



Diminishing numbers of male southern elephant seals (*Mirounga leonina* Pinnipedia: Phocidae, Linnaeus, 1758) at the Vestfold Hills, East Antarctica (1957–2022)

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Abstract: A proportion of the southern elephant seal (*Mirounga leonina*) population that breeds in the Kerguelen Plateau region seasonally migrates between their natal sub-Antarctic islands and moult haul-out locations on the Antarctic coastline. Analyses of survey data collated for one moult location at the Vestfold Hills, East Antarctica, showed that there had been no appreciable change in the timing (phenology) of maximum seal arrivals between 1974 and 2022; however, the maximum number of seals moulting at that site had declined by ~90% over the same time interval. Spatial analyses showed rates of population change were survey area dependent, as seal numbers decreased most rapidly at haul-out areas closest to the permanently occupied Davis Station, suggesting that a relationship exists between seal numbers and human activities. The range of potential factors that contribute to population change for southern elephant seals moulting at the Vestfold Hills includes changes in status at primary source populations, one of which has not been surveyed since the 1990s, and species relocation. Should numbers of southern elephant seals in the Vestfold Hills continue to decrease at the current average rate of change (-7.78 seals/year) the species could vanish from the area by c. 2040.

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Introduction

Carl Linnaeus described humans (*Homo sapiens*) and southern elephant seals (*Mirounga leonina*) together in 1758, but since then the latter has experienced a range of often negative interactions with the former. First, as a component of the whale oil industry came a period (1790s to late 1800s) of intense commercial harvesting, known then as 'elephanting', at which time southern elephant seal populations were substantially reduced, some to extinction. However, coincident with the demise of the blubber oil industry was a period of population rebound, itself then closely followed by inexplicable decreases in seal numbers at most breeding locations (Hindell *et al.* 2016). Eight potential explanatory factors were proposed, and after competition with commercial fisheries and human disturbance were discounted only interspecific competition and environmental change remained as significant plausible explanations for the observed population changes (McMahon *et al.* 2005). Southern elephant seals are now listed as of Least Concern globally by the International Union for Conservation of Nature; however, this species is variously listed by New Zealand as Nationally Critical (Hitchmough *et al.* 2007) and by Australia as Vulnerable (DCCEEW 2023), and it is explicitly protected within the Antarctic Treaty Area under the Convention for the

Conservation of Antarctic Seals (Hofmeyr 2015, Bester *et al.* 2020). Against a background of continued global anthropogenesis, the outlook for the species is highly likely to include continued and cumulative interactions with human activities both on land and at sea (McKee *et al.* 2004, van den Hoff *et al.* 2017, Bester *et al.* 2020, Orgeret *et al.* 2022).

Southern elephant seals are a cryptic species, spending ~85% of their lives at sea, with ~90% of that time spent submerged. The remainder (~15%) of an elephant seal's life is one of imposed fasting, as individuals are twice-annually bound to a terrestrial existence, once for breeding and once for moulting (Le Boeuf & Laws 1994). The largest southern elephant seal breeding aggregations can be observed during September to late November, mainly but not exclusively on islands scattered throughout the sub-Antarctic zone between ~45° S and ~55° S (Le Boeuf & Laws 1994). Before extirpation, their breeding distribution extended north to 37° S along the eastern South Pacific coast (Acevedo *et al.* 2019) and to King Island, Bass Strait, Australia (39.90° S, 143.97° E; Ling 2002). South of 60° S their breeding aggregations are mainly on islands adjacent to the Antarctic Peninsula; birthing elsewhere on the Antarctic continent south of the mean spring sea-ice limits remains infrequent (Bester *et al.* 2020).

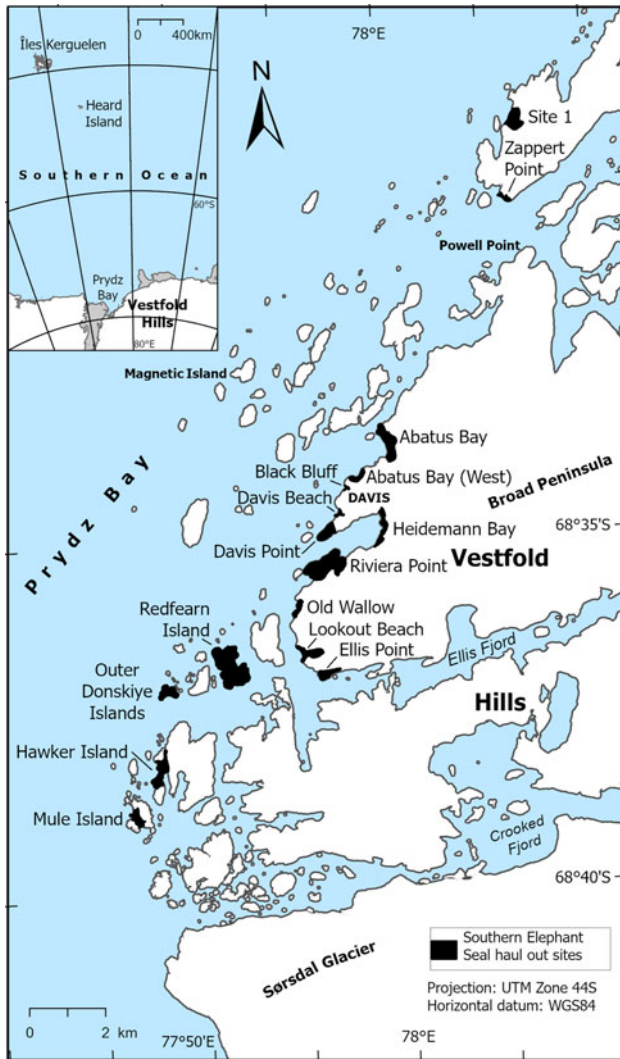


Figure 1. Locations and naming convention for southern elephant seal (*Mirounga leonina*) moult haul-out areas at the Vestfold Hills and offshore islands, Prydz Bay, East Antarctica.

Owing to the relatively late exploration of the Antarctic continent compared with the sub-Antarctic and the Antarctic Peninsula, southern elephant seals were not known there until non-breeding aggregations were seen in East Antarctica during February 1957 at the Vestfold Hills (68° S, 78° E) and during December 1958 at the Windmills Islands (66.0° S, 110.5° E; Ingham 1960); only isolated individuals had been reported prior to that (Erickson & Hofman 1974). There is, however, compelling evidence for a much longer history of southern elephant seal occupation in Antarctica. For example, the Vestfold Hills and Vincennes Bay regions have sites where accumulations of moulted hair and carcasses have been frozen into a matrix of sand and faeces up to 0.71 m deep (Tierney 1977; author's unpublished data 2007). Mummified remains of

southern elephant seals were also discovered at Inexpressible Island, western Ross Sea, and have been ^{14}C dated at > 3,000 years into the Holocene period (Koch *et al.* 2019). There are also ice-free areas that have yet to be fully surveyed for southern elephant seals at the time of their moult, and therefore the existence of additional moulting areas on coastal Antarctica remains open to speculation.

Male southern elephant seals occurred primarily over the summer period on land at the Vestfold Hills, the fringing fast ice having regulated their presence over the winter period (Johnstone *et al.* 1973). In early spring (November and December), well-fattened non-moulting individuals were seen in close proximity to a coastal polynya that had formed at the terminus of the Sørsvdal Glacier, Prydz Bay, and also hauled out on nearby Hawker and Mule islands in the southern Vestfold Hills (Fig. 1; Johnstone *et al.* 1973, Gales & Burton 1989). East Antarctic coastal polynyas are now generally accepted as seasonally dynamic foraging areas for male southern elephant seals originating from natal islands on the Kerguelen Plateau (Labrousse *et al.* 2018, Arce *et al.* 2022). The coincidence of the southward transit of males from sub-Antarctic breeding islands into Antarctic waters (Hindell *et al.* 2016, 2021), the annual recession of the fast ice between October and December (Tierney 1977) and the onset of the annual moult in January culminate in the greatest accumulations of southern elephant seals in East Antarctica during March in each year (Gales & Burton 1989, van den Hoff *et al.* 2003). By April, the sea-ice cover is re-establishing, and the remaining newly moulted seals must cross several kilometres of ice to reach open water (Johnstone *et al.* 1973).

Mark-recapture and telemetry studies have shown moulting male southern elephant seals are faithful to both their natal and potential breeding sub-Antarctic islands and distant moult sites at Antarctic coastal ice-free areas. The vast majority of male southern elephant seals that were either sampled for genetic analyses, fitted with tracking devices or individually marked (flipper-tagged) at the Vestfold Hills were representative of the greater Kerguelen genetic stock, mostly from Heard Island and Îles Kerguelen (Tierney 1977, Bester 1988, Bester *et al.* 2020, Hindell *et al.* 2021, Chua *et al.* 2022). The terrestrial habitat requirements for seals moulting in Antarctica (ice-free, gently sloping sand beaches) can result in their co-occurrence with humans. For example, the once-harvested southern elephant seal population on the South Shetland Islands remains in close proximity to permanently occupied stations (Fudala & Bialik 2020), and seals moulting at the Vestfold Hills - once shot as a source of dog food (Gales & Burton 1989) - aggregate close to Davis Station and associated infrastructures (Burton 1985, Bester *et al.* 2020).

Quasi-annual surveys and observations of the southern elephant seal population at the Vestfold Hills were undertaken from 1957 to 2022. Here, I have collated those data with the objectives to: 1) explore them for changes in phenology and population status for the species over the time series and 2) predict the future status of the population at the most southerly terrestrial haul-out site of the species.

Materials and methods

Study area

The ice-free land of the Vestfold Hills (68°35' S, 78° E) lies on the eastern coast of Prydz Bay, East Antarctica (Fig. 1). The approximately triangular area of ~400 km² is skirted by the East Antarctic Ice Sheet to the east and the Sørsdal Glacier to the south, and the waters of Prydz Bay lap the rocky north-west-facing coastline (O'Brien *et al.* 2015). Coastal fast ice forms from approximately mid-March and reaches maximum thickness and extent in October–November before clearing out in late December (Heil 2006).

Data acquisition

Spatial and temporal occurrences of southern elephant seals at the Vestfold Hills have been recorded over the period 1957–2022. Data previously presented by Johnstone *et al.* (1973), Tierney (1977) and Gales & Burton (1989) are supplemented here with survey data collected for the period 1986–2022. Individuals that were not clearly within a predefined haul-out area during that later period were assigned to the nearest predefined area.

The ~18 km length of mainland coast between Powell Point and Ellis Point (Fig. 1) was the area most often surveyed on foot. Offshore islands were surveyed either from the air or on foot after being accessed using over-water (summer) or over-ice (winter) transport. Each sighting record contained the date, a location, a count of the number of seals, the sex of each individual and their age class whenever observer experience allowed. Two different age classification methods have been used over the study period: that in Tierney (1977) and a visual age classification based on Laws (1953) introduced from *c.* 2018. This change made it possible for non-specialists to estimate age from appearance rather than estimates of length. Class I seals were aged 1–3 years, class II seals were aged 4–6 years, class III seals were aged 7–9 years and class IV seals were aged 9+ years, which approximately equated to fig. 22c,d,e,f, respectively, in Laws (1953).

Observed and predicted numbers

Count data were not standardized within and between years (e.g. counts were daily in some years but not in

others) and not all areas were surveyed in all years. Nevertheless, the phenology of elephant seal arrivals and departures during their terrestrial phases is highly predictable and can be described using stochastic models, such as the normal distribution with a mean and a standard deviation (Slip & Burton 1999). In that way, the number and day of maximum seals ashore and the day of maximum arrival rate can be predicted from inconsistent count data.

Modelling southern elephant seal phenology at the Vestfold Hills followed the general approaches detailed by Slip & Burton (1999) and Authier *et al.* (2011), with the exception that the average residence period (d) was fixed at 37.97 days (i.e. the mean duration of the moult for male southern elephant seals at the Vestfold Hills; Gales & Burton 1989). I assumed d was consistent across age classes; however, moult duration can vary with age in females (de Kock *et al.* 2021). Model parameters were estimated using a non-linear mixed effects approach (Pinheiro & Bates 2000) generalized to allow maximum seal abundance (N_{\max}) to vary from year to year, with random effects for timing of maximum arrivals (a) and fixed effects for residence time (d , above) and the standard deviation for the day of arrival (s).

Population parameters

Annual finite rates of population change (λ) were estimated as N_{t+1}/N_t , where $N = N_{\max}$ and $t = \text{year}$. The average annual rate of change (r) was estimated as the slope of the linear regression for N_{\max} over the chosen time intervals (Hone 1999).

Statistics

Anomalies were calculated as the difference between the annual mean for a given year and the long-term annual mean. The predicted day of the maximum rate of arrivals (a) was used here as a measure of potential shifts in phenology. All statistical analyses were done using *R* 3.5.0 (R Core Team 2018). Regression analyses were done within the *car* package (Fox & Weisberg 2019) and results were graphed using *ggplot2* (Wickham 2016). Unless otherwise specified, means are accompanied by standard errors (s.e.).

Results

Winter presence

Over-ice surveys undertaken during the winters of 1957 and the early 1970s confirmed that hundreds of southern elephant seals occurred in the area of Hawker and Mule islands close to the Sørsdal Glacier (Fig. 1). Total numbers of seals sighted in the Mule and Hawker



Figure 2. Southern elephant seals (*Mirounga leonina*) at the Vestfold Hills, East Antarctica. **a.** Impression of a seal left on the fast ice near Sørsdal Glacier (22 July 2022); in this case, the yellow ice indicates a male seal was present (photograph: Derryn Harvie). **b.** The carcass of a male seal in the process of being incorporated into the accumulation of frozen hair/sand/faeces at Old Wallow. Living, moulting seals can be seen in the background (8 February 2019; photograph: Kris Carlyon). Note the polished rocks suggesting long-term haul-out area usage. **c.** A large male (>9 years of age) resting on Davis beach, a gently sloping sandy beach adjacent to Davis Station. Note the proximity of the wharf infrastructure (5 February 2019; photograph: Kris Carlyon). **d.** An unusual influx of under-yearling seals on Davis beach (18 March 2019; photo credit unknown). The view in **d.** is behind the photographer taking the image in **c.**

islands area varied from 0 (September) to 358 (December) over the period 6 July 1957–17 December 1957, with numbers increasing most rapidly in early November (source: https://data.aad.gov.au/metadata/Biology_Log_Mawson_1950s). Seals were also seen during April 1957 on the fast ice adjacent to a polynya at the terminus of the Sørsdal Glacier (Fig. 1). While no live seals were seen in that polynya area in recent times, their presence was

established from their imprints in the snow covered fast ice (Fig. 2a).

Fifty-two individuals were seen on one occasion at Magnetic Island (Fig. 1) during the third week of April 1957. There have been no reports of future occurrences at that island. No seals were recorded during winter at the Davis beach haul-out area adjacent to the permanently occupied Davis Station.

Moult haul-out area locations and usage

Up to 16 separate moulting haul-out areas have been recognized from repeated seal occurrences and from accumulations of moulted hair (Figs 1 & 2b). Not all haul-out areas were used in each year; some appeared to have been abandoned for some considerable period (e.g. Site 1 and Zappert Point; Fig. 1), whereas others were apparently used on an irregular basis.

The naming convention for haul-out areas in the Vestfold Hills has evolved over the study period to a point where aggregations of seals separated by as little as 100 m were assigned to separate haul-out areas (e.g. Davis beach and Davis wallow = Davis beach; North and South Heidemann Point = Riviera Point). Here, I have reviewed that naming convention and provide a

simplified convention that might be used in future years (Fig. 1). The approximate boundaries for the renamed moult haul-out areas are shown in Fig. 1, bearing in mind that these boundaries can move both within and between survey years.

Phenology of arrivals and departures at the Davis beach haul out

The Davis beach haul-out area is within 100 m of the permanently occupied Davis Station (Figs 1 & 2c,d), and therefore it was the most consistently and comprehensively surveyed of all haul outs in this study. There was at least one survey in that area during 48 of 65 possible seasons between 1957 and 2022 inclusive, noting that the station was unoccupied for four seasons

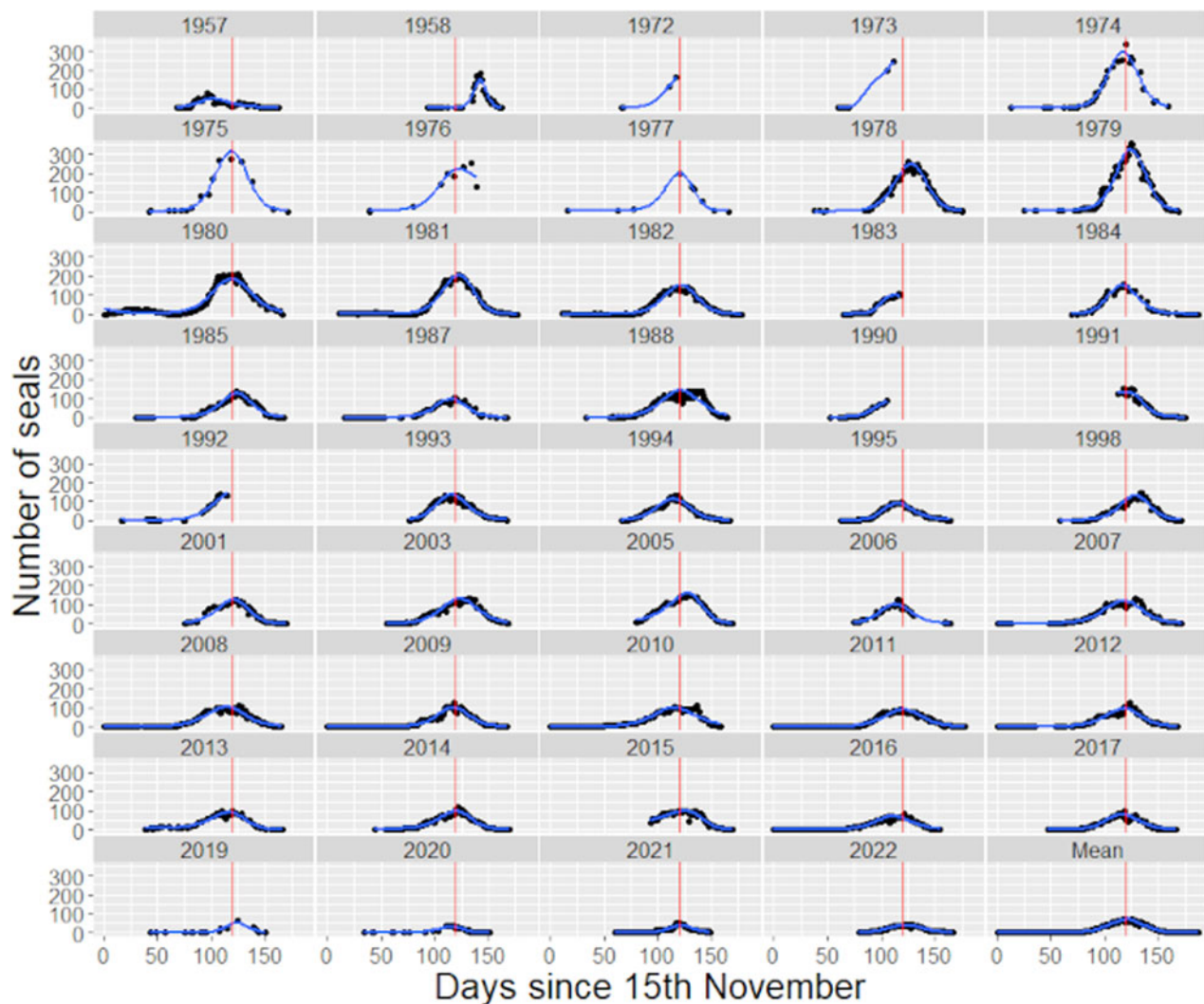


Figure 3. Phenology of arrivals and departures and diminishing maximum numbers of southern elephant seals (*Mirounga leonina*) at the Davis beach moult haul-out area, Vestfold Hills, East Antarctica (1957–2022). Day 0 = 15 November in the previous year (e.g. day 0 for the 1957 plot = 15 November 1956). The curved blue lines represent the normal distribution model fitted to the observational data (black dots). The vertical red lines indicate the arithmetic mean ($n = 44$) for the date of maximum seal numbers (15 March).

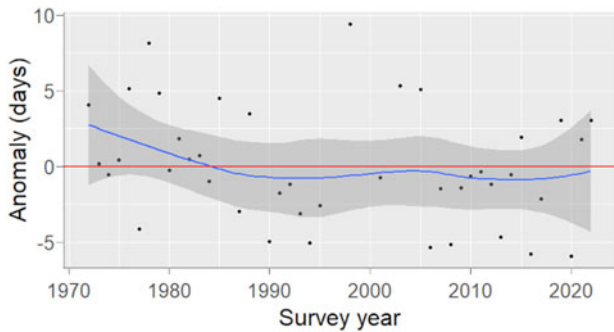


Figure 4. Anomalies for the predicted day of maximum arrival rate (*a*) for southern elephant seals (*Mirounga leonina*) at the Davis beach haul-out area, Vestfold Hills, East Antarctica (1972–2022). Blue line = the locally weighted mean fitted curve with 95% confidence intervals (grey shading). Red line = overall mean (23 February). A negative anomaly = a later arrival date. The non-linear mixed effects approach was generalized to allow seal abundance to vary from year to year, with random effects for timing of *a* and fixed effects for residence time and the standard deviation for the day of arrival.

between January 1965 and February 1969. On average, the Davis beach haul-out area was surveyed 74 ± 55 times within a season (range: 0–178).

The 1957 and 1958 seasons are curious in that the timings of arrivals at Davis beach were different from most other survey years (Fig. 3). Commentary in the January 1957–December 1958 station log book suggested that the sudden drop in seal numbers in late February 1957 could be attributed to the direct removal (shooting) of seals for dog food, and the late arrival of moulting seals in 1958 appears to be linked with the late disappearance (30 March) of the fast ice from the beach front (Fig. 3).

Excluding the pre-1958 data, the general bell-shaped patterns of seal arrivals and departures were consistent between years. Insufficient temporal spread of count data contributed most to failures of model fitting and thus to the exclusion of seasons 1971/1972, 1972/1973, 1982/1983, 1989/1990 and 1991/1992 from analyses. Models fitted to the remaining observational data suggested 100% of seals (i.e. N_{max}) arrived at Davis beach sometime between 13 and 20 March, with a mean date of 15 March ($n = 37$). Approximately 5% of seals arrived by 1 February and 95% by 13 March, ~5% had departed by 19 March and 95% were gone by 24 April (lower right panel in Fig. 3). The predicted mean date of maximum seal arrival rate (*a*) was consistently near 23 February (± 3.8 days).

There was a statistically weak linear change for the timing of maximum arrivals (*a*) over the period from 1972 to 2022, *a* was earlier at a mean rate of -0.06 ± 0.04 days with each passing year ($F_{(1,40)} = 2.59$, $P = 0.11$, $R_{adj} = 0.04$). Neither *survey year* or N_{max} , nor their

interactions, was a significant predictor of change in *a* (global interaction model: $F_{(3,38)} = 1.54$, $P = 0.22$, $R_{adj} = 0.04$). There was considerable but consistent variation in anomalous values for *a* over the study period (Fig. 4). Anomalous values for *a* were latest during the 1970s but have remained relatively unchanged since c. 1980 (Fig. 4).

Maximum numbers of seals (N_{max})

Predicted values for N_{max} at Davis beach were in good agreement with observed values ($R_{adj} = 0.96$, $F_{(1,39)} = 902.6$, $P < 0.001$), the former providing the larger sample size for the following analyses. Predicted N_{max} at Davis beach decreased from a high of ~330 individuals in 1974 to ~46 individuals in 2022 at an average (*r*) of $-3.89 (\pm 0.42)$ seals per year ($F_{(1,40)} = 83.14$, $P = 0.001$, $R_{adj} = 0.67$). A locally weighted curve fitted to the modelled values (Fig. 5) showed strong evidence of a stepwise change in predicted N_{max} over the time series. There were two well-defined periods of decrease: 1972–1990 and 2005 onward, when *r* was -10.0 and -5.5 , respectively. Those periods of decrease were interrupted by a period of relative stability (c. 1990–2005), when *r* was < -1 (Fig. 5). If the rate of decrease in seal numbers on Davis beach continues unabated at its current rate of -5.5 per year, we might expect there to be no seals in the area by c. 2030–2035.

In line with the Davis beach area, the whole of the Vestfold Hills population has decreased over the 45 year period from ~467 southern elephant seals in 1975 to ~117 individuals in 2020, at an *r* of -7.78 seals per year (Table 1). If *r* for the whole of the Vestfold Hills population continues unmitigated into the future, southern elephant seals could vanish from the area by c. 2040.

In both 1975 and 2020 (the years with the most comprehensive survey efforts), most (> 50%) of the seals

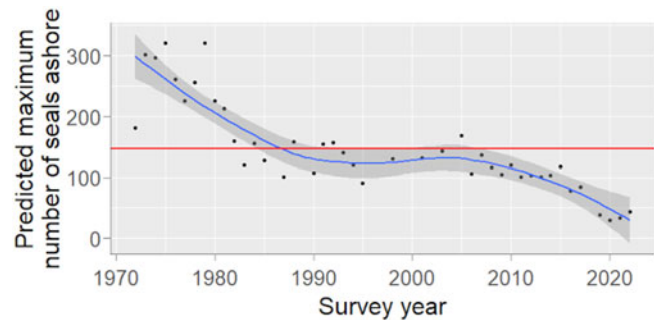


Figure 5. Predicted maximum numbers of southern elephant seals (*Mirounga leonina*) ashore annually within the Davis beach haul-out area, Vestfold Hills, East Antarctica (1972–2022). Blue line = the locally weighted mean curve. Red line = mean (1972–2022). Grey shading = 95% confidence intervals.

Table I. Estimates of maximum population size (N_{\max}) and annual finite rates of change (λ) for the southern elephant seal (*Mirounga leonina*) populations within three haul-out areas at the Vestfold Hills, East Antarctica. Numbers in parentheses are percentages of the population in the haul-out area.

Haul-out area	N_{\max}			λ
	18 March 1958	13 March 1975	11 March 2020	
Davis beach to Long Fjord	NA	275 (59)	63 (54)	-4.71
Riviera Point	NA	140 (30)	35 (30)	-2.33
Old Wallow to Ellis Point	NA	52 (11)	19 (16)	-0.73
Broad Peninsula total	457	467	117	-7.78

NA = not available.

in the Broad Peninsula area were observed at haul-out sites between Davis beach and Black Bluff, ~30% were within the Riviera Point area and < 20% were at sites between Old Wallow and Ellis Point inclusive (Fig. 1 & Table I). Area-specific finite rates of annual population change (λ) increased with increasing proximity to Davis Station infrastructure, and λ was slowest for the section of coast between Old Wallow and Ellis Fjord (Table I).

Age structure

A broad range of age classes of moulting male southern elephant seals were observed at the Vestfold Hills. Generally, a smaller proportion of the population was classified into age classes I and II compared with age classes III or above (Figs 2c & 6). There was an influx of under-yearling seals at the Davis beach haul-out area on 18 March 2019 (Fig. 2d).

Discussion

Judging from ^{14}C dating for basal sediments of accumulated hair deposits, it seems probable that southern elephant seals have aggregated to moult at the Vestfold Hills for *c.* 3500 years (author's unpublished data 2007). Remains of southern elephant seals, some older than 4000 years, are known from the Victoria Valley Coast, Ross Sea, but the presence of living individuals has discontinued in that region relative to late Holocene advances in sea ice (de Bruyn *et al.* 2009). Only Vincennes Bay and the Vestfold Hills are known to have aggregations of living southern elephant seals (Gales & Burton 1989, van den Hoff *et al.* 2003), and both of these locations are within the Australian Antarctic Territory.

The results of this study at the Vestfold Hills have shown that some aspects of the current (2022) population of moulting male southern elephant seals were consistent

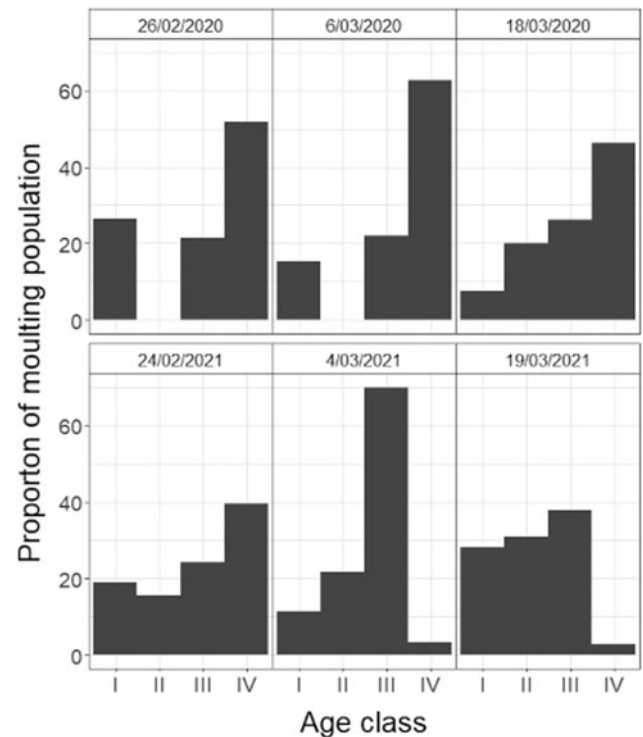


Figure 6. Proportions of the Vestfold Hills southern elephant seal (*Mirounga leonina*) population grouped by age class, March 2020 and 2021. Class I = 1–3 years old, class II = 4–6 years old, class III = 7–9 years old and class IV = 9+ years old.

with previous descriptions, whereas others have changed. Early surveys found non-moulting individuals were on Hawker and Mule islands during winter (Johnstone *et al.* 1973), and their winter presence in that area was recently evidenced only from imprints left in the snow-covered fast ice (Fig. 2a). Access to prey associated with a polynya at the terminus of Sørsdal Glacier is a plausible explanation for the seasonal presence of male southern elephant seals in that area (Ingham 1960, Johnstone *et al.* 1973, Arce *et al.* 2022). The close proximity of the polynya to suitable moulting habitat may also play a role because individuals foraging at the polynya during the post-breeding to pre-moult pelagic phase need not cross almost 2500 km of ocean to return to their natal islands for the moult. The absence of southern elephant seals from the Vestfold Hills during September–December continues to coincide with the breeding season for the species at natal sub-Antarctic islands (Johnstone *et al.* 1973).

A change in age classification methods made it difficult to determine whether there has been a temporal shift in the age structure of the population of male southern elephant seals at the Vestfold Hills. Nevertheless, individuals classified into age classes III and IV predominated during February and March of 2020 and 2021 (Figs 2c & 6), and they also predominated during the study by

Tierney (1977). A lower proportion of individuals classified into age classes I and II not only reflects differences in moult timing (Hindell & Burton 1988) but also reflects the general southward shift in foraging ranges as males age (Field *et al.* 2005, Chaigne *et al.* 2013).

Of interest from this study was the appearance of multiple (> 20) under-yearling southern elephant seals at Davis beach on a single day in March 2019 (Fig. 2d). That observation not only attests to the capacity of young individuals to undertake very long-distance migrations between natal sites and the Antarctic coast when sea-ice conditions are favourable; it also suggests considerable flexibility in foraging niche width for juvenile southern elephant seals, which is in contrast to the notion of individual age/sex-related 'ecological species' as proposed by Field *et al.* (2005). Finally, the presence of multiple individuals on the same day allows for speculation that under-yearling southern elephant seals might exhibit collective behaviours. Collective foraging behaviours have yet to be confirmed for elephant seals, but other pinnipeds exhibit such behaviours (Heithaus & Dill 2009).

One constant throughout this study has been the near-complete absence of adult female southern elephant seals at the Vestfold Hills, and, moreover, no births have been documented there since human occupation began (Tierney 1977, Gales & Burton 1989). The absence of adult females at the Vestfold Hills is not entirely unexpected as several factors conspire against their presence in Antarctica. Adult females are typically faithful to their natal islands, they forage at the edge of the sea-ice zone moving northward as the ice field expands away from Antarctica and their moulting season commences at a time when the land-fast ice has yet to clear (Bester 1988, Slade *et al.* 1998, Heil 2006, Hindell *et al.* 2016). However, current models predict a reduced ice cover with increasing global temperatures (Urbański & Litwicka 2022), potentially (re)opening habitat on the Antarctic coastline at a time suited to breeding and moulting for females. Warming has been proposed as a factor in early Holocene occurrences of southern elephant seals on the Ross Sea coastline, Victoria Land Coast (de Bruyn *et al.* 2009). For adult female southern elephant seals to aggregate for breeding at high latitudes (> 65° S) on the Antarctic continent would require flexibility in evolved behaviours, including faithfulness to foraging areas and natal islands in the sub-Antarctic. Indeed, there may be some evidence of this already occurring as southern elephant seal populations expand into new habitat created with the warming of the west Antarctic Peninsula area (Siniff *et al.* 2008).

All southern elephant seals moult annually, and the replacement of the pelage is thought to be coordinated with seasonal gradients of photoperiod acting through

neuro-endocrine pathways, an environmental cue that is inextricably linked to the periodicity of the Earth's rotation (Ling 1970). Since the periodicity of the Earth's rotation changes only over geological time scales (Denis *et al.* 2011), it is not surprising that a strong relationship should exist between survey date (time) and southern elephant seal moulting. Although there were acknowledged shortcomings in the modelling approaches used during previous studies, the model approaches that were chosen provided some biologically meaningful parameters (Condy 1979, Hindell & Burton 1988, Slip & Burton 1999, Authier *et al.* 2011). One parameter - the date of maximum arrival rate (a) - was considered here as a means of comparing changes in moulting phenology at the population level. Analyses showed weak evidence of a linear trend towards an earlier timing over the study period (slope = -0.06 ± 0.03 days), but overall values for a remained statistically unchanged over the 50 year study period (Fig. 4). The phenology of the moult in adult female southern elephant seals at Marion Island also remained unchanged over a 32 year study period, and, as opposed to findings for Davis beach (Fig. 4), there was a weak linear trend towards a later moult arrival date for seals at Marion Island (de Kock *et al.* 2021).

One environmental factor that might impact the phenology of male southern elephant seal arrivals at moult sites on the coast of East Antarctica is a temporal change in the timing of fast-ice presence. Heil (2006) has shown evidence for a 0.43 day year⁻¹ delay in fast-ice breakout at the Vestfold Hills over similar timespans as this study, but so far the timing of maximum arrival for seals moulting on Davis beach (model parameter a) appears statistically unaffected, perhaps because mean ice breakout was complete by early January and mean date of maximum seal arrivals was mid- to late February.

The conservation status of the southern elephant seal has been, and in some cases remains, a matter of concern as reports of substantial decreases in numbers of adult females at most breeding locations first surfaced in the 1980s (McMahon *et al.* 2005, Hofmeyer 2015, DCCEEW 2023), and the importance of long-term survey data in continually (re)assessing the status of species cannot be understated in that regard. This long-term study has shown evidence of a stepwise downward trend in N_{\max} at the Davis beach haul-out area (Fig. 5). Moreover, the severity of the downward trend was area-specific, being greatest nearest to Davis Station, which is coincidentally the census area with the greatest data acquisition and nearest to associated human activities compared with more remote sub-areas (Table I). Past speculation suggested that low numbers of seals in the Davis beach haul-out area were the result of seals being taken for dog food and/or the cumulative effects of human activities (Johnstone *et al.* 1973, Gales

& Burton 1989). Although no seals have been shot for dog food in some considerable time, the potential impacts of station-associated human activities, whether cumulative or not, on southern elephant seal population status at Davis beach remain unmeasured and therefore cannot be discounted. Should the rate of population change continue along its present downward trajectory, male southern elephant seals are predicted to vanish from the Vestfold Hills within 100 years of human occupation, perhaps earlier at moult haul-out areas nearest to Davis Station.

Past studies have looked to population status at source populations to explain the status of male southern elephant seals in East Antarctica (Gales & Burton 1989, van den Hoff *et al.* 2003). Indeed, visual comparisons of census results of seals at Davis beach (this study) and at Courbet Peninsula, Îles Kerguelen (Guinet *et al.* 1999, Authier *et al.* 2011), a known source population for seals moulting at the Vestfold Hills, showed that numbers of male southern elephant seals ashore at Davis beach (Fig. 5) mirrored changes in numbers of females at the source island, at least for the period from *c.* 1970 to the late 1990s. With the benefit of long-term data collection, we can now see evidence that the population trajectories diverged during the mid-2000s (compare Fig. 5 of this study with Laborie *et al.* 2023). The causes of such a divergence could be multifaceted and presently are speculative, but one possibility is a change in regional foraging behaviour (C. Guinet, personal communication 2023). As the proportion of the male seals from Îles Kerguelen feeding close to Antarctica has been shown to be decreasing over time (Authier *et al.* 2011, Chaigne *et al.* 2013), it might follow that fewer males are electing to moult on the Antarctic continent.

Another source of uncertainty comes from our limited understanding of the population trajectory for southern elephant seals at Heard Island; after Îles Kerguelen, Heard Island is the next largest source population to the Vestfold Hills. The Vestfold Hills and Heard Island populations shared similar trajectories up until the Heard Island population was last counted in 1992 (Slip 1999). The recent and expanding gap in data acquisition for Heard Island does not allow me to compare population trajectories for the two source populations and against the Vestfold Hills population. Therefore, potential recent (post-2005) influences of the Heard Island population cannot be accounted for in the Vestfold Hills story.

There may be other explanatory variables, such as survey design, contributing to the observed Vestfold Hills population trajectory that require further investigation. For example, in the case of this study, the survey area was inconsistent between years and often constrained to the coast between Ellis and Long fjords or individual areas within that greater area (Fig. 1) that

were accessible on foot. Such a constrained survey area leads to the (remote) possibility that the Vestfold Hills population has actually remained stable and a 'decreasing' population status could be a consequence of the redistribution of seals into un(der)surveyed areas. At the local scale of the Vestfold Hills, seals may be present but undetected at suitable habitats on offshore islands such as Magnetic Island, where seals have been recorded in the past. At a broader scale, moulting male southern elephant seals may now be concentrating at undiscovered haul-out habitats along the coast of Antarctica. Unknown moult haul-out locations might be identifiable from high-resolution satellite imagery of ice-free areas (e.g. Obu *et al.* 2020) taken in March combined with locations of dry phases (i.e. the seal is *not* in the water) in present and future telemetry data.

The main outcomes from this study of population change in moulting southern elephant seals at the Vestfold Hills are that:

- 1) In order to attribute explanatory variables, there is a need to better monitor the status of southern elephant seals in proximity to human activities in the broader East Antarctic context and at source populations.
- 2) There may be undiscovered southern elephant seal moult haul-out habitats on the Antarctic coast.
- 3) A precautionary approach may be necessary to mitigate against perceived negative impacts of human activities on southern elephant seal population status, especially where the seals and humans are in close contact.

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Data accessibility

van den Hoff, J. 2023. Vestfold Hills, Davis Station southern elephant seal numbers 1957–2022, Ver. 1. Australian Antarctic Data Centre. Retrieved from https://data.aad.gov.au/metadata/AAS_2265_Elephant_seal_counts_Vestfold_Hills.

References

- ACEVEDO, J., VARGAS, R., TORRES, D. & AGUAYO-LOBO, A. 2019. Northerly births of the southern elephant seal (*Mirounga leonina*) in their former southeast Pacific distribution. *Aquatic Mammals*, **45**, 293–298.
- ARCE, F., HINDELL, M.A., MCMAHON, C.R., WOTHERSPOON, S.J., GUINET, C., HARCOURT, R.G. & BESTLEY, S. 2022. Elephant seal foraging success

- is enhanced in Antarctic coastal polynyas. *Proceedings of the Royal Society B*, **289**, 20212452.
- AUTHIER, M., DELORD, K. & GUINET, C. 2011. Population trends of female elephant seals breeding on the Courbet Peninsula, Îles Kerguelen. *Polar Biology*, **34**, 319–328.
- BESTER, M.N. 1988. Marking and monitoring studies of the Kerguelen stock of southern elephant seals *Mirounga leonina* and their bearing on biological research in the Vestfold Hills. *Hydrobiologia*, **165**, 269–277.
- BESTER, M.N., BORNEMANN, H., DANERI, G.A. & VAN DEN HOFF, J. 2020. Southern elephant seals (*Mirounga leonina* L.) in the Antarctic Treaty Area. Retrieved from <https://environments.aq/publications/southern-elephant-seals-mirounga-leonina-l-in-the-antarctic-treaty-area/> (accessed 30 May 2022).
- BURTON, H.R. 1985. Tagging studies of male southern elephant seals (*Mirounga leonina* L.) in the Vestfold Hills area, Antarctica, and some aspects of their behaviour. In LING J.K. & BRYDEN, M.M. eds, *Studies of sea mammals in south latitudes*. Adelaide: South Australian Museum, 19–30.
- BURTON, H.R. 1986. A substantial decline in numbers of the southern elephant seal at Heard Island. *Tasmanian Naturalist*, **86**, 4–8.
- CHAIGNE, A., AUTHIER, M., RICHARD, P., CHEREL, Y. & GUINET, C. 2013. Shift in foraging grounds and diet broadening during ontogeny in southern elephant seals from Kerguelen Islands. *Marine Biology*, **160**, 977–986.
- CHUA, M., HO, S.Y., MCMAHON, C.R., JONSEN, I.D. & DE BRUYN, M. 2022. Movements of southern elephant seals (*Mirounga leonina*) from Davis Base, Antarctica: combining population genetics and tracking data. *Polar Biology*, **45**, 1163–1174.
- CONDY, P.R. 1979. Annual cycle of the southern elephant seal *Mirounga leonina* (Linn.) at Marion Island. *African Zoology*, **14**, 95–102.
- DCCEE. 2023. *Mirounga leonina* (southern elephant seal). Department of Climate Change, Energy, the Environment and Water. Retrieved from <https://www.dcceew.gov.au/environment/biodiversity/threatened/conservation-advice/mirounga-leonina> (accessed 14 March 2023).
- DE BRUYN, M., HALL, B.L., CHAUKE, L.F., BARONI, C., KOCH, P.L. & HOELZEL, A.R. 2009. Rapid response of a marine mammal species to Holocene climate and habitat change. *PLoS Genetics*, **5**, e1000554.
- DE KOCK, L., OOSTHUIZEN, W.C., BELTRAN, R.S., BESTER, M.N. & DE BRUYN, P.J. 2021. Determinants of moult haulout phenology and duration in southern elephant seals. *Scientific Reports*, **11**, 1–13.
- DENIS, C., RYBICKI, K.R., SCHREIDER, A.A., TOMECKA-SUCHOŃ, S. & VARGA, P. 2011. Length of the day and evolution of the Earth's core in the geological past. *Astronomische Nachrichten*, **332**, 24–35.
- ERICKSON, A.W. & HOFMAN, R.J. 1974. Antarctic seals. *Antarctic Map Folio Series*, **18**, 4–12.
- FIELD, I.C., BRADSHAW, C.J., BURTON, H.R., SUMNER, M.D. & HINDELL, M.A. 2005. Resource partitioning through oceanic segregation of foraging juvenile southern elephant seals (*Mirounga leonina*). *Oecologia*, **142**, 127–135.
- FOX, J. & WEISBERG, S. 2019. *An R companion to applied regression* (3rd edition). Thousand Oaks, CA: Sage.
- GALES, N. & BURTON, H. 1989. The past and present status of the southern elephant seal (*Mirounga leonina* Linn.) in Greater Antarctica. *Mammalia*, **53**, 35–47.
- GUINET, C., JOUVENTIN, P. & WEIMERSKIRCH, H. 1999. Recent population change of the southern elephant seal at Îles Crozet and Îles Kerguelen: the end of the decrease?. *Antarctic Science*, **11**, 193–197.
- HEIL, P. 2006. Atmospheric conditions and fast ice at Davis, East Antarctica: a case study. *Journal of Geophysical Research - Oceans*, **111**, 10.1029/2005JC002904.
- HEITHAUS, M.R. & DILL, L.M. 2009. Feeding strategies and tactics. In *Encyclopedia of marine mammals*. Cambridge, MA: Academic Press, 414–423.
- HINDELL, M.A. & BURTON, H.R. 1988. Seasonal haul-out patterns of the southern elephant seal (*Mirounga leonina* L.), at Macquarie Island. *Journal of Mammalogy*, **69**, 81–88.
- HINDELL, M.A., MCMAHON, C.R., JONSEN, I., HARCOURT, R., ARCE, F. & GUINET, C. 2021. Inter- and intrasex habitat partitioning in the highly dimorphic southern elephant seal. *Ecology and Evolution*, **11**, 1620–1633.
- HINDELL, M.A., MCMAHON, C.R., BESTER, M.N., BOEHME, L., COSTA, D., FEDAK, M.A., et al. 2016. Circumpolar habitat use in the southern elephant seal: implications for foraging success and population trajectories. *Ecosphere*, **7**, e01213.
- HITCHMOUGH, R., BULL, L. & CROMARTY, P. 2007. *New Zealand threat classification system lists*. Wellington: Department of Conservation, 194 pp.
- HOFMEYR, G.J.G. 2015. *Mirounga leonina*. In *The IUCN Red List of Threatened Species* 2015. Retrieved from <https://dx.doi.org/10.2305/IUCN.UK.2015-4.RLTS.T13583A45227247.en> (accessed 14 March 2023).
- HONE, J. 1999. On rate of increase (*r*): patterns of variation in Australian mammals and the implications for wildlife management. *Journal of Applied Ecology*, **36**, 709–718.
- INGHAM, S.E. 1960. The status of seals (Pinnipedia) at Australian Antarctic stations. *Mammalia*, **24**, 422–430.
- JOHNSTONE, G.W., LUGG, D.J. & BROWN, D.A. 1973. The biology of the Vestfold Hills, Antarctica. *Australian National Antarctic Research Expeditions Scientific Reports, Series B (I) Zoology*, **123**, 44–49.
- KOCH, P.L., HALL, B.L., DE BRUYN, M., HOELZEL, A.R., BARONI, C. & SALVATORE, M.C. 2019. Mummified and skeletal southern elephant seals (*Mirounga leonina*) from the Victoria Land Coast, Ross Sea, Antarctica. *Marine Mammal Science*, **35**, 934–956.
- LABORIE, J., AUTHIER, M., CHAIGNE, A., DELORD, K., WEIMERSKIRCH, H. & GUINET, C. 2023. Estimation of total population size of southern elephant seals (*Mirounga leonina*) on Kerguelen and Crozet archipelagos using very high-resolution satellite imagery. *Frontiers in Marine Science*, **10**, 1149100.
- LABROUSSE, S., WILLIAMS, G., TAMURA, T., BESTLEY, S., SALLÉE, J.B., FRASER, A.D., et al. 2018. Coastal polynyas: winter oases for subadult southern elephant seals in East Antarctica. *Scientific Reports*, **8**, 1–15.
- LAWS, R.M., 1953. The elephant seal (*Mirounga leonina*, Linn.): I. Growth and age. *Falkland Islands Dependencies Survey, Scientific Reports* **3**, 1–11.
- LE BOEUF, B.J. & LAWS, R.M. 1994. Elephant seals. In LE BOEUF, B.J. & LAWS, R.M., eds, *Elephant seals: population ecology, behavior, and physiology*. Berkeley, CA: University of California Press, 1–26.
- LING, J.K. 1970. Pelage and molting in wild mammals with special reference to aquatic forms. *The Quarterly Review of Biology* **45**, 16–54.
- LING, J.K. 2002. Impact of colonial sealing on seal stocks around Australia, New Zealand and subantarctic islands between 150 and 170 degrees east. *Australian Mammalogy*, **24**, 117–126.
- MCKEE, J.K., SCIULLI, P.W., FOOCE, C.D. & WAITE, T.A. 2004. Forecasting global biodiversity threats associated with human population growth. *Biological Conservation*, **115**, 161–164.
- MCMAHON, C.R., BESTER, M.N., BURTON, H.R., HINDELL, M.A. & BRADSHAW, C.J. 2005. Population status, trends and a re-examination of the hypotheses explaining the recent declines of the southern elephant seal *Mirounga leonina*. *Mammal Review*, **35**, 82–100.
- O'BRIEN, P.E., SMITH, J., STARK, J.S., JOHNSTONE, G., RIDDLE, M. & FRANKLIN, D. 2015. Submarine geomorphology and sea floor processes along the coast of Vestfold Hills, East Antarctica, from multibeam bathymetry and video data. *Antarctic Science*, **27**, 566–586.

- OBU, J., WESTERMANN, S., VIEIRA, G., ABRAMOV, A., BALKS, M.R., BARTSCH, A., *et al.* 2020. Pan-Antarctic map of near-surface permafrost temperatures at 1 km² scale. *The Cryosphere*, **14**, 497–519.
- ORGERET, F., THIEBAULT, A., KOVACS, K.M., LYDERSEN, C., HINDELL, M.A., THOMPSON, S.A., *et al.* 2022. Climate change impacts on seabirds and marine mammals: the importance of study duration, thermal tolerance and generation time. *Ecology Letters*, **25**, 218–239.
- PINHEIRO, J.C. & BATES, D.M. 2000. *Mixed-effects, odels in S and S-PLUS*. Berlin: Springer, 528 pp.
- R CORE TEAM. 2018. *R: a language and environment for statistical computing*. Vienna: R Foundation for Statistical Computing. Retrieved from <https://www.R-project.org>
- SINIFF, D.B., GARROTT, R.A., ROTELLA, J.J., FRASER, W.R. & AINLEY, D. 2008. Projecting the effects of environmental change on Antarctic seals. *Antarctic Science*, **20**, 425–435.
- SLADE, R.W., MORITZ, C., HOELZEL, A.R. & BURTON, H.R. 1998. Molecular population genetics of the southern elephant seal *Mirounga leonina*. *Genetics*, **149**, 1945–1957.
- SLIP, D.J. & BURTON, H.R. 1999. Population status and seasonal haulout patterns of the southern elephant seal (*Mirounga leonina*) at Heard Island. *Antarctic Science*, **11**, 38–47.
- TIERNEY, T.J. 1977. The southern elephant seal, *Mirounga leonina* (L.), in the Vestfold Hills, Antarctica. *Wildlife Research*, **4**, 13–24.
- URBAŃSKI, J.A. & LITWICKA, D. 2022. The decline of Svalbard land-fast sea ice extent as a result of climate change. *Oceanologia*, **64**, 535–545.
- VAN DEN HOFF, J., DAVIES, R. & BURTON, H. 2003. Origins, age composition and change in numbers of moulting southern elephant seals (*Mirounga leonina* L.) in the Windmill Islands, Vincennes Bay, east Antarctica, 1988–2001. *Wildlife Research*, **30**, 275–280.
- VAN DEN HOFF, J., KILPATRICK, R. & WELSFORD, D. 2017. Southern elephant seals (*Mirounga leonina* Linn.) depredate toothfish longlines in the midnight zone. *PLoS ONE*, **12**, e0172396.
- WICKHAM, H. 2016. *ggplot2: elegant graphics for data analysis*. New York: Springer-Verlag. Retrieved from <https://ggplot2.tidyverse.org>