

Abundance estimates of killer whales at subantarctic Marion Island

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ABSTRACT: Killer whales *Orcinus orca* are apex predators known to have important effects on marine ecosystems. A fundamental step towards understanding their role in ecosystems, and vital for their informed management and conservation, is the rigorous estimation of their abundance. Studies concerning this species have used mark-recapture analytical techniques to estimate abundance, but enumeration of identifiable individuals is more common. This study estimated the abundance of killer whales occurring inshore at subantarctic Marion Island. Mark-recapture analyses were performed using nearly 10 000 photographs taken from 2006 to 2009. Using careful quality control criteria, we identified 37 ind. The evident capture heterogeneity violates the underlying assumptions of the open population POPAN parameterization in the software program MARK we initially used. We thus used the simpler Chapman modified Lincoln-Petersen estimator, calculating a population size of 37 ind. (95% CI = 29 to 44) for the period 2006 to 2007 and 32 ind. (95% CI = 30 to 33) for 2007 to 2008. Both estimates are close to the catalogue size, suggesting that enumeration is an accurate measure of abundance in this study. Our results are comparable to recent abundance estimates for the neighbouring Crozet Archipelago (~1000 km due east). No rigorous approach has been used previously to estimate the abundance of killer whales at Marion Island. This estimate provides a foundation for further research related to the sociality and potential ecological impact of this population of killer whales in the Southern Ocean.

KEY WORDS: *Orcinus orca* · Photo-identification · Population size · Mark-recapture · Southern Ocean · Count

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INTRODUCTION

Killer whales, *Orcinus orca*, are cosmopolitan (Heynig & Dahlheim 1988) apex predators with different populations preying on a variety of taxa including cephalopods, bony and cartilaginous fishes, reptiles, birds and mammals (Hoyt 1990, Jefferson et al. 1991, Ford 2009). As apex predators they potentially have important effects on marine ecosystems (e.g. Estes et al. 1998, Williams et al. 2004) and the diversity of their prey means they can influence ecosystems at various levels and intensities (e.g. Springer et al. 2003, Ford & Ellis 2006). In the Southern Ocean, southern elephant seals, *Mirounga leonina*, underwent a population decline between the 1950s and 1990s throughout most of their breeding range (McMahon et al. 2005) and killer whale predation has been suggested as one of the

causes of this decline at 2 breeding locations: Marion Island (Condy et al. 1978) and the Crozet Archipelago (Guinet et al. 1992).

A critical step towards understanding the role of killer whales in ecosystems, however, and necessary for quantitatively evaluating the effects of killer whales in ecosystems, is the estimation of their abundance. Moreover, abundance estimates are vital for the informed management and conservation of cetaceans (e.g. Karczmarski et al. 1999, Keith et al. 2002, Parra et al. 2006) and trends in the abundance of marine top predators may be useful in detecting environmental changes in marine ecosystems (Weimerskirch et al. 2003, Boyd et al. 2006).

Forney & Wade (2007) reviewed worldwide killer whale abundance, estimating a minimum global population size of 50 000, but abundance data are poor for

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many regions and the authors identified the need for further estimates. Regional abundance estimates for the Southern Ocean, based on line-transect surveys, indicate that killer whales are relatively common in these waters. Hammond (1984) estimated 38 278 (CV = 0.63) killer whales in the Indian Ocean sector of the Southern Ocean, Kasamatsu & Joyce (1995) estimated 80 400 (CV = 0.15) individuals in the Southern Ocean with uncorrected abundance estimates for the Indian Ocean sector totalling 12 093 (CV = 0.44 to 0.96), and most recently Branch & Butterworth (2001) estimated 24 790 (CV = 0.23) killer whales south of 60° S.

In the southern Indian Ocean, rigorous local population size estimates are only available for Possession Island (Crozet Archipelago). Poncelet et al. (2010) used mark-recapture (MR) methodology to estimate the population size at 98 animals between 1988 and 1989 (95% CI = 70 to 156) and 37 ind. between 1998 and 2000 (95% CI = 32 to 62). Their analyses show a worrying decline in population size and survival rates, which the authors speculate is due to changes in prey availability (southern elephant seals and large whales) and lethal interactions with illegal fisheries targeting the Patagonian toothfish *Dissostichus eleginoides* (see also Tixier et al. 2010). At Marion Island, no rigorous population size estimates have been produced. Keith et al. (2001) identified 26 individual killer whales from 159 photographs taken opportunistically from 1975 to 1989 and, based on simultaneous island-wide observations on a single day, Pistorius et al. (2002) approximated the population size at 25 to 30 individuals.

MR analyses of photographic identification data have been used to estimate population size in killer whales (Kuningas et al. 2007, Williams & Thomas 2009, Poncelet et al. 2010, Durban et al. 2010) but this approach has generally been necessitated by logistical (e.g. large populations where individuals are encountered infrequently, or large and/or remote areas) or financial constraints (see Williams & Thomas 2009, Durban et al. 2010). More commonly, the abundance of small, well-studied killer whale populations is determined by a count of known individuals (e.g. Dahlheim et al. 1997, Matkin et al. 1999, Ford et al. 2000).

We aim to provide information required for the assessment of the ecological role of killer whales at Marion Island, and to furnish baseline information for their management and conservation there and in the broader southern Indian Ocean. Using photographic

identification data collected from 2006 to 2009, we established an identification catalogue of individuals at Marion Island and used MR analyses, as well as 2 simpler methods (proportion of identifiable individuals and enumeration), to estimate the abundance of killer whales.

MATERIALS AND METHODS

Study area. Subantarctic Marion Island (46° 54' S, 37° 45' E; Fig. 1) is the larger (296 km²) of a pair of islands comprising the Prince Edward Islands group. It is situated in the southern Indian Ocean with the nearest landmass being the Crozet Archipelago, approximately 1000 km to the east at a similar latitude. The interplay between the Antarctic Circumpolar Current and the prominent bottom topography of the Southwest Indian Ridge results in productive turbulent water masses around the Prince Edward Islands (Ansorge & Lutjeharms 2005), sustaining the large breeding populations of seals and seabirds.

Field methods. Land-based sightings of killer whales at Marion Island were recorded from April 2006 to April 2009. Small-vessel-based surveys are impossible because of logistic and safety concerns regarding the isolation of Marion Island and the very poor weather and sea conditions (Prince Edward Islands Management Plan Working Group 1996). Sightings were of 2 types: (1) opportunistic observations, which were recorded

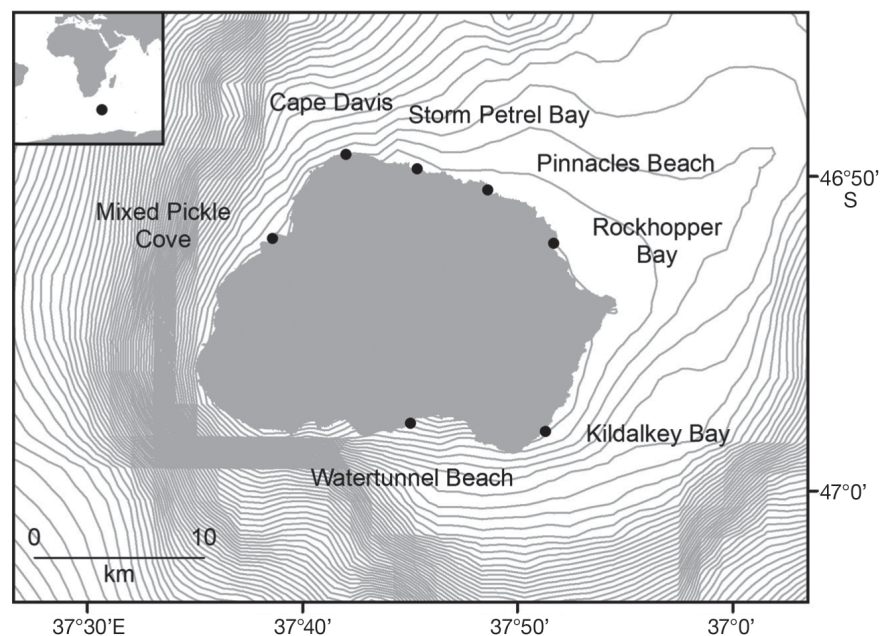


Fig. 1. Marion Island, showing killer whale observation points at the Island and approximate 50 m isobaths. The inset shows Marion Island's location in relation to Africa and Antarctica

Table 1. Hours of observation effort (parentheses: no. of observation sessions) monthly at various sites on Marion Island (see Fig. 1 for locations). Long (10 h) sessions were performed at all sites; short (2 to 3 h) sessions were performed only at Rockhopper Bay, and are presented separately from the long sessions. Dashes: no observations made

Site	2008								2009				Total
	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Jan	Feb	Mar	Apr	
Mixed Pickle Cove	-	-	-	-	-	-	-	-	10 (1)	10 (1)	-	-	20 (2)
Cape Davis	-	-	-	-	-	10 (1)	-	-	-	10 (1)	10 (1)	-	30 (3)
Storm Petrel Bay	-	-	-	10 (1)	10 (1)	20 (2)	20 (2)	-	-	10 (1)	-	-	70 (7)
Pinnacles Beach	-	-	-	10 (1)	10 (1)	20 (2)	10 (1)	20 (2)	-	-	-	-	70 (7)
Rockhopper Bay	-	-	-	-	-	-	10 (1)	20 (2)	-	-	-	-	30 (3)
Kildalkey Bay	-	-	-	10 (1)	20 (2)	20 (2)	30 (3)	20 (2)	-	10 (1)	10 (1)	-	120 (12)
Watertunnel Beach	-	-	-	10 (1)	30 (3)	20 (2)	30 (3)	10 (1)	-	20 (2)	-	-	120 (12)
All sites (long sessions)	-	-	-	40 (4)	70 (7)	90 (9)	100 (10)	70 (7)	10 (1)	60 (6)	20 (2)	-	460 (46)
Rockhopper Bay (short sessions)	14 (7)	25 (12)	24 (12)	24 (8)	27 (9)	18 (6)	21 (7)	24 (8)	24 (8)	15 (5)	27 (9)	6 (2)	249 (93)

from April 2006 to April 2009 while observers were engaged in various field activities, mostly systematic pinniped monitoring (see de Bruyn et al. 2008 for further pinniped monitoring details); and (2) dedicated observation sessions, which were conducted at various points on the north, east and south coasts of the island (Fig. 1) from May 2008 to April 2009 (Table 1). We consider these locations a representative inshore sampling/survey area as killer whales mainly patrol beaches along the eastern half of the island (Keith et al. 2001, Pistorius et al. 2002). During these sessions, a trained observer would remain at a point and visually search for killer whales for a predetermined length of time. Such dedicated observation sessions were either short or long. Short (2 to 3 h) observation sessions were performed 93 times at Rockhopper Bay (Fig. 1), totalling 249 h (Table 1). Sessions were performed at regular intervals throughout each month (approximately every 3 d), starting at the same time (approximately 11:00 or 14:00 h). Long (10 h uninterrupted) observation sessions were performed 46 times at 8 locations from August 2008 to March 2009, totalling 460 h (Table 1). Sessions were conducted on a weekly cycle.

For all types of observation, the location, group size and age and/or sex class composition of the group, as well as direction of movement, were recorded for each sighting. Distance from shore was recorded following Condry et al. (1978), where Zone 1 is within 5 m of shore; Zone 2 is 5 to 100 m from shore, usually extending to the first kelp (*Macrocystis* sp.) belt; Zone 3 is 100 to 500 m from shore, usually extending to the second kelp belt; and Zone 4 is beyond 500 m from shore. As many individuals as possible were photographed using an 8 megapixel Canon 350D with a Canon 75–200 mm f4.5–5.6 lens, or a 10.2 megapixel Nikon D200 with either a Nikon 80–200 mm f2.8 lens or a Nikon 80–400 mm f4.5–5.6 lens. To minimize capture hetero-

geneity, observers made a conscious effort to direct equal photographic effort at all individuals, independent of any noticeable marks on the individuals. Observers continued to take photographs as long as a group was within photographic range, irrespective of whether all individuals were photographed.

Treatment of photographs. Photographs were carefully examined and assigned a quality (*Q*) score from 1 (unusable for MR analyses) to 5 (excellent), independent of the distinctiveness of the individual represented. The *Q* score took into account the size of the dorsal fin in the photograph, focus, lighting, exposure, the angle of the dorsal fin to the photographer and the proportion of the dorsal fin obscured by water. Photographs of *Q*4 and *Q*5 were well exposed and well lit, in focus and the dorsal fin was sufficiently large in the photograph, relatively perpendicular to the photographer and not obscured by water. Although photographs of *Q*1 to *Q*5 were considered for the catalogue of identifiable individuals, only photographs of *Q*4 to *Q*5 were considered for MR analyses (Friday et al. 2000).

Individuals were identified based on natural markings of the dorsal fin and saddle patch (Bigg et al. 1987), mainly the pattern of nicks, notches and mutilations along the trailing edge of the dorsal fin. Individuals that were considered recognizable were assigned a unique numeric identifier, and included in a catalogue with which all subsequent photographs were compared (see Tosh et al. 2008). Both left and right side images of dorsal fins were used, as they could reliably be matched to the same individual. Catalogued individuals were not rated according to their distinctiveness, rather all catalogued individuals were considered reliably identifiable from photographs of *Q*4 to *Q*5, other than calves, which were excluded from MR analyses.

For all photographs of *Q*4 and *Q*5, a ratio was calculated relating the number of dorsal fins that could be

reliably identified (excluding calves) to the total number of photographed fins. This calculation was performed for each sighting, and subsequently an overall ratio was calculated representing the proportion of identifiable individuals (θ).

Analyses. MR analyses of the sighting histories of recognizable individuals were firstly performed using the software program MARK (White & Burnham 1999). Per-sighting captures were pooled into monthly capture events, thus a single calendar month constituted a sampling occasion. Population parameters were estimated using the open-population POPAN parameterization (Schwarz & Arnason 1996, 2009) The initial analysis is based on the fully time-dependent Cormack-Jolly-Seber (CJS) model ($\Phi_t p_t b_t$, where Φ is survival, p is probability of capture, b is probability of entry) and the first step in the analysis involves goodness-of-fit (GOF) tests for the CJS model using the program RELEASE GOF to validate model assumptions. Models were constructed for combinations of time-dependence (t) and consistency (\cdot) for Φ and p , and seasonal (s) variation was allowed for p . Based on the seasonal abundance of killer whales at Marion Island (Reisinger et al. 2011), September to December of each year was considered 'peak' occurrence whereas January to August was considered 'low' abundance. The most appropriate model was selected using the small-sample corrected Akaike's information criterion (AIC_c ; Burnham & Anderson 1998). Based on the GOF results of TEST 2 + TEST 3 in program RELEASE, a *post hoc* variance inflation factor (\hat{c}) may be estimated to adjust for extra-binomial variation in the data, resulting in a quasi- AIC_c ($QAIC_c$). Median and bootstrap GOF are not available in the POPAN parameterization.

Because of sparse data, overparameterization and possible violation of one of the assumptions underlying the POPAN approach (see 'Results' and 'Discussion'), we also calculated abundance using the Chapman-modified Lincoln-Petersen 2-occasion estimator (Chapman 1951). Captures in September to December (the months of peak killer whale occurrence at Marion Island; Reisinger et al. 2011) were pooled into a single capture occasion for each year (2006, 2007 and 2008) and abundance was estimated for 2006 to 2007 and 2007 to 2008. Pooling captures from the peak occurrence months min-

imized the effects of temporary immigration and emigration on this closed population model.

Finally, we calculated abundance simply as the number of non-calf individuals determined from photographs of Q4 to Q5 during the study period, divided by the proportion of identifiable individuals (θ).

The MR abundance estimates apply only to the population of marked animals (excluding calves) and these estimates were expanded to include the entire population (including calves) by dividing N (the MR population size estimate) by θ , yielding total abundance (N_{total}). Variance was estimated using the delta method as:

$$\text{var}(N_{\text{total}}) = N_{\text{total}}^2 \left(\frac{\text{var}(N)}{N^2} + \frac{1-\theta}{n\theta} \right) \quad (1)$$

where n is the total number of dorsal fins from which θ was calculated. Confidence intervals for N_{total} assumed the same error distribution as the MR estimates (Wilson et al. 1999).

RESULTS

From April 2006 to April 2009 (inclusive), killer whales were sighted 846 times at Marion Island and 9724 photographs were taken. Table 2 shows the number of sightings per year, the number of photographs taken in various categories and the number of photographic identifications in various categories. Killer whales were regularly observed close inshore; 50% of sightings included sightings in Zone 1 and 65% included sightings in Zones 1 & 2. Group size ranged from 1 to 13 ind. (Fig. 2) and the proportion of individuals photographed in each group per occasion ranged from 0 to 100%. In total, 37 ind. were identified, of which 7 were classified as adult males, 22 as adult females, 5 as unknown age-sex class and 3 as calves (born during the study period and identified by their colouration, relative size, close association with an adult female and previous absence from groups). Left and right side dorsal fin images were available for 30 ind.; the remaining 7 were photographed from one side only. Only 30 ind. were included in the POPAN MR analyses, the remaining 7 were calves (3 ind.) or

Table 2. Sightings of killer whales at Marion Island, photographic effort, number of identifications and individuals identified, April 2006 to April 2009. Q1–Q5: see 'Treatment of photographs' in 'Materials and methods'

Period	Sightings		Photographs		Identifications		Unique individuals sighted	New individuals identified
	All	Photographic	Q1–Q5	Q4–Q5	Q1–Q5	Q4–Q5		
2006–2007	239	83	334	49	190	37	21	21
2007–2008	166	94	1334	86	299	54	21	10
2008–2009	441	209	8056	1446	4075	1283	30	6
2006–2009	846	386	9724	1581	4564	1374	37	37

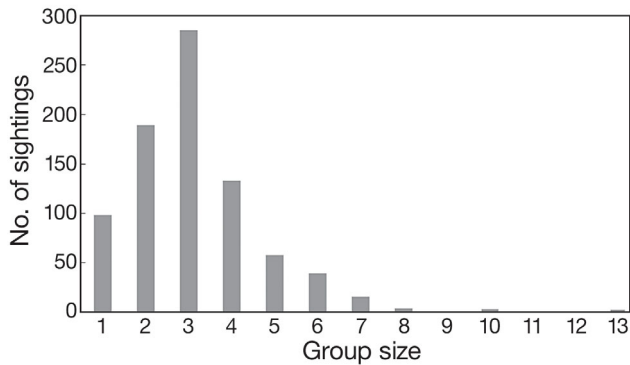


Fig. 2. Frequency distribution of group sizes of killer whales sighted at Marion Island, April 2006 to April 2009

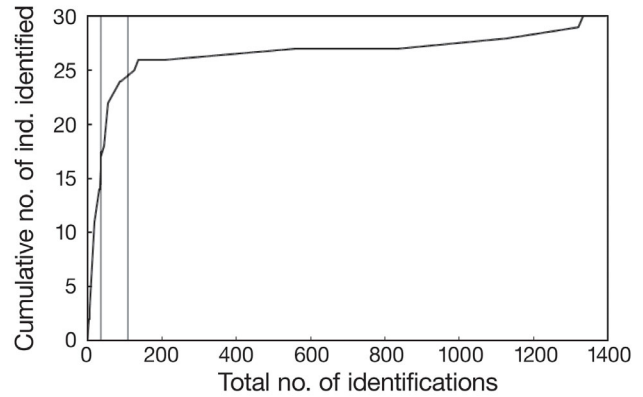


Fig. 4. Discovery curve, or cumulative number of individuals identified, for killer whales at Marion Island, April 2006 to April 2009 (photographs of Q4 to Q5 only, calves excluded). Vertical lines indicate the period including study years (2006–2007, 2007–2008 and 2008–2009)

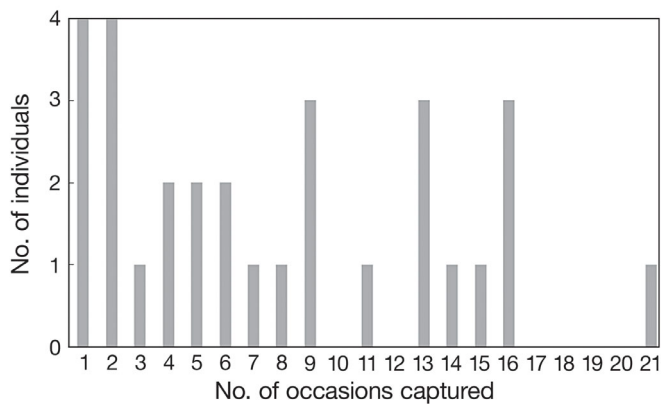


Fig. 3. Sighting frequency distribution of identifiable killer whales at Marion Island from April 2006 to April 2009 (photographs of Q4 to Q5 only — see ‘Treatment of photographs’ in ‘Materials and methods’; calves excluded)

were not identified in photos of Q4–Q5 (4 ind.). Fig. 3 shows the sighting frequency distribution of these animals and Fig. 4 shows the discovery curve, or the cumulative number of identified individuals (both figures used Q4 to Q5 only and calves were excluded). Only 27 ind. were included in the Chapman MR analyses; of the 10 excluded individuals, 3 were calves and 7 were not identified in photos of Q4 to Q5 in the sampling occasions (September–December of each year).

Of the 6 biologically sensible model combinations tested in the POPAN approach, one did not reach numerical convergence. Parameters for each occasion were often inestimable because of sparse data. Although the result of TEST 2 + TEST 3 in program RELEASE GOF (= 1.30; Table 3) indicated only slight overdispersion in the data (Cooch & White 2009), program RELEASE reported insufficient data to perform tests for a number of occasions and TEST 2 was rejected. The most parsimonious model according to the QAIC_c scores was $\Phi. p_s b_t$ (constant survival, probabil-

ity of capture varies seasonally and probability of entry varies with capture occasion), and this model estimated population size at 33 ind. (SE = 2.91, 95% CI = 27 to 38). No models had a $\Delta QAIC_c$ (difference between the QAIC_c of the model in question and that of the top-ranked model) of <2 units, which would have indicated that they were also likely descriptors of the data (Burnham & Anderson 1998). The proportion of identifiable individuals was 0.77 (SE = 0.34) and, based on model $\Phi. p_s b_t$, total abundance was estimated at 42 ind. (SE = 3.83, 95% CI = 35 to 50).

Test	\hat{c}	χ^2	df	p
TEST 2 + TEST 3	1.30	41.58	32	0.12
TEST 2	2.11	40.12	19	0.00
TEST 3	0.11	1.46	13	1.00
TEST 3.SR	0.08	0.53	7	1.00
TEST 3.SM	0.17	0.94	6	0.99

The Chapman-modified Lincoln-Petersen estimator yielded total population sizes of 37 and 32 ind. in 2006 to 2007 and 2007 to 2008, respectively (Table 4), and the simple abundance estimate (number of individuals identified from photographs of Q4 to Q5, excluding calves, divided by θ) yielded 39 ind.

Table 4. Chapman-modified Lincoln-Petersen estimates of the abundance of killer whales at Marion Island

Period	Marked population			Total population		
	N	SE	95% CI	N	SE	95% CI
2006–2007	29	4.72	23–35	37	6.15	29–44
2007–2008	25	0.87	23–26	32	1.21	30–33

DISCUSSION

The observed group sizes (Fig. 2) of killer whales at Marion Island are consistent with earlier observations for the island (Condy et al. 1978, Keith et al. 2001, Tosh et al. 2008), as well as for populations of pinniped-eating killer whales elsewhere, likely an optimal group size for maximizing energy intake in such populations (Baird & Dill 1996). The most frequent group size observed (3 ind.) is comparable to average group sizes of 4.2 (Condy et al. 1978), 3.6 (Keith et al. 2001) and 3.4 (Tosh et al. 2008) reported previously at Marion Island, 3.2 (modal group size of 2) at Punta Norte (Lopez & Lopez 1985) and a modal group size of 3 at Vancouver Island, British Columbia (Baird & Dill 1996). The largest groups observed at Marion Island included identified individuals that were mostly observed separately on other occasions (Tosh et al. 2008, P.J.N.d.B. unpublished data), indicating that large groups formed temporarily during interactions of smaller groups, likely for socializing and perhaps cooperative hunting (Baird & Dill 1996). This illustrates that, albeit for killer whales in different habitats and aquatic ecosystems, a stable group size aligned with the energetic constraints of predation on marine mammals has evolved (e.g. Baird & Dill 1996).

The number of individuals identified in the present study is substantially larger than that identified by Keith et al. (2001) but the proportion of adult females in the current catalogue (59%) is almost identical to that in Keith et al.'s study (58%), although the proportion of adult males differs markedly (19% in the present study compared with 35%). The opportunistic nature of Keith et al.'s (2001) study may have meant that males were more likely to be observed because of their much larger dorsal fins, potentially explaining the higher proportion of males in that study. The number of individuals identified here is similar to photographic identification studies at Punta Norte (30 ind. in 1975 to 1997; Iñíguez 2001) and Possession Island (32 ind. in 1998 to 2000; Poncet et al. 2010). The sighting frequency distribution (Fig. 3) suggests a population of regularly occurring animals; only 4 ind. were seen during one month only and the majority of animals were seen in a number of months during the study period. The presence of a

large proportion of transient (not to be confused with the eastern North Pacific killer whale ecotype) or migratory animals is therefore unlikely. Further, there is no suggestion of separate populations of transient/migratory and resident (again, not to be confused with the eastern North Pacific killer whale ecotype) animals, as sighting frequencies are relatively evenly distributed without clear clustering.

The discovery curve (Fig. 4) shows the expected rapid initial increase in 2006 to 2007 and 2007 to 2008 but, despite the far greater photographic effort in 2008 to 2009 (Table 2) and the larger number of sightings, it appears to level off. This asymptotic tendency in the discovery curve indicates that most individuals in the population have been identified; however, only continuation of the photographic MR effort in a structured protocol can confirm this (e.g. Wilson et al. 1999, Baker et al. 2006).

Assumptions: validation and violations

Validation of the assumptions underlying MR methods is critical in providing relatively unbiased estimates of population parameters (Begon 1983). The natural characteristics used to identify killer whales have proven to be long-lasting, allowing individuals to be recognized for years in long-term studies (e.g. Bigg et al. 1987, Bigg et al. 1990, Baird & Whitehead 2000, Parsons et al. 2009, Ivkovich et al. 2010). This makes killer whales conducive to MR analysis following rigorous photographic surveying and we therefore considered mark loss in this study as being negligible. Sampling was instantaneous, and sampling effort was consciously similarly distributed between marked and unmarked animals, although heterogeneous capture probabilities because of differences in the behaviour of individuals are present in many photographic identification MR studies (e.g. Hammond 1986, see also Baird & Dill 1995). Any further violations of equal capture probabilities were minimized by imposing careful photographic quality criteria; however, capture heterogeneity is evident in this study. In the POPAN approach, TEST 2 (capture heterogeneity) in program RELEASE was rejected (Table 3). The most likely explanations are differences in behaviour of individuals (Hammond 1986) and slight temporary emigration.

MR estimates compared with simpler methods

Capture homogeneity is one of the key assumptions underlying the POPAN and other Jolly-Seber approaches, and violation of this assumption casts severe doubt on estimates using this method. Evidence of

capture heterogeneity in this study thus leads us to prefer the simpler Chapman-modified Lincoln-Petersen estimator to the POPAN approach, so the 2 simplest approaches we took to estimate abundance seem most appropriate in this case.

Applying the proportion of identifiable individuals (θ) to the number of non-calf individuals identified from photos of Q4–Q5 yields a population size of 39 ind. — close to the number of individuals in the catalogue (37 ind.), the POPAN MR estimates (42, 95% CI = 35 to 50) and the Chapman MR estimates (37, 95% CI = 29 to 44 and 32, 95% CI = 30 to 33). This agreement, combined with the sighting frequency pattern (Fig. 3) and the asymptotic tendency of the discovery curve (Fig. 4), indicates that most of the identifiable proportion of the population has been included in the catalogue, and lends confidence to the catalogue size (complete enumeration over time) as a rigorous abundance estimate free of the assumptions underlying MR estimates. Although the catalogue may also be subject to some bias, it is more precise than MR estimates. Our estimate is based on only 3 yr of data, and continued study is undoubtedly required and may resolve problems with the MR analyses. The thorough establishment of a photographic identification catalogue and the continuation of the photographic identification study will be of future use to investigate various questions related to population parameters, social ecology and movement of individuals.

Comparison with other studies and defining the 'population'

Our catalogue size should not be compared with that of Keith et al. (2001) with a view to identify abundance trends, because of the highly opportunistic nature of that study. In broad terms, our population size estimates are similar to the most recent estimate at Possession Island (37 ind., 95% CI = 32–62; Poncet et al. 2010). Although the Possession Island population has undergone a marked decline, no comparable data are available for Marion Island. The birth of at least 3 calves at Marion Island during 2008 to 2009 suggests a higher fecundity than that reported at Possession (Guinet & Bouvier 1995).

This begs the question as to what constitutes the 'population'. In terms of the MR methodology, the 'population' refers to individuals available to be captured during the study, and thus refers to any killer whales that may occur in the inshore area. We have discussed why it is unlikely that such a population includes a large proportion of transient individuals and can broadly refer to the population in this case as those killer whales that occur, at least seasonally, inshore at

Marion Island (however, it should be noted that there may be differences among groups in the use of inshore areas; Baird & Dill 1995). This population likely includes animals occurring at neighbouring Prince Edward Island. Prince Edward Island is only 19 km from Marion Island, a much smaller distance than the more than 40 km of coastline included in our survey area, and the only photograph available of a killer whale at Prince Edward Island (provided by R. Tarr, Oceans and Coasts, Department of Environmental Affairs, Rogge Bay, South Africa) was reliably identified as an individual included in the Marion catalogue.

Because our data are completely biased to killer whales occurring inshore, we cannot exclude the existence of a separate population of offshore animals (as exists in the eastern North Pacific; Dahlheim et al. 2008), and our abundance estimate would not apply to such a population. No studies have been conducted on the medium- and large-scale movement of killer whales at Marion Island, but inshore abundance data (Reisinger et al. 2011, see also Condy et al. 1978, Keith et al. 2001) indicate potential seasonal movement offshore or increased range, both of which may be accompanied by a potential diet switch (e.g. Mikhalev et al. 1981).

Future research

Although our abundance estimate is a novel and critical step in elucidating the role of killer whales in the Marion Island marine ecosystem—as well as being valuable for any conservation and management decisions in the region and for comparisons with other killer whale populations—the current photographic identification study should continue. Future research investigating the population structure and spatiotemporal distribution of killer whales at Marion Island can now be initiated in the context of this rigorous abundance estimate.

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