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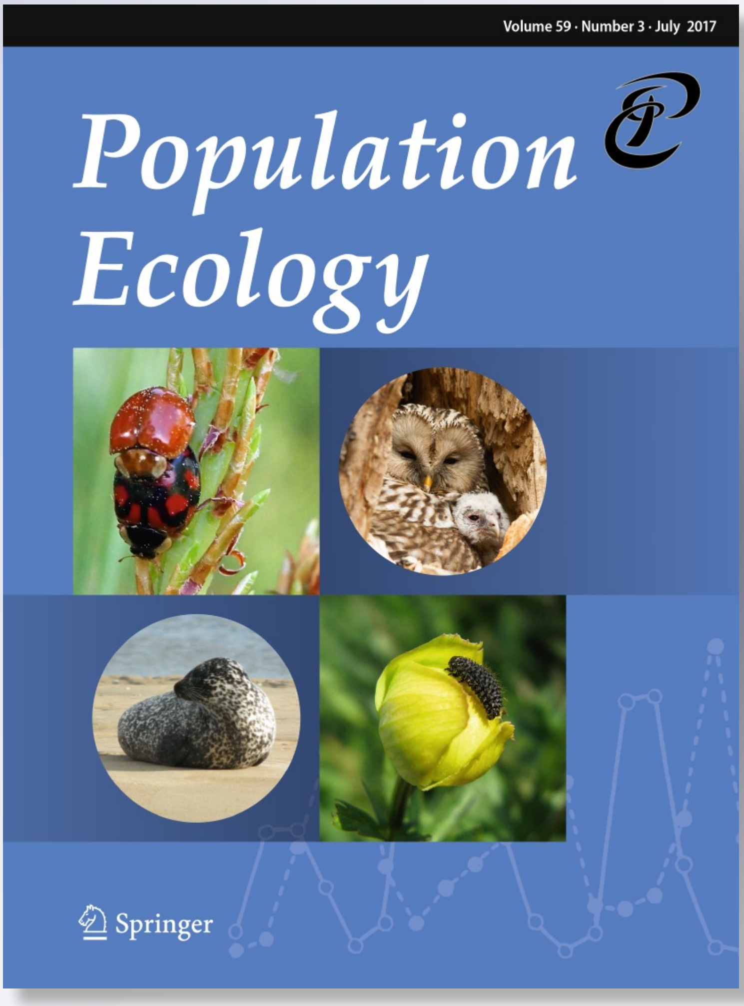

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ORIGINAL ARTICLE

Disentangling the effects of predation and oceanographic fluctuations in the mortality of two allopatric seabird populations

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Abstract Life-history traits of migratory seabirds are influenced by changing conditions at breeding and wintering grounds. Climatic conditions and predation are known to impact populations' survival rates, but few studies examine their effect simultaneously. We used multievent capture–recapture models to assess mortality due to environmental conditions and predation in breeding European storm petrels (*Hydrobates pelagicus*) in two allopatric colonies (Mediterranean and Atlantic). Predatory mortality at the colonies showed annual variation, being around 0.05 in certain years. Mortality at sea differed between the two oceanic basins, and was lower in the Mediterranean colony [0.11, 95% CI (0.09, 0.14)] when compared to the Atlantic colony [0.18, 95% CI (0.15, 0.22)]. The Western Mediterranean Oscillation index (WeMOi) explained 57% of the temporal variability in mortality of Mediterranean breeders. In comparison, 43% of the temporal variability in mortality of Atlantic breeders was explained by the winter St Helena index (wHIX) and El Niño-Southern Oscillation index (wENSO). Our results suggest that Mediterranean breeders remain in this basin for wintering where they may face lower migratory costs and more favourable environmental conditions. In contrast, Atlantic breeders' mortality may be due to higher cost of migration, changing upwelling conditions in the Benguela current and heavy storms over their migratory route during La Niña events. This study underlines the importance of modelling separately different causes of mortality when testing the effects of climatic covariates.

Keywords Capture–recapture · Climate · Multievent · Storm petrel · Survival

Introduction

There are critical moments during the annual cycle of animals in which their risk of mortality increases. Particularly, long-distance migratory species can experience increased mortality risks during migration (Klaassen et al. 2014; Lok et al. 2015; Sanz-Aguilar et al. 2015a) or at wintering areas when conditions are unfavourable (Schaub et al. 2005; Sanz-Aguilar et al. 2012). Seabirds in temperate regions typically perform medium to long-distance migrations between wintering areas and breeding sites (Schreiber and Burger 2001). Pelagic species are ideal bioindicators of the marine environment, as they spend more than 90% of their life at sea, only coming to land during the breeding season (Furness and Camphuysen 1997). Unfavourable weather conditions and lack of resources drive variation of survival rates in seabirds, especially during periods of vulnerability and high energy expenditure such as migration (Genovart et al. 2013; Payo-Payo et al. 2016).

In long-lived species with low fecundity, adult survival is the most critical parameter for population viability and

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usually displays low variability over time (Sæther and Bakke 2000; Gaillard and Yoccoz 2003; Oro 2014). As a result, any additional mortality during breeding or wintering seasons can severely impact population viability (Jones et al. 2008; Schaub et al. 2010; Sanz-Aguilar et al. 2015b, 2016). For example, the introduction of alien carnivore species at islands has contributed to rapid declines in seabird populations (Martin et al. 2000; Jones et al. 2008; Le Corre 2008). Furthermore, in some areas, sympatric native avian predators, such as raptors, seagulls or skuas prey on large numbers of small seabirds, including storm petrels (Votier et al. 2004; Oro et al. 2005).

In order to relate the probability of mortality to corresponding disturbance, a spatial scale partitioning is required for the separation of breeding season (predation risk) from the non-breeding season (climatic factors) (Oro 2014). Nevertheless, different factors operating in separate spatio-temporal scales are rarely taken into account when studying animal survival (Stenseth et al. 2002; Brook et al. 2008).

In this study, we modelled and tested the effects of winter and migration environmental conditions and predation at breeding colonies on the mortality probabilities of a small pelagic seabird, the European storm petrel (*Hydrobates pelagicus*). The European storm petrel is the smallest Palearctic seabird (medium wingspan of 36 cm and average weight of 28 g; Cramp and Simmons 1977). The two subspecies of *H. pelagicus* (Cagnon et al. 2004) are *H. p. pelagicus* (Linnaeus 1758) (distributed along eastern Atlantic coast) and *H. p. melitensis* (Schembri 1843) (which breeds in the Mediterranean basin). These birds usually nest in rock crevices and under boulders on islands free of mammalian predators (Del Hoyo et al. 1992). As an evolutionary strategy, storm petrels at land are active at night to avoid diurnal avian predators, such as seagulls (Warham 1990). Atlantic storm petrels are transequatorial migrants that leave their European colonies in autumn and travel to the coast of south and southeast Africa (Fowler 2002; Fig. 1). The wintering grounds of the Mediterranean populations remain unknown, but it is suspected that most of the birds do not depart Mediterranean basin (Hashmi and Fliege 1994; Soldatini et al. 2014).

Our first objective was to estimate and compare mortality probabilities due to predation and environmental conditions out of the breeding season of storm petrels in two allopatric breeding colonies, one located in the Atlantic and the other in the Mediterranean basin (Fig. 1). Next, we aimed to evaluate the effects of different environmental covariates on mortality probabilities during migration and wintering. We used multievent capture–recapture models (Pradel 2005) to estimate mortality during breeding and non-breeding seasons due to predation and migration to wintering areas, respectively. This was performed using long-term individual capture–recapture data. As predation at breeding colonies exists and influences storm petrel mortality (Sanz-Aguilar et al. 2009a), it must be considered separately when testing the potential effects of climatic conditions on mortality during non-breeding season (Genovart et al. 2013; Lok et al. 2015). We tested the effects of oceanographic and climatic conditions at sea by using climatic indices as proxies of oceanic and atmospheric fluctuations, which drive spatio-temporal differences in marine biological productivity and serve as indicators of climate variability (Genovart et al. 2013; Ramírez et al. 2016). Climatic conditions may influence mortality of storm petrels either directly (through weather signature) or indirectly (through bottom-up control).

Materials and Methods

Data collection at breeding colonies

We used long-term individual data collected from two different monitoring programs: one colony of *H. p. pelagicus* in the North-East Atlantic basin, located at the Enez Kreiz islet of Molène archipelago (48°21′N, 4°46′W, France), and a colony of the Mediterranean subspecies *H. p. melitensis*, located at the island of Benidorm (38°30′N, 0°08′E, Spain) (Fig. 1). Both colonies were visited during the breeding period every 1–3 weeks. Breeding individuals were caught once per year on their nests, when incubating an egg or rearing a chick, and marked with stainless steel rings with a unique alpha-numeric code. In Benidorm both partners were typically captured while at Enez Kreiz only one member of the breeding pair was caught annually. A standardized systematic search for recoveries of predated storm petrels was implemented in 2001 at Enez Kreiz and in 2002 at Benidorm, following each visit to the studied colonies. At Enez Kreiz, the main predator of storm petrels is the great black-backed gull (*Larus marinus*, Linnaeus 1758) followed by grey heron (*Ardea cinerea*, Linnaeus 1758) (Cadiou 2001, 2013), while at Benidorm the main avian predator is the yellow-legged gull (*Larus michahellis*, J. F. Naumann 1840) (Oro et al. 2005). The rings of predated storm petrels can be easily found in pellets around predators' nests and in the storm petrel colonies (Sanz-Aguilar et al. 2009a). For the purpose of this study, we used individual encounter history data (both live recaptures and dead recoveries) of breeding adults from 2002 to 2014 at Benidorm Island and from 2001 to 2014 at Enez Kreiz Island.

Climatic covariates

Some studies have demonstrated that large-scale climatic indices can perform better than local weather factors in

Fig. 1 Location of the two studied breeding colonies of Atlantic and Mediterranean storm petrels (*stars*) and recaptures/recoveries during winter months (November to February) of storm petrels ringed in the Atlantic ($n = 76$; *black dots*) and in the Mediterranean ($n = 4$; *white dots*). Data was obtained from EURING Data Bank (du Feu et al. 2009)

explaining impacts of oceanographic processes on demographic parameters of seabird populations (Rodríguez and Bustamante 2003; Hallett et al. 2004). However, other researchers argue that individual indices are too simple to assess complex ecological processes in aquatic ecosystems (Blenckner and Hillebrand 2002). Additionally, certain global climatic indices can indirectly influence seabird vital rates, primarily by bottom-up control (i.e., by food limitation), directly affecting the spawning or recruitment of seabird prey (Davis et al. 2005). Here we tested the effects of seven different climatic indices on non-breeding survival: winter (December to March) NAO, ENSO, MEI, SOI and HIX and both winter (December to March) and annual (July to June) WeMOi (see details below). The South Oscillation Index (SOI, http://www.cpc.ncep.noaa.gov/data/indices/soi) and the North Atlantic Oscillation Index (NAO, https://climatedataguide.ucar.edu/climate-data/hurrell-north-atlantic-oscillation-nao-index-station-based) were used as proxies for large-scale patterns of atmospheric circulation variability over the Atlantic and Mediterranean basin

(Durant et al. 2004; Hurrell and Deser 2015). The NAO is a major teleconnection index dominant throughout the year in the Northern Hemisphere that exhibits more than a third of total variance in sea level pressure during winter (Cayan 1992; Hurrell et al. 2013). Positive values of NAO depict warm weather conditions over North Atlantic and dry conditions in the Mediterranean. Negative values show the opposite pattern: colder winter in Northern Europe, while the Mediterranean receives more precipitation (Hurrell 1995). The latter conditions are potentially connected with higher density of prey items for seabirds (Ottersen et al. 2001), including storm petrels (Hemery et al. 2008). SOI represents the standardized anomalies in observed sea level pressure differences between Tahiti and Darwin. Although this index is specific for equatorial Pacific Ocean, it has a global impact. For example, during La Niña events (the positive phase) there is more hurricane activity in the Atlantic Ocean (Knutson et al. 2008; Latif and Grötzner 2000). ENSO (El Niño-Southern Oscillation) is a proxy for sea surface temperature (SST) and air pressure across the equatorial Pacific Ocean (Philander 1990). To quantify this index, we used a three month running period of Oceanic Niño Index for winter months (DJF, JFM, FMA) from NOAA database (http://www.cpc.ncep.noaa.gov/products/analysis_monitoring/ensostuff/ensoyears.shtml). Multivariate Enso Index (MEI) exhibits the same phases like the ENSO index, with opposite signature than SOI, meaning that the negative values correspond to cold La Niña conditions and positive values to warm El Niño conditions. But unlike ENSO, MEI consists of six different variables: sea level pressure, surface wind components, sea surface temperature, surface air temperature and total cloudiness (Wolter and Timlin 1993). The bimonthly values of winter months for MEI were obtained from NOAA database (http://www.esrl.noaa.gov/psd/enso/mei/table.html). Under La Niña conditions we would expect higher mortality of storm petrels due to stronger Atlantic hurricane activity during migration, as has been found for Cory's shearwaters (*Calonectris borealis*) (Ramos et al. 2012) and Scopoli's shearwaters (*C. diomedea*) (Boano et al. 2010; Genovart et al. 2013).

Recaptures and recoveries of Atlantic European storm petrels suggest that they may spend the winter off the southwest coast of Africa (Fowler 2002) using the biologically productive Benguela upwelling system (southwestern Africa) (Fig. 1). The signals of atmospheric elements carried by trade winds to the island of St Helena in the south-east Atlantic show the interannual fluctuations of SST in this region, creating temporal coefficient index, proposed as St Helena Island Climate Index (HIX) (Feistel et al. 2003). Its negative values are indicators of abnormally warm episodes and suppressed Benguela upwelling, while positive values show the opposite pattern (Hagen et al. 2005). Since upwelling brings the nutrient rich water to the surface and favours increase in zooplankton biomass and abundance (Cury et al. 2000), negative values of HIX may indicate a depletion of food resources available for storm petrels. Interannual changes in the Benguela upwelling region can also be associated with strengthening of the south-east trade wind components (Hagen et al. 2005), which can imply stormy weather potentially affecting survival of the species. HIX index values were obtained from the Baltic Sea Research Institute database (http://www.io-warnemuende.de/en_hix-st-helena-island-climate-index.html).

Within the Mediterranean basin, where Mediterranean storm petrels are suspected to remain the whole year, we used the Western Mediterranean Oscillation Index (WeMOi) as a proxy of heavy precipitation and river run-off. It depicts difference of the standardised values in surface atmospheric pressure in San Fernando (Spain) and Padua (Italy) (Martin-Vide and Lopez-Bustins 2006). WeMOi is positively correlated with fish landings in the North Western Mediterranean (Barausse et al. 2011). Furthermore, this index influences the strength of winds and torrential rainfall (Martin-Vide and Lopez-Bustins 2006), which could have direct impact on Mediterranean birds' mortality. WeMOi signature is reversed between the Western and the Eastern Mediterranean (Burić et al. 2014). Annual (July–June period) and winter WeMO index values (December–March) were obtained from the database of Climatology group of University of Barcelona (http://www.ub.edu/gc/English/wemo.htm). All climatic covariates were tested for inter-correlation after they were defined (Table 5, Appendix 1).

Statistical analysis

Mortality due to predation during the breeding season (m_c = mortality at the colony) and mortality due to other factors affecting petrels during the whole year (m_s = mortality at sea) were modelled by means of multievent capture–recapture modelling (Pradel 2005). The first step in the capture–recapture modelling was the assessment of the goodness-of-fit (GOF) of the Jolly-Movement (JMV) model using the program U-CARE 2.2.2. (Choquet et al. 2009a). Here we detected a significant trap-dependence effect in both datasets and a transient effect for the birds at Benidorm colony (Table 3, Appendix 1). Consequently, we included these effects in all the models performed. Two apparent age classes models in mortality were used to account for transient effects (Pradel et al. 1997). Differential recapture probabilities for individuals captured and not captured in the previous occasion were used to account for trap-dependence (Pradel and Sanz-Aguilar 2012). A transient effect was also tested in the models for Enez Kreiz colony (see Results). To account for the remaining lack of fit, model deviances were scaled using a variance inflation parameter ($\hat{c}$), calculated as the χ^2 over its degrees of freedom. The values used were $\hat{c} = 1.00$ and $\hat{c} = 1.77$, for Enez Kreiz and Benidorm colony, respectively (Table 3, Appendix 1). Given that dispersal between the two colonies has never been documented, mortality probabilities of adult breeders at each colony were estimated using individual capture–recapture data through two separate multievent capture–recapture analyses, implemented in program E-SURGE (Choquet et al. 2009b).

We used a modelling approach that included five biological states and three events (see details in Appendix 2). In each capture/recapture occasion, the possible events were: individual not captured ("0"); individual captured ("1"); individual recovered dead in the colony within a predator's pellet ("2"). The individual states considered were: individual alive and captured at its nest in the current occasion (AH); individual alive but not captured in the current occasion (AS); individual recently dead by predation at the colony (RDc); individual recently dead at sea (RDs); and long dead bird (LD). The initial state in the models was always AH (Vector 1).

$$\text{Inital state} = \begin{array}{cccc} \text{AH} & \text{AS} & \text{RDc} & \text{RDs} \\ (1 & 0 & 0 & 0) \end{array} \qquad \text{(Vector 1).}$$

For the purpose of this study, transition between states was modelled in a two-step approach: mortality (m_c and m_s: the transition between alive and dead states that differentiate the causes of mortality, Matrix 1) and recapture (p, the transition between the captured and not captured states, Matrix 2).

$$\text{Mortality} = \begin{array}{c} \\ \text{AH} \\ \text{AS} \\ \text{RDc} \\ \text{RDs} \\ \text{LD} \end{array} \begin{array}{ccccc} \text{AH} & \text{AS} & \text{RDc} & \text{RDs} & \text{LD} \\ 1-m_c-m_s & 0 & m_c & m_s & 0 \\ 0 & 1-m_c-m_s & m_c & m_s & 0 \\ 0 & 0 & 0 & 0 & 1 \\ 0 & 0 & 0 & 0 & 1 \\ 0 & 0 & 0 & 0 & 1 \end{array} \qquad \text{(Matrix 1)}$$

$$\text{Recapture} = \begin{array}{c} \\ \text{AH} \\ \text{AS} \\ \text{RDc} \\ \text{RDs} \\ \text{LD} \end{array} \begin{array}{ccccc} \text{AH} & \text{AS} & \text{RDc} & \text{RDs} & \text{LD} \\ p_h & 1-p_h & 0 & 0 & 0 \\ p_s & 1-p_s & 0 & 0 & 0 \\ 0 & 0 & 1 & 0 & 0 \\ 0 & 0 & 0 & 1 & 0 \\ 0 & 0 & 0 & 0 & 1 \end{array} \qquad \text{(Matrix 2)}$$

In order to separate mortality causes, the multievent model considered that probability of recovery for individuals dead at the colony was one (i.e., all predated individuals were detected, see event in Matrix 3 and details in Appendix 2). This is a necessary assumption to make model parameters identifiable, but this is not necessarily true (i.e., a small number of pellets may be lost in the sea, or removed by wind or rain). Given this assumption and the observed annual variation in the number of rings recovered in predators' pellets, all the models included time dependent variation in mortality probabilities due to predation at the colonies.

$$\text{Event} = \begin{array}{c} \\ \text{AH} \\ \text{AS} \\ \text{RDc} \\ \text{RDs} \\ \text{LD} \end{array} \begin{array}{ccc} 0 & 1 & 2 \\ 0 & 1 & 0 \\ 1 & 0 & 0 \\ 0 & 0 & 1 \\ 1 & 0 & 0 \\ 1 & 0 & 0 \end{array} \qquad \text{(Matrix 3)}$$

Based on previous analysis of the data (Table 4, Appendix 1) all models included parallel time dependent variation (i.e., additive time effects) in recapture probabilities of individuals captured and not captured in the previous occasion (i.e., trap-dependence), and additive transient effects (Sanz-Aguilar et al. 2010).

First, we tested the potential differences in mortality between newly marked and resident birds (i.e., transient effect; Pradel et al. 1997). Then we tested the effects of time and environmental covariates in the probabilities of mortality at sea. Model selection was based on the Akaike's Information Criterion adjusted for small sample size (c) and overdispersion (Q), calculated as: $\text{QAIC}_c = \frac{\text{Dev}}{\hat{c}} + 2\text{np}$ where Dev is model deviance, $\hat{c}$ is variance inflation factor, and np is the number of parameters in the model. Furthermore, for each model i, the Akaike weights (w_i) was calculated, as an index of its relative plausibility (Burnham and Anderson 2002).

The effect of environmental covariates on mortality at sea was tested by analysis of deviance (ANODEV) with a Fisher-Snedecor distribution (Skalski et al. 1993), calculated as:

$$F(1, \text{np}(\text{M}_t) - \text{np}(\text{M}_{\text{cov}})) = \frac{\text{Dev}(\text{M}_{\text{cnt}}) - \text{Dev}(\text{M}_{\text{cov}})}{(\text{Dev}(\text{M}_{\text{cnt}}) - \text{Dev}(\text{M}_t))/(\text{np}(\text{M}_t) - \text{np}(\text{M}_{\text{cov}}))}$$

where np is the number of estimable parameters of the models, Dev is the deviance estimated for the constant model (M_{cnt}), the model with environmental covariate (M_{cov}) and the time-dependent model (M_t). The proportion of the temporal variance explained by environmental covariate (R^2) was calculated as:

$$R^2 = \frac{\text{Dev}(\text{M}_{\text{cnt}}) - \text{Dev}(\text{M}_{\text{cov}})}{\text{Dev}(\text{M}_{\text{cnt}}) - \text{Dev}(\text{M}_t)}$$

Results

Model selection started with the general model that included transient and time effects on mortality probabilities at the colonies and at sea, and trap-dependence and time effects on recapture probabilities (Models 1, Table 1). Simpler structures of recapture did not reduce QAIC_c value of Model 1 for both datasets (Table 4, Appendix 1), so this recapture structure was used for modelling mortality. We first modelled mortality at the colony (Models 1–4, Table 1). Models including a transient effect in mortality at the colony due to predation were not supported (Table 1).

We continued model selection by testing the effects of time and transient on mortality at sea (Models 5–6, Table 1). For the Enez Kreiz colony a model with transient and no time effects for the mortality at sea, i.e., constant model (Model 5 EK, Table 1), was better supported than a temporal model (Model 2 EK, Table 1). In contrast, for Benidorm colony a model with additive

Table 1 Model selection for mortality probabilities (μ) of European storm petrel (*Hydrobates pelagicus*) on Enez Kreiz Islet, Western Brittany (EK) and Benidorm Island, Western Mediterranean (B)

Model	m_c	m_s	np	Dev	QAIC_c	$\Delta\mathrm{QAIC}_c$	w_i	R^2	F	P
12 EK	***t***	**a + wHIX + wENSO**	**31**	**2603.44**	**2667.43**	**0.00**	**0.56**	**0.43**	**7.47**	**0.02**
13 EK	*t*	a + wHIX + wSOI	31	2606.39	2670.39	2.96	0.13	0.30	4.35	0.06
14 EK	*t*	a + wHIX + wMEI	31	2606.67	2670.66	3.23	0.11	0.29	4.12	0.07
11 EK	*t*	a + wHIX	30	2610.01	2671.88	4.45	0.06	0.15	1.96	0.19
10 EK	*t*	a + wENSO	30	2610.74	2672.61	5.18	0.04	0.12	1.50	0.25
5 EK	*t*	a	29	2613.60	2673.34	5.91	0.03			
9 EK	*t*	a + wMEI	30	2612.66	2674.53	7.10	0.02	0.04	0.45	0.52
8 EK	*t*	a + wSOI	30	2612.77	2674.64	7.21	0.02	0.03	0.40	0.54
6 EK	*t*	.	28	2617.47	2675.10	7.67	0.01			
2 EK	*t*	a + *t*	41	2589.83	2675.33	7.90	0.00			
7 EK	*t*	a + wNAO	30	2613.56	2675.43	8.00	0.01	0.00	0.02	0.89
4 EK	.	a + *t*	29	2616.40	2676.15	8.72	0.01			
1 EK	a + *t*	a + *t*	42	2588.96	2676.64	9.21	0.01			
3 EK	a	a + *t*	30	2616.40	2678.27	10.84	0.00			
13 B	***t***	**a + WeMOi**	**28**	**3535.67**	**2054.34**	**0.00**	**0.29**	**0.57**	**13.01**	**0.01**
14 B	*t*	a + WeMOi + wHIX	29	3533.22	2055.01	0.67	0.21	0.61	13.98	0.01
18 B	*t*	a + WeMOi + wNAO	29	3533.92	2055.40	1.06	0.17	0.60	13.29	0.01
17 B	*t*	a + WeMOi + wSOI	29	3535.56	2056.33	1.99	0.11	0.57	11.80	0.01
15 B	*t*	a + WeMOi + wENSO	29	3535.66	2056.39	2.05	0.10	0.57	11.72	0.01
16 B	*t*	a + WeMOi + wMEI	29	3535.66	2056.39	2.05	0.10	0.57	11.72	0.01
2 B	*t*	a + *t*	38	3510.83	2060.96	6.62	0.01			
1 B	a + *t*	a + *t*	39	3510.76	2062.99	8.65	0.00			
11 B	*t*	a + wHIX	28	3554.60	2065.03	10.69	0.00	0.23	3.05	0.11
12 B	*t*	a + wWeMOi	28	3556.41	2066.05	11.71	0.00	0.20	2.54	0.14
10 B	*t*	a + wENSO	28	3558.04	2066.98	12.64	0.00	0.17	2.10	0.18
9 B	*t*	a + wMEI	28	3559.22	2067.64	13.30	0.00	0.15	1.81	0.21
4 B	.	a + *t*	27	3563.95	2068.26	13.92	0.00			
8 B	*t*	a + wSOI	28	3560.56	2068.40	14.06	0.00	0.13	1.49	0.25
3 B	a	a + *t*	28	3563.75	2070.21	15.86	0.00			
5 B	*t*	a	27	3567.99	2070.54	16.20	0.00			
7 B	*t*	a + wNAO	28	3567.85	2072.52	18.18	0.00	0.00	0.02	0.89
6 B	*t*	.	26	3594.50	2083.47	29.13	0.00			

m_c mortality at the colony due to predation, m_s mortality at sea, *np* number of estimable parameters, *Dev* relative deviance, $QAIC_c$ Akaike's information criterion adjusted for small sample size (c) and overdispersion (Q), $\Delta QAIC_c$ difference between current model and the model with the lowest QAIC_c, w_i Akaike's weights, R^2 proportion of variance explained by the covariate, *F* ANODEV test values, *P* value of statistical significance. "*wHIX*" winter St.Helena Index, "*wENSO*" winter Oceanic Niño 3.4 Index, "*wMEI*" winter Multivariate Enso Index, "*wSOI*" winter Southern Oscillation Index, "*wNAO*" winter North Atlantic Oscillation index, "*WeMOi*" annual Western Mediterranean Oscillation Index, "*wWeMOi*" winter Western Mediterranean Oscillation Index, "*t*" time effect, "*a*" transient effect, "." constant/no effects considered. The model with the highest w_i is in bold. The recapture probabilities for all the models took into account time and trap dependence effects (Table 4, Appendix 1)

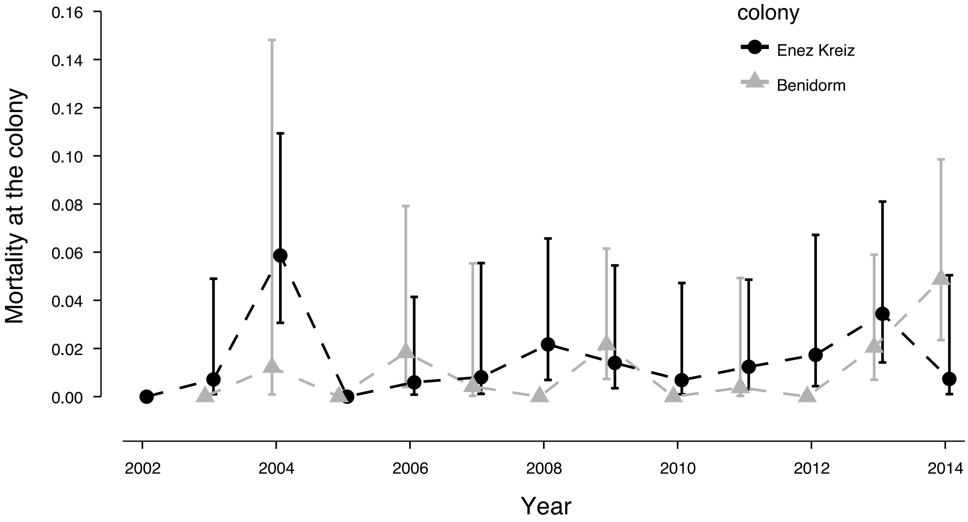

Fig. 2 Annual estimates (and 95% confidence intervals) of mortality probabilities at the colonies due to predation of European storm petrels breeding at Enez Kreiz and Benidorm islands (Models 12 EK and 13 B, Table 1)

Table 2 Mean estimates of European storm petrel mortality at sea at Enez Kreiz and Benidorm Island colonies, with 95% confidence intervals (CI) and standard error (SE) estimated by multievent capture–recapture modelling

Colony	Apparent age classes	Mean	95% CI	SE
Enez Kreiz	Newly marked	0.27	(0.20, 0.35)	0.04
	Residents	0.18	(0.15, 0.22)	0.02
Benidorm	Newly marked	0.23	(0.18, 0.29)	0.03
	Residents	0.11	(0.09, 0.14)	0.01

The estimates were derived from Model 5 (Table 1)

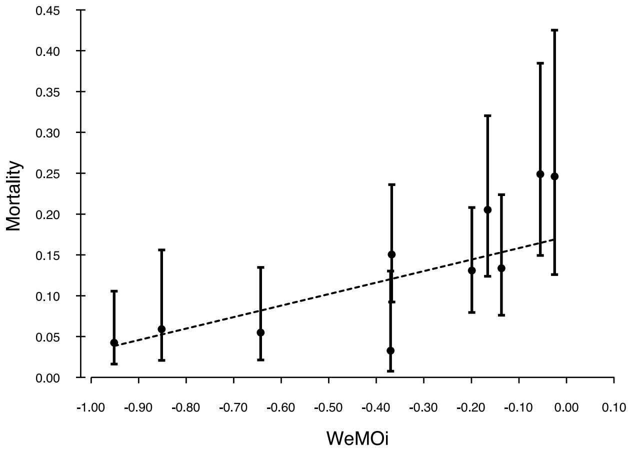

Fig. 3 Annual variation in mortality probabilities at sea of resident European storm petrels breeding at Benidorm Island in relation with annual WeMOi values. Estimates (*dots* with 95% CI) were obtained from the time dependent model (Model 2 B, Table 1) and the *dotted line* represents the mortality estimates of the model including the WeMOi covariate (Model 13 B, Table 1)

time and transient effects for the mortality at sea, i.e., time-dependent model (Model 2B, Table 1), was better supported than the constant model (Model 5B, Table 1). Finally, we tested the effects of environmental covariates (Models 7–18, Table 1). The best model for Benidorm colony was the one with the effect of climatic index WeMOi (Model 13 B, Table 1). The best model for Enez Kreiz colony was the one with the combined effect of the climatic index wHIX and the climatic index wENSO (Model 12 EK, Table 1).

Estimates of mortality due to predation for both study sites showed large variability between years, varying between 0.00 and 0.06 at Enez Kreiz, and between 0.00 and 0.05 at Benidorm colony (Fig. 2). Mean estimates of mortality at sea were slightly higher at Enez Kreiz colony but confidence intervals greatly overlapped (Table 2). Mortality probabilities of newly marked birds and residents were more similar at Enez Kreiz colony than at Benidorm (Table 2), which is in agreement with the failure to detect a transient effect by GOF tests in this colony (Table 3, Appendix 1). The WeMOi covariate explained 57% of temporal variability in mortality at sea (not due to predation) for Benidorm breeders (Model 13 B, Table 1). Higher mortality was related with higher WeMOi values (Fig. 3). For Atlantic breeders, wHIX and wENSO explained together only 43% of temporal variability in mortality at sea (Model 12 EK, Table 1). Here, higher mortality was related with lower wHIX and wENSO values (Figs. 4,5).

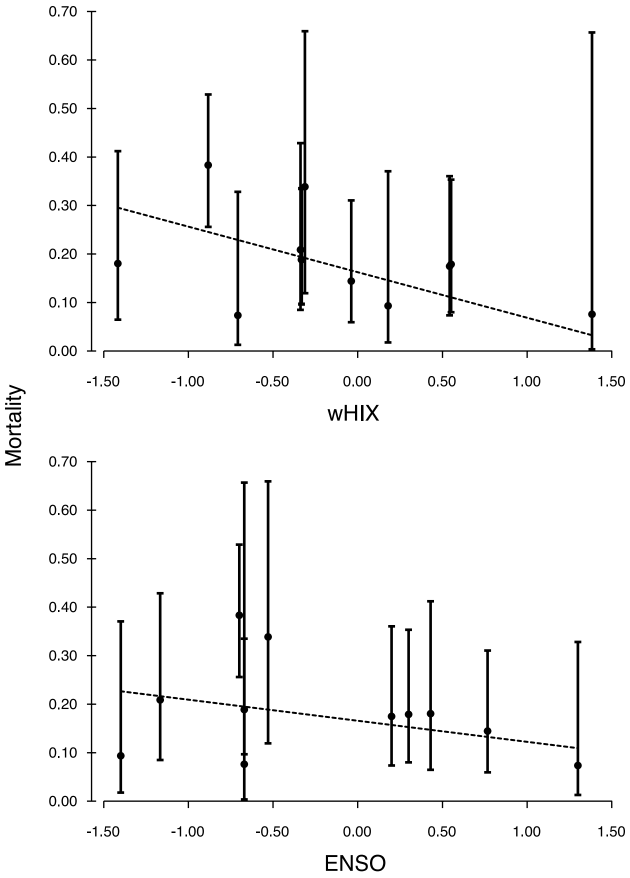

Fig. 4 Annual variation in mortality probabilities at sea of resident European storm petrels breeding at Enez Kreiz Island in relation with annual St. Helena index (wHIX) and winter ENSO index. Estimates (*dots* with 95% CI) were obtained from the time dependent model (Model 2 EK, Table 1) and the *dotted line* represents the mortality estimates of the models including the covariates (Models 10–11 EK, Table 1)

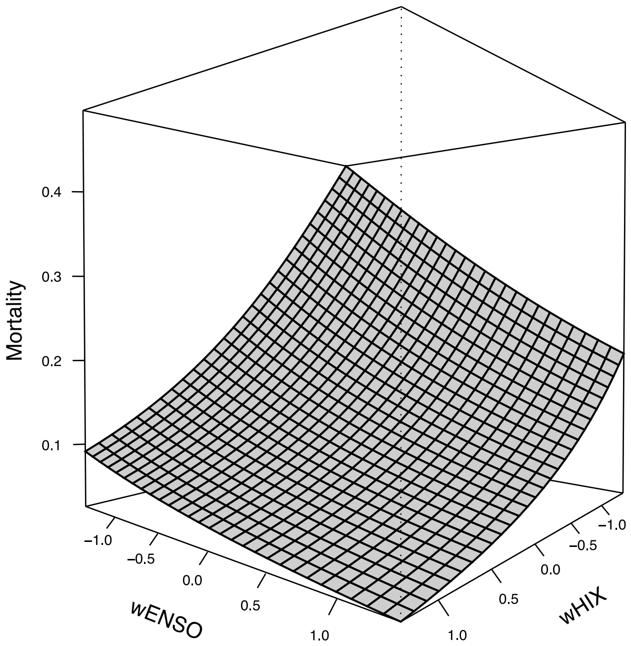

Fig. 5 Predicted mortality probabilities at sea of resident European storm petrels breeding at Enez Kreiz Island in relation with St. Helena index (wHIX) and winter ENSO index (Model 12 EK, Table 1)

Discussion

Mortality at sea

Seabirds are potentially important indicators of marine environmental variability at large spatio-temporal scales, owing to their long life-expectancy and integration of oceanic resources over wide areas (Ballerini et al. 2009; Genovart et al. 2013; Oro 2014). Climate influences vital rates (survival and reproduction) of numerous seabird species breeding all around the world (Jenouvrier 2013; Descamps et al. 2015). Migratory species face different environmental conditions during the year at breeding areas, migration routes and wintering quarters. During wintering and migration, individuals from different distant populations can use similar areas and be exposed to similar environmental conditions (Oro 2014). For example, the survival of Cory's and Scopoli's shearwaters breeding in the Atlantic and the Mediterranean is similarly affected by shared wintering oceanographic conditions, showing higher mortality during La Niña events (Jenouvrier et al. 2009; Ramos et al. 2012; Genovart et al. 2013). Similar results have been found for some terrestrial bird species such as white storks (*Ciconia ciconia*) (Schaub et al. 2005). Unfortunately, little is known about the European storm petrel's migration routes and wintering areas. Some birds ringed in Atlantic colonies have been recaptured or recovered during winter along the African coast as far as the Indian Ocean, especially in South Africa and Namibia (Fowler 2002) (Fig. 1). On the other hand, the extent of transequatorial migration and the spatial location of wintering areas of Mediterranean storm petrels remain largely unknown (Hashmi and Fliege 1994). This complicates the application of climatic indices in the right spatial scale when modelling vital rates (van de Pol et al. 2013; Oro 2014).

Our results clearly indicate that the Atlantic and Mediterranean subspecies were not affected by the same environmental factors, and showed different annual mortality, thus indicating the use of distinct migration routes and wintering quarters. The higher mortality of storm petrels from Enez Kreiz could be the result of a cost of longer migration to their wintering quarters, i.e., more energy expenditure during their journey to the south or south-eastern African waters, as it has been found for other long-lived and long-distance migrants (Schaub et al. 2005; Sanz-Aguilar et al. 2012). Moreover, our results indicate that Atlantic petrels are affected by different oceanographic conditions over their large migratory route, thus preventing association of their mortality to a single factor. Part of the temporal variability of adult mortality of Atlantic breeders was explained by wHIX and wENSO indices combined (Fig. 5). The wHIX climatic index operates at Benguela area, where some Atlantic birds have been detected during winter (Fig. 1; Fowler 2002), and higher mortality occurred when the Angola-Benguela upwelling was suppressed (Fig. 4; Hagen et al. 2005). Besides this bottom-up control, governed by supressed upwelling, mortality of Atlantic storm petrels was also influenced by negative values of ENSO, during La Niña conditions, when waters of tropical Pacific are cooling down and stronger hurricane season is expected in the eastern Atlantic (Fig. 4; Boano et al. 2010). This relationship has been also documented for other seabird species wintering in the Central and South Atlantic such as Cory's and Scopoli's shearwaters (Ramos et al. 2012; Genovart et al. 2013).

Mediterranean storm petrels probably remain in the basin throughout the year, experiencing reduced costs of migration compared with Atlantic migrants. Their mortality outside the colony was positively correlated with the WeMO index. The positive phase of WeMOi indicates favourable foraging conditions and lower heavy rainfall events in North Western Mediterranean (Martin-Vide and Lopez-Bustins 2006), but WeMOi signature in North Eastern Mediterranean is the opposite (Burić et al. 2014). When conditions are favourable in the western part of the basin, the movements of cyclones from west to east may generate unfavourable environmental conditions in the eastern part (Milošević et al. 2016). Extreme weather events, such as storms and gales, are known to cause direct mortality in the species (Warham 1990). Since 57% of the temporal variation in mortality of Mediterranean breeders was positively correlated with the climatic covariate WeMOi, it seems reasonable that Benidorm storm petrels might overwinter in the eastern Mediterranean. Nevertheless, without fully knowing the migration routes of *H. p. melitensis* it is difficult to select specific environmental covariates as a proxy for local weather drivers when studying mortality (van de Pol et al. 2013). Much work remains to be done regarding the effects of WeMO index at different spatial locations and on different components of food chains (Criado-Aldeanueva and Soto-Navarro 2013).

Mortality at colonies, top–down processes

As it has been found for other seabirds, the main mortality of storm petrels occurred at sea (Igual et al. 2009). However, mortality due to predation reached 5% in some years, representing a locally important cause of mortality (Sanz-Aguilar et al. 2009a). Adult mortality in some seabird species is governed by predator-driven processes compared to nutrient-driven control (Horswill et al. 2014, 2016). Unlike larger seabird species, upon which predators mainly prey on chicks and eggs (Igual et al. 2009), storm petrels are the smallest and are highly susceptible to top–down control by predation (Oro et al. 2005). Although newly marked individuals are potentially younger and less experienced (Sanz-Aguilar et al. 2008), we did not find an effect of age since marking (transience) on mortality probabilities by predation. This is probably because all the breeders have a similar behaviour outside their breeding site—walking rapidly inside their site after landing or flying rapidly at departure. Mortality due to predation showed a large annual variation, likely reflecting different temporal and spatial predation pressures. This could be explained by three nonexclusive hypotheses. First, predators may opportunistically prey on storm petrels when there is a depletion in their other food sources (Oro and Martinez-Vilalta 1994). Secondly, number of predators may change (Votier et al. 2004). Thirdly, predators may specialize and improve their hunting efficiency (Sanz-Aguilar et al. 2009a). It has already been shown that an increase in number of breeding aerial predators, and a decline in their other food supply, caused increased rate of predation on smaller seabirds (Votier et al. 2004). In general, mortality by predation was higher in Enez Kreiz, where no culling was performed on any predator (Cadiou 2001, 2013). In colonies free of predators (e.g., Skokholm Island 1966–1969 and Marettimo Island 1991–2006) total annual mortality of adult storm petrels was estimated around 10–11% (Scott 1970; Sanz-Aguilar et al. 2009b). Long-lived Procellariiform species, as storm petrels, have evolved in predator-free sites and lack specific anti-predatory behaviour apart from being nocturnal (Warham 1990).

In conclusion, we found that mortality in two allopatric colonies of storm petrels was linked to complex processes operating during breeding, migration and wintering seasons, generating important inter-population differences. This study emphasizes the necessity of modelling separately different causes of mortality when studying the effects of climate on vital rates.

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Appendix 1

See Tables (3, 4, 5).

Table 3 Goodness-of-fit (GOF) tests of the multistate Jolly Movement model and the transient and trap-dependence multistate models, for birds at Enez Kreiz Island, Brittany (noted EK) and birds at the at Benidorm Island (noted B)

Colony	EK		B	
Goodness-of-fit components	χ^2	*df*	χ^2	*df*
JMV model total	94.04	74	**141.33**	**47**
WBWA	0	0		
3G.SR transient effect	16.15	12	**43.56**	**11**
3G.SM	20.84	20	20.92	13
MITEC trap-dependence effect	**35.03**	**19**	**55.41**	**12**
MLTEC	22.02	23	**21.45**	**11**
Model with transients and trap-dependence	42.86	43	**42.37**	**24**
$\hat{c}$—Model with transients and trap-dependence	1.00		1.77	

Significant Chi square statistics ($P < 0.05$) are in bold

Table 4 Model selection for recapture probabilities (*p*) of European storm petrel (*Hydrobates pelagicus*) on Enez Kreiz Island, Western Brittany (EK) and Benidorm Island, Western Mediterranean (B)

Model	m_c	m_s	p	np	Dev	QAIC$_c$	ΔQAIC$_c$
1 EK	**a + *t***	**a + *t***	**trap + *t***	**42**	**2588.96**	**2676.64**	**0.00**
1b EK	a + *t*	a + *t*	trap	30	2622.56	2684.43	7.79
1 B	**a + *t***	**a + *t***	**trap + *t***	**39**	**3510.76**	**2062.99**	**0.00**
1b B	a + *t*	a + *t*	trap	28	3564.63	2070.70	7.71

m_c mortality at the colony due to predation, m_s mortality at sea, *np* number of estimable parameters, *Dev* relative deviance, *QAIC$_c$* Akaike's information criterion adjusted for small sample size (c) and overdispersion (Q), *ΔQAIC$_c$* difference between current model and the model with the lowest QAIC$_c$, "*t*" time effect, "*a*" transient effect, "*trap*" trap dependence effect. The model with the highest w_i is in bold

Table 5 Correlation between climatic covariates with Pearson's *r* test below the diagonal and *P* value of a *t* test above the diagonal

	wNAO	wSOI	wMEI	wENSO	wHIX	WeMOi	wWeMOi
wNAO		0.56	0.36	0.24	**0.03**	0.92	0.48
wSOI	0.18		**0.00**	**0.00**	0.35	0.12	0.72
wMEI	−0.28	**−0.97**		**0.00**	0.43	0.09	0.84
wENSO	−0.35	**−0.90**	**0.97**		0.51	0.10	0.87
wHIX	**0.60**	0.28	−0.24	−0.20		0.23	0.11
WeMOi	0.05	−0.48	0.48	0.50	0.36		0.14
wWeMOi	0.22	−0.11	0.06	−0.05	0.46	0.43	

The values in bold indicate that there is statistically significant correlation between covariates

Appendix 2

Specification of the multievent modelling approach in program E-SURGE

Multievent models were built in several stages using program E-SURGE (Choquet et al. 2009b). Multievent model uses three kinds of parameters: the initial state probabilities, the transition probabilities, and the event probabilities (conditional on the underlying states). Here the parameters of interest were mortality (*m*) and recapture probabilities (*p*). We used a specific structure of transition probabilities (decomposed in two steps, see below) that allows the differential modelling of two types of mortality (Pradel 2005) and accounts for trap-dependence effects (i.e., differential recapture probabilities in time $t+1$ of alive individuals captured and not captured in time *t*) (Pradel and Sanz-Aguilar 2012).

The multievent framework distinguishes the events, coded in the capture histories, from the states, which must be inferred. The possible events were:

0 = "not seen".
1 = "captured on the nest".
2 = "recovered dead in a pellet".

And the underlying biological states were:

AH	alive captured
AS	alive non-captured
RDc	recently dead at the colony
RDs	recently dead at sea
LD	long dead

The symbols for parameters were

m	mortality probability
p	recapture probability

The transition probabilities are presented in stochastic matrices form with departure states in rows and arrival states in columns (see specific matrices below). Each row corresponds to a multinomial. Consequently, the total of cell probabilities was 1. Because of this constraint, one and only one cell probability in each row will be calculated as the complement to 1 of the others. This particular cell is denoted with a '*' symbol. Inactive cells, i.e., cells whose associated probability is structurally 0 are denoted with a '-' symbol. An active cell receives an arbitrary letter.

As every individual in presented data set was captured alive for the first time, all initial state probabilities (Vector 1) were 1 for the state "AH" and this kind of parameter was not used here.

Initial State probabilities

$$\text{Inital state} = \begin{array}{cccc} \text{AH} & \text{AS} & \text{RDc} & \text{RDs} \\ (1 & 0 & 0 & 0) \end{array} \quad \text{(Vector 1)}.$$

The initial state probabilities vector is specified in GEPAT (E-SURGE) as:

1	2	3	4
*	–	–	–

Transition probabilities, step 1: Mortality

In the first step of transitions, the probabilities of mortality at the colony (m_c) and at sea (m_s) of alive individuals (states AH and AS) were modelled (Matrix 1). The last state—long dead 'LD' can only be reached from recently dead states (RDc and RDs) with probability 1, and once in this state an individual will remain in it forever (transition from 'LD' to 'LD' is 1: last row, last column).

$$\text{Mortality} = \begin{array}{cccccc} & \text{AH} & \text{AS} & \text{RDc} & \text{RDs} & \text{LD} \\ \text{AH} & 1-m_c-m_s & 0 & m_c & m_s & 0 \\ \text{AS} & 0 & 1-m_c-m_s & m_c & m_s & 0 \\ \text{RDc} & 0 & 0 & 0 & 0 & 1 \\ \text{RDs} & 0 & 0 & 0 & 0 & 1 \\ \text{LD} & 0 & 0 & 0 & 0 & 1 \end{array} \quad \text{(Matrix 1)}$$

Matrix 1 is specified in GEPAT (E-SURGE) as:

	1	2	3	4	5
1	*	–	m	m	–
2	–	*	m	m	–
3	–	–	–	–	*
4	–	–	–	–	*
5	–	–	–	–	*

Transition probabilities, step 2: recapture

In the second step of transitions, only the probabilities of recapture of alive individuals (states AH and AS) were modelled (Matrix 2), as dead individuals cannot be captured alive and the only possibility is to remain dead.

$$\text{Recapture} = \begin{array}{cccccc} & \text{AH} & \text{AS} & \text{RDc} & \text{RDs} & \text{LD} \\ \text{AH} & p_h & 1-p_h & 0 & 0 & 0 \\ \text{AS} & p_s & 1-p_s & 0 & 0 & 0 \\ \text{RDc} & 0 & 0 & 1 & 0 & 0 \\ \text{RDs} & 0 & 0 & 0 & 1 & 0 \\ \text{LD} & 0 & 0 & 0 & 0 & 1 \end{array} \quad \text{(Matrix 2)}.$$

Matrix 2 is specified in GEPAT (E-SURGE) as:

	1	2	3	4	5
1	p	*	–	–	–
2	p	*	–	–	–
3	–	–	*	–	–
4	–	–	–	*	–
5	–	–	–	–	*

Event probabilities, step 1

The event probabilities relate the observations coded in the capture histories to the underlying biological states (Matrix 3). Consequently, individuals alive and captured (AH) always have a code 1, and individuals alive but not captured (AS) always have a code 0. Dead individuals at the colony will have a code 2 with a probability 1 which assumes that every predated individual was recovered. Dead individuals at sea cannot be recovered in pellets and have a code 0 with a probability of 1.

$$\text{Event} = \begin{array}{cccc} & 0 & 1 & 2 \\ \text{AH} & 0 & 1 & 0 \\ \text{AS} & 1 & 0 & 0 \\ \text{RDc} & 0 & 0 & 1 \\ \text{RDs} & 1 & 0 & 0 \\ \text{LD} & 1 & 0 & 0 \end{array} \quad \text{(Matrix 3)}$$

Matrix 3 is specified in GEPAT (E-SURGE) as:

	1	2	3
1	–	*	–
2	*	–	–
3	–	–	*
4	*	–	–
5	*	–	–

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