

Summer distribution of marine mammals encountered along transects between South Africa and Antarctica during 2007 – 2012 in relation to oceanographic features

Claude R. Joiris^{1,2*}, Grant R.W. Humphries³ & Alain De Broyer²

¹ Laboratory for Polar Ecology (PoE), 26130 Saint-Restitut, France;

² Conservation Biology Unit, Royal Belgian Institute for Natural Sciences (RBINS), 1000 Brussels, Belgium;

³ Department of Ecology and Evolution, Stony Brook University, Stony Brook, New York, USA 11794

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Abstract The at-sea summertime distribution of marine mammals between South Africa and Antarctica was determined along eight transects surveyed between December 2007 and January 2012. During 1930 30-minute transect counts, 1390 marine mammal individuals were attributed to 19 species: eight toothed whales (*Odontoceti*), six pinnipeds, and five baleen whales (*Mysticeti*). An additional two toothed-whale species were encountered 'out of effort'. The four most numerous species accounted for 85% of the total number of individuals encountered: crabeater seal (*Lobodon carcinophagus*), humpback whale (*Megaptera novaeangliae*), Antarctic Minke whale (*Balaenoptera bonaerensis*) and fin whale (*B. physalus*). The distribution of these species was related to oceanographic features, such as water masses and fronts, pack ice and ice edge: These differences were statistically highly significant. Biodiversity was compared with other polar marine ecosystems.

Keywords marine mammals, at-sea distribution, Antarctica

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1 Introduction

Our long-term study on upper trophic level species (*i.e.*, seabirds and marine mammals) in polar marine ecosystems aims to deepen understanding of the basic mechanisms influencing the distributions of species 'at sea.' Decades of research has demonstrated that water masses and fronts, pack ice, the ice edge and eddies are the main hydrological features explaining the distribution of seabirds and marine mammals in the ocean^[1-9], with particular attention given to seabirds and mammals^[7], cetaceans^[8] and a southern sea case study on the Antarctic Minke whale *Balaenoptera bonaerensis*^[9].

High density at-sea distributions of upper trophic-level species can reveal areas of high biological productivity, given

that predators depend on high local prey availability^[6,10-13]. In addition to filling in gaps of information on the distribution of some less-common marine mammal species in the southern seas, these at-sea distributional data might also be valuable for detecting future shifts in species distribution connected to global changes, such as increasing water temperature and reduced ice coverage.

2 Materials and methods

Counts of marine mammals were performed from the bridge of the icebreaking MS *Ivan Papanin* (19.5 m above sea level) and RV *Polarstern* (18 m above sea level) during summer along eight transects between South Africa and Antarctica, surveyed between December 2007 and January 2012. Transect counts were not constrained by distance to the

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* Corresponding author (email: crjoiris@gmail.com)

ship, lasted 30 min, and covered a 90° angle from the bow to one side (the bridge being too broad for allowing simultaneous counting on both sides by one observer). Cruise tracks, transect positions and basic information about each survey are presented in a sister paper on seabird distribution^[14]. Mammals were identified and counted using 10×42 mm binoculars, as per an established methodology^[6,13,15]. Results are presented as unmodified data, *i.e.*, numbers encountered per count. An index of density was calculated from these data by determining the surface covered during each count on the basis of specific detection distances based on their size, color and behavior (“jizz”)^[6,13,15] and mean ship speed: 10 knots in open water and 5 knots in ice covered areas.

Water temperature and salinity were continuously recorded aboard *Polarstern* by thermo-salinometer, as well as sub-surface fluorimetric evaluation of chlorophyll (on the keel, –10 m). Ice cover was estimated from the bridge and expressed as % cover within a 500-m radius of the ship.

On the basis of water temperature, salinity and ice coverage^[16–17], without taking into account the South African coastal waters the following north-south water masses and fronts were recognized (Table 1): Sub-Tropical Water (STW), Sub-Tropical Front (STF), Antarctic Circumpolar Current (ACC), Sub-Antarctic Front (SAF), Polar Frontal Zone (PFZ), Polar Front (PF), Antarctic Zone (AAZ), and Antarctic Surface Water (AASW), including ice edge and pack ice (PI)^[14]. Biological production, especially (primary) productivity as reflected by chlorophyll pigments (fluorescence), was greatest along oceanographic fronts and at the ice edge. These observations are consistent with earlier reports^[18–19].

We used a Generalized Linear Model (GLM^[20]) with a Poisson function distribution attributed to the response variable (*i.e.*, counts of marine mammals are of a Poisson distribution; right skewed) in the statistical software JMP (version 10) in the program SAS (Statistical Analysis System). This was done to test if the numbers of marine mammals were significantly correlated to oceanographic regions as defined by water temperature, salinity and ice coverage. We further analysed the importance of oceanographic regions in determining mammal distributions by applying boosted regression tree models (generalized boosted regression

modelling, GBM^[21]) to the data in program R (version 3.0.^[22]). GBMs function by creating a series of decision trees based on the relationships between the response (*i.e.*, presence/absence of marine mammals) and explanatory variables (*in situ* oceanographic data). These decision trees represent a series of “if/then” statements (*i.e.*, a rule set) which can be applied to new data to make predictions. The success of GBMs is determined by how well a model predicts to an independent set of data. To do this we created GBMs using data from the *Polarstern* (region, ice coverage, salinity and water temperature); neither salinity nor water temperature data were available for *Ivan Papanin* surveys. We transformed raw count data to binary presence/absence data, then created models for the south-bound leg of both trips (using the return, north-bound data to assess model fit). The south-bound survey (versus the north-bound survey) was chosen because it had more sightings of Minke and fin whales with which to construct models. GBMs were applied to north-bound data, with model accuracy calculated using the area under the receiver operating characteristic curve (AUC) as an independent metric of model performance. AUC values are a combined representation of the number of correctly classified categories in a model and therefore higher AUC values are generally representative of better models^[23]. Although there is no convention for what makes a “good” AUC value, we use the academic point system (*i.e.*, graded from a score of 0 to 100%, with 100% being the highest score) as a proxy for model accuracy (0.90–1 = excellent, 0.80–0.90 = good, 0.70–0.80 = fair, 0.60–0.70 = poor, 0.50–0.60 = fail: An AUC of 0.50 means the model is simply random^[23]). We also report ‘sensitivity’ (based on the number of correctly classified presences) and ‘specificity’ (based on the number of correctly classified absences) of the model. Models were run both with and without ‘region’ as an explanatory variable to determine the importance of this variable in defining the distribution of marine mammals. We also ran models with and without distance-to-ice-edge (DTI), due to the higher numbers of fin and humpback whales observed around this feature. Finally, models were run at different temporal scales to examine the effect of time (season) on distributions of species. All model runs included salinity, temperature, ice cover and chlorophyll (fluorescence) data.

Table 1 Transect between South Africa and Antarctica: main water masses, fronts and pack ice. Data collected from RV *Polarstern* in December 2011, from North to South

	Latitude/°S	Water temperature/°C	Salinity	Ice cover/%
Sub-Tropical Water, STW		18.9 (22.8 to 13.5)	35.4 (35.1 to 35.6)	0
Sub-Tropical Front, STF	40			
Antarctic Circumpolar Current*, ACC		11.2 (13.5 to 10.2)	34.6 (35.0 to 34.6)	0
Antarctic Front, AF	45			
Polar Frontal Water, PFW		5.9 (5.3 to 9.7)	33.9 (33.8 to 34.6)	0
Polar Front, PF	50			
Antarctic Water, AW		0.26 (2.6 to –1.52)	33.8 (33.8 to 33.9)	0
Ice edge, Front	58			
Weddell Gyre; Antarctic Surface Water; Pack Ice, PI		–1.7 (–1.8 to –1.5)	34.2 (33.7 to 34.4)	36.6 (0 to 98)

Note: * Sub-Antarctic Water

3 Results

In total, 21 mammal species were recorded during the eight surveys, including two species 'out of effort' (*i.e.*, seen when the ship was stationary or when recorders were not on the bridge): 10 toothed cetaceans (*Odontoceti*), six pinnipeds and five baleen whales (*Mysticeti*) (Table 2). We

detected 1390 mammals during 1930×30 minute surveys: 805 pinnipeds, 465 baleen whales and 120 toothed whales. Of these, four taxa represented 85% of all species recorded: the crabeater seal, *Lobodon carcinophaga* (730 individuals, *i.e.*, 90% of identified pinnipeds, though probably more, given unidentified seals mainly belonged to this species and because no correction was applied for their daily hauling-

Table 2 Marine mammals encountered during four return transects between South Africa and Antarctica during summer. Total numbers recorded; *n* = number of half-hour transect counts; mean number per count for totals > 25 identified individuals

	Expedition	BELARE07	ANT25/2	BELARE08	ANT28/2		
	Ship	<i>I.Papanin</i>	<i>Polarstern</i>	<i>I.Papanin</i>	<i>Polarstern</i>		
	Period	Dec. 2007	2008/ 09	2008/ 09	2011/ 12	Total	Mean
Species	Species/ <i>n</i>	201	686	444	596	1927	N/count
Sub-Antarctic/Antarctic fur seal	<i>Arctocephalus tropicalis/ gazella</i>		2	3	15	20	
S African fur seal ^I	<i>Arctocephalus [pusillus] doriferus</i>	*	5	*		5	
fur seal sp	<i>Arctocephalus sp.</i>				8	8	
leopard seal	<i>Hydrurga leptonyx</i>	2	4		5	11	
Weddell seal	<i>Leptonychotes weddellii</i>	5		17	6	28	0.015
crabeater seal	<i>Lobodon carcinophaga</i>	35	167	325	205	732	0.38
Ross seal	<i>Ommatophoca rossii</i>	1	3	3	3	10	
seal sp		18	54	101	13	186	
long-finned pilot whale	<i>Globicephala melas</i>	40 + 50**				40	0.021
hourglass dolphin	<i>Lagenorhynchus cruciger</i>	6				6	
dusky dolphin	<i>Lagenorhynchus obscurus</i>			19 + 40**		19	
killer whale	<i>Orcinus orca</i>	24**		5**		0	
bottlenose dolphin	<i>Tursiops truncatus</i>		2			2	
sperm whale	<i>Physeter macrocephalus</i>		31	7		38	0.020
Arnoux's beaked whale	<i>Berardius arnuxii</i>	6**				0	
southern bottlenose whale ^{II}	<i>Hyperodon planifrons</i>	4	2	1**		6	
Gray's beaked whale ^I	<i>Mesoplodon gravi</i>			3		3	
Cuvier's beaked whale	<i>Ziphius cavirostris</i>			4		4	
dolphin sp ^{III}		75				75	
Antarctic Minke whale	<i>Balaenoptera bonaerensis</i>	16	36	41	11	104	0.054
sei whale	<i>Balaenoptera borealis</i>	2	10	1		13	
southern blue whale	<i>Balaenoptera [musculus] intermedia/brevicauda</i>				2	2	
fin whale	<i>Balaenoptera physalus</i>		29	5	16	50	0.026
humpback whale	<i>Megaptera novaeangliae</i>	5	76	197	17	295	0.15
large whale sp		*	46	*	15	61	
total all		209	467	726	316	1718	
total identified		116	367	625	280	1388	
mean identified per count		0.58	0.53	1.41	0.47	0.72	0.72

Notes: * not recorded; ** out of effort: not included in calculations.

Remark: I, off S African coast. II, mostly off S African coast. III, probable dusky or common.

out rhythm; humpback whales (*Megaptera novaeangliae*, 300 individuals, though probably more, considering most large unidentified cetaceans likely belonged to this species); Antarctic Minke whales (*Balaenoptera bonaerensis*, 100 individuals, of which some may have been misidentified dwarf Minke whales (*B. acutorostrata*)); and fin whales, *B. physalus* (50 individuals). The last three of these species represent 97% of identified baleen whales (64%, 22% and 11% respectively, Table 2).

Observations on the behavior or distributions of select species follow to augment known accounts for these species or region^[24-30].

Weddell (*Leptonychotes weddellii*) and Ross seals (*Ommatophoca rossii*) were observed in close pack ice not far from the Antarctic continent, south of 67°S. Ross seals have been encountered in large concentrations in medium and close pack ice between 12°E and 6°W^[26-27], though no comparable aggregation was encountered during our surveys.

Seven pods of long-finned whales (*Globicephala melas*) numbering at least 90 individuals were observed close to South African waters, of which three (totalling 50 individuals) were observed out of effort.

Our single sighting of the hourglass dolphin (*Lagenorhynchus cruciger*) comprised six individuals that approached the ship on December 4, 2007 (48.60°S, 21°E). This position is considered typical of this species for deep-water populations^[31]. Three pods of dusky dolphins (*L. obscurus*), comprising at least 19 individuals, were sighted on December 11, 2008 between 43.50° and 44.45°S, 18.40° and 18.70°E. One pod was actively feeding, attracting white-headed (*Pterodroma lessonii*) and soft-plumaged (*P. mollis*) petrels, the latter birds being considerably beyond their normal distribution range, more than 1 000 km from the South African or Prince Edward and Marion Island populations.

A pod of five killer whales (*Orcinus orca*), probably including one adult male, two females and two younger individuals, was encountered at 69.55°S, 06.45°E on December 19, 2008. These individuals appeared to be feeding as they sometimes circled together or dived for short periods of time. All were quite small. The shape of the eye patch and the contrast between the black cape, paler flanks and area behind the saddle are consistent with their being 'C Ecotype' individuals, as to be expected in and around Antarctic pack ice^[32].

Sperm whale (*Physeter macrocephalus*) observations varied considerably between surveys in all open-water zones, which may reflect their migratory movements.

Arnoux's beaked whales (*Berardius arnuxi*) were encountered on December 11, 2007 (70°S, 5.20°E) while stationary (*i.e.*, not during counting effort): three probable adult females with three calves dived regularly along the ice edge for about 1 h. Three dives lasted 11, 14 and 15 min, separated by 4-minute surface rests. The calves remained beside an adult within the group. A pod of three Gray's beaked whales (*Mesoplodon grayi*) was sighted close to South African waters on January 14, 2009 (35°S, 17.45°E). A pod of

at least four Cuvier's beaked whales (*Ziphius cavirostris*) was observed on December 8, 2008 (37.15°S, 17.20°E).

Southern bottlenose whales (*Hyperoodon planifrons*) were almost exclusively encountered in STW (35°–36°S), with the exception of one individual encountered further south (58°S, 25.50°E) on December 6, 2007.

Humpback whales were mostly encountered in pods of two to 10 individuals, of which many were adult, most likely being females accompanied by calves. Most were encountered between 55.20° and 57.75°S on January 9, 2009: 190 individuals in 19 successive counts, with a maximum of 38 at one count at 56°S. Whales were either stationary, resting or surface feeding (*i.e.*, some diving and displaying their flukes). Moreover, two large groups of approximately 100 individuals were observed during another *Polarstern* expedition in the same area on January 22, 2008, at about 62°S, 0°E (H. Robert, pers. com.).

The influence of water masses was strong, as summarized in Table 3. The vast majority of mammals were present in AASW and PI: crabeater seals in close pack ice, Antarctic Minke whales in loose pack ice around icebergs and ice floes, and humpback and fin whales at the ice edge and open AAZ south of the SAF. As a result, 70% of the most abundant species (seals and baleen whales) were encountered in AASW and PI, and 17% in AAZ. In contrast, toothed whales occurred mainly in STW off the South African coast, with the exception of the sperm whale, which was observed in all open water masses except PI. A similar segregation of toothed and baleen whales has been described from the Weddell Sea^[33]. Humpback whales were observed in AAZ primarily around the ice edge front, with a mean of 1.1 per count, followed by crabeater seals in PI as expected (0.73 per count), fin whales in AAZ and PI (0.15 and 0.012 per count respectively) and Antarctic Minke whales in PI and AAZ (0.08 and 0.04 per count respectively). In contrast, six toothed cetacean species were observed in lower numbers, mainly in STW, ACC and PFZ, partially in South African coastal waters, though male sperm whales could be encountered in all open water zones. A few toothed cetacean species, *e.g.*, dusky dolphin, were encountered far from their usual range. This created substantial differences in marine mammal density when all species were pooled: from 0.14 individuals per count in STW, 0.16 in ACC, 0.21 in PFZ to 0.89 in PI and 1.40 in AAZW.

We tested the importance of specific regions on the distributions of the four main species encountered using a GLM. The GLMs identified a strong statistically significant relationship between oceanographic region on all species except the fin whale, which was slightly significant ($p < 0.05$, Table 3). GBM models generally performed well (*e.g.*, AUC close to and higher than 0.80 in most cases).

For humpback whales, the model with the highest AUC (0.85) included regions and data for all years, but not DTI, though this model had a specificity of 0.56 (meaning only 56% of predicted data were correctly classified as presences). Although AUC for models which included regions, DTI and

Table 3 Marine mammals encountered between South Africa and Antarctica during summer, grouped according to water mass. Data: *Papanin* 2008/2009, *Polarstern* 2008/2009 and 2011/2012^I; total numbers recorded; mean N/count for main species (total > 25); N/km with speed of 10 knots in open water and 5 knots in ice covered areas; calculated density with specific detection limits; *n* = number of half-hour counts

Zone ^{II}	STW	ACC	SAZ	AAZ	AASW/ PI	all	N/count	N/count	N/km	Detection	N/km ²	Signifi-
Species/ <i>n</i>	276	152	131	246	939	1744	all	PI	PI	Limit/m	PI	cance ^{III}
Sub-Antarctic/ Antarctic fur seal				2	18	20						
S African fur seal	5					5						
leopard seal				1	8	9						
Weddell seal					23	23						
crabeater seal				13	684	697	0.40	0.73	0.16	400	0.40	$p < 0.001$
Ross seal					9	9						
Σ pinnipeds						763	0.44					
long-finned pilot whale	40					40	0.022					
hourglass dolphin			6			6						
dusky dolphin		19				19						
bottlenose dolphin	2					2						
sperm whale	19	2	15	2		38	0.022					
southern bottlenose whale	2					2						
Gray's beaked whale	3					3						
Cuvier's beaked whale	4					4						
Σ toothed whales						114	0.065					
Antarctic Minke whale			1	11	76	88	0.050	0.081	0.022	3000	0.07	$p < 0.001$
sei whale	1	3		4	3	11						
southern blue whale					2	2						
fin whale	3			36	11	50	0.029	0.012	0.005	5000	0.001	$p < 0.05$
humpback whale	3		12	275		290	0.17		0.013	5000	0.003	$p < 0.001$
Σ baleen whales						441	0.25					
total	39	24	28	344	834	1269	0.73	0.89				
mean per count	0.14	0.16	0.21	1.40	0.89	0.73						

Notes : I, Since no data on salinity nor water temperature are available for *Papanin* 2007. II, STW: Sub-Tropical Water; ACC: Antarctic Circumpolar Current; AAZ: Antarctic Zone; AASW: Antarctic Surface Water; PI: pack ice. III, Based on GLM analysis.

all-yearly data, and those limited to just DTI and yearly data (excluding regions), had AUC values of 0.79 (considered a “fair” model), sensitivity in both cases was 0.78; for determining where humpback whales occur, these latter models performed best.

Models for fin whales performed best when variables were limited to DTI and all-yearly data (excluding regions) (AUC = 0.96: “excellent”), whereas model performance was “poor” when limiting variables to oceanographic parameters (AUC = 0.65). In the best models for fin whales, which included DTI as a predictor, 99% of predicted presences were correctly classified.

Models for Antarctic Minke whales performed least-well overall, scoring “fair” (AUC 0.70–0.80), with the best model including regions and all-yearly data (excluding DTI) (AUC = 0.79, sensitivity = 0.65, specificity = 0.75). Although the sensitivity was highest for a Minke whale model that included regions and DTI for 2008 (72% correctly classified presences), specificity was very low (55% correctly classified absences) with an AUC of only 0.70.

Crabeater seal models were all “good” with AUC values ranging from 0.80 to 0.84, with the most successful models being those that included DTI and regions (for all years and 2008; AUC values of 0.84) (Table 4).

Table 4 GBM model performance of models assessing the importance of region, distance to ice edge and year in predicting the distribution of the four most abundant marine mammals along transects between South Africa and Antarctica

Species	Regions included Distance to ice (DTI) included Years included	AUC*				
		Yes	Yes	Yes	Yes	No
		Yes	Yes	Yes	No	Yes
		all years	2008	2011	all years	all years
crabeater seal	mean	0.84	0.84	0.81	0.83	0.83
<i>Lobodon carcinophaga</i>	(sensitivity / specificity)	(0.72/0.76)	(0.74/0.74)	(0.78/0.95)	(0.74/0.75)	(0.73/0.74)
Antarctic Minke whale	mean	0.75	0.70	**	0.79	0.71
<i>Balaenoptera bonaerensis</i>	(sensitivity / specificity)	(0.62/0.73)	(0.72/0.55)		(0.65/0.75)	(0.57/0.73)
fin whale	mean	0.95	**	**	0.65	0.96
<i>Balaenoptera physalus</i>	(sensitivity / specificity)	(0.92/0.99)			(0.60/0.82)	(0.91/0.99)
humpback whale	mean	0.79	0.77	**	0.85	0.79
<i>Megaptera novaeangliae</i>	(sensitivity / specificity)	(0.78/0.76)	(0.70/0.77)		(0.56/0.82)	(0.78/0.76)

Notes: * = Area Under the receiver operating characteristic Curve (see text); ** = Too few observations to accurately calculate AUC values.

4 Discussion and conclusions

Humpback whales are often the most common baleen whale species in western Antarctica^[34-35], whereas Antarctic Minke whales are most common in the Weddell Sea^[33]. Humpback and Minke whales appear to avoid each other, possibly to limit competition for similar food sources^[34-39]. The spring arrival time of various species also differs, with pygmy blue whales (*Balaenoptera musculus*, s.sp. *intermedia/brevicauda*) arriving first, followed by humpback, fin and sei whales *B. borealis*^[40].

During the first leg of the EPOS 1 expedition (European Polarstern Study, October–November 1988) in the adjacent Weddell Sea, departing from South America, using the same team, platform, and counting method, 12 mammal species were counted (6 pinnipeds, 4 toothed whales and 2 baleen whales^[33]), whereas 21 were detected in this study (n.b. total effort was different in this study, which would affect the detection of less-abundant species). Numbers of individuals were also much higher in the ice-covered Weddell Sea^[33]: a mean of 26 pinnipeds per count, of which 12 were crabeater seals, compared with 0.73 pinnipeds per count in PI in this study. For cetaceans, mean values were more comparable: 0.18 individuals per count (of which 0.16 were Antarctic Minke whales) in the Weddell Sea compared with 0.25 per count (of which 0.17 were humpback whales) in this study. Similar data were collected in the western Weddell Sea during the second leg of EPOS 1^[41]. The low number of species and high number of individuals indicate lower marine mammal diversity in the Weddell Sea, though total biological production seems to be greater as mammal biomass is also greater, consistent with seabird populations in these regions^[14]. Patchiness should also be taken into account instead of expressing data as mean values: The presence of very local large concentrations could obviously strongly influence such calculations, e.g., up to 300 fin whales in a limited area around Elephant Island, including

100 in one count^[42].

Modelling indicates the distributions of humpback and Minke whales and crabeater seals are independent of year, based on comparable AUC values between 2008 models and those using all-yearly data. However, because of the low number of presences, we were unable to test this. The low incidence of encounter of these three species in 2011 could suggest a change from the 2008 season, either by a decrease in the number of whales or seals, or a geographic shift in their migratory behavior (e.g., only five detections of Minke whale on the northbound trip in 2011, as opposed to 25 in 2008). However, the few sightings of fin and humpback whales during the 2011 survey do occur within the vicinity of the 2008 survey (Figure 1). Humpback whale model sensitivity was impacted by the removal of DTI as a variable. Most humpback whale sightings occurred along the ice edge; other reports could be migrating individuals or groups (Figure 1).

The accuracy of fin whale models was driven primarily by region and DTI, with a drastic reduction in accuracy when both were removed from analyses. This indicates a high regional dependency of these whales, and that temperature, ice cover or salinity may not drive their distribution during summer. We also see that a good-fitting model can be created for fin whales without including regions, indicating, that at least of those variables we have taken into consideration, this species appears to be dependent on or closely associated with the ice edge.

The accuracy of models for Minke whales was similar, though when including region as a variable, model performance improves. As seen in Figure 1, it is not surprising that removing region affects model accuracy. However, model assessments are only “fair” for this species indicating that factors other than those we include in our models (Chlorophyll (fluorescence), water temperature, salinity and ice cover) may affect their distribution, such as current speed, seabed depth, distance from land mass, prey aggregation, or primary productivity to name a few.

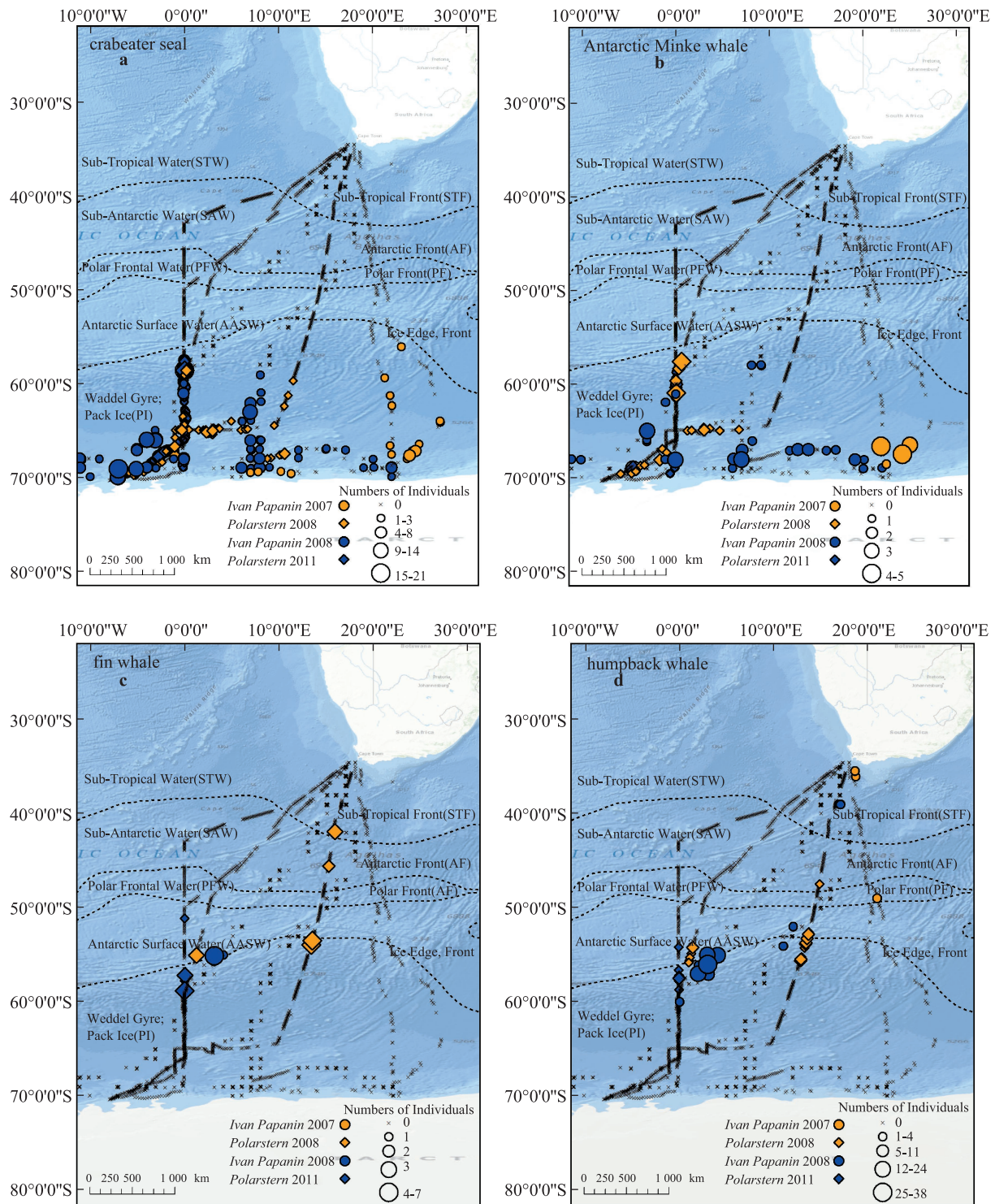


Figure 1 Examples of marine mammal distribution for most abundant species. Numbers per half-hour transect count: **a**, crabeater seal *Lobodon carcinophaga*; **b**, Antarctic Minke whale *Balaenoptera bonaerensis*; **c**, fin whale *Balaenoptera physalus*; **d**, humpback whale *Megaptera novaeangliae*. Dotted lines depict the mean position of fronts separating different water masses.

The accuracy of models for crabeater seals was broadly comparable, though we were surprised that ‘region’ did not affect model assessment (Figure 1) to the extent we thought it might have, probably because our oceanographic variables better explained data variation than ‘region’.

Finally, the accuracy of models for Minke whales and

crabeater seals were similar when modelled data were limited to oceanographic variables, indicating these species may be more sensitive to environmental conditions than either fin or humpback whales. Our results are comparable to earlier accounts those from this same area^[14,43] and on a broader scale^[18], demonstrating that southern-sea upper trophic level

assemblages are driven primarily by latitudinal gradients, water temperature, salinity and ice cover.

We conclude that the geographic structure of “top predator” distributions must probably be bound to differences of ecological functioning of the water column resulting in differences in species composition — including age structure and size classes — density and availability of their main prey: zooplankton and krill, nekton and small fish^[43].

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References

- Wynne-Edwards V C. On the habits and distribution of birds on the North Atlantic. Boston: Boston Society of Natural History, 1935: 233–346
- Joiris C R. Seabirds recorded in the northern North Sea in July: the ecological implications of their distribution. *Gerfaut*, 1978, 68: 419–440
- Pocklington R. An oceanographic interpretation of seabird distributions in the Indian Ocean. *Mar Biol*, 1979, 51(1): 9–21
- Kinder T H, Hunt G L Jr, Schneider D, et al. Correlations between seabirds and oceanic fronts around the Pribilof Islands, Alaska. *Estuar Coastal Shelf Sci*, 1983, 16(3): 309–319
- Elphick C, Hunt G L Jr. Variations in the distributions of marine birds with water mass in the Northern Bering Sea. *Condor*, 1993, 95(1): 33–44
- Joiris C R, Falck E. Summer at-sea distribution of little auks *Alle alle* and harp seals *Pagophilus (Phoca) groenlandica* in the Fram Strait Greenland Sea: impact of small-scale hydrological events. *Polar Biol*, 2011, 34(4): 541–548
- Bost C A, Cotté C, Bailleul F, et al. The importance of oceanographic fronts to marine birds and mammals in the southern oceans. *J Mar Syst*, 2009, 78(3): 363–376
- Ainley D G, Dugger K M, Toniolo V, et al. Cetacean occurrence patterns in the Amundsen and Southern Bellingshausen Sea sector, Southern Ocean. *Mar Mamm Sci*, 2007, 23(2): 287–305
- Ainley D G, Jongsomijt D, Ballard G, et al. Modeling the relationship of Antarctic Minke whale to major ocean boundaries. *Polar Biol*, 2012, 35: 281–290
- Hunt G L Jr. The pelagic distribution of marine birds in a heterogeneous environment. *Polar Res*, 1990, 8: 43–54
- Bost C A, le Maho Y. Seabirds as bio-indicators of changing marine ecosystems: new perspectives. *Acta Oecolo Int J Ecol*, 1993, 14: 463–470
- Furness R W, Camphuysen C J K. Seabirds as monitors of the marine environment. *ICES J Mar Sc*, 1997, 54(4): 726–737
- Joiris C R. At-sea distribution of seabirds and marine mammals in the Greenland and Norwegian seas: impact of extremely low ice coverage. Symposium “European Research on Polar Environment and Climate”, Brussels, 5–6 March 2007. http://ec.europa.eu/research/environment/newsanddoc/agenda0307_en.htm
- Joiris C R, Humphries G R W, De Broyer A. Seabirds encountered along return transects between South Africa and Antarctica in summer in relation to hydrological features. *Polar Biol*, 2013, 36(1): 1633–1647
- Joiris C R. Possible impact of decreasing Arctic pack ice on the higher trophic levels: seabirds and marine mammals. *Adv Environ Res*, 2011, 23: 207–221
- Orsi A H, Nowlin W D Jr, With worth III T. On the circulation and stratification of the Weddell Gyre. *Deep-Sea Res I*, 1993, 40(1): 169–203
- Orsi A H, Whithworth III T, Nowlin W D Jr. On the meridional extent and fronts of the Antarctic Circumpolar Current. *Deep-Sea Res I*, 1995, 42(5): 641–673
- Tynan C T. Ecological importance of the southern boundary of the Antarctic circumpolar current. *Nature*, 1998, 392(6677): 708–710
- Nicol S, Pauly T, Bindoff N L, et al. Ocean circulation off East Antarctica affects ecosystem structure and sea-ice extent. *Nature*, 2000, 406(6795): 505–507
- Nelder A J A, Wedderburn R W M. Generalized Linear Models. J Royal Statistical Soc, Series A (General), 1972, 135: 370–384
- Elith J, Leathwick J, Hastie T. A working guide to boosted regression trees. *J Anim Ecol*, 2008, 77(4): 802–813
- R Development Core Team. A language and environment for statistical computing. R Foundation for Statistical Computing, 2014, Vienna, Austria
- Swets J A. Measuring the accuracy of diagnostic systems. *Science*, 1988, 240: 1285–1293
- Shirihai H. A complete guide to Antarctic wildlife. The birds and marine mammals of the Antarctic continent and the Southern Ocean 2nd edn. London: A & C Black, 2007: 544
- Laws R M. Seals. In: Laws R M. Antarctic Ecology, vol. 2. London: Academic Press, 1984: 621–715
- Laws R M. Antarctic seals; research methods and techniques. Cambridge: Cambridge University Press, 1993, 390
- Shirihai H, Jarrett B. Whales, dolphins and seals. London: A & C Black, 2006, 384
- Best P B, Ansorge I, Lutjeharms L, et al. Whales and dolphins of the southern African subregion. Cambridge: Cambridge University Press, 2008, 352
- Hall-Martin A J. Observations on population density and species composition of seals in the King Haakon VII Sea, Antarctica. *S Afri J Antarct Res*, 1974, 4: 34–39
- Wilson V J. A second survey of seals in the King Haakon VII Sea, Antarctica. *S Afri J Antarct Res*, 1975, 5: 31–36
- Dellabianca N, Sciosia G, Schiavini A, et al. Occurrence of hourglass dolphin (*Lagenorhynchus cruciger*) and habitat characteristics along the Patagonian Shelf and the Atlantic Ocean sector of the Southern Ocean. *Polar Biol*, 2012, 35(12): 1921–1927
- Pitman R L, Ensor P. Three forms of killer whales in Antarctic waters. *J Cetacean Res Manage*, 2003, 5: 131–139
- Joiris C R. Spring distribution and ecological role of seabirds and marine mammals in the Weddell Sea, Antarctica. *Polar Biol*, 1991, 11(7): 415–424
- Thiele D, Chester E T, Moore S E, et al. Seasonal variability in whale encounters in the Western Antarctic Peninsula. *Deep-Sea Res II*, 2004, 51(17–19): 2311–2325
- Friedlaender A S, Halpin P N, Qian S S, et al. Whale distribution in relation to prey abundance and oceanographic processes in shelf waters of the Western Antarctic Peninsula. *Mar Ecol Progr Ser*, 2006, 317: 297–310
- Kawamura A. A review of baleen whale feeding in the Southern Ocean. *Intl Whaling Comm*, 1994, 44: 261–272
- Kasamatsu F, Matsuoka K, Hakamada T. Interspecific relationships in density among the whale community in the Antarctic. *Polar Biol*, 2000, 23(7): 446–473
- Branch T A. Abundance estimates for Antarctic Minke whales from

- three completed circumpolar sets of surveys, 1978/79 to 2003/04. Intl Whaling Comm, SC/58/IA18, 2006
- 39 Friedlaender A S, Lawson G L, Halpin P N. Evidence of resource partitioning between humpback and Minke whales around the western Antarctic Peninsula. *Mar Mamm Sci*, 2009, 25(2): 402–415
- 40 Wilson E, Mittelmeier R A. Handbook of the mammals of the world. Vol 4: Sea Mammals. Lynx Editions, Barcelona, 2014, 614
- 41 van Franeker J A. Top predators as indicators for ecosystem events in the confluence zone and marginal ice zone of the Weddell and Scotia seas, Antarctica, November 1988 to January 1989 (EPOS leg 2). *Polar Biol*, 1992, 12(1): 93–102
- 42 Joiris C R, Dochy O. A major autumn feeding ground for fin whales, southern fulmars and grey-headed albatrosses around the South Shetland Islands, Antarctica. *Polar Biol*, 2013, 36(11): 1649–1658
- 43 Croll D A, Tershy B R, Hewitt R P, et al. An integrated approach to the foraging ecology of marine birds and mammals. *Deep-Sea Res II*, 1998, 45: 1353–1371