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Transnational mortality from Spanish longline fisheries bycatch is shaping the decline of a vulnerable French seabird

Nicolas Courbin [a,*], Aurélien Besnard [b], David Grémillet [a,c]

[a] CEFE, Univ Montpellier, CNRS, EPHE, IRD, Montpellier, France
[b] CEFE, Univ Montpellier, CNRS, EPHE-PSL University, IRD, Montpellier, France
[c] Percy FitzPatrick Institute of African Ornithology, University of Cape Town, Rondebosch, South Africa

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ABSTRACT

The marine realm suffers from cumulative causes of biodiversity erosion and world seabird community declined by 50 % since 1970. Seabirds routinely transgress regional and international boundaries and threat assessments should be performed at large spatial scales. We studied the demographic consequences of transnational Spanish longline fisheries bycatch on vulnerable Scopoli's shearwater (*Calonectris diomedea*) populations in the French Mediterranean. First, we assessed space use for 174 shearwaters breeding in the Calanques National Park (NP) using GPS-tracking between 2011 and 2022. By matching this information with a published bycatch risk map for Mediterranean Spain, we found that shearwaters largely overlapped with Spanish longline fisheries. Second, we calculated Spanish demersal longline bycatch on shearwater populations of Calanques and Port-Cros NPs, using bycatch reports, ring recoveries and ringing effort. Annually, Spanish demersal longline fisheries killed 5.3 birds (95 % CI = 0.4–14.2; 0.5 % of the population) from the Calanques NP and 8.1 birds (0.5–21.6; 2.6 % of the population) from Port-Cros NPs. Third, we assessed the demographic consequences of this bycatch using multi-event capture-recapture models and matrix population modeling based on long-term nest monitoring. Adult survival was low (0.84 to 0.92) relative to other Procellariiforms. Even though annual shearwater casualties on Spanish demersal longline seem modest, they may compromise the persistence of several French Scopoli's populations within 50 years. We demonstrate the importance of designing marine conservation at international scales for highly mobile species, to fully embrace the cumulative effects of marine anthropogenic threats on adult seabird survival, the main leverage effect for long-lived vulnerable populations.

1. Introduction

Marine ecosystems suffer from cumulative human impacts at regional and global scales. Those affect most marine biota and organisms, from unicellular organisms to top predators (Halpern et al., 2008; Micheli et al., 2013; Halpern et al., 2015). Among them, seabirds face the cumulative threats of habitat loss, predation by introduced species (e.g. feral cats and rats), fisheries bycatch, climatic changes leading to extreme weather events and changes in prey distributions, pollution, wind farms impacts, and competition with fisheries (Furness et al., 2013; Green et al., 2016; Genovart et al., 2017; Grémillet et al., 2018; Dias et al., 2019; Le Bot et al., 2019; Rodríguez et al., 2019; Clairbaux et al., 2021). Worldwide, seabird populations consequently suffered a 50 % decline between 1970 and 2010 (Grémillet et al., 2018) and seabirds are, together with parrots, the most vulnerable bird group (Dias et al., 2019).

Long-distance travellers such as seabirds are also exposed to anthropogenic threats over large spatial scales extending beyond the national territory of their breeding grounds, i.e., during extensive foraging trips off breeding colonies and along migration routes. The additive impact of transnational sources of stress on adult survival is of primary concern considering the key role of adult survival for the population dynamics of these long-lived species, characterized by a slow pace of life (Saether and Bakke, 2000; Caswell, 2001). Yet, the effect of transnational mortality on the faith of vulnerable seabird populations is seldom studied.

With >500,000 annual casualties worldwide (Anderson et al., 2011; Žydelis et al., 2013), seabird bycatch on gillnets and longlines is one of the most prominent threats for seabird populations (Dias et al., 2019). In some areas such as the Southern Ocean, efficient technical and

* Corresponding author at: CEFE-CNRS, 1919 route de Mende, 34293 Montpellier cedex 5, France.
E-mail address: nicolas.courbin@cefe.cnrs.fr (N. Courbin).

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operational mitigation measures applied to fisheries led to seabird population recoveries (e.g., bird-scaring streamer lines, line weighting, night-setting and no-take areas, Baker et al., 2024). This is notably the case for white-chinned petrels (*Procellaria aequinoctialis*) from Possession Island in the Crozet archipelago (Dasnon et al., 2022). Yet, in other areas such as the Mediterranean Sea, there is a striking lack of data on bycatch rates, due to the high proportion of small-scale fisheries and the rarity of fishery control programs (e.g., Anderson et al., 2011; Rodríguez et al., 2019). Notably, there is no robust scientific data on seabird bycatch in the French Mediterranean, in the absence of a properly-designed survey program. When such valuable data exist, bycatch is generally assessed in the context of local fisheries only (e.g. Cortés et al., 2017; Genovart et al., 2018). The impact of foreign fisheries on local population dynamics is therefore rarely considered, limiting appropriate conservation measures at large spatial scales.

The Mediterranean Sea is a biodiversity hotspot under immense pressure from cumulative threats (Micheli et al., 2013), especially for seabirds (Coll et al., 2012; Genovart et al., 2016; Genovart et al., 2018; Grémillet et al., 2018). The Mediterranean notably hosts three endemic shearwater species: Scopoli's (*Calonectris diomedea*, vulnerable in France), vulnerable yelkouan (*Puffinus yelkouan*) and the critically endangered Balearic shearwater (*Puffinus mauretanicus*), all of them undergoing a current population decline (IUCN, 2023). In the Western Mediterranean, current knowledge shows that shearwater survival is already compromised by accidental mortality due to longline fishing activities, with strong effects of small and medium-scale demersal longliners (Cortés et al., 2018; Genovart et al., 2018). Consequently, regional populations apparently act as sinks at metapopulation level (Sanz-Aguilar et al., 2016). The Scopoli's shearwater is a long-lived migratory species and individuals breeding in France perform foraging trips and use migration routes across French and Spanish national waters (Péron and Grémillet, 2013; Courbin et al., 2018; Péron et al., 2018; Fig. 1). Therefore, assessing the additive current mortality due to foreign bycatch is crucial, to design international appropriate conservation measures at sea.

We developed a three-steps analytical framework to model the impacts of current bycatch by Spanish demersal longline fisheries, on the French population dynamics of Scopoli's shearwaters breeding in the Calanques National Park (NP) off Marseille, one of the largest French Scopoli's shearwater population, and in the Port-Cros NP off Hyères. First, we identified the spatial extent of Spanish bycatch risk for shearwaters breeding in Calanques NP tracked by GPS across 2011–2022, by crossing shearwater space-use with a published map of Spanish longline bycatch risk. Second, we estimated mortality by Spanish demersal longliners for the Scopoli's shearwater populations of the two National Parks based on existing bycatch data for Spanish waters. Third, we modelled the effects of this bycatch on shearwater population dynamics. For this purpose, we estimated demographic parameters and population dynamics of the Scopoli's shearwater populations based on long-term demographic monitoring and ringing program (1981–2016 in the Calanques NP and 2004–2017 in the Port-Cros NP). We thereby assessed the negative demographic consequences of Spanish demersal longline bycatch, by contrasting different bycatch scenarios, to infer the impact of transnational Spanish fisheries on the French Scopoli's shearwater populations.

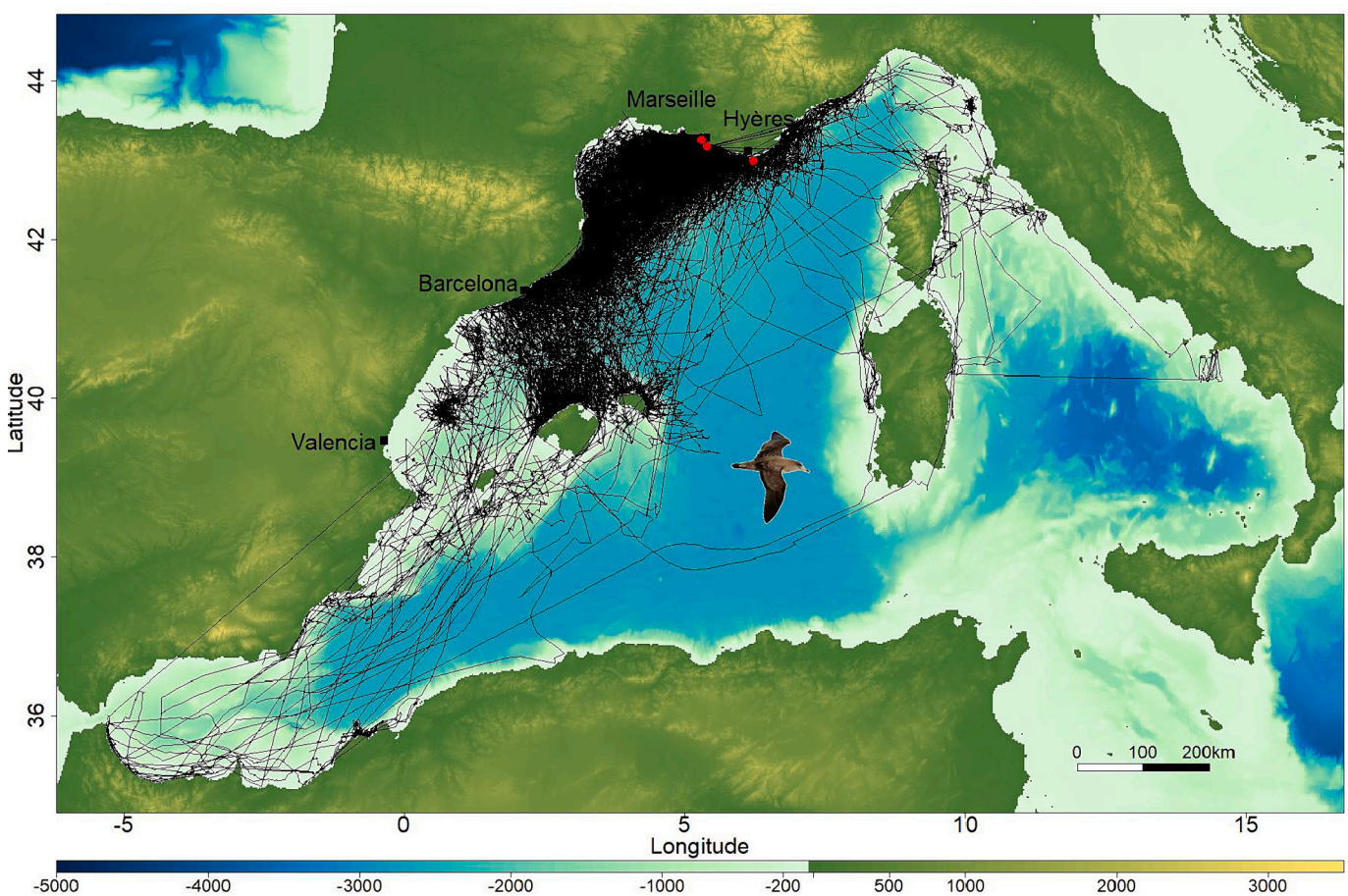

Fig. 1. Tracks of the 174 Scopoli's shearwaters followed with GPS during the breeding period (March to October) between 2011 and 2022 from Riou and Frioul Islands in Calanques NP off Marseille (red dot). We also show the Porquerolles Island in Port-Cros NP off Hyères (red dot). The color scale indicates the bathymetry/altitude. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

2. Material and methods

2.1. Study site

Field work took place in the Calanques National Park (Marseille, France), on the archipelagos of Riou (43°11′00″ N, 05°23′00″ E) and Frioul (43°16′32″ N, 5°18′24″ E), and in the Port-Cros National Park (Hyères, France), on the Porquerolles Island (43°00′02″ N, 6°13′38″ E), located in the Western Mediterranean Sea. Approximately 520 and 155 pairs of Scopoli's shearwaters breed in Calanques NP and Port-Cros NP, respectively (Cadiou et al., 2004; Calanques National Park). Shearwaters stay in the Mediterranean Sea between March and October, and migrate off West Africa and into the South Atlantic during the winter period (Péron and Grémillet, 2013). They are highly philopatric (Igual et al., 2007; Sanz-Aguilar et al., 2011). During the breeding season, shearwaters of both sexes mainly forage in the Gulf of Lion and adjacent waters, within 50 km of the colony for birds from Calanques NP in the early chick-rearing period, but also within the Balearic Sea, during extensive foraging trips and before migrating toward the Atlantic (Péron and Grémillet, 2013; Courbin et al., 2018; Péron et al., 2018). They may cover a daily distance of several hundred kilometres to feed on small pelagic fish (*Engraulis encrasicolus*, *Sprattus sprattus*, *Sardina pilchardus*) and mesozooplankton (Courbin et al., 2018). Shearwaters are exposed to introduced predators: black rats (*Rattus rattus*) and cats (*Felis catus*, except in Riou Island), while colonies are protected against human disturbances.

2.2. Tracking seabird movements

We tracked the at-sea movements of 154 breeding adults during the chick-rearing period (30th July to 16th August) between 2011 and 2020 (except in 2013) and of 20 breeding adults during their whole period of presence in the Mediterranean in 2021–2022, in Calanques NP. We caught breeding adults by hand at the nest during night-time. Before 2021, we equipped birds with GPS loggers (IgotU-GT120, Perthold Engineering LCC, USA, 47x30x13 mm, 22 g or Earth and Ocean Technologies, Germany, 47x23x12 mm, 12.5 g). We encapsulated GPSs in heat-shrink tubing, attached to back feathers with black Tesa® tape, and we recovered them at the nest after one to several foraging trips. Tagging load of GPS represented ~3.6 % of average bird body mass (mean body mass in 2011–2021 = 612 g, range: 490–780 g). A previous study at the same site showed no effect of carrying this type of loggers on breeding performances and divorce rate for 34 Scopoli's shearwaters (Authier et al., 2013). The GPS loggers recorded positions every 30 s, 1 or 2 min depending on the year. We rediscretized/interpolated data with a regular 60 s interval for analyses. In 2021–2022, we equipped birds with GPS-GSM (OrniTrack-10 Ornitela, Lithuania, 47x18x12mm, 10-12 g) fitted in leg-loop with teflon harness. Tagging load of GPS-GSM represented ~2.0 % of average bird body mass (mean body mass = 608 g, range: 510–790 g). GPS-GSM took a location every 10 min, 30 min or 1 h depending on battery charge. Handling was generally performed in <15 min. The potential impacts of our second deployment technique on shearwater fitness are currently being investigated. Here, all tags transmitted data until the post-breeding migration (<3 months) and 13 tags out of 20 were still transmitting after one year. Considering an estimated adult survival of ~0.9 (see Results), we can expect two bird casualties, and the five missing birds could simply reflect the detachment of the harness. The recapture rate being low (~0.2, Table A.5), it is currently difficult to determine the potential impact of the harness-based deployment, which will become clearer with time and more recapture opportunities at the nest.

2.3. Shearwater distribution at sea

We estimated the utilization distribution (UD) of the birds from Calanques NP during their whole period of presence in the Mediterranean (8 months from early March to early November) on a 5-km resolution grid covering Western Mediterranean waters. We used the biased random bridge method (BRB; Benhamou, 2011) that accounted for autocorrelation in GPS locations within individuals. We fitted individual UDs for three specific monitoring periods during the breeding season and then averaged individual UDs for each period: 1) UD of early August to mid-August was based on 178 individual-years tracked by GPS and 20 individuals followed by GPS-GSM, 2) UD of mid-August to early November resulted from UDs of the 20 birds followed by GPS-GSM, and 3) UD of early March to late July was the combination of the UDs of the 12 individuals equipped by GPS-GSM that returned in Mediterranean in 2022. Then, we averaged the three period-specific UDs and weighted the mean by the duration that each UD covered (i.e., weights were 0.5/8, 2.5/8 and 5/8 for $UD_{\text{early August to mid-August}}$, $UD_{\text{mid-August to early November}}$ and $UD_{\text{early March to late July}}$, respectively). Individuals UDs were fitted with the *adehabitatHR* package (Calenge, 2006) for the R software (R Development Core Team, 2019).

We then estimated the expected density of birds d per km^2 within our study area during the whole breeding period $d = (\hat{u}_x \times N_{CalanquesNP}) / 5$, where $\hat{u}_x$ is the empirical probability density of use of pixel x by shearwaters as determined by UD and $N_{CalanquesNP}$ is the size of the breeding populations in Calanques NP, i.e., 1040 individuals (Calanques National Park).

2.4. Estimation of mortality through Spanish demersal longline bycatch

We estimated the number of Scopoli's shearwaters from Calanques NP and Port-Cros NP killed per year through Spanish demersal longline bycatch using published information. Based on on-board observations and longline fishermen declarations collected between 2011 and 2015 in the regions of Catalonia and Balearic Islands, the total annual mortality (i.e., not just the one reported), N_{dead}, was estimated at 683 (95 % CI: 46 and 1818) Scopoli's shearwaters by the Spanish demersal fleet (Cortés et al., 2017). We can therefore approximate the annual mortality of birds from a site i (Calanques or Port-Cros NP) caused by Spanish demersal longliners as $n_{dead_i} = N_{dead} \times p_i$, with p_i the expected proportion of birds from Calanques or Port-Cros NP bycaught by Spanish demersal longliners. The Spanish demersal bycatch mortality rate for birds from site i was thus $h = n_{dead_i} / N_i$, with N_i the colony size in site i, and its 95 % CI was calculated using the lower and upper limit of the 95 % CI for N_{dead}.

We estimated p_i using published information. Based on Cortés et al. (2018), 251 Scopoli's shearwaters were reported bycaught by Spanish longliners (72 % by demersal longliners and 28 % by pelagic longline vessels) between 2003 and 2015 in the Balearic sea, including 34 ringed birds. Among those 34 birds ringed, 22 birds came from Spain, three birds from Italy, and nine birds from France including one from Calanques NP, one from Port-Cros NP and seven from Lavezzi Islands and Bonifacio in Corsica (Cortés et al., 2018). To correctly infer the proportion of bycaught birds from different origins, we have to consider differences in ringing effort between countries. Between 2000 and 2015, the mean annual ringing effort was 2.77 % in Mediterranean Spain (excluding Chafarinas Islands in the Alborean Sea) considering 2055–7055 pairs of breeding birds (Reyes-González, 2022) and an equivalent of 176.5 adult birds ringed annually on average (Data bank of Aranzadi Ringing Scheme, 2024; SEO/BirdLife, 2024), i.e., the number of adults ringed and the number of juveniles ringed weighted by the estimated probability to become an adult 0.77^{-5} (see Section 3.2 in the Results). In France (excluding Calanques and Port-Cros NPs), birds were all ringed in Lavezzi Islands and Bonifacio, with a ringing effort of 1.28 % considering 586–761 pairs of breeding birds (Cadiou et al., 2004; Gotti et al., 2020) and an equivalent of 17.0 adult birds ringed annually on average (Dehorter and CRBPO, 2024). In Calanques NP, the ringing effort was 6.73 % with 520 breeding pairs (Calanques National Park) and an equivalent of 70.0 adults ringed annually on average (Dehorter and CRBPO, 2024). In Port-Cros NP, the ringing effort was 4.43 % considering 106–204 pairs of breeding birds (Cadiou et al., 2004) and an

equivalent of 12.4 adult birds ringed annually on average (Dehorter and CRBPO, 2024). Finally, the ringing effort was 0.58 % in Italy considering 2909–5543 pairs of breeding birds (excluding colonies from Adriatic Sea and Sicily Channel; Cadiou et al., 2004; Baccetti et al., 2009; Mazzoleni, 2015; Gotti et al., 2020) and an equivalent of 43.9 adult birds ringed annually on average based on EURING Data Bank. Thus, if we assume that birds from different countries/colonies had equal likelihood to be recaptured in a parsimonious hypothesis, we should find an expected proportion p_i of birds bycaught from country/colony *i*:

$$p_i = \frac{N_{exp_bycaught_i}}{\sum N_{exp_bycaught}}$$

with $N_{exp_bycaught_i}$ the expected number of birds from country/colony *i* bycaught:

$$N_{exp_bycaught_i} = \frac{Ringing_rate_{Spain}}{Ringing_rate_i} \times N_{obs_bycaught_i}$$

with $Ringing_rate_{Spain}$ the ringing rate in Spain (0.0277), $Ringing_rate_i$ the ringing rate in the country/colony *i*, and $N_{obs_bycaught_i}$ the observed number of birds from country/colony *i* bycaught, and $\sum N_{exp_bycaught}$ the expected total number of birds bycaught:

$$\sum N_{exp_bycaught} = N_{obs_bycaught_Spain} + \sum \left(\frac{Ringing_rate_{Spain}}{Ringing_rate_i} \times N_{obs_bycaught_i} \right)$$

with $N_{obs_bycaught_Spain}$ the observed number of birds from Spain bycaught (22). Thus, we can approximate the expected proportion of birds from Calanques NP and Port-Cros NP bycaught by Spanish longliners $p_{CalanquesNP} = 0.0078$ and $p_{Port\text{-}CrosNP} = 0.0119$. Eighty six percent of the Spanish population of Scopoli's shearwaters occur in the Balearic Sea during the breeding period (Reyes-González, 2022) and we believed that $N_{obs_bycaught_Spain}$ was reliable and did not bias our estimation of p_i.

2.5. Estimating demographic parameters

We used a long-term monitoring of shearwater nests and a ringing program (PP n°380 in Calanques NP, PP n°445 in Port-Cros NP, CRBPO MNHN). In Calanques NP, the survey started in 1981 on Frioul archipelago, extended to Riou archipelago in 2002 with an increase in monitoring effort since 2003. Overall, 6812 shearwater nest-years were recorded between 1981 and 2016. In Port-Cros NP, 257 shearwater nest-years were recorded between 2003 and 2017. We calculated annual breeding success as the ratio between the number of nests with a fledgling chick at the end of the breeding season and the number of nests occupied at the beginning of the breeding season (see data in Table A.1).

2.5.1. Estimating adult survival

Between 1981 and 2016, 1239 adult shearwaters and 1565 shearwater chicks were fitted with a metal ring at the Calanques NP. Sex was determined for 82 % of adults based on their calls (females have a low pitch and male a high pitch), and the presence of ringed individuals at nest sites was recorded during each breeding season. We modelled adult survival with a multi-event capture-recapture model (Pradel, 2005) based on individual capture histories of birds ringed as adults, and capture histories after the minimum age at first reproduction for birds ringed as chicks (observed at five years in our study site). Specifically, the model estimated sex-dependent adult survival probability (ϕ_a) and capture probability (p_a), even if sex is unknown for some individuals (Pradel et al., 2008). The model considered *events* resulting from field observations at each capture-recapture occasion (i.e., each year) and coded in capture histories, and *states* were user-defined (Pradel, 2005). We considered four *events*: individual not seen (0), female seen alive (1), male seen alive (2), and individual of unknown sex seen alive (3). A goodness-of-fit test adjusted with U-CARE v2.3.4 (Choquet et al., 2009a) revealed two sources of bias: transience ($\chi^2 = 5.4648$, df = 30, $P < 0.001$), and trap-dependence (i.e., $\chi^2 = -2.6509$, df = 30, $P = 0.008$). Simultaneous presence of both biases suggested capture heterogeneity between individuals (Pradel and Sanz-Aguilar, 2012). Therefore, the model considered five biological *states*: female alive with a high recapture rate, female alive with a low recapture rate, male alive with a high recapture rate, male alive with a low recapture rate, and dead (not observable state). Transitions between states were modelled in two steps: survival and recapture probability (conditional to survival). See complete model structure in Table A.2.

Considering temporal variation in capture-recapture effort along the survey in Calanques NP and to avoid any confounding effect of period on adult survival estimation, we distinguished the effect of two periods on ϕ_a: 1981–2002 when effort was low (19 % of ringed birds and 23 % of the total number of resights) on Frioul, and Riou was only poorly prospected in 2002, and 2003–2016 when effort was high (81 % of ringed birds and 77 % of the total number of resights) on both archipelagos. Also, we considered intrinsic differences in ϕ_a between archipelagos (e.g., level of predation and potentially human disturbance is much higher on Frioul than on Riou, *unpub data*). We added a time effect (year of observation) on p_a. In addition, we controlled for spatial heterogeneity in prospecting and fixed to 0 the recapture probability of birds that were occupying islands that were not prospected some years knowing that shearwaters are extremely faithful to their breeding site. The multi-event capture-recapture model was fitted with E-SURGE (Choquet et al., 2009b) and has the following structure:

$$\phi_a\ (sex + obs.period + archip), p_a\ (ch + time)$$

with ϕ_a depending on *sex* (female and male), *obs.period* the period of observation (1981–2002 and 2003–2016) and *archip* the archipelago (Frioul and Riou), and p_a the adult capture probability depending on *ch*, which was the capture heterogeneity between individuals (high and low) and *time*, the year of observation.

In Port-Cros NP, 142 adult shearwaters and 68 shearwater chicks were fitted with a metal ring between 2004 and 2017, almost exclusively (95 %) on Porquerolles Island. Determination of sex of individuals being rare, we used a simplified version of the previous multi-event capture-recapture model (Pradel, 2005). We considered two *events* at each capture-recapture occasion (year): bird not seen (0), bird seen alive (1). A goodness-of-fit test adjusted with U-CARE v2.3.4 (Choquet et al., 2009a) revealed two sources of bias: transience ($\chi^2 = 2.4462$, df = 12, $P < 0.02$), and trap-dependence (i.e., $\chi^2 = -3.8676$, df = 12, $P \leq 0.001$). Because of capture heterogeneity between individuals, we considered three biological *states*: bird alive with a high recapture rate, bird alive with a low recapture rate, and dead (not observable state). The initial state can be one of the two first *states*. Transitions between *states* represented survival. As previously, we controlled for spatial heterogeneity in prospecting. The multi-event capture-recapture model has the following structure:

$$\phi_a, p_a\ (ch + time)$$

with p_a the adult capture probability depending on *ch*, which was the capture heterogeneity between individuals (high and low) and *time*, the year of observation. See complete model structure in Table A.3.

2.5.2. Estimating pre-adult survival

Pre-adult survival is the survival of individuals from fledging to the minimum age of first reproduction, estimated at five years empirically in our study area. We fitted a multi-events capture-recapture model (Pradel, 2005) based on individual capture histories of birds ringed as chicks, to model pre-adult survival probability $\phi_{pre\text{-}adult}$ and pre-adult recapture probability $p_{pre\text{-}adult}$. We have only used data from the Calanques NP because too little data has been collected on chicks from the Port-Cros NP. We considered two *events* at each capture-recapture occasion (year): individual not seen (0) and individual seen alive (1). Few individuals were observed at the colonies before their first

reproduction and we thus had to consider $\phi_{pre\text{-}adult}$ constant over their first five years. We specified two age classes, pre-adult and adult, in the model. A goodness-of-fit test fitted with U-CARE v2.3.4 (Choquet et al., 2009a) indicated transience ($\chi^2 = 15.348$, df = 22, $P < 0.001$), and trap-dependence ($\chi^2 = -3.6134$, df = 22, $P < 0.001$). Therefore, models considered three *states*: individual alive with low recapture rate, individual alive with high recapture rate, and dead (not observable state). The initial state can be one of the two first *states*. Transitions between *states* represented survival. As previously, we fixed to 0 the recapture probability of birds that were occupying islands that were not prospected. The multi-event capture-recapture model structure was:

$$\phi_{pre-adult}\,(age.class), p_{pre-adult}\,(ch)$$

with $\phi_{pre\text{-}adult}$ being shearwater pre-adult survival probability depending on *age.class*, the age class of birds (pre-adult and adult), and $p_{pre\text{-}adult}$ the pre-adult capture probability depending on *ch*, the capture heterogeneity between individuals (high and low). The multi-event capture-recapture model was fitted with E-SURGE (Choquet et al., 2009b). See complete model structure in Table A.4.

The 5-year apparent survival is the combination of juvenile survival $\phi_{juvenile}$ during the first year and the immature survival $\phi_{immature}$ during the next four years, and can be expressed as:

$\phi_{pre-adult} = \phi_{juvenile} \times \phi^4_{immature}$, with immature survival assumed to be identical to adult survival (Sanz-Aguilar et al., 2016; Genovart et al., 2017). We then back-calculated juvenile survival using female adult survival estimate for Frioul archipelago.

2.6. Spanish demersal longline bycatch effect on Scopoli's French populations

We determined the growth rate λ of Scopoli's shearwater populations from Riou and Frioul archipelagos (Calanques NP) and Port-Cros NP. We adapted a prebreeding matrix population model described by Genovart et al. (2017) for this species, and incorporated demographic stochasticity (Table 1 and see below) and several sources of mortality. The model considered only females and a monogamous hypothesis (Oro et al., 2004), and represented a 10-stages life cycle depending on age and reproductive status of individuals (Fig. A.1, Table A.5). Immatures seem to be less affected by fishing gears than adults (Genovart et al., 2017) and juveniles generally stay in Atlantic all year round. Therefore, we considered an effect of Spanish demersal longline bycatch on adult only and expressed adult survival ϕ_a as following:

$$\phi_a = 1 - (h + Other)$$

with *h* the Spanish bycatch mortality rate (see Section 2.4 Estimation of mortality through Spanish demersal longline bycatch) and *Other* the additional causes of death (e.g., other bycatch sources, predation, starvation, etc.). Compensation by natural mortality is low in long-lived species (Péron, 2013; Simon and Fortin, 2019) and we do not consider it in the model. Considering that $Other = 1 - \phi_a^{'}$, with $\phi_a^{'}$ the expected adult survival in absence of Spanish bycatch, we can reformulate $\phi_a = \phi_a^{'} - h$.

To assess the additive effect of Spanish bycatch, we considered demographic matrix models corresponding to three scenarios: 1) under the current estimated Spanish demersal longline bycatch mortality rate *h* with the estimated adult survival ϕ_a, 2) hypothetical absence of Spanish bycatch following improvements in fishing techniques, and we considered the adult survival $\phi_a^{'} = \phi_a + h$ for each stage ≥5 years old of the life cycle, and 3) potential high Spanish bycatch rate, using h_{max} the upper limit of the 95 % CI for *h*, and we considered the adult survival $\phi_a^{''} = \phi_a^{'} - h_{max}$ for each stage ≥5 years old of the life cycle (Table 1, and Fig. A.1, Table A.5).

For each scenario, we adjusted a deterministic model with constant demographic parameters to estimate the distribution of population at equilibrium at each stage, and the sensitivity and elasticity of demographic parameters, to infer their relative contribution (Caswell, 2001). Then, we used a stochastic model to mimic the temporal variation in demographic parameters and determine the mean stochastic population growth rate λ_s, make populations projections and estimate the risk of quasi-extinction (≤ 10 breeding females). We performed 10,000 Monte-Carlo simulations (i.e., 10,000 population trajectories) over a period of 100 years. Values of adult, immature and juvenile survival were randomly picked up within a uniform distribution limited between ±0.1 around the model estimates (Table 1). We thereby used values of breeding success drawn randomly in a uniform distribution bounded between the lowest and highest annual values estimated empirically. For the demographic parameters excerpted from the literature, we used a uniform distribution bounded between ±0.1 around the value when a unique value was found, or values were drawn uniformly between the lowest and highest values found. We fitted analyses with the package *popbio* (Stubben and Milligan, 2007) for R (R

Table 1
Demographic parameters used to model the dynamics of Scopoli's shearwater populations of Calanques National Park (NP) and Port-Cros National Park, with mean estimates used in the deterministic model and the range of values used in the stochastic model.

Parameters	Frioul, Calanques NP		Riou, Calanques NP		Porquerolles, Port-Cros NP	
	Mean	Range	Mean	Range	Mean	Range
Sex-ratio (ρ)	0.5	_	0.5	_	0.5	_
Breeding success (f)[a]	0.554	0.340;0.950	0.704	0.340;0.950	0.777	0.250;1.000
Juvenile survival (S1, first year)[a]	0.451	0.351;0.551	0.451	0.351;0.551	0.451	0.351;0.551
Immature survival (S2)[a]	0.881	0.781;0.981	0.923	0.823;0.999	0.845	0.835;0.945
Adult survival for non-breeders (S3)[a]	0.881	0.781;0.981	0.923	0.823;0.999	0.845	0.835;0.945
Adult survival for breeders (S4)[a]	0.881	0.781;0.981	0.923	0.823;0.999	0.845	0.835;0.945
Adult survival for breeders at 5 years (Sb5)[b]	0.180	0.080;0.280	0.180	0.080;0.280	0.180	0.080;0.280
Probability of being a non-breeder after being a breeder ($P_{R\text{-}NR}$)[b]	0.140	0.060;0.140	0.140	0.060;0.140	0.140	0.060;0.140
Probability of staying a non-breeder ($P_{NR\text{-}NR}$)[b]	0.660	0.410;0.660	0.660	0.410;0.660	0.660	0.410;0.660
Recruitment probability at 5 years (r5)[b,d]	0.030	0.001;0.130	0.030	0.001;0.130	0.030	0.001;0.130
Recruitment probability at 6 years (r6)[b]	0.100	0.001;0.200	0.100	0.001;0.200	0.100	0.001;0.200
Recruitment probability at 7 years (r7)[b]	0.230	0.130;0.330	0.230	0.130;0.330	0.230	0.130;0.330
Recruitment probability >7 years[b]	1.000	_	1.000	_	1.000	_
N breeding females[c]	100	_	420	_	155	_
Survival adjustment under scenario of absence of Spanish bycatch[a]	0.005	_	0.005	_	0.026	_
Survival adjustment under scenario of high risk of Spanish bycatch[a]	−0.009	_	−0.009	_	−0.044	_

[a] Values estimated in our study.
[b] Values estimated in Igual et al. (2009), Bourgeois and Dromzée (2012), Sanz-Aguilar et al. (2016).
[c] Size estimated by the Calanques NP and Cadiou et al. (2004).
[d] Birds that start to reproduce at five years may entail a high survival cost.

Development Core Team, 2019). We provided the Rcodes in Supplementary Materials.

3. Results

3.1. Shearwaters overlapped with Spanish longline fisheries

During the breeding period, birds from Calanques NP covered an area of 76,875 km^2 (95 % UD) mainly located within the Eastern part of the continental shelf of the Gulf of Lion and along its continental slope, and also within the Balearic Sea along the Catalan coast and close to the Balearic Islands where longline Spanish fisheries are active (Figs. 1 and 2A). Overall, shearwaters largely overlapped with Spanish longline fisheries hotspots during their whole presence in Mediterranean (Fig. 2B). The shearwater population of Calanques NP comprising ca. 1040 breeding birds, absolute bird densities remained low, with a maximum of ca. 8 individuals per km^2 within the first 5 km of the colonies and < 1 bird per km^2 farther than 15 km from the colonies, within the Gulf of Lion and Spanish waters.

3.2. Shearwater demography: a concerning low adult survival

Based on long-term nest monitoring, the mean yearly reproductive success was 0.554 ± 0.034 (± SD) on Frioul and 0.704 ± 0.034 on Riou, both archipelagos of the Calanques NP, during the 2003–2016 period, and 0.777 ± 0.050 on Porquerolles Island in Port-Cros NP (details in Table A.1). This was similar to that found in a rapidly declining colony (Genovart et al., 2017). We collected 1341 capture histories for adult in Calanques NP, with 48 % of individuals ringed as adults resighted at least once. For the 2003–2016 period, female shearwater adult survival in our study area ϕ_a was rather low compared to what is expected for this species and was estimated at 0.881 (95 % CI: 0.831;0.918) on Frioul. Female adult survival was higher on Riou, 0.923 (0.889;0.947), and similar to male shearwater adult survival for both archipelagos: 0.927 (0.893;0.951) on Frioul and 0.923 (0.873;0.955) on Riou, respectively. The situation was worse in Port-Cros NP and adult survival was estimated at 0.845 (0.793;0.886) based on 145 capture histories for adult, with 55 % of individuals ringed as adults resighted at least once. Only 7 % of ringed chicks in Calanques NP were resighted. Pre-adult survival $\phi_{pre\text{-}adult}$ was 0.770 (0.681;0.841) and the back-calculated juvenile survival was 0.451. More details in Tables A.6, A.7 and A.8.

3.3. Additive mortality effect of Spanish bycatch

Under the current bycatch situation, the stochastic population growth rate λ_s was 0.950 in Frioul, 0.979 in Riou, and 0.912 in Port-Cros NP. Without immigration, shearwater populations would collapse within 50 years in Port-Cros NP (quasi-extinction risk was 0.99), have a low risk of extinction within 50 years in Frioul (risk was 0.06), whereas the larger population size and higher female adult survival rate on Riou prevent extinction within 100 years (Fig. 3A, B, C). Sensitivity and elasticities analyses indicated that the population growth rate was largely affected by changes in the probability that a breeding adult survived and reproduced again the next year, and few by fecundity (Tables A.9, A.10 and A.11).

We estimated that Spanish demersal longliners bycaught 5.3 (95 % CI = 0.4;14.2) Scopoli's shearwaters from Calanques NP, i.e. 0.51 % (0.03;1.37) of the population, and 8.1 (0.5;21.6) birds from Port-Cros NP, i.e., 2.62 % (0.18;6.97) of the population, over their whole breeding period each year. Spanish demersal longline bycatches had substantial impact on modelled population trajectories of Scopoli's shearwaters of France and compromised their potential population persistence. In the absence of Spanish bycatch mortality, the mean λ_s increased to 0.955 in Frioul and the population extinction became unlikely at 50 years (mean quasi-extinction risk was <0.01, Fig. 3D). This effect was even greater at Porquerolles, with λ_s increasing to 0.935 and the risk of population extinction at 50 years dropping from 0.99 to 0.23 (Fig. 3F). In Riou, Scopoli's population would decrease slowly without Spanish bycatch with $\lambda_s = 0.985$ (Fig. 3E).

Considering a scenario with a high Spanish bycatch rate, the additive mortality reached 14.2 birds in Calanques NP (i.e., 1.37 % of the population) per breeding period and population decline accelerated for both archipelagos, $\lambda_s = 0.943$ in Frioul and $\lambda_s = 0.972$ in Riou. Under such conditions, risk of shearwater population extinction was 0.34 in 50 years for Frioul but remained unlikely in 100 years for Riou (Fig. 3G, H). We estimated 21.6 shearwaters from Port-Cros NP bycaught (i.e., 6.97 % of the population) per breeding period. The λ_s was 0.871 in Port-Cros NP and the shearwater population would extinct in 30 years (risk was 0.96; Fig. 3I).

4. Discussion

Using an exceptionally large, long-term data set on Scopoli's shearwater demography combined with at-sea movements, we provide a key example of transnational human threats on seabird population trajectories. Notably, French shearwater at-sea distribution overlaps significantly with Spanish longline fisheries during the breeding period. Consequently, birds are exposed to high Spanish bycatch on demersal longline fishing hooks, estimated to kill on average 5.3 to possibly up to 14.2 birds each year in Calanques NP (0.51 to 1.37 % of the population), and average 8.1 to possibly up to 21.6 shearwaters each year in Port-Cros NP (2.62 to 6.97 % of the population). The mortality estimate is, however, a rough approximation due to uncertainty in some of the data used. Birds have also relatively low adult survival, comprised between 0.84 and 0.92 during the same period, as elsewhere in the Western Mediterranean (Genovart et al., 2017; Genovart et al., 2018). We therefore predict that some populations of France, notably shearwater population of Port-Cros NP and birds breeding on Frioul in Calanques NP might face extinction within 50 years, if they were not supported by immigration. Our demographic model shows that the current Spanish bycatch mortality decreased the λ_s of populations from Calanques NP of 0.006 and the λ_s of population from Port-Cros NP of 0.023. Hence, the suppression of Spanish demersal longline bycatch would notably decrease the extinction risk of the colony in Port-Cros NP within 50 years and would ensure the persistence of the small colony in Frioul within the short-term (> 50 ans). However, the trajectory of the Riou colony in Calanques NP, one of the largest French Scopoli's shearwater population was little influenced by Spanish fisheries within the next 100 years.

The impact of transnational bycatch on the French Scopoli's colonies depends not only on colony size, but also on seabird at-sea space use. Notably, Cortés et al. (2018) found that 7 out of 34 shearwaters bycaught by Spanish fisheries came from Lavezzi Islands and Bonifacio colony (Corsica), the other largest French Scopoli's shearwater population (>1340 breeding individuals, Cadiou et al., 2004; Gotti et al., 2020). Consequently, after correcting for differences in ringing effort between the different country/colonies, we can expect that Spanish demersal longliners bycaught 196 birds annually from the Lavezzi Islands and Bonifacio population on average, i.e.14.6 % of the population. There is no doubt that this is a crucial driver for the population dynamics. As a thought experiment, if we apply the demographic model of the Riou colony to Lavezzi population (for which no demographic model is currently available, but both colonies are similar in size), we find that removing Spanish bycatch would reverse the demographic trend (λ_s moves from 0.98 to 1.17) and lead to an increase in the size of the Lavezzi and Bonifacio population.

The Scopoli's shearwater is an endemic species of Mediterranean seabird, and the French state bares substantial responsibility with respect to the long-term persistence of populations breeding on islands under its jurisdiction. Those populations are already under major threats, with many disturbances on breeding islands and at sea, through predation by introduced predators such as rats and feral cats (Genovart et al., 2017; Rodríguez et al., 2019), food competition with fisheries

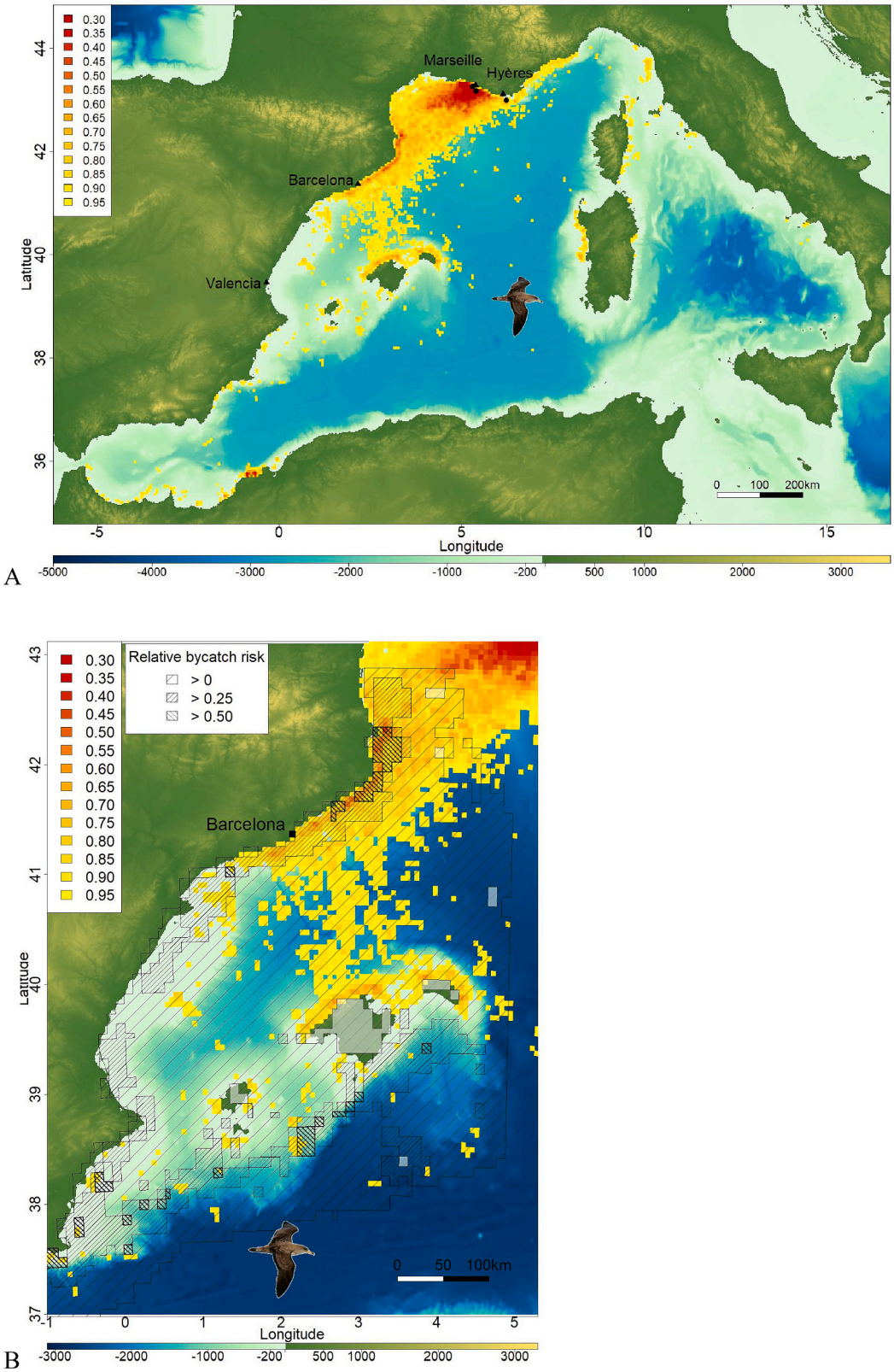

Fig. 2. A. Utilization distribution of breeding Scopoli's shearwaters tracked from Riou and Frioul Islands in Calanques National Park (black dot) between 2011 and 2022 within the Western Mediterranean. B. Zooming on the Balearic Sea with crossing information on the bycatch risk by Spanish longliners for Scopoli's shearwater (adapted from Genovart et al., 2018; Fig. 1 in it). The risk map had a spatial resolution of 0.1° × 0.1°, and each pixel represents the relative bycatch risk by pelagic and demersal longliners (ranged between 0 and 1) considering temporal variations in fishing effort (relative abundance of vessels and maximum number of hooks), and capture probability depending on the month and the longline modalities (small-scale demersal, medium-scale demersal, semi-industrial pelagic) for the whole period of presence of birds in Mediterranean Sea (see details in Genovart et al., 2018). The color scale indicates the bathymetry/altitude. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

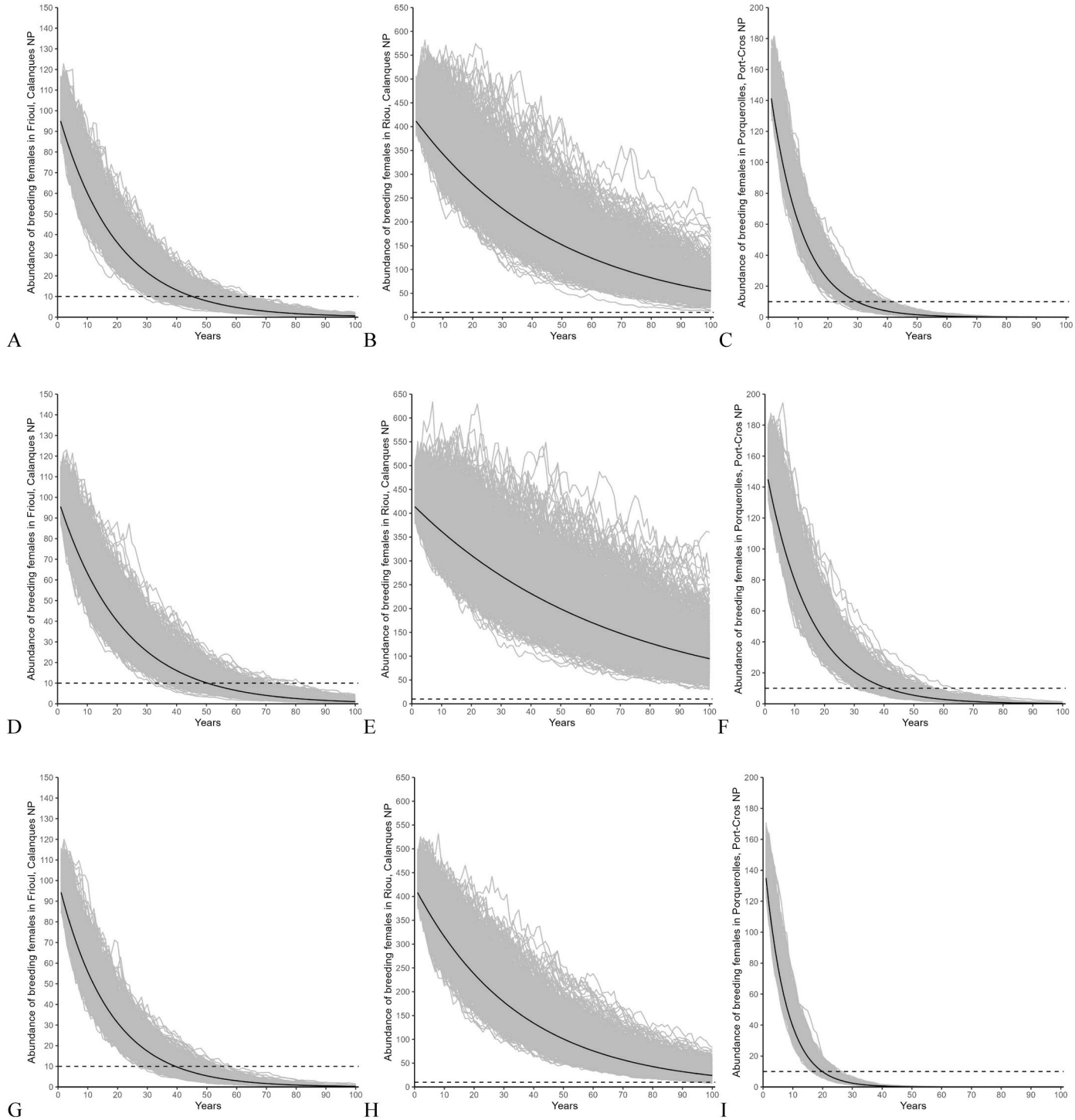

Fig. 3. Stochastic projections of the abundance of breeding female shearwaters in (A, D, G) Frioul and (B, E, H) Riou archipelagos in Calanques National Park, and in (C, F, I) Porquerolles Island in Port-Cros National Park for the next 100 years under three scenarios: (A, B, C) the current Spanish bycatch situation, (D, E, F) absence of Spanish bycatch situation, (G, H, I) a high Spanish bycatch risk. We show 1000 simulations (grey lines) along with the mean trajectory expected with the estimated stochastic lambda (black line). Horizontal dotted line indicates a critical population size with 10 breeding females.

(Grémillet et al., 2015), and depletion in the quality of their main prey species (zooplankton and small pelagic fish; Menu et al., 2023) linked to human-induced global changes. Additional mortality due to bycatch on fishing gear strongly enhances their population decline, as in many seabird populations (Lewison et al., 2012; Dias et al., 2019; Rodríguez et al., 2019).

Bycatch mortality is already known as one of the main threats to worldwide seabirds (Micheli et al., 2013; Dias et al., 2019) including Spanish shearwater populations in the North-western Mediterranean (Cortés et al., 2017; Genovart et al., 2017; Genovart et al., 2018; Rodríguez et al., 2019). Here, we provide the first evidence of Spanish Mediterranean longline bycatch impact on a foreign seabird population. The impact of fisheries bycatch on French shearwater populations is likely even higher, as other fishing gears could also produce bycatch, both in Spain (Genovart et al., 2017) and across the whole range of the species distribution, including French waters during the breeding period

where levels of bycatch are undetermined, and Atlantic waters off West Africa during migration (Péron and Grémillet, 2013; Grecian et al., 2016). In the latter area, seabirds are also intentionally harvested in some instances, for illegal seabird export toward Asian food markets (Grémillet et al., 2015). Ultimately, transnational bycatch effects accumulate all across shearwater life cycles with probably substantial impact on French shearwater populations. Transnational bycatch accumulation could therefore jeopardize Scopoli's metapopulation viability in the long-term. For example, the Scopoli's shearwater population from Pantaleu (Balearic Archipelago) is not self-maintained but rescued by massive yearly recruiting of immigrants (10–12 % of the total population, Sanz-Aguilar et al., 2016) probably coming from the enormous colonies in the central Mediterranean, e.g. Zembra Island, which hosts ~80 % of the world breeding population (~142,000 breeding pairs, Defos du Rau et al., 2015). The mechanism is probably similar in the Calanques and Port-Cros NPs, with the immigration flow from large colonies partly offsetting the reduced apparent adult survival.

While fisheries impact persists, and in the current context of numerous threats on land and at sea that may be of concern to the Scopoli's shearwaters, a new threat is looming at sea as a result of the energy transition taking place in several European countries. The potential additive risk posed by the planned explosion of offshore wind turbines in the Mediterranean along Spanish, French and Italian coasts may represent the final blow for Scopoli's shearwaters and other sensitive seabirds (e.g., Balearic and Yelkouan shearwater). Disturbingly, a future area dedicated to wind farms is <50 km East of one of the largest French Scopoli's shearwater colony (Ministère de la Transition Ecologique, 2022), and shearwaters routinely forage and rest there (Courbin et al., 2018).

Overall, our results highlight that the main mitigation actions should be aimed at increasing adult survival within seabird populations. However, we show, for the marine component, that such a mitigation action goes beyond the scope of local stakeholders. Even if conservation actions on land have to be conducted and in most of places reinforced (e.g., introduced mammal control and/or eradication, habitat preservation/restauration, tourism frequentation regulation), there is also an urgent need to coordinate marine conservation actions on an international scale (Beal et al., 2021). Therefore, we hereby plead for human development accounting for cumulative effects at regional and transnational scales in the marine realm (Micheli et al., 2013; Willsteed et al., 2023), and mandate bycatch mitigation on every fishing boat, such as a night-setting (Cortés and González-Solis, 2018), accompanied by extensive and international observer programs. In particular, such programs need to be properly scaled to detect rare mass-mortality events, which occur for shearwaters (Genovart et al., 2017), and reassess the impact of fisheries at large scales on population dynamics. We call for the continued reduction of seabird bycatch in the Mediterranean and worldwide through effective mitigation efforts (e.g., bird-scaring streamer lines, line-weighting, night-setting and no-take areas; Baker et al., 2024).

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CRediT authorship contribution statement

Nicolas Courbin: Writing – original draft, Visualization, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Aurélien Besnard:** Writing – review & editing, Supervision, Methodology, Formal analysis, Conceptualization. **David Grémillet:** Writing – review & editing, Supervision, Methodology, Funding acquisition, Data curation, Conceptualization.

Declaration of competing interest

The authors declare that they have no competing interests.

Data availability

Tracking data are available via Birdlife International's Seabird Tracking Database and MoveBank (*Calonectris diomedea* - Scopoli's shearwater - Riou Marseille France – ID_PROG 1190).

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Appendix A. Supplementary data

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