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Assessing the impact of extreme adverse weather on the biological traits of a European storm petrel colony

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Abstract Climate change affects the climatic disturbance patterns and regimes and is altering the frequency and intensity of subtropical cyclones. These events can affect population dynamics of seabirds (e.g., survival, reproduction). In this work we tested the effect of adverse weather on a colony of European storm petrels (Hydrobates pelagicus) located in a small islet (Aketx) in northern Spain. Over a long-term monitoring period (1993–2014) we ringed 3728 petrels. From 2003 onwards we also monitored breeding success, the percentage of immature individuals and moult scores. We used Cormack-Jolly-Seber models and Underhill and Zucchini models to analyze the effects of climatic conditions on a number of biological traits (survival, breeding parameters, moulting patterns). Our analyses revealed a constant value of adult survival over the 26-year monitoring period. Recapture probability, however, tended to be positively influenced by NAO conditions in spring, and negatively influenced by NAO conditions in winter (although this would only affect to a fraction of first-captured birds). Moreover, the impact of adverse weather, especially in 2011 and 2014, resulted in an increasing proportion of yearlings in the breeding population, a lower breeding success and a delayed onset of moult. These effects were similar to those observed during the Prestige oil spill catastrophe.

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Introduction

Ecological disturbance is defined as any relatively discrete event in time that disrupts an ecosystem, community or population structure and alters the resource availability or the physical environment (White and Pickett 1985; Turner et al. 2003). The weather in the northern hemisphere is greatly affected by changes in atmospheric pressure over the North Atlantic. These alterations are known as the North Atlantic Oscillation (NAO). When there is a large difference between the low pressure area over Iceland and the high pressure area over the Azores (i.e., a high, positive NAO index), the westerly wind coming from the Atlantic to Europe is stronger. This gives rise to frequent, heavy storms during the winter period (Draycott 2012). In more recent times this index has been highly-positive (Hurrell and Van Loon 1997), leading to increasing temperatures and precipitations over Western Europe (Stenseth et al. 2003). Climate change is causing changes in disturbance patterns and regimes and is also altering the frequency and intensity of subtropical cyclones (Knutson et al. 2010; Baatsen et al. 2015). These events affect marine food webs and the complex bottom-up and top-down processes found in marine ecosystems (Thompson and Ollason 2001; Drinkwater et al. 2003; Frederiksen et al. 2007; Rossoll et al. 2012). However, the community and ecosystem responses to stochastic disturbances, such as storms, are difficult to observe in the open sea (Fiedler et al. 2013).

Seabirds are considered indicators of environmental change, as they range over large areas of the ocean and are therefore directly affected by any changes that may occur

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(Thompson et al. 1998; Barbraud et al. 2012; Soldatini et al. 2014). Wind patterns associated with the distribution of the high and low pressure systems over oceans have a significant effect on the at-sea distribution and long-range trajectories of many seabird species such as petrels and allies (Procellariiformes; Guinet et al. 1998; Barbraud and Weimerskirch 2003; Adams and Flora 2010; Boano et al. 2010). Blomqvist and Peterz (1984) suggested that petrels in the open ocean avoid flying into cyclone centres. Indeed, they may be capable of avoiding cyclones altogether (Fiedler et al. 2013). When subjected to protracted periods of continuous gale-force winds petrels are prevented from feeding, hence they become exhausted and severely weakened. Fat reserves are utilised, leading to weight loss and leaving birds without insulation from their wet environment (Elkins 2004). Moreover, changes in prey abundance and quality during pre-breeding and chick rearing periods may result in variations in adult body condition which affect the birds' quality as breeders and/or their survival (Soldatini et al. 2014).

The capacity of petrels and other seabirds to avoid perturbations or even to take advantage of these events (Fiedler et al. 2013) makes it difficult to find relationships between weather conditions and the biological traits of these birds (see Soldatini et al. 2014). In the case of the smaller species in this large group (i.e., storm petrels), satellite tracking devices cannot be used, since unfortunately they are still too heavy. This hampers our ability to answer questions related to wintering foraging areas, movements during the breeding and non-breeding seasons and relationships with oceanic weather conditions. For the time-being indirect cues must be used to analyse population dynamics, which are often conditioned by the above factors. In the case of European storm petrels (Hydrobates pelagicus Linnaeus, 1758) capture-recapture programmes have been the main method used to estimate population trends, survival and recruitment (Furness and Baillie 1981; Ratcliffe et al. 1998; Sydeman et al. 1998; Insley et al. 2002; Sanz-Aguilar et al. 2009; Zabala et al. 2011a; Soldatini et al. 2014), whereas breeding success has been used to find relationships between weather and sea conditions (Soldatini et al. 2014).

Due to energy constraints, most bird species avoid overlapping moult with other energetically demanding activities such as breeding or migration (Barshep et al. 2013). In many species, moult starts shortly after the breeding season is completed. Arroyo et al. (2004) described the moult pattern of the European storm petrel for two populations, one in the Bay of Biscay and another in the Mediterranean. They found a 1-month difference in the start of the moult period, largely related to the onset of the breeding season at the two sites. The inner primary moult of storm petrels begins either near the end of or following chick rearing (Ainley et al. 1976). Moult can therefore serve as an indicator for other life-history stages that cannot be quantified directly. For instance, in species that make a single breeding attempt per season, an early onset of the moult may indicate breeding failure (e.g., Barshep 2011; Barshep et al. 2011). The variance in the start date of moult could serve as an indicator for variability in reproductive success (Barshep 2011; Rayner et al. 2013). It should be noted that unpredictable food resources and feeding opportunities during the winter months are also reasons for the early start of moult (Underhill 2003; Summers et al. 2004, 2010).

Containing more than 5000 adult breeding birds (Zuberogoitia et al. 2007), the European storm petrel colony on the Aketx islet is likely to be one of the largest colonies in the Bay of Biscay. In November of 2002, the tanker "Prestige" sank about 120 miles from northwest Spain, generating a 77,000 t crude oil spill. By December of 2002, the first oil-slicks had reached the eastern coast of the Bay of Biscay and from then on they were continuously washed ashore. Overall, 23,181 dead birds were found along the coasts of Iberia and France; however, 115,000-230,000 birds in total were likely to have been affected (García et al. 2003). Nonetheless, data from the Aketx colony revealed a decrease in the sampling effortcorrected population size, higher percentage of yearlings (1-year-old birds in their first-breeding attempt), poorer body condition and lower breeding success during the two breeding years (2003-2004) subsequent to the oil spill (Azkona et al. 2006). However, Zabala et al. (2011a, b) showed no effect of the oil spill on adult survival rates and concluded that the species can minimise the impact of pollution or other adverse short-term accidents by skipping reproduction in unfavourable years. At the same time, these bad years could be used by some birds to breed. Thus, when local experienced birds decide to skip reproduction, birds of given characteristics (e.g., floaters) may try to breed as there would be less competition to find nesting site or feeding sources around the colony (Gaston 2004). If this occurs, we should expect a higher proportion of transients (birds that would be captured in 1 year but would never return to the colony) in these "bad" years. Moreover, if local birds skip reproduction in given years, we should expect a relatively constant survival rate, but variable values of recapture probability: bad years may be characterized by lower recapture rates, simply since some birds would not be present at the colony in these years. Finally, the proportion of first breeders breeding again in subsequent years after their first breeding attempt might be lower than that of experienced and established breeders (Weimerskirch 1992; Wooller and Coulson 2008), and also be more sensitive to subsequent environmental conditions.

The monitoring of the Aketx colony through to 2014 encompasses years in which the winters or springs had very high positive NAO values (Fig. 1), giving rise to frequent, heavy storms (e.g., 2011, 2012, 2014). We suspected that these atypical years might have had effects similar to those observed during the Prestige oil spill. In this paper we aimed to test for the effect of this presumably adverse weather on the European storm petrel population breeding on Aketx. Particularly, we focused on four sets of biological indicators: (1) survival and proportion of transients, including potential differences in probability of recapture after the first capture, (2) percentage of yearling breeding birds, (3) breeding success, and (4) onset of moult.

Materials and methods

Study area

The study was carried out on the Aketx colony (Biscay, north of Spain). Aketx is a small limestone islet of 6 ha, 80 m high, situated 800 m offshore to the north of the coast. The eastern part of the island has vertical, inaccessible cliffs with crevices and caves where yellow-legged gulls *Larus michahellis*, shags *Phalacrocorax aristotelis*

and European storm petrels breed. The western side is covered by rocky outcrops and large boulders. The terrain is steep here but, unlike the eastern face, it is partially covered by vegetation, mainly stunted holm-oaks *Quercus ilex*, wild olives *Olea europea* var. *silvestris* and fig trees *Ficus carica* (Zuberogoitia et al. 2007). The summit of the islet is flat and covered with shrubs and nitrophilous vegetation. The climate is oceanic, with north-westerly winds being dominant. The average annual temperature is 13 °C and average annual precipitation is 1200 l/m², with between 150 and 200 days of rainfall per year (for more details see Zabala et al. 2011a).

Sampling protocol

The first storm petrel studies involving ringing on Aketx took place in 1990 and 1991, when European storm petrels were captured using mist nets and tape lures (Mínguez et al. 1995; Zabala et al. 2011a). From 1993 to 2014 a systematic survey of the colony was undertaken, consisting of a minimum of one capture day per year in mid-July (breeding period, Table 1). In the second period tape-lures were not used, to minimise the likelihood of attracting transients and non-breeders to the nets and also to avoid adding variance in the probability of capture/recapture



European storm petrels per sampling day on the Aketx islet and mean NAO index for winter (WNAO) and spring (SNAO) during the study period (1993–2014)

Fig. 1 Number of captures of

Table 1 Sampling years andthe total number of samplingdays per year at the Europeanstorm petrel colony on theAketx Islet (north of Spain)

Year	Sampling days
1993	1
1995	1
1996	1
1997	1
1999	1
2001	1
2003 ^a	3
2004	3
2005	2
2006	1
2011	2
2012	1
2013	2
2014	2

^a 2003 was the year following the Prestige oil spill

attributable to differences in wind conditions or broadcasting power between and/or during the sampling visits (Furness and Baillie 1981; Sanz-Aguilar et al. 2008; Zabala et al. 2011a). These surveys used three mist nets (each measuring 12.0×2.5 m) always placed in the same position from 22:30 to 05:30 h. The sampling effort was therefore constant and the number of captures per year was directly comparable. Furthermore, although the islet harbours more than 5000 petrels, the sampled area is on a small corner of it and most parts of the islet, like the unreachable large cliffs of the northwest, north and east shore, are not prone to be sampled. Sampling was suspended in some years (Table 1), due to bad weather or for logistical reasons. Following the Prestige oil spill, we increased the number of sampling days per year to a maximum of three (for details see Table 1).

Captured petrels were ringed. From 2003 onwards they were aged, either as yearlings (petrels hatched the previous year which still had juvenile plumage in their wings) or adults (older birds), and moult was scored on each primary feather following Ginn and Melville (1983): 0, old, non-moulted feather; 1, old feather lost and new one starting to grow; 2–4, growing feather (from <1/3 to >2/3 of the mature feather length); 5, new, fully-grown feather. These scores were summed to give an overall moult score of between 0 and 50 (Erni et al. 2013). All these measurements were made over a period of less than 30 min after capture.

From 2003 onwards, we recorded the breeding success in 17 nests situated close to the point where we ringed the birds. We numbered these nests and surveyed them (presence of incubating adults, eggs or chicks) during each visit to the colony. The breeding success was defined as the proportion of nests in which we detected chicks. This proportion could be above the real success level, since some of these chicks could have died before fledging. However, the sampling design did not allow for a better estimation.

We obtained the mean NAO index for the months of December–March (winter NAO: WNAO) and from April to June (spring NAO: SNAO) to obtain a proxy of the prevailing conditions during the winter and at the beginning of the breeding period, respectively (http://www.win dows2universe.org/earth/climate/nao.html). We used this index since it represents general weather conditions within the region where the study was carried out. We did not use alternative (or complementary) indices such as the sea surface temperature because we ignore the non-breeding quarters of the birds from our study colony.

Survival and transient proportions (data 1993-2014)

Both survival and the proportion of transients were calculated using Cormack-Jolly-Seber (CJS) models, which allow us to estimate apparent survival (ϕ ; probability that a bird survives from t to t + 1) and re-sighting (recapture) probability (p; probability that a bird seen at t and still alive in t + 1 is seen at t + 1) separately. Overall, we obtained a matrix of 13 columns (years 1993-2014; 2003 excluded; for details see Table 2) by 2623 rows (individuals). Nonsampling years were taken into account in capture-recapture models, just by indicating the number of time intervals (years) elapsed between subsequent sampling years in MARK software. The model selection was conducted using the small sample size-corrected Akaike Information Criterion (AIC_c) values (Burnham and Anderson 2002). Models differing in less than 2 AIC_c values were considered to fit to the data equally well (Burnham and Anderson 2002).

Goodness of fit (GOF) was used to test the fit of the data to CJS assumptions (no trap-dependence, no transients (Lebreton et al. 1992; Choquet et al. 2009) using U-CARE software (Choquet et al. 2001). The global GOF test was significant ($\chi^2 = 80.78$, P < 0.001), as was the specific test to detect transients (z = 6.09, P < 0.001), but not the specific test used to detect trap-dependence (z = -1.41, P = 0.16). Therefore we parametrized models for the presence of transients.

Previous to any test of the effect of several covariate factors on either ϕ or p, we ran a set of 26 alternative models considering constant, time- and age-dependence on ϕ or p. In models assuming age-dependence we forced ϕ (or p) to vary between two age classes (ϕ_{t1} : annual apparent survival of previously unmarked birds to next year; ϕ_{t2} : annual apparent survival in subsequent years). In this set, the models assuming time-dependence on ϕ_{t1} ,

Year	R_i	R_i Number of recaptures												
		1993	1995	1996	1997	1999	2001	2004	2005	2006	2011	2012	2013	2014
1993	141		0	0	0	1	4	1	1	0	1	0	0	0
1995	90			4	4	0	0	0	0	0	0	0	0	0
1996	204				5	2	0	0	0	1	0	0	0	0
1997	175					5	3	3	0	1	0	0	0	0
1999	187						3	2	0	1	0	0	0	1
2001	242							7	1	5	0	1	1	1
2004	278								8	4	2	3	0	0
2005	282									4	1	1	0	2
2006	216										1	2	1	3
2011	215											6	11	4
2012	113												11	8
2013	253													11

Table 2 M-array table summarising the data used to run the CJS models

The term R_i refers to the number of birds "released" each year. Recaptures refers to the number of recaptures obtained from each cohort. Recaptures within the same year and outside the study Aketx islet were not considered

constant ϕ_{t2} [i.e., $\phi_{t1}(t)$, ϕ_{t2}] gained 99.9 % of the AIC_c weight (see Table 6 in Appendix). Regarding *p*, however, the data fitted a number of different candidate models equally well (see Table 6 in Appendix).

Given this, we parameterized models to analyse the effects of environmental covariates (SNAO and WNAO) on ϕ . In particular, we replaced time-dependence in $[\phi_{t1}(t), \phi_{t2}]$ by a SNAO or WNAO effect [e.g., ϕ_{t1} (SNAO), ϕ_{t2}]. This NAO effect can be only tested with parameters calculated over 1 year-interval. Thus, survival values remained unconstrained (i.e., time-dependent) for those years where there was no sampling in the previous year (e.g., in 1995, as we were not able to survey the colony in 1994; Table 1). We ran two alternative NAO-dependent models, assuming (1) NAO effect, with unconstrained time-dependent for the years in which it was not possible to include NAO effects (such models were named as SNAO and WNAO); (2) NAO effect, with constant survival values for the years in which it was not possible to include NAO effects (such models were named as SNAO' and WNAO'). We also tested for the possible effect of SNAO or WNAO on p. This analysis was carried out since we found that storm petrels would be able to skip breeding if they find bad conditions (e.g., Zabala et al. 2011a, b). Alternative models tested in this case replaced time-dependence by SNAO, SNAO', WNAO or WNAO' in models (1) p(t), (2) $p_{t1}(t)$, $p_{t2}(t)$, and (3) $p_{t1}(t)$, p_{t2} . Finally, we also added a model including an effect of sampling effort (Table 1) on p. All models were ran using the MARK software (White and Burnham 1999) and the logit link function implemented in it.

Moult pattern (data 2003-2014)

The proportion of yearlings, breeding success and moult was only recorded from 2003 onwards. Therefore, we did not have sufficient data to run Generalized Linear Models with an acceptable statistical power. As an alternative, we tested whether these three dependent variables varied from year to year and checked whether the years showing significant differences were also those coinciding with abnormally high, positive NAO indexes (2012, 2014).

To analyse whether the primary moult starting date varied from year to year we used the models of Underhill and Zucchini (1988) and Underhill et al. (1990). These models estimate the duration of moult and the mean (\pm SD) starting date of this process. The models are based on an index of moult which increases linearly with time. We only considered birds in moult for these analyses (i.e., Type 3, Erni et al. 2013). We used the Julian day (June 1 is day 1) as the time scale in the analyses and graphs. Specifically, we tested if the moult start date varied from year to year, considering two candidate models: m1, the null model and m2, with year as a covariate that may influence the onset of moult. The models were ranked according to their AIC_c value (Burnham and Anderson 2002).

The analyses were performed with R (R Development Core Team 2013) using lme4 (Bates et al. 2012) and Moult (Erni et al. 2013) packages. Statistical significance was set at P < 0.05.

Results

Overall, we ringed 3728 storm petrels from 1993 to 2014. The standardised mid-July number of captures ranged from 134 (in 2004) to 242 (in 2001, Fig. 1).

Survival analyses revealed that the best models did not consider any effect of NAO on apparent survival (ϕ). Models considering transients and constant survival after the first recapture {i.e., [$\phi_{t1}(t)$, ϕ_{t2}]} ranked higher than the rest of tested models (Table 3), indicating that the proportion of transients varied with time (ϕ_{t1} is affected by the occurrence of transients), whilst survival of non-transients was constant over time (mean \pm SE 0.86 \pm 0.02).

Regarding probability of capture (*p*), the best model was that assuming a positive effect of SNAO on *p* (B-parameter: $+0.10 \pm 0.18$) (Table 3). However, several models

ranked within 2 AIC_c values from the best model. These included: (1) an sampling effort effect on p (with increasing values of p within an increasing sampling effort; model 2); (2) a positive effect SNAO' on p (B-parameter: +0.08 ± 0.18; model 3); and (3) a negative effect of WNAO' on p_{t1} (B-parameter: +0.48 ± 0.35; model 4). Thus, overall, we found evidence suggesting that p tended to be positively correlated with NAO conditions in spring and higher sampling effort, and at the same time probability of capture of petrels first-captured in a previous year tended to be negatively influenced by NAO values during the winter.

The proportion of yearlings in the sample was almost negligible, except in 2003, during the Prestige oil spill, 2006, 2011 and 2014 (Table 4). The breeding success (Table 4) was 100 % or close to 100 % except in 2003,

Models	AIC _c	ΔAIC_c	AIC _c weight	np	Deviance
$\phi_{t1}(t), \phi_{t2}, p(\text{SNAO})$	1400.98	0.00	0.25	20	163.71
$\phi_{t1}(t), \phi_{t2}, p(\text{effort})$	1402.09	1.11	0.14	15	174.97
$\phi_{t1}(t), \phi_{t2}, p(\text{SNAO}')$	1402.28	1.30	0.13	15	175.16
$\phi_{t1}(t), \phi_{t2}, p_{t1}(WNAO'), p_{t2}$	1402.48	1.50	0.12	16	173.33
$\phi_{t1}(t), \phi_{t2}, p(WNAO)$	1403.73	2.76	0.06	20	166.46
$\phi_{t1}(t), \phi_{t2}, p_{t1}(\text{SNAO}'), p_{t2}$	1403.96	2.98	0.06	16	174.81
$\phi_{t1}(t), \phi_{t2}, p_{t1}(WNAO), p_{t2}$	1404.22	3.24	0.05	21	164.91
$\phi_{t1}(t), \phi_{t2}, p_{t1}(WNAO'), p_{t2}(WNAO')$	1404.27	3.30	0.05	17	173.10
$\phi_{t1}(t), \phi_{t2}, p(WNAO')$	1405.42	4.45	0.03	15	178.31
$\phi_{t1}(t), \phi_{t2}, p_{t1}(SNAO), p_{t2}$	1405.88	4.90	0.02	21	166.57
$\phi_{t1}(t), \phi_{t2}, p_{t1}(\text{SNAO}'), p_{t2}(\text{SNAO}')$	1405.98	5.00	0.02	17	174.80
$\phi_{t1}(t), \phi_{t2}, p_{t1}(WNAO), p_{t2}(WNAO)$	1408.69	7.71	0.01	27	157.13
$\phi_{t1}(\text{SNAO}), \phi_{t2}, p(t)$	1413.84	12.86	0.00	20	176.57
ϕ_{t1} (WNAO), ϕ_{t2} , $p(t)$	1414.91	13.93	0.00	20	177.64
$\phi_{t1}(t), \phi_{t2}, p_{t1}(SNAO), p_{t2}(SNAO)$	1415.32	14.34	0.00	27	163.77
ϕ_{t1} (SNAO), ϕ_{t2} , p_{t1} , p_{t2}	1420.38	19.40	0.00	10	203.37
ϕ_{t1} (WNAO), ϕ_{t2} , p_{t1} , p_{t2}	1421.14	20.16	0.00	10	204.13
$\phi_{t1}(\text{SNAO}'), \phi_{t2}, p(t)$	1430.50	29.52	0.00	15	203.38
$\phi_{t1}(t), \phi_{t2}(t), p_{t1}(t), p_{t2}(t)$	1431.43	30.45	0.00	46	140.67
$\phi_{t1}(WNAO'), \phi_{t2}, p(t)$	1435.39	34.41	0.00	15	208.27
$\phi_{t1}(\text{SNAO}'), \phi_{t2}, p_{t1}, p_{t2}$	1435.54	34.56	0.00	5	228.59
$\phi_{t1}, \phi_{t2}, p_{t1}, p_{t2}$	1440.89	39.92	0.00	4	235.96
ϕ , $p(t)$	1440.93	39.95	0.00	13	217.86
ϕ_{t1} (WNAO'), ϕ_{t2} , p_{t1} , p_{t2}	1442.84	41.86	0.00	5	235.89
ф, <i>р</i>	1448.49	47.52	0.00	2	247.57
$\phi(t), p(t)$	1448.72	47.74	0.00	23	205.33
$\phi(t), p$	1450.89	49.91	0.00	13	227.82

AIC_c, small sample sizes-corrected Akaike values; Δ AIC_c, difference in AIC_c values in relation to the top model; np, number of parameters. Models: ϕ_{t1} , survival between first capture year to following year; ϕ_{t2} , annual survival in subsequent years; *t*, time-dependent; SNAO and WNAO, spring and winter NAO effect, with unconstrained time-dependence for the years in which it was not possible to include NAO effects; SNAO' and WNAO', spring and winter NAO effects; which unconstrained to the years in which it was not possible to include NAO effects; *p*, recapture probability

 Table 3
 Ranking of the models

 used to test for the effect of
 several factors on European

 storm petrel annual apparent
 survival

Year	Number of second-year birds (proportion)	Number of successful nests (breeding success)	Number of monitored nests (n)
2003	6 (3.0 %)	2 (16.7)	12
2004	1 (0.4 %)	6 (100.0)	6
2005	1 (0.4 %)	14 (93.3)	15
2006	5 (2.3 %)	_	11
2011	10 (4.5 %)	11 (64.7)	17
2012	0 (0.0 %)	-	12
2013	2 (0.8 %)	11 (91.7)	12
2014	22 (5.8 %)	1 (12.5)	8

Table 4 Number of yearlings and proportion respect to the annual captures and number of successful nests and annual breeding success (proportion of nests with chicks)

We also show the number of nests over which the breeding success was calculated. We only developed one sampling day during the breeding seasons of 2006 and 2012 due to bad sea conditions and therefore, we could not monitor the breeding success

 Table 5 Results of multi-model evaluation applied to the moult scores of storm petrels

Models	AIC	ΔΑΙϹ	AIC weight	np
Year, type 3	-1745.59	0.00	1.00	9
Null model, type 3	-1687.11	58.48	0.00	3

Models are estimated and ranked according to their AIC value. Δ AIC, difference in AIC values in relation to the top model

following the Prestige oil spill, when it was only 16.7 %. We also calculated a low rate of 64.7 % for 2011 and 12.5 % for 2014. On 23rd July 2014 only one nestling was found in the eight monitored nests. However, it is important to note that we detected six incubating adults and caught two gravid females on that date, suggesting delayed breeding that year.

Storm petrels started to moult on 21st July (SD 11.95 days). The first birds with active moults were detected on 2nd July, and the last captures still found to be moulting some primary feathers were obtained on 12th August (we did not sample after this date). The mean start of moult varied significantly from year to year (Table 5). In fact, the moult was significantly delayed in 2011 and 2014 (Fig. 2).

Discussion

Seabirds are vulnerable to episodic weather events regardless of the time of year when these occur (Descmaps et al. 2015). Storm petrel wrecks have been widely documented, although it is often unclear which breeding population they belong to, as populations of distinct breeding origin can meet at given areas during the non-breeding period (Newton 2013). Zabala et al. (2011a) showed that



Fig. 2 Mean start of moult (Julian days from 1st June) of European storm petrels on the Aketx islet. The *bars* indicate 95 % confidence intervals

European storm petrels, in common with other long-lived oceanic species, have behavioral traits allowing them to minimise the impact of extreme weather or pollution by skipping reproduction. This may explain the constant value of adult survival found in the target population of European storm petrels on the Aketx islet over the 26 monitoring years.

Interestingly, despite adult apparent survival being constant, we observed that recapture rate was positively influenced by NAO values in spring. This suggests that the pre-breeding environmental conditions affect the probability of skipping or not the reproduction (Erikstad et al. 1997). In the same way, one of the models ranking within 2 AIC_c units of the best one showed that recapture of those petrels which were first-captured in the previous year tended to be negatively influenced by NAO values during the winter. First-captures are composed by a mixture of

transients, first breeding birds and older, more experienced individuals that have not been captured in previous occasions. Our result is compatible with the idea that a fraction of these first-captures, probably composed by still inexperienced birds, might be more prone to skip reproduction in the following year if they experience adverse weather conditions during the winter (Weimerskirch 1992; Wooller and Coulson 2008).

Breeding yearlings (birds breeding in their second calendar year) only appeared in the colony in four out of the 14 study years. This happened during the Prestige oil spill, and in 2006, 2011 and 2014. Zabala et al. (2011a) suggested that an increase in yearlings during the Prestige oil spill might have been due to the skipping of reproduction by older experienced birds, while inexperienced birds would have tried to breed. In line with this statement, we may expect the causes of an increase in yearling proportion in recent years to be related with unfavorable weather conditions. In parallel, we found a lower breeding success and delayed onset of moult both in 2011 and 2014. Delayed onset of moult is closely related to delayed breeding (Rohwer et al. 2009). During the Prestige oil spill, however, an early onset of moult could have been an indication of early breeding failures (e.g., Barshep 2011; Barshep et al. 2011).

Although it is hard to find statistical relationships between biological traits and particular events (Descmaps et al. 2015; Mesquita et al. 2015), our results suggest an impact of adverse weather on key life history aspects, such as breeding or moulting. The NAO value for April 2011 (2.48) was two-fold the maximum value reached in this month over the period 1992-2014, and the second higherranked over this period (the highest was in December 2011: 2.52). The NAO value during the winter of 2014 (December-March) was 0.84. However, from 11th December to 30th March the Bay of Biscay suffered continuous extratropical cyclones (i.e., Hercules, Christina, Ulla). Overall there were 24 days with winds of over 80 km/h and a further 35 days with maximum winds of over 100 km/h, reaching a peak of 265 km/h on 10th January. In the line with our results, other research teams monitoring seabirds in the Bay of Biscay registered notably delayed breeding in shags (Phalacrocorax aristotelis, J. Hidalgo, personal communication).

Overall, adverse weather, including continuous rain or heavy swell, may have led to the bad breeding performance or delayed moult via carry-over effects. The passage of vigorous depressions probably hampers feeding, which might have a severe impact on both breeding and moulting performance (Elkins 2004). Population dynamics of storm petrels may be affected by very extreme weather conditions, which occur at unpredictable times. In such cases, the detection of deleterious effects on population dynamics would likely require hierarchical analyses to evaluate the influence of within-year or within-season weather events (Rotenberry and Wiens 1991). Additionally, the vagrant movements of storm petrels during winter and spring are still far from being fully understood. European storm petrels winter in the south Atlantic but it is also possible to detect them in the Bay of Biscay during the winter season (SEO/Birdlife 2012). It is hard to relate weather events in the northern Atlantic when the target birds may be far away (i.e., off the southwestern coast of Africa). Soldatini et al. (2014) suggested that sea conditions may induce storm petrels to skip reproduction in years with high surface temperatures and low chlorophyll levels at wintering sites, resulting in lower encounter rates with these birds during the subsequent breeding season.

In conclusion, our results showed that harsh environmental conditions, such as climatic perturbations or the knock-on effects of oil spills, affect the biological cycle of storm petrels. The species seems adapted and its particular life cycle permits it to absorb the consequences of occasional impacts and recover the population rhythm within a few years. However, we do not know how storm petrels will respond if the frequency and intensity of these types of events increase in the future, as some authors have suggested (Baatsen et al. 2015).

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Appendix

See Table 6.

Table 6 List of 26 models used to test for constant, time- and age-dependence on ϕ or *p*

Models	AIC _c	ΔAIC_{c}	AIC _c weight	np	Deviance
$\phi_{t1}(t), \phi_{t2}, p_{t1}, p_{t2}$	1405.44	0.00	0.46	15	178.33
$\phi_{t1}(t), \phi_{t2}, p_{t1}, p_{t2}(t)$	1406.27	0.83	0.30	25	158.80
$\phi_{t1}(t), \phi_{t2}, p(t)$	1406.78	1.34	0.23	25	159.31
$\phi_{t1}(t), \phi_{t2}, p_{t1}(t), p_{t2}$	1413.73	8.29	0.01	26	164.22
$\phi_{t1}(t), \phi_{t2}, p_{t1}(t), p_{t2}(t)$	1417.05	11.61	0.00	36	147.00
$\phi_{t1}(t), \phi_{t2}(t), p_{t1}, p_{t2}(t)$	1419.80	14.36	0.00	35	151.81
$\phi_{t1}(t), \ \phi_{t2}(t), \ p(t)$	1421.08	15.64	0.00	35	153.09
$\phi_{t1}(t), \phi_{t2}(t), p_{t1}, p_{t2}$	1426.59	21.15	0.00	25	179.12
$\phi_{t1}(t), \phi_{t2}(t), p_{t1}(t), p_{t2}$	1426.96	21.52	0.00	36	156.92
$\phi_{t1}, \phi_{t2}(t), p_{t1}, p_{t2}$	1428.98	23.54	0.00	7	218.02
$\phi_{t1}(t), \phi_{t2}(t), p_{t1}(t), p_{t2}(t)$	1431.43	25.99	0.00	46	140.67
$\phi_{t1}, \phi_{t2}(t), p_{t1}, p_{t2}(t)$	1431.78	26.34	0.00	17	200.61
$\phi_{t1}, \phi_{t2}, p(t)$	1437.51	32.07	0.00	14	212.42
$\phi_{t1}, \phi_{t2}, p_{t1}(t), p_{t2}(t)$	1438.07	32.63	0.00	25	190.60
$\phi_{t1}, \phi_{t2}, p_{t1}, p_{t2}(t)$	1438.55	33.11	0.00	14	213.46
$\phi_{t1}, \phi_{t2}(t), p(t)$	1440.00	34.56	0.00	24	194.58
$\phi_{t1}, \phi_{t2}, p_{t1}(t), p_{t2}$	1440.43	34.99	0.00	15	213.31
$\phi_{t1}, \phi_{t2}, p_{t1}, p_{t2}$	1440.89	35.45	0.00	4	235.96
ϕ , $p(t)$	1440.93	35.49	0.00	13	217.86
$\phi_{t1}, \phi_{t2}(t), p_{t1}(t), p_{t2}$	1442.12	36.68	0.00	25	194.65
$\phi_{t1}, \phi_{t2}(t), p_{t1}(t), p_{t2}(t)$	1445.19	39.75	0.00	35	177.20
ϕ, p_{t1}, p_{t2}	1445.48	40.04	0.00	3	242.55
$\phi(t), p_{t1}, p_{t2}$	1448.38	42.94	0.00	14	223.29
φ, <i>p</i>	1448.49	43.05	0.00	2	247.57
$\phi(t), p(t)$	1448.72	43.28	0.00	23	205.33
$\phi(t), p$	1450.89	45.45	0.00	13	227.82

AIC_c, small sample sizes-corrected Akaike values; Δ AIC_c, difference in AIC_c values in relation to the top model; np, number of parameters. Models: ϕ_{r1} , survival between first capture year to following year; ϕ_{r2} , annual survival in subsequent years; *t*, time-dependence; *p*, recapture probability

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