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Tracking of marine predators to protect Southern Ocean ecosystems

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Projected shifts in the foraging habitat of crabeater seals along the Antarctic Peninsula

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Crabeater seals exhibit extreme dietary specialization, feeding almost exclusively on Antarctic krill. This specialization has inextricably linked habitat use, life history and evolution of this pinniped species to the distribution of its prey. Therefore, the foraging habitat of crabeater seals can be used to infer the distribution of Antarctic krill. Here, we combined seal movements and diving behaviour with environmental variables to build a foraging habitat model for crabeater seals for the rapidly changing western Antarctic Peninsula (WAP). Our projections show that future crabeater seal foraging habitat and, by inference, krill distribution will expand towards offshore waters and the southern WAP in response to changes in circulation, water temperature and sea ice distribution. Antarctic krill biomass is projected to be negatively affected by the environmental changes, which are anticipated to manifest as a decrease in krill densities in coastal waters, with impacts on the land-/ice-based krill predator community, particularly in the northern WAP.

Polar marine ecosystems are particularly vulnerable to changes induced by warming air and ocean temperatures, as these affect the concentration, extent and seasonality of sea ice, which in turn shape ecosystem dynamics from primary producers to top predators[1]. Furthermore, polar marine ecosystems are undergoing some of the fastest rates of environmental change on the planet. The western Antarctic Peninsula (WAP) has recently experienced air temperature warming rates above 0.6 °C per decade and rates of reduction in sea ice extent of ~10% per decade[2].

The WAP continental shelf marine environment is controlled by processes that occur at the air–sea interface and at the outer continental margin[3]. The shelf break along the WAP is influenced by the southern boundary of the Antarctic Circumpolar Current (ACC), which episodically produces intrusions of warmer, saltier and nutrient-rich waters (Circumpolar Deep Water (CDW)) onto the continental shelf (Fig. 1a). These waters mix upward into the surface layers, affecting the oceanographic properties and sea ice concentration[3], and supporting elevated biological productivity[4].

The elevated primary productivity of the WAP sustains high and persistent biomass of Antarctic krill *Euphausia superba*[5]—a species that shapes the dynamics of the entire ecosystem[6]. The WAP krill biomass supports large populations of warm-blooded predators (whales, seals and penguins)[7]—species with elevated metabolic rates and large body sizes, possibly representing the most important community of marine endothermic predators in the world in terms of energy flux[8]. However, the strong seasonality that dominates the Antarctic continental shelf regions determines the structure of this community of krill-dependent predators. Many of these predator species leave Antarctic waters during the austral winter months, whereas others display dietary shifts to include fish prey items during the winter[9].

The crabeater seal *Lobodon carcinophaga*—a permanent pack ice resident—is one of the most abundant species of large marine predators in the world. With a local WAP population of >1.8 million individuals[10], the success of this species depends on Antarctic krill, which account for >90% of its diet[11]. The crabeater seal is one of the most extreme examples of dietary specialization in mammals, making it an ideal sentinel species for the Antarctic ecosystem, as changes in its ecology, distribution and behaviour reflect changes in the Antarctic krill population[12].

The high level of dietary specialization in crabeater seals was probably shaped evolutionarily by the abundance and accessibility of krill in the Southern Ocean, as well as the spatial overlap between foraging and resting (sea ice) areas (Fig. 2a). The co-occurrence of these two habitat requirements (food and resting substrate) results in maximization of foraging efficiency because crabeater seals do not have to invest energy in travelling between foraging and resting areas, as do central place foragers[13]. Another benefit of this overlap is the reduced probability of predation, as the seals avoid offshore open waters, where they would be more exposed to their natural predators, particularly killer whales (*Orcinus orca*)[14].

Here, we use the term habitat to refer to the foraging habitat of crabeater seals, unless otherwise stated. We combined data on crabeater seal movement and diving behaviour[15,16] (Fig. 1b) with environmental data obtained from animal-borne instruments, remote sensing and oceanographic circulation models to build a model to investigate seals' foraging habitat as a function of oceanographic conditions, sea ice and bathymetry along the WAP (Fig. 3 and Supplementary Table 1).

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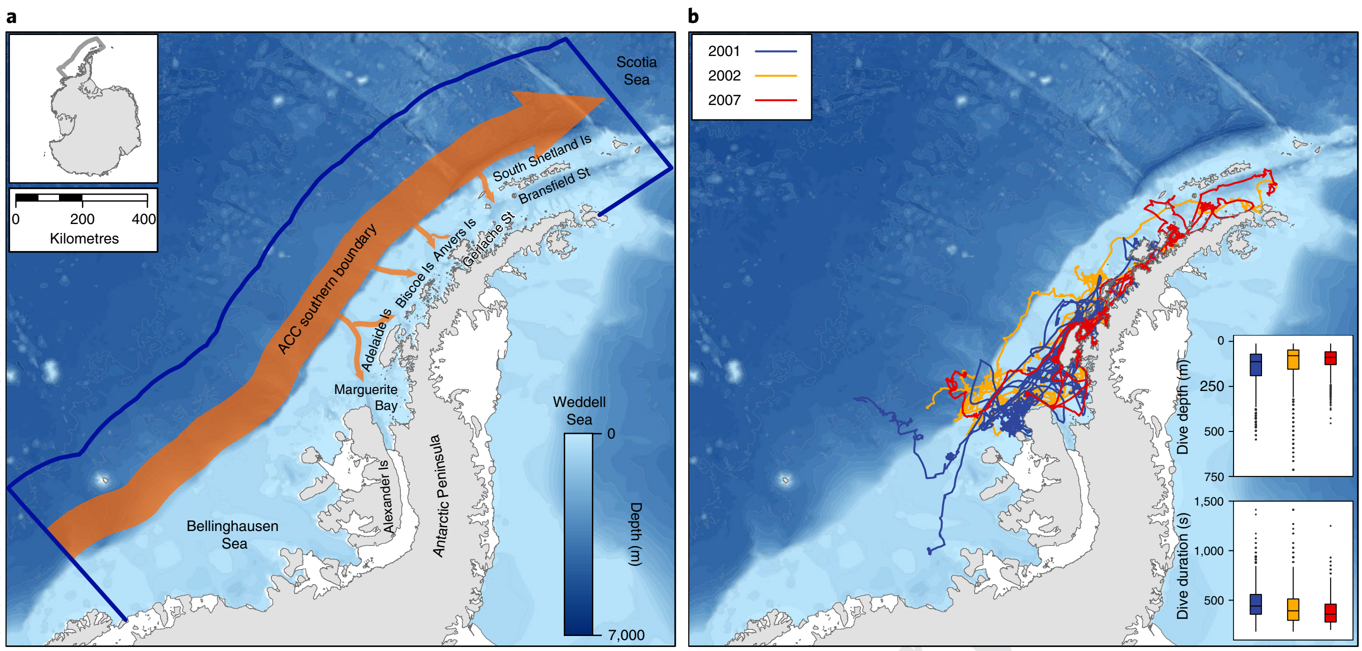

Fig. 1 | Habitat utilization of crabeater seals along the WAP. a, Map of the study area (that is, the WAP), indicating the approximate location of the southern boundary of the ACC and sites of CDW intrusions onto the continental shelf (orange). The spatial domain of the coupled circulation–sea ice model is shown within the blue lines. **b**, Movement patterns of individual crabeater seals from the WAP. Seals were captured in 2001 ($n=16$; blue), 2002 ($n=19$; yellow) and 2007 ($n=8$; red). Differences in diving depth (top inset) and diving duration (bottom inset) of crabeater seals between 2001, 2002 and 2007 are also shown. The centre lines represent the median, box limits represent the 25th and 75th quantiles, vertical lines indicate 1.5× the interquantile range and dots represent outliers. Seals in 2001 dived longer and deeper than those in 2002 and 2007 (Kruskal–Wallis test). Is, island; St, station.

Model simulations of current habitat show that the subsurface environment has a fundamental role in the foraging habitat selected by this species, in addition to the variables traditionally used in marine species distribution modelling, such as surface and bathymetric conditions (Fig. 3). The monthly variability in current habitat importance and departures from the average showed seasonal differences in the foraging habitat of crabeater seals along the WAP (Supplementary Video). Our model showed that current foraging habitat expands into open waters over the continental shelf during summer months (when sea ice cover is at its minimum), in contrast with the use of inner shelf waters during winter months and Naata dramatic reduction in the use of the area between Gerlache Strait and Marguerite Bay.

The at-sea behaviour of marine predators can be used to infer prey distribution and density, as their habitat usage is inextricably determined by the occurrence of their prey[12]. Crabeater seals travel by swimming at the surface (<10 m), whereas their dives (defined here as descents >10 m in depth) are indicative of foraging behaviour (that is, when they are searching for and/or capturing prey)[17]. In contrast with traditional habitat models based on tracking data, our approach additionally models the foraging habitat of crabeater seals by including dives (that is, foraging) as a response variable (Supplementary Table 1).

Crabeater seals eat krill almost exclusively[11], so their foraging habitat along the WAP should reflect the distribution of this mid-trophic species. Indeed, our simulated current seal foraging habitat is consistent with the distribution of krill along the northern WAP obtained from plankton net tows[18] (although with the caveats imposed by the differences in location and timing of traditional net sampling; Extended Data Fig. 7), and corresponds to areas where acoustic surveys have identified high biomasses of Antarctic krill[5,19,20].

Along the WAP, adult krill spawn in the outer shelf in summer to then migrate to the inner shelf in autumn, remaining in coastal waters until the next summer[20,21]. The simulated crabeater seal habitat agrees with this seasonal temporal shift in adult krill distribution (Supplementary Video). Our simulations also identify coastal areas near offshore krill spawning habitats that are similar to those identified for this area using a different modelling approach[22,23]. These comparisons indicate that the habitat model has sufficient strength to be used as a putative indicator of krill distribution (Extended Data Fig. 7).

The crabeater seal foraging habitat model was implemented under expected future atmospheric and oceanographic conditions (that is, increased wind strength and modified ACC characteristics[24]) to assess the impacts these variables are likely to have on the extent and location of the foraging habitat of crabeater seals (and inferred krill distribution), as well as the potential impacts on the krill-dependent predator community (Figs. 2 and 4). The simulations indicated that foraging areas of crabeater seals along the WAP will expand offshore beyond the continental shelf break and the southern boundary of the ACC (Fig. 2b,c). Foraging habitat will be reduced between Bransfield Strait and Anvers Island and around the South Shetland Islands (Fig. 4). Importantly, these reductions in foraging habitat will occur primarily during the summer months when there is increased competition from other krill predators, many of which have restrictions in foraging range imposed by pup or chick rearing (fur seals and penguins) at this time of the year. Our results also showed more extended habitat in the southern latitudes (south of Alexander Island and in the Bellinghausen Sea) for the projected atmospheric and oceanographic conditions (Extended Data Fig. 1).

The fitness of a species is directly linked to its ability to efficiently acquire food while minimizing energy expenditure in doing so[25]. Molecular evidence indicates that the crabeater seal population underwent a sudden increase about 1.6 million years ago, coinciding with expansion of the pack ice season and extent of the pack

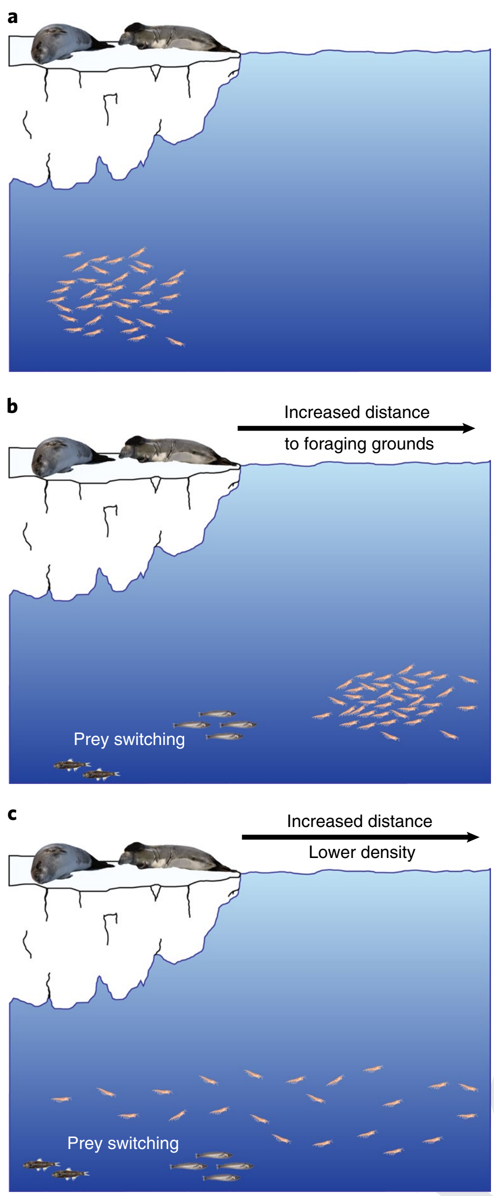

Fig. 2 | Schematic of changes in crabeater seal foraging capability in response to projected habitat changes and decreased Antarctic krill density along the WAP. a, The life history of the crabeater seal has been shaped by the spatial overlap in their haulout sites and foraging areas, reducing the energetic costs associated with travelling to foraging grounds. **b**–**d**, Crabeater seal responses to projected offshore expansion in foraging habitat and inferred krill distribution away from the sea ice edge include: incurring elevated energetic expenses associated with increased travel between haulout sites and foraging areas (**b**) and/or encountering lower krill density as their habitat expands offshore away from the sea ice (**c**). Alternatively, crabeater seals could switch to other prey that occur closer to their haulout sites (**b** and **c**).

ice (due to decreasing temperatures during the Pleistocene[26]). This was accompanied by an increase in krill biomass[27]. The highly specialized diet and de-centralized distribution, along with the overlap between foraging and resting habitats, probably allowed crabeater seals to maximize krill intake, producing the high seal abundances seen today[10].

In contrast with fur seals and penguins, crabeater seals are not restricted to a colony and do not display site fidelity—a strategy that provides flexibility to move over large distances and follow prey aggregations in the pack ice[28] (Fig. 2a). This strategy also minimizes exposure to predators and provides homogeneous access to a stable haulout substrate. Crabeater seals do not have a well-defined circumpolar population structure[29], which provides them with the ability to move and follow prey aggregations.

The spatial distribution, biomass and density of krill will be impacted by projected changes in environmental conditions[5,6,23]. Increased CDW transport onto the continental shelf from stronger winds and changed ACC characteristics will enhance heat transport to the upper-shelf waters and reduce sea ice extent. An increase in productivity is a possible outcome but may be offset by the deepening of the mixed layer depth (MLD)[23]. The projected environmental conditions are not likely to impact the spawning-to-larvae cycle of krill in the WAP, but a reduction of winter sea ice will impact the overwintering survival of larvae, and thermal stress resulting from increased water temperatures may impact krill growth, effectively shifting their distribution to higher latitudes[22,23]. This reduction in inferred krill distribution is relevant for the top-predator community in the northern WAP, the Scotia Sea and South Georgia, which depend on inputs of juvenile krill produced to the south in the central WAP to support the recruitment of adult krill[5].

Krill biomass will probably be negatively affected by environmental changes[30], and the inferred future offshore expansion of adult krill (Fig. 4) will further decrease krill densities along the central and northern WAP. Projections of future krill inferred distribution also indicate a potential advection of the population offshore and beyond the southern boundary of the ACC[22]. However, the fate of the krill biomass is uncertain and depends on the ability of new areas to provide primary and secondary production that can support the krill population.

These changes in the prey field have implications for land- and ice-based krill predators, such as fur seals and penguins[31]. These species are primarily supported by the abundant concentrations of krill that occur near their haulout/resting areas during the austral spring/summer that offset the increased energetic demands and mitigate range limitations imposed by offspring rearing[19,32]. Our spatial projections obtained for expected future conditions show a marked decrease in inferred nearshore krill habitat in the northern sectors of the WAP during summer months (Fig. 4). As the krill range expands away from coastal waters, predators will need to travel longer distances to reach the same krill densities, incurring elevated energy expenditures. Alternatively, they will have to switch their diet to incorporate other prey items (Fig. 2b,c).

The projected changes in krill distribution will also affect winter foraging because crabeater seals are one of the few krill-dependent predators that remain in pack ice-covered waters throughout the year. Today, the bulk of the krill biomass shifts to inshore waters and remains associated with canyons and troughs during the winter[19], making prey easily accessible to the crabeater seals[15]. By 2100, a 90-d delay in the formation of winter sea ice in the area of the WAP, Bellinghausen Sea and Amundsen Sea is anticipated[22], and sea ice is projected to be mostly land-locked or limited to southern waters. These changes imply that distances between crabeater seal haulout sites and foraging areas will increase (Fig. 2b and Extended Data Fig. 2), effectively forcing longer transits from the ice edge to potential offshore foraging grounds, with attendant increased energy expenditure.

Our study indicates that changes in the wind strength, ACC characteristics and sea ice extent and duration projected for the WAP for the future will strongly modify the foraging habitat of crabeater seals and the distribution of adult krill in the region, with potential impacts on the entire krill-dependent predator community. Crabeater seal foraging habitat and inferred krill distribution will expand towards offshore waters and the southern sectors of the WAP, decreasing the density of adult krill available for the community

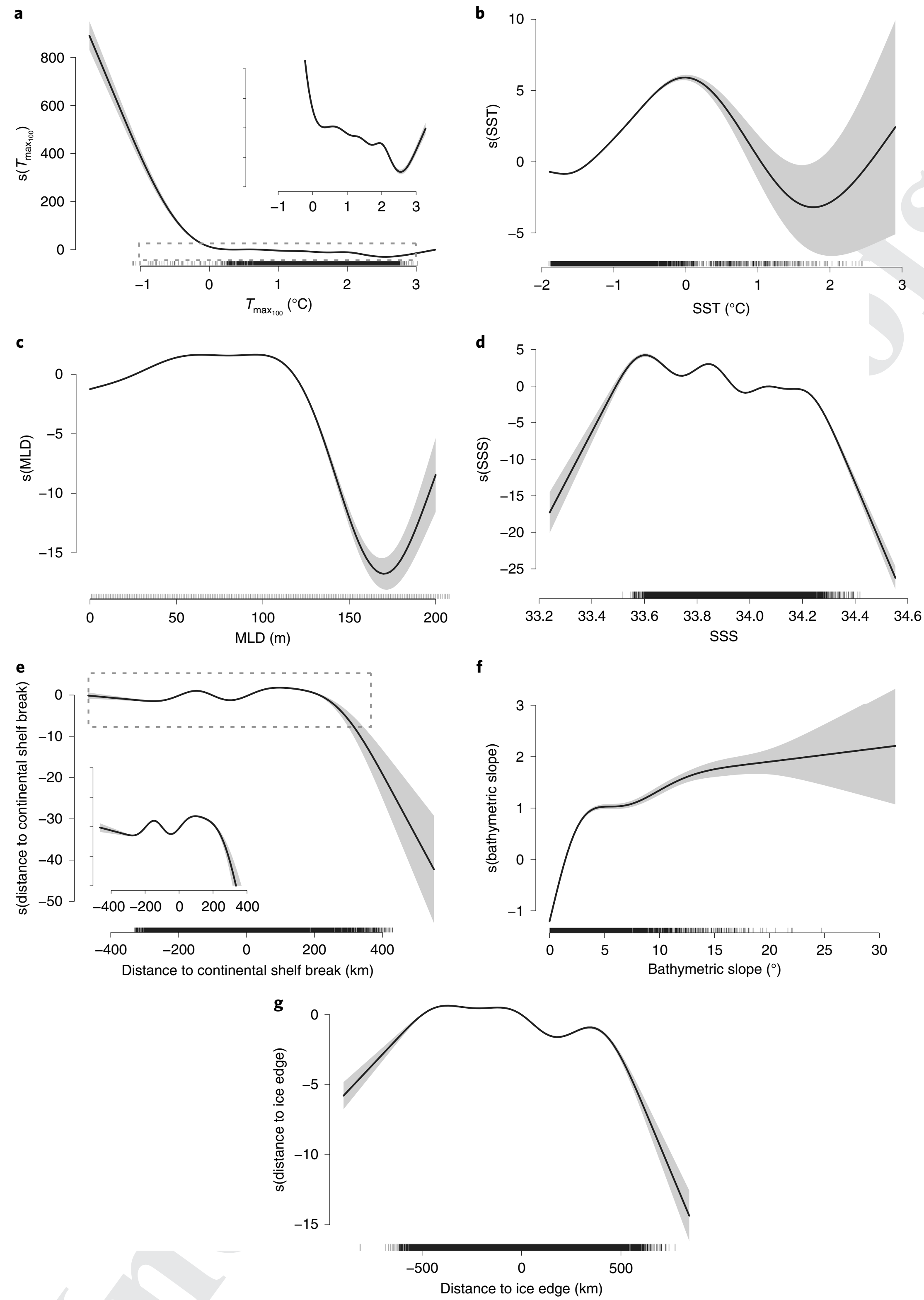

Fig. 3 | Relationship between the foraging habitat of crabeater seals and environmental covariates. a–g, Generalized additive mixed model smoothers and confidence intervals (shaded areas) of the relationship between habitat importance (*y* axis) and the indicated environmental covariates: $T_{max_{100}}$ (**a**); SST (**b**); MLD (**c**); SSS (**d**); distance to the continental shelf break (dist2shelf) (**e**); bathymetric slope (**f**); and distance to the ice edge (**g**). The detailed shapes of the smoothers for the areas indicated by dashed lines are shown as insets. The habitat model details are provided in the Supplementary Information.

of bird and mammal predators in the central and northern WAP. The potential redistribution of prey implies that, to survive, land-based predators will need to modify their distribution (southward movement along the WAP) and/or foraging behaviour (diet switching to other prey), or incur longer foraging trips and exposure to predators (central place forager). Each of these response mechanisms incurs a cost, and the future of the krill predator community depends on the ability to adapt to these changes.

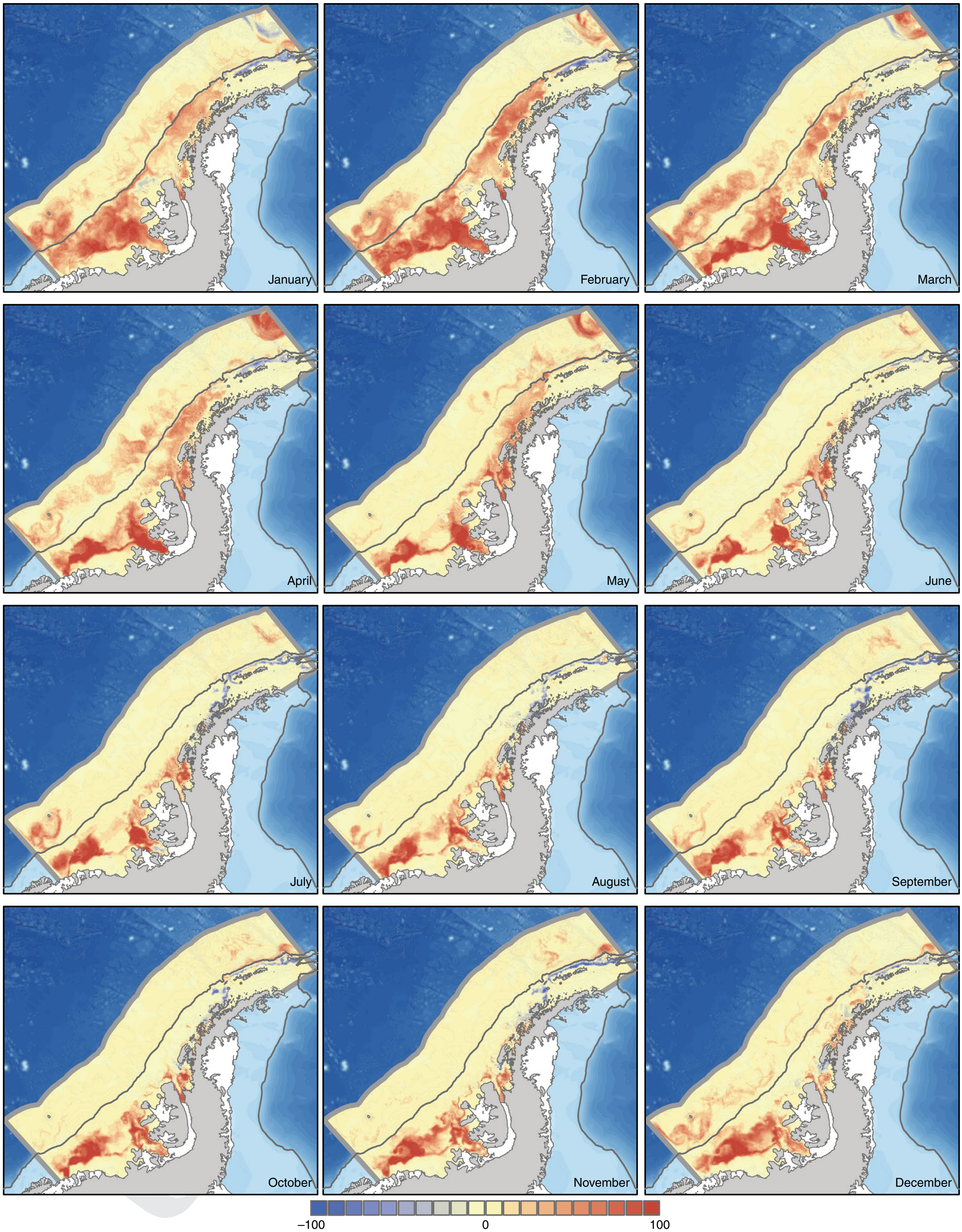

Fig. 4 | Monthly anomalies (percentage change) in predicted habitat importance for crabeater seals under expected future environmental conditions along the WAP. Regions of increase (red), decrease (blue) and no change (yellow) are indicated, in addition to the 1,000-m isobath (thin grey line). The foraging habitat of the highly specialized crabeater seal is a proxy for the distribution of its preferred prey, Antarctic krill.

Online content

Any methods, additional references, Nature Research reporting summaries, source data, extended data, supplementary information, acknowledgements, peer review information; details of author contributions and competing interests; and statements of data and code availability are available at https://doi.org/10.1038/s41558-020-0745-9.

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Methods

Animal captures and instrumentation. Crabeater seals ($n=42$) were captured in the WAP on three cruises (aboard the RV *Lawrence M. Gould*) to the area along the WAP incorporating Crystal Sound, Laubeuf Fjord and Marguerite Bay (Fig. 1) during the autumn and/or winter seasons of 2001, 2002 (US Southern Ocean Global Ocean Ecosystems Dynamics (SO GLOBEC) research programme[33]) and 2007[34]. Tracking and diving data for the animals captured in 2001–2002 have been presented elsewhere[15,16,35,36].

Animals were captured and sedated, as described in refs. [15,35], and instrumented with three different models of Sea Mammal Research Unit satellite relay data loggers (SRDLs) (see refs. [15,34,35]). In 2001 ($n=16$), seals were instrumented with regular Sea Mammal Research Unit SRDL tags, which determine at-sea location and diving behaviour. Animals in 2002 ($n=18$) were instrumented with temperature SRDL tags, which along with the location and diving data also recorded the temperature of the water column. Finally, animals in 2007 ($n=8$) were instrumented with conductivity–temperature–depth SRDL tags, which have the additional capability of measuring the salinity of the water column. The behavioural (diving) and, when available, environmental data collected by these instruments were processed and compressed on board (see Fedak et al.[37]) and transmitted via the Argos satellite system.

Track analysis. We pre-filtered Argos location data using a forward/backward speed filter (20 km h^{-1}) to remove aberrant positions[38] and then applied a state–space model (SSM)[39]. The SSM allows the estimation of regularly spaced positions from the Argos location data, by measuring the errors associated with each location class, as provided by the Argos system, and from dynamics of the movement process[38–40]. This methodology allows for statistically robust predictions that embrace the inherent uncertainty in the position data. For this study, we configured the SSM to generate a position estimate every 4 h. To determine the location of the dives, temperature (2002) and conductivity–temperature–depth profiles (2007), we used linear interpolation based on the filtered tracks and time of each dive.

Track and dive simulation. Because the tracking data only provide presence locations, we used correlated random walks (CRWs) to generate pseudo-absences in our habitat model (10,000 simulated tracks for every individual in our sample). A CRW model is considered an appropriate model to describe animal movement since it introduces a correlation factor to the simpler random walk, which accounts for the tendency of animals to go forward[41]. Moreover, modelling animal movement using CRWs assumes that habitat use is rather homogeneous, and that animal behaviour is consistent with time[42–44].

For the CRW simulations, we calculated the distributions for both step length (km) and turning angle (°) for every individual seal based on their actual tracks, and used these parameters to simulate the tracks. We used the first real location for that individual (that is, the first track location) as the initial point for all corresponding simulated tracks. Since the purpose of this part of the study was to model the habitat available to crabeater seals, we restricted the simulations to only generate positions at sea, by implementing a custom-made land mask of the study area.

The second step was to create one simulated dive for each real dive in our dataset. For every real dive conducted by a seal at time i, we randomly selected a subset of three simulated tracks from the 10,000 created for that individual, estimated the locations at time i and placed a dive at each simulated point in space and time. Taking into consideration computational limitations and the risk of artificially increasing the number of false absences, we decided to use a conservative criterion and to use three pseudo-absences to capture the variability in the environment that the individual did not use. The parameter of interest for each simulated dive was diving depth (used later to extract environmental data at the bottom of the dive (see 'Environmental data sources' and 'Data analysis')). This parameter was randomly drawn from the distribution of actual diving depths for all seals in our sample, to capture the physiological limits of the species and avoid creating dives to unreasonable depths that the seals cannot reach. A different subset of three simulated tracks was then selected for diving time $i+1$, and three new diving locations and depths were assigned as previously described. This process was repeated until every real dive performed by the seal had three corresponding simulated dives. We explicitly restricted the depths of the simulated dives based on bathymetry, so that if the diving depth was deeper than the bathymetry for that location, as defined in the Regional Ocean Modeling System (ROMS) model (see 'Environmental data sources'), a new random location (and dive) was selected for the analysis.

Since all simulated tracks had the first real location for that individual as the point of origin, we added a buffer, consisting of the first five dives for both the real and simulated tracks, which were eliminated from the analysis, thus preventing spatial overlap between the real and simulated dives. As well, we only accepted simulated dives that were located at >4 km from the real dive at any specific time, again avoiding spatial overlap between real and simulated dives. This distance threshold (4 km) was selected since it corresponds to the size of the grid cells from the oceanographic model used to obtain the environmental data (see 'Environmental data sources').

Finally, both datasets (presences and pseudo-absences) were merged ($n=906{,}306$ dives) and used for the habitat modelling analysis.

Environmental data sources. We used a complementary approach to obtain the environmental data for real and simulated dives from four different sources: ice data, bathymetric data, animal-borne instruments and oceanographic modelling.

Ice data. Daily sea ice concentrations for 2001 and 2002 were obtained from the National Snow and Ice Data Centre dataset of Special Sensor Microwave/Imager products. These data are provided on a 25-km grid. For 2007, daily sea ice concentrations were obtained from the National Snow and Ice Data Centre dataset of the Advanced Microwave Scanning Radiometer for the Earth Observing System, with a resolution of 6.25 km. These datasets were also used to calculate the ice edge (see 'Data analysis').

Bathymetric data. Data on sea floor depth were obtained primarily from the SO GLOBEC bathymetry dataset, with a 75-m grid resolution (http://www.whoi.edu/science/PO/so_globec/get_data.html). In addition to sea floor depth, these data were also used to calculate the bottom slope (°) (see 'Data analysis').

Animal-borne instruments. Satellite tags deployed on crabeater seals in 2002 and 2007 also provided data on temperature (hereafter, T_{profile}) for 2002, and temperature and salinity (hereafter, $\mathrm{TS}_{\mathrm{profile}}$) for 2007. These data were quality controlled before analysis by comparing them against the monthly climatological profiles provided by the World Ocean Database (WOD13). For every 1° cell within the study area, we created a mean temperature and salinity profile with its corresponding standard deviation, by taking all data within a radius of 2.5° from the centre of that particular cell. The seal data were then compared against this 1° mean monthly profile and values that differed by more than two standard deviations were flagged as suspicious and visually inspected before confirming their elimination from further analysis. Since dive and T_{profile}/$\mathrm{TS}_{\mathrm{profile}}$ did not necessarily correspond in time, we matched each dive in the analysis with the closest T_{profile}/$\mathrm{TS}_{\mathrm{profile}}$ in time. The dive had to have occurred within 0.5 d of the T_{profile}/$\mathrm{TS}_{\mathrm{profile}}$, otherwise, the dive was not included in the analysis.

Oceanographic modelling. Finally, oceanographic data (temperature, salinity and current velocity (vectors **u** and **v**)) were obtained for both real and simulated dives from a coupled ocean circulation/ice shelf/sea ice ROMS model developed for the study area[24,45]. The ROMS model, with a spatial resolution of 4 km, was run for 2001, 2002 and 2007, generating an output file for every 48-h period. We then extracted the environmental data for each dive (both real and simulated) from the closest output file in time (that is, the maximum time lag between the dive and its corresponding environmental data obtained from the oceanographic model was 24 h). Large changes in environmental conditions in the WAP are not expected at such a temporal scale, so we assumed that the 48-h output from the ROMS model was appropriate for this analysis and captured the environmental variability.

Future environment in the WAP. Polar oceans are changing rapidly, but our ability to use the available climate models to simulate current conditions or project future changes is rather limited[46]. During the past several decades, western Antarctica has experienced the fastest warming in both air and ocean temperatures in the Southern Hemisphere[47,48]. As a consequence of this warming, sea ice cover has decreased in extent and the duration of the open water season has lengthened, particularly in the northern Antarctic Peninsula[49,50].

The dominant mechanism of variability in the atmospheric circulation of the Southern Hemisphere (that is, the Southern Annular Mode (SAM))[51] has shown an unprecedented positive trend during austral summers since the 1940s, probably associated with the increase in the atmospheric concentration of GHGs, as well as the depletion in stratospheric ozone[46,52,53]. This positive trend in SAM values results in the strengthening of the westerlies[54], increased frequency of mesoscale cyclones and a decrease in sea ice cover.

Although there are conflicting opinions on whether the positive trends in SAM will continue after the hole in the stratospheric ozone layer is patched, general circulation models indicate that future increasing GHG atmospheric concentrations will continue the positive trend in SAM[46,54]. These changes in the winds, triggered by the positive trend in the SAM, have resulted in an increase in CDW intrusions onto the continental shelf of the WAP, and this is likely to continue[55].

Given the high uncertainty regarding the mechanisms that are currently operating (or will be during the next decades), as the atmospheric concentration of GHGs continues to rise, we have opted for simulating future conditions in our study using the same approach as Dinniman et al.[24] and Piñones at al.[23]: a 20% increase in wind speed (a conservative estimate of the environment for the future decades[56,57]) and 5% increased transport by the ACC[24].

Data analysis. A set of environmental variables was derived from the 'Environmental data sources' for the construction of the habitat models:

(1) Bathymetric variables. We created grids of bottom depth (m), and slope (°) from the SO GLOBEC bathymetric dataset and the corresponding values

were obtained for each seal dive. The continental shelf break, defined here as the 1,000-m depth contour, was calculated for the study area, and the minimum distance between this contour and each dive was calculated. To account for animals on versus off the shelf, we assigned negative distances when the dive locations were located on the shelf and positive distances when dives were located beyond the limit of the shelf break. All of these calculations were performed using the Spatial Analyst toolbox in ArcGIS version 10.5.

(2) Ice conditions. Daily sea ice concentrations were obtained for each dive location, as well as measures of the distance to the ice edge (5% sea ice concentration contour) using a custom-written algorithm in MATLAB. Sea ice variation was estimated by calculating the standard deviation in sea ice concentration for the 10 d before the day of the observation.

(3) Sea surface variables. Sea surface temperature (SST) and sea surface salinity (SSS) were calculated as the mean value for the first 5 m of the water column. These temperature values were obtained from either the animal tags or the ROMS model.

(4) Water column properties. The reconstructed profiles of temperature and salinity were used to derive the following oceanographic variables for the water column: (1) MLD, calculated as the depth at which the gradient in the temperature profile over 3 m was greater than 0.05 °C; (2) maximum temperature below 100 m ($T_{max_{100}}$); (3) depth of $T_{max_{100}}$, as obtained from the interpolated temperature profile; (4) horizontal distance to the 1 °C isotherm at 200 m; (5) water column stability, derived from the Brunt–Väisäla frequency (N^2) estimated at the maximum dive depth; (6) temperature and salinity at the maximum dive depth, obtained as described for SST and SSS; and (7) current velocity in its two components, **u** and **v**, at the surface and at the maximum dive depth. As the maximum depth reached for crabeater seals in our study was close to 700 m, values of $T_{max_{100}}$, depth of $T_{max_{100}}$ and MLD were limited to 1,000 m.

Habitat models. Habitat preference may differ depending on the behavioural state of the animal and the environmental requirements[58]. For instance, foraging might have different environmental requirements from breeding, leading to differences in the preferred habitat between these two states. For this study, we were interested in describing the preferred foraging habitat of crabeater seals along the WAP; therefore, we used the presence of dives as the modelled response variable since these vertical incursions of seals are concomitantly related to the process of searching, pursuing and catching prey.

We used a multivariate modelling approach to study the habitat preference of crabeater seals along the WAP, following Raymond et al.[59]. First, boosted regression trees (BRTs)[60] were used to model the relationship between the presence of crabeater seal dives and the environmental covariates in the dataset. Model tuning and selection were automated using the packages gbm and caret in R version 3.5 (ref. [61]), and model assessment was performed using k-fold cross-validation across the individuals in our dataset by randomly assigning individuals to one of ten data folds. BRTs provide an estimate of the strength of the influence that each variable has on the response, or relative influence, that sums to 100 for all covariates in the model. Variables with a relative influence >3 were kept for the final model[60].

Generalized additive mixed models were chosen to build the final model due to their ability to deal with nonlinearity[62]. For our study, the presence or absence of dives was modelled with a logit link function, using thin plate regression splines with shrinkage as a smoother and individual as a random effect, using the package mgcv[63] in R. The fixed structure of the model was determined from the BRT, after checking for collinearity (Pearson correlation coefficients and variance inflation factors). This method does not estimate a real probability of occurrence, but the output can be interpreted as a measure of habitat importance (0–100%) for the species (see ref. [59]).

The full dataset was randomly split: two-thirds were used for model fitting and the remaining one-third was used for model validation. Model evaluation was based on the receiver operating characteristic curve—a graphical method representing the relationship between the fraction of true positives (sensitivity) and the fraction of false positives at various threshold settings. In this case, the area under the curve, corresponding to the area between the receiver operating characteristic curve and the 45° line, evaluates the ability of the model to correctly classify the presence of a dive. Area under the curve values >0.5 indicated that the model performed better than random, whereas values >0.75 indicated that the model showed a useful amount of discrimination at predicting the presence of a dive[64].

Predicting habitat utilization of crabeater seals. The ROMS model was used to extract the dynamic environmental covariates retained in the final habitat model to predict the current (2001, 2002 and 2007) and projected habitat of crabeater seals. Current conditions were obtained by forcing the model using actual wind data for the years in our study. Plausible future environmental conditions were simulated by running the model under a 20% increase in wind speed and 5% increased transport by the ACC[24] (see 'Future environment in the WAP' above).

Daily gridded fields of predicted habitat (and estimated standard error, as a measure of uncertainty) were created for the study area (grid cell: 10 km × 10 km), and current and projected annual predictions of habitat importance were generated in ArcGIS version 10.5 by averaging daily rasters. Seasonal (month to month) anomalies in patterns of habitat importance (current and projected) were calculated as the difference between the predicted monthly habitat and the gridded average (either current or projected), allowing us to estimate temporal trends in departures from the average habitat importance. Likewise, we calculated an anomaly in habitat importance as the difference between projected and current habitat.

Finally, we defined the 50% habitat importance contour as the most important habitat for crabeater seals and calculated the areas of the resulting polygons. Additionally, as crabeater seals range from the coast to open waters, we estimated the habitat width as the distance between the 50% contour and the coastline. Habitat width was then used to identify latitudinal and spatial shifts in the size and distribution of the most important habitat for crabeater seals between current and projected conditions using a linear model of the form: habitat width ~ latitude × period (current and projected) (Extended Data Fig. 2).

While this approach relies exclusively on habitat attributes as covariates to model foraging habitat preference (as they are assumed to be proxies of prey distribution), there are other factors that influence the habitat preference of marine top predators that were not accounted for in our study (for example, predator distribution and the presence of inter- and intra-species competitors, among several others). These unaccounted-for factors are not likely to influence our results or interpretation, yet they do constitute a caveat to our modelling approach.

All statistical analyses were performed in R. The data are presented as means ± standard deviation unless otherwise specified.

Ethics. All animal captures and procedures were authorised under National Marine Fisheries Service permits (numbers 87-1593 and 87-1851-00) and approved by the Institutional Animal Care and Use Committee at the University of California, Santa Cruz. Fieldwork in Antarctica was approved by the Antarctic Conservation Act.

Reporting Summary. Further information on research design is available in the Nature Research Reporting Summary linked to this article.

Data availability

All crabeater seal movement data analysed during the current study are included in the Retrospective Analysis of Antarctic Tracking Data (RAATD) project[65]. Crabeater seal diving data are available from https://doi.org/10.5281/zenodo.3600555.

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Author contributions

L.A.H., D.P.C., D.E.C., J.E.M. and E.E.H. conceived of the study. L.A.H., B.I.M., D.P.C., D.E.C. and J.M.B. conducted the fieldwork and collected the data. L.A.H., D.M.P., A.P. and M.S.D. analysed the data. L.A.H. drafted the manuscript. All authors contributed to subsequent drafts.

Competing interests

The authors declare no competing interests.

Additional information

Extended data is available for this paper at https://doi.org/10.1038/s41558-020-0745-9.

Supplementary information is available for this paper at https://doi.org/10.1038/s41558-020-0745-9.

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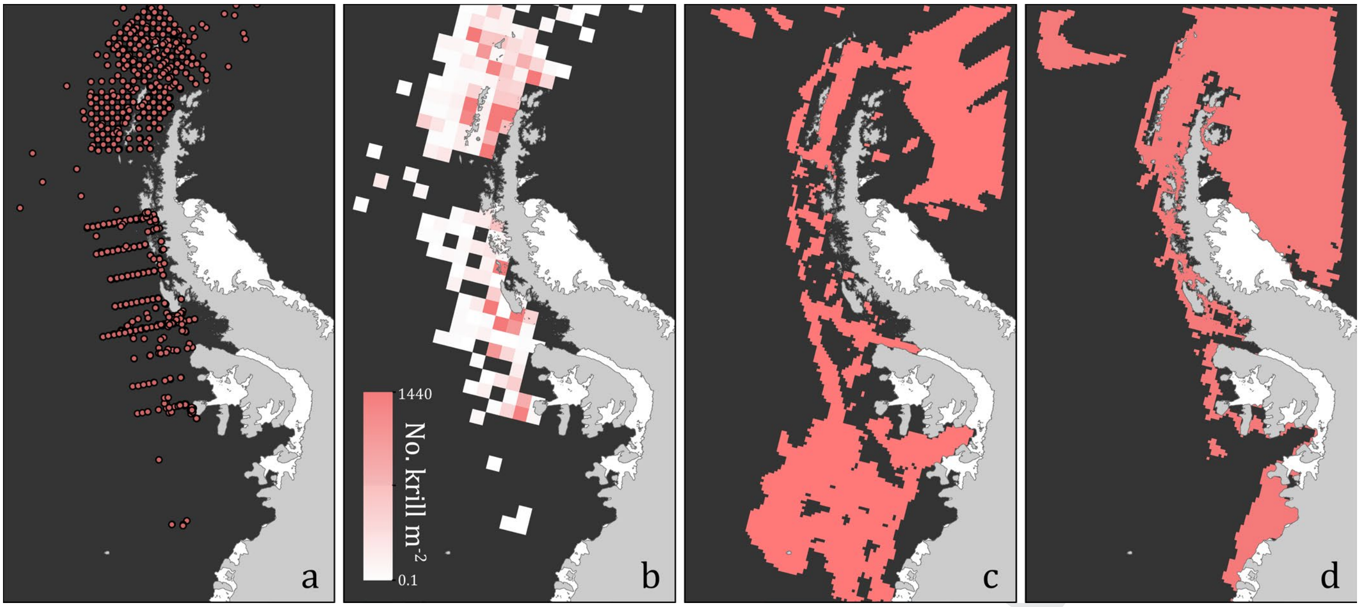
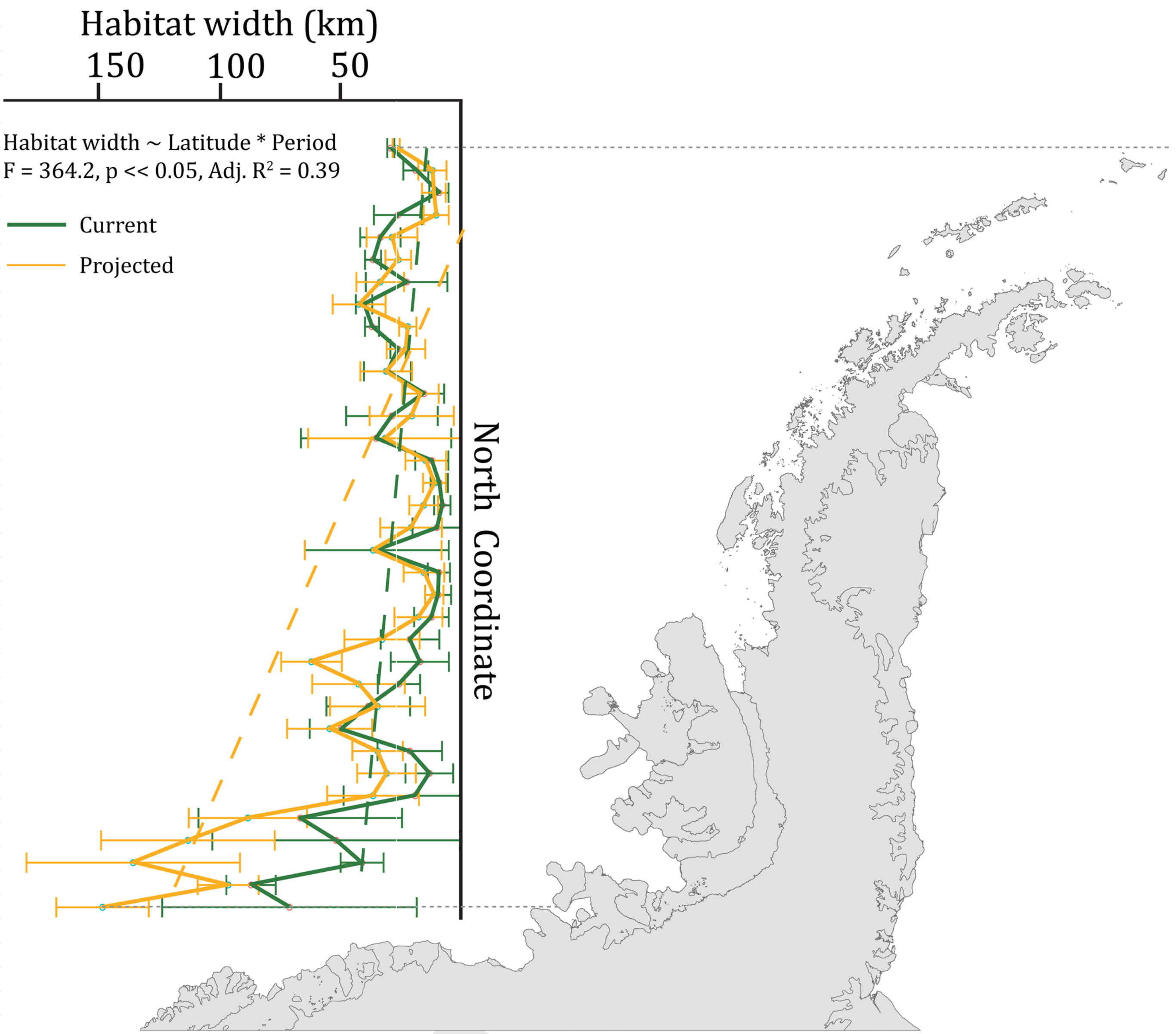
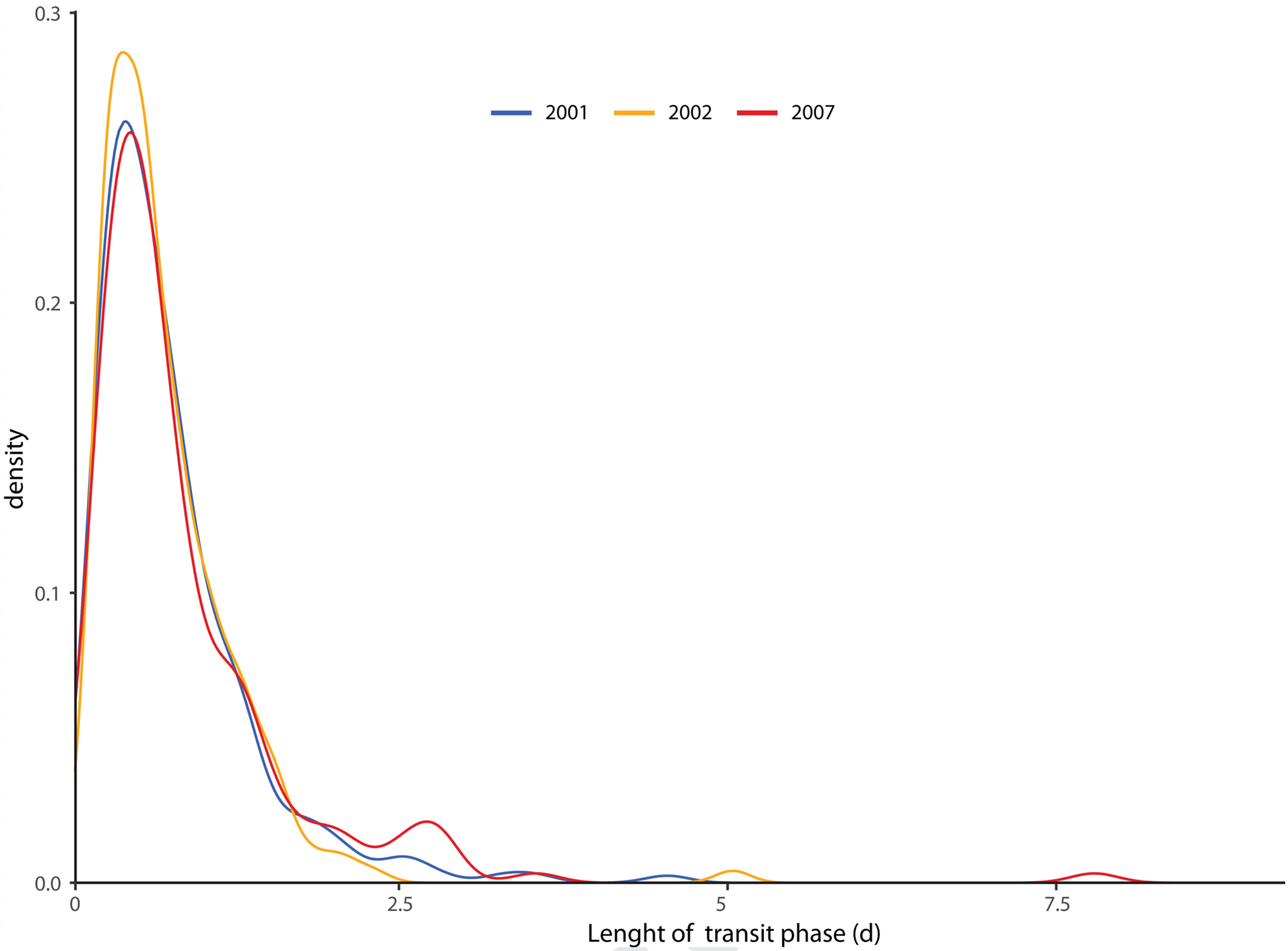


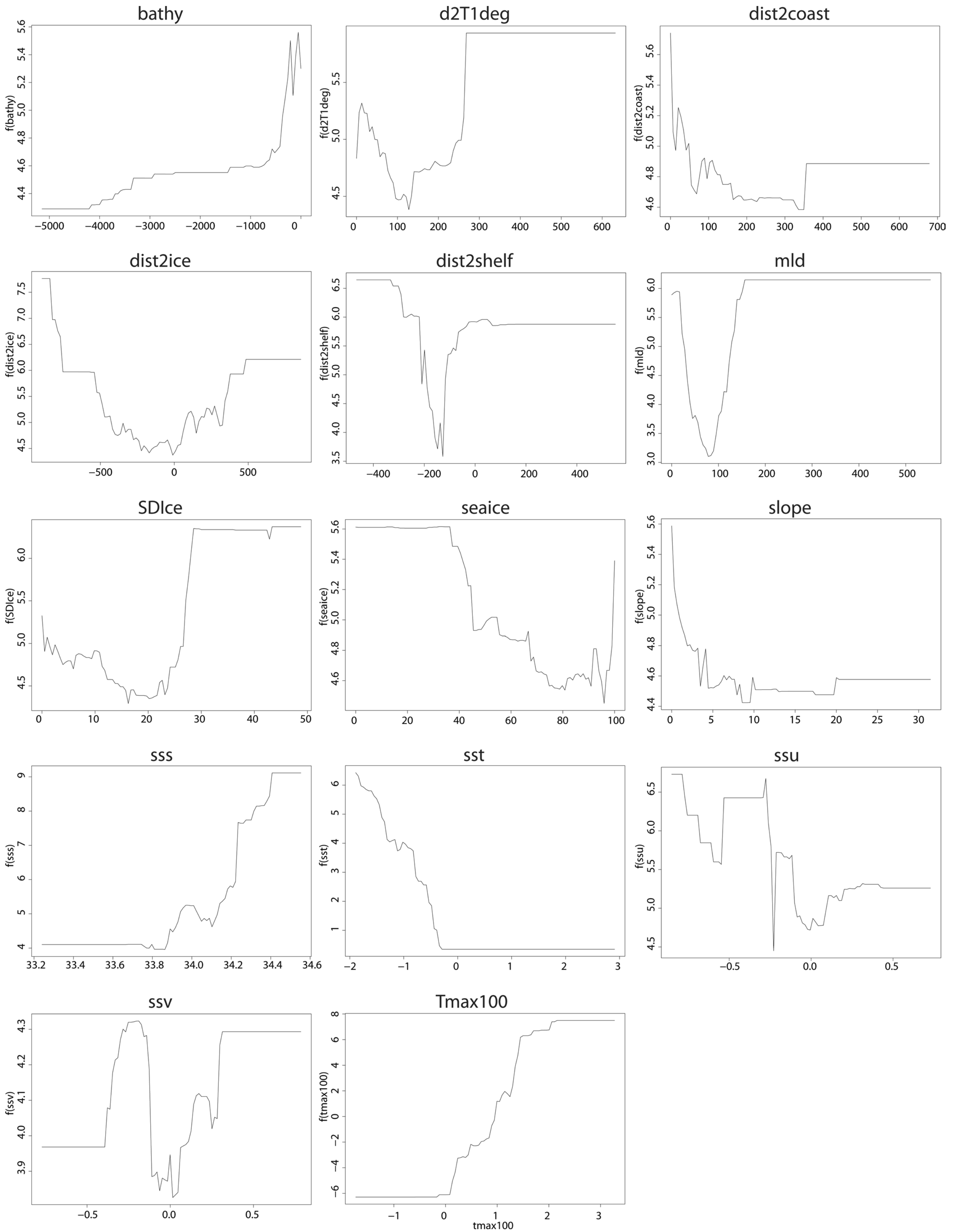
Extended Data Fig. 1 | Krill distribution comparisons. Comparison between krill distribution and current crabeater seal foraging habitat. **a**, Sampling locations included in KRILLBASE between 2000 and 2016; **b**, krill densities (No. krill m^{-2}) obtained from KRILLBASE between 2000 and 2016 (Atkinson et al 2017); **c**, krill spawning habitat along the wAP (Piñones and Fedorov 2016); **d**, crabeater foraging habitat (inferred krill distribution) as modeled in this study).



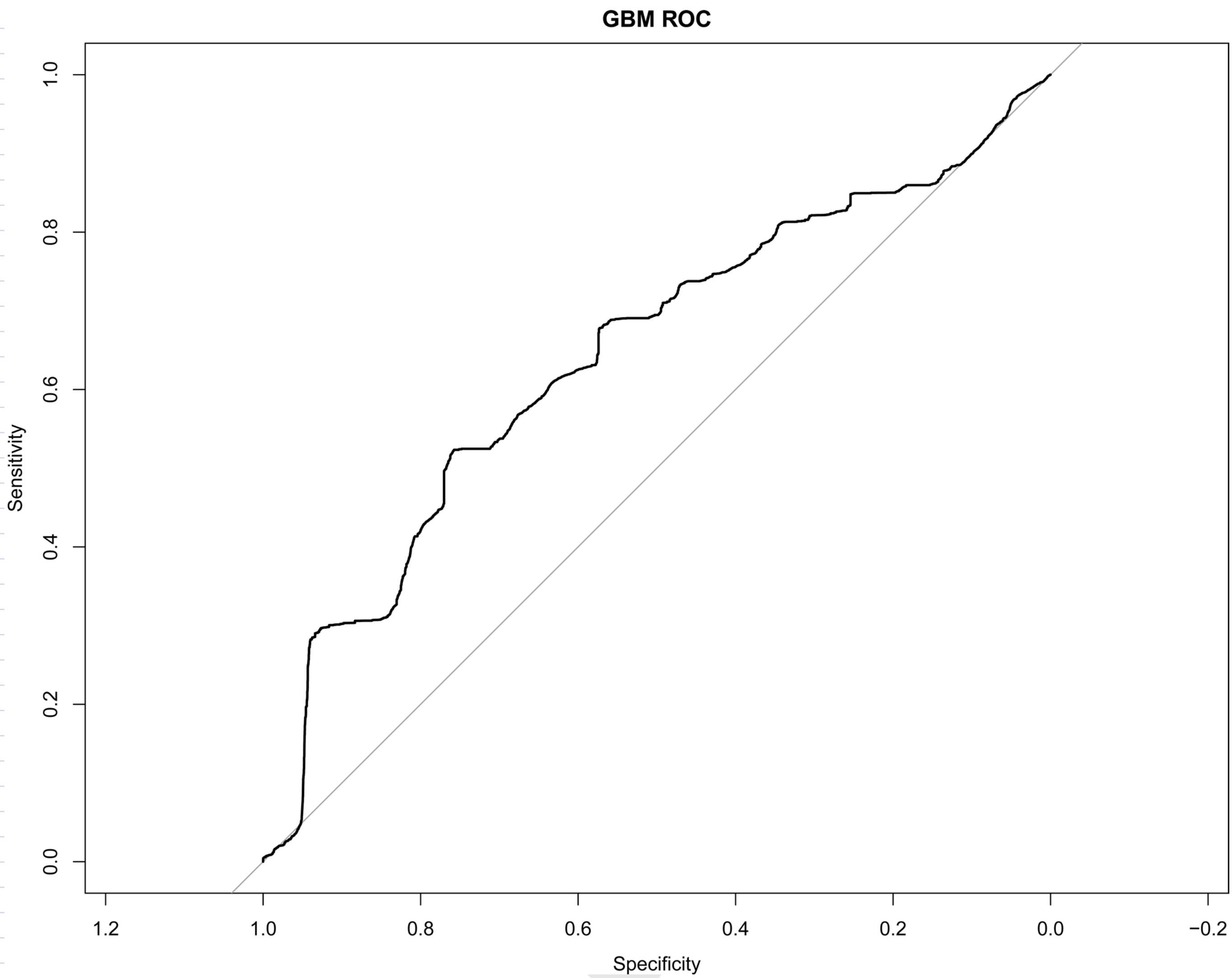
Extended Data Fig. 2 | Projected expansion in habitat. Projected future offshore expansion of the habitat of crabeater seals along the western Antarctic Peninsula (Linear regression model: *Habitat width ~ Latitude * Period*). Habitat width was defined as the mean distance between the coast and the 50% habitat importance contour for 50 km bins in the North coordinate. Error bars indicate the standard deviation of the habitat width for the bins. Colour dashed lines indicate the fitted linear regressions. Green indicates current habitat width. Yellow is projected habitat width under projected environmental changes.



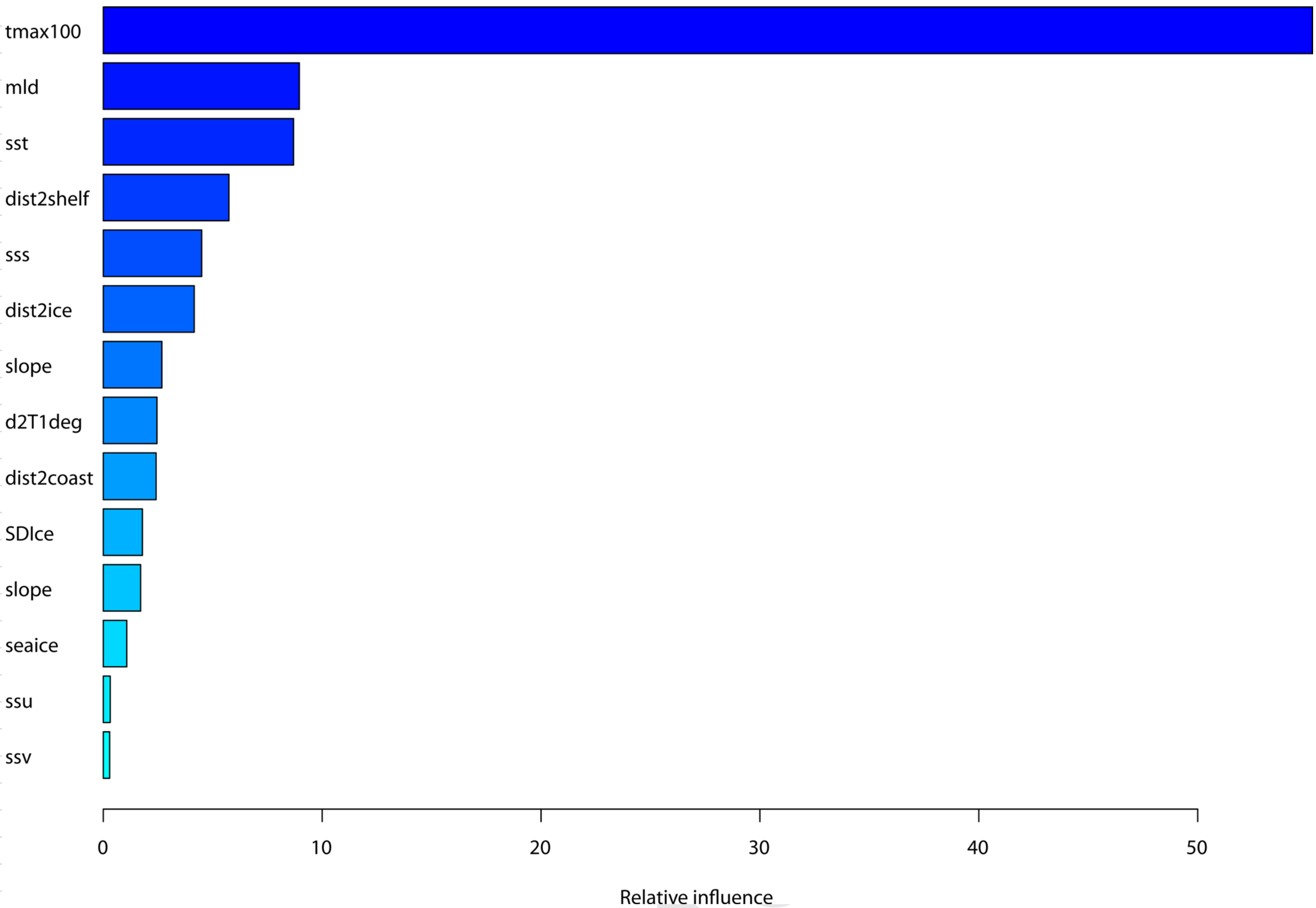
Extended Data Fig. 3 | Density of Transit Phases. Frequency distribution of the duration of continuous travel segments, as identified from satellite telemetry, for crabeater seals from the western Antarctic Peninsula.



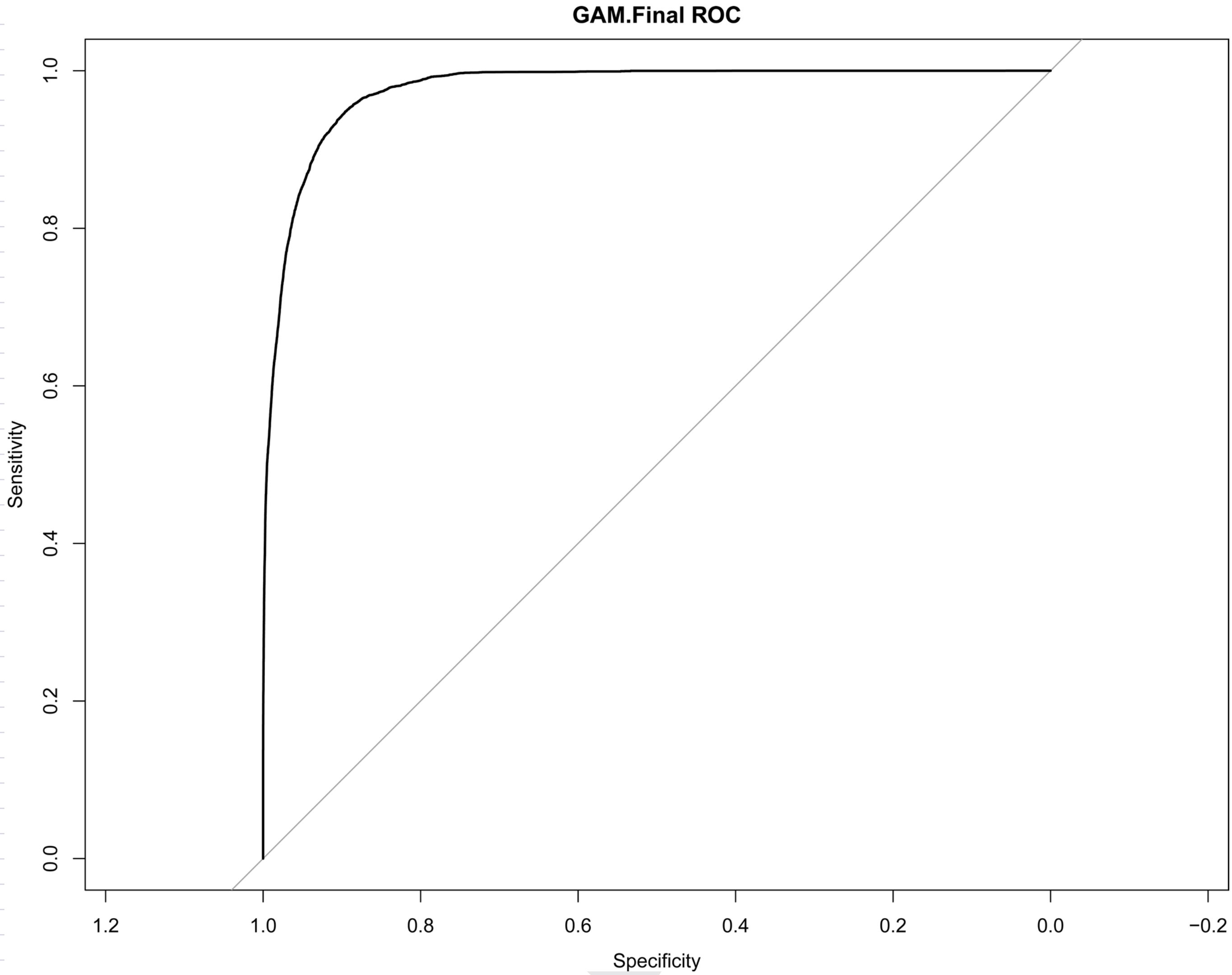
Extended Data Fig. 4 | Boosted Regression Trees – Partial Dependence Plots. Boosted Regression Tree (BRT). Partial dependence plots of the relationship between environmental covariates and presence/absence of crabeater seals along the western Antarctic Peninsula.



Extended Data Fig. 5 | Boosted Regression Trees – ROC. Boosted Regression Tree (BRT) Analysis. Receiver Operator Curve (ROC) shows a low performance of the final BRT model selected (Area Under the Curve, AUC = 0.64).



Extended Data Fig. 6 | Boosted Regression Trees – Variable Influence. Boosted Regression Tree (BRT) Analysis. Relative influence of environmental variables used in the BRT models to predict foraging habitat of crabeater seals. The relative influence indicates the proportion of variation in the data explained by each variable with respect to the rest of the variables.



Extended Data Fig. 7 | GAMM – ROC. Receiver Operator Curve (ROC) to estimate the performance of the final Generalised Additive Mixed Model (GAMM) to predict the foraging habitat of crabeater seals from the western Antarctic Peninsula. The final selected model performance was estimated based on the Area Under the Curve (AUC) of 0.97.

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Our web collection on statistics for biologists contains articles on many of the points above.

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Policy information about availability of computer code

Data collection	Animal movement, diving and environmental data from animals were collected using Sea Mammal Research Unit (SMRU) Satellite Relay Data Loggers with a proprietary data collection, processing and transmission on-board algorithm (Fedak et al. 2001).
Data analysis	The coupled ocean circulation/ice shelf/seaice ROMS model is described in Dinniman et al. (2003). Details about the ROMS framework, along with documentation and packages can be found in www.myroms.org Tracking data filtering was conducted in R using the packages 'argosfilter' and 'bsam'. Simulated tracks and dives were created using a custom written algorithm in Matlab. Statistical modeling was conducted in R using the packages 'gbm' and 'caret' (boosted regression trees) and 'mgcv' (GAMMs). Habitat importance predictions were also built in R, using the command 'predict'. Model performance evaluation was estimated using the ROC curve, calculated using the package 'pROC'. Predictions raster and spatial analyses were conducted in ArcGIS 10.5, using the Spatial Analyst and Raster toolboxes. Likewise, predicted habitat importance contours were calculated in ArcGIS 10.5m and the linear model relating habitat width to latitude was run in R using the function 'lm'.

For manuscripts utilizing custom algorithms or software that are central to the research but not yet described in published literature, software must be made available to editors/reviewers. We strongly encourage code deposition in a community repository (e.g. GitHub). See the Nature Research guidelines for submitting code & software for further information.

Data

Policy information about availability of data

All manuscripts must include a data availability statement. This statement should provide the following information, where applicable:

- Accession codes, unique identifiers, or web links for publicly available datasets
- A list of figures that have associated raw data
- A description of any restrictions on data availability

The tracking data used in this study will be available shortly as part of an In Press article coming out in Nature Scientific Data by Ropert-Coudert et al. The retrospective analysis of Antarctic tracking data project, SDATA-18-00258A. As of today, the article is still under embargo.

All movement data analysed during the current study are included in the Retrospective Analysis of Antarctic Tracking Data (RAATD) project (Ropert-Coudert et al. 2019. The retrospective analysis of Antarctic tracking data project. Nature Scientific Data), available in the Australian Antarctic Division Data Centre with the DOI: doi.org/10.4225/15/5afcb927e8162

Diving data are available from the corresponding author GitHub, under the DOI: doi.org/10.5281/zenodo.3600555

Field-specific reporting

Please select the one below that is the best fit for your research. If you are not sure, read the appropriate sections before making your selection.

☐ Life sciences ☐ Behavioural & social sciences ☒ Ecological, evolutionary & environmental sciences

For a reference copy of the document with all sections, see nature.com/documents/nr-reporting-summary-flat.pdf

Ecological, evolutionary & environmental sciences study design

All studies must disclose on these points even when the disclosure is negative.

Study description	Here, we present a habitat model for a conspicuous predator of the wAP, the crabeater seal (Lobodon carcinophaga), considered a highly-specialized predator of Antarctic krill (Euphausia superba), and likely the largest consumer of krill in the world. The characteristics of the species, such as its rather limited feeding niche (as implied from the highly specialized diet), relatively low mobility, and high dependence on sea ice as substrate, make the crabeater seal a species of high interest in studies of effects of climate change, since it is likely that this species will be highly impacted by the drastic environmental changes predicted for the area. The goal of our study was to develop a foraging habitat model for the crabeater seal along the wAP using animal diving behaviour and movement data (as obtained from satellite telemetry) combined with environmental properties of the water column obtained from animal-borne instruments and oceanographic models developed for the study area, as well as to predict how the distribution of the crabeater seal will be affected under the predicted environmental changes in the area as a consequence of global climatic change.
Research sample	Our study involved outfitting 42 adult crabeater seals (Lobodon carcinophaga) with satellite tags in the Crystal Sound/Lau Beouf fjord/Marguerite Bay areas along the western Antarctic Peninsula. Number of animals tagged every year was a function of budget (number of instruments available) and conditions in the field determining occurrence of seals and accessibility to their haul-out areas given the ice conditions. Individual masses varied between 118 and 413 kg (average mass = 252 kg), and our sample consisted of 24 females and 18 males (the species does not present sexual dimorphism)
Sampling strategy	Due to the nature of our study, sample size was not predetermined, but instead was determined by the availability of satellite tags purchased each year given the budget approved for the study. For analysis of spatial and vertical movements of animals, power analysis is not useful for determining the sample size because of the many different variables that are measured. This number is determined based on our previous knowledge of tracking and diving of pinnipeds. We have found that about 50% of the variability in Antarctic seals foraging ecology can be explained by the inter-individual variability, so a number of at least 15-20 individuals is necessary to detect the, so far, unexplained variability in foraging ecology. Our sample size (n = 42) is consistent with the current range of individuals used in recently carried out tracking studies. Our design aims at minimizing the individual impact of animal handling on individual seals, while keeping a sample size small enough but that will provide us with robust scientific data to fulfill our study objectives.
Data collection	Diving behaviour, temperature and salinity data were collected and processed on-board by the SRDL-CTD tags. Location was estimated using the Argos satellite system (Toulusse, France). SRDL-CTD tags are programmed to transmit the data using the Argos satellite system, so no recovery is necessary. Because we attached the instruments to the pelage of the seals using 5-min marine epoxy, the tags fall off during the seals' annual moult in the Austral summer (Jan-Feb).
Timing and spatial scale	Satellite tag deployments were conducted as part of three different scientific cruises to the western Antarctic Peninsula. The timing of the cruises was specifically designed to take place right after the annual moult to maximise the length of the individual records and obtain data on animal movement through the winter season. The first two cruises (2001 and 2002) were part of the US Southern Ocean GLOBEC project, whereas the 2007 data were part of a different scientific project. The mean total distance travelled by seals was 2586.6 ± 1720.8 km; whereas the mean maximum distance travelled from the tagging location was 555.9 ± 425.3.
Data exclusions	No data were excluded from the study

Reproducibility	Does not apply
Randomization	Animals were chosen randomly in the area of study, although we actively selected adult animals that looked healthy
Blinding	Does not apply

Did the study involve field work? ☒ Yes ☐ No

Field work, collection and transport

Field conditions	Field work was conducted on the pack ice covered waters of the western Antarctic Peninsula. Due to the natural harsh conditions and limitations to the correct functioning of our gas anesthesia equipment, we only worked when the air temperature was above -20 degrees Celsius
Location	Animal captures were conducted in the Crystal Sound/Lau Beouf fjord/Marguerite Bay along the western Antarctic Peninsula, between 65 and 68 degrees of Latitude South, and between the coastline and the 1000 m isobath
Access and import/export	Field work was conducted under approval from the National Marine Fisheries Service permits no. 87-1593, 87-1851-00, and approved by the Institutional Animal Care and Use (IACUC) at UC Santa Cruz. Fieldwork in Antarctica was approved by the Antarctic Conservation Act.
Disturbance	Individuals were selected based on a healthy appearance, accessibility, alertness, and proximity to other alert individuals. Animals were captured using remote darting and physical capture. Our group has considerable experience with all of these capture methods, with this and other species. Animals were restrained using a combination of chemical immobilization, gas anesthesia, and/or physical restraint. These methods are widely employed in our field. We minimized adverse effects by paying close attention to dosage, body size, physical condition and environmental factors. As outlined above, we were prepared to administer emergency drugs and provide supplemental mechanical ventilation in the event the animal exhibited any respiratory distress or other complications during sedation. Close contact was maintained among all investigators who use chemical sedation on seals with the aim of sharing information and thus increasing the margin of safety of the procedure. We have extensive experience working with these species and these drugs, which helped us to minimize adverse effects to the animals and our crew.

Reporting for specific materials, systems and methods

We require information from authors about some types of materials, experimental systems and methods used in many studies. Here, indicate whether each material, system or method listed is relevant to your study. If you are not sure if a list item applies to your research, read the appropriate section before selecting a response.

Materials & experimental systems

n/a	Involved in the study
☒	☐ Antibodies
☒	☐ Eukaryotic cell lines
☒	☐ Palaeontology
☐	☒ Animals and other organisms
☒	☐ Human research participants
☒	☐ Clinical data

Methods

n/a	Involved in the study
☒	☐ ChIP-seq
☒	☐ Flow cytometry
☒	☐ MRI-based neuroimaging

Animals and other organisms

Policy information about studies involving animals; ARRIVE guidelines recommended for reporting animal research

Laboratory animals	This study did not involve laboratory animals
Wild animals	Adult crabeater seals (Lobodon carcinophaga) were captured in the fall and/or winter of 2001, 2002 and 2007 during three cruises along the western Antarctic Peninsula on board of the RV Lawrence M. Gould. Animals were sighted from the bridge of the vessel and approached by foot or inflatable boat to deliver an intramuscular injection of Telazol (0.8 to 1.2 mg per kg body weight or Midazolan (0.5 to 0.75 mg per kg body weight), administered via a jab-stick of dart gun to sedate each animal. After induction, animals were manually restrained with a hoop net and isofluorane combined with oxygen was administered via a gas masks. Handling of animals lasted in average 1 hour, when seals were outfitted with Satellite Relay Data Loggers, biological samples and morphometrics data were collected. At the end of the procedures animals were monitored while administering oxygen until full recovery and finally released. Animals body masses ranged between 118 and 413 kg (mean = 253 kg). Females represented the 58% of the animals sampled in our study; males represented the 42% of the sample.
Field-collected samples	Although biological samples were collected during animal handling, this study does not involve biological samples
Ethics oversight	All animal captures and procedures were authorized under the National Marine Fisheries Service permit Nos. 87-1593,

Ethics oversight	87-1851-00, and approved by the Institutional Animal Care and Use (IACUC) at UC Santa Cruz. Fieldwork in Antarctica was approved by the Antarctic Conservation Act

Note that full information on the approval of the study protocol must also be provided in the manuscript.