Foraging plasticity of yellow-eyed penguins (Megadyptes antipodes) in their subantarctic range

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Title page

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Running page head

Variable foraging in yellow-eyed penguins

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Author Statement

CGM conceived and designed the experiments, carried out the fieldwork, analysed the data, and wrote the paper. RKF assisted with fieldwork and data collection, and data analysis. AC, AK, and YR-C supplied GPS devices and gave advice on data analysis. BLC and PFB provided general oversight, and assisted with ecological aspects of the project. All authors reviewed the manuscript and gave final approval for publication.

ABSTRACT

Foraging behaviour is crucial to the breeding success for marine predators, including seabirds. Yellow-eyed penguins (*Megadyptes antipodes*) are central-place predominantly benthic foragers around mainland New Zealand. The mainland population of this iconic species is declining, with changes in the marine environment a suspected cause, in particular, warming water and poorer foraging success. Here, we undertook a detailed foraging study of the ancestral subantarctic population which is genetically separate from the northern population. Over two breeding seasons, we collected GPS logs

from 94 deployments on 75 breeding yellow-eyed penguins foraging from Enderby Island, Auckland Islands, New Zealand. Birds foraged up to 47 km from shore, more than twice as far as yellow-eyed penguins in many areas around mainland New Zealand. Foraging area size and maximum range (distance from shore) were larger in a year of greater breeding effort (2016), and also for females, and birds undertaking pelagic foraging trips. Differences in foraging behaviour are likely influenced by local bathymetry, environmental conditions, and individual preference. Despite comparable bathymetry in some areas, the southern population shows greater foraging plasticity than seen in the northern population, implying foraging conditions may be less restricted in the subantarctic. However, previous studies have shown breeding success at the Auckland Islands is inconsistent, and differing foraging behaviour between years indicates foraging conditions are likely variable. Prey availability and foraging success are also expected to be affected by warming water, with implications for future breeding success particularly from the effects of climate change and El Niño Southern Oscillations (ENSO).

1. INTRODUCTION

Many marine predators are central-place foragers, such as 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 conditions, 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, Catry et al. 2013, Agnew et al. 2015, Ropert-Coudert et al. 2015, Poupart et al. 2017). 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, other 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 are 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). These dives tend to have a shorter bottom time 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 (hōiho, *Megadyptes antipodes*) are endangered (Couch-Lewis et al. 2016, IUCN 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, Figure 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). Over 60% of the total yellow-eyed penguin population breeds in the subantarctic (Couch-Lewis et al. 2016, 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 since the 1980s (Moore 1992, Muller et al. 2020b). Analysis of ancient DNA has shown that the original endemic mainland species *M. waitaha* went extinct soon after Polynesian settlement of New Zealand c.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 prior to the increase of European settlers in the late 1800s (Boessenkool et al. 2009a). However, there is currently almost no migration (<2%) between the mainland and subantarctic, meaning these areas represent separate populations and management units (Boessenkool et al. 2009b). Despite the importance of the southern population to the species, there is little information available on yellow-eyed penguin foraging behaviour in the subantarctic, and whether foraging differs from the northern population.

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 offshore where they have access to a large shelf area (Moore 1999, Mattern et al. 2007, Mattern et al. 2013). Around mainland New Zealand, foraging trips are typically up to 25 km from shore and over mid-shelf areas, as confirmed by VHF and GPS tracking studies (Moore 1999, Mattern et al. 2013), although the mean foraging range can be as short as 6.2 km offshore at some locations (Mattern et al. 2007). While diet studies in the 1990s showed occasional indications of pelagic foraging (van Heezik 1990, Moore et al. 1995), more recent dive data had demonstrated a predominantly benthic foraging strategy for the mainland population (Mattern et al. 2007, Mattern et al. 2013, Chilvers et al. 2014). In contrast, birds in the southern population utilise 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 depth of 134 m for benthic dive bouts, and 115 m for pelagic dives (Muller et al. 2020a).

Yellow-eyed penguin foraging is negatively influenced by warmer water in the northern population (Young 2014, Mattern & Ellenberg 2018). 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 (Young 2014). El Niño conditions result in more variable breeding success than in neutral ENSO conditions (Peacock et al. 2000, Darby 2003). 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 individuals' 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. Therefore, in light of this variability, and the importance of the subantarctic population to the species, a study of foraging parameters was urgently needed in the southern population.

This study determined the size and location of foraging areas used by yellow-eyed penguins breeding at Enderby Island in the New Zealand subantarctic (Figure 1). We compared foraging habitats to published data for the northern population. Given the importance of the southern population to the species, the knowledge of foraging area use by subantarctic yellow-eyed penguins is vital to complement research on diving behaviour and breeding success in the subantarctic. This information

could assist with future conservation management of the species and marine-based threats in these isolated subantarctic areas.

2. MATERIALS & METHODS

2.2. 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, Figure 1) for three breeding seasons; 2015 (Nov 2015–Feb 2016), 2016 (Nov 2016–Feb 2017), and 2017 (Nov 2017–Jan 2018). GPS data were collected in 2016 and 2017, while dive and breeding success data were collected in all three years in parallel studies (Muller et al. 2020a, Muller et al. 2020b). Nests were located using manual ground searches, ground-based VHF telemetry, and an Unmanned Aerial Vehicle (UAV) equipped with a Very High Frequency (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, Palmerston North, New Zealand) for permanent identification (Muller et al. 2020b) 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 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, Beiersdorf, Germany) (Muller et al. 2020a) to the lower back to optimise streamlining and orientation to the sky during the typical posture adopted during swimming or brooding. Other data loggers were taped to the upper back on the midline to maximise streamlining (Figure 2). GPS loggers were customised CatTraQ™ GPS loggers, 14 × 35 × 70 mm, weight ~30 g (Catnip Technologies, USA) modified for underwater use with the

addition of a magnetic on/off switch, and a moulded resin housing (Pelletier et al. 2014). GPS loggers were programmed to record a fix every 3 minutes, providing a battery life of approximately 4–5 days. After programming, each unit was waterproofed with heat-shrink tubing (TE Connectivity, Schaffhausen, Switzerland) before deployment. Time Depth Recorders (TDR) and VHF transmitters were also attached following a similar protocol (Muller et al. 2020a). Where possible, loggers were deployed for one foraging trip before being recovered to minimise potential disturbance. All deployments in 2016 consisted of a GPS and TDR logger (Table 1). Of the total deployments in 2017, a subset of 31 birds received two logger deployments of either a GPS + TDR, or a TDR only, followed by the alternative in a subsequent trip, with the deployment order randomised (Muller et al. 2020a). The remaining unpaired trips in 2017 included 10 GPS + TDR deployments, and two TDR only deployments.

2.3. Data Analysis

GPS data files were downloaded and filtered by deleting any duplicate records (those with a distance of 0 m between subsequent positions), then interpolated to account for missed GPS fixes (at 3 min intervals) when the unit was underwater during a scheduled fix attempt. Interpolation assumed a constant heading and velocity between recorded locations and used an automated script in Python 3.5.2 (Python Software Foundation, Beaverton USA, available at www.python.org). Where multiple foraging trips were recorded in one deployment, the data were considered as separate trips (Muller et al. 2020a). Data were displayed in ArcGIS 10.2.2 (ESRI), with NIWA New Zealand region bathymetry data at 50 m depth contours overlaid for comparison (Mitchell et al. 2016). Points on land were deleted using a spatial selection tool in ArcGIS. Data were projected in the NZTM coordinate system, and geodesic distance calculations between points were automated in a Python script using the GeoPy library.

The foraging range (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) were calculated from interpolated data. Summary data were calculated from these distances (mean + SD). When calculating mean distances, short trips (<10 km foraging range, or <25 km total distance) and with low GPS fix success (<20%) were excluded to avoid biasing distance measurements, since these may not have represented the furthest distance travelled. However, all GPS fixes were included for area calculations and other analyses.

Foraging range areas were analysed using GME 0.7.3.0 (www.spatialecology.com) and ArcGIS functions (Beyer 2012, Locher & Lindenberg 2016). Kernel Density Estimates (KDE) were determined with smoothed cross-validation bandwidth which provided the best visually-estimated match with data point concentrations, 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 generated for spatial analysis in ArcGIS. Foraging area calculations were determined using the 95% confidence interval. The intersection between 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 the previous AND following dive. Foraging trips were also classified, with benthic trips having more than 3.6% benthic dives, which ensured that remaining trips classified as pelagic contained entirely pelagic diving bouts (Muller et al. 2020a). Dive analysis included all dives greater than 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. Only GPS data were used to

determine foraging areas to avoid skewing habitat use, i.e. excluding interpolated positions which were more likely to occur during transits to and from foraging locations when penguins swim quickly and surface only briefly (Mattern et al. 2007).

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). Linear mixed effects models were used to compare maximum foraging range and total trip distance with year and forage type (as fixed variables), and with bird ID as a random effect (since some birds made more than one trip). ANOVA tests were used to determine the significance of these effects in each model. Graphs were generated in R, including the ggplot2 package (Wickham 2010).

3. RESULTS

3.1. Foraging Area

A total of 87 GPS foraging tracks were collected (52 in 2016, and 35 in 2017), from 69 individual birds (Table S1). These data included 48 trips made by 38 females and 38 trips by 30 males, plus one trip by one bird of unknown sex. Yellow-eyed penguins foraged on an offshore continental shelf plateau approximately 30 – 40 km south-east of Enderby Island (Figure 3), where the water depth is predominantly 50 – 100 m, with some spill-over into deeper water up to 150 m deep. Of all tracks, 32 corresponded to benthic and 52 corresponded to pelagic foraging trips. Dive type could not be determined for three trips where there were no corresponding dive records. A small subset of eleven birds (seven in 2016 and four in 2017) travelled to the northwest to forage off the northern coast of Auckland Island (Figure 3), with nine of these (82%) conducting pelagic foraging trips.

Birds travelled over a more extensive range in 2016 compared to 2017 (Figure 3A, upper and middle panels), with an estimated total foraging area size of 801 vs 462 km^2, respectively (Table 2). Analysis

of the intersection (overlap) between years (Figure 3A, bottom panel) showed only 37% of birds foraged in the overlap area in 2016, compared to 64% of birds in 2017 (Table 2). Benthic foraging trips covered a smaller area than pelagic trips (Figure 3B, upper and middle panels), with estimated total foraging areas of 571 vs 985 km^2, respectively (Table 2). Across all years the benthic foraging area than was smaller than for pelagic foraging. The shared home range area had a 91% overlap with the foraging area used by individuals undertaking benthic foraging (Figure 3B, bottom panel), compared to only 53% overlap with the area used by pelagic foragers (Table 2). Females foraged over a much larger range than males (Figure 3C, upper and middle panels), with foraging areas of 963 vs 585 km^2, respectively (Table 2) and 85% of males foraged in this overlap area (Figure 3C, bottom panel), compared to only 52% of females (Table 2).

3.1. Foraging Distances

The largest foraging range was 46.7 km offshore, with a mean of 27.8 ± 7.5 km. The longest total trip distance was 151.9 km, with a mean value of 69.2 ± 26.7 km (Table 3). Linear mixed-effects models showed that the foraging range was significantly greater in 2016 than 2017 (χ^2=19.78, p<0.0001) and was also significantly greater for benthic foragers than for pelagic (χ^2=8.53, p=0.014). Although pelagic foragers used a greater geographical area including travelling furthest from shore (Figure 3B) their shorter mean foraging range can be explained by the wide variation (Figure S2A), with the mean value of the core foraging range closer to shore than for benthic foragers (50% contours, Figure 3B). The total trip distance was also significantly greater in 2016 compared to 2017 (χ^2=13.82 p<0.001) but there was no significant difference between benthic or pelagic foraging trip types (χ^2=4.86, p=0.088). Sex was not significant for foraging range (p=0.36), or total trip distance (p=0.187).

3.2. Foraging Changes

In 2016, individuals foraged over a larger area and had a smaller overlap of shared areas indicating birds were foraging more widely than in 2017, when the foraging home range area reduced in size by

340 km^2 or 42% (Figure 3A). Birds also foraged further offshore in 2016 (Table 3), and on average foraging range was greater for benthic foragers than pelagic foragers in both years (Figure S2A). However, pelagic foragers had a much wider spread in their foraging range including travelling the greatest distance offshore (Table S1, Figure S2), and had a much larger foraging home range at the 95% CI (Figure 3B). The total trip distance showed a similar trend (Figure S2B) although this was not significantly different between benthic and pelagic foraging.

4. DISCUSSION

Foraging by breeding yellow-eyed penguins was concentrated over a plateau to the east of Enderby Island where the maximum water depth is up to 150 m (Mitchell et al. 2016), and the substrate is a mixture of coarse sand, broken shells, coral, and pebbles (Tidey & Hulbe 2019, LINZ 2020). The foraging range of Enderby birds averaged up to 30.5 km offshore in 2016, with a maximum of 46.7 km (Table 3), but was less in other years. This is larger than ranges reported for the northern population which typically forage a maximum of 25 km from shore around mainland New Zealand (Moore 1999, Mattern et al. 2007, Mattern et al. 2013). The total distance travelled per trip by Enderby Island birds was also greater than at many northern population locations, where penguins typically swam around 31 ± 10 km per trip with extremes of 55 ± 12 km recorded (Mattern et al. 2013). The northern population are considered to be predominantly benthic foragers with only benthic dives published in studies using dive loggers (Mattern et al. 2007, Mattern et al. 2013, Chilvers et al. 2014), although there is possible evidence for occasional pelagic foraging from diet and other studies (van Heezik 1990, Moore et al. 1995, Mattern et al. 2018). Conversely, birds in the subantarctic Auckland Islands show a much greater degree of diving plasticity. They demonstrate 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 changes between years, with trips in 2017 significantly shorter than trips in 2015 and 2016, but there is no difference between the sexes (Muller et al. 2020a).

4.1. Changes in foraging behaviour

Individuals foraged over a larger area with a smaller overlap in 2016 than in 2017. Mean foraging range was greater for benthic foragers than pelagic foragers in both years. This difference suggests that while benthic foragers may have travelled further offshore on average to reach their foraging area, pelagic foragers generally covered similar distances while searching for prey although they utilised a much larger and more variable area. 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. In all years benthic foraging took place over a smaller area than pelagic 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.

Dive logger data from the same study published elsewhere showed the proportion of pelagic foraging trips increased each year from none in 2015, to 79% in 2017 (Muller et al. 2020a). Pelagic foraging was associated with a larger foraging area size in our data (Figure 3B) which might be expected to result in increasing foraging area size over the same period. However, while the highest proportion of pelagic diving was in 2017, the foraging area was actually smaller in 2017 than in 2016 (Figure 3A), although sample size was also smaller in 2017. Foraging area use is therefore likely affected by additional complexity in the type of prey species and their spatial distribution each year. During 2017 a total of 28% of birds changed their diving behaviour on a subsequent trip in the same year, and 56% changed their behaviour between different years (Muller et al. 2020a). This indicates diving plasticity is

present in the subantarctic, and given the link between diving behaviour and foraging this implies plasticity in foraging area use also. 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 (Figure 3C), with only 51.6% overlap with the shared foraging area, compared to 85.1% overlap for males.

In comparison, mean foraging ranges for mainland New Zealand yellow-eyed penguins ranged from 6.2 ± 0.8 (SD) km to 23.3 ± 11.2 (SD) km (Table 3), although these included data collected using different methods, and during different breeding phases and years where birds may have foraged more widely (Moore 1999, Mattern et al. 2007, Mattern et al. 2013). Mean and maximum mainland foraging ranges 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 utilising the same foraging areas consistently over different years (Mattern et al. 2007). However, while mainland birds tend to be either inshore or offshore foragers, some could switch strategies (Moore 1999), and foraging areas (Moore et al. 1995, Moore 1999), indicating some foraging plasticity in the northern population as well. Differences are likely due to the local environment and prey availability (Muller et al. 2020a), rather than any inherent behavioural differences between these genetically similar populations (Boessenkool et al. 2009a).

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 five times larger for little penguins (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 range in winter was significantly larger (up to eight 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 described here should be regarded as a minimum estimate of the total area used by yellow-eyed penguins from Enderby Island, which may be considerably larger. Our data also tended to show that larger datasets with more positions represented larger foraging areas, so more data may reveal additional use areas. However, these sample sizes were considerably larger than for comparable studies on the northern population, and increasing the sample size is likely impractical due to logistics and ethical concerns for this endangered species.

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) did not have a biologically significant effect on diving behaviour or deployment order (the difference was 0.55 m, which was less than the error margin of the loggers).

4.3. Foraging and breeding success

In the Auckland Islands, there was a much greater number of breeding birds and a higher overall breeding success (total number of fledged chicks) in 2016 than in 2015 or 2017 (Muller et al. 2020b). This also coincided with an increase in pelagic foraging from 2015 to 2017 (Muller et al. 2020a). A foraging strategy's success will depend on the trip duration, distance travelled and the return for effort, which will be affected by the distribution and quality of prey, and the effort required for capture (Costa

2015). Therefore, the switch from predominantly benthic foraging behaviour in 2015 indicates that during 2016 and 2017 pelagic foraging likely provided greater returns that outweighed benthic foraging. A favourable pelagic food source may have provided nutritional benefits outweighing the energy requirement of foraging over a larger area to obtain it. However, while the breeding population and breeding success both declined in 2017 (Muller et al. 2020b), the proportion of pelagic foraging trips continued to increase compared to previous years (Muller et al. 2020a). This difference suggests a more complex interaction between foraging and breeding success, suggesting that conditions for all types of foraging were less favourable in 2017.

The 2015 breeding season corresponded with severe El Niño conditions (Null 2019), which have been linked to a local decline of prey species and poorer foraging and breeding outcomes for yellow-eyed penguins than during neutral ENSO conditions (Peacock et al. 2000, Darby 2003). The 2016 and 2017 seasons both had weak La Niña conditions (Null 2019) which have a stronger negative effect on northern yellow-eyed penguin breeding success than El Niño conditions (Young 2014). Benthic foraging generally took place over a smaller area (Figure 3B), and the proportion of benthic foraging was greatest during the El Niño season in 2015 (Muller et al. 2020a). Therefore, the 95% CI of the foraging home range would also be expected closer to shore during El Niño conditions. While we do not have GPS data from 2015 to confirm this, trip times in 2015 were significantly shorter than in 2016 (Muller et al. 2020a), implying a more compact foraging area, and possibly closer to shore. It is not known whether prey assemblages are consistent in this area during different ENSO conditions, so 2015 may not have been representative of all El Niño seasons. Yellow-eyed penguin prey species in the subantarctic are unknown, as is their distribution in space and time, so this would require further research to confirm.

Travelling greater distances can result in longer times at sea, although this is not always the case. For subantarctic yellow-eyed penguins, pelagic foraging trips are not significantly different in time duration from benthic trips (Muller et al. 2020a), or in total trip length (Figure S2B), although individual trip distances could vary. Trips in 2017 were of significantly shorter time than in 2016 (Muller et al. 2020a), which is consistent with the smaller foraging area utilised (Figure 3A). Longer foraging trips in seabirds including Magellanic (*Spheniscus magellanicus*), Adélie (*Pygoscelis adeliae*), and little penguins (*Eudyptula minor*) are 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. Therefore, 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.

4.4. Foraging and conservation management

Enderby Island holds 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 predators are removed from Auckland Island (Muller et al. 2020b). Only part of the foraging area used by Enderby Island birds is protected from fisheries interactions by the Auckland Islands Motu Maha Marine Reserve which extends 12 nm from shore (Figure 3) Although there was no mortality of yellow-eyed penguins

reported as bycatch in the trawl fishery around the Auckland Islands reserve 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), and 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 would be 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 km^2 (81%) of foraging area within the marine reserve. However, the areas presented here represent minimum estimates of the habitat used, and therefore should be regarded as the minimum areas where protection should be considered. Additionally, birds breeding at Carnley Harbour in the south may have a smaller foraging area available, as water depths drop to 150 m within only 11 km of the harbour entrance.

CONCLUSIONS

This study found foraging trips of longer distance and the use of a larger foraging area by the southern population. These differences are likely a result of local conditions, rather than any inherent differences between these two genetically similar populations. Yellow-eyed penguins have many factors currently impacting their survival as a species including land- and sea-based mortality and have been classified as endangered since 2000, with the population continuing to decline (IUCN 2020). These impacts should receive ongoing monitoring and mitigation to ensure they do not combine with poor foraging seasons to exacerbate population declines in both locations. For the southern population, removing introduced mammalian predators from Auckland Island should be an essential step for future management of subantarctic yellow-eyed penguins. The foraging area size and distance varied at

Enderby Island between years, likely due to changing climate effects bringing changes in prey availability, with considerable variability in breeding success between years. 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. Therefore, this variable breeding success remains a cause for concern for subantarctic populations, as successive poor breeding seasons in the future could lead to similar declines to those observed in the northern population.

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FIGURES & TABLES

Table 1: Data logger deployments on breeding yellow-eyed penguins from Enderby Island, showing the number of trips with loggers of each type in each year of the study. In 2015 only TDRs were deployed, and in 2016 all birds received both types of logger. In 2017 a subset of 31 birds carried data loggers on two separate occasions (one with GPS + TDR, and one with TDR only) with the order randomised. Additional single deployments of GPS + TDR loggers were also made on eight other individuals. Where multiple foraging trips were recorded in one deployment, the data were divided into separate trips.

Year	TDR only	GPS + TDR	TOTAL
2015	13	0	13
2016	0	51	51
2017	31	39	70
TOTAL	44	90	134

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 of kernel density estimates representing the combined home range area used by all birds, and the 50% confidence interval representing the combined core foraging area. For each comparison, Intersect 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 with each parameter. Spatial representations of the areas for all parameters are shown on separate maps (Figure 3).

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

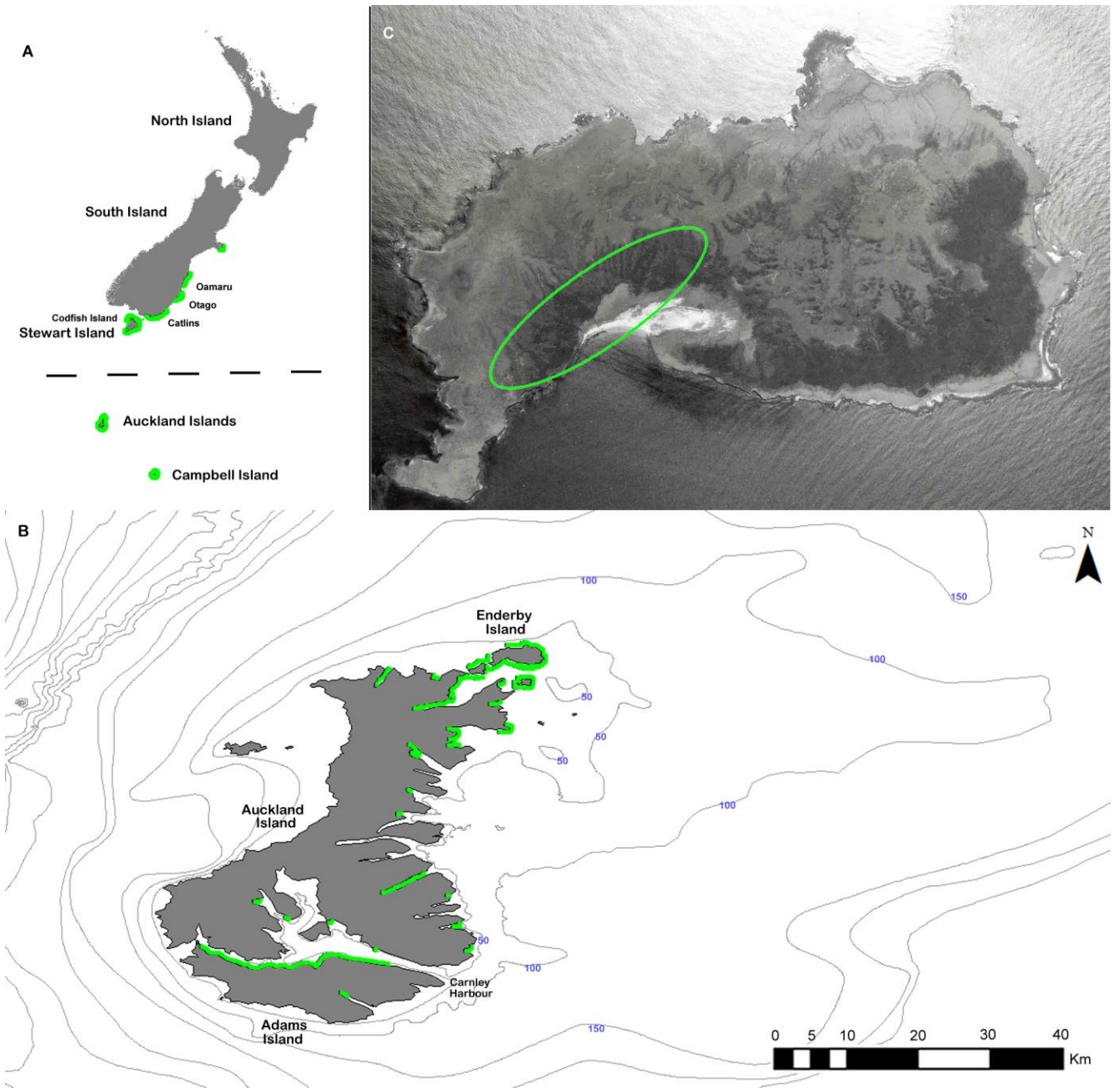
Table 3: Foraging range (maximum distance from shore) and total trip distance (cumulative distance travelled) of breeding yellow-eyed penguins from Enderby Island in different years. Short trips (<10 km foraging range, or <25 km total distance) and with low GPS fix success (<20%) were ignored for distance calculations to avoid bias. Also shown are the number of individual foraging trips, and the number of birds which returned with valid GPS logs each season. Grey highlights show data from mainland sites for comparison.

1

Reference	Year	Location	Site	Year	Phase	Foraging range (km)			Total distance (km)			No. Birds	No. Trips
						Mean	SD	Max	Mean	SD	Max		
This study	2016	Subantarctic	Enderby Is	2016	guard	30.5	5.7	46.7	74.6	25.6	151.9	52	42
	2017	Subantarctic	Enderby Is	2017	guard	19.2	5.9	30.0	50.1	22.1	98.9	29	13
	2016-17	Subantarctic	Enderby Is	2016-17	guard	27.8	7.5	46.7	69.2	26.7	151.9	81	55
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	
Moore	1999	Mainland	Boulder Beach, Otago	1990	post-guard	14.4	7.2					6	
		Mainland	Boulder Beach, Otago	1991	incubation	23.3	11.2					13	
		Mainland	Boulder Beach, Otago	1991	guard	13.4	6.1					10	
		Mainland	Boulder Beach, Otago	1991	post-guard	15.5	8.7					10	
		Mainland	Boulder Beach, Otago	1992	incubation	14.0	8.6					14	
		Mainland	Boulder Beach, Otago	1992	guard	14.4	5.8					10	
		Mainland	Boulder Beach, Otago	1992	post-guard	12.4	6.1					10	
		Mainland	Long Point, Catlins	1991	post-guard	11.1	7.2					9	

	Mainland	Long Point, Catlins	1992	post-guard	9.4	5.3		10

1


A
North Island
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Catlins
Stewart Island
Auckland Islands
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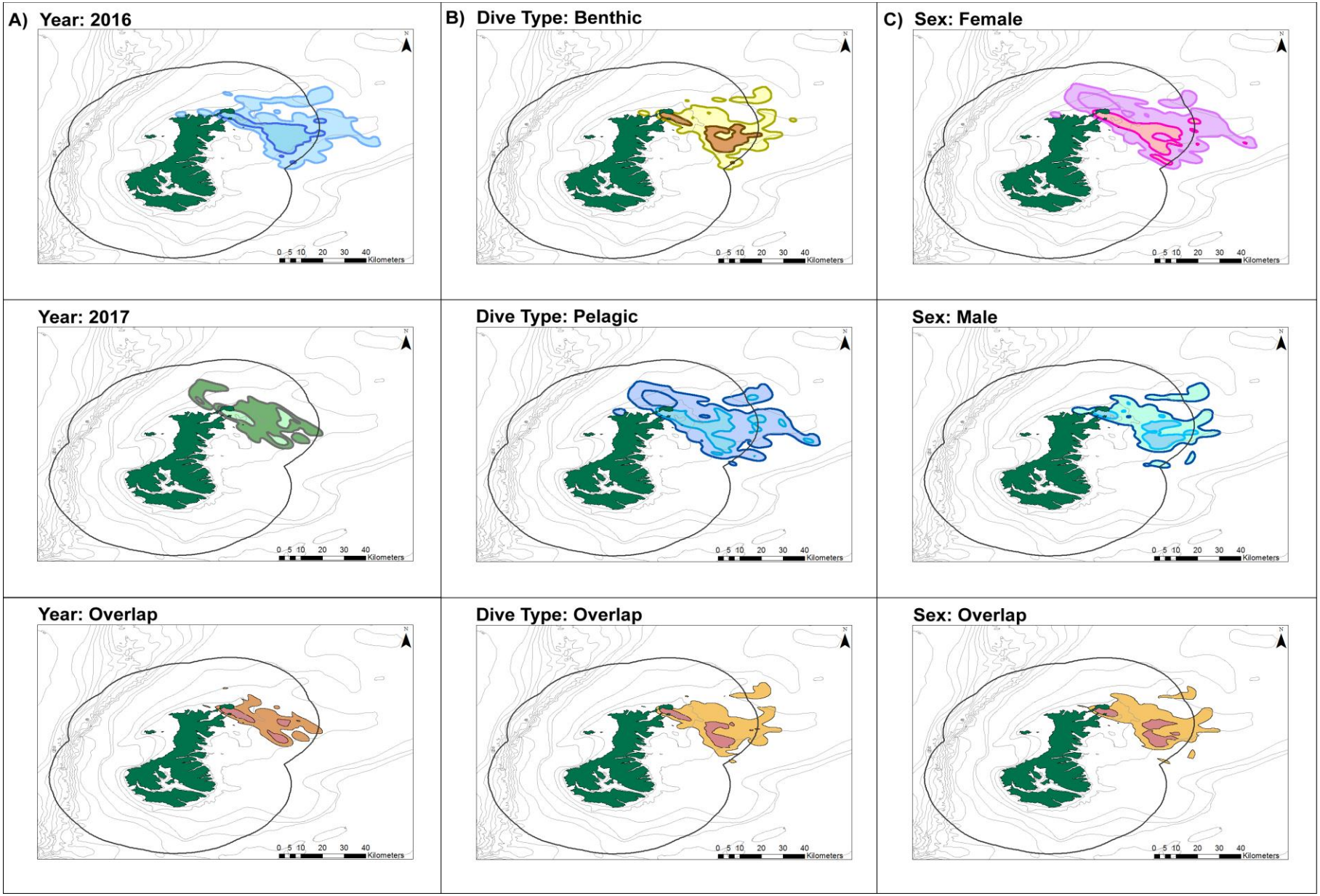
Adams Island
0 5 10 20 30 40
Km

1

Figure 1: (A) The breeding range of yellow-eyed penguins (green highlights) around the New Zealand mainland (above the dashed line) and in the subantarctic (below the dashed line). (B) The Auckland Islands archipelago with Enderby Island to the NE. Selected depth contours are shown in blue, from Mitchell et al. (2016). (C) A close-up of Enderby Island showing the area where breeding birds were sampled (green ellipse). Modified from Muller et al (2020a), Fig. 1.

Figure 2: Nesting yellow-eyed penguin with a Time-Depth Recorder and VHF transmitter attached to the upper back, and GPS logger attached to the lower back. Enderby Island, Auckland Islands, New Zealand subantarctic. Photo credit: CG Muller


A) Year: 2016
B) Dive Type: Benthic
C) Sex: Female
Year: 2017
Dive Type: Pelagic
Sex: Male
Year: Overlap
Dive Type: Overlap
Sex: Overlap
0 5 10 20 30 40
Kilometers

1

1

Figure 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 polygon) indicate combined home range use, and 50% contours (inner polygon) indicate combined core foraging area use. The spatial intersection of kernel density estimates (lower panels) shows the overlap area common to both parameters (upper and middle panels). 95% contours (orange) indicate shared home range use and 50% contours (red) indicate shared core foraging use. Also shown on all maps are 50 m depth contours (light grey) with selected depth values per Figure 1, and the extent of the marine reserve 12 nm from shore (black line).

Supplementary materials

Table S1: Foraging trips by breeding yellow-eyed penguins from Enderby Island. Data were derived from simultaneous GPS and TDR deployments, and are ordered chronologically. Where multiple foraging trips were recorded in one deployment the data were separated into individual trips. Trip times are shown from GPS logs. Foraging type was determined from dive logs, where available (Muller et al. 2020a). GPS fix success was calculated from the theoretical number of possible fixes between the first and last GPS position times per trip.

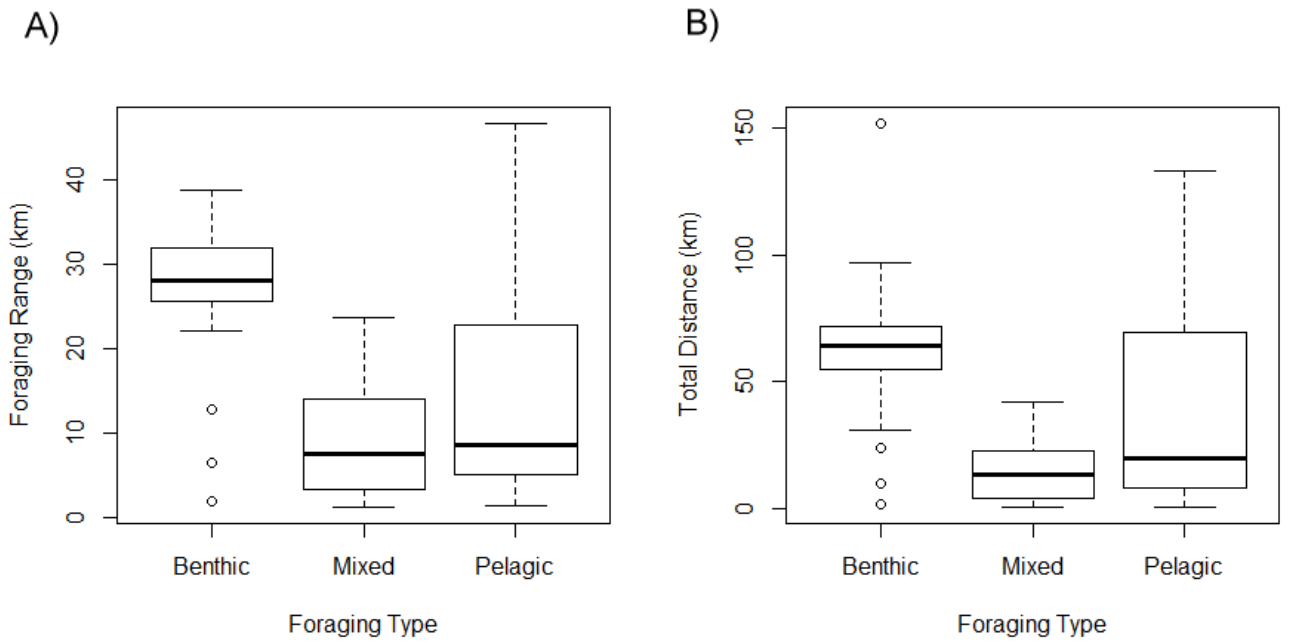
BirdID	Sex	Year	Deploy No.	Start Date	Start Time	End Date	End Time	GPS Fix Success	Foraging Range (km)	Total Distance (km)	Forage Type
bird186	F	2016	1	5/12/2016	05:27:04	5/12/201	20:46:59	6%	6.41	9.89	Benthic
bird187	F	2016	1	7/12/2016	05:19:04	8/12/201	11:55:09	4%	1.95	1.77	Benthic
bird001	M	2016	1	8/12/2016	20:10:04	10/12/20	08:03:59	19%	31.18	52.21	Benthic
bird052	F	2016	1	9/12/2016	15:03:04	10/12/20	14:06:59	11%	32.76	63.96	Benthic
bird053	F	2016	1	9/12/2016	17:48:04	10/12/20	19:22:59	13%	25.72	31.18	Benthic
bird086	M	2016	1	10/12/201	05:32:04	10/12/20	15:01:59	8%	6.47	11.57	Pelagic
bird030	M	2016	1	10/12/201	05:58:04	12/12/20	16:07:59	21%	30.67	72.75	Benthic
bird019	M	2016	1	10/12/201	07:05:04	11/12/20	20:41:59	6%	24.89	56.24	Benthic
bird143	F	2016	1	10/12/201	07:25:04	11/12/20	20:29:59	12%	34.09	95.59	Benthic
bird117	M	2016	1	10/12/201	15:09:04	11/12/20	16:44:59	8%	26.94	59.63	Benthic
bird142	F	2016	1	12/12/201	14:05:04	15/12/20	19:16:59	11%	33.36	81.02	Pelagic
bird042	F	2016	1	12/12/201	16:45:04	14/12/20	14:46:59	3%	2.58	4.67	Pelagic
bird106	M	2016	1	12/12/201	17:59:04	13/12/20	17:38:59	11%	25.01	56.79	Benthic
bird107	M	2016	1	13/12/201	14:47:04	15/12/20	10:55:59	6%	25.60	53.40	Benthic
bird175	F	2016	1	13/12/201	16:35:04	15/12/20	22:21:59	10%	29.18	72.86	Benthic
bird132	M	2016	1	14/12/201	05:46:04	16/12/20	00:30:59	4%	3.56	5.45	Pelagic
bird189	M	2016	1	14/12/201	15:01:04	14/12/20	19:49:59	7%	1.31	0.89	Pelagic
bird022	F	2016	1	14/12/201	18:15:04	18/12/20	14:25:59	5%	35.72	143.37	Pelagic
bird145	F	2016	1	15/12/201	05:19:04	17/12/20	16:03:59	10%	27.84	85.48	Benthic
bird111	F	2016	1	15/12/201	05:27:04	16/12/20	18:52:59	9%	37.18	87.35	Pelagic
bird101	F	2016	1	16/12/201	18:19:04	17/12/20	17:30:59	11%	23.08	56.19	Pelagic
bird192	M	2016	1	17/12/201	16:41:04	18/12/20	19:34:59	14%	22.03	70.89	Benthic
bird172	M	2016	1	17/12/201	18:17:04	19/12/20	11:06:59	5%	8.66	20.98	Pelagic

bird171	M	2016	1	17/12/201	22:48:04	19/12/20	10:08:59	4%	7.18	12.44	Pelagic
bird191	M	2016	1	17/12/201	23:58:04	19/12/20	20:41:59	12%	36.41	83.15	Benthic
bird170	F	2016	1	18/12/201	06:07:04	18/12/20	22:00:59	3%	7.12	14.84	Pelagic
bird164	F	2016	1	24/12/201	13:25:04	26/12/20	08:00:59	27%	35.71	70.43	Pelagic
bird155	M	2016	1	24/12/201	16:01:04	25/12/20	16:23:59	30%	33.92	67.14	Benthic
bird154	M	2016	1	24/12/201	17:03:04	25/12/20	15:03:59	33%	32.30	64.08	Benthic
bird161	F	2016	1	24/12/201	17:36:04	25/12/20	17:47:59	40%	35.71	76.51	Pelagic
bird159	M	2016	1	24/12/201	20:00:04	25/12/20	20:44:59	29%	36.57	73.41	Benthic
bird205	F	2016	1	25/12/201	16:47:04	27/12/20	08:48:59	30%	33.23	67.19	Pelagic
bird207	F	2016	1	25/12/201	16:59:04	26/12/20	17:26:59	45%	25.62	62.15	Benthic
bird210	F	2016	1	25/12/201	17:00:04	28/12/20	07:30:44	16%	32.10	122.78	Benthic
bird206	M	2016	1	25/12/201	17:40:04	26/12/20	21:07:59	43%	27.60	66.17	Benthic
bird120	F	2016	1	25/12/201	17:40:04	28/12/20	03:57:59	34%	33.64	96.97	Benthic
bird160	M	2016	1	25/12/201	18:46:04	27/12/20	03:36:59	30%	29.32	66.42	Benthic
bird208	F	2016	1	25/12/201	20:40:04	26/12/20	20:51:59	29%	24.53	53.08	Benthic
bird149	F	2016	1	25/12/201	22:04:04	27/12/20	05:41:59	29%	33.07	69.76	Pelagic
bird162	F	2016	1	25/12/201	22:52:04	27/12/20	22:21:59	28%	34.51	133.11	Pelagic
bird032	F	2016	1	26/12/201	05:21:04	28/12/20	12:16:59	30%	46.73	110.35	Pelagic
bird183	F	2016	1	26/12/201	18:31:04	27/12/20	19:18:59	25%	17.21	36.61	Pelagic
bird064	?	2016	1	26/12/201	19:37:04	28/12/20	23:20:59	11%	38.78	151.88	Benthic
bird209	M	2016	1	27/12/201	05:25:04	28/12/20	03:54:59	23%	31.50	62.94	Benthic
bird215	F	2016	1	30/12/201	03:47:04	1/01/201	09:42:59	7%	28.14	57.90	Benthic
bird213	F	2016	1	30/12/201	05:17:04	31/12/20	18:13:59	45%	36.97	79.56	Pelagic
bird217	M	2016	1	30/12/201	15:39:04	1/01/201	13:22:59	22%	30.32	70.55	Benthic
bird214	F	2016	1	30/12/201	16:00:04	31/12/20	18:21:59	16%	8.97	18.43	Pelagic
bird216	M	2016	1	31/12/201	18:08:04	1/01/201	18:09:59	31%	27.13	65.80	Benthic
bird065	F	2016	1	16/12/201	06:42:48	19/12/20	19:09:53	3%	21.02	53.93	unkno
bird204	M	2016	1	25/12/201	19:27:20	26/12/20	20:27:47	29%	23.09	60.49	unkno
bird193	M	2016	1	18/12/201	04:03:08	20/12/20	14:50:08	3%	30.84	72.70	unkno
bird249	M	2017	1	4/12/2017	01:14:04	5/12/201	21:37:59	3%	1.17	0.61	Pelagic
bird250	F	2017	1	4/12/2017	02:29:04	6/12/201	23:32:59	23%	29.95	64.59	Benthic
bird247	F	2017	1	4/12/2017	05:44:04	4/12/201	19:54:59	5%	4.04	5.24	Pelagic
bird233	F	2017	1	4/12/2017	06:01:04	4/12/201	17:54:59	3%	3.33	3.61	Pelagic
bird244	M	2017	1	4/12/2017	18:33:04	5/12/201	18:16:59	7%	6.45	19.89	Pelagic
bird117	M	2017	1	10/12/201	15:16:04	12/12/20	23:15:59	8%	27.25	49.57	Benthic
bird068	M	2017	1	10/12/201	15:37:04	11/12/20	15:52:59	4%	12.82	23.76	Benthic
bird142	F	2017	1	11/12/201	05:19:04	13/12/20	20:52:59	2%	5.53	17.38	Pelagic
bird095	F	2017	1	11/12/201	15:55:04	12/12/20	13:30:59	38%	18.36	26.94	Pelagic
bird053	F	2017	1	13/12/201	15:39:04	15/12/20	11:57:59	13%	11.62	31.90	Pelagic
bird035	M	2017	1	13/12/201	17:30:04	15/12/20	18:11:59	2%	9.83	18.60	Pelagic
bird013	M	2017	1	14/12/201	14:00:04	16/12/20	23:18:59	16%	22.87	98.95	Pelagic
bird042	F	2017	1	15/12/201	05:33:04	15/12/20	15:42:59	4%	2.39	2.72	Pelagic
bird052	F	2017	1	15/12/201	05:51:04	18/12/20	13:47:59	31%	23.61	42.32	Pelagic
bird155	M	2017	1	16/12/201	04:49:04	16/12/20	20:13:59	5%	6.19	9.91	Pelagic

bird245	F	2017	1	16/12/201	06:29:04	16/12/20	20:12:59	2%	1.58	1.06	Pelagic
bird244	M	2017	2	16/12/201	11:09:04	17/12/20	00:57:59	4%	4.16	6.67	Pelagic
bird254	F	2017	1	16/12/201	15:23:04	17/12/20	10:02:59	26%	20.14	53.81	Pelagic
bird249	M	2017	2	17/12/201	05:34:04	17/12/20	20:41:59	1%	4.29	5.63	Pelagic
bird247	F	2017	2	17/12/201	05:34:04	18/12/20	16:12:59	3%	5.59	11.77	Pelagic
bird086	M	2017	1	17/12/201	05:49:04	17/12/20	19:48:59	16%	8.97	17.12	Pelagic
bird233	F	2017	2	18/12/201	05:50:04	18/12/20	17:13:59	9%	22.58	65.33	Pelagic
bird025	F	2017	1	19/12/201	16:06:04	20/12/20	12:46:59	12%	5.11	8.79	Pelagic
bird106	M	2017	1	21/12/201	15:47:04	22/12/20	22:09:59	2%	1.65	1.17	Pelagic
bird160	M	2017	1	23/12/201	06:00:04	23/12/20	16:47:59	25%	15.49	28.90	Pelagic
bird161	F	2017	1	23/12/201	18:17:04	25/12/20	16:40:59	15%	18.08	71.96	Pelagic
bird101	F	2017	1	24/12/201	05:46:04	24/12/20	18:26:59	5%	5.79	8.55	Pelagic
bird160	M	2017	2	24/12/201	13:22:04	24/12/20	21:59:59	9%	4.72	7.40	Pelagic
bird050	M	2017	1	24/12/201	19:52:04	25/12/20	16:52:59	9%	2.65	3.29	Pelagic
bird161	F	2017	2	26/12/201	05:28:04	26/12/20	11:34:59	4%	1.62	3.24	Pelagic
bird022	F	2017	1	27/12/201	05:55:04	27/12/20	13:16:59	6%	3.65	5.70	Pelagic
bird267	F	2017	1	2/01/2018	07:04:04	2/01/201	19:18:59	33%	12.68	25.30	Pelagic
bird270	F	2017	1	2/01/2018	13:03:04	2/01/201	21:00:59	17%	7.22	14.03	Pelagic
bird268	M	2017	1	3/01/2018	13:33:04	3/01/201	21:40:59	15%	7.51	12.18	Pelagic
bird269	F	2017	1	3/01/2018	14:58:04	4/01/201	15:03:59	49%	13.58	41.15	Pelagic

1

2



3

4 Figure S2: A) Foraging range (maximum distance travelled offshore), and B) Total distance

5 (cumulative distance travelled per foraging trip) by foraging type for breeding yellow-eyed penguins

from Enderby Island. Distance was determined from GPS logs and foraging type was determined from analysis of simultaneous dive (TDR) logs (Muller et al. 2020a).