

Large-scale oceanographic fluctuations drive Antarctic petrel survival and reproduction

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Polar Regions are experiencing environmental changes at unprecedented rates. These changes can spread throughout entire food webs from lower trophic levels to apex predators. As many top predators forage over large areas, these indirect effects may be associated with large-scale patterns of climate variability. Using global climate indices that are known to impact the Southern Ocean ecosystem (the El Niño Southern Oscillation and Antarctic Oscillation Indices) we assessed their efficacy to predict variation in the demographic parameters of Antarctic seabirds. First, we used a long-term dataset on adult survival (estimated from capture–mark–recapture data) and reproduction of Antarctic petrel *Thalassoica antarctica*, from the largest known breeding colony (Svarthamaren, Dronning Maud Land) and examined whether large-scale oceanographic fluctuations impact survival and reproduction. Second, we conducted an exhaustive literature review to determine whether the effects of large-scale environmental variability on Antarctic seabirds have a coherent fingerprint across the Antarctic continent and nearby islands. We found that most of the variation in both reproductive success, timing of hatching, and survival of Antarctic petrels can be accurately modeled using the two modes of large-scale climate variability in Antarctica. The literature review, combined with the results from our field study, suggests that while the anticipated trends in the global patterns of climatic variability will generally have detrimental effects on populations of top predators in the Southwest Atlantic, these conclusions cannot be extrapolated to all seabird populations in Antarctica without additional data.

Given the comparatively recent and unprecedented rate of increase in multiple environmental stressors facing free-living populations, identifying the linkages between environmental variation and population demographics is of utmost importance. This need becomes especially true in polar systems that are changing more rapidly than other areas of the planet (Post et al. 2013, Intergovernmental Panel on Climate Change 2014). In the Southern Hemisphere, the strongest rates of atmospheric warming are occurring in the western Antarctic Peninsula and the islands of the Scotia Arc, where there have also been increases in oceanic temperatures and large regional decreases in winter sea ice extent and duration (Larsen et al. 2014).

Environmental conditions in the Southern Ocean are primarily determined by two modes of large-scale climate variability, the Antarctic Oscillation (AAO) and the El Niño–Southern Oscillation or ENSO (Kwok and Comiso 2002, Turner 2004, Yuan 2004, Stammerjohn et al. 2008, Forcada and Trathan 2009). The AAO, also referred to as the Southern Annular Mode (SAM), represents the periodical change in the strength of the circumpolar vortex, i.e. a belt of tropospheric westerlies surrounding the Antarctic

continent (Abram et al. 2014). The positive phase of the AAO corresponds to low-pressure anomalies over Antarctica (Abram et al. 2014) and wind, temperature, sea ice drift, and precipitation show widespread and significant AAO-related signals in Antarctica (Meredith et al. 2008). For example, when the vortex is strong (high AAO index), northwesterly flow anomalies cause warming over the Antarctic Peninsula and adjacent regions in west Antarctica and the Weddell Sea (van den Broeke and van Lipzig 2004).

The ENSO is an anomalous large-scale oceanic and atmospheric system causing strong fluctuations in ocean currents and temperatures (Philander 1983, Trenberth 1997). It characterizes variation in both the sea temperature of the tropical eastern Pacific and the air surface pressure in the tropical western Pacific. It is triggered in the equatorial/tropical Pacific but has teleconnections to the Southern Ocean and Antarctica via both atmospheric and oceanic processes (Turner 2004, Yuan 2004). The strength of the ENSO is accurately estimated by the Southern Oscillation Index or SOI (Lockwood 1984, Deser and Wallace 1987, Philander 1990), which is a standardized index based on the difference in sea level pressure between Tahiti and Darwin, Australia.

Prolonged periods of negative SOI values coincide with abnormally warm waters across the eastern tropical Pacific, which is typical of El Niño episodes (<www.ncdc.noaa.gov/teleconnections/enso/indicators/soi.php>). Periods of high SOI (i.e. La Niña) are characterized by fewer storms, warmer conditions, and less sea ice in the western Weddell Sea, but with opposite conditions (i.e. more storms and colder conditions) in the Ross Sea (Yuan 2004). This phenomenon is known as the Antarctic Dipole (Yuan 2004).

Both the SOI and the AAO are linked to the abundance and/or distribution of crustaceans, fish and squid in Antarctica and sub-Antarctica (Waluda et al. 2004, Salinger 2013). In particular, several studies have reported linkages between the SOI/AAO and the abundance of Antarctic krill *Euphausia superba* (Quetin and Ross 2003, Murphy et al. 2007b) likely through effects on sea temperatures and sea ice distribution (Simmonds and Jacka 1995, Harangozo 2000, Kwok and Comiso 2002, Turner 2004, Yuan 2004, Stammerjohn et al. 2008). Antarctic krill is a key ice-dependent species in the Southern Ocean, being the primary prey for most top predators in the South West Atlantic (Fraser and Hofmann 2003, Smetacek and Nicol 2005, Murphy et al. 2007b). Several studies have identified links between top predator populations and fluctuations in the SOI/AAO, with the most likely mechanism involving indirect effects mediated through krill (Murphy et al. 2007b, Trathan et al. 2007, Forcada and Trathan 2009) although direct effects may also exist (Weimerskirch et al. 2012).

In this study, our first goal was to examine whether large-scale oceanographic fluctuations affect the survival and reproduction (breeding phenology and chick production), of an Antarctic krill predator, the Antarctic petrel *Thalassoica antarctica*. Free-living populations are generally not affected by a single weather or oceanographic component, but instead by the co-occurrence of several dependent variables (Stenseth et al. 2003, Oro 2014). As such, large scale climate indices may capture this complexity in the association between weather and/or oceanography and ecological processes (Stenseth et al. 2003, Hallett et al. 2004, Stenseth and Mysterud 2005). Large-scale indices are also often associated with environmental conditions over large geographical areas (see Hurrell et al. 2001 for an example on the NAO) and are thus very suitable for assessing the effects of climate or oceanographic processes on populations whose distribution is widespread.

We used a long-term dataset on survival (estimated from capture-mark-recapture) and reproduction of Antarctic petrels from the largest known breeding colony (Svarthamaren, Dronning Maud Land, Lorentsen et al. 1998). High SOI and high AAO values in the Weddell Sea correspond to warm waters and less sea ice, and thus potentially low krill availability in the Weddell Sea (Murphy et al. 2007a, b, Trathan et al. 2007), where Antarctic petrels from Svarthamaren forage during and outside the breeding season (see Fauchald and Tveraa 2006 for the summer distribution at sea; unpublished results from the winter distribution). Therefore, we predicted that high SOI and high AAO values would be associated with lower adult survival, lower reproductive success and delayed breeding phenology (as petrels may need more time to acquire the necessary nutritional reserves to initiate reproduction).

Our second goal was to integrate these results within a broader context to determine whether the effects of

large-scale environmental variability on seabirds can be generalized, or whether they are temporally-, spatially-, or species-dependent. This was achieved by an exhaustive literature review of all the studies published to date that have examined links between large-scale climatic variability and seabirds in Antarctica.

Overall, our study indicates very strong links between those large scale climatic indices and the life-history of Antarctic petrels. Despite large complexity in the relationships between SOI or AAO and seabird life history traits, seabird populations in South West Atlantic show a globally coherent response to changes in the AAO. An increasingly positive trend in AAO, as observed in recent decades (Turner et al. 2007, Abram et al. 2014, Zhang et al. 2014) may thus have important detrimental consequences on top predators in this Antarctic region.

Methods

Study system and the Antarctic petrel

The focal study was carried out at the Svarthamaren Antarctic petrel colony (71°53'S, 5°10'E) in Dronning Maud Land, Antarctica between 1992 and 2014 (Antarctic summers 1991/1992 and 2013/2014, respectively). This colony is located 200 km inland and is the largest known breeding colony for this species (Mehlum et al. 1988, van Franeker et al. 1999). Breeding numbers fluctuated between ca 100 000 and 250 000 pairs during the study period. The Antarctic petrel is a long-lived seabird weighing approximately 600 g, lays a single egg at the end of November/early December, and both parents contribute to incubation and chick-rearing. Hatching occurs around mid-January and fledging in early March, and parents alternate foraging and chick-guarding duties for the first 7–15 d following hatching (Lorentsen and Røv 1995). Diet of the Antarctic petrel consists mainly of crustaceans, with Antarctic krill being the main prey (Lorentsen et al. 1998), at least during the chick-rearing period. The only predator of petrels at the Svarthamaren colony is the south polar skua *Catharacta maccormicki* which mainly preys upon eggs and chicks (Brooke et al. 1999, unpubl.).

Adult Antarctic petrels were captured, ringed (metal ring only), and recaptured within one of four monitored plots (Lorentsen et al. 1993) in summers 1991/1992–1994/1995, 1996/1997, 1997/1998, 2000/2001 and 2011/2012–2013/2014. Breeding-site fidelity is extremely high for Antarctic petrels and individuals use the exact same nest site year after year. During these 10 breeding seasons, a total of 2029 petrels were ringed, and the hatching date of between 82 and 491 nests was recorded in each of seven years (1992, 1997, 1998, 2001 and 2012–2014). To estimate hatching dates, nests were visited every day in January in years 1992, 1997, 1998, and 2001, and every other day in the period 2012–2014.

Productivity monitoring

To estimate Antarctic petrel productivity (i.e. the number of chicks produced at Svarthamaren after the peak

of hatching), a grid of 201 plots (40 × 40 m each) was established in 1992 (Lorentsen et al. 1993). Plots were evenly spaced throughout the surface area of the colony, and the centre of each plot was permanently marked, and the number of active nests in each plot within a circle of 10 m² (circle of 1.78 m radius centered in the plot) was counted. Usually, a very small number of nests were still active but with an egg and not a chick during our surveys (i.e. hatching had not occurred yet). Those active nests have been included to calculate our productivity index. Antarctic petrel productivity was estimated at the end of January using this protocol in 10 study years (1992–1995, 1997, 1998, 2001, 2012–2014). In addition to this data, estimates of productivity were also available from previously published studies of the same colony for 1985 and 1990 (Mehlum et al. 1988, Røv 1991). The method used for these censuses (1985 and 1990) differed slightly from the one used from 1992 onward as it was based on three transects comprising 96 plots of 9 m² each. We included these two additional data points in our analyses as there is no reason to believe that doing so could bias the observed results since the sampling locations in both methods spread over the entire colony.

Large scale environmental variables

To test for a link between the Southern Oscillation Index (SOI), and the Antarctic Oscillation (AAO) with petrel survival, we considered the average annual values calculated from monthly data obtained at < www.cpc.ncep.noaa.gov >. Indeed, Antarctic petrels forage all year round within more or less the same broad geographical area (eastern Weddell Sea), and we have no reason to believe that conditions during a specific period of the year are more important in driving variation in survival. For productivity and breeding phenology analyses, we considered the spring SOI and AAO averages (averages calculated over the months Sept–Oct–Nov) given that conditions just before the breeding season are likely key determinants of petrel reproductive traits (Trathan et al. 1996, Sorensen et al. 2009).

The SOI and AAO variables are expected to affect Antarctic petrels via the food chain, and in particular via Antarctic krill availability. An effect of environmental variation on krill reproduction may in fact impact Antarctic petrels only one to three years later, i.e. when juvenile krill become available as prey to petrels (Siegel and Loeb 1994). Moreover, it may take time for the effects of atmospheric or oceanographic anomalies resulting from extreme AAO or SOI values to propagate into the foraging area of petrels (Murphy et al. 2007a). We therefore also considered time lags of one to three years in our analyses of SOI and AAO. Only the spring AAO was correlated with itself with a 1-yr time lag (Pearson's $r = -0.41$, $p = 0.03$); otherwise, all other series were independent from their lagged values (all p -values > 0.08 for period 1985–2013). Moreover, the AAO and SOI time series were only moderately correlated during the period of our study (Pearson's $r = 0.21$ for the spring SOI and spring AAO and Pearson's $r = 0.36$ for the annual SOI and AAO in period 1985–2014).

Statistical methods

Survival modeling

Annual survival of Antarctic petrels was estimated using the capture history from 2029 individuals (breeding adults) ringed and resighted between 1991/1992 and 2013/2014. The average resighting probability (in years where fieldwork was performed) was 0.79 (Supplementary material Appendix 1) and the average annual survival was 0.90.

The first step in capture–recapture survival modeling is to assess the goodness-of-fit (GOF) of the most general model (Lebreton et al. 1992). The goodness-of-fit of the fully-time-dependent or Cormack–Jolly–Seber (CJS) model was assessed using software U-CARE (Choquet et al. 2009a). This GOF test indicated significant lack of fit and over-dispersion in our data ($\chi^2 = 113.13$, $DF = 79$, $p = 0.007$). This was mostly due to significant trap-dependence, i.e. heterogeneity among birds in their resighting probability (reduced GOF test without test 2.CT: $\chi^2 = 90.36$, $DF = 67$, $p = 0.03$). We therefore corrected for trap-dependence into our models following Pradel and Sanz-Aguilar (2012). The moderate remaining heterogeneity had no simple biological meaning and was not due to transience (test 3.SR: $\chi^2 = 30.89$, $DF = 27$, $p = 0.28$). To take this remaining heterogeneity into account within our model selection, we adjusted our information criterion with an overdispersion coefficient of $\hat{c} = \frac{90.36}{67} = 1.35$.

Model selection was based on Akaike information criterion corrected for over-dispersion (QAIC). A difference in QAIC of less than 2 units between the model considered and the model with lowest QAIC (i.e. the Δ QAIC) indicates that these models cannot be distinguished in their ability to fit the data (Burnham and Anderson 2002). When the Δ QAIC was < 2 between two nested models, the most parsimonious model was retained. Model selection and parameter estimation were performed with software E-SURGE 1.7 (Choquet et al. 2009b). In a first step, we tested for the effects of the environmental parameters one at a time. We also tested for a linear trend to detect any long-term changes in petrel life-history independent of changes in SOI or AAO. In a second step, we considered a global model including all parameters that were significant in the previous step (based on ANODEV tests, see below).

For years where no field work was conducted, recapture rates were set to 0, and annual survival rates could not be estimated separately before and after those years with no recapture/resighting (e.g. no fieldwork occurred in 1996 so that recapture rate was set to 0 in 1996, and only the 2-yr average survival rate from 1995 to 1997 could be estimated). When testing for the effect of environmental covariates, we considered the average value for the entire interval where survival was averaged. In the previous example, we considered the average values for the SOI and AAO for the period 1995–1997.

The percentage of variance in petrel survival explained by environmental covariates was estimated using two indices. We considered the percentage of deviance explained (%Dev) calculated as: $\frac{Dev. - Dev_{cov}}{Dev. - Dev_i}$ where Dev_{cov} represents the deviance of the model including a covariate, Dev_i represents

the deviance of the model where survival was constant, and Dev_t represents the deviance of the model where survival was time-dependent (Grosbois et al. 2008). We also calculated the square of the Pearson correlation coefficient between survival estimates from the ‘environmental covariate models’ and survival estimates from the general time-dependent model (Zheng and Agresti 2000). To test whether the environmental parameters had a significant effect on survival, we performed analysis of deviance (ANODEV) tests (Grosbois et al. 2008).

Linear regression

We used linear models (GLMs) to assess the relationship between the environmental parameters defined above and Antarctic petrel productivity (defined as the number of chicks per square meter estimated after the hatching period) and breeding phenology (mean hatching date). All computations were implemented in software R 3.1.1 (R Development Core Team) using the `lm()` function. Partial correlations were calculated using the `parcor()` function from package `ggm`.

Considering our rather short time-series, we tested for the effects of the environmental parameters by testing them one at a time. As with survival, we also tested for a linear trend in breeding phenology and productivity since a common trend in both the environmental parameter and the variable of interest could lead to a spurious significant relation. Because we lacked data from the period 2002–2011, a significant trend in one of the traits considered could instead mean that this trait had a lower value on average in recent (2012–2014) rather than previous years (1985–2001). This is not necessarily equivalent to a linear trend where the trait is expected to gradually decrease during the study period. However, for the three traits considered (survival, productivity, breeding phenology), including a linear trend in the model improved the fit much more than including a two-level variable. This suggests that the declines observed in our study were not only due to a difference between the two main periods (1985–2001 and 2012–2014) but rather represent gradual declines that already began prior to 2001 (see Discussion).

After testing each environmental parameter separately, we ran a global model including all parameters found to be significant in the first step. To test for links between SOI/AAO and productivity, we included the number of storm days (between early December and late January, when the petrel productivity was estimated) into the models as this strongly impacts Antarctic petrel breeding success (Descamps et al. 2015a). The annual AAO and spring SOI (with and without time lags) were standardized prior to all analyses.

Data available from the Dryad Digital Repository: <<http://dx.doi.org/10.5061/dryad.ds63c>> (Descamps et al. 2015b).

Results

Temporal variation in survival

Survival of adult Antarctic petrels at Svarthamaren showed strong and statistically significant inter-annual variation, from 0.87 in 1994/1995 up to 0.96 in 1997/1998 (Fig. 1; Table 1). Survival of Antarctic petrels decreased slightly, but

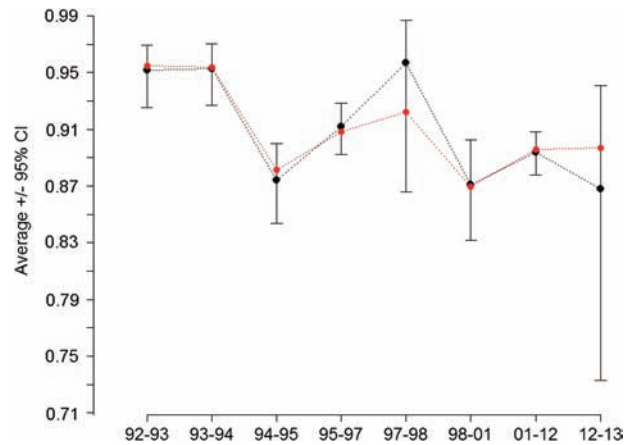


Figure 1. Average annual adult survival (\pm 95% confidence intervals) of Antarctic petrels breeding at Svarthamaren, Dronning Maud Land, Antarctica (black symbols). Red symbols represent the estimated survival rates when survival is constrained to follow a linear trend and to be a linear function of the Antarctic Oscillation (AAO) with a time lag of 1 yr.

significantly, over the study period (Table 1; Fig. 1). Temporal variation in survival was very well explained (%Dev = 0.76, $r^2 = 0.64$) by the AAO with a 1-yr time lag (Fig. 1; Table 1) via a negative effect on petrel survival. The SOI (with no lag) tended to negatively affect survival ($p = 0.06$; Table 1), but this effect disappeared when a linear temporal trend was included (Table 1). This suggests that the apparent effect of the SOI on survival is due to a common long-term trend, but that short-term fluctuations in SOI did not affect short-term fluctuations in survival. No other environmental parameters had statistically significant effects (Table 1). A model including both a linear temporal trend and the AAO with a 1-yr lag explained 81% of the variance in survival (and 94% of the deviance).

Temporal variation in productivity

The number of chicks after the peak of hatching was negatively related to the number of storm days, and showed a negative and significant trend over the study period (Table 2). Moreover, after accounting for the variation due to the storms and for the linear trend, we found that petrel productivity was, contrary to our prediction, positively associated with the spring SOI (with no time lag; Table 2; Fig. 2). These three variables explained 85% of the inter-annual fluctuation in petrel productivity (Fig. 2).

Temporal variation in phenology

Antarctic petrel chicks at Svarthamaren hatched approximately two days later in recent years than in the 1990s (average hatching date: 12 January in period 1992–2001, $n = 1039$ collected over 4 seasons, and 14 January in period 2012–2014, $n = 390$ collected over 3 seasons; 95% CI: [12.6, 12.9] and [14.5–14.9]; Table 2). Hatching was spread over 15 d (95% confidence interval [11, 19]) in 1992–2001 and over 12 d (95% confidence interval [11, 14]) in 2012–2014

Table 1. Model selection for the survival of adult Antarctic petrels breeding at Svarthamaren, Dronning Maud Land, Antarctica (71°53'S, 5°10'E). Dev represents the deviance of the model and np its number of estimable parameters. QAIC represents the Akaike's information criterion adjusted for an over-dispersion $\hat{c}=1.35$; Δ QAIC represents the difference in QAIC between the model considered and the model with lowest QAIC. Subscript t, g and f represent time, group (plot within the colony) and trap-dependence effects, respectively. Symbol Φ represents the adult survival probabilities and symbol p the recapture probabilities.

Model	np	Dev	QAIC	Δ QAIC
$\Phi_t p_{t,g}$	39	9579.069	7173.607	0.000
$\Phi_t p_{t,g+f}$	41	9574.578	7174.280	0.673
$\Phi_{t+g} p_{t,g+f}$	44	9566.678	7174.428	0.821
$\Phi_{t,g} p_{t,g+f}$	59	9548.169	7190.718	17.111
$\Phi_{t,g} p_{t,g}$	58	9553.743	7192.847	19.240
$\Phi_t p_{t+g}$	21	9656.470	7194.941	21.334
$\Phi_g p_{t,g+f}$	36	9626.607	7202.820	29.213
$\Phi_{t,g} p_{t,g,f}$	70	9536.195	7203.848	30.241
$\Phi p_{t,g+f}$	33	9639.069	7206.051	32.444
$\Phi_{t,g} p_{t+g+f}$	44	9612.603	7208.447	34.840
$\Phi_{t,g} p_{t+g}$	42	9618.298	7208.665	35.058
$\Phi_i p_{t,g}$	32	9649.035	7211.434	37.827
$\Phi_{t,g} p_{t+f}$	40	9659.845	7235.440	61.833
$\Phi_{t,g} p_{t,g}$	39	9666.398	7238.295	64.688
$\Phi_{t,g} p_{g+f}$	36	9937.310	7432.970	259.363
$\Phi_{t,g} p_g$	35	9944.792	7436.513	262.906
$\Phi_{t,g} p.$	32	10012.214	7480.456	306.849

b) Testing for environmental effects (recapture probabilities were modeled as $p_{t,g}$). %Dev represents the % of deviance explained by a given covariate or set of covariates. ANODEV (F-statistics and associated p-value) stands for analysis of deviance (see Methods for details)

Model	np	Dev	QAIC	Δ QAIC	%Dev	ANODEV
$\Phi_{AAO-lag 1 + trend}$	34	9583.142	7166.623	0.000	0.94	$F_{2,6} = 48.53, p < 0.001$
$\Phi_{AAO-lag 1 + SOI + trend}$	35	9583.112	7168.612	1.989	0.94	$F_{3,5} = 27.18, p = 0.0016$
$\Phi_{AAO-lag 1 + SOI}$	34	9586.269	7168.940	2.317	0.90	$F_{2,6} = 26.15, p = 0.001$
Φ_f	39	9579.069	7173.607	6.984		
$\Phi_{AAO-lag 1}$	33	9595.906	7174.079	7.456	0.76	$F_{1,7} = 22.09, p = 0.002$
Φ_{trend}	33	9612.995	7186.737	20.114	0.52	$F_{1,7} = 7.43, p = 0.03$
$\Phi_{SOI + trend}$	34	9612.894	7188.662	22.039	0.52	$F_{2,6} = 3.20, p = 0.11$
Φ_{SOI}	33	9619.928	7191.873	25.250	0.42	$F_{1,7} = 4.99, p = 0.061$
$\Phi_{SOI-lag 1}$	33	9630.378	7199.613	32.990	0.27	$F_{1,7} = 2.55, p = 0.15$
$\Phi_{AAO-lag 2}$	33	9639.373	7206.276	39.653	0.14	$F_{1,7} = 1.12, p = 0.33$
$\Phi_{SOI-lag 2}$	33	9641.211	7207.637	41.014	0.11	$F_{1,7} = 0.88, p = 0.38$
$\Phi_{AAO-lag 3}$	33	9641.905	7208.152	41.529	0.10	$F_{1,7} = 0.79, p = 0.40$
Φ_{AAO}	33	9645.709	7210.970	44.347	0.05	$F_{1,7} = 0.35, p = 0.57$
Φ_i	32	9649.035	7211.434	44.811		
$\Phi_{SOI-lag 3}$	33	9648.389	7212.955	46.332	0.01	$F_{1,7} = 0.065, p = 0.81$

(Supplementary material Appendix 1). Almost no hatching has been observed before 10 January in period 2012–2014, whereas it was not rare in years 1991–2001 (Supplementary material Appendix 2). Hatching dates were significantly

and negatively related to the spring SOI with no lag; a model including both a linear trend and the spring SOI explained 88% of the temporal variance in hatching date (Table 2; Fig. 3).

Table 2. Environmental effects (slopes \pm SE) on the productivity (i.e. number of chicks produced per square meter after the peak of hatching at the colony scale) and average hatching dates of Antarctic petrels breeding at Svarthamaren, Dronning Maud Land, Antarctica (71°53'S, 5°10'E). All variables (trend, storm days and spring SOI) have been standardized. R^2 values correspond to the coefficient of determination. Partial R^2 represent the squared partial correlations.

	Best model	Slope \pm SE	t	p	Partial R^2	R^2
Productivity	Trend	-0.17 \pm 0.033	-5.34	0.0007	0.78	0.85
	+ Storm days	-0.082 \pm 0.029	-2.81	0.023	0.50	
	+ Spring SOI	0.092 \pm 0.032	2.91	0.020	0.51	
Average hatching date	Trend	1.89 \pm 0.35	5.37	0.006	0.88	0.88
	+ Spring SOI	-1.22 \pm 0.35	-3.45	0.026	0.75	

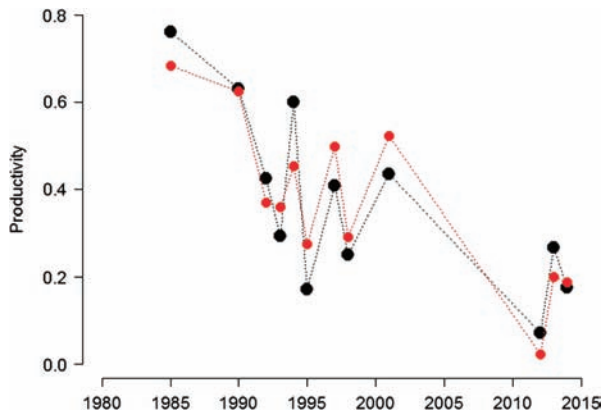


Figure 2. Breeding productivity (i.e. number of chicks produced m^{-2} after the peak of hatching) of Antarctic petrels breeding at Svarthamaren, Dronning Maud Land, Antarctica (black symbols). Red symbols represent the estimated productivity when constrained to follow a linear trend and to be a linear function of the Southern Oscillation Index (SOI) and the number of storm days per breeding season.

Discussion

The life history of Antarctic petrels is strongly correlated with the Southern Oscillation (SOI) and Antarctic Oscillation (AAO) indices, which are the two modes of large-scale climatic variability in Antarctica. Indeed, these two indices explained most of the temporal variation in adult survival, productivity and breeding phenology over the last decades. More specifically, the annual AAO with a time lag of 1 yr and the spring SOI (with no lag) were the best predictors for these three critical life history traits. As predicted, a higher AAO index (warmer sea conditions and lower ice concentration in the Weddell Sea) was associated with decreased adult survival. However, a high spring SOI (warmer conditions, and less sea ice in the Weddell Sea) was, contrary to our prediction, associated with higher petrel productivity and earlier breeding in the current year.

Adult survival and chick production of the Antarctic petrel colony at Svarthamaren have significantly decreased during the last three decades and the timing of breeding has

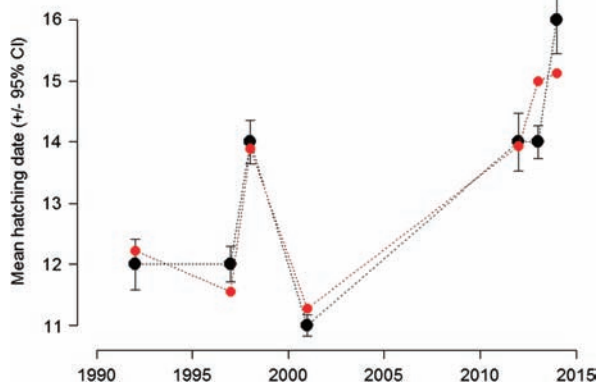


Figure 3. Mean hatching date (January date, $\pm 95\%$ confidence intervals) of Antarctic petrels breeding at Svarthamaren, Dronning Maud Land, Antarctica (black symbols). Red symbols represent the estimated hatching dates when constrained to follow a linear trend and to be a linear function of the Southern Oscillation Index (SOI).

been significantly delayed by ca 2 d, even after controlling for the effects of SOI or AAO. Delayed breeding has also been demonstrated in multiple seabirds in Adélie Land, Antarctica (delay of ca 2 d since 1950, Barbraud and Weimerskirch 2006). While these declines in vital rates and changes in the timing of breeding are statistically significant, this does not necessarily mean that these particular life history traits have changed gradually over the past 25 yr. Indeed, it could be that in recent years (2012–2014), environmental conditions were not optimal for Antarctic petrels (i.e. years of low krill availability) due to stochastic fluctuations (i.e. a bad period in 2011–2014) rather than a linear degradation of the environment. However, in our analyses, a linear trend received much larger support than a two modality variable regardless of the trait considered. These results provide strength to the hypothesis that gradual changes in survival, breeding productivity, and breeding phenology have occurred since the 1980s, rather than simply a recent change in the 2012–2014 period. Nonetheless, further data are needed to disentangle these two alternatives and confirm, or reject, these trends.

Effect of the Antarctic Oscillation (AAO)

High values of the AAO are associated with warmer conditions and less sea ice around the Antarctic Peninsula and in adjacent regions such as the Weddell and Scotia Seas (van den Broeke and van Lipzig 2004, Whitehouse et al. 2008, Pezza et al. 2012). Consequently, our results suggest that a warmer sea and lower ice concentration negatively impact the survival of adult Antarctic petrels. To our knowledge, only one other study has identified links between the AAO and seabird survival (southern giant petrel *Macronectes giganteus* in the South Shetland Island, Krüger et al. 2011), although the study found a positive association over a 6-yr period (1987–1992). Such a positive relationship might be surprising considering the negative effect of higher values of the AAO index on sea ice extent in this region (Pezza et al. 2012). However, since giant petrels mostly prey upon other seabirds or marine mammals (Hunter and Brooke 1992, Gonzalez-Solis et al. 2000, Descamps et al. 2005) a poor year for krill-dependent seabirds might represent a suitable year for seabird predators like the giant petrel (e.g. through a higher rate of nest abandonment and thus a higher access to prey eggs/chicks for giant petrels).

More generally, our literature review (Supplementary material Appendix 3; Fig. 4) suggests that the AAO has been found to affect seabird populations in different directions. Nevertheless, the distribution of the studies indicating that a higher AAO index had negative impacts on seabird demography or population dynamics was likely not random, and indeed all colonies were located in the South West Atlantic (South Orkneys, South Georgia, Weddell Sea) and Antarctic peninsula (Fig. 4). These results fit with the reported negative association between the AAO and sea ice conditions in this region (van den Broeke and van Lipzig 2004, Pezza et al. 2012), which can have negative impacts on krill availability (Whitehouse et al. 2008, Saba et al. 2014).

In the other parts of Antarctica, the majority of the studies did not identify any significant association between variation in AAO and variation in seabird life history traits or

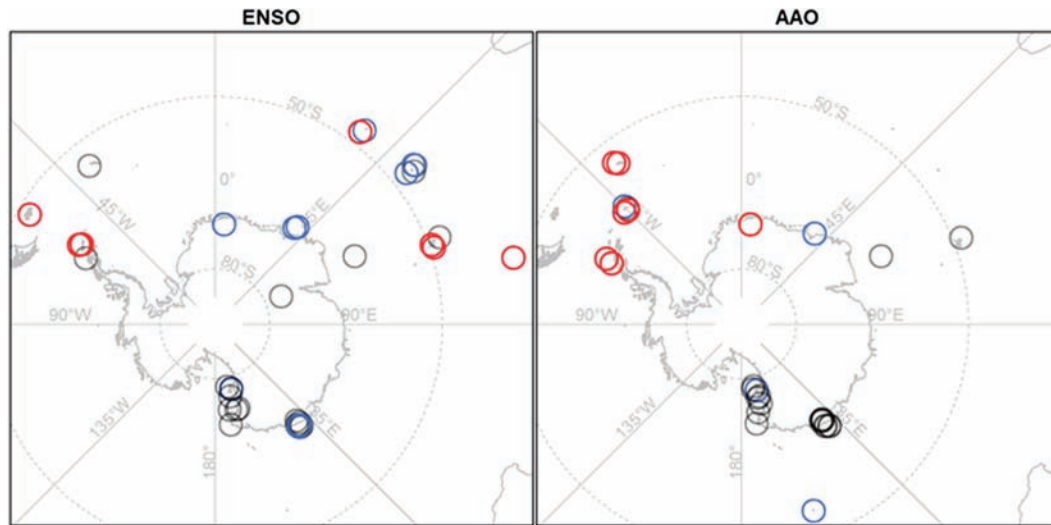


Figure 4. Sign of the relationships between large-scale climatic variability and seabird life history traits or population dynamics. Each circle corresponds to one species at a given breeding location. Red circles represent breeding sites where a significant negative relationship between seabird survival, reproduction and/or population growth rate and the ENSO or AAO has been identified. Blue circles indicate studies where a significant positive relationship has been found and grey circles sites where no clear relationship has been found (i.e. no significant relationship, or variation of the sign of the relationship through time, or positive effect on some traits but negative on others; see Supplementary material Appendix 2 for details). Note that a positive effect on breeding phenology (2 cases) was identified as a red circle as late breeding is generally associated with detrimental effects on reproductive output.

population dynamics (Fig. 4; Supplementary material Appendix 2). Studies that did not find any significant association were not shorter than the ones reporting a positive or negative effect (Supplementary material Appendix 4), suggesting that this lack of effect was not due to a lower statistical power. The positive phase of the AAO was in fact associated with positive sea ice anomalies and lower sea temperatures in several areas around the Antarctic continent (Lefebvre and Goosse 2005, Whitehouse et al. 2008, Pezza et al. 2012). This suggests that the effects of variability in the AAO on oceanographic conditions (e.g. sea ice extent, duration, sea temperature) are highly complex and may show large spatial heterogeneity depending on the scale considered. Consequently, effects of AAO fluctuations on seabird species may also exhibit large spatial variation being more or less pronounced depending on the area considered. Moreover, the association between the AAO and local oceanographic conditions may also vary temporally (Marshall et al. 2013). Unfortunately, the number of studies reported in our literature review and their temporal coverage did not allow us to test whether the association between seabird life history traits and the AAO has changed through time. Finally, the effect of the AAO on seabirds may also vary among species and their primary prey. Our review indicated that the vast majority of the studies representing a significant effect of the AAO were on penguins (Supplementary material Appendix 2) but again, the relatively limited number of studies reported and the potential confounding effect of the study areas prevented an adequate test of inter-specific variation in the response to changes in the AAO.

Effect of the Southern Oscillation Index on Antarctic seabirds

Our results indicate that variation in Antarctic petrel reproduction is very well explained by local as well as large-scale

environmental parameters. Indeed, the number of storm days and the SOI (combined with a linear trend) explained more than 85% of the temporal variation in chick production in period 1985–2014. These effects may be explained by changes in breeding success directly (i.e. egg or chick survival) and/or indirectly by changes in the total number of breeding pairs at the beginning of the season (and thus changes in mean breeding propensity). Unfortunately, no data were available to disentangle between those two non-exclusive hypotheses.

Similarly, the spring SOI explained more than 85% of the inter-annual variation in breeding phenology. The spring SOI had a positive effect on petrel reproduction (high spring SOI was associated with a higher chick production and an earlier breeding), which corresponds to a negative effect of the ENSO. This is similar to previous studies on seabirds in the South West Atlantic (Baylis et al. 2012). However, low ENSO values, or more specifically La Niña events, are associated with low sea ice extent and warmer water in the Scotia and Weddell Seas (Yuan 2004, Murphy et al. 2007a). This does not fit with our prediction of lower chick production and delayed breeding phenology in warmer years and years with negative sea ice anomalies, which may also correspond to years of low krill availability (Fraser and Hofmann 2003, Quetin and Ross 2003, Trathan et al. 2003, 2007). Several explanations can be proposed for these apparent anomalies. First, the relationships between the ENSO and oceanographic conditions around Antarctica show important spatial heterogeneity (Yuan 2004). The positive association between sea ice extent or sea temperature and the ENSO reported in the Weddell Sea is mostly valid for the western Weddell Sea (Turner 2004, Yuan 2004). However, even in the Weddell Sea, relationships between sea ice and the ENSO are not homogeneous and in some areas the relationship is even opposite (Pezza et al. 2012). Different relationships between the ENSO and sea ice or sea temperature

may thus prevail in the core area used by petrels during the breeding or pre-breeding season which could explain the positive association we detected between the SOI and Antarctic petrel reproduction. Second, the ENSO-oceanography relationships may change through time and among seasons. Indeed, even if the Weddell sector tends to hold less sea ice in La Niña years in most seasons, the opposite effect has been observed in summer (Pezza et al. 2012). The relationships between the ENSO and sea temperature or sea ice may also change depending on the time lag considered. Indeed, even though this relationship is generally described as positive, its sign may change after some years. For example, Murphy et al. (2007a) showed that in the South Georgia sector, sea temperatures were negatively correlated with sea temperatures in the tropical Pacific (which corresponds with the general idea that in El Niño years, temperatures will be colder around South Georgia), but only when no time lag was considered. When a three-year time lag was considered, the sign of the relation changed (Fig. 1 in Murphy et al. 2007a). This result is supported by the correlation coefficient observed between the maximum sea ice extent in the entire Weddell Sea and the SOI (Supplementary material Appendix 5) which changed depending on the lag considered. Therefore, without a detailed understanding of the links between the ENSO, sea temperature, sea ice dynamics and prey (krill) dynamics in the specific area used by petrels, understanding the mechanisms linking the ENSO to petrel demography and life history remains challenging.

Such complexity in the relationships between the ENSO and oceanographic conditions may explain why no clear pattern emerged when examining the sign of the relationship between the ENSO and seabird life history and population dynamics in Antarctica (Supplementary material Appendix 3; Fig. 4). Indeed, our review showed various effects of the ENSO all around Antarctica and these effects were either positive or negative for different species breeding at the same location, or indeed within the same species breeding at different locations (Supplementary material Appendix 3; Fig. 4). However, most of the reported significant effects of the ENSO on seabirds were negative (Supplementary material Appendix 2). With the exception of the Weddell/Scotia Sea region where the ecosystem is highly dependent on Antarctic krill and where the links between the ENSO and krill abundance are relatively well appreciated (Murphy et al. 2007a, b), very little is known about associations between the ENSO, sea ice, sea temperature, and prey biomass in other regions of Antarctica. Different regions in Antarctica may well be dominated by different food webs, not necessarily centered on Antarctic krill, and different food webs may in turn respond differentially to a similar environmental signal. Combining these interactions with complex time lags between the ENSO and local oceanographic conditions may explain why no clear or homogenous signal was detected. Such homogeneity can simply not exist and relationships between the ENSO and seabirds may be highly dependent on the region considered and highly variable at a small spatial scale.

Conclusion

Our study identified very strong relationships between the most important modes of large-scale environmental

variability in Antarctica, and Antarctic petrel reproduction and survival. Although these results are based on relatively short time series, they revealed that very simple models accounting only for variation in the Antarctic Oscillation (AAO) or the Southern Oscillation Index (SOI) explained a very large proportion of the inter-annual fluctuation in both petrel survival and reproduction. The mechanisms may involve changes in primary productivity and krill availability, through changes in sea ice distribution or phenology. However, additional data is still needed to test such effects, including data on the fine scale distribution of Antarctic petrels throughout the year and over several years. Based on our extensive literature review and the focal results from our Antarctic petrel studies, it seems realistic to predict that an increasingly positive trend in AAO, as observed in the last decades (Turner et al. 2007, Abram et al. 2014, Zhang et al. 2014), will have detrimental effects on top predator populations in the southwest Atlantic. However, our work also suggests that such conclusions cannot yet be extrapolated to other areas, and that further studies are clearly needed to understand the relationships between fluctuations in the AAO and SOI/ENSO and top predator populations in Antarctica. Ideally, those studies should aim to identify the foraging areas and primary prey of those top-predators, while assessing the linkages between SOI/AAO fluctuations and oceanographic and climatic parameters in those areas. Although this type of data would increase our knowledge of the mechanistic relationships between climate or oceanographic variation and seabird population changes, it remains a very challenging task especially for highly mobile species using a large geographical area.

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References

- Abram, N. J. et al. 2014. Evolution of the Southern Annular Mode during the past millennium. – *Nat. Clim. Change* 4: 564–569.
- Barbraud, C. and Weimerskirch, H. 2006. Antarctic birds breed later in response to climate change. – *Proc. Natl Acad. Sci. USA* 103: 6248–6251.
- Baylis, A. M. M. et al. 2012. Climate as a driver of population variability in breeding gentoo penguins *Pygoscelis papua* at the Falkland Islands. – *Ibis* 154: 30–41.
- Brooke, M. D. et al. 1999. Exploitation of inland-breeding Antarctic petrels by south polar skuas. – *Oecologia* 121: 25–31.
- Burnham, K. P. and Anderson, D. R. 2002. Model selection and multimodel inference: a practical information-theoretic approach, 2nd ed. – Springer.
- Choquet, R. et al. 2009a. U-CARE: utilities for performing goodness of fit tests and manipulating CAPture-REcapture data. – *Ecography* 32: 1071–1074.
- Choquet, R. et al. 2009b. Program E-SURGE: a software application for fitting multievent models. – In: Thomson, D. L. et al. (eds), *Modeling demographic processes in marked populations*. Springer, pp. 845–865.

- Descamps, S. et al. 2005. Impact of predation on king penguin *Aptenodytes patagonicus* in Crozet Archipelago. – *Polar Biol.* 28: 303–310.
- Descamps, S. et al. 2015a. Demographic effects of extreme weather events: snow storms, breeding success, and population growth rate in a long-lived Antarctic seabird. – *Ecol. Evol.* 5: 314–325.
- Descamps, S. et al. 2015b. Data from: Large-scale oceanographic fluctuations drive Antarctic petrel survival and reproduction. – Dryad Digital Repository, <<http://dx.doi.org/10.5061/dryad.ds63c>>.
- Deser, C. and Wallace, J. M. 1987. El Niño events and their relation to the Southern Oscillation 1925–1986. – *J. Geophys. Res. Oceans* 92: 14189–14196.
- Fauchald, P. and Tveraa, T. 2006. Hierarchical patch dynamics and animal movement pattern. – *Oecologia* 149: 383–395.
- Forcada, J. and Trathan, P. N. 2009. Penguin responses to climate change in the Southern Ocean. – *Global Change Biol.* 15: 1618–1630.
- Fraser, W. R. and Hofmann, E. E. 2003. A predator's perspective on causal links between climate change, physical forcing and ecosystem response. – *Mar. Ecol. Prog. Ser.* 265: 1–15.
- Gonzalez-Solis, J. et al. 2000. Foraging partitioning between giant petrels *Macronectes* spp. and its relationship with breeding population changes at Bird Island, South Georgia. – *Mar. Ecol. Prog. Ser.* 204: 279–288.
- Grosbois, V. et al. 2008. Assessing the impact of climate variation on survival in vertebrate populations. – *Biol. Rev.* 83: 357–399.
- Hallett, T. B. et al. 2004. Why large-scale climate indices seem to predict ecological processes better than local weather. – *Nature* 430: 71–75.
- Harangozo, S. A. 2000. A search for ENSO teleconnections in the west Antarctic Peninsula climate in Austral winter. – *Int. J. Climatol.* 20: 663–679.
- Hunter, S. and Brooke, M. D. 1992. The diet of giant petrels *Macronectes* spp. at Marion Island, Southern Indian Ocean. – *Colon. Waterbirds* 15: 56–65.
- Hurrell, J. W. et al. 2001. The North Atlantic Oscillation. – *Science* 291: 603–605.
- Intergovernmental Panel on Climate Change 2014. Climate change 2014: impacts, adaptation and vulnerability. Working Group II Contribution to the IPCC 5th Assessment Report. – <www.ipcc.ch/report/ar5/wg2/>.
- Krüger, L. et al. 2011. Responses of an Antarctic southern giant petrel population to climate change. Annual activity report. – National Inst. of Science and Technology – Antarctic Environmental Research.
- Kwok, R. and Comiso, J. C. 2002. Southern Ocean climate and sea ice anomalies associated with the Southern Oscillation. – *J. Clim.* 15: 487–501.
- Larsen, J. N. et al. 2014. Polar regions. – In: Barros, V. R. et al. (eds), Climate change 2014: impacts, adaptation, and vulnerability. Part B: regional aspects. Contribution of Working Group II to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change, pp. 1567–1612.
- Lebreton, J. D. et al. 1992. Modeling survival and testing biological hypotheses using marked animals – a unified approach with case-studies. – *Ecol. Monogr.* 62: 67–118.
- Lefebvre, W. and Goosse, H. 2005. Influence of the Southern Annular Mode on the sea ice-ocean system: the role of the thermal and mechanical forcing. – *Ocean Sci.* 1: 145–157.
- Lockwood, J. G. 1984. The Southern Oscillation and El Niño. – *Prog. Phys. Geogr.* 8: 102–110.
- Lorentsen, S. H. and Røv, N. 1995. Incubation and brooding performance of the Antarctic petrel *Thalassoica antarctica* at Svarthamaren, Dronning Maud Land. – *Ibis* 137: 345–351.
- Lorentsen, S. H. et al. 1993. Documentation of the demography and population monitoring systems for Antarctic petrels at Svarthamaren, Dronning Maud Land. – NINA Oppdragsmelding.
- Lorentsen, S. H. et al. 1998. Diet and prey consumption of Antarctic petrels *Thalassoica antarctica* at Svarthamaren, Dronning Maud Land, and at sea outside the colony. – *Polar Biol.* 19: 414–420.
- Marshall, G. J. et al. 2013. A predominant reversal in the relationship between the SAM and east Antarctic temperatures during the twenty-first century. – *J. Clim.* 26: 5196–5204.
- Mehlum, F. et al. 1988. Census of breeding Antarctic petrels *Thalassoica antarctica* and physical features of the breeding colony at Svarthamaren, Dronning Maud Land, with notes on breeding snow petrels *Pagodroma nivea* and south polar skuas *Catharacta maccormicki*. – *Polar Res.* 6: 1–9.
- Meredith, M. P. et al. 2008. On the interannual variability of ocean temperatures around South Georgia, Southern Ocean: forcing by El Niño/Southern Oscillation and the Southern Annular Mode. – *Deep-Sea Res. Part II* 55: 2007–2022.
- Murphy, E. J. et al. 2007a. Climatically driven fluctuations in Southern Ocean ecosystems. – *Proc. R. Soc. B* 274: 3057–3067.
- Murphy, E. J. et al. 2007b. Spatial and temporal operation of the Scotia Sea ecosystem: a review of large-scale links in a krill centred food web. – *Phil. Trans. R. Soc. B* 362: 113–148.
- Oro, D. 2014. Seabird and climate: knowledge, pitfalls, and opportunities. – *Front. Ecol. Evol.* 2: 79.
- Pezza, A. B. et al. 2012. Climate links and recent extremes in antarctic sea ice, high-latitude cyclones, Southern Annular Mode and ENSO. – *Clim. Dyn.* 38: 57–73.
- Philander, S. G. (ed.) 1990. El Niño, La Niña, and the Southern Oscillation. – Elsevier.
- Philander, S. G. H. 1983. El-Niño Southern Oscillation phenomena. – *Nature* 302: 295–301.
- Post, E. et al. 2013. Ecological consequences of sea-ice decline. – *Science* 341: 519–524.
- Pradel, R. and Sanz-Aguilar, A. 2012. Modeling trap-awareness and related phenomena in capture–recapture studies. – *PLoS One* 7: 32666.
- Quetin, L. B. and Ross, R. M. 2003. Episodic recruitment in Antarctic krill *Euphausia superba* in the Palmer LTER study region. – *Mar. Ecol. Prog. Ser.* 259: 185–200.
- Røv, N. 1991. The density of breeding and non-breeding Antarctic petrels at Svarthamaren, Dronning Maud Land, 1990. – *Fauna Norv. Ser. C Cinclus* 14: 49–53.
- Saba, G. K. et al. 2014. Winter and spring controls on the summer food web of the coastal west Antarctic Peninsula. – *Nat. Comm.* 5: 4318.
- Salinger, M. J. 2013. A brief introduction to the issue of climate and marine fisheries. – *Clim. Change* 119: 23–35.
- Siegel, V. and Loeb, V. 1994. Length and age at maturity of Antarctic krill. – *Antarct. Sci.* 6: 479–482.
- Simmonds, I. and Jacka, T. H. 1995. Relationships between the interannual variability of Antarctic sea-ice and the Southern Oscillation. – *J. Clim.* 8: 637–647.
- Smetacek, V. and Nicol, S. 2005. Polar ocean ecosystems in a changing world. – *Nature* 437: 362–368.
- Sorensen, M. C. et al. 2009. Carry-over effects in a Pacific seabird: stable isotope evidence that pre-breeding diet quality influences reproductive success. – *J. Anim. Ecol.* 78: 460–467.
- Stammerjohn, S. E. et al. 2008. Trends in Antarctic annual sea ice retreat and advance and their relation to El Niño-Southern Oscillation and Southern Annular Mode variability. – *J. Geophys. Res. Oceans* 113: CO3S90.
- Stenseth, N. C. and Mysterud, A. 2005. Weather packages: finding the right scale and composition of climate in ecology. – *J. Anim. Ecol.* 74: 1195–1198.
- Stenseth, N. C. et al. 2003. Studying climate effects on ecology through the use of climate indices: the North Atlantic Oscillation, El Niño Southern Oscillation and beyond. – *Proc. R. Soc. B* 270: 2087–2096.

- Trathan, P. N. et al. 1996. Dynamics of Antarctic penguin populations in relation to interannual variability in sea ice distribution. – *Polar Biol.* 16: 321–330.
- Trathan, P. N. et al. 2003. Oceanographic variability and changes in Antarctic krill (*Euphausia superba*) abundance at South Georgia. – *Fish. Oceanogr.* 12: 569–583.
- Trathan, P. N. et al. 2007. Environmental forcing and Southern Ocean marine predator populations: effects of climate change and variability. – *Phil. Trans. R. Soc. B* 362: 2351–2365.
- Trenberth, K. E. 1997. The definition of El Niño. – *Bull. Am. Meteorol. Soc.* 78: 2771–2777.
- Turner, J. 2004. The El Niño-southern oscillation and Antarctica. – *Int. J. Climatol.* 24: 1–31.
- Turner, J. et al. 2007. An Arctic and Antarctic perspective on recent climate change. – *Int. J. Climatol.* 27: 277–293.
- van den Broeke, M. R. and van Lipzig, N. P. M. 2004. Changes in Antarctic temperature, wind and precipitation in response to the Antarctic Oscillation. – *Ann. Glaciol.* 39: 119–126.
- van Franeker, J. A. et al. 1999. Distribution and abundance of the Antarctic petrel. – *Waterbirds* 22: 14–28.
- Waluda, C. M. et al. 2004. Synchronicity in southern hemisphere squid stocks and the influence of the Southern Oscillation and Trans Polar Index. – *Fish. Oceanogr.* 13: 255–266.
- Weimerskirch, H. et al. 2012. Changes in wind pattern alter albatross distribution and life-history traits. – *Science* 335: 211–214.
- Whitehouse, M. J. et al. 2008. Rapid warming of the ocean around South Georgia, Southern Ocean, during the 20th century: forcings, characteristics and implications for lower trophic levels. – *Deep-Sea Res. Part I* 55: 1218–1228.
- Yuan, X. J. 2004. ENSO-related impacts on Antarctic sea ice: a synthesis of phenomenon and mechanisms. – *Antarct. Sci.* 16: 415–425.
- Zhang, Z. et al. 2014. Is the Antarctic oscillation trend during the recent decades unusual? – *Antarct. Sci.* 26: 445–451.
- Zheng, B. Y. and Agresti, A. 2000. Summarizing the predictive power of a generalized linear model. – *Stat. Med.* 19: 1771–1781.

Supplementary material (Appendix ECOG-01659 at <www.ecography.org/readers/appendix>). Appendix 1–5.