Demographic parameters, foraging and responses to environmental variation of little penguins (*Eudyptula minor*)

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Abstract

Long-term monitoring for the purpose of establishing demographic parameters is critical to the understanding of trends in animal populations. Demographic parameters vary annually via complex pathways that include variation in foraging behaviour driven by prey distribution and abundance and are further influenced by environmental variation. Long-term monitoring can be used to untangle the relative roles of natural variability and anthropogenic impacts such as climate change, in population change. The aim of the research presented in this thesis was to combine an investigation into the demographic parameters, foraging behaviour and relationships with environmental variations in an increasing population of little penguins (*Eudyptula minor*) at Oamaru, South Island, New Zealand.

Long-term data were collected at the Oamaru Blue Penguin Colony during 20 consecutive breeding seasons, 1993-2012. These data were analysed to quantify reproductive performance and survival rates of little penguins. Estimates obtained were amongst the highest reported for the species (breeding success: 1.89 mean chicks fledged per female annually). Median lay date, breeding success and the proportion of females double brooding were highly correlated, indicating that high breeding success was attributable to the regular occurrence of double brooding. The onset of egg laying was highly variable, occurring any time between early May and late September. Impacts from storms on the penguins and their responses to variation in sea surface temperature (SST) and marine productivity (represented by chlorophyll *a* concentrations) were examined. Median lay dates were delayed by 12 days with every decrease in chlorophyll by 0.1 (mg m^{-3}) during the January-April prior to breeding. Storms caused multiple impacts on the penguins, beginning with a drop in the number of penguins arriving ashore each evening. A drop in arrivals disrupted breeding and reduced chick growth. Rough seas and the re-suspension of sediment during storms likely affect the foraging abilities of little penguins, being visual foragers. Adult survival rates decreased with increasing storm intensity and decreasing chlorophyll. An increase in the frequency and intensity of storms is a likely consequence of global climate change, likely impacting the breeding and survival of little penguins at Oamaru. How variation in productivity will be affected by climate change, and subsequently affect little penguins, is unknown.

I studied foraging behaviour of the penguins over three consecutive breeding seasons, 2010-2012, using Global Positioning System and Time-Depth recording devices to establish foraging locations and distances, and diving behaviour. The penguins tended to travel northwards towards the Waitaki River mouth when at sea for more than a day. Foraging behaviour changed as the season progressed, coinciding with time of year rather than the stage of breeding. Dive depth decreased as the season progressed, suggesting that the penguins adjusted their foraging in response to changing prey abundance and distribution.

The penguins’ ability to vary foraging behaviour in response to a changing environment, and their proficiency at double brooding appear to be key factors driving their population increase at Oamaru. In contrast, the penguins cope poorly with storms which impact the population on multiple levels.

Acknowledgements

Firstly, I would like to recognise and give thanks to the many people that have been involved with the Oamaru Blue Penguin Colony at Oamaru. Before the commercial phase of penguin-watching was established there were very divided opinions on the occupancy of the former quarry by the penguins. At a borough council meeting, in 1985, the Mayor of Oamaru stated that the penguins were “trespassing in our quarry”. He went on to suggest that idea of the penguins nesting at the quarry becoming a tourist attraction was “ludicrous” (Oamaru Mail, 1985). Were it not for the insight and drive of many individuals and conservation groups he may well have been correct. Consistent provision of nesting habitat and protection from predators has helped the birds recover, and those involved should be proud of their contribution to the colony’s success. The consistent weekly monitoring, started in 1993 by Dave Houston, has been a very important asset to the colony management, and to our understanding of these birds.

The study would never have happened without Jason Gaskill’s vision for improving the research carried out at the colony. The first step in his vision was to have a PhD conducted at the colony and he was the driving force behind facilitating funding for the work. I am incredibly grateful to Jason for such an amazing opportunity, he has supported me every step of the way, through difficult times in the early days of data collections and later, during the equally challenging write-up. He also ensured I had assistance in the field, whenever I needed it, from employees at the colony. The project was fully funded by the Oamaru Blue Penguin Colony. I owe great thanks to the board of directors for agreeing to support the project, and for continuing to do so.

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Chapter 1 :

General Introduction

1.1 Background

Demographic parameters of animal populations vary annually via complex pathways that include variation in foraging behaviour driven by prey distribution and abundance, in turn influenced by climate (Weimerskirch 2001; Jenouvrier 2013). Monitoring of demographic parameters on a scale covering generations rather than breeding seasons helps determine the relative role of annual variability versus long-term trends, and also helps to identify rare events (Porzig et al. 2011). Results from long-term monitoring establish baseline data on demographic parameters, providing a yardstick by which to measure change and identify underlying mechanisms of change (Saracco et al. 2008). Given the growing threats to animal populations worldwide, the need for long-term monitoring data is greater than ever (Hilton-Taylor et al. 2009).

Global climate change is likely to have a major impact on animals in the future (Foden et al. 2009). Concerns about the effects of climate change on bird species have grown. For example, the International Union for the Conservation of Nature (IUCN) assessed the demographic parameters of 9856 threatened bird species and found that 35% were susceptible to climate change (Foden et al. 2009). Increasing our understanding of the impacts of global climate change is likely to be crucial for future conservation management. The predicted consequences of climate change are varied and far-reaching; from snow and ice melt and sea level rise, to increases in the frequency and intensity of extreme weather events (IPCC 2013). While physical indicators of climate change can be measured directly, effects on animal species are complex. In a recent review of threats to penguins, environmental variability and climate change were identified as potential threats to penguins in the future, however, it was acknowledged that it is difficult to gain direct evidence of the nature of impacts (Trathan et al. 2014). The magnitude and frequency of extreme climatic events may be more important for penguins than average climatic change (Boersma and Rebstock 2014; Lescroël et al. 2014).

There are 18 species of penguin (family Spheniscidae; IUCN 2013). With the exception of the Galápagos penguin (*Spheniscus mendiculus*) which straddles the equator, penguins are found exclusively in the southern hemisphere, and are concentrated in cooler waters (Brooke 2001). The abundances of 12 of the 18 species are decreasing, three are stable and three increasing (IUCN 2013). Current anthropogenic pressures on penguins causing decreases in abundance include terrestrial habitat degradation, marine pollution and fisheries interactions (Trathan et al. 2014).

Penguins live in two worlds: they breed on land but feed at sea. They can be regarded as ‘sentinel’ species that enable insight into how marine species are likely to respond to changing ocean patterns (Boersma 2008). A penguin’s ability to find food during breeding determines how much energy it can invest in reproduction (Weimerskirch 2001) and is influenced by both the location and density of prey (Boersma et al. 2007). The location of a foraging area determines the time spent travelling, the duration spent foraging (Ropert-Coudert et al. 2004) and is reflected in the rate of provisioning to offspring (Boersma and Rebstock 2009b). Prey distribution changes through the breeding season (Collins et al. 1999; Charrassin et al. 2002), and penguins adapt their behaviour in response (Clarke et al. 2006). How well they do so is potentially reflected in their reproductive performance.

Penguins are inherently difficult animals to study; much of their life is spent away from land, and therefore they are poorly accessible to scientists. For this reason, the kind of research that has been possible has been highly dependent on available technology. Early research was restricted to land-based studies of their biology (e.g. Richdale 1957). Subsequent work has embraced the development of new technology, particularly in the form of tracking and data-logging devices (reviews in: Wilson et al. 2002; Ropert-Coudert and Wilson 2005; Burger and Shaffer 2008). These devices not only provide insight into the behaviour of individuals at sea (Lescroël et al. 2010) but also they also allow sampling of the physical parameters of the marine environment (Sokolov et al. 2006). With the development of such devices it is important to monitor and quantify any effects of their use, not only for the welfare of the individuals but to ensure validity of data collected (Wilson and McMahon 2006).

1.2 Little penguins (*Eudyptula minor*)

As their common name suggests, little penguins are the smallest of all penguins, standing approximately 30 cm tall and weighing around 1 kg (Marchant and Higgins 1990). Little penguins are found along the coastal mainland and offshore islands of New Zealand and southern Australia. The total breeding population is thought to be approximately 600,000 individuals: 500,000 in Australia and 100,000 in New Zealand (Dann 2013). Despite a threat status of “Least concern” (IUCN 2013) due to their large population and widespread distribution, little penguins are believed to be in decline in both New Zealand (Dann 1994; Heber et al. 2008) and Australia (Dann 1992; Stevenson and Woehler 2007). The main cause of decline is predation ashore by introduced mammals and terrestrial habitat loss (Taylor 2000), with other threats including road traffic (Heber et al. 2008), oil spills (Goldsworthy et al. 2000) and gill-nets (Stevenson and Woehler 2007). In areas where these anthropogenic threats appear to be minimal, populations still face pressure from fluctuations in food availability (Dann et al. 2000; Chiaradia et al. 2010) and potentially from climate change (Chambers et al. 2011).

The taxonomic status of little penguins has been the subject of intensive research and review. The species was once partitioned into six subspecies based on morphology, colouration and breeding biology (Kinsky and Falla 1976). In contrast to the existence of six subspecies, later studies of mitochondrial DNA revealed two deeply divergent lineages (Banks et al. 2002), one in Australia and south-east New Zealand ("Australian" clade) and the other elsewhere in New Zealand (New Zealand clade), a result further supported by Peucker et al. (2009). Banks et al. (2002) suggested the species originated in New Zealand, dispersed to Australia and then back to the south-east region of New Zealand. Peucker et al. (2009) supported this and further suggested that there was a local extinction of the New Zealand clade in the south-east region that may have resulted from the Australia birds being competitively superior. Oamaru, in the south-east of the South Island, is the northern limit of distribution of the Australian clade in New Zealand; 93% of birds there belonging to the Australian clade and 7% to the New Zealand clade (Clark et al. 2013).

Much of what is known about the biology of little penguins originates from Phillip Island, southern Australia, where data collection began in 1968 (Reilly and Cullen 1979, 1981, 1982). Early research focused on documenting adult survival (Reilly and Cullen 1979), breeding biology (Reilly and Cullen 1981), and chick dispersal and survival (Reilly and Cullen 1982). Subsequent research has documented reproductive success in relation to extrinsic and intrinsic factors (Dann et al. 2000; Robinson et al. 2005; Nisbet and Dann 2009) not only at Phillip Island but at other sites around Australia (Rogers et al. 1995; Fortescue 1999; Priddel et al. 2008). Studies in New Zealand have documented breeding biology at various colonies (Bull 2000; Perriman and Steen 2000; Heber et al. 2008; Braidwood et al. 2011), with the longest duration of any published study being that located at Banks Peninsula (1996-2009; Allen et al. 2011). Across all studies, the highest reproductive performance was recorded on the Otago Peninsula, south-east New Zealand (Johannesen et al. 2002a), and North Harbour, Sydney, Australia (Priddel et al. 2008).

The onset of egg-laying for little penguins occurs during the austral winter (Reilly and Cullen 1981) and, if laying occurs early enough during winter, it is possible for pairs to lay a second clutch of eggs after chicks from the first brood have fledged (termed double brooding; Gales 1985). Double brooding occurs in Australia (Fortescue 1999; Knight and Rogers 2004; Priddel et al. 2008) and in south-eastern New Zealand (Johannesen et al. 2003) but not elsewhere in New Zealand (Heber et al. 2008; McKenzie 2011).

Adult survival has also been studied in Australia (Dann and Cullen 1990; Sidhu et al. 2007) and New Zealand (Johannesen et al. 2002b; Johannesen et al. 2003). Starvation and disease account for the majority of little penguin deaths in New Zealand (Jansen van Rensburg 2010). Survival was lowest in April and May following the annual moult (Johannesen et al. 2002b). Annual survival rates at Phillip Island increased with age up to 13 years and then progressively decreased (Sidhu et al. 2007). Before the current study, age-specific survival had not been investigated in New Zealand.

Little penguins are visual predators, foraging during daylight hours and returning to the breeding colony after dark (Chiaradia and Kerry 1999). They take a wide variety of small pelagic prey from near-shore waters, a pattern established by several comprehensive studies in Australia (Klomp and Wooller 1988; Montague and Cullen 1988; Gales and Pemberton 1990; Cullen et al. 1992; Chiaradia et al. 2003) and in New Zealand (Fraser and Lalas 2004; Flemming et al. 2013). The main prey of little penguins at Phillip Island are small pelagic schooling fish, most commonly anchovy (*Engraulis australis*) and pilchard (*Sardinops sagax*) (Montague and Cullen 1988). These species are not present in the diet all of the time, however, some studies document a shift towards other pelagic species during the year and between years (Cullen et al. 1992; Chiaradia et al. 2003). Variability in the abundance and species composition of prey fish within the little penguins' foraging range (Hobday 1992) was reflected in the penguins' diet (Cullen et al. 1992) and foraging range (Weavers 1992). Stable isotope work on little penguins near Auckland, New Zealand, also found evidence of temporal and spatial variation in diet (McKenzie 2011). Small, pelagic schooling fish form the mainstay of the diet of little penguins at Oamaru. These are most commonly slender sprat (*Sprattus antipodum*) and Graham's gudgeon (*Grahamichthys radiata*) (Fraser and Lalas 2004; Flemming et al. 2013).

Although little penguins feed on similar prey species throughout their range, location and the environment can influence their diving behaviour and reproductive performance (Chiaradia et al. 2007). In a study of four colonies, two in Australia and two in New Zealand, dive depth was deeper and diving effort higher at colonies with lower fledging success (Chiaradia et al. 2007). Foraging area and bathymetry were examined as potential influences, however clear relationships were not found (Chiaradia et al. 2007). In New Zealand, previous research on foraging ecology compared little penguins from Oamaru and 500 km further north at Motuara Island (Numata et al. 2000; Mattern 2001; Numata et al. 2004). The Oamaru birds exhibited lower foraging effort, better body condition and higher breeding success.

Annual variations in sea surface temperature (SST) appear to affect the timing and success of breeding and the survival rates of juvenile little penguins in Australia (Dann and Chambers 2013). The nature of these relationships varies across Australia. Breeding success increased with increasing SST in the south-east (Cullen et al. 2009) but decreased with increasing SST in the west (Cannell et al. 2012). In the south-east, juvenile survival also increased with SST (Sidhu et al. 2012). Such variation in responses makes it difficult to judge how increasing SST, predicted to occur with climate change (IPCC 2007), will affect little penguins.

1.3 The marine environment off south-east New Zealand

Oceanic circulation along the south-east coast of the South Island is strongly influenced by New Zealand’s position at the crossroads of five important water masses (Heath 1981). The Subtropical Convergence or Subtropical Front (STF) separates two water masses: relatively warm, saline subtropical waters in the north and cooler, less saline subantarctic waters in the south (Heath 1981, 1985). The STF is a global feature extending around the Southern Ocean at about 40°S and flowing eastwards across the Tasman Sea at about 45°S, before deviating further south below New Zealand. Along the south-east coast of the South Island the STF follows the continental shelf northwards and is referred to as the Southland Front (Figure 1.1; Heath 1981, 1985). Three water masses are present off this coast; first, closest to shore, is neritic water influenced by freshwater runoff; second is subtropical surface water; and third, furthest seaward, is subantarctic surface water (Jillett 1969; Heath 1972; Shaw et al. 1999). The Southland Front separates the subtropical and subantarctic waters (Shaw et al. 1999) and closely follows the continental slope at the 500 m isobath (Figure 1.1; Shaw and Vennell 2001). The front's proximity to the coast and its interaction with the Waitaki Canyon (offshore from the Waitaki River), causing upwelling, may enhance primary productivity in the region (Beentjes et al. 2002). The Waitaki River provides another source of terrestrial nutrients, further increasing productivity in the area (Beentjes et al. 2002).

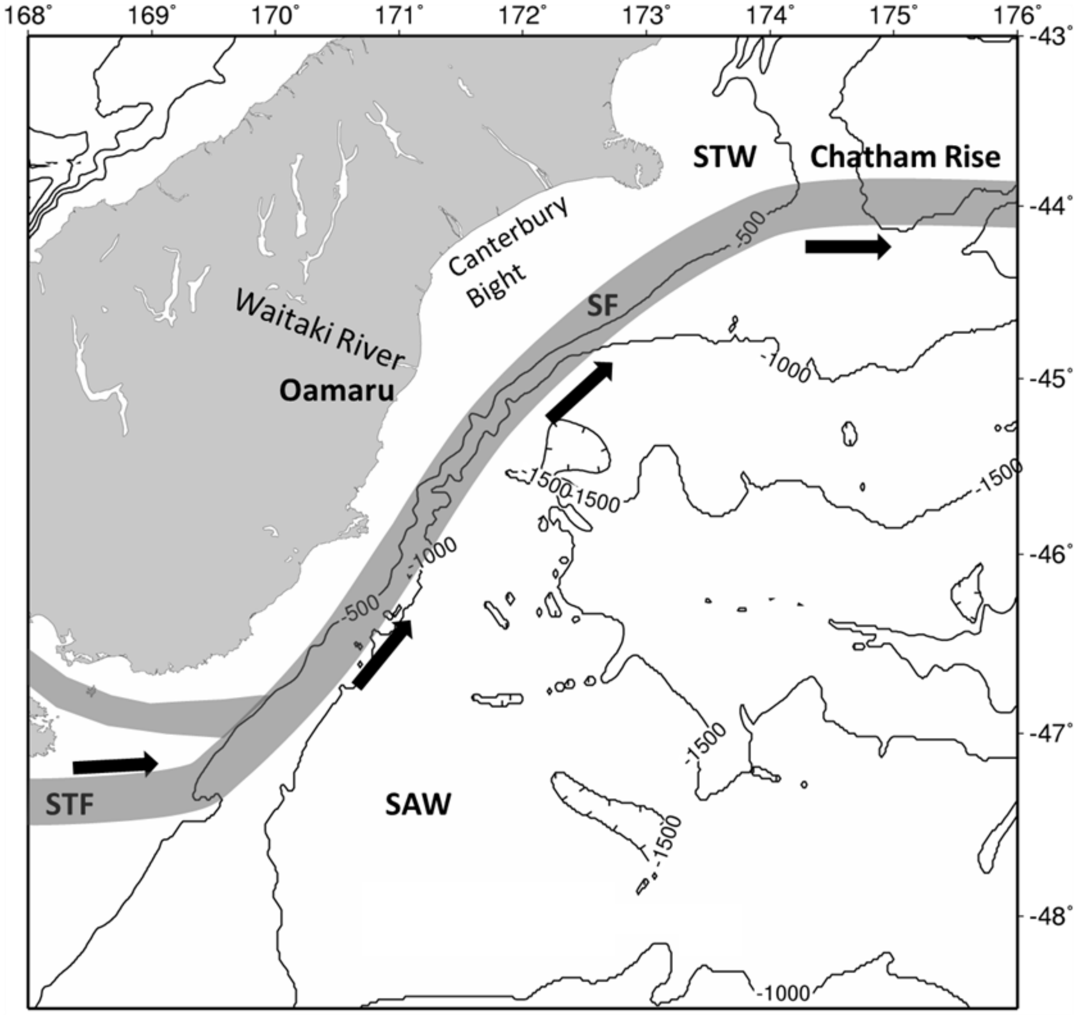

Figure 1.1. The approximate location of the Subtropical Front (STF; dark grey) off southern New Zealand (after Shaw and Vennell 2001). The front separates the subantarctic waters (SAW) and the subtropical waters (STW) and is termed the Southland Front (SF) off eastern South Island. Isobaths are shown at 500 m intervals.

1.4 Oamaru Blue Penguin Colony

Oamaru is a small town (population approximately 12,000) on the south-eastern coastline of the South Island, New Zealand. The Oamaru Blue Penguin Colony (OBPC) (45°07'S, 170°58'E) is situated approximately 2 km from the centre of the township at the south-eastern corner of Oamaru Harbour (Figure 1.2). The 2 ha site consists of a visitor's centre, penguin viewing facility and breeding. The site was originally a harbour-side quarry that operated from 1865 until the mid-1980s. The first penguins nested at the site in the 1970s and were viewed as a pest by the quarry owners due to the obstruction caused (Higham and Lück 2002). Soon after the quarry closed, the first artificial nest boxes were installed by the Waitaki Branch of the Royal Forest and Bird Protection Society (Houston 1999). By the early 1990s the penguins were no longer viewed as a pest and a solution to the issue of how to manage the area was sought. A "Penguin Liaison Committee" was established and a survey was carried out by Dr Peter Dann in 1991-92 to determine the distribution of penguins along the Otago coastline, including Oamaru (Dann 1994). The intention of the survey at Oamaru was to identify a suitable site for establishing public viewing of the penguins during their arrival ashore after dark, in a manner similar to Phillip Island's "Penguin Parade". Dann (1994) found 218 breeding pairs located around Oamaru with the majority of birds at two sites 1 km apart: one in the vicinity of the quarry, and the other extending from the main wharf to the mouth of Oamaru Creek (Figure 1.2). The former quarry site was considered suitable for a commercial tourism operation, which was established in 1992. The colony at the second site was fenced to exclude people, and augmented with nesting boxes. Public access to this second site (now named "Oamaru Creek Penguin Refuge") was discouraged so that it could be monitored as a control colony for investigating potential effects of the tourism operation at the quarry (Perriman et al. 2000). The conservation aims of the tourism operation at the quarry was to manage visitors viewing the penguins coming ashore in the evening, and to provide the penguins with a safe breeding habitat, free from introduced predators and with minimal disturbance by people (Johannesen et al. 2003). Trapping of introduced mammalian predators, (ship rats *Rattus rattus*, Norway rats *R. norvegicus*, weasels *Mustela nivalis*, stoats *M. erminea* and ferrets *M. putorius furo*) was carried out and the presence of domestic dogs (*Canis lupus familiaris*) was prohibited at both sites. The area was fenced so members of the public could not enter the penguins' breeding habitat. The site was cleared and mounds of soil created on which nesting boxes were placed. Nesting boxes had a removable lid, allowing easy examination of nest contents (Houston 1999). Few birds built their nests in natural burrows, most preferring to use the nesting boxes (Johannesen et al. 2003). Weekly nest checks at both sites began in August 1993 to monitor the penguins' breeding and survival and quantify any negative effects of the tourism operation. Early research at the two sites found similar population growth and breeding success rates (Perriman et al. 2000).

Visitor numbers grew from around 13,000 in the second full year of operation in 1994 to around 75,000 in 2012 (OBPC unpublished data). Evening viewing of the penguins ends around 10 pm during the height of the tourist season in the austral summer; a late hour that favours the use of local accommodation by tourists (Higham and Lück 2002). The continued success of the little penguins at Oamaru is paramount not only for the preservation of a stronghold of the species on mainland New Zealand (10.5% of breeding pairs along the Otago coastline; Dann 1994) but also for the benefit to the local economy.

Figure 1.2. Location of the study site at Oamaru Blue Penguin Colony and the Oamaru Creek Penguin Refuge, New Zealand.

1.5 Thesis aims and structure

Research into foraging behaviour and long-term demographic parameters, combined with environmental influences on New Zealand's little penguins is currently lacking. The little penguins at Oamaru are highly successful; the population is increasing due to protection from anthropogenic threats (Perriman et al. 2000; Johannesen et al. 2003) and relatively high breeding success (Numata et al. 2000). Foraging effort is lower than in other populations (Numata et al. 2000). Studying the population at Oamaru is crucial for improving our understanding of how foraging relates to reproductive performance within and between breeding seasons, and how the population responds to change in the marine environment. This research offers an opportunity to learn how this population will respond to global climate change, and refine predictions for how other populations will fare.

Specifically the aims of this thesis are to:

- Quantify annual variation in the reproductive performance of little penguins at Oamaru over a 19-year period and examine relationships among reproductive variables
- Quantify annual and age-related variations in the survival rates of little penguins at Oamaru
- Quantify effects on body weight, breeding and survival of data-logging devices attached to individual penguins during pre-egg, incubation and chick rearing
- Investigate variation in foraging behaviour during pre-egg, incubation and chick rearing during three consecutive breeding seasons, 2010-2012
- Investigate relationships between environmental variables (represented by storms, chlorophyll *a* and sea surface temperatures) and demographic parameters

This thesis comprises seven chapters with introductory (Chapter 1) and concluding (Chapter 7) chapters bounding five research chapters (Chapters 2 to 6) each written in a format for publication. Chapters 2-6 have been published, are submitted for publication or are in preparation for submission. As a result there may be some overlap of introductory materials and methods in some of the chapters. This will be minimised by cross-referencing where possible.

Chapters 2 and 3 begin by extracting demographic parameters for the little penguin population at Oamaru using a long-term dataset of 20 years. The data were recorded from weekly checks of all nesting boxes in the OBPC colony from 1993 to 2012. Chapter 2 examines reproductive variables focusing on temporal variation and relationships among variables and chapter 3 examines age-related variations in annual survival probabilities.

Chapter 2 has been published as:

Agnew P., Houston D., Lalas C., Wright J. (2014) Variation in reproductive performance of little penguins (*Eudyptula minor*) attributable to double brooding. Journal of Ornithology 155: 101-109

The next section of the thesis examines foraging behaviour of little penguins in relation to reproductive performance. Chapter 4 addresses potential effects of data-logging devices and examines whether it is feasible to attach devices repeatedly during the breeding season with minimal impacts. This was the first publication from the thesis work, and presented data collected in the 2010 and 2011 breeding seasons:

Chapter 4 has been published as:

Agnew P., Lalas C., Wright J., Dawson S. (2013) Effects of attached data-logging devices on little penguins (*Eudyptula minor*). Marine Biology 160: 2375-2382

Chapter 5 examines annual and seasonal variation in foraging behaviour during three breeding seasons, 2010-2012, in relation to reproductive performance at each stage.

Chapter 6 combines results from Chapters 2 and 3 in relation to environmental variables (SST and significant wave height) with the aim of examining the potential effects of global climate change on the penguins.

Chapter 7 summarises conclusions from the five research chapters with recommendations for future research and management of the little penguins at Oamaru.

1.6 Author contribution

I am senior author for the publications that arose from this thesis. I designed the sampling procedures, collected all the data on foraging ecology and collected the monitoring data from October 2006 onwards; I analysed all data and wrote all sections of this thesis. Dave Houston (Department of Conservation) organised and was involved in monitoring at the colony from 1993 to 2005, created an electronic database and collated the data into the database until 2005. He therefore is a co-author in Chapter 2. My three supervisors have provided advice and editorial input. Dr Chris Lalas (Department of Marine Science, University of Otago) was my primary supervisor, reviewed all thesis chapters and is co-author on all published manuscripts. Dr Janine Wright (Department of Mathematics and Statistics, University of Otago) was secondary supervisor and provided statistical advice throughout; she reviewed all chapters and is co-author on all published manuscripts. Professor Steve Dawson (Department of Marine Science, University of Otago) was my third supervisor; he reviewed all chapters and is co-author on the manuscripts for the publications from Chapters 3–6.

Chapter 2 :

Variation in reproductive performance of little penguins (*Eudyptula minor*) attributable to double brooding[1]

2.1 Abstract

Little penguin populations on the south-eastern coastline of the South Island, New Zealand, thrive at locations where they are protected from predation by introduced mammals and disturbance by people. Our objectives was to investigate the reproductive performance of a population of little penguin at Oamaru over a period of 19 years. Long-term monitoring of the population began in 1993 and involved a weekly check of all nests in the breeding colony to record the numbers of adult penguins, eggs and chicks present. All breeding adults and fledged chicks were flipper-banded. Breeding seasons with an early onset of egg-laying had more double brooding. Annual breeding success through 19 breeding seasons (1994–2012) averaged 1.89 chicks per female, the highest recorded for the species. The study showed that an early onset of egg-laying and the occurrence of double brooding resulted in high breeding success at the Oamaru population.

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[1] Published as: Agnew P., Houston D., Lalas C., Wright J. (2014) Variation in reproductive performance of little penguins (*Eudyptula minor*) attributable to double brooding. Journal of Ornithology 155: 101-109

2.2 Introduction

The threat status of little penguins (*Eudyptula minor*) is ‘Least concern’ (IUCN 2013) due to their widespread distribution around the New Zealand and southern Australian coasts. Numbers have declined in some areas (Dann 1994; Stevenson and Woehler 2007; Heber et al. 2008) and increased in others (Perriman et al. 2000; Preston et al. 2008; Sutherland and Dann 2012). Agents of decline include predation by introduced mammals and habitat loss (Taylor 2000), with other threats including road traffic (Heber et al. 2008), oil spills (Goldsworthy et al. 2000) and recreational gill-nets (Stevenson and Woehler 2007). At locations where human-induced threats have been reduced populations still face pressure from fluctuations in food availability (Dann et al. 2000; Chiaradia et al. 2010) and potentially climate change (Chambers et al. 2011). Understanding the population dynamics of little penguins is vital to the conservation management of the species and studying managed populations protected from anthropogenic threats ashore has the potential to provide a yardstick against which to assess impacts elsewhere. In New Zealand, the south-eastern coastline of the South Island is a region where populations are increasing at locations protected from introduced mammalian predators and from human disturbance (Perriman and Steen 2000; Johannesen et al. 2003).

Little penguins generally lay two eggs per clutch and incubate them for around 35 days (Kemp and Dann 2001). Chicks are guarded continuously by either parent for the first 2-3 weeks, fledge at 7-9 weeks, and then spend the majority of their first year at sea (Reilly and Cullen 1982). Adult little penguins first breed at 2-3 years old and thereafter breed annually at the same colony, often in the same area within the colony (Reilly and Cullen 1981). Breeding little penguins have an average life expectancy at Phillip Island, south-eastern Australia, of 6.5 years (Reilly and Cullen 1979), with the oldest individual recorded living to 25 years (Dann et al. 2005). The timing of the annual cycle is highly variable both across locations and years (Reilly and Cullen 1981; Dann et al. 2000; Johannesen et al. 2003; Dann 2013). Variation in the onset of egg-laying is likely to be driven by sea surface temperatures affecting food availability (Hobday 1992; Mickelson et al. 1992; Cullen et al. 2009). If the onset of egg-laying is early enough in the season it is possible for little penguins to produce a second clutch of eggs after the chicks of the first brood have fledged, termed ‘double brooding’ (Gales 1985). The highest breeding success of greater than two chicks fledged per pair was recorded for little penguins in the Otago region, on the south-eastern coastline of the South Island, New Zealand (Perriman et al. 2000; Johannesen et al. 2002a).

Reproductive performance of little penguins on the south-eastern coast of New Zealand, at Oamaru, was examined in relation to climate (Perriman et al. 2000) and survival of individuals (Johannesen et al. 2003). Double breeding (as opposed to double brooding) was defined to include pairs that laid a second clutch after incubating the first clutch past 35 days, regardless of whether the eggs hatched or chicks fledged from the first clutch (Perriman et al. 2000; Johannesen et al. 2003). These studies were carried out from 1993 to 1998 (Perriman et al. 2000) and 1993 to 1997 (Johannesen et al. 2003). The onset of egg laying was later and the proportion of double breeders lower during La Niña conditions than El Niño and normal years (Perriman et al. 2000). Double breeding birds had a higher probability of surviving until and breeding during the following season than single breeders (Johannesen et al. 2003). The objective of the current study was to quantify the reproductive performance of a population of little penguins at Oamaru over a 19 year period (1994 to 2012) and determine the importance of breeding variables on breeding success.

2.3 Methods

The Oamaru Blue Penguin Colony (OBPC) (45°07’S, 170°58’E) is situated 2 km from the centre of Oamaru township at the south-eastern corner of Oamaru Harbour. The colony was established as the OBPC tourism facility in 1992, which aimed to manage visitors viewing the penguins coming ashore in the evening and provide the penguins with a safe breeding habitat (Johannesen et al. 2003). The area was cleared and fenced, so members of the public could not enter the breeding area, and mounds of soil were made to place nesting boxes. In 1993, 87 nesting boxes were added (Johannesen et al. 2003) and 250 boxes were in place by 2012, all with a removable lid that allowed easy access for inspection of the nest by colony workers (Houston 1999). Few birds (<5% of pairs) made their nests in natural burrows, preferring to use the nesting boxes. Trapping of introduced mammalian predators, (rats *Rattus* sp., weasels, stoats and ferrets *Mustela* sp.) was carried out and the presence of domestic dogs (*Canis lupus familiaris*) was prohibited at the site.

2.3.1 Data collection

Following the establishment of the penguin colony as a tourism operation, a monitoring programme of the penguins to weekly check all nests and their contents was put in place. Adult penguins were banded on the right flipper with an individually numbered metal band. Banding began in the area in 1985 and then continued infrequently until regular weekly nest checks began in 1993. Adults were sexed by bill measurements (Hocken and Russell 2002) and by association with known-sex individuals. Chicks were weighed weekly and banded when around six weeks old. Chicks were recorded as fledged when they were absent from the colony past the age of six weeks when they had therefore reached the potential fledging age of seven weeks. The fledging weight of each chick was recorded as the weight at its last nest check. We used data from 1994-2012, where birds were followed the entire season, to calculate breeding variables.

Breeding seasons, referred to by the calendar year in which breeding began, started on 1 May and finished on 30 April of the following year (Perriman and Steen 2000). Birds were breeders when found in a nest incubating eggs or guarding chicks. An average of 3 (SE = 0.65) females and 2 (SE = 0.43) males changed mate mid-season and continued breeding; to accommodate this complex behaviour we focused on the female penguins for the calculation of variables. We defined breeding success as the number of chicks fledged per female per season; hatching success, the proportion of eggs hatched out of eggs laid; fledging success, the proportion of chicks fledged out of eggs hatched; egg success, the proportion of chicks fledged out of eggs laid, following Reilly and Cullen (1981). Double brooders were defined as females that laid a second clutch following the successful fledging of one or more chicks from the first brood. Single clutches were defined as eggs laid by females that laid only one clutch. Replacement clutches were defined as the laying of a second clutch following the failure of the first.

Exact lay dates are known only within 7 days so were estimated from the date that eggs were first found and the number of eggs present both on that date and the week following. Eggs are laid two to four days apart (Marchant and Higgins 1990; Kemp and Dann 2001), so the lay date was estimated as half way between the earliest possible lay date and the latest possible lay date between visits and depended on whether one or two eggs were present. For analyses, lay dates were designated as the nominal date eggs were laid as an integer day from day one onwards, with day one being 1 May of the calendar year, and were presented as the actual date for clarity. We defined the date of first eggs as the lay date of first eggs for the entire colony and defined median lay dates of first clutches as the median date first clutches were laid per season. Median lay dates were calculated to account for outliers in the data.

Predation by ferrets occurred during December 1999 over a two week period, resulting in around one third of chicks and eggs disappearing from nests but no breeding adults disappeared. The group of ferrets comprised a female and her litter of five offspring and were eventually caught in traps. Nests with chicks or eggs missing due to predation during 1999 were excluded from analyses.

To test for an effect of the experience of breeders we separated breeding pairs each season into three categories: pairs comprising two experienced birds, pairs comprising one experienced (male or female) and one new breeder, and pairs comprising two new breeders. We examined the median lay date of birds in each category compared to the overall median, breeding success of each and the proportion of females in each category that laid a replacement clutch or double brood.

2.3.2 Statistical analyses

Principal components analysis (PCA) was applied to the variables that related to breeding success: season, number of breeders, lay date of first eggs for the colony, median lay date of first clutches, proportion of females that laid replacement clutches, proportion of females that were double brooders, chicks fledged per female, chick fledge weights, hatching success, fledging success and egg success. A second PCA analysis included egg success variables: lay date of first eggs for the colony, median lay date of second clutches for double brooders, egg success for single clutches, egg success of replacement clutches, and egg success of first and second clutches for double brooders. PCA determines the correlation between the components and original variables and the total variation explained by each component. The PCA was computed on a correlation matrix; correlations are the covariances of standardized variables (Legendre and Legendre 2012), we standardized the variables as they were expressed on different measurement scales or with different orders of magnitude. We presented correlations of the variables with principal components that had an eigenvalue greater than one (Legendre and Legendre 2012) and a variable factor map of the first two components. The factor map allowed for the observation of correlation between variables. PCA was performed with R software, version 2.15.3 (R Development Core Team 2013) using the FactoMineR package (Le et al. 2008).

Confidence intervals for the difference between two means were calculated for the difference in mean egg success of different clutch-types and breeding variables of pairs with varying experience.

2.4 Results

The number of breeding little penguins in the study area at Oamaru increased from 42 males and 43 females in 1994 to 171 and 162 in 2012. The number of breeders increased most from 1994 to 1998 and from 2002 to 2009 (Figure 2.1). During the 1999 season there were 93 breeding females in total, however only 59 females were included in the reproductive analyses as the remainder lost eggs or chicks to predation by a ferret in December.

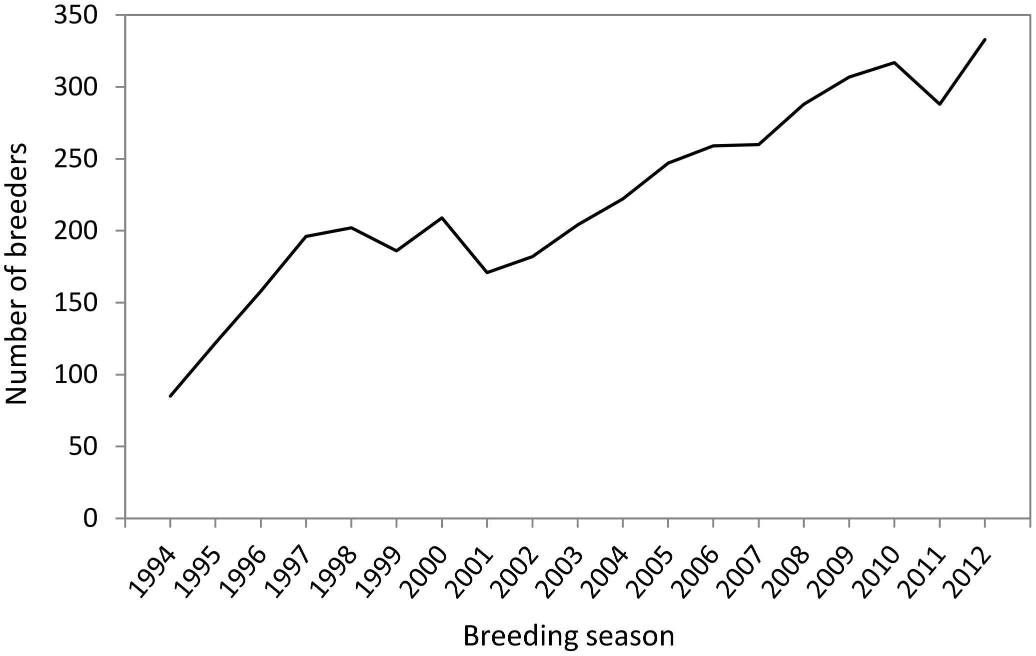

Figure 2.1. The number of breeding little penguins at Oamaru 19 breeding seasons, 1994-2012.

The date of first eggs for little penguins at Oamaru during the 19 breeding seasons ranged from 2 May in 1996 to 30 September in 1999, with a median date of 17 July. It was common for eggs to be found in only one or two nests at the beginning of the season, with other pairs laying up to one month later. The earliest two clutches on 18 May 1995 and 2 May 1996 (laid by the same breeding pair), were followed by clutches laid by other breeding pairs 30 and 28 days later. The median lay date of all first clutches per season ranged from 11 August in 2003 to 23 October in 2008, with a median for all seasons of 18 September. All first clutches of double brooders were laid prior to 18 September; with a median lay date of 13 August. The earliest lay date for the second clutch of a double brood was also 18 September and the median lay date for second clutches of double brooders was 29 November. The median lay date of single clutches was 5 October and for replacement clutches was 8 November. The latest date eggs were laid occurred early January. Seven of the 19 breeding seasons saw double brooding by < 10% of females, therefore we examined the median proportion of females that were double brooders each season. The median was 0.31, ranging from 0 up to 0.62, with an interquartile range of 0.03 – 0.42.

Annual breeding success averaged 1.89 chicks per female (Table 2.1) ranging from 1.29 in 1999 and 2004, to 2.48 in 2003 (Figure 2.2). The occurrence of replacement clutches (up to 23%) and double broods increased the number of chicks fledged per female per season by up to 75%, in 2003 (Figure 2.2). Breeding success fluctuated in relation to the number of chicks produced from double broods; the number of chicks fledged per female for first and single clutches showed less variation than the total number of chicks fledged per female (Figure 2.2). A mean of 77% of double brooding females per season fledged at least one chick from the second clutch (range: 67-86%, $n = 12$).

Table 2.1. Mean breeding parameters of the population of little penguins at Oamaru for 19 breeding seasons, 1994-2012.

Breeding parameter	Mean	SE	95% CI
Proportion of females that laid replacement clutches	0.12	0.01	0.12 – 0.13
Mean chicks fledged per female per season	1.89	0.09	1.72 – 2.06
Mean chicks fledged from all first clutches	1.42	0.02	1.37 – 1.46
Hatching success	0.75	0.01	0.73 – 0.77
Fledging success	0.92	0.01	0.90 – 0.94
Egg success – All	0.69	0.01	0.67 – 0.71
Egg success – Single clutches only	0.77	0.01	0.74 – 0.79
Egg success – First clutches of double brooders	0.88	0.01	0.86 – 0.91
Egg success – Second clutches of double brooders	0.67	0.01	0.65 – 0.70
Egg success – Replacement clutches	0.52	0.02	0.45 – 0.59
Mean chick fledge weight (g)	1065	10.30	1045 - 1085

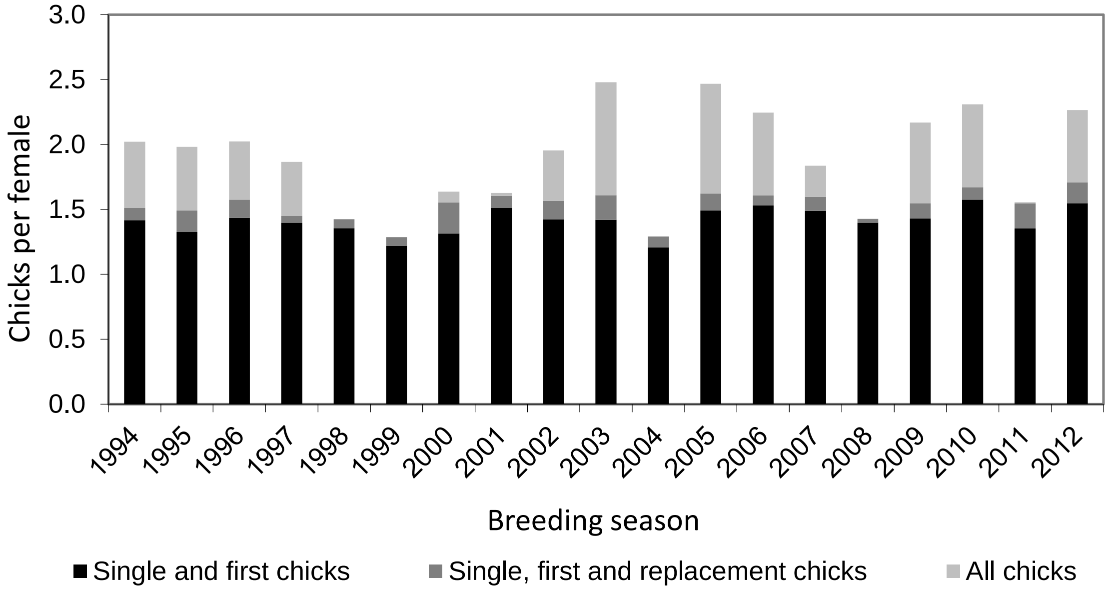

Figure 2.2. Chicks fledged per female from single and first clutches only (without the second clutch of double broods or replacements clutches); single, first clutches and the chicks fledged from replacement clutches (without including chicks from the second clutch of double broods); and all chicks fledged, for little penguins at Oamaru, 1994-2012.

The first three components of the PCA for reproductive parameters explained 86% of the total variance and were the only components with an eigenvalue greater than 1 (Table 2.2). The proportion of females double brooding, chicks fledged per female and the median lay date of first clutches per season were highly correlated with the first principal component (Table 2.2). The angle between the proportion double brooding and chicks per female in the variable factor map was small (Figure 2.3) indicating a high positive correlation between the two variables and both were 180° from the median lay date, indicating a strong negative correlation between this variable and the other two. The lay date of first eggs for the colony was also correlated with the first principal component and the direction of the variable in the factor map indicated that it was correlated to the median lay date (Figure 2.3). Not surprisingly, hatching success and egg success were closely correlated (Table 2.2, Figure 2.3). The number of breeders, breeding season and the proportion of females that laid replacement clutches were highly correlated with the second principal component. The number of breeders increased with season, where the proportion of replacement clutches decreased with both season and the number of breeders. Chick fledging weights and fledging success were positively correlated (Table 2.2, Figure 2.3).

Table 2.2. First three principal component correlations with breeding variables of little penguins at Oamaru, 1994-2012. Variation explained and eigenvalue of each component also shown.

Variables	Dim.1	Dim.2	Dim.3
Season	0.33	0.87	-0.06
Number of breeders	0.30	0.87	-0.08
Chicks per female	0.98	-0.14	-0.01
First eggs for colony	-0.69	0.49	0.24
Hatching success	0.71	0.51	-0.01
Fledging success	0.14	-0.10	0.91
Egg success	0.66	0.33	0.61
Fledge weights	0.06	-0.47	0.80
Proportion of double brooders	0.92	-0.19	-0.16
Proportion of replacement clutches	0.35	-0.73	-0.30
Median lay date of first clutches	-0.93	0.18	0.12
Variation explained (%)	40.1	27.0	18.6
Eigenvalue	4.4	3.0	2.0

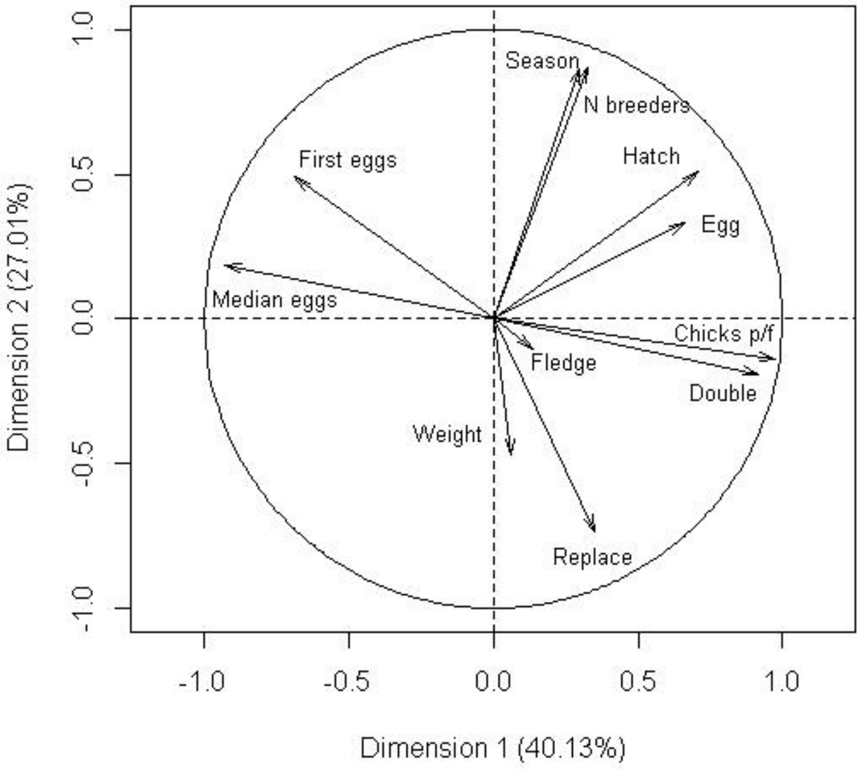

Figure 2.3. Variable factor map for PCA results on reproduction variables for little penguins at Oamaru each season, 1994-2012: season, number of breeders (N breeders), lay date of first eggs for the colony (First eggs), median lay date of first clutches (Median eggs), chick fledge weights (Weight), proportion of females that laid replacement clutches (Replace), fledging success (Fledge), proportion of females that were double brooders (Double), chicks fledged per female (Chicks p/f), egg success (Egg) and hatching success (Hatch).

Egg success of females that laid replacement clutches by definition was zero for their first clutches. The mean for the replacement clutch during the 19 year study (Table 2.1) was significantly lower than egg success of first (95% CI: 0.28, 0.44) and second clutches for double brooding females (95% CI: 0.07, 0.23) and eggs from females who laid a single clutch only (95% CI: 0.17, 0.33). Egg success of the first clutch of double brooders was significantly higher than the egg success of single clutches (95% CI: 0.08, 0.16) and the second clutch of double brooders (95% CI: 0.17, 0.25). Egg success of single clutches was significantly higher than the second clutch of double brooders (95% CI: 0.05, 0.13).

The first three components of the PCA for egg success explained 75% of the total variance and all had an eigenvalue greater than 1 (Table 2.3). Egg success of replacement clutches was highly correlated with the first component (Table 2.3). The median lay date of second clutches for double brooders and egg success of second clutches for double brooders were also correlated with the first component (Table 2.3) and were negatively correlated; egg success of second clutches declined as the lay date became later during the season (Figure 2.4). The remaining egg success variables were not correlated.

Table 2.3. First three principal component correlations with egg success of little penguins at Oamaru, 1994-2012. Variation explained and eigenvalue of each component also shown.

Variables	Dim.1	Dim.2	Dim.3
Median date of all first clutches	-0.50	0.77	-0.03
Egg success single clutches	-0.29	-0.53	-0.37
Egg success first clutches for double brooders	0.26	0.20	0.84
Egg success second clutches for double brooders	-0.66	-0.41	0.19
Egg success replacement clutches	0.81	-0.47	0.08
Median date second clutches double brooders	0.59	0.48	-0.48
Variation explained (%)	30.7	25.6	18.6
Eigenvalue	1.8	1.5	1.1

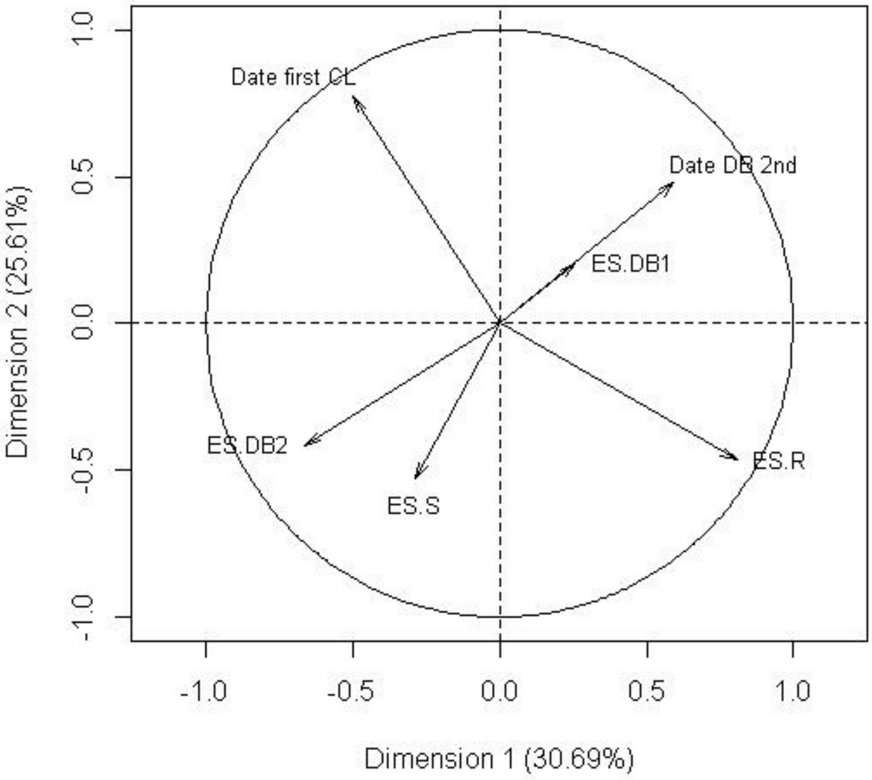

Figure 2.4. Variable factor map for PCA results on egg success variables for female little penguins at Oamaru (only seasons included where >0.10 double brooding occurred, *n* = 12): lay date of first eggs for the colony (Date first CL), median lay date of second clutches for double brooders (Date DB 2nd), egg success for single brooders (ES.S), egg success of replacement clutches (ES.R), and egg success of first (ES.DB1) and second (ES.DB2) clutches for double brooders.

Pairs of two experienced breeders laid eggs earlier than pairs with only one experienced breeder (95% CI: 23.1, 35.6) or two new breeders (95% CI: 29.9, 42.7) (Table 2.4). There was no significant difference between the pairs with one new breeder and pairs with two new breeders (95% CI: -0.66, 14.51). Breeding success was also significantly higher for experienced breeders compared to pairs with only one experienced breeder (95% CI: 0.39, 0.90), attributable to a higher proportion of these breeders double brooding (95% CI: 0.15, 0.43). While the proportion of pairs that laid a replacement clutch was higher for pairs with one experienced breeder and one new breeder, the difference was not significant (cf. experienced breeders, 95% CI: 0.00, 0.16). Egg success in this instance excluded first and second clutches of double brooders since inexperienced birds did not double brood. Egg success of eggs laid by two experienced breeders was higher than those laid by two new breeders (Table 2.4, 95% CI: 0.02, 0.18) but there was no difference between experienced breeders and pairs with one experienced and one new breeder (95% CI: -0.02, 0.14).

Table 2.4. Mean (SE) breeding parameters for little penguin pairs with two experienced breeders, one experienced (male or female) and one new, and two new breeders, at Oamaru 1994-2012.

Variable	Two experienced	One experienced, one new	Two new
Proportion of females	0.72 (0.02)	0.12 (0.01)	0.16 (0.01)
Difference between lay date and median	6.89 (1.65)	-22.5 (2.59)	-29.4 (2.69)
Breeding success	2.11 (0.10)	1.46 (0.07)	1.27 (0.09)
Mean proportion double brooding	0.35 (0.07)	0.06 (0.02)	0.05 (0.02)
Mean proportion laid replacement clutch	0.11 (0.01)	0.19 (0.04)	0.12 (0.02)
Egg success (excludes double broods)	0.65 (0.02)	0.60 (0.03)	0.56 (0.03)

2.5 Discussion

The onset of egg laying through the 19 seasons of this study varied across a five month period from May to September. An early onset of egg laying, where first eggs for the colony were laid in either May or June, gave a seven to eight month potential laying period for the season. The onset of egg laying provided an early indication of breeding success for the season. All breeding pairs that produced a double brood laid their first clutch prior to mid-September. Therefore, the number of pairs that lay eggs during June-August each season provides an indication of the proportion of pairs that were expected to double brood.

Breeding success and the proportion of females that produced a double brood each season declined with increasing median lay dates. Egg success of the second clutch also declined with increasingly late laying of second clutches. The most productive breeding seasons with >2 chicks fledged per female exhibited median lay dates in August and >50% of females double brooding. Variation in the onset of egg laying that extends over several months has been documented at Taiaroa Head on the Otago Peninsula, New Zealand (Perriman and Steen 2000) and Phillip Island (Reilly and Cullen 1981), however at other colonies in Australia, further north of Phillip Island, the mean lay date occurred within a few days from one season to the next (Lion Island: Rogers et al. 1995; Bowen Island: Fortescue 1998). The link between the timing of egg-laying and proportion double brooding has been established at Taiaroa Head (Gales 1985; Perriman and Steen 2000) and Phillip Island (Reilly and Cullen 1981). At Bowen Island and Lion Island the proportion double brooding was not related to the timing of egg laying on a colony scale, however individuals that began laying earlier during the season were more likely to double brood (Rogers et al. 1995; Fortescue 1998). Our study quantified the effect that double brooding had on breeding success at Oamaru, variation in breeding success increased three-fold with the addition of chicks from replacement clutches and double broods. Replacement clutches and double broods increased breeding success by as much as 75% per season (from 1.42 to 2.48 in 2003). Breeding success peaked at 1.58 chicks per female for single clutches only, but peaked at 2.48 chicks per female with all chicks included. Breeding success at Oamaru was the highest recorded for little penguins in any population, with only a few locations, at North Harbour near Sydney in Australia and Taiaroa Head, approaching this level of success (Table 2.5). The high proportion of pairs double brooding exhibited at Oamaru also occurred at these other two sites. Double brooding did not guarantee high breeding success at Phillip Island (Table 2.5). Robinson et al. (2005) regarded a ‘good’ breeding season at Phillip Island as a season with more than 1.3 chicks fledged per pair and a ‘poor’ season less than 0.7 chicks per pair. In contrast, at Oamaru the seasons with lowest breeding success (1.29 chicks per female in 2004) was similar to a good season for Phillip Island. In Australia double brooding does not occur in Tasmania due to a shortened breeding season; eggs are laid only after September (Hodgson 1975; Gales and Green 1990).

Table 2.5. Population size, mean breeding success, proportion of double brooders and egg success at colonies of little penguins. Locations are listed from north to south in each country.

Location	Population size (N breeders)	Breeding success	Proportion double brooding	Egg success	Year	Reference
Australia:						
Lion Island	600	1.37	0.14	0.60	1991-1993	Rogers et al. (1995)
North Harbour	100	1.71	0.24	0.70	2002-2005	Priddel et al. (2008)
Bowen Island	15,600	1.46	0.14	0.78	1987-1997	Fortescue (1995; 1998)
Phillip Island	26,000	0.71	0.16	0.26	1968-1978	Reilly and Cullen (1981), Dann and Norman (2006)
New Zealand:						
Wellington	80	0.94	0	0.47	1995-1996	Bull (2000)
Buller District	80	1.18	0	0.66	2006	Heber et al. (2008)
Banks Peninsula	2,100	1.29	0	0.64	1996-2009	Allen et al. (2011)
Oamaru	300	1.89	0.27	0.69	1994-2012	This study
Taiaroa Head	600		0-0.48	0.63	1992-1998	Perriman and Steen (2000)
Taiaroa Head		1.74			1993-1997	Johannesen et al. (2002a)

In New Zealand, double brooding does not occur outside the Otago region. Replacement clutches are rare at Banks Peninsula (Allen et al. 2011) and Wellington (Bull 2000), and do not occur in populations in the Buller District or South Westland (Braidwood et al. 2011). While these studies sampled only a few breeding seasons, the lack of double brooding outside of the Otago region has previously been recognized by Gales (1985). The lack of double brooding at other New Zealand regions is not due to the timing of the onset of egg laying however, as eggs are regularly laid prior to September. These regions (with the exception of Wellington, Table 2.5) exhibit similar egg success to Oamaru, therefore, it is the lack of double brooding that lowers breeding success. Breeding success of birds at Oamaru of first and single clutches only was similar (although slightly higher) to breeding success at other New Zealand colonies.

Early breeding and a high proportion of double brooding at the northern colonies in Australia are likely related to a constant and abundant food supply (Rogers et al. 1995), likewise variation in breeding at Phillip Island was linked to fluctuations in food supply (Chiaradia et al. 2010). Dann and Norman (2006) suggested it is not only fluctuations in food supply but competition for food due to the size of the Phillip Island population that has lead to reduced breeding success. While this may be the case for Phillip Island it does not explain the reduced breeding success at other sites; Bowen Island and Banks Peninsula show the next largest populations (Table 2.5), yet double brooding occurrs at one and not the other. The relationship between food supply and breeding success suggests that other regions around New Zealand and Tasmania do not experience the same abundance of food as the south-eastern region of the South Island.

For little penguins with previous breeding experience there is a clear advantage in pairing with another experienced individual. Experienced breeders are most likely to begin breeding early during the season and produce a double brood. This may be the result of early and regular attendance at the colony during the pre-egg stage of the season, re-establishing pair-bonds and re-claiming a nest.

Our study provided substantial evidence that researchers studying little penguins need to be clear and consistent when defining double brooding. Double brooding as originally defined by Gales (1985) only included birds that successfully fledged at least one chick from the first clutch, whereas other researchers have re-defined it as double breeding and included first clutches that have only been incubated to completion without including the criteria of fledging chicks from the first clutch (Perriman et al. 2000; Johannesen et al. 2003). We suggest that replacement clutches cannot be combined with second clutches from double broods as we have established that the success of replacement clutches is significantly lower than all other clutch-types. Johannesen et al. (2003) treated double breeding as a fitness parameter suggesting that double breeding may be evidence of a difference in the quality of breeders. We suggest this cannot be the case as birds that lay replacement clutches were significantly less successful at hatching and raising chicks in our study. The significantly lower egg success of replacement clutches compared to other clutch types was not due to being laid later during the season as the median lay date was earlier than the second clutch of double broods.

Overall mean fledge weight of chicks at Oamaru (1065g) was similar to the mean for the North Harbour colony, which was 1059g across three seasons: 2002-2004 (Priddel et al. 2008). These mean weights were higher than other colonies both in New Zealand (Numata et al. 2004) and Australia (Fortescue 1999; Chiaradia and Nisbet 2006), again potentially related to food availability. Dann and Norman (2006) found that chick mass decreased with increasing colony size of little penguins in Australia. However, in New Zealand a study of chick growth from two similar sized colonies, at Oamaru and Motuara Island in the Marlborough Sounds, found Oamaru chicks had higher growth rates and fledging mass (Numata et al. 2004).

At Oamaru, chick fledge weights were related to fledging success but unrelated to other breeding parameters. During a breeding season with poor breeding success at Oamaru it was still possible for birds to produce heavy chicks at fledging. Therefore, although breeding success provided an indication of a poor season in terms of the number of chicks produced per pair, it did not provide an indication of chick condition. This raises questions about what influences breeding success and chick growth. In Australia, food availability driven by local sea temperatures influence the onset of egg laying and reproductive performance (Hobday 1992; Mickelson et al. 1992; Cullen et al. 2009). However, similar to Oamaru, breeding success does not directly relate to chick growth or fledge weights (Chiaradia and Nisbet 2006). Instead there is evidence that parents adapt their foraging behaviour to compensate for a food shortage and as a result, meal mass and chick growth during poor breeding seasons are not significantly different to other seasons (Chiaradia and Nisbet 2006).

Our study demonstrates that the timing of egg laying and breeding success is highly variable. Accurate measures of lay dates, breeding success and double brooding rates rely on regular nest checks from May onwards and comprehensive marking of individuals and checking of all nests is necessary to determine breeding success. Regular nest visits are needed to examine the link between breeding experience and breeding success.

Chapter 3 :

First-year and adult survival estimates of little penguins (*Eudyptula minor*)

3.1 Abstract

Identifying variation in survival probabilities is fundamental to understanding population dynamics. We quantified variation in survival of little penguins (*Eudyptula minor*) at Oamaru, New Zealand, over 19 years, 1993-2011. Specifically survival in relation to age and breeding status were investigated. We used a multi-state capture-mark-recapture model to examine survival and recapture probabilities of known-age penguins flipper-banded as chicks, and breeding penguins of unknown age banded as adults. Survival of little penguins in their first year was lower than all older ages and averaged 0.43 (SE = 0.03). The mean annual survival rate of breeding adult penguins was 0.86 (SE = 0.02). The observed proportion of fledglings that later recruited into the breeding population in the study colony mirrored first-year survival estimates from the model. We detected no significant effect of age on survival for breeding penguins. Survival was however, related to breeding status; survival was lower in pre-breeding penguins relative to breeding penguins of the same age. The comprehensive, long-term monitoring programme in place at Oamaru resulted in very high recapture rates of breeding penguins, highly precise estimates of survival, and negligible bias.

3.2 Introduction

Population growth rates of long-lived bird species are highly sensitive to variation in adult survival probabilities (Sæther and Bakke 2000; Doherty et al. 2004; Stahl and Oli 2006). Growth is also influenced by a high inter-annual variability in survival from fledging to breeding (Harris et al. 2007; Gaston and Descamps 2011). Determining patterns of variation in survival is therefore fundamental to understanding population dynamics and managing populations. Variation in survival may be attributed to age or breeding status (Francis et al. 1992; Sidhu et al. 2007). Typically, seabird survival is lowest during adolescence (Weimerskirch et al. 1992; Emmerson and Southwell 2011), increases with age (Mauck et al. 2012) then decreases with senescence (Coulson and Wooller 1976; Nussey et al. 2013). Lower survival early in life is likely attributable to young birds lacking skills or experience in foraging or predator avoidance (Greig et al. 1983; Marchetti and Price 1989). Young birds have an immature immune system and as a consequence are more susceptible to disease and parasites (Harrigan 1992). These vulnerabilities result in annual first-year survival rates being more variable than adult survival (Horswill et al. 2014; Sherley et al. 2014). Decreased survival at advanced age is considered to be due to physiological deterioration (Williams 1957). Survival also varies over time and space in response to environmental variation such as climatic cycles (Bertram et al. 2005), prey abundance (Crawford et al. 2008), or variation in weather (Frederiksen et al. 2008). (Horswill et al. 2014).

Survival analyses are typically based on the capture and recapture of marked animals (Lebreton et al. 1992). Recapture of seabirds varies considerably with age and breeding status (Sandvik et al. 2008). Generally seabirds are rarely seen in their first year, because they venture far away from the natal colony (Thiebot et al. 2011; Thiebot et al. 2013) and often the chance of being seen will depend on their location relative to the level of human habitation (Sidhu et al. 2007). Accurate estimates of first-year survival are difficult to obtain as a result (Weimerskirch 2001). Recapture probabilities increase as individuals begin prospecting for a nest in the breeding colony and remaining high after initiating breeding (Horswill et al. 2014). Breeders must attend the breeding colony regularly to share incubation and chick feeding duties, and are available for recapture (Stenhouse and Robertson 2005).

Little penguins (*Eudyptula minor*) typically begin breeding at 2-3 years old (Reilly and Cullen 1981; Weimerskirch 2001). Thereafter they show strong fidelity to their breeding colony (Johannesen et al. 2002a). Nest fidelity is high, and birds often return to the same area within the colony or the same nest each season (Reilly and Cullen 1981; Rogers and Knight 2006). Breeders do not migrate away from the breeding colony during non-breeding months, they may spend longer periods at sea but still exhibit regular attendance at the colony (Reilly and Cullen 1981). Survival and recapture probabilities of little penguins vary with age (Sidhu et al. 2007). At Phillip Island, Australia, survival was lowest during the first year of life (0.17), peaked in adults aged 3-9 years (0.71 - 0.83), and decreased in birds older than 13 years (0.76) (Sidhu et al. 2007). Our study aimed to determine if a similar trend in age-related survival was present for little penguins at Oamaru, New Zealand. We expected that survival would be lower in the penguins' first year and then increase with age. We also expected that the survival and recapture probabilities of pre-breeders and breeding penguins would differ and vary through time. We examined these predictions by quantifying: (1) inter-annual variations in the survival of first-year, pre-breeding and breeding penguins; (2) age-specific variations in known-age breeding penguins; and (3) recapture of individuals at a second colony approximately 1 km away. For first year birds, modelled estimates were compared with data on the proportion of fledglings that later recruited into the breeding population. For breeding birds, modelled estimates were compared with data on the proportion of breeding penguins surviving from one season to the next.

3.3 Methods

3.3.1 Data collection

The study was carried out at the Oamaru Blue Penguin Colony (OBPC) (45°07’S, 170°58’E), situated 2 km from the centre of Oamaru township at the south-eastern corner of Oamaru Harbour. The OBPC was established as a tourist facility in 1992 to manage visitors watching the penguins come ashore in the evening and provide safe breeding habitat for the penguins (Johannesen et al. 2003). For details of the study site and weekly monitoring protocols, see Agnew et al (2013; 2014).

Little penguins in the study colony were identified with uniquely-numbered metal flipper bands. Flipper bands were made from an aluminium and stainless blend until 2008 when they were changed to stainless only. Bands were placed around the upper right flipper using pliers. When fitting, care was taken to ensure the join between the two edges of the band was smooth and flat. Bands were applied to individuals as chicks prior to fledging or when first encountered breeding in the colony. The first penguins were banded in Oamaru in 1985 but regular banding did not occur until weekly nest checks began in 1993, when all breeders and their offspring were banded. Two breeding colonies were monitored weekly, the OBPC and a second colony approximately 1 km to the north, the Oamaru Creek Penguin Refuge (Creek) (see Figure 1.2). Areas surrounding both colonies were the subject of irregular surveys (OBPC unpublished data). Monitoring data and incidental sightings and recovery of carcases from outside the colonies were incorporated into a database. It is not likely, however, that the database contains a perfect record of all such resightings and recoveries. We examined data over 19 breeding seasons from 1993 to 2011.

3.3.2 Statistical analyses

The data were analysed using mark-recapture models in which animals are marked during the initial capture, released and recorded on each subsequent encounter. Conventional mark-recapture models assume that survival and recapture probabilities do not vary between individuals in a group (Lebreton et al. 1992). To satisfy this assumption and to incorporate known-age individuals (banded as chicks) and unknown-age breeders into the same model, we used a multi-state model (Lebreton et al. 2009) in program MARK (version 6.2, White and Burnham 1999). This model had the advantage of grouping birds likely to have similar recapture probabilities. To further satisfy this assumption we focused only on individuals that fledged from the study colony and were recaptured back at the study colony or at the Creek colony. Inclusion of data from outside either colony would have violated the assumption because individuals that resided outside did not have the same probability of recapture.

A breeding season was referred to by the calendar year in which breeding began; and was defined to start on 1 May and finish 30 April of the following year. This definition followed the annual cycle of the penguins: eggs are laid from as early as May and as late as December with chicks fledged at the latest in March (Agnew et al. 2014); and adults moult after breeding (Reilly and Cullen 1981). Recapture data were extracted from the weekly monitoring programme and multiple records within a breeding season (May-April) were treated as a single recapture per breeding season in the encounter history matrix. Each breeding season was defined as one time interval in the model.

We defined four states (*F*: fledgling; *P*: pre-breeder at the study colony; *B*: breeder at the study colony; *O*: individual recaptured at the second colony) and two groups (*g*) (A: birds banded as breeding adults; C: birds banded as chicks). Fledglings were first-year individuals and pre-breeders were individuals in their second year onwards until they began breeding. We estimated survival (*S*) and recapture (ρ) probabilities for each state, and transition (ψ) probabilities from fledgling to pre-breeder, fledgling to present at the second colony, pre-breeder to breeder and transitions from the second colony back to the study colony. We developed a general model which assumed that survival probabilities for each state and group were time-dependent (*t*), and recapture probabilities of breeders in each group were time-dependent. The transition probabilities were constant over time in the general model. Parameters that we knew were biologically impossible: survival, recapture and transition probabilities for fledglings or pre-breeders in the group of individuals banded as adults; recapture of fledglings; backward transitions of breeders to pre-breeders or any state to fledglings, were fixed to zero. Using an information-theoretic approach (Burnham and Anderson 2002) we reduced the general model to develop a set of candidate models which incorporated variation in the states and groups. We used a two-step process; first we examined models with variation in the structure of recapture probabilities of breeders, then used the best recapture structure to examine variation in survival probabilities. The recapture-varying models included: time-dependent but constant over the two groups, group-dependent but constant over time, constant over time and groups, or age-dependent to 19 years for each group. The age-effect became an effect of time since the onset of breeding for survival of unknown-age breeders (banded as adults). The recapture probability structure resulting in the model with the lowest AIC in that set was then used in all models examined survival structure. Variation in the following was examined: survival probability of fledglings with time or constant over time; variation in pre-breeder survival with time, age to five years and constant over time; variation in adult survival with time for each group separately, with time but constant over the two groups, group-dependent but constant over time, constant over time and group, age to 19 and 13 years for each group. There were 40 possible models in the complete set.

We assessed the model fit of the general model using a parametric bootstrap goodness-of-fit (GoF) procedure performed in program MARK (Cooch and White 2012). This procedure generates simulated data using the estimates from the model being evaluated. Data are encounter histories for each animal, in which random numbers (between 0 and 1) are generated and compared to the survival estimates from the original data to decide on the status (survived/died) of each animal at each time interval. Simulated data exactly met the assumptions of the model. Once the encounter histories are generated, the model is run to compute the deviance and the process is repeated for 100 replicates. The over-dispersion parameter ($\hat{c}$) was estimated as the observed deviance of the general model divided by the mean expected deviance from the 100 replicates, which provided a measure of the amount of over-dispersion in the data. The general model was deemed acceptable if values of $\hat{c} = 1$ to 3 (Sandercock et al. 2005). Model selection was based on the difference in Akaike's Information Criterion, corrected for small sample size (ΔAIC_c). The models with the most substantial support had $\Delta AIC_c \leq 2$ compared to the model with the lowest AIC_c, models with ΔAIC_c from 3 to 7 showed some support (Burnham and Anderson 2002).

We examined the observed proportion of surviving fledglings from each breeding season that later recruited into the breeding population. To further test the accuracy of estimated survival probabilities of breeding penguins, we carried out a regression analysis on the modelled survival estimates of breeders in relation to the observed proportions that survived from one season to the next.

3.4 Results

We banded 3970 fledglings from the study area at Oamaru from 1993 to 2012. From 1993 to 2009 (allowing three years for birds to reach breeding age), 3016 chicks fledged and 18% (543) subsequently returned to the colony to begin breeding. A further 177 individuals were recaptured in the colony, but did not begin breeding there, and 47 were recaptured at the Creek colony. There were 32 re-sighted elsewhere and 34 recovered dead that were not included in the model. We banded 426 adult breeders of unknown origin (223 females; 203 males) in the colony. A further 31 individuals (19 females; 12 males) were banded elsewhere as adults or chicks before entering the breeding population at the study colony. They were banded at the Creek colony (19), at nests found elsewhere around Oamaru (9), or at Taiaroa Head (3) on Otago Peninsula. Of the 426 birds of unknown origin, 38 were banded as adults prior to routine monitoring (during 1991 and 1992) and another 76 were banded as adults during the first three years of the study (1993-1995). The total number of identified adult breeders from all breeding seasons (1993-2012) was 1039.

The general model (Model 5, Table 3.1) was an adequate fit to the data (GOF test, $\hat{c}$ = 1.95). Models 1 to 5 (Table 3.1) determined the best structure explaining variation in breeder recapture probabilities. The best model in the set of five held recapture of both groups constant over time (Model 1, Table 3.1). The best supported model in the set examining variation in survival probabilities incorporated time-dependent survival of fledglings, age-dependent variation in survival of pre-breeders, and time-dependent survival of breeders without a group effect (Model 6, Table 3.1). Estimates of first-year survival, from the best supported model, varied widely among years, from 0.27 in 2003 to 0.68 in 1994, with an overall average of 0.43 (*n* = 17 seasons, SE = 0.03; Figure 3.1). Temporal variation in the observed proportion of fledglings that subsequently recruited into the breeding population mirrored first-year survival estimates (Figure 3.1). Both first-year survival and the proportion of each cohort that recruited were higher for the first three breeding seasons than for the subsequent 14 seasons. The first-year survival estimate was lowest in 2003, however the lowest proportion recruited was from the cohort that fledged in 1997. The transition probability of fledgling to pre-breeder was 0.54 (SE = 0.03) and from fledgling to an individual present at the second colony was 0.04 (SE = 0.01). This accounted for 0.58 of fledglings that survived their first year of life, 0.42 could not be allocated to a state which means they were not recaptured in the first year.

Table 3.1. Five models (numbers 1 to 5) investigating recapture probabilities (*ρ*) of breeding little penguins at Oamaru, 1993-2011. Top ten models (numbers 6 to 15) investigating survival probabilities (*S*) of little penguins in four states: F: fledglings; P: pre-breeders at study colony; B: breeders at study colony; O: recaptured at other colony. The best supported model with lowest AICc in bold. Transition probabilities had the structure: $\psi_.^{FP}, \psi_.^{FB}, \psi_.^{FO}, \psi_.^{PB}, \psi_.^{PO}, \psi_g^{BO}, \psi_.^{OP}\psi_g^{OB}$.

Model number	Models	AICc	Δ AICc	*w_i*	*K*	Deviance
Models testing recapture of breeders:						
1	$S_t^F, S_t^P, S_{g*t}^B, S_.^O;\ \rho_.^P, \rho_.^B, \rho_.^O$	12420.95	70.16	0.00	89	2981.97
2	$S_t^F, S_t^P, S_{g*t}^B, S_.^O;\ \rho_.^P, \rho_g^B, \rho_.^O$	12422.19	71.40	0.00	90	2981.16
3	$S_t^F, S_t^P, S_{g*t}^B, S_.^O;\ \rho_.^P, \rho_{t,age-19}^B, \rho_.^O$	12429.64	78.85	0.00	127	2912.57
4	$S_t^F, S_t^P, S_{g*t}^B, S_.^O;\ \rho_.^P, \rho_t^B, \rho_.^O$	12449.20	98.41	0.00	107	2973.32
5	$S_t^F, S_t^P, S_{g*t}^B, S_.^O;\ \rho_.^P, \rho_{g*t}^B, \rho_.^O$	12480.50	129.70	0.00	127	2963.42
Models testing survival:						
6	$\boldsymbol{S_t^F, S_{age-5}^P, S_t^B, S_.^O;\ \rho_.^P, \rho_.^B, \rho_.^O}$	**12350.79**	**0.00**	**1.00**	**58**	**2974.97**
7	$S_t^F, S_{age-5}^P, S_{g*t}^B, S_.^O;\ \rho_.^P, \rho_.^B, \rho_.^O$	12361.62	10.82	0.00	75	2951.22
8	$S_t^F, S_{age-5}^P, S_{g*age-13}^B, S_.^O;\ \rho_.^P, \rho_.^B, \rho_.^O$	12390.98	40.18	0.00	63	3005.00
9	$S_t^F, S_{age-5}^P, S_{g*age-19}^B, S_.^O;\ \rho_.^P, \rho_.^B, \rho_.^O$	12394.95	44.16	0.00	75	2984.55
10	$S_t^F, S_.^P, S_t^B, S_.^O;\ \rho_.^P, \rho_.^B, \rho_.^O$	12403.72	52.93	0.00	55	3033.99
11	$S_.^F, S_{age-5}^P, S_{g*t}^B, S_.^O;\ \rho_.^P, \rho_.^B, \rho_.^O$	12409.80	59.01	0.00	57	3036.01
12	$S_t^F, S_t^P, S_t^B, S_.^O;\ \rho_.^P, \rho_.^B, \rho_.^O$	12410.00	59.21	0.00	72	3005.72
13	$S_t^F, S_t^P, S_{g*t}^B, S_.^O;\ \rho_.^P, \rho_.^B, \rho_.^O$	12414.52	63.73	0.00	72	3010.24
14	$S_t^F, S_{age-5}^P, S_g^B, S_.^O;\ \rho_.^P, \rho_.^B, \rho_.^O$	12428.11	77.32	0.00	40	3088.74
15	$S_t^F, S_.^P, S_{g*age-19}^B, S_.^O;\ \rho_.^P, \rho_.^B, \rho_.^O$	12447.86	97.06	0.00	72	3043.57

AICc: Akaike's information criterion, the selection criterion corrected for small sample size; ΔAICc: the difference between the AICc values for each model and the best model; w_i: Akaike weights; *K*: number of estimated parameters; Deviance: model deviance; *t*: time; age-5, age-13, age-19: age varying up to the fifth, 13th and 19th years of life respectively; constant (.).

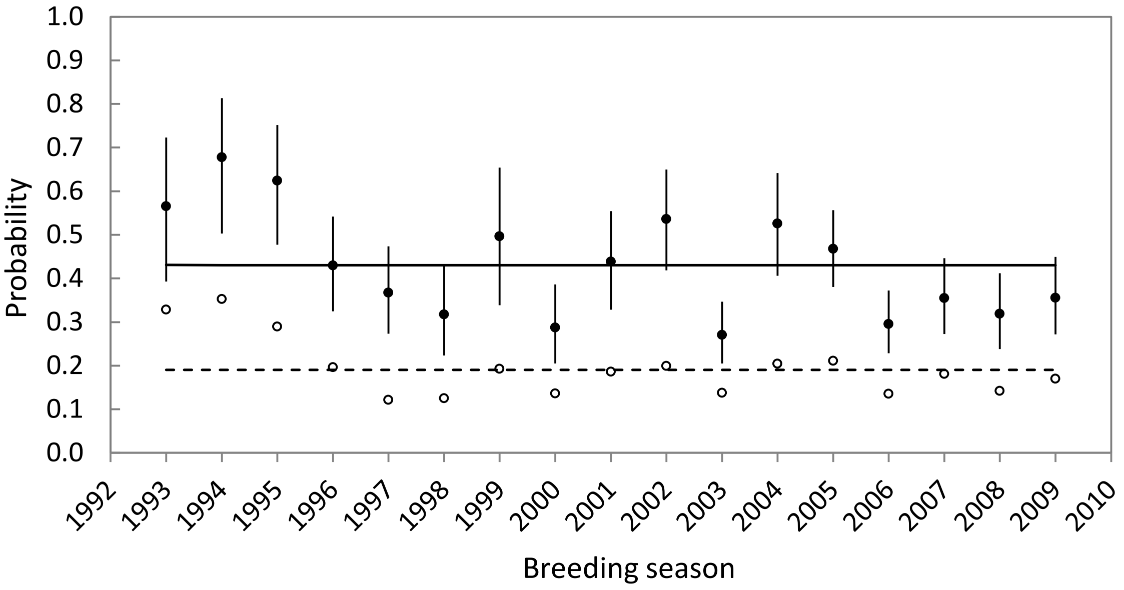

Figure 3.1. Annual survival probabilities (± 95% CI) of little penguins in their first-year (closed circles) and the proportion of fledglings from each season that recruited into the breeding population (open circles), from 17 consecutive cohorts, 1993-2009, at Oamaru. Solid horizontal line represents mean first-year survival for the period and dashed line represents the mean cohort recruitment. Parameter estimates for first-year survival were from the best supported model ($S_t^F, S_{age-5}^P, S_t^B, S_.^O;\ \rho_.^P, \rho_.^B, \rho_.^O$).

The survival probability of pre-breeding penguins in their second year was 0.85 (SE = 0.02; Figure 3.2), considerably higher than first-year survival. The survival probability of pre-breeders decreased with age to the fourth year of life, the wide confidence interval for survival of individuals in their fifth year of life and older indicated a small sample size for this age group (Figure 3.2). This meant that individuals which did not transition to become breeders in the colony died or moved away and did not stay in the colony without breeding. The transition probability of pre-breeders to breeders at the study colony was 0.72 (SE = 0.02). The recapture probability of pre-breeders was 0.67 (SE = 0.02). No breeding adults moved from one colony to the other; individuals only migrated soon after fledging.

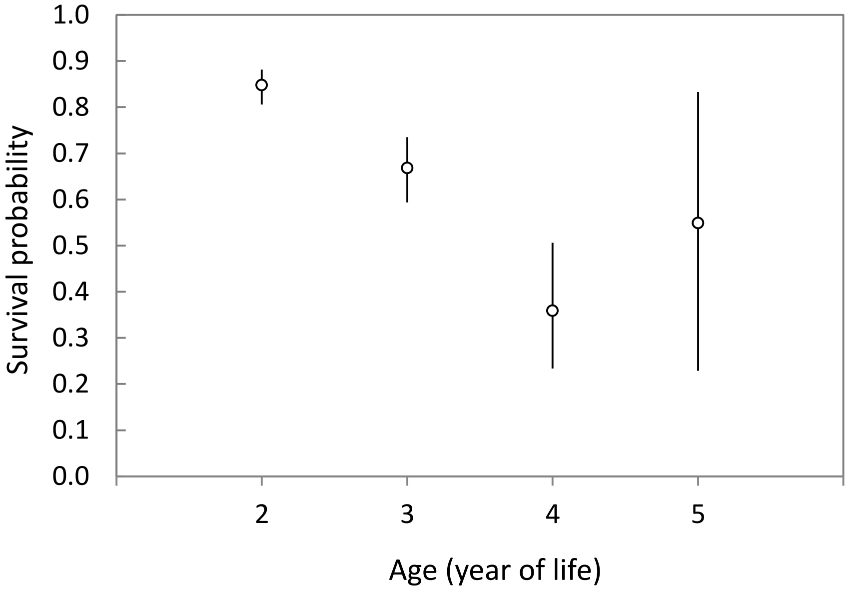

Figure 3.2. Age-specific survival probabilities (± 95% CI) of pre-breeding little penguins in their second year of life and older, for penguins fledged from 1993 to 2009 at Oamaru. Penguins in their fifth year of life and older were grouped together. Estimates were from the best supported model ($S_t^F, S_{age-5}^P, S_t^B, S_.^O;\ \rho_.^P, \rho_.^B, \rho_.^O$).

Estimates of breeder survival from the best supported model varied from 0.75 in 2001 to 1.00 in 1994, with an overall average of 0.86 (*n* = 19 seasons, SE = 0.02; Figure 3.3). A group effect was not included in the best supported model indicating there was no difference in survival between breeders banded as adults and breeders banded as chicks. The recapture probability of breeding adults was 1.00 (SE = 0.00). The high probability of recapture meant that modelled survival estimates were very close to the observed proportion of breeders that survived annually ($y = 1.01x$, $R^2 = 0.98$, $P < 0.0001$; Figure 3.4).

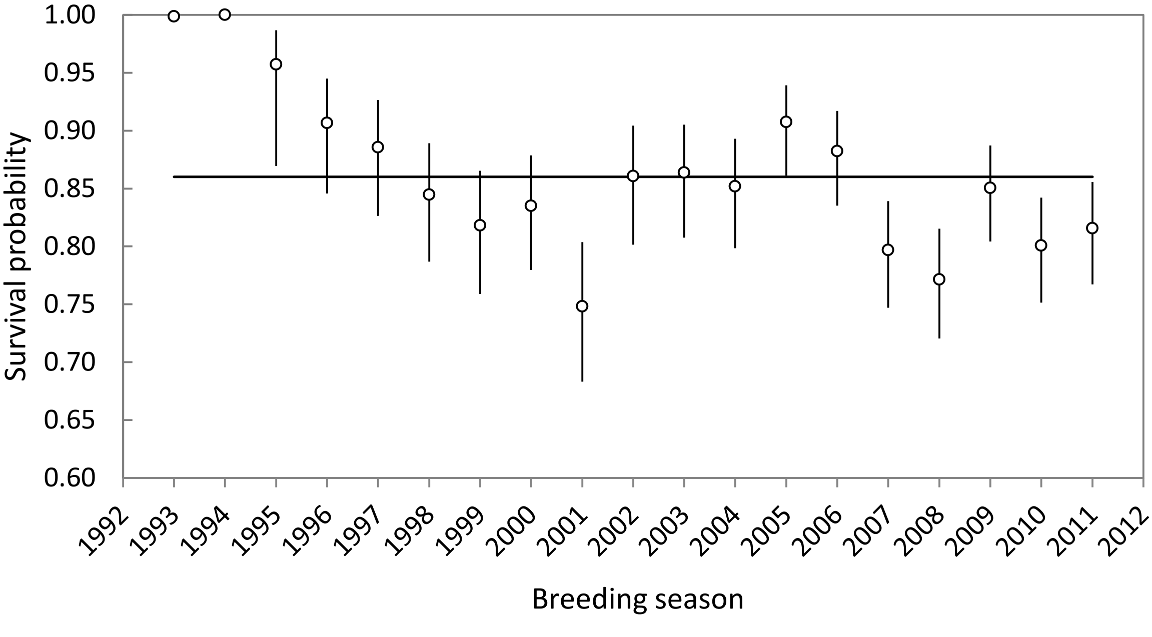

Figure 3.3. Annual survival probabilities (± 95% CI) of breeding little penguins, from 19 breeding seasons 1993-2011, at Oamaru. Solid horizontal lines represent the mean survival. Parameter estimates obtained from the best supported model $(S_t^F, S_{age-5}^P, S_t^B, S_.^O;\ \rho_.^P, \rho_.^B, \rho_.^O)$.

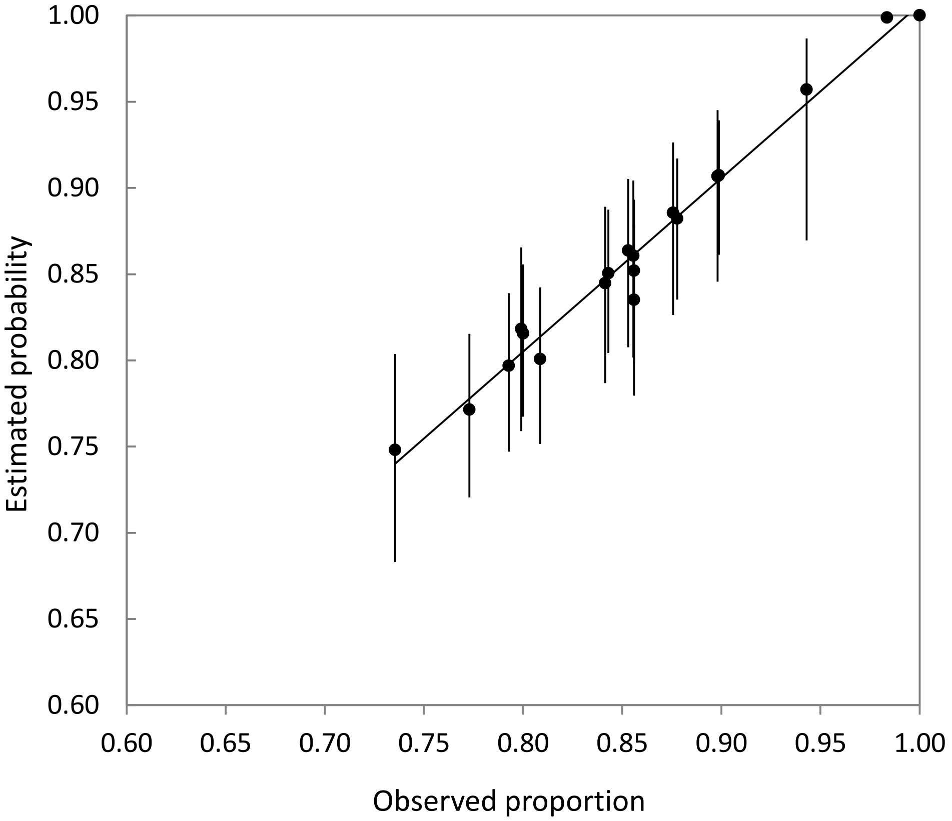

Figure 3.4. The relationship between the observed proportion of breeding little penguins surviving from one breeding season to the next, and the estimated survival probabilities (± 95% CI) from the best supported model ($S_t^F, S_{age-5}^P, S_t^B, S_.^O;\ \rho_.^P, \rho_.^B, \rho_.^O$), from 19 breeding seasons 1993-2011, at Oamaru. Linear regression (solid line): $R^2 = 0.98$, $P < 0.0001$, $y = 1.01x$.

The high annual variability in survival of breeders meant that the best models incorporated time-dependent effects on survival. While age-specific effects on breeding penguins were not included in the best supported model (see model 8, Table 3.1), they still may have been biologically significant and hence are presented (Figure 3.5). The survival of breeding penguins in their third year of life (Figure 3.5; 0.92, 95% CI: 0.89, 0.94) was significantly higher than pre-breeders of the same age (0.67, 95% CI: 0.59, 0.73). While there was a decrease in survival over the 13th year, the associated confidence intervals overlap comprehensively (Figure 3.5).

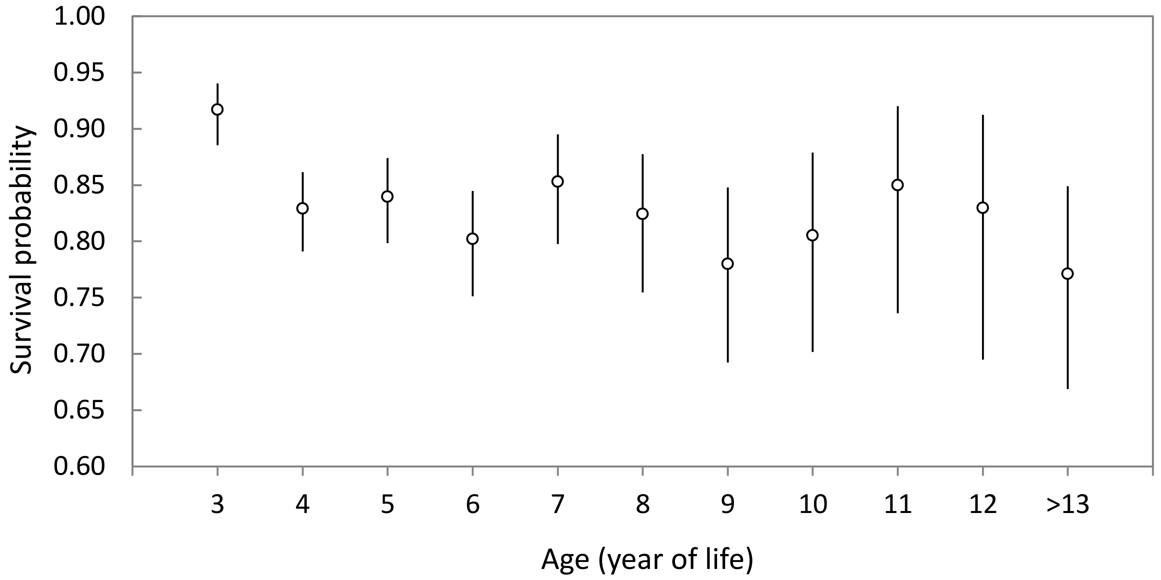

Figure 3.5. Age-specific survival probabilities (± 95% CI) for breeding, known-age penguins in their third year of life and older, for little penguins fledged from 1993 to 2009 at Oamaru. Parameter estimates obtained from the model: $S_t^F, S_{age-5}^P, S_{g*age-13}^B, S_.^O;\ \rho_.^P, \rho_.^B, \rho_.^O$.

3.5 Discussion

As expected, survival estimates for little penguins in their first year were lower than for older penguins. Average annual survival probability of known-age birds in their first-year was 0.43 (n = 17, 1993-2009). Average survival rates for breeding adults was double this figure. A 36-year dataset from little penguins at Phillip Island showed that survival was also lowest in the first year of life (0.17) compared to adults (0.71 - 0.83). This is a generally consistent pattern across studies of other penguins (e.g. Emmerson and Southwell 2011; Horswill et al. 2014; Ludynia et al. 2014). In contrast, in king penguins (*Aptenodytes patagonicus*) average juvenile survival was 0.77 (Saraux et al. 2011c), much closer to published adult survival rates (0.90-0.95; Weimerskirch et al. 1992). King penguins exhibit low breeding success and so a suggested reason for high juvenile survival was that chicks are already subject to strong selective pressure prior to fledgling (Saraux et al. 2011c). Juvenile and adult survival rates were also similar for southern rockhopper penguins (*Eudyptes chrysocome*) (0.81 and 0.98; Dehnhard et al. 2014), thought to be due to favourable environmental conditions during their study. Dehnhard et al. (2014) examined juvenile survival from only two breeding seasons, however. Lower survival may have been recorded over a longer study duration.

Survival of little penguins at Oamaru did not decrease with old age, a result in contrast to findings at Phillip Island, where survival gradually declined in older penguins to 0.76 by age 13 (Sidhu et al. 2007). Comparable survival in older penguins was perhaps due to the smaller population size at Oamaru compared to Phillip Island (see Table 2.5). In a smaller population there may be more food available for individuals (Dann and Norman 2006) and a reduced sample size of older penguins (Nisbet 2001).

Gaining accurate estimates of first-year survival of seabirds is especially difficult because these birds disperse, and often do so into areas where re-sighting or recovery is impossible. The recapture of first-year and pre-breeding little penguins in our study was lower than breeding penguins, a result consistent with other penguin studies. The recapture of rockhopper penguins in their first year was 0.55 compared to 0.97 for birds 2-4 years old (Dehnhard et al. 2014) and macaroni penguins (*Eudyptes chrysolophus*) in their first year was only 0.10, increasing to 1.00 by age 4 (Horswill et al. 2014). Low recapture rates are likely to result from young birds spending less time at the breeding colony: Saraux et al (2011) found that 56% of king penguins, that returned to the colony in their first year, stayed in the colony for less than a week. In other seabirds the probability of recapturing young seabirds is near-zero and this age class is frequently treated as an unobservable state (e.g. Monticelli and Ramos 2012; Maness and Anderson 2013). For example, sooty shearwaters had a mean age of first return to the breeding colony of 4.8 years and few birds were first observed prior to two years (Fletcher et al. 2013). In our study, even though recapture of juveniles was lower than older birds, the recapture of more than half that were alive will have increased the accuracy of our first-year survival estimates. The proportion of fledged little penguins that survived to recruit into the breeding population at Oamaru mirrored survival estimates for first-year penguins. These results strongly suggest that our estimates of first-year survival are accurate; unbiased by dispersal.

Once recorded in one colony as a pre-breeder or breeder, the birds in our study did not migrate to the other colony. Some individuals recorded as pre-breeders were also later recaptured as pre-breeders. These findings suggest high site fidelity after the first year. The survival of pre-breeding penguins in their third year of life was significantly lower than the survival of breeding penguins of the same age. We also found a decrease in pre-breeder survival with age. High site fidelity would suggest that penguins that disappear at this time have died rather than migrated.

It is inevitable that some individuals will be of higher intrinsic “quality” than others, and that this would be shown in higher survival and earlier breeding. Aubry et al. (2011) found black-legged kittiwakes (*Rissa tridactyla*) that delayed recruitment, suffered a higher mortality risk than early recruits. Birds that recruited early may have had intrinsic reproductive, survival and competitive abilities allowing them to achieve higher fitness (Aubry et al. 2011). Long-term monitoring of little penguins at Oamaru makes testing this idea possible, by quantifying lifetime reproductive success of individuals, age at first breeding and survival.

Survival of first-year and breeding penguins varied through time. Temporal variation in survival can, in part, be attributed to a number of environmental factors that drive prey abundance and availability (e.g. Dehnhard et al. 2013b). Variation in prey abundance occurs in response to multiple factors, such as variation in weather patterns (Bergeron 2000), global climatic events (Surman and Nicholson 2009) and varying sea surface temperatures - which affect productivity and water stratification (Hansen et al. 2001). Environmental variation can affect first-year and adult individuals differently (Pardo et al. 2013). Young individuals may be more sensitive to environmental variation and reductions in prey availability, due to their poorer foraging skills (Marchetti and Price 1989), or immature immune system making them more susceptible to parasites (Harrigan 1992). Daunt et al. (2007) found juvenile European shags (*Phalacrocorax aristotelis*) compensated for reduced foraging proficiency by increasing foraging duration. An increase in juvenile mortality during winter resulted from a reduction in available foraging time, because birds are obligate visual foragers (Daunt et al. 2007). Compared with juveniles, breeding birds have a restricted foraging range (Hoskins et al. 2008). They are susceptible to environmental variation in the immediate area and are unable to foraging further away and return within the same day to feed chicks.

3.5.1 Potential effects of flipper bands

The use of bands to mark penguins remains controversial, and while there are studies that show reductions in survival of banded penguins (Froget et al. 1998; Saraux et al. 2011a), there are studies that document minimal effects (Hindell et al. 1996; Boersma and Rebstock 2009a, 2010) and others with inconsistent results (Clarke and Kerry 1998; Dugger et al. 2006). Clarke and Kerry (1998) found, over six years, the survival of Adélie penguins (*Pygoscelis adeliae*) was not statistically different between birds marked with bands compared to transponders. During one year of their study however, mortality of flipper banded penguins was higher following a severe food shortage (Clarke and Kerry 1998), suggesting that band effects may be only become under adverse environmental conditions. Survival of the penguins at Phillip Island was negatively impacted by the application of flipper-bands (Dann et al. 2014): survival in the year after banding and subsequent years (0.75 and 0.87), was lower than survival of those marked with a passive integrated transponder (0.81 and 0.91). A food shortage during the first of six years of the study at Phillip Island (Dann et al. 2000) may have increased mortality of banded birds the first year after marking relative to those marked with a transponder. At Oamaru little penguins have higher reproductive performance (Agnew et al. 2014) than those at Phillip Island (Reilly and Cullen 1981; Dann and Norman 2006) and have been increasing in numbers since 1993 (Agnew et al. 2014) while the Phillip Island population has remained stable since 1995 (Sutherland and Dann 2014). Survival rates at Oamaru were comparable with those of unbanded penguins at Phillip Island. A hypothesis of greater food availability at Oamaru versus Phillip Island could mitigate any negative effects of flipper bands on the penguins. At Matiu/Somes Island in Wellington Harbour, New Zealand, a 5-year study found the survival of banded little penguins was not lower than those with inserted transponders (Cotter 2012). We are confident despite researcher concern regarding the application of bands, that the Oamaru penguins are not impacted by flipper bands and that our results are applicable to unbanded conspecifics.

3.5.2 Conclusion

Population growth rates of long-lived animals are, in general, highly sensitive to adult survival (Sæther and Bakke 2000). If we wish to understand population change and responses to environmental fluctuations, it is essential to gain accurate estimates of adult survival. The current study demonstrates that precise and unbiased estimates of adult little penguin survival can be obtained from regular nest searches encompassing the colony. Several features of the penguins' breeding biology facilitates good survival estimates: (1) breeders occupied the same nest area in the colony each season, (2) once they began breeding at the study colony, birds did not leave to breed elsewhere and, (3) few birds skipped breeding for a season, without being recorded in the colony at some stage (Reilly and Cullen 1981). These features, in combination with the comprehensive monitoring programme in place in Oamaru, result in very high recapture rates, highly precise estimates of survival, and negligible bias.

Chapter 4 :

Effects of attached data-logging devices on little penguins (*Eudyptula minor*)[2]

4.1 Abstract

Data-logging devices are commonly used to study the foraging behaviour of individual seabirds. Such studies need to examine the potential effects of using devices on instrumented individuals, not only for ethical reasons but also to ensure the validity of data gathered. We studied the effects of two types of device (time depth recorder and global positioning system) on little penguins (*Eudyptula minor*) during the 2010 and 2011 breeding seasons at Oamaru, New Zealand. Mixed-effect models were used to test for effects of devices by comparing changes in body weight, chick growth and breeding performance between instrumented and control individuals. We found no detectable effects of the attached devices on body weight change, hatching success, fledging success, chick growth parameters or adult survival. We conclude that it is possible to attach data-logging devices to adult little penguins for extended periods during the breeding season with minimal impacts.

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[2] Published as: Agnew P., Lalas C., Wright J., Dawson S. (2013) Effects of attached data-logging devices on little penguins (*Eudyptula minor*). Marine Biology 160: 2375-2382

4.2 Introduction

The use of data-logging devices to track the behaviour of seabirds at sea is becoming widespread (reviews in: Wilson et al. 2002; Ropert-Coudert and Wilson 2005; Burger and Shaffer 2008). Such devices not only provide insight into the foraging behaviour of individuals (e.g. Cook et al. 2006) but also into the environment in which the animals live (e.g. Sokolov et al. 2006), allowing collection of data that are otherwise very difficult to obtain. The objective of using data-logging devices is to measure ‘normal’ behaviour of individuals, behaviour that is representative of unequipped conspecifics. Therefore, any effects of the devices should be minimised, not only for the well-being of the animal but also for the reliability of data collected.

The advantages of using attached devices can be marred by potential detrimental effects on the device carrier (Barron et al. 2010). At sea, device effects result principally from additional weight for flying birds and additional hydrodynamic drag for diving birds. Increased drag can reduce swimming speeds affecting diving behaviour, decreasing foraging range, increasing foraging duration (Boersma and Rebstock 2009a) and increasing energy expenditure (Wilson et al. 1986; Culik and Wilson 1991; Ropert-Coudert et al. 2007b). These effects potentially reduce breeding success due to failure to incubate eggs successfully (Beaulieu et al. 2010) or provide chicks with enough food (Croll et al. 1996; Kidawa et al. 2012). Standardised procedures for the application of data-loggers have been established informally. Device effects have been found to increase with increasing device size (Hull 1997); therefore, the general consensus is that devices should be as small and streamlined as possible (Ballard et al. 2001). Devices should be inconspicuous colours, attached at a point that minimises drag, and attached using methods that preserve the integrity of feathers (Ballard et al. 2001; Ropert-Coudert et al. 2003). The ideal situation would be that the animal shows no reaction to the attachment of a device but this aspiration can be difficult to achieve (Wilson et al. 2002), therefore, research using such devices should closely monitor their effects (Wilson et al. 1986; Casper 2009; McMahon et al. 2012).

Previous researchers have measured effects of attached devices on different aspects of seabird biology: for example, investigating the hydrodynamic properties of real (Culik et al. 1994) and model animals (Bannasch et al. 1994); foraging trip durations (Hull 1997); colony attendance (Sohle et al. 2000); chick growth patterns (Ackerman et al. 2004; Adams et al. 2009); and breeding success (Ballard et al. 2001; Barbraud and Weimerskirch 2012). The number of published papers in which devices have been used on seabirds has increased during the past three decades, yet there has not been a comparative increase in the documentation of the effects of the devices on individuals (Barron et al. 2010; Vandenabeele et al. 2011). Only 11.8% of papers examined by Vandenabeele et al. (2011) focused on effects on the device carrier. This is also true of papers specific to little penguins (*Eudyptula minor*). Device effects on little penguins have been addressed indirectly, via recording body weight before and after device attachment and/or breeding success during and after device attachment (e.g. Ropert-Coudert et al. 2003; Preston et al. 2010). However, few researchers have presented detailed results of such analyses or used proper controls (individuals without devices) to quantify effects of attached devices on little penguins (Collins et al. 1999). Few published papers have focused on device effects as their central objective (Ropert-Coudert et al. 2007a).

Our objective was to quantify any effects of data-logging devices attached to little penguins through various stages of the breeding season via measuring changes in body weight, breeding performance and survival of adult little penguins, and also effects on chick growth. Adult body weight of little penguins provides a measure of physical condition, and may influence the timing of breeding (Robinson et al. 2005), the potential for egg desertion (Numata et al. 2000), chick survival (Numata et al. 2004; Saraux et al. 2011b) and overall breeding success (Numata et al. 2004). We predicted that individuals with devices attached would gain less body weight at sea than individuals without devices and chicks belonging to parents with devices attached would experience reduced growth rates.

4.3 Methods

The study was conducted at the Oamaru Blue Penguin Colony (45°07’S, 170°58’E), Oamaru, South Island, New Zealand. This study population is located in a disused quarry at the foot of an artificial breakwater that forms the eastern arm of Oamaru Harbour. The location is managed to mitigate impacts of introduced predatory mammals and human disturbance. The penguins nest in nesting boxes, with each box checked weekly as part of a systematic monitoring programme that began in 1993 (Johannesen et al. 2003). During monitoring each nest is checked and the presence of eggs, chicks and/or adults recorded. All breeding adults have been banded with a metal flipper-band on their right flipper. Chicks are banded prior to fledging. The study population increased from 33 breeding pairs in 1993 (Perriman et al. 2000) to 160 breeding pairs in the 2010 breeding season and then dropped to 145 pairs during 2011.

4.3.1 Data collection

We attached two types of data-logging devices independently to little penguins; Global Positioning System (GPS) devices (Earth & Ocean Technologies, Germany) measuring 47 x 23.5 x 13 mm (Figure 4.1), with a cross-sectional area of 293 mm^2 and weighing 14 g in air, and cylindrical Time-Depth Recorder (TDR) devices (Lotek, Canada) measuring 8 mm diameter x 32 mm length (Figure 4.1), with a cross-sectional area of 50 mm^2 and weighing 3.4 g in air. The GPS devices were 5%, and the TDR devices 1% of the frontal cross-sectional area (5500 mm^2; Lovvorn et al. 2001) of little penguins. Devices were attached on the lower back (Bannasch et al. 1994) with waterproof tape (Tesa®, Germany) following Wilson et al. (1997b), in accordance with permits from Otago University Animal Ethics Committee (83/09) and Department of Conservation, New Zealand. Birds were caught in their nesting boxes during the day and hand-held for less than 5 min while devices were attached.

Figure 4.1. Time-depth recording device (top) and Global Positioning System device used on little penguins at Oamaru.

The study was carried out during the 2010 and 2011 breeding seasons. Breeding seasons were defined as beginning 1 May and ending 30 April of the following calendar year and referred to by the calendar year in which they began. Birds included at the beginning of the study were all known-age individuals present during the pre-egg stage of the 2010 season. Individuals that survived from 2010 to 2011 were included again during 2011 (provided they remained breeding with a known-age partner), along with additional known-age birds present at the beginning of the 2011 season. A total of 113 little penguins were included; 58 during 2010 and 96 during 2011 (41 of which were involved in both seasons).

To assess effects of the devices, changes in body weight of birds with devices attached were compared to control individuals without a device. Individuals were randomly assigned as ‘instrumented’ individual (with a device attached) or ‘control’ (without), with no more than one instrumented individual per pair. There were 20 instrumented and 38 control individuals during 2010 and 36 instrumented and 60 control individuals during 2011. Each instrumented individual had the same device-type each time, with an equal number of males and females for each device. GPS devices were deployed for single foraging trips, due to limited battery life and were deployed twice per individual during incubation. The TDR devices were left attached for successive foraging trips, since the capacity of the unit was based on the amount of data collected and not restricted by battery life. The control group was separated into GPS-control individuals and TDR-control individuals, so that procedures for monitoring individuals were the same for the instrumented and control individuals.

Body weight was measured to the nearest 10 g (< 1 kg) or 20 g (> 1 kg) using Pesola spring balances and was recorded initially when individuals were included in the study and again following periods of time spent on land or at sea. Body weights for GPS-instrumented individuals and GPS-control individuals were recorded at the beginning and end of a foraging trip. Corresponding body weights for TDR-instrumented individuals and TDR-control individuals were recorded at the beginning and end of a deployment period which covered a number of successive foraging trips.

To avoid unnecessary disturbance caused by weighing individuals every day, the equation:

$$W_d = W_t e^{-kt}$$

(Croxall 1982), was used to estimate body weight on the day individuals departed the colony, where W_d is the weight at departure, W_t is the weight when the bird was weighed t days before departure and k is the proportion of body mass lost per day (estimated for each individual). Individual estimates of the proportion of body mass lost per day were based on the rates that each individual lost weight during successive days spent on land.

To assess the effects of devices on the growth of offspring, devices were attached to adults after the first chick in each nest reached one week old. TDR devices were deployed for a minimum of five foraging trips and GPS devices deployed for a minimum of two successive trips, which required handling the bird in between to replace the battery. Chicks were weighed from one week old, every 3-4 days until the chicks fledged. Chicks were identified by marking the first chick with a piece of string tied around the right leg until they were banded at six weeks of age. Weighing of adults was kept to a minimum during chick-rearing to limit disturbance in the nest. Chick growth parameters recorded (for each chick that fledged) followed Chiaradia and Nisbet (2006): linear growth rate (LGR, gd^{-1}), the slope of the regression line fitted to data from first weighing to 35 days; peak mass (g), the maximum mass recorded; and age at peak mass (days). For these analyses all chicks from nests where both parents were control adults were grouped together as control chicks, to be compared to chicks from nests in which one adult had a GPS device attached and to chicks from nests where one adult had a TDR device attached.

Breeding performance was recorded as eggs laid, eggs hatched and chicks fledged for pairs from the Oamaru study population. Hatching success was defined as the proportion of eggs hatched out of eggs laid and fledging success, the proportion of chicks fledged out of eggs hatched. Survival rates recorded for instrumented individuals were compared with those for control individuals and for all other breeders for both breeding seasons.

4.3.2 Statistical analyses

We tested the effects of devices on body weight change of instrumented individuals using a set of a priori models (Anderson et al. 2000). We used mixed-effects models with nest site number for each breeding pair and band number as random effects, and device (GPS or TDR), age (integer years), gender (male or female), initial body weight (g) and season as fixed effects. Interaction effects between device and all other fixed effects were also examined, giving a set of 18 models for each device-type. To examine the effects of attached devices on the chicks of instrumented individuals, nest site number was also included as a random effect, and device (chicks from an instrumented parent compared to controls), hatch date (integer day beginning 1 May) and mean parental age (average of both parents) were included as fixed effects. We ran the statistical models using a Monte Carlo Markov Chain (MCMC) simulation implemented in the package JAGS (Plummer

2009) in R software version 2.13.0 (http://www.r-cran.org/, accessed 30 March 2012). We ran three MCMC chains for 1,000,000 iterations each, with a 500,000 “burn-in” period (Plummer 2009) (retaining every 100th sample). Chain convergence was checked using the Gelman-Rubin diagnostic R-hat (Gelman and Rubin 1992) in the R package coda (Plummer et al. 2006). R-hat values close to one indicated chain convergence. Due to the inclusion of random effects, models were compared using the deviance information criterion (DIC) as described in Spiegelhalter et al. (2002). For each model, the pD, DIC, DIC difference (ΔDIC) and model weight (w_i) were calculated. The pD is the effective number of parameters in a model (Spiegelhalter et al. 2002). The ΔDIC is the difference between the DIC of the candidate model and the highest ranked model with the lowest DIC. Models regarded as having substantial support have ΔDIC ≤ 2 (Burnham and Anderson 2004). The model weight is the likelihood of a model given the data and is represented as the proportional weight of evidence for each model relative to the entire set (Johnson and Omland 2004). The 95% credible intervals (CrI) (Plummer et al. 2006) on the regression coefficients for fixed effects were also presented; significant effects had a credible interval that did not span zero.

A generalized linear mixed-effect model (GLMM) (using R package Ime4) was used to test for variation in hatching success between pairs with one GPS adult, pairs with one TDR adult, pairs with two control individuals and all other breeding pairs (collectively defined as group). The model had eggs hatched as a binary response (0 = not hatched, 1 = hatched), nest site number as a random effect and group as a fixed effect. The model was tested using a log-likelihood ratio χ^2 statistic to assess closeness of fit to a model without the group effect included, the model was regarded as a good fit when $P < 0.05$.

Monthly survival rates of instrumented, control and other breeders were estimated for 2010 and 2011 using the Cormack-Jolly-Seber model (Lebreton et al. 1992) in program MARK (White and Burnham 1999). Recapture data were extracted from the weekly monitoring programme; multiple records within a month were treated as a single recapture in the encounter history matrix. The matrix had 13 columns (one per month from May onwards until May of the following season) and one row per individual. The encounter histories were based on weekly monitoring to satisfy the assumption that the probability of recapture was the same for all individuals.

4.4 Results

The penguins exhibited a regular pattern of attendance during the pre-egg stage of both breeding seasons: they were ashore for 7-14 consecutive days alternating with a similar duration at sea. To minimise loss of GPS devices and ensure that an entire foraging trip was recorded in each deployment, they were used after egg-laying began. The TDR devices were deployed during the pre-egg stage of both 2010 and 2011 seasons.

During 2010, egg laying by study pairs began on 27 July and continued until 11 September for first clutches. Twenty-eight pairs laid eggs, 24 of which successfully fledged chicks and 20 of those pairs laid a second clutch for the season. Egg laying by study pairs began around the same period during 2011, on 24 July. An unusually long fetch and long-lasting southerly storm from 14-17 August brought snow to sea level along the South Island east coast, sustained low temperatures at Oamaru (8th lowest mean temperature over 48 hours since 1972), sustained gale to storm force winds, and swells of up to 13.8 m (measured at the nearest wave buoy, at Banks Peninsula, c. 240km away). All nine pairs that had laid eggs by this date failed to raise chicks; seven pairs abandoned their eggs and two pairs had chicks die a few days after hatching. No more eggs were laid until 26 September 2011. Overall, 45 pairs laid eggs, 38 of which successfully fledged chicks. Due to the late re-start to the 2011 breeding season, no pairs laid another clutch after successfully fledging chicks. Analyses were restricted to incubation of the first clutch and rearing of first broods for the 2010 season and incubation of clutches laid and rearing of broods from September onwards for the 2011 season (for sample sizes see Table 4.1).

Table 4.1. Sample sizes of adult little penguins for each group during the incubation stage of the 2010 and 2011 breeding seasons at Oamaru. Device-type included a Global Positioning System (GPS) device attached or a Time-Depth Recorder (TDR) attached.

Breeding season	Device-type	Instrumented	Handled control	Total
2010	GPS	10	20	30
	TDR	9	17	26
2011	GPS	18	30	48
	TDR	15	27	42

Instrumented and control individuals for both types of device, on average, gained weight while at sea during incubation (Figure 4.2). Unexpectedly, males with GPS devices gained more weight than control males and male penguins carrying TDR devices gained less weight than control males. Instrumented females showed the opposite trend, though not significantly so (Figure 4.2). A number of fixed effects contributed to the variation in body weight gain by GPS and control individuals, including initial weight, age and gender (Table 4.2). The best three models all showed substantial support with ΔDIC ≤ 2 (Burnham and Anderson 2004). The best model for weight gain by the TDR and control individuals (Table 4.2) had device (95% CrI: -28.5, -0.07), age (95% CrI: -1.2, 0.4) and the interaction between the two (95% CrI: -0.3, 3.5) as fixed effects, with device the only significant variable.

Table 4.2. Top five models for mean estimated daily body weight gain of GPS instrumented and handled control individuals, and TDR instrumented and handled control individual little penguins during incubation in the 2010 and 2011 breeding seasons, at Oamaru. pD: an estimate of the effective number of parameters; DIC: deviance information criterion; ΔDIC: difference between each model and the best model; w_i: model weight.

Device group	Model	pD	DIC	ΔDIC	w_i
GPS	Device*Initial weight + Gender	74.4	1216.7	0.0	0.45
	Age*Device + Gender + Initial weight	74.0	1218.4	1.7	0.19
	Device*Initial weight + Age + Gender	76.6	1219.0	2.3	0.14
	Device*Initial weight	73.9	1221.1	4.4	0.05
	Device*Initial weight + Age	74.6	1221.6	4.9	0.04
TDR	Age*Device	96.6	586.6	0.0	0.71
	Device	99.9	590.5	3.9	0.10
	Season	100.8	591.7	5.1	0.06
	Age*Device + Gender	102.0	591.8	5.2	0.05
	Age*Device + Initial weight	102.3	592.6	6.0	0.04

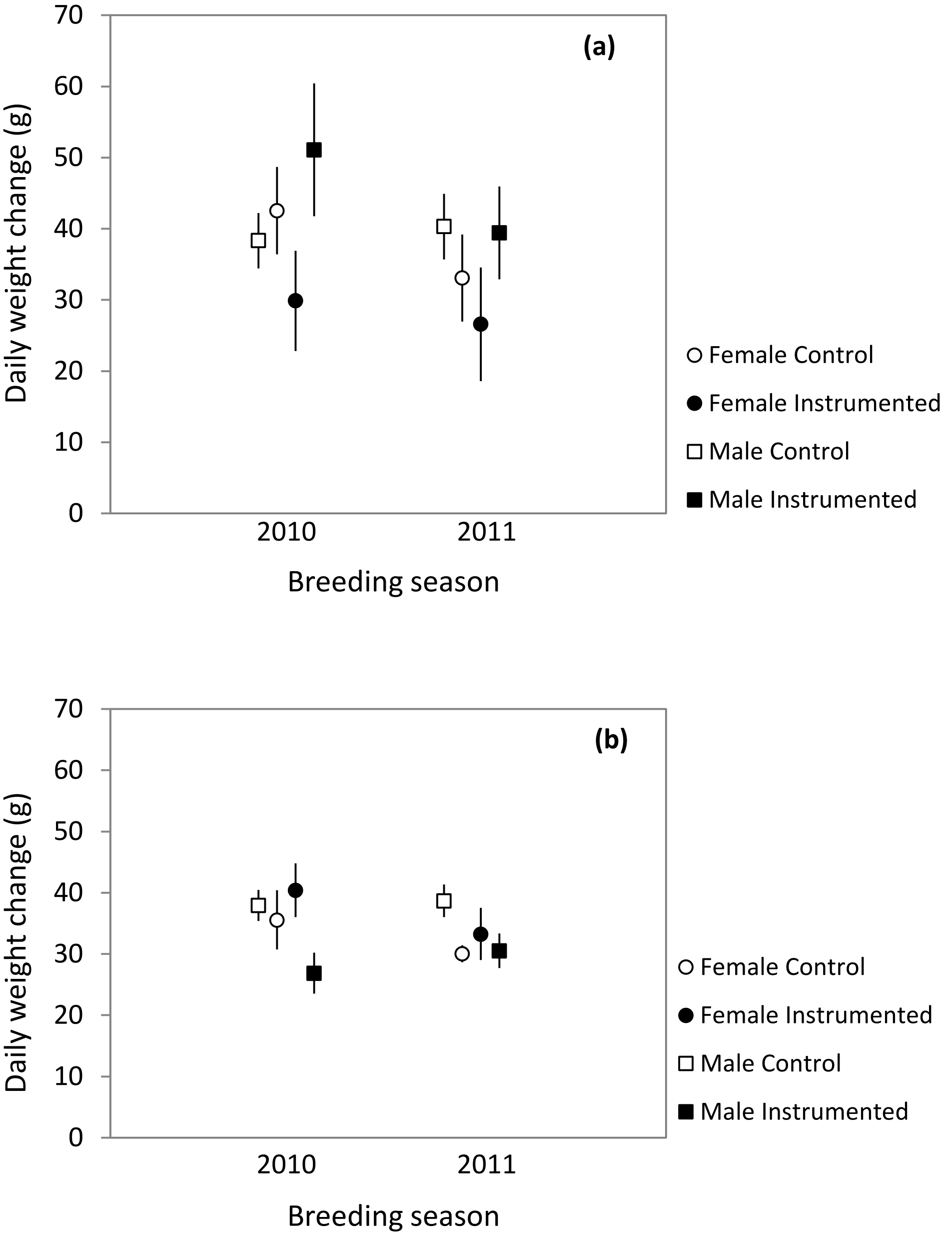

Figure 4.2. Mean estimated body weight change per day while at sea (± SE), of instrumented and control little penguins during incubation in the 2010 and 2011 breeding seasons at Oamaru: (a) instrumented individuals with a Global Positioning System (GPS) device attached and GPS-controls and (b) instrumented individuals with a Time-Depth Recorder (TDR) attached and TDR-controls.

The attachment of devices to adults did not impact the growth rates of offspring during either breeding season as the mean growth rates were almost identical (<1 g difference; Table 4.3). Peak mass and age at peak mass were similar (< 1 g and <1 day, respectively) for chicks from control pairs and pairs in which one adult had a device attached, during the 2010 breeding season (Table 4.3). During the 2011 season, chicks belonging to control pairs reached higher mean peak mass, at an older age (Table 4.3). The model with fixed effects of device (95% CrI: -57.8, 0.5), hatch date (95% CrI: -1.5, -0.7) and the interaction between the two (95% CrI: -0.04, 0.3) was the best model for explaining variation in peak mass for both seasons (Table 4.3). However, hatch date was the only significant variable; the negative value for the regression coefficient indicating that peak mass decreased as hatch date increased. The model with fixed effects of device (95% CrI: -2.6, 10.1), mean parental age (95% CrI: -0.3, 0.9) and the interaction between the two (95% CrI: -1.5, 0.03) was the best model for explaining variation in the age at peak mass data for both seasons (Table 4.3), yet the variables were not significant.

Table 4.3. Mean linear growth rate (LGR), peak mass and age at peak mass of chicks (SE) from control nests, nests where one parent had a Global Positioning System (GPS) device attached and nests where one parent had a Time-Depth Recorder (TDR) attached during chick-rearing in the 2010 and 2011 breeding seasons at Oamaru; *n*: number of chicks per group.

Season	Group	*n*	LGR (g^{-d})	Peak mass (g)	Age at peak mass (days)
2010	Control	13	30.3 (0.8)	1215 (26.4)	45.2 (1.6)
	GPS	18	30.6 (1.1)	1216 (25.6)	46.4 (0.9)
	TDR	14	31.5 (0.8)	1214 (25.8)	45.1 (1.2)
2011	Control	16	30.1 (0.9)	1179 (18.9)	47.3 (1.3)
	GPS	31	31.0 (0.4)	1145 (13.2)	43.8 (0.9)
	TDR	22	30.9 (0.8)	1144 (24.4)	44.5 (1.0)

Table 4.4. Top five models for mean peak mass and age at peak mass of chicks, from control nests and nests where one parent had a device attached, during chick-rearing in the 2010 and 2011 breeding seasons at Oamaru. pD: an estimate of the effective number of parameters; DIC: deviance information criterion; ΔDIC: difference between each model and the best model; w_i: model weight.

Response variable	Model	pD	DIC	ΔDIC	*wi*
Peak mass	Device*Hatch date	963.2	3782.1	0.0	1.00
	Hatch date	971.7	3797.2	15.1	<0.001
	Device*Mean parental age	1070.7	3977.8	195.7	<0.001
	Device*Season	1062.9	3989.8	207.7	<0.001
	Mean parental age	1059.9	3993.0	210.9	<0.001
Age at peak mass	Device*Mean parental age	83.7	752.9	0.0	0.99
	Device	94.2	763.9	11.0	<0.001
	Device*Season	96.4	766.2	13.3	<0.001
	Season	101.2	770.7	17.8	<0.001
	Device*Hatch date	102.5	771.5	18.6	<0.001

Hatching success of pairs was not significantly affected by the attachment of devices during either season, as the GLMM with the group effect included did not fit the data well compared to the model without group (2010: $P = 0.617$, 2011: $P = 0.638$). The attachment of devices also did not affect fledging success of pairs with an instrumented adult, as these pairs successfully fledged all chicks (Table 4.5). Survival of instrumented penguins was not significantly affected by the attachment of devices (Figure 4.3).

Table 4.5. Hatching and fledging success (SE) of pairs with one instrumented adult (Global Positioning System (GPS) or Time Depth Recorder (TDR) attached), pairs with two handled-control adults and non-handled control little penguins during the 2010 and 2011 breeding seasons at Oamaru. Clutches included were first clutches during 2010 and clutches laid after 1 September during 2011.

Season	Group	Hatching success	Fledging success
2010	GPS	0.90 (0.07)	1.00 (0.00)
	TDR	0.78 (0.10)	1.00 (0.00)
	Handled controls	0.79 (0.10)	0.87 (0.09)
	Non-handled controls	0.84 (0.02)	0.94 (0.02)
2011	GPS	0.86 (0.06)	1.00 (0.00)
	TDR	0.73 (0.08)	1.00 (0.00)
	Handled controls	0.82 (0.08)	0.89 (0.08)
	Non-handled controls	0.81 (0.03)	0.97 (0.01)

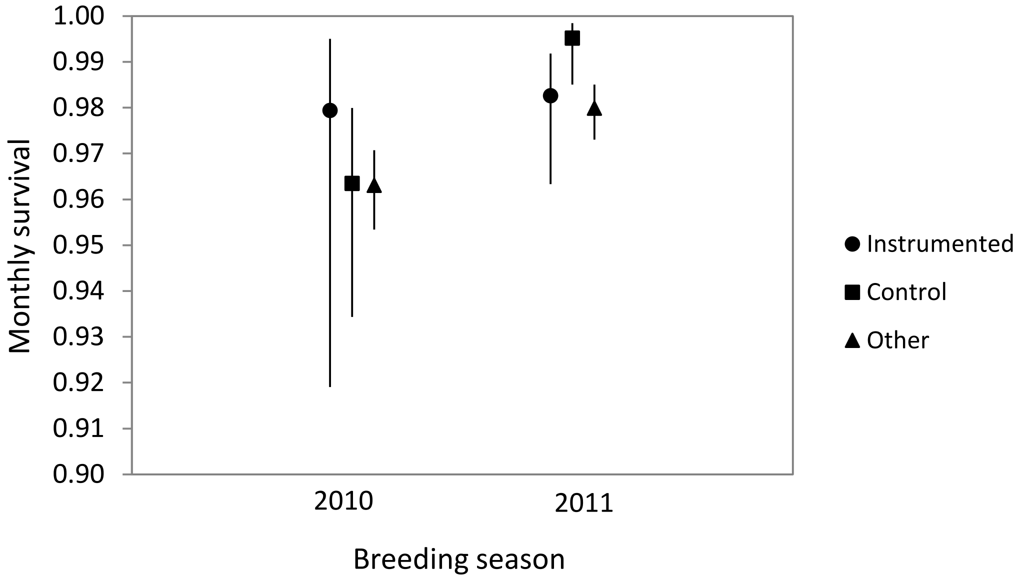

Figure 4.3. Mean monthly survival rates of instrumented, control and other breeding little penguins (95% CI), at Oamaru during the 2010 and 2011 breeding seasons.

4.5 Discussion

Comparisons of instrumented and control little penguins in our study established that attached devices had no detectable effects on adult body weight, chick growth, breeding success or survival. We expected that the larger device, the GPS, would have a more profound effect than the TDR. The size difference between our devices was substantially larger than previous studies comparing devices of differing size attached to penguins (Hull 1997; Ropert-Coudert et al. 2007a), yet the larger device showed no obvious effect. Previous research suggests that little penguins are able to adjust their diving behaviour to accommodate for increased drag and energy expenditure caused by attached devices. Ropert-Coudert et al. (2007a) found that little penguins carrying the larger of two attached devices made more dives, of shorter duration and shallower depth. Females with larger devices increased their descent rate, presumably to reduce transit time to the bottom of the dive (Ropert-Coudert et al. 2007a). The paper did not report whether diving behaviour was a key factor in weight gain and breeding success. The ability of little penguins to compensate for an attached device by increasing foraging effort may explain why instrumented penguins in our study were able to maintain or increase their body weight compared to control individuals. However, it does not explain why individuals carrying larger devices in our study gained more weight than controls. Ample food supply may be another reason why the penguins were able to compensate for the increased drag of the attached devices. Evidence for this relates to the amount the penguins (with and without devices) were able to feed to their chicks compared to penguins at Phillip Island. Chicks belonging to Oamaru birds showed a higher linear growth rate and peak mass than chicks at Phillip Island, while achieving peak mass at around the same age (Chiaradia and Nisbet 2006).

The attached devices had no detectable impact on breeding performance. Collins et al. (1999) showed no difference in fledging success between instrumented and control little penguins, but found lower hatching success by instrumented individuals in two of three seasons studied. Negative effects of attached devices on breeding performance by individuals have been reported for other penguin species (Croll et al. 1996; Hull 1997; Beaulieu et al. 2010) and other seabird species (Ackerman et al. 2004; Whidden et al. 2007; Adams et al. 2009). The period of attachment of devices is considerably longer in projects involving larger penguin species and flying seabirds, due to the lifespan of the device (Whidden et al. 2007). Therefore, such researchers often deploy devices for the duration of the breeding season (Beaulieu et al. 2009) or at least for the duration of incubation (Beaulieu et al. 2010) or chick rearing (Whidden et al. 2007). While we did not attach devices for the duration of the breeding season, we established that it is possible to attach devices for repeated deployments and for longer periods than previous studies of little penguins with no detectable effects.

While there have been standard procedures informally established for the attachment of devices to seabirds, we recommend that the criteria for attachment should begin with a comparative study of instrumented versus control individuals. Researchers should not assume that the use of the smallest, most streamlined devices available will equate to minimal effects on the device carrier. We also recommend that several aspects of seabird biology are examined, due to the potential for indirect effects on chick growth and demographic parameters.

Chapter 5 :

Seasonal and annual variation in foraging of little penguins (*Eudyptula minor*)

5.1 Abstract

Seabirds must alter their foraging throughout the year to cope with variation in prey availability and the demands of breeding. We sampled foraging ranges and diving behaviour of breeding little penguins (*Eudyptula minor*) at Oamaru, New Zealand, using Global Positioning System and time-depth recording devices. We attached the devices during pre-egg, incubation and chick rearing stages over three breeding seasons (2010, 2011 and 2012). We aimed to determine how little penguins adjust their foraging depending on their breeding activity and to determine if variation in foraging relates to reproductive performance. Total distance travelled increased while dive depth decreased as the breeding season progressed. We found travel distance was similar among breeding seasons. Diving effort was similar when adults were incubating or rearing chicks. Among seasons, diving effort was higher during the rearing of second broods in 2010 compared to 2012. Breeding success was reduced during the 2010 breeding season attributed to a strong storm. Diving effort was, however, already high before the storm. We conclude that extrinsic factors were more important than stage-related demands of breeding in influencing little penguin foraging at Oamaru.

5.2 Introduction

Over the course of a year seabirds face variation and fluctuations in prey abundance that influence their reproduction. Prey abundance and availability varies due to a combination of factors, including variations in sea surface temperatures (Hansen et al. 2001), weather patterns (Beentjes and Renwick 2001), ocean currents (Chiswell and Schiel 2001), primary productivity and water stratification (Chiswell 2011). During the breeding season, seabirds are central place foragers (Orians and Pearson 1979) because they must commute to their feeding areas but return regularly to share incubation duties and feed offspring. Hence, seabirds must alter their foraging behaviour to obtain sufficient food for both reproduction and their own future survival (Charrassin et al. 2002; Ronconi and Burger 2008). Research on seasonal variation in seabird foraging behaviour can provide insights beyond foraging; it can indicate ecosystem health and change (Piatt et al. 2007; Cury et al. 2011; Dänhardt and Becker 2011). Examples of the strategies seabirds employ to increase foraging success include changes in foraging trip durations (Burke and Montevecchi 2009), range (Clarke et al. 2006), number of dives (Monaghan 1996; Peery et al. 2009) and dive depth (Kato et al. 2009; Miller et al. 2009; Lyver et al. 2011).

In penguins, foraging ranges are broadly proportional to body size, with smaller species generally having more limited foraging ranges due to slower swimming speeds than larger species (Sato et al. 2010). Hence smaller species would be expected to be particularly sensitive to variation in prey availability, which could impact both foraging behaviour and breeding success (Dänhardt and Becker 2011). Little penguins are the smallest of the 18 penguin species (Trathan et al. 2014) standing around 30 cm tall and weighing c. 1 kg. Unsurprisingly, they have the most restricted foraging range, not only in terms of distance from the colony but also in achievable diving depth (Ropert-Coudert et al. 2006a). As visual foragers they are further restricted to foraging during daylight hours (Cannell and Cullen 1998). Foraging behaviour of little penguins varies across their distribution and correlates with variation in breeding success: across four colonies in Australia and New Zealand, dive depth and foraging effort was higher in colonies with lower fledging success (Chiaradia et al. 2007). In New Zealand, little penguins at Motuara Island in the Marlborough Sounds show increased foraging effort (higher dive frequency, greater depth and duration; Mattern 2001) and lower body condition and breeding success (Numata et al. 2000; 2004) than those at Oamaru, approximately 500 km to the south. The lower foraging effort and higher breeding success at Oamaru suggested a greater abundance of prey (Numata et al. 2004). Few researchers have examined variation in foraging through time at any one breeding colony of little penguins, instead restricting sampling to single stages of the breeding season and single deployments of attached devices (Chiaradia et al. 2007). Increased miniaturization of data-logging devices makes it is possible to attach devices repeatedly to individual little penguins through the season with no detectable impacts (Agnew et al. 2013). Repeated attachment would aid our understanding of how foraging relates to the breeding cycle and varies across breeding seasons.

Our study was designed to investigate variation in foraging behaviour of little penguins within and among three consecutive breeding seasons, at Oamaru. Specifically, we wished to explore two main predictions; that foraging effort would increase during chick rearing relative to incubation or pre-egg stages, and that foraging effort would vary with breeding success. Finally, we examined foraging behaviour in response to variation in marine productivity within the penguins’ foraging zone.

5.3 Methods

5.3.1 Data collection

The study location was the Oamaru Blue Penguin Colony (OBPC) (45°07’S, 170°58’E), Oamaru, New Zealand. The study location and weekly nest-checking methodology have been described previously (Agnew et al. 2013; 2014). We attached data-logging devices prior to egg-laying, during incubation and chick rearing of the 2010/11, 2011/12 and 2012/13 breeding seasons. The onset of egg-laying varies annually and occurs between May and September, we therefore defined a breeding season to begin 1 May and finish 30 April of the following calendar year and referred to each breeding season by the calendar year in which breeding began (Agnew et al. 2014).

We attached two types of devices separately to different individuals; cylindrical Time-Depth Recorders (TDRs; Lotek, Canada; LAT1500, 512k; measuring 8 mm diameter x 32 mm length, with a cross-sectional area of 50 mm^2 and weighing 3.4 g in air) and Global Positioning System (GPS; Earth & Ocean Technologies, Germany; mGPS-2; measuring 47 x 23.5 x 13 mm, with a cross-sectional area of 293 mm^2 and weighing 14 g in air). Devices were attached to feathers on the lower back (Bannasch et al. 1994) with waterproof tape (Tesa®, Germany) following Wilson et al. (1997b), in accordance with permits from Otago University Animal Ethics Committee (83/09) and Department of Conservation, New Zealand. Device attachment took less than five minutes.

The TDRs measured hydrostatic pressure to an accuracy of ± 1%. Prior to deployment we checked the zero-offset of each device by manually lowering the devices to known depths in seawater. To conserve memory and ensure at least 5 days of recording per deployment, the tags recorded pressure (at 1Hz) every second only if pressure was greater than 1 dbar (c.1 m deep).

To conserve battery power, our GPS tags could be programmed to search for satellites only at specific intervals. After trialling intervals of 2, 5, 10 or 20 minutes we set devices to search for a satellite every 2 or 5 minutes ending the search after 5 minutes (when the device would switch off for five minutes). GPS devices were set to begin recording around sunrise on the date we predicted the penguins would go to sea. Attachment naturally involved some guesswork, however the penguins swapped duties on the nest regularly during incubation and daily during the guard stage. Therefore it was possible to predict when individuals were likely to go to sea, and attach devices beforehand. According to the manufacturer's specifications the accuracy of the GPS devices in intermittent mode was <20 m for 90% of position fixes.

During the pre-egg stage individuals were randomly selected for inclusion in the study; we aimed to use the same individuals each breeding season with the addition of new individuals if previously sampled individuals disappeared. We identified five stages during the breeding season: pre-egg stage (PE), incubation of first clutch (I1), rearing of chicks from the first brood (C1), incubation of the second clutch of a double brood (I2) and rearing of chicks from the second brood of a double brood (C2). Devices were deployed during all five stages. During the chick stage devices were attached only after the first chick in the nest was > 1 week old.

Reproductive performance during the three breeding seasons was examined as: median lay date of first clutches per breeding season; breeding success, the number of chicks fledged per female per breeding season; hatching success, the proportion of chicks hatched from eggs laid; and fledging success, the proportion of chicks fledged from chicks hatched (Agnew et al. 2014). Among breeding seasons we compared body weights for adults that fledged ≥1 chick (following Agnew et al. 2013) and for chicks at fledging (following Agnew et al. 2014).

Chlorophyll *a* data were extracted from a global dataset produced by the National Oceanic and Atmospheric Administration (NOAA) National Climate Data Center and made available on the Physical Oceanography Distributed Active Archive Center (PO.DAAC) website (http://thredds.jpl.nasa.gov/las/getUI.do, NASA Jet Propulsion Laboratory, Pasadena, CA). The chlorophyll *a* data, captured by the Moderate-resolution Imaging Spectroradiometer (MODIS), had a monthly temporal resolution and a spatial resolution of 4 km.

5.3.2 Statistical analyses

We used Multitrace Dive software (Jensen Software Systems, Germany) to process raw dive data. For each dive we obtained the dive duration (s), bottom phase duration (s), dive depth (maximum depth in metres reached during a dive), dive shape ('V' dives were symmetrical dives without a bottom phase, 'U' shape dives had a bottom phase; Bost et al. 2007) and the proportion of bottom time (calculated as the bottom phase duration/dive duration for U-shaped dives). Dive durations of less than 5 s were excluded as they were likely to represent near-surface travelling behaviour (Bengtson et al. 1993; Ropert-Coudert et al. 2001). The beginning and ending of the bottom phase of a dive were determined by a change in the vertical speed of the penguin to less than 0.3 m/sec, following recommendations from Jensen Software Systems based on our data.

We then calculated the median values of dive variables per penguin per day instead of means as many of the data were not normally distributed. These daily dive variables per penguin were the number of foraging dives, the daily total duration of dives ≥5 s long (h, defined as diving effort), total vertical distance travelled (km), total duration of the bottom phase (h), proportion of the day spent diving, proportion of dives that were U-shaped and proportion of consecutive dives to the same depth zone (intra-depth zone dives, IDZ). The total vertical distance travelled was defined as twice the sum of the maximum dive depth for each dive (Horning and Trillmich 1997). The proportion of the day spent diving was calculated as the daily total duration of diving divided by the total daylight hours (which ranged from 8.75 h on 22 June, around the beginning of the breeding season, to 15.50 h on 22 December, towards the end of the breeding season). Intra-depth zone dives were defined as dives with a maximum depth to within 10% of the preceding dive (Tremblay and Cherel 2000). From the GPS data we calculated the maximal distance from the colony and the total foraging distance, as the sum of the distances between each GPS location recorded for each penguin per foraging trip beginning and ending at the colony.

To reduce the number and examine the relatedness of dive variables we carried out a principal components analysis (PCA) on the daily medians and summary dive variables using R software version 2.15.3 (R Development Core Team 2013). An aim of PCA is to reduce the dimensionality in the data by combining related variables (Jolliffe 2005). The procedure transforms the original (possibly) correlated variables into uncorrelated variables (principal components). The first few components explain most of the variability in the data (Jolliffe 2005). The PCA was computed on a correlation matrix; correlations are the covariances of standardised variables (Legendre and Legendre 2012). The PCA was then rotated using Varimax on the components that had an eigenvalue >1 to facilitate interpretation of the components, using package *psych* in R software.

Based on the results of the PCA we then selected original dive variables to examine further. We had multiple days of dive data for each penguin at each stage of breeding, so we first calculated the mean per penguin per stage, and used these to calculate means for each stage of the three breeding seasons. We also calculated means of the foraging distance data for each stage of each breeding season. We then used linear mixed models (LMM) on the complete dataset (not the averaged data) in package *nlme* in R software to compare foraging variables among breeding seasons, date of the foraging trip and stages of the breeding season. For analyses, foraging date was designated as the nominal date as an integer from day one (1 May) onwards. We examined stage of breeding both as a continuous (“stage”) and a categorical (“stage 2”) effect to identify if changes in variables were continual through the breeding season or occurred only in specific stages. Daily summary data were tested for normality and log-transformed if non-normal. Breeding season was classed as a categorical rather than continuous effect as we were not looking at linear changes over time. In models with a categorical effect, the first level becomes the reference level. Breeding season, stage and the date of foraging were fixed effects and individual identity (band number) was included as a random effect to avoid pseudo-replication. Each fixed effect was examined individually in the model plus an interaction effect between the date of foraging and breeding season. We compared models based on the difference in Akaike's Information Criterion (ΔAIC). Models were considered to have "substantial" support if their ΔAIC values were within 2 points of the lowest AIC score and "some" support if within 3 to 7 AIC points (Burnham and Anderson 2002). We present the models with the lowest AIC scores and those with ΔAIC values ≤ 2. We also used LMM to compare foraging variables between incubation and chick stages; this model was tested using a log-likelihood ratio χ^2 statistic to assess closeness of fit to a model without the fixed effect included (the null model). The model was regarded as a good fit when $P < 0.05$.

5.4 Results

5.4.1 Reproductive performance and adult body weight

The first eggs for the colony were laid each season on 7 July 2010, 17 July 2011 and 17 June 2012. Breeding success was higher during the 2010 and 2012 breeding seasons (chicks fledged per female: 2.31, 2.27 respectively) compared to the long-term mean of 1.86 for the Oamaru colony through the previous 16 years, 1994–2009 (Agnew et al. 2014). Breeding success was below average during the 2011 breeding season (1.56), attributed to a winter storm during August (Agnew et al. 2013). The storm occurred on 14 August and was so severe that clutches already laid were abandoned. The penguins did not re-commence laying until late September (Agnew et al. 2013). We defined clutches laid after the storm as first clutches, which meant that the median lay date of first clutches was later during 2011 than the other two seasons (Table 5.1) and resulted in no double brooding.

There was also a summer storm from 18–25 January 2011, towards the end of the 2010 breeding season. The storm was less severe than the August 2011 storm but sustained higher wave heights than would be typical for austral summer months (around 2m compared to < 1m, MetOcean Solutions unpublished data), high waves persisted for five days. The number of penguins arriving ashore in the evening dropped from 162 to 35 over a few days and continued to remain below average (OBPC unpublished data). Many chicks were not fed and 17 of the 125 second-brood chicks died, resulting in fledging success significantly lower than 2012 (Table 5.1, Fisher's exact test: P = 0.003). Hatching success and fledging success of first broods were similar for the three seasons. Chicks from the second brood during 2010 fledged lighter than chicks from the second brood during 2012 (mean difference = 42 g; 95% CI = 6 − 78). With the exception of the first brood during 2012, chick fledge weights from the current study (Table 5.1) were lower than the long-term mean (of 1069 g) from 1994-2009 for all chicks (Agnew et al. 2014).

There was no difference between the body weight of breeding little penguins during the pre-egg stage of the 2010 and 2012 breeding seasons (mean difference = 18 g; 95% CI = -33 − 69), however body weight was significantly heavier during the pre-egg stage of both 2010 (mean difference = 63 g; 95% CI = 17 − 109) and 2012 (mean difference = 80 g; 95% CI = 33 − 128) compared to 2011 (Table 5.2). The percentage of body weight lost from the pre-egg stage to the chick stage of first broods was greater during 2010 (mean difference = 6.3%; 95% CI = 3.5 – 9.1) and 2012 (mean difference = 10.9%; 95% CI = 7.2 – 14.6), compared to 2011, and also greater during 2012 compared to 2010 (mean difference = 4.6%; 95% CI = 1.4 – 7.8). The percentage of body weight lost from the pre-egg stage to the chick stage of second (of double) broods was similar for the 2010 and 2012 breeding seasons (Table 5.2, mean difference = -3.3%; 95% CI = 0.3 - -7.0).

Table 5.1. Breeding parameters and mean chick fledge weights for the population of little penguins at Oamaru during the three breeding seasons, 2010-2012. *n* = number of chicks.

	Median lay date		Hatching success		Fledging success		Chick fledge weights, g (*n* , SE)	
Season	1st	2nd	1st	2nd	1st	2nd	1st	2nd
2010	20-Aug	2-Dec	0.85	0.75	0.95	0.81	1040 (262, 8)	987 (101, 14)
2011	20-Oct		0.80		0.97		1057 (223, 8)	
2012	2-Sep	29-Nov	0.82	0.74	0.96	0.95	1073 (274, 7)	1029 (91, 12)

Table 5.2. Mean body weight (SE) of breeding little penguins during the pre-egg stage of the season and percentage of weight lost (SE) from the pre-egg stage to each of the other stages: from pre-egg to incubation of first clutch (I1), raising of first brood (C1), incubation of the second clutch of a double brood (I2) and raising of the second brood of a double brood (C2).

			% weight lost at stage:			
Season	*n*	Pre-egg body weight (g)	I1	C1	I2	C2
2010	34	1189 (18)	1.9 (1.1)	8.6 (0.9)	5.5 (0.9)	13.3 (1.1)
2011	61	1127 (15)	3.2 (1.0)	2.3 (1.2)		
2012	38	1207 (17)	5.6 (1.5)	13.1 (1.4)	4.3 (1.6)	10.0 (1.5)

5.4.2 Success of devices

We made 143 deployments of TDR devices using 26 individuals (13 females and 13 males), of which 135 deployments were successful. Eight deployments were not used due to: trialling a deeper ‘switch on’ depth (3), no data due to device failure (2), device loss (1) or non-return of the penguin they were attached to (2). The longest duration of deployment was 26 days and maximum duration of data collection was 14 days. We gathered 860 days of dive data from the 135 deployments. From the 135 deployments we excluded data collected from three penguins (one in 2010, two in 2012, totalling 30 days) with replacement clutches (clutches laid after the failure of the first clutch) as the sample size was considered too small to be representative of this stage in breeding.

We deployed the GPS devices on 241 occasions using 22 individuals (10 females and 12 males). We discovered during pre-egg deployments that the GPS devices did not stay attached to the penguins for long durations; based on how loose the tape had become we estimated the maximum attachment would be around nine days. The reason for device loss was tape wear on the top of the device; hence we attached GPS devices only during incubation and chick rearing stages only. Complete foraging trip data were obtained for 100 single-day trips (two of which were obtained from a single deployment). We also gained partial trip information for 19 longer (> 1 day) trips with the longest duration of operation being two full days of a six day trip. Of the deployments with incomplete trip information (total = 123) five were due to device loss, 44 returned no data, and the remaining 74 returned data for less than half of the foraging trip. The most likely reason for short functioning time was from battery exhaustion due to the penguins not surfacing for long enough for the device to obtain a fix. In that case the device continued to search until the search period times out, and used more battery power in this process than it did when it got a fix, and turned off.

5.4.3 Dive variables

Most of the variation present in the data for dive variables was explained by the first three components of the PCA (92%, Table 5.3). Dive depth, dive duration, IDZ dives and bottom phase duration were strongly correlated with the first principal component. Total vertical distance travelled, diving effort, number of dives, the proportion of the day spent diving and total duration of the bottom phase were strongly correlated to the second principal component. The proportion of bottom time and the proportion of dives that were U-shaped had the strongest contribution to the third principal component (Table 5.3). We selected four variables to examine further: median dive depth, diving effort, the number of dives per day per individual and the proportion of bottom time (Table 5.4).

Table 5.3. First three principal component loadings (after Varimax rotation) of daily dive variables of little penguins at Oamaru, 2010-2012. Variation explained and eigenvalue of each component also shown. Highest correlation for each variable in bold. Diving effort: total individual daily duration of diving (h).

Daily variables	PC1	PC2	PC3
Bottom phase as proportion of dive duration	-0.11	0.04	**0.94**
IDZ dives	**0.86**	0.20	0.16
Median bottom phase duration	**0.78**	0.15	0.58
Median dive depth	**0.94**	0.17	-0.16
Median dive duration	**0.93**	0.18	0.16
Number of dives	-0.40	**0.88**	0.00
Proportion of day spent diving	0.51	**0.74**	0.23
Proportion of total dives U-shaped	0.57	0.06	**0.74**
Total bottom phase duration	0.34	**0.72**	0.56
Diving effort	0.30	**0.93**	0.15
Total vertical distance	0.38	**0.89**	-0.15
Variation explained (%)	38	33	21
Eigenvalue	6.02	2.40	1.68

Median dive depth decreased through the 2010 and 2012 breeding seasons, and also decreased following incubation to chick stage of the 2011 breeding season (Table 5.4). For the set of LMMs on the (log transformed) median dive depths, the model with the lowest AIC included the categorical effect of stage as a predictor, with substantial support for the model with an interaction effect between the date of foraging and breeding season (Table 5.5). Diving effort increased during the first three stages of the 2010 and 2012 breeding seasons, then kept increasing during 2010 but decreased during 2012 (Table 5.4). The number of dives per day also increased with stage during 2010. The second chick-rearing stage of the 2010 breeding season showed the highest diving effort and the number of dives per day (Table 5.4). The best LMM for these two dive variables both included an interaction between the date of foraging and breeding season with a weight of 1.00 for each model (Table 5.5). There was little variation in the proportion of bottom time across breeding seasons (Table 5.4).

Table 5.4. Mean daily dive variables (SE) for little penguins at Oamaru during each stage of the breeding season, 2010-2012.

Season	Stage	*n*	Median dive depth (m)	Diving effort	Number of dives per day	Bottom time/ Dive duration
2010	PE	7	11.60 (0.70)	4.18 (0.16)	461 (15)	0.42 (0.01)
	I1	9	9.99 (0.65)	4.90 (0.38)	566 (42)	0.41 (0.01)
	C1	8	12.67 (0.95)	6.11 (0.41)	696 (60)	0.41 (0.01)
	I2	6	7.31 (0.57)	5.78 (0.28)	874 (57)	0.44 (0.01)
	C2	4	7.91 (0.56)	8.59 (0.28)	1264 (151)	0.46 (0.03)
2011	PE	9	8.49 (0.85)	4.94 (0.30)	584 (35)	0.47 (0.02)
	I1	15	10.27 (0.80)	7.05 (0.50)	836 (55)	0.46 (0.01)
	C1	13	6.66 (0.60)	4.17 (0.40)	727 (73)	0.44 (0.01)
2012	PE	6	9.74 (1.32)	4.89 (0.24)	620 (72)	0.47 (0.01)
	I1	17	8.28 (0.42)	5.31 (0.21)	754 (36)	0.44 (0.01)
	C1	13	9.80 (0.68)	6.26 (0.28)	898 (47)	0.42 (0.01)
	I2	9	6.31 (0.58)	3.38 (0.42)	597 (73)	0.44 (0.01)
	C2	7	5.06 (0.28)	3.90 (0.45)	838 (68)	0.42 (0.01)

n = number of individuals; Stages were – PE: pre-egg stage; I1: incubation of first clutch; C1: raising of first brood; I2: incubation of the second clutch of a double brood; C2: raising of the second brood of a double brood. Diving effort: total individual daily duration of diving (h).

Table 5.5. Set of models examining variation in each of three daily dive variables for little penguins at Oamaru, 2010-2012.

Variable	Model	df	AIC	ΔAIC	w_i
(Log) Median dive depth	Stage 2	7	968.72	0.00	0.67
	Date*Season	8	970.14	1.43	0.33
	Date	4	980.59	11.87	0.00
	Stage	4	1000.71	31.99	0.00
	Season	5	1051.07	82.35	0.00
	Null	3	1065.80	97.09	0.00
Diving effort	Date*Season	8	3370.19	0.00	1.00
	Stage 2	7	3418.91	48.71	0.00
	Season	5	3477.91	107.72	0.00
	Date	4	3489.34	119.14	0.00
	Null	3	3494.31	124.12	0.00
	Stage	4	3492.75	122.55	0.00
Number of dives per day	Date*Season	8	11425.42	0.00	1.00
	Date	4	11466.04	40.62	0.00
	Stage 2	7	11487.80	62.38	0.00
	Stage	4	11511.78	86.36	0.00
	Season	5	11631.35	205.93	0.00
	Null	3	11637.40	211.98	0.00

AIC: Akaike’s information criterion; ΔAIC: value of the difference between each model and the best model; w_i: Akaike weights; Date: date of the foraging trip; Season: breeding season; Stage: stage of the breeding season as a continuous effect; Stage 2: stage of breeding as a categorical effect. Diving effort: total individual daily duration of diving (h).

Median dive depth did not differ significantly from the pre-egg to first incubation and chick rearing, but was significantly shallower during the second incubation and chick rearing compared to the pre-egg stage (Table 5.6). Incubation of second clutches occurred during December and rearing of second broods during January (Figure 5.1). These two months showed the majority of dives were performed in the top 10 m of the water column (Figure 5.1). Median dive depth was also less variable during the later months (Figure 5.1). There was also evidence from the second best model (Table 5.6) of a negative relationship between median dive depth and the date of foraging. The slope of the relationship for the 2012 season was significantly different (further negative) to the slope for 2010 (Table 5.6).

There was a significant positive relationship between diving effort and the date of foraging in 2010 (Table 5.6, Figure 5.2), diving effort increased by approximately 30 minutes for every 30 days through the season. The slope of the relationships for 2011 and 2012 were negative, but not significantly so (Figure 5.2). The number of dives per day increased throughout each breeding season (Table 5.6).

Table 5.6. Results of the best models (ΔAIC ≤ 2) for three daily dive variables for little penguins at Oamaru, 2010-2012 (from Table 5.5).

Variable	Model	Parameter	Estimate	SE	*t*-value	*P*-value
(Log) Median dive depth	Stage (categorical)	(Intercept)	2.14	0.05	44.47	<0.001
		I1	-0.003	0.04	-0.07	0.95
		C1	-0.007	0.04	-0.16	0.87
		I2	-0.37	0.05	-7.21	<0.001
		C2	-0.48	0.06	-7.99	<0.001
(Log) Median dive depth	Date*Season	(Intercept)	2.49	0.07	34.43	<0.001
		Date	-0.002	0.00	-4.76	<0.001
		Season[2011]	-0.09	0.15	-0.59	0.56
		Season[2012]	0.05	0.10	0.48	0.63
		Date:Season[2011]	-0.00003	0.00	-0.04	0.97
		Date:Season[2012]	-0.001	0.00	-2.26	0.02
Diving effort	Date*Season	(Intercept)	2.83	0.30	9.46	<0.001
		Date	0.017	0.00	9.59	<0.001
		Season[2011]	4.40	0.64	6.91	<0.001
		Season[2012]	3.47	0.44	7.91	<0.001
		Date:Season[2011]	-0.025	0.00	-6.97	<0.001
		Date:Season[2012]	-0.025	0.00	-10.07	<0.001
Number of dives per day	Date*Season	(Intercept)	196.23	44.53	4.41	<0.001
		Date	3.30	0.22	14.92	<0.001
		Season[2011]	407.32	81.81	4.98	<0.001
		Season[2012]	417.81	57.42	7.28	<0.001
		Date:Season[2011]	-2.33	0.45	-5.14	<0.001
		Date:Season[2012]	-2.55	0.32	-8.06	<0.001

Date: date of the foraging trip; Season: breeding season; Stage: stage of the breeding season as a continuous effect; Stage 2: stage of breeding as a categorical effect, Diving effort: total individual daily duration of diving (h).

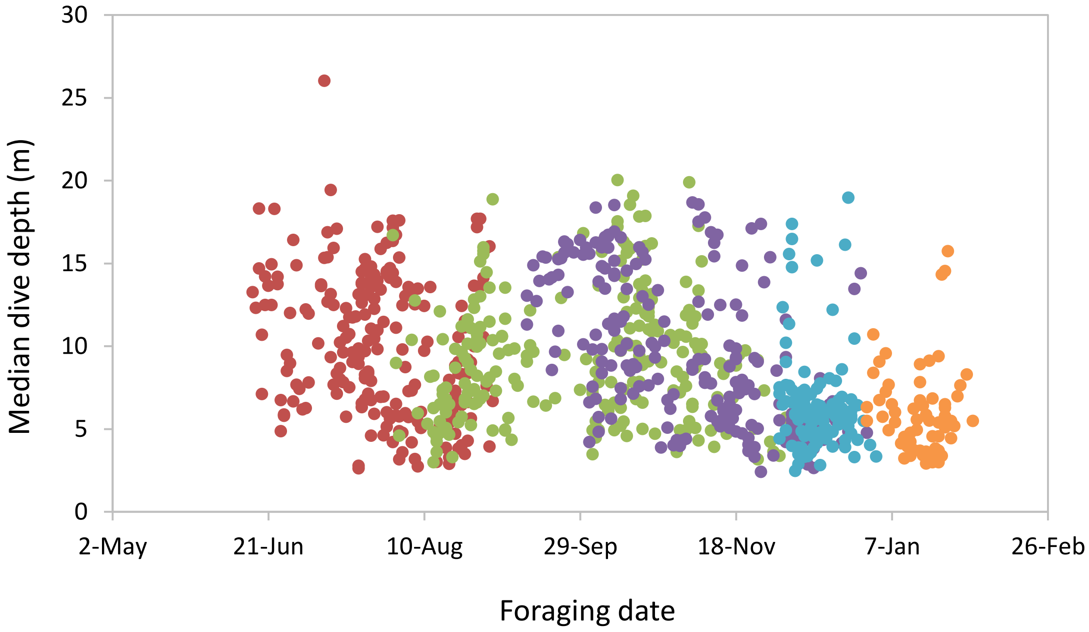

Figure 5.1. Daily median dive depth (m) in relation to foraging date of little penguins during the 2010-2012 breeding seasons at Oamaru. Differentially coloured marks represent the five stages of the breeding cycle: pre-egg stage; incubation of first clutch; raising of first brood; incubation of the second clutch of a double brood; raising of the second brood of a double brood.

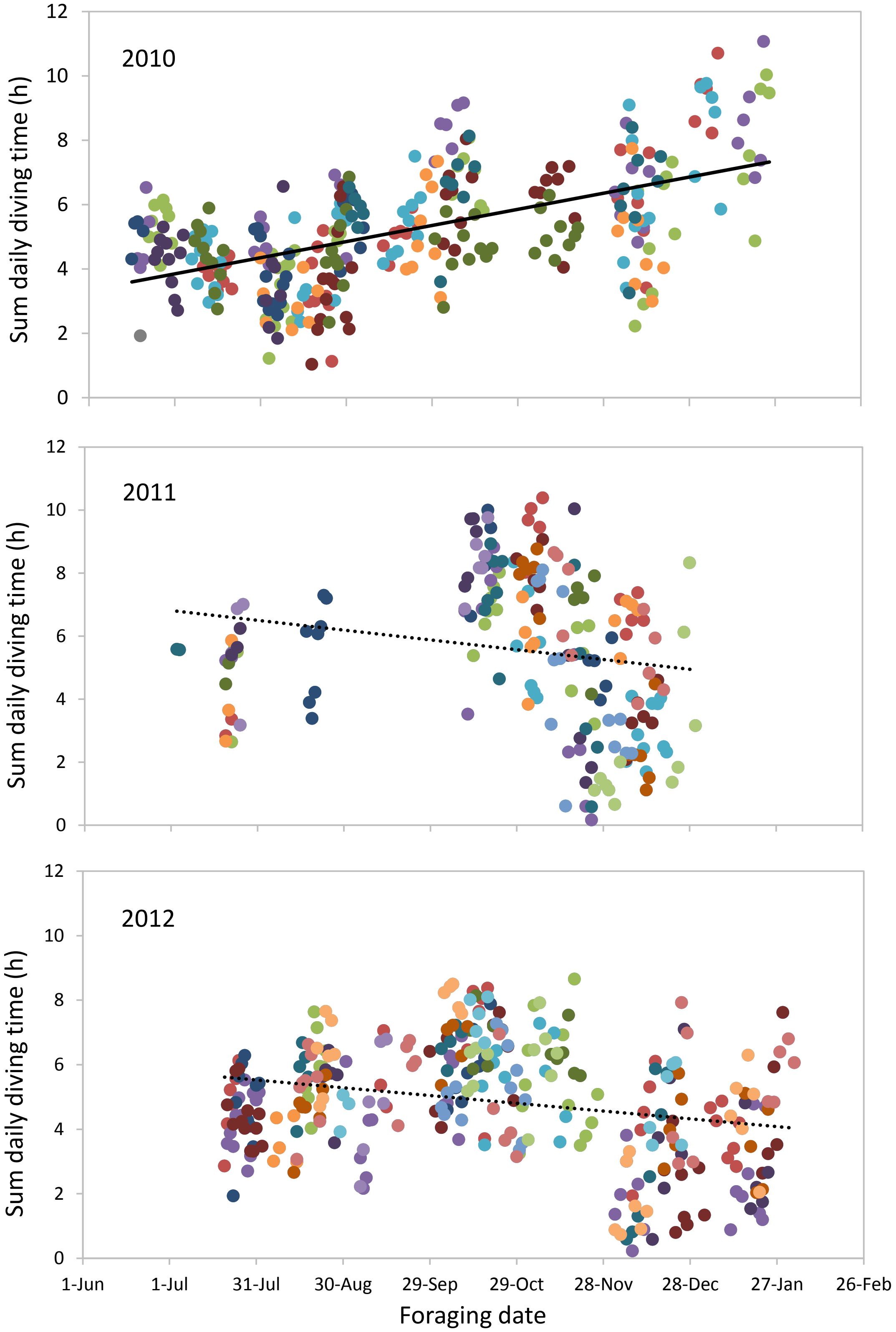

Figure 5.2. Diving effort (total daily diving time) of individual little penguins at Oamaru, in relation to foraging date during the 2010, 2011 and 2012 breeding seasons. Different individuals are depicted by different coloured marks. Linear regression for 2010 (solid line): $R^2 = 0.31$, $P < 0.001$, $y = 0.017 * \text{Date} + 2.83$. Dashed line shows non-significant regressions.

Diving effort appeared similar when adults were incubating eggs or feeding chicks as the model was not improved compared to the null when what the adults were doing were included in the model ($P = 0.64$). Diving effort was greater during the second incubation and chick stages ($P = 0.03$) but this was due to the influence of 2010 ($P < 0.0001$) rather than 2012 ($P = 0.22$). We compared diving effort prior to and during the summer storm of the 2010 breeding season (January 2011) to determine if that was the reason for the increase late during the 2010 breeding season however the difference between the two periods was not significant. The LMM with the storm effect included did not fit the data well compared to the null model ($P = 0.86$).

5.4.4 Foraging distances

Tagged penguins foraged predominantly in water < 50 m deep and within 20 km of the coastline. Trips > 2 days were generally spent travelling northwards of the Waitaki River mouth (14 of 19 trips) and all trips north occurred during incubations (Figure 5.3 compared to Figure 5.4). The penguin travelling the shortest maximal distance was only 5.6 km away from the colony compared to the one travelling the longest that reached 35.2 km away (Table 5.7). The two penguins that travelled the longest distances covered 75.4 km and 74.8 km, respectively, on a single-day trip. These birds also reached the most southerly latitudes during the entire study period (Figure 5.4). As both of these trips were significantly longer than other trips recorded at the same stage that season and they occurred on the same day (22 January 2011) during the summer storm, we assume the storm may have influenced the distance travelled by the penguins. A third penguin foraging on the same day in the same area (Figure 5.4) stayed away for another five days.

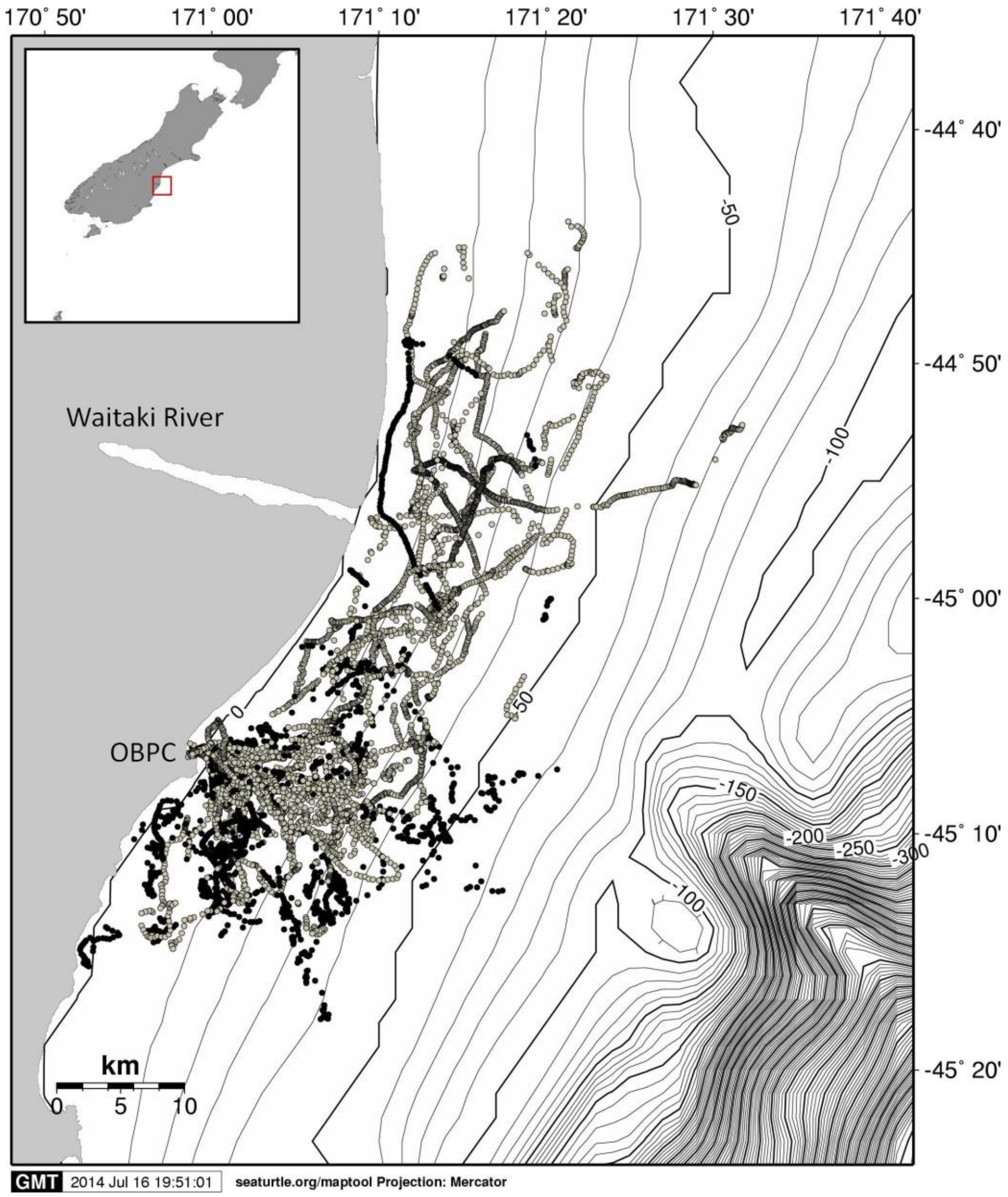

Figure 5.3. Global positioning system locations recorded from 22 individual little penguins during incubation at the study colony (OBPC) near Oamaru, 2010-2012. Points are presented for first clutches (grey) and second (of double) clutches (black). Map was created using Maptool (Seaturtle.org 2002), showing bathymetry in 10 m intervals.

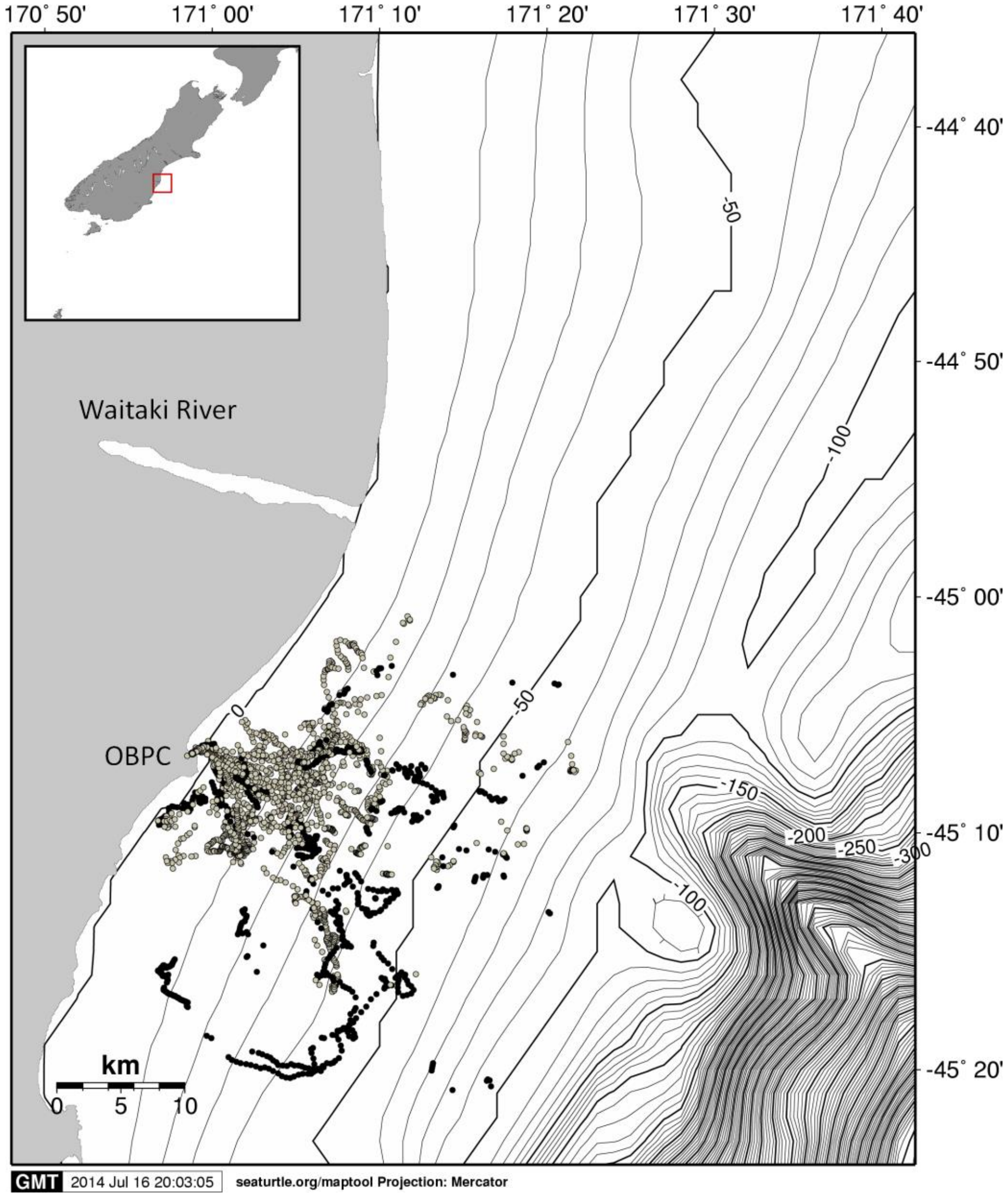

Figure 5.4. Global positioning system locations recorded from 18 individual little penguins during chick rearing at the study colony (OBPC) near Oamaru, 2010-2012. Points are presented for first broods (grey) and second (of double) broods (black). Map was created using Maptool (Seaturtle.org 2002), showing bathymetry in 10 m intervals.

Table 5.7. Mean (SE) and maximum distance measured (km) in a straight line from the colony to the farthest point and total distance travelled (km) during one-day foraging trips by little penguins at Oamaru during each stage of the breeding season, 2010-2012.

Season	Stage	*n*	Mean farthest point	Maximum farthest point	Mean total distance	Maximum total distance
2010	PE	6	13.2 (0.79)	16.0	38.9 (1.09)	43.1
	I1	8	14.2 (0.64)	17.2	39.5 (1.80)	50.8
	C1	8	11.7 (0.85)	15.6	38.7 (2.10)	45.5
	I2	9	16.4 (1.62)	26.6	43.0 (2.27)	57.6
	C2	4	22.6 (5.99)	35.2	57.6 (11.64)	75.4
2011	I1	3	18.4 (2.12)	23.7	47.0 (3.52)	57.5
	C1	10	17.8 (2.20)	30.0	46.4 (4.08)	70.0
2012	I1	10	12.8 (0.84)	19.2	33.6 (1.47)	43.1
	C1	4	16.5 (3.15)	25.6	40.8 (6.08)	57.8
	I2	8	19.4 (1.60)	28.7	46.5 (5.63)	58.6
	C2	8	18.3 (2.22)	27.7	43.9 (6.92)	60.0

n = number of individuals; Stages were – PE: pre-egg stage; I1: incubation of first clutch; C1: raising of first brood; I2: incubation of the second clutch of a double brood; C2: raising of the second brood of a double brood.

For the set of LMMs on the (log-transformed) total foraging distance, the model with lowest AIC had the date of foraging as a fixed effect. There was some support for models with stage (as a continuous variable) and an interaction between the date of foraging and breeding season (Table 5.8). The best three models all established that total foraging distance increased through the breeding season (Table 5.9). Over the three breeding seasons there was no obvious difference between the total foraging distance during incubation compared to the chick stage; the LMM with the (stage) effect included did not fit the data well compared to the null model (*P* = 0.10).

Table 5.8. Set of models examining variation in the log-transformed total foraging distance by little penguins at Oamaru, 2010-2012.

Variable	Model	df	AIC	ΔAIC	w_i
(Log) Total distance	Date	4	-9.82	0.00	0.62
	Stage	4	-7.51	2.31	0.19
	Date*Season	8	-7.12	2.70	0.16
	Stage2	7	-3.24	6.57	0.02
	Null	3	1.02	10.84	0.00
	Season	5	2.47	12.29	0.00

AIC: Akaike's information criterion; ΔAIC: value of the difference between each model and the best model; w_i: Akaike weights; Date: date of the foraging trip; Season: breeding season; Stage: stage of the breeding season as a continuous effect; Stage 2: stage of breeding as a categorical effect.

Table 5.9. Results for the best models (ΔAIC ≤ 2) for the log-transformed total foraging distance for little penguins at Oamaru, 2010-2012 (from Table 5.8).

Model	Parameter	Estimate	SE	*t*-value	*P*-value
Stage	(Intercept)	3.51	0.07	52.95	<0.001
	Stage	0.06	0.02	3.30	<0.001
Date*Season	(Intercept)	3.53	0.10	35.29	<0.001
	Date	0.001	0.001	1.99	0.05
	Season[2011]	0.08	0.76	0.11	0.92
	Season[2012]	-0.35	0.18	-1.92	0.06
	Date:Season[2011]	-0.0002	0.004	-0.05	0.96
	Date:Season[2012]	0.002	0.001	1.65	0.10

Date: date of the foraging trip; Season: breeding season; Stage: stage of the breeding season as a continuous effect; Stage 2: stage of breeding as a categorical effect.

5.4.5 Ocean productivity

During August chlorophyll concentrations decreased with increasing distance from the coastline (Figure 5.5), however the same was not the case during December and January (Figure 5.6). A drop in chlorophyll during August occurred at the approximate location of the continental shelf. Diving effort averaged for each month was not related to the monthly area-averaged chlorophyll within the penguins’ foraging range (linear regression: $R^2 = 0.02$, $P = 0.59$). Of the three breeding seasons diving effort was greatest in December 2010 and January 2011 however this was not the period of lowest productivity, chlorophyll was actually higher during these two months than at the same time in 2011 and 2012 (Figure 5.6). Areas of highest productivity included waters near the coastline and along the coastline towards (and north of) the Waitaki River mouth.

Since we had reliable foraging distance data for single-day trips only, we examined the total distance travelled in one day in relation to chlorophyll concentrations at a site immediately offshore from the penguin colony. The relationship showed a negative trend of increasing foraging distance with decreasing chlorophyll ($y = -3.72x + 46.89$, $R^2 = 0.12$), but was not significant ($P = 0.22$). The farthest foraging trips occurred during January 2011, however chlorophyll was comparatively high close to the colony and offshore from the Waitaki River mouth during that month (Figure 5.6).

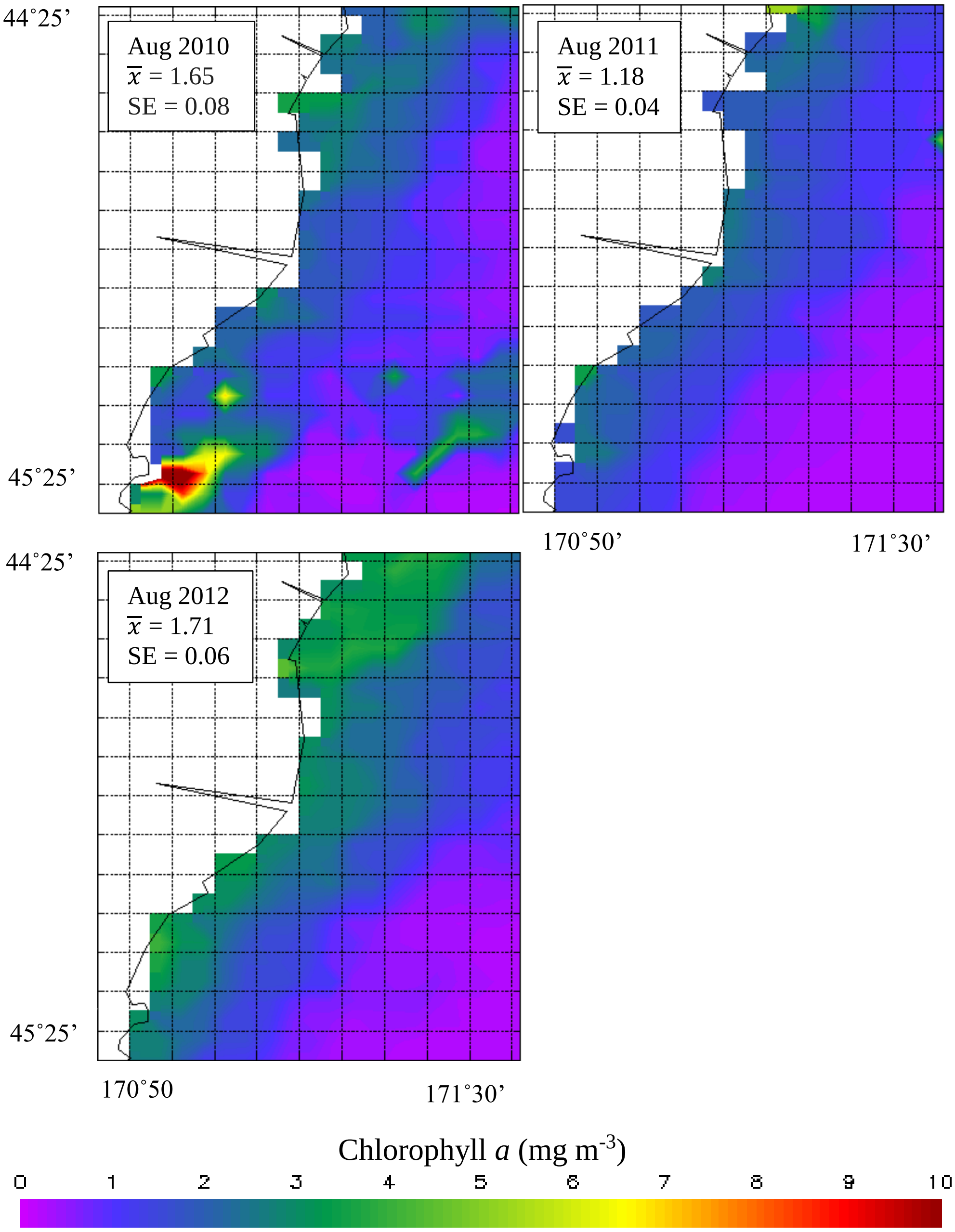

Figure 5.5. Monthly mapped chlorophyll *a* (mg m^{-3}) for the foraging area of little penguins at Oamaru during August 2010-2012.

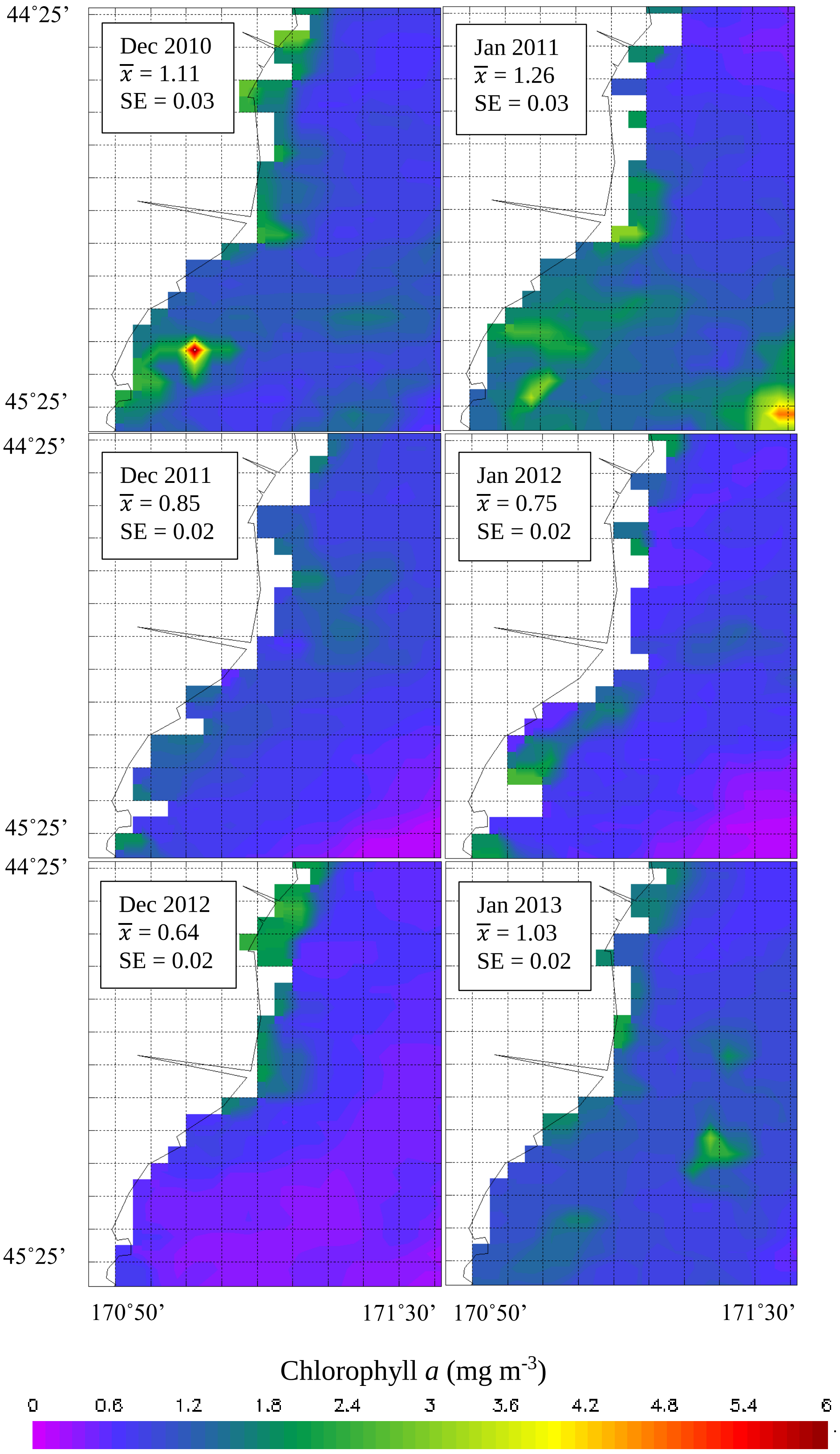

Figure 5.6. Monthly mapped chlorophyll *a* (mg m^{-3}) for the foraging area of little penguins at Oamaru during December-January, 2010-2012.

5.5 Discussion

The penguins laid their first eggs at similar dates each year during the study. Hatching and fledging success and chick fledge weights for the first broods were also similar. A disruption to egg-laying in 2011 led to below-average breeding success in that season, and fledging success and chick fledge weights for the second broods were lower during 2010 than 2012; these reductions in reproductive output were both attributable to a persistent storm. Storms increase the turbidity in the water column via increased wind and wave action. Increased turbidity impacts on seabirds via reduced prey availability and ease of capture (Taylor 1983; Finney et al. 1999; Braby et al. 2011) and may subsequently cause an interruption to breeding (Wright et al. 2013). The two farthest single-day foraging trips occurred during the storm during the 2010 season. This suggests that the storm forced birds to forage further away from the colony and caused the recorded drop in the number of birds returning to the colony each night.

Dive depth was correlated with several other dive variables: dive duration, bottom phase duration and the proportion of IDZ dives, consistent with studies on rockhopper penguins (*Eudyptes chrysocome*), in which dive duration and bottom phase duration were closely related to dive depth (Wilson et al. 1997a). Previously, preferred dive depths of little penguins at Oamaru, during December and January 2000, were found to average only 6 m (Mattern 2001), similar to dive depths during the same months in the current study. The observed variation in diving behaviour through the breeding season in the current study highlights the importance of account for time of year when generalising about dive depths for little penguins at different locations. Mattern (2001) compared dive depths of Oamaru little penguins with those at Motuara Island, Marlborough Sounds, New Zealand, and found (during September – November) Motuara birds dove significantly deeper (mean = 10 m). This deeper diving may have related to the time of year rather than location. Further comparisons of Mattern's results with Phillip Island little penguins concluded that Phillip Island penguins dove deeper than Oamaru and Penguin Island (Western Australia) birds (Chiaradia et al. 2007). The study at Penguin Island was carried out in September (Ropert-Coudert et al. 2003) but it was not stated in published literature when the Phillip Island study occurred. Our results were consistent with other research at Phillip Island (mean dive depth during November: 10 m, December: 6 m; Pelletier et al. 2012). Pelletier et al. (2012) also found dive depth decreased with time through the five week duration of their study, consistent with our findings also. Prior work found shallower diving through time by little penguins at Phillip Island was related to an increase in the number of dives per day and a decrease in prey pursuit time (Zimmer et al. 2011). Diving effort by the penguins at Oamaru decreased towards the later months of 2011 and 2012, which interestingly coincided with the longest day length. Shifts in dive depth and effort through time could be attributable to changes in prey distribution (Kato et al. 2003) or prey species targeted (Moore et al. 1999). Little penguins at Oamaru target small pelagic prey, typically 5-10 cm long; either, juveniles and adults of small species (e.g. slender sprat *Sprattus antipodum* and Graham's gudgeon *Grahamichthys radiata*), or juveniles of larger species (e.g. red cod *Pseudophycis bachus*, barracouta *Thyrsites atun* and arrow squid *Nototodarus sloanii*) (Fraser and Lalas 2004; Flemming et al. 2013). Fraser and Lalas (2004) found the total mass of prey taken each day during the 1994 breeding season was around 25g between July and November and increased from then until reaching 125 g/day in February, attributable not only to the number but also the size of prey taken. The largest fish were taken during January through April (Fraser and Lalas 2004).

Double brooding occurred during the 1994 breeding season (Agnew et al. 2014), which meant that from November onwards birds would be incubating eggs and raising chicks from late first broods or from second broods. The increase in total mass of prey taken was likely a result of an increase in prey availability or abundance rather than an increase in the demands of breeding because birds would also have been incubating eggs and raising chicks earlier during the season. A similar increase in prey may have occurred during the 2011 and 2012 seasons but perhaps not during 2010, explaining the higher diving effort late 2010. If a drop in prey abundance did occur during 2010, the birds were able to compensate through increased diving effort - because their body weight was not affected. The percent of weight lost by adults by the time of the second brood was no greater than in 2012.

Fish production is related to primary productivity (Iverson 1990); for example, the growth of European anchovies (*Engraulis encrasicolus*) at different locations varies according to chlorophyll concentrations at each (Basilone et al. 2004). There is also evidence that seabird distributions are associated with chlorophyll (Culik 2001; Weichler et al. 2004) and subsequently that chlorophyll concentrations determine foraging distances (Boersma et al. 2009). While it was difficult to know whether the little penguins at Oamaru targeted chlorophyll rich areas during individual foraging trips, they generally appeared to focus on areas that were higher in chlorophyll, these being near-shore (< 20 km from the coast) and north towards the Waitaki River mouth. The observed increase in diving effort that occurred late 2010 did not result from a decrease in ocean productivity.

As median dive depth increased, the proportion of dives to the same depth zone (IDZ dives) increased, potentially attributable to penguins diving to the seabed (Ropert-Coudert et al. 2006b). Ropert-Coudert *et al*. (2006b) suggested that little penguins encounter their prey in the demersal zone and pursue them down to the seabed to reduce their ability to escape capture. An alternative explanation could be an increase in the proportion of IDZ dives due to the presence of a thermocline. A thermocline in well-stratified water concentrates prey by creating a physical barrier via a rapid change in temperature with depth (Ropert-Coudert et al. 2009). Prey for little penguins are likely to be less dispersed in well-stratified water, which allows for greater rate of prey encounter (Ropert-Coudert et al. 2009). By attaching GPS and TDR (with external temperature sensor) devices to the same individual, future research at Oamaru could further examine variation in dive depth in relation to the water depth and temperature profile of the water column.

We expected that the increased pressure of provisioning offspring would be reflected by increases in foraging effort. This was not the case: across all three seasons diving effort and distance travelled (during single-day trips) were similar between chick rearing and incubation stages. This both supports (Kato et al. 2009) and contrasts with previous seabird research (Benvenuti et al. 2002; Humphreys et al. 2006), indicating that differences in foraging behaviour between stages of breeding are not only species- and site-specific but may also vary between years. For example, the diving activity of the marbled murrelets (*Brachyramphus marmoratus*) during incubation and chick rearing did not differ during years of abundant food supply but increased during both stages when food supply was low (Ronconi and Burger 2008). The lack of a difference between incubation and chick rearing at Oamaru may mean there is plentiful food for the penguins throughout the year.

The penguins increased their diving effort during 2010 which, without the confounding issue of the storm, may have been enough to maintain sufficient food supply to their chicks without resulting in a decrease in fledge weights and fledging success that occurred. We conclude that extrinsic factors determining the availability of prey were more important than stage-related demands of breeding in influencing little penguin foraging behaviour at Oamaru. Further research into prey abundance near Oamaru is required to determine ecological mechanisms involved.

Chapter 6 :

Variation in breeding success and survival of little penguins in response to global climate change

6.1 Abstract

Climate change is likely to result in continued warming of the oceans and an increase in the frequency and intensity of storms. Uncertainty surrounds the potential effects of such changes on seabird species. We aimed to determine whether variation in sea surface temperature (SST), chlorophyll *a* concentrations and the occurrence of severe storms affected breeding and survival in little penguins at Oamaru. We examined the impact of prolonged, extreme storms using the 99th percentile of significant wave heights. Long durations of above-average wave heights at Oamaru were associated with a reduction in the number of penguins arriving ashore each evening and a reduction in the survival rate of breeders. Productivity positively influenced the penguins: survival of breeders and recruitment of fledglings into the breeding population were positively related to increases in chlorophyll and egg-laying became earlier. Global climate change is highly likely to have negative impacts on the population of little penguins at Oamaru through impacts from storms. It is uncertain how chlorophyll concentrations will change through time and hence will affect the penguins. Potential increases in chlorophyll through increased nutrient input from the land will have positive effects on the penguins.

6.2 Introduction

Comprehensive studies investigating relationships between demographic parameters of seabirds and environmental variation indicate the likely ecological consequences of global climate change. Environmental variation can affect foraging behaviour (Catry et al. 2013) and subsequently breeding success and survival (e.g., Ramos et al. 2002; Sandvik et al. 2005; Bertram et al. 2009; Cubaynes et al. 2011). Foraging behaviour of seabirds is directly linked to a combination of prey abundance and prey availability (e.g., Barrett and Krasnov 1996; Henkel 2006), which are strongly influenced by environmental factors such as mixed layer depth and turbidity (e.g., Bertram et al. 2009; Bergeron and Masse 2011).

Globally, ocean temperatures warmed during the 20th Century (Levitus et al. 2012) and are likely to continue warming in the future (IPCC 2007). This trend has been apparent in New Zealand waters, where temperatures increased by around 0.6˚C between 1871 and 1993 (Folland and Salinger 1995). Increasing SST can impact top predators directly via negative relationships between sea surface temperature (SST) and fish abundance: increased egg mortality and reduced spawning occurs in warmer than average SSTs (Potts et al. 2014) shown by effects on commercial fish catches (Beentjes and Renwick 2001). Increasing SST can also affect predators indirectly via the associated reduction in productivity (Behrenfeld et al. 2006; Boyce et al. 2010). Increasing SST decreases productivity by reducing surface mixing of the water column and increasing the depth of the mixed layer which limits nutrient supply to phytoplankton (Boyce et al. 2010). While chlorophyll *a* (a reliable measure of productivity) has decreased through the 20th century by around 1% per year globally, it is uncertain how it will change in coastal waters in the future (Boyce et al. 2010). Through increased runoff and input of nutrients into the ocean, coastal waters at some sites have increased in productivity since the 1980s and may continue to do so

(Gregg et al. 2005). Seabirds alter their foraging habits in response to variation in productivity. For example, foraging trip distances of Magellanic penguins (*Spheniscus magellanicus*) increased with decreasing productivity at different breeding colonies (Boersma et al. 2009). Foraging distances affected reproductive success, such that the probability of nest failure increased with distanced travelled (Boersma and Rebstock 2009b).

Research into demographic parameters of various penguin species: e.g., emperor (*Aptenodytes forsteri*) (Jenouvrier et al. 2012), rockhopper (*Eudyptes chrysocome* and *E. moseleyi*) (Dehnhard et al. 2013b) and king penguins (*A. patagonicus*) (Le Bohec et al. 2008), has predicted that climate change will negatively impact breeding success and survival. Research on little penguins (*Eudyptula minor*) in New Zealand has suggested that warming will delay the onset of egg laying (Perriman et al. 2000). In Australia, however, effects appear to depend on location. Breeding success decreased following periods of relatively high SST in Western Australia (Cannell et al. 2012) but increased in Victoria (Cullen et al. 2009).

For southern New Zealand, climate change is also predicted to result in an intensification of storms during winter (Mullan et al. 2011). Increased wind speeds and wave heights associated with storms bring marine sediments into suspension and the longer increased wave activity lasts, the longer those materials remain in suspension (Verspecht and Pattiaratchi 2010). Increased river outflow following heavy rain also acts to reduce water clarity and lower the foraging efficiency of seabirds (Braby et al. 2011) which rely on vision to detect prey underwater. Further, mixing of the water column caused by storms can act to disperse fish aggregations associated with stratified layers (e.g. thermoclines)

(Peterman and Bradford 1987; Bergeron and Masse 2011), making prey less available to little penguins (Ropert-Coudert et al. 2009). The energetic demands of foraging increase under difficult conditions, while food intake is likely to decrease (Grubb 1977; Dehnhard et al. 2013a). Other storm-related impacts on seabirds include reduction in survival rates (Harris and Wanless 1996; Frederiksen et al. 2008), abandonment of breeding (Wright et al. 2013), chick deaths due to increased rainfall (Boersma and Rebstock 2014) or reduction in the amount of food delivered to chicks (Finney et al. 1999; Stienen et al. 2000).

Little penguins are a near-shore forager, with restricted foraging ranges due to their small size. Foraging in near-shore coastal waters means they are vulnerable to changes within that environment as they cannot forage further afield and breed successfully. At Oamaru, New Zealand the reproductive performance and survival of little penguins has been studied in detail in an increasing population (Agnew et al. 2014), however the impact of environmental variation on their breeding and survival is largely unknown. Our objective is to determine whether variation within the coastal marine environment represented by storms, SST and chlorophyll fluctuations, affect the timing of breeding and/or annual survival of little penguins at Oamaru.

6.3 Methods

6.3.1 Penguin data

The study was conducted at the Oamaru Blue Penguin Colony (45°06’37”S, 170°58’47”E), Oamaru, South Island, New Zealand. The colony was established as a tourism facility in 1992, which aimed to manage visitors viewing the penguins coming ashore in the evening and provide the penguins with a safe breeding habitat (Johannesen et al. 2003). Staff at the colony recorded the number of penguins arriving ashore for one hour after the arrival of the first penguin every evening from January 1993 onwards. Beginning in August 1993, weekly monitoring of the penguins involved a check of every nest in the colony, with monitoring procedures documented in Agnew et al. (2013; 2014).

At Oamaru the lay date of first eggs in each breeding season has varied by up to five months from May to September (Agnew et al. 2014). For analysis, we defined breeding seasons as beginning 1 May and finishing 30 April of the following calendar year. Breeding seasons are referred to by the year in which breeding began (Agnew et al. 2014). For analysis of survival of breeders with respect to environmental variables, we divided breeding seasons into four-month periods: May-August, September-December and January-April. This division was used in preference to a standard (three-monthly) seasonal division as it more appropriately represents changes in breeding activity through the breeding season. The penguins began breeding as early as May in some years (Agnew et al. 2014); therefore May through August incorporated early breeding activity, September through December were predominantly incubating and chick rearing, and January-April final chicks fledged and breeders moulted. For consistency environmental variables were averaged over the same periods.

6.3.2 Environmental variables

Data on significant wave height (four times the square root of the sea surface variance) were obtained from hind-casts generated using numerical modelling by MetOcean Solutions Limited (metocean.co.nz) (Beamsley et al. 2009). The dataset was available as a three-hourly time series from 1 January 1979 to 31 December 2012. Spatial resolution was 5 km, with data obtained from the nearest offshore node (45°07’55”S, 171°01’00”E), situated 3.8 km south-east of the study area. We examined monthly and annual significant wave heights and then concentrated on the 99th percentile value of all three-hourly records (as an indicator of extreme values; Mullan et al. 2011) between 1 May 1993 and 30 April 2012. We used the number of consecutive three-hourly records that exceeded the 99th percentile, defined as “P99 exceedence”, as an indicator of the severity of the most extreme storms each four-month period.

Data on sea surface temperature were extracted from a global dataset produced by the National Oceanic and Atmospheric Administration (NOAA) National Climate Data Center and made available on the Physical Oceanography Distributed Active Archive Center (PO.DAAC) website (http://thredds.jpl.nasa.gov/las/getUI.do, NASA Jet Propulsion Laboratory, Pasadena, CA). The SST data were part of a product referred to as the Group for High Resolution Sea Surface Temperature (GHRSST) global Level 4 sea surface temperature analysis. The analysis used optimal interpolation (OI) of SSTs measured in-situ and satellite derived SSTs from the (version 5) time series provided by the NOAA Advanced Very High Resolution Radiometer (AVHRR) Pathfinder. The data were available from 1985 to the present and were produced daily on a 0.25 degree (c. 28 km) grid (Reynolds et al. 2007). This analysis was documented originally by Reynolds and Smith (1994) and re-analysed by Reynolds et al. (2002). We calculated area-averaged four-month means for the region 44˚25’- 45˚50’S and 170˚45’ - 171˚35’E, where little penguins from the Oamaru colony are known to forage during the breeding season (Chapter 5). Chlorophyll *a* data were also downloaded from the NASA website made available by the Sea-viewing Wide Field-of-view Sensor (SeaWiFS) mission. The monthly 9-km chlorophyll data are available from September 1997 to September 2010, we calculated the four month mean for these data also.

6.3.3 Statistical analysis

Our metric for immediate effects of storms on the daily number of penguins arriving ashore was the number of days during and after an increase in wave height that penguin arrivals were below the lower quartile of arrival numbers prior to the storm (from 1 May to the first day of the storm). We used the lower quartile value instead of the median to ensure that metric was not triggered by normal fluctuations in arrival numbers.

To quantify short-term effects of a storm on the survival of breeding penguins we estimated survival probabilities within the breeding season using mark-recapture. Recapture data for breeding penguins were extracted from the weekly monitoring programme data and divided into the three four-month periods of the breeding season. Multiple records within a four-month period were treated as a single recapture in the encounter history matrix. This process generated an encounter history matrix with 54 columns: beginning May-August 1994 (1993 was excluded due to regular monitoring occurring after the beginning of the breeding season) and finishing January-April 2012, at the end of the 2011 season. We used the Cormack-Jolly-Seber (CJS) live recapture model in program MARK for each period (i) to estimate apparent survival probability (φ_i), the probability of surviving and returning to the study area from time period i to i+1; and the probability of recapture (p_i), the probability of recapture in the study area from i to i+1. The standard CJS model assumes that survival and recapture probabilities do not vary between individuals (Lebreton et al. 1992). We then used a logistic regression (Generalised Linear Models: GLM) in R software version 2.15.3 (R Development Core Team 2013) to determine the relationship between survival probabilities and the P99 exceedence for the May-August period of each breeding season.

For analysis of annual survival we used the proportion of fledglings that later recruited into the breeding population as a proxy for first-year survival and the observed survival rate for survival of breeding adults each season (Chapter 3). We tested for relationships between environmental variables and the annual survival probabilities using logistic regression models for the years we had representative data (1998-2010). Year was included to look for variation through time and we also examined the intercept-only (Null) model. For each model, the Akaike's Information Criterion corrected for small sample size (AICc), AICc difference (ΔAICc) and model weight (w_i).

The lay date of first eggs for the breeding colony, and median lay dates of first clutches, were used as proxies for breeding success due to the significant relationship between lay dates and breeding success via double brooding (Agnew et al. 2014). The median lay date of the first clutch by pairs with previous breeding experience was earlier than that of pairs with no previous experience (Agnew et al. 2014). To account for this we examined relationships between environmental variables and median lay date of the first clutch for all pairs together, and also for experienced pairs only. We examined relationships between lay dates of first eggs and SST and chlorophyll, with linear regressions for each four-month mean from the current and from the previous breeding season. All three variables were included in linear regression models with the response variable being median lay date of first clutches.

6.4 Results

6.4.1 Environmental variables

Significant wave height modelled for the ocean immediately offshore from Oamaru, for the 19 years from 1 May 1993 to 30 April 2012, ranged from 0.13 to 3.78 m with a mean of 1.05 m and 99th percentile of 2.32 m. The direction of the largest waves was between 90°T and 160°T with a median of 132°T (south-easterly). The period from May-August had the greatest number of above 2.32m, though this varied among years (Table 6.1). A linear regression analysis of the trend in P99 for each year through time for the complete data set (1979-2012) revealed that P99 did not increase significantly through the period ($y = 0.0009 * \text{year} + 5.8$, $R^2 = 0.002$). While the relationship between year and May-August SST explained little variation in the data (23%), the increase with time was significant for the period 1985-2012 (Figure 6.1). Temperature increased by 0.03˚C each year, increasing by 0.7˚C over the period. The trend for September-December was positive but not significant, as were the trends for chlorophyll through the period 1997-2010 (Figure 6.2).

Table 6.1. Monthly and annual wave statistics for three-hourly significant wave height (m) data near Oamaru, 1993-2011. *n* = number of records, P99 = 99th percentile, Max = maximum recorded for the period.

	Mean	SE	*n*	P99	Count of records > 2.32m	Max
May	1.13	0.02	4712	2.50	91	3.49
Jun	1.20	0.02	4560	2.41	72	3.28
Jul	1.19	0.02	4712	2.77	139	3.68
Aug	1.22	0.02	4712	2.55	93	3.78
Sep	1.05	0.02	4560	2.34	51	3.13
Oct	0.97	0.01	4712	2.02	15	3.04
Nov	0.98	0.01	4560	2.04	8	2.52
Dec	0.91	0.01	4712	1.97	4	2.45
Jan	0.92	0.01	4712	2.16	21	2.70
Feb	0.96	0.01	4296	2.02	17	2.94
Mar	1.00	0.01	4712	2.03	16	3.12
Apr	1.04	0.02	4560	2.19	26	2.68
1993	1.10	0.01	2920	2.25	23	2.78
1994	1.06	0.01	2920	2.29	28	3.25
1995	1.05	0.01	2928	2.21	16	3.05
1996	1.04	0.01	2920	2.17	19	2.59
1997	0.98	0.01	2920	2.20	22	2.67
1998	1.00	0.01	2920	1.92	1	2.40
1999	1.02	0.01	2928	2.53	68	3.12
2000	0.97	0.01	2920	2.33	34	3.28
2001	1.05	0.01	2920	2.58	57	3.30
2002	1.06	0.01	2920	2.20	17	2.98
2003	1.04	0.01	2928	2.11	7	2.94
2004	1.08	0.01	2920	2.27	22	2.60
2005	1.00	0.01	2920	2.05	9	2.77
2006	1.04	0.01	2920	2.16	15	2.52
2007	1.04	0.01	2928	2.43	42	3.68
2008	1.12	0.01	2920	2.53	57	3.30
2009	1.15	0.01	2920	2.34	31	2.79
2010	1.11	0.01	2920	2.56	39	3.49
2011	1.06	0.01	2928	2.71	52	3.78

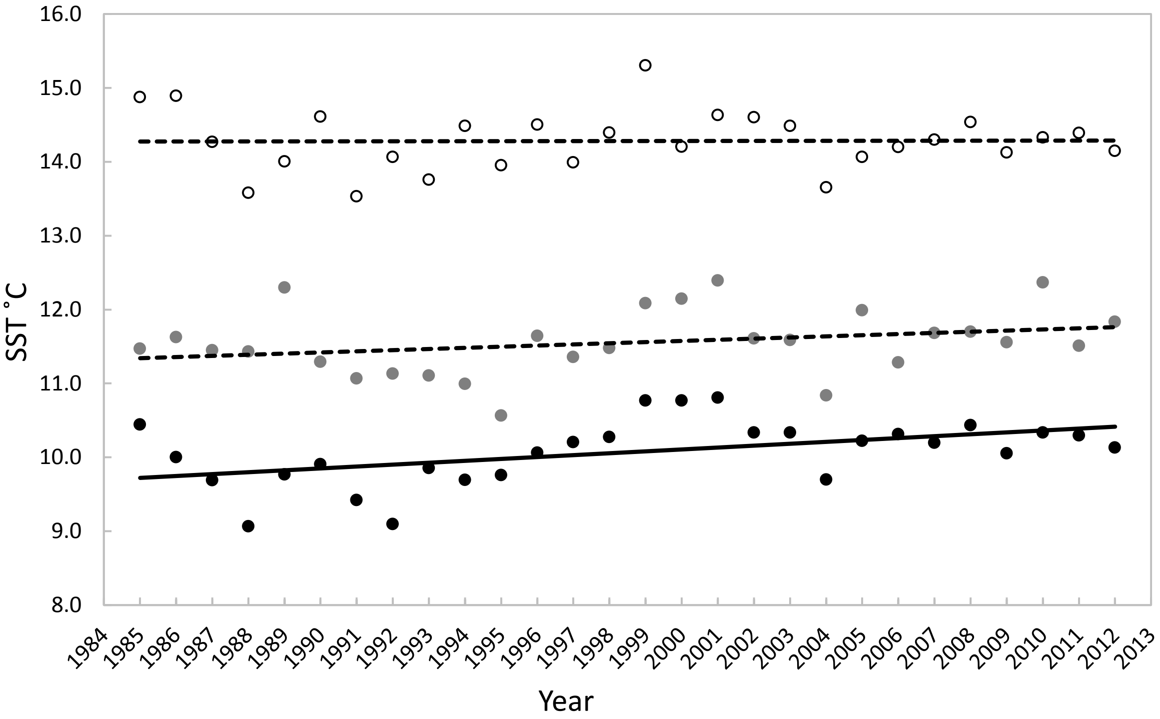

Figure 6.1. Four-month mean sea surface temperatures (SST) for January-April (open circles), May-August (black circles) and September-December (grey circles) each year for the region offshore from Oamaru, 1985-2012. Significant linear regression (solid line) for May-August: $R^2 = 0.23$, $P = 0.01$, $y = 0.026x - 41.4$. Dashed lines show non-significant linear regressions.

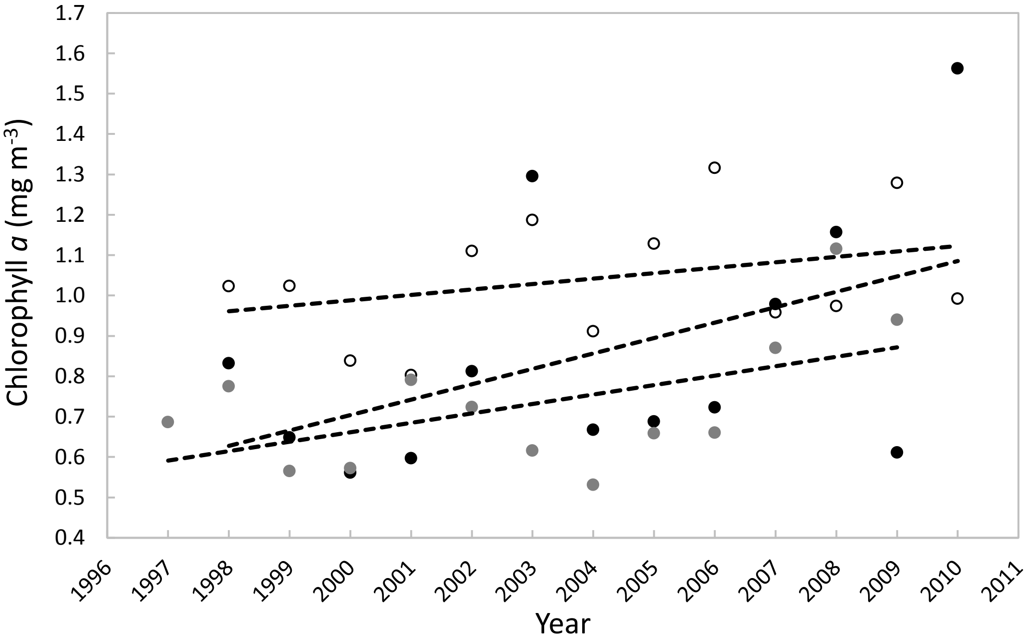

Figure 6.2. Four-month mean chlorophyll *a* for January-April (open circles), May-August (black circles) and September-December (grey circles) each year for the region offshore from Oamaru, September 1997- September 2010. Dashed lines show non-significant linear regressions.

6.4.2 Immediate effects of storms

Persistent extreme significant wave heights had a clear effect on the daily numbers of penguins arriving ashore. The higher the P99 exceedence the greater the number of days that arrival numbers remained low (Figure 6.3). Each extra three-hourly duration of extreme significant wave heights was met with an increase of nearly one day (0.88) of reduced arrivals of penguins (below the lower quartile), and the model explained 47% of the variation in the data (Figure 6.3). The 2011 breeding season was a potential outlier in the relationship; the number of consecutive days may have remained low due to the birds having started breeding already (and therefore more incentive to return to the colony). There appeared to be two scenarios depending on the severity of the storm. During low storm severity (< 13 consecutive records above the P99 threshold) the duration of low penguin numbers occurred for shorter durations (< 10 days). Alternatively, during high storm severity (> 20 consecutive records above the P99 threshold) the duration of low attendance was > 10 days). The difference in the duration of low attendance between low and high storm severity was significant (mean difference: 23.5, 95% CI: 10.0, 37.0). Four of the six worst storm years (1999, 2001, 2007 and 2011) also had the lowest adult survival through the period May-August (Figure 6.4). The 2007, 2010 and 2011 data points had high leverage, reducing the fit of the model and hence the model could not fit the outlying data points. The trend however did show that persistence of extreme wave heights had a negative effect on adult survival (Figure 6.4: β = -0.04, 95% CI: -0.05, -0.03).

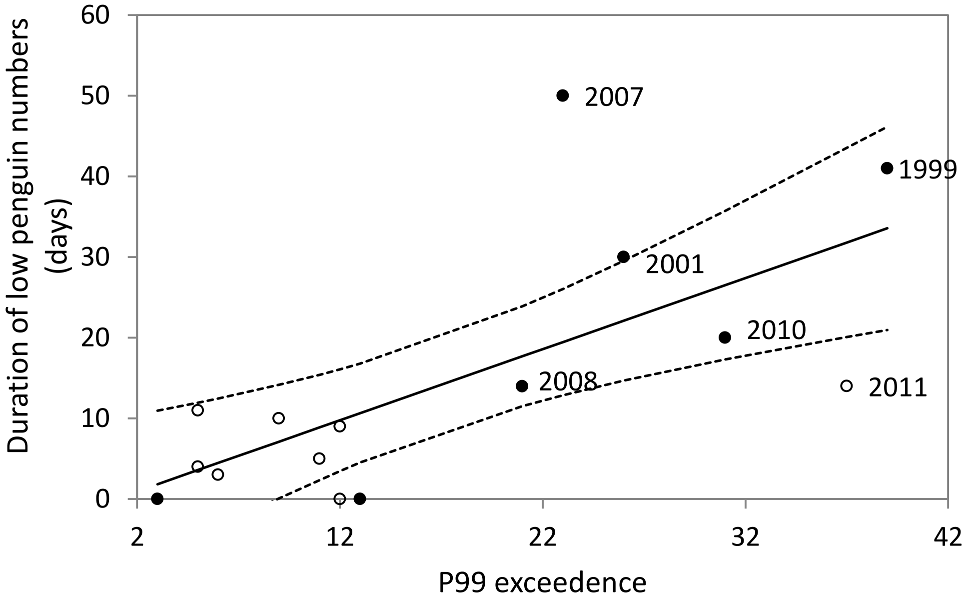

Figure 6.3. The relationship between the number of consecutive three-hourly records above the 99th percentile significant wave height (P99 exceedence) and the corresponding number of consecutive days the number of little penguins arriving ashore was below the lower quartile value during evening viewing at Oamaru each breeding season, 1994-2011. Open circles show seasons in which breeding had begun prior to the storm and closed circles when breeding began after the storm. Data labels identify the worst affected years. Linear regression (solid line) and 95% confidence intervals (dashed lines): $R^2 = 0.47$, $P = 0.005$, $y = 0.88x - 0.80$.

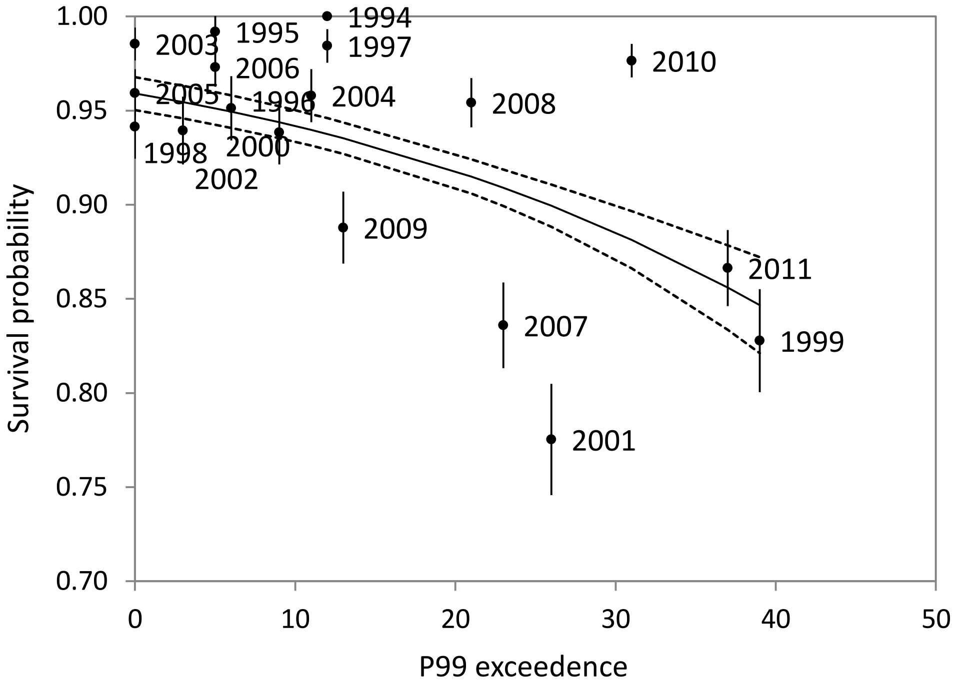

Figure 6.4. The relationship between the number of consecutive three-hourly records above the 99th percentile significant wave height value (P99 exceedence) and the survival probability (95% CI) of adult little penguins during the period May-August of the 1994-2011 breeding seasons at Oamaru. Logistic regression model (solid line): logit(φ) = 3.22 – 0.04 * P99.

6.4.3 Impacts on annual survival and recruitment

The best model (lowest AICc) for the survival rate of breeders included the four-month mean chlorophyll for January-April prior to the current breeding season plus P99 exceedence (Table 6.2). Observed survival probabilities were within the predicted estimate confidence intervals for 10 of 13 breeding seasons (Figure 6.5). Survival rate increased with increasing chlorophyll ($\beta = 0.93$, 95% CI: 0.25, 1.60, $P = 0.007$) and decreasing consecutive records of extreme significant wave height ($\beta = -0.01$, 95% CI: -0.02, -0.005, $P = 0.001$). Examined separately, the model with P99 exceedence as the predictor resulted in a lower AICc than the model with chlorophyll by 3 points (Table 6.2), indicating that P99 exceedence had slightly more importance in determining survival rates. Models with SST ranked low compared to chlorophyll and P99. Variation in survival through time also was not important in determining survival rates as this model was not amongst the top ten. Other combinations of variables did not lower AICc values.

The best model for the proportion of fledglings recruited into the breeding population included the P99 exceedence for the season following fledging (Table 6.2). Recruitment increased with decreasing P99 exceedence (Figure 6.6, $\beta = -0.01$, 95% CI: -0.02, -0.002, $P = 0.02$). There was also support for the model that included chlorophyll from the same breeding season the chicks fledged, recruitment increased with increasing chlorophyll ($\beta = 0.73$, 95% CI: 0.06, 1.40, $P = 0.03$). While the variables showed a significant effect on recruitment there was also some support for the null model (Table 6.2).

Table 6.2. Top ten generalised linear models examining variation in annual survival rate of breeding little penguins at Oamaru, 1998-2010, and the proportion of each cohort of fledglings recruited to the breeding population of little penguins at Oamaru, 1998-2009, in relation to four-month mean sea surface temperatures (SST), four-month mean chlorophyll *a* (Chl) and the number of consecutive three-hourly records above the 99th percentile significant wave height value (P99) in the season of breeding for adults and the season after fledging for recruits.

Variable	AICc	ΔAICc	w_i
Adult survival:			
P99 + Chl-PJA	91.32	0	0.86
P99	95.28	3.96	0.12
Chl-PJA	98.49	7.17	0.02
SST-SD	109.91	18.58	0.00
SST-MA	110.33	19.01	0.00
Chl-SD	110.41	19.09	0.00
SST-PJA	111.52	20.20	0.00
SST-PMA	114.41	23.08	0.00
Chl-MA	115.24	23.92	0.00
SST-PSD	116.73	25.41	0.00
Proportion of fledglings recruited:			
P99	75.90	0	0.37
Chl-JA	77.11	1.21	0.20
Null	78.73	2.83	0.09
Chl-MA	79.36	3.46	0.07
SST-PSD	80.01	4.11	0.05
SST-MA	80.27	4.37	0.04
SST-SD	81.15	5.24	0.03
SST-PMA	81.15	5.25	0.03
SST-PJA	81.17	5.27	0.03
Chl-PJA	81.33	5.43	0.02

AICc: Akaike’s information criterion, the selection criterion corrected for small sample size; ΔAICc: value of the difference between each model and the best model; w_i: Akaike weights; PMA: Previous May-August; MA: current May-August; PSD: previous September-December; SD: current September-December; PJA: previous January-April; JA: current January-April.

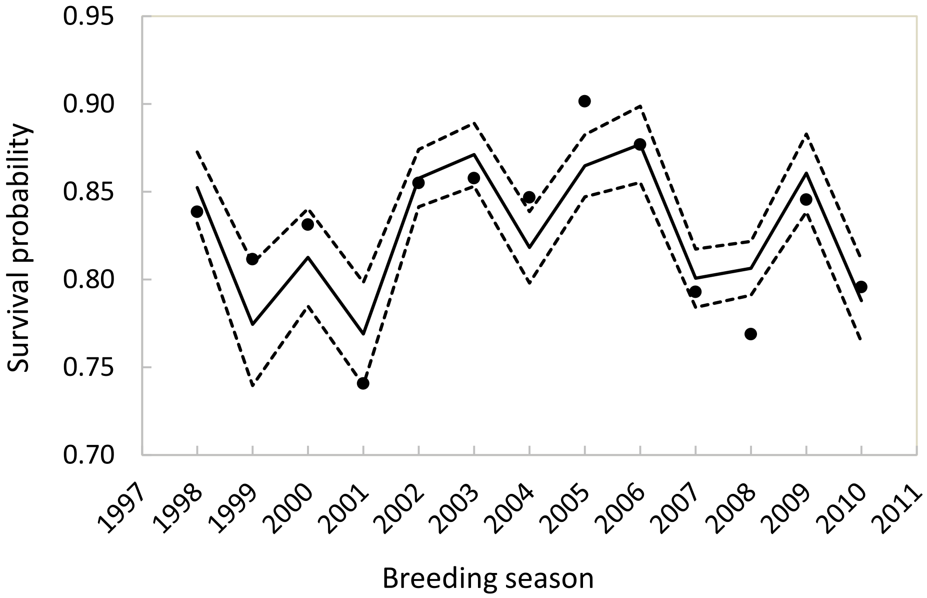

Figure 6.5. Observed (data points) and predicted (solid line) estimates of survival probability of breeding little penguins at Oamaru, 1998-2010. Predicted estimates (± 95% CI: dashed lines) generated from the fit of the model with the lowest AICc (Table 6.2), in relation to the four-month mean chlorophyll *a* from January-April prior to the breeding season and the number of consecutive three-hourly records above the 99th percentile significant wave height value.

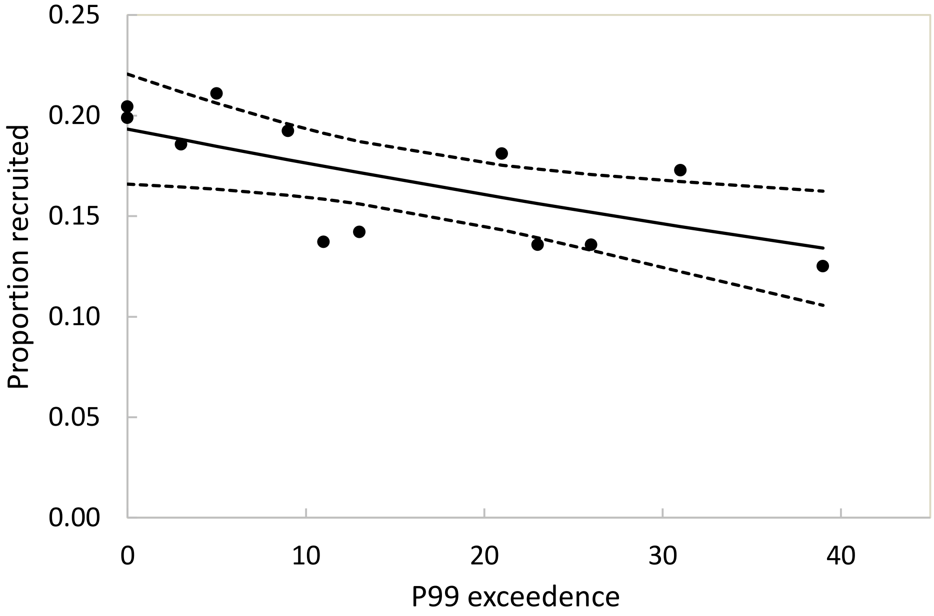

Figure 6.6. Observed (data points) and predicted (solid line) estimates of the proportion of each cohort of fledglings recruited to the breeding population of little penguins at Oamaru, 1998-2009. Predicted estimates (± 95% CI: dashed lines) generated from the fit of the model with the lowest AICc (Table 6.2), in relation to the number of consecutive three-hourly records above the 99th percentile significant wave height value (P99 exceedence) from the season after fledging.

6.4.4 Impacts on breeding

The proxy for storms (P99 exceedence) was excluded from the analyses of lay date of first eggs because the date of P99 exceedence occurred after the onset of egg laying in 6 of the 13 breeding seasons from 1998-2010. The two best supported models for lay date of first eggs included the four-month mean chlorophyll and SST for January-April prior to the breeding season (Table 6.3). These variables explained little variation in lay dates however, as the third model in the set, the null model, also had ΔAIC < 2.

For the median lay dates, the best model included the four-month mean chlorophyll for January-April prior to the breeding season (Table 6.3). Median lay dates were 12 days earlier during the breeding season for every increase in chlorophyll by 0.1 mg m^{-3}, the relationship was significant ($P = 0.008$) and explained 49% of variation in the data (Figure 6.7). The next two models in the set were only slightly better supported than the null model but still within ΔAIC ≤ 7. In the two models, median lay dates were later with increasing P99 exceedence ($R^2 = 0.16$) and earlier through time ($R^2 = 0.25$).

Table 6.3. Top ten linear models examining variation in the lay date of first eggs for the colony and median lay date of first clutches of little penguins at Oamaru, 1998-2010, in relation to four-month mean sea surface temperatures (SST), four-month mean chlorophyll *a* (Chl) and the number of consecutive three-hourly records above the 99th percentile significant wave height value (P99).

Variable	AICc	ΔAICc	w_i
First eggs:			
Chl-PJA	132.48	0	0.25
SST-PJA	133.07	0.59	0.19
Null	133.42	0.94	0.16
SST-MA	134.92	2.44	0.07
SST-JA	135.05	2.57	0.07
Chl-SD	135.47	2.99	0.06
Year	135.52	3.04	0.05
Chl-MA	135.91	3.43	0.05
SST-PMA	136.03	3.55	0.04
SST-SD	136.67	4.19	0.03
Median eggs:			
Chl-PJA	122.31	0	0.69
P99	126.13	3.82	0.10
Year	127.40	5.09	0.05
Null	127.64	5.33	0.05
SST-JA	129.60	7.29	0.02
SST-MA	129.67	7.36	0.02
SST-PJA	129.86	7.55	0.02
Chl-MA	129.90	7.59	0.02
SST-PMA	130.09	7.78	0.01
Chl-SD	130.91	8.60	0.01

AICc: Akaike's information criterion, the selection criterion corrected for small sample size; ΔAICc: value of the difference between each model and the best model; w_i: Akaike weights; PMA: Previous May-August; MA: current May-August; PSD: previous September-December; SD: current September-December; PJA: previous January-April; JA: current January-April.

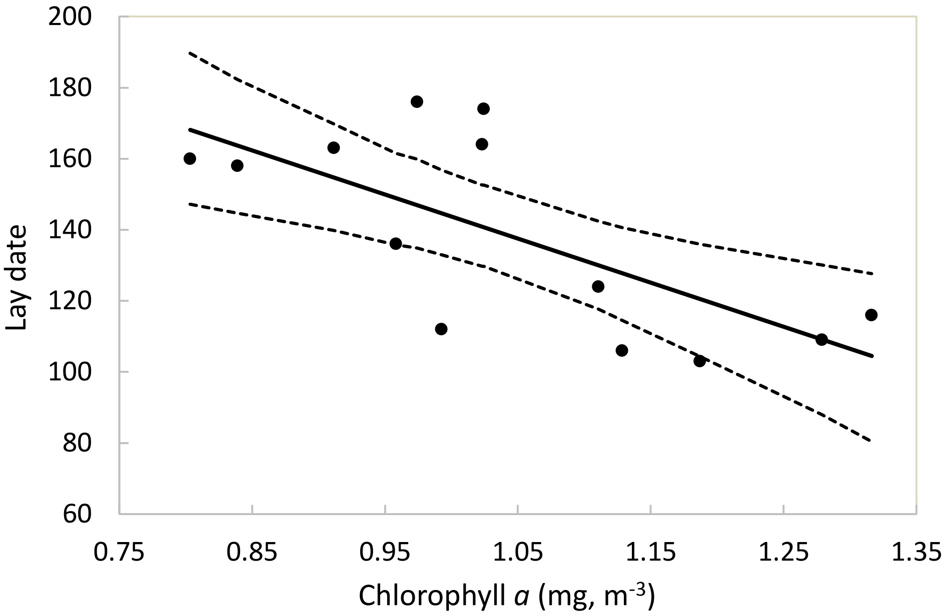

Figure 6.7. Observed (data points) and predicted (solid line) estimates of the median lay date of first clutches for experienced breeding pairs of little penguins at Oamaru, 1998-2010. Predicted estimates (± 95% CI: dashed lines) generated from the fit of the model with the lowest AICc (Table 6.3), in relation to the four-month mean chlorophyll *a* from January-April prior to the breeding season. Linear regression: $R^2 = 0.49$, $P = 0.008$, $y = -123.8 * \text{Chl-a} + 267.5$.

6.5 Discussion

Uncertainty surrounds how global climate change will affect various regions and ecosystems around the globe. Documented research (Folland and Salinger 1995; Lundquist et al. 2011) and findings from this study, suggest that winter SSTs, at least, are increasing around New Zealand. What increasing SST means for productivity and trophic relationships in the area is largely unknown however. Open ocean productivity may be decreasing as a result of increasing SST (Boyce et al. 2010) but it seems that this decline has not occurred in near-shore waters off the coast of Oamaru. A longer time series of data may be required to be certain of any trends and enable predictions around how productivity will respond to global climate change. Extreme wave heights have not increased through time but are predicted to with climate change (Mullan et al. 2011). The current study offered insights into how little penguins, and potentially other near-shore foraging animals will respond to changes in the marine environment.

At Oamaru, fewer penguins came ashore during periods of rough seas. The longer a storm persisted, the longer the number of penguin arrivals ashore remained low. High winds and wave action during more intense storms likely caused increased mixing of the water column resulting in the re-suspension of sediments, reducing water clarity (Verspecht and Pattiaratchi 2010) and impeding visual feeding. This raises the question of why the penguins prefer to stay at sea during what would seem to be energetically-expensive conditions. Other seabirds species have been found to reduce foraging time during rough seas, preferring to ‘sit out’ difficult conditions (Daunt et al. 2006).

We observed a reduction in annual survival of breeders in the years with the highest P99 exceedence. Foraging difficulty, decreased food intake and subsequent loss of body mass is probably the mechanism driving the relationship between storms and the survival rate of penguins. Difficulty foraging during storms reduced prey capture success and diving rate for terns (Taylor 1983; Braby et al. 2011). Long term, an increase in the frequency and intensity of extreme storms is likely to increase variation in adult survival, due to increasing numbers of breeding seasons with reduced survival rates. Population growth rates in long-lived vertebrates are highly sensitive to variation in adult survival rates (Sæther and Bakke 2000). Frederiksen et al. (2008) showed that increasing temporal variation in survival attributable to the occurrence of storms with strong onshore winds and high rainfall during winter would lead to reduced population growth and increased probability of extinction of European shags (*Phalacrocorax aristotelis*).

In addition to impacts from storms, chlorophyll was an important variable determining survival of breeding little penguins. Annual survival increased with increasing chlorophyll recorded during January-April prior to the breeding season. The proportion of fledglings recruited also increased with increasing chlorophyll January-April of the season of fledging. A negative relationship was apparent between chlorophyll and the median date of egg-laying; indicating earlier onset of laying with increasing chlorophyll from January-April prior to breeding. Small, inshore schooling fish predominate in the diet of little penguins at Oamaru: mainly slender sprat (*Sprattus antipodum*) and Graham’s gudgeon (*Grahamichthys radiata*) (Fraser and Lalas 2004; Flemming et al. 2013). Slender sprat grow to 120 mm in length (Whitehead et al. 1985), spawn from June to November (Colman 1979; Robertson 1980) and are very abundant in Canterbury Bight, including off Oamaru (Colman 1979). Fish production is influenced both by spawning conditions and primary productivity that influences growth (Basilone et al. 2004). The abundance of sprat may be influenced by both conditions during spawning and the year following. Slender sprat eaten by little penguins at Oamaru during the 1994 breeding season were largest (50 - 60 mm) during January to April (Fraser and Lalas 2004). Our study found that chlorophyll was generally highest during January to April and since these months are the most productive during the year, the variability in productivity between years may influence the abundance and size of fish available to little penguins. Correlations between chlorophyll and body growth have been found for other marine fish species (Iverson 1990; Basilone et al. 2004). Fish abundance during the January-April prior to breeding therefore may act as an indicator of prey availability for penguins in the coming year.

Studies examining the effects of environmental variation on little penguins have reached contrasting conclusions. An earlier onset of egg laying and higher breeding success of little penguins at Phillip Island, Australia, was associated with warmer SST (Cullen et al. 2009), yet earlier work found the opposite (Mickelson et al. 1992), as did studies in Western Australia (Cannell et al. 2012) and New Zealand (Perriman et al. 2000). Cullen et al. (2009) and Cannell et al. (2012) both attributed relationships to variation in fish abundance, however the ecological mechanisms were unknown as warm water was predicted to decrease fish abundance in Western Australia yet increase it in Victoria. Investigations of relationships with chlorophyll variation during each of the studies in Australia may have helped explain the results, as lay dates related to chlorophyll rather than SST at Oamaru. Links between productivity and penguin reproductive success have been found in other temperate penguin species (Boersma and Rebstock 2009b; Boersma et al. 2009).

Productivity is predicted to decline with increasing SST in open oceans (particularly at low latitudes) as a result of global climate change, and increase with SST at high latitudes

(Behrenfeld et al. 2006). Seabirds at both extreme of latitude are sensitive to variation in productivity. For example, tropical roseate terns (*Sterna dougallii*) were more successful (higher chicks/breeding pair) in years of higher chlorophyll and phytoplankton growth than years of weak growth (Monticelli et al. 2007). Seabirds in the Southern Ocean concentrate their foraging on high productive areas (Peron et al. 2010). Productivity is highly variable in coastal environments due to the complex nature of land-sea interactions, which makes predictions surrounding global climate change difficult (Cloern 1996; Cloern and Jassby 2008). There may actually be an increase in productivity in coastal waters due to increased nutrient input from the land (Gregg et al. 2005). For seabirds it may mean that species will be differential affected depending on their location and foraging proximity to land. We suggest that extreme events linked to global climate change are likely to affect little penguins at Oamaru. How variation in productivity will be affected by climate change, and subsequently affect little penguins is unknown, but may be positive and potentially mitigate impacts from other sources.

Chapter 7 :

Discussion and recommendations

In an effort to better understand the population dynamics of little penguins, this thesis has addressed three interrelated topics; quantifying demographic parameters, describing foraging behaviour, and investigating relationships between demographics and environmental variables.

Long-term monitoring has clear benefits for understanding demographic parameters and population growth (Porzig et al. 2011). My study showed that comprehensive long-term monitoring has had profound advantages for estimating little penguin demographic parameters accurately at Oamaru. These parameters are not constant – only by many years of study can an overall average be discerned from annual fluctuations. For example, the consecutive years from 1998 to 2001 had lower reproductive output compared to the prior breeding seasons. Had these four seasons been the focus of a study, I would have reported much lower breeding success for this species at Oamaru. Based on a drop in breeding success from 1993-1997 to 1998-2001, Johannesen et al. (2003) suggested that density-dependent depletion of resources limited breeding success as this colony increased in size. My study, with a further ten seasons of data, shows that this is not the case. Instead, it is clear that breeding success is somewhat variable year to year, and that long term study is vital to elucidate overall trends in demographic parameters.

The reproductive performance measured over 19 years at Oamaru was the highest reported for little penguins (Table 2.5, Chapter 2). Survival probabilities were higher at Oamaru than those at Phillip Island (Chapter 3). The combination of these demographic parameters is driving an increase in the population size at Oamaru. High breeding success was attributable to double brooding, resulting from early onset of egg laying. Double brooding and the laying of replacement clutches increased breeding success by as much as 75% per season relative to single clutches. Double brooding does not occur everywhere throughout the little penguins' range (e.g. west coast of New Zealand; Heber et al. 2008) and where it occurs it does not guarantee high breeding success, such as at Phillip Island (Reilly and Cullen 1981; Robinson et al. 2005). Double brooding is more likely to occur in tropical or subtropical seabirds, and in penguins has only been recorded for African penguins (*Spheniscus demersus*, Crawford et al. 1999*)*, Humboldt penguins (*S. humboldt*, Paredes et al. 2002), Galápagos penguins (*S. mendiculus,* Boersma 1978) and little penguins (Gales 1985). All species exhibit an extended laying period, particularly the Galápagos penguins which lay year-round if conditions permit (Vargas et al. 2006). Double brooding is unique among temperate penguins due to the compressed breeding season, therefore the extended laying period by little penguins is atypical for temperate penguins. The current study is the first to quantify double brooding in a temperate seabird and to show the contribution of double brooding to annual productivity.

Penguins are regarded as sentinels of the marine environment (Boersma 2008), providing insights into ecosystem change (e.g. Piatt et al. 2007; Mallory et al. 2010). This is because their relatively high trophic status and restricted foraging range during the breeding season, make them sensitive to local environmental change (Chiaradia et al. 2010; Durant et al. 2010). The continued growth of the Oamaru colony, particularly the high survival and reproductive output of its birds, indicates that the penguins do not experience food shortages that little penguins at other colonies do (e.g. Phillip Island). This is particularly evident when demographic parameters of this population are compared with those measured at Phillip Island. The onset of egg laying by little penguins at Oamaru was highly variable over the study period, suggesting that this is one of the ways that the birds respond to fluctuations in food availability. Interestingly, even during breeding seasons with a late onset of egg laying, the conditions driving the late laying did not seem to persist through the season as the birds did not fledge lighter chicks; fledge weights were similar across ‘normal’ and ‘late’ breeding seasons.

Before describing foraging behaviour of little penguins in relation to reproductive performance, I first addressed potential impacts of attaching data-logging devices repeatedly to little penguins through the breeding season (Chapter 4). The results established that it is possible to do so with no negative impacts on body condition, hatching success, fledging success, chick growth parameters or adult survival. The study benefitted from the inclusion of control individuals subjected to the same handling as instrumented individuals. Previous research investigating effects of data-logging devices on seabirds have shown impacts occur on breeding success (Croll et al. 1996), hatching success (Collins et al. 1999), chick growth (Ackerman et al. 2004; Adams et al. 2009), and adult body condition (Passos et al. 2010). Impacts result from the disruption to streamlining, increasing energy costs (Ropert-Coudert et al. 2000), a reduction in colony attendance (Whidden et al. 2007) and increased stress due to the presence of the device (Beaulieu et al. 2010). The importance of testing for device effects is, in part, to ensure, for ethical reasons, that effects remain small. Additionally, and just as importantly, such studies increase confidence that results obtained from the device represent normal behaviour - undistorted by effects of attachment. Data-logging devices are proving to be an important research tool in seabird ecology, however, I recommend that all studies should monitor potential effects of their use by including control individuals as a comparison. I also encourage the reporting of non-significant that do not show evidence of an impact because there is a need to show if the increased miniaturisation of devices mitigates impacts on individuals studied.

My study has been able to identify important foraging areas and quantify the foraging range of little penguins at Oamaru (Chapter 5). When away from the colony for several days, the penguins travelled northwards towards and north of the Waitaki River mouth. The addition of nutrients into the marine environment at the river mouth may increase the productivity in the area; Zeldis (1985) found large aggregations of the galatheid krill *Munida gregaria* in the area of the Waitaki River plume. Trawl surveys have also found high densities of fish northwards of the river mouth (Beentjes et al. 2002). The river mouth may also be important for other seabird species such as red-billed gulls (*Larus novaehollandiae scopulinus*) (Perriman and Lalas 2012). Studying the foraging behaviour of birds residing at the second colony at Oamaru (c. 1 km away from OBPC) would further discriminate whether this preference is restricted to the study colony and perhaps certain individuals or if it is due to the nature of the local marine environment. During single-day trips the penguins generally foraged within 20 km of the colony. This distance from the colony, during single-day trips, was similar to little penguins in Victoria, Australia, found by Hoskins et al. (2008).

Foraging behaviour depended on the time of year rather than stage (incubation versus chick rearing) of breeding. Diving effort was lowest during the austral summer of 2012.

Considering the penguins are visual foragers, one might have expected higher diving effort during the summer because of the longer daylight period (i.e. more time for foraging). It seems most likely that prey were simply more available at this time, and hence the birds did not have to expend so much energy on feeding, nor did they dive as deep. Dive depth decreased as the season progressed, suggesting a response to changing prey abundance and distribution (diving shallower during the austral summer months). A decrease in prey density in winter has been suggested as the likely reason for extended bottom durations by king penguins in winter compared to summer (Charrassin et al. 2002).

Two severe storms during the three years of foraging research of the study caused complications for relating foraging behaviour to reproductive output. Without their impact the penguins' reproductive performance during the studied breeding seasons would likely have been quite similar. In addition to the productive marine environment, plasticity in foraging behaviour appears to help birds cope with change, and hence aids population growth at Oamaru. Gentoo penguins at the South Shetland Islands, Antarctica, exhibited plasticity in their foraging behaviour while maintaining reproductive success: diving behaviour varied over 5 years yet chick-rearing success remained constant (Miller et al. 2009). Miller et al. (2009) suggested this behavioural plasticity helped the populations in the region to remain stable.

An outcomes of global climate change is potentially an increase in the frequency and intensity of winter storms (Mullan et al. 2011; IPCC 2013). This study was the first to document impacts of storms on little penguins. Storms caused a drop in the number of penguins arriving ashore (Chapters 5 and 6), which lead to a reduction in chick growth during the 2010 breeding season and a disruption to egg-laying during 2011 (Chapter 5).

Adult survival was also impacted (Chapter 6). Impacts of storms on seabirds occur both in the terrestrial environment, via increased rainfall during breeding, which causes flooding of nests (Wright et al. 2013), and in the marine environment via rough seas increasing turbidity, which restricts visual foraging (Braby et al. 2011). The terrestrial effects of storms on little penguins at Oamaru are limited, not only because they nest in artificial boxes that do not flood, but also because during storms they spend most of their time at sea. The multiple effects of storms on penguins, found in this study, suggest that other seabirds foraging in same region that are also visual foragers might be similarly affected.

The top 100m of the water column is predicted to warm by 0.6˚C to 2˚C by the end of the 21st century (IPCC 2013). Increasing SSTs are likely to result in a decrease in productivity through many tropical and open ocean areas (Behrenfeld et al. 2006), however what will happen in coastal waters is uncertain (Gregg et al. 2005). The current study supported the SST trend by showing an increase in mean May-August SST through time but did not show an increase/decrease in chlorophyll or storm intensity near Oamaru. Median lay dates were correlated with the average chlorophyll of the January-April prior to breeding (Chapter 6), perhaps due to a match in productivity around an important growth period for their preferred prey species. Median lay dates became 12 days earlier for every 0.1 (mg m^{-3}) increase in chlorophyll. Earlier egg laying will help to increase the likelihood of double brooding and increase breeding success. Annual recruitment of fledglings and breeder survival were also positively related to chlorophyll during January-April. The ecological mechanisms driving prey abundance are complex and even though SSTs are predicated to increase with global climate change, chlorophyll my also increase for unrelated reasons (Gregg et al. 2005). As the current study on little penguins at Oamaru emphasises, it is therefore important to consider the effects of multiple environmental variables on several demographic parameters.

7.1 Recommendations for future research

As expected, the current study raised questions concerning seabird conservation. Specifically:

- What are the specific threats within the penguins’ foraging zone? Management practices aiming to conserve and protect little penguins (and other seabirds) will rely on measuring the impact of extrinsic factors within the penguins’ foraging range. The penguins forage offshore from the Waitaki River mouth, where pollutants from intensive agriculture (especially dairy farming) in the Waitaki Valley may be introduced into the sea, as occurred in Tasman Bay (Cornelisen et al. 2011). Further research should look for further correlations with the ecology of the Waitaki River, from chlorophyll and river output, to water quality and effects on prey species particularly during increased rainfall, all with the aim of identifying the consequences for seabirds. Impacts from entanglement in set-net fisheries are undocumented, but likely. Yellow eyed-penguins (*Megadyptes antipodes*) have been caught frequently in the Otago region (Darby and Dawson 2000) and four were caught in commercial set-nets in the 2008-09 fishing season off the North Otago coastline, three of which were close to the Waitaki River mouth (Abraham and Thompson 2011). If we consider that observer coverage on commercial vessels in that season was 2.2% (and zero on recreational fishers) it is clear that the majority of captures would not be reported.

- Are the effects of storms on little penguins similar at other colonies to those found at OBPC? Do they affect other seabird species similarly? How is water clarity affected by storms, and how does it influence penguin foraging? This could be investigated using small attached cameras.
- Much could be learned from examining the differences between single and double brooders. First to identify whether there are birds that only ever single brood, or always double brood, and second to identify whether these groups have different foraging behaviours, chick growth weights (and rates).
- How will population growth rates vary under different climate change scenarios? This could be explored using demographic parameters from the current study in a population model that can incorporate predicted levels of climate change, and greater variability in climate, to estimate the likely impact on population trajectories.

7.2 Management recommendations

The current study highlighted the high value of the current monitoring programme at Oamaru and I recommend that this continues at the same standard. Assuming that the population continues to sustain the current rates of survival and breeding success, it will be necessary to allow for population growth. The provision of nesting habitat, primarily via more nesting boxes or nesting area, needs to precede population growth to minimise competition for available nests. Provision for growth at OBPC is essential for continued success of both the little penguins and the tourism operation that is reliant upon them.

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