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Important marine habitat off east Antarctica revealed by two decades of multi-species predator tracking

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Satellite telemetry data are a key source of animal distribution information for marine ecosystem management and conservation activities. We used two decades of telemetry data from the East Antarctic sector of the Southern Ocean. Habitat utilization models for the spring/summer period were developed for six highly abundant, wide-ranging meso- and top-predator species: Adélie *Pygoscelis adeliae* and emperor *Aptenodytes forsteri* penguins, light-mantled albatross *Phoebetria palpebrata*, Antarctic fur seals *Arctocephalus gazella*, southern elephant seals *Mirounga leonina*, and Weddell seals *Leptonychotes weddellii*. The regional predictions from these models were combined to identify areas utilized by multiple species, and therefore likely to be of particular ecological significance. These areas were distributed across the longitudinal breadth of the East Antarctic sector, and were characterized by proximity to breeding colonies, both on the Antarctic continent and on subantarctic islands to the north, and by sea-ice dynamics, particularly locations of winter polynyas. These areas of important habitat were also congruent with many of the areas reported to be showing the strongest regional trends in sea ice seasonality. The results emphasize the importance of on-shore and sea-ice processes to Antarctic marine ecosystems. Our study provides ocean-basin-scale predictions of predator habitat utilization, an assessment of contemporary habitat use against which future changes can be assessed, and is of direct relevance to current conservation planning and spatial management efforts.

Quantitative knowledge of the distribution and abundance of marine predators is a cornerstone of our understanding of the structure and function of their ecosystems. Predators are sensitive to environmental changes that affect the distribution and abundance of their prey, and can be studied at a range of temporal and spatial scales. Many aspects of their life history integrate the lower trophic levels of the system. This makes them valuable sentinels of ecosystem change (Reid and Croxall 2001, Durant et al. 2009). Linking the distribution of higher order biota to fundamental bio-physical factors is therefore essential for understanding and predicting the effects of changing climate, as well as for conservation and management (Bost et al. 2009). Species distribution and habitat utilization models play a prominent role in this process and are used extensively to inform fisheries management and by-catch mitigation regimes (Burger and Shaffer 2008). Telemetry studies (i.e. location tracking, using e.g. Argos, GLS, or GPS tags) offer vital information on the spatial distribution and foraging activity of predators (Péron et al. 2012). However, studies to date have generally been conducted on a species-by-species basis and few have been able to consider representative multi-species datasets. Comparing and contrasting the behaviours of multiple species serves to bring an ecosystem-level focus to predator studies (Costa et al. 2010). Areas that are utilized by multiple predator species simultaneously are indicative of characteristics such as high prey abundance and predictability, and may require particular attention in ecosystem modelling, monitoring, and management activities (Block et al. 2011, Hindell et al. 2011). In practice, few studies have the resources to undertake regional-scale, simultaneous tracking deployments on multiple predator species. The largest, most comprehensive example to date is the Tagging of Pacific Predators project (Block et al. 2011), a component of the Census of Marine Life. However, there are a number of regions where multiple studies have occurred over a number of years, often focusing on different species at different times. Integration of data from these studies is currently the only viable alternative for obtaining multi-species inferences in these regions.

The Southern Ocean is home to large populations of higher-order predators, many of which are potentially vulnerable to the effects of climate change (Turner et al. 2013). An extensive portfolio of studies has used telemetry and other data to identify and characterize important Southern Ocean habitats, which include polynyas, fronts, and sea-ice and bathymetric features (Bost et al. 2009, Tynan et al. 2010). However, regional and multi-species syntheses of such information are still needed. Identifying ecologically important areas and their environmental drivers will provide important management information and insights into how this region might respond to predicted environmental changes.

The aim of this study was to bring together existing animal tracking data to identify important areas of marine habitat in the East Antarctic region, which lies in the Indian Ocean sector of the Southern Ocean. Specifically, data from seven predator species were used to develop region-wide, species-specific habitat utilization models. Expert knowledge and previously published research were used to guide the selection of environmental predictor variables. Individual species models were then combined to identify areas of multi-species overlap, which are likely to be areas of particular ecological significance.

Material and methods

We used existing telemetry data collected from the East Antarctic region by Australian and French Antarctic research teams. These data are available from public repositories: the Australian Antarctic Data Centre (<http://data.aad.gov.au/aadc/argos>), the Integrated Marine Observing System (<http://imos.org.au>), ANTABIF (<http://data.biodiversity.aq>), and the BirdLife International Seabird Tracking Database (<http://seabirdtracking.org>). Additional southern elephant seal data from Kerguelen Island, collected as part of the SEaOS (Southern Elephant seals as Oceanographic Samplers) and MEOP (Marine Mammals Exploring the Oceans Pole to Pole) projects, were provided by the Southern Ocean MEMO project (Mammifère marin Echantillonneur du Milieu Océanique; principal investigator C. Guinet). Further details of these data, and references to their studies of origin, are provided in Supplementary material Appendix 1, Table A1. Telemetry data were predominantly captured by Argos-type tags, with GPS-based units deployed on Adélie penguins at Dumont d'Urville. For breeding animals making multiple foraging trips from their colony, tracks were partitioned into individual trips. Argos data were Kalman filtered to account for measurement errors and unequal sampling intervals (Patterson et al. 2010). Positions were interpolated to regular intervals (3, 6, or 12 h depending on species) using a Kalman smoother (Patterson et al. 2010). GPS tracks were speed-filtered and interpolated but without Kalman filtering/smoothing.

Models were constructed for seven species: female Weddell seals *Leptonychotes weddellii*, crabeater seals *Lobodon carcinophagus,* southern elephant seals *Mirounga leonina*, male Antarctic fur seals *Arctocephalus gazella*, light-mantled albatross *Phoebetria palpebrata*, and Adélie *Pygoscelis adeliae* and emperor *Aptenodytes forsteri* penguins. The preferred habitat of each species was identified using a habitat selectivity approach, by modelling the environmental characteristics of the locations where the animals were recorded to be present (utilized habitat) relative to the areas that they could potentially have used (available habitat). Available habitat was estimated by simulating tracks (a similar approach to e.g. Wakefield et al. 2010). For each observed trip by each individual animal, 20 simulated trips were computed from the same deployment location, using a first-order vector autoregressive model. These simulated tracks indicate where the animals could potentially have travelled if they did not have any preferences in terms of environmental conditions, while still respecting the constraints on their trip duration and travel speed.

Environmental conditions $\boldsymbol{w}$ were collated at each point on the observed and simulated tracks, and binomial generalized additive models (GAMs) with logit link were fitted, where the response variable s took the value $s = 1$ if the point was from an observed track, or $s = 0$ for a simulated track. The estimates $\mathrm{p}(s = 1|\boldsymbol{w})$ from this type of model (known as a presence-background or habitat selectivity model) can be interpreted as a description of habitat use relative to availability (Wakefield et al. 2010). They are not direct estimates of the probabilities $\mathrm{p}(q = 1|\boldsymbol{w})$ that the species utilizes habitat $\boldsymbol{w}$, but rather are monotonically related, with the relationship being dependent on the prevalence of the species (Phillips et al. 2009). Direct comparison of $\mathrm{p}(s = 1|\boldsymbol{w})$ between species with differing prevalences is therefore not meaningful. However, the study area can be partitioned into areas of decreasingly important habitat by applying a set of thresholds to the $\mathrm{p}(s = 1|\boldsymbol{w})$ values. This yields a transformed prediction map, wherein each value is a habitat importance percentile by area. The monotonic relationship means that the same results are obtained from $\mathrm{p}(s = 1|\boldsymbol{w})$ as from $\mathrm{p}(q = 1|\boldsymbol{w})$ (see Supplementary material Appendix 1 for details). These percentile values can be compared across species, allowing overlap between different species to be quantified.

For repeated observations of individuals, models with random effects are often used. In this instance, there is no advantage to including a random intercept term, because the intercept simply represents the ratio of the number of observed to simulated points for each individual, which is constant. In the GAM framework, it is possible to include random smooth terms that would allow individual variability in response to environmental covariates (i.e. generalized additive mixed models, or GAMMs; Wood 2006). However, these are computationally demanding and potentially problematic for species with small samples. For consistency across species and computational tractability, regular GAMs were used throughout.

The fitted model for each species was used to predict the habitat preference for that species over the entire region of interest, for each month November–February, then averaged to give an overall summer species prediction. For Adélie penguins, separate models were fitted to the incubation and chick-rearing periods; similarly, for the chick-rearing and pre-moult periods for emperor penguins. A single model was used for each of the remaining species on the basis of relatively consistent at-sea behaviour over the study period.

Environmental predictor variables used in each model were selected from 28 available variables that characterized various aspects of the physical environment. Variables related to physical oceanographic properties (temperature, sea surface height, and water depth) typically act as proxies for discriminating water masses and fronts, which can represent areas of different prey and prey-aggregation (Bost et al. 2009). Sea-ice variables (fast- and sea-ice mean coverage and variability, time since melt, distance to nearest fast- and sea-ice, and distance to nearest polynya location) offer insights into accessibility (lack of open water) as well as ecosystem structure and prey abundance, which is typically elevated near the ice edge (Brierley et al. 2002). Productivity-related variables (chlorophyll-*a* and primary productivity estimates) also relate to prey availability. Benthic characteristics (geomorphology, slope, and seafloor water temperature) are potentially relevant for deep-diving predators such as southern elephant seals and emperor penguins. Transport cost was calculated as the distance from the colony or deployment location, weighted by wind considerations for flying birds or currents for swimming predators (see Supplementary material Appendix 1 for details). This provides information about the accessibility of different geographic areas, particularly for breeding animals with restricted ranges from their colonies. A complete list of predictor variables including details such as their original source and spatial resolution is provided in Supplementary material Appendix 1, Table A3.

Cross-validation was used for model assessment and to guide variable selection. Individual animals were randomly assigned to one of ten data folds (or as many folds as individuals, where the sample included less than ten individuals). Each model was trained on all-but-one folds and tested on the remaining one, withholding each fold in turn. Predictive performance (the area under the receiver operating curve; AUC) was then aggregated across the ten sets of results. Estimates of uncertainty in spatial predictions were calculated using a similar cross-validation method, but additionally including swapping of predictor variables (Supplementary material Appendix 1).

Individual species predictions were combined to quantify overlap. The predator suite here is diverse, and it would not be expected that important ecological areas would necessarily involve every species. For each grid cell in the study region, the top four habitat importance values (i.e. the highest four values from the individual species results for that grid cell) were averaged. Species compositions of the regions of overlap were assessed using UPGMA clustering and multidimensional scaling, with Bray–Curtis dissimilarity index. An independent data set of at-sea observations of seabirds spanning 1980–2006, available from <http://data.aad.gov.au/aadc/wov> (Woehler 1997), was used to corroborate the final results. Briefly, GAMs were used to estimate both the abundance (Poisson, log link) and probability of presence (binomial, logit link) of various species of seabirds as functions of the habitat overlap values. The species included two for which tracking data were analysed (Adélie and emperor penguins) and a number of other high-Antarctic species not represented in the tracking data (specifically, Antarctic petrels *Thalassoica antarctica*, snow petrels *Pagodroma nivea*, south polar skua *Catharacta maccormicki*, southern fulmar *Fulmarus glacialoides*, and Antarctic *Sterna vittata* and Arctic *S. paradisaea* terns). The two tern species were combined due to difficulty of identification at sea. Overlap importance values were also compared with estimates of breeding seabird biomass in 5° longitude sectors (Woehler 1990) using rank correlation.

All analyses were conducted in Matlab 8.1 (Mathworks, Natick MA) and R 2.15 (R Development Core Team).

Results

The input data and models are summarized in Table 1, Supplementary material Appendix 1, Table A1 and A2, and Fig. A1, the predicted habitat importance maps in Fig. 1, and their uncertainties in Supplementary material Appendix 1, Fig. A2. Predictions were made for each month November–February inclusive, then combined to give a single composite spring/summer prediction for each species. The model for crabeater seals did not perform adequately (i.e. area under the receiver operating curve (AUC) not significantly better than 0.5) and so is not presented here nor included in the calculations of species overlap. The AUC values for the other models ranged from 0.615 to 0.949 (Table 1).

Important habitat for Adélie penguins was generally predicted to be close to breeding colonies, and particularly so during the chick-rearing period when the parents must return regularly to provision their chicks. Emperor penguins were similarly constrained during the chick-rearing period, but utilized more distant offshore habitat during the pre-moult period. Light-mantled albatrosses, which foraged in Antarctic waters while rearing chicks on subantarctic Heard and Macquarie islands to the north, utilized open ocean areas south of their colonies, and north of the Antarctic shelf slope. The southern-most extent of this range was coincident with the near-Antarctic easterly wind band. Post-breeding male Antarctic fur seals, also foraging from colonies located on subantarctic islands, showed similar habitat usage to light-mantled albatrosses, but with a range extending further south. Male and female southern elephant seals, which disperse widely from their subantarctic colonies after breeding, concentrated on shallow parts of the Antarctic continental shelf, including areas of winter polynyas. They avoided areas of persistent ice cover, presumably due to lack of breathing/haul-out access, or risk of entrapment. Post-breeding female Weddell seals utilized shallow shelf waters close to both fast ice and winter polynya locations.

The individual species predictions were combined to identify areas of overlap. The results obtained by averaging the top four habitat importance values within each grid cell

Table 1. Summary of data and model results. Known details of breeding status, age, and sex are indicated in parentheses next to the species name. Area under the receiver-operating curve (AUC) values are given as mean (SD); asterisks denote values significantly better than 0.5 ($p < 0.05$; Wilcoxon signed-rank test). Only indicative references to original studies are included here: a full list appears in Supplementary material Appendix 1, Table A1.

Species	N individuals	N trips	N positions	N days	Date range of data	Predictors selected in model	AUC score
Antarctic fur seal (post-breeding sub-adult/adult males) (Gales et al. 2004, updated 2010)	11	11	3559	452	1-Jan–28-Feb	Mean summer chl-*a* Transport cost Distance to polynya	0.952 (0.035)*
Adélie penguin (incubation) (Clarke et al. 2006, Cottin et al. 2012)	47	47	2597	504	24-Nov–29-Dec	Transport cost Sea-ice cover Distance to upper slope	0.743 (0.132)*
Adélie penguin (chick-rearing) (Clarke et al. 2006, Cottin et al. 2012)	100	186	3966	669	22-Dec–16-Feb	Bathymetry Sea-ice summer variability Sea-ice cover Transport cost Distance to upper slope	0.711 (0.122)*
Crabeater seal (Wall et al. 2007)	22	22	6273	795	1-Nov–6-Jan	Mean summer sea surface temperature (SST) Fast ice cover Distance to sea-ice (monthly)	0.535 (0.159)
Emperor penguin (chick-rearing) (Wienecke et al. 2004)	7	10	60	36	5-Dec–13-Dec	Transport cost Fast ice cover	0.810 (0.071)*
Emperor penguin (pre-moult) (Wienecke et al. 2004)	8	8	615	311	15-Dec–26-Feb	Bathymetry Distance to fast ice	0.615 (0.109)*
Light-mantled albatross (chick-rearing) (Weimerskirch and Robertson 1994, Lawton et al. 2008)	17	45	1437	221	14-Nov–28-Feb	Zonal wind summer Sea-ice days since melt Transport cost	0.752 (0.225)*
Southern elephant seal (post-breeding/post-moult males and females) (Biuw et al. 2007, Bestley et al. 2012)	36	36	3594	471	11-Nov–28-Feb	Distance from deployment Bathymetry Sea-ice cover monthly	0.783 (0.204)*
Weddell seal (post-breeding females) (Lake et al. 2006, Andrews-Goff et al. 2010)	20	20	1073	273	1-Nov–28-Feb	Bathymetry Distance to fast ice Distance to polynya	0.702 (0.271)*

are shown in Fig. 2 (note that results obtained by averaging the top three or five values were very similar and so are not shown). A high degree of overlap occurred in six regions in particular (numbered 1–6 in Fig. 3a): 1) small patches off the Riiser-Larsen Peninsula (30–35°E) and a relatively narrow band off Cape Ann at approximately 50°E; 2) east of Cape Ann to the western edge of Prydz Bay (approximately 60–70°E); 3) the eastern side of Prydz Bay to the West Ice Shelf (75–80°E); 4) off and between the West and Shackleton ice shelves (85–100°E); 5) off Vincennes Bay (110°E); and 6) off Terre Adélie (130–150°E).

Areas of overlap were all located in the southern part of the study region, generally over the Antarctic shelf and waters immediately to its north, excluding deep, open oceanic areas. Three of the overlaps (1, 2, and 5) were largely restricted to shelf areas; the remainder included both shelf and offshore habitats. The species compositions of the overlaps showed a latitudinal structuring (Fig. 3b, c), with female Weddell seals, and to a lesser extent emperor penguins, most strongly associated with near-coastal areas. Light-mantled albatrosses displayed opposing trends, with decreasing representation nearer to the Antarctic coast. The remaining species showed more uniform distributions. The species composition of area 5 differed from the remainder, with decreased importance for male Antarctic fur seals.

Each of the areas of overlap was associated with a polynya (Fig. 3a); however, not all polynyas were associated with overlaps. Of the 19 polynyas in the study region, four are located more than 150 km from the nearest penguin colony, and none of these four were associated with an overlap. Of the 15 polynyas located closer than 150 km to the nearest penguin colony only one (the Lutzöw-Holm Bay polynya at 40°E) was not associated with an overlap (but note that the results for Lutzöw-Holm Bay were affected by missing data, shown as white in Fig. 2). Areas of overlap that did not extend off the continental shelf (overlaps 1, 2, and 5) were those that were most distant from subantarctic islands and apparently beyond the foraging ranges of light-mantled albatrosses and male Antarctic fur seals.

Figure 3d shows a multidimensional scaling plot of the environmental characteristics of the relatively-near-shore part of the study region (within 390 km of the Antarctic coastline, which was the 90th percentile of overlap grid cell distances from the coast). Grey points (grid cells not associated with overlaps) are prevalent in the upper part of the plot, and correspond to deep, oceanic waters. The lower part of this plot is dominated by coloured points (i.e. corresponding to overlap grid cells), but also contains grey points. These generally correspond to grid cells that are distant from subantarctic islands or have persistent sea-ice cover.

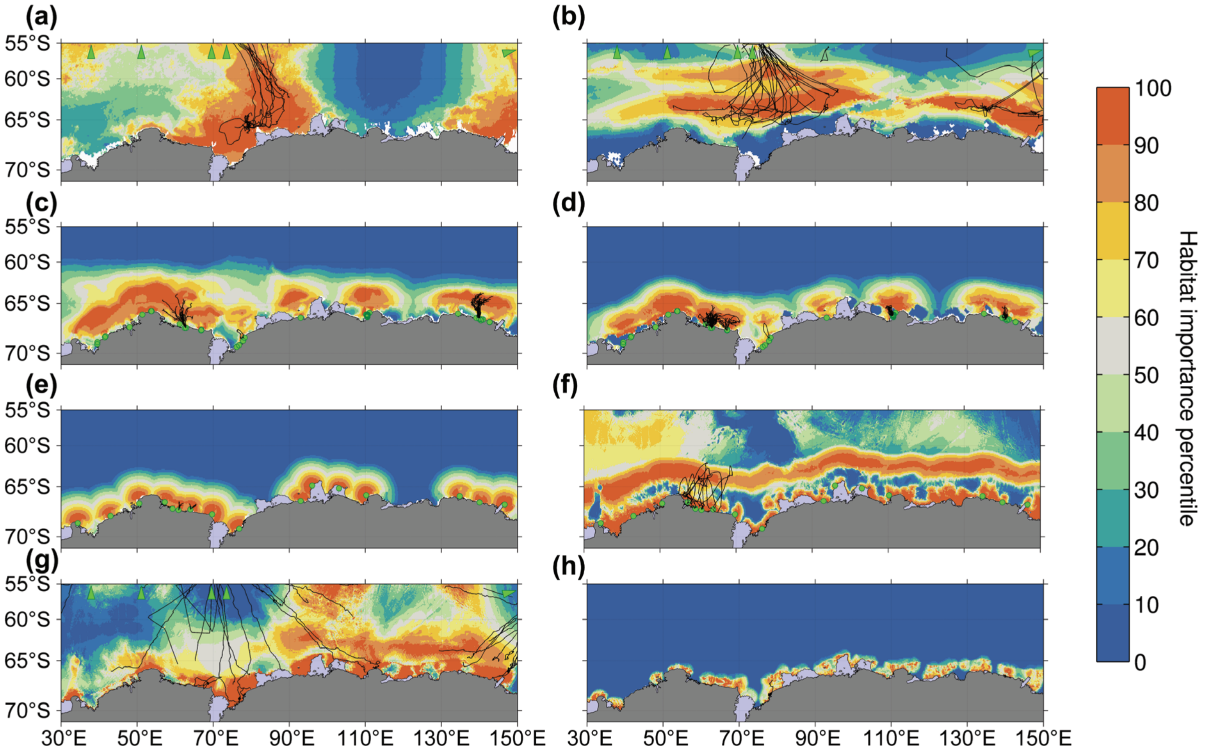

Figure 1. Predicted habitat importance for individual species. (a) male Antarctic fur seals, (b) light-mantled albatrosses, Adélie penguins during the (c) incubation and (d) chick-rearing periods, emperor penguins during the (e) chick-rearing and (f) pre-moult periods, (g) southern elephant seals, and (h) female Weddell seals. Black points show the filtered and interpolated position locations. Green points show colony locations for the Antarctic-breeding Adélie and emperor penguins; green arrows show the direction of (from west to east) subantarctic Marion and Prince Edward, Crozet, Kerguelen, Heard, and Macquarie islands, which host breeding colonies of Antarctic fur seals, southern elephant seals, and light-mantled albatrosses.

The overlap results were corroborated using independent data: at-sea sightings of seabirds, and estimates of seabird breeding colony biomass. The at-sea sighting data showed that both the abundance (number of individuals sighted per survey) and the encounter rate (probability of observation of one or more individuals) generally increased with increasing overlap importance (Fig. 4). That is, areas of habitat that were deemed important by analysis of the tracking data were also associated with higher abundances and encounter rates of these high-Antarctic seabird species. Overlap importance (averaged within 5° longitude sectors) was also correlated with seabird breeding colony biomass (Spearman $r = 0.62$, $p < 0.05$).

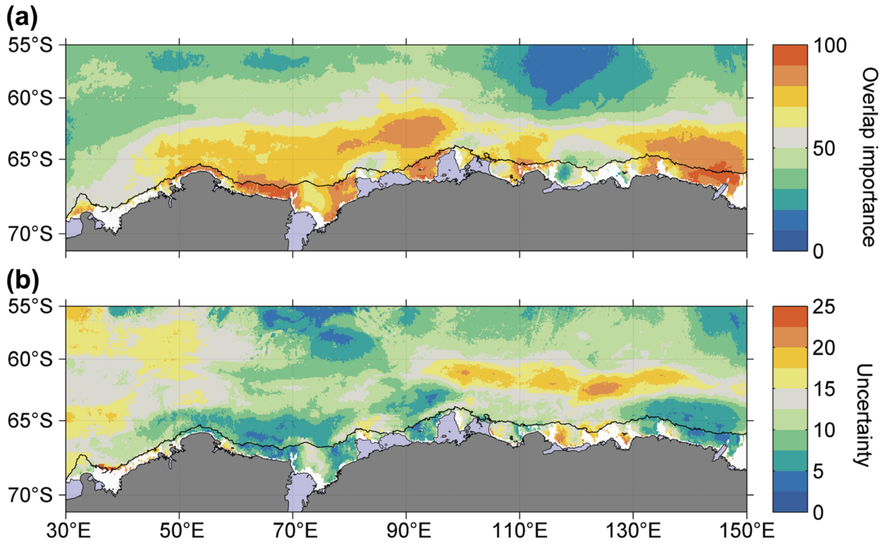

Figure 2. Multi-predator overlap. (a) Overlap importance, calculated as the average of the top four habitat importance values from the six species shown in Fig. 1. (b) Uncertainty in the overlap importance, calculated as the interquartile range of overlap importance values using a resampling procedure (see text). The black line shows the 1000 m bathymetric contour, which approximately delineates the Antarctic continental shelf.

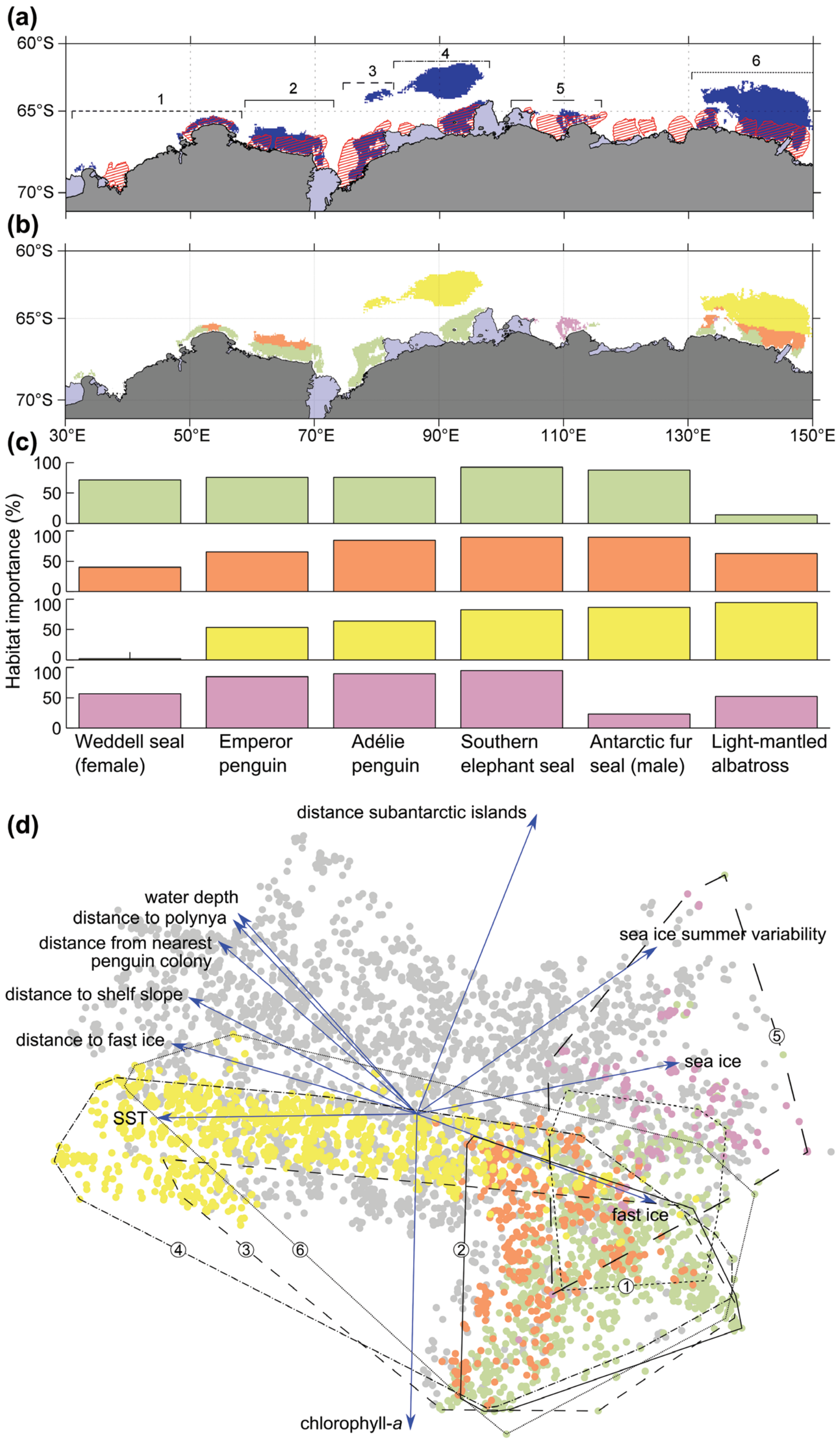

Figure 3. Areas of overlap, their species compositions, and environmental characteristics. (a) Areas of overlap (blue), identified as those areas with overlap importance of 80% or more in Fig. 2. Zones of overlap are numbered for discussion purposes. Red hatched areas show polynya locations (Arrigo and van Dijken 2003). (b) As for panel (a), but with colour according to species composition, determined by cluster analysis (see text). (c) Species compositions of the clusters shown in panel (b). (d) Nonmetric multidimensional scaling plot of the environmental characteristics of the grid cells (stress = 0.12). Colours correspond to those in panels (b) and (c); grey markers indicate grid cells within 390 km of the Antarctic continent that were not associated with areas of overlap. Dotted black lines show the convex hulls of points associated with each of the numbered zones of overlap in panel (a).

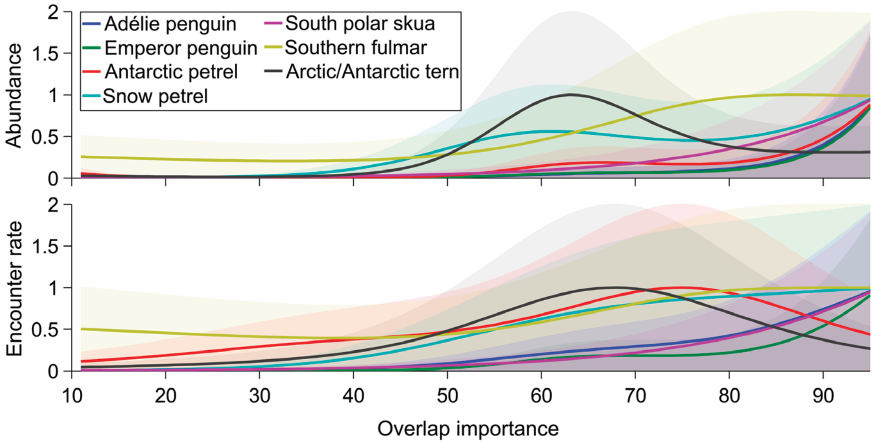

Figure 4. Variations in at-sea sightings of seabirds with respect to overlap importance from Fig. 2, showing abundance (number of individuals per survey), and encounter rate (probability of observation of at least one individual in a survey). Abundances and encounter rates have been normalized (the maximum of the fitted mean has been scaled to unity) to assist with visual comparison. Shaded areas show ± 1 SE on the fitted means.

Discussion

Combining tracking data from a diverse suite of Antarctic marine predators has revealed the importance of several regions and features. Despite differences in habitat preference amongst the individual species, regions of overlap were evident, and these areas shared key environmental characteristics. The primary factors associated with areas of overlap were accessibility from Antarctic and subantarctic breeding colonies, and proximity to winter polynya areas. Areas of overlap were generally located on the Antarctic continental shelf near breeding colonies, with some extending northwards off the shelf into oceanic waters. The latter were those that were within potential foraging range of subantarctic-breeding species. This study focused on the austral spring/summer period, and so for species that breed in this period, proximity to breeding colonies is a natural consequence of the responsibilities of the adults to their young. Colony locations are governed in part by terrestrial characteristics such as substrate and exposure (Olivier and Wotherspoon 2006). While these factors were not investigated here, the results nevertheless highlight the importance of terrestrial processes in the context of marine conservation planning (Sloan et al. 2007). The accessibility of high Antarctic foraging areas to subantarctic-breeding predators was found here to be related to distance, but also to wind and ocean current patterns. These are known to affect travel routes and foraging locations of flying seabirds, penguins, and marine mammals (Lea et al. 2009, Raymond et al. 2010, Cottin et al. 2012, Weimerskirch et al. 2012), and changes in the prevailing wind patterns have been shown to impact on seabird reproductive success (Weimerskirch et al. 2012).

Polynyas provide access to open water, particularly during the winter months (McMahon et al. 2002), and are areas of increased productivity (Arrigo and van Dijken 2003, Tynan et al. 2010) and food availability, including access for diving predators to under-ice prey such as Antarctic krill *Euphausia superba* (Brierley et al. 2002). In the spring/summer period (the focus of this study) these areas are generally not strictly polynyas, because the surrounding ice has typically broken out or melted, but they remain biologically important (Arrigo and van Dijken 2003). Polynyas also play a role in determining colony location and size (Arrigo and van Dijken 2003). While much of East Antarctica has shown relative minor changes in sea-ice seasonality since 1979, a number of coastal areas have shown significant trends (Massom et al. 2013). Many of these areas correspond, or are adjacent to coastal polynyas, and hence to the areas of important habitat identified in this study. These include areas near Davis, Mawson, and Dumont d'Urville stations, and around Cape Ann (Massom et al. 2013). Likely future changes in sea-ice characteristics in these areas, and more broadly across East Antarctica, due to both climate change and abrupt events like glacier tongue calving, are not well understood and are an active area of research (Massom and Stammerjohn 2010). However, changes in sea-ice seasonality and polynya regimes are known to have major impacts on the ecosystem, and are reflected in indices such as penguin breeding success (Emmerson and Southwell 2008). As an example, the Mertz Glacier Tongue (~145°E) calved in early 2010, affecting sea-ice production and polynya activity in the area (Tamura et al. 2012, Dragon et al. 2014). Subsequent Adélie penguin breeding success at Dumont d'Urville (140°E) in the 2011/2012 and 2012/2013 seasons has been poor (T. Raclot pers. comm.).

Modelling approaches allow inferences to be made for areas where predator tracking has not been undertaken. For example, important habitat for male Antarctic fur seals was predicted off Terre Adélie (130–150°E; Fig. 1a). This area lies south of Macquarie Island and within potential foraging range of its fur seal colonies; however, tracking deployments have not been made on Macquarie Island to enable this prediction to be tested. The predictive accuracy of these models, and of related approaches such as species distribution modelling, is influenced by a range of factors. An important assumption is that the predictor variables – at their available spatial and temporal resolutions – adequately describe environmental factors and processes that are relevant to the species of interest. One of the strongest determinants of predator distribution is prey availability; however, direct measurements (e.g. ship-based acoustic estimates) do not have synoptic coverage. Regional-scale modelling is thus dependent on remotely-sensed or modelled products with broad spatial coverage, and which characterize processes related to prey abundance and distribution (Bost et al. 2009, Raymond et al. 2010). Some of the fitted environmental dependencies here are consistent with prey distribution factors. Emperor penguins were found to prefer deep areas of the shelf, which have been shown to correspond to increased densities of silverfish *Pleuragramma antarcticum* larvae (Koubbi et al. 2011). Similarly, Adélie penguin utilization of the shelf break and slope corresponds to increased densities of krill (Jarvis et al. 2010). However, the information available from synoptic environmental data is typically not directly related to the conditions experienced by the animals. This mismatch may reflect issues related to spatial resolution, or the inability of satellite sensors to measure sub-surface conditions. For benthic-foraging or sea-ice specialist species, informative predictors can be particularly difficult to obtain. Development of more directly-relevant predictor variables is likely to improve the utility of modelling exercises such as this. An alternative approach to collecting environmental data at more relevant spatial and temporal scales is to use instruments attached to the animals (Biuw et al. 2007), but this cannot be used for regional extrapolations because the same data will not be available across the region.

Other recent studies have investigated multi-species overlap from telemetry data by assessing spatial overlap directly from the track locations, and then applying regression models to explain the overlap in terms of environmental conditions (Kappes et al. 2010, Block et al. 2011). Our approach differs in that individual species habitat preferences were first modelled, and then spatial overlap was assessed from the model predictions (similar to Žydelis et al. 2011, Hazen et al. 2013). This provides additional flexibility to accommodate deployments made from different areas (yielding tracking data that might not necessarily overlap in geographic space). Implicit in this approach is the assumption that data from a limited set of deployment locations can be used to make inferences about the same species in other areas. In the present study, inter-colony differences in habitat use strategies were not explicitly modelled. Doing so would be strongly limited by the available data: the majority of colonies (of any species) have not been the subject of tracking studies. Methods to accommodate colony-specific information in regional model predictions are a focus of current research, but not sufficiently mature for use here.

The predator data available for a study such as this will clearly influence the conclusions that are drawn and the areas that are identified as important. Tracking deployments at high latitudes are tightly constrained by logistics and cost. Access to field sites is difficult, highly seasonal, and often only intermittently possible. Studies are often directed at breeding individuals because of their accessibility while ashore, and the generally greater interest of breeding individuals to policy development and management activities. Colony-breeding seals, penguins, and large flying seabirds thus comprise the bulk of Antarctic tracking deployments. Patterns exhibited by non-breeding individuals, and at other times of year, may well differ from those presented here. The sample sizes are also uneven across species, leading to differing sensitivities of the individual species results to factors such as individual variability and quirks of particular tracks. Additional tracking data would potentially resolve some of these issues and broaden the relevance of these results; however, it also needs to be acknowledged that full data coverage in this remote region will never be practicable. Effective management may be better served by a pro-active approach based on existing data and knowledge (Grantham et al. 2009), with the option of later refinement as additional data becomes available.

Post-hoc synthesis of independently-collected tracking data has highlighted a number of data-oriented issues, including differences in data format, degree of documentation, tag types and settings (Breed et al. 2011), and data availability. Multi-species monitoring is a component of a number of large Southern Ocean science initiatives (e.g. the Southern Ocean Observing System, SOOS; and Integrating Climate and Ecosystem Dynamics in the Southern Ocean, ICED), and might be assisted by tighter coordination of details such as these. Multi-species predator modelling is also the focus of the Retrospective Analysis of Antarctic Tracking Data (RAATD), which is a joint initiative between the Commission for the Conservation of Antarctic Marine Living Resources (CCAMLR) and the Scientific Committee on Antarctic Research (SCAR) through its expert groups on birds and marine mammals, and Antarctic biodiversity informatics. The scope of RAATD is broader (circum-Antarctic) and more species-diverse than the work presented here, but these methods and results are relevant to that project.

The results of this work are also relevant to Southern Ocean conservation planning efforts, including the establishment of marine protected areas (MPAs). Australia, France, and the European Union have jointly proposed a system of seven MPAs in the East Antarctic sector (Delegations of Australia and France 2011). Some of the tracking data used here were also considered in the preparation of that MPA proposal. Nevertheless, our results indicate that, even though designed for ecosystem representation, the coverage of those proposed MPAs is broadly congruent with important predator habitats. This reinforces the notion that areas of predator overlap will tend to occur in regions of high ecological diversity, and that the scales of the proposed MPAs are consistent with the spatial scales of these habitats.

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Supplementary material (Appendix ECOG-01021 at <www.ecography.org/readers/appendix>). Appendix 1.

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