



## Trend changes in sympatric Subantarctic and Antarctic fur seal pup populations at Marion Island, Southern Ocean

MIA WEGE,<sup>1</sup> Mammal Research Institute, Department of Zoology & Entomology, University of Pretoria, Private Bag X20, Hatfield, Pretoria, 0028, South Africa; MARIE-PIERRE ETIENNE, UMR AgroParisTech INRA MIA-518, F-75005 Paris, France; W. CHRIS OOSTHUIZEN, RYAN R. REISINGER,<sup>2</sup> MARTHÁN N. BESTER, P. J. NICO DE BRUYN, Mammal Research Institute, Department of Zoology & Entomology, University of Pretoria, Private Bag X20, Hatfield, Pretoria, 0028, South Africa.

### ABSTRACT

Recent pup population estimates of sympatric Subantarctic (*Arctocephalus tropicalis*) and Antarctic fur seals (*A. gazella*) at Marion Island are presented. Published pup population estimates of *A. tropicalis* (1995 and 2004) with an unpublished total island count in 2013, and annual counts on subsets of rookeries (2007–2015) were analyzed using a hierarchical Bayesian model. The pup population declined by 46% (95% credible interval CI: 43%–48%) between 2004 (mean = 15,260, CI: 14,447–16,169 pups) and 2013 (mean = 8,312, CI: 7,983–8,697), mirrored by a 58%–60% decline at rookeries counted annually (2007–2015). Population decline was highest at high-density west and north coast rookeries, despite negligible change in female attendance patterns, pup mortality or median pupping date over the previous 25 yr. A better understanding of foraging behavior and its effects on reproductive success and survival in this *A. tropicalis* population is needed before we can attribute population decline to any external factors. In contrast, total island counts of *A. gazella* pups in 2007, 2010, and 2013, suggest that this population is still increasing although the annual intrinsic rate of population growth decreased from 17.0% (1995–2004, 744 pups) to 4.0% (2010–2013, 1,553 pups). The slowed growth of *A. gazella* is likely the result of saturation at the main rookery.

**Key words:** *Arctocephalus*, Subantarctic fur seal, Antarctic fur seal, population estimate, Marion Island, hierarchical Bayesian model, detection probability, sympatry, density, count.

Population size assessments are central to ecological studies. Quantifying population trend change is crucial to evaluate its current state, facilitating decisions related to conservation or management interventions (Sutherland and Norris 2002). Monitoring recovery in previously exploited populations allows for quantification of the four phases (survival, establishment, recolonization, and maturity)

<sup>1</sup>Corresponding author (e-mail: mwege@zoology.up.ac.za).

<sup>2</sup>Department of Zoology, Nelson Mandela Metropolitan University, PO Box 77000, Port Elizabeth, 6031, South Africa

of population growth (Bester 1980, Roux 1987) and provides insight into population growth dynamics (Sinclair 1996). Monitoring consequently permits investigation into underlying mechanisms of how environmental fluctuations influence population growth.

All fur seals (family Otariidae) were hunted for their furs; several species, including the Southern Hemisphere species (genus *Arctocephalus*), were hunted close to extinction (Bonner and Laws 1964). Small populations survived on a few subantarctic islands, which facilitated subsequent recovery (Bonner and Laws 1964). Similar to other subantarctic islands, Marion Island was subjected to sealing from the 17th century. Sealing continued intermittently until 1931 when only a small population of Subantarctic fur seals (*Arctocephalus tropicalis*; SAFS) remained (Kerley 1987). Marion Island is currently home to the largest sympatric populations of Subantarctic and Antarctic fur seals (*A. gazella*) (Hofmeyr *et al.* 2006). The first population census at Marion Island was done in 1952 (Rand 1956) but regular population censuses only commenced in 1974 (Condy 1978; Kerley 1987; Wilkinson and Bester 1990; Hofmeyr *et al.* 1997, 2006) and started opportunistically at neighboring Prince Edward Island in 1981 (Kerley 1987; Wilkinson and Bester 1990; Bester *et al.* 2003, 2009).

Between 1952 and the late 1970s the SAFS population on Marion Island followed the first stage of the classic population recolonization trajectory: a period of survival, where population numbers remained low and increased slowly (Bester 1980, Roux 1987). From the late 1970s until the late 1980s a phase of rapid recolonization and exponential increase was recorded (12.9% per annum; Wilkinson and Bester 1990), but from the end of the 1980s to 1995, annual population growth slowed to 2% (Hofmeyr *et al.* 1997). Although it was suggested that the population had reached the maturity phase, a 2004 census showed an annual rate of population increase of 5.2% over the intervening 9 yr (Hofmeyr *et al.* 2006). Therefore, the population might not have been in the maturity phase as yet but had certainly passed the peak period of population increase by 2004 (Hofmeyr *et al.* 2006). The largest rookeries (mostly on the western aspect of Marion Island) showed slowed growth, while smaller rookeries elsewhere on the island increased in number and size. Hofmeyr *et al.* (2006, 2007) argued that the overall reduced population growth was probably due to limited breeding space at the source rookeries, rather than a lack of resources at sea. It is not known whether Antarctic fur seals (AFS) used to breed on Marion Island prior to sealing (Rand 1956). AFS numbers were last shown to increase at 17% annually (1995–2004); thus in the exponential growth phase (Hofmeyr *et al.* 2006). The end point of these trends corresponded to the most recent increased abundance estimates of both species at Marion Island of *ca.* 80,000 SAFS and *ca.* 5,800 AFS in 2004 (Hofmeyr *et al.* 2006).

The synchronous breeding of high-latitude fur seals (*e.g.*, Payne 1977) and the presence of aggressive territorial males make direct counts on the beach during peak breeding season impossible (Shaughnessy 1986). Counting is often done from a vantage point above the beach (*e.g.*, Bester *et al.* 2003, 2009; Gibbens and Arnould 2009); from a ship, counting adult females ashore (Boyd 1993); through aerial surveys, or some combination of these (*e.g.*, Pemberton and Kirkwood 1994, Huckle-Gaete *et al.* 2004). All these methods have inherent counting errors, and often depend on the density of animals on the beach (*e.g.*, Boyd 1993). Alternatively, population trends can be estimated through pup population changes (*e.g.*, Chapman and Johnson 1968, Bonner 1968, Guinet *et al.* 1994, Shaughnessy *et al.* 1995, Hofmeyr *et al.* 2007). Pups are easily distinguishable from other age classes and most importantly remain at colonies for months after birth (Pemberton and Kirkwood 1994). In

contrast, adult individuals spend time both at sea and on land during this period, while subadult individuals are not present on land during this period (Kerley 1983). This makes comprehensive population counts of separate age classes infeasible (Shaughnessy 1986). Pup production can also serve as an indicator of environmental pressures on the population. Precipitous declines in pup production have been linked to El Niño events in several otariid species (Trillmich and Ono 1991, Guinet *et al.* 1994). Declines have been correlated with positive sea-surface temperature anomalies in AFS (Forcada *et al.* 2005) and have been negatively correlated with sea-surface temperature and positively correlated with female body condition for Australian fur seals (*A. pusillus doriferus*; Gibbens and Arnould 2009). Australian sea lion (*Neophoca cinerea*) pup production was negatively influenced by adult sea lion bycatch of shark fishery activities (Shaughnessy *et al.* 2013).

In this paper, we reassess the pup population status of *Arctocephalus* spp. at Marion Island and provide revised estimates of pup numbers and trends for the period 2004–2013. To achieve this, for SAFS we use (1) annual pup count data from a subset of rookeries on Marion Island (2007–2015), (2) total island surveys (2004 and 2013), and (3) minimum pup mortality. Changes in AFS pup numbers are represented by triennial total island surveys (2007, 2010, and 2013).

## METHODS

Marion Island is part of the Prince Edward archipelago in the Indian sector of the Southern Ocean. Marion Island is approximately 300 km<sup>2</sup> in area, with a coastline of *ca.* 107 km (Meiklejohn and Smith 2008). On Marion Island, AFS have a median pupping date of 5–7 December, whereas the median pupping date for SAFS is 16–20 December (Hofmeyr *et al.* 2007). AFS pups wean at 110 d and SAFS pups at 300 d (Kerley 1983). Breeding seasons span from the end of one calendar year into the next and are referred to by the year in which the pups wean, for example, “2007” refers to pups born in December 2006 and weaned in 2007.

### *Subantarctic Fur Seal Pup Counts: Field Methods*

SAFS prefer to breed on boulder/jumbled rocky beaches (Bester 1982). At Marion Island, pup numbers are predominantly estimated by direct counting while observers traverse beaches on foot (but by capture-mark-recapture at Fur Seal Peninsula, the largest breeding area). Previous studies indicated that direct counts underestimate pup numbers but that it is colony specific due to topography (Shaughnessy *et al.* 1995, Kirkwood *et al.* 2005). To account for imperfect observation of pups during direct counts (*e.g.*, pups hiding out of sight underneath boulders), we use (1) capture-mark-recapture (CMR) methods in combination with direct counts at a single beach to estimate detection probability when counting directly (Shaughnessy *et al.* 1995), and (2) cliff-top counts in combination with direct counts at a single beach to estimate the detection probability when beaches could only be counted by direct observation from the top of a cliff (lower detection expected in this case). Each of these counting methods is explained in more detail below.

*Annual (2007–2015) and island-wide direct counts (2004, 2013)*—The coastline of Marion Island is made up of a series of distinct, naturally segregated beaches interspersed with sheer cliffs that drop directly into the ocean. An observer can easily move on foot between and across beaches and record the number of pups present on

these. In each year, all counts were made by a single, experienced observer moving on foot across each beach. Live and dead pups were counted by systematically searching beaches and vegetated areas adjacent to beaches. Where over 100 pups were counted on a beach, multiple (2–4) counts were done. Annual counts were made along a small stretch of coastline (Fig. 1) at the conclusion of the pupping season from the middle to the end of January (Kerley 1983); total island counts extended into early February. Consistent with all previous total population estimates of SAFS at Marion Island (Condy 1978; Kerley 1983; Wilkinson and Bester 1990; Hofmeyr *et al.* 1997, 2006), pups on the entire coastline were counted in 2013 with the exception of inaccessible stretches of four bays (Crawford, Rooks, Goodhope and part of Triegaardt

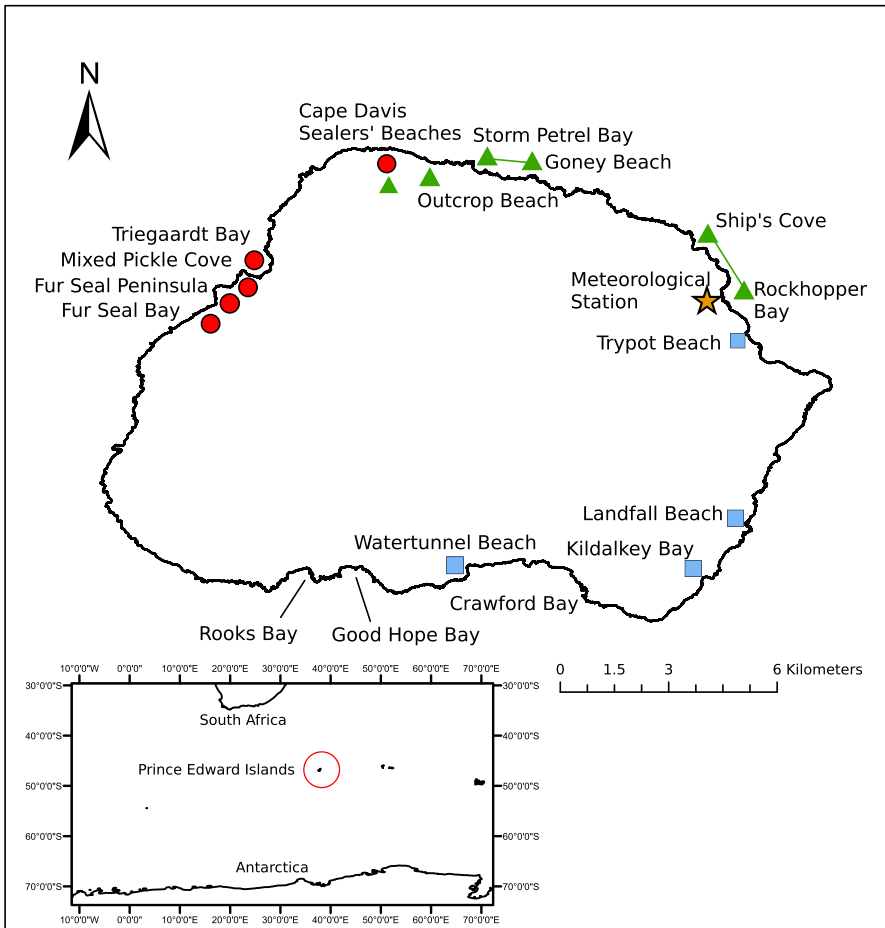


Figure 1. Marion Island. The five high density Subantarctic fur seal rookeries (circles), four high density Antarctic fur seal rookeries (squares) and Meteorological Station (star) are shown. The annual Subantarctic fur seal pup count beaches are between the Cape Davis Sealers' Beaches and Outcrop Beach, between Storm Petrel Bay and Goney Beach and from Ship's Cove to Rockhopper Bay, represented by triangles. Insert: The Prince Edward Islands' location in relation to South Africa and Antarctica.

Bay; Fig. 1). Situated at the foot of precipitous cliffs, these narrow stretches of coastline are presumed to contribute little to overall pup numbers.

*Fur Seal Peninsula CMR study (2004, 2013)*—Given the large number of pups born at Fur Seal Peninsula (Fig. 1) and the size of the area, CMR is more suitable than direct counts to estimate pup numbers for this area (Hofmeyr *et al.* 2006). In 2004 (9–10 February 2004), 500 pups (with a 50:50 sex ratio) were clearly marked with long lasting (>6 d) road paint across the shoulder blades. Similarly, in 2013, 735 pups were marked (21–23 January 2013). To avoid paint washing off, no wet or swimming pups were marked and freshly painted pups were prevented from swimming for ~30 s after release (*i.e.*, enough time to let the paint settle in the fur). Pups were allowed to reintegrate into the rookery for more than 1 d before “recaptures” started by way of a single observer moving slowly along parallel transects that covered the whole peninsula. In 2004, the peninsula was divided into five transects; whereas in 2013, 12 shorter transects were used. All marked and unmarked live and dead pups were counted within 3 m of the observer. Each transect was counted three times over two consecutive days. Transects were evenly spaced to cover the entire area.

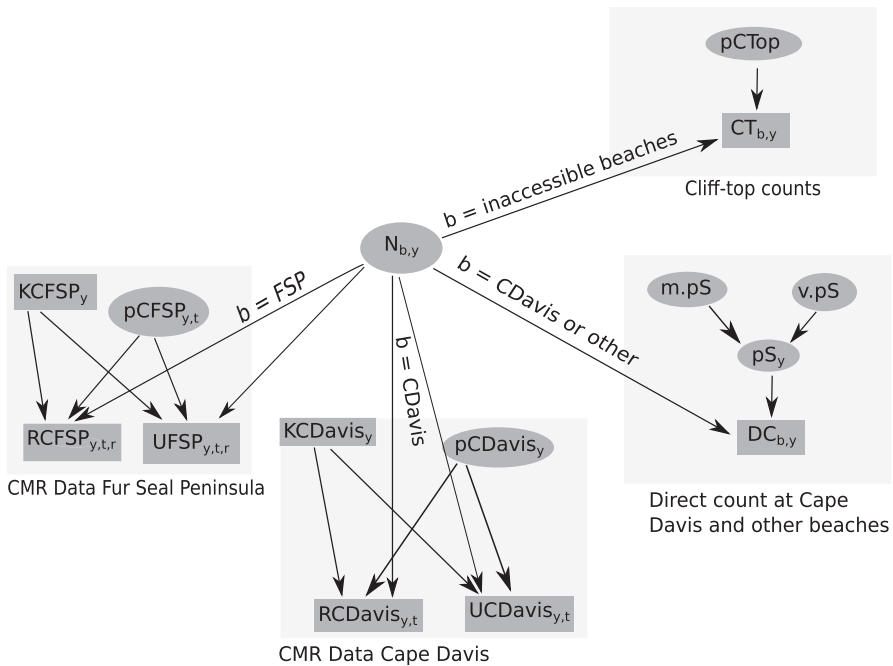
*CMR study to estimate detection probability: Cape Davis (1995, 2007–2015)*—To estimate detection probability during direct counts, pup numbers at Cape Davis Beach (Fig. 1) were estimated annually by both direct counting and CMR. Logistical constraints prevented us from estimating detection probability at multiple beaches, but Cape Davis is topographically representative of an assortment of beaches at the island with large boulders, backed by a vegetated area. In each year, between 150 and 200 pups were caught by hand and marked as described above. Pups were allowed to reintegrate into the rookery for one full day before “recaptures” started (as above) along 7–9 transects covering the entire beach and backing vegetated area. Each transect was counted three times over two consecutive days. In addition to CMR counts, pups at Cape Davis were counted directly. Detection probability was estimated by comparing the CMR estimate and number of pups directly counted (refer to hierarchical Bayesian model methods sections below for a comprehensive explanation). No CMR study was done at Cape Davis in 2004. However, the same observer counted pups in 1995 and 2004, thus the detection probability estimated from the 1995 CMR study was used as a proxy for that in 2004 (Hofmeyr *et al.* 2006).

*Estimating detection probability of cliff-top counts (2004, 2013)*—Several beaches along Marion Island’s coastline are backed by high cliff-faces, making them inaccessible. During total island counts in 2004 and 2013, pups at these beaches were carefully counted with binoculars from a clear vantage point at the top of the backing cliff. To account for a lower detection probability at beaches only counted from the cliff-top compared to direct counts, a unique cliff-top detection probability was also obtained at three of the Cape Davis Sealers’ Beaches (including Cape Davis Beach and two neighboring beaches). These cliff-lined beaches are also accessible on foot, and were first counted with binoculars from the top of the cliff and thereafter directly while walking across the beach. This was repeated three times for each of the beaches. The difference between direct and cliff-top counts was subsequently used to determine detection probability from cliff-tops (refer to hierarchical Bayesian model methods sections below for a comprehensive explanation).

*Data Analysis: Hierarchical Bayesian Model*

A hierarchical Bayesian model was used to analyze the complete data set, *i.e.*, CMR data from Cape Davis (1995, 2007–2015) and Fur Seal Peninsula (2004, 2013), as well as direct and cliff-top counts at different beaches (2004, 2007–2015). The integrated model is described in the subsections below. Each section presents a specific part of the full hierarchical Bayesian model, which might be thought as an aggregation of different submodels (see Parent and Rivot 2013). The direct acyclic graph in Figure 2 provides a graphical representation of the full hierarchical Bayesian model.

*Annual count model*—Following a standard closed population CMR model (King *et al.* 2010) the CMR data collected at Cape Davis Beach were used to estimate both



*Figure 2.* Direct acyclic graph of the hierarchical Bayesian model used to estimate the Subantarctic fur seal pup population. Ovals denote stochastic quantities (*i.e.*, parameters that are estimated); squares denote known quantities (*i.e.*, counts made). The Fur Seal Peninsula (FSP) specific capture-mark-recapture (CMR) model is presented by parameters  $KCFSP_y$  (total number of pups marked),  $RCFSP_{y,t,r}$  (number of pups recounted),  $UFSP_{y,t,r}$  (number of untagged pups counted) and  $pCFSP_{y,t}$  (estimated detection probability); where  $y = \text{year}$ ,  $t = \text{transect}$ , and  $r = \text{replicate}$ . The CMR submodel for Cape Davis (CDavis) is presented by  $KCDavis_y$  (total number of pups marked),  $RCDavis_{y,t}$  (number of marked pups recounted),  $UCDavis_{y,t}$  (number of unmarked pups counted) and  $pCDavis_y$  (estimated detection probability) where  $y = \text{year}$  and  $t = \text{transect}$ . The cliff-top count specific model is given by  $CT_{b,y}$  (cliff-top direct count and beach  $b$  in year  $y$ ) and  $pCTop$  (estimated probability of detecting a pup on beaches only counted from a cliff-top). The annual and direct count specific model is presented by  $DC_{b,y}$  (number of pups counted directly on beach  $b$  in year  $y$ ),  $pSy$  (the overall probability of detecting a pup in year  $y$ ),  $m \cdot pS$  and  $v \cdot pS$  (the mean and variance of  $pS$  respectively). All these submodels are combined to estimate  $N_{b,y}$  (the estimated number of pups on beach  $b$  in year  $y$ ).

the "true" number of pups at Cape Davis for a given year  $y$  ( $N_{CDavis,y}$ ) and the probability of detection ( $p_{CDavis,y}$ ). In a closed population CMR model for a given year  $y$ , all pups are assumed to have the same probability of capture and behave independently. Therefore, given  $K_{CDavis,y}$  (the number of marked pups in year  $y$ ), the number of recaptured pups ( $R_{CDavis,y}$ ), and the number of unmarked pups ( $U_{CDavis,y}$ ) are assumed to follow a binomial distribution. As Cape Davis main beach is topographically relatively homogeneous, each transect was considered as an independent realization of the same model. The full specification for year  $y$  and transect  $t$  is:

$$R_{CDavis,yt} \sim \text{Bin}(K_{CDavis,y}, p_{CDavis,y}), y = 2004, 2007, \dots, 2015, t = 1, \dots, 10$$

$$U_{CDavis,yt} \sim \text{Bin}(N_{CDavis,y} - K_{CDavis,y}, p_{CDavis,y})$$

To estimate the probability of detecting a pup ( $p_{S,y}$ ), the above mentioned Cape Davis CMR model was combined with the direct count data at Cape Davis (hereafter referred to as the "direct count model"). Under this model, for year  $y$ , and repeat direct count of Cape Davis  $r$ , the direct counts of Cape Davis are assumed to follow a binomial distribution with parameters  $N_{CDavis,y}$  (estimated by the previous model) and  $p_{S,y}$ . To estimate the variation in capture probability between years, parameter  $p_{S,y}$  was treated as a random effect within a hierarchical model to borrow strength from other years (as classically done in spatial analysis; Waller and Carlin 2010). Therefore  $\text{logit}(p_{S,y})$  is assumed to follow a normal distribution with mean  $m \cdot p_S$  and variance  $v \cdot p_S$ .

*Fur Seal Peninsula specific model*—Fur Seal Peninsula CMR data were also analyzed with a standard closed population CMR model (King *et al.* 2010). In contrast to Cape Davis, Fur Seal Peninsula is a large heterogeneous beach. This potential heterogeneity in capture probability is accounted for by means of transect dependent probability of capture  $p_{CFSP,yt}$ , where  $y$  = year and  $t$  = transect. This fine-scale modeling is possible due to repeat counts for each transect, where  $r$  = replicate. Given  $K_{CFSP,y}$  (the number of marked pups in year  $y$ ), the number of recaptured pups in ( $R_{CFSP,ytr}$ ) and the number of unmarked pups ( $U_{FSP,ytr}$ ), the CMR model for Fur Seal Peninsula for year  $y$ , transect  $t$  and replicate  $r$  is therefore:

$$R_{CFSP,ytr} \sim \text{Bin}(K_{CFSP,y}, p_{CFSP,yt}), y = 2004, 2013, t = 1, \dots, 15, r = 1, \dots, 3$$

$$U_{FSP,ytr} \sim \text{Bin}(N_{FSP,y} - K_{CFSP,y}, p_{CFSP,yt})$$

*Direct count specific model*—To determine the "true" number of pups on the beaches that were only counted directly we used the probability of detecting a pup ( $p_{S,y}$ ) in year  $y$ , determined by the Cape Davis CMR study, to correct for observer undercount on each beach. The direct count data from beach  $b$  in year  $y$  is combined with parameter  $p_{S,y}$  and modeled by

$$DC_{by} \sim \text{Bin}(N_{by}, p_{S,y}), y = 2004, 2007, \dots, 2015, b = 1, \dots, 76$$

*Cliff-top count specific model*—To estimate the probability of detecting a pup on beaches only counted from a cliff-top ( $p_{CTop}$ ), the data from Cape Davis Sealers' Beaches with cliff-top and direct counts were used in a binomial model that assumed pups behave independently and share the same probability of detection. Detection probability ( $p_{CTop}$ ) was estimated using (1) the cliff-top counts at Cape Davis Sealers' Beaches  $CT_{yb}$ , for year  $y$  and beach  $b$ , and (2)  $N_{yb}$ , the estimated "true" number of pups

on the beach  $b$  in year  $y$ . Parameter  $N_{yb}$ , was estimated using the direct count data from Cape Davis Sealers' Beaches and the probability of detection,  $p_{\mathcal{S}y}$ , determined by the "direct count model" above. Initial fitting of the model indicated that cliff-top counts made in 2004 were too few to enable  $pCTop$  to be estimated separately for each year. Consequently, for the sake of parsimony, a single estimate of  $pCTop$  was calculated by combining cliff-top counts made in both 2004 and 2013.

In a Bayesian framework the full model requires the prior distribution of the parameters to be specified. The prior distributions of  $p_{CDavis}$ ,  $p_{CFSP}$ , and  $pCTop$  were specified as a uniform distribution between 0 and 1. The parameters that dictate the normal distribution on the random effects,  $\logit(p_{\mathcal{S}})$  and  $m \cdot p_{\mathcal{S}}$ , were assumed to be drawn from an uninformative normal distribution with mean 0 and variance 1,000. The variance  $v \cdot p_{\mathcal{S}}$  was assumed to be drawn from an inverse gamma distribution with shape and scale parameters equal to 0.01. The model was fit using JAGS 3.4.0 (<http://mcmc-jags.sourceforge.net/>) through R (R Core Team 2014) using the *rjags* package (Plummer 2015). Convergence of the Markov Chain Monte Carlo (MCMC) approach was checked visually and by using Gelman-Rubin statistics (Gelman and Rubin 1992). A single Markov chain of length 100,000 iterations with a burn-in of 1,000 iterations and a thinning parameter of 200 gave 500 samples of the joint posterior distribution. The model code is provided in Appendix S1.

#### *Triennial Antarctic Fur Seal Pup Counts and Estimation of Rate of Population Change*

Following the last published AFS total island pup count in 2004 (Hofmeyr *et al.* 2006), total island pup counts of AFS were done in 2007, 2010, and 2013. The last counts (2010 and 2013) were made by the same observer (MW). Counts were made from the middle to the end of January. AFS prefer to breed on open pebble beaches, backed by flat vegetated areas (Kerley 1984), and because of this, it is assumed that few pups are missed by observers obviating undercount corrections for this species (Hofmeyr *et al.* 2006). As for the SAFS direct counts, a single observer walked through beaches systematically counting pups. Observers separated SAFS and AFS pups based on descriptions in Bester and Wilkinson (1989).

Using the pup numbers, the intrinsic rate of population change ( $r$ ) was calculated using the exponential function

$$N_t = N_0 e^{rt}$$

where  $N_t$  = pup population estimate at time  $t$ ,  $N_0$  = previous pup population estimate,  $e$  = the base of natural logarithms,  $r$  = the intrinsic rate of pup population change and  $t$  = the time elapsed between the two counts (Caughley 1977). The intrinsic rate of pup population change was converted to a mean annual percentage change ( $\lambda$ ) (Caughley 1977) using

$$\lambda = (e^r - 1) \times 100.$$

#### *Pup Mortality*

Dead and live pups of both species were counted during the 2013 total island count. The incidence of pup mortality for each beach was calculated by dividing the number of dead pups by the total number of pups found on the beach (*i.e.*, live + dead



pups; Hofmeyr *et al.* 2007) and expressed as a percentage. Pup mortality at Fur Seal Peninsula was calculated by summing the total number of dead pups counted in all transects and dividing it by the sum of the dead pups and the average number of live pups counted (marked and unmarked) during the transect-counting. When it was not possible to identify a dead pup as SAFS or AFS, it was classed into the more abundant breeding species of the specific beach. SAFS and AFS have differential preferences for breeding substrate and are generally well segregated on Marion Island. Thus, confusion between species was unlikely.

## RESULTS

Between 2004 and 2013 the total island pup estimates of Subantarctic fur seals declined from 15,260 (95% credible interval CI: 14,447–16,169) to 8,312 (CI: 7,983–8,697), which corresponds to a 46% decline (CI: 43%–48%; Fig. 3, Table 1). Fur Seal Peninsula estimates decreased by 60.8% (CI: 56%–66%; Fig. 4, Table 1). Between 2004 and 2015 Cape Davis declined by 60% (CI: 59%–62%; Fig. 5) and the beaches where pups were counted annually, excluding Cape Davis, were reduced by 58% (CI: 57%–59%; between 2004 and 2015 (Fig. 6). These values were calculated using the posterior means of [(the number of pups in 2004) – (number of pups in 2013)/number of pups in 2004]. The declines at Cape Davis and the other beaches that were counted annually were rapid between 2004 and 2010; thereafter pup numbers remained stable (Fig. 5, 6; Table 1). Cape Davis is considered a medium-density beach whereas the other beaches counted annually are smaller, low-density beaches. We calculated pup numbers and percentage change separately for these to see if

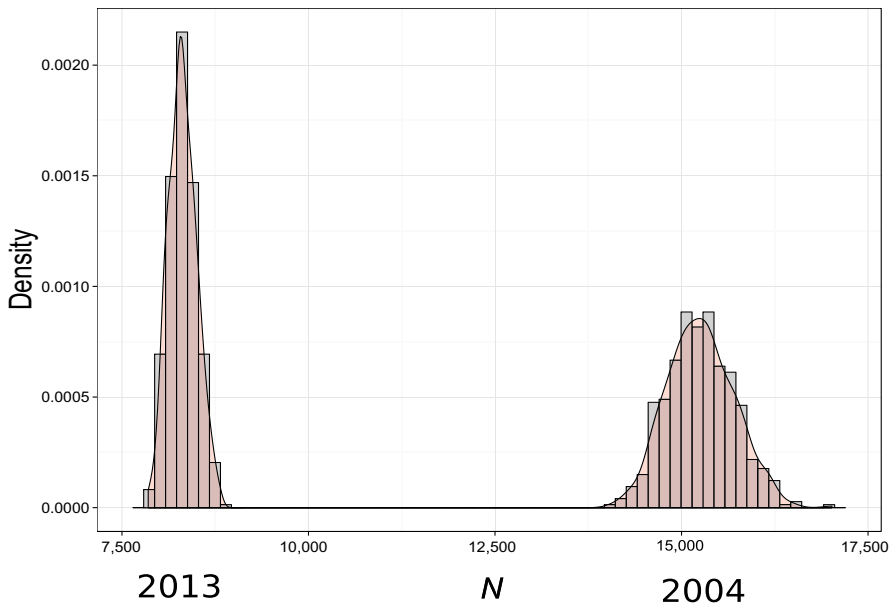


Figure 3. Posterior distribution of the total number of Subantarctic fur seal pups ( $N$ ) estimated on Marion Island during 2004 (right) and 2013 (left).

rookery density had an effect on pup decline; however, the rate of decline is similar to that of Cape Davis. There were clear dissimilarities in how pup numbers changed between the different stretches of coastline. By far the largest reduction was observed on the west coast, followed by the north coast. The northeast and east coast minimally had fewer pups recorded in 2013 compared to 2004 and no change in pup numbers was detected along the south coast (Fig. 7, Table 1).

The probability of seeing a pup during direct counts ( $pS$ ) was much lower during 1995 ( $pS_{1995}$  was used for 2004 too) than for any of the other years (Fig. 8, Table 1). The larger errors estimated for  $pS_{2007}$ ,  $pS_{2008}$ , and  $pS_{2010}$  are likely because in 2007, 2008, and 2010 CMR transects were only done once, not three times like other years. In 2008, 2011, and 2012, pups were counted by the same observer (WCO) and a second observer in 2010 and 2013 (MW). Despite this, the hierarchical Bayesian model showed that irrespective of whether or not the same observer counted, the probability of observing a pup still varies among years (Fig. 8, Table 1) as evidenced by the skewed distribution of the variance of  $pS$  (Fig. 9B, Table 1).

The AFS pup counts and, hence, estimated population growth rate remained positive (Table 2) although it slowed over the last 9 yr (Fig. 10), largely due to diminishing increase in pup numbers at Watertunnel Beach (where the majority of pups were born: 77.1%–81.7%) and Landfall Beach. At the remaining rookeries pup numbers fluctuated, either increasing or decreasing (Table 2) and several new, small rookeries (1–7 pups) were established around Marion Island.

Pup mortality of SAFS at Fur Seal Peninsula was estimated at 6.4% during 2013. Table 3 presents the uncorrected incidence of pup mortality of SAFS pups in relation to the density on the beaches. Dead AFS pups were only found at four of the main

Table 1. Posterior summary statistics calculated by means of Markov chain Monte Carlo for each of the parameter values used in the hierarchical Bayesian model used to estimate Subantarctic fur seal (*Arctocephalus tropicalis*) pup numbers at Marion Island.

Parameter	Mean	Median	95% Credible interval	
			Lower	Upper
$pS_{1995}^a$	0.48	0.47	0.45	0.51
$pS_{2007}$	0.69	0.7	0.58	0.8
$pS_{2008}$	0.83	0.83	0.77	0.89
$pS_{2009}$	0.91	0.91	0.87	0.94
$pS_{2010}$	0.84	0.85	0.77	0.90
$pS_{2011}$	0.87	0.87	0.84	0.90
$pS_{2012}$	0.91	0.91	0.88	0.93
$pS_{2013}$	0.81	0.82	0.77	0.86
$pS_{2014}$	0.77	0.77	0.73	0.81
$pS_{2015}$	0.79	0.79	0.76	0.82
$m \cdot pS$	1.46	1.46	0.96	1.97
$v \cdot pS$	0.71	0.58	0.27	1.83
$p \cdot Top$	0.53	0.53	0.50	0.56
NFSPen2004	5,385	5,376	4,768.0	6,112.2
NFSPen2013	2,109	2,104	1,988.5	2,242.5
N2004	15,260	15,243	14,447	16,169
N2013	8,312	8,303	7,983	8,697

<sup>a</sup>Was also used to correct for undercount of 2004 data.

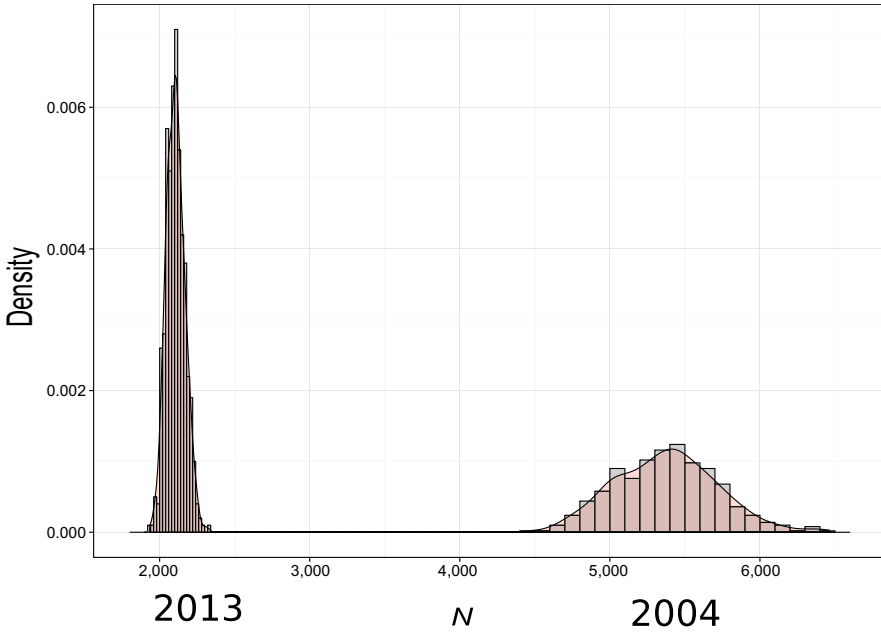


Figure 4. Posterior distribution of the capture-mark-recapture model for the number of Subantarctic fur seal pups ( $N$ ) estimated at Fur Seal Peninsula, Marion Island during 2004 (right) and 2013 (left).

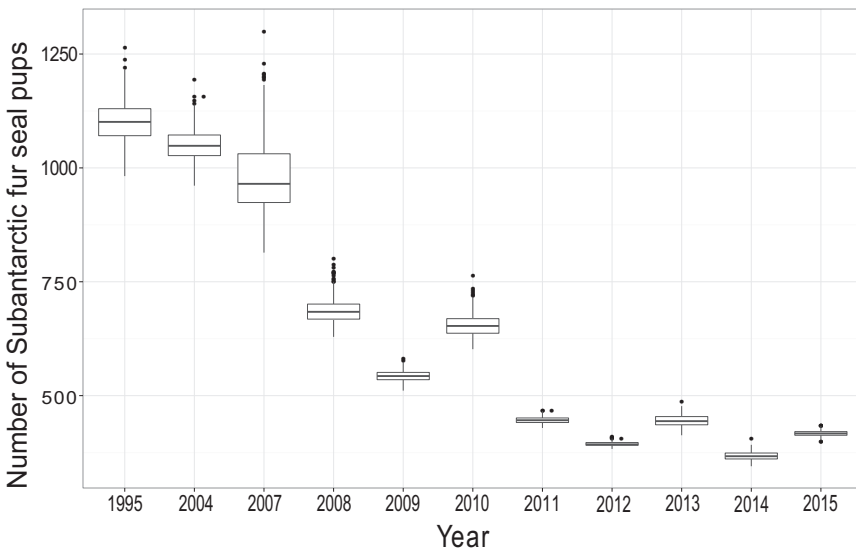


Figure 5. Posterior distribution of the total number of Subantarctic fur seal pups estimated at Cape Davis main beach, Marion Island, in 1995, 2004, and 2007–2015.

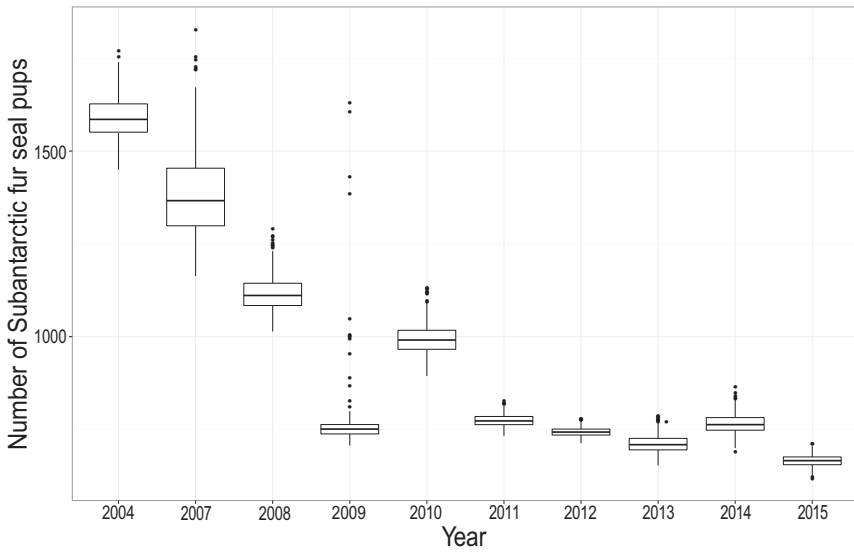


Figure 6. Posterior distribution of the total number of Subantarctic fur seal pups estimated, and summed, at the remainder of the annual count beaches on Marion Island in 2004 and 2007–2015.

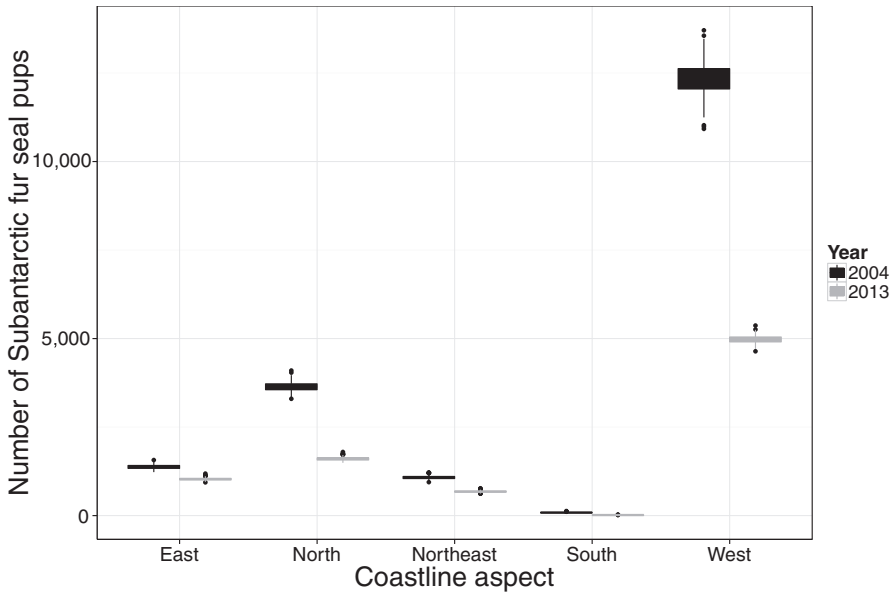


Figure 7. Differences in the number of Subantarctic fur seal pups estimated between 2004 and 2013 divided into the different stretches of coastline around Marion Island.

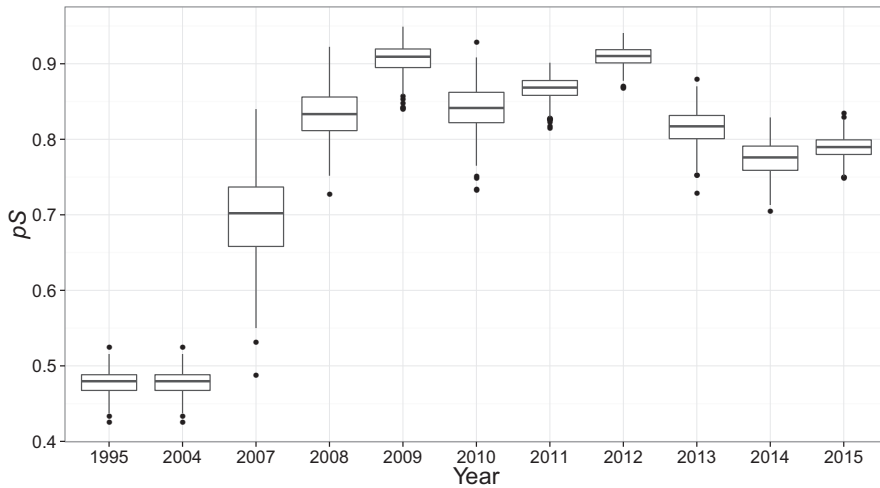


Figure 8. Posterior distribution of the annual variation in the probability to observe a Subantarctic fur seal pup ( $pS$ ) in 1995, 2004, and 2007–2015.

beaches and mortality rates were 1.67% at Kildalkey Bay, 3.03% at Landfall and Trypot beaches, and 3.72% at Watertunnel Beach.

## DISCUSSION

Over the past decade population growth based on pup counts changed considerably for both *Arctocephalus* spp. at Marion Island, where the largest sympatric populations of SAFS and AFS occur. The number of SAFS pups estimated decreased by 46% over the last decade, whereas AFS are still increasing but at a reduced annual rate (4% in 2010–2013 *vs.* 17% in 1995–2004). It is unusual to observe two different population trajectories from the same locality for such closely related species (*e.g.*, Croxall *et al.* 2002, Forcada *et al.* 2006).

The 2013 total population estimate of SAFS pups (8,312; 95% CI: 7,983–8,697) is equivalent to that of 1989 when the population was still increasing exponentially (8,684 pups; Wilkinson and Bester 1990). The 46% decrease in the pup population between 2004 and 2013 is not a symptom of a singular, anomalous year; it is due to a real decline evidenced by continuous annual decrease in pup numbers (2007–2015) at Cape Davis and several smaller beaches on the north coast. It is unclear why the SAFS pup population is declining. The annual percentage reduction in pup numbers at Cape Davis (medium density rookery) is no different from that at smaller, low density rookeries. All these beaches are situated on the north and northeast coast of Marion Island. The greatest reduction in pup numbers occurred on beaches on the west coast, followed by those on the north coast, where the highest density rookeries are situated. Superficially, it appears that coastline orientation may be a strong indicator of pup number reduction, however, the interaction between coastline orientation and rookery density still needs to be explored further.

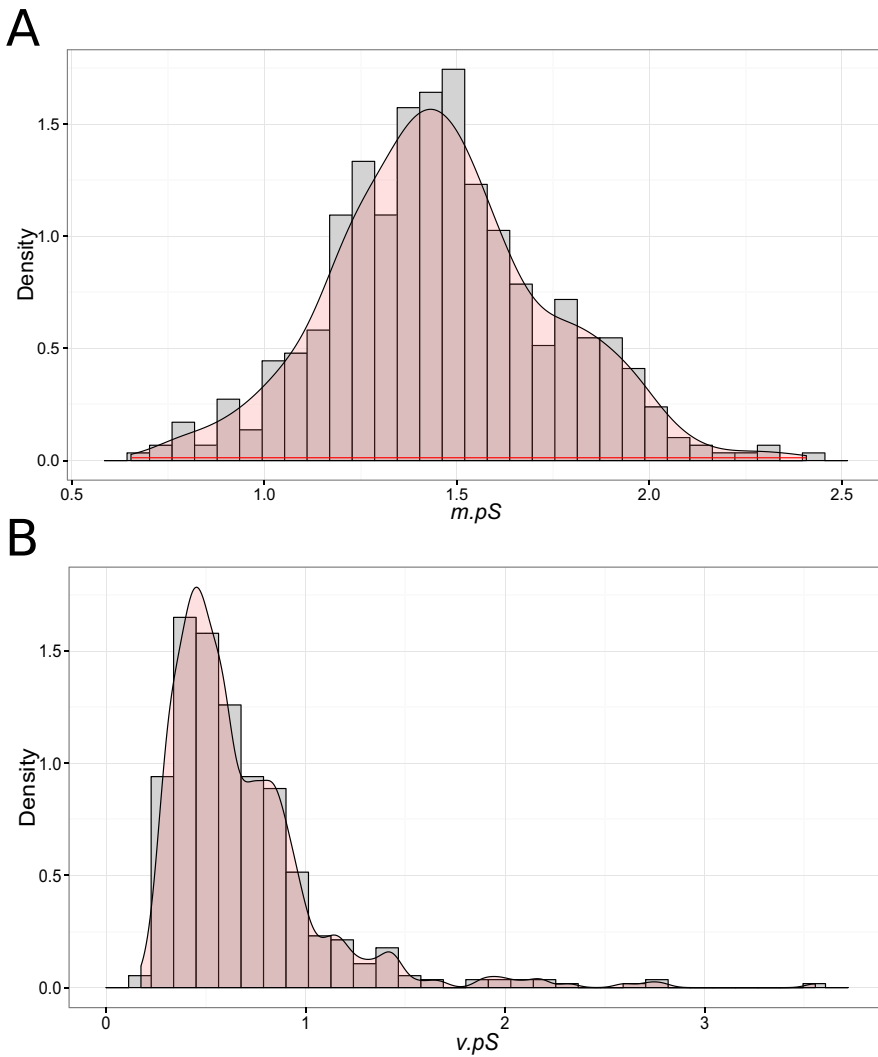


Figure 9. Posterior distribution of model parameters (A) the mean of direct count sighting probability ( $m.pS$ ); (B) The variance of direct count sighting probability ( $v.pS$ ).

Density dependence in pup mortality and consequently pup numbers is a well-established phenomenon (Doidge *et al.* 1984, Harcourt 1992, Reid and Forcada 2005). This is mostly related to a lack of breeding space, fatal injuries caused by territorial males and adult females, as well as failure of females to bond with pups after birth, resulting in starvation (Doidge *et al.* 1984, Reid and Forcada 2005). However, no drastic changes in pup mortality were observed at Marion Island from 2004 to 2013 (2013 mortality range 2.03%–8.34%, *vs.* 2004 range 0.8%–10%, Hofmeyr *et al.* 2007). Mortality estimates are generally negatively biased and these values only represent the lowest possible mortality rates because several carcasses would have been

Table 2. The number of live Antarctic fur seal pups (*Arctocephalus gazella*) counted at each of the four highest density rookeries on Marion Island and the remainder of the island for each of the total island censuses done from 1975 to 2013. Values in parentheses represent the mean annual percentage pup population change for that beach in relation to the previous count. Where multiple counts of a beach were done, mean  $\pm$  standard deviation is presented.

	1975	1982	1989	1995	2000	2001	2004	2007	2010	2013
Waterunnel Beach				211			615 $\pm$ 5	903 $\pm$ 9 (13.7%)	1,108 $\pm$ 26 (7.1%)	1,198 $\pm$ 58 (2.6%)
Landfall Beach				3			69	127 (22.6%)	174 $\pm$ 0.6 (11.1%)	192 $\pm$ 6 (3.3%)
Trypot Beach							21	26 (7.4%)	51 (25.2%)	64 (7.9%)
Kildalkey Bay							12	26 (29.4%)	29 (3.7%)	59 (26.7%)
Rest of the Island				19			27	23 (-5.2%)	17 (-9.6%)	40 (33.0%)
Total	15 <sup>a</sup>	43 <sup>a</sup>	91 <sup>a</sup>	233	343 <sup>a</sup>	464 <sup>a</sup>	744	1,105	1,379	1,553

<sup>a</sup>It was not specified in the literature at which beach on Marion Island these pups were counted and thus only the total values are presented.

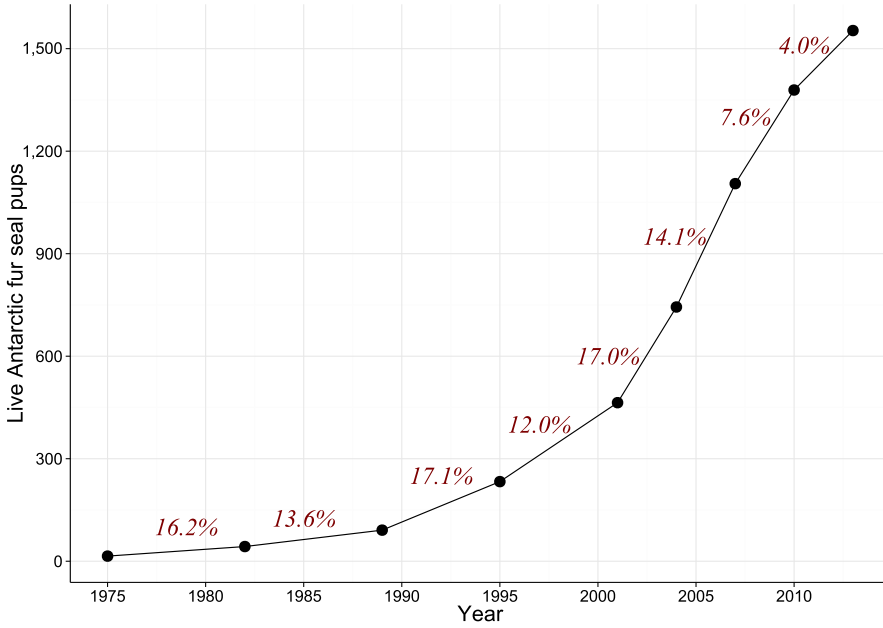


Figure 10. Estimates of Antarctic fur seal pups on Marion Island from 1975–2013. Italicized numbers are the mean annual percentage change between the respective censuses.

Table 3. Incidence of minimum pup mortality of Subantarctic fur seal pups (*Arctocephalus tropicalis*) in relation to rookery size at Marion Island in 2013.

Rookery size	N <sup>a</sup>	Average ± SD mortality %
0–100 pups	133	3.09 ± 15.18
101–200 pups	9	2.05 ± 1.52
201–300 pups	2	2.03 ± 2.88
301–500 pups	3	4.27 ± 3.48
501+ pups	2	8.34 ± 2.77
Total	149	3.11 ± 14.35

<sup>a</sup>N = Number of rookeries.

washed away by high seas, fallen into gaps between boulders or destroyed by scavenging Giant Petrels (*Macronetes* spp.; de Bruyn *et al.* 2007) or trampled by other seals (Kerley 1987, Hofmeyr *et al.* 2007). Although it is difficult to quantify pup mortality accurately, especially early in the pupping season, the timing of our counts is consistent with that of Hofmeyr *et al.* (2006). This minimizes any bias in the comparison of mortality estimates between these specific counts.

Adult female fur seals do not breed annually. In AFS, from 40%–50% of pregnancy failures were related to previous year pregnancy and a female’s survival was also negatively influenced by her pregnancy rate (Boyd *et al.* 1995). However, if the precipitous decline in SAFS pups at Marion Island was only related to annual variations in adult female pregnancy rates, it would have fluctuated from year to year and not



shown a consistent decline over several years. As the Marion Island population of SAFS recovered, it is also expected that the average age of females in the population increased. Senescence of the population could influence population growth. For instance, adult female AFS pregnancy rate peaked at 8 yr and declined thereafter (Boyd *et al.* 1995). On the other hand, if the population of SAFS females on Marion Island aged to such an extent that it would influence the population pregnancy rate, we would have also observed a change in breeding phenology (*e.g.*, Gibbens and Arnould 2009). However, over the last two decades breeding phenology (*i.e.*, median pupping date) of both species at Marion Island has remained stable (Hofmeyr *et al.* 2007; MRI, unpublished data).

In 2006 a mass die-off of adult male SAFS (250–300 individuals) occurred at Fur Seal Peninsula and around the rest of the island (~50 individuals) (de Bruyn *et al.* 2008). SAFS are highly polygynous and there is generally a surplus of sexually mature males. Therefore, changes in the number of adult males available to breed would have had little impact on population dynamics of the species (Gentry and Kooyman 1986).

Sudden population decreases can also occur when density-dependent controls are reinforced by stochastic environmental events (Barbraud and Weimerskirch 2003). However, neither weak El Niño events nor sea-surface temperature anomalies that occurred over the last 10 yr affected the pup-attendance patterns of lactating SAFS (Wege 2013). To assess whether environmental fluctuations modulated by density-dependent factors have influenced the SAFS population growth at Marion Island, we need to understand the mechanisms that influence foraging behavior and how that affects reproductive success and survival.

Furthermore, no significant changes in lactating SAFS female attendance patterns (foraging trip and on-shore attendance bout duration) were observed over the last two and a half decades (Bester and Bartlett 1990, Kirkman *et al.* 2002, Wege *et al.* 2015). SAFS pup weaning mass is also higher at Marion Island (Kirkman *et al.* 2002, Oosthuizen *et al.* 2015) than at Gough Island where seals occur at very high densities (Bester and van Jaarsveld 1994, 1997).

Neighboring Prince Edward Island is considered to be in the maturity phase of population growth of SAFS with a slight reduction of -0.3% in pup production recorded in the 2009 breeding season (Bester *et al.* 2009). Emigration from Marion Island to Prince Edward Island (19 km northeast of Marion Island) is unlikely (see Bester 1989) and probably not the cause for the reduced pup production at Marion Island. Although both islands are frequented by a population of killer whales (*Orcinus orca*; Pistorius *et al.* 2012), top down control by this predator is unlikely to be the primary driver of the SAFS pup production decline (Reisinger *et al.* 2011).

The probability of seeing a pup during direct counts ( $pS$ ) was lowest in 1995 (same  $pS$  used in 2004) and is likely related to the higher number of pups to count on the beach—more pups present in the same sized area are more difficult to count as pups tend to scatter as an observer approaches. Annual variation in  $pS$  was likely also influenced by prevailing weather conditions during the CMR experiment. Pups tend to hide under large boulders when it is warmer and are therefore more difficult to count. During stormy rainy days, pups swim more, and extreme Southern Ocean storms can make counting difficult (see Hofmeyr *et al.* 2006 for a detailed discussion).

Detection of pups on beaches is imperfect and our methods involve several caveats, such as the influence of daily weather fluctuations on pup behavior (Hofmeyr *et al.* 2006). However, reanalyzing previously published and new data by combining the various types of pup counts (*i.e.*, direct count, CMR and cliff-top undercount

estimation) under a hierarchical Bayesian framework made pup number estimates comparable and also accounted for several of these caveats in an unbiased manner. Although counting pups only provides a minimum estimate of the population size and does not account for females that do not breed every year, we showed a definite decline in pup production over 12 yr (2004–2015). As SAFS females reach sexual maturity at 4–6 yr with a decline in the pregnancy rate from age 12 (Bester 1995), fewer pups born over so many years would have influenced the number of new individuals recruited to the breeding population by this stage (this study).

Although the AFS population is still increasing, the annual rate of increase has slowed considerably (4% in 2010–2013) from the previous estimate (17% in 1995 and 2004). Watertunnel Beach represents 77%–81% (2007–2013) of the total AFS population on Marion Island, and the slowed growth may simply indicate that this beach is reaching saturation. This is potentially similar to what happened with the SAFS population between 1989 and 2004: high density rookeries reached a saturation point (1989–1995) which resulted in a slowed overall annual population growth (Hofmeyr *et al.* 1997) and new rookeries were established around the remainder of the island during 1995–2004 (Hofmeyr *et al.* 2006). These newly formed rookeries took some time to develop beyond the establishment phase and enter a rapid growth phase. Currently, the same may be true for the AFS population at Marion Island. The AFS pup numbers for the remainder of the island (outside the main, established breeding rookeries) fluctuated between the three triennial counts, which possibly indicated the establishment of new rookeries. It is unlikely that this slowed growth and the decrease in SAFS population is a result of interspecific competition for breeding space. SAFS prefer to breed on boulder/jumbled rocky beaches (Bester 1982), whereas AFS prefer small-pebble beaches backed by vegetated slopes (Kerley 1984).

An alternative interpretation is that the direct count at Watertunnel Beach is no longer effective at determining rookery size. Pups were counted ~1.5 mo after the median pupping date when older pups were spending time in the inshore shallows and hence were difficult to count. A larger pup cohort can result in larger inherent error and potential underestimation of pup numbers. Consequently, our confidence in the accuracy of AFS counts at Watertunnel Beach decreased recently. Future counts will take imperfect detection into account, especially considering the timing of the counts late in the season. Such change in techniques would indicate whether the slowed growth of AFS pup production is an artifact of counting methods or saturation at the main rookery on Watertunnel Beach.

### Conclusion

Over the past decade population growth has changed considerably for both *Arctocephalus* spp. on Marion Island. It is unclear why SAFS pup production is declining and AFS population growth rate is decreasing. As central-place foragers, lactating females of both species forage within the vicinity of the island (de Bruyn *et al.* 2009, Arthur *et al.* 2015). Although the diets of the two species overlap to a certain degree (Makhado *et al.* 2008, 2013), it is largely unknown to what extent their core foraging areas overlap (in time and space, including foraging depth distribution) and how their other population life-history traits (such as survival and breeding success) compare. Pronounced population changes of long-lived large vertebrates are cause for concern because they could be indicative of large-scale changes in ecosystem structure and functioning (Barbraud and Weimerskirch 2003). However, it is difficult to pinpoint mechanisms behind changing population trends, mainly because population

fluctuations are often the result of a complex interplay among several factors (e.g., Boyd *et al.* 2006, Trites *et al.* 2007).

The global population status of SAFS and AFS differ; some populations are increasing while others are stable or decreasing (SCAR EGS 2008, Bester *et al.* 2009, Forcada and Hoffman 2014). Both species experienced a rapid rate of increase for more than 50 yr throughout the Southern Ocean. It is likely that in the larger metapopulation of the Southern Ocean some areas are reaching saturation while new colonies are still being established elsewhere. The recent changes on Marion Island could be resultant fluctuations of historically perturbed species. For example, some AFS populations are declining in part of their distribution range (Forcada and Hoffman 2014), but not elsewhere. Fur seals are able to travel extensive distances (e.g., Bester and Reisinger 2010, Bester *et al.* 2014) and settle at new rookeries (Wynen *et al.* 2000). We therefore require a holistic picture of top-predator population dynamics throughout the Southern Ocean to understand the larger metapopulation dynamics and the effects of environmental perturbations.

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#### LITERATURE CITED

- Arthur, B., M. Hindell, M. N. Bester, *et al.* 2015. Return customers: Foraging site fidelity and the effect of environmental variability in wide-ranging Antarctic fur seals. *PLOS ONE* 10:e0120888.
- Barbraud, C., and H. Weimerskirch. 2003. Climate and density shape population dynamics of a marine top predator. *Proceedings of the Royal Society of London, B* 270:2111–2116.
- Bester, M. N. 1980. Population increase in the Amsterdam Island fur seal *Arctocephalus tropicalis* at Gough Island. *South African Journal of Zoology* 15:229–234.
- Bester, M. N. 1982. Distribution, habitat selection and colony types of the Amsterdam Island fur seal *Arctocephalus tropicalis* at Gough Island. *Journal of Zoology, London* 196:217–231.
- 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. 1995. Reproduction in the female subantarctic fur seal *Arctocephalus tropicalis*. *Marine Mammal Science* 11:362–375.
- Bester, M. N., and P. A. Bartlett. 1990. Attendance behaviour of Antarctic and subantarctic fur seal females at Marion Island. *Antarctic Science* 2:309–312.

- Bester, M. N., and R. R. Reisinger. 2010. Vagrant Antarctic fur seals at Gough Island in 2009. *Polar Biology* 33:709–711.
- Bester, M. N., and A. S. van Jaarsveld. 1994. Sex-specific and latitudinal variance in postnatal growth of the Subantarctic fur seal (*Arctocephalus tropicalis*). *Canadian Journal of Zoology* 72:1126–1133.
- Bester, M. N., and A. S. van Jaarsveld. 1997. Growth in Subantarctic fur seal pups as a possible indicator of offshore food availability. Pages 88–91 in M. Hindell and C. S. Kemper, eds. *Marine mammal research in the Southern Hemisphere*. Volume 1. Surrey Beatty and Sons, Chipping Norton, U.K.
- Bester, M. N., and I. S. Wilkinson. 1989. Field identification of Antarctic and Subantarctic fur seal pups. *South African Journal of Wildlife Research* 19:140–144.
- Bester, M. N., P. G. Ryan and B. M. Dyer. 2003. Population numbers of fur seals at Prince Edward Island, Southern Ocean. *South African Journal of Marine Science* 25:549–554.
- Bester, M. N., P. G. Ryan and J. Visagie. 2009. Summer survey of fur seals at Prince Edward Island, southern Indian Ocean. *African Journal of Marine Science* 31:451–455.
- Bester, M. N., P. G. Ryan, W. A. Bester and T. Glass. 2014. Vagrant Antarctic fur seals at the Tristan da Cunha Islands. *Polar Biology* 37:1701–1703.
- Bonner, W. N. 1968. The fur seal of South Georgia. *British Antarctic Survey Scientific Report*, No. 56. 81 pp.
- Bonner, W. N., and R. M. Laws. 1964. Seals and sealing. Pages 163–190 in R. Priestley, R. J. Adie and G. D. Q. Robin, eds. *Antarctic research*. Butterworths, London, U.K.
- Boyd, I. L. 1993. Pup production and distribution of breeding Antarctic fur seals (*Arctocephalus gazella*) at South Georgia. *Antarctic Science* 5:17–24.
- Boyd, I. L., J. P. Croxall, N. J. Lunn and K. Reid. 1995. Population demography of Antarctic fur seals: The costs of reproduction and implications for life-histories. *Journal of Animal Ecology* 64:505–518.
- Boyd, I., S. Wanless and C. J. Camphuysen. 2006. *Top predators in marine ecosystems: Their role in monitoring and management*. Cambridge University Press, Cambridge, U.K..
- Caughley, G. 1977. *Analysis of vertebrate populations*. Wiley, New York, NY.
- Chapman, D. G., and A. M. Johnson. 1968. Estimation of fur seal pup populations by randomized sampling. *Transactions of the American Fisheries Society* 97:264–270.
- Condy, P. R. 1978. Distribution, abundance, and annual cycle of fur seals (*Arctocephalus* spp.) on the Prince Edward Islands. *South African Journal of Wildlife Research* 8:159–168.
- Croxall, J. P., P. N. Trathan and E. J. Murphy. 2002. Environmental change and antarctic seabird populations. *Science* 297:1510–1514.
- de Bruyn, P. J. N., J. Cooper, M. N. Bester and C. A. Tosh. 2007. The importance of land-based prey for sympatrically breeding giant petrels at sub-Antarctic Marion Island. *Antarctic Science* 19:25–30.
- de Bruyn, P. J. N., A. D. S. Bastos, C. Eadie, C. A. Tosh and M. N. Bester. 2008. Mass mortality of adult male Subantarctic fur seals: Are alien mice the culprits? *PLOS ONE* 3 (11):e3757.
- de Bruyn, P. J. N., C. A. Tosh, W. C. Oosthuizen, M. N. Bester and J. P. Y. Arnould. 2009. Bathymetry and frontal system interactions influence seasonal foraging movements of lactating Subantarctic fur seals from Marion Island. *Marine Ecology Progress Series* 394:263–276.
- Doidge, D. W., J. P. Croxall and J. R. Baker. 1984. Density-dependent pup mortality in the Antarctic fur seal *Arctocephalus gazella* at South Georgia. *Journal of Zoology (London)* 202:449–460.
- Forcada, J., and J. I. Hoffman. 2014. Climate change selects for heterozygosity in a declining fur seal population. *Nature* 511:462–465.
- Forcada, J., P. N. Trathan, K. Reid and E. J. Murphy. 2005. The effects of global climate variability in pup production of Antarctic fur seals. *Ecology* 86:2408–2417.

- Forcada, J., P. N. Trathan, K. Reid, E. J. Murphy and J. P. Croxall. 2006. Contrasting population changes in sympatric penguin species in association with climate warming. *Global Change Biology* 12:411–423.
- Gelman, A. and D. B. Rubin. 1992. Inference from iterative simulation using multiple sequences. *Statistical Science* 7:457–472.
- Gentry, R. L., and G. L. Kooyman. 1986. *Fur seals: Maternal strategies on land and at sea*. Princeton University Press, Princeton, NJ.
- Gibbens, J., and J. P. Y. Arnould. 2009. Interannual variation in pup production and the timing of breeding in benthic foraging Australian fur seals. *Marine Mammal Science* 25:573–587.
- Guinet, C., P. Jouventin and J-Y. Georges. 1994. Long term population changes of fur seals *Arctocephalus gazella* and *Arctocephalus tropicalis* on subantarctic (Crozet) and subtropical (St. Paul and Amsterdam) islands and their possible relationship to El Niño Southern Oscillation. *Antarctic Science* 6:473–478.
- Harcourt, R. 1992. Factors affecting early mortality in the South American fur seal (*Arctocephalus australis*) in Peru: Density related effects and predation. *Journal of Zoology*, London 226:259–270.
- Hofmeyr, G. J. G., M. N. Bester and F. C. Jonker. 1997. Changes in population sizes and distribution of fur seals at Marion Island. *Polar Biology* 17:150–158.
- Hofmeyr, G. J. G., M. N. Bester, A. B. Makhado and P. A. Pistorius. 2006. Population changes in Subantarctic and Antarctic fur seals at Marion Island. *South African Journal of Wildlife Research* 36:55–68.
- Hofmeyr, G. J. G., M. N. Bester, P. A. Pistorius, *et al.* 2007. Median pupping date, pup mortality and sex ratio of fur seals at Marion Island. *South African Journal of Wildlife Research* 37:1–8.
- Hucke-Gaete, R., L. P. Osman, C. A. Moreno and D. Torres. 2004. Examining natural population growth from near extinction: The case of the Antarctic fur seal at the South Shetlands, Antarctica. *Polar Biology* 27:304–311.
- Kerley, G. I. H. 1983. Comparison of seasonal haul-out patterns of fur seals *Arctocephalus tropicalis* and *A. gazella* on subantarctic Marion Island. *South African Journal of Wildlife Research* 13:71–77.
- Kerley, G. I. H. 1984. The relationship between two species of fur seals *Arctocephalus tropicalis* (Gray) and *A. gazella* (Peters) on Marion Island. M.Sc. thesis, University of Pretoria, Pretoria, South Africa. 108 pp.
- Kerley, G. I. H. 1987. *Arctocephalus tropicalis* on the Prince Edward Islands. Pages 61–64 in J. P. Croxall and R. L. Gentry, eds. Status, biology, and ecology of fur seals. Proceedings of an International Symposium and Workshop, Cambridge, England, 23–27 April 1984. U.S. Department of Commerce, NOAA Technical Report NMFS-51.
- King, R., B. J. T. Morgan, O. Gimenez and S. P. Brooks. 2010. Bayesian analysis for population ecology. Chapman & Hall/CRC, Boca Raton, FL.
- Kirkman, S. P., M. N. Bester, G. J. G. Hofmeyr, P. A. Pistorius and A. B. Makhado. 2002. Pup growth and maternal attendance patterns in Subantarctic fur seals. *African Zoology* 37:13–19.
- Kirkwood, R., R. Gales, A. Terauds, *et al.* 2005. Pup production and population trends of the Australian fur seal (*Arctocephalus pusillus doriferus*). *Marine Mammal Science* 21:260–282.
- Makhado, A. B., M. N. Bester, S. P. Kirkman, P. A. Pistorius, J. W. H. Ferguson and N. T. W. Klages. 2008. Prey of the Antarctic fur seal *Arctocephalus gazella* at Marion Island. *Polar Biology* 31:575–581.
- Makhado, A. B., M. N. Bester, S. Somhlaba and R. J. M. Crawford. 2013. The diet of the Subantarctic fur seal *Arctocephalus tropicalis* at Marion Island. *Polar Biology* 36:1609–1617.
- Meiklejohn, K. I., and V. R. Smith. 2008. Surface areas of altitudinal zones on sub-Antarctic Marion Island. *Polar Biology* 31:259–261.

- Payne, M. R. 1977. Growth of a fur seal population. *Philosophical Transactions of the Royal Society of London* B279:67–79.
- Oosthuizen, W. C., P. J. N. de Bruyn, M. Wege and M. N. Bester. 2015. Geographic variation in Subantarctic fur seal pup growth: Linkages with environmental variability and population density. *Journal of Mammalogy*. doi:10.1093/jmammal/gyv181.
- Parent, E., and E. Rivot. 2013. Introduction to hierarchical Bayesian modeling for ecological data. Chapman and Hall/CRC Press, Boca Raton, FL.
- Pemberton, D., and R. J. Kirkwood. 1994. Pup production and distribution of the Australian fur seal, *Arctocephalus pusillus doriferus*, in Tasmania. *Wildlife Research* 21:341–352.
- Pistorius, P. A., M. A. Meÿer, R. R. Reisinger and S. P. Kirkman. 2012. Killer whale predation on subantarctic fur seals at Prince Edward Island, Southern Indian Ocean. *Polar Biology* 35:1767–1772.
- Plummer, M. 2015. rjags: Bayesian graphical models using MCMC. R package version 3-15. Available at <http://CRAN.R-project.org/package=rjags>.
- R Core Team. 2014. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.
- Rand, R. W. 1956. Notes on the Marion Island fur seal. *Proceedings of the Royal Society (London)* 126:65–82.
- Reid, K., and J. Forcada. 2005. Causes of offspring mortality in the Antarctic fur seal, *Arctocephalus gazella*: The interaction of density dependence and ecosystem variability. *Canadian Journal of Zoology* 83:604–609.
- Reisinger, R. R., P. J. N. de Bruyn and M. N. Bester. 2011. Predatory impact of killer whales on pinniped and penguin populations at the Subantarctic Prince Edward Islands: Fact and fiction. *Journal of Zoology* 285:1–10.
- Roux, J. P. 1987. Recolonization processes in the Subantarctic fur seal, *Arctocephalus tropicalis*, on Amsterdam Island. Pages 189–194 in J. P. Croxall and R. L. Gentry, eds. Status, biology, and ecology of fur seals. Proceedings of an International Symposium and Workshop, Cambridge, England, 23–27 April 1984. U.S. Department of Commerce, NOAA Technical Report NMFS-51.
- SCAR EGS. 2008. Scientific Committee for Antarctic Research—Expert Group on Seals Report. Available at <http://www.seals.scar.org/pdf/statusofstocs.pdf>.
- Shaughnessy, P. D. 1986. Estimating population size in colonially breeding pinnipeds. Pages 57–59 in P. D. Shaughnessy, ed. Report of CSIRO Marine Mammal Workshop, March 1986. Division of Wildlife and Rangelands Research, Canberra, Australia. Technical Memorandum No. 26.
- Shaughnessy, P. D., J. W. Testa and R. M. Warneke. 1995. Abundance of Australian fur seal pups, *Arctocephalus pusillus doriferus*, at Seal Rocks, Victoria, in 1991–92 from Petersen and Bayesian estimators. *Wildlife Research* 22:625–632.
- Shaughnessy, P. D., S. D. Goldworthy, P. Burch and T. E. Dennis. 2013. Pup numbers of the Australian sea lion (*Neophoca cinerea*) at The Page Islands, South Australia, over two decades. *Australian Journal of Zoology* 61:112–118.
- Sinclair, A. R. E. 1996. Mammal populations: Fluctuations, regulation, life history theory and their implications for conservation. Pages 127–154 in R. B. Floyd, A. W. Sheppard and P. J. De Barro, eds. *Frontiers of population ecology*. CSIRO Publishing, Melbourne, Australia.
- Sutherland, W. J., and K. Norris. 2002. Behavioural models of population growth rates: Implications for conservation and prediction. *Philosophical Transaction of the Royal Society, London B* 357:1273–1284.
- Trillmich, F., and K. A. Ono. 1991. Pinnipeds and El Niño: Responses to environmental stress. Springer-Verlag, Berlin, Germany.
- Trites, A. W., A. J. Miller, H. D. G. Maschner, et al. 2007. Bottom-up forcing and the decline of Steller sea lions (*Eumetopias jubatus*) in Alaska: Assessing the ocean climate hypothesis. *Fisheries Oceanography* 16:46–67.

- Waller, L., and B. Carlin. 2010. Disease mapping. Pages 217–244 in A. E. Gelfand, P. Diggle, P. Guttorp and M. Fuentes, eds. Handbook of spatial statistics. CRC Press, Boca Raton, FL.
- Wege, M. 2013. Maternal foraging behaviour of Subantarctic fur seals from Marion Island. M.Sc. thesis, University of Pretoria, Pretoria, South Africa. 154 pp.
- Wege, M., M. Nevoux, P. J. N. de Bruyn and M. N. Bester. 2015. Multistate mark-recapture models as a novel approach to estimate factors affecting attendance patterns of lactating Subantarctic fur seals from Marion Island. *Antarctic Science* 27:252–262.
- Wilkinson, I. S., and M. N. Bester. 1990. Continued population increase in fur seals, *Arctocephalus tropicalis* and *A. gazella*, at the Prince Edward Islands. *South African Journal of Antarctic Research* 20:58–63.
- Wynen, L. P., S. D. Goldsworthy, C. Guinet, *et al.* 2000. Post-sealing genetic variation and population structure of two species of fur seal (*Arctocephalus gazella* and *A. tropicalis*). *Molecular Ecology* 9:299–314.

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#### SUPPORTING INFORMATION

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*Appendix S1.* The JAGS code of the hierarchical Bayesian model.