Foraging ecology of a winter breeder, the Fiordland penguin

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ABSTRACT: Breeding in most species is timed to coincide with the greatest availability of food resources to support the increased energetic needs of reproduction. Correspondingly, the majority (76%) of seabird species in temperate and polar regions breed in spring/summer, matching the peak in ocean productivity. The Fiordland penguin Eudyptes pachyrhynchus is one of only 34 seabird species worldwide that have part of their breeding cycle during the winter, and its chicks fledge when the eggs of congeneric Eudyptes species in the same region are only starting to hatch. Little is known of the foraging ecology of this species and the factors that may influence its timing of breeding. In the present study, the foraging behaviour of breeding individuals from Taumakana/Open Bay Island, New Zealand, was investigated using GPS, dive recorder and tri-axis accelerometer data loggers. In total, 35 individuals (4 males, 31 females) were tracked at sea, revealing extensive use of continental shelf slope (200–1000 m) habitat within 42 ± 5 km of the colony. Individuals foraged mostly during daylight in the epi-pelagic zone (mean modal depth 22 ± 2 m) and prey encounter events occurred in 50% of dives. Blood isotopic signatures suggest a trophic level indicative of squid consumption, supporting previous findings that winter-spawning squid are the most important prey type. The results of the present study suggest that a winter-breeding strategy by seabirds can reflect locally abundant prey resources and suitable conditions at the time for breeding.

KEY WORDS: Foraging behaviour · Winter breeding · Bio-logging · Prey encounter · Eudyptes pachyrhynchus · New Zealand

1. INTRODUCTION

The survival of any animal depends on its capacity to match food intake to energy requirements. Throughout the life cycle, energy requirements vary and environmental fluctuations alter food availability. Energetically demanding activities such as reproduction (Speakman 2008) are thus restricted to favourable times. Income-breeder species fuelling their reproductive investment with current trophic intake (Stearns 1989) have a breeding schedule synchronised with the time of the year giving the best chance of survival to the offspring (Lack 1954). This timing is typically a fixed life history trait, and is considered an adaptive evolutionary response to the predominant environmental conditions.

In temperate and polar environments, contrasting seasons throughout the year lead to variability in primary production. At sea, the warmer conditions and longer day length during spring and summer en-
hance phytoplankton blooms, which support a cascade of large biomasses in primary and secondary consumers (Verity & Smetacek 1996), providing an important food resource for pelagic fish and higher predators. In contrast, primary production is reduced in autumn, and at a minimum in winter (Alvain et al. 2008), making this period unfavourable for heterotrophic organisms. Correspondingly, in temperate and polar latitudes, breeding activities of predators are typically scheduled in spring and summer to coincide with favourable environmental conditions.

Seabirds (347 species; Croxall et al. 2012) are among the most numerous marine predators, and play a key role within marine food webs (Brooke 2004). Their colonial breeding and central-place foraging habits, coupled with the increased energetic costs of chick rearing, can lead to a total predator demand of >200 tons km⁻² yr⁻¹ (Murphy 1995) at sea around their colonies during summer. Consequently, the timing of reproduction in seabirds is closely linked to the temporal and spatial productivity of oceanic features (Bost et al. 2009) and, correspondingly, the vast majority of polar and temperate seabirds breed in summer (197 species, ca. 481 million ind.). In contrast, breeding in winter (i.e. incubation or chick rearing during the winter months) occurs in only 34 species (ca. 30 million ind.; Croxall et al. 2012).

Winter is considered a period of reduced prey availability and harsh environmental conditions for seabirds (Newton 1998) that induces an energetic bottleneck, often leading to increased mortality (Camphuysen et al. 1999, Fort et al. 2009). Correspondingly, most temperate and polar seabirds avoid these negative effects through migration towards more beneficial areas for their non-breeding period (Guilford et al. 2009). Resident species have to buffer these challenging conditions and compensate for the shorter day length with nocturnal foraging (Daunt et al. 2006). Paradoxically, winter-breeding species endure these conditions while experiencing the additional demands of reproduction (Salamolard & Weimerskirch 1993). Seasonal studies have reported that penguins dive longer and deeper in winter than summer (Green et al. 2005), with associated changes in diet, while feeding a chick during winter (Charrassin et al. 2002). However, little is known of the biological and ecological factors influencing winter-breeding or its energetic and reproductive consequences on seabirds (Zotier 1990).

The largest winter-breeding seabird community in the world is found in New Zealand, with 17 species of winter-breeding procellariiforms, cormorants and penguins (Croxall et al. 2012). It includes the Fiordland penguin Eudyptes pachyrhynchus, which is endemic to the coast and offshore islands south-west of the South Island. Unique within its genus, the breeding cycle of the species starts during the austral winter (Warham 1974), with egg laying occurring in July/August; the chick-fledging period starts in late spring when congenerics at similar latitudes are just starting to hatch (Warham 1972, García-Borboroglu & Boersma 2013). The small population of <7000 individuals nests in loose aggregations containing fewer than 10 pairs, dispersed over long stretches of coastline in dense vegetation, overhangs and small caves. This is in contrast to other Eudyptes species, which breed in very large colonies at high nesting densities in open spaces.

Given the apparent challenge of winter breeding and its small population, the Fiordland penguin may experience reduced food availability during reproduction, and may have to compensate for such conditions by increasing its foraging range and expend an increased effort (e.g. higher dive rate, deeper, longer and anaerobic dives) compared to its 7 summer-breeding congenerics. While the diet of Fiordland penguin has been reported to be composed of cephalopods, fish and crustaceans (Van Heezik 1989, 1990), very little is known of its foraging behaviour and the environmental factors influencing foraging in this species (Mattern 2013). Such information is crucial to understanding how the species, which has a Vulnerable conservation status (IUCN 2018), may respond to environmental variability and climate change (Otley et al. 2018). The objectives of the present study, therefore, were to examine (1) at-sea movements and habitat use, (2) diving behaviour and foraging effort, (3) trophic niche level and width and (4) potential intrinsic and environmental factors influencing these parameters in Fiordland penguins over the breeding season.

2. MATERIALS AND METHODS

2.1. Study site and field procedures

The study was conducted on Taumaka/Open Bay Island (43.859° S, 168.885° E), 4.5 km off the west coast of New Zealand’s South Island (see Fig. 1). This 20 ha island hosts one of the largest populations of Fiordland penguins with at least 150 breeding pairs (McLean & Russ 1991). Individuals were sampled (once throughout the study) during different breeding stages (incubation, guard and créche) over 2 breeding seasons (2016 and 2017). The birds were
observed from hides as they returned to the island and were captured by hand as they walked to, or were at, their nest. Once captured, they were fitted with a cloth hood to minimise stress and weighed using a spring scale (±20 g; Pesola).

To determine at-sea movements and marine habitat use, the birds were equipped with a GPS data logger (i-gotU Mobile Action Technology) accurate to ±10 m (Morris & Conner 2017). The device was removed from its original casing to reduce drag effect and sealed in a waterproof heat-shrink tubing (Tyco Electronics). During incubation, model GT 600 units (45 × 39 × 13 mm, 26.5 g) were deployed, programmed to sample at 2 min intervals. During guard and creche stages, model GT-120 units (45 × 25 × 12 mm, 15 g) were deployed, programmed to sample at 1 and 2 min intervals, respectively. The data loggers were attached to the mid-line dorsal feathers on the lower back with black waterproof tape (TESA 4651; Beiersdorf AG) following Wilson et al. (1997).

To obtain information on diving behaviour, the same individuals were simultaneously instrumented during the guard and creche stages with a dive behaviour/accelerometer data logger (40 × 15 × 11 mm, 6.5 g; Axy-Depth, Technosmart, or 21 × 13 × 4 mm, 1.7 g; WACU, MIBE/IPHC) recording depth (±5 cm) and temperature (±0.1°C) every 1 s and tri-axial body acceleration at 25 Hz. In total, attached devices represented ca. 1% of the penguins’ body mass in air and ca. 2.6% of their cross-sectional surface area, and therefore are likely to have had negligible impact on the individual’s foraging behaviour (Agnew et al. 2013). Handling procedures lasted 10–15 min before the animals were released near their nest to resume normal behaviours.

After 1 or 2 foraging trips to sea, individuals were recaptured and the data loggers were removed. Culmen length and bill depth were measured using Vernier callipers (±0.1 mm) to sex the birds using a discriminant function previously established at this site (Murie et al. 1991). A 0.1 ml blood sample was collected by venipuncture of a tarsal vein and stored in 70% ethanol for later analysis of stable isotopes for trophic niche estimation.

2.2. Data handling and processing

GPS data were processed within the R statistical environment (R Core Team 2017). Foraging trips were defined as the time spent at sea between the departure and the return (land-based points removed). A speed filter with a threshold at 8.2 km h⁻¹ (Brown 1987) was applied to remove erroneous locations. The following trip metrics were calculated using the package ‘adehabitatHR’ (Calenge 2006): trip duration, total horizontal distance travelled, mean horizontal speed, maximum distance from the colony and compass bearing to the most distal point.

Raw depth data were downloaded from the data loggers and converted using the software Axy Manager (Technosmart Europe). Submergences of >1 m depth were considered dives and were processed within the R software to calculate their parameters (maximum depth, duration, descent and ascent rates, bottom time, post-dive interval) using the package ‘diveMove’ (Luque 2007). Maximum depth of successive dives were compared to assess the intra depth zone (IDZ; Tremblay & Cherel 2000). For each individual trip, the proportion of time spent diving and the dive frequency were determined. For individuals providing sufficient data, the behavioural aerobic dive limit (bADL) was estimated from the dive duration and post-dive interval. As 98% of post-dive intervals were ≤60 s (and those lasting longer were not related to dive sequences), this threshold was used to investigate the bADL. The bADL was determined from the intersection of quantile regressions fitted on a moving average of 5 successive dives (Fig. S1 in the Supplement at www.int-res.com/articles/suppl/m614p183_supp.pdf), to account for oxygen payoff delay (Horning 2012). Lastly, dive data were visually inspected to ascertain dive shape profiles (Wilson et al. 1996). Dive occurrence was investigated in relation to local sunrise, sunset and nautical twilight times (www.timeanddate.com, retrieved for Haast, 10 km east of the colony) in order to describe their temporal distribution (dawn, day, dusk and night).

Foraging effort was assessed from the vertical dive rate (total vertical distance / trip duration, m h⁻¹). The acceleration data along the 3 axes (surge, heave and sway) were analysed within IGOR Pro software v.7 (Wavemetrics). Gravity-related acceleration, determined by a 1 s running mean, was subtracted from the raw acceleration to calculate vectorial dynamic body acceleration (VeDBA; Gleiss et al. 2011), a measure of whole body activity. Assuming that sudden, sharp movements were associated with prey pursuits (Chimienti et al. 2016), peaks above 0.15 g during dives on a 1 s moving average VeDBA were considered to represent prey encounter events (PEEs; Fig. S2) following the method described in Sánchez et al. (2018). Intervals of ≤2 s between VeDBA peaks were considered to be related to the same prey item, as inspection of the frequency distri-
bution of interval durations revealed a sharp decrease in the number of PEEs above this threshold. The PEEs were then aligned with the diving behaviour and the interpolated GPS coordinates in order to describe their vertical and spatio-temporal distribution along the foraging trip.

To investigate the important environmental factors driving Fiordland penguin habitat use, oceanographic variables considered to be influential (Reisinger et al. 2018) were gathered on the penguins’ foraging area. Remote-sensed sea surface chlorophyll $a$ (chl $a$) concentration was excluded, as it has been reported as an imprecise index of the water column stock of chl $a$ in these inshore waters influenced by coastal run-off (Vincent et al. 1991). Bathymetry and sea floor slope were obtained from 250 m gridded bathymetry data (www.niwa.co.nz/our-science/oceans/bathymetry). Daily sea surface temperature (SST) and SST anomaly were obtained at 0.01° resolution (https://coastwatch.pfeg.noaa.gov/). Daily sea surface height (SSH), mixed layer thickness (MLT), salinity (SAL) and sea water eastward and northward velocity data were obtained at 0.08° resolution (http://marine.copernicus.eu/). Current speed was calculated as:

\[
\text{current speed} = \sqrt{\text{northward velocity}^2 + \text{eastward velocity}^2}
\]

Within square grid cells of 0.01° (ca. 1 km$^2$) matching the finest resolution of the oceanographic data, the linearly interpolated GPS tracks at 1 min were converted in a standardised proportion of time spent in area, using the package ‘trip’ (Sumner 2015). As individuals spend more time where they forage, it is a spatial index of the foraging effort (Péron et al. 2012). The time spent in area values were then spatio-temporally matched with the above oceanographic variables using the package ‘raster’ (Hijmans & Van Etten 2016).

The trophic niche of individuals was investigated using the analysis of stable isotopes (SIA) of nitrogen ($\delta^{15}$N) and carbon ($\delta^{13}$C), a widely used method to infer a consumer’s trophic level and quantify its niche within the food web (Bearhop et al. 2004). SIA was conducted on whole blood samples, which reflects the assimilated diet signature with a half-life turnover of 12−14 d for a penguin of this size (Barquetti et al. 2013). Samples were oven-dried for 24 h at 60°C, ground and 0.5 mg sub-samples loaded into tin capsules. Analyses were conducted at the National Isotope Centre (GNS Science) with an elemental analyser (EuroVector) coupled to a mass spectrometer (Isoprime). Isotopic ratios are reported in δ notation relative to the international standards, Viennaa Pee Dee Belemnite limestone for carbon and atmospheric N$_2$ for nitrogen. Their isotopic deviation is defined as $\delta(\%) = [(R_s/R_{ref})/R_{ref}] \times 1000$, where $R_s$ is the isotopic ratio measured for the sample and $R_{ref}$ is the reference standard. Internal laboratory standards (Leucine) indicate an analytical precision of ±0.2‰ for C and ±0.3‰ for N (±1 SD). The isotopic niche position and width of Fiordland penguins was estimated and compared between breeding stages in a 2-dimensional (2D) isotopic space, using the ellipse area-based metrics of the SIBER package (Jackson et al. 2011). The isotopic niche was estimated by the 40% standard ellipse area corrected for sample size (SEAb$\alpha$) and by the Bayesian standard ellipses areas (SEAB$_\alpha$) on 10$^5$ replicates, which quantified uncertainty and allowed robust statistical comparisons (Jackson et al. 2011). The niche overlap between stages was quantified by the isotopic area of overlap from the maximum likelihood ellipses for 2 given stages.

2.3. Statistical analyses

All statistical analyses were conducted within the R software (R Core Team 2017). Different tests were used to assess variable normality (Shapiro-Wilk test), variance homogeneity of unbalanced samples (Bartlett test), the distribution between departures and returns times (Wilcoxon test) and their variation between breeding stages (Kolmogorov-Smirnov tests). The uniformity of range bearings was tested with a Kuiper’s test. To investigate variables influencing foraging behaviour of the instrumented individuals, different mixed models were fitted to account for the hierarchical structure of the tracking data (Bolker et al. 2009) using individuals as a random factor. Generalized linear mixed models (GLMMs) were used to investigate the influence of year, breeding stage and sex (explanatory variables) on the maximum distance from the colony, mean horizontal speed, trip duration and total horizontal distance travelled (response variables), using the package ‘nlme’ (Pinheiro et al. 2014). Allowing for non-linear relationships between the response variable and its covariables (Wakefield et al. 2009), generalized additive mixed models (GAMMs) were used to investigate the influence of the year, time of day, breeding stage and sex (explanatory variables) on the dive rate, depth, duration and percentage of anaerobic dives (response variables). The temporal autocorrelation of the dives was taken into account by an autoregressive component (rho) using the package ‘mgcv’ (Wood & Wood 2015). A GAMM was also used to investigate the influence
of oceanographic variables on the foraging effort index. Prior to modelling, oceanographic variables were scaled and checked for collinearity, with a cut-off criterion of \( r_s = 0.5 \) for inclusion in the model. Generalized linear models (GLMs) were used to investigate the influence of year, breeding stage and sex on the isotopic values (\( \delta^{13}C \) and \( \delta^{15}N \)).

Model selection was based on Akaike’s information criterion corrected for small sample sizes (AICc), ranking all candidate models using the package ‘MuMIn’ (Barton 2016). The best-supported model was chosen, or in the case of several candidate models with substantial support (\( \Delta AIC < 4 \)), the most parsimonious model was chosen (Table S1) after a model-averaging procedure identifying the most important predictor variables (Burnham et al. 2011). Selected models were validated by examination of the residuals (Zuur et al. 2009). Variable influence was considered significant at \( p < 0.05 \). Unless otherwise stated, data are presented as means ± SE.

3. RESULTS

3.1. At-sea movements and habitat use

Due to logistical constraints, not all stages could be sampled equally in both years of the study. Device malfunctions and loss at sea of some devices meant that complete data sets were not available from all individuals (Table 1). Data on at-sea movements were obtained for 35 individuals (37 trips), totalling 1427 h at sea and 22470 filtered locations (27 removed). There was a significant difference between the sexes in the body mass of departing birds, with males weighing 3.4 ± 0.1 kg and females 2.8 ± 0.0 kg (ANOVA, \( p < 0.001 \)), but not between year or breeding stage. When recaptured, the same birds were weighed with an average mass gain of 44 ± 33 g.

Movements from the colony occurred throughout most of the day (01:00–22:00 h) with departures occurring mainly before sunrise (67%), while returns to the colony were spread throughout the afternoon until sunset (70%). This pattern was consistent across breeding stages. During incubation, individuals conducted multi-day trips (3–5 d), whereas during the guard stage trips were mostly for a single day (8–15 h, 64%) or shorter multi-day trips (2 d, 36%). During the crèche stage, all trips consisted of longer multi-day trips (2–7 d).

Individuals travelled in a non-random direction across breeding stages (Kuiper test, \( D = 4.5, p < 0.01 \)), in a northerly direction over a narrow peri-insular shelf (Fig. 1). They reached a maximum distance from the colony of 115 km, making a total home range area of 3877 km². Their total horizontal distance travelled ranged from 11 to 379 km, covered at a mean horizontal speed of 3.1 ± 0.1 km h⁻¹. GLMMs indicated an influence of breeding stage and year on trip parameters (Table 2). Guard-stage trips were closer to the colony by 62 ± 11 km, had trip durations that were shorter by 70 ± 9 h, and the birds travelled shorter horizontal distances by 187 ± 25 km (all \( p < 0.001 \)). During 2017, birds travelled shorter maximum distances from the colony (17 ± 8 km) compared to 2016. Sex had no influence on trip parameters.

At sea, individuals spent most of their time in shelfslope waters (200–1000 m, 68%), followed by neritic shelf waters (0–200 m, 22.9%), and oceanic waters (>1000 m, 9%). SST ranged between 11 and 14°C with an associated temperature anomaly between −0.6 and 1.2°C. SAL ranged between 34.6 and 35.2 psu, SSH between 0.007 and 0.2 m, and MLT varied from 10 and 228 m depth. GAMM modelling revealed that the time spent in area was influenced negatively by salinity above 35 psu (\( p < 0.001 \)) and positively by seafloor slope between 0 and 29° (\( p < 0.01 \), Fig. S3).

Table 1. Logger deployments on Fiordland penguins (M: males; F: females) at Taumaka/Open Bay Island, New Zealand, and their GPS trip metrics according to breeding stage (mean ± SE)

<table>
<thead>
<tr>
<th>Year</th>
<th>Incubation 2016</th>
<th>Guard 2016</th>
<th>Crèche 2016</th>
<th>Crèche 2017</th>
</tr>
</thead>
<tbody>
<tr>
<td>Individuals equipped (n)</td>
<td>4 (3 F, 1 M)</td>
<td>21 (20 F, 1 M)</td>
<td>5 (3 F, 2 M)</td>
<td></td>
</tr>
<tr>
<td>Body mass (kg)</td>
<td>2.7 ± 0.1</td>
<td>2.8 ± 0.1</td>
<td>3 ± 0.05</td>
<td>3 ± 0.08</td>
</tr>
<tr>
<td>Trips recorded (n)</td>
<td>4</td>
<td>5</td>
<td>23</td>
<td>5</td>
</tr>
<tr>
<td>Trip duration (h)</td>
<td>101 ± 9</td>
<td>31 ± 4</td>
<td>17 ± 2</td>
<td>106 ± 16</td>
</tr>
<tr>
<td>Max. distance from the colony (km)</td>
<td>89 ± 9</td>
<td>42 ± 6</td>
<td>25 ± 3</td>
<td>88 ± 13</td>
</tr>
<tr>
<td>Total horizontal distance travelled (km)</td>
<td>250 ± 29</td>
<td>96 ± 13</td>
<td>56 ± 6</td>
<td>254 ± 46</td>
</tr>
<tr>
<td>Mean horizontal speed (km h⁻¹)</td>
<td>2.4 ± 0.07</td>
<td>3.1 ± 0.2</td>
<td>3.3 ± 0.1</td>
<td>2.7 ± 0.1</td>
</tr>
<tr>
<td>Trip bearing (°)</td>
<td>8 ± 1.3</td>
<td>350 ± 2</td>
<td>0.01 ± 2.1</td>
<td>30 ± 1.2</td>
</tr>
</tbody>
</table>
3.2. Diving behaviour and foraging effort

Diving behaviour data were obtained from 23 individuals (25 trips) totalling 970 h at sea and 23172 dives. Individuals spent 72 ± 2% of their time at sea submerged, with the number of dives recorded ranging from 253 to 4790 trip⁻¹, reflecting the variation in trip duration. Dives were conducted primarily during daylight, not only during the 14 single-day trips (98.8%) but also for the 11 multi-day trips (87.2%) which included 1–6 successive nights at sea. Outside of daylight, diving activity was reduced but not absent, with 0.9% occurring at dawn, 3.8% at dusk and 7.9% at night. Dives were epi-pelagic along the trips, characterised by shallow dives in the vicinity of the colony followed by sequences of deeper diving further off-shore (Fig. 2) with typical V-, U- and irregular U-shaped profiles.

Dive depths (max. 154 m) and duration (max. 206 s) were not normally distributed and so modes were calculated for each trip. Mean modal dive depth across all individuals was 22 ± 2 m, with 35 ± 1% of dives occurring sequentially within the same IDZ. Mean modal dive duration was 74 ± 11 s with a mean modal post-dive interval of 20 ± 1 s. These dives characteristics led to a dive frequency of 19 ± 2 dives h⁻¹ and to a

Fig. 1. (A) Study site. (B,C,D) Fiordland penguins’ foraging trips from Taumaka/Open Bay Island expressed as standardised time spent in area within 0.01° cells during the different breeding stages: (B) incubation, (C) guard and (D) crèche. Study site location (black point in A) is represented in regards to the breeding populations’ locations (green points) and to the average position of the subtropical front (dashed line), and is framed by a rectangle showing the area plotted in (B–D). New Zealand islands are shaded in grey; bathymetry is indicated by 200 and 1000 m isobaths.
mean dive rate of $1141 \pm 64$ m h$^{-1}$ (Table 3). Most individuals did not conduct apparent anaerobic dives, and the bADL could be calculated for 2 males ($155 \pm 2$ s) and 2 females ($154 \pm 2$ s) during the crèche stage, and 7 females during the guard stage ($146 \pm 1$ s). No significant difference was found between sexes ($t_{2.1} = -2.3$, $p = 0.13$) or breeding stage ($t_{1.4} = -1.7$, $p = 0.26$). While only 6% of the total foraging dives were anaerobic, there was substantial inter-individual variation in their proportions (range 0–38%). All these dive parameters varied temporally according to the hour of the day (all $p < 0.001$; Table 4). At midday, the dive rate increased due to deeper, longer and, hence, more anaerobic dives. Concurrently, individuals encountered fewer prey at this time (Fig. 3). Breeding stage influenced some dive parameters, with dive rate increasing by 262 $\pm 107$ m h$^{-1}$ and maximum depth by 11 $\pm 4$ m in the crèche stage compared to the guard stage. Sex did not influence the dives parameters.

Across all individuals, PEEs were recorded in 50 $\pm 2$% of dives. Within these dives, PEEs occurred 1.0 $\pm 0.1$ dive$^{-1}$, primarily during the bottom phase (74.7%), with the remainder during the descent (13.4%) and the ascent (11.8%) phases of dives. Overall, individuals encountered prey at a rate of 33 $\pm 3$ PEEs h$^{-1}$ during their foraging trips, without influence of sex or breeding stage (GLMM, $p > 0.05$). Based on a linear interpolation of the GPS tracks, the horizontal distance between successive PEE dives

<table>
<thead>
<tr>
<th>Model</th>
<th>Response variable</th>
<th>Predictor variable</th>
<th>Parametric coefficients</th>
<th>Approximate significance of smooth terms</th>
<th>p-value</th>
</tr>
</thead>
</table>
| GLMM        | Max. distance from the colony      | Stage (guard)      | $-62.0$ 11.3 9.1        | --                                     | $<0.001$
| GLMM        | Trip duration                      | Stage (guard)      | $-70.6$ 9.6 $-7.3$      | --                                     | $<0.001$
| GLMM        | Max. distance travelled            | Stage (guard)      | $-187.3$ 25.2 $-7.4$   | --                                     | $<0.001$
| GAMM        | Log(time spent in area)            | Intercept          | $-0.19$ 0.27 $-0.72$   | --                                     | 0.4     
|             |                                    | Slope              | --                     | 1 7.1                                  | 0.007   |
|             |                                    | Current            | --                     | 6.3 1.9                               | 0.059   |
|             |                                    | Salinity           | --                     | 8.0 6.1                               | $<0.001$

Table 2. Model outputs used to assess trends in foraging trip parameters of breeding Fiordland penguins at Taumaka/Open Bay Island. Significant p-values are highlighted in bold. Edf: estimated degrees of freedom, GLMM: generalized linear mixed model; GAMM: generalized additive mixed model.

Fig. 2. Typical Fiordland penguin dive profile (in blue) along a 2 d foraging trip, overlaid with bathymetry (dotted pattern below) and distance to the colony (above). The diving activity with repeated dives at high frequency is concentrated during the day, and reduced at dawn and dusk (light grey shaded areas) and night-time (dark grey shaded areas).
was 92 ± 15 m. The vertical distribution of the PEE in the water column ranged between 2 and 105 m depth, with time spent encountering prey positively increasing with depth (Fig. S4).

### 3.3. Trophic level and isotopic niche width

Stable isotope values of whole blood (mean ± SD) were −19.8 ± 0.3‰ for $\delta^{13}C$ and 12.2 ± 0.3‰ for $\delta^{15}N$, with an associated C:N ratio of 3.3 ± 0.1. The GLMs indicated that $\delta^{15}N$ values were not influenced by year, breeding stage or sex (null model selected). The $\delta^{13}C$ values were not influenced by sex, but were significantly reduced by 0.5 ± 0.1‰ in 2017 (p < 0.001), and reduced by 0.2 ± 0.1‰ during the guard stage (p = 0.01). Therefore, isotopic data from both sexes were pooled together and were clustered by year and breeding stage (Fig. 4). The isotopic niche area during incubation was estimated at $SE_{A_c} = 0.37\%^2$ and $SE_{A_B} = 0.31\%^2$, with a high probability of being larger than during the guard stage (2016: $SE_{A_c} = 0.29\%^2$, $SE_{A_B} = 0.20\%^2$; 2017: $SE_{A_c} = 0.27\%^2$, $SE_{A_B} = 0.19\%^2$) and was statistically similar to isotopic niche area during the crèche stage ($SE_{A_c} = 0.35\%^2$, $SE_{A_B} = 0.37\%^2$) (Table S2). All isotopic niche areas from $SE_{A_B}$ overlapped to some extent. In order of importance, the overlap was high between incubation/crèche, incubation/guard 2016, guard 2016/crèche, medium between guard 2017/crèche, and low between guard 2017/crèche and guard 2016/guard 2017 (Table S2).

### Table 3. Diving behaviour of 23 Fiordland penguins (25 trips including 23172 dives) provisioning chicks at Taumaka/Open Bay Island, New Zealand. According to their distributions, parameters are summarized by either the mean (normality), mode (skewed between individuals) or the mean of the modes (skewed within individuals)

<table>
<thead>
<tr>
<th>Dive parameter</th>
<th>Mean/ mode</th>
<th>Mean of the modes</th>
<th>SE</th>
<th>Range</th>
</tr>
</thead>
<tbody>
<tr>
<td>% Time spent diving</td>
<td>72†</td>
<td>–</td>
<td>2</td>
<td>44–77</td>
</tr>
<tr>
<td>Dive frequency (h⁻¹)</td>
<td>23†</td>
<td>–</td>
<td>1</td>
<td>14–56</td>
</tr>
<tr>
<td>Dive rate (m h⁻¹)</td>
<td>1141</td>
<td>–</td>
<td>64</td>
<td>629–1775</td>
</tr>
<tr>
<td>Dive depth (m)</td>
<td>–</td>
<td>22</td>
<td>2</td>
<td>1–56</td>
</tr>
<tr>
<td>Duration (s)</td>
<td>–</td>
<td>74</td>
<td>11</td>
<td>1–182</td>
</tr>
<tr>
<td>Post-dive interval (s)</td>
<td>–</td>
<td>19</td>
<td>2</td>
<td>12–29</td>
</tr>
<tr>
<td>Bottom time (s)</td>
<td>–</td>
<td>1</td>
<td>0</td>
<td>1–1</td>
</tr>
<tr>
<td>Descent rate (m s⁻¹)</td>
<td>0.6</td>
<td>–</td>
<td>0.4</td>
<td>0.2–2</td>
</tr>
<tr>
<td>Ascent rate (m s⁻¹)</td>
<td>0.6</td>
<td>–</td>
<td>0.4</td>
<td>0.2–2</td>
</tr>
<tr>
<td>Anaerobic dives (%)</td>
<td>0</td>
<td>–</td>
<td>1.7</td>
<td>0–38</td>
</tr>
<tr>
<td>Intra depth zone dives (%)</td>
<td>35</td>
<td>–</td>
<td>1</td>
<td>37–86</td>
</tr>
<tr>
<td>Dives with prey encounter events (PEEs) (%)</td>
<td>50</td>
<td>–</td>
<td>2</td>
<td>28–75</td>
</tr>
<tr>
<td>PEE rate (h⁻¹)</td>
<td>33</td>
<td>–</td>
<td>3</td>
<td>13–66</td>
</tr>
<tr>
<td>Number of PEEs within</td>
<td>1†</td>
<td>–</td>
<td>0.06</td>
<td>1–2</td>
</tr>
<tr>
<td>Horizontal distance between PEE dives (m)</td>
<td>–</td>
<td>92</td>
<td>15</td>
<td>3–213</td>
</tr>
</tbody>
</table>

### Table 4. Generalized additive mixed model (GAMM) outputs used to assess the trends in the diving behaviour of Fiordland penguins provisioning chicks at Taumaka/Open Bay Island. Significant p-values are highlighted in bold

<table>
<thead>
<tr>
<th>Response variable</th>
<th>Predictor variable</th>
<th>Parametric coefficients</th>
<th>Approximate significance of smooth terms</th>
<th>p-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Dive rate</td>
<td>Intercept</td>
<td>1051</td>
<td>60</td>
<td>17.4</td>
</tr>
<tr>
<td></td>
<td>Stage (crèche)</td>
<td>262</td>
<td>107</td>
<td>2.4</td>
</tr>
<tr>
<td></td>
<td>Hour of the day</td>
<td>–</td>
<td>–</td>
<td>–</td>
</tr>
<tr>
<td>Dive depth</td>
<td>Intercept</td>
<td>18.9</td>
<td>1.7</td>
<td>11.0</td>
</tr>
<tr>
<td></td>
<td>Stage (crèche)</td>
<td>11.0</td>
<td>4.1</td>
<td>2.6</td>
</tr>
<tr>
<td></td>
<td>Sex (male)</td>
<td>–7.8</td>
<td>4.3</td>
<td>–1.8</td>
</tr>
<tr>
<td></td>
<td>Hour of the day</td>
<td>–</td>
<td>–</td>
<td>–</td>
</tr>
<tr>
<td>Dive duration</td>
<td>Intercept</td>
<td>84.4</td>
<td>3.6</td>
<td>23.0</td>
</tr>
<tr>
<td></td>
<td>Stage (crèche)</td>
<td>9.4</td>
<td>6.3</td>
<td>1.4</td>
</tr>
<tr>
<td></td>
<td>Hour of the day</td>
<td>–</td>
<td>–</td>
<td>–</td>
</tr>
<tr>
<td>% of anaerobic dives</td>
<td>Intercept</td>
<td>12</td>
<td>3.7</td>
<td>3.2</td>
</tr>
<tr>
<td></td>
<td>Stage (crèche)</td>
<td>10.4</td>
<td>5.8</td>
<td>1.7</td>
</tr>
<tr>
<td></td>
<td>Hour of the day</td>
<td>–</td>
<td>–</td>
<td>–</td>
</tr>
<tr>
<td>Time spent in prey encounter events</td>
<td>Intercept</td>
<td>56.9</td>
<td>32.8</td>
<td>1.7</td>
</tr>
<tr>
<td></td>
<td>Stage (crèche)</td>
<td>163.2</td>
<td>98.6</td>
<td>1.6</td>
</tr>
<tr>
<td></td>
<td>Sex (male)</td>
<td>163.7</td>
<td>98.5</td>
<td>1.6</td>
</tr>
<tr>
<td></td>
<td>Hour of the day</td>
<td>–</td>
<td>–</td>
<td>–</td>
</tr>
</tbody>
</table>
4. DISCUSSION

With a winter-time breeding phenotype, the Fiordland penguin is unique amongst its congenerics. The combined results of the at-sea movement, diving behaviour, prey field estimation and isotopic niche obtained in this study revealed that individuals breeding at Taumaka/Open Bay Island engaged in short and directional foraging trips towards a close peri-insular shelf slope. During foraging trips, individuals dived within the epi-pelagic zone primarily during the day. Isotopic examination of the trophic niche showed a small niche width that corresponds to a squid-dominated diet. This foraging strategy was consistent between sexes, and only constrained to a shorter distance from the colony during the chick-guard stage by the need for more regular chick feedings. Despite the shorter available daylight hours (11−13 h in winter versus 14−17 h in summer), individuals did not display any detectable compensation by foraging more at night. While winter is considered a period of low food availability for many seabird species, this study revealed that individuals encounter prey at a sufficiently high abundance that they do not need to forage at a higher effort than their summer-breeding conspecifics.

4.1. At-sea movements and habitat use

The early morning departures and afternoon returns to the colony by Fiordland penguins observed in the present study were consistent with previous observations on this (Warham 1974) and other penguins species, displaying a typical diurnal pattern consistent with their reliance on ambient light as visual foragers (Bost et al. 2002). During the
incubation stage, males and females alternated foraging trips until hatching. Whereas females usually assume all the foraging duties in the guard stage while males brood the chicks (Warham 1974), the present study found one male alternated guard duties with its female partner. A sexing error is unlikely as both individuals of the pair were instrumented for the study. During the crèche stage, as in other penguin species, both sexes were simultaneously engaged in foraging trips to cope with the high energy demands of larger chicks (Green et al. 2005).

The tracked individuals made directional movements which suggest the use of predictable profitable prey areas close to the colony (Barlow & Croxall 2002). In 2016, females foraged further away during the guard stage than in 2017, which could reflect inter-annual variation in prey distribution (Garthe et al. 2011). Breeding stage influenced the foraging trip parameters, with distance and duration typically reduced during the guard stage when small offspring need to be provisioned more frequently, while incubation and crèche trips parameters were similarly longer. Despite the sexes being dimorphic and there being sex-specific differences in energetic constraints in the various breeding stages, sex did not influence foraging trip parameters in the present study. This is in contrast to that reported in other *Eudyptes* species, where males forage in prolonged trips further from the colony than females (Barlow & Croxall 2002, Ludynia et al. 2013), enabling preparation for, and in recuperation of, long fasting periods by males associated with the guard stage. However, due to logistical constraints, a sample with equal sex ratios could not be obtained in the present study, so it is possible that sex differences in habitat use do exist in Fiordland penguins.

Whereas most *Eudyptes* recover from the energy deficit of fasting during courtship, egg laying and incubation with trips of long duration to distant oceanic areas (Table 5), the Fiordland penguins from Taumaka/Open Bay Island foraged close to the colony on short trips during this period. Similarly, during the crèche stage, individuals in the present study supported the higher nutritional requirements of large chicks with foraging trips of shorter duration and closer to the colony than congenerics (Table 5). Tracked individuals foraged mostly over the shelf slope, where their time per grid cell was influenced by the sea-surface salinity and seafloor bathymetry slope only. This is in contrast with the summer-breeding congenerics that use mesoscale (eddies) and sub-mesoscale (filaments) cues to locate favourable foraging conditions in the oceanic environment (Bon et al. 2015, Whitehead 2017). Instead, Fiordland penguins from Taumaka/Open Bay Island targeted the adjacent shelf slope, likely reflecting ready access to favourable waters, where lower salinity could indicate areas of mixing (Heath 1985).

### 4.2. Diving behaviour and foraging effort

In the present study, individuals started foraging soon after leaving the colony, with no apparent commuting phase, and spent the majority of their time at sea diving. Despite an ability to reach deeper-water prey, predominant aerobic and epi-pelagic dives reflect prey availability at shallower depths. Diving behaviour varied throughout the day, with the deepest and longest dives occurring in the middle of the day when the rate of prey encounter decreased. This strongly suggests an adaptation to diel vertically migrating prey (Bost et al. 2002) and is similar to other *Eudyptes* species where temporal variation in epi-pelagic dives corresponds to vertically migrating prey (Wilson et al. 1997, Tremblay & Cherel 2003, Deagle et al. 2008). Breeding stage influenced dive depth and foraging effort, showing a slight increase during the crèche stage. This is in accordance with the changing energy demands of chick rearing (Green et al. 2009), and is similar to that reported for congeneric species (Schiavini & Rey 2004, Booth et al. 2018, Deagle et al. 2008). Within the limited samples sizes of the present study, diving parameters
were not influenced by sex, despite the presence of sexual dimorphism and unequal breeding duties between male and female Fiordland penguins (Warham 1974). This is similar to that observed in royal/macaroni penguins (Hull 2000, Deagle et al. 2008) but in contrast to that reported in rockhopper penguins where females dived to greater depths than males (Ludynia et al. 2013). These contrasted results could potentially reflect site-specific prey accessibility and density-dependence triggering the intra-specific competition (Lewis et al. 2001). Given the imbalanced sex ratio in the present study, further investigations are required to see if females have more time to forage and if this could potentially reflect sex differences in diving behaviour and foraging effort in Fiordland penguins.

Assuming the foraging behaviour of a predator reflects the availability of its prey (Elliott et al. 2008), the observed PEE rate (~1 dive$^{-1}$) was low in comparison to that reported in other penguin species (Watanabe & Takahashi 2013, Sutton et al. 2015) achieving multiple prey captures per dive associated with small schooling prey. Hence, the results of the present study suggest individuals have foraged predominantly on less aggregated or solitary larval prey. Future studies using animal-borne cameras are needed to confirm the identity of prey species and the quantification of prey consumption (Watanabe & Takahashi 2013, Morrison 2015; Whitehead 2017; Otley et al. 2018; Booth et al. 2018; Values calculated per hour underwater, for comparison purposes)

### Table 5. Comparison of breeding and foraging parameters among the *Eudyptes* genus. Data from the present study are shown in *italics*, other data are from Garcia-Borboroglu & Boersma (2013), except data indicated by superscripts. NA: not available

<table>
<thead>
<tr>
<th>Eudyptes penguin species</th>
<th>Southern rockhopper</th>
<th>Eastern rockhopper</th>
<th>Northern rockhopper</th>
<th>Erect-crested</th>
<th>Fiordland</th>
<th>Snares</th>
<th>Macaroni</th>
<th>Royal</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>E. chrysolophus</em></td>
<td><em>E. chrysolophus</em></td>
<td><em>E. chrysolophus</em></td>
<td><em>E. chrysolophus</em></td>
<td><em>E. chrysolophus</em></td>
<td><em>E. chrysolophus</em></td>
<td><em>E. chrysolophus</em></td>
<td><em>E. chrysolophus</em></td>
<td><em>E. chrysolophus</em></td>
</tr>
<tr>
<td><strong>Egg laying period</strong></td>
<td>November</td>
<td>December</td>
<td>September-October</td>
<td>October</td>
<td>July-August</td>
<td>September-October</td>
<td>November-December</td>
<td>October-November</td>
</tr>
<tr>
<td><strong>Main prey</strong></td>
<td>Crustaceans</td>
<td>Crustaceans</td>
<td>Crustaceans</td>
<td>Fish</td>
<td>Fish</td>
<td>Fish</td>
<td>Fish</td>
<td>Fish</td>
</tr>
<tr>
<td><strong>Habitat</strong></td>
<td>Patagonian shelf and slope</td>
<td>Polar frontal zone, shelf</td>
<td>Peri-insular shelf</td>
<td>NA</td>
<td>Peri-insular shelf</td>
<td>Subtropical front</td>
<td>Polar frontal zone, shelf</td>
<td>Polar frontal zone</td>
</tr>
<tr>
<td><strong>Trip duration and range</strong></td>
<td>Incubation</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>0.3−22 d (9−190 km)</td>
<td>14 d$^a$ NA</td>
<td>NA</td>
<td>NA</td>
<td>3−5 d (76−115 km)</td>
<td>10 ± 2 d 200 km</td>
<td>10−26 d (300−700 km)</td>
<td>19 ± 7 d (415−600 km)</td>
</tr>
<tr>
<td></td>
<td>Guard</td>
<td>6−67 h$^b$ (1−78 km)</td>
<td>11−19 h NA</td>
<td>NA</td>
<td>8−41 h (11−134 km)</td>
<td>34 ± 8 h (121 ± 31 km)</td>
<td>4−64 h (12−98 km)</td>
<td>6 ± 3 d (22−406 km)</td>
</tr>
<tr>
<td></td>
<td>Crèche</td>
<td>27−28 h (30 km)</td>
<td>1−336 h$^b$ (2−420 km)</td>
<td>12 ± 1$^d$ NA</td>
<td>2−7 d (42−111 km)</td>
<td>NA</td>
<td>NA</td>
<td>NA</td>
</tr>
<tr>
<td><strong>Mean dive depth range (m)</strong></td>
<td>14−27 48</td>
<td>13−18 NA</td>
<td>20 23</td>
<td>15−60 32</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>Dive rate (m h$^{-1}$)</strong></td>
<td>1716−2909$^e$</td>
<td>1544$^e$</td>
<td>1530 NA</td>
<td>1141 (=1782$^e$) NA</td>
<td>1205, 1457$^e$ NA</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>Chick fledge duration (d)</strong></td>
<td>66−73 68</td>
<td>63−70 70</td>
<td>74 75</td>
<td>60−70 65</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>Mean breeding success</strong></td>
<td>0.35−0.61 0.47</td>
<td>0.36 NA</td>
<td>0.61$^c$ 0.41</td>
<td>0.35 0.53</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

$^a$Morrison (2015); $^b$Whitehead (2017); $^c$Otley et al. (2018); $^d$Booth et al. (2018); $^e$Values calculated per hour underwater, for comparison purposes
4.3. Trophic level and isotopic niche width

The δ¹⁵N values observed in the present study are similar to that observed in other penguin species in New Zealand inshore waters that are known to have a squid-dominated diet (Flemming & Van Heezik 2014). This is consistent with the stomach contents of Fiordland penguins previously analysed at Taumaka/ Open Bay Island, indicating that squid (ranging in mantle lengths from 20−140 mm) represents 71% of the diet by mass (Van Heezik 1989). Furthermore, the small isotopic ellipses and the absence of δ¹⁵N variation between sexes and breeding stages corroborate, respectively, the low prey diversity and lack of sex difference in stomach contents (Van Heezik 1989). However, the constant trophic level observed between breeding stages in the present study contrasts with the diet shift seen during chick rearing in southern rockhopper (Schiavani & Rey 2004) and northern rockhopper (Tremblay & Cherel 2003, Booth et al. 2018) penguins, also provisioning chicks during the crèche by foraging on the shelf. The δ¹³C values, reflecting the carbon source in the food chain with a gradient between inshore−offshore habitats (Hobson et al. 1994), indicated small variations between breeding stages and years. These isotopic results are also consistent with the GPS trips and dive parameters discussed above. The different time scales between time integration of whole blood isotopes and the duration of the tracked foraging trips complicate their spatio-temporal interpretation, especially in a region of such intermittent water mixing processes (Vincent et al. 1991). Future studies should consider analysing the stable isotopes of blood plasma, integrating a shorter period of time (Barquet et al. 2013) to gain accuracy.

The narrowness of the trophic niche observed in the present study is typical of specialist Eudyptes species, having little deviation in their stable isotopes values (Cherel & Hobson 2007) and few prey taxa in their stomach contents (Cooper et al. 1990). However, while Eudyptes species rely mostly on crustacean or fish (Table 5), the Fiordland penguin appears to be a squid specialist during the breeding season off the west coast of New Zealand’s South Island (Van Heezik 1989). This is consistent with the local oceanic conditions, with a weak eastward flow bringing the oligotrophic and iron-limited subtropical waters of the Tasman Sea to this region (Ellwood et al. 2008). Undergoing a mixed layer deepening in winter that recharges the photic zone in nutrients and rises over the peri-insular shelf where intermittent wind-driven coastal upwelling and large river outflows occur (Heath 1985, Vincent et al. 1991), these waters have an increased phytoplankton production in winter that peaks in September–October before decreasing in summer (Longhurst 1995, Murphy et al. 2001). Numerous species, including arrow squid Nototodarus sloanii and warty squid Moroteuthis ingens which are the main prey of the Fiordland penguin (Van Heezik 1989), take advantage of these conditions to spawn during winter (Uozumi & Forch 1995, Jackson 1997). Other fish prey such as sprat Sprattus antipodum, red cod Pseudophycis bachus or hoki Macruronus novaezelandiae also spawn in winter on this shelf (Colman 1979, Coombs & Cordue 1995, Beentjes & Renwick 2001).

In summary, the present study found no compelling evidence that Fiordland penguins at Taumaka/Open Bay Island experience particularly challenging prey availability conditions during their winter breeding period. Instead, the results suggest that Fiordland penguins breeding at this location match their breeding activity to a predictable prey resource, potentially winter-spawning squid. This close prey resource is likely to explain the shorter foraging range and similar foraging effort that lead to a high breeding success after a similar chick-rearing period compared to the other Eudyptes species (Table 5). However, these apparently favourable foraging conditions are at odds with the low population size and the negative population trend for the species (Mattern 2013, Otley et al. 2018). While introduced predators are known to reduce the breeding success of Fiordland penguins nesting on the mainland (Mattern 2013), the results of the present study were obtained on an island free from introduced mammalian predators. This suggests that the species may experience a local energetic bottleneck at other times of the year, limiting their population growth. For instance, the local availability of squid is known to decrease in summer (Mattlin 1985), when Fiordland penguins shift foraging location towards distant oceanic fronts during the pre-moult trip (Mattern et al. 2018), and are not observed near their breeding sites during the non-breeding period.

It will be necessary to gather further information on the Fiordland penguin’s foraging ecology throughout the annual cycle (Marra et al. 2015) to understand the full range of its ecological requirements and potential threats at sea. This is especially important in view of its reliance on a narrow continental shelf associated with a narrow trophic niche dimension, reflecting a high degree of specialization and little plasticity during the breeding period, which may make this population highly sensitive to environmental perturba-
tions (Laidre et al. 2008). The present study was conducted in a small proportion of the species’ range, with many populations occurring further south closer to the subtropical front (Fig. 1) where individuals are likely to face different marine conditions and are known to have a fish-dominated diet at Codfish Island (Van Heezik 1990). The degree to which the foraging characteristics of this relatively large population of the Fiordland penguin breeding at the study site reflects that of other smaller breeding groups remains to be investigated. Therefore, additional studies are needed across the species’ range to better understand the drivers and consequences of winter breeding.

Other seabird species with long breeding cycles that extend chick rearing into winter (e.g. king penguin *Aptenodytes patagonicus*, Charriasin et al. 2002, or wandering albatross *Diomedea exulans*, Salamolard & Weimerskirch 1993) forage in oceanic waters with a higher effort (longer trip durations and greater distances) to rear chicks. In contrast, the present study suggests winter breeding in Fiordland penguins is a strategy to match favourable pelagic conditions. These findings extend the knowledge on species that commence breeding in winter, currently limited to the emperor penguin *Aptenodytes forsteri* and gentoo penguin *Pygoscelis papua*, which are capable of benthic foraging (Rodary et al. 2000, Lescroël & Bost 2005). In addition to taking advantage of a winter resource, the absence of the numerous migratory summer-breeding species during winter could constitute another advantage. More studies involving different winter-breeding seabirds from other parts of the world and considering year-round prey availability are needed to improve our understanding of the evolution of winter breeding. Studies on flying species, more constrained by surface prey availability, would be especially important. Such temporal resource segregation with summer-breeding species is likely to have played a major role in speciation. For instance, this could be the case in the *Eudyptes* radiation and the divergence between the summer-breeding snares penguin and the winter-breeding Fiordland penguin during the Pleistocene (Baker et al. 2006). In addition, ongoing climate change and anthropogenic impacts on the oceans at a global scale might influence the cost/benefit of the winter-breeding strategy, on which much remains to be discovered.

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