CHAPTER 4

COHORT AND TAG-SITE SPECIFIC TAG-LOSS RATES IN MARK-RECAPTURE STUDIES: A SOUTHERN ELEPHANT SEAL CAUTIONARY CASE

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Abstract

Marker-loss is a common feature of mark-recapture studies and important as it may bias parameter estimation. A slight alteration in tag-site of double tagged southern elephant seals (*Mirounga leonina*) marked at Marion Island from 1983 - 2005 in an ongoing mark-recapture program, had important consequences for tag-loss. We calculated age-specific tag-retention rates and cumulative tag-retention probabilities using a maximum likelihood model selection approach in the software application TAG_LOSS 3.2.0. Under the tag-loss independence assumption, double tag-loss of inner interdigital webbing tags (IIT; 17 cohorts) remained below 1% in the first 5 years and increased monotonically as seals aged, with higher tag-loss in males. Lifetime cumulative IIT tag-loss was 11.9 % for females and 18.4 % for males, and equivalent for all cohorts. Changing the tag-site to the outer interdigital webbing (OIT; 6 cohorts) resulted in increased and cohort dependent tag-loss, although the variation (mean ± 95% CI) in cumulative tag-loss probabilities never exceeded 5.3% between cohorts at similar age. Although different studies may homogenize techniques, we advocate the importance of dataset-specific assessment of tag-loss rates to ensure greatest confidence in population parameters obtained from mark-recapture experiments. Permanent marking should be implemented where feasible.

Key-words: cohort heterogeneity, double tagging, mark-resight, marker-loss, *Mirounga leonina,* Marion Island, phocids, tag shedding, tag placement

Introduction

Mark-recapture studies are frequently used by ecologists and wildlife managers to estimate demographic parameters of wildlife populations. These parameters provide insight into population processes and allow implementation of appropriate management policies. Mark-recapture data analyses have largely been based on Cormack-Jolly-Seber (CJS) parameterizations (Lebreton *et al.* 1992). However, violations of the assumptions of the CJS model can severely bias parameter estimates (Arnason and Mills 1981, McDonald *et al.* 2003). Fundamental assumptions are that marks do not affect future survival, are not lost or missed during resights (Seber 1982), and are correctly identified (Stevick *et al.* 2001). However, these assumptions are potentially violated by many marking techniques and may be inherent to all long-term tagging regimes. Marker-loss and marker-induced mortality result in population size overestimates through negatively biased survival rates, since individuals that have lost their marks cannot be identified anymore and appear 'dead' to the observer (Arnason and Mills 1981, Pollock *et al.* 1990, McDonald *et al.* 2003). Additionally, if recaptured, such individuals appear to be immigrants, biasing recruitment rates upward (Cowen and Schwarz 2006). Time or group dependent marker-loss may additionally result in non-uniform biases in survival estimates through heterogeneous recapture probabilities among groups or over time (Pollock *et al.* 2001). Therefore, knowledge of violations of fundamental assumptions such as marker-loss is crucial to obtain robust information of life-history data that allows informed decision making (McMahon and White 2009).

The extensive use of non-permanent markers to identify individuals in mark-recapture studies for investigations of life-history, demographics, dispersal, growth and behaviour makes estimation of marker-loss rates widely applicable to numerous ecological research disciplines and wildlife authorities across a wide range of species. An increasing number of studies incorporate quantitative estimates of marker-loss rates in conjunction with analytical advances in this field (Barrowman and Meyers 1996, Conn *et al.* 2004, Cowen and Schwarz 2006). These include tag-loss in invertebrates (Kneib and Huggler 2001), terrestrial and marine vertebrates, (Stobo and Horne 1994, Diefenbach and Alt 1998, Adam and Kirkwood 2001, Casale *et al.* 2007) and neckband failure (Johnson *et al.* 1995) and band loss in birds (Spendelow *et al.* 1994). Marker-loss is usually estimated by double marking individuals and approximating marker-loss by following subjects through time and noting whether one or two marks are retained. In the absence of a permanent mark (in addition to the two temporary markers), marker-loss independence is assumed, where the probability of losing the second marker is independent of the probability of losing the first marker. This assumption is difficult to test because permanent marking is not easily accomplished. However, in cases where permanent marks facilitated assessment of the assumption, assuming independence has been shown to underestimate tag-loss (e.g., Diefenbach and Alt 1998, Bradshaw *et al.* 2000, McMahon and White 2009). However, aside from the potential errors associated with the independence assumption, researchers should attempt to quantify inconsistent marker-loss over time or variation therein between groups of marked animals (Spendelow *et al.* 1994). Failure to account for marker-loss differences between juveniles and adults for example, may lead to erroneous conclusions about the importance of juvenile and adult survival as population growth determinants. Similarly, a false indication of processes such as density dependent survival may be indicated when marker-loss differs according to the population density, physical environment or tagger proficiency at specific colonies or study sites.

Many pinniped species are ideal mark-recapture study subjects due to their ubiquitous terrestrial phases, generally high site fidelity and thus their temporal and spatial accessibility to researchers. Individuals are usually marked by double tagging in the connective tissue of the interdigital webbing of each hind flipper in true seals (Phocidae) or in the trailing edge of both front flippers in fur seals and sea lions (Otariidae) (Erickson *et al.* 1993). However, in contrast to permanent markings such as branding or tattoos, tag-loss can be substantial (e.g., Stobo and Horne 1994, McMahon and White 2009) and if left uncorrected may severely bias survival estimates. On sub-Antarctic Marion Island (46^{o}54'S, 37^{o}45'E), southern elephant seals *Mirounga leonina* L. have been subject to a 25-year (1983 - 2008) ongoing mark-recapture study. The mark-recapture program forms the foundation of investigations into life-history, demography, dispersal and philopatry of southern elephant seals at Marion Island (e.g., Bester 1989, Pistorius *et al.* 1999, 2004, Kirkman *et al.* 2003, 2004, McMahon and Burton 2005, McMahon *et al.* 2005). Two previous studies have estimated tag-loss for this population, to incorporate tag-loss adjustments into demographic data. Wilkinson and Bester (1997) used a ratio method to calculate tag-loss over the period 1983 to 1990 and Pistorius *et al.* (2000) improved on this method, estimating linear tag-loss (1983 - 1993) based on the time at liberty of tagged seals in a maximum likelihood framework. Age and sex specific tag-loss rates from Pistorius *et al.* (2000) were subsequently used to correct mark-recapture survival estimates of southern elephant seals at Marion Island.

The physical placement of markers can be central to the accuracy of estimates gained from mark-recapture experiments. Incorrect tag placement can result in increased mortality (Kneib and Huggler 2001) or reduced apparent survival as a consequence of increased tag-loss. Tag placement has nonetheless received limited attention in studies beyond fisheries management (e.g., Brennan *et al.* 2007). Limpus (1992), however, evaluated tag placement in turtles, where tag-loss was higher in the more distal tagging positions on the front flipper. The hind flipper tag-site used to mark elephant seals at Marion Island changed in 2000 from the inner interdigital webbing (between digits two and three or three and four; 1983 - 1999) to the upper, outer interdigital webbing of the hind flippers (between digits one and two; 2000 - 2008) (Figure 4.1). The tag-site adjustment aimed at improving tag visibility for resighting, because the tags placed in the inner interdigital webbing are often obscured by the flipper digits when animals are hauled out on land. The effect of tag-site on tag-loss has not been quantified here or directly for other pinnipeds and such an adjustment may have important consequences for demographic analyses.

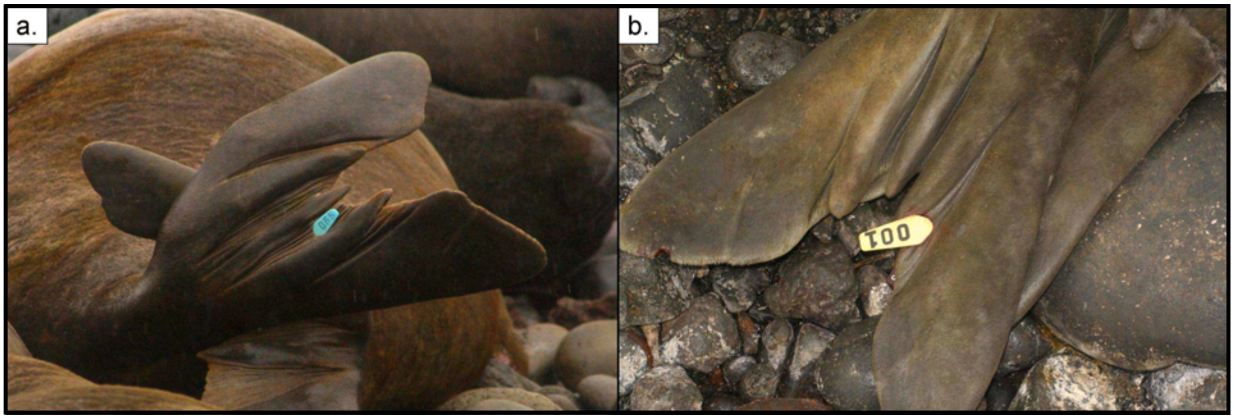

Figure 4.1. a. Inner interdigital tag (IIT). The tag is applied to the center of the inner section of the interdigital webbing of the hind flipper between digits three and four. b. Outer interdigital tag (OIT). The tag is applied to the center of the upper interdigital webbing of the hind flipper between digits one and two.

We estimate and compare tag-loss rates for 17 cohorts of southern elephant seals double tagged in the inner interdigital webbing (inner interdigital tags: IIT), and six cohorts double tagged in the upper, outer interdigital webbing (outer interdigital tags: OIT). Variation in tag-loss due to seal age and sex, tagging protocol (tag-site, *i.e.,* IIT and OIT) and tagging proficiency by different personnel (resulting in cohort specific tag-loss rates) are considered.

Methods

Mark-resight framework

Data from cohorts of southern elephant seals born on Marion Island from 1983 to 2005 and resighted up to April 2008 were used. During each breeding season, virtually all recently weaned southern elephant seal pups born on Marion Island were sexed and double tagged in the interdigital webbing of the hind flippers with identical, uniquely numbered, colour-coded plastic Dal 008 Jumbotags® (Dalton Supplies Ltd., Henley-on-Thames, United Kingdom). These two-piece self-piercing tags are applied with an applicator, and have favorable retention rates as compared to other tag types (Testa and Rothery 1992). The male component of all tags was positioned on the outer surface of the flipper (*i.e.,* the point of this component protrudes from the inner surface). From 1983 to 1999 tags were applied to the center of either of the two inner sections of interdigital webbing of the hind flipper (webbing between digits two and three or three and four; IIT). From 2000 to 2005, tags were applied to the center of the upper interdigital webbing of the hind flipper (between the first and second digit; OIT) (Figure 4.1). At tagging, one third of the tag extended past the trailing edge of the interdigital webbing. During all years tags were applied by two dedicated field personnel, all of whom were trained by MNB (except from 1986 to 1988 when up to six pairs of trained field personnel tagged pups). Further details regarding the tagging procedure appear in Wilkinson and Bester (1997) and de Bruyn *et al.* (2008).

During most of the study period (1983 - 2008), the resighting effort remained constant and included all beaches along a 51.9 km coastline where southern elephant seals can haul out. During the moulting and winter periods (mid-November - mid-August), all beaches were searched for tagged seals every ten days, but in the breeding season (mid-August - mid-November) this was done on a seven-day cycle to allow for increased seal numbers and harem density. During the early study period (1983 - 1988), no resights were made during winter (mid-April - mid-August). For every tagged seal that was resighted, the date and locality of the sighting, tag colour combination and three-digit number, number of tags remaining (one or two), and the sex of the seal (if identified) were recorded. We assume similar and accurate resight rates of single and double tags owing to the high and constant resight effort by trained personnel on Marion Island, where both flippers of each animal was always inspected for the presence of tags. This was done to prevent different reporting rates for single or double tags which may bias estimates (Adam and Kirkwood 2001). The haulout pattern of elephant seals (Kirkman *et al.* 2003, 2004) allowed for confirmation of recorded tag data with subsequent resights, often several times over a season. Shed tags were not replaced.

Estimation of tag-loss

We estimated tag-loss using a maximum likelihood method for individually identifiable mark-resight study subjects in the software application TAG_LOSS (Version 3.2.0;

http://www.ese.u-psud.fr/epc/conservation/Tag_Loss/Tag_Loss.html) as presented by Rivalan *et al.* (2005). This program provides quasi-continuous tag-loss probabilities and incorporates assessment of different trends in tag-loss rates over time. Quasi-continuous tag-loss probabilities based on exact time at liberty remove bias associated with pooled observations (Xiao 1996*,* Diefenbach and Alt 1998). Model functions described the time-dependent daily probability of tag-loss $p(t)$ (see Rivalan *et al.* 2005). Model selection was based on Akaike's Information Criteria (AIC), where the model with the smallest AIC value provided the most parsimonious fit (Burnham and Anderson 1998). AIC weights (w_i) provided the relative support for each model. Pups initially tagged with only one tag, seals of unknown sex and pups double tagged, but never resighted, were excluded from analyses. Tagged seals that were not resighted most likely died during their first pelagic foraging trip (60 - 65% first year mortality; McMahon *et al.* 1999, Pistorius and Bester 2002) or emigrated from the study area (Bester 1989). Double tag-loss within the first year is suggested to be minimal (see Results and Discussion).

The regularity of the annual haulout cycle of elephant seals (which includes obligatory and facultative haulouts per annum), combined with the continuous high resight effort in the current study permits calculation of reliable estimates of tag time at liberty, in contrast to studies where few resights are possible (e.g., leatherback sea turtles *Dermochelys coriacea,* Rivalan *et al.* [2005] and loggerhead sea turtles *Caretta caretta,* Casale *et al.* [2007]). We constructed individual capture histories for all individuals tagged on day zero (at weaning), and subsequently resighted (n = 7849, cohort range n = 228 - 479). Three sets of capture histories were considered, following Rivalan *et al.* (2005): (1) The individual was resighted with two tags intact for the duration of its presence in the study, to estimate the minimum number of days without tag-loss (N_{22}; n = 6786). (2) We initially observed the individual with two remaining tags (N_{22}), but subsequently with only one tag intact (N_{21}). This capture history calculates both the minimum number of days without tag-loss (N_{22}) and the interval length (mean = 212 days) during which one tag was lost (N_{21}; n = 952). (3) Subsequent to double tagging, we only observed the individual with one tag intact for the duration of its presence in the study (N_{21}; n = 111). Because permanent marks were absent, we could not reliably identify animals that had lost both tags (N_{20} or N_{10}; known n = 10 from other identifiable marks, e.g., scarring), and therefore did not consider such cases. This necessitated the assumption of tag-loss independence, where the probability of losing one tag did not affect the probability of losing the second tag.

We tested three different trends in daily tag-loss over time: constant rate, monotonic increase/decrease and a two-step function (e.g., rapid initial tag-loss, followed by a decreased continuous loss pattern and then a further increase or decrease with varying slope; this function can adjust to many different daily tag-loss rate modalities over time). Tag-loss patterns were assessed separately for each sex and cohort and also for cohorts and sexes pooled over time. We used the best fitting trend to test for a sex, cohort and tag-site effect on tag-loss. For the sex and cohort variables, we compared the AIC model fit for separate sex/cohort models, compared to a single model grouping sexes/cohorts. Constructing models that separated IIT and OIT and subsequently evaluating model fit assessed tag-site variability. TAG_LOSS 3.2.0 converted parameter estimates from the best model to daily tag-loss probabilities, age-specific tag-loss probabilities and cumulative tag-loss rates (Rivalan *et al.* 2005). Age-specific tag-loss is the conditional probability that a tag is lost during one year among the tags that were still present at the beginning of that year. Standard errors of parameters were calculated by the square-root of the inverse of the Fisher information matrix (Abt and Welch 1998). The proportion of animals retaining at least one tag is presented as identification probabilities (1 - cumulative tag-loss probability). Identification probabilities therefore represent the proportion of individuals still identifiable (retaining either one or two tag/s) for each age group.

Results

Tag-loss was best described by a monotonic increase of tag-loss rate with time for both male and female groups (AIC $w_{i\ (\text{monotonic})} = 1$) (Table 4.1). Although several cohorts showed support for the constant model or two-step function, few of these cohorts showed substantial support against the monotonic increasing model. Males from cohort 17 deviated most from the monotonic trend (ΔAIC = 17.01), while only one other cohort (cohort 10 females) with a ΔAIC value > 4 (ΔAIC = 7.95) indicated some support for an alternate model. Both these groups received support for the two-step function model, indicating initial high tag-loss soon after tagging, but leveling off over time.

Table 4.1 (below). Model selection results for tests of southern elephant seal tag-loss trend over time, at Marion Island. For each sex, model parameterizations specify one of three different trends in daily tag-loss over time: constant rate, monotonic increase/decrease or a two-step function. For monotonic functions, ‘direction’ indicates a positive or negative slope of the daily tag-loss function over time.

		Males				Females			
Cohort	Tag-site	Model of change of tag-loss rate				Model of change of tag-loss rate			
		Constant	Monotonic	direction	2 steps	Constant	Monotonic	direction	2 steps
1	IIT	119.52	**112.51**	**+**	116.50	171.85	**169.18**	**+**	173.17
2	IIT	120.48	**117.53**	**+**	121.41	**200.60**	201.12	**+**	205.12
3	IIT	278.71	**273.20**	**+**	277.20	300.49	**291.10**	**+**	295.10
4	IIT	**170.28**	173.42	**-**	177.44	257.17	**254.50**	**+**	258.50
5	IIT	227.20	**224.72**	**+**	228.70	221.33	**216.38**	**+**	219.98
6	IIT	245.02	**237.28**	**+**	240.87	258.25	**256.04**	**+**	259.28
7	IIT	258.11	**257.76**	**+**	261.74	**247.33**	251.28	+	255.26
8	IIT	239.07	**234.04**	**+**	238.04	**229.30**	230.17	+	234.16
9	IIT	214.48	**213.38**	**+**	217.38	327.08	**322.64**	**+**	326.64
10	IIT	222.12	220.40	**-**	**219.05**[a]	400.89	404.89	=	**396.93**[b]
11	IIT	248.59	**248.45**	**+**	252.38	288.61	285.10	**+**	**284.12**
12	IIT	134.55	**134.05**	**+**	138.05	278.11	**277.29**	**+**	280.93
13	IIT	**153.06**	155.56	+	156.82	177.04	**175.69**	**+**	179.17
14	IIT	162.68	158.19	+	**156.42**[b]	378.33	**367.55**	**+**	371.54
15	IIT	219.67	**199.89**	**+**	203.88	215.89	**205.05**	**+**	209.05
16	IIT	**175.11**	178.12	+	181.36	**318.64**	319.25	+	323.20
17	IIT	167.68	171.69	=	**154.68**[a]	210.59	205.46	-	**202.98**[c]
18	OIT	224.71	**199.69**	**+**	203.69	243.94	**218.45**	**+**	221.40
19	OIT	189.52	**180.91**	**+**	184.91	305.19	**289.70**	**+**	293.70
20	OIT	268.39	**265.37**	**+**	269.37	**324.18**	325.70	+	328.43
21	OIT	345.78	**339.70**	**+**	343.70	**483.32**	486.05	+	490.04
22	OIT	**89.64**	90.72	+	93.55	**167.01**	169.35	+	171.97
23	OIT	**378.02**	378.56	-	381.46	**393.78**	397.78	-	401.28
Total AIC		4852.39	**4765.10**		4818.59	6398.92	**6319.70**		6381.97
Δ AIC		87.25	0.00		53.45	79.22	0.00		62.27
AIC w_i		0.00	1.00		0.00	0.00	1.00		0.00

[a] High tag-loss rate soon after tagging. Rate becomes null after 1500 days

[b] High tag-loss rate soon after tagging

[c] Tag-loss rate becomes null after 2000 days

Tag-site had a significant effect on tag-loss rates, with cohort and sex differences in tag-loss also dependent on the tag-site. Tag-loss did not differ between cohorts with IIT, and the model with a general estimate calculated over all 17 cohorts received the most AIC support (Table 4.2).

In contrast, strong support for variable tag-loss rate between cohorts was found for OIT (cohorts grouped, $\Delta AIC_{18\ -\ 23} = 190.03$) (Figure 4.2). Cohort dependent OIT tag-loss was not unexpected, as field observations indicated that cohort 23 showed uncharacteristically high

Table 4.2. Model performance based on AIC for cohort dependent and independent tag-loss rates in southern elephant seals at Marion Island.

Cohort grouping	Males	Δ AIC	AIC w_i
1,..,23	4765.14	25.59	0.00
1-17, 18,..,23	**4739.55**	0.00	1.00
1,..,17, 18-23	4860.33	120.78	0.00
1-17, 18-23	4834.75	95.19	0.00
1-23	4910.24	170.68	0.00

Cohort grouping	Females	Δ AIC	AIC w_i
1,..,23	**6319.70**	0.00	0.93
1-17, 18,..,23	6324.90	5.19	0.07
1,..,17, 18-23	6421.61	101.91	0.00
1-17, 18-23	6426.81	107.10	0.00
1-23	6511.57	191.87	0.00

Cohort grouping	M+F	Δ AIC	AIC w_i
1,..,23	11084.85	12.06	0.00
1-17, 18,..,23	**11072.78**	0.00	1.00
1,..,17, 18-23	11274.87	202.09	0.00
1-17, 18-23	11262.81	190.03	0.00
1-23	11431.83	359.05	0.00

initial tag-loss associated with suboptimal (shallow - tag extends more than one third past the trailing edge of the flipper webbing) tagging . In addition, we suspected that cohorts 19 and 20 might show different tag-loss rates that could lead to inter-cohort variation as these tags were sometimes tagged too deep (tag not extending by one third past the trailing edge of the flipper webbing). We subsequently removed cohorts 19, 20 and 23 from the OIT model, to test whether cohort variability existed among the remaining three cohorts. Cohort specific variability persisted (cohorts grouped $\Delta AIC_{18,\ 21,\ 22}$ = 59.34, cohorts separate ΔAIC = 0), and we continued analyses considering all OIT cohorts separately. Separate sex models, with increased tag-loss in males, improved model fit for IIT (Table 4.3). Conversely, a single model for males and females combined was sufficient to describe tag-loss for OIT cohorts.

Table 4.3. Model selection for a sex-effect, dependent on tag-site, for southern elephant seal tag-loss from Marion Island. Males in cohorts 1-17 showed higher tag-loss rates than females.

Cohorts	Sexes separated	Sexes grouped	Δ AIC	AIC w_i
1-17	**7722.49**	7730.82	8.333	0.98
18-23	3539.07	**3531.99**	7.073	0.97

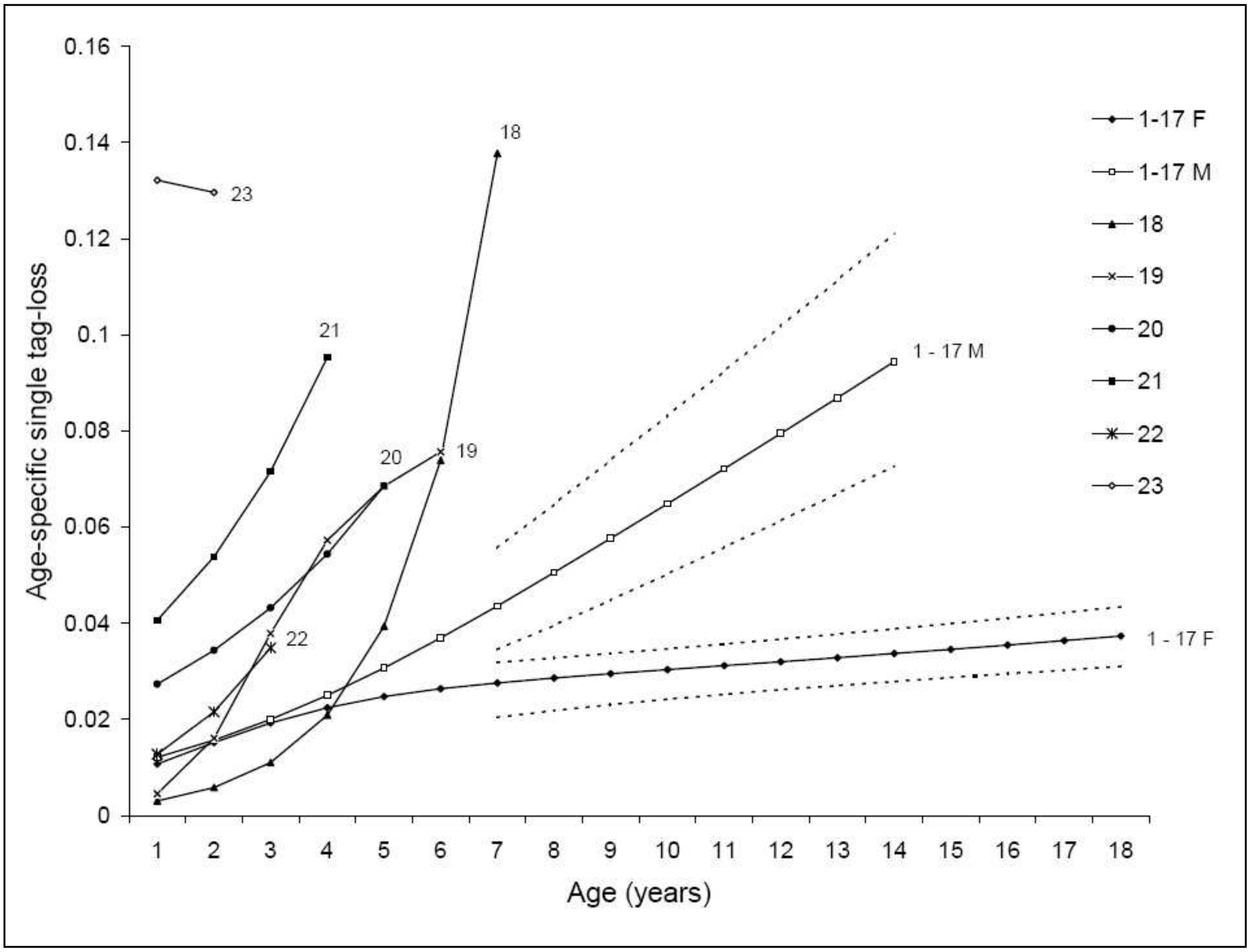

Figure 4.2. Maximum likelihood functions for age-specific single tag-loss rates over time. Inner interdigital tags (IIT; cohorts 1-17) are represented by two general functions for males and females. Standard errors (tag-loss probability ± 2SE) are presented for IIT tags above age 7. Numbers at the end of each line depict the cohort.

Age-specific tag-loss rates (Figure 4.2) were derived for cohorts 1 - 17 (IIT; grouped), and cohorts 18 - 23 (OIT; separately). IIT showed low initial tag-loss rates that increased monotonically over time. Age-specific tag-loss of adult females followed a slight convex curve, with tag-loss increasing at a low rate for adult females above age five. Cumulative IIT tag-loss rates (double tag-loss; Fig. 3) were less than 1% up to age five for both sexes. Tag-loss in males increased more as they aged when compared with females, although older age classes are represented by fewer males than females (e.g., 13 males and 106 females above age 12), leading to greater confidence in female retention rates to this age. Near the maximum life expectancy, close to 82% of males, and 88% of females were expected to remain identifiable under the tag-loss independence assumption (Table 4.4). Age-specific tag-loss rates for OIT were generally higher than those of IIT and predominantly increased over time, apart from cohort 23 in which tag-loss declined after high initial loss. Cumulative tag-loss rates increased from cohort 18 to 23 (Figure 4.3), with the exception of cohort 22 (cumulative tag-loss cohort 18 < 19 < 22 < 20 < 21 < 23), *i.e.,* apart from cohort 22, tag-loss increased as resight time decreased.

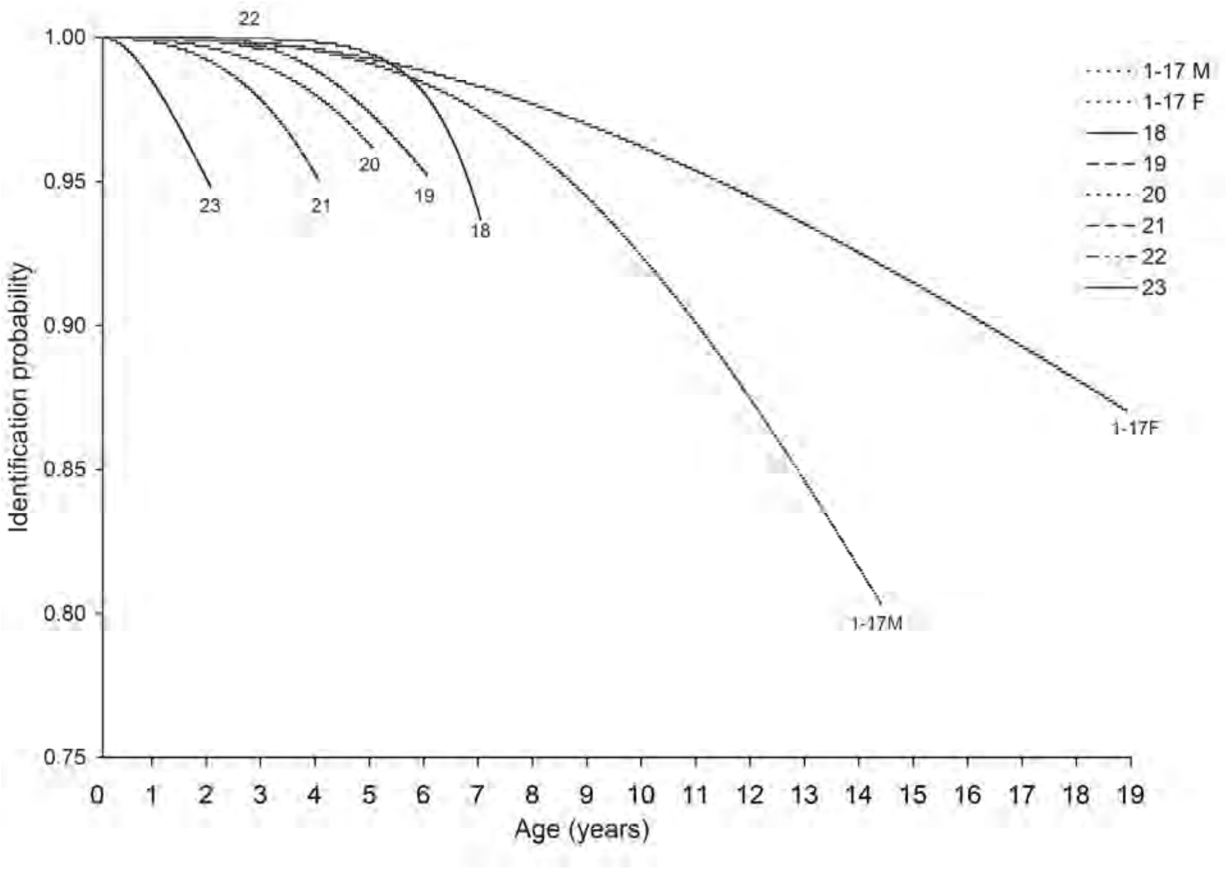

Figure 4.3. Identification probabilities of double tagged southern elephant seal cohorts at Marion Island. An individual is rendered unidentifiable when both tags are lost.

The variation in cumulative tag-loss rates between individual OIT cohorts and between grouped OIT and grouped IIT cohorts was relatively small, despite model-supported separation. The maximum difference observed between IIT and OIT cohorts was for cohort 23, indicating a 5.2% lower identification probability at age 2 as compared to cohorts with IIT. When cohort 23 was not considered, OIT inter-cohort variation did not differ by more than

0.16% ± 0.16 (mean ± 95%CI) for ages 0-2. Cohort variation for OIT increased as animals aged (age 3-7), but 95% confidence intervals never spanned more than 5.3% for any age (Figure 4.4).

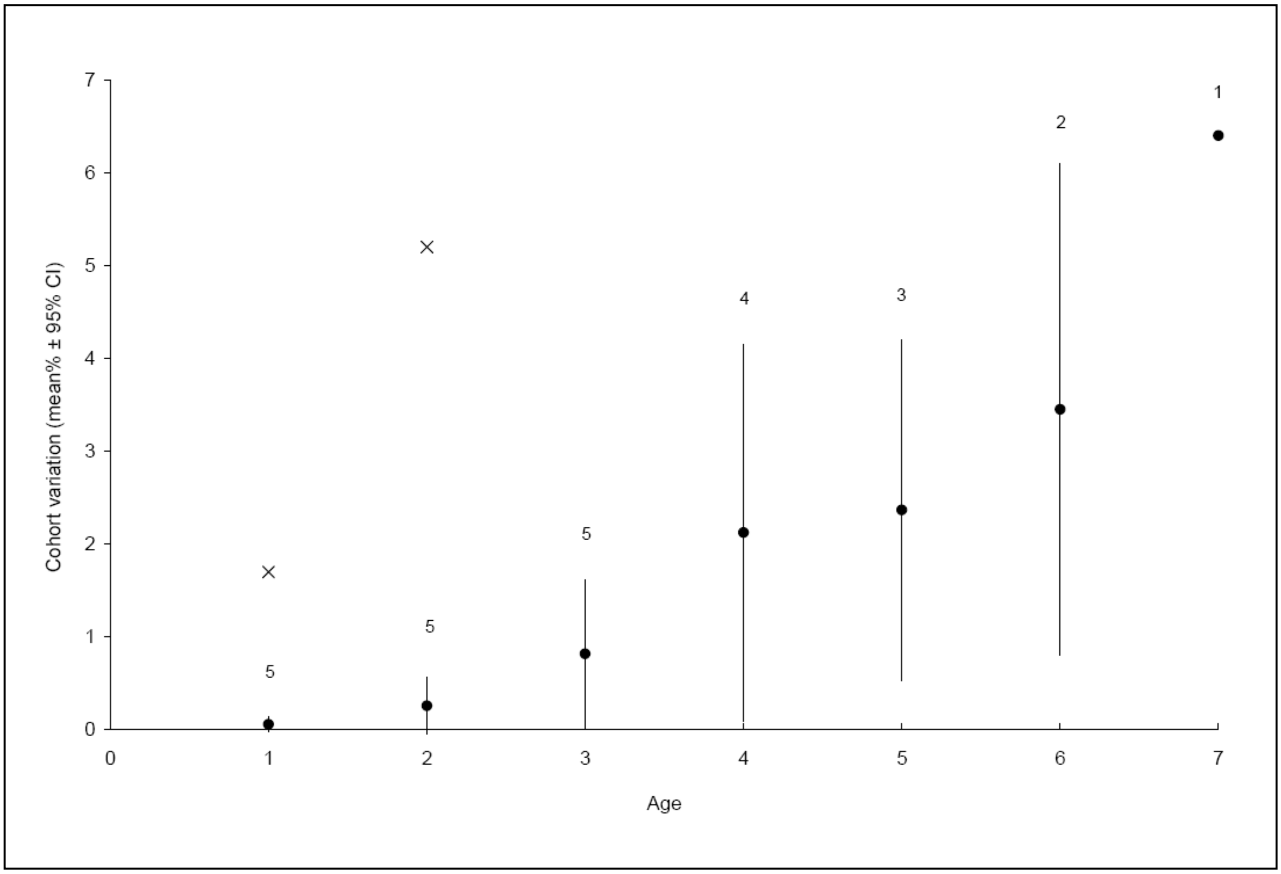

Figure 4.4. Variation in southern elephant seal tag-loss rates between cohorts 18 - 23, double tagged in the outer interdigital webbing of the hind flipper (OIT). Points represent the mean tag-loss rate over cohorts 18 - 22, with numerical values indicating the available sample size (number of cohorts). Cohort 23 (× at ages 1 and 2) is not included in the calculation of mean cohort differences.

Table 4.4. Estimated cumulative age specific tag retention probabilities for southern elephant seals at Marion Island. Cohort independent, sex specific probabilities are given for inner interdigital tags (IIT; cohorts 1 to 17), while outer interdigital tags are separated by cohort (OIT; cohorts 18 to 23).

Age	1-17 F	1-17 M	18	19	20	21	22	23
1	1.000	1.000	1.000	1.000	0.999	0.998	1.000	0.983
2	0.999	0.999	1.000	1.000	0.996	0.992	0.999	0.948
3	0.998	0.998	1.000	0.997	0.990	0.977	0.995	
4	0.996	0.995	0.998	0.988	0.979	0.950		
5	0.992	0.991	0.994	0.973	0.962			
6	0.988	0.984	0.979	0.952				
7	0.983	0.974	0.936					
8	0.977	0.961						
9	0.970	0.944						
10	0.962	0.924						
11	0.954	0.900						
12	0.945	0.874						
13	0.935	0.846						
14	0.925	0.816						
15	0.915							
16	0.904							
17	0.893							
18	0.881							

Discussion

Tag-loss for both IIT and OIT cohorts of southern elephant seals is best described by a monotonic increase over time, although the pattern of tag-loss did deviate in some cohorts. Because all tags were applied to recently weaned individuals (~23 - 30 days old; see de Bruyn *et al.* 2008), tag-time and seal age cannot be differentiated. The increase in tag-loss rates over time is assumed to be generally related to an increase in seal- and flipper size and webbing thickness, rather than tag failure due to breakage (Pistorius *et al.* 2000). Extreme sexual dimorphism is present in adult elephant seals and the higher tag-loss rates in males tagged with IIT reflect this. Age-specific IIT tag-loss probabilities of males increased relative to those of females from age 3 to 4 onwards. Sexual body size differences become evident at age 3, whereas extreme sexual dimorphism manifests after male elephant seals undergo a secondary growth spurt between ages 4 and 6 (Laws 1984). In contrast, model selection favoured a combined male and female model for OIT cohorts. The lack of a sex effect for the OIT cohorts may possibly be explained by a lack of statistical power, due to fewer years post-tagging (maximum = 7 years) to detect such effects. For IIT, model selected support for different sex models was only present when all cohorts were grouped, and not for individual cohorts (results not shown). Therefore, there may be insufficient statistical power to detect sex differences when using individual cohorts, or only a few combined cohorts (OIT, *n* = 6). However, seals tagged in the outer webbing of the hind flipper at Macquarie Island, similarly did not show sex differences in tag-loss (McMahon and White 2009). This may indicate that the influence of flipper size may be important for IIT-loss, but less so for tags applied to the outer webbing (OIT).

Cumulative tag-loss rates for both IIT and OIT are low in comparison with other phocid studies (e.g., Stobo and Horne 1994, McMahon and White 2009) and with previous assessments for a shorter time-series of this same mark-recapture program (Pistorius *et al.* 2000). Cumulative tag-loss rates from birth to age 15 computed by Pistorius *et al.* (2000) were 35% and 17% for males and females respectively, which is higher than those reported here (18.4 and 8.5% for males and females up to age 15 respectively). Pistorius *et al.* (2000) included 11 cohorts (1983 - 1993), with resighting data up to 1998. Our data included an additional 6 cohorts with IIT, and a further 10 years of resighting data. The added cohorts, and more importantly the longer resighting time period would modify the tag-loss estimation. This may be especially important for the adult age categories (e.g., 13 males over age 12 in this study *vs.* only 2 males in Pistorius *et al.* 2000). The different analytical approach between this study and Pistorius *et al.* (2000) furthermore contributed to these differences. The Pistorius *et al.* (2000) function constrained tag-loss to be a straight line, with the younger age categories (the region in the graph that has the more weight in the likelihood output, because more individuals are included) guiding the initial slope of the linear trend line. Age-specific IIT tag-loss (this study) did not fit the linear function exactly, but were rather slightly concave up (males) or convex down (females), leading to lower cumulative loss.

Outer interdigital tags were shed at a higher rate than IIT. In aquatic mammals, body and fin/flipper undulations pass water posterior along the body with increasing force, creating body-bound vorticity. This vorticity is transmitted along the body to the trailing edge of the fin, or flipper, where it is shed in a thrust jet (Fish *et al.* 2008). In swimming phocids, the center of the flipper is in addition more rigid than the flipper extremities (Fish *et al.* 1988). While swimming, OIT may thus be subjected to increased drag and movement, leading to increased tag-loss. On land, IIT are usually protected from the substrate and environmental variables (e.g., ultraviolet light) because the tag is typically enclosed in the folds of the resting flipper (between adjacent flipper digits). OIT visibly protrude more, improving tag visibility for resighting and reducing disturbance to seals during tag resighting (the objective of the change in tag-placement in this study program). However, OIT are therefore also more likely to make contact with the substrate, plausibly leading to more abrasion and snagging, and potential loss from the flipper. Additionally, OIT exposed to more UV radiation than the enclosed IIT may become weakened over time and result in increased tag breakage, although we rarely observed such breakage.

McMahon and White (2009) compared tag-loss rates at Macquarie Island to Marion Island, and suggested that tag placement may affect tag-loss as tag-loss rates was much greater at Macquarie Island (OIT) than at Marion Island (IIT, from Pistorius *et al.* 2000). Our results support their interpretation. However, the large difference in tag-loss between the OIT from Macquarie Island (McMahon and White 2009) and Marion Island (this study) indicate that other factors are also important. We suggest that the timing of tagging is a critical determinant in life-time retention rates. At Marion Island, pups are always tagged post-weaning (age ~ 23 - 30 days), while pups on Macquarie Island were tagged at birth. McMahon and White (2009) rejected this hypothesis, as they calculated tag-loss from weaning (when pups were branded) only; and not birth. However, it is probable that flipper damage from tagging at birth may lead to increased tag-loss post-weaning and not necessarily only during the pre-weaning period as assumed by McMahon and White (2009). For example, newborn pups may be more immuno-compromised than weaned pups. Tag-loss due to immune reaction may, however, only occur in a few months time, rather than within the 3 - 4 week pre-weaning age. Weaned pups, in contrast, may be less susceptible to infection of the tag-site than newborn pups, leading to lower tag-loss. We recommend that pups are tagged at weaning only and suggest an alternative method to identify pre-weaned pups (de Bruyn *et al.* 2008). On Marion Island, pre-weaned pups are marked with temporary Supersmall® tags (Dalton Supplies Ltd., Henley-on-Thames, U.K.) that are designed to minimize injury to the tag-site on the pre-weaned pup's delicate hind flipper. These tags are applied to the inner interdigital webbing of the hind flipper. At weaning (when hind flippers are sturdier), pups are tagged in the outer webbing of the hind flipper with the more robust Jumbotags®. This tagging protocol allows identification of pre-weaned pups (de Bruyn *et al.* 2008), while postponing marking with long-lasting tags to a period when; a) the pup flipper is stronger; b) the pup is generally in better condition and has greater immunity than at birth; and c) tagging of weaned pups occurs well outside the harem (without the need to return the pup to the harem) that enable the precise placing of tags without interference from breeding seals, which is required for low loss rates. The correlation between tag-loss, tag-site and time of tagging between Marion Island and Macquarie Island may further be influenced by different tag types used (Dal 008 Jumbotags® [Marion] vs. Supertag® Size 1 [Macquarie]; Dalton Supplies Ltd., Henley-on-Thames, United Kingdom) and possibly the practice of cutting and filing the tag pin on Macquarie Island. If this procedure puts any strain on the tag itself (e.g., holding the tag to file it down, while the pup tries to move the flipper), tag-loss may be increased due to damage/enlargement of the tag-site during this procedure.

Differences in tagging proficiency of personnel may lead to heterogeneous tag-loss. Tag-loss in South African fur seals *Arctocephalus pusillus pusillus*, for example, varied between 6.8 - 33.8% for different tagging personnel (Shaughnessy 1994). Stobo and Horne (1993) reported cohort variation in tag-loss among year-old grey seals *Halichoerus grypus* which varied between 7.2 - 18.8%. In the present study, interannual variation in tagging proficiency may result in cohort specific tag-loss rates, despite stringent efforts to maintain constant tagging technique. Wilkinson and Bester (1997) compared tag-loss of one-year old elephant seals at Marion Island, and found no significant variation amongst 8 cohorts. This trend continued for all age groups in the 17 IIT cohorts, and no important variation in tag-loss between cohorts was evident. Conversely, OIT tag-loss varied by cohort. Field observation indicated that tag placement in three of the OIT cohorts were marginally suboptimal. It thus appears as if tag placement for OIT needs to be even more exact (~ 5mm) as compared with IIT, as only a slight misplacement of the tags (OIT) at tagging may render tags attached too deep (cohorts 19 and 20) or too shallow (cohort 23). Tags applied too deep in the webbing may increase infection and tissue necrosis of the tag-site as the flippers grow while tags applied too shallow are more likely to tear out of the trailing edge of the flipper. The outer webbing of the hind flipper also provides a smaller surface area in which to place a tag as compared to the neighboring inner webbings between digits two and tree and three and four. This may therefore explain the cohort dependence observed (and the suggested need for more precise tag placement) for OIT, but not IIT.

Although tag location on the outer interdigital webbing may lead to a lower retention rate, it is assumed that loss of tags should occur randomly among cohorts when they are similarly tagged. Yet, even when we removed cohorts that we *a priori* believed might have been responsible for the observed bias, the remaining three cohorts still could not be grouped. The estimates of OIT are hampered by a lower sample size (6 cohorts) for a maximum time at liberty of 7 years, compared to 17 cohorts at a maximum time at liberty of over 24 years for IIT cohorts. As such, OIT resight data exists for only five cohorts of adult females, and two cohorts of adult males (based on the age at maturity for this species at Marion Island; Kirkman *et al.* 2003). Tag-loss probabilities are based on the time at liberty of tags: the time from application of the tag, to the last occasion that the individual was seen with two tags (N_{22}) or first seen with one tag (N_{21}). However, cohorts have different maximum times at liberty (maximum resight time decreases by one year for successive cohorts) which could influence parameter estimates, especially when the time at liberty is relatively short. This potential bias is apparent in the current study, significantly more so for OIT with shorter time at liberty and few sexually mature cohorts. For example, cohort 23 tags have a maximum time at liberty of around 900 days, in comparison with the first OIT cohort (18) at liberty for more than 2700 days. Inter-cohort variation should be more pronounced when the data are sparse, and a few random cases of tag-loss could potentially help to drive cohort specific differences. For five of the six OIT cohorts (cohort 22 being the exception), tag-loss estimates increased as absolute cohort age was younger. Therefore, we attribute at least part of the cohort specific tag-loss rates observed for OIT as an effect of fewer days to maximum time at liberty (specifically the time-span of N_{22}). We suspect that as more data becomes available, tag-loss of OIT should become more homogenous among cohorts, although at higher rates than the IIT cohorts.

The cohort effect observed for OIT necessitates caution when deriving life-history parameter estimates (such as age-specific survival rates) from these cohorts. Because animals from separate OIT cohorts lose tags at different rates, the proportion of marked animals in the population at any period will differ between cohorts, and not represent a homogenous group with respect to tag-loss. An increase in tag-loss rate between IIT and OIT *per se* does not present considerable analytical drawbacks as survival rate corrections may simply be structured to represent the two different tag-sites. Extreme cohort variability, however, would negate the implementation of survival models structured at a population level (rather than a cohort level) as population level survival trends might be influenced by cohort specific tag-loss rates.

To demonstrate the differences in tag-loss rates between OIT cohorts, we considered an arbitrary cohort of 500 double tagged pups, a good approximation of the number of pups born annually on Marion Island in recent years (Mammal Research Institute, unpublished data). On average, at age 2, cumulative tag-loss will render all individuals identifiable for three of the OIT cohorts (and all of the IIT cohorts). Tag-loss in cohort 20 and 21 will result in double tag-loss in 2 and 4 pups respectively, while tag-loss in cohort 23 rendered 26 pups unidentifiable. Therefore, in a mark-recapture framework, within the first two years of life, only cohort 23 had biologically meaningful variation in tag-loss rates - which may lead to a decrease of 5% in apparent survival rate [1- (26/500) = 0.948]. The maximum variance in OIT loss was present at age 4, where one (cohort 18) or 25 (cohort 21) pups out of 500 are expected to lose both tags, leading to a 4.8% decrease in apparent survival rate of cohort 21 at this age. Survivorship is chiefly responsible for population regulation at Marion Island (see Pistorius *et al.* 1999, 2004), and indeed in many mammal populations where immigration and emigration is limited; accurate estimates of these rates are therefore invaluable. In this case, apparent survival rates for juveniles should not be biased by tag-loss even if IIT and OIT cohorts were combined in survival analysis (excluding cohort 23). However, variation in tag-loss between cohorts can negatively bias estimates for subadult male and adult age classes if such cohorts are pooled.

Assumption of independent tag-loss

The results presented assume tag-loss independence. Violations of the independence assumption will result in a greater proportion of animals retaining two or losing two tags, with few animals retaining only one tag. This would result in an overestimate in tag retention rates, and negative bias in survival rates. Testing for dependence in tag-loss requires the permanent marking of study subjects. Permanent marking of southern elephant seals at Marion Island is not possible to facilitate testing of this assumption. Tattoos for example (Diefenbach and Alt 1998), although useful in a mark-recapture framework, are not realistic in our mark-resight design. Southern elephant seals have been successfully branded on Macquarie Island with no long-term influence on survival or condition (McMahon *et al.* 2006a). This protocol has allowed testing of the independent assumption for the period where flipper tagging and branding overlapped (McMahon and White 2009). However, branding is logistically impractical at Marion Island and this technique incorporates animal welfare concerns (Jabour Green and Bradshaw 2004) that resulted in the termination of the Macquarie Island southern elephant seal monitoring program (McMahon *et al.* 2006b, 2007). Passive Integrated Transponder (PIT tags) have been successfully used to mark numerous species (Gibbons and Andrews 2004) including southern elephant seals (Galimberti *et al.* 2000). PIT tags facilitate reliable long-term identification of elephant seals up to adult age classes for both sexes (F. Galimberti, personal communication)[1]. However, in contrast to external hind flipper tags which can be sighted from a distance, PIT tags require scanning each seal from a close distance (<20cm) with an electronic reader. This is often impossible to achieve, in particular for breeding females within harems, and aggregations of seals during the moult haulout (F. Galimberti, personal communication)[1]. PIT tags are additionally more invasive than external tags, may itself incur tag-loss (Gibbons and Andrews 2004) and are expensive. Therefore, by comparison, double tagging with plastic tags remains the preferred choice of marking in elephant seals. Still, where PIT tags can be used in combination with double-tagging to provide an additional mark this method will be useful to improve tag-loss estimates. Previously tagged animals can in some cases be identified through scarring, and Bradshaw *et al.* (2000) used flipper scarring in New Zealand fur seal *Arctocephalus forsteri* pups to address dependence in tag-loss estimates. Such scarring (tag punctures in the flipper) is sometimes visible in elephant seals, but it is virtually impossible to regularly and accurately distinguish seals that have lost both tags from untagged seals (e.g., transients/immigrants).

Several studies have provided evidence of dependent tag-loss, and the assumption of independence appears to be biologically unrealistic. Double ear tag-loss in sea otters *Enhydra lutris* (Siniff and Ralls 1991) and black bears *Ursus americanus* (Diefenbach and Alt 1998), and flipper tag-loss in fur seal pups (Bradshaw *et al.* 2000) and leatherback sea turtles (Rivalan *et al.* 2005) were all greater than expected under the independence assumption. Similar results for elephant seals from Macquarie Island have been shown (McMahon and White 2009), and the expectation is therefore that tag-loss at Marion Island would also be dependent. Dependent tag-loss varies according to individual attributes, leading to heterogeneous tag-loss probabilities (McMahon and White 2009). In black bears, individual behaviour such as fighting, mother-pup grooming or playing probably influences tag-loss (Diefenbach and Alt 1998). In fur seal pups, mechanical abrasion is thought to induce tag-loss, which is likely influenced by substrate, pup behaviour and condition (Bradshaw *et al.* 2000). Dependent tag-loss in leatherback sea turtles is probably related to individual immunity, as the majority of tags are lost as a result of tissue necrosis. Individuals prone to infection may therefore be more likely to lose the second tag if the first tag was already lost

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[1] Elephant Seal Research Group, Sea Lion Island, Falkland Islands, 15 April 2009.

(Rivalan *et al.* 2005). Tag-loss in elephant seals at Macquarie Island seems to be more dependent on pup wean mass. Lower wean mass concurrent with lowered immuno-competence is suggested to result in a greater incidence of dependent tag-loss, while larger pups generally exhibit independent tag-loss (McMahon and White 2009). To what extent observations from different species or different marking protocols can be used to infer dependent tag-loss in individual elephant seals at Marion Island is unsure. Even species-specific comparison is intricate due to the large difference in age-specific single tag-loss rates between Marion Island (0.0 - 0.14, this study) and Macquarie Island (0.0 - 0.364, McMahon and White 2009). Ideally, because the degree of tag-loss heterogeneity varies among study species, physical environment and tagging protocol, with the bias associated with assuming tag-loss independence reliant on the magnitude of tag-loss, dataset-specific assessment of this assumption will be of greatest value.

Pistorius *et al.* (2000) expected a low degree of bias caused by dependent tag-loss for the Marion Island tagging regime owing to; a) an observed increase in tag-loss rate over time instead of an apparent decline (see Xiao *et al.* 1999); b) low absolute tag-loss rates resulting in modest bias; c) high resight frequency, where most animals are seen multiple times per year, reducing the probability of missing tag transition from N_{22} - N_{20} (*i.e.,* not seeing the seal changing tag status from two to one tag), and d) the relatively high proportion of resightings of seals with one tag remaining for extended periods. Diefenbach and Alt (1998) predicted from observations of permanently marked animals that low tag-loss and frequent resightings should result in little bias from dependent tag-loss. Therefore, as the rate of tag-loss from two tags to one tag (N_{21}) is markedly lower at Marion Island than at Macquarie Island (Figure 4.5), dependence of tag-loss should result in a smaller bias of survival rate at Marion Island, and results should be fairly robust in dealing with these violations, especially for IIT. However, we acknowledge the potential bias in our results and agree that the tag-loss estimates provided here will be underestimated due to partial dependence of tag-loss in individuals. In cohorts with relatively high tag-loss (cohort 23 for example), the bias in survival rates will be higher.

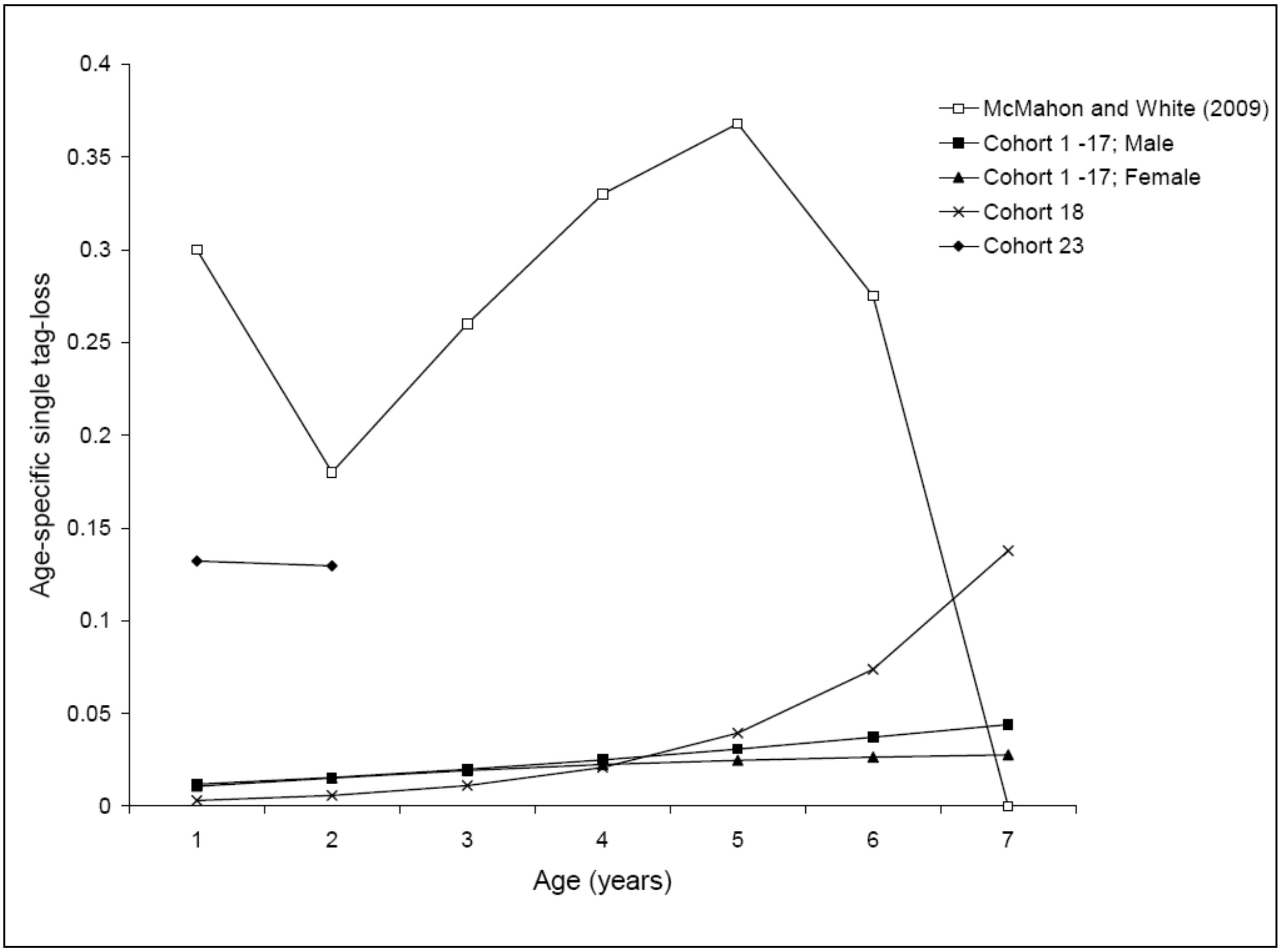

Figure 4.5. Age-specific single tag-loss (N_{21}) in southern elephant seals from Macquarie Island (McMahon and White 2009) and Marion Island (data shown for IIT [cohort 1-17 males and females] and OIT cohorts 18 [longest OIT time-series] and 23 [cohort with greatest tag-loss measured]). Tag-transition from two to one tag is accurately measured at both locations, and not influenced by the independence of tag-loss assumption.

Conclusion

Generally, small shifts in demographic rates of large-mammal populations, especially adult female survival, are able to produce a change in population growth (Eberhardt and Siniff 1977, Pistorius *et al.* 1999, McMahon *et al.* 2005). This illustrates the importance of accurate estimation of survival rates in mark-recapture studies, as biased estimates of demographic rates may result in erroneous conclusions and implementation of inappropriate management strategies leading to failure in management objectives (Brook *et al.* 1997, McMahon and White 2009). Tag-loss corrections in mark-recapture studies improve accuracy by adjusting survival estimates upwards. Double tagging with high retention tags, in conjunction with permanent marking (where possible) should be used, while frequent resight/recapture occasions should improve life-history estimates (McDonald *et al.* 2003). Fluctuation in tag-loss rates between years, tag-site and other variables (e.g., colony and habitat differences) must be considered. We illustrate that small changes in tagging methodology can have potentially serious consequences for life-history estimates of a population if such changes are not investigated and, ideally, quantified. While homogenizing techniques for extensive use across study locations are appropriate for comparative purposes, we advocate the importance of dataset-specific assessment of tag-loss rates to ensure greatest confidence in population parameters obtained from mark-recapture experiments.

References

Abt, M. and Welch, W.J. 1998. Fisher information and maximum-likelihood estimation of covariance parameters in Gaussian stochastic processes. *The Canadian Journal of Statistics* 26: 127-139.

Adam, M.S. and Kirkwood, G.P. 2001. Estimating tag-shedding rates for skipjack tuna, *Katsuwonus pelamis* off the Maldives. *Fishery Bulletin* 99: 193-196.

Arnason, A.N. and Mills, K.H. 1981. Bias and loss of precision due to tag loss in Jolly-Seber estimates for mark-recapture experiments. *Canadian Journal of Fisheries and Aquatic Sciences* 38: 1077-1095.

Barrowman, N.J. and Myers, R.A. 1996. Estimating tag-shedding rates for experiments with multiple tag types. *Biometrics* 52: 1410-1416.

Bester, M.N. 1989. Movements of southern elephant seals and Subantarctic fur seals in relation to Marion Island. *Marine Mammal Science* 5: 257-265

Bradshaw, C.J.A., Barker, R.J. and Davis, L.S. 2000. Modeling tag loss in New Zealand fur seal pups. *Journal of Agricultural Biological and Environmental Statistics* 5: 475-485.

Brennan, N.P., Leber, K.M. and Blackburn, B.R. 2007. Use of coded-wire and visible implant elastomer tags for marine stock enhancement with juvenile red snapper *Lutjanus campechanus*. *Fisheries Research* 83: 90-97.

Brook, B.W., Lim, L., Harden, R. and Frankham, R. 1997. Does population viability analysis software predict the behaviour of real populations? A retrospective study on the Lord Howe Island woodhen *Tricholimnas sylvestris* (Sclater). *Biological Conservation* 82: 119-128.

Burnham, K.P. and Anderson, D.R. 1998. *Model selection and inference. A practical information-theoretic approach*. Springer-Verlag, New York.

Casale, P., Mazaris, A.D., Freggi, D., Basso, R. and Argano, R. 2007. Survival probabilities of loggerhead sea turtles (*Caretta caretta*) estimated from capture-mark-recapture data in the Mediterranean Sea. *Scientia Marina* 71: 365-372.

Conn, P.B., Kendall, W.L. and Samuel, M.D. 2004. A general model for the analysis of mark-resight, mark-recapture, and band-recovery data under tag loss. *Biometrics* 60: 900-909.

Cowen, L., and Schwarz, C.J. 2006. The Jolly-Seber model with tag loss. *Biometrics* 62: 699-705.

de Bruyn, P.J.N., Tosh, C.A., Oosthuizen, W.C., Phalanndwa, M.V. and Bester, M.N. 2008. Temporary marking of unweaned southern elephant seal (*Mirounga leonina* L.) pups. *South African Journal of Wildlife Research* 38: 133-137.

Diefenbach, D.R. and Alt, G.L. 1998. Modeling and evaluation of ear tag loss in black bears. *Journal of Wildlife Management* 62: 1292-1300.

Eberhardt, L.L. and Siniff, D.B. 1977. Population dynamics and marine mammal management policies. *Journal of the Fisheries Research Board of Canada* 34:183-190.

Erickson, A.W., Bester, M.N. and Laws, R.M. 1993. Marking techniques. In: Laws, R.M. (Ed). *Antarctic seals: research methods and techniques*. pp. 89-118. University Press, Cambridge.

Fish, F.E., Innes, S. and Ronald, K. 1988. Kinematics and estimated thrust production of swimming harp and ringed seals. *Journal of Experimental Biology* 137: 157-173.

Fish, F.E., Howle, L.E. and Murray, M.M. 2008. Hydrodynamic flow control in marine mammals. *Integrative and Comparative Biology* 48: 788-800.

Galimberti, F., Sanvito, S. and Boitani, L. 2000. Marking of southern elephant seals with Passive Integrated Transponders. *Marine Mammal Science* 16:500-504.

Gibbons, J.W. and Andrews, K.M. 2004. PIT tagging: simple technology at its best. *BioScience* 54: 447-454.

Jabour Green, J. and Bradshaw, C.J.A. 2004. The "capacity to reason" in conservation biology and policy: the southern elephant seal branding controversy. *Journal for Nature Conservation* 12: 25-39.

Johnson, S.R., Schieck, J.O. and Searing, G.F. 1995. Neck band loss rates for lesser snow geese. *Journal of Wildlife Management* 59: 747-752.

Kirkman, S.P., Bester, M.N., Pistorius, P.A., Hofmeyr, G.J.G., Jonker, F.C., Owen, R. and Strydom, N. 2003. Variation in the timing of moult in southern elephant seals at Marion Island. *South African Journal of Wildlife Research* 33: 79-84.

Kirkman, S.P., Bester, M.N. Hofmeyr, G.J.G., Jonker, F.C., Pistorius, P.A., Owen, R. and Strydom, N. 2004. Variation in the timing of the breeding haulout of female southern elephant seals at Marion Island. *Australian Journal of Zoology* 52: 379-388.

Kneib, R.T. and Huggler, M.C. 2001. Tag placement, mark retention, survival and growth of juvenile white shrimp (*Litopenaeus setiferus* Pérez Farfante, 1969) injected with coded wire tags. *Journal of Experimental Marine Biology and Ecology* 266: 109-120.

Laws, R.M. 1984. Seals. In: Laws, R.M. (Ed). *Antarctic Ecology*. pp. 621-715. Academic Press, London.

Lebreton, J.D., Burnham, K.P., Clobert, J. and Anderson, D.R. 1992. Modeling survival and testing biological hypotheses using marked animals: a unified approach with case studies. *Ecological Monographs* 62: 67-118.

Limpus, C.J. 1992. Estimation of tag loss in marine turtle research. *Wildlife Research* 19: 457-469.

McDonald, T.L., Amstrup, S.C. and Manly, B.F.J. 2003. Tag loss can bias Jolly-Seber capture-recapture estimates. *Wildlife Society Bulletin* 31: 814-822.

McMahon, C.R. and Burton, H.R. 2005. Climate change and seal survival: evidence for environmentally mediated changes in elephant seal, *Mirounga leonina*, pup survival. *Proceedings of the Royal Society of London B* 272: 923-928.

McMahon, C.R. and White, G.C. 2009. Tag loss probabilities are not independent: Assessing and quantifying the assumption of independent tag transition probabilities from direct observations. *Journal of Experimental Marine Biology and Ecology* 372: 36-42.

McMahon, C.R., Burton, H.R. and Bester, M.N. 1999. First-year survival of southern elephant seals, *Mirounga leonina*, at sub-Antarctic Macquarie Island. *Polar Biology* 21: 279-284.

McMahon, C.R., Hindell, M.A., Burton, H.R. and Bester, M.N. 2005. Comparison of southern elephant seal populations, and observations of a population on a demographic knife-edge. *Marine Ecology Progress Series* 288: 273-283.

McMahon, C.R., Burton, H.R., van den Hoff, J., Woods, R. and Bradshaw, C.J.A. 2006a. Assessing hot-iron and cryo-branding for permanently marking southern elephant seals. *Journal of Wildlife Management* 70: 1484-1489.

McMahon, C.R., Bradshaw, C.J.A. and Hays, G.C. 2006b. Branding can be justified in vital conservation research. *Nature* 439: 392-392.

McMahon, C.R., Bradshaw, C.J.A. and Hays, G.C. 2007. Applying the heat to research techniques for species conservation. *Conservation Biology* 21: 271-273.

Pistorius, P.A. and Bester, M.N. 2002. Juvenile survival and population regulation in southern elephant seals at Marion Island. *African Zoology* 37: 35-41.

Pistorius, P.A., Bester, M.N. and Kirkman, S.P. 1999. Survivorship of a declining population of southern elephant seals, *Mirounga leonina*, in relation to age, sex, and cohort. *Oecologia* 121: 201-211.

Pistorius, P.A., Bester, M.N., Kirkman, S.P. and Boveng, P.L. 2000. Evaluation of age- and sex-dependent rates of tag loss in southern elephant seals. *Journal of Wildlife Management* 64: 373-380.

Pistorius, P.A., Bester, M.N., Lewis, M.N., Taylor, F.E., Campagna, C. and Kirkman, S.P. 2004. Adult female survival, population trend, and the implications of early primiparity in a capital breeder, the southern elephant seal (*Mirounga leonina*). *Journal of Zoology, London* 263: 107-119.

Pollock, K.H., Nichols, J.D., Brownie, C. and Hines, J.E. 1990. Statistical inference for capture-recapture experiments. *Wildlife Monographs* 107: 1-97.

Pollock, K.H., Hoenig, J.M., Hearn, W.S. and Calingaert, B. 2001. Tag reporting rate estimation: 1. An evaluation of the high-reward tagging method. *North American Journal of Fisheries Management* 21: 521-532.

Rivalan, P., Godfrey, M.H., Prévot-Julliard, A-C. and Girondot, M. 2005. Maximum likelihood estimates of tag loss in leatherback sea turtles. *Journal of Wildlife Management* 69: 540-548.

Seber, G.A.F. 1982. *The estimation of animal abundance and related parameters (2nd Edition).* Charles Griffin & Company Ltd, London.

Shaughnessy, P.D. 1994. Tag-shedding from South African fur seals *Arctocephalus pusillus pusillus*. *South African Journal of Marine Science* 14: 89-94.

Siniff, D.B., and Ralls, K. 1991. Reproduction, survival and tag loss in California sea otters. *Marine Mammal Science* 7: 211-229.

Spendelow, J.A., Burger, J., Nisbet, I.C.T., Nichols, J.D., Hines, J.E., Hays, H., Cormons, G.D. and Gochfeld, M. 1994. Sources of variation in loss rates of color bands applied to adult roseate terns (*Sterna dougallii*) in the western north Atlantic. *Auk* 111: 881-887.

Stevick, P.T., Palsbøll, P.J., Smith, T.D., Bravington, M.V. and Hammond, P.S. 2001. Errors in identification using natural markings: Rates, sources, and effects on capture-recapture estimates of abundance. *Canadian Journal of Fisheries and Aquatic Sciences* 58: 1861-1870.

Stobo, W.T. and Horne, J.K. 1994. Tag loss in grey seals (*Halichoerus grypus*) and potential effects on population estimates. *Canadian Journal of Zoology* 72: 555-561.

Testa, W.J. and Rothery, P. 1992. Effectiveness of various cattle ear tags as markers for Weddell seals. *Marine Mammal Science* 8: 344-352.

Wilkinson, I.S. and Bester, M.N. 1997. Tag-loss in southern elephant seals, *Mirounga leonina*, at Marion Island. *Antarctic Science* 9: 162-167.

Xiao, Y. 1996. A general model for estimating tag-specific shedding rates and tag interactions from exact or pooled times at liberty for a double tagging experiment. *Canadian Journal of Fisheries and Aquatic Sciences* 53: 1852-1861.

Xiao, Y., Brown, L.P., Walker, T.I. and Punt, A.E. 1999. Estimation of instantaneous rates of tag shedding for school shark, *Galeorhinus galeus*, and gummy shark, *Mustelus antarcticus*, by conditional likelihood. *Fishery Bulletin* 97: 170-184.

CHAPTER 5

INTRA-ARCHIPELAGO MOULT DISPERSION OF SOUTHERN ELEPHANT SEALS AT THE PRINCE EDWARD ISLANDS, SOUTHERN INDIAN OCEAN

W.C. Oosthuizen *et al.*

Abstract

During three summer surveys at Prince Edward Island (PEI), Southern Ocean (2001, 2004 and 2008), we inspected 416 southern elephant seals *Mirounga leonina* for identification tags. We found 42 seals that had been tagged as weaned pups at their natal site on Marion Island (MI), 37 of which could be individually identified by resighting their tag numbers. The majority of the MI-tagged seals were yearlings or subadults, and all but one were hauled out at PEI for the annual moult. The attendance rate of the known individuals at their natal island during the annual moult was only 40%, based on their resighting histories. This was significantly lower than the 75 ± 6% moult attendance rate estimated for a random MI population sample drawn from the same cohorts (based on 10 000 replications). Annual resight probabilities (when all haulout phases are considered) were 58% per annum for the MI seals seen at PEI, and 80 ± 4% for the simulation. Seasonal and annual absences of seals from MI violate the ‘homogeneity of capture’ assumption of mark-recapture models. When multiple sightings during any year are treated as a single sighting, resights during other haulouts (e.g., breeding) compensate only partially for absences during the moult. Therefore, mark-recapture studies undertaken in archipelagos should ideally include both marking and resighting of individuals on all islands which will allow discrimination between mortality and local migration.

Keywords: capture heterogeneity, dispersal, Marion Island, mark-resight, *Mirounga leonina*, movement, site fidelity, sub-Antarctic

Introduction

The Prince Edward Islands (PEIs) in the sub-Antarctic region of the southern Indian Ocean (Figure 5.1) comprise two islands, Marion Island (MI, 300 km^2) and Prince Edward Island (PEI, 46 km^2). The PEIs constitute an isolated surface feature within this region of the Southern

Ocean and large populations of seabirds and three species of seals use the terrestrial habitat as breeding and moulting sites (Ryan and Bester 2008). The archipelago's southern elephant seal *Mirounga leonina* population is relatively small (ca. 520 and 130 pups born annually on MI and PEI respectively [Bester and Hofmeyr 2005, Mammal Research Institute, unpublished data]) and forms part of the larger Kerguelen 'stock', along with Îles Crozet, Îles Kerguelen and Heard Island (Figure 5.1) (Laws 1994). Southern elephant seals haul out onto both MI and PEI - usually returning to the vicinity of their natal beaches (Hofmeyr 2000) to rest (chiefly immature seals), breed (adults) and moult (annual obligatory haulout for all the seals) (Kirkman *et al.* 2001, 2003, 2004).

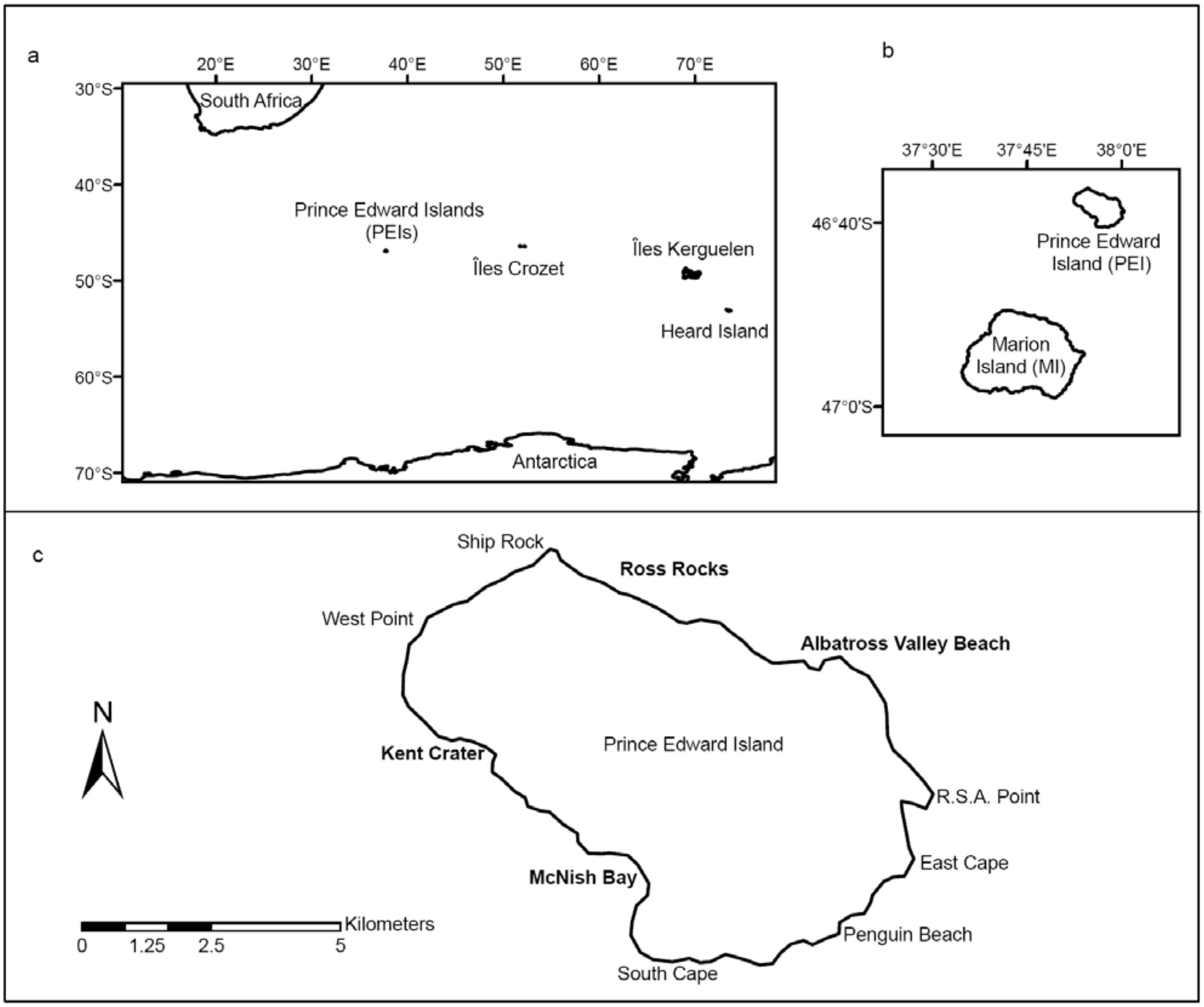

Figure 5.1. Maps showing (a) the position of the Prince Edward Islands group in the Southern Ocean, (b) the two islands within the archipelago, and (c) the elephant seal survey areas on Prince Edward Island.

Each year at MI since 1983, all or nearly all of the weaned elephant seal pups of each birth cohort have been tagged for future identification, by fieldworkers stationed at the island. To resight these marked animals, most of the beaches utilised by elephant seals at MI have been frequented every 7-10 days throughout this long-term study. In contrast, mark-resight effort at PEI has been extremely low: only a portion of a single elephant seal cohort has been tagged (in 2004) and resightings of tagged animals have only occurred on 13 days over the past 15 years. The reason for this is that visits to PEI are restricted, to protect its relatively pristine environment (PEIMPWG 1996). The operative inaccessibility of PEI potentially results in an observational ’sink area’ for tagged MI-seals (seals alive and present at the PEIs, but not resighted) in sharp contrast to the detectability of marked seals at MI which approaches 100%. Although it is assumed that emigration of southern elephant seals from MI has a negligible influence on modeling of population parameters for this population (e.g., Pistorius *et al.* 1999), at least in autumn-winter, some elephant seals marked at MI have been recorded at PEI, 19 km distant and the only other island in the PEI archipelago (Bester 1989). Even if such displacement is temporary, it could have implications for the MI mark-resight study: if some individuals temporarily disperse from MI while others are perpetually available for resighting, heterogenous capture probabilities would result in violation of mark-resight model assumptions.

Survey expeditions to PEI in the summers of 2001, 2004 and 2008 allowed us to investigate movements of tagged elephant seals between MI and PEI during the season of the moult, to contemplate the possible effects of observed movements for the ongoing mark-resight programme at MI. More specifically, the aims of this study were as follows:

(1) to investigate intra-archipelago movements of elephant seals in the PEI group, including (a) resights of MI-tagged seals during three summer surveys on PEI, and (b) resights of seals tagged at PEI in 2004, at MI;
(2) to determine whether or not the resighting histories of MI-tagged seals observed at PEI are typical for individuals of the MI population, by assessing the frequency of haulouts at MI throughout their recorded life histories;
(3) to discuss the significance of the findings for the ongoing mark-resight programme at MI.

Methods

MI mark-resight protocol

Recently weaned elephant seal pups have been double-tagged annually at MI from 1983 to 2008 (total 12 370, range 389 - 700 per year) with uniquely numbered, colour-coded plastic Dal 008 Jumbotags® (Dalton Supplies Ltd., Henley-on-Thames, UK). Throughout each year, all MI beaches where elephant seals regularly haulout were searched for seals every 7-10 days, and the numbers of all untagged and tagged seals were recorded. For every tagged seal that was resighted (including non-MI tags), the date and locality of the sighting, tag colour combination and three-digit number were recorded to identify the seal (see de Bruyn *et al.* 2008, Oosthuizen *et al.* 2009 for details).

PEI summer surveys

Elephant seal surveys at PEI were conducted during 17-22 December 2001, 18-19 November 2004 and 16-20 December 2008. The November survey, which coincided with the end of the breeding season and the onset of the juvenile moult, presented the only opportunity for the marking of weaned pups at this locality to date (Bester and Hofmeyr 2005). The timing of the two December surveys corresponded with the peak moult haulout period for subadult males and subadult to young adult females (Kirkman *et al.* 2003). The survey area covered most of the coastline where elephant seals are likely to haul out, from (a) Kent Crater in the north-west to Ross Rocks Peninsula in the north-east, and (b) Albatross Valley Beach in the east to McNish Bay in the south-west (Figure 5.1), with the following exceptions: in the 2001 survey, it was not possible to check all the likely moulting sites in the Penguin Beach surroundings for seals, due to a lack of time and manpower; in 2004, only Albatross Valley Beach to McNish Bay was surveyed. During the 2004 survey, 90 of the 130 weaned pups encountered were double-tagged (Bester and Hofmeyr 2005).

We noted the following number of: seals present at each site, seals that could be inspected for the presence of tags, and seals with tags. For all seals with tags, we attempted to record tag-resight data as described for MI (above). Untagged seals were subjectively classified by experienced observers as weaned pups, under-yearlings, yearlings, subadults, adult females and adult males, using morphological comparisons with known age of seals from MI. In some cases, beach topography or breeding colonies of subantarctic fur seal *Arctocephalus tropicalis* and Antarctic fur seal *A. gazella* prevented access to elephant seals. In such cases, we only noted the number of seals present without conducting tag resights.

Analyses

The MI-resighting history of each tagged individual that was observed at PEI during any of the summer surveys was scrutinised. For each of these individuals, it was first determined whether or not it had been recorded as present at MI during each moult season between birth and the last time it was resighted alive, including the year(s) that it was observed on PEI. 'Seal years' between the last resighting record of an individual and the end of the study (April 2009) were disregarded because the status of the animal (e.g., alive, dead or permanently emigrated) would have been uncertain during this period. A seal year corresponds to 15 October$_{(t)}$ to 14 October$_{(t+1)}$, as it was assumed that the seals aged a year on 15 October, the peak haulout date for breeding females at MI (Kirkman *et al.* 2004). Secondly, for each of these individuals, their overall annual capture probability was calculated, taking all haulout phases during a year into account and treating multiple sightings within a year as a single sighting. Annual capture probabilities are typically used in estimation of annual survival estimates (e.g., Pistorius *et al.* 1999).

To determine whether or not the MI resight histories of the MI-tagged seals recorded at PEI are typical for individuals of the MI population, we compared resight histories of the observed dataset (MI-tagged seals recorded at PEI) to a simulated dataset (10 000 replications) based on individuals selected at random from corresponding birth cohorts. Individuals from the observed dataset, as well as individuals that were never resighted after their first year, were excluded from the simulation dataset. The observed and simulated groups were compared by calculating the capture probability $P = X/n$, where X represents the number of 'successes' (present at MI) in n possible years. Proportions were taken over the total sample size and not individual seals (i.e. the sampling units; see Crawley 2007). Analyses were performed in R 2.9.1 (R development Core Team 2009) and probabilities were considered statistically significant at $p < 0.01$.

Results

Resights of MI seals at PEI

The timing of the PEI surveys corresponded to the early moult season, with yearlings and subadults as the age classes that were best represented in the counts (Table 5.1). In total, 42, or 10% of the 416 seals inspected for tags at PEI, were tagged as weaned pups at MI (Table 5.2). Additionally, three seals tagged at PEI in 2004 were encountered at PEI. Thirty-eight of the resighted MI-tagged seals could be individually identified; the other four individuals were not identified because their tag numbers could not be resighted with confidence. The proportion of seals inspected for tags that had tags was the same for the two December survey periods when subadults were the predominant moulting group, but higher during the November survey when yearlings were the predominant moulting group (Table 5.2). All tagged seals except one were associated with the moult haulout, the exception being an under-yearling (a recently weaned pup, FB269) recorded on 18 December 2008 that had been recorded at MI shortly before on 11 December 2008. The sex ratio among the resighted tagged seals (22 females, 17 males, 3 unidentified) was not significantly different to parity ($X^2 = 0.65$, df = 1, $p = 0.42$).

Table 5.1. Age class distribution of southern elephant seals (marked and unmarked) encountered at Prince Edward Island during three summer surveys.

Survey period	Adult males	Adult females	Sub adults	Yearlings	Under-yearlings	Weaned pups	Unknown	Total
December 2001	5	29	61	22			41	158*
November 2004	10	15	32	42		130		229
December 2008		23	150	32	4		37	246

*Undercount

Table 5.2. Number of tagged southern elephant seals encountered during three summer surveys at Prince Edward Island. MI and PEI tags indicate seals tagged at Marion Island and Prince Edward Island respectively.

Survey Period	Seals observed	Seals inspected for tags	MI tags	MI tags identified	Ratio: MI tag/untagged	PEI tags
December 2001	158*	117	9	8	0.077	-
November 2004	229	90	18	16	0.200	-
December 2008	246	209	15	14	0.072	3
Total	633	416	42	38	-	3

*Undercount

Life-history comparisons

Resight histories of the 37 MI-tagged seals that were recorded moulting at PEI totalled 119 seal years (115 moult seasons; birth to last known age alive) up to 2009. Moulting occurred at PEI in 37 of these years ($P = 0.32$), in 46 of these years at MI ($P = 0.40$) and a further 32 ($P = 0.28$) of the moult seasons were unaccounted for (absent from MI, possibly present at PEI, but no resights made; Figure 5.2). In contrast, the simulations based on individuals selected randomly from the same birth cohorts showed that MI-tagged individuals had a 0.77 ± 0.06 capture probability at MI at the time of the moult (mean ± SD, 10 000 replicates; Figure 5.2). The total moult attendance ($P = 0.4$) of the MI-tagged seals that were recorded moulting at PEI falls well outside the normal distribution range of the simulated sample (Z = 37.51, 2.5th percentile = 64.86%, 97.5th percentile = 87.49%, $p < 0.01$). When resights made during all haulout phases within a year were considered, the probability of observing the MI-tagged seals recorded at PEI increased to $P = 0.58$ per annum, however, this is still significantly lower than the annual recapture probability for the simulation ($P = 0.80 \pm 0.04$, $Z = 33.46$, 2.5^{th} percentile = 72.69%, 97.5th percentile = 87.66%, $p < 0.01$).

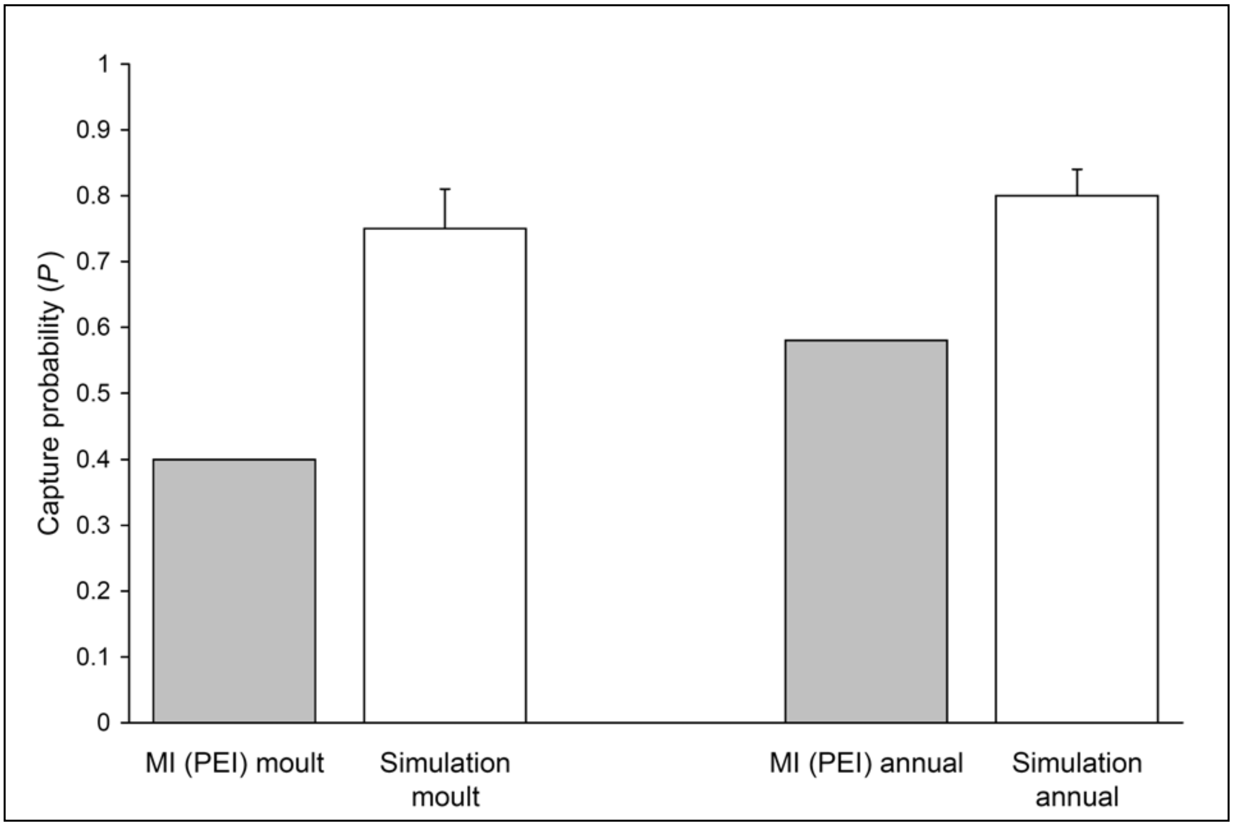

Figure 5.2. Capture probabilities of southern elephant seals at Marion Island (MI). Grey bars represent capture probabilities (at MI) of the group of MI-tagged seals resighted at Prince Edward Island (PEI) during three summer surveys. The first column show capture probabilities that were calculated during the moult haulout only (MI(PEI) moult) whereas the second column show capture probabilities derived from using all haulout phases within a year (MI(PEI) annual). Dotted bars represent the capture probabilities of a random MI population simulation (10 000 replicates) at MI using resights during the moult only and all annual resights respectively. MI-tagged seals recorded moulting at PEI have significantly lower capture probabilities, even when all haulout phases within a year are considered.

Resights of PEI seals at MI

Over a period of 5 years, 32 of the 90 weaned pups tagged at PEI hauled out on MI as immature seals during the winter (*n* = 40 occasions) and moult (*n* = 28 occasions). Males (*n* = 20) outnumbered females (*n* = 10) but this is unsurprising because nearly twice as many males (*n* = 57) than females (*n* = 29) were initially tagged at PEI. In all, 15 PEI-tagged seals were seen during more than one haulout phase at MI (mean number of haulout phases of PEI-tagged seals at MI = 2.09 ± 1.67 SD, *n* = 32). One subadult male hauled out on MI during the winter and moult of every year (up to and including the moult of 2008) since its birth in

2004. None of the 29 PEI-tagged females bred at MI during 2007 or 2008 (at age 3-4). However, based on current survival estimates from MI (de Bruyn 2009), juvenile and subadult mortality would have reduced the surviving PEI-tagged female cohort to only approximately 10 individuals by this age. Only a single PEI female that previously hauled out at MI to winter and moult is known to have been alive subsequent to these breeding seasons.

Discussion

Intra-archipelago movement

Southern elephant seals are good mark-recapture study subjects (Bester 1988). During the predictable haulout phases of the life cycle, it is relatively easy to mark large numbers of seals, while resighting of marked seals is facilitated by the high site fidelity that is characteristic of the species (Hofmeyr 2000). However, although island populations appear to be relatively isolated, movement between islands within an archipelago (e.g., between MI and PEI) or even movements between locations on larger islands, may hamper mark-recapture resighting schedules. Few study protocols are capable of incorporating such spatial variation (but see Baker and Thompson 2007 for a Hawaiian monk seal *Monachus schauinslandi* example) and consequently, discrimination between mortality and emigration to alternative sites is often impossible. Mark-recapture estimates of southern elephant seal populations, including those at MI, are assumed to have little emigration bias due to high site fidelity by individuals (Pistorius *et al.* 1999). However, caution should be exercised when inferring site fidelity using data from individuals actually present at MI (de Bruyn 2009). Whereas Hofmeyr (2000) showed that site fidelity at an island scale (between different beaches on the same island) was high for seals returning to MI (i.e. seals usually haul out in the vicinity of their natal beach or site of first reproduction when they return to the island), these results excluded individuals that did not return to MI (de Bruyn 2009). High beach-specific, island-scale site fidelity of individuals returning to MI should therefore be distinguished from archipelago site fidelity with associated temporary or permanent emigration between islands within the group.

The increased ratio of MI-tagged seals relative to untagged seals observed at PEI during the peak yearling moult (Table 5.2) is consistent with findings of reduced site fidelity of under-yearlings and yearlings at MI (Hofmeyr 2000) and peak dispersion of juveniles during the moult from Macquarie Island (van den Hoff 2001). No discernable sex difference among the MI juveniles that dispersed to PEI was observed or expected (Hofmeyr 2000), as opposed to breeding dispersal or long range dispersal (e.g., between archipelagos) which are predicted to be male biased (Slade *et al.* 1998). The occurrence of the recently weaned MI pup (FB269) at PEI is not unexpected; weaned pups are known to disperse between their natal sites and other haulout sites in the vicinity during the post-natal period ashore, before finally departing on their first true pelagic trip during late November and early December (Wilkinson and Bester 1990). At this time, untagged weaned pups are occasionally found at MI beaches as well. These seals most likely originate from PEI as all of the pups born at MI are tagged shortly after weaning, and under-yearlings from Îles Crozet only haul out from January onwards (Mammal Research Institute, unpublished data, Chapter 6).

Intra-archipelago movement and the MI mark-resight programme

The annual moult is obligatory for all elephant seals, but elephant seals of the MI population do not always moult at MI. This is illustrated by the animals observed moulting on PEI in this study, and the resighting histories of several other individuals that could be identified in the MI mark-resight database. For example, one tagged female, GW506 returned to MI to breed 12 times between 1992 and 2008, but was recorded only twice at MI during the moult over her 20-year lifespan. It is unlikely that she or other individuals that were not recorded during the moult were in fact present and escaped observation, considering the long duration of the moult (approximately a month) and the intensive resighting effort at MI. Such individuals therefore most likely moulted at PEI or further afield (e.g., Îles Crozet, Bester 1989). Given that site fidelity of returning MI-tagged seals is generally high (Hofmeyr 2000) as supported by the result of the random simulations in this study, individuals that disperse elsewhere for certain haulout phases appear to be the exception rather than the rule. However, it does emphasize the need to (1) consider all the haulout phases for mark-resight based population studies of elephant seals, and (2) where one or more neighbouring islands exist that animals may alternate between, studies should ideally include both marking and resighting of individuals on all islands as single island mark-recapture studies will still include variable capture probabilities of individuals, even when all haulout phases are considered.

That some elephant seals disperse from MI to PEI during the moult does not necessarily result in, or imply, permanent emigration from the MI population. Most of these seals are observed at MI as well, although at a lower incidence than a random population sample. Such temporary emigration from the study area violates the mark-recapture Cormack-Jolly-Seber (CJS) model assumption that every marked animal present in the population at time i should have the same probability of recapture p_i (Pledger *et al.* 2003). For annual comparisons of survival (e.g., Pistorius *et al.* 1999, de Bruyn 2009), where all resights made within a seal year are condensed to one encounter history event, such variation in recapture probability are reduced as seals may be resighted during alternative haulout phases. However, this may remain problematic for juvenile seals, where no breeding haulout is present and because non-wintering seals (or seals possibly wintering at PEI) also have low recapture probabilities in the moult, compared with seals that rest at MI during autumn-winter (Pistorius *et al.* 2002). Furthermore, as many adult females do not breed every year (de Bruyn 2009), their absence during the moult may result in annual variation in recapture probability. Finally, variation in the moult haulout attendance may also be important when intra-annual comparisons of survival are being assessed (e.g., Pistorius *et al.* 2008). Although mark-recapture analyses incorporate reduced recapture probabilities to produce unbiased survival estimates, the lack of fit of the CJS model caused by heterogeneity in capture probability requires adjustments for extra binomial variation in the data. To accommodate lack of model fit, a variance inflation factor is typically incorporated in model selection, which reduces the level of AIC support for models with more parameters (Burnham and Anderson 1998). Where considerable capture heterogeneity is present, a multistate modeling approach that includes an ‘unobservable’ state may be better suited to model survival in combination with temporary emigration (Kendall and Nichols 2002).

Conclusion

The tag resights made during the three summer surveys at PEI provide a snapshot of the moult dispersion patterns of mostly immature seals from MI to PEI. The study is hampered by the low resight effort and small marked population of elephant seals at PEI. This in itself has, however, allowed discussion of the potential problems associated with archipelago mark-recapture studies where not all islands are equally sampled (see Baker and Thomson 2007). It remains unclear to what extent MI seals may emigrate or disperse from MI either temporarily or permanently, i.e. use of PEI as a breeding site. Insight into the breeding dispersal of elephant seals between MI and PEI will only be gained if resights of tagged seals can be made at PEI during the breeding season, and PEI seals there can be marked on a regular basis. The information gained from such studies will be invaluable in augmenting population demographic research of the southern elephant seal population at the PEIs.

References

Baker, J.D. and Thompson, P.M. 2007. Temporal and spatial variation in age-specific survival rates of a long-lived mammal, the Hawaiian monk seal. *Proceedings of the Royal Society B* 274: 407-415.

Bester, M.N. 1988. Marking and monitoring studies of the Kerguelen stock of southern elephant seals, *Mirounga leonina*, and their bearing on biological research in the Vestfold Hills. *Hydrobiologia* 165: 269-277.

Bester, M.N. 1989. Movements of southern elephant seals and Subantarctic fur seals in relation to Marion Island. *Marine Mammal Science* 5: 257-265.

Bester, M.N. and Hofmeyr, G.J.G. 2005. Numbers of elephant seals at Prince Edward Island, Southern Ocean. *South African Journal of Wildlife Research* 35: 85-88.

Burnham, K.P. and Anderson, D.R. (Eds). 1998. *Model selection and inference: a practical information-theoretic approach*. Springer-Verlag, New York.

Crawley, M.J. (Ed). 2007. *The R Book*. John Wiley & Sons, Ltd, Chichester.

de Bruyn, P.J.N. 2009. Life history studies of the southern elephant seal population at Marion Island. PhD thesis, University of Pretoria, South Africa.

de Bruyn, P.J.N., Tosh, C.A., Oosthuizen, W.C., Phalanndwa, M.V. and Bester M.N. 2008. Temporary marking of unweaned southern elephant seal (*Mirounga leonina* L.) pups. *South African Journal of Wildlife Research* 38: 133-137.

Hofmeyr, G.J.G. 2000. Dispersal and dispersion in the southern elephant seal *Mirounga leonina* at Marion Island. M Sc thesis, University of Pretoria, South Africa.

Kendall, W.L. and Nichols, J.D. 2002. Estimating state-transition probabilities for unobservable states using capture-recapture/resighting data. *Ecology* 83: 3276-3284

Kirkman, S.P., Bester, M.N., Pistorius, P.A., Hofmeyr, G.J.G., Owen, R. and Mecenero, S. 2001. Participation in the winter haulout by southern elephant seals (*Mirounga leonina*). *Antarctic Science* 13: 380-384.

Kirkman, S.P., Bester, M.N., Pistorius, P.A., Hofmeyr, G.J.G., Jonker, F.C., Owen, R. and Strydom, N. 2003. Variation in the timing of moult in southern elephant seals at Marion Island. *South African Journal of Wildlife Research* 33: 79-84.

Kirkman, S.P., Bester, M.N., Hofmeyr, G.J.G., Jonker, F.C., Pistorius, P.A., Owen, R. and Strydom, N. 2004. Variation in the timing of the breeding haulout of female southern elephant seals at Marion Island. *Australian Journal of Zoology* 52: 379-388.

Laws, R.M. 1994. History and present status of southern elephant seal populations. In: Le Boeuf, B.J. and Laws, R.M. (Eds). *Elephant seals: population ecology, behavior and physiology*. pp. 49-65. University of California Press, Los Angeles.

Oosthuizen, W.C., de Bruyn, P.J.N., Bester, M.N. and Girondot M. 2010. Cohort and tag-site specific tag-loss rates in mark-recapture studies: a southern elephant seal cautionary case. *Marine Mammal Science* 26: 350-369.

PEIMPWG (Prince Edward Islands Management Plan Working Group). 1996. *Prince Edward Islands Management Plan*. Department of Environmental Affairs and Tourism, Pretoria. pp 1-64.

Pledger, S., Pollock, K.H. and Norris, J.L. 2003. Open capture-recapture models with heterogeneity: I. Cormack-Jolly-Seber Model. *Biometrics* 59: 786-794.

Pistorius, P.A., Bester, M.N. and Kirkman, S.P. 1999. Survivorship of a declining population of southern elephant seals, *Mirounga leonina*, in relation to age, sex, and cohort. *Oecologia* 121: 201-211.

Pistorius, P.A., Kirkman, S.P., Bester, M.N. and Taylor, F.E. 2002. Implications of the winter haulout for future survival and resighting probability of southern elephant seals at Marion Island. *South African Journal of Wildlife Research* 32: 59-63.

Pistorius, P.A., Bester, M.N., Hofmeyr, G.J.G., Kirkman, S.P. and Taylor, F.E. 2008. Seasonal survival and the relative cost of first reproduction in adult female southern elephant seals *Journal of Mammalogy*: 89: 567-574.

R Development Core Team. 2009. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, URL http://www.R-project.org.

Ryan, P.G. and Bester, M.N. 2008. Pelagic predators. In: Chown, S.L. and Froneman, P.W. (Eds). *The Prince Edward Islands. Land-sea interactions in a changing ecosystem*. pp. 121-164. African Sun Media, Stellenboch.

Slade, R.W., Moritz, C., Hoelzel, A.R. and Burton, H.R. 1998. Molecular population genetics of the southern elephant seal *Mirounga leonina. Genetics* 149: 1945-1957.

van den Hoff, J. 2001. Dispersal of southern elephant seals (*Mirounga leonina*) marked at Macquarie Island. *Wildlife Research* 28: 413-418.

Wilkinson, I.S. and Bester, M.N. 1990. Duration of post-weaning fast and local dispersion in the southern elephant seal, *Mirounga leonina*, at Marion Island. *Journal of Zoology, London* 222: 591-600.

CHAPTER 6

DISPERSAL AND DISPERSION OF SOUTHERN ELEPHANT SEALS IN THE KERGUELEN PROVINCE, SOUTHERN OCEAN

W.C. Oosthuizen ***et al.***

Abstract

Southern elephant seals *Mirounga leonina* in the southern Indian Ocean move within the Kerguelen province between Marion Island (MI), Îles Crozet (IC) and Îles Kerguelen (IK) despite the high site fidelity characteristic of this species. From 1987 to 2002, 199 IC individuals, or 11.63% of the tagged population there, were resighted at MI, 1000 km distant. Resights of IC seals at MI peaked during the juvenile moult (45% of all haulouts) and autumn/winter mid-year haulout. Equal numbers of male and female seals were identified. The age frequency distribution of tagged IC seals was strongly juvenile biased and seals aged 0 to 2 represent 66% of all resights made. The return rate of IC seals following their first haulout at MI depended on the age of the seal when the first haulout was made. Seals hauling out at MI for the first time as under-yearlings were often resighted during subsequent haulouts (62.5% return rate); however, seals hauling out for the first time as yearlings (48% return rate) and subadults (14% return rate) were commonly not recorded again. Dispersing breeding females (*n* = 22, in 33 seasons) outnumbered dispersing breeding males (*n* = 6, in 16 seasons), after initially emigrating from IC to MI as juvenile seals (natal dispersal). Greater male-mediated gene flow was ultimately attained due to the polygynous mating system and some extremely successful males. One male from IC controlled harems for 6 consecutive breeding seasons at MI where 196 females, or 7.6% of the breeding population, bred from 1996 - 2001. Of 132 seals fitted with satellite-relay data loggers at MI, six hauled out at IC and three at IK. Two of the seals which migrated to IC were born at MI; all others were unmarked subadult or adult males that probably hauled out at MI in the course of foraging migrations from IC and IK respectively. Immigration sufficiently modifies the population growth rate for the small southern elephant seal population at MI and dispersal should ideally be considered when assessing vital rates for this and other southern Indian Ocean populations.

Keywords: gene flow, Îles Crozet, Îles Kerguelen, inter-island movement, mark-resighting, migration, *Mirounga leonina*, Marion Island, Prince Edward Islands, tag recovery

Introduction

The movement of organisms from one location to another is a fundamental biological process shaping the distribution, structure and dynamics of populations and ultimately influencing communities (Nathan 2001). Dispersal, defined as the movement of an organism from its birth site to a site where it reproduces, or would have reproduced if it survived and had access to a mate (Howard 1960), affect both local and global population dynamics by modifying the composition of populations (Clobert *et al.* 2001). Specifically, natal dispersal (the movement from the natal site to the site where reproduction is first attempted) can be distinguished from breeding dispersal, the latter which is defined as a change in breeding sites between two successive breeding attempts (Greenwood 1980). Long distance dispersal events are especially important to maintain genetic connectivity between populations and although occurring at low frequency, such events have disproportionate impact on populations (Nathan 2001, Trakhtenbrot *et al.* 2005). Dispersal - through the processes of individual movement, survival and reproduction - thus maintain metapopulation structures and enable gene flow between distant sites, influencing the geographical distribution and persistence of populations (Nathan 2001, Clobert *et al.* 2001).

An alternative strategy to dispersal is known as philopatry, where individuals are faithful to the natal site and attempt to reproduce at the natal site or recruit to the natal colony (Greenwood 1980). Movements away from the natal site are then associated with non-reproductive purposes, for example foraging. Migration is defined as a periodic (cyclic or seasonal) departure and return (i.e., it involves a return trip), to be distinguished from immigration and emigration, which are one-way inward and one-way outward processes respectively (van den Hoff 2001). Dispersion, defined by Nicholls (1970) as “the changing distribution during the life of an animal”, is used here to describe the presence of individuals at a non-natal site for non-reproductive purposes.

Southern elephant seals (*Mirounga leonina*) have a circumpolar distribution in the Southern Ocean (McMahon *et al.* 2005a) and all seals migrate annually between terrestrial haulout sites (where they may breed, moult or winter) and pelagic foraging areas. During the pelagic phase, seals migrate to foraging areas that may be more than 3000 km from the previous haulout site (e.g., Jonker and Bester 1998, Bailleul *et al.* 2007, Tosh 2010). Despite the long range migrations, most elephant seals are philopatric and return to their natal island to breed and moult (Nicholls 1970, Lewis *et al.* 1996, Hofmeyr 2000). This high site fidelity results in limited exchange of breeding individuals between major populations and four genetically distinct provinces/populations are recognized: the South Georgia province in the southern Atlantic Ocean, the Macquarie province in the southern Pacific Ocean, the Kerguelen province in the southern Indian Ocean and the Peninsula Valdés population on the Argentinean coast in the southern Atlantic Ocean (the only continental breeding population) (Figure 6.1, Hoelzel *et al.* 2001, McMahon *et al*. 2005a). Although movement of individuals between these provinces/populations are rare (Fabiani *et al.* 2003), movement between sub-populations within a province may be more frequent and an equally important population process.

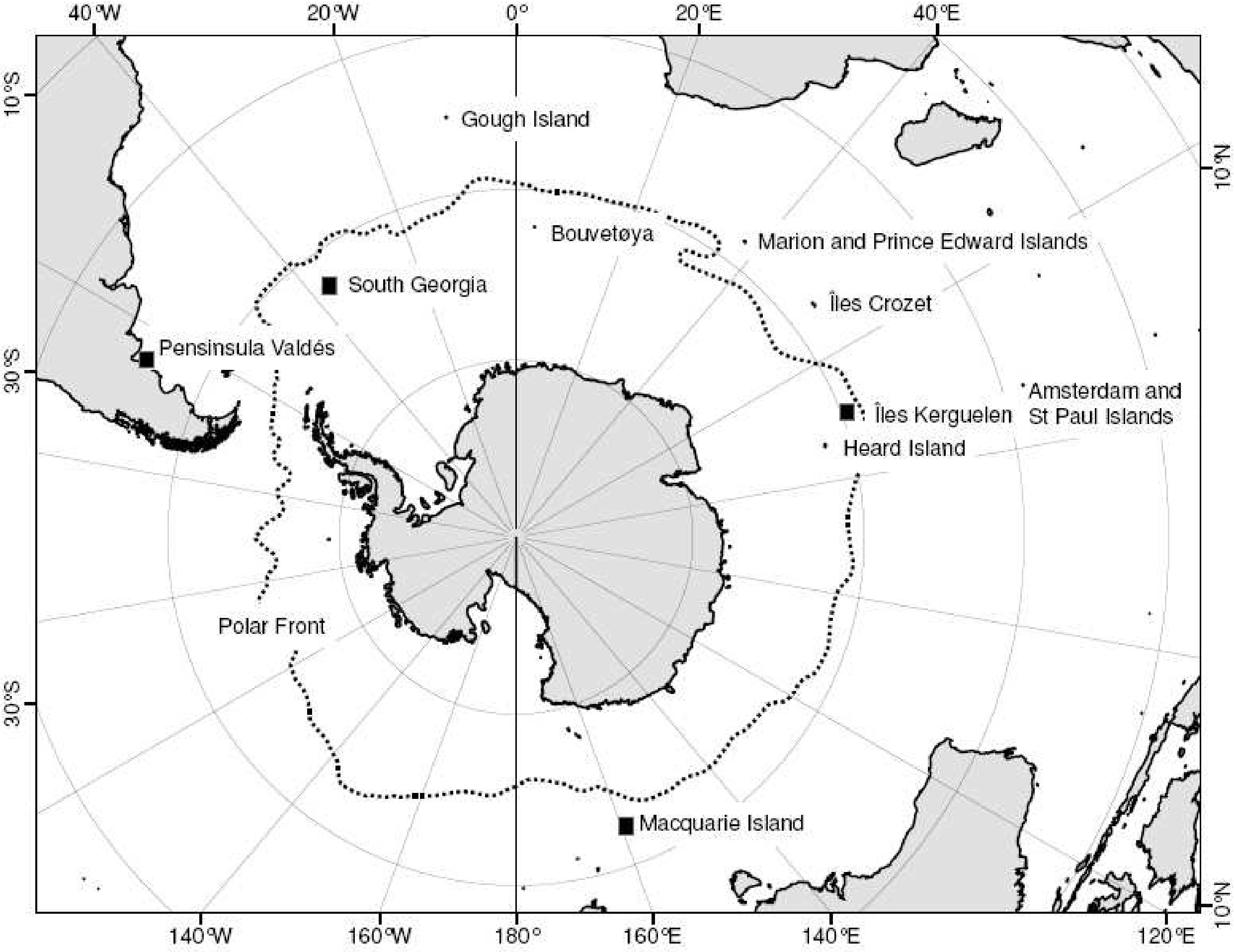

Figure 6.1. The four major populations of southern elephant seals in each geographical province (squares) and locations of sub-populations of southern elephant seals within the southern Atlantic and Indian oceans mentioned in the text.

Within the Kerguelen province, two large principal elephant seal populations are found at Îles Kerguelen and Heard Island, together with smaller sub-populations at Îles Crozet and the Prince Edward Islands (Marion Island and Prince Edward Island, Figure 6.1) (McMahon *et al.* 2005a). A long-term mark-resight programme at Marion Island (MI) and intermittent elephant seal research at Heard Island (HI), Îles Kerguelen (IK) and Îles Crozet (IC) have indicated some inter-island movement between MI and other sub-populations within this province (Bester 1989 and references therein, Guinet *et al.* 1992). Resights of individuals marked with plastic hind flipper tags suggest that in relation to MI, movement between MI and IC occurs most frequently within this province, that movements are migratory and that it mainly involves immature seals (Bester 1989). Dispersal between MI and other islands seems rare: from 1973 to 1986, a single breeding female from IC dispersed to MI (Bester 1989), while two MI females bred at IC in 1988 and 1989 respectively (Guinet *et al.* 1992).

Marking of elephant seals at IC along with concurrent resights of tagged seals at MI allow assessment of dispersal and dispersion of tagged southern elephant seals from IC to MI. A lack of resight effort at IC precludes examination of movement in the opposite direction (i.e. MI to IC). We use tag resight data from MI from 1987 to 2009 to address the following aims, specifically for seals originating from IC:

1. To what extent are dispersion and/or dispersal occurring?
2. Can dispersal be described as natal- or breeding dispersal and is gene flow occurring (i.e., do dispersing individuals reproduce)?
3. Are there temporal, haulout type, sex or age class differences in dispersion/dispersal?
4. Are IC seals transient visitors to MI (occur only once) rather than potential immigrants to the population (repeatedly sighted)?

The modest marking and resight effort at localities other than at MI within the Kerguelen province during this study period curbs quantitative assessment of inter-island movement, however, indications of such movement are presented. Satellite telemetry may, in addition to tag resight data, provide evidence of inter-island movement. Movement from MI to other islands within the Kerguelen province is qualitatively discussed based on deployments of satellite-relay data loggers on southern elephant seals at MI from 1999 to 2008. A population projection simulation model, using published survival and fecundity rates together with dispersal rates of elephant seals to MI, then gauges the demographic impact of dispersal on the MI elephant seal population.

Methods

Study area

Marion Island (MI; 300 km^2) and Prince Edward Island (PEI; 46 km^2; 19 km north-east of MI) form the Prince Edward Islands (PEIs) archipelago. The nearest landmass to the PEIs is the five constituent islands of Îles Crozet (IC), approximately 1000 km to the east. Elephant seal research is largely restricted to MI and Île de la Possession (Possession Island, PI; 150 km^2, 1140 km from MI) at the PEIs and IC respectively. Îles Kerguelen (IK) and Heard Island (HI) are 2640 km and 2740 km to the east of the PEIs, respectively (Figure 6.1).

Marion Island (MI)

Nearly all weaned elephant seals pups born at MI from 1983 - 2008 were sexed and double tagged with uniquely numbered, colour-coded plastic Dal 008 Jumbo-tags® (Dalton Supplies Ltd., Henley-on-Thames, United Kingdom) in an ongoing mark-recapture study (de Bruyn *et al.* 2008). During this time, resights of elephant seals were made on a 7- or 10-day cycle at all beaches along a 51.9 km coastline where southern elephant seals regularly haul out. Once a month, beaches on the western side of the island (where seals rarely haul out) were checked for the presence of seals. No censuses were conducted during the winter (mid-May to mid-August) of 1987 and 1988. Data of PI tag resights made at MI from September 1998 to May 1999 were lost.

For every tagged seal that was resighted at MI (including PI tags), the date and locality of the sighting, tag colour combination and tag number were recorded to identify the seal, along with information about the age class, sex (if identified) and social status (breeding status, moult stage or winter haulout). Seals were grouped into the following age class categories: under-yearling (< 1 year), yearling (1 to < 2 year), subadult (2 to < 3 [females]; 2 to < 5 [males]), adult female (>3 [if breeding]), adult male (>6 year). During the breeding season, the social status indicated whether male seals were “beachmasters” (exclusive control of a harem) or “bachelors” (subordinate males at the periphery of harems not challenging the beachmaster) and whether or not a female has given birth to a pup. “Assistant beachmasters” and “challenger bulls” are uncommon at Marion Island due to the small size of harems (Wilkinson and van Aarde 1999). Possession Island tag resight records (C. Guinet, unpublished data)[2] were authenticated against the original tagging records to confirm the natal island, year of birth and sex (if recorded at tagging).

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[2] Centre d'Etudes Biologiques de Chizé, Centre National de la Recherche Scientifique, Villiers en Bois, France

From 1999 to 2008, 132 satellite-relay data loggers (SRDLs) were deployed at MI (Tosh 2010). Logistical constraints often precluded stringent selection of SRDL carriers, but the quasi-representative data set included male and female seals from nearly all age classes and pelagic phases following all haulout types (winter, post-moult, post-breeding; Tosh 2010). Devices were mostly deployed on MI tagged individuals, however, in April 1999 (*n* = 8), April 2002 (*n* = 9), April 2004 (*n* = 4) and April 2005 (*n* = 3) SRDLs were deployed on unmarked/untagged (presumably non-native) seals hauled out at MI. From 2006 - 2008, the probability of device recovery was improved by selecting tagged individuals that had regularly returned to MI during previous breeding and moult haulouts.

Îles Crozet (IC) - Possession Island (PI)

Recently weaned elephant seal pups were marked at PI from 1984 - 1991 (Table 6.1). Seals were either single tagged (*n* = 683) or double tagged (*n* = 1639) with Jumbo-rototags® (Dalton Supplies Ltd). Every year during the peak breeding season, from 1980 - 1997, a total island census was done at PI (Guinet *et al.*1992); however, no tag resight data is available. As such, movement of MI seals to PI and migrations of PI seals (from PI to MI and back to PI) could not be assessed (e.g., van den Hoff 2001).

Îles Kerguelen (IK)

Large numbers of elephant seal pups (*n* = 13 818) were tagged between 1970 and 1979 at IK (van Aarde and Pascal 1980, Lenglart and Bester 1982), but only sporadically since then. In 2006, 200 weaned pups were tagged on the Courbet Peninsula (C. Guinet, unpublished data)[2]. Low resight effort prevents assessment of seal movement from MI to IK (Bester 1989; this study).

Analyses: Tag resights

Encounter history profiles were constructed for each of the PI seals resighted at MI. On 58 occasions, seals were identified as PI animals in the field, but individual tag numbers could not be read. Most of these resights (*n* = 51) were excluded from all analyses. Four unidentified PI breeding females and one breeding male could be recognized as unique individuals within a season based on tag colour and haulout locality and were consequently included in some analyses, even though their identity and resight history remain unknown (*n* = 7 resights). Multiple resights of the same tagged individual during any single haulout period were reduced to one encounter event (the first sighting of the seal). Sightings of the same tagged individual

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in different haulout periods were considered as separate encounters of that individual. Seal age was estimated by subtracting the birth date (taken as 15 October every year [the peak haulout date for breeding females at PI; Guinet *et al.* 1992]) from the resight date.

Pearson's chi-square goodness of fit test (significance set as $p < 0.05$) was used to establish whether the frequency distribution of PI seals that haul out at MI differs from the expected distribution in relation to sex, age class and time (monthly variation). The encounter history profiles of breeding individuals were scrutinized to determine the age of first breeding at MI and to establish whether breeding haulouts were preceded by non-breeding haulouts. The return rate of seals (whether or not seals were seen after their first haulout) was related to the age at which the first haulout at MI was made and tested for departure of expected frequency distribution using Pearson's chi-square test.

The proportion of tagged seals moving between PI and MI was calculated from birth cohorts 1986 to 1991, based on numbers of seals tagged and resighted at the respective localities. Juvenile haulouts in 1985 and 1986 for seals tagged in 1984 and 1985 pre-dated this study (these were reported by Bester 1989); as a result these cohorts were not included in this analysis. Proportions were calculated by dividing the total number of foreign tagged seals in each cohort resighted at MI by the total number of pups tagged in the specific cohort, not accounting for tag-loss or survival. The mean value of proportions calculated for 1986 - 1991 were used to predict the total number of female seals immigrating to MI annually. Seals were assumed to have immigrated to the population if they were resighted in more than one haulout.

Analyses: Satellite telemetry

At-sea locations were filtered according to a 10 km h^{-1} velocity algorithm to remove positions that required unrealistic travel distances per unit time (McConnell *et al.* 1992). Location positions were subsequently averaged to a daily location to provide regular trajectories over time and mapped in ArcMap (ArcGIS) (see Tosh *et al.* 2009; Tosh 2010 for details). We extracted all tracks where seals hauled out at locations other than MI or PEI and discuss these qualitatively without attempting a rigorous analysis.

Analyses: Simulation model

The numbers of breeding female seals provide a suitable index of population size and status (McMahon *et al.* 2005b). We constructed a Leslie matrix (Caswell 2001) to project the change in female population size through time as a function of age-specific survival (de Bruyn 2009) and fecundity (McMahon *et al.* 2003). Survival rates were calculated for the period of population decline, from 1983 to 1998 (de Bruyn 2009). Fecundity, the number of female offspring born per female in every year, was assumed to be 50% of all pups born per annum and constant for adult females aged 8 and above (McMahon *et al.* 2003). For simplicity, we did not allow for stochastic variation in vital rates, but modeled the deterministic population trend. Immigration was modelled by adding females to the population; seals entered the population according to the age-frequency distribution of resights from this study, which formed the baseline of the simulated values. Seals entered the population at ages 1 ($n = 6$), 2 ($n = 6$) and 3 ($n = 1$). The number of seals immigrating in each age class was allowed to vary by a standard deviation of 1 per iteration, assuming a normal distribution function (100 replicates). Once immigrant seals entered the population, we assumed that they survived and reproduced at a rate similar to that of the MI population. The predicted annual population growth rate r (calculated as the slope of the log transformed population counts) was calculated for scenarios with zero immigration and incorporating immigration. These are compared to the observed population growth rate, as determined by annual counts of breeding females during the peak haulout period (McMahon *et al.* 2009).

Results

PI tag resights at MI

From 1987 to 2002, 1198 resights of 199 individually identified PI tagged southern elephant seals were made at MI. These 199 seals were resighted during 510 separate haulout periods, including 222 autumn/winter, 239 moult and 49 breeding haulouts. Seven of these seals were also seen at MI prior to 1987 (reported in Bester 1989) whereas no PI tagged seals were resighted from April 2002 to present. Seals occurred throughout the year but numbers of PI seals resighted per month fluctuated significantly and correlated to the annual haulout cycle of southern elephant seals ($X^2 = 194.8$, df = 11, $p < 0.01$, $n = 510$). Resights peaked during the juvenile moult (November, December in particular and January, when 45% of all haulouts of PI tagged elephant seals occurred), and during the autumn/winter mid-year haulout (April to May) (Figure 6.2). Similar numbers of male and female seals could be identified (78 males, 80 females, 41 unidentified; $X^2 = 0.03$, df = 1, $p = 0.87$). The age frequency distribution of PI seals resighted at MI was strongly juvenile biased ($X^2 = 54.30$, df = 3, $p < 0.01$, $n = 505$) and collectively, seals aged 1 and 2 made up 52% of all PI seal resights made at MI (Figure 6.3). Possession Island under-yearlings hauled out at MI from as young as 4 months of age and under-yearlings accounted for 14.1% of all resights. The oldest females recorded were aged 8 ($n = 2$), with the tail of the age frequency distribution attributed to three males reaching ages of 9, 10 and 13 respectively.

From 1989 to 1998, 22 PI females bred 33 times at MI, with pupping confirmed in 27 of these seasons. Adult males ($n = 6$) were present during 16 breeding seasons, from 1989 to 2001, and three males successfully gained 'beachmaster' status in 10 of these seasons. One PI male controlled harems for 6 consecutive breeding seasons (1996 - 2001). During this time, 196 females bred in his harems, representing 7.6% of all females breeding at MI in this period.

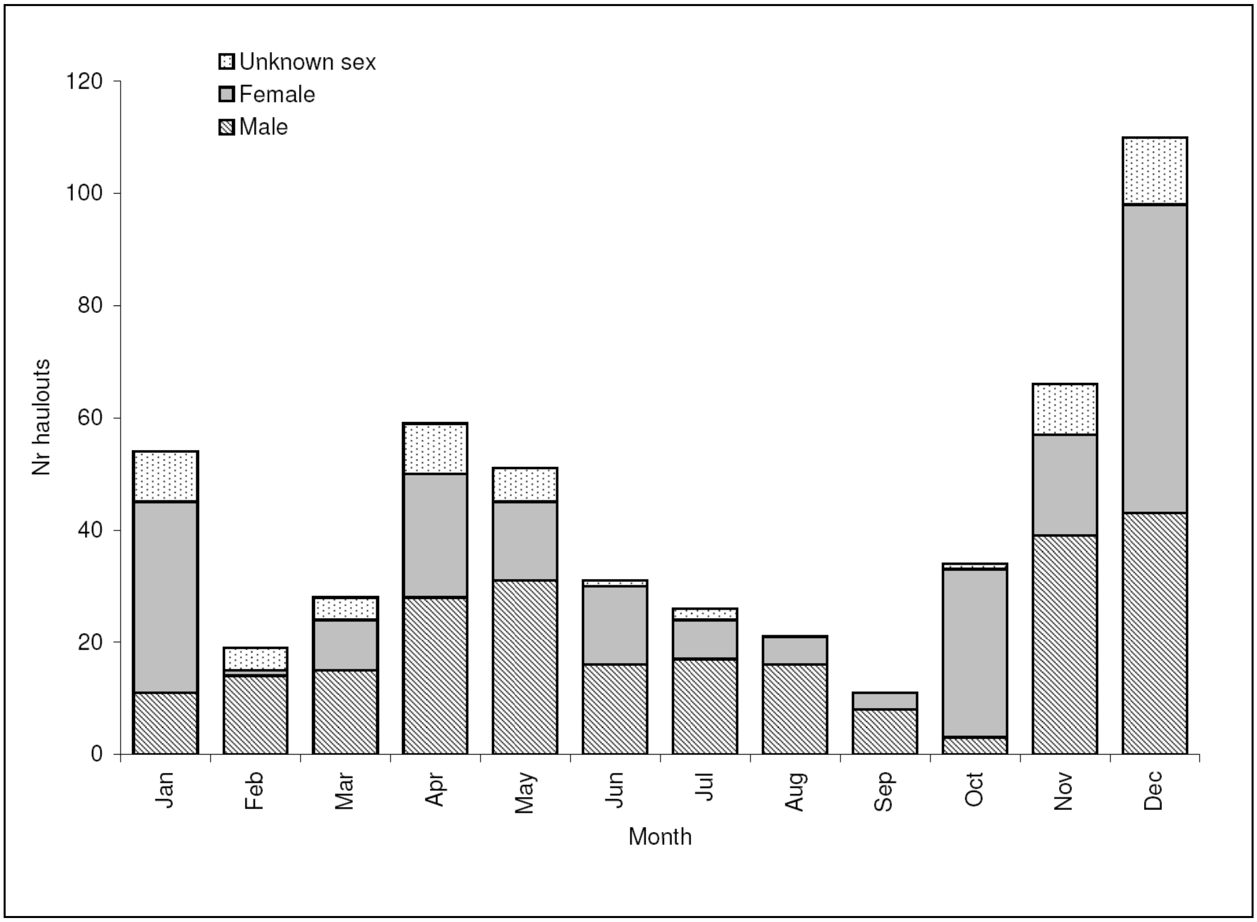

Figure 6.2. Cumulative monthly distribution (1987 - 2002) of numbers of southern elephant seals from Possession Island hauling out at Marion Island. Only the first observation of an individual during every haulout is included (n = 510).

Natal or breeding dispersal

Of the 23 known PI breeders (male and female) at MI, 21 were seen at MI prior to their first breeding haulout. Only two female elephant seals were seen breeding at age 4, without being observed previously. All of the 21 seals seen prior to breeding, moulted at least once at MI. Eleven moulted at MI for the first time at age 1, eight at age 2, and one at age 3. Including winter haulouts, these seals hauled out at MI as juveniles for the first time at age 1.21± 0.60 years (mean ± SD) an average of 5.05 (± 4.09) times prior to breeding. Females were observed to breed for the first time at MI at age 3 (n = 7), age 4 (n = 6), age 5 (n = 2) and age 6 (n = 3), with the mean age of first (observed) breeding of 4.05 yr. Males participated in the breeding season for the first time at age 6 (n = 1), age 7 (n = 2) and age 8 (n = 2).

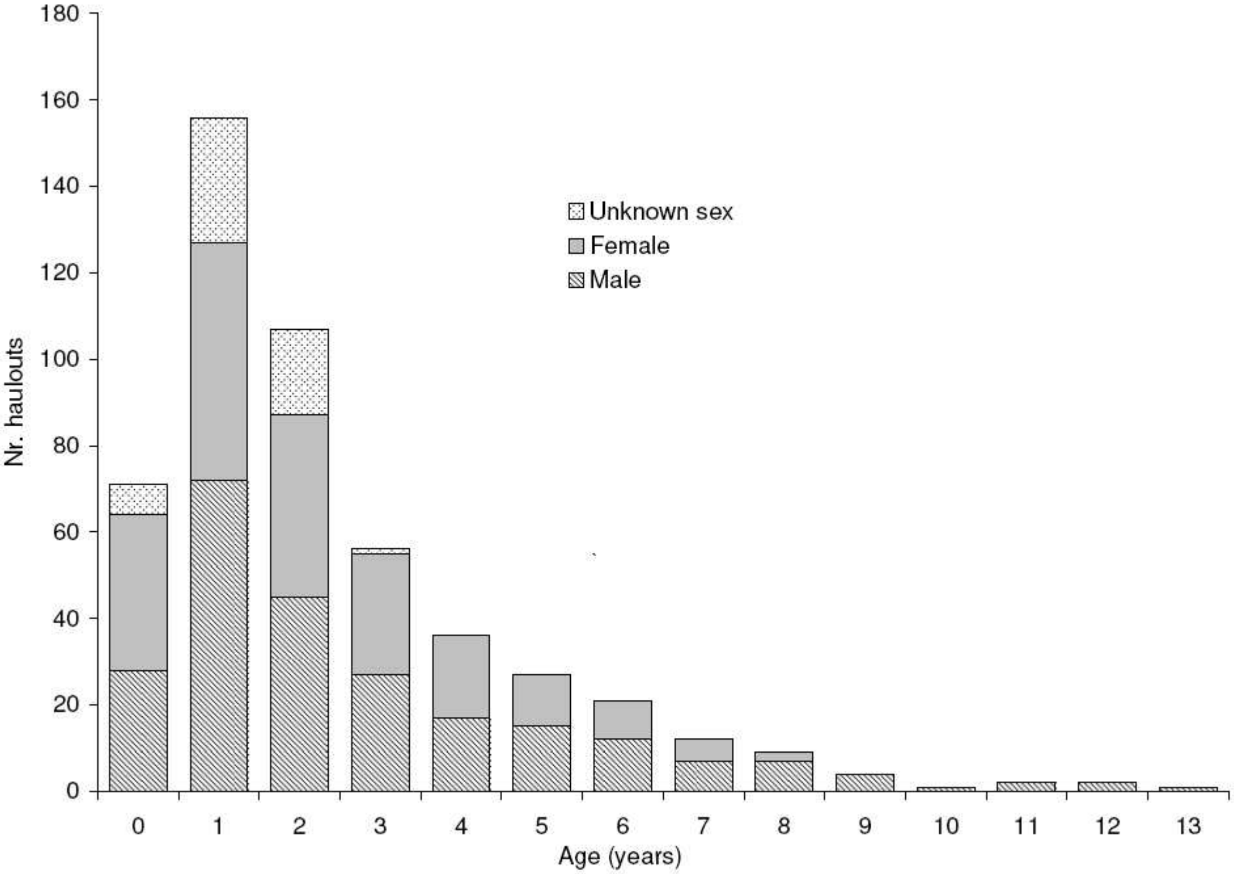

Figure 6.3. Age frequency distribution of southern elephant seals from Possession Island hauling out at Marion Island. Age signifies the initial age, e.g., age 0 is equivalent to 0 to 364 days. Only the first observation of an individual (n = 199) during every haulout (n = 505) is included.

Transient and immigrant movement

The return rate of seals following their first haulout was significantly influenced by the age of the seal at the first haulout ($X^2 = 27.85$, df = 2, $p < 0.01$, $n = 196$). More than half (56%) of the PI seals seen at MI were observed during only one haulout ($n = 112$); these were predominantly yearlings ($n = 42$) and subadults ($n = 43$). Seals hauling out for the first time as yearlings showed equal likelihood of returning or not returning for a second haulout (48%, $n = 82$), whereas seals hauling out at MI for the first time as subadults (14%, $n = 50$) or adults (<1%, $n = 3$) were commonly not recorded again (Figure 6.4). In contrast, 62.5% of PI seals which hauled out at MI as under-yearlings ($n = 64$) returned to MI for subsequent haulouts (Figure 6.4). Seals that returned to MI often did so within the first two years of life (age of first haulout 1.44 ± 0.86 years; age of second haulout 1.79 ± 0.92 years, mean ± SD).

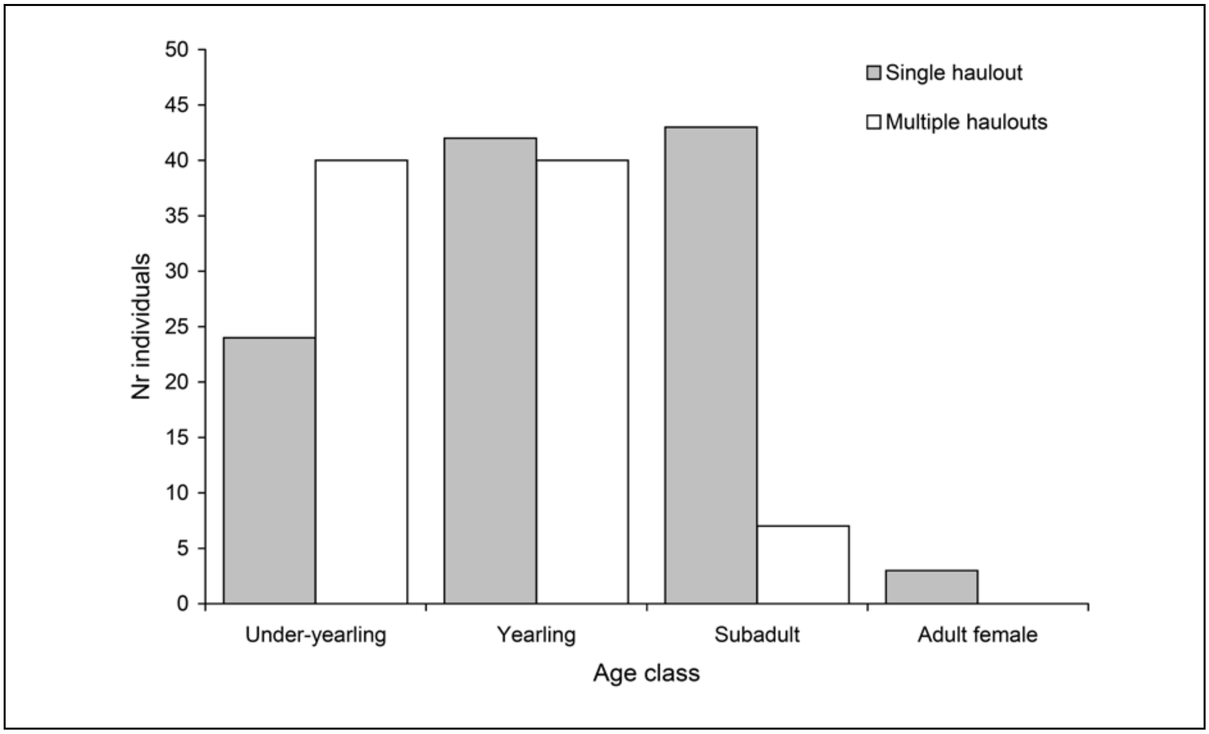

Figure 6.4. The return rate (single or multiple haulouts) of Possession Island southern elephant seals following their first haulout at Marion Island (MI). Seals that haul out at MI for the first time as under-yearlings are likely to return to MI for subsequent (multiple) haulouts. Seals that haul out at MI for the first time as subadults or adult females have lower return rates. None of the marked PI seals hauled out at Marion Island for the first time as an adult male.

Proportion of PI tagged seals at MI

Nearly 1500 seals were tagged from 1986 to 1991 at PI (Table 6.1); 173, or 11.63% of these were resighted at MI. Overall resight rates ranged from 5.2% to 28% for different birth cohorts, the lowest resight rates corresponding to birth cohorts 1986 and 1987 (Figure 6.5). The female elephant seal breeding population at PI remained stable between 1990 and 1997, at 553 ± 32 females (mean ± SD) per year (Guinet *et al.* 1999). If 11.63% of pups born to these females were to migrate to MI, some 64 seals from each birth cohort would haul out at MI at some stage. The proportion of seals migrating to MI may be as high as 21.45% or 119 individuals per cohort (upper 95% confidence interval calculated from resight rates between 1986 and 1991, *n* = 6). Approximately 44% of PI seals that haul out at MI once return for subsequent (i.e., multiple) haulout periods (Table 6.2). This translates to approximately 28 seals (both sexes) predicted to immigrate (i.e. haul out more than once in their lifetime) from PI to the MI population annually, taking age class specific variation in return rates into account. Approximately half of these are expected to be females (1:1 sex reatio observed in this study).

Table 6.1. Numbers of southern elephant seals tagged from 1984 to 1991 at Possession Island, Îles Crozet (C. Guinet, unpublished data)[2] *and numbers of individuals belonging to each cohort resighted at Marion Island from 1987 to 2002. Resights at Marion Island from the 1984 and 1985 cohorts is biased low as observations for this study only commenced in 1987. The number of seals predicted to disperse to Marion Island (Table 6.2) is derived from birth cohorts 1986 - 1991 (n = 173 resights).*

Year (cohort)	Single tagged	Double tagged	Resighted at MI (1987 - 2002)
1984	346	18	1
1985	336	145	25
1986	1	285	15
1987		324	21
1988		234	20
1989		247	40
1990		200	56
1991		196	21

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Table 6.2. The number of southern elephant seals predicted to disperse from Possession Island (PI), Îles Crozet to Marion Island (MI), assuming seals resighted multiple times at MI immigrate into the population. Tag-resights at MI suggest that up to 11.63% of the tagged population at PI haul out at MI, which can be extrapolated to 64 seals in the total population.

Total tagged population [PI] (1986 - 1991 cohorts)	1487 individuals
Percent of above tagged population (1986 - 1991 cohorts) resighted at MI (1987 - 2002)	11.63% (*n* = 173)
Source population size (Guinet *et al.* 1999)	553 ± 32 females year^{-1}
Mean nr. of source population migrating to MI	64 seals year^{-1}

Age class	A. Observed single haulout (*n* individuals)	B. Observed multiple haulouts (*n* individuals)	C. % Multiple haulouts (= B / 199)	D. Predicted annual multiple haulouts (*n*) (= C x 64)
Under-yearling	24	40	20.10	13
Yearling	42	40	20.10	13
Subadult	43	7	3.52	2
Adult female	3	0	0.00	0

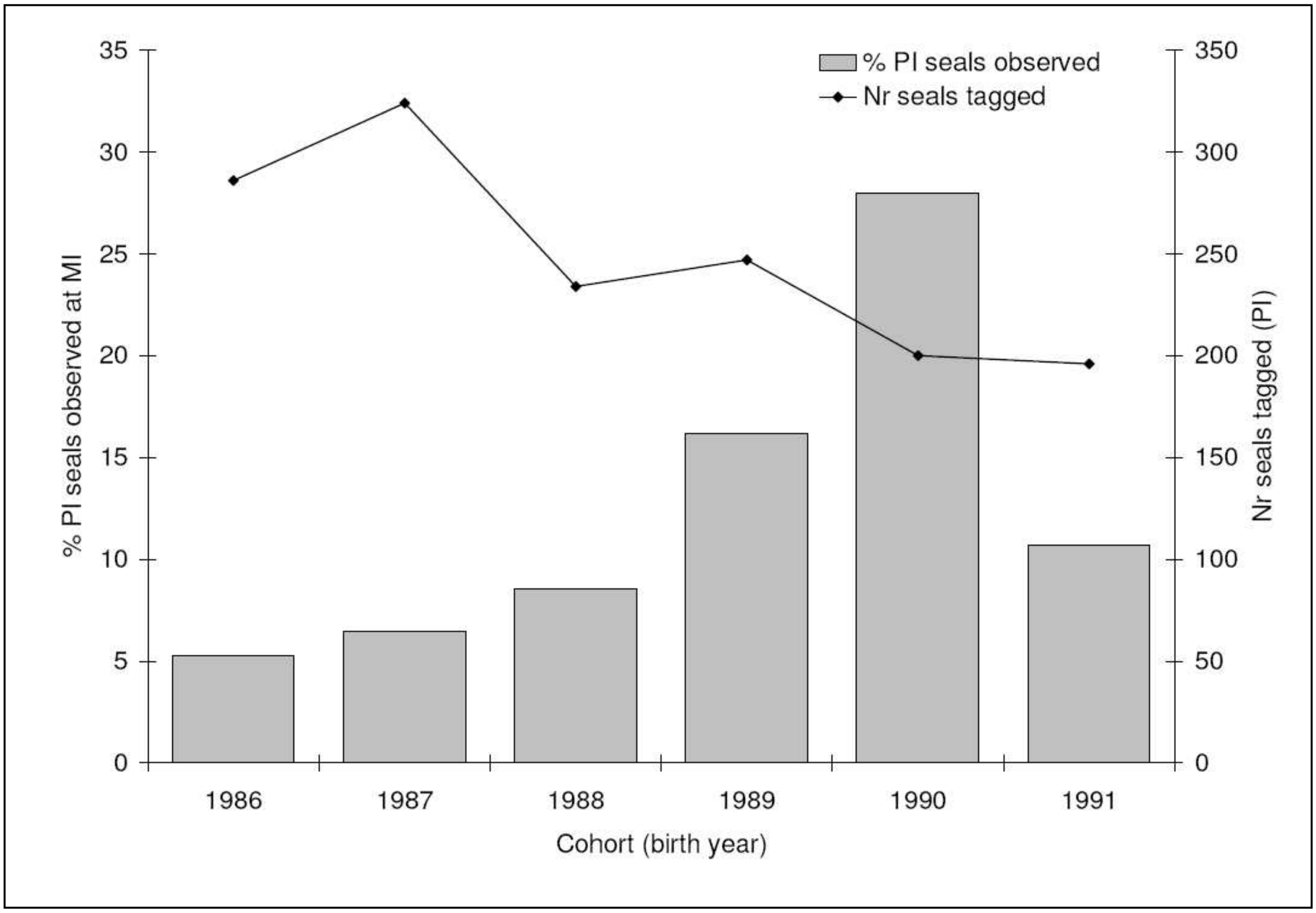


Figure 6.5. The total number of southern elephant seals tagged in every cohort on Possession Island from 1986 - 1991 (line) and the percentage of these seals subsequently resighted at Marion Island (bars). The percentage of seals resighted from the 1986 and 1987 cohorts is biased low because no tag resights were made at Marion Island during the winters of 1987 and 1988.

Other tag resights at MI

In 2006, 200 weaned pups were tagged at Îles Kerguelen (IK). One of these was resighted at MI as an under-yearling in August 2007, but not thereafter.

Satellite telemetry

In total, nine seals tracked from MI hauled out at locations away from the PEIs. Three untagged males fitted with SRDLs during April 1999 (*n* = 2) and April 2002 (autumn/winter haulout at MI), subsequently migrated to IK (Figure 6.6). Individual A, an adult male (Figure

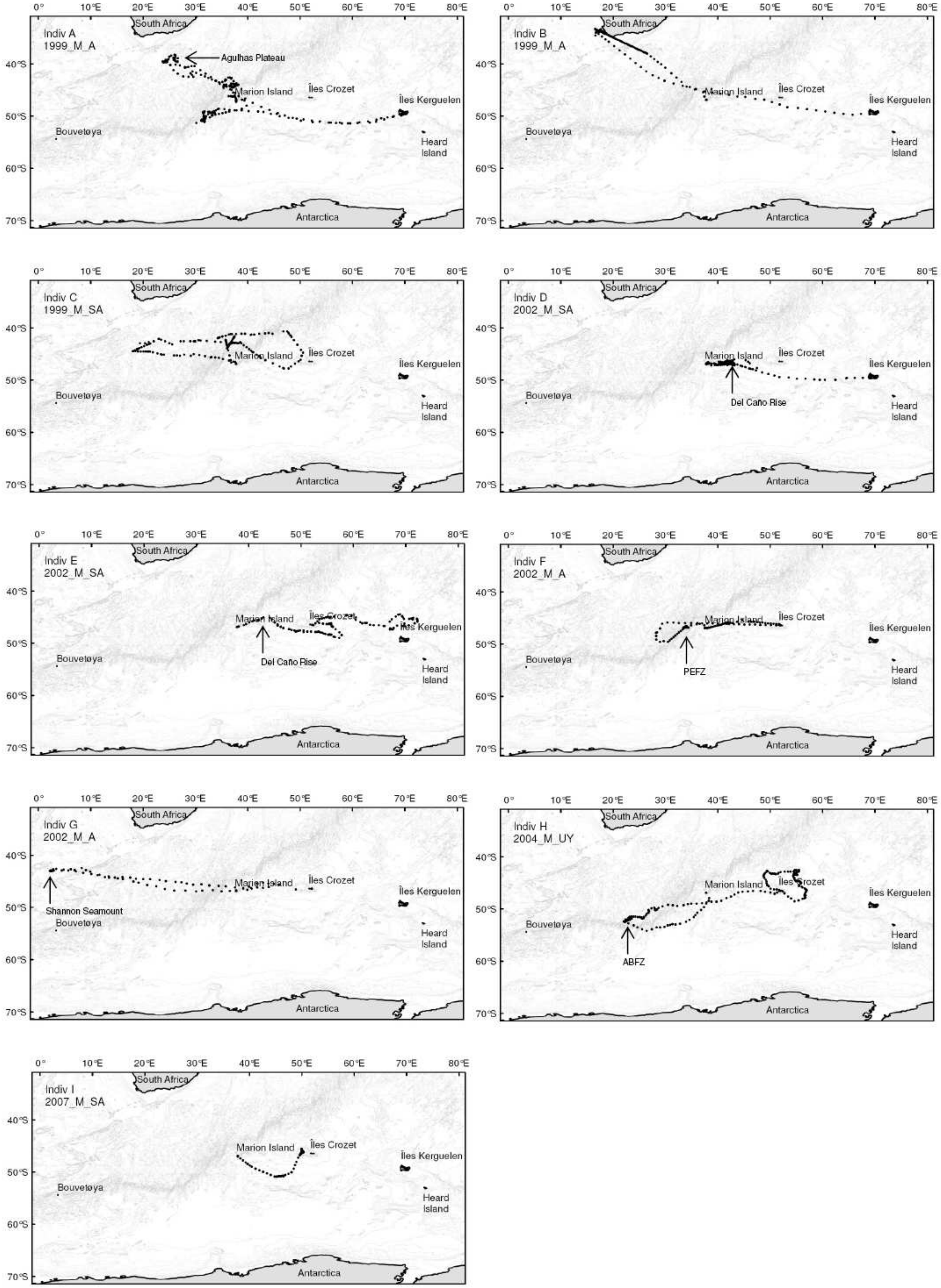
6.6), departed from MI on 17 April 1999 and, after foraging immediately north of the island, travelled to the northwest of the islands, concentrating movement over the Agulhas Plateau. It subsequently travelled to IK, passing due north of MI on 11 September and arriving at the Gallieni Peninsula (Bay of Audierne, IK) on 2 October 1999. It spent the breeding season ashore on the southern end of the Gallieni Peninsula, to the west of Cap des Grottes. It departed from IK on 27 November and travelled along the same route back towards MI. It was due south of MI on 20 December, subsequently moving to the southwest of MI. The last SRDL location was at MI on 23 March 2000 when the seal hauled out for the moult. Individual B, an adult male, departed from MI on 16 April 1999 and travelled to the southwest coast of South Africa, remaining in this area from 30 May to 24 July without hauling out. It subsequently returned towards MI on a route south of the outward trip, passed north of MI (15 August) and south of IC (24 August) before arriving at the Courbet Peninsula, IK for the breeding haulout on 4 September. It stayed in the area between Cap Ratmanoff and Cap Digby (IK) until 17 November when data transmission from the SRDL stopped. Individual D, a subadult male fitted with a SRDL in 2002, departed from MI on 4 May 2002, and travelled east to the Del Caño Rise where it foraged (Tosh 2010). It returned to MI on 14 July for a winter haulout before returning to the Del Caño Rise where it stayed until 19 October, before travelling to the Gallieni Peninsula of IK where it hauled out at the Îles du Prince de Monaco (Bay of Audierne) on 8 November. On 15 November it relocated to the Plaine Ampère region to moult. The last transmission was received on 4 Dec 2002.

Six males hauled out at Îles Crozet in 1999, 2002 (*n* = 3), 2004, and 2007 respectively. All of them departed from MI in April/May following an autumn/winter haulout at which time they were fitted with SRDLs. Four of these seals were untagged. Individual C, an untagged subadult male, departed to the north of MI on 19 April 1999, before heading southeast and hauling out at Île aux Cochons (Îles Crozet) on 17 July 1999 for a winter haulout. On 4 August it departed on the return leg of the migration and first travelled northwest, before heading west, passing MI to the north. The seal returned to MI on 15 November 1999 for the moult haulout. Individual E, an untagged subadult male left MI on 29 April 2002, travelling east via the Del Caño Rise and initially passing southward of IC, before hauling out on the southern coast of Île de l'Est (IC) on 6 July. From here, it travelled further east, with the last position recorded to the north of IK, on 1 September 2002. Individual F, an untagged adult male, departed from MI on 8 May 2002 and travelled westward, before turning south and northeast, concentrating foraging around the Prince Edward Fracture Zone (PEFZ, Figure 6.6; Tosh

2010). It subsequently travelled east, passing northward of MI and hauling out at PI on 19 September 2002. This male remained at PI for the breeding season, before, on 8 November, it migrated west to MI, concentrating movement at the Del Caño Rise during this passage. The seal hauled out at MI on 10 January 2003 for the moult. Individual G, an untagged adult male departed from MI on 19 April 2002 and after a short eastward trip, travelled directly westward to the Shannon Seamount where it foraged in a restricted area from 31 May to 2 September (Tosh 2010). From here, it travelled eastwards, passing the PEIs on 25 September and hauling out for the breeding season on Île de l'Est, IC on 4 October. SRDL data was last received from Anse de l'Aventure (Aventure Cove), Île de l'Est, on 26 October 2002.

Two seals that were born at MI travelled to IC. An under-yearling, individual H (YY232), departed from MI on 25 April 2004, travelling southwest to the Andrew Bain Fracture Zone (ABFZ) in the Southwest Indian Ridge where it foraged from 19 May to 30 June. Next, it travelled eastwards on a track north of the outbound trip and passed MI to the south, heading further east. It hauled out on PI from 19 to 26 August 2004 for a winter haulout before making a clockwise loop to the northeast of IC. SRDL data was last received on 23 November, the location just off the southern coast of PI. The seal may have hauled out on PI on this date, but it did not moult there as it was resighted at MI (without a device but identified by its flipper tags) when it hauled out to moult nine days later. Individual I (BB116), a subadult male, left MI on 25 April 2007 and travelled to IC. It spent the majority of its time (78% of locations) foraging within 65 km to the west of Île aux Cochons (Tosh 2010) and eventually hauled out there on 7 August for a winter haulout. The SRDL stopped transmitting on 17 October 2007 with the seal still in the area to the west of Île aux Cochons. BB116 was not recorded at MI during the 2007/2008 moult haulout and therefore probably moulted at IC. It was next seen at MI on 22 April 2008 during a winter haulout.

Figure 6.6 (below). Movement tracks of southern elephant seals (n = 9) fitted with SRDL devices at Marion Island and migrating to either Îles Crozet or Îles Kerguelen. The upper left corner of each box contains the following information: the individual track identity (e.g, Indiv A), the year of deployment, sex (M = male) and age class (UY = under-yearling, SA = subadult, A = adult).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Îles Crozet
Îles Kerguelen
Heard Island
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Indiv C
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Indiv D
2002_M_SA
Del Caño Rise
Indiv E
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Del Caño Rise
Indiv F
2002_M_A
PEFZ
Indiv G
2002_M_A
Shannon Seamount
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Indiv I
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Population projection

The MI female population decreased at a mean rate of *r* = -6.27% per annum in the projection model where immigration was nil. Within 60 generations, the population size decreased to less than 20 females. When juvenile females (*n* = 13) immigrated into the modeled population, the rate of decrease slowed to *r* = -1.27 ± 0.03% (mean ± SD) per annum. At this rate, a population of 868 females (adults and juveniles) will decrease to 243 females after 100 generations (Figure 6.7).

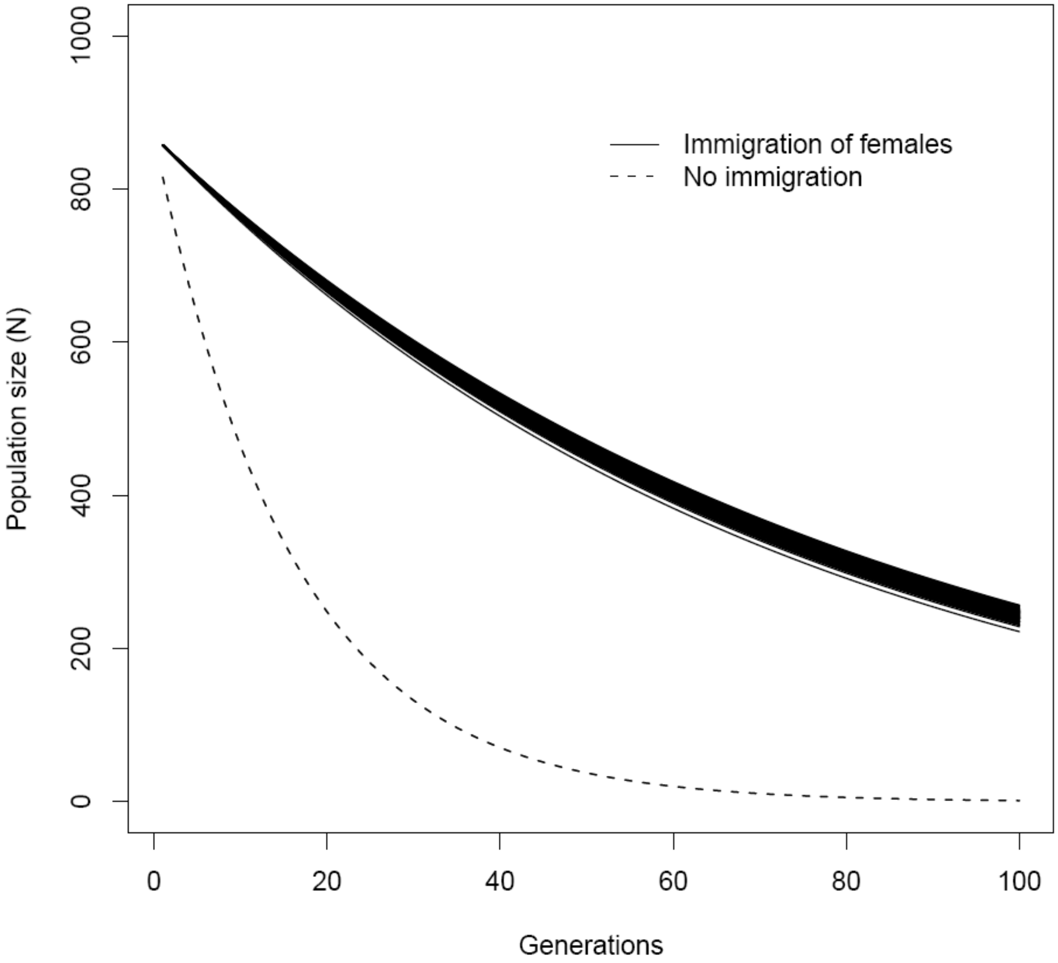

Figure 6.7. Population projection of southern elephant seals at Marion Island over 100 generations based on survival estimates from 1983 to 1998 (de Bruyn 2009) and fecundity estimates from 1993 to 1997 (McMahon et al. 2003). The dotted line represents the deterministic population growth with no immigration; solid lines represent 100 replicates of population growth when six females are added to ages 1 and 2 (±1 SD), and one female to age 3 (±1 SD).

Discussion

Movement, migration and especially breeding dispersal are key processes in any study of population biology (Clobert *et al.* 2001). Several methods enable direct or indirect evaluation of dispersal (and dispersion or migration) in southern elephant seals, including mark-recapture, satellite telemetry and genetic analyses. Intra-island and local archipelago dispersal and dispersion (Hofmeyr 2000, Setsaas *et al.* 2008, Oosthuizen *et al.* 2009) and long range inter-island movements (Bester 1988; Bester 1989; Guinet e*t al.* 1992; Hindell and McMahon 2000; van den Hoff 2001, van den Hoff *et al.* 2003) have been documented through resights of marked individuals. To provide robust quantitative estimates of movement rates, this method relies on large numbers of tagged subjects and an intensive resighting regime over large temporal and spatial scales. Recovery rates are often low when research programmes are not temporally aligned, leading to inadequate data for distant unobservable sites. In our study, for example, no resight data for seals hauling out on IC or IK were available. Satellite telemetry, apart from providing insight to the pelagic foraging behaviour of elephant seals, may additionally provide evidence of inter-island movement. Although often dealing with small sample sizes, tracking the at-sea movements of southern elephant seals from MI (this study) confirmed movement of seals between the MI, IC and IK populations. However, non-random selection of individuals (favouring those that regularly return) excludes the use of tracking data to quantify dispersal rates from MI. Genetic approaches that indirectly quantify effective dispersal rates, have suggested that significant gene flow between some distant populations may occur (Slade *et al.* 1998, Fabiani *et al.* 2003). Genetic dispersal from MI is male biased, but includes female-mediated gene flow (i.e., female dispersal) between MI and HI (Chauke 2008). While no comparisons could be made with IC and IK populations due to a lack of population genetic data, gene flow between these populations within the Kerguelen province is plausible (this study, Chauke 2008).

Juvenile southern elephant seals are less philopatric than adults (Hofmeyr 2000), and are known to haul out on non-native islands to rest or moult (e.g., Bester 1989, van den Hoff 2001). This study confirms MI as an important winter resting and moult haulout site for immature seals from IC, with up to 28% of pups tagged in a birth cohort hauling out at MI. The abundance of IC seals at MI suggests that elephant seals from PI may be foraging to the west of IC, encountering MI during their foraging migrations. Marion Island elephant seals generally forage to the west of MI (Tosh 2010), but the extent of foraging area overlap (Bradshaw *et al.* 2002), and whether seals from the two populations compete for the same (limiting) food resource (Pistorius *et al.* 1999, McMahon *et al.* 2003), is unknown. At a community level, migrant and immigrant IC seals will add nutrients to the MI terrestrial ecosystem via excreta and moulted skin (Panagis 1984, Smith 2008). Migrant and immigrant seals may also fall prey to the resident killer whale (*Orcinus orca*) population at MI which take elephant seals (Condy *et al.* 1978) and are most abundant during the summer (October to December, Keith *et al.* 2001) following the elephant seal breeding season and at a time when juvenile elephant seals haul out to moult.

Despite the relatively large numbers of elephant seals dispersing to MI during the winter and moult, breeding dispersal is less common. However, immigrant seals of both sexes do recruit to the MI breeding population. Dispersal in mammals (Greenwood 1980) including marine mammals (e.g., Lyrholm *et al.* 1999, Möller and Beheregaray 2004, Herreman *et al.* 2009) are generally male biased. Due to the extreme polygynous mating system, elephant seal males are predicted to be the dispersing sex (Greenwood 1980) and greater male dispersal has been indicated by both genetic (Slade *et al.* 1998; Hoelzel *et al*. 2001; Fabiani *et al*. 2003) and mark-recapture studies (e.g., van den Hoff 2001, Lewis *et al.* 2006) of elephant seals, although long range female migrations may occur (e.g., Hindell and McMahon 2000). This study recorded more individual dispersing females than males; however greater male-mediated gene flow was ultimately attained due to the polygynous mating system and one or two extremely successful immigrant males. A single successful dispersal event by a male may therefore have correspondingly large effects on population genetics. Elephant seal males have higher pre-breeding mortality than females due to delayed sexual maturity (age 6, compared to age 3 to 4 for females at MI) and higher mortality rates. Consequently, although absolute numbers of immigrant males in the breeding population may be lower than that of females, the proportion of dispersing males as estimated from the surviving population may be higher than that of females. Males therefore do not have a predisposition to disperse less than females, but they may do so in lower numbers due to higher pre-breeding mortality.

Most immigrant breeders hauled out repeatedly at MI prior to breeding, often as under-yearlings for the first time, whereas seals hauling out as yearlings or subadults were more likely to be transient, often not returning to MI. The mean age of first breeding (primiparity) for MI females is 3.95 yr (McMahon *et al.* 2003). The mean age of first (observed) breeding of IC females at MI was 4.05 yr. Seven IC females breeding at MI were definite first time breeders (age 3). Although breeding probabilities of age 3 females are relatively low (Pistorius *et al.*

2001), we cannot say with certainty that females older than 3 had not bred previously. Still, with the observed age of first breeding of IC females at MI approaching primiparity, dispersal can be best described as ‘natal dispersal’.

Resights of tagged seals is likely to underestimate true dispersion and dispersal rates. Resight rates for the 1986 and 1987 PI cohorts are visibly biased low as no tag resights were made at MI during the winters of 1987 and 1988 when a number of juvenile seals from these cohorts would have been wintering at MI. Apart from PI, the immigration model ignored the other four constituent islands of the IC archipelago population where unknown numbers of elephant seals breed. Furthermore, numbers were not corrected for tag-loss and although tag-loss may be low for juveniles (Oosthuizen *et al.* 2010), higher tag-loss among adult age classes and especially males may have decreased the number of adult male seals resighted, compared to females. Seals marked with a single tag are also expected to become unidentiafiable more rapidly (van Aarde and Pascal 1980), lowering resighting rates.

Although PEI and IC are the closest islands to MI, these localities have relatively small elephant seal populations and the large populations at IK and HI, although more distant, may significantly contribute immigrant seals to MI. Pup production exceeds 43 000 at the Courbet Peninsula, IK (Guinet *et al*. 1999) and approximately 18 000 pups are born per annum at HI (Slip and Burton 1999). Even if emigration rates are low (< 1%), many unmarked seals from these localities may arrive at MI. Initially, IK seals immigrating to MI appear negligible in number, given that of approximately 14 000 tags that had been deployed at IK prior to 1987 only two of these seals were recorded at MI. However, resight effort at MI was low during, and for the four subsequent years to the end of the IK marking period (1970 - 1979). Elephant seals from IK often forage around the Antarctic continental shelf and pelagic areas with marginal sea-ice south of the Antarctic Polar Front (Bailleul *et al*. 2007). From 2004 to 2009, SRDLs were deployed on 110 juvenile, adult female and adult male elephant seals at IK. None were observed to haul out on IC, MI or PEI (C. Guinet, unpublished data)[2], although one breeding female was observed to forage in the vicinity of IC and MI after initially foraging at the Antarctic shelf (see Fig 3 (A) Ind n°5 in Bailleul *et al*. 2007). From our small sample of tracked unmarked (untagged) males that hauled out at MI during autumn (April), two were tracked to IK where they hauled out for the breeding season. Because these seals migrating from MI were untagged, tracking them to IK more likely represents migration of IK seals to MI, followed by a return journey to the natal site during the breeding season. One male was

[2] Centre d'Etudes Biologiques de Chizé, Centre National de la Recherche Scientifique, Villiers en Bois, France

tracked back to MI for the subsequent moult haulout, and it is probable that such dispersion may occur more frequently. Seals that disperse from the natal island for non-breeding purposes only may be faithful to that behaviour throughout their lives, possibly because long-term fidelity to particular foraging regions has some advantages for lifetime foraging success (Bradshaw *et al.* 2004). The large distances between populations within the Kerguelen province is no barrier for any sex or age class as elephant seal under-yearlings are already capable of moving such distances. Because immigration into a distant population appears to be more likely if seals haul out at the locality early on in life (this study), this capability increases the chances that migratory individuals may relocate permanently between these populations.

Population exchange has important consequences for population demographics and dispersal may mediate the genetic and ecological factors regulating closed populations (Ferriere *et al.* 2000). With little evidence suggesting significant dispersal between MI and other island populations, together with the difficulty of incorporating quantitative dispersal figures into demographic models, dispersal was hitherto often assumed to be negligible (e.g., Pistorius *et al*. 1999, 2004, McMahon *et al*. 2009). Even so, earlier population modeling showed that immigration of as few as 8 female elephant seals (aged 1 to 4) per year to MI has a dramatic effect on the predicted future population size (McMahon *et al.* 2005b). The current attempt to quantify migratory rates to improve population survivorship models and estimates of future population size, shows that in the population simulation the rate of population decrease slowed from -6.27% to -1.27% with the addition of 13 juvenile females per annum. The observed rate of decrease of the MI population for 1986 to 1997 falls between these two estimates (-3.7%, McMahon *et al.* 2009). If the survival and fecundity rates for the corresponding period are accurate, the model results suggest that although immigration adds seals to the population, our rates overestimate the number of females eventually recruited into the breeding population. Although the applicability of these estimates in quantitative modeling requires corroboration (see below), it is evident that dispersal should be considered when assessing vital rates for this and other southern elephant seal populations in the southern Indian Ocean.

Future research

This study incorporated data from two temporally overlapping tagging regimes. Currently, MI is the only island in the southern Indian Ocean where elephant seals are tagged annually and resighted at regular intervals. Accordingly, a new marking protocol was recently initiated at MI aiming to address some of the unanswered questions regarding dispersal and dispersion between MI and other islands. Untagged seals hauling out at MI during winter as under-yearlings and during the moult (age 1) are tagged with uniquely identifiable tags to mark them as “non-native seals”. This approach is possible as virtually all MI born seals are tagged every year (de Bruyn *et al.* 2008), and tag-loss from weaning to age 1 is negligible (Oosthuizen *et al*. 2010). This marking protocol aims to further quantify dispersal and dispersion involving the MI population, even if the source populations of these seals remain unknown. Assessment of gene flow between populations in the southern Indian Ocean will complement the current study and previous genetic studies (Chauke 2008).

The extent of emigration of seals from MI remains unclear. Because the majority of MI seals forage to the west and south-west of MI (Tosh 2010) where the closest elephant seal population is on Bouvetøya (*c.* 2500 km distant), we hypothesize that the amount of immigration to MI from IC and IK to the east overshadows emigration from MI. Although several SRDL females from MI travelled to the immediate vicinity of Bouvetøya during their pelagic migration, none has hauled out there. Also, no MI tagged seals have been observed at Bouvetoya during the moulting periods in five expeditions there over the course of ~ 15 years (Norwegian Polar Institute, unpublished data). Yet, MI tagged elephant seals resighted at Gough Island, south Atlantic Ocean, (Reisinger and Bester, [in review]) and IC (Bester 1989) to the west and east of MI respectively, suggest some emigration, although some of these movements may be migratory. Furthermore, local dispersal and dispersion (temporary or permanent) to neighbouring PEI occurs at low but apparently consistent levels (Oosthuizen *et al.* 2009).

References

Bailleul, F., Charrassin, J-B, Ezraty, R, Girard-Ardhuin, F., McMahon, C.R., Field, I.C. and Guinet, C. 2007. Southern elephant seals from Kerguelen Islands confronted by Antarctic Sea ice. Changes in movements and in diving behaviour. *Deep-Sea Research II* 54: 343-355.

Bester, M.N. 1988. Marking and monitoring studies of the Kerguélen stock of southern elephant seals *Mirounga leonina* and their bearing on biological research in the Vestfold Hills. *Hydrobiologia* 165:269-277.

Bester, M.N. 1989. Movements of southern elephant seals and Subantarctic fur seals in relation to Marion Island. *Marine Mammal Science* 5:257-265.

Bradshaw, C.J.A., McMahon, C.R., Hindell, M.A. Pistorius, P.A. and Bester, M.N. 2002. Do southern elephant seals show density dependence in fecundity? *Polar Biology* 25: 650-655.

Bradshaw, C.J.A., Hindell, M.A., Sumner, M.D. and Michael, K.J. 2004. Loyalty pays: potential life history consequences of fidelity to marine foraging regions by southern elephant seals. *Animal Behaviour* 68: 1349-1360.

Caswell, H. 2001. *Matrix population models: construction analysis and interpretation.* Sinauer Associates, Sunderland, MA.

Chauke, L.F. 2008. Genetic variation and population structure of southern elephant seals *Mirounga leonina* from Marion Island. M.Sc. Dissertation, University of Pretoria, Pretoria.

Clobert, J., Danchin, E., Dhondt, A.A. and Nichols, J.D. 2001. *Dispersal*. Oxford University Press, New York.

Condy, P.R., van Aarde, R.J. and Bester, M.N. 1978. The seasonal occurrence and behaviour of killer whales *Orcinus orca,* at Marion Island. *Journal of Zoology, London* 184: 449-464.

de Bruyn, P.J.N., Tosh, C.A., Oosthuizen, W.C., Phalanndwa, M.V. and Bester M.N. 2008. Temporary marking of unweaned southern elephant seal (*Mirounga leonina* L.) pups. *South African Journal of Wildlife Research* 38: 133-137.

de Bruyn, P.J.N. 2009. Life history studies of the southern elephant seal population at Marion Island. PhD thesis, University of Pretoria, Pretoria

Fabiani, A., Hoelzel, A. R., Galimberti, F. and Muelbert, M. M. C. 2003. Long-range paternal gene flow in the southern elephant seal. *Science* 299: 676.

Ferriere, R., Belthoff, J.R., Olivieri, I. and Krackow, S. 2000. Evolving dispersal: where to go next? *Trends in Ecology and Evolution* 15: 5-7.

Greenwood, P.J. 1980. Mating systems, philopatry and dispersal in birds and mammals. *Animal Behaviour* 28: 1140-1162.

Guinet, C., Jouventin, P. and Weimerskirch, H. 1992. Population changes, movements of southern elephant seals on Crozet and Kerguelen Archipelagos in the last decades. *Polar Biology* 12:349-356.

Guinet, C., Jouventin, P. and Weimerskirch, H. 1999. Recent population change of the southern elephant seal at Îles Crozet and Îles Kerguelen: the end of the decrease? *Antarctic Science* 11:193-197.

Herreman, J.K., Blundell, G.M., McDonald, D.B. and Ben-David, M. 2009. Asymmetrical male-mediated gene flow between harbor seal (*Phoca vitulina*) populations in Alaska. *Canadian Journal of Zoology* 87: 498-507.

Hindell, M.A. and McMahon, C.R. 2000. A long distance movement of a southern elephant seal (*Mirounga leonina*) from Macquarie Island to Peter 1ØY. *Marine Mammal Science* 16: 504-507.

Hoelzel, A.R., Campagna, C. and Arnbom, T. 2001. Genetic and morphometric differentiation between island and mainland southern elephant seal populations. *Proceedings of the Royal Society London B* 268: 325-332.

Hofmeyr, G.J.G. 2000. Dispersal and dispersion in the southern elephant seal *Mirounga leonina* at Marion Island. M.Sc. Dissertation, University of Pretoria, Pretoria

Howard, W.E. 1960. Innate and environmental dispersal of individual vertebrates. *American Midland Naturalist* 63: 152-161.

Jonker, F.C. and Bester, M.N. 1998. Seasonal movements and foraging areas of adult southern female elephant seals, *Mirounga leonina*, from Marion Island. *Antarctic Science*: 10: 21-30.

Keith, M., Bester, M.N., Bartlett, P.A. and Baker, D. 2001. Killer whales (*Orcinus orca*) at Marion Island, Southern Ocean. *African Zoology* 36: 163-175.

Lenglart, P.Y. and Bester, M.N. 1982. Post-weaning dispersion of southern elephant seal *Mirounga leonina* underyearlings at Kerguelen. *Review de Ecologie (Terre et la Vie)* 36: 175-186.

Lewis, M., Campagna, C. and Quintana, F. 1996. Site fidelity and dispersion of southern elephant seals from Patagonia. *Marine Mammal Science* 12: 138-147.

Lewis, M., Campagna, C. Marin, M.R. and Fernandez, T. 2006. Southern elephant seals north of the Antarctic Polar Front. *Antarctic Science* 18: 213-221.

Lyrholm, T., Leimar, O., Johanneson, B. and Gyllensten, U. 1999. Sex-biased dispersal in sperm whales: contrasting mitochondrial and nuclear genetic structure of global populations. *Proceedings of the Royal Society of London B* 266: 347-354.

McConnell, B.J., Chambers, C. and Fedak, M.A. 1992. Foraging ecology and southern elephant seals in relation to bathymetry and productivity of the Southern Ocean. *Antarctic Science* 4: 393-398.

McMahon, C.R., Burton, H.R. and Bester, M.N. 2003. A demographic comparison of two southern elephant seal populations. *Journal of Animal Ecology* 72: 61-74.

McMahon, C.R., Bester, M.N., Burton, H.R., Hindell, M.A. and Bradshaw, C.J.A. 2005a. Population status, trends and a re-examination of the hypotheses explaining the recent declines of the southern elephant seal *Mirounga leonina*. *Mammal Review* 35:82-100.

McMahon, C.R., Hindell, M.A., Burton, H.R. and Bester, M.N. 2005b. Comparison of southern elephant seal populations, and observations of a population on a demographic knife-edge. *Marine Ecology Progress Series* 288: 273-283.

McMahon, C.R., Bester, M.N., Hindell, M.A., Brook, B.W. and Bradshaw, C.J.A. 2009. Shifting trends: detecting environmentally mediated regulation in long lived marine vertebrates using time-series data. *Oecologia* 159: 69-82.

Möller, L.M. and Beheregaray, L.B. 2004. Genetic evidence for sex-biased dispersal in resident bottlenose dolphins (*Tursiops aduncus*). *Molecular Ecology* 13: 1607-1612.

Nathan, R. 2001. The challenges of studying dispersal. *Trends in Ecology and Evolution* 16: 481-483.

Nicholls, D.G. 1970. Dispersal and dispersion in relation to the birthsite of the southern elephant seal, *Mirounga leonina* (L.), of Macquarie Island. *Mammalia* 34: 598-616.

Oosthuizen, W.C., Bester, M.N., de Bruyn, P.J.N. and Hofmeyr, G.J.G. 2009. Intra-archipelago moult dispersion of southern elephant seals at the Prince Edward Islands, southern Indian Ocean. *African Journal of Marine Science* 31: 457-462.

Oosthuizen, W.C., de Bruyn, P.J.N., Bester, M.N. and Girondot, M. 2010. Cohort and tag-site specific tag-loss rates in mark-recapture studies: a southern elephant seal cautionary case. *Marine Mammal Science* 26: 350-369.

Panagis, K. 1984. Influence of southern elephant seals, *Mirounga leonina*, on the coastal moulting areas at Marion Island. *South African Journal of Science* 80: 30.

Pistorius, P.A., Bester, M.N. and Kirkman, S.P. 1999. Survivorship of a declining population of southern elephant seals, *Mirounga leonina*, in relation to age, sex, and cohort. *Oecologia* 121: 201-211.

Pistorius, P.A., Bester, M.N., Kirkman, S.P. and Taylor, F.E. 2001. Temporal changes in fecundity and age at sexual maturity of southern elephant seals at Marion Island. *Polar Biology* 24: 343-348.

Pistorius, P.A., Bester, M.N., Lewis, M.N., Taylor, F.E., Campagna, C. and Kirkman, S.P. 2004. Adult female survival, population trend, and the implications of early primiparity in a capital breeder, the southern elephant seal (*Mirounga leonina*). *Journal of Zoology, London* 263: 107-119.

Reisinger, R.R. and Bester, M.N. (in review) Long distance breeding dispersal of a southern elephant seal. *Polar Biology*

Setsaas, T.H., Bester, M.N., Van Niekerk, J.H., Roux, J.P. and Hofmeyr, G.J.G. 2008. Dispersion during the moult haulout of southern elephant seals at the Courbet Peninsula, Iles Kerguelen. *Polar Biology* 31: 249-253.

Slade, R.W., Moritz, C., Hoelzel, A.R. and Burton, H.R. 1998. Molecular population genetics of the southern elephant seal *Mirounga leonina*. *Genetics* 149: 1945-1957.

Slip, D.J. and Burton, H.R. 1999. Population status and seasonal haulout patterns of the southern elephant seal (*Mirounga leonina*) at Heard Island. *Antarctic Science* 11: 38-47.

Smith, V.R. 2008. Energy flow and nutrient cycling in the Marion Island terrestrial ecosystem: 30 years on. *Polar Record* 44: 211-226.

Tosh, C.A. 2010. Oceanographic signatures and foraging areas of southern elephant seals. PhD thesis, University of Pretoria, Pretoria.

Tosh, C.A., Bornemann, H., Ramdohr, S., Schröder, M., Martin, T., Carlini, A., Plötz, J. and Bester, M.N. 2009. Adult male southern elephant seals from King George Island utilize the Weddell Sea. *Antarctic Science* 21: 113-121.

Trakhtenbrot, A., Nathan, R. Perry, G. and Richardson, D.M. 2005. The importance of long-distance dispersal in biodiversity conservation. *Diversity and Distributions* 11: 173-181.

van Aarde, R.J. and Pascal, M. 1980. Marking southern elephant seals on Îles Kerguelen. *Polar Record* 20: 61-65.

van den Hoff, J. 2001. Dispersal of southern elephant seals (*Mirounga leonina*) marked at Macquarie Island. *Wildlife Research* 28:41-418.

van den Hoff, J., Davies, R. and Burton, H. 2003. Origins, age composition and change in numbers of moulting southern elephant seals (*Mirounga leonina*) in the Windmill Islands, Vincennes Bay, east Antarctica, 1988-2001. *Wildlife Research* 30: 275-208.

Wilkinson, I.S. and van Aarde, R.J. 1999. Marion Island elephant seals: the paucity-of-males hypothesis tested. *Canadian Journal of Zoology* 77: 1547-1554.

CHAPTER 7

GENERAL CONCLUSION

Synthesis

Long-term mark-recapture experiments of long-lived animals are of considerable importance if the causal factors that drive population dynamics are to be identified (Clobert *et al.* 1994). Such experiments have inherent complexity and estimation of parameters of interest, such as survival and fecundity, may be biased if 'nuisance parameters' such as marker-loss, emigration and immigration are not accounted for (Pollock 2000). Marker-loss results in negatively biased survival rates (Arnason and Mills 1981) and additionally, if recaptured, individuals that have lost their identifying marks appear to be immigrants, biasing recruitment rates upward (Cowen and Schwarz 2006). Emigration influences survival rate estimation in mark-recapture experiments by generating variable recapture probabilities, which is reduced for temporary emigrants and zero (equivalent to mortality) for permanent emigrants (Schaub *et al.* 2004). Immigration has important consequences for population demographics and may mediate the genetic and ecological factors regulating closed populations (Ferriere *et al.* 2000).

Extensive analyses on mark-recapture data of the southern elephant seal population at Marion Island have identified the importance of survival (juvenile survival, McMahon *et al.* 2003, 2005a; adult female survival, Pistorius *et al.* 1999, 2004; juvenile and adult survival, de Bruyn 2009) in population regulation. Variable fecundity appears to have a limited effect on the rate of population change (McMahon *et al.* 2003), but recruitment by means of immigration may significantly influence population growth (McMahon *et al*. 2005a). Field observations of large numbers of untagged seals suggest that immigration may be an important component of population demography. Furthermore, violation of the "homogeneity of recaptures" assumption of mark-recapture survival analyses (de Bruyn 2009) suggests that temporary emigration of marked seals may be occurring. Dispersal is a challenging facet of population biology (Nathan 2001) and has received comparatively little attention in the well-studied Marion Island elephant seal population. Inter-island movement of seals during the winter and moult, mostly by juveniles, has been recorded (Bester 1989) but evidence of permanent immigration and breeding at non-native islands has largely been lacking, although the potential impact of such dispersal have been illustrated (McMahon *et al.* 2005a).

This study established that Marion Island is an important winter and moult haulout locality for seals from the Kerguelen province. Investigation into the foraging ranges and potential intra-specific competition between seals from the different populations in the region is timely. The potential foraging range overlap for elephant seal populations in the Kerguelen province has been suggested before (Bradshaw *et al.* 2002), with consequences for interpretation of the ‘food limitation hypothesis’ (Pistorius *et al.* 1999), for example. Significant overlap of foraging ranges in the presence of either divergent population growth rates or the temporal asynchrony of population trends within the Kerguelen province (Bradshaw *et al.* 2002), would suggest that food limitation alone is not driving population trends. This may support hypotheses regarding the importance of killer whale (*Orcinus orca*) predation as a regulating factor of small populations (McMahon *et al.* 2005b, de Bruyn 2009).

Additionally, this study provides evidence of immigration and successful breeding of both sexes of Îles Crozet elephant seals at Marion Island. However, the findings based on resightings of marked seals are likely to underestimate the true rate of dispersal as marking effort has been, and continues to be, very low at all other islands in this region. In an attempt to further quantify dispersal and dispersion involving the Marion Island population, a new marking protocol was initiated where untagged under-yearlings hauling out at Marion Island during the winter and first-year moult are tagged with uniquely identifiable tags to mark them as “non-native seals”. Although the source populations of these seals will remain unknown, it is anticipated that such a marking practice will improve quantitative estimates of immigration rates. Unfortunately, a similar ‘single island approach’ will not assist evaluation of the extent of permanent emigration from Marion Island, which remains unclear and difficult to quantify. Temporary emigration, which was shown to occur between Marion Island, Price Edward Island and Îles Crozet, can from an analytical perspective, be accounted for in a multistate modeling approach with an ‘unobservable’ state (Schaub *et al.* 2004), an necessary advance in analyses of Marion Island mark-resight data proposed by de Bruyn (2009).

References

Arnason, A.N., and Mills, K.H. 1981. Bias and loss of precision due to tag loss in Jolly-Seber estimates for mark-recapture experiments. *Canadian Journal of Fisheries and Aquatic Sciences* 38: 1077-1095.

Bester, M.N. 1989. Movements of southern elephant seals and Subantarctic fur seals in relation to Marion Island. *Marine Mammal Science* 5: 257-265.

Bradshaw, C.J.A., McMahon, C.R., Hindell, M.A. Pistorius, P.A. and Bester, M.N. 2002. Do southern elephant seals show density dependence in fecundity? *Polar Biology* 25: 650-655.

Clobert, J., Lebreton, J.-D., Allaine, D. and Gaillard, J.M. 1994. The estimation of age-specific breeding probabilities from recapture or resightings in vertebrate populations: II. Longitudinal models. *Biometrics* 50: 375-387.

Cowen, L., and Schwarz, C.J. 2006. The Jolly-Seber model with tag loss. *Biometrics* 62: 699-705.

de Bruyn, P.J.N. 2009. Life history studies of the southern elephant seal population at Marion Island. PhD thesis, University of Pretoria, Pretoria.

Ferriere, R., Belthoff, J.R., Olivieri, I. and Krackow, S. 2000. Evolving dispersal: where to go next? *Trends in Ecology and Evolution* 15: 5-7.

McMahon, C.R., Burton, H.R. and Bester, M.N. 2003. A demographic comparison of two southern elephant seal populations. *Journal of Animal Ecology* 72: 61-74.

McMahon, C.R., Hindell, M.A., Burton, H.R. and Bester, M.N. 2005a. Comparison of southern elephant seal populations, and observations of a population on a demographic knife-edge. *Marine Ecology Progress Series* 288: 273-283.

McMahon, C.R., Bester, M.N., Burton, H.R., Hindell, M.A. and Bradshaw, C.J.A. 2005b. Population status, trends and a re-examination of the hypotheses explaining the recent declines of the southern elephant seal *Mirounga leonina*. *Mammal Review* 35:82-100.

Nathan, R. 2001. The challenges of studying dispersal. *Trends in Ecology and Evolution* 16: 481-483.

Pistorius, P.A., Bester, M.N. and Kirkman, S.P. 1999. Survivorship of a declining population of southern elephant seals, *Mirounga leonina*, in relation to age, sex and cohort. *Oecologia* 121: 201-211.

Pistorius, P.A., Bester, M.N., Lewis, M.N., Taylor, F.E., Campagna, C. and Kirkman, S.P. 2004. Adult female survival, population trend, and the implications of early primiparity in a capital breeder, the southern elephant seal. *Journal of Zoology, London* 263: 107-119.

Schaub, M., Gimenez, O., Schmidt, B.R. and Pradel, R. 2004. Estimating survival and temporary emigration in the multistate capture-recapture framework. *Ecology* 85: 2107-2113.

Pollock, K.H. 2000. Capture-recapture models. *Journal of the American Statistical Association* 95: 293-296.

“They will soar on wings like eagles”

(Photo: Johann Jamneck)

(Photo: Paul Visser)