

## RESEARCH ARTICLE

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# Diet plasticity and links to changing foraging behaviour in the conservation of subantarctic yellow-eyed penguins (*Megadyptes antipodes*)

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## Abstract

1. Diet is a key factor affecting seabird foraging behaviour, ultimately influencing survival, breeding success and long-term population viability. The density and distribution of prey species in the marine environment are influenced by many factors including climate effects such as El Niño southern oscillation and climate change that alter water temperature.
2. While poor quality diet has been implicated as a contributing factor in the decline of some mainland New Zealand yellow-eyed penguin (*Megadyptes antipodes*) populations, little is known about their diet in the subantarctic where the majority of the species breeds.
3. Blood and feather samples (n = 63) were collected for stable isotope analysis of diet from 25 individual birds breeding on subantarctic Enderby Island, Auckland Islands, New Zealand, from 2015 to 2018.
4. Diet data were analysed by factors such as breeding year, sex and foraging behaviour. Stable isotope analysis demonstrated significant changes in diet during each year of the study, which included both El Niño and La Niña conditions.
5. Diet during El Niño conditions comprised lower trophic level prey, which were more benthic, and found closer to shore than diet during La Niña.
6. Coupled with the reported variable breeding success of yellow-eyed penguins in the subantarctic, variable diet suggests prey availability is likely to be a limiting factor in some years. Prey availability is therefore expected to be a major influence on survival and breeding success of this endangered species in the future, particularly if the effects of climate change become more pronounced.
7. This research highlights an urgent conservation need to identify prey species utilized by the southern population, along with their distribution in time and space, and therefore also the effect of diet on long-term population stability.

## KEYWORDS

Auckland Islands, benthic diving, carbon isotope, climate change, El Niño southern oscillation, GPS logger, nitrogen isotope, pelagic diving, stable isotope analysis, time depth recorder

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## 1 | INTRODUCTION

The diet of long-lived marine predators is a key indicator of individual foraging success (Emlen, 1966; MacArthur & Pianka, 1966), as it affects adult survival (Keymer et al., 2001), chick provisioning (Jodice et al., 2006), and ultimately breeding success and long-term population viability (Emlen, 1966; MacArthur & Pianka, 1966; Olsson, 1997; Moreno et al., 1999; McClung et al., 2004; Jodice et al., 2006; Crawford et al., 2008). Prey availability is determined by the density and distribution of prey species, with horizontal and vertical distribution affecting predators' travel distance and dive depth (Croxall, Reid & Prince, 1999; Inchausti et al., 2003; Boersma & Rebstock, 2009). Prey species can be affected by changes in environmental conditions such as water temperature, with diet quality predicted to decrease for many marine species due to climate change (Worm et al., 2006; Cury et al., 2011). Studying broader changes in prey trophic level can shed light on foraging behaviour even where prey species are not directly analysed (Chilvers, 2017a; Chilvers, 2017b). Changes in the diet of a diving seabird can indicate variability in prey species utilized between years, sexes and age classes (Cherel, Hobson & Weimerskirch, 2000; Ainley et al., 2003; Tremblay & Cherel, 2003), and, therefore, foraging variability. Interpretation of dive data often relies on the assumption that sampling a small number of foraging trips is representative of diving behaviour over a whole breeding season, which may not be the case (Amélineau et al., 2021). However, diet studies can be used to interpret dive results, since significant differences in diet between individuals in the same population can indicate that different foraging behaviours were occurring, and that these were maintained across multiple foraging trips for the period in question.

Stable isotope analysis (SIA) is a method of analysing diet composition by determining the chemical makeup of prey items that have been incorporated into body tissues (Hobson & Clark, 1992a; Cherel, Hobson & Weimerskirch, 2000; Bearhop et al., 2002; Bearhop et al., 2006). Stable isotope analysis offers advantages over other techniques such as stomach contents analysis, which often represent diet from only a single meal, and can be biased by differing prey digestibility (Duffy & Jackson, 1986; van Heezik & Seddon, 1989; van Heezik, 1990a; Pütz, 1995). Techniques such as faecal analysis, and particularly faecal DNA analysis, can be used to determine prey species over extended periods and multiple individuals to avoid the single meal constraint, and faecal DNA avoids differential digestion issues (Deagle et al., 2010; Young et al., 2020). However, DNA samples need to be stored at  $-20^{\circ}\text{C}$  to prevent degradation (Young et al., 2020), so transport from the subantarctic is logistically difficult. While results are easier to obtain from SIA than DNA analysis (especially from feathers), SIA allows identification of prey to trophic level only (Hobson, Piatt & Pitocchelli, 1994), making it useful for measuring broad-scale taxonomic-level changes in the diet of marine predators. Stable isotope analysis measures the dietary components of prey species, which are assimilated in the tissues of consumers in a reliable and predictable way (DeNiro & Epstein, 1978; DeNiro & Epstein, 1981; Hobson & Clark, 1992a; Hobson & Clark, 1992b).

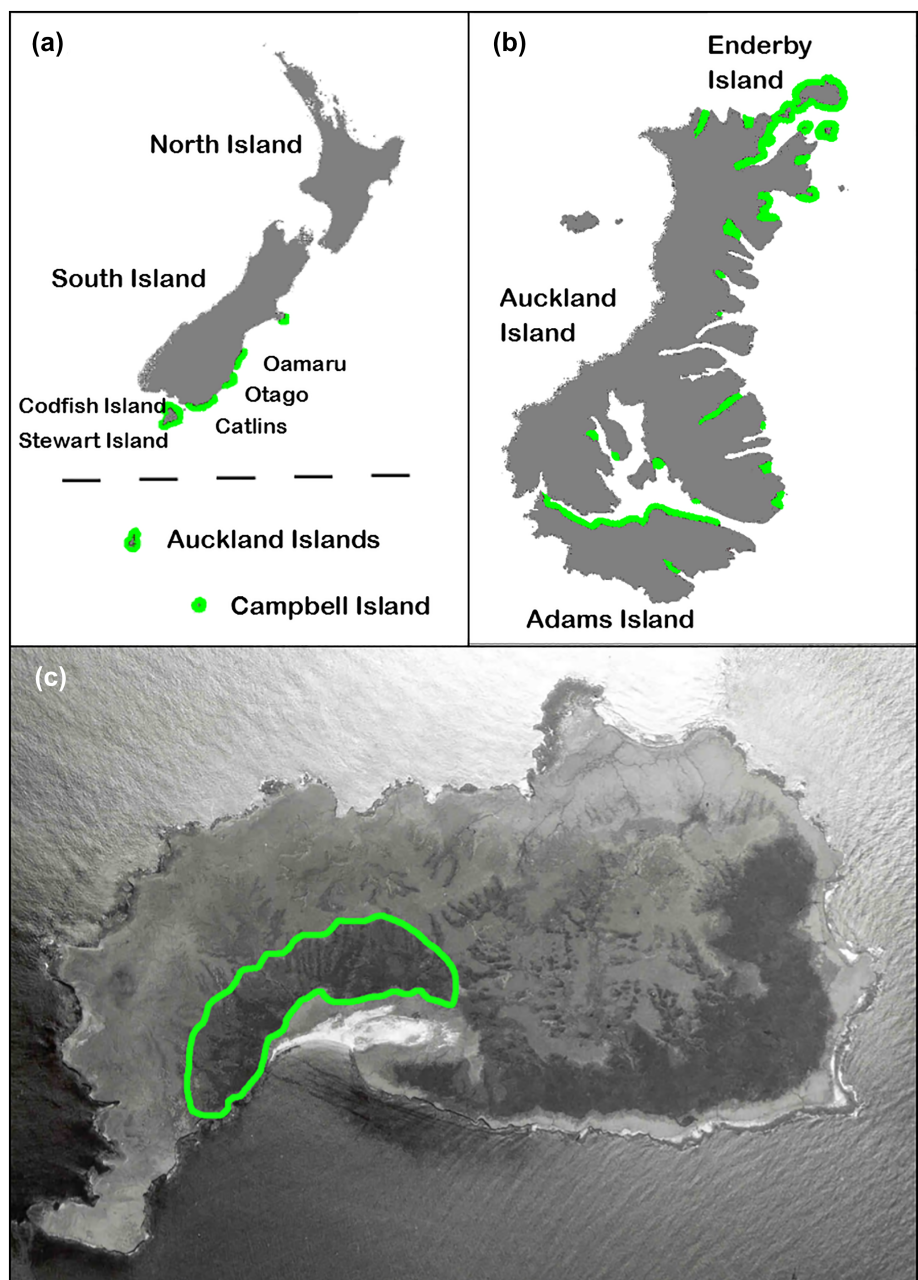
Chemical elements with more than one isotopic form have different molecular mass, and differing ratios of these can distinguish between prey from different sources. The isotopic ratio of nitrogen ( $^{15}\text{N}/^{14}\text{N}$ ) indicates which trophic level an animal is feeding at (DeNiro & Epstein, 1981; Bodey, Bearhop & McDonald, 2011), with fish and cephalopods higher than zooplankton prey (Owens, 1988; Hobson, Piatt & Pitocchelli, 1994). The isotopic ratios of carbon ( $^{13}\text{C}/^{12}\text{C}$ ) can be used to confirm foraging location, with higher (less negative) values indicating more inshore versus offshore feeding (Hobson, Piatt & Pitocchelli, 1994; Kelly, 2000) and more benthic versus pelagic (Hobson, Piatt & Pitocchelli, 1994; Cherel et al., 2007). Stable isotopes can be analysed from body samples such as feathers and blood, which represent diet over different time frames (Bearhop et al., 2002). Nitrogen and carbon signatures persist in blood for around 1–5 weeks after prey consumption (Hobson & Clark, 1992a; Haramis et al., 2001; Bearhop et al., 2002; Pearson et al., 2003; Cherel, Hobson & Hassani, 2005), with a half-life of around 2 weeks (Bearhop et al., 2002). Feather samples are logistically simpler and less invasive to obtain than taking blood, or some other methods of determining diet, such as stomach flushing. Isotope signatures in feathers are stable but reflect the diet at the time they were grown (Hobson & Clark, 1992a; Haramis et al., 2001; Bearhop et al., 2002; Pearson et al., 2003; Cherel, Hobson & Hassani, 2005) meaning they represent a portion of the diet of the total breeding season. Unlike other seabirds, most species of penguin generally undergo a single annual feather moult, which often occurs during a period of fasting at the end of the breeding season (Adams & Brown, 1990). Since penguins remain on shore and rely on stored energy reserves during the period new feathers are grown (Adams & Brown, 1990), the SIA signature in the feathers is therefore homogenous and represents the nutritional content of the diet for a period of around 4–6 weeks during the pre-moult period (Flemming & van Heezik, 2014; Chilvers, 2017a).

Breeding penguins are central-place foragers that must frequently travel from their nest to their foraging area at sea, and return to feed chicks (Williams, 1995; Borboroglu & Boersma, 2013). Consequently, breeding penguins and other seabirds are particularly vulnerable to localized prey depletion, as well as to changes affecting the location or depth of prey, which can increase the effort required to find and exploit a food source (Birt et al., 1987). Penguins are diving predators, capturing and consuming live prey underwater. The predominant dive types are benthic diving (to the sea floor), which is characterized by repeated dives to a uniform maximum depth limited by seabed depth (Tremblay & Cherel, 2000); and pelagic diving, which occurs mid-water with a more variable maximum depth between dives since prey could be encountered anywhere in the water column (Tremblay & Cherel, 2000). Deeper dives require more energy expenditure, so benthic foraging can be more energetically expensive than pelagic foraging, especially in deeper water (Costa et al., 2004). However, benthic prey species tend to be a predictable, evenly distributed prey source, although often occurring at low densities within a habitat (Costa et al., 2004; Chilvers & Wilkinson, 2009). Conversely, while pelagic foraging is unpredictable and may require birds to travel larger

distances to search for prey, pelagic prey are often found in higher-density aggregations, such as schools and bait balls, providing a richer food source once located (Chilvers & Wilkinson, 2009). Overall, pelagic prey are often more influenced by oceanographic and weather conditions such as El Niño southern oscillation (ENSO) than are benthic prey (Costa et al., 2004), meaning benthic prey may be a more reliable food source when prey are less abundant. Successful foraging must balance the energy expenditure required to catch prey with their nutritional quality. Fish generally have a higher lipid and energy content than do cephalopods or zooplankton and therefore represent higher quality prey (Clarke & Prince, 1980; Cherel & Ridoux, 1992; Meynier et al., 2008). Penguins feeding on a higher proportion of fish are therefore expected to be in better body condition, and the body

condition of penguin chicks is positively correlated with the proportion of fish in their diet (Forero et al., 2002). Factors affecting the makeup of prey species in the diet can therefore affect foraging success, which in turn has implications for both nutrition and chick provisioning.

The yellow-eyed penguin (hoiho, *Megadyptes antipodes*) is classified as Endangered (Couch-Lewis et al., 2016; Birdlife International, 2020) and endemic to New Zealand, with a highly restricted distribution. The northern population includes breeding areas in the south east of the South Island, and Stewart and Codfish Islands (Figure 1, above dotted line), and the southern population includes the subantarctic Auckland and Campbell Islands (Figure 1, below dotted line) (Seddon, Ellenberg & Van Heezik, 2013), with



**FIGURE 1** (a) Map of yellow-eyed penguin breeding range around New Zealand (green), with the northern population above the dotted line, and southern population below the line. Also shown is (b) an enlarged view of the subantarctic Auckland Islands with Enderby Island to the north east, and (c) a close-up of Enderby Island showing the area where breeding birds were sampled (green ellipse). Modified from Muller et al. (2020a)

these areas representing discrete populations for conservation management (Boessenkool et al., 2009). Most populations around mainland New Zealand are in serious decline due to successive poor breeding seasons and ongoing high adult mortality, believed to be due to threats at sea including poor foraging success, fisheries interactions, pollution and human disturbance (Couch-Lewis et al., 2016; Mattern et al., 2017; Mattern & Wilson, 2018). The southern yellow-eyed penguin population comprises at least 60–79% of the total population (Couch-Lewis et al., 2016; Muller et al., 2020b), and while apparently not declining in the 2010s, there were large fluctuations in breeding success, and counts have reduced since the 1980s (Moore, 1992; Moore, Fletcher & Amey, 2001; Muller et al., 2020b). As in most other penguin species, yellow-eyed penguins typically moult after breeding; in late March on mainland New Zealand (Seddon, Ellenberg & Van Heezik, 2013), or during April in the subantarctic (Moore, Fletcher & Amey, 2001). Warmer water has a detrimental effect on foraging and breeding success in the northern population (Young, 2014; Mattern & Ellenberg, 2018). The warmer water and more stochastic weather and wind patterns associated with strong La Niña conditions around mainland New Zealand negatively affect yellow-eyed penguin breeding success (Moore & Wakelin, 1997; Darby, 2003; Young, 2014; Mattern et al., 2017). However, there are few data on the effects of ENSO on foraging and breeding success in the southern population, although a greater proportion of pelagic foraging was observed during La Niña conditions (Muller et al., 2021). Breeding yellow-eyed penguins typically forage in coastal and mid-shelf waters around mainland New Zealand (Moore, 1999; Mattern et al., 2007; Mattern et al., 2013), while, at the subantarctic Auckland Islands, yellow-eyed penguins forage further offshore than many mainland birds do (Muller et al., 2021) and at greater depths (Muller et al., 2020a). Dive data from the northern population revealed predominantly benthic foraging behaviour (Seddon & van Heezik, 1990; Moore et al., 1995; Mattern, 2006; Mattern et al., 2007; Mattern et al., 2013; Chilvers, Dobbins & Edmonds, 2014). Earlier diet studies suggested that some pelagic prey species were utilized (van Heezik, 1990b); however, more recently, prey were interpreted as being mainly demersal (Moore & Wakelin, 1997). A predominantly benthic foraging strategy in the northern population may be influenced by changes in prey availability and environmental conditions, with some pelagic foraging occurring when visibility is poor at the sea bed (Mattern & Ellenberg, 2018). In contrast, Enderby Island birds displayed apparently greater diving plasticity, with foraging behaviour switching from benthic to almost 80% pelagic in some years, as well as trips consisting almost entirely of pelagic dives (Muller et al., 2020a), a diving behaviour not common in the northern population. It is likely that diving and foraging plasticity is a function of the physical environment and changes in prey availability and location, rather than an inherent characteristic of either population (Muller et al., 2021).

Knowledge of diet diversity is important for ecosystem-based management plans (Shiffman et al., 2012). Understanding diet and foraging behaviour is essential for conservation monitoring because it allows for informed management decisions such as predicting where

and how poor diet may affect population viability, and how to address that when it occurs. Poor diet can result in poorer chick condition in yellow-eyed penguins (van Heezik & Davis, 1990), leading to decreased post-fledging survival rates (McClung et al., 2004). Poor foraging success has also been linked to reduced adult survival, with negative long-term population outcomes (Couch-Lewis et al., 2016; Mattern & Wilson, 2018; Department of Conservation, 2020). Variable breeding success is evident in the southern population, probably linked to changes in foraging success (Muller et al., 2020b; Muller et al., 2021). As yellow-eyed penguin foraging is influenced by climate patterns (Moore & Wakelin, 1997; Darby, 2003; Young, 2014; Mattern et al., 2017; Muller et al., 2021), a comprehensive understanding of diet and foraging ecology across the range of the species is essential for monitoring yellow-eyed penguin breeding and guiding effective conservation management, particularly as the effects of climate change are expected to become more pronounced in the future (Collins et al., 2013; Ramírez et al., 2017). While variable foraging behaviour has been identified in the subantarctic (Muller et al., 2020a; Muller et al., 2021), little information on diet is available for the southern population. Better knowledge of yellow-eyed penguin diet will also help determine whether food availability or quality might be limiting factors, and as a result, to anticipate any possible impacts on successful breeding for these populations. The aims of this study were therefore to better understand diet and foraging in the southern population, by: (i) identifying changes in diet between years and relating these to population-level changes in foraging, breeding and ENSO state; (ii) identifying variability in diet between sexes, or birds utilizing different foraging behaviours in order to identify pressure on particular cohorts; and (iii) comparing diet trends in the subantarctic with data published for mainland birds to identify specific regional threats to the southern population.

## 2 | METHODS

### 2.1 | Fieldwork

Ground-based fieldwork was carried out on Enderby Island, Auckland Islands, in the New Zealand subantarctic (50°29'45"S 166°17'44"E, Figure 1) for three breeding seasons 2015 (November 2015–February 2016), 2016 (November 2016–February 2017), and 2017 (November 2017–January 2018). GPS foraging data were collected during concurrent research in 2016 and 2017 (Muller et al., 2021), and dive and breeding success data were collected in all three years (Muller et al., 2020a; Muller et al., 2020b). Nests were located using manual ground searching, ground-based very high frequency radio tracking, and aerial tracking using an unmanned aerial vehicle equipped with a very high frequency receiver (Muller et al., 2019). Adult penguins were captured by hand as they returned to the shore in the evening following a foraging trip at sea, and transferred to a custom-made holding bag. This held the wings against the body but left the head and feet exposed for processing and collection of morphometric data using a spring balance and callipers. Birds were marked with a

microchip for permanent individual identification (Muller et al., 2020b), and sex was determined using the relationship between head plus beak length and foot length (Setiawan, Darby & Lambert, 2004), or the relative sizes between breeding partners with males assumed to be the larger (Setiawan, Darby & Lambert, 2004). Blood and feather samples for SIA were taken while birds were restrained.

## 2.2 | Sampling and stable isotope analysis

Blood samples were collected in November 2015 only, due to logistical constraints. A 1-ml sample of blood was taken using a 25-gauge needle from either the medial metatarsal vein (inside of the leg) or dorsal digital vein (on top of the foot) while penguins were restrained in the holding bag. Blood samples were transferred to an Eppendorf tube then spun in the field using a centrifuge, and the serum and red blood cell components were transferred into separate tubes and frozen in liquid nitrogen for transfer back to the mainland. Serum samples were then freeze-dried and ground to a fine powder for SIA analysis.

Feather samples were collected in the 2015, 2016 and 2017 breeding seasons (representing diet during pre-moult periods in the 2014, 2015 and 2016 seasons, respectively). Six feathers were cut with scissors from haphazard locations on the central and lower back of each bird. Feathers were cleaned by soaking for 5 min each in distilled water, followed by a 2:1 solution of chloroform and methanol to remove lipids, then rinsed in clean distilled water again for 1 min to remove solvents (Cherel et al., 2007). Feathers were dried using clean paper towels, and placed in clean Ziploc bags for storage.

Stable isotope analysis of blood and feathers was conducted by Waikato Stable Isotope Unit (Department of Biological Sciences, University of Waikato). Blood samples were compared with feather samples from the same bird, representing a similar nutritional period (i.e. feathers collected during the following breeding season in 2016). Feathers and powdered serum were weighed and packed in tin-foil capsules, and carbon and nitrogen isotope ratios were determined by a Dumas elemental analyser (Europa Scientific ANCA-SL) interfaced to an isotope mass spectrometer (Europa Scientific 20–20 Stable Isotope Analyser). Results are presented in the conventional notation relative to a laboratory standard or reference for sucrose ( $^{13}\text{C}$ ) and urea ( $^{15}\text{N}$ ), with urea calibrated relative to atmospheric nitrogen. Quality-control samples were run before and after every 12 samples, and unless otherwise stated, data are presented as means  $\pm$  SE and results are considered significant at the  $P < 0.05$  level.

Statistical analyses were performed in R Studio version 1.1.456 running R version 3.5.1 (R. Core Team, 2017), and using the lme4 package (Bates et al., 2015). All continuous variables were visually assessed to be normally distributed using histograms and Q-Q plots, so dependent variables were not transformed. Stable isotope analysis results were analysed using general linear mixed effects models, with bird ID (an individual identifier) as a random effect to avoid pseudo-replication. A separate ANOVA test of models with and without bird

ID was used to test whether bird ID significantly improved the model fit, based on the resulting corrected Akaike's information criterion (AICc) values. This hypothesis-driven test was used to investigate whether any individual preferences in diet existed. Graphs were generated in R including the ggplot2 package (Wickham, 2016).

## 2.3 | Dive type and foraging distance

Concurrent dive data were collected using Lotek LAT 1400 time depth recorders attached to the middle of the back using waterproof tape, as described in Muller et al. (2020a). Dives were categorized as benthic if the depth change between subsequent dives was  $< 2.9\%$ , with the remainder of dives classed as pelagic (Muller et al., 2020a). Foraging trips were also classified using Bayesian analysis, with benthic trips having  $> 3.6\%$  benthic dives, accounting for the large proportion of non-feeding travelling dives and ensuring that the remaining trips classified as pelagic contained no significant instances of benthic diving (Muller et al., 2020a).

Foraging data were collected using customized CatTraQ GPS loggers modified for underwater use according to Pelletier et al. (2014), and attached to the lower back (Muller et al., 2021). GPS data were interpolated to account for missed fixes, and distance measures were calculated including the foraging distance (maximum straight-line distance away from shore, measured from the sea access point) and the total trip distance (cumulative distance travelled between all points in a foraging trip) (Muller et al., 2021). Where possible, electronics were deployed for only one foraging trip before being recovered to minimize attachment time. However, if penguins undertook more than one foraging trip before electronics were recovered, the data were divided into separate trips. For full methodology refer to Muller et al. (2021).

## 3 | RESULTS

### 3.1 | Summary

A total of 63 SIA samples were processed, from 25 individual birds (14 males and 11 females; Table S1). This included 10 blood samples from 10 different birds collected in 2015, and 53 feather samples

**TABLE 1** Isotope values (‰) for blood and feather samples from yellow-eyed penguins breeding on Enderby Island

	Blood		Feathers	
	$\delta^{15}\text{N}$	$\delta^{13}\text{C}$	$\delta^{15}\text{N}$	$\delta^{13}\text{C}$
Min	10.28	-20.99	10.98	-19.01
Max	11.40	-20.10	12.75	-17.58
Difference	1.12	0.89	1.77	1.43
Mean	10.69	-20.50	11.78	-18.40
SD	0.40	0.28	0.38	0.32

from 25 birds collected from 2015 to 2017 and representing diet years 2014 ( $n = 10$ ), 2015 ( $n = 23$ ) and 2016 ( $n = 20$ ). Included in the feather samples were seven birds sampled in all three years, 14 birds sampled in two different years, and four birds sampled in a single year only. SIA data were matched with 22 dive logs, including 15 benthic and seven pelagic foraging trips (Muller et al., 2020a). A comparison ( $n = 9$  pairs) was also made between blood and feathers representing the 2015 diet year (Figure S1). Foraging data were analysed in detail in concurrent studies (Muller et al., 2020a; Muller et al., 2021). Summary data are provided for each individual bird (Table S1).

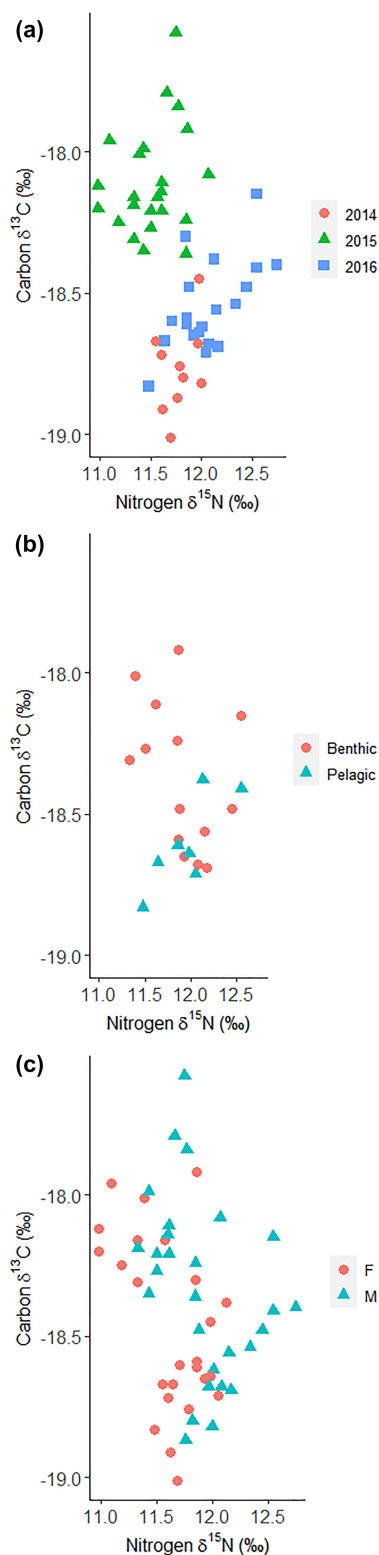
### 3.2 | Blood versus feathers

The nitrogen ( $\delta^{15}\text{N}$ ) values for blood and feathers had a range of 1.1 and 1.8‰, respectively, and the carbon ( $\delta^{13}\text{C}$ ) values had a range of 0.9 and 1.4‰, respectively (Tables 1, S1). Blood SIA values generally followed a similar trend to feather samples from the same diet year, but were offset lower. This was the case for all  $\delta^{13}\text{C}$  and most  $\delta^{15}\text{N}$  measures (Figure S1). General linear models comparing isotope values confirmed that blood and feather samples were significantly different for both  $\delta^{15}\text{N}$  ( $t = 8.278$ ,  $P = 1.31\text{e-}11$ ) and  $\delta^{13}\text{C}$  ( $t = 19.62$ ,  $P < 2\text{e-}16$ ). Therefore, although their trends were similar, SIA results for blood and feathers needed to be considered separately. Since blood was collected only in 2015, feather samples were analysed to compare diet with other factors between multiple years, although feathers were not available for the final breeding year.

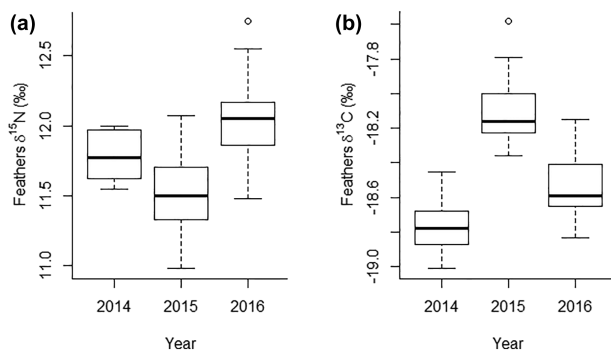
### 3.3 | Isotope analysis

The  $\delta^{15}\text{N}$  isotope values were lowest in 2015 (Figures 2a and 3a). General linear models comparing nitrogen isotope values showed that all were significantly different between years; 2016 and 2015 were both significantly different from 2014 ( $t = 2.717$ ,  $P = 0.00897$ , and  $t = -2.521$ ,  $P = 0.01486$  respectively), and 2014 and 2015 were both significantly different from 2016 ( $t = -2.717$ ,  $P = 0.00897$ , and  $t = -6.623$ ,  $P = 2.14\text{e-}08$  respectively). A linear mixed effects model with bird ID as a random effect (to account for individual birds' preferences as a potential confounding effect) had the same result, with a significant difference between years ( $\chi^2 = 114.73$ ,  $P < 2.2\text{e-}16$ ).

The  $\delta^{13}\text{C}$  isotope values were the inverse of nitrogen values, and were highest in 2015 (Figure 2a, Figure 3a). General linear models comparing carbon isotope values showed that all years were significantly different; 2016 and 2015 were both significantly different from 2014 ( $t = 3.417$ ,  $P = 0.00125$ , and  $t = 10.089$ ,  $P = 9.53\text{e-}14$ ), and 2014 and 2015 were both significantly different from 2016 ( $t = -3.417$ ,  $P = 0.00125$ , and  $t = 8.312$ ,  $P = 4.74\text{e-}11$  respectively). A linear mixed effects model with bird ID as a random effect (to account for individual bird's preferences as a potential confounding effect) also found that year was significant ( $\chi^2 = 230.06$ ,  $P < 2.2\text{e-}16$ ).



**FIGURE 2** Comparison of stable isotope analysis results extracted from feathers for different groups of foraging yellow-eyed penguins, breeding on Enderby Island in the New Zealand subantarctic ( $n = 54$  birds). Results show nitrogen ( $\delta^{15}\text{N}$ ) and carbon ( $\delta^{13}\text{C}$ ) isotopes in ‰ for: (a) the diet year when feather samples were formed (during the pre-moult period); (b) birds conducting different dive types (benthic or pelagic) as per Muller et al. (2020a); and (c) for birds of different sex



**FIGURE 3** Comparison of stable isotope analysis results extracted from feathers for foraging yellow-eyed penguins breeding on Enderby Island in the New Zealand subantarctic ( $n = 54$  birds) in different diet years (when feathers were formed), showing isotopes in ‰ for: (a) nitrogen  $\delta^{15}\text{N}$  (left); and (b) carbon  $\delta^{13}\text{C}$  (right). N and C values in all years were significantly different from each other

A general linear model comparing  $\delta^{15}\text{N}$  isotope values with foraging type (Figure 2b) was not significant ( $t = 0.492$ ,  $P = 0.628$ ); however, sex was significant ( $t = -2.795$ ,  $P = 0.00725$ ), with males tending towards larger  $\delta^{15}\text{N}$  values (Figure 2c). This was not the case when only blood samples were analysed, with no significant difference evident between sexes in this case ( $t = 1.432$ ,  $P = 0.19$ ), although sample sizes were much smaller ( $n = 5$  males and 5 females for blood sample analysis). While carbon  $\delta^{13}\text{C}$  isotope values were generally lower for benthic foragers (Figure 2b) and some males tended towards smaller (less negative)  $\delta^{13}\text{C}$  values (Figure 2c), these values were not significantly different for either foraging type ( $t = -2.069$ ,  $P = 0.0517$ ) or sex ( $t = -1.403$ ,  $P = 0.167$ ). Individual bird ID (as a random effect) significantly improved the linear mixed effects model fit for  $\delta^{15}\text{N}$  ( $\chi^2 = 11.097$ ,  $P = 0.0008647$ ), and  $\delta^{13}\text{C}$  ( $\chi^2 = 7.9297$ ,  $P = 0.004863$ ).

General linear models comparing isotope values with foraging distances in 2016 (Table S1) showed that foraging distance (maximum distance offshore) had no significant effect on  $\delta^{15}\text{N}$  ratios ( $t = -2.083$ ,  $P = 0.0561$ ); however, the total foraging distance (cumulative distance travelled) did have a significant effect on  $\delta^{15}\text{N}$  ( $t = -2.162$ ,  $P = 0.0484$ ). Neither maximum distance nor cumulative distance travelled had a significant effect on  $\delta^{13}\text{C}$  ( $t = -1.031$ ,  $P = 0.32$ ,  $t = -0.48$ ,  $P = 0.638$  respectively). Distance and year could not be tested in the same model since there was only one year where both GPS and SIA data were available (2016).

## 4 | DISCUSSION

Significant differences were evident in the isotope ratios of both nitrogen and carbon in different breeding seasons, indicating dietary shifts by foraging yellow-eyed penguins. The models including bird ID were a better fit, implying that individual diet preferences were present for both nitrogen (approximating trophic level) and carbon (approximating foraging location) isotopes.

### 4.1 | Blood versus feathers comparison

Isotope values for blood and feathers followed similar trends to each other; however, all  $\delta^{13}\text{C}$  and most  $\delta^{15}\text{N}$  blood values were significantly lower than feather samples from the same diet year (Figure S1), meaning that they could not be grouped together for analysis. This is consistent with Cherel, Hobson & Hassani (2005) who found significantly lower isotope values for blood compared to feathers in all penguin species studied, and is due to fractionation differences, which mean that SIA signatures of feathers are typically enriched relative to blood for many seabird species (Ogden, Hobson & Lank, 2004; Quillfeldt et al., 2008; Bond & Jones, 2009).

### 4.2 | Nitrogen 15 analysis (trophic level)

Isotopic ratios of nitrogen ( $^{15}\text{N}/^{14}\text{N}$ ) represent the trophic level at which an animal is feeding (DeNiro & Epstein, 1981; Bodey, Bearhop & McDonald, 2011), with fish being a higher trophic level to cephalopods to zooplankton prey (Owens, 1988; Hobson, Piatt & Pitocchelli, 1994). The  $\delta^{15}\text{N}$  isotope levels of prey obtained by breeding yellow-eyed penguins in the subantarctic were significantly different in each year, indicating that penguins consumed differing proportions of prey from different trophic levels in different breeding seasons. A change of  $\delta^{15}\text{N}$  isotope levels of around 2.3–3.4‰ is considered to represent a change in trophic level (McCutchan et al., 2003). The  $\delta^{15}\text{N}$  results had a range of 1.8‰ for feathers, which was lower than this threshold, meaning that the variability in the diet of yellow-eyed penguins probably relates to differing amounts of prey from each trophic level rather than comprehensive switches between trophic levels.

The trophic level inferred from nitrogen isotope levels was not significantly affected by dive type, implying that benthic and pelagic foragers were generally feeding at similar trophic levels. There was also no significant effect from the maximum foraging distance away from the colony, indicating that there was no consistent correlation between distance from the colony and the availability of different trophic level prey. However, the trophic level was affected by the cumulative total foraging distance (length of trip), implying that birds undertaking trips of longer total distance may have been targeting prey at a different trophic level.

Nitrogen isotope levels were also affected by sex, with females having a lower  $\delta^{15}\text{N}$  value implying feeding at a lower trophic level or consuming greater amounts of lower trophic level prey. However, sex was not significant when only blood samples were analysed. The variances in feather and blood samples were similar (0.14 and 0.16, respectively) so this is unlikely to have influenced this result; however, the sample size for blood was smaller so may not have been representative. There is no evidence for different diving behaviour between sexes from mainland New Zealand (Seddon & van Heezik, 1990; Moore, 1999; Mattern et al., 2007). This is also true in the subantarctic, although some individual birds of each sex may consistently use benthic foraging in preference to other methods

(Muller et al., 2020a), and females may use a larger foraging area during the guard phase (Muller et al., 2021). These foraging trends suggest that some females in the southern population may target different prey species (or differing amounts of each species) than males.

### 4.3 | Carbon 13 analysis (foraging location)

Isotopic ratios of carbon ( $^{13}\text{C}/^{12}\text{C}$ ) can be used to infer foraging location, differentiating between inshore versus offshore and benthic versus pelagic feeding (Kelly, 2000; Cherel et al., 2007). The  $\delta^{13}\text{C}$  isotope levels of prey obtained by breeding yellow-eyed penguins in the subantarctic were significantly different in all years, implying that penguins were feeding at different locations or on prey with different carbon inputs in different breeding seasons. While this implies changing foraging locations, carbon inputs in the same physical location may also be influenced by ocean currents bringing varying amounts of nutrients (Cherel & Hobson, 2007). The  $\delta^{13}\text{C}$  isotope levels were highest (less negative) in 2015, indicating that foraging was associated with more inshore and benthic habitats during this severe El Niño season. This is consistent with the higher proportion of benthic foraging trips evident in 2015 (Muller et al., 2020a). Carbon isotope levels were not affected by the maximum foraging distance away from the colony, or the cumulative foraging distance (length of trip). There was also no difference evident between sexes or dive types.

### 4.4 | Diet plasticity

Dietary partitioning has also been demonstrated in other penguin species using SIA analysis. SIA of blood from breeding Adélie penguins was able to distinguish between prey at a broad taxonomic level (e.g. fish vs. krill), and this was confirmed by stomach contents analysis (Tierney et al., 2008). They also found that diet composition changed during the breeding season. SIA demonstrated broad diet composition (e.g. fish, cephalopod, crustacean) in little blue penguins, with greater accuracy than stomach sampling (Flemming & van Heezik, 2014). In that study, blood isotopes had narrower confidence intervals but also mirrored trends for feathers.

Yellow-eyed penguins are predominantly benthic divers in the northern population (Mattern et al., 2007; Mattern et al., 2013; Chilvers, Dobbins & Edmonds, 2014). The greater variability in diet at Enderby Island was also consistent with greater plasticity in diving and foraging behaviour, with significant proportions of pelagic diving, probably influenced by different foraging conditions affecting prey species availability and their distribution over time (Muller et al., 2020a).

In multiple trips recorded for the same individuals, the majority of birds (72%) displayed consistent foraging behaviour during multiple trips within a season (Muller et al., 2020a). This is also consistent with the significant differences evident in dietary stable isotopes when

individual bird ID was included as a factor, demonstrating that individual foraging preferences were maintained over the period while feathers were formed.

### 4.5 | Yellow-eyed penguin diet

The diet of the northern population consists primarily of demersal fish species. The main prey species in the 1980s by frequency eaten, were sprat (*Sprattus antipodum*), and by proportion of mass eaten, were red cod (*Pseudophycis bachus*) and opalfish (*Hemerocoetes* spp.), with smaller amounts of other fish species, and arrow squid (*Nototodarus sloanii*), other cephalopods and crustaceans (van Heezik, 1990a). There were considerable differences in diet between locations and years (van Heezik, 1990a). Later studies revealed a dietary shift to less feeding on red cod, and more blue cod (*Paraperchis colias*) along with opalfish (Moore & Wakelin, 1997; Mattern et al., 2017; Mattern & Ellenberg, 2018; Mattern & Wilson, 2018). Regional differences in diet composition are evident for the northern population, probably due to differing benthic habitat (Mattern & Ellenberg, 2018). Diet can also be influenced in regions exposed to disturbance caused by bottom trawls favouring scavenging species such as blue cod (Mattern et al., 2013), which can be more difficult for penguins to locate and capture (Mattern et al., 2018), and as a food source such prey may therefore be restricted to individuals with acquired foraging experience (Forslund & Pärt, 1995). In the northern population, larval fish, gelata and other mid-water species were targeted during short periods of pelagic foraging but only when poor visibility prevented benthic foraging (Mattern et al., 2017; Mattern et al., 2018; Mattern & Ellenberg, 2018).

Diet composition of the southern population was unknown prior to this study. Consequently, there is no information on subantarctic prey species targeted by yellow-eyed penguins. Furthermore, many of the northern prey species do not occur in the subantarctic. Diet of the northern population includes juveniles of some commercial species (van Heezik, 1990a; van Heezik, 1990b; Moore & Wakelin, 1997; Browne et al., 2011) and this may also be the case in the subantarctic (Table S2). Diversity of reef fishes is negatively correlated with latitude, and the subantarctic Auckland and Campbell Islands have a low diversity of reef fishes compared to other New Zealand ecosystems (Francis, 1996), which would be expected to reduce the number of benthic fish species available as a food resource for penguins (Table S2). Benthic diving occurs at Campbell Island (P. Moore, personal communication), with pelagic dives possible but not confirmed there, and prey species similarly unknown.

Future SIA work in the subantarctic would benefit from a reference collection of yellow-eyed penguin prey species and determination of their isotopic signatures, enabling the use of mixing models to estimate relative contributions of specific prey types. Faecal DNA analysis can also assist with identifying diet to species level (Young et al., 2020), provided suitable logistics can be arranged for DNA samples to be transported to New Zealand for analysis. In combination with data on foraging area and diving behaviour from

GPS/time depth recorder device deployment (Muller et al., 2020a; Muller et al., 2021), this could provide more detailed information on yellow-eyed penguin foraging ecology in the face of climate change.

#### 4.6 | Breeding success

Adult seabirds may be able to compensate for declining availability of high-energy prey by bringing back a larger volume of prey (Suryan, Irons & Benson, 2000; Litzow et al., 2002). However, declining diet quality has been linked to selective provisioning and poor reproductive success of yellow-eyed penguins on Stewart and Codfish Islands in the northern population (Browne et al., 2011). Stable isotope analysis has shown that poorer chick nutrition was associated with unsuccessful foraging trips by parents, as well as prey species having a lower energetic content, or being unsuitable for chicks to eat (Browne et al., 2011). Larger food items are less suitable for feeding to chicks, and can result in poorer nutritional outcomes (Moore & Wakelin, 1997; Mattern et al., 2017; Mattern & Ellenberg, 2018), and a corresponding reduction in breeding success (Browne et al., 2011; Mattern & Ellenberg, 2018). However, there is no evidence that prey size is an issue for chick nutrition in the southern population.

The amount and distribution of many fish species around New Zealand are affected by water temperature, with warmer water leading to lower recruitment and subsequent biomass (Francis, 1996; Beentjes & Renwick, 2001), and increasing water temperature since the mid-1990s has been implicated in reduced survival rates and population decline for the northern yellow-eyed penguin population (Mattern et al., 2017).

#### 4.7 | Climate

In New Zealand waters, El Niño corresponds to a cooler and wetter climate, with implications for many marine species including yellow-eyed penguins (see Peacock, Paulin & Darby, 2000 for review). In the northern population, colder temperatures (including air and sea surface temperatures) and wetter conditions are generally more favourable for breeding success (Peacock, Paulin & Darby, 2000; Darby, 2003), and warmer conditions, such as warm water events associated with La Niña, generally result in poorer and more variable breeding success outcomes (Moore & Wakelin, 1997; Young, 2014; Mattern et al., 2017). High air temperatures around mainland New Zealand can also subject nesting birds to heat stress, which can affect breeding success (Seddon & Davis, 1989; Clark, Mathieu & Seddon, 2015). This study suggests that subantarctic populations may differ from the mainland, and El Niño conditions may be less productive or even detrimental to breeding success. However, it may also be the case that any severe climate effects are detrimental, regardless of type.

El Niño conditions were present in 2014 (weak) and 2015 (severe), and both 2016 and 2017 were mild La Niña years

(Null, 2019). At Enderby Island, the  $\delta^{15}\text{N}$  isotope levels were lowest in 2015, suggesting that birds were feeding more on lower trophic level prey during this severe El Niño season, and levels were highest in 2016 during mild La Niña conditions. Lower trophic level prey generally have a lower energy content than prey of higher trophic level (Meynier et al., 2008), which indicates poorer-value prey during the El Niño conditions in 2015. Stable isotope analysis of carbon indicated foraging (based on prey species composition) was on average closer to shore and more benthic in 2015 than in 2016 or 2017. This corresponded with a high incidence of benthic foraging recorded for subantarctic yellow-eyed penguins in 2015 (Muller et al., 2020a), and a lower breeding population and breeding attempts during El Niño conditions these years (Muller et al., 2020b).

Studies on many prey species have shown poorer recruitment and lower biomass related to periods of warmer water, including for red cod (Beentjes & Renwick, 2001), an important part of the diet of the northern population, and for southern blue whiting, an important species in subantarctic fisheries (Hanchet & Renwick, 1999). Southern blue whiting are also negatively affected by other weather events in the subantarctic (Willis, Fu & Hanchet, 2007). Our study indicates that diet and foraging for the southern yellow-eyed penguin population are variable, and may also be affected by ENSO index, with implications for breeding success.

These results corresponded to poorer breeding success during the severe El Niño in 2015, and also the La Niña in 2017, but positive breeding success during a weak La Niña in 2016 (Muller et al., 2020b). Since weather conditions can be more severe in the subantarctic (Eden, 1955; Higham, 1991), it may be that individual weather events play a more significant role than ENSO state in the region, although climate changes that lead to an increase in number or severity of severe weather events would be expected to have a detrimental effect on yellow-eyed penguin population stability.

#### 4.8 | Conservation considerations

In addition to direct impact on individual foraging success, climate effects can also increase the pressure on a population rendering it less able to respond to non-climate related impacts, such as fisheries interactions, habitat degradation, human disturbance, and prey availability, which have all been implicated in declines in the northern yellow-eyed penguin population (Mattern et al., 2017). This study demonstrates that yellow-eyed penguin diet is variable in the subantarctic, probably influenced by local climatic conditions including ENSO. Diet during El Niño conditions comprised lower trophic level and more benthic prey, and during La Niña conditions was more pelagic and associated with greater foraging distances. By implication, prey availability is probably also a limiting factor in this region in some years, and therefore a major influencer of future survival and breeding success. This could be exacerbated if the effects of climate change become more pronounced as predicted (Easterling et al., 2000; Ramírez et al., 2017). Therefore, the findings of this study suggest that poor breeding seasons driven by reduced prey availability could

become more common in the future. Subantarctic yellow-eyed penguins are also vulnerable to other threats such as nest predation on islands with introduced predators, potential negative interactions with commercial fisheries in the area, including resource competition as well as adult mortality, and to catastrophic events such as oil spills (Muller et al., 2020b), all of which could compound the effects of a poor breeding season. Unlike in the northern population, logistical constraints largely prevent direct intervention in the subantarctic to rehabilitate individual adults or chicks in poor condition. As a result, intervention is likely to be only possible at a population level to attempt to mitigate large-scale threats. Therefore, ongoing future monitoring of population and breeding success is needed to identify declines and allow intervention as soon as possible. Any potential threats to yellow-eyed penguin survival and foraging need to be investigated in greater detail, and if necessary, pre-emptive interventions made to ensure they do not become a significant contributor to declines in yellow-eyed penguin foraging efficiency or population. The isotope signatures collected for this study provide a foundation to match with the SIA signatures of individual prey species, and this could be expanded on by the use of DNA diet analysis to identify prey species around the Auckland Islands archipelago. This is a key step to understanding the distribution of prey species in space and time, in order to model and predict future constraints on food availability. Future management of the species will benefit from greater knowledge of all potential threats to foraging success, and therefore also to breeding success and population stability.

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#### CONFLICT OF INTEREST

The authors declare no conflict of interest. All authors reviewed the manuscript and gave final approval for publication.

#### DATA AVAILABILITY STATEMENT

Summarized data that support the findings of this study are available in the Supplementary Materials for this paper. Raw data are available from the corresponding author upon reasonable request.

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#### REFERENCES

- Adams, N.J. & Brown, C.R. (1990). Energetics of molt in penguins. In: L.S. Davis, J.T. Darby (Eds.) *Penguin Biology*, Vol. Penguin Biology. London, UK: Academic Press.
- Ainley, D.G., Ballard, G., Barton, K.J., Karl, B.J., Rau, G.H., Ribic, C.A. et al. (2003). Spatial and temporal variation of diet within a presumed metapopulation of Adélie penguins. *Condor*, 105(1), 95–106. [https://doi.org/10.1650/0010-5422\(2003\)105\[95:SATVOD\]2.0.CO;2](https://doi.org/10.1650/0010-5422(2003)105[95:SATVOD]2.0.CO;2)
- Amélineau, F., Saraux, C., Ropert-Coudert, Y., Kato, A., Hobson, K.A., Raymond, B. et al. (2021). Intra- and inter-individual changes in little penguin diving and isotopic composition over the breeding season. *Marine Biology*, 168(5), 62. <https://doi.org/10.1007/s00227-021-03867-2>
- Bates, D., Maechler, M., Bolker, B. & Walker, S. (2015). Fitting linear mixed-effects models using lme4. *Journal of Statistical Software*, 67, 1–48. Available at: <https://arxiv.org/abs/1406.5823>
- Bearhop, S., Phillips, R.A., McGill, R., Cherel, Y., Dawson, D.A. & Croxall, J.P. (2006). Stable isotopes indicate sex-specific and long-term individual foraging specialisation in diving seabirds. *Marine Ecology Progress Series*, 311, 157–164. <https://doi.org/10.3354/meps311157>
- Bearhop, S., Waldron, S., Votier, S.C. & Furness, R.W. (2002). Factors that influence assimilation rates and fractionation of nitrogen and carbon stable isotopes in avian blood and feathers. *Physiological and Biochemical Zoology*, 75(5), 451–458. <https://doi.org/10.1086/342800>
- Beentjes, M.P. & Renwick, J.A. (2001). The relationship between red cod, *Pseudophycis bachus*, recruitment and environmental variables in New Zealand. *Environmental Biology of Fishes*, 61(3), 315–328. <https://doi.org/10.1023/A:1010943906264>
- Birdlife International. (2020). *Megadyptes antipodes* (Yellow-eyed Penguin). IUCN Red List of Threatened Species. Available at: <http://www.iucnredlist.org> [Accessed 24 February 2021].
- Birt, V.L., Birt, T.P., Goulet, D., Cairns, D.K. & Montevecchi, W.A. (1987). Ashmole's halo: Direct evidence for prey depletion by a seabird. *Marine Ecology Progress Series*, 40(3), 205–208. <https://doi.org/10.3354/meps040205>
- Bodey, T., Bearhop, S. & McDonald, R. (2011). Invasions and stable isotope analysis—informing ecology and management. In: *Island Invasives: Eradication and Management*. Gland, Switzerland: IUCN, pp. 148–151.
- Boersma, P.D. & Rebstock, G.A. (2009). Foraging distance affects reproductive success in Magellanic penguins. *Marine Ecology Progress Series*, 375, 263–275. <https://doi.org/10.3354/meps07753>
- Boessenkool, S., Star, B., Waters, J.M. & Seddon, P.J. (2009). Multilocus assignment analyses reveal multiple units and rare migration events in the recently expanded yellow-eyed penguin (*Megadyptes antipodes*). *Molecular Ecology*, 18(11), 2390–2400. <https://doi.org/10.1111/j.1365-294X.2009.04203.x>
- Bond, A.L. & Jones, I.L. (2009). A practical introduction to stable-isotope analysis for seabird biologists: Approaches, cautions and caveats. *Marine Ornithology*, 37(3), 183–188. Available at: <http://research.library.mun.ca/id/eprint/565>

- Borboroglu, P. & Boersma, P. (2013). *Penguins: Natural History and Conservation*. Seattle: University of Washington Press.
- Browne, T., Lalas, C., Mattern, T. & Van Heezik, Y. (2011). Chick starvation in yellow-eyed penguins: Evidence for poor diet quality and selective provisioning of chicks from conventional diet analysis and stable isotopes. *Austral Ecology*, 36(1), 99–108. <https://doi.org/10.1111/j.1442-9993.2010.02125.x>
- Cherel, Y. & Hobson, K.A. (2007). Geographical variation in carbon stable isotope signatures of marine predators: A tool to investigate their foraging areas in the Southern Ocean. *Marine Ecology Progress Series*, 329, 281–287. <https://doi.org/10.3354/meps329281>
- Cherel, Y., Hobson, K.A., Guinet, C. & Vanpe, C. (2007). Stable isotopes document seasonal changes in trophic niches and winter foraging individual specialization in diving predators from the Southern Ocean. *Journal of Animal Ecology*, 76(4), 826–836. <https://doi.org/10.1111/j.1365-2656.2007.01238.x>
- Cherel, Y., Hobson, K.A. & Hassani, S. (2005). Isotopic discrimination between food and blood and feathers of captive penguins: Implications for dietary studies in the wild. *Physiological and Biochemical Zoology: Ecological and Evolutionary Approaches*, 78(1), 106–115. <https://doi.org/10.1086/425202>
- Cherel, Y., Hobson, K.A. & Weimerskirch, H. (2000). Using stable-isotope analysis of feathers to distinguish moulting and breeding origins of seabirds. *Oecologia*, 122(2), 155–162. <https://doi.org/10.1007/PL00008843>
- Cherel, Y. & Ridoux, V. (1992). Prey species and nutritive-value of food fed during summer to King Penguin *Aptenodytes patagonica* chicks at Possession Island, Crozet Archipelago. *Ibis*, 134(2), 118–127. <https://doi.org/10.1111/j.1474-919X.1992.tb08388.x>
- Chilvers, B.L. (2017a). Comparison of New Zealand's little blue penguins, *Eudyptula minor*, diving behaviour. *Polar Biology*, 40(10), 1965–1974. <https://doi.org/10.1007/s00300-017-2112-5>
- Chilvers, B.L. (2017b). Stable isotope signatures of whisker and blood serum confirm foraging strategies for female New Zealand sea lions (*Phocarctos hookeri*) derived from telemetry. *Canadian Journal of Zoology*, 95(12), 955–963. <https://doi.org/10.1139/cjz-2016-0299>
- Chilvers, B.L., Dobbins, M.L. & Edmonds, H.K. (2014). Diving behaviour of yellow-eyed penguins, Port Pegasus/Pikihati, Stewart Island/Rakiura, New Zealand. *New Zealand Journal of Zoology*, 41(3), 161–170. <https://doi.org/10.1080/03014223.2014.908931>
- Chilvers, B.L. & Wilkinson, I.S. (2009). Diverse foraging strategies in lactating New Zealand sea lions. *Marine Ecology Progress Series*, 378, 299–308. <https://doi.org/10.3354/meps07846>
- Clark, R.D., Mathieu, R. & Seddon, P.J. (2015). Selection for protection from insolation results in the visual isolation of Yellow-eyed Penguin *Megadyptes antipodes* nests. *Bird Conservation International*, 25(2), 192–206. <https://doi.org/10.1017/S0959270914000082>
- Clarke, A. & Prince, P.A. (1980). Chemical composition and calorific value of food fed to mollymauk chicks *Diomedea melanophrys* and *Diomedea chrysostoma* at Bird Island, South Georgia. *Ibis*, 122(4), 488–494. <https://doi.org/10.1111/j.1474-919X.1980.tb00903.x>
- Collins, M., Knutti, R., Arblaster, J., Dufresne, J.-L., Fichetef, T., Friedlingstein, P. et al. (2013). Long-term climate change: projections, commitments and irreversibility. In: *Climate Change 2013-The Physical Science Basis: Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change*. Cambridge University Press, pp. 1029–1136.
- Costa, D.P., Kuhn, C.E., Weise, M.J., Shaffer, S.A. & Arnould, J.P.Y. (2004). When does physiology limit the foraging behaviour of freely diving mammals? *International Congress Series*, 1275, 359–366. <https://doi.org/10.1016/j.ics.2004.08.058>
- Couch-Lewis, Y., McKinlay, B., Murray, S. & Edge Hill, K.-A. (2016). Yellow-eyed penguin stock-take report - he pūrongo mō te hoiho - a report of progress against the hoiho recovery plan (Department of Conservation, 2000) objectives and actions. Retrieved from Dunedin, New Zealand.
- Crawford, R.J.M., Makhado, A.B., Upfold, L. & Dyer, B.M. (2008). Mass on arrival of rockhopper penguins at Marion Island correlated with breeding success. *African Journal of Marine Science*, 30(1), 185–188. <https://doi.org/10.2989/AJMS.2008.30.1.19.469>
- Croxall, J., Reid, K. & Prince, P. (1999). Diet, provisioning and productivity responses of marine predators to differences in availability of Antarctic krill. *Marine Ecology Progress Series*, 177, 115–131. <https://doi.org/10.3354/meps177115>
- Cury, P.M., Boyd, I.L., Bonhommeau, S., Anker-Nilssen, T., Crawford, R.J. M., Furness, R.W. et al. (2011). Global seabird response to forage fish depletion: One-third for the birds. *Science*, 334(6063), 1703–1706. <https://doi.org/10.1126/science.1212928>
- Darby, J.T. (2003). The yellow-eyed penguin (*Megadyptes antipodes*) on Stewart and Codfish Islands. *Notornis*, 50(3), 148–154.
- Deagle, B.E., Chiaradia, A., McInnes, J. & Jarman, S.N. (2010). Pyrosequencing faecal DNA to determine diet of little penguins: Is what goes in what comes out? *Conservation Genetics*, 11(5), 2039–2048. <https://doi.org/10.1007/s10592-010-0096-6>
- DeNiro, M.J. & Epstein, S. (1978). Influence of diet on the distribution of carbon isotopes in animals. *Geochimica et Cosmochimica Acta*, 42(5), 495–506. [https://doi.org/10.1016/0016-7037\(78\)90199-0](https://doi.org/10.1016/0016-7037(78)90199-0)
- DeNiro, M.J. & Epstein, S. (1981). Influence of diet on the distribution of nitrogen isotopes in animals. *Geochimica et Cosmochimica Acta*, 45(3), 341–351. [https://doi.org/10.1016/0016-7037\(81\)90244-1](https://doi.org/10.1016/0016-7037(81)90244-1)
- Department of Conservation. (2020). *Te Kaweka Takohaka mō te Hoiho - A strategy to support the ecological and cultural health of hoiho*. Retrieved from Wellington, New Zealand.
- Duffy, D.C. & Jackson, S. (1986). Diet studies of seabirds: A review of methods. *Colonial Waterbirds*, 9(1), 1–17. <https://doi.org/10.2307/1521138>
- Easterling, D.R., Meehl, G.A., Parmesan, C., Changnon, S.A., Karl, T.R. & Mearns, L.O. (2000). Climate extremes: Observations, modeling, and impacts. *Science*, 289(5487), 2068–2074. <https://doi.org/10.1126/science.289.5487.2068>
- Eden, A.W. (1955). *Islands of despair: Being an account of a survey expedition to the sub-antarctic islands of New Zealand*: Andrew Melrose.
- Emlen, J.M. (1966). The role of time and energy in food preference. *The American Naturalist*, 100(916), 611–617. <https://doi.org/10.1086/282455>
- Flemming, S.A. & van Heezik, Y. (2014). Stable isotope analysis as a tool to monitor dietary trends in little penguins *Eudyptula minor*. *Austral Ecology*, 39(6), 656–667. <https://doi.org/10.1111/aec.12128>
- Forero, M.G., Hobson, K.A., Bortolotti, G.R., Donazar, J.A., Bertelotti, M. & Blanco, G. (2002). Food resource utilisation by Magellanic penguin evaluated through stable isotope analysis: Segregation by sex and age and influence of offspring quality. *Marine Ecology Progress Series*, 234, 289–299. <https://doi.org/10.3354/meps234289>
- Forslund, P. & Pärt, T. (1995). Age and reproduction in birds – hypotheses and tests. *Trends in Ecology & Evolution*, 10(9), 374–378. [https://doi.org/10.1016/S0169-5347\(00\)89141-7](https://doi.org/10.1016/S0169-5347(00)89141-7)
- Francis, M.P. (1996). Geographic distribution of marine reef fishes in the New Zealand region. *New Zealand Journal of Marine and Freshwater Research*, 30(1), 35–55. <https://doi.org/10.1080/00288330.1996.9516695>
- Hanchet, S. & Renwick, J. (1999). New Zealand fisheries assessment research document 99/55.
- Haramis, G.M., Jorde, D.G., Macko, S.A. & Walker, J.L. (2001). Stable-isotope analysis of Canvasback winter diet in upper Chesapeake Bay. *The Auk*, 118(4), 1008–1017. <https://doi.org/10.1093/auk/118.4.1008>
- Higham, T. (1991). *New Zealand's subantarctic islands: A guidebook*. Wellington, New Zealand: Southland Conservancy, Department of Conservation.
- Hobson, K.A. & Clark, R.G. (1992a). Assessing avian diets using stable isotopes I: Turnover of <sup>13</sup>C in tissues. *Condor*, 94(1), 181–188. <https://doi.org/10.2307/1368807>

- Hobson, K.A. & Clark, R.G. (1992b). Assessing avian diets using stable isotopes II: Factors influencing diet-tissue fractionation. *Condor*, 94(1), 189–197. <https://doi.org/10.2307/1368808>
- Hobson, K.A., Piatt, J.F. & Pitocchelli, J. (1994). Using stable isotopes to determine seabird trophic relationships. *Journal of Animal Ecology*, 63(4), 786–798. <https://doi.org/10.2307/5256>
- Inchausti, P., Guinet, C., Koudil, M., Durbec, J.-P., Barbraud, C., Weimerskirch, H. et al. (2003). Inter-annual variability in the breeding performance of seabirds in relation to oceanographic anomalies that affect the Crozet and the Kerguelen sectors of the Southern Ocean. *Journal of Avian Biology*, 34(2), 170–176. <https://doi.org/10.1034/j.1600-048X.2003.03031.x>
- Jodice, P.G.R., Roby, D.D., Turco, K.R., Suryan, R.M., Irons, D.B., Piatt, J.F. et al. (2006). Assessing the nutritional stress hypothesis: Relative influence of diet quantity and quality on seabird productivity. *Marine Ecology Progress Series*, 325, 267–279. <https://doi.org/10.3354/meps325267>
- Kelly, J.F. (2000). Stable isotopes of carbon and nitrogen in the study of avian and mammalian trophic ecology. *Canadian Journal of Zoology*, 78(1), 1–27. <https://doi.org/10.1139/z99-165>
- Keymer, I.F., Malcolm, H.M., Hunt, A. & Horsley, D.T. (2001). Health evaluation of penguins (Sphenisciformes) following mortality in the Falklands (South Atlantic). *Diseases of Aquatic Organisms*, 45(3), 159–169. <https://doi.org/10.3354/dao045159>
- Litzow, M.A., Piatt, J.F., Prichard, A.K. & Roby, D.D. (2002). Response of pigeon guillemots to variable abundance of high-lipid and low-lipid prey. *Oecologia*, 132(2), 286–295. <https://doi.org/10.1007/s00442-002-0945-1>
- MacArthur, R.H. & Pianka, E.R. (1966). On optimal use of a patchy environment. *The American Naturalist*, 100(916), 603–609. <https://doi.org/10.1086/282454>
- Mattern, T. (2006). Marine ecology of offshore and inshore foraging penguins: The snares penguin and yellow-eyed penguin. (PhD thesis), University of Otago, New Zealand. (June)
- Mattern, T. & Ellenberg, U. (2018). Yellow-eyed penguin diet and indirect effects affecting prey composition - collation of biological information. Retrieved from Wellington, New Zealand.
- Mattern, T., Ellenberg, U., Houston, D.M. & Davis, L.S. (2007). Consistent foraging routes and benthic foraging behaviour in yellow-eyed penguins. *Marine Ecology Progress Series*, 343, 295–306. <https://doi.org/10.3354/meps06954>
- Mattern, T., Ellenberg, U., Houston, D.M., Lamare, M., Davis, L.S., Van Heezik, Y. et al. (2013). Straight line foraging in yellow-eyed penguins: New insights into cascading fisheries effects and orientation capabilities of marine predators. *PLoS ONE*, 8(12), e84381. <https://doi.org/10.1371/journal.pone.0084381>
- Mattern, T., McPherson, M.D., Ellenberg, U., van Heezik, Y. & Seddon, P.J. (2018). High definition video loggers provide new insights into behaviour, physiology, and the oceanic habitat of a marine predator, the yellow-eyed penguin. *PeerJ*, 6, e5459. <https://doi.org/10.7717/peerj.5459>
- Mattern, T., Meyer, S., Ellenberg, U., Houston, D.M., Darby, J.T., Young, M. et al. (2017). Quantifying climate change impacts emphasises the importance of managing regional threats in the endangered Yellow-eyed penguin. *PeerJ*, 5, e3272. <https://doi.org/10.7717/peerj.3272>
- Mattern, T. & Wilson, K.J. (2018). New Zealand penguins - current knowledge and research priorities. Retrieved from Dunedin, New Zealand.
- McClung, M.R., Seddon, P.J., Massaro, M. & Setiawan, A.N. (2004). Nature-based tourism impacts on yellow-eyed penguins *Megadyptes antipodes*: Does unregulated visitor access affect fledging weight and juvenile survival? *Biological Conservation*, 119(2), 279–285. <https://doi.org/10.1016/j.biocon.2003.11.012>
- McCutchan, J.H., Lewis, W.M., Kendall, C. & McGrath, C.C. (2003). Variation in trophic shift for stable isotope ratios of carbon, nitrogen, and sulfur. *Oikos*, 102(2), 378–390. <https://doi.org/10.1034/j.1600-0706.2003.12098.x>
- Meynier, L., Morel, P., MacKenzie, D., MacGibbon, A., Chilvers, B.L. & Duignan, P.J. (2008). Proximate composition, energy content, and fatty acid composition of marine species from Campbell Plateau, New Zealand. *New Zealand Journal of Marine and Freshwater Research*, 42(4), 425–437. <https://doi.org/10.1080/00288330809509971>
- Moore, P., Fletcher, D. & Amey, J. (2001). Population estimates of Yellow-eyed Penguins, *Megadyptes antipodes*, on Campbell Island, 1987–98. *Emu*, 101(3), 225–236. <https://doi.org/10.1071/MU00037>
- Moore, P.J. (1992). Yellow-eyed penguin population estimates on Campbell and Auckland Islands 1987–90. *Notornis*, 39(1), 1–15.
- Moore, P.J. (1999). Foraging range of the yellow-eyed penguin *Megadyptes antipodes*. *Marine Ornithology*, 27(1–2), 56–58. Available at: <http://www.marineornithology.org/content/get.cgi?rn=423>
- Moore, P.J., Wakelin, M., Douglas, M.E., McKinlay, B., Nelson, D. & Murphy, B. (1995). Yellow-eyed penguin foraging study, South-Eastern New Zealand, 1991–1993. Retrieved from Wellington, New Zealand.
- Moore, P.J. & Wakelin, M.D. (1997). Diet of the yellow-eyed penguin *Megadyptes antipodes*, South Island, New Zealand, 1991–1993. *Marine Ornithology*, 25(1–2), 17–29. Available at: <http://www.marineornithology.org/content/get.cgi?rn=377>
- Moreno, E., Barbosa, A., de Leon, A. & Fargallo, J.A. (1999). Phenotypic selection on morphology at independence in the Chinstrap penguin *Pygoscelis antarctica*. *Journal of Evolutionary Biology*, 12, 507–513. <https://doi.org/10.1046/j.1420-9101.1999.00032.x>
- Muller, C.G., Chilvers, B.L., Barker, Z., Barnsdale, K.P., Battley, P.F., French, R.K. et al. (2019). Aerial VHF tracking of wildlife using an unmanned aerial vehicle (UAV): Comparing efficiency of yellow-eyed penguin (*Megadyptes antipodes*) nest location methods. *Wildlife Research*, 46(2), 145–153. <https://doi.org/10.1071/WR17147>
- Muller, C.G., Chilvers, B.L., French, R.K. & Battley, P.F. (2020a). Diving plasticity in the ancestral range of the yellow-eyed penguin, *Megadyptes antipodes*, an endangered marine predator. *Marine Ecology Progress Series*, 648, 191–205. <https://doi.org/10.3354/meps13415>
- Muller, C.G., Chilvers, B.L., French, R.K. & Battley, P.F. (2021). Foraging areas and plasticity of yellow-eyed penguins (*Megadyptes antipodes*) in their subantarctic range. *Marine Ecology Progress Series*, 679, 149–162. <https://doi.org/10.3354/meps13911>
- Muller, C.G., Chilvers, B.L., French, R.K., Hiscock, J.A. & Battley, P.F. (2020b). Population estimate for yellow-eyed penguins (*Megadyptes antipodes*) in the subantarctic Auckland Islands, New Zealand. *Notornis*, 67, 299–319.
- Null, J. (2019). El Niño and La Niña years and intensities. Available at: <https://ggweather.com/enso/oni.htm>
- Ogden, L.J.E., Hobson, K.A. & Lank, D.B. (2004). Blood Isotopic ( $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$ ) Turnover and Diet-Tissue Fractionation Factors in Captive Dunlin (*Calidris alpina pacifica*). *The Auk*, 121(1), 170–177. <https://doi.org/10.1093/auk/121.1.170>
- Olsson, O. (1997). Effects of food availability on fledging condition and post-fledging survival in king penguin chicks. *Polar Biology*, 18(3), 161–165. <https://doi.org/10.1007/s003000050172>
- Owens, N.J.P. (1988). Natural variations in  $^{15}\text{N}$  in the marine environment. In: J.H.S. Blaxter, A.J. Southward (Eds.) *Advances in Marine Biology*, Vol. 24: Academic Press, pp. 389–451.
- Peacock, L., Paulin, M. & Darby, J. (2000). Investigations into climate influence on population dynamics of yellow-eyed penguins *Megadyptes antipodes*. *New Zealand Journal of Zoology*, 27(4), 317–325. <https://doi.org/10.1080/03014223.2000.9518241>

- Pearson, S.F., Levey, D.J., Greenberg, C.H. & Del Rio, C.M. (2003). Effects of elemental composition on the incorporation of dietary nitrogen and carbon isotopic signatures in an omnivorous songbird. *Oecologia*, 135(4), 516–523. <https://doi.org/10.1007/s00442-003-1221-8>
- Pelletier, L., Chiaradia, A., Kato, A. & Ropert-Coudert, Y. (2014). Fine-scale spatial age segregation in the limited foraging area of an inshore seabird species, the little penguin. *Oecologia*, 176(2), 399–408. <https://doi.org/10.1007/s00442-014-3018-3>
- Pütz, K. (1995). The post-moult diet of Emperor Penguins (*Aptenodytes forsteri*) in the eastern Weddell Sea, Antarctica. *Polar Biology*, 15(7), 457–463. <https://doi.org/10.1007/BF00237459>
- Quillfeldt, P., Bugoni, L., McGill, R.A.R., Masello, J.F. & Furness, R.W. (2008). Differences in stable isotopes in blood and feathers of seabirds are consistent across species, age and latitude: Implications for food web studies. *Marine Biology*, 155(6), 593–598. <https://doi.org/10.1007/s00227-008-1048-2>
- R. Core Team. (2017). R: a language and environment for statistical computing. Available at: <https://www.R-project.org/>
- Ramírez, F., Afán, I., Davis, L.S. & Chiaradia, A. (2017). Climate impacts on global hot spots of marine biodiversity. *Science Advances*, 3(2), e1601198. <https://doi.org/10.1126/sciadv.1601198>
- Seddon, P., Ellenberg, U. & Van Heezik, Y. (2013). The Yellow-eyed Penguin. In: G.P. Borboroglu, D. Boersma (Eds.) *Penguins: Natural History and Conservation*, Vol. 1. Seattle and London: University of Washington Press, pp. 90–110.
- Seddon, P.J. & Davis, L.S. (1989). Nest-Site Selection by Yellow-Eyed Penguins. *Condor*, 91(3), 653–659. <https://doi.org/10.2307/1368116>
- Seddon, P.J. & van Heezik, Y. (1990). Diving depths of the yellow-eyed penguin *Megadyptes antipodes*. *Emu*, 90(1), 53–57. <https://doi.org/10.1071/MU9900053>
- Setiawan, A.N., Darby, J.T. & Lambert, D.M. (2004). The use of morphometric measurements to sex yellow-eyed penguins. *Waterbirds*, 27(1), 96–101. [https://doi.org/10.1675/1524-4695\(2004\)027\[0096:TUOMMT\]2.0.CO;2](https://doi.org/10.1675/1524-4695(2004)027[0096:TUOMMT]2.0.CO;2)
- Shiffman, D., Gallagher, A., Boyle, M., Hammerschlag-Peyer, C. & Hammerschlag, N. (2012). Stable isotope analysis as a tool for elasmobranch conservation research: A primer for non-specialists. *Marine and Freshwater Research*, 63(7), 635–643. <https://doi.org/10.1071/MF11235>
- Suryan, R.M., Irons, D.B. & Benson, J. (2000). Prey switching and variable foraging strategies of black-legged kittiwakes and the effect on reproductive success. *The Condor*, 102(2), 374–384. <https://doi.org/10.1093/condor/102.2.374>
- Tierney, M., Southwell, C., Emmerson, L.M. & Hindell, M.A. (2008). Evaluating and using stable-isotope analysis to infer diet composition and foraging ecology of Adelie penguins *Pygoscelis adeliae*. *Marine Ecology Progress Series*, 355, 297–307. <https://doi.org/10.3354/meps07235>
- Tremblay, Y. & Cherel, Y. (2000). Benthic and pelagic dives: A new foraging behaviour in Rockhopper Penguins. *Marine Ecology Progress Series*, 204, 257–267. <https://doi.org/10.3354/meps204257>
- Tremblay, Y. & Cherel, Y. (2003). Geographic variation in the foraging behaviour, diet and chick growth of Rockhopper Penguins. *Marine Ecology Progress Series*, 251, 279–297. <https://doi.org/10.3354/meps251279>
- van Heezik, Y. (1990a). Diets of yellow-eyed, Fiordland crested, and little blue penguins breeding sympatrically on Codfish Island, New Zealand. *New Zealand Journal of Zoology*, 17(4), 543–548. <https://doi.org/10.1080/03014223.1990.10422952>
- van Heezik, Y. (1990b). Seasonal, geographical, and age-related variations in the diet of the yellow-eyed penguin (*Megadyptes antipodes*). *New Zealand Journal of Zoology*, 17, 201–212. <https://doi.org/10.1080/03014223.1990.10422597>
- van Heezik, Y. & Davis, L. (1990). Effects of food variability on growth rates, fledging sizes and reproductive success in the Yellow-eyed Penguin *Megadyptes antipodes*. *Ibis*, 132(3), 354–365. <https://doi.org/10.1111/j.1474-919X.1990.tb01055.x>
- van Heezik, Y. & Seddon, P. (1989). Stomach Sampling in the Yellow-Eyed Penguin: Erosion of Otoliths and Squid Beaks (*Megadyptes antipodes*). *Journal of Field Ornithology*, 60(4), 451–458. Available at: <https://www.jstor.org/stable/4513468>
- Wickham, H. (2016). *ggplot2: Elegant graphics for data analysis*. New York: Springer-Verlag.
- Williams, T. (1995). *The penguins: Spheniscidae; bird families of the world*. Oxford: Oxford University Press.
- Willis, T., Fu, D. & Hanchet, S. (2007). Correlates of southern blue whiting year class strength. New Zealand Fisheries Assessment Report, 40.
- Worm, B., Barbier, E.B., Beaumont, N., Duffy, J.E., Folke, C., Halpern, B.S. et al. (2006). Impacts of biodiversity loss on ocean ecosystem services. *Science*, 314(5800), 787–790. <https://doi.org/10.1126/science.1132294>
- Young, M.J. (2014). Determining the drivers of yellow-eyed penguin productivity. (MSc thesis), University of Otago, New Zealand.
- Young, M.J., Dutoit, L., Robertson, F., van Heezik, Y., Seddon, P.J. & Robertson, B.C. (2020). Species in the faeces: DNA metabarcoding as a method to determine the diet of the endangered yellow-eyed penguin. *Wildlife Research*, 47(6), 509–522. <https://doi.org/10.1071/WR19246>

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