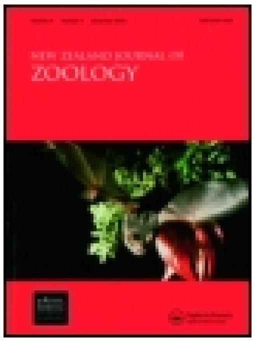

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RESEARCH ARTICLE

Variability in the foraging range of *Eudyptula minor* across breeding sites in central New Zealand

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ABSTRACT
The little penguin *Eudyptula minor* is primarily an inshore forager with its range generally limited to c. 30 km of breeding sites during the nesting period. However, exceptions with greater foraging distances have been recorded in Australia. To investigate the foraging range plasticity in New Zealand we used GPS tracks gathered on 68 individuals in three regions of central New Zealand between 2011 and 2016. Foraging patterns varied between sites and between years. Tracks revealed that penguins can rely on distant foraging areas while incubating, with nesting birds travelling up to 214 km to feed. Isotope analyses of blood samples showed that this distant food across deep waters (0–200 m) is likely to be squid dominated. During the chick rearing period, birds undertook a diet shift to a higher trophic level while foraging closer to their colony, and possibly near river plumes. These findings highlight the need to consider the little penguins' large potential foraging ranges when managing threats and changes to the environment.

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Conservation; *Eudyptula minor*; foraging range; GPS tracking; isotopes; little penguin; population variability

Introduction

The little penguin (*Eudyptula minor*) is endemic to Australasia with a breeding range between 26°S–47°S and 115°E–176°W (Marchant and Higgins 1990). One species of little penguin is currently recognised by New Zealand authorities (Gill et al. 2010), although DNA analyses by Grosser et al. (2015) suggest two distinct lineages treated as separate species: *Eudyptula novaehollandiae*, predominantly in Australia and southeastern New Zealand (hereafter, the Australian taxon) and *Eudyptula minor*, occurring throughout the remainder of New Zealand and the Chatham Islands (hereafter, the New Zealand taxon) (Overeem et al. 2008; Peucker et al. 2009; Grosser et al. 2016). The Australian taxon is known to feed predominantly within 30 km of its nests during the chick rearing stage (Hoskins et al. 2008; Agnew 2014; Pelletier et al. 2014), as does the New Zealand taxon

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(Mattern et al. 2001; Zhang et al. 2015). Unusually long foraging trips have been recorded only in the eastern Great Australian Bight where penguins foraged up to 118 km from their nests (Wiebkin et al. 2005).

Little penguins breed in waters of annual mean sea surface temperature (SST) between 14–22 °C in Australia and 11–18 °C in New Zealand (Uddstrom & Oien 1999). They forage by diving mostly at depths less than 50 m (Chiaradia et al. 2007) to feed on fish, squid and crustaceans. Their diet is dominated by pilchard (*Sardinops sagax*) and anchovy (*Engraulis australis*) in Australia (Chiaradia et al. 2010), while in New Zealand the key prey are the slender sprat (*Spratelloides gracilis*), Graham's gudgeon (*Grahamichthys radiata*) (Fraser & Lalas 2004) and arrow squid (*Nototodarus sloanii*; Flemming et al. 2013), although there is variation in dietary composition between sites.

Many other aspects of the little penguin's biology also vary across its range. The breeding schedule spans the period between April and December with both intra and interpopulation variation (Marchant & Higgins 1990). Different environmental drivers affecting the onset of breeding have been identified: for the Australian taxon (including Otago populations), earlier laying dates within a colony have been correlated with a higher SST at some sites (Cullen et al. 2009), but with lower SST at others (Perriman et al. 2000; Berlincourt & Arnould 2015). Further, higher SST has been correlated with both higher (Cullen et al. 2009; Agnew et al. 2015) and lower breeding success (Cannell et al. 2012).

In contrast to the Australian taxon, the penguins in the New Zealand taxon raise only one clutch per breeding season (Bull 2000; Heber et al. 2008). The foraging behaviour and breeding success also differ between the two taxa (Mattern et al. 2004; Numata et al. 2004). These complex relationships suggest a range of factors influencing the habitat suitability for little penguins. Although the species has received considerable research (Chambers et al. 2014), spatial requirements for the New Zealand taxon have been studied only twice, each time during a single breeding season (Mattern et al. 2001; Zhang et al. 2015).

The penguins' foraging areas are known to be influenced by areas of enhanced productivity such as frontal zones (Bost et al. 2009), eddies (Bon et al. 2015), upwelling (Crawford et al. 2007) or seamounts (Kokubun et al. 2015) where food resources are more predictable within a highly variable marine environment. As a result of terrestrial runoff, river plumes with a high nutrient concentration enhance primary production in a down-plume direction (Dagg et al. 2004). These areas of high productivity are also selectively used as foraging areas by flying seabirds (Matsumoto et al. 2016) and the little penguins in Australia (Kowalczyk et al. 2015b).

Given the variability observed in the breeding and foraging behaviour of little penguins across their range, we used tracking devices and analyses of isotope ratios to examine the foraging behaviour of the New Zealand little penguin taxon at three different breeding sites (with different marine habitat characteristics), and over several years. We expected to find plasticity in the species' behaviour as they adapt to local environmental variations. We also examined whether penguins selectively foraged near river plumes when these occurred within their range.

Methods

The study was conducted in three regions of New Zealand (Figure 1). The first site, Wellington, included three colonies within Wellington Harbour: Balaena Bay (−41.292°S,

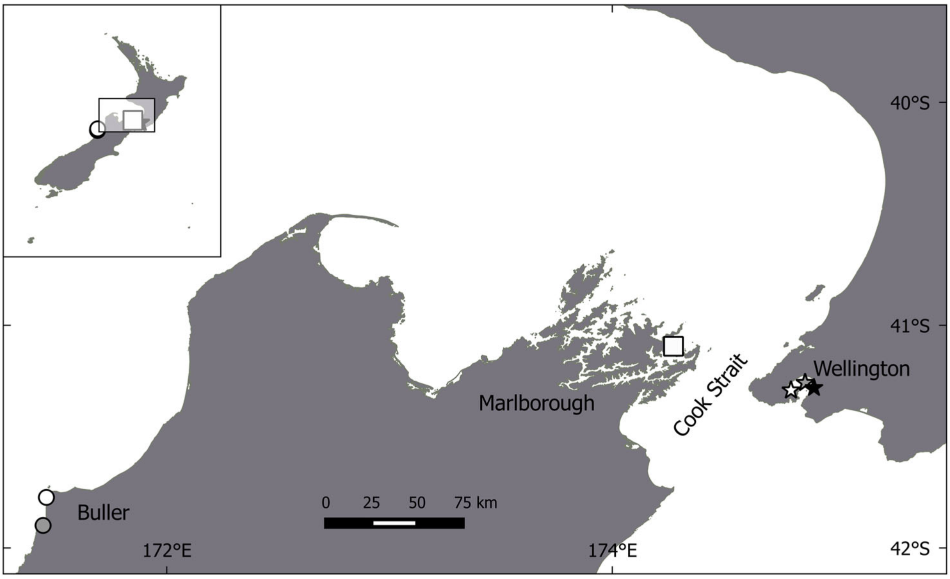

Figure 1. Location of the study sites in central New Zealand. Sites are in Buller Region at Nile River (grey circle) and Cape Foulwind (white circle); Marlborough at Motuara Island (white square) and Wellington at Balaena Bay (white star), Matiu/Somes Island (grey star) and Days Bay (black star).

174.802°E); Matiu/Somes Island (−41.258°S, 174.865°E); and Days Bay (−41.276°S, 174.903°E), which together host c. 200 breeding pairs of little penguins. Banding records show bird exchange between these colonies (G. Taylor, pers. obs.). Wellington Harbour is shallow, with depth mostly less than 20 m (NIWA 2016) and it receives the discharge from the Hutt River, on average 22 m^3/s (Young & Foster 1986). The second site, in Marlborough Region, was at Motuara Island (−41.094°S, 174.272°E) near the mouth of Queen Charlotte Sound (hereafter, the Sound) where c. 300 pairs breed (Renner & Davis 1999). The Sound does not have any major rivers draining into it, and it is mostly less than 50 m deep. It opens onto Cook Strait, which plunges to depths of 100 m only 9 km north of the colony. The third site, in the Buller Region, included two colonies: Cape Foulwind (−41.093°S, 174.271°E) and Nile River (−41.890°S, 171.453°E). These two colonies were 15 km distant from each other and together they contain c. 75 pairs (K-J. Wilson, pers. obs.). The bathymetry at this site follows the gently sloping continental shelf: 50 m deep at 7 km offshore; 100 m at 13 km; and 150 m at 23 km. The Nile River, a river of 16 m^3/s (K. Walter, NIWA, 2017), and the very large Buller River (423 m^3/s) occur to the south and north of these colonies, respectively.

Unmarked breeding birds were captured by hand at their nest or near the nest on their way to/from the sea. GPS tracking devices were attached to the bird, with a maximum of one bird per nest per breeding stage. The aim was to record one foraging trip for each deployment. Handling procedures lasted less than 10 min and the heads of the penguins were covered to minimise stress. Both males and females were tracked during incubation and/or the chick rearing stage. Loggers were deployed on the central dorsal area (Chiaradia et al. 2005) with Tesa 4651 waterproof tape following Wilson et al. (1997) in order to minimise feather damage. As the dataset was collected by several different teams, different kinds of GPS loggers and satellite search times were used (Table 1). Sample sizes and numbers of tracks recorded per site are shown in Table 2. Zhang et al. (2015) describes attachment techniques used at Matiu/Somes Island. The most commonly used loggers for the remaining studies were IgotU GT-120 GPS units (Mobile Action Technology), sealed in waterproof heat-shrink tubing and measuring 80 × 25 × 12 mm. The dry-weight of the whole package was 25 g and represented 2.5 ± 0.2% of the bird's weight. Most birds were weighed in a bag with a spring balance (± 25 g) prior to and after their trips. Breeding success was defined as the mean number of chicks fledged per pair, monitored by weekly burrow checks with burrowscope Taupe (Sextant Technology Ltd.) until 9 November (chicks fledging) for Marlborough and by nest box checks at the start and end of the breeding season for penguins in the Wellington and Buller study sites.

Spatial analysis

A foraging trip was defined by the time spent at sea by an individual between its departure from the colony and its return. All the locations were filtered using the method of Austin et al. (2003) in the package 'DiveMove' (Luque 2007) developed in the R software (R Core Team 2016). Unrealistic travel speed greater than 2 m/s (Hoskins et al. 2008) were removed, involving 3% of the locations. The GPS technology we used show where the penguins went and how long they stayed there. When the sample sizes were equal or greater than three individuals, their spatial distribution was determined by the kernel-density estimation (Worton 1989) with the *KernelUD* function in R package 'adehabitat' (Calenge 2006). The 95% utilisation distribution (UD) represent the overall activity area, including transit and foraging with no distinction (Brothers et al. 1998). However, the 50% UD, referred to as the focal area, represent the places where the largest concentrations of locations occurred. Hence, the focal area is likely to represent the most important foraging areas (Wood et al. 2000). A test with resampled tracks (to get the same sampling interval between loggers) against the pooled data showed no significant difference between resulting UDs. As kernels rely on a probability function (Worton 1989) rather than the number of locations, we kept the pooled data. The *h* smoothing factor, which depends on the spread of the UDs, was defined for the first time by the software (hdef method) and then by ourselves, with a value fitting all the results from the same site or same period in order to allow accurate comparisons (Table 1). Areas were calculated using the *kernel.area* function.

Table 1. GPS loggers used to track little penguins at each study site each year.

	Wellington	Marlborough	Buller
2011	Earth&Ocean GPS (5)	–	–
2012	IgotU GT120 GPS (1)	–	–
2013	–	–	IgotU GT120 GPS (5)
2014	IgotU GT120 GPS (3)	IgotU GT120 GPS (3)	–
	Fastloc II GPS (3)	Fastloc II GPS (3)	–
	Kiwisat PTT (60)	Kiwisat PTT (60)	–
2015	–	IgotU GT120 GPS (15 for incubation, 5 for chick rearing)	IgotU GT120 GPS (15 for incubation, 5 for chick rearing)
2016	–	–	IgotU GT120 GPS (15 for incubation, 5 for chick rearing)

In parentheses, the satellite search interval (minutes).

Table 2. Tracking parameters (mean ± SD) obtained from 68 little penguins tracked at three sites in central New Zealand between 2011 and 2016.

Region	Wellington				Marlborough				Buller				
Year	2011	2012		2014	2014		2015		2013	2015		2016	
Month	Nov	Oct / Nov / Dec	Oct	Oct / Nov	Oct / Nov	Oct / Nov	Sep / Oct	Oct / Nov	Oct	Sept	Sept / Oct	Oct	Oct
Breeding stage	Chick	Chick	Egg	Chick	Egg	Chick	Egg	Chick	Chick	Egg	Chick	Egg	Chick
Birds tracked/tracks recorded	4/4	8/13	4/18	6/7	1/1	5/5	14/24	15/28	3/3	1/1	3/7	1/1	3/4
Mean maximum range (km)	7 ± 7	9 ± 8	11 ± 4	12 ± 11	155	49 ± 32	102 ± 69	11 ± 9	17 ± 7	57	15 ± 6	25	22 ± 2
Mean travelled distance (km)	–	–	69 ± 24	54 ± 22	482	213 ± 182	253 ± 189	28 ± 18	–	170	34 ± 15	108	34 ± 23
Mean trip duration (d)	–	1 ± 0	2 ± 1	2 ± 1	16	7 ± 5	7 ± 4	1 ± 1	–	5	1 ± 1	2	1 ± 0
95% UD area (km^2)	137	228	244	344	4,776	2,665	16,521	1,016	159	–	359	–	278
50% UD area (km^2)	32	43	30	36	810	487	4,062	107	22	–	54	–	42
h smoothing factor (km)	1.5	1.5	1.5	1.5	–	3	10	3	1.2	–	1.2	–	1.2
Breeding success (cpp (*n*))	–	–	1.2 (6)*		0.13 (30)		1.0 (43)		0.7 (41)	0.81 (31)		0.53 (1)	

–, no metrics calculated due to incomplete tracks or data.

*1.1 chicks per pair were observed at 29 nests monitored at other sites around Wellington Harbour in 2014 (K. Wiley, Places for penguins, pers. comm., 2016).

To investigate similarity in foraging areas over the years, the spatial overlap between 50% UDs was calculated using the *kerneloverlap* function. The overlap index was calculated with the Bhattacharyya's Affinity as it is appropriate to quantify the overall similarity between UDs (Fieberg & Kochanny 2005). All the kernels were plotted in the software QGIS (QGIS Development Team 2016). Tracking parameters (maximum range, total distance travelled, trip duration) were calculated for complete tracks only (Table 2). Incomplete tracks due to logger failures were excluded from the calculations.

To investigate a possible influence of river outflow on penguin foraging range, we calculated the distance between the mouth of the nearest large river and each study colony in GIS (QGIS Development Team 2016). A river was arbitrarily considered large when its mean flow was greater than 10 m^3/s (Young & Foster 1986). The distance was plotted against the mean maximum foraging distance known for the colony. We used our study sites and added data from Agnew (2014) for a study of penguins near Oamaru in these analyses. The relationship between maximum foraging range and distance to a large river was tested using a linear regression with data pooled across years at each site.

Isotope analyses

To estimate the potential diet of penguins, blood samples were collected from birds at the Marlborough study site in 2015. A sample of 0.1 mL blood was taken from the tarsal vein at logger retrieval and stored in 70% ethanol. We investigated potential differences in the penguins' diet between breeding stages, using the stable isotope ratios of carbon ($^{13}C/^{12}C$) and nitrogen ($^{15}N/^{14}N$) in the whole blood. These ratios change in a predictable and quantifiable way along the food chain (Hobson & Clark 1992a, 1992b). As $\delta^{15}N$ increases with the trophic level and $\delta^{13}C$ varies according to the area that prey come from, isotopes allow determination of the relative trophic levels and detection of prey consumption from inshore versus offshore waters (Hobson et al. 1994). Less intrusive than stomach flushing techniques, the isotopic niche is a proxy of the trophic niche (Jaeger et al. 2010). Isotope ratios in whole blood reflect a period of dietary integration of about 4 weeks (Bearhop et al. 2002). Blood samples were freeze-dried for processing and subsampled with 0.5 mg of ground and dried blood loaded into separate tin capsules. Carbon and nitrogen content and isotopic composition were analysed in duplicate using an Isoprime isotope ratio mass spectrometer interfaced to a EuroEA elemental analyser in continuous-flow mode (EA-IRMS). Working reference standards (leucine, EDTA, caffeine, hair and sucrose) were calibrated against international reference materials (IAEA-N1, IAEA-N2, IAEA-CH6 and IAEA-CH7) and blanks were included during each run for calibration. Isotopic ratios ($^{15}N/^{14}N$ and $^{13}C/^{12}C$) are expressed as isotopic deviations defined as:

$$\delta(‰) = \frac{R_s - R_{\mathrm{ref}}}{R_{\mathrm{ref}}} \times 1000$$

where R_s is the isotopic ratio measured for the sample and R_{ref} is the international standard. The $\delta^{13}C$ value is relative to the international Vienna Pee Dee Belemnite (VPDB) standard, and the $\delta^{15}N$ value is relative to atmospheric air. Raw values were normalised using internal standards calibrated to international standards and results are expressed in points per thousand (‰) versus the specific reference. Analytical precision of the measurements is ± 0.2‰, and reproducibility of the results is within ± 0.2‰ for carbon and ± 0.3‰ for nitrogen (1σn). Isotopic niches were compared between stages from Bayesian standard ellipses computed in the R package 'siar' (Parnell & Jackson 2013).

Statistics

Due to the small sample sizes at some sites, and the lack of data for some years, statistics were limited to site and/or breeding stage comparisons within the same year. We reduced possible autocorrelation of trips by considering only the birds' first foraging trip, when they did several consecutive short trips. Prior to performing statistical tests, data exploration revealed non-normality, so site and breeding stage comparisons were performed with a non-parametric Kruskal-Wallis rank sum test. With the isotope results we tested for differences in isotopic niche between breeding stages at one site using a one-way ANOVA. Results are shown by mean ± standard deviation.

Results

Inter-stage variability

Wellington penguins foraged mostly within Wellington Harbour and within 12 ± 12 km of their colony (Figure 2). During the incubation and chick rearing stages, trip duration was between 1 and 3 days. Two incubating birds also did trips into Cook Strait and Palliser Bay up to 36 km from their colony. The tracking parameters (Table 2) showed no differences in their range ($H(1) = 1.63$, $P = 0.2$), distance travelled ($H(1) = 0.4$, $P = 0.5$) or trip duration ($H(1) = 0.1$, $P = 0.6$) between breeding stages.

At the other study sites, trip parameters did differ between stages (Table 2). In Marlborough in 2015, incubating birds foraged within 102 ± 69 km of their colony (minimum = 1 km, maximum = 214 km) and their trips lasted 7 ± 4 days (minimum = 1 day, maximum = 16 days). Three birds undertook short-distance trips within 10 km of the colony. Three other birds undertook medium-distance trips 40–75 km from the colony towards Cook Strait and other areas of the Marlborough Sound. Eight birds crossed

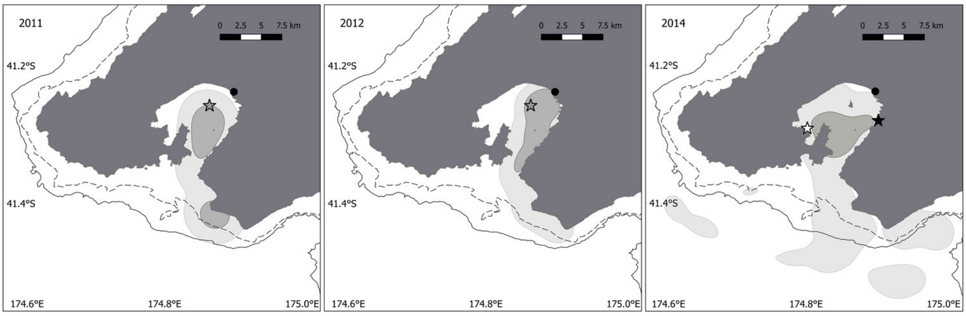

Figure 2. Inter-annual variability of Wellington penguins foraging areas between 2011, 2012 and 2014. The light grey area represents the home range (95% UD), the dark grey the focal area (50% UD). Study colonies are shown by stars: grey for Matiu/Somes Island, white for Balaena Bay and black for Days Bay. The black circle shows the Hutt River mouth. The dashed line is 50 m bathymetric contour; the solid line is 100 m.

Cook Strait to forage 93–214 km away, as far as the Taranaki Bight on the west coast of the North Island (Figure 3). After trips during the incubation period, birds came back 75 ± 70 g heavier (minimum = −50 g, maximum = + 175 g).

A total of 66% of the nests belonging to birds undertaking short-distance trips were successful (breeding success = 1 ± 1 chick per pair). In contrast, all the nests tended by birds undertaking medium-distance trips failed: the chicks hatched but were not fed. However, a total of 75% of nests tended by birds undertaking long-distance trips (range = 104–173 km, up to 13 days) were successful. Only two birds (which went 169 and 214 km away for 9 and 11 days, respectively) failed to provision their chicks. Such long trips did not reduce breeding success ($H(2) = 0.5$, $P = 0.9$; Figure 4) and eventually these nests had the best breeding success (1.3 ± 0.9 chick per pair).

At chick rearing stage, birds undertook shorter trips ($H(1) = 9.6$, $P = 0.001$) closer to the colony ($H(1) = 10.6$, $P = 0.001$). They fed within 6–10 km in and outside the Sound during 1-day trips, and 36–43 km away in Cook Strait during 2-day trips. They came back to the colony 57 ± 86 g heavier (minimum = −75 g, maximum = + 225 g), but these measures may be biased as some birds were weighed before feeding chicks and others afterwards.

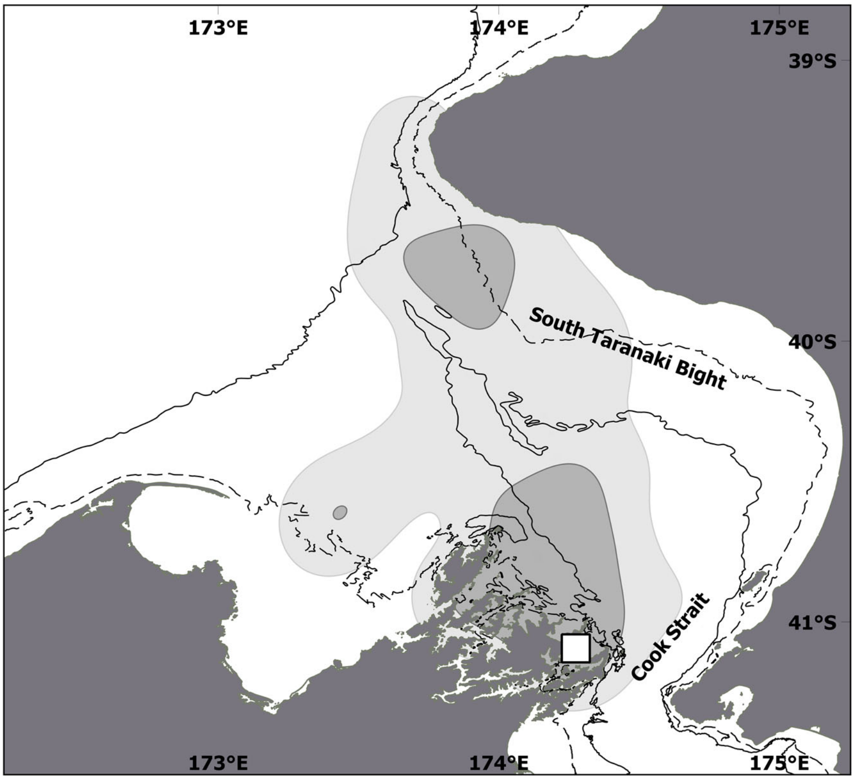

Figure 3. Foraging areas of Motuara Island little penguins during incubation stage in 2015. The light grey area represents the home range (95% UD), the dark grey the focal area (50% UD). Study colony is shown by the white square. The dashed line is 50 m bathymetric contour; the solid line is 100 m.

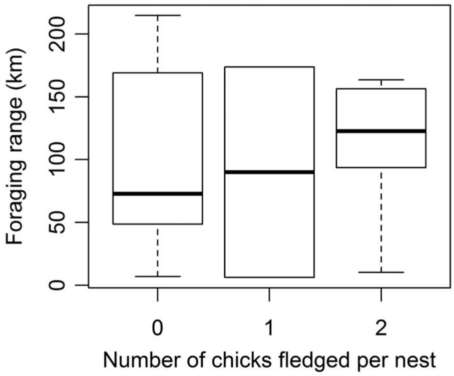

Figure 4. Boxplot of the incubation foraging range distributions by breeding success ($n = 14$). Long foraging trips are also undertaken by successful birds.

Inter-stage differences were also evident in Buller Region with longer tracks undertaken during incubation (Figure 5), but the sample sizes ($n = 1$ for both 2015 and 2016) were too small to be statistically tested.

Inter-site variability

Within each year, the penguins' tracks showed significant differences between sites (Table 2). Marlborough penguins performed longer duration trips ($H(1) = 3.75$, $P = 0.003$), travelled to locations farther away ($H(1) = 6.72$, $P = 0.009$) and covered more distance ($H(1) = 3.83$, $P = 0.05$) than the Wellington Harbour penguins tracked during the same months in 2014. Marlborough penguins showed no significant differences when compared to Buller birds in their range ($F(1) = 1.4$, $P = 0.24$), distance travelled ($F(1) = 0.65$, $P = 0.42$) or trip duration ($H(1) = 48$, $P = 0.06$) while raising chicks in 2015.

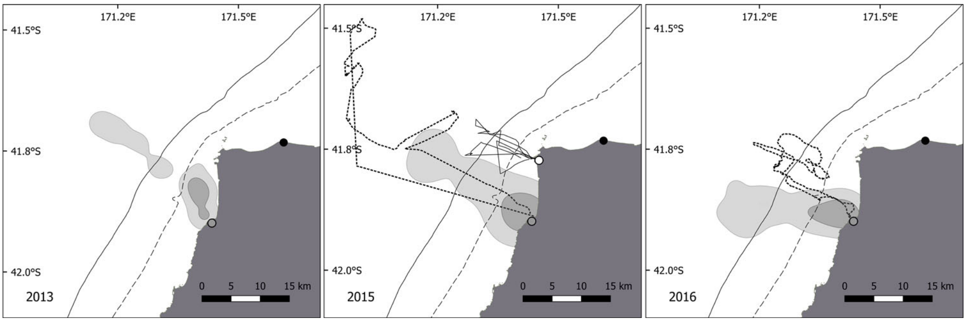

Figure 5. Inter-annual variability of Buller little penguin foraging areas between 2013, 2015 and 2016. The light grey area represents the home range (95% UD), the dark grey the focal area (50% UD). Study colonies are shown by the circles: grey for Nile River, white for Cape Foulwind. Tracks not included in kernel calculation due to small samples sizes are shown: in 2015, incubation track from Nile River (dotted line) and chick-rearing stage track from Cape Foulwind (black line), and in 2016 an incubation track from Nile River (dotted line). The black circle shows the Buller River mouth. The dashed line is 50 m bathymetric contour; the solid line is 100 m.

Inter-annual variability

Between years, the Wellington and Buller penguins used a similar range. At Wellington, over 3 years (Figure 2), no significant differences occurred in their range distance ($H(2) = 3.11$, $P = 0.21$). On a scale from 0 to 1, their focal areas overlapped by 0.87, 0.75 and 0.8 for 2011/2012, 2012/2014 and 2011/2014 comparisons, respectively. In Buller (Figure 5) the birds also used a similar range over 3 years ($H(2) = 2.4$, $P = 0.3$) and the overlap in focal areas was 0.63, 0.42 and 0.77 for 2013/2015, 2013/2016 and 2015/2016 comparisons, respectively. However, inter-annual variations occurred in Marlborough (Figure 6). Penguins raising chicks spent longer at sea ($H(1) = 15.7$, $P = < 0.001$), travelled greater distances ($H(1) = 5.3$, $P = 0.02$) and went further away ($H(1) = 6.6$, $P = 0.01$) in 2014 than in 2015. These differences were reflected in the breeding outputs, with productivity per pair of 0.13 and 1 chicks fledged per pair in 2014 and 2015, respectively (Table 2). In 2014, penguins also used a foraging area two times larger, including visited localities not used in 2015 (Figure 6).

Isotopic niche

The stable isotope ratios for Marlborough birds in 2015 revealed a dietary shift between breeding stages. Both δ^{13}C and δ^{15}N values were significantly different ($F(1) = 7.3$, $P = 0.01$ and $F(1) = 4.9$, $P = 0.03$, respectively). Isotopic niches, represented by the ellipses (Figure 7), showed an area of 0.8 for incubating birds compared with 0.3 for birds raising chicks. This suggests that birds sampled during the incubation period fed on a broader range of offshore-dominated prey. In contrast, birds sampled while feeding chicks fed on a narrower range of prey from higher trophic levels, from inshore-dominated prey. The small overlap between the two isotopic niches (3.8% of the incubation ellipse and 10.9% of the chick rearing ellipse) showed a clear segregation between

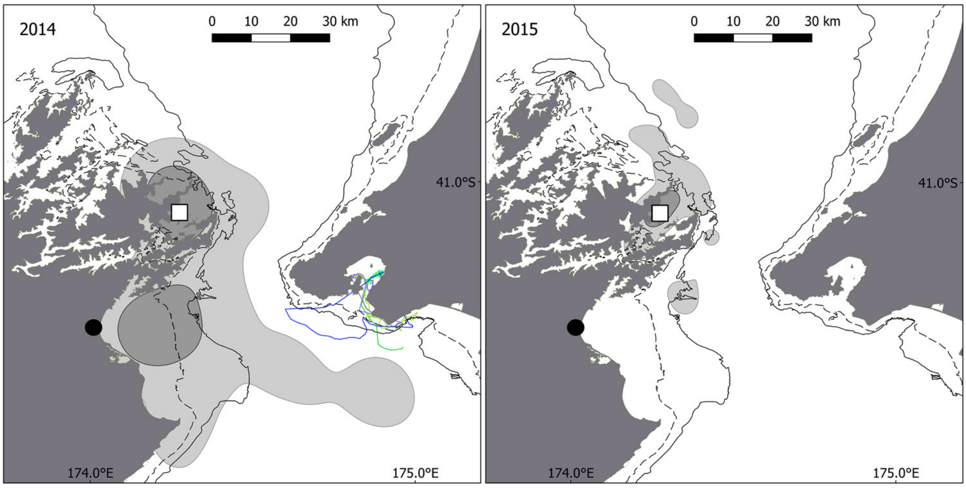

Figure 6. Inter-annual variability of Marlborough little penguin foraging areas between 2014 and 2015. The light grey area represents the home range (95% UD), the dark grey the focal area (50% UD). Study colony is shown by the white square; the black circle shows the Wairau River mouth. The dashed line is 50 m bathymetric contour; the solid line is 100 m.

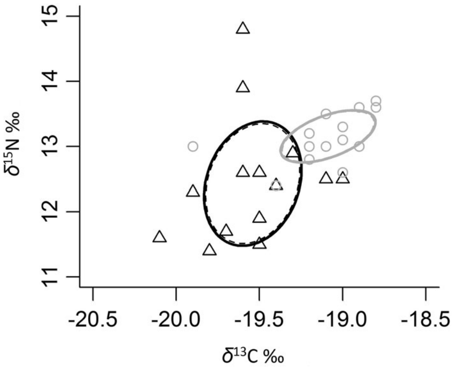

Figure 7. Whole blood $\delta^{13}C$ and $\delta^{15}N$ values of tracked little penguins during incubation (black triangles, $n = 14$) and during chick rearing (grey circles, $n = 16$). Standard Bayesian ellipse areas corrected (solid line) and uncorrected (dashed lines) for small sample sizes are shown for incubation and chick rearing (black and grey lines, respectively).

stages, coinciding with a spatial shift in their foraging areas. The offshore carbon signature corresponded to birds foraging mostly across the Cook Strait, while the inshore carbon signature corresponded to birds foraging mostly in and off the mouth of the Sound.

River distance

Birds nesting further from large rivers foraged at greater distances from their nests. We found a positive relationship between the mean maximum foraging distance and distance to a large river. This correlation did not hold during chick rearing ($R^2 = 0.06$, $t = 0.2$, NS) but was significant during incubation ($R^2 = 0.96$, $t = 6.8$, $P = 0.02$) (Figure 8).

Discussion

Inter-site variability

The foraging range of little penguins in central New Zealand showed strong differences between sites. Our study of GPS tracks revealed that most of the variability in foraging ranges between colonies occurred during the incubation period. Furthermore, the tracks we obtained from penguins at the Buller and Marlborough sites challenge the assumption that little penguins are exclusive near-shore feeders. Thus, the long trips of little penguins reported by Wiebkin et al. (2005) from the Great Australian Bight are not an exception; rather, they demonstrate the adaptability of this species to a range of marine habitats. Strong site effects appear to influence the foraging behaviour of little penguins across their range. Similar results have been found for the Magellanic penguin (*Spheniscus magellanicus*; Wilson et al. 2005) and the Humbolt penguin (*S. humbolti*; Hennicke & Culik 2005), and explained by site-specific prey distributions and abundance. As the foraging trip distance is negatively correlated with prey availability (Inchausti et al. 2003; Ballard et al. 2010), it is likely that little penguins undertook long foraging trips offshore because of poorer prey accessibility near the colony.

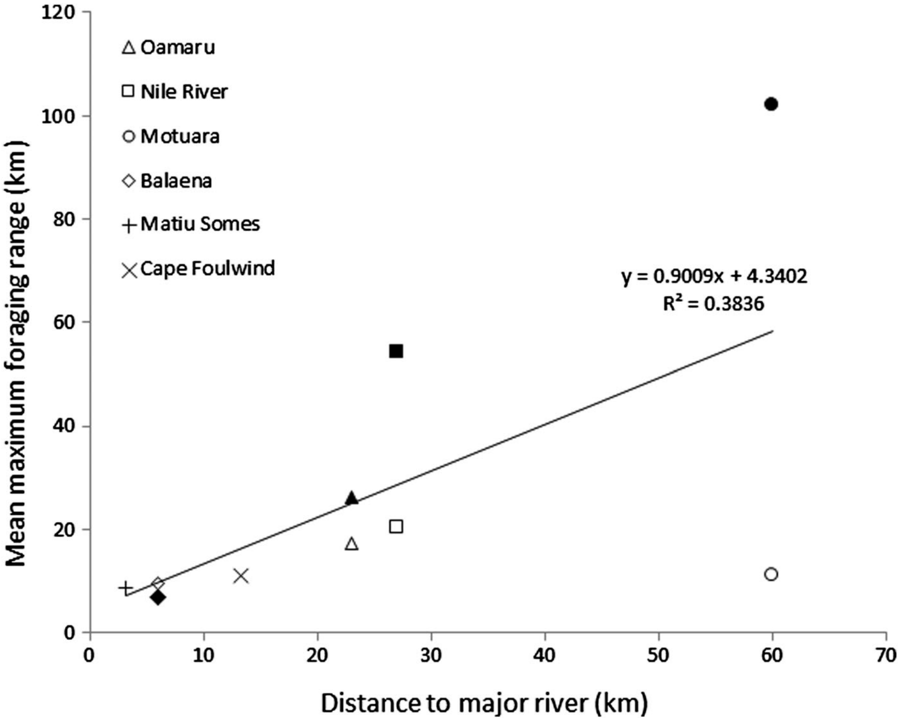

Figure 8. Relationship between the mean maximum foraging range and the distance from colony to a major river (> 10 m^3/s). Little penguins nesting far from a river had a greater foraging range. Study colonies are shown by symbols. Solid symbols represent data for the incubation stage and open symbols for the chick-rearing stage.

In contrast to the behaviour of penguins during the incubation stage, birds behaved more like classic inshore foragers during the chick rearing stage, as noted in the previous tracking results from Motuara Island (Mattern et al. 2001), Wellington (Zhang et al. 2015), Otago (Agnew 2014) and Australia (Hoskins et al. 2008; Pelletier et al. 2014; Kowalczyk et al. 2015a). It is likely that the limited ability of chicks to fast constrains the breeders' range at this stage. Only at Motuara Island in 2014 did birds maintain a large foraging range. The birds at this site are known to have a high diving effort (Mattern et al. 2004; Chiaradia et al. 2007) and these long trips appear to be associated with low prey availability (Inchausti et al. 2003; Ballard et al. 2010) in the Sound. Only the breeding birds from inside a large harbour (Wellington) showed a stable foraging range. Further work associating prey abundance, foraging strategy and isotopic niche in a gradient of oceanic to sheltered inshore breeding sites would be useful to understand how environmental conditions influence breeding strategies and how little penguins from both New Zealand and Australian taxa can adapt to perturbations in their environment (Ancel et al. 2013).

Inter-annual comparisons

Little penguins at the Wellington site showed a consistency between years, as was also recorded at Oamaru in New Zealand (Agnew 2014), in Bass Strait (Hoskins et al. 2008;

Berlincourt & Arnould 2015) and at Port Phillip Bay (Kowalczyk et al. 2015a) in Australia. For Marlborough birds, the long-distance foraging trips had been suspected by previous workers at the same colony (Numata et al. 2000; Mattern et al. 2001; Renner & Davis 2001) and our records suggest that the South Taranaki Bight may be used each year during incubation. Inter-annual variability occurred at Motuara Island at chick rearing stage. As reproductive success is correlated with prey density (Croll et al. 2006) and foraging trip length (Boersma & Rebstock 2009), the differences in breeding success and foraging range observed between 2014 and 2015 suggest that little penguins experienced different prey availability within the Sound between years. Little penguins appear to adapt to low prey availability by increasing their foraging range and area. However, their low breeding success showed that they were unable to fully compensate for low prey availability during unusual environmental events conditions (Ropert-Coudert et al. 2015).

Inter-stage differences

While no significant effect of breeding stage was apparent for the Wellington Harbour nesting birds, penguins on the West Coast and Marlborough Sound sites did show clear differences between breeding stages. Incubating penguins usually undertook longer trips than chick rearing birds (Hull et al. 1997; Charrassin et al. 1998; Collins et al. 1999). This breeding stage difference was reinforced by the isotope results for Marlborough birds.

The nitrogen ratios from Motuara Island birds are among the lowest recorded for this species, comparable to those recorded at Stewart Island (Flemming & van Heezik 2014) where penguins have a squid dominated diet (*Nototodarus sloanii*) and comparable to a few individuals from Phillip Island (Chiaradia et al. 2016) where *N. gouldi* contribute to the diet. Penguins that feed mostly on fish species show isotope ratios that indicate a higher trophic level (Chiaradia et al. 2010; Flemming & van Heezik 2014; Chilvers et al. 2015). The eastern South Taranaki Bight, where Motuara Island penguin forage during incubation, is known to receive by horizontal advection the upwelled waters from the Tasman Basin (Bowman et al. 1983; Shirtcliffe et al. 1990). This phenomenon induces a phytoplankton bloom at intervals of 10–15 days, as well as a high macro-zooplankton biomass (James & Wilkinson 1988; Bradfordgrieve et al. 1993). This area of continental shelf also hosts two species of arrow squid (*N. sloanii* and *N. gouldi*) with a main spawning area for the latter (Uozumi & Forch 1995; Hurst et al. 2012). These squids hatch in April–May and, according to the ageing regression of Uozumi & Forch (1995), they should have a dorsal mantle length (DML) between 40 mm and 64 mm by September (123 to 153 days later) when penguins forage there. Squids of comparable size (total length between 90–120 mm) are taken by little penguins (Flemming et al. 2013). Hence, the South Taranaki Bight squids are very likely to be part of the diet of Motuara Island penguins.

At chick rearing stage, trophic level enrichment has been recorded by Chiaradia et al. (2012) with little penguins targeting small fish such as anchovies or pilchards (Dann et al. 2000). Peak energy requirements occur during chick rearing (Chiaradia & Nisbet 2006) when more 'valuable' prey such as energetically-rich fish are taken (Hislop et al. 1991). Marlborough penguins follow the same pattern, which can indicate a possible intentional search for fish or reflect just an opportunistic use of higher trophic level prey near the colony (Chiaradia et al. 2016). A pilchard fishery existed in Marlborough and Tasman

Bay from the 1880s, but the fishery collapsed and closed in 1950 (Paul et al. 2001). Pilchard stock shortage is known in Australia to negatively affect the penguin populations (Dann et al. 2000), but we do not know how New Zealand penguins responded to this overfishing. To date, it is not known whether the fish stock has recovered, but it is noteworthy that pilchard has not been identified as a prey for penguins in New Zealand (Van Heezik 1990; Fraser & Lalas 2004; Lalas et al. 2004; Flemming et al. 2013).

Motuara Island, a predator-free site adjacent to a marine reserve, would initially appear to be an ideal habitat for little penguins. Surprisingly, they rely on a > 16,000 km^2 area to feed, shunning the marine reserve. The Sound provided only part of their food in some years and then low prey availability led to poor breeding success. The Sound ecosystem is undergoing change, with sedimentation from forestry (Fahey & Coker 1992) and mussel aquaculture (Kaspar et al. 1985), as well as seabed dredging from scallop fisheries (Bull 1989). Tracking penguins nesting further into the Sound would be useful to explore in detail how the local ecosystem is used by the species. Birds nesting at the head of the Sound are likely to be too far from the open ocean to regularly feed in Cook Strait.

The westerly wind-driven upwelling (Stanton 1976; Bowman et al. 1983), which sustains the South Taranaki Bight food web, exposes the Marlborough penguins to wind variability. Wind direction and speed had significant influence on foraging mass gain for rockhopper penguins (*Eudyptes chrysocome*), with greatest gain with moderate westerlies and least gain with strong easterlies and storm conditions (Dehnhard et al. 2013). As wind can have a strong influence on little penguin prey availability (Dann & Chambers 2013), this may make some little penguin colonies in New Zealand sensitive to climate change if patterns of wind change as a result (Boning et al. 2008; Langlais et al. 2015).

Foraging area characteristics and relation to rivers

The relationship between foraging range and distance to a major river suggests that penguins could forage closer to the colony when a river enters the sea nearby. Nutrient-rich freshwater enhances phytoplankton production in the sea, with a maximum production in a downplume direction located at an intermediate salinity gradient (Dagg et al. 2004). These fine-scale fronts, which are likely to attract penguin prey, induce a selective foraging at Port Philipp Bay (Kowalczyk et al. 2015b). River input can consist of a tongue-like freshwater mass at the river mouth, and penguin tracks showed movement by birds towards the Waitaki River mouth from the Oamaru colonies (Mattern et al. 2001; Agnew 2014) and the Ruamahanga River mouth from Wellington birds (C. Bost, Te Papa Tongarewa, unpubl. data, 2014). Large discharges and cumulative effects of rivers can also enhance a buoyant low-salinity surface layer transported by wind and current (Stanton 1976; Vincent et al. 1991) further offshore: 33‰ salinity surface water can be found up to 35 km off the west coast of New Zealand's South Island (Stanton 1976). With large rainfall in New Zealand, freshwater-induced surface layers could be an alternative predictable prey resource, especially when the wind-driven coastal upwellings (Stanton 1976; Bowman et al. 1983) are subdued.

These freshwater inputs are undergoing change from agricultural intensification, with both water abstraction for irrigation and nutrient concentration changes (Wilcock et al. 2011). Through altering water quality, remote land-based activities can affect marine ecosystems (Fahey & Coker 1992; Schramm et al. 1996). Are little penguins affected by changes in freshwater inputs? With a potential relationship between New Zealand little penguins and large river outflows, this is a conservation management question worthy of further study.

Conservation implications of long-distance foraging

Our findings highlight the need for more research into the at-sea requirements of little penguins. Foraging range and main prey types vary between colonies, leading to potentially different habitat and resource requirements across the range of the species. Conservation efforts need to take this variation into account to protect little penguins which are currently in decline across New Zealand (BirdLife International 2016). Variable foraging ecology may expose little penguins to threats that, when it was thought only small ranges were used for foraging at sea, were not previously considered important. Our improved understanding of foraging range shows that little penguins may be exposed to dredging or seabed mining on foraging habitat far from known colonies. Penguins at the colonies we studied in Wellington, Buller and Marlborough all feed in areas where seabed mining and dredging activities have been proposed. Proposals for significant seabed disturbance are currently being assessed in the South Taranaki Bight and the west coast including Buller (Trans-Tasman Resources 2016), in Wellington Harbour and Cook Strait (CentrePort 2016). There are potential adverse effects of these activities for penguin populations because of sustained benthic disturbance increasing water turbidity and disrupting marine food webs. This may affect the penguins' foraging efficiency, survivorship and breeding. A recent review of the status of little penguin populations in New Zealand (BirdLife International 2016) showed that there were few large (> 200 pairs) populations of little penguins in New Zealand (K-J. Wilson, West Coast penguin Trust, Te Papa, unpubl. data), of which two are in Marlborough and in Wellington Harbour. Threats to these populations therefore are significant at the taxon level.

Conclusion

Variable foraging ranges, and possibly influences of freshwater outflows in determining key foraging areas, appear to be a feature of New Zealand little penguin populations studied to date. The long distances travelled by little penguins also highlight the potential for adverse effects of dredging or seabed mining activities, even at some distance from known breeding sites. Even though little penguins are considered one of the better studied seabirds in the Australasian region (Chambers et al. 2014), the ecological processes driving the intra- and inter-population variability are still to be discovered. Further work for the New Zealand taxon is needed to assess the population's viability in the face of a changing environment.

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