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Title: Differential adult survival at close seabird colonies: the importance of spatial foraging segregation and bycatch risk during the breeding season

Running Head – Survival and bycatch risk in a long-lived species

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Abstract

Marine megafauna, including seabirds, are critically affected by fisheries bycatch. However, bycatch risk may differ on temporal and spatial scales due to the uneven distribution and effort of fleets operating different fishing gear, and to focal species distribution and foraging behaviour. Scopoli's shearwater *Calonectris diomedea* is a long-lived seabird that experiences high bycatch rates in longline fisheries and strong population-level impacts due to this type of anthropogenic mortality. Analyzing a long-term data set on individual monitoring, we compared adult survival (by means of multi-event capture-recapture models)

among three close predator-free Mediterranean colonies of the species. Unexpectedly for a long-lived organism, adult survival varied among colonies. We explored potential causes of this differential survival, by: (1) measuring egg volume as a proxy of food availability and parental condition; (2) building a specific longline bycatch risk map for the species; and (3) assessing the distribution patterns of breeding birds from the three study colonies via GPS tracking. Egg volume was very similar between colonies over time, suggesting that environmental variability related to habitat foraging suitability was not the main cause of differential survival. On the other hand, differences in foraging movements among individuals from the three colonies expose them to differential mortality risk, which likely influenced the observed differences in adult survival. The overlap of information obtained by the generation of specific bycatch risk maps, the quantification of population demographic parameters and the foraging spatial analysis should inform managers about differential sensitivity to the anthropogenic impact at mesoscale level and guide decisions depending on the spatial configuration of local populations. The approach would apply and should be considered in any species where foraging distribution is colony-specific and mortality risk varies spatially.

KEYWORDS

bycatch, conservation, marine predators, multi-event capture–recapture, risk map, seabirds, spatial mortality, survival

INTRODUCTION

Understanding the demographic processes driving population dynamics is crucial from a theoretical point of view to assess life-history theory, but also from an applied viewpoint for conservation purposes and ecosystem management. For both purposes, it is important to estimate demographic parameters and to disentangle the factors driving their variation. While the exploration of within-population variation, such as variation over time or among groups of individuals (e.g. sex, age), has been thoroughly analyzed, variation among wild populations of the same species has been seldom assessed, probably due to the challenges of gathering suitable data for rigorous comparisons (Frederiksen *et al.*, 2005) but see (Altwegg *et al.*, 2007; Papadatou *et al.*, 2011; Lee *et al.*, 2016). However, demographic parameters may also vary at a spatial scale due to the heterogeneous environments inhabited by individuals (Frederiksen *et al.*, 2005; Grosbois *et al.*, 2008, 2009) or to differing population features (e.g., age-structure, strength of density-dependence) (Tavecchia *et al.*, 2008; Sanz-Aguilar *et al.*, 2009).

The population growth rate in long-lived species is highly sensitive to changes in adult survival (Gaillard *et al.*, 2000). To persist in the face of environmental variation, adult survival in long-lived species is high and relatively invariable (Pfister, 1998; Gaillard *et al.*, 2000), and when strong variations in adult survival occur, species persistence may be jeopardized. Agents of global change, such as anthropogenic mortality and overharvesting, increase environmental variability and unpredictability and may result in large declines in adult survival. Additionally, temporal and spatial scales should be taken into account when assessing anthropogenic mortality risk, as both animal and anthropogenic threat may vary at a spatial and a temporal scale (Bradbury *et al.*, 2014; Brown *et al.*, 2015; Guil *et al.*, 2015).

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Of particular concern in the case of marine megafauna, is fisheries bycatch mortality (Lewison *et al.*, 2004, 2014). This source of mortality has increased throughout all marine ecosystems in the last decades due to fisheries expansion, increased harvesting rates, fishing technology and power, and changes in fish market consumption due to social changes in human societies (e.g. Curtin & Prelezo, 2010). Other agents of global change such as climate warming and pollution may exacerbate the impacts of bycatch in certain regions and also in the temporal scale (Brander, 2010; Sguotti *et al.*, 2016). Despite the mounting evidence of the occurrence of megafauna bycatch, it is difficult to quantify mortality rates and evaluate its impact in most species and populations (but see Genovart *et al.*, 2016, 2017). Additionally, non-negligible differences may exist in bycatch rates at a temporal and spatial scales (Tuck *et al.*, 2003; Anderson *et al.*, 2011; Lewison *et al.*, 2014; Roe *et al.*, 2014). Thus it would be desirable for conservation planning to build maps of fisheries bycatch risk for each species or community affected that take into account spatio-temporal scales of risk and specific features characterizing fishing gear.

The degree of overlap between bycatch risk and seabird preferences for oceanic habitat influences their vulnerability (Hyrenbach *et al.*, 2002; Inchausti & Weimerskirch, 2002). For any given species, the greater the overlap of risky longline fisheries and species distribution, at both temporal and spatial scales, the higher the mortality risks. In this regard, some species may show spatial foraging segregation among populations (Grémillet *et al.*, 2004; Louzao *et al.*, 2011; Wakefield *et al.*, 2013), with possible consequences at the level of bycatch probability. Tracking technology presently offers the opportunity to accurately assess this segregation and to obtain information about foraging grounds and range in highly vagile marine species, information that is otherwise difficult, if not impossible, to obtain (Wilson *et al.*, 2002; BirdLife International, 2004). While cross-taxa and cross-gear bycatch assessment is necessary for good global fisheries management schemes, for both a better understanding

and the successful management of most species, it is also extremely useful to cross information on specific maps of bycatch risk and species foraging distribution. The generation of spatially explicit risk maps for anthropogenic impacts related to global change is a useful tool for prioritizing conservation actions targeting threatened populations, species and communities (Jaiswal *et al.*, 2002; Lewison *et al.*, 2009; Venette *et al.*, 2010; Bradbury *et al.*, 2014; Brown *et al.*, 2015; Certain *et al.*, 2015).

The Mediterranean Sea has been identified as one of the hottest spots of bycatch impact on marine megafauna worldwide (ICES 2013; Lewison *et al.*, 2014; FAO 2016). One of the taxa most affected by fisheries bycatch is Scopoli's shearwater *Calonectris diomedea* (García-Barcelona *et al.*, 2010; Karris *et al.*, 2013; Báez *et al.*, 2014; Cortés *et al.*, 2017) and previous works have pointed to the potential factors that may drive this bycatch (Belda & Sanchez, 2001; Laneri *et al.*, 2010; Soriano-Redondo *et al.*, 2016). Additionally, one recent study showed a strong population-level effect of this anthropogenic impact and demonstrated that urgent conservation actions are required to ensure the viability of some populations of this long-lived species (Genovart *et al.*, 2017). However, this study was based only on a single colony, and hence, it is important to gather information from other colonies to shed light on the global status of the species and to assess how source-sink dynamics may influence population functioning (Sanz-Aguilar *et al.*, 2016a).

Here, we take advantage of the long-term monitoring of three rat- and carnivore-free colonies of Scopoli's shearwater (authors unpublished data) and a 17-year individual mark-recapture dataset to jointly analyze potential spatio-temporal variation in vital rates and assess factors affecting these differences. We also build the first detailed longline bycatch risk map in the western Mediterranean for this species, gathering and analyzing detailed information on longline fisheries (i.e., type of longline, power, temporal and spatial vessel distribution, fishing effort, number of hooks). Furthermore, this information is useful not only for other

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seabird species, but also for other megafauna affected by longline bycatch in the study area. We additionally analyzed data on GPS-tracking of 75 breeding adults from the three colonies, to assess both their foraging distribution pattern during the breeding period and the longline bycatch risk depending on the colony. The present study specifically aims to: 1) rigorously estimate adult survival and breeding performance at three western Mediterranean colonies of Scopoli's shearwater; 2) build a longline bycatch risk map for this species for the western Mediterranean; 3) assess the foraging range and spatial segregation of the individuals from the three different study colonies; and 4) assess longline bycatch risk of individuals breeding at each colony. In the absence of any anthropogenic impact, we would expect survival to be almost constant in this long-lived species, especially when individuals breed in predatory-free colonies and inhabit the same geographical area. If spatial variation appears, we expect this to be linked to differential bycatch mortality risk among colonies.

Materials and methods

Study species

Scopoli's shearwater is a long-lived Procellariiform that breeds at colonies on the Mediterranean islands. It was recently split from the closely related Atlantic form, Cory's shearwater *Calonectris (d.) borealis* (Sangster et al., 2012; but see Genovart et al., 2013a). This Mediterranean form carries out long-distance migrations to Sub-tropical and South Atlantic waters, with most individuals arriving in the Mediterranean by early March and breeding from May to October (Cramp & Simmons, 1977; Karris 2014; de los Reyes-González & González-Solís, 2016). The species lays one egg and is characterized by biparental care during incubation and chick-feeding (Cramp & Simmons, 1977; del Hoyo et al., 1992; Sánchez-Codoñer & Castilla, 1997). The species feeds mostly on fish, squid and crustaceans, but also exploits fishing discards and experiences high mortality

in longlines (García-Barcelona et al., 2010; Báez et al., 2014; Karris et al. 2015; Genovart et al., 2017).

Bycatch risk map

Longline fishing is an extensive fishing practice in the Spanish Mediterranean, with substantial variability in configuration and practices. Overall, we can define three major types of longline, all of them contributing to seabird bycatch: (a) small-scale demersal; (b) medium-scale demersal; and (c) pelagic (García-Barcelona *et al.*, 2010; Cortés *et al.*, 2017). Vessels conducting pelagic longline are the largest (12-27 m) and tend to operate at larger scales. The two classes of demersal longliners defined here are quite heterogeneous, with vessels ranging from 6 to 18 m, but medium-scale vessels are specifically licensed for demersal longlining and tend to be slightly larger, whereas small-scale vessels are polyvalent and can alternate between different gears.

We built a longline bycatch risk map for Scopoli's shearwater covering the Spanish Mediterranean waters from the coastline off to 2800 m depth, and from the French border and slightly beyond in the NE (42.8°N) to almost Gibraltar in the SW (36.3°N) (Fig. 1). To that aim, we used a grid of 0.1° x 0.1°, a spatial resolution that allows to correctly grouping the information of the VMS data, but without losing spatial detail. For each grid cell, a bycatch risk index was estimated, taking in consideration fishing effort and the likelihood to capture birds according to the period and the type of bycatch. Each type of bycatch was first considered separately, and then values were averaged taking into account the relative risk of each type of bycatch for the Scopoli's shearwaters (i.e. according to bycatch rates; García-Barcelona et al., 2010; Laneri et al., 2010; Cortés et al., 2017).

Fishing effort was estimated as the relative abundance of vessels on any given cell across time (for each month during the four years of study), and also taking into account the maximum number of hooks potentially set by each type of longline vessel (BOE 2012) (Table 1). To assess vessel distribution, whenever possible we used Vessel Monitoring System (VMS) data, provided by the Spanish Government (Centro de Seguimiento de Pesca, Ministerio de Agricultura y Pesca, Alimentación y Medio Ambiente - MAPAMA) for the period 2008-2012. However, VMS only applies to vessels over 12 m long, so it was mostly appropriate to assess pelagic longliners distribution (as about 60% of the fleet overpasses that length; Bécares & Cama, 2013). However, for the demersal longliners most vessels are small and lack VMS data. In this case we relied on the fleet statistics also provided by the Spanish Government (Subdirección General de la Flota Pesquera, MAPAMA). This provided the number of vessels per port, and from that we inferred their abundance at sea considering a radius of action of 75 km (and 500 m depth) for the medium-scale demersal longliners and 50 km (and 200 m depth) for the small-scale vessels, based on the available data from studies with observers onboard and questionnaires (Laneri et al., 2010; Cortés et al., 2017; Tarzia et al. 2017). In the case of the small-scale vessels, taking into account information from questionnaires (SEO/BirdLife 2014), we assumed that about 20% of them used demersal longline at some point, and that one third of their time was devoted to longline. This assumption is rough and subject to strong variability, but fishing statistics do not provide this type of information and hence available data did not allow making a more refined assessment. In the case of the Balearic Islands, however, the bulk of the small-scale fleet concentrates in the fishing of lobsters (with nets and traps) from April to August, so we disregarded small-scale vessels for that period.

Regarding the likelihood of captures, we only used data from months in which Scopoli's shearwaters are present in the Mediterranean (March to October, de los Reyes-González & González-Solís, 2016). Moreover, since bycatch rates appear to vary along the season (Cortés *et al.*, 2017), we weighted data to generate a pelagic longline risk map by month (Table 1). Thus, the highest risk occurs in May (value = 1.00), followed by April (0.28), June (0.14), and the remaining months (<0.10) (BOE 2012; SEO/BirdLife. 2014).

Study colonies and field methods

Data were collected from three rat- and carnivore-free western Mediterranean colonies: Aire Island in Menorca (39°48' N, 4°17'E), Pantaleu islet in Mallorca (39°34' N, 2°21' E), both in the Balearic Archipelago, and Columbretes Islands off the eastern Iberian coast (39°55'N, 0°40'E) (Fig. 1). Aire, Pantaleu and Columbretes hold ca. 60, 200 and 65 breeding pairs, respectively (Sanz-Aguilar *et al.*, 2016b; Authors unpublished data).

At the three colonies, adults and chicks were trapped during daylight on their nesting burrows (or at night in burrow surroundings), and marked with stainless-steel bands with a unique code to allow identification, or recaptured if they had been previously marked. For the statistical analyses, we only considered individuals captured as adults. Our capture-recapture dataset includes data from 1999 to 2016 for Aire and Columbretes and from 2000 to 2016 for Pantaleu.

Remote tracking of Scopoli's shearwaters

To analyze the overlap between longline fishing activity and shearwater distribution at sea we used GPS tracking data obtained between 2007 and 2012 during the late incubation and chick-rearing periods. Birds were equipped with CatTrack GPS loggers (Perthold, 2011), sealed using a rubber shrink tube to ensure waterproof. Loggers were programmed to collect

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locations every 5 minutes, which allowed for a battery life of 10–15 days. The weight of the sealed devices was approximately 20g, roughly representing 3–5% of the bird's body mass (Wilson et al., 2002; Phillips et al., 2003). We used data from Mallorca (6 individuals from Pantaleu monitored in 2007), Menorca (4 individuals from Aire monitored in 2007 and 34 individuals from Cala Morell monitored in 2007 and 2010) and Columbretes (31 individuals monitored in 2011 and 2012). Data from the two colonies in Menorca (Cala Morell and Aire) were pooled together to obtain a larger sample size and based on the fact that birds from both colonies forage at the same fishing grounds, as determined by GPS tracking (see Fig. S1 in Appendix).

To determine the overlap between shearwaters and high bycatch risk areas, we calculated the percentage of time that each individual spent in high-risk cells (risk value > 3rd quartile). We averaged the value of all individuals from each study colony to determine if there were statistically significant differences among colonies. We employed a permutation test to evaluate differences, and a pairwise permutation test as a post-hoc method (coin and rcompanion package in R, <http://www.R-project.org>).

Egg volume

Egg volume is a good indicator of food availability and adult conditions during first stages of breeding (Ratcliffe *et al.*, 1998; Oro *et al.*, 2004). Thus, to compare early breeding conditions between colonies we measured and compared egg volumes between Aire Island and Pantaleu Islet. We measured egg length and width at nests from Pantaleu Islet between 2001 and 2016, and from Aire Island between 2009-2016, with no egg measurements taken in 2013. No egg measurements from Columbretes were available for the study period because most eggs were inaccessible.

Egg volume (in cm³) was calculated as: $V=0.00051*\text{egg length (in cm)}*(\text{egg width(in cm)})^2$ (Hoyt, 1979; Mougin, 1998). We then estimated the annual mean egg volume for each colony and assessed which factors affected its spatio-temporal variability. We tested for the influence of the North Atlantic Oscillation (NAO) Index, as the NAO affects water column hydrodynamics and may drive the production, distribution and abundance of the organisms upon which birds feed (Stenseth, 2004; Gordo *et al.*, 2011). To test the NAO effect, we selected the extended annual winter NAO (i.e., December–March) with positive values related to windy and warmer conditions, and negative values to colder air and wetter conditions in the Mediterranean (<http://www.cgd.ucar.edu/cas/jhurrell/indices.html>) (Hurrell, 1995). To do this, we carried out generalized linear models in R, with egg volume as the response variable, colony and year as explanatory factors, and NAO as a covariate. Additionally, to complementarily assess the amount of variation explained by the NAO index, we also performed an analysis of deviance test (ANODEV) (Skalski *et al.*, 1993). The percentage of variation that was explained by the NAO (r^2) was estimated as:

$$r^2 = \frac{Dev(M_{cnt})-Dev(M_{cov})}{Dev(M_{cnt})-Dev(M_t)}$$

Where Dev is the deviance estimated for the constant model (M_{cnt}), the model with climatic covariate (M_{cov}) and the time dependent model (M_t).

Analysis of survival

We jointly analyzed adult survival at the three colonies. To assess the fit of our models, we first carried out a goodness-of-fit (GOF) test using U-care (Choquet *et al.*, 2009a). To estimate annual survival probability we used multi-event capture-recapture modeling and

models were fitted in the program E-SURGE (Pradel, 2005; Choquet *et al.*, 2009b). These models hold two levels in capture-recapture data: field observations, called “events”, encoded in the capture histories, and “states” defined to match the biological questions and which can only be inferred. Individuals were classified into three groups based on their breeding colony and only adults were included in the analysis. To correct for trap heterogeneity (see results) we differentiated individuals depending on whether they had been previously observed (Aware) or not (Unaware) (Pradel & Sanz-Aguilar, 2012). Thus, our models included three biological states: individual alive aware (AA); individual alive unaware (AU); and dead (D). The latter state was non-observable. The initial state in our models was always AA. Transitions between states were modelled in a two-step approach: survival and recapture probability (conditional on survival). On each capture-recapture occasion (t), we considered two possible events: individual not seen (noted 0); and individual seen alive (noted 1). Details on the multi-event models can be found in Appendix S1. As we found a strong transient effect (see results below), we included one different survival for individuals captured for the first time and another for those captured more than once. Based on previous results (Genovart *et al.*, 2013b), we tested for a time variant survival, and for an effect of the Southern Oscillation Index (SOI) (<http://www.cru.uea.ac.uk/cru/data/soi/soi.dat>), in an additive and interaction manner with colony. As an exploratory model, we also ran a model to estimate mean adult survival, including transients and residents. Given the different capture-recapture efforts made annually in the three colonies, we kept the recapture probability time variant and colony dependent. Model selection relied on QAICc (i.e., the Akaike Information Criterion duly corrected for overdispersion and small sample size) (Burnham & Anderson, 2002).

RESULTS

Bycatch risk and foraging patterns

Our longline bycatch risk map showed that the areas with higher risk were those corresponding to the Iberian continental shelf, particularly off Central and North Catalunya and from Cape La Nao to Cape Palos, and the deep waters south of the Balearic Archipelago (the latter mostly related to pelagic longline). On the other hand, lower risk areas were deep waters between the Catalan coast and the Balearic archipelago (Fig. 1).

Despite the fact that the colonies were closely situated, we observed a clear segregation at sea among individuals from different colonies (Fig. 2). Individuals breeding at Menorca (Aire and Cala Morell) mainly foraged in the area of the Mallorca-Menorca Canal, whereas individuals from Columbretes mainly foraged in waters around the archipelago, at distances of ca. 100km around the colony. Individuals from Pantaleu mainly foraged in coastal waters, at the Balearic southern coasts and at waters off Cape La Nao.

When assessing the risk of longline bycatch for individuals at the three colonies we observed that individuals from Pantaleu had a higher probability of longline bycatch due to a greater overlap between areas of high bycatch risk and foraging (Fig. 2). Both individuals from Columbretes (post-hoc pairwise permutation test; p -value=0.0316), and especially those from Menorca (p -value=0.00067), showed a lower risk of longline bycatch than those from Pantaleu Islet in Mallorca. Individuals from Menorca also showed a lower risk of longline bycatch than those from Columbretes (p -value=0.0267, Fig. 2).

Egg volume

We measured 123 and 789, eggs at Aire and Pantaleu, respectively. Egg volume varied annually and in a similar way between Pantaleu and Aire; annual differences were influenced in both colonies by the NAO index (Table 2 and Fig. 3), with smaller volumes when higher NAO index values. The ANODEV test performed revealed a relevant effect of the NAO index, explaining a significant 74% of the annual egg volume variation ($F_{1,7} = 19.72$, $p < 0.005$).

Analysis of survival

We analyzed 1561 individual capture-recapture histories from the three colonies; 231 from Aire, 876 from Pantaleu and 454 from Columbretes. When analyzing the complete data set, the GOF for the Cormack-Jolly-Seber model was poor ($\hat{c} = 2.76$) mainly due to both the presence of transients and trap-heterogeneity. All of our models included two ages to correct for transience and a trap effect and we corrected for remaining overdispersion with a lower inflation factor ($\hat{c} = 1.42$).

The most parsimonious model indicated that adult survival differed between colonies and also depended on the annual SOI value (Model 1, Table 3). The SOI globally explained about 21% of the variance in annual survival ($F_{1,16} = 4.38$, $p = 0.05$). Adult survival probability was highest for breeders from Aire and lowest for individuals from Pantaleu, whereas shearwaters from Columbretes showed an intermediate annual survival probability (Table 4). When not correcting for a transient effect and thus assuming equal survival probability for those individuals seen for the first time and those residents (Model 9, Table 3), mean adult survival probability (and 95% confidence intervals) for individuals breeding at Aire, Pantaleu and Columbretes were 0.877 (0.846-0.902), 0.819 (0.802-0.834) and 0.860 (0.826-0.887), respectively, again showing the same pattern of differences among colonies.

DISCUSSION

Unexpectedly for a long-lived species, we found a strong spatial variation in adult survival. The fact that we found differences in survival between colonies but not in egg volume suggests that probably those differences are related to spatial heterogeneity in mortality risk and not to food availability. Indeed, crossing information from a detailed and rigorous longline bycatch risk map with foraging distribution patterns of individuals from the three study colonies, we conclude that differential bycatch mortality between colonies may be taking place. Furthermore, adult survival in Pantaleu and Columbretes (but not in Aire) was much lower than expected for Scopoli's shearwaters (Jenouvrier *et al.*, 2009; Genovart *et al.*, 2017) and for a long-lived organism. As previously demonstrated, our study also points to longline bycatch as an additive and high source of mortality for this (Genovart *et al.*, 2017) and closely-related species (Genovart *et al.*, 2016).

Wakefield *et al.* (2013) provide strong evidence that seabirds in neighboring colonies avoid direct food competition by segregating in largely mutually exclusive areas. In agreement with this and other previous studies (Grémillet *et al.*, 2004; Wiley *et al.*, 2012; Corman *et al.*, 2016), we show such a foraging segregation between relatively close colonies (140 to 250 km apart) despite the fact that Procellariiforms are highly vagile. In our study case, the spatial foraging segregation between colonies differently affected the risk of mortality due to longline bycatch. This was due to the heterogeneous distribution of fishing effort within the study region, related to topographical and oceanographic features, as well as differences in longline modalities and practices across the region, as well as an uneven distribution of the longline fleet across ports. As a result, non-negligible spatial differences in survival may occur even at a small scale, and this should be taken into account when assessing species bycatch risk and its impact on different populations, even at relatively close distances or even when assessing global species status. More research should be done to determine spatial

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bycatch risk in the wintering areas to assess if there is also differential bycatch mortality during the wintering phase (González-Solís *et al.*, 2007a; Rayner *et al.*, 2011; Thiebot *et al.*, 2011).

Although our results come from a temporally static bycatch risk, it is also likely that temporal variations of risk mortality occur in the long term. For instance, even though long-term seabird bycatch data is seldom available, it is known that recent development and expansion of some longline fleets has triggered the appearance of seabird bycatch in several regions of the world (Tuck *et al.*, 2003). Contrarily, bycatch mitigation measures implemented in some fisheries may decrease mortality risk for seabirds, turtles and marine mammals (Lewison *et al.*, 2004; Read *et al.*, 2006). Additionally selection filter acting on heritable traits of individuals prone to follow fishing fleets may decrease the percentage of those individuals in populations, with a resulting recovering of population densities (Barbraud *et al.*, 2013; Tuck *et al.*, 2015). It is also expected that the temporal variability of other global change agents, such as climate, overharvesting and invasive species, may interact with the trends in bycatch mortality risk, either exacerbating or buffering its effects on marine megafauna.

We also show that global climatic indices play an important role in the population dynamics of this long-lived seabird species. Apart from the differential mortality between colonies due to anthropogenic effects, we confirm that El Niño-Southern Oscillation (ENSO) is driving adult survival in all the colonies, with lower survival in years with low SOI values. It has been previously suggested that SOI affects adult survival in this species via annual differences in the intensity and frequency of hurricanes in the wintering season (Bricchetti *et al.*, 2000; Genovart *et al.*, 2013b). While an indirect effect of the SOI on survival via changes in food availability cannot be ruled out, long-lived organisms mostly maintains a constant adult survival rate despite temporal environmental variability (Lescroël *et al.*, 2009), thus we

would only expect a decrease when facing very drastic disturbances and extended to a very large area. On the other hand, egg volume seems to be partially driven by the NAO index, which probably influences food availability prior to and during the egg-laying period (see also Michel *et al.*, 2003).

The demographic buffering process allows populations to persist in the face of environmental change by favouring traits that buffer most sensitive vital rates from temporal environmental variation (Pfister, 1998; Gaillard *et al.*, 2000). Thus, adult survival in long-lived species population dynamics is often high and shows little temporal and spatial variation (Stearns, 1992; *i.e.* Altwegg *et al.*, 2007 and Baker & Thompson, 2007). However, if global change agents act, as bycatch does in this species, strongly decreasing adult survival, and especially if this effect is prolonged over time, it may compromise population and species persistence (see Genovart *et al.*, 2017). In two of the three colonies, survival is critically low, compromising populations and perhaps species' persistence (see Genovart *et al.*, 2017). Foraging segregation between colonies may desynchronize population growth rates and thus confer some resilience to the species (Royama, 1992; Heino *et al.*, 1997). This may be especially true because Menorca, where bycatch impact was low, actually holds one of the largest Scopoli's shearwater numbers in the western Mediterranean. The spatio-temporal heterogeneity for the intensity of anthropogenic impacts may also alter source-sink dynamics and the rescue effect potentially provided by source populations (Sanz-Aguilar *et al.*, 2016a). However, given the survival estimates obtained and the bycatch rates estimated for the species (Belda & Sanchez, 2001; Laneri *et al.*, 2010; Soriano-Redondo *et al.*, 2016), urgent bycatch mitigation actions should be taken to reduce anthropogenic adult mortality. Finally, selection pressure over individuals more prone to bycatch-related mortality may exert evolutionary rescues in impacted populations (Barbraud *et al.*, 2013; Carlson *et al.*, 2014).

This approach may be suitable, not only when assessing bycatch risk, but also when dealing with other potential anthropogenic threats, such as wind farms, electrocution by electric towers or even oil spills (Bevanger, 1998; Drewitt & Langston, 2006; De Lucas *et al.*, 2008; Tintó *et al.*, 2010; Issaris *et al.*, 2012; Hermann Hötter & Oliver Krone, 2017) and to mitigate conflicts for human resources use and preserving wildlife. For instance, some electric towers are known to have a more dangerous design for birds than others, but this difference should be higher or lower depending on the overlap between the foraging areas and the occurrence of a specific tower design. Bird collision in wind farms does not only vary with bird abundance (Bradbury *et al.*, 2014) but also with turbine type, configuration and location (De Lucas *et al.*, 2008; Ferrer *et al.*, 2012). Our approach would apply to any population of a colonial animal where foraging distribution is colony-specific and mortality risk varies spatially. Distribution of foraging by breeding social animals is likely colony-specific (Wilson *et al.*, 2017; Brown & Brown, 2002; Masello *et al.*, 2010) and in turn mortality risk should also be colony-specific, as suggested by our study. Contrarily colony-specific wintering areas occur rather at regional scale that might result in a similar spatial variation in mortality risk during winter (Hedd & Gales, 2005; González-Solís *et al.*, 2007; but see Genovart *et al.*, 2013). The overlap of information obtained by the generation of specific risk maps, the quantification of population demographic parameters and the foraging spatial analysis should inform managers about differential sensitivity of an anthropogenic impact at a mesoscale and guide their decisions depending on the spatial configuration of local populations.

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Table 1. Weight assigned to each longline fishing fleet operating in the study area based on the size of the different fleets, the number of hooks and the time spent using longline gears.

Fishing gear	Number of boats in the study area (2008) ¹	Maximum hooks per boat	% of boats longline fishing	Time dedicated to longline fishing	Weight
Small-scale longline	1052	2000	20% *	33% *	0.20
Bottom longline	59	3000	100%	100%	0.25
Pelagic longline	79	5000	100%	100%	0.55

¹ data given by "Subdirección General de la Flota Pesquera" (MAPAMA)

Table 2. Model selection for assessing factors affecting egg volume variation between colonies of Scopoli's shearwater. Data are from Aire Island and Pantaleu Islet, during 2009-2016. Best model is shown in bold. Np = number of parameters, QAICc = AIC value corrected for overdispersion, Δ AIC = AIC difference points from the best model, w_i = weight of model i from all the models tested; “*” and “+” show interaction and additive effect between factors, respectively.

Model	Deviance	np	AICc	Δ AIC	w_i
Constant	2877.982	2	5759.963	27.134	0.00
Year	2858.245	9	5734.489	1.660	0.18
Colony	2877.351	3	5760.702	27.873	0.00
NAO	2863.415	3	5732.829	0	0.42
Colony + Year	2857.828	10	5735.656	2.827	0.10
Colony * Year	2855.897	16	5743.793	10.964	0.00
NAO+ Colony	2863.216	4	5734.432	1.603	0.19
NAO* Colony	2862.855	5	5735.711	2.882	0.10

Table 3. Model selection (see Methods) for estimating survival in Scopoli's shearwater in three western Mediterranean colonies. All models assumed a time variant and colony-specific recapture probability. Best model is shown in bold and the model for estimating annual mean survival at each colony is shown in italics. T/R: two ages, transients and residents. "+" indicates additivity between factors and "*" interaction.

Model	Survival	np	Deviance	QAICc	Δ QAICc	w_i
1	(T/R) * colony + SOI	57	9452.72	6867.364	0	0.73
2	(T/R) + colony + SOI	55	9463.05	6870.65	3.28	0.14
3	(T/R) * colony	56	9461.18	6871.36	3.99	0.10
4	(T/R) * colony. SOI	62	9448.10	6874.33	6.96	0.02
5	(T/R) * colony + t	72	9421.81	6876.13	8.77	0.01
6	(T/R) + SOI	53	9478.59	6877.65	10.29	0.00
7	(T/R) + colony +t	70	9430.26	6878.04	10.68	0.00
8	(T/R) + t	68	9447.18	6883.98	16.62	0,00
9	<i>(T/R) * colony</i>	56	<i>9481.09</i>	<i>6885.58</i>	<i>18.21</i>	<i>0.00</i>
10	colony + SOI	54	9490.27	6888.04	20.68	0.00
11	colony	53	9495.24	6889.55	22.18	0.00
12	colony + t	69	9454.73	6893.46	26.10	0.00
13	(T/R) * t + colony	84	9413,46	6894,99	27,63	0,00
14	(T/R) * t	82	9429.57	6902.35	34.99	0,00
15	colony * t	96	9416.00	6921.75	54.39	0.00
16	(T/R) * colony * t	141	9335.45	6958.95	91.59	0.00

Table 4. Estimates of mean survival (and 95% Confidence Intervals in parentheses) and recapture probabilities for Scopoli's shearwaters on the islands of Aire, Pantaleu and Columbretes (from model 9, Table 3).

	Aire	Pantaleu	Columbretes
Adult survival ¹	0.688 (0.584-0.776)	0.756 (0.715-0.793)	0.768 (0.666-0.845)
Adult survival	0.924 (0.890-0.948)	0.843 (0.824-0.859)	0.869 (0.833-0.898)
Recapture			
Unaware	0.253 (0.213-0.298)	0.620 (0.573-0.664)	0.226 (0.189-0.267)
Aware	0.468 (0.418-0.519)	0.809 (0.788-0.829)	0.431 (0.387-0.477)
¹ First encounter			

Figure 1. Map of longline risk bycatch in western Mediterranean waters for Scopoli's shearwater. In the upper panels we show the risk for different longline modalities, and in the lower panel we show a global longline risk map for the area and the location of the three study colonies.

Figure 2. Map showing the foraging patterns of individuals from the three colonies obtained from GPS remote sensing and areas of high longline bycatch risk. Trajectories from each colony are shown in different colours: black for individuals from Menorca, red for individuals from Columbretes and blue for individuals from Pantaleu Islet. The same codes are used for the location of each colony. The inner box plot graph shows longline bycatch risk estimated for each colony depending on the percentage of time spent in high risk zones (> 3rd quartile). These zones of ochreous mottling are shown on the map.

Figure 3. Boxplot of the annual mean egg volume (in cm^3 , from 2009 to 2016) of Scopoli's shearwater breeding at Aire Island (green boxes) and Pantaleu Islet (yellow boxes). Outliers are also plotted as individual points.





