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Coexistence of mesopredators in an intact polar ocean ecosystem: The basis for defining a Ross Sea marine protected area

Grant Ballard [a,*], Dennis Jongsomjit [a,1], Samuel D. Veloz [a,2], David G. Ainley [b,3]

[a] PRBO Conservation Science, 3820 Cypress Drive #11, Petaluma, CA 94954, United States
[b] H.T. Harvey & Associates, 983 University Avenue, Los Gatos, CA 95032, United States

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ABSTRACT

Designation of an effective marine protected area (MPA) requires substantial knowledge of the spatial use of the region by key species, particularly those of high mobility. Within the Ross Sea, Antarctica, the least altered marine ecosystem on Earth, unusually large and closely interacting populations of several marine bird and mammal species co-exist. Understanding how that is possible is important to maintaining the ecological integrity of the system, the major goal in designating the Ross Sea as an MPA. We report analyses of niche occupation, two-dimensional habitat use, and overlap for the majority (9) of mesopredator species in the Ross Sea considering three components: (1) diet, (2) vertical distribution and (3) horizontal distribution. For (1) and (2) we used information in the literature; for (3) we used maximum entropy modeling to project species' distributions from occurrence data from several ocean cruises and satellite telemetry, correlated with six environmental variables. Results identified and ranked areas of importance in a conservation prioritization framework. While diet overlapped intensively, some spatial partitioning existed in the vertical dimension (diving depth). Horizontal partitioning, however, was the key structuring factor, defined by three general patterns of environmental suitability: (1) continental shelf break, (2) shelf and slope, and (3) marginal ice zone of the pack ice surrounding the Ross Sea post-polynya. In aggregate, the nine mesopredators used the entire continental shelf and slope, allowing the large populations of these species to co-exist. Conservation prioritization analyses identified the outer shelf and slope and the deeper troughs in the Ross Sea shelf to be most important. Our results substantially improve understanding of these species' niche occupation and imply that a piecemeal approach to MPA designation in this system is not likely to be successful.

1. Introduction

Ecology is the study of organisms in relation to their environment. A cornerstone of the science involves determining the spatial aspect of a species' occurrence, which usually means defining its habitat, determining the biological and physical mechanisms of its existence there, and determining why the species does not occur elsewhere (Grinnell, 1917; MacArthur, 1972). Thereby, ecology seeks to define a species' niche within the specified "resource utilization space," which includes habitat parameters, diet, and patterns of co-existence with other species (Elton, 1927; MacArthur and Levins, 1964; Diamond and Case, 1986; Wiens et al., 2009). According to classic niche theory, especially where resource choices are limited, species should be distributed among habitat types according to their capabilities to exploit respective resources, and fewer species should occupy habitats with more unpredictable attributes (Lack, 1954; MacArthur and Levins, 1964). Understanding how that is accomplished in a region is key to preserving the full function of an ecosystem.

As ecology has matured, the study of species' occurrence patterns has benefited from the development of modeling techniques for making species-habitat relationships spatially explicit across unsampled space (commonly referred to as species distribution models; Elith et al., 2006; Phillips et al., 2006; Wiens et al., 2009). Owing to the high costs both in time and resources to sample the ocean, the use of spatial models is critical to quantifying occurrence patterns, and their overlap, among marine species. This ability has, in theory, increased the relevance of "systematic conservation planning" that seeks to identify portions of the ocean deserving special management in the face of competing pressures from human use of resources and other anthropogenic disturbances (Margules and Pressey, 2000; Airame et al., 2003; Lombard et al., 2007). Invoking such planning in the extensively altered ecosystems that currently exist in most of the world ocean (see Halp-

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* Corresponding author. Tel.: +1 707 781 2555x340.
E-mail addresses: gballard@prbo.org (G. Ballard), djongsomjit@prbo.org (D. Jongsomjit), dainley@penguinscience.com (D.G. Ainley).
[1] Tel.: +1 707 781 2555x346.
[2] Tel.: +1 707 781 2555x308.
[3] Tel.: +1 408 458 3200.

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ern et al., 2008) can be a challenge (Longhurst, 2010, and references therein).

The Ross Sea, which is the largest continental shelf ecosystem south of the Antarctic Polar Front but which comprises just 2% of the Southern Ocean, is one of the better known stretches of South Polar seas (Ainley et al., 2010; Smith et al., 2007, 2012). Importantly, owing to its relative isolation from human civilization and protection of its coastal habitat under the Antarctic Treaty, including several Antarctic Specially Protected Areas, it is the anthropogenically least-affected stretch of ocean remaining on Earth (Halpern et al.. 2008). It still has a full suite of upper-trophic-level predators, including large fish, birds, seals and whales, which all exist in huge numbers (Ainley, 2010; Ainley et al., 2010). This wealth of apex and mesopredators in part must result from the Ross Sea's unusually high primary production (estimated to be 28% of the total primary production of the Southern Ocean south of 50°) – implying that there are higher than expected amounts of phytoplankton available at the base of the trophic pyramid (Arrigo et al., 1998, 2008; Smith and Comiso, 2008) and thus the potential for a very robust food web (Smith et al., 2012). Contributing to this exemplary phytoplankton concentration, grazer standing stocks (e.g., krill) occur in lower than expected levels, in turn potentially explained by the unusual (in today's world) prevalence of their upper-level predators (Table A.1; Ainley et al., 2006; Baum and Worm, 2009; Smith et al., 2012), some of which have been shown to act together to deplete middle-trophic-level prey (smaller fish and krill; Ainley et al., 2006; Ainley and Siniff, 2009; Ainley et al., 2010). For these reasons, elucidating the patterns of co-occurrence of the Ross Sea mesopredator fauna within its relatively small confines and highly variable environmental conditions not only will offer ecological insights not possible elsewhere in the world ocean, where most top predators have been severely depleted (e.g., Pauly and Maclean, 2003; Longhurst, 2010), but could also serve as a model for identifying relevant boundaries of marine protected areas (MPA's) designed for maintaining "pristine ecosystems."

The Antarctic Treaty signatory powers, through the Convention for the Conservation of Antarctic Marine Living Resources (CCAMLR), are currently working to designate a network of MPA's in the Southern Ocean by 2012, in accordance with a recommendation adopted at the 2003 United Nations Conference on Sustainable Development calling for the establishment of MPAs to protect biodiversity and ecosystem processes throughout the world's oceans. The Ross Sea is one area selected for closer scrutiny by a "bioregionalization" process using mostly physical measures of habitat heterogeneity (CCAMLR, 2007, 2008). Toward achieving that goal, we report results of analyses of niche occupation of all abundant air-breathing mesopredators in the Ross Sea, considering three important components: (1) diet, (2) vertical distribution (diving depth) and (3) horizontal distribution. To our knowledge this is the first study to employ maximum entropy modeling within a conservation prioritization framework in a large scale marine setting. Our results substantially improve understanding of habitat use by key species in the Ross Sea, previously only described using heuristic approaches (Ainley et al., 1984; Ainley, 1985; Smith et al., 2007, 2012) and identify areas of highest conservation priority for this intact polar ocean ecosystem.

2. Methods

2.1. Depth of foraging

We obtained information on maximum diving depth, a measure of foraging capability, from the literature (Fig. 1A; Appendix A.6). While mean foraging depth might be more ecologically meaningful, such information was not available for minke whale, killer whale, and the petrels (see Appendix A.1 for scientific names of all species studied). Moreover, depth of foraging varies with bottom and prey depth. Therefore, for each species pair, we determined the amount of overlap in maximum foraging depth by dividing the depth of the species having shallowest dives by that of the one having deeper dives.

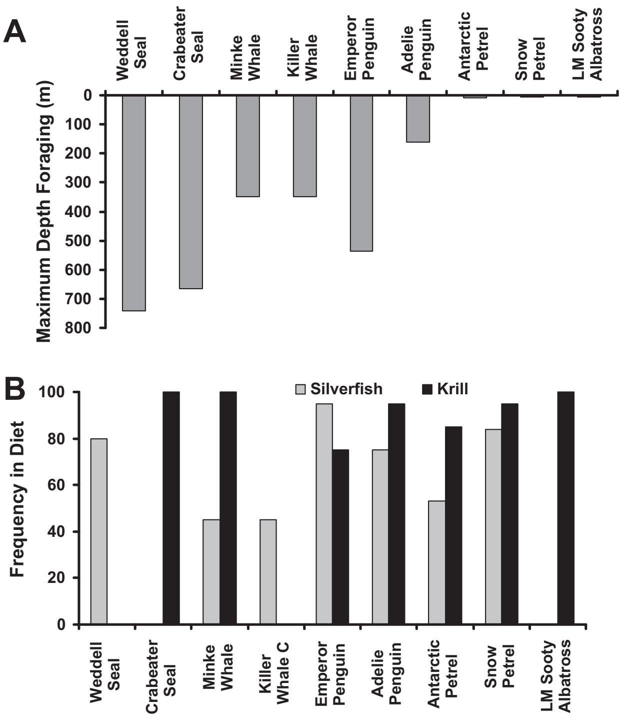

Fig. 1. (A) Overlap in maximum diving depths of top-trophic (air-breathing) predators of the Ross Sea shelf and slope. Source Data and more details are listed in Appendix A.5. (B) Prevalence of Antarctic silverfish and krill (all species) in the diet of (air breathing) mesopredators over the Ross Sea shelf and slope, indexing degree of diet overlap. Source Data and more details are listed in Appendix A.6.

2.2. Diet

We created an index of the amount of diet overlap among species pairs using data from the literature on frequency of occurrence of krill (*Euphausia superba*, *Euphausia crystallorophias*) and silverfish (*Pleuragramma antarctica*) in the diet (Fig 1B; Appendix A.7). These are the predominant prey in this system (summarized in Smith et al., 2007; Smith et al., 2012; see also Ainley et al., 2010). We could not use other measures, such as diet based on mean mass of prey nor index of relative importance, because sufficient detail was not available for several species (e.g., minke whale, killer whale). For krill, and then independently for silverfish, we determined the percent of overlap by dividing the frequency of occurrence in the diet for the species having the lowest frequency by that having the higher; we then averaged the two (krill, silverfish comparisons) for each species pair. Species preying on only one of the two diet species (e.g., Weddell seal: silverfish only) compared to a predator preying only on the other (e.g., crabeater seal: krill only), were considered to have 0% overlap.

2.3. Species distribution models: explanatory variables

We defined the study area as all ocean waters south of 63°S between 165°E and 150°W; the study area entirely contains the Ross Sea, constituting the broadest continental shelf (with slope) in the

Southern Ocean (Fig. 2). Environmental covariates, obtained from various sources (Table A.2; Ainley et al., 2010), were as follows: chlorophyll concentration, depth, percent ice cover, prevalence of Circumpolar Deep Water, distance to Shelfbreak Front, and bathymetric gradient.

Before inclusion in species distribution models, covariate data were resampled to 5 km resolution in ArcMap 9.3.1 (ESRI, 2008) using bilinear interpolation or (for sea-ice and chlorophyll) nearest-neighbor assignment. Although higher resolution bathymetric data are available for parts of the study area (Davey, 2004), we resampled the data to match the 5 km bathymetry available for the entire study area, especially since the resolution of almost all other datasets was no better than this (Table A.2). Satellite-derived monthly mean percent sea-ice cover was obtained for July to September (winter; used for Weddell seal models only – see Section 2.4.3) and December to January (summer) for 10 years, 1998–2008, and averaged across all years to obtain one mean grid for each season. Ice cover data were collected on several of the

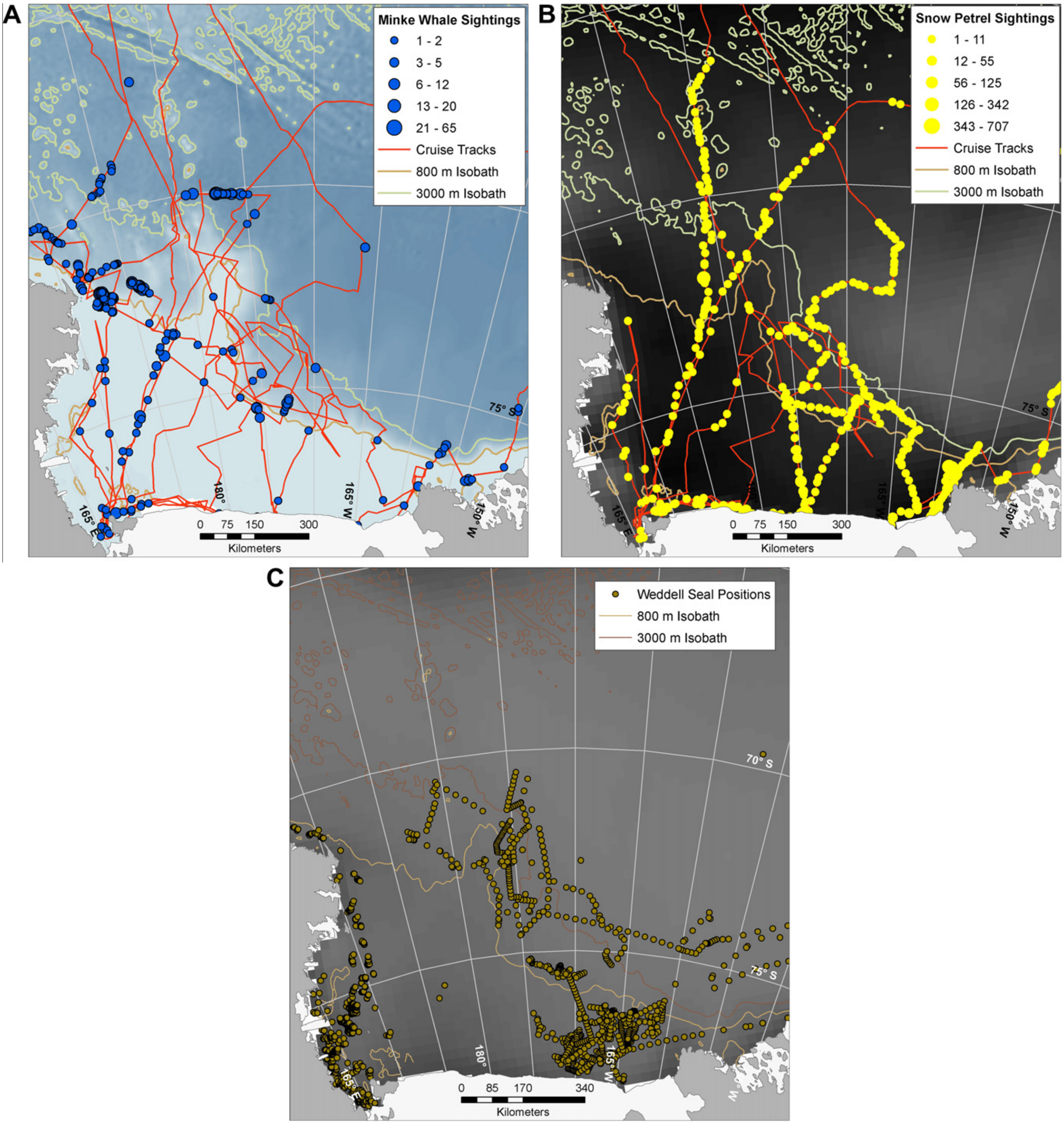

Fig. 2. (A): cruise tracks on which minke whales were surveyed, with bathymetry as base layer (lighter = shallower). (B): tracks on which seabirds and pinnipeds were surveyed (snow petrel sightings used for example), with typical sea-ice cover for coincident season (mean December-January ice concentration from December 1997 to January 2008; black = no ice, lighter shades of gray = more ice). (C) Positions of Weddell seals during winter (from determined satellite transmitters) and typical sea ice cover for coincident season (mean July–September ice concentration for 1997–2007; black = no ice, lighter shades of gray = more ice). Seals were initially tagged outside the Eastern boundary of the map and subsequently moved into the Ross Sea over the next several months.

cruises, but these data were not available for all locations, and preliminary evaluation of models including these data for subsamples of locations did not improve model performance (Section 2.5). Bathymetric slope was calculated as the maximum change in depth (degrees) between a given cell and its eight neighboring cells.

We calculated Pearson correlation coefficients for each pair of environmental covariates to aid in covariate selection and interpretation of model results (Table A.3). Prevalence of Circumpolar Deep Water (CDW) was relatively highly (negatively) correlated with bathymetry (82%) and chlorophyll (73%), somewhat complicating interpretation of the relative influence of CDW vs. these variables. Since our primary goal was to create the best possible projections of species occurrences rather than to explain why these patterns exist in relation to covariates, and since they were not completely correlated with one another, we included all in the modeling, especially given the paucity of available covariates.

2.4. Species distribution models: dependent variables

There are 13 species of upper level trophic predators which regularly occur in the Ross Sea (Appendix A.1 and Table A.1; Ainley et al., 2010; Smith et al., 2012), however, rarity and paucity of sightings meant that only nine could be included in this study (see Table 1).

2.4.1. Survey methods for minke whale, crabeater seal, and seabirds

Ships and dates for the nine data collection cruises are listed in Table A.4, and examples of tracks are shown in Fig. 1. Surveys were occurred in early summer (15 December to 4 January) and late summer (16 January to 21 February). Field methods for collecting occurrence data are described in Appendix A.3. Other than for the Ross Sea, systematic observations of marine animals this far south are virtually non-existent for early summer because of the heavy sea ice.

2.4.2. Survey methods for killer whale

Some data on killer whales were available from the surveys described in Section 2.4.1, but most came from the International Whaling Commission database gathered during the Southern Ocean Whale Research cruises 1987–2005. On the basis of pod size (Ainley et al., 2010) we partitioned sightings into Ross Sea killer whale (ecotype C; pod size ⩾20) and ecotype A and B (combined; pod size ⩽10; Pitman and Ensor, 2003), and excluded the later two types from analyses presented here.

2.4.3. Survey method for Weddell seal

During the summer, Weddell seals are concentrated on coastal fast ice, where even icebreakers rarely travel. Therefore we only used satellite positions, mostly from March–October, when the seals are free to leave coastal ice cracks to exploit the remaining Ross Sea (Fig. 1; sources in Table A.2, more details in Ainley et al., 2010).

2.5. Species distribution models: maximum entropy modeling

We modeled the environmental suitability for each species using environmental data and species presence (>0 counted) localities from surveys and sources described above (Table 1). Presence data were aggregated for each 5 km cell in the study area, and locations that fell outside of the extent of any of the environmental layers were not used. We used a machine learning, "maximum entropy" modeling method called Maxent, and its logistic output format (v.3.3.3a; Phillips et al., 2006; Phillips and Dudík, 2008), to estimate environmental suitability in each cell given the modeled relationship between a given species and environmental covariates. Maxent tends to out-perform all other existing distribution modeling algorithms when compared to known distributions, including superior performance using a limited number of presence locations (Phillips et al., 2006; Elith et al., 2006; Hernandez et al., 2006; Wisz et al., 2008; Phillips and Dudík, 2008). To evaluate model performance, we produced Receiver Operating Characteristic (ROC) plots (true positives vs. false positives) based on presence and target background ("bias corrected pseudo-absence") data selected from the area within one gridcell of ship's tracks (Phillips et al., 2006, 2009; Elith et al., 2011). The ROC area under the curve (AUC) values for a randomly selected 25% test portion of the data in each of 30 replicate model runs was used to evaluate model performance for each species (Table 1). More details about species selection criteria, Maxent analyses, and model performance evaluation are given in the Appendix.

2.6. Species distribution models: comparison of spatial overlap, environmental niche similarity, overall species richness, and identification of conservation priorities

Using results from the species distribution models, we created an index of the amount of spatial overlap between every pair of species. To constrain our overlap analysis to those areas that best represented presence of a species according to the model projections, we applied a threshold to each model that maximized training sensitivity and specificity (Phillips et al., 2006) and converted all values above the threshold to 1 (predicted presence) and all values below the threshold to 0 (predicted absence). We chose this method of conversion because other methods, such as setting an arbitrary fixed threshold for all species, have been shown to bias results (Liu et al., 2005). We then divided the number of cells where both species were predicted to be present by the total num-

Table 1

Species distribution model performance (mean AUC ± standard deviation for 30 bootstrapped runs) and heuristic estimates of percent contribution of each variable to the Maxent model. Bold font indicates most influential variable in each species' model; winter sea ice cover used for Weddell seals (for others: summer sea ice).

Common name	AUC ± SD	locations	Relative importance to distribution model (permutation importance)					
			Chl	Bathy	Sea ice cover	Presence CDW	Distance SB front	Bathy gradient
Minke whale	0.739 ± 0.035	174	15.7	11.0	15.1	22.9	**30.9**	4.3
Ross Sea killer whale	0.812 ± 0.075	38	8.0	9.7	10.3	5.2	**40.2**	26.7
Crabeater seal	0.720 ± 0.048	96	9.7	12.7	**28.0**	20.5	12.6	16.5
Weddell seal	0.926 ± 0.004	1023	3.7	**40.9**	7.3	20.0	27.2	0.9
Emperor penguin	0.813 ± 0.06	48	3.2	17.7	**32.6**	13.1	29.6	3.8
Adélie penguin	0.795 ± 0.036	136	5.0	**28.1**	18.1	13.8	25.3	9.7
Antarctic petrel	0.643 ± 0.029	329	**25.3**	16.0	12.8	16.7	**25.3**	3.9
Snow Petrel	0.693 ± 0.028	337	19.6	16.1	**24.1**	13.8	14.8	11.7
Light-mantled sooty albatross	0.839 ± 0.053	20	**51.8**	6.2	10.4	27.4	1.9	2.3
Total			142.0	158.4	158.7	153.4	**207.8**	79.8

Table 2
Index of spatial overlap (%; left side), and environmental niche similarity index (I; right side) for species in the Ross Sea region during summer, except for Weddell seal (winter only, in italics). Spatial overlap values >13% (the median for summer species co-occurrence) are shown in bold font, as are significant values of I as determined from randomization tests.

Species	1	2	3	4	5	6	7	8	9
	Environmental niche similarity index (*I*)								
1. Minke whale	–	0.62	**0.87**	**0.89**	**0.89**	**0.73**	**0.75**	**0.85**	*0.70*
2. Ross Sea killer whale	**18**	–	0.69	0.58	**0.71**	0.44	**0.71**	**0.74**	*0.62*
3. Crabeater seal	**16**	9	–	**0.78**	**0.90**	**0.76**	**0.89**	**0.94**	*0.59*
4. Emperor penguin	12	1	**57**	–	**0.86**	**0.68**	0.61	**0.73**	*0.64*
5. Adélie penguin	**15**	8	**47**	**55**	–	0.60	0.73	**0.87**	*0.66*
6. LM sooty albatross	5	0	4	2	1	–	**0.80**	**0.77**	*0.33*
7. Antarctic Petrel	8	9	**31**	**19**	9	12	–	**0.95**	*0.48*
8. Snow petrel	**15**	12	**62**	**44**	**30**	6	**52**	–	*0.59*
9. Weddell Seal	***16***	***30***	***17***	*13*	***17***	*7*	*12*	***22***	–
	Spatial overlap index (%)								

ber of cells where either species was predicted to be present to calculate an index of spatial overlap for each species pair.

Additionally, we quantified the overlap of species in environmental space using a recently introduced technique that accounts for bias in the spatial resolution of the environmental data and corrects for the availability of data within the study region (Broennimann et al., 2011). We used a principal components analysis (PCA) to transform the environmental space of the predictor variables into a two dimensional surface defined by the first and second principal components that explained the most variation in the data. To calculate the PCA we used the environmental data at presence and target background points and then projected the PCA onto a 100 × 100 PCA unit grid of cells bounded by the minimum and maximum PCA values that occur in the target background data. A smoothed density of each species in each cell of the PCA grid was then estimated using a kernel density function based on the observed species occurrences (Broennimann et al., 2011). We then used a niche similarity statistic (I; Warren et al., 2008, corrected per Warren pers. comm.) to measure the degree of environmental niche overlap between each species pair. I ranges from 0 [completely dissimilar environmental niches] to 1 [identical niches]). An important difference between this method and the spatial overlap index is that the comparison in environmental space corrects for common environments; species co-occurring in a common environment could have high spatial overlap but a low environmental overlap if only one of the species can also occur in another less common environment. We tested for the equivalence and similarity of the environmental niches between pairs of species using randomization tests (see Appendix A.5 for details). Weddell seal was included in both overlap analyses, comparing its winter occurrence patterns with the summer patterns of other species.

We used an index of species richness to identify potentially important places within the study area. The species richness index was calculated by summing all species' predicted presence/absence values (i.e., 0's and 1's for below and above threshold values, respectively, as described above) for each pixel (Wiens et al., 2009).

We used the hierarchical reserve selection software Zonation (v. 3.0; Moilanen et al., 2005) to evaluate the relative importance of each pixel in the study area to all species. Zonation emphasizes conservation priorities from a biodiversity perspective and has been used to evaluate potential large scale MPA's (Leathwick et al., 2008) and terrestrial conservation priorities (Kremen et al., 2008; Carroll et al., 2010). Zonation offers three advantages over other reserve design software from our perspective: (1) it creates a continuous, hierarchical prioritization of the entire study area based on the conservation values of each site (pixel); (2) it works from grids rather than polygons, which means that the user is not required to draw any pre-conceived lines on the map to serve as planning units; and (3) users are not required to set *a priori* conservation targets, such as "20% of species X's range." We used a "no cost constraint" approach, where all cells were assumed to have equal potential conservation costs and prioritization was established by evaluating species' projected distributions, with equal weight given to all species' "conservation value". Species' projected distributions were discounted by subtracting an "uncertainty surface" for each species (Moilanen et al., 2006). The uncertainty surface was proportional to the standard deviation of the bootstrapped Maxent models for each species, thus emphasizing areas with higher model certainty, and followed the default Zonation presets (uncertainty parameter $\alpha = 1$). Because we had a definite list of species for which we wished to rank locations and because we wanted to emphasize locations with the highest environmental suitability, we chose to use a "core area" definition of marginal loss in the Zonation software, which prioritizes the inclusion of high-quality locations for all species (Moilanen et al., 2005; Moilanen, 2007; Leathwick et al., 2008; Carroll et al., 2010). The mathematical details and other methodological information pertaining to core-area Zonation are provided by Moilanen et al. (2005) and Moilanen (2007).

Table 3
(A) Percent overlap in maximum diving depth among Ross Sea top mesopredators. (B) Approximate average percent overlap in diet among Ross Sea mesopredators; overlap based on frequency of occurrence of silverfish in the diet averaged with that of krill in the diet.

Species	1	2	3	4	5	6	7	8
A.								
1. Minke whale								
2. Killer whale C	1.00							
3. Crabeater seal	0.53	0.53						
4. Weddell seal	0.47	0.47	0.81					
5. Emperor penguin	0.65	0.65	0.80	0.72				
6. Adélie penguin	0.40	0.40	0.21	0.19	0.26			
7. LM sooty albatross	0.00	0.00	0.00	0.00	0.00	0.01		
8. Antarctic petrel	0.01	0.01	0.01	0.01	0.01	0.04	0.20	
9. Snow petrel	0.00	0.00	0.00	0.00	0.00	0.01	1.00	0.20
B.								
1. Minke whale								
2. Killer whale C	0.45							
3. Crabeater seal	0.50	0.00						
4. Weddell seal	0.28	0.63	0.00					
5. Emperor penguin	0.58	0.53	0.35	0.42				
6. Adélie penguin	0.80	0.67	0.47	0.47	0.76			
7. LM sooty albatross	0.50	0.00	1.00	0.00	0.35	0.47		
8. Antarctic petrel	0.85	0.50	0.40	0.37	0.70	0.68	0.40	
9. Snow petrel	0.75	0.30	0.45	0.47	0.82	0.91	0.45	0.74

3. Results

3.1. Partitioning of vertical space and diet

For the Ross Sea mesopredators in our study a high degree of partitioning of the continental shelf and slope exists in the vertical dimension, but with overlap among groups of deep, medium and shallow divers. Species with strong use of the shelf, and which are present during the winter as well, i.e., Weddell and crabeater seals and emperor penguin (and adult, therefore neutrally buoyant, Antarctic toothfish, a 10th mesopredator not included further in our analyses; Fuiman et al., 2002), all are capable of using the entire water column from the shelf bottom to the surface (deep divers) and, thus, experience among themselves >70% overlap in foraging depth (Fig. 1A, Table 3). Only over the deeper waters of the slope could any vertical spatial partitioning be expressed, other than that aspect of dive behavior affected by the prey being targeted. Deep diving by the seals and emperor penguin provides access to maximum water volume without needing much horizontal movement, which would be constrained by the heavy pack ice conditions of winter. The remaining mesopredators are composed of medium-deep divers (whales), shallow divers (Adélie penguin), and surface foragers (petrels, albatross). Complete overlap in foraging depth exists among the aerial birds and among the whales. Otherwise, there is little overlap in foraging depth for the majority of species.

The deep-diving year-round/winter inhabitants, i.e., Weddell seal and emperor penguin, are mainly piscivorous, particularly preying on Antarctic silverfish (Fig. 1B, Table 3). The silverfish, or “herring of the Antarctic” (DeWitt and Hopkins, 1977), is also confined to the shelf, and perhaps its existence is key to the wintertime presence and deep diving of these predators. As noted above, these predators, along with adult toothfish, also completely overlap in foraging depth. The Ross Sea killer whale (ecotype C) to a small degree may be included in this diet pattern. Feeding just on fish, it likely does not dive as deeply as other killer whales, and probably departs the area during winter (R. Pitman pers. comm.).

The degree of overlap in diet among the remaining species other than the near-surface feeding petrels and albatross, is appreciable though less than the above, i.e., ~50%, in most comparisons. Predators that forage heavily on krill, and tend to not dive deeply, occur principally over the slope (minke whale, crabeater seal, albatross). The outer shelf and slope is where krill biomass is maximum (Ainley et al., 2010). The extensive overlap in diet indicates that species use of vertical but especially horizontal space is key to understanding the co-existence of the mobile, upper level predators in this system.

3.2. Horizontal habitat use

Model (test data) AUC scores ranged from 0.643 (Antarctic petrel) to 0.926 (Weddell seal) and averaged 0.775 (Table 1). The most influential variable in species distribution models overall was distance to the shelf break, which was negatively correlated with environmental suitability for all species except Weddell seal. Species' environmental suitability scores were mixed in response to ice cover and ocean depth, the second and third most influential variables, respectively. Bathymetric gradient was the least influential variable. Response curves and standard deviations for variable influences for all models are in Appendix B.

Three patterns of spatial use of the Ross Sea were apparent at the mesoscale (Fig. 3): (1) shelf break: restricted mostly to the continental shelf break, which includes outer shelf and slope (light-mantled sooty albatross); (2) shelf and slope: full use of both the continental shelf and the slope (Ross Sea killer whale, Weddell seal); and (3) marginal ice zone (MIZ; pack ice surrounding the Ross Sea post-polynya): combinations in which the slope is the main habitat but western and eastern portions of the shelf, where sea ice is persistent, are used as well (minke whale, crabeater seal, penguins, petrels). This last pattern is consistent with correlation to the presence of relatively high concentrations of pack ice, either over the continental slope or over the shelf (cf. Karnovsky et al., 2007).

There was relatively little overlap among species in use of horizontal space at the small scale (individual 5×5 km cells). The highest overlap was between crabeater seal and snow petrel (62%; Table 2), while most species did not overlap more than 20% (median = 13%) in projected probability of co-occurrence, thus indicating relatively distributed occupation of the most highly suitable areas. By contrast, species pairs had relatively high environmental niche index similarities (median = 0.73), indicating similar relationships between habitat suitability for most species on a cell by cell basis. The similarities between the two petrel species and between crabeater seal and snow petrel were highest (0.95 and 0.94, respectively). For all species pairs, the null hypothesis of niche equivalence was rejected indicating that each species had a distinct environmental niche, but in 21 of the 36 comparisons, the observed environmental niche overlap was greater than would be expected by chance (Table 2).

3.3. Species richness and conservation ranking

The species richness analysis integrated the spatial models of nine major upper-trophic-level predators (among 13 total). Even more than the individual models, species richness highlighted the importance to Ross Sea biodiversity of the deeper water areas on the shelf, as well as several areas along the shelfbreak slope (Fig. 4A). Largely these are areas of more consistent pack ice presence and to some extent places where the intrusion of Circumpolar Deep Water was predicted to be most prevalent (Ainley et al., 2010; Dinniman et al., 2003, pers. comm.). While CDW was negatively correlated with most species' habitat suitability indices (Appendix B), this is likely because of its prevalence in the pelagic (off shelf) portion of our study area, where most of the modeled species were less likely to occur.

Zonation conservation ranking results confirmed the importance of many of these same areas, and elevated the importance of the eastern Ross Sea shelf, western slope, southwest Ross Sea, and pelagic waters overlying areas of bathymetric complexity (ridges in northern part of study area; Fig. 4B).

4. Discussion

4.1. Overall patterns

Polar oceans are recognized as being low in species diversity but high in biomass or species abundance. Both the importance of the outer continental shelf and slope to the Ross Sea mesopredator community and the mosaic spatial pattern in which these predators used this habitat were noteworthy, and demonstrated how very abundant upper-trophic-level predators were able to coexist, despite their relatively high similarities in environmental niche indices and diet. In accord with the mosaic, unlike temperate and tropical seas, there are few multispecies foraging flocks in the high latitude Southern Ocean (DGA, pers. obs.). To our knowledge this is the first time that modeling of niche occupation and overlap among the majority of mesopredators has been attempted for a polar (or any) marine ecosystem. It has been done for terrestrial habitats (reviewed in Diamond and Case, 1986), particularly in the context of recent “experiments” undertaken when apex predators

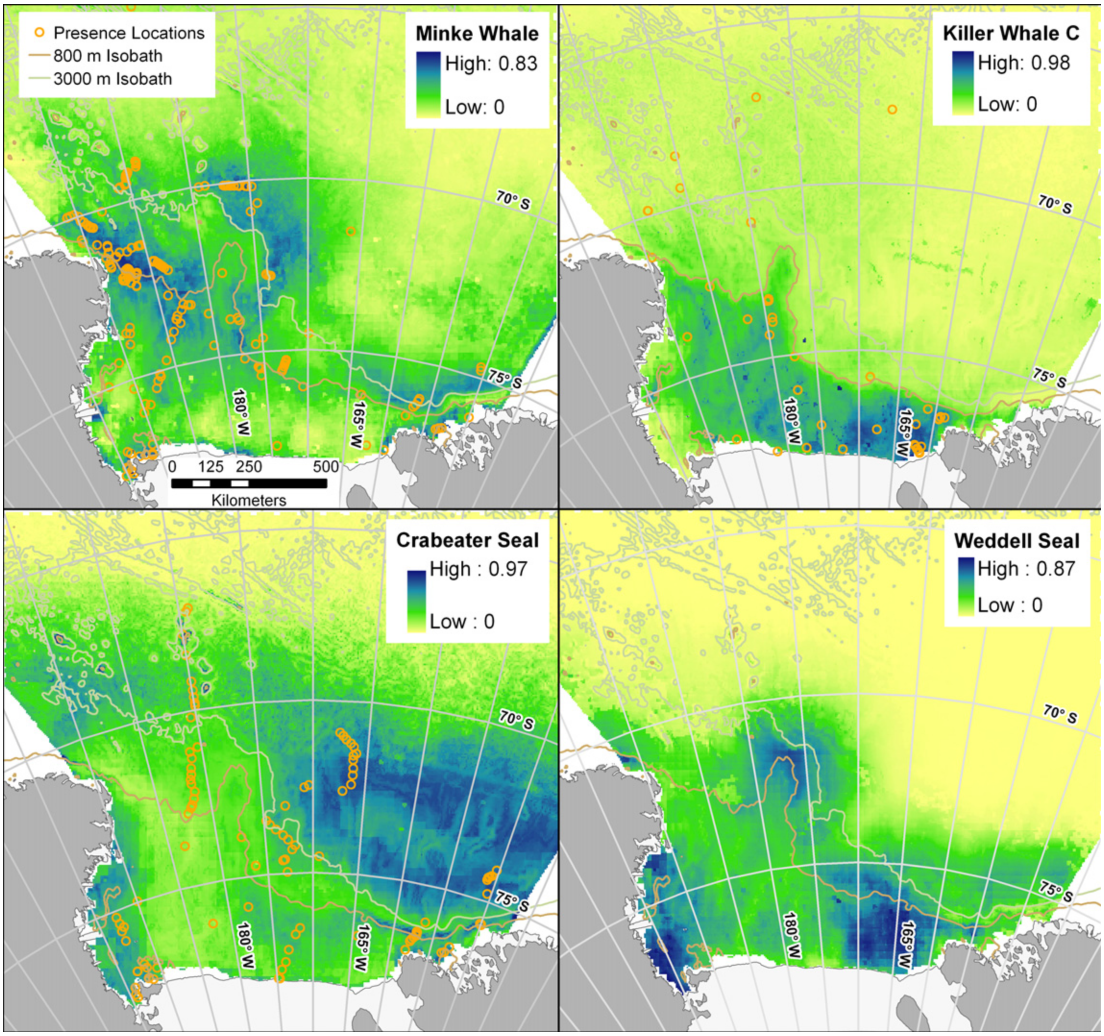

Fig. 3. Mean (from 30 bootstrapped runs) modeled environmental suitability for predators in the Ross Sea; results of maximum entropy modeling. Presence locations are displayed as orange circles (see Fig. 1 for Weddell seal presence locations, and for full survey effort). Map for Weddell seal is for winter distribution (all others are summer), when no longer confined mostly to haul outs along coastal tide cracks in fast ice not adequately sampled by ship-based surveys.

were re-introduced after a long absence, with resulting cascading effects on the diet and spatial use of mesopredators (McLaren and Peterson, 1994; Ripple and Beschta, 2004; Prugh et al., 2009).

In marine systems, understanding of trophic relationships has been improved by recent food web modeling, for instance the analyses for the Baltic Sea (Österblom et al., 2007), the Benguela Current (Watermeyer et al., 2008a,b), and Ross Sea (Pinkerton et al., 2010). But this modeling does not include the spatial and behavioral aspects that also structure ecosystems, which are of great importance to species' existence and coexistence in a given region. Aspects of coexistence have been investigated for portions of upper trophic levels in some marine systems, for instance among predatory fish, seabirds and cetaceans in the California Current (Ainley et al., 2009; Ainley and Hyrenbach, 2010), studies in which spatial and temporal use patterns, as well as behavior and diet were important. It was found, for example, that predatory fish and cetaceans can affect the niche space of seabirds through both facilitation and competition (see Section 4.3).

The mesopredators of the Ross Sea are dominated by year-round or near year-round species. Only the albatross and the cetaceans are seasonal visitors, and the cetaceans are not central place foragers, so only the albatross could be characterized as a commuter (Ainley et al., 1984). Therefore, we believe our modeling has identified the "critical habitat" (as opposed to commuting habitat) of this fauna.

In a mosaic of habitat use, respective spatial use of the Ross Sea among mesopredators had three patterns common to various groups of species: most of continental shelf and slope, mostly slope, and MIZ (which includes waters overlying the slope), reinforcing earlier analyses which found both the Ross Sea Shelfbreak Front, overlying the slope, and the MIZ to be important to these organisms (see Ainley and Jacobs, 1981; Karnovsky et al., 2007). Our model of species richness (spatial use of all predators together) and the Zonation results (showing areas of relative importance to all species) integrated these studies and showed that the Ross Sea continental shelf and slope, in a spatio-temporal mosaic, are a natural history unit at the community scale. Individual and combined models also showed the consistent importance of the shelf in determining environmental suitability, with distance to slope (and Shelfbreak Front) being the most influential covariate we examined; increasing distance from shelf break led to decreasing habitat suitability for all species except Weddell seal (Appendix B).

These findings are reinforced by a year-round analysis of Ross Sea use by Adélie penguins (Ballard et al., 2010), and an assessment of the importance of ocean fronts to Southern Ocean seabirds (Ribic et al., 2011). In the latter case, Antarctic-wide, where the Antarctic

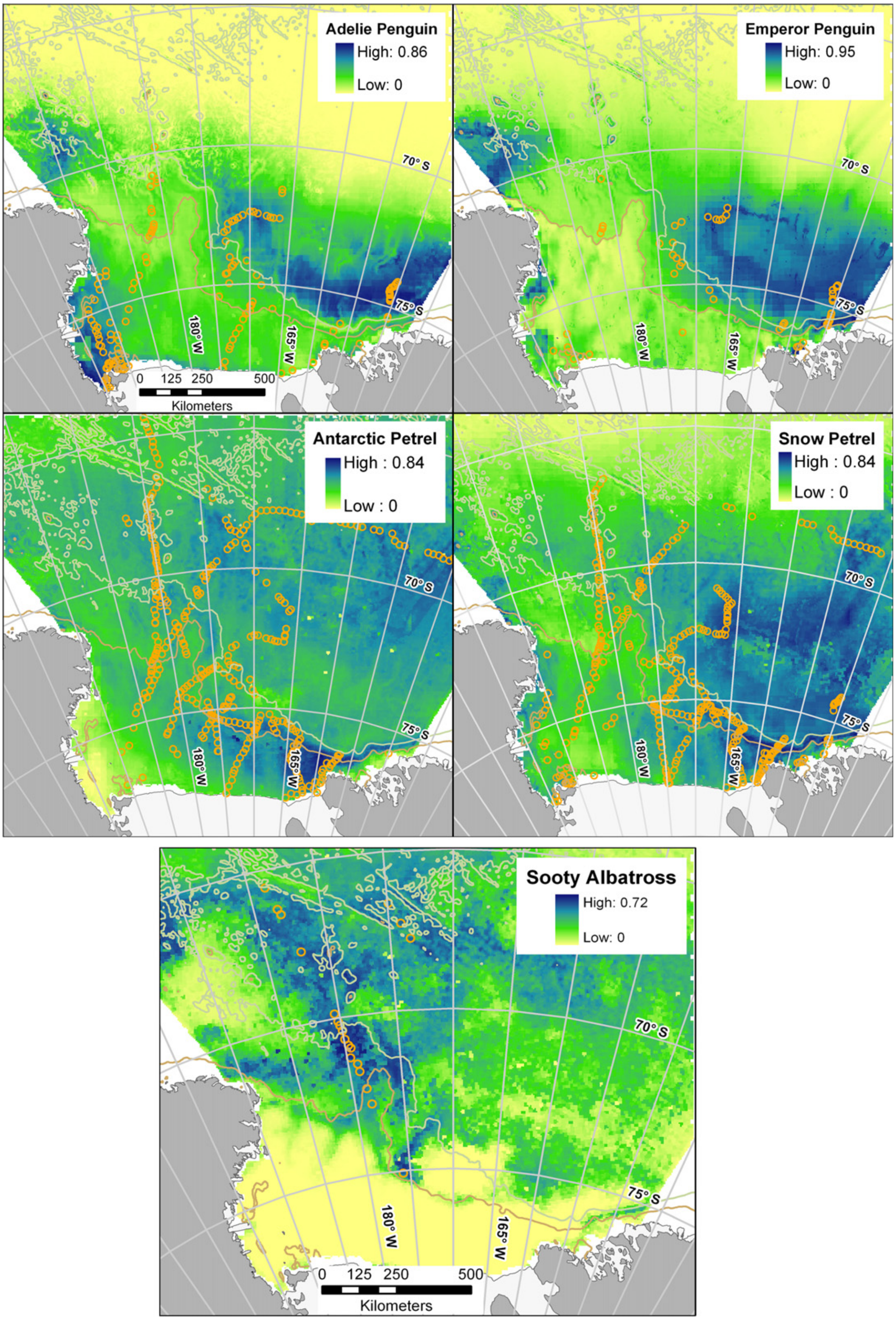

Fig. 3 (*continued*)

Shelfbreak Front coincides with various MIZs, it is the oceanic front rather than the ice front that is more important in explaining species occurrence. In the Ross Sea, the MIZ represents a habitat where the microbial community, namely the prevalence of diatoms, is the basis for a much more complex food web than that originating with *Phaeocystis antarctica*, a colonial alga that dominates the central-southern Ross Sea shelf where sea ice is less persistent (reviewed in Smith et al., 2012). Accordingly, many Ross Sea upper-trophic-level species appear to avoid the central-southern Ross Sea shelf, where the main predators are pteropods.

The importance of the outer shelf and slope to Ross Sea predators returns us to the questions raised in the Introduction: how can such large populations of predators, apex- and meso-alike, exist in the relatively small confines of the Ross Sea, and how can we pre-

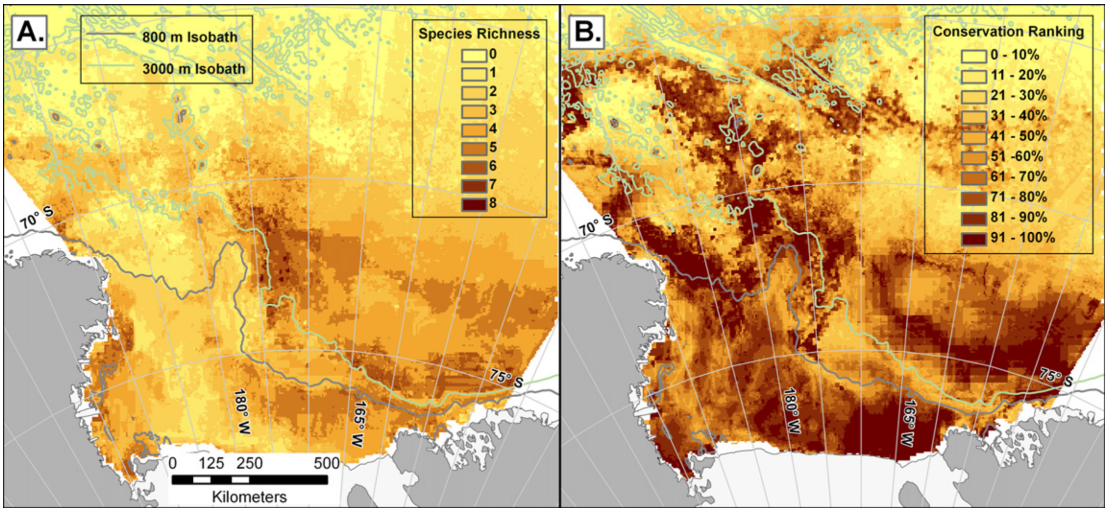

Fig. 4. (A) Modeled species richness (sum of individual species' Maxent-modeled environmental suitability) of mesopredators of the Ross Sea: minke whale, Ross Sea killer whale (ecotype C), crabeater seal, Weddell seal, Adélie penguin, emperor penguin, Antarctic petrel, snow petrel, and light-mantled sooty albatross. (B) Relative conservation importance for same species; results from Zonation core area analysis with all species given equal conservation priority (darker colors represent higher conservation ranking). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

serve this structure? The fact that there are very large populations of Ross Sea mesopredators seemingly explains the documented trophic cascade in which zooplankton standing stock is kept low, with lower-than-usual grazing on phytoplankton, and therefore higher phytoplankton concentrations (summary in Baum and Worm, 2009; Smith et al., 2012).

A spatial mosaic among mobile species at the fine scale is also part of the mechanism of coexistence in this system, with diet segregation having, if any, a negative effect. Diet overlap among mesopredators ranges from medium to high, and is especially high among the petrels and Adélie penguins, and between the albatross and crabeater seal. The fact that diet overlaps extensively is not surprising given that just three species are the main prey consumed in this system by mesopredators. The relative abundance of these prey (compared to other anthropogenically altered systems), resulting from the high level of primary production, probably further facilitates diet overlap among these mesopredators. Indeed, where diet becomes an important component of niche separation, often it is expressed mainly when food availability is low (Grant and Grant, 1993; Grant, 1999; Ainley and Boekelheide, 1990), which is not the case in the Ross Sea. By contrast, it appears that differences in depth of foraging are important to species' coexistence, especially for those having similar diet, as is the spread of areas where different species concentrate.

To an important degree the spread of spatial use among species is due to temporally out-of-phase natural history cycles. For example, the penguins and the Weddell seal, being central place foragers associated with the coast for breeding, are constrained to exist near land during spring and summer. Other than the extreme western and eastern portions of the Ross Sea, where most penguin colonies and Weddell seal haulouts are located, there is much of the outer shelf and slope devoid of them (other than non-breeding members of their population) during spring-summer, and thus providing little overlap with other mesopredator species at that time. In the late summer-autumn the penguins move from the western Ross Sea to the eastern Ross Sea shelf break where they fatten and then molt; the Weddell seals move out into the Ross Sea beginning late autumn and into the winter, a time when other species are migrating out of the area (Ainley et al., 2010). Other species exhibit analogous, temporally-defined use of Ross Sea space.

4.2. Limitations of the study

Predicting species habitat suitability from presence only data is not an ideal approach – further insights could be gained by using true absence information along with abundance data to create projections of numbers of individuals utilizing each grid cell. We chose not to include absence or abundance data, which were available for some (but not all) datasets for three primary reasons: (1) given the limited survey effort for the study area, relative to many others, especially terrestrial studies (generally only a single visit to any sampling location in the Ross Sea), we were not confident that that the absence data available were representative of "true" absences, due to incomplete and possibly biased survey coverage, which can lead poor modeling results (Mackenzie, 2005); (2) we wished to use a consistent approach for all species to make results directly comparable and to facilitate inclusion in the species richness and Zonation analyses; (3) Maxent is specifically designed for working well with presence-only data, and has been used in similar conservation prioritization situations previously (Kremen et al., 2008; Carroll et al., 2010). Additionally, for the two penguins and crabeater seals, besides cruise data, we also have satellite tracking data (Ainley et al., 2010), which show concordance with the habitat use identified by the models for these species. In other words, the occupation of waters overlying the shelfbreak front, primarily, and the shelf is obvious. Of course, more data collection would likely improve matters as well, especially if covariate data were collected contemporaneously. That being said, a multiple-species suite of mesopredators in very few areas of the Southern Ocean have been investigated as thoroughly as in the Ross Sea.

Indeed, our study benefitted from the wealth of data that have been aggregated over several decades by researchers working in the study area (Ainley et al., 2010). We were limited, however, in our ability to include environmental covariates collected at the same time as species' observations. Many of the datasets were collected prior to the availability of satellites, and high spatial resolution data are still not available for sea ice or chlorophyll (limited to 12.5 km now, 25 km for much of the study period). Although several of the environmental variables used in our model are temporally dynamic, they do hold distinct spatial patterns over long time periods. Still, it would be better to be able to use data collected at the time of the survey. Future studies will benefit from higher spatio-temporal resolution of covariates, assuming the food web remains intact long enough for these studies to be undertaken. Even so, our goal was to project patterns of current usage at a 5 km scale rather than to explore mechanisms explaining these patterns. Doing the latter would be of great interest, but would require a new multi-investigator effort.

4.3. Conclusions

The fact that the Ross Sea ecosystem is still largely intact provides a chance to investigate the sorts of phenomena and other factors that once structured marine ecosystems elsewhere but which can now usually be investigated only indirectly (e.g., Österblom et al., 2007; Christensen and Richardson, 2008). An intact ecosystem also allows investigation of the apparent large-scale trophic cascade that exists in the Ross Sea (Smith et al., 2012), and which may have been prevalent once in other ocean ecosystems (Pauly and Maclean, 2003). For these reasons, preservation of this ecosystem is a priority (ASOC, 2010).

The agency overseeing biotic resource exploitation in the Southern Ocean, the Commission for the Conservation of Antarctic Living Marine Resources (CCAMLR), is in the process of designating MPA’s (CCAMLR, 2007, 2008). So far it has designated one area, in the waters south of the South Orkney Islands, based primarily on foraging areas of breeding penguins and petrels (CCAMLR, 2009), and not including information from the non-breeding period or from other (non-avian) taxa. Since animals use different areas at different times of their life cycle in the Ross Sea, and since data are available for a broader time period and for a wider array of species in the Ross Sea than for the South Orkney Islands, we recommend a different approach for this region. At the least, consideration should be given to all the areas ranked highly in our Zonation analysis (i.e., most of the shelf break and large areas of the shelf), especially since this is the least-anthropogenically-affected marine ecosystem remaining on the planet (Halpern et al., 2008). We have been engaged in exactly such a process with the US delegation to CCAMLR, using the conservation prioritization grids as a context for evaluating the relative benefits of various potential MPA boundaries. For example, for any given boundary, which in practice has been suggested considering a wide range of economic, political, and environmental factors, we can calculate the proportion of the top 50%, 75%, and 95% conservation prioritization pixels that are included or excluded. Other methods of inclusion of this information are possible, such as kernel analyses or other methods of finding polygon boundaries based on the conservation prioritization values of clusters of pixels. However, there are a wide range of challenges in designing MPA boundaries that emphasize mobile species, including the fact that alteration of the abundance of one species (mobile prey) by fishing, can change the spatial extent of habitat use by other species (Pichegru et al., 2010, this issue). In the Ross Sea, this phenomenon is exhibited by foraging cetaceans (rather than fishing vessels), which alter the colony-based foraging range of penguins (Ainley et al., 2006), and by the foraging of seals, which alter the local presence of toothfish (Ainley and Siniff, 2009). As noted by Longhurst (2010, and references therein) thoughtful consideration of species’ natural history, spatio-temporal habitat use and species’ interactions, such as those reviewed herein, is key to designating the boundaries of an effective MPA.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.biocon.2011.11.017.

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