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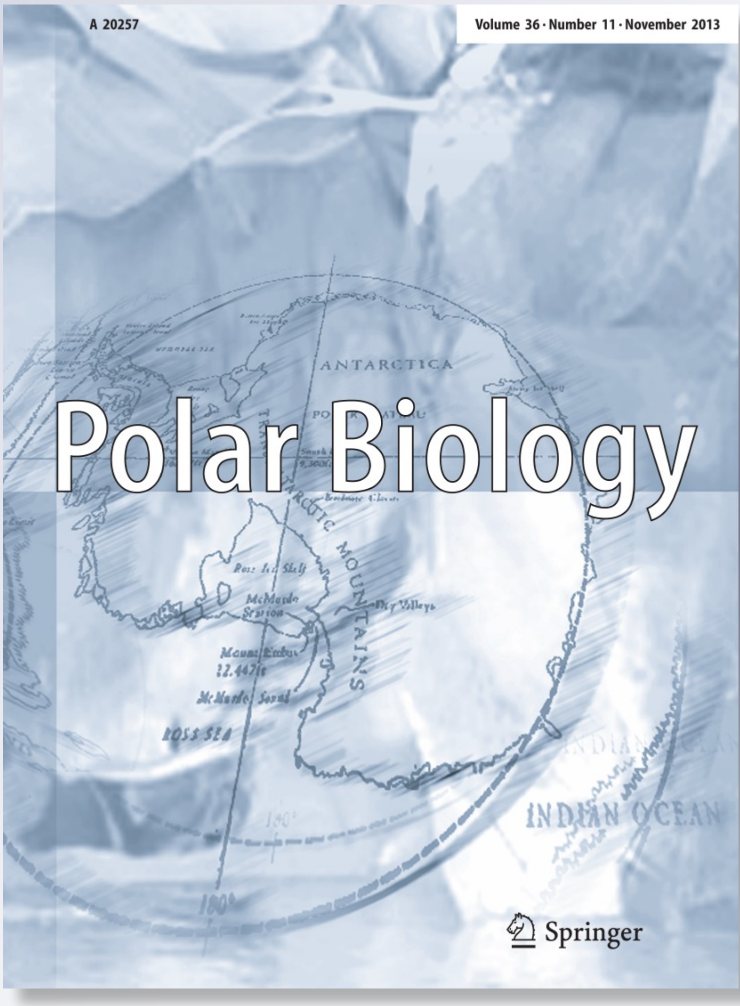

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ORIGINAL PAPER

Seabirds encountered along return transects between South Africa and Antarctica in summer in relation to hydrological features

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Abstract The first aim of our long-term study on the at-sea distribution of the upper trophic levels—seabirds and marine mammals—in polar marine ecosystems is to identify the main factors affecting their distribution: water masses and pack ice, fronts and ice edge as defined on the basis of water temperature, salinity and ice overage. In this study, seabird at-sea distribution was determined in the south-eastern Atlantic Ocean in summer along four return transects between Cape Town, South Africa, and Queen Maud Land, Antarctica: two on board icebreaking *MS Ivan Papanin* and two on board icebreaking *RV Polarstern* between December 2007 and January 2012. During a total of 1,930 half-an-hour transect counts devoted to seabird recording, 69,000 individuals were encountered, belonging to 57 species (mean: 36 individuals per count, all species and expeditions pooled). In comparison, the adjacent Weddell Sea shows a lower seabird biodiversity (30 species and 150 individuals per count) than in the area covered by this study. European Arctic seas reflect an intermediate biodiversity, with 30 species and 60 individuals per count; the major difference is observed in closed pack ice, almost empty in the Arctic but showing a very high biomass in the Antarctic. On the other hand, following the same route in different years allowed to compare results: density and abundance were found to be homogenous and reproducible between years for some species, while very important patchiness was detected for others, causing large heterogeneities and differences between expeditions.

Keywords Seabirds at-sea · Antarctic · Southern seas · Water masses · Fronts · Pack ice · Ice edge

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Introduction

The main aims of our long-term study on the at-sea distribution of the upper trophic levels—seabirds and marine mammals—in polar marine ecosystems are to quantify their distribution and to deepen the basic mechanisms influencing them. Water masses and fronts, pack ice and ice edge, and eddies are the main hydrological factors explaining the distribution of seabirds and marine mammals in the ocean: this has been known for decades (Wynne-Edwards 1935; Joiris 1979; Pocklington 1979; Kinder et al. 1983) and has been confirmed by other more recent studies (e.g. Elphick and Hunt 1993; Joiris and Falck 2010). Recent publications summarize the situation in the southern seas for seabirds and mammals in general (Bost et al. 2009) or for minke whale in particular (Ainley et al. 2012).

Studies on the distribution of seabirds at-sea allow us to locate areas of high biological production because upper-level predators, e.g. seabirds and marine mammals, depend on high local prey abundance (Hunt 1990; Bost and le

Maho 1993; Furness and Camphuysen 1997; Joiris 2007; Joiris and Falck 2010). Moreover, these data allow us to detect temporal and spatial evolutions on a larger time scale, possibly connected to global changes such as increasing temperature and changing ice coverage. Finally, information on the distribution of some seabird species far off their breeding grounds is sparse and thus deserves special attention.

Biological studies in the Antarctic marine ecosystems, especially of the upper trophic levels—seabirds and marine mammals—tend to concentrate on the Weddell Sea (Joiris 1991; van Franeker 1992) and the Ross Sea (Ainley et al. 1984) and to a lesser extent, the Amundsen and Bellingshausen seas. In this paper, we report on the at-sea distribution of seabirds in the poorly studied south-eastern Atlantic sector of the Southern seas along return transects between Cape Town, South Africa, and the Princess Elisabeth station (Belgium) and Neumayer station (Germany), Queen Maud Land, Antarctica, during summer. The main aims are to identify the importance of hydrological factors for seabird distribution, to deepen their knowledge and to make use of successive visits on the same transect for studying both the reproducibility of the counting method and the heterogeneity/patchiness of seabird distribution.

Materials and methods

Seabirds and marine mammals were recorded from the bridge of the icebreaking *MS Ivan Papanin* (19.5 m above sea level)—sometimes from outside, weather and visibility allowing—and from the bridge of the icebreaking *RV Polarstern* (18 m above sea level) during transect counts without width limitation, lasting half-an-hour each and covering a 90° angle from the bow to one side, the bridge being too broad for allowing simultaneous counting on both sides by one observer. Basic information about the four return expeditions is presented in Table 1, and cruise tracks and position of counts are presented in Fig. 1. The animals were detected with the naked eye, and observations confirmed and complemented with binoculars (10 × 42). Followers were identified as far as possible and counted as snapshots, once in each count: this includes birds following the ship, circling at some distance, and sometimes flying above the ship (see detail and discussion of the methodology in Joiris 2007; Joiris and Falck 2010; Joiris 2011). When useful, photographic material was also used, especially for rare or difficult to identify species. Results are presented as basic unmodified data, *i.e.* numbers encountered per half-an-hour transect count. Density was calculated as well, the surface covered during each count being evaluated on the basis of specific detection distances (Joiris 2007; Joiris and Falck 2010; Joiris 2011) and mean ship's speed: 10 knots in open water and 5 knots in ice-covered areas.

Ice cover was evaluated by us from the bridge and expressed as % coverage within a range of 500 m around the ship. Water temperature and salinity were continuously recorded on board *Polarstern* with a thermo-salinometer, as well as a fluorimetric evaluation of chlorophyll pigments, at sub-surface sampling (keel: −10 m). Field data were collected between December 2007 and January 2012.

Statistical significance of seabird numbers between the geographical regions as defined by water temperature, salinity and ice coverage was tested using a GLM (Generalized Linear Model) based on a Poisson function since the distribution of values is not normal; software: JMP10 (SAS). We further analysed the importance of hydrographic regions in determining seabird distributions by applying a GBM (boosted regression trees; Elith et al. 2008) to the data. The success of a GBM is determined by how well a set of data predicts to an independent set of data. To do this, we created GBMs using data from the *Polarstern* (salinity, temperature, ice coverage and region). We were interested here in determining whether these variables were important in determining the presence of individuals, so we transformed the data into presence/absence binary data. Data were then modelled for the southern bound leg of both trips. Those models were then applied to the northern bound leg of the trips and model accuracy was calculated using Area under the receiver operating characteristic curve (AUC). Models were run with and without region as an explanatory variable to determine the importance of region in defining the distribution of seabirds.

Results

In total, about 69,000 individual seabirds belonging to 57 species were encountered during 1,930 transect counts, without taking into account 6 strictly coastal South African species: Cape cormorant *Phalacrocorax capensis*, Cape gannet *Morus capensis*, Cape and Hartlaub's gulls *Larus vetula* and *Chroicocephalus hartlaubii*, Sandwich and swift terns *Sterna sandvicensis* and *Sterna bergii* (Table 2).

From North to South, the following water masses and fronts were identified in this study, without taking into account the African coastal waters (after Orsi et al. 1993, 1995): Sub-Tropical Water (STW), Sub-Tropical Front (STF), Antarctic Circumpolar Current (ACC) (=Sub-Antarctic Water), Antarctic Front (AF), Polar Frontal Water (PFW), Polar Front (PF), Antarctic Water (AW) and Antarctic Surface Water in the Weddell Gyre, including ice edge and pack ice PI. Biological production, especially (primary) productivity as reflected by chlorophyll pigments

Table 1 Return expeditions between South Africa (Cape Town) and Antarctica (Neumayer and Princes Elizabeth stations, Queen Maud Land) during summer

Ship	Expedition	Dates from	to	Observers
MS Ivan Papanin	BELARE 07	01.12.2007	28.12.2007	A. De Broyer, R-M. Lafontaine
RV Polarstern	ANT 25/2	06.12.2008	04.01.2009	C. Gruwier, X. Vanderpuyen
MS Ivan Papanin	BELARE 08	08.12.2008	14.01.2009	A. De Broyer, H. Robert, A. Joris
RV Polarstern	ANT 28/2	03.12.2011	05.01.2012	D. Verbelen, J. Haelters

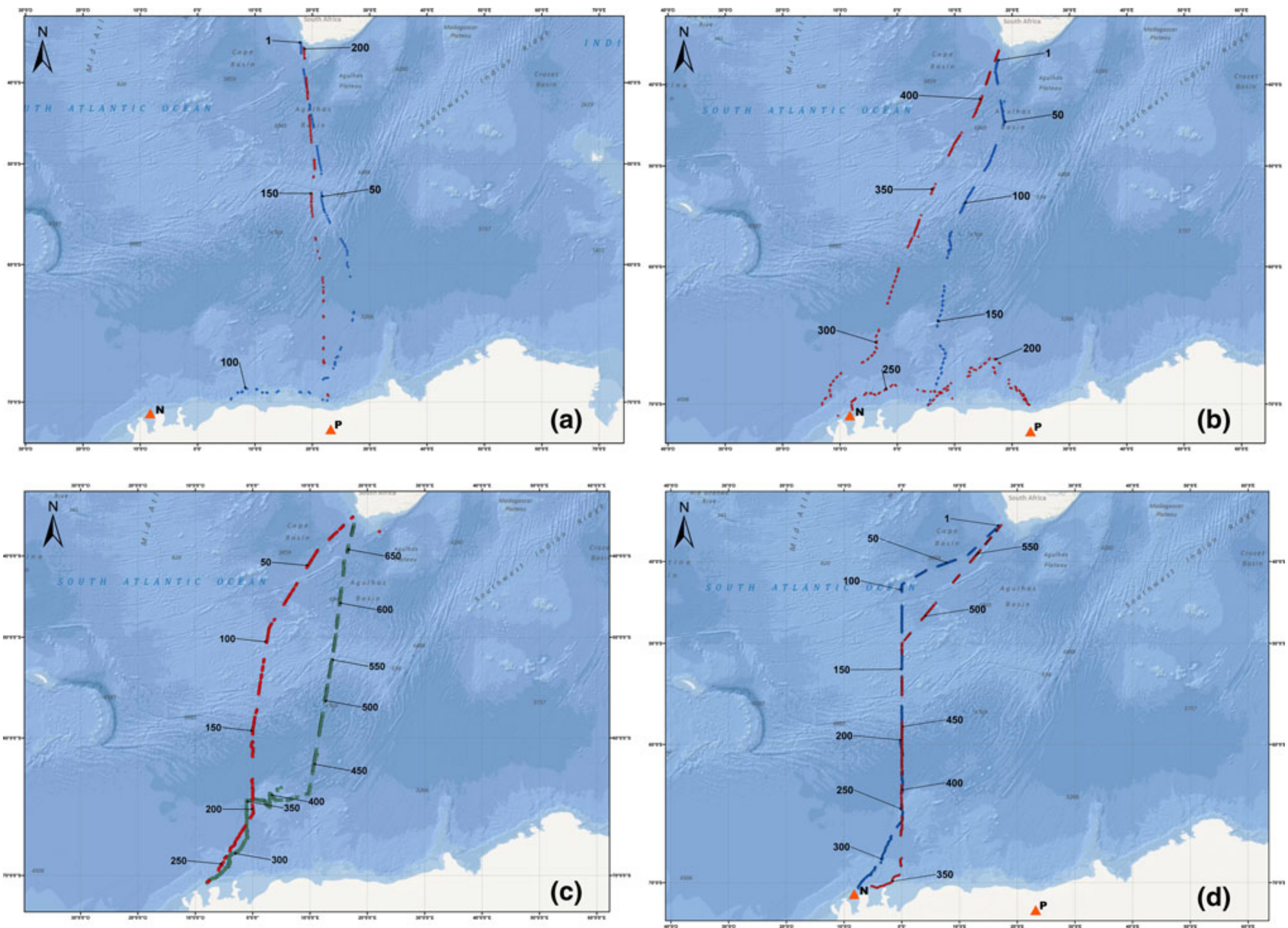


Fig. 1 Cruise track and geographical distribution of the seabird transect counts during summer expeditions on board *MS Ivan Papanin* (**a**, **c**) and *RV Polarstern* (**b**, **d**); numbering of the half-an-hour transect counts; N: Neumayer station (Germany); P: Princess Elisabeth station (Belgium); prepared by C. Gruwier

(fluorescence), was maximal at the fronts and ice edge (Table 3; Fig. 1).

The influence of water masses was obvious and can be summarized as follows (main species based on a selected example in Table 4). Some species were present in all zones, often with differences in density from one zone to the other. Such quantitative differences cause significant geographical heterogeneities for black-browed albatross *Thalassarche [melanophrys] melanophrys,* soft-plumaged petrel *Pterodroma mollis*, black-bellied storm-petrel *Fregetta tropica* with a much higher density in AW or Salvin's/Antarctic prions (with a much lower density in STW). For wandering albatross *Diomeda [exulans] sp*, most of the individuals were encountered in STW and ACC, confirming their high density between 40° and 70°S (Jameson 1958), this area being one of the three geographical zones with highest numbers in the southern seas (Dixon 1933). Other species, even if detected in all zones, presented a high affinity for some of them: great shearwater *Puffinus gravis* in STW, ACC and PFW, Cape petrel *Daption capense* and Southern giant petrel *Macronectes giganteus* in PI. As expected, other albatross species were bound to STW, e.g. Atlantic yellow-nosed

Table 2 Seabirds encountered during four return transects between South Africa and Antarctica during summer; total numbers recorded; n = number of half-an-hour transect counts

Species		Expedition > BELARE 07 Ship > *I. Papanin* Period > Dec. 2007 n > 201	ANT 25/2 *Polarstern* 2008/09 686	BELARE 08 *I. Papanin* 2008/09 444	ANT 28/2 *Polarstern* 2011/12 596	Total 1927	Remark
Emperor penguin	*Aptenodytes forsteri*	18	197	190	114	519	
Adélie penguin	*Pygoscelis adeliae*	31	302	432	306	1071	
Chinstrap penguin	*Pygoscelis antarctica*	294	220	264	910	1688	
Macaroni penguin	*Eudyptes chrysolophus*	9	1		6	16	
Wandering albatross	*Diomedea [exulans] sp.*	69	36	51	133	289	
Northern royal albatross	*Diomedea [epomorpha] sanfordi*		1			1	
Southern royal albatross	*Diomedea [epomorpha] epomorpha*	6	8	4		18	
Large albatross sp.	*Diomedea [exulans]/[epomorpha] sp.*		1			1	
Shy albatross	*Thalassarche [cauta] cauta*	53	38	2	3	96	
Salvin's albatross	*Thalassarche [cauta] salvini*		1			1	Photographic material
Black-browed albatross	*Thalassarche [melanophrys] melanophrys*	61	62	88	42	253	
Grey-headed albatross	*Thalassarche chrysostoma*	15	23	23	8	69	
Atlantic yellow-nosed albatross	*Thalassarche [chlororhynchos] chlororhynchos*	7	11	17	12	47	
Indian yellow-nosed albatross	*Thalassarche [chlororhynchos] carteri*	22	18	4	2	46	
Yellow-nosed albatross sp.	*Thalassarche [chlororhynchos] sp.*	7		23	6	36	
Sooty albatross	*Phoebetria fusca*	17	26	46	47	136	
Light-mantled sooty albatross	*Phoebetria palpebrata*	54	85	673	49	861	
Southern giant petrel	*Macronectes giganteus*	14	43	32	48	137	
Northern giant petrel	*Macronectes halli*	9	9	13	17	48	
Giant petrel sp.	*Macronectes sp.*	13	8	13	8	42	
Southern fulmar	*Fulmarus glacialoides*	31	216	5147	157	5551	
Antarctic petrel	*Thalassoica antarctica*	591	1130	4751	2544	9016	
Cape petrel	*Daption capense*	59	352	688	185	1284	1 *"australe"*; photographic material: ESM_1
Snow petrel	*Pagodroma [nivea] sp.*	554	1015	1802	422	3793	
Kerguelen petrel	*Pterodroma brevirostris*	165	246	568	210	1189	
Great-winged petrel	*Pterodroma [macroptera] macropetra*	324	227	705	304	1560	
Soft-plumaged petrel	*Pterodroma mollis*	1426	470	1644	694	4234	Dark morph: 9
White-headed petrel	*Pterodroma lessonii*	124	47	171	30	372	
Atlantic petrel	*Pterodroma incerta*	1	3		26	30	
White-chinned petrel	*Procellaria aequinoctialis*	257	212	49	95	613	
Spectacled petrel	*Procellaria conspicillata*			9	27	36	
Grey petrel	*Procellaria cinerea*	14	47	15	3	79	

Table 2 continued

Species		Expedition > BELARE 07 Ship > *I. Papanin* Period > Dec. 2007 n > 201	ANT 25/2 *Polarstern* 2008/09 686	BELARE 08 *I. Papanin* 2008/09 444	ANT 28/2 *Polarstern* 2011/12 596	Total 1927	Remark
Barau's petrel	*Pterodroma baraui*			1		1	Photographic material: Fig. 3
Great shearwater	*Puffinus gravis*	13	98	146	116	373	
Flesh-footed shearwater	*Puffinus carneipes*	1		1		2	
Sooty shearwater	*Puffinus griseus*	369	189	36	23	617	
Antarctic little shearwater	*Puffinus assimilis elegans*	74	14	305	25	418	
Manx shearwater	*Puffinus puffinus*	4		2		6	
Cory's shearwater	*Calonectris diomedea borealis*	250	143	229	194	816	
Broad-billed prion	*Pachyptila vittata*	21	2	1559	21	1603	
Fairy prion	*Pachyptila turtur*	143	46	1376		1565	
Slender-billed prion	*Pachyptila belcheri*	85	835	2752	1	3673	
Prion sp. (Salvin's/Antarctic)	*Pachyptila sp. (salvini/desolata)*	4133	1923	10981	858[a]	17895	
Blue petrel	*Halobaena caerulea*	371	627	3740	748	5486	
Wilson's storm-petrel	*Oceanites oceanicus*	5	26	40	21	92	
European storm-petrel	*Hydrobates pelagicus*	1	1	5		7	
White-bellied storm-petrel	*Fregetta grallaria*	35	4	28	9	76	
Black-bellied storm-petrel	*Fregetta tropica*	233	103	231	182	749	
Leach's storm-petrel	*Oceanodroma leucorhoa*	4	7	347	2	360	
Storm-petrel sp.	*Oceanites/Fregetta sp.*				9	9	
S Georgian diving-petrel	*Pelecanoides georgicus*	2				2	Most probable determination; photographic material: Fig. 4
Diving-petrel sp.	*Pelecanoides sp.*	25	18	104	36	183	Mainly common *P. urinatrix*
Cape cormorant	*Phalacrocorax capensis*		160		14	174	Off African coast
Cape gannet	*Morus capensis*		79	22		101	Off African coast
Grey (red) phalarope	*Phalaropus fulicarius*		55	42	49	146	
Subantarctic skua	*Catharacta [skua] antarctica*	4	19	6	8	37	
South polar skua	*Catharacta [skua] maccormicki*			5	4	9	
Pomarine skua	*Stercorarius pomarinus*			4	3	7	
Arctic skua	*Stercorarius parasiticus*		6	1	1	8	
Long-tailed skua	*Stercorarius longicaudus*	111	33	22	22	168	
Skua sp.	*Stercorarius sp.*	3	7	22		32	Probably long-tailed
Cape gull	*Larus vetula*		34		34	68	Off African coast
Sabine's gull	*Xema sabini*	3	134		91	228	Off African coast
Hartlaub's gull	*Chroicocephalus hartlaubii*		2			2	Off African coast

Table 2 continued

Species		Expedition > BELARE 07 Ship > *I. Papanin* Period > Dec. 2007 n > 201	ANT 25/2 *Polarstern* 2008/09 686	BELARE 08 *I. Papanin* 2008/09 444	ANT 28/2 *Polarstern* 2011/12 596	Total 1927	Remark
Arctic tern	*Sterna paradisaea*	99	196	883	103	1281	
Sandwich tern	*Sterna sandvicencis*				58	58	Off African coast
Swift tern	*Sterna bergii*		113		54	167	Off African coast
Antarctic tern	*Sterna vittata*		34			34	
Arctic/Antarctic tern	*Sterna sp.*		63			63	
Total all seabirds		10234	10026	40314	8236	69648	
Mean per count		50.9	14.6	90.8	13.8	35.7	

[a] Prions sp, not identified

Thalassarche [chlororhynchos] chlororhynchos, or to STW and ACC, e.g. sooty *Phoebetria fusca*, with the exception of light-mantled sooty *Phoebetria palpebrata* in PFW, AW and PI. Penguins and most of the medium-sized tubenoses were bound to PI, even if some were present in AW in lower numbers: emperor *Aptenodytes forsteri*, Adélie *Pygoscelis adeliae* and chinstrap *Pygoscelis antarctica* penguins, southern fulmar *Fulmarus glacialoides*, Antarctic petrel *Thalassoica antarctica*, snow petrel *Pagodroma [nivea] sp*, Kerguelen petrel *Pterodroma brevirostris*, blue petrel. Few species were bound to STW or STW and ACC: great-winged petrel *Pterodroma [macroptera] macroptera*, white-headed petrel *Pterodroma lessonii,* white-chinned petrel *Procellaria aequinoctialis,* spectacled petrel *Procellaria conspicillata*, sooty and Cory's shearwaters *Puffinus griseus* and *Calonectris diomedea borealis*, while grey phalarope's *Phalaropus fulicarius* distribution was limited to ACC (see below). It was found that there were clear differences between zones for most species, as confirmed by their very high statistical significance ($P < 0.01$) both for the concerned species and their pooled sum; moreover, for each species significant differences between zones are shown as well (Table 4; selected illustration in Fig. 4). This is in accordance with the work we performed in the Arctic showing that the hydrological regions accounted for 90 % of data variability, on the basis of a principal component analysis (Fig. 3 in Joiris 2000).

Some species of note are presented below in groups and in decreasing order of abundance. Comments on their geographical distribution will be expressed in comparison with the synopsis by Shirihai (2007).

Prions and blue petrel formed the most numerous group of species, with a total of 30,200 individuals, including 17,000 registered during the Papanin 2008/2009 expedition (Table 2). During the two *Papanin* expeditions, for example, 25,100 individuals were observed at a bit more than 200 counts, representing half of the total of 50,400 birds encountered during 645 counts. All observations were obtained between 40 and 62°S, reflecting a strong link between prions and the ACC and AW and between blue petrel and AW. They presented a very high patchiness, 11,340 being noted in 16 counts, including peaks of thousands: 4,800 at 2 successive counts around 42°30′S (broad-billed and Salvin's/Antarctic prions sp), and 5,750 at 8 successive counts around 49°S, *i.e.* close to the PF (fairy, slender-billed and Salvin's/Antarctic prions sp). Blue petrels were seen between 53° and 62°S, with a major concentration of more than 3,000 between 57° and 58°S at the ice edge in association with tens of humpback whales *Megaptera novaeangliae*. Such high concentrations were not detected by the other team present on board *Polarstern* in the same region during the same period, thus reflecting the high patchiness of their distribution.

Table 3 Transect between South Africa and Antarctica: main water masses, fronts and pack ice; data Polarstern 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[a] (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)	37 (0 to 98)

[a] Sub-Antarctic Water

Table 4 Seabirds encountered between South Africa and Antarctica during summer, grouped per water masses; data: Polarstern 2011/12; main species (total ≥ 25); total numbers recorded; calculated density; n = number of half-an-hour counts

Species	Zone[a]> STW n> 106	ACC 74	PFW 67	AW 64	PI 280	All 591	Mean 591	Detection Limit (m)	Density (N/km2)	Significance
Emperor penguin	0[b]	0	0	0	114[b]	114	0.19	700	0.060	***
Adélie penguin	0[b]	0	0	0	36[b]	36	0.06	700	0.019	***
Chinstrap penguin	0[b]	0	0	17[b]	97[b]	114	0.19	700	0.060	***
Wandering albatross	66[b]	19[b]	36[b]	2	1[b]	124	0.21	800	0.029	***
Black-browed albatross	19[b]	11[b]	5	6	6[b]	47	0.08	600	0.015	***
Sooty albatross	13[b]	22[b]	1[b]	2	0[b]	38	0.06	600	0.012	***
Light-mantled sooty albatross	0[b]	1	24[b]	22[b]	18[b]	65	0.11	600	0.020	***
Southern giant petrel	2[b]	1	3	1[b]	42	49	0.08	600	0.030	***
Southern fulmar	0[b]	2	1	31[b]	142[b]	176	0.30	450	0.108	***
Antarctic petrel	0	0	0	1[b]	2544[b]	2545	4.31	450	1.57	***
Cape petrel	1[b]	6	13	43[b]	161	224	0.38	450	0.138	***
Snow petrel	0[b]	0	0	1[b]	442[b]	443	0.75	500	0.329	***
Kerguelen petrel	0[b]	1	0	16[b]	147[b]	164	0.28	450	0.067	***
Great-winged petrel	32[b]	2	0	0	0	34	0.06	450	0.014	***
Soft-plumaged petrel	222	18[b]	168[b]	114[b]	59[b]	581	0.98	450	0.239	***
White-headed petrel	24[b]	3[b]	3[b]	0	0	30	0.05	450	0.012	***
White-chinned petrel	84[b]	3	4	4	3[b]	98	0.17	450	0.040	***
Spectacled petrel	27[b]	0	0	0	0	27	0.05	450	0.011	***
Great shearwater	48[b]	22[b]	38[b]	8	1[b]	117	0.20	450	0.048	***
Antarctic little shearwater	1[b]	24[b]	0	0	0	25	0.04	400	0.011	***
Cory's shearwater	194[b]	0	0	0	0	194	0.33	250	0.143	***
Prion sp. (Salvin's/Antarctic)	18	151[b]	237[b]	347[b]	176[b]	929	1.57	200	0.859	***
Blue petrel	0[b]	0	0	241[b]	748	989	1.67	200	1.83	***
Black-bellied storm-petrel	31[b]	6	7	137[b]	57[b]	238	0.40	200	0.220	***
Diving-petrel sp.	0[b]	0	21[b]	15[b]	13	49	0.08	200	0.045	***
Grey (red) phalarope	0[b]	49[b]	0	0	0	49	0.08	200	0.045	***
Total	839[b]	355	575	1022[b]	4826	7617	12.9		5.974	***
Mean	7.9	4.8	8.6	16	17.2	12.9			0.208	

[a] *STW* Sub-Tropical Water, *ACC* Antarctic Circumpolar Current (Sub-Antarctic Water), *PFW* Polar Frontal Water, *AW* Antarctic Water, *PI* pack ice; statistical significance: *** $P < 0.01$; b: $P < 0.01$

The second most abundant group was the medium-sized tubenoses, fulmar and petrels: they represented a total of 28,000 individuals belonging to 13 species, including 3,800 snow petrels bound to pack ice. The most numerous species of this group was Antarctic petrel with 9,000 individuals (peaking around 58°S, *i.e.* at the ice edge), followed by Antarctic fulmar (5,500), soft-plumaged petrel (4,200), great-winged petrel (1,550), Cape petrel (1,300) and Kerguelen petrel (1,200). Worth mentioning is the observation of dark morphs of soft-plumaged petrels (at least 9 between 41° and 53°S) since their distribution is poorly known; some intermediate individuals were also sighted in the same area. The vast majority of Cape petrels were of the nominate race *D. c. capense*, with the exception of a *D. c. australe*, very far of its known distribution (Online Resource 1). The other species were encountered with less than 1,000 individuals, listed in decreasing order of abundance: white-chinned petrel, white-headed petrel, grey petrel (*Procellaria cinerea),* spectacled petrel, Atlantic petrel, to finish with the rare Barau's petrel (*Pterodroma baraui),* of which one individual was recorded on 8 December 2008 at the Sub-Tropical Front (39°S, 17°E; Fig. 2), well away from its usual distribution in the tropical Indian Ocean. Finally, Antarctic little shearwater was present between 42°30′ and 44°30′S (420 individuals) with a peak of 240 in 2 counts at 43°20′, *i.e.* out of its known range.

Three species formed the bulk of the penguin populations: chinstrap (1,700 individuals), Adélie (1,100), and emperor (520), all being as expected bound to PI even if chinstraps tend to be noted at the ice edge and thus in open AW as well, as mentioned before (Joiris 1991). Of note were 16 macaroni *Eudypes chrysolopus* recorded in open AW.

Medium-sized albatrosses and giant petrels were represented by 10 species, the most numerous ones being light-mantled sooty albatross (860 individuals), black-browed albatross (250), Southern giant petrel (140), sooty albatross (135), shy albatross *Thalassarche [cauta] cauta* (96), grey-headed albatross *Thalassarche chrysostoma* (70) and 3 species below 50 individuals: Northern giant petrel *Macronectes halli,* Atlantic and Indian yellow-nosed albatrosses *Thalassarche [chlororhynchos] chlororhynchos* and *carteri.* A single Salvin's albatross *Thalassarche [cauta] salvini* was observed and its determination confirmed by photographic material.

Storm-petrels were mainly black-bellied (750 individuals) and Leach's *Oceanodroma leucorhoa* (360 mainly between 35° and 38°S, of which 300 at 14 successive counts on January 14th, 2009), as well as Wilson's *Oceanites oceanicus* (90) and white-bellied *Fregetta grallaria* (75, mainly around 42°S), and few European *Hydrobates pelagicus* (7 close to South Africa), while diving-petrels were common *Pelecanoides urinatrix* (130, mainly between 48° and 53°S) and a few most probable South Georgian *P. georgicus* (at least 2 at 50°S on 4 December 2007: Fig. 3). Both species were sighted out of their known range (Figs. 4, 5).

Among the large albatrosses, the main species was wandering with 290 individuals, followed by southern royal *Diomedea [epomorpha] epomoropha* (18), all in the ACC, mainly between 40° and 50°S.

Grey phalaropes (150) were encountered farther south than expected: 40° to 46°30′S close to the Antarctic Front; most birds were seen in small groups flying at c. 30 m above the sea.

Observations of long-tailed skuas *Stercorarius longicaudus* reflect an overwintering zone farther south than expected, around 40°S with a peak of 55 in one count (40°10′S, 27 December 2007, *i.e.* close to STF): although its winter repartition is considered to be just north of the Subtropical Convergence in general, this species was considered as irregular south of 35°S in the South African area (Malling Olsen and Larsson 1997; Shirihai 2007).

A quantitative comparison of data collected during the different expeditions was prepared for the most numerous species in order to determine the reproducibility of the counting method and the heterogeneity (patchiness) of seabird distribution. Some obvious differences in numbers between expeditions, however, concern some species and could be explained by seasonal movements, e.g. for Arctic tern *Sterna paradisaea,* Sabine's gull *Xema sabini* and the northern skua species (Arctic *Stercorarius parasiticus*, pomarine *Stercorarius pomarinus* and long-tailed *Stercorarius longicaudus*). Moreover, some differences could also be due to slight differences in the followed route from one expedition to the other, especially in its southern part (Fig. 1). From the quantitative point of view, data were analysed for the most numerous species ($n \geq 25$ individuals in total). A simple comparison was based on the maximal to minimal means ratio. The lowest value was 1,3 for southern giant petrel, allowing us to consider the reproducibility as very high. A large group of species showed a ratio between 2 and 9, reflecting a relatively stable and homogenous distribution: in increasing order of max to min ratio, they were Atlantic yellow-nose albatross, Kerguelen petrel, sooty albatross, black-browed albatross, emperor and Adélie penguins, great-winged albatross, great shearwater, Cape petrel, grey-headed albatross, snow petrel, Cory's shearwater, Adélie penguin, wandering albatross, diving-petrel, blue petrel. Very high ratios reflected patchiness and heterogeneity of the distribution of other species, between 10 and 75, in increasing order of ratio: soft-plumaged, white-headed and white-chinned petrels, prions, light-mantled sooty and Indian yellow-nosed albatrosses, Antarctic little shearwater and southern fulmar. The ratio was obviously much higher, but could not be quantified since some expeditions showed no observation at all, reflecting an extremely high patchiness: spectacled petrel and grey (red)

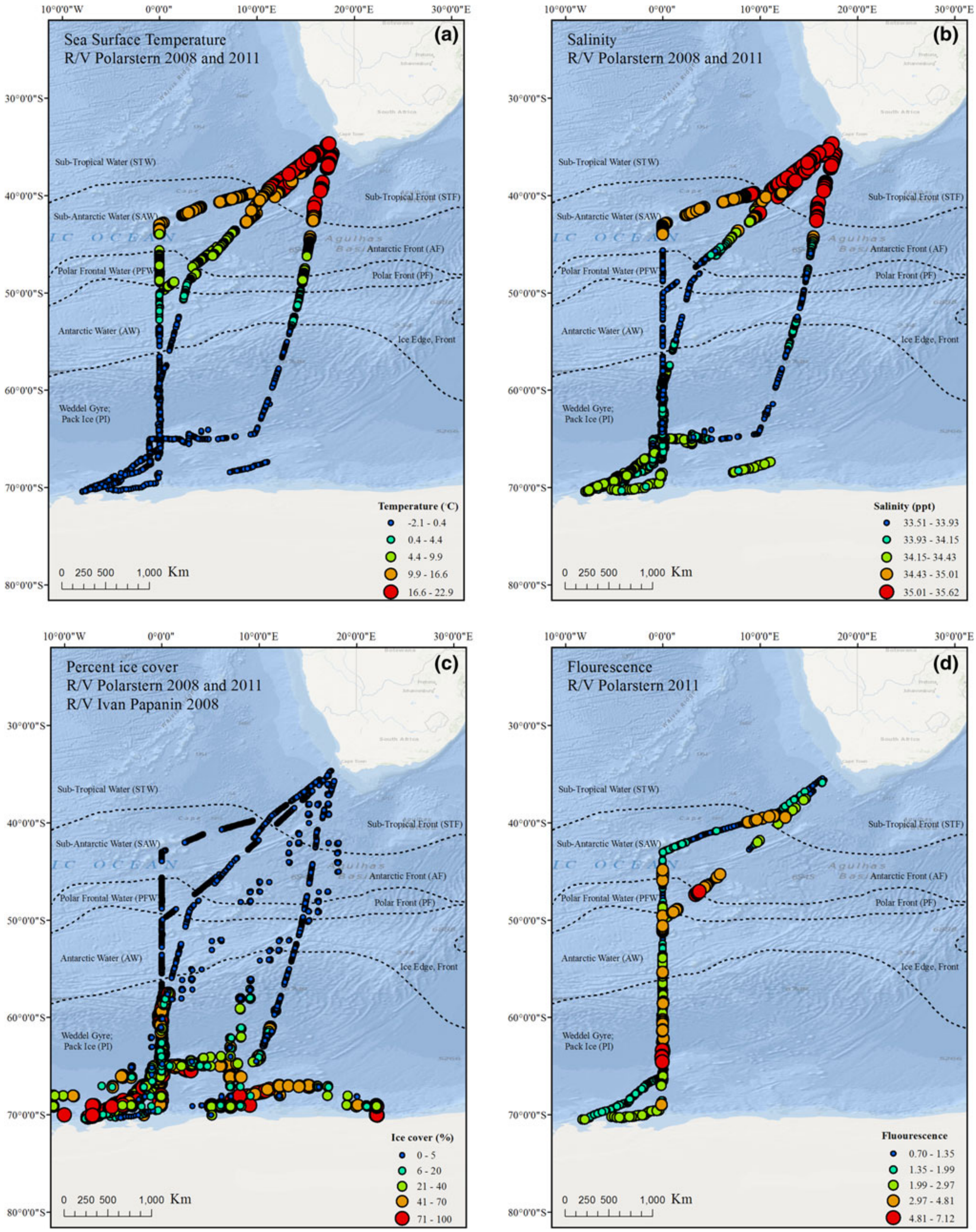


Fig. 2 Hydrological data collected on board *RV Polarstern*: water temperature (°C) (**a**), salinity (**b**), ice coverage (%) (**c**), chlorophyll pigments as fluorescence (**d**)

Fig. 3 Barau's petrel *Pterodroma baraui*, 39°S, 17°20′E, 8 December 2008; photo ADB

Fig. 4 Most probable South Georgian diving-petrel *Pelecanoides georgicus*, 50°S, 4 December 2007; photo ADB

phalarope. As an example, data on the prion species and blue petrel are shown in some detail in Table 5.

GBMs performed very well in general (e.g. AUC > 0.80 in most cases), highlighting the fact that using temperature, ice cover, salinity and region are primary drivers in determining the distribution of many Antarctic seabird species (Table 6). The models that performed poorest were the black-browed albatross (AUC 0.68 to 0.74) and the southern giant petrel (AUC 0.57 to 0.59). Between years (2008 and 2011 trips), AUC values for most species were comparable suggesting that year may not be a large factor in predicting the distribution of these species. AUC did highly differ between years for the white-headed petrel (AUC 0.86 in 2008, and 0.54 in 2011) and the blue petrel (AUC 0.97 in 2008 and 0.74 in 2011). We also found that when we removed region as a predictor variable, the AUC values decreased for 12 of the modelled species, while AUC actually increased when removing region for 6 of the modelled species.

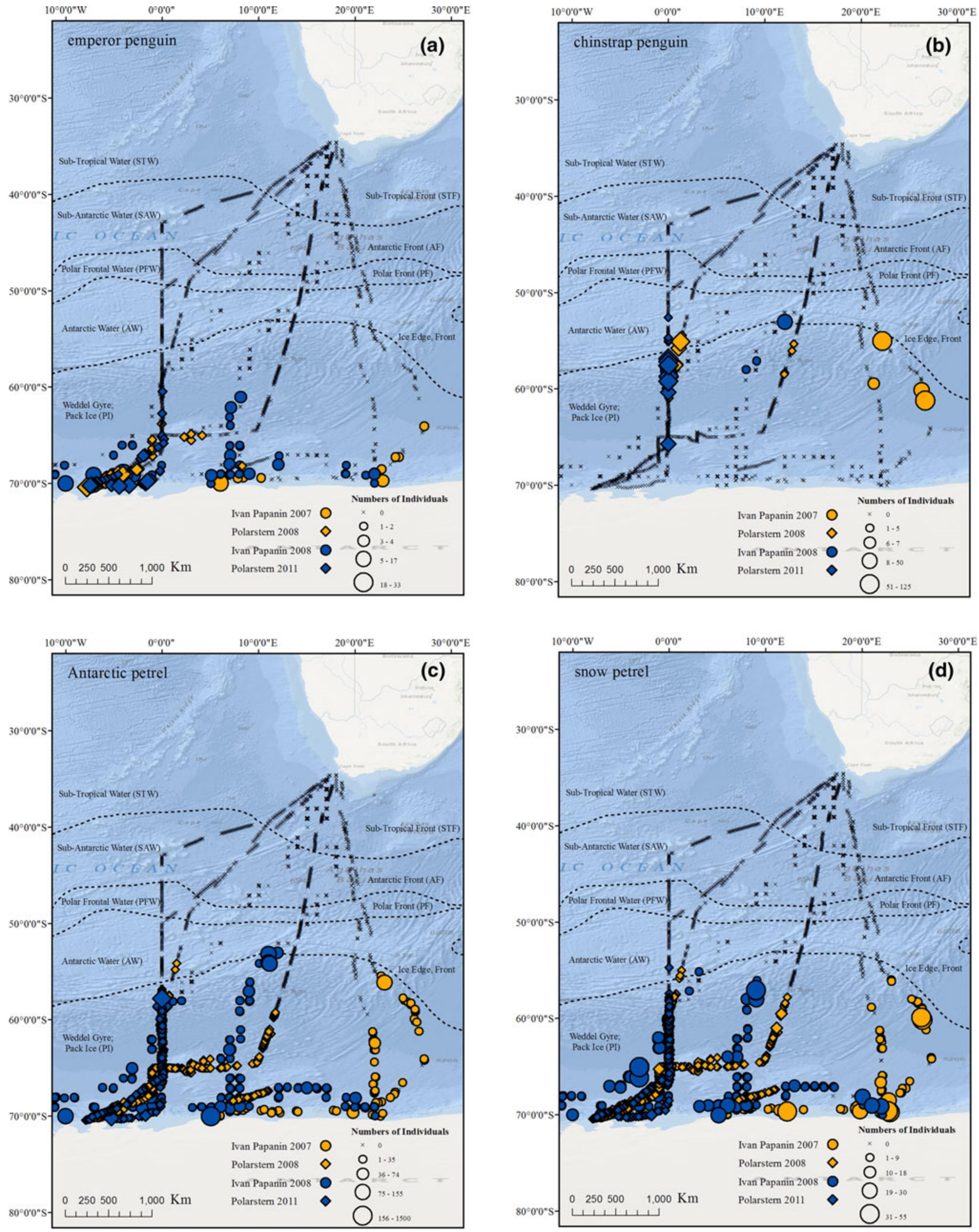
Fig. 5 Examples of seabird distribution: numbers per half-an-hour transect count: emperor penguin *Aptenodytes forsteri* (**a**), chinstrap penguin *Pygoscelis antarctica* (**b**), Antarctic petrel *Thalassoica antarctica* (**c**), snow petrel *Pagodroma [nivea] sp.* (**d**), soft-plumaged petrel *Pterodroma mollis* (**e**), Antarctic little shearwater *Puffinus assimilis elegans* (**f**), black-bellied storm-petrel *Fregetta tropica* (**g**), grey (red) phalarope *Phalaropus fulicarius* (**h**) ▶

Discussion

The data basically show a very good homogeneity between expeditions for some species, reflecting both the stability of seabird distribution and the good reproducibility of the counting method. Some species show high heterogeneity and patchiness with very high local concentrations and thus variability between expeditions, even when quasi-simultaneous (*Papanin* and *Polarstern,* 2008/2009, Table 2) (notably prions and blue petrel, Table 6). This patchiness was also the reason for important differences between expeditions and years in total numbers of individuals—all species pooled: from 14 to 90 per count with an overall mean of 36 (Table 2). It also results in the fact that quantitative discussions of data collected during a single or a low number of expeditions in a given area have a very low significance only: more expeditions are needed. An obvious consequence is that data do not show a normal distribution, so that mean and standard deviation values should not be applied, as it is usually the case in such field studies. Means were shown here, however, to allow comparison with literature data.

Modelling efforts confirm the fact that many of the species counted were homogeneous in time and in space. Hydrographic regions as defined by salinity, ice and temperature allowed for the creation of models with high accuracy. Models that had decreased AUC values when removing region as a predictor suggest that there are other factors which may influence the presence of certain species. When AUC values increased after region was removed, we can assume that we are over-complicating the models and that a more simple model can be adopted for predicting the distributions of these species. These results are confirmed by other works in the same area showing that seabird assemblages in the Southern Ocean are in fact driven primarily by latitudinal gradients, sea surface temperature and ice cover (Commins et al. 2013).

As expected, sibling species having a similar diet were geographically separated and so was competition for food avoided (Competitive Exclusion Principle, Gause 1934; Hardin 1960): e.g. chinstrap penguin at the ice edge and Adélie penguin in closed pack ice (see Joiris 1991) or sooty albatross in STW and ACC, and light-mantled sooty albatross in PFW and AW.



emperor penguin
(a)
chinstrap penguin
(b)
Antarctic petrel
(c)
snow petrel
(d)
10°0'0"W
0°0'0"
10°0'0"E
20°0'0"E
30°0'0"E
30°0'0"S
40°0'0"S
50°0'0"S
60°0'0"S
70°0'0"S
80°0'0"S
Sub-Tropical Water (STW)
Sub-Tropical Front (STF)
Sub-Antarctic Water (SAW)
Antarctic Front (AF)
Polar Frontal Water (PFW)
Polar Front (PF)
Antarctic Water (AW)
Ice Edge, Front
Weddel Gyre; Pack Ice (PI)
Numbers of Individuals
Ivan Papanin 2007
Polarstern 2008
Ivan Papanin 2008
Polarstern 2011
0 250 500 1,000 Km
0
1 - 2
3 - 4
5 - 17
18 - 33
1 - 5
6 - 7
8 - 50
51 - 125
1 - 35
36 - 74
75 - 155
156 - 1500
1 - 9
10 - 18
19 - 30
31 - 55

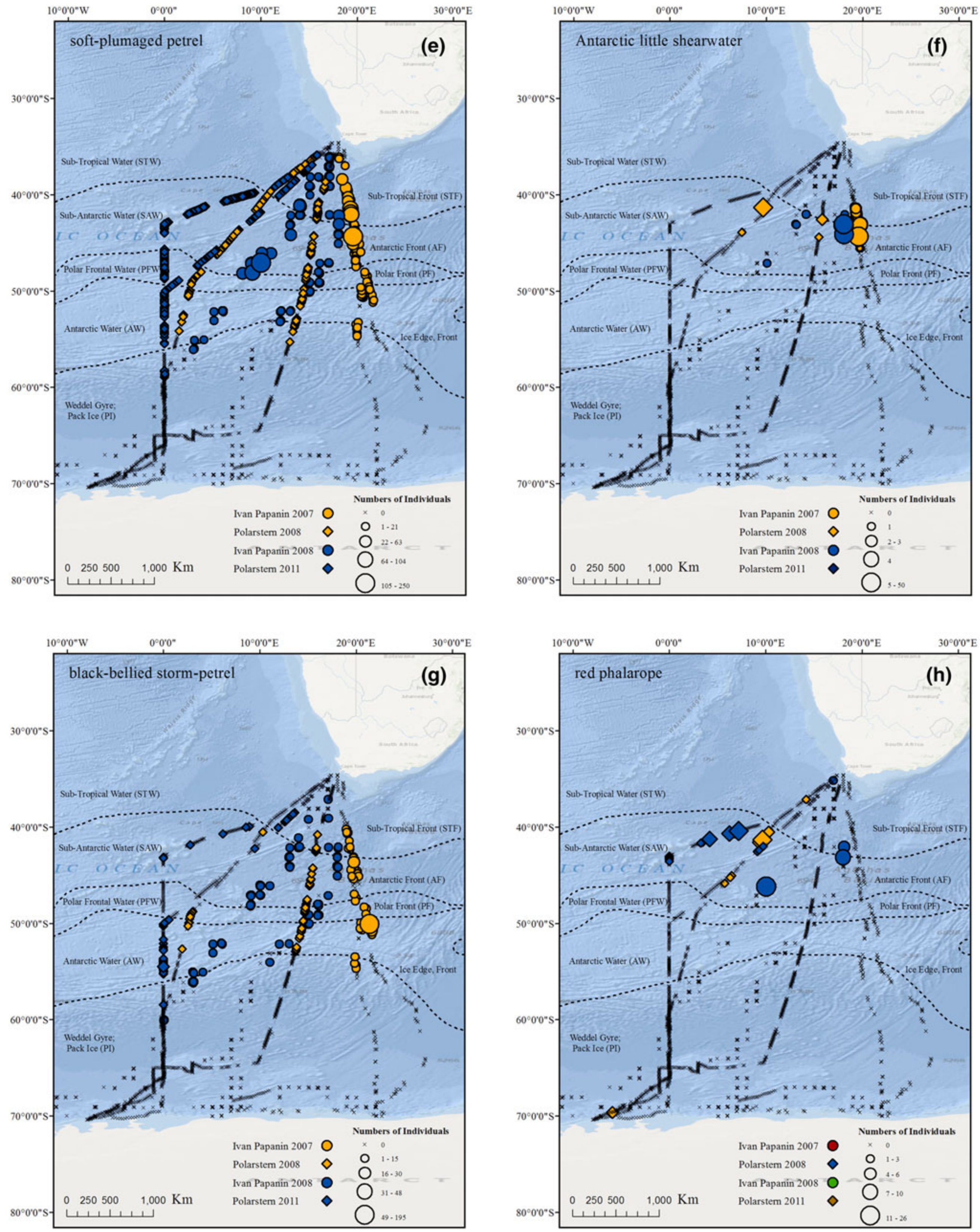


Fig. 5 continued

Table 5 Geographical distribution of prions and blue petrel recorded during two return transects between South Africa and Antarctic a total numbers; n = number of positive counts

Species	Expedition>	BELARE 07				BELARE 08				Total	
		Route S		Route N		Route S		Route N			
	Zone: from to	40°S 60°15′S	*n*	49°S 62°S	*n*	42°S 60°S	*n*	42°S 58°15′S	*n*		*n*
Broad-billed prion		21	3			3	3	1556[a]	8	1580	14
Fairy prion		24	8	119	8	1376[b]	9			1519	25
Slender-billed prion		21	6	64	10	2651[b]	20	101	5	2837	41
Prion sp (Salvin's/Antarctic)		2819	50	1314	33	4432[b]	65	6547[a]	54	15112	202
Blue petrel		159	23	212	19	993	28	2702[c]	9	4066	79

[a] Including high concentrations at two successive counts at 42°30′S: 1400 broad-billed prions and 3400 prions sp (Salvin's/Antarctic)

[b] Including high concentrations at 8 successive counts from 48°30′S to 49°15′S: 1,900 prions sp (Salvin's/Antarctic), 2,600 slender-billed prions and 1,250 fairy prions

[c] Including a high concentration of 2690 blue petrels at 6 successive counts from 57°10′S to 57°50′S

Table 6 AUC values for GBM models run on seabirds encountered during *Polarstern* transects in 2008/2009 and 2011/2012. AUC calculated on an independent data set from respective years

Species	2008/2009	2011/2012	Both years	Both years–no region
Emperor penguin	0.79	0.85	0.83	0.79
Adélie penguin	0.82	0.96	0.90	0.88
Chinstrap penguin		0.90	0.86	0.78
Wandering albatross	0.93	0.81	0.84	0.84
Black-browed albatross	0.68		0.69	0.74
Grey-headed albatross			0.86	0.85
Atlantic yellow-nosed albatross			0.86	0.86
Sooty albatross			0.69	0.73
Light-mantled sooty albatross	0.76	0.90	0.83	0.84
Southern giant petrel	0.57		0.57	0.59
Southern fulmar	0.89	0.89	0.86	0.88
Antarctic petrel	0.95	0.89	0.92	0.93
Cape petrel	0.88	0.76	0.83	0.81
Snow petrel	0.95	0.90	0.92	0.89
Kerguelen petrel	0.92	0.95	0.96	0.95
Great-winged petrel	0.96	0.98	0.97	0.96
Soft-plumaged petrel	0.91	0.94	0.95	0.95
White-headed petrel	0.86	0.54	0.79	0.79
White-chinned petrel	0.87	0.80	0.80	0.80
Great shearwater		0.79	0.84	0.84
Cory's shearwater	0.98	0.98	0.98	0.98
Prion sp. (Salvin's/Antarctic)	0.91	0.87	0.89	0.87
Blue petrel	0.97	0.74	0.93	0.92
Black-bellied storm-petrel	0.80	0.93	0.84	0.83
Diving-petrel sp.			0.77	0.73

Conclusion

Hydrological features were as expected the main factor explaining the seabird distribution, a few species only being present in all water masses, many bound to two or three zones, and a few limited to one zone. For selected (main) species recorded during the *Polarstern* 2011/2012 expedition, for example (Table 4), this resulted in similar numbers of species in each zone: between 18 and 22. Total numbers of individuals, however, varied from 5 per count in ACC, 8 in STW, 9 in PFW, with maximal values in AW and PI as 16 and 17, respectively; this last figure being strongly influenced by the large numbers of southern fulmar and petrels recorded, e.g. 2,550 Antarctic petrels for a total of 4,830 birds in PI. These differences were statistically highly significant ($P < 0.01$, Table 4). We speculate that the geographical structure of seabird distribution must be bound to differences in density, availability and species composition of their prey, mainly zooplankton. Precise information on the diet of the different species, mainly the tubenoses, is, however, scarce, so that seabird preferences for prey are difficult to establish, especially out of the breeding season when adults bring food to their chicks.

In comparison with data obtained in the adjacent Weddell Sea by the same team, same platform (*Polarstern*) and same counting method during the EPOS 1 expedition *(European Polarstern Study*, leg 1, October–November 1988), total number of species was 31 in the Weddell Sea and 57 in this study, not taking into account the 6 African coastal species. Numbers of individuals were, however, much higher in the Weddell Sea: 150 as a mean (Joiris 1991), compared to 36 in this study. Both figures, low number of species and high number of individuals, reflect a lower biodiversity in the Weddell Sea even if total biological production seems to be more important since the seabird biomass was much higher. The difference is qualitative as well, the most numerous species in PI being Antarctic petrel in this study but Adélie penguin and Cape (pigeon) petrel in the Weddell Sea (Joiris 1991, 2000). Similarly, a comparison with European Arctic marine ecosystems reflects an intermediate biodiversity, with 30 species and 60 individuals per count (Joiris 2000). Patchiness in the Arctic can be extreme, with most seabirds—mainly northern fulmar *Fulmarus glacialis*—and cetaceans (humpback whales) being concentrated in a very limited area (Joiris 2011). The major difference is observed in closed pack ice, almost empty in the Arctic but showing a very high biomass in the Antarctic, mainly of Adélie penguins, Cape petrels and crabeater seals *Lobodon carcinophagus* (Joiris 1991, 2000).

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