Global climate patterns explain range-wide synchronicity in survival of a migratory seabird

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Abstract

To predict the impact of climate change over the whole species distribution range, comparison of adult survival variations over large spatial scale is of primary concern for long-lived species populations that are particularly susceptible to decline if adult survival is reduced. In this study, we estimated and compared adult survival rates between 1989 and 1997 of six populations of Cory's shearwater (*Calonectris diomedea*) spread across 4600 km using capture–recapture models. We showed that mean annual adult survival rates are different among populations along a longitudinal gradient and between sexes. Variation in adult survival is synchronized among populations, with three distinct groups: (1) both females and males of Corsica, Tremiti, and Selvagem (annual survival range 0.88–0.96); (2) both females and males of Frioul and females from Crete (0.82–0.92); and (3) both females and males of Malta and males from Crete (0.74–0.88). The total variation accounted for by the common pattern of variation is on average 71%, suggesting strong environmental forcing. At least 61% of the variation in survival is explained by the Southern Oscillation Index fluctuations. We suggested that Atlantic hurricanes and storms during La Niña years may increase adult mortality for Cory's shearwater during winter months. For long-lived seabird species, variation in adult survival is buffered against environmental variability, although extreme climate conditions such as storms significantly affect adult survival. The effect of climate at large spatial scales on adult survival during the nonbreeding period may lead to synchronization of variation in adult survival over the species' range and has large effects on the meta-population trends. One can thus worry about the future of such long-lived seabirds species under the predictions of higher frequency of extreme large-scale climatic events.

Keywords: adult survival, capture–recapture models, climate, Cory's shearwater, Southern Oscillation, synchrony

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Introduction

The global climate is warming, with important consequences for animal and plant populations (Walther

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et al., 2002). Population changes are caused by variation in vital rates (demographic parameters), and many long-lived species have low population growth rates resulting from their life histories (small litter size, late recruitment, and high adult survival; Stearns, 1992). Population growth rates for long-lived species are strongly influenced by adult survival (Lebreton & Clobert, 1990). Adult survival may vary little, because

variability is selectively disadvantageous for long-lived iteroparous species, and the variability of vital rates that has greatest impact on the population growth rate should be low (i.e. environmental canalization process; Saether & Bakke, 2000; Gaillard & Yoccoz, 2003).

Adult survival of long-lived species is affected by climate variation (e.g. Jenouvrier et al., 2003). The effect of climate may vary within a year according to the life history of the species (e.g. breeding and wintering seasons; see Jenouvrier et al., 2005), and may depend on the severity of environmental change at these different times of the year. Extreme climate events may particularly reduce adult survival, ultimately causing the population to crash (e.g. emperor penguin *Aptenodytes forsteri*, Jenouvrier et al., 2005; barn owl *Tyto alba*, Altwegg et al., 2006).

Climate effects could be critical during the nonbreeding season for long-lived migratory species when individuals from a wide range of breeding populations migrate to a same area, because any reduction in adult survival will cause a decrease in the whole meta-population. Moreover, climatic influence during the nonbreeding season may cause synchrony in adult survival variability between breeding populations over a large spatial range (Harris et al., 2005; Schaub et al., 2005), and potentially increase the risk of species extinction (Royama, 1992). Therefore, comparison of adult survival variations over a wide spatial range is of primary concern to study the influence of climate on populations, and hence predict the impact of climate changes over the whole species distribution range.

Comparative studies focusing on variation in the vital rates within a species and covering a substantial part of the species' range are very rare (Frederiksen et al., 2005). Most of the comparative studies to date compare previously published data (e.g. Frederiksen et al., 2005). Few species are studied at the individual level with capture–recapture in population across their geographical range, to provide a rigorous joint analysis of original data from all sites (but see Harris et al., 2005). Here, we compared the variation of adult survival of a procellariiform seabird (i.e. petrel), the Cory's shearwater (*Calonectris diomedea*), over a substantial range of its distribution. We estimated adult survival with a joint analysis from the original capture–recapture data for six breeding populations over 4600 km apart during 9 years.

Adult survival of several petrel species is affected by climate variability (e.g. Jenouvrier et al., 2003), and also other factors that may interact with the effect of climate variability, such as sex (e.g. Jenouvrier et al., 2005), density dependence (Barbraud & Weimerskirch, 2003), and fisheries (Rolland et al., 2008). For Cory's shearwater, several potential nonexclusive factors may affect adult survival, including physical factors (e.g. large climatic oscillation; Brichetti et al., 2000), biological factors related to the environment (e.g. oceanographic productivity), factors specific to the species (e.g. sex, body size, and migration pattern), and finally human factors (harvesting and fisheries bycatch). Because seabird activity varies with season, these different factors may act at different spatial scales and time periods within a year. We first compared the average Cory's shearwater annual adult survival between the six populations and between sexes. The Cory's shearwater is sexually dimorphic (Ristow & Wink, 1980) and differences between sexes are thus expected. Moreover, we expect a longitudinal gradient in adult survival due to geographical variation in ocean productivity (Margalef, 1985; Caddy et al., 1995; Freudenthal et al., 2002), body size (Rabouam et al., 1998), and migration patterns (Ristow et al., 2000). Human impacts on adult survival also differed between the breeding sites; Cory's shearwater is harvested in the Sicily channel and is commonly fisheries bycatch in the Mediterranean (Belda & Sánchez, 2001).

Secondly, we studied temporal variability in adult survival. During the breeding season, the potential factors affecting survival involve specific local processes. Because the six breeding populations studied here are spread over 4600 km, we expect differences in temporal variation among populations if environmental conditions affect survival mainly during the breeding season. During the nonbreeding season, seabirds have a widespread distribution across vast oceanic ranges and can simply select a different area with better climate or trophic conditions (Harris et al., 2005). Therefore, during the nonbreeding season, factors affecting adult survival variations are likely extreme events occurring at large spatial scales. Such events have the potential to result in synchrony in time series of adult survival (Schaub et al., 2005). Moreover, we expect little variability in adult survival under the environmental canalization hypothesis (Saether & Bakke, 2000; Gaillard & Yoccoz, 2003), although it would be surprising if adverse climate and trophic conditions did not affect survival at all. For instance, many seabird wrecks (i.e. large numbers of seabirds washing ashore) appear to be related to periods of stormy weather (Hudson, 1985).

Finally, we studied the potential influence of large-scale climate oscillations on temporal adult survival variations. Causal relationships between adult survival and large-scale climatic phenomena are not easily identified (Sandvik et al., 2005), although large-scale climatic oscillations are remarkably good predictors of ecological responses to climate (Hallett et al., 2004). Large-scale climatic oscillations are defined as temporal

fluctuations of pressure anomalies, and are treated as a 'proxy' for different climatic processes (Stenseth *et al.*, 2003). Large-scale climatic oscillations affect the local climate and oceanographic constraints (Ottersen *et al.*, 2001) and thus may affect adult survival of long-lived species directly by increasing mortality during extreme environmental events (e.g. Brichetti *et al.*, 2000), or indirectly through its effect on the abundance and distribution of prey (e.g. Sandvik *et al.*, 2005). We tested whether variability in adult survival is driven by large-scale climatic processes through direct or indirect effects. Atlantic hurricanes and storms during La Niña years of the Southern Oscillation (SO) may affect directly adult survivorship by increasing the mortality of migrating birds (Brichetti *et al.*, 2000). The North Atlantic Oscillation (NAO) may affect indirectly adult survivorship by its effect on the food web (Stenseth *et al.*, 2004).

Material and methods

Study species and sites

Cory's shearwaters are typical long-lived seabirds, with low fecundity (a single egg is laid per year), low first-year survival (Jenouvrier *et al.*, 2008), and delayed sexual maturity (see review in Thibault *et al.*, 1997; Mougin *et al.*, 2000; Jenouvrier *et al.*, 2008). The Cory's shearwater is sexually dimorphic (Ristow & Wink, 1980), and there are sex differences in vocalizations (Bretagnolle & Lequette, 1990). They forage at sea and feed on fish, molluscs, and offal (Sarà, 1993). They breed on islands and cliffs from the end of February to mid-October. Data on their wintering range are scarce, but observations suggest that the wintering area is very large and encompasses the entire Atlantic, potentially reaching the Indian Ocean (Thibault *et al.*, 1997). Birds from Atlantic populations seem to winter more westward in the Atlantic than those from the Mediterranean (Ristow *et al.*, 2000), although they are both observed in similar areas in different abundances (Camphuysen & Van Der Meer, 2001).

Studies were carried out on six breeding populations of Cory's shearwater on six islands from the eastern Atlantic to the eastern Mediterranean (Fig. 1). At the western and eastern edges of the Cory's shearwater breeding distribution range, the population number at Selvagem Island is the highest (30 000 birds) and at Crete the lowest (500–700 birds).

Data collection

In each population, birds were caught in their burrows or at the burrow's entrance and ringed. In subsequent
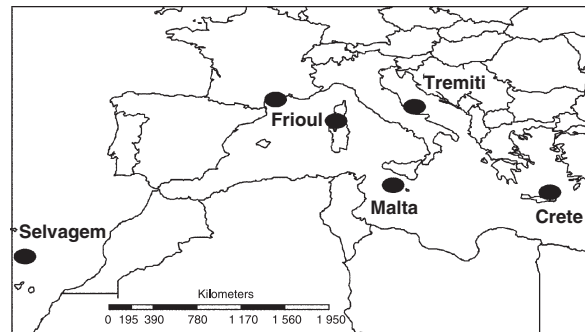

Fig. 1 Map of the study sites of the six studied populations of Cory's shearwater.

years, they were recaptured intensively in annually visited plots. The period of capture–recapture differed among population, because the present comparison was not intended when the authors independently started their fieldwork.

Birds were sexed on the basis of voice, bill measurements (length and height), or the sex of their breeding partner. Cory's shearwater body size decreases gradually eastward from the Atlantic to the Mediterranean (Thibault *et al.*, 1997; Rabouam *et al.*, 1998). Weight is used as a proxy of body size, although weight variations are influenced by stomach contents and fat stores, and thus showed important variations within a population.

Environmental variables

We tested the effect of Southern Oscillation Index (SOI available at http://www.cru.uea.ac.uk/cru/data/soi.htm) and the NAO (http://www.cgd.ucar.edu/cas/jhurrell/indices.html) on adult survival of Cory's shearwater. The SO is a large-scale oscillation in atmospheric mass between the southeastern (Darwin) and southwestern (Tahiti) Pacific waters, and the NAO between the subtropical high (Azores) and the polar low (Iceland). We used the annual indices averaged over the entire year for SOI, because previous time series analysis detected strong annual variation and no significant seasonal variability in the SOI fluctuations (unpublished results), and over winter for the NAO (Stenseth *et al.*, 2004).

The effect of the SO is most pronounced in the southeastern Pacific Ocean, although other marine ecosystems are also affected, such as the Southern Atlantic (e.g. Duffy, 1990) where Cory's shearwaters spend the winter. Sustained negative values of the SOI indicate El Niño episodes, while positive values indicate La Niña episodes. La Niña episodes favor tropical storms and

hurricanes in the Atlantic that likely influence the survivorship of Cory's shearwaters by causing increased heat loss, displacing birds to areas with less food, or making foraging more difficult because common fish prey species move deeper into the water column (Brichetti et al., 2000).

The NAO may affect seabird mortality directly (wind) and/or indirectly (prey availability), although several studies suggest that these effects are indirect rather than direct (Harris et al., 2005; Sandvik et al., 2005). In our case, because birds wintered in the Southern Atlantic and the equatorial zone, a direct effect of the NAO on mortality is not expected because the storms occur in the North Atlantic Ocean. NAO may affect seabird mortality during the breeding season through its lagged effects on the abundance of lower trophic level species (e.g. phytoplankton, zooplankton, and fish; Stenseth et al., 2004). Because Cory's shearwaters forage on lower trophic species with short life cycle, lags are expected to be seasonal rather than yearly. Therefore, we assumed a lag of one season, and we used the NAO during winter to test its effect on adult survival during the following breeding season.

Data analysis and modeling

The analysis is based on capture–recapture histories of birds of unknown age when ringed, and recaptured in the subsequent years as breeders from populations where the same burrows have been checked each year. Datasets differed in length, and the analysis was restricted to the common period from 1989 to 1997.

We used capture–mark–recapture (CMR; Lebreton et al., 1992) models to estimate adult annual survival rates. CMR models distinguish survival (noted Φ), defined as the probability that a shearwater alive at year t survives at year $t + 1$, and recapture probabilities (noted P), defined as the probability that a shearwater alive at year t is caught during the breeding season of year t. The Cormack–Jolly–Seber model (CJS) is noted Φ_t, P_t, where both survival and capture probabilities varied freely over time, denoted t.

Two classical sources of lack of fit in capture–recapture studies arise from transient and trap dependence effects. The transient effect arises with birds that disperse from the study population in spite of breeding, or birds that breed in an inaccessible crevice nearby in future years (Tavecchia et al., 2001). Trap dependence and especially trap happiness (a bird seen in year t is much more likely to be seen in year $t + 1$ than a bird not seen in year t) is common in seabird capture–recapture

data because most of the seabirds are extremely faithful to their breeding colony (Jenouvrier et al., 2005). To detect transient and trap-dependent effects, goodness-of-fit (GOF) tests for the CJS model were computed for each location and sex (see Table A1) using the program U-Care (Choquet et al., 2005). Overall, there were large discrepancies between study sites and sex. Trap happiness (denoted by m) is detected for males in Corsica and females in Crete, and the trap dependence models (Φ_t, $P_{t \cdot m}$) fit the data ($P = 0.13$ and 0.85, respectively). A transient effect is detected only for Selvagem birds for both sexes and is denoted by $a2$ for two classes of apparent 'age' (i.e. time elapsed since marking). The transient model ($\Phi_{t \cdot a2}$, P_t) fits the data ($P = 0.84$ and 0.23 for females and males, respectively).

The umbrella (i.e. most general) model is thus ($\Phi_{t \cdot s}$ Corsica, Crete, Frioul, Malta, Tremiti $\Phi_{t \cdot s \cdot a2}$ Selvagem, $P_{t \cdot \male}$ Corsica, $\female$ Crete, $P_{t \cdot s}$ Frioul, Malta, Tremiti, Selvagem $P_{t \cdot m}$ $\female$ Corsica, $\male$ Crete), and its construction is detailed in the Appendix (see also Gimenez et al., 2003 for model development, and Frederiksen et al., 2004 and Crespin et al., 2006 for applications to other species). From the umbrella model, simpler models are fitted successively and Akaike's information criterion corrected for small sample size (AIC$_c$; see Anderson & Burnham, 1999) is used for model comparison. The best model is the one with the lowest AIC$_c$, [i.e. the most parsimonious model in terms of the number of parameters and data fit (model deviance)]. These analyses were run in the program M-SURGE (Choquet et al., 2004). To enable identification of biological processes responsible for variation in survival rates, the total variance was decomposed into sampling variance and process variance (Gould & Nichols, 1998), and the process variance was estimated with program MARK (White & Burnham, 1999). To compare process variance among the populations, the process variance was calculated relative to the maximum possible variance (Morris & Doak, 2004).

The similarity of temporal variability in survival was calculated between all possible pairs among the six populations (Harris et al., 2005; and Table A2). The tests of covariate effects are based on an analysis analogous to analysis of variance called ANODEV (Table A2). Under H_0, the covariate did not explain any of the survival variance. To assess the effects of covariates, the amount of variation in survival accounted for by covariates (R^2) was estimated according to the model's deviance (Table A2; Gaillard et al., 1997), or the process variance [calculated as $(\sigma^2 - \sigma^2_{res})/\sigma^2$, where σ^2 refers to the total process variance and σ^2_{res} to estimated residual variance when the effects of covariate are accounted for; see Loison et al., 2002].

Table 1 Modeling (a) capture and (b) survival probabilities for Cory's shearwater

Question	Model name	k	Dev	ΔAIC_c
(a)				
Umbrella model	$\Phi_{t \cdot s}$ Corsica, Crete, Frioul, Malta, Tremiti	207	7197	33
	$\Phi_{t \cdot s \cdot a2}$ Selvagem,			
	$P_{t\ \male}$ Corsica, $\female$ Crete, $P_{t \cdot s}$ Frioul, Malta,			
	Tremiti, Selvagem			
	$P_{t \cdot m\ \female}$ Corsica, $\male$Crete			
1. Trap dependence effect?	$P_{t \cdot s}$ Corsica, Crete, Frioul, Malta,	193	7247	55
	Tremiti, Selvagem			
2. Additive trap dependence effect?	$P_{t \cdot s\ \male}$ Corsica, $\female$ Crete, Frioul, Malta,	197	7219	35
	Tremiti, Selvagem			
	$P_{t + m\ \female}$ Corsica, $\male$Crete			
3. Additive sex effect?	$P_{t + s}$ Frioul, Malta, Tremiti, Selvagem	161	7261	5
	$P_{t + s + m}$ Corsica, Crete			
4. Sex effect according to different study sites?	P_t Frioul, Malta, Tremiti, Selvagem	157	7279	15
	$P_{t + s + m}$ Corsica, Crete			
For sake of simplicity, we did not show the	P_t Malta, Tremiti, Selvagem	158	7262	0
test for each study site	$P_{t + s}$ Frioul			
	$P_{t + s + m}$ Corsica, Crete			
5. Additive time effect?	$P_{t + (}$Malta, Tremiti, Selvagem, $+ s$ Frioul,	123	7737	405
	$s + m$ Corsica, Crete)			
6. Time effect?	$P_{.}$ Malta, Tremiti, Selvagem	120	7716	378
	P_s Frioul			
	$P_{s + m}$ Corsica, Crete			
(b)				
Umbrella model	$\Phi_{t \cdot s}$ Corsica, Crete, Frioul, Malta, Tremiti	158	7262	72
	$\Phi_{a2 \cdot t \cdot s}$ Selvagem			
	P_t Malta, Tremiti, Selvagem			
	$P_{t + s}$ Frioul			
	$P_{t + s + m}$ Corsica, Crete			
1. Transient effect?	$\Phi_{t \cdot s}$ Corsica, Crete, Frioul, Malta, Tremiti, Selvagem	145	7302	86
2. Additive transient effect?	$\Phi_{t \cdot s}$ Corsica, Crete, Frioul, Malta, Tremiti	148	7273	63
	$\Phi_{(a2 + t) \cdot s}$ Selvagem			
3. Additive sex effect?	$\Phi_{t + s}$ Corsica, Crete, Frioul, Malta, Tremiti	109	7312	24
	$\Phi_{a2 + t + s}$ Selvagem			
4. Sex effect according to different study sites?	Φ_t Corsica, Crete, Frioul, Malta, Tremiti	98	7322	12
	$\Phi_{a2 + t}$ Selvagem			
For sake of simplicity, we did not show the	Φ_t Corsica, Frioul, Malta, Tremiti	101	7315	11
test for each study site	$\Phi_{t + s}$ Crete			
	$\Phi_{a2 + t}$ Selvagem			
5. Additive time effect?	$\Phi_{t + (}$Corsica, Frioul, Malta, Tremiti, $s +$ Crete,	68	7377	7
	$a2 +$ Selvagem)			
6. Time effect according to different study sites?	$\Phi_{t +}$ {1.(Corsica, Tremiti, $a2$ Selvagem);	**64**	**7378**	**0**
	2. (Crete $\female$, Frioul);			
	3.(Crete $\male$, Malta)			
All the possible combinations of study sites are not	$\Phi_{.}$ {1.(Corsica, Tremiti, $a2$ Selvagem),	57	7413	21
showed here for sake of simplicity	2. (Crete $\female$, Frioul,)			
	3. (Crete $\male$, Malta)}			

Akaike's information criterion corrected for small sample size (AIC_c) is used for model comparison, and for the identification of the best model (lowest AIC_c). ΔAIC_c is the difference of AIC between the specified model and the best one (i.e. $\Delta AIC_c = 0$ for the best model) in each table. k refers to the number of parameters estimated and Dev to the deviance of the model. The CJS model is $\Phi_t P_t$, with the survival probability (Φ) and capture probability (P) varying with time (t). An effect of sex on survival or capture rate is denoted by s, the letter m denotes apparent 'trap happiness' on recapture rates, and a transient effect on adult survival is denoted by $a2$ (see 'Material and methods' for more details).

Table 2 Effect of longitude and body size on adult survival variation of the six studied populations of Cory's Shearwater

Models	Dev	k	Slope	ICL	ICH	ANODEV $F_{(1,11)}$	P-value	R^2 σDev
Sex × study sites	7431.1	65						
Longitude	7455.3	55	−0.0015	−0.023	−0.006	5.7	0.04	30–34
Body size	7465.8	55	0.0730	−0.027	0.173			
Constant	7467.9	54						

Dev is the deviance, k the number of parameters estimated, while IC refers to the 95% confidence intervals of the slope. To assess the effect of covariates, we determined whether the slope of the relationship between adult survival and the environmental variable was significant (i.e. does 0 belong to the confidence interval of the slope estimate?). If the slope is significant, we thus used the ANODEV to test for the covariate effect. The threshold P-value used for ANODEV was 0.05. We estimated the proportion of explained temporal variation in adult survival accounted by covariates (R^2) based on the process variance (σ), and based on the deviance, respectively.

Results

Recapture rates

The most parsimonious model constrained detection probabilities to vary between years with additive trap happiness for males in Corsica and females in Crete, and with differences between sexes in the localities of Frioul, Corsica, and Crete (Table 1a). Recapture rates were highly divergent across study sites (Fig. 2a), and this is due to the differences in sampling schemes of the monitoring programs. For example, on Lavezzi capture–recapture efforts occurred during the prelaying stage when females visit their nests irregularly, whereas males visit them nearly every night. This favored the capture of males vs. females.

Adult survival

The mean annual adult survival rate of Cory's shearwater was 0.90 and the relative process variance (i.e. process variance taken relative to the maximum possible variance) is 0.0049. Mean annual adult survival ranges from 0.83 ± 0.0016 (mean ± relative process variance) for both sexes in Malta to 0.95 ± 0.009 for females from Selvagem (Fig. 3a). There is evidence of a longitudinal gradient among the population (ANODEV, P = 0.04; Table 2, Fig. 3a), with 34% of the variation among population explained by a longitudinal gradient. There is no evidence of a body mass effect on adult survival (ANODEV, P = 0.43; Table 2), although there is a tendency for larger birds to have higher survival rates (Fig. 3b).

The most parsimonious model constrained adult survival to vary synchronously between localities, with differences between sexes in Crete and a transient effect in Selvagem (Table 1b). Adult survival probabilities were not dissimilar between the following groups: (1) both females and males from Selvagem, Corsica, Tremiti; (2) both females and males from Frioul and

females from Crete; and (3) both females and males from Malta and males from Crete (Fig. 2b). Adult survival probabilities varied from year to year between (1) 0.88 and 0.96, (2) 0.82 and 0.92, and (3) between 0.74 and 0.88. Lower survival rates occurred in 1990 and 1995; if these values are excluded, the relative process variance relative is reduced by 82% (0.09). The fraction of variability accounted for by the common patterns among possible pairs of localities ranges from 37% for Frioul/Crete to 92% for Tremiti/Malta, and is overall very high (average 71%) (Table 3). The temporal adult survival variations are affected by SOI (ANODEV, P < 0.0001; Table 4, Fig. 3c), but not by NAO (Table 4). The proportion of explained variation in survival by SOI was high (92% based on deviance and 62% based on the process variance).

Discussion

Our results showed that temporal variations in Cory's shearwater adult survival from six breeding populations were synchronized over a wide range of the species' distribution between 1989 and 1997. Adult survival varied between 0.88 and 0.96 for birds breeding in Selvagem, Corsica, and Tremiti Islands; 0.82 and 0.92 for females breeding in Crete and birds from Frioul Island; and between 0.74 and 0.88 for males breeding in Crete and birds from Malta.

Adult survival varied little from year to year, except during 1990 and 1995, where it decreased strongly. As expected for a long-lived species such as the Cory's shearwater, the interannual adult survival variations are small because of the effect of environmental canalization (Saether & Bakke, 2000; Gaillard & Yoccoz, 2003). If the 1990 and 1995 lower adult survival years are removed, the process variance of adult survival drops by 82%. These results suggest that extreme events might be a likely factor affecting adult survival of Cory's shearwater.
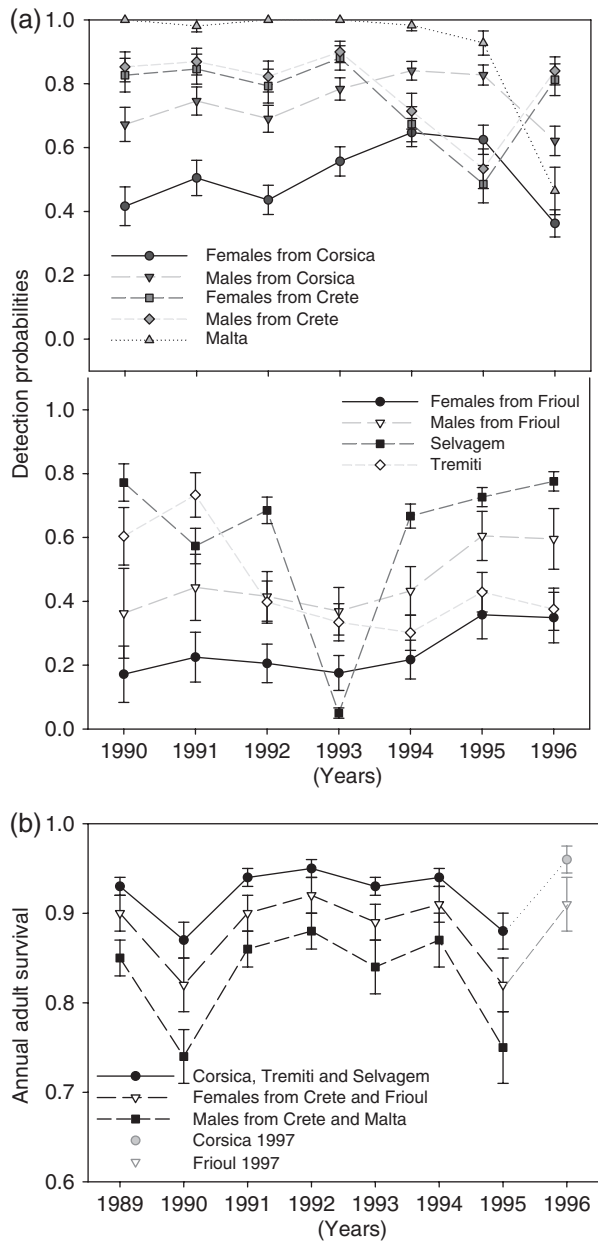
Fig. 2 (a) Capture probabilities and (b) survival rates according to study sites. Estimates ± standard errors were computed from the best model $\Phi_{t\,+\,\{1.(Corsica,\,Tremiti,\,a2\,Selvagem);\,2.(Crete\,\female,\,Frioul);\,3.(Crete\,\male,\,Malta)\}}\,P_{t}$ Malta, Tremiti, Selvagem $P_{t\,+\,s}$ Frioul $P_{t\,+\,s\,+\,m}$ Corsica, Crete. Because trap-dependent models have severe identifiability problems (Pradel, 1993), we showed the estimates of adult survival from Corsica and Frioul in 1996, computed by another analysis over the entire period of the study (unpublished results). The estimates ± standard errors were computed from the best model $\Phi_{t}\,P_{t\,+\,s\,+\,m}$ and $\Phi_{t}P_{t\,+\,s}$ for Corsica between 1978 and 2004 and Frioul between 1981and 2004, respectively. For the sake of visibility, we represented the variability in detection probabilities in two panels.
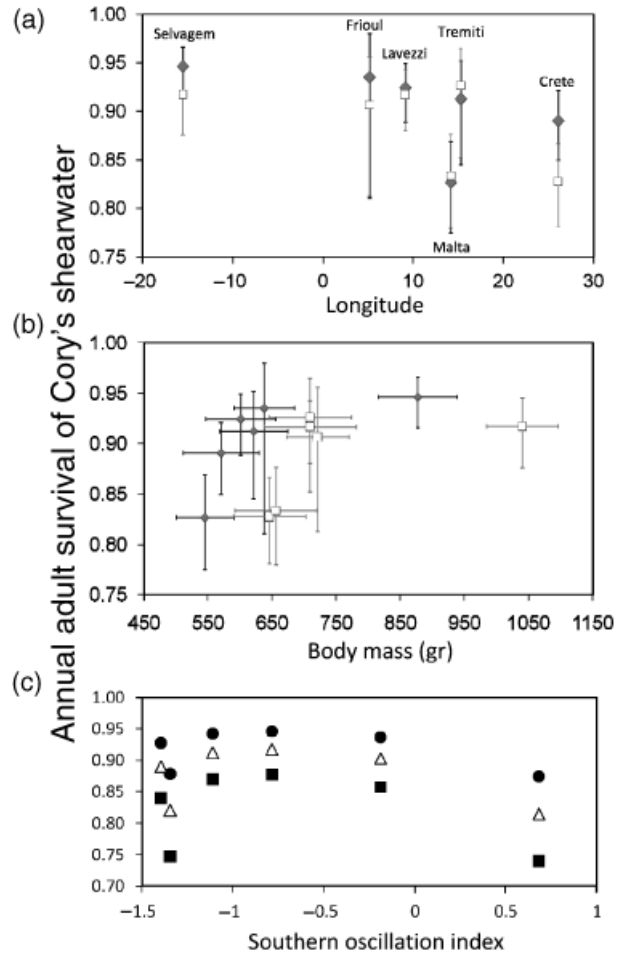

Fig. 3 Cory's shearwater mean adult survival rate for both sexes and across studies sites as a function of (a) longitude and (b) body mass. Gray diamonds represent females and black squares represent males. Estimates ± standard errors are computed from the model $\Phi_{(Crete,\,Corsica,\,Frioul,\,Malta,\,Tremiti,\,a2\,Selvagem)\,\cdot\,s}$. (c) Temporal variations in Cory's shearwater adult survival rate between 1989 and 1997 as a function of the Southern Oscillation Index for the three groups (1) both females and males from Selvagem, Corsica, Tremiti (black circles), (2) both females and males from Frioul and females from Crete (triangles), and (3) both females and males from Malta and males from Crete (black squares). Estimates ± standard errors are computed from the best model $\Phi_{t\,+\,1.(Corsica,\,Tremiti,\,a2\,Selvagem);\,2.(Crete\,\female,\,Frioul);\,3.(Crete\,\male,\,Malta)}$.

Synchronicity explains on average 71% of adult temporal variations. Spatial synchronization of annual survival rates might be caused by the effect of environmental conditions during the nonbreeding season, when migratory seabirds originating from different breeding populations congregate in similar areas (Schaub *et al.*, 2005). Cory's shearwaters appeared to

migrate to a widespread range in the South Atlantic, with birds breeding in the Atlantic (Selvagem) wintering more westward than those breeding in the Mediterranean (Ristow *et al.*, 2000). The widespread distribution during winter over a vast oceanic range allows seabirds to leave an area with adverse weather or trophic conditions (Harris *et al.*, 2005), and extreme environmental events occurring at large spatial scale may be a likely factor affecting adult survival. Wrecks of large numbers of seabirds, including Cory's shearwaters, have been recorded related to autumn and northern-winter storms in the course of migration and wintering area of Cory's shearwater (Brichetti *et al.*, 2000).

Our results support the hypothesis that extreme events due to large-scale climate oscillations occurred during the nonbreeding season and influenced Cory's shearwater adult survival. The SOI appears to be an important source for the temporal variation of Cory's shearwater adult survival, whereas the NAO has no effect. The NAO affects the North Atlantic and Mediterranean climate where the breeding populations are located, whereas the effect of the SO is expected only during the nonbreeding season when the birds migrate southward in the Atlantic. Adult survival is negatively affected by the SOI (positive SOI values indicated La Niña years), with at least 62% of the variation in survival explained by SOI fluctuations. During La Niña years, the greater number of Atlantic hurricanes and storms may cause a decrease in adult

survival for Cory's shearwater. Wrecks of pelagic seabirds following hurricanes and storms generally tend to be dominated by juvenile birds rather than adults. Therefore, the effect of storms during La Niña suggested here for adults will likely affect juvenile survival even more.

Our results showed that large-scale climate forces affect and synchronize the adult survival of wide-ranging migratory bird over its entire range. The consequences of this result in terms of population dynamics depend on complex demographic processes (e.g. fecundity, recruitment, immigration, density dependence, and so on) and require modeling the meta-population, which is beyond the scope of this study. However, we speculate that the spatial synchronization of annual survival variations may unlikely translate into the spatial synchronization of interannual fluctuations in populations. Indeed, for long-lived species, Saether & Bakke (2000) suggested that variation in fecundity and recruitment contributes more to the population fluctuations than variations in adult survival. Spatial synchronization of fecundity and recruitment variability is unlikely for seabirds because the potential factors affecting them (e.g. ocean productivity around the breeding site, habitat quality, predation, etc.) may differ significantly among geographically distinct populations. Nevertheless, the synchronized reduction in adult survival for all populations during extreme climate events may likely have a direct consequence on the meta-population, because long-lived species population growth rate is very sensitive to adult survival. Ultimately, it will result in higher species extinction risk, especially if extreme climate events become more frequent.

Our results also highlight that mean adult survival rates differed between populations and between sexes for birds breeding in Crete. A longitudinal gradient explains 34% of the variance observed among mean adult survival. Adult survival is higher for birds breeding in the Atlantic (mean ± relative process variance: 0.95 ± 0.03 for females, 0.93 ± 0.04 for males in Selvagem) than in the eastern part (0.89 ± 0.03 for females, 0.83 ± 0.03 for males in Crete). Several

Table 3 Covariation among study sites time series from 1989 to 1997

	Selvagem	Frioul	Lavezzi	Malta	Tremiti	Crete
Selvagem		58	77	88	90	51
Frioul			74	60	88	37
Lavezzi				46	79	87
Malta					92	51
Tremiti						86
Crete						

Fraction of variation explained by a common pattern between study sites time series (%).

Table 4 Effect of SOI and NAO on adult survival variation of the six studied populations of Cory's shearwater

Models	Deviance	k	Slope	ICL	ICH	ANODEV $F(1,7)$	p_{ANODEV}	R^2 σ-deviance (%)
Time	7378.1	64						
SOI	7408.2	58	−0.22	−0.41	−0.04	78.7	<0.0001	62–92
NAO	7713.1	58	−0.09	−0.47	0.29			
Constant	7746.7	57						

See Table 3 for legend. The threshold *P*-value used for ANODEV is 0.05 and a Bonferroni correction for two tests is applied.
SOI, Southern Oscillation Index; NAO, North Atlantic Oscillation.

nonexclusive factors potentially explain this observed longitudinal gradient, including oceanographic constraints around the breeding populations, body size, and human impacts.

Oceanographic productivity around the breeding populations decreases eastward. The eastern Mediterranean is a nutrient-poor region with low productivity (Caddy *et al.*, 1995). In the Western Mediterranean, productivity is enhanced by cooler water from large rivers and currents from Atlantic along North Africa coasts (Margalef, 1985; Caddy *et al.*, 1995). Between Morocco and Selvagem Islands in the Atlantic, productivity is enhanced by strong upwelling with colder and richer waters (Freudenthal *et al.*, 2002).

Previous studies showed a longitudinal gradient in body size, with larger birds in the Atlantic than in the eastern Mediterranean (Rabouam *et al.*, 1998). This is probably a result of the selective pressure in relation to the observed water productivity gradient. Our analysis does not support an effect of body mass on Cory's shearwater. However, body weight had been collected at random, and the random weight of an individual varies by 15% within days whereas the weight distribution of a population shows a much smaller standard deviation (Ristow & Wink, 1980). To study the influence of body size on adult survival, the quality of the data should be improved in future studies by taking weights only at the end of the prelaying period to minimize the variation in weight among individuals, or by using measurements of skeletal features of birds.

Harvesting of Cory's shearwater and incidental bycatch by longline fisheries may also influence adult survival, with contrasting effects between the Atlantic and Mediterranean. Sixty-six percent of the birds killed as incidental bycatch are mainly adult Cory's shearwaters around Columbretes Islands in the Western Mediterranean (Belda & Sánchez, 2001). Interaction with fisheries varies depending on location (Cooper *et al.*, 2003), but more information is needed to quantify the impact of longline fisheries on Cory's shearwater mortality. The practice of harvesting of birds has sharply declined among most Mediterranean populations since the 1970s, with the exception of the Sicily channel where birds are killed illegally by fishermen in Malta (Borg & Cachia-Zammit, 1998). Birds breeding in Malta showed the lowest adult survival (0.827 ± 0.03 for females, 0.833 ± 0.03 for males), highlighting the effects of human harvesting.

Conclusion

Despite uncertainties over causal mechanisms, these findings add to the body of evidence that large-scale climate variations could affect seabird adult survival over large spatial scales. We argue here that for long-lived seabird species, adult survival is buffered against regular environmental variability. Extreme climate conditions, such as storms, significantly affect adult survival at large spatial scales during the nonbreeding period. Whatever the exact causes may be, the effects of large-scale climatic processes are dramatic for species with high adult survival and low fecundity, because even minimal reductions in survival have large effects on population trends. Moreover, we showed here that variation in adult survival was synchronized over the entire distribution of the Cory' shearwater, resulting in reduced persistence of meta-populations. The future of such long-lived seabirds species has the potential to be dire under future global changes, especially because there are predictions of higher frequency extreme large-scale climatic events, such as El Niño/La Niña events.

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Appendix A: Goodness of fit test and model

Goodness-of-fit tests

Table A1 Results of goodness-of-fit (GOF) tests of CJS model (Φ_t, P_t), for each location and sex

| | | | Test | | | | | | | | GOF test for the umbrella model with . . . | | | | | | | | | |
| | | | 3SR | | | 3SM | | | 2CT | | | 2CL | | | TraP dePendence | | | Transients | | | None (CJS model) | | | |
Location		df	χ^2	P	df	χ^2	P	df	χ^2	P	df	χ^2	P	df	χ^2	P	df	χ^2	P	df	χ^2	P	Chosen model
CORSICA	♀	7	2.2	0.949	7	18.3	**0.011**	6	7.7	0.259	6	5.8	0.444	20	26.3	0.156	19	31.8	**0.033**	26	34.0	0.134	$\Phi_t\, P_t$
	♂	6	8.5	0.206	7	9.7	0.204	6	27.0	**0.000**	5	6.7	0.242	18	24.9	0.127	18	43.5	**0.001**	24	52.0	**0.001**	$\Phi_t\, P_{t\cdot m}$
CRETE	♀	7	2.4	0.937	6	7.7	0.265	6	22.7	**0.001**	5	2.0	0.846	18	12.0	0.845	17	32.4	**0.013**	24	34.8	0.072	$\Phi_t\, P_{t\cdot m}$
	♂	6	3.6	0.728	6	0.8	0.993	6	3.2	0.787	3	3.4	0.334	15	7.8	0.932	15	7.3	0.948	21	11.0	0.964	$\Phi_t\, P_t$
MALTA	♀	6	4.3	0.631	2	0.5	0.775							8	4.9	0.773	2	0.5	0.775	8	4.9	0.773	$\Phi_t\, P_t$
	♂	6	8.3	0.220	3	2.8	0.430	1	1.2	0.271				9	11.0	0.274	4	4.0	0.410	10	12.2	0.270	$\Phi_t\, P_t$
FRIOUL	♀	5	6.4	0.267				6	7.5	0.274	5	2.2	0.818	10	8.7	0.566	11	9.8	0.552	16	16.2	0.440	$\Phi_t\, P_t$
	♂	7	4.8	0.681	6	7.7	0.262	6	5.2	0.520	5	4.1	0.534	18	16.6	0.549	17	17.0	0.455	24	21.8	0.590	$\Phi_t\, P_t$
SELVAGE	♀	7	22.3	**0.002**	7	5.5	0.599	6	4.0	0.677	5	2.7	0.746	19	30.5	**0.046**	18	12.2	0.837	25	34.5	**0.098**	$\Phi_{a2\cdot t}\, P_t$
	♂	6	17.5	**0.008**	6	10.8	0.096	6	4.8	0.564	5	5.3	0.379	17	33.6	**0.009**	17	20.9	0.230	23	38.4	**0.023**	$\Phi_{a2\cdot t}\, P_t$
TREMITI	♀	5	2.5	0.783	5	6.2	0.284	6	7.1	0.310	6	3.0	0.809	16	11.7	0.764	17	16.4	0.498	22	18.8	0.656	$\Phi_t\, P_t$
	♂	6	7.9	0.243	5	6.8	0.233	6	3.1	0.801	5	7.9	0.161	16	22.7	0.122	16	17.8	0.335	22	25.8	0.262	$\Phi_t\, P_t$

When the specific tests for transients or trap-happiness were significant, we tested the GOF of the more general model ($\Phi_{t\cdot a2}$, P_t) or (Φ_t, $P_{t\cdot m}$). For each study locality, we first assessed the fit of the most general model ($\Phi_{t\cdot s}$, $P_{t\cdot s}$) with both survival and recapture rate varying among years and sexes, using TEST2 and TEST3. TEST 2 examines the independence between year of last release and year of next recapture. TEST 3 checks the homogeneity of resighting histories at any release time (Burnham *et al.*, 1987). In cases when model ($\Phi_{t\cdot s}$, $P_{t\cdot s}$) did not fit the data, we used the sum of TEST 2 + TEST 3SM to assess the goodness of fit (GOF) of model that take into account 'transients' ($\Phi_{t\cdot s\cdot a2}$, $P_{t\cdot s}$) and the sum of TEST 3 + TEST 2CL to assess the goodness of fit of model that consider 'trap dependence' ($\Phi_{t\cdot s}$, $P_{t\cdot s\cdot m}$) (see Pradel, 1993). Empty boxes refer to cases when there were not sufficient data to compute GOF test, and significant tests appear in bold.

Model development

Gimenez *et al.* (2003) showed that a model taking into account both the effects of trap dependence on detection probabilities and transience on survival probabilities could be written in a multi-state framework as:

$$
\Phi_t = \begin{matrix} & \text{Seen at } t & \text{Not seen at } t \\ \text{Seen before} & \begin{pmatrix} \Phi_{a2 \cdot t} P_t & \Phi_{a2 \cdot t}(1 - P_t) \\ \Phi_{a2 \cdot t} P_t^* & \Phi_{a2 \cdot t}(1 - P_t^*) \end{pmatrix} \\ \text{Not seen before} & \end{matrix}
$$

$$
P_t = \begin{matrix} \text{Seen before} & \\ & \begin{pmatrix} 1 \\ 0 \end{pmatrix} \\ \text{Not seen before} & \end{matrix}
$$

Where P_t and P_t^* are the capture probabilities at time t for an individual caught at the previous occasion or not, respectively; Φ_t is the survival probabilities between time t and $t + 1$. Trap happiness stands for $P_t > P_t^*$. To include transient effects, we took into account an age effect on survival, noted $a2$ with $\Phi_{a1 \cdot t} < \Phi_{a2 \cdot t}$. (Table A2)

Table A2 Summary of the calculations used to study the similarity of variability in temporal survival among the six populations and the effect of covariates on survival probabilities

Question of interest	Calculation	Notation of models (M) and parameters
similarity of temporal survival variation	$[DEV(M_p) - DEV(M_{p+t})]/$ $[DEV(M_p) - DEV(M_{p \cdot t})]$	M_p: constant survival according to population, M_{p+t}: similar time variations between populations M_{p*t}: time effect for each population.
effects of body size and longitudinal gradient on adult survival	F-statistic of the ANODEV test: $[DEV(M_.) - DEV(M_c)]/[(DEV(M_c) - DEV(M_g))/k-1]$	$M_.$: constant survival M_c: covariate M_g: constant survival according to study sites and sex (g standing for 12 groups, 2 sex · 6 study sites), k: number of parameters of the survival vector (12 for 12 groups)
amount of variation in survival accounted for by covariates (R^2)	$[DEV(M_c) - DEV(M_.)]/$ $[DEV(M_g) - DEV(M_.)]$	
effects of climatic oscillations on adult survival	F-statistic of the ANODEV test: $[DEV(M_.) - DEV(M_c)]/$ $[(DEV(M_c) - DEV(M_t))/k-1]$	$M_.$: constant survival M_c: covariate M_t: time varying survival
amount of variation in survival accounted for by covariates (R^2)	$[DEV(M_c) - DEV(M_.)]/$ $[DEV(M_t) - DEV(M_.)]$	k: number of parameters of the survival vector (8 for 8 years)

The calculations are based on the deviance (DEV) of specific models. The effects of covariates are tested with an analysis analogous to analysis of variance, called ANODEV. Under H_0, the covariate does not explain any of the survival variance [$F \sim F(1, k-1)$].