 2016. 'Effects of a strengthening western boundary current on the foraging success of penguins'. Oral presentation at the Ocean Sciences Meeting, New Orleans, USA 2016

Carroll, G., Everett, J., Harcourt, R., Slip, D., Jonsen, I. 2016. 'Hunting in hotspots: influence of a warm and strengthening current on the foraging success of little penguins'. Oral presentation at the World Seabird Conference, Cape Town, South Africa 2015

Ladds, M., **Carroll, G.**, Salton, M., O'Hara, D., Slip, D. and Harcourt, R. 2013. "Multi species tracking for identification of Areas of Ecological Significance (AES)." Poster presented at: Student Conference on Conservation Science, Brisbane, Australia

Grants and Awards:

Jonsen, I., **Carroll, G.**, Harcourt, R., Slip, D., Cox, M., Suthers, I., Doblin, M., Roughan, M. Australian Research Council Linkage Grant 2016: 'Resolving the warming East Australian Current's impact on a marine food web' (AUD \$330,000)

Carroll, G. Emu – Austral Ornithology Research Award 2015: 'Validating the use of feather corticosterone as an index of heat stress in juvenile little penguins' (AUD \$4500)

Carroll, G. Australian Bird Environment Foundation grant 2014: 'Mitigating the effects of extreme heat on breeding little penguins' (AUD \$1500)

Carroll, G. Rice Memorial Field Research Proposal Award 2014 (AUD \$500)

1st Prize for presentation of laboratory based research at Macquarie University Student Conference 2014 (AUD \$250)

Macquarie University Research Excellence Scholarship 2013 2017 (AUD \$97,000)

Additional publications:

Carroll, G., Turner, E., Dann, P., & Harcourt, R. (2016). 'Prior exposure to capture heightens the corticosterone and behavioural responses of little penguins (*Eudyptula minor*) to acute stress' *Conservation Physiology*, 4(1), cov061.

Carroll, G., Hedley, S., Bannister, J., Ensor, P. & Harcourt, R. (2014) 'No evidence for recovery in a population of sperm whale bulls off Western Australia, 30 years post whaling' *Endangered Species Research* 24:33 43

Acknowledgements

The years spent doing this PhD have been the best of my life so far. This is in huge part because I've had the privilege of meeting and working with wonderful people who offered me support and guidance, and who made me think and laugh.

First and foremost, I'd like to thank my three supervisors: Lesley Hughes, David Slip and Ian Jonsen. I couldn't imagine three more different people, yet together they formed the most complementary supervisory team I could have hoped for. Lesley, thank you for your wisdom and insight into academic life, and for being such a wonderful, strong female role model. You gave me your time and guidance, and wanted nothing in return except for my success. Dave, thank you for the many long conversations about science and life, and for always being willing to explore ideas with me. Your passion for knowledge and your curiosity about the world have been infectious, and your calm competence and good nature in the field and at the zoo were invaluable. Ian, thank you for your enormous input into this project. You gave me ideas when my mind was swamped, and clarity and direction when I couldn't see the wood for the trees. Your guidance has given me confidence and opened up the path to an exciting career.

Thanks to Martin Cox, for his acoustic and statistical expertise on the prey field work. Thanks also to Jason Everett for his insights into the East Australian Current and for helping me start down the path towards becoming something that resembles a "biological oceanographer". I enjoyed working with you both immensely and hope to continue to do so into the future.

Thanks to Taronga Conservation Society Australia for their financial support, and to the keepers at Taronga Zoo for their enthusiasm in facilitating research on their penguins. The captive work provided a tool that helped me to understand the behaviour of wild penguins better, and without it this project would have been far weaker. Thanks to the National Parks and Wildlife Service at Narooma for all the

logistical and administrative support that made fieldwork on Montague Island possible. In particular, a big thank you to the field officers: Francois, Hutcho, Ian, Jim, Brent, Shane, Mark, Mitch and especially Kel. I had some of the best times of my life on Montague laughing and exploring and doing crazy fun things and it wouldn't have been half as enjoyable without the kindness, intelligence and humour that you brought to the place. A big thanks also to everyone who volunteered their time to help and support me on and around Montague Island during this project: Mary Anne Lea, Marine Desprez, Kim Kliska, Marcus Salton, Lisa Marie Harrison, Nicolette Armansin, Ben Pitcher, Vanessa Pirotta, Adam Wilkins, Andrew Irvine, Dustin O'Hara. I hope you all had as much fun as I did.

To the Marine Predator Research Group in all its different forms throughout the last 4 years, thank you so much for all the good times!!! PhD life would not have been the same without the hours watching animal videos, sitting in the sun sharing food and coffee and wine, playing squash or talking about dolphin sex. Special thanks to Vanessa, Lisa Marie and Dustin for their energy, laughter and positivity. Ben, thank you for being such a great companion, especially for two really fun months on Montague. Thanks for Moon Moon and otters and VG&Ts and everything else. Thanks Nic for your friendship, thoughtfulness and support, and for making life heaps funner.

Thanks to all my friends and family, and in particular to Mum and Dad: thanks for always loving and supporting me, even when you were unsure about the path I was taking.

Finally, Rob: there are so many ways in which you deserve my thanks. Thank you for your time and energy and ideas on this project. Thank you for your dogged support, patience and loyalty, and for your kind and generous spirit. Thank you for exploring wild places with me, looking for beautiful creatures. It's been such a fun adventure.

*Slip into the dawn
Sea like spilled ink,
Time stretched thin
Over quiet waves.*

*Seek a place where waters
Collide: warm and clear
With cold and dark,
Plankton-rich.*

*Where does light scatter
And dance from the deep,
Writhing silver and blue -*

Where are the fish?

Table of Contents

Chapter One	1
1.1 General Introduction	1
1.2 Thesis aims	5
1.3 Thesis Structure	6
Chapter Two	10
2.1 Introduction	11
2.2 Materials and Methods	14
2.3 Results	23
2.4 Discussion	27
Chapter Three	33
3.1 Introduction	34
3.2 Materials and Methods	37
3.3 Results	44
3.4 Discussion	54
3.5 Conclusions	59
3.6 Supporting information for Chapter Three	60
Chapter Four	67
4.1 Introduction	69
4.2 Materials and Methods	71
4.3 Results	78
4.4 Discussion	88
4.5 Supporting information for Chapter Four	91
Chapter Five	96
5.1 Introduction	97
5.2 Materials and Methods	99
5.3 Results	104
5.4 Discussion	112
5.5 Conclusions	115
5.6 Supporting information for Chapter Five	116
Chapter Six	120
6.1 General Discussion	120
6.2 Conclusion	126
References	127
Appendix One: published manuscript version of Chapter Two	154
Appendix Two: published manuscript version of Chapter Three	163
Appendix Three: published manuscript version of Chapter Four	176
Appendix Four: Animal Research Authority 2011-2014	187
Appendix Five: Animal Research Authority 2014-2016	188

Chapter One

1.1 General Introduction

In an era of climate change (Parmesan & Yohe 2003), habitat degradation (Tilman et al. 2001), and intense competition with humans (Darimont et al. 2015), predators must forage for prey resources in increasingly altered systems. Studying where, when and how much prey predators consume, and how this changes under different environmental conditions are therefore important topics in animal ecology (Marker et al. 2003). As well as providing information that can assist with the conservation of vulnerable predator species (Novack et al. 2005), conducting detailed studies of predator foraging ecology provides a top down perspective on how environmental changes affect ecosystems (Estes et al. 2011).

Studying interactions between predators and their prey can be challenging. There are logistical difficulties to observing foraging behaviour under natural conditions, especially if predators are cryptic or forage in remote locations (e.g. Wang et al. 2015). To address this, the field of bio logging (using animal borne instruments to collect physical and biological data) has undergone rapid technological advances that provide unprecedented insight into the foraging ecology of wild animals (Bograd et al. 2010; Kays et al. 2015; Hussey et al. 2015). Data loggers that record information on an animal's trajectory (e.g. Jonsen et al. 2005), three dimensional path (e.g. Mitani et al. 2004), head or body acceleration (e.g. Nathan et al. 2012; Wang et al. 2015), jaw opening events (e.g. Liebsch et al. 2007; Okuyama et al. 2009), stomach or oesophageal temperatures (e.g. Grémillet & Plös 1994; Ancel et al. 1997), or video streams from the animal's perspective (e.g. Moll et al. 2007; Watanabe & Takahashi, 2013), have enabled the remote identification of foraging behaviour in predators as diverse as vultures (Nathan et al. 2012) and blue whales (Goldbogen et al. 2013).

Bio logging technologies can give novel insight into when (e.g. Austen et al. 2006), where (e.g. Weimerskirch et al. 2007) and even how (e.g. Tremblay et al. 2014)

predators locate and consume prey. However, additional context is required to understand why animals feed where they do, and if and how this may change under different conditions. Remote sensing of environmental data provides a growing opportunity to estimate habitat composition, and track environmental change over spatial and temporal scales that can be matched to the movement and behaviour of animals (Kerr & Ostrovsky 2003; Handcock et al. 2009). Linking feeding by predators to aspects of the physical environment provides important context regarding the biophysical processes that govern prey abundance and distribution (e.g. Chavez et al. 2003) as well as other habitat requirements of predators for foraging, such as their thermal preference (Blouin Demers & Weatherhead 2001; Sims et al. 2006a), their need to mitigate predation risk (Heithaus & Dill 2002), or their need to enhance the detectability or catchability of prey (Hopcraft et al. 2005; Balme et al. 2007; Cox et al. 2016). From this, we can determine which set of conditions comprise an animal's foraging niche (Bestley et al. 2010; Scales et al. 2015), and predict how species distributions may shift given expected future changes in habitat (Hazen et al. 2013).

Direct measurements of prey distribution can add a further dimension to predator foraging studies (Karanth et al. 2004). While patterns of prey encounter and consumption by predators can provide a proxy for prey availability (Thums et al. 2011), predators almost always have imperfect information on the location of prey (Vogel & Beauchamp, 1999), and often have constraints on their movements and behaviour that prevent them from tracking prey density (Mitani et al. 2004). Additionally, predators exhibit varying degrees of flexibility in their foraging ecology, with some species readily switching prey species, foraging strategies or foraging location in response to changing prey availability (Schmidt 2008; Grémillet & Charmantier 2010; Paiva et al. 2010), and others exhibiting more rigid foraging behaviour (Bradshaw et al. 2004). These factors make it difficult to determine how foraging habitat selection by a predator relates to prey availability in the environment, or how prey intake by predators may be affected by changes in prey abundance and distribution. Having measures of prey availability that are contemporaneous with foraging by predators can give unique insights into how patterns of prey aggregation shape the hunting strategy and distribution of predators (Sims et al. 2006b).

Furthermore, it can allow us to evaluate the ability of animals to assess and match the distribution of their prey at varying densities and under different environmental conditions (Fauchald & Erikstad 2002; Karanth et al. 2004; Grémillet et al. 2008).

In the ocean, low trophic level species are distributed patchily in three dimensions (Fauchald 1999), and are highly sensitive to changes in the physical environment (Chavez et al. 2003). Consequently, marine predators including seabirds, seals, sharks and cetaceans must track patchy and variable prey, often over wide expanses of ocean (Block et al. 2011). Marine predators are important regulators of marine ecosystems (Heithaus et al. 2008; Estes et al. 2011), and many taxa have suffered massive global declines (Dulvey et al. 2008; Schipper et al. 2008; Paleczny et al. 2015), making it important to understand how their populations respond to changing resource availability (Sydeman et al. 2015). Marine predators can also be more conspicuous and accessible than their prey, making them useful indicators of prey availability and distribution under changing environmental conditions (Boyd & Murray 2001; Ainley et al. 1995). While the difficulties of observing interactions between predators and their prey at sea are substantial (e.g. Costa 1993), coupling advances in marine vertebrate movement ecology (Ponganis 2007; Hussey et al. 2015) with remotely sensed information on the environment has provided exciting new avenues to understand how marine predators and their prey may be affected by environmental change (Hazen et al. 2013; Hobday et al. 2013; Sydeman et al. 2015).

Study system

The East Australian Current is the western boundary current of the south Pacific gyre. It transports warm, tropical water down the east coast of Australia to temperate latitudes (Suthers et al. 2011). The flow of the East Australian Current is highly dynamic due to the influence of an “avenue” of meso scale eddies that are generated when the current separates from the coast and meanders east into the Tasman Sea (Figure 1.1, Everett et al. 2012). Although the current itself is generally nutrient poor, the action of these eddies drives nutrient upwelling onto the continental shelf (Tranter et al. 1986), supporting spawning stocks of small pelagic fish such as sardines and mackerel (Stewart et al. 2010; Ward et al. 2015) that in turn sustain populations

of upper trophic level marine predators including seabirds, seals, large teleost fish and sharks (Graham et al. 2001; Shaughnessy et al. 2008; Trebilco et al. 2010; Brodie et al. 2015).

There has been substantial emphasis on understanding the physical dynamics of the East Australian Current (Roughan et al. 2003; Ridgway, 2007; Cetina Heredia et al. 2014), and the influence of these processes on phytoplankton (Armbrecht et al. 2014; Everett et al. 2014), zooplankton (Tranter et al. 1983; Everett et al. 2011) and larval fish (Gray & Miskiewicz 2000; Uehara et al. 2005; Condie et al. 2011; Mullaney & Suthers 2013) communities. However, apart from a small number of papers on pelagic fisheries (e.g. Young et al. 2011; Brodie et al. 2015), there have been few studies explicitly linking East Australian Current dynamics to mid and upper trophic level species in this region. Understanding these links is important, as like other western boundary currents (Wu et al. 2012), the East Australian Current is intensifying, with sea surface temperatures in its path increasing 2–3 times faster than the global average (Cai et al. 2005; Ridgway 2007; Wu et al. 2012; Cetina Heredia et al. 2014). Understanding the effects of physical changes in this hotspot of ocean warming may give insight into the resilience of this ecosystem, and may shed light on how ecosystems in parts of the world that are warming less rapidly will change in the coming decades.

The little penguin is the world's smallest species of penguin, and is native to southern Australia and New Zealand (Stahel & Gales 1987). Little penguins prey on low trophic level 'forage fish' species including small pelagic fish, krill and squid (Montague & Cullen 1988; Chiaradia et al. 2012). Because it is both small and flightless, the little penguin is limited in the distances it can travel to find prey. This makes it heavily reliant on local prey availability during some parts of the breeding cycle (< 100 km from the colony during incubation and < 25 km from the colony during brooding). Due to the little penguin's sensitivity to changes in its forage fish prey (Chiaradia et al. 2010), coupled with its accessibility on land during breeding, little penguin foraging ecology provides a means to explore interactions among predators, prey availability and the physical environment in the East Australian Current system.

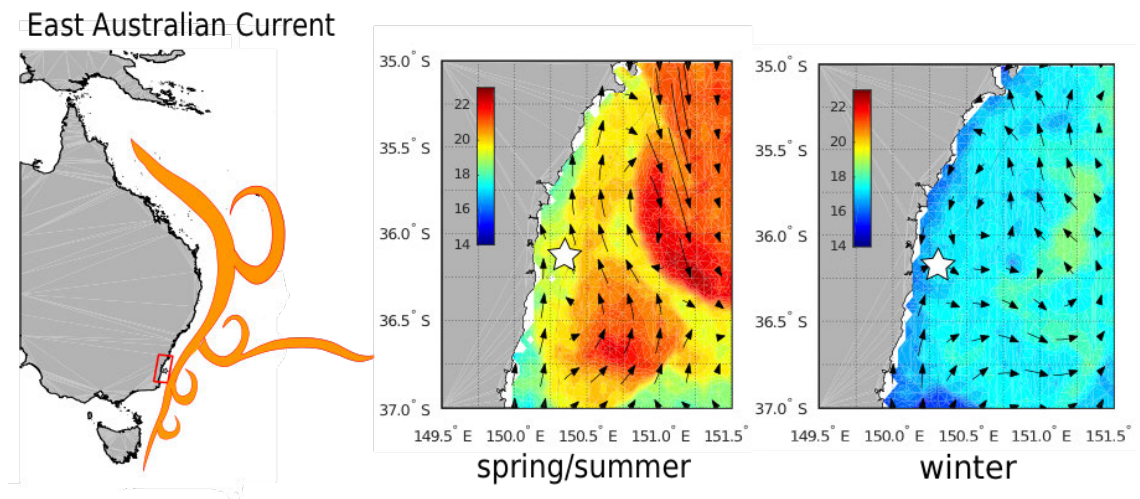


Figure 1.1. Schematic showing the East Australian Current and the ‘avenue’ of meso-scale eddies that it generates. To the right are representations of seasonal sea surface temperatures on the south coast of New South Wales, when the East Australian Current penetrates the region in spring/summer, and when the current is largely absent in winter. The location of the study site, Montague Island, is shown by the white star.

1.2 Thesis aims

In this thesis, I examined the foraging ecology of little penguins breeding on Montague Island, New South Wales, in relation to prey availability and physical processes associated with the East Australian Current. The main aims of the thesis were:

1. To develop and validate a method of identifying feeding events by penguins at sea (**Chapter Two**).
2. To determine whether prey capture success by penguins is influenced by dynamics of the East Australian Current, both seasonally and inter annually (**Chapter Three**).
3. To determine whether patterns of prey capture by penguins reflect underlying patterns in the distribution of their prey (**Chapter Four**).
4. To understand strategies used by penguins to maximise prey capture in response to short term variability in their foraging environment (**Chapter Five**).

1.3 Thesis Structure

The thesis is comprised of this introduction, four data chapters and a general discussion. The data chapters are written as standalone papers. However, each builds upon previous components of the study by adding new layers of insight into factors underpinning the foraging success of little penguins in the East Australian Current system.

In **chapter two**, I developed and validated a method of identifying prey capture by penguins in the wild. I recorded the behaviour of little penguins in captivity during feeding, and annotated it onto the stream of data acquired from accelerometers carried by the penguins. I trained a machine learning algorithm called a support vector machine (Shawe Taylor & Christianini 2004) to classify the acceleration data into two behaviours: 'swimming' and 'handling prey'. I tested the accuracy of the algorithm on unseen portions of the captive data, then applied it to accelerometry data attained from foraging trips by wild penguins. I showed that dives during which prey captures

were identified by the model were longer, deeper, had longer bottom times and faster ascent and descent rates, consistent with predictions from foraging theory. I found that the algorithm performed well, with a final estimated probability of falsely detecting a feeding event at sea of 0.09%. This method provided the basis for the rest of the thesis, and each of the subsequent chapters used this technique to assess the physical and biological factors associated with prey capture by penguins at various spatial and temporal scales. Chapter two has been published as:

Carroll, G., Slip, D., Jonsen, I. & Harcourt, R. (2014) 'Supervised accelerometry analysis can identify prey capture by penguins at sea' *Journal of Experimental Biology* 217(24), 4295-4302.

In **chapter three**, I applied the prey capture detection algorithm to three years of tracking data from little penguins foraging from Montague Island during their breeding season. I related prey capture success to sea surface temperature, as a proxy for the influence of the warm East Australian Current. I showed that prey capture was related to sea surface temperature at multiple spatial and temporal scales. The year with the highest prey capture success had mean sea surface temperatures that were lower than the decadal mean, while the year with lowest prey capture success was anomalously warm. I found that overall, there was an optimal offshore sea surface temperature associated with prey capture success of 19 – 21 °C, with reduced success at both lower and higher temperatures. Spatially, penguins targeted pockets of cool, inshore water and avoided foraging in the East Australian Current water mass. This chapter gives insight into how increased penetration of the EAC may negatively affect the availability of resources for upper trophic level species in southeast Australia. It also provides an example of the utility of applying a prey capture detection algorithm to better understand the consequences of habitat change on predator ecology.

Chapter three has been published as:

Carroll, G., Everett, J. D., Harcourt, R., Slip, D., & Jonsen, I. (2016). 'High sea surface temperatures driven by a strengthening current reduce foraging success by penguins' *Scientific Reports*, 6.

In **chapter four**, I investigated spatial patterns of prey capture success by little penguins in relation to patterns in the distribution of their prey. I analysed tracking data from 20 penguins over 3 consecutive days during the chick guard period, when they were constrained to foraging within approximately 25 km of the colony. I explored synchronies between where prey captures occurred and the distribution of aggregations of potential forage fish prey, which were mapped using boat based active acoustics. I found that prey distribution influenced prey capture at multiple, nested spatial scales. At the broadest scale, the overall distribution of prey captures matched the distribution of prey within the penguins' foraging range, when both were estimated using complementary resource selection functions. The patchiness of prey distribution also influenced prey capture, with the distance between consecutive prey captures by penguins following a bimodal distribution that appeared to correspond to within and between patch movements. Finally, I showed that specific characteristics of aggregations enhanced prey capture success, with dense, shallow and compact aggregations having higher local prey capture success. This chapter demonstrates a functional relationship between prey intake by a predator and the underlying distribution of its prey and provides insight into whether penguins can effectively track prey availability in the East Australian Current system. Chapter 4 is in press:

Carroll, G., Cox, M., Harcourt, R., Pitcher, B., Slip, D., Jonsen, I. (2017). 'Hierarchical influences of prey distribution on patterns of prey capture by a marine predator.'

Functional Ecology

In **chapter 5**, I examined how little penguin foraging decisions may be shaped by the East Australian Current system. I tracked 20 penguins throughout the brooding period, and examined relationships between their foraging location and foraging success on consecutive trips. I tested theories of site fidelity to determine whether penguins behave in a flexible way that is consistent with the environment being dynamic at the two day scale at which penguins make decisions about where to forage. Penguins were more likely to return to a site when they caught more prey on the previous trip, suggesting some degree of predictability in the foraging environment at short spatial

and temporal scales. However, penguins behaved flexibly, sometimes switching to opposite parts of their home range on consecutive trips, and achieving high prey capture success when they did so. Penguins foraged closer to where other penguins were foraging on the same day than they did to their own previous site, suggesting that local conditions and social cues may be more important determinants of foraging than their experience on the previous trip. This chapter demonstrates a 'win stay, lose switch' strategy in little penguins, and suggests that this species exhibits a similar flexibility in their foraging strategy to seabirds in unpredictable tropical environments.

Chapter Two

Supervised accelerometry analysis can identify prey capture by penguins at sea

This chapter has been published as:

Carroll, G., Slip, D., Jonsen, I. & Harcourt, R. (2014) 'Supervised accelerometry analysis can identify prey capture by penguins at sea' *Journal of Experimental Biology* 217(24), 4295-4302.

Abstract

Determining where, when and how much animals eat is fundamental to understanding their ecology. We developed a technique to identify a prey capture signature for little penguins from accelerometry, in order to quantify food intake remotely. We categorised behaviour of captive penguins from HD video and matched this to time series data from back-mounted accelerometers. We then trained a support vector machine (SVM) to classify the penguins' behaviour at 0.3s intervals as either 'prey handling' or 'swimming'. We applied this model to accelerometer data collected from foraging wild penguins to identify prey capture events. We compared prey capture and non-prey capture dives to test the model predictions against foraging theory. The SVM had an accuracy of $84.95 \pm 0.26\%$ and a false positive rate of $9.82 \pm 0.24\%$ when tested on unseen captive data. For wild data, we defined three independent, consecutive prey handling observations as representing true prey capture, with a false positive rate of 0.09%. Dives with prey captures had longer duration and bottom times, were deeper, had faster ascent rates, and had more 'wiggles' and 'dashes' (proxies for prey encounter used in other studies). The mean number of prey captures per foraging trip was 446.60 ± 66.28 . By recording the behaviour of captive animals on HD video and using a supervised machine learning approach, we show that accelerometry signatures can classify the behaviour of wild animals at unprecedentedly fine scales.

2.1 Introduction

Identifying with confidence where and when animals find food is integral to studies of foraging ecology. Accurately detecting feeding behaviour can enable energy intake to be estimated (Rothman et al. 2012), and can give insights into the distribution of food and the processes by which animals search for it (Bestley et al. 2008). However, it is difficult in practice to identify specific feeding events if directly observing the animal foraging in the wild is impractical or impossible. In these cases, bio logging technologies can provide insight into the behaviour of wild animals, with the added value of simultaneously recording contextual information about the environment (Ropert Coudert & Wilson 2005).

Accelerometry is increasingly being used to classify behaviour states based on patterns of animal movement, and is a promising tool for identifying feeding events remotely (Lagarde et al. 2008; Grünewälder et al. 2012; Nathan et al. 2012). Extensive high resolution data describing continuous profiles of animal movement can now be collected reliably and cost effectively, and the computational tools to mine this information are being accessed by ecologists (e.g. Bidder et al. 2014). Accelerometry can improve our understanding of the way that animals move through three dimensional space and interact with the environment to acquire resources at unprecedentedly fine scales (e.g. Goldbogen et al. 2013). However, there are relatively few examples of studies in which analytical methods have been both a) validated and b) applied to wild animals to give insight into ecological processes (but see e.g. Nathan et al. 2012; Watanabe & Takahashi 2013; Watanabe et al. 2014).

There are two main approaches to using accelerometry data to infer the behaviour of animals. The first is an 'unsupervised' classification approach, by which accelerometer data are grouped by similarities in movement patterns either by visual inspection of the data (in the form of a line graph), or by using techniques such as cluster analyses (Sakamoto et al. 2009) or spectral analyses (Watanabe et al. 2005; Ropert Coudert et al. 2006b). Unsupervised approaches have the benefit of being readily applicable to both new and existing datasets without the explicit need to ground truth the

information (Sakamoto et al. 2009), although validation can be done *post hoc* to confirm or improve estimates of behaviour. However, searching accelerometer data for groups of patterns related to various activities can be problematic, as this relies heavily on assumptions about how we expect animals to move and behave. For example, rapid increases in the speed of locomotion may reflect pursuit of prey, but may also signify intraspecific interaction or predator avoidance.

The second approach is 'supervised' classification, in which a model is trained on segments of movement data that have been given behaviour labels after direct observation of the animal carrying the accelerometer (Nathan et al. 2012). These ground truthed models can then be applied to new accelerometer output to classify unobserved behaviour into pre determined classes. Examples of this approach include machine learning techniques such as support vector machines (SVMs), classification and regression trees (CART) and artificial neural networks (ANNs), and these provide computationally powerful methods of data classification that can detect complex patterns that are not evident to the human eye. Thus, the models can identify intrinsic differences between similar behaviours or locomotory types when applied to acceleration data (Martiskainen et al. 2009). Another advantage of supervised models for determining animal behaviour is that the accuracy of the model can be tested on portions of data that are held out from model training, enabling the error rate to be clearly quantified during the model development process (Bidder et al. 2014).

Studies using accelerometry to identify feeding events in wild marine animals have favoured unsupervised models, due to the obvious logistical difficulties of ground truthing datasets. In larger animals, accelerometers have been placed on the head, or on both the head and back to identify dynamic head movements thought to be related to 'lunging' for prey (Kokubun et al. 2011; Gallon et al. 2013; Ydesen et al. 2014) and jaw mounted accelerometers have been used to identify mouth opening events that may result in prey ingestion (Viviant et al. 2010). In smaller marine species, back mounted accelerometry is currently the best or only option. In these cases, periods when the wing/flipper/tail beat frequency or amplitude (identifiable from the 'heaving' (wing/flipper) or 'swaying' (tail) axis of the accelerometer data) spike above

a threshold are determined to be ‘dashes’ – increases in speed when the animal may have encountered and pursued prey (Ropert Coudert et al. 2006b). When validation has been undertaken in the marine realm (by attaching a video camera alongside the accelerometer) it has tended to focus on validating prey capture attempts (e.g. head lunges) rather than validating the actual capture and consumption of prey (Watanabe & Takahashi 2013). This distinction is important, as it is impossible to quantify an animal’s foraging efficiency or its energy intake if the success of prey capture remains uncertain.

Several little penguin (*Eudyptula minor*, Forster, 1781) populations around the south coast of Australia are experiencing declines that seem at least partially related to changes in the availability of the small baitfish that constitute its primary prey (Cannell et al. 2012). There is therefore an urgent need to understand the energetic requirements and feeding ecology of this species at fine scales, both to predict its vulnerability to environmental change that may alter the abundance and distribution of prey, and to assess the need for conservation measures such as restrictions on fishing activity around breeding colonies. The relative ease of studying little penguins both in captivity and in the wild also makes them a suitable model species for developing analytical techniques that can be applied to other marine fauna.

Here, we develop a supervised machine learning approach to identifying feeding events at sea from observations of little penguins wearing accelerometers while they handled prey in captivity. Due to their small size, it is not yet possible to equip little penguins with cameras in the wild, and the captive setting provides a means of observing feeding behaviour in great detail. Although translating observations made in captivity to the behaviour of wild animals is inherently problematic due to the diversity of natural behaviours and contexts, by developing a classification model based on the handling of prey rather than on pursuits or capture attempts, we can be more confident that this approximates natural feeding behaviour. This is because the physical process of prey handling and consumption are likely to be similar even if other predator prey interactions may differ between captive and wild settings. By taking this approach we also aim to remove some of the uncertainties of prey capture

variability as well as uncertainties resulting from the presence of rapid movements that are unrelated to prey encounters.

We then apply this model to wild penguin acceleration data and compare ‘successful’ vs ‘unsuccessful’ foraging dives as a means of further exploring the validity of the model on wild data, and to characterise foraging success and its determinants in little penguins. We also attempt to quantify the number of prey items ingested during a day of foraging, and validate this information in relation to what is known about little penguin energetics.

2.2 Materials and Methods

The field study was conducted on Montague Island (36.252777°, 150.227110°), 9km off the southeast coast of NSW, Australia. The island supported approximately 5000 breeding pairs of little penguins in 2000 (Weerheim et al. 2003) however there have been no recent, reliable estimates of population size on the island. Extensive habitat restoration on Montague Island has necessitated the use of nest boxes to accommodate a large portion of the breeding penguin population. Data used in this analysis were collected during the breeding season in September, November and December 2013. Penguins were captured in their artificial wooden nest boxes at night, and sex was determined by comparing the morphology of the two adults present in the nest (males are generally slightly larger in body size and have thicker bills with a pronounced hook at the tip).

Accelerometer data loggers (G6a and G6a+, CEFAS Technology Pty Ltd, Suffolk, UK) were attached to feathers just below the mid point of the back with cloth tape (Tesa, Hamburg, Germany) the night before a penguin went to sea. The units recorded acceleration in 3 axes: anterior posterior (surging), lateral (swaying) and dorso ventral (heaving) with a range of ± 2 g (see Figure 2.1). The accelerometers recorded depth, temperature and acceleration and were programmed in two modes: “shallow” mode (<1.37 m: 1.5% of the full scale pressure range) where parameters were recorded every 10 seconds, and “dive” mode (>1.37 m) where the same parameters were

recorded at a rate of 30Hz. When the penguins returned from a foraging trip they were recaptured in their nest boxes, the loggers were removed and they were weighed in a calico bag using a spring balance scale (Pesola, AG Switzerland).

Validation of acceleration signal

To identify a unique signal from acceleration data that corresponds to prey handling in little penguins, we attached the same accelerometers to captive penguins at Taronga Zoo, Sydney, Australia using the same technique as for wild penguins. The accelerometers were programmed to record depth and tri axial movement continuously at 30Hz. Three underwater cameras (GoPro Hero 3, San Mateo, California) filming in HD 1080 at 60 frames per second were fixed in the pool and angled to give coverage of the entire swimming area. The accelerometers were attached using uniquely coloured cloth tape so that each penguin with an accelerometer could be individually identified from the video. First, we attached accelerometers to 5 penguins and recorded their behaviour as they swam around their enclosure with other members of their captive group for one hour. In subsequent experiments, accelerometers were attached to 25 penguins in the morning, and were programmed to start recording before the afternoon feeding session. Two GoPro cameras were then strategically placed to provide coverage of the feeding area at the start of each feeding session.

The behaviour of the penguins was determined from the video footage and recorded directly onto the accelerometer output file. This created a behaviour label for each 30Hz accelerometer reading. Exact pairing of the video footage with accelerometer data to the 30Hz level was achieved by a combination of a) identifying the exact frame within a given second in which a change in behaviour occurred on the video, and b) visually identifying rapid changes in acceleration associated with a change in

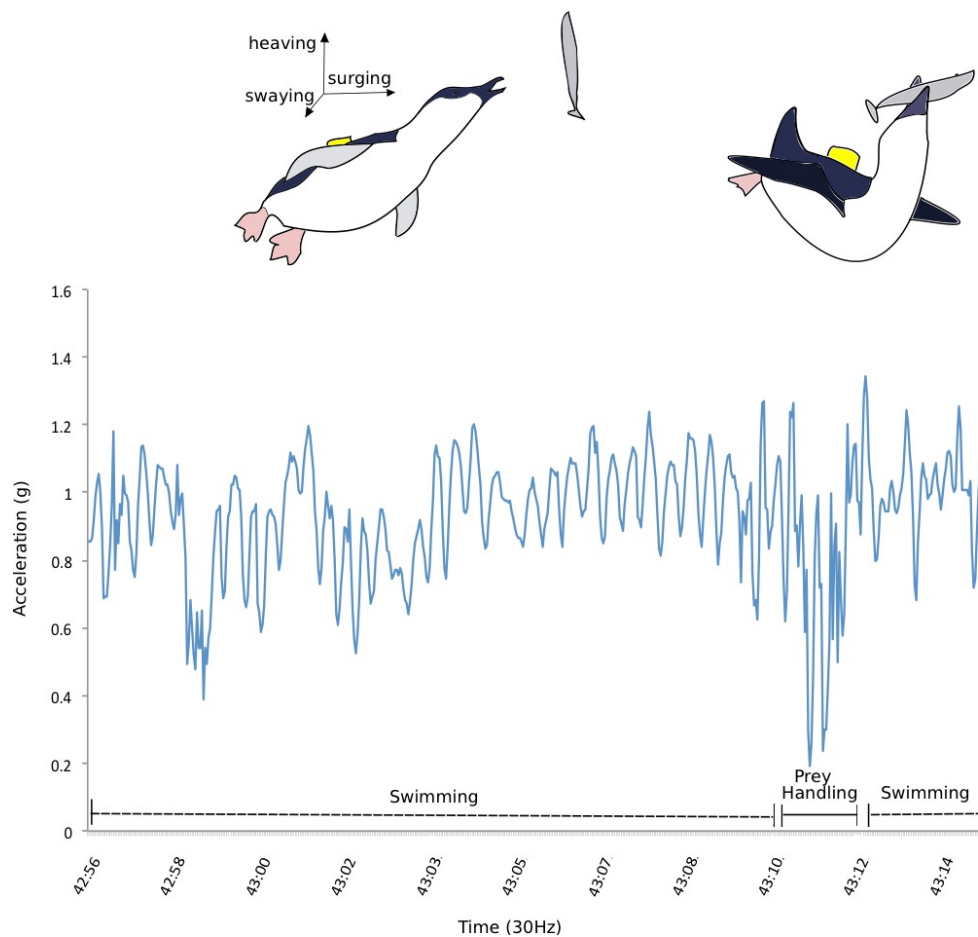


Figure 2.1. Schematic of a little penguin wearing an accelerometer (yellow) swimming towards a fish and handling prey. The accelerometer axes (heaving, surging and swaying) are shown on the left. Beneath is a sample raw accelerometry profile from the 'heaving' axis (g) (recorded at 30Hz) of a penguin swimming and handling prey in captivity 'labelled' with the associated behaviours identified from HD video.

behaviour from plotted accelerometer data. Behaviour was scored as being one of 'swimming', 'surface swimming' or 'prey handling'.

Due to ethical and practical considerations, live prey was not used in feeding trials. Instead, handfuls of dead pilchards were thrown into the pool until the penguins were satiated. 'Prey handling' was recorded from the time that the penguin grabbed a fish in the water until the first powerful flipper stroke as it began to swim away after swallowing the fish. We believe that this reasonably approximates the prey handling behaviour of wild penguins, as: 1) the captive penguins approached a fish at high speeds and with dynamic movement as there were usually several penguins competing for each fish and 2) the captive penguins performed characteristic behaviours such as striking at the head of the fish to 'immobilise' it before swallowing it head first. All other behaviour, including all feeding behaviour leading right up to grabbing a fish, was recorded as 'swimming' unless the penguin was at the surface. All observations where the penguin was recorded as 'surface swimming' were later removed from the analysis, as the wild data did not capture times when the birds rested at the surface at the same 30Hz resolution.

SVM and data processing

Twenty two summary statistics were calculated from the raw accelerometer output using a rolling window of 10 data points (0.3s). For each axis (heaving, surging and swaying), we calculated mean, s.d., minimum, maximum, skewness and kurtosis. We also calculated pairwise correlations between the 3 axes as well as overall dynamic body acceleration (ODBA), an estimate of activity specific metabolic rate (Wilson et al. 2006). Rather than pre segmenting the data into groups representing single behaviours for the training/testing process (e.g. Nathan et al. 2012), we took the behaviour label of each 10 data point rolling window to be whichever behaviour was represented by most (>5) observations. Having behaviour inputs that are mixed in this way introduces uncertainty and is therefore likely to reduce the accuracy of our model when tested on captive data. However, this should result in a model that can be applied with increased confidence to wild accelerometry, where the model must be robust to data that are not grouped into classes.

Several powerful supervised machine learning methods have been successfully employed to classify the behaviour of terrestrial animals from accelerometry, including classification and regression trees, random forests, artificial neural networks and support vector machines (SVMs). Each of these models performs to a high standard when classifying animal behaviour (see Nathan et al. 2012; Martiskainen et al. 2009). We selected the SVM to classify feeding because it is robust and consistently among the best performers in comparisons of machine learning methods. Rather than comparing a variety of statistical methods we focus instead on exploring the ability of a single method to give insight into fine scale ecological processes.

SVMs are used in many pattern recognition applications and we attempt to describe the underlying mechanisms of the model here in relation to classifying animal behaviour (for a detailed explanation see Shawe Taylor & Christiani 2004). As in all supervised machine learning problems, the model is trained on data that have been given class labels. In this case the data are the summary statistics derived from the acceleration data, and the labels are the behaviours that the animal was observed performing from the video that correspond to the acceleration data. The model 'learns' the relationship between features of the data and these behaviour labels, and is then able to classify new unlabelled data into these classes.

The SVM can be visualised conceptually in two dimensions, with points representing two linearly separable classes, e.g. 'swimming' and 'prey handling' (See Figure 2.2). There are many lines that could be drawn that would separate the data into these two classes. The SVM algorithm aims to determine the line (or 'hyperplane') that is able to separate the data with the largest possible margin. This large margin makes the model robust to new data that may fall outside the range of the observations used to train the model. The optimal hyperplane determined during the training process is then used to classify new examples.

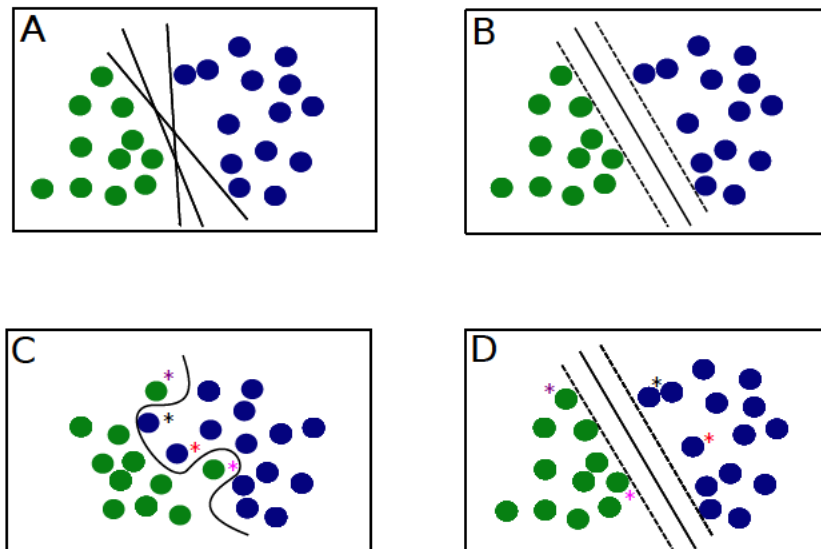


Figure 2.2. Conceptual 2D representation of how SVMs separate data into two classes: A) a series of possible lines that could separate data of two classes; B) the optimal line or 'hyperplane' determined by a support vector machine that separates the data with the largest margin; C) data that cannot be linearly separated; D) the effect of applying a 'kernel trick' to increase the distance between the classes in C by projecting them in hyperspace. Points with the same coloured asterisk in C and D represent the same data point.

Rather than classifying data in two dimensions, in reality the space is n dimensional, where each dimension represents a different user specified feature of the data. In this case, features could be any number of summary statistics derived from the raw accelerometer data across some time window (e.g. the mean of the 'heaving' accelerometer axis over 0.3s) and many features are usually required for the model to accurately detect patterns. Unsurprisingly, separating the two classes with a linear classifier is often not possible. A kernel represented by $k(x_i, y_i)$, (where x_i is the sample vector input as training data, and y_i is the class label of x_i), is therefore employed to increase the distance between the classes by transforming or 'mapping' them in a high dimensional feature space. The type of kernel that is selected defines this feature space.

We trained an SVM to classify the behaviour of the penguins as 'swimming' or 'prey handling' from the labelled data in the freely available R statistical software (R Core Team 2013) package e1071 (Meyer et al. 2014). The data were randomly split into two sets in a 70:30 ratio (training:testing). Tuning of the SVM parameters was performed using 10 fold cross validation. We trialled a range of available kernels (radial, linear, second, third and fourth order polynomial kernels), and selected a second order polynomial kernel (represented by $k(x_i, y_i) = (x_i, y_i)^2$) as the model developed with this kernel showed the highest overall accuracy. Mean and standard deviation of the overall accuracy and false positive rate, a measure of how often the model misclassifies a point as 'prey handling' when it should be 'swimming', (incorrect 'prey handling'/incorrect 'prey handling' + true 'swimming') of the best model were obtained by generating random 70:30 splits, re training and testing the accuracy of the model on each of these datasets.

Application of SVM to wild accelerometer profiles

When the best model had been selected, we then applied it to the wild dataset, after pre processing the data using the same statistics and 10 data point (0.3s) rolling window. We classified a 'prey capture event' as any sequence of three or more consecutive 'Prey handling' classifications, to reduce the misclassification of transient events. We determined a threshold for the amount of time that separated discrete

feeding events by plotting a survival curve showing the frequency of seconds (1–100 s) between prey handling events for each individual penguin. The breakpoint of the curve was used to define the threshold, which was between 5 and 9 seconds for all penguins. We took the timestamp of these feeding events (to the nearest second) to be the 5th data point of the sequence of 10 data points used in calculating the summary statistics.

We calculated a number of summary statistics in order to characterise intrinsic differences between dives in which the SVM identified prey capture and those in which it did not. We first calculated maximum depth, dive duration, bottom time duration, mean ascent and descent rates, ‘wiggle’ presence and ‘dash’ presence. We included wiggles and dashes in this part of the analysis as they have been used as proxies for prey encounter in previous studies, and we wished to understand whether their presence was related to predictions of prey capture derived from the SVM. Dashes are instances where the penguin increases the amplitude of its flipper strokes, possibly to pursue prey (Ropert Coudert et al. 2006b; Zimmer et al. 2011a). For the ‘dash’ analysis, we identified an upper amplitude threshold for flipper strokes (identifiable in the vertical ‘heaving’ axis) by plotting a survival curve of amplitude frequency from the raw accelerometer data. We calculated thresholds separately for the descent, bottom time and ascent phases of dives and for each individual bird. As penguins must stroke harder in the top part of the water column to compensate for buoyancy, the descent phase of a dive was not analysed if the depth was less than 4 m (Zimmer et al. 2011b).

Wiggles are undulations in the bottom phase of dives thought to be related to hunting strategy, and have been shown to be a proxy for prey encounter in other species of penguins (Simeone and Wilson 2003; Bost et al. 2007) and whales (Goldbogen et al. 2013). We defined a wiggle as a change in depth during bottom time occurring at > 0.5m/s (See Figure 2.3). We defined the start and end of bottom time as the first and last time within a dive that the rate of change in depth was < 0.25m/s (Kato et al. 2008).

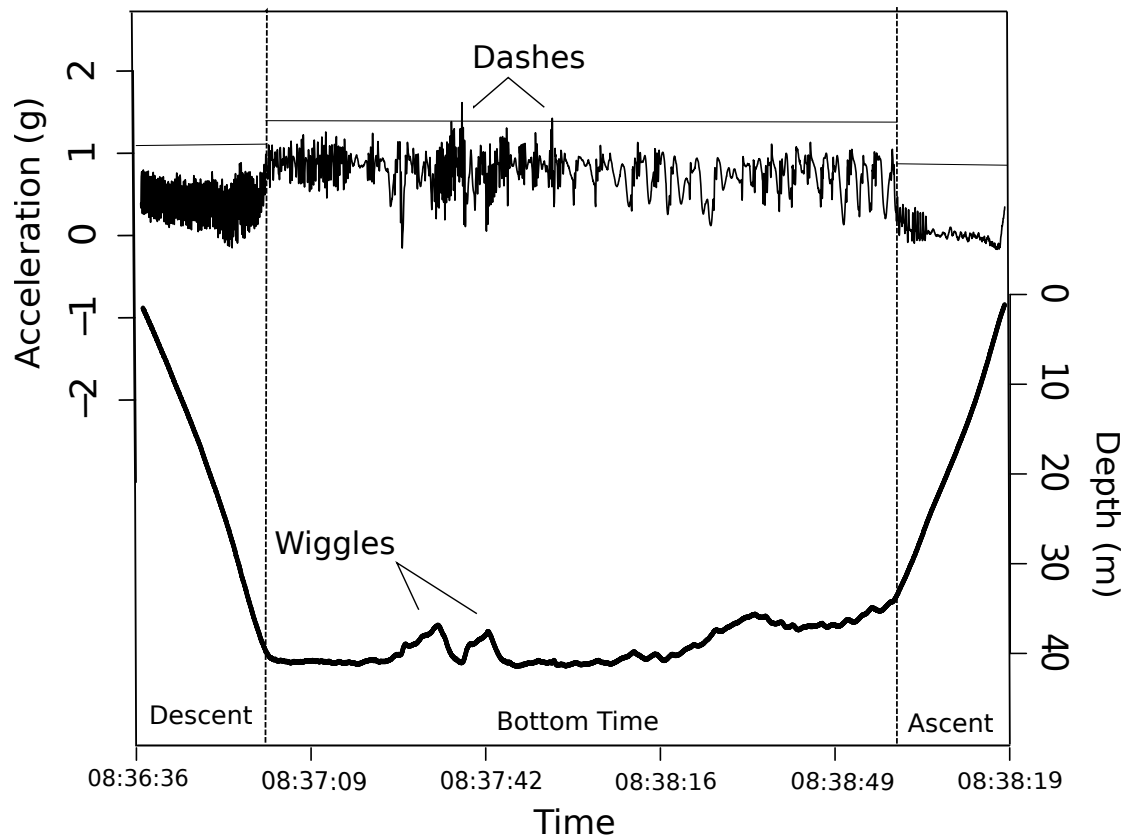


Figure 2.3. Depth and acceleration in the vertical heaving axis during a sample little penguin dive that included both wiggles and dashes. Wiggles are undulations in the bottom phase of the dive occurring at $>0.5 \text{ m s}^{-1}$; dashes are spikes above an acceleration threshold determined using a survival curve. Both wiggles and dashes have been used as proxies for prey encounter and are included in this paper to understand their relationship with predictions from the SVM estimates of prey capture.

To determine which of these features are important components of prey capture vs. non prey capture dives, we used a binomial generalised linear mixed model (GLMM) in the R package lme4 (Bates et al. 2015). As dive duration, maximum depth and bottom duration were all strongly, linearly correlated, we calculated the 'dive residual': a measure of dive duration after removing the effect of maximum depth, and dropped both maximum depth and dive duration from the model. The dive residual is likely to be a proxy for bottom duration, with removal of the contribution of time spent travelling to and from depth. We therefore also omitted bottom time duration from the GLMM. Fixed effects were dive residual, mean ascent rate, mean descent rate, wiggle presence and dash presence. As these variables are naturally autocorrelated at the single dive scale (the presence or absence of prey capture in one dive is not an independent observation if the penguin is foraging in bouts) we ran the GLMM on a random sub sample representing 90% of the dives, to reduce the autocorrelation. Penguin ID was included as a random effect.

2.3 Results

SVM performance on captive data

We analysed 20 accelerometry profiles recorded by 7 different captive penguins on 8 days. A total of 5244 behaviour observations (3971 'Swimming'; 1273 'Prey handling') were extracted after processing the data into 0.3s blocks. These observations were randomly split into 3670 training and 1574 testing points for the initial parameter tuning run, and for each subsequent iteration when evaluating the model's performance. The overall mean accuracy of the SVM in classifying both 'Swimming' and 'Prey handling' events correctly on the unseen testing data was 84.95% (S.E. \pm 0.26%, $n = 12$ iterations). As we are interested in how well the model is likely to correctly predict prey handling in the wild, a more important measure of model performance is the false positive rate, i.e. the likelihood of misclassifying an event as 'prey handling' when it should have been 'swimming'. On our unseen testing data this measure was 9.8% (S.E. \pm 0.24%).

Month	Breeding stage	Sex	Mean mass (g)	Total dives	Prey capture dives/total dives	Prey captures/day	Prey captures/diving minute
Sep	Incubation = 3 Guard = 3 Post guard = 3 Total = 9	F = 5 M = 4	1184 (± 115.68)	15557	0.42 (± 0.28)	443.82 (± 289.81)	1.92 (± 1.14)
Nov	Guard = 2 Post guard = 5 Total = 7	F = 5 M = 2	1103 (± 108.54)	7434	0.37 (± 0.23)	465.43 (± 454)	1.22 (± 0.93)
Dec	Guard = 6 Post guard = 1 Total = 7	F = 7	1043 (± 163.78)	5797	0.47 (± 0.26)	431.36 (± 227.29)	1.39 (± 0.91)
Total	Incubation = 3 Guard = 11 Post guard = 9 Total = 23	F = 17 M = 6	1125 (± 129.67)	28,788	0.42 (± 0.25)	446.61 (± 317.86)	1.54 (± 1.02)

Table 2.1. Summary of the attributes of wild little penguins deployed with accelerometers in 2013, and measures of their foraging efficiency calculated using a support vector machine

<i>Parameter</i>	<i>Slope</i>	<i>SE</i>	<i>P</i>
Dive Residuals	9.82253	0.33185	<0.0001
Mean Descent Rate	0.21976	0.26772	0.334
Mean Ascent Rate	4.01958	0.15780	<0.0001
Wiggle Presence	0.87131	0.04277	<0.0001
Dash Presence	0.46260	0.04259	<0.0001

Table 2.2. Slope, standard error and *P* values for a binomial generalised linear mixed model characterising dive parameters in prey capture vs non prey capture dives during 23 little penguin foraging trips. Parameters in bold were significant.

Application of the SVM to wild accelerometer profiles

Accelerometer profiles were obtained for 21 penguins performing 23 single day foraging trips in 2013 (two birds were sampled twice at different times of the year and in different breeding stages for information about penguins, their foraging trips and measures of their foraging efficiency see Table 2.1). We classified a prey capture event as three consecutive observations of 'prey handling', in order to reduce the misclassification of transient events. As each datum is treated as an independent observation by the SVM, the probability of the model incorrectly classifying three consecutive observations as 'Prey handling' when they should all be 'Swimming' is 0.0009 ($0.098 \times 0.098 \times 0.098$). This is strong evidence that the prey capture events identified by the model were likely to reflect true instances when the penguin had captured and handled prey.

Comparison of prey capture vs non prey capture dives

We analysed 28,788 dives and identified prey capture events in 38%. The number of prey caught per successful dive ranged from 1 (75% of successful dives) to 6 (0.02% of successful dives). We found that prey capture dives were longer in duration and bottom time, were deeper, and were more likely to contain wiggles and dashes (see Figure 2.4). A random subsample of 25,910 (90%) of these dives were included in the binomial GLMM. These results showed that dive residual (a measure of dive duration corrected for depth), mean ascent rate, wiggle presence and dash presence were all significant parameters ($p < 0.0001$), while mean descent rate was not significant ($p = 0.33$) (See Table 2.2).

Comparison of SVM predictions with wiggles and dashes

Wiggles (undulations in the bottom phase of a dive) occurred in 71% of prey capture dives, 40% of non prey capture dives, and 54% of all dives. Dashes (periods where the amplitude of the 'heaving' axis, a proxy for flipper strokes, spiked above a threshold) occurred in 61% of prey capture dives, 52% of non prey capture dives, and 56% of all dives. Wiggles and dashes were present together in 33% of all dives, and of these 53% were successful dives and 47% were unsuccessful dives.

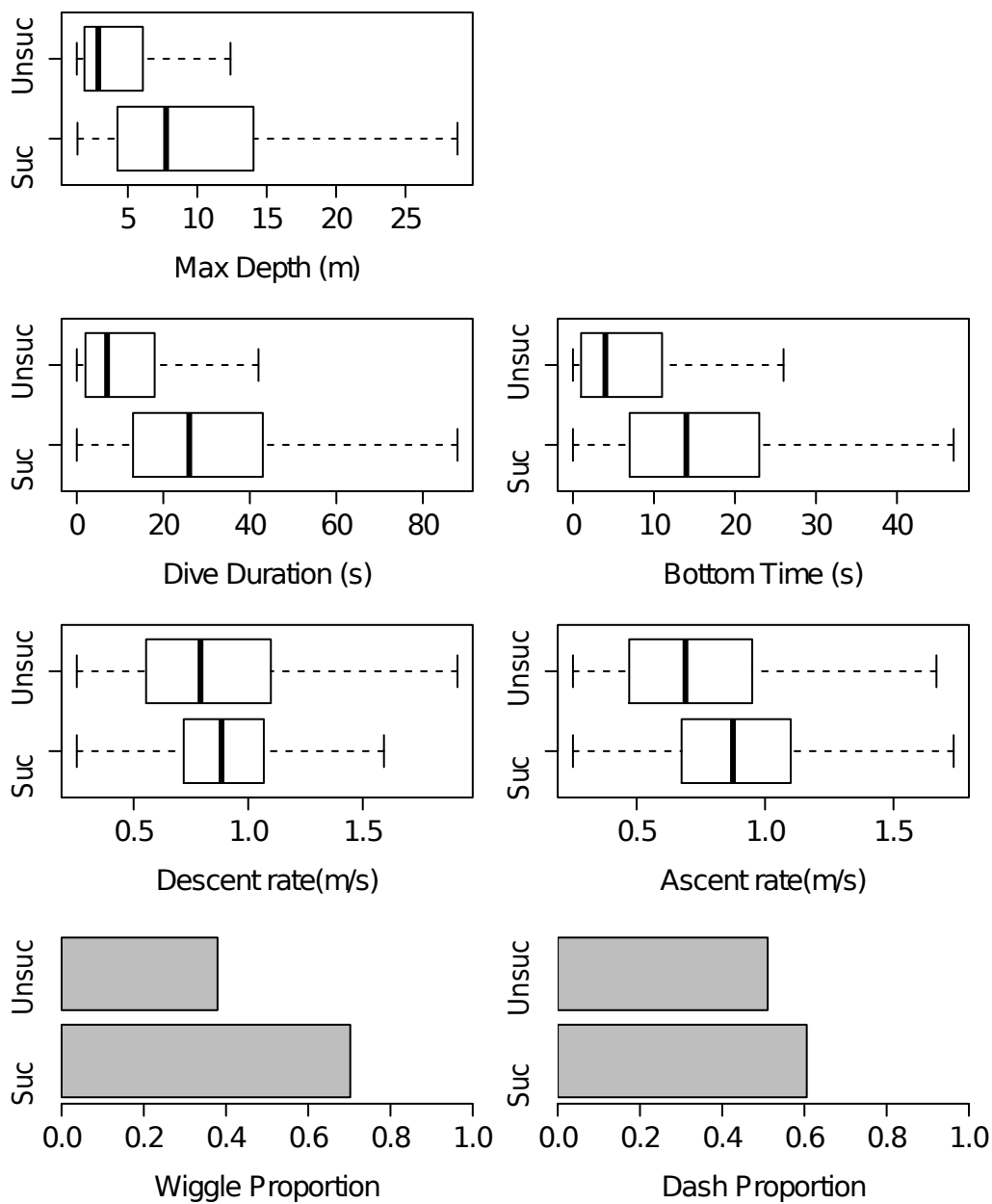


Figure 2.4. A comparison of little penguin dive attributes in 2013, for dives in which the support vector machine detected a prey capture ('Suc') and those in which it did not ('Unsuc').

Little penguin foraging efficiency

The number of discrete prey captures by each penguin per foraging day determined by the model was highly variable, ranging from 120 to 1368 with a mean of 446.61 (S.E. \pm 66.28) and a median of 305. The proportion of successful prey capture dives also varied between individuals, from 0.11 – 0.88 with a mean of 0.40 (S.E. \pm 0.05). Prey captures per minute diving (averaged over the whole foraging trip) ranged from 0.30 – 4.0, with a mean of 1.54 (S.E. \pm 0.21) and a median of 1.56.

2.4 Discussion

There are several emerging analytical techniques that attempt to elucidate the relationships between patterns of acceleration and behaviour in animals. Although each approach can give biological meaning to movement data, identifying and validating prey captures in a wild setting remains difficult, and very few accelerometry studies have attempted to quantify prey ingestion (Watanabe & Takahashi 2013). The results of the present study are promising. The SVM trained on captive penguin accelerometry performed well on unseen captive data, with an 84.95% overall accuracy and 9.8% false positive which is similar to those found in studies on captive terrestrial animals (Nathan et al. 2012, Bidder et al. 2014). The clear differences that we identified between dives in which the SVM identified prey capture and those in which it did not are also encouraging for the translation of this technique to wild datasets. However, assessing model performance on data collected in the wild is challenging as it requires several assumptions, the validity of which we explore below.

Prey captures and foraging strategy

Air breathing divers such as penguins must frequently leave prey patches to return to the surface to breathe during foraging trips. This constraint confers expectations on the way that they are likely to behave while foraging. Foraging animals should make decisions that will maximise their potential for resource acquisition, and are therefore expected to spend more time foraging where food availability is high (Charnov 1976). This prediction holds true for diving animals including wild Adélie penguins, which increase the duration of their dives in response to the rate of short term krill capture

success (Watanabe et al., 2014). Theory also predicts that shallow dives, which constituted most of the dives performed by penguins in this study (77% of all dives and 61% of successful dives were above 10m in depth), should be aborted if prey is not encountered in the upper part of the water column (Thompson & Fedak 2001). Therefore, successful prey capture dives are likely to be not only longer, but deeper than non prey capture dives. The strong differences in duration and depth that we observed between prey capture and non prey capture dives support these theories.

Penguins are observed to have sharper angles of ascent when bottom duration is longer (Sato et al. 2004), and when prey capture has been identified by oesophageal temperature loggers (Robert Coudert et al. 2001). This is probably because if successful prey capture dives are longer and deeper, animals are likely to be foraging closer to their aerobic dive limit and should optimise their return to the surface to replenish their oxygen stores (Viviant et al. 2014). Our results are consistent with these observations, as significantly higher mean ascent rates were observed during successful dives. Descent rate was not a determinant of prey capture in this study, indicating that there was no strong pre conception by the penguins about whether prey was available at the single dive scale.

There was a clear relationship between the presence of both wiggles and dashes, which have been used as proxies for prey encounters in diving animals (Simeone & Wilson 2003; Zimmer et al. 2011a), and the presence of a prey capture identified by the SVM. Wiggles were a better indicator of prey capture than dashes, corresponding to 71% of dives in which the model identified a prey capture event compared with 61% for dashes. Studies using proxies for prey encounter such as wiggles, dashes and head movements have assumed that a) all prey that is encountered is pursued (Robert Coudert et al. 2006b) and b) once prey is encountered, the likelihood of prey capture is high (Zimmer et al., 2011a). However, there are many factors that are likely to affect the rate of prey capture success in relation to the prey that is encountered. These include the effects of prey patch density on prey capture success (Draulans 1987; Darby et al. 2012), the effects of light level on the foraging success of visual predators (Robert Coudert et al. 2006b), the presence of competition from other

predators (Minderman et al. 2006) and the effects of individual experience (Daunt et al. 2007). For these reasons, rates of prey capture cannot be inferred from prey encounter, and methods that focus on prey encounters or capture attempts alone could significantly over estimate the prey consumed by foraging animals.

Foraging efficiency and prey capture rates

Prey acquisition is difficult to quantify in marine animals. Techniques such as diet analyses based on stomach flushing are prone to bias as different prey types have differential digestion rates, and hard parts such as otoliths and squid beaks, if consumed, may not always be retained in the gut (Gales 1988). For animals performing longer foraging trips, stomach contents on return to the colony may only represent the most recent bout of feeding. Such studies generally report the relative occurrence of prey types, rather than attempting to quantify the number of prey items that have been ingested. However, approximate quantities can be estimated by back calculating the wet mass of key prey types required to fulfil the daily energy requirements of individuals based on known metabolic rates (Adams et al. 1993; Watanabe and Takahashi 2013) or they can be determined via water and sodium influxes (Gales & Green 1990).

To determine whether the SVM result provides a reasonable estimate of the quantity of prey items ingested we estimate the possible feeding requirements of little penguins from what is known about their energetics. The SVM identified a mean of 447 prey capture events per penguin per day. The relationship between the daily metabolic rate of little penguins during the breeding season and the food that they require is complicated by the penguins' need to consume a surplus to account for fasting days and the extra mass of food required to provision growing chicks. The metabolic rate of little penguins during the breeding season has been determined to be between $661 \text{ kJ.kg}^{-1} \text{ d}^{-1}$ (for a fasting, incubating bird) to $2532 \text{ kJ.kg}^{-1} \text{ d}^{-1}$ (for a foraging bird late in the chick provisioning phase) using the doubly labelled water method (Gales & Green 1990). The mean energy value of the little penguin diet, with varying proportions of fish, squid and krill across the annual cycle is approximately

3.87kJ/g. Food consumption based on water and sodium influxes has been calculated as being up to 664g.kg 1.d⁻¹ (Gales & Green 1990).

Multiplying the standardised metabolic rate by the mean mass of the penguins in this study (1.125kg), foraging penguins provisioning chicks require up to 2848kJ/d. This approximate energy requirement could be met with 736g of food, a similar mass to the 747g obtained when the mass of food estimated by water and sodium influx is also multiplied by 1.125kg (Gales & Green 1990). Food consumption has also been estimated for little penguin chicks using water and sodium influxes, with an estimated mean rate of intake of 256g/d for older (post guard stage) chicks (Green et al. 1988). This means that approximately 1259g of food could be eaten on an average day by a foraging penguin provisioning two chicks. This estimate may be lower for incubating birds and those with very small chicks, however this figure provides a benchmark on which to sanity test our observations.

If all prey captures identified by the SVM represent actual prey captures, prey consumed by little penguins in our study had a mean mass of approximately 2.8g. Mean mass of ingested fish species estimated from diet reconstruction for little penguins at Phillip Island, Victoria, Australia, ranged from 0.9g (red cod) to 10.7g (garfish) with a mean of approximately 4.9g per item across all fish species (Cullen et al. 1992). Small (1-5cm) schooling fish were the primary component of the diet of little penguins around Montague Island in 2013, with penguins also eating krill when transient swarms enter the area (G. Carroll, unpublished data). Our estimate of mean prey ingestion quantities is consistent with this provided that handling of small size classes of fish and krill are considered in the same way as the handling of larger fish by the SVM.

As the model was trained on penguins handling one type of prey (pilchards), whether or not the capture of other prey types can be identified with the same accuracy is uncertain. This is a limitation of the interpretability of nonlinear SVMs, which are to some extent 'black box' algorithms with non transparent decision rules (Rosenbaum et al. 2011). Logically, the capture and handling of any prey type (live or dead) is more

likely to resemble the physical action of handling dead pilchards than of swimming. It is probable that when the accelerometer records these events, the SVM classifies the observations as 'prey handling', and the number of prey captures recorded in our study supports the notion that the capture of small prey items are being detected.

However, in this study we made a number of assumptions regarding the amount of time it takes for a little penguin to handle prey in the wild. By setting a prey capture event at 3 consecutive 0.3 s observations of prey handling, the minimum observable prey handling time was 0.9s which may not be at a fine enough resolution to detect the rapid consumption of small prey. Similarly, by using a survival curve to determine the amount of time between consecutive prey captures it is possible that we also underestimated prey capture rates when prey density was high. Without validating the handling of more prey types (particularly small fish and krill) and of both dead and live prey, there will remain a level of uncertainty, and the absolute estimates of prey capture quantity should be interpreted with caution at this early stage.

Benefits of supervised accelerometry analysis and future applications

The ability to determine the quantity and timing of prey consumption in wild animals has immense value in ecological studies. The supervised accelerometry approach provides a reliable and minimally invasive method to assess and monitor foraging efficiency, and to estimate the energy intake of predators. Further value can be added by integrating this information with fine scale location data and environmental covariates such as temperature and light level (Guinet et al. 2014). This will lead to an improved understanding of the factors governing the distribution of resources in both space and time, and enable better predictions of the effects of environmental change on predator populations (Hazen et al. 2013).

Although identifying and quantifying the consumption of prey gives us valuable information in the little penguin example, supervised accelerometry analysis can be equally applied to other behaviours of interest. We have shown here that fine scale behaviours that correspond to transient events lasting less than a second can be detected accurately with a machine learning model such as an SVM. Therefore, this

technique is potentially valuable for identifying other behaviours of interest that are variable, transient or occur relatively rarely, e.g. aggressive interactions or copulation.

In order to detect events at such a fine scale, the accelerometry data must be high resolution (30Hz or greater, Broell et al. 2013) and behaviour analysis must occur at the same resolution in order to pinpoint the transition between behaviour states with precision. Ground truthing accelerometry data in captivity is valuable in this respect, as high quality video can be collected from angles that clearly show the whole organism and all its movements to allow for more precise coding of behaviour. The opportunity also exists to experimentally increase the frequency of a particular activity, whereas data must be collected in a much more opportunistic fashion in the wild. Although critter cams are valuable for gaining insight into the natural behaviours of wild animals, they may not always show a behaviour from the best angle, making it difficult for example to determine whether prey capture was successful (Watanabe & Takahashi 2013). They are also a sub optimal method for animals that operate primarily in low light conditions such as nocturnal or deep diving animals, due to the potential interference of the camera's light source with the animal's normal behaviour (Heaslip & Hooker 2008). Ideally, observation of animals in the wild is the best way to remove doubts regarding the validity of acceleration signatures for identifying the full range of their natural behaviours. However, if this is impractical and if captive animals perform behaviours that adequately reflect the natural behaviour of their wild conspecifics, the captive environment provides a useful setting to begin to model their fine scale behaviour using accelerometry.

Chapter Three

High sea surface temperatures driven by a strengthening current reduce foraging success by penguins

This paper is published as:

Carroll, G., Everett, J. D., Harcourt, R., Slip, D., & Jonsen, I. (2016). 'High sea surface temperatures driven by a strengthening current reduce foraging success by penguins' *Scientific Reports*, 6.

Abstract

The world's oceans are undergoing rapid, regionally specific warming. Strengthening western boundary currents play a role in this phenomenon, with sea surface temperatures (SST) in their paths rising faster than the global average. To understand how dynamic oceanography influences food availability in these ocean warming "hotspots", we use a novel prey capture signature derived from accelerometry to understand how the warm East Australian Current shapes foraging success by a meso predator, the little penguin. This seabird feeds on low trophic level species that are sensitive to environmental change. We found that in 2012, prey capture success by penguins was high when SST was low relative to the long term mean. In 2013 prey capture success was low, coincident with an unusually strong penetration of warm water. Overall there was an optimal temperature range for prey capture around 19–21°C, with lower success at both lower and higher temperatures, mirroring published relationships between commercial sardine catch and SST. Spatially, higher SSTs corresponded to a lower probability of penguins using an area, and lower prey capture success. These links between high SST and reduced prey capture success by penguins suggest negative implications for future resource availability in a system dominated by a strengthening western boundary current.

3.1 Introduction

To understand how changes in the physical properties of oceans affect food webs, it is essential to develop appropriate indicators of resource availability. Remote sensing of environmental data including sea surface temperature (SST) and chlorophyll *a* provides valuable insight into the processes driving spatial and temporal changes in primary productivity (Behrenfeld et al. 2006). Linking these changes to outcomes for mid and upper trophic level predators is more challenging, despite the importance of this information for predicting ecosystem responses to climate change (Doney et al. 2012). As it is difficult to directly measure prey abundance on scales relevant to marine predators, studies have often used tracking technology to identify correlations between oceanography, primary productivity and predator foraging behaviour (Dragon et al. 2010; Suryan et al. 2012). However, without a measure of foraging success, it is difficult to estimate how much prey animals encounter and consume while foraging under different environmental conditions.

Accelerometry has shown great potential to provide fine scale information on the activity of wild animals. Machine learning algorithms have been applied to recognise patterns in acceleration data, providing robust links between the behaviour of animals and their movement profiles, such that behaviour can be determined remotely (Nathan et al. 2012). One application of these behaviour classification methods has been to identify movement patterns associated with feeding (Watanabe & Takahashi 2013; Carroll et al. 2014; Ydesen et al. 2014). The next step in this rapidly evolving field is to use information on prey capture events to answer important ecological questions relating to resource availability that were previously difficult to address. By linking foraging success to physical oceanography, we can gain insight into the mechanisms dictating resource availability and predict if and how marine predators and their prey are vulnerable to environmental change.

Western boundary currents are a significant source of global heat transport, advecting warm water from the tropics to temperate latitudes (Jayne & Marotzke 2002). Although these systems are considered nutrient poor compared with cold eastern

boundary currents, they generate eddies (Everett et al. 2012) that drive nutrient upwelling (Tranter et al. 1986). Subsequently, they are able to support fisheries (Olson 2001) and populations of marine predators such as seabirds (e.g. Jiménez et al. 2011). Western boundary currents are strengthening, increasing the pole ward penetration of warm water. For example, the East Australian Current (EAC) is the western boundary current of the South Pacific Gyre, and its intensification is causing regional sea surface temperature (SST) to rise much faster than the global average (Wu et al. 2012). The global significance of changes to currents means that it is important to understand how their physical processes drive variation in productivity (Everett et al. 2015), and to identify the effects of this variability at all trophic levels.

Seabirds provide a useful model to examine the effects of environmental change on resources, as they are highly responsive to fluctuations in prey availability (Einoder 2009). The little penguin (*Eudyptula minor*) is the world's smallest species of penguin and has a breeding colony at Montague Island, off southeast Australia (774 ± 61 breeding pairs on the southern part of the island in 2015; Peter Fullagar, unpublished data). Montague Island is situated halfway across the continental shelf, with surrounding waters heavily influenced by the dynamics of the EAC and its eddy field (Figure 3.1A). To assess the consequences of variation in EAC penetration on the amount of prey (low trophic level species, or “forage fish”, including small pelagic fish, krill and squid) caught by penguins, we used a prey capture signature derived from their acceleration profiles (Carroll et al. 2014). As little penguins are highly constrained in the range and duration of foraging trips during the breeding season, we determined mechanistic links between foraging success and the environment on fine spatial (< 25km) and temporal (< 10 day) scales.

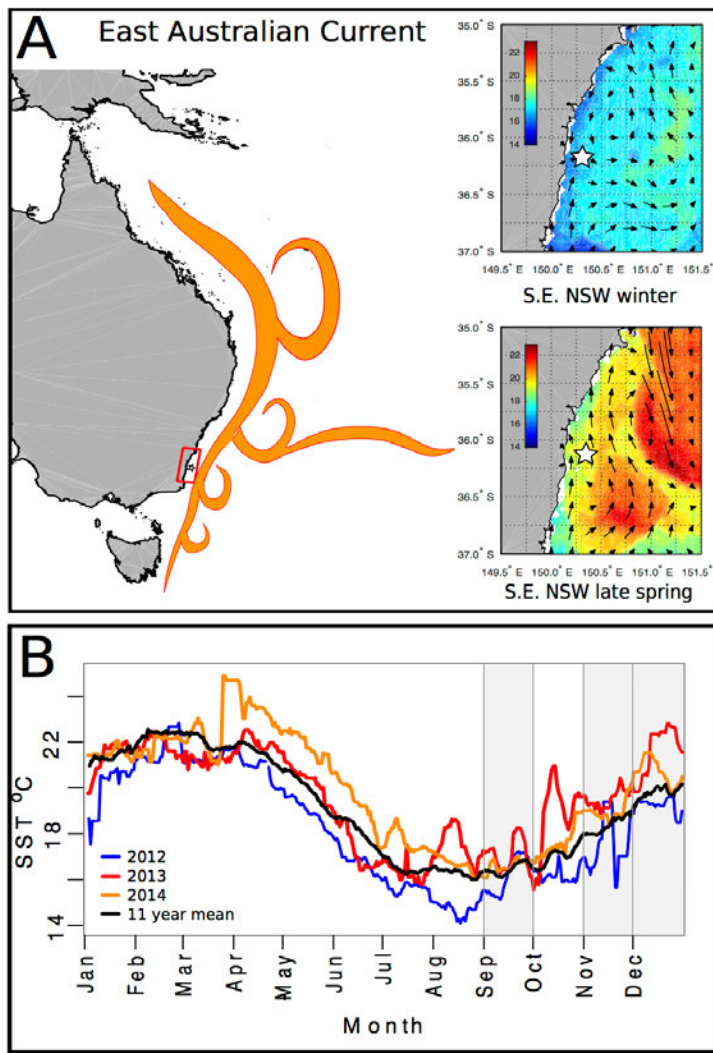


Figure 3.1. A) Schematic showing the general characteristics of the East Australian Current (left). The area of this study (southeast NSW) is indicated by the red box, and the white star marks the location of Montague Island. On the right are examples of typical winter (top) and late spring (bottom) sea surface temperature and current directions in southeast NSW around Montague Island (white star). Inset maps were produced in MATLAB R2014b using data available from <http://imos.aodn.org.au/imos/>. B) Annual time series of sea surface temperature measured offshore from Montague Island during 2012, 2013 and 2014 with a rolling 10 day mean. Grey windows represent the months (Sep, Nov, Dec) in which penguins were tracked from 2012 2014.

Specifically, our aims were to: 1) understand the temporal variability of prey capture success by little penguins determined using accelerometry, and assess how this variability was related to the EAC; 2) understand spatial variability in foraging location determined using GPS, and assess how environmental features dictate the way that penguins use available foraging habitat; 3) assess spatial variability in prey capture success determined from GPS, accelerometry and depth recorders in relation to the EAC. We discuss the insight that our findings give into the relative availability of low trophic level species to predators in the context of western boundary current intensification.

3.2 Materials and Methods

Fieldwork

The field study was conducted on Montague Island (36.253°, 150.227°), 9km off the southeast coast of New South Wales, Australia, in September, November and December 2012–2014. This period covers the peak of the little penguin's breeding season, which can be highly asynchronous (Robinson et al. 2005). Adults show biparental care during incubation and rearing offspring. During incubation, foraging trips are on average 3.5 days in length (Chiaradia & Kerry 1999). When offspring are young (< 2 weeks) one parent stays behind to guard the chicks while the other goes to sea usually for a single day, and as the chicks grow both parents go to sea simultaneously, often for multiple days. When conditions are good, little penguins can raise two clutches in succession (Johannesen et al. 2003). Sampling periods comprised 6–15 days tracking penguins in each month.

The night before a penguin went to sea, it was caught in its nest box and equipped with a GPS logger (CatTrack, South Carolina, USA) modified with epoxy resin to withstand pressure at depth. The loggers were inserted into heat shrink tubing, then attached to feathers on the lower back with cloth tape (Tesa, Hamburg, Germany), positioned so as to reduce drag but not impede tail movement. These tags were 43 mm in length, 27 mm in width and 13 mm in height, and weighed 55 g in air and 17.4 g in seawater. A range of sampling frequencies was used over the study period to adjust

the trade off between battery life and spatial resolution. For penguins expected to perform single day trips (birds rearing small chicks), sampling frequency ranged from 7 – 45 s. For birds expected to perform multiple day trips (incubating birds and birds with larger chicks), the sampling frequency ranged from 30–115 s, however at these sampling frequencies the loggers were still rarely able to record complete multiple days, so spatial analyses were restricted to single day trips. When penguins returned from a foraging trip they were recaptured in their nest boxes, loggers removed and the penguin was weighed in a calico bag using a spring balance scale (Pesola, AG Switzerland).

Accelerometer data loggers (G6a and G6a+, CEFAS Technology Pty Ltd, Suffolk, UK) were attached immediately in front of the GPS units (towards the head) on the middle back for a subset of penguins from November 2012. These tags were 40 mm in length, 28 mm in width and 15 mm in height, and weighed 7.8 g in air and 2.3 g in seawater. The accelerometers recorded acceleration in 3 axes: anterior posterior (surging), lateral (swaying) and dorso ventral (heaving) with a range of ± 2 g. The accelerometers recorded depth, temperature and acceleration and were programmed in two modes: “shallow” mode (<1.5 m: 1.5% of the full scale pressure range) where parameters were recorded every 10 seconds, and “dive” mode (>1.5 m) where the same parameters were recorded at 30 Hz.

Combined tag weight for penguins that were equipped with both accelerometers and GPS was 62 g in air and 19.7 g in seawater, which is < 5% and < 2% of mean bodyweight (~1100 g) respectively. Handling time was kept to a minimum, and in most cases was less than 5 min for both deployment and retrieval of devices. All animal research protocols were carried out in accordance with guidelines approved by the Macquarie University Animal Ethics Committee (Animal Research Authority 2011/14).

Prey capture signature

We previously developed a motion signature to identify prey capture by wild penguins at sea, using a support vector machine algorithm that identified prey handling by wild penguins with a false positive rate of 0.09%. A thorough description of this method

and its validation in the wild is detailed in Carroll et al. (2014). We showed that dives during which prey capture occurred were longer in duration, deeper, had longer bottom times, more undulations in the bottom phase of the dive and faster ascent and descent rates, consistent with predictions from foraging theory and previous empirical studies of marine predator foraging ecology (Charnov 1976; Thompson & Fedak 2001; Sato et al. 2004).

Analysis

Temporal variability in prey capture success

We assessed temporal patterns of prey capture success by breeding little penguins between November 2012 and December 2014. All available accelerometry profiles were used in this analysis, from both single and multiple day foraging trips. The penguins in this study were not individually marked, so it is not known whether they were resampled in multiple years. However, only 9 birds of the same sex from the same nest were sampled more than once (13%). We used the mean number of prey caught per 90 min period across a foraging trip as an index of prey capture success for that trip. As we might expect penguins to adjust their foraging effort to the availability of prey, we also calculated a measure of catch per unit effort (CPUE), which was the mean value across a foraging trip of the number of prey caught per 90 min window as a function of time spent diving below 1.5 m within that window. We used the mean value over discrete time windows rather than a daily value, as this allowed for comparison among foraging trips of different lengths. We tested a range of time windows (1, 5, 10, 20, 30, 45, 60, 90, 120 and 240 min) on a subset of eight pooled single and multiple day foraging trips and found that 90 minutes was the window that minimised the standard deviation of the mean foraging trip CPUE (see Figure 3.S1 in Section 3.6). For trips longer than one day, we removed all 90 min intervals that occurred at night, as penguins do not forage after dark (Cannell & Cullen 1998). In this study time spent diving was usually < 1min per 90 min window after sunset.

To assess the temporal influence of the EAC on foraging success, we first described relationships between different environmental variables to find a suitable means of representing EAC penetration. We obtained measurements of satellite derived SST

(MODIS Aqua), chlorophyll *a* (OC3) and geostrophic velocity (derived from altimetry from NASA/CNES (Jason 1 and 2) and ESA (ENVISAT) satellites) from the Integrated Marine Observing System (IMOS) Data Portal (<http://imos.aodn.org.au/imos/>). Daily SST and Chlorophyll *a* data were obtained at a location 5.5 km offshore (east) from Montague Island (36.26°S, 150.29°E) in November and December 2012–14 and September 2013–14 (accelerometry data was not collected during September 2012). This offshore location is halfway between Montague Island and the edge of the continental slope where the EAC is centred (Suthers et al. 2011), and therefore should provide an index of the incursion of offshore EAC waters onto the shelf. We used oceanographic data from this location after comparison with data taken from a location 3 km inshore (west), halfway between Montague Island and the mainland (36.26°S, 150.19°E), and values averaged over the penguin foraging area. The single offshore location better captured the variability associated with EAC penetration, as indicated by the fact that Akaike's Information Criterion (AIC) scores were lowest with offshore SST, when the same models were run with each of these variables in turn (see below for model details). North-south geostrophic velocity was obtained at the closest pixel to the SST data (36.2°S, 150.4°E) and rotated 19 degrees to be in the alongshore direction.

Using linear regression we examined the relationship between offshore SST, chlorophyll *a* from the same location, and geostrophic current velocity (see Figure 3.S2 in Section 3.6). As expected, a stronger alongshore current was correlated with warmer water (adjusted $R^2 = 0.17$, $p < 0.0001$) and chlorophyll *a* concentration decreased with warmer water (adjusted $R^2 = 0.36$, $p < 0.0001$). Due to these correlations we chose not to model the effect of more than one of these environmental variables on foraging success simultaneously, although they are each likely to explain a portion of its variance. We chose to use offshore SST as a single proxy for penetration of the EAC, as the EAC brings warm water down Australia's southeast coast from the tropics in a series of highly variable mesoscale eddies, rather than a continuous southward flowing stream (Everett et al. 2012; Suthers et al. 2011). Increasing temperature brought by these warm influxes is likely to be of greater biological relevance to larger organisms than for example, an increase in the speed of

the current. Furthermore, the measurement of SST in coastal systems is more reliable than measurement of chlorophyll a , and occurs at a higher sampling frequency (daily) compared to geostrophic velocities, which are calculated from satellite altimetry data and collated and interpolated over a 10 day cycle.

To characterize seasonal patterns of EAC penetration, we plotted a time series of daily SST values offshore from Montague Island for 2012–2014, and applied a 10 day rolling mean to smooth the data. To place our findings in a longer term context, we calculated the mean SST for each calendar day over a period of 11 years (2003–2014). We also calculated the mean SST for each month that penguins were tracked.

We used generalised additive models (GAMs) with Gaussian error distributions to estimate the relationship between SST and our two measures of foraging success (mean number of prey caught per 90min window and CPUE). For each penguin foraging trip, we averaged SST over a four day window centred on the trip dates. If the foraging trip was longer than four days, we used the mean over the length of the trip. This helped to reduce gaps in satellite data arising from cloud cover, but was still relevant for penguins foraging on short temporal scales.

Spatial variability in foraging location

We used locations recorded by GPS loggers to determine the relationship between spatial habitat use and SST. For these analyses we only used single day foraging trips, as these were comparable in terms of the maximum distance that the penguins travelled from the island (~25km per day). By focusing on single day trips, we were also able to use the most complete GPS tracks, as tracks of multiple day foraging trips were often incomplete due to limitations in GPS battery life on these small loggers.

To determine the relationship between foraging location and SST, we created a grid with 1km² cells spanning the penguins' potential single day foraging range (25km north and south of Montague Island and east to the shelf edge). The 1km² grid was the finest resolution available for the remotely sensed MODIS Aqua SST data. We averaged SST over the days when we tracked penguins (e.g. if there were penguins

tracked on the 3rd, 4th, 6th, 8th and 11th of September, we averaged gridded SSTs for these days). We chose this method after testing two others that masked relationships between SST and foraging success: a) taking the mean of SST for all days within the range of dates that penguins were tracked (e.g. 3rd – 11th September) and b) averaging over 15 days regardless of the tracking date range (15 days being the longest tracking period).

We spatially binned locations recorded by the GPS tags onto the same 1km² grid, resulting in counts of locations within each grid cell that we summed for each sampling period (Sep, Nov & Dec 2012–14). To avoid artificially over sampling in some areas where penguins rested at the surface, and under sampling in other areas where gaps were recorded in the GPS data due to the penguins spending more time underwater, we linearly interpolated the raw GPS location data at regular 10 min intervals. Interpolation also allowed us to homogenise the different GPS sampling frequencies used during the study period. We determined a 10 min sampling frequency to be the most appropriate as little penguins travel at a mean speed of 1.8m/s (Bethge et al. 1997), and therefore move, on average, ~ 1km every 10 minutes. Thus, 1km² areas that penguins moved through without foraging would get on average a single count (or fewer if the penguin was moving more quickly), whereas areas where they encountered prey and engaged in area restricted search were likely to contain substantially more observations.

We analysed the relationship between SST and penguin location counts using a hurdle model (Jackman 2015). This model accounts for the zero inflation present in the count data (there were large areas where the penguins did not go and hence many zero counts in grid cells) as well as over dispersion (some cells had few detections while others had many). The hurdle model uses two processes to model data. The first assesses the relationship between the predictor variable (in this case SST) and counts (the number of times penguins were observed in a cell). The second assesses the relationship between the predictor variable (SST) and the zero observations (presence/absence of penguins in a cell) using a binomial distribution. The model assumes that SST might differentially affect a) whether penguins do or do not go to an

area at all (habitat suitability) and b) how much time they spend there (habitat quality).

To test whether penguins are responding to relative SST or absolute temperatures, we assessed both SST and SST anomaly (deviance of SST for each 1km² grid cell from the mean SST of all grid cells). We compared three measures (SST, SST anomaly (continuous predictor) and SST anomaly (binary predictor; warmer or cooler than the mean)) in separate hurdle models and compared them using Akaike's Information Criterion (AIC), to best capture the relationship between SST and both penguin presence/absence and the number of observations within grid cells. We created a visual representation of the relationship between foraging location and SST by overlaying raw GPS tracks on a map with spatial SST anomaly (pixels were coloured according to how much they deviated from the mean temperature of the study area).

Spatial variability in prey capture success

We assessed the spatial distribution of prey capture events in relation to SST. We performed a linear interpolation between GPS locations at 1 s intervals to integrate the accelerometry record and the GPS tracks. When a location was determined for each prey capture event, we used only these locations in the analysis. We used the same 1km² grid and counted prey capture events recorded in each cell. We analysed only the cells in which prey capture occurred, using a GAM to assess relationships between prey capture density and SST. We then examined the time series of SST encountered by penguins through the course of single day trips (mean SST of grid cells visited per 10% increment by all penguins within a sampling period) in relation to the prey caught through the course of single day trips. We also determined the mean depth of prey capture events during each foraging trip, and the mean distance of prey captures from the colony during each foraging trip, and assessed how these varied intra and inter annually in relation to offshore SST (described previously). All analyses conducted in this study were performed in the R statistical programming framework (R Core Team 2015).

3.3 Results

Oceanography

Penetration of the East Australian Current was variable over the three study years (Figure 3.1B). In 2012, SSTs were almost always lower than the long term average. By contrast, both 2013 and 2014 had summer SSTs that were generally warmer than average. In particular, SSTs appeared anomalously high in 2013 during the penguin breeding season, with high variability and strong pulses of warm water penetrating the study region. The timing of the onset of warm water penetration in 2013 was notable, with an unusual infiltration of warm water in August resulting in SSTs more than 1 °C warmer than the long term mean. In October 2013 there was a spike in SST of almost +4 °C from the mean and in December 2013 an increase of around +3 °C. 2014 was less variable, but there was an anomalous spike of + 1 °C in late October to mid November 2014, and another of +1.5 °C in December 2014.

Temporal variability in prey capture success

We obtained accelerometry profiles for 63 penguin foraging trips between Nov 2012 and Dec 2014 (Nov 2012 n = 3; Dec 2012 n = 10; Sep 2013 n = 9; Nov 2013 n = 7; Dec 2013 n = 7; Sep 2014 n = 16; Nov 2014 n = 7; Dec 2014 n = 4). The mean number of prey caught per 90 minute period varied both intra and inter annually (see Figure 3.2) (mean \pm s.e.: Sep 2013 = 51.65 ± 10.97 , Sep 2014 = 19.18 ± 3.97 ; Nov 2012 = 75.74 ± 6.10 , Nov 2013 = 44.22 ± 15.74 , Nov 2014 = 57.04 ± 17.47 ; Dec 2012 = 88.09 ± 9.22 , Dec 2013 = 40.86 ± 8.52 , Dec 2014 = 63.24 ± 20.77). We tested whether inter annual differences were significant using a generalised linear model (GLM) for each of the three months, assessing the relationship between 90 min prey capture success and year. Where there were 3 years (November and December), 2012 was the reference year as it always had the highest prey capture success. In September, 2014 was significantly worse for prey capture success than 2013 (32.47 ± 9.69 , $t = -3.350$, $p = 0.003$). In November, there were no significant differences, and in December, 2013 had significantly lower prey capture success than 2012 (47.23 ± 14.64 , $t = -3.22$, $p = 0.005$). CPUE followed the same general trend as the 90 min catch data, although in

September penguins spent less time actively foraging relative to the number of prey caught, thereby reducing the difference in CPUE between 2013 and 2014.

In November and December, the monthly SST anomaly (SST relative to mean SST for that month across the 3 study years) showed a broad correlation with prey capture success as determined by both 90 minute prey capture and CPUE metrics. 2012 was the year with lowest SSTs (Nov = -1.34°C ; Dec = -1.25°C relative to the mean), and saw the highest foraging success. 2013 was anomalously warm, (Nov = $+0.67^{\circ}\text{C}$; Dec = $+1.08^{\circ}\text{C}$) and saw the lowest foraging success. 2014 was intermediate in both SST and foraging success (Nov = $+0.09^{\circ}\text{C}$ and Dec = $+0.07^{\circ}\text{C}$). In September this trend was reversed with 2013 being warmer with higher prey capture success, although there was low variability in SST between the two years (Sep 2013 = $+0.26^{\circ}\text{C}$, Sep 2014 = $+0.18^{\circ}\text{C}$).

Offshore SST had a quadratic relationship with both log transformed prey captures per 90 min and CPUE (Figure 3.3). For the 90 min prey capture data, low SSTs (16°C – 18.5°C)

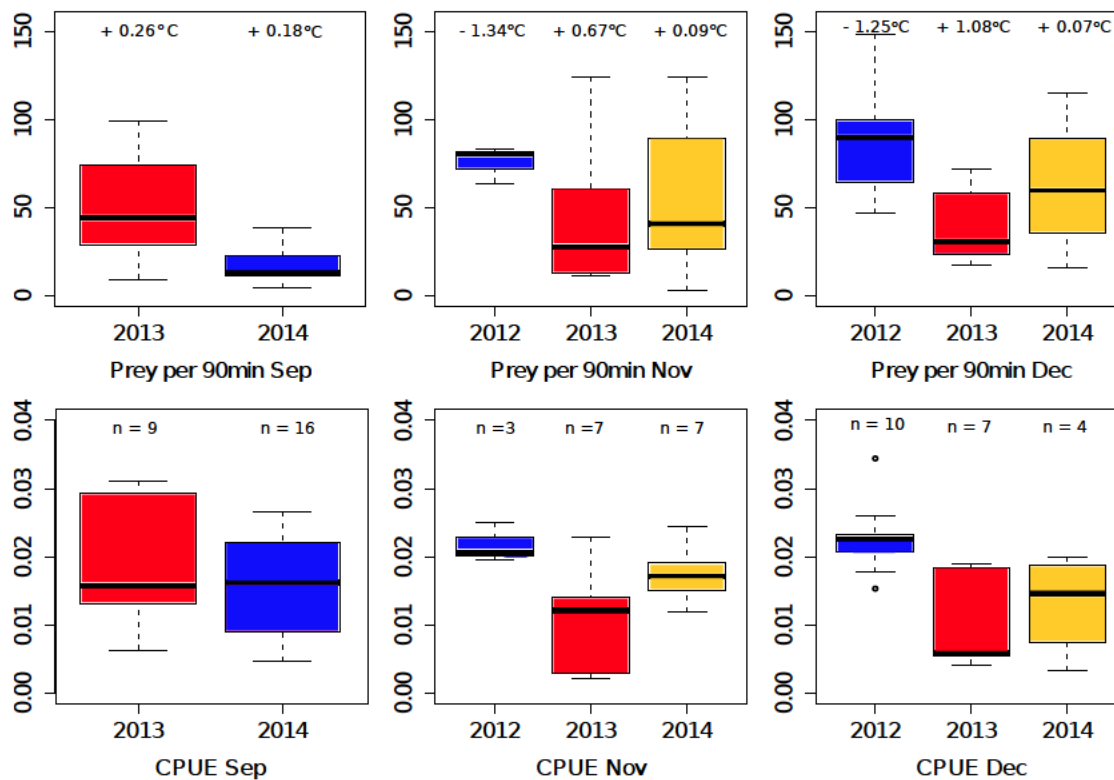


Figure 3.2. Mean prey caught per 90min window and mean CPUE (prey caught per minute spent diving below 1.5m) per 90min window by month in 2012, 2013 and 2014. Box plots are coloured according to the SST relative to the mean SST of that month in the other two study years (red being the warmest of the 3 years for each month, blue being the coldest). Sample size and deviation from the mean monthly temperature (°C) are noted on the prey capture plot (top) and samples sizes are shown on the CPUE plot (bottom).

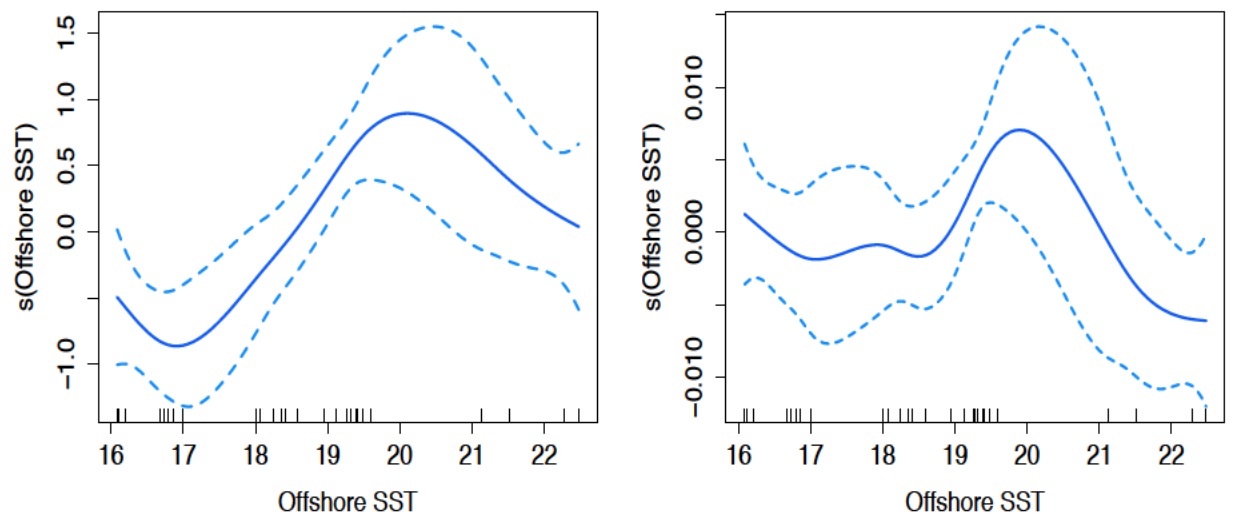


Figure 3.3. Generalised additive model relationships between log transformed prey capture by penguins per 90 min and offshore SST (left); and catch per unit effort (number of prey caught by penguins/amount of time spent diving > 1.5m) & offshore SST (right).

corresponded to the lowest prey capture success. A peak in prey captures occurred at around 20 °C before dropping off (GAM $R^2 = 0.31$, $F = 5.79$, $p = 0.0002$). There was no strong relationship between CPUE and SST between 16 °C and 19 °C, when again the model showed a strong peak in CPUE around 20 °C before a drop off between 21 °C and 22 °C (GAM $R^2 = 0.17$, $F = 2.57$, $p = 0.03$).

Spatial variability in foraging location

For the habitat use analysis, we analysed GPS tracks from a total of 112 single day penguin foraging trips in September, November and December 2012 14 (Sep 2012 $n = 31$; Nov 2012 $n = 6$; Dec 2012 $n = 10$; Sep 2013 $n = 15$; Nov 2013 $n = 19$; Dec 2013 $n = 12$; Sep 2014 $n = 9$; Nov 2014 $n = 6$; Dec 2014 $n = 4$). 82% of 1km² grid cells that penguins could have visited during single day trips did not contain observations of penguins, indicating that penguins were selective in their habitat choice, foraging in similar locations within a given time period.

Penguins appeared to seek out water that was colder than the mean of all available habitat (Figure 3.4). When a grid cell was colder than average, we were 42% more likely to observe a penguin than if the grid cell was warmer than average (26% of cells colder than average recorded penguin presence c.f. 15% of cells that were warmer than average). Similarly, the time that penguins spent in a cell was related to its SST anomaly: areas colder than average had 50% higher counts than areas warmer than average (cold = 2.76, warm = 1.38).

The hurdle model using SST averaged over the sampling days as a predictor performed better than models using SST anomaly either as a continuous or binary variable (see Table 3.S1). The count part of the hurdle model, which explains variation in the number of times penguins are observed in a cell, showed that lower counts were recorded as SST increased (SST estimate = 0.02, S.E. = 0.01, Z value = 3.00, P value = 0.003). For the zero part of the hurdle model, which explains variation in whether penguins were observed in

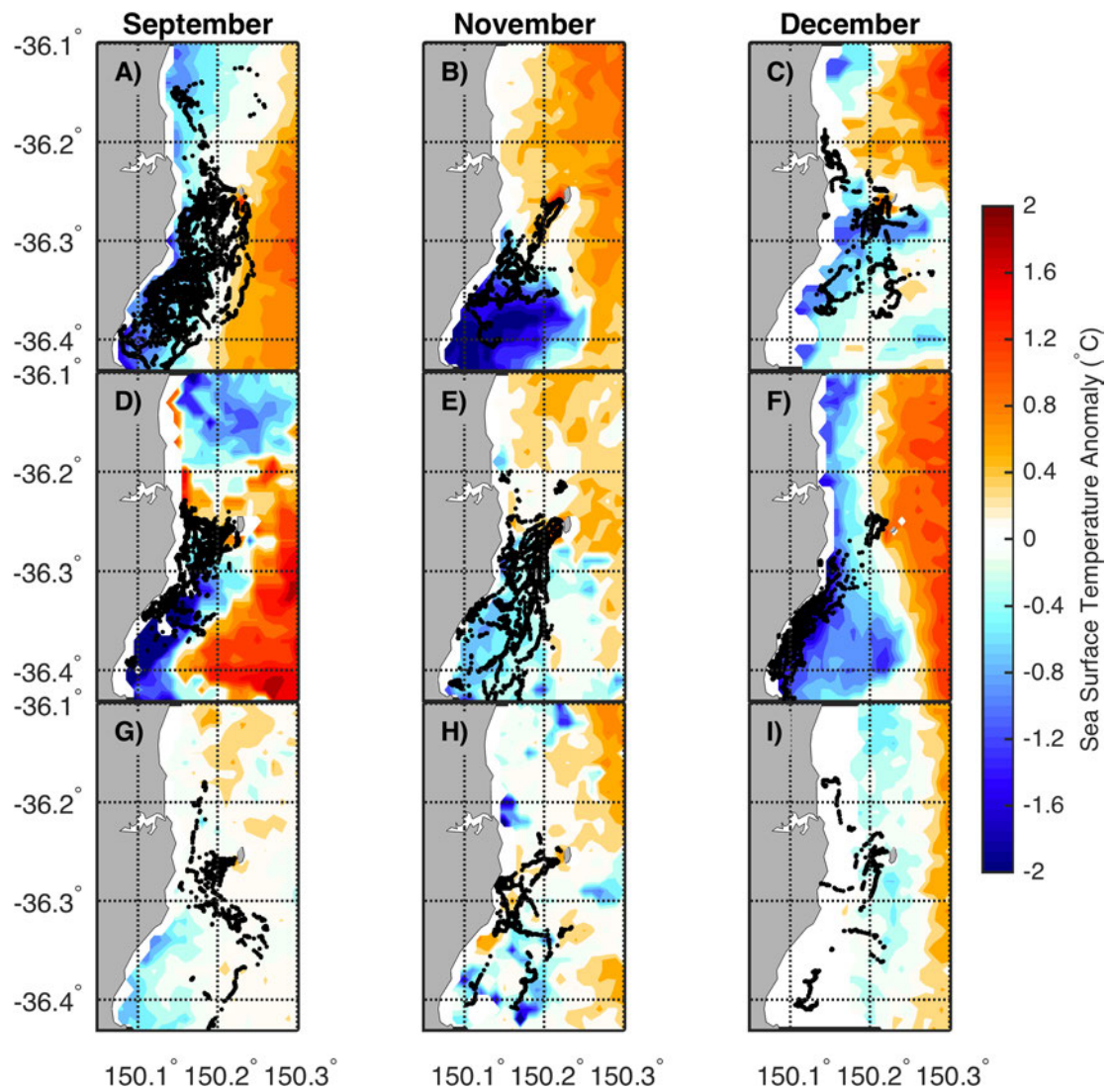


Figure 3.4. Raw GPS tracks of penguins performing single day foraging trips in relation to sea surface temperature anomalies (SST of 1km^2 grid cell – mean SST of all 1km^2 grid cells in study area). Top row is 2012, second is 2013 and bottom row is 2014. Plot regions represent the area gridded on a 1km^2 scale for spatial analyses. Maps were produced in MATLAB R2014b using data available from <http://imos.aodn.org.au/imos/>.

a cell at all, showed that as SST increased, penguins were increasingly less likely to visit that cell (SST estimate = 0.28, S.E. = 0.03, Z value = 10.45, P value = < 0.0001).

Spatial variability in prey capture success

To assess the effect of SST on the spatial distribution of prey captures, we integrated accelerometry profiles and GPS tracks of 50 complete single day penguin foraging trips in

November and December 2012–14, and September 2013–14 (Nov 2012 n = 3; Dec 2012 n = 10; Sep 2013 n = 6; Nov 2013 n = 8; Dec 2013 n = 8; Sep 2014 n = 7; Nov 2014 n = 4; Dec 2014 n = 4). Sample penguin tracks with prey capture locations in relation to gridded SST are shown in Figure 3.5. These illustrate habitat selection by the penguins, with penguins tending to forage in cooler waters, particularly in warmer months (e.g. in December 2013). Examples of gridded prey capture densities by all penguins within each month in 2013 are shown in Figure 3.S3. There were signs of a relationship between SST and the number of prey caught within a 1km² grid cell at the coldest and warmest temperatures observed during this study (Figure 3.S4). The GAM showed that the highest density of prey captures occurred when penguins were in areas with the lowest recorded temperatures (~13.5 °C). Prey capture success was variable at intermediate SST and fell when temperatures were > 20 °C. Even after removing the effect of unsuitable habitat where there may be no prey at all, there was an effect of SST on the spatial distribution of prey captures. However, the modelled relationships retained some uncertainty and the amount of variance explained was low (GAM R² = 0.11, F = 4.05, p < 0.0001).

The GAM only assessed the effect of SST on prey capture success in areas where prey capture occurred. To assess the relationship between prey capture and the SSTs encountered over the course of a foraging trip, we plotted a time series of the mean SST of grid cells visited by penguins in 10% increments of trips within a sampling period (September, November and December 2012–14). We then overlaid the mean number of prey captures identified using accelerometry within the same 10% increments within a

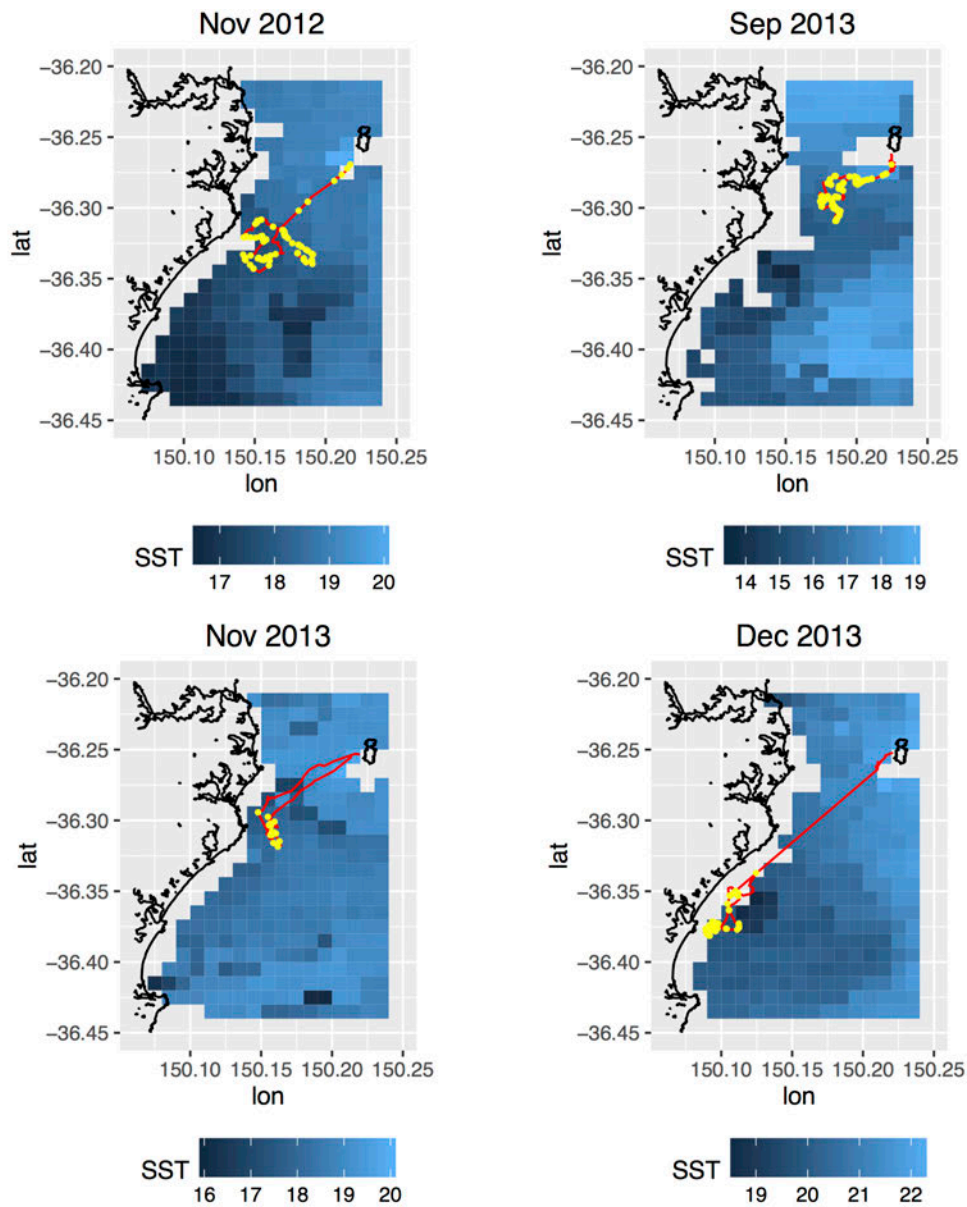


Figure 3.5. Sample foraging trips by little penguins in relation to gridded sea surface temperature (<http://imos.aodn.org.au/imos/>), showing foraging trajectory (red) and prey capture locations (yellow). Panels have different scales in order to highlight penguin habitat selection relative to the distribution of sea surface temperatures within each period.

sampling period (November and December 2012 14, September 2013 14) (see Figure 3.6).

This analysis confirmed that penguins seek out areas with lower relative SSTs, with encountered temperatures always decreasing during a foraging trip before increasing again towards the end of a journey. It also showed that in December 2012 14 and November 2012 and 2014, there was good agreement between the spatial distribution of prey capture success and SST, with areas/periods of lowest SST encountered by penguins on a foraging trip related to the highest prey capture success. However, in September 2013 14 and November 2013 there was no clear relationship between spatial prey capture and SST distribution.

In order to explore whether subsurface water properties such as thermoclines might affect little penguin foraging success differently from SST, we assessed the relationship between the mean SST in a 1 km² grid cell and the mean temperature at the point of prey capture in the same grid cell, calculated from the temperature sensors on board the accelerometers. We found a near linear, 1:1 relationship between SST and prey capture temperature above 16 °C (GAM $R^2 = 0.53$, $F = 28.02$, $P < 0.0001$) (Figure 3.S5). This is unsurprising, as prey capture by penguins generally occurred in the upper part of the water column, with the mean depth of prey captures across foraging trips being less than 10 m in all months (mean \pm s.e.: Sep 2013 = 4.26 ± 0.20 , Sep 2014 = 4.57 ± 0.35 ; Nov 2012 = 6.77 ± 0.81 ; Nov 2013 = 8.46 ± 0.59 , Nov 2014 = 8.49 ± 0.70 ; Dec 2012 = 9.93 ± 0.82 , Dec 2013 = 9.18 ± 0.99 , Dec 2014 = 6.89 ± 1.49). There were no obvious patterns between depth of prey capture and the relative SST for each month (Figure 3.S6).

The mean distance from the colony at which penguins caught prey ranged from 8 km to 16 km (Sep 2013 = 8.18 ± 0.79 , Sep 2014 = 7.28 ± 0.86 ; Nov 2012 = 8.55 ± 0.91 ; Nov 2013 = 13.32 ± 2.30 , Nov 2014 = 8.18 ± 0.49 ; Dec 2012 = 8.07 ± 1.04 , Dec 2013 = 15.68 ± 0.84 , Dec 2014 = 12.94 ± 3.47). It appears that prey captures occurred further from the colony

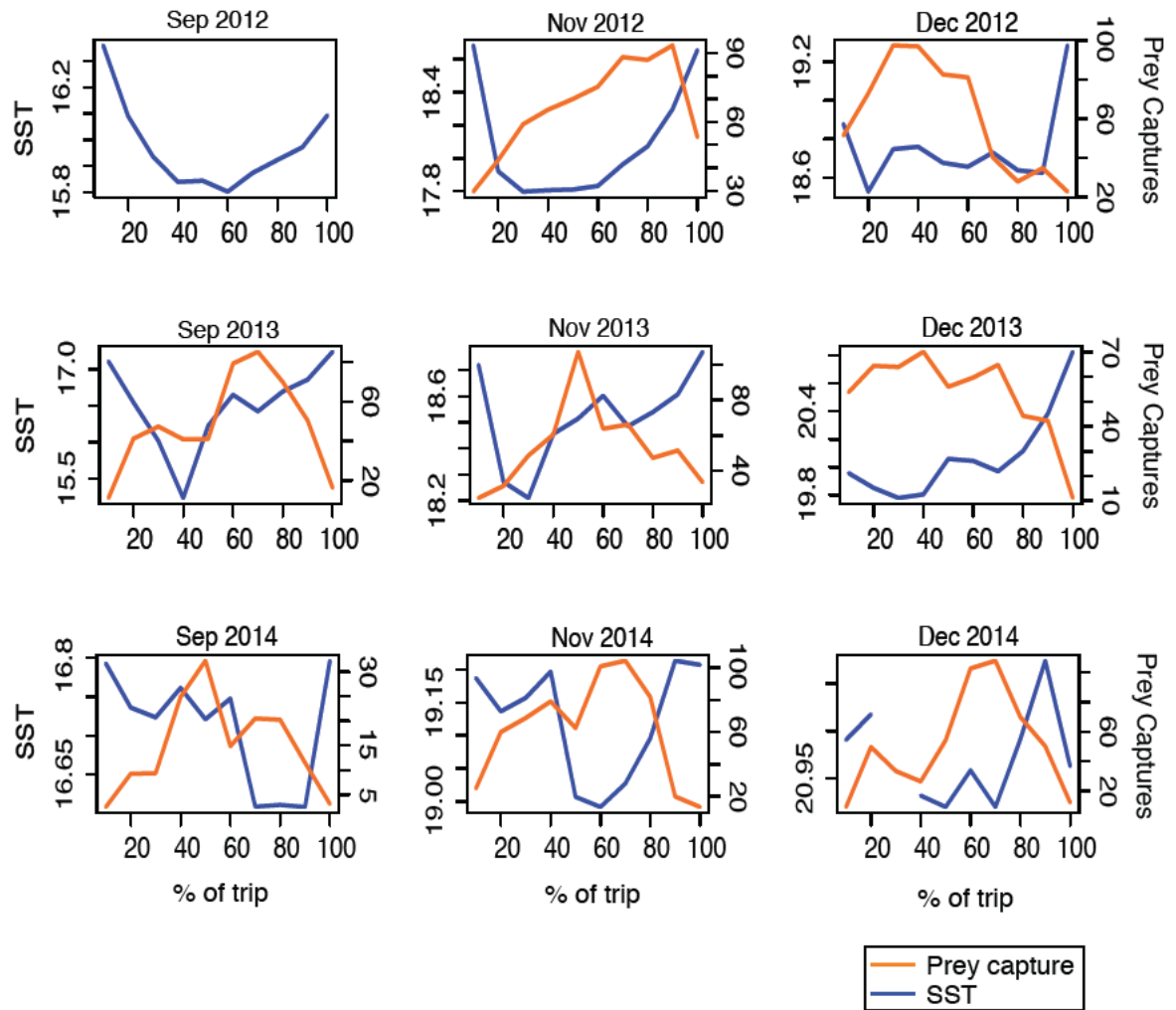


Figure 3.6. SST (blue lines) and prey capture events (orange lines) as a function of time elapsed in a foraging trip (each trip was divided into 10% quantiles). SST values are the mean of the SSTs encountered by all GPS equipped penguins in 1km² grid cells in each 10% interval. Prey capture values are the mean of the number of prey captures recorded by accelerometer and GPS equipped penguins in each 10% interval.

when SST was relatively warm (Figure 3.S6). This was confirmed by a GAM that showed a general increasing trend between offshore SST and distance of prey capture from the colony, which became steepest at temperatures $> 19.5^{\circ}\text{C}$ ($R^2 = 0.46$, $F = 9.602$, $P < 0.0001$) (Figure 3.S7).

3.4 Discussion

Southeast Australia is a hotspot for ocean warming driven by the EAC, with SST rises of 0.7 – 1.4°C predicted by 2030, and 2 – 3°C by 2100 (Ridgway & Hill 2009). To better understand the ecological effects of this strengthening western boundary current, we used accelerometry in conjunction with remotely sensed environmental data to link the foraging success of a marine predator to local SST. We observed a consistent relationship between high SST and low penguin foraging success, both temporally and spatially. These findings may give important insights into resource availability in a changing system, and we discuss them below.

Temporal variability in foraging success

Little penguins feed on a variety of low trophic level species, with “forage fish” e.g. small pelagic fish, squid and krill comprising most of their diet throughout their range (Klomp & Wooller 1988; Deagle et al. 2010). Globally, forage fish are important commercial stocks, and sustain many marine predator populations (Pikitch et al. 2014). These species feed on phytoplankton and zooplankton, the abundance and distribution of which are tightly linked to nutrient upwelling in boundary current systems (Lanz et al. 2009). For example, in southeast Australia where waters are generally nutrient poor, upwelling events driven by wind or the dynamic action of the EAC can enrich coastal waters (Roughan & Middleton 2002). These ephemeral events lead to significantly increased biomass of plankton in upwelling areas (Baird et al. 2006), which forage fish prey on. Forage fish can be highly sensitive to changes in upwelling dynamics and to environmental conditions such as temperature, and their populations can exhibit ‘boom bust’ dynamics (Chavez et al. 2003). Fluctuations in forage fish abundance have in turn been shown to have major effects on the productivity of predators (Cury et al. 2011), including little penguins (Dann et al.

2000).

Although we only studied prey capture by penguins over three breeding seasons, SST during the study period varied substantially around the long term mean, situating our findings within a climatological context. This was due to variable dynamics of the EAC, with unusual spikes of warm water penetrating the region in the spring and summer of 2013 and 2014. We found that a simple but reliable predictor of relative foraging success in November and December was whether SST was high or low relative to the same month in the other study years, with the year with the lowest mean temperatures (2012) having the highest success and the year with the highest mean temperatures (2013) having the lowest (Figure 3.2).

A broad correlation between anomalously high SST and the availability of forage fish is seen in other western boundary current systems. In the Sea of Japan, which is influenced by the warm Kuroshio Current, sardine catches are lowest when SST is high (Yasuda et al. 1999). In the same region, the proportion of anchovy in the diet of rhinoceros auklets was also very low during a period of high SST (Thayer et al. 2008). As well as reducing the abundance of adult fish, high SST is related to higher mortality (Noto & Yasuda 1999) and lower recruitment (Lindegren & Checkley 2012) of juvenile sardines. This suggests a potentially poor outcome for clupeoid fish species and their predators as SST rises in western boundary current regions such as southeast Australia.

Although high SST was inversely related to foraging success on a monthly scale, our modelled data showed that the functional relationship between prey capture success and SST was not linear. At the lowest SSTs, prey capture success was also low. At latitudes around Montague Island ($\sim 36.5^\circ\text{S}$), a major phytoplankton bloom occurs each spring that increases local chlorophyll *a* concentrations by around 150%. This bloom is driven by a seasonal increase in SST, greater availability of dissolved nitrate and silicate, and a shallowing of the mixed layer depth: conditions that promote rapid phytoplankton growth and reproduction (Everett et al. 2014). Reduced prey capture success occurring at low SSTs may therefore represent a period when the water is not

yet warm enough to facilitate the production of high phytoplankton densities, that in turn increase local abundance of planktivorous forage fish (Nevárez Martínez et al. 2001). The timing of this spring bloom is likely to be important for the breeding phenology of predators, and may explain the spring/summer breeding cycle of seabirds and seals in the study area, compared with winter breeding, which is common in western Australia.

Our models suggest an optimal offshore temperature range for prey capture success of 19–21 °C, with lower success outside that range (Figure 3.3). Although the SST values used in this part of the analysis provide a more general index of EAC driven temperatures affecting the shelf rather than conditions in the precise location of penguin foraging, it is notable that this ‘thermal optimum’ mirrors established relationships between sardine (*Sardinops sagax*) catches and SST in the Gulf of California, South Africa and South Australia (Agenbag et al. 2003; O’Donoghue et al. 2010a, Lanz et al. 2009; Doubell et al. 2015). The area around Montague Island is the most northerly summer sardine spawning ground on the east coast of Australia (Thayer et al. 2008), and there is a commercial sardine fishery operating in this region. Catch rates are unavailable for the study period, however landings for the ~110km region of coast incorporating the penguin foraging ground were on average 75 t per month in Sep and Nov, and 10 t per month in Dec between 1984 and 2008 (Stewart et al. 2010). The importance of this area to sardines and their established distribution in relation to SST suggest that the patterns of prey capture success that we identified using accelerometry may reflect processes that govern the local availability of sardines to penguins. Future tracking studies incorporating diet analysis of predators such as seabirds, animal borne video cameras and/or direct sampling of the prey field in relation to environmental conditions would be valuable to provide further insight into the predator-prey relationships in this system.

Our results imply that offshore SST > 21 °C is related to lower prey capture success by penguins breeding on Montague Island. In an average year, these temperatures are not experienced until January, the tail end of the little penguin’s breeding season. However, in anomalous years such as 2013, pulses of warm water arrive earlier and

coincide with the peak chick provisioning period, a time of high energetic demand (Gales & Green 1990). Reduced food availability at crucial times in the breeding cycle is likely to have poor outcomes for breeding success and survival in range restricted species (Oro & Furness 2002; Crawford et al. 2006). A link between high SST and low reproductive success has been established for little penguins in other parts of their range (Hobday 1992; Mickelson et al. 1992; Cannell et al. 2012) and for some other seabird species globally (Inchausti et al. 2003, Frederiksen et al. 2007). Although there was no demographic study on Montague Island running concurrent to this foraging study, and the effect of the observed variation in prey availability on breeding success is therefore unknown, our findings provide some evidence that any future decrease in the fitness of meso predators related to rising SST in the EAC system may be a function of variation in local prey availability.

Spatial variability in foraging location

It is apparent from overlaying tracks on SST anomaly maps and from the hurdle model results that little penguin foraging tends to be focused in habitat with lower SST (Figure 3.4, Table 3.S1). Little penguins are small (~1.1 kg; 40cm in length) and have a limited ability to assess available habitat quality relative to flying seabirds that can cover greater distances and map their environment efficiently from an aerial perspective using visual and olfactory cues (Davoren et al. 2003; Nevitt et al. 2008). It is somewhat surprising therefore, that the penguins in this study appeared to be able to reliably select the coolest habitat for foraging. Across the study period the coolest area around Montague Island tended to be inshore to the southwest, and this was the destination of almost all of the penguins tracked during this study. This persistent oceanographic feature may be influenced by the shape of the coastline at this location, which curves inwards with a prominent headland, perhaps functioning as a trap for cooler water being pushed inshore by the EAC. Heading south from the colony until encountering colder water could therefore be a risk minimising foraging strategy for penguins, if prey abundance is predictably higher in this cooler than average area. Future work characterising the fine scale oceanography in this region may shed light on the local features that enhance productivity and/or concentrate prey in certain areas.

Spatial variability in foraging success

We found a relationship between prey capture success and SST that was not accounted for by habitat preference. Even within the cooler areas that penguins selected for foraging, and in those areas that actually contained prey, the amount of prey caught was related to SST. The coldest areas provided the highest prey capture success, and the warmest areas provided the lowest prey capture success, indicating that prey distribution may be responsive to fine scale SST. An inverse relationship between local forage fish distribution and SST has also been observed in eastern South Africa, where sardines appear to be spatially aggregated in the coolest available habitat, pushed inshore to small patches of suitable habitat by shoreward movement of the warm Agulhas current (O'Donoghue et al. 2010b).

The penguins in this study appeared to consistently forage near the surface (< 10 m). This suggests that the distribution of the prey species that they were targeting was similar throughout the study period, and that the penguins maintain a relatively consistent foraging strategy, even though prey capture success can be highly variable. In previous studies of little penguins (Pelletier et al. 2012) and other diving seabirds (Takahashi et al. 2008), features such as thermoclines have been identified as potential foraging cues. The relationship between the vertical distribution of forage fish and the temperature profile of the water column is generally poorly studied, including in the path of the EAC. However, as the mixed layer depth on the shelf at this time was likely to be around 20 m (CSIRO Atlas of Regional Seas (CARS); <http://www.marine.csiro.au/~dunn/cars2009/>) and there was no evidence of a thermocline from the tag temperature data at the depths at which penguins were catching prey, it seems that whichever prey species the penguins were primarily feeding on during this period were not consistently aggregated around such subsurface features that may be related to EAC dynamics.

Our results suggest a relationship between the distance from the colony at which penguins catch most of their prey and offshore SST, with the highest SSTs being associated with the furthest foraging distances. This was influenced by penguins

travelling unusually far in December 2013 and 2014, when SST was comparatively high. Increases in foraging effort (e.g. distance travelled and dive behaviour) in response to shifts in the location of profitable feeding areas may ultimately affect population dynamics (Bost et al. 2015). We recommend future longitudinal studies mapping the prey field using active acoustics (Boyd et al. 2015), alongside the collection of high resolution *in situ* environmental data. This will shed light on the types and densities of prey in the area at different times, and their fine scale distribution in relation to the environment. Tracking studies of breeding seabirds could assess the 'energy landscape' in the region by estimating spatial gradients of energy expenditure (Wilson et al. 2011) and prey capture success from accelerometry. This could then be related back to fitness metrics such as breeding success, in order to gain more direct insight into how variability in rapidly changing ocean systems such as the EAC may affect the ability of predator populations to be sustained into the future.

3.5 Conclusions

Marine predator populations are vulnerable to reductions in prey availability (Oro & Furness 2002; Crawford et al. 2006) and some forage fish populations are vulnerable to rising SST (Yasuda et al. 1999; Lanz et al. 2009; Noto & Yasuda 1999; Lindegren & Checkley 2012). We have shown that short term variability in SST is related to prey capture success by little penguins, and that future increases in SST driven by a strengthening western boundary current may alter the abundance and distribution of forage fish. By using a prey capture signature to assess the effects of environmental variation on the relative availability of resources, we can direct future research into the way that climate change will affect species at multiple trophic levels.

3.6 Supporting information for Chapter Three

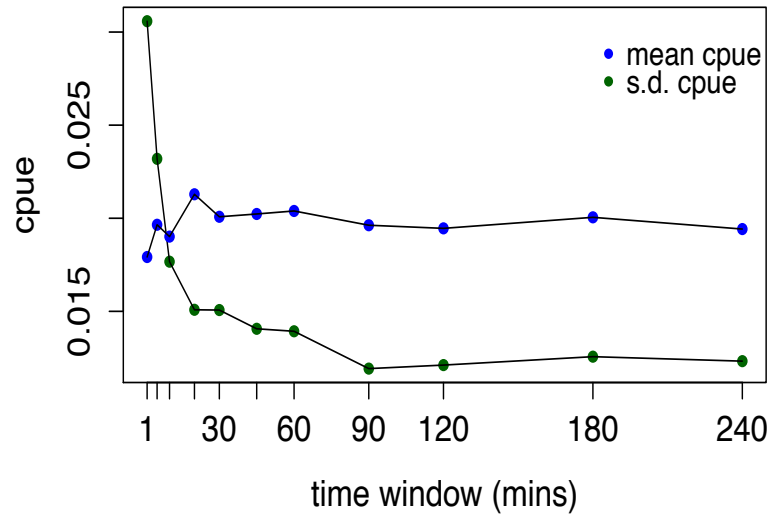


Figure 3.S1. Mean and standard deviation of CPUE data for different time windows pooled across a subset of 8 little penguin foraging trips. 90 minutes was chosen as the most suitable window for binning data, as this showed the lowest variability between periods.

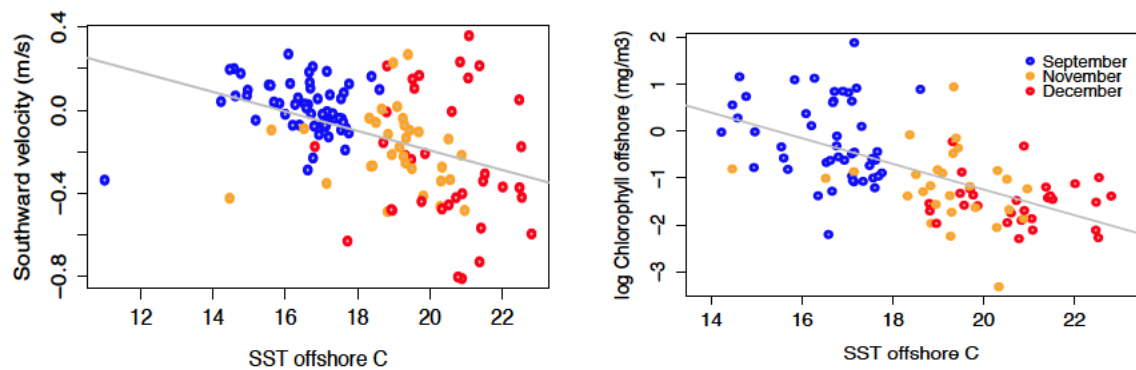
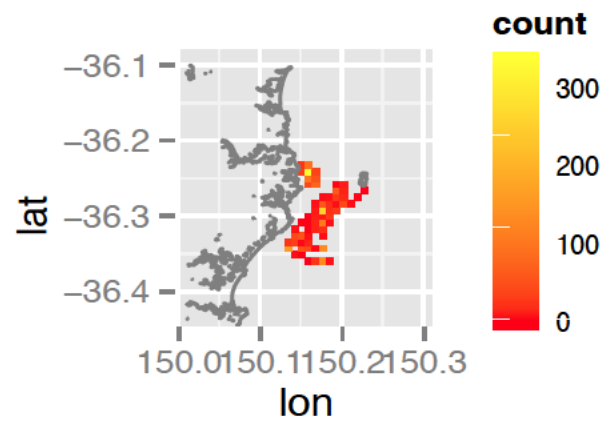
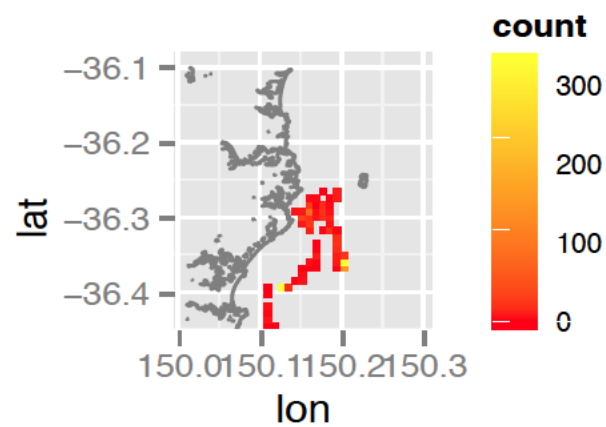


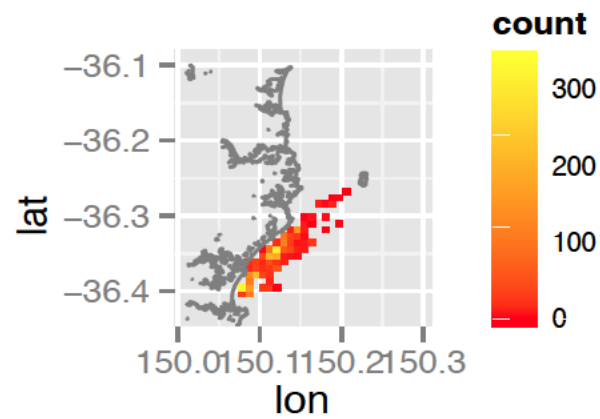
Figure 3.S2. Relationships between southward current velocity & SST measured 5.5 km offshore from Montague Island (left) and log transformed chlorophyll concentrations offshore & SST offshore measured 5.5 km offshore from Montague Island (right)



Sep 2013



Nov 2013



Dec 2013

Figure 3.S3. Map showing prey capture densities in 1km² grid cells during September, November and December 2013.

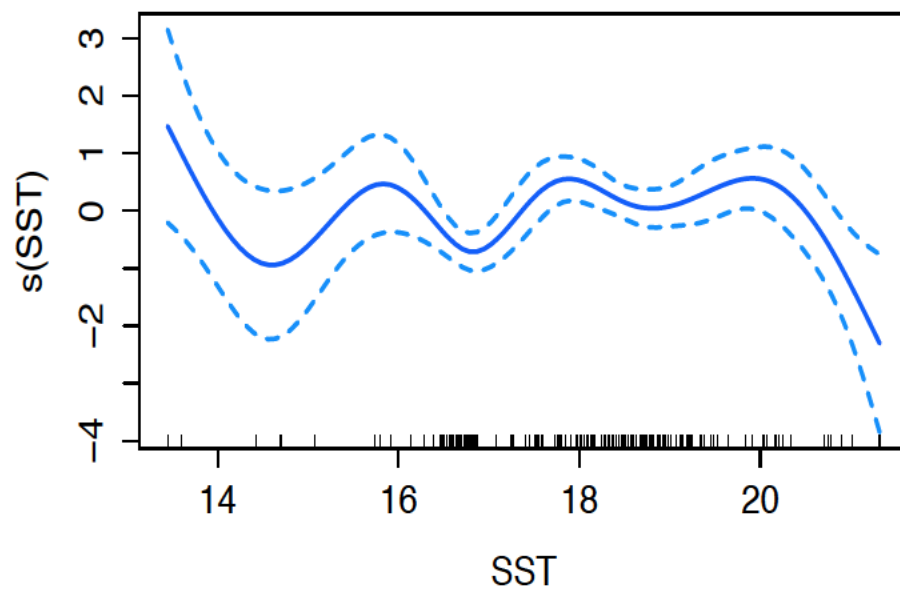


Figure 3.S4. Generalised additive model relationship between the SST in a 1km² cell and the log-transformed number of prey captures in that cell. Only cells in which prey captures were recorded were included in this analysis.

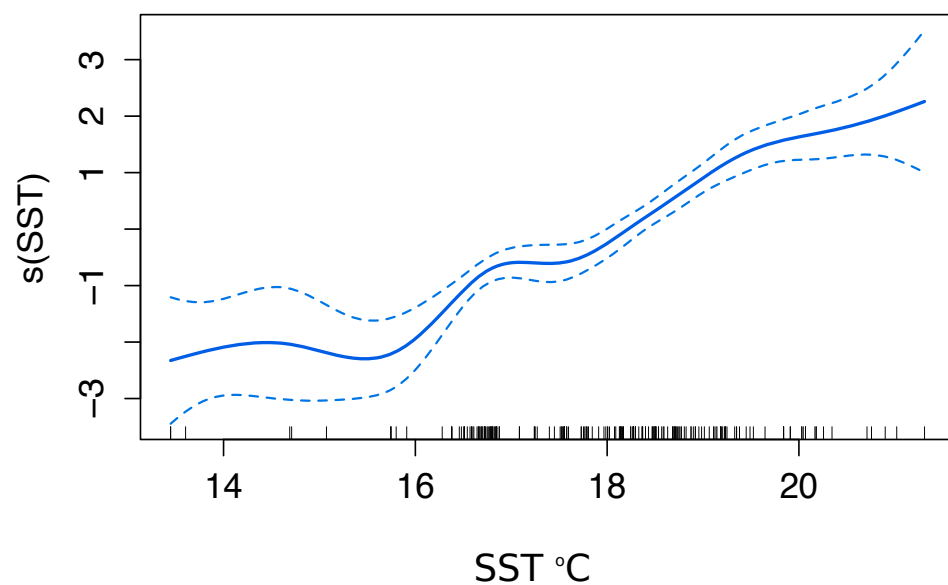


Figure 3.S5. Generalised additive model relationship between the mean SST in a 1 km² grid cell and the mean temperature at which prey capture occurred in that grid cell, taken from the temperature sensor on board the accelerometer tags at the point of prey capture in the water column.

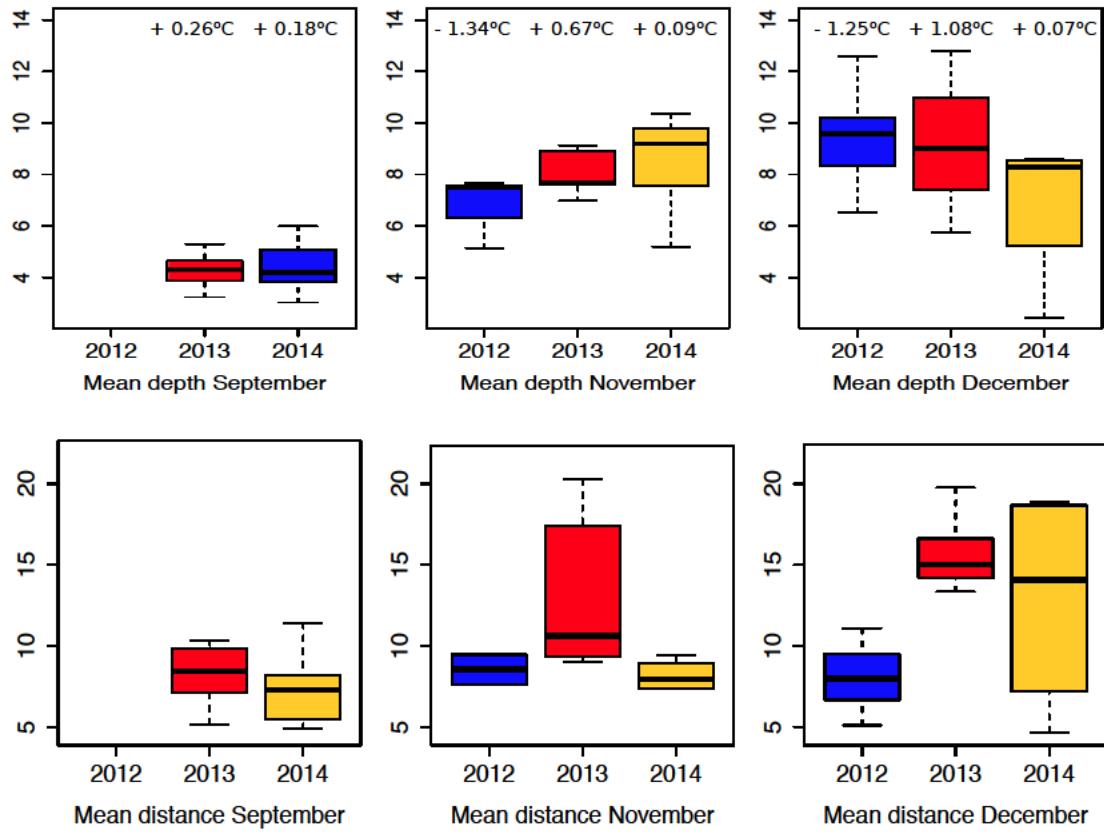


Figure 3.S6. Boxplots showing the mean depth (m) at which prey capture occurred, and the mean distance (km) from the colony at which prey capture occurred. Box plots are coloured according to the SST relative to the mean SST of that month in the other two study years (red being the warmest of the 3 years for each month, blue being the coldest). Sample size and deviation from the mean monthly temperature ($^{\circ}\text{C}$) are noted on the top series of plots.

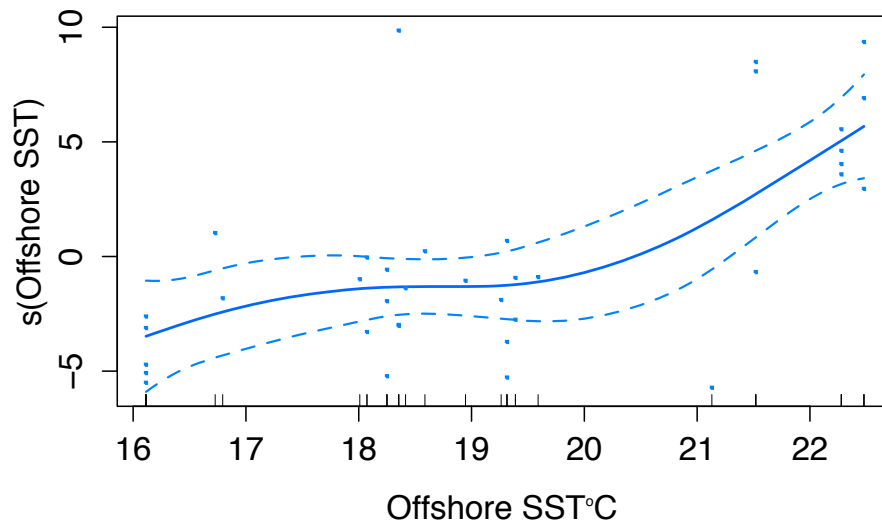


Figure 3.S7. Generalised additive model relationship between SST recorded offshore from Montague Island and the mean distance from the colony at which penguins caught prey.

Count model	Estimate	Std. Error	Z value	P value	AIC	Δ AIC
Intercept	2.30	0.01	178.25	<0.0001	13440	42
SST anomaly	0.01	0.02	0.89	0.37		
Zero model	Estimate	Std. Error	Z value	P value		
Intercept	1.45	0.04	32.45	<0.0001		
SST anomaly	0.50	0.05	9.06	<0.0001		

Count model	Estimate	Std. Error	Z value	P value	AIC	Δ AIC
Intercept	2.21	0.02	114.43	<0.0001	13422	24
SST anomaly bin	0.17	0.02	6.62	<0.0001		
Zero model	Estimate	Std. Error	Z value	P value		
Intercept	1.72	0.06	27.18	<0.0001		
SST anomaly bin	0.66	0.09	7.56	<0.0001		

Table 3.S1. Output from hurdle models describing the distribution of counts (number of penguin GPS locations in 1km² grid cells) and the distribution of zeros (presence vs absence of penguin GPS locations in 1km² grid cells) in relation to sea surface temperature (SST) and SST anomaly (both as a continuous and binary variable) in those cells.

Chapter Four

Hierarchical influences of prey distribution on patterns of prey capture by a marine predator

This paper is published as:

Carroll, G., Cox, M., Harcourt, R., Pitcher, B., Slip, D., Jonsen, I. (2017). 'Hierarchical influences of prey distribution on patterns of prey capture by a marine predator.'

Functional Ecology doi:10.1111/1365_2435.12873

Abstract

Prey distribution acts at multiple spatial scales to influence foraging success by predators. The overall distribution of prey may shape foraging ranges, the distance between patches may influence the ability of predators to detect and move between profitable areas, and individual patch characteristics may affect prey capture efficiency. In this study, we assessed relationships between spatially explicit patterns of prey capture by a central place forager, the little penguin (using GPS tracking and accelerometry), and the distribution of aggregations of potential forage fish prey (using boat based active acoustics) in eastern Australia. We used complementary resource selection functions to estimate the distribution of both prey captures and aggregations across the study area, based on a suite of habitat characteristics. We found that 99% of prey captures by penguins occurred in the top 20 m of the water column. The estimated distribution of prey captures across the study area was similar to the distribution of aggregations above 20 m depth, indicating that penguins effectively matched the local distribution of their prey. The distances between consecutive prey captures followed a bimodal distribution, with means of 8.1 ± 2.2 m and 57.4 ± 1.7 m. Based on the length of aggregations and the distances separating aggregations along survey transects, this implies that foraging behaviour occurs on multiple spatial scales corresponding to within patch and between patch movements respectively. Morphological characteristics of aggregations above 20 m depth were important for explaining variance in the number of prey caught by penguins in an

area, with penguins catching more prey where aggregations were relatively dense, compact and shallow. These results reveal spatially explicit patterns of prey capture, and provide a framework for understanding how features of prey distribution influence prey intake by predators in patchy environments.

4.1 Introduction

In dynamic ecological systems, prey can be distributed hierarchically in space. Dense aggregations of individual prey items are clustered and nested within patches of lower prey density, that are in turn separated by areas where prey is scarce (Hassell & Southwood, 1978; Kotliar & Wiens 1990, Wu & Loucks 1995; Fauchald et al. 2000). In these systems, predators may use hierarchical foraging tactics, employing search patterns that maximise their chance of encountering aggregations of prey across patchy landscapes (Bartumeus et al. 2005; Sims et al. 2006b), then using features of aggregations at finer scales to maximise rates of prey consumption (Wellenreuther & Connell, 2002). Understanding the nature of these scale dependent predator prey interactions provides insight into the specific ways that predator foraging traits are a response to the selective pressures exerted by patterns of variability in their environment.

In the open ocean, resources follow a hierarchical, patchy distribution in three dimensions (Fauchald et al. 2000). The pelagic environment can be highly dynamic, necessitating the evolution of predator foraging strategies that account for variability in resource distribution at different scales (e.g. Weimerskirch et al. 2005a; Sommerfeld et al. 2015). Despite the importance of these prey field characteristics to understanding drivers of fitness and behaviour in marine predators, rarely are studies of marine predator foraging ecology able to combine simultaneous, independent estimates of prey distribution and *in situ* foraging success. This is because it is difficult to measure prey distribution at spatial and temporal scales that are relevant for wide ranging marine animals, and because measuring prey intake by predators at sea is challenging (Watanabe & Takahashi 2013).

One result of these challenges is that characteristics of the movement of marine predators at sea are often used as proxies for prey encounter (Jonsen et al. 2005; Ropert Coudert et al. 2006b). However, functional relationships between predator foraging movements and the underlying abundance and distribution of prey are not straightforward. For example, in some cases where prey distribution has been independently assessed alongside marine predator foraging movements there is a spatial mismatch between where predators forage and where the highest density of prey was observed (Grémillet et al. 2008; Benoit Bird et al. 2013a, Boyd et al. 2015). As in the terrestrial realm (Hopcraft et al. 2005; Fuller, Harrison & Vashon, 2007), accessibility of prey appears to be an important driver of marine predator foraging. Proximity to the breeding colony (for central place foragers; Grémillet et al. 2008), prey depth (Boyd et al. 2015; Friedlaender et al. 2016b) and patch density (Benoit Bird et al. 2013a) have been shown to be important predictors of foraging behaviour. However, the specific ways that these features of prey distribution influence prey consumption often remain unclear.

In this study, we examined relationships between prey distribution and spatially explicit patterns of prey capture by a marine predator, the little penguin (*Eudyptula minor*). To do this, we used active acoustics to identify and describe aggregations of potential prey (primarily small pelagic fish such as sardines and Australian sprat; Bester 1997) within the penguins' single day foraging range. In tandem with these estimates of prey distribution, we combined GPS tracking and a prey capture signature derived from accelerometry (Carroll et al. 2014) to assess where penguins caught prey.

We pose the following questions: 1) How closely matched is the distribution of prey captures with the distribution of prey? 2) Does distance between consecutive prey captures mirror the spatial scales of prey patchiness? 3) Are there characteristics of individual aggregations that enhance prey consumption? By addressing these questions, we hope to clarify functional relationships between prey distribution and foraging success at nested spatial scales.

4.2 Materials and Methods

Penguin tracking

The tracking study was conducted on Montague Island (36.253° S, 150.227° E), 9 km off the southeast coast of New South Wales, Australia over three days from the 30th September to the 2nd October 2015. The study was designed to coincide with the peak of the period when little penguins were brooding small chicks (< 2 weeks old). During this time, one parent stays behind to guard the chicks, while the other goes to sea for a single day foraging trip, returning after sunset.

Penguins performing single day trips are restricted to foraging within a maximum distance of approximately 25 km from the colony. By tracking only birds at this breeding stage, we were able to conduct the acoustic survey over a relatively small area, and remove the effect of differential habitat selection strategies caused by the different foraging ranges and energetic requirements of birds at different breeding stages (Gales & Green, 1990). The short temporal window of the field study (three days) also reduced unmeasured effects of environmental variability on prey distribution and penguin foraging behaviour.

The night before a penguin went to sea it was caught in its nest box, weighed in a calico bag using a spring balance scale (Pesola, AG Switzerland) and equipped with a GPS logger (CatTrack, South Carolina, USA) modified with epoxy resin to withstand pressure at depth. The loggers were inserted into waterproof heat shrink tubing, then attached to feathers on the lower back with cloth tape (Tesa, Hamburg, Germany), positioned to reduce drag but not impede tail movement. These tags were 43 mm in length, 27 mm in width and 13 mm in height, and weighed 55 g in air and 17.4 g in seawater. Tags were programmed to record a location every 15 s.

Accelerometer data loggers (G6a+, CEFAS Technology Pty Ltd, Suffolk, UK) were then attached immediately anterior of the GPS units on the middle back. These tags were 40 mm in length, 28 mm in width and 15 mm in height, and weighed 7.8 g in air and 2.3 g in seawater. The accelerometers recorded acceleration in 3 axes: anterior

posterior (surging), lateral (swaying) and dorso ventral (heaving) with a range of ± 2 g. The accelerometers recorded depth, temperature and acceleration and were programmed in two modes: “shallow” mode (<1.5 m: 1.5% of the full scale pressure range) where variables were recorded every 10 seconds, and “dive” mode (>1.5 m) where the same variables were recorded at 30 Hz.

When penguins returned from a foraging trip they were recaptured in their nest boxes, loggers were removed and the penguin was reweighed. Combined tag weight for penguins that were equipped with both accelerometers and GPS was 62 g in air, which was $< 6\%$ of mean bodyweight ($1060 \text{ g} \pm 89 \text{ s.d.}$ in this study). Handling time was kept to a minimum, and in most cases was < 5 min for both deployment and retrieval of devices. Penguins during this study were only handled twice, once for deployment and once for removal of devices to minimise stress associated with handling (Carroll et al. 2016b). All animal research protocols were carried out in accordance with guidelines approved by the Macquarie University Animal Ethics Committee (Animal Research Authority 2014/057).

Prey capture signature

We previously developed a model to identify a movement signature associated with prey capture by penguins at sea, using a support vector machine algorithm that identified prey handling by wild penguins with a false positive rate of 0.09 % (Carroll et al. 2014).

Prey captures were assigned a location by matching their time signature to those of GPS tracks after linear interpolation to a 1 s resolution. To remove prey captures with a substantial degree of uncertainty surrounding their location, we removed all interpolated prey capture positions that occurred during gaps in the GPS record > 5 min. This corresponded to only 8% of the total number of prey captures, indicating that lengthy gaps when the GPS units do not record locations may generally reflect periods when the penguins are travelling between locations, rather than when they are spending a lot of time submerged during active foraging.

Active acoustic data collection and processing

We conducted an acoustic survey of the region around Montague Island over the same three days as we tracked penguins (30th September to the 2nd October 2015). The survey was undertaken from a 6 m rigid hulled inflatable vessel travelling at 4 knots. We surveyed seven cross shelf transects (a total of 84.4 km) spaced 3.5 km apart, spanning a total of 25 km north to south along the continental shelf. The survey encompassed an area where penguins typically forage during single day trips (inshore to the southwest of the island), as well as areas further offshore where penguins are observed foraging less frequently (see Carroll et al. 2016a, Fig. 4).

A calibrated Simrad EK80 scientific echosounder operating at 70 kHz in continuous wave mode was mounted on a pole connected to the vessel via a retractable arm (depth = 0.75 m). The split beam transducer's beam width was 18°, the transmit power was 280 W and had a 1.024 ms pulse duration and a 2 Hz ping rate (See Table 4.S1 for calibration parameters).

Acoustic data were processed using Echoview v7 (Echoview, Hobart, Australia). Seabed returns and surface noise were removed from the acoustic data prior to echo integration, being put on a grid of dimensions 50 pings along transect by 5 m deep with a 80 dB re 1 m⁻¹ minimum integration threshold. Aggregations were isolated from the acoustic record by applying the SHAPES algorithm implemented in the 'Schools Detection' module of Echoview v7.0 to a 3 x 3 identity matrix convolution of the processed acoustic data. The minimum detection threshold was 65 dB re 1 m⁻¹ (Diner 2001), and schools detection parameters (Table 4.S2). School descriptor bias was minimised by ensuring that the relative school image with respect to beam shape was greater than 1.5 for all aggregations (Diner 2001).

A measure of aggregation density was described using the line backscatter coefficient, s_L (units = m) which is a measure of total acoustic echo strength integrated over a portion of the transect. s_L was calculated as:

$$s_L = \int \int_A s_v dx dz$$

where, A is the area of the aggregation and s_v is the volume backscatter coefficient (see MacLennan, Fernandes & Dalen 2002).

Aggregations were described using the approach of Reid et al. (2000), and the following aggregation morphological metrics were calculated: depth (to top of aggregation), length (along the transect), and height. Aggregation morphology metrics were corrected for transducer beam pattern effect (Diner 2001).

We were unable to undertake trawl or video work to identify aggregations to species level during the survey, although *in situ* observations of surface aggregations were all of small forage fish likely to be suitable penguin prey. A systematic video survey undertaken during the same period in 2016 identified all observed aggregations < 20 m as being small forage fish including sardines and mackerel (Carroll et al. unpublished data).

Environmental variables

We used observed relationships with environmental variables to estimate the distributions of both aggregations of potential prey and prey capture by penguins across the study area. We obtained static variables such as seabed depth (Geosciences Australia, 250 m x 250 m resolution), distance from the coast and distance from Montague Island as well as satellite derived measures of sea surface temperature (SST) and chlorophyll a averaged over the three survey days at a resolution of $0.01^\circ \times 0.01^\circ$ (<http://imos.aodn.org.au/imos/>). In addition, we used *in situ* conductivity, temperature and depth (CTD) measurements taken along the transects during the survey by lowering a CTD unit (CastAway CTD, Sontek, San Diego, CA) on a 30 m line at sampling stations 3.5 km apart. We used the mean salinity at 0 to 0.5 m, and the mean temperature and salinity at 5 to 10 m, 10 to 15 m, 15 to 20 m and 20 to 25 m. These environmental variables were measured at different locations and at different spatial

resolutions, and were not available for the precise locations where animals were observed. We therefore used a geostatistical interpolation approach called ordinary kriging that uses spatial correlation to estimate trends in environmental variables across a surface (Cressie 1988). We employed this method to smooth environmental predictors onto a 250 x 250 m prediction grid that covered the study area using the R package *gstat*, with automated variogram fitting (Pebesma 2004). An example of *in situ* observations, interpolation and spatially explicit variance are presented in Figure 4.S1.

Data analysis

Resource selection function – penguin prey captures

We estimated the spatially explicit probability of prey capture by penguins using a resource selection function. Although resource selection functions are generally used in telemetry studies to describe habitat selection by animals (Aarts et al. 2008), we use this approach here to understand the occurrence of a specific behaviour (prey capture) rather than the occurrence of the animals themselves (e.g. Abrahms et al. 2015). This approach allows us to examine which combinations of environmental variables describe the locations where penguins caught prey, and generate predictions of the distribution of prey captures across the study area, accounting for the fact that not all penguins in the greater population were tracked. We used the location of prey captures as presence points and selected twice this number of pseudo absence points, i.e. points drawn randomly from across the study area that sample the range of environmental conditions in which prey capture could have occurred. To account for complex, non linear relationships between prey capture and the environment, we used a generalized additive model (GAM) framework with a binomial distribution using the R package *mgcv* (Wood, 2011). To account for biases in sampling effort toward data rich individuals, and to reduce the effect of serial autocorrelation in consecutive presence point locations by an individual penguin, we fitted models with individual as a random effect. We also included a random effect term for sex of the penguin.

We assigned both presence and pseudo absence points the values of environmental variables drawn from the closest point on the 250 m x 250 m prediction grid. Some environmental variables were highly correlated as they varied spatially over similar gradients. To reduce the worst effects of multicollinearity (or concurvity, the equivalent phenomenon in the GAM framework) on the precision of standard errors (Fox 1997), we performed variable selection before model fitting. We removed candidate covariates one at a time until variance inflation factors for the suite of variables were below 10, and Spearman's correlation coefficients were below 0.80 (Berry & Feldman 1985). Although there was some collinearity remaining in the data, we opted not to reduce the candidate variable set further, as the primary goal of this analysis was to accurately interpolate and compare the distribution of prey captures and aggregations within the study area during the survey period, not to extrapolate beyond the extent of our data into novel conditions (Elith & Leathwick 2009). The variables retained were: distance from Montague Island, distance from the coast, SST, chlorophyll *a*, salinity in the top 0.5 m, salinity at 10 to 15 m and temperature at 15 to 20 m. We also included an isotropic surface smooth over two variables: distance to coast and distance to Montague Island. As well as being a spatially explicit term that is likely to reduce the probability of spatial autocorrelation due to unmeasured variables being omitted from the model, it also created a proxy for differential accessibility of areas of the foraging range to penguins (Aarts et al. 2008).

Models were fitted using maximum likelihood estimation (ML), then the best model was determined by Akaike's Information Criterion (AIC). We used a receiver operating characteristic (ROC) to calculate an area under the curve (AUC) as a means of testing the performance of the model in predicting the occurrence of prey capture (Boyce et al. 2002).

Resource selection function – aggregations

We used a similar approach to estimate the distribution of aggregations across the study area. As aggregations were in most cases much shorter than the 250 m scale of the environmental data, we used only the centre coordinate of each aggregation as 'presence' points in our models to avoid pseudo replication. Due to the relative

scarcity of aggregations compared with the absence points generated during the acoustic survey, using all observed absence points in the models would have resulted in substantial zero inflation. We therefore chose ten times the number of presence points randomly from regions along the transects outside the boundaries of aggregations as ‘absence’ points. To examine robustness to the selection of these points, we refitted models 1000 times with different subsets of absences. Each presence and absence point along the transect was associated with the same reduced set of environmental variables as used in the penguin analysis (distance from Montague Island, distance from the coast, SST, chlorophyll a , salinity in the top 0.5 m, salinity at 10 to 15 m and temperature at 15 to 20 m), by assigning it the smoothed values corresponding to the closest cell on the 250 m x 250 m prediction grid. We used GAMs with binomial distributions to find the relationship between the incidence of aggregations and environmental features. Models containing different combinations of candidate covariates were compared using AIC. We generated the mean predicted probability of aggregation presence over 1000 runs of the best model for the 250 m x 250 m prediction grid encompassing the study area and calculated the median AUC over 1000 model runs to test how well the best model fit the observations.

Similarity between distributions

To compare the interpolated distribution of prey captures by penguins with the interpolated presence of aggregations, we calculated a Spearman’s correlation coefficient between paired aggregation and prey capture maps, and used a quantile quantile plot to assess the similarity in distributions.

Scales of foraging in relation to aggregation distribution

To determine the spatial scales at which penguin foraging occurs in relation to aggregation size and patchiness, we fitted a finite Gaussian mixture model using the R package *mclust* (Fraley et al. 2002) to the distances separating consecutive prey captures by penguins. This process iteratively fit different mixtures of normal distributions to these prey capture step lengths, and used the Bayesian information criterion (BIC) to determine which combination of distributions best described

modality in the frequency distribution. We then compared the distributions of distances separating prey captures with the distributions of aggregation lengths and the distances between neighbouring aggregations, in order to determine whether scales of foraging movements could represent within patch and between patch movements.

Aggregation characteristics

To determine the relationship between the number of prey caught by penguins and aggregation characteristics, we divided each transect into segments and calculated mean morphological and density metrics (height, length, depth to aggregation top and acoustic density (sL)) for aggregations in each section. We then related these values to the number of prey caught by penguins in proximity to each segment. As this analysis was likely to be sensitive to the size of the areas chosen, we ran models for segments of 250 m, 500 m, 1 km and 2 km along the transect, and for prey captures observed within distances of 150 m, 250 m, 500 m and 1 km either side of the transect. We fitted generalized linear models (GLMs) with Poisson error distributions, and determined the best model for each of the 16 possible spatial scales using AIC. We then compared the adjusted deviance explained by each of these best models to determine which spatial scale showed the strongest relationships between aggregation characteristics and the number of nearby prey captures.

4.3 Results

Resource selection function – penguin prey capture

After removing prey captures occurring in gaps of > 5 min in the GPS data, 9199 prey capture locations from foraging trips by 20 penguins (11 females, 9 males) were used in the resource selection function (Figure 4.1A). These prey captures were most common close to shore in inner continental shelf waters (0 to 60 m depth) but also occurred further offshore in the deeper middle shelf zone (60 to 130 m depth). While some prey captures occurred on the inshore edge of the warm, saline East Australian Current water mass (Suthers et al. 2011), the current appeared to restrict the penguins' movements offshore.

The best model describing penguin prey captures as determined by AIC contained a smooth of distance from the coast and distance from Montague Island, as well as smoothed terms for SST, chlorophyll *a*, salinity at 0 to 0.5 m, salinity at 10 to 15 m, temperature at 15 to 20 m, and a random effect term for penguin ID (Table 4.1). Upon examination, the number of knots was constrained to 10 for each smooth, and 30 for the isotropic smooth of distance from the coast and distance from Montague Island. These smoothing parameters were decided upon as we wished to use broad relationships between occurrence and the environment for prediction, rather than overfitting to the observations. The random effect term increased the deviance explained by the model by only 2%, indicating that while individual differences contributed to habitat preference, the environment was more important (Table 4.S3). The sex term did not significantly improve the model, suggesting no spatial niche partitioning between male and female penguins. Spatially explicit probabilities of prey capture occurrence from this model are shown in Figure 4.2A, estimated from the fixed effects. The adjusted R^2 of the best model was 0.58 and the AUC was 0.94, indicating a good fit to the data.

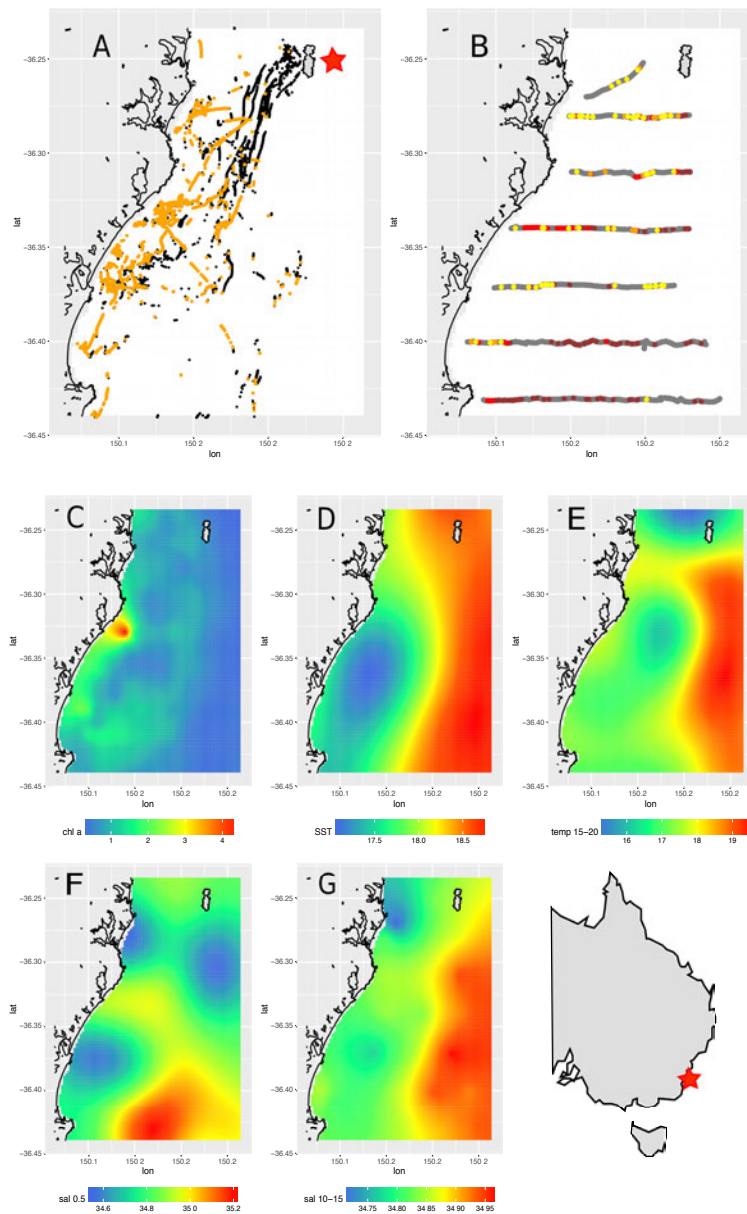


Figure 4.1. A) GPS tracks from 20 little penguins performing single day foraging trips during brooding, with prey capture locations indicated in orange. B) Acoustic survey transects (dark grey) with the locations of aggregations < 10 m (yellow), < 20 m (orange), < 30 m (red), and > 30 m (maroon). C – G) Interpolated environmental variables (chlorophyll *a*, sea surface temperature, temperature at 15–20 m, salinity in the top 0.5 m and salinity at 10–15 m) used in resource selection functions. The red star denotes the location of Montague Island, NSW, Australia.

Smooth term	EDF	Chi sq	p-value
Distance to Montague, distance to coast	28.38	2423.9	< 0.0001
Chl <i>a</i>	8.11	183.4	< 0.0001
SST	8.92	333.3	< 0.0001
Temperature 15 – 20 m	8.12	390.7	< 0.0001
Salinity 0 – 0.5 m	8.70	397.1	< 0.0001
Salinity 10 – 15 m	8.61	575.8	< 0.0001
Random effect (penguin id)	18.40	465.9	< 0.0001
Deviance explained = 58 % AUC = 0.94			

Table 4.1. Summary of the best binomial generalised additive mixed model estimating the relationship between the occurrence of prey capture by penguins and features of the environment. Shown are the estimated degrees of freedom (EDF), chi square and p values for each environmental parameter, as well as the percent deviance explained and area under the curve as measures of model performance.

Resource selection function – aggregations

On the acoustic transects we observed 238 aggregations, ranging in depth from 1.7 m to 119.0 m at their top (mean depth at top = 15 ± 0.8 m). Of these 238 aggregations, 63 (26%) were in the top 10 m, 92 (39%) were in the top 20 m and 144 (61%) were in the top 30 m of the water column (Figure 4.1B). As 99% of prey captures by penguins occurred in the top 20 m of the water column (mean depth = 7.4 ± 0.04 m, max depth = 32.0 m), we focus on describing aggregations that were above 20 m depth at their top. Aggregations < 20 m depth occurred most often inshore, but also along the inner margin of the warm, saline East Australian Current water mass. No aggregations < 20 m were observed where water was warmest, in the offshore portion of the study area.

The best model for predicting the incidence of aggregations < 20 m depth contained a smooth of distance from the coast and distance from Montague Island, as well as smoothed terms for SST, chlorophyll *a*, salinity at 0 to 0.5 m, salinity at 10 to 15 m and temperature at 15 to 20 m (Table 4.S4) although not all these variables were significant in all model runs (Table 4.2). The number of knots was constrained to 10 for each smooth, and 30 for the isotropic smooth of distance from the coast and distance from Montague Island. Over 1000 runs, the best GAM had a median deviance explained of 41.3 % and a median AUC of 0.92, indicating a good fit to the data. A mean of 1000 predictions for aggregation occurrence using different subsets of absence points is presented in Figure 4.2B; standard errors of predictions from these 1000 runs are presented in Figure 4.S2.

Smooth term	Median EDF	Median Chi sq	% significant
Distance to Montague, distance to coast	27.03	44.54	77 %
Chlorophyll <i>a</i>	1.00	0.33	2 %
Sea surface temperature	4.68	13.36	61 %
Temperature 15 – 20 m	6.95	18.08	69 %
Salinity 0 – 0.5 m	3.78	4.71	17 %
Salinity 10 – 15 m	8.66	19.01	68 %
Median deviance explained = 41 % Median AUC = 0.92			

Table 4.2. Summary of the best binomial generalised additive model estimating the relationship between the occurrence of aggregations of potential penguin prey and the environment. The best model was run 1000 times with different subsets of absence points, shown are median values for estimated degrees of freedom (EDF) and chi square values over 1000 model runs, and the percent of runs where each environmental parameter was significant at $p < 0.05$. Median deviance explained and area under the curve values over 1000 runs are presented as measures of model performance.

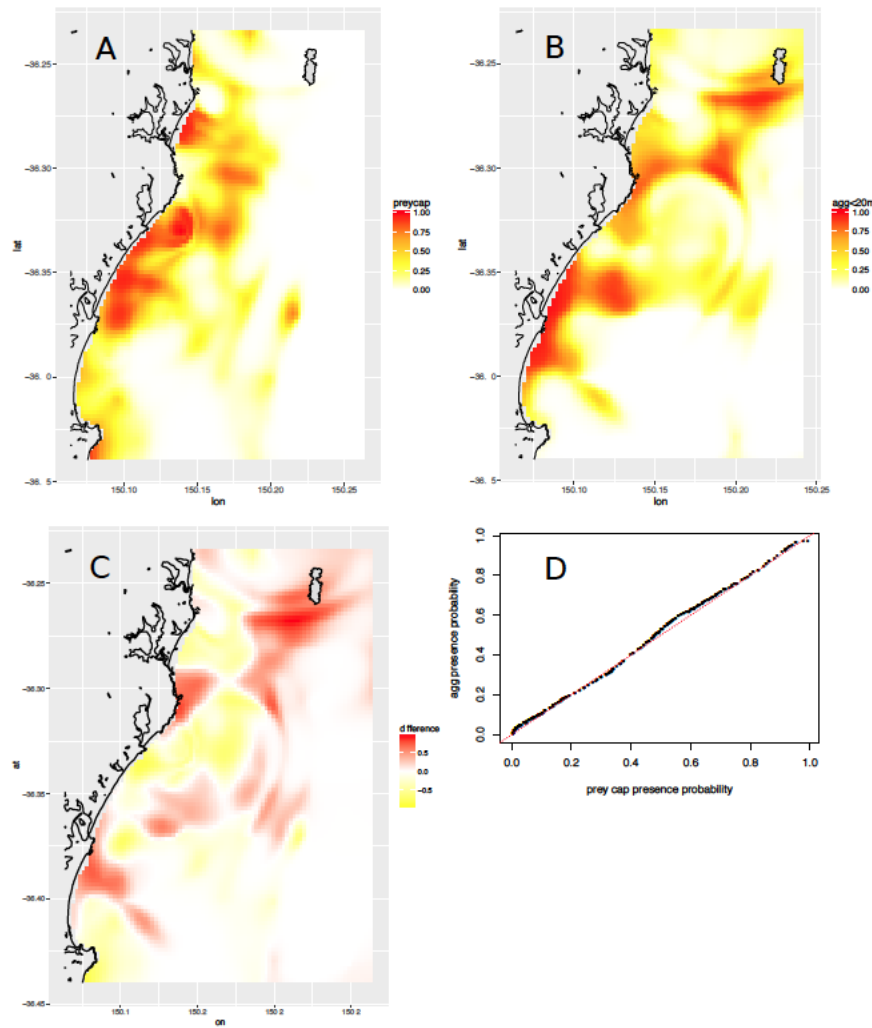


Figure 4.2. A) Spatially explicit probability of prey capture by penguins, based on the relationship between the incidence of prey captures and environmental variables. B) Spatially explicit probability of the incidence of aggregations < 20 m, based on the relationship between the incidence of aggregations and environmental variables. C) Difference in probability of aggregation presence < 20 m depth and probability of prey capture by penguins. Red areas are where aggregations were more likely to occur than prey captures, yellow areas are where prey capture was more likely than aggregations, white areas are where differences are close to zero. D) Quantile quantile plot of the probabilities of aggregation presence and prey capture presence. The red dashed line denotes a hypothetical 1:1 relationship

Similarity between distributions

The predicted spatial distributions of aggregations < 20 m depth and prey captures by penguins had a Spearman's correlation coefficient of 0.50. A quantile quantile plot of the paired probabilities showed close agreement between the two distributions, with the probability of aggregation presence tending to be slightly higher than the probability of prey capture presence in a given area (Figure 4.2D).

Scales of foraging in relation to aggregation distribution

The horizontal distance separating consecutive prey captures had a bimodal distribution, indicating that foraging movements occurred at two spatial scales with means (\pm s.d.) of 8.1 ± 2.2 m and 57.4 ± 1.7 m (Figure 4.3). The first scale was considerably shorter than mean aggregation length (19 ± 2 m), indicating that this likely relates to within patch foraging movements. The second scale was larger than almost all aggregations, indicating that this may represent between patch movements. As penguins occasionally caught prey on the outward or homeward portion of the trip near Montague Island, there were sometimes very large distances separating consecutive prey captures (max distance = 16.2 km). Due to underlying assumptions of normality, the best Gaussian mixture model described these data by classifying distances into three distributions, with the third class accounting for the very large step lengths (mean = 124.0 ± 4.5 m).

Aggregation characteristics

The characteristics of aggregations that were important for determining the number of prey captures were acoustic line backscatter coefficient (S_L), depth to the top of the aggregation and aggregation height (Table 4.3). The best model included these variables and considered the number of prey caught within an area 500 m along the transect by 250 m either side of the transect. Penguins caught more prey where nearby aggregations had a higher line backscatter coefficient (higher relative internal density) and less prey where aggregations were deeper and of greater height in the water column. The adjusted deviance explained of the best model was 0.42.

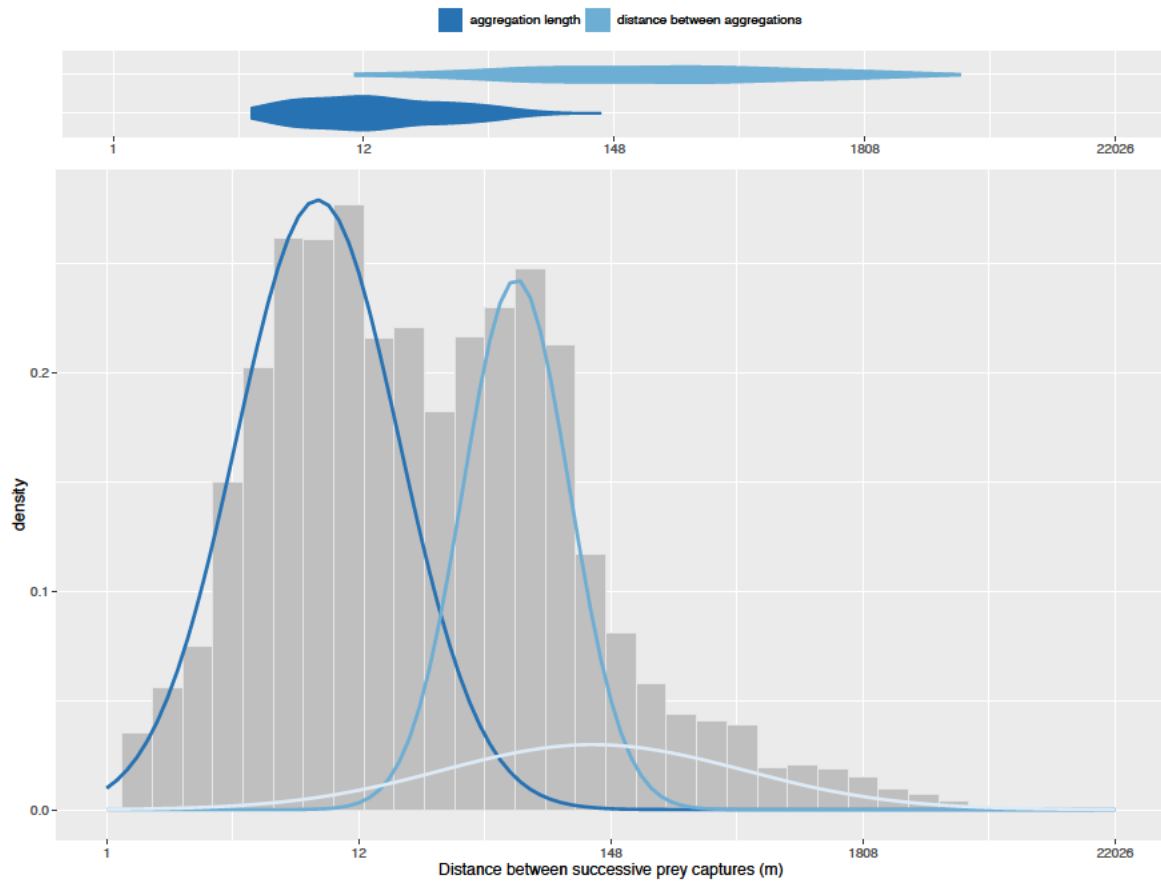


Figure 4.3. Gaussian finite mixture model describing the distribution of step lengths separating consecutive prey captures. The best model identified three classes of step lengths, with mean (\pm s.d.) of 8.1 ± 2.2 m, 57.4 ± 1.7 m, and 124.0 ± 4.5 m. The distribution of aggregation lengths and distances separating aggregations are shown at the top of the figure as violin plots.

	Estimate	Std. Error	z value	p value
Intercept	0.07	0.14	0.50	0.62
Mean line backscatter coefficient (relative internal density)	0.15	0.04	4.10	< 0.0001
Mean depth to aggregation top	2.81	0.14	20.76	< 0.0001
Mean aggregation height	0.83	0.08	9.95	< 0.0001

Table 4.3. Poisson generalised linear model summary showing the relationship between the number of prey caught by penguins and characteristics of nearby aggregations. Prey captures occurred within an area 250 m either side of 500 m transect segments. Aggregation characteristics are the mean of all aggregations observed in each segment above 20 m depth; values were mean centred and scaled by their standard deviations to assess their relative importance.

4.4 Discussion

We incorporated an index of feeding activity by a predator with contemporaneous, independent measures of prey occurrence. Our results show that prey distribution acts at multiple, nested spatial scales to influence *in situ* foraging success. First, prey capture events overlapped spatially with the distribution of prey, with both related in similar ways to the environment. Second, aggregation size and the scale of aggregation patchiness was reflected in the distances between consecutive prey captures. Third, characteristics of individual aggregations (short length, shallow depth and high density) enhanced prey consumption.

The ability for animals to match the overall distribution of prey within their foraging range is related to their ability to efficiently detect and access prey across the landscape. Prey accessibility is an important predictor of foraging activity in marine and terrestrial predators (Butler & Gillings, 2004; Hopcraft et al. 2005; Wilson et al. 2005; Boyd et al. 2015). In marine systems, the depth of prey is an important component of its accessibility, particularly to air breathing marine predators such as seabirds that are physiologically constrained in their ability to access prey at depth (e.g. Sala et al. 2015). In this study, penguins preferentially targeted relatively shallow, accessible prey < 20 m depth despite being capable of deeper dives (Robert Coudert et al. 2006a) and despite the availability of deeper aggregations. This suggests a trade off between the potential energy gains provided by prey resources, and the costs of accessing them. Such trade offs can drive prey selection, and result in different behavioural responses to the same prey when encountered by a predator under conditions conferring different physiological constraints (Hazen et al. 2015).

Relationships between prey distribution and the environment are likely to regulate the availability of prey to predators (Butler & Gillings, 2004). For example, features of the environment that promote prey occurrence in the top part of the water column are likely to drive foraging distribution by near surface feeding marine predators (Boyd et al. 2015). We found an agreement between the spatial distribution of aggregations above 20 m depth and the location of prey captures by penguins, when

we estimated both distributions using complementary resource selection functions. The similarity between these predictions is driven by the underlying environmental niches that both sets of observations occupied (Elith & Leathwick 2009), with features of the East Australian Current water mass such as high water temperatures, high salinity and low chlorophyll *a* (Suthers et al. 2011) providing non preferred habitat. The small pelagic fish such as sardines (*Sardinops sagax*) that little penguins primarily feed on (Bester 1997; Sutton, Hoskins & Arnould 2015), and which are dominant in this study area (Stewart et al. 2010), are known to be highly responsive to the physical environment (e.g. Nevarez Martinez et al. 2001; Agenbag et al. 2003). Our study provides evidence that habitat selection by predators in dynamic environments is coupled with the environmental preferences of their prey (e.g. Carroll et al. 2016a).

The distribution of distances between prey capture events provides direct information on the spatial scales at which predators find and consume prey (Adachi et al. 2016; Weimerskirch et al. 2005). In our study, the distances separating consecutive prey captures had a bimodal distribution, reflecting two main scales of foraging displacement. The larger scale (mean 57.4 m), was likely to correspond to between patch movements. These displacements were larger than most single aggregations, yet reflected relatively short distances separating neighbouring aggregations. This suggests that penguins were able to detect and move between neighbouring prey patches most easily in areas where they were clustered together. This may reflect the distance over which they can perceive prey using visual or olfactory cues (e.g. Nevitt et al. 2008). However, some predators have been shown to enhance the probability of detecting prey by employing movement characteristics that approximate the structure of prey organisation (Turchin 1998, Fauchald 1999, Sims et al. 2006b; Benoit Bird et al. 2013b). Theoretically, in hierarchical systems, predators engage in large, directed movements until they encounter a medium scale patch, then use shorter steps and sharper turning angles to track the presence of clustered aggregations (Kareiva & Odell 1987, Fauchald 1999). This corresponds to our findings of a relatively short distance between prey captures at the between aggregation scale, with the large tail on the distribution reflecting the fact that sometimes prey was caught

opportunistically *en route* to or from the colony, when penguins were travelling in a directed fashion (Thums et al. 2011).

The peak at shorter prey capture distances (8.1 m) suggests that prey items were frequently caught within relatively small patches. Targeting aggregations of prey rather than individual prey items can enhance foraging success (Sutton et al. 2015). Specific characteristics of aggregation morphology and density can also influence patterns of prey consumption by enhancing the efficiency with which predators access numerous prey items in rapid succession. Penguins caught more prey where aggregations had a higher relative internal density, were shallower and less tall in the water column. These characteristics may represent measures of prey accessibility to seabirds, with compact, high density aggregations in the top part of the water column more detectable and less energetically costly to predate (Davoren 2000; Benoit Bird et al. 2011; Benoit Bird et al. 2013a).

Our study demonstrates that in a system where prey is distributed patchily, prey capture by a predator is influenced by prey distribution over multiple levels of spatial organisation. These influences appear to be hierarchical, with prey capture being related to large scale prey distribution over the foraging range, the level of patchiness among neighbouring aggregations, and aggregation characteristics. The distributions of both predators and their prey were related to characteristics of the three dimensional physical environment such as temperature and salinity at depth. The accessibility of prey also played an important role in prey capture, with areas where patches were close together in shallow, compact aggregations enhancing prey capture success. Our findings provide empirical insight into the complex factors regulating prey consumption in a wild marine predator, and provide a basis for further work examining spatiotemporal dynamics in pelagic food webs.

4.5 Supporting information for Chapter Four

Parameter	Estimate
Gain	20.47 dB
s_A correction	0.03
Alongship beam width	21.6°
Athwartship beam width	21.7°
Alongship beam offset	0.13°
Athwartship beam offset	0.11°
Target strength RMS error	0.067

Table 4.S1. Calibration parameters for the 70 kHz split-beam transducer. Calibration was carried out using standard sphere techniques (Foote et al., 1987).

Parameter	Value (m)
Minimum total school length	3
Minimum total school height	1
Minimum candidate school length	3
Minimum candidate school height	1
Maximum vertical linking distance	2
Maximum horizontal linking distance	3

Table 4.S2. Schools detection parameters used to isolate bait fish schools from the acoustic data.

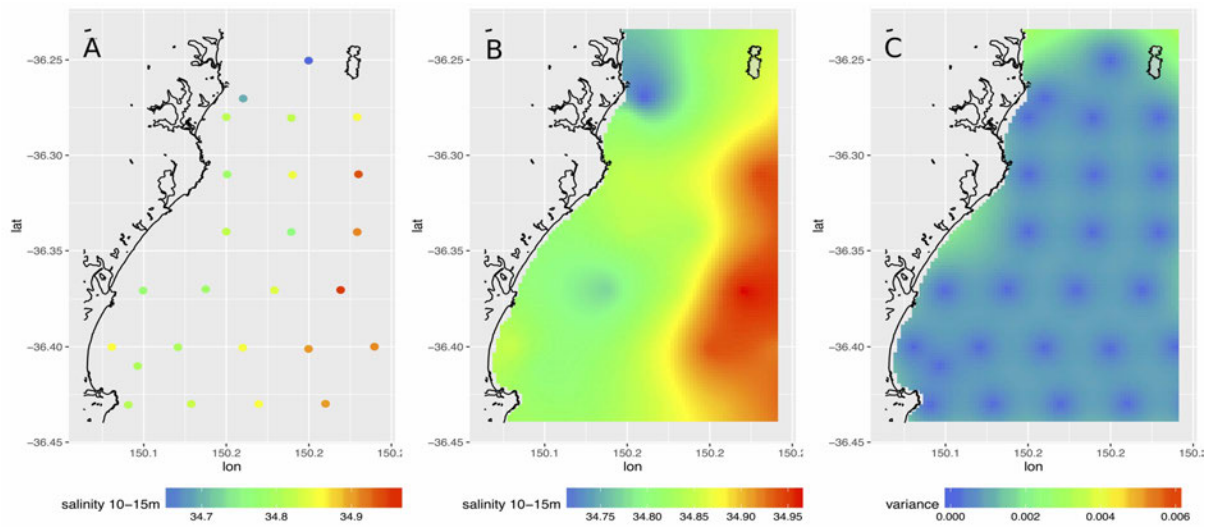


Figure 4.S1. Example of the spatial interpolation process: A) original *in situ* conductivity temperature depth cast observations (salinity at 10 to 15 m), B) interpolation estimated from ordinary kriging, and C) spatially explicit estimates of the variance in interpolated predictions.

Description of binomial generalised additive model	Environmental variables included as smooth terms	df	Δ AIC	Dev. expl	Adj. R ²
All environmental variables + random effect of penguin id	distance to Montague * distance to coast + chl a + SST + salinity 0.5 m + salinity 10-15 m + temp 15-20 + id	92.13	0	53%	0.58
All environmental variables + random effect of penguin id + random effect of sex	distance to Montague * distance to coast + chl a + SST + salinity 0.5 m + salinity 10 15 m + temp 15 20 + id + sex	92.13	0.01	52.8%	0.57
All environmental variables	distance to Montague * distance to coast + chl a + SST + salinity 0.5 m + salinity 10 15 m + temp 15 20 m	74.11	497	51.5%	0.56
Static environmental variables and in situ oceanographic variables	distance to Montague * distance to coast + salinity 0.5 m + salinity 10 15 m + temp 15 20 m	55.95	1082	49.7%	0.54
Static environmental and remotely sensed oceanographic variables	distance to Montague * distance to coast + chl a + SST	46.98	2407	45.9%	0.50
Static environmental variables	distance to Montague * distance to coast	29.44	3964	41.4%	0.46
Oceanographic variables	chl a + SST + salinity 0.5 m + salinity 10 15 m + temp 15 20 m	45.34	6390	34.5%	0.38

Table 4.S3. Model selection for candidate generalised additive models assessing relationships between the incidence of prey captures by penguins and environmental variables. Candidate models were chosen that had combinations of both static (smooth term for distance from coast and distance from Montague Island), and oceanographic variables. Oceanographic variables were further divided into in situ (observations from CTD casts during surveys; temperature at 15 – 20 m, salinity in the top 0.5 m and salinity at 20 – 25 m) and remotely sensed observations (sea surface temperature, chlorophyll a). The best model contained all environmental variables plus a random effect for individual penguin, and is shown in bold.

Description	Model specifications (Binomial generalized additive models)	df	Δ AIC	Dev. expl	Adj. R^2
All environmental variables	distance to Montague * distance to coast + chl a + SST + salinity 0.5 m + salinity 10-15 m + temp 15-20 m	49.26	0	37.4%	0.26
Static environmental variables and in situ oceanographic variables	distance to Montague * distance to coast + salinity 0.5 m + salinity 10 15 m + temp 15 20 m	41.29	4	34.1%	0.24
Static environmental and remotely sensed oceanographic variables	distance to Montague * distance to coast + chl a + SST	32.30	27	27.5%	0.16
Oceanographic variables	chl a + SST + salinity 0.5 m + salinity 10 15 m + temp 15 20 m	29.50	30	26.1%	0.18
Static environmental variables	distance to Montague + distance to coast	26.16	37	24%	0.13

Table 4.S4. Model selection for candidate generalised additive models assessing relationships between the incidence of aggregations < 20 m depth and environmental variables. Candidate models were chosen that had combinations of both static (smooth term for distance from coast and distance from Montague Island), and oceanographic variables. Oceanographic variables were further divided into in situ (observations from CTD casts during surveys; temperature at 15 – 20 m, salinity in the top 0.5 m and salinity at 20 – 25 m) and remotely sensed observations (sea surface temperature, chlorophyll a). The best model contained all environmental variables and is shown in bold.

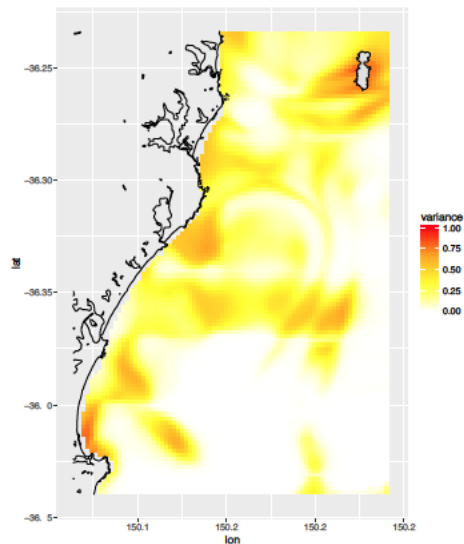


Figure 4.S2. Mean standard error for the best model predictions of aggregation occurrence, over 1000 runs with different combinations of absence points

References for supporting information

Foote, K. G., Knudsen, H. P., Vestnes, G., MacLennan, D. N., and Simmonds, E. J. (1987). Calibration of acoustic instruments for fish density estimation: a practical guide. ICES Cooperative Research Report, 144. 57 pp

Chapter Five

Flexible foraging strategies for a dynamic environment: relationships among site fidelity, foraging success and the environment in a marine predator

Gemma Carroll, Robert Harcourt, Benjamin J. Pitcher, David Slip, Ian Jonsen

Abstract

Foraging site fidelity allows animals to increase their efficiency by returning to sites where they were successful in the past. However, this strategy relies on the predictability of prey distribution at the spatial and temporal scales at which foraging decisions are made. In this study, we examined relationships among environmental variability, prey capture success and site fidelity by a marine predator foraging in a dynamic western boundary current system. We studied little penguins (*Eudyptula minor*) during brooding, when they are restricted to foraging within 25 km of the colony and undertake a single foraging trip every second day. We found that sea surface temperature, a proxy for current driven processes, was dynamic at the two day scale at which penguins forage, and that the predictability and quality of available foraging habitat were spatially heterogeneous. Penguins exhibited some site fidelity, but foraged on average 2.74 km closer to where other penguins foraged on the same day than they did to the location of their previous foraging trip, suggesting that they were adaptively responding to dynamic cues of prey distribution. For every kilometre closer together penguins foraged on the same day, the mean number of prey captures increased by 9 %. Penguins foraged closer to their own previous trip's site if they were more successful on the last trip, with proximity increasing by 4 % for every 100 additional prey caught. This indicates some preference by penguins to return to areas remembered to have high productivity on the previous trip. However, penguins were more successful relative to the previous trip when they foraged furthest (> 12 km) from the previous trip's site. This suggests that penguins made large changes in foraging site only when conditions in a new site were favourable enough to offset costs of switching. Together, these findings illustrate how a predator can integrate

past and present information in a flexible way to cope with changing prey distribution in a dynamic environment.

5.1 Introduction

Foraging site fidelity enables animals to increase their foraging efficiency by returning to locations where productivity was previously high (e.g. Gonzalez Gomez & Vasquez 2006). However, this strategy should be most efficient if prey distribution is predictable at the spatial and temporal scales at which animals forage (Weimerskirch 2007). Under predictable conditions, an animal should return to a location where it was previously successful, and choose an alternative site if it was unsuccessful: a 'win stay, lose switch' strategy (Switzer 1993; Schmidt 2001; Hoover 2003; Chalfoun & Martin 2010). Conversely, if the environment is unpredictable, an animal should not base its decision to return to a site on its past success there, as the probability of experiencing the same outcome again is low (Switzer 1993). However, animals might be expected to return to the same site even in unpredictable conditions if there are fitness benefits of site familiarity (Piper 2011) or if the mean quality of all available sites is similar, and there is no advantage to switching (Switzer 1993). In cases where the environment is both unpredictable and heterogeneous in quality, animals might be expected to show lower site fidelity, but greater use of environmental cues that help them to adaptively locate prey (Weimerskirch et al. 2005b; Garthe et al. 2011).

Understanding what constitutes predictability and heterogeneity on scales that are meaningful to animals making foraging decisions is challenging. For example, the marine environment is generally considered less predictable than terrestrial environments, as water circulation patterns result in a dynamic distribution of organisms at the base of the food web (Abraham 1998). Additionally, mismatches have sometimes been demonstrated between areas of high primary productivity and areas of the highest availability of meso pelagic prey (Grémillet et al. 2008; Sherley et al. 2017). However, some wide ranging species of pelagic animal demonstrate foraging site fidelity within and between years (Bradshaw et al. 2004; Wakefield et al. 2015; Arthur et al. 2015; Patrick & Weimerskirch 2017). It has been suggested that this

indicates the occurrence of stable mesoscale (1 – 100 km) features of the ocean environment that enhance the presence of prey (Weimerskirch 2007). This is supported by observations of animals making ‘commuting’ trips toward oceanic features such as bathymetric structures, fronts and upwelling zones, where they initiate intensive search behaviour (Weimerskirch et al. 1993; Scales et al. 2014). Although these features may themselves be variable, they are likely to represent relatively predictable areas of enhanced productivity in an otherwise dynamic and heterogeneous seascape.

While the return of animals to a foraging site gives some indication that resources are predictable, the interplay between site fidelity, foraging success and habitat characteristics are often unknown. Animals are likely to combine different types of information at different spatial and temporal scales, and the degree to which their decision making reflects prior experience at a site rather than contemporary information such as prey encounter or environmental cues may vary under different conditions (Spencer 2012). Most studies that have assessed site fidelity were unable to incorporate information on foraging success, and the mechanisms underpinning site fidelity and its fitness consequences in complex systems are therefore usually unknown (Piper 2011).

In this study, we assess foraging site fidelity by the little penguin (*Eudyptula minor*), a marine predator that feeds on forage fish in dynamic coastal environments (Hoskins et al. 2008; Carroll et al. 2016a). We tracked penguins during brooding when they undertake single day trips every second day, and are limited to foraging within ~ 25 km of their colony off southeast Australia. Under these constraints, penguins must find prey that is distributed patchily (Carroll et al. 2017), in a complex marine environment dominated by incursions of the warm, nutrient poor East Australian Current (Suthers et al. 2011; Carroll et al. 2016a).

Here, we first describe the environment and its predictability over a 2 day window – the temporal scale at which penguins make foraging decisions. We assess relative habitat quality using a prey capture signature derived from the movement profiles of

penguins (Carroll et al. 2014), recording for each location within the foraging range a) the total number of prey caught, and b) the mean number of prey caught per visit. We then examine whether penguins forage in locations that are more similar to their own previous trip or are closer in proximity to the locations of other penguins foraging on the same day. We also assess whether penguins exhibit greater site fidelity after a more successful previous trip, and whether penguins catch more prey when they are faithful to their previous foraging site.

By systematically testing predictions of site fidelity on a trip by trip basis, we aim to shed light on how animals use different types of information to maximise foraging success in complex and changeable environments.

5.2 Materials and Methods

Penguin tracking

The study was conducted on Montague Island (36.253° S, 150.227° E), 9 km off the southeast coast of New South Wales, Australia over 44 days from the 18th September to the 31st October 2016. The study was designed to coincide with the peak of the period when little penguins were brooding small chicks (< 2 weeks old). During this stage of the breeding cycle, one parent remains at the nest to guard the chicks, while the other goes to sea for a single day foraging trip, returning after sunset.

Consequently, individuals at this breeding stage usually undertake foraging trips every second day. Penguins undertaking single day trips are restricted to foraging within a maximum distance of approximately 25 km from the colony. By selecting only birds at this breeding stage for tracking, we were able to remove the effect of differential habitat selection strategies caused by the varying foraging ranges and energetic requirements of birds at different breeding stages (Gales & Green, 1990).

The night before a penguin went to sea it was captured from its nest box, weighed in a calico bag using a spring balance scale (Pesola, AG Switzerland) and equipped with a GPS logger (CatTrack, South Carolina, USA) modified with epoxy resin to withstand pressure at depth. The loggers were inserted into waterproof heat shrink tubing, then

attached to feathers on the lower back with cloth tape (Tesa, Hamburg, Germany), positioned to reduce drag but not impede tail movement. These tags were 43 mm in length, 27 mm in width and 13 mm in height, and weighed 55 g in air and 17.4 g in seawater. Tags were programmed to record a location every 2–6 s.

Accelerometer data loggers (G6a+, CEFAS Technology Pty Ltd, Suffolk, UK) were attached immediately anterior of the GPS units on the middle back. These tags were 40 mm in length, 28 mm in width and 15 mm in height, and weighed 7.8 g in air and 2.3 g in seawater. The accelerometers recorded acceleration in 3 axes: anterior posterior (surging), lateral (swaying) and dorso ventral (heaving) with a range of ± 2 g. The accelerometers recorded depth, temperature and acceleration and were programmed in two modes: “shallow” mode (<1.5 m: 1.5% of the full scale pressure range) where variables were recorded every 10 seconds, and “dive” mode (>1.5 m) where the same variables were recorded at 30 Hz. Once loggers had been attached, penguins were released into their nest box.

When penguins returned from a foraging trip they were recaptured in their nest boxes, loggers were removed and the penguin was reweighed. Combined tag weight for penguins that were equipped with both accelerometers and GPS was 62 g in air, which was $< 6\%$ of mean bodyweight ($1038.76 \text{ g} \pm 8.89$ in this study).

We minimised handling time and in most cases total time spent at a nest including deployment and retrieval of devices was < 10 min. To reduce potential stress caused by repeated handling (Carroll et al. 2016b), penguin pairs were given a respite from tracking for five to seven days in the middle of sampling, during which time the nest was not visited. Throughout the study the mass of chicks and adults were monitored, and tracking of an individual was ceased if it lost more than 15 % body mass over the study period, dropped below 900 g or changed their nest attendance patterns. Animal research protocols were carried out in accordance with guidelines approved by the Macquarie University Animal Ethics Committee (Animal Research Authority 2014/057).

Data analysis

GPS tracks and prey capture signature

We tracked 20 penguins from 10 nests during the chick guard period, giving 159 foraging trips where GPS tracks were recorded, and 148 trips where both GPS and accelerometry data were recorded (mean number of trips per penguin = 7.95 ± 0.60 and 7.4 ± 0.54 respectively). To regularise the tracking data, we interpolated GPS positions to 30 s intervals using a state space model (Jonsen et al. 2005). To determine where prey captures occurred along the track, we used a support vector machine algorithm that classified movement profiles from accelerometry data as 'swimming' or handling prey'. This algorithm identified prey handling by wild penguins with a false positive rate of 0.09 % (Carroll et al. 2014). Prey captures were assigned a location by matching their time signature to those of GPS tracks after linearly interpolating the positions estimated by the state space model to a 1 s resolution.

Predictability of foraging habitat

We used sea surface temperature (SST) as a proxy for variability in the marine environment. This is because the study region is dominated by the influence of the warm, southward flowing East Australian Current (Suthers et al. 2011). Incursions of warm, nutrient poor tropical water onto the continental shelf are driven by the action of offshore eddies, resulting in a highly dynamic foraging area around Montague Island. A previous study showed that prey capture by penguins in this region was related to SST both spatially and temporally, with high SSTs being associated in general with lower foraging success across multiple spatial and temporal scales (Carroll et al. 2016a).

Day/night composite SST data (Satellite, processed by L3S) at a $0.02^\circ \times 0.02^\circ$ spatial resolution were sourced from the Integrated Marine Observing System's online data access portal (www.imos.org.au). There were 23 days during the study period when satellite coverage was high (usually > 80%), and these were included in analyses. To fill in gaps associated with cloud cover on these days, we smoothed data onto a 2 km x 2 km grid using ordinary kriging, a geostatistical interpolation technique (Cressie 1988).

We used automated variogram fitting in the R package *gstat* (Pebesma 2004). The original data along with the smoothed surfaces are shown in Figures 5.S1 and 5.S2.

From these daily SST surfaces, we calculated the mean difference in SST over a sliding window with a two day lag. This represents spatially explicit variability in the environment at the temporal scale at which penguins leave the colony to forage.

Heterogeneity in habitat quality

As measures of relative habitat quality, we calculated the total number of prey captures recorded by penguins in each 2 km x 2 km grid cell, as well as the number of prey captures divided by the number of foraging trips on which a cell was visited. These indices give insight into the relative productivity of each part of the foraging range, in relation to their use by penguins.

To describe relationships between the physical characteristics of foraging habitat and habitat quality, we used generalised additive models (GAMs). We modelled the total number of prey caught in each cell, and the mean number of prey caught in each cell per visit as functions of both mean SST and mean SST differences over a two day rolling window. We compared GAMs with Poisson and negative binomial error distributions (to account for potential over dispersion) for total counts, and Gaussian error distributions for mean prey captures. We constrained the number of knots in these GAMs to 5 per smooth term, to give broad, directional relationships and to avoid over fitting the data. GAMs were fit using the R package *mgcv* (Wood 2011).

Site Fidelity

To determine whether penguins returned to the same area on consecutive foraging trips, we first calculated the 95% kernel utilisation distribution (KUD) of state space model filtered GPS locations for each foraging trip using the R package *adeHabitatHR* (Calenge, 2006). We used a bivariate normal kernel to estimate the KUD of all trips on a grid of approximately 1 km x 1 km. Where penguins had consecutive foraging trips that were two days apart (separated by a day guarding chicks on the nest), we calculated the distance in kilometres between the centroid of the first foraging trip's

KUD and the centroid of the second foraging trip's KUD. We selected the distance between centroids as a continuous measure of site fidelity, after also testing KUD overlap. KUD overlap contained a high proportion of zero values that were largely uninformative about the relative similarity of two trips, therefore the continuous distance measure was preferred.

Proximity of penguins and relationship with foraging success

We paired the distance between a penguin's own consecutive KUD centroids and the mean distance between its centroid and the centroids of all other tagged penguins foraging on the same day. We took the difference of these two values, and used a one sample t test to test whether the differences were not equal to zero. We then determined whether the mean distance separating penguins foraging on the same day was related to how successful they were that day (mean number of prey caught that day), using a least squares regression.

Site fidelity and foraging success

To assess whether site fidelity was influenced by a penguin's foraging success on the previous trip, we tested the correlation between the distance between the centroid of each consecutive foraging trip's KUD and the number of prey caught on the first foraging trip. To determine how successfully penguins foraged as a function of their prior success and their fidelity to the previous foraging site, we related the difference in the number of prey captures between two consecutive trips to the distance between the two foraging sites. We also tested the relationship between the difference in prey captures on two consecutive trips and the distance between sites at the upper range of distances (> 12 km separating consecutive trips = upper 50 % of the range of distances), to determine which factors contributed to the largest shifts in foraging location. For these analyses we developed candidate model sets that included least squares regressions and linear mixed effects models fit in *lme4* (Bates et al. 2015), with Penguin ID and day included as random intercept terms. Model selection was performed using Akaike's Information Criterion. Continuous response variables were checked for normality and log transformed if necessary; data

presented are means \pm standard error. All analyses were performed in R version 3.3.2 (R Core Team 2016).

5.3 Results

Predictability of the foraging environment

Over the study period, SST was generally lowest inshore, and highest offshore where the flow of the warm East Australian Current is generally strongest (Figure 5.1A, Suthers et al. 2011).

At the two day temporal scale at which penguins make decisions regarding where to forage, SST in the penguins' foraging range was variable, and this variability was spatially

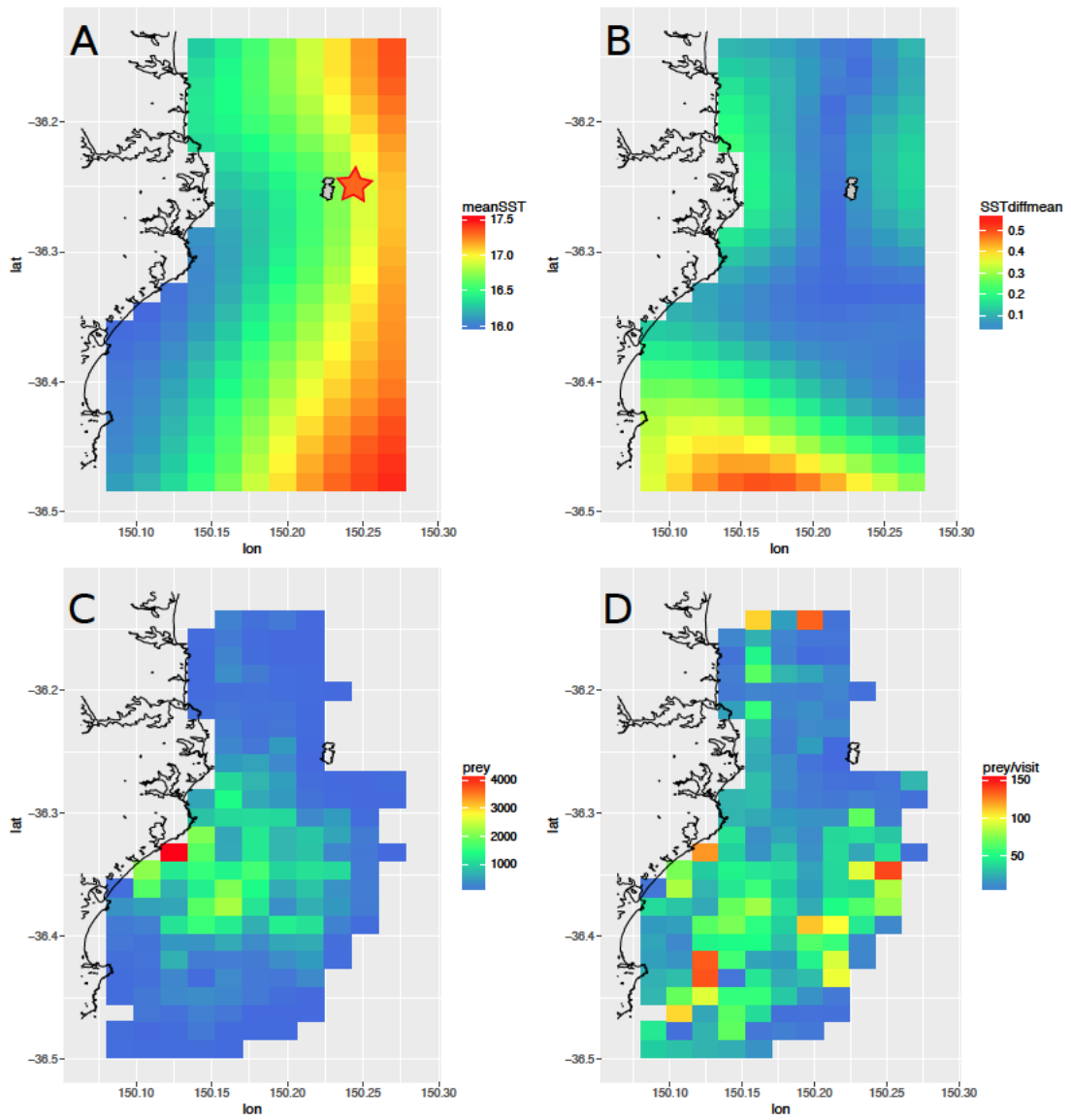


Figure 5.1. A) Mean sea surface temperature over the 30 day study period. B) Mean difference in SST over a two day rolling window. C) total number of prey captures recorded by little penguins, D) number of prey captures per cell visit. Montague Island is indicated by the red star on panel A.

heterogeneous. The mean difference in each cell's SST over a two day window showed that the most predictable area at this scale was immediately to the south of Montague

Island, where temperatures changed on average $< 0.1^{\circ}\text{C}$ over two days. The area of highest variability was to the far south of the penguins' foraging range, where temperatures differed by means of up to 0.5°C (Figure 5.1B).

Heterogeneity in habitat quality

Habitat quality was spatially heterogeneous within the foraging area, with penguins catching most prey items in the area inshore and southwest of Montague Island.

When the number of times that a site was visited was taken into account, quality was less heterogeneous. However, the area to the south of the island was still generally of higher quality than the area to the north.

The Poisson GAM describing the total number of prey captures performed better than the negative binomial GAM, indicating that over dispersion was unlikely to be a major problem for these count data. The best GAM showed a peak at mean SSTs of approximately $16.4 - 17.1^{\circ}\text{C}$, with fewer prey caught in areas with higher and lower mean temperatures (Figure 5.2A). The model also showed that when accounting for mean SST values, prey captures were highest in areas where the difference in SST over the two day period was lowest, with a steep drop off in prey captures where variability was very high (difference $> 0.4^{\circ}\text{C}$; Figure 5.2B). This model explained 36.2% of the deviance in total prey captures.

The Gaussian GAM describing the relationship between mean prey capture and mean SST showed a peak at approximately 16.4°C with lower success at both lower and higher temperatures (Figure 5.2C). This model was not improved by adding the difference in SST over a two day period. This model explained 13.5% of the deviance in mean prey captures.

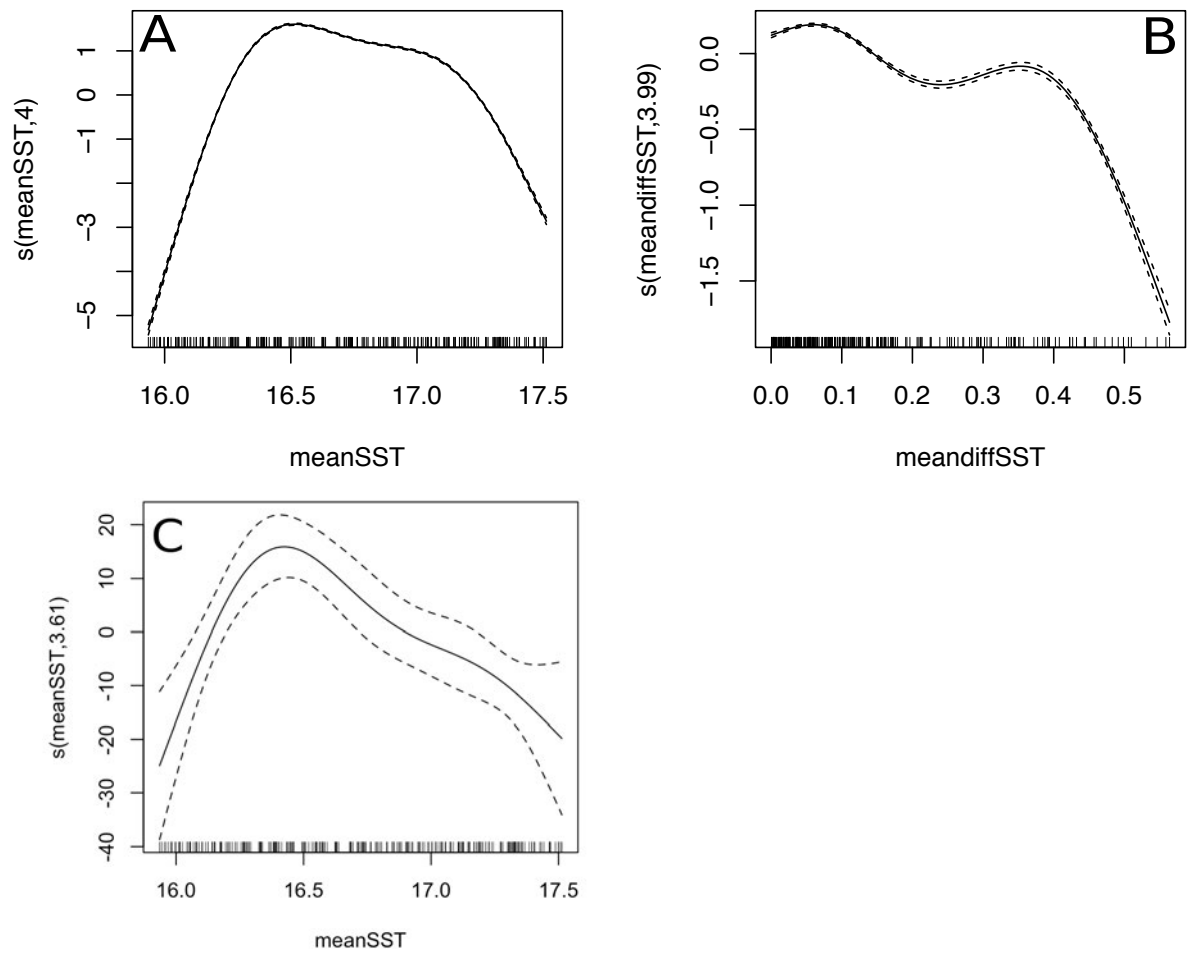


Figure 5.2. Generalised additive model partial plots for two models showing: A & B) the relationship between mean sea surface temperature & mean difference in sea surface temperature at the two day scale, and the total number of prey caught in a grid cell; C) the relationship between mean sea surface temperature and mean prey caught per cell visit.

Site fidelity

Of the 159 foraging trips recorded during this study, 88 had a consecutive trip occurring 2 days later. On these 88 paired trips, the mean distance between the centroids of each pair of 95% KUDs was 7.25 (± 0.51) km. In general, site fidelity by individual penguins was variable (Figure 5.S3), and it did not appear that there were consistent, divergent site fidelity strategies among individuals e.g. with some being specialists and others generalists, as seen in other marine species (Arthur et al. 2015; Patrick & Weimerskirch, 2017).

Proximity of penguins on the same day and relationship with foraging success

Of the penguins we tracked in this study, the mean distance between the centre of a penguin's foraging site and the centres of the sites of other penguins foraging on the same day was 5.35 (± 0.57) km. Distances between foraging sites by penguins on the same day were significantly lower than the distances separating consecutive foraging sites by individual penguins (mean difference = 2.74 km, one sample t test: $df = 46$, $t = 3.66$, $p = 0.0007$).

When tracked penguins foraged closer together on the same day, they had significantly higher mean prey capture success (Figure 5.3; linear model, intercept = 6.80 ± 0.20 , distance = 0.09 ± 0.03 , t value = 2.89, p value = 0.007, Adjusted $R^2 = 0.20$). The best model showed that for every kilometre further apart penguins foraged on average, the mean number of prey captures decreased by a factor of 0.91.

Site fidelity in relation to prior success

The number of prey caught on the first day's foraging trip was negatively correlated with the distance between the centroids of that trip and the trip two days later (Figure 5.4; linear model, intercept = 2.02 ± 0.11 , prior success = 0.0004 ± 0.0001 , t value = 2.88, p value = 0.004, adjusted $R^2 = 0.08$). This model showed that for every 100 additional prey

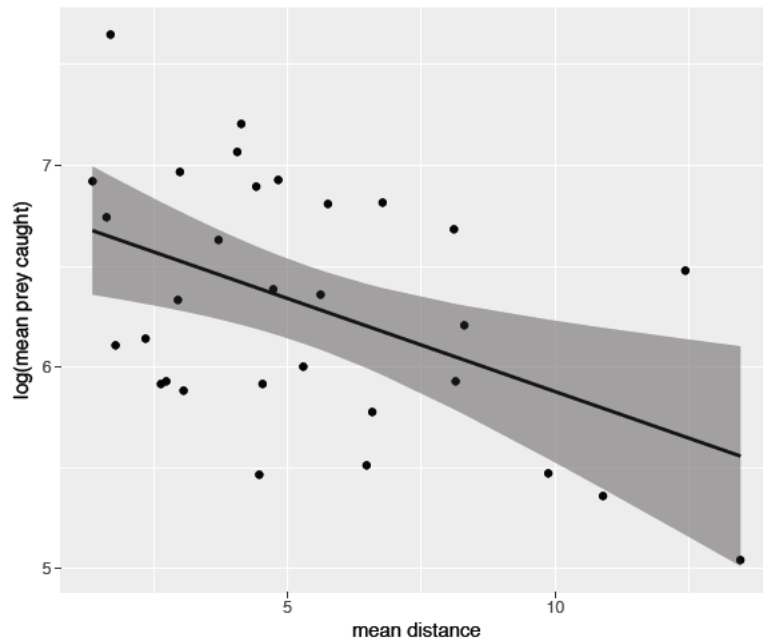


Figure 5.3. Relationship between the mean number of prey caught by penguins on a day and the mean distance between the centroid of all penguins' foraging sites on that day. Fitted line and confidence limits are shown for a linear model with an adjusted R^2 of 0.20.

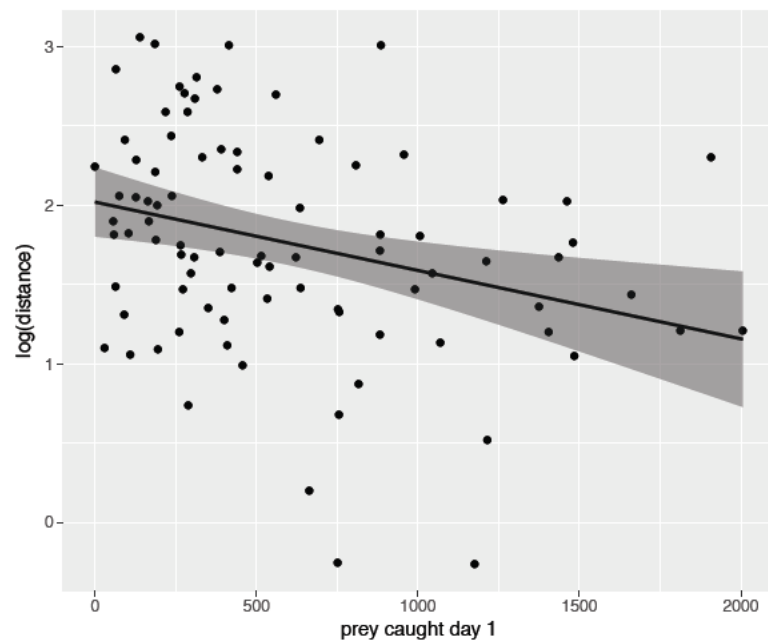


Figure 5.4. Relationship between the number of prey caught on a foraging trip and the log distance between the centroid of that trip and the trip two days later. Fitted line and confidence limits are shown for a linear model with an adjusted R^2 of 0.08.

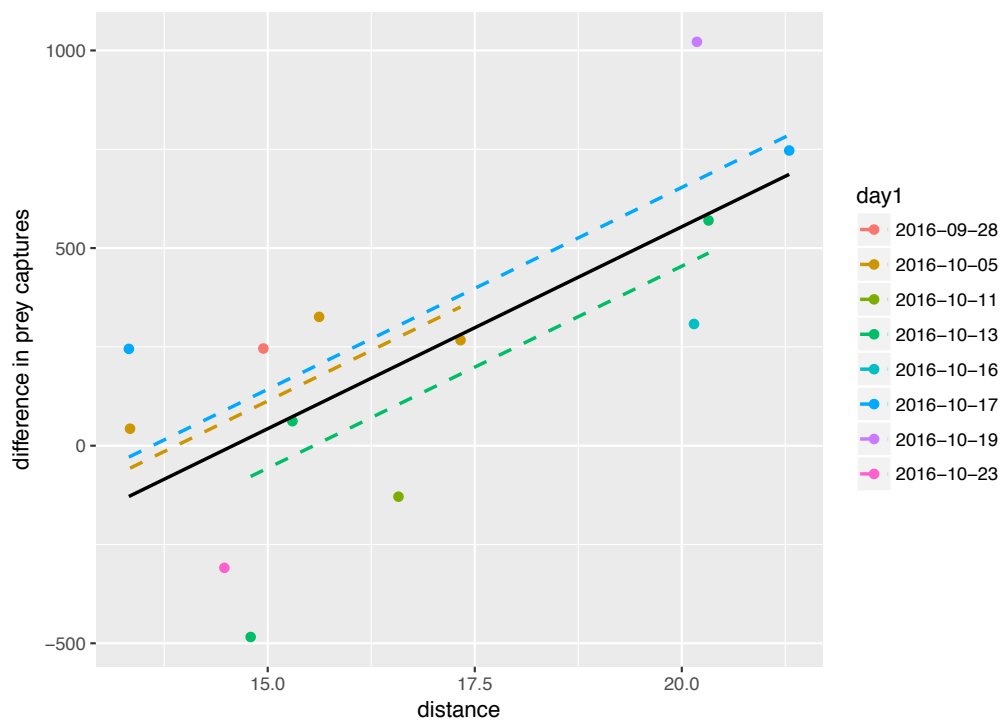


Figure 5.5. Relationship between the distance (km) between centroids of consecutive foraging trips > 12 km, and the difference in prey captures between the two trips. Fitted lines from a linear mixed model are shown for the population (black solid line) as well as random intercepts for day.

caught by penguins on the first trip, the distance separating the two trips decreased by a factor of 0.96.

Foraging success in relation to prior success and site fidelity

Penguins caught more prey on the second trip relative to the first trip when they foraged further from the site of the first trip (Linear mixed effects model, Table 5.S1). However, there was some uncertainty surrounding this relationship, and the distance coefficient in the best model was not significant. When we considered only trips that exhibited the lowest site fidelity (> 12 km separating consecutive trips = upper 50 % of the range of distances) using the same model we found a strong, positive relationship between distance and the difference in the number of prey captures between two trips (Figure 5.5).

5.4 Discussion

Studies in both marine (e.g. Broderick et al. 2007; Wakefield et al. 2015) and terrestrial (e.g. Duchamp et al. 2000; Schaefer et al. 2000) systems have demonstrated remarkable levels of foraging site fidelity in some species, whereby individual animals repeatedly return to particular locations to feed, within and between years. High fidelity to foraging sites is likely to be favoured in cases where resources are highly predictable (Broderick et al. 2007), where quality among available foraging habitats is homogeneous (Bedard & LaPointe 1984a,b), where an individual is specialised to a type of prey or hunting technique (Mattern et al. 2007), where competition is high (e.g. Grémillet et al. 2004) or where there are high energetic or survival costs to switching to unfamiliar sites (Yoder et al. 2004; Brown et al. 2008). Under this 'always stay' strategy, animals make a trade off between flexibility and familiarity, relying on advantages conferred by specialising on a known site (Piper 2011). But if conditions at their preferred site deteriorate, specialised foragers may not be able to compensate behaviourally by switching foraging sites, and site fidelity can therefore confer vulnerability on individuals and populations (Bolnick et al. 2002).

In our study, we found that penguins showed some evidence of a 'win stay, lose switch' foraging strategy (Switzer 1993). Penguins used information about prior foraging success to return to profitable areas, while retaining the flexibility to adapt to local conditions on a trip by trip basis. These findings suggest that the environment was predictable enough, at the spatial and temporal scales at which penguins made decisions about where to forage, to warrant returning to approximately the same area if they were successful previously. This likely reflects patterns in the persistence of prey patches in this system, with the locations of prey aggregations being spatially and temporally correlated (Zach & Falls 1979). This is supported by the fact that penguins preferentially foraged where the average magnitude of variability in SST was lowest at the two day scale (Figure 5.1). However, penguins showed flexibility in selecting their foraging sites, and some environmentally variable areas that were visited less frequently had higher mean prey capture returns. This suggests that while selecting stable foraging habitat may be a risk minimising strategy, flexibility in foraging locations when conditions change may ultimately benefit foragers in a dynamic system (Weimerskirch et al. 2005b).

Generally, penguins foraged closer to where other penguins foraged on the same day than they did to their own previous foraging site. Although only a limited sample of the population was tracked during this study, the relative proximity of these penguins to one another during foraging suggests that local conditions may be a more important determinant of foraging location than prior experience. This could be a result of local enhancement (Thiebault et al. 2014), cooperative foraging increasing opportunities for prey encounter (Sutton et al. 2015), or penguins independently using the same signals in the environment to locate prey, such as sea surface temperature or olfactory cues (Nevitt et al. 2008). Similar to some terrestrial birds and bats (Wilkinson & Boughman 1998), little penguins use contact calls at sea, indicating a potential social component to foraging. However, the mechanisms by which penguins may integrate social cues with environmental cues remain unknown.

When penguins foraging on the same day were closer together, the mean number of prey caught by penguins on that day was higher. Previous studies have shown that

group foraging does not enhance rates of prey consumption in little penguins, at least at the patch scale (Sutton et al. 2015). Our finding more likely suggests that when prey was abundant and accessible, penguins were best able to cue in to productive locations either independently, or through communicating with conspecifics, leading to higher net prey consumption. Conversely, days when penguins foraged further from each other may represent periods when prey was more dispersed or more difficult to locate, resulting in penguins making more frequent large displacements in their search for prey (Kareiva & Odell 1987), and resulting in a net decrease in foraging success. These hypotheses are supported by studies showing that predators including little penguins forage more intensively in areas where aggregations of prey are spatially clustered (Benoit Bird et al. 2013a; Carroll et al. 2017) and where prey is easily accessible (Hopcraft et al. 2005; Boyd et al. 2015; Carroll et al. 2017).

When penguins did switch sites, they tended to be more successful when they foraged further from the previous day's site. This difference in success was greatest at relatively large distances (15 – 20 km separating two sites). For an animal that is constrained to foraging within 25 km of the colony, these distances represent substantial shifts to opposite parts of the foraging range. That penguins were significantly more successful when they made these large shifts indicates that any costs of switching through lost familiarity (Piper 2011) were offset by encountering favourable conditions at the alternative site (Linkhart & Reynolds 2007). It is unclear how penguins gain insight into habitat quality in other parts of the range, if their own success is their primary measure of quality (Switzer 1997). One mechanism may be that penguins leaving the colony sometimes either encounter prey directly, or encounter conditions that signal prey availability. Following these cues from the start of the trip may substantially alter their foraging trajectory. If penguins do not encounter such strong cues, they may head towards their previous site or to the area with the most predictable quality, where prey capture success may not be guaranteed. Independent information on the spatio temporal dynamics of prey predictability and its influence on foraging behaviour will help to resolve these uncertainties.

5.5 Conclusions

In this study, we showed that penguins employ foraging strategies consistent with the environment being to some extent predictable at the spatial and temporal scales at which penguins forage, with penguins demonstrating a 'win stay, lose switch' strategy (Switzer 1993; Weimerskirch 2007). However, we found greater evidence that penguins could adaptively alter their foraging locations on a trip by trip basis, and that this could result in enhanced foraging success at the individual and group levels. This suggests that for animals in dynamic environments, any benefits of site familiarity are offset by the need for flexible foraging strategies to locate prey. Our findings highlight the complexity of decision making by foraging animals, and give new insights into the way that animals integrate spatio temporal information about the foraging environment to maximise net energy gain.

5.6 Supporting information for Chapter Five

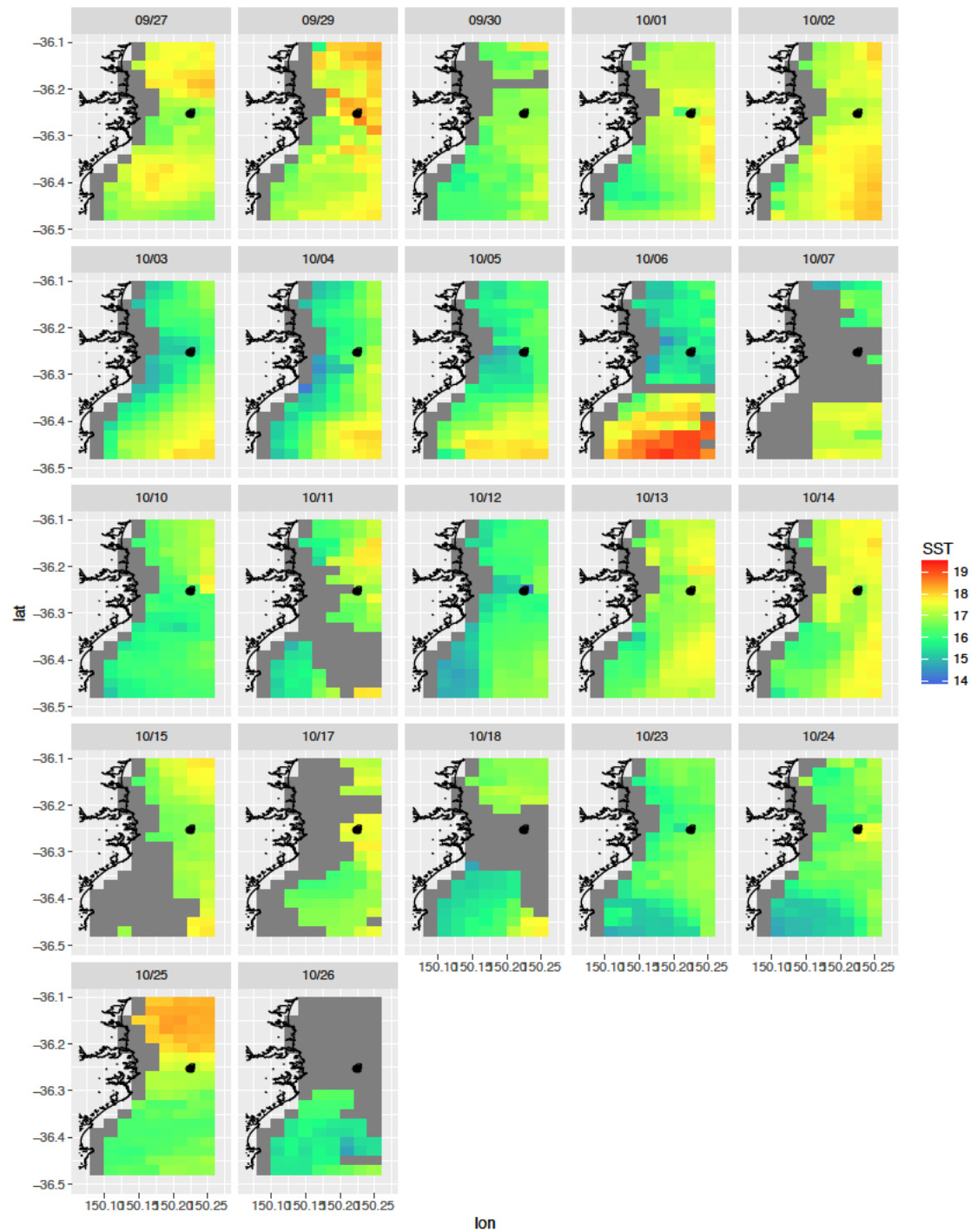


Figure 5.S1. Satellite-derived sea surface temperature values on days used in analyses

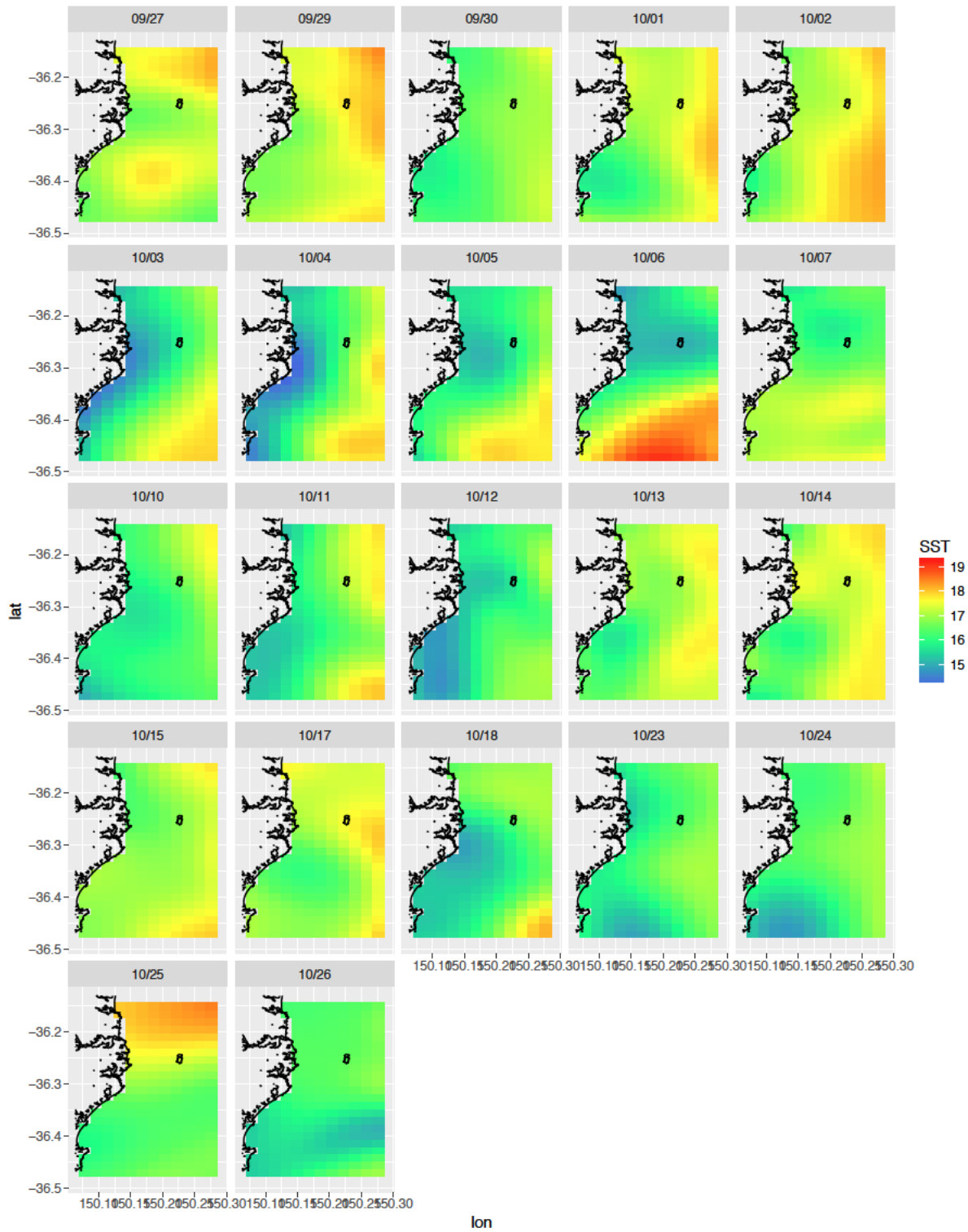


Figure 5.S2. Satellite-derived sea surface temperatures smoothed onto a 2 km x 2 km grid using ordinary kriging

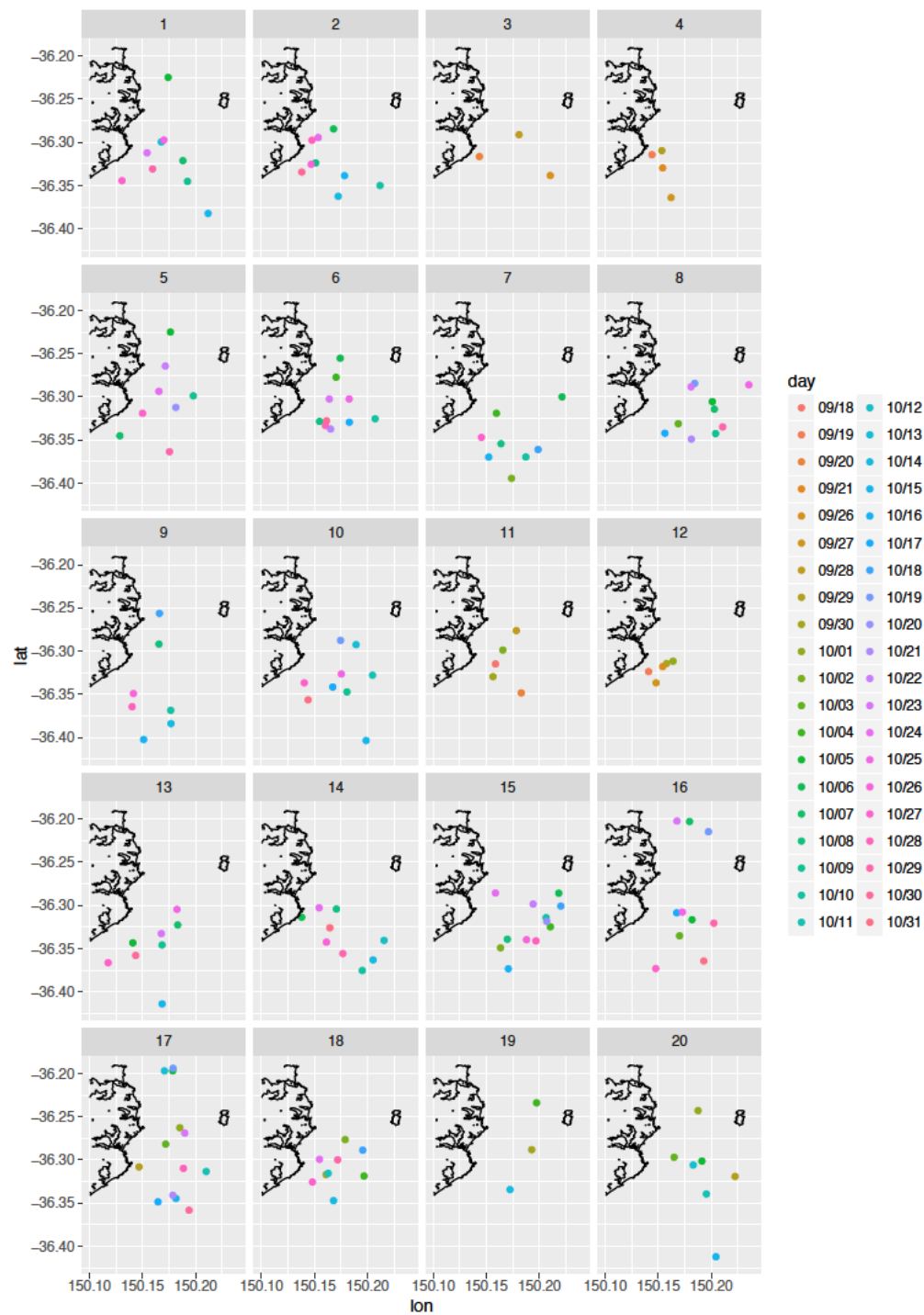


Figure 5.S3. Centroids of each penguin's foraging trip during the study. There did not appear to be consistent, divergent site fidelity strategies among this sample of penguins, e.g. with some being specialists to particular foraging locations and others being generalists.

Fixed Effects	Estimate	Std. Error	t value
Intercept	68.67	104.50	0.66
Distance	55.84	67.80	0.82
Random Effects		Variance	Std. Dev.
Day	Intercept	270587	520.2
Residual		240478	490.4

Table 5.S1. Summary table describing the best linear mixed effects model for the relationship between the difference between the number of prey caught by a penguin on two consecutive trips and the distance between the centroids of the two trips. The distance metric is mean centred and scaled.

Chapter Six

6.1 General Discussion

To understand the spatial ecology of predators, it is useful to have information on when and where they find and consume prey (Marker et al. 2003), and how prey consumption is mediated by components of the biophysical environment (e.g. Friedlaender et al. 2016b). This thesis presents an innovative method for identifying predator prey interactions by a marine predator, and shows how an index of prey capture can be combined with information on the environment, prey distribution and the foraging behaviour of conspecifics to provide textured insight into the factors underpinning foraging success in a complex and changing natural system.

In this final chapter, I synthesise information from the preceding chapters, and discuss implications of this body of work for understanding predator prey interactions. I also outline future research questions arising from my work that will enable a deeper understanding of the pelagic food web off the east coast of Australia.

Accelerometry as a tool to understand predator prey interactions

There is a rapidly increasing number of studies in which pattern recognition tools have been developed for classifying animal behaviour from accelerometry data (e.g. Martiskainen et al. 2009; Sakamoto et al. 2009; Bidder et al. 2014; Resheff et al. 2014; Collins et al. 2015; Leos Barajas et al. 2017; Ladds et al. 2017). These analytical methods each have unique benefits and drawbacks, and their application to individual species and behaviours requires careful adaptation and testing (e.g. Nathan et al. 2012; Ladds et al. 2016). Although the development of these tools provides significant advances to behavioural ecology (Valletta et al. 2017), the true potential of accelerometry for understanding animal lives is only just beginning to be realised through the application of these techniques to data obtained from wild animals under varying ecological conditions (e.g. Abrahms et al. 2015; McClune et al. 2015).

The support vector machine algorithm that I developed in Chapter Two to detect prey capture was based on observations of little penguins feeding in captivity. This ‘supervised’ approach allowed the matching of penguin feeding behaviour to their movement profiles at a very high temporal resolution under controlled conditions, and allowed the model’s accuracy and precision to be estimated during model development (Nathan et al. 2012). In addition to this testing phase in captivity, ground truthing the model by assessing differences in behaviour between prey capture and non prey capture dives by wild penguins was an important component of this study that enabled confident application of the model to wild data in the subsequent chapters. This *in situ* validation step was important in this system given the constraint of feeding the captive penguins only sardines, which constitute a substantial yet incomplete portion of the penguins’ diet in the wild (Montague & Cullen 1988; Chiaradia et al. 2012). Validation of behaviour estimates from accelerometers attached to wild animals, e.g. using other tag sensors and ‘common sense’ expectations of how animals behave in the wild (e.g. Chimienti et al. 2016; Wilson et al. 2017), should be performed in all similar studies where possible to increase the robustness of inferences from accelerometry in the field.

Having a behavioural index of prey consumption provides a useful tool with which to understand predator ecology. By identifying when, where and how animals find food in the wild, we can gain a deeper understanding of the factors underlying predator movements (Jonsen et al. 2003). For example, accelerometry techniques have been applied in a series of related studies on large baleen whales to answer diverse questions regarding the ecological processes that underpin foraging behaviour in these species (e.g. Goldbogen et al. 2015; Hazen et al. 2015; Friedlaender et al. 2016a,b). Application of this tool has uncovered complex behavioural trade offs between energy expenditure and energy consumption in relation to prey density and distribution (Goldbogen et al. 2015; Hazen et al. 2015; Friedlaender et al. 2016b), and anthropogenic disturbance (Friedlaender et al. 2016a). Using a prey capture signature in multiple, connected studies to answer a series of questions in this manner gives detailed, multi layered insight into how animals interact with their environment, and how their foraging strategies and success vary under different ecological constraints.

In Chapters Three, Four and Five of this thesis, I used the prey capture index as a spatial tool to understand how patterns of foraging habitat use by penguins were linked to the physical environment and prey distribution. This approach allowed the parts of the penguins' tracks that were associated with successful foraging to be separated from the parts that were associated with other behaviours such as resting, transit, searching or unsuccessful foraging. This provided more precise estimates of how penguins used the environment for foraging, and exposed underlying spatial patterns of relative profitability in the seascape around Montague Island. Combining animal tracking studies with an accelerometry derived index of feeding is a valuable but currently under utilised approach for understanding where predators find and consume prey. This method could be employed in many marine and terrestrial systems to design spatial conservation strategies for predators that are based on identifying important feeding areas (e.g. Game et al. 2009), or to provide protection for prey (e.g. livestock or native species) from pest predators (e.g. Darimont et al. 2015).

As well as using the prey capture index as a spatial tool, I also used it as a means to quantify relative prey capture success under different foraging scenarios. In Chapter Three, I related the rate of prey capture to offshore sea surface temperature and in Chapter Five I determined how the overall number of prey caught on a trip influenced foraging site fidelity. Having an indication of foraging performance is rare in animal ecology, but gives deeper insight into the fitness outcomes of different foraging conditions (Grémillet et al. 2016), and sheds light on the evolution of diverse foraging strategies (Goldbogen et al. 2015). Having an index of prey consumption allows a predator's influence on the food web to be investigated (Preisser et al. 2005), and provides a more mechanistic approach to understanding how predators might respond to changing conditions.

Factors influencing foraging success by Montague Island little penguins

While little penguin foraging ecology has been studied in other parts of Australia (e.g. Ropert Coudert et al. 2006b; Pelletier et al. 2014), this thesis represents the first

collection of studies to use bio logging technology to examine the oceanographic drivers of little penguin foraging behaviour on the east coast. In this thesis, I explored a number of specific factors in relation to their influence on foraging success by penguins in the East Australian Current system.

I found that prey capture by little penguins was related to sea surface temperature at multiple spatial and temporal scales. Sea surface temperature is a defining feature of underlying oceanographic processes in this system, differentiating the tropical water carried by the East Australian Current from the temperate waters of the Tasman Sea (Suthers et al. 2011). Spatially, I found that penguins usually foraged in cool, inshore waters (Chapters Three, Four and Five), suggesting that these conditions support a relatively high density of forage fish prey (e.g. Ward et al. 2015). However, penguins sometimes caught prey in the frontal zone between the edge of the current and the inshore Tasman Sea water, which appeared to present an unpredictable yet sometimes highly profitable foraging opportunity (Chapters Four and Five; Scales et al. 2014; Cox et al. 2016). The position of the edge of the East Australian Current was variable at a daily scale (Chapter Five), and this likely had a major influence on local prey distribution, with both prey aggregations and foraging activity by penguins being limited in their offshore extent by the East Australian Current water mass (Chapters Three, Four and Five).

In Chapter Four, I found that spatial patterns of prey capture by little penguins were related to prey distribution at nested spatial scales. At the broadest scale, penguins appeared to be able to match the local distribution of prey aggregations across their home range. Penguins caught consecutive prey items at distances that reflected the size of prey aggregations, and the clustering of neighbouring aggregations. At the finest scale, penguins caught more prey where aggregations were compact, dense and shallow. It is rare to have the opportunity to combine estimates of spatially explicit predator foraging success with an independent assessment of the distribution of prey (e.g. Hazen et al. 2015). In this study, having a measure of prey distribution provided novel insight into how little penguin foraging strategies are shaped by the patchiness and relative accessibility of their prey across the seascape (Benoit Bird et al. 2013a;

Boyd et al. 2015). The synchrony that I found between penguin foraging and prey distribution also confirms that patterns of foraging habitat selection in Chapters Three and Five are likely to represent patterns in the underlying distribution of prey around Montague Island (Ward et al. 2015).

Little penguins appeared to use information about their prior foraging success as well as responding flexibly to *in situ* conditions to maximise prey consumption in the dynamic East Australian Current system (Chapter Five). Penguins exhibited evidence of a ‘win stay, lose switch’ strategy between consecutive foraging trips (Switzer 1993). The tendency of penguins to return to a site where they were successful suggests that patterns of prey availability generally persisted over at least a two day foraging window, likely driven by sub mesoscale features of the marine environment operating at this temporal scale (Zach & Falls 1979; Switzer 1993; Hazen et al. 2013). However, penguins were also able to take advantage of new foraging opportunities when conditions changed. Site fidelity by little penguins appeared lower than by some marine predators in temperate environments that exhibit an ‘always stay’ foraging strategy (e.g. Wakefield et al. 2015). This suggests that the area around Montague Island may exhibit similarities to tropical systems, where seabirds also exhibit more dynamic foraging strategies to cope with unpredictable and patchy resources (Weimerskirch et al. 2005b). The findings in Chapter Five attest to the ability of penguins to respond in a flexible way to changes in the foraging environment, within the constraints of being restricted to foraging within 25 km of the colony during brooding.

Future research directions

While studying little penguins gave novel and useful insights into patterns of resource availability, taking an integrated approach across trophic levels and ecological disciplines would strengthen future studies in this and other dynamic marine systems. The area around Montague Island that was the focus of this study provides an ideal model system within which to conduct an innovative food web study that integrates sampling from phytoplankton to penguins, to understand trophic links in a changing environment (e.g. Grémillet et al. 2008). Boat based acoustic surveys (described in

Chapter Four) should be extended as a platform to collect more detailed information about fish communities in this area under different oceanographic conditions (McInnes et al. 2017), while simultaneously collecting information about plankton biomass that could be used to understand patterns of primary and secondary production (Kiørboe 1993; Suthers et al. 2006). This would add new context to information on the foraging dynamics of marine predators such as penguins, and enable a better understanding of the mechanisms governing prey availability within their home range (McInnes et al. 2017).

Temporal patterns in predator prey environment interactions are difficult to address in ecological studies (e.g. Bunnell & Huggard 1999), but could be considered using the sampling protocol outlined above. By surveying the same parts of the prey field for plankton and forage fish at nested time intervals (e.g. daily, weekly, monthly and inter annually), it would be possible to build knowledge about the directions and magnitude of natural variability in pelagic systems. This variability in prey abundance and distribution could then be related to the foraging strategies and performance of predators such as penguins, to understand temporal patterns in foraging performance and the way that animals accumulate and use information over increasing timescales (Clayton et al. 2003). The multi trophic level information obtained through this type of study could then be related to physical oceanography through a numerical model describing water properties, current flow, and upwelling dynamics at fine spatial and temporal scales (e.g. Colette et al. 2016). This detailed suite of information would give insight into the unique characteristics of the pelagic food web that may not be apparent from static snapshots in time (e.g. Chapter Four, Benoit Bird et al. 2013b; Boyd et al. 2015). Consequently, this would provide a more holistic picture of how this ecosystem might change as the East Australian Current intensifies.

In addition to spatio temporal information from the prey field, a time series of the demography and reproductive success of marine predators in this area would greatly enhance our ability to infer how changes in the physical environment affect this ecosystem (Ainley et al. 1995; Boyd & Murray 2001; Sydeman et al. 2017). This information was largely unavailable for little penguins during this study, due to the

logistical difficulty of monitoring the long, asynchronous breeding season of penguins on the relatively remote Montague Island. Having information on the fitness of animals concurrent to estimates of foraging success is rare, but extremely valuable (Morales et al. 2010). This would enable a better understanding of whether penguins are able to offset variability in foraging success under different environmental conditions (Bost et al 2015). In combination with predictive modelling of East Australian Current intensification, this would shed further light on the ability of predators such as little penguins to persist in the East Australian Current system into the future.

6.2 Conclusion

As a body of work, this thesis provides new perspectives on resource availability in the pelagic ecosystem off eastern Australia, through examination of little penguin foraging ecology. I applied a novel prey capture detection algorithm to accelerometry data, to understand where penguins catch prey, and under which environmental conditions prey capture is enhanced or reduced. I showed that prey capture by penguins followed specific relationships with the physical environment, with more prey caught at cool to intermediate sea surface temperatures inside the margin of the dynamic East Australian Current water mass. I showed that little penguins behaved in ways that enabled them to match the local distribution of aggregations of their forage fish prey within this suitable foraging habitat. Prey capture by penguins was lowest when penetration of the East Australian Current was strongest, suggested by higher offshore sea surface temperature. This indicates that despite the flexibility that penguins exhibit when foraging, there may be negative outcomes for penguins and their prey as the East Australian Current intensifies (Chapter Two; Cai et al. 2005; Wu et al. 2012). There remains much to be done to understand this system and how it will change in the future, but my work suggests that the rapid rise in sea surface temperature off southeast Australia may have serious consequences for marine predators such as penguins, and for the rest of the pelagic food web in this region.

References

- Aarts, G., MacKenzie, M., McConnell, B., Fedak, M., & Matthiopoulos, J. (2008). Estimating space use and habitat preference from wildlife telemetry data. *Ecography*, **31**, 140–160.
- Abraham, E. R. (1998). The generation of plankton patchiness by turbulent stirring. *Nature*, **391**, 577–580.
- Abrahams, B., Jordan, N. R., Golabek, K. A., McNutt, J. W., Wilson, A. M., & Brashares, J. S. (2015). Lessons from integrating behaviour and resource selection: activity specific responses of African wild dogs to roads. *Animal Conservation*, **19**, 247–255.
- Adachi, T., Costa, D. P., Robinson, P. W., Peterson, S. H., Yamamichi, M., Naito, Y., & Takahashi, A. (2017). Searching for prey in a three dimensional environment: hierarchical movements enhance foraging success in northern elephant seals. *Functional Ecology*, **31**, 361–369.
- Adams, N. J., Moloney, C., and Navarro, R. (1993). Estimated food consumption by penguins at the Prince Edward Islands. *Antarctic Science*, **5**, 245–252.
- Agenbag, J. J., Richardson, A. J., Demarcq, H., Fréon, P., Weeks, S., & Shillington, F. A. (2003). Estimating environmental preferences of South African pelagic fish species using catch size and remote sensing data. *Progress in Oceanography*, **59**, 275–300.
- Ainley, D. G., Sydeman, W. J., & Norton, J. (1995). Upper trophic level predators indicate interannual negative and positive anomalies in the California Current food web. *Marine Ecology Progress Series*, **118**, 69–79.
- Ancel, A., Horning, M., & Kooyman, G. L. (1997). Prey ingestion revealed by oesophagus and stomach temperature recordings in cormorants. *Journal of Experimental Biology*, **200**, 149–154.
- Armbrecht, L. H., Roughan, M., Rossi, V., Schaeffer, A., Davies, P. L., Waite, A. M., & Armand, L. K. (2014). Phytoplankton composition under contrasting oceanographic conditions: Upwelling and downwelling (Eastern Australia). *Continental Shelf Research*, **75**, 54–67.
- Arthur, B., Hindell, M., Bester, M., Trathan, P., Jonsen, I., Staniland, I., ... & Lea, M. A. (2015). Return customers: Foraging site fidelity and the effect of environmental variability in wide ranging Antarctic fur seals. *PloS one*, **10**, e0120888.
- Austin, D., Bowen, W. D., McMillan, J. I., & Boness, D. J. (2006). Stomach temperature telemetry reveals temporal patterns of foraging success in a free ranging marine mammal. *Journal of Animal Ecology*, **75**, 408–420.
- Baird, M. E., Timko, P. G., I. M., & Middleton, J. H. (2006). Coupled physical–biological modelling study of the East Australian Current with idealised wind forcing. Part I: Biological model intercomparison. *Journal of Marine Systems*, **59**, 249–270.

- Balme, G., Hunter, L., & Slotow, R. (2007). Feeding habitat selection by hunting leopards *Panthera pardus* in a woodland savanna: prey catchability versus abundance. *Animal Behaviour*, **74**, 589–598.
- Bartumeus, F., da Luz, M. E., Viswanathan, G. M., & Catalan, J. (2005). Animal search strategies: a quantitative random walk analysis. *Ecology*, **86**, 3078–3087.
- Bates, D., Maechler, M., Bolker, B., Walker, S. (2015). Fitting Linear Mixed Effects Models Using lme4. *Journal of Statistical Software*, **67**, 1–48.
- Bedard, J. and LaPointe, G. (1984a) Banding returns, arrival times, and site fidelity in the savannah sparrow. *Wilson Bulletin*. **96**, 196–205.
- Bedard, J. and LaPointe, G. (1984b) The savannah sparrow territorial system: can habitat features be related to breeding success? *Canadian Journal of Zoology*, **62**, 1819–1828.
- Behrenfeld, M. J., O'Malley, R. T., Siegel, D. A., McClain, C. R., Sarmiento, J. L., Feldman, G. C., M. J. Milligan, A.J., Falkowski, P.G., Letelier, R.M. & Boss, E. S. (2006). Climate driven trends in contemporary ocean productivity. *Nature*, **444**, 752–755.
- Benoit Bird, K. J., Battaile, B. C., Heppell, S. A., Hoover, B., Irons, D., Jones, N., Kuletz, K.J., Nordstrom, C.A., Paredes, R., Suryan, R.M. & Waluk, C. M. (2013a). Prey patch patterns predict habitat use by top marine predators with diverse foraging strategies. *PLoS One*, **8**, e53348.
- Benoit Bird, K. J., Battaile, B. C., Nordstrom, C. A., & Trites, A. W. (2013b). Foraging behavior of northern fur seals closely matches the hierarchical patch scales of prey. *Marine Ecology Progress Series*, **479**, 283–302.
- Benoit Bird, K. J., Kuletz, K., Heppell, S., Jones, N., & Hoover, B. (2011). Active acoustic examination of the diving behavior of murres foraging on patchy prey. *Marine Ecology Progress Series*, **443**, 217–235.
- Berry, W.D., Feldman, S. (1985). Multiple Regression in Practice (Quantitative Applications in the Social Sciences) SAGE Publications; Thousand Oaks. CA
- Bester, A. (1997) A comparison of the feeding ecology of seabirds on Montague Island, New South Wales. *Honours Thesis, Charles Sturt University, Albury, Australia*
- Bestley, S., Patterson, T. A., Hindell, M. A., & Gunn, J. S. (2010). Predicting feeding success in a migratory predator: integrating telemetry, environment, and modeling techniques. *Ecology*, **91**, 2373–2384.
- Bestley, S., Patterson, T. A., Hindell, M. A., and Gunn, J. S. (2008). Feeding ecology of wild migratory tunas revealed by archival tag records of visceral warming. *Journal of Animal Ecology*, **77**, 1223–1233.
- Bethge, P., Nicol, S., Culik, B. M., & Wilson, R. P. (1997). Diving behaviour and energetics in breeding little penguins (*Eudyptula minor*). *Journal of Zoology*, **242**, 483–502.
- Bidder, O. R., Campbell, H. A., Gómez Laich, A., Urgé, P., Walker, J., Cai, Y., Gao, L., Quintana, F. & Wilson, R. P. (2014). Love thy neighbour: automatic animal

- behavioural classification of acceleration data using the k nearest neighbour algorithm. *PLoS One*, **9**, e88609.
- Block, B. A., Jonsen, I. D., Jorgensen, S. J., Winship, A. J., Shaffer, S. A., Bograd, S. J., Hazen, E.L., Foley, D.G., Breed, G.A., Harrison, A.L. & Ganong, J. E. (2011). Tracking apex marine predator movements in a dynamic ocean. *Nature*, **475**, 86–90.
- Blouin Demers, G., & Weatherhead, P. J. (2001). Habitat use by black rat snakes (*Elaphe obsoleta obsoleta*) in fragmented forests. *Ecology*, **82**, 2882–2896.
- Bograd, S. J., Block, B. A., Costa, D. P., & Godley, B. J. (2010). Biologging technologies: new tools for conservation. Introduction. *Endangered Species Research*, **10**, 1–7.
- Bolnick, D. I., Svanbäck, R., Fordyce, J. A., Yang, L. H., Davis, J. M., Hulsey, C. D., & Forister, M. L. (2002). The ecology of individuals: incidence and implications of individual specialization. *The American Naturalist*, **161**, 1–28.
- Bost, C. A., Cotté, C., Terray, P., Barbraud, C., Bon, C., Delord, K., Gimenez, O., Handrich, Y., Naito, Y., Guinet, C. & Weimerskirch, H. (2015). Large scale climatic anomalies affect marine predator foraging behaviour and demography. *Nature Communications*, **6**, 1–9.
- Bost, C. A., Handrich, Y., Butler, P. J., Fahlman, A., Halsey, L. G., Woakes, A. J., and Ropert Coudert, Y. (2007). Changes in dive profiles as an indicator of feeding success in king and Adélie penguins. *Deep Sea Research Part II* **54**, 248–255.
- Boyce, M. S., Vernier, P. R., Nielsen, S. E., & Schmiegelow, F. K. (2002). Evaluating resource selection functions. *Ecological Modelling*, **157**, 281–300.
- Boyd, C., Castillo, R., Hunt, G. L., Punt, A. E., VanBlaricom, G. R., Weimerskirch, H., & Bertrand, S. (2015). Predictive modelling of habitat selection by marine predators with respect to the abundance and depth distribution of pelagic prey. *Journal of Animal Ecology*, **84**, 1575–1588.
- Boyd, I. L., & Murray, A. W. A. (2001). Monitoring a marine ecosystem using responses of upper trophic level predators. *Journal of Animal Ecology*, **70**, 747–760.
- Bradshaw, C. J., Hindell, M. A., Sumner, M. D., & Michael, K. J. (2004). Loyalty pays: potential life history consequences of fidelity to marine foraging regions by southern elephant seals. *Animal Behaviour*, **68**, 1349–1360.
- Broderick, A. C., Coyne, M. S., Fuller, W. J., Glen, F., & Godley, B. J. (2007). Fidelity and over wintering of sea turtles. *Proceedings of the Royal Society of London B: Biological Sciences*, **274**, 1533–1539.
- Brodie, S., Hobday, A. J., Smith, J. A., Everett, J. D., Taylor, M. D., Gray, C. A., & Suthers, I. M. (2015). Modelling the oceanic habitats of two pelagic species using recreational fisheries data. *Fisheries Oceanography*, **24**, 463–477.
- Broell, F., Noda, T., Wright, S., Domenici, P., Steffensen, J. F., Auclair, J. P., and Taggart, C. T. (2013). Accelerometer tags: detecting and identifying activities in fish and the effect of sampling frequency. *Journal of Experimental Biology*, **216**, 1255–1264.

- Brown, C. R., Brown, M. B., & Brazeal, K. R. (2008). Familiarity with breeding habitat improves daily survival in colonial cliff swallows. *Animal Behaviour*, **76**, 1201–1210.
- Bunnell, F. L., & Huggard, D. J. (1999). Biodiversity across spatial and temporal scales: problems and opportunities. *Forest ecology and Management*, **115**, 113–126.
- Butler, S. J., & Gillings, S. (2004). Quantifying the effects of habitat structure on prey detectability and accessibility to farmland birds. *Ibis*, **146**, 123–130.
- Cai, W., Shi, G., Cowan, T., Bi, D., & Ribbe, J. (2005). The response of the Southern Annular Mode, the East Australian Current, and the southern mid latitude ocean circulation to global warming. *Geophysical Research Letters*, **32**, 1–4.
- Calenge, C. (2006) The package adehabitat for the R software: a tool for the analysis of space and habitat use by animals. *Ecological Modelling*, **197**, 516–519.
- Cannell, B. L., & Cullen, J. M. (1998). The foraging behaviour of little penguins *Eudyptula minor* at different light levels. *Ibis*. **140**, 467–471.
- Cannell, B. L., Chambers, L. E., Wooller, R. D. & Bradley, J. S. (2012). Poorer breeding by little penguins near Perth, Western Australia is correlated with above average sea surface temperatures and a stronger Leeuwin Current. *Marine and Freshwater Research*, **63**, 914–925.
- Carroll, G., Cox, M., Harcourt, R., Pitcher, B., Slip, D., Jonsen, I. (2017). Hierarchical influences of prey distribution on patterns of prey capture by a marine predator. *Functional Ecology* doi:10.1111/1365-2435.12873
- Carroll, G., Everett, J. D., Harcourt, R., Slip, D., & Jonsen, I. (2016a). High sea surface temperatures driven by a strengthening current reduce foraging success by penguins. *Scientific reports*, **6**, 1–13.
- Carroll, G., Slip, D., Jonsen, I. & Harcourt, R. (2014). Supervised accelerometry analysis can identify prey capture by penguins at sea. *Journal of Experimental Biology* **217**, 4295–4302.
- Carroll, G., Turner, E., Dann, P., & Harcourt, R. (2016b). Prior exposure to capture heightens the corticosterone and behavioural responses of little penguins (*Eudyptula minor*) to acute stress. *Conservation Physiology*, **4**, cov061.
- Cetina Heredia, P., Roughan, M., Van Sebille, E., & Coleman, M. A. (2014). Long term trends in the East Australian Current separation latitude and eddy driven transport. *Journal of Geophysical Research: Oceans*, **119**, 4351–4366.
- Chalfoun, A. D., & Martin, T. E. (2010). Facultative nest patch shifts in response to nest predation risk in the Brewer's sparrow: a "win stay, lose switch" strategy? *Oecologia*, **163**, 885–892.
- Charnov, E.L. (1976). Optimal foraging: the marginal value theorem. *Theoretical Population Biology*, **9**, 129–136.
- Chavez, F. P., Ryan, J., Lluch Cota, S. E., & Niquen, M. (2003). From anchovies to sardines and back: multidecadal change in the Pacific Ocean. *Science*, **299**, 217–221.

- Chiaradia, A., Forero, M. G., Hobson, K. A., & Cullen, J. M. (2010). Changes in diet and trophic position of a top predator 10 years after a mass mortality of a key prey. *ICES Journal of Marine Science: Journal du Conseil*, **67**, 1710–1720.
- Chiaradia, A., Forero, M. G., Hobson, K. A., Swearer, S. E., Hume, F., Renwick, L., & Dann, P. (2012). Diet segregation between two colonies of little penguins *Eudyptula minor* in southeast Australia. *Austral Ecology*, **37**, 610–619.
- Chiaradia, A.F. & Kerry, K.R. (1999). Daily nest attendance and breeding performance in the little penguin *Eudyptula minor* at Phillip Island, Australia. *Marine Ornithology*, **27**, 13–20.
- Chimienti, M., Cornulier, T., Owen, E., Bolton, M., Davies, I. M., Travis, J. M., & Scott, B. E. (2016). The use of an unsupervised learning approach for characterizing latent behaviours in accelerometer data. *Ecology and evolution*, **6**, 727–741.
- Clayton, N. S., Bussey, T. J., & Dickinson, A. (2003). Can animals recall the past and plan for the future? *Nature Reviews Neuroscience*, **4**, 685–691.
- Colette, K., Powell, B., Roughan, M., & Oke, P. (2016). Development and evaluation of a high resolution reanalysis of the East Australian Current region using the Regional Ocean Modelling System (ROMS 3.4) and Incremental Strong Constraint 4 Dimensional Variational (IS4D Var) data assimilation. *Geoscientific Model Development*, **9**, 3779.
- Collins, P. M., Green, J. A., Warwick Evans, V., Dodd, S., Shaw, P. J., Arnould, J. P., & Halsey, L. G. (2015). Interpreting behaviors from accelerometry: a method combining simplicity and objectivity. *Ecology and evolution*, **5**, 4642–4654.
- Condie, S. A., Mansbridge, J. V., & Cahill, M. L. (2011). Contrasting local retention and cross shore transports of the East Australian Current and the Leeuwin Current and their relative influences on the life histories of small pelagic fishes. *Deep Sea Research Part II: Topical Studies in Oceanography*, **58**, 606–615.
- Costa, D. P. (1993). The secret life of marine mammals. *Oceanography*, **6**, 120–128.
- Cox, S. L., Miller, P. I., Embling, C. B., Scales, K. L., Bicknell, A. W. J., Hosegood, P. J., Morgan, G., Ingram, S.N. & Votier, S. C. (2016). Seabird diving behaviour reveals the functional significance of shelf sea fronts as foraging hotspots. *Royal Society Open Science*, **3**, 160317.
- Crawford, R. J. Barham, P. J., Underhill, L. G., Shannon, L. J., Coetzee, J. C., Dyer, B. M., Leshoro, T.M. & 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.
- Cressie, N. (1988). Spatial prediction and ordinary kriging. *Mathematical Geology*, **20**, 405–421.
- Cullen, J. M., Montague, T. L., and Hull, C. (1992). Food of little penguins *Eudyptula minor* in Victoria: comparison of three localities between 1985 and 1988. *Emu*, **91**, 318–341.
- Cury, P. M. Boyd, I. L., Bonhommeau, S., Anker Nilssen, T., Crawford, R. J., Furness, R. W., Mills, J.A., Murphy, E.J., Österblom, H., Paleczny, M. & Piatt, J. F. (2011).

Global seabird response to forage fish depletion—one third for the birds. *Science*. **334**, 1703 1706.

- Dann, P., Norman, F. I., Cullen, J. M., Neira, F. J., & Chiaradia, A. (2000). Mortality and breeding failure of little penguins, *Eudyptula minor*, in Victoria, 1995–96, following a widespread mortality of pilchard, *Sardinops sagax*. *Marine and Freshwater Research*, **51**, 355 362.
- Darby, P.C., Fujisaki, I. & Mellow, D.J. (2012). The Effects of Prey Density on Capture Times and Foraging Success of Course Hunting Adult Snail Kites. *Condor*, **114**, 755 763.
- Darimont, C. T., Fox, C. H., Bryan, H. M., & Reimchen, T. E. (2015). The unique ecology of human predators. *Science*, **349**, 858 860.
- Daunt, F., Wanless, S., Harris, M. P., Money, L., & Monaghan, P. (2007). Older and wiser: improvements in breeding success are linked to better foraging performance in European shags. *Functional Ecology*, **21**, 561 567.
- Davoren, G. K., Montevecchi, W. A., & Anderson, J. T. (2003). Search strategies of a pursuit diving marine bird and the persistence of prey patches. *Ecological Monographs*. **73**, 463 481.
- Davoren, G.K. (2000). Variability in foraging in response to changing prey distributions in rhinoceros auklets. *Marine Ecology Progress Series*, **198**, 283 291.
- Deagle, B. E., Chiaradia, A., McInnes, J., & Jarman, S. N. (2010). Pyrosequencing faecal DNA to determine diet of little penguins: is what goes in what comes out? *Conservation Genetics*. **11**, 2039 2048.
- Diner, N. (2001). Correction on school geometry and density: approach based on acoustic image simulation. *Aquatic Living Resources*, **14**, 211 222.
- Doney, S. C., Ruckelshaus, M., Duffy, J. E., Barry, J. P., Chan, F., English, C. A., Galindo, H.M., Grebmeier, J.M., Hollowed, A.B., Knowlton, N. & Polovina, J. (2012). Climate change impacts on marine ecosystems. *Annual Review of Marine Science* **4**, 11 37.
- Doubell, M.J, Ward, T.M., Watson, P., James, C., Carroll, J. and Redondo Rodriguez, A. (2015). Optimising the size and quality of Sardines through real time harvesting. Prepared by the South Australian Research and Development Institute (Aquatic Sciences), Adelaide, 1 47.
- Dragon, A. C., Monestiez, P., Bar Hen, A., & Guinet, C. (2010). Linking foraging behaviour to physical oceanographic structures: southern elephant seals and mesoscale eddies east of Kerguelen Islands. *Progress in Oceanography* **87**, 61 71.
- Draulans, D. (1987). The effect of prey density on foraging behaviour and success of adult and first year grey herons (*Ardea cinerea*). *Journal of Animal Ecology*, **56**, 479 493.
- Duchamp, J. E., Sparks, D. W., & Whitaker, Jr, J. O. (2004). Foraging habitat selection by bats at an urban–rural interface: comparison between a successful and a less successful species. *Canadian Journal of Zoology*, **82**, 1157 1164.

- Dulvy, N. K., Baum, J. K., Clarke, S., Compagno, L. J., Cortés, E., Domingo, A., Fordham, S., Fowler, S., Francis, M.P., Gibson, C. & Martínez, J. (2008). You can swim but you can't hide: the global status and conservation of oceanic pelagic sharks and rays. *Aquatic Conservation: Marine and Freshwater Ecosystems*, **18**, 459–482.
- Einoder, L. D. A review of the use of seabirds as indicators in fisheries and ecosystem management. *Fish. Res.* **95**, 6–13 (2009).
- Elith, J., & Leathwick, J.R. (2009). Species distribution models: ecological explanation and prediction across space and time. *Annual Review of Ecology, Evolution, and Systematics*, **40**, 677.
- Estes, J. A., Terborgh, J., Brashares, J. S., Power, M. E., Berger, J., Bond, W. J., Carpenter, S.R., Essington, T.E., Holt, R.D., Jackson, J.B. & Marquis, R. J. (2011). Trophic downgrading of planet Earth. *Science*, **333**, 301–306.
- Everett, J. D., Baird, M. E., & Suthers, I. M. (2011). Three dimensional structure of a swarm of the salp *Thalia democratica* within a cold core eddy off southeast Australia. *Journal of Geophysical Research: Oceans*, **116**, 1–14.
- Everett, J. D., Baird, M. E., Oke, P. R., & Suthers, I. M. (2012). An avenue of eddies: Quantifying the biophysical properties of mesoscale eddies in the Tasman Sea. *Geophysical Research Letters*, **39**, 1–5.
- Everett, J. D., Baird, M. E., Roughan, M., Suthers, I. M., & Doblin, M. A. (2014). Relative impact of seasonal and oceanographic drivers on surface chlorophyll *a* along a Western Boundary Current. *Progress in Oceanography*, **120**, 340–351.
- Everett, J.D. & Doblin, M.A. (2015). Characterising primary productivity measurements across a dynamic western boundary current region. *Deep Sea Research Part I*. **100**, 105–116.
- Fauchald, P. (1999). Foraging in a hierarchical patch system. *The American Naturalist*, **153**, 603–613.
- Fauchald, P., & Erikstad, K. E. (2002). Scale dependent predator-prey interactions: the aggregative response of seabirds to prey under variable prey abundance and patchiness. *Marine Ecology Progress Series*, **231**, 279–291.
- Fauchald, P., Erikstad, K. E., & Skarsfjord, H. (2000). Scale dependent predator-prey interactions: the hierarchical spatial distribution of seabirds and prey. *Ecology*, **81**, 773–783.
- Fox, J. (1997). Applied regression analysis, linear models, and related methods. *Sage Publishing, CA*
- Fraley, C., Raftery, A.E., Murphy, T.B. & Scrucca, L. (2002). Model based Clustering, Discriminant Analysis and Density Estimation *Journal of the American Statistical Association*, **97**, 611–631.
- Frederiksen, M., Edwards, M., Mavor, R. A., & Wanless, S. (2007). Regional and annual variation in black legged kittiwake breeding productivity is related to sea surface temperature. *Marine Ecology Progress Series*, **350**, 137.

- Friedlaender, A. S., Hazen, E. L., Goldbogen, J. A., Stimpert, A. K., Calambokidis, J., & Southall, B. L. (2016a). Prey mediated behavioral responses of feeding blue whales in controlled sound exposure experiments. *Ecological Applications*, **26**, 1075–1085.
- Friedlaender, A. S., Johnston, D. W., Tyson, R. B., Kaltenberg, A., Goldbogen, J. A., Stimpert, A.K., Curtice, C., Hazen, E.L., Halpin, P.N., Read, A.J. and Nowacek, D.P. (2016b). Multiple stage decisions in a marine central place forager. *Royal Society Open Science*, **3**, 160043.
- Fuller, A. K., Harrison, D. J., & Vashon, J. H. (2007). Winter habitat selection by Canada lynx in Maine: prey abundance or accessibility? *Journal of Wildlife Management*, **71**, 1980–1986.
- Gales, R. P. (1988). The use of otoliths as indicators of Little Penguin *Eudyptula minor* diet. *Ibis*, **130**, 418–426.
- Gales, R., & Green, B. (1990). The annual energetics cycle of little penguins (*Eudyptula minor*). *Ecology*, **71**, 2297–2312.
- Gallon, S., Bailleul, F., Charrassin, J. B., Guinet, C., Bost, C. A., Handrich, Y., and Hindell, M. (2013). Identifying foraging events in deep diving southern elephant seals, *Mirounga leonina*, using acceleration data loggers. *Deep Sea Res Part II*. **88**, 14–22.
- Game, E. T., Grantham, H. S., Hobday, A. J., Pressey, R. L., Lombard, A. T., Beckley, L. E., Gjerde, K., Bustamante, R., Possingham, H.P. & Richardson, A. J. (2009). Pelagic protected areas: the missing dimension in ocean conservation. *Trends in Ecology & Evolution*, **24**, 360–369.
- Garthe, S., Montevecchi, W. A. and Davoren, G. K. (2011). Inter annual changes in prey fields trigger different foraging tactics in a large marine predator *Limnology and Oceanography*, **56**, 802–812.
- Goldbogen, J. A., Calambokidis, J., Friedlaender, A. S., Francis, J., DeRuiter, S. L., Stimpert, A. K., Falcone, E. and Southall, B. L. (2013). Underwater acrobatics by the world's largest predator: 360° rolling manoeuvres by lunge feeding blue whales. *Biology Letters* **9**, 20120986.
- Goldbogen, J. A., Hazen, E. L., Friedlaender, A. S., Calambokidis, J., DeRuiter, S. L., Stimpert, A. K., & Southall, B. L. (2015). Prey density and distribution drive the three dimensional foraging strategies of the largest filter feeder. *Functional Ecology*, **29**, 951–961.
- González Gómez, P. L., & Vasquez, R. A. (2006). A Field Study of Spatial Memory in Green Backed Firecrown Hummingbirds (*Sebanoides sebanoides*). *Ethology*, **112**, 790–795.
- Graham, K. J., Andrew, N. L., & Hodgson, K. E. (2001). Changes in relative abundance of sharks and rays on Australian South East Fishery trawl grounds after twenty years of fishing. *Marine and Freshwater Research*, **52**, 549–561.

- Gray, C. A., & Miskiewicz, A. G. (2000). Larval fish assemblages in south east Australian coastal waters: seasonal and spatial structure. *Estuarine, Coastal and Shelf Science*, **50**, 549 570.
- Green, B., Brothers, N., and Gales, R. (1988). Water, Sodium and Energy Turnover in Free Living Little Penguins, *Eudyptula minor*. *Australian Journal of Zoology*, **36**, 429 440.
- Grémillet, D. J., & Plös, A. L. (1994). The use of stomach temperature records for the calculation of daily food intake in cormorants. *Journal of Experimental Biology*, **189**, 105 115.
- Grémillet, D., & Charmantier, A. (2010). Shifts in phenotypic plasticity constrain the value of seabirds as ecological indicators of marine ecosystems. *Ecological Applications*, **20**, 1498 1503.
- Grémillet, D., Dell’Omo, G., Ryan, P. G., Peters, G., Ropert Coudert, Y., & 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., Huggett, J. A., Coetzee, J. C., Verheye, H.M., Daunt, F., Wanless, S. & Ryan, P. G. (2008). Spatial match–mismatch in the Benguela upwelling zone: should we expect chlorophyll and sea surface temperature to predict marine predator distributions? *Journal of Applied Ecology*, **45**, 610 621.
- Grémillet, D., Lewis, S., Drapeau, L., van Der Lingen, C.D., Huggett, J.A., Coetzee, J.C., Verheye, H.M., Daunt, F., Wanless, S. and Ryan, P.G. (2008). Spatial match–mismatch in the Benguela upwelling zone: should we expect chlorophyll and sea surface temperature to predict marine predator distributions? *Journal of Applied Ecology*, **45**, 610 621.
- Grémillet, D., Péron, C., Kato, A., Amélineau, F., Ropert Coudert, Y., Ryan, P. G., & Pichegru, L. (2016). Starving seabirds: unprofitable foraging and its fitness consequences in Cape gannets competing with fisheries in the Benguela upwelling ecosystem. *Marine biology*, **163**, 1 11.
- Grünewälder, S., Broekhuis, F., Macdonald, D. W., Wilson, A. M., McNutt, J. W., Shawe Taylor, J., and Hailes, S. (2012). Movement activity based classification of animal behaviour with an application to data from cheetah (*Acinonyx jubatus*). *PloS One*, **7**, e49120.
- Guinet, C., Vacquié Garcia, J., Picard, B., Bessigneul, G., Lebras, Y., Dragon, A. C., Viviant, M., Arnould, J.P.Y. and Bailleul, F. (2014). Southern elephant seal foraging success in relation to temperature and light conditions: insight into prey distribution. *Marine Ecology Progress Series*, **499**, 285 301.
- Handcock, R. N., Swain, D. L., Bishop Hurley, G. J., Patison, K. P., Wark, T., Valencia, P., Corke, P. & O’Neill, C. J. (2009). Monitoring animal behaviour and environmental interactions using wireless sensor networks, GPS collars and satellite remote sensing. *Sensors*, **9**, 3586 3603.

- Hassell, M., & Southwood, T. R. E. (1978). Foraging strategies of insects. *Annual Review of Ecology and Systematics*, **9**, 75–98.
- Hazen, E. L., Friedlaender, A. S., & Goldbogen, J. A. (2015). Blue whales (*Balaenoptera musculus*) optimize foraging efficiency by balancing oxygen use and energy gain as a function of prey density. *Science Advances*, **1**, e1500469.
- Hazen, E. L., Jorgensen, S., Rykaczewski, R. R., Bograd, S. J., Foley, D. G., Jonsen, I. D., Shaffer, S.A., Dunne, J.P., Costa, D.P., Crowder, L.B. & Block, B. A. (2013). Predicted habitat shifts of Pacific top predators in a changing climate. *Nature Climate Change*, **3**, 234–238.
- Heaslip, S. G., and Hooker, S. K. (2008). Effect of animal borne camera and flash on the diving behaviour of the female Antarctic fur seal (*Arctocephalus gazella*). *Deep Sea Res Pt I*, **55**, 1179–1192.
- Heithaus, M. R., & Dill, L. M. (2002). Food availability and tiger shark predation risk influence bottlenose dolphin habitat use. *Ecology*, **83**, 480–491.
- Heithaus, M. R., Frid, A., Wirsing, A. J., & Worm, B. (2008). Predicting ecological consequences of marine top predator declines. *Trends in Ecology & Evolution*, **23**, 202–210.
- Hobday, A. J., Young, J. W., Abe, O., Costa, D. P., Cowen, R. K., Evans, K., Gasalla, M.A., Kloser, R., Maury, O. & Weng, K. C. (2013). Climate impacts and oceanic top predators: moving from impacts to adaptation in oceanic systems. *Reviews in fish biology and fisheries*, **23**, 537–546.
- Hobday, D. K. (1992). Abundance and distribution of pilchard and Australian anchovy as prey species for the little penguin *Eudyptula minor* at Phillip Island, Victoria. *Emu*, **91**, 342–354.
- Hoover, J. P. (2003). Decision rules for site fidelity in a migratory bird, the prothonotary warbler. *Ecology*, **84**, 416–430.
- Hopcraft, J. G. C., Sinclair, A. R. E., & Packer, C. (2005). Planning for success: Serengeti lions seek prey accessibility rather than abundance. *Journal of Animal Ecology*, **74**, 559–566.
- Hoskins, A. J., Dann, P., Robert Coudert, Y., Kato, A., Chiaradia, A., Costa, D. P., & Arnould, J. P. (2008). Foraging behaviour and habitat selection of the little penguin *Eudyptula minor* during early chick rearing in Bass Strait, Australia. *Marine Ecology Progress Series*, **366**, 293–303.
- Hussey, N. E., Kessel, S. T., Aarestrup, K., Cooke, S. J., Cowley, P. D., Fisk, A. T., Harcourt, R.G., Holland, K.N., Iverson, S.J., Kocik, J.F. & Flemming, J. E. M. (2015). Aquatic animal telemetry: a panoramic window into the underwater world. *Science*, **348**, 1255–1262.
- Inchausti, P., Guinet, C., Koudil, M., Durbec, J. P., Barbraud, C., Weimerskirch, H., Cherel, Y. & Jouventin, P. (2003). Inter annual variability in the breeding performance of seabirds in relation to oceanographic anomalies that affect the Crozet and the Kerguelen sectors of the Southern Ocean. *Journal of Avian Biology*, **34**, 170–176.

- Jackman, S. (2015). pscl: Classes and Methods for R Developed in the Political Science Computational Laboratory, Stanford University. Department of Political Science, Stanford University. Stanford, California. R package version 1.4.9.
- Jayne, S. R., & Marotzke, J. (2002). The oceanic eddy heat transport. *Journal of Physical Oceanography*, **32**, 3328–3345.
- Jiménez, S., Domingo, A., Abreu, M., & Brazeiro, A. (2011). Structure of the seabird assemblage associated with pelagic longline vessels in the southwestern Atlantic: implications for bycatch. *Endangered Species Research* **15**, 241–254.
- Johannesen, E., Houston, D. & Russell, J. (2003). Increased survival and breeding performance of double breeders in little penguins *Eudyptula minor*, New Zealand: evidence for individual bird quality? *Journal of Avian Biology*, **34**, 198–210.
- Jonsen, I. D., Flemming, J. M., & Myers, R. A. (2005). Robust state–space modelling of animal movement data. *Ecology*, **86**, 2874–2880.
- Jonsen, I. D., Myers, R. A., & Flemming, J. M. (2003). Meta analysis of animal movement using state space models. *Ecology*, **84**, 3055–3063.
- Karanth, K. U., Nichols, J. D., Kumar, N. S., Link, W. A., & Hines, J. E. (2004). Tigers and their prey: predicting carnivore densities from prey abundance. *Proceedings of the National Academy of Sciences of the United States of America*, **101**, 4854–4858.
- Kareiva, P. & Odell, G. (1987). Swarms of predators exhibit “prey taxis” if individual predators use area restricted search. *American Naturalist* **130**, 233–270.
- Kato A, Ropert Coudert Y, Chiaradia A (2008) Regulation of trip duration by an inshore forager, the little penguin (*Eudyptula minor*), during incubation. *Auk* **125**, 588–593.
- Kays, R., Crofoot, M. C., Jetz, W., & Wikelski, M. (2015). Terrestrial animal tracking as an eye on life and planet. *Science*, **348**, 1–9.
- Kerr, J. T., & Ostrovsky, M. (2003). From space to species: ecological applications for remote sensing. *Trends in Ecology & Evolution*, **18**, 299–305.
- Kjørboe, T. (1993). Turbulence, phytoplankton cell size, and the structure of pelagic food webs. *Advances in marine biology*, **29**, 1–72.
- Klomp, N. I., & Wooller, R. D. (1988). Diet of little penguins, *Eudyptula minor*, from Penguin Island, western Australia. *Mar. Freshwater. Res.* **39**, 633–639.
- Kokubun N, Kim JH, Shin HC, Naito Y, Takahashi A. (2011). Penguin head movement detected using small accelerometers: A proxy of prey encounter rate. *Journal of Experimental Biology*, **214**, 3760–3767
- Kotliar, N. B., & Wiens, J. A. (1990). Multiple scales of patchiness and patch structure: a hierarchical framework for the study of heterogeneity. *Oikos*, **59**, 253–260.
- Ladds, M. A., Thompson, A. P., Kadar, J. P., Slip, D., Hocking, D., & Harcourt, R. (2017). Super machine learning: improving accuracy and reducing variance of behaviour classification from accelerometry. *Animal Biotelemetry*, **5**, 1–8.

- Ladds, M. A., Thompson, A. P., Slip, D. J., Hocking, D. P., & Harcourt, R. G. (2016). Seeing It All: Evaluating Supervised Machine Learning Methods for the Classification of Diverse Otariid Behaviours. *PloS one*, **11**, e0166898.
- Lagarde, F., Guillon, M., Dubroca, L., Bonnet, X., Ben Kaddour, K., and Slimani, T. (2008). Slowness and acceleration: a new method to quantify the activity budget of chelonians. *Animal Behaviour*, **75**, 319–329.
- Lanz, E., López Martínez, J., Nevárez Martínez, M., & Dworak, J. A. (2009). Small pelagic fish catches in the Gulf of California associated with sea surface temperature and chlorophyll. *Calif. Coop. Oceanic Fish. Invest. Rep.* **50**, 134–146.
- Leos Barajas, V., Photopoulou, T., Langrock, R., Patterson, T. A., Watanabe, Y. Y., Murgatroyd, M., & Papastamatiou, Y. P. (2017). Analysis of animal accelerometer data using hidden Markov models. *Methods in Ecology and Evolution*, **8**, 161–173.
- Liebsch, N., Wilson, R. P., Bornemann, H., Adelung, D., & Plötz, J. (2007). Mouthing off about fish capture: Jaw movement in pinnipeds reveals the real secrets of ingestion. *Deep Sea Research Part II: Topical Studies in Oceanography*, **54**, 256–269.
- Lindgren, M., & Checkley Jr, D. M. (2012). Temperature dependence of Pacific sardine (*Sardinops sagax*) recruitment in the California Current Ecosystem revisited and revised. *Canadian Journal of Fisheries and Aquatic Science*, **70**, 245–252.
- Linkhart, B. D., & Reynolds, R. T. (2007). Return rate, fidelity, and dispersal in a breeding population of flammulated owls (*Otus flammeolus*). *The Auk*, **124**, 264–275.
- MacLennan, D. N., Fernandes, P. G., & Dalen, J. (2002). A consistent approach to definitions and symbols in fisheries acoustics. *ICES Journal of Marine Science: Journal du Conseil*, **59**, 365–369.
- Marker, L. L., Muntifering, J. R., Dickman, A. J., Mills, M. G. L., & Macdonald, D. W. (2003). Quantifying prey preferences of free ranging Namibian cheetahs. *South African Journal of Wildlife Research*, **33**, 43–53.
- Martiskainen, P., Järvinen, M., Skön, J. P., Tiirikainen, J., Kolehmainen, M., & Mononen, J. (2009). Cow behaviour pattern recognition using a three dimensional accelerometer and support vector machines. *Applied Animal Behaviour Science*, **119**, 32–38.
- Mattern, T., Ellenberg, U., Houston, D. M., & Davis, L. S. (2007). Consistent foraging routes and benthic foraging behaviour in yellow eyed penguins. *Marine Ecology Progress Series*, **343**, 295–306.
- McClune, D. W., Marks, N. J., Delahay, R. J., Montgomery, W. I., & Scantlebury, D. M. (2015). Behaviour time budget and functional habitat use of a free ranging European badger (*Meles meles*). *Animal Biotelemetry*, **3**, 1–7.

- McGregor, H. W., Legge, S., Jones, M. E., & Johnson, C. N. (2014). Landscape management of fire and grazing regimes alters the fine scale habitat utilisation by feral cats. *PLoS One*, **9**, e109097.
- McInnes, A. M., Ryan, P. G., Lacerda, M., Deshayes, J., Goschen, W. S., & Pichegru, L. (2017). Small pelagic fish responses to fine scale oceanographic conditions: implications for the endangered African penguin. *Marine Ecology Progress Series*, **569**, 187–203.
- Meyer, D., Dimitriadou, E., Hornik, K., Weingessel, A. and Leisch F. (2014). e1071: Misc Functions of the Department of Statistics (e1071), TU Wien. R package version 1.6 2. <http://CRAN.R-project.org/package=e1071>
- Mickelson, M. J., Dann, P., & Cullen, J. M. (1992). Sea temperature in Bass Strait and breeding success of the little penguin *Eudyptula minor* at Phillip Island, south eastern Australia. *Emu*, **91**, 355–368.
- Minderman, J., Lind, J., and Cresswell, W. (2006). Behaviourally mediated indirect effects: interference competition increases predation mortality in foraging redshanks. *Journal of Animal Ecology* **75**, 713–723.
- Mitani, Y., Watanabe, Y., Sato, K., Cameron, M. F., & Naito, Y. (2004). 3D diving behavior of Weddell seals with respect to prey accessibility and abundance. *Marine Ecology Progress Series*, **281**, 275–281.
- Moll, R. J., Millspaugh, J. J., Beringer, J., Sartwell, J., & He, Z. (2007). A new ‘view’ of ecology and conservation through animal borne video systems. *Trends in ecology & evolution*, **22**, 660–668.
- Montague, T. L., & Cullen, J. M. (1988). The diet of the little penguin *Eudyptula minor* at Phillip Island, Victoria. *Emu*, **88**, 138–149.
- Morales, J. M., Moorcroft, P. R., Matthiopoulos, J., Frair, J. L., Kie, J. G., Powell, R. A., Merrill, E.H. and Haydon, D.T., & Haydon, D. T. (2010). Building the bridge between animal movement and population dynamics. *Philosophical Transactions of the Royal Society B: Biological Sciences*, **365**, 2289–2301.
- Mullaney, T. J., & Suthers, I. M. (2013). Entrainment and retention of the coastal larval fish assemblage by a short lived, submesoscale, frontal eddy of the East Australian Current. *Limnology and Oceanography*, **58**, 1546–1556.
- Nathan, R., Spiegel, O., Fortmann Roe, S., Harel, R., Wikelski, M., & Getz, W. M. (2012). Using tri axial acceleration data to identify behavioral modes of free ranging animals: general concepts and tools illustrated for griffon vultures. *Journal of Experimental Biology*, **215**, 986–996.
- Nevárez Martinez, M. O., Lluch Belda, D., Cisneros Mata, M. A., Santos Molina, J. P., De los Angeles Martinez Zavala, M., & Lluch Cota, S. E. (2001). Distribution and abundance of the Pacific sardine (*Sardinops sagax*) in the Gulf of California and their relation with the environment. *Progress in Oceanography*, **49**, 565–580.
- Nevitt, G. A., Losekoot, M., & Weimerskirch, H. (2008). Evidence for olfactory search in wandering albatross, *Diomedea exulans*. *Proceedings of the National Academy of Sciences*, **105**, 4576–4581.

- Noto, M., & Yasuda, I. (1999). Population decline of the Japanese sardine, *Sardinops melanostictus*, in relation to sea surface temperature in the Kuroshio Extension. *Canadian Journal of Fisheries and Aquatic Science*, **56**, 973–983.
- Novack, A. J., Main, M. B., Sunquist, M. E., & Labisky, R. F. (2005). Foraging ecology of jaguar (*Panthera onca*) and puma (*Puma concolor*) in hunted and non hunted sites within the Maya Biosphere Reserve, Guatemala. *Journal of Zoology*, **267**, 167–178.
- O'Donoghue, S. H., Drapeau, L., & Peddemors, V. M. (2010b). 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.
- O'Donoghue, S. H., Drapeau, L., Dudley, S. F., & Peddemors, V. M. (2010a). The KwaZulu Natal sardine run: shoal distribution in relation to nearshore environmental conditions, 1997–2007. *African Journal of Marine Science*, **32**, 293–307.
- Okuyama J, Kawabata Y, Naito Y, Arai N, Kobayashi M (2009) Monitoring beak movements with an acceleration datalogger: a useful technique for assessing the feeding and breathing behaviors of sea turtles. *Endangered Species Research*, **10**, 39–45.
- Olson, D.B. (2001). Biophysical dynamics of western transition zones: a preliminary synthesis. *Fisheries Oceanography*, **10**, 133–150.
- Oro, D., & Furness, R. W. (2002). Influences of food availability and predation on survival of kittiwakes. *Ecology*, **83**, 2516–2528.
- Paiva, V. H., Geraldes, P., Ramírez, I., Meirinho, A., Garthe, S., & Ramos, J. A. (2010). Foraging plasticity in a pelagic seabird species along a marine productivity gradient. *Marine Ecology Progress Series*, **398**, 259–274.
- Paleczny, M., Hammill, E., Karpouzi, V., & Pauly, D. (2015). Population trend of the world's monitored seabirds, 1950–2010. *PLoS One*, **10**, e0129342.
- Parmesan, C., & Yohe, G. (2003). A globally coherent fingerprint of climate change impacts across natural systems. *Nature*, **421**, 37–42.
- Patrick, S. C., & Weimerskirch, H. (2017). Reproductive success is driven by local site fidelity despite stronger specialisation by individuals for large scale habitat preference. *Journal of Animal Ecology*, **86**, 674–682.
- Pebesma, E.J., 2004. Multivariable geostatistics in S: the gstat package. *Computers & Geosciences*, **30**, 683–691.
- Pelletier, L., Chiaradia, A., Kato, A., & Ropert Coudert, Y. (2014). Fine scale spatial age segregation in the limited foraging area of an inshore seabird species, the little penguin. *Oecologia*, **176**, 399–408.
- Pelletier, L., Kato, A., Chiaradia, A. & 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.

- Pikitch, E. K., Rountos, K. J., Essington, T. E., Santora, C., Pauly, D., Watson, R., Sumaila, U.R., Boersma, P.D., Boyd, I.L., Conover, D.O. & Cury, P. (2014). The global contribution of forage fish to marine fisheries and ecosystems. *Fish and Fisheries* **15**, 43–64.
- Piper, W. H. (2011). Making habitat selection more “familiar”: a review. *Behavioral Ecology and Sociobiology*, **65**, 1329–1351.
- Ponganis, P. J. (2007). Bio logging of physiological parameters in higher marine vertebrates. *Deep Sea Research Part II: Topical Studies in Oceanography*, **54**, 183–192.
- Preisser, E. L., Bolnick, D. I., & Benard, M. F. (2005). Scared to death? The effects of intimidation and consumption in predator–prey interactions. *Ecology*, **86**, 501–509.
- R Core Team (2013). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL <http://www.R-project.org/>.
- R Core Team (2015). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.
- R Core Team (2016). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL <https://www.R-project.org/>.
- Reid, D. G., Scalabrin, C., Petitgas, P., Masse, J., Aukland, R., Carrera, P., and Georgakarakos, S. 2000. Standard protocols for the analysis of school based data from echosounder surveys. *Fisheries Research*, **47**, 125–136.
- Resheff, Y. S., Rotics, S., Harel, R., Spiegel, O., & Nathan, R. (2014). AcceleRater: a web application for supervised learning of behavioral modes from acceleration measurements. *Movement Ecology*, **2**, 27.
- Ridgway, K. & Hill, K. The East Australian Current. In *A Marine Climate Change Impacts and Adaptation Report Card for Australia 2009* (Eds. E.S. Poloczanska, A.J. Hobday and A.J. Richardson), NCCARF Publication 05/09 (2009).
- Ridgway, K. R. (2007). Long term trend and decadal variability of the southward penetration of the East Australian Current. *Geophysical Research Letters*, **34**, 1–5.
- Robinson, S., Chiaradia, A. & Hindell, M.A. (2005). The effect of body condition on the timing and success of breeding in Little Penguins *Eudyptula minor*. *Ibis*, **147**, 483–489.
- Robert Coudert, Y. and Wilson, R. P. (2005). Trends and perspectives in animal attached remote sensing. *Frontiers in Ecology and the Environment*, **3**, 437–444.
- Robert Coudert, Y., Chiaradia, A., & Kato, A. (2006a). An exceptionally deep dive by a little penguin, *Eudyptula minor*. *Marine Ornithology*, **34**, 71–74.

- Ropert Coudert, Y., Kato, A., Baudat, J., Bost, C. A., Le Maho, Y., and Naito, Y. (2001). Time/depth usage of Adélie penguins: an approach based on dive angles. *Polar Biology*, **24**, 467 470.
- Ropert Coudert, Y., Kato, A., Wilson, R. P., & Cannell, B. (2006b). Foraging strategies and prey encounter rate of free ranging Little Penguins. *Marine Biology*, **149**, 139 148.
- Rosenbaum, L., Hinselmann, G., Jahn, A., and Zell, A. (2011). Interpreting linear support vector machine models with heat map molecule coloring. *Journal of Chemical Information and Modeling*, **3**, 1 12.
- Rothman, J. M., Chapman, C. A., and Van Soest, P. J. (2012). Methods in primate nutritional ecology: a user's guide. *International Journal of Primatology* **33**, 542 566.
- Roughan, M. & Middleton, J. H. (2002). A comparison of observed upwelling mechanisms off the east coast of Australia. *Continental Shelf Research*, **22**, 2551 2572.
- Roughan, M., Oke, P. R., & Middleton, J. H. (2003). A modelling study of the climatological current field and the trajectories of upwelled particles in the East Australian Current. *Journal of Physical Oceanography*, **33**, 2551 2564.
- Sakamoto, K. Q., Sato, K., Ishizuka, M., Watanuki, Y., Takahashi, A., Daunt, F., & Wanless, S. (2009). Can ethograms be automatically generated using body acceleration data from free ranging birds? *PloS one*, **4**, e5379.
- Sala, J. E., Wilson, R. P., & Quintana, F. (2015). Foraging effort in Magellanic penguins: balancing the energy books for survival? *Marine Biology*, **162**, 501 514.
- Santora, J. A., Ralston, S., & Sydeman, W. J. (2011). Spatial organization of krill and seabirds in the central California Current. *ICES Journal of Marine Science: Journal du Conseil*, fsr046.
- Sato, K., Charrassin, J. B., Bost, C. A., and Naito, Y. (2004). Why do macaroni penguins choose shallow body angles that result in longer descent and ascent durations? *Journal of Experimental Biology*, **207**, 4057 4065.
- Scales, K. L., Miller, P. I., Embling, C. B., Ingram, S. N., Pirodda, E., & Votier, S. C. (2014). Mesoscale fronts as foraging habitats: composite front mapping reveals oceanographic drivers of habitat use for a pelagic seabird. *Journal of the Royal Society Interface*, **11**, 20140679.
- Scales, K. L., Miller, P. I., Ingram, S. N., Hazen, E. L., Bograd, S. J., & Phillips, R. A. (2016). Identifying predictable foraging habitats for a wide ranging marine predator using ensemble ecological niche models. *Diversity and Distributions*, **22**, 212 224.
- Schaefer, J. A., Bergman, C. M., & Luttich, S. N. (2000). Site fidelity of female caribou at multiple spatial scales. *Landscape Ecology*, **15**, 731 739.
- Schipper, J., Chanson, J. S., Chiozza, F., Cox, N. A., Hoffmann, M., Katariya, V., Lamoreux, J., Rodrigues, A.S., Stuart, S.N., Temple, H.J. & Baillie, J. (2008). The

- status of the world's land and marine mammals: diversity, threat, and knowledge. *Science*, **322**, 225–230.
- Schmidt KA (2001) Site fidelity in habitats with contrasting levels of nest predation and brood parasitism. *Evolutionary Ecology Research*, **3**, 633–648
- Schmidt, K. (2008). Behavioural and spatial adaptation of the Eurasian lynx to a decline in prey availability. *Acta Theriologica*, **53**, 1–16.
- Shaughnessy, P. D., Nicholls, A. O., & Briggs, S. V. (2008). Do tour boats affect fur seals at Montague Island, New South Wales? *Tourism in Marine Environments*, **5**, 15–27.
- Shawe Taylor J, Cristianini N (2004) Kernel Methods for Pattern Analysis. Cambridge, UK: Cambridge University Press.
- Sherley, R. B., Ludynia, K., Dyer, B. M., Lamont, T., Makhado, A. B., Roux, J. P., Scales, K.L., Underhill, L.G. & Votier, S. C. (2017). Metapopulation tracking juvenile penguins reveals an ecosystem wide ecological trap. *Current Biology*, **27**, 563–568.
- Simeone A. and Wilson R.P. (2003) In depth studies of Magellanic penguin (*Spheniscus magellanicus*) foraging: can we estimate prey consumption by perturbations in the dive profile? *Marine Biology*, **143**, 825–831.
- Sims, D. W., Wearmouth, V. J., Southall, E. J., Hill, J. M., Moore, P., Rawlinson, K., Hutchinson, N., Budd, G.C., Righton, D., Metcalfe, J.D. & Nash, J. P. (2006a). Hunt warm, rest cool: bioenergetic strategy underlying diel vertical migration of a benthic shark. *Journal of Animal Ecology*, **75**, 176–190.
- Sims, D. W., Witt, M. J., Richardson, A. J., Southall, E. J., & Metcalfe, J. D. (2006b). Encounter success of free ranging marine predator movements across a dynamic prey landscape. *Proceedings of the Royal Society of London B: Biological Sciences*, **273**, 1195–1201.
- Sommerfeld, J., Kato, A., Ropert Coudert, Y., Garthe, S., Wilcox, C., & Hindell, M. A. (2015). Flexible foraging behaviour in a marine predator, the Masked booby (*Sula dactylatra*), according to foraging locations and environmental conditions. *Journal of Experimental Marine Biology and Ecology*, **463**, 79–86.
- Spencer, W. D. (2012). Home ranges and the value of spatial information. *Journal of Mammalogy*, **93**, 929–947.
- Stahel, C. and Gales, R. (1987) *Little Penguin: Fairy Penguins in Australia*, UNSW Press, Kensington, Australia
- Stewart, J., Ballinger, G. & Ferrell, D. (2010) Review of the biology and fishery for Australian sardines (*Sardinops sagax*) in New South Wales. Industry & Investment NSW.
- Suryan, R. M., Santora, J. A., & Sydeman, W. J. (2012). New approach for using remotely sensed chlorophyll a to identify seabird hotspots. *Marine Ecology Progress Series*. **451**, 213–225

- Suthers, I. M., Taggart, C. T., Rissik, D., & Baird, M. E. (2006). Day and night ichthyoplankton assemblages and zooplankton biomass size spectrum in a deep ocean island wake. *Marine Ecology Progress Series*, **322**, 225–238.
- Suthers, I. M., Young, J. W., Baird, M. E., Roughan, M., Everett, J. D., Brassington, G. B., Byrne, M., Condie, S.A., Hartog, J.R., Hassler, C.S. & Hobday, A. J. (2011). The strengthening East Australian Current, its eddies and biological effects—an introduction and overview. *Deep Sea Research Part II: Topical Studies in Oceanography*, **58**, 538–546.
- Sutton, G.J., Hoskins, A.J., & Arnould, J.P. (2015). Benefits of group foraging depend on prey type in a small marine predator, the little penguin. *PloS one*, **10**, e0144297.
- Switzer, P. V. (1993). Site fidelity in predictable and unpredictable habitats. *Evolutionary Ecology*, **7**, 533–555.
- Switzer, P. V. (1997). Past reproductive success affects future habitat selection. *Behavioral Ecology and Sociobiology*, **40**, 307–312.
- Sydeman, W. J., Poloczanska, E., Reed, T. E., & Thompson, S. A. (2015). Climate change and marine vertebrates. *Science*, **350**, 772–777.
- Sydeman, W. J., Thompson, S. A., Piatt, J. F., García Reyes, M., Zador, S., Williams, J. C., Romano, M. & Renner, H. M. (2017). Regionalizing indicators for marine ecosystems: Bering Sea–Aleutian Island seabirds, climate, and competitors. *Ecological Indicators*, **78**, 458–469.
- Takahashi, A., Matsumoto, K., Hunt, G. L., Shultz, M. T., Kitaysky, A. S., Sato, K., Iida, K. & Watanuki, Y. (2008). Thick billed murre use different diving behaviors in mixed and stratified waters. *Deep Sea Research Pt. I*, **55**, 1837–1845.
- Thayer, J.A., Bertram, D.F., Hatch, S.A., Hipfner, M.J., Slater, L., Sydeman, W.J. & Watanuki, Y. (2008). Forage fish of the Pacific Rim as revealed by diet of a piscivorous seabird: synchrony and relationships with sea surface temperature. *Canadian Journal of Fisheries and Aquatic Sciences*, **65**, 1610–1622.
- Thiebault, A., Mullers, R. H., Pistorius, P. A., & Tremblay, Y. (2014). Local enhancement in a seabird: reaction distances and foraging consequence of predator aggregations. *Behavioral Ecology*, **25**, 1302–1310.
- Thompson, D., and Fedak, M. A. (2001). How long should a dive last? A simple model of foraging decisions by breath hold divers in a patchy environment. *Animal Behaviour*, **61**, 287–296.
- Thums, M., Bradshaw, C. J., & Hindell, M. A. (2011). In situ measures of foraging success and prey encounter reveal marine habitat dependent search strategies. *Ecology*, **92**, 1258–1270.
- Tilman, D., Fargione, J., Wolff, B., D'Antonio, C., Dobson, A., Howarth, R., Schindler, D., Schlesinger, W.H., Simberloff, D. & Swackhamer, D. (2001). Forecasting agriculturally driven global environmental change. *Science*, **292**, 281–284.

- Tranter, D. J., Carpenter, D. J., & Leech, G. S. (1986). The coastal enrichment effect of the East Australian Current eddy field. *Deep Sea Research Part A. Oceanographic Research Papers*, **33**, 1705–1728.
- Tranter, D. J., Tafe, D. J., & Sandland, R. L. (1983). Some zooplankton characteristics of warm core eddies shed by the East Australian Current, with particular reference to copepods. *Marine and Freshwater Research*, **34**, 587–607.
- Trebilco, R., Gales, R., Lawrence, E., Alderman, R., Robertson, G., & Baker, G. B. (2010). Characterizing seabird bycatch in the eastern Australian tuna and billfish pelagic longline fishery in relation to temporal, spatial and biological influences. *Aquatic Conservation: Marine and Freshwater Ecosystems*, **20**, 531–542.
- Tremblay, Y., Thiebault, A., Mullers, R., & Pistorius, P. (2014). Bird borne video cameras show that seabird movement patterns relate to previously unrevealed proximate environment, not prey. *PLoS One*, **9**, e88424.
- Turchin, P. (1998) Quantitative analysis of movement: measuring and modeling population redistribution in animals and plants. Sinauer Associates, Sunderland, Massachusetts, USA.
- Uehara, S., Syahailatua, A., & Suthers, I. M. (2005). Recent growth rate of larval pilchards *Sardinops sagax* in relation to their stable isotope composition, in an upwelling zone of the East Australian Current. *Marine and Freshwater Research*, **56**, 549–560.
- Valletta, J. J., Torney, C., Kings, M., Thornton, A., & Madden, J. (2017). Applications of machine learning in animal behaviour studies. *Animal Behaviour*, **124**, 203–220.
- Viviant, M., Monestiez, P., and Guinet, C. (2014). Can We Predict Foraging Success in a Marine Predator from Dive Patterns Only? Validation with Prey Capture Attempt Data. *PloS One*, **9**, e88503.
- Viviant, M., Trites, A. W., Rosen, D. A., Monestiez, P., and Guinet, C. (2010). Prey capture attempts can be detected in Steller sea lions and other marine predators using accelerometers. *Polar Biology*, **33**, 713–719.
- Vogel, J. L., & Beauchamp, D. A. (1999). Effects of light, prey size, and turbidity on reaction distances of lake trout (*Salvelinus namaycush*) to salmonid prey. *Canadian Journal of Fisheries and Aquatic Sciences*, **56**, 1293–1297.
- Wakefield, E. D., Cleasby, I. R., Bearhop, S., Bodey, T. W., Davies, R. D., Miller, P. I., Newton, J., Votier, S.C. & Hamer, K. C. (2015). Long term individual foraging site fidelity—why some gannets don't change their spots. *Ecology*, **96**, 3058–3074.
- Wang, Y., Nickel, B., Rutishauser, M., Bryce, C. M., Williams, T. M., Elkaim, G., & Wilmers, C. C. (2015). Movement, resting, and attack behaviors of wild pumas are revealed by tri axial accelerometer measurements. *Movement Ecology*, **3**, 1–12.
- Ward, T.M., Burnell, O., Ivey, A. Carroll, J. Keane, J., Lyle, J., Sexton, S. South Australian Research and Development Institute (Aquatic Sciences) (2015). Summer

- spawning patterns and preliminary Daily Egg Production Method survey of Jack Mackerel and Sardine off the East Coast, March.
- Watanabe, S., Izawa, M., Kato, A., Ropert Coudert, Y., and Naito, Y. (2005). A new technique for monitoring the detailed behaviour of terrestrial animals: a case study with the domestic cat. *Applied Animal Behaviour Science*, **94**, 117–131.
- Watanabe, Y. Y., & Takahashi, A. (2013). Linking animal borne video to accelerometers reveals prey capture variability. *Proceedings of the National Academy of Sciences*, **110**, 2199–2204.
- Watanabe, Y. Y., and Takahashi, A. (2013). Linking animal borne video to accelerometers reveals prey capture variability. *Proceedings of the National Academy of Sciences*, **110**, 2199–2204.
- Watanabe, Y.Y., Ito, M., Takahashi, A. (2014). Testing optimal foraging theory in a penguin–krill system. *Proceedings of the Royal Society B*, **281**, 20132376.
- Weerheim, M. S., Klomp, N. I., Brunsting, A. M., and Komdeur, J. (2003). Population size, breeding habitat and nest site distribution of little penguins (*Eudyptula minor*) on Montague Island, New South Wales. *Wildlife Research*, **30**, 151–157.
- Weimerskirch, H. (2007). Are seabirds foraging for unpredictable resources? *Deep Sea Research Part II: Topical Studies in Oceanography*, **54**, 211–223.
- Weimerskirch, H., Gault, A., & Cherel, Y. (2005a). Prey distribution and patchiness: factors in foraging success and efficiency of wandering albatrosses. *Ecology*, **86**, 2611–2622.
- Weimerskirch, H., Le Corre, M., Jaquemet, S., & Marsac, F. (2005b). Foraging strategy of a tropical seabird, the red footed booby, in a dynamic marine environment. *Marine Ecology Progress Series*, **288**, 251–261.
- Weimerskirch, H., Pinaud, D., Pawlowski, F., & Bost, C. A. (2007). Does prey capture induce area restricted search? A fine scale study using GPS in a marine predator, the wandering albatross. *The American Naturalist*, **170**, 734–743.
- Weimerskirch, H., Salamolard, M., Sarrazin, F., & Jouventin, P. (1993). Foraging strategy of wandering albatrosses through the breeding season: a study using satellite telemetry. *The Auk*, **110**, 325–342.
- Wellenreuther, M., & Connell, S. D. (2002). Response of predators to prey abundance: separating the effects of prey density and patch size. *Journal of Experimental Marine Biology*, **273**, 61–71.
- Wilkinson, G. S., & Boughman, J. W. (1998). Social calls coordinate foraging in greater spear nosed bats. *Animal Behaviour*, **55**, 337–350.
- Wilson, K., Littnan, C., Halpin, P., & Read, A. (2017). Integrating multiple technologies to understand the foraging behaviour of Hawaiian monk seals. *Royal Society Open Science*, **4**, 160703.
- Wilson, R. P., Quintana, F. & Hobson, V. J. (2011). Construction of energy landscapes can clarify the movement and distribution of foraging animals. *Proceedings of the Royal Society B*, **282**, 975–980.

- Wilson, R. P., Sclaro, J. A., Grémillet, D., Kierspel, M. A., Laurenti, S., Upton, J., Gallelli, H., Quintana, F., Frere, E., Müller, G. & Straten, M. T. (2005). How do Magellanic Penguins cope with variability in their access to prey? *Ecological Monographs*, **75**, 379–401.
- Wilson, R. P., White, C. R., Quintana, F., Halsey, L. G., Liebsch, N., Martin, G. R., and Butler, P. J. (2006). Moving towards acceleration for estimates of activity specific metabolic rate in free living animals: the case of the cormorant. *Journal of Animal Ecology*, **75**, 1081–1090.
- Wood, S.N. (2011) Fast stable restricted maximum likelihood and marginal likelihood estimation of semiparametric generalized linear models. *Journal of the Royal Statistical Society B*, **73**, 3–36
- Wu, L., Cai, W., Zhang, L., Nakamura, H., Timmermann, A., Joyce, T., McPhaden, M.J., Alexander, M., Qiu, B., Visbeck, M. & Chang, P. (2012). Enhanced warming over the global subtropical western boundary currents. *Nature Climate Change*, **2**, 161–166.
- Yasuda, I., Sugisaki, H., Watanabe, Y., Minobe, S. S., & Oozeki, Y. (1999). Interdecadal variations in Japanese sardine and ocean/climate. *Fish. Oceanogr.* **8**, 18–24.
- Ydesen, K. S. Ydesen, K.S., Wisniewska, D.M., Hansen, J.D., Beedholm, K., Johnson, M. and Madsen, P.T. (2014). What a jerk: prey engulfment revealed by high rate, super cranial accelerometry on a harbour seal (*Phoca vitulina*). *Journal of Experimental Biology* **217**, 2239–2243.
- Yoder, J. M., Marschall, E. A., & Swanson, D. A. (2004). The cost of dispersal: predation as a function of movement and site familiarity in ruffed grouse. *Behavioral Ecology*, **15**, 469–476.
- Young, J. W., Hobday, A. J., Campbell, R. A., Kloser, R. J., Bonham, P. I., Clementson, L. A., & Lansdell, M. J. (2011). The biological oceanography of the East Australian Current and surrounding waters in relation to tuna and billfish catches off eastern Australia. *Deep Sea Research Part II: Topical Studies in Oceanography*, **58**, 720–733.
- Zach, R. & Falls, J.B. (1979) Foraging and territoriality of male ovenbirds (Aves: Parulidae) in a heterogeneous habitat. *Journal of Animal Ecology*, **48**, 33–52.
- Zimmer, I., Ropert Coudert, Y., Kato, A., Ancel, A., and Chiaradia, A. (2011a). Does foraging performance change with age in female little penguins (*Eudyptula minor*)? *PloS One*, **6**, e16098.
- Zimmer, I., Ropert Coudert, Y., Poulin, N., Kato, A., and Chiaradia, A. (2011b). Evaluating the relative importance of intrinsic and extrinsic factors on the foraging activity of top predators: a case study on female little penguins. *Marine Biology*, **158**, 715–722.

Pages 148-155 of this thesis have been removed as they contain published material under copyright. Removed contents published as:

Carroll, G., Slip, D., Jonsen, I., & Harcourt, R. (2014) Supervised accelerometry analysis can identify prey capture by penguins at sea, *Journal of Experimental Biology*, vol. 217, pp. 4295-4302, doi.org/10.1242/jeb.113076.

SCIENTIFIC REPORTS

OPEN

High sea surface temperatures driven by a strengthening current reduce foraging success by penguins

Received: 23 September 2015

Accepted: 09 February 2016

Published: 29 February 2016

Gemma Carroll¹, Jason D. Everett², Robert Harcourt¹, David Slip³ & Ian Jonsen¹

The world's oceans are undergoing rapid, regionally specific warming. Strengthening western boundary currents play a role in this phenomenon, with sea surface temperatures (SST) in their paths rising faster than the global average. To understand how dynamic oceanography influences food availability in these ocean warming "hotspots", we use a novel prey capture signature derived from accelerometry to understand how the warm East Australian Current shapes foraging success by a meso-predator, the little penguin. This seabird feeds on low trophic level species that are sensitive to environmental change. We found that in 2012, prey capture success by penguins was high when SST was low relative to the long-term mean. In 2013 prey capture success was low, coincident with an unusually strong penetration of warm water. Overall there was an optimal temperature range for prey capture around 19–21 °C, with lower success at both lower and higher temperatures, mirroring published relationships between commercial sardine catch and SST. Spatially, higher SSTs corresponded to a lower probability of penguins using an area, and lower prey capture success. These links between high SST and reduced prey capture success by penguins suggest negative implications for future resource availability in a system dominated by a strengthening western boundary current.

To understand how changes in the physical properties of oceans affect food webs, it is essential to develop appropriate indicators of resource availability. Remote sensing of environmental data including sea surface temperature (SST) and chlorophyll *a* provides valuable insight into the processes driving spatial and temporal changes in primary productivity¹. Linking these changes to outcomes for mid- and upper-trophic level predators is more challenging, despite the importance of this information for predicting ecosystem responses to climate change². As it is difficult to directly measure prey abundance on scales relevant to marine predators, studies have often used tracking technology to identify correlations between oceanography, primary productivity and predator foraging behaviour^{3,4}. However, without a measure of foraging success, it is difficult to estimate how much prey animals encounter and consume while foraging under different environmental conditions.

Accelerometry has shown great potential to provide fine-scale information on the activity of wild animals. Machine learning algorithms have been applied to recognise patterns in acceleration data, providing robust links between the behaviour of animals and their movement profiles, such that behaviour can be determined remotely⁵. One application of these behaviour classification methods has been to identify movement patterns associated with feeding^{6–8}. The next step in this rapidly evolving field is to use information on prey capture events to answer important ecological questions relating to resource availability that were previously difficult to address. By linking foraging success to physical oceanography, we can gain insight into the mechanisms dictating resource availability and predict if and how marine predators and their prey are vulnerable to environmental change.

Western boundary currents are a significant source of global heat transport, advecting warm water from the tropics to temperate latitudes⁹. Although these systems are considered nutrient poor compared with cold eastern boundary currents, they generate eddies¹⁰ that drive nutrient upwelling¹¹. Subsequently, they are able to support

¹Department of Biological Sciences, Faculty of Science and Engineering, Macquarie University, Sydney NSW 2109, Australia. ²Evolution & Ecology Research Centre, School of Biological Earth and Environmental Sciences, University of New South Wales, Sydney NSW 2052, Australia. ³Taronga Conservation Society Australia, Bradleys Head Rd Mosman, Sydney NSW 2088, Australia. Correspondence and requests for materials should be addressed to G.C. (email: gemma.carroll@mq.edu.au)

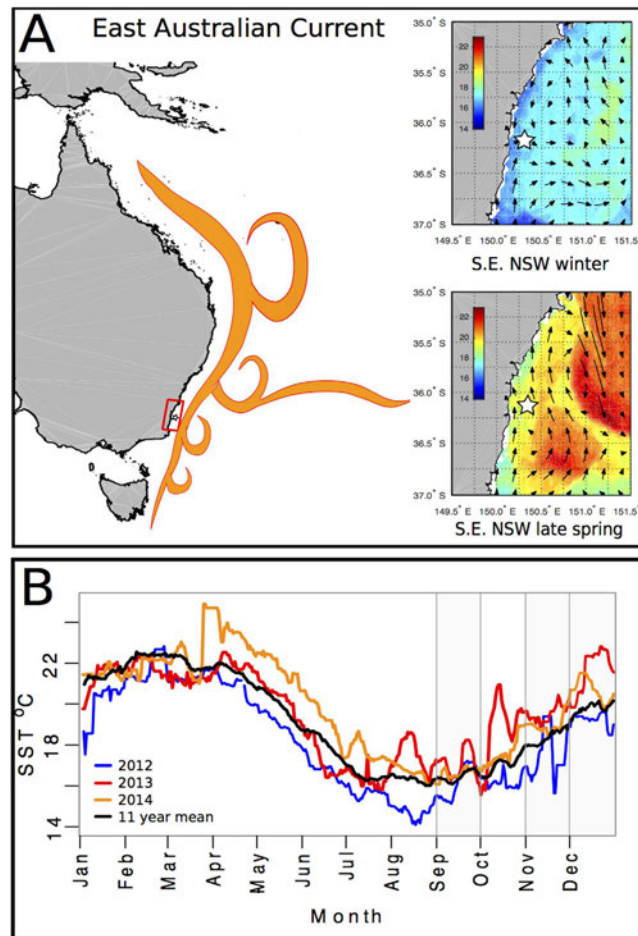


Figure 1. (A) Schematic showing the general characteristics of the East Australian Current (left). The area of this study (southeast NSW) is indicated by the red box, and the white star marks the location of Montague Island. On the right are examples of typical winter (top) and late spring (bottom) sea surface temperature and current directions in southeast NSW around Montague Island (white star). Inset maps were produced in MATLAB R2014b using data available from <http://imos.aodn.org.au/imos/>. (B) Annual time series of sea surface temperature measured offshore from Montague Island during 2012, 2013 and 2014 with a rolling 10-day mean. Grey windows represent the months (Sep, Nov, Dec) in which penguins were tracked from 2012–2014.

fisheries¹² and populations of marine predators such as seabirds (e.g.)¹³. Western boundary currents are strengthening, increasing the pole-ward penetration of warm water. For example, the East Australian Current (EAC) is the western boundary current of the South Pacific Gyre, and its intensification is causing regional sea surface temperature (SST) to rise much faster than the global average¹⁴. The global significance of changes to currents means that it is important to understand how their physical processes drive variation in productivity¹⁵, and to identify the effects of this variability at all trophic levels.

Seabirds provide a useful model to examine the effects of environmental change on resources, as they are highly responsive to fluctuations in prey availability¹⁶. The little penguin (*Eudyptula minor*) is the world's smallest species of penguin and has a breeding colony at Montague Island, off southeast Australia (774 ± 61 breeding pairs on the southern part of the island in 2015; Peter Fullagar, unpublished data). Montague Island is situated halfway across the continental shelf, with surrounding waters heavily influenced by the dynamics of the EAC and its eddy field (Fig. 1A). To assess the consequences of variation in EAC penetration on the amount of prey (low trophic level species, or “forage fish”, including small pelagic fish, krill and squid) caught by penguins, we used a prey capture signature derived from their acceleration profiles⁷. As little penguins are highly constrained in the range and duration of foraging trips during the breeding season, we determined mechanistic links between foraging success and the environment on fine spatial (<25 km) and temporal (<10 day) scales.

Specifically, our aims were to: 1) understand the temporal variability of prey capture success by little penguins determined using accelerometry, and assess how this variability was related to the EAC; 2) understand spatial variability in foraging location determined using GPS, and assess how environmental features dictate the way that penguins use available foraging habitat; 3) assess spatial variability in prey capture success determined from GPS, accelerometry and depth recorders in relation to the EAC. We discuss the insight that our findings give

into the relative availability of low trophic level species to predators in the context of western boundary current intensification.

Methods

Fieldwork. The field study was conducted on Montague Island (-36.253° , 150.227°), 9 km off the southeast coast of New South Wales, Australia, in September, November and December 2012–2014. This period covers the peak of the little penguin's breeding season, which can be highly asynchronous¹⁷. Adults show bi-parental care during incubation and rearing offspring. During incubation, foraging trips are on average 3.5 days in length¹⁸. When offspring are young (<2 weeks) one parent stays behind to guard the chicks while the other goes to sea usually for a single day, and as the chicks grow both parents go to sea simultaneously, often for multiple days. When conditions are good, little penguins can raise two clutches in succession¹⁹. Sampling periods comprised 6–15 days tracking penguins in each month.

The night before a penguin went to sea, it was caught in its nest box and equipped with a GPS logger (CatTrack, South Carolina, USA) modified with epoxy resin to withstand pressure at depth. The loggers were inserted into heat shrink tubing, then attached to feathers on the lower back with cloth tape (Tesa, Hamburg, Germany), positioned so as to reduce drag but not impede tail movement. These tags were 43 mm in length, 27 mm in width and 13 mm in height, and weighed 55 g in air and 17.4 g in seawater. A range of sampling frequencies was used over the study period to adjust the trade-off between battery life and spatial resolution. For penguins expected to perform single day trips (birds rearing small chicks), sampling frequency ranged from 7–45 s. For birds expected to perform multiple day trips (incubating birds and birds with larger chicks), the sampling frequency ranged from 30–115 s, however at these sampling frequencies the loggers were still rarely able to record complete multiple days, so spatial analyses were restricted to single day trips. When penguins returned from a foraging trip they were recaptured in their nest boxes, loggers removed and the penguin was weighed in a calico bag using a spring balance scale (Pesola, AG Switzerland).

Accelerometer data loggers (G6a and G6a+, CEFAS Technology Pty Ltd, Suffolk, UK) were attached immediately in front of the GPS units (towards the head) on the middle back for a subset of penguins from November 2012. These tags were 40 mm in length, 28 mm in width and 15 mm in height, and weighed 7.8 g in air and 2.3 g in seawater. The accelerometers recorded acceleration in 3 axes: anterior-posterior (surging), lateral (swaying) and dorso-ventral (heaving) with a range of $+/-2$ g. The accelerometers recorded depth, temperature and acceleration and were programmed in two modes: "shallow" mode (<1.5 m: 1.5% of the full scale pressure range) where parameters were recorded every 10 seconds, and "dive" mode (>1.5 m) where the same parameters were recorded at 30 Hz.

Combined tag weight for penguins that were equipped with both accelerometers and GPS was 62 g in air and 19.7 g in seawater, which is $<5\%$ and $<2\%$ of mean bodyweight (~ 1100 g) respectively. Handling time was kept to a minimum, and in most cases was less than 5 min for both deployment and retrieval of devices. All animal research protocols were carried out in accordance with guidelines approved by the Macquarie University Animal Ethics Committee (Animal Research Authority 2011/14).

Prey capture signature. We previously developed a motion signature to identify prey capture by wild penguins at sea, using a support vector machine algorithm that identified prey handling by wild penguins with a false positive rate of 0.09%. A thorough description of this method and its validation in the wild is detailed in Carroll *et al.*⁷. We showed that dives during which prey capture occurred were longer in duration, deeper, had longer bottom times, more undulations in the bottom phase of the dive and faster ascent and descent rates, consistent with predictions from foraging theory and previous empirical studies of marine predator foraging ecology^{20–22}.

Analysis. *Temporal variability in prey capture success.* We assessed temporal patterns of prey capture success by breeding little penguins between November 2012 and December 2014. All available accelerometry profiles were used in this analysis, from both single and multiple day foraging trips. The penguins in this study were not individually marked, so it is not known whether they were resampled in multiple years. However, only 9 birds of the same sex from the same nest were sampled more than once (13%). We used the mean number of prey caught per 90 min period across a foraging trip as an index of prey capture success for that trip. As we might expect penguins to adjust their foraging effort to the availability of prey, we also calculated a measure of catch per unit effort (CPUE), which was the mean value across a foraging trip of the number of prey caught per 90 min window as a function of time spent diving below 1.5 m within that window. We used the mean value over discrete time windows rather than a daily value, as this allowed for comparison among foraging trips of different lengths. We tested a range of time windows (1, 5, 10, 20, 30, 45, 60, 90, 120 and 240 min) on a subset of eight pooled single and multiple day foraging trips and found that 90 minutes was the window that minimised the standard deviation of the mean foraging trip CPUE (see Figure S1 in Supplementary Material). For trips longer than one day, we removed all 90 min intervals that occurred at night, as penguins do not forage after dark²³. In this study time spent diving was usually <1 min per 90 min window after sunset.

To assess the temporal influence of the EAC on foraging success, we first described relationships between different environmental variables to find a suitable means of representing EAC penetration. We obtained measurements of satellite-derived SST (MODIS-Aqua), chlorophyll *a* (OC3) and geostrophic velocity (derived from altimetry from NASA/CNES (Jason-1 and 2) and ESA (ENVISAT) satellites) from the Integrated Marine Observing System (IMOS) Data Portal (<http://imos.aodn.org.au/imos/>). Daily SST and Chlorophyll *a* data were obtained at a location 5.5 km offshore (east) from Montague Island (36.26° S, 150.29° E) in November and December 2012–14 and September 2013–14 (accelerometry data was not collected during September 2012). This offshore location is halfway between Montague Island and the edge of the continental slope where the EAC is centred²⁴, and therefore should provide an index of the incursion of offshore EAC waters onto the shelf. We used

oceanographic data from this location after comparison with data taken from a location 3 km inshore (west), halfway between Montague Island and the mainland (36.26°S, 150.19°E), and values averaged over the penguin foraging area. The single offshore location better captured the variability associated with EAC penetration, as indicated by the fact that Akaike's Information Criterion (AIC) scores were lowest with offshore SST, when the same models were run with each of these variables in turn (see below for model details). North-south geostrophic velocity was obtained at the closest pixel to the SST data (36.2°S, 150.4°E) and rotated 19-degrees to be in the alongshore direction.

Using linear regression we examined the relationship between offshore SST, chlorophyll *a* from the same location, and geostrophic current velocity (see Figure S2 in Supplementary Material). As expected, a stronger alongshore current was correlated with warmer water (adjusted $R^2 = 0.17$, $p < 0.0001$) and chlorophyll *a* concentration decreased with warmer water (adjusted $R^2 = 0.36$, $p < 0.0001$). Due to these correlations we chose not to model the effect of more than one of these environmental variables on foraging success simultaneously, although they are each likely to explain a portion of its variance. We chose to use offshore SST as a single proxy for penetration of the EAC, as the EAC brings warm water down Australia's southeast coast from the tropics in a series of highly variable mesoscale eddies, rather than a continuous southward-flowing stream^{10,24}. Increasing temperature brought by these warm influxes is likely to be of greater biological relevance to larger organisms than for example, an increase in the speed of the current. Furthermore, the measurement of SST in coastal systems is more reliable than measurement of chlorophyll *a*, and occurs at a higher sampling frequency (daily) compared to geostrophic velocities, which are calculated from satellite altimetry data and collated and interpolated over a 10-day cycle.

To characterize seasonal patterns of EAC penetration, we plotted a time series of daily SST values offshore from Montague Island for 2012–2014, and applied a 10-day rolling mean to smooth the data. To place our findings in a longer-term context, we calculated the mean SST for each calendar day over a period of 11 years (2003–2014). We also calculated the mean SST for each month that penguins were tracked.

We used generalised additive models (GAMs) with Gaussian error distributions to estimate the relationship between SST and our two measures of foraging success (mean number of prey caught per 90 min window and CPUE). For each penguin foraging trip, we averaged SST over a four-day window centred on the trip dates. If the foraging trip was longer than four days, we used the mean over the length of the trip. This helped to reduce gaps in satellite data arising from cloud cover, but was still relevant for penguins foraging on short temporal scales.

Spatial variability in foraging location. We used locations recorded by GPS loggers to determine the relationship between spatial habitat use and SST. For these analyses we only used single day foraging trips, as these were comparable in terms of the maximum distance that the penguins travelled from the island (~25 km per day). By focusing on single day trips, we were also able to use the most complete GPS tracks, as tracks of multiple day foraging trips were often incomplete due to limitations in GPS battery life on these small loggers.

To determine the relationship between foraging location and SST, we created a grid with 1 km² cells spanning the penguins' potential single day foraging range (25 km north and south of Montague Island and east to the shelf edge). The 1 km² grid was the finest resolution available for the remote-sensed MODIS-Aqua SST data. We averaged SST over the days when we tracked penguins (e.g. if there were penguins tracked on the 3rd, 4th, 6th, 8th and 11th of September, we averaged gridded SSTs for these days). We chose this method after testing two others that masked relationships between SST and foraging success: a) taking the mean of SST for all days within the range of dates that penguins were tracked (e.g. 3rd – 11th September) and b) averaging over 15 days regardless of the tracking date range (15 days being the longest tracking period).

We spatially binned locations recorded by the GPS tags onto the same 1 km² grid, resulting in counts of locations within each grid cell that we summed for each sampling period (Sep, Nov & Dec 2012–14). To avoid artificially over-sampling in some areas where penguins rested at the surface, and under-sampling in other areas where gaps were recorded in the GPS data due to the penguins spending more time underwater, we linearly interpolated the raw GPS location data at regular 10 min intervals. Interpolation also allowed us to homogenise the different GPS sampling frequencies used during the study period. We determined a 10 min sampling frequency to be the most appropriate as little penguins travel at a mean speed of 1.8 m/s²⁵, and therefore move, on average, ~1 km every 10 minutes. Thus, 1 km² areas that penguins moved through without foraging would get on average a single count (or fewer if the penguin was moving more quickly), whereas areas where they encountered prey and engaged in area restricted search were likely to contain substantially more observations.

We analysed the relationship between SST and penguin location counts using a hurdle model²⁶. This model accounts for the zero-inflation present in the count data (there were large areas where the penguins did not go and hence many zero counts in grid cells) as well as over-dispersion (some cells had few detections while others had many). The hurdle model uses two processes to model data. The first assesses the relationship between the predictor variable (in this case SST) and counts (the number of times penguins were observed in a cell). The second assesses the relationship between the predictor variable (SST) and the zero observations (presence/absence of penguins in a cell) using a binomial distribution. The model assumes that SST might differentially affect a) whether penguins do or do not go to an area at all (habitat suitability) and b) how much time they spend there (habitat quality).

To test whether penguins are responding to relative SST or absolute temperatures, we assessed both SST and SST anomaly (deviance of SST for each 1 km² grid cell from the mean SST of all grid cells). We compared three measures (SST, SST anomaly (continuous predictor) and SST anomaly (binary predictor; warmer or cooler than the mean)) in separate hurdle models and compared them using Akaike's Information Criterion (AIC), to best capture the relationship between SST and both penguin presence/absence and the number of observations within grid cells. We created a visual representation of the relationship between foraging location and SST by overlaying raw GPS tracks on a map with spatial SST anomaly (pixels were coloured according to how much they deviated from the mean temperature of the study area).

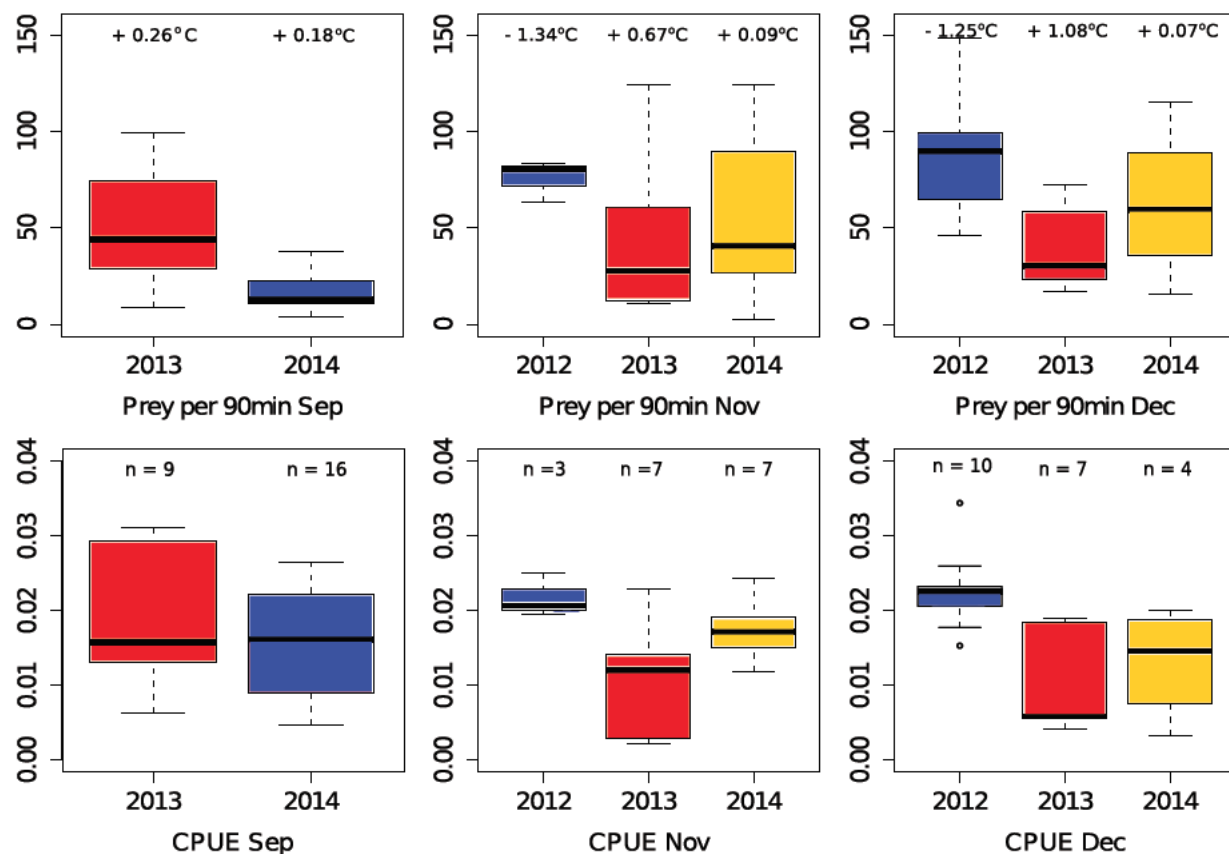


Figure 2. Mean prey caught per 90 min window and mean CPUE (prey caught per minute spent diving below 1.5 m) per 90 min window by month in 2012, 2013 and 2014. Box plots are coloured according to the SST relative to the mean SST of that month in the other two study years (red being the warmest of the 3 years for each month, blue being the coldest). Sample size and deviation from the mean monthly temperature (°C) are noted on the prey capture plot (top row) and samples sizes are shown on the CPUE plot (bottom row).

Spatial variability in prey capture success. We assessed the spatial distribution of prey capture events in relation to SST. We performed a linear interpolation between GPS locations at 1 s intervals to integrate the accelerometry record and the GPS tracks. When a location was determined for each prey capture event, we used only these locations in the analysis. We used the same 1 km² grid and counted prey capture events recorded in each cell. We analysed only the cells in which prey capture occurred, using a GAM to assess relationships between prey capture density and SST. We then examined the time series of SST encountered by penguins through the course of single day trips (mean SST of grid cells visited per 10% increment by all penguins within a sampling period) in relation to the prey caught through the course of single day trips. We also determined the mean depth of prey capture events during each foraging trip, and the mean distance of prey captures from the colony during each foraging trip, and assessed how these varied intra- and inter-annually in relation to offshore SST (described previously).²⁷

All analyses conducted in this study were performed in the R statistical programming framework²⁷.

Ethics statement. The Macquarie University Animal Ethics Committee approved all animal research protocols, which were undertaken in accordance with guidelines set out by Australian law (Animal Research Authority 2011/14).

Results

Oceanography. Penetration of the East Australian Current was variable over the three study years (Fig. 1,B). In 2012, SSTs were almost always lower than the long-term average. By contrast, both 2013 and 2014 had summer SSTs that were generally warmer than average. In particular, SSTs appeared anomalously high in 2013 during the penguin breeding season, with high variability and strong pulses of warm water penetrating the study region. The timing of the onset of warm water penetration in 2013 was notable, with an unusual infiltration of warm water in August resulting in SSTs more than 1 °C warmer than the long-term mean. In October 2013 there was a spike in SST of almost +4 °C from the mean and in December 2013 an increase of around +3 °C. 2014 was less variable, but there was an anomalous spike of +1 °C in late October to mid-November 2014, and another of +1.5 °C in December 2014.

Temporal variability in prey capture success. We obtained accelerometry profiles for 63 penguin foraging trips between Nov 2012 and Dec 2014 (Nov 2012 n = 3; Dec 2012 n = 10; Sep 2013 n = 9; Nov 2013

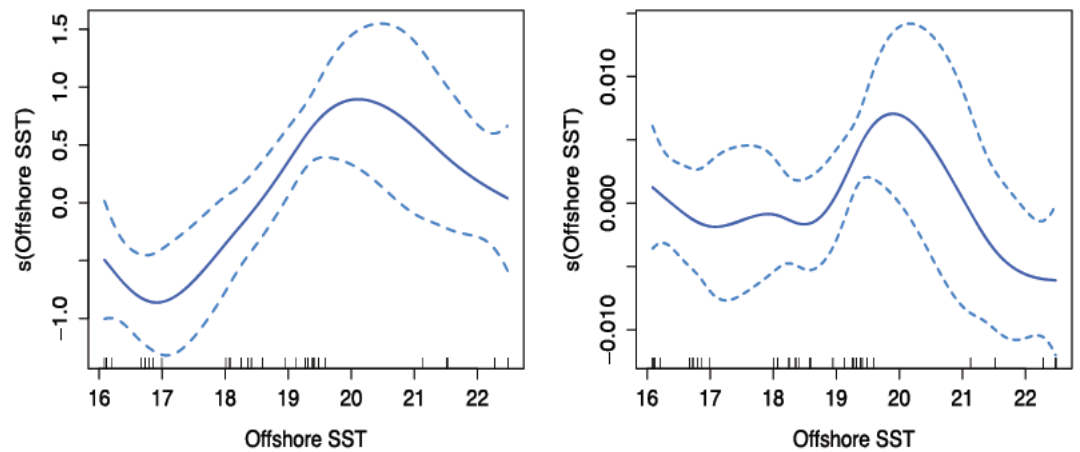


Figure 3. Generalised additive model relationships between log transformed prey capture by penguins per 90 min and offshore SST (left); and catch per unit effort (number of prey caught by penguins/amount of time spent diving > 1.5m) & offshore SST (right).

n = 7; Dec 2013 n = 7; Sep 2–14 n = 16; Nov 2014 n = 7; Dec 2014 n = 4). The mean number of prey caught per 90 minute period varied both intra- and inter-annually (see Fig. 2) (mean \pm s.e.: Sep 2013 = 51.65 ± 10.97 , Sep 2014 = 19.18 ± 3.97 ; Nov 2012 = 75.74 ± 6.10 , Nov 2013 = 44.22 ± 15.74 , Nov 2014 = 57.04 ± 17.47 ; Dec 2012 = 88.09 ± 9.22 , Dec 2013 = 40.86 ± 8.52 , Dec 2014 = 63.24 ± 20.77). We tested whether inter-annual differences were significant using a generalised linear model (GLM) for each of the three months, assessing the relationship between 90 min prey capture success and year. Where there were 3 years (November and December), 2012 was the reference year as it always had the highest prey capture success. In September, 2014 was significantly worse for prey capture success than 2013 (-32.47 ± 9.69 , $t = -3.350$, $p = 0.003$). In November, there were no significant differences, and in December, 2013 had significantly lower prey capture success than 2012 (-47.23 ± 14.64 , $t = -3.22$, $p = 0.005$). CPUE followed the same general trend as the 90 min catch data, although in September penguins spent less time actively foraging relative to the number of prey caught, thereby reducing the difference in CPUE between 2013 and 2014.

In November and December, the monthly SST anomaly (SST relative to mean SST for that month across the 3 study years) showed a broad correlation with prey capture success as determined by both 90-minute prey capture and CPUE metrics. 2012 was the year with lowest SSTs (Nov = -1.34°C ; Dec = -1.25°C relative to the mean), and saw the highest foraging success. 2013 was anomalously warm, (Nov = $+0.67^\circ\text{C}$; Dec = $+1.08^\circ\text{C}$) and saw the lowest foraging success. 2014 was intermediate in both SST and foraging success (Nov = $+0.09^\circ\text{C}$ and Dec = $+0.07^\circ\text{C}$). In September this trend was reversed with 2013 being warmer with higher prey capture success, although there was low variability in SST between the two years (Sep 2013 = $+0.26^\circ\text{C}$, Sep 2014 = $+0.18^\circ\text{C}$).

Offshore SST had a quadratic relationship with both log transformed prey captures per 90 min and CPUE (Fig. 3). For the 90 min prey capture data, low SSTs ($16^\circ\text{C} - 18.5^\circ\text{C}$) corresponded to the lowest prey capture success. A peak in prey captures occurred at around 20°C before dropping off (GAM $R^2 = 0.31$, $F = 5.79$, $p = 0.0002$). There was no strong relationship between CPUE and SST between 16°C and 19°C , when again the model showed a strong peak in CPUE around 20°C before a drop off between 21°C and 22°C (GAM $R^2 = 0.17$, $F = 2.57$, $p = 0.03$).

Spatial variability in foraging location. For the habitat use analysis, we analysed GPS tracks from a total of 112 single day penguin foraging trips in September, November and December 2012–14 (Sep 2012 n = 31; Nov 2012 n = 6; Dec 2012 n = 10; Sep 2013 n = 15; Nov 2013 n = 19; Dec 2013 n = 12; Sep 2014 n = 9; Nov 2014 n = 6; Dec 2014 n = 4). 82% of 1 km^2 grid cells that penguins could have visited during single day trips did not contain observations of penguins, indicating that penguins were selective in their habitat choice, foraging in similar locations within a given time period.

Penguins appeared to seek out water that was colder than the mean of all available habitat (Fig. 4). When a grid cell was colder than average, we were 42% more likely to observe a penguin than if the grid cell was warmer than average (26% of cells colder than average recorded penguin presence c.f. 15% of cells that were warmer than average). Similarly, the time that penguins spent in a cell was related to its SST anomaly: areas colder than average had 50% higher counts than areas warmer than average (cold = 2.76, warm = 1.38).

The hurdle model using SST averaged over the sampling days as a predictor performed better than models using SST anomaly either as a continuous or binary variable (see Table S1). The count part of the hurdle model, which explains variation in the number of times penguins are observed in a cell, showed that lower counts were recorded as SST increased (SST estimate = -0.02 , S.E. = 0.01 , Z value = -3.00 , P value = 0.003). For the zero part of the hurdle model, which explains variation in whether penguins were observed in a cell at all, showed that as SST increased, penguins were increasingly less likely to visit that cell (SST estimate = -0.28 , S.E. = 0.03 , Z value = -10.45 , P value = < 0.0001).

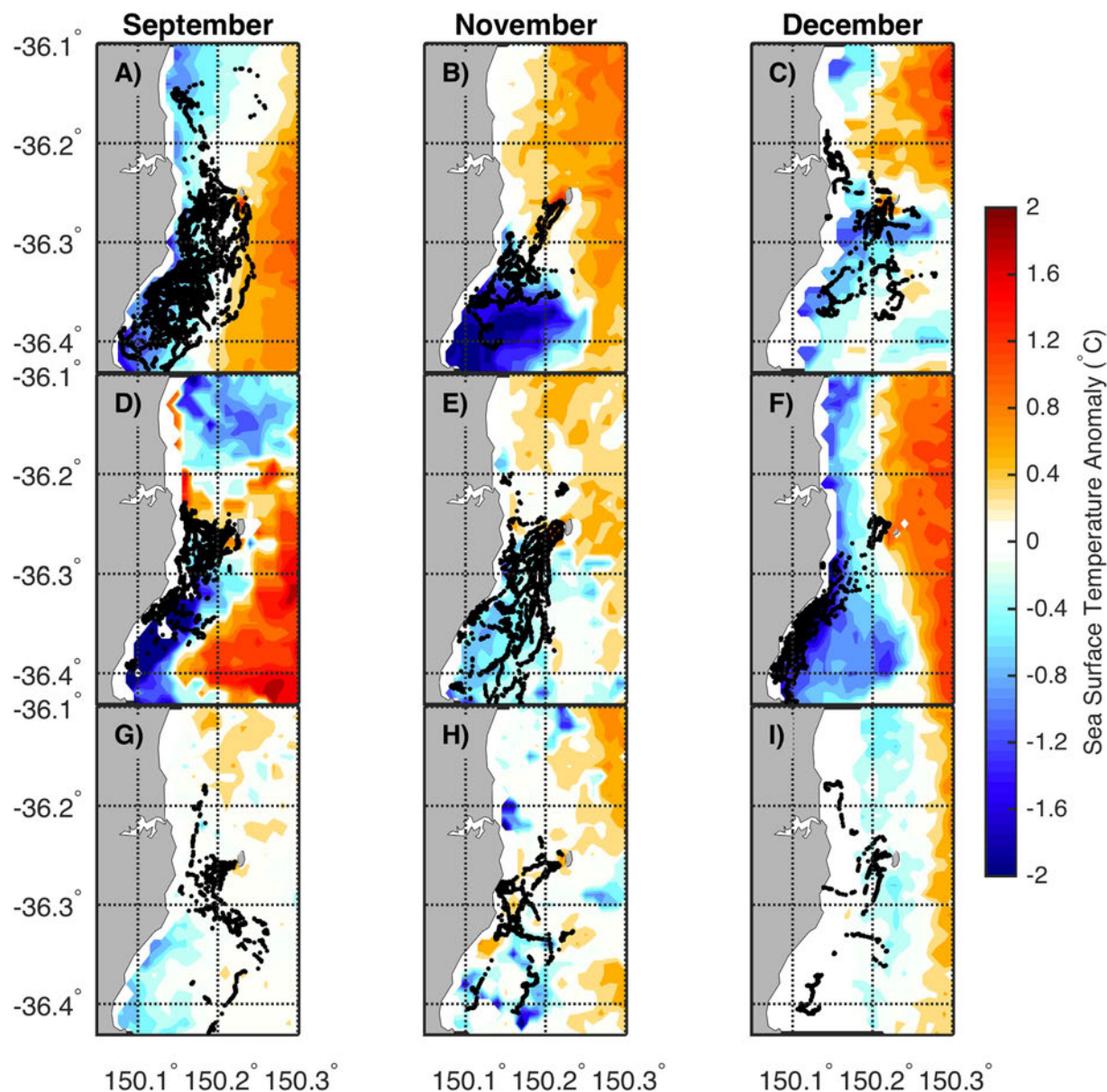


Figure 4. Raw GPS tracks of penguins performing single day foraging trips in relation to sea surface temperature anomalies (SST of 1 km² grid cell – mean SST of all 1 km² grid cells in study area). Top row is 2012, second row is 2013 and bottom row is 2014. Plot regions represent the area gridded on a 1 km² scale for spatial analyses. Maps were produced in MATLAB R2014b using data available from <http://imos.aodn.org.au/>

Spatial variability in prey capture success. To assess the effect of SST on the spatial distribution of prey captures, we integrated accelerometry profiles and GPS tracks of 50 complete single day penguin foraging trips in November and December 2012–14, and September 2013–14 (Nov 2012 n = 3; Dec 2012 n = 10; Sep 2013 n = 6; Nov 2013 n = 8; Dec 2013 n = 8; Sep 2014 n = 7; Nov 2014 n = 4; Dec 2014 n = 4). Sample penguin tracks with prey capture locations in relation to gridded SST are shown in Fig. 5. These illustrate habitat selection by the penguins, with penguins tending to forage in cooler waters, particularly in warmer months (e.g. in December 2013). Examples of gridded prey capture densities by all penguins within each month in 2013 are shown in Figure S3. There were signs of a relationship between SST and the number of prey caught within a 1 km² grid cell at the coldest and warmest temperatures observed during this study (Figure S4). The GAM showed that the highest density of prey captures occurred when penguins were in areas with the lowest recorded temperatures (~13.5°C). Prey capture success was variable at intermediate SST and fell when temperatures were > 20°C. Even after removing the effect of unsuitable habitat where there may be no prey at all, there was an effect of SST on the spatial distribution of prey captures. However, the modelled relationships retained some uncertainty and the amount of variance explained was low (GAM R² = 0.11, F = 4.05, p < 0.0001).

The GAM only assessed the effect of SST on prey capture success in areas where prey capture occurred. To assess the relationship between prey capture and the SSTs encountered over the course of a foraging trip, we

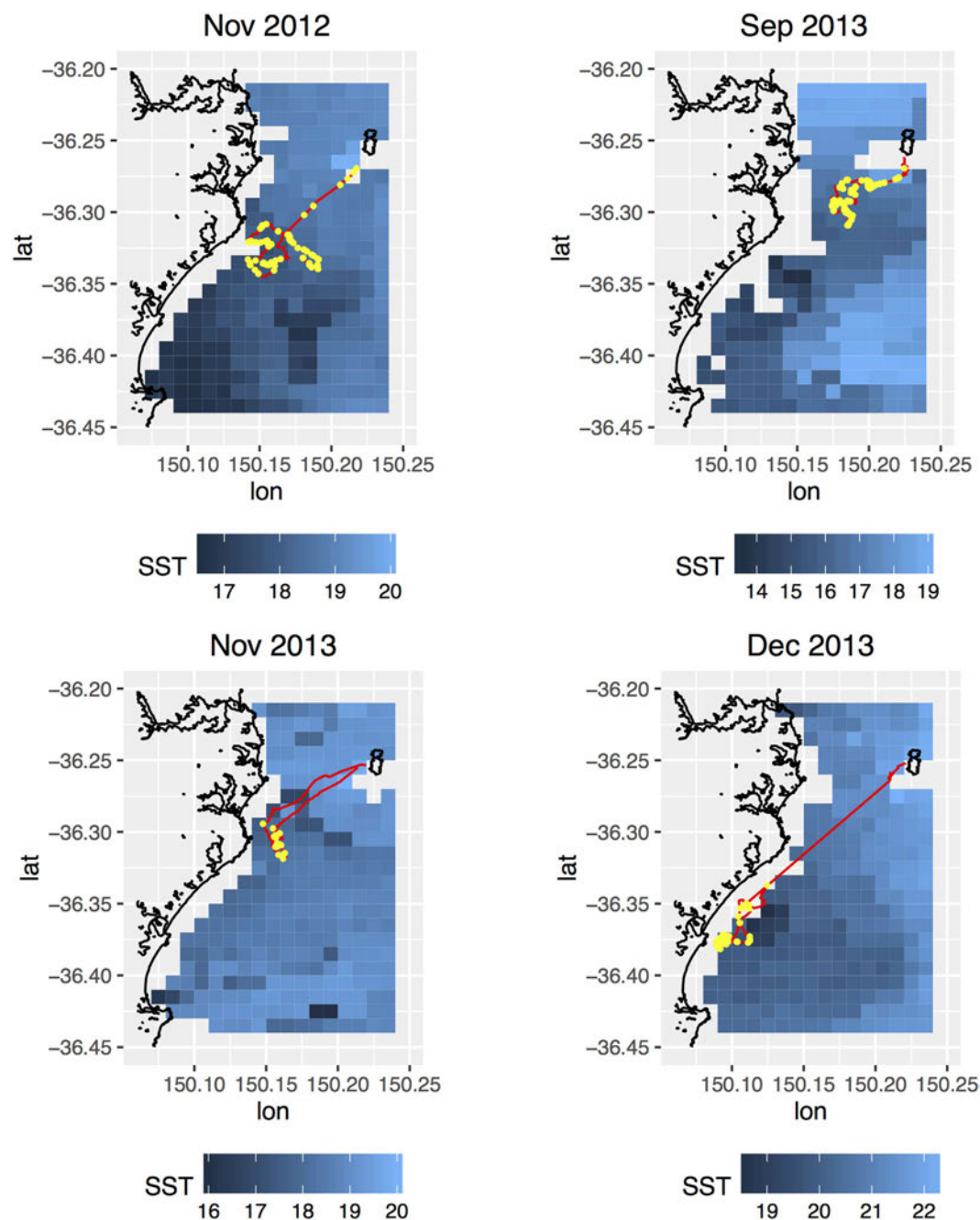


Figure 5. Sample foraging trips by little penguins in relation to gridded sea surface temperature (<http://imos.aodn.org.au/imos/>), showing foraging trajectory (red) and prey capture locations (yellow). Panels have different scales in order to highlight penguin habitat selection relative to the distribution of sea surface temperatures within each period. Plot created using *ggplot2*⁶⁴ in R version 3.2.3²⁷.

plotted a time-series of the mean SST of grid cells visited by penguins in 10% increments of trips within a sampling period (September, November and December 2012–14). We then overlaid the mean number of prey captures identified using accelerometry within the same 10% increments within a sampling period (November and December 2012–14, September 2013–14) (see Fig. 6).

This analysis confirmed that penguins seek out areas with lower relative SSTs, with encountered temperatures always decreasing during a foraging trip before increasing again towards the end of a journey. It also showed that in December 2012–14 and November 2012 and 2014, there was good agreement between the spatial distribution of prey capture success and SST, with areas/periods of lowest SST encountered by penguins on a foraging trip related to the highest prey capture success. However, in September 2013–14 and November 2013 there was no clear relationship between spatial prey capture and SST distribution.

In order to explore whether subsurface water properties such as thermoclines might affect little penguin foraging success differently from SST, we assessed the relationship between the mean SST in a 1 km² grid cell and

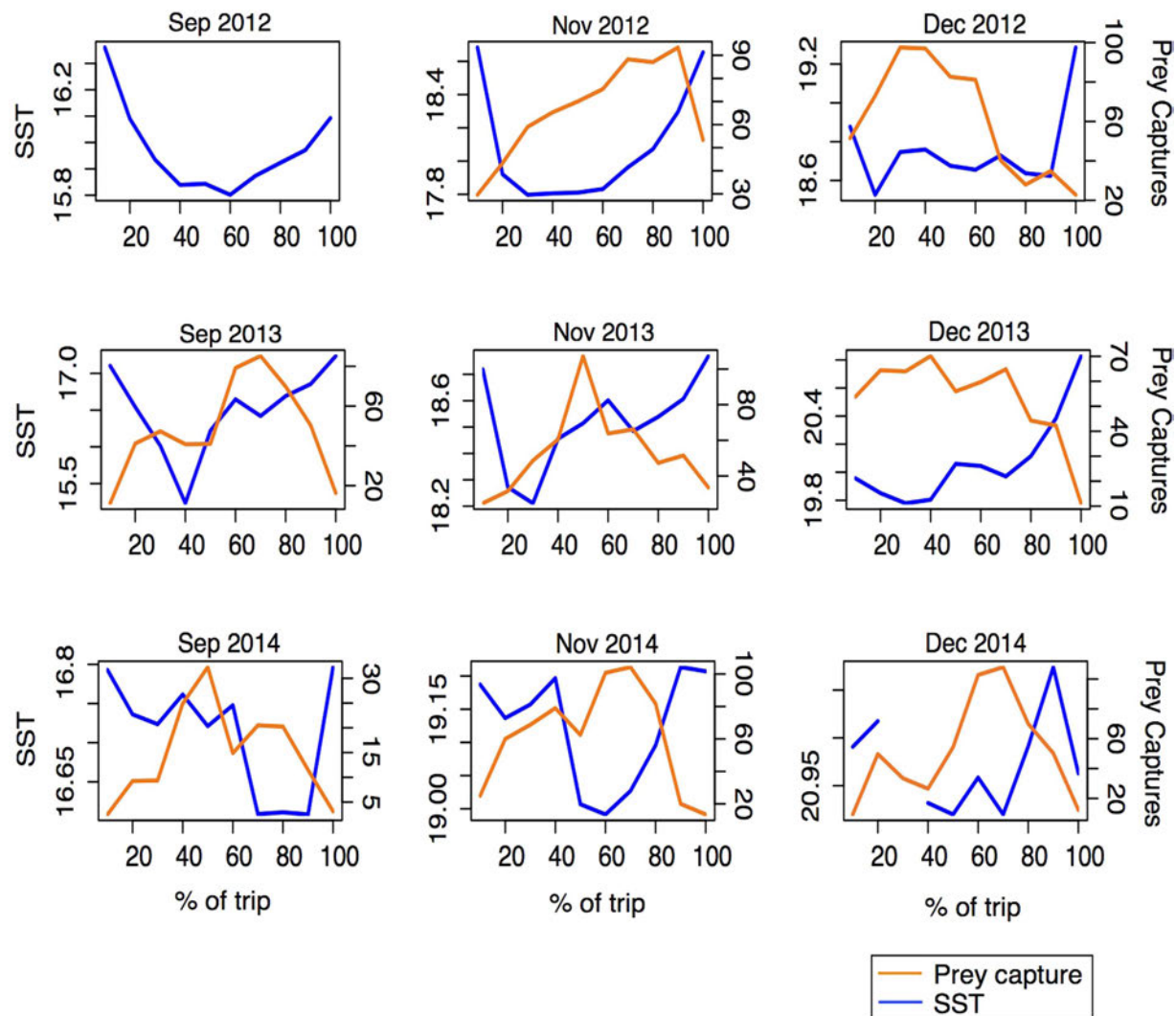


Figure 6. SST (blue lines) and prey capture events (orange lines) as a function of time elapsed in a foraging trip (each trip was divided into 10% quantiles). SST values are the mean of the SSTs encountered by all GPS-equipped penguins in 1 km² grid cells in each 10% interval. Prey capture values are the mean of the number of prey captures recorded by accelerometer- and GPS-equipped penguins in each 10% interval.

the mean temperature at the point of prey capture in the same grid cell, calculated from the temperature sensors on board the accelerometers. We found a near linear, 1:1 relationship between SST and prey capture temperature above 16 °C (GAM $R^2 = 0.53$, $F = 28.02$, $P < 0.0001$) (Figure S5). This is unsurprising, as prey capture by penguins generally occurred in the upper part of the water column, with the mean depth of prey captures across foraging trips being less than 10 m in all months (mean (m) \pm s.e.: Sep 2013 = 4.26 ± 0.20 , Sep 2014 = 4.57 ± 0.35 ; Nov 2012 = 6.77 ± 0.81 ; Nov 2013 = 8.46 ± 0.59 , Nov 2014 = 8.49 ± 0.70 ; Dec 2012 = 9.93 ± 0.82 , Dec 2013 = 9.18 ± 0.99 , Dec 2014 = 6.89 ± 1.49). There were no obvious patterns between depth of prey capture and the relative SST for each month (Figure S6).

The mean distance from the colony at which penguins caught prey ranged from 8 km to 16 km (Sep 2013 = 8.18 ± 0.79 , Sep 2014 = 7.28 ± 0.86 ; Nov 2012 = 8.55 ± 0.91 ; Nov 2013 = 13.32 ± 2.30 , Nov 2014 = 8.18 ± 0.49 ; Dec 2012 = 8.07 ± 1.04 , Dec 2013 = 15.68 ± 0.84 , Dec 2014 = 12.94 ± 3.47). It appears that prey captures occurred further from the colony when SST was relatively warm (Figure S6). This was confirmed by a GAM that showed a general increasing trend between offshore SST and distance of prey capture from the colony, which became most steep at temperatures > 19.5 °C ($R^2 = 0.46$, $F = 9.602$, $P < 0.0001$) (Figure S7).

Discussion

Southeast Australia is a hotspot for ocean warming driven by the EAC, with SST rises of 0.7–1.4 °C predicted by 2030, and 2–3 °C by 2100²⁸. To better understand the ecological effects of this strengthening western boundary current, we used accelerometry in conjunction with remote-sensed environmental data to link the foraging success of a marine predator to local SST. We observed a consistent relationship between high SST and low penguin

foraging success, both temporally and spatially. These findings may give important insights into resource availability in a changing system, and we discuss them below.

Temporal variability in foraging success. Little penguins feed on a variety of low trophic level species, with “forage fish” e.g. small pelagic fish, squid and krill comprising most of their diet throughout their range^{29,30}. Globally, forage fish are important commercial stocks, and sustain many marine predator populations³¹. These species feed on phytoplankton and zooplankton, the abundance and distribution of which are tightly linked to nutrient upwelling in boundary current systems³². For example, in southeast Australia where waters are generally nutrient poor, upwelling events driven by wind or the dynamic action of the EAC can enrich coastal waters³³. These ephemeral events lead to significantly increased biomass of plankton in upwelling areas³⁴, which forage fish prey on. Forage fish can be highly sensitive to changes in upwelling dynamics and to environmental conditions such as temperature, and their populations can exhibit ‘boom-bust’ dynamics³⁵. Fluctuations in forage fish abundance have in turn been shown to have major effects on the productivity of predators³⁶, including little penguins³⁷.

Although we only studied prey capture by penguins over three breeding seasons, SST during the study period varied substantially around the long-term mean, situating our findings within a climatological context. This was due to variable dynamics of the EAC, with unusual spikes of warm water penetrating the region in the spring and summer of 2013 and 2014. We found that a simple but reliable predictor of relative foraging success in November and December was whether SST was high or low relative to the same month in the other study years, with the year with the lowest mean temperatures (2012) having the highest success and the year with the highest mean temperatures (2013) having the lowest (Fig. 2).

A broad correlation between anomalously high SST and the availability of forage fish is seen in other western boundary current systems. In the Sea of Japan, which is influenced by the warm Kuroshio Current, sardine catches are lowest when SST is high³⁸. In the same region, the proportion of anchovy in the diet of rhinoceros auklets was also very low during a period of high SST³⁹. As well as reducing the abundance of adult fish, high SST is related to higher mortality⁴⁰ and lower recruitment⁴¹ of juvenile sardines. This suggests a potentially poor outcome for clupeoid fish species and their predators as SST rises in western boundary current regions such as southeast Australia.

Although high SST was inversely related to foraging success on a monthly scale, our modelled data showed that the functional relationship between prey capture success and SST was not linear. At the lowest SSTs, prey capture success was also low. At latitudes around Montague Island (~ -36.5 S), a major phytoplankton bloom occurs each spring that increases local chlorophyll *a* concentrations by around 150%. This bloom is driven by a seasonal increase in SST, greater availability of dissolved nitrate and silicate, and a shallowing of the mixed-layer depth: conditions that promote rapid phytoplankton growth and reproduction⁴². Reduced prey capture success occurring at low SSTs may therefore represent a period when the water is not yet warm enough to facilitate the production of high phytoplankton densities, that in turn increase local abundance of planktivorous forage fish⁴³. The timing of this spring bloom is likely to be important for the breeding phenology of predators, and may explain the spring/summer breeding cycle of seabirds and seals in the study area, compared with winter breeding, which is common in western Australia.

Our models suggest an optimal offshore temperature range for prey capture success of 19–21 °C, with lower success outside that range (Fig. 3). Although the SST values used in this part of the analysis provide a more general index of EAC-driven temperatures affecting the shelf rather than conditions in the precise location of penguin foraging, it is notable that this ‘thermal optimum’ mirrors established relationships between sardine (*Sardinops sagax*) catches and SST in the Gulf of California, South Africa and South Australia^{32,44–46}. The area around Montague Island is the most northerly summer sardine spawning ground on the east coast of Australia, and there is a commercial sardine fishery operating in this region. Catch rates are unavailable for the study period, however landings for the ~110km region of coast incorporating the penguin foraging ground were on average 75 t per month in Sep and Nov, and 10 t per month in Dec between 1984 and 2008⁴⁷. The importance of this area to sardines and their established distribution in relation to SST suggest that the patterns of prey capture success that we identified using accelerometry may reflect processes that govern the local availability of sardines to penguins. Future tracking studies incorporating diet analysis of predators such as seabirds, animal-borne video cameras and/or direct sampling of the prey field in relation to environmental conditions would be valuable to provide further insight into the predator-prey relationships in this system.

Our results imply that offshore SST > 21 °C is related to lower prey capture success by penguins breeding on Montague Island. In an average year, these temperatures are not experienced until January, the tail end of the little penguin’s breeding season. However, in anomalous years such as 2013, pulses of warm water arrive earlier and coincide with the peak chick-provisioning period, a time of high energetic demand⁴⁸. Reduced food availability at crucial times in the breeding cycle is likely to have poor outcomes for breeding success and survival in range-restricted species^{49,50}. A link between high SST and low reproductive success has been established for little penguins in other parts of their range^{51–53} and for some other seabird species globally^{54,55}. Although there was no demographic study on Montague Island running concurrent to this foraging study, and the effect of the observed variation in prey availability on breeding success is therefore unknown, our findings provide some evidence that any future decrease in the fitness of meso-predators related to rising SST in the EAC system may be a function of variation in local prey availability.

Spatial variability in foraging location. It is apparent from overlaying tracks on SST anomaly maps and from the hurdle model results that little penguin foraging tends to be focused in habitat with lower SST (Fig. 4, Table S1). Little penguins are small (~1.1 kg; 40 cm in length) and have a limited ability to assess available habitat quality relative to flying seabirds that can cover greater distances and map their environment efficiently from an aerial perspective using visual and olfactory cues^{56,57}. It is somewhat surprising therefore, that the penguins in

this study appeared to be able to reliably select the coolest habitat for foraging. Across the study period the coolest area around Montague Island tended to be inshore to the southwest, and this was the destination of almost all of the penguins tracked during this study. This persistent oceanographic feature may be influenced by the shape of the coastline at this location, which curves inwards with a prominent headland, perhaps functioning as a trap for cooler water being pushed inshore by the EAC. Heading south from the colony until encountering colder water could therefore be a risk-minimising foraging strategy for penguins, if prey abundance is predictably higher in this cooler-than-average area. Future work characterising the fine-scale oceanography in this region may shed light on the local features that enhance productivity and/or concentrate prey in certain areas.

Spatial variability in foraging success. We found a relationship between prey capture success and SST that was not accounted for by habitat preference. Even within the cooler areas that penguins selected for foraging, and in those areas that actually contained prey, the amount of prey caught was related to SST. The coldest areas provided the highest prey capture success, and the warmest areas provided the lowest prey capture success, indicating that prey distribution may be responsive to fine-scale SST. An inverse relationship between local forage fish distribution and SST has also been observed in eastern South Africa, where sardines appear to be spatially aggregated in the coolest available habitat, pushed inshore to small patches of suitable habitat by shoreward movement of the warm Agulhas current⁵⁸.

The penguins in this study appeared to consistently forage near the surface (<10 m). This suggests that the distribution of the prey species that they were targeting was similar throughout the study period, and that the penguins maintain a relatively consistent foraging strategy, even though prey capture success can be highly variable. In previous studies of little penguins⁵⁹ and other diving seabirds⁶⁰, features such as thermoclines have been identified as potential foraging cues. The relationship between the vertical distribution of forage fish and the temperature profile of the water column is generally poorly studied, including in the path of the EAC. However, as the mixed layer depth on the shelf at this time was likely to be around 20 m (CSIRO Atlas of Regional Seas (CARS); <http://www.marine.csiro.au/~dunn/cars2009/>) and there was no evidence of a thermocline from the tag temperature data at the depths at which penguins were catching prey, it seems that whichever prey species the penguins were primarily feeding on during this period were not consistently aggregated around such subsurface features that may be related to EAC dynamics.

Our results suggest a relationship between the distance from the colony at which penguins catch most of their prey and offshore SST, with the highest SSTs being associated with the furthest foraging distances. This was influenced by penguins travelling unusually far in December 2013 and 2014, when SST was comparatively high. Increases in foraging effort (e.g. distance travelled and dive behaviour) in response to shifts in the location of profitable feeding areas may ultimately affect population dynamics⁶¹. We recommend future longitudinal studies mapping the prey field using active acoustics⁶², alongside the collection of high resolution *in situ* environmental data. This will shed light on the types and densities of prey in the area at different times, and their fine-scale distribution in relation to the environment. Tracking studies of breeding seabirds could assess the 'energy landscape' in the region by estimating spatial gradients of energy expenditure⁶³ and prey capture success from accelerometry. This could then be related back to fitness metrics such as breeding success, in order to gain more direct insight into how variability in rapidly changing ocean systems such as the EAC may affect the ability of predator populations to be sustained into the future.

Conclusions

Marine predator populations are vulnerable to reductions in prey availability^{49,50} and some forage fish populations are vulnerable to rising SST^{32,38,40,41}. We have shown that short-term variability in SST is related to prey capture success by little penguins, and that future increases in SST driven by a strengthening western boundary current may alter the abundance and distribution of forage fish. By using a prey capture signature to assess the effects of environmental variation on the relative availability of resources, we can direct future research into the way that climate change will affect species at multiple trophic levels.

References

- Behrenfeld, M. J. *et al.* Climate-driven trends in contemporary ocean productivity. *Nature*, **444**, 752–755 (2006).
- Doney, S. C. *et al.* Climate change impacts on marine ecosystems. *Mar. Sci.* **4**, (2012).
- Dragon, A. C., Monestiez, P., Bar-Hen, A. & Guinet, C. Linking foraging behaviour to physical oceanographic structures: southern elephant seals and mesoscale eddies east of Kerguelen Islands. *Prog. Oceanogr.* **87**, 61–71 (2010).
- Suryan, R. M., Santora, J. A. & Sydeman, W. J. New approach for using remotely sensed chlorophyll a to identify seabird hotspots. *Mar. Ecol. Prog. Ser.* **451**, 213–225 (2012).
- Nathan, R. *et al.* Using tri-axial acceleration data to identify behavioral modes of free-ranging animals: general concepts and tools illustrated for griffon vultures. *J. Exp. Biol.* **215**, 986–996 (2012).
- Watanabe, Y. Y. & Takahashi, A. Linking animal-borne video to accelerometers reveals prey capture variability. *Proc. Natl. Acad. Sci.* **110**, 2199–2204 (2013).
- Carroll, G., Slip, D., Jonsen, I. & Harcourt, R. Supervised accelerometry analysis can identify prey capture by penguins at sea. *J. Exp. Biol.* **217**, 4295–4302 (2014).
- Ydesen, K. S. *et al.* What a jerk: prey engulfment revealed by high-rate, super-cranial accelerometry on a harbour seal (*Phoca vitulina*). *J. Exp. Biol.* **217**, 2239–2243 (2014).
- Jayne, S. R. & Marotzke, J. The oceanic eddy heat transport. *J. Phys. Oceanogr.* **32**, 3328–3345 (2002).
- Everett, J. D., Baird, M. E. & Suthers, I. M. An avenue of eddies: Quantifying the biophysical properties of mesoscale eddies in the Tasman Sea. *Geophys. Res. Lett.* **39**, p.L16608 (2012).
- Tranter, D., Carpenter, D. & Leech, G. The coastal enrichment effect of the East Australian Current eddy field. *Deep-Sea Res. Pt I* **33**, 1705–1728 (1986).
- Olson, D. B. Biophysical dynamics of western transition zones: a preliminary synthesis. *Fish. Oceanogr.* **10**, 133–150 (2001).
- Jiménez, S., Domingo, A., Abreu, M. & Brazeiro, A. Structure of the seabird assemblage associated with pelagic longline vessels in the southwestern Atlantic: implications for bycatch. *Endangered Species Res.* **15**, 241–254 (2011).

14. Wu, L. *et al.* Enhanced warming over the global subtropical western boundary currents. *Nature Clim. Change*. **2**, 161–166 (2012).
15. Everett, J. D. & Doblin, M. A. Characterising primary productivity measurements across a dynamic western boundary current region. *Deep-Sea Res. Pt I*. **100**, 105–116 (2015).
16. Einoder, L. D. A review of the use of seabirds as indicators in fisheries and ecosystem management. *Fish. Res.* **95**, 6–13 (2009).
17. Robinson, S., Chiaradia, A. & Hindell, M. A. The effect of body condition on the timing and success of breeding in Little Penguins *Eudyptula minor*. *Ibis*, **147**, 483–489 (2005).
18. Chiaradia, A. F. & Kerry, K. R. Daily nest attendance and breeding performance in the little penguin *Eudyptula minor* at Phillip Island, Australia. *Mar Ornithol.* **27**, 13–20 (1999).
19. Johannessen, E., Houston, D. & Russell, J. Increased survival and breeding performance of double breeders in little penguins *Eudyptula minor*, New Zealand: evidence for individual bird quality? *J. Avian Biol.* **34**, 198–210 (2003).
20. Charnov, E. L. Optimal foraging: the marginal value theorem. *Theor. Popul. Biol.* **9**, 129–136 (1976).
21. Thompson, D. & Fedak, M. A. How long should a dive last? A simple model of foraging decisions by breath-hold divers in a patchy environment. *Anim Behav.* **61**, 287–296 (2001).
22. Sato, K., Charrassin, J. B., Bost, C. A. & Na to, Y. Why do macaroni penguins choose shallow body angles that result in longer descent and ascent durations? *J. Exp Biol.* **207**, 4057–4065 (2004).
23. Cannell, B. L. & Cullen, J. M. The foraging behaviour of little penguins *Eudyptula minor* at different light levels. *Ibis*. **140**, 467–471 (1998).
24. Suthers, I. M. *et al.* The strengthening East Australian Current, its eddies and biological effects—an introduction and overview. *Deep-Sea Res. Pt. II*. **58** 538–546 (2011).
25. Bethge, P., Nicol, S., Culik, B. M. & Wilson, R. P. Diving behaviour and energetics in breeding little penguins (*Eudyptula minor*). *J. Zool.* **242**, 483–502 (1997).
26. Jackman, S. pscl: Classes and Methods for R Developed in the Political Science Computational Laboratory, Stanford University. Department of Political Science, Stanford University. Stanford, California. R package version 1.4.9 (2015).
27. R Core Team. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria (2015).
28. Ridgway, K. & Hill, K. The East Australian Current. In *A Marine Climate Change Impacts and Adaptation Report Card for Australia 2009* (Eds. E. S. Poloczanska, A. J. Hobday & A. J. Richardson), NCCARF Publication 05/09 (2009).
29. Klomp, N. I. & Wooller, R. D. Diet of little penguins, *Eudyptula minor*, from Penguin Island, western Australia. *Mar. Freshwater Res.* **39**, 633–639 (1988).
30. Deagle, B. E., Chiaradia, A., McInnes, J. & Jarman, S. N. Pyrosequencing faecal DNA to determine diet of little penguins: is what goes in what comes out? *Conserv. Genetics*. **11**, 2039–2048 (2010).
31. Pikitch, E. K. *et al.* The global contribution of forage fish to marine fisheries and ecosystems. *Fish. Fish.* **15**, 43–64 (2014).
32. Lanz, E., López-Martínez, J., Nevárez-Martínez, M. & Dworak, J. A. Small pelagic fish catches in the Gulf of California associated with sea surface temperature and chlorophyll. *Calif. Coop. Oceanic Fish. Invest. Rep.* **50**, 134–146 (2009).
33. Roughan, M. & Middleton, J. H. A comparison of observed upwelling mechanisms off the east coast of Australia. *Cont. Shelf Res.* **22** 2551–2572 (2002).
34. Baird, M. E., Timko, P. G., 3, I. M. & Middleton, J. H. Coupled physical–biological modelling study of the East Australian Current with idealised wind forcing. Part I: Biological model intercomparison. *J. Mar. Sys.* **59**, 249–270 (2006).
35. Chavez, F. P., Ryan, J., Lluch-Cota, S. E. & Niquen, M. From anchovies to sardines and back: multidecadal change in the Pacific Ocean. *Science*. **299**, 217–221 (2003).
36. Curry, P. M. *et al.* Global seabird response to forage fish depletion—one-third for the birds. *Science*. **334**, 1703–1706 (2011).
37. Dann, P., Norman, F. I., Cullen, J. M., Neira, F. J. & Chiaradia, A. Mortality and breeding failure of little penguins, *Eudyptula minor*, in Victoria, 1995–96, following a widespread mortality of pilchard, *Sardinops sagax*. *Mar. Freshwater Res.* **51**, 355–362 (2000).
38. Yasuda, I., Sugisaki, H., Watanabe, Y., Minobe, S. S. & Oozeki, Y. Interdecadal variations in Japanese sardine and ocean/climate. *Fish. Oceanogr.* **8**, 18–24 (1999).
39. Thayer, J. A. *et al.* Forage fish of the Pacific Rim as revealed by diet of a piscivorous seabird: synchrony and relationships with sea surface temperature. *Can. J. Fish. Aquat. Sci.* **65**, 1610–1622 (2008).
40. Noto, M. & Yasuda, I. Population decline of the Japanese sardine, *Sardinops melanostictus*, in relation to sea surface temperature in the Kuroshio Extension. *Can. J. Fish. Aquat. Sci.* **56**, 973–983 (1999).
41. Lindegren, M. & Checkley Jr, D. M. Temperature dependence of Pacific sardine (*Sardinops sagax*) recruitment in the California Current Ecosystem revisited and revised. *Can. J. Fish. Aquat. Sci.* **70**, 245–252 (2012).
42. Everett, J. D., Baird, M. E., Roughan, M., Suthers, I. M. & Doblin, M. A. Relative impact of seasonal and oceanographic drivers on surface chlorophyll a along a Western Boundary Current. *Prog. Oceanogr.* **120**, 340–351 (2014).
43. Nevárez-Martínez, M. O. *et al.* Distribution and abundance of the Pacific sardine (*Sardinops sagax*) in the Gulf of California and their relation with the environment. *Prog. Oceanogr.* **49**, 565–580 (2001).
44. Agenbag, J. J. *et al.* Estimating environmental preferences of South African pelagic fish species using catch size-and remote sensing data. *Prog. Oceanogr.* **59**, 275–300 (2003).
45. O'Donoghue, S. H., Drapeau, L., Dudley, S. F. & Peddemors, V. M. The KwaZulu-Natal sardine run: shoal distribution in relation to nearshore environmental conditions, 1997–2007. *Afr. J. Mar. Sci.* **32**, 293–307 (2010a).
46. Doubell, M. J. *et al.* South Australian Research and Development Institute (Aquatic Sciences) Optimising the size and quality of Sardines through real-time harvesting (2015).
47. Stewart, J., Ballinger, G. & Ferrell, D. Industry & Investment NSW. Review of the biology and fishery for Australian sardines (*Sardinops sagax*) in New South Wales. (2010).
48. Gales, R. & Green, B. The annual energetics cycle of little penguins (*Eudyptula minor*). *Ecology*. 2297–2312 (1990).
49. Oro, D. & Furness, R. W. Influences of food availability and predation on survival of kittiwakes. *Ecology*. **83**, 2516–2528 (2002).
50. Crawford, R. J. *et al.* The influence of food availability on breeding success of African penguins *Spheniscus demersus* at Robben Island, South Africa. *Biol Conserv.* **132**, 119–125 (2006).
51. Hobday, D. K. Abundance and distribution of pilchard and Australian anchovy as prey species for the little penguin *Eudyptula minor* at Phillip Island, Victoria. *Emu*, **91**, 342–354 (1992).
52. Mickelson, M. J., Dann, P. & Cullen, J. M. Sea temperature in Bass Strait and breeding success of the little penguin *Eudyptula minor* at Phillip Island, south-eastern Australia. *Emu*, **91**, 355–368 (1992).
53. Cannell, B. L., Chambers, L. E., Wooller, R. D. & Bradley, J. S. Poorer breeding by little penguins near Perth, Western Australia is correlated with above average sea surface temperatures and a stronger Leeuwin Current. *Mar. Freshwater Res.* **63**, 914–925 (2012).
54. Inchausti, P. *et al.* Inter-annual variability in the breeding performance of seabirds in relation to oceanographic anomalies that affect the Crozet and the Kerguelen sectors of the Southern Ocean. *J. Avian Biol.* **34**, 170–176 (2003).
55. Frederiksen, M., Edwards, M., Mavor, R. A. & Wanless, S. Regional and annual variation in black-legged kittiwake breeding productivity is related to sea surface temperature. *Mar. Ecol. Prog. Ser.* **350**, 137 (2007).
56. Davoren, G. K., Montevecchi, W. A. & Anderson, J. T. Search strategies of a pursuit-diving marine bird and the persistence of prey patches. *Ecol Monogr.* **73**, 463–481 (2003).
57. Nevitt, G. A., Losekoot, M. & Weimerskirch, H. Evidence for olfactory search in wandering albatross, *Diomedea exulans*. *Proc. Natl. Acad. Sci.* **105**, 4576–4581 (2008).

58. O'Donoghue, S. H., Drapeau, L. & Peddemors, V. M. Broad-scale distribution patterns of sardine and their predators in relation to remotely sensed environmental conditions during the KwaZulu-Natal sardine run. *Afr. J. Mar. Sci.* **32**, 279–291 (2010b).
59. Pelletier, L., Kato, A., Chiaradia, A. & Ropert-Coudert, Y. Can thermoclines be a cue to prey distribution for marine top predators? A case study with little penguins. *PLoS ONE*. **7**, e31768 (2012).
60. Takahashi, A. *et al.* Thick-billed murre use different diving behaviors in mixed and stratified waters. *Deep-Sea Res. Pt. I*, **55**, 1837–1845 (2008).
61. Bost, C. A. *et al.* Large-scale climatic anomalies affect marine predator foraging behaviour and demography. *Nat. Comms.* **6** (2015).
62. Boyd, C. *et al.* Predictive modelling of habitat selection by marine predators with respect to the abundance and depth distribution of pelagic prey. *J. Anim. Ecol.* **84**, 1575–1588 (2015).
63. Wilson, R. P., Quintana, F. & Hobson, V. J. Construction of energy landscapes can clarify the movement and distribution of foraging animals. *Proc. Roy. Soc. B.* **282** (2011).
64. Wickham, H. *ggplot2: Elegant Graphics for Data Analysis*. (Springer-Verlag, 2009).

Acknowledgements

We thank the NSW National Parks and Wildlife Service for their ongoing commitment to this project and logistical support. We thank all those who assisted with penguin tracking, and Yan Ropert-Coudert and Akiko Kato for technical assistance and modification of GPS units. Satellite-derived data are freely available from the Australian Integrated Marine Observing System (IMOS; <http://www.imos.org.au>), an initiative of the Australian Government being conducted as part of the National Collaborative Research Infrastructure Strategy and the Super Science Initiative. This project was funded by an Australian Research Council Linkage Grant (LP110200603), supported by Taronga Conservation Society Australia. G.C. is supported by a Macquarie University Research Excellence Scholarship and I.J. is supported by a Macquarie University Vice Chancellor's Innovation Fellowship. J.D.E. was funded by an ARC Discovery Project (DP120100728).

Author Contributions

G.C. conceived the study design, collected data, performed data analysis and drafted the manuscript. J.D.E. provided oceanographic expertise and data that shaped both the analysis and writing. R.H. and D.S. were involved in study design, data collection and writing. I.J. contributed to data collection, writing and data analysis. All authors approved the final version of this manuscript.

Additional Information

Supplementary information accompanies this paper at <http://www.nature.com/srep>

Competing financial interests: The authors declare no competing financial interests.

How to cite this article: Carroll, G. *et al.* High sea surface temperatures driven by a strengthening current reduce foraging success by penguins. *Sci. Rep.* **6**, 22236; doi: 10.1038/srep22236 (2016).



This work is licensed under a Creative Commons Attribution 4.0 International License. The images or other third party material in this article are included in the article's Creative Commons license, unless indicated otherwise in the credit line; if the material is not included under the Creative Commons license, users will need to obtain permission from the license holder to reproduce the material. To view a copy of this license, visit <http://creativecommons.org/licenses/by/4.0/>

Pages 169-179 of this thesis have been removed as they contain published material under copyright. Removed contents published as:

Carroll, G., Cox, M., Harcourt, R., Pitcher, B.J., Slip, D. and Jonsen, I. (2017), Hierarchical influences of prey distribution on patterns of prey capture by a marine predator. *Functional Ecology*, vol. 31, pp. 1750-1760, doi.org/10.1111/1365-2435.12873

ANIMAL RESEARCH AUTHORITY (ARA)

AEC Reference No.: 2011/054-6

Date of Expiry: 12 December 2014

Full Approval Duration: 13 December 2011 to 12 December 2014 (36 months)

This ARA remains in force until the Date of Expiry (unless suspended, cancelled or surrendered) and will only be renewed upon receipt of a satisfactory Progress Report before expiry.

Principal Investigator:

Professor Rob Harcourt
Dept of Environment and Geography
Macquarie University, NSW 2109
robert.harcourt@mq.edu.au
(02) 9850 797 0421 780 434

Associate Investigators:

Gemma Carrol 0422 775 086
Matt Carr 0417 041 086
Justin Clarke 0412 025 434
Marcus Salton 0400 596 139
Dustin O'Hara 0403 881 958
Monique Ladds 0449 693 029

Other principal Investigators:

Iain Field 0427 355 879
David Slip 0432 886 278

In case of emergency, please contact:

**Principal investigator – 0421 780 434 or The Associate Investigators named above, or
Animal Welfare Officer - 9850 7758**

The above-named are authorised by MACQUARIE UNIVERSITY AEC to conduct the following research:

Title of the project: Marine predators, marine parks and marine hotspots: is zoning and effective conservation tool in a changing environment?

Type of animal research: 7: Environmental Study

Aims of project: This project aims to identify the underlying physical and biological drivers of Areas of Ecological Significance, by observing the movement of eight predator species and analysis in relation to the dynamic oceanographic conditions of the region and the static boundaries of marine reserves.

Surgical Procedures category: 3 (Minor Conscious Intervention)

All procedures must be performed in accordance with the AEC approved protocol.

Maximum numbers approved (for the Full Approval Duration):

Species	Age	Total	Source
<i>Arctocephalus forsteri</i> New Zealand Fur Seal	Adult/Juveniles	120/150	Wild
<i>Arctocphalus pusillus doriferu</i> Australian fur seal	Adult/Juveniles	120/150	Wild
<i>Eudyptula minor</i> Little Penguin	Adult	270	Wild
<i>Puffinus tenuirostris</i> Short tailed shearwater	Adult	150	Wild
<i>Puffinus pacificus</i> Wedge tailed shearwater	Adult	150	Wild
<i>Puffinus griseus</i> Sooty shearwater	Adult	150	Wild
<i>Thalasseus bergii</i> Greater crested tern	Adult	150	Wild
<i>Larus novaehollandiae</i> Silver gull	Adult	150	Wild
TOTAL		1560	

Location: Montague Island, Jervis Bay and Batemans Bay marine parks

Amendments considered and approved by the AEC since initial approval:

1. Addition of Marcus (approved April 2012)
2. Addition of Dustin O'Hara and Monique Ladds (Approved 20 June 2012)
3. Two species studies and rectification for animal numbers (Approved 19 July 2012)
4. Addition of Monique Ladds as AI (Approved 20 June 2012)
5. Add number of animal (90 penguins per annum) (Approved 5 December 2013)
6. Addition of stomach flushing for dietary studies (for seabirds only) (Approved 5 December 2013)
7. Adding new experimental procedure (Approved at AEC meeting 18 September 2014)

Conditions of initial Approval:

1. No more than 5% of blood volume (BV) is sampled. (A suggested estimate of BV is 60ml per Kg of body weight)
2. Copies of NPWS and MPA permit/licences are submitted to animal.ethics@mq.edu.au prior to research beginning

Being animal research carried out in accordance with the Code of Practice for a recognised research purpose and in connection with animals (other than exempt animals) that have been obtained from the holder of an animal suppliers licence.

Professor Mark Connor (Chair, Animal Ethics Committee)

Approval Date: 18 September 2014

Adapted from Form C (issued under part IV of the Animal Research Act, 1985)



AEC Reference No.: 2014/057-8

Date of Expiry: 23 December 2017

Full Approval Duration: 23 December 2014 to 23 December 2017

This ARA remains in force until the Date of Expiry (unless suspended, cancelled or surrendered) **and will only be renewed upon receipt of a satisfactory Progress Report before expiry (see Approval email for submission details).**

Principal Investigator:

Professor Robert Harcourt
Biological Sciences
Macquarie University, NSW 2109
0421 780 434
Robert.harcourt@mq.edu.au

Associate Investigator:

Justin Clarke	0412 025 434
Paolo Momigliano	0416 979 417
Benjamin Pitcher	02 9852 2103
Monique Ladds	0449 693 029
Lisa Harrison	0459 723 705
Marcus Salton	0400 596 139
Kimberley Kliska	0411 425 788
Dave Slip	0432 886 278
Ian Jonsen	02 9850 7998
Gemma Carroll	0422 775 086
Clive McMahon	0419 870 275
Michelle Power	0414 350 344

In case of emergency, please contact:
the Principal Investigator / Associate Investigator named above
OR Animal Welfare Officer: 9850 7758 / 0439 497 383

The above-named are authorised by MACQUARIE UNIVERSITY ANIMAL ETHICS COMMITTEE to conduct the following research:

Title of the project : Marine predators, marine parks and marine hotspots: is zoning an effect conservation tool in a changing environment?

Purpose: 7 - Research: Environmental Study

Aims: 1. Quantify foraging and movements of seals and seabirds, using GPS, accelerometers and other loggers 2. Characterise the spatio-temporal distribution of prey density and associated environmental drivers through in-situ sampling and acoustic surveys 3. Establish the sensitivity of seals and penguins to DMS concentrations in controlled and natural settings 4. Determine the relationship between DMS concentrations and the distribution/density of prey relevant to little penguins and other mid-trophic level predators 5. Experimentally assess the influence of DMS on prey tracking and foraging behaviour of predators 6. Integrate predator behaviour, environmental and prey density information to infer how foraging strategies and associated energetic demands may respond to future environmental change. 7. To examine the sensitivity of little penguins to DMS. 8. Measure the energy requirements of nesting little penguins.

Surgical Procedures category: 4 - Minor Surgery With Recovery

All procedures must be performed as per the AEC-approved protocol, unless stated otherwise by the AEC and/or AWO.

Maximum numbers approved (for the Full Approval Duration):

Species	Strain	Sex/Age/Weight	Total	Supplier/Source
4E Pinnipedia	Australian and New Zealand Fur Seal	Any	120	Wild
20 native Wild	little penguin, silver gull, crested tern, short-tailed shearwater, wedge-tailed shearwater	Any	900	Wild
20 native Wild	little penguins – Metabolic studies	Any	36	Wild
20 native Wild	little penguins – DMS Observational	Any	10,000	Wild
20 native Wild	little penguins – Scent recognition	Any – Chicks	20	Wild
20 native Wild	little penguins – Scent recognition	Any - Adults	20	Wild
		TOTAL	11,096	

Location of research:

Location	Full street address
In - Situ / Wild	Montague Island Nature Reserve, Montague Island via Narooma NSW, Jervis Bay, NSW Booderee National Park (Parks Australia), Jervis Bay Territory ACT, Jervis Bay Marine Park, NSW Batemans Marine Park, Batemans Bay, NSW
Sydney Harbour	

Amendments approved by the AEC since initial approval:

- Amendment #1 – Amend experimental design and number of animals
- Amendment #2 – Addition of Dr Clive McMahon as Associate Investigator (Executive approved, ratified by AEC 16 July 2015)
- Amendment #3 – Add location of research – Sydney Harbour (Executive approved, ratified by AEC 14 July 2016).
- Amendment #4(a) – Amend experimental design, Amendment #4(b) – Amend procedure and Amendment #4(c) – Amend number and type of animals (Approved by AEC 18 August 2016).
- Amendment #5 – Amend Technique (Executive approved, ratified by AEC 15 September 2016).
- Amendment #6 – Add Michelle Power as Associate Investigator (Executive approved, ratified by AEC 12 April 2017).

Conditions of Approval:

- Amendment #2 – Dr Clive McMahon is to complete the Research Animal Care and Ethics (RACE) Training 2015

Being animal research carried out in accordance with the Code of Practice for a recognised research purpose and in connection with animals (other than exempt animals) that have been obtained from the holder of an animal suppliers licence.

Associate Professor Jennifer Cornish (Chair, Animal Ethics Committee)

Approval Date: 12 April 2017