# ROSS SEA BIOREGIONALIZATION, PART II: PATTERNS OF CO-OCCURRENCE OF MESOPREDATORS IN AN INTACT POLAR OCEAN ECOSYSTEM

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9 10 Abstract. We report results of analyses of niche occupation among mesopredators in the Ross Sea region, Antarctica, considering three important components: 1) projected distribution and 11 12 overlap across the surface of the ocean, 2) capacity to utilize differing amounts of the water 13 column (foraging depth) and 3) diet. Species included were: Antarctic Minke Whale, Ross Sea 14 Killer Whale (ecotype C), Crabeater Seal, Weddell Seal, Emperor Penguin, Adélie Penguin, 15 Light-mantled Sooty Albatross, and Antarctic and Snow petrel. The apex predators, Leopard 16 Seal and Killer Whale ecotype A/B, were not included because of their rarity and, therefore, lack 17 of adequate sighting data on which to generate spatial models. We also did not have adequate 18 data to model Arnoux's Beaked Whales, Antarctic Toothfish nor Colossal Squid, which likely 19 are also important mesopredators, particularly adult toothfish. We modeled mesopredator species 20 distributions at a 5km/pixel scale, using environmental data and species presence localities from 21 at-sea surveys and other sources. A machine learning, "maximum entropy" modeling algorithm 22 (Maxent) was used to model spatial patterns of species' probabilities of occurrence, and these 23 data were used to identify areas of importance to species in a conservation prioritization 24 framework (Zonation). Data on depth of diving and diet were taken from the literature.

25 Three patterns of horizontal spatial use of the Ross Sea were apparent: 1) Shelf Break: 26 restricted mostly to the shelf break, which includes outer continental shelf and slope (Light-27 mantled Sooty Albatross); 2) Shelf and Slope: full use of both the shelf and the slope (Ross Sea 28 Killer Whale, Weddell Seal); and 3) Marginal Ice Zone (MIZ; pack ice surrounding the Ross Sea 29 post-polynya): combinations in which the slope is the main habitat but western and eastern 30 portions of the shelf (where sea ice is persistent) are used as well (Minke whale, Crabeater Seal, 31 penguins, petrels). Diet composition overlapped extensively, but use of foraging space was well partitioned by depth of diving. Horizontally, the entire suite of mesopredators used the entire 32 33 shelf and slope in a mosaic pattern although, not necessarily during the same season.

Spatial modeling of species richness, supported by Zonation analysis, indicated the outer shelf and slope, as well as deeper troughs in the Ross Sea Shelf and Ross Island vicinity to be particularly important to the upper trophic level organisms of the Ross Sea. Our results

37 substantially improve understanding of these species' niche occupation previously only

- 38 described using heuristic approaches.
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40 INTRODUCTION

41 Ecology is the study of organisms in relation to their environment. A basic thrust in the science

42 involves determining the spatial aspect of a species' occurrence, which usually means defining

43 its habitat, determining the biological and physical mechanisms of its existence there, and

44 determining why the species does not occur elsewhere (Grinnell 1917, MacArthur 1972). In this

45 process, ecology thereby seeks to define a species' niche within the specified "resource

46 utilization space," which includes habitat parameters, diet, and patterns of co-existence with

Appendix. Response curves for variables included in Maxent models.

These figures (one species per page) show mean (red line) and standard deviation (blue shading) modeled predictions of effect of the six included environmental variables on probability of species occurrence, keeping all other environmental variables at their average sample value. Results are from 30 bootstrapped Maxent runs. Relative influence of each environmental variable is given in Table 5.



Figure A1. Light-mantled Sooty Albatross



# Figure A2. Ross Sea Killer Whale

# Figure A3. Antarctic Petrel



# Figure A4. Adélie Penguin



# Figure A5. Emperor Penguin



# Figure A6. Snow Petrel



# Figure A7. Crabeater Seal



# Figure A8. Weddell Seal



# Figure A9. Minke Whale



other species (Elton 1927, MacArthur & Levins 1964, Diamond & Case 1986, Wiens et al.
2009). According to classic niche theory, especially where resources are limited, species should
be allocated among habitat types according to their relative capabilities to exploit respective
resources, and fewer species should occupy habitats with more unpredictable attributes (Lack

51 1954, MacArthur & Levins 1964).

52 In the earliest days of ecology, detailed records were kept on the conditions present where a 53 given species was encountered, including field sketches or photographs and the notes made on 54 specimen tags. In the context of the disappearance or movement of species in the present time of 55 rapid environmental change, such information has become increasingly valuable in order to 56 reconstruct a species' recent history of habitat use (e.g. Barry et al. 1995, Klanderud & Birks 57 2003). As the science of ecology has matured, the value of species' occurrence records has 58 benefited from the development of modeling techniques for revealing species-habitat 59 relationships, often from somewhat sparsely collected data (Elith et al. 2006, 2008, Phillips et al. 60 2006, Wiens et al. 2009). This is especially important for areas where little or no sampling has been directly carried out. Of course, with more and more ground- (or sea-) truthing, models are 61 62 improved and validated.

Owing to the high costs both in time and resources to sample the ocean, the use of models and spatial analysis has become particularly important to project occurrence patterns of marine species, for many of whom data are spatially clumped and otherwise sparse. This ability has, at least theoretically, increased the relevance of the "systematic conservation planning" that is

67 involved in identifying portions of the ocean that might deserve special management in the face
68 of competing pressures from human use of resources and other anthropogenic disturbances
69 (Margules & Pressey 2000, Ariame et al. 2003, Lombard et al. 2007).

70 Fortunately, the Ross Sea, which is the largest continental shelf ecosystem south of the 71 Antarctic Polar Front but which comprises just 2% of the Southern Ocean, is one of the better 72 known stretches of south polar seas due to a long history of investigation (see Ross Sea 73 Bioregionalization, Part I). Importantly, owing to its relative isolation from human civilization, 74 and protection of its coastal habitat under the Antarctic Treaty, including several Antarctic 75 Specially Protected Areas involving marine species, it is the anthropogenically least-affected stretch of ocean remaining on Earth (Halpern et al. 2008). It still has a full suite of top predators, 76 77 including large fish, birds, seals and whales (Ainley 2010), and some of these have been shown 78 to act together to deplete middle-trophic-level species (smaller fish and krill; Ainley et al. 2006, 79 Smith et al. in press). This wealth of apex and mesopredators in part must result from the Ross 80 Sea's unusually high primary production (estimated to be 28% of the total primary productivity 81 of the Southern Ocean south of  $50^{\circ}$ ) – implying that there are higher than expected amounts of phytoplankton available at the base of the so-called trophic pyramid (Arrigo et al. 1998, 2008; 82 83 Smith & Comiso 2008) and thus the potential for a very robust food web (Smith et al. in press). 84 Contributing to this exemplary phytoplankton concentration, as perceived by chlorophyll 85 measurements, is that phytoplankton 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 86 their upper-level predators (Table 1; Ainley et al. 2006, Baum & Worm 2009, Smith et al. in 87 88 press). For these reasons, and especially its relatively pristine condition, elucidating the patterns 89 of co-occurrence of this Ross Sea fauna within its relatively small confines may offer ecological 90 insights not possible elsewhere in the world ocean where most top predators have been severely 91 depleted for a long time (e.g., Pauly & Maclean 2003), and could help to answer the question of 92 how so many predators can exist there. Here we report results of analyses of niche occupation of all air-breathing mesopredators in the Ross Sea, considering three important components: 1)

projected distribution and overlap across the surface of the ocean, 2) capacity to utilize differing
 amounts of the water column (foraging depth) and 3) diet.

96 We knew from the outset (see Ross Sea Bioregionalization, Part I) that certain species would 97 be too rare or data insufficient to include in spatial modeling, such as Arnoux's Beaked Whale 98 Berardius arnouxii (rare) and Colossal Squid Mesonychoteuthis hamiltoni (sparse data, perhaps 99 rare). It also proved true that data for Antarctic toothfish (Dissostichus mawsoni), coming from 100 an industrial fishery, were too much affected by a strategy to maximize catch (kilograms) per 101 unit effort, and have not been summarized by fish size, for use in our modeling of adults (fish 102 >100 cm TL). It is the adults who, at least by analysis of stable isotopes, occupy the same trophic 103 level as Weddell Seals (Ainley & Siniff 2009). The lack of information about the distribution of 104 this mesopredator is unfortunate, given that in most oceans fish are the main predators (Sheffer et 105 al. 2005), and there is reason to expect an important predatory role in the Ross Sea foodweb as 106 well (Eastman (1993) characterizes the toothfish as the most important piscine predator in the 107 Southern Ocean). We also explored including the semi-apex predator, Leopard Seal (Hydrurga 108 *leptonyx*), and the apex Killer Whale (Orcinus orca) ecotype A/B (see Pitman and Ensor 2003), 109 but we had few sightings of the seal in our database (see Ross Sea Bioregionalization, Part I), 110 owing to their relative rarity and highly localized occurrence pattern during summer (near to 111 penguin colonies). We made an attempt to model the A/B Killer Whale, which would be the true apex predator in this system but, as our results show, we failed, likely because of their highly 112 nomadic life-history. Nevertheless, a broad array of mesopredators was available for analysis and 113 114 our results substantially improve understanding of their spatial occurrence patterns in the Ross

115 Sea, previously only described using heuristic approaches (Ainley et al. 1984, Ainley 1985).

#### 116 117 METHODS

# 118 *1a. Species Distribution Models: Explanatory Variables*

119 We defined the study area as all ocean waters south of 63° S between 165°E and 150°W (Figure

Environmental covariates were obtained from various sources (Table 2; see also Ross Sea
 Bioregionalization, Part I, for further discussion of these variables, including mapped displays).
 Before inclusion in species distribution models, all covariate data were resampled to 5 km
 resolution in ArcMap 9.3.1 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 conducted this resampling so that data could be easily matched to

126 the 5 km bathymetry available for the entire study area (ADD 2000), especially since the 127 resolution of almost all other source datasets was no better than this (Table 1). Monthly mean

128 percent sea-ice cover grids were obtained for July to September (winter ice) and December to

129 January (summer) for ten years, 1998-2008, from the National Snow and Ice Data Center

(Cavalieri et al. 2008) and averaged across all years to obtain one mean grid for each season
 (winter and summer). Ice cover data were collected on several of the cruises, but these data were

not available for all locations, and preliminary evaluation of models including these data for

133 subsamples of locations where they were available did not improve model performance (see

134 below for description of model evaluation). Slope (rate of change in depth) was derived from the

bathymetry layer (ADD 2000) and was calculated as the maximum change between a given celland its 8 neighboring cells, expressed as degrees.

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141 Table 1. Summary of the population size of upper trophic level predators in the Ross Sea, Antarctica, i.e. the waters

142 overlying the continental shelf and slope. Percentages give, as noted, the portion of the world or Southern Ocean (by 143 sector) population that occurs within the Ross Sea.

		Percent of	
	Number	World	
Species	Individuals	Population	Source
Antarctic Minke Whale	21,000	6 %	Branch 2006, Ainley
Balaenoptera bonaerensis			2010
Ross Sea (Ecotype C) Killer Whale	3350	~50 %?	Ainley 1985, Ainley et
Orcinus (orca) sp. nov.			al. 2009a, Morin et al.
			2010
Ecotype-A/B Killer Whale	70	?	Ainley 1985, Ainley et
Orcinus orca			al. 2009a
Weddell Seal Leptonychotes	30,000-	50-72 %	Stirling 1969, Ainley
weddellii	50,000	Pacific	1985, Erickson &
		sector	Hanson 1990
Crabeater Seal Lobodon	204,000	17 %	Ainley 1985, Erickson
carcinophagus		Pacific	& Hanson 1990
		sector	
Leopard Seal Hydrurga leptonyx	8,000	12 %	Ainley 1985
		Pacific	
		sector	
Adélie Penguin Pygoscelis adeliae	3,000,000	38 %	Woehler 1993
Emperor Penguin Aptenodytes	200,000	26 %	Woehler 1993
forsteri			
Antarctic Petrel Thalassoica	5,000,000	30 %	Ainley et al. 1984, van
antarctica			Franeker et al. 1999
Snow Petrel Pagodroma nivea	1,000,000	?	Ainley et al. 1984

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146 We calculated Pearson correlation coefficients for each pair of environmental covariates to 147 aid in covariate selection and interpretation of model results (Table 3). Prevalence of 148 Circumpolar Deep Water was relatively highly (negatively) correlated with bathymetry (82%) 149 and chlorophyll (73%), somewhat complicating interpretation of the relative influence of CDW 150 versus these variables. However, since our primary goal was to create the best possible 151 projections of species occurrences rather than to explain why these patterns exist in relation to 152 covariates, and since they were not completely correlated with one another, we kept them all in 153 the modeling process, especially given the relative paucity of potential covariates.

155 156 Table 2. Variables used in species distribution models, years of data collection, spatial resolution and source of

6	original data; see R	oss Sea Bioregion	alization, Part I, fo	or mapped display	ys of much of these data.
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			Original	
Data Tuna	Definition	Voors	sample	Source
Environmental	Demittion	1 cars	resolution	Source
Data				
Bathymetry (BTH)	Depth in meters		5km	ADD 2000
Prevalence of Circumpolar Deep Water (CDW)	Temperature and salinity defined water mass		5km	Orsi & Wiederwohl 2009; http://wocesoatlas.tamu.edu. Also, Dinniman et al. 2003, M. Dinniman, pers. comm.
Summer Sea Ice (SSI)	Mean percent cover (Dec - Jan)	1998 - 2008	25km	Cavalieri et al. 2008.
Winter Sea Ice (WSI); used for Weddell Seal only	Mean percent cover (Jul – Sen)	1998 - 2007	25km	Cavalieri et al. 2008.
Chlorophyll (CHL)	Mg x m <sup>-3</sup> averaged over 10 years (Nov – Jan)	1997- 2006	12.5km	NASA, J. Comiso, pers. comm.
Distance to Shelfbreak Front (DSH)	Euclidean distance (m) to the 800-m isobath			
Bathymetric gradient (SLP)	The angle of maximum change between cells in bathymetry grid (degrees)		5km	
Species Occurrence	Data			
Minke Whale distribution		1976- 1983, 1994, 2004	5km	D. Thiele, AnSlope cruises (2004); D. Ainley, RISP and NBP cruises.
Killer whale distribution		1976- 2004	5km	IWC, R.L. Brownell, Jr, pers.comm.; D. Thiele, AnSlope cruises, D. Ainley, RISP and NBP cruises.
Seal and seabird distributions		1976- 1981, 1994	5km	D. Ainley, RISP and NBP cruises.
Weddell Seal distribution	Positions of seals with satellite tags	1993- 1995, 1997- 2000	1km	Pers. comm.: B. Stewart, W. Testa, J. Burns, J. Bengtson, P. Boveng

157 Table 3 Pearson correlation coefficients for each pair of environmental covariates (see Table 2 for explanation of

acronyms).

	BTH	CDW	SSI	WSI	CHL	DSH
BTH	-					
CDW	-0.82	-				
SSI	-0.35	0.23	-			
WSI	-0.47	0.34	0.69*	-		
CHL	0.59	-0.73	-0.20	-0.22	-	
DSH	-0.47	0.37	-0.46	-0.28	-0.35	-
SLP	-0.03	0.24	-0.29	-0.18	-0.20	0.27

\* SSI and WSI were not included in the same models.

161 *Ib. Species Distribution Models: Dependent Variables* 

162 Sample sizes for all species included in modeling are shown in Table 4.

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164 <u>Minke Whale, Crabeater Seal, and seabirds.</u> Cruises were made aboard ice breakers as listed 165 below (Fig. 1). Dates encompass periods when the ships were within the study area and are

divided into early summer (15 December to 4 January) and late summer (16 January to 21

February). Before (and since), systematic observations of seabirds this far south were virtually

non-existent for early summer because of the heavy sea ice. Ships and dates of early summer

169 cruises were: USCGC Northwind, 15 December, 1976 to 4 January, 1977, and 19 December,

170 1979 to 2 January, 1980; and USCGC Burton Island, 23 December to 29 December, 1977. Late

summer cruises were made on USCGC Burton Island, 16 to 19 and 22 to 26 January, 1977;

172 USCGC Glacier, 2 to 21 February, 1979; R/V Nathaniel B. Palmer, 12-20 February 1994, and

173 (AnSlope cruises) 24 February-1 April and 21 October-5 December 2004.

174 Counts by (usually) two observers were made from the ice breakers' bridge wings, where eye 175 level was ~16 m above the sea surface, during hours that the ship traveled at speeds exceeding 6 knots during daylight (more or less continuous). The ships cruised at a maximum 10-12 knots in 176 177 open water. In all but AnSlope cruises, in which line transects were made for whales only 178 (involving >2 observers), continuous surveys were broken into half-hour segments equivalent to 179 a "transect." Transects were not made when visibility was <800 m, but rarely was visibility other 180 than excellent. In all but AnSlope cruises, we censused only birds and seals that passed within 181 300 m, and cetaceans with 800 m, of the side (forequarter) of the ship on which we positioned 182 ourselves to experience the least glare (AnSlope line transects were to the horizon). Transect 183 width was determined using a range finder. Ship's position, updated half-hourly, was determined 184 by satellite navigation. The distance traveled during each half-hour transect, multiplied by the 185 transect width, provided the area of the strip samples; dividing animal numbers by this area gave 186 an estimate of density. Birds that followed or circled the ship were counted only if they initially flew to it from the forequarter being censused. Binoculars (8X) were used to sweep the outer part 187 188 of the census strip visually about once every 1-2 min. We also scanned carefully for swimming 189 penguins.

190 Other than AnSlope cruises, counts of seals and whales were corrected by time of day, pod 191 size and probability of detection (see details in Ainley 1985). We know for certain that the

penguin survey results included all age-classes, as juveniles are identifiable by plumage (see

maps in Ainley et al. 1984); in fact, the younger age classes may be represented

194 disproportionately, as some portion of adults were at colonies during cruises. Results also

included all age classes of petrels on the basis of inspecting specimens collected at sea (Ainley et

<sup>160</sup> 

al. 1984), and we have reason to believe that all age classes of marine mammals that utilize thearea were represented, too.

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199 Killer whale. Some data on killer whales were available from the surveys described above, but

200 most of the presence data used herein came from the International Whaling Commission data

201 base gathered during the SOWR cruises 1987-2005. On the basis of pod size, as described in

202 Ross Sea Bioregionalization, Part I, we partitioned sightings into Ross Sea Killer Whale (=

- 203 ecotype C; pod size  $\geq$ 20) and ecotype A and B (combined; pod size  $\leq$ 10; see Pitman & Ensor
- 204 2003).
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Table 4. Number of locations where each species was detected and used for creating Maxent species distribution models.

Species	No. locations
Minke Whale	174
Ross Sea Killer Whale	38
Killer Whale A/B	72
Crabeater Seal	96
Weddell Seal	1023
Emperor Penguin	48
Adélie Penguin	136
Antarctic Petrel	329
Snow Petrel	337
Light-mantled Sooty Albatross	20
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Figure 1. Left panel: cruise tracks on which minke whales were surveyed, with bathymetry as base layer (lighter = shallower). Right panel: tracks on which seabirds and pinnipeds were surveyed (snow petrel sightings used for example). Right panel also shows typical sea-ice cover for period when most of the cruises were undertaken (mean

213 Dec-Jan ice concentration from Dec 1997 to Jan 2008 shown – black = no ice, lighter shades of gray = more ice).

214 See Ross Sea Bioregionalization, Part I for more details.

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## 217 Ic. Species Distribution: Maximum Entropy Modeling

218 We modeled probability of species occurrence using environmental data and species presence 219 (>0 counted) localities from surveys and sources described in Table 2. Presence data were 220 aggregated for each 5 km cell in the study area, and locations that fell outside of the extent of any 221 of the environmental layers were not used. We used a machine learning, "maximum entropy" 222 modeling method called Maxent (v.3.3.1; Phillips et al 2006, Phillips & Dudík 2008) to estimate 223 probability of each species' occurrence in each cell given the modeled relationship between a 224 given species and the environmental covariates, using Maxent's logistic output format (Phillips 225 & Dudík 2008). This is a method that has been used several times recently to achieve goals 226 similar to ours (Kremen et al. 2008, Stralberg et al. 2009, Carroll et al. 2010). Maximum entropy 227 modeling can predict species' distributions from relatively sparse amounts of presence-only 228 information by estimating the probability distribution that has maximum entropy (most uniform 229 or spread out across prediction space) while meeting the constraints imposed by the (incomplete) 230 information available about the actual distribution and avoiding any other assumptions (Jaynes 231 1957; Phillips et al. 2006; Phillips & Dudík 2008). These constraints require that the mean of 232 each environmental covariate across the entire prediction space in the model selected by Maxent 233 be approximately equal to the empirical average of this variable across all sample locations. How 234 close to equal these means are is a parameter (called "regularization") that is automatically 235 optimized by Maxent for each model, but which can be manually specified, with higher values 236 resulting in lower likelihood of model over-fitting, but also potentially in lower model specificity 237 (Phillips & Dudík 2008). We ran each model 30 times using a bootstrapping approach using the 238 full dataset available in a random sort order each time. Thus, the model results presented are the 239 ensemble means.

240 Covariate data in Maxent are allowed to have six types of relationship to the species 241 occurrence likelihood – linear, quadratic, product (i.e., interaction of two covariates), threshold, 242 hinge, and category indicator; each type is evaluated with respect to creating the model with the 243 highest entropy, with the best version retained. Threshold and hinge covariates allow modeling 244 of an arbitrary response of the species to the covariate from which they are derived (Phillips and 245 Dudík 2008). Maxent out-performs almost all other existing distribution modeling algorithms 246 and at least equals the best known methods when compared to known distributions, including 247 good performance using a limited number of presence locations (Phillips et al. 2006, Elith et al. 248 2006, Hernandez et al. 2006, Wisz et al. 2008, Phillips & Dudík 2008).

249 We produced Receiver Operating Characteristic (ROC) plots (true positives vs. false 250 positives) based on presence and background ("pseudo-absence") data (Elith 2002, Phillips et al. 251 2006). The ROC area under the curve (AUC) values for a randomly selected 25% test portion of 252 the data in each of 30 model runs was used to evaluate model performance (Table 5). Because 253 we did not have true absence data, AUC scores represent the probability that a randomly chosen 254 presence location was assessed to be more likely to have the species present than a randomly 255 selected pseudo-absence location chosen from the entire study area (Phillips et al. 2006). A 256 model that does not perform better than random would have an AUC of 0.5, while a perfect 257 model would have an AUC of 1.0. Models with AUC above 0.75 are considered potentially 258 useful, 0.80 to 0.90 good, and 0.90 to 1.0 excellent (Swets 1988, Elith 2002). While this method 259 is not perfect (Lobo et al. 2007), several of the criticisms of AUC do not apply in the context of 260 this paper (e.g., weighting omission and commission errors equally does not impact our findings, the spatial extent of the models was all the same; Lobo et al. 2007). Model outputs were also

- visually inspected and compared to location data and previous expert-based mapping efforts (see
- Ross Sea Bioregionalization, Part I). In preliminary validation model runs we investigated
- 264 contributions of individual covariates for evidence of model over-fitting and evaluated the effect
- of raising the Maxent regularization value above the default settings, with and without bootstrapping. In all cases best model performance (in terms of test AUC) was achieve
- bootstrapping. In all cases best model performance (in terms of test AUC) was achieved by
   accepting the default Maxent regularization parameter and bootstrapping. In several cases,
- however, inspection of the covariate response curves suggested over-fitting, and increasing
- regularization did not penalize AUC substantially (generally 1 3%). Thus, for these species we
- present bootstrapped results with regularization coefficients set to 2 (i.e., default regularization x
  2), and these are the values used in subsequent analyses for Antarctic Petrel, Adélie Penguin,
- 272 Snow Petrel, Crabeater Seal, Weddell Seal, and Minke Whale.

273 We evaluated another machine learning method for predicting species occurrence, boosted 274 regression trees, using presence/absence and abundance data (Elith et al. 2008, Leathwick et al. 275 2008) to validate the maximum entropy results, and to investigate whether multiple interactions 276 among covariates (up to 5) were influential in predicting species occurrence/absence. We noted 277 no substantial improvements in results (e.g., in AUC values), and we were not able to use this 278 method consistently for all species due to the lack or incomplete availability of absence and 279 abundance data available for some (Weddell Seal, Minke Whale, and both Killer Whale species) 280 Also, given the limited survey effort for the study area, relative to many other, especially 281 terrestrial studies (generally only a single visit to any sampling location), we were not confident 282 that that the absence data available were representative of "true" absences, due to incomplete and 283 possibly biased survey coverage, which can lead poor modeling results (Mackenzie 2005). For 284 these reasons we chose to use Maxent for all results reported herein.

For all species other than Weddell Seal, data represent distribution during December-February (killer whales to April), and ice and chlorophyll data from that portion of the year was used in the modeling. During that period, Weddell Seals are concentrated on coastal fast ice, where even icebreakers rarely pass. Therefore, for Weddell Seals, satellite positions were used, and mostly from March – October when the seals are free to leave coastal ice cracks and we used ice data from the middle of that portion of the year (July-September; Fig. 3).

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293 294 295 296 297 Figure 3. Positions of Weddell Seals during winter as determined by satellite transmitters. Also shown is typical sea ice cover for the period when positions were determined (mean Jul - Sep ice concentration for 1997 to 2007 shown; black = no ice, lighter shades of gray = more ice; white is continental ice). These seals were initially tagged outside the Eastern boundary of the map and subsequently moved into the Ross Sea over the next several months.

298 Id. Species Distribution: Comparison of Spatial Overlap, Overall Species Richness, and

*identification of relative conservation importance* 

300 Using results from the species distribution models, we created an index of the amount of spatial 301 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 302 303 each model that maximized training sensitivity and specificity (Phillips et al. 2006) and removed 304 areas that fell below this threshold. We chose this method of conversion because other methods, 305 such as setting an arbitrary fixed threshold for all species, have been shown to bias results (Liu et 306 al. 2005). We then multiplied the values of the remaining pixels between each species pair and 307 calculated the overall mean to get an index of co-occurrence, which equals the mean probability 308 that both species occurred in any given pixel within their combined ranges. The remaining pixels 309 were also used to calculate the total area of probable occurrence for each species and of co-310 occurrence for each species pair (i.e., the combination of both species' total area of probable 311 occurrence) in km<sup>2</sup>. Weddell Seal was included in this analysis, out of interest, comparing its winter occurrence patterns with the summer patterns of other species. 312

To estimate species richness and identify potentially important zones within the study area, we summed pixel-level probabilities of occurrence (i.e., the original, continuous values produced by Maxent) across all species.

316 We used the hierarchical reserve selection software Zonation 2.0 (Moilanen et al. 2005) to 317 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 318 319 potential large scale Marine Protected Areas (Leathwick et al. 2008) and terrestrial conservation 320 priorities (Kremen et al. 2008, Carroll et al. 2010). Zonation offers three advantages over other 321 reserve design software from our perspective: 1) it allows the creation of a continuous, 322 hierarchical surface of conservation values across the entire study area; 2) it works from grids 323 rather than polygons, which simplifies use with other software (especially geographic 324 information systems) and means that the user is not required to draw any pre-conceived lines on 325 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 simple, unconstrained or "no cost 326 327 constraint" approach, where all cells were assumed to have equal potential conservation costs 328 and prioritization was established simply by evaluating species' projected distributions and 329 connectivity, with equal weight given to all species' "conservation value." Because we had a 330 definite list of species for which we wished to rank locations and because we wanted to 331 emphasize locations with the highest occurrence probabilities we chose to use a core area 332 definition of marginal loss in the Zonation software, which prioritizes the inclusion of high-333 quality locations for all species (Moilanen et al. 2005, Moilanen 2007, Leathwick et al. 2008, 334 Carroll et al. 2010). For our purposes, the important characteristic of this type of Zonation 335 analysis is that, assuming comparison of two identical locations with identical projected occurrence for two different species, the one given higher rank is the one that contains the 336 337 species that has lost more of its distribution up to that point in the modeling run. The grid cells given the lowest ranks are ones that do not contain high occurrence probabilities for any of the 338 339 target species, whereas the cells given highest ranks are the ones that contain the highest 340 probabilities of occurrence for the most species, bearing in mind that species which do not 341 overlap any others would still need to have some locations retained. The mathematical details 342 and other methodological information pertaining to core-area Zonation are provided by Moilanen 343 et al. (2005) and Moilanen (2007).

- 344
- 345 2. Depth of Foraging

346 We obtained information on maximum depth of diving, a measure of foraging capability, from

347 the literature (Fig. 4). Obviously, the ideal would be to investigate all the Ross Sea

348 mesopredators simultaneously, as seemingly food availability and competitive interactions would

349 affect diving behavior; indeed, Adélie Penguins forage deeper when in the company of Minke 350

- Whales (Ainley et al. 2006; Ballard et al. unpubl. data). In any case, we could not use mean 351 depth of foraging in any situation, as this information is not available for all species, i.e., not for
- 352 Minke Whale, which was estimated on the basis of body size, killer whale, nor the petrels. For
- 353 each species pair, we then determined degree of overlap by dividing the depth of the species
- 354 having shallowest dives by that of the one having deeper dives.
- 355



356 357 Figure 4. Overlap in the maximum diving depths exhibited among top-trophic (air-breathing) predators of the Ross 358 Sea shelf and slope. Data on diving depths from: Kooyman 1989, Schreer & Kovacs 1997, Baird et al. 2003, Burns 359 et al. 2004, Ballard et al. unpublished data. Depth for minke whale estimated based on comparable body size to 360 killer whales (Baird et al. 2003); diving depth generally correlates to body size in vertebrates (see Kooyman 1989). 361 Instrumented Weddell Seals have been constrained by bottom depth in regard to the maximum depths that they 362 could attain (thus likely an underestimate?); the much smaller Crabeater Seal, on the other hand, has been 363 investigated where bottom depth would not constrain deep diving. On the basis of arguments presented in Kooyman 364 (1989), Weddell Seal should be capable of diving much deeper than has been measured.

- 365
- 366 3. Diet

367 We determined an index to the degree of diet overlap among species pairs using data from the

368 literature on frequency of occurrence of krill (Euphausia superba, E. crystallorophias) and 369 silverfish (*Pleuragramma antarctica*) in the diet (Fig 5). These are the two prey types/species

- 370 that predominate in this system (summarized in Smith et al. 2007, in press; see also Ross Sea 371 Bioregionalization, Part I). We could not use other measures, such as diet based on mean mass of
- prev nor index of relative importance, because not all species had sufficient detail available (e.g.
- 372 373 minke whale, killer whale). For krill, and then independently for silverfish, we determined the
- 374 percent of overlap by dividing the species having the lowest frequency by that having the higher;

376 preying on one of the two diet species (e.g. Weddell Seal: silverfish only) compared to a predator

not preying on the other (e.g. Crabeater Seal: krill only), we considered this 0% overlap rather
 than 50% overlap.

379



380 381

Figure 5. Prevalence of Antarctic silverfish and krill (all species) in the diet of (air breathing) top-predators over the
Ross Sea shelf and slope, thus indexing degree of diet overlap. Data from Ainley et al. 1984, 2003; Burns et al.
1998, Cherel & Kooyman 1998, Green & Burton 1987, Pitman & Ensor 2003, and Ichii et al. 1998. Values shown
for minke whales are a large underestimate for silverfish, as Ichii et al. only presented the proportion of samples in
which silverfish was the *dominant* prey, not the proportion of samples in which silverfish occurred; values for killer
whales are a guess (the only fish available to them in any quantity would be silverfish and toothfish; see Ainley et al.
2009a).

388 389

# 390 RESULTS

391 *Model Performance* 

392 Model (test data) AUC scores ranged from 0.745 (Killer Whale A/B) to 0.926 (Weddell Seal and

Light-mantled Sooty Albatross) and averaged 0.857 (Table 5). The most influential variable in

394 species distribution models overall was distance to the shelf break, followed by prevalence of 395 Circumpolar Deep Water. Distance to shelf break was negatively correlated with probability of

396 occurrence for all species except Weddell Seal (Appendix). Slope was the least influential

397 variable overall. Response curves and standard deviations for variable influences for all models

398 are in the Appendix.

Three patterns of spatial use of the Ross Sea became apparent: 1) Shelf Break: restricted mostly to the shelf break, which includes outer shelf and the slope (Light-mantled Sooty

401 Albatross; Fig. 6); 2) Shelf and Slope: full use of both the shelf and the slope (Ross Sea Killer

402 Whale, Weddell Seal; Fig. 6); and 3) Marginal Ice Zone (MIZ; pack ice surrounding the Ross

403 Sea post-polynya): combinations in which the slope is the main habitat but western and eastern 404 portions of the shelf are used as well (Minke Whale, Crabeater Seal, penguins, petrels; Fig. 6).

404 portions of the shell are used as well (Minke whale, Crabeater Seal, penguins, petiels, Fig. 6). 405 This last pattern is consistent with correlation to the presence of pack ice, either over the slope or

406 over the shelf (cf. Karnovsky et al. 2007).

107	Table 5 Spacing	distribution mode	l marfarmanaa (maaa	ALIC   standard derivation	n for 20 hootstronged muse using all
40/	Table 5. Species	s distribution mode	i periormance (mea	$1 \text{ AUC} \pm \text{standard deviatio}$	In for 50 bootstrapped runs using an
100	1		1		11 8
AANO	1 / 1 1 1			1 111 111	110100

408	data) and heuristic estimates of pe	rcent contribution of each variable to the Maxent model. Bold font indicates most
400	influential contrability and have a	$r^{2}$ and $r^{2}$ do not the second second for $W_{2}$ do $11$ Secold (for otherwork even and $r^{2}$ is $r^{2}$

409	influential variable in each species	model; winter sea ice cover used for Weddell Seals (for others: summer sea ice)
		Percentage Contribution to distribution model

			rereentage	Contributio	in to distribut	ion model	
						Distance	
				Sea Ice	Prevalence	Shelfbreak	Bathy
Common Name	$AUC \pm SD^1$	Chloro	Bathy	Cover	CDW	Front	Gradient
Minke Whale	$0.923 \pm 0.008$	14.7	9.4	9.3	13.3	49.5	3.9
Ross Sea Killer	$0.934\pm0.02$	8.0	9.0	6.7	57.0	13.2	6.2
Whale							
Killer Whale A/B	$0.814\pm0.03$	9.2	23.7	16.9	16.8	15.4	18.0
Crabeater Seal	$0.871 \pm 0.015$	5.3	6.4	15.5	19.8	48.8	4.2
Weddell Seal	$0.926\pm0.002$	3.7	40.9	7.3	20.0	27.2	0.9
Emperor Penguin	$0.928\pm0.01$	4.0	12.3	13.6	8.5	52.5	9.0
Adélie Penguin	$0.906 \pm 0.009$	7.9	13.6	6.2	30.6	39.1	2.6
Antarctic Petrel	$0.820\pm0.008$	6.2	3.3	22.7	23.6	41.8	2.4
Snow Petrel	$0.852\pm0.008$	12.5	6.3	12.1	18.9	46.9	3.3
Light-mantled	$0.962 \pm 0.008$	27.2	20.0	24.9	14.9	9.4	3.5
Sooty Albatross							
Total		98.7	144.9	135.2	223.4	343.8	54.0

410 <sup>1</sup>AUC's reported in table are for full dataset used in models. AUC's for bootstrapped test data (random 25% subset 411 of each of 30 model runs): Minke Whale:  $0.896 \pm 0.02$ ; Ross Sea Killer Whale:  $0.881 \pm 0.05$ ; Killer Whale A/B:

 $0.745 \pm 0.07$ ; Crabeater Seal:  $0.803 \pm 0.03$ ; Weddell Seal:  $0.926 \pm 0.004$ ; Emperor Penguin:  $0.884 \pm 0.04$ ; Adélie 413 penguin:  $0.885 \pm 0.02$ ; Antarctic Petrel:  $0.797 \pm 0.02$ ; Snow Petrel:  $0.823 \pm 0.02$ ; Light-mantled Sooty Albatross:

 $0.926 \pm 0.04$ .

416 Figure 6. Mean (from 30 bootstrapped runs) modeled probability of occurrence for marine predators in the Ross Sea, 417 Antarctica; results of maximum entropy modeling using Maxent. Presence locations from which models were

418 created are displayed as orange circles (see Figure 3 for Weddell Seal presence locations, and see Figure 1 for full

419 survey effort). Map for Weddell Seal is for winter distribution (all others are summer). During summer Weddell

420 seals are confined mostly to haul outs along the coast, i.e. tide cracks between fast ice and shore. Such habitat was



Figure 6 (continued)



#### Figure 6 (continued)



422

744	
423	Analysis of species overlap indicated relatively little overlap in horizontal space. The highest
424	overlap was between Antarctic and Snow petrels (26%; Table 6), while most species did not
425	overlap more than 20% (median = 15%) in projected probability of co-occurrence, thus
426	indicating relatively well-distributed occupation of potential spatial niches. In other words, these
427	species' occurrence constituted a sort of mosaic of Ross Sea space. The test AUC score for Killer
428	Whale A/B was <0.75 and the resulting model did not appear to discriminate based on any
429	habitat covariates in particular. This relatively poor modeling score was likely due to the fact that
430	these are two nomadic forms of killer whale, and associate with mammal prey of several types
431	(seals, whales) rather than specific habitat (see Pitman & Ensor 2003). Indeed satellite tags
432	placed on Killer Whale B's showed them to be highly mobile, passing quickly between areas
433	where potential prey (Emperor Penguins, Weddell Seals) congregate (Andrews et al. 2008). This
434	is the only model that we view as unsatisfactory, and we therefore did not include this species in
435	further analyses.
436	

437 438 439 Table 6. Total area of modeled probable occurrence and index of probability (%) of co-occurrence of species in the Ross Sea region during summer, except for Weddell Seal (winter only, in italics). Overlap indices >15% (the median for summer species co-occurrence) are shown in hold font

					Perc	ent Ov	erlap		
	Species Area,						_		
Species	km <sup>2</sup>	1	2	3	4	5	6	7	8
1. Minke Whale	441,200	-							
2. Ross Sea Killer Whale	247,050	11	-						
3. Crabeater Seal	627,750	16	10	-					
4. Emperor Penguin	331,625	13	7	18	-				
5. Adélie Penguin	548,000	15	9	19	16	-			
6. LM Sooty Albatross	271,375	7	4	8	6	4	-		
7. Antarctic Petrel	643,475	19	13	21	15	15	12	-	
8. Snow Petrel	738,700	17	12	23	17	18	8	26	-
9. Weddell Seal	424,975	15	14	19	17	18	5	18	20

# 442 Species Richness and Conservation Ranking

The species richness and conservation ranking
The species richness analysis integrated the spatial models of all upper trophic level predators.
Even more than the individual models, the species richness model highlighted the importance to
Ross Sea biodiversity of the shelf break region, and other places on the shelf (the troughs
between banks; Fig.7A) where the intrusion of Circumpolar Deep Water was most prevalent, and
also the Ross Island vicinity. See maps of CDW in Ross Sea Bioregionalization, Part I (also
Dinniman et al. 2003, and pers. comm.). While CDW generally was negatively correlated with

species' probabilities of occurrence (Appendix), this is likely because of its prevalence in the
 pelagic portion of our study area, where most species were less likely to occur.

Zonation conservation ranking results also highlighted the importance of most of the Ross
Sea shelf break (outer shelf and slope), Ross Island vicinity, and troughs in the shelf, but also
elevated the importance of the Eastern Ross Sea shelf and pelagic waters overlying areas of

- 454 bathymetric complexity (ridges in northern part of study area; Figure 7B).



Figure 7. (A) Modeled species richness (sum of individual species' Maxent-modeled probabilities of occurrence) of
mesopredators of the Ross Sea: Ross Sea Killer Whale (ecotype C), Minke Whale, Crabeater Seal, Weddell Seal,
Emperor Penguin, Adélie 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).

### 466 Partitioning of Vertical Space and Diet

- 467 A review of the literature revealed that among Ross Sea mesopredators a high degree of
- 468 partitioning of the shelf and slope habitat exists in the vertical dimension. Species with strong
- use of the shelf, and which are present during the winter as well, i.e. Weddell and Crabeater seals
- 470 and Emperor Penguin (and adult, therefore neutrally buoyant, Antarctic Toothfish), all are
- 471 capable of using the entire water column from the shelf bottom to the surface and, thus,
- 472 experience among themselves >70% overlap in foraging depth (Figure 3, Table 7). Only over the
- 473 deeper waters of the slope could any vertical spatial partitioning be expressed, other than that
- 474 aspect of dive behavior affected by the prey being targeted. Deep diving by the seals and
   475 Emperor Penguin provides access to maximum water volume without needing much horizontal
- Emperor Penguin provides access to maximum water volume without needing much horizontalmovement, which would be constrained by the heavy pack ice conditions of winter. The
- 477 remaining mesopredators are composed of medium-deep divers (whales), shallow divers (Adélie
- 478 Penguin), and surface foragers (petrels, albatross). Complete overlap in foraging depth exists
- 479 among the aerial birds and among the whales. Otherwise, there is little overlap in foraging depth
- 480 by the majority of species.
- 481

482 Ta	able 7. Percent c	overlap in ma	ximum diving	depth among	g Ross Sea toj	p mesopredators.
--------	-------------------	---------------	--------------	-------------	----------------	------------------

		0 1	U					
Species	1	2	3	4	5	6	7	8
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

483

Based on a literature review of mesopredator diet, it appears that the deep-diving yearround/winter inhabitants, Weddell Seal and Emperor Penguin, are mainly piscivorous,
particularly preying on Antarctic silverfish (Fig 5, Table 8). The silverfish, or "herring of the
Antarctic" (DeWitt and Hopkins 1977), is also confined to the shelf, and perhaps its existence is

488 key to the wintertime presence and deep diving of these predators. As noted above, these
 489 predators, along with adult toothfish, also completely overlap in depth of foraging. The Ross Sea

490 Killer Whale (ecotype C) to a small degree may be included in this diet pattern. Feeding just on

491 fish, it likely does not dive as deep and, as far as is known, probably departs the area during

492 winter (R. Pitman pers. comm.).

493 Otherwise, the degree of overlap in diet among the remaining species, except for the near494 surface feeding petrels and albatross, is appreciable though less than the above, i.e. ~50%, in
495 most comparisons. Predators that forage heavily on krill, and tend to not dive deeply, occur
496 principally over the slope (Minke Whale, Crabeater Seal, albatross). The outer shelf and slope is

497 where krill biomass is maximum (Ross Sea Bioregionalization, Part I).

498

Table 8. 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
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

501

502 503

# 504 DISCUSSION

Both the importance of the outer shelf and slope to the Ross Sea mesopredator community and
 the mosaic spatial pattern by which these predators used this habitat was noteworthy. To our

507 knowledge this is the first time that modeling of spatial use and niche overlap among the

508 majority of mesopredators within an ecosystem — cetaceans, pinnipeds and seabirds —has been

509 attempted in a marine setting. It has been done for terrestrial habitats, particularly in the context

510 of the recent "experiments" undertaken when apex predators have been re-introduced, with

511 resulting cascading effects on the diet and space use of mesopredators, the apex predators having

been absent for decades (McLaren & Peterson 1994, Ripple & Beschta 2004, Prugh et al. 2009).
Competition and niche overlap has also been investigated among numerous, closely related

513 Competition and niche overlap has also been investigated among numerous, closely related 514 assemblages of terrestrial vertebrate species, such as birds, lizards, and small mammals

515 (reviewed in Diamond & Case 1986).

516 In marine systems, recent food web modeling could be used to assess trophic overlap, if only 517 indirectly, as for instance the analyses of Österblom et al. (2007) for the Baltic Sea, Watermeyer

et al. (2008a, b) for the Benguela Current, or even Pinkerton et al. (2008) for the Ross Sea.

519 However, this modeling does not include the spatial and behavioral aspects that also structure

520 ecosystems, are of great importance to species' coexistence, and in fact are important to a species

521 existence in a given region. Aspects of coexistence have been investigated for portions of upper

522 trophic levels in some marine systems, for instance among predatory fish, seabirds and cetaceans

523 in the California Current (Ainley et al. 2009b, Ainley & Hyrenbach 2010), studies in which

524 spatial and temporal use patterns, as well as behavior and diet proved to be important. It was 525 found, for example, that predatory fish and cetaceans can affect the niche space of seabirds,

525 Found, for example, that predatory fish and cetaceans can affect the mene space of seatones, 526 sometimes through facilitation and others through competition, a subject which we will return to 527 helew.

527 below.

528 The mesopredators of the Ross Sea are dominated by year-round (seals, Emperor Penguin,

529 possibly the petrels, which forage well in the dark; Ainley et al. 1992) or near year-round species

530 (Adélie Penguin). Only the albatross and the cetaceans are seasonal visitors, and the cetaceans

are not central place foragers. Therefore, we believe our modeling has identified the "critical

532 habitat" (as opposed to commuting habitat) of this fauna. In a mosaic of habitat use, respective 533 spatial use of the Ross Sea among mesopredators had three patterns common to various groups 534 of species: most of shelf and slope, mostly slope, and MIZ (which includes waters overlying the 535 slope). It is not surprising that earlier separate analyses found both the Ross Sea Shelfbreak Front 536 and the MIZ to be important to these organisms (see Ainley & Jacobs 1981, Karnovsky et al. 537 2007). Our model of species richness (spatial use of all predators together) and the Zonation 538 results (showing areas of relative importance to all species) integrated these studies, as well as 539 the spatial use patterns of the individual mesopredators, and showed that the Ross Sea shelf and 540 slope, in a spatio-temporal mosaic are a natural history unit at the community scale. Individual 541 and combined models also showed the consistent importance of the shelf in determining 542 likelihood of occurrence, with distance to slope (and Shelfbreak Front) being the most influential 543 covariate we examined (increasing distance from shelf break led to decreasing probability of 544 occurrence for all species except Weddell Seal). This is further reinforced by a year-round 545 analysis of Ross Sea use by Adélie Penguins (Ballard et al. 2010; see also Rosss Sea 546 Bioregionalization, Part I), and a recent comparison of the importance of ocean fronts to 547 Southern Ocean seabirds, Antarctic-wide: in cases where the Antarctic Shelfbreak Front 548 coincided with various MIZs, it is the oceanic front rather than the ice front that is the more 549 important in explaining species occurrence (Ribic et al. 2010). On the other hand, in the Ross 550 Sea, the MIZ represents a habitat where the microbial community, namely the prevalence of 551 diatoms, is the basis for a much more complex food web than that originating with *Phaeocystis* 552 antarctica, a colonial alga that dominates the central-southern Ross Sea shelf where sea ice is 553 less persistent (reviewed in Smith et al., in press). Accordingly, many Ross Sea upper trophic 554 level species appear to avoid the central-southern Ross Sea shelf, where the main predators 555 appear to be pteropods.

The importance of the outer shelf and slope to Ross Sea predators returns us to the question 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? The fact that there are so many Ross Sea mesopredators seemingly explains the documented trophic cascade in which zooplankton standing stock is kept low, with lower-than-usual grazing on phytoplankton (summary in Baum & Worm 2009, Smith et al. in press).

562 Spatial separation mosaic is part of the mechanism of species coexistence in this system, with 563 diet segregation playing a minimal part. Diet overlap among mesopredators ranges from medium 564 to high. Diet overlap is especially high among the petrels and Adélie Penguins, and between the 565 albatross and Crabeater Seal. The fact that diet overlaps extensively is not surprising given that 566 just three prey are the main species consumed in this system (two krill species, silverfish). The 567 relative abundance of these prev (compared to other anthropogenically altered systems), resulting from the high level of primary productivity, would further facilitate the diet overlap among 568 569 mesopredators. Indeed, where diet becomes an important component of niche separation, often it 570 is expressed mainly when food availability is low (Grant & Grant 1993, Grant 1999, Ainley & 571 Boekelheide 1990), which is not the case in the Ross Sea. On the other hand, it appears that 572 differences in depth of foraging are very important to various species' coexistence, especially for 573 those species having similar diet, as is the spread of areas where different species concentrate. 574 To some degree the spread of spatial use may be an artifact of out-of-phase natural history 575 cycles, which actually would contribute to co-existence at the Ross Sea scale. (1) The penguins 576 and the Weddell Seal, being central place foragers, are constrained to exist very close to land

577 during spring and summer (Their confinement was one factor that we propose caused the poor

578 performance of the spatial model of the apex predator, Killer Whale B, in that these killer whales 579 would be keying on several different prey, penguins and seals, and not necessarily habitat). Other 580 than the extreme western and eastern portions of the Ross Sea, where most penguin colonies and 581 Weddell Seal haulouts are located, there is much of the outer shelf and slope devoid of them 582 (other than non-breeding members of their population) during spring-summer, and thus 583 providing little overlap with other species. In the late summer-autumn the penguins move from 584 the western Ross Sea to the eastern Ross Sea Shelfbreak region in order to fatten and molt; the 585 Weddell Seals move out into the Ross Sea beginning late autumn and into the winter, a time 586 when other species are migrating out of the area (see Ross Sea Bioregionalization, Part I). The 587 seals tend to occur over deeper areas. (2) Most of the petrels that frequent the Ross Sea slope do 588 so from the east, apparently closer to (mostly unknown) breeding areas in the mountains of 589 Marie Byrd Land and Ellsworth Land (Ainley et al. 1984). These petrels forage as they go, 590 mainly along the shelfbreak, which is close to shore where they begin their flights over the 591 ocean; thus including waters over which they are merely commuting is not an issue. This eastern 592 portion of the Ross Sea is the area frequented late in the summer by the penguins during molt, 593 but coexistence is possible among petrels and penguins owing to a disparate depth of foraging. 594 (3) Light-mantled Sooty Albatross, although not abundant and therefore somewhat 595 inconsequential, competitively speaking, are more prevalent in the western Ross Sea slope (and 596 waters to the north), also possibly being a function of proximity to closest nesting sites (in the 597 New Zealand subantarctic islands). In fact, their occurrence immediately north of the Shelfbreak 598 Front, unlike the continent-breeding petrels, may to some extent be due to the detection of 599 commuting birds. (4) Minke Whales are most abundant in the western slope region, too, an area 600 in which Blue Whales (Balaenoptera musculus intermedia) were once more abundant; it is likely 601 that minkes are now more abundant in the Ross Sea as a consequence (Laws 1977, Ainley 2010). 602 If they need to, Minke Whales can forage deeper than the petrels, albatrosses and Adélie 603 penguins that co-occur with them, and where Minke Whales are abundant, it is true that penguins 604 have to adjust their foraging behavior (Ainley et al. 2006).

605 Competition surely plays a role in spatial use patterns. As noted, we know that when and 606 where Minke Whales are abundant within the space used by (foraging) breeding penguins, the 607 whales' (or whales' and penguins' together) foraging causes prev to become less available. 608 causing expanding foraging area for penguins (and presumably the whales), and deeper diving 609 for Adélies (Ainley et al. 2006). We expect that this phenomenon occurs along the western Ross 610 Sea outer shelf and slope as well, which is adjacent to very large (uninvestigated) penguin 611 colonies in northern Victoria Land, and where Minke Whales are most abundant according to our 612 model (as well as empirical data; see Ross Sea Bioregionalization, Part I). Indeed, without the 613 ability to exploit the entire water column. Adélie Penguins are forced by intra- and interspecific 614 competition to enlarge their foraging areas mostly horizontally as they force the decreased 615 availability of their prey: large colonies expand foraging areas even more than smaller ones (Ballance et al. 2009). Emperor Penguins, however, do not show the pattern of seasonal change 616 617 in foraging extent (see Ross Sea Bioregionalization, Part I); but if they experience the same sort of competition that leads to expanded foraging area among Adélies (facilitated by diet 618 619 competition with Weddell Seals, and Ross Sea Killer Whales), Emperors hypothetically have a 620 much better capacity to expand the vertical aspect of foraging than do Adélies. This supposition 621 in regard to Emperor Penguins needs to be investigated with season-long deployment of time-622 depth recorders, as has been done with Adélies (Lescroel et al. 2010). Finally, it is known that 623 large toothfish disappear from areas where Weddell seals are concentrated. Whether this is due

to depletion by the predating seals, or movement away by the toothfish owing to competition for

- 625 silverfish or harassment by the seals requires more investigation (reviewed in Ainley & Siniff
- 626 2009). It is another example of how species interactions may modify spatial use of the Ross Sea,

as indicated in the models generated based on habitat features alone.

- 628 We surmise that competition helps to explain some of the other spatial patterns observed. For
- 629 instance, why are there no Humpback Whales (*Megaptera novaeangliae*) in the Ross Sea, but
- large numbers immediately to the west (cf. Branch 2009, Ainley 2010)? Is this the result of thelarge number of Minke Whales, a known competitor (Friedlaender et al. 2008)? Is it just an
- artifact that our model shows relatively few Ross Sea Killer Whales (fish eating) in the
- 633 southwestern Ross Sea, where Weddell Seals are probably the most concentrated during summer
- of anywhere in Antarctica? These patterns, too, require additional research for a better
- 635 of anywhere in Antarctea? These patients, too, require additional research for a better635 understanding of causation.
- 636
- 637 Limitations of the Study and Final Thoughts
- 638 Predicting species probability of occurrences from presence only data is not an ideal approach –
- 639 it would be more powerful to have the capability to use true absence information along with
- abundance data to create projections of numbers of individuals utilizing each grid cell. As
- described in Methods, we did do some comparisons with results from boosted regression trees
- 642 for the species for which we had potentially suitable information and did not note any important
- 643 differences in patterns of spatial distribution or areas of apparent importance. For the two
- 644 penguins and Crabeater Seals, we also have satellite tracking data (displayed in Ross Sea
- Bioregionalization, Part I: table 2 and figures 35, 40-43), 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. Finally, Maxent is specifically
- 648 designed for working with presence-only data, and has been used in similar conservation
- 649 prioritization situations previously (Kremen et al. 2008, Carroll et al. 2010). Of course, more
- data collection would likely improve matters as well, especially if covariate data were collected
   contemporaneously. This is said, however, knowing that the mesopredators in very few areas of
- the Southern Ocean have been investigated as well as in the Ross Sea.
- 653 Our study benefitted from the wealth of data that have been aggregated over several decades 654 by researchers working in the study area (see Ross Sea Bioregionalization, Part I). We were 655 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, 656 657 and high spatial resolution data are still not available for sea ice or chlorophyll (limited to 658 12.5km so far, 25km for much of the study period). Although several of the environmental 659 variables used in our model are temporally dynamic, they do hold distinct spatial patterns over long time periods, but it would be better to be able to use data collected at the time of the survey. 660
- 661 Future studies will benefit from higher spatio-temporal resolution of covariates, assuming the 662 food web remains intact long enough for these studies to be undertaken. Even so, our goal was to
- project general patterns of current usage at a 5km scale rather than to explore mechanisms
   explaining these patterns. Doing the latter would be of great interest, but would require a directed
- multi-investigator effort, something which is difficult to achieve in recent years.
  The fact that the Ross Sea is still largely intact allows a chance to investigate these sorts of
  phenomena and other factors that once structured marine ecosystems elsewhere but which can
  now be investigated only indirectly (see, e.g. Österblom et al. 2007, Christensen & Richardson
  2008). An intact ecosystem also allows investigation of the apparent large-scale trophic cascade

- 670 that exists in the Ross Sea (see Smith et al. in press), and which could well have been of a sort
- 671 prevalent once in other ocean ecosystems (Pauly & Maclaean 2003).
- 672
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