THE ROYAL SOCIETY
PUBLISHING

Elephant seal foraging success is enhanced in Antarctic coastal polynyas

Fernando Arce[1,2], Mark A. Hindell[1], Clive R. McMahon[1,3,5], Simon J. Wotherspoon[1,2], Christophe Guinet[4], Robert G. Harcourt[5] and Sophie Bestley[1]

[1]Institute for Marine and Antarctic Studies, University of Tasmania, Private Bag 129 Hobart, TAS 7001, Australia
[2]Australian Antarctic Division, 203 Channel Highway, Kingston, TAS 7050, Australia
[3]IMOS Animal Tagging, Sydney Institute of Marine Science, Mosman, NSW 2088, Australia
[4]Centre d'Etudes Biologiques de Chizé, CNRS, Villiers en Bois 79360, France
[5]Department of Biological Sciences, Macquarie University, North Ryde, NSW 2113, Australia

FA, 0000-0002-7622-3791; MAH, 0000-0002-7823-7185; CRM, 0000-0001-5241-8917; SJW, 0000-0002-6947-4445; CG, 0000-0003-2481-6947; RGH, 0000-0003-4666-2934; SB, 0000-0001-9342-669X

Antarctic polynyas are persistent open water areas which enable early and large seasonal phytoplankton blooms. This high primary productivity, boosted by iron supply from coastal glaciers, attracts organisms from all trophic levels to form a rich and diverse community. How the ecological benefit of polynya productivity is translated to the highest trophic levels remains poorly resolved. We studied 119 southern elephant seals feeding over the Antarctic shelf and demonstrated that: (i) 96% of seals foraging here used polynyas, with individuals spending on average 62% of their time there; (ii) the seals exhibited more area-restricted search behaviour when in polynyas; and (iii) these seals gained more energy (indicated by increased buoyancy from greater fat stores) when inside polynyas. This higher-quality foraging existed even when ice was not present in the study area, indicating that these are important and predictable foraging grounds year-round. Despite these energetic advantages from using polynyas, not all the seals used them extensively. Factors other than food supply may influence an individual's choice in their use of feeding grounds, such as exposure to predation or the probability of being able to return to distant sub-Antarctic breeding sites.

1. Introduction

Polynyas are recurrent areas of open water or fragmented thin ice surrounded by higher-density sea ice [1]. Around Antarctica, during autumn and winter, coastal polynyas are generally maintained by katabatic winds advecting newly formed sea ice away [2,3]. The brine rejection during recurrent sea-ice formation results in dense water that sinks, enhancing the vertical transfer of nutrients and gases, and acting as a precursor of the Antarctic bottom water which forms the deepest layer of the world ocean [4]. These physical processes linking atmospheric-ocean-ice dynamics contribute to high values of oceanic heat loss [5], ocean ventilation, plus drawdown of atmospheric CO_2 due to primary productivity [6–8], making them relevant to the mitigation of human-induced climate change [9]. Because Antarctic polynyas maintain a thin ice cover during winter [10–12] they are the first areas to melt during spring [13], enabling earlier and larger seasonal phytoplankton blooms thereby enhancing energy transfer through the food web [7,13]. Through increased vertical carbon flux, polynyas can also support rich benthic communities [14,15].

During spring and summer, when polynyas are no longer in the active sea-ice production phase, these locations may be regarded as 'post-polynyas' [13,16]. The benefits of high seasonal primary productivity described above, often boosted by iron supply from nearby coastal glacier basal melt, persist through the summer season and into autumn [7,13]. Because these post-

polynyas are geographically stable and because they retain many of the biologically (and biogeochemically) important features such as enhanced productivity, they remain areas that attract larger predators such as marine mammals and seabirds [16,17]. Consequently, polynyas are considered important 'biological hotspots' for organisms from all trophic levels, forming rich ecosystems and representing important year-round habitat for air-breathing marine predators [17–24].

Due to their predictable recurrence within the otherwise highly variable sea-ice environment [1,25], polynyas provide areas of open water where diving predators can resurface for air [19,24], especially important in winter when the continental shelf and surrounding waters are largely ice-covered [12,26]. Exactly how the potential ecological benefit of polynya productivity is translated to the highest trophic level (e.g. via increased foraging opportunities, enhanced growth and/or reproduction), has rarely been quantified and remains poorly resolved [13,27,28]. Consequently, whether polynyas actually offer enhanced energetic benefit for foraging Antarctic predators, as opposed to fulfilling a physical habitat requirement (such as access to open water), remains somewhat speculative [13,23,29].

Southern elephant seals (*Mirounga leonina*) are large, wide-ranging predators that forage seasonally within Antarctic shelf waters, including coastal polynyas [23,24], where they feed on benthic, epi-benthic and mid-water prey [30,31]. They are one of the few upper trophic species where it is possible to evaluate the importance of polynyas because of the capacity to quantify *in situ* changes in their body condition [32–34]. As capital breeders with a catastrophic moult, individual seals fast on land for several weeks during the two energetically demanding breeding and moult periods, with the energy for these fasts needing to be acquired at sea beforehand [35]. Hence, elephant seals show lower body condition after these fasting periods, typically followed by a progressive increase in condition as they recommence foraging and replenish their energetic reserves [32]. These changes may be identified through changes in buoyancy manifested in their vertical drift rates [32,36].

Focusing on elephant seals tracked in the East Antarctic region (from the Kerguelen plateau population), we first examine polynya usage with respect to their movement behaviour, foraging success, sex and tag deployment location. We then test whether the seals that forage in post-polynya areas gained more condition than seals that forage outside these areas (in the surrounding Antarctic waters), thereby directly quantifying the ecological importance of polynyas to higher trophic species such as seals.

2. Material and methods

(a) Seal tagging data

More than two hundred southern elephant seals have been instrumented in the Indian sector of the Southern Ocean over the last decade under the Australian Integrated Marine Observing System [37] and the Service National d'Observation Mammifères Echantillonneurs du Milieu Oceanique (SNO-MEMO as part of the France's National Antarctic Program (Institut Polaire Français Paul Emile Victor, IPEV) (electronic supplementary material, table S1). The seals were tagged with conductivity temperature depth – satellite relayed data loggers (CTD-SRDLs; Sea Mammal Research Unit, University of St Andrews, UK) on Îles Kerguelen ($n = 112$),

the main breeding site of the species in the Southern Indian Ocean, or at one of two moulting sites in East Antarctica, Prydz ($n = 48$) and Vincennes Bay ($n = 42$). See electronic supplementary material, table S1 for detailed information of tagging numbers by year, sex and location. The capture and sedating procedures are fully described elsewhere [38,39]. CTD-SRDLs record dive depth data summarized by a broken-stick algorithm [40,41] and transmitted through the ARGOS satellite system [42]. Due to transmission constraints, the final diving dataset for each seal represents a random subsample of all dives comprising around 80% of the total number of dives [40,43].

We used a widely applied hierarchical state-space model [44,45] to filter ARGOS Doppler locations and provide an estimate of the seals' movement behaviour. The hierarchical state-space model was implemented using the R package *bsam* [44,45] in R v. 3.5.2 [46]. In brief, this approach models a behavioural process whereby animals switch between two different correlated random walks (behavioural states), as introduced by [44], thereby differentiating periods of relatively directed (in-transit) and more sinuous (area-restricted search) horizontal movements. Tracks were processed in batches defined by deployment year/location [47] with location and behavioural state estimates provided at regular 6 h intervals.

(b) Estimating changes in body condition

In approximately 3–4% of dives each day, elephant seals are inactive and drift through the water column [33,34]. These drift dives are characterized by having a phase during which the seal drifts passively in the water column [32,48], when the rate (cm s^{-1}) and the magnitude and direction of the vertical displacement depends largely on the seals' buoyancy. The buoyancy of elephant seals is primarily determined by the ratio of blubber : lean tissue [32]; negatively buoyant seals will descend passively in the water column when inactive, while positively buoyant seals will ascend. We processed the CTD-SRDL dive information after Arce, Bestley [34], identifying all dives with a high probability of being drift dives ($Z > 0.5$). To assign an average drift rate to each 6 h location estimate, we fitted to each seal a generalized additive model (GAM) with a custom link function that considers the buoyancy model implemented in R package *slimmingDive* [49].

(c) Definition of temporal coverage, geographical study region and Antarctic foragers

We focused on the seals' winter post-moult trips, during which they are at sea for 8–10 months (figure 1). After moulting, seals have relatively low body condition that must be recovered [50]. The speed of recovery of fat reserves is highest during the early phase of the trip, after which the seals approach neutral buoyancy; at neutral buoyancy, their cost of transport within the water column is minimal [51]. This typically occurs during mid-summer to late autumn when large areas of the Antarctic shelf are ice-free and available to foraging seals [7]. Therefore, during this time, we can test behavioural and foraging differences between post-polynya areas and the rest of the Antarctic region. To focus on this critical period of recovering body condition, we analyse drift dive data over the first two months (60 days) each seal spent foraging at sea. In most cases, this covers February–April but there is variability between individuals (figure 1b).

The use of the Southern Indian Ocean by elephant seals can be broadly considered as either sub-Antarctic or Antarctic [30,31,52]. A density plot of latitudes obtained from the tracks shows a strong bimodal distribution matching these two categories. We demarcated the latitude with the minimum density value (58.50° S) as the sub-Antarctic/Antarctic threshold (electronic supplementary material, appendix S2, figure S1) and defined Antarctic foragers
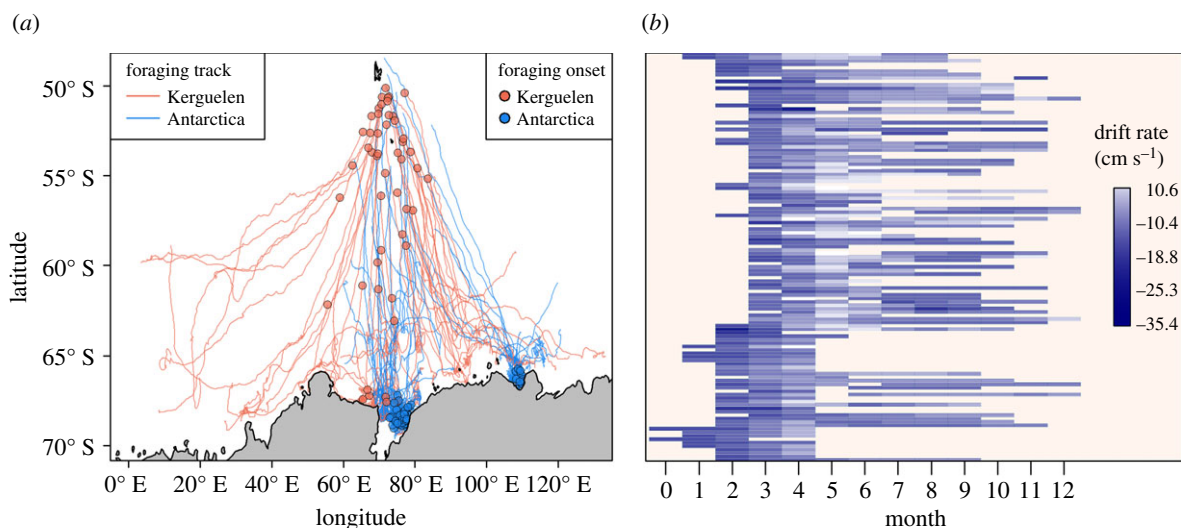
Figure 1. (*a*) Map showing filtered post-moult foraging tracks of 119 southern elephant seals instrumented at Îles Kerguelen (KI; red, *n* = 50; 49.35° S, 70.22° E) and in the East Antarctic (blue, *n* = 69; tagging locations are nearby the polar research stations at Casey (CS) [66.28° S, 110.53° E] and Davis (DS) [68.58° S, 77.97° E]). The commencement of drift diving behaviour (considered onset of foraging) is represented by a coloured circle. (*b*) Heatmap showing drift rates (cm s^{-1}) indicating seal body condition through time, where darker blue indicates poorer condition whereas at the lightest colour seals are positively buoyant (i.e. cm s^{-1} > 0). One individual seal is represented per row (*n* = 119). Horizontal axis shows month; here 1 to 12 is continuous, with month 12 referring to December for tags that transmitted throughout the year (i.e. cessation before moult). Month 0 is prefixed for those seals tagged in December the year prior. (Online version in colour.)

as those seals which spent at least 50% of the 60-day period south of 58.50° S. All individuals providing drift rate information for at least 10 days were included, as they provide drift rate change trajectories of sufficient duration to quantify changes in condition. Electronic supplementary material, appendix S2, table S1 provides a summary of the seal data (*n* = 119 individuals) considered in this study.

Seals may delay the start of foraging while in transit to the forage grounds or commence feeding opportunistically *en route* [36]. Since drift dives are thought to be related to food processing and resting [36,53,54], we defined the start of foraging for individual seals (time zero [t_0]) when seals first made a drift dive. We then calculated the rate of change in the drift rate for each subsequent location (ΔDr_i) as the difference between the drift rate values, obtained from the GAM smoothing at the current (Dr_i) and previous (Dr_{i-1}) locations, divided by the time increment between them (ΔT_i):

$$\Delta Dr_i = \frac{(Dr_i - Dr_{i-1})}{\Delta T_i}. \tag{2.1}$$

(d) Quantifying polynya usage and foraging success

Following other recent ecological studies [16,55], we used the East Antarctic coastal polynyas areas identified by Arrigo & van Dijken [13] (as shown in their fig. 1*b*). These are calculated based on the percentage of ice-free winter days and considering the horizontal extent of the associated phytoplankton blooms [13]. As stated above, outside the active ice-formation periods the geographic location of these polynyas may be regarded as 'post-polynyas'.

We evaluated the ecological importance of polynyas to elephant seals in two ways, looking at: (i) predictors of polynya usage and then (ii) quantifying their ecological benefit. For the first we fit generalized linear mixed models with the response variable being whether a seal location was inside or outside a polynya area, using a binomial distribution. This was done to establish if seal foraging behaviour varied in and out of polynyas. For this, the fixed effects were *behavioural state* (ranging between 1: in-transit and 2: area-restricted search), *sex* (male or female), *tagging location* (Îles Kerguelen or Antarctic coast) and ΔDr (i.e. the drift rate change). Seal identity was included as a random effect in all mixed models. We fitted the candidate

models using R package *lme4* [56], assessing all combinations of fixed effects using the R package *MuMIn* [57] and comparing them using AICc [58].

For (ii), we then established whether foraging success was different when seals were in or out of polynyas. Here, we fitted linear mixed models using ΔDr rate (as measure of foraging success) as the response variable. Fixed effects were *polynya* (inside or outside), *tagging location* (Îles Kerguelen or Antarctic coast), *behavioural state* estimate (ranging between 1: in-transit and 2: area-restricted search) and *sex* (male or female). We incorporated a continuous time autocorrelation structure (corCAR1) given the values generated by the (smoothing) GAM function were not independent. Again, seal identity was included as a random effect in all mixed models. We fitted candidate models with the R package *nlme* [59] and compared them as above. The dataset supporting this article is available in the electronic supplementary material, appendix S1.

3. Results

(a) Number of seals using the Antarctic region

Overall, 45% (*n* = 50) of seals instrumented at Îles Kerguelen spent at least half their time within the Antarctic region. More males 50% (*n* = 28) than females 33% (*n* = 22) used the Antarctic region (electronic supplementary material, appendix S2 and table S1). The first drift dive was recorded either during transit or after arriving at the Antarctic shelf, at an overall average distance of 837 km from the island (s.d. = 579, *n* = 50; figure 1*a*; electronic supplementary material, appendix S2 and figure S2). Of those seals instrumented in Antarctica, 96% remained as Antarctic foragers (electronic supplementary material, appendix S2, table S1), commencing foraging at an average distance of 67 km (s.d. = 48, *n* = 69) from the tagging location (figure 1*a*; electronic supplementary material, appendix S2, figure S1).

(b) Body condition at the onset of foraging

Elephant seals had negative drift rates at the start of their post-moult foraging trips (figure 1*b*). The mean overall drift rate at the start of the foraging period was −29 cm s^{-1} (s.d. = 6 cm s^{-1}, *n* = 119), and drift rate was lower for individuals instrumented
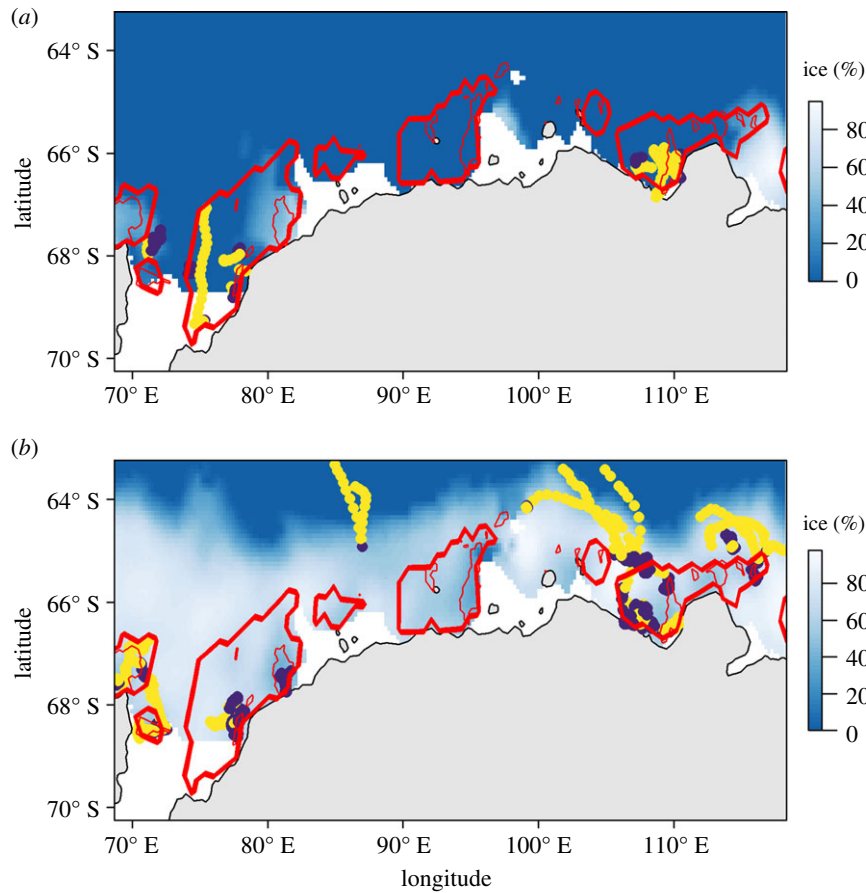
Figure 2. Maps showing the ice concentration in the study site on 7 March and 24 April 2012. We have chosen 2012 as this was the year with the greatest number of instrumented seals using the Antarctic continental shelf. Also shown are the tracks of seals (coloured points: yellow indicates in-transit and indigo indicates more resident behaviour; see figure 3) in the region 3 days either side of those dates. Background colour shows ASI Algorithm AMSR-E sea-ice concentration (%) data at 6.25 km resolution obtained from the Integrated Climate Date Center (ICDC, icdc.cen.uni-hamburg.de/), University of Hamburg, Hamburg, Germany [60,61]. The red polygons indicate the seven post-polynya areas [13] located within the study domain. (Online version in colour.)

at Îles Kerguelen (mean = −31.95, s.d. = 5.96, $n = 50$) than those instrumented in Antarctica (mean = −27.52, s.d. = 5.12, $n = 69$; t-test = −4.14, $p < 0.001$). Males instrumented at Îles Kerguelen and Antarctica had mean starting drift rates of −33 cm s^{-1} (s.d. = 6, $n = 28$) and −28 cm s^{-1} (s.d. = 5, $n = 67$), respectively. Females instrumented at Îles Kerguelen had a mean starting drift rate of −30 cm s^{-1} (s.d. = 5, $n = 22$), while the two females instrumented in Antarctica had starting values of −14 and −26 cm s^{-1}, respectively.

(c) Polynya usage and movement behaviour

Ice extent and concentration changed considerably during the study period (figure 2). In early March, when the seals arrived on the Antarctic shelf, very little of the region had any ice cover, but some of the seals used post-polynya areas. By the end of the study period in late April, the ice extended northwards over the shelf, with seals using regions of both high and low ice concentration, within and outside the permanent polynyas.

Twenty-seven of the 28 Antarctic foraging males instrumented at Îles Kerguelen (96%) spent some time in coastal polynyas or post-polynyas (median = 62% of total time, range = 3.4–100%; electronic supplementary material, appendix S2, figure S3). All the male seals instrumented in Antarctica ($n = 67$) similarly spent some time inside polynyas or post-polynyas (median = 64% of total time, range = 1.4–100%). In comparison, only four of 22 (18%) females from Îles Kerguelen that travelled
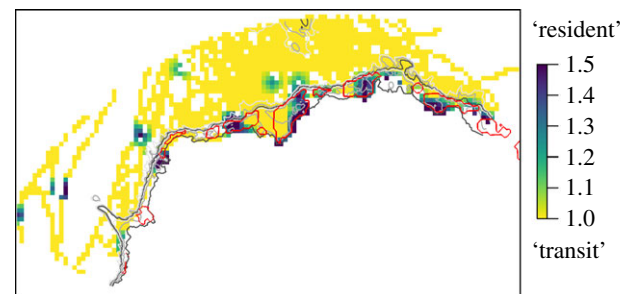

Figure 3. Map showing movement behaviour as estimated using hierarchical state-space switching models (see Material and methods). Yellow (values close to 1) indicates in-transit areas and darker colours indicate more resident behaviour (indicative of area-restricted search). Red polygons demarcate post-polynya areas [13]. Data shown as average values per 50 km grid cell aggregated across all individual seals. (Online version in colour.)

to the Antarctic region spent time in coastal polynyas or post-polynyas (0.4, 2.5, 27 and 40% of their total time; electronic supplementary material, appendix S2, figure S3). The two females instrumented in Antarctica remained as Antarctic foragers but unlike the male seals spent little time inside polynyas (1.6 and 36% of their total time).

Seal movements exhibited clear transit behaviour between the breeding colony and the Antarctic shelf when outbound from Îles Kerguelen (figure 2). Once over the Antarctic shelf region, area-restricted search behaviour was

Table 1. Results of mixed effect models for predicting (*a*) polynya usage and (*b*) foraging success (i.e. positive drift rates). Parameters with statistically significant slopes ($p < 0.05$) are highlighted in italics. For factor variables, the parentheses indicate which factor level is represented; for example, in (*a*) Kerguelen males represent the reference level, and the effects of sex (females) and tagging location (Antarctic deployments) are reported relative to this.

(a) polynya usage			
fixed effects	coefficient ± s.e.	*z*-value	*p*-value
intercept (Kerguelen male)	−0.14 ± 0.37	−0.38	0.70
behavioural state	*0.65 ± 0.02*	*32.32*	*<0.001*
Δ drift rate	*0.22 ± 0.02*	*9.23*	*<0.001*
sex (female)	*−6.19 ± 0.64*	*−9.61*	*<0.001*
tagging location (Antarctic)	0.74 ± 0.43	1.70	0.089
(b) foraging success (Δ drift rate)			
fixed effects	coefficient ± s.e.	*t*-value	*p*-value
intercept (Kerguelen male)	*0.05 ± 0.009*	*5.06*	*<0.001*
polynya usage (in)	*0.01 ± 0.003*	*2.93*	*0.003*
sex (female)	0.01 ± 0.013	1.04	0.30
tagging location (Antarctic)	*0.05 ± 0.011*	*4.41*	*<0.001*
behavioural state	*0.01 ± 0.002*	*4.85*	*<0.001*

evident inside and immediately around the post-polynya regions (figure 3).

The best model for polynya usage retained *sex*, ΔDr and *behavioural state* as predictors (table 1). The two highest ranked models (with or without *tagging location*) were essentially equivalent (i.e. ΔAIC < 1; electronic supplementary material, appendix S2, table S2). Antarctic foraging males that were instrumented at Îles Kerguelen or on the Antarctic continent were therefore equally likely to visit polynya areas, while females, regardless of their tagging location, were much less likely to visit polynyas than males. Locations inside polynyas were associated with more area-restricted search behaviour and with positive changes in drift rates (electronic supplementary material, appendix S2, figures S4–S6).

(d) Relative foraging success in polynyas as determined from changes in drift rate

For seals ($n = 90$), with drift rate information for the full 60-day period, the mean drift rate was −11 cm s^{-1} (s.d. = 13) with an average increase of 0.31 cm d^{-1} (s.d. = 0.21) over the 60-day period. While almost all seals gained body condition during this time, the rate of body condition change (ΔDr_i) was higher inside than outside polynya or post-polynya areas (table 1; electronic supplementary material, appendix S2, table S3). This is illustrated in figure 4 where seals with relatively low polynya usage had drift rate of around −15 cm s^{-1} at the end of 60 days compared to seals with high use of polynyas which had drift rates around 0 cm s^{-1} (or neutral buoyancy) after 60 days. There were no significant differences in terms of the rate of change between males and females (table 1). However, Antarctic instrumented seals (predominantly males) with high use of polynyas gained condition faster (mean = 0.11 cm d^{-1}, s.d. = 0.16 cm d^{-1}) than equivalent seals from Îles Kerguelen

(mean = 0.07 cm d^{-1}, s.d. = 0.07 cm d^{-1}), hence there is a bimodal distribution evident in drift rates (figure 4).

4. Discussion

Antarctic coastal polynyas and post-polynyas are biological hotspots that support high rates of primary production, and the productivity associated with these polynyas is thought to be a critical food source for some of the most abundant top predators in Antarctic waters including penguins, albatrosses and seals. However, few studies have directly demonstrated the foraging benefit of energy consumed within polynyas by upper trophic levels. Our study directly quantifies both polynya usage and the differential benefit for elephant seals foraging within and outside Antarctic coastal polynyas. The use of a valuable proxy for fat:lean tissue, available while animals are at sea, shows foraging success is greater inside polynyas.

Most seals that foraged on the Antarctic continental shelf used polynyas, with individuals spending an average of 62% of their time in a polynya. Seals inside polynyas exhibited more area-restricted search behaviour and gained more energy (indicated by increased buoyancy from greater fat stores) than seals outside of the polynyas. This clearly demonstrates that polynyas are productive feeding locations, providing corroborating evidence that polynyas provide higher prey resources. However, the underlying mechanisms for how this occurs remains unclear. One hypothesis is that higher primary production translates to higher biomass of potential prey, but the empirical demonstration of this in terms of foraging success has been elusive. The magnitude of annual production in coastal polynyas can help explain the variance in Adélie penguin (*Pygoscelis adeliae*) colony size [13]. Recent work showed pup production by ice-dependent Weddell seals (*Leptonychotes weddellii*) to be positively
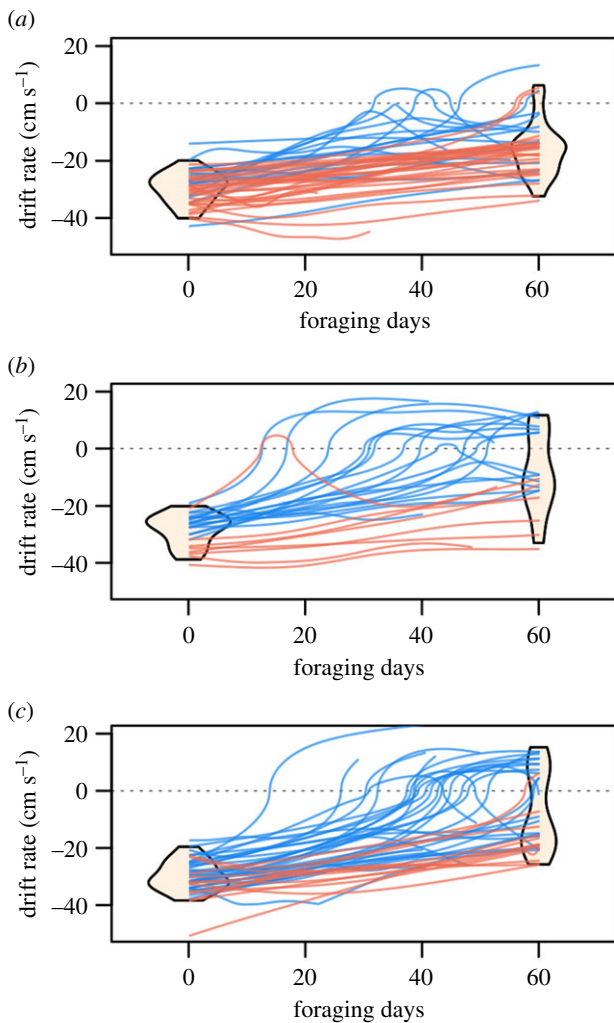
Figure 4. Drift rate (cm s^{-1}) time series for Antarctic foraging elephant seals ($n = 119$). For visualization, the time series from individuals are separated according to usage of post-polynya areas: seals that spent less than one-third of their time inside post-polynya areas (a) (low polynya usage), between one-third and two-thirds of their tracked time inside post-polynya areas (b) (medium polynya usage) and more than two-thirds of their time inside post-polynya areas (c) (high polynya usage). Lines show the estimated drift rate from the fitted GAMs for seals instrumented at Îles Kerguelen (red, $n = 50$), and in Antarctica (blue, $n = 69$). Violin plots show the distribution of drift rates at the start and end of the 60-day period. (Online version in colour.)

associated with annual primary production in the McMurdo Sound polynya, Ross Sea [27]. Our study shows a direct improvement in elephant seal body condition in polynya-foraging animals in the East Antarctic. By inference, polynyas should also provide better foraging for other predators that rely on mesopelagic prey, such as emperor penguins (*Aptenodytes forsteri*) [62], although this species sometimes favours smaller and ephemeral polynyas, rather than the large, predictable ones [29].

Seals also spent some time outside polynyas (on average 38% of their time), despite polynyas offering a clear advantage in terms of resource availability. This may be because not all Antarctic polynyas are equally biologically productive [7] due to differences in nutrient inputs (primarily iron; for example from ice shelf melt [63,64]), which may also translate to different prey field characteristics (e.g. [65]). Our study has undertaken a broad-scale assessment of the relative importance of polynyas without accounting for individual differences among polynyas, as this would require a much larger sample of seals to resolve. However, coastal polynyas may differ considerably in size, intensity (ice formation rates), physical structure and water transformation processes, seasonal persistence and productivity [66]. Along with a greater sampling effort inside and outside of polynyas, future work quantifying the importance of productivity within specific polynyas for the performance of the broad suite of animals using them would allow us to more accurately account for differences at the regional scale.

Seals and penguins will also forage in open water features other than polynyas, such as leads and tide cracks, where they may catch sufficient food to meet their energetic requirements [28]. Animals do not necessarily need to forage in the best available habitat and can succeed in habitats that are 'good enough' [67]. Alternatively, animals may balance food acquisition with potential risks, such as increased predation at the best foraging spots [68]. Presumably, if an area is important to meso-predators such as seals or penguins it is also likely to be attractive to their predators, such as killer whales (*Orcinus orca*) [31,69]. Risk of predation has been shown in other systems to displace animals to sub-optimal forage habitat [70]. However, given the dearth of information on the presence, distribution and behaviour of apex predators such as killer whales during the late summer and winter periods in the Antarctic much remains to be learnt on the predator–prey dynamics in polynyas and how it influences animals there [71–73].

Sex-specific differences have been previously identified in the use of polynyas, with adult female southern elephant seals rarely using polynyas and the Antarctic continental shelf [30,31,74], noting that these studies used a subset of the same seals that we report on here. Even though females rarely use polynyas, when they do, they have similar levels of foraging success to the males indicating that polynyas are a potential high resource area for both sexes. The question then arises, why don't more females exploit this resource? A potential explanation could be sex-specific resource partitioning driven by the different absolute energetic requirements for males and females as a consequence of their extreme sexual dimorphism [31]. This hypothesis is supported by an increase in trophic level of males as they age [75,76], whereas females do not exhibit a major dietary shift in relation to their age and breeding status [52]. The winter sea-ice environment is highly dynamic both within and between years [77] presenting a challenging environment for the animals that live there. The benefit of foraging in polynya or post-polynya regions may not compensate for the risks of (i) females being entrapped by ice when ready to return to breeding colonies to pup [78] or (ii) a higher risk of predation [31,79]. However, quantifying at-sea mortality and ascribing it to a specific predation event is difficult [69]. Immature male seals, unlike females, are not obliged to return to breeding colonies and may therefore trade off potentially higher risk for enhanced feeding opportunities that allow faster growth rates and increased size. The benefits of size are manifest in greater breeding opportunities given that only the largest males successfully hold harems and have the greatest reproductive output [80,81]. Consequently, there is a strong selection for the sexes using different foraging areas that have different prey assemblages.

There is low confidence in the prognoses for polynya activity in the future [9]. Calving and collapsing ice shelves

(e.g. Mertz Glacier Tongue, Larsen A and B), creating polynyas in their wake, can increase local primary production [82,83]. Changes in basal ice shelf melt rates could increase iron supply and water column productivity. Under anthropogenic climate change, some models indicate that surface freshening caused by increased precipitation will reduce polynya occurrence [84]. The implications for dependent predators foraging in these areas are unclear and may change phases over scales of decades or centuries. Improved observations of biophysical interactions [85,86], linking iron supply, polynya productivity and foraging predators is a priority for developing prognoses of ecosystem change in these Antarctic biological hotspots.

References

1. Morales Maqueda MA, Willmott AJ, Biggs NRT. 2004 Polynya dynamics: a review of observations and modeling. *Rev. Geophys.* **42**, 1. (doi:10.1029/2002RG000116)

2. Adolphs U, Wendler G. 1995 A pilot study on the interactions between katabatic winds and polynyas at the Adélie Coast, eastern Antarctica. *Antarct. Sci.* **7**, 307–314. (doi:10.1017/S0954102095000423)

3. Massom RA, Harris PT, Michael KJ, Potter MJ. 1998 The distribution and formative processes of latent-heat polynyas in East Antarctica. *J. Glaciol.* **27**, 420–426. (doi:10.3189/1998AoG27-1-420-426)

4. Markus T, Kottmeier C, Fahrbach E. 1998 Ice formation in coastal polynyas in the Weddell sea and their impact on oceanic salinity. In *Antarctic sea ice: physical processes, interactions and variability* (eds T Markus, C Kottmeier, E Fahrbach), pp. 273–292. Washington, DC: American Geophysical Union.

5. Renfrew IA, King JC, Markus T. 2002 Coastal polynyas in the southern Weddell Sea: variability of the surface energy budget. *J. Geophys. Res.* **107**, 16-11–16-22. (doi:10.1029/2000JC000720)

6. Arrigo KR, Robinson DH, Worthen DL, Dunbar RB, DiTullio GR, VanWoert M, Lizotte MP. 1999 Phytoplankton community structure and the drawdown of nutrients and CO_2 in the southern ocean. *Science* **283**, 365–367. (doi:10.1126/science.283.5400.365)

7. Arrigo KR, van Dijken GL, Strong AL. 2015 Environmental controls of marine productivity hot spots around Antarctica. *J. Geophys. Res.* **120**, 5545–5565. (doi:10.1002/2015JC010888)

8. Stein K, Timmermann A, Kwon EY, Friedrich T. 2020 Timing and magnitude of Southern Ocean sea ice/carbon cycle feedbacks. *Proc. Natl Acad. Sci. USA* **117**, 4498–4504. (doi:10.1073/pnas.1908670117)

9. Meredith M et al. 2019 Polar Regions. Chapter 3, IPCC Special Report on the Ocean and Cryosphere in a Changing Climate.

10. Tamura T, Ohshima KI, Fraser AD, Williams GD. 2016 Sea ice production variability in Antarctic coastal polynyas. *J. Geophys. Res.* **121**, 2967–2979. (doi:10.1002/2015JC011537)

11. Nihashi S, Ohshima KI, Tamura T. 2017 Sea-ice production in Antarctic coastal polynyas estimated from AMSR2 data and its validation using AMSR-E and SSM/I-SSMIS data. *IEEE J. Selected Topics Appl. Earth Observ. Remote Sens.* **10**, 3912–3922. (doi:10.1109/JSTARS.2017.2731995)

12. Nihashi S, Ohshima KI. 2015 Circumpolar mapping of Antarctic coastal polynyas and landfast sea ice: relationship and variability. *J. Clim.* **28**, 3650–3670. (doi:10.1175/jcli-d-14-00369.1)

13. Arrigo KR, van Dijken GL. 2003 Phytoplankton dynamics within 37 Antarctic coastal polynya systems. *J. Geophys. Res.* **108**, Artn 3271. (doi:10.1029/2002jc001739)

14. Grebmeier JM, Barry JP. 2007 Chapter 11 benthic processes in polynyas. In *Elsevier oceanography series* (eds WO Smith, DG Barber), pp. 363–390. Amsterdam, The Netherlands: Elsevier.

15. Jansen J et al. 2018 Abundance and richness of key Antarctic seafloor fauna correlates with modelled food availability. *Nat. Ecol. Evol.* **2**, 71–80. (doi:10.1038/s41559-017-0392-3)

16. Raymond B et al. 2015 Important marine habitat off east Antarctica revealed by two decades of multi-species predator tracking. *Ecography* **38**, 121–129. (doi:10.1111/ecog.01021)

17. Stirling I. 1997 The importance of polynyas, ice edges, and leads to marine mammals and birds. *J. Mar. Sys.* **10**, 9–21. (doi:10.1016/S0924-7963(96)00054-1)

18. Stirling I. 1980 The biological importance of polynyas in the Canadian Arctic. *Arctic* **10**, 303–315.

19. Ancel A et al. 1992 Foraging behaviour of emperor penguins as a resource detector in winter and summer. *Nature* **360**, 336–339. (doi:10.1038/360336a0)

20. McMahon C, Hindell M, Dorr T, Massom RA. 2002 Winter distribution and abundance of crabeater seals off George V Land, East Antarctica. *Antarct. Sci.* **14**, 128–133. (doi:10.1017/S0954102002000688)

21. Thiele D, Gill PC. 1999 Cetacean observations during a winter voyage into Antarctic sea ice south of Australia. *Antarct. Sci.* **11**, 48–53. (doi:10.1017/S0954102099000073)

22. Karnovsky N, Ainley DG, Lee P. 2007 The impact and importance of production in polynyas to top-trophic predators: three case histories. In *Elsevier oceanography series* (eds WO Smith, DG Barber), pp. 391–410. Amsterdam, The Netherlands: Elsevier.

23. Labrousse S *et al.* 2018 Coastal polynyas: winter oases for subadult southern elephant seals in East Antarctica. *Sci. Rep.* **8**, 1–15. (doi:10.1038/s41598-018-21388-9)

24. Malpress V, Bestley S, Corney S, Welsford D, Labrousse S, Sumner M, Hindell M. 2017 Bio-physical characterisation of polynyas as a key foraging habitat for juvenile male southern elephant seals (*Mirounga leonina*) in Prydz Bay, East Antarctica. *PLoS ONE* **12**, 1–24. (doi:10.1371/journal.pone.0184536)

25. Labrousse S *et al.* 2015 Winter use of sea ice and ocean water mass habitat by southern elephant seals: the length and breadth of the mystery. *Prog. Oceanogr.* **137**, 52–68. (doi:10.1016/j.pocean.2015.05.023)

26. Fraser AD, Massom RA, Michael KJ, Galton-Fenzi BK, Lieser JL. 2012 East Antarctic landfast sea ice distribution and variability, 2000–08. *J. Clim.* **25**, 1137–1156. (doi:10.1175/jcli-d-10-05032.1)

27. Paterson JT, Rotella JJ, Arrigo KR, Garrott RA. 2015 Tight coupling of primary production and marine mammal reproduction in the Southern Ocean. *Proc. R. Soc. B* **282**, 20143137. (doi:10.1098/rspb.2014.3137)

28. Saenz BT, Ainley DG, Daly KL, Ballard G, Conlisk E, Elrod ML, Kim SL. 2020 Drivers of concentrated predation in an Antarctic marginal-ice-zone food web. *Sci. Rep.* **10**, 7282. (doi:10.1038/s41598-020-63875-y)

29. Labrousse S *et al.* 2019 Dynamic fine-scale sea icescape shapes adult emperor penguin foraging habitat in East Antarctica. *Geophys. Res. Lett.* **46**, 11 206–11 218. (doi:10.1029/2019GL084347)

30. Hindell MA *et al.* 2016 Circumpolar habitat use in the southern elephant seal: implications for foraging success and population trajectories. *Ecosphere* **7**, e01213. (doi:10.1002/ecs2.1213)

31. Hindell MA, McMahon CR, Jonsen I, Harcourt R, Arce F, Guinet C. 2021 Inter- and intrasex habitat partitioning in the highly dimorphic southern elephant seal. *Ecol. Evol.* **11**, 1620–1633. (doi:10.1002/ece3.7147)

32. Biuw M, McConnell B, Bradshaw CJA, Burton H, Fedak M. 2003 Blubber and buoyancy: monitoring the body condition of free-ranging seals using simple dive characteristics. *J. Exp. Biol.* **206**, 3405–3423. (doi:10.1242/jeb.00583)

33. Biuw M *et al.* 2007 Variations in behavior and condition of a Southern Ocean top predator in relation to in situ oceanographic conditions. *Proc. Natl Acad. Sci. USA* **104**, 13 705–13 710. (doi:10.1073/pnas.0701121104)

34. Arce F, Bestley S, Hindell MA, McMahon CR, Wotherspoon S. 2019 A quantitative, hierarchical approach for detecting drift dives and tracking buoyancy changes in southern elephant seals. *Sci. Rep.* **9**, 1–13. (doi:10.1038/s41598-019-44970-1)

35. Fedak MA, Arnbom TA, McConnell B, Chambers C, Boyd IL, Harwood J, McCann T. 1994 Expenditure, investment, and acquisition of energy in southern elephant seals.

36. Crocker DE, Boeuf BJL, Costa DP. 1997 Drift diving in female northern elephant seals: implications for food processing. *Can. J. Zool.* **75**, 27–39. (doi:10.1139/z97-004)

37. IMOS. 2019 Animal tracking facility—satellite relay tagging program—delayed mode data. See https://catalogue-imosaodnorgau/geonetwork/srv/eng/catalogsearch#/metadata/06b09398-d3d0-47dc-a54a-a745319fbece (accessed on 21 April 2019).

38. McMahon CR, Burton H, Slip D, McLean S, Bester M. 2000 Field immobilisation of southern elephant seals with intravenous tiletamine and zolazepam. *Vet. Rec.* **146**, 251–254. (doi:10.1136/vr.146.9.251)

39. Field IC, Bradshaw CJA, McMahon CR, Harrington J, Burton HR. 2002 Effects of age, size and condition of elephant seals (*Mirounga leonina*) on their intravenous anaesthesia with tiletamine and zolazepam. *Vet. Rec.* **151**, 235–240. (doi:10.1136/vr.151.8.235)

40. Fedak M, Lovell P, McConnell B, Hunter C. 2002 Overcoming the constraints of long range radio telemetry from animals: getting more useful data from smaller packages. *Integr. Comp. Biol.* **42**, 3–10. (doi:10.1093/icb/42.1.3)

41. Photopoulou T, Lovell P, Fedak MA, Thomas L, Matthiopoulos J. 2015 Efficient abstracting of dive profiles using a broken-stick model. *Methods Ecol. Evol.* **6**, 278–288. (doi:10.1111/2041-210x.12328)

42. Argos. 2016 Argos user's manual. See https://wwwargos-systemorg/wp-content/uploads/2016/08/r363_9_argos_users_manual-v166pdf.

43. Fedak MA, Lovell P, Grant S. 2001 Two approaches to compressing and interpreting time-depth information as collected by time-depth recorders and satellite-linked data recorders. *Mar. Mammal. Sci.* **17**. (doi:10.1111/j.1748-7692.2001.tb00982.x)

44. Jonsen ID, Flemming JM, Myers RA. 2005 Robust state-space modeling of animal movement data. *Ecology* **86**, 2874–2880. (doi:10.1890/04-1852)

45. Jonsen I. 2016 Joint estimation over multiple individuals improves behavioural state inference from animal movement data. *Sci. Rep.* **6**, 20625. (doi:10.1038/srep20625)

46. R Core Team. 2020 *R: a language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing. See http://www.R-project.org R version 4.0.3.

47. Bestley S, Jonsen ID, Hindell MA, Harcourt RG, Gales NJ. 2015 Taking animal tracking to new depths: synthesizing horizontal–vertical movement relationships for four marine predators. *Ecology* **96**, 417–427. (doi:10.1890/14-0469.1)

48. Webb P, Crocker D, Blackwell S, Costa D, Boeuf B. 1998 Effects of buoyancy on the diving behavior of northern elephant seals. *J. Exp. Biol.* **201**, 2349–2358. (doi:10.1242/jeb.201.16.2349)

49. Arce F., Bestley S., Hindell MA., McMahon CR., Wotherspoon S. 2019 slimmingDive: flexible,

50. Hindell MA, Slip DJ, Burton HR. 1994 Body mass loss of moulting female southern elephant seals, Mirounga leonina, at Macquarie Island. *Polar Biol.* **14**, 275–278. (doi:10.1007/BF00239176)

51. Aoki K, Watanabe YY, Crocker DE, Robinson PW, Biuw M, Costa DP, Miyazaki N, Fedak MA, Miller PJO. 2011 Northern elephant seals adjust gliding and stroking patterns with changes in buoyancy: validation of at-sea metrics of body density. *J. Exp. Biol.* **214**, 2973–2987. (doi:10.1242/jeb.055137)

52. Bailleul F, Authier M, Ducatez S, Roquet F, Charrassin JB, Cherel Y, Guinet C. 2010 Looking at the unseen: combining animal bio-logging and stable isotopes to reveal a shift in the ecological niche of a deep diving predator. *Ecography* **33**, 709–719. (doi:10.1111/j.1600-0587.2009.06034.x)

53. Mitani Y, Andrews RD, Sato K, Kato A, Naito Y, Costa DP. 2010 Three-dimensional resting behaviour of northern elephant seals: drifting like a falling leaf. *Biol. Lett.* **6**, 163–166. (doi:10.1098/rsbl.2009.0719)

54. Watanabe YY, Baranov EA, Miyazaki N. 2015 Drift dives and prolonged surfacing periods in Baikal seals: resting strategies in open waters? *J. Exp. Biol.* **218**, 2793–2798. (doi:10.1242/jeb.125898)

55. Harcourt R *et al.* 2021 Regional variation in winter foraging strategies by Weddell Seals in Eastern Antarctica and the Ross Sea. *Front. Mar. Sci.* **8**, 1262. (doi:10.3389/fmars.2021.720335)

56. Bates D, Mächler M, Bolker B, Walker S. 2015 Fitting linear mixed-effects models using lme4. *J. Stat. Softw.* **67**, 1–48. (doi:10.18637/jss.v067.i01)

57. Bartoń K. 2020 MuMIn: multi-model inference. R package version 1.43.17. See https://CRANR-projectorg/package=MuMIn.

58. Burnham KP, Anderson DR. 2002 Information and likelihood theory: a basis for model selection and inference. In *Model selection and multimodel inference: a practical information-theoretic approach* (eds KP Burnham, DR Anderson), pp. 49–97. New York, NY: Springer.

59. Pinheiro J, Bates D, DebRoy S, Sarkar D, R-Core-Team. 2020 nlme: Linear and nonlinear mixed effects models. R package version 3.1-151. See https://CRAN.R-project.org/package=nlme.

60. Kaleschke L, Lüpkes C, Vihma T, Haarpaintner J, Bochert A, Hartmann J, Heygster G. 2001 SSM/I sea ice remote sensing for mesoscale ocean-atmosphere interaction analysis. *Can. J. Remote Sens.* **27**, 526–537. (doi:10.1080/07038992.2001.10854892)

61. Spreen G, Kaleschke L, Heygster G. 2008 Sea ice remote sensing using AMSR-E 89-GHz channels. *J. Geophys. Res.* **113**, C2. (doi:10.1029/2005JC003384)

62. Jafari V, Maccapan D, Careddu G, Sporta Caputi S, Calizza E, Rossi L, Costantini ML. 2021 Spatial and temporal diet variability of Adélie (*Pygoscelis adeliae*) and emperor (*Aptenodytes forsteri*) penguin: a multi tissue stable isotope analysis. *Polar Biol.* **44**, 1869–1881. (doi:10.1007/s00300-021-02925-1)

hierarchical selection of drift dives (v0.1.0). *Zenodo* See https://doiorg/105281/zenodo3255153.

63. Wang S, Bailey D, Lindsay K, Moore JK, Holland M. 2014 Impact of sea ice on the marine iron cycle and phytoplankton productivity. *Biogeosciences* **11**, 4713–4731. (doi:10.5194/bg-11-4713-2014)

64. Wolff EW *et al.* 2006 Southern Ocean sea-ice extent, productivity and iron flux over the past eight glacial cycles. *Nature* **440**, 491–496. (doi:10.1038/nature04614)

65. Bestley S *et al.* 2018 Predicting krill swarm characteristics important for marine predators foraging off East Antarctica. *Ecography* **41**, 996–1012. (doi:10.1111/ecog.03080)

66. Narayanan A, Gille ST, Mazloff MR, Murali K. 2019 Water Mass characteristics of the Antarctic margins and the production and seasonality of dense shelf water. *J. Geophys. Res.* **124**, 9277–9294. (doi:10.1029/2018JC014907)

67. Benoit-Bird KJ *et al.* 2013 Prey patch patterns predict habitat use by top marine predators with diverse foraging strategies. *PLoS ONE* **8**, e53348. (doi:10.1371/journal.pone.0053348)

68. Beltran RS *et al.* 2021 Lightscapes of fear: how mesopredators balance starvation and predation in the open ocean. *Sci. Adv.* **7**, eabd9818. (doi:10.1126/sciadv.abd9818)

69. Henderson AF, McMahon CR, Harcourt R, Guinet C, Picard B, Wotherspoon S, Hindell MA. 2020 Inferring variation in southern elephant seal at-sea mortality by modelling tag failure. *Front. Mar. Sci.* **7**, 796. (doi:10.3389/fmars.2020.517901)

70. Heithaus MR, Frid A. 2003 Optimal diving under the risk of predation. *J. Theor. Biol.* **223**, 79–92. (doi:10.1016/S0022-5193(03)00073-0)

71. Cornejo-Donoso J, Antezana T. 2008 Preliminary trophic model of the Antarctic Peninsula Ecosystem (Sub-area CCAMLR 48.1). *Ecol. Model.* **218**, 1–17. (doi:10.1016/j.ecolmodel.2008.06.011)

72. Durban JW, Pitman RL. 2012 Antarctic killer whales make rapid, round-trip movements to subtropical waters: evidence for physiological maintenance migrations? *Biol. Lett.* **8**, 274–277. (doi:10.1098/rsbl.2011.0875)

73. Van Opzeeland I, Hillebrand H. 2020 Year-round passive acoustic data reveal spatio-temporal patterns in marine mammal community composition in the Weddell Sea, Antarctica. *Mar. Ecol. Prog. Ser.* **638**, 191–206. (doi:10.3354/meps13258)

74. Labrousse S *et al.* 2017 Variability in sea ice cover and climate elicit sex specific responses in an Antarctic predator. *Sci. Rep.* **7**, 43236. (doi:10.1038/srep43236)

75. Martin C, Bentaleb I, Steelandt S, Guinet C. 2011 Stable carbon and nitrogen isotope variations in canine dentine growth layers of Kerguelen southern elephant seals. *Mar. Ecol. Prog. Ser.* **439**, 295–305. (doi:10.3354/meps09331)

76. Authier M, Martin C, Ponchon A, Steelandt S, Bentaleb I, Guinet C. 2012 Breaking the sticks: a hierarchical change-point model for estimating ontogenetic shifts with stable isotope data. *Methods Ecol. Evol.* **3**, 281–290. (doi:10.1111/j.2041-210X.2011.00162.x)

77. Parkinson CL. 2019 A 40-y record reveals gradual Antarctic sea ice increases followed by decreases at rates far exceeding the rates seen in the Arctic. *Proc. Natl Acad. Sci. USA* **116**, 14 414–14 423. (doi:10.1073/pnas.1906556116)

78. Bailleul F, Charrassin J-B, Ezraty R, Girard-Ardhuin F, McMahon CR, Field IC, Guinet C. 2007 Southern elephant seals from Kerguelen Islands confronted by Antarctic Sea ice: changes in movements and in diving behaviour. *Deep-Sea Res. Part II Topical Stud. Oceanogr.* **54**, 343–355. (doi:10.1016/j.dsr2.2006.11.005)

79. Van Den Hoff J, Morrice MG. 2008 Sleeper shark (Somniosus antarcticus) and other bite wounds observed on southern elephant seals (*Mirounga leonina*) at Macquarie Island. *Mar. Mamm. Sci.* **24**, 239–247. (doi:10.1111/j.1748-7692.2007.00181.x)

80. Le Boeuf BJ, Peterson RS. 1969 Social status and mating activity in elephant seals. *Science* **163**, 91–93. (doi:10.1126/science.163.3862.91)

81. Le Boeuf B, Condit R, Reiter J. 2019 Lifetime reproductive success of northern elephant seals (*Mirounga angustirostris*). *Can. J. Zool.* **97**, 1203–1217. (doi:10.1139/cjz-2019-0104)

82. Cape MR, Vernet M, Kahru M, Spreen G. 2014 Polynya dynamics drive primary production in the Larsen A and B embayments following ice shelf collapse. *J. Geophys. Res.* **119**, 572–594. (doi:10.1002/2013JC009441)

83. Shadwick EH, Tilbrook B, Currie KI. 2017 Late-summer biogeochemistry in the Mertz Polynya: East Antarctica. *J. Geophys. Res.* **122**, 7380–7394. (doi:10.1002/2017JC013015)

84. de Lavergne C, Palter JB, Galbraith ED, Bernardello R, Marinov I. 2014 Cessation of deep convection in the open Southern Ocean under anthropogenic climate change. *Nat. Clim. Change* **4**, 278–282. (doi:10.1038/nclimate2132)

85. McMahon CR *et al.* 2021 Animal Borne Ocean Sensors–AniBOS–an essential component of the Global Ocean Observing System (GOOS). *Front. Mar. Sci.* **8**, 751840. (doi:10.3389/fmars.2021.751840)

86. Bestley S *et al.* 2020 Marine ecosystem assessment for the Southern Ocean: birds and marine mammals in a changing climate. *Front. Ecol. Evol.* **8**, 338. (doi:10.3389/fevo.2020.566936)

87. Arce F, Hindell MA, McMahon CR, Wotherspoon S, Guinet C, Harcourt R, Bestley S. 2022 Elephant seal foraging success is enhanced in Antarctic coastal polynyas. Figshare.