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Population changes of *Arctocephalus* spp. at Marion Island

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

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 Published pup population estimates of *A. tropicalis* (1995 and 2004) with an unpublished total island count in 2013, and annual counts on subsets of rookeries (2007-2015) were analyzed using a Hierarchical Bayesian model.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 beaches 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. However, 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

Introduction

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) 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 1970's until the late 1980's 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, Hucke-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, Shaughnessy *et al.* 1995, Guinet *et al.*1994, 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 sub-adult 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 doriferu*s; 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 re-assess the pup population status of *Arctocephalus* spp. at Marion Island and provide revised estimates of pup numbers and trends for the period 2004 to 2013. To achieve this, for SAFS we use 1) annual pup count data from a subset of beaches 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^2 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 (Shaugnessy *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 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 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 ~30s 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 one day 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 5 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 section 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 Sealer's 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 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 sub-models (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 the 'true' number of pups at Cape Davis for a given year y ($NCDavis_y$) and the probability of detection ($pCDavis_y$). 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 $KCDavis_y$ (the number of marked pups in year y), the number of recaptured pups ($RCDavis_y$), and the number of unmarked pups ($UCDavis_y$) 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:*

$$RCDavis_{yt} \sim \text{Bin}\,(KCDavis_y, pCDavis_y), \quad y=2004, 2007,...2015, t=1, \ldots,10$$

$$UCDavis_{yt} \sim \text{Bin}\,(NCDavis_y - KCDavis_y, pCDavis_y)$$

To estimate the probability of detecting a pup (pS_y), the above mentioned Cape Davis CMR model was combined with the direct count data at Cape Davis (hereafter referred to 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 $NCDavis_y$ (estimated by the previous model) and pS_y. To estimate the variation in capture probability between years, parameter pS_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 $logit(pS_y)$ is assumed to follow a normal distribution with mean $m.pS$ and variance $v.pS$.

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 $pCFSP_{yt}$, where y=year and t=transect. This fine-scale modeling is possible due to repeat counts for each transect, where r=replicate. Given $KCFSP_y$ (the number of marked pups in year y), the number of recaptured pups in ($RCFSP_{ytr}$) and the number of unmarked pups ($UFSP_{ytr}$), the CMR model for Fur Seal

Peninsula for year y, transect t and replicate r is therefore:

$$RCFSP_{ytr} \sim \text{Bin}\ (KCFSP_{y}, pCFSP_{yt}),\quad y=2004, 2013, t=1, \ldots,15, r=1, \ldots 3$$

$$UFSP_{ytr} \sim \text{Bin}\ (NFSP_{y} - KCFSP_{y}, pCFSP_{yt})$$

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 (pS_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 pS_y and modeled by

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

Cliff-top count specific model

To estimate the probability of detecting a pup on beaches only counted from a cliff-top (*pCTop)*, 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 (*pCTop)* 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, pS_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 *pCDavis*, *pCFPenin*, and *pCTop* were specified as a uniform distribution between 0 and 1. The parameters that dictate the normal distribution on the random effects (logit(*pS*) and *m.pS*), were assumed to be drawn from an uninformative normal distribution with mean 0 and variance 1000. The variance *v.pS* 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 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 as supplementary material (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

$$N_t = N_0e^{rt}$$

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 (λ)(Caughley 1977) using

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

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 to 16,169) to 8312 (CI: 7,983 to 8,697), which corresponds to a 46% decline (CI: 43% to 48%; Fig.3; Table 1). Fur Seal Peninsula estimates decreased by 60.8% (CI: 56% to 66%; Fig.4; Table 1). Between 2004 and 2015 Cape Davis declined by 60% (CI: 59% to 62%; Fig.5) and the beaches where pups were counted annually, excluding Cape Davis, were reduced by 58% (CI: 57% to 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 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 decreased pup counts at Watertunnel Beach (where the majority of pups were born: 77.1% - 81.7%) and Landfall Beach. At the remaining rookeries pup counts 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 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 to 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.

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 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 (Kerley1987, Hofmeyr *et al.* 2007). Although it is difficult to accurately quantify pup mortality, 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.* In Press.) 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 north-east 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, re-analyzing 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 to 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 to 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 inter-specific 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: 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.

Acknowledgements:

The Department of Environmental Affairs supplied logistic support within the South African National Antarctic Programme. Financial support was provided by the Department of Science and Technology, through the National Research Foundation (NRF), in support of the Marion Island Marine Mammal Programme of the MRI. Greg Hofmeyr helped plan the 2013 total island count, and provided the 1995 and 2004 data as well as valuable insight. For assistance in the field we are grateful to Dawn Cory-Toussaint, Cheryl Tosh, Santjie du Toit, Mashudu Phalanndwa, Paul Visser, Derek van der Merwe, Hugh Purdon, Christiaan Conradie, Shadrack Podile, Thomas Mufanadzo, Johan van der Vyver, Nadia Hansa, Daniël Kotzé, and Liezl Pretorius. All the above procedures have ethics clearance from the Animal Use and Care Committee (AUCC) of the Faculty of Natural and Agricultural Sciences, University of Pretoria, South Africa, under AUCC 040827-023. MNB benefitted from a Hanse-Wissenschaftskollege (Institute for Advanced Study) Fellowship during the final stages of preparing this manuscript.

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Figure Legends:

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 Sealer's 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.

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 = year, t=transect and r=replicate. The CMR sub-model for Cape Davis (CDavis) is presented by $KCDavis_y$ (total number of pups marked),

$RCDavis_y$ (number of marked pups recounted), $UCDavis_y$ (number of unmarked pups counted) and $pCDavis_y$ (estimated detection probability) where y=year and t=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), $m.pS$ and $v.pS$ (the mean and variance of pS respectively). All these sub-models are combined to estimate $N_{b,y}$ (the estimated number of pups on beach b in year y).

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

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.

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)*.

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

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.

			95% Credible Interval	
Parameter	**Mean**	**Median**	**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.pS	1.46	1.46	0.96	1.97
v.pS	0.71	0.58	0.27	1.83
pcTop	0.53	0.53	0.50	0.56
NFSPen2004	5385	5376	4768.0	6112.2
NFSPen2013	2109	2104	1988.5	2242.5
N2004	15260	15243	14447	16169
N2013	8312	8303	7983	8697

[a] Was also used to correct for undercount of 2004 data

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 1975-2013. Values in brackets represent the mean annual percentage population change for that beach in relation to the previous count. Where multiple counts of a beach was done, mean ± standard deviation is presented.

Year	**1975**	**1982**	**1989**	**1995**	**2000**	**2001**	**2004**	**2007**	**2010**	**2013**
Watertunnel Beach				211			615 ± 5	903 ± 9	1108 ± 26	1198 ± 58
								(13.7%)	*(7.1%)*	*(2.6%)*
Landfall Beach				3			69	127	174 ± 0.6	192 ± 6
								(22.6%)	*(11.1%)*	*(3.3%)*
Trypot Beach							21	26	51	64
								(7.4%)	*(25.2%)*	*(7.9%)*
Kildalkey Bay							12	26	29	59
								(29.4%)	*(3.7%)*	*(26.7%)*
Rest of the Island				19			27	23	17	40
								(-5.2%)	*(-9.6%)*	*(33.0%)*
Total:	**15**[a]	**43**[a]	**91**[a]	**233**	**343**[a]	**464**[a]	**744**	**1105**	**1379**	**1553**

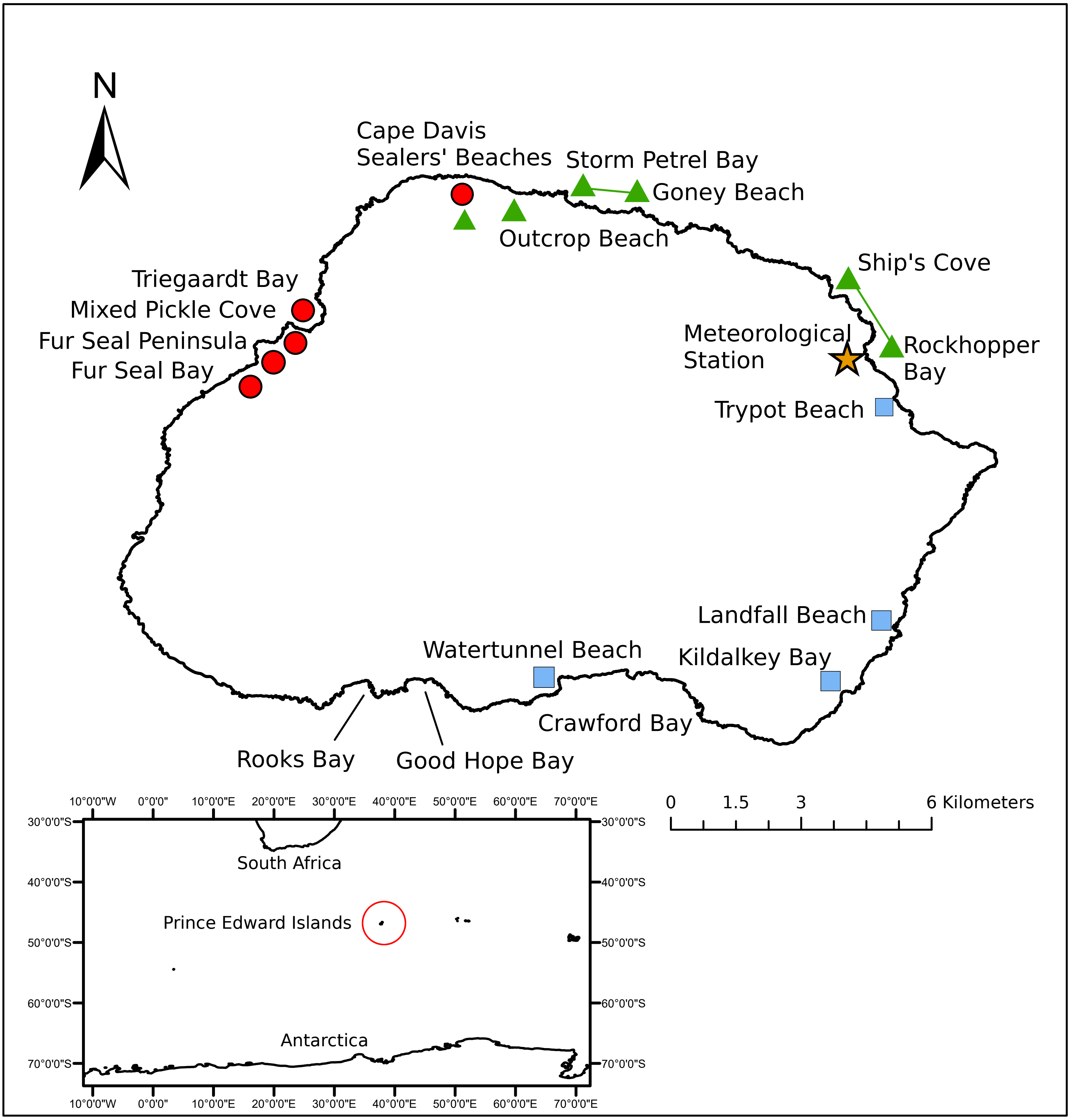
[a] It was not specified in the literature at which beach on Marion Island these pups were counted and thus only the total values are presented.

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*[a]	Average ± SD[b] 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**

[a] *N* = The number of rookeries

[b] SD = Standard deviation


N
Cape Davis
Sealers' Beaches
Storm Petrel Bay
Goney Beach
Outcrop Beach
Triegaardt Bay
Mixed Pickle Cove
Fur Seal Peninsula
Fur Seal Bay
Ship's Cove
Meteorological
Station
Rockhopper
Bay
Trypot Beach
Landfall Beach
Watertunnel Beach
Kildalkey Bay
Crawford Bay
Rooks Bay
Good Hope Bay
0
1.5
3
6 Kilometers
10°0'0"W
0°0'0"
10°0'0"E
20°0'0"E
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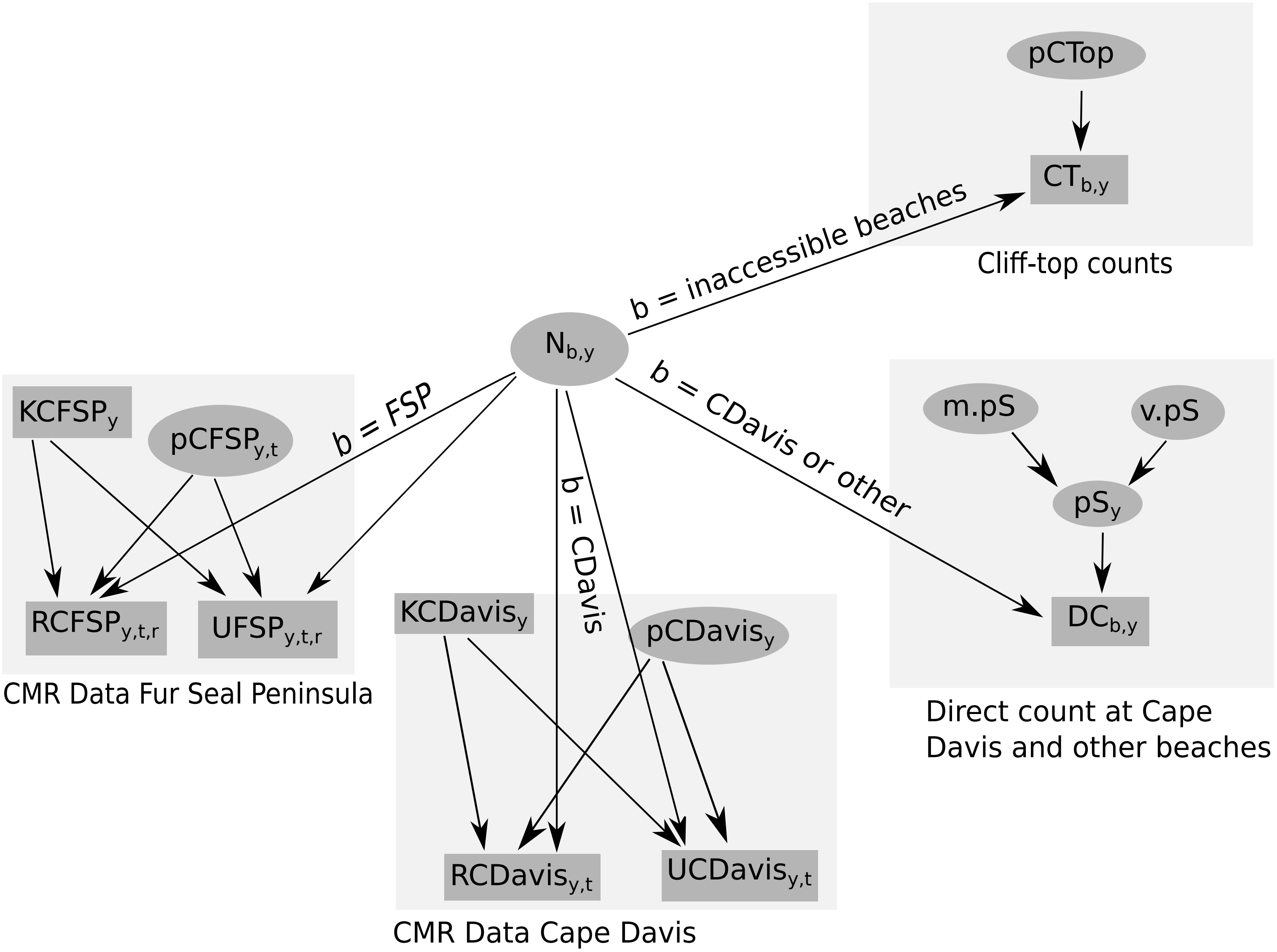
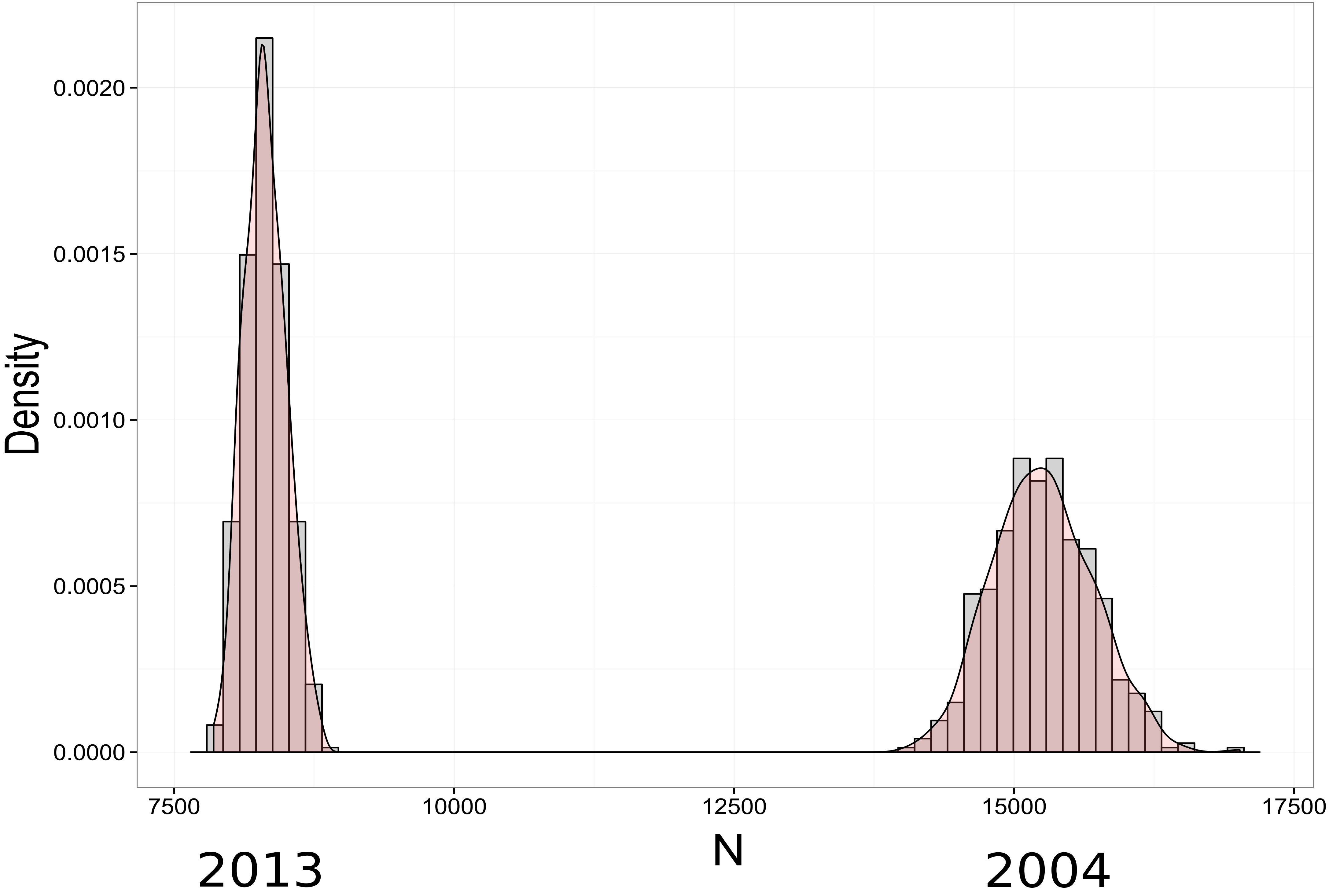
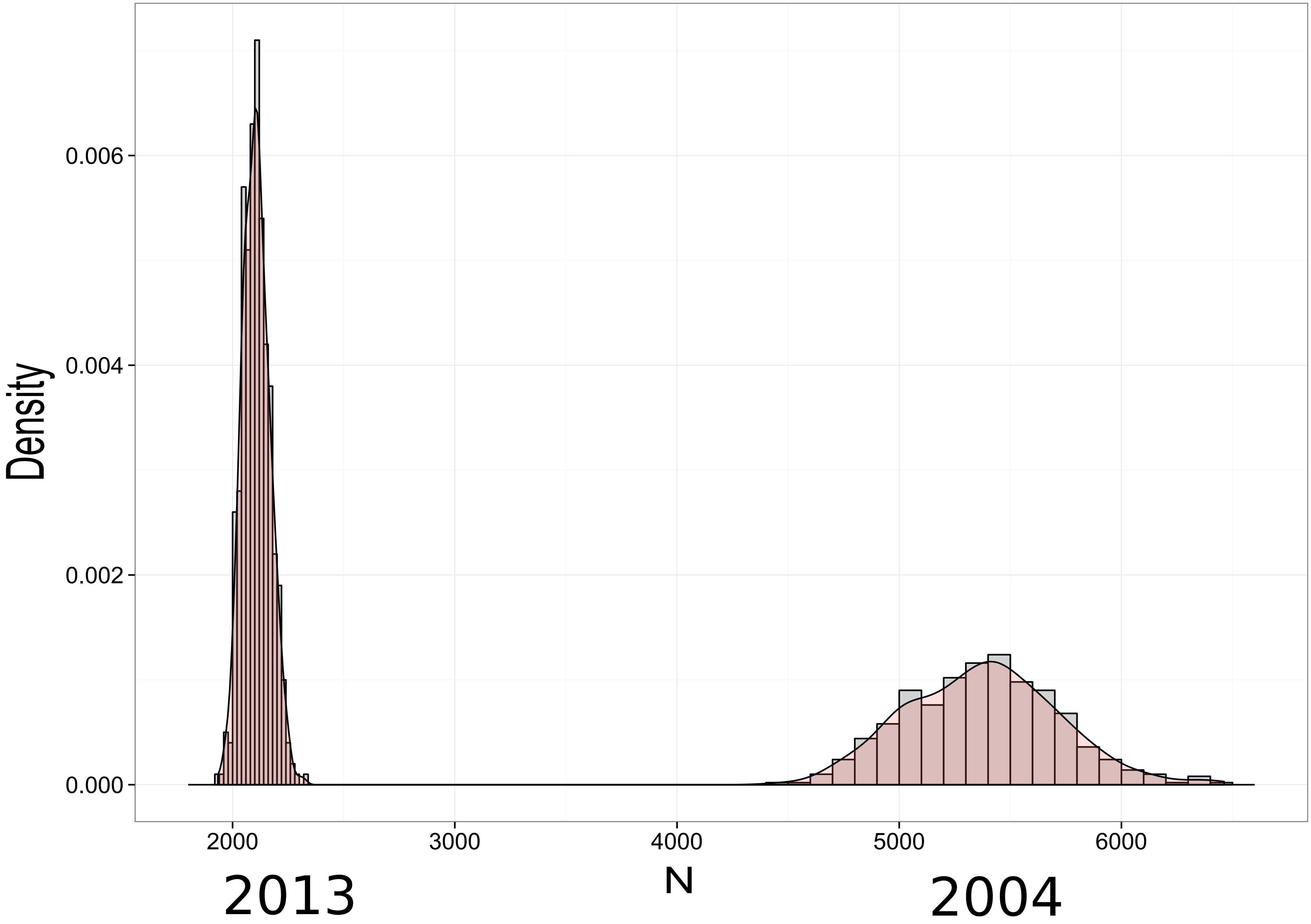
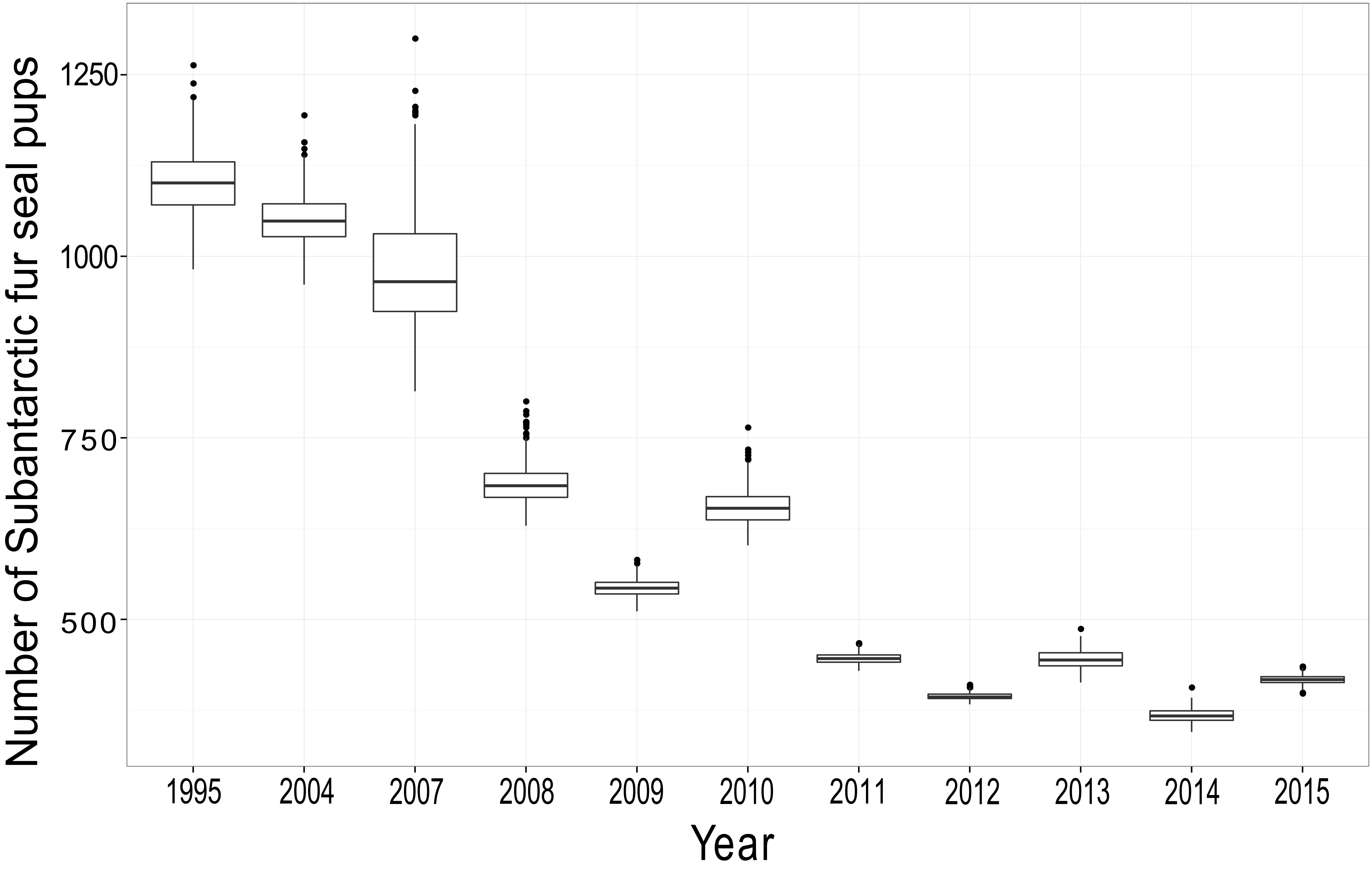
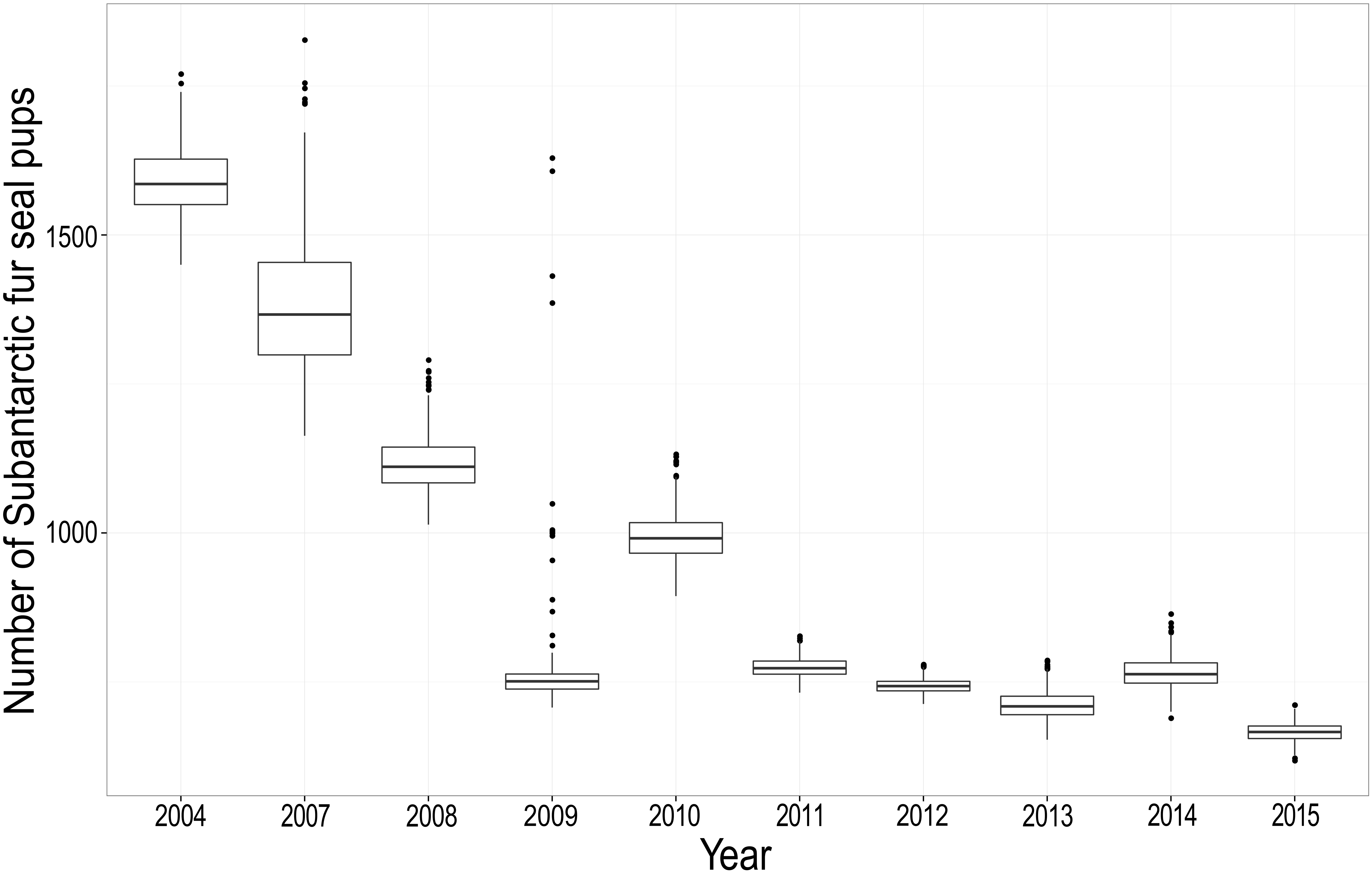
South Africa
Prince Edward Islands
Antarctica


pCTop
$CT_{b,y}$
Cliff-top counts
b = inaccessible beaches
$N_{b,y}$
b = FSP
b = CDavis
b = CDavis or other
$KCFSP_{y}$
$pCFSP_{y,t}$
$RCFSP_{y,t,r}$
$UFSP_{y,t,r}$
CMR Data Fur Seal Peninsula
$KCDavis_{y}$
$pCDavis_{y}$
$RCDavis_{y,t}$
$UCDavis_{y,t}$
CMR Data Cape Davis
m.pS
v.pS
pS_{y}
$DC_{b,y}$
Direct count at Cape Davis and other beaches

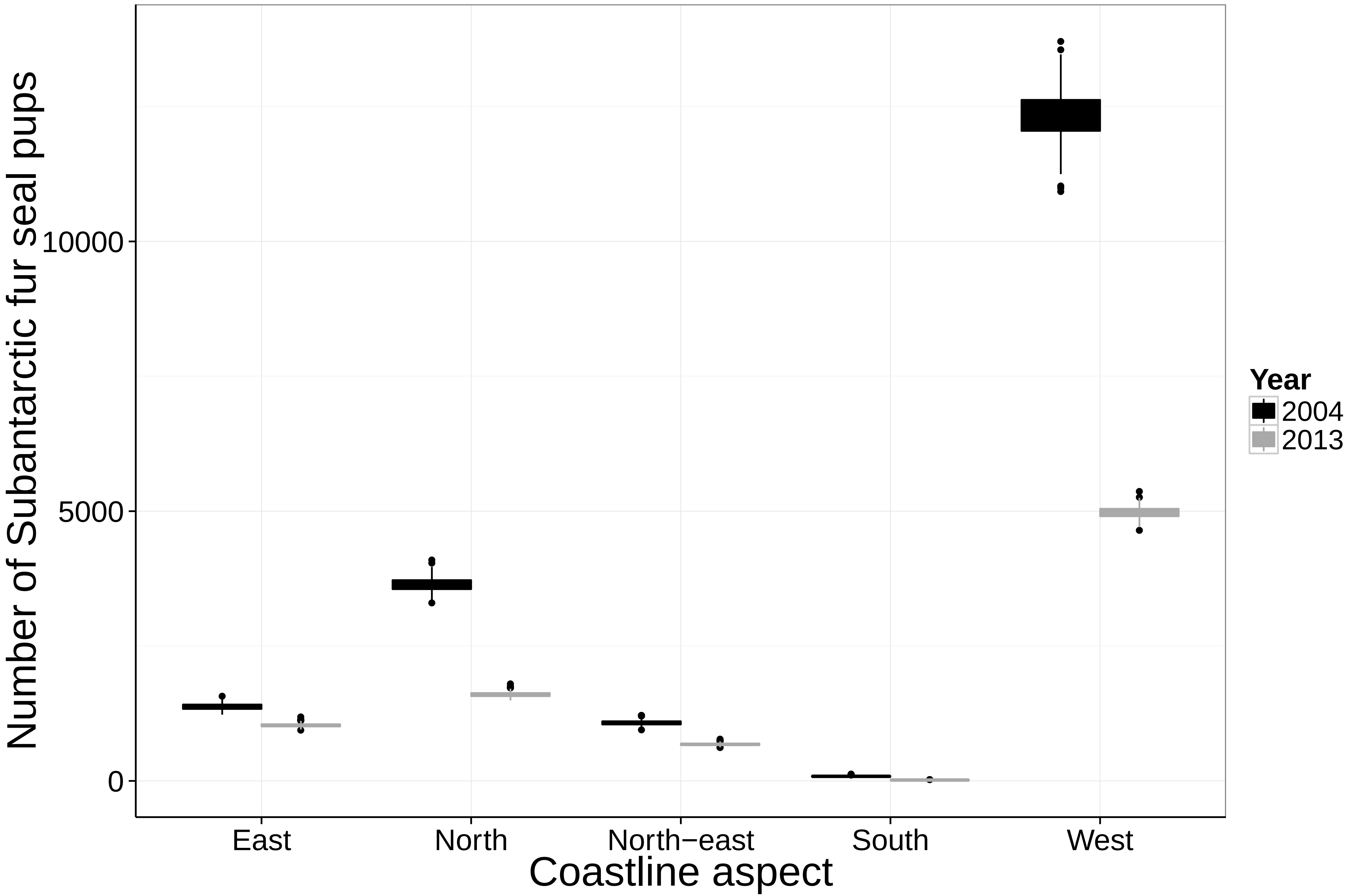

0.0020
0.0015
0.0010
0.0005
0.0000
Density
7500
10000
12500
15000
17500
N
2013
2004

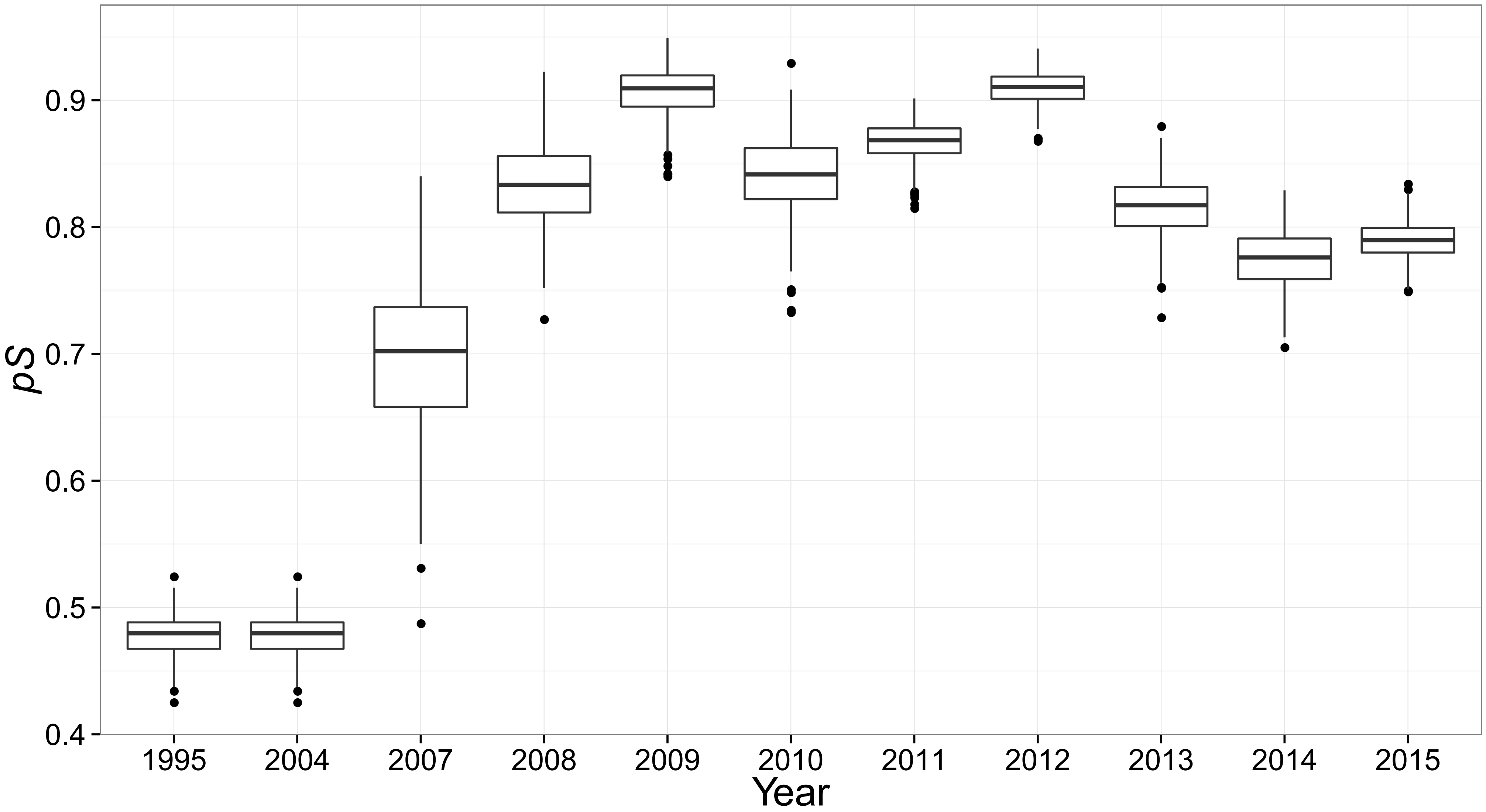

Density
0.006
0.004
0.002
0.000
2000
3000
4000
5000
6000
N
2013
2004


Number of Subantarctic fur seal pups
1250
1000
750
500
1995
2004
2007
2008
2009
2010
2011
2012
2013
2014
2015
Year

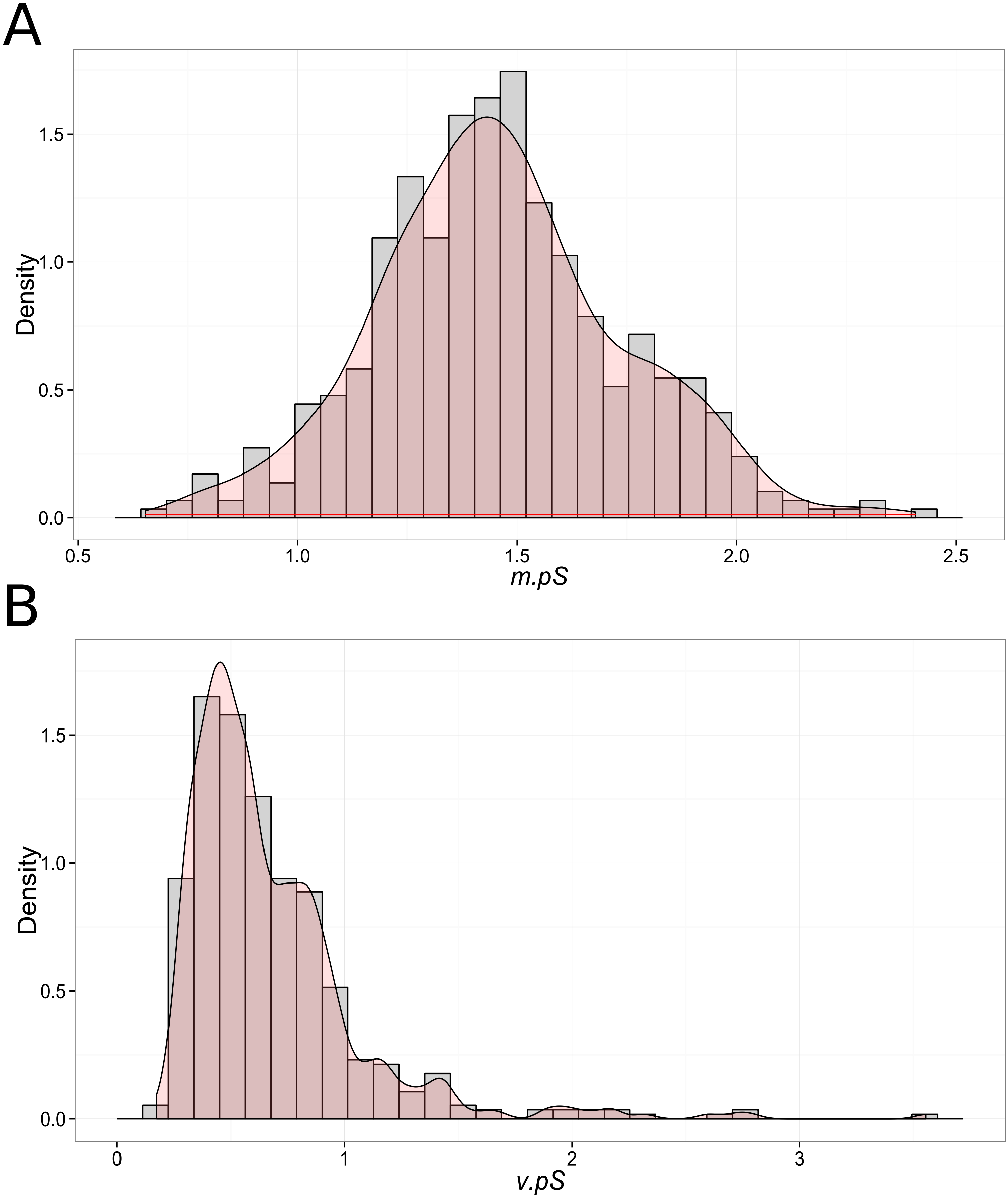


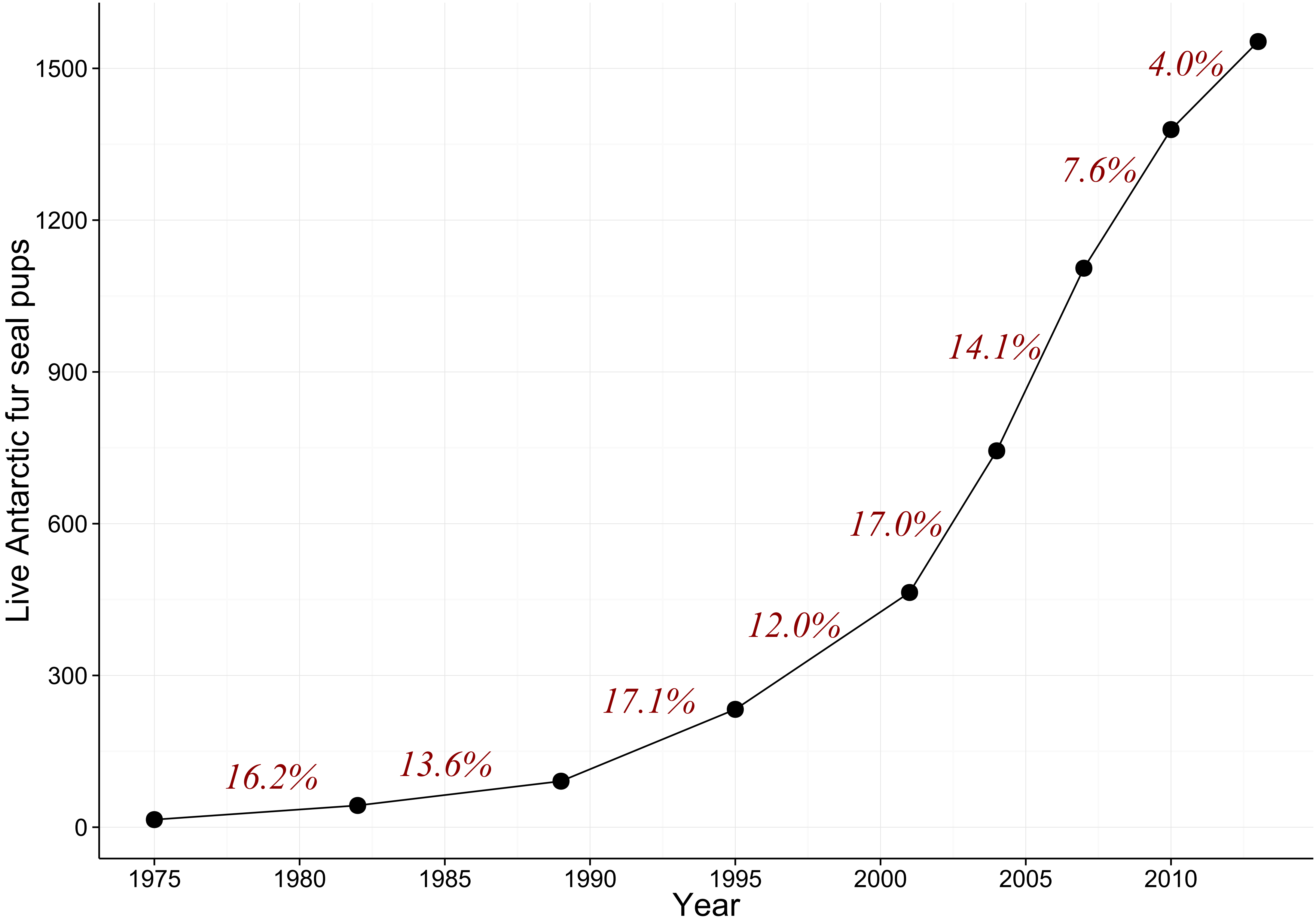
Number of Subantarctic fur seal pups
1500
1000
2004
2007
2008
2009
2010
2011
2012
2013
2014
2015
Year


Number of Subantarctic fur seal pups
10000
5000
0
East
North
North−east
South
West
Coastline aspect
Year
2004
2013



pS
0.4
0.5
0.6
0.7
0.8
0.9
1995
2004
2007
2008
2009
2010
2011
2012
2013
2014
2015
Year


A
Density
1.5
1.0
0.5
0.0
0.5
1.0
1.5
2.0
2.5
m.pS
B
Density
1.5
1.0
0.5
0.0
0
1
2
3
v.pS


Live Antarctic fur seal pups
0
300
600
900
1200
1500
Year
1975
1980
1985
1990
1995
2000
2005
2010
16.2%
13.6%
17.1%
12.0%
17.0%
14.1%
7.6%
4.0%