

**Relationships between foraging behaviour, diet and
reproductive success at an urban colony of little
penguins (*Eudyptula minor*), St Kilda, Australia**

A thesis submitted for the degree of Doctor of Philosophy

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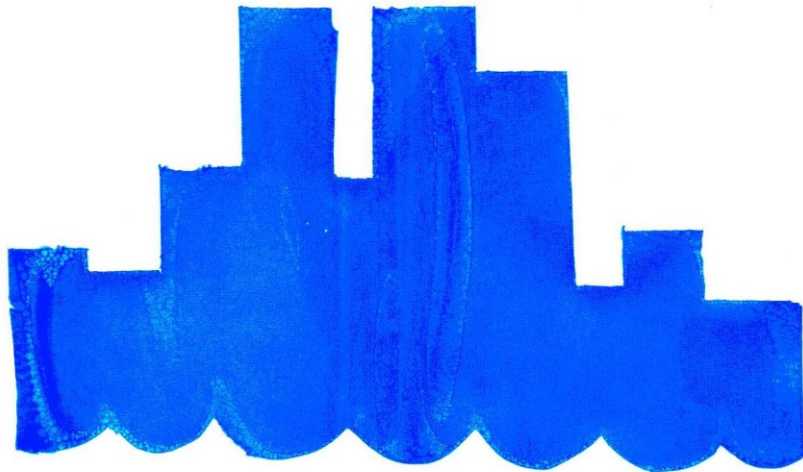
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I have often had the impression that, to penguins, man is just another penguin - different, less predictable, occasionally violent, but tolerable company when he sits still and minds his own business.

- Bernard Stonehouse



Little penguins (*Eudyptula minor*) in a nest at the St Kilda breakwater.

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Abstract

Little penguins have shown an overall pattern of decline throughout their distribution, thus it was considered unusual for a new colony to establish themselves recently near the heart of a city at St Kilda, Victoria, Australia. Since they were first observed in the 1970's, this colony has grown from a few breeding pairs to ~1000 individuals. It is the factors that have contributed to this population success that this study aims to examine, specifically the relationships between colony's foraging behaviour, diet and subsequent reproductive success.

Penguin foraging behaviour was studied during three breeding seasons by satellite transmitters, global positioning system (GPS) loggers and time-depth recorders (TDR). Results revealed that the penguins have a small foraging area ~1500 ha in the north of Port Phillip bay. Maximum distance travelled from the colony each day is ~13 kms and total horizontal distance covered is ~34 km, less than that cited for other penguin colonies. Diving was conducted mostly to depths ≤ 10 m, with ~800 dives performed in a day, comparable to other little penguin colonies. Use of the combined GPS and TDR revealed that the penguins spent a disproportionately high amount of time foraging in the artificially dredged shipping channels that occur within their foraging area. This foraging study also found that the combined loggers providing more accurate and useful data at the small scale than separately deployed satellite transmitters and TDRs.

Diet at the penguin colony was monitored continuously over a two year period using stomach content and stable isotope analysis. Stable isotopes were better able to detect seasonal variation in diet, while stomach contents were useful for determining dietary diversity and age cohorts of the prey consumed. The diet was dominated by Australian anchovy (*Engraulis australis*) and southern garfish (*Hypobamphus melanochir*). Australian anchovies were common during the pre-breeding and early stages of breeding throughout

spring and early summer. Southern garfish increased in the diet from chick-rearing through the non-breeding season. Adult penguins switched from Australian anchovy to southern garfish to feed their chicks, presumably due to the higher energetic, protein and fat content of this species.

Reproductive success determined by the number of chicks fledged per pair and peak chick weights was similarly low in all years of this study. The mean egg-laying date was earlier in 2008 than other years, and the reproductive success was also greatest in this year, being considered 'average' for little penguins. Double brooding was highest in 2006, but this was also the year with the latest mean egg-laying date and the lowest fledging rate from first clutches. Successful breeding was associated with quality prey rather than increased double brooding.

St Kilda little penguin colony is an example of a native animal population that has successfully exploited changes in both the terrestrial (breakwater) and marine (shipping channel) environments. Prey availability in close proximity to their colony is essential for the continuation of this population; their survival in the urban environment can be supported through the careful management of their prey stocks.

General Declaration

In accordance with Monash University Doctorate Regulation 17 / Doctor of Philosophy and Master of Philosophy (MPhil) regulations the following declarations are made:

I hereby declare that this thesis contains no material which has been accepted for the award of any other degree or diploma at any university or equivalent institution and that, to the best of my knowledge and belief, this thesis contains no material previously published or written by another person, except where due reference is made in the text of the thesis.

This thesis includes two original papers published in peer reviewed journals and two unpublished publications. The core theme of the thesis is the investigation of the foraging ecology, diet and resultant reproductive success of an urban colony of little penguins. The ideas, development and writing up of all the papers in the thesis were the principal responsibility of myself, the candidate, working within the School of Biological Sciences under the supervision of Richard Reina and André Chiaradia.

The inclusion of co-authors reflects the fact that the work came from active collaboration between researchers and acknowledges input into team-based research.

In the case of chapters 2 and 3, my contribution to the work involved the following:

Thesis chapter	Publication title	Publication status*	Nature and extent of candidate's contribution
2	Foraging behaviour of little penguins <i>Eudyptula minor</i> in an artificially modified environment	Published	Data collection, interpretation, writing.
3	Fine scale tracking and biologging for conservation of an inshore marine animal	Published	Data collection, interpretation, writing.

Signed: 

Date: 13/9/2010 (corrections 20/2/2011)

Acknowledgements

Personal Acknowledgements

I firstly have to acknowledge the penguins themselves. They may be the smallest of all penguins, but Little Penguins have big characters, which is why I love working with them.

I hope that this study will ultimately be of benefit to the St Kilda colony, with the information collected used to help manage and protect it well into the future. My appreciation goes out to all those involved in the great work of protecting these penguins, past, present and future.

I want to thank my supervisors, Richard Reina and André Chiaradia, who together make a fantastic team. Richard has kept me focussed and on track, as well as being supportive throughout the whole process. I wish to thank André, the self proclaimed “loose cannon”, for his enthusiasm for the project and the knowledge that he has passed on to me. I have enjoyed the many conversations and laughs I’ve been provided with by both over the past few years.

I am ever so grateful to the amazing Zoe Hogg of Earthcare St Kilda for all of her help and support. Her energy and enthusiasm is unmatched by anyone I know. I must also thank all of the Earthcare St Kilda volunteers. There are too many to name, but I would particularly like to thank Louise Kelly, Sue Mason, Andrew McCutcheon, Clare McCutcheon, Ben Waincymer, Linda Grootendorst, Huon Clark, Alysson Svennson, Bob Tammick, Katrina Fine and Neil Blake. My gratitude also to Marcus Salton, Tracy Shaw, Meagan Dewar and Nicole Schumman, all of whom helped with fieldwork and were a great source of gossip that helped us endure the cold nights on the breakwater.

I would like to thank all the staff at the Phillip Island Nature Park for being so welcoming, I have always enjoy visiting the research centre and sharing morning tea. Thank you to

Peter Dann, Roger Kirkwood, Leanne Renwick, Julie McInnes, Marg Healy and Roz Jessop for helping with data analysis, field techniques and handling permits. I am grateful to Fiona Hume for patiently teaching me the difference between anchovy and pilchard otoliths. I also want to thank Yan Ropert-Courdert and Akiko Kato for helping me through the initial splash into the world of diving profiles and being supportive ever since.

At Monash University I'd like to thank my fellow post-graduate students for their ongoing support, particularly Sherrie Caarels, Lorenz Frick, Chris Johnstone and Tony Rafferty. My gratitude to Belinda Lees, who always came up with a brilliant solution to every challenge I put forward and to Stuart Kerr for help with freeze drying. My appreciation to all of the administrative staff in the School of Biological Sciences also.

From Parks Victoria I want to acknowledge all the staff at the Williamstown office, particularly Angeline Tew and Edena Critch. I appreciate the efforts made in dealing with the media and responding to any issues arising on the breakwater with such good humour. I would like to extend my deepest thanks to my friends and family that have safely navigated me through the rough seas of the PhD by helping me to keep it all in perspective. Thanks especially to my mum, Sharrelle and the Matics, for their support. I would also like to recognise my dad, who always lovingly encouraged my pursuits.

Lastly I want to thank Ash, who first referred to me as 'penguin girl'. He has helped in many ways, from assisting with fieldwork to putting up with penguin samples in the fridge, he has given unwavering support throughout it all.

Funding Acknowledgements

I was fortunate to have funding and equipment from a number of sources for this project.

I would like to thank all people and organisations that have generously supported this project, without their assistance this would not have been possible.

Australian Conservation Foundation

BHP-Billiton

Birds Australia

Dan Costa

Earthcare St Kilda Inc

Holsworth Wildlife Research Endowment

Monash University

National Institute of Polar Research (Japan)

Parks Victoria

Phillip Island Nature Parks

The Penguin Foundation

Toyota Australia

I would particularly like to thank Monash University for providing me with the Faculty of Science Deans Scholarship that has allowed me conduct this research.

Permit Acknowledgements

The field site was accessed with permission of the St Kilda Breakwater Wildlife

Management Co-operative Area committee. Research was conducted under animal ethics

permit BSCI/2006/12 from Monash University. Wildlife permits 10003374 and 10003848

were granted from the Department of Sustainability and Environment, Victoria.

Chapter 1: General Introduction

1.1 Little penguins in an urban environment

As human developments expand and put increased pressure on sensitive areas, such as coastal environments, a rise in interactions between people and native animals also occurs. Managing the impact of the urban environment on native animals can only be effective when informed by knowledge of the animal's requirements and potential threats to their survival. Study of urban foraging ecology is increasingly common (Rutz, 2006, Chipman et al., 2008, Eguchi et al., 2010), as we strive to retain populations of animals within our cities and developed areas.

Facilitated by anthropogenic changes to the environment together with an absence of natural predators, populations of introduced species often grow rapidly in urban areas. Unfortunately such invasive species and development can impede the persistence of native populations and lead to the litany of species that are now considered threatened, or indeed are extinct (Clavero and Garcia-Berthou, 2005). However, there are some examples of native species that have adapted to live in developed areas and may indeed benefit from introduced animals as a source of prey (e.g. the peregrine falcon, Rejt, 2001). In the face of mass extinctions it is important that we understand what factors influence both the failure and success of native populations. The reasons for species decline are often obvious and catastrophic, but those behind population success can be subtle and complicated. By addressing the causes of population decline and understanding the factors that determine population success we can more effectively act to conserve native animal species, albeit often at a much reduced carrying capacity than prior to initial disturbance events.

In this study we investigate a colony of little penguins, *Endiaptula minor*, that has successfully established and grown in a location close to many anthropogenic activities and developments. Several temperate species of penguins have populations that coincide with

human settlements, but most of these were established prior to human encroachment (e.g. Galapagos *Spheniscus mendiculus* and yellow-eyed *Megadyptes antipodes* penguins), while some were established more recently to a mixed response from residents (e.g. little penguins at Oamaru, New Zealand, and African penguins *Spheniscus demersus* at Simons Town, South Africa). Penguins fall into a group of animals that rely on two distinctly different habitats for their survival. Most of the penguin life is spent at sea foraging for food, but essential life history phases of courtship, breeding and moulting are necessarily conducted on land. Unfortunately for these animals they are consequently subject to two sets of potential anthropogenic disturbances. At sea, common threats to penguin health and survival come in the form of overfishing, oiling, entanglement and now global warming (Hays, 1984, Simeone et al., 1999, Boersma, 2008). On land the threats are most commonly habitat destruction or disturbance, introduced predators and contact with humans (Dann, 1992b, Simeone and Schlatter, 1998, Walker et al., 2005). Of the 18 penguin species, only five are considered as 'least concern' on the IUCN Red List (www.iucnredlist.org, accessed 29/09/2009), the rest are either decreasing in population or are at such small population levels that they are considered threatened with extinction due to a combination of the above threatening processes.

The little penguin (*Eudyptula minor*) is a temperate species that is considered common, but has suffered population decline within its range due to a number of threatening processes (Dann, 1992b, Stevenson and Woehler, 2007). The sensitivity of this species to human activities both on land and in the water makes it surprising that a colony of penguins would not only establish itself, but grow to a self-sustaining size within a heavily used area such as St Kilda.

1.2 St Kilda little penguin population

The St Kilda penguin colony is located on a 650 m long man-made breakwater wall that was built for the 1956 Melbourne Olympic Games. Most of the breakwater has been fenced off for approximately 20 years, but a section of ~100 m still remains open to the public (Giling et al., 2008). The breakwater is located at the end of a 450 m pier, approximately 5 km from the heart of Melbourne (37° 51' S, 144° 57' E), which has a population of approximately 4 million people (see Fig 1, Chapter 2). Penguins were first officially reported breeding on the breakwater in 1974 (Eades, 1975), at which time there were only a few breeding pairs. Study of the penguin colony started in 1986 by Prof. Mike Cullen of Monash University and has continued through the establishment of the volunteer group Earthcare St Kilda Inc. Management of the penguin colony is overseen by the St Kilda Breakwater Wildlife Management Co-operative Area committee, which is composed of members from a number of management organisations.

Prior to the establishment of the St Kilda penguin colony, little penguins had been recorded breeding at a few scattered locations within Port Phillip bay (Garnett et al., 1986), but no colony had been established. It is unknown whether little penguins nested within Port Phillip prior to European settlement. Phillip Island (approximately 110 km swimming distance from St Kilda) is the likely origin of penguins that settled at St Kilda (Cullen et al., 1996, Overeem et al., 2007), as penguins from Phillip Island use Port Phillip bay extensively during winter (Norman, 1992, Collins et al., 1999). However, there appears to be little migration between the colonies now (Z. Hogg, *unpublished data*) and St Kilda is considered a self-sustaining colony.

The population of penguins at the St Kilda colony has been estimated by Earthcare St Kilda (using estimates of breeding birds in the population, Dann and Cullen, 1990) for each year of study. This annual estimate provides valuable information on trends in the

population and it has shown a gradual rise in the estimated number of penguins from 100 individuals in 1987 to 1000 in 2005 (Z. Hogg, *unpublished data*).

Aside from the work of volunteers at this colony, there was a brief note on the establishment of this colony (Eades, 1975), their breeding success and foraging movements (using radio telemetry) in the 1990's (Cullen et al., 1996), genetic samples taken in 2003 (Overeem et al., 2007) and dietary samples collected in 2003-2004 (Chiaradia et al., *In review*).

The fieldwork for this PhD was conducted from 2006 to 2009 during the proposal and execution of a large-scale dredging project within the penguins foraging range. Reference to this specific project is made throughout the thesis chapters as an example of a large scale disturbance that is typical within many coastal environments.

1.3 Foraging behaviour of little penguins

Study of little penguin foraging behaviour has to date been limited to using separately deployed devices in order to minimise drag and weight on the penguins carrying them.

Little penguins have been tracked at sea using radio-telemetry and satellite transmitters, primarily at their eastern Australia colonies (Gales et al., 1990, Weavers, 1992, Cullen et al., 1996, Hull et al., 1998, Collins et al., 1999, Fortescue, 1999, Wiebkin et al., 2005, Hoskins et al., 2008). These studies have found that little penguins have one of the smallest ranges of all seabirds during breeding (Dann and Norman, 2006).

Depth recorders and accelerometers deployed on little penguins show variation in their behaviour, both at the level of individual (Ropert-Coudert et al., 2003) and colony (Chiaradia et al., 2007), employing both benthic and pelagic diving strategies (Ropert-Coudert et al., 2006b, Hoskins et al., 2008, Ropert-Coudert et al., 2009).

1.4 Diet of little penguins

Gales and Green (1990) found that little penguins consumed between 74 and 664 g kg⁻¹ d⁻¹ of fish, squid and krill, with the greatest consumption rates occurring during chick-rearing. The composition of the diet of little penguins varies both spatially (Cullen et al., 1992) and temporally (Fraser and Lalas, 2004). Most colonies of little penguins have a varied diet and are opportunistic feeders (Cullen et al., 1992), but there are reported cases where colonies will feed primarily on a single prey species (Fraser and Lalas, 2004, Wiebkin, 2009). Studies have shown that the diet of little penguins is influenced by environmental conditions (Hoskins et al., 2008, Ropert-Coudert et al., 2009), and dietary changes may influence breeding success in this species (Dann et al., 2000, Lalas et al., 2004).

Until very recently the diet of little penguins has been studied through the use of the stomach flushing technique (Gales, 1987), but stable isotope and DNA sampling is now starting to emerge as a dietary sampling tool in this species (Chiaradia et al., 2010, Deagle et al., 2010).

1.5 Reproductive success of little penguins

The reproductive success of little penguins is highly variable between years and colonies (Reilly and Cullen, 1981). Little penguins may abandon breeding attempts at any stage (incubation, chick-guard or post-guard) and will often attempt to raise two clutches in a single season (Reilly and Cullen, 1981, Numata et al., 2000). Reproductive success has been classified in terms of the number of chicks fledged per female per season using the following scale; >1.2 high, ≤1.2 to >0.7 average, ≤0.7 low (Chiaradia et al., 2003).

Fortescue (1999) described a pattern of decreasing breeding success at little penguin colonies running from north to south along the east coast of Australia. He hypothesised that this pattern in reproductive success was due to the quality of breeding habitat and the influence of the East Australian Current. Sea temperature has been found to effect the

timing and overall success of breeding seasons in south-eastern Australia (Cullen et al., 2009), either through a longer breeding season or greater prey availability. Colony size may also have an influence on reproductive success, as Dann and Norman (2006) proposed with their theory that both available breeding area and intra-specific competition for prey determine population size.

1.6 Aims of the study

There has been little migration between the St Kilda penguin population and other colonies, based on the recovery of tagged individuals (Z. Hogg, *unpublished data*). Hence, the growth of the population over time has been attributed to high rates of reproductive success (Cullen et al., 1996, Fortescue, 1999). However, the factors attributable to this reproductive success have remained largely unknown, but high consumption of Australian anchovy (*Engraulis australis*) during the breeding season has been postulated as a contributing factor (Chiaradia et al., *In review*). Furthermore, the proximity of this colony to a large human settlement is unusual for this species, as it is threatened by a number of anthropogenic processes at other colonies (Stevenson and Woehler, 2007). What impacts the urban and highly modified environment has had on this colony have not been described. Therefore, the overall aim of this study is to investigate the relationships between the foraging behaviour, diet and reproductive success in this colony of little penguins in the context of the busy, artificially modified marine environment in which it occurs, and its previous population growth (Cullen et al., 1996).

Previous radio-tracking at this colony suggested that the penguins at St Kilda had a very small foraging range (Cullen et al., 1996). Due to technological limits of that study though, it was unknown how the penguins at this urban colony used the shallow water column and the anthropogenic shipping channels that occurred near their breeding colony. This study aims to expand upon this initial research and describe the foraging behaviour of the St

Kilda penguin colony in the context of the modified environment that they occur in, as well as confirm the extent of their foraging area and effort. To do this I deployed time-depth recorders and satellite transmitters to breeding birds (this foraging study was limited to the breeding penguins in order to retrieve the devices) during two seasons. The study was continued for a third breeding season when a mini-GPS device became available to me and was combined with a time-depth recorder, enabling the collection of horizontal and vertical movement data on the same individual.

Diet was thought to influence the success of breeding at the St Kilda colony as it has done at other little penguin colonies (Dann et al., 2000, Chiaradia et al., *In review*). However, nothing was known of this colony's diet during the pre-breeding season, which has been associated with seabird reproductive success (Becker et al., 2007a, Sorensen et al., 2009). Knowledge of prey stock movements in Port Phillip bay is limited, but inter-annual changes in the abundance of marine prey stocks have been associated with fishing, predators, salinity, productivity and sea temperature (Nakken, 1994, Rogers and Millner, 1996, Dimmlich et al., 2004, Montevecchi, 2007). I investigated whether the prey of penguins changed seasonally, and if there was any relationship between prey consumed, local environmental parameters, phenology and reproductive success. To measure this, I sampled the penguin's diet continuously for two years using stomach contents and stable isotope analysis to provide information on their dietary composition and trophic position. The reproductive success rate at St Kilda was known to be good, with a large rate of double broods and high peak chick weights (Cullen et al., 1996). To compare the foraging behaviour and diet with the resultant reproductive success at this colony, it was necessary to measure parameters of reproductive success in each year of the study. Here I measured phenology and reproductive success through mean egg laying date, number of broods per pair, chicks per pair and peak chick weight over three breeding seasons.

1.7 Thesis structure

This thesis is comprised of six chapters, which are organised into four papers, this general introduction and a general discussion to conclude. The second chapter is a published paper (Preston et al., 2008) on the foraging behaviour of penguins from St Kilda and the potential impacts of the dredging program (referred to in section 1.2) within their foraging range. Chapter three is a follow up publication (Preston et al., 2010) that describes the foraging behaviour of the penguins in more detail through the deployment of loggers measuring both horizontal and vertical movements on the same individual. It also compares the methods used in chapter two of separate location and diving data, to the new method for this species of combining global positioning system devices with diving loggers. Chapter four is written as a paper in preparation, examining conventional and contemporary seabird dietary sampling methods by comparing data collected from stomach flushing with the results of whole blood stable isotope analysis. The fifth chapter is also written as a paper in preparation and examines the influence of environmental parameters and diet on the phenology and success of breeding in this little penguin population. All references are presented at the end of the thesis.

Chapter 2: Foraging behaviour of little penguins *Eudyptula minor* in an artificially modified environment

Monash University

Declaration for Thesis Chapter 2

In the case of chapter 2, contributions to the work involved the following:

Name	% contribution	Nature of contribution
T. J. Preston	70%	Conception, execution and writing
Y. Ropert-Coudert	6%	Data analysis, interpretation and advice
A.Kato	6%	Data analysis, interpretation and advice
A.Chiaradia	6%	Interpretation and advice
R. Kirkwood	4%	Data analysis
P. Dann	3%	Interpretation, advice and provision of satellite trackers
R. Reina	5%	Advice and writing assistance

Declaration by co-authors

The undersigned hereby certify that:

- (1) they meet the criteria for authorship in that they have participated in the conception, execution, or interpretation, of at least that part of the publication in their field of expertise;
- (2) they take public responsibility for their part of the publication, except for the responsible author who accepts overall responsibility for the publication;
- (3) there are no other authors of the publication according to these criteria;
- (4) potential conflicts of interest have been disclosed to (a) granting bodies, (b) the editor or publisher of journals or other publications, and (c) the head of the responsible academic unit; and
- (5) the original data are stored at the following location(s) and will be held for at least five years from the date indicated below:

Location(s)

School of Biological Sciences, Clayton Campus, Monash University
Research Centre, Phillip Island Nature Parks, Phillip Island
Institut Pluridisciplinaire Hubert Curien, Strasbourg, France

Signature 1		13/7/10
Signature 2		20/7/10
Signature 3		20/7/10
Signature 4		17/8/10
Signature 5		16/8/10
Signature 6		4/8/10
Signature 7		15/7/10



CC

THEME SECTION

Foraging behaviour of little penguins *Eudyptula minor* in an artificially modified environment

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ABSTRACT: We investigated the 3-dimensional foraging behaviour of little penguins *Eudyptula minor* breeding on an artificially constructed breakwater near dredged shipping channels in Port Phillip Bay, southern Australia. Breeding penguins were fitted with either satellite trackers or time-depth recorders during the 2006-2007 breeding season to record foraging locations and diving behaviour, which were then compared with local bathymetry. Diving appeared to be both mid-water and demersal, and on 1 d trips penguins reached a mean maximum distance from the colony of 13.8 km. Penguins were recorded in locations containing artificially constructed shipping channels, and examination of their diving profiles suggests that they probably forage within these channels. Little penguins at this urban colony have benefited from anthropogenic alterations in the terrestrial environment, but their location exposes them to many potential anthropogenic threats in their marine environment, including a large-scale dredging operation to deepen the existing shipping channels.

KEY WORDS: Anthropogenic · Dredge · Satellite · Foraging · Dive · *Eudyptula minor*

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INTRODUCTION

Anthropogenic alteration of the natural environment is a widespread and obvious phenomenon. There are numerous examples of the deleterious effect of artificial habitat changes on wildlife, such as the reduction in species diversity caused by dam constructions (Pringle 2000, Gehrke et al. 2002) or the range of animals affected by land-clearing (see examples in Vos & Chardon 1998, Crooks 2002, Lehman et al. 2006). However, a few animal populations are capable of adapting to and benefiting from anthropogenic changes, such as peregrine falcons *Falco peregrinus* nesting in high rise buildings (Gilbert 1989, Cade & Bird 1990).

The effects of human activities in the marine environment are less conspicuous than on land, but they

are often extensive, particularly in coastal areas. While the local influence of anthropogenic habitat modification can be readily assessed for sessile organisms such as algae, seagrass and coral (e.g. Richmond 1993, Nyström et al. 2000, Duarte 2002), the effect on mobile marine animals is more difficult to determine. Ongoing miniaturisation of remote monitoring tools, such as satellite transmitters and diving loggers, is providing increased opportunities to identify how highly mobile animals use the marine environment (Ropert-Coudert & Wilson 2005) and to examine the influence of human alterations on them.

The little penguin is an ideal model for studying local oceanic alterations because it is part of a relatively short food chain (Cullen et al. 1992) and has a restricted foraging range during the chick-rearing phase

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of the breeding season (Collins et al. 1999). Little penguins are capable of acquiring only local resources at this time because they need to return regularly to their terrestrial nest site to feed their chicks (Chiaradia et al. 2007). This central place foraging behaviour facilitates the attachment and removal of data loggers, which allow their at-sea behaviour to be studied.

Although considered common, little penguins have been adversely affected by human settlement and activities in some places. Introduced mammalian predators and habitat loss have been the major causes of decline in this species on Phillip Island and south-eastern Tasmania in Australia, and the Otago region of New Zealand (Dann 1992a,b, Stevenson & Woehler in press). Other potential threats of anthropogenic origin also exist at sea, such as oil spills, over fishing, gill-netting, introduction of diseases to prey populations and dredging (Dann 1992b, Dann et al. 2000, Goldsworthy et al. 2001, Stevenson & Woehler in press).

A colony of little penguins resides on a breakwater wall constructed at St Kilda, 5 km from the centre of the city of Melbourne, Australia. The colony is close to both marine and terrestrial urban developments. This is the only established little penguin colony within Port Phillip Bay, which seems otherwise largely unsuitable for the establishment of penguin populations due to a lack of appropriate nesting sites, terrestrial threats from introduced predators and on-land habitat distur-

bance. Although extensive habitat alteration and other anthropogenic effects occur within this colony's foraging range, the population has grown to approximately 1000 individuals (Z. Hogg unpubl. data) since the first breeding pairs were discovered in 1974 (Eades 1975). Population growth is attributed to the proximity of food resources in northern Port Phillip Bay, within 20 km of the colony (Cullen et al. 1996), but is also likely to be due in part to the general absence of predators. A secure fence prevents access to the breakwater by roaming dogs and foxes, which may otherwise decimate the colony.

We investigated the 3-dimensional foraging behaviour of little penguins at the St Kilda colony during the 2006-2007 breeding season in order to examine how penguins use a highly modified marine habitat. Using satellite transmitters and time-depth recorders, we assessed whether the penguins have adapted their foraging strategy to use bathymetric variations of the sea floor (including dredged shipping channels) that are present within their foraging range.

MATERIALS AND METHODS

Study site. The diving behaviour and foraging zone occupancy of little penguins were examined at St Kilda, Melbourne, Australia (37° 51' S, 144° 57' E, Fig. 1)

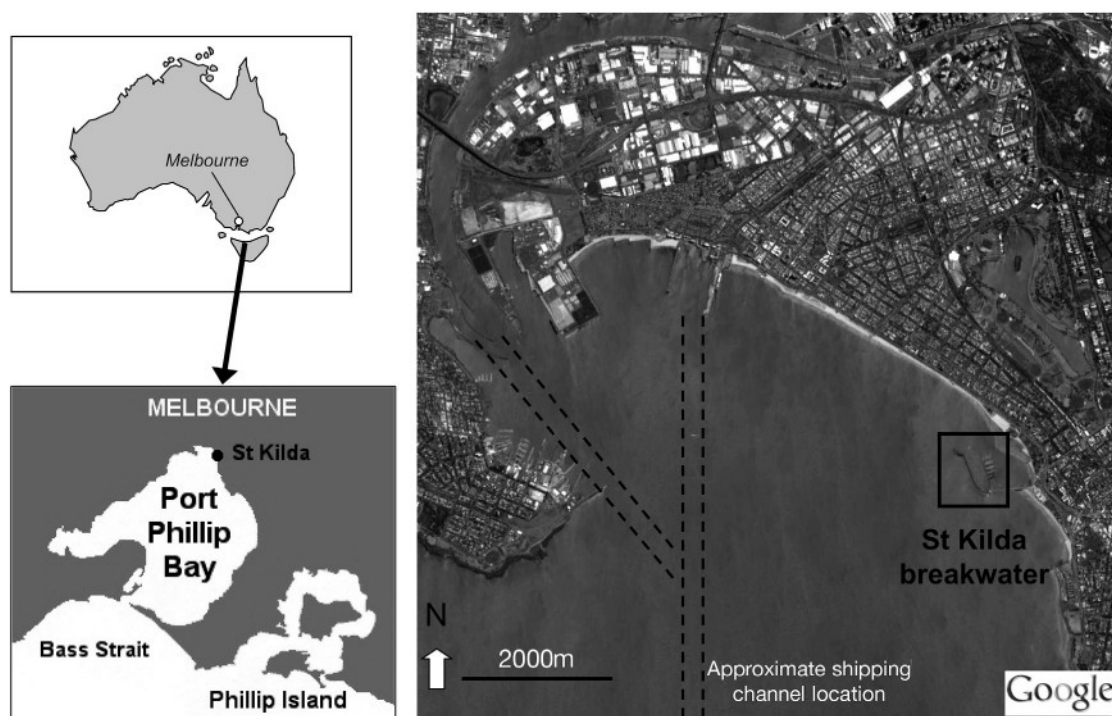


Fig. 1. Location of St Kilda penguin colony inside Port Phillip Bay, relative to Melbourne and Phillip Island. Satellite image taken from Google Earth™

during November and December of the 2006-2007 breeding season. Penguins were monitored in their nests 3 times wk^{-1} to determine their stage of breeding and were permanently identified by either a passive integrated transponder (Trovan®) or a flipper band.

At St Kilda, penguins forage inside Port Phillip Bay (Cullen et al. 1996), a bay of 1950 km^2 , with an average depth of 13 m and a maximum depth of 24 m (although some trenches at the entrance extend deeper). Several large shipping channels exist in the north and west of Port Phillip Bay, as well as the south where Port Phillip Bay joins Bass Strait (Fig. 1). The shipping channel ranges between 12-17 m depth and 180-240 m width.

Deployment of satellite trackers and time-depth recorders. Satellite tracking and time-depth recording devices were deployed separately on penguins. Although data from both devices on single birds could have proved useful, we considered the encumbrance resulting from their deployment together too great for a 1 kg bird. Only 1 penguin (O53F) was fitted with both devices, the time-depth recorder during incubation and satellite transmitter during chick-guard.

Satellite tracking was conducted on 13 birds from the chick-guard stage (chicks up to 2 wk old) using platform transmitter terminals (PTT, KiwiSat model 202 by Sirtrack, 60 · 31 · 20 mm, cross-sectional area 514 mm^2 , mass in air 43 g, antenna 18 cm spring mounted at 60°). In parallel, miniature time-depth recorders (TDR, M190-DT by Little Leonardo 49 · 15 mm, cross-sectional area 177 mm^2 , mass in air 14 g) were fitted to 14 penguins, 9 at the egg incubation stage and 5 at the chick-guard stage. Little penguins typically make trips of up to 3 consecutive days at sea during egg incubation and just 1 day at sea during the chick-guard stage, but the duration may increase during poor breeding seasons (Chiaradia & Nisbet 2006). TDRs collected data every 1 s in the 0-190 m depth range with a 12-bit resolution and 0.1 m accuracy.

All devices were attached to the penguins' feathers using waterproof tape (Tesa® 4651) (Wilson et al. 1997) along the mid-line of the lower back to minimise drag (Wilson & Culik 1994). We applied a thin strip of adhesive compound (Mastic, Denso) between the feathers and the device, to reduce friction and prevent loosening. All devices and adhesives were removed from the penguin upon its return to the colony after a foraging trip. Attachment and removal each took < 5 min. Penguins were weighed to the nearest 20 g using a spring balance (Pesola 42500) before and after instrumentation.

Data analysis. Penguin locations from the PTTs and the accuracy of these locations were provided by CLS Argos and plotted using Elsa Pro software (CLS Argos, 2005). Only locations where accuracy was 1 km or better (Classes 1, 2 and 3) were included in the analysis. We filtered the locations in the R statistical program

(R Development Core Team 2005) using TimeTrack, a custom designed software package (Sumner 2006).

TimeTrack uses the algorithms described by McConnell et al. (1999) to filter out locations that result from unreasonable speeds for a particular species. Using the maximum swimming speed of 3.3 ms^{-1} reported by Bethge et al. (1997), none of the Class 1, 2 or 3 locations were eliminated. Time-in-area analysis was calculated by interpolation of locations at 10 min intervals between the predicted locations, assuming straight-line travel at an even speed between the 2 locations (Austin et al. 2003), and assigning time spent to 1 km^2 grid-squares.

Bathymetry contours (at 5 m depth intervals) of Port Phillip Bay (provided by D. Ball, Primary Industries Research Victoria) were plotted using ArcView GIS version 3.0 (Environmental Systems Research Institute, 2004) and overlain with the time-in-area data.

G Power analysis (Faul et al. 2007) was used *a posteriori* to calculate the power of our sample size in describing the foraging area at 95% confidence interval. We used the number of grid-squares visited per penguin and conducted 50 permutations of adding the data from each penguin sequentially and in a random order. In this way, we derived a curve for the cumulative increase in grid-squares visited with each additional penguin. We then used the mean and standard deviations of the data to calculate the power of our sample size.

Diving data were downloaded from TDRs and analyzed (surface-align and dive detection) using IGOR Pro version 5.0 (Wavemetrics). Based on the relative accuracy of the logger, we adopted a dive threshold of 1 m. Diving activity was defined by the following parameters: maximum depth, dive duration, bottom phase (calculated as the period in the dive between when vertical speed first drops below and last rises above 0.25 m s^{-1} vertical speed), depth amplitude within bottom phase (the difference between the maximum and minimum depths reached during the bottom phase), descent and ascent rates, and number of undulations in the dive profile (Kato et al. 2006, Ropert-Coudert et al. 2006). For analysis of these diving parameters, we filtered data to exclude dives without a bottom phase (15.4%). Predominately, they were shallow (86.5% were ≤ 5 m deep) and were likely to be dives performed during travel. Dive shapes were analyzed using Multi-Trace Dive (Jensen Software Systems), excluding only dives < 1 m. Based on observation of the dive profiles, demersal dives generally had descent rates $\geq 0.8 \text{ ms}^{-1}$ and were performed at depths ≥ 6 m.

We conducted all other statistical analysis in SYSTAT Version 10 (SPSS). The statistical threshold was set at 0.05 and the values are presented as means with 1 SD.

RESULTS

Satellite tracking

The 13 penguins fitted with PTTs made either 1 or 2 d foraging trips and the total number of unfiltered locations of all classes was 279. After filtering, this was reduced to 11 penguins tracked from 98 Class 1, 2 or 3 locations, 10 of which performed single day trips and 1 (penguin O53F) performed a 2 d trip. By interpolating between satellite data, we calculated that the penguins spent time in 222 different 1 km² grid-squares within Port Phillip Bay. Time spent in each square ranged from 1 to 668 min.

Little penguins making 1 d trips from St Kilda remained in the north of the bay within 22 km of the colony (Fig. 2). They headed out in a south-westerly direction from St Kilda that included and crossed the shipping channels. Mean maximum distance from the colony on 1 d trips was 13.8 ± 4.1 km. Our sample size of 10 penguins had a power of 0.95 at 95% confidence interval to represent the foraging area within 1 d trip at the chick-guard stage.

On average, penguins on 1 d trips spent 10.8% of their time in the 1 km² grid-squares containing the shipping channels and 31.5% of their time < 2 km from the northern shipping channel (i.e. the 1 km² grid-squares containing, and on either side of, the shipping channel). These grid-squares accounted for 9.3 and

22.5%, respectively, of all grid-squares visited on 1 d trips. The penguin that performed a 2 d trip travelled in waters <15 m deep to the western channel achieving a maximum distance from the colony of 51 km.

Dive behaviour

We retrieved TDRs from all penguins after 1 or 2 trips, except for 1 penguin at the incubation stage and 3 at the guard stage; these penguins had abandoned their nests. We do not think that nest abandonment was related to device attachment, because 57% of the monitored nests in the colony were abandoned prior to chick fledging, whether the birds had been part of this study or not. Reproductive success of the colony as a whole was poor during the 2006-2007 breeding season (T. J. Preston unpubl. data). Trip durations for retrieved dive loggers ranged from 1 to 11 d, with a total of 48 foraging days and 32 690 dives from 10 birds (Table 1).

Diving was exclusively diurnal, with dive depths being greatest during the middle of the day. Excluding dives <1 m, the total number of dives for an individual ranged from 422 to 6321 (Table 1). The maximum depth recorded was 26.5 m and the maximum dive duration was 79 s. Penguins dived to a mean depth of 8.4 ± 1.8 m, with a mean diving duration of 28.5 ± 3.8 s. Most (82.7%) dives were to depths of between 2 and 13 m (Fig. 3). Just under half ($44.3 \pm 4.6\%$) of all dives were made to a depth ± 1 m of the previous dive.

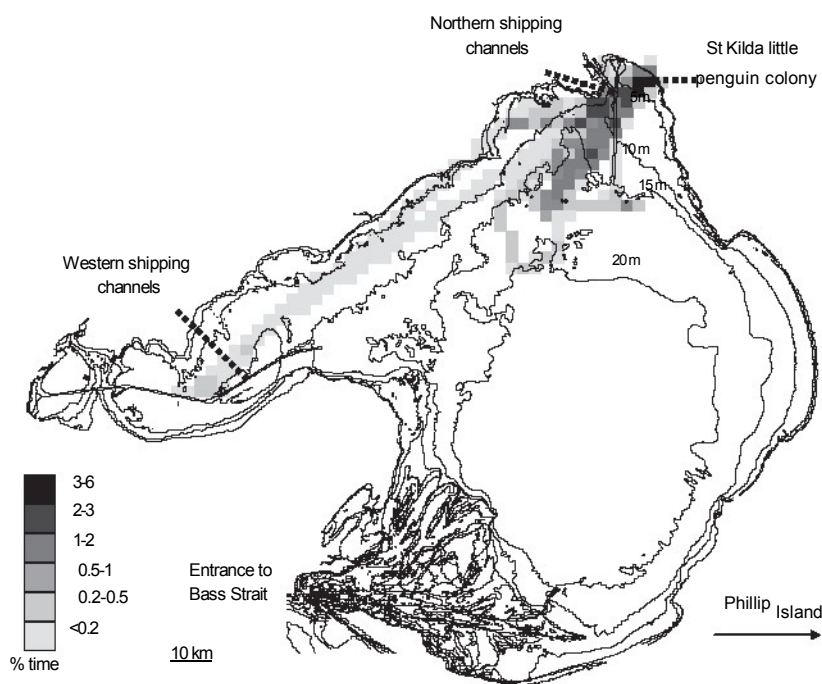


Fig. 2. Bathymetry contours and dredged shipping channels in Port Phillip Bay, and foraging areas of little penguins at the chick-guard stage from the St Kilda colony. Areas were determined from satellite tracking with shading indicating the relative amount of time penguins spent within 1 km² areas

Analysis of dives with a bottom phase (84.6 %) found that the bottom phase accounted for almost half ($49.7 \pm 7.3\%$) of each dive time (Table 1). In $60.7 \pm 7.0\%$ of dives, at least half of the bottom phase occurred in the lowest depth quartile and these dives had either flat bottoms, several small undulations (<1 m amplitude) or ragged shapes (Fig. 4).

As location and diving data was collected separately, it was not possible to identify definitively which dives were made inside the shipping channels. However, penguins in the present study did exhibit some unusual dive profiles that contained a flat bottom phase usu-

ally followed, but sometimes preceded, by a rapid change in depth (Fig. 5). Many of these dives appeared to be made mid-water, as indicated by the surrounding dives and low descent rates, but 248

were considered demersal. Of these, 180 correspond with the depth profile of the shipping channels (outside channel

Table 1. *Eudyptula minor*. Trip and diving information (mean $\pm$ SD) for penguins fitted with time-depth recorders. F: female; M: male

Penguin	Breeding stage	Trip duration (d) ^a	Total no. of dives	Diving depth (m)	Dive duration (s)	Bottom phase duration (s)
B14M	Incubation	1, 7	5533	8.1 $\pm$ 3.9	25.1 $\pm$ 11.7	46.7 $\pm$ 19.9
B33M	Incubation	1	561	7.9 $\pm$ 4.6	26.3 $\pm$ 14.5	47.0 $\pm$ 20.9
C93F	Incubation	7	5365	9.9 $\pm$ 4.6	34.0 $\pm$ 13.5	48.9 $\pm$ 17.4
I53F	Incubation	6	3532	9.7 $\pm$ 5.2	29.2 $\pm$ 13.8	43.8 $\pm$ 19.7
O53M	Incubation	6	4116	8.5 $\pm$ 4.6	27.8 $\pm$ 15.3	46.6 $\pm$ 21.6
O63M	Incubation	11	6321	11.0 $\pm$ 5.8	31.4 $\pm$ 16.0	39.3 $\pm$ 19.3
L24F	Incubation	1	422	8.0 $\pm$ 4.2	33.0 $\pm$ 15.1	53.3 $\pm$ 18.9
O53F	Incubation	4, 1	3800	5.4 $\pm$ 3.1	23.1 $\pm$ 12.5	56.2 $\pm$ 20.0
O03F	Chick-guard	1	922	5.6 $\pm$ 2.8	24.5 $\pm$ 9.8	65.7 $\pm$ 17.0
O74M	Chick-guard	2	2118	10.0 $\pm$ 4.4	31.1 $\pm$ 15.1	49.9 $\pm$ 19.1

^aTwo values denote 2 trips made by the same penguin

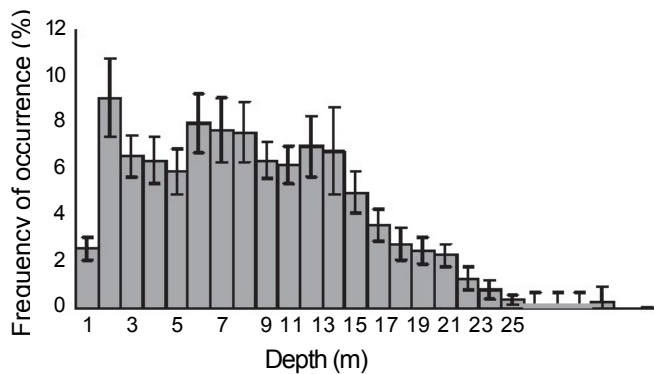


Fig. 3. *Eudyptula minor*. Frequency of occurrence and maximum depth of dives with bottom phase (n = 32 690, $\pm$ 1 SE)

6-10 m, inside 11-17 m, depth between outside and inside $\geq$ 3 m). These dives could have been made by the penguins entering or leaving the shipping channels. The remaining dives were deeper and all made by penguins on trips >1 d that may have travelled to deeper trenches at the mouth of the bay.

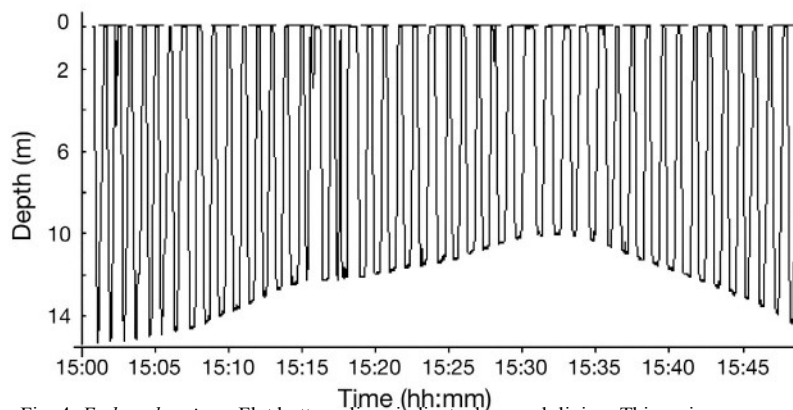


Fig. 4. *Eudyptula minor*. Flat bottom dives indicate demersal diving. This series of dives suggests that penguins follow the topography of the sea floor

DISCUSSION

Many studies of penguin behaviour at sea now combine both location and diving information for the same bird (e.g. Pütz et al. 1998, Charrassin et al. 2004, Ryan et al. 2004, Sokolov et al. 2006, Mattern et al. 2007); this allows direct correlation between behaviour of the animal and bathymetry of the area. Unfortunately, the instruments required to combine this information are

still too large to be deployed on little penguins. Accordingly, our data on location and diving behaviour were collected separately. We have no reason to believe, however, that over a comparable time-frame the penguins fitted with TDRs foraged in different areas to those fitted with PTTs. The foraging area of all PTT carrying birds on 1 d trips were similar and the diving depths recorded by TDRs on single day trips were within the ranges of depths over which PTT-bearing birds foraged. Time spent at sea is a determining factor in how far penguins can travel from the colony, and those penguins at sea for >1 d may have travelled further than the 1 d foraging area described.

Attachment of external devices to penguins is known to affect their foraging performance (Wilson et al. 1986). Decreasing the device size and judicious placement on the lower back minimises the effects (Ropert-Coudert et al. 2007). In the present study, we used the smallest devices available to us. The difference in cross-sectional area between the TDRs and PTTs, as well as the presence of an aerial (cf. Wilson et al. 2004), may have resulted in differences in diving capabilities, but it is unlikely that this will lead to a difference in foraging area used by penguins fitted with PTTs compared with those fitted with TDRs. Aban-

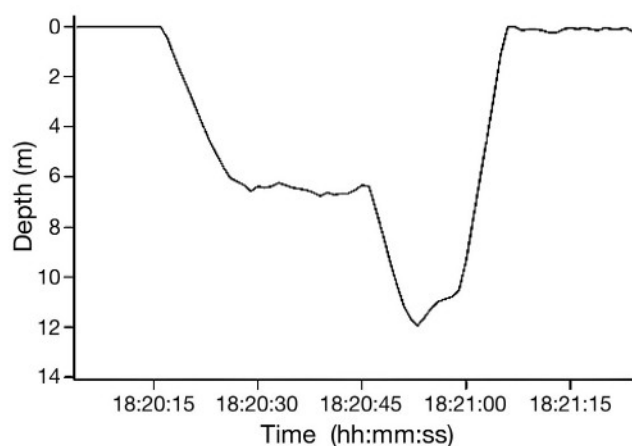


Fig. 5. *Eudyptula minor*. Example of a dive thought to be made into the shipping channel. Flat bottom phase is equivalent to the depth of the sea floor outside the shipping channel, while sharp increase in depth corresponds with the shipping channel wall

donment of nests during the 2006-2007 breeding season was high (57%) for all breeding pairs in the colony. Interestingly, though, the breeding success of birds that carried devices was actually higher than the colony average (colony 29.5%, TDR or PTT carried by at least 1 parent on 1 trip: 38.0 and 44.5%, respectively).

The distribution of tracked penguins at the chick-guard stage from St Kilda was concentrated in the north of Port Phillip Bay, similar to the non-breeding distribution recorded by radio tracking (Cullen et al. 1996). This foraging area is inclusive of the northern shipping channels that lie to the west of the colony. The limited foraging range of little penguins caring for young chicks was reflected in the low maximum distance travelled from the colony, which was slightly lower than the value reported for little penguins on 1 d trips from Phillip Island (Collins et al. 1999).

The west of Port Phillip Bay was used by 1 penguin in our study that spent 2 d at sea and travelled between shipping channels in the north and west. Little penguins from Phillip Island (Fig. 1) are known to occur in both the north and west of Port Phillip Bay (Collins et al. 1999), which suggests high prey availability and highlights the importance of these areas to both populations. Penguins have also been observed in the central part of Port Phillip Bay, but it was not identified whether they came from St Kilda, Phillip Island or elsewhere (Port of Melbourne Corporation 2007). We can expect that little penguins from St Kilda, if not restricted in their foraging trip duration, might also sometimes forage in the west of the bay.

Little penguins commonly dive to mid-levels of the water column (Bethge et al. 1997, Chiaradia et al.

2007), but demersal diving has also been reported in this species (Ropert-Coudert et al. 2006). Penguins in the present study appeared to use both mid-water and demersal diving strategies, as suggested by the length and shape of dive profiles (Fig. 4, Table 1). Penguins dived to ± 1 m of the previous dive depth on a mean of 44.3% of occasions, comparable with rockhopper penguins *Eudyptes chrysocome* employing a mixture of benthic and pelagic dives, to within $\pm 10\%$ of the previous dive depth around 53% of the time (Tremblay & Cherel 2000). Given the shallow nature of Port Phillip Bay and reasonable natural variations in the sea floor topography, we considered that a threshold of ± 1 m was more appropriate than $\pm 10\%$ for this study.

The mean bottom phase duration of penguins from St Kilda was similar to that reported for demersal diving little penguins from Penguin Island, Western Australia (Ropert-Coudert et al. 2006). In contrast, little penguins from other colonies that engage primarily in mid-water or shallow-water diving spend less time in the bottom phase of the dive (Chiaradia et al. 2007). Penguins in present study could move from the shallow area around their colony (< 5 m) to the deepest part of the bay (> 20 m), a distance of approximately 20 km, in around 3 h (based on average swimming speed, Bethge et al. 1997). Subsequently we saw frequent changes in the depth profile throughout the day, which makes differentiation between demersal and mid-water dives difficult.

Little penguins from St Kilda have an unusual monospecific diet of anchovy (*Engraulis australis*; A. Chiaradia unpubl. data), with apparently few supplementary or alternative prey species in the diet (T. J. Preston unpubl. data). Anchovy is generally regarded as a shallow water pelagic species, occurring in the top 20 m of the water column (Kailola et al. 1993). Penguin species including the Humboldt *Spheniscus humboldti* and African *Spheniscus demersus* that feed on pelagic schooling fish, including anchovy, have been found to seize prey from below, as the fish are easier to locate as a silhouette rather than from the side or above (Wilson & Duffy 1986, Wilson et al. 1989), and this is likely to be the case for penguins at St Kilda that feed almost exclusively on anchovy.

Little penguins from St Kilda had some unusual dive profiles that displayed a sharp increase in depth during the bottom phase (Fig. 5). Unpublished accounts of these types of dives in Snares *Eudyptes robustus* (T. Mattern pers. comm.) and Magellanic penguins *Spheniscus magellanicus* (R. Wilson pers. comm.) suggest that these dives are made mid-water, as do the characteristics of many of the dives made in this study. However, benthic diving yellow-eyed penguins *Megadyptes antipodes* are also known to make dives of similar shape (T. Mattern pers. comm.). The surrounding dives to consistent depth and the high

descent rates of a number of the unusual dives made by the little penguins in the present study indicated that they were demersal, and probably reflect penguins following changes in the sea floor topography. To precisely determine the location of these dives requires simultaneous collection of these data from an individual bird, but this currently presents significant technical challenges for animals of small size. However, from our knowledge of bathymetry in the area, the shipping channels are the most likely place for these dives to occur and some of the recorded dive profiles probably represent penguins diving into or out of the channels. It is possible that the penguins use both the sea floor and the 3-dimensional structure of the shipping channels to trap their prey, a foraging strategy similar to that suggested for the little penguins at Penguin Island (Ropert-Coudert et al. 2006). Although numerous studies exist on the benthic and demersal diving patterns of various marine birds and mammals (see Tremblay & Cherel 2000 for review), this is the first reported instance where anthropogenic features in the sea floor are probably being used by a species for foraging, and may benefit them by reducing the prey escape field.

Physical modifications to both the marine and terrestrial environments seem to have benefited this population of little penguins, but their exploitation of these modifications has consequently placed them in close proximity to a large human settlement and associated potential threats. One such potential threat is the current proposal to deepen the shipping channels in the north and south of Port Phillip Bay by dredging.

The proposed dredging to increase the depth of shipping channels by approximately 3 m is much larger in scale than the routine dredging that has taken place since the channels were first constructed in the 1860s. The main immediate potential effect of the dredging on little penguins in the vicinity will be the increased water turbidity, the extent and concentration of which are likely to vary at any one time and place. In all, the dredging will produce suspended sediment above 5 mg l⁻¹ that is predicted to spread over an area approximately 4 km wide and 18 km long before it settles, immediately surrounding and east of the shipping channels in the north of Port Phillip Bay (Port of Melbourne Corporation 2007). This area overlaps approximately 30% of the penguin foraging range described in this study and is situated between the penguin colony and their main foraging area to the west of the shipping channels. The reactions of little penguins to turbidity are unknown, but they are considered visual predators (Cannell & Cullen 1998, Ropert-Coudert et al. 2006) and as such it is unlikely that they will be able to forage within highly turbid areas of the suspended sediment plume,

particularly in the area of the channels where the suspended sediments originate from the sea floor. Whether the penguins will travel across the densest areas of the plume or swim around them in order to reach clear foraging areas is not known.

Much of the recruitment biology and spawning dynamics of the anchovy inside Port Phillip Bay is uncertain, but the north of the bay, including areas to be affected by the dredging plume, has been identified as a spawning ground for this species in several studies (Blackburn 1950, Jenkins 1986, Neira & Tate 1996). Spawning takes place from September to March, peaking in January (Jenkins 1986), which coincides with the scheduled dredging in the north of the bay (Port of Melbourne Corporation 2007). The foraging behaviour of anchovy may be affected by the turbidity plume, as they are generally regarded as visual predators (Chiappa-Carrara & Gallardo-Cabello 1993). Physiological effects of the suspended sediment on anchovy, particularly eggs and larvae, may result in high levels of mortality (Wilber & Clarke 2001), decreasing recruitment and ultimately leading to a decline in the population size. Reduction of available cape anchovy *Engraulis capensis* has been implicated in the breeding failure of African penguins *Spheniscus demersus* (Crawford & Dyer 1995, Crawford 1998), and a widespread decline of pilchards *Sardinops sagax* was associated with high levels of adult mortality and very low breeding success in little penguins from Phillip Island (Dann et al. 2000). Similar levels of breeding failure and adult mortality may be expected for the St Kilda little penguin colony if there was a significant reduction or an absence of anchovies and alternative food sources as a result of the dredging. The population of > 52 000 little penguins at Phillip Island may also be affected by the channel dredging, as radio-tracking has determined that they use Port Phillip Bay extensively in winter and spring (Collins et al. 1999) and anchovy is a major prey component of their diet (Cullen et al. 1992).

The St Kilda colony of little penguins appears to have adapted to and benefited from some artificial environmental modifications in the past; construction of a breakwater wall provided a suitable nesting habitat and shipping channels reduced the prey escape field. However, this adaptation to artificial environmental modifications now puts little penguins in a precarious position where significant changes in their spatially limited marine habitat, such as the proposed dredging, have the potential to severely affect this population.

Acknowledgements. We thank E. Buik, T. Shaw, Z. Hogg and volunteers of Earthcare St Kilda for field assistance. We also thank M. Sumner for kindly providing advice and assistance with analysing satellite data. D. Ball from Primary

Industries Research Victoria, Queenscliff, provided the bathymetry data for Port Phillip Bay. Funding for satellite tracking was provided by Toyota Australia, The Penguin Foundation and Dan Costa. Diving study was supported by a grant from BHP-Billiton. The study site was accessed with permission from Parks Victoria and the St Kilda Breakwater Wildlife Management Co-operative Area committee. Research was conducted under animal ethics permit BSCI/2006/12 from the Monash University AEC and wildlife permits 10003374 and 10003848 from the Department of Sustainability and Environment, Victoria. Picture in Fig. 1 accessed from Google EarthTM.

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- Editorial responsibility: Rory Wilson, Swansea, UK*
- Submitted: September 13, 2007; Accepted: November 6, 2007*
- Proofs received from author(s): November 20, 2007*

Chapter 3: Fine scale tracking and biologging for conservation of an inshore marine animal

Monash University

Declaration for Thesis Chapter 3

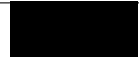
In the case of chapter 3, contributions to the work involved the following:

Name	% contribution	Nature of contribution
T.J. Preston	85%	Conception, execution and writing
A. Chiaradia	5%	Advice, interpretation and writing assistance
S.A. Caarels	5%	Statistical analysis, interpretation and advice
R.D. Reina	5%	Advice, interpretation and writing assistance

Declaration by co-authors

The undersigned hereby certify that:

- (1) they meet the criteria for authorship in that they have participated in the conception, execution, or interpretation, of at least that part of the publication in their field of expertise;
- (2) they take public responsibility for their part of the publication, except for the responsible author who accepts overall responsibility for the publication;
- (3) there are no other authors of the publication according to these criteria;
- (4) potential conflicts of interest have been disclosed to (a) granting bodies, (b) the editor or publisher of journals or other publications, and (c) the head of the responsible academic unit; and
- (5) the original data are stored at the following location(s) and will be held for at least five years from the date indicated below:

Location(s)	School of Biological Sciences, Clayton Campus, Monash University	
Signature 1		13/07/10
Signature 2		27/07/10
Signature 3		27/07/10
Signature 4		17/7/10



Fine scale biologging of an inshore marine animal

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ARTICLE INFO

Article history:

Received 11 January 2010

Received in revised form 22 April 2010

Accepted 22 April 2010

Keywords:

Biologging

Marine conservation

Small scale

Tracking

ABSTRACT

We compared the results of two biologging techniques used to study the foraging behaviour of a colony of small inshore predators, little penguins (*Eudyptula minor*). The first technique involved the use of satellite transmitters and diving loggers deployed on separate individuals, which has been the conventional method of tracking the movements and behaviour of this species for >10 years. The second technique combined a diving logger and a global positioning system (GPS) logger deployed on the same individual, which is similar to the biologging methods presently being developed and used for many other species. We then considered the value of each technique as a conservation tool operating at the small scale (foraging area <5000 ha and duration <1 day).

We found that the separately deployed satellite transmitters significantly underestimated the penguins' foraging area size. However, the size of the foraging area and other foraging parameters, such as total distance travelled, were influenced by the degree of GPS location sub-sampling. Furthermore, only the combined diving and GPS loggers could confidently describe the diving behaviour of the penguins in relation to the sea floor and identify that they were using small areas of conservation interest (shipping channel) inside their foraging area. Hence, the method employed to assess habitat use at fine scales can influence conservation measures that rely upon the data collected. We suggest that researchers fast-track their adoption of high resolution multi-loggers for increased data confidence when tracking animals at a fine scale, but also consider the potential effect of sampling rate on the calculation of parameters of interest.

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1. Introduction

Biologging science (use of animal-attached devices, Rutz and Hays, 2009) is commonly employed to identify animal foraging behaviour and areas of conservation significance in a wide range of species (Cooke, 2008). In the marine environment, biologging is often conducted on vertebrates that travel over extensive spatial and temporal scales such as turtles, seals, whales and seabirds (e.g. Guinet et al., 1997; Hays et al., 2006; Kirkwood et al., 2006; Robinson et al., 2007; Lagerquist et al., 2008). However, many breeding colonies and populations of marine vertebrates that are restricted to shallow environments are necessarily coastal, and often coincide with anthropogenic pressures such as run-off pollution, development, fishing, boating and dredging (for example Borboroglu and Yorio, 2007; Hines et al., 2008; Skov and Thomsen, 2008). Conservation of animals that live within such inshore areas requires accurate information about their movements and home range in order to designate appropriate protective measures, such as marine protected areas. Studies of animal movements within coastal areas

have been conducted using both Argos (Boersma et al., 2002; Thompson et al., 2003; Zbinden et al., 2007; Seney and Landry, 2008) and global positioning system (GPS) technologies (Heithaus et al., 2002; Schofield et al., 2007; Nanami and Yamada, 2008), yet few studies have compared the efficacy of these techniques to calculate animal movements at small spatial and temporal scales in the marine environment (Yasuda and Arai, 2005; Hazel, 2009).

The Argos satellite network is used to remotely identify the location of many marine vertebrates, but the raw data from this system often gives inaccurate positions (Vincent et al., 2002; Costa et al., 2010). Over large spatial and temporal scales these locations may still prove useful in identifying general movement patterns (Tougaard et al., 2008), but at the small scale position accuracy is very important (Hays et al., 2001) and a high degree of data filtering is required, removing a large number of the locations. To better understand the behaviour of a diving animal it is important to identify its vertical distribution, commonly determined through the use of diving recorders. However, diving data alone do not provide direct information on location at sea. Use of a combination of location and depth to determine the movement of diving animals is becoming more common, particularly with the recent advancements in GPS technology (e.g. Gremillet et al., 2004; Mattern et al., 2007; Schofield et al., 2007), which is able to provide a greater number of locations and accuracy than the Argos network. In some systems the Argos

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network is now being used as a means to remotely transmit data that has been collected by GPS and/or depth loggers back to the user (e.g. Fossette et al., 2008; Sims et al., 2009; Schofield et al., 2010), removing the necessity to retrieve the logging devices.

A good example of a spatially restricted forager is the little penguin (*Eudyptula minor*), distributed through southern Australia and New Zealand. Little penguins are a colonial species that have one of the smallest foraging ranges among seabirds during breeding (Dann and Norman, 2006). The movement of little penguins at sea has been examined through the use of radio-transmitters, satellite transmitters (also known as platform terminal transmitters, PTT) and diving loggers (time-depth recorders, TDR) in a number of studies (e.g. Collins et al., 1999; Ropert-Coudert et al., 2003; Chiaradia et al., 2007; Hoskins et al., 2008; Fallow et al., 2009) that have examined vertical and horizontal activity ranges and diurnal patterns. However, none of these studies have combined location with diving behaviour in the same individual at the same time, due to size limitations of devices that can be used on this small species (approx. 1 kg adult body mass). This means that interpretation of penguin behaviour at sea has been limited to assumptions made from location and dive data collected separately, which has caveats as a management tool. For instance, in our initial study using satellite transmitter and diving logger data collected separately in 2006, we considered it highly likely that the penguin foraging area overlapped with a shipping channel subject to a major dredging project, but we were unable to confirm this with a high level of certainty (Preston et al., 2008).

In this study, we used a miniaturized GPS device that was small enough to be deployed together with a diving logger on little penguins. By combining the GPS with a diving logger on the same individual, we eliminated the problems of interpretation associated from separately collected location and diving data. We analysed how this high resolution multi-logger approach compared with separately deployed satellite transmitters and dive loggers. Our aim was to determine if data on animal distribution and behaviour differed significantly between the two biologging techniques when collected over small spatial (<5000 ha) and temporal (<1 day) scales. In doing so, we also sub-sampled the GPS data at a number of time intervals to examine whether different data collection rates effected calculation of foraging parameters. This study is particularly relevant as the current trend in biologging research continues toward developing higher resolution multi-logging devices. The results of this study could be particularly useful to researchers and managers working with inshore species that require biologging information on which to base conservation decisions.

2. Methods

2.1. Study site and field procedures

The St Kilda colony of little penguins numbers approximately 800 individuals and is located on the St Kilda breakwater, Melbourne, Australia, within close proximity to commercial shipping channels (37° 51' S, 144° 57' E, Fig. 1). The study site and field work is described in detail in Preston et al. (2008). Externally attached diving and location recording devices were deployed on breeding penguins during the 2007 and 2008 breeding seasons (approximately October–December). Deepening of the shipping channels occurred in the non-breeding season between the two sampling periods. Thus, there was no turbidity as a result of dredging activity during the time of our sampling, which may affect penguin foraging because they are visual predators (Cannell and Cullen, 1998).

To permit comparison between the two methods, this study considered only single foraging trips made by penguins at the chick-guard stage (first 2-weeks after hatching) when the trip duration is one day (considered typical at this stage of breeding, Chiaradia and Nisbet, 2006). We used data from 13 penguins fitted with a PTT and

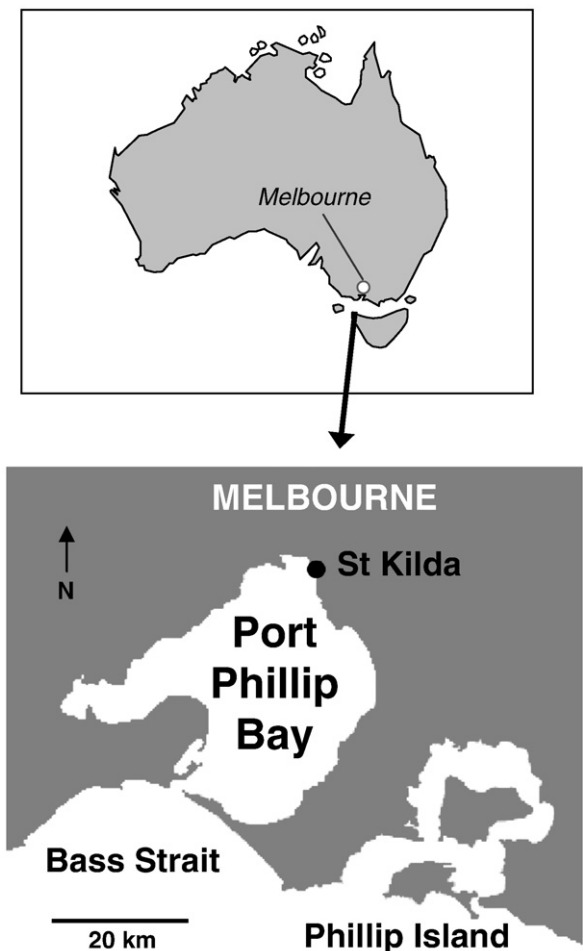


Fig. 1. Location of St Kilda penguin colony in Port Phillip bay where penguins forage.

five penguins fitted with a TDR in 2007, and 17 penguins fitted with both a GPS and TDR in 2008.

The PTTs used were Sirtrack KiwiSat 202 (New Zealand, 60 × 31 × 20 mm, cross-sectional area 514 mm², mass in air 43 g, 18 cm antenna spring mounted at 60°) operating on the Argos satellite network and the time-depth recorders were Cefas G5 (United Kingdom, 36 × 11 mm, cross-sectional area 95 mm², mass in air 5.8 g, set to record pressure and temperature at 1 s intervals).

The same TDR units were used in 2008, together with the mini-GPSlog by Earth & Ocean Technologies (Germany, 46.5 × 31 × 16 mm, cross-sectional area 496 mm², mass in air 29 g, acquisition time 1 to 3 s). The TDR was attached horizontally to the lower end of the GPS with waterproof tape (Tesa® 4651) to improve streamlining (GPS plus TDR mass in air, including tape, 37.7 g). Both GPS and TDR clocks were synchronised on the same computer to local time (eastern Australian daylight-savings) and were set to start approximately 1–2 h before sunrise when penguins left the colony. The GPS only recorded locations when the penguin was at the surface, but it was in continuous search mode (recording interval of 1 s) as the battery was able to last the length of the full deployment (1 day) and trials with longer search intervals were unsuccessful (A. Chiaradia and T. Preston, unpublished data).

All devices were attached using waterproof tape (Wilson et al., 1997) and a strip of adhesive compound (Mastic, Denso) to feathers along the mid-line of the lower back. Attachment and removal of all devices took <5 min and penguins were weighed to the nearest 10 g before and after deployments. Devices were retrieved for data

download when the penguins returned to the colony in the evening of the day of deployment.

2.2. Data analyses

Dive profiles were analysed using Multi-Trace Dive (Jensen Software Systems, Germany) with 1 m as the dive threshold. The following parameters were compared over the 2 years using Welch's (for unequal sample size) or randomization (for non-normality) *t*-tests: total number of dives, dive depth, dives with a bottom phase (period of dive when vertical speed first drops below and last rises above 0.25 m s^{-1}), bottom phase proportion of dive and number of dives to the intra-depth zone (based on dives within 1 m of previous dive, which is more appropriate to our data logger accuracy at these shallow depths than the 10% threshold of Tremblay and Cherel, 2000). The experimental design was randomised, with TDRs deployed on 5 individuals (2 males and 3 females) in 2007 and 17 individuals (10 males and 7 females) in 2008.

PTT data were filtered to exclude all Argos location class (LC) 0, A, B and Z positions (for which no estimate of error is provided, CLS, 2008), leaving only positions with an accuracy of between 250 and 1500 m or better (this has recently been revised up from 150 to 1000 m or better, CLS, 2008). Positions from GPS with horizontal dilution of precision >9 were filtered out of the dataset and accuracy of at least 90% of positions was within 6 m. Swimming speeds greater than the maximum of 3.3 ms^{-1} for little penguins were also filtered out of both types of data (Bethge et al., 1997). GPS data was further sub-sampled at 10 s, 1 min, 10 min, 30 min and 1 h time scales to represent various data collection regimes (Wilson et al., 1995). Each time interval was taken as a minimum period between locations, to simulate biologging interval mode where the GPS is switched off for certain periods of time to conserve battery power.

Satellite data were plotted using ArcGIS 9.1 (ESRI, Redlands, CA, U.S.A.). PTTs were deployed on 13 individuals in 2007 (5 males and 8 females) and 17 in 2008 (10 males and 7 females). Location parameters were analysed using randomised, type III, two-factor ANOVA models since the design was unbalanced and several penguins were re-sampled in consecutive years. Specifically, models were used to investigate differences in: maximum straight-line distance from the colony, total distance travelled (assuming straight line travel between successive locations), total foraging area (90% kernel density estimators, Borger et al., 2006) and amount of shipping channel occupied (expressed as a percentage of the total length of the shipping channel) between sexes and years. These variables were calculated using Hawth's Analysis Tools extension (downloaded from <http://www.spatial ecology.com/index.php/3/3/09>).

Combined GPS and TDR data were used to compare the diving depth with water depth and the amount of time spent at each water depth (where GPS data were available). Water depth was determined every 5 min (or as close as possible thereto) along the GPS path using bathymetry data of the foraging area plotted in 5 m contours (provided by D. Ball, Department of Primary Industries, Victoria, Australia). Intervals of 5 min were appropriate to the accuracy of our bathymetry data and the maximum speed at which little penguins can travel (Bethge et al., 1997). Calculating the proximity of dives to

the sea floor was limited by the accuracy of the bathymetry data (plotted in 5 m bins) and the shipping channel was assigned to a depth of 15.5 m (the depth it is maintained to, although it may be deeper in parts).

We examined the proportion of dives repeatedly made to the same depth (intra-depth zone dives, IDZ) at each known depth and whether those IDZ dives were benthic, as this pattern of diving often indicates (Tremblay and Cherel, 2000). Further, we determined the proportion of time spent and dives made by penguins in the shipping channel, the area of main conservation interest.

Statistical analysis was conducted using R (R Development Core Team, 2009). The statistical threshold was set at $P < 0.05$ and results are presented as mean $\pm$ s.e.

3. Results

3.1. Comparing methods

Body mass did not differ significantly between sexes and consecutive years after deployment for both PTT or combined GPS/TDR devices ($P > 0.05$, mean weight change PTT: $20 \pm 9 \text{ g}$, GPS/TDR: $12 \pm 13 \text{ g}$).

3.2. Diving behaviour

The number of intra-depth zone dives made by individuals was significantly higher (approximately 24% on average) in 2008 than in 2007 ($t = 3.13$, randomisations = 5000, $P = 0.009$). There were no significant differences in other diving parameters measured between years (Table 1).

3.3. Penguin location

Initial filtering resulted in a mean of 11766 ± 1103 GPS locations per day compared with 8 ± 1 for the PTT. After we sub-sampled the GPS data at several time intervals and compared the results to the satellite tracking data, we found in all cases that both the number of locations and size of the foraging area significantly greater (Table 2). Maximum distance travelled from the colony did not differ between the two methods at any of the GPS sub-sampling levels and the total distance travelled was only significantly different from that calculated from the PTT data when GPS data were sub-sampled at 10 s. The amount of the shipping channel covered by the foraging area was significantly greater when calculated from the GPS compared to the PTT data, at 1, 10 and 30 min intervals (Fig. 2).

The mean size of the foraging area was greatest when calculated at the 10 min interval for GPS data, followed by the shorter time intervals of 1 min and 10 s (Fig. 3). For GPS data, estimates of the total distance travelled were quite low at the larger time intervals, increasing to distances slightly greater than that calculated by the PTT when sub-sampled at 10 min intervals (Fig. 4). The shortest sub-sampling time intervals of 1 min and 10 s gave the greatest estimate of the mean total distance travelled.

It is noted that there were no significant effects of sex, nor sex by year interactions for all location parameters (not presented).

Table 1
Mean values of diving parameters measured in 2007 and 2008 are presented in left hand columns. Results of statistical tests performed on data collected using the two methods are presented in the right hand columns (significant *P*-values in bold).

Diving parameters	2007 Mean $\pm$ se	2008 Mean $\pm$ se	df	<i>t</i> (<i>t</i> -test)	<i>P</i> -value
Number of dives	776.4 $\pm$ 58.4	825.4 $\pm$ 28.4	6.0	0.75 (Welch's)	0.479
Dive depth (m)	8.6 $\pm$ 0.8	7.7 $\pm$ 0.4	6.0	0.96 (Welch's)	0.375
Dives with bottom phase (%)	74.0 $\pm$ 1.7	78.2 $\pm$ 1.6	<i>R</i> = 5000	1.79 (Randomization)	0.051
Bottom phase as % total dive	44.6 $\pm$ 1.8	46.1 $\pm$ 0.9	5.9	−0.77 (Welch's)	0.475
Dives to intra-depth zone (%)	43.8 $\pm$ 1.8	55.3 $\pm$ 3.2	<i>R</i> = 5000	−3.13 (Randomization)	0.009

Table 2
Location parameters measured using the PTT and GPS sub-sampled at different time intervals. The difference between the PTT and GPS values are presented, significant P-values in bold.

Parameters	PTT		GPS 1 h		GPS 30 min		GPS 10 min		GPS 1 min		GPS 10 s	
	Mean ± se	F, P	Mean ± se	F, P	Mean ± se	F, P	Mean ± se	F, P	Mean ± se	F, P	Mean ± se	F, P
# Locations	8.1 ± 1.2	5.042(1,26), 0.034	10.8 ± 0.5	5.042(1,26), 0.034	19.6 ± 1.1	47.275(1,26), <0.001	49.8 ± 3.9	76.937(1,26), <0.001	377.1 ± 36.3	4.268(1,26), 0.049	1353.6 ± 132.2	70.742(1,26), <0.001
Area (ha)	727.8 ± 84.5	6.531(1,26), 0.017	993.8 ± 67.3	6.531(1,26), 0.017	1382.4 ± 127.7	15.295(1,26), <0.001	1557.5 ± 162.5	16.194(1,26), <0.001	1487.7 ± 157.5	14.360(1,26), <0.001	1402.0 ± 152.9	11.949(1,26), 0.002
Max distance (km)	11.1 ± 1.8	0.001(1,26), 0.981	11.2 ± 1.1	0.212(1,26), 0.649	10.2 ± 1.1	0.212(1,26), 0.649	10.4 ± 1.1	0.138(1,26), 0.713	10.5 ± 1.0	0.100(1,26), 0.754	10.5 ± 1.0	0.100(1,26), 0.754
Total distance (km)	26.0 ± 3.0	0.218(1,26), 0.645	24.3 ± 2.3	0.218(1,26), 0.645	23.2 ± 1.9	0.627(1,26), 0.436	28.5 ± 1.9	0.522(1,26), 0.476	32.91 ± 1.8	4.107(1,26), 0.053	34.6 ± 1.8	6.319(1,26), 0.018
Shipping channel (%)	7.8 ± 2.3	1.104(1,26), 0.303	11.0 ± 2.9	1.104(1,26), 0.303	15.6 ± 3.1	4.571(1,26), 0.043	16.8 ± 3.3	5.281(1,26), 0.029	15.3 ± 3.2	70.834(1,26), <0.001	15.3 ± 3.6	3.577(1,26), 0.069

3.4. Combined GPS and TDR: where both position and diving information are known

During periods of extensive diving, little penguins did not stay at the surface long enough for the GPS to record their location. Hence, all results presented here are from when both location and diving information are known, which accounts for 50.3% of the dives recorded during 2008.

Penguins spent an equal amount of time in areas that were 15 and 20 m deep, which constituted the major portion of the foraging area (Table 3). The amount of diving was roughly proportional to the time spent in an area. The least and greatest amount of dives were performed in regions that were 5 and 15 m deep, respectively.

Penguins showed a preference for performing dives to ≤ 10 m regardless of the water depth. Over 80% of time at sea was spent in areas ≥ 15 m, but only 35% of all dives were made to ≥ 11 m.

Intra-depth zone dives made to within ± 1 m of the previous dive were common at the shallow depths and within the shipping channel, but less so at depths ≥ 20 m (Table 3). Approximately one-quarter (28%) of these IDZ dives appear to be benthic (within 5 m of the sea floor, excluding data from the 5 m and 10 m areas), with most (39%) occurring within the shipping channels.

4. Discussion

Global positioning systems are being increasingly used by biologists due to the greater number and accuracy of locations obtained compared to the commonly used Argos satellite tracking system. A lot of studies have focused on the usefulness of Argos and GPS to describe animal behaviour patterns at sea (Bradshaw et al., 2007; Jonsen et al., 2007; Tremblay et al., 2007; Pinaud, 2008), but few have examined how the calculation of marine animal home ranges differ using the two technologies at a small scale (Yasuda and Arai, 2005; Hazel, 2009). The work by Yasuda and Arai (2005) found that GPS data resulted in smaller, but more realistic, home range estimates due to the inclusion of Argos data from all location classes in their calculations and comparatively few GPS locations. Hazel (2009) on the other hand, who used approximately 50 times more GPS than Argos positions and only LC 1, 2 or 3 Argos locations, reported home ranges for green turtles were larger when calculated by Fastloc GPS. This is similar to the results obtained in our study, where GPS positions determined that little penguins used a foraging area around twice the size of that calculated from the satellite transmitters operating on the Argos system, when both datasets were stringently filtered.

However, inter-annual variations in home ranges may be accounted for by changes in environmental conditions in some cases (Schofield et al., 2010). Little penguin distribution is known to be affected by prey availability (Weavers, 1992; Collins et al., 1999), and at a small scale has been linked with sea-surface temperature (Hoskins et al., 2008) and the presence of thermoclines (Ropert-Coudert et al., 2009). Large amounts of rainfall in the catchment (which could potentially cause stratification in the otherwise well mixed shallow bay) did not occur during the period of our study in either year (rainfall data accessed at <http://www.bom.gov.au> 16/3/2010) and a slightly higher (approximately 1–2 °C) sea-surface temperature (SST) in the north of Port Phillip during 2007 (data accessed <http://www.earthsci.unimelb.edu.au/~awatkins/temps.html> accessed 16/3/2010) did not result in a greater foraging area that year, as would be predicted based on typical prey responses to SST (Hobday, 1992; Mickelson et al., 1992). Therefore, considering that maximum distances travelled from the colony did not differ between the 2 years and the overall pattern of distribution looked very similar, the differences between foraging area size can be attributed to the different methods used and the significantly different number of locations obtained. The number of locations is also responsible for differences between GPS time intervals in calculating

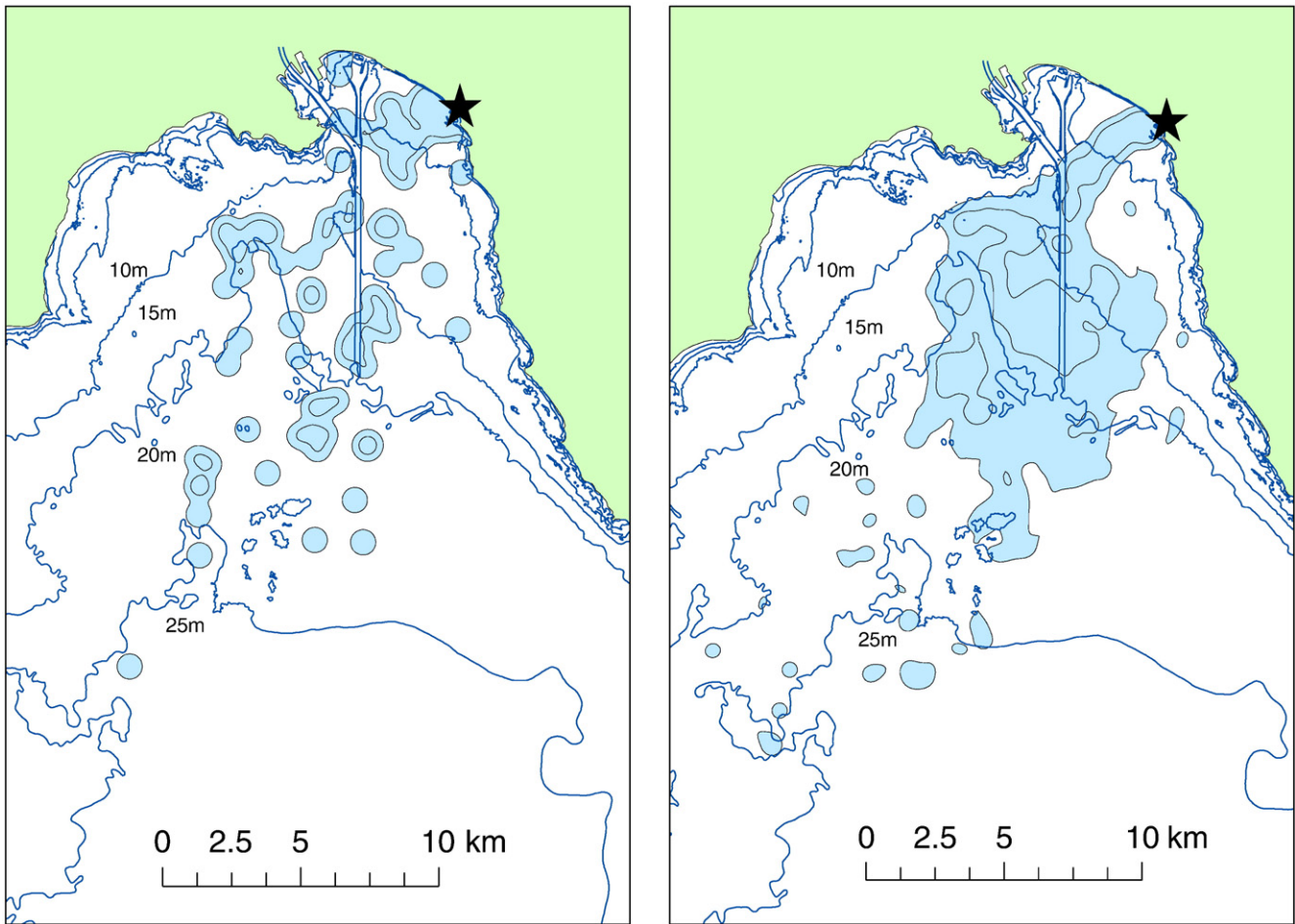


Fig. 2. Penguin foraging areas calculated by 90% fixed kernel density estimators based on PTT data (left) and GPS data sub-sampled at 10 min intervals (right). Location of penguin colony is indicated with star and bathymetry (including that of the shipping channel) is in dark blue. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

total distance travelled (Ryan et al., 2004), foraging area size and amount of shipping channels contained within the foraging area.

A distinct advantage of the combined GPS and TDR over the separately deployed PTT and TDR was that it provided simultaneous information on the penguin's three-dimensional space usage, which

is essential in conservation applications for animals with limited foraging ranges. GPS data were also capable of describing penguin behaviour within the small, defined area of the shipping channel in much greater detail than the satellite transmitter. This is due both to

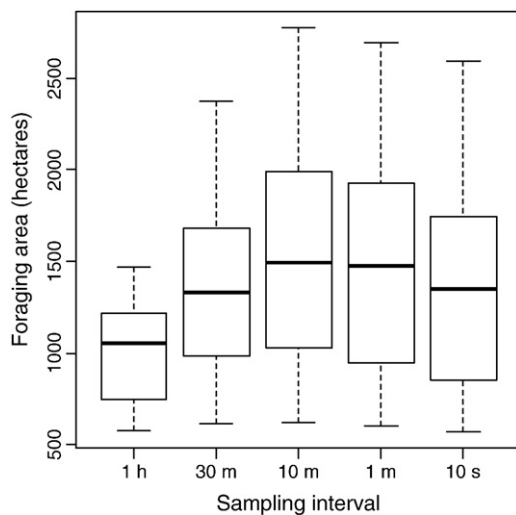


Fig. 3. Foraging area calculated from GPS data sub-sampled at various time intervals.

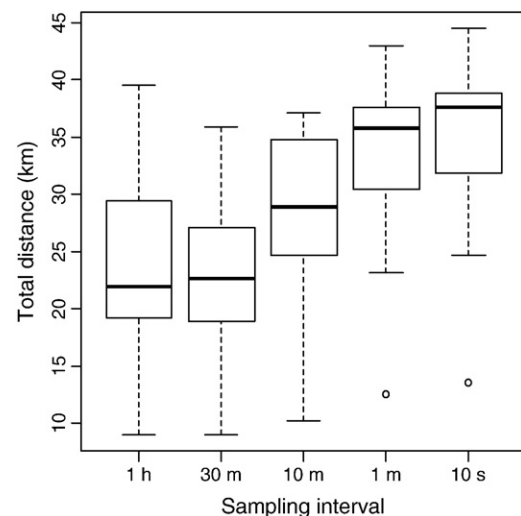


Fig. 4. Total daily distance swum by penguins calculated from GPS data sub-sampled at various time intervals.

Table 3

Foraging zone and diving behaviour by water depth, where known from GPS locations (filtered by 10 min intervals).

Sea depth (m)	Mean dive depth (m)	% Foraging zone	% Time spent	% Dives made	% Dives IDZ
5	2.45 ± 0.21	3.8	6.2	0.9	50
10	5.32 ± 0.10	16.3	13.0	14.7	69.9
15	8.48 ± 0.07	28.0	32.6	37.3	48.7
20	9.95 ± 0.12	44.5	32.6	29.8	31.6
25	10.54 ± 0.40	4.3	4.2	4.4	23.5
Shipping channel	7.73 ± 0.15	3.0	11.4	13.0	62.3

the number and accuracy (within 6 m) of those locations collected by the GPS. Even with the best location accuracy of the PTT on the Argos network (to within 250 m), the data are of limited value when determining use of small habitat areas in the penguin's activity range such as the shipping channel (that is approximately 200 m wide). Further, given that errors are often greater than that reported by the service provider (see Hazel, 2009 for review), the use of the PTT data at this scale for conservation purposes is open to criticism that may undermine the results presented. Prior to the use of GPS, we speculated that penguins were making benthic dives in the channel and pursuing prey from below (Preston et al., 2008). Deepening of the channel occurred before our device deployments in 2008, so we cannot be certain as to whether the increased depth has altered penguin behaviour in this area. However, our results show that a large amount of diving made in the channels is benthic and the penguins spend a disproportionately high amount of time there compared to the size it occupies within the foraging range, so the shipping channel appears to be an important foraging area for this colony.

This study compared two different methods of describing foraging behaviour using externally attached devices of three different sizes, which can potentially affect the behaviour of little penguins (Ropert-Coudert et al., 2007). The larger cross-sectional area and drag created by the external antenna of the satellite transmitter may have had a greater affect on the foraging behaviour of the penguins than the combined GPS and diving loggers, but the change in penguin body mass after deployment with these devices was not significantly different. This suggests that the significant differences between years for the size of the foraging area are a result of the higher number of locations collected by the GPS, which would affect calculation of kernel density estimators, rather than an effect of the different devices used in this study. Additionally, we found no significant differences in the number of dives or bottom phase proportion of the dive, parameters that are likely to change as a result of device size (Ropert-Coudert et al., 2007), thus it is unlikely that there was an effect on the diving behaviour between the methods used.

Most diving parameters measured were similar in both years, but the interpretation of 2007 diving behaviour was limited as geographic location was unknown. In studies of fish, horizontal movements are often interpreted from barometric pressure or light determined from diving recorders (Le Port et al., 2008; Hobson et al., 2009). Likewise, with penguins the shape of dives or intra-depth zone dives may give an indication of which part of the water column penguins are utilizing (Tremblay and Cherel, 2000; Hoskins et al., 2008). Penguins in this study made most of their dives with long bottom phases indicative of demersal diving (Ropert-Coudert et al., 2006) and commonly made dives to the intra-depth zone, which may be indicative of benthic diving when repeatedly made within a diving bout (Tremblay and Cherel, 2000). However, when diving profiles were combined with penguin location, we found that most of the dives were performed to mid-water in areas 15–20 m. About a quarter of intra-depth zone dives were made to within 5 m of the sea floor (the accuracy of our bathymetric data) and thus, the majority of the flat bottomed demersal dives were actually performed mid-water column. Visual examination of the diving bouts in areas of known depth suggests

that the penguins employ some diving strategies near to the sea floor, but more dives are made to the mid-water column than previously thought (Preston et al., 2008).

Use of highly accurate combined location and diving data provided better estimates of the area used by foraging animals, and were also capable of identifying behaviour within small areas of interest, such as the shipping channel, which was not possible with separately collected data or location data with the accuracy of the Argos network. However, the calculation of parameters varied depending on the time interval GPS data at which was sub-sampled. Compared with 1 h and 30 min GPS intervals the PTT provided a greater estimate of total distance travelled, which may due to relative error associated with PTT that may artificially increase the distance between actual concurrent locations. The higher total foraging distances calculated by 10 s and 1 min GPS sub-sampling are more representative of actual foraging length, as they are approximately 70% of the total length calculated from all 1 s GPS data, which takes into account the influence of measurement error (Ryan et al., 2004). Overall, we found that the data collected at short-medium time intervals provided us with the greatest estimates for each of the foraging parameters and was also suitable for describing diving behaviour in relation to the sea floor.

Further improvements to our data collection method could be made by using GPS units with longer battery life to provide more sampling time. Improving miniaturized Fastloc® or TrackTag® GPS units to be used on diving animals would provide quicker acquisition of positions for diving animals during periods of extensive diving (Rutz and Hays, 2009). The results of our study justify the continued advancement and use of biologgging technologies, including the miniaturization of devices that is required for many small animals (Burger and Shaffer, 2008), such as little penguins. Of particular benefit from these technological developments will be animals that forage over small temporal and spatial scales, or within coastal areas that are subject to a high level of anthropogenic disturbance.

Acknowledgements

We wish to thank A. Matic, Z. Hogg, T. Shaw, C. McCutcheon and volunteers of Earthcare St Kilda for field assistance. Our gratitude also to N. Schumann for advice on GIS programs. Funding and equipment for this research was provided by Monash University, Earthcare St Kilda, Australian Conservation Foundation, Toyota Australia, BHP-Billiton, The Penguin Foundation, Dan Costa and Parks Victoria. We wish to also acknowledge P. Dann and Phillip Island Nature Park research staff for provision of PTTs and collation of the data from ARGOS. Bathymetry data was provided by Department of Primary Industries, Queenscliff. The field site was accessed with permission of the St Kilda Breakwater Wildlife Management Co-operative Area committee and research was conducted under animal ethics permit BSCI/2006/12 from Monash University and wildlife permits 10003374 and 10003848 from the Department of Sustainability and Environment, Victoria. The authors also wish to thank the two anonymous reviewers whose comments greatly improved the quality of this manuscript. [SS]

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Glossary

Biologging: the science of attaching remote logging or tracking devices to animals, to record information on their movements, behaviour and environment
GPS: global positioning system
TDR: time-depth recorder, a biologging device to record animal dives
PTT: platform terminal transmitter, satellite tracking biologging device
Argos: a global satellite network

Chapter 4: Comparison of stomach content and stable isotope analysis for describing the diet and prey of seabirds

Declaration for Thesis Chapter 4

In the case of chapter 4, contributions to the work involved the following:

Name	% contribution	Nature of contribution
T.J. Preston	88%	Conception, execution, statistical analysis and writing
A. Chiaradia	5%	Advice, interpretation and writing assistance
S.A. Caarels	2%	Statistical advice
R.D. Reina	5%	Advice, interpretation and writing assistance

Declaration by co-authors

The undersigned hereby certify that:

- (1) they meet the criteria for authorship in that they have participated in the conception, execution, or interpretation, of at least that part of the publication in their field of expertise;
- (2) they take public responsibility for their part of the publication, except for the responsible author who accepts overall responsibility for the publication;
- (3) there are no other authors of the publication according to these criteria;
- (4) potential conflicts of interest have been disclosed to (a) granting bodies, (b) the editor or publisher of journals or other publications, and (c) the head of the responsible academic unit; and
- (5) the original data are stored at the following location(s) and will be held for at least five years from the date indicated below:

Location(s)	School of Biological Sciences, Clayton Campus, Monash University	
Signature 1		20/08/10
Signature 2		31/08/10
Signature 3		3/09/10
Signature 4		20/08/10

Abstract

Dietary analysis of seabirds is conducted using a number of methods, all with advantages and disadvantages. Many studies are now using more than one method, particularly when describing the diet of seabirds over longer periods such as during the non-breeding season. In this study I compared the information provided by two commonly combined dietary sampling methods, stomach content and stable isotope analysis. By studying a colony of resident little penguins (*Eudyptula minor*), I was able to collect samples using both methods on a monthly basis across two years and compare the ability of each method to detect seasonal and inter-annual differences in the diet. Additionally, as the colony I studied has a limited foraging range, I was able to use the information from this diet study to provide an insight into the age and presence of some prey stocks in their foraging area.

No correlations were found between the diet composition estimated by the two methods. Stomach contents and stable isotopes provided significantly different estimates of the proportion of prey items in the diet each month, with stomach contents estimating 23% more Australian anchovy, *Engraulis australis*, and 6% more luminous bay squid, *Loliolus noctiluca*, in the diet than stable isotopes. However, stable isotopes estimated that 36% more southern garfish, *Hyporhamphus melanochir*, was consumed by penguins each month than was indicated by the stomach contents.

The two methods also differed in their ability to reveal changes in the dietary composition over time, but there was some seasonality apparent for the anchovy and garfish when both methods were correlated. Stomach contents did not show any significant differences in the three main prey species between seasons and years. Stable isotopes showed several significant differences in their seasonal and yearly values, both the nitrogen and carbon isotopes differed significantly in their year by season interactions and carbon also differed between the two years studied.

It was only through the stomach contents that I was able to determine the full range of species consumed by the penguins. Size and age data of prey determined from the stomach contents was supported by the composition of the diet through stable isotope mixing models, with both being used to describe the seasonal presence of garfish and anchovy of varying ages within the foraging area. I found that each of the methods provide distinctly different information and are complementary in assessing the diet and prey of seabirds, but direct comparison of the dietary composition determined separately by the two methods should be avoided.

Introduction

Seabirds are mostly generalists and one of the largest natural consumers of marine fisheries stocks (Brooke, 2004). Changes in seabird reproductive success and population size are often associated with diet (Boersma and Parrish, 1998, Jodice et al., 2006, Becker et al., 2007b, Sorensen et al., 2009), and as such responses to prey availability means that they can play a role in revealing prey movements and estimating prey abundances for fisheries and conservation management (Cairns, 1992, Barrett, 2002, Petersen et al., 2006, Ainley and Blight, 2009). Thus, seabird diets are widely studied to provide information both about the state of their populations and that of their prey (Barrett et al., 2007).

Conventional methods of seabird dietary sampling typically involve observation of food delivery to chicks, or the collection of regurgitate, stomach content or faecal samples (e.g. Sydeman et al., 1997, Xavier et al., 2006, Montevecchi, 2007, Deagle et al., 2008), which provide direct information on the species and size of prey consumed. However, these samples only reflect food ingested over a very short period (Gales, 1987, van Heezik and Seddon, 1989) and may misrepresent the overall diet consumed between sampling events. Indeed, most studies of seabird diet are conducted during the breeding season when

observation and capture are easily facilitated (Guinet et al., 1996), but their diet during this period covers only a portion of their life history and may be influenced by reproductive constraints (Gales and Green, 1990). This provides an incomplete picture of seabird prey consumption patterns and renders estimates of their annual consumption rates difficult (Karpouzi et al., 2007). This gap in our knowledge of seabird diets has been recognised (Barrett et al., 2007), with studies now trying to address this information deficit (Xavier et al., 2006, Phillips et al., 2009, Sorensen et al., 2009).

One alternative approach to studying diet is stable isotope analysis, which is able to reveal an animals' trophic position, dietary composition and feeding location (Hobson et al., 1994, Hobson, 1999, Phillips, 2001) across the sampled tissue's turnover period, which can range from days to months (Hobson and Clark, 1992). It can be used to determine the diet across times when seabirds are not resident at their colonies, and as such it is gaining momentum as a method of examining seabird diets during both the breeding and non-breeding seasons (e.g. Forero and Hobson, 2003, Quillfeldt et al., 2005, Becker et al., 2007a, Sorensen et al., 2009). The pros and cons of conventional (i.e. stomach content analysis) and stable isotope dietary analysis have been well documented (Fry, 2006, Barrett et al., 2007, Pasquaud et al., 2007), with both methods offering distinctly different information. Stomach contents provide direct information on the prey species consumed and their size, while stable isotopes add information about the trophic position and foraging areas that the predators are feeding at. Both stomach content and stable isotope analysis may be used to provide an estimate of the dietary composition.

When stomach content and stable isotope analysis are combined, the results from each can be complementary, as demonstrated by research into estuarine and inshore food webs (Penchaszadeh et al., 2006, Pasquaud et al., 2010), fish (Azzurro et al., 2007, Ho et al., 2007, Fanelli and Cartes, 2008, Paradis et al., 2008) and marine mammals (Dehn et al., 2007).

However, whilst most studies using both methods find that stable isotopes confirm what is

found by stomach contents and vice-versa, this is not always the case. Using these methods, both Winemiller et al. (2007), who investigated a saltmarsh food web and Meckstroth et al. (2007), who determined the diet of introduced terrestrial vertebrates, found differences in results between stable isotopes and stomach contents in terms of the prey trophic level and the actual food consumed, respectively. Erroneous interpretations of the diets examined in these studies would likely have resulted if they had not used both stable isotopes and stomach content analyses. A number of seabird dietary studies have used stable isotopes in addition to stomach contents, concurrently (Sydeman et al., 1997, Karnovsky et al., 2008, Ito et al., 2009, Karnovsky et al., 2009, Browne et al., 2010, Chiaradia et al., 2010) and during periods when stomach contents were unable to be collected (Ainley et al., 2003, Mattern et al., 2009). However, none of the studies using the two techniques simultaneously have been conducted over a prolonged continuous period in order to examine whether the results are similar year-round and if they are each able to detect seasonal and inter-annual patterns in diet.

Year-round access to a little penguin (*Eudyptula minor*) colony enabled me to conduct a dietary study using both stable isotopes and stomach samples continuously over a two year period, incorporating both the breeding and non-breeding seasons. I collected samples monthly to examine any changes in dietary composition over time, and used the results of each method to determine whether stable isotopes provide different or complementary information to stomach contents. The colony of little penguins I sampled have a small foraging area inside a large marine embayment (Preston et al., 2008), which also allowed for the consideration of these methods to describe prey stocks in the area without the potentially confounding factor of penguins from the same colony using spatially distinct foraging regions.

Methods

Study site

The St Kilda penguin colony is located 5 km from the centre of Melbourne, Australia (37° 51' S, 144° 57' E, Fig. 1), with a population of approximately 1000 individuals (Z. Hogg, *pers.comm.*). Penguins nest on a constructed breakwater 650 m long, landing all along the leeward side (facing the shore). The population forages in the north of Port Phillip (Preston et al., 2010), a large marine embayment that joins Bass Strait.

Field procedures

Stomach content samples

Ten penguins were caught coming ashore at St Kilda each month between August 2006 and October 2008 (except January 2008). Penguins were identified by passive integrated transponder (PIT) tag or flipper band, weighed by spring balance to the nearest 10 g and sexed by bill measurements (Arnould et al., 2004). In the interests of animal well-being, penguins that had been sampled within the previous 12 months or weighed <900 g were released without sampling (numbers not recorded). Remaining penguins' stomachs were gently massaged with the palm of a hand prior to flushing, to break up any food bolus and assess the level of stomach fullness. When a stomach was considered full to capacity (i.e. the stomach would not move when gentle pressure was applied), the penguin was released to avoid overstretching of the stomach and potential injury (total number 13). Resultantly, 174 samples were collected over the two year period (88 female, 86 male).

Stomach contents from the sampled penguins were obtained using a modified water offloading technique (Chiaradia et al., 2003). Water was administered via an oesophageal tube that was connected to a 140 ml syringe. Rather than filling the stomach with water until water overflowed from the bill, a small volume of water (normally $\approx$ 70-100 ml depending on stomach fullness) was given at a constant slow speed. The tube was then

removed and penguins were held over a collection bucket while their stomach was gently pressed to induce regurgitation. The whole process was repeated a maximum of three times per penguin. The tube inserted into the oesophagus was cleaned in a solution of either Milton or F10SC for approximately 5 min then rinsed in fresh water between individual penguins, to avoid transmission of pathogens that may occur in the oesophageal microflora (Dewar, 2007).

Blood samples

Monthly blood samples were collected from 6 male and 6 female randomly caught adult penguins at St Kilda from September 2006 – October 2008 (different individuals to those stomach flushed, to minimise stress and risk of overheating). As it was not essential that these penguins had just returned from sea, a higher number of penguins could be captured than was possible for stomach flushing, and could also be selected on the basis of sex. Approximately half of these penguins were sampled once and the other half sampled >1 time (mean 2.4 times). Power analysis found that the isotope variation between samples (within a sex, within a month) was very low (typically 5% at 0.8 power), so it is unlikely that re-sampled penguins would skew the results. Monthly sampling was chosen as stable isotopes are known to turn over in the blood approximately every three to four weeks (Hobson and Clark, 1993). Blood samples of 80 µl were collected by capillary tube from the tarsal vein and stored in 1 ml 70% ethanol at room temperature until analysis (Hobson et al., 1997).

Sample analysis

Stomach samples

Stomach samples were frozen at -18°C until sorting, when they were defrosted, drained and left to air-dry before being weighed to the nearest 0.05 g. Prey items were identified from otoliths and squid beaks using several references (including Lu and Ickeringill, 2002,

Furlani et al., 2007 and a reference collection used in Chiaradia et al., 2003) and measured to nearest 0.1 mm. The length (most were measured to standard length, but it did vary for some species according to the reference) and weight of each fish and squid was calculated from published regression equations of otoliths and beaks respectively (Cullen et al., 1992, Lu and Ickeringill, 2002, Furlani et al., 2007). *Engraulis australis*, the Australian anchovy, were categorized into broad age classes according to size, based on data from anchovies collected within Port Phillip bay (Parry and Stokie, 2008b). The 0+ year cohort corresponded to standard lengths <63 mm, 1+ year 63-91mm and 2+ year 92+ mm (none larger than 98 mm were recorded), recognising that there is overlap in size between the age cohorts.

Stable Isotopes

Prey samples analysed for stable isotopes were whole specimens collected from St Kilda penguin stomach contents. The penguin blood samples had ethanol removed. Both prey flesh and whole blood were then freeze dried and ground prior to analysis by SINLAB, Canada. There, samples were weighed into tin capsules and combusted in an AS128 autosampler at 1050°C. The CO₂ and N₂ gases were analysed for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ in either a Thermo-Finnigan Delta Plus or Delta XP isotope-ratio mass spectrometer (Bremen, Germany) using a continuous flow system. Data were corrected with three internal laboratory standards and one out of every 20 samples was tested twice to ensure that results were consistent. Results are presented in δ notation as parts per thousand (‰) deviation from the standard PDB (C) and AIR (N).

Statistical analysis

Statistical analysis was conducted in R version 2.9.1 (R Development Core Team, 2009). The statistical threshold was set at $P < 0.05$ and results are presented as mean $\pm$ SE.

Stomach content samples were quantified using the weighted relative occurrence method adapted from Montague and Cullen (1988). The percentage contribution of each item to the sample based on weight (calculated by linear regressions) was determined and this was then averaged across all samples to give a value for each prey item for the month. The overall diet composition across the two years was based on prey item weight as a percentage of the total weight of all prey items recovered. Stomach content analyses excluded stomach content samples that were empty (158 analysed, 79 male and 79 female). Using the mean monthly value of dual isotopes ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) and three sources (*Engraulis australis*, *Hyporhamphus melanochir* and *Loliolus noctiluca*) in the mixing model Isosource (Phillips and Gregg, 2003), I estimated the relative proportion of the main dietary components (determined from stomach contents) in the penguins diet each month. As no specific data on discrimination factors or trophic enrichment exist for little penguins, I calculated the fractionation factor from the stable isotope values taken in my first month of sampling (September 2006) when the diet according to stomach contents consisted of >90% *Engraulis australis* for two consecutive months (August and September 2006). This assumes that the diet was dominated by *Engraulis australis*, throughout the month leading up to the September 2006 blood sampling. The resultant fractionation was 2.51‰ $\delta^{15}\text{N}$ and 1.2‰ $\delta^{13}\text{C}$. This is similar to the mean $\delta^{15}\text{N}$ values reported for all birds reported in Caut et. al. (2009) and for rockhopper penguins (*Endiptes chrysocome*) in Cherel et. al. (2005). My higher fractionation value of $\delta^{13}\text{C}$ is likely to be due to interspecific variation and because I did not remove lipids from the prey samples (Becker et al., 2007a).

Type III ANOVA's were used to compare the results of stomach content dietary composition (of the three main prey species) and stable isotope $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values between years and seasons (summer = Dec/Jan/Feb, autumn = Mar/Apr/May, winter = Jun/Jul/Aug, spring = Sep/Oct/Nov, added as a factor). Seasonality and inter-annual differences in anchovy sizes were also determined by type III ANOVA's. Where

significant interactions were found, the data were randomized 10000 times to create a new F-distribution and P value from this is presented, to account for any possible influences from re-sampling the same penguins.

Multiple time series correlation analysis and paired t-tests were conducted on the monthly main prey items estimated by both stomach flushing and the mixing model.

Autocorrelation and partial autocorrelation functions were used to determine any cross-correlations between the two methods and any periodicity in the estimates using each method. Monthly estimates of each prey species in the diet are presented for each of the methods, together with a three-month moving average applied to the stomach content data in order to smooth out the point sampling and make it more comparable to the integrated mixing model data.

Results

Stomach contents

The majority of stomach contents were fish (Table 1), specifically *Engraulis australis* (Australian anchovy) and *Hyporhamphus melanochir* (southern garfish). Cephalopods comprised only a small proportion of the diet overall (Table 1), with *Loliolus noctiluca* (luminous bay squid) being the most common species. Several types of crustacea were found, but not identified to species level due to their low overall importance in the diet (Table 1). The stomach content sampling showed no significant difference (type III ANOVA, results presented in Table 2) between year or season for the three main species consumed, *Engraulis australis*, *Hyporhamphus melanochir* and *Loliolus noctiluca*. No seasonality was apparent from the partial autocorrelation analysis for any of the three main prey types, and there were no significant time-lag correlations (Fig 2a).

Mean size of *Engraulis australis* calculated from published otolith-standard length regression equations was approximately 72 mm, corresponding to anchovies of approximately 1+ year class (Parry and Stokie, 2008b). Anchovies in the 1+ year class were most common in the penguin diet, accounting for 71% of all anchovies eaten (Fig. 3). Anchovies in their first year (0+ year class) were most abundant in the penguin diet in the summer months and accounted for 28% of the anchovies consumed. Those in the 2+ year class were taken rarely (1% of all anchovies), mostly in the winter months, but there was no significant difference in the size of anchovies taken either by year (type III ANOVA, $F_{1,22}=1.762$, $P=0.204$) or season ($F_{3,22}=2.383$, $P=0.110$).

Based on standard length, all *Hyporhamphus melanochir* consumed by penguins were immature (mean standard length approximately 129 mm) and <18 months old (Ling, 1958). The mean length of *Loliolus noctiluca* calculated from beak-mantle length regression equations was approximately 32 mm.

Stable isotopes

Analysis of the three main prey items showed *Loliolus noctiluca* to have the highest $\delta^{15}\text{N}$ values and *Hyporhamphus melanochir* the lowest, with *Engraulis australis* $\delta^{15}\text{N}$ values in between and with lower $\delta^{13}\text{C}$ values (Fig. 4).

There was a significant year by season interaction in $\delta^{15}\text{N}$ values (Table 3) in the penguin blood, where $\delta^{15}\text{N}$ was significantly lower in the spring of 2007 than 2006, whilst it was higher during the winter in 2007 than 2008 (Fig. 5a). There was also a significant year by season interaction (type III ANOVA, Table 3) for $\delta^{13}\text{C}$ values, which were greater during the autumn and winter of 2008 than 2007 (Fig. 5b). Both $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values differed significantly by season in each year (Table 3) and displayed a similar pattern by season in both years (Fig. 5a & b).

Partial autocorrelation analysis indicated that there was significant positive correlation between 1 month lag periods, and significant negative correlations between 3 month lag periods for both *Engraulis australis* and *Hyporhamphus melanochir* (Fig. 2b). Plots in figure 2b indicate some seasonality in these two prey species, but not *Loliolus noctiluca*.

Direct comparison of methods

The greatest contributor to the penguin diet overall, *Engraulis australis* was significantly more common in the stomach contents than the mixing model (paired $t_{(24)}=2.8$, $p<0.01$, Fig. 6a), by a monthly average of 22.8% over the study period. Conversely, mean monthly estimates of *Hyporhamphus melanochir* in the diet were on average 36% lower when calculated by stomach contents than when determined by the mixing model (paired $t_{(24)}=4.5$, $p<0.01$, Fig. 6b). *Loliolus noctiluca* was the lowest contributor to the penguin diet out of the three main prey species, but significantly more was found in stomach contents than indicated by the mixing model (paired $t_{(24)}=2.8$, $p<0.01$, mean difference 5.6%, Fig. 6c). In the multiple time series analysis, plots of autocorrelation (Fig. 7) displayed no significant relationships between the two methods, indicating that there was no relationship between the techniques, including any time-lag that may occur due to incorporation of stable isotopes.

Discussion

Stomach contents collected from the St Kilda colony of little penguins indicated that the main prey consumed throughout the year was Australian anchovy *Engraulis australis*, in agreement with the finding that anchovy are amongst the most common fish larvae found in Port Phillip bay (Neira and Sporcic, 2002). While there were fluctuations in the quantity of the penguins main prey species from month to month and over time, no significant seasonal or inter-annual variations were detected in the stomach contents. In contrast, the

stable isotope and mixing model values changed relatively steadily from month to month, indicating that there were significant seasonal and inter-annual patterns in the penguins' diet that were not detected by stomach content analysis. Stomach contents and stable isotope mixing models differed in their estimate of all three main prey items each month, indicating that they do not give the same information on diet composition, so direct comparison of the diet between the two methods is not possible.

The methodological constraints of each sampling technique differ (Barrett et al., 2007) and the effect of these must be considered when reviewing the differences in results obtained. Although the examination of seabird stomach contents is a method that has been in use for >50 years (Ealey, 1954), it has been recognised amongst the biological community that this method can lead to the reporting of erroneous figures due to its underestimate of prey items that break down rapidly (Meckstroth et al., 2007) and the relatively short time period that it represents (Barrett et al., 2007). The digestion of prey generally occurs over 8-16 hours in little penguins (Gales, 1987), which means that much of what is consumed early in the day may not be retrieved by stomach flushing upon return to the colony in the evening. This can bias the results toward what is caught later on in the day, which may not represent what the adult is consuming if they are partitioning prey to chicks as some seabird species do (Forero et al., 2002, Suryan et al., 2002, Browne et al., 2010). Conversely, stable isotopes represent food consumed over a relatively long time, requiring complex analysis (Barrett et al., 2007), which only provides a comparably rough estimate of the prey proportions consumed compared with the accuracy that can be obtained through stomach content analysis. However, my study shows differences in the stable isotopes and stomach contents year round, suggesting that prey delivery to chicks is not responsible for the difference in results found here and stomach contents may provide an inaccurate account of what adults are eating both during breeding and non-breeding stages. The variation in prey composition between individual stomach content samples was greater than that for

stable isotopes, suggesting that on a daily basis the dietary composition of individual penguins within a population will differ, but when measured over a longer time interval those differences are less variable. Smoothing the results of the stomach contents with a moving average helped to reduce the fluctuation in results caused by variation between individual samples.

Mixed modelling found southern garfish *Hyporhamphus melanochir* to play a much larger role in the diet of these little penguins than stomach contents showed. Such discrepancies in diet composition between the two methods were also found through similar sampling on yellow-eyed penguins at Stewart Island by Browne *et al.* (2010). The considerably lower rate of southern garfish found by stomach contents as opposed to stable isotopes in this study is peculiar, as southern garfish (including otoliths) are very distinctive, and as such are unlikely to be misidentified in a stomach content sample. Some species digest quicker in the seabird gut than others (van Heezik and Seddon, 1989), which may partially account for the underestimate of southern garfish and the overestimate of luminous bay squid *Loliolus noctiluca*. These findings indicate that stable isotopes are more sensitive than stomach contents for determining dietary composition, but the main prey species need to be known in order to be included in the mixing model, which can only be achieved through conventional methods such as stomach content analysis.

The stable isotope analysis and subsequent mixed modelling found trends in the penguins diet composition over the two years studied, but there was no periodicity apparent from stomach content samples. Seasonal and inter-annual variation in $\delta^{13}\text{C}$ values are generally considered to be due to inshore versus offshore feeding locations (Hobson and Welch, 1992), but as this little penguin colony forages at inshore locations year-round (Preston *et al.*, 2010, Dann, P. and Preston, T.J. unpublished data) changes are more likely to be due to the prey consumed. Fluctuations in $\delta^{15}\text{N}$ values generally infer changes in the trophic level of the prey consumed (Fry, 2006), and here they indicated that Australian anchovy

decreased in the diet at the end of the breeding season during late summer and autumn. This corresponds with the time of year that anchovies in the 0+ age cohort peaked in the diet and those in the more commonly taken 1+ age cohort decreased. There was a slight pattern of Australian anchovy decrease in the smoothed stomach sample data during these times, but the mixing model clearly indicated that southern garfish was the dominant prey item during those periods. The seasonal patterns of prey consumption were evident from stable isotope data despite significant differences in values between years. The cause of those significantly different values is unknown, as stomach contents confirm that the diet did not change to completely different species between the years.

Although the level of anchovy larvae in Port Phillip bay is amongst the highest recorded in Australia (Jenkins, 1986, Dimmlich et al., 2004), it is unknown whether they form a self-recruiting population that resides inside the bay or are actually part of a larger coastal population that would be more subject to environmental variation (Neira and Sporcic, 2002) and possibly different $\delta^{13}\text{C}$ values. However, the stomach content data showed that most of the Australian anchovies consumed by the penguins were 1+ years old and therefore are likely to have spent their whole life in Port Phillip (Blackburn, 1950).

Likewise, all southern garfish consumed by the penguins were immature (Ling, 1958). Very little is known about southern garfish movements locally, although their larvae is found within the bay from December to March (Neira and Sporcic, 2002) and they are hypothesised to have large scale movements during their life history (Fowler et al., 2008). Additionally, my stomach flushing and stable isotope results indicate that luminous bay squid is present within the penguin diet in low amounts year-round, so this squid species must be present in Port Phillip throughout the year.

I found more than 15 different prey species in the stomach of penguins and while most of these appeared in small quantities, it informs us that these species were present in the bay and they appear to be supplementary or opportunistic prey for the penguins. Assessing

prey stocks from seabird diet has limitations as the responses of seabirds to changing prey availability are typically non-linear (Cairns, 1992, Piatt et al., 2007) and it is not known whether these little penguins were selectively feeding on particular prey types (e.g. Kerry et al., 1997) or if they were consuming what was available. Hence, I cannot assume the complete prey stock structure in the penguins foraging area based on their diet, but my findings do support a survey conducted in 2008 that found clupeoid species (such as pilchard and sprat) compose only 1% of the anchovy biomass within the bay (Parry and Stokie, 2008a). At the St Kilda penguin colony where frequent collection of stomach content samples is possible, this type of sampling may be employed to add to our understanding of prey species and become a useful binary stock assessment tool in the future, but further study is first needed into penguin responses to prey availability (Piatt et al., 2007).

This study provides the most comprehensive long-term comparison of stomach content and stable isotope dietary analysis techniques for wild seabirds that I am aware of, and has highlighted that stomach sampling may have more caveats in terms of describing changes in the diet than previously thought. Despite this, I was only able to determine the full range of prey species consumed by penguins through examination of the stomach contents. Thus, each technique is suited to different applications and the decision to use one over the other will depend on the research questions being posed. Those directed at dietary diversity, prey size and age would be better suited to use of the stomach content method, while those interested in dietary composition changes over time are best suited to stable isotopes. Stomach contents provide the ability to point-sample the diet, which may be appropriate for addressing questions about a specific period of time, while stable isotopes are more appropriate to longer-term studies and detecting seasonality.

It is not recommended to directly compare the dietary composition determined separately by these two methods, as this study demonstrated by that they provide significantly

different results. However, if used together stomach content and stable isotope analysis can be complementary in describing seabird dietary composition and prey attributes.

Figures and tables

Figure 1: Location of the St Kilda penguin colony in Port Phillip, Victoria, Australia.

Figure 2: Partial autocorrelation analysis of mean monthly a) stomach contents and b) mixing model estimates for (L-R) *Engraulis australis*, *Hyporhamphus melanochir* and *Loliolus noctiluca*.

Figure 3: Age composition of anchovies recovered from little penguin stomach contents each month over two years, calculated from otolith size regression equations for standard length.

Figure 4: Mean ($\pm$ SE) stable isotope values of the penguins' three most commonly taken prey items, *Engraulis australis*, *Hyporhamphus melanochir* and *Loliolus noctiluca*.

Figure 5: Mean ($\pm$ SE) value of a) $\delta^{15}\text{N}$ and b) $\delta^{13}\text{C}$ in penguin whole blood each season for two years (spring 2006 - winter 2008).

Figure 6: Mean ($\pm$ SE) percentage of a: *Engraulis australis*, b: *Hyporhamphus melanochir* and c: *Loliolus noctiluca* in the diet of little penguins, determined by stomach contents and estimated by stable isotope mixing models.

Figure 7: Autocorrelation between mean monthly stomach content and mixing model estimates of (L-R) *Engraulis australis*, *Hyporhamphus melanochir* and *Loliolus noctiluca*.

Table 1: Prey items recovered from the stomach of penguins at St Kilda over 25 months of sampling and their contribution to the overall diet based on weight.

<u>Prey common name</u>	<u>Scientific name</u>	<u># months recorded</u>	<u>% contribution to diet</u>
Cephalopods			
Luminous bay squid	<i>Lololus noctiluca</i>	22	6.31
Arrow squid	<i>Nototodarus gouldi</i>	3	0.57
	All cephalopods		6.89
Crustacea			
Isopod spp.		9	<0.50
Amphipod spp.		6	<0.50
Copepod spp.		3	<0.50
	All crustacea		<0.50
Fish			
Australian anchovy	<i>Engraulis australis</i>	24	81.58
Southern garfish	<i>Hyporhamphus melanochir</i>	17	7.91
Eroded otoliths		16	0.73
Australian sprat	<i>Sprattus novaehollandiae</i>	9	0.66
Blue sprat	<i>Spratelloides robustus</i>	7	0.54
Smallscale hardyhead	<i>Atherinason hepsetoides</i>	2	0.58
Hardyhead spp.		8	<0.50
Sandy sprat	<i>Hyperlophus vittatus</i>	6	<0.50
Unidentified postlarva		5	<0.50
Warehou spp.		2	<0.50
Australian pilchard	<i>Sardinops neopilchardus</i>	2	<0.50
King George whiting	<i>Sillaginodes punctatus</i>	1	<0.50
Leatherjacket spp.		1	<0.50
	All fish		>92.00
Miscellaneous			
Shellgrit		6	<0.50
Terrestrial plant material		4	<0.50
Seagrass		3	<0.50
	All miscellaneous		<0.50

Table 2: Year and season effects on the three main species found in stomach contents (type III ANOVA).

	df	<u><i>Engraulis australis</i></u>		<u><i>Hyporhamphus melanochir</i></u>		<u><i>Loliolus noctiluca</i></u>	
		F	P	F	P	F	P
Year	1	<0.001	0.987	0.801	0.385	0.001	0.974
Season	3	0.680	0.577	1.408	0.279	1.346	0.297
Year:Season	3	0.249	0.861	0.327	0.806	0.846	0.490

Table 3: The effect of year and season on penguin whole blood $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values (type III ANOVA, significant P-values in bold).

		<u>Nitrogen</u>		<u>Carbon</u>	
	df	F	P	F	P
<u>Main effects</u>					
Year	1	0.14	0.763	36.50	< 0.001
Season	3	54.05	< 0.001	40.36	< 0.001
<u>Interactions</u>					
Year:Season	3	7.94	0.006	5.42	0.019
Year					
Summer	1	1.20	0.278	3.39	0.073
Autumn	1	1.01	0.124	22.51	< 0.001
Winter	1	4.12	0.048	27.27	< 0.001
Spring	1	16.13	< 0.001	0.10	0.752
Season					
Year 1	3	48.66	< 0.001	9.47	< 0.001
Year 2	3	13.14	< 0.001	37.00	< 0.001

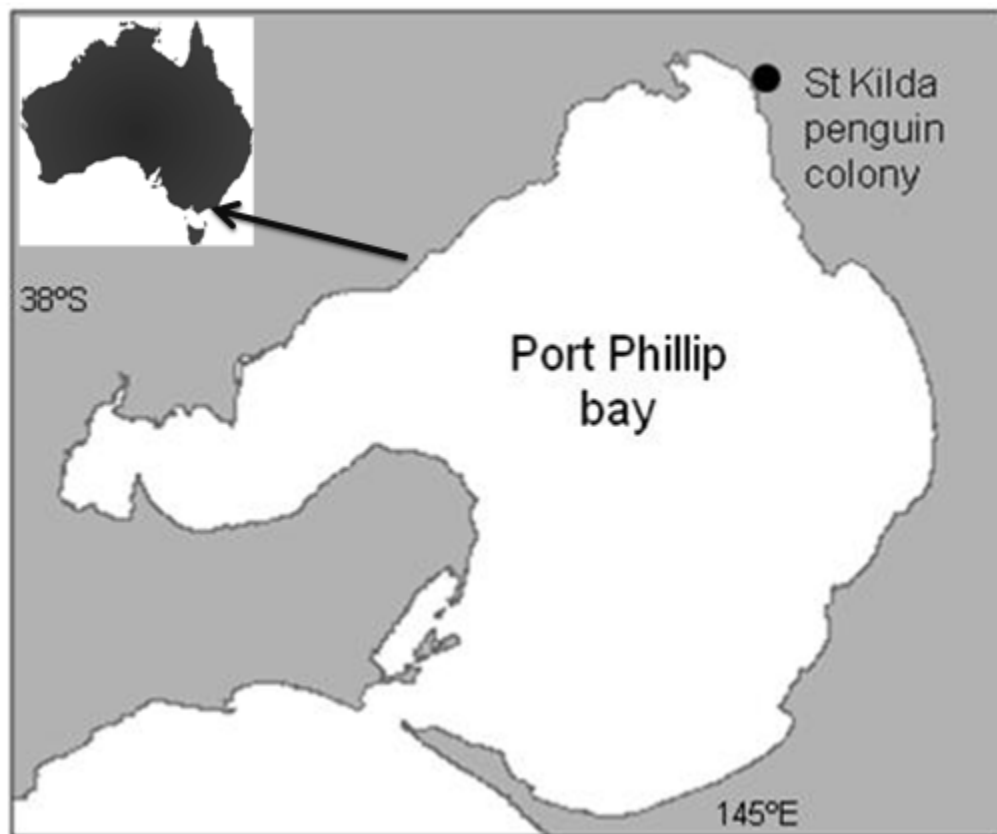


Figure 1

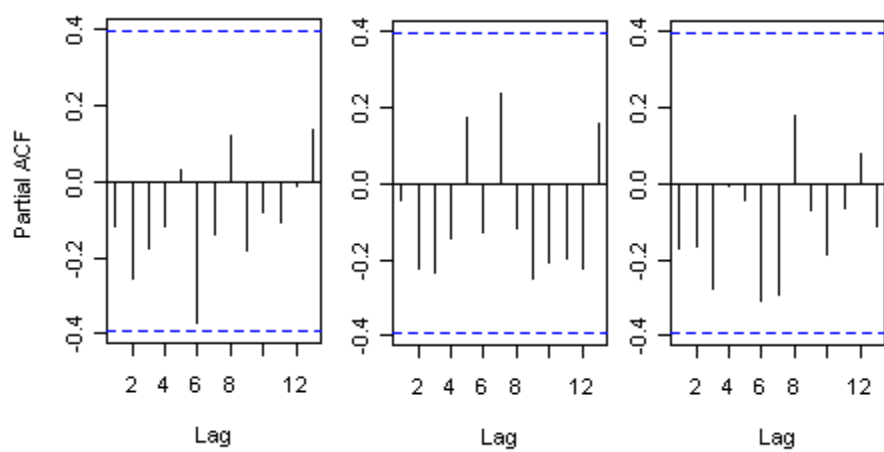


Figure 2a

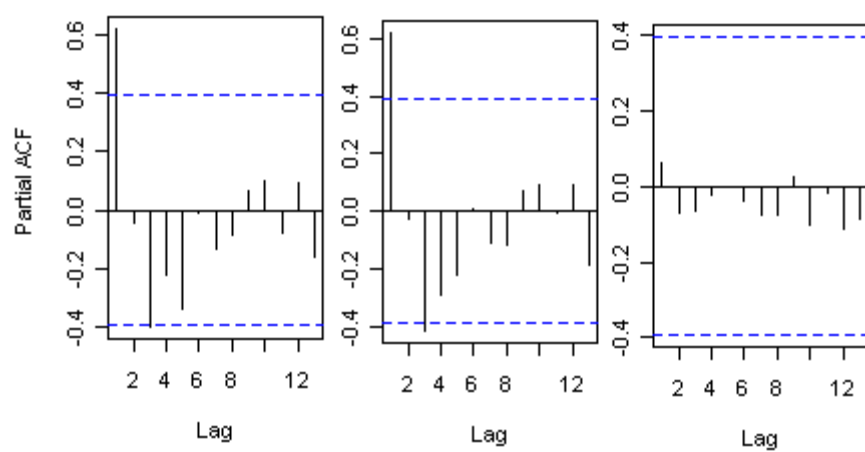


Figure 2b

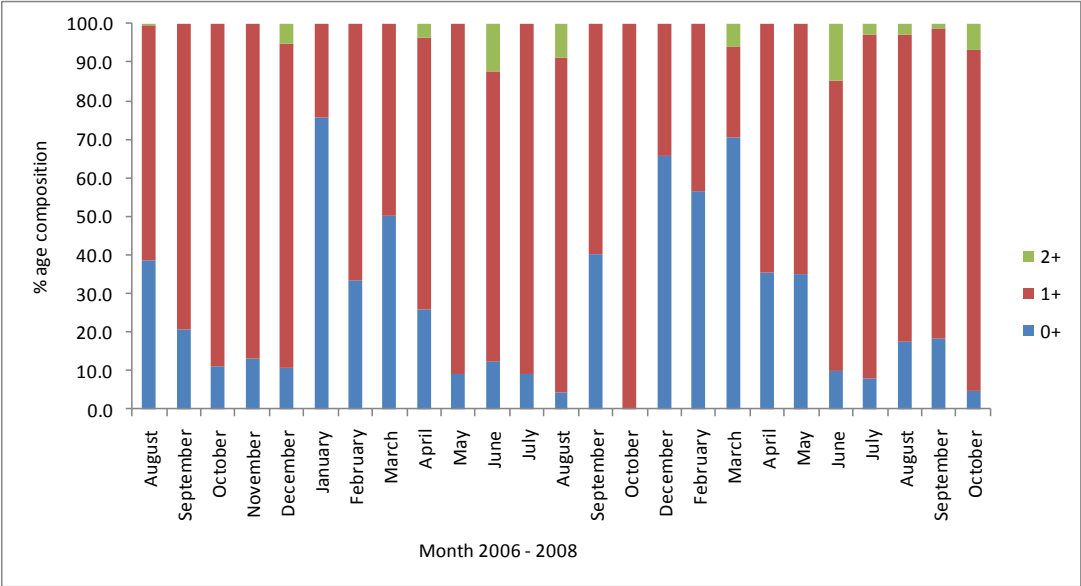


Figure 3

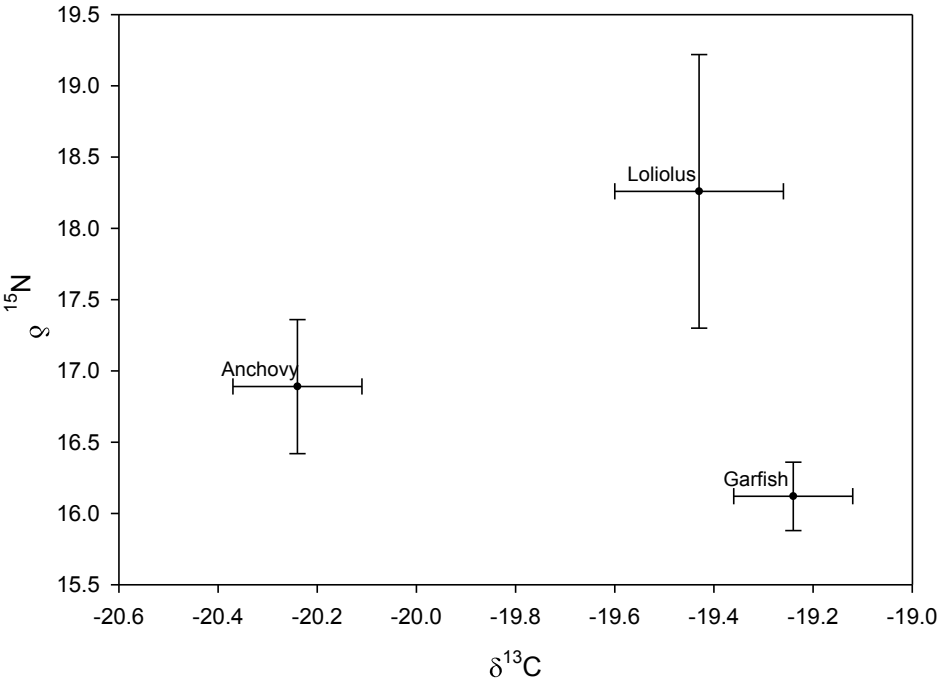


Figure 4

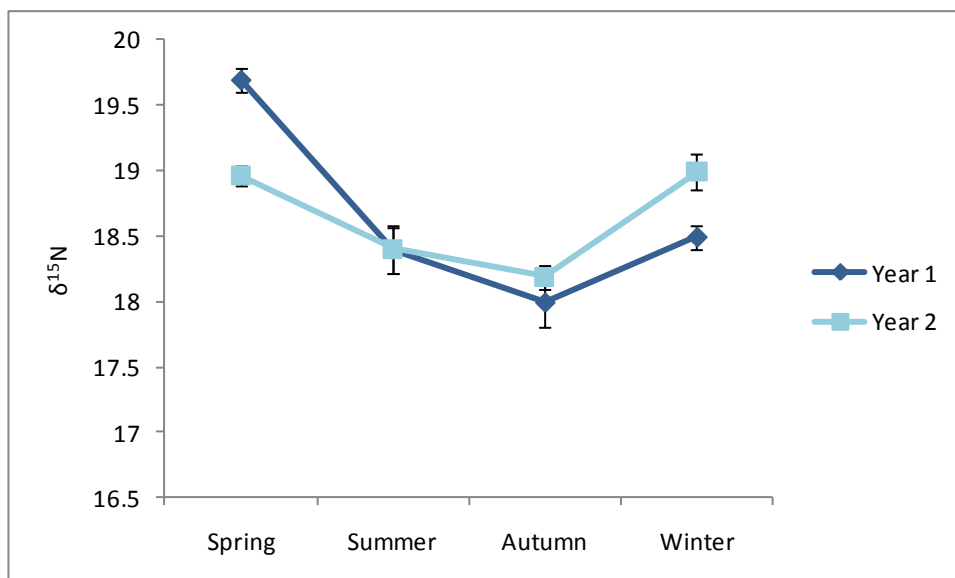


Figure 5a

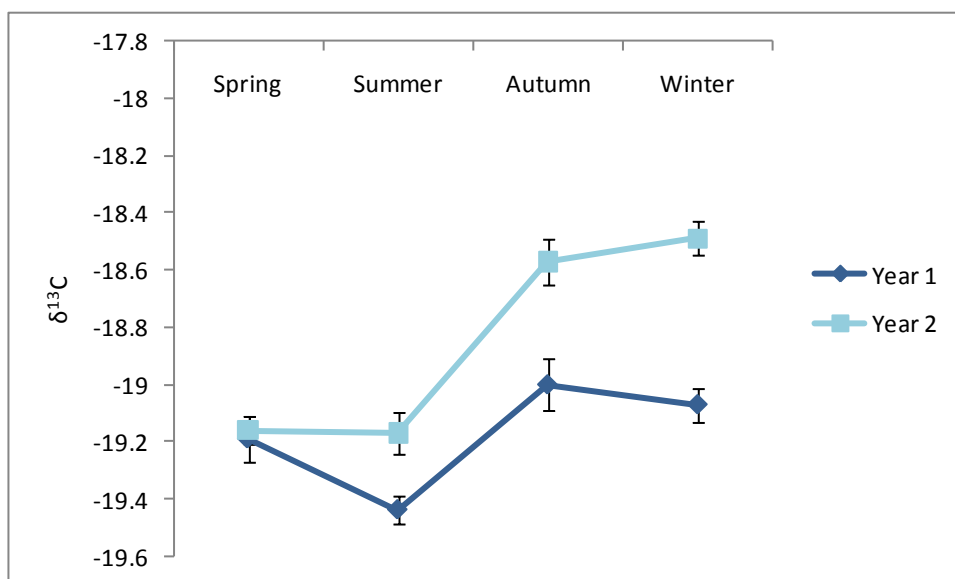


Figure 5b

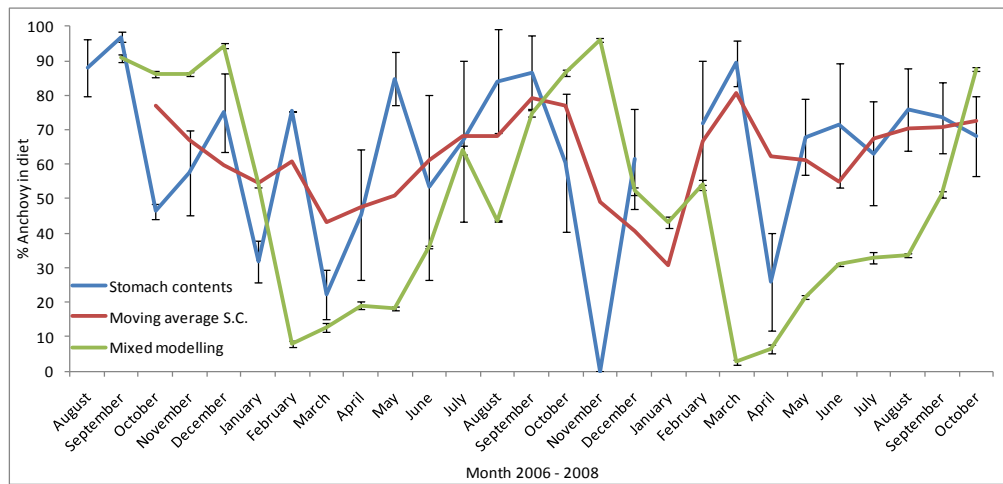


Figure 6a

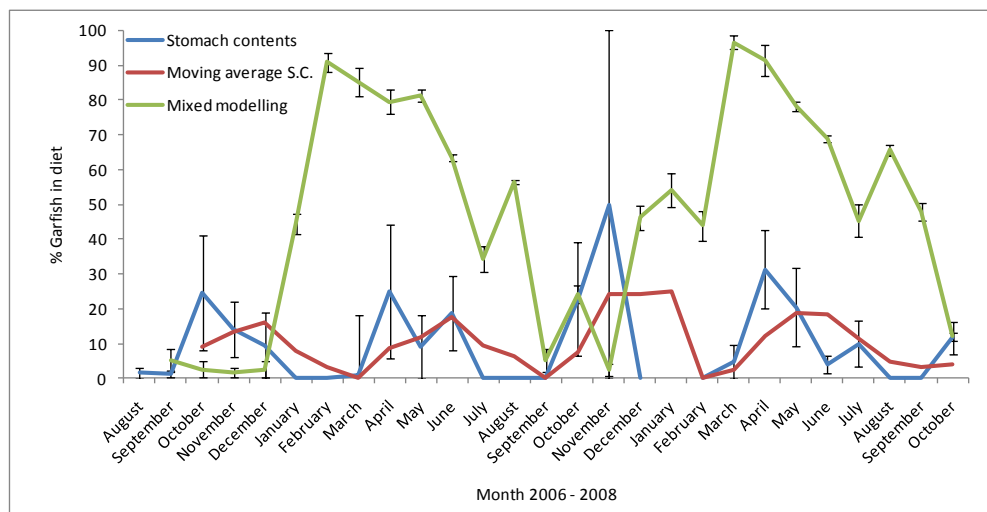


Figure 6b

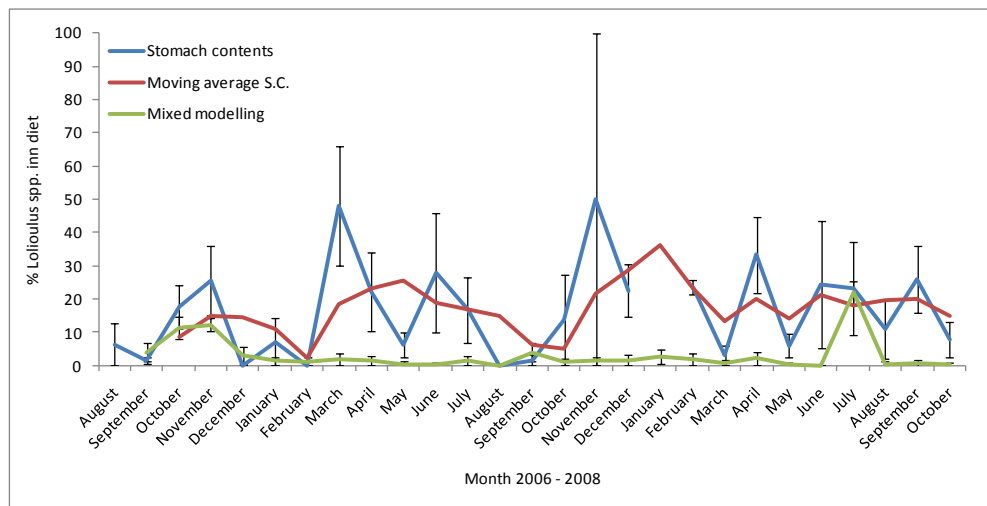


Figure 6c

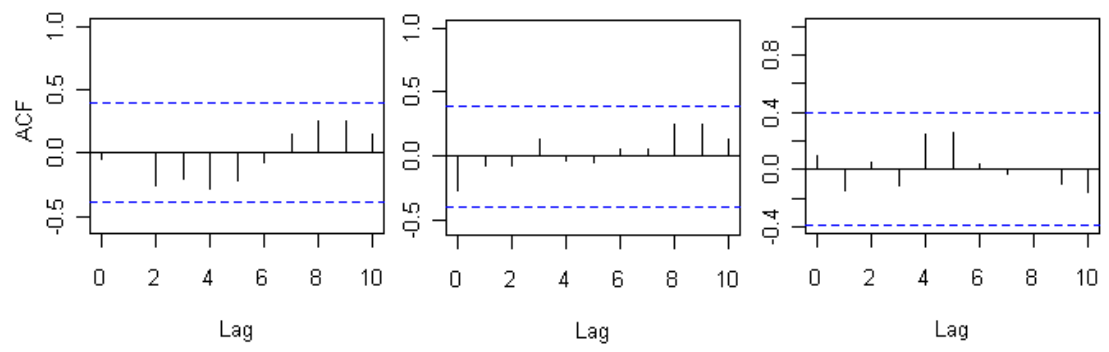


Figure 7

Chapter 5: Factors influencing the timing and success of breeding at a little penguin colony within a large bay

Declaration for Thesis Chapter 5

In the case of chapter 5, contributions to the work involved the following:

Name	% contribution	Nature of contribution
T.J. Preston	90%	Conception, execution, statistical analysis and writing
A. Chiaradia	5%	Advice, interpretation and writing assistance
R.D. Reina	5%	Advice, interpretation and writing assistance

Declaration by co-authors

The undersigned hereby certify that:

- (1) they meet the criteria for authorship in that they have participated in the conception, execution, or interpretation, of at least that part of the publication in their field of expertise;
- (2) they take public responsibility for their part of the publication, except for the responsible author who accepts overall responsibility for the publication;
- (3) there are no other authors of the publication according to these criteria;
- (4) potential conflicts of interest have been disclosed to (a) granting bodies, (b) the editor or publisher of journals or other publications, and (c) the head of the responsible academic unit; and
- (5) the original data are stored at the following location(s) and will be held for at least five years from the date indicated below:

Location(s)	School of Biological Sciences, Clayton Campus, Monash University	
Signature 1		31/08/10
Signature 2		27/08/10
Signature 3		30/08/10

Abstract

Inter-annual variation in the timing and success of breeding in many species is tightly coupled with environmental cues and prey availability. Such factors are often influenced by both localised environmental changes and large scale perturbations. Understanding how species respond to environmental parameters and prey availability can help us predict how populations will cope in the face of climate change and equip us to better manage their populations.

Here I studied the phenology and reproductive success of a colony of little penguins (*Endiaptula minor*) that live in a large marine embayment, from 2006-2008. As the bay they occur in has little influence from oceanic currents, I compared the reproductive success with local environmental parameters of sea-surface temperature, ambient temperature and rainfall, together with their diet over this period.

Breeding success was considered poor for little penguins in 2006 and 2007, but average in 2008. The number of second broods was highest in 2006, which had the poorest fledging rates from first breeding attempts. All years of the study were conducted in a drought, where rainfall in the catchment area was lower than the long-term average.

An earlier mean egg-laying date was coupled with greater reproductive success, but not as a result of increased double brooding. The penguins switch from Australian anchovy (*Engraulis australis*) to southern garfish (*Hyporhamphus melanochir*), a species with a greater energy, protein and fat content, during chick-rearing, thus the success of the broods may depend on timing chick fledging with southern garfish availability. Low breeding success at this colony corresponded with years of drought and high temperature, but was not related to sea-surface temperature. It is possible that this colony living in an embayment is more sensitive to terrestrial influences than changes in the marine environment.

Introduction

Inter-annual variation in environmental conditions is known to influence the timing and success of reproductive efforts in seabirds, most commonly through indirect means of affecting prey availability and distribution (Becker et al., 2007b, Ito et al., 2009). The phenology of many species is thought to be initiated by environmental cues that signal the beginning of a highly productive period which will match the individual and offspring energetic requirements (Weimerskirch et al., 2001, Shultz et al., 2009). Reproductively failure is the likely result when these highly energetic life cycle phases are mismatched with ecosystem productivity (e.g. Bertram et al., 2009). Understanding the effect of fluctuating environmental variables is important to predicting changes in population viability, such as responses to climate change (Edwards and Richardson, 2004, Votier et al., 2009).

Despite the flexible breeding strategies exhibited by many seabirds (Chiaradia and Nisbet, 2006, Shultz et al., 2009), as long-lived animals they will ultimately abandon breeding attempts in poor seasons where individual survival is at risk, in order to preserve their future reproductive potential (Weimerskirch et al., 2001). Seabirds are central place foragers during breeding and the cues they respond to reflect their foraging range. Small-scale foragers like rhinoceros auklets (*Cerorhinca monocerata*) are influenced by localised conditions, such as sea-surface temperature (Takahashi et al., 2001), but highly dispersive species like the black-legged kittiwake (*Rissa tridactyla*) may be influenced by large scale environmental cues, such as global oscillations (Frederiksen et al., 2004). Even within species there is often a broad range of timing and success of reproductive efforts across their distribution (Wilson and Martin, 2010). Additionally, population size is another factor that has been linked with reproductive success at seabird colonies (Votier et al., 2009), where intra-specific competition limits the locally available resources.

Here I investigate the phenology and reproductive success of a small little penguin (*Eudyptula minor*) colony with a history of high reproductive success and a growing population (Cullen et al., 1996, Priddel et al., 2008). Like other seabirds, reproductive success in little penguins varies across their distribution (Fortescue, 1999) and between colonies of different sizes (Dann and Norman, 2006). The onset and success of reproduction in little penguins has been linked with sea-surface temperature (SST) at several little penguin colonies, but often in contrasting ways (Wooller et al., 1991, Fraser and Lalas, 2004, Cullen et al., 2009). The colonies studied throughout the species range from Western Australia to New Zealand are subject to major oceanic currents and/or El Niño Southern Oscillation, which are thought to effect little penguin reproduction through influences on prey at the local ecosystem level (Cullen et al., 2009). However, it is still not fully understood whether the increased success in some years is attributable to a longer breeding season that allows for double brooding or because better quality prey is influenced by SST (Cullen et al., 2009).

While little penguins from many colonies throughout their distribution are influenced by oceanic currents and oscillations, the penguins from St Kilda, Victoria, in this study reside in a bay that has only small exchanges with the sea (Harris et al., 1996). Within shallow (<25 m) Port Phillip bay, SST reaches cooler temperatures in winter and higher temperatures in summer than connecting Bass Strait (Harris et al., 1996). Additionally, the northern area of the bay where this colony of penguins forage (Preston et al., 2010) is influenced by nutrient inputs from the Yarra River (Harris et al., 1996), thus rainfall in the catchment area of Melbourne is a potentially important localised influence on this marine ecosystem. Hence, this colony of penguins are year-round inshore foragers and potentially respond to a different set of environmental conditions that are much more localised than those faced by other little penguin colonies. Here I investigate the timing and success of

reproductive efforts at the St Kilda little penguin colony from 2006-2008 in tangent with their diet and localised environmental parameters of SST, ambient temperature and rainfall.

Methods

Study site

The St Kilda penguin colony has a population estimated at between 800-1000 individuals (Fig. 1, Z. Hogg, *unpublished data*) and is located 5 km from the city of Melbourne, Australia (37° 51' S, 144° 57' E). The penguin foraging area is limited to within ~13 km from their colony (Preston et al., 2010), located in the north of Port Phillip bay near the mouth of the Yarra River (Fig. 2).

Breeding success

A sub-set of 20 nests were checked for reproductive success three times per week during the 2006/07 and 2007/08 breeding seasons, and once per week during 2008/09 (Reilly and Cullen, 1981, Chiaradia and Nisbet, 2006). Penguins within these nests were identified by PIT tags or flipper bands and chicks were painted with different coloured food dye until they were old enough to be injected with a PIT tag. Chicks were measured with a spring balance to the nearest 10 g at each visit. Chicks were assumed to have fledged if they were last seen alive at least six weeks after hatching. Success of the breeding season is based on the number of chicks fledged per pair (CPP) using the categories defined by Chiaradia *et al.* (2003) where ≤ 0.7 CPP is low, $>0.7-\leq 1.2$ CPP is average and >1.2 CPP is high.

Diet

Data on adult penguin blood stable isotope values are from chapter 4, with the addition of chick blood samples that were collected at the guard (first 2 weeks after hatching) and post-guard (from the end of the guard stage until fledging) stages (6 chicks at each stage in the 2006 and 2007 breeding seasons). All collection, sample analysis and mixed modelling

methods are the same as those described for the adults in Chapter 4. Adult blood stable isotope values analysed here are those collected during the breeding season (approximately September –January) corresponding with the penguin breeding stages of pre-laying, incubation, guard.

Sea-surface temperature, ambient temperature and rainfall

Daily figures (averaged composite over the previous 6 days) of sea-surface temperature (SST) in the north of Port Phillip bay for 2001 – 2009 determined from satellite images at a 6 x 6 km resolution (CSIRO Marine and Atmospheric Research, data obtained from A. Watkins) were used to provide an average monthly SST for the penguins foraging area. Mean monthly temperatures across the year were pooled to compare anomalies in the three years of the study compared with the 9 year average for the same period. Additional comparisons were conducted for spring (September-November), as this corresponds with the time that Australian anchovies are thought to migrate into Port Phillip bay (Parry and Stokie, 2008a) and coincides with their appearance in the penguin diet (Chapter 4). Monthly rainfall and ambient temperature values for 2006, 2007 and 2008 were compared with each other and the long-term average for Melbourne (averaged from 1855-2010 data accessed from www.bom.gov.au 19/7/10 and 3/1/11) using paired t-tests. Yearly and spring rainfall figures were also plotted against the long-term average rainfall data.

Statistical analysis

Statistical analysis was conducted in SYSTAT version 10 (SPSS) and R version 2.9.1 (R Development Core Team, 2009). The statistical threshold was set at $P < 0.05$ and results are presented as mean $\pm$ SE.

The breeding parameters of mean laying date, chicks fledged per pair and peak chick weight were compared between the three breeding seasons using ANOVA and Tukeys HSD post-hoc test.

Results

Breeding success

Breeding success at St Kilda was considered poor in 2006 and 2007, but average in 2008 (Table 1). The success of first clutches in 2006 was low and the overall chick fledging rate was boosted by a higher number of second broods than in 2007. Although all second attempts were successful in 2008 and the overall success was considered average, the number of chicks fledged per pair for this year did not differ significantly from the previous 2 years ($F_{(2,72)}=0.54$, $p=0.59$).

The mean date of egg-laying was earliest in 2008, followed by 2007 then 2006 (Table 1). Peak chick weight was greatest in 2008, followed by 2007 and 2006, but there were no significant differences between any of the three years for peak chick weight ($F_{(2,34)}=1.31$, $p=0.28$) or mean laying date ($F_{(2,67)}=1.03$, $p=0.36$).

Diet

Estimates of the diet consumed by the penguins at the various breeding stages are presented in Figure 3. Due to the lag between consumption and stable isotope change in the blood, guard chick diet is a reflection of that from the pre-laying period, which was similar in both years. Post-guard chicks reflect the diet consumed during the late adult guard to early post-guard stage, and the chick diet in both years was intermediate between the adult diet at these stages.

Sea-surface temperature, ambient temperature and rainfall

Average SST was observed for 2008, but 2006 was characterised by lower than average SST anomalies, while 2007 was higher than average (Fig. 4). The spring anomalies were similar to the yearly ones in all cases except 2006 which recorded higher than average spring SST. Average maximum monthly ambient temperature was significantly higher in each year of

the study than the long-term average (Fig. 5, 2006 paired $t_{(11)}=3.0$, $p=0.01$, 2007 paired $t_{(11)}=7.3$, $p<0.01$, 2008 paired $t_{(11)}=2.8$, $p=0.02$), but not significantly different between the years (06/07 paired $t_{(11)}=1.9$, $p=0.07$, 06/08 paired $t_{(11)}=0.12$, $p=0.91$, 07/08 paired $t_{(11)}=-1.6$, $p=0.13$). All years of the study recorded significantly less monthly rainfall than the long-term average in Melbourne (Fig. 6, 2006 paired $t_{(11)}=-2.4$, $p=0.03$; 2007 paired $t_{(11)}=-2.7$, $p=0.02$; 2008 paired $t_{(11)}=-2.4$, $p=0.03$). Between each of the years there were no significant differences (06/07 paired $t_{(11)}=-0.08$, $p=0.93$; 06/08 paired $t_{(11)}=-0.09$, $p=0.93$; 07/08 paired $t_{(11)}=-0.02$, $p=0.99$).

Discussion

The low rates of reproductive success measured during this study were not expected based on the previous reports of high fledging success rates at St Kilda (Cullen et al., 1996). There was a corresponding decline in the estimated population during the study period, from a peak of 1025 in 2005, down to 821 in 2006, 854 in 2007 and 789 in 2008. However, these population estimates are based on the number of reproductive sites and hence reproductive effort in a year, rather than recapture rates of individuals. As the reproductive effort is the basis of the population estimate, I have calculated the long-term and annual rate of reproductive effort for this colony based on volunteer collected data (Cullen and Blake, 2001, Z. Hogg, *unpublished data*). From 1987-2009, the reproductive effort increased by $3.7 \pm 1.7\%$ (mean $\pm$ s.e.) per year. However, during my study it fell to -4.3% in 2006, 0.8% in 2007 and -1.6% 2008, based on the previous years effort. Thus, my study was conducted during a prolonged period of below-average reproductive effort at this colony and the low rate of reproductive success is not an artefact of the sampling regime, where only small sample sizes could be obtained due to the difficulty of following the same individuals over the course of multiple breeding seasons at St Kilda.

The higher rate of chicks fledged per pair and peak chick weight corresponded with an earlier mean egg-laying date in 2008. This supports the findings of several other studies that have also found earlier breeding to be more successful in this species (Reilly and Cullen, 1981, Chiaradia and Kerry, 1999, Cullen et al., 2009). However, the number of second broods was greatest in 2006 and amongst the highest reported for little penguins (Priddel et al., 2008). This high rate of second broods followed on from a very low number of chicks fledged from the first attempt and the latest mean-egg laying date from the three year studied, which contradicts other studies that have found second broods to indicate good foraging conditions (Stahel and Gales, 1987, Priddel et al., 2008) or an early start to the breeding season (Cullen et al., 2009). Hence, my study supports the notion of Fraser and Lalas (2004) that double brooding may be a mechanism used in two ways by little penguins, to boost fledging rates when initial breeding attempts are largely unsuccessful (e.g. this study), or to take advantage of abundant resources in productive years (Reilly and Cullen, 1981, Fortescue, 1999).

During the two years of continuous dietary study (Chapter 4) there was a distinct trend toward increased consumption of the Australian anchovy *Engraulis australis* during the pre-breeding and early breeding seasons, with the southern garfish *Hyporhamphus melanochir* increasing during the period of chick-rearing and the non-breeding season. Adult penguins were generally feeding their chicks on the same prey as themselves, but the diet switched to lower trophic level southern garfish (Chapter 4) during the chick rearing part of the breeding season, which is represented by the post-guard stage and month following, due to the 3-4 week integration of stable isotopes into the blood (Hobson and Clark, 1993).

Given that the 1+ year anchovies that the penguins feed on (Chapter 4) are thought to be in the northern area of the bay until early autumn (Blackburn, 1950), this suggests that the penguins may selectively feed on southern garfish, as the diet moves toward the lower trophic level prey as early as December to coincide with the periods of chick feeding.

However, without concurrent fish distribution data this cannot be confirmed, and the penguins' diet could reflect an absence or reduction in Australian anchovy during the chick-rearing periods for the years of this study. Concurrent study of the abundance and distribution of prey within the penguins foraging area together with study of the penguins reproductive success is required to confirm whether the penguins are selectively foraging or not, as several studies have shown that the relationship between seabird diet and prey availability is not simply linear (Montevecchi et al., 1988, Cairns, 1992, Piatt et al., 2007). Different seabird species have been recorded as feeding chicks on both low (Browne et al., 2010) and high (Forero et al., 2002, Ito et al., 2009) trophic level prey, with the reasons behind shifts related to prey availability (e.g. Ito et al., 2009) and/or energetic value (e.g. Forero et al., 2002). Bunce (2001) reported that southern garfish from Port Phillip bay were slightly higher in protein and energy than Australian anchovy, and contained almost double the amount of crude fat. Chick diets high in protein and fat have been associated with higher growth in seabirds (Boersma and Parrish, 1998) and the continuation of this higher quality diet in the non-breeding season may also help adults during their moult and recovery that occurs after breeding has finished. Thus, the patterns of dietary shift in the penguins at St Kilda are probably a combination of prey availability when the anchovies reach their peak during spring (Blackburn, 1950), and prey selection for the higher quality southern garfish during important growth periods for both chicks and adults. The low fledging success of first attempts in 2006 coincided with the increased rates of squid consumption during this season, which indicates that these foraging attempts were mismatched with the availability of prey species containing more energy.

As reproductive success was similarly low across the three years of this study, SST, ambient temperature and rainfall should also show consistent patterns if they are influencing factors on the timing and success of breeding at this colony. This was the case for rainfall and ambient temperature, where this study coincided with drought conditions that meant all

years were hotter and received significantly less rainfall than average. Therefore, in this respect the bay environment is affected by large-scale climate fluctuations, and the effects of these perturbations are centred on the small foraging area of the little penguins that coincides with the mouth of the Yarra River. Port Phillip bay is considered nitrogen limited, the major sources being the Yarra River and the sewage treatment plant at Werribee (Harris et al., 1996). In years of below average rainfall, it is likely that the penguins foraging area adjacent to the Yarra River experiences lower nutrient inputs and this could result in lower primary productivity and subsequently zooplankton, which is associated with Australian anchovy spawning (Jenkins, 1986). Ambient temperatures higher than the long-term average in all years of the study may have affected the penguins breeding attempts, with heat stress beginning at temperatures above 30°C (Stahel and Nicol, 1982). The lowest rates of chicks fledged occurred in 2007 when the temperature was also highest. However, unlike rainfall and ambient temperature, the pattern of SST anomalies across the years was not consistent. Close to average SST in the penguins foraging area was experienced during spring and throughout 2008, but above average SST characterised 2007, while 2006 showed disparities between the SST throughout the year and during spring. The variations in SST do not match with the slight differences in phenology or reproductive success observed at the penguin colony during these years. If little penguin breeding success is an indicator of prey availability, then the results of this study suggest that prey movements within the bay may not be as tightly coupled with local SST as has been observed elsewhere in oceanic environments (Weimerskirch et al., 2001, Ito et al., 2009). However, a study of little penguin colonies throughout Victoria suggested that nesting sites, not food were the limiting factor in population growth at small little penguin colonies (Dann and Norman, 2006). Observation of penguin nest use suggests that St Kilda penguins are not constrained by nest availability though, with a high rate of nest swapping and unused nests at any one time (T.P., *personal observation*). Thus, the colony

at St Kilda may still have the potential to grow at this stage, but inter-annual variations in breeding success and subsequent recruitment are likely due to fluctuating prey availability rather than nest availability, which does not change between years.

Spawning of the Australian anchovy has been associated with high SST levels (Dimmlich et al., 2004), but this does not necessarily represent the factors controlling the movements of the 1+ year anchovies consumed by the penguins from St Kilda. These anchovies are known to be conspicuous in the penguins foraging area during the warmer months (Blackburn, 1950), but their movements during winter are largely unknown (Parry and Stokie, 2008a). However, only mature anchovies of at least 2+ are thought to migrate out of the bay (Parry and Stokie, 2008a), therefore the anchovies taken by the penguins are bay residents (Blackburn, 1950) and not directly affected by oceanic currents. Seasonal movements and life history of the Australian anchovy are complex and need more research (Blackburn, 1950, Parry and Stokie, 2008a) to understand the environmental factors controlling their distribution. Likewise, little information has been published on the movements of the southern garfish in relation to environmental parameters, aside to say that recruitment is probably influenced by such (Fowler et al., 2008). Despite this species being commercially harvested in Port Phillip (Department of Primary Industries, 2006), it's movements within the bay are unknown, but it has been associated with seagrass beds (Klumpp and Nichols, 1983). This study confirms the presence of immature southern garfish (Chapter 4) in the northern areas of Port Phillip predominantly during late summer and autumn, but little occurs in the penguin diet during spring. The southern garfish diet of seagrass and crustaceans (Klumpp and Nichols, 1983) is likely to be closely coupled with production (driven by nutrients washed into the bay from local rainfall), as is the zooplankton based diet of anchovy (Jenkins, 1986). Thus, other unexamined environmental and/or biological parameters are probably playing a significant role in determining prey distribution in the inshore environment of the penguins foraging area.

Inter-annual fluctuations in breeding success are normal for little penguins (Priddel et al., 2008), and the three years of low reproductive rates recorded during this study are not dissimilar to periods of poor breeding success reported for other colonies (Fortescue, 1999). However, without comparative data on diet and environmental parameters from years of contrasting reproductive success it is difficult to identify what factors influence the timing and success of reproduction at St Kilda (Weimerskirch et al., 2001). Thus, more research is needed at this colony during years of average and high reproductive success to compare with the results found during this study. Ongoing research into the penguin colony found that the rate of reproductive success reached a rate of 1 chick per pair in 2009 (considered average for little penguins, Dann and Norman, 2006), but at least one year of high reproductive success would also be desirable to compare conditions between contrasting years.

Nonetheless, I have confirmed through my research that earlier mean egg-laying dates can correspond with greater reproductive success, but the driver is more likely high quality prey rather than greater rates of double brooding. The factors controlling the prey availability remain unknown, but as the penguins from this colony predominantly consume immature fish, the fish are likely to remain in the bay throughout the year and not be directly influenced by oceanic currents. Whether local rainfall, ambient temperature and SST influence prey and act as a cue for the penguins to start breeding remains unknown. Given the high inter-annual fluctuations in local SST observed during the three years of this study, it appears that this colony may be influenced more strongly by terrestrial factors than changes in the marine environment. The relationships between environmental parameters and prey movements need to be resolved before any predictions on the long-term effects of climate change can be made for this colony, but the location of the colony in an area that is affected by rainfall and drought means that even with a small foraging range this colony of little penguins may be influenced by large-scale environmental fluctuations.

Figures and tables

Figure 1: Estimated penguin population at St Kilda based on the number of breeding sites found per year over 20 years from 1988-2008.

Figure 2: Location of little penguin colony at St Kilda within Port Phillip bay, which joins with Bass Strait. Major sources of nitrogen into the bay come from the Yarra River and Werribee sewage treatment plant.

Figure 3: Mean mixing model estimates of diet from stable isotope values of whole blood collected from adult penguins and chicks at different breeding stages in 2006 and 2007.

Figure 4: SST anomalies derived from monthly mean temperatures for the whole year (blue) and spring (red) in the north of Port Phillip.

Figure 5: Ambient temperature anomalies (from Melbourne long term average 1855-2010) derived from monthly mean temperatures for the whole year (blue) and spring (red).

Figure 6: Yearly (blue) and spring (red) rainfall in Melbourne for 2006, 2007, 2008 compared with the long-term average.

Table 1: Breeding parameters measured at St Kilda penguin colony over three breeding seasons. Success rates are based on the percentage of chicks fledged from the number of breeding attempts.

<u>Parameter</u>	<u>2006</u>	<u>2007</u>	<u>2008</u>
Egg-lay date	5 Oct	20 Sep	15 Sep
(mean, range)	(3 Jul – 6 Dec)	(29 Jun – 7 Dec)	(30 Apr – 25 Nov)
Mean # attempts	1.45	1.15	1.15
1st attempt success	0.40	0.60	0.60
2nd attempt success	0.55	0.00	1.00
Chicks per pair	0.65±0.04	0.60±0.04	0.75±0.04
Peak chick weight (g)	1070±30	1120±50	1160±40

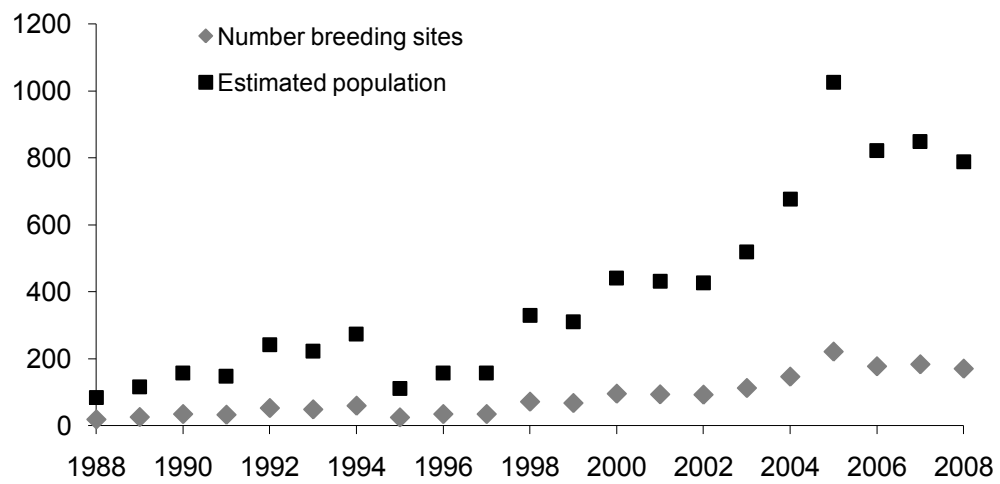


Figure 1

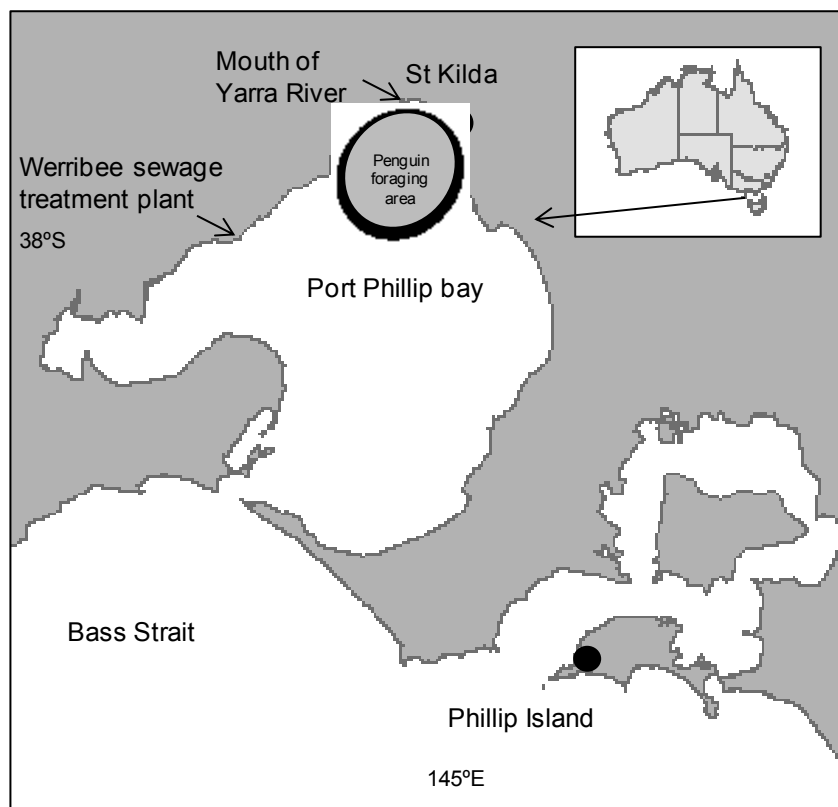


Figure 2

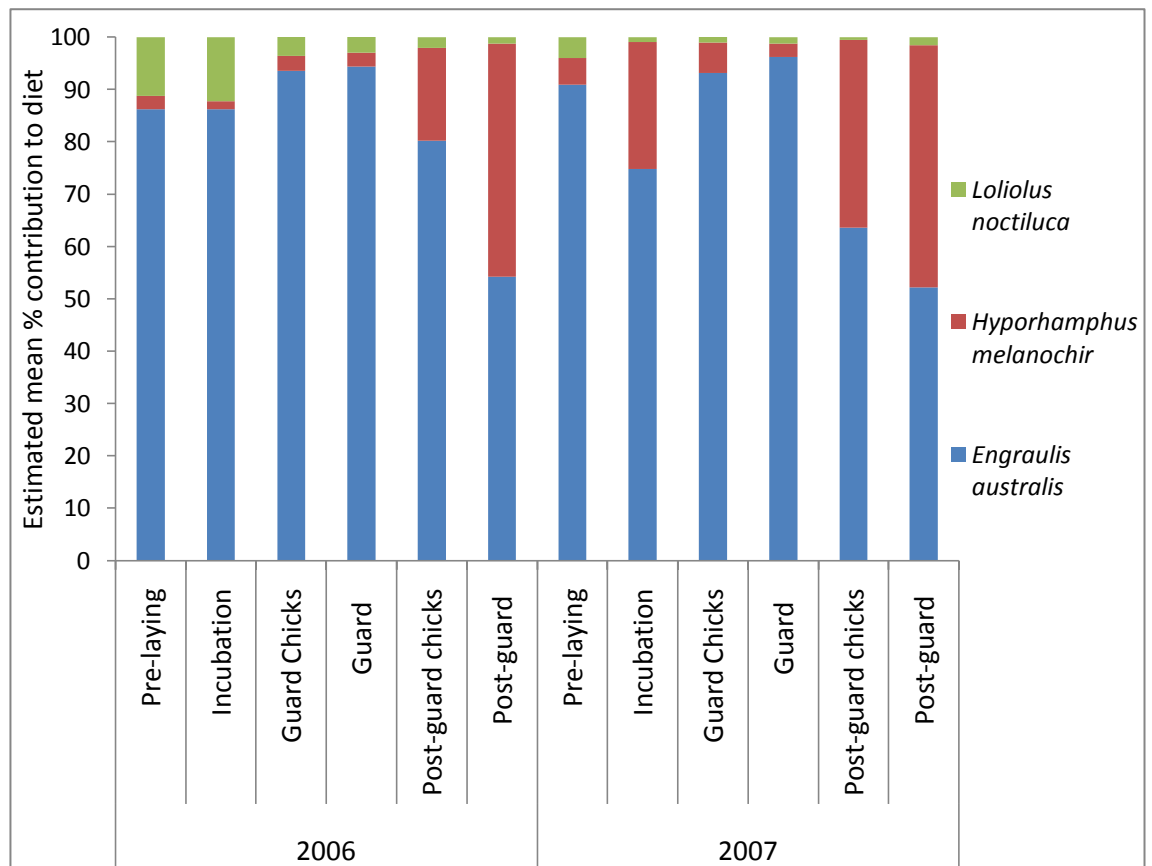


Figure 3

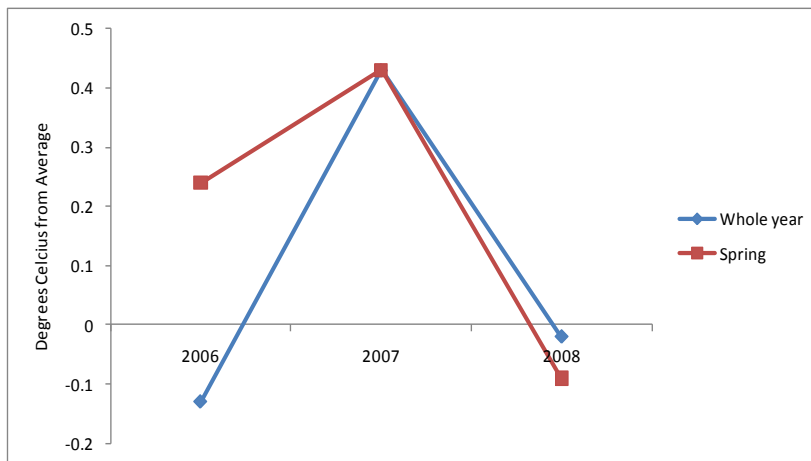


Figure 4

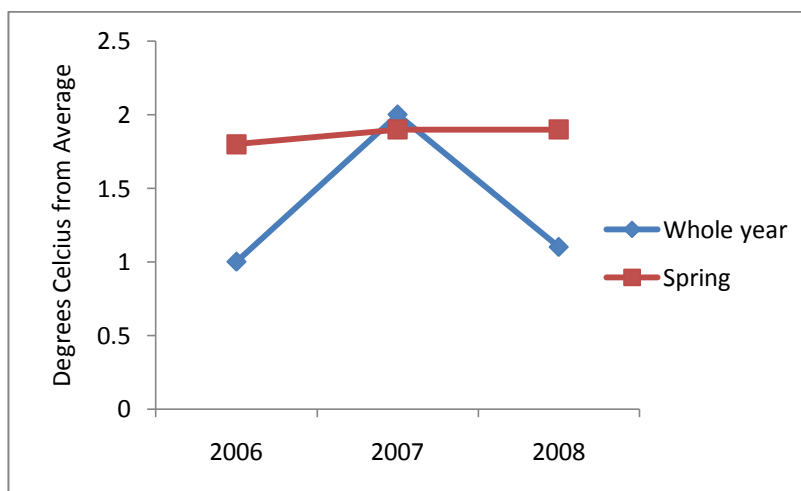


Figure 5

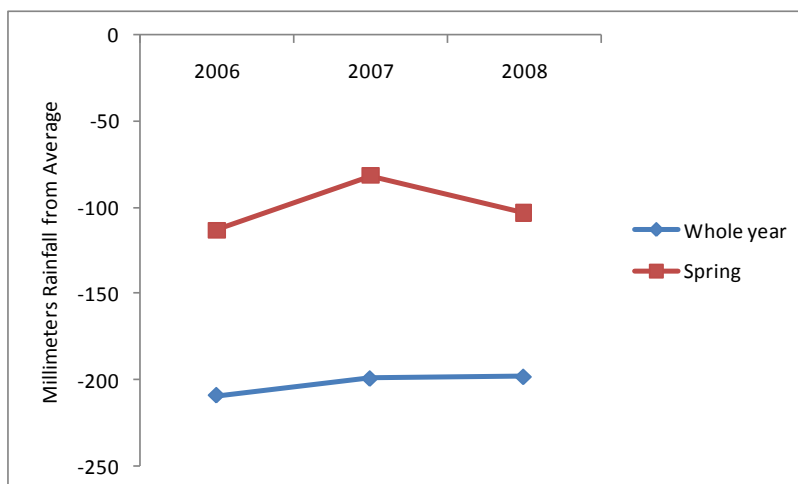


Figure 6

Chapter 6: General discussion

6.1 Findings of the study

Here I provide a brief summary of the main findings already discussed in detail in the previous chapters. Environmental conditions were characterised by slightly lower than average local SST during 2006 and 2008, and slightly higher than average SST in 2007 (Chapter 5). All years of the study were affected by drought conditions, with higher than average ambient temperatures and lower than average rainfalls in Melbourne bringing less fresh water and nutrients to the north of the bay.

Foraging patterns of the penguins were consistent over the three breeding seasons (Chapters 2 and 3), with this colony of little penguins having a foraging area of ~1500 ha and travelling a daily horizontal distance of ~34 km. The number of dives performed per day was ~800 to a mean dive depth of ~8 m. Through use of the mini-GPS and TDR devices combined, I was able to confirm that the penguins dived most commonly to depths of ≤ 10 m regardless of the depth of water they were in. The number of dives in an area was proportional to the amount of time spent in that area, with penguins spending the majority of their time areas 15-20 m deep. Penguins preference for water of 15-20 m depth was also apparent from the time they spent in the shipping channels. Although these channels only accounted for ~3% of the foraging area, the penguins spent >11% of their time foraging there.

Monthly dietary sampling across two years recorded at least 15 different species in the stomach contents of penguins, but the most commonly consumed prey items were Australian anchovy (*Engraulis australis*), southern garfish (*Hyporhamphus melanochir*) and luminous bay squid (*Loliolus noctiluca*), respectively (Chapter 4). Significant differences were found between stomach contents and stable isotope mixing models when estimating the proportions of these prey items in the diet each month. Stable isotopes were found to be a

more sensitive and appropriate tool to detect change in the diet over the long time frame of this study, but stomach contents were useful for identifying prey species and attributes.

The diet was dominated by Australian anchovy during pre-breeding and early stages of the breeding season, but the amount of southern garfish increased during chick feeding and non-breeding periods. All Australian anchovy consumed were < 3 years old and all southern garfish taken by penguins were immature.

Over the three breeding seasons studied I found reproductive success to be considered low in the first two years, and average in the third (Chapter 5). None of the reproductive parameters measured in each year differed significantly, but breeding started earlier and was slightly more successful in 2008/09 than the previous two years. Second broods were higher in 2006/07 which had the lowest rate of chick fledging success from first broods.

This study employed conventional and contemporary methods for the foraging and dietary studies, the results of which were compared to assess the usefulness of each technique to other researchers. Methods used to describe foraging behaviour were specific to small scale inshore foragers, an area of biologging science that perhaps does not get as much attention as large-scale foraging, but is applicable to many species (as discussed in Chapter 3). The use of stable isotopes and stomach contents continuously over a two-year period allowed this study to not only describe the penguin's diet, but provide useful comparative information on the two commonly employed dietary methods (as outlined in Chapter 4).

6.2 Success of the colony

Despite these years of low reproductive success, the rate of fledging success (represented as the success rate of each breeding attempt in Chapter 5) at St Kilda in the years of this study was still often better than that reported for little penguin colonies at Montague Island, Bruny Island and Phillip Island in Fortescue (1999). This colony appears to benefit from the inshore bay environment where they cover comparatively small horizontal distances (Hoskins et al., 2008) and avoid deep dives that require long recovery times (Ropert-

Coudert et al., 2006a). Even during the years of low breeding success they appear to have a food source available in close proximity to the colony and do not need to diversify their diet (Chiaradia et al., 2003). This is probably also due in part to their small population size that limits competition for food within the population (Dann and Norman, 2006) and the restriction of foraging to the north of Port Phillip is probably a mechanism to avoid intra-specific competition with the penguins from Phillip Island that commonly feed in the southern and middle sections of the bay (Collins et al., 1999).

As examined in Chapter 5, the exact influences on reproductive success at St Kilda are difficult to assign as limited comparative data exists on diet and foraging behaviour during years of good or average reproductive success at this colony. Environmental parameters have been associated with little penguin reproductive success at other colonies (Cullen et al., 2009), but here it is unclear whether the local SST, ambient temperature and rainfall (which delivers nutrients through the Yarra River, Harris et al., 1996) has a long-term influence on reproductive success. Studies over longer time frames that incorporate years of average and/or good reproductive success, together with research into the environmental parameters influencing southern garfish and Australian anchovy movements are needed to resolve this relationship. However, it appears that prey stocks are less sensitive to environmental fluctuations within the bay than has been demonstrated for species in oceanic environments (Ito et al., 2009, Shultz et al., 2009).

Additionally, St Kilda penguin colony has been referred to as a mainland colony (Priddel et al., 2008), but in many ways the pier (approximately 450 m long) acts to prevent access to the colony by many introduced predators and thus the colony is more like an island. This has resulted in a much lower adult mortality rate from foxes, cats and dogs than experienced at other colonies (Dann, 1992b, Stevenson and Woehler, 2007, Priddel et al., 2008), which is a contributing factor to the success here.

6.3 Impact of the urban environment

The St Kilda colony of penguins is no doubt influenced by their urban habitat, from the constructed breakwater that they nest on to the dredged shipping channel that they forage in. Part of the colony that is still open to visitor access has a lower nest abundance than the protected section (Giling et al., 2008), indicating some impact of human presence. All of my study was conducted on penguins captured within the protected area though, where human impacts on breeding should be lowest.

Despite the foraging area of the penguins being within a busy shipping area, the boat-strike rate appears to be very low based on long-term recapture records of individual penguins and number of reported injuries. This is probably attributable to the amount of large commercial ships that operate in the area, which restricts the use of recreational boating and hence propeller cuts. However, an observed increase in the use of recreational jet-skis in the area (I. Preston, *personal observation*) has the potential to affect penguins as they congregate near and approach the breakwater of an evening.

The penguins foraging area also overlaps with commercial anchovy fisheries, but the number of operations has diminished greatly over time, from approximately 30 in the early 1900's (Blackburn, 1950) to less than 5 today. Capture of penguins within purse-seine nets is possible, but the main operator in the area is aware of the penguin colony and uses nets that the penguins are able to roll out of (P. McAdam, *personal communication*), thus reducing mortality rates from net entanglement. Unfortunately entanglement of the penguins in fishing line and litter either left on the breakwater or washed into the bay through stormwater is common, and probably the greatest threat to individual mortality. The abundance of natural predators (i.e. sharks and New Zealand fur seals) appears to be quite low in the northern areas of Port Phillip, with shark populations centred around the deeper sections to the south of the penguins foraging area (Parry et al., 1995) and the bay

dominated by Australian fur seals (Scarparci et al., 2005), which have not been reported to consume little penguins (Hume et al., 2004, Page et al., 2005).

By far the biggest influence of the urban environment on the penguins at sea is the shipping channels. Although they only account for around 3% of the penguins foraging area, the penguins spent about 11% of their time at sea foraging within them. This indicates that these areas may either harbour a higher proportion of fish, or the penguins prefer to use the unique bathymetry of the channels to trap fish.

The penguin's use of the shipping channels continued after their dredging in 2008, but it is not known whether the dredging had any direct impact on the penguins at the time through increased turbidity or other interactions. Based on the penguin's diet, it appears that the dredging did not have a significant impact upon their prey as the composition and size of prey were similar between years. Reproductive success was low in 2008 following dredging, but not significantly different from the two years prior. Ongoing study of the colony found that the reproductive success returned to higher levels in 2009 (T. Preston and Z. Hogg, *unpublished data*), indicating no short-medium term impact of the dredging on breeding. However, long-term effects of dredging may still be a problem for the penguins through bioaccumulation (Choong et al., 2007), as much of the sediment that was dredged was contaminated with toxins that had accumulated from past industrial practices. These contaminated sediments were dumped in a spoil ground that occurs within the penguins foraging area and were capped with sand, which is designed to contain the contaminants for ~30 years.

6.4 Broader research applications

Little penguins are not listed as a threatened species at the national level in Australia or New Zealand, but many of their populations are considered to be threatened or extinct (Stevenson and Woehler, 2007, Priddel et al., 2008). They are sensitive to both anthropogenic activity and perturbations in the environment (Mickelson et al., 1992,

Ropert-Coudert et al., 2009), and as such the reasons behind the success of the colony at St Kilda is of interest to managers at other little penguin colonies. It appears that much of the success of this colony is related to their mostly protected breeding area and the environment in which they forage, factors that are difficult or impossible to control and manage at other sites. The bay environment is unlike oceanic sites that are highly influenced by currents and stratification, and although management of fisheries may influence the abundance of prey for other sites, it will not control the distribution of that prey, which appears to be a key factor in the success of this colony.

This study provides an interesting example to urban ecologists of the way a native species can utilise both terrestrial and aquatic anthropogenic structures. Neither the breakwater nor the shipping channels were designed to provide habitat to penguins, but their location near a food source has made them suitable as such. Other examples of native animals exploiting human developments and activities in the terrestrial (e.g. peregrine falcons using tall buildings for nesting, Cade and Bird, 1990) and aquatic environments (e.g. green turtles staying in the area of warm water from a power plant during winter, Eguchi et al., 2010) do exist, but I am not aware of a population using both terrestrial and aquatic developments.

In future, the design of coastal developments may be considered in terms of their potential use as habitat, such as the many housing estates in greater Melbourne now featuring wetlands, one aspect of which is to provide habitat to native animals, including the endangered growling grass frog, *Litoria raniformis* (T.Preston, *personal observation*).

St Kilda little penguins are exceptional in terms of their ability to succeed in close proximity to human settlement, but they exemplify that if food stocks are available in the urban environment then some native populations will persist given that their habitat needs are met (in this case the breakwater) and disturbance, particularly during breeding, is kept to a minimum. Anthropogenic structures can be designed to be suitable breeding structures,

but access to foraging areas must also be available, something which can be difficult in terrestrial environs.

6.5 Implications for management of St Kilda penguin colony

My study shows that double brooding at St Kilda is not necessarily associated with good years of reproductive success. Additionally, little penguins can change nests and/or partners within a breeding season, therefore the number of nest sites (and reproductive effort) is not necessarily the best way to calculate population. Thus, estimates of reproductive success and population at this colony need review so that the state of the population can be more accurately determined each year and changes followed more closely. Ongoing drought, a symptom of climate change, may have an effect on the reproductive success at this colony, but further study into this relationship is required. Throughout this study the diet of the St Kilda penguins exhibited a high reliance on two immature prey stocks, Australian anchovy and southern garfish. Successful spawning from each of these species every year is necessary to support the consumption needs of the penguins. These requirements should be taken into consideration in the management of each of these prey stocks as alternative clupeoid species (e.g. sprat spp. and pilchard) only compose approximately 1% of the anchovy biomass in Port Phillip (Parry and Stokie, 2008a), and thus are not a reliable alternative.

Additionally, now that this colony's foraging area has been well established, any changes to activities within this area that could affect the penguins should be reviewed carefully by management authorities, such as Parks Victoria. Limits on the use of jet-skis in the vicinity of the penguins colony should exist, particularly during the period when penguins return to the colony. A recommended exclusion zone of 1 km around the colony from one hour prior to sunset each evening would be sufficient to ensure that the penguins were not disturbed or harmed by jet-skis.

6.6 Future research

The foraging area of the penguins at St Kilda is now well established, and so it is the changes that occur within that area which will determine the ongoing success of this colony. It would be advantageous to the management of this penguin colony to identify the patterns and causes of prey movement within the penguins foraging area. This will require detailed studies of Australian anchovy and southern garfish both inside the bay and moving between Port Phillip and Bass Strait. Additionally, further study into little penguin responses to prey availability may make this population useful in prey stock assessments within the bay.

Further study into the effect of diet on breeding success is also required at this colony, particularly information that examines the diet when rates of reproductive success are considered average and high. Data on the amount of food intake between years of differing reproductive rates would add to our understanding of factors controlling breeding success. The implementation of an automated penguin measuring system (APMS) would be the best way to indirectly monitor the amount of food delivered to chicks, but its installation at this site would be difficult due to the lack of a central landing location at this colony. Dietary analysis through feather stable isotopes offers another method that could be employed to monitor the penguins diet with minimal disturbance, but this would only reflect the diet of the penguins post-breeding as their feathers only grow during the moult period.

Another factor that was not considered for this study was the mortality rate and time after fledging that chicks return to the colony. Through exploration of the long-term data I have noted that approximately 30% of chicks identified before fledging return to the colony, which is similar to that recorded at Phillip Island (Dann and Cullen, 1990). However, most chicks return to St Kilda in the first year, sooner than generally recorded elsewhere (Reilly and Cullen, 1982, Priddel et al., 2008) and indicates that they probably do not leave Port

Phillip bay. Additionally, the recovery rate in the first twelve months is the lowest, and it appears to increase with penguin age. Thus, low mortality rates of adult penguins may also be a contributing factor to the success of this colony, but this work needs further detailed examination.

Although not the subject of this study, the large scale dredging that occurred in the bay during the period of field work involved the removal of contaminated sediment from within the penguins foraging area. Study into the contaminant levels within the penguin's tissues should be monitored over the course of several years to ensure that contaminants do not bioaccumulate to potentially fatal levels.

The continuation of the volunteer research is encouraged, as this will be the earliest indicator of any changes in the population stability at this colony. Adoption of a mark-recapture based method of calculating population size (such as program MARK), which is independent of breeding effort, is strongly recommended.

6.7 Conclusions

Little penguins from the St Kilda colony have a highly variable rate of breeding effort, but overall the colony has grown with a modest rate of increase in annual reproductive effort over time. Even during the years of low breeding effort and poor reproductive success that my study was conducted in, the penguins still successfully raised ~0.6 chicks per pair, which is higher than what many other little penguin colonies produce in years of low reproductive success (Fortescue, 1999). Much of the success of this population is due to the location of their colony, near food sources in a shallow bay that appears not to be subject to the high variability of prey distribution that occurs at many other little penguin colonies (Gales and Pemberton, 1990, Cullen et al., 1992). This colony has only established in this location because of the breakwater construction, establishment of a colony on the foreshore of this size would be almost impossible due to the lack of suitable nesting sites, predators and shifting sands that affect the area.

The results of this study suggest that the little penguins are highly reliant on two prey species, Australian anchovy and southern garfish, throughout the year. As long as these prey species are available within the north of Port Phillip I expect that the colony will continue to exist, but if either of these species diminishes it could have catastrophic results for this population. Little penguins are adaptable and will feed on other prey species (Chiaradia et al., 2003), but the availability and abundance of alternative prey within their foraging area appears to be minimal (Parry and Stokie, 2008a). Expansion of the St Kilda populations foraging area into the south of Port Phillip bay would mean intra-specific competition for resources with the penguins from Phillip Island. The long-term carrying capacity of this population will likely be determined by prey availability rather than nest sites, as there appears to be many potential nest sites on the breakwater that are not utilised and an extension to the breakwater that will provide further habitat is planned for the near future.

Adoption of my recommendations for ongoing research at this colony will help guide the management of the St Kilda penguin colony well into the future.

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