Habitat- based density models of pack-ice seal distribution in the southern Weddell Sea, Antarctica

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ABSTRACT: Climate variability and changes in sea ice dynamics have caused several ice-obligate or krill-dependent populations of marine predators to decline, eliciting concern about their demographic persistence and the indirect ecological consequences that predator depletions may have on marine ecosystems. Pack-ice seals are dominant ice-obligate predators in the Antarctic marine ecosystem, but there is considerable uncertainty about their abundance and population trends. We modelled the density and distribution of pack-ice seals as a function of environmental covariates in the southern Weddell Sea, Antarctica. Our density surface modelling approach used data from aerial surveys of pack-ice seals collected in the 2013/14 austral summer. Crabeater seals *Lobodon carcinophaga*, the most numerous pack-ice seal we observed, occurred at the highest densities in areas with extensive sea ice near the continental shelf break, but were almost absent in areas of similar sea ice concentration in the southern extent of the Weddell Sea. The highest densities of Weddell seals *Leptonychotes weddelli*, which were less abundant than crabeater seals within the pack ice habitat, were predicted to occur over the continental shelf, near the shelf break. The

distribution of both seal species broadly corresponded with the distribution and relative abundance of their main prey (Antarctic krill *Euphausia superba* and Antarctic silverfish *Pleuragramma antarctica*) obtained from concurrent ecosystem surveys. Ross seals *Ommatophoca rossii* and leopard seals *Hydrurga leptonyx* were not detected at all and are apparently rare within the southern Weddell Sea. These results can contribute to biodiversity assessments in the context of marine protected area planning in this region of the Southern Ocean.

1. INTRODUCTION

The seasonal advance and retreat of Antarctic sea ice is one of the defining features of the physical environment of the Southern Ocean, one of the largest and most productive marine ecosystems on earth (Constable et al. 2003). The area covered by sea ice varies seasonally from a minimum of about 3 million km^2 in February to a maximum of about 19 million km^2 in September (Simmonds et al. 2005). Sea ice plays a pivotal role in the Southern Ocean ecosystem: productivity of ice algae and the phenology of Antarctic krill Euphausia superba, a species that sustains millions of marine predators and a commercial fishery, are integrally linked to sea ice (Deppeler & Davidson 2017). Sea-ice associated seals and seabirds not only prey on abundant under-ice meso- and macrozooplankton and fish communities, but also use sea ice as a platform for resting, breeding and moulting (Ainley et al. 2003). As a result, the population dynamics of these predators may be particularly vulnerable to changes in the extent, duration and seasonality of sea ice (Siniff et al. 2008, Hückstädt et al. 2020).

Four seal species in the family Phocidae have circumpolar distributions in the sea ice habitat surrounding the Antarctic continent. These pack-ice seals (crabeater seal *Lobodon carcinophaga*, Weddell seal *Leptonychotes weddelli*, leopard seal Hydrurga leptonyx and Ross seal Ommatophoca rossii) breed on ice and are therefore especially sensitive to biological and physical variations in the sea ice environment (Siniff et al. 2008). Two other seal species, the southern elephant seal Mirounga leonina and Antarctic fur seal Arctocephalus gazella, also forage within pack ice habitats (Bornemann et al. 2000, Tosh et al. 2009), but these seals almost exclusively breed on ice-free islands (Bester et al. 2017). Crabeater seals are by far the most abundant of the pack-ice seals, but even regional population abundance estimates are highly uncertain (Southwell et al. 2012). In fact, apart from a few long-term study colonies such as the Erebus Bay Weddell seal population in the Ross Sea (Rotella et al. 2009), the population sizes and demographic trends of all 4 pack-ice seal species remain extremely poorly known. Although we have limited understanding of even the most basic population parameters, there is little doubt that pack-ice seals have far-reaching impacts on the Southern Ocean ecosystem structure, functioning and resilience through top-down control of prey abundance and biomass. For example, regional estimates of

population size and bioenergetics models for crabeater seals inhabiting the Weddell–Scotia confluence zone of the Southern Ocean suggest that these seals eat more Antarctic krill than is taken by the krill fishery, or consumed by the great whales and populations of other krill-dependent predators such as penguins (Forcada et al. 2012).

Crabeater seals are specialist krill predators and the only pack-ice seal species to feed almost exclusively on krill (Hückstädt et al. 2012). However, krill also makes up the largest proportion of the diet of leopard seals, especially in winter (Krause et al. 2020). Long-term climate-driven declines of Southern Ocean krill stocks (Atkinson et al. 2004, 2019) are therefore predicted to have negative effects on the population dynamics of crabeater and leopard seals in particular. Weddell seals, which primarily inhabit coastal fast ice rather than pack ice, prey mostly on fish species such as Antarctic silverfish Pleuragramma antarctica, Trematomus spp. and other notothens including commercially harvested Antarctic toothfish Dissostichus mawsoni (Plötz et al. 2001, Goetz et al. 2017). Mid- to deep-water squid and fish appear to be the primary prey of Ross seals, the least abundant Antarctic pack-ice seal species (Brault et al. 2019).

In this paper, we develop spatially explicit habitat models to estimate the density and distribution of pack-ice seals in the southern Weddell Sea, Antarctica. The marine predator guild of this remote ecosystem, one of the most ecologically intact ecosystems worldwide (Halpern et al. 2008), is poorly studied relative to many other sectors of the Southern Ocean. Our analysis is based on aerial surveys of pack-ice seals performed in November 2013 and January to February 2014 that centred round the Filchner Trough (Fig. 1). We used these survey data and density surface models (Miller et al. 2013) to map pack-ice seal density and distribution in relation to multiple spatially explicit physical environmental variables. Additionally, we used pack-ice seal prey species data obtained from concurrent ecosystem surveys to explore the correlation between model-predicted pack-ice seal densities and measures of prey abundance. This study contributes novel results about the distribution and abundance of pack-ice seals and their prey in the area of the Filchner Trough that can contribute to biodiversity assessments in the context of marine protected area planning in this region of the Southern Ocean (Teschke et al. 2020).

2. MATERIALS AND METHODS

2.1. Survey region

The Weddell Sea is a deep embayment that, together with the Ross Sea, comprises the southernmost open ocean areas on earth. Heavy sea ice conditions typically occur year-round in the southern Weddell Sea, and the average summer sea ice concentration in this region has increased in recent decades (Turner et al. 2020). In the southern Weddell Sea, the continental shelf extends some 500 km north of the Filchner-Ronne Ice Shelf. The continental shelf, with seabed depths of 300–500 m, is intersected by the Filchner Trough, a deep glacial trough that extends from the ice shelf cavity to the shelf break (Fig. 1). Large volumes of dense Ice Shelf Water (ISW) formed below the Filchner-Ronne Ice Shelf via ocean–ice shelf interaction exit

the continental shelf via the Filchner Sill (Foldvik et al. 2004). Here, ISW interacts with Warm Deep Water (WDW), a derivative of Circumpolar Deep Water, flowing westward at mid-depth (500–1000 m) along the continental slope as part of the Weddell Gyre (Fahrbach et al. 1992). The continental shelves upstream of the Filchner Trough are governed by cold and fresh water masses, resulting in a density gradient across the continental shelf break, called the Antarctic Slope Front (ASF), which is associated with a strong westward flow (Fahrbach et al. 1992). Shelf break fronts such as the ASF can be important habitat areas for Antarctic marine predators (Bost et al. 2009 and references therein). In the southern Weddell Sea, upwelling of nutrient-rich WDW along the continental shelf break slopes and on-shelf transport of WDW across the ASF (Ryan et al. 2017) may increase local biological productivity, inducing prey and predator concentrations.

2.2. Survey methods

2.2.1. Digital strip transect survey

The fixed-wing research aircraft 'Polar6' (Alfred-Wegener-Institut Helmholtz-Zentrum für Polar- und Meeresforschung 2016) conducted a digital strip transect survey across the Filchner Sill, continental shelf break and shelf break slope on 15 and 16 November 2013. This period corresponds with the late breeding season of crabeater and Weddell seals (Southwell et al. 2003, Rotella et al. 2016). The survey comprised 11 parallel transects (separated by 37 km) perpendicular to the 1000 m shelf break bathymetric contour (Fig. 1). Transect length summed to a total distance of 1448.45 km, with individual transects measuring 131.68 ± 9.63 km in length (mean ± SD). A 21.1 megapixel single-lens reflex digital camera with a 36 × 24 mm full-frame sensor and 14 mm, f 2.8 lens was mounted in the belly port of the aircraft. Images were continuously recorded and successive photographs overlapped to cover the entire length of these transects. At a target flight altitude of 200 m, this configuration produced a strip-width of 171 m. Because the mean flight altitude varied somewhat between transects (194–221 m), we calculated strip-width separately for each transect (166–189 m).

Strip transect sampling assumes that all objects in the covered strip are detected (Buckland et al. 2015). In our case, this means always detecting a seal when present in an image. Three trained observers independently examined all images on high-definition LCD screens and noted the presence or absence of seals in each image. Though none of the observers had perfect detection probability, the overall probability of detection when combining observer data approached unity (i.e. all seals were detected; see Text S1 in Supplement 1, all Supplements are available at www.int-res.com/articles/suppl/m123p456_supp.pdf). Seals within 2 body lengths of each other were assumed to occur as a group. All seals in an image were counted and the geographic coordinates of the image tagged in a GIS layer. Images were not of sufficient resolution to classify seals to species level and therefore the digital survey results refer to pack-ice seals in a generic sense.

2.2.2. Visual line transect survey

Visual line transect surveys were conducted from a Bölkow Blohm helicopter deployed from RV 'Polarstern' in January and February 2014 (Knust & Schröder 2014, Alfred-Wegener-Institut Helmholtz-Zentrum für Polar- und Meeresforschung 2017). Visual surveys therefore coincided with the moult of pack-ice seals (Southwell 2005). The survey area again included the Filchner Sill and continental shelf break region but also extended to the southernmost eastern shelf region of the Filchner Trough. The realised survey design comprised 20 transect lines flown on 12 d from 13 January to 9 February 2014. Each transect was traversed once, flying at 111 km h–1 (60 knots) and 61 m (200 ft) altitude. Six transects (totalling 425.54 km) orientated perpendicular to the coast crossed the Filchner Trough in the southern extent of the study area. Fourteen transects (totalling 1270.12 km) spaced at 18.5 km intervals and positioned perpendicular to the 1000 m continental shelf break bathymetric contour sampled the sea ice habitat in the vicinity of the Filchner Sill. Ideally, there should not have been a gap in survey coverage between the northern and southern transect clusters (Fig. 1), but logistical constraints (ship position, ice cover, helicopter range limits and inclement weather) prevented implementation of a survey design with equal coverage throughout the whole region. When estimating animal densities with line transect sampling, well-designed surveys with sufficient spatial spread and representative coverage with regard to habitat are always preferable. While the model-based (cf. design-based methods) abundance estimation approach we used does not hinge on the formal randomisation and uniform coverage sampling assumptions required by conventional design-based line transect methods (Hedley & Buckland 2004, Miller et al. 2013), the gap in survey coverage is undesirable, as it means that we lack direct empirical data from this connecting geographic area.

Portside and starboard observers independently searched for seals hauled out on ice or swimming at the water surface, and identified seals sighted to species level. Each observer counted seals through sighting bars (aligned markers on the windows of the helicopter) that enabled observations to be grouped into non-overlapping 'bins' based on the perpendicular distance from the transect line (Buckland et al. 2015). Observers counted seals in 6 bins placed at 10° angles from the horizon (0°) to 60°. During analysis, we accounted for the obscured area directly below the helicopter by left-truncation. Observers used digital voice recorders to log count data; this ensured uninterrupted search effort. Continuous recording of GPS positions allowed spatial referencing of all observations. Seals within 2 body lengths of each other were assumed to occur as a group. One observer visually assessed sea ice structure to control for its possible effect on probability of detection. Sea ice structure was scored as: even (relatively flat surface, little or no structure that could make it difficult to spot a seal); undulating (ice with some structure [e.g. pressure ridges] that could conceal hauled out seals); and upheaved (large areas of ice with major structure [e.g. many multi-year pressure ridges]). All flights were flown between 11:00 and 16:00 h local apparent time to coincide survey effort with the maximum proportion of seals hauled out on the ice (Southwell 2005, Boehme et al. 2016).

2.3. Spatial modelling of density

We fitted density surface models (DSMs; Hedley & Buckland 2004, Miller et al. 2013) to both the digital strip transect survey and visual line transect survey data. Density surface modelling uses a 2-stage approach to estimate spatially explicit density or abundance. A detection function is first fitted to the observed count data to account for a decline in detectability at larger distances. Subsequently, generalized additive models (GAMs) (Wood 2006) and spatially referenced covariates are used to predict density or abundance across an area of interest.

2.3.1. Fitting a detection function

For the visual surveys, the distribution of sightings within distance bins was used to estimate the probability that a seal in the covered region was detected. The strip directly beneath the aircraft and the bin that extended to the horizon were excluded from analysis (truncated at perpendicular distances of 35 and 345 m, respectively). We assumed that all seals within the immediate vicinity of the track line were detected (i.e. $g(0) = 1$). Half-normal and hazard-rate detection functions were fitted via maximum likelihood to describe the decrease in detection probability with distance from the observer. Covariates that affected the scale parameter of the detection probability function were also included (Buckland et al. 2015). Observer (left/right), group size (range 1 to 6, fitted as a factor with 2 levels [1, ≥2] or as a continuous covariate), seal species, visibility (below standard/good, subjectively judged by observers) and ice structure (even/undulating/upheaved) were included as covariates. Akaike's information criterion (AIC) was used to select among candidate detection functions. A chi-squared goodness of fit test was used to verify the fit of the most parsimonious detection function which was subsequently used for DSMs. Detection functions were fitted using the package 'Distance' (Miller 2017, Miller et al. 2019) in R 3.6.3 (R Core Team 2020). A detection function was not required for the digital strip transect survey.

2.3.2. Accounting for availability bias

Seals are not always available (i.e. hauled out on ice or swimming at the water surface) to be counted. Because a proportion of the population is always diving and unavailable for detection, counts of seals sighted had to be appropriately inflated to account for this availability bias. Since we only detected seals hauled out on ice (and none swimming), we used the time spent in and out of the water by satellite tagged crabeater and Weddell seals (Southwell 2005, Bengtson et al. 2011, Forcada et al. 2012) to correct on-ice abundance estimates. These studies showed that the probability of being hauled out consistently peaked around 0.7 in the hours on either side of local mid-day (Figs. S1–S4 in Supplement 2), when most of our surveys were conducted. Our analysis thus assumed that 70% of seals were available for detection during both the digital and visual surveys. To evaluate the sensitivity of model outputs to this haulout factor, our final DSMs were refitted using availability parameters that varied from 0.5 up to 0.9 (e.g. Winiarski et al. 2013).

2.3.3. Density surface model specification and selection

GAMs were used to describe the relationship between environmental covariates and seal abundance. We split the visual survey transect lines into contiguous segments of length l_j (median $l_j = 6.04$ km, mean $l_j = 6.06$ km, range $l_j = 2.28$–7.42 km), and estimated the abundance per segment ($\hat{N}_j$) using the estimates of average detection probability obtained from the detection function in a Horvitz Thompson-like estimator (Borchers & Burnham 2004, Miller et al. 2019). The digital strip transect survey was similarly divided into contiguous segments (median $l_j = 10.01$ km, mean $l_j = 10.04$ km, range $l_j = 9.60$–10.40 km). Seeing that we did not have a detection function with covariates in the digital survey, we used the number of seals counted (N_j) in each segment (rather than the Horvitz Thompson-like estimated abundance) as the response. Both $\hat{N}_j$ and N_j were skewed by a high proportion of zeros. We considered negative binomial and Tweedie distributions with a log link function between the linear predictor and the mean as possible response distributions. The most appropriate response distribution was selected by visual inspection of QQ- and randomised quantile residual plots, and by comparing model AIC scores.

We fitted DSMs to the digital survey data, and separately for crabeater seal and Weddell seal observations obtained from visual surveys. We used Duchon splines, a generalisation of thin plate splines that reduces edge effects (i.e. inflated predictions far away from the observed data) as the basis for the models' smooth terms (Miller & Wood 2014). To avoid fitting excessively complex models, we set an upper limit of 5 degrees of freedom for splines and used restricted maximum likelihood as the smoothness selection method (Marra & Wood 2011). Several pairs of environmental covariates were highly collinear (Spearman rank correlation coefficients >0.7 or <–0.7; Dormann et al. 2013); these covariates were fitted in separate DSMs. We used a double penalty approach (Marra & Wood 2011) to carry out variable selection in each model fitted. Smoothing penalties included a small shrinkage component so that the smooth term could automatically be eliminated from the full model (i.e. the effective degrees of freedom [edf] could decrease to near zero; Marra & Wood 2011). Covariates that made no contribution to the model were thus penalized away altogether during model fitting. DSMs were fitted using the package 'dsm' (Miller et al. 2017) in R 3.6.3 (R Core Team 2020).

2.3.4. Predicting density and uncertainty analysis

Information on animal densities beyond surveyed areas are often needed for management and conservation actions, but extrapolations to conditions outside the range of those encountered in surveys can easily lead to unreasonable results (Mannocci et al. 2015, Sequeira et al. 2018). We therefore conducted a quantitative assessment of extrapolation to limit our model predictions to areas of multivariate environmental space (cf. geographic extrapolation) that was informed by reference (survey) data (Figs. S5–S10 in Supplement 3). Specifically, our prediction grid was delineated using 2 metrics of extrapolation obtained via the R package 'dsmextra': the extrapolation detection (ExDet) tool and the percentage of data

nearby (%N) (Bouchet et al. 2020). The ExDet tool (Mesgaran et al. 2014) uses Euclidean and Mahalanobis distances to distinguish interpolation (predictions in unsampled geographic space that are within the range of sampled environmental space) from predictions that require univariate or combinatorial extrapolation (Bouchet et al. 2020). We limited our prediction area to cells where environmental conditions were within the sampled range of the covariate data and avoided both univariate and combinatorial extrapolation. The percentage of data nearby (%N) metric quantified the amount of reference (survey) data lying within a radius of 1 geometric mean Gower's distance of any prediction cell that were available to inform model predictions (King & Zeng 2007, García-Barón et al. 2019, Bouchet et al. 2020). As such, %N provided a quantitative measure of the proportion of reference data lying within the 'neighbourhood' of any prediction cell; we expect that predictions will be more reliable in the proximity of a larger amount of sample data, and less reliable where predictions occur in sparsely sampled regions, even when interpolating within the sampled environmental space (Mannocci et al. 2018, Bouchet et al. 2020). We focussed our DSM inference on areas that were informed by at least 10% reference data (%N ≥ 10%) in the neighbourhood of prediction cells. Predictions in areas where %N was between 0 and 10% (%N > 0%) are more speculative and are highlighted in the density maps to appropriately caution the reader (e.g. Fifield et al. 2017, Mannocci et al. 2017).

Inference was based on the DSMs with the lowest AIC values (Burnham & Anderson 2002). We used a 12.5 × 12.5 km spatially referenced grid (Antarctic Polar Stereographic Projection, EPSG:3031) with boundaries for model predictions demarcated by the extrapolation analysis described above. Each grid cell therefore had a 156.25 km2 area. Uncertainty in density estimates was calculated using the 'dsm.var.gam' function in the R package 'dsm' (Miller et al. 2017), which assumes independence between the detection function and the spatial GAM, and combined the uncertainty estimates from the 2 model stages via the Delta method to obtain an estimate of the overall variance (Miller et al. 2013). We could not propagate uncertainty from the detection function to the spatial model (e.g. Williams et al. 2011) because 'observer' was included in the selected detection function (Miller et al. 2013). The variance predictions were plotted over the study area as the coefficient of variation (CV).

2.3.5. Environmental covariates used in modelling

We used environmental covariates related to bathymetry and sea ice to model the habitat of pack-ice seals. The mid-point of each transect segment was used to extract values for environmental covariates. For dynamic covariates, we matched the segment's survey date to the nearest available environmental data in space and time (the prediction grid contained the mean environmental conditions observed across surveys). We extracted bathymetry data (at an original resolution of 0.05°) from the General Bathymetric Chart of the Oceans (British Oceanographic Data Centre; www.gebco.net) using the 'raster' package (Hijmans 2016) in R and calculated depth (m), bottom slope (°), distance to the shelf break (defined as the 1000 m bathymetry contour at the continental shelf edge) (km) and distance to the nearest coast (km) from these data. Sea ice concentration (%) and distance to the nearest ice edge (defined as the 15% sea ice concentration contour) (km) were derived from National Snow and Ice Data

Center sea ice data (Cavalieri et al. 1996; https://nsidc.org/data/nsidc-0051) at a grid cell size of 25×25 km. The ice edge covariate thus represents the distance to partially covered open water areas, including those at the borders of large coastal polynyas, a key foraging habitat for several Antarctic marine predators (Labrousse et al. 2018, Michelot et al. 2020). We used the proportion of time that a grid cell was covered by pack ice of concentration 85% or higher over a 7 yr period (January 2003 to December 2010) as a proxy of multiyear consistency in sea ice concentration ('long-term sea ice cover'; https://data.aad.gov.au/metadata/records/Polar_Environmental_Data). We include additional information (Text S4) and maps of environmental covariates (Figs. S11 & S12) in Supplement 4.

2.3.6. Predator–prey spatial correlations

Physical environmental covariates may influence marine predators directly, but these covariates are often used to model marine predator habitat use under the assumption that they indirectly impact predators through modifying the distribution, abundance or composition of their prey (Reisinger et al. 2018). Physical covariates are typically required as proxies of biological productivity as detailed surveys of prey abundance and distribution are rarely available, especially for wide-ranging Southern Ocean marine predators. Scientific bottom trawl catches of fish and multiple-opening rectangular midwater trawl (M-RMT) hauls for macrozooplankton were made from RV 'Polarstern' in January and February 2014, potentially providing data on the spatial distribution, species composition and biomass of demersal and pelagic fish fauna and macrozooplankton that overlap in time and space with the visual line transect surveys for pack-ice seals (see Knust & Schröder 2014 and Text S5, Supplement 5, for methodological details). Unfortunately, logistical constraints prevented a grid-like sampling scheme, and too few stations were sampled to estimate fish or macrozooplankton (specifically Euphausia krill species) distribution and abundance within the entire study area through model-based interpolation (e.g. Herr et al. 2016). Consequently, data on fish (Pleuragramma antarctica and Trematomus spp.) and Euphausia spp. distribution and relative abundance collected in January and February 2014 were not included as spatially explicit covariates in the DSMs. Instead, we extracted pack-ice seal densities (as predicted by visual survey DSMs fitted with physical environmental covariates) at the prey sampling points, and examined the relationship between our model predictions and the prey field using linear regression models.

3. RESULTS

3.1. Digital strip transect survey

A total of 221 seals hauled out on ice were photographed in the digital survey. Observations were mostly of individual animals (n = 102) and pairs (n = 45), with few larger groups (up to 5 seals) recorded. The mean group size was 1.42. Seals were present in 86 of 144 (60%) segments used to fit DSMs. We fitted 6 DSMs, with each model including different combinations of environmental covariates (Table S1 in Supplement 6). QQ- and

randomised quantile residual plots indicated good fit of all models, with AIC scores being lower for models with a Tweedie distribution (Fig. S13 in Supplement 6). The model with the lowest AIC value explained 24.80% of the deviance (Table 1). Double penalty variable selection indicated that long-term sea ice cover (the fraction of time that a grid cell had ice concentration ≥85% over several years) was the strongest predictor of seal density. The highest densities of seals occurred in areas with consistently high sea ice concentration (see Figs. 2 & 3). Depth was reduced to a near-linear term (edf < 1), while ice concentration at the time of the surveys and distance to the continental shelf was penalized to a zero effect (edf approaches 0) (Table 1). However, sea ice concentration varied little across the study area during the November survey, with compact to close pack ice (where sea ice concentration >90%) occurring throughout all but the easternmost section of the study area (Fig. S11 in Supplement 4 and Fig. S14 in Supplement 7). The model predicted low seal densities in this easternmost section, i.e. where sea ice concentration was lowest during the study period and over the long term (Fig. 2). The predicted abundance estimate of 39939 seals (95% confidence interval 33582–47500 seals) over a prediction area of 57031 km2 corresponds to a mean density of 0.70 seals km^{-2}.

3.2. Visual line transect survey

We detected a total of 759 seals during helicopter surveys. Crabeater seals were most frequently encountered (n = 593 seals), while Weddell seals (n = 166) occurred in comparatively low numbers in the pack ice. Other Antarctic seal species (e.g. leopard seals, Ross seals) were not sighted at all (in or out of transect). Again, the majority of detections (n = 495, or 81%) were of solitary seals, with groups of up to 6 seals accounting for the remainder of detections. The mean group size was 1.24. A hazard-rate detection function with observer as factor covariate was selected by AIC as an appropriate detection function (Table S2 and Fig. S15 in Supplement 8). The average probability of detection was estimated as 0.57 (CV = 0.04), and a chi-squared goodness of fit test showed that the detection function fitted the data well ($\chi_1^2 = 0.02$, p = 0.88).

The 20 survey transects were divided into 281 segments; of these segments, 196 (70%) contained one or more seals. Crabeater seals were detected in 167 segments and Weddell seals in 87 segments. However, only a single crabeater seal was encountered in the southern extent of the study area, i.e. on 426 km of transects surveyed deep in the Filchner Trough. Spearman correlation coefficients again showed collinearity between some environmental covariates, prompting us to fit 3 DSMs with different covariate combinations (Tables S3 & S4 in Supplement 9). DSMs with Tweedie distributions were selected for both seal species. Deviance residuals indicated some overdispersion in the Weddell seal data, but the overall model fit was acceptable (Figs. S16 & S17 in Supplement 9).

For crabeater seals, distance to the shelf break, distance to the coast and long-term sea ice cover (proportion time with ice concentration >85%) were retained as important non-linear terms in the model with the lowest AIC value (deviance explained = 44.92%) (Table 1, Fig. 3). Depth and bottom slope were penalized out of the model. Models that included the covariates distance to the ice edge and ice concentration at the time of the surveys were less

parsimonious (ΔAIC > 8). We also considered a north vs. south stratification of the study area with a categorical 'habitat' variable fitted in DSMs, but this did not improve parsimony of the spatial model. The AIC-selected model predicted extremely low densities of crabeater seals (mean = 0.02 seals km^{-2}) in the southernmost extent of the study area, with higher densities along the shelf break, on either side of the Filchner Sill (Fig. 2). The average density of crabeater seals across the northern prediction area (45781 km2) was 1.60 seals km^{-2}, and the total estimated abundance in this region was 71876 seals (95% CI: 60388–85551).

Most of the seals encountered along the 6 transects deep in the southern Weddell Sea were Weddell seals, but their predicted densities were lower than those of crabeater seals nearer to the Filchner Sill and shelf break (Fig. 2). Weddell seals were predicted to occur at an average density of 0.55 seals km^{-2} in the northern prediction area (25267 [19724–32368] individuals), and at an average density of 0.21 seals km^{-2} in the southern prediction area (4271 [2649–6884] individuals). These estimates are based on the most parsimonious Weddell seal DSM (deviance explained = 18.7%; Table 1) that retained distance to the shelf break, long-term sea ice cover and bottom slope as significant covariates. Weddell seal densities were predicted to be low on the steep slopes of the continental shelf break (over deeper water) and declined with distance from the shelf break (Fig. 3). Higher densities were predicted to occur over the continental shelf (at depths of 400–500 m) near the shelf break (Fig. 2).

3.3. Predator–prey spatial correlations

Both predator and prey species occurred at higher densities near the shelf break than deep in the Filchner Trough. Macrozooplankton biomass and fish catches made from RV 'Polarstern' at the same time as the visual pack-ice seal surveys were clearly lower in the southern section of the Filchner Trough than along the continental shelf break (Fig. 4). Antarctic krill Euphausia superba were well represented in catches near the Filchner Sill and shelf break, but almost entirely absent in the south where ice krill E. crystallorophias represented the most abundant euphausiid taxa (Fig. 4A). Antarctic silverfish Pleuragramma antarctica, the main prey of Weddell seals (Plötz 1986), were also more abundant near the continental shelf break, especially on the eastern shelf. Both silverfish and Trematomus spp. were almost absent from stations sampled deep in the Filchner Trough (Fig. 4B). The DSM-predicted density of pack-ice seals extracted at prey sampling stations did not correlate significantly with prey density or biomass (Fig. 5). Nonetheless, the predicted density of crabeater seals and that of Antarctic krill, their main prey species, was weakly positively correlated, whereas the densities of both seal species showed weak positive correlation with the biomass of Antarctic silverfish.

4. DISCUSSION

In this study, we provide habitat-based density estimates of pack-ice seals in the Filchner Trough area situated in the south-eastern limit of the Weddell Sea. Little dedicated pack-ice seal survey effort had previously been allocated to this area of the deep Weddell Sea.

Despite tremendous circumpolar effort, even the multinational Antarctic Pack Ice Seals (APIS) survey program that was initiated in the late 1990s extrapolated pack-ice seal densities to our study area, based on surveys conducted elsewhere in the Weddell Sea (Forcada et al. 2012, Southwell et al. 2012). Our study therefore contributes new information on pack-ice seal densities in this region of the Southern Ocean that can inform ecosystem models, spatial planning and marine conservation efforts.

The most striking feature of our results is the low density of pack-ice seals, and crabeater seals in particular, in the southern extent of the Weddell Sea. Previous studies of crabeater seal foraging behaviour indicate that they avoid consolidated pack ice (where sea ice concentration is 100%), but that they are not excluded from areas of high (90%) ice cover (Ribic et al. 1991, Burns et al. 2004). Indeed, our results showed that crabeater seals occurred at the highest densities (2–3 ind. km–2) in areas with extensive (>80%) sea ice near the continental shelf break, but not in areas of similar sea ice concentration deep in the Weddell Sea (see Fig. S12 in Supplement 4). The crabeater seal density estimates we obtained near the continental shelf break are comparable to those previously estimated for the eastern Weddell Sea (Gurarie et al. 2017), western Weddell Sea (Flores et al. 2008, Forcada et al. 2012), east Antarctica (Southwell et al. 2008a) and the Amundsen and Ross Seas (Bengtson et al. 2011). In the Amundsen and Ross Seas, crabeater seals occur primarily in the outer pack ice and in pack ice habitats near the continental shelf; the highest densities (0.85 seals km–2) were found in areas of 50–90% ice concentration (Bengtson et al. 2011). Unusually high (but also very localised) densities of crabeater seals have previously been observed near the coastline in the eastern Weddell Sea, but these estimates were obtained in an anomalous El Niño year with almost no summer pack ice, which led to high concentrations of seals confined to small areas of pack ice (Bester & Odendaal 2000, Gurarie et al. 2017). The highest regional densities of crabeater seals in the Southern Ocean are probably found in the West Antarctic Peninsula, where sea ice cover has significantly declined since 1979 (Forcada et al. 2012).

Weddell seals were not abundant in the pack ice, though they were more common than crabeater seals in the southern extent of the Weddell Sea. However, it is important to emphasise that our results pertain solely to the pack ice habitat. Aerial surveys did not include fast ice habitat adjacent to the continent, where Weddell seals are known to breed and moult along tidal cracks. Our Weddell seal densities are therefore only comparable to other areas of pack ice. In East Antarctica, the density of Weddell seals in fast ice habitats (0.46 seals km–2) markedly exceeds that in the sea ice (0.08 seals km–2) (Bengtson et al. 2011). This trend is likely to hold true in the southern Weddell Sea, as approximately 200 Weddell seals were counted opportunistically on a reconnaissance flight over a relatively small area of coastal fast ice near 78° S in January 2014 (W. C. Oosthuizen & H. Bornemann pers. obs.). Weddell seals are also known to haul out elsewhere along the Luitpold Coast (Bester et al. 2018), such as at coastal fast-ice covered inlets at the Brunt Ice Shelf (near 75° S) (Nachtsheim et al. 2019). It is possible that many of the Weddell seals encountered in the pack ice were younger, non-reproductive adults. Such individuals may disperse extensively, from the Filchner-Ronne Ice Shelf to the Weddell Gyre off the continental shelf, without ever hauling out on coastal fast ice (Boehme et al. 2016, Langley et al. 2018, Nachtsheim et al. 2019). In contrast, Weddell

seals of breeding age often forage within the pack ice, but return to the fast ice to haul out, even outside of breeding periods (Nachtsheim et al. 2019). Ross seals and leopard seals were not detected during surveys, or opportunistically from ship or air. Ross seals are apparently absent from the inner reaches of the Weddell Sea (south of about 73° S) in summer (Bester et al. 2020). Even though cryptic behaviour may lead to false absences (Southwell et al. 2008b), it is probable that leopard seals are also uncommon in this region.

Crabeater and Weddell seals showed varied relationships with environmental covariates, but densities of both species tended to decrease with distance from the shelf break. The fraction of time that a grid cell had ice concentration >85% (over several years) appeared to be a better predictor of seal density than ice concentration measured at the time of the study period, perhaps because it better represented sea ice structure (e.g. thickness and surface structure [even, undulating or upheaved]). For example, although sea ice concentration varied little during the November digital survey, images nonetheless showed that the easternmost section of the study area, where seals were predicted to be least common, had lower ice thickness than elsewhere. Ice thickness is one of several characteristics of sea ice, including ice concentration, floe size and age (e.g. new ice or multiyear ice). Crabeater seal densities have previously been related to ice thickness (McMahon et al. 2002, Flores et al. 2008), and it is possible that seals avoided the easternmost section of the study area in November because the comparatively thin ice was unsuitable for haul out during the breeding season.

Optimal foraging theory (Pyke 1984) predicts that predators should modify their movement behaviour in relation to the availability and spatial distribution of prey. Thus, in environments where resources are heterogeneously distributed, we expect marine predators to associate with areas of enhanced productivity, or areas where physical–biological interactions lead to an accumulation of prey organisms. Concurrent surveys of macrozooplankton, fish and pack-ice seal communities suggest that the haul out distribution of pack-ice seals broadly reflects patterns of prey distribution within the southern Weddell Sea. The relative abundance of meso- and macrozooplankton in the southern Filchner Trough was lower than along the eastern Weddell Sea shelf break, at approximately 75° S. Antarctic krill occurred along the shelf break, but was scarce in the southern part of the study area. Ice krill occurred only in lower abundances in the Filchner Trough than further north along the eastern shelf break. Crabeater seal distribution thus broadly overlapped with that of its main prey species, Antarctic krill. Within the southern Filchner Trough, the zooplankton community was dominated by copepods (Calanus propinquus, Calanoides acutus, Metridia gerlachei, Paraeuchaeta antarctica) and the pteropods Limacina spp. at the time of our surveys (Auel et al. 2014). These species do not contribute significantly to the diets of pack-ice seals. At most of the stations sampled in January to February 2014 (Fig. 4), zooplankton was also still in a very early stage of seasonal succession, probably because of high concentrations of sea ice. For example, many C. acutus females had not started feeding yet, and only one copepod female in an experimental series covering 9 stations actually produced eggs (Auel et al. 2014). These results suggest that productivity and zooplankton biomass were low in the southern Filchner Trough during the time of the study. This conclusion is supported by earlier work showing lower abundance of meso- and macrozooplankton in the epipelagic zone of the

southern Weddell Sea compared to the north-eastern continental shelf (Boysen-Ennen & Piatkowski 1988).

Weddell seals and several other Antarctic marine predators prey extensively on Antarctic silverfish, the most abundant fish species inhabiting the high Antarctic continental shelf ecosystem (Plötz 1986, La Mesa et al. 2004). The results of the fish surveys (Fig. 4) made from RV 'Polarstern' at the same time as the visual pack-ice seal surveys indicate a higher biomass of silverfish, as well as demersal notothens such as Trematomus spp., near the eastern shelf break. Some of the highest densities of Weddell seals predicted by the DSM (Fig. 2) also occurred in this general area, especially where silverfish biomass was high (Fig. 5). As for zooplankton, the biomass and abundance of both demersal and pelagic fishes were substantially lower in the very south. Bathymetric features such as shelf breaks and seamounts often constitute important foraging habitats for pelagic vertebrates (Bost et al. 2009, Bouchet et al. 2015). The south-eastern Weddell Sea continental shelf break is a region of energetic turbulent mixing, due to strong tidal flow over the complex topography, while the shelf farther south is more quiescent (Fer et al. 2016). Turbulence is created by the downwelling and mixture of cold, dense ISW with relatively warm WDW at the sill of the Filchner Trough. This turbulence and the upwelling of nutrient-rich WDW may increase productivity at the continental shelf break (Boehme et al. 2016), resulting in a richer food supply for marine predators.

Given that detailed surveys of prey abundance and distribution are rarely available for wide-ranging marine predators, physical environmental covariates are commonly used as surrogates of variation in productivity and prey resources when modelling the spatial distribution of such predators (Reisinger et al. 2018). Our DSM approach thus relied exclusively on using physical environmental covariates, assumed to be proxies of prey distribution, to model seal density. We acknowledge the limitations of this approach. Basic environmental metrics do not fully capture the complexity of landscapes and prey fields on their own (Hobday & Hartog 2014). As a result, not all spatial variation was captured by the DSMs since some covariates that are important predictors of seal density and distribution were missing (because they were unknown or unmeasured). DSM predictions into unsurveyed areas should therefore be interpreted cognisant of the uncertainties underlying model projections. In an effort to achieve reliable predictions for unsampled space, we avoided extrapolation beyond the range of sampled covariates used to build the DSMs and limited predictions to areas informed by a larger amount of sample data. Even so, the geographic gap in survey coverage between the northern and southern transect clusters means that part of the range of environmental covariates such as 'distance to shelf break' was not sampled, which increases the uncertainty of the transferability of our model projections. Despite these challenges, our estimates of pack-ice seal density and distribution in the southern Weddell Sea are the first to be informed by local data (and not extrapolations from surveys conducted elsewhere in Antarctica) and thus contribute new information about the marine predator guild in this region of the Southern Ocean.

We conducted our surveys around midday, when variation in haulout behaviour between seals is low (Southwell 2005; Figs. S1–S4 in Supplement 2). Nonetheless, estimates

of availability are another source of uncertainty inherent to distance sampling surveys of marine mammals. In the present study, the mean abundance estimates obtained when 60 or 80% availability were assumed, fell within the 95% confidence limits of abundance we report (i.e., when 70% availability was assumed) (Fig. S18 in Supplement 10).

Bias in predator–prey spatial correlations may also arise if the true distributions of the predator or prey fields were not fully captured by DSMs and relatively sparse prey sampling. Another possible sampling caveat is that in ice-covered waters, the bulk of the Antarctic krill population resides at the ice–water interface, where it cannot be reached by pelagic nets, but may be easily targeted by seals (Marschall 1988, Flores et al. 2012). Therefore, the true spatial distribution or relative abundance of Antarctic krill prey available to seals may have been somewhat different from the distribution patterns derived from our M-RMT catches. The relationship we drew between DSM-predicted seal density and measures of prey abundance are thus subject to model uncertainty and potential sampling biases, and should be considered with due caution.

Density maps (i.e. spatially explicit abundance estimates) of marine predators are integral to systematic conservation planning (Hammond et al. 2013), including the development of marine protected areas (Williams et al. 2014). Here we provide novel information on pack-ice seal densities in the deep Weddell Sea that can inform ecosystem models, spatial planning and marine conservation efforts. A potential caveat relevant to conservation management is that our surveys only provide snapshots of pack-ice seal distribution and abundance. In temporally variable systems, patterns of occupancy or abundance may fluctuate in response to many factors, and we must be cautious when extrapolating the findings of this short-term study to longer temporal scales. Our result of higher densities of seals along the shelf break than deeper in the Filchner Trough is, however, supported by longer-term satellite telemetry data from Weddell seals (Boehme et al. 2016, Langley et al. 2018, Photopoulou et al. 2020). These authors studied the at-sea distribution of adult Weddell seals during multiple seasons by deploying satellite telemetry devices on seals hauled out on both sides of the Filchner Trough. Their results clearly show that Weddell seals (males in particular) tracked from February to June mostly foraged and hauled out near the continental shelf break. We are not aware of any satellite telemetry work on crabeater seals conducted in the immediate vicinity of the Filchner Trough that can corroborate our survey data for this species. However, some crabeater seals equipped with satellite transmitters at the Drescher Inlet in the eastern Weddell Sea (72.85° S, 19.26° E) foraged along and to the north of the Weddell Gyre continental shelf break, but did not show area-restricted behaviour south of the shelf break (Nachtsheim et al. 2017). Elsewhere in Antarctica, crabeater seals also mostly forage along the edges of continental shelf breaks (Southwell et al. 2005, Wall et al. 2007, Bengtson et al. 2011). However, projections suggest that crabeater seal foraging distributions may change in future in response to ongoing environmental change (Hückstädt et al. 2020).

Worldwide declines of marine predators such as sharks, seabirds and marine mammals elicit concern about their demographic persistence and the indirect ecological consequences (e.g. cascading effects) that predator depletions may have on marine ecosystems (Heithaus et

al. 2008). Consistent with global trends, many Southern Ocean marine predator populations have decreased in abundance in recent decades, possibly due to changes in environmental conditions. For example, increasing climate variability since 1990 has led to frequent reductions in Antarctic krill availability in the Scotia Sea, causing a decline in the krill-dependent Antarctic fur seal population at South Georgia (Forcada et al. 2008). High variability in annual sea ice extent also influences the population trends of the ice-obligate emperor penguin Aptenodytes forsteri, with several colonies having decreased or declined to extinction in recent years (Jenouvrier et al. 2012). We currently do not have sufficient data to judge whether Southern Ocean pack-ice seal populations may have experienced similar declines. Pack-ice seals are dominant predators in the Antarctic marine ecosystem, but there is still considerable uncertainty about their abundance and population trends in space and time (Southwell et al. 2012). Among the pack-ice seals, crabeater seals are especially important in the krill-based food web of the Southern Ocean, and the paucity of reliable spatially integrated abundance estimates for this species in particular complicates conservation and fisheries management in the Southern Ocean.

This study contributes novel results about the distribution and abundance of pack-ice seals from a previously undersampled area. Still, our results about the pack-ice seal community of the southern Weddell Sea stem from a small sample of the target population and limited spatial coverage across part of the survey region. Validation of our model predictions will be an important step when more data become available. Reliable data on pack-ice seal density and distribution are currently still scarce or non-existent for large parts of Antarctica, but the limitations of ship- and helicopter-based surveys may in future be resolved by conducting surveys using unmanned aerial vehicles (Colefax et al. 2018) or counting pack-ice seals on high-resolution satellite images (LaRue et al. 2011, Wege et al. 2020). While remote sensing is a promising tool to better monitor these predators, it does not currently yield as detailed information as traditional visual surveys made from ship or manned aircraft as it is still difficult to reliably detect or distinguish species from remote sensing platforms. Nonetheless, further advances in remote sensing platforms and automated image processing (Gonçalves et al. 2020) will make regional and Southern Ocean-wide spatiotemporal monitoring of pack-ice seal population trends possible.

Data availability. All data and related meta-information are available via the Data Publisher for Earth & Environmental Science PANGAEA (www.pangaea.de; Bester et al. 2015).

LITERATURE CITED

Ainley DG, Tynan CT, Stirling I (2003) Sea Ice: a critical habitat for polar marine mammals and birds. In: Thomas DN, Dieckmann G (eds) Sea Ice - an introduction to its physics, chemistry, biology and geology. Blackwell Publishing, Oxford, UK, p 240 – 266

Alfred-Wegener-Institut Helmholtz-Zentrum für Polar- und Meeresforschung (2016) Polar aircraft Polar5 and Polar6 operated by the Alfred Wegener Institute. Journal of large-scale research facilities 2:A87

Alfred-Wegener-Institut Helmholtz-Zentrum für Polar- und Meeresforschung (2017) Polar Research and Supply Vessel POLARSTERN Operated by the Alfred-Wegener-Institute. Journal of large-scale research facilities 3:A119

Atkinson A, Siegel V, Pakhomov E, Rothery P (2004) Long-term decline in krill stock and increase in salps within the Southern Ocean. Nature 432:100-103

Atkinson A, Hill SL, Pakhomov EA, Siegel V and others (2019) Krill (*Euphausia superba*) distribution contracts southward during rapid regional warming. Nat Clim Change 9:142–147

Auel H, Dürschlag J, Janssen D, Ksionzek K and others (2014) Biological and biogeochemical processes in sea ice and the pelagic realm. In: Knust R, Schröder M (eds) The expedition PS82 of the Research Vessel Polarstern to the southern Weddell Sea in 2013/2014. Berichte zur Polar- und Meeresforschung 680:52-60

Bengtson JL, Laake JL, Boveng PL, Cameron MF and others (2011) Distribution, density, and abundance of pack ice seals in the Amundsen and Ross Seas, Antarctica. Deep-Sea Res II 58:1261-1276

Bester MN, Odendaal PN (2000) Abundance and distribution of Antarctic pack ice seals in the Weddell Sea. In: Davison W, Howard-Williams C, Broady P (eds) Antarctic Ecosystems: Models for Wider Ecological Understanding. Caxton Press, Christchurch, New Zealand, p 51-55

Bester MN, Oosthuizen WC, Bornemann H (2015) SEAFOS seal census survey at Filchner Outflow System during campaign FIL2014. Alfred Wegener Institute, Helmholtz Centre

for Polar and Marine Research, Bremerhaven, PANGAEA, https://doi.org/10.1594/PANGAEA.855259

Bester MN, Bornemann H, McIntyre T (2017) Antarctic marine mammals and sea ice. In: Thomas DN (ed) Sea Ice (3rd Edition). John Wiley and Sons Ltd, Oxford, UK, p 534 – 555

Bester MN, Wege M, Bornemann H (2018) Foraging ecology of Ross seals in the south-western Weddell Sea. In: Schröder M (ed) The Expedition PS111 of the Research POLARSTERN to the southern Weddell Sea in 2018. Berichte zur Polar- und Meeresforschung 718:63-74

Bester MN, Wege M, Oosthuizen WC, Bornemann H (2020) Ross seal distribution in the Weddell Sea: fact and fallacy. Polar Biol 43:35-41

Boehme L, Baker A, Fedak M, Årthun M and others (2016) Bimodal winter haul-out patterns of adult Weddell seals (*Leptonychotes weddellii*) in the southern Weddell Sea. PLOS ONE 11:e0155817

Borchers, DL, Burnham KP (2004) General formulation for distance sampling. In: Buckland ST, Anderson DR, Burnham KP, Laake JL, Borchers DL, Thomas L (eds) Advanced Distance Sampling. Oxford University Press, Oxford, UK, p 6-30

Bornemann H, Kreyscher M, Ramdohr S, Martin T and others (2000) Southern elephant seal movements and Antarctic sea ice. Antarct Sci 12:3-15

Bost CA, Cotté C, Bailleul F, Cherel Y and others (2009) The importance of oceanographic fronts to marine birds and mammals of the southern oceans. J Mar Syst 78:363–376

Bouchet PJ, Meeuwig JJ, Salgado Kent CP, Letessier TB, Jenner CK (2015) Topographic determinants of mobile vertebrate predator hotspots: Current knowledge and future directions. Biol Rev 90:699-728

Bouchet PJ, Miller DL, Roberts JJ, Mannocci L and others (2020) dsmextra: Extrapolation assessment tools for density surface models. Methods Ecol Evol 11: 1464–1469

Boysen-Ennen E, Piatkowski U (1988) Meso- and macrozooplankton communities in the Weddell Sea, Antarctica. Polar Biol 9:17-35

Brault EK, Koch PL, Costa DP, McCarthy MD and others (2019) Trophic position and foraging ecology of Ross, Weddell, and crabeater seals revealed by compound-specific isotope analysis. Mar Ecol Prog Ser 611:1-18

Buckland ST, Rexstad EA, Marques TA, Oedekoven CS (2015) Distance Sampling: methods and applications. Springer International Publishing, Switzerland

Burnham KP, Anderson DR (2002) Model selection and multimodel inference. A practical information theoretic approach. Second edition. Springer-Verlag, New York, New York, USA

Burns JM, Costa DP, Fedak MA, Hindell MA and others (2004) Winter habitat use and foraging behavior of crabeater seals along the Western Antarctic Peninsula. Deep-Sea Res II 51:2279–2303

Cavalieri DJ, Parkinson CL, Gloersen P, Zwally HJ (1996, updated yearly) Sea Ice Concentrations from Nimbus-7 SMMR and DMSP SSM/I-SSMIS Passive Microwave Data, Version 1. Boulder, Colorado USA. NASA National Snow and Ice Data Center Distributed Active Archive Center. https://doi.org/10.5067/8GQ8LZQVL0VL

Colefax AP, Butcher PA, Kelaher BP (2018) The potential for unmanned aerial vehicles (UAVs) to conduct marine fauna surveys in place of manned aircraft. ICES J Mar Sci 75: 1-8

Constable AJ, Nicol S, Strutton PG (2003) Southern Ocean productivity in relation to spatial and temporal variation in the physical environment. J Geophys Res 108:8079-9000

Deppeler SL, Davidson AT (2017) Southern Ocean phytoplankton in a changing climate. Front Mar Sci 4:40

Dormann CF, Elith J, Bacher S, Buchmann C and others (2013) Collinearity: a review of methods to deal with it and a simulation study evaluating their performance. Ecography 36:27–46

Fahrbach E, Rohardt G, Krause G (1992) The Antarctic coastal current in the southeastern Weddell Sea. Polar Biol 12:171-182

Fer I, Darelius E, Daae, KB (2016) Observations of energetic turbulence on the Weddell Sea continental slope. Geophys Res Lett 43:760-766

Fifield DA, Hedd A, Avery-Gomm S, Robertson GJ and others (2017) Employing predictive spatial models to inform conservation planning for seabirds in the Labrador Sea. Front Mar Sci 4:149

Flores H, Haas C, van Franeker JA, 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 Res II 55:1068–1074

Flores H, van Franeker JA, Siegel V, Haraldsson M and others (2012) The association of Antarctic krill *Euphausia superba* with the under-ice habitat. PLOS One 7:e31775

Foldvik A, Gammelsrød T, Østerhus S, Fahrbach E and others (2004) Ice shelf water overflow and bottom water formation in the southern Weddell Sea. J Geophys Res 109:C02015

Forcada J, Trathan PN, Murphy EJ (2008) Life history buffering in Antarctic mammals and birds against changing patterns of climate and environmental variation. Glob Change Biol 14:2473-2488

Forcada J, Trathan PN, Boveng PL, Boyd IL and others (2012) Responses of Antarctic pack ice seals to environmental change and increasing krill fishing. Biol Conserv 149:40-50

García-Barón I, Authier M, Caballero A, Vázquez JA and others (2019) Modelling the spatial abundance of a migratory predator: a call for transboundary marine protected areas. Divers Distrib 25:346–360

Goetz KT, Burns JM, Hückstädt LA, Shero MR, Costa DP (2017) Temporal variation in isotopic composition and diet of Weddell seals in the western Ross Sea. Deep-Sea Res II 140:36–44

Gonçalves BC, Spitzbart B, Lynch HJ (2020) SealNet: A fully-automated pack ice seal detection pipeline for sub-meter satellite imagery. Remote Sens Environ 239:111617

Gurarie E, Bengtson JL, Bester MN, Blix AS and others (2017) Distribution, density and abundance of Antarctic ice seals off Queen Maud Land and the eastern Weddell Sea. Polar Biol 40:1149-1165

Halpern BS, Walbridge S, Selkoe KA, Kappel CV and others (2008) A global map of human impact on marine ecosystems. Science 319:948-952

Hammond PS, Macleod K, Berggren P, Borchers DL and others (2013) Cetacean abundance and distribution in European Atlantic shelf waters to inform conservation and management. Biol Conserv 164:107–122

Hedley SL, Buckland ST (2004) Spatial models for line transect sampling. J Agric Biol Environ Stat 9:181-199

Heithaus MR, Frid A, Wirsing AJ, Worm B (2008) Predicting ecological consequences of marine top predator declines. Trends Ecol Evol 23:202-210

Herr H, Viquerat S, Siegel V, Kock K-H and others (2016) Horizontal niche partitioning of humpback and fin whales around the West Antarctic Peninsula: evidence from a concurrent whale and krill survey. Polar Biol 39:799–818

Hijmans RJ (2016) raster: Geographic data analysis and modeling. R package version 2.5-8. Retrieved from https://CRAN.R-project.org/package=raster

Hobday AJ, Hartog JR (2014) Derived ocean features for dynamic ocean management. Oceanography 27:134-145

Hückstädt LA, Burns JM, Koch PL, McDonald BI and others (2012) Diet of a specialist in a changing environment: the crabeater seal along the western Antarctic Peninsula. Mar Ecol Prog Ser 455:287-301

Hückstädt LA, Piñones A, Palacios DM, McDonald BI and others (2020) Projected shifts in the foraging habitat of crabeater seals along the Antarctic Peninsula. Nat Clim Change 10:472-477

Jenouvrier S, Holland M, Stroeve J, Barbraud C and others (2012) Effects of climate change on an emperor penguin population: analysis of coupled demographic and climate models. Glob Change Biol 18:2756-2770

King G, Zeng L (2007) When can history be our guide? The pitfalls of counterfactual inference. Int Stud Q 51: 183-210

Knust R, Schröder M (2014) The expedition PS82 of the Research Vessel Polarstern to the southern Weddell Sea in 2013/14. Berichte zur Polar- und Meeresforschung 680: 1-155

Krause DJ, Goebel ME, Kurle CM (2020) Leopard seal diets in a rapidly warming polar region vary by year, season, sex, and body size. BMC Ecol 20:32

La Mesa M, Eastman JT, Vacchi M (2004) The role of notothenioid fish in the food web of the Ross Sea shelf waters: a review. Polar Biol 27:321-338

Labrousse S, Williams G, Tamura T, Bestley S and others (2018) Coastal polynyas: winter oases for subadult southern elephant seals in East Antarctica. Sci Rep 8: 3183

Langley I, Fedak M, Nicholls K, Boehme L (2018) Sex-related differences in the postmolt distribution of Weddell seals (*Leptonychotes weddellii*) in the southern Weddell Sea. Mar Mam Sci 34:403–419

LaRue MA, Rotella JJ, Garrott RA, Siniff DB and others (2011) Satellite imagery can be used to detect variation in abundance of Weddell seals (*Leptonychotes weddellii*) in Erebus Bay, Antarctica. Polar Biol 34:1727-1737

Mannocci L, Monestiez P, Spitz J, Ridoux V (2015) Extrapolating cetacean densities beyond surveyed regions: Habitat-based predictions in the circumtropical belt. J Biogeogr 42:1267– 1280

Mannocci L, Roberts JJ, Miller DL, Halpin PN (2017) Extrapolating cetacean densities to quantitatively assess human impacts on populations in the high seas. Conserv Biol 31: 601-614

Mannocci L, Roberts, JJ, Halpin PN, Authier M and others (2018) Assessing cetacean surveys throughout the Mediterranean Sea: a gap analysis in environmental space. Sci Rep 8: 3126

Marra G, Wood SN (2011) Practical variable selection for generalized additive models. Comput Stat Data Anal 55:2372-2387

Marschall HP (1988) The overwintering strategy of Antarctic krill under the pack-ice of the Weddell Sea. Polar Biol 9:129-135

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

Mesgaran MB, Cousens RD, Webber BL (2014) Here be dragons: A tool for quantifying novelty due to covariate range and correlation change when projecting species distribution models. Divers Distrib 20: 1147-1159

Michelot C, Kato A, Raclot T, Shiomi K and others (2020) Sea-ice edge is more important than closer open water access for foraging Adélie penguins: evidence from two colonies. Mar Ecol Prog Ser 640:215–230

Miller DL, Burt ML, Rexstad EA, Thomas L (2013) Spatial models for distance sampling data: recent developments and future directions. Methods Ecol Evol 4:1001–1010

Miller DL (2017) Distance: distance sampling detection function and abundance estimation. R package version 0.9.7. https://CRAN.R-project.org/package=Distance

Miller DL, Wood SN (2014) Finite area smoothing with generalized distance splines. Environ Ecol Stat 21:715–731

Miller DL, Rexstad E, Burt L, Bravington MV, Hedley S (2017) dsm: Density Surface Modelling of distance sampling data. R package version 2.2.15. https://CRAN.R-project.org/package=dsm

Miller DL, Rexstad E, Thomas L, Marshall L, Laake JL (2019) Distance Sampling in R. J Stat Softw 89:1

Nachtsheim D, 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 Biol 40:961-976

Nachtsheim DA, Ryan S, Schröder, M, Jensen L and others (2019) Foraging behaviour of Weddell seals (*Leptonychotes weddellii*) in connection to oceanographic conditions in the southern Weddell Sea. Prog Oceanogr 173:165–179

Photopoulou T, Heerah K, Pohle J, Boehme L (2020) Sex-specific variation in the use of vertical habitat by a resident Antarctic top predator. Proc R Soc Lond B 287:20201447

Plötz J (1986) Summer diet of Weddell seals (*Leptonychotes weddelli*) in the eastern and southern Weddell Sea, Antarctica. Polar Biol 6:97-102

Plötz J, Bornemann H, Knust R, Schröder A, Bester MN (2001) Foraging behaviour of Weddell seals, and its ecological implications. Polar Biol 24:901-909

Pyke GH (1984) Optimal foraging theory: a critical review. Annu Rev Ecol Evol Syst 15:523-575

R Core Team (2020) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org/

Reisinger RR, Raymond B, Hindell MA, Bester MN and others (2018) Habitat modelling of tracking data from multiple marine predators identifies important areas in the Southern Indian Ocean. Divers Distrib 8: 24:535–550

Ribic CA, Ainley DG, Fraser WR (1991) Habitat selection by marine mammals in the marginal ice zone. Antarct Sci 3:181-186

Rotella, JJ, Link WA, Nichols JD, Hadley GL and others (2009) An evaluation of density-dependent and density-independent influences on population growth rates in Weddell seals. Ecology 90:975-984

Rotella JJ, Paterson JT, Garrott RA (2016) Birth dates vary with fixed and dynamic maternal features, offspring sex, and extreme climatic events in a high-latitude marine mammal. Ecol Evol 6:1930-1941

Ryan S, Hattermann T, Darelius E, Schröder M (2017) Seasonal cycle of hydrography on the eastern shelf of the Filchner Trough, Weddell Sea, Antarctica. J Geophys Res Oceans 122:6437-6453

Sequeira AMM, Bouchet PJ, Yates KL, Mengersen K, Caley MJ (2018) Transferring biodiversity models for conservation: opportunities and challenges. Methods Ecol Evol 9: 1250-1264

Simmonds I, Rafter A, Cowan T, Watkins AB, Keay K (2005) Large-scale vertical momentum, kinetic energy and moisture fluxes in the Antarctic sea-ice region. Bound-Layer Meteorol 117:149-177

Siniff DB, Garrott RA, Rotella JJ, Fraser WR, Ainley DG (2008) Projecting the effects of environmental change on Antarctic seals. Antarct Sci 20:425-435

Southwell C (2005) Optimising the timing of visual surveys of crabeater seal abundance: haulout behaviour as a consideration. Wildl Res 32:333–338

Southwell C, Kerry K, Ensor P, Woehler EJ, Rogers T (2003) The timing of pupping by pack ice seals in East Antarctica. Polar Biol 26:648-652

Southwell CJ, Kerry KR, Ensor PH (2005) Predicting the distribution of crabeater seals *Lobodon carcinophaga* off east Antarctica during the breeding season. Mar Ecol Prog Ser 299:297-309

Southwell C, Paxton CGM, Borchers D, Boveng P, de la Mare W (2008a) Taking account of dependent species in management of the Southern Ocean krill fishery: estimating crabeater seal abundance off east Antarctica. J Appl Ecol 45:622–631

Southwell CJ, Paxton CGM, Borchers D, Boveng P and others (2008b) Uncommon or cryptic? Challenges in estimating leopard seal abundance by conventional but state-of-the-art methods. Deep-Sea Res II 55:519-531

Southwell C, Bengtson J, Bester MN, Blix AS and others (2012) A review of data on abundance, trends in abundance, habitat use and diet of ice-breeding seals in the Southern Ocean. CCAMLR Sci 19:49-74

Teschke K, Pehlke H, Siegel V, Bornemann H and others (2020) An integrated compilation of data sources for the development of a marine protected area in the Weddell Sea. Earth Syst Sci Data 12:1003–1023

Tosh CA, Bornemann H, Ramdohr S, Schröder M and others (2009) Adult male southern elephant seals from King George Island utilize the Weddell Sea. Antarct Sci 21: 113-121

Turner J, Guarino MV, Arnatt J, Jena B and others (2020). Recent decrease of summer sea ice in the Weddell Sea, Antarctica. Geophys Res Lett 47:e2020GL087127

Wall SM, Bradshaw CJA, Southwell CJ, Gales NJ, Hindell MA (2007) Crabeater seal diving behaviour in eastern Antarctica. Mar Ecol Prog Ser 337:265-277

Wege M, Salas L, LaRue M (2020) Citizen science and habitat modelling facilitates conservation planning for crabeater seals in the Weddell Sea. Divers Distrib 26: 1291–1304

Williams R, Hedley SL, Branch TA, Bravington MV and others (2011) Chilean blue whales as a case study to illustrate methods to estimate abundance and evaluate conservation status of rare species. Conserv Biol 25: 526-535

Williams R, Grand J, Hooker SK, Buckland ST and others (2014) Prioritizing global marine mammal habitats using density maps in place of range maps. Ecography 37:212-220

Winiarski KJ, Miller DL, Paton PWC, McWilliams SR (2013) Spatially explicit model of wintering common loons: conservation implications. Mar Ecol Prog Ser 492: 273-283

Wood SN (2006) Generalized Additive Models: An introduction with R. Chapman & Hall/CRC, BocaRaton, FL, USA

Table 1. Approximate significance of environmental covariates included in density surface models of pack-ice seals in the southern Weddell Sea, Antarctica. We used a double penalty approach to carry out variable selection in a single step. Thus, model terms with effective degrees of freedom (edf) near 0 (<0.01) have effectively been eliminated from the model. Models with the lowest Akaike's information criterion (AIC) scores are presented (see Table S1 in Supplement 6 and Tables S3 & S4 in Supplement 9 for summary of all models fitted). Abundance was predicted to a prediction grid that did not require univariate or combinatorial extrapolation and that had more than 0% (%N > 0%) or at least 10% (%N ≥ 10%) reference data nearby (Fig. 2)

Model terms	edf	*F*	p
Digital strip transect survey			
s(ice concentration)	<0.01	0.00	0.41
s(time with ice ≥85%)	2.63	6.77	<0.01
s(depth)	0.79	0.77	0.03
s(distance to shelf break)	<0.01	0.00	0.35

Deviance explained: 24.80%

Abundance estimate (%N ≥ 10%): 39939 (95% CI: 33582–47500) over 57031 km2

Abundance estimate (%N > 0%): 54442 (95% CI: 45697–64860) over 81094 km2

Model terms	edf	*F*	p
Visual line transect survey – crabeater seals			
s(time with ice ≥85%)	2.39	2.20	<0.01
s(distance to shelf break)	2.01	6.18	<0.01
s(depth)	<0.01	0.00	0.49
s(bottom slope)	<0.01	0.00	1.00
s(coast)	2.33	3.11	<0.01

Deviance explained: 44.92%

Abundance estimate (%N ≥ 10%): 72323 (95% CI: 60682–86196) over 65625 km^2

Abundance estimate (%N > 0%): 105386 (95% CI: 82312–134927) over 124063 km^2

Model terms	edf	*F*	p
Visual line transect survey – Weddell seals			
s(time with ice ≥85%)	3.48	6.47	<0.01
s(distance to shelf break)	0.96	7.13	<0.01
s(depth)	<0.01	0.00	0.76
s(bottom slope)	1.59	4.16	<0.01
s(coast)	<0.01	0.00	0.45

Deviance explained: 18.70%

Abundance estimate (%N ≥ 10%): 29538 (95% CI: 23143–37700) over 65625 km^2

Abundance estimate (%N > 0%): 54695 (95% CI: 39968–74850) over 124063 km^2
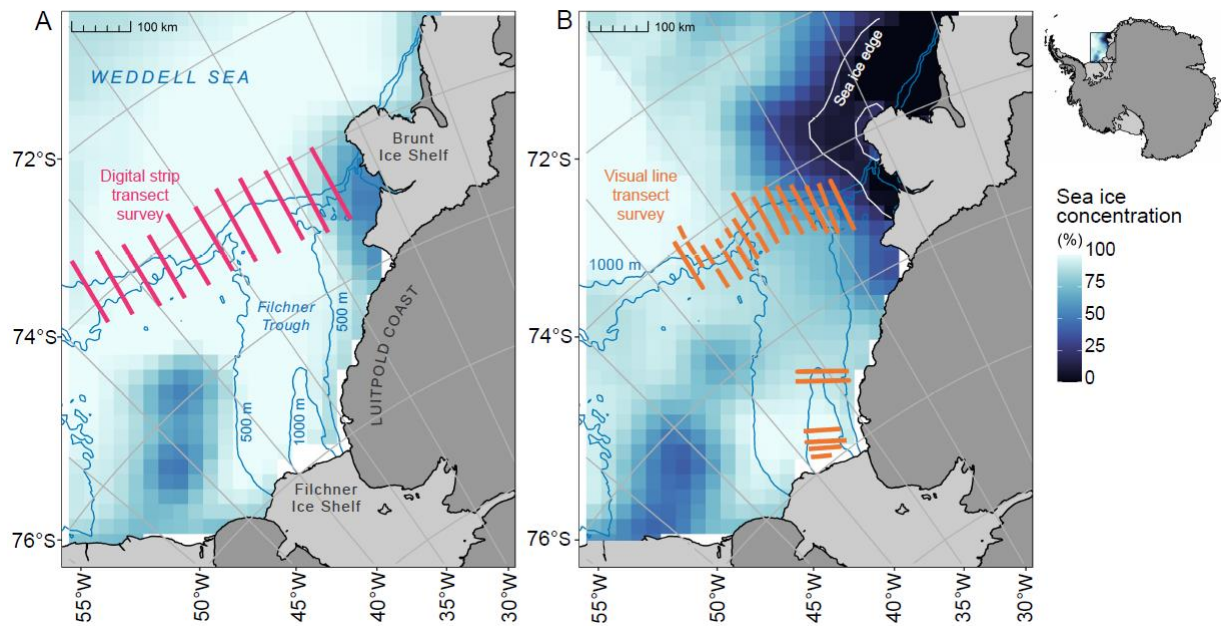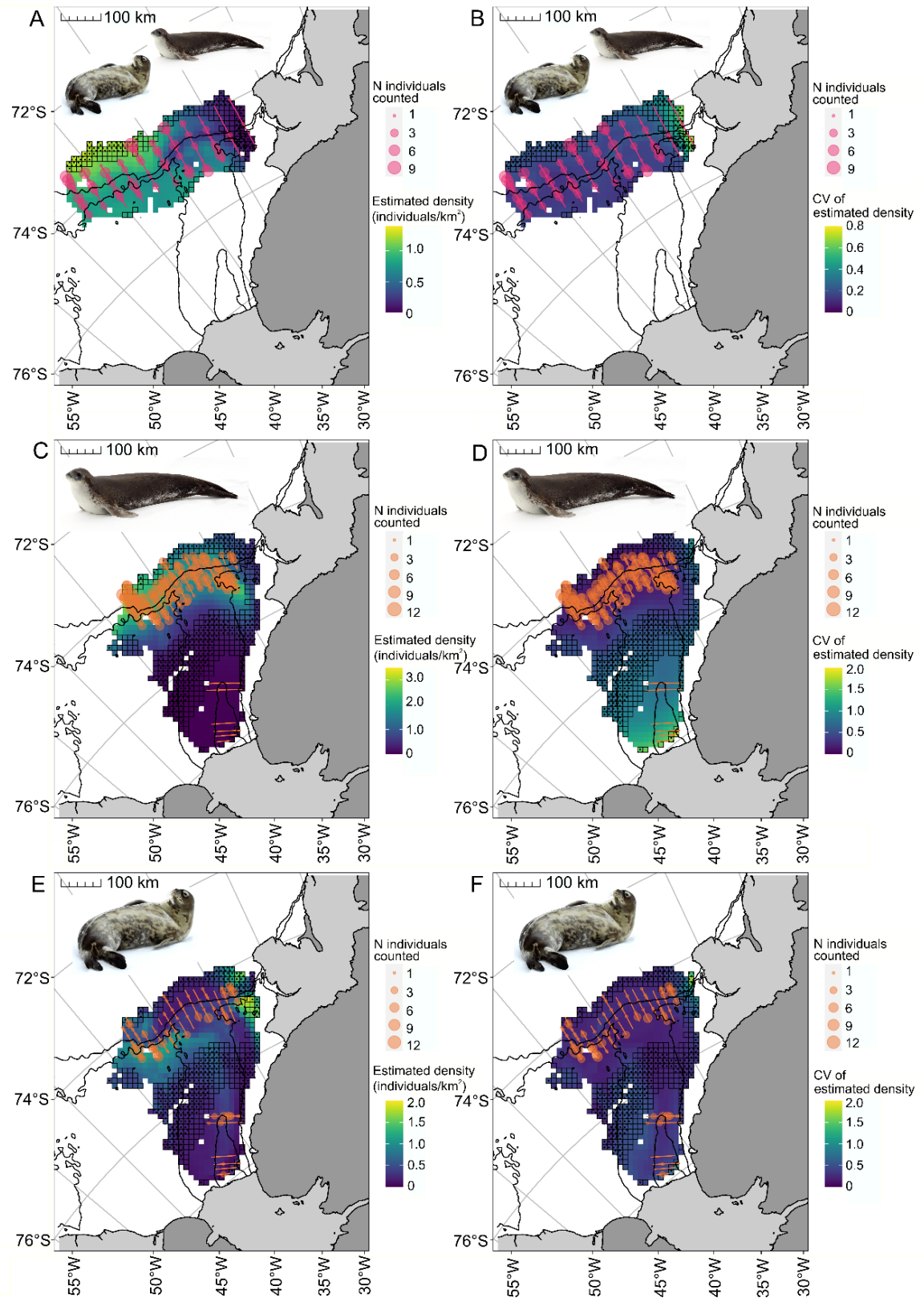
Fig. 1. Study area in the southern Weddell Sea, showing locations of (A) digital strip transect surveys and (B) visual line transect surveys. The background shows sea ice concentration on (A) 15 November 2013 and (B) 27 January 2014. Blue lines indicate 500 and 1000 m bathymetry contours. The inset on the right shows the position of the study area in relation to the Antarctic continent

Fig. 2. Predicted densities and coefficients of variation (CV) of pack-ice seals in the southern Weddell Sea. (A,B) Results from the digital strip transect survey data conducted in November 2013. Also shown are (C,D) crabeater seal and (E,F) Weddell seal densities and CVs estimated from visual line transect survey data collected in January and February 2014. Transect lines and observations are overlaid. The prediction area is limited to cells where environmental conditions were within the sampled range of the covariate data. Prediction cells with black borders have <10% reference data (%N < 10%) in the neighbourhood of that cell; dotted cells have %N < 5%. Predictions in these areas are less reliable and must be interpreted with extreme caution
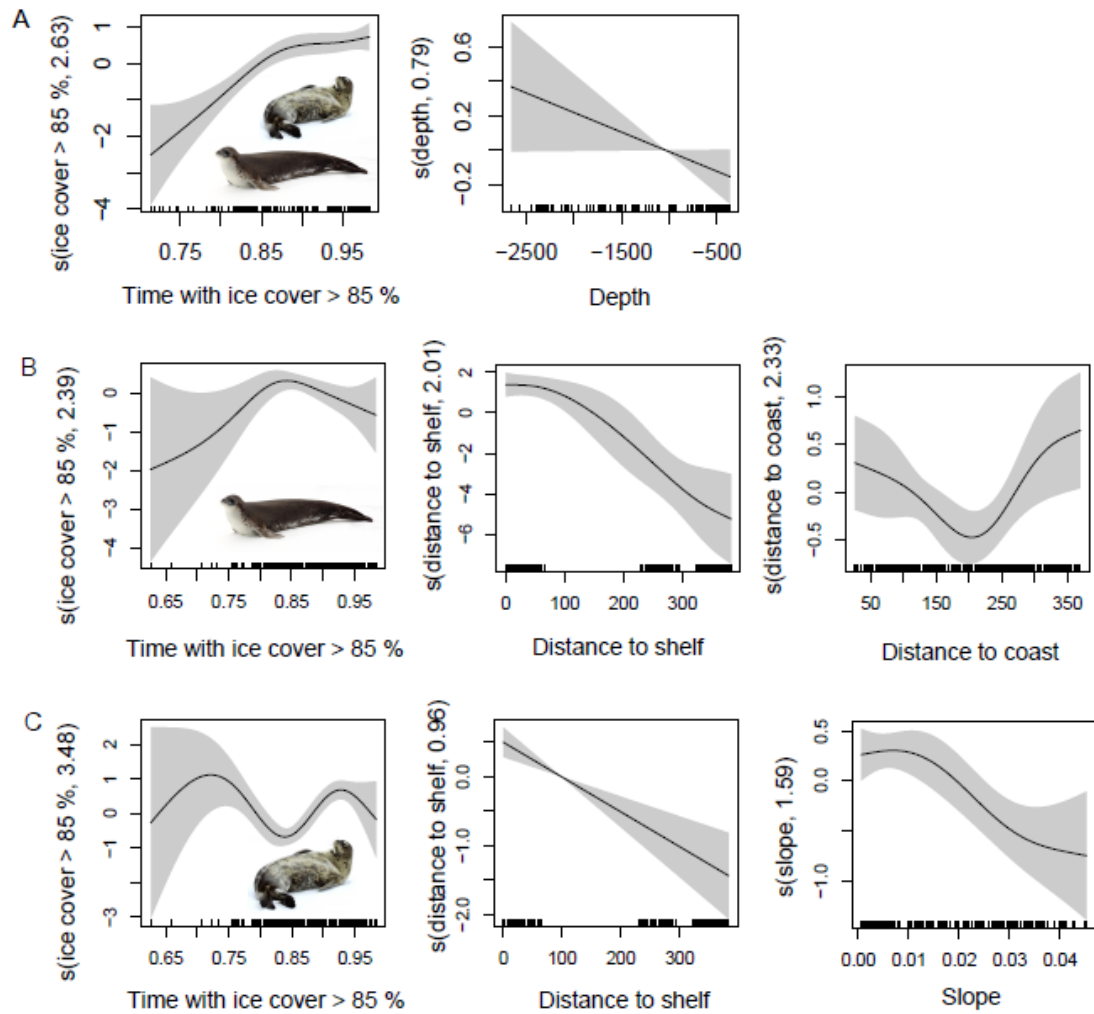
Fig. 3. Generalized additive model smooth functions (solid lines) with 95% confidence intervals (grey shading) for the models with the lowest AIC score in (A) the digital strip transect survey, and in visual line transect surveys for (B) crabeater seals and (C) Weddell seals. The *x*- axes show the environmental covariate values; the *y*- axes represent the contribution of the smooth term (s) to the models (on the scale of the linear predictor). The effective degrees of freedom (edf) for each smooth are indicated in the *y*- axis labels. Smooth terms with edf near 0 are not shown
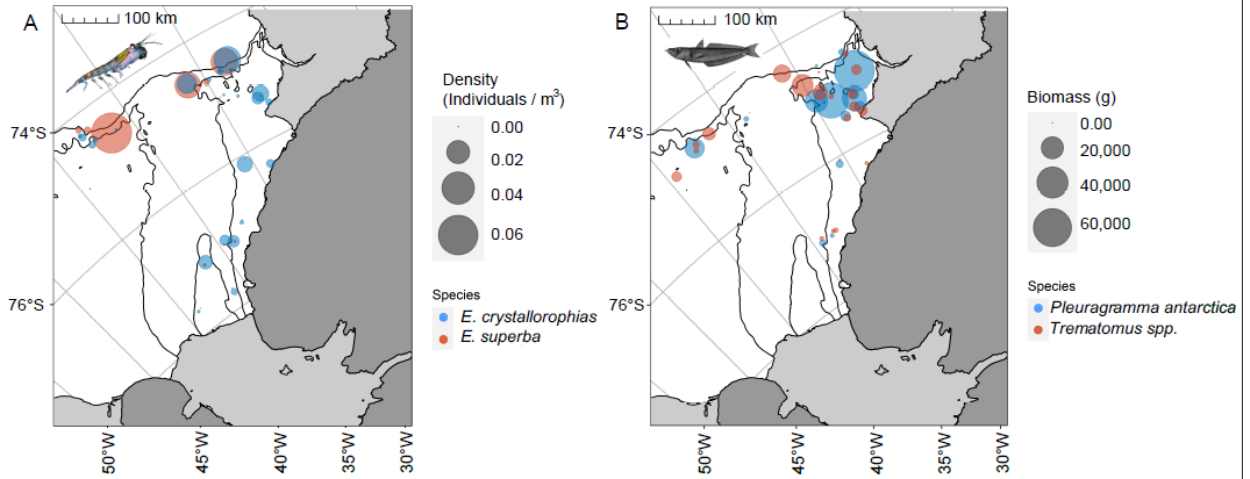
Fig. 4. Relative abundance of pack-ice seal prey species sampled in the southern Weddell Sea during January and February 2014. (A) Density of krill (*Euphausia superba* and *E. crystallorophias*) collected per multiple-opening rectangular midwater trawl haul (n = 22). (B) Biomass of notothen fish (*Pleuragramma antarctica* and *Trematomus* spp.) obtained from scientific bottom trawls (n = 21)
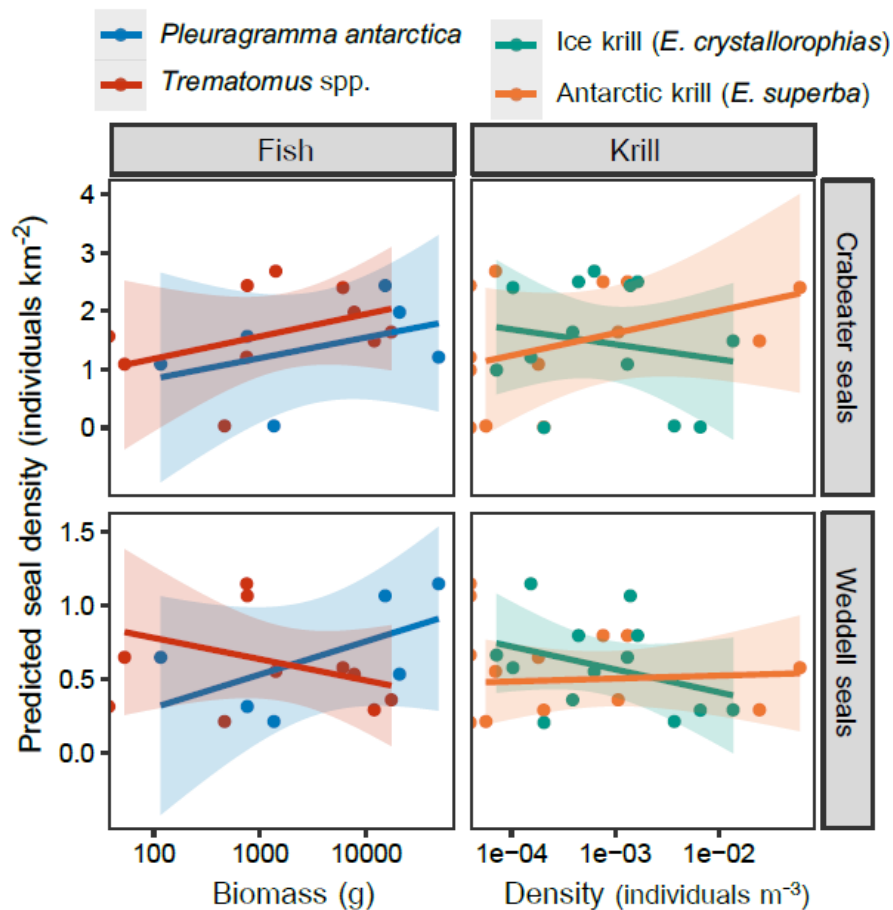
Fig. 5. Density of pack-ice seals (predicted by density surface models) plotted against relative abundance (on the log scale) of pack- ice seal prey species (left panels: notothen fish *Pleuragramma antarctica* and *Trematomus* spp.; right panels: krill *Euphausia superba* and *E. crystallorophias*) sampled in the southern Weddell Sea during January and February 2014. Seal densities were extracted from the prediction grid with ≥ 10% reference data in the neighbourhood (%N ≥ 10%) (see Fig. S19 in Supplement 11 for regressions using all sampled prey data, which required seal densities to be extracted from the prediction grid with %N > 0%). Linear regressions between predicted seal densities and measures of prey abundance are indicated (shaded areas are 95% confidence intervals)