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Source: Wildlife Biology, 2020(4)

Published By: Nordic Board for Wildlife Research

URL: <https://doi.org/10.2981/wlb.00732>

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Abundance, survival and population growth of killer whales *Orcinus orca* at subantarctic Marion Island

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Killer whales, *Orcinus orca*, are a cosmopolitan species with large ecological and demographic variation across populations. Population-specific demographic studies are, therefore, crucial in accurately assessing the status and trends of local killer whale populations. Such studies require long-term datasets and remain scarce, particularly in the Southern Ocean where detailed population specific studies have only been conducted at a single archipelago – Îles Crozet. Here, we analysed 12 years of capture–recapture data (comprising nearly 90 000 identification photographs taken from 2006 to 2018) of killer whales at subantarctic Marion Island (46°54'S, 37°45'E) to estimate the abundance, survival and growth rate of this population. Demographic parameters were estimated using multistate capture recapture models, and Pradel Survival-Lambda and POPAN single-state models implemented in the program MARK. Annual survival probability (0.98 [95% CI: 0.96–0.99]) was constant over time, and no important differences between sexes and age-classes (calves, juveniles, adults) were found. This estimate of survival suggests a life expectancy of approximately 48 years. Realised mean population growth rate (λ) was 1.012 (0.987–1.037) with an estimated population size of 54 (54–60) individuals and a mean calving rate of 0.13 (0.06–0.20) calves born per year per reproductive female. The survival and reproduction rates of killer whales at Marion Island are similar to those of killer whale populations in the eastern North Pacific, Norway and Îles Crozet. However, subtle differences in survival and reproduction rates are present. These are likely the result of local differences in resource abundances, historical impacts on social structure and/or stressors. Also, the presence and scale of fisheries (legal and illegal) in the area may provide opportunities for direct interactions with fishing activities impacting survival and reproduction rates.

Keywords: abundance, calving rate, demography, environmental variation, fisheries

Geographically separated animal populations of the same species often exist in decidedly different ecological conditions. Local adaptation and variation in diet, behaviour, morphology and demographic parameters (e.g. survival and reproductive rates) are common among such populations (McMahon et al. 2003, Tremblay and Cherel 2003, Gabrey 2010, Jordaan et al. 2019b). Yet, these population differences are often overlooked in ecological studies. Single, well-studied populations are frequently assumed to typify a species' behaviours and demographic traits, with the characteristics of these populations becoming the species 'standard' (Foster 1999). This is problematic as single populations may poorly represent the diversity in life history traits that opti-

mize fitness in different environments. Information obtained from studies conducted throughout a species' distributional range is therefore vital to understand the underlying causes of phenotypic plasticity and adaptive differentiation between populations.

Killer whales, *Orcinus orca*, are apex marine predators that occupy every ocean (Heyning and Dahlheim 1988). All killer whales currently belong to the same taxonomic group, but sympatric and geographically separated populations of killer whales vary in their genetic make-up (see Morin et al. 2010 for proposed taxonomic differentiation based on phylogenetic analysis), behavioural ecology (diet, social structure, movement patterns and dialects) and morphology (Hoelzel and Dover 1991, Ford et al. 1998, Pitman and Ensor 2003, Pitman et al. 2010, de Bruyn et al. 2013, Durban et al. 2016, Lefort et al. 2020). Populations of killer whales with different ecological adaptations can be differentiated into ecotypes. Distinct ecotypes have been described in the eastern North Pacific (ENP) ($n = 3$)

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(Ford 2002), North Atlantic ($n=2$) (Foote et al. 2009) and Southern Oceans ($n=5$) (Pitman and Ensor 2003, Pitman et al. 2010, Durban et al. 2016). While many killer whale ecotypes are well-defined, definitive ecotype designation is not possible in some cases (de Bruyn et al. 2013). Regardless, allopatric populations of killer whales often occur in oceans with markedly different environmental conditions and prey species availability. This variability has resulted in substantial ecological variation in this species reflected in the dietary specialisation of many killer whale populations with some being highly specialised fish or mammal predators while others are more generalist predators (Ford et al. 1998, Pitman and Ensor 2003, Pitman et al. 2010, de Bruyn et al. 2013, Durban et al. 2016, Lefort et al. 2020). Local prey availability and dietary specialisation may lead to variation in social and demographic patterns across populations and impact the viability or persistence of (sub)populations.

Globally, the demography of killer whales has been best studied in the coastal waters of British Columbia and Washington State in the ENP and in the Gulf of Alaska (Bigg et al. 1990, Olesiuk et al. 1990, 2005, Brault and Caswell 1993, Foster et al. 2012, Matkin et al. 2012, DFO 2019, Towers et al. 2019, Natrass et al. 2020). It is from these long-term longitudinal studies that most of our understanding of killer whale life-history and demography arises, such as age- and sex-specific survival rates. In the Northern Hemisphere, outside of the ENP, killer whale demography remains poorly understood, though estimates of survival and population size are available for the killer whale population in northern Norway (Kuningas et al. 2014), in the Strait of Gibraltar (Esteban et al. 2016) and off the west coast of the British Isles (Beck et al. 2014). In the Southern Hemisphere, killer whale demography has been studied in New Zealand (Visser 2000), at Îles Crozet (Poncelet et al. 2010, Guinet et al. 2015, Tixier et al. 2015, Tixier et al. 2017), in Antarctica (Pitman et al. 2018, Fearnbach et al. 2019) and in South African waters (Best et al. 2010).

The preceding studies cover a wide range of oceans and represent killer whale populations of different ecotypes with underlying differences in ecology and demographic traits. The apparent survival of killer whales in northern Norway that eat Norwegian spring-spawning herring, *Clupea harengus*, differs between sexes. Females ($\Phi=0.977$: 95% CI=0.959–0.995) have greater survival than males ($\Phi=0.971$: 95% CI=0.955–0.987) (Kuningas et al. 2014). The age structure of the small population in British and Irish waters is highly skewed (towards older individuals) with no recruitment and a declining population growth ($\lambda < 1.0$) rate during the time they were studied (Beck et al. 2014). In the Strait of Gibraltar, the adult survival ($\Phi=0.901$: 95% CI=0.803–0.999), population growth rate ($\lambda=1.0$) and calving rates (0.02: 95% CI=0.0004–0.04) of tuna-eating killer whales, that do not interact (i.e. non-depredating) with fishing vessels, are known (Esteban et al. 2016). Furthermore, in this population, the adult survival ($\Phi=0.991$: 95% CI=0.969–1), population growth rate ($\lambda=1.04$) and calving rate (0.22: 95% CI=0.18–0.26) of killer whales that depredate tuna from drop-line fishing vessels is also known.

Depredation occurs when fish are removed from fishing hooks, an act that in some cases evokes lethal responses from fishers, an additional negative effect to the threat of entanglement (Matkin 1986, Lewison et al. 2004). Depredation may, however, also affect individuals positively by providing a feeding strategy with low foraging effort (Northridge and Hoffman 1999, Tixier et al. 2017, 2020).

In the Southern Hemisphere, demographic results from New Zealand, where killer whales prey predominantly on elasmobranchs, are limited to estimates of total population size (115 in 1997: range 65–167) and structure (three subpopulations) (Visser 2000). Population size estimates are available for fish eating type C killer whales in Antarctica (Pitman et al. 2018) while more detailed survival estimates ($\Phi=0.98$: 95% CI=0.74–1.0) of type A killer whales (marine mammal feeders) exist (Fearnbach et al. 2019). Killer whale estimated life expectancy (approximately 25 and 18 years for females and males respectively) and calving intervals (3–4 years) off the South African coast are exclusively known from the necropsy of stranded and harvested individuals (Best et al. 2010). These whales appear to prey mainly on marine mammals (Best et al. 2010). The Southern Hemisphere's most detailed demographic information to date (e.g. temporally variable calving rates and age class- and sex-specific survival rates) has been obtained from individual life-history data of killer whales around Îles Crozet (which prey on seals, whales, fish and penguins) and from groups depredating commercial longline fishing vessels in the region (Tixier et al. 2017, 2019).

Killer whale abundance has previously been estimated at Marion Island, situated approximately 950 km due west of Îles Crozet in the southern Indian Ocean (Reisinger et al. 2011a), but this is the only demographic information that exists for this population. Genetically, Marion Island killer whales are most closely related to Antarctic type B killer whales (Moura et al. 2015). This small population (37 (95% CI=29–44) individuals in 2006–2008; Reisinger et al. 2011a) preys on a range of species, including southern elephant seals *Mirounga leonina*, Subantarctic fur seals *Arctocephalus tropicalis*, various penguins, Patagonian toothfish *Dissotichus eleginoides* and possibly cephalopods (Reisinger et al. 2011b, 2016). Killer whale presence at Marion Island varies seasonally, with peaks between September and December and between April and May (Reisinger et al. 2011b). When not at the island, tracked individuals have shown restricted movement behaviour at seamounts north of the archipelago where they dived to depths of up to 767 m (Reisinger et al. 2015). Socially, group sizes range between 1 and 16 individuals with a modal group size of three individuals (Tosh et al. 2008, Reisinger et al. 2017).

Here, we investigate the survival, life expectancy, population growth rate, population size and calving rates of the killer whale population at Marion Island. We achieve this by analysing individual life-histories obtained from a long-term, uninterrupted, photo-identification study (2006–2018). These parameters are compared to other killer whale populations and we discuss the potential effects of local ecology on demography.

Methods

Study site

Marion Island (296 km²) and the neighbouring Prince Edward Island (45 km²) together form the Prince Edward Islands (PEIs) archipelago (46°54'S, 37°45'E) in the southern Indian Ocean (Fig. 1). This archipelago lies approximately 1800 km south east of South Africa and 1000 km west of Îles Crozet. The PEIs sustain large breeding populations of seals and seabirds as a result of productive turbulent water masses that surround the islands (Ryan and Bester 2008). The inshore abundance of killer whales at the archipelago peaks when inshore prey availability (predominantly elephant seals and penguins) is high (Reisinger et al. 2011b).

Data collection and processing

At Marion Island, identification photographs of killer whales were collected from shore during the period May 2006 to April 2018. Photographs were taken with various digital camera and lens combinations. Photographs were taken during sightings of killer whales observed either opportunistically (e.g. when observers were completing other field work) or during dedicated observation sessions. Dedicated observation sessions were done by trained observers that remained at various locations (Fig. 1) around the island and visually searched for killer whales for a predetermined, uninterrupted, period ranging from 2 to 10 h. These observation locations cover areas of the coastline most frequented by killer whales (Keith et al. 2001, Reisinger et al. 2015).

For all types of sightings, when a group was sighted, the observer would estimate the group's size, movement direction and age/sex composition. Additionally, the observer attempted to photograph the dorsal fin of each individual within the group and would continue to do so until the group was no longer in photographic range or the observer needed to terminate the observation. Photo-identification effort was thus continued irrespective of whether all animals were deemed to have been photographed.

Individual killer whales were identified by carefully examining the dorsal fins and saddle patches in photographs for any nicks, notches and mutilations (Bigg et al. 1987) and comparing these to individuals in an existing photographic identification catalogue (Tosh et al. 2008, Reisinger et al. 2011a, Reisinger and de Bruyn 2014, Jordaan et al. 2019a). All photographs were assigned a quality score ranging from 1 (unusable) to 5 (excellent) based on focus, lighting and exposure and the size, level of obscurity and angle of the dorsal fin in the photograph. Only identifications of killer whales obtained from photographs with a quality score ≥ 3 were considered for analyses (Reisinger et al. 2011a). Additionally, all individuals seen only during one year, and not observed socialising with other known individuals, were removed from the data set as there is a high probability that these individuals were vagrants and not part of the main population.

Data analysis

Individual identification data were summarised in an encounter history matrix with 12 occasions, each occasion

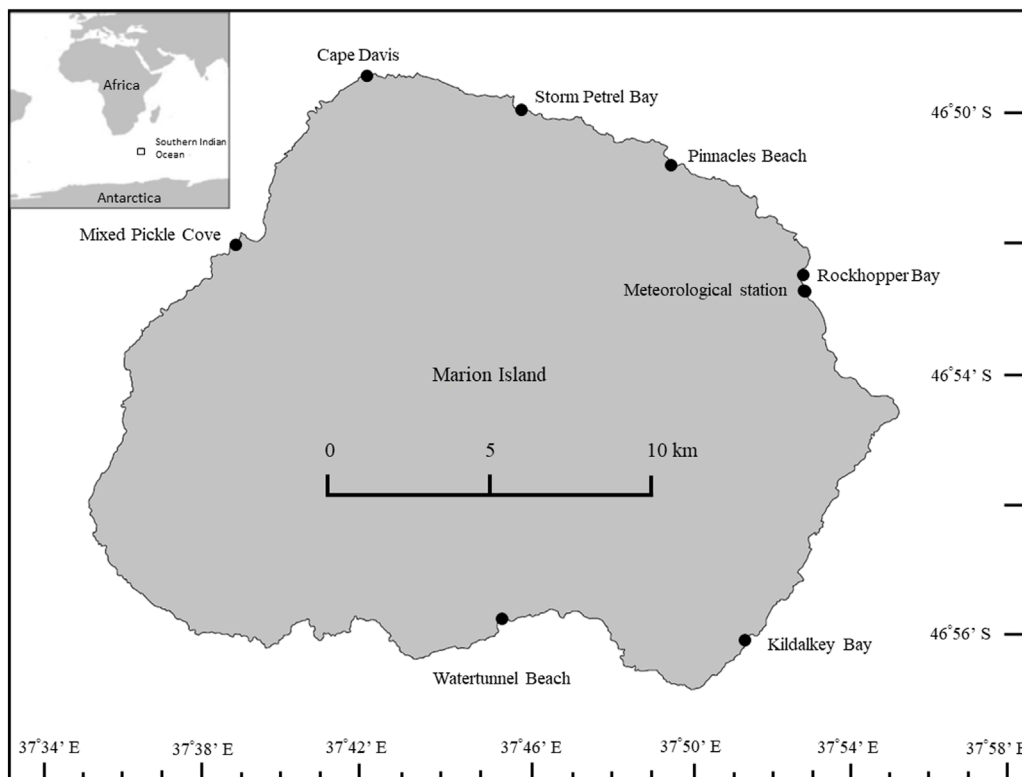


Figure 1. Map of Marion Island indicating the location in the Southern Ocean and the sites where dedicated observations were conducted on the island.

one year in length, starting on 1 May and ending on 30 April the following year. These dates coincide with the period that research teams over-wintered at Marion Island; dedicated observers thus remained unchanged during this period. Multiple sightings of an individual within a year (May–April) were treated as a single detection in modelling. The encounter history matrix incorporated information on age class, so that individuals could transition from calf and juvenile states to adult states. Age classes used were calf (male and female: 0–3 years), juvenile (male: 3–13 years, female: 3–10 years) and adult (male > 13 years, female > 10 years) (Olesiuk et al. 1990, Best et al. 2010). Individuals not born during the study period were assigned an age class based on the size and rate of growth of their dorsal fin between years. Sexes were only assigned to individuals that had reached sexual maturity (no growth in fin size over a five-year period), when females gave birth to calves and to others where sex-specific ventral markings were clearly observed (Olesiuk et al. 1990).

Data were analysed by calling MARK (White and Burnham 1999) through the RMark package (Laake 2013) in R (<www.r-project.org>). Program MARK uses maximum likelihood methods to estimate survival and other population parameters, such as transition probability between states, population size (n) and population growth rate (λ) from multiple encounters of animals with natural or artificial markings. Statistical inference was based on model selection and parsimony, i.e. ranking biologically plausible models using a model selection criterion and favouring models that represent the structure in the data with the minimum number of parameters (Burnham and Anderson 2002). We used Akaike's information criterion corrected for small sample sizes (AICc) to rank models. The model with the lowest AICc value represents the best compromise between model complexity and model fit (Burnham and Anderson 2002). Relative model support was based on differences in AICc values (ΔAICc); $\Delta\text{AICc} < 2$ suggested that two models received approximately equivalent support from the data (Burnham and Anderson 2002). The model selection approach assumed that the set of models considered included a general model that adequately fits the data. Therefore, we verified whether the Jolly–Move (JMV) multistate model (Pradel et al. 2005) reasonably fitted the data. The underlying assumptions of the JMV model are homogeneous survival and detection probabilities among marked animals that behave independently (Pradel et al. 2005). More generally, capture recapture models assume that marks are not lost, individuals are not mis-identified, and sampling is instantaneous relative to the interval between occasions. Goodness-of-fit testing was performed in U-CARE ver. 2.2.2 (Choquet et al. 2009).

We used multistate capture recapture models to estimate survival (Φ), state transition (Ψ) and detection probabilities (p) of killer whales at Marion Island. For Φ and Ψ and p , a limited set of predictor variables (time-dependence ($-$ time), time-consistency ($-$ 1), sex ($-$ sex) and age class ($-$ state) was used to build additive covariate models (with a maximum of two predictor variables per parameter). Some transition parameters between age classes were impossible (adult to calf, adult to juvenile, juvenile to calf and calf to adult) and were fixed to 0. For detection probability, additional covariates of observer effort were also added to test if the

number of dedicated observation sessions, observation hours or photos taken influenced detectability between years. The significance of these covariates was evaluated using an analysis of deviance (ANODEV) test (Grosbois et al. 2008). Mean life expectancy was estimated from the most parsimonious model as (Seber 1982):

$$\text{Life expectancy} = \frac{1}{\ln(\text{Survival})}$$

We used a single state encounter history matrix to estimate population growth rate (λ) with Pradel Survival-Lambda (PSL) models (Pradel 1996) and population size (n) with the POPAN generalization of the Jolly–Seber model (Schwarz and Arnason 1996). Sex was also omitted as a covariate for these models due to the lack of support for sex differences in multistate analyses. Pradel Survival-Lambda and POPAN models were built using all possible combinations of time-dependence ($-$ time) and time-consistency ($-$ 1) for survival (Φ), detection probability (p) and probability of entry (pent) (POPAN only). We derived single estimates for mean population growth rate (λ) (PSL only) and mean population size (n) (POPAN only) during the study period.

Annual calving rates were calculated in two ways. Firstly, we calculated calving rates as the total number of calves born during a given year relative to the total number of 'reproductively available' females in the population that year. A female was deemed 'reproductively available' if she was estimated (based on recent fin growth) to be at least 10 years old (the average age of sexual maturity in female killer whales) (Olesiuk et al. 2005). Females with 1 and 2-year-old calves (i.e. females that calved in the previous two years) were omitted from the 'reproductively available' group as they were deemed to still be lactating (Tixier et al. 2015). Secondly, per capita calving rates were determined as the number of calves born in a year per number of animals (males and females, including juveniles) within the population for that year (Olesiuk et al. 1990).

Results

From May 2006 to April 2018, observers at Marion Island conducted 1997 dedicated killer whale observation sessions totalling 11 194 h. During this time, 2668 sightings were recorded (0.24 h^{-1}). In addition, 2071 opportunistic sightings were recorded during the study period. A total of 54 unique killer whales were identified from 89 792 photographs with 41 814 of these photographs having a suitable quality score (>3). Of these, 19 killer whales were born into the population during the study period and were excluded from the discovery curve which shows the number of individuals identified plotted against the total number of identifications (Fig. 2). This number ($n=54$), includes 8 individuals seen at both Marion Island and Îles Crozet and excludes 13 individuals which were removed from the data set as they were deemed to not be part of the main population. These individuals were seen once at Marion Island only, either singularly or in groups, and have not been recorded elsewhere (i.e. at Îles Crozet). Figure 2 therefore depicts how

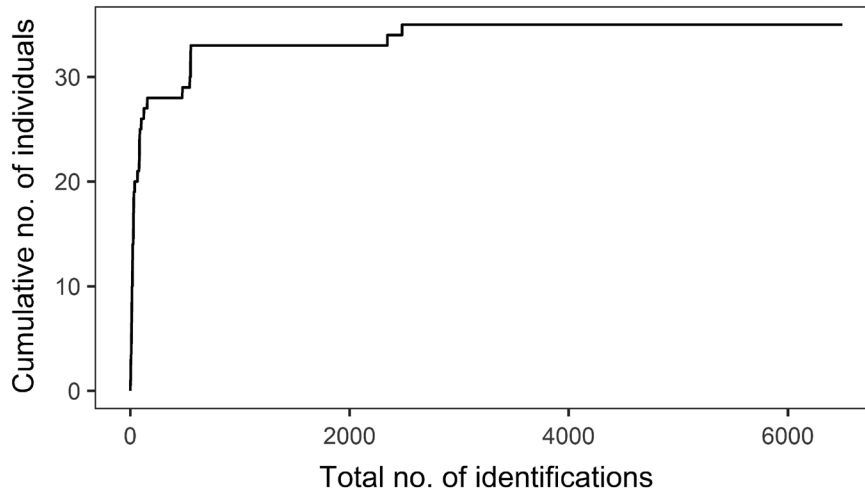


Figure 2. Discovery curve showing the cumulative number of individual killer whales identified ($n = 35$) at Marion Island during the period April 2006–2018, plotted against the total number of identifications. Calves ($n = 19$) were excluded. Identifications were made during dedicated and opportunistic sightings.

many new individuals are seen over time, excluding those seen once at Marion Island (deemed vagrants).

Goodness-of-fit test results for the multistate encounter history data showed non-significant results for component tests and the overall Jolly–Move (JMV) model (Table 1). These results indicate that the data fits the model assumptions. Multistate capture–recapture model selection indicated that the model with constant survival, state dependent transition and time-dependent detection was most parsimonious (Table 2). This model was approximately five times better supported by the data compared to the second-ranked model that included state (age class) dependent survival ($\Delta\text{AICc} = 3.35$; $w = 0.64/0.12 = 5.33$). The estimated annual survival probability of 0.98 (95% confidence interval (CI): 0.96–0.99) translates to an approximate mean life expectancy of 48 years (95% CI: 28.07–66.17 years). Survival did not differ meaningfully between sexes ($\Delta\text{AICc} = 4.33$). The probability to transition from the calf to juvenile state ($\Psi = 0.36$ [95% CI: 0.24–0.51]) was higher than the probability of moving from the juvenile to adult state ($\Psi = 0.12$ [0.07–0.21]). The probability of detection varied over time and ranged from 0.63 to 1 (Supplementary material Appendix 1 Fig. A1) (mean $p = 0.89$ [95% CI: 0.86–0.92]). Covariates of observation ‘effort’ did not explain the temporal pattern in detection probability between years (Table 3).

The most parsimonious PSL model suggested that survival was constant and probability of detection was time dependent (Table 4). The estimate of mean population growth rate was 1.012 (95% CI: 0.987–1.037). The most parsimonious POPAN model assumed constant survival, probability of entry and population size and time dependent detection probability (Table 5). This analysis suggested a probability of entry into the population of 0.028 (95% CI: 0.017–0.045) and estimated the population size at 54 (95% CI: 54–60) individuals.

The number of reproductive females ranged from 7 to 16 individuals per year while the entire (observed) population ranged between 20 and 42 individuals per year (Table 6). The number of calves born per year ranged between

0 and 4. This equates to a mean calving rate of 0.13 (95% CI: 0.06–0.20) calves born per year per reproductive female and a per capita birth rate of 0.04 (95% CI: 0.02–0.06).

Discussion

Killer whales at Marion Island show survivorship trajectories closely resembling those for neighbouring Îles Crozet, northern Norway and the ‘residents’ of the ENP (Olesiuk et al. 1990, Kuningas et al. 2014, Guinet et al. 2015, Tixier et al. 2017). Additionally, this population currently has a marginally positive mean growth rate and healthy calving rate.

Global comparison

Our results suggest that overall survival in this population is constant during our study period with no differences in survival detected between sexes and/or age classes. Studies in the ENP, the Mediterranean and northern Norway suggest that killer whale survival differs between sexes and age classes (Olesiuk et al. 1990, Kuningas et al. 2014, Esteban et al. 2016). Sexual differences in survival translate to dissimilarities in estimated maximum ages of ENP southern residents between females (80–90 years) and males (50–60 years). This increased post-reproductive lifespan of resident females is beneficial to inclusive fitness through increasing the survival of their grandoffspring and through the transfer of ecological

Table 1. Goodness-of-fit test results for the JollyMove (JMV) model fitted to multistate data of killer whales at Marion Island (2006–2018). Test 3G assesses for transience (i.e. differences in future encounter probabilities between newly identified and previously identified individuals). Test M tests for heterogeneity in detection (e.g. trap-dependence – changes in detection following ‘captures’ (i.e. sightings)).

	χ^2	p	df
Test 3G	11.79	0.44	14
Test M	5.2	0.13	4
JMV model	16.98	0.41	18

Table 2. Model selection results for survival (Φ), detection probability (p) and the probability of moving between age-class states (Ψ) obtained from multistate analysis of killer whale sighting histories at Marion Island (2006–2018). The number of parameters (K), model deviance, ΔAICc (the difference in AICc between the model with the lowest AICc value and the relevant model) and AICc weight (w_i) (the relative support by the data of a model, in relation to the other models) are presented. Only models with a $\Delta\text{AICc} < 15$ are shown (see Supplementary material Appendix 1 Table A1 for all models fitted). ~ 1 = constant, $\sim\text{time}$ = full time dependence and $\sim\text{state}$ = age class.

Model			K	Deviance	ΔAICc	w_i
Survival	Detection probability	Probability of moving between age-class states				
~ 1	$\sim\text{time}$	$\sim\text{state}$	15	350.38	0.00	0.64
$\sim\text{state}$	$\sim\text{time}$	$\sim\text{state}$	17	349.36	3.35	0.12
~ 1	$\sim\text{time}$	$\sim\text{state} + \text{time}$	25	331.91	3.82	0.09
$\sim\text{sex}$	$\sim\text{time}$	$\sim\text{state}$	17	350.35	4.33	0.07
~ 1	$\sim\text{time}$	~ 1	13	360.66	5.97	0.03
$\sim\text{state}$	$\sim\text{time}$	$\sim\text{state} + \text{time}$	27	330.85	7.37	0.02
$\sim\text{sex}$	$\sim\text{time}$	$\sim\text{state} + \text{time}$	27	331.88	8.40	0.01
$\sim\text{state}$	$\sim\text{time}$	~ 1	15	359.61	9.23	0.01
~ 1	$\sim\text{time}$	$\sim\text{sex}$	15	360.40	10.02	0.00
$\sim\text{sex}$	$\sim\text{time}$	~ 1	15	360.64	10.26	0.00
~ 1	$\sim\text{time}$	$\sim\text{time}$	23	345.38	12.74	0.00
$\sim\text{state}$	$\sim\text{time}$	$\sim\text{sex}$	17	359.34	13.33	0.00
$\sim\text{time}$	$\sim\text{time}$	$\sim\text{state}$	25	341.78	13.69	0.00
$\sim\text{sex}$	$\sim\text{time}$	$\sim\text{sex}$	17	360.37	14.35	0.00

* Omitted 126 models (total of 140 models).

knowledge (Foster et al. 2012, Brent et al. 2015, Croft et al. 2017, Natrass et al. 2020). The apparent absence of sex differences in survival for the Marion Island population may be due to an incomplete dataset where most calves and juveniles have not yet been sexed, the relatively short time series (relative to lifespan) and the small number of individuals in the population (sample size). Our estimated survival at Marion Island translates to an estimated life expectancy of 48 years, similar to that experienced by males in the ENP. It is likely that our estimate of survival, which had low statistical power to detect age and sex differences in survival, underestimates female longevity, which is characterised by a prolonged post-reproductive lifespan.

The total births per capita (0.04) at Marion Island are similar to that of ENP resident killer whales (0.03–0.05 births per capita; Olesiuk et al. 1990) but the Marion Island calving rate (0.13) is intermediate of depredating (0.22: 95% CI = 0.18–0.26) and non-depredating (0.02: 95% CI = 0.0004–0.04) killer whales in the Strait of Gibraltar (Esteban et al. 2016). Fecundity and survival in northern and southern ENP residents is highly correlated with the abundance of Chinook salmon, *Oncorhynchus tshawytscha*, (Ward et al. 2009, Ford et al. 2010), suggesting the possibility that prey availability may also impact the fecundity and survival of Marion Island's killer whales. Despite a similar total

number of births per capita, the mean population growth rate of the Marion Island population ($\lambda = 1.012$) is marginally lower than that of the northern residents ($\lambda = 1.022$) and depredating Strait of Gibraltar killer whales ($\lambda = 1.04$) but higher than the southern residents in the ENP ($\lambda = 0.998$) as recorded between 1979 and 2017 (Towers et al. 2015, Esteban et al. 2016, DFO 2019). The resident populations are now listed as 'Threatened' (northern residents) and 'Endangered' (southern residents) due to their small population sizes, recent low reproductive rates and a net loss of individuals between 2011 and 2016 (COSEWIC 2008, United States Environmental Protection Agency). The mean Marion Island growth rate is, however, higher than that reported in British and Irish waters ($\lambda < 1$) and compared to non-depredating Strait of Gibraltar killer whales ($\lambda = 1.0$) although the British and Irish population is small ($n = 10$) (Beck et al. 2014, Esteban et al. 2016).

Local comparison

Comparisons between the Marion Island population, the ENP resident population and Strait of Gibraltar population are interesting due to the differences, particularly in diet, between these populations. These populations differ not only in diet, but also in vast geographical separation. Perhaps more relevant comparisons can be made to killer whale populations in neighbouring waters such as Antarctic type A killer whales in the western Antarctic Peninsula. This form is known to feed on marine mammals (Pitman and Ensor 2003), and shows survival rates (0.98: 95% CI = 0.74–1.0) similar to Marion Island killer whales (Fearnbach et al. 2019). In recent years, this population has also been increasing in abundance, possibly as a result of increased access to feeding areas due to changing ice conditions (Fearnbach et al. 2019). Our estimate of survival ($\Phi = 0.98$), without differences between sexes, is similar to the survival of Crozet killer whales (0.99, 95% CI: 0.99–0.99) prior to the commencement of illegal fisheries around those islands in 1996 (Guinet et al. 2015, Tixier et al. 2017). Survival estimates for

Table 3. Analysis of deviance (ANODEV) test results showing the non-significant effect of effort covariates on annual detection probability. Variation (%) indicates the amount of temporal variation in detection probability explained by a covariate.

	df	Deviance	F	p	Variation (%)
Constant model	5	394.91			
Time dependent model	15	350.38			
Difference	10	44.53			
Covariate: photos	6	384.44	2.77	0.13	23.52
Covariate: hours	6	392.09	0.61	0.46	6.34
Covariate: observations	6	392.44	0.53	0.49	5.56

Table 4. Model selection results for Pradel Survival-Lambda analysis of survival (Φ), detection probability (p) and population growth rate (λ) of killer whales at Marion Island (2006–2018). The number of parameters (K), model deviance, ΔAICc and AICc weight (w_i) are presented. ~1 = constant and ~time = full time dependence.

Model						
Survival	Detection probability	Population growth rate	K	Deviance	ΔAICc	w_i
~1	~time	~1	14	166.42	0.00	0.98
~time	~time	~1	24	152.57	8.09	0.02
~1	~1	~1	3	247.53	58.16	0.00
~time	~1	~1	13	229.32	60.76	0.00

Crozet killer whales subsequently decreased (0.92, 95% CI: 0.90–0.94) during the illegal fishing period between 1996 and 2002 due to lethal means (the use of explosives and firearms) adopted by fishers to prevent whales from depredating on their lines (Poncelet et al. 2010, Tixier et al. 2017). Survival estimates increased (0.94, 95% CI: 0.92–0.96) between 2003 and 2011 after illegal fishing ceased (Poncelet et al. 2010, Tixier et al. 2017).

Like in the ENP and the Strait of Gibraltar, the fecundity and survival of Crozet killer whales is positively correlated to food availability where females that depredated legal longline Patagonian toothfish fisheries near Îles Crozet show greater calving and survival rates than sympatric individuals that do not depredate (Tixier et al. 2015, 2017). As with killer whales in the Strait of Gibraltar, the mean calving rate of 0.13 calves born per year at Marion Island is greater than the calving rate of non-depredating Crozet killer whales (0.064) but less than the calving rate of killer whales depredating Patagonian toothfish fishing vessels (0.195) between 2003 and 2012 (i.e. after illegal fishing ceased) (Tixier et al. 2015). Depredation comes at a cost to individuals associating with illegal longline fisheries in the same area, as these individuals suffered high mortality rates (due to the lethal responses taken against depredating killer whales by fishers) compared to those who did not depredate (Guinet et al. 2015). Furthermore, the social groups of depredating killer whales were disrupted by these lethal responses resulting in reduced fitness of surviving individuals (Busson et al. 2019). The differences between these subgroups is amplified when population growth rate is considered: both the depredating ($\lambda = 1.0062$ [95% CI: 1.0058–1.0067]) and non-depredating ($\lambda = 0.9273$ [95% CI 0.9269–0.9276]) Crozet killer whales (Tixier et al. 2017) show lower growth rates compared to the Marion Island population ($\lambda = 1.012$), although confidence intervals overlap with the former.

Comparisons between the Marion Island and Îles Crozet populations are intriguing due to the relatively small geographical distance (allowing connectivity) and the similar-

ity of available prey and diet between the two populations. Despite these similarities, differences in survival and fecundity are present. These may be attributed to differences in natural prey abundance and/or differences in Patagonian toothfish fishery activities between the two populations such as the continued presence of illegal fishing vessels around Îles Crozet (resulting in continued mortality of depredating killer whales) and the level of killer whale interaction with these fisheries (Ford et al. 2010, Tixier et al. 2019, 2020, CCAMLR 2020). Killer whale prey abundances at Îles Crozet have decreased in the last several decades as a result of over-exploited toothfish stocks and substantial decreases in penguin, southern elephant seal and large whale population sizes (Guinet et al. 1992, Clapham et al. 1999, Weimerskirch et al. 2018). During this same period, Marion Island experienced decreases in penguin population sizes but increases in fur seal and southern elephant seal population sizes (Crawford et al. 2003, Hofmeyr et al. 2006, Bester et al. 2011). Furthermore, although seasonal and not year-round, the current legal fishery at Îles Crozet is estimated to be bigger (11 845 versus 4373 longline sets between 2006 and 2018) with more depredation taking place (21% (179 tonnes) versus 6% (15 tonnes) of total catch per year) when compared to the fishery surrounding Marion Island where stocks were substantially impacted by illegal fishing prior to 2006 (Boonzaier et al. 2012, Tixier et al. 2020). Depredating, and non-depredating, killer whales at Îles Crozet are therefore exposed to different natural and artificial resources, which, in addition to a disrupted social structure, could account for differences in their fecundity and survival rates.

Annual detection probability was high, and the total Marion Island killer whale population size estimated by capture recapture modelling ($n = 54$) is close to the population size reported in the discovery curve (Fig. 2). The population has increased from 37 (95% CI = 29–44) individuals in 2006–2009 (Reisinger et al. 2011a). This increase is attributed to births ($n = 11$ since 2009) and new identifications of older individuals. High annual detection probability and the

Table 5. Model selection results for POPAN analysis of survival (Φ), detection probability (p), probability of entry ($pent$) and population size (n) of killer whales at Marion Island (2006–2018). The number of parameters (K), ΔAICc and AICc weight (w_i) are presented. Main column headings are the same as in Table 4. Only models with a $\Delta\text{AICc} < 25$ are shown (see Supplementary material Appendix 1 Table A2 for all models fitted).

Model						
Survival	Detection probability	Probability of entry	n	K	ΔAICc	w_i
~1	~time	~1	~1	15	0.00	0.99
~time	~time	~1	~1	25	9.13	0.01
~1	~time	~time	~1	25	23.59	0.00

* Omitted five models (total of eight models).

Table 6. Summary of annual calving rates of killer whales at Marion Island. Calving rate (total) was determined as the number of calves born per killer whale observed at Marion Island during the specific year. Calving rate (female) is the number of calves born per female available for reproduction in the population.

Year	Total (n)	Reproductive females (n)	Calves born (n)	Calving rate (total)	Calving rate (female)
2006–2007	20	10	1	0.00	0.10
2007–2008	24	10	3	0.08	0.30
2008–2009	38	12	4	0.08	0.33
2009–2010	26	7	0	0.00	0.00
2010–2011	35	12	0	0.00	0.00
2011–2012	39	16	1	0.03	0.06
2012–2013	37	15	1	0.03	0.07
2013–2014	40	15	2	0.05	0.13
2014–2015	40	12	4	0.10	0.33
2015–2016	42	11	1	0.02	0.09
2016–2017	35	9	0	0.00	0.00
2017–2018	41	13	2	0.05	0.15
Mean (SE)	34.75 (2.11)	11.83 (0.77)	1.58 (0.42)	0.04 (0.01)	0.13 (0.04)

similarity of population size estimates obtained from capture recapture models and the discovery curve indicate that enumeration by photographic identification is still an accurate measure of abundance for this small, well-observed population suggesting that the current sampling design and effort is well suited to this population (Reisinger et al. 2011a).

Conclusion

This study provides a demographic baseline for Marion Island's killer whales and increases our knowledge of this population and of killer whales in the Southern Ocean. Furthermore, these results suggest that survival and reproduction in this population are similar to populations of killer whales elsewhere in the world. We speculate that the subtle differences among populations may be partly due to their local ecology and/or stressors because killer whale survival, population growth rates and reproduction are known to be impacted by prey preferences and abundances and by fishing activity (Ford et al. 2010, Esteban et al. 2016, Tixier et al. 2017, 2019). Future investigations on this population of killer whales should determine the response of demography and reproduction to changes in measured environmental conditions and prey abundances.

Acknowledgements – We thank the many fieldworkers and individuals who collected long-term data on killer whales at Marion Island. Marion Island killer whale research was conducted pursuant to the provisions of the Marine Living Resources Act, 1998 (Act 18 of 1998) and the Prince Edward Islands Management Plan v0.2 (2010).

Funding – Funding was provided through the Department of Science and Innovation (DSI) by the National Research Foundations' SANAP and Thuthuka Funding instruments, and additionally supported through the International Whaling Commission Southern Ocean Research Partnership, as well as the Mohamed bin Zayed Species Conservation Fund (project number: 10251290). Additionally, RKJ was supported by a FILAMO Mobility grant.

Permits – The project has ethics clearance from the Animal Ethics Committee (AEC) of the Faculty of Veterinary Science, University of Pretoria, under EC077-15. All research was also carried out under permit from the Director-General: Department of Environment, Forestry and Fisheries (DEFF), South Africa. The DEFF provided logistical support for on-going fieldwork at Marion Island, through the South African National Antarctic Program (SANAP).

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Supplementary material (available online as Appendix wlb-00732 at <www.wildlifebiology.org/appendix/wlb-00732>). Appendix 1.