

'La Niña'-driven Atlantic storms affect winter survival of Mediterranean Cory's Shearwaters

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Abstract

To test a previous hypothesis of a relationship between the adult survival rates of Mediterranean Cory's Shearwaters (*Calonectris d. diomedea*) and La Niña-driven Atlantic storms, we analysed 18 years of capture–mark–recapture data of adults ringed at a breeding colony in the Tremiti Islands. We used the program MARK to model survival and capture probabilities as functions of time-specific external variables such as the effect of temporal variations on capture probability and of climatic (ENSO, NAO, SST) and non-climatic factors (oil spills and fishery production) on shearwater survival. The model selection process of the program indicated that survival declined the most in La Niña years, when a greater number of storms were expected in the wintering range; oil spills and interaction with fisheries are worthy of attention too. Our analysis confirms the results of previous work, suggesting that the El Niño Southern Oscillation (ENSO) cycle is the main force governing climatic and ecological factors responsible for lowering Cory's Shearwater survival rates during La Niña years, probably through the effects of the enhanced Atlantic hurricane season.

Keywords: *Cory's Shearwater, survival, ENSO, NAO, oil spill*

Introduction

Many aspects of seabird life history respond directly to climatic conditions such as temperature and wind intensity, while oceanographic conditions (e.g. water temperature, currents, storms) may have an indirect effect through their influence on abundance and distribution of seabird prey (Durant et al. 2004).

The best example comes from the effects of the El Niño–Southern Oscillation (ENSO) on food chains and fisheries along the Pacific coast of South America and its devastating effects on sea-bird populations (Duffy et al. 1988; Schreiber & Schreiber 1989).

Moreover, ENSO is now known to have global influence (teleconnections) on temperature, precipitation patterns and storm frequencies in many regions of the world (Cane 1983; Ropolewski & Halpert 1997; Tremberth et al. 1998); therefore, even though the ecological effect of ENSO is most pronounced in the south-eastern Pacific Ocean, a number of studies document its effect on survival and reproduction of many seabird populations in

other parts of the Southern Oceans (e.g. Duffy 1990; Chastel et al. 1993; Guinet et al. 1998).

Other, less pronounced, climatic oscillations are known from other oceanic regions, the best studied of which is the North Atlantic Oscillation (NAO) (Hurrell et al. 2003; Hurrell & Dickson 2004). The impacts of the NAO appear less extreme (and less clear) than ENSO, without mass mortality episodes, and it is only since the mid-1990s that temporal patterns in the NAO have been related to variability in biological populations (Ottersen et al. 2001; Stenseth et al. 2002). Reported effects of the NAO on the abundance of zooplankton and key fish prey suggest that the NAO may influence the dynamics of seabird populations, but only recently have studies started to explore these relationships (Grosbois & Thompson 2005).

NAO effects on seabirds generally seem to be lagged, and meteorological parameters probably affect seabird mortality only indirectly, likely due to prey availability according to Sandvik et al. (2005), based on their study of five species of North Atlantic

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seabirds. However, Votier et al. (2005) found that lower overwinter survival of Guillemots (*Uria aalge*) was associated with high winter NAO indices, although the mortality rate was doubled by major oil pollution incidents.

Alongside with other climatic variables such as sea surface temperature (SST) – an index of global warming, a largely accepted phenomenon with a diffuse and complex influence on marine ecology – other well known seabird mortality factors are mainly anthropogenic, such as oil spills (see for example Piatt et al. 1990; Lima et al. 2004; Votier et al. 2008) and fisheries, which cause direct mortality due to fishing lines, but may also have a favourable influence due to enhanced food availability from discarded fish (Furness 2003; Votier et al. 2004).

Evidence of an influence of climatic variability or pollution on seabird life histories is even scantier in the Mediterranean, where the number of seabird species and their populations are lower than in the North Atlantic or Pacific coasts. We thus think it useful to present a new analysis of the capture–mark–recapture data collected from 1988 onwards on the Cory's Shearwater population breeding on the Tremiti Islands (Southern Adriatic Sea), focusing on adult survival, one of the key life history parameters of animal populations.

Cory's Shearwaters spend on average 80 days in their wintering areas, plus 40 days flying to and from them; this represents a substantial proportion of their annual life cycle (Gonzalés-Solis et al. 2007) and in light of their wanderings of 15,000–35,000 km over the Atlantic Ocean, this is certainly a key period for the survival of this species. Moreover, the findings of Jenouvrier et al. (2008), which showed that adult survival varied in synchrony for six different breeding populations of Mediterranean Cory's Shearwaters, strongly suggest that mortality occurs principally on the wintering grounds, and is affected by large-scale (hemisphere-scale) global factors; emphasizing the interest of such an analysis even on a single colony.

The objective of this new paper is thus to test our hypothesis (Brichetti et al. 2010) with a longer-term data set (18 years), and other possible covariates not previously considered, such as NAO, SST, and the effects of oil pollution and fisheries.

Materials and methods

Study site and field methods

Cory's Shearwater (*Calonectris diomedea diomedea*) has a breeding population in the Mediterranean Sea

that probably exceeds 65,000 pairs; although some spend the winter in the Mediterranean, most migrate to the Central Atlantic and Southern Atlantic Ocean (Thibault 1997; Ristow et al. 2000; Camphuysen & Van der Meer 2001; Gonzalés-Solis et al. 2007).

Our ringing site was located on the Tremiti Islands (S Italy, 42° 8' N, 15°30' E), where about 300–400 pairs of Cory's breed (Lo Valvo & Massa 1992; Brichetti & Fracasso 2003), in three different nest site typologies: (a) burrows occupied by single breeding pairs, (b) small caves with 1–4 pairs, (c) large caves with tens of pairs. We worked in two caves of the third type. In the first three years, our search efforts extended to some isolated burrows; subsequently, we felt that limiting our efforts to the largest, most accessible caves was sufficient for our purposes: we visited the main cave on San Domino island (cave A) and several other caves of Capraia island (cave B) regularly for 18 years; we exclude from this study small caves and burrows on the island of Capraia, which we visited only occasionally.

Ringing operations were carried out annually from the second half of May to the first half of June; we inspected about 40 nest cavities of Cory's Shearwater once a year, after eggs were laid. Birds in the nests were captured by hand and immediately released after banding and measuring (wing, bill, tarsus, weight). The ring number of previously banded birds was recorded. We were able to sex 89% of the birds (48% males) by biometry and vocalizations according to Ristow and Wink (1980).

Since the incubation shifts of the partners last about 4–8 days (Thibault 1997) and our banding sessions usually lasted 1–4 days, we expected each year to mark about 50% of the breeding adults, depending on the search effort. Cohorts of marked birds were composed of birds marked as breeding in the same year, but probably not hatched in the same year. After some years of banding, it was possible that unmarked birds were in their first breeding attempt, but we detected only seven birds (mean 8 years; range 6–10) previously banded by us as nestlings in this colony.

Data analysis

Theory and practice of capture–mark–recapture analysis is now well developed, and we refer to Williams et al. (2002) for general concepts and methodology.

Analysis started with program RELEASE (Burnham et al. 1987) and U-CARE (Choquet et al. 2005) to compute the goodness-of-fit test of the most general model, test for differences between sexes, and other specific tests for transience and trap

Table I. Environmental variables examined.

Variable	Expected effects	Source
ENSO (MEI Dec–Jan index)	negative/positive	http://www.cdc.noaa.gov/people/klaus.wolter/MEI/table.html
La Niña year	negative	http://www.cpc.ncep.noaa.gov/products/analysis_monitoring/ensostuff/ensoyears.shtml
Extended winter NAO index	positive/negative	http://www.cgd.ucar.edu/cas/jhurrell/nao.stat.winter.html
Mean Jan. SST	positive/negative	http://jisao.washington.edu/data/global_sstanomts/
Numbers of Atlantic storms	negative	http://www.wxresearch.com/outlook/comp2004.htm and http://atmos.colostate.edu/forecasts/2004/dec2004/
World amount of oil spills in tonnes	negative	http://www.itopf.com/stats.html
Number of spills on the African Atlantic coasts	negative	http://www.lastingnews.com/maps/oilspill.php
Small pelagic fish (<30 cm) landings in Canary Current	positive/negative	http://aerl06.aerl.ubc.ca/LME/lme.aspx
Small pelagic fish (<30 cm) landings in Guinea Current	positive/negative	http://aerl06.aerl.ubc.ca/LME/lme.aspx
Small pelagic fish (<30 cm) landings in Benguela Current	positive/negative	http://aerl06.aerl.ubc.ca/LME/lme.aspx

dependence. Then, models making further restrictions were fitted with program MARK (White & Burnham 1999; Cooch & White 2002), including models where temporal variation in survival is modelled as a logit-link function of specific covariates. The selection of the most appropriate model was based on the Akaike's Information Criterion (AIC) (Burnham et al. 1995; Anderson & Burnham 1999). In this study AICc values (AIC approximated for small samples) were adopted (White & Burnham 1999).

The explanatory variables fitted to the models are described hereafter.

Environmental variables

All environmental variables are listed in Table I with their expected effects and internet sources of the data used.

In particular, starting from our previous study (Brichetti et al. 2000), we tested for the effect of El Niño–Southern Oscillation (ENSO) on adult survival of Cory's Shearwaters. We used the Multivariate ENSO Index (MEI) as a proxy for overall climate conditions in the southern hemisphere. The MEI is calculated from six variables combined: sea-level pressure, zonal and meridional components of the surface wind, sea surface temperature (SST), surface air temperature, and total cloudiness fraction of the sky; negative values of the MEI represent the cold ENSO phase (La Niña), while positive MEI values represent the warm ENSO phase (El Niño) (Wolter & Timlin 1993). During La Niña episodes, waters in the central and eastern tropical Pacific Ocean become cooler and a stronger hurricane season is expected

in the Atlantic. The strongest La Niña year in the considered period was in 1988/89; other La Niña episodes took place in 1998/99 and 2000/01. The long-lasting (1990–1995) El Niño event ended in early 1995 and the succeeding development of La Niña was followed, later that year, by one of the most active Atlantic hurricane seasons on record. To emphasize the effect of La Niña years, we also tested a model obtained simply by coding the Niña years as '1' and all other years as '0'.

We then used the North Atlantic Oscillation index, NAO, as a proxy of winter climate variability in the North Atlantic and Mediterranean. The NAO is a large-scale oscillation in atmospheric mass between the subtropical high and the polar low (Hurrell et al. 2003). The positive NAO index phase shows a stronger than usual subtropical high-pressure centre and a deeper than normal Icelandic low. The increased pressure difference results in more numerous and stronger winter storms crossing the Atlantic Ocean on a more northerly track. This results in warm wet winters in Europe, while cold dry winters prevail in the Mediterranean area. The NAO and Mediterranean precipitation are also correlated, with negative anomalies for the positive phase of the oscillation and northward shifts of the storm track during the positive phases of the oscillation (Delitala et al. 2000; Baldi et al. 2004).

In our analyses we used the annual mean of monthly values of those global indices, and MEI and NAO were not significantly correlated (Pearson correlation coefficient: $r = -0.41$, $p = 0.31$, normality test $p = 0.76$, constant variance test $p = 0.50$).

As an index of global warming, we then selected the mid-winter (January) mean global sea surface temperature (SST).

Other variables, also considered in our previous work, were Atlantic hurricane and storm activity. Despite great interannual and interdecadal variability (Fink & Schrage 2007), Atlantic storminess seems to be related to La Niña episodes (Gray 1984; Pielke & Landsea 1999) and may be one of the most significant climatic influences on the life of shearwaters at sea. Because of the strong correlations among all four indexes of storminess (number of storms, storm days, number of hurricanes, hurricane days), we only retained the first for this analysis.

Along with these climatic indexes, we also tested oil spill statistics both at the global level (quantity of oil spilled) and the local level (oil spills off the African coast) as indexes of marine pollution. In these cases, we invariably expect a negative correlation with shearwater survival, due to mortality from oiled feathers and a degraded marine environment.

Finally, we attempted to evaluate the direct effects of food availability, measured by the quantity of fish (pelagic fish less than 30 cm long) caught in the regions in which shearwaters winter or pass through on migration. This index can be interpreted as a prey availability index, and should thus be positively correlated with shearwater survival, unless fisheries compete with birds for resources or cause mortalities in fishing nets.

The main problem, however, remains defining the most important wintering areas for Cory's Shearwaters, since Mediterranean breeding birds (*C. d. diomedea*) are generally thought to be trans-Equatorial migrants, moving south to the Benguela Current off Southern Africa, while Atlantic breeding birds (*C. d. borealis*) concentrate first off the eastern United States and later in the year off South American waters (Thibault et al. 1997). Recently, however, satellite telemetry data suggest that at least some Mediterranean breeding birds (*C. d. diomedea*) do not cross the Equator but winter off north-west Africa (Ristow et al. 2000), and recent observations off Southern Africa suggest *C. d. borealis* greatly outnumber *C. d. diomedea* in most areas there (Camphuysen & Van der Meer 2001). We are thus forced to consider the fish catch of all the three potentially interested regions: the Canary, Guinea and Benguela Currents (Figure 1).

Finally, the percentage of variation explained by the addition of covariates was calculated using analysis of deviance (ANODEV), calculated as the difference in variance between the constant model and the covariate model, divided by the difference between the constant model and the time dependent model (Skalski et al. 1993).

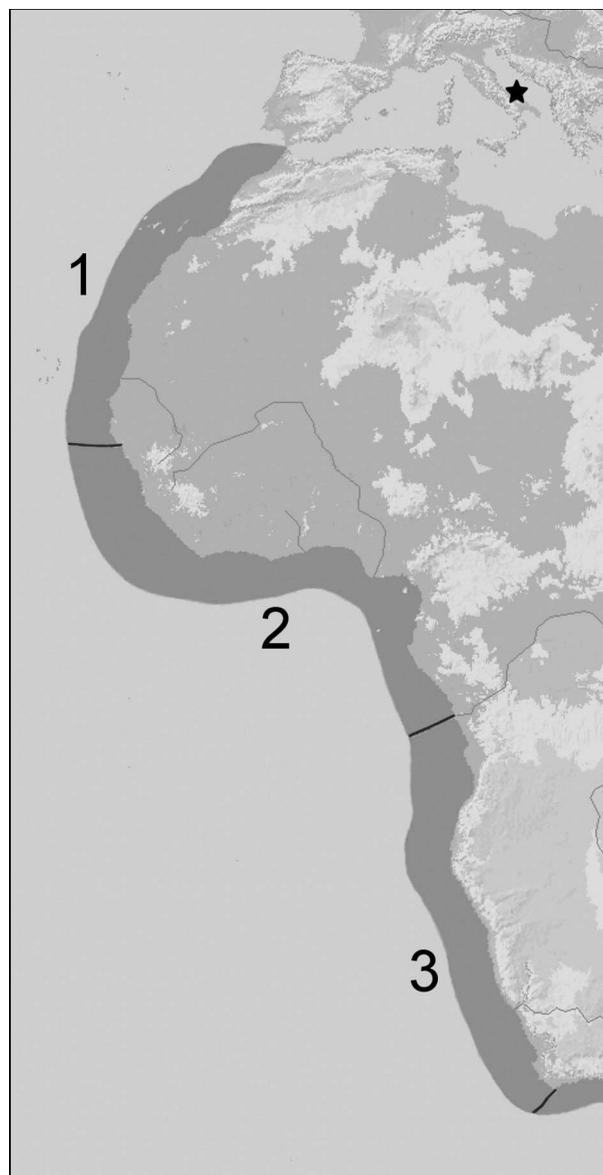


Figure 1. African coast fishing regions: Canary Current (1), Guinea Current (2) and Benguela Current (3).

Results

From 1988 to 2005 we ringed 144 adult Cory's Shearwaters, and many of them were recaptured for several years, for a total of 478 capture events (Table II). We computed the goodness-of-fit test of the fully time-dependent general model (CJS model) and specific tests for transience and trap-dependence with the programs RELEASE 3.0 and U-CARE 2.0. As we previously found (Brichetti et al. 2000), the RELEASE test for differences between groups (sexes) failed to find any differences in survival or capture rates (TEST 1 = 16.65; df = 33; $P = 0.992$), allowing the pooling of males, females and a few

Table II. Capture–recapture data for Tremiti breeding adult Cory’s Shearwaters summarized in $m(i)$ array. Year 1 = 1988. $R(i)$ = Marked birds released in year (i); columns denote period of next capture.

Year	j																		Total
	$R(i)$	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	
1	40	20	5	1	0	0	0	1	0	0	2	0	0	0	0	0	0	0	29
2	36		20	7	2	0	0	0	1	0	0	0	0	0	0	0	0	0	30
3	41			26	2	2	1	3	1	1	0	0	0	0	0	0	0	0	36
4	50				21	8	2	4	2	1	1	0	1	1	0	0	0	0	41
5	41					13	13	2	2	1	2	0	0	0	0	0	0	0	33
6	33						6	12	3	2	0	0	0	0	0	0	0	0	23
7	27							10	6	1	1	0	0	0	1	0	0	0	19
8	34								10	4	3	2	0	1	1	0	0	0	21
9	29									10	6	3	0	0	1	2	1	0	23
10	29										13	6	3	1	1	0	0	0	24
11	30											8	6	4	2	1	1	0	22
12	26												10	7	3	0	0	0	20
13	21													5	6	2	0	1	14
14	19														8	4	2	1	15
15	23															8	5	1	14
16	17																8	1	9
17	17																	9	9

unsexed birds for further analysis. Further testing with pooled data was made with the program U-CARE (Choquet et al. 2005). We computed the goodness-of-fit test of the general model (CJS model) ($df = 63$, Quadratic $\chi^2 = 59.50$, P -level = 0.60 ($\hat{C} = 0.94$) and the specific tests for transience ($df = 14$, Quadratic $\chi^2 = 9.64$, P -level = 0.79) and for trap-dependence ($df = 15$, Quadratic $\chi^2 = 9.13$, P -level, two-sided test = 0.39), all of which were non-significant.

To investigate the effects of selected variables, we further fitted models with time constraints on capture and survival rates, using the program MARK. The output provides the deviance of the model fitted to an additive constant that depends on the data set but not on the model. This relative deviance is used to compute likelihood-ratio tests (LRT) and the AIC of the models. We used AICc and not QAICc because we have no overdispersion of the data ($\hat{C} = 0.94$) (Cooch & White 2002).

We first tested for a time effect alternatively on recapture and survival rate and we noted that the re-encounter probabilities in the first three years were constantly higher; they were lower in all successive years and relatively constant, in accordance with our more intensive efforts in the first three years. We thus decided to include in the model selection procedure a model with two levels of re-encounter probabilities, one for the first three years and one for all the others (coded ‘2p’), significantly improving the performance of our model.

To further test the hypothesis that environmental variables affected the survival of shearwaters, we

then added constraints to this last model to force the survival probabilities during each year to be functions of all the selected indices (Table I).

The results of the model selection process are shown in Table III; the first shows the model fitted with MEI December–January index, the second shows the model ($\text{PHI}_{\text{Niña}}$) and the third shows the model fitted with the numbers of Atlantic storms, all with very high likelihood and with very similar test performance.

The other climatic models show weaker relationships with the observed survival estimates (Delta AIC = 3.83 or greater) and also the relationship with the index of oil spills show a similar support, with a Delta AIC of 3.83 for the number of oil spills along the West African coast.

Among the models that consider African coastal fisheries, we noted the good performance of the relationship with Benguela Current fisheries (Delta AIC = 1.33).

In summary, we can retain the results of the Model $\text{PHI}_{\text{Niña}}$ (shown in Table IV) as a good approximation of the survival in ‘bad’ (0.85) and ‘good’ (0.92) years, but the annual variability in survival rates is best defined by the ‘ENSO–MEI’ Model (Figure 2).

Discussion

On the basis of methodological and biological considerations (see Brichetti et al. 2000), we believe that our model-based estimates are good approximations of

Table III. Model selection results.

Model	AICc	Delta AICc	AICc weights	Model likelihood	Num. par.	Deviance
{Phi(MEI DJ index) p(2p) }	1581.36	0.00	0.12	1.00	4	908.46
{Phi(Niña years) p(2p) }	1581.60	0.24	0.11	0.89	4	908.70
{Phi(n storms) p(2p) }	1582.06	0.69	0.09	0.71	4	909.16
{Phi(small pelagic fish Benguela) p(2p) }	1582.70	1.33	0.06	0.51	4	909.80
{Phi(.) p(2p) }	1584.24	2.88	0.03	0.24	3	913.37
{Phi(n oil afrcoast) p(2p) }	1585.19	3.83	0.02	0.15	4	912.29
{Phi(SST jan) p(2p) }	1585.20	3.83	0.02	0.15	4	912.30
{Phi(world tonn oil p(2p) }	1585.75	4.39	0.01	0.11	4	912.80
{Phi(djfm NAO index) p(2p) }	1586.18	4.81	0.01	0.09	4	913.28
{Phi(small pelagic fish Guinea) p(2p) }	1586.25	4.89	0.01	0.09	4	913.35
{Phi(small pelagic fish Canary) p(2p) }	1586.25	4.89	0.01	0.09	4	913.35
{Phi(t) p(2p) }	1595.12	13.75	0.00	0.00	15	899.33
{Phi(.) p(.) }	1602.61	21.24	0.00	0.00	2	933.76
{Phi(.) p(t) }	1602.88	21.51	0.00	0.00	18	900.67
{Phi(t) p(t) }	1614.19	32.83	0.00	0.00	31	883.24
{Phi(t) p(.) }	1620.16	38.80	0.00	0.00	15	924.37

Table IV. Results of the Model {Phi(Niña years) p(2p)}.

Parameter	Estimate	SE	95% Confidence interval	
			Lower	Upper
1: Phi(Niña years)	0.85	0.02	0.79	0.89
2: Phi(not-Niña years)	0.92	0.02	0.88	0.95
1: p	0.62	0.05	0.52	0.70
2: p	0.38	0.02	0.39	0.42

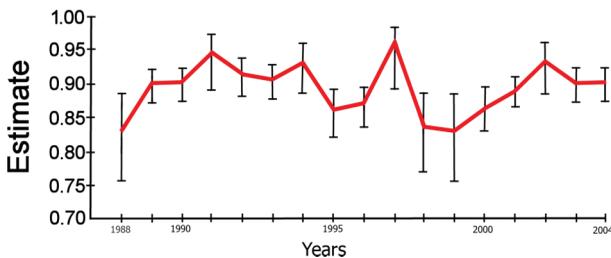


Figure 2. Annual variability of Cory's Shearwater survival estimates according to the model Phi(ENSO-MEI) p(2p).

the actual survival and expect our data to fit the assumptions of the general model.

Survival rates are similar (Figure 2; Table II) to those recorded in eastern (89–90%: Ristow et al. 1990) or western Mediterranean (86–96%: Thibault 1997) Cory's Shearwater populations (see also Jenouvrier et al. 2008), but more interesting are the reasons for the observed temporal variation in survival rates, with the best model being the one constrained with the MEI index, with a notably negative effect of La Niña years (i.e. negative value of

MEI), in accordance with the analysis of six Cory's Shearwater populations made by Jenouvrier et al. (2008).

However, some other models, comprised in the so-called 'rule of the thumb' of 2 Delta AIC (Burnham & Anderson 2002), deserve attention, while other variables tested seem not to be involved in the observed survival variability.

We now discuss them starting from those that are least correlated with shearwater survival.

First of all, although there is now evidence that the winter NAO influences, directly or indirectly, the adult survival of the northern fulmar (*Fulmarus glacialis*) (Grosbois & Thompson 2005) and other North Atlantic birds (Sandvik et al. 2005; Votier et al. 2005), we found no indications of an influence of NAO on our shearwater population. This is perhaps not surprising, because the NAO effects are mainly restricted to the northern Atlantic and the Mediterranean, where probably only a few Cory's remain in winter.

Average SST, as an index of global warming, was not found to be a good predictor of observed survival rates, and all the climatic indexes cited above were not found to enhance the performance of the models even when lagged $-1/-2$ years, as in our exploratory analysis.

The weak relationship between oil spills and survival was more unexpected, considering the importance of major oil spills as causes of seabird mortality. In fact, the relationship with the global number of tonnes of oil spilled also move in an unexpected direction (better survival in worse years), and so is probably due simply to chance, but the number of oil spills along the West African coast seems deserving attention in view of the well-known effects of oil

pollution. Generally they are strongest and more evident near the coast and for breeding colonies, but occasionally wintering birds also show high mortality rates. For example, in 1994, due to an oil spill along the Brazilian coast, approximately 10,000 birds of 21 species were killed. The high mortality was caused by the accident involving an oil tanker from Nigeria that caused a large oil spill which flooded the coast of Salvador and extended northward along the coast of Bahia. During this study, *Calonectris d. borealis* accounted for most of the birds found on the beach. The specimens were mostly young birds that left their nests from three months to one year before dying in their first or second flight across the Atlantic. This accounts for their frailty when facing storms or sea pollution. The adult birds of this species are more experienced and have already lived through many storms and are therefore not involved in the mortality phenomenon (Lima et al. 2004).

Moreover, using a long-term data set, Votier et al. (2005, 2008) showed that over-winter survival of adult common guillemots (*Uria aalge*) was negatively affected by both the incidence of four major oil spills in their wintering grounds and high values of the NAO index.

Our data do not exclude the possibility of additional mortality due to this cause (which is potentially much higher for young birds excluded from our analysis); however, a more likely explanation of the observed results is that, fortunately, the wintering area of *C. d. diomedea* was not particularly affected by oil spills in the years under study, with only three episodes registered in two different years.

The results regarding fish landings are more contradictory. First of all, any possible correlation between estimated survival rate and the fish landing in the Canary and Guinea Currents, where good numbers of Mediterranean Cory's Shearwaters winter (Ristow et al. 2000; Gonzalés-Solis et al. 2007) are clearly rejected. On the other hand, the 'good statistical performance' on the selection process of the model constrained with Benguela Current fisheries is very intriguing. Results from this model are counterintuitive, since they show lower shearwater survival rates in years in which fish landings are higher. If we accept this as a biologically meaningful result, it can only be explained by the complex relationship between fisheries and seabirds. In fact, industrial fisheries may reduce the availability of lipid-rich shoaling fish to seabirds either directly or through disturbance (Frederiksen et al. 2004); moreover, the Benguela Current fishing area is known for intensive long-lining effort and high by-catch rates of Procellariiformes (Tuck et al. 2003)

and for the considerable risk of incidental mortality in trawl fisheries. According to González-Solis et al. (2007), a substantial proportion of the Mediterranean Cory's Shearwater population (29%) winters in the Benguela Current, although it is outnumbered there by *borealis*. We do not comment further on this result, which deserves further investigation in light of increasing information on the effects of by-catch and on the actual wintering areas of each population.

The best models, according to AIC, corroborate our previous hypothesis of an influence of ENSO on Cory's Shearwater survival, due once again to the effects of Atlantic storminess during La Niña years. The results do not seem as strong as in our previous work (Delta AIC between the better model and the model with constant Phi being only 2.9) and the amount of variation now explained by climate (35%) is much inferior to our initial result (88.5%) or the result of the multi-colonial analysis of Jenouvrier et al. (2008). This is probably to be expected, since in recent years no strong La Niña events (such as that of 1988/89) were detected and the strong hurricane season of 1995 (with 121 storm days!) was not equalled. A recent La Niña event was detected in 2007, so a continued ringing effort will provide us with better testing opportunities.

Despite uncertainties over causal mechanisms, these findings add to the body of evidence that large-scale climate variation and its effects on the oceans can affect seabird population dynamics. In fact, large-scale indices (such as ENSO and NAO) seem to be better predictors of ecological processes than local climate. The ability of large-climatic indices (such as NAO) to outperform proxies of local climatic conditions in explaining variation in ecological processes has been demonstrated repeatedly, but seems counterintuitive given the mechanisms by which climatic variation imposes energetic stresses and influences resource availability in the wild. One explanation may be the complicated and temporally variable associations between local climate and ecological processes, which monthly climatic averages fail to capture, but which the large climatic index can incompletely reflect (Hallet et al. 2004).

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