**ORIGINAL PAPER**

# Population status of southern elephant seals (*Mirounga leonina*) at Peninsula Potter breeding colony, Antarctica

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## Abstract

Southern elephant seals (*Mirounga leonina*) are apex predators that spend several months at sea feeding over vast areas. Their population trends are related to food availability during winter, which in turn is influenced by environmental conditions; thus, fluctuations in their populations reflect changes in the ecosystems. Although population trends for this species are available for large populations, there are still small colonies for which information is scarce, as is the case for the colony located at Peninsula Potter, South Shetland Islands. At this colony, field censuses of the number of breeding females conducted from 1995 to 2018 revealed an overall decline of 11.9% at an annual rate of 0.6%. However, contrasting trends before and after 2008 were observed. A decrease of 46.5% at an annual rate of 4.6% was registered before 2008, while for the subsequent period (2008–2018) the number of females increased by 64.5% at an annual rate of 5%. A positive association was observed between the extent of sea ice in winter foraging areas and population numbers between 1995 and 2008. The females of this colony feed on the edge of the sea ice, so in years of low sea ice extension the effort required to reach these areas is greater. This could lead individuals to choose to breed in areas closer to their feeding grounds in order to avoid the energetic expenditure of body reserves acquired during winter that would sustain the return trip to their natal colony.

**Keywords** Marine mammals · Southern Ocean · Population trend · Sea ice extent · Weaning weight · Dispersal

## Introduction

Estimating the population status of a species and monitoring its changes over time are key tasks for its management and conservation, especially in species that live in ecosystems exposed to climatic changes such as the Antarctic marine environment (Rogers et al. 2019; Convey and Peck 2019). Monitoring the effects of climate change on the entire ecosystem can be difficult. However, studying the response of some of its most conspicuous residents, such as mammals, can shed light on other aspects of the ecosystem. For instance, it is known that the demography and abundance of Antarctic top predators is affected by the availability of prey, which in turn is influenced either by changes in primary productivity, by variations in the physical and chemical conditions of the environment, or by a combination of both (Weimerskirch et al. 2003; Ainley et al. 2005; de Little et al. 2007; Orgeret et al. 2022).

Among Antarctic marine mammals, the southern elephant seal (*Mirounga leonina*; hereafter SES) has been widely studied throughout its distribution. Shifts in the trajectories of its populations and vital rates have been related to environmental changes such as sea ice extent and dynamics (de Little et al. 2007; Hindell et al. 2016; Hindell et al. 2017; Volzke et al. 2021).This ice-tolerant species has a circumpolar distribution in the southern hemisphere and globally is made up of four geographically and genetically differentiated populations i.e., the Macquarie Island stock in the south

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Pacific Ocean; the Îles Kerguelen stock located in the south Indian Ocean; the Peninsula Valdés stock in Argentina; and the South Georgia stock in the south Atlantic Ocean (Hoelzel et al. 1993; Hoelzel et al. 2001; Slade et al. 1998; McMahon et al. 2005a; Corrigan et al. 2016).

A global decline in the population size of SES during the second part of the twentieth century was reported by several authors (e.g., McMahon et al. 2005a; Authier et al. 2011; Pistorius et al. 2011). Currently, some of those populations, like Kerguelen, South Georgia, and Peninsula Valdés, are stable or even increasing, while the population at Macquarie Island is still decreasing (Hindell et al. 2017). The largest group (in terms of number of animals) is the South Georgia stock and includes subpopulations at South Georgia, South Orkney, South Shetland, Gough, Bouvet, and Malvinas Islands among others (Laws 1994; Mc Mahon et al. 2005a). The majority of the breeding colonies belonging to the South Georgia stock are stable; however, the current population status for some other subpopulations of this stock is unknown or needs to be updated. This is the case for one of the southernmost subpopulations situated at the Antarctic Specially Protected Area (ASPA) N°132 "Peninsula Potter", 25 de Mayo/King George Island. The first estimate of the population trend for this SES colony was in the 1980s when it was observed that the intrinsic rate of population growth was positive between 1980 and 1988 (Vergani 1985; Vergani et al. 1987; Vergani and Stanganelli 1990). Then, between 1989 and 1994, the maximum number of females ashore varied slightly from 559 to 423 individuals (Vergani et al. 2004). From that date to the present, preliminary reports showed a decrease in the number of reproductive females in this colony between 1995 and 2011 (Mennucci et al. 2012). Population trends of SES in Antarctica are linked to the environmental conditions of their foraging sites (Clausius et al. 2017; Hindell et al. 2017; McMahon et al. 2017), where sea ice in particular seems to play an important role.

Sea ice affects the foraging behavior of predators in contrasting ways, since while a large extension of ice could prevent them from accessing areas with a large amount of prey (van Den Hoff et al. 2014), it could also favor productivity by providing shelter and food for certain key ecosystem components such as krill (Nicol 2006), thus, generating foraging hot spots for predators. In eastern Antarctica, there is evidence that the positive trend in the extent and duration of sea ice in the foraging areas of breeding female SESs on Macquarie Island is negatively affecting the population trend (van Den Hoff et al. 2014). The greater extent of sea ice in the Western Antarctic Peninsula (WAP) in certain years was also linked both to low body condition of females that came to breed at Peninsula Potter as well as to the weight of their pups at weaning, apparently because these ice conditions are unfavorable for potential SES prey during winter (Vergani et al. 2001; Vergani et al. 2008; Carlini 2010).

Sea ice trends in Antarctica vary regionally. While in the east both the extent and duration have increased, there are other sectors, such as the WAP, where the trend is opposite. This area has experienced the fastest warming in the southern hemisphere (Vaughan et al. 2003), especially during fall and winter (Turner et al. 2013), and consequently a decrease in the regional extent and duration of the sea ice sheet in the WAP was recorded during the second half of the last century (Stammerjohn et al. 2008; Stammerjohn et al. 2012; Turner et al. 2015). Adult female SESs that breed on Peninsula Potter forage during winter in the WAP area (Bornemann et al. 2000), so this decrease in the extent of sea ice may have been affecting the population for past decades. In this context, we hypothesized that the decline in the extent of sea ice observed in the WAP would positively influence the foraging success of SES females, which would ensure they have sufficient energy reserves for their pups, thus increasing the probability of their survival and consequently an increase in the number of individuals that are recruited for breeding at the colony of Peninsula Potter. To test this hypothesis, we analyzed whether there was a relationship between the trends of both the extent and duration of sea ice during the post-reproductive foraging months of females in the WAP and their population trends in the Peninsula Potter colony between 1995 and 2018. Furthermore, since the foraging success of the females and consequently the size and mass of their young at weaning have been related to population trends (Clausius et al. 2017), we also explore if pup weights at weaning at Peninsula Potter show a relationship with population trend. The small size of the Peninsula Potter population, the accessibility of its coast, and the small size of harems (mean harem size $27.6 \pm 28$; Carlini et al. (2006)) allow us to obtain counts of the entire colony in a single day, thus minimizing the sampling error and allowing accurate dates to obtain when the maximum number of females were on land.

## Materials and methods

### *Study area*

The study was carried out within the ASPA N°132 "Peninsula Potter" (62°14′S, 58°40′W) on the 25 de Mayo/King George Island (Fig. 1). The ASPA stretches along a coastal zone around 5.4 km from Potter Cove (to the southwest) to the Polar Club glacier (to the northeast), with variable width from the coastline to the cliff (Fig. 1). The coastal area is composed of both sandy and gravel beaches with gentle slopes and pebble beaches with steeper slopes.
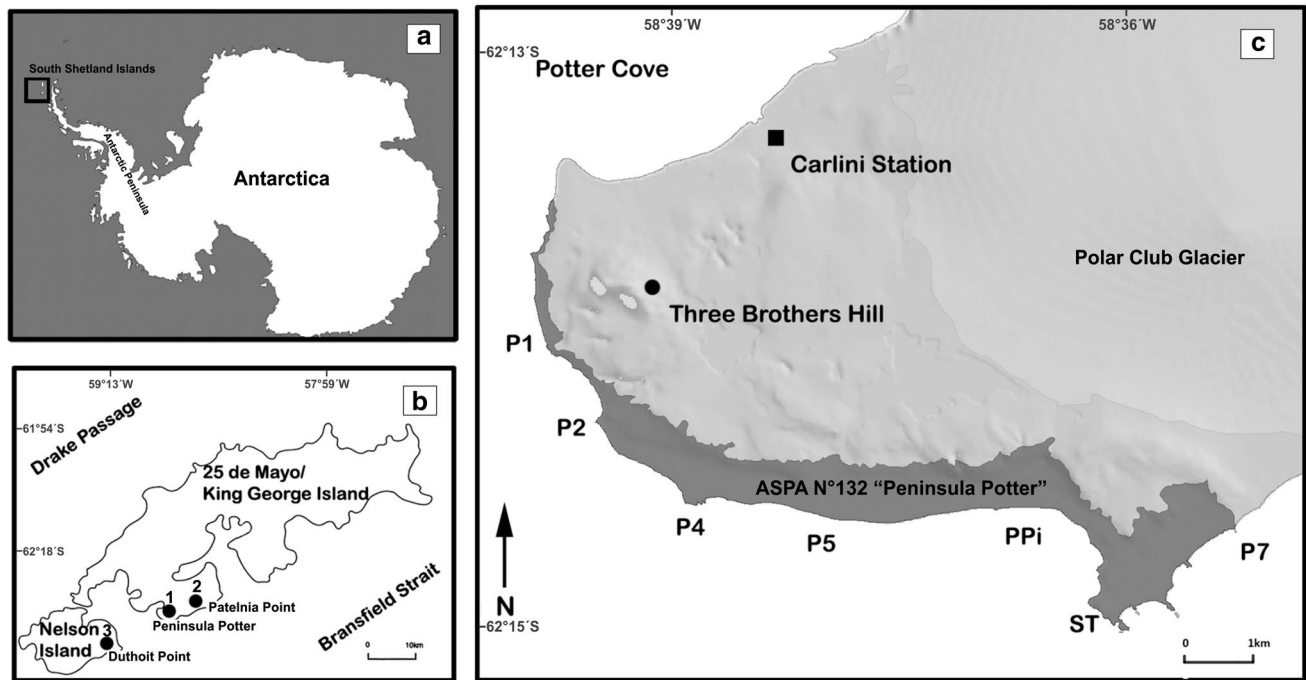
**Fig. 1** Map of the study site location: **a** Location of 25 de Mayo/King George Island in the Antarctic continent; **b** detail of 25 de Mayo/King George Island and Nelson Island, where numbers 1, 2 and 3 correspond to Peninsula Potter, Patelnia Point, and Duthoit Point colonies, respectively; **c** detail of the Peninsula Potter area with references P1 to P7 identifying census sites. Dark gray area represents ASPA Nº132

## Individual marking

Since 1995 a mark-recapture program of the seals born at Peninsula Potter has been conducted. In most of the breeding seasons studied, around 30% of the Peninsula Potter SES pups were individually marked by hot-iron brands (alphanumeric code) and double tagged in the interdigital webbing of the hind flippers with uniquely numbered plastic Allflex Pig-Sheep tags (Allflex ®). Plastic tags allowed rapid recognition of the marked individuals, however, as these types of marks can be lost, seals were also hot-iron branded so they could be identified even if they lost both tags. This long-term, durable marking technique allowed us to record their presence in nearby colonies and to accurately estimate demographic and life history parameters without compromising seal survival (McMahon et al. 2006).

## Census information

The life cycle of SES involves two main terrestrial phases, molting and reproduction, which alternate with two phases at sea where seals forage (Carrick et al. 1962). At the Peninsula Potter colony, the breeding season begins in mid-September when adult males arrive on the beaches and extends until approximately the last week of November when females have weaned their pups and leave the colony to begin their post-reproductive foraging trips. We used counts of the female SES during the reproductive season to identify changes in population status. This is because females have a higher degree of philopatry to a specific site of the breeding colony (Nicholls 1970). Field censuses were conducted to record the number of SES adult females, pups, and weanlings between 1995 and 2018, with the exception of 2009 due to logistical limitations. Every year, the census began between the last week of September and October 1st and continued until the last week of November on alternate days between 10:00 and 14:00 h (local time). They were conducted from the Carlini Antarctic Station (formerly known as Jubany Base) to the end of ASPA N° 132, identified by a rocky formation known as "Peñón 7" (P7; Fig. 1, 62°15′21.81″S, 58°37′50.26″W). The area was explored on foot by two observers who counted all SES between the coast and the base of the cliffs. Since most of the harems have a relatively small size (mean harem size 27.6 ± 28; Carlini et al. (2006)) and it was possible to visualize all the individuals simultaneously, they were counted directly. In cases where harems were greater than the average, three consecutive counts were made and the mean count value was used. In addition, around the estimated peak of abundance in the area (last week of October), field surveys were also conducted at Duthoit Point on Nelson Island and Patelnia Point on Isla 25 de Mayo (Fig. 1), the closest SES breeding areas to the study colony. These censuses were carried out to verify if the females born at Peninsula Potter chose other

nearby places to reproduce, which would be evidence of a dispersal of females during the reproductive season, contributing in part to the decline observed in that colony.

## Number of adult females

In order to compare our results with those previously obtained for this colony, the maximum number of females on land, defined here as "female haul-out peak date", was estimated following the methodology of Vergani and Stanganelli (1990). This consists of adding the maximum number of females on land, the number of weaned pups, and the accumulated number of dead pups at the date of female haul-out peak. This allows us to estimate not only the number of females that are on the beach at that time but also the number of those females that have already left the colony, either because they have weaned their pups or because their pups died during the season.

## Population changes

The intrinsic rate of change in the number of breeding females, recorded at peak haul-out date, was determined following Caughley (1977):

$$r = (\ln Nt - \ln N0)/t,$$

where $r$ is the intrinsic rate of change; $ln\ Nt$ is the natural logarithm of the number of breeding females at time t; $ln\ N0$ is the natural logarithm of the number of breeding females at the starting time; and $t$ is the time interval between population counts.

The count data were log-transformed to fit a normal distribution. Simple linear regressions (log number of females regressed on time) were performed throughout the analyzed census period (1995–2018) and for the periods before and after the breakpoint identified in the general trend (see ahead). Since population trends may vary over time and as we analyzed more than 20 years of count data, we followed a breakpoint linear regression analysis of the natural log-transformed number of breeding females (estimated at the female haul-out peak date). To identify if there was a breakpoint in the time series data, we used SegReg software (Oosterbaan 2017) following Garcia-Aguilar (2018). The intrinsic rate of change was calculated for each segment (i.e., up to the breakpoint and after it).

## Weight of pups at weaning

Between 1998 and 2015, a subset of 1589 pups born at Peninsula Potter were weighed (range 29–171 pups weighted per annum) at their weaning date or two days after at most. Weanlings were weighed in a plasticized canvas bag with a

Challenger AZM electronic scale (1000 ± 0.5 kg capacity) suspended from an aluminum pole resting on the shoulders of two researchers. For each year, the mean weight of pups at weaning were obtained and then linearly regressed against the number of females at haul-out peak both for the study period and for the time periods before and after the breakpoint identified in the trend.

## Sea ice extent and duration vs. population trend analyses

Given that the pre-reproductive foraging areas of the females from the Peninsula Potter colony are located in the WAP (Bornemann et al. 2000), we used sea ice data collected from Palmer Station Antarctica (Palmer Long-Term Ecological Research). Sea ice extent refers to the total surface area inside the ice edge and sea ice duration to the days elapsed between the maximum advance and retreat of sea ice (Palmer Station Antarctica LTER and Stammerjohn 2020a). To identify if environmental conditions during either of the seal's at-sea foraging periods had greater impact upon foraging success we used monthly sea ice extent and sea ice duration values for March to September and June to September. Log-transformed numbers of females that breed at Peninsula Potter were regressed against those mean sea ice extent values. In addition, the sea ice duration (i.e., days elapsed between advance and retreat of sea ice (Palmer Station Antarctica LTER and S. Stammerjohn 2020b) was also regressed to log-normal transformed numbers of females. These analyses were performed for the study period 1995–2018 and for the time series before and after the breakpoint (i.e., 1995–2008 and 2008–2018, respectively). All regressions were conducted with R software v.3.6.0 (R Core Team 2018) in RStudio software v.1.1.463 (RStudio Team 2018) by using the "lm" function in the R package nlme (Pinheiro et al. 2018).

# Results

## Abundance records at Peninsula Potter

The number of adult females breeding at Peninsula Potter between 1995 and 2018 ranged between 204 and 555 individuals (Table 1). During that period, the female haul-out peak at Peninsula Potter occurred during the last week of October (mean date = 27 October, range 23–31 October, $n = 21$ see Table 1).

## Population trend and rates

In the study period, the number of adult females decreased by 11.9% at an annual rate of − 0.6%. Although this decline was not significant ($F_{(1,21)} = 3.1$, $p = 0.09$, *adjusted $r^2 = 0.1$*),

**Table 1** Abundance records of breeding adults on the Peninsula Potter colony during the study period (1995–2018) and weaning mass of pups born there. For each season in which data were available, mean ± SD values of pup weights at weaning are presented. The number of pups weighed in each season (n) is given in parentheses

| Female haul-out peak date | Number of adult females | Number of adult males | Weigth of weanlings (kg) |
|---|---|---|---|
| 26/10/1995 | 469 | 51 | 157.8 ± 21.5 (29) |
| 25/10/1996 | 471 | 68 | |
| 26/10/1997 | 444 | 70 | |
| 1/11/1998 | 555 | 39 | 156.9 ± 25.5 (70) |
| 28/10/1999 | 296 | 36 | |
| 26/10/2000 | 340 | 44 | |
| 26/10/2001 | 360 | 29 | 162.2 ± 24.6 (79) |
| 30/10/2002 | 432 | 39 | 159.5 ± 28.4 (171) |
| 31/10/2003 | 307 | 42 | 154.5 ± 24.9 (133) |
| 28/10/2004 | 408 | 47 | 160.9 ± 28.1 (116) |
| 27/10/2005 | 317 | 51 | 153.2 ± 23.6 (100) |
| 25/10/2006 | 285 | 45 | 165.1 ± 23.6 (147) |
| 30/10/2007 | 204 | 46 | 159.9 ± 26.6 (99) |
| 27/10/2008 | 251 | 44 | 163.9 ± 25.7 (119) |
| 27/10/2010 | 314 | 54 | 158.8 ± 30 (104) |
| 23/10/2011 | 379 | 67 | 164.1 ± 27.5 (116) |
| 27/10/2012 | 388 | 81 | 146.6 ± 28.6 (102) |
| 25/10/2013 | 304 | 38 | 156.8 ± 33.1 (118) |
| 29/10/2014 | 359 | 59 | 156.2 ± 27.4 (50) |
| 30/10/2015 | 321 | 43 | 158.9 ± 32.3 (36) |
| 29/10/2016 | 368 | 70 | |
| 27/10/2017 | 304 | 40 | |
| 21/10/2018 | 413 | 40 | |

a breakpoint was observed in the 2008 season (Fig. 2). From 1995 to the identified breakpoint in the population trend (2008), a linear regression of the log-normal transformed number of females against time showed a significant decline of 46.5% ($F_{(1,12)} = 19.1$, $p < 0.001$, *adjusted* $r^2 = 0.6$) at an annual rate of -4.6% (i.e., from 469 to 251 individuals). In contrast, for the period after the breakpoint (2008–2018), the number of females increased by 64.5% at an annual rate of 5% (i.e., from 251 to 413 individuals), though this increase was not statistically significant ($F_{(1,8)} = 2.6$, $p = 0.24$, *adjusted* $r^2 = 0.2$). Despite the general trend between 1995 and 2018, the number of reproductive females fluctuated, showing both decreases and increases between years (Fig. 3).

## Sea ice extent and duration vs population trends

Of all the regressions carried out between the abundance of females in the colony and the ice conditions in the winter foraging areas, only positive and statistically significant associations were observed between the number of females before the breakpoint (1995–2008) and mean values of both the extension ($F_{(1,12)} = 5.6$, $p = 0.03$, *adjusted* $r^2 = 0.3$) and the duration of sea ice ($F_{(1,12)} = 5.2$, $p = 0.04$, *adjusted* $r^2 = 0.3$) in the WAP between June and September.

## Weight of pups at weaning and population trends

The mean pup weaning weight (Table 1) did not vary with time either between 1998 and 2015 ($F_{(1,13)} = 0.3$, $p = 0.58$, *adjusted* $r^2 = -0.1$) or during the period prior to the breakpoint when the colony size decreased ($F_{(1,7)} = 1.0$, $p = 0.35$, *adjusted* $r^2 = 0.0$). Although the years of weaning weight



**Fig. 2** Population trend of southern elephant seals breeding at Peninsula Potter colony. Log-transformed number of SES breeding females (solid dots) counted at Peninsula Potter between 1995 and 2018. Population trend (solid lines) and the 95% confidence interval (dotted lines) calculated by the software SegReg (Oosterbaan 2017)
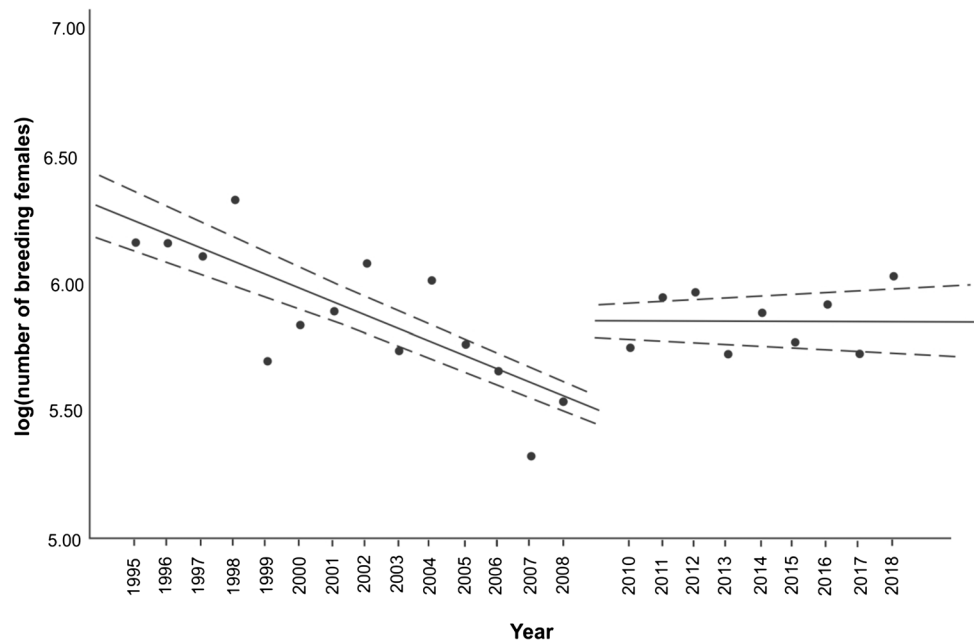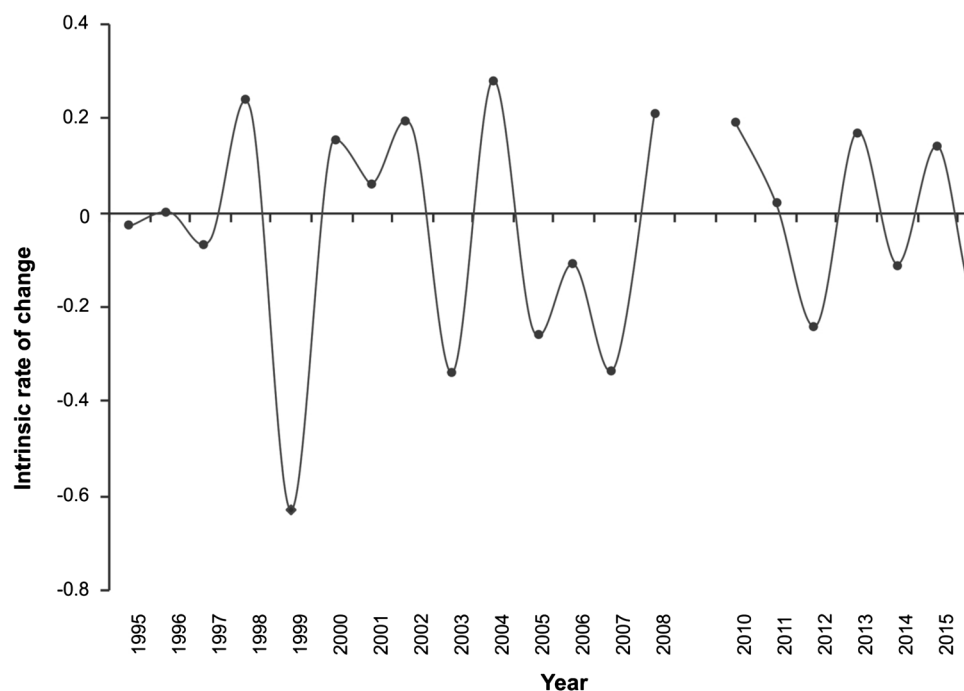
**Fig. 3** Interannual fluctuations in the number of breeding females at the Peninsula Potter colony. The Y axis represents the variation in the values of the intrinsic rates of change calculated from the counts of breeding females at "female haul-out peak date" between 1995 and 2018



and count data do not coincide completely, we assume that the analysed dataset ($n = 15$, between 1998 and 2015) is representative of the count period (1995–2018). No significant correlations were found between the number of females in the Peninsula Potter colony and the weaning weight of their pups either for the entire study period ($F_{(1,13)} = 0.7$, $p = 0.41$, *adjusted* $r^2 = -0$.) or for the periods before ($F_{(1,7)} = 0.5$, $p = 0.52$, *adjusted* $r^2 = -0.1$) and after ($F_{(1,5)} = 1.8$, $p = 0.22$, *adjusted* $r2 = 0.1$) the breakpoint of 2008.

## Dispersal of females

Between 1997 and 2018, Duthoit Point was visited in 10 breeding seasons (approximately one week after the female haul-out peak date at Peninsula Potter). During 7 out of those 10 censuses, a total of 36 branded females (i.e., females that were born at Peninsula Potter) were observed breeding there. The number of branded females observed (mean = 2.4, range 2–8) represented 0.9 to 10% of the total number of females breeding at Duthoit Point (mean = 125.2, range 35–206).

At Patelnia Point, only 4 censuses were carried out (2002, 2003, 2012, and 2013) around the female haul-out peak. A total of 9 branded females (mean = 2.4, range 2–3) were observed, representing from 0.6 to 1% of females breeding at this site (mean = 261.2, range 226–291).

All branded females observed at these two colonies were adult individuals rearing their pups and their ages ranged from 4 to 14 years old.

## Discussion

With the exception of the colonies of the Macquarie stock that are still decreasing, the global situation of southern elephant seal (SES) populations is now one of stability (Hindell et al. 2017) after a considerable decline in most of the large reproductive colonies in the second half of the twentieth century (e.g., McMahon et al. 2005a; Authier et al. 2011; Pistorius et al. 2011). However, there are some small colonies which require a population data update. This is the case for the Peninsula Potter colony and that is why one of our objectives was to report the population trend between 1995 and 2018 and its relationship with one of the most important environmental changes (decline in the extend and duration of sea ice (Massom and Stammerjohn 2010) within the main foraging area (WAP) of females.

### Abundance records and population trends at Peninsula Potter

From 1995 to 2018, the female haul-out peak at Peninsula Potter always occurred during the last week of October, in line with the dates recorded by Vergani and Stanganelli (1990). The authors reported a maximum of 825 females breeding at Peninsula Potter in 1980. If we consider that value, the number of breeding females decreased significantly between 1980 and 2018 by 49.9% from 825 to 413 individuals at an annual rate of -1.8%. However, the scenario seems to be more favorable in the period between 1995 and 2018 since the general decline was much less pronounced (11.9%). During this period, a breakpoint in the general

trend of the colony was identified in 2008 and opposite trends before and after this year were recorded. Possible reasons for these differences in trends and the observed interannual fluctuation in female abundance are not yet clear. The growth of a population depends, in part, on the survival of young individuals that will later be recruited as reproductive adults (Caughley 1977). For the SES, it is the survival of younger animals that has a profound influence on the growth of a population (Hindell 1991; Hindell et al. 1994; McMahon et al. 1999; McMahon et al. 2000). In turn, this survival depends largely on the weight of the pups at weaning, since the higher the weight the greater the probability of surviving by relying on fat reserves until they feed successfully (McMahon et al. 2000). SES are capital breeders, which means they fast during lactation and therefore much of the weight gain of pups will depend on the energy reserves accumulated by females during foraging prior to reproduction (Fedak et al. 1996; Boyd 2000). In this context, changes in prey availability as a consequence of environmental variations in the feeding areas of females can affect their weight gain and indirectly the weight and size of their pups at weaning, which in turn can affect their survival during the first year of life, the probability of recruitment, and consequently the population growth (McMahon et al. 2000; McMahon et al. 2015; McMahon et al. 2017; Clausius et al. 2017; Oosthuizen et al. 2018).

## Sea ice extent and duration vs population trends and weaning mass

Extrinsic factors have been linked to changes in the number of SES at different populations (McMahon et al. 2005b; de Little et al. 2007; Clausius et al. 2017; Hindell et al. 2016; Hindell et al. 2017 among others). For example, population trends for SES breeding on Macquarie Island were negatively related to the extent and concentration of sea ice on the east coast of Victoria Land and the west of the Ross Sea where females forage in winter (van den Hoff 2014; Hindell et al. 2017). The decrease in the success of foraging females and consequently a lower acquisition of reserves to raise their young, which would ultimately affect their chances of survival, were recently related to the population decline observed at Macquarie Island (Clausius et al. 2017). SES females that breed at Peninsula Potter forage in the coastal shelf waters of the WAP that reach the Bellingshausen Sea and at the pack ice edge of that area (Bornemann et al. 2000; Daneri et al. 2015). The regional extent and duration of the sea ice sheet in the WAP decreased during the second half of the last century in association with particular phases of the Southern Annular Mode (SAM) and the high-latitude response to El Niño–Southern Oscillation (ENSO) (Massom and Stammerjohn 2010; Stammerjohn et al. 2008,

2012; Turner et al. 2015). For the Peninsula Potter population, changes in sea ice conditions related to ENSO were linked to both the body condition of the females that came to breed (Carlini 2010) and the weight of pups at weaning (Vergani et al. 2001; Vergani et al. 2008; Carlini 2010). These authors found a negative relationship between the extent of sea ice and the weight of the pups at weaning. They hypothesized that physical conditions in foraging areas during years of increased sea ice extent could be unfavorable to the growth and availability of SES prey and thus indirectly impact on the foraging success and the body condition of Peninsula Potter SES females. The weaning weights of SES pups at Peninsula Potter were negatively related to the El Niño phenomenon (Vergani et al. 2008) and the authors speculated that there might be a greater availability or larger size of the cephalopod *Psychroteuthis glacialis* during La Niña events that allowed females to gain greater weight during their feeding phases. However, this conclusion was questioned by other authors, especially because they did not take into account the possible variation in diet and the potential importance of fish (McMahon et al. 2008). On the other hand, the decline in sea ice extent in the WAP was negatively correlated with the abundance of another common prey of SES, the Antarctic silverfish (*Pleuragramma antarctica)* (Mintenbeck & Torres 2017; Corso et al.2022). Therefore, the link between sea ice extent and SES foraging success in the WAP could be highly variable depending on the predominant prey in the diet.

During our study period (1995–2018), the mean weight of the pups at weaning in the Peninsula Potter colony did not change significantly. Moreover, mean values of the weight of weanlings obtained in this study are well above those reported for declining colonies (e.g., Burton et al. 1997; Clausius et al. 2017) and they are within the range of weights that pups should reach to obtain an advantage when surviving the first years of life (Oosthuizen et al. 2018). This would indicate that, at least at the time analyzed, the foraging success of a large proportion of the females that arrived at the colony was not significantly affected. In addition, we did not find any association between the mean weight of the pups and the observed population trend recorded in this study. Our results indicate that most of the females that arrived at the colony had enough reserves to allocate to their pups for them to reach a weight that would benefit their survival and therefore their probable recruitment in successive years back to the colony as breeders, as reported for other colonies (Oosthuizen 2015, 2018). In this context, we must also consider that the variation in sea ice extent interacts with population trends in other ways that may not be strictly related to female foraging success.

## Dispersal of females

Climate-related shifts in the ecosystem may also affect populations by increasing or restricting access to certain parts of the habitat, thus altering dispersal patterns. Movements between subpopulations and latitudinal expansions of SES colonies appear to have occurred in response to the emerging, ice-free, terrestrial habitat in warm climatic conditions during the Holocene (Hall et al. 2006). The increase in ice-free land areas along the WAP (Lee et al. 2017) as a consequence of the retreat of ice fields and glaciers increases the suitable beach habitat for SES to breed and molt, thus potentially expanding their possible distribution (Siniff et al. 2008). Contrary to our main hypothesis and predictions, our analyses showed a positive relationship between the number of females that reproduce in Peninsula Potter and the extent of sea ice in the WAP. Since the ice conditions during winter do not seem to have affected greatly the foraging success of females, as indicated by changes in the weight of their pups, our alternative hypothesis is that during years of low sea ice extent in winter foraging areas, some females from that colony (probably those that forage at sea ice edge, see Bornemann et al. 2000) select to breed in new ice-free sites closer to foraging areas further south. Since this is a capital breeding species, it may be desirable to reduce energy costs of traveling between feeding and breeding grounds.

The migration of females to ice-free beaches available south of Peninsula Potter during certain years is a plausible explanation for the inter-annual fluctuation in the number of females observed. Although they are scarce, there are sites located south of Peninsula Potter and in close proximity to the foraging areas of the females of this colony where SES were observed breeding, as is the case of Anvers Island (64° 36′S, 63° 30′W), where in the early 1980s a small group of females were observed giving birth and raising their pups (Heimark and Heimark 1986). Between that date and 2005, the number of elephant seals at Anvers Island has increased (Siniff et al. 2008), coinciding in part with the period of decline observed at Peninsula Potter. Unfortunately, the information available for this colony does not allow us to corroborate if females from Peninsula Potter are breeding there.

Although statistically significant, the regression values between the number of females at Peninsula Potter and sea ice in the winter foraging areas does not seem to explain much of the observed changes in abundance, which would indicate that other variables are. A second alternative explanation, although not exclusive of the previous one, is that in certain years the females encounter adverse local conditions in their natal sites and therefore are forced to change to other colonies at the beginning of the reproductive season. For example, at Peninsula Potter, excessive ice accumulation was observed on the coast during the beginning of the 2007 breeding season (September–October) when the lowest number of breeding females was recorded. This "icefoot" was an average of 1.5 m high, which made it difficult for the animals to access the beach from the sea. As a consequence, females were observed forming harems in other areas close to the ASPA that are not part of the censuses given that there had not been registered animals breeding there previously (J.N. personal observation). It is probable that during years of great accumulation of snow, and consequently a greater amount of ice adhering to the coast, certain individuals select nearby areas to breed. Local movements (intra-island and intra-archipelago) of SES have already been reported elsewhere (Hofmeyr 2000; Setsaas et al. 2008; Oosthuizen et al. 2009; Oosthuizen et al. 2011) and the redistribution of breeding females belonging to the colony under study in nearby sites such as Duthoit Point (Fig. 1) was also previously reported (Carlini et al. 2003). Our results indicate that these movements both within the 25 de Mayo Island (i.e., Patelnia Point) and within the South Shetland archipelago (i.e., Duthoit Point in Nelson Island) were not isolated events and occurred several times throughout the study period. Although the percentage of females from Peninsula Potter that were recorded breeding in these colonies is low, it could well be underestimated since censuses were sometimes carried out at least one week after the estimated peak date for female abundance at these latitudes (Carlini et al. 2003), so some individuals may have left the beach for that date. The ages of the marked females observed at both locations range between four and fourteen years old, thus a breeding or even a natal dispersal (Greenwood 1980) could be taking place at Peninsula Potter. The breeding female dispersal observed here may appear low and could be assumed to be negligible, however simulation of SES female migration rates, even those where a small number of animals are involved, can contribute considerably to small colony population dynamics (McMahon et al. 2005c).

When we compare the general decline observed between 1995 and 2018 with available data from the South Shetland islands, we observed that it is opposite to the population trend observed at other localities in the archipelago, like Livingston Island (Gil Delgado et al. 2013) and Elephant Island (Hindell et al. 2016), where recent reports noted an increase in the number of breeding females. However, it is difficult to make accurate comparisons in the population trends between these colonies and Peninsula Potter given the disparity in the time series available. For example, the latest reports for the Elephant Island colony indicate a growth since 2010 (Hindel et al. 2016) which coincides with the trends observed at Peninsula Potter, however there would appear to be a period of time before that date where, to our knowledge, there were no population trend data available in the literature. The same situation occurs when comparing our results with the Livingston Island colony since, although at present the numbers

have increased, the comparisons were made between two counts separated by more than two decades (Gil Delgado et al. 2013). If we consider there has been a general population decline between 1995 and 2018 our results are opposite to most of the current trends in other localities whose population status shows stability or growth, with the exception of the colonies belonging to Prince Edward Island, Gough Island, and all the Macquarie stocks (see Table 6 in Hindell et a 2016). However, the situation changes when analyzing the trends observed after the breakpoint identified in 2008, since the current growth status, although not statistically significant, coincides with that of other populations such as Peninsula Valdes, Possession, Marion and the Crozet Islands (see Table 6 in Hindell et al. 2016). Considering the contrasting trends observed here and the increasing numbers from other localities in the archipelago of the South Shetland Islands, we believe that metapopulational studies are required to better understand population dynamics of this species in an area where there are numerous small nearby colonies.

## Conclusions

Our work provides an update on the population status of this breeding colony and new information for future studies by shedding light on probable causes of the reported population trend. In addition, the population increase registered since 2008 is encouraging and relevant for the conservation efforts and management strategies that are being carried out in ASPA N° 132. Monitoring both this colony as well as those nearby will be important to examine whether females are moving among the colonies during reproduction in order to consider the value that places such as Duthoit Point may have for the population dynamics of this species in the archipelago and to evaluate the possibility of including them in a system of protected areas such as the ASPAs. Finally, we show there is a relationship between population trends and the environmental conditions encountered by the females in winter while foraging, but further studies that include other demographic aspects (i.e., fecundity, mortality and emigration rates) as well as other intrinsic and extrinsic factors are necessary in order to have a clearer picture of the population dynamics of this species at Peninsula Potter.

## Declarations

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