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RESEARCH ARTICLE

Diving behaviour of Little Penguins from four colonies across their whole distribution range: bathymetry affecting diving effort and fledging success

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Abstract Little Penguins, *Eudyptula minor*, breed in several small colonies in New Zealand and Australia. In this study, we compare the birds' diving performances at different sites situated throughout their breeding range. Environmental conditions and breeding success vary drastically amongst colonies, but all birds feed on similar types of prey and face similar limitations on their foraging range. We examined several diving parameters and calculated the proportion of foraging zone available during breeding to examine whether oceanographic and geographic factors in the foraging zone can explain variations in diving behaviour and fledging success among the different colonies. In colonies with high fledging success, Penguin Island and Oamaru, penguins made shallow dives <50 m depth and had lower diving effort. More than 90% of the foraging zone was in waters <50 m depth in these colonies. Motuara Island also has shallow waters with 95% <50 m depth, but the fledging success was low. Phillip Island has only 42% of waters <50 m and comparatively low fledging success. Thus, penguins dived deeper and showed a higher diving effort in colonies with lower fledging success (Motuara Island and Phillip Island), indicating that they were disadvantaged compared to conspecifics from other colonies that dived shallower and with a lesser diving effort. We concluded that bathymetry is an important factor, but not the only one, which influences fledging success.

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Introduction

In the marine environment, prey–predator relationships are primarily determined by the distribution of prey in the water column and the swimming and diving ability of the predators (Baldwin 1988). Penguins feed on mobile prey species such as fish, squid and krill and this requires considerable searching effort and flexibility in foraging behaviour (Williams et al. 1992; Hull 2000). The diving patterns of Gentoo Penguins *Pygoscelis papua* and Macaroni Penguins *Eudyptes chrysolophus* follow the behaviour of their prey, as the Gentoo Penguins change their dive depth according to the prey type and the Macaroni Penguins exploit the natural vertical migration of Antarctic krill *Euphausia superba* (Croxall et al. 1988). The speed and escape trajectories of prey (cf. Arnott et al. 1999), the topography of the oceanic floor (Scolaro and Suburo 1991) and the light levels (Cannell and Cullen 1998; Ropert-Coudert et al. 2006) may also influence the maximum dive depths of predators.

The maximum depth at which an air-breathing animal can dive also depends on a number of physiological and biomechanical variables such as haemoglobin binding capacity (Bethge et al. 1997) and buoyancy (Wilson et al.

1992). In this regard, body mass is a good factor explaining the diving capacities of penguins, at least for depth and duration, when compared with other air-breathing diving vertebrates (Schreer and Kovacs 1997). Wilson (1995), using data from time-depth recorders, derived an empirical relationship between body mass (x in kg) and maximum diving depth (y in m): $y = 18x + 47.6$, $r^2 = 0.81$. Following this equation, a 1,100 g bird could theoretically reach a maximum depth of 67.4 m. Such a mass corresponds to the average mass of Little Penguins, *Eudyptula minor*, the world's smallest Spheniscidae. These birds are endemic in Australia and New Zealand and breed in several small colonies among which environmental conditions and breeding success vary dramatically. Throughout these breeding locations, Little Penguins feed on similar types of schooling and pelagic prey, mainly Clupeiformes (Klomp and Wooller 1988; Cullen et al. 1992; Fraser and Lalas 2004).

While the equation of Wilson (1995) predicts that Little Penguins are vertically restricted to the upper 70 m of the water column, Little Penguins travel no further than 20 km from the colony while feeding chicks (Klomp and Wooller 1988; Chiaradia and Kerry 1999; Collins et al. 1999). Thus, all chick-rearing Little Penguins face similar diving and dispersal limitations across their distribution range. We expect, therefore, the water depth and geographical features of the foraging zones to influence considerably the foraging strategies used by penguins, thus ultimately affecting their breeding success (Rodary et al. 2000).

In this paper, using miniature time-depth recorders (Ropert-Coudert and Wilson 2005), we compared the diving performance of Little Penguins from four colonies distributed across their entire distribution range: two in New Zealand (Motuara Island and Oamaru) and two in Australia (Phillip Island and Penguin Island). We examined diving as a function of the bathymetry and used published data from other breeding sites on colony size, fledging success and site geographic location to calculate the proportion of foraging zone available within a 20 km radius (Collins et al. 1999) during breeding. We examined which oceanographic and geographic factors in the foraging zone, if any, could explain variations in diving behaviour and fledging success among different colonies.

Methods

Diving behaviour

The diving behaviour of Little Penguins was examined in four colonies located on the entire range of their distribution (black dots in Fig. 1): two colonies in Australia in 2001 and 2002 (Penguin Island: 32°18′S, 115°41′E and Phillip Island: 38°31′S, 145°09′E); and two colonies in New Zealand in 2000 (Oamaru: 45°07′S, 170°59′E and Motuara Island: 41°06′S, 174°17′E). We sampled penguins at the guard stage when parents mostly make one-day trips. We used three types of miniature data loggers with comparable dimensions and sensor resolutions (Table 1). Field-work protocol for the four sites and methods of attachment are described elsewhere (Oamaru and Motuara Island: Mattern 2001; Penguin Island: Ropert–Coudert et al. 2003; Phillip Island: Yorke 2003). All loggers were streamlined and attached to the lower back of the penguins using waterproof TESA tape, allowing quick attachment and recovery of the loggers and minimising the damage to the feathers of the birds (Wilson et al. 1997).

Dive analysis

All logger data recovered from all locations were analysed using IGOR Pro (Wavemetrics Inc., USA, 2000, Version 5.0). All datasets were re-sampled to 2 s for homogeneity and analysed using the same hand-written software (Ropert–Coudert et al. 2006). The mean of each variable per penguin was used in the analysis of variance (ANOVA), followed by a Tukey post-hoc test to compare among colonies (Quinn and Keough 2002). The dives consisted of three phases: the descent from the surface to the deepest portion of the dives, the bottom around the deepest portion of the dive and the ascent phases, i.e. the return from the deepest part of the dive to the surface (Le Boeuf et al. 1986). The starting and ending of the bottom phases were defined as the first and the last time the depth change rate became <0.25 m s^{-1} during a dive. The *proportion of bottom time* was calculated as bottom phase duration/dive duration. *Diving effort* was calculated as the total diving duration per hour per bird and then plotted as hourly mean per colony in an accumulative curve. Diving efficiency was calculated as: [bottom phase duration/(dive duration + post-dive interval)], according to Ydenberg and Clark (1989). We filtered the data to eliminate non-foraging dives and long-rest periods from the analysis using a modified criterion from Takahashi et al. (2003). Most dives <1 m did not have a bottom phase and dive durations <5 s were too short to accurately measure the bottom phase of the dive using our 2 s sampling interval. Therefore, they were not included in the analysis. Post-dive intervals >100 s were outliers, i.e. they heavily skewed the distribution and accounted for <2% of the total dives. They were also excluded from the analysis.

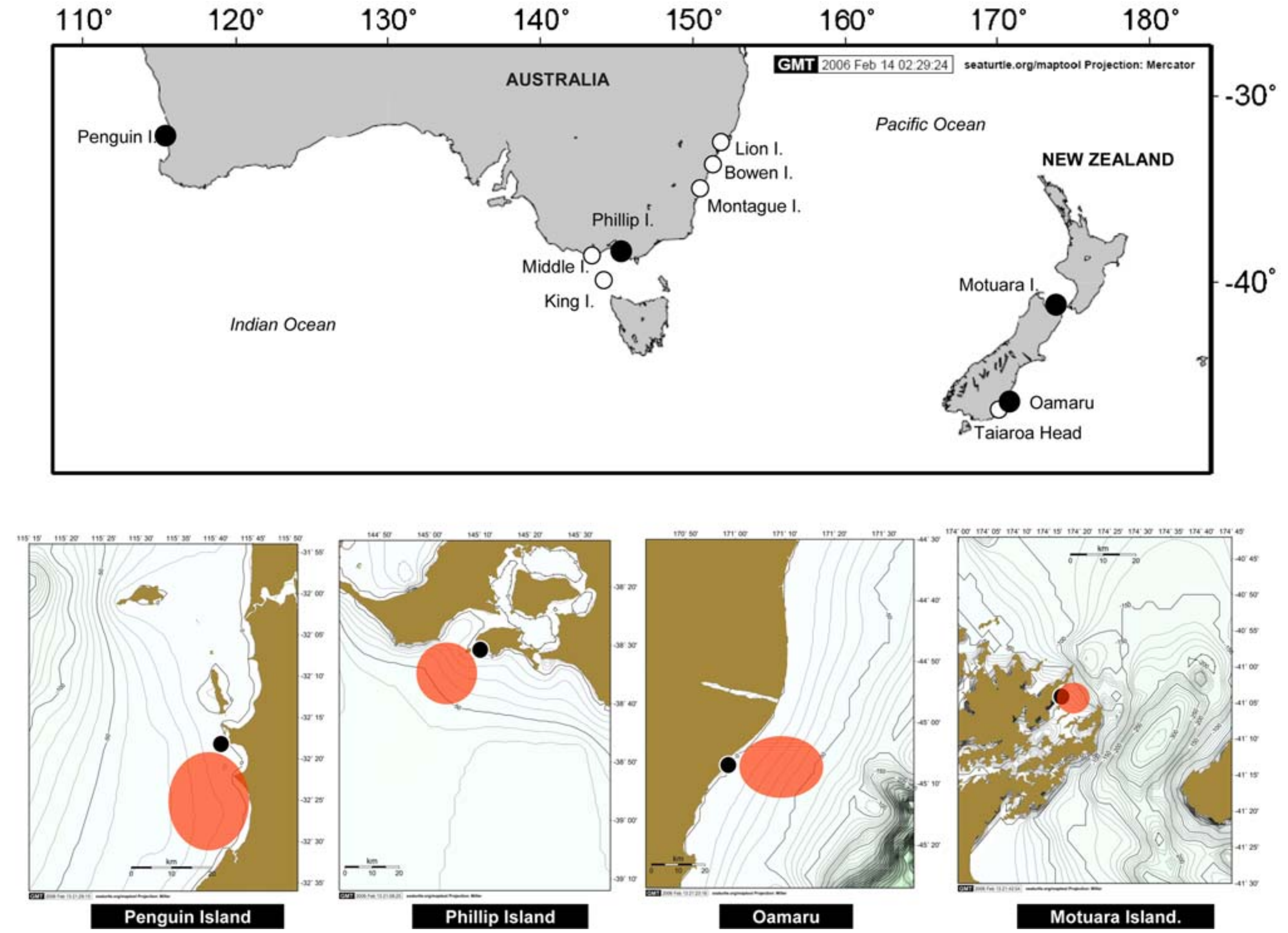

Fig. 1 Location, bathymetry and foraging area of the four colonies (*black dots*) of Little Penguins studied in Australia and New Zealand. Bathymetry (10 m intervals) and foraging area (*red transparent circles*) are detailed for each colony. Breeding data and colony size from literature were used from further six colonies in this study (*white dots*). Maps were created using Maptool in Seaturtle.org (2002)

Table 1 Sample numbers, fledging success, population size and loggers used at four locations in this study

Location	Number of penguins	Number of dives	Fledging success	Population size	Foraging area [b] (%)	Time-depth logger	Logger's dimensions and weight	Logger's percent of the Penguin's frontal area
Phillip Island	22	19,580	0.5	12,000	89	LTD 1200-100, Lotek, Canada	62 mm × 18 mm, 17 g [c]	4.9
Motuara Island	4	9,909	0.5	600	62	MK7 Wildlife Computers, USA	65 mm × 12 mm × 8 mm, 32 g [d]	1.8
Penguin Island	8	16,071	0.7[a]	1,000	65	M190-D2GT, Little Leonardo, Japan	52 mm × 15 mm, 16 g [c]	3.4
Oamaru	4	7,511	0.8	6,000	51	MK7 Wildlife Computers, USA	65 mm × 12 mm × 8 mm, 32 g [d]	1.8

[a] Fledging success at Penguin Island was based on historical data only (Wienecke et al. 1995)

[b] Foraging area is the area available for foraging within 20 km of the colony (see text)

[c] The dimensions are given in length and diameter for cylindrical loggers

[d] The dimensions are given in length, width and height for rectangular loggers

Fledging success

We estimated breeding success by the number of chicks fledged per chicks hatched. This number is hereafter referred to as fledging success, using contemporaneous data from this study and historical data for Penguin

Island (Wienecke et al. 1995), where contemporaneous breeding data were not available (Tables 1, 2).

Bathymetry and diving depth

In order to examine the influence of bathymetry on the diving behaviour of Little Penguins, we plotted these two parameters together for each colony (Fig. 2). First, we calculated the foraging range of penguins using the contour plot of all penguin locations at sea during the guard stage. Penguin locations at Oamaru and Motuara Island (Mattern 2001) and Phillip Island (Collins et al. 1999) were obtained from published radio-tracking data. Tracking data were not available for Penguin Island, but penguins are known to forage within a 20 km radius from this colony (Wienecke et al. 1995). We then used published bathymetry data (NOAA, http://www.ngdc.noaa.gov/mgg/image/2minrelief.html) to determine the proportion of depth categories available within the 20 km radius foraging range. Bathymetry in the foraging area and penguin diving depths are represented in proportion per depth in 1 m interval (Fig. 2) in order to make possible the comparison among colonies, since the number of points for each colony was disproportional.

Foraging area available

We also calculated how much foraging area was available to penguins after considering the land barriers around the breeding sites. The calculation was based on the proportion of water/land within a 20 km radius of the breeding sites. This radius is the mean maximum distance Little Penguins travel within a one-day trip (Collins et al. 1999). Apart from the four sites used in this study, we used six other localities to calculate the foraging area (Montague Island: 36°15′S, 150°13′E, King Island: 39°51′S, 143°59′E, Lion Island: 33°33′S, 151°19′E, Middle Island: 38°24′S, 142°28′E, and Bowen Island: 35°07′S, 150°46′E and Taiaroa Head: 45°47′S, 170°44′E; white dots, Fig. 1). Population size and breeding data for these six sites are given in references in Table 2. The foraging area was then correlated with fledging success and colony size (Tables 1, 2).

Results

We recorded 53,071 dives of 38 penguins from four Little Penguin colonies (Table 1). The fledging success at Penguin Island and Oamaru was higher than that at Phillip and Motuara Islands (Table 1).

Penguins from Motuara and Phillip Islands dived deeper and showed higher diving efforts than penguins from Penguin Island and Oamaru (Figs. 2, 3; Table 3). In other words, lower diving effort and shallower diving activity were observed in the colonies where a high fledging success was observed (Fig. 2, Tables 1, 3).

The diving efficiency was the highest at Penguin Island and the lowest at Phillip Island (Table 3). Penguins from Oamaru and Motuara Islands showed no significant difference in their diving efficiency, but they were both significantly different from those at Penguin and Phillip Islands (Table 3).

Although the calculated maximum depth that a 1,200 g penguin can potentially reach is 70 m (Wilson 1995), most Little Penguin dives were <50 m (Fig. 2). More than 90% of the foraging zone was in waters shallower than 50 m in colonies of high fledging success, i.e. Penguin Island and Oamaru. Motuara Island also has 95% of waters under 50 m depth, but waters <20 m were rare and the fledging success there was low. Phillip Island had only 42% of its waters <50 m and had an intermediate to low fledging success. In addition, penguins from colonies of high fledging success had a higher proportion of bottom phase duration than penguins from colonies of low fledging success, except for Motuara Island (Table 3).

The colony size increased with the foraging area available ($r^2 = 0.44$, $P = 0.038$, and Fig. 4), but the available foraging area was not significantly correlated with fledging success ($r^2 = 0.21$ and $P = 0.18$).

Table 2 Fledging success, population size and the foraging area available within 20 km of the colony of six penguin colonies (Fortescue 1995)

	Fledging success	Population size	Foraging area available (%)	Source
Taiaroa Head	0.9	300	62	Perriman and Steen (2000)
Middle Island	0.8	400	49	Overeem (2000)
Lion Island	0.8	600	34	Knight and Rogers (2004)
King Island	0.8	4,000	69	P. Dann (pers. communication)
Montague Island	0.4	10,000	71	Weber (1994)
Bowen Island	0.8	14,000	65	Fortescue (1995)

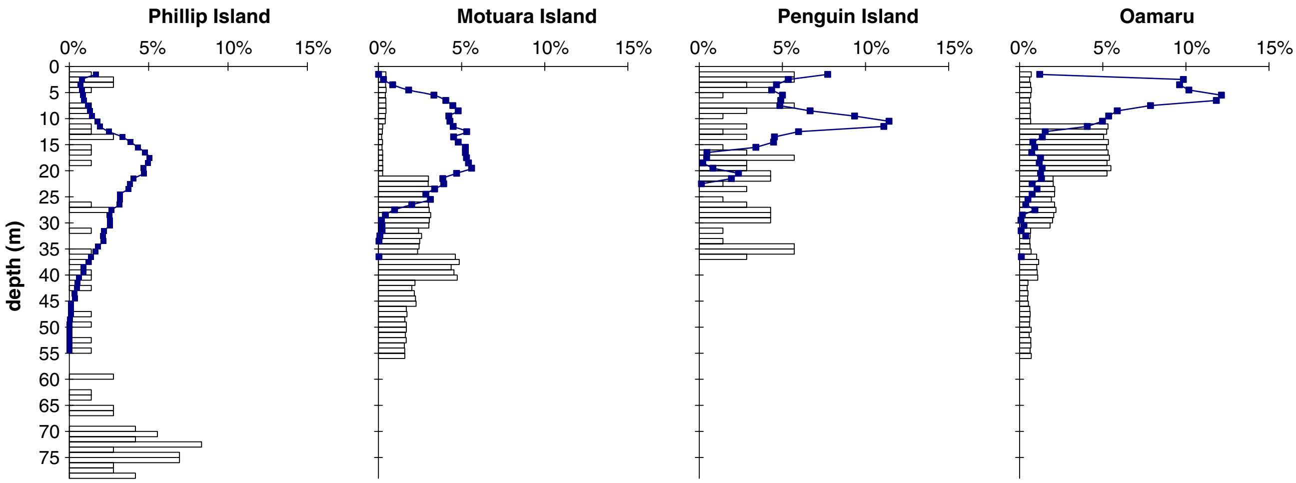

Fig. 2 The proportion of foraging area depth (*bathymetry, clear bars*) and diving depths (*dark squares and lines*) per 1 m interval for Little Penguins in Australia (Phillip Island and Penguin Island) and New Zealand (Motuara Island and Oamaru). Note, Phillip Island and Motuara Island have higher proportions of deeper depths within the penguins' foraging zones

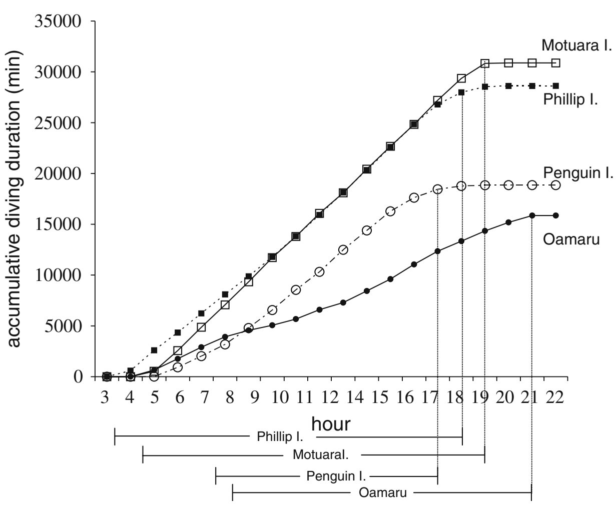

Fig. 3 Diving efforts shown as the accumulative sum of diving duration per hour of the day at each of the four locations. *Horizontal bars* show the range between the beginning and end of the diving activity in a day. Note the short diving activity and therefore less diving effort at Penguin Island, but increasing at Oamaru, Motuara Island and Phillip Island, respectively

Discussion

Changes in strength of water current in Western Australia, seasonal changes in food supply at Phillip Island and the presence of upwelling in New Zealand have all been related to changes in breeding success among Little Penguins (Wooller et al. 1991, Chiaradia and Nisbet 2006; Mattern 2001). These factors would affect prey distribution and availability, which would have a strong influence on the diving behaviour and breeding success (Hobday 1992; Chiaradia and Nisbet 2006). If the search for prey is unsuccessful, penguins may have to travel greater distances to increase prey encounters or, alternatively, increase their diving effort and search deeper in the water column (Wilson and Wilson 1990). In our study, penguins dived deeper and showed higher diving efforts in colonies with lower fledging success (Motuara Island and Phillip Island), indicating that they were disadvantaged compared to conspecifics from other colonies that dived shallow and with a lesser diving effort.

The differences observed between colonies may be related to the small differences in the frontal area of the logger types (Table 1), since this would influence the diving behaviour of penguins (Ropert-Coudert et al. in press). However, while these differences would quantitatively affect the results, they would not modify the trend between colonies. For instance, the loggers used in the two colonies in New Zealand (Motuara and Oamaru) were identical, but penguins still displayed significant differences in their diving behaviour. In addition, the difference in behaviour due to differences in logger size, as recorded by Ropert-Coudert et al. (unpublished data), was much smaller than that observed in the present study.

The main prey in the diet of Little Penguins is the Clupeiformes. These are distributed from the surface down to depths >200 m (Kailola et al. 1993). Thus, in zones of deep waters, Clupeiformes can seek refuge at depths well beyond the <50 m attained by penguins under normal foraging conditions (this study). Conversely, Clupeiformes in shallow waters <50 m cannot escape to greater depths, thus giving them fewer options to avoid the penguins (cf. Takahashi et al. 2003; Ropert-Coudert et al. 2006). For instance, more

Table 3 Depth, diving efficiency (bottom phase duration/(dive duration + post-dive duration) and proportion of bottom duration (bottom phase duration/dive duration) of dives of Little Penguins at four colonies

	Phillip Island	Motuara Island	Penguin Island	Oamaru	F	*n*	
Depth (m)	13 ± 3.9^{b}	11 ± 2.7^{b}	6 ± 3.5^{a}	5 ± 0.9^{a}	11.8	38	$P < 0.001$
Efficiency	0.14 ± 0.04^{a}	0.21 ± 0.05^{b}	0.32 ± 0.06^{c}	0.16 ± 0.04^{ab}	8.13	38	$P = 0.010$
Bottom duration (%)	22 ± 5^{a}	32 ± 6^{b}	47 ± 4^{c}	34 ± 6^{b}	56	38	$P < 0.001$

We used ANOVA with Tukey's post-hoc test to compare the four colonies

[a, b,c] Values in the same line without a letter in common are significantly different from each other. a Indicates the lowest value followed by b and c, which indicate the next higher value

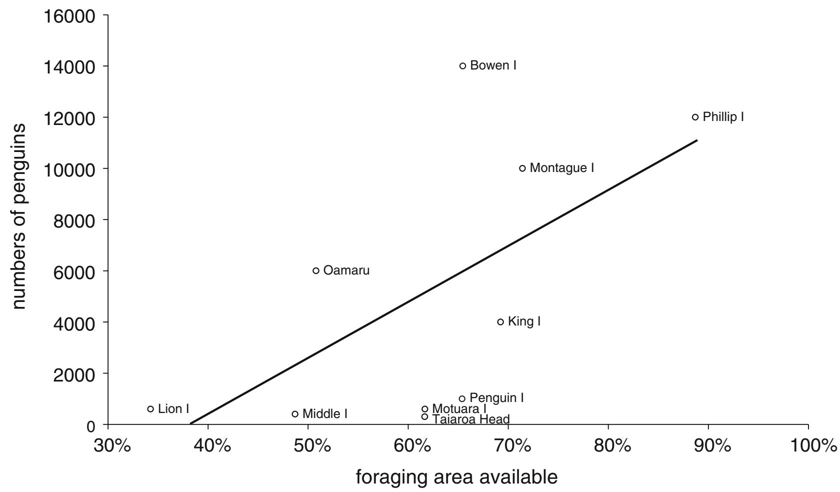

Fig. 4 Linear relationship ($r^2 = 0.44$ and $P = 0.038$) between the proportion of foraging area available within a 20 km radius of the breeding sites and the population size (= number of breeding penguins). In addition to the four sites used in this study, we added another six penguin sites to calculate the foraging area

than 90% of the Penguin foraging zones in colonies of high fledging success at Penguin Island and Oamaru consisted of waters <50 m. On the other hand, at Phillip Island, with intermediate to low fledging success (Dann et al. 2000, this study), less than half of the penguin's foraging zone is in shallow waters.

Penguins, including Little Penguins (Ropert-Coudert et al. 2006), are known to feed mainly during the bottom phase of dives (Takahashi et al. 2003; Ropert-Coudert et al. 2000, 2001). In the highly productive colony of Penguin Island, the foraging area consists of shallow waters, thus corresponding to penguins showing a greater proportion of their diving time spent at the bottom phase. Such behaviour represents demersal diving activity (Tremblay and Cherel 2000). Demersal feeding in shallow waters can be advantageous, as the distance between the surface and the bottom is predictable and penguins can use the seabed to trap their prey (Ropert-Coudert et al. 2006). This agrees with our observations, since the diving efficiency of birds in Penguin Island was also high. Although the foraging area at the second highly productive area of Oamaru comprised an important proportion of deep waters, the penguins foraged near the surface (Fig. 2). In contrast, in the low-productive colonies of Phillip and Motuara Islands, the penguins dived deeper, showing a greater diving effort. Under these conditions, adult penguins with chicks at the guard-stage in low-productive colonies would return every night with less food to feed their growing chicks, thus decreasing the chance of survival of the offspring (Dann 1987; Perriman and Steen 2000). This decrease was indeed observed in Motuara Island where several chicks died of starvation (Mattern 2001).

At Motuara Island, other factors are probably more influential on fledging success than bathymetry alone. This colony showed low fledging success, although it is surrounded by shallow waters. The island is limited by the geographic features of Queen Charlotte Sound and the waters of Cook Strait that represent a natural boundary to the Sound. The Strait's strong currents would not only require higher travelling efforts by the penguins, but may also considerably influence the distribution of the prey (Hunt 1990; Hunt et al. 1992). The distribution of fish in deeper waters is often affected by bathymetric features like rocks or islands that may create local upwelling. This phenomenon results in higher productivity around these areas (Miller 2003). The effort penguins have to make to reach rocks and islands in Cook Strait is probably too great to make them suitable destinations for one-day foraging trips. Therefore, trips into Cook Strait are likely to result in long-term foraging trips. During guard-stage when Little Penguins travel mostly for 1 day (Chiaradia and Kerry 1999; this study), the penguins from Motuara Island have only one choice to enhance their foraging success—to increase dive activity and search greater volumes of the water column within the outer Queen Charlotte Sound.

Based on our results, we conclude that bathymetry is an important factor, but not the only one, influencing the fledging success of Little Penguins. Indeed, even the proportion of landmass acting as geographic barrier seems to dictate colony size (Fig. 4), but not fledging success. Nevertheless, we suspect that a decline in prey availability affecting two colonies similarly would have a stronger negative impact on the fledging success of penguins feeding in deeper waters. This study is, to our knowledge, the first one to investigate simultaneously the fledging success, the bathymetry in the foraging zones and the diving behaviour of penguins across their breeding distribution. An increase in the number of sites monitored would help us to confirm the role of bathymetry in determining the fledging success of penguins. If the trend observed here is confirmed, bathymetry could be regarded as an important factor for breeding site selection in Little Penguins. In other words, the decision of penguins to breed at a specific location would be a result of on-land and at-sea factors, with constraints of the foraging zones probably as critical as those of the nesting sites.

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