



Foraging areas and plasticity of yellow-eyed penguins *Megadyptes antipodes* in their subantarctic range

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ABSTRACT: Foraging behaviour is crucial to breeding success for marine predators, including seabirds. Yellow-eyed penguins *Megadyptes antipodes* are central-place, predominantly benthic foragers around mainland New Zealand. The northern (mainland) population of this Endangered species is declining, with changes in the marine environment a suspected cause, particularly warming water and poorer foraging success. We undertook a detailed foraging study of the data-deficient subantarctic population, which is distinct from the northern population. Over 2 breeding seasons, we collected 91 GPS foraging logs from 69 breeding yellow-eyed penguins from Enderby Island, Auckland Islands, New Zealand. The mean foraging distance was 24 km from shore (max 47 km). Foraging area size was greater for females and for pelagic foragers, although benthic foragers travelled further from shore on average. Diving plasticity was evident both in diving behaviour and foraging area use. Foraging area and distance from shore were greater for all birds in a year of greater breeding effort and fledging success (2016). Foraging occurred over continental shelf waters, similar to the mainland, and in areas up to 150 m deep, so any differences in foraging behaviour compared to those reported for the northern population are likely influenced by local bathymetry, environmental conditions, and individual preference. Despite comparable bathymetry in some areas, the southern population showed greater foraging plasticity, with 62% of foraging trips categorised as pelagic, implying that subantarctic foraging conditions may differ from the predominantly benthic mainland foraging. Variable foraging conditions may therefore have implications for future breeding success in the subantarctic.

KEY WORDS: Foraging behaviour · GPS · VHF tracking · Time–depth recorder · Subantarctic Auckland Islands · Diving behaviour · Climate change · El Niño Southern Oscillation

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1. INTRODUCTION

Many marine predators are central-place foragers, including seabirds and pinnipeds that breed on land but forage at sea, returning ashore to provide for their young (Boyd et al. 1994, Boersma & Rebstock

2009, Jones et al. 2020). Finding food is essential for breeding success and population viability for long-lived marine predators (Villegas-Amtmann et al. 2008, Chilvers & Wilkinson 2009), including seabirds (Sandvik et al. 2005, Catry et al. 2013). Seabird foraging success can vary between years, as oceanic con-

ditions, reflected in indices such as the El Niño Southern Oscillation (ENSO), can change and may affect prey abundance and distribution (Boyd et al. 1994, Miller & Sydeman 2004, Grémillet & Boulinier 2009, Ropert-Coudert et al. 2009, 2015, Catry et al. 2013, Agnew et al. 2015, Poupart et al. 2017).

Foraging plasticity describes the adaptability of an organism to changes in its environment with respect to foraging behaviour. While this can include changes in the type of foraging method used (e.g. benthic vs. mid-water or pelagic diving), plasticity can also include other changes related to foraging location. Foraging over a greater area may increase the time and effort required, while foraging closer to or further from shore may also correspond to changes in water depth, and all foraging changes can expose a predator to different prey assemblages. Benthic prey are less influenced by oceanographic perturbations such as ENSO and they may be a more reliable food source than pelagic prey over time (Costa et al. 2004). However, changes to the benthos can affect benthic penguin foraging (Browne et al. 2011). One approach to classify benthic and pelagic dives is by determining dive shape and depth. Benthic dives to the seafloor are characterised by a U- or square-shaped dive profile with a uniform maximum depth limited by bathymetry (Wilson 1995, Tremblay & Cherel 2000, Pütz & Cherel 2005, Bost et al. 2007). Conversely, pelagic dives occur in mid-water and display a V- or W-shaped dive profile with a more variable maximum depth between dives, with the former sometimes considered exploratory behaviour, and the latter linked with prey-pursuit activity (Wilson 1995, Ropert-Coudert et al. 2000, Pütz & Cherel 2005). Pelagic dives tend to have a shorter bottom time and maximum depth, given that prey could be encountered anywhere in the water column (Wilson 1995, Tremblay & Cherel 2000, Pütz & Cherel 2005, Bost et al. 2007). When foraging, most penguin species rely on pelagic feeding dives, catching prey within the water column (Ratcliffe & Trathan 2011), although some species such as southern rockhopper penguins *Eudyptes chrysocome filholi* have a mixed strategy incorporating both pelagic and benthic diving (Tremblay & Cherel 2000).

Yellow-eyed penguins (hoiho, in Maori) *Megadyptes antipodes* are Endangered (Couch-Lewis et al. 2016, BirdLife International 2020, Department of Conservation 2020) and endemic to New Zealand. Their distribution is restricted to the south-east of the South Island, Stewart and Codfish Islands (the northern population), and subantarctic Auckland and Campbell Islands (the southern population; Fig. 1)

(Seddon et al. 2013). The northern population is undergoing a severe decline due to successive poor breeding seasons and high adult mortality, thought to be primarily a result of 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, Department of Conservation 2020). At least 60–79% of the total yellow-eyed penguin population is estimated to breed in the subantarctic (Couch-Lewis et al. 2016, Department of Conservation 2020, Muller et al. 2020b), which is considered the stronghold for the species. The subantarctic population appears stable at present, but with evidence of wide fluctuations and a possible decline at the Auckland Islands since the 1980s (Moore 1992, Muller et al. 2020b). The Campbell Island population also fluctuated from 1987 to 1998 (Moore et al. 2001), but no recent data are available. Analysis of ancient DNA has shown that the original endemic mainland species *M. waitaha* went extinct soon after Polynesian settlement of New Zealand ca. 1280 CE (Boessenkool et al. 2009a, Collins et al. 2014). Yellow-eyed penguins from the subantarctic expanded their range into this vacant niche and colonised the mainland in the last few hundred years, prior to the increase of European settlers in the late 1800s (Boessenkool et al. 2009a). However, there is currently very little migration (<2%) between the mainland and subantarctic, meaning these areas represent separate populations and management units (Boessenkool et al. 2009b). Basic population ecology information is required for the southern population, which is data deficient (Muller et al. 2020b).

During breeding, yellow-eyed penguins are central-place foragers, and the northern population feeds in shallow coastal waters adjacent to their breeding area, and over mid-shelf areas further from shore where they have access to a large shelf area (Moore 1999, Mattern et al. 2007, 2013). Around mainland New Zealand, foraging trips are typically up to 25 km from shore and over mid-shelf areas, as confirmed by very high frequency (VHF) radio and GPS tracking studies (Moore 1999, Mattern et al. 2013), although the mean foraging distance can be as short as 6.2 km from shore at some locations (Mattern et al. 2007). Birds from Codfish Island may forage further from shore and over a wider area than birds from neighbouring Stewart Island (Mattern 2006). Many published studies on the northern population involved small numbers of birds, from different locations, in different years, and in some cases during different breeding phases (see Table 3). Consequently,

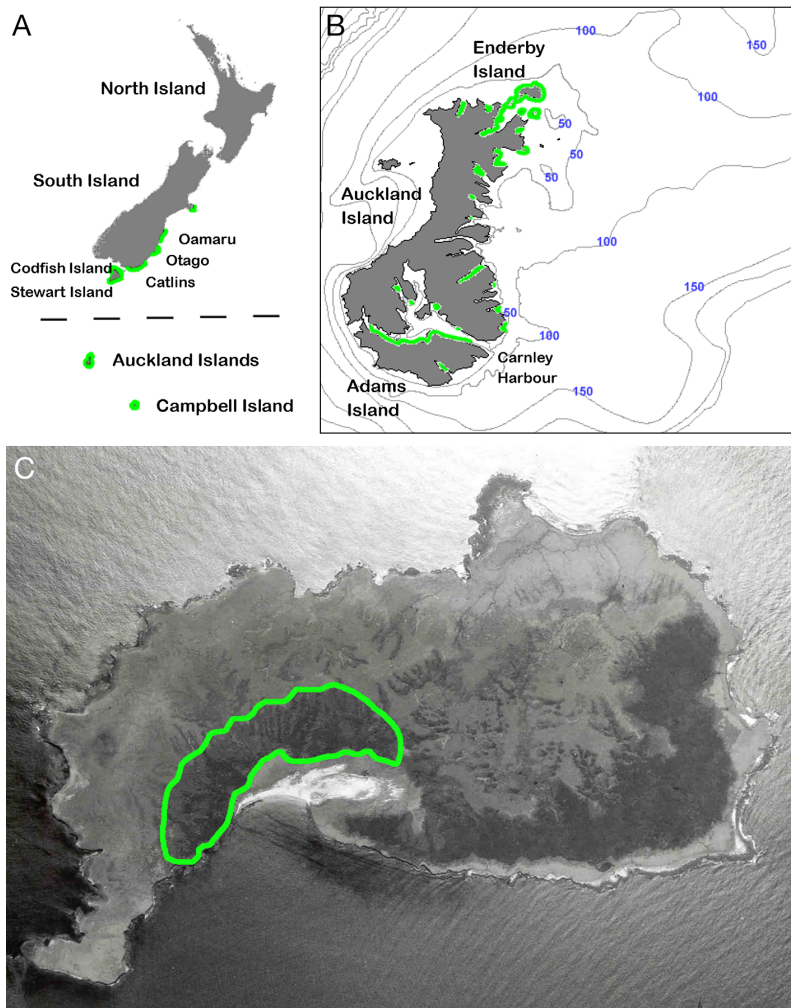


Fig. 1. (A) Breeding range of yellow-eyed penguins (green highlights) around the New Zealand mainland (northern population; above the dashed line) and in the subantarctic (southern population; below the dashed line). (B) Auckland Islands archipelago, with Enderby Island to the northeast (ca. 4.5 km wide, 50° 29' 45" S, 166° 17' 44" E). Selected depth contours are labelled in blue, from Mitchell et al. (2016). (C) Close-up of Enderby Island, showing the area where breeding birds were sampled (green). Modified from Fig. 1 in Muller et al. (2020a)

while some studies give a relatively good picture of what was happening during a particular time period and location, they may not represent the full range of foraging behaviour of the entire northern population. While diet studies in the 1990s showed occasional indications of pelagic foraging (van Heezik 1990, Moore et al. 1995), more recent dive data demonstrated a predominantly benthic foraging strategy for the mainland population (Mattern et al. 2007, 2013, Chilvers et al. 2014). In contrast, birds in the southern population use a mixed strategy incorporating varying amounts of pelagic foraging at the subantarctic Auckland Islands, including solely pelagic foraging

trips (Muller et al. 2020a). Moreover, subantarctic yellow-eyed penguins forage at greater depths than in many northern areas, with a maximum recorded depth of 134 m for benthic dive bouts, and 115 m for pelagic dives for Enderby Island birds (Muller et al. 2020a).

The ENSO is a weather phenomenon which influences rainfall, sea surface temperature (SST), and wind patterns in the Pacific Ocean (Null 2019). The 2015 austral summer was a very strong El Niño ($\geq 2.0^{\circ}\text{C}$ SST anomaly), and the 2016 and 2017 summers were both weak La Niña events (-0.5 to -0.9°C SST anomaly) (Null 2019). Yellow-eyed penguin foraging is negatively influenced by warmer water in the northern population (Young 2014, Mattern & Ellenberg 2018). Strong La Niña conditions result in warmer water and more stochastic weather and wind patterns in the New Zealand region, with an adverse effect on yellow-eyed penguin breeding success in the northern population (Young 2014). Increasing SST, which can result from La Niña conditions, may cause declines in the northern population in some years (Darby 2003, Mattern et al. 2017). SST and rainfall have the greatest effect on breeding parameters, including some lag effects in subsequent years (Peacock et al. 2000), although more research is needed to determine how variation in prey productivity is related to climate. There is no information about the effects of ENSO and climate variability on foraging and breeding success in subantarctic yellow-eyed penguins, and whether this may vary from the northern population.

The southern population displays widely variable breeding success, which is likely linked to foraging success (Moore 1992, Muller et al. 2020b). Foraging parameters are a product of the physical environment, changing environmental parameters, or individual preference to target specific prey in particular habitats. The subantarctic populations forage in deeper water and over greater distances than many mainland birds (Muller et al. 2020a) and may be expected to expend more energy foraging. There-

fore, the aims of this study were to determine the size and location of foraging areas used by yellow-eyed penguins breeding at Enderby Island in the New Zealand subantarctic (Fig. 1), as well as any differences in foraging area size and distance from shore between birds of different sex, diving behaviour, or between different years. We compared foraging habits to published data for the northern population. Given the importance of the southern population to the species, greater knowledge of foraging behaviour by subantarctic yellow-eyed penguins is vital to inform research on diving behaviour and breeding success in the area. This information will also assist with future conservation management of the species and marine-based threats in these isolated subantarctic areas.

2. MATERIALS AND METHODS

2.1. Fieldwork and equipment

Fieldwork was carried out on Enderby Island, Auckland Islands, in the New Zealand subantarctic (50° 29' 45" S, 166° 17' 44" E, Fig. 1). GPS data were collected for 2 breeding seasons; 2016 (November 2016–February 2017), and 2017 (November 2017–January 2018), while dive and breeding success data were collected for the 2015–2017 seasons in parallel studies (Muller et al. 2020a,b). Nests were located using manual ground searches, ground-based VHF telemetry, and an unmanned aerial vehicle equipped with a VHF radio receiver (Muller et al. 2019). Adult yellow-eyed penguins were captured by hand as they returned from sea and placed in a capture bag for processing and collection of morphometric data using a spring balance and callipers. Birds were marked with a microchip (Allflex) for permanent identification (Muller et al. 2020b), and sex was determined using the relationship between head length (including beak) and foot length (Setiawan et al. 2004), or the relative sizes between breeding partners with males assumed to be the larger individual (Setiawan et al. 2004).

Data loggers were deployed during late November and December, corresponding to the guard phase of breeding. GPS loggers were attached using waterproof tape (TESA) to the lower back to optimise streamlining (Bannasch et al. 1994) and orientation to the sky during the typical posture adopted during swimming or brooding (Muller et al. 2020a). For consistency, time–depth recorder (TDR) loggers were always taped to the centre of the back, below the



Fig. 2. Nesting yellow-eyed penguin with a time–depth recorder and very high frequency transmitter attached to the centre of the back, and a GPS logger attached to the lower back: inset shows close-up view. Enderby Island, Auckland Islands, New Zealand subantarctic. Photo credit: C. G. Muller

shoulder blades (Fig. 2) even when no other electronics were attached. GPS loggers were customised CatTraQ™ GPS loggers (Catnip Technologies), with time-to-fix of 45 s cold start, 35 s warm start, 1 s hot start. Units were modified for underwater use with the addition of a magnetic on/off switch, and a moulded resin housing (Pelletier et al. 2014), 45 × 30 × 12 mm, weight ~25 g. These GPS loggers have been used in a number of penguin foraging studies (Pelletier et al. 2014, Carpenter-Kling et al. 2017, Sánchez et al. 2018, Phillips et al. 2019). GPS loggers were programmed to record a fix every 3 min, providing a battery life of approximately 4–5 d. This was necessary, as birds remained on the nest for a period of time before commencing their logged foraging trip; the maximum foraging trip duration of all TDR deployments from 2015–2017 (n = 134) was up to 113.3 h (4.7 d) (Muller et al. 2020a), and fine-scale position logging was not needed to identify foraging locations. After programming, each GPS logger was waterproofed with heat-shrink tubing, weighing ~5 g (TE Connectivity) before deployment. TDR tags were LAT 1400 loggers with 128 kB of memory, 11 × 35 mm, weight 5 g (Lotek). These were programmed to log pressure every 5 s when wet, to allow sufficient data storage for long trips. VHF transmitters, V1G118A with 150 or 220 mm whip antenna, 20 × 13 × 6 mm, weight 4.5–5 g (Sirtrack) were attached to the dive loggers to monitor when penguins were ashore and assist with recovery of electronics. TDRs and VHF transmitters were attached following a similar protocol (Muller et al. 2020a). Where possible, loggers were retrieved after one foraging trip to minimise attachment time. Additional TDR-only deploy-

ments were carried out in 2015 and 2017, and 31 paired deployments in 2017 allowed comparison of dive behaviour with and without the addition of the larger GPS logger (Muller et al. 2020a).

2.2. Data analysis

Total trip duration was determined using the wet/dry switch on the TDR logger, as this was considered more accurate than the GPS log. GPS data files were downloaded and filtered by deleting any duplicate records (those with a distance of 0 m between subsequent positions), and any with implausible changes in distance or speed. Positions were interpolated to account for missed GPS fixes when the unit was underwater during a scheduled fix attempt. Interpolation used a custom-made script in Python 3.5.2 (Python Software Foundation, www.python.org), which added missed positions (at 3 min intervals) assuming a constant heading and velocity between recorded locations. Where multiple foraging trips were recorded in one deployment, the data were considered as separate trips (Muller et al. 2020a). Spatial analyses were performed in ArcGIS 10.2.2 (ESRI), with the National Institute of Water and Atmospheric Research (NIWA) New Zealand region bathymetry data at depth contours in 50 m increments overlaid for comparison (Mitchell et al. 2016). Points on land, generated before or after a foraging trip, were deleted using a spatial selection tool in ArcGIS. Data were projected in the New Zealand Transverse Mercator coordinate system, and geodesic distance calculations between points were automated in a Python script using the 'GeoPy' library.

The foraging distance (maximum straight-line distance away from the shore, measured from the sea access point) and the total trip distance (cumulative distance travelled between all points in a foraging trip, including the start and end location at the sea access point) were calculated from interpolated data. Summary data were calculated from these distances (mean \pm SD). Comparisons with trip data collected independently using the wet-dry switch on the TDR logger (Muller et al. 2020a) indicated that some GPS logs may have been partial trips, and may not accurately represent the furthest distance travelled. Consequently, these values represent minimum estimates of the actual foraging distances. For comparison, foraging distance means were also calculated with some partial trips ($\leq 5\%$ GPS fix success) removed. All

GPS fixes were included for all other distance analyses, statistical tests, and when determining area calculations.

Foraging areas were analysed using GME 0.7.3.0 (Spatial Ecology) and ArcGIS functions (Beyer 2012, Locher & Lindenberg 2016). Position data were grouped according to year, dive type, and sex for kernel density estimates (Worton 1989), which were determined with smoothed cross-validation bandwidth, and a cell size of 50 m. Values were calculated using 95 and 50% kernel contours to represent the home range and core foraging areas, respectively (Hamer et al. 2007), and isopleth and polygon features were imported into ArcGIS for further spatial analysis. The intersection between home range kernel density polygons was used to compare the percentage overlap of foraging activity location between groups of interest representing different years, sexes, and dive types (i.e. benthic or pelagic diving).

Dive data were categorised separately using Bayesian analysis (see Muller et al. 2020a). Individual dives were classified as benthic if they displayed an inter-dive depth change of less than 2.9% from both the previous and following dives. Foraging trips were also classified, with benthic trips having more than 3.6% benthic dives, which ensured that remaining trips classified as pelagic contained almost exclusively pelagic diving bouts (Muller et al. 2020a). Dive analysis included all dives > 2 m depth which likely included some travelling dives to and from the foraging area. Polygon areas were calculated in ArcGIS, along with percentage of spatial overlap between different foraging areas. All GPS data were used to determine foraging areas. When commuting, penguins swim quickly and surface only briefly (Mattern et al. 2007). Therefore, due to the time-to-fix and programmed fix rate of the GPS loggers, whenever a GPS fix was collected, the penguin was most likely resting at the surface between dives, rather than commuting.

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. Linear mixed effects models were used to compare maximum foraging distance and total trip distance with year, dive type, and sex (as fixed variables), and with bird ID as a random effect (since some birds made more than 1 trip). For each model, the homogeneity of variance was visually confirmed using residuals vs. fitted value plots. ANOVAs were

used to determine the significance of effects in each model. For comparison, statistical tests on distance were also repeated with subsequent trips by the same individual excluded from analysis, and separately with suspected partial trips ($\leq 5\%$ GPS fix success) excluded to see if these significantly affected the model results. Trip duration was also compared with foraging distance and total distance using a linear model. Graphs were generated in R, including the 'ggplot2' package (Wickham 2010).

3. RESULTS

3.1. Foraging area

A total of 91 GPS foraging tracks were collected (55 in 2016, and 36 in 2017), from 69 individual birds (Table 1; Table S1 in the Supplement at www.int-res.com/articles/suppl/m679p149_supp.pdf). These data included 51 trips made by 38 females and 39 trips by 30 males, plus 1 trip by 1 bird of unknown sex. Seven birds had GPS tracks logged for 2 or more foraging trips in 2017 and 2 birds in 2016, and 12 birds were tracked in both years, with 3 individuals tracked for multiple trips both between years, and during a year. Yellow-eyed penguins foraged over a continental shelf plateau approximately 30–40 km south-east of Enderby Island (Fig. 3), where the water depth is

Table 1. Summary of foraging logs collected from breeding yellow-eyed penguins from Enderby Island, New Zealand, showing the number of logs collected in each category, and the number of individual birds. Where multiple foraging trips were recorded in one deployment, the data were divided into separate trips. Not all deployments were successful, and in at least one case a logger collected multiple foraging trips before being recovered. More detail on the GPS tracks collected (including analysis by category) is summarised in Section 3, and the full list of foraging trips is shown in Table S1

Foraging logs		Individuals	
Year		Birds	
2016	55	Males	30
2017	36	Females	38
Total	91	Unknown	1
Sex		Total	69
Males	39		
Females	51		
Total	90		
Dive type			
Benthic	35		
Pelagic	52		
Total	87		

predominantly 50–100 m, with some spill-over into deeper water up to 150 m deep. Of the 87 GPS tracks where dive type was determined from accompanying TDR data, 35 (40%) corresponded to benthic and 52 (60%) to pelagic foraging trips, with 42% pelagic foraging in 2016 and 81% in 2017 (Table S1). Dive type could not be determined for 4 trips for which there were no corresponding dive records. A small subset of 11 birds (7 in 2016 and 4 in 2017) travelled to the northwest to forage off the northern coast of Auckland Island (Fig. 3), with 9 of these (82%) conducting pelagic foraging trips.

Birds travelled over a more extensive foraging area in 2016 compared to 2017 (Fig. 3A), with an estimated total foraging area size of 801 vs. 462 km², respectively (Table 2). Analysis of the intersection (overlap) between years (Fig. 3A) showed that only 37% of birds foraged in the overlap area in 2016, compared to 65% of birds in 2017 (Table 2). Benthic foraging trips covered a smaller area than pelagic trips (Fig. 3B), with estimated total foraging areas of 571 vs. 985 km², respectively (Table 2). Across all years, the benthic foraging area was smaller than the pelagic foraging area. The shared foraging area for dive type had a 91% overlap with the foraging area used by individuals undertaking benthic foraging (Fig. 3B), compared to only 52% overlap with the area used by pelagic foragers (Table 2). Females foraged over a much larger range than males (Fig. 3C), with foraging areas of 963 vs. 585 km², respectively (Table 2), and 85% of males foraged in this overlap area (Fig. 3C), compared to only 52% of females (Table 2).

3.2. Foraging distances

The largest foraging distance was 46.7 km from shore, and the mean across both years was 19.5 ± 12.6 (SD) km for all trips, or an estimated 23.8 ± 11.2 km with some suspected partial trips ($\leq 5\%$ GPS fix success, Fig. S2) removed. Foraging distance averaged an estimated 28.1 ± 9.2 km from shore in 2016 (max 46.7 km), and 14.8 ± 9.4 km from shore in 2017 (max 36.1 km) (Table 3). Total trip distance was also greater in 2016, with a maximum of 136.7 km and an estimated mean of 70.7 ± 25.8 km travelled (Table 3). Linear mixed-effects model results (Table S2) showed that the foraging distance was significantly greater in 2016 than 2017 (ANOVA, $\chi^2 = 24.63$, $p < 0.001$) and was also significantly greater for benthic than for pelagic foragers (ANOVA, $\chi^2 = 5.45$, $p = 0.020$). Pelagic foragers used a greater geographical

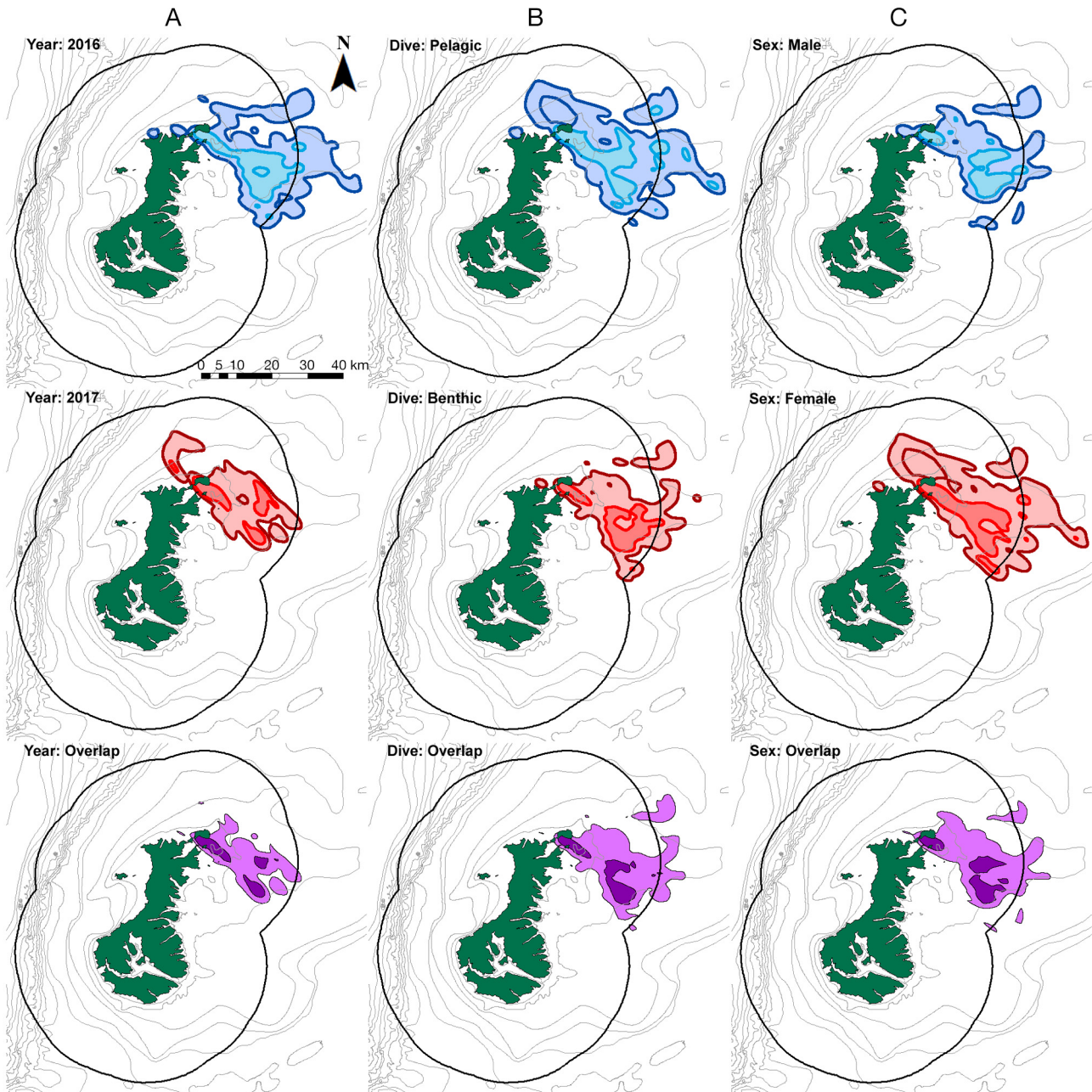


Fig. 3. Kernel density estimates of yellow-eyed penguin foraging trips to compare different parameters showing comparison by (A) year, (B) dive type, and (C) sex. In all cases, 95% contours (outer polygons) indicate combined home range use, and 50% contours (inner polygons) indicate combined core foraging area use. The spatial intersection of kernel density estimates (lower panels) show the overlap areas common to both parameters (upper and middle panels). The overlap outer 95% contours (violet) indicate shared home range use and inner 50% contours (purple) indicate shared core foraging use. Also shown on all maps are depth contours (light grey), for which selected depth values are labelled in Fig. 1, and the extent of the marine reserve 12 nautical miles from shore (black line)

area including travelling furthest from shore (Fig. 3B; Table S1). However, they also had a wider variation in foraging distance (Fig. S1A), and on average the pelagic foraging distance was closer to shore than for benthic foragers (Fig. 3B), suggesting that a greater number of pelagic birds foraged closer to shore. The

total trip distance was also significantly greater in 2016 compared to 2017 (ANOVA, $\chi^2 = 20.62$, $p < 0.001$), and benthic trips had significantly greater total distance than pelagic foraging trips ($\chi^2 = 6.45$, $p = 0.011$), although they showed a similar trend to foraging distance (Fig. S1B). Sex was not significant

Table 2. Combined foraging area size of breeding yellow-eyed penguins from Enderby Island, comparing different parameters (year, dive type, and sex). Areas were calculated from GPS data with the 95% confidence interval (CI) of kernel density estimates representing the combined foraging area used by all birds, and the 50% CI representing the combined core foraging area. For each comparison, the intersect parameter shows the size of the spatial overlap indicating the shared area common to both parameters, and overlap shows the percentage overlap of the shared intersect area for each parameter. Spatial representations of the areas for all parameters are shown on separate maps (Fig. 3)

Comparison	Parameter	Foraging area (95% CI)		Core foraging area (50% CI)	
		Area (km ²)	Overlap (%)	Area (km ²)	Overlap (%)
Year	2016	801	37	196	29
	2017	462	65	91	63
	Intersect	299	100	57	100
Dive type	Benthic	571	91	134	64
	Pelagic	985	52	203	42
	Intersect	517	100	86	100
Sex	Females	963	52	191	48
	Males	585	85	132	69
	Intersect	497	100	91	100

for foraging distance ($p = 0.2$), but males had a significantly shorter total trip distance (ANOVA, $\chi^2 = 4.8657$, $p = 0.0274$). There was a significant relationship between trip duration and foraging distance ($t = 4.40$, $p < 0.001$), and also total distance ($t = 5.60$, $p < 0.001$), with travelling further taking longer (Fig. S3). For the statistical tests on distance, the significance was the same when subsequent trips by the same individual were excluded from analysis. Significance was also the same when all trips were included as when some partial trips were excluded, except for foraging type, which was not significant for both foraging distance ($p = 0.15$) and total distance ($p = 0.07$) when partial trips were excluded. This suggests the relationship between dive type and distance is not as strong as for other factors.

4. DISCUSSION

Foraging by breeding yellow-eyed penguins during the guard phase was concentrated over a continental shelf plateau to the east of Enderby Island and primarily in water 50–100 m deep (Mitchell et al. 2016), where the substrate is a mixture of coarse sand, broken shells, coral, and pebbles (Tidey & Hulbe 2019, LINZ 2020). Foraging plasticity was evident between years, both for diving behaviour and foraging area use. Foraging distances were greater in 2016 than in 2017, and also greater than many data reported during the guard phase around mainland New Zealand where birds typically forage less than 25 km from shore (Moore 1999, Mattern et al. 2007, 2013). In 2017, in particular, there was evi-

dence that a subset of birds had shorter foraging distances (<10 km from shore), although there was some uncertainty due to the presence of partial trip records. This finding is comparable with mainland data, where birds foraged closer to shore during the guard phase, and some individuals habitually foraged <5 km from shore (Moore 1999). Together, these data suggest that 2016 may have been an unusual year at the Auckland Islands, with much longer and more widespread foraging trips. The foraging area size and distance from shore are related to the shape and size of the available continental shelf close to the breeding area, although use of this area can vary between breeding phases. In some years, foraging trips at Enderby Island appear to have longer duration during incubation than in other breeding phases (Muller et al. 2020b), so may result in a greater foraging area than these data from the guard phase. This is true for the northern population, where birds can be at sea for up to 6 d during incubation (Moore 1999), and where birds had greater foraging distances during incubation than during guard and post-guard breeding phases (Moore 1999). Trip duration was shorter on subantarctic Campbell Island during the guard phase, with some birds making 2 short foraging trips per day (Moore & Moffat 1990), likely indicating close proximity to foraging areas at that locality. Similarly at Long Point on mainland New Zealand, some individual birds made 2–3 trips per day (Moore 1999).

The total distance travelled per trip by Enderby Island birds was a mean of 48.7 ± 33.5 km (59.7 ± 30.2 km when some partial trips were excluded), and a maximum of 136.7 km, which was greater than at

Table 3. Foraging distance (maximum distance from shore) and total trip distance (cumulative distance travelled) of breeding yellow-eyed penguins from Enderby Island in different years. The first data series includes all trip data, including partial trips, therefore distances are likely underestimates. The second data series shows estimated (Est) means with some suspected partial trips ($\leq 5\%$ GPS fix success) removed for comparison. Also shown are the numbers of individual birds and foraging trips with valid GPS logs in each data series. Additional data from previous studies conducted at mainland sites are included for comparison

Reference	Location	Site	Year	Phase	Foraging distance (km)			Total distance (km)			No. birds	No. trips
					Mean	SD	Max	Mean	SD	Max		
This study	Subantarctic	Enderby Is	2016 (All)	Guard	25.2	11.4	46.7	63.2	30.7	136.7	52	55
	Subantarctic	Enderby Is	2017 (All)	Guard	10.8	9.1	36.1	26.7	24.6	95.4	29	36
	Subantarctic	Enderby Is	2016–17 (All)	Guard	19.5	12.6	46.7	48.7	33.5	136.7	69	91
	Subantarctic	Enderby Is	2016 (Est)	Guard	28.1	9.2	46.7	70.7	25.8	136.7	44	45
	Subantarctic	Enderby Is	2017 (Est)	Guard	14.8	9.4	36.1	37.1	26.1	95.4	20	22
	Subantarctic	Enderby Is	2016–17 (Est)	Guard	23.8	11.2	46.7	59.7	30.2	136.7	56	67
Mattern (2013)	Mainland	Boulder Beach, Otago	2004	Guard	21.1	5.9		54.5	12.0		8	
	Mainland	Boulder Beach, Otago	2005	Guard	11.0	3.1		30.5	10.3		4	
	Mainland	Boulder Beach, Otago	2012	Guard, post-guard	10.8	6.2		33.6	18.9		11	
Mattern (2007)	Mainland	Bushy Beach, Oamaru	2003	Guard, post-guard	6.2	0.8		15.9	1.2		5	
	Mainland	Bushy Beach, Oamaru	2003	Guard, post-guard	17.5	2.5		47.5	1.8		5	
	Mainland	Bushy Beach, Oamaru	2004	Guard	18.2	1.1		46.0	3.0		4	
	Mainland	Bushy Beach, Oamaru	2005	Guard	11.4	2.7		29.5	1.0		3	
Mattern (2006)	Stewart Is	Golden, Rollers beaches	2005	Guard	24.3	4.8		66.9	9.5		6	
	Codfish Is	Sealers Bay	2005	Guard	11.7	4.8		37.0	5.1		3	
	Stewart Is	Golden, Rollers beaches	2004	Post-guard	55.4	6.2		139.9	26.3		3	
	Codfish Is	Sealers Bay	2005	Post-guard	14.4	7.2					6	
Moore (1999)	Mainland	Boulder Beach, Otago	1990	Post-guard	23.3	11.2					13	
	Mainland	Boulder Beach, Otago	1991	Incubation	13.4	6.1					10	
	Mainland	Boulder Beach, Otago	1991	Guard	15.5	8.7					10	
	Mainland	Boulder Beach, Otago	1991	Post-guard	14.0	8.6					14	
	Mainland	Boulder Beach, Otago	1992	Incubation	14.4	5.8					10	
	Mainland	Boulder Beach, Otago	1992	Guard	12.4	6.1					10	
	Mainland	Boulder Beach, Otago	1992	Post-guard	11.1	7.2					9	
Mattern (2013)	Mainland	Long Point, Catlins	1991	Post-guard	9.4	5.3					10	
	Mainland	Long Point, Catlins	1992	Post-guard								

many northern population locations where penguins typically swam a total of 31 ± 10 km per trip with extremes of 55 ± 12 km recorded (Mattern et al. 2013). The northern population is considered to comprise predominantly benthic foragers with only benthic dives published in studies using dive loggers (Mattern et al. 2007, 2013, Chilvers et al. 2014), although there is evidence for some pelagic foraging from diet and other studies (van Heezik 1990, Moore et al. 1995, Mattern et al. 2018). In contrast, our data demonstrate that birds in the subantarctic Auckland Islands show a much greater degree of diving plasticity. They have a mixed diving strategy incorporating varying amounts of pelagic foraging between and within seasons, including solely pelagic foraging trips (Muller et al. 2020a). Changes in diving behaviour between years also corresponded with changes in foraging behaviour, including home range size and distance travelled. Foraging trip duration in the subantarctic also changed between years, with trips in 2017 significantly shorter than trips in 2015 and 2016, although there was no difference evident between the sexes (Muller et al. 2020a).

4.1. Changes in foraging behaviour

In 2016, birds foraged further from shore, over a larger area, and with a smaller overlap of shared areas than in 2017, when the foraging home range area reduced in size by 340 km^2 or 42% (Fig. 3A). Mean foraging distance was significantly greater for benthic foragers than pelagic foragers in both years. The majority of benthic foraging took place in an area centred approximately 20–25 km from shore (Fig. 3B), and utilising a smaller

area than pelagic foraging. However, pelagic foragers also displayed greater variance in foraging distance, with the majority of foraging closer to shore than benthic foragers, but others using a much larger and more variable area, including travelling further from shore than benthic foragers (Fig. 3B). Benthic diving, especially in deep water, can use more energy than other types of diving (Costa et al. 2004, Chilvers & Wilkinson 2009), so this may represent a greater energy expenditure by birds conducting benthic foraging. Given that both benthic and pelagic diving occurred together in some locations (the overlap areas), this indicates that dive type was not governed by bathymetry or water depth in these shared areas.

Additional dive logger data showed that the proportion of pelagic foraging trips increased each year with none recorded in 2015 (Muller et al. 2020a) and increasing proportions in 2016 and 2017. Since pelagic foraging was associated with a larger foraging area size (Fig. 3B), it might be expected that the overall foraging area size would be greater in 2017 when the highest proportion of pelagic diving was recorded. However, the foraging area was actually smaller in 2017 than in 2016 (Fig. 3A), although sample size was also smaller in 2017. Foraging area use is therefore likely influenced by additional complexity related to the type and distribution of prey species available each year, and possibly conditions for all types of foraging were less favourable in 2017. Cameras deployed on mainland birds indicated that pelagic foraging there was generally on poorer quality prey items such as jellyfish and other gelata, and was associated with poor visibility at the sea floor which prevented benthic foraging (Mattern & Ellenberg 2018).

During 2017, a total of 28% of birds changed their diving behaviour (from benthic to pelagic, or vice versa) on a subsequent trip in the same year, and 56% changed their behaviour between different years (Muller et al. 2020a). This demonstrates plasticity of dive type for individual birds, and the general change in foraging locations between years also suggests a large degree of plasticity in foraging area use. There is no difference in diving behaviour between male and female birds in the subantarctic (Muller et al. 2020a), although females may have been foraging over a wider area during the guard phase (Fig. 3C), with only 51.6% overlap with the shared foraging area, compared to 85.1% overlap for males.

Mean \pm SD foraging distances for mainland New Zealand yellow-eyed penguins ranged from 6.2 ± 0.8 to 23.3 ± 11.2 km (Table 3), although these included

data collected using different methods, and during different breeding phases and years when birds may have foraged differently (Moore 1999, Mattern et al. 2007, 2013). Mean and maximum mainland foraging distances were closer to shore than in the subantarctic; however, statistical comparison between these data sets was not possible. The northern population displays a generally consistent benthic foraging strategy, using the same foraging areas consistently over different years (Mattern et al. 2007). However, while mainland birds tend to forage either close to shore or further from shore, some could switch strategies (Moore 1999) and foraging areas (Moore et al. 1995, Moore 1999), indicating a degree of foraging plasticity in the northern population as well. Since these populations are genetically similar (Boessenkool et al. 2009a), any differences are likely due to the local environment and prey availability (Muller et al. 2020a), rather than any inherent behavioural differences.

This study reports on the foraging area used by breeding penguins during the guard phase when parental attendance at the nest is high (Richdale 1957, Darby et al. 1990). However, many penguin species forage over considerably larger areas during incubation and post-guard phases of the breeding season compared to the guard phase (Jouventin et al. 1994), including an area over 5 times larger for little penguins *Eudyptula minor* (Sánchez et al. 2018). In little penguins, foraging closer to the colony during chick-rearing was also associated with a diet switch to higher trophic level prey (Poupart et al. 2017), and the mean maximum foraging distance in winter was significantly larger (up to 8 times greater) than during the breeding season (Hoskins et al. 2008, McCutcheon et al. 2011). Yellow-eyed penguins in the northern population travel further from the breeding area during incubation and post-guard stages (Moore 1999) and in winter (M. Young pers. comm.). Therefore, given that no foraging data are available for other breeding phases in the subantarctic, the foraging areas and distances described here should be regarded as minima for yellow-eyed penguins from Enderby Island. Our data also tended to show that larger datasets represented larger foraging areas, so collecting additional data may reveal additional areas used by penguins. However, sampling a greater number of birds than in this study is likely impractical due to logistics and ethical concerns for this Endangered species.

While the attachment of any device to a diving animal can introduce hydrodynamic drag, this was minimised by using smaller individual loggers, and by

attaching the loggers as far back as possible to maintain streamlining (Bannasch et al. 1994). In particular, it is possible that carrying the larger GPS loggers may have influenced behaviour. However, Muller et al. (2020a) showed that the type of loggers deployed (TDR only, or TDR + GPS), or the deployment order did not have a biologically significant effect on diving behaviour (the difference in dive depth was 0.55 m, which was less than the error margin of the loggers).

4.2. Foraging and breeding success

The weak La Niña conditions during the 2016 and 2017 seasons corresponded to increasing amounts of pelagic foraging (Muller et al. 2020a), as well as to greater breeding effort and success in 2016 (Muller et al. 2020b). Strong La Niña conditions can increase SST and have a greater negative effect on northern yellow-eyed penguin breeding success than during El Niño conditions (Young 2014), although effects on breeding success can manifest in subsequent years (Peacock et al. 2000). Therefore, more investigation is needed on the interaction between the strength of ENSO cycles, foraging, diet, and breeding success in the subantarctic. During 2015, the proportion of benthic foraging at Enderby Island (100%) was greater than in subsequent years (Muller et al. 2020a), and since benthic foraging generally took place over a smaller area (Fig. 3B), it follows that smaller foraging areas would be expected during El Niño conditions. While we do not have GPS data from 2015 to confirm this, trip times in 2015 (mean and maximum duration) were longer than in 2016, which would be consistent with more benthic foraging, although the difference was not significant (Muller et al. 2020a). Yellow-eyed penguin prey species in the subantarctic are unknown, and it is not known whether prey assemblages at the Auckland Islands are consistent in the region during different ENSO conditions. Further research is needed to confirm how ENSO conditions may affect prey species distribution in space and time, and to what extent this affects yellow-eyed penguin foraging and breeding success.

Travelling greater distances resulted in longer times at sea, although this may not always be the case. For subantarctic yellow-eyed penguins, pelagic foraging trips were not significantly different in time duration from benthic trips (Muller et al. 2020a), or in total trip length (Fig. S1B), although individual trip distances could vary. Trips in 2016 were significantly longer in duration than in 2017 (Muller et al. 2020a),

and foraging areas were also larger (Fig. 3A), although breeding success was better (Muller et al. 2020b). These findings tend to contradict the conclusions of other studies. For example, longer foraging trips in other seabirds including Magellanic *Spheniscus magellanicus*, Adélie *Pygoscelis adeliae*, and little penguins were directly related to lower breeding success (Chiaradia & Nisbet 2006, Boersma & Rebstock 2009). Changes in prey availability, particularly the distance travelled to obtain it, will affect the effort required (Miller & Sydeman 2004). This, in turn, affects both adult energetics and chick provisioning; longer travel or search times by foraging parents can result in less-frequent feeding of chicks, and may result in lower growth rates and fledging weights for chicks (Kitaysky et al. 2000, Davoren & Montevecchi 2003, Pinaud et al. 2005). Longer foraging trips may also result in more food digestion, with less available for transfer to offspring (Weimerskirch et al. 1994, Ropert-Coudert et al. 2004). Increased energy expenditure by foraging adults may lead to a reduction in their body condition (Arnould et al. 1996, Shaffer et al. 2003), as well as breeding success (Inchausti et al. 2003), thereby influencing long-term survival and evolutionary fitness of breeders. However, the larger foraging area in 2016 may have allowed birds to exploit prey which was further from shore, or distributed more widely, but which justified traveling greater distances to obtain it. Nevertheless, any factors affecting the type and distribution of prey which may require travelling greater distances or spending more time at sea could have a negative effect on future yellow-eyed penguin breeding success.

4.3. Foraging and conservation management

Enderby Island represents over 50% of the breeding population for the Auckland Islands archipelago, and will likely continue to be the main breeding location in the future unless introduced predators are removed from Auckland Island (Muller et al. 2020b). Only part of the foraging area used by Enderby Island birds is protected from potential fisheries interactions by the Auckland Islands Motu Maha Marine Reserve, which extends 12 nautical miles (22.22 km) from shore (Fig. 3). Although no yellow-eyed penguins were reported as bycatch in the trawl fishery around the Auckland Islands during the period of this study (Ministry of Primary Industries 2018), fisheries activities such as bottom-trawling modify the benthos and may affect penguin foraging (Browne et al. 2011). Indirect competition with fisheries has been

linked to declines in some mainland yellow-eyed penguin populations (Ellenberg & Mattern 2012). Therefore, research into the direct and indirect impacts of fishing activities on yellow-eyed penguins in the Auckland Islands area is crucial for their long-term conservation. The core foraging areas (represented by the 50% isopleths) were contained within the marine reserve boundary, and the home range of all penguins we examined (represented by the 95% isopleths) contained 595 km² (81%) of foraging area within the marine reserve. However, the areas presented here represent minimum estimates of the habitat used, and therefore a larger area than the current marine reserve would be required to fully protect the yellow-eyed penguin at the Auckland Islands. Further research is needed into foraging area use during other breeding phases, including incubation, post-guard, pre-moult, and winter foraging, as foraging areas may be larger at these times. Additionally, we recommend further research on other breeding populations in the Auckland Islands area, as foraging conditions may differ. For example, birds breeding at Carnley Harbour in the south may have a smaller foraging area available, as the shelf drops off to 150 m deep and beyond benthic diving range within only 11 km of the harbour entrance.

5. CONCLUSIONS

The yellow-eyed penguin was classified as Endangered in 2000 and numbers have continued to decline, particularly for the northern population (Couch-Lewis et al. 2016, BirdLife International 2020, Department of Conservation 2020). This study of yellow-eyed penguins at Enderby Island found foraging plasticity between years, including differing foraging behaviour and locations. Some foraging trips during the guard phase covered greater distance and area compared with northern populations, with any differences likely a result of local conditions, rather than any inherent differences between these 2 genetically similar populations. However, the subantarctic environment may predispose the southern population to more difficult foraging conditions. Ongoing monitoring of foraging and breeding success is needed to ensure timely warnings if poor foraging seasons combine with other factors to initiate or exacerbate population declines in the subantarctic. Management should also include appropriate protection of foraging areas used by yellow-eyed penguins, with the data presented here considered as a minimum estimate.

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