

Climate and density shape population dynamics of a marine top predator

Christophe Barbraud* and Henri Weimerskirch

Centre d'Études Biologiques de Chizé, CNRS-UPR 1934, 79360 Villiers en Bois, France

Long-term studies have documented that climate fluctuations affect the dynamics of populations, but the relative influence of stochastic and density-dependent processes is still poorly understood and debated. Most studies have been conducted on terrestrial systems, and lacking are studies on marine systems explicitly integrating the fact that most populations live in seasonal environments and respond to regular or systematic environmental changes. We separated winter from summer mortality in a seabird population, the blue petrel *Halobaena caerulea*, in the southern Indian Ocean where the El Niño/Southern Oscillation effects occur with a 3–4-year lag. Seventy per cent of the mortality occurred in winter and was linked to climatic factors, being lower during anomalous warm events. The strength of density dependence was affected by climate, with population crashes occurring when poor conditions occurred at high densities. We found that an exceptionally long-lasting warming caused a *ca.* 40% decline of the population, suggesting that chronic climate change will strongly affect this top predator. These findings demonstrate that populations in marine systems are particularly susceptible to climate variation through complex interactions between seasonal mortality and density-dependent effects.

Keywords: blue petrel; climatic fluctuations; density dependence; density independence; seasonal survival

1. INTRODUCTION

Long-term studies have documented that climate fluctuations influence the dynamics of populations (McCarty 2001; Stenseth *et al.* 2002; Walther *et al.* 2002), but the underlying mechanisms, in particular the interaction between stochastic and density-dependent effects, are poorly understood and debated (Leirs *et al.* 1997). The majority of work exploring the influence of density-dependent and independent processes on vital rates and population dynamics has used either time-series analyses (e.g. Forchhammer *et al.* 1998; Grenfell *et al.* 1998), or analyses based on long-term detailed individual-based data. This second approach has detected important processes influencing population dynamics that time-series methodologies may have overlooked (Leirs *et al.* 1997; Saether *et al.* 2000; Coulson *et al.* 2001). However, the overwhelming majority of work using these approaches to shed light on the processes influencing population dynamics has been conducted on terrestrial populations (mammals: ungulates, rodents, carnivores; birds: passerines, waders; see Stenseth *et al.* (2002) and Walther *et al.* (2002) for recent reviews). Thus, there is a crucial need for studies on marine or coupled marine–terrestrial systems to permit the approach of a general insight on the relative roles of stochastic and density-dependent effects on populations. Such studies are especially needed if one wants to predict the response of oceanic ecosystems to climatic changes.

Disentangling the density-dependent and density-independent structure that interacts with the climatic signal requires understanding the poorly explored seasonal patterns of mortality. Most populations respond to regular or systematic environmental fluctuations because individuals

are exposed to changes in resource abundance and face variable mortality risks during the different stages of the annual cycle (Fretwell 1972). In addition, season duration and climate may be differentially affected by climate warming (Houghton *et al.* 2001; Parkinson & Cavalieri 2002). However, quantitative studies that explicitly integrate seasonal variation in survival throughout the annual cycle when examining density and climate interactions are few (Sillert *et al.* 2000), reliable estimates of seasonal survival rates are rare (Gauthier *et al.* 2001) and non-existent, to our knowledge, for long-lived top predators in which population growth rate is mostly sensitive to changes in adult survival (Lebreton & Clobert 1991).

In this paper, the data used are long-term capture–recapture data from which are extracted survival, recruitment and population size in a seabird population to identify the period during which most of the mortality occurs, and to explore how density-independent processes (ocean climate fluctuations) interact with population density and affect the demographic parameters and the population dynamics of a marine top predator.

2. METHODS

(a) *Study population and life history*

Data came from a capture–recapture study on a population of blue petrels (*Halobaena caerulea*) on Kerguelen Islands between 1986 and 2001. The blue petrel, a small (190 g) long-lived seabird, breeds at only six sub-Antarctic islands (Warham 1990). It forages over oceanic waters and preys mainly on small crustaceans and fishes from Antarctic waters south of the Antarctic convergence (Cherel *et al.* 2002). Blue petrels remain between the Antarctic convergence and the northern limit of the pack ice throughout the year. The birds are burrowers. A single egg is laid in late October and the chick fledges in February. In mid-April the birds return to their burrows and stay about one

*Author for correspondence (barbraud@cebc.cnrs.fr).

month (Paulian 1953) before leaving the colony and dispersing at sea until the next breeding season. The study colony was located on Mayes Island, a 5 km² uninhabited island in the Kerguelen archipelago (48°38' S, 68°38' E), southern Indian Ocean. Each year, between 71 and 238 individually marked burrows, fitted with an observation window above the nest chamber, were inspected in early November (to search for occupied nest sites and record marked adults), and mid-April (to record marked adults returning to their burrows). Each year, new individuals found in studied burrows were marked.

(b) Modelling survival, climate fluctuations and density dependence

We estimated seasonal survival rates of adults from November 1986 to November 2001 ($k = 31$ occasions; 15 summers, 15 winters), using the Cormack–Jolly–Seber (CJS) model implemented in the MARK computer program (White & Burnham 1999). This method allows the estimation of unbiased capture and survival probabilities (Lebreton *et al.* 1992). Summer survival was defined as the probability of survival from November of year t to April of year $t + 1$, and subsequent winter survival as the probability of survival from April of year $t + 1$ to November of year $t + 1$.

(c) Modelling survival

A model with season and time dependence in both survival and capture probabilities ($\phi_{s(t)*w(t)}, p_{s(t)*w(t)}$, where ϕ is the survival probability, t the year, s and w for summer and winter indicate variation within seasons, and p the capture probability) was considered as a biological starting point. The fit of this model to the data was tested using the RELEASE software (Burnham *et al.* 1987). Because we detected dependence in sighting probabilities (see § 3a), we used the modification of the CJS model proposed by Pradel (1993) for trap dependence. Because of the seasonal nature of our dataset, we expected trap dependence over two occasions (1 year), so that the probability of observing an individual depended on whether or not it had been observed the year before in the same time interval. The non-significant component 2.Cm ($\chi^2(27) = 32.855$, $p = 0.202$) for the annual dataset indicated that trap dependence did not extend beyond 1 year. To model this, we used a model structure with 'three age classes' for resighting probability. The general model then becomes ($\phi_{s(t)*w(t)}, p_{s(t)*w(t)*m}$), where m is Markovian dependence in sighting probability p .

Even when accounting for trap dependence in sighting probabilities, the tests from RELEASE still indicated a lack of fit (see § 3a). To account for that extra-binomial variation, we computed a conservative variance inflation factor, \hat{c} (Lebreton *et al.* 1992), which is the ratio of the residual χ^2 goodness-of-fit tests of RELEASE (i.e. excluding the component 2.Ct, which is taken into account by the model with immediate trap dependence in p) on its residual degrees of freedom. Because we controlled for long-term trap dependence this should, in theory, reduce the \hat{c} value. Because there is no simple goodness-of-fit test for such a model the previous \hat{c} value was retained, and this makes our comparisons between models slightly more conservative (Gauthier *et al.* 2001).

Model selection was based on the estimation of an information-theoretic criterion as an estimate of expected relative Kullback–Leibler information (Burnham & Anderson 2002). The second-order approximation Akaike information criterion accounting for overdispersion (QAICc) was used to select the most parsimonious model. Models were ranked and scaled using

respectively Δ QAICc and Akaike weights (w_i), and model inference was based on evidence ratios (w_i/w_j) following Burnham & Anderson (2002).

(d) Estimating population size and recruitment rate

Because mortality was very low during summer (see § 3b) the population was considered as closed, and population size estimates were obtained using the program CAPTURE (White *et al.* 1982). The model selection procedure of CAPTURE recommended model M_{tth} (where the probability of capture is specific to each individual, varies from occasion to occasion, and depends on whether the individual has been previously captured) as an appropriate model for the data and for each secondary capture session. However, since no population size estimator is available for this model we used estimators of the next most complex model as ranked by the model selection procedure, which was model M_{tth} (where the probability of capture is specific to each individual and depends on whether the individual has been previously captured). The population size estimators obtained with model M_{tth} were a function of the number of monitored burrows ($r = 0.53$, $n = 15$, $p = 0.042$). Thus, we used the detrended population size estimators to estimate variations in the population size.

The recruitment rate of the population (defined as the number of new individuals in the population at time t per individual in the population at time $t - 1$) was obtained from capture–recapture data analysis using Pradel's models (Pradel 1996) implemented in program MARK. Because of the trap response, the approach of Pradel for estimating recruitment may not work well. We thus obtained a goodness-of-fit statistic for the standard CJS model (no trap response) and used the resulting variance inflation factor (4.7359) to increase recruitment rate variances.

(e) Modelling climatic effects and density dependence

Time variation in summer capture probability (November) was modelled as a function of sea-surface temperature anomalies (SSTA) south of Kerguelen as earlier studies have shown that SSTA directly affect the body condition of blue petrels (Guinet *et al.* 1998), and hence their propensity to breed (Chastel *et al.* 1995). The SSTA data derived from ship, buoy and satellite data (Reynolds & Smith 1994), were obtained from the Integrated Global Ocean Service System (IGOSS) at <http://ingrid.ldgo.columbia.edu/SOURCES/IGOSS/nmc>.

Time variation in winter survival was modelled as a function of the winter (from July to October) El Niño/Southern Oscillation Index (SOI) with 3- and 4-year lags, as portions of the SSTA associated with the SOI generated in the south Pacific Ocean follow the hemispheric course of the Antarctic Circumpolar Current and reach Kerguelen 3–4 years later (White & Peterson 1996; Xie *et al.* 2002). The SOI reflects a large-scale pattern of climate variability in the Southern Ocean and accounts for major variations in weather and sea-surface temperature (Philander 1990). In the southern Indian Ocean, the response includes a basin-wide increase of sea-surface temperatures and wind stress (Xie *et al.* 2002), which in turn negatively affect primary and presumably secondary productivity (Comiso *et al.* 1993; Pakhomov & McQuaid 1996). Because blue petrels and other marine top predators feed on crustaceans and fishes, these anomalies may affect directly or indirectly (via modification of the food web) their dynamics. The SOI was obtained

Table 1. Statistical capture–recapture models.

(Δ_i is the difference in QAICc between the lowest QAICc model and QAICc of model i ; w_i the Akaike weights, and np the number of parameters estimated by MARK. * and + respectively denote models with and without interactions. $p_{s(SSTA)}$ indicates that summer recapture probability is a function of SSTA. (.) indicates no time effect.)

model	QAICc	Δ_i	w_i	np	deviance
1. $\phi_{s(.)} w(SOI-3+SOI-4)*N_{t-1} p_{s(SSTA)+w(t)+m3}$	3899.88	0.00	0.9831	23	1390.60
2. $\phi_{s(.)} w(SOI-3+SOI-4) p_{s(SSTA)+w(t)+m3}$	3909.31	9.42	0.0088	23	1400.02
3. $\phi_{s(.)} w(SOI-3+SOI-4+N_{t-1}) p_{s(SSTA)+w(t)+m3}$	3910.78	10.89	0.0042	24	1399.47
4. $\phi_{s(.)} w(SOI-3) p_{s(SSTA)+w(t)+m3}$	3911.06	11.18	0.0037	22	1403.81
5. $\phi_{s(.)} w(SOI-4) p_{s(SSTA)+w(t)+m3}$	3918.40	18.52	0.0001	22	1411.15
6. $\phi_{s(.)} w(t) p_{s(SSTA)+w(t)+m3}$	3921.19	21.31	0.0000	31	1395.64
7. $\phi_{s(t)*w(t)} p_{s(SSTA)+w(t)+m3}$	3924.00	24.12	0.0000	39	1380.06
8. $\phi_{s(t)*w(t)} p_{s(t)+w(t)+m3}$	3925.76	25.88	0.0000	38	1385.91
9. $\phi_{s(.)} w(.) p_{s(SSTA)+w(t)+m3}$	3927.63	27.74	0.0000	21	1420.37
10. $\phi_{s(t)*w(t)} p_{s(t)*w(t)*m3}$	3997.71	97.83	0.0000	107	1313.64

from the Bureau of Meteorology (Australia) at ftp://ftp.bom.gov.au/anon/home/ncc/www/sco/soi.

To test for the effects of SOI on survival, we examined a logit-linear relationship of survival with SOI:

$$\text{logit } \phi_{w(t)} = a + b \times \text{SOI}.$$

Density dependence on survival was incorporated in this logit-linear relationship without and with interactive effects with SOI, respectively, as

$$\text{logit } \phi_{w(t)} = a + b \times \text{SOI} + c \times N_{t-1}$$

and

$$\text{logit } \phi_{w(t)} = a + b \times \text{SOI} + c \times N_{t-1} + d \times \text{SOI} \times N_{t-1}$$

where N_{t-1} is the population size at time $t - 1$. Thus, when an interactive effect between density and climate was incorporated in the model, climate affected the strength of density dependence.

In addition to the above models we also fitted the model proposed by Maynard-Smith & Slatkin (1973) (hereafter referred to as MS), and often used in similar studies for terrestrial populations:

$$\phi_{w(t)} = \frac{\phi_{w(0)}}{(1 + (N_{t-1}/K)^\beta \times \text{SOI})}$$

where N_{t-1} is the density of the population at time $t - 1$, $\phi_{w(0)}$ is the maximum winter survival, K is a parameter closely related to the carrying capacity or the stable equilibrium density, and β is a parameter expressing the degree of density dependence (the larger it is the stronger is the degree of density dependence).

The proportion of variation in survival explained by the covariates, which is akin to r^2 , was estimated using two methods. First, the random-effects models (available in MARK) permitted calculation of the proportion of process variance in survival explained by covariates as (Loison *et al.* 2002)

$$r^2 = 1 - \sigma_{\text{cov}}^2 / \sigma_t^2,$$

where σ_{cov}^2 and σ_t^2 are respectively the variances in survival in the presence and in the absence of the relationship with the covariate. Second, we used the analysis of deviance (Skalski *et al.* 1993) to estimate the total variance in survival explained by the covariates, which is defined as (deviance(constant model) – deviance(covariate model)) / (deviance(constant model) – deviance(time-dependent model)).

3. RESULTS

(a) Goodness-of-fit tests

The goodness-of-fit statistic of the general model ($\phi_{s(t)*w(t)}$, $p_{s(t)*w(t)}$) provided evidence of a lack of fit ($\chi^2(164) = 422.47$, $p < 0.001$). A large part of this χ^2 statistic was explained by Test 2.Ct ($\chi^2(25) = 97.297$, $p < 0.001$), and Test 2.Cm ($\chi^2(70) = 195.481$, $p < 0.001$), respectively indicating immediate and long-term trap dependence (trap happiness in this case) effects on capture. A goodness-of-fit test accounting for trap dependence on capture was calculated by considering only the components of Test 3 and Test 2.Cm but there was still evidence for a lack of fit ($\chi^2(139) = 325.173$, $p < 0.001$). To correct for this overdispersion, we used an inflation factor in the remaining analysis ($\hat{c} = 2.339$).

(b) Seasonal variation in survival

A model with only additive effects across years on the sighting probabilities (model 8) was preferred over the general model (model 10; table 1). As predicted, a model with an effect of SSTA in winter on the summer sighting probabilities (model 7) was preferred over model 8. A model where summer survival was constant across years (model 6) was preferred over model 7, but a model with constant winter survival was rejected (model 9). Winter survival varied across years and was on average lower (0.924, s.e. = 0.014) than summer survival (0.967, s.e. = 0.016) over the study period (figure 1a). Thus, most (ca. 70%) of the annual mortality occurred during the winter period.

(c) Effect of climate and density

Winter SOI with a 3-year lag (SOI-3) strongly affected winter survival (model 4 versus model 6; slope = 0.084, s.e. = 0.032; figure 1b), indicating that blue petrels survived less in winters during negative phases of the winter SOI, i.e. when sea-surface temperatures were warmer than average. There was an additive effect of SOI-4 (model 2 versus model 4; slope = 0.049, s.e. = 0.020 (there was no significant relationship between SOI-3 and SOI-4: Pearson $r = -0.062$, $p = 0.842$)), indicating the existence of prolonged effects of the SOI on oceanographic conditions off Kerguelen. Based on w_i values, the evidence ratio of model 2 versus model 6 was $w_2/w_6 = 442$, providing strong

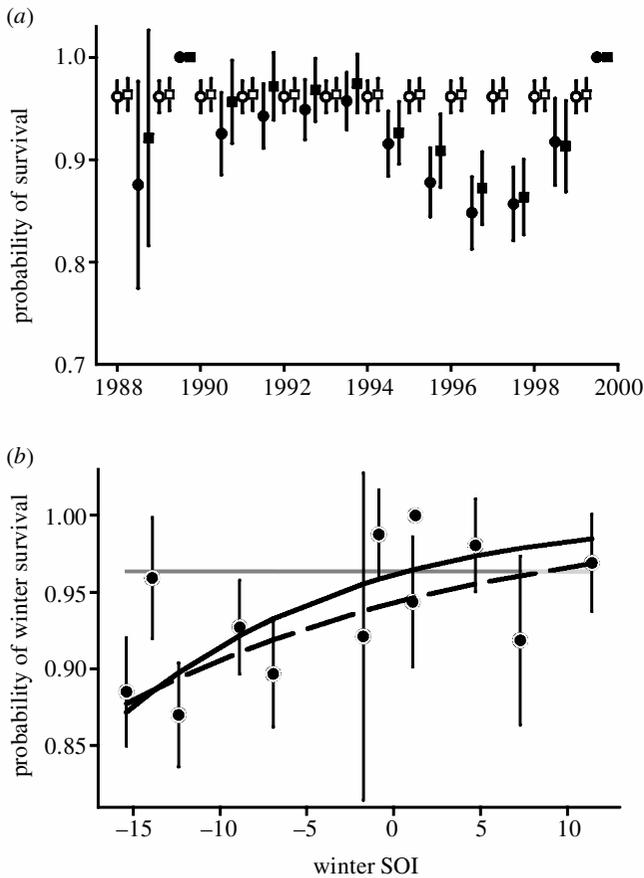


Figure 1. Adult survival of blue petrels. (a) The annual variations in summer (open symbols) and winter (filled symbols) survival estimated from model $(\phi_{s(c)} w(t) p_{s(SSTA)+w(t)+m3})$ (circles) and from model $(\phi_{s(c)} w(t) p_{s(t)+w(t)+m3})$ (squares), where summer survival is constant, winter survival is time dependent, summer recapture rate is respectively a function of winter SSTA and time, and winter recapture rate is time dependent. (b) The probability of winter survival plotted against the winter SOI with a 4-year lag (plain line) and the winter SOI with a 3-year lag (dashed line). Estimates are from models $(\phi_{s(c)} w(SOI-3) p_{s(SSTA)+w(t)+m3})$ and $(\phi_{s(c)} w(SOI-4) p_{s(SSTA)+w(t)+m3})$, respectively. The grey line indicates summer survival. Bars indicate ± 1 s.e.

evidence for an effect of SOI-3 and SOI-4 on winter survival.

The ecologically plausible model combining density-dependent and density-independent effects non-additively was the most parsimonious (model 1), and had a strong weight of evidence ($w_1 > 0.98$; evidence ratio versus the second best ranked model according to QAICc: $w_1/w_2 = 111$). Winter survival decreased at higher densities, particularly under poor oceanographic conditions (slopes for SOI-3 and SOI-4 with an interaction with density: -0.036 , s.e. = 0.013 , and -0.029 , s.e. = 0.015 , respectively). There was strong evidence that climate affected the strength of density dependence as suggested by the evidence ratio of model 1 versus model 3 ($w_1/w_4 = 232$). The evidence for the MS model was similar to the evidence for model 1 ($w_1/w_{MS} = 1.2$), i.e. both models were equivalent in describing the variability in the data ($\beta = 0.385$, s.e. = 0.138 for model MS). Model 1 explained 73.9% and 14.5% of the total and process variance in winter adult survival, respectively (figure 2c).

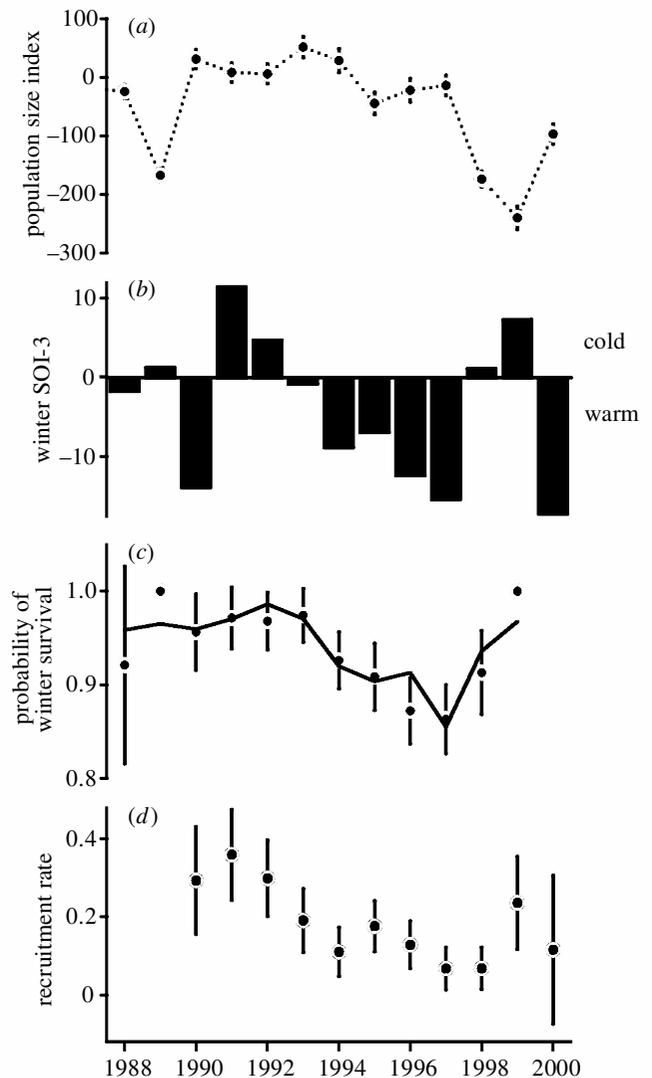


Figure 2. The annual variation of demographic parameters in the blue petrel and climatic parameters. (a) The population size index. (b) The winter SOI-3. (c) The probability of winter survival. The filled circles represent survival estimates from model $(\phi_{s(c)} w(t) p_{s(SSTA)+w(t)+m3})$. The solid line represents survival estimates predicted from the best-fit model $(\phi_{s(c)} w(SOI-3+SOI-4)*N_{t-1} p_{s(SSTA)+w(t)+m3})$. The last survival estimate is not identifiable and is not indicated on the figure. (d) The recruitment rate, estimated from a Pradel's model where survival, recapture and recruitment probabilities are all time dependent. Recruitment rates for the first 2 years (1988 and 1989) are not indicated as this corresponded to the beginning of the study when many birds were marked. Bars indicate ± 1 s.e.

There was a major decrease (*ca.* 40%) of the population size following four consecutive years with high winter mortality associated with negative winter SOI (1994 to 1997; figure 2a,b). The recruitment rate decreased during positive winter SOI-3 conditions ($p = 0.026$; $r^2 = 0.35$; figure 2d), but was not density dependent ($p = 0.634$; $r^2 = 0.02$), indicating that fewer individuals were recruited in the population during warm events.

4. DISCUSSION

This study demonstrates that large-scale climatic fluctuations and density are key factors that influence winter

survival rates and the population dynamics of a marine top predator. The strength of density dependence was affected by climate. At low population densities, winter survival decreases when climatic conditions become unfavourable (negative SOI values and warm sea-surface temperatures), but remains sufficiently high (*ca.* 0.925) to avoid major population declines ($\lambda = 0.992$, based on a matrix population model (Caswell 2001) with seven age classes (age at first reproduction 4 years, juvenile survival rate 0.5, immature survival rate 0.88, fecundity 0.4)). When condition deteriorates at high population densities, winter survival declines dramatically through density-dependent effects (down to 0.865) and population crashes occur ($\lambda = 0.914$). Such combined effects have not, to our knowledge, previously been reported for a marine top predator. This suggests that both density and climatic fluctuations may affect populations in marine systems, as has been previously shown for terrestrial systems (Leirs *et al.* 1997; Coulson *et al.* 2001).

Competition acting mainly through lower food availability at sea during winter in the Southern Ocean (Comiso *et al.* 1993; Daly & Smith 1993; Moore & Abbott 2000) may be the mechanism leading to the association between survival rates and density. Blue petrels may have to compete for food resources with conspecifics or with individuals from species showing overlap in the resource needs such as *Pachyptila* sp. (Cherel *et al.* 2002). Warm sea-surface temperatures off Kerguelen in the winter are known to negatively affect zooplankton communities (Pakhomov & McQuaid 1996) and the body condition of blue petrels (Guinet *et al.* 1998). Blue petrels mainly forage on prey species living south of Kerguelen (ex: *Themisto gaudichaudii* and *Euphasia superba* (Cherel *et al.* 2002)), whose abundance is negatively affected by warm sea-surface temperatures (Marinovic *et al.* 2002). Our results thus suggest that survival variability may be mainly driven by abundance of resources.

Summer survival was relatively high and varied little between years. This result seems surprising because, as estimated, summer survival includes the costs of breeding and moulting. This is probably because breeding and moulting occur during a period when primary (phytoplankton) and secondary (zooplankton) productivities in the southern Indian Ocean are high (Daly & Smith 1993; Moore & Abbott 2000). In addition, the effect of the reproductive effort made during the summer might only appear during winter. For example, a late moult or a demanding breeding might result in a poor preparation for the winter and its subsequent effect on mortality. Thus, winter survival was the main determinant of annual survival. Although this is a common assumption in ecology, it has never been explicitly estimated previously for such a long-lived organism.

The study period was characterized by the occurrence of an exceptionally long-lasting warming of the southern Indian Ocean (1994–1997) corresponding (with a lag) to the longest record of successive negative SOI values (McPhaden 1993), that had probably profound effects on all components of the marine ecosystem (Jaksic 2001). The blue petrel population decreased dramatically following this long warming event. Our results suggest that populations of marine top predators are able to sustain short-term anomalous climatic events (for example by not

breeding), but that long-lasting anomalies result in population crashes (see also Barbraud & Weimerskirch 2001). Probably, a chronic increase in sea-surface temperatures of the Southern Ocean would result in a population decrease of blue petrels but also in other marine top predators.

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REFERENCES

- Barbraud, C. & Weimerskirch, H. 2001 Emperor penguins and climate change. *Nature* **411**, 183–186.
- Burnham, K. P. & Anderson, D. R. 2002 *Model selection and multimodel inference*. New York: Springer.
- Burnham, K. P., Anderson, D. R. & White, G. C. 1987 Design and analysis methods for fish survival experiments based on release–recapture. *Am. Fish. Soc. Monogr.* **5**, 1–437.
- Caswell, H. 2001 *Matrix population models*. Sunderland, MA: Sinauer.
- Chastel, O., Weimerskirch, H. & Jouventin, P. 1995 Body condition and seabird reproductive performance: a study of three petrel species. *Ecology* **76**, 2240–2246.
- Cherel, Y., Bocher, P., Trouvé, C. & Weimerskirch, H. 2002 Diet and feeding ecology of blue petrels *Halobaena caerulea* at Iles Kerguelen, Southern Indian Ocean. *Mar. Ecol. Prog. Ser.* **228**, 283–299.
- Comiso, J. C., McClain, C. R., Sullivan, C. W., Ryan, J. P. & Leonard, C. L. 1993 Coastal zone color scanner pigment concentrations in the southern ocean and relationships to geophysical surface features. *J. Geophys. Res.* **98**, 2419–2451.
- Coulson, T., Catchpole, E. A., Albon, S. D., Morgan, B. J. T., Pemberton, J. M., Clutton-Brock, T. H., Crawley, M. J. & Grenfell, B. T. 2001 Age, sex, density, winter weather, and population crashes in Soay sheep. *Science* **292**, 1528–1531.
- Daly, K. L. & Smith, W. O. 1993 Physical–biological interactions influencing marine plankton production. *A. Rev. Ecol. Syst.* **24**, 555–585.
- Forchhammer, M. C., Stenseth, N. C., Post, E. & Langvatn, R. 1998 Population dynamics of Norwegian red deer: density-dependence and climatic variation. *Proc. R. Soc. Lond. B* **265**, 341–350. (DOI 10.1098/rspb.1998.0301.)
- Fretwell, S. D. 1972 *Populations in a seasonal environment*. Princeton University Press.
- Gauthier, G., Pradel, R., Menu, S. & Lebreton, J.-D. 2001 Seasonal survival of greater snow geese and effect of hunting under dependence in sighting probability. *Ecology* **82**, 3105–3119.
- Grenfell, B. T., Wilson, K., Finkenstadt, B. F., Coulson, T. N., Murray, S., Albon, S. D., Pemberton, J. M., Clutton-Brock, T. H. & Crawley, M. J. 1998 Noise and determinism in synchronised sheep dynamics. *Nature* **394**, 674–677.
- Guinet, C., Chastel, O., Koudil, M., Durbec, J.-P. & Jouventin, P. 1998 Effects of warm sea-surface temperature anomalies on the blue petrel at the Kerguelen Islands. *Proc. R. Soc. Lond. B* **265**, 1001–1006. (DOI 10.1098/rspb.1998.0390.)
- Houghton, J. T., Ding, Y., Griggs, D. J., Noguer, M., Van der Linden, P. J., Dai, X., Maskell, K. & Johnson, C. A. 2001 *Climate change 2001: the scientific basis*. Cambridge University Press.

- Jaksic, F. M. 2001 Ecological effects of El Niño in terrestrial ecosystems of western South America. *Ecography* **24**, 241–249.
- Lebreton, J.-D. & Clobert, J. 1991 Bird population dynamics, management, and conservation: the role of mathematical modelling. In *Bird population dynamics, management, and conservation: the role of mathematical modeling* (ed. C. M. Perrins, J.-D. Lebreton & G. J. M. Hirons), pp. 105–125. Oxford University Press.
- Lebreton, J.-D., Burnham, K. P., Clobert, J. & Anderson, D. R. 1992 Modelling survival and testing biological hypotheses using marked animals: a unified approach with case studies. *Ecol. Monogr.* **62**, 67–118.
- Leirs, H., Stenseth, N. C., Nichols, J. D., Hines, J. E., Verhagen, R. & Verheyen, W. 1997 Stochastic seasonality and nonlinear density-dependent factors regulate population size in an African rodent. *Nature* **389**, 176–180.
- Loison, A., Saether, B.-E., Jerstad, K. & Røstad, O. W. 2002 Disentangling the sources of variation in the survival of the European dipper. *J. Appl. Stat.* **29**, 289–304.
- McCarty, J. P. 2001 Ecological consequences of recent climate change. *Conserv. Biol.* **15**, 320–331.
- McPhaden, M. J. 1993 TOGA-TAO and the 1991–93 El Niño–Southern Oscillation event. *Oceanography* **6**, 36–44.
- Marinovic, B. B., Croll, D. A., Gong, N., Benson, S. R. & Chavez, F. P. 2002 Effects of the 1997–1999 El Niño and La Niña events on zooplankton abundance and euphausiid community composition within the Monterey Bay coastal upwelling system. *Progr. Oceanogr.* **54**, 265–277.
- Maynard Smith, J. & Slatkin, M. 1973 The stability of predator–prey systems. *Ecology* **54**, 384–391.
- Moore, J. K. & Abbott, M. R. 2000 Phytoplankton chlorophyll distribution and primary production in the Southern Ocean. *J. Geophys. Res.* **105**, 28 709–28 722.
- Pakhomov, E. A. & McQuaid, C. D. 1996 Distribution of surface zooplankton and seabirds across the Southern Ocean. *Polar Biol.* **16**, 271–286.
- Parkinson, C. L. & Cavalieri, D. J. 2002 A 21 year record of Arctic sea-ice extents and their regional, seasonal and monthly variability and trends. *Ann. Glaciol.* **34**, 441–446.
- Paulian, P. 1953 Pinnipèdes, cétacés, oiseaux des Iles Kerguelen et Amsterdam. *Mem. Inst. Scient. Madagascar* **8**, 111–234.
- Philander, S. G. 1990 *El Niño, La Niña, and the Southern Oscillation*. New York: Academic.
- Pradel, R. 1993 Flexibility in survival analysis from recapture data: handling trap-dependence. In *Marked individuals in the study of bird population* (ed. J.-D. Lebreton & P. M. North), pp. 29–37. Basel, Switzerland: Birkhäuser.
- Pradel, R. 1996 Utilization of capture–mark–recapture for the study of recruitment and population growth rate. *Biometrics* **52**, 703–709.
- Reynolds, R. W. & Smith, T. M. 1994 Improved global sea-surface temperature analyses. *J. Climate* **7**, 929–948.
- Saether, B.-E., Tufto, J., Engen, S., Jerstad, K., Røstad, O. W. & Skåtan, J. E. 2000 Population dynamical consequences of climate change for a small temperate songbird. *Science* **287**, 854–856.
- Sillett, T. S., Holmes, R. T. & Sherry, T. W. 2000 Impacts of a global climate cycle on population dynamics of a migratory songbird. *Science* **288**, 2040–2042.
- Skalski, J. R., Hoffmann, A. & Smith, S. G. 1993 Testing the significance of individual- and cohort-level covariates in animal survival studies. In *Marked individuals in the study of bird population* (ed. J.-D. Lebreton & P. M. North), pp. 9–28. Basel, Switzerland: Birkhäuser.
- Stenseth, N. C., Mysterud, A., Ottersen, G., Hurrell, J. W., Chan, K.-S. & Lima, M. 2002 Ecological effects of climate fluctuations. *Science* **297**, 1292–1296.
- Walther, G.-R., Post, E., Convey, P., Menzel, A., Parmesan, C., Beebee, T., Fromentin, J.-M., Hoegh-Guldberg, O. & Bairlein, F. 2002 Ecological responses to recent climate change. *Nature* **416**, 389–395.
- Warham, J. 1990 *The petrels: their ecology and breeding systems*. London: Academic.
- White, G. C. & Burnham, K. P. 1999 Program MARK: survival estimation from populations of marked animals. *Bird Study Suppl.* **1** **46**, S120–S139.
- White, G. C., Anderson, D. R., Burnham, K. P. & Otis, D. L. 1982 Capture–recapture and removal methods for sampling closed populations. Report LA-8787-NERP, Los Alamos, USA.
- White, W. B. & Peterson, R. G. 1996 An Antarctic circum-polar wave in surface pressure, wind, temperature and sea-ice extent. *Nature* **380**, 699–702.
- Xie, S.-P., Annamalai, H., Schott, F. A. & McCreary Jr, J. P. 2002 Structure and mechanisms of South Indian Ocean climate variability. *J. Climate* **15**, 864–878.