

Citizen science and habitat modelling facilitates conservation planning for crabeater seals in the Weddell Sea

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Abstract

Aim: Creating a network of marine protected areas in the Southern Ocean requires extensive knowledge on species' abundances, distributions and population trends especially in the Weddell Sea where year-round pack ice makes most of the Weddell Sea inaccessible. We combine satellite images and citizen science to model habitat suitability for crabeater seals (*Lobodon carcinophaga*) throughout the Weddell Sea.

Location: Weddell Sea, Antarctica.

Methods: High-resolution satellite images covering 18,219 km² of the Weddell Sea during crabeater seal breeding season (October–November) were hosted on the crowd-sourcing platform Tomnod (DigitalGlobe). Citizen scientists marked “maps” where seals were present/absent and these votes were compared with the votes of an experienced observer. Correction factors were used to correct votes to either a continuous probability of seal presence, or a binary seal presence/absence value. We modelled probability of seal presence using ensemble models of Random Forests (RF), Boosted Regression Trees (BRT) and Support Vector Machines (SVM), and used fitted Maxent models to model seal presence/absence data.

Results: Model predictive power was low (RF: $R^2 = 0.076 \pm 0.002$; BRT: $R^2 = 0.086 \pm 0.0008$; SVM: $R^2 = 0.082 \pm 0.003$) to average (Maxent: $AUC = 0.71 \pm 0.004$). Distance to the ice edge and bathymetry were the most important variables that influenced crabeater seal distribution.

Main conclusions: Crabeater seals were more likely to be present over abyssal water, which coincides with typical adult Antarctic krill habitat – crabeater seal preferred prey. Where ice concentrations were more variable, that is more accessible, crabeater seals were also more likely to occur. Results agreed with the known ecology of crabeaters seals and the abundance, distribution and ecology of Antarctic krill. We were able to survey the largest area ever surveyed in the Weddell Sea and provide a model to assist furthering policy around the proposed protected area.

KEYWORDS

Antarctic krill, boosted regression tree, citizen science, ensemble modelling, machine learning, Maxent, random forests, support vector machines

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1 | INTRODUCTION

The Commission for the Conservation of Antarctic Marine Living Resources (CCAMLR) member states started considerable efforts to designate marine protected areas (MPA) in the Southern Ocean (CCAMLR, 2011). MPAs are a means to facilitate biodiversity conservation through, among others, the recovery of intensely exploited areas and biomass increases (Gell & Roberts, 2003; Lester & Halpern, 2008). The most recent of CCAMLR's proposed MPAs is a German-led initiative to establish a 1.8-million km² MPA in the Weddell Sea (Teschke et al., 2020). Here, we present information on the distribution of a key predator, the crabeater seal that may help drive decisions on the placement of the MPAs. We evaluate and discuss the ecological drivers of the seal's distribution in the Weddell Sea, and the relevance of our results for the goal of conserving the biodiversity of this globally important ecosystem.

The Weddell Sea is a key production area of super-cooled Antarctic Bottom Water and Circumpolar Deep Water, and the Weddell Gyre is fundamental to global ocean circulation and gas exchange with the atmosphere (Vernet et al., 2019). It is an environment of high benthic species richness (Gutt, Sirenko, Smirnov, & Arntz, 2004), and the breeding and foraging ground for several marine predators (Croxall, Trathan, & Murphy, 2002; Forcada et al., 2012; Fretwell et al., 2012; Gurarie et al., 2017). The proposed MPA aims to conserve the biodiversity of the region mainly through regulation of fishing for key Antarctic fish species such as Antarctic toothfish (*Dissostichus mawsoni*) and Antarctic krill (*Euphausia superba*; Teschke et al., 2016).

The larger Weddell Sea region, south of 55°S, between 90°W and 0°W (the Atlantic Sector of the Southern Ocean and including the Scotia Sea to the north) contains roughly 70% of the global Antarctic krill stock (Atkinson et al., 2008). Antarctic krill is a key dietary resource for several predators, for example baleen whales, Antarctic fur seals (*Arctocephalus gazella*), Adélie (*Pygoscelis adeliae*), chinstrap (*Pygoscelis antarctica*) and gentoo (*Pygoscelis papua*) penguins, and several species of albatross, fish, squid and other invertebrates (Croxall & Prince, 1980; Lynnes, Reid, & Croxall, 2004). Subsequently, variability in the abundance and distribution of Antarctic krill are believed to have substantial effects on reproductive performance of krill-dependent predators, especially species that specialize on krill (Croxall, Reid, & Prince, 1999; Forcada et al., 2012; Reid, Croxall, Briggs, & Murphy, 2005). In the Scotia Sea (north) and Weddell Sea (south) areas, pack-ice seals, and specifically crabeater seals (*Lobodon carcinophaga*), are the major krill consumers (CCAMLR, 2008).

The only Antarctic pack ice seal whose diet is ~90% Antarctic krill is the crabeater seal (Hückstädt et al., 2012; Laws, 1977; Øritsland, 1977; Zhao, Castellini, Mau, & Trumble, 2004). Native to the Southern Ocean, their circumpolar population estimate ranges between 7 and 30 million individuals (Bengtson, 2009; Bester, Bornemann, & McIntyre, 2017; Erickson & Hofman, 1974; Southwell et al., 2012). Although the population estimates are wide and population trends of this species are unknown (but previously suspected

to have increased (Erickson & Hofman, 1974)), all evidence suggests that this numerous krill predator likely has a substantial impact on the abundance and distribution of Antarctic krill – and vice versa (Daly & Macaulay, 1991; Forcada et al., 2012).

Specialist predators are often more susceptible to fluctuations in prey abundance because they might not be capable of switching prey species (Terraube, Arroyo, Madders, & Mougeot, 2011), which makes them vulnerable and at greater risk of extinction than generalist predators (Angermeier, 1995; Shultz, Bradbury, Evans, Gregory, & Blackburn, 2005). Crabeater seals are therefore especially vulnerable to changes in krill abundance and this vulnerability further makes them a potentially valuable tool for monitoring krill stock and ecosystem health (CCAMLR, 2008).

The CCAMLR Ecosystem Monitoring Programme (CEMP) was initiated to understand how species will respond to climate change and over-fishing as a means to monitor ecosystem changes through measurements of the distribution and abundance of Antarctic predators (Agnew, 1997). However, collecting sufficient information to use a higher-order predator as an effective monitoring tool in the Southern Ocean, particularly the crabeater seal that uses the inaccessible pack ice, is challenging and existing data are limited. The Weddell Sea is dominated by vast areas with year-round dense pack ice, which makes most of it inaccessible throughout the year, and conducting adequate region-wide surveys nearly impossible.

To date, census efforts of pack-ice seals have been completed using helicopter and ship surveys (Bester, Ferguson, & Jonker, 2002; Bester, Wege, Lübcker, Postma, & Syndercombe, 2019; Flores, Haas, van Franeker, & Meesters, 2008; Gurarie et al., 2017; Nordoy, Folkow, & Blix, 1995). But these are as follows: (a) mainly focussed to the eastern parts of the Weddell Sea in Dronning Maud Land and Princess Martha Coast, or along the Scotia Arc in the Marginal Ice Zone (Erickson, 1984; Flores et al., 2008; Gurarie et al., 2017); (b) covering a relatively small area per survey and (c) are restricted to the moulting season in December–February when ice coverage is at its minimum. Survey effort is constrained by logistical requirements of Antarctic stations, ice densities, ship-time requirements of other research, and substantial costs of ship and helicopter time.

To use a species' distribution and abundance as an effective monitoring tool, the study area needs to be sufficiently large to be a true representation of the population and needs to be surveyed in a relatively short amount of time (to avoid moving in and out of the study area), while still remaining cost-effective. Using satellite imagery to count animals from space can cover large areas in a short amount of time at a low cost. It is increasingly used and proven to be an effective tool to study Antarctic species breeding on Antarctic fast ice (Fretwell et al., 2012; LaRue et al., 2011; LaRue, Ainley, et al., 2020; LaRue, Salas, et al., 2019; Lynch & LaRue, 2014).

Here, citizen scientists looked for crabeater seals in very high-resolution (VHR) satellite images in 18,219 km² of the Weddell Sea during their breeding season (October–November). Our aims are to gain a better understanding of (a) crabeater seal distribution during a key time in their life history that has not previously been explored, and (b) how distribution is influenced by bottom-up processes. We

further use habitat ensemble modelling to determine crabeater seal distribution throughout the entire Weddell Sea.

2 | METHODS

2.1 | Image selection and study design

We selected images in the Weddell Sea from DigitalGlobe's (<http://www.digitalglobe.com>) online platform of available VHR images, ranging in spatial resolution of ~0.31 cm–0.50 cm; seals (length: ~160–280 cm; Laws, Baird, & Bryden, 2003) can be detected on images with spatial resolution from ~0.60 m (LaRue, Ainley, et al., 2020; LaRue et al., 2011). Image selection considered a range of criteria, including acquisition date, off-nadir angle, cloud cover percentage (typically < 20%), image quality (i.e., discarded images that were over-exposed or striped; LaRue et al., 2011) and location. In coordination with the SCAR Expert Group on Birds and Marine Mammals (EG-BAMM) and the Polar Geospatial Centre at the University of Minnesota, image acquisition was placed on “spec” tasking with DigitalGlobe in 2016. Spec tasking refers to a request to acquire images provided there is enough space on the platform to do so: there is no guarantee of successful image acquisition. During the first round of spec tasking, we requested images on the 800 m bathymetrical contour (the depth at which the continental shelf ends) spaced every 150 km apart. Then, for this project in particular, we requested image acquisition (and later obtained) from DigitalGlobe directly based on a stratified sampling design of ice concentration with an equal number of images selected from low (5%–34%), medium (35%–64%) and high (65%–94%) ice concentration average from mid-December over the last decade. Thirdly, satellite images were selected around peak pupping dates to capture the breeding haul out of crabeater seals, primarily during October 2018. The earliest recorded sighting of a crabeater mother-pup pair was on 2 October and the latest sighting on 15 December and the ratio of crabeater pups to adults increased rapidly between 16 and 25 October (Southwell, Kerry, Ensor, Woehler, & Rogers, 2003). Lastly, images were chosen to fall within the maximum haul-out hours of crabeater seals (09h00–15h00; Southwell, 2005) to avoid missing seals swimming in the water.

Although there is no way to identify seals to species, Weddell seals (*Leptonychotes weddellii*) – which are large enough to be confused with a crabeater seal – breed on the fast ice during this time of year, and breeding individuals are not present in the pack ice during October (Siniff, 1991). Secondly, Ross seals (*Ommatophoca rossii*) are pelagic foragers and breed in the outer fringes of the consolidated pack ice when they return from the open ocean (Blix & Nordøy, 2007), making it unlikely that they would be present in the southern Weddell Sea. Furthermore, Ross seals are typically smaller than crabeater seals, making them more difficult to detect on VHR images. The leopard seal (*Hydrurga leptonyx*) is the only pack-ice breeding species that we could have mistaken crabeater seals for, given that leopard seals grow up to ~4.5 m long (Laws, 1981). However,

leopard seals have a much lower abundance and overall density than crabeater seals (leopard seal global population estimate: 220,000–440,000; Bester et al., 2017), which means that for every leopard seal there are ~32–68 crabeater seals. Furthermore, leopard seals are typically found in higher densities around the pack-ice edge compared with the inner pack ice (Bester et al., 2002; Siniff, 1991) and some spend winter travelling outside of the pack ice and around neighbouring islands (Walker et al., 1998). Thus, they are unlikely to be found in the inner fringes of the pack-ice close to the Antarctic continent in the Weddell Sea (but see Hall-Aspland & Rogers, 2004; Rogers, Hogg, & Irvine, 2005). Although we cannot discount that we mistook leopard seals for crabeater seals, the likelihood of doing so is small.

Full VHR images were sub-divided into 0.25 km² (500 m × 500 m) maps – from here, we use “image” to refer to the full extent of VHR images (ranging from ~200–900 km², depending on swath length), and “map” to refer to the 0.25 km² sub-areas within each image.

2.2 | Citizen Scientist component

Tomnod (now “Geohive,” part of Maxar: <https://www.maxar.com/>) is a geospatial content server and web application that hosts DigitalGlobe's VHR satellite imagery for crowdsourcing and image classification. We used Tomnod's existing infrastructure to host the satellite images and we recruited voters through television promotion (in New Zealand in particular) and social media (primarily Twitter; LaRue, Ainley, et al., 2020). Prior to voting, participants were given a comprehensive set of instructions (see Appendix S1) to identify seals, with examples of seals on the ice versus melt pools, cracks and ridges on the ice (LaRue, Ainley, et al., 2020). Tomnod's platform then presented voters with a random 0.25 km² map where they were asked to vote whether seals were present (“Seals”) or absent (“No Seals”; Figure 1). The online campaign ran from 16 March 2019 to 27 June 2019. Data containing the voters' unique identification numbers, maps searched and seal presence/absence were recorded and stored by Tomnod in a PostgreSQL database, exported as geojson files, and converted to geospatial shapefiles and databases within R (R Core Team, 2019). To arrive at an “answer” as to whether a seal was likely present on a map or not, we employed Tomnod's proprietary algorithm, CrowdRank, which is a scoring system that relies on consensus among voters (LaRue, Ainley, et al., 2020; LaRue, Salas, et al., 2019; Salas et al.,). Tomnod's proprietary algorithm shows voters maps at random; maps where voters disagree with one another are shown more often to new voters (i.e., voters are not shown the same map more than once). Maps were retired from voting rotation once a sufficient number of high-quality voters had viewed and voted on the map or where voters agreed with one another. One of our initial goals was to count the number of seals present on all the images. However, inspection of the citizen science vote results indicated that this would be unfeasible given the variability of results. Pups were also too small to clearly discern from shadows formed by compressed multi-year sea ice. For these reasons, we opted to only

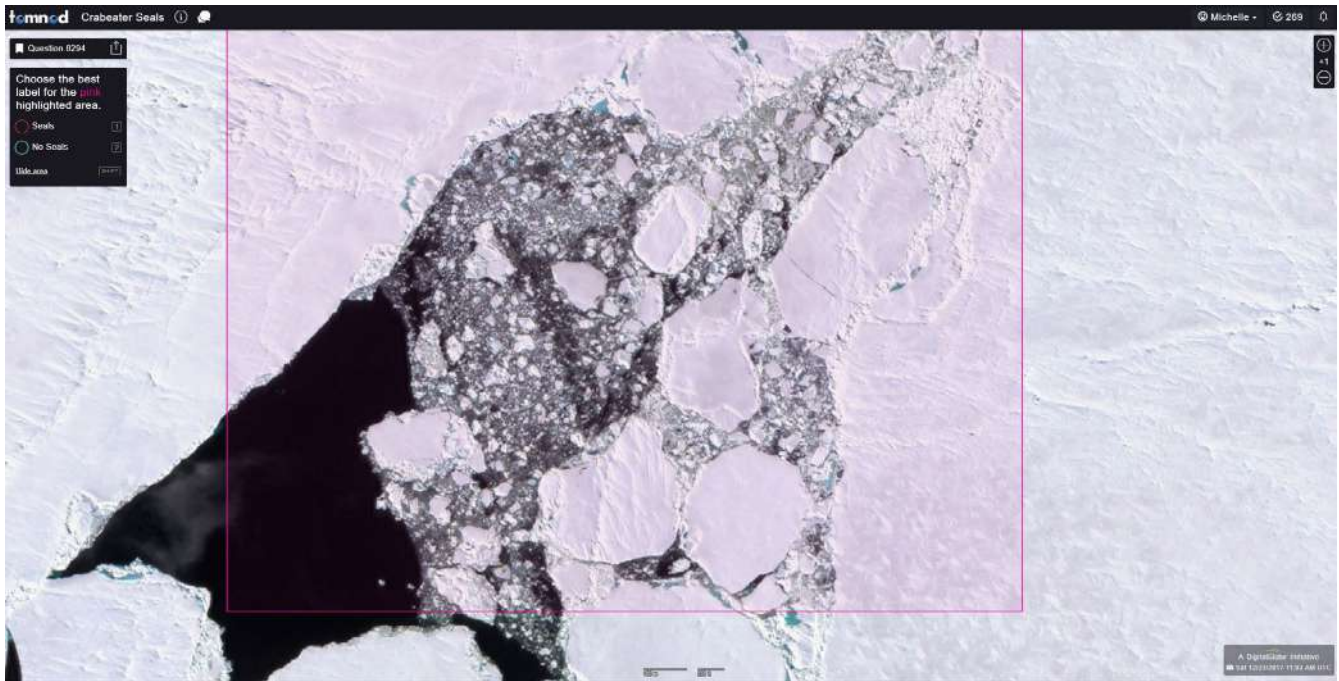


FIGURE 1 Example of a 0.25 km² map that citizen scientists voted on with crabeater seals present

build habitat models based on seal presence-absence using a very conservative modelling approach.

2.3 | Probability of seal presence correction factor

We compared Tomnod participants' votes to that of an expert voter who developed the techniques for estimating seal populations via satellite imagery (MLR) and created a confusion matrix for each voter that overlapped with MLR to calculate the probability of a vote being a false positive (pFP) or a false negative (pFN) for each voter. The accuracy for each voter that overlapped with MLR was then calculated as the ratio between false positives and negatives following:

$$pCES_i = vCES_{ij} \times \frac{1 - pFP_i}{pFN_i} \quad (1)$$

where $pCES_i$ is the probability a crabeater seal (CES) is present for voter i ; $vCES_{ij}$ is the seal present (1) or absent (0) vote of voter i in map j ; pFP_i is voter i probability of a false positive and pFN_i the probability of a false negative. The sample of $pCES_i$ from all participants that overlapped with MLR was fitted to a Gamma distribution using a maximum likelihood approach in the "fitdistrplus" library in R (Delignette-Muller & Dutang, 2015; R Core Team, 2019). A Gamma distribution typically is used to model continuous variables that are always positive and have skewed distributions. We calculated mean $pCES$, using the shape (α) divided by the rate (β). For each map, we calculated the proportion of times seals were voted to be present by using the mean $pCES$ from the Gamma distribution as the correction factor. We multiplied it by the proportion of times seals were voted to be present in each map by all voters who voted on that map. The correction factor deflated

the voters' mean votes with their overall mean accuracy and gave us a corrected probability of a seal being present in each map (pSeal). This value was converted to the logistic scale (Formula 2 below) to enable us to use the normal distribution to model crabeater seal habitat suitability.

$$\text{logitSeal} = \log(p\text{Seal}) - \log(1 - p\text{Seal}) \quad (2)$$

For each map, we converted logitSeal to seal presence/absence by back-transforming from Equation (2) and comparing the value to the landscape prevalence of crabeater seals found by MLR (Jiménez-Valverde & Lobo, 2007; Liu, Newell, & White, 2016). All maps, where logitSeal was higher than the landscape prevalence, were considered to have seals present.

2.4 | Environmental covariates

We used 24 remotely sensed environmental covariates to describe the habitat use of crabeater seals in the Weddell Sea (Table 1). These variables are known to affect marine predator foraging and haul-out behaviour through the mixing of water masses, distribution of nutrients and subsequent prey, size and thickness of ice floes, and accessibility of ice through cracks (Gurarie et al., 2017; Labrousse et al., 2018; LaRue, Salas, et al., 2019; Raymond et al., 2015; Reisinger et al., 2018; Southwell, Kerry, & Ensor, 2005; Wege, de Bruyn, Hindell, Lea, & Bester, 2019). We include details on how these data sources were prepared in the Appendix S1 (Table S1). Several of these variables are inherently collinear; we filtered for the most informative set by calculating variable inflation factors for the entire Weddell Sea region using the R library "fmsb" (Nakazawa, 2018). Variables with a

TABLE 1 Environmental variables used as covariates in habitat suitability models for crabeater seals (*Lobodon carcinophaga*) in the Weddell Sea

Abbreviation	Variable	Unit
bath	Bathymetry	m
slope	Ocean floor slope	°
sst	Sea surface temperature	°C
sstA	Sea surface temperature anomalies	°C
sst_grad	Sea surface temperature gradient	°
ssh	Sea surface height	m
currmag	Horizontal geostrophic current magnitude	cm/s
eke	Eddy kinetic energy	cm ² /s ²
windmag	Horizontal wind magnitude	m/s
dist_shelf	Distance to continental shelf – i.e., the 800 m isobath	m
dist_polynya	Distance to nearest polynya	m
dist_canyon	Distance to canyon	km
ice	Ice concentration	%
dist_ice_edge	Distance to ice edge	m
ice_sd	Ice standard deviation	NA
ice_thick	Ice thickness	
oldice	Old ice: Proportion of time the ocean is covered by sea ice of concentration 85% or higher 2003–2010	%
oldice_cv	Old ice coefficient of variation	NA
shflux	Surface heat flux	W/m ²
shflux_sd	Surface heat flux standard deviation	NA
vmix	Vertical mixing	m/s
vmix_sd	Vertical mixing standard deviation	NA
sal200_600	Salinity difference between 200 m and 600 m depth	psu
sal0_200	Salinity difference between 0 m and 600 m depth	psu

variance inflation factor larger than 10 were excluded, because this is a good indication of strong collinearity (Nakazawa, 2018).

2.5 | Habitat ensemble models

We used ensemble models of random forests (RF), boosted regression trees (BRT) and support vector machines with a radial kernel (SVM) to model crabeater seal habitat suitability, with logitSeal as the response variable, and set the models to follow a Gaussian distribution. These algorithms typically perform and combine well as species distribution models (Drake, Randin, & Guisan, 2006; Elith,

Leathwick, Hastie, & Leathwick, 2008; Kirkman, Yemane, Lamont, Meÿer, & Pistorius, 2016; Reisinger et al., 2018). Modelling was done in the “caret” library of R (Kuhn et al., 2019), which employs functions from the libraries “ranger,” “gbm” and “kernlab” for each of the models respectively (Greenwell, Boehmke, Cunningham, & Developers, 2019; Karatzoglou, Smola, Hornik, & Zeileis, 2004; Wright & Ziegler, 2017). We used Maxent (Maximum Entropy; Phillips, Anderson, & Schapire, 2006; Phillips & Dudik, 2008) models as our fourth model in the ensemble using corrected seal presences and absences as the response variable. The “ENMeval” library in R (Muscarella et al., 2014) was used to train Maxent models because it provided more freedom to tune the models and use a stricter regularization parameter. The default settings in Maxent have been shown to produce models that over-fit the data (Muscarella et al., 2014), and it is crucial to model accuracy to choose model specific tuning parameters (Merow, Smith, & Silander, 2013).

For all models, we held out 20% of the data (test data, $n = 1,964$ records) to evaluate model performance, while the remaining 80% of the data was used to train the models. The hold-out data were equally balanced between corrected seal presence and absence points ($n = 982$ records for each). Given the unbalanced and skewed nature of the response variable, we made use of a bootstrapping method and ran each of the four model-types on sub-sets of the data. This also reduces the amount of spatial-autocorrelation often found in habitat models (Hijmans, 2012). Each bootstrap contained all the corrected seal presence records ($n = 3,929$) and a random sample of equal size ($n = 3,929$) of corrected seal absence records. Without balancing the data set, the models would optimize on predicting absences at the expense of increased error in predicted presence. Our bootstrap samples of $n = 7,858$ records were used to train each of the models in the ensemble with each bootstrap. We ran 500 bootstraps for each of the four constituent models. The RF, BRT and SVM models were tuned respectively in each bootstrap using the “tuneGrid” function in “caret” through compiling a range of candidate models and choosing the best candidate model based on the R^2 value that was calculated from 10-fold cross-validation. Cross-validation folds were created by randomly dividing bootstrap records into 10-fold containing an approximately equal number of records. We calculated the R^2 value as the goodness-of-fit measure for the RF, BRT and SVM models of each bootstrap using the 20% hold-out test data. To tune the Maxent models we trained bootstrap models with a 10-fold cross-validation, a range of regularization parameters (RM) ranging from 0.5 to 4, and trying various combinations of feature classes (linear, quadratic, product, threshold and hinge). The area under the random-receiver operator curve (AUC) predicted in the model was used to select the best model in each bootstrap. An out-of-bag AUC value was calculated for each bootstrap using the 20% hold-out test data and was subsequently used as the Maxent goodness-of-fit measure.

Using the environmental layers, we predicted to the rest of the Weddell Sea for each bootstrap of each of the four constituent models using the “predict” function in the R-library “raster” (Hijmans, 2016). However, Maxent is a Poisson point-process model

and cannot calculate true probability of seal presence values (Phillips et al., 2006). Instead, a threshold value is calculated and seal presence/absence is determined from it by evaluating if the point-process relative predicted probability falls below or above the threshold value. We calculated the threshold value based on the overall estimated landscape prevalence of the Weddell Sea calculated using the “threshold” function in the R-library “dismo” (Hijmans, Phillips, Leathwick, & Elith, 2017).

2.6 | Goodness of fit measurements and model weighting

The mean, standard deviation (*SD*) and coefficient of variation ($CV = SD/\text{mean}$) predicted layer for each constituent model was calculated using the 500 layers from the bootstraps. Thereafter, we calculated the mean and standard deviation of the R^2 -values from the bootstraps for the RF, BRT and SVM models, which was used to calculate a model-specific weight using $\text{mean}(R^2)/SD^2(R^2)$. This weighting accounts for both a good fit and for the variance in goodness-of-fit throughout the bootstraps. A weighted average of the three models' predicted habitat suitability was calculated using the raster library's “weighted.mean” function; each respective model's mean predicted layer, and model weight (Hijmans, 2016). We repeated this to calculate an overall weighted mean of the CV of habitat suitability. The weighted mean predicted habitat use layer was converted back from the logit-scale into the probability scale and the CV layer was multiplied with the mean layer to ultimately determine the weighted standard deviation.

The presence/absence post-threshold Maxent layers (consisting of 1's and 0's) of the 500 bootstraps were averaged and for every cell where a Maxent bootstrap predicted seals to be present (1's) 80% of the time or more, a 1 was assigned to that cell (i.e., predicted seal presence). The remainder of the cells was assigned a 0 (i.e., predicted seal absence).

2.7 | Variable importance

For each of the bootstrap samples, we calculated permutation variable importance for the RF and SVM models. R library “gbm” (Ridgeway, 2015) calculates the percentage contribution each variable of the BRT model. Percentage contribution was also calculated for each of the Maxent bootstraps. To understand the processes (not just the individual variables) that influence crabeater seal distribution, we grouped different variables together into three different groups: “ice,” “water” and “geomorphology.” Bathymetry (bathy), distance to canyon (dist_canyon), distance to continental shelf (dist_shelf) and slope (slope) were considered together as “geomorphology” variables. Salinity difference between 200 m and 600 m (sal200_600), surface heat flux (shflux) and its standard deviation (shflux_sd), vertical mixing (vmix) and its standard deviation (vmix_sd), and sea-surface temperature (sst) were grouped under “water.”

Distance to ice edge (ice_edge_dist), ice concentration standard deviation (ice_sd), long-term ice concentration coefficient of variation (oldice_cv) and wind magnitude (windmag) were grouped together under “ice.” The relative proportions each of these variables contributed to a specific cluster were calculated. This also enables us to compare permutation importance with percentage relative influence importance values produced by the different models.

3 | RESULTS

We used 62 satellite images that were broken up into 71,891 maps (0.25 km² each) covering an area of 18,219 km² in the Weddell Sea (Figure 2). In total, 2,225 people voted on maps 156,994 times. Participants voted on average 60 times (range: 1–11,255 times), while each map was voted on, on average twice (range: 1–326 votes per map; Figure 2). Voters found seals in only 92 of the maps. The expert voter (MLR) voted on 1,711 of the 71,891 maps and found seals in 52 of these, resulting in an overall landscape prevalence for the Weddell Sea region of crabeater seals 0.03.

3.1 | Correction factor and pSeal

In total, 276 voters overlapped with MLR on >15 maps. The Gamma distribution's shape and rate were $\alpha = 1.4$ and $\beta = 3.2$, respectively, resulting in a mean accuracy correction factor of 0.44 (95% confidence intervals = [0.02; 1.4]). The deflated probability of seal presence in any given map averaged at 0.014 (range: 0–0.44) and using the landscape prevalence of 0.03, means that the corrected dataset resulted in 4,911 “seals present” and 66,980 “seals absent” records.

3.2 | VIF

The Variance Inflation Factors indicated high collinearity between several variables and consequently, only 14 of the 24 variables were retained for habitat modelling: bathy, dist_canyon, dist_shelf, ice_edge_dist, ice_sd, oldice_cv, sal200_600, slope, vmix, vmix_sd, windmag, sst, shflux, shflux_sd.

3.3 | Habitat models

The RF, BRT and SVM models had low overall performance, while the Maxent model overall performed better (Table 2), but the predicted landscape prevalence agreed with training data's landscape prevalence and the models converged successfully. A summary of the models tuned hyperparameters is in Table S2.

Figure 3 illustrates the spatial distribution of predicted seal probability and the coefficient of variation, while Figure 4 compares the threshold seal presence/absence maps between the ensemble models and the Maxent model.

FIGURE 2 Locations of the satellite images within the Weddell Sea, indicating the number of votes each map received from citizen scientists. Inset: Location of the Weddell Sea in relation to the rest of Antarctica

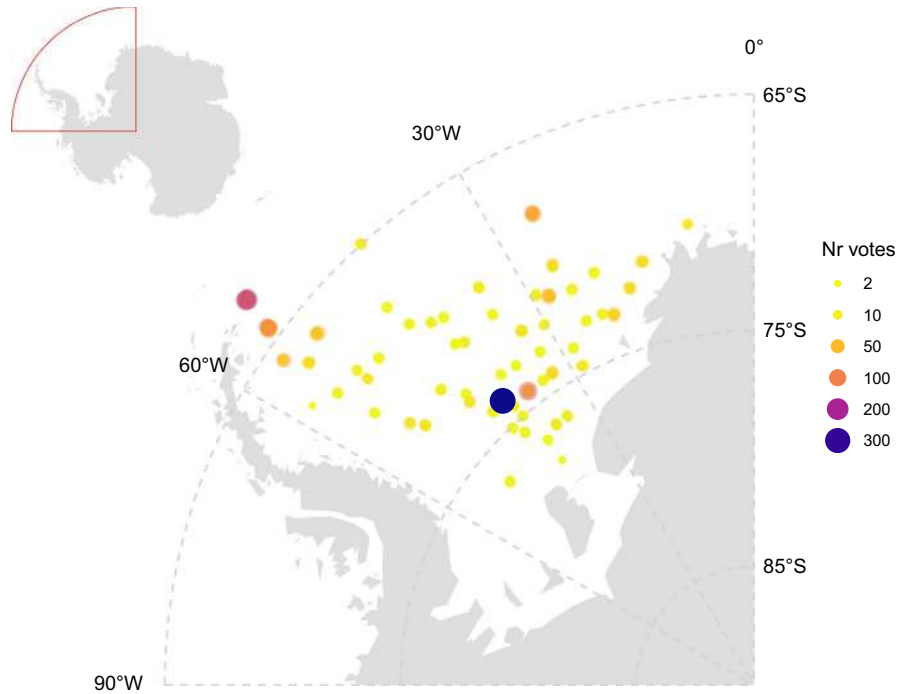


TABLE 2 Summary of the Goodness of Fit metric for each of the constituent models

Model	Goodness of fit metric (mean ± SD)	Model weight (mean(R ²)/SD ²)
RF	R ² = 0.076 ± 0.002	19,438.63
BRT	R ² = 0.086 ± 0.0008	115,275.17
SVM	R ² = 0.082 ± 0.003	10,540.82
Maxent	AUC = 0.71 ± 0.004	NA

3.4 | Variable importance

Relative variable importance for the BRT, SVM and Maxent models were highest for the ice variables, whereas RF models' shown an equal amount of importance for the ice and geomorphology variables (Figure 5). Individual variable importance is shown in Figure S1.

4 | DISCUSSION

We present the first-ever habitat models of crabeater seals during the breeding season in the Weddell Sea. Our study covered an extraordinary, and mostly ice-covered 18,219 km² – the largest area ever surveyed for crabeater seal in a single study over a single breeding season. We were further able to search for crabeater seals in parts of the Weddell Sea where this has never formally been done before due to the dense year-round pack ice that the Weddell Sea is known for. This once again illustrates the effectiveness of VHR satellite imagery to cover large, areas that are potentially inaccessible to ships or within the reach of helicopters in a safe and time- and cost-effective manner.

4.1 | Factors influencing seal distribution

The spatial distribution of predicted seal presences and absences, and higher probabilities of seeing seals (Figures 3 and 4) was consistent with previous research (Erickson, 1984; Forcada et al., 2012; Southwell et al., 2005): seals have a higher probability of being present in the outer fringes of the pack ice around the Scotia Arc and again east of 30° W towards the Antarctic continent (Figure 3; this study). These areas have higher abundance of Antarctic krill, with the highest krill densities in the Southern Ocean found around the Scotia Arc (Atkinson et al., 2008; Siegel, 2005). The continental shelf break and vicinity is the centre of adult krill distribution (Bestley et al., 2018; Nicol, 2006). During the early spring, adult female krill migrate from under the ice of the continental shelf over deeper abyssal waters, and in fact, >87% of the global krill stock occur over water deeper than 2,000 m from October to January (Atkinson et al., 2008). We found crabeater seals more likely to be present over water depth of 1,000–2,000 m, 200–400 km away from a canyon, and only about 200–400 m away from the continental shelf edge. Similarly, the only other habitat models that exist for crabeater seal during the breeding season (off east Antarctica; Southwell et al., 2005) found that crabeater seal was also more likely to be present around depths of 2,500 m and around the continental shelf break. These ecological traits of Antarctic krill would explain why distance to the ice edge and these bathymetric features were the top predictor variables for all ensemble models (Figure S1); and why partial dependence plots for distance to the ice-edge and bathymetry show that crabeater seal is more likely to be present away from the ice edge, into the pack ice and over deeper water, close to the continental shelf edge (Figure 6). Though our results are ecologically sensible, our interpretations are based on the variables on the model. Since some variables were excluded due to their high variance inflation factor, it is unclear if the

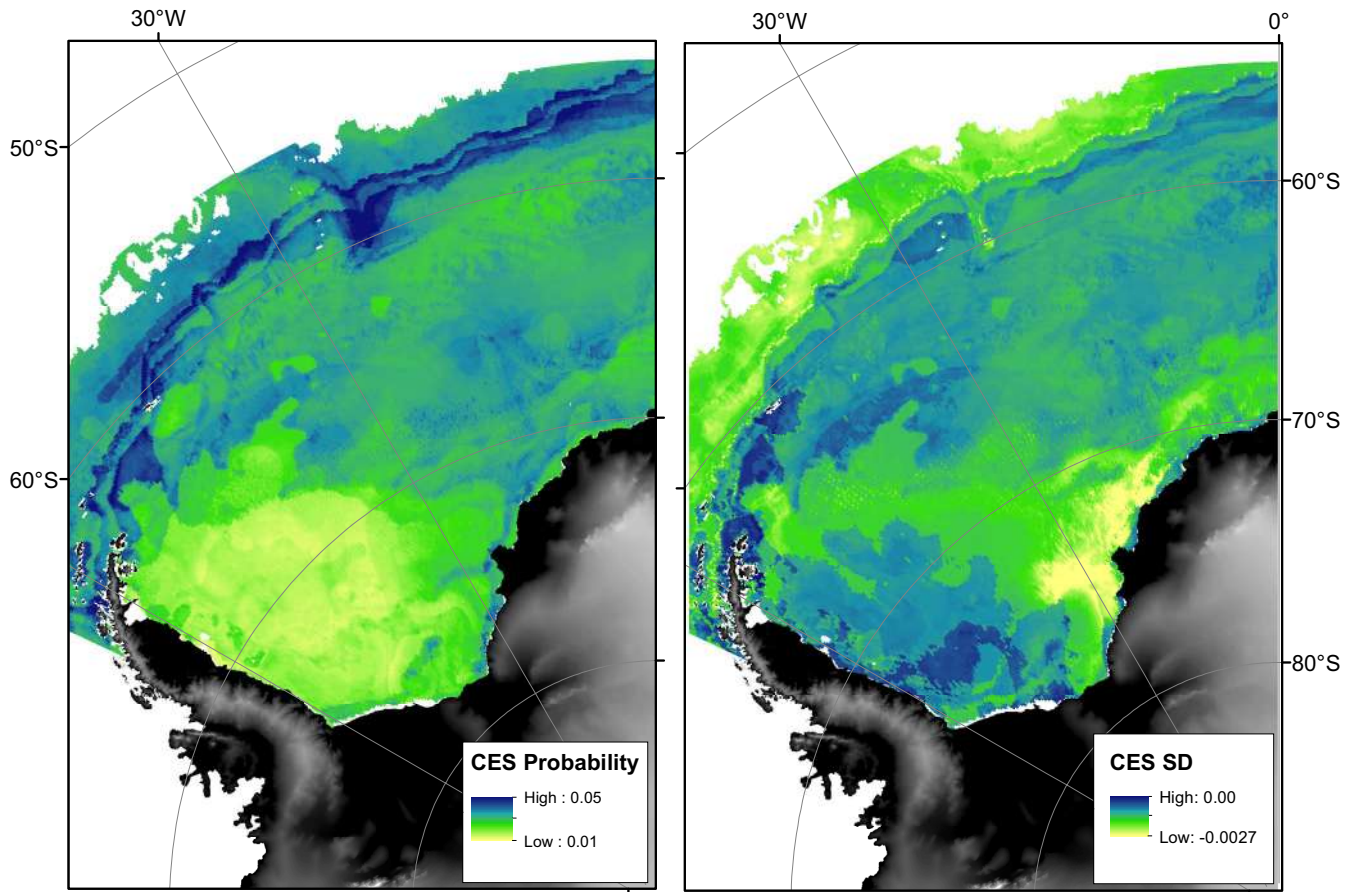


FIGURE 3 Weighted mean ensemble prediction (left) and standard deviation (right) for crabeater seal habitat suitability in the Weddell Sea. Ensemble models were built from Random Forests, Boosted Regression Trees and Support Vector Machines

discarded variables, and not the variables kept for modelling, are the covariates that are affecting the habitat selection by seals.

The south-western area in the deep Weddell Sea where crabeater seals are predicted to be absent during breeding season is an area of high concentrations of multi-year pack ice. This persistent pack ice is maintained by the clockwise rotating Weddell Gyre that pushes pack ice into the arm of the Antarctic Peninsula and retains it within the south-western Weddell Sea throughout summer (Harder & Fischer, 1999; Yaremchuk, Nechaev, Schröter, & Fahrback, 1998). Indeed, ice concentration standard deviation contributed a large amount to all the ensemble models. Ice concentration standard deviation perhaps serves as a proxy for accessibility – the more variable the ice concentration, the more accessible it is to swimming seals. The partial dependence plot (Figure 6) supports this and show that higher ice concentration variability coincides with higher probabilities of crabeater seal presence.

For the BRT, SVM and Maxent ensemble models, ice variables were the most important variables that influenced crabeater seal distribution and were equally as important as the geomorphological variables in the RF ensembles (Figure 5). Ice is the dominant force in the Southern Ocean, it provides a platform for species to haul out on to breed and rest, and it can restrict the movements of individuals and provide valuable nutrients when melting (Ainley,

Jacobs, Ribic, & Gaffney, 1998; Croxall et al., 2002; Southwell et al., 2005; Van Franeker, Bathmann, & Mathot, 1997). Indeed, previous habitat modelling approaches to quantify crabeater seal distribution and abundance also found ice to be a dominant predictor in their distribution and abundance (Flores et al., 2008; Gurarie et al., 2017; Nachtsheim, Jerosch, Hagen, Plötz, & Bornemann, 2017). Off east Antarctica, crabeater seal presence/absence during the breeding season was influenced by bathymetry and distance to the ice-edge was positively correlated with seal presence (Southwell et al., 2005), similar to this study. Although crabeater seals are capital breeders who do not need to forage during the breeding haul-out phase, the spatial overlap between food resources (krill) and haul-out areas on the ice means that crabeater seals can breed close to food resources. This is likely a result of their extremely specialist diet and would explain why breeding haul-out areas overlap with typical adult krill habitat – although ice accessibility and stability also contributes to the selection of haul-out sites.

Their highly specialized diet and spatial overlap between haul out and foraging habitat, make them ideal indicator species; however, CEMP does not consider crabeater seals to be good indicator species to use for monitoring of krill availability because they live in the pack ice, which is hard to access and not manageable through

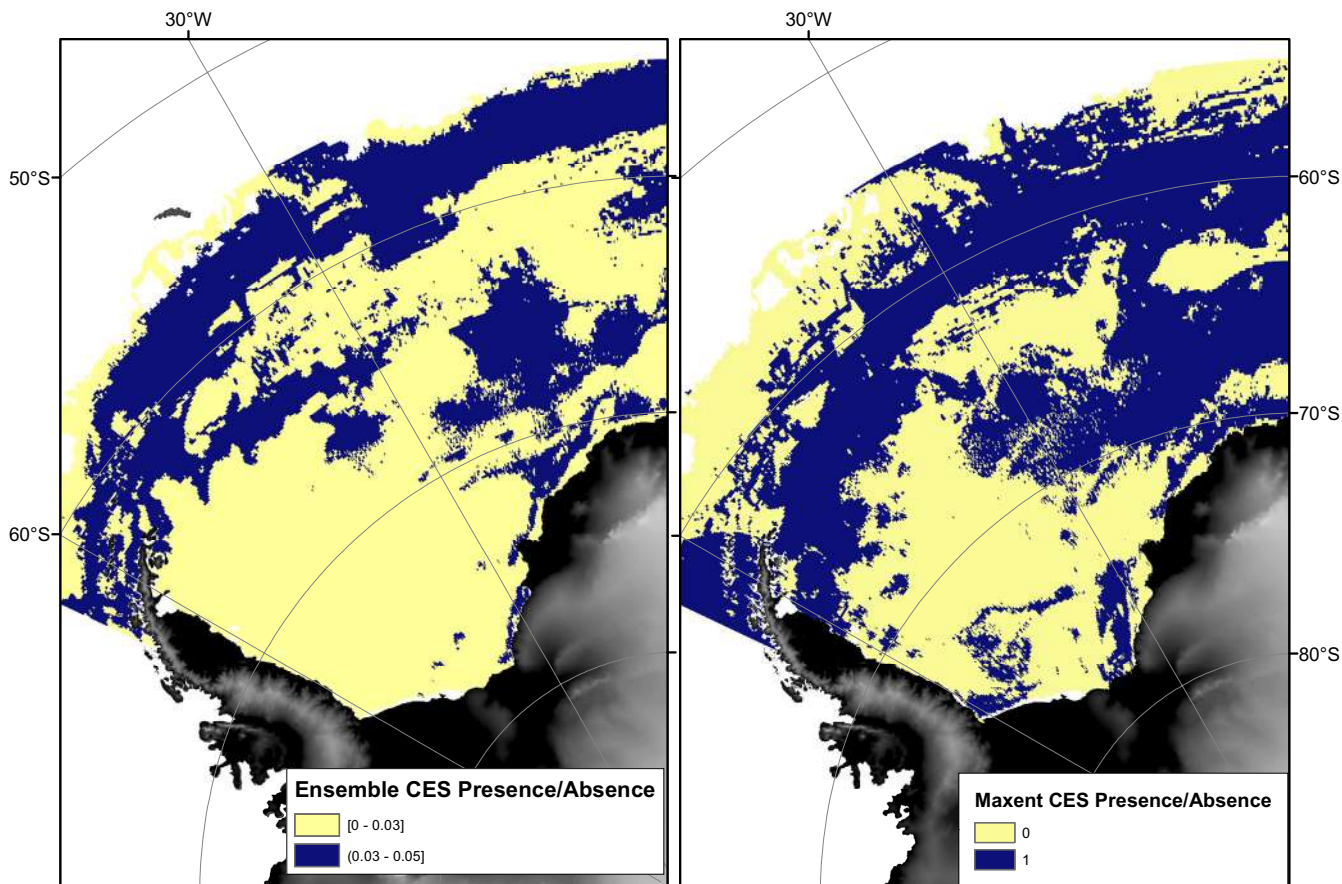
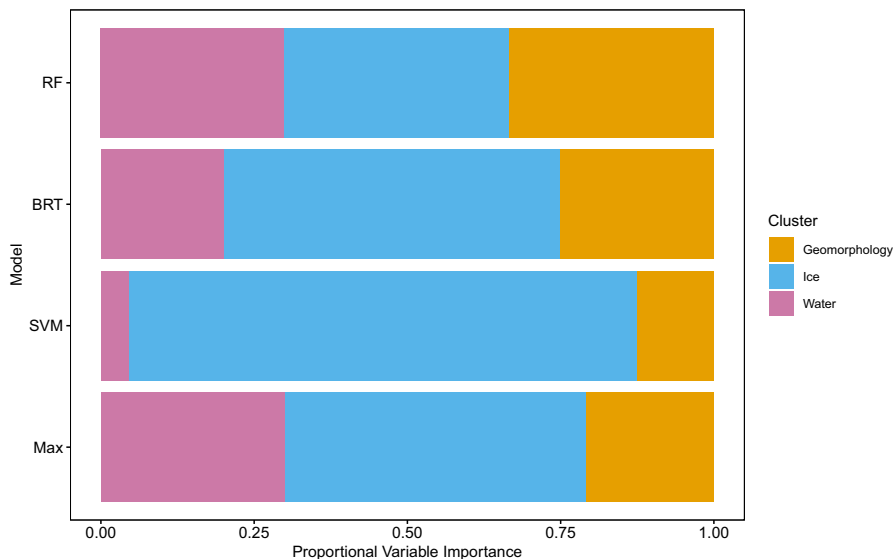


FIGURE 4 Left: Weighted mean ensemble prediction in the Weddell Sea, where the predicted probability of presence is higher (blue) or lower (light yellow) than the overall landscape prevalence of crabeater seals. Right: The average Maxent model prediction of seal presence (1: blue)/ absence (0: light yellow) after a landscape prevalence threshold was applied to each of the bootstrap Maxent models

FIGURE 5 Proportional variable importance of the environmental predictor variables used in the Random Forests (RF), Boosted Regression Trees (BRT), Support Vector Machines (SVM) and Maxent (Max) models. Ice variables: ice_edge_dist, ice_sd, oldice_cv and windmag. Geomorphology variables: bathy, dist_canyon, dist_shelf, and slope. Water variables: sal200_600, shflux, shflux_sd, vmix, vmix_sd, and sst



repeated monitoring (CEMP: <https://www.ccamlr.org/en/science/ccamlr-ecosystem-monitoring-program-cemp>.) However, VHR presents a cost-effective manner to monitor large inaccessible areas. Krill forms the base of the short food chains in Antarctica and is a key prey species for many predators.

In terms of the planned Weddell Sea MPA, it is clear that the deeper and inner Weddell Sea is not ideal crabeater seal (this study) or krill habitat (this study; Teschke et al., 2020), while the outer fringes around the Scotia Arc and closer to Princess Martha Coast are import crabeater seal and krill areas (this study; (Nachtsheim

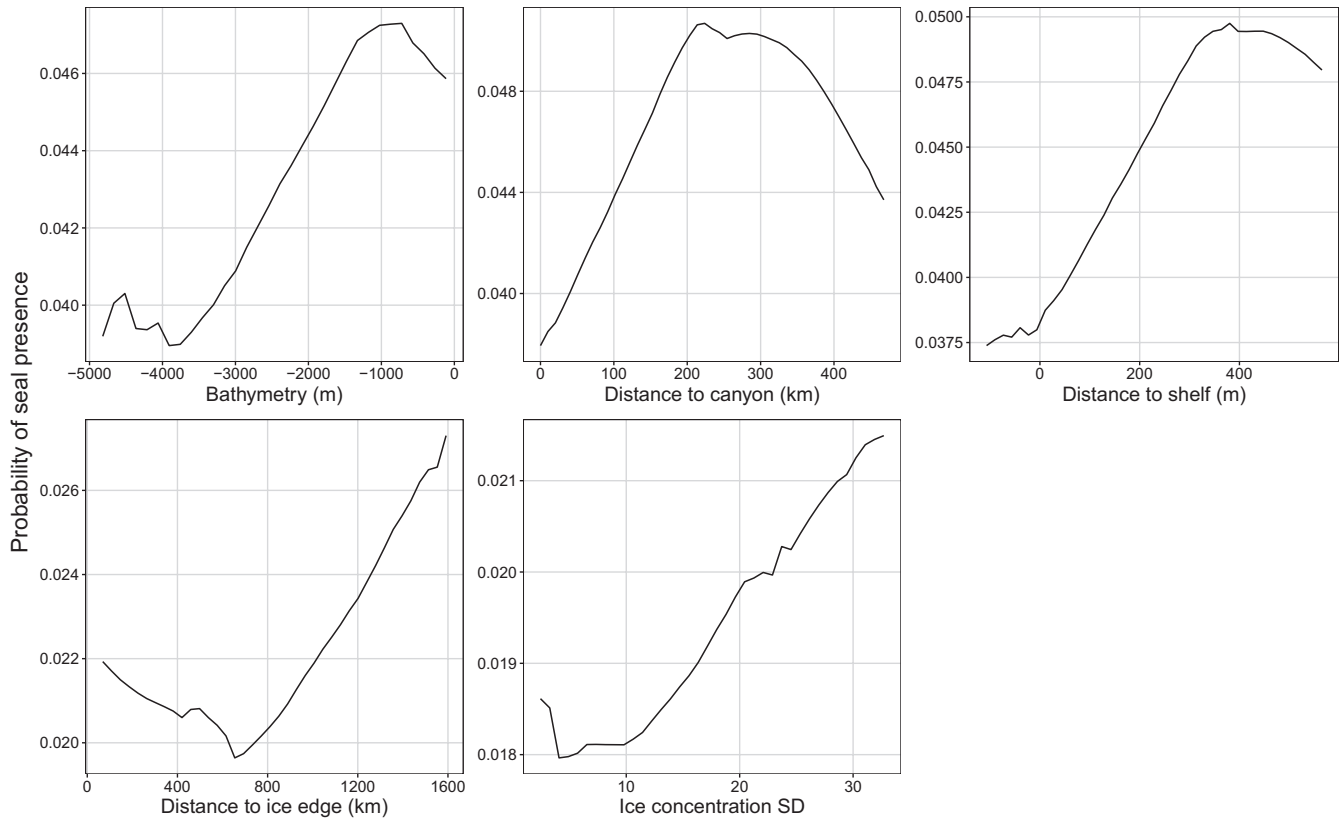


FIGURE 6 Average partial dependence plots for the model ensemble (RF, BRT and SVM models), presenting the relationship between probability of crabeater seal presence and the top five environmental predictor variables

et al., 2017; Teschke et al., 2020). Although the southern areas of the Weddell Sea have never been commercially fished (Teschke et al., 2020) this study shows that these areas are not ideal krill harvesting areas.

4.2 | Caveats of the data

The low prevalence of seals in the data set (3%) could potentially be due to difficulty in seeing seals on the ice (Figure 1). This low prevalence and resulting low number of detections, results in a large number of false-negative data, which in turn causes the models in the ensemble to have very low R^2 . Maxent's modelling approach treats the absences as pseudo-absences, and thus results in a better fit. Despite the low R^2 , the ensemble models are able to find some information in the data to discern potentially good from less desirable crabeater seal habitat, and indeed results largely converge with the Maxent results. However, the current method is not able to provide abundance estimates. The roughness of the terrain in the Antarctic pack ice and the available quality of satellite images still makes it difficult to discern between two seals lying next to each other and to distinguish pups from adults. Although making use of citizen scientist votes and comparing it to an expert voter is biased, automated image recognition only detects 30% of seals, even

during summer when the ice floes are smaller and flatter, and seals haul out in high numbers close to each other (Gonçalves, Spitzbart, & Lynch, 2020).

To date, satellite images have not been used to study a pack-ice breeding species, such as the crabeater seal, because of the complexity of the background of the sea ice. Weddell seals and Emperor penguins (*Aptenodytes forsteri*) breed on fast ice, which is generally flat with minimal ridges and melt pools. This makes seeing seals and penguins from satellite imagery easier and more feasible than trying to look for seals on pack ice with multiple pressure ridges, melt pools, shadows and multi-year ice (Fretwell et al., 2012; LaRue et al., 2011; Figure 1). However, despite these difficulties in detecting seals, we believe it is rather the locations of where the satellite images were taken that is the cause for low crabeater seal prevalence. The satellite images, by way of our stratified random sampling design, were focussed on areas deeper in the Weddell Sea, where ice concentrations during spring is higher and cracks and leads were unlikely to be open through which crabeater seal can access these areas. Furthermore, although the northern areas of the Weddell Sea in the Scotia Sea is home to 70% of the global Antarctic krill population (Atkinson et al., 2008), the deeper Weddell Sea has some of the lowest Antarctic krill abundances within its circumpolar range (Atkinson et al., 2008; Teschke et al., 2020). These characteristics make most of the areas where

the satellite images were taken, unfavourable seal habitat given that they were taken in high ice concentration areas and unlikely krill habitat (Teschke et al., 2020).

Finally, during the citizen science phase we only asked the citizen scientists to vote on whether seals were present or absent. We took this approach based on results reported in LaRue, Ainley, et al. (2020), which found that citizen scientists accurately detected (97%) Weddell seals on Antarctic fast ice, and in fact over-identified "seal" maps (false-positive rate of 67%). We therefore built on this previous work and assumed the same could be true with crabeater seals. This combined with the fact that the proportion of seal maps detected by "the crowd" and by the expert (MLR) are nearly identical (~3%) re-emphasizes our results – crabeater seals may in fact be present in fewer locations within the Weddell Sea than previously reported (e.g., Erickson & Hanson, 1990). Using images from drones or ground counts to inform these models further could also improve the models, however, this negates the fact that we surveyed areas in the Weddell Sea during spring that would be inaccessible to ships and to date have never been surveyed.

Despite challenges in working with VHR imagery to find crabeater seal in the Weddell Sea pack ice and the low predictive power of the ensemble models, the results still agreed with what we know about the ecology of crabeater seal and the abundance, distribution and ecology of Antarctic krill – the prey that make up 90% of their diet. Future improvements of our methods might make this approach the only tool that could quantify crabeater seal abundance with more confidence than the current suggested estimate of 7–30 million individuals. We identified key areas for this abundant mesopredator in the Weddell Sea during breeding season, a vital life-stage and also provided insights into the close linkage between their breeding haul-out locations and the distance to likely foraging habitat across 18 219 km². Our modelling exercise provides CCAMLR with a concrete model to assist furthering policy around the Weddell Sea MPA, especially in relation to protecting potential krill habitat: the prey of most of Antarctica's predators.

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REFERENCES

Agnew, D. J. (1997). The CCAMLR Ecosystem Monitoring Programme. *Antarctic Science*, 9(3), 235–242.

Ainley, D. G., Jacobs, S. S., Ribic, C. A., & Gaffney, I. A. N. (1998). Seabird distribution and oceanic features of the Amundsen and southern

Bellingshausen seas. *Antarctic Science*, 10(2), 111–123. <https://doi.org/10.1017/S0954102098000169>

Angermeier, P. L. (1995). Ecological attributes of extinction prone species: Loss of freshwater species of fishes of Virginia. *Conservation Biology*, 9, 143–158.

Atkinson, A., Siegel, V., Pakhomov, E. A., Rothery, P., Loeb, V., Ross, R. M., ... Fleming, A. H. (2008). Oceanic circumpolar habitats of Antarctic krill. *Marine Ecology Progress Series*, 362, 1–23. <https://doi.org/10.3354/meps07498>

Bengtson, J. L. (2009). Crabeater seal *Lobodon carcinophaga*. In W. Perrin, B. Wursig, & J. Thewissen (Eds.), *Encyclopedia of marine mammals* (pp. 290–292). Cambridge, MA: Academic Press.

Bester, M. N., Bornemann, H., & McIntyre, T. (2017). Antarctic marine mammals and sea ice. In D. N. Thomas (Ed.), *Sea Ice* (3rd ed., pp. 534–555). Hoboken, NJ: John Wiley & Sons Ltd.

Bester, M. N., Ferguson, J. W. H. W. H., & Jonker, F. C. C. (2002). Population densities of pack ice seals in the Lazarev Sea, Antarctica. *Antarctic Science*, 14(2), 139–143. <https://doi.org/10.1017/S0954102002000676>

Bester, M. N., Wege, M., Lübcker, N., Postma, M., & Syndercombe, G. (2019). Opportunistic ship-based census of pack ice seals in eastern Weddell Sea, Antarctica. *Polar Biology*, 42(1), 225–229. <https://doi.org/10.1007/s00300-018-2401-7>

Bestley, S., Raymond, B., Gales, N. J., Harcourt, R. G., Hindell, M. A., Jonsen, I. D., ... Cox, M. J. (2018). Predicting krill swarm characteristics important for marine predators foraging off East Antarctica. *Ecography*, 41, 996–1012. <https://doi.org/10.1111/ecog.03080>

Blix, A. S., & Nordøy, E. S. (2007). Ross seal (*Ommatophoca rossii*) annual distribution, diving behaviour, breeding and moulting, off Queen Maud Land, Antarctica. *Polar Biology*, 30(11), 1449–1458. <https://doi.org/10.1007/s00300-007-0306-y>

CCAMLR (2008). *Report of the Twenty-Seventh Meeting of the Scientific Committee Report. SC-CAMLR-XXVII/Annex 4, Hobart, Australia*. Retrieved from <http://www.ccamlr.org>

CCAMLR. (2011). *Commission for the Conservation of Antarctic Marine Living Resources, "Conservation Measure 91-04: General Framework for the Establishment of CCAMLR Marine Protected Areas"*. Retrieved from <https://www.ccamlr.org/en/measure-91-04-2011>

Croxall, J. P., & Prince, P. A. (1980). Food, feeding ecology and ecological segregation of seabirds at South Georgia. *Biological Journal of the Linnean Society*, 14(1), 103–131. <https://doi.org/10.1111/j.1095-8312.1980.tb00101.x>

Croxall, J. P., Reid, K., & Prince, P. A. (1999). Diet, provisioning and productivity responses of marine predators to differences in availability of Antarctic krill. *Marine Ecology Progress Series*, 177, 115–131.

Croxall, J. P., Trathan, P. N., & Murphy, E. J. (2002). Environmental Change and Antarctic Seabird populations. *Science*, 297(5586), 1510–1514. <https://doi.org/10.1126/science.1071987>

Daly, K., & Macaulay, M. (1991). Influence of physical and biological mesoscale dynamics on the seasonal distribution and behavior of *Euphausia superba* in the antarctic marginal ice zone. *Marine Ecology Progress Series*, 79(1–2), 37–66. <https://doi.org/10.3354/meps079037>

Delignette-Muller, M. L., & Dutang, C. (2015). *fitdistrplus: An r package for fitting distributions*. *Journal of Statistical Software*, 64(4), 1–34.

Drake, J. M., Randin, C., & Guisan, A. (2006). Modelling ecological niches with support vector machines. *Journal of Applied Ecology*, 43, 424–432. <https://doi.org/10.1111/j.1365-2664.2006.01141.x>

Elith, J., Leathwick, J. R., Hastie, T., & Leathwick, R. J. (2008). A working guide to boosted regression trees. *Journal of Animal Ecology*, 77, 802–813. <https://doi.org/10.1111/j.1365-2656.2008.01390.x>

Erickson, A. W. (1984). Aerial census of seals, whales, and penguins in the pack ice of the northwestern Weddell Sea, November 1983. *Antarctic Journal of the United States*, 19, 121–124.

- Erickson, A. W., & Hanson, M. B. (1990). Continental estimates and population trends of Antarctic Ice Seals. In K. Kerry, & G. Hempel (Eds.), *Antarctic ecosystems, ecological change and conservation* (pp. 253–264). Berlin, Germany: Springer.
- Erickson, A. W., & Hofman, R. J. (1974). Antarctic Seals. In V. C. Bushnell (Ed.), *Antarctic Mammals, Antarctic Map Folio Series No. 18*. New York, NY: American Geographic Society.
- Flores, H., Haas, C., van Franeker, J. A., & Meesters, E. (2008). Density of pack-ice seals and penguins in the western Weddell Sea in relation to ice thickness and ocean depth. *Deep-Sea Research Part II: Topical Studies in Oceanography*, 55(8–9), 1068–1074. <https://doi.org/10.1016/j.dsr2.2007.12.024>
- Forcada, J., Trathan, P. N., Boveng, P. L., Boyd, I. L., Burns, J. M., Costa, D. P., ... Southwell, C. J. (2012). Responses of Antarctic pack-ice seals to environmental change and increasing krill fishing. *Biological Conservation*, 149(1), 40–50. <https://doi.org/10.1016/j.biocon.2012.02.002>
- Fretwell, P., LaRue, M. A., Morin, P., Kooyman, G. L., Wienecke, B., Ratcliffe, N., ... Trathan, P. N. (2012). An emperor penguin population estimate: The first global, synoptic survey of a species from space. *PLoS One*, 7(4), e33751. <https://doi.org/10.1371/journal.pone.0033751>
- Gell, F. R., & Roberts, C. M. (2003). Benefits beyond boundaries: The fishery effects of marine reserves. *Trends in Ecology and Evolution*, 18(9), 448–455. [https://doi.org/10.1016/S0169-5347\(03\)00189-7](https://doi.org/10.1016/S0169-5347(03)00189-7)
- Gonçalves, B. C., Spitzbart, B., & Lynch, H. J. (2020). SealNet: A fully-automated pack-ice seal detection pipeline for sub-meter satellite imagery. *Remote Sensing of Environment*, 239, 111617. <https://doi.org/10.1016/j.rse.2019.111617>
- Greenwell, B., Boehmke, B., Cunningham, J., & Developers, G. B. M. (2019). *gbm: Generalized Boosted Regression Models (R package version 2.1.5)*. Retrieved from <https://cran.r-project.org/package=gbm>
- Gurarie, E., Bengtson, J. L., Bester, M. N., Blix, A. S., Cameron, M., Bornemann, H., ... Boveng, P. (2017). Distribution, density and abundance of Antarctic ice seals off Queen Maud Land and the eastern Weddell Sea. *Polar Biology*, 40(5), 1149–1165. <https://doi.org/10.1007/s00300-016-2029-4>
- Gutt, J., Sirenko, B. I., Smirnov, I. S., & Arntz, W. E. (2004). How many macrozoobenthic species might inhabit the Antarctic shelf? *Antarctic Science*, 16(1), 11–16. <https://doi.org/10.1017/S0954102004001750>
- Hall-Aspland, S. A., & Rogers, T. L. (2004). Summer diet of leopard seals (*Hydrurga leptonyx*) in Prydz Bay, Eastern Antarctica. *Polar Biology*, 27(12), 729–734. <https://doi.org/10.1007/s00300-004-0662-9>
- Harder, M., & Fischer, H. (1999). Sea ice dynamics in the Weddell Sea simulated with an optimized model. *Journal of Geophysical Research – Oceans*, 104, 11151–11162. <https://doi.org/10.1029/1999JC900047>
- Hijmans, R. J. (2012). Cross-validation of species distribution models: Removing spatial sorting bias and calibration with a null model. *Ecology*, 93(3), 679–688. <https://doi.org/10.1890/11-0826.1>
- Hijmans, R. J. (2016). *raster: Geographic Data Analysis and Modeling. R package version 2.5-8*. Retrieved from <https://CRAN.R-project.org/package=raster>
- Hijmans, R. J., Phillips, S. J., Leathwick, J., & Elith, J. (2017). *dismo: Species Distribution Modeling. R Package Version 1.1-4*. Retrieved from <https://cran.r-project.org>
- Hückstädt, L. A., Burns, J. M., Koch, P. L., McDonald, B. I., Crocker, D. E., & Costa, D. P. (2012). Diet of a specialist in a changing environment: The crabeater seal along the western Antarctic Peninsula. *Marine Ecology Progress Series*, 455, 287–301. <https://doi.org/10.3354/meps09601>
- Jiménez-Valverde, A., & Lobo, J. M. (2007). Threshold criteria for conversion of probability of species presence to either-or presence-absence. *Acta Oecologica*, 31(3), 361–369. <https://doi.org/10.1016/j.actao.2007.02.001>
- Karatzoglou, A., Smola, A., Hornik, K., & Zeileis, A. (2004). kernlab - An S4 Package for Kernel Methods in R. *Journal of Statistical Software*, 11(9), 1–20.
- Kirkman, S. P., Yemane, D. G., Lamont, T., Meyer, M. A., & Pistorius, P. A. (2016). Foraging behavior of subantarctic fur seals supports efficiency of a Marine Reserve's Design. *PLoS One*, 11(5), e0152370. <https://doi.org/10.1371/journal.pone.0152370>
- Kuhn, M., Wing, J., Weston, S., Williams, A., Keefer, C., Engelhardt, A., ... Hunt, T. (2019). *caret: Classification and Regression Training (R package version 6.0-83)*. Retrieved from <https://cran.r-project.org/package=caret>
- Labrousse, S., Williams G., Tamura T., Bestley S., Sallée J-B., Fraser A. D., ... Charrassin J-B. (2018). Coastal polynyas: Winter oases for sub-adult southern elephant seals in East Antarctica. *Scientific Reports*, 8, (1), 3183. <http://dx.doi.org/10.1038/s41598-018-21388-9>
- LaRue, M. A., Ainley D. G., Pennycook J., Stamatou K., Salas L., Nur N., ... Barrington L. (2020). Engaging 'the crowd' in remote sensing to learn about habitat affinity of the Weddell seal in Antarctica. *Remote Sensing in Ecology and Conservation*, 6, (1), 70–78. <http://dx.doi.org/10.1002/rse2.124>
- LaRue, M. A., Rotella, J. J., Garrott, R. A., Siniff, D. B., Ainley, D. G., Stauffer, G. E., ... Morin, P. J. (2011). Satellite imagery can be used to detect variation in abundance of Weddell seals (*Leptonychotes weddellii*) in Erebus Bay. *Antarctica. Polar Biology*, 34(11), 1727–1737. <https://doi.org/10.1007/s00300-011-1023-0>
- LaRue, M. A., Salas, L., Nur, N., Ainley, D. G., Stammerjohn, S. E., Barrington, L., ... Nakamura, H. (2019). Physical and ecological factors explain the distribution of Ross Sea Weddell seals during the breeding season. *Marine Ecology Progress Series*, 612, 193–208. <https://doi.org/10.3354/meps12877>
- Laws, R. M. (1977). Seals and whales of the Southern Ocean. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences*, 279(963), 81–96.
- Laws, R. M. (1981). Biology of Antarctic seals. *Science Progress*, 67(267), 377–397.
- Laws, R. M., Baird, A., & Bryden, M. M. (2003). Size and growth of the crabeater seal *Lobodon carcinophagus* (Mammalia: Carnivora). *Journal of Zoology*, 259(1), 103–108. <https://doi.org/10.1017/S0952836902003072>
- Lester, S. E., & Halpern, B. S. (2008). Biological responses in marine no-take reserves versus partially protected areas. *Marine Ecology Progress Series*, 367, 49–56. <https://doi.org/10.3354/meps07599>
- Liu, C., Newell, G., & White, M. (2016). On the selection of thresholds for predicting species occurrence with presence-only data. *Ecology and Evolution*, 6(1), 337–348. <https://doi.org/10.1002/ece3.1878>
- Lynch, H. J., & LaRue, M. A. (2014). First global census of the Adélie Penguin. *The Auk*, 131(4), 457–466. <https://doi.org/10.1642/AUK-14-31.1>
- Lynnes, A. S., Reid, K., & Croxall, J. P. (2004). Diet and reproductive success of Adélie and chinstrap penguins: Linking response of predators to prey population dynamics. *Polar Biology*, 27(9), 544–554. <https://doi.org/10.1007/s00300-004-0617-1>
- Merow, C., Smith, M. J., & Silander, J. A. (2013). A practical guide to MaxEnt for modeling species' distributions: What it does, and why inputs and settings matter. *Ecography*, 36(10), 1058–1069. <https://doi.org/10.1111/j.1600-0587.2013.07872.x>
- Muscarella, R., Galante, P. J., Soley-Guardia, M., Boria, R. A., Kass, J. M., Uriarte, M., & Anderson, R. P. (2014). ENMeval: An R package for conducting spatially independent evaluations and estimating optimal model complexity for Maxent ecological niche models. *Methods in Ecology and Evolution*, 5(11), 1198–1205. <https://doi.org/10.1111/2041-210x.12261>

- Nachtsheim, D. A., Jerosch, K., Hagen, W., Plötz, J., & Bornemann, H. (2017). Habitat modelling of crabeater seals (*Lobodon carcinophaga*) in the Weddell Sea using the multivariate approach Maxent. *Polar Biology*, 40(5), 961–976. <https://doi.org/10.1007/s00300-016-2020-0>
- Nakazawa, M. (2018). *fmsb: Functions for medical statistics book with some demographic data. R Package Version 0.6.3*. Retrieved from <https://cran.r-project.org/package=fmsb>
- Nicol, S. (2006). Krill, currents, and Sea Ice: *Euphausia superba* and its changing environment. *BioScience*, 56(2), 111–120. [https://doi.org/10.1641/0006-3568\(2006\)056\[0111:KCASIE\]2.0.CO;2](https://doi.org/10.1641/0006-3568(2006)056[0111:KCASIE]2.0.CO;2)
- Nordoy, E. S., Folkow, L., & Blix, A. S. (1995). Distribution and diving behaviour of crabeater seals (*Lobodon carcinophagus*) off Queen Maud Land. *Polar Biology*, 15, 261–268. <https://doi.org/10.1007/BF00239846>
- Øritsland, T. (1977). Food consumption of seals in the antarctic pack ice. In G. A. Llano (Ed.), *Adaptations within Antarctic ecosystems, Third Symposium on Antarctic Biology*. Scientific Committee for Antarctic Research.
- Phillips, S. J., Anderson, R. P., & Schapire, R. E. (2006). Maximum entropy modeling of species geographic distributions. *Ecological Modelling*, 190, 231–259. <https://doi.org/10.1016/j.ecolmodel.2005.03.026>
- Phillips, S. J., & Dudik, M. (2008). Modeling of species distributions with Maxent: New extensions and a comprehensive evaluation. *Ecography*, 31, 161–175. <https://doi.org/10.1111/j.2007.0906-7590.05203.x>
- R Core Team (2019). *R: A language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing. Retrieved from <http://www.R-project.org>
- Raymond, B. (2018). *Polar Environmental Data Layers Australian Antarctic Data Centre - CAASM Metadata*. Retrieved from https://data.aad.gov.au/metadata/records/Polar_Environmental_Data
- Raymond, B., Lea, M.-A., Patterson, T., Andrews-Goff, V., Sharples, R., Charrassin, J.-B., ... Hindell, M. A. (2015). Important marine habitat off east Antarctica revealed by two decades of multi-species predator tracking. *Ecography*, 38, 121–129. <https://doi.org/10.1111/ecog.01021>
- Reid, K., Croxall, J. P., Briggs, D. R., & Murphy, E. J. (2005). Antarctic ecosystem monitoring: Quantifying the response of ecosystem indicators to variability in Antarctic krill. *ICES Journal of Marine Science*, 62(3), 366–373. <https://doi.org/10.1016/j.jicesms.2004.11.003>
- Reisinger, R. R., Raymond, B., Hindell, M. A., Bester, M. N., Crawford, R. J. M., Davies, D., ... Pistorius, P. A. (2018). Habitat modelling of tracking data from multiple marine predators identifies important areas in the Southern Indian Ocean. *Diversity and Distributions*, 24, 535–550. <https://doi.org/10.1111/ddi.12702>
- Ridgeway, G. (2015). *gbm: Generalized Boosted Regression Models. R package version 2.1.1*. Retrieved from <https://CRAN.R-project.org/package=gbm>
- Rogers, T. L., Hogg, C. J., & Irvine, A. (2005). Spatial movement of adult leopard seals (*Hydrurga leptonyx*) in Prydz Bay, Eastern Antarctica. *Polar Biology*, 28, 456–463. <https://doi.org/10.1007/s00300-004-0703-4>
- Shultz, S., Bradbury, R. B., Evans, K. L., Gregory, R. D., & Blackburn, T. M. (2005). Brain size and resource specialization predict long-term population trends in British birds. *Proceedings of the Royal Society B: Biological Sciences*, 272(1578), 2305–2311. <https://doi.org/10.1098/rspb.2005.3250>
- Siegel, V. (2005). Distribution and population dynamics of *Euphausia superba*: Summary of recent findings. *Polar Biology*, 29, 1–22. <https://doi.org/10.1007/s00300-005-0058-5>
- Siniff, D. B. (1991). An Overview of the Ecology of Antarctic Seals. *American Zoologist*, 31(1), 143–149. <https://doi.org/10.1093/icb/31.1.143>
- Southwell, C. J. (2005). Optimising the timing of visual surveys of crabeater seal abundance: Haulout behaviour as a consideration. *Wildlife Research*, 32, 333–338. <https://doi.org/10.1071/WR04085>
- Southwell, C. J., Bengtson, J. L., Bester, M. N., Blix, A. S., Bornemann, H., Boveng, P. L., ... Trathan, P. N. (2012). A review of data on abundance, trends in abundance, habitat use and diet of ice-breeding seals in the Southern Ocean. *CCAMLR Science*, 19, 1–26.
- Southwell, C. J., Kerry, K. R., & Ensor, P. H. (2005). Predicting the distribution of crabeater seals *Lobodon carcinophaga* off east Antarctica during the breeding season. *Marine Ecology Progress Series*, 299, 297–309. <https://doi.org/10.3354/meps299297>
- Southwell, C. J., Kerry, K., Ensor, P., Woehler, E. J., & Rogers, T. L. (2003). The timing of pupping by pack-ice seals in East Antarctica. *Polar Biology*, 26, 648–652. <https://doi.org/10.1007/s00300-003-0534-8>
- Sumner, M. D. (2015). *raadtools: Tools for synoptic environmental spatial data*. Retrieved from <https://github.com/AustralianAntarcticDivision/raadtools>
- Terraube, J., Arroyo, B., Madders, M., & Mougeot, F. (2011). Diet specialisation and foraging efficiency under fluctuating vole abundance: A comparison between generalist and specialist avian predators. *Oikos*, 120(2), 234–244. <https://doi.org/10.1111/j.1600-0706.2010.18554.x>
- Teschke, K., Beaver, D., Bester, M. N., Bombosch, A., Bornemann, H., Brandt, A., ... Brey, T. (2016). *Scientific background document in support of the development of a CCAMLR MPA in the Weddell Sea (Antarctica) - Version 2016 - Part A: General context of the establishment of MPAs and background information on the Weddell Sea MPA planning area WG-EMM-16/01* (Issue November).
- Teschke, K., Pehlke H., Siegel V., Bornemann H., Knust R., Brey T. (2020). An integrated compilation of data sources for the development of a marine protected area in the Weddell Sea. *Earth System Science Data*, 12, (2), 1003–1023. <http://dx.doi.org/10.5194/essd-12-1003-2020>
- Van Franeker, J. A., Bathmann, U. V., & Mathot, S. (1997). Carbon fluxes to Antarctic top predators. *Deep Sea Research II*, 44, 435–455. [https://doi.org/10.1016/S0967-0645\(96\)00078-1](https://doi.org/10.1016/S0967-0645(96)00078-1)
- Vernet, M., Geibert, W., Hoppema, M., Brown, P. J., Haas, C., Hellmer, H. H., ... Verdy, A. (2019). The Weddell Gyre, Southern Ocean: Present knowledge and future challenges. *Reviews of Geophysics*, 57, 623–708. <https://doi.org/10.1029/2018RG000604>
- Walker, T. R., Boyd, I. L., McCafferty, D. J., Huin, N., Taylor, R. I., & Reid, K. (1998). Seasonal occurrence and diet of leopard seals (*Hydrurga leptonyx*) at Bird Island, South Georgia. *Antarctic Science*, 10(1), 75–81.
- Wege, M., de Bruyn, P. J. N., Hindell, M. A., Lea, M. A., & Bester, M. N. (2019). Preferred, small-scale foraging areas of two Southern Ocean fur seal species are not determined by habitat characteristics. *BMC Ecology*, 19, 36. <https://doi.org/10.1186/s12898-019-0252-x>
- Wright, M. N., & Ziegler, A. (2017). {ranger}: A fast implementation of random forests for high dimensional data in {C++} and {R}. *Journal of Statistical Software*, 77(1), 1–17. <https://doi.org/10.18637/jss.v077.i01>
- Yaremchuk, M., Nechaev, D., Schröter, J., & Fahrback, E. (1998). A dynamically consistent analysis of circulation and transports in the southwestern Weddell Sea. *Annales Geophysicae - Atmospheres, Hydrospheres and Space Sciences*, 16, 1024–1038. <https://doi.org/10.1007/s00585-998-1024-7>
- Zhao, L., Castellini, M. A., Mau, T. L., & Trumble, S. J. (2004). Trophic interactions of Antarctic seals as determined by stable isotope signatures. *Polar Biology*, 27(6), 368–373. <https://doi.org/10.1007/s00300-004-0598-0>

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Author contributions: MLR conceived and designed the research, and acted as the expert voter. MW and LS did the analyses. MW wrote the manuscript with contributions from all other authors.

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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