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Abstract

Long-term demographic studies have recently shown that global climate change together with increasing direct impacts of human activities, such as fisheries, are affecting the population dynamics of marine top predators. However, the effects of these factors on species distribution and abundance at sea are still poorly understood, particularly in marine ecosystems of the southern hemisphere. Using a unique long-term data set of at-sea observations, we tested for interdecadal (1980s vs. 2000s) changes in summer abundance and distribution of 12 species of Albatrosses and Petrels along a 30° latitudinal gradient between tropical and Antarctic waters of the southern Indian Ocean. There were contrasting effects of climate change on subantarctic seabird distribution and abundance at sea. While subtropical waters showed the highest rate of warming, the species that visited this water mass showed the greatest changes in distribution and abundance. The abundance of Wandering Albatrosses (*Diomedea exulans*), White-chinned Petrels (*Procellaria aequinoctialis*) and Giant Petrels (*Macronectes* sp.) declined markedly, whereas the other species showed contrasting trends or did not change. With the exception of the White-chinned Petrel, these decreases were at least partly related to regional increase in sea surface temperature. The southward shift of Wandering Albatross and Prions (*Pachyptila* spp.) distributions could be ascribed to species redistribution or decrease in abundance due to warming of the subtropical waters. Surprisingly, White-chinned Petrel distribution shifted northward, suggesting more complex mechanisms. This study is the first to document a shift in species range in the Southern Ocean related to climate change and contrasting abundance changes. It suggests that some species might experience more severe impacts from climate change depending on the water masses they visit. As climate changes are predicted to continue in the next decades, understanding species responses to climate change is crucial for conservation management, especially when their conservation status is critical or unknown.

Keywords: at-sea survey, Bayesian, climate change, mixture model, populations trends, Procellariiform, zero inflation

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Introduction

The Earth's climate has experienced an unprecedented warming since the 1970s (IPCC, 2007) that has already affected both marine and terrestrial ecosystems (Walther *et al.*, 2002). Climate changes are affecting species physiology, phenology, abundance and distribution, and thus the structure and composition of communities (Hughes, 2000; Root *et al.*, 2003; Votier *et al.*, 2005). Depending on the pace of changes, a species can either adapt to its new environment, track its former preferred habitat, or go extinct (Davis *et al.*, 2005). These responses will depend on species standing genetic variation, dispersal ability as well as biotic interactions. However, given the current rate of warming, changes in

distribution and abundance are the most likely and immediate responses for most species (Bennett, 1997). Indeed, several studies have reported population declines and/or poleward shifts in distribution consistent with climate warming (reviewed in Parmesan, 2006). Whereas such changes have been widely studied in the northern Atlantic (Beaugrand & Reid, 2003; Genner *et al.*, 2004) and Pacific Oceans (Roemmich & McGowan, 1995; Hyrenbach & Veit, 2003), the ecological impact of climate change on marine ecosystems is less well documented in the southern hemisphere where large-scale and long-term data sets are logistically difficult to obtain. As climate changes differ between both hemispheres, we might expect differences in biological responses.

The Southern Ocean is a major component of the global ocean and climate system and several studies documented an increase in air and sea surface tempera-

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tures (SST; King, 1994; Smith *et al.*, 1999; Gille, 2002) over the past 50 years, concomitant with important changes in sea-ice extent (Zwally *et al.*, 2002) and surface wind stress (Fyfe *et al.*, 2007). Such changes in oceanographic conditions are related to atmospheric circulation, water mass dynamics and the position of frontal structures (Hall & Visbeck, 2002; Kostianoy *et al.*, 2004), known to affect distribution and abundance of marine pelagic species (e.g., plankton, fish and squids; Hunt *et al.*, 1981; Lehodey *et al.*, 1997) and, consequently, the availability of prey to top predators. Given the shifts in the at-sea distribution and abundance of several marine species in some other parts of the world (e.g., Lehodey *et al.*, 1997; Beaugrand *et al.*, 2003; McMahon & Hays, 2006), we may expect environmental changes to have an impact on the Southern Ocean communities. For instance, Atkinson *et al.* (2004) documented the long-term changes in Antarctic krill (*Euphausia superba*) density and distribution and their effects on the Southern Ocean food web.

As top predators, seabirds are thought to integrate marine food webs across space and time (Trathan *et al.*, 2007) and can therefore provide information on ecosystem changes. They are important components of the ecosystems and are by far the most studied taxa in the Southern Ocean marine environment with long-term demographic studies on land.

Whereas changes in the demographic parameters and population sizes of several Antarctic and subantarctic seabird species have been related to both local and large-scale climatic changes (Weimerskirch *et al.*, 2003; Trathan *et al.*, 2007; Forcada *et al.*, 2008), there are few similar studies investigating the long-term changes in at-sea distribution based on tracking or at-sea observations. Vessel-based surveys are precious tools to investigate species range expansions or contractions and/or changes in abundance as seabirds spend most of their time at sea. Their advantages are to provide information on abundance of (1) species inaccessible on land (Balance, 2007) and (2) the nonbreeding fraction of the population, a component frequently ignored by land-based monitoring (Aebischer & Wanless, 1992).

Most of the vessel-based surveys conducted in the Southern Ocean aimed at characterizing seabird communities and their oceanographic habitats using short-term monitoring surveys (Ainley *et al.*, 1994; Van Franeker *et al.*, 2002; Raymond & Woehler, 2003; Hyrenbach *et al.*, 2007). To our knowledge, the only long-term study of seabird abundance and distribution at sea in the Southern Ocean was conducted by Woehler (1997) in Prydz Bay (Antarctica). This study revealed a decrease in abundance of five nonresident subantarctic species (Black-browed Albatross *Diomedea melanophrys*, Wandering Albatross *Diomedea exulans*, Northern Giant Pet-

rel *Macronectes halli*, White-chinned Petrel *Procellaria aequinoctialis* and Light-mantled sooty Albatross *Phoebastria palpebrata*) between the summers of 1980 and 1992.

The novelty of our study is to analyze a unique long-term data set of at-sea observations made repeatedly over two time periods separated by 20 years to examine changes in seabird occurrence and abundance at a large spatial scale. Cruises encompassed a 30° latitudinal gradient from tropical to Antarctic waters of the Southern Indian Ocean that allowed us to investigate the effect of rising SST on 12 species of Albatrosses and Petrels breeding on the subantarctic islands. We favored a Bayesian approach for data analysis to account for the heterogeneity of observational data and to fit less standard distributions (Gelman & Hill, 2007).

Our objectives were to test (1) whether the northern limit of the range and/or abundance of subantarctic seabirds changed over a 20-year time period and (2) whether any changes were consistent throughout the latitudinal gradient. We also tested how seabird occurrence and abundance responded to ocean warming by studying the relationships between species distribution and SST anomalies (SSTa). We expected species-specific responses since long-term responses to climate warming depend on species' ecology, such as affinity to warm or cold waters (Hyrenbach & Veit, 2003; Hemery *et al.*, 2008) or feeding guilds (Van Franeker *et al.*, 2002). Given the threats remaining over these species (Delord *et al.*, 2008), studying their response to climate change may provide valuable information for conservation management.

Materials and methods

Study area

Data were collected on board R.V. Marion Dufresne I and II during logistic or oceanographic cruises between La Réunion Island (21°06'S; 55°6'E) and the French subantarctic islands of Crozet (46°30'S; 51°00'E) and Kerguelen (49°30'S; 69°30'E). We analyzed 12 southward surveys conducted during two time periods: 1981–1984 and 2002–2007 in November and December (Table 1), corresponding to the breeding period of the 12 studied species. These 2 months were the most frequently surveyed and exhibited comparable oceanographic patterns (Kostianoy *et al.*, 2004). Transect lines crossed a large latitudinal gradient encompassing five distinct biogeographic domains (Fig. 1): the tropical waters (SST > 24 °C, TRW), the subtropical waters (SST = 17–24 °C, STW), the convergence zone (SST = 13–17 °C, CZ), the subantarctic waters (SST = 4 °C–13 °C, SAW) and the Antarctic waters (SST < 4 °C, ANW).

Seabird surveys

Seabirds were recorded using the strip transect method (Tasker *et al.*, 1984) and survey effort was maintained through-

Table 1 Description of the surveys including the start/end dates, duration and geographical ranges

No.	Start date GMT	End date GMT	Decade	No. of stations	No. of days	North (°S)	South (°S)	West (°E)	East (°E)
1	07/12/1981	18/12/1981	1980	65	8	23.57	49.75	51.93	70.08
2	22/12/1982	29/12/1982	1980	65	7	23.93	49.33	52.03	66.00
3	05/11/1984	16/11/1984	1980	39	8	20.95	48.92	52.47	66.27
4	06/12/1984	13/12/1984	1980	60	7	23.62	48.35	52.03	66.08
5	02/12/2002	10/12/2002	2000	51	6	23.92	48.37	52.40	67.95
6	05/12/2004	12/12/2004	2000	68	7	24.17	49.03	51.97	69.82
7	05/11/2005	13/11/2005	2000	38	7	21.17	49.60	51.95	68.02
8	03/12/2005	20/12/2005	2000	67	7	23.63	48.68	52.00	69.07
9	05/11/2006	14/11/2006	2000	89	8	21.53	48.23	51.97	66.45
10	06/12/2006	13/12/2006	2000	39	6	33.90	48.47	51.95	68.68
11	04/11/2007	12/11/2007	2000	75	6	23.37	48.32	52.33	67.25
12	04/12/2007	10/12/2007	2000	52	6	23.77	47.77	51.95	58.73

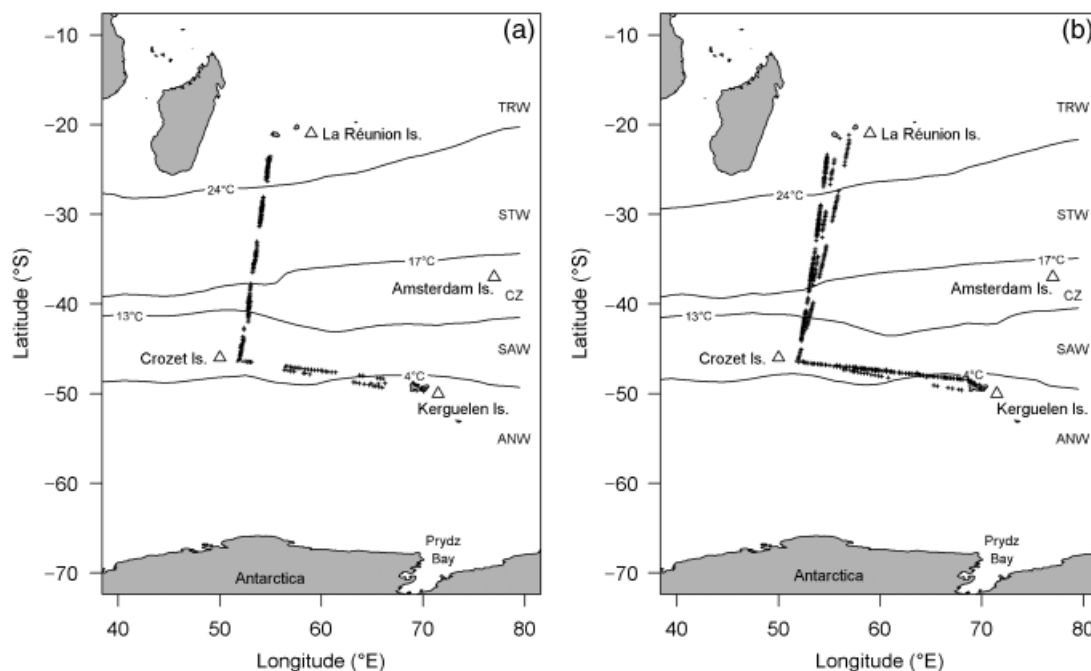


Fig. 1 Maps of the Southern Indian Ocean showing the survey stations (+) in (a) the 1980s and (b) in the 2000s. The sea-surface isotherms are delimiting five distinct biogeographic domains: the tropical waters (SST > 24 °C, TRW), the subtropical waters (SST = 17–24 °C, STW), the convergence zone (SST = 13–17 °C, CZ), the subantarctic waters (SST = 4 °C–13 °C, SAW) and the Antarctic waters (SST < 4 °C, ANW). The SST data were obtained by averaging the November and December monthly composites derived from the latest version of Reynolds Optimally Interpolated SST for the two time periods (1981–1984 and 2002–2007) at 1° × 1° spatial resolution.

out daylight hours on the one side of the vessel with best visibility (least sun glare). Seabird counts were performed by highly experienced or trained observers so that identifications were made to the lowest possible taxonomic level. Prions (genus *Pachyptila*) and Giant Petrels (genus *Macronectes*) were not identified at the species level due to their difficult identification when at-sea. Sighting position was determined by the Positioning System of the ship and observation conditions were recorded before each count (visibility, wind force and

sea state). We selected censuses made when the vessel cruising-speed was between eight and 15 knots, visibility was more than 3 km and sea state was not stronger than rough (swell lower than 4 m) to avoid bias in detection probability, especially that of small-sized species (Tasker *et al.*, 1984; Spear *et al.*, 2004).

As many subantarctic species tend to follow ships (hereafter termed ship-followers), two types of counts were performed. The first type of count consisted in recording all birds from the

Table 2 Decadal comparisons of total abundance, occurrence and mean latitude of first sighting of the 12 studied seabirds species ($n_{1980} = 229$ stations, $n_{2000} = 479$ stations)

Species	Code	Mean abundance (ind/ count \pm SD)		Freq Occ. (%)		Mean latitude of first sighting ($^{\circ}$ S \pm SD)		Group
		1980	2000	1980	2000	1980	2000	
<i>Ship-followers (instantaneous counts)</i>								
Wandering Albatross <i>Diomedea exulans</i>	WAAL	0.94 \pm 1.77	0.59 \pm 1.20	38.43	27.97	33.96 \pm 3.43	38.38 \pm 4.67	Warm
Black-browed Albatross <i>Thalassarche melanophrys</i>	BBAL	0.09 \pm 0.39	0.22 \pm 0.67	6.55	12.32	44.85 \pm 3.17	44.35 \pm 4.51	Cold
Light-mantled sooty Albatross <i>Phoebastria palpebrata</i>	LMSA	0.09 \pm 0.41	0.03 \pm 0.35	6.55	2.09	47.12 \pm 0.22	46.78 \pm 1.27	Cold
Grey-headed Albatross <i>Diomedea chrysostoma</i>	GHAL	0.05 \pm 0.23	0.07 \pm 0.31	4.37	5.43	46.18 \pm 3.75	44.81 \pm 2.98	Cold
Yellow-nosed Albatross <i>Thalassarche chlororhynchos</i>	YNAL	0.04 \pm 0.23	0.01 \pm 0.10	3.93	1.04	37.98 \pm 2.51	40.63 \pm 4.74	Warm
Giant Petrel sp. <i>Macronectes</i> sp.	GPSP	0.47 \pm 0.92	0.43 \pm 1.25	26.20	16.91	37.57 \pm 3.21	42.08 \pm 4.54	Warm
White-chinned Petrel <i>Procellaria aequinoctialis</i>	WCPE	7.37 \pm 10.38	4.81 \pm 6.98	58.95	52.19	33.35 \pm 4.01	32.91 \pm 3.83	Warm
Cape Petrel <i>Daption capense</i>	CAPE	0.41 \pm 1.55	0.22 \pm 1.05	10.92	8.56	43.79 \pm 4.41	46.78 \pm 1.75	Cold
Prions spp. <i>Pachyptila</i> spp.	PRSP	3.59 \pm 13.16	5.69 \pm 27.53	20.52	23.38	42.32 \pm 2.82	41.23 \pm 1.7	Cold
Wilson's storm Petrel <i>Oceanites oceanicus</i>	WISP	0.28 \pm 1.11	0.07 \pm 0.36	9.17	4.80	39.18 \pm 4.94	38.02 \pm 3.65	Cold
<i>Flying past (10 min counts)</i>								
Soft-plumaged Petrel <i>Pterodroma mollis</i>	SPPE	0.38 \pm 1.00	0.49 \pm 1.15	19.65	24.06	34.95 \pm 0.50	34.72 \pm 3.44	Warm
Blue Petrel <i>Halobaena caerulea</i>	BLPE	0.04 \pm 0.23	0.004 \pm 0.06	3.05	0.42	45.71 \pm 1.01	46.79 \pm 1.36	Cold

Species of the 'Warm' group, with mean latitude of first sighting lower than 38°S in the 1980s appear in bold.

bow to 90° off one side during 10 min. The second count was made immediately after the first one at the rear of the boat as an instantaneous picture of birds following in the wake. The observation protocol of the 10 min count at the front of the ship changed between the two decades. During the 1980s, seabird abundance was assessed regardless of distance (Brown *et al.*, 1975), whereas in the 2000s, counts were made within a 300 m strip (Tasker *et al.*, 1984; Spear *et al.*, 2004). Moreover, during the 1980s, time interval between censuses was variable, while it was kept strictly constant each hour in the 2000s. The snapshot count at the rear of the boat was however performed identically during the two decades. Among the 40 Procellariiform species recorded in the study area (list of species in Table S1), we focused on the 12 most frequently sighted species (i.e., total occurrence higher than 2%, Table 2). As 10 out of 12 species (listed in Table 2) had already been reported as ship-followers (Griffiths, 1982; Cherel *et al.*, 1996; Weimerskirch *et al.*, 2000), we chose to use the instantaneous count made at the rear of the boat for those species in order to (1) compare distribution and abundance with the same counting method, (2) avoid overestimation of abundance as ship-followers are likely to enter and exit the quadrant repeatedly during the 10 min count (Spear *et al.*, 1992; Hyrenbach, 2001). Ship-followers abundance was thus estimated as the number of birds sighted during the snapshot count at the rear of the boat, whereas abundances of Blue Petrels (BLPE, *Halobaena caerulea*)

and Soft-plumaged Petrels (SPPE, *Pterodroma mollis*), which are not ship-following species (Ryan & Moloney, 1988), were assessed as the number of birds recorded during the 10 min count performed on the side of the vessel. The change in counting method (from the bow to 90° off one side during 10 min) is unlikely to have an effect on abundance estimates of SPPE and BLPE given their low detection probability beyond 300 m (<30%, Barbraud & Thiebot, 2009). Spatial coverage of survey effort was comparable between decades (Fig. S1) with lower effort at latitudes covered at night and in the vicinity of islands as counts were stopped to minimize the effect of land and/or colony attraction. We constrained the time interval between two consecutive counts to be longer than 40 min in order to reduce autocorrelation, i.e., the tendency of seabirds to stay around the ship (Hyrenbach, 2001). For instance, La Cock & Schneider (1982) reported that Wandering Albatrosses, one of the most common species encountered in this region, followed their research vessel for an average of 44 min.

Oceanographic data

We investigated the effect of SSTa on abundance and distribution because it was the only environmental variable available since the 1980s. Several studies have documented the effect of SST on seabird populations through demographic parameters

(Barbraud & Weimerskirch, 2001; Pinaud & Weimerskirch, 2002; Sandvik *et al.*, 2005) or density estimates derived from at-sea surveys (Oedekoven *et al.*, 2001). Summer SSTa were derived from the latest version of the Reynolds Optimally Interpolated SST (Reynolds *et al.*, 2002) available at the IRI/LDEO Climate Data Library (<http://ingrid.ldeo.columbia.edu/>). The anomalies were calculated over the 1981–2007 period at two spatial scales. We used monthly SSTa at a spatial resolution of $1^\circ \times 1^\circ$ as a covariate in our models, whereas they were averaged on a 5° longitudinal strip (50 – 55°E) from La Réunion to Crozet (20 – 45°S) and on a 14° longitudinal strip (56 – 70°E) from Crozet to Kerguelen (46 – 50°S) to investigate summer decadal trends. Long-term temporal trends were analyzed with linear regressions.

Analytical methods

Our data are largely observational: it is unbalanced with heterogeneity due to variability in observers (Van der Meer & Camphuysen, 1996), at-sea conditions and spatial sampling. Because of these features, a Bayesian approach was favored as it easily accounts for the structure of the data and fits less-standard distributions (Gelman & Hill, 2007).

Because counts started shortly after leaving La Réunion Island (i.e., at latitudes where our focal species were absent), our data contain many zeros due to the real absence of birds. The exact latitude at which a species can be observed, however, is unknown. Removing all zeros would assume a probability of detection close to 1, an unreasonable assumption for most species (Barbraud & Thiebot, 2009). Instead, we modeled occurrence and abundance simultaneously using zero-altered distributions, such as a Zero-Inflated Poisson (ZIP) or a Zero-Inflated Negative Binomial (ZINB). Observed zeros can either stem from: (1) a true absence of the species caused by unsuitable habitat or chance or (2) a false absence due to

imperfect detection or a temporary absence (Fig. S2; Martin *et al.*, 2005). False absences can result from a too small sampling area or a too short census duration relative to the temporal and spatial scale of movements of the focal species (Tyre *et al.*, 2003).

We were not interested in performing model selection but in reproducing the observed patterns using a few biological meaningful predictors. In a preliminary analysis we tested the ability of a ZIP and a ZINB to predict the observed proportion of individuals, and found the ZINB to provide a better fit, especially for nonzero observations (see Martin *et al.*, 2005; Wenger & Freeman, 2008). We therefore focused on the ZINB model to detect any decadal differences in occurrence and/or abundance of species.

For all studied species, survey identity was included as a random effect to account for the variability due to observers, differing locations of the counts and weather conditions. We could not model a decadal effect explicitly (because it had only two levels) as this would mean including decade as a random effect, with survey nested within decade. Treating decade as a fixed factor would ignore this nested structure. Nevertheless, to account for the latter, we pooled estimates of the random effects of surveys made in the 1980s and of those made in the 2000s to look for systematic differences between their modes.

For all species, occurrence and abundance were modeled as functions of latitude (continuous data) and SSTa (categorical data: positive or negative). We studied the effect of SSTa independently from latitude as they were not strongly correlated (Pearson's $\rho = 0.26$, $P < 0.01$). For species with $< 90\%$ zero-observations (Table 3), the probability of observing a false absence was modeled as a straight line with varying slopes and a fixed intercept. For the remaining species, occurrence was modeled with fixed intercept and slope, because presence values were too sparse to detect decadal changes in occurrence. Abundance was modeled on a log scale as a straight line with a fixed slope and varying intercepts for all species except

Table 3 ZINB model detailed parameters ($N = 708$), species with more than 90% zero observations appear in bold

Species name	Proportion of zero values (%)	Occurrence		Abundance	
		Intercept	Slope	Intercept	Slope
<i>Warm species</i>					
Wandering Albatross	68.6	Fixed	Varying	Varying	Varying
Yellow-nosed Albatross	98.0	Fixed	Fixed	Varying	Fixed
Giant Petrel sp.	80.1	Fixed	Varying	Varying	Fixed
White-chinned Petrel	45.6	Fixed	Varying	Varying	Varying
Soft-plumaged Petrel	77.4	Fixed	Varying	Varying	Varying
<i>Cold species</i>					
Black-browed Albatross	89.6	Fixed	Varying	Varying	Fixed
Light-mantled sooty Albatross	96.5	Fixed	Fixed	Varying	Fixed
Grey-headed Albatross	94.9	Fixed	Fixed	Varying	Fixed
Cape Petrel	90.7	Fixed	Fixed	Varying	Fixed
Wilson's storm Petrel	93.8	Fixed	Fixed	Varying	Fixed
Prions sp	77.5	Fixed	Varying	Varying	Fixed
Blue Petrel	93.2	Fixed	Fixed	Varying	Fixed

ZINB, zero-inflated negative binomial.

White-Chinned Petrel (WCPE), Wandering Albatross (WAAL) and SPPE (Table 3). For the latter three, varying slopes were included as well. For nonfollowing species (BLPE and SPPE), we included a categorical 'METHOD' covariate because the protocol changed between the two decades. A sensibility analysis was conducted in order to assess whether this methodological bias could have been detected given the sample sizes (see details in the supplementary information 'Ability to detect a methodological bias', Fig. S7).

To summarize, occurrence was modeled for 6 species (WAAL, WCPE, SPPE, BBAL, PRSP, GPSP) as

$$\log(p(x_{i,j})) = a_0 + (a_1 + \alpha_{1,j}) \cdot \text{LAT}_{i,j} + a_2 \cdot \text{SSTa}_{i,j}, \quad (1)$$

where $p(x_{i,j})$ is the probability that observation i in survey j belongs to a negative binomial distribution, a_0 is a fixed intercept, a_1 and $\alpha_{1,j}$ are, respectively, fixed and random slope parameters of latitude, and a_2 is a fixed slope parameter of SSTa.

Abundance was modeled as

$$\log(\lambda(z_{i,j})) = (b_0 + \beta_{0,j}) + (b_1 + \beta_{1,j}) \cdot \text{LAT}_{i,j} + b_2 \cdot \text{SSTa}_{i,j}, \quad (2)$$

for WCPE, WAAL and SPPE (random intercept and slope), and

$$\log(\lambda(z_{i,j})) = (b_0 + \beta_{0,j}) + b_1 \cdot \text{LAT}_{i,j} + b_2 \cdot \text{SSTa}_{i,j}, \quad (3)$$

for other species (random intercept and fixed slope), where $\lambda(z_{i,j})$ is the number of individuals per count at location i and survey j , b_0 and $\beta_{0,j}$ are, respectively, the fixed and random intercept of latitude, b_1 and $\beta_{1,j}$ are, respectively, the fixed and random slope parameters of latitude, and b_2 is the fixed parameter of SSTa.

We then calculated the difference in the slope parameters of latitude between decades as

$$\Delta \text{Occurrence}_{\text{slope}} = \frac{\sum_{j=1}^{n_{2000s}} \alpha_{1,j}}{n_{2000s}} - \frac{\sum_{j=1}^{n_{1980s}} \alpha_{1,j}}{n_{1980s}}, \quad (4)$$

where n_{1980s} and n_{2000s} are the number of surveys in each decade (4 and 8, respectively), and $\alpha_{1,j}$ the random effect of latitude at each survey. This difference reflects the latitudinal changes in the distribution of birds: if intercept (a_0) and Δ Occurrence slope have the same/opposite signs, it corresponds to a northward/southward shift of species' distribution.

Likewise, we calculated

$$\Delta \text{Abundance}_{\text{intercept}} = \frac{\sum_{j=1}^{n_{2000s}} \beta_{0,j}}{n_{2000s}} - \frac{\sum_{j=1}^{n_{1980s}} \beta_{0,j}}{n_{1980s}}, \quad (5)$$

$$\Delta \text{Abundance}_{\text{slope}} = \frac{\sum_{j=1}^{n_{2000s}} \beta_{1,j}}{n_{2000s}} - \frac{\sum_{j=1}^{n_{1980s}} \beta_{1,j}}{n_{1980s}}, \quad (6)$$

where $\beta_{0,j}$ and $\beta_{1,j}$ are the random effects of latitude at each survey on the intercept and slope parameters, respectively. A negative (positive) $\Delta \text{Abundance}_{\text{intercept}}$ indicates a decrease (increase) in number of birds sighted at sea throughout the latitudinal gradient, whereas $\Delta \text{Abundance}_{\text{slope}}$ does not reflect any decadal changes in abundance but a redistribution of the abundance along the gradient.

Models were fitted using WinBUGS version 1.4 (Spiegelhalter *et al.*, 2003). In a Bayesian analysis, one must specify prior distributions which summarize information about uncertain parameters independent of that provided by the data. We used weakly informative priors (Gelman, 2006) and inferences were

drawn for posterior distributions based on 1 000 000 Markov Chain Monte Carlo simulations with every 500th sample retained to reduce autocorrelation (see Inference details and WinBUGS codes in supplementary information). Half Sample estimators of the mode and 95% highest density probability (HDP) intervals are reported. The goodness of fit of the model was assessed using a Kolmogorov–Smirnov test.

Furthermore, we distinguished between species that were first sighted north of 38°S ('Warm' group) and those observed south of 38°S ('Cold' group) in the 1980s (Table 2), to perform a meta-analysis using output parameters from the 12 models (one by species). The threshold of 38°S was retained in light of the strong increase in SSTa above that latitude, corresponding to the northern limit of the convergence zone between subtropical and subantarctic waters. Parameters describing the differences in abundance (for both groups) and occurrence (only for the 'Warm' group, as there was not enough data for 'Cold' species) were modeled with a skew-normal distribution (Fig. S3, Ghosh *et al.*, 2007).

Results

The most abundant species recorded were White-chinned Petrels, Prions (*Pachyptila* spp.) and Wandering Albatrosses with, respectively, 3990, 3546 and 497 individuals recorded following the ship and a frequency of occurrence of 54.4%, 22.5% and 31.3%. The nine remaining species had a frequency of occurrence lower than 20% which leads to high proportion of zero values (Table 3). The 12 models provided a good fit to the data with no significant differences between observed and predicted distributions of abundance (Kolmogorov–Smirnov test, $P > 0.13$). It is noteworthy that the models accurately predicted zero-observations (Fig. S6).

Decadal variations in SSTa along the latitudinal gradient

Spatio-temporal variations of summer SSTa along the latitudinal gradient revealed a higher frequency of positive anomalies since the 2000s (Fig. 2), particularly in subtropical waters (north of 38°S) where positive SSTa have been recorded since the late 1990s. Maximum warming trends were observed at latitudes from 25 to 30°S and 30 to 35°S with increasing rates of 0.029 and 0.039 °C yr⁻¹, respectively. These trends correspond to an increase of 0.6–0.8 °C over the 20 years time period.

Decadal and latitudinal changes in occurrence

Decadal comparisons of occurrence were performed for the six species with <90% zero-observations (Table 3). We were not able to fit the model by decade for the remaining species because of the large proportion of zeros in the data set. Decadal changes in latitudinal distribution were contrasting as evidenced by the delta

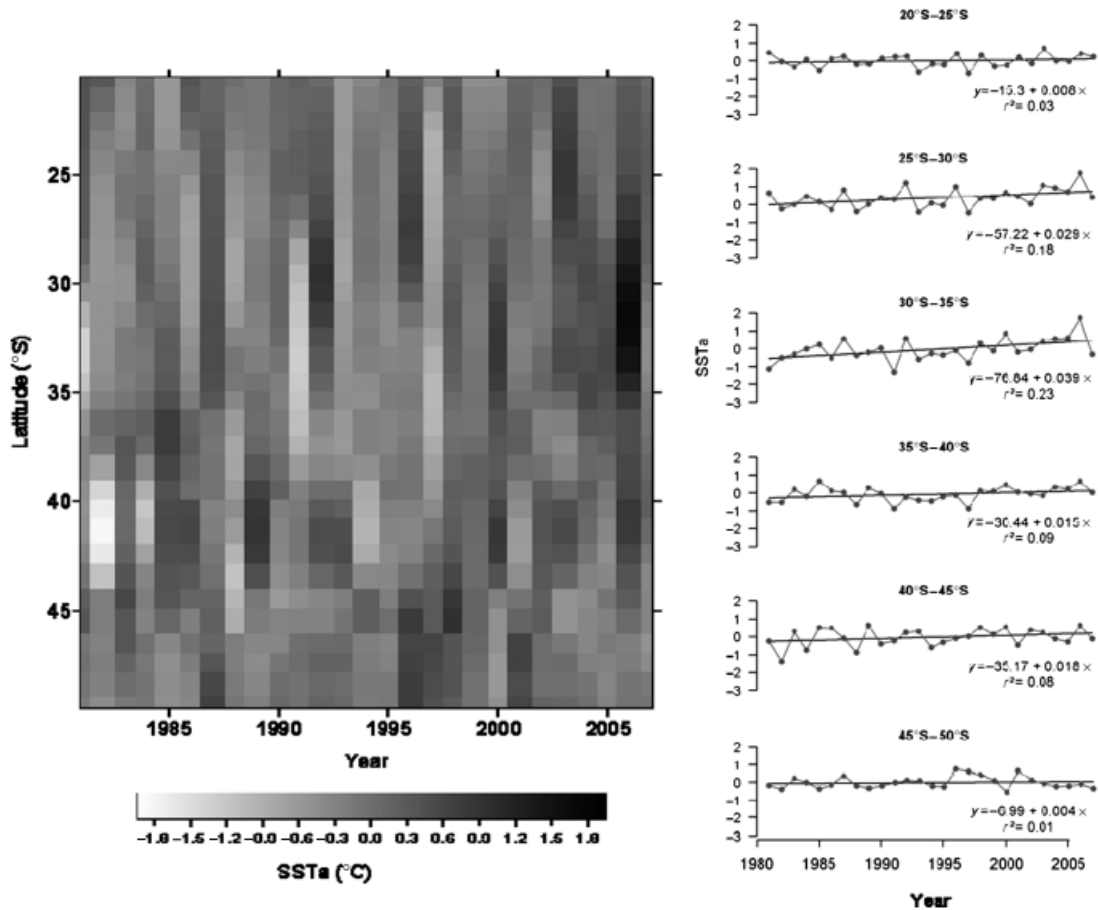


Fig. 2 Spatio-temporal variations of sea-surface temperature anomalies (SSTa) averaged over November and December in $1^\circ \times 5^\circ$ latitude-longitude blocks from 1981 to 2007 and linear trends of SSTa time series in $5^\circ \times 5^\circ$ blocks (50–55°E).

coefficients and the shape of the probability of presence (Fig. 3). The positive delta coefficient of WCPE ($\Delta\text{Occurrence}_{\text{slope}} = 1.45$, $\text{CI}_{95} = [-0.01; 6.37]$) revealed a significant change in its distribution, with a higher probability of presence in the northern part of the study area (29–35°S) and a lower one in the southern part in the 2000s compared with the 1980s (Fig. 3). Unlike WCPE, decadal comparisons of WAAL and PRSP slope parameters (Fig. 3) revealed a southward shift of their distributions (delta coefficients, off-centered from zero). The spatial distribution of GPSP, SPPE and BBAL did not change between the two decades.

Decadal and latitudinal changes in abundance

Decadal differences in the intercept of the models suggested a decrease in abundance for three species (Fig. 4): WAAL, WCPE and GPSP, for which confidence intervals were narrow and did not include zero, or only marginally. Similarly, the abundance of YNAL and LMSA tended to decrease whereas BBAL tended to

increase between the two decades. No trends were apparent for the remaining species. For WAAL, WCPE and SPPE, the random effect on the slope of the latitude allowed investigation of whether changes in abundance were consistent along the latitudinal gradient or constrained to a specific range of latitude. Decadal change in slopes of WCPE widely included zero ($\Delta\text{Abundance}_{\text{slope}} = -0.02$, $\text{CI}_{95} = [-0.64; 0.71]$), so that the decline was consistent throughout the latitudinal gradient. By contrast, the intercept of the abundance model of SPPE did not change significantly between the decades but the difference in slope parameters of WAAL and SPPE tended to be negative ($\Delta\text{Abundance}_{\text{slope}} = -0.38$, $\text{CI}_{95} = [-1.63; 0.31]$, $\Delta\text{Abundance}_{\text{slope}} = -0.45$, $\text{CI}_{95} = [-2.10; 0.38]$, respectively) suggesting a redistribution of abundance towards higher latitudes. We found no effect of the 'METHOD' covariate on abundances of SPPE and BLPE, suggesting a weak impact of the width of the strip (300 m vs. to horizon) for these two species. Decadal comparisons of abundance did not reveal any

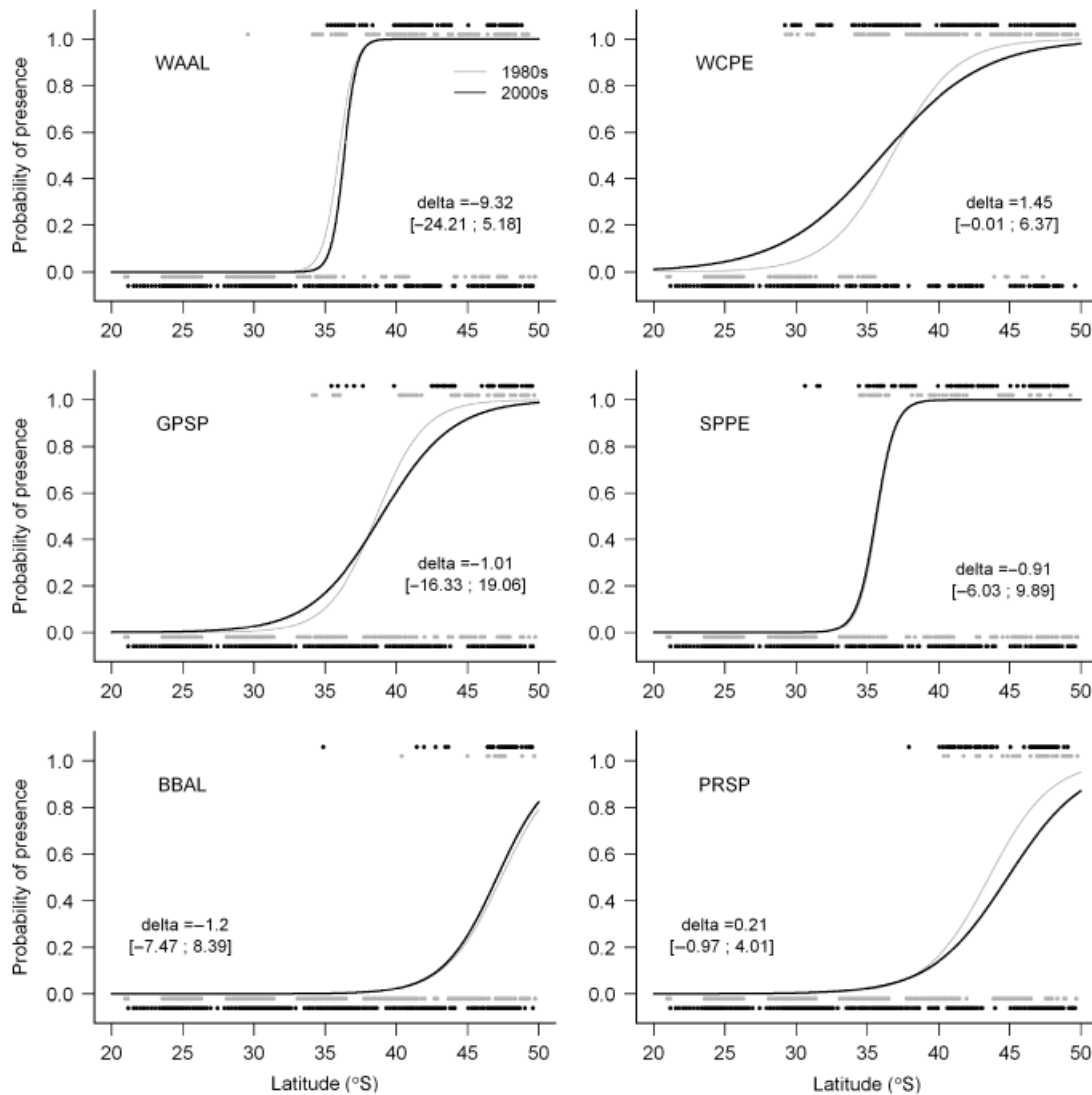


Fig. 3 Predicted probability of presence (occurrence) along the latitudinal gradient (lines) and observed presence (1) and absence (0) in dots for the two decades. Delta corresponds to the mean decadal difference and confidence interval (95%) between the slopes of the Occurrence–Latitude linear relationship on a logit scale.

trends for the others species of Petrels and GHAL, as confidence intervals were often large and centered on zero.

Effect of SSTa on occurrence and abundance

The effects of SSTa on occurrence and abundance were contrasting (Fig. 5). HPD intervals of SSTa coefficients were much larger for occurrence than abundance. On one hand, we found no effect of SSTa on occurrence (values close to zero and large variance), except for PRSP that tended to occur more frequently when SSTa were positive. On the other hand, models revealed different effects of SSTa on abundance depending on

species. Models of WAAL, GPSP and BBAL showed a negative relationship between abundance and SSTa ($b_2 = -0.43$, $CI_{95} = [-0.78; -0.09]$, $b_2 = -0.63$, $CI_{95} = [-1.18; -0.13]$, $b_2 = -1.20$, $CI_{95} = [-2.47; -0.19]$, respectively), whereas abundances of the others Albatross species, WCPE, BLPE and WISP were not affected by SSTa. SPPE and CAPE abundances tended to be negatively related to SSTa unlike PRSP which was the only species positively affected.

Decadal changes of 'Warm' vs. 'Cold' water species

The meta-analysis conducted on 'Warm' and 'Cold' species (Table 4) reflected a higher decadal decrease in at-sea

abundance of the 'Warm' group ($\Delta Abundance_{intercept} = -0.75$, $CI_{95} = [-1.35; -0.13]$), compared with the 'Cold' group whose confidence interval marginally included zero

($\Delta Abundance_{intercept} = -0.37$, $CI_{95} = [-1.05; 0.10]$). Occurrence of the 'Warm' group did not change between the two decades, which reflects the contrasting trends of the species included in the 'Warm' group.

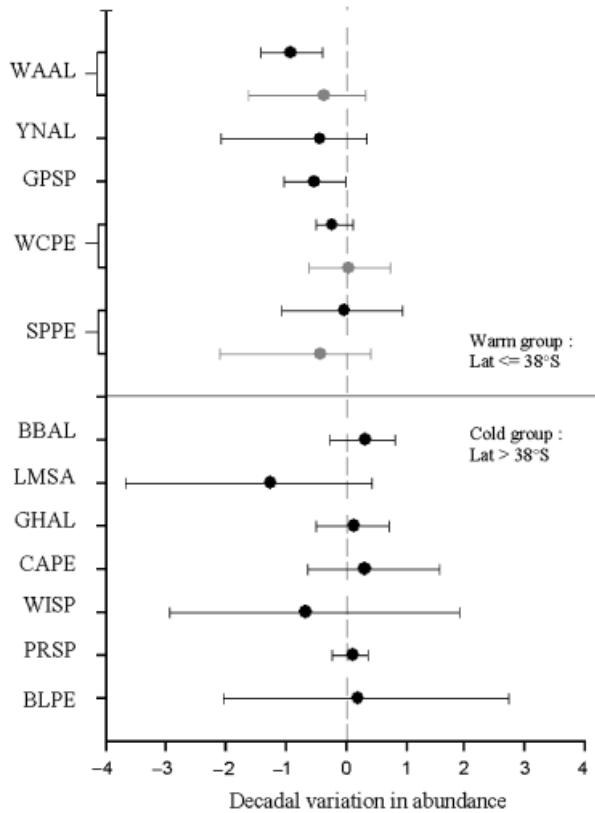


Fig. 4 Decadal difference and confidence interval (95%) between the intercept (black) and slope (gray) of the abundance model for each species.

Discussion

During the study period, the 12 seabird species exhibited contrasting decadal trends in their distributions and abundances at-sea. While subtropical waters had the highest rate of warming in the study area, cosmopolitan species that visited these waters during summer exhibited most changes in distribution and abundance. Occurrence of WCPE revealed a northward shift since the 1980s, whereas other species did not change or tended to shift southward (WAAL and PRSP). Abundance of 'Warm' species declined significantly between the two decades compared with 'Cold' ones, which declined to a lesser extent. The abundance of WAAL, WCPE, GPSP, YNAL and LMSA declined or tended to decline, whereas BBAL tended to increase and the remaining species did not change. SSTa affected mainly seabird abundance but their effects varied with species. Most of the species declining in abundance were adversely affected by positive SSTa.

Latitudinal shifts

Tracking long-term changes in distribution of far-ranging mobile animals is challenging as they are able to disperse over large spatial scales and respond rapidly to shifting water mass distributions (Hyrenbach & Veit,

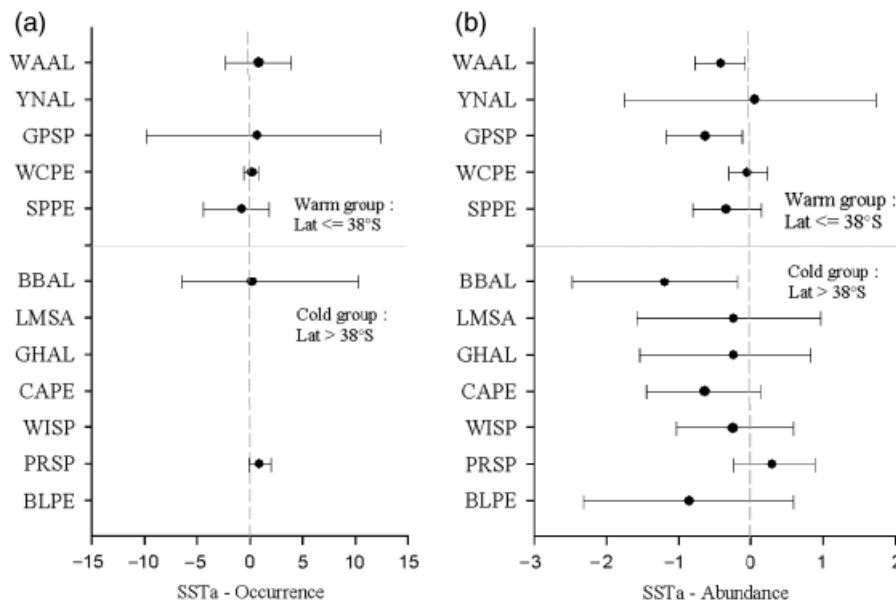


Fig. 5 Mean estimates and confidence intervals (95%) of the sea-surface temperature anomalies (SSTa) effect on occurrence (a) and abundance (b) for each species.

Table 4 Meta-analysis of the inter decadal differences of the ZINB models

Group	Δ Abundance _{intercept}			Δ Occurrence _{slope}		
	No. of species	Mean \pm SE	HDP 95%	No. of species	Mean \pm SE	HDP 95%
Warm	5	-0.75 ± 0.48	[-1.35 to -0.13]	4	-1.45 ± 2.48	[-8.43 to 3.9]
Cold	7	-0.37 ± 0.35	[-1.05 to 0.10]	–	–	–

HDP 95% corresponds to the confidence interval of the highest density probability. ZINB, zero-inflated negative binomial.

2003). Consequently, monitoring surveys often cover a small part of their entire range (Parmesan, 2006). In our case, the surveys encompassed the northern part of the species ranges, which narrows our interpretation of change in spatial distribution. The ZINB model proved to be appropriate to predict zero-observations and consequently to estimate the 'real' occurrence (the probability of presence even when a species is not observed), often confounded with the probability of detecting a species (Altwegg *et al.*, 2008).

Owing to the consistency of positive SSTa observed in the subtropical waters since the early 2000s, we might have expected a latitudinal shift of seabird's northern distribution towards cooler waters. Surprisingly, the 'Warm' group did not display any consistent shift of its northern range limit. Among the six species whose occurrence was investigated, WAAL and PRSP latitudinal range tended to shift in the expected direction (e.g., poleward), whereas the range of WCPE moved northward. The absence of SSTa effect on frequency of occurrence of the six species except PRSP, suggests that other factors may be involved, such as change in wind force (Fyfe *et al.*, 2007), which is known to influence seabird dispersal capacities (Alerstam *et al.*, 1993). We can also suspect that the range of the positive SSTa was too small (0–1.8°C) to trigger any large distributional change. The southward shift of WAAL is consistent with its global decline in abundance and the trend for redistribution towards southern latitudes, as in most cases there is a positive relationship between abundance and occurrence (Selmi & Boulinier, 2004). Indeed, when spatial distribution is scattered, the less abundant is a species, the lower its probability of presence. On the contrary, the northward shift of WCPE is surprising given its decline in abundance at-sea; yet it may pertain to a few individuals dispersing northward in the 2000s. Several explanations could be proposed such as a reduction of competition with other species that shifted southward or a specialization of some individuals following fishing vessels, as fisheries activity has largely expanded in subtropical waters since the 1980s (Tuck *et al.*, 2003). Fishing vessels are known to influence distribution of ship-following species that feed on fish-

ery discards (Ryan & Moloney, 1988), but it is suspected to concern a small proportion of populations (Freeman, 1997).

Changes in abundance

A significant proportion of the individuals observed in the study area during summer is likely to breed on subantarctic islands located in the southern part of the transects, since breeders are spatially constrained by incubation and chick-provisioning. Therefore, comparisons with long-term demographic studies could be related to changes in at-sea abundance. Several demographic studies have linked seabirds survival or breeding success to local SSTa or other climatic factors as well as longline fisheries' bycatch (Barbraud & Weimerskirch, 2001; Croxall *et al.*, 2002; Rolland *et al.*, 2008). However, such comparisons may be hazardous as individuals sighted at sea are likely to come from various colonies and the species-level response to climate change can vary within geographically differentiated communities (Genner *et al.*, 2004).

Decline of the warm group abundance

The abundance of the 'Warm' group significantly declined in the study area over the past 20 years. While long-term changes in at-sea abundance have already been reported at various trophic levels in marine ecosystems of the Northern Hemisphere (Hyrenbach & Veit, 2003; Grandgeorge *et al.*, 2008; Hemery *et al.*, 2008), similar studies in the Southern Ocean mainly focused on Antarctic krill (Atkinson *et al.*, 2004). Woehler (1997) documented for the first time a decrease in summer at-sea abundance of five subantarctic seabird species in Antarctic waters (Prydz Bay) between 1980 and 1992. Three of these species (WAAL, WCPE and Northern Giant Petrel *Macronectes halli*) showed similar declines within our study area between 1981 and 2007.

Whereas WCPE decline was not related to SSTa, most of the declining 'Warm' species were negatively affected by SSTa. Rising SST may influence seabird distribution

either directly at their range limits or indirectly through availability of prey (Frederiksen *et al.*, 2006). Indeed, 'Warm' species forage partly in subtropical waters and feed on temperature-dependent resources such as fish, squid or krill when observed at sea (Ridoux, 1994). Thus, subantarctic species that forage at higher trophic levels in latitudinal limits of their range during the breeding period may be more susceptible to rising SST. Hyrenbach & Veit (2003) reported such an influence of SST in the California Current System where they observed a concurrent increase in the abundance of warm water taxa and a decline in cold water ones, following the SST increase between 1987–1990 and 1995–1998. Rising SST may alter seabird community structure and eventually modify species interactions. The absence of SSTa effect on WCPE abundance is consistent with the findings of Barbraud *et al.* (2008), suggesting that adult survival was affected by large-scale oceanographic variables (e.g., Southern Oscillation Index) rather than small-scale SSTa variations.

In addition, all the species included in the 'Warm' group, except SPPE have been reported as ship-followers and thus, are dramatically affected by incidental mortality caused by pelagic and demersal longline fisheries in both subtropical and subantarctic waters (Gales *et al.*, 1998; Nel *et al.*, 2002; Delord *et al.*, 2005). During the 1990s, the Southern Indian Ocean witnessed an intensification of tuna longline fisheries in subtropical waters and the development of demersal longline fisheries for Patagonian toothfish *Dissostichus eleginoides* in subantarctic waters (Tuck *et al.*, 2001). Moreover, this mortality is suspected to mainly affect nonbreeding birds, which are directly included in at-sea records (Weimerskirch *et al.*, 2006).

Comparing at-sea abundance and land-based population trends of WAAL and some other species of Albatross and Petrel (GPSP) is more complex as juveniles and nonbreeders can exhibit circumpolar movements (Weimerskirch *et al.*, 1985; Prince *et al.*, 1998; Croxall *et al.*, 2005; Trebilco *et al.*, 2008; H. Weimerskirch, unpublished data). Individuals sighted along the transect lines are likely to come from various breeding localities where population trends may be contrasted.

The model fitted for the WAAL suggests both a decline and redistribution of its abundance towards southern latitudes. This observed decline is congruent with population trends observed at South Georgia (Poncet *et al.*, 2006) but contrasts with increasing population trends estimated on Crozet Is. and Marion Is. during the study period (Nel *et al.*, 2002; Delord *et al.*, 2008). Unfortunately, the collection of tracking data does not inform us on redistribution patterns as it only started in the early 1990s. On the other hand, tracking studies of WCPE suggest that most birds observed

along our surveys during the breeding period come from Crozet Is. and Kerguelen Is. where large populations occur (Weimerskirch *et al.*, 1999; Catard *et al.*, 2000; Barbraud *et al.*, 2008). Similarly, YNAL sighted at-sea probably came from surrounding islands since tracking studies indicated that YNAL from Amsterdam Is. are foraging in our study area during the breeding season (Pinaud *et al.*, 2005). The declining trend of these two species is in accordance with the population trends inferred from land-based surveys on Crozet Is. (Barbraud *et al.*, 2008), Marion Is. (Nel *et al.*, 2002) and the more distant South Georgia (Berrow *et al.*, 2000) for WCPE, and Amsterdam Is. for YNAL, where the main population of the Indian Ocean decreased heavily (Rolland *et al.*, 2009). Given the constancy of the decline in abundance of WCPE and YNAL along the 30° latitudinal gradient and their sensitivity to SST and/or fisheries, we favor the hypothesis of a decline in population sizes over the redistribution hypothesis. Unfortunately, Giant Petrels were not identified at the species level, which limits the interpretation of the decline observed in the study area because long-term demographic trends contrast between breeding sites and species. NGPE populations estimates are quite stable at Crozet Is. (Delord *et al.*, 2008), declining at Marion Is. (Nel *et al.*, 2002; Crawford *et al.*, 2003) and increasing at South Georgia (Gonzalez-Solis *et al.*, 2000), whereas SGPE populations are increasing at Crozet Is. (Delord *et al.*, 2008), Falkland Is. and Gough Is., fluctuating at Marion Is. (Nel *et al.*, 2002; Crawford *et al.*, 2003) and are stable at South Georgia (Gonzalez-Solis *et al.*, 2000). Finally, SPPE abundance did not change but its distribution has shifted towards southern latitudes. As SPPE was the only 'Warm' species spared by fishery bycatch, this change is likely to be essentially driven by oceanographic changes occurring in the subtropical waters as evidenced by the negative trend of SSTa on its abundance. This result is particularly interesting as demographic studies and tracking data are nonexistent for this inconspicuous burrow nesting species. From a methodological point of view, if surveying a shorter strip in the 2000s had an impact (Fig. S7), and yet no decadal abundance changes are detected, then the true pattern would be an abundance increase of SPPE and BLPE.

Overall, our study suggests that climate change had a significant effect on abundance and distribution of several seabird species in the Southern Indian Ocean, with fisheries potentially having an additional effect on abundance. The respective impact of climate and fisheries on abundance is difficult to assess from at-sea surveys, but demographic studies suggest contrasting impact according to species considered (Barbraud *et al.*, 2008; Rolland *et al.*, 2009, 2010).

Change in cold species abundance

'Cold' species abundance tended to decrease but their low occurrence was responsible for the low precision of this parameter. At the species level, these trends were consistent with Woehler (1997) observations in Prydz Bay, except for BBAL. LMSA abundance tended to decline in both studies whereas the other species remained stable. Despite accounting for its low detection probability, the gregarious at-sea behavior of PRSP may have hidden any decadal changes in abundance. Indeed, abundance was highly dependent on the probability of encountering a flock during the count and its size. Within the 'Cold' species group, BBAL was the unique small Albatross species vulnerable to bycatch mortality found to be also affected by SSTa, confirming their sensitivity to climate fluctuations (Rolland *et al.*, 2008). The lack of SSTa effect on the remaining species was consistent with the absence of decadal changes in their abundances. BLPE breeding population trends are fluctuating in one colony monitored at Kerguelen Is. (Barbraud & Weimerskirch, 2003) but, to our knowledge, population trends are unknown at others localities. Likewise, no information is currently available for breeding PRSP, CAPE and WISP. Trends in at-sea abundance of LMSA and GHAL have to be considered with caution regarding the small number of sightings. Still, our study provides interesting additional information on their status as their breeding population trends vary between localities (Crozet Is.: Delord *et al.*, 2008; Marion Is.: Nel *et al.*, 2002; Crawford *et al.*, 2003; South Georgia: Prince *et al.*, 1994; Poncet *et al.*, 2006). Finally, the increase in abundance of BBAL in our study area is not consistent with the long-term demographic trend on Kerguelen Is., where breeding pairs have fluctuated since the 1980s but remained stable (Rolland *et al.*, 2008), or in South Georgia, where they have decreased (Prince *et al.*, 1994). The observed increase of BBAL in the study area combined with its disappearance in Prydz Bay (Woehler, 1997) may support the hypothesis of a change in distribution with a range contraction, resulting in a higher abundance close to subantarctic islands.

Implications

Our study highlights the importance of conducting long-term systematic seabird surveys at-sea in order to complement population trends assessed by demographic monitoring, or to provide new insights on species when demography, and consequently conservation status, are poorly known. Despite some drawbacks (observational data), platforms of opportunity reduce costs of collecting data on seabirds at-sea and provide

complementary information to that of tracking data. Unfortunately, long-term data sets of at-sea observations are scarce, often discontinuous and need suitable statistical methods to deal with data heterogeneity. A mixture modeling approach turned out to be appropriate when comparing occurrence and abundance over multiple years: our study is yet another example of the suitability of hierarchical models for the analysis of complex ecological data sets.

The four vessel-based surveys conducted in the 1980s allowed us to illustrate the alteration of marine top predator community structure linked to recent regional warming and/or fisheries.

The concordance between at-sea observations and demographic trends on land suggests that many populations are affected and probably that all components of the population (juveniles, immatures and adults) contribute to the observed trends rather than breeding birds only. Species-specific responses suggest that the susceptibility of marine top predators to climate change and fishery activities depends on their behavior, spatial range (water masses affinity) and adaptability to changing environmental conditions. Since climate models predict that mean annual global surface temperature will increase by 1–3.58 °C by 2100, with warming more pronounced at higher latitudes (Hughes, 2000), we may expect the colder species to be impacted in the next few decades.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Figure S1. Comparison of latitudinal distribution of the survey effort (mean number of counts \pm SD) between the two decades. Low efforts correspond to segments often surveyed during nighttime.

Figure S2. Diagram of the mixture modeling procedure, following Martin *et al.* (2005).

Figure S3. Posterior probability densities of the delta abundance intercept for the twelve studied species. The dashed grey line indicates the Half-Sample Mode of the distribution (Poncet 2007). Note that all distributions are left-skewed apart from that of the YNAL.

Figure S4. Sensitivity analysis to prior specification. Mean decadal difference in the slope parameter linking occurrence and latitude for the 'Warm' group and its 95% Highest Probability Density interval are represented. Cauchy priors with two different scales (10 and 2 governing the spread of the prior distribution around zero, i.e. the Cauchy2 prior brings more information, or equivalently shrinks more the posterior estimate toward zero, than the Cauchy10 prior) and a uniform prior were used. Cauchy priors were used according to Gelman *et al.* (2008). Note that point estimates agree between different priors, but that coverage of the 95% HPD interval varies. Nevertheless, all 95% HPD intervals of the mean effect include zero.

Figure S5. Sensitivity analysis to prior specification. Mean decadal difference in the intercept parameter linking abundance and latitude for the 'Warm' group (A) and the 'Cold' group (B); and its 95% Highest Probability Density interval are represented. Cauchy priors with two different scales (10 and 2 governing the spread of the prior distribution around zero, i.e. the Cauchy2 prior brings more information, or equivalently shrinks more the posterior estimate toward zero, than the Cauchy10 prior) and a uniform prior were used. Note that point estimates and 95% HPD interval coverage largely agree between different priors. For the 'Warm' group, none of the 95% HPD intervals of the mean effect includes zero, while they all include zero for the 'Cold' group.

Figure S6. Goodness of fit of the predicted distribution of abundance (black lines) compared to the observed data (grey histograms). Distribution of abundance was modeled using mixture modeling, following Martin *et al.* 2005 (Fig. 2). As data contained a large proportion of zeros, we squared-root transformed the proportion of counts for readability reason. A Kolmogorov-Smirnoff test was performed on each model to assess the goodness of fit statistically. All models provide accurate predictions ($P > 0.13$).

Figure S7. Model ability to detect a methodological bias due to extra birds counting during the 1980s for the Soft-plumaged Petrel.

Table S1. List of the seabird species encountered in November and December along the latitudinal gradient from La Réunion Is. to Kerguelen Is. via Crozet Is., over the twelve years of the study. The number of individuals in counts of flying seabirds (front of the boat) and following seabirds (behind the boat) are reported all years included. Species in bold indicate the twelve species under investigation in our study.

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