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# Variable breeding success and its implication in the conservation of endangered yellow-eyed penguin (*Megadyptes antipodes*) at the New Zealand subantarctic Auckland Islands

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## Abstract

1. Knowledge of breeding success is essential for conservation, as it is required for monitoring populations and survival trends. Seabird reproductive success can be negatively affected by prey availability, marine-based stochasticity, extreme weather events, individual breeders' performance and direct threats such as disease, predation and fisheries interactions.
2. The endangered yellow-eyed penguin (*Megadyptes antipodes*) is declining in mainland New Zealand, however, little is known about its breeding success in the subantarctic where the majority of the species breeds.
3. Yellow-eyed penguin breeding success data were collected from a total of 167 nests on subantarctic Enderby Island, Auckland Islands, New Zealand, from the 2015 to 2017 breeding seasons. This included egg and chick mortality and fledging rates, plus a wider sample of the fledgling condition of 276 chicks.
4. Fledging success was higher than in mainland New Zealand in some years, although chicks were smaller and lighter on average, highlighting the need for more information on juvenile survival probabilities in the subantarctic.
5. Breeding success measures were similar in 2015 and 2016, but a large egg mortality in 2017 caused a significant reduction in breeding success that year. Such variability requires more investigation into the correlates of breeding success, including possible stressors such as foraging success, adverse weather and environmental effects, and pathogens.
6. These results demonstrate the need for ongoing monitoring of yellow-eyed penguin breeding success across the subantarctic in order to establish baselines for normal variation and to determine whether anthropogenic (manageable) factors may be contributing to low productivity.
7. This research highlights an important consideration for endangered species conservation; that breeding success may not be consistent over time, or across a species' entire range. Additional monitoring of all breeding populations should be

carried out to ensure up-to-date information is available to inform conservation management decisions for the species.

**KEYWORDS**

chick mortality, chick weight, climate change, egg mortality, fledgling weight

## 1 | INTRODUCTION

An understanding of breeding biology is essential for monitoring population success and determining survival trends (Miller et al., 2017). Seabirds are vulnerable to threats affecting adult survival, breeding success and chick survival (Cairns, 1988; Purvis et al., 2000; Ricklefs, 1990). Reproductive success can be negatively affected by prey availability, marine-based stochasticity, extreme weather events and the performance of individual breeders, including prior experience (Forslund & Pärt, 1995; Fowler, 1995; Moreno, 2003; Wendeln & Becker, 1999). Oceanographic shifts affecting sea surface temperature (SST), such as the El Niño-Southern Oscillation (ENSO) and climate change, exert a major influence on environmental variability and therefore also on seabird productivity (Gregg et al., 2003; Lewison et al., 2012). Threats to breeding birds can also come from disease, predation and negative fisheries interactions (Croxall et al., 2012). Long-term research is useful to provide sufficient detail on adult survival and long-term trends, particularly for factors affecting parental condition which can vary over time (Moreno, 2003). However, research is logistically difficult in isolated locations, and therefore, research aims need to fit within the practical constraints of fieldwork. Regular monitoring is important for wildlife conservation and management, particularly for long-lived species where changes may not be evident in the short term, and this can be used to assess the impact of threats and environmental changes as well as the effectiveness of any management actions (Lindenmayer & Likens, 2009; Purvis et al., 2000; Witmer, 2005). Demographic monitoring is an important measurement of survival rates (including of different age classes and genders) and breeding productivity but can be labour-intensive as it often requires capturing and marking birds for ongoing re-sighting or re-capture over their lifetime (Dowding, 2012), however, long-term monitoring effort can be difficult to sustain. Breeding success monitoring requires an understanding of population parameters such as individual nesting success, reproductive output and fledgling health (Armstrong et al., 2002). The fledgling condition can also have an important bearing on juvenile survival and likely future recruitment into the breeding population, which is true for many seabirds species (Reid et al., 2000; Sagar & Horning, 1998) including yellow-eyed penguins (*Megadyptes antipodes*, hoiho in Māori) (McClung et al., 2004). If long-term data are impractical to collect, data from individual breeding seasons can still be useful for discrete analysis and as benchmarks for future comparisons.

The yellow-eyed penguin is one of the larger penguin species, around 65 cm tall, with a mean adult mass between 4.2 and 8.5 kg based on studies of mainland New Zealand birds (Marchant & Higgins, 1990; Seddon et al., 2013). The species is endemic to New Zealand, with a distribution restricted to the southeast coast of the South Island, Stewart and Codfish Islands (the northern population; Figure 1a, above dotted line), and the subantarctic Auckland and Campbell Islands (the southern population; Figure 1a, below dotted line) (Seddon et al., 2013). There is <2% estimated migration between these areas, and therefore, it is considered they should be regarded as separate populations for conservation management (Boessenkool et al., 2009).

The yellow-eyed penguin is classified as endangered (BirdLife International, 2020; Couch-Lewis et al., 2016), and the northern population is declining due to successive poor breeding seasons and ongoing high adult mortality (Couch-Lewis et al., 2016; Mattern et al., 2017; Mattern & Wilson, 2018). Threats are believed to be primarily at sea, including poor foraging success, fisheries interactions, pollution and human disturbance (Couch-Lewis et al., 2016; Mattern et al., 2017; Mattern & Wilson, 2018). In the subantarctic, population estimates at the Auckland Islands fluctuated in the 2010s, and numbers may have declined since the 1980s (Muller, Chilvers, French, Hiscock, & Battley, 2020). On Campbell Island the population numbers varied, decreasing by 41% between 1988 and 1992, with a partial recovery towards the end of the 1990s (Moore et al., 2001). However, there are no recent data for Campbell Island. Threats in the subantarctic are believed to relate primarily to climate and other factors affecting prey availability and foraging success, although fisheries interactions require further investigation, as well as the effect of introduced mammalian predators present on the main Auckland Island (French et al., 2020; Muller et al., 2022).

Age at first breeding for yellow-eyed penguins is an average of 2.6 years in females and 4.3 years in males (Richdale, 1957), although breeding success is lower for inexperienced breeders (Richdale, 1957; Williams, 1995). On the New Zealand mainland, eggs are usually laid in late September and hatch in November, following an incubation period of 39–51 days (Seddon, 1989). The timing of breeding is delayed by approximately 2 weeks in the subantarctic (Moore, 1990). Two eggs are normally laid per pair with each having an equal survival probability, based on mainland research (Edge et al., 1999; van Heezik & Davis, 1990).

Yellow-eyed penguins nest in coastal forests up to 1 km from shore (Darby et al., 1990; Ellenberg & Mattern, 2012), with nests hidden in dense vegetation and visually isolated from other nests (Seddon & Davis, 1989). In data from mainland New Zealand, nests are sited an average of 12–32 m and up to 78 m from other nests (Seddon & Davis, 1989), and nesting pairs seldom use the same nest bowl between years, with 55% of females moving their nest site

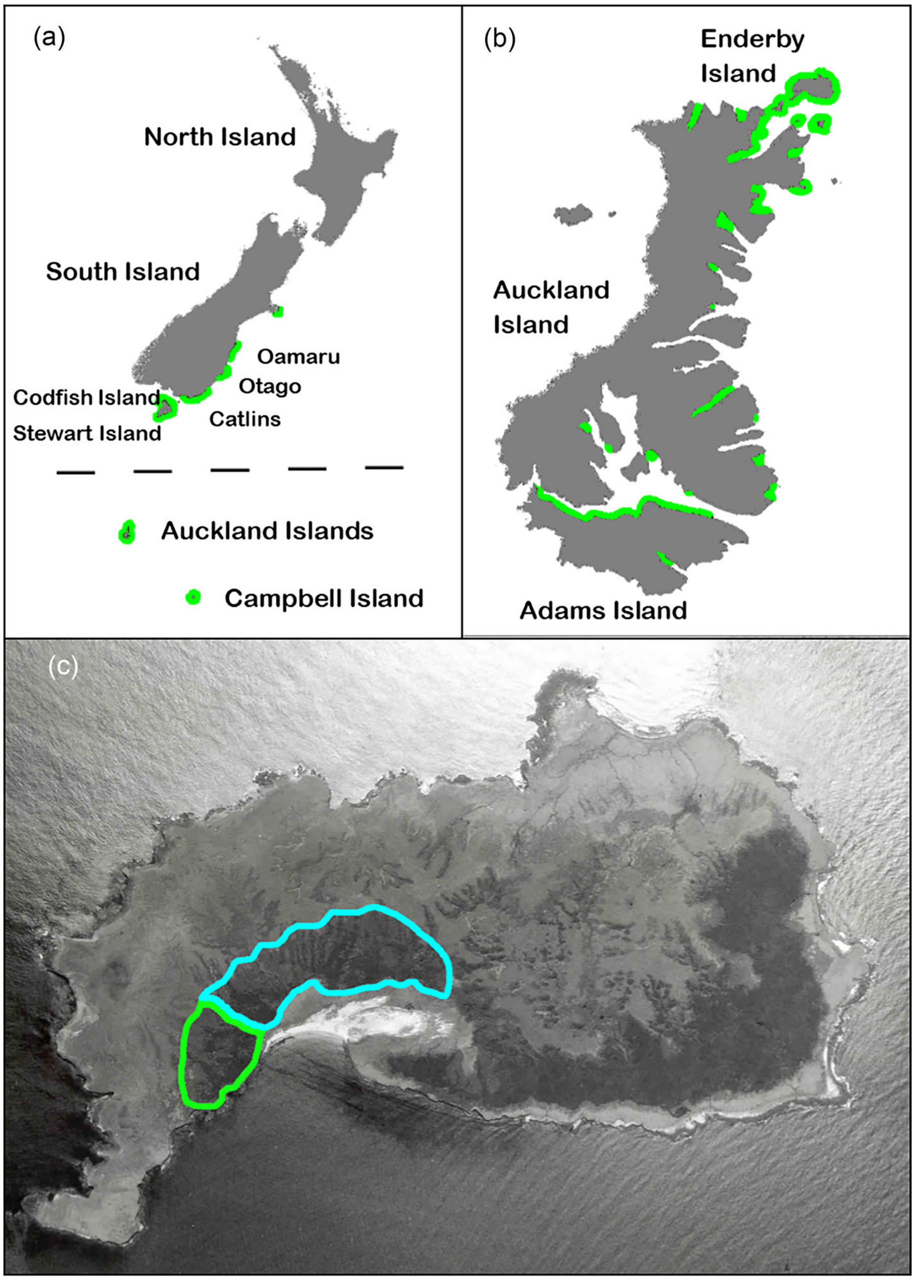

**FIGURE 1** (a) Map of yellow-eyed penguin breeding range around New Zealand (green), with the northern population above the dotted line, and southern population below the line. Also shown is (b) an enlarged view of the subantarctic Auckland Islands with Enderby Island to the NE, and (c) a close-up of Enderby Island showing the areas where breeding birds were sampled; Rocky Ramp (lower left, green border), and Sandy Bay (right, blue border). Modified from Muller, Chilvers, French, and Battley (2020).

more than 20 m away (Setiawan et al., 2005). An average of 63% of birds breed with the same partner in the following breeding season, with the majority of partner swaps being due to the death of a partner (31%) (Setiawan et al., 2005). Only 6% of partner swaps are due to divorce, but failure to fledge any chicks has a significant effect on the likelihood of divorce (Setiawan et al., 2005). The likelihood of a bird missing a breeding season is generally low but is significantly higher if birds are not with the same partner, particularly for males. The probability of a male bird missing a breeding season if their previous mate had died or divorced was 30% and 56%, respectively, and 11% and 27% for females. In comparison, for birds who retained their previous partner, the likelihood of missing a breeding season is only 6% for males and 2% for females (Setiawan et al., 2005), suggesting that any factors affecting pair bonds could be detrimental to overall breeding effort in the population.

Little is known about yellow-eyed penguin breeding behaviour in the subantarctic. Access and logistics are complex in the isolated subantarctic islands, making research in this area difficult.

On Campbell Island, Moore et al. (2001) carried out band resights which showed that a large number of breeding adults (10%–44%) disappeared in the winter following a breeding season, and did not return the following breeding season, although there was some uncertainty as bands were difficult to read. Flipper bands have been shown to decrease foraging success and increase mortality (Stonehouse, 1999), and consequently their use has been discontinued (Department of Conservation, 2012).

At the Auckland Islands, all breeding success research to date has been carried out on Enderby Island. Argilla et al. (2013) found a high chick mortality (over 50%) in the 2007 breeding season, possibly as a result of starvation and disease caused by *Leucocytozoon*, an avian haemoparasite. Disturbance to transiting birds has been postulated to affect breeding success, although this was not proven in the subantarctic (French et al., 2019; Young, 2009). French (2018) provided a more detailed breeding success analysis for a single breeding season (2016), including determining that tourism disturbance did not significantly affect breeding success. Research on breeding success at the Auckland Islands has been limited to single-year studies, with one exception; multi-year nesting success data in the form of fledgling counts for 2015–2017 were presented by Muller, Chilvers, French, Hiscock, and Battley (2020). The current study provides a more in-depth analysis of this dataset including a breakdown of specific mortality affecting chicks and eggs and a measure of fledgling condition.

The aims of this research were therefore to further analyse data from the 2015–2017 study to monitor nesting effort and breeding success at Enderby Island. The goal was to identify any significant causes of concern affecting egg or chick survival, to inform ongoing conservation management of the species at the Auckland Islands, and to compare with the findings presented in the literature for mainland New Zealand populations.

## 2 | METHODS

### 2.1 | Fieldwork

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 (Nov 2015–Feb 2016), 2016 (Nov 2016–Feb 2017) and 2017 (Nov 2017–Jan 2018). Additional data were collected during concurrent research including foraging location in 2016 and 2017 (Muller et al., 2021), dive profiles (Muller, Chilvers, French, & Battley, 2020) and diet (Muller et al., 2022) in all 3 years. Parental foraging behaviour was categorised using a combination of foraging and diving behaviour and stable isotope analysis of diet (Muller et al., 2022).

Adults and chicks were caught by hand and transferred to a custom-made holding bag. This held the wings against the body but left the head and feet exposed for the collection of morphometric data using a spring balance and callipers. Adults were fitted with a microchip for permanent individual identification (Department of Conservation, 2012; Muller, Chilvers, French, Hiscock, & Battley, 2020), and sex was determined using the relationship between head plus beak length and foot length (Setiawan et al., 2004), or the relative sizes between breeding partners with males assumed to be the larger (Setiawan et al., 2004).

Nests were located using manual ground searching, ground-based very high frequency (VHF) radio tracking and aerial tracking using an unmanned aerial vehicle (UAV) equipped with a VHF receiver (Muller et al., 2019). Once located, all nests were regularly visited in person to identify adults and check breeding status, and the location was recorded with a handheld GPS (Garmin International, Kansas, USA). Birds on the nest were scanned using a hand-held microchip reader (Allflex, Palmerston North, New Zealand).

### 2.2 | Breeding success

The estimated number of breeding birds on Enderby Island was too large to attempt to sample every nest (Muller, Chilvers, French, Hiscock, & Battley, 2020), so a smaller reference population was identified at Rocky Ramp (Figure 1c). This was a discrete sub-population of breeding birds defined by physical boundaries (including cliffs, creeks and non-breeding habitats). All nests in this area were located and monitored, and this was verified using microchip and trail camera records of birds as they transited to and from the area to the sea (Muller, Chilvers, French, Hiscock, & Battley, 2020). This sub-population represented the geographic area of Rocky Ramp although it included some birds which may occasionally have transited to the sea via the landing area at Penguin Alley on the western edge of Sandy Bay (Figure 1c). Comparisons of nest numbers were made between years for the Rocky Ramp population, with breeding success measures (including the number of eggs laid, the number of chicks hatched and the number of chicks fledged) determined for all breeding attempts.

Nests were located during the incubation phase and were visited every 3–4 days until eggs hatched or the nest was abandoned, and at least every 7 days after hatching to monitor chicks. Hatch date was noted if hatching was observed, or was estimated based on the condition of young chicks up to 3 days old (Darby et al., 1990; van Heezik & Davis, 1990). Chicks older than 3 days could not be estimated using this method, but an approximate hatch date could still be estimated based on the date of the previous visit (French, 2018). Nests found later in the season during the post-guard phase (when an adult was not continuously in attendance at the nest) were excluded from breeding success analysis to avoid bias towards nests with live chicks which would have been easier to locate (Armstrong et al., 2002).

In the neighbouring breeding area at Sandy Bay (Figure 1c), additional nests representing a subset of those in the area were located and monitored to provide additional chick weight data. A random sample of birds was captured as they returned from sea, and VHF transmitters were attached, allowing them to be tracked back to their nest, see Muller et al. (2019) for methods. Any nests encountered on the way to the target bird were also included in the sample. The area included a sub-area of western Sandy Bay known as Penguin Alley. Chicks were captured by hand during the post-guard phase (1–17 February in 2016, and 3–10 January in 2017). Birds were weighed using a spring balance and custom canvas weigh bag, and head and foot measurements were collected using a custom wooden measuring board (Department of Conservation [DOC], New Zealand). Permission was not granted to weigh chicks in 2015 so fledglings were counted only. In 2015, one chick was not located during fledging checks, but no evidence could be found to indicate whether it had died or fledged. Therefore, this nest was excluded from fledging calculations, but it was included in egg and chick counts because these data were available. In 2016, a total of 67 nests were located in the area, however, two nests with one chick in each were found late in the season. Because no information was available on the original number of eggs laid or chicks hatched, these were excluded from the summary table (Table 1).

In the 2017 breeding season, abandoned eggs were collected during the post-guard phase (10–11 January 2018) and opened to check for the presence of embryos. All embryos were photographed and measured using callipers to give a relative measure for size comparison.

### 2.3 | Analysis

Statistical analyses were conducted in R Studio version 1.1.456 running R version 3.5.1 (R. Core Team, 2017). Generalised linear models with a Poisson family and log link were used to analyse the number of eggs, chicks and fledglings per nest, as count data. The predictor variables year (2015, 2016 or 2017), nest location (Rocky Ramp or Sandy Bay) and the parents' forage type (benthic, pelagic or mixed) were included in the models. Benthic dives were to the seafloor, whereas pelagic dives were in mid-water (MullerMuller, Chilvers, French, & Battley, 2020), and mixed foraging included birds which changed their foraging behaviour on subsequent trips (Muller et al., 2022). However, nest location and forage type were not significant in any model, so were removed. Graphs were generated using R, including the package ggplot2 (Wickham, 2016).

The probability of survival to fledging was calculated using a generalised linear model with a binomial family and logit link. The year was included as a fixed effect, and male and female bird ID as random effects to avoid pseudo-replication due to possible differences between parenting ability or nest site selection. The model was run using the lme4 package, and data were analysed and plotted using ggeffects and ggplot2 in R.

Nesting distances were calculated using a custom script in Python 3.5.2 (Python Software Foundation, www.python.org), including the geopy library. This calculated the geodesic distance between nest location coordinates from different years, and instances of partner changes between years were determined after identifying breeding pairs. Only known birds from identified nests breeding in multiple years were included in this calculation. Boolean partner fidelity data (as a fixed variable) were analysed using linear mixed-effects (LMER) models to determine the effect on nest distance (the distance between nest locations in subsequent years) for birds with the same, or a different partner. Nest ID (a unique identifier assigned to each nest in each year) was used in all models as a random effect with a random intercept to avoid pseudo-replication. Results were tested for statistical significance using an ANOVA test and the lme4 package (Bates et al., 2015).

## 3 | RESULTS

### 3.1 | Nesting effort

For the Rocky Ramp reference population, the total number of nests was 50 in 2015, 65 in 2016, and 52 in 2017 (Table 2). Mean hatch dates were 27 November ±4 days (SE 0.55) in 2016, and 29 November ±4 days (SE 0.67) in 2017. The earliest hatch date was 18 November in 2016 and 2017, from the same breeding pair. Accurate hatch dates were not calculable for 2015 as research effort was prioritised towards ground searching for nests, preventing regular revisits.

The number of returning breeders varied between years, with a larger percentage of returning breeders in 2017 (Table S1). In 2017, 81% of breeders had also bred the previous year (2016), whereas 97% had previously bred during any year of the study (either 2016 or 2015). Of 102 birds identified as breeding in two consecutive breeding seasons, 78 (76%) were with the same partner (Table S2). The mean distance between nest sites in subsequent years was 37.9 (SE 4.9) m. For birds confirmed nesting with the same partner the mean distance was smaller at 30.7 (SE 2.9) m. Nesting distance was significantly greater for birds confirmed with a different partner with a mean of 60.3 (SE 20.6) m ($\chi^2 = 6.2028$, df = 2, $p = 0.04$).

### 3.2 | Breeding success

At the Rocky Ramp reference population, there was no significant difference in the average number of eggs laid per nest between years ($p > 0.01$ for all samples) (Table 1). However, in 2017, the average number of chicks hatched per nest was significantly lower than in all other years (2017 vs. 2016; $z = -2.326$, $p = 0.0200$, and 2017 vs. 2015; $z = -2.223$, $p = 0.0262$). This was primarily due to a high percentage of egg mortality in 2017 (Figure 2). The average number of chicks fledged per nest also reduced significantly between 2016 and 2017 ($z = -2.582$, $p = 0.00982$) as a consequence of the larger egg mortality in 2017. However, the number of chicks fledged was not significantly different between other years (2015 vs. 2016; $z = -0.540$, $p = 0.58886$, and 2015 vs. 2017; $z = -1.948$, $p = 0.05139$).

**TABLE 1** The number of nests at the Rocky Ramp reference population on Enderby Island for each year of the study.

| | Nests | Nests with two eggs laid | | Nests with two chicks hatched | |
|---|---|---|---|---|---|
| Year | No. | No. | Proportion | No. | Proportion |
| 2015 | 50 | 48 | 0.96 | 38 | 0.76 |
| 2016 | 65 | 61 | 0.94 | 49 | 0.75 |
| 2017 | 52 | 50 | 0.96 | 28 | 0.54 |

**TABLE 2** Breeding success per year for the reference population at Rocky Ramp on Enderby Island (Figure 1c), where all nests were located in each year of the study. Survival data are shown for all offspring per stage (eggs or chicks), with nest failures showing the proportion of nests reaching 0 surviving offspring in that stage. Breeding data (grey highlight) show the total breeding success (combined survival and nest failures for all breeding stages) in that year.

| Breeding stage | Year | Number produced | Mean production per nest (SE) | Survival per stage % | Nest failures per stage % |
|---|---|---|---|---|---|
| Eggs | 2015 | 99 | 1.98 (0.008) | 85.9% | 8.0% |
| | 2016 | 126 | 1.94 (0.007) | 86.5% | 7.7% |
| | 2017 | 102 | 1.96 (0.008) | 58.8% | 38.5% |
| Chicks | 2015 | 84 | 1.68 (0.016) | 84.5% | 8.0% |
| | 2016 | 109 | 1.68 (0.012) | 92.7% | 6.2% |
| | 2017 | 60 | 1.15 (0.019) | 86.7% | 5.8% |
| Breeding | 2015 | 70 | 1.43 (0.018) | 82.0% | 16.0% |
| | 2016 | 101 | 1.55 (0.013) | 86.2% | 13.9% |
| | 2017 | 52 | 1.00 (0.019) | 55.8% | 44.2% |

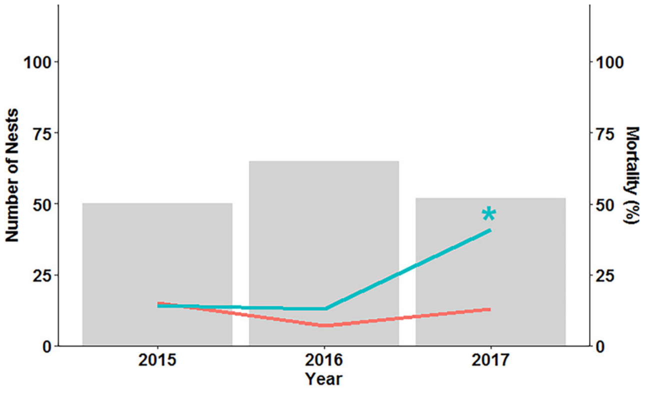

**FIGURE 2** Combined breeding success measures for the reference population at Rocky Ramp on Enderby Island, where all nests present were monitored in each year of the study. The left axis shows numbers of nests (grey bars), and the right axis shows percentage mortality of eggs (blue line) and chicks (red line) in each year. Only egg mortality in 2017 was significantly different from any other year.

The attrition in the average number of offspring per nest between chick hatching and fledging was similar in 2016 and 2017 (a decrease of 0.15), indicating a similar rate of chick mortality after hatching. However, in 2015, there was a steeper decline of 0.25, which highlights higher chick mortality that year. The probability of survival to fledging was significantly lower in 2017 (Figure 3) compared with 2015 ($p = 0.03158$, $z = -2.150$) and 2016 ($p = 0.000168$, $z = -3.763$) due to the high egg mortality in 2017 (Figure 2).

In the 2017 breeding season, there were 42 unhatched eggs (Tables 1 and S3), significantly more than in any other year (Figure 2). In mid-January 2018, 26 failed eggs from 15 nests were opened to check their developmental stage. Other failed eggs had already been broken or lost by the adults and so were not available for examination at the end of the season. Of the sampled eggs, 18 (69%) had clearly identifiable embryos present, measuring between 7.5 and 45.5 mm. The remaining 8 eggs examined (31%) had no visible embryo indicating either a very early-stage death or infertile eggs.

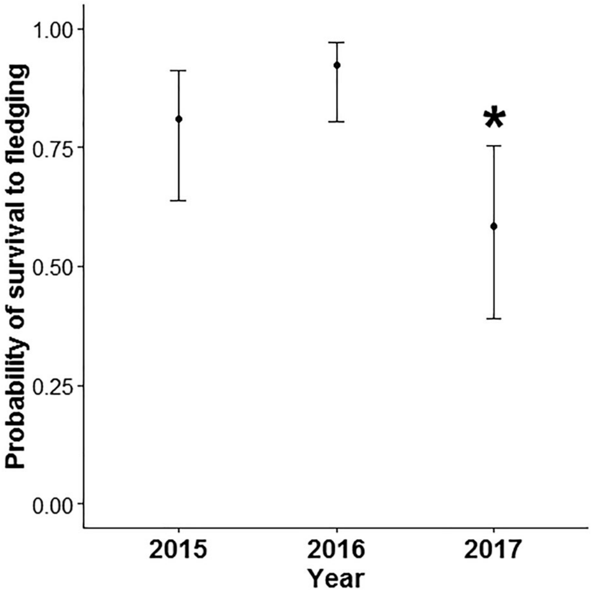

**FIGURE 3** Probability of survival to fledging for all eggs laid in the Rocky Ramp study area on Enderby Island, for the 2015–2017 breeding seasons. Error bars show 95% confidence intervals. Asterisk denotes significant difference from all other years ($p < 0.05$).

There was no significant difference ($p > 0.05$) in breeding success between adults undertaking different foraging types (benthic or pelagic). There was no evidence of predation of eggs or chicks on Enderby Island, except for one egg found broken on open ground.

## 3.3 | Breeding condition

A total of 437 breeding adults were weighed over the 3 years of this study. Mean bodyweight was 5.3 ± 0.02 (SE) kg, with a range of 4.0–6.8 kg. Morphometric measurements illustrate the size of a bird and can be used to determine sex (Setiawan et al., 2004). The sum of head and foot measurements was 263.2 ± 0.45 (SE) mm, with a range of

**TABLE 3** Chick growth indices (weights and measurements) for the reference population at Rocky Ramp (RR) and Sandy Bay (SB) on Enderby Island, for the 2016 and 2017 breeding seasons (grey highlight). Chicks were weighed at a mean age of 38 days since hatching in 2017, and 73 days in 2016. Mainland chick growth indices at a similar age are shown for comparison (van Heezik & Davis, 1990). No chicks were weighed in 2015.

| Location | Sub location | Year | Calculated age (days) | Weight (kg) mean (SE) | Foot length (mm) mean (SE) | Head + beak length (mm) mean (SE) | *n* |
|---|---|---|---|---|---|---|---|
| Enderby Island | RR + SB | 2017 | 38 ± 5 | 2.80 (0.007) | 123.89 (0.025) | 103.67 (0.026) | 95 |
| South Island | Nugget Point | 1984 | 38 | 3.1 | 125 | 110 | 24 |
| South Island | Nugget Point | 1985 | 38 | 2.6 | 125 | 110 | 15 |
| South Island | Boulder Beach | 1984 | 38 | 2.8 | 125 | 110 | 11 |
| South Island | Boulder Beach | 1985 | 38 | 2.8 | 130 | 125 | 18 |
| Enderby Island | RR + SB | 2016 | 73 ± 5 | 4.53 (0.004) | 126.73 (0.011) | 126.64 (0.012) | 181 |
| South Island | Nugget Point | 1984 | 73 | 5.1 | 130 | 140 | 24 |
| South Island | Nugget Point | 1985 | 73 | 3.9 | 125 | 140 | 15 |
| South Island | Boulder Beach | 1984 | 73 | 4.8 | 125 | 140 | 11 |
| South Island | Boulder Beach | 1985 | 73 | 4.8 | 125 | 130 | 18 |

222.0–284.0 mm. Individual head and foot measurement means were 135.0 ± 0.24 (SE) mm and 128.2 ± 0.25 (SE) mm, respectively.

Growth indices including weights and morphometrics were collected from a total of 276 chicks at the Rocky Ramp and Sandy Bay breeding areas (181 in 2016, and 95 in 2017) (Table S4). The mean chick age at weighing was 73 ± 5 (SD) days in 2016, with a mean weight of 4.53 ± 0.04 (SD) kg, and 38 ± 5 (SD) days in 2017, with a mean weight of 2.80 ± 0.46 (SD) kg. Chick growth data appear comparable to data from mainland New Zealand (Table 3), although statistical comparisons between data sets were not possible as raw mainland weights were not available.

## 4 | DISCUSSION

Knowledge of breeding biology is essential for monitoring breeding success and determining survival trends (Miller et al., 2017). All of these parameters are important components of endangered species management. The northern yellow-eyed penguin population is declining due to successive poor breeding seasons and ongoing high adult mortality (Couch-Lewis et al., 2016; Mattern et al., 2017; Mattern & Wilson, 2018), with regular ongoing monitoring of breeding success to inform management decisions. In contrast, few breeding success data exist for the southern population, although population estimates and breeding numbers are known to vary significantly between years at the Auckland Islands (Muller, Chilvers, French, Hiscock, & Battley, 2020) and Campbell Island (Moore et al., 2001), making detailed knowledge of breeding biology important.

Around 37%–49% of the species breeds at the Auckland Islands, and of this, around 50% of the Auckland Islands population breeds at Enderby Island (Muller, Chilvers, French, Hiscock, & Battley, 2020), making it an important breeding population for the species. While breeding success measures (the proportion of surviving eggs, chicks and fledglings) were generally similar between years, we documented a greater breeding effort and therefore number of surviving chicks in 2016, compared with 2015 and 2017. There was also a large egg mortality in the 2017 breeding season which caused a significant reduction in reproductive success that year.

### 4.1 | Nesting

In the Rocky Ramp reference area on Enderby Island, between 59% and 81% of birds returned to nest in the following year, although a total of 97% returned during the course of the study (Table S1). This suggests that some birds may have either taken a year off or moved to a different location to breed in some years. The mean nest distance was significantly further from the previous nest location for birds that had changed their partner from the previous year, with a much greater variance. Birds with the same partner were more likely to breed closer to their previous nest location. This is consistent with research from the northern population where birds did not nest in a different area, or a large distance away from the previous nest (Darby et al., 1990; Richdale, 1949). Additionally, northern population birds were also less likely to skip a breeding season or change partner unless their previous partner had died or divorced (Setiawan et al., 2005). Evidence of partner changes in the subantarctic could therefore indicate adult mortality or previous breeding failure, with associated conservation implications. Additional long-term monitoring of breeders is needed to investigate trends and whether outcomes are related to foraging and breeding success.

### 4.2 | Breeding success

While egg and chick mortality were both lower in 2016 (Figure 3, Table S3), there was no significant difference in egg or chick survival between years, apart from 2017 which had a high proportion of unhatched eggs, and a large proportion of nests which failed at the egg stage (Table 1). Embryos ranged in size from 7.5 to 45.5 mm, indicating that embryonic development had most likely stopped during early development (possibly late September or early October given a mean hatch date in late November). Egg mortality occurred before researchers or tourists were present on the island so was unlikely to be due to human disturbance of nesting birds. No mammalian predators are present on Enderby Island, and disease is more likely to kill chicks than eggs (Argilla, 2015), so the cause of egg mortality was possibly due to cold exposure. Eggs need to be kept warm during incubation (Seddon, 1989), and death could therefore be due to reduced parental attendance at the nest leading to low-temperature fatality. The widespread egg mortality may be due to one or more extreme weather events, adults spending longer at sea foraging, or some other reason causing adults to leave the nest. Embryonic death at this time could therefore have been the result of environmental conditions, or other factors affecting the nest attendance or foraging schedule of the parents. Nests located post-hatching may be easier to find than pre-hatching, as young chicks can increase the visibility of nests (Armstrong et al., 2002). While we excluded nests found later in the season from breeding success measures, we did include nests found within a week of hatching so there may have been some bias towards successful nests. However, any bias is likely to be small. As nests with unhatched eggs were still able to be discovered, it would only have been unmonitored nests where eggs were lost that may have been under-reported.

The number of chicks successfully fledging in 2016 was higher than in other years, which also corresponded to a higher estimated population and number of breeders that year (Muller, Chilvers, French, Hiscock, & Battley, 2020). This adds further weight to the suggestion that 2016 was a good breeding year, with all measures of breeding success higher than in both the previous and following breeding seasons, including nesting attempts and the number of eggs, chicks and fledglings produced. This pattern also matched similar fluctuations in the population estimates for the Auckland Islands during this time (Muller, Chilvers, French, Hiscock, & Battley, 2020). Yellow-eyed penguin foraging and diving behaviour vary between years in the subantarctic (Muller, Chilvers, French, Hiscock, & Battley, 2020; Muller et al., 2021), and this is reflected in changes to their diet (Muller et al., 2022). Penguins undertook a greater proportion of pelagic dives and foraged further from shore during La Niña conditions, with their diet including greater amounts of higher-trophic-level prey (Muller et al., 2022). This corresponded to improved breeding success during La Niña conditions in 2016, although breeding effort was not as high during similar ENSO conditions the following year. In addition to direct effects on nesting birds, extreme weather events can also reduce foraging success in penguins, and these effects can persist for several days following a storm event (Barreau et al., 2021). Short-term stochastic weather events can therefore have an extended impact on penguin foraging success, which can translate into reduced breeding success (Barreau et al., 2021). Together, this suggests that foraging and breeding success are the result of more complex interactions affecting prey availability and nest attendance, and extreme weather events may be as significant as ENSO status or other climate measures. Consequently, these factors are expected to have a major effect on the survival and breeding success of subantarctic yellow-eyed penguins in the future, particularly if the effects of climate change intensify.

Breeding success is a combination of hatching success and fledging success, which may be subject to different pressures. Breeding success (the number of chicks fledged per pair) on mainland New Zealand ranged from 1.39 at an undisturbed site (Green Island), to 0.75 at a site subject to tourism disturbance (Sandfly Bay) in Otago (Ellenberg et al., 2007). In comparison, the maximum breeding success at Enderby Island was 1.5 (Table 1), and breeding success was generally higher than at the undisturbed mainland site, except for 1.0 in 2017 which had low hatching success due to a large egg mortality. On subantarctic Campbell Island, breeding success was 1.4 chicks per nest (Moore, 1992), which was within the range of values for Enderby Island during the present study. Breeding success was previously investigated on Enderby Island during the 2008 breeding season. Fledging success was not measured, although a high chick mortality (55%) was reported (Argilla et al., 2013). Together, these results suggest that breeding success in the subantarctic is generally comparable to a good season at an undisturbed mainland breeding area, however, poor breeding seasons with significantly reduced productivity can also occur (Table 1). A high variability in breeding success has also been documented in mainland New Zealand (Seddon et al., 2013).

Other seabirds breeding at the Auckland Islands also display variable breeding success between breeding locations and years, such as the rockhopper penguin (*Eudyptes chrysocome*) (Cunningham & Moors, 1994; Morrison et al., 2015) and giant petrel (*Macronectes halli*) (Parker et al., 2016; Parker et al., 2020). Some albatross species commonly take a breeding sabbatical every second season, including the southern royal albatross (*Diomedea epomophora*) and Gibson's wandering albatross (*Diomedea antipodensis gibsoni*), which also breed in the Auckland Islands (Childerhouse et al., 2003; Robertson, 1972; Walker & Elliott, 2001). Seabird breeding success is likely influenced by prey availability and also by various terrestrial and marine threats such as predation by introduced mammals, climate change and negative fisheries interactions including competition and bycatch (Croxall et al., 2012). In addition to climate change affecting seabirds' food supply and availability (Worm et al., 2006), it can also be responsible for localised effects including extreme weather events (Saraux et al., 2016), and damage to breeding areas with associated population declines (Chilvers & Hiscock, 2019). Localised threats can affect population size and breeding success differently, including populations elsewhere in the subantarctic for giant petrels (summarised in Parker et al., 2020) and rockhopper penguins (Morrison, 2015; Pütz et al., 2001), highlighting the need to monitor species across their entire range to determine breeding trends.

## 4.3 | Breeding condition

The bodyweight of yellow-eyed penguin fledglings from mainland New Zealand is strongly correlated with their expected survival probability as juveniles (McClung et al., 2004). Chicks were weighed at different ages in different studies, making direct comparisons difficult, although mean chick weights do not fluctuate significantly during the last month before fledging (van Heezik, 1988). While fledging success was higher on Enderby Island, comparison with chick breeding conditions from mainland New Zealand (van Heezik & Davis, 1990) shows that chick weights and measurements are comparable. Enderby Island chicks may tend towards being lighter and smaller, particularly at the 73-day mark (Table 3), although this may indicate birds are lighter and smaller in the subantarctic in general. A later mainland study by McClung et al. (2004) found a mean fledging weight of 5.3 kg (range 4.1–6.1) at a site subject to tourism disturbance (Sandfly Bay), compared with means from 5.5 to 5.7 kg (range 4.1–7.1 kg) for other undisturbed sites. These correspond to predicted post-fledging survival probabilities of approximately 0.25 and 0.29 for disturbed and undisturbed sites, respectively. In comparison, the mean weights in 2016 at Enderby Island at the same age would correspond to a lower estimated survival probability of around 0.21 using this measure. This is lower than the survival rate at a disturbed mainland colony, although there is no evidence of tourism disturbance affecting yellow-eyed penguin breeding success on Enderby Island (French, 2018). Consequently, it is reasonable to conclude that birds may be generally lighter and smaller in the subantarctic (Table 3), and therefore comparisons with the mainland may not be valid because lighter-weight birds may not be under as much nutritional stress. Chick growth rates likely differ between the northern and southern populations, as parental foraging behaviour also differs in the subantarctic (Muller, Chilvers, French, & Battley, 2020; Muller et al., 2021; Muller et al., 2022). Foraging efficiency may also fluctuate between years in the subantarctic as a result of climate and other factors affecting prey availability, and this can affect parental diet (Muller et al., 2022) as well as breeding effort (Muller, Chilvers, French, & Battley, 2020). The mean fledging weight on subantarctic Campbell Island during the 1987 breeding season was 5.1 kg at 108 days since hatching (Moore, 1992), which is larger than chick weights recorded on Enderby Island at 73 days since hatching. This may indicate more favourable breeding or foraging conditions on Campbell Island in general, or in the late 1980s when these data were collected. Simultaneous comparisons of breeding success across the Auckland Islands, and at Campbell Island would provide a clearer picture of breeding success and threats in the subantarctic. More longer-term subantarctic data sets are therefore needed to investigate fledging condition of chicks during years of different prey availability, as well as documenting the survival probability of juveniles to recruitment into the adult population.

## 4.4 | Direct causes of breeding mortality

Most New Zealand subantarctic islands are now pest-free, including Enderby and Campbell Islands. However, introduced mammalian predators including cats (*Felis catus*) and pigs (*Sus scrofa*) are present on Auckland Island and are suspected of depredating yellow-eyed penguins and nests (Challies, 1975; Moore, 1990). Mice (*Mus musculus*) are also present on Auckland Island (Taylor, 1971) and are known to attack albatross chicks on other subantarctic islands (Cuthbert & Hilton, 2004). Auckland Island contains around 66% of the land area of the archipelago but only around 29% of the yellow-eyed penguin population in the area breeds there, with predation on land thought to be a factor (Muller, Chilvers, French, & Battley, 2020). Eradication of introduced predators would therefore be expected to increase the breeding habitat available to yellow-eyed penguins.

Natural predators in the subantarctic include the brown skua (*Catharacta antarctica*) and northern giant petrel (*M. halli*), which kill smaller penguins such as rockhoppers (Morrison et al., 2017; Ryan et al., 2008), although they have not been documented killing yellow-eyed penguins. These avian predators do not usually enter forested areas where yellow-eyed penguins nest and no interactions have been observed on land (pers. obs.). There was no evidence of predation of eggs or chicks on Enderby Island, except for one egg found broken on open ground, which was consistent with damage caused by a skua. This egg came from a nest in low scrub (<30 cm high) and located less than 0.5 m from the edge of vegetation cover so may have been accessible to a skua. No skuas or giant petrels were observed under vegetation cover (pers. obs.) so the majority of nests were assumed to be safe from these naturally occurring avian predators. Breeding success data are required for other breeding populations in the area, particularly on the main Auckland Island where introduced mammalian predators are thought to be responsible for lower yellow-eyed penguin population estimates (Muller, Chilvers, French, & Battley, 2020). The eradication of introduced predators should therefore also be a priority for yellow-eyed penguin conservation on the Auckland Islands.

During all three breeding seasons of this study, the majority of dead chicks died in their first week after hatching due to unknown causes, with a large gap until a smaller peak of mortality near fledging age, most likely due to starvation. A similar pattern was documented in the 2008 breeding season on Enderby Island with two separate peaks of chick mortality; a larger peak at 1 week, and a smaller peak at 4 weeks of age (Argilla et al., 2013). In that study, the causes of mortality were not clear, but it was thought that disease might be more likely a contributing factor in the death of older chicks. In the present study, one post mortem was conducted in Feb 2017 on a dead chick near fledging age. The diagnosis was possible starvation which was consistent with the chick's very low bodyweight (under 3 kg). Dead chicks were collected but no early season post mortems were able to be carried out, so causes of death for young chicks in this study are unknown. Several disease-causing organisms are present on Enderby Island, including *Leucocytozoon* (Argilla et al., 2013), *Coccidia* and *Plasmodia* (Kay, 2021), and these have been linked to the deaths of chicks and some adults. However, while several disease epidemics and mass mortality of adults have been reported for yellow-eyed penguins around mainland New Zealand (Alley et al., 2017; Argilla, 2015; Gartrell et al., 2017), none have been reported in the subantarctic, although this could be due to a lack of regular monitoring. More information is therefore needed on disease-causing organisms present in the subantarctic, and in particular, causes of death of young chicks which represent the larger mortality peak.

## 4.5 | Conservation implications

The endangered yellow-eyed penguin faces numerous threats, and although the mainland population is declining and at greater risk of immediate collapse, unique threats are present in the subantarctic with important consequences for the future viability of the southern population, and therefore the species. Variable breeding success in the subantarctic indicates that the species is vulnerable to changing environmental conditions, particularly those that may affect foraging success, and therefore chick provisioning. Foraging success can be influenced by changes in prey availability as a result of climatic variations, and in turn, this can translate to a reduction in breeding success. Poor breeding outcomes could increase in frequency and become more pronounced in the future due to increasing water temperature associated with ENSO oscillations or climate change. Low breeding success in some years will translate to future low recruitment when that cohort reaches breeding age. As a long-lived, slow-growing species with low average fecundity, this means the breeding population is also vulnerable to any large-scale adult mortality, but also to any large or ongoing decline in breeding success. The significant egg mortality documented in this study is a particular cause for concern and could indicate that extreme weather events may have a disproportionate effect on breeding success, even if other factors are generally favourable.

Manageable threats such as the eradication of introduced terrestrial predators, and the prevention of any potential negative fisheries interactions should be controlled as an essential step for future management of subantarctic yellow-eyed penguins. This is necessary to ensure they do not compound with other threats such as climate change, prey availability or other marine-based threats which are more difficult to mitigate.

Population fluctuations were evident in the Campbell Island population in the 1990s (Moore et al., 2001), although no studies have been carried out since then, meaning recent population estimates and breeding success data are required for Campbell Island (French & Muller, 2021). Variable breeding success in the southern population is a cause for concern, as a combination of successive poor breeding seasons in the future could result in population decline. As a consequence of this uncertain and highly variable breeding output, ongoing future monitoring of breeding success and population numbers is needed to identify issues as early as possible, allowing investigation in greater detail, and if necessary, pre-emptive actions to mitigate their effects. Monitoring should ideally include long-term studies of known individuals over multiple breeding seasons, as well as measuring the survival rate of juveniles to recruitment into the breeding population. While logistical constraints make subantarctic research difficult and expensive, this population is vital to the survival of the species and continuing monitoring efforts are critical to conservation efforts.

Similar factors are evident in the conservation of the New Zealand sea lion (*Phocarctos hookeri*) which also has separate breeding populations in the subantarctic and mainland New Zealand (Childerhouse & Gales, 1998). Mainland breeding success is primarily affected by negative interactions with humans on land and with coastal fisheries at sea (Augé et al., 2015; Thompson, 2022). Whereas for the larger subantarctic breeding population, breeding success and mortality are affected by pelagic fisheries and disease leading to high pup mortality on land (Castinel et al., 2007; Chilvers, 2008; Maloney et al., 2009; Robertson & Chilvers, 2011).

This research highlights an important consideration for all endangered species conservation; that breeding success may not be consistent over time, or across a species' entire range, as environmental conditions and threats may differ. Therefore, ongoing monitoring of all breeding populations or representative areas should be carried out to ensure up-to-date information is available to inform conservation management decisions for the species.

## AUTHOR CONTRIBUTIONS

C. G. Muller conceived and designed the experiments, carried out the fieldwork, analysed the data and wrote the paper. R. K. French assisted with fieldwork and data analysis. B. L. Chilvers and P. F. Battley provided general oversight and funding and assisted with the ecological aspects of the project. All authors reviewed the manuscript and gave final approval for publication.

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## CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

## DATA AVAILABILITY STATEMENT

The data that supports the findings of this study are available in the supplementary material of this article.

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## SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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