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RESEARCH ARTICLE

Future climate-induced distribution shifts in a sexually dimorphic key predator of the Southern Ocean

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Abstract

The response to climate change in highly dimorphic species can be hindered by differences between sexes in habitat preferences and movement patterns. The Antarctic fur seal, *Arctocephalus gazella*, is the most abundant pinniped in the Southern Hemisphere, and one of the main consumers of Antarctic krill, *Euphausia superba*, in the Southern Ocean. However, the populations breeding in the Atlantic Southern Ocean are decreasing, partly due to global warming. Male and female Antarctic fur seals differ greatly in body size and foraging ecology, and little is known about their sex-specific responses to climate change. We used satellite tracking data and Earth System Models to predict changes in habitat suitability for male and female Antarctic fur seals from the Western Antarctic Peninsula under different climate change scenarios. Under the most extreme scenario (SSP5-8.5; global average temperature +4.4°C projected by 2100), suitable habitat patches will shift southward during the non-breeding season, leading to a minor overall habitat loss. The impact will be more pronounced for females than for males. The reduction of winter foraging grounds might decrease the survival of post-weaned females, reducing recruitment and jeopardizing population viability. During the breeding season, when males fast on land, suitable foraging grounds for females off the South Shetland Islands will remain largely unmodified, and new ones will emerge in the Bellingshausen Sea. As Antarctic fur seals are income breeders, the foraging grounds of females should be reasonably close to the breeding colony. As a result, the new suitable foraging grounds will be useful for females only if nearby beaches currently covered by sea ice emerge by the end of the century. Furthermore, the colonization of these new, ice-free breeding locations might be limited by strong female philopatry. These results should be considered when managing the fisheries of Antarctic krill in the Southern Ocean.

KEYWORDS
Antarctic fur seal, Antarctic krill, Antarctic Peninsula, *Arctocephalus gazella*, climate change, *Euphausia superba*, habitat suitability, philopatry, sex-specific

1 | INTRODUCTION

Climate change is one of the dominant forces driving the transformation of Planet Earth (Kortsch et al., 2015; Pörtner et al., 2022; Sage, 2020). Many species respond to climate change by shifting their distribution range, which has implications ranging from individual performance to global biogeographic patterns (Pinsky et al., 2020; Rebelo et al., 2010; Sousa-Guedes et al., 2020). Suitable habitat for marine species is also quickly shifting due to climate change (Lenoir et al., 2020; Poloczanska et al., 2013), and distribution shifts are projected to intensify during the current century, particularly in polar oceans (Cheung et al., 2009; Gordó-Vilaseca et al., 2023). Monitoring these changes presents major logistical challenges, particularly when it comes to land-breeding species that spend part of their time at sea and part on land, such as pinnipeds and seabirds.

Pinnipeds are referred to as sentinel species for at least three reasons. First, they have generally broad geographical ranges and long lifespans (Boyd, 2009; Kovacs et al., 2012); second, they can easily modify their movement patterns in response to changes in prey availability and environmental conditions (Pinsky et al., 2020); and third, they are highly sensitive to trophic amplification processes (Lotze et al., 2019). Furthermore, pagophilic pinniped species are expected to be adversely affected by temperature rise, whereas non-ice-dependent species may benefit from ice receding and hence expand their distribution (Bester et al., 2017; Kelly, 2001; Siniff et al., 2008).

Pinniped species also differ in their degree of sexual dimorphism, from nearly complete monomorphic taxa (e.g., ringed seal *Pusa hispida*; Krüger et al., 2014) to species with extreme sexual size dimorphism (e.g., Southern elephant seal *Mirounga leonina*; Cullen et al., 2014; Kienle et al., 2022). As body size determines diving performance and thermoregulation in pinnipeds (Favilla & Costa, 2020), highly dimorphic species often exhibit sexual segregation in their foraging behavior, with males and females using different foraging grounds during winter months (Blanchet et al., 2013; Breed et al., 2006; Kienle et al., 2022). This means that global warming will impact differently on males and females of the same species, and hence the species' response will depend on the more vulnerable sex.

The Antarctic fur seal, *Arctocephalus gazella*, is a highly dimorphic, non-pagophilic species with a breeding distribution restricted to the Southern Ocean, in its Atlantic and Indian sectors (Kaschner et al., 2019). It is the second most abundant pinniped in the world and the most abundant species in the Southern Hemisphere (Forcada et al., 2023). Male and female Antarctic fur seals differ not only in body size (120–140 kg males vs. 25–50 kg females; Blanchet et al., 2013) but also in their winter habitats (Arthur et al., 2015, 2017; Lowther et al., 2020; March et al., 2021). Furthermore, they rely on ice-free areas of land for breeding, and females are highly philopatric (Hoffman & Forcada, 2012). Antarctic krill, *Euphausia superba*, is the staple food of both sexes during the summer months in the Atlantic sector of the Southern Ocean (Atkinson et al., 2022; Borras-Chavez et al., 2023; Drago et al., 2023; Osman et al., 2004; Polito & Goebel, 2010) and for males during the winter months (Drago et al., 2023). However, females rely mostly on myctophid fishes and squid in winter (Walters, 2014). Global warming was initially predicted to have a neutral effect on Antarctic fur seal populations (Siniff et al., 2008), but there is increasing evidence of population declines both in colonies breeding close to the Antarctic Convergence (Forcada et al., 2023; Forcada & Hoffman, 2014) and in the South Shetland Islands (Krause et al., 2022, 2023; Schwarz et al., 2013). It is worth noting that the three subpopulations in the Atlantic Sector of the Southern Ocean (South Georgia Islands, South Shetland Islands and Bouvet Island) are demographically independent (Krause et al., 2023) and that the reasons for their decline are also different, although at least partially related to global warming (Forcada et al., 2023; Krause et al., 2022, 2023). For all these reasons, the species constitutes an excellent model to test whether males and females will respond differently to global warming.

Here, we evaluate future habitat suitability for the Antarctic fur seals from the declining population of the Western Antarctic Peninsula during breeding and non-breeding seasons throughout the next century under two diverging climate change scenarios (Shared Socioeconomic Pathways [SSPs]; SSP1-2.6 and SSP5-8.5). To do so, we have combined tracking data and outputs from four Earth System Models (ESM). Using a machine-learning modeling approach (boosted regression trees [BRT]), we test the hypothesis that males and females will have differential responses to future environmental change based on their sexual dimorphism and ecological strategies throughout their biological cycle.

2 | MATERIALS AND METHODS

2.1 | Animal capture and instrumentation

Tracking data was collected from individuals captured in two islands 40 km apart in the South Shetland Islands, off the Western Antarctic Peninsula (i.e., Deception Island: males; and Cape Shirreff, Livingston Island: females) between the years 2006 and 2019. Both sexes spend the non-breeding season at sea, although males remain close to Antarctica and females move to the northern limit of the Southern Ocean (Arthur et al., 2015, 2017; Lowther et al., 2020; March et al., 2021). They also differ widely in their behavior during the breeding season. At that time, females behave as income breeders and central-place foragers that must return to shore to feed their pups (Borras-Chavez et al., 2023). Conversely, males are polygynous and spend most of their time at the beach to maximize their mating opportunities, performing only a few sporadic foraging trips or none at all (Staniland & Robinson, 2008). For this reason, the at-sea behavior of both sexes was studied during the non-breeding season, but only that of females was studied during the breeding season.

2.1.1 | Males in the non-breeding season

Antarctic fur seal males ($n = 14$) were captured from February to March 2019 at Collins Point, Deception Island (South Shetland Islands; 62.96° S, 60.62° W; Figure 1b) and instrumented with satellite tag-linked platform terminal transmitters (PTTs) KiwiSat STANDARD series (model K2G 276A; 95 g; $n = 10$) or KiwiSat DIVE series (model K2G 276A with depth sensor; 95 g; $n = 4$), manufactured by Sirtrack, currently Lotek (www.lotek.com), which recorded and transmitted location using the ARGOS satellite service. The duty cycle was 24 h on every day and tags did not stop transmitting when individuals hauled out. Data on males is restricted to winter, as they

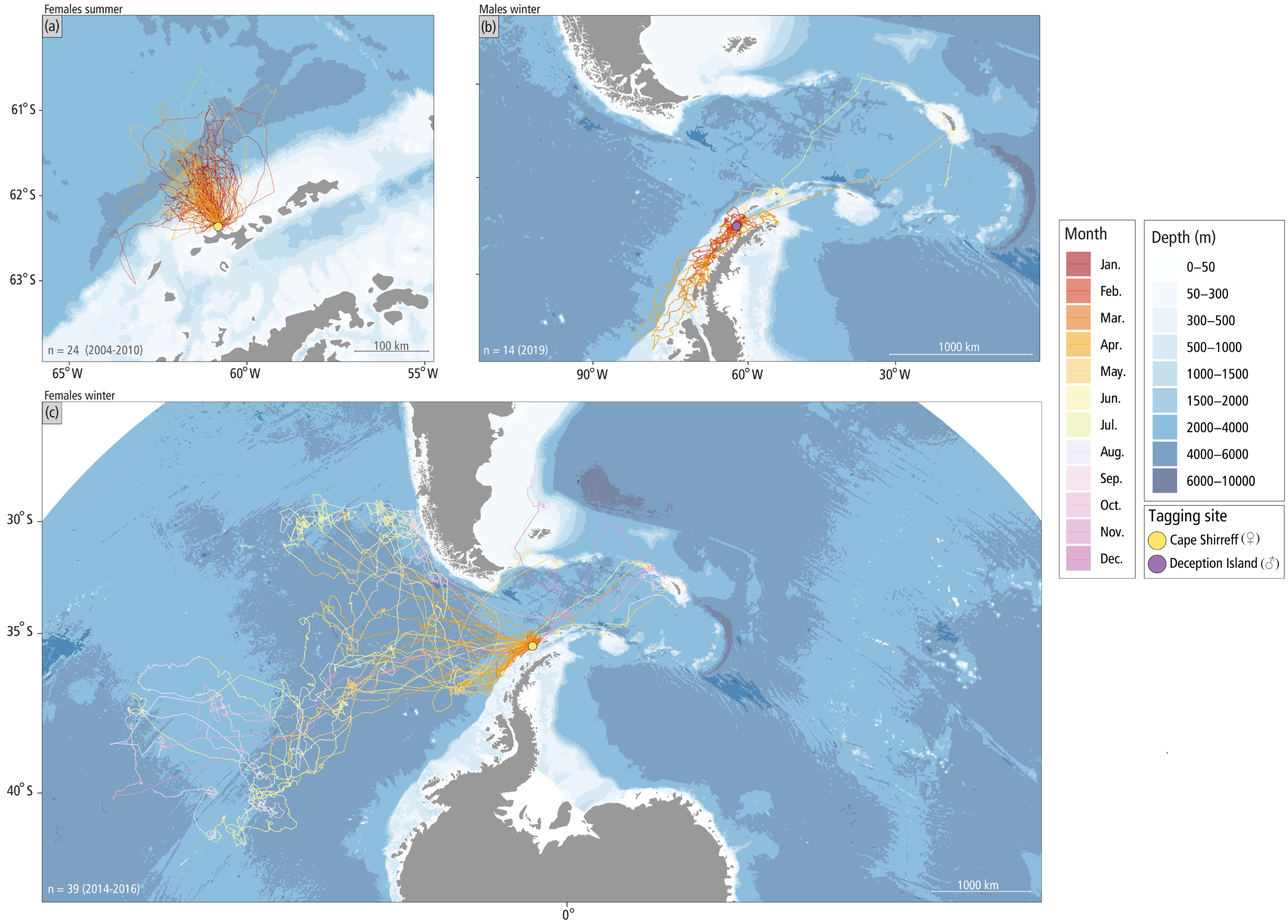

FIGURE 1 Tracks of Antarctic fur seals *Arctocephalus gazella* used for modelling. (a) Females from Cape Shirreff during the breeding season ($n = 24$). (b) Males from Deception Island during the non-breeding season ($n = 14$). (c) Females from Cape Shirreff during the non-breeding season ($n = 39$). Tracks are color-coded by month. The background shows bathymetry, and circles show the tagging sites: Cape Shirreff (females) and Deception Island (males).

spend most of the summer on the breeding beaches (Grebieniow et al., 2020). Animal handling and device attachment procedures followed those outlined in March et al. (2021).

2.1.2 | Females in the non-breeding season

Female Antarctic fur seals breeding at Cape Shirreff (Livingston Island, South Shetland Islands; 62.46° S, 60.79° W; Figure 1c) were captured and instrumented with PTTs (model SPOT5; 119 g; $n = 39$), manufactured by Wildlife Computers (https://wildlifecomputers.com) in 2006, 2008, 2009 and 2010, 3–4 weeks before the end of lactation and tracked throughout the following non-breeding season. Animal handling and device attachment procedures are detailed in Arthur et al. (2015).

2.1.3 | Females in the breeding season

Female Antarctic fur seals breeding at Cape Shirreff (Livingston Island, South Shetland Islands; 62.46° S, 60.79° W; Figure 1a) were captured early in the breeding season (December) of 2014, 2015 and 2016, instrumented with Mk10 FastLoc TDRs (132 g; $n = 24$), manufactured by Wildlife Computers (https://wildlifecomputers.com), and tracked until March of the following year. Animal handling and device attachment procedures are detailed in Borras-Chavez et al. (2023).

2.2 | Geolocation data processing

Individual tracks were trimmed into individual trips (i.e., ocean tracks in between haul-outs). Near-duplicate positions, defined as animal positions that occurred 2 min or less after an existing position fix from the same animal, were removed (Ropert-Coudert et al., 2020). Tracks were filtered using a speed, distance, and angle filter (Freitas et al., 2008; Sequeira et al., 2021). Although this method may result in errors of several tenths of km, this magnitude is acceptable considering the resolution of the environmental data used (1° × 1° pixel size, see below). Specifically, all points with unrealistic swimming speeds (>3 ms; Bonadonna et al., 2001; Lea & Dubroca, 2003) or unlikely turning angles (all spikes with angles smaller than 15° and lengths greater than 2.5 km or angles smaller than 25° and lengths greater than 5 km) were removed using the "argosfilter" R Package (Freitas et al., 2008). In addition to this first filter, in ARGOS data from males and females in winter, all location class Z values ("invalid locations") were deleted. FastLoc GPS data accuracy (from females in summer) is around four times greater than that of ARGOS (Costa et al., 2010), and there are no location classes in the data obtained from these tags. Tracks with data gaps longer than 7 days were broken up for separate modeling (i.e., each portion of the track was treated independently), as a lack of data can lead to unlikely location predictions within those gaps (Vogel et al., 2021). A state-space model (SSM) was used to estimate locations at regular time intervals (6 h) and account for measurement error in the original observations using the "foieGras" R Package (Jonsen et al., 2019, 2020). The updated version of this package is called "aniMotum" (Jonsen et al., 2023). We fitted the SSM using a correlated random walk model with the Template Model Building for fast estimation. After checking for convergence, all tracks were retained for further analyses.

2.3 | Pseudoabsences

Satellite tracks represent only presence data. To use a binomial response (i.e., presence and absence) and create a habitat preference model, we generated simulated tracks to represent the available habitat (i.e., where the animals could go given their movement characteristics and duration of each track). For each real track, we simulated 50 pseudo-tracks by fitting a first-order vector autoregressive model characterized by the step lengths and turning characteristics of the observed track (Raymond et al., 2015; Reisinger et al., 2018). The number of simulations was selected as a compromise between computing cost and the number of generated locations for further random sampling (see Section 2.6). Simulations were generated using the "availability" R package (https://github.com/AustralianAntarcticDivision/availability). For winter simulations (males and females), we fixed the initial location (i.e., the first track location) and restricted the following locations to the sea by defining a custom land mask of the study area using the GEBCO bathymetry (www.gebco.net) within a region defined by the minimum convex polygon around satellite tracks. In the case of females in summer, we also fixed the last track location in the colony; in this way, the simulated tracks matched the central-place foraging behavior of breeding females (Hindell et al., 2020). All simulations recreate the movement characteristics of the original tracks, considering their autocorrelation structure (Hazen et al., 2021; O'Toole et al., 2021) but are independent of the underlying environment. However, simulated tracks can generate replication at the same locations of the real track, hence leading to contradictory information in binomial models (i.e., same location and date defined as either presence or absence), and potentially reducing model performance. To reduce the amount of pseudo-replication and prevent overlap between real and simulated tracks, we gridded all presence and pseudo-absence locations per individual at 1° degree for each day and filtered out pseudo-absences that were adjacent to any presence grid cell (i.e., all individuals considered) within a temporal window of 2 days (March et al., 2021). This reduces the probability that presences and pseudo-absences at adjacent grid cells have similar environmental conditions on similar dates, to maximize model performance, although other temporal windows could also be useful.

2.4 | Environmental data and climate change scenarios

We used a suite of 12 environmental variables (four static: bathymetry, slope, distance to shore and distance to the colony; and eight dynamic: sea surface temperature [SST], salinity, eddy kinetic energy, mixed layer depth, chlorophyll concentration, carbon from diatoms, sea ice concentration, and distance to ice edge. Table S1), which were matched to the gridded presences and pseudoabsences to assess the habitat use of Antarctic fur seals. Environmental variables were chosen because it has been suggested that they are relevant for the distribution of Antarctic fur seals (Arthur et al., 2017; Lea & Dubroca, 2003; March et al., 2021; Raymond et al., 2015) or their prey (Atkinson et al., 2019, 2022). Eddy kinetic energy is a proxy for mesoscale variability in the ocean due to eddies and meanders; the mixed layer depth is a proxy for the thickness of the top layer of the water column mixed by wind action. Outputs from the Sixth Phase of the Coupled Model Intercomparison Project Phase 6 (CMIP6) were extracted from the Inter-Sectorial Impact Model Intercomparison Project (ISIMIP) portal (2022, https://data.isimip.org/). The latest iteration of scenarios used for CMIP6 are the SSP, which represent alternative narratives about how the world might develop under different policy scenarios (and therefore under different greenhouse gas emissions). We used three of these future scenarios (Chambault et al., 2022; Tittensor et al., 2021): a low forcing scenario (SSP1-2.6; global average temperature +1.4°C projected by 2100), a mid-forcing scenario (SSP3-7.0; global average temperature +3.6°C projected by 2100) and a high forcing future scenario (SSP5-8.5; global average temperature +4.4°C projected by 2100). Most of the CMIP6 models agree on the direction that environmental changes will take in the current century. However, in some parameters, there is inter-model variability in the magnitudes of the projected change (i.e., some are more extreme than others). Aiming to integrate these differences between models, we used an ensemble of four ESM (Table S2; Figure S1) from CMIP6: GFDL-ESM4, IPSL-CM6A-LR, MPI-ESM1-2-HR, and UKESM-1-0-LL (i.e., we averaged monthly model outputs across the four ESM). All covariates were bilinearly interpolated to a common extent (i.e., encompassing all observed and simulated tracks) and resolution ($1° \times 1°$ pixel size). Each presence and absence location were temporally (i.e., same month) and spatially matched to environmental data by averaging their values within a 150 km radius (1° of longitude represents ca. 100 km in the latitudes involved), hence accounting for uncertainty in covariate data that arise from observational error and filling in missing data.

2.5 | SSPs ensemble for the tracking period and sensitivity analysis

Tracking datasets overlapped both with the hindcast (1850–2014) and forecast (2015–2100) phases of the CMIP6 ESM. In the hindcast phase (i.e., ESM covering historical time), only one monthly layer for each environmental variable exists. However, in the forecast phase (projection/forcing phase), there were as many monthly layers for each environmental variable as available SSP (i.e., future climate projections; upper-right part of Figure S2). Therefore, a specific analysis was needed to determine whether the environmental conditions differed notably in the different forcing scenarios that overlapped temporally with the tracking datasets. More in detail, this was done to assess whether we needed to fit a habitat suitability model for each SSP, or if we could use a monthly average of the three scenarios (SSP1-2.6, SSP3-7.0, and SSP5-8.5) to fit a single model for each sex/season combination (males in winter, females in winter, or females in summer). To this end, we computed all possible mean SST differences between scenarios on a monthly basis (e.g., mean January SST for SSP1-2.6 [2015–2019] minus mean January SST for SSP5-8.5 [2015–2019]; 2015–2019 being the years where there is an overlap of the CMIP6 forecast phase and our tracking data). We then compared these differences to the root mean square error (RMSE) of each ESM: if the differences (in °C) between scenarios were smaller than the RMSE of the model, we could assume that differences were not critical. Differences including the historical period (e.g., mean January SST for SSP1-2.6 [2006–2014] minus mean January SST for SSP5-8.5 [2015–2019]; 2016–2014 being the years where there is an overlap of the CMIP6 hindcast phase and our tracking data) were computed to check whether there was a strong variation of environmental conditions in the hindcast phase in relation to the forecast one. We obtained smaller differences than RMSE in all cases (Figure S3), so we fitted a single model for each sex/season combination (lower part of Figure S2). All SST values were extracted from the minimum convex polygon determined by the tracking data of each sex/season combination. This analysis was only performed for SST. Finally, we obtained an environmental data repository to fit the habitat suitability models extending from 2006 up to 2019 (the period covered by the tracking data) that consisted of a monthly layer for each environmental variable, which was a product of averaging the monthly data of the three SSP considered within each ESM, and a subsequent averaging of the four ESM used (Figures S1 and mid part of S2).

2.6 | Habitat suitability model

We developed three species distribution models (males in winter, females in winter and females in summer) using BRT, a machine-learning method commonly used to model animal tracking data and to predict future species distributions (Chambault et al., 2022; Hazen et al., 2018; Hindell et al., 2020; Hückstädt et al., 2020). The BRT algorithm demonstrates improved performance when using an equal number of pseudo-absences compared to the available presences. Consequently, we employed a stratified random subsampling approach to select the same number of pseudo-absence data points as presence observations per day and individual. This 1:1 ratio has been recommended for machine-learning methods (Barbet-Massin et al., 2012), and applied in species distribution models of animal telemetry (Hazen et al., 2018, 2021). Although collinearity between environmental variables does not affect BRT predictions, it can affect the interpretation of the model (Dormann et al., 2013). Therefore, we assessed collinearity among variables by calculating the Spearman pairwise correlation coefficient. Correlations varied in the different sex/season combinations. We represented the Spearman rank correlation coefficients by using a cluster analysis (Figures S4–S6), which helped decide which variables should be kept for further modeling (Table S1). Variables retained for each model are shown in Table S1. Bathymetry, slope, SST, salinity, and eddy kinetic energy were used in the three models. Distance to shore and distance to colony were used only in the model for females in winter; mixed layer depth was used only in both female models. Chlorophyll concentration was used only in the winter models and carbon from diatoms was used only in the model for females in summer.

We used the “dismo” package (Hijmans et al., 2020) in R to fit the BRT using a Bernoulli family, appropriate to the response variable of presence (1) and absence (0). BRT requires the optimization of four parameters (Elith et al., 2008): the number of trees (boosting iterations), tree complexity, the learning rate (shrinkage), and the bag fraction (proportion of data randomly selected at each iteration). We created combinations for potential values: number of trees = 50–10,000 in 50 tree increments; tree complexity = 1, 3, or 5; learning rate = 0.005, 0.001, 0.05, 0.01; and bag fraction = 0.5, 0.6, or 0.7. Following previous recommendations (Elith et al., 2008), we selected the combination with >1000 trees that minimized the area under the receiver operating characteristic curve (AUC, a measure of model predictive performance) during cross-validation. In the case of ties, we prioritized models with larger learning rates, smaller tree complexities, and fewer trees to reduce overfitting. To account for the repeated-measures structure derived from telemetry data, we incorporated a block factor in the cross-validation process (March et al., 2021; Reisinger et al., 2018; Roberts et al., 2017). We used individual Antarctic fur seals as folds in a leave-one-out cross-validation, meaning that all data from a given animal (both observed and simulated locations) were excluded from the training dataset and used to validate the model. After running the parameter optimization, we selected the parameters to fit the final model. Males in winter: number of trees = 3650, tree complexity = 5, learning rate = 0.005, bag fraction = 0.7; females in winter: number of trees = 3250, tree complexity = 5, learning rate = 0.01, bag fraction = 0.5; females in summer: number of trees = 3250, tree complexity = 5, learning rate = 0.005, bag fraction = 0.5 (Tables S3–S5). Variable selection in BRT is achieved because the model largely ignores non-informative predictors when fitting the trees (Elith et al., 2008). However, to drop unimportant variables the model included an additional variable, with a random number between 1 and 100, to serve as an indicator for variables that have influence greater or less than random (Scales et al., 2017). All environmental variables had an influence greater than the random number variable and were included in the final model.

2.7 | Spatial predictions of habitat suitability

We used the fitted model to generate spatial predictions of the habitat suitability for the entire study region monthly. To simplify our output, we only show predictions for the two extreme SSPs (SSP1-2.6; low forcing/SSP5-8.5; high forcing). To account for model stochasticity and estimate the uncertainty associated with these predictions, we used a bootstrap approach (Elith et al., 2008; Hazen et al., 2018). We fitted the model 50 times by sampling half the data (with replacement) to map daily predictions, using the median, for the study region (Hindell et al., 2020; March et al., 2021). As a measure of uncertainty, we calculated the 95% confidence interval range of the 50 values in each cell. Our habitat suitability predictions range from 0 to 1, with 0 representing the least environmentally suitable locations and 1 representing the most suitable ones. To summarize winter seasonal trends (for males and females), we generated averages from monthly predictions by grouping winter data in early (March, April, May), mid (June, July, August), and late winter (only September for males in winter and September, October, and November for females in winter; adapted from Arthur et al., 2017). Habitat suitability for females in summer was assessed in a single timeslot (i.e., the whole summer), as their movement is highly influenced by their central-place foraging behavior, so there are no latitudinal month-related differences in that period. It is worth noting that habitat suitability here refers only to foraging grounds (i.e., at sea) and does not consider breeding habitat (i.e., on land).

2.8 | Accessibility model

The modeling approach described above estimates the habitat suitability of a given location based on its environmental characteristics. However, it does not consider the accessibility of a given cell. Following previous works, we used a second set of models to account for this factor (Hindell et al., 2020; Reisinger et al., 2018). Given that males and females do not behave as central-place foragers in winter, we modeled the accessibility of a given grid cell as a function of distance beyond the sea ice edge (15% sea ice concentration) using a binary response (Hindell et al., 2020): accessible (i.e., cells with any observed or simulated location) or non-accessible (i.e., cells with no observed or simulated locations). On the other hand, females behave as central-place foragers during the breeding season and hence both sea ice concentration and distance to the colony were considered to determine the accessibility of a given cell for females at that time. Under this assumption, the modeling consisted of fitting binomial models with a smooth, monotonic decreasing constraint using the “scam” R package (Pya & Wood, 2015), as accessibility should decrease with the distance to the ice edge and/or distance to the colony. Antarctic fur seals may occur in areas where sea ice concentration is >15% (Reiss et al., 2017; Ribic et al., 1991), but satellite telemetry data indicates that they usually avoid such areas (Arthur et al., 2017; March et al., 2021) and hence those were considered not to be accessible in our models. As in the habitat model, we used a bootstrap approach to account for model uncertainty and fitted the model 50 times by sampling half the data (with replacement). Predictions from the habitat suitability model were then weighted by the predictions of the accessibility model. This modeling approach deems as inaccessible any suitable foraging patch that may develop further away from the current female movement ranges; it therefore fails to identify environmentally suitable areas that could be used by females if they shifted their breeding grounds. Accordingly, we ran a second accessibility model for females in summer including only sea ice concentration, to identify suitable foraging grounds far from the current breeding area, accessible under a relaxed philopatry scenario.

2.9 | Direction of habitat suitability changes

The geographic direction of variations in habitat suitability was assessed by calculating the centroid of the predicted habitat suitability distribution monthly (i.e., mean latitude and longitude coordinate of the area with habitat suitability ≥0.1) all along the forecast phase of the CMIP6 ESM used (2015–2100).

2.10 | Quantification of habitat suitability changes

To quantify the amount of habitat that will be potentially gained or lost in the different climate change scenarios, we first calculated the area of suitable habitat (habitat suitability ≥0.1) monthly through all the different periods (present–2100), then we calculated annual averages and finally, fitted linear regressions (area ~ year) to assess the trends in habitat suitability (gain, loss, or preservation; Ouled-Cheikh et al., 2022; Ramírez et al., 2022). From these, we extracted: (1) the slope and (2) the *p*-value, assessing the trend in the area of optimal habitat versus time and whether it was statistically significant or not.

2.11 | Ethics statement

Animal handling protocols to capture males at Deception Island were reviewed and approved by the Ethics Committee in Animal Experimentation of the University of Barcelona and the Government of Catalonia (project No. 10292) by relevant guidelines and regulations. The procedures adhered to the ARRIVE guidelines and requirements of the ethics committee of the Spanish Polar Institute that approved all our fieldwork under permit No. CPE-2018-4. Captures of females at Cape Shirreff were conducted under the USA Marine Mammal Protection Act Permit No. 20599 granted by the Office of Protected Resources, National Marine Fisheries Service, and the USA Antarctic Conservation Act Permit Nos. 2012-005, 2017-012, the USDA Permit No. 42994, and the NMFS-SWFSC Institutional Animal Care and Use Committee Permit No. SWPI 2014-03R and the Scientific Ethical Committee of Environmental and Animal Care of the Universidad Católica de Chile (Code 150617016).

3 | RESULTS

3.1 | Model assessment

Model assessment using cross-validation procedures suggests a good fit to the observed data for the three models tested (males in the non-breeding season, females in the non-breeding season, and females in the breeding season), with a cross-validated deviance of 0.374, 0.628, and 0.112, respectively, and having high predictive performance with cross-validated AUC score: 0.97, 0.94, and 0.99, respectively (Tables S3–S5). Top predictors were bathymetry (for males in the non-breeding season; 54%; Figure S7), SST (for females in the non-breeding season; 36%; Figure S8), and eddy kinetic energy (for females in the breeding season; 52%; Figure S9). All three models showed non-linear response curves (Figures S10–S12).

3.2 | Extent of suitable habitat for males in winter

Currently, the distribution of suitable habitats for Antarctic fur seal males during the non-breeding season shifts in accordance with sea ice dynamics: they cluster off the Western Antarctic Peninsula in the early winter and move northward as winter progresses and sea ice expands (Figure 2). Under SSP1-2.6, only slight changes are expected by 2100 in the distribution of suitable habitat patches (Figure 3), although the total extent of the suitable habitat (from an environmental point of view) is projected to decrease overall. More notable changes are expected by 2100 under SSP5-8.5 (Figure 2), as habitat suitability is projected to increase and expand southward off the Western Antarctic Peninsula in the early winter. Mid and late winter habitat suitability projections present a southward and southeastward shift respectively, with the latter being a consequence of the seasonal, bell-shaped growth of sea ice in the Weddell Sea (Figure S13). Also, new suitable habitats may appear in the reduced sea ice limit of the Weddell Sea.

3.3 | Extent of suitable habitat for females in winter

Currently, suitable habitat for Antarctic fur seal females throughout winter occurs over a much wider area than that of males, both in latitude and longitude, spanning from the eastern Pacific and to the western Atlantic sectors of the Southern Ocean (Figure 4). When comparing present-day habitat suitability distribution with that expected by the end of the century, major suitable habitat reductions emerge under both SSP1-2.6 and SSP5-8.5 (Figure 3). Suitable habitat in the early winter is projected to be extensively lost by 2100 in the Pacific sector of the Southern Ocean in the

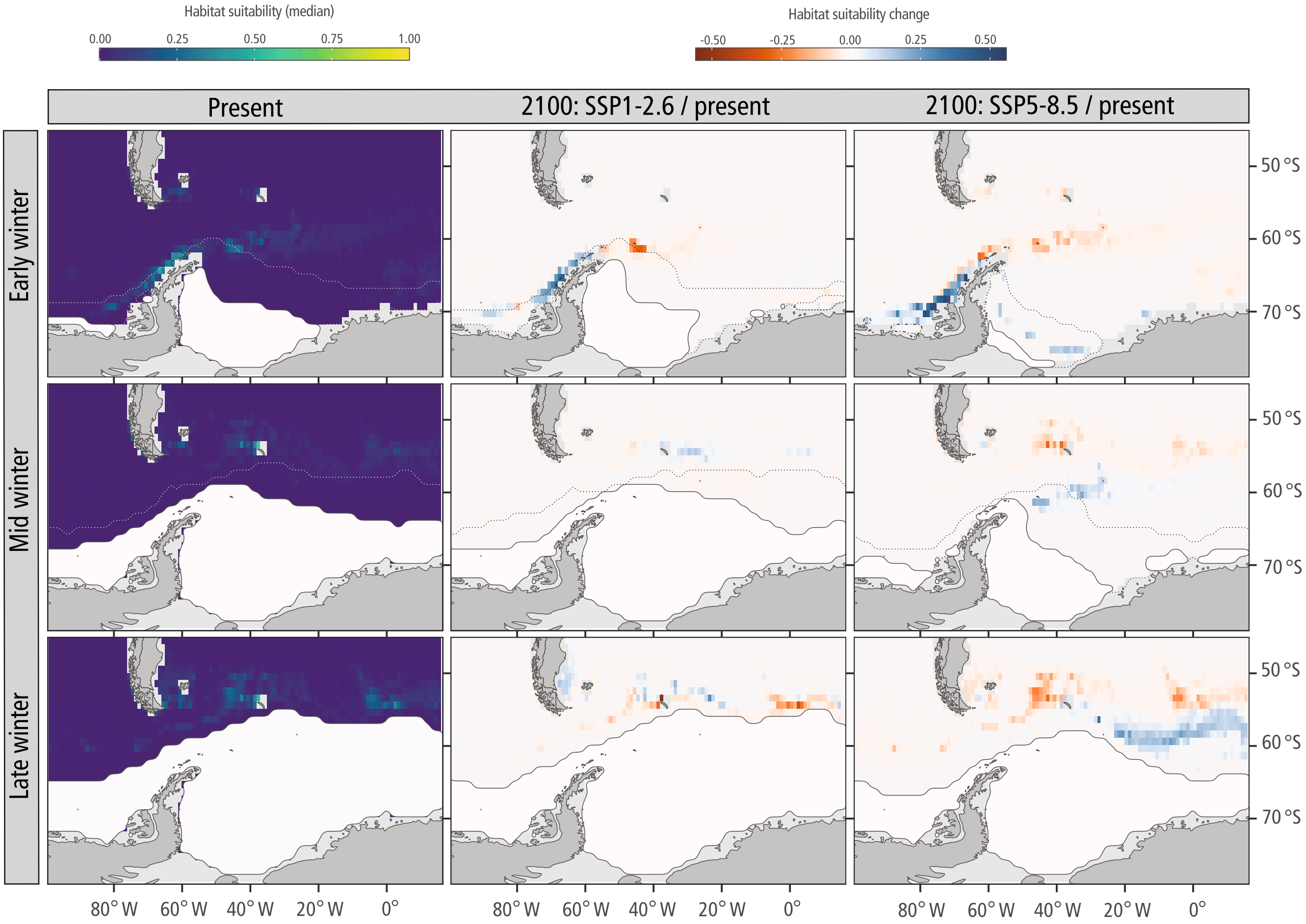

FIGURE 2 Predicted habitat suitability for Antarctic fur seal males throughout the non-breeding season. Early winter: (March–May), mid winter (June–August), late winter (September). First column (Present) shows the median of the bootstrapped habitat suitability predictions ($n = 50$) averaged for the 2019–2025 period. SSP1-2.6 column shows the difference between habitat suitability in 2100 and the present, where blues indicate a gain in suitable habitat and reds a loss. SSP5-8.5 column shows the difference between habitat suitability in 2100 and the present, where blues indicate a gain in suitable habitat and reds a loss. White polygon shows the area covered by a sea ice concentration >15% (this includes open water areas at sub-pixel resolution; Stammerjohn & Smith, 1997) in the minimum extent and the dotted line at the maximum. Map lines delineate study areas and do not necessarily depict accepted national boundaries. SSP, Shared Socioeconomic Pathway.

SSP1-2.6 scenario, with a slight increase in the Atlantic sector. This pattern vanishes in mid and late winter, when suitable patches occur both in the Pacific and the Atlantic sectors, but over a much smaller extent than currently. A clearer spatial pattern emerges under SSP5-8.5, with the loss of a massive area of suitable habitat between 40° S and 60° S. In contrast to the pattern for males, habitat close to the coast of the Western Antarctic Peninsula is not projected to be suitable for females in the early winter, with only some patches of new suitable habitat in the northernmost part of the Weddell Sea, but not accessing up to the minimum sea ice limit (Figure S14).

3.4 | Extent of suitable habitat for females in the breeding season

Currently, suitable habitat for females during the breeding season is concentrated within 100 km north of Livingston Island, with a decreasing gradient of habitat suitability all along the South Shetland Islands and the Western Antarctic Peninsula. Under the SSP1-2.6 scenario, new patches of suitable foraging habitat are projected to develop south of Livingston Island, when distances both to sea ice and the colony are included in the accessibility model (strong philopatry scenario). For SSP5-8.5, suitable foraging patches may occur mostly southward and further away from Livingston Island, under the same accessibility drivers (Figures 3 and 5; Figure S15). However, extensive patches of suitable foraging grounds develop up to 1500 km from Livingston Island in the Bellingshausen and Weddell Sea both under SSP1-2.6 and SSP5-8.5 scenarios when the distance to the colony is removed from the accessibility model (relaxed philopatry scenario).

4 | DISCUSSION

We created habitat suitability models for male and female Antarctic fur seals by integrating tracking data and outputs from four ESM and

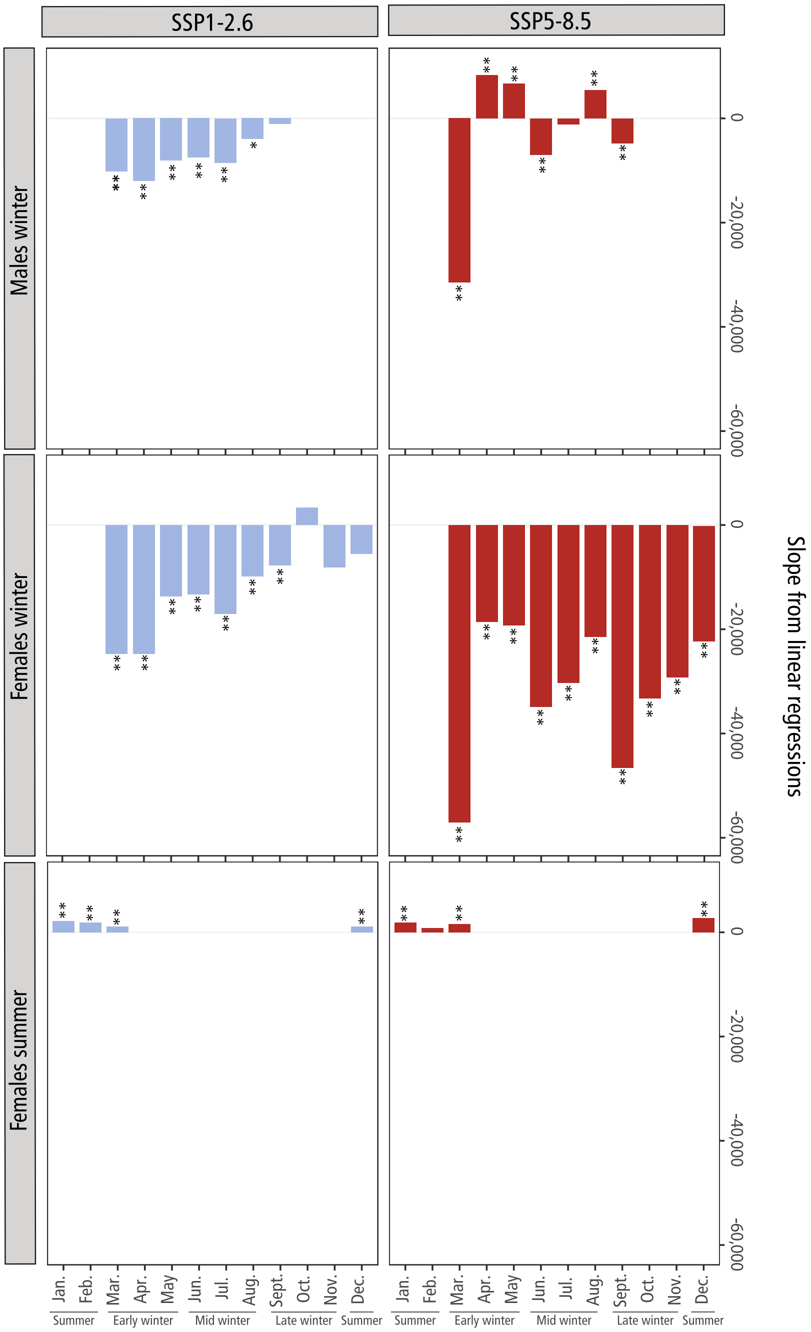

FIGURE 3 Habitat suitability trends (linear trend of the yearly habitat suitability; ≥0.1). Barplots show the slope from the linear regressions fitted monthly between "year" and the area of suitable habitat from the present until 2100 for males in winter (upper panels), females in winter (mid panels), and females in summer (lower panels) split in the two SSP (SSP1-2.6; left, SSP5-8.5; right). Asterisks denote statistically significant linear regressions (*$p < .05$; **$p < .01$). SSP, Shared Socioeconomic Pathway.

projected potential changes in habitat suitability for this species up to 2100. Our cross-validated model performance metrics highlight that all of the models that we developed have a high predictive performance, so we expect them to have a strong ability to discriminate between suitable and unsuitable areas.

The findings presented in this study revealed that both males and females will experience a major poleward distribution shift during the non-breeding season (Figures 2 and 4). It is worth noting that suitable foraging grounds for females during the breeding season will likely persist near to current breeding colonies at Cape Shirreff (Livingston Island), but extensive patches of environmentally suitable foraging grounds may also arise in the Bellingshausen Sea (Figure 5). Accessing these new potential foraging grounds would require longer foraging trips if females remain faithful to their current breeding colonies. Alternatively, much shorter foraging trips would be required if females moved for breeding to new, ice-free breeding beaches, a response dependent on their degree of philopatry.

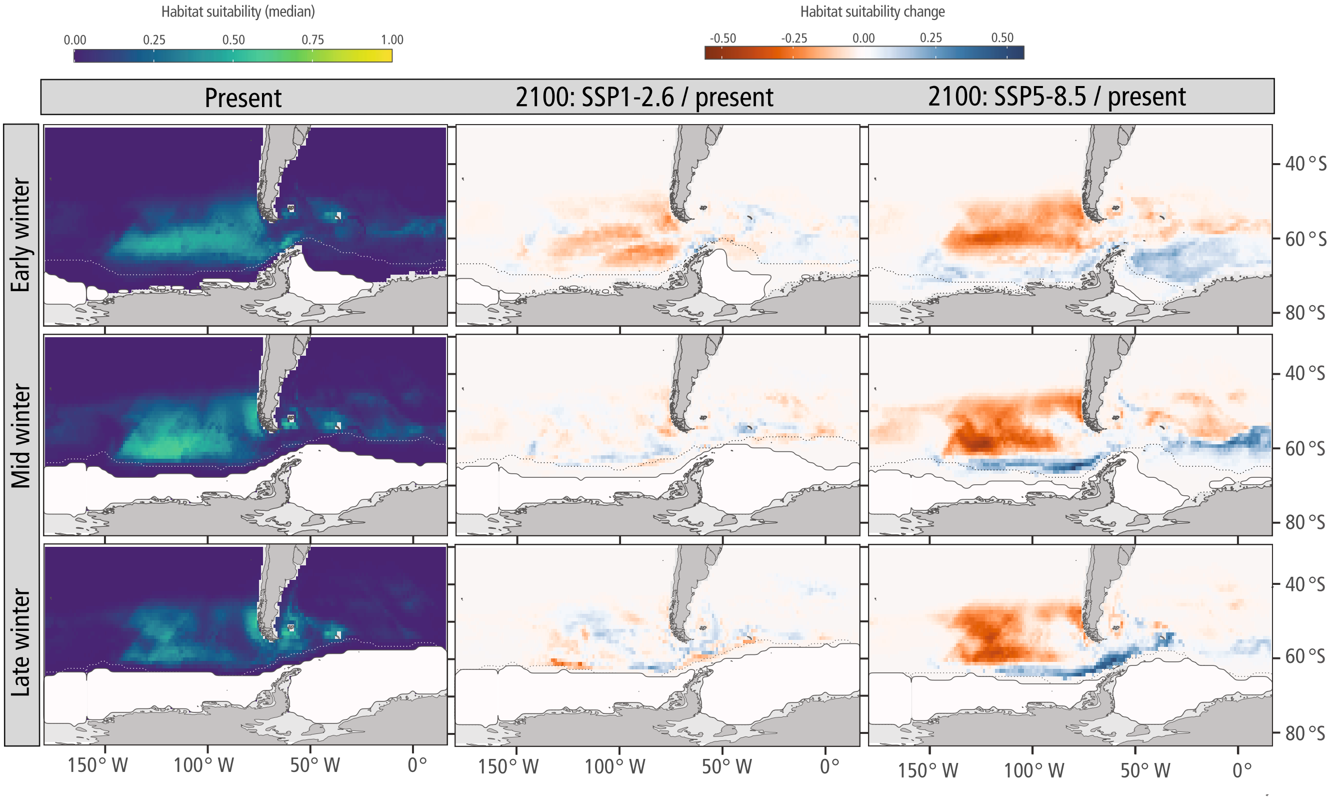

FIGURE 4 Predicted habitat suitability for Antarctic fur seal females throughout the non-breeding season. Early winter: (March–May), mid winter (June–August), late winter (September–December). First column (Present) shows the median of the bootstrapped habitat suitability predictions ($n = 50$) averaged for the 2019–2025 period. SSP1-2.6 column shows the difference between habitat suitability in 2100 and the present, where blues indicate a gain in suitable habitat and reds a loss. White polygon shows the area covered by a sea ice concentration >15% (this includes open water areas at sub-pixel resolution; Stammerjohn & Smith, 1997) in the minimum extent and the dotted line at the maximum. Map lines delineate study areas and do not necessarily depict accepted national boundaries. SSP, Shared Socioeconomic Pathway.

It should be noted that males and females tagged for the present study were sampled at different sites, in different years, and during contrastingly different sea ice conditions. However, the impact of these confounding factors is thought to be small, particularly the difference in sampling sites. This is because they were only 40 km apart and males were captured at a haul-out site where they congregate after the breeding season to molt. In this regard, males and females can be assumed to belong to the same regional population, thus overcoming the limitations of this as a potential confounding factor. On the other hand, differences in sea ice conditions during the years when males and females were tracked represent a more important methodological and analytical limitation. This is because the females tracked in winter experienced extended sea ice cover, whereas the extent of sea ice cover was smaller during the year when males were tracked. More extensive sea ice cover may certainly result in a more northerly location of the winter foraging grounds, but this is unlikely to be the reason for the differences reported here between the winter foraging grounds of males and females, more than 1000 km apart. Previous research using stable isotope analysis and satellite telemetry and conducted over several years has already demonstrated that males forage closer to Antarctica than females during the winter months, both in the Atlantic and the Indian sectors of the Southern Ocean (Arthur et al., 2017; Cherel et al., 2009; Drago et al., 2023; Jones et al., 2020; Kernaléguen et al., 2012, 2015, 2016; Lowther et al., 2020; March et al., 2021; Raymond et al., 2015; Walters, 2014). Hence, interannual differences in the extent of sea ice may certainly influence the exact location of the winter foraging grounds of each sex, but there is little doubt that males remain closer to Antarctica than females during the winter months, irrespective of sea ice extent.

The reasons for the winter segregation of males and females are poorly understood but might be related to the winter migration of Antarctic krill to areas deeper than 100 m over the continental shelf (Atkinson et al., 2008; Reiss et al., 2017). The average body mass of adult female Antarctic fur seals from Cape Shirreff is 42 kg, their average aerobic dive limit is 1.6 min, and their average dive duration is 1.3 min (Borras-Chavez et al., 2023; Costa et al., 2001). Oxygen stores have not been calculated for adult male Antarctic fur seals to the best of our knowledge, but their average body mass is larger than 100 kg (Lowther et al., 2020; Payne, 1979). As oxygen stores depend on lung volume, blood volume, body mass, and hemoglobin and myoglobin (Costa et al., 2001), the differences in body mass reported above suggest that the oxygen stores of adult males should be at least twice those of females, unless major differences exist between the

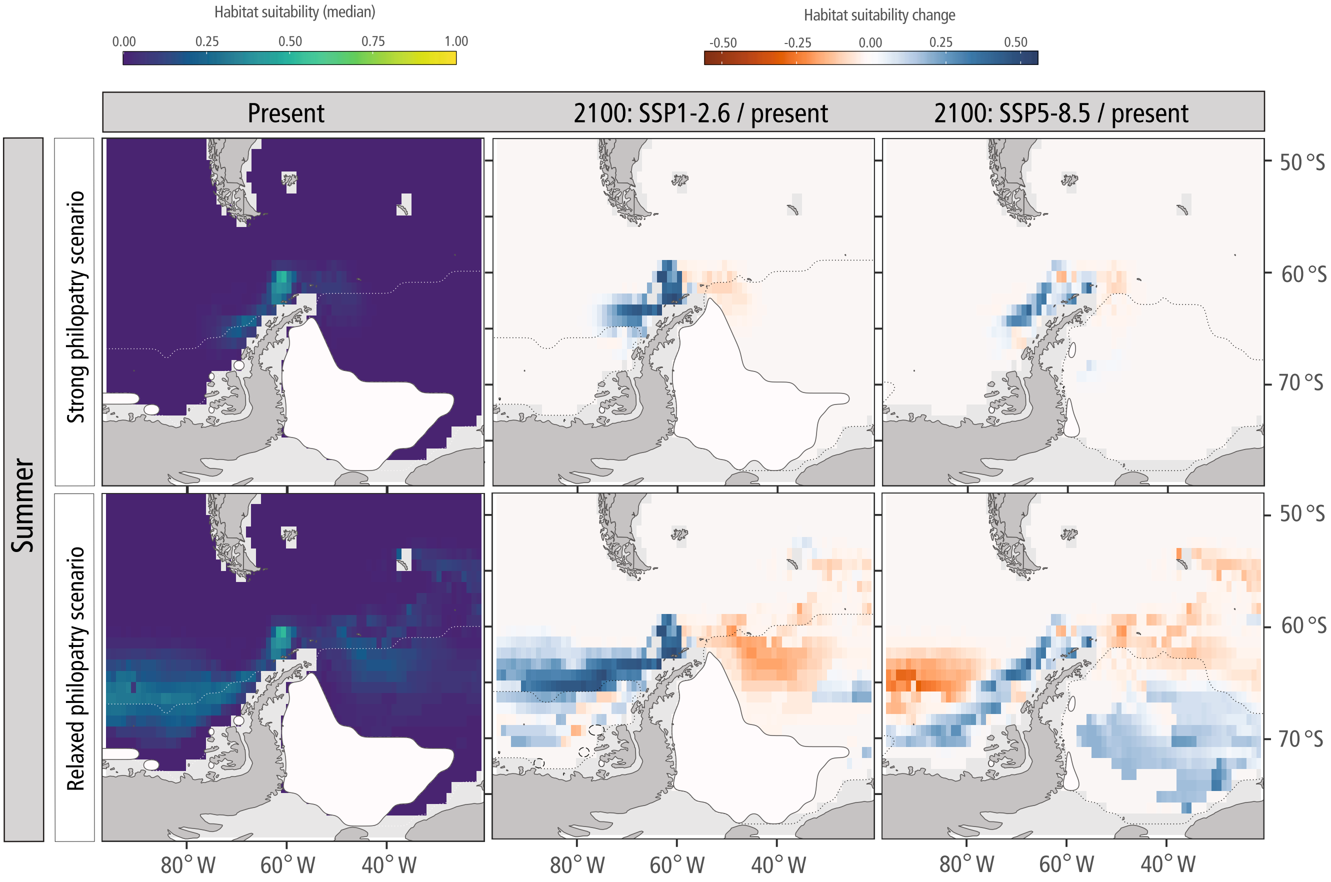

FIGURE 5 Predicted habitat suitability for Antarctic fur seal females throughout the breeding season. First column (Present) shows the median of the bootstrapped habitat suitability predictions (*n* = 50) averaged for the 2019–2025 period. SSP1-2.6 column shows the difference between habitat suitability in 2100 and the present, where blues indicate a gain in habitat suitability and reds a loss. White polygon shows the area covered by a sea ice concentration >15% (this includes open water areas at sub-pixel resolution; Stammerjohn & Smith, 1997) in the minimum extent and the dotted line at the maximum. Map lines delineate study areas and do not necessarily depict accepted national boundaries. SSP, Shared Socioeconomic Pathway.

hemoglobin and myoglobin contents of adult female and male fur seals. This explains why the average dive time of adult males from the South Georgia Islands in summer is 3.9 min, compared to 1.4 min in females (Staniland & Robinson, 2008). A longer dive time allows males to reach greater depths, which in turn explains why the average depth of male dive in the Atlantic sector during the summer months is 100 m and that of females less than 50 m (Biuw et al., 2009; Costa et al., 2000, 2001; Staniland & Robinson, 2008). Females dive much deeper on average in the Indian sector, but never deeper than 100 m (Blanchet et al., 2013; Jeanniard-du-Dot et al., 2017; Lea et al., 2002; Lea & Dubroca, 2003). On the contrary, the deepest male dives reach 270 m and the average depth of the deepest daily dive of males increases significantly as winter advances, with most males regularly diving deeper than 100 m (Lowther et al., 2020; March et al., 2021). The overall evidence suggests that krill remaining at 100–200 m of depth during the winter months may be out of reach of females but is still accessible to males. This explains why krill remains the staple food of males in the Atlantic sector year-round (Drago et al., 2023), whereas females move to northern foraging grounds and shift to myctophid fishes and squid (Walters, 2014). It should also be noted that segregation between male and female Antarctic fur seals at winter foraging grounds emerges before they reach sexual maturity (Jones et al., 2021; Kernaléguen et al., 2016), which can be explained by the larger size of males since weaning (Payne, 1979). Additionally, Antarctic fur seals are one of the few fur-bearing marine mammals of Antarctica and as such, they have high energetic demands when foraging at high latitudes (Liwanag, 2008). The greater mass and body size of males result in smaller surface-to-volume ratios and thus less relative area to lose heat to the marine environment. This difference may also contribute to explain the disparities in the winter distribution disparities between sexes.

These differences align with our findings, as our results pointed out that the most informative variable to explain habitat suitability for males in winter months was bathymetry, with distance to the sea ice edge also playing a significant role at finer spatial scales (March et al., 2021). Bathymetry and sea ice edge may be selected as relevant as they characterize a region of open water immediately off the sea ice edge along the Western Antarctic Peninsula, where males spend winter months. Although bathymetry is independent of warming, male fur seals avoid areas with a very high sea ice concentration (March et al., 2021; Reiss et al., 2017; Ribic et al., 1991), which are usually closer to the continent and therefore shallower. For this reason, their winter distribution is predicted to shift poleward and expand, as new ice-free areas open in the southernmost sectors of the Bellingshausen and Weddell Seas currently covered with ice year-round (Waluda et al., 2010). In contrast, we found that the winter foraging grounds of females are primarily influenced by SST, in agreement with previous studies (Arthur et al., 2017). As SST increases in the northernmost part of their current winter foraging distribution, the extent of suitable winter habitat will not only shift southward but also contract. Furthermore, the southward expansion of both males and females is restricted by the Antarctic landmass, leading to a net loss of suitable habitat area during the winter months all along the current century.

During summer, adult males remain stationary on breeding beaches, performing few to no foraging trips (Staniland & Robinson, 2008), while the income-breeding lactating females perform central-place foraging trips as they suckle their pups. As a result, the existence of food-rich patches at a short distance from the colony is critical for their reproductive success (Forcada & Hoffman, 2014). In this case, the best descriptor for the locations chosen by females in the summer was the eddy kinetic energy, a proxy for mesoscale activity features such as eddies or meanders. These oceanographic features may enhance primary productivity by locally increasing nutrient availability (Frenger et al., 2018), which draws mesopredators and top predators (Keates et al., 2022). From an environmental point of view, our models predicted an increase in suitable habitat around the Cape Shirreff colony in 2100, as well as the development of favorable environmental conditions all along the Western Antarctic Peninsula. This is particularly meaningful, as it highlights that females would find increasing areas of environmentally suitable foraging habitat for both the weakest and the strongest forcing scenarios throughout the current century during the breeding seasons, which is critical for the species' survival.

Potential changes in the Antarctic fur seal's distribution and spatial use, derived from our habitat suitability models, will largely depend on the response of their prey to increased warming. Antarctic krill is the staple diet of male Antarctic fur seals throughout the year (Drago et al., 2023) and has already experienced a southward distribution shift induced by climate change, especially in the Bellingshausen Sea (shift for larvae: 832 km SW; for adults: 1400 km SW; Atkinson et al., 2019, 2022). Overall, winter foraging grounds of male Antarctic fur seals may align with the projected shift in krill distribution by 2100, particularly during the early and mid winter months. The winter diet of females from Cape Shirreff is less known, but evidence suggests a high reliance on myctophid fishes and squid (Walters, 2014); this is because during winter they forage in areas where krill is scarce or absent but myctophids abound (Collins et al., 2012; Koubbi et al., 2011; Saunders et al., 2019). The diversity, abundance, and body size of myctophids are known to decline in warmer areas and periods (Agiadi et al., 2023; Klemmedson et al., 2020; Schwarzhans & Carnevale, 2021) and projections for the Southern Ocean suggest changes in their geographic and vertical distribution (McMahon et al., 2019). This implies a potential reduction in food availability for females at their current winter foraging grounds and a virtual poleward shift of areas with high myctophid biomass, mirroring our study's projected shift in winter female foraging areas. In addition, as income breeders, their reproductive success is primarily determined by the quantity and quality of food available to females during the lactation period (Sparling et al., 2006) and the survival of post-weaned juvenile female fur seals is greatly influenced by food availability during the winter months (Beauplet et al., 2005; Rutishauser et al., 2004). Interestingly, the population decline observed since 2004 in the Antarctic fur seal population breeding at the South Shetland Islands has been attributed to poor recruitment, resulting from a combination of increased predation by leopard seals on pups before weaning and low survival of post-weaned females at sea (Krause et al., 2022; Schwarz et al., 2013). The recession of environmentally suitable habitat during winter, which currently serves as a foraging ground for adult females in preparation for the breeding season, and as a foraging area for post-weaned juvenile females during their first winter, presents an unfavorable sign for reversing the present population trend.

In contrast to the non-breeding season, a major mismatch between predator and prey distribution may arise during the breeding season. Krill is the main prey item of Antarctic fur seal females breeding at the South Shetland Islands (Atkinson et al., 2022; Borras-Chavez et al., 2023; Osman et al., 2004; Polito & Goebel, 2010), and current evidence suggests that krill distribution is shifting southwards (Atkinson et al., 2019, 2022). Our results show that suitable foraging grounds will still exist close to Livingston Island by 2100, both in the strong and relaxed philopatry scenarios. However, fidelity to current summer foraging grounds (Arthur et al., 2015; Bonadonna et al., 2001) may delay the shift of adult females to new, more productive foraging grounds. Furthermore, strong female philopatry (Hoffman & Forcada, 2012) might prevent the colonization of new breeding areas and hence restrict the use of new krill-rich area in the Bellingshausen Sea. A possible delay in the colonization of the new suitable summer foraging grounds and breeding areas is supported by genetic evidence, as Antarctic fur seals needed approximately a century to recolonize some of the islands from which they were extirpated by sealers (Paijmans et al., 2020). If so, colonies breeding currently at the South Shetland Islands may track the poleward shift of krill in the weaker forcing scenarios but not in the strongest one. The recent colonization of Hugo Island (64.95° S, 65.75° W) by a few breeding females (Fraser, personal observation) might be the onset of such a southward shift, but the vagaries in the numbers of breeding females at the South Orkney Islands (Waluda et al., 2010) demonstrates how tenuous new settlements can be in marginal environments. On the other hand, the populations breeding in the Indian sector of the Southern Ocean may respond differently, as females rely mostly on myctophid fish and squid, which respond to global warming differently to Antarctic krill (McMahon et al., 2019). The responses of Antarctic fur seals predicted by our models also differ from those suggested for other pinnipeds such as the pagophilic crabeater seal *Lobodon carcinophaga*. Crabeaters are a monomorphic, non-philopatric krill predator, highly dependent on sea ice for breeding (Hückstädt et al., 2020). This species may initially adapt faster than Antarctic fur seals to the southward shift of krill, as they breed on sea ice and are not constrained by philopatry (Hückstädt et al., 2020; Wege et al., 2021). However, crabeater seals may experience a major population decline in the long term due to the massive reduction of sea ice extent in the strongest forcing scenarios (Hückstädt et al., 2020; Wege et al., 2021). In contrast, Antarctic fur seals in the Atlantic sector of the Southern Ocean may respond more slowly, due to their philopatry, but thrive in the long run if they can track the southward shift of krill. Other ice-dependent pinnipeds such as the Weddell seal, *Leptonychotes weddellii*, may also be greatly impacted by the projected losses of sea ice during the current century, even though they have a generalist diet and they breed in more stable fast ice than do to crabeater seals (Wege et al., 2021).

Globally, our results give significant insights into how the future may look for a key predator of the Southern Ocean. We argue that the consequences of climate change on this species may be particularly driven by how females deal with the great loss of environmentally suitable habitat during winter months, as habitat suitability during summer was not projected to worsen. Part of the relevance of this study lies in the fact that the Antarctic fur seal is an abundant mesopredator widespread in the Southern Ocean, which may be a useful sentinel species for tracking climate change off the Western Antarctic Peninsula. Moreover, this population is restricted to the Atlantic and Pacific sectors of the Southern Ocean and hence it might integrate the environmental and prey dynamics of this area, signaling changes using shifts in population dynamics, foraging areas, or body condition. This indicates the great value of continuous monitoring of this species, which in turn, will provide important information about climate change-induced environmental variations. It is important to note that our models only use environmental information to discriminate along the gradients of habitat suitability presented and that the spatial resolution we used may hinder local processes such as fine-scale ice dynamics. Furthermore, the marine environment has many more layers of complexity, where prey response and other ecological interactions among organisms and functional groups play key roles in defining the spatial distribution of focal species. There are many other krill consumers whose future dynamics have not yet been studied, as well as a commercial fishery targeting krill in the same foraging grounds used by Antarctic fur seals. It is also worth noting here that commercial sealing decimated Antarctic fur seals during the 19th century (Paijmans et al., 2020) and whales during the 20th century (Hoffman et al., 2022; Laws, 1977), but not other krill consumers, like crabeater seals. Anthropogenic-induced warming will again modify the abundance and distribution of those species in this remote region of the planet. It would be of great value to tackle the interactions between all those species using ecosystem-level mechanistic models and incorporating the results into the management of the krill fishery. Finally, continued monitoring over the current century will ensure that conservation and exploitation policies are based on up-to-date, science-based evidence.

AUTHOR CONTRIBUTIONS

Jazel Ouled-Cheikh: Conceptualization; data curation; formal analysis; investigation; methodology; visualization; writing – original draft; writing – review and editing. **David March:** Conceptualization; data curation; formal analysis; methodology; supervision; writing – review and editing. **Renato Borras-Chavez:** Conceptualization; data curation; investigation; writing – review and editing. **Massimiliano Drago:** Methodology. **Michael E. Goebel:** Funding acquisition; investigation; resources; supervision; writing – review and editing. **José M. Fariña:** Methodology. **Manel Gazo:** Methodology. **Marta Coll:** Conceptualization; funding acquisition; investigation; methodology; supervision; writing – review and editing. **Luis Cardona:** Conceptualization; funding acquisition; investigation; methodology; project administration; resources; supervision; writing – review and editing.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest regarding the publication of this article.

DATA AVAILABILITY STATEMENT

Raw data and results (produced prediction TIFF files) can be openly found in the repository of the University of Barcelona (https://doi.org/10.34810/data1064).

CODE AVAILABILITY STATEMENT

All the R code used in this study is available in the following GitHub repository (https://github.com/jazelouled/AntarcticFurSeal_ClimateChange; https://zenodo.org/doi/10.5281/zenodo.10610953).

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SUPPORTING INFORMATION

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