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RESEARCH

Variability of little blue penguin (*Eudyptula minor*) diving behaviour across New Zealand

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Abstract: Foraging strategies of penguin species can vary according to the quality of the marine environment, and this influences their abundance and breeding success. Little blue penguins (*Eudyptula minor*) are considered a candidate species for assessing near-shore marine productivity due to their usually limited foraging ranges and reliance on local resources, particularly while rearing chicks. Understanding the variability of little blue penguins diving behaviours will inform whether the species can be used as an environmental monitor. This research investigates diving behaviours and feather stable isotope values (as indicators of diet) of little blue penguins from Motuara Island, Marlborough Sounds, New Zealand, and compares them with little blue penguins from three other locations distributed across the country. The diving behaviour of little blue penguins, including dive depth and duration, were highly variable indicating that little blue penguins are an environmentally adaptable species. Because of the highly variable marine environments they inhabit, the use of little blue penguins as local monitors of New Zealand's changing marine environment requires an understanding of area and population specific diving and foraging behaviour.

Keywords: diet, foraging behaviour, stable isotope analysis

Introduction

Coastal areas are changing rapidly due to shoreline development and increased shipping, mining and fishing pressures (Blaber et al. 2000; Newson et al. 2009). In temperate marine environments, penguins are thought to be useful near-shore indicators or environmental monitors of environmental change because they are both top predators and land-based breeders (Croxall & Davis 1999; Dann & Chambers 2013). Penguin foraging ranges are generally reduced during the breeding period, particularly when provisioning chicks, as they must return to land to brood and feed offspring on a regular basis. It is commonly thought that individuals rely on the availability of prey within close proximity of their nesting site (Chiaradia et al. 2007; Ropert-Coudert et al. 2009; McCutcheon et al. 2011); however, recent research in New Zealand indicates that during incubation foraging distances can be quite extensive (Poupart et al. 2017). If little blue penguins are reliant on near-shore marine ecosystems with variable productivity (prey availability) during chick rearing, there is likely to be immediate impacts on penguin breeding success and possibly flow-on effects in population size and distribution (Boersma 2008).

In New Zealand, there are six penguin species (Robertson & Heather 2005). The most widespread of these species is the little blue penguin (*Eudyptula minor*), which is recognised as having several sub-species (Robertson et al. 2017). Recent genetic analysis has suggested that there could be two distinct species: *E. minor*, occurring around most of New Zealand (and the focus of this paper), and *E. novaehollandiae*, throughout southern Australia and the Otago and Canterbury regions of New Zealand (Grosser et al. 2015). Little blue penguins are the world's smallest penguins, weighing approximately 1 kg, and begin breeding from winter to spring (May–October; Perriman et al. 2000; Agnew et al. 2014). One to two eggs are laid and incubated for approximately 36 days (Kemp & Dann 2001), with parents taking turns to incubate while the other forages at sea. Once hatched, the chicks are guarded and brooded by both parents on alternate days, with the guard stage lasting for 2 to 3 weeks. During the post-guard stage, when the chicks are older and more capable of thermoregulating, both parents forage at sea during the day, returning after dark to feed their chicks (Nisbet & Dann 2009).

Changes in little blue penguin diet and foraging behaviour have previously been used to indicate changes in the availability of prey in near-shore areas (Flemming et al. 2013). In Australia, El Niño events of the Southern Oscillation (ENSO) result in increased sea-surface temperatures and can cause the prey of little blue penguins to change distribution, becoming locally scarce (Perriman et al. 2000; Dann & Chambers 2013). Such changes have been reported to cause increased foraging effort in little blue penguins and disrupt their regular breeding, in turn affecting the entire breeding population in an area (Dann et al. 2000; Numata et al. 2004; Robinson et al. 2005; Ropert-Coudert et al. 2009; Chiaradia et al. 2010). Similarly, variations in the availability of food have resulted in delays to the start of the breeding period, reduced likelihood that a second clutch

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will be produced, and increased chick mortality (Dann et al. 2000; Nisbet & Dann 2009; Chiaradia et al. 2010). Reduction in food availability can also lead to poor adult and chick body condition, resulting in reduced chick immunity and longer fledging periods (Dann et al. 2000; Chiaradia et al. 2010).

The diving behaviour of little blue penguins varies across New Zealand (Mattern 2001; Chiaradia et al. 2007; Chilvers et al. 2015; Chilvers 2017). Their shallow diving behaviour indicates they are epipelagic divers (i.e. they forage in the uppermost part of the ocean where there is sufficient sunlight to allow photosynthesis to occur), with mean dive depths usually ranging between 5 and 14 m (Chilvers 2017). Their foraging ranges also vary significantly between locations and in some areas between breeding stages (i.e. incubation compared with chick rearing; Poupart et al. 2017). In New Zealand, little blue penguins are visual predators, foraging predominantly on squid (*Nototodarus* spp.) and small fish such as Graham's gudgeons (*Grahamichthys radiata*; Flemming et al. 2013).

Stable isotope analysis of little blue penguin blood and feathers can be used to reflect diets over different time frames: blood representing a period of days to weeks; and feathers reflecting diet just prior to moulting the previous year (Hilton et al. 2006; Tierney et al. 2008; Flemming & Van Heezik 2014; Chilvers 2017). Stable isotope analysis has been used to infer diet (including the trophic levels of prey) and foraging areas for sea birds (Hobson et al. 1994). Stable carbon and nitrogen isotope ratios ($\delta^{13}C$ and $\delta^{15}N$) of marine predators define their isotopic niche along two dimensions, with $\delta^{13}C$ and $\delta^{15}N$ values reflecting the predators' foraging habitat and trophic level, respectively (Newsome et al. 2010).

This study examined the diving behaviour and feather stable isotopes (an indicator of diet during the pre-moult period, from mid-February to mid-April; Johannessen et al. 2002) of little blue penguins from Motuara Island, in the outer Marlborough Sounds, New Zealand, in November 2014. The Motuara Island little blue penguin diving behaviour is compared with the behaviours of little blue penguins from three other locations across New Zealand to determine whether the species might provide a useful environmental monitor.

Material and methods

Study sites and animal captures

The diving behaviour of little blue penguins was examined at Motuara Island, 32 km from Picton in the outer Marlborough Sounds, New Zealand (41.01946°S, 174.2744°E; Fig. 1). Motuara Island is a New Zealand Department of Conservation Scenic Reserve covered in native forest. Rats were eradicated from the island in 1992 and since then saddleback/tīeke (*Philesturnus carunculatus*), South Island robin/toutouwai (*Petroica australis*), and yellow-crowned parakeet/kākāriki (*Cyanoramphus auriceps*) have been transferred to the island. Little blue penguins occur naturally in the area; however, there are no population size estimates for the breeding population on Motuara Island.

In mid-November 2014 ten little blue penguin were captured while returning to their nests. Weights and beak and head lengths were measured. To reduce the disturbance at nests, individuals were not followed or captured at nests. This method meant that birds could not be confirmed as breeding individuals, although all birds were checked to confirm brood pouches in an attempt to capture breeders. While captured, seven of the penguins were tagged with time-depth recorders (TDRs; Lotek LAT1400, 6 g, 30 × 10 mm) and VHF transmitters (3 g, 20 × 8 mm, Sirtrack, Havelock North, New Zealand) and all ten had five feathers removed from their lower backs for stable isotopes analysis. To reduce drag from the fitted device, the recorders and transmitters were taped together before being attached to the lower back of the penguins using waterproof TESA tape (TESA tape, No. 4651, Baiersdorf AG, Hamburg, Germany). The TESA tape allows the quick attachment and recovery of the loggers, minimising any damage to the feathers of the birds (Wilson et al. 1997). TDRs were programmed to record depth every 2 s when wet. The instruments were recovered 1–3 days after deployment. Due to the TDRs small size, they could only store data from one foraging trip for each bird. However, penguins were tagged during the late guard stage, when parents predominantly make one-day foraging trips.

Little blue penguin dive data from Motuara Island were compared with little blue penguin dive data collected using the same methodology, at the same time of year, from three other locations: Pearl Island (off Stewart Island), Adele Island (Abel Tasman National Park; Chilvers 2017) and Leisure Island (near Tauranga; Chilvers et al. 2015); see Figure 1.

Stable isotope analysis

Surface contaminants were removed from the feathers by rinsing for 5 mins in a 2:1 chloroform : methanol solution. All feathers from each penguin were then cut and ground together. Approximately 3–4 mg of ground material was loaded into tin capsules for measurement of $\delta^{13}C$ and $\delta^{15}N$ isotope ratios. Samples were combusted to N_2 and CO_2 gas in a Dumas Elemental Analyser (Europa Scientific ANCA-SL) interfaced to an isotope mass spectrometer (Europa Scientific 20-20 Stable Isotope Analyser). Isotope ratios are reported in δ notation as part per thousand ($^{0}/_{00}$) (Bond & Hobson 2012). Results from this research were compared with stable isotope values from the three other research sites (Fig. 1) and tested for significant difference using a one-way ANOVA and Tukey *B* post-hoc test to identify significant differences between colonies.

Dive analysis

Diving data were analysed using Multitrace (Jensen Software Systems) to produce summary statistics for each dive, and for each penguin (including the number of dives per trip and dives per hour, percentage time spent diving to 1 m or greater at sea, mean and maximum dive depths, dive duration, surface intervals, percentage of time spent in the bottom 85% of a dive, and dive shapes). A foraging trip was defined as the time the TDR recorded the penguin to be in the water, as the TDR recorded only when the instrument was submerged in water. Foraging effort was defined as the percentage of time spent diving per day (Takahashi et al. 2003). Dive shapes were classified as V, U or W shaped as described by Halsey et al. (2007). V dives were those that have no bottom time with direct ascent and descents; U dives were dives with time spent at depths exceeding 85% of the maximum depth for each dive; W dives (also referred to as wiggles) are dives where the dive profile has a 'zigzag' shape usually in the bottom of the dive, as there is an increase in depth followed by a decrease in depth and then another increase in depth, before returning to the surface. Sensor (zero-offset) and drift in the depth values for each tag were corrected manually within Multitrace. Only dives >1 m in depth were used for the analyses, as Chiaradia et al. (2007) determined that most little blue penguin dives <1 m had a duration of <5 secs and 5 secs was considered too short to accurately measure dives given the study's 2 s

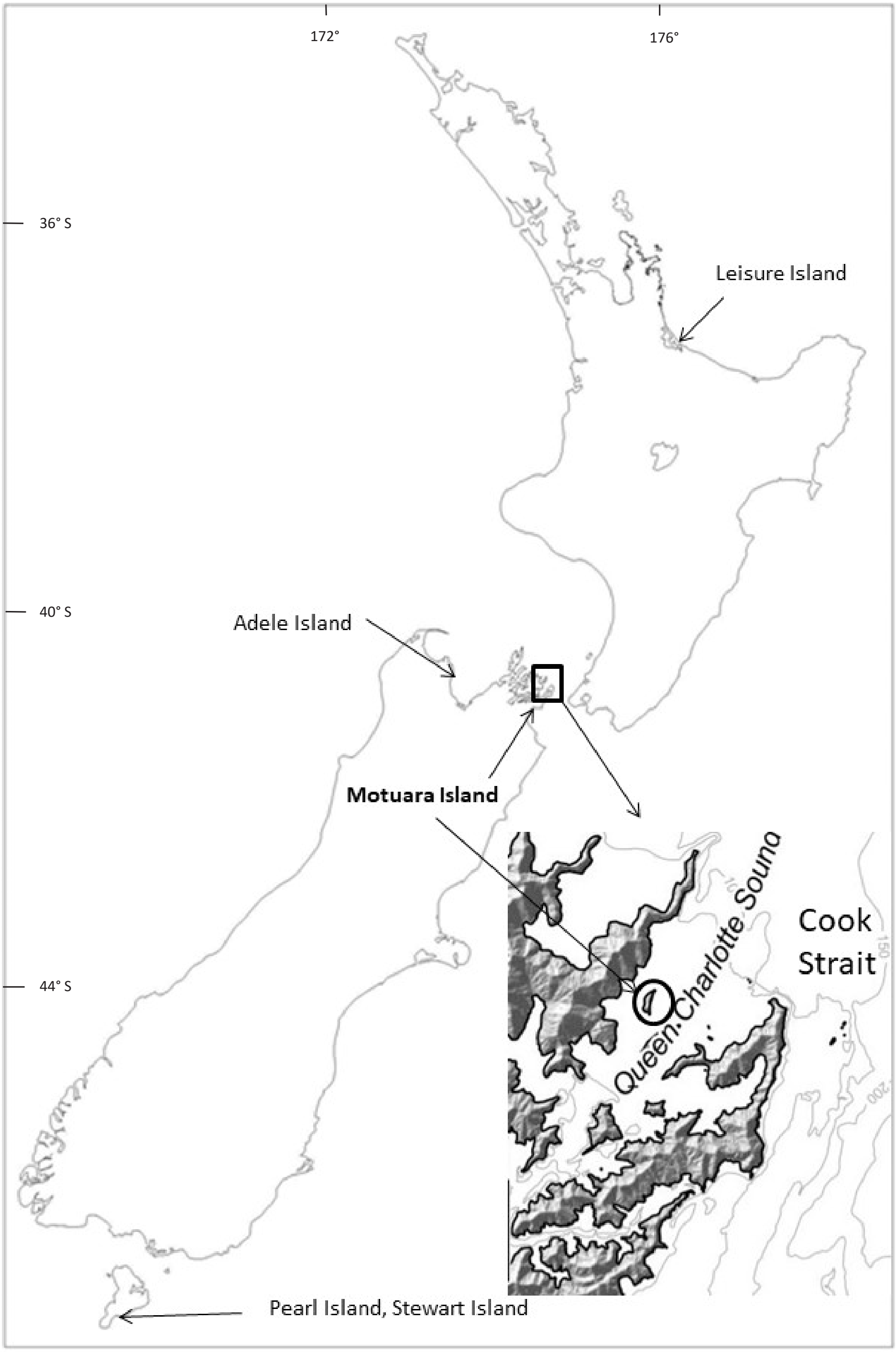

Figure 1. Map of New Zealand showing all locations where the diving behaviour or stable isotope analysis of little blue penguins (*Eudyptula minor*) used in this research have been studied. A. Bathymetry of the area around Motuara Island and Cook Strait, specifically the deep 100 m depths close to Motuara Island in Cook Strait.

sampling interval. Surface intervals >100 s were excluded from surface interval analysis to differentiate between surface time attributed to post-dive recovery or surface travelling (Chiaradia et al. 2007).

All statistical analyses were conducted in SPSS 24 (SPSS Inc., 2004). Comparisons of dive parameters between this study site and others from New Zealand were made using GLMs using nested ANOVAs with individuals nested within island groups. Depth was included as a covariate to analyse dive duration, as dive depth is usually correlated with dive duration. Tukey *B* post-hoc testing was used to detect significant differences in dive parameters between colonies. Means are presented ±1 standard error unless otherwise stated.

Results

One foraging trip was recorded for each of the seven little blue penguins tagged, with 7098 individual dives recorded in total. On average, Motuara Island little blue penguins spent 60% of their time at sea diving to depths of >1 m and undertook 68 ± 8.7 dives per hour (Table 1). Their mean dive depth was 11.5 ± 0.1 m with one penguin diving to a maximum recorded depth of 35.3 m (Table 1). The mean dive duration was 31.7 ± 0.2 secs, with on average similar but more variable surface interval lengths of 19.3 ± 1.1 secs (Table 1). The Motuara Island little blue penguins spent on average 16% of their dive time at >85% of the max. depth of their dives and predominantly

Table 1. Summary statistics of the diving records of little blue penguins (*Eudyptula minor*) from Motuara Island, Marlborough Sounds (n = 7), New Zealand. Data are from one foraging trip for each bird. Means ± SE.

Penguin VHF #	Sex	Penguin mass (g)	# dives per trip	% time at sea spent diving	Dives per hour	Mean depth (m)	Max depth (m)	Mean duration (sec)	Mean surface interval (sec)	% bottom time	% U dives	% V dives	% W dives
10	F	1000	1374	70	90	10.3 ± 0.23	33.8	28 ± 0.5	12 ± 0.9	16 ± 0.5	40	43	17
12	F	1050	395	21	27	9.6 ± 0.37	32.6	28 ± 0.8	27 ± 2.0	13 ± 0.9	30	49	21
20	F	1200	962	60	66	9.9 ± 0.18	31.1	33 ± 0.4	22 ± 4.8	22 ± 0.6	56	24	20
24	M	1120	1071	73	71	16.6 ± 0.25	35.2	14 ± 0.8	13 ± 0.7	13 ± 0.5	38	45	16
30	M	1350	1111	70	73	12.0 ± 0.15	25.0	35 ± 0.4	14 ± 1.5	17 ± 0.6	41	38	21
40	M	1300	1378	68	89	9.0 ± 0.16	31.1	27 ± 0.3	13 ± 0.7	12 ± 0.4	30	50	20
50	M	1150	1167	73	79	12 ± 0.20	35.3	33 ± 0.5	12 ± 1.4	17 ± 0.5	45	36	19
Average			1014 ± 135	60 ± 8.2	68 ± 8.7	11.5 ± 0.1	31.7 ± 1.5	31.7 ± 0.2	19.3 ± 1.1	16 ± 0.2	40 ± 4.0	40 ± 4.0	20 ± 0.7

undertook U and V shaped dives (Table 1). Overall, the little blue penguins from Motuara Island dived significantly deeper, and for longer, than any previously recorded little blue penguins (Table 2; Chilvers et al. 2015; Chilvers 2017). The percentage of dives in each depth range by the Motuara Island little blue penguins were fairly evenly spread down to the significantly deep depth of 30 m (Fig. 2). Most dives were between 4 and 12 m deep; however, the overall distribution of dive depths was significantly deeper than all other locations (Fig. 2). The increased depth and duration of dives is reflected in the lower number of dives per trip and dives per hour undertaken by the Motuara Island penguins (Table 2).

Across all four islands studied, there were significant differences between almost all of the dive parameters recorded (Table 2). As there was a significant correlation between dive depth and dive duration (Pearson correlation = 0.791, $p<0.0001$), depth was used as a covariate in the GLM analysis and it was found that significantly shorter dives were being undertaken at the northern and southern colonies (Pearl and Leisure Islands) relative to the two colonies in the Cook Strait area, even at similar dive depths ($p<0.0001$, Table 2). In general, the deeper the penguins dive, the longer their dive durations, and the fewer dives per trip and per hour. The four little blue penguins from the southern-most colony, Pearl Island, showed the least energetic diving parameters, with short, shallow dives, minimal bottom time and predominantly V shape dives, while Motuara Island birds showed the most energetic diving parameters, with longer, deeper dives.

The isotopic values of feathers from the Motuara Island little blue penguins are presented in Figure 3 and Table 3, along with previously reported isotopic values from little blue penguins from the three other locations (Fig. 1; Chilvers et al. 2015; Chilvers 2017). The $\delta^{13}C$ and $\delta^{15}N$ values of the four little blue penguin populations differed significantly (Table 3). The Tukey *B* test showed a significant difference in $\delta^{15}N$ values from Pearl Island relative to all other colonies, while the $\delta^{13}C$ values differed significantly between Motuara and Leisure Islands, with Adele and Pearl Island populations having values not significantly different from those on either Motuara or Leisure Islands (Table 3).

Discussion

This study examined diving behaviour and feather stable isotope ratios of little blue penguins from Motuara Island, Marlborough Sounds, and compared them with little blue penguins from three other locations measured at similar time of the breeding stage (late October–November; Table 2) in the same year (Leisure Island) or 2 and 3 years previous (Pearl and Adele Islands, respectively). The aim was to better understand if little blue penguins could be used as an environmental monitor by studying their diving behaviour. Across all four sites there were significant differences between the diving parameters of the penguins. Motuara Island penguins had the deepest, longest, most energetic diving behaviour, with these long deep dives reflected in fewer dives per hour than any of the other locations studied. Penguins from the southern-most locality (Pearl Island) had the shallowest, shortest dives, longest surface intervals and spent less time diving while at sea than the more northern penguins (Table 2).

The foraging behaviours of little blue penguins are thought to be limited by local geographical and bathymetrical features. Chiaradia et al. (2007) undertook a comparison of the diving behaviour of little blue penguins from breeding colonies across Australia and New Zealand and showed that penguins that appeared to have the most energetic diving parameters (diving deeper and longer) had reduced breeding success in terms of lower fledging success than penguins that carried out shallower dives with less diving effort. Chiaradia et al. (2007) considered these differences to be predominantly driven by the geography and bathymetry of the penguins' local environment.

However, as can be seen in Table 2, the significant variation between the diving behaviours of little blue penguins across New Zealand does not appear to relate to their geographical surroundings. Motuara Island penguins performed the deepest dives of the four locations, with the penguins having deep (greater than 100 m) water within 2 km of their nesting sites. In contrast, Pearl Island penguins undertook the shallowest dives even though they also have a 100 m deep trench within tens of metres of their nesting sites (Chilvers 2017; Fig. 1). These results suggest it is not bathymetry or geography alone

Table 2. Summary statistics of the diving records of little blue penguins (*Eudyptula minor*) all collected in November, throughout New Zealand. Means ± SE. Superscripts denote statistically significant differences (p<0.05) between values in each column, as indicated by Tukey *B* post-hoc testing.

Location (reference / year of study)	*n*	% time at sea diving	# dives per trip	Dives per hour	Mean depth (m)	Max depth (m)	Mean duration (sec)	Mean surface interval (sec)	% bottom time	% U dives	% V dives	% W dives
Motuara Island (this study / 2014)	7	60 ± 8.2^{b}	1014 ± 135^{a}	68 ± 8.7^{a}	11.5 ± 0.1^{d}	31.7 ± 1.5^{c}	31.7 ± 0.2^{c}	19.3 ± 1.1^{c}	16 ± 0.2^{b}	40 ± 4.0	40 ± 4.0^{a}	20 ± 0.7^{b}
Pearl Island (Chilvers 2017 / 2011)	4	43 ± 0.1^{a}	1283 ± 208^{ab}	81 ±12.6^{a}	5.2 ± 0.4^{a}	15.0 ± 0.9^{a}	19.6 ± 0.12^{a}	26.9 ± 0.88^{d}	9.6 ± 0.2^{a}	28 ± 6.7	65 ± 6.7^{b}	7 ± 0.4a
Adele Island (Chilvers 2017 / 2012)	4	62 ± 0.1^{b}	1447 ± 110^{ab}	98 ± 7.4^{ab}	6.4 ± 0.3^{c}	21.9 ± 1.5^{b}	24.6 ± 0.16^{b}	15.2 ± 0.43^{b}	20.3 ± 0.3^{c}	49 ± 4.4	43 ± 4.2^{a}	8 ± 0.4^{a}
Leisure Island (Chilvers et al. 2015 / 2014)	14	71 ± 0.1^{b}	1750 ± 126^{b}	131 ± 9.0^{b}	6.1 ± 0.6^{b}	16.3 ± 0.9^{a}	20.1 ± 1.3^{a}	8.2 ± 0.58^{a}	16 ± 1^{b}	44 ± 3.7	44 ± 3.2^{a}	12 ± 1.6^{a}
Statistical results		$F_{3,28}$= 7.6, p=0.001	$F_{3,28}$= 4.7, p=0.01	$F_{3,28}$= 8.5, p<0.0001	$F_{3,42872}$= 498, p<0.0001	$F_{3,28}$= 39.8, p<0.0001	$F_{3,42872}$= 40.4, p<0.0001	$F_{3,42872}$= 10.9, p<0.0001	$F_{3,42872}$= 91.7, p<0.0001	n.s.	$F_{3,28}$= 4.5, p=0.01	$F_{3,28}$= 8.6, p<0.0001

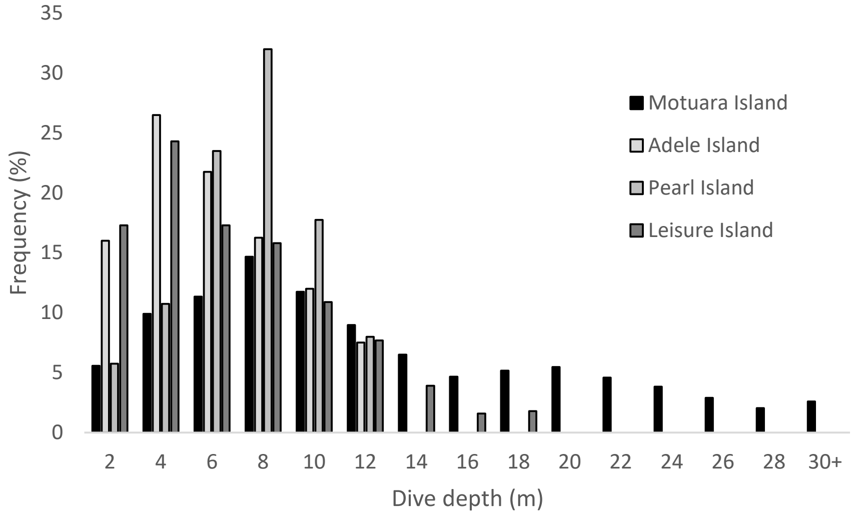

Figure 2. Frequency of dives in each depth category for little blue penguins (*Eudyptula minor*) from Motuara Island (n = 7), Adele Island (n = 4), Pearl Island (n = 4) and Leisure Island (n = 14), New Zealand.

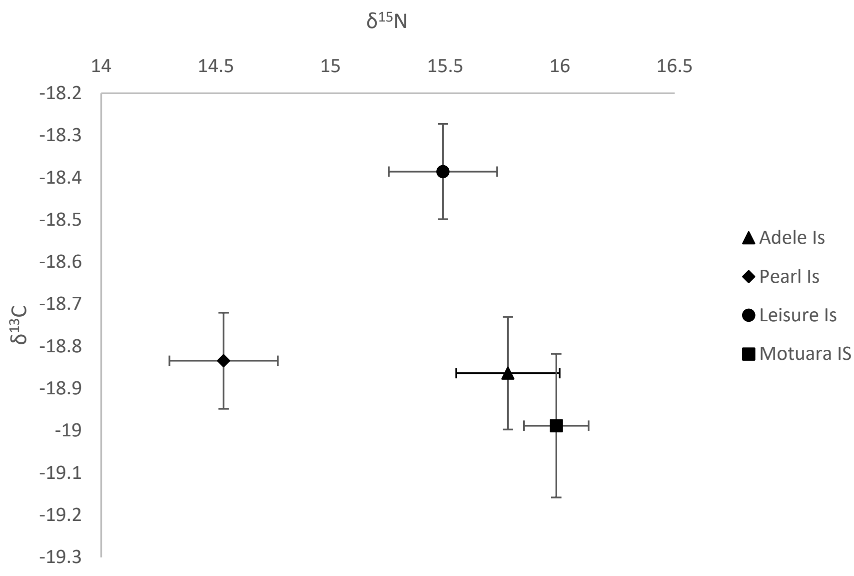

Figure 3. Bi-plots of $\delta^{15}N$ and $\delta^{13}C$ (μ±σ) of adult little blue penguins (*Eudyptula minor*) feathers from Motuara Island, Adele Island, Pearl Island and Leisure Island, New Zealand.

Table 3. Summary statistics of the stable isotope values of feathers from little blue penguins (*Eudyptula minor*) all collected in November, throughout New Zealand. Means ± SE. Superscripts represent Tukey *B* post-hoc testing, means with different superscript letters differ significantly from each other (p<0.05).

Location (reference / year of study)	n	$\delta^{15}N$	$\delta^{13}C$
Motuara Island (this study / 2014)	10	15.9 ± 0.14^{b}	-18.9 ± 0.17^{a}
Pearl Island (Chilvers 2017 / 2011)	10	14.5 ± 0.24^{a}	-18.8 ± 0.11^{ab}
Adele Island (Chilvers 2017 / 2012)	10	15.8 ± 0.23^{b}	-18.8 ± 0.13^{ab}
Leisure Island (Chilvers et al. 2015 / 2014)	20	15.5 ± 0.09^{b}	-18.4 ± 0.11^{b}
Statistical results		$F_{3,46} = 12.9$, $p<0.0001$	$F_{3,46} = 4.9$, $p=0.005$

that is influencing the diving behaviour of these penguins. Other influences that need consideration include water and wind movement (e.g. currents, eddies or upwellings) that can enhance nutrients and productivity in an area (Torres 2013; Poupart et al. 2017). Both Pearl and Motuara Islands are located in areas with strong currents and tidal and upwelling movements, which are likely to provide potential differences in prey abundance and distribution (Chiswell 1995). In contrast, Adele and Leisure Islands are in areas that are sheltered from strong currents (Fig. 1; Stanton et al. 1997; Tuckey et al. 2006). It is likely all of these factors will influence prey species type, abundance, and distribution between the sites, requiring the penguins to dive to different depths and have different dive frequencies to achieve the required prey intake.

Foraging behaviour and reproductive success

Foraging behaviour during incubation and chick rearing (including diving behaviour, foraging range and trip length) impacts the reproductive success of little blue penguins (Dann et al. 2000; Nisbet & Dann 2009; Chiaradia et al. 2010). Poupart et al. (2017) undertook foraging location research on Motuara Island little blue penguins contemporaneously with this study in 2014, and again in 2015. They reported significant differences in foraging range and area between individuals, breeding stages (incubation vs chick rearing, with foraging range and trip distances being significantly greater during incubation) and years during the chick rearing stage. In 2015, incubating birds foraged within 102 ± 69 km of their colony with their trips lasting 7 ± 4 days. Individuals either constantly undertook short-distance trips (c. 10 km of the colony), medium-distance trips (40–75 km from colony) or long foraging trips that involved crossing Cook Strait to forage 93–214 km from the breeding site. There were significant differences in breeding success between these birds. Two out of the three birds undertaking short-distance trips bred successfully (at least one chick fledged), while all nests tended by medium-distance foraging trips failed (the chicks hatched but were not fed), and birds undertaking long-distance trips had a 75% success rate. The results of Poupart et al. (2017), combined with the dive data presented here, show that the Motuara Island little blue penguins have a highly energetic diving behaviour and indicate that these birds appear to be able to adapt their foraging behaviour in an area with apparently low prey availability. However, doing so appears to have some trade-off in terms of breeding success. The results from the combined research indicates that Motuara Island little blue penguins may not be able to compensate or alter their foraging behaviour if there is either an unusual environmental occurrence or if subjected to severe resource competition lowering prey availability (Ropert-Coudert et al. 2015).

Stable isotope analysis

All keratin structures of animals (i.e. hair, whiskers, nails and feathers) are inert (inactive) once grown. Therefore, stable isotope analysis of keratin structures provides a coarse proxy for diet at the time the keratin was laid down, which for little blue penguin feathers is only once a year (during the pre-moult period, mid-February to mid-April; Johannessen et al. 2002). Consequently, the stable isotope analysis diet analysis reported here (Chilvers et al. 2015; Chilvers 2017), refers to the time period 7 months prior to the collection of the dive data and, therefore, there may be some bias in comparing the stable isotope analysis and diving datasets. In particular, the pre-moult diet in little blue penguins usually contains higher tropic level species, resulting in higher $\delta^{15}N$ values than diet recorded outside of the pre-moult period (Cullen et al. 1992; Fraser & Lalas 2004). However, for comparison between sites, it is assumed that the scale and direction of the bias in diet is similar for all areas studied, as all populations of little blue penguins would have foraged higher trophic level prey prior to moulting (Cullen et al. 1992; Flemming & Van Heezik 2014).

Little blue penguins from Motuara Island had the highest $\delta^{15}N$ and lowest $\delta^{13}C$ values recorded in this study (Fig. 3; Table 3). The low $\delta^{13}C$ values indicate these birds were foraging in areas with lower carbon input, which could mean they are foraging off shore or are foraging in an environment with lower terrestrial carbon input into the marine environment (i.e. further from river mouths); both are likely given our understanding of the foraging locations of the Motuara Island penguins. Some birds forage into and across Cook Strait, while others forage closer to their breeding island where the surrounding land has an extensive cover of native bush and no major river outflows (Poupart et al. 2017). The $\delta^{13}C$ levels were similar to those recorded from the blood of penguins from this colony during the incubation and chick rearing periods in the following year, 2015 (Poupart et al. 2017).

The $\delta^{15}N$ values of Motuara Island little blue penguins indicates the consumption of higher trophic level prey than birds at the other locations. These $\delta^{15}N$ values are in contrast to blood $\delta^{15}N$ values during the incubation and chick rearing periods in the following year, 2015 (Poupart et al. 2017). However, as previously noted and recorded for other little blue penguin species, higher $\delta^{15}N$ values are expected from pre-moult stable isotope samples (Cullen et al. 1992; Fraser & Lalas 2004; Flemming & Van Heezik 2014). Poupart et al. (2017) hypothesised that the low $\delta^{15}N$ values they recorded indicated the penguins were foraging predominantly on lower trophic level species such as squid during chick rearing rather than higher trophic level prey such as fish (Chiaradia et al. 2010; Flemming & van Heezik 2014; Chilvers et al. 2015). This hypothesis matches the foraging locations recorded during incubation and chick rearing (Poupart et al. 2017). As is expected, it appears that this prey intake changes to higher tropic level species prior to moult, reflecting the higher $\delta^{15}N$ values recorded in the feathers.

In contrast (and considering that feather $\delta^{15}N$ values should reflect the timing of the highest trophic level prey consumption), the $\delta^{15}N$ values for the most southerly location, Pearl Island, indicate the little blue penguins there were feeding on a lower trophic level prey prior to moult (Fig. 3; Table 3). Lower trophic level prey generally has a lower energy value than higher trophic level prey (Meynier et al. 2008). Little blue penguins from Pearl Island had the shallowest, shortest dives and spent the least time in a day at sea diving, indicating that the area is most likely a high productivity area. In this case, the little blue penguins were able to undertake minimal diving and eat lower energy content, yet still consume sufficient resources to survive and breed, as all the bird caught had healthy mass and were assumed breeding birds (Chilvers 2017).

Research limitations

There are a number of limitations to this research. First, the population sizes and trends of the little blue penguin colonies studied are unknown, including whether the populations in each area are stable, increasing or decreasing. The lack of knowledge about population sizes and trends is common for little blue penguin colonies throughout New Zealand and is reflected in their national threat classification listing(s) as 'data poor' (Robertson et al. 2017).

Second, only one day's diving behaviour was collected per bird to minimise the impact of carrying loggers on animal's behaviour and foraging ability (Chiaradia et al. 2007; Ropert-Coudert et al. 2009; Chilvers et al. 2015; Zhang et al. 2015). Although this appears to be a low sample size, it is comparable to similar little blue penguin research (Chiaradia et al. 2007; Ropert-Coudert et al. 2009; Chilvers et al. 2015; Zhang et al. 2015).

Finally, the breeding sites in this study were studied over 2 different years. When comparing the diving behaviours of marine species across years, differences in marine conditions (such as the Southern Oscillation) may have an influence and should be considered. However, neither of the 2 years in this study had either a strong El Niño or La Niña influence (https://ggweather.com/enso/oni.htm), therefore reducing the likelihood that this factor had a major impact on the results.

Conclusion

The aim of this research was to investigate little blue penguin diving behaviour and diet, to assess whether the species could be used as an environmental monitor in New Zealand. Given the variability in both diving and foraging behaviours of little blue penguins throughout New Zealand, and likely differences in prey as indicated by stable isotope analysis (this study; Poupart et al. 2017), the species appears to be highly adaptive to local environments. Therefore, the results suggest that little blue penguins would not make a good environmental monitor. Some environments may be more difficult for little blue penguins to adapt to than others, as reflected by the longer, deeper dives and greater foraging ranges for little blue penguins at Motuara Island and corresponding reduction in some indicators of breeding success (Numata et al. 2004; Poupart et al. 2017). Little blue penguins may prove to be useful environmental monitors for changes in the marine environment at individual sites, particularly if long-term monitoring at these sites was combined with an understanding of local population trends.

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