Varying demographic impacts of different fisheries on three Mediterranean seabird species

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Abstract
Fisheries have an enormous economic importance, but reconciling their socio-economic features with the conservation and sustainability of marine ecosystems presents major challenges. Bycatch mortality from fisheries is clearly among the most serious global threats for marine ecosystems, affecting a wide range of top predators. Recent estimates report ca. 200,000 seabirds killed annually by bycatch in European waters. However, there is an urgent need to rigorously estimate actual mortality rates and quantify effects of bycatch on populations. The Mediterranean Sea is one of the most impacted regions. Here, we estimate for the first time both bycatch mortality rates and their population-level effects on three endemic and vulnerable Mediterranean taxa: Scopoli’s shearwater, Mediterranean shag, and Audouin’s gull, that die in different types of fishing gears: longlines, gillnets and sport trolling, respectively. We use multi-event capture–recapture modelling to estimate crucial demographic parameters, including the probabilities of dying in different fishing gears. We then build stochastic demography models to forecast the viability of the populations under different management scenarios. Longline bycatch was particularly severe for adults of Scopoli’s shearwaters and Audouin’s gulls (ca. 28% and 23% of total mortality, respectively) and also for immature gulls (ca. 90% of mortality). Gillnets had a lower impact, but were still responsible for ca. 9% of juvenile mortality on shags, whereas sport trolling only slightly influenced total mortality in gulls. Bycatch mortality has high population-level impacts in all three species, with shearwaters having the highest extinction risk under current mortality rates. Different life-history traits and compensatory demographic mechanisms between the three species are probably influencing the different bycatch impact: for shearwaters, urgent conservation actions are required to ensure the viability of their populations. Results will be very useful for guiding future seabird conservation policies and moving towards an ecosystem-based approach to sustainable fisheries management.

Keywords
bycatch, conservation, marine predators, multi-event capture–recapture, parameter uncertainty, population models, PVA, seabirds, stochasticity, survival
1 INTRODUCTION

Humans have extensively altered the global environment, and among the habitats most affected by anthropogenic activities are the marine ecosystems, mainly due to fisheries (Coll et al., 2010; Halpern et al., 2008; Jackson, 2008; Pauly, Watson, & Alder, 2005). Fisheries have an enormous economic importance, with an estimated direct value of ca. US $80–85 billion annually (Dyck & Sumaila, 2010) and are a major protein source for human populations in both affluent and developing countries. As a consequence, it is a challenge to reconcile economic and social issues involving fish and fisheries with efforts to improve marine conservation and sustainability (Crowder et al., 2008; Hilborn, 2016).

Seabirds have long interacted with fisheries, including both positive and negative effects of human activities. But, the industrialization of fisheries has dramatically increased their impacts on seabirds and other marine top predators (e.g. Furness, 2003; Lewison et al., 2014; Tasker et al., 2000; Wagner & Boersma, 2011). But even now, fisheries create a mix of different effects. For example, trawling fisheries make a huge amount of extra food, in the form of discards (>7 million tonnes each year worldwide, (Kelleher, 2005), available to seabirds; this bounty is scavenged by at least 143 species representing all seabird families (Bugoni, McGill, & Furness, 2010; Garthe, Camphuysen, & Furness, 1996; Oro, Cam, Pradel, & Martinez-Abraín, 2004; Oro, Pradel, & Lebreton, 1999; Oro & Ruiz, 1997). In a few cases, the benefits of consuming discards have been quantified for seabirds, and, when discards are available, demographic performance can be significantly enhanced by increases in fecundity and survival (Oro, Jover, & Ruiz, 1996; Payo-Payo, Genovart, Bertolero, Pradel, & Oro, 2016) but see (Gremillet et al., 2008). In contrast to the positive effects obtained from trawler discards, seabirds are also attracted to other fishing fleets (such as longlines, gillnets, purse-seiners or sport trolling fishing) that generate incidental mortality (Croxall et al., 2012; Davoren, 2007; Lewison, Crowder, Read, & Freeman, 2004; Regular, Montevercchi, Hedd, Robertson, & Wilhelm, 2013; Tull & Germain, 1972; Žydelis, Small, & French, 2013). Bycatch mortality from these fisheries is clearly among the most serious global threats for marine ecosystems, affecting not only seabirds but also a wide range of other top predators, from large fish to turtles and marine mammals (Furness, 2003; Lewison et al., 2014).

Seabirds are among the most threatened group of birds, with one third of species threatened with extinction, and bycatch is considered one of the main causes of population declines in many populations (Paleczny, Hammill, Karpouzi, & Pauly, 2015; Phillips et al., 2016). Most prior research on bycatch has focused on long-line fisheries (mainly because it affects multiple pelagic top predators such as dolphins, turtles or albatrosses) and it has been focused on Atlantic and Pacific waters (Barbraud et al., 2012; Dunn & Steel, 2001; Ramos et al., 2012; Tasker et al., 2000). However, bycatch is also prevalent in the Mediterranean (Báez et al., 2014; Belda & Sanchez, 2001; Cooper et al., 2003; Dimech et al., 2008; Karris et al., 2013; Laneri et al., 2010); a worldwide review suggests that this region together with the southwest Atlantic is experiencing large bycatch impacts (Lewison et al., 2014). In the case of the Mediterranean, this impact is of particular conservation concern since most of the seabird taxa are endemic and they have small and threatened populations (Zotier, Bretagnolle, & Thibault, 1999).

Recently, attempts have been made to quantify the total number of birds that may die due to incidental bycatch (Anderson et al., 2011; Baker et al., 2007; Lewison & Crowder, 2003). For instance, International Council for the Exploration of the Sea (ICES; http://www.ices.dk) reported ca. 200,000 seabirds killed annually in European Union (EU) waters by fisheries bycatch. Unfortunately, the reliability of these estimates is sometimes low due to the paucity of data in most fisheries, unreliable extrapolations, and unchecked assumptions and the large spatio-temporal variability in bycatch rates. There is an urgent need to go beyond these rough numbers to assess not just total numbers killed, but the effects of bycatch caused by different fishing gears by estimating actual mortality rates and their impact on the viability of their populations (Komoroske & Lewison, 2015). Only a few studies have been able to quantify how seabird survival may be affected by bycatch rates (Barbraud, Marteau, Ridoux, Delord, & Weimerskirch, 2008). For instance, Véran et al. (2007), using capture–recapture modelling, found that longline fishing explained more than 40% of the variation in adult survival in a species of albatross. However, to directly estimate not only the survival probability, but also the probabilities of dying by fisheries bycatch, recoveries and not only resightings should be analysed. Due to the difficulty of obtaining recoveries of marked individuals and the need to apply complex capture–recapture modelling, we are aware of only one previous study that has been able to directly estimate the probability of a seabird dying in fishing gear (Genovart et al., 2016).

The present study aims to rigorously quantify the bycatch effect from different types of fishing gears on vulnerable seabirds, and to build realistic population models to forecast their population viability in the face of bycatch-generated mortality. To accomplish these goals, we use multi-event capture–recapture modelling (Pradel, 2005, 2009) to estimate the probabilities of dying in different fishing gears together with crucial demographic parameters such as survival and recruitment. We then use these demographic estimates and information on other parameters to build age-structured stochastic population models with which to assess population viability (Bakker & Doak, 2008; Morris & Doak, 2002). We focus on three endemic Mediterranean taxa included in the EU Birds Directive that appear to be primarily impacted by different types of fishing gear: the Scopoli’s shearwater Calonectris diomedea diomedea, impacted mainly by longlines; the Mediterranean shag Phalacrocorax aristotelis desmarestii, impacted by gillnets; and the Audouin’s gull Larus audouinii, impacted by longlines and sport trolling.

More broadly, our manuscript aims to help to understand the biological and population effects of fishing bycatch to help developing careful ecosystem-based approaches to sustainable fisheries management, which are essential to carry out more effective conservation planning (FAO 2010, FAO 2016; Bicknell, Oro, Camphuysen, & Votier, 2013; Votier, Bicknell, Cox, Scales, & Patrick, 2013; Hilborn, 2016).
2 | MATERIALS AND METHODS

2.1 | Study species

The Scopoli's shearwater is a long-distance migrant and colonial Procellariform breeding on the northeast Atlantic and Mediterranean islands. This subspecies is endemic to the Mediterranean, and it has recently been suggested that it should be treated as a separate species (Sangster et al., 2012) (but see Genovart et al., 2013). The species feeds mostly on fish, squid and crustaceans, but also exploits fishing discards (Karris, Ketsilis-Rinis, Kalogeropoulou, Xirouchakis, & Machias, 2016; Oro & Ruiz, 1997). Previous work showed low survival rates not expected in a long-lived species (Genovart, Sanz-Aguilar, et al., 2013), and there is evidence of suffering high mortality in fishing gears (Báez et al., 2014; García-Barcelona, Ortiz de Urbina, de la Sema, Alot, & Macías, 2010).

The Mediterranean shag is a coastal colonial seabird subspecies endemic of the Mediterranean and listed in the EU Birds Directive. The species is largely sedentary although some populations, as the Adriatic, are migratory (Sponza, Cosolo, & Kralj, 2013) and feed on fish predominantly near the seabed (Cosolo, Privileggi, Cimador, & Sponza, 2011; Sponza, Cimador, Cosolo, & Ferrero, 2010), but may eventually exploit trawling discards. Gillnets and fish traps, especially when permanently located close to the sea shore, have been suggested to be responsible for killing significant numbers of shags (Gallo-Orsi, 2003; Žydelis et al., 2013).

The Audouin’s gull is a colonial seabird endemic to the Mediterranean. It is a coastal species that may perform larger foraging trips than other gull species (Oro, 1998). It was classified as Endangered during the 1970s, then Vulnerable and now is classified as Least concern (BirdLife International, 2015) due to the exponential growth of the largest colony (Ebro Delta) over the last three decades. However, this large population is now in strong regression, calling into question the conservation status of the species. The species’ diet consists mostly of epipelagic fish, but it also extensively exploits discards (Oro, 1998). There is some evidence of mortality in longliners (Belda & Sanchez, 2001; Cooper et al., 2003), and monitoring at some breeding colonies also indicates mortality in trolling sport fishing (authors' personal observations).

2.2 | Features of the fisheries

Two categories of fisheries generate seabird bycatch in our study: commercial and sport. Longlines and gillnets are set by professional fishermen (commercial), whereas sport trolling is a leisure activity mostly performed during weekends and holidays. In the Mediterranean, longlines and gillnets set in more coastal areas are used by an artisanal fleet, composed of a large number of boats of generally low tonnage (Farrugio, Oliver, & Biagi, 1993). Bottom longliners cause more seabird mortality than pelagic drifting longliners because of the size of the hooks and their operations are more coastal and more predictable in space and time, increasing the probabilities of birds being there. Even within these broad categories there is a lot of variability in fishing operations that may influence bycatch rates, according to differences in target fish species, operational depth and technical features (García-Barcelona et al., 2010). Gillnets are also very variable, ranging from drift nets to gill nets fixed to the coastline.

2.3 | Study area, field methods and data sets

For Scopoli’s shearwater, data were collected at Pantaleu Islet (Mallorca) in the Balearic Archipelago (39°34’N, 2°21’E), a legally protected colony with ca. 200 breeding pairs that it is free of carnivores and rats (Sanz-Aguilar, Igual, Oro, Genovart, & Tavecchia, 2016). Between 1985 and 2013, adults and chicks were trapped in the burrow, and marked (or recaptured) with stainless-steel bands with a unique code to allow identification. Dead recoveries were obtained from the Spanish banding office (SEO/BirdLife) and provided by fishermen, researchers and wildlife recovery centres. Each recovery was assigned as caused by fishing longlines (carrying a hook) or unknown.

Breeding success was calculated for each year between 2001 and 2014, as the proportion of chicks that fledge from all nests with an egg laid (more details in Genovart, Sanz-Aguilar, et al., 2013; Sanz-Aguilar, Igual, Oro et al. 2016).

For the Mediterranean shag, data were collected at six colonies, composed by a total of 15 islands, in Croatia, at North Adriatic, between 2005 and 2013. Three colonies are located off the western coast of the Istria peninsula near Vrsar (45°09’N, 13°35’E), Rovinj (between 45°03’–45°04’N and 13°37’–3°38’E) and on the Brijuni archipelago (between 44°53’–44°56’N and 13°42’–13°47’E). The other three colonies are located on Oruda (44°33’N, 14°34’E), Morovnik and Olib (44°26’N–14°44’E) and on Silanski Grebeni (between 44°19’–44°20’N and 14°41’–14°43’E) islands (Sponza et al., 2013). At least 1300–1500 pairs of the Mediterranean Shag breed in the north and central Adriatic Sea (Sponza et al., 2013) and up to 4000 individuals of all age classes were counted on the communal roosts in the north Adriatic during late summer and autumn (Škornik, Utmar, Kravos, Candotto, & Crnkovic, 2011). Adults and chicks were trapped by hand at colonies and marked with alphanumeric plastic bands with a unique code to allow identification. Recoveries were obtained from the banding offices, fishermen and researchers. Each recovery was assigned as caused by fishing gears or by other causes, including unknown cause of death. For the Audouin’s gull, data were collected at the protected area of the Punta de la Banya, Catalonia (40°37’N, 00°35’E). The site was colonized by Audouin’s gulls in 1981 and in 2012 it held 60% of the Audouin’s Gull world population (Oro, 1998). During 1992–2012 chicks were individually marked at fledging using a plastic band with a unique alphanumeric code. Resightings were made during the breeding season using spotting scopes from a distance (Genovart, Pradel, & Oro, 2012). We also included in the analysis recoveries obtained by the authors or by the local environmental agencies in the breeding areas or abroad. Each recovery was assigned a cause of either: longline bycatch, bycatch in trolling sport fishing, other causes (e.g. predation or starving), or unknown cause of death.
success was calculated for each year as the number of chicks that fledge from all nests with eggs laid (see details in Oro & Ruxton, 2001).

For the three species, in a few cases a bird was resighted or recaptured in the colony early in spring and subsequently recovered before the end of the breeding season in the same year. We addressed this by moving the recovery date of such birds to the next recovery year, as if they had died just after the breeding period.

2.4 | Analysis of demographic parameters

To estimate demographic parameters such as survival, and probability of dying in fishing gears, we used multi-event capture–recapture modelling (Pradel, 2005). These models hold two levels in capture–recapture data: the field observations, called "events", encoded in the capture histories, and the "states" defined to match the biological questions, that can only be inferred. Models were fitted in program E-SURGE (Choquet, Rouan, & Pradel, 2009). In these models, we did not allow for error in the probability of ascertaining the cause of death; as a consequence, estimated probabilities of dying in fishing gear represent minimum bycatch probabilities (because some individuals, without a definitive cause of death, certainly died from bycatch). Details on multi-event models for each species can be found on Appendix S1.

Model selection relied on QAICc, that is the Akaike Information Criterion corrected for overdispersion and for small sample sizes (Burnham & Anderson, 2002). Since there is no goodness-of-fit test available for these multi-event models, we assessed the fit of a uni-state model without recoveries (Cormack–Jolly–Seber type models) using U-care (Choquet, Lebreton, Gimenez, Reboulet, & Pradel, 2009).

Additionally, for all species, once we estimated the probability of bycatch, we also estimated the hypothetical survival without incidental capture, both for immature and adult birds. We did so by removing the estimated probability of dying in fishing gears from the total estimated mortality probability estimated for each age class. We assumed that mortality from fisheries was additive.

To build mean projection models (see Population Modelling section), we needed an estimate of the mean adult survival probabilities. In cases for which the best supported survival model was time varying, we then also ran a model assuming constant annual survival.

2.4.1 | Scopoli’s shearwater survival models

Individuals were classified in two groups based on their age at first capture (chicks or adults). As we detected trap heterogeneity with the GOF test, all our models corrected for this effect by assuming that, when an animal is caught or seen, it will be more easily trapped or seen at the next occasion (Aware). However, if it is not caught, it revert immediately to a “trip unaware” state (Unaware) (see details in Pradel & Sanz-Aguilar, 2012). Thus our models included five biological states: individual alive aware (AA); individual alive unaware (AU); individual recently dead by longline bycatch (Rf); individual recently dead by other causes (Rc); and dead (D), this last state being nonobservable. The initial state in our models was always AA.

Transitions between states were modelled in a three-step approach: survival, probability to die in bycatch events and recapture probability (both conditional on the previous steps: survival and cause of death). In each capture–recapture occasion (“t”) we considered four possible events: individual not seen (noted 0); individual seen alive (noted 1); individual found recently dead by bycatch (noted 2); individual found recently dead by unknown causes (noted 3).

We assumed at least two different survivals, one for immature and another for adults, the former including either only individuals 1 year old in some models (juveniles) or all immature birds (1–3 years old) in others. As we also found a strong transient effect in adults (see results below), that means that many individuals only found once, we modelled two different survivals, one survival for the individuals captured as adults for the first time, and one for individuals seen more than once. We also tested for a time variant survival, both for immature and adults. We estimated the probability of dying on fishing gears and we additionally tested an age effect on this probability, that is separately for immature (1–3 year) and adults. Given the different capture–recapture effort made during the study, we distinguished one period from 1985 to 2001, where the effort was minor, and another second period, from 2002, when the Population Ecology Group at IMDEA started to monitor the colony, and the effort was larger. As we lacked enough data to check whether recovery probability varied over time, we kept it constant. However, we considered different recovery rates depending on the cause of death. A list of all models fit to the data for this species is in Table S1.

2.4.2 | Mediterranean shag survival models

Individuals were classified in two groups based on their age at first capture (chicks and adults). Models included four biological states: individual alive (A); individual recently found dead by bycatch (RF); individual recently found dead by unknown causes (RD); and dead (D), this last state being nonobservable. The initial state in our models was always A. Transitions between states were modelled in a two-step approach: survival and probability to die in bycatch events (conditional on survival). In each capture–recapture occasion (“t”) we considered four possible events: individual not seen (noted 0); individual seen alive (noted 1); individual found recently dead by bycatch (noted 2); individual found recently dead by unknown causes (noted 3).

We tested different survivals depending on age: one age (all ages with the same probability of survival), two ages (juvenile survival for the first year and adult survival including all individuals older than one year old) and three ages (one first-year survival probability, one two-year survival probability and one adult survival, including all individuals older than two years). We also tested for a time variant survival for juveniles and immatures (<3 year) and adults (>3 year). We estimated the probability of dying on fishing gears and we additionally tested an age effect on this probability, with different probability for juveniles (1 year) and adults (>1). We modelled recapture
probability as time variant, and constant. We also tested for a time variation in recovery rate, and we tested whether recovery rate was equal irrespectively of the cause of death or not. A list of all models fit to the data for this species is in Table S2.

### 2.4.3 Audouin’s gull survival models

Models included six biological states: individual alive aware (AA) and individual alive unaware (AU), to correct for trap dependence; individual recently dead by sport fishing bycatch (FS); individual recently dead by longline bycatch (FL); individual recently dead by other causes (RO); and dead (D), this last state being nonobservable. The initial state in our models was always AA. Transitions between states were modelled in a three-step approach: survival, probability to die by different causes, and recapture probability (both conditional on survival). As for this species we found individuals dead by two fishing gears and also individuals dead by other causes (i.e. predation), in each capture-recapture occasion (“t”) we considered six possible events: individual not seen (noted 0); individual seen alive (noted 1); individual found recently dead by bycatch in sport trolling fishing (noted 2); individual found recently dead by bycatch in longline fishing gear (noted 3); individual found recently dead by other causes (noted 4); and individual found recently dead by unknown causes (noted 5).

We run different models to test for different survivals depending on age and for a time variant survival. We estimated the probability of dying on both fishing gears (longline and sport) and by other causes, and we additionally tested an age effect on these probabilities, either by assuming different survival for juveniles (1 year) and adults, or by assuming different survival for immatures (1–2 years old) and adults. Given the different capture-recapture effort made during the study, and the different probability of individuals being in the colony depending on their age, we included age and time effects when modelling recapture probability. As we lacked enough data to check if recovery probability varied over time, we kept it constant. However, we allowed different recovery rates depending on the cause of death. As individuals dead from other causes than bycatch were only recovered in the colony, and chicks left the colony at fledging and almost never come back during the first two years, we included this age effect on this recovery rate. This approach does not work for bycatch recovery rates because bycatch could kill birds outside the breeding area; however, to be thorough, we also tested for an age effect in bycatch recovery rates. A list of all models fit to the data for this species is in Table S3.

### 2.5 Population modelling

All our models followed a prebreeding census format, and were based only on females, assuming equal survival between sexes and monogamy (Genovart et al., 2012, Genovart, Sanz-Aguilar, et al., 2013; Harris, Buckland, Russell, & Wanless, 1994).

#### 2.5.1 Deterministic analysis

For all three species, we first constructed a deterministic model that is based on the mean values of the estimated vital rates and yield the deterministic population growth rate or $\lambda$ (Caswell, 2001). We also used this deterministic model to account for variability in those rates and hence the risk of population decline or extinction. To do so, we picked random values for survival or fertility rates from beta distributions in each year of simulations, using the mean and variance values from our field data and capture-recapture analysis in most cases, and from previous studies when necessary (see details below). 5000 Monte Carlo simulations for 100 years each were run. For each 100-year simulation, we estimated the mean stochastic population growth rate ($\lambda_s$) over a short and relevant time horizon of 100 years, and then estimated a mean stochastic growth rate across all 5000 simulate trajectories for each scenario:

$$\lambda_s = \frac{1}{5000} \sum_{t=1}^{5000} \exp \left( \frac{\ln(N(t=100)) - \ln(N(t=0))}{100} \right).$$

We report this mean and 95% confidence intervals for these estimates.

All projection models were developed and executed in program R (http://cran.r-project.org).

#### 2.5.3 Parameter uncertainty and covariance

Our stochastic projections included parameter uncertainty in almost all demographic parameters except in a few cases when uncertainty was unknown (detailed below) (Bakker et al., 2009). In our models we also took into account, when possible, the covariance between some vital rates, such as between juvenile and adult survival (Morris & Doak, 2002). We did not include model uncertainty because parameter estimates from the second-best models were almost equivalent (at least second decimal) (see Results section).

Details on each model can be found below in each species section.

#### 2.5.4 Scopoli’s shearwater population model

We formulated a ten stage-class matrix population model (Table S4, Fig. 1). The population model included the possibility of individuals having different survivals depending on the age-stage, and we also
include the probability for some individuals to skip breeding (Genovart, Sanz-Aguilar et al., 2013; Sanz-Aguilar et al., 2011). Recent work has shown that 5-year-old first-time breeders may be paying a very high cost of reproduction (Sanz-Aguilar, Igual, Oro et al. 2016), so we included in the population model a different survival for these individuals. As a conservative measure, and based on our own results and those recently found by Sanz-Aguilar, Igual, Oro et al. (2016), we consider immature survival (2–3 years old) equal to adult survival; we used the value of adult survival corresponding to individuals seen more than once, assuming that the strong transient effect was mainly due to individuals that breed for the first time at the age of 5. All the vital rates used in the model were derived from this study, except the probability of sabbatical and recruitment, which we obtained from previous works on the same species and population (Sanz-Aguilar, Igual, Oro et al. 2016). Survival estimates from all the best ranked models were exact to the 4th decimal; thus, we did not include model uncertainty in our simulations. However as we could not rule out an equal bycatch probability for the two age classes considered, and given the large CI for the age-specific estimates (see Results), we estimated the hypothetical annual local survival probability without longline bycatch based on both, the age-specific and also the mean bycatch estimates for simulations without bycatch mortality. We thus ran four scenarios: the first scenario projected the population under current conditions and with current bycatch rates (“current 1”); the second scenario projected current conditions but assuming no cost of first reproduction for 5-year-old first-time breeders (“current 2”); the third and the fourth scenarios projected populations with the same demographic parameters than scenario one, but assuming higher survival due to no bycatch impact; n the third scenario (“no bycatch 1”), the hypothetical survival was calculated taking into account the estimated mean bycatch rate, assuming no differences in bycatch rates between ages; and in the fourth scenario (“no bycatch 2”), the hypothetical survival was calculated taking into account the age-specific bycatch probability (see Results and Table 1). In all scenarios survival of nonbreeders was considered to be equal to the survival of breeders, because we assumed that environmental stochasticity equally affected the two groups of birds. In this species, the best capture-recapture model pointed out a constant survival over time, and when decomposing annual survival we found that all variation was due to sampling variance and not to process variance, thus we only included stochasticity in fecundity. To initialize the models, we used the actual estimate of the colony of ca. 200 breeding pairs (Sanz-Aguilar, Igual, Oro et al. 2016).

### 2.5.5 Mediterranean shag population model

We formulated a five stage-class matrix population model (Table S5, Fig. 2). Survival estimates were derived from this study, and other vital rates such as the probability of sabbatical and breeding success come from previous studies of other populations. Based on previous studies, we accounted for sabbaticals (Aebischer & Wanless, 1992; Cairns, 1992), assuming a conservative annual probability of about 10%, and fixed a probability of starting reproduction at two years old of 0.47, with all remaining individuals starting reproduction at three years (Velando & Freire, 2002). In all simulations survival of nonbreeders was considered to be equal to the survival of breeders. We ran models under two different scenarios: with current fisheries’ impact and assuming no bycatch impact (see Results and Table 2). We based our initial values for population size on the estimated total population size obtained at communal roosts in the north Adriatic during late summer and autumn (Skornik et al., 2011).

### 2.5.6 Audouin’s gull population model

We formulated a seven stage-class matrix population model (Table S6, Fig. 3), with age-dependent survival rates. Based on previous studies, we assumed that three-year-old first-time breeders have lower breeding success than older or experienced breeders and that full recruitment occurred at 6 years old. We used survival estimates and breeding success estimated in this manuscript, and available information from the same population for other parameters such as recruitment rates (M. Genovart, R. Pradel & D. Oro, unpublished data). We ran models under two different scenarios: with current fisheries’ impact and assuming no bycatch impact (see Results and Table 3). We based our initial values for population size on the estimated population size in the Punta de la Banya in 2014.

### 3 RESULTS

#### 3.1 Scopoli’s shearwater

During 1985–2013 a total of 3071 individuals were captured and banded at the study colony, corresponding to 1981 chicks (65%) and 1090 adults (35%) and these were recaptured 2083 times. We obtained 28 recoveries, 14 from longline bycatch and 14 from unknown causes.

When analysing the complete data set, the GOF for the Cormack–Jolly–Seber model was very poor (c = 9.0566) mainly due to the presence of transients among individuals banded as chicks (c = 41.18) but also for individuals marked as adults (c = 2.36). We also detected strong trap heterogeneity among both chicks and adults. All our models included an age and a trap effect and we corrected for remaining overdispersion with a c = 3.08.

Four alternative models were almost equally parsimonious (Models 1–4, Tables 4a and S1). All these models supported three different groups with distinct survivals: juveniles (1 year old), breeders captured for the first time, and adults breeding more than once. In these four best models, survival did not vary significantly over time and juvenile survival was much lower than adult survival (Table 5). Three of these models suggest a different bycatch probability for juveniles and immatures versus adults (Models 1–3, Tables 4a and S1) although we cannot rule out an equal bycatch probability between ages (Model 4, Table 4a), probably due to a lack of statistical power. Our survival estimate for 2-year-old individuals should be taken with caution because we almost do not have data to disentangle survival at 2 years old from that of one-year-olds (most individuals do not return
Mean incidental capture in longlines for all ages was estimated at 0.5001 (95% CI: 0.4387–0.5633) (Model 4, Table 4a), which meant that a minimum of about half of mortality was caused by bycatch. From those that die, the probabilities of dying by longline bycatch were 0.0165 (95% CI: 0.0008–0.2530) and 0.2815 (95% CI: 0.0204–0.8806) for immatures (1–3 year) and adults, respectively (Tables 5 and S7). Thus, the annual percentage of immatures and adults dying in longlines were estimated at ca. 1.2% and 3.4%, respectively, based on those bycatch probabilities, and 35% and 6% based on the estimated mean bycatch probability (Table S7). However, these values should be taken with caution due to the large confidence intervals of the age-dependent 

**TABLE 1** Estimates of demographic parameters used in population models in Scopoli's shearwater (standard errors in brackets) for each scenario considered. "current 1": population under current conditions; “current 2”: current conditions but assuming no cost of first reproduction for 5-year-old first-time breeders; “no bycatch 1”: scenario without bycatch impact, survival estimated taking into account the mean bycatch probability; “no bycatch 2” scenario without bycatch impact assuming an age-specific bycatch probability. Sex ratio was set to 0.5 in all models. Recruitment and sabbatical estimates were common for all scenarios; recruitment was 1 for 6 years old and older individuals.

<table>
<thead>
<tr>
<th>Scenario</th>
<th>Adult survival for breeders (s3)</th>
<th>Adult survival for nonbreeders (s4)</th>
<th>Survival for 5 year first-time breeders (sf5)</th>
<th>Immature survival (2–3 year) (s2)</th>
<th>Juvenile survival (1 year) (s1)</th>
<th>Breeding success</th>
<th>Sabbatical probability after breeding</th>
<th>Sabbatical probability after sabbatical</th>
<th>Recruitment probability at 5 year</th>
<th>at 6 year</th>
<th>at 7 year</th>
<th>at &gt;7 year</th>
</tr>
</thead>
<tbody>
<tr>
<td>current 1</td>
<td>0.878 (0.006)</td>
<td>0.878 (0.006)</td>
<td>0.18 (0.17)</td>
<td>0.878 (0.006)</td>
<td>0.29 (0.025)</td>
<td>0.663 (0.06)</td>
<td>0.14 (0.020)</td>
<td>0.66 (0.071)</td>
<td>0.03 (0.02)</td>
<td>0.23 (0.08)</td>
<td>0.32 (0.11)</td>
<td>1</td>
</tr>
<tr>
<td>current 2</td>
<td>0.878 (0.006)</td>
<td>0.878 (0.006)</td>
<td>0.18 (0.17)</td>
<td>0.878 (0.006)</td>
<td>0.29 (0.025)</td>
<td>0.663 (0.06)</td>
<td>0.14 (0.020)</td>
<td>0.66 (0.071)</td>
<td>0.03 (0.02)</td>
<td>0.23 (0.08)</td>
<td>0.32 (0.11)</td>
<td>1</td>
</tr>
<tr>
<td>no bycatch 1</td>
<td>0.939 (0.006)</td>
<td>0.939 (0.006)</td>
<td>0.18 (0.17)</td>
<td>0.939 (0.006)</td>
<td>0.647 (0.025)</td>
<td>0.663 (0.06)</td>
<td>0.14 (0.020)</td>
<td>0.66 (0.071)</td>
<td>0.03 (0.02)</td>
<td>0.23 (0.08)</td>
<td>0.32 (0.11)</td>
<td>1</td>
</tr>
<tr>
<td>no bycatch 2</td>
<td>0.912 (0.006)</td>
<td>0.912 (0.006)</td>
<td>0.18 (0.17)</td>
<td>0.912 (0.006)</td>
<td>0.302 (0.025)</td>
<td>0.663 (0.06)</td>
<td>0.14 (0.020)</td>
<td>0.66 (0.071)</td>
<td>0.03 (0.02)</td>
<td>0.23 (0.08)</td>
<td>0.32 (0.11)</td>
<td>1</td>
</tr>
</tbody>
</table>

**FIGURE 1** Life cycle diagram used to project Scopoli’s shearwater population (prebreeding census). Birds indicated age-stage classes Ni: individuals i years old (from 1 to 4); N5NB: individuals 5 years old not recruited; N6NB: individuals 6 years old not recruited; N7NB: individuals 7 years old not recruited; N5B: individuals 5-year-old first-time breeders; N6: experienced breeders or first-time breeders older than 5 years old; N7B: animals in sabbatical, they have bred at least once; Y1: sabbatical probability after breeding; Y2: sabbatical probability after sabbatical; r5,6,7: recruitment probability (probability of breeding for the first time) at 5, 6 and 7 years old, respectively; p: hatching sex ratio; S1: survival of the first year of life; S2: immature survival for individuals from 2 to 4 years old; S3: adult survival for nonbreeder; S4: adult survival for a breeder older than 5 years old; S5: adult survival for a first-time breeder 5 years old; f: fertility (fledging/female year) for an experienced breeder or a >5-year-old first-time breeder; f5: fertility for first-time breeders 5 years old.
bycatch probabilities, which may also account for the disparity between the estimates for immature bycatch. Local survival assuming no bycatch occurrence was estimated at 0.6473 and 0.9393 for scenario "no bycatch 1" for juveniles and adults (>1 year), respectively, and 0.3016 and 0.9122 for scenario "no bycatch 2".

The estimated deterministic $\lambda$ under current conditions was 0.9280, reflecting an annual decline of about 7% in population size, and a time to extinction of 81 years. Generation time for the species was 17.5 years and the stable stage distribution for the species showed that 52% of females were breeders (Table S8). Sensitivity and elasticity analysis showed that changes in survival of breeding adults, and to a smaller extent the probability of a bird on sabbatical to reproduce again, had the largest effect on the population growth rate (Table S8).

When adding environmental stochasticity under current conditions of bycatch impact, the mean growth rate for the population $\lambda_s$ was 0.9287 (95% CI: 0.9151–0.9417) (Table 6). The mean time to extinction was estimated at 81 years and the probability of extinction in 100 years was high (0.9798). Even in the absence of costs of reproduction, the population showed a strong decreasing trend (Fig. 4). For the two scenarios assuming no bycatch impact, the probabilities of extinction in 100 years were almost null, although the only scenario with a stable or increasing trend was the one with no bycatch impact and assuming no differential bycatch probability between ages ("no bycatch 1", Table 6, Fig. 4). In this species even the maximum value of fertility would not be able to compensate for adult survival values lower than 0.90 (Fig. 5a).

### 3.2 Mediterranean shag

During 2005–2013 a total of 297 individuals were captured and banded at the study colony, corresponding to 269 chicks (91%) and 28 adults (9%). We obtained a total of 799 recaptures and 29 recoveries, nine dead from bycatch and 20 from unknown causes.

When analysing the data set to look for deviations from the Cormack–Jolly–Seber model, the GOF was 1.69. We included age in our models and corrected for the remaining overdispersion with a $\hat{c} = 1.5$.

The model with the lowest QAICc value (model 1, Tables 4b and S2) assumed different survival for juveniles and older birds, that...
temporally change in parallel between both age classes. Models suggesting three different survivals (model 2 and 4 Table S2), one for each age class (first year, individuals of age 2 and older individuals), were at two or less QAICc points from models assuming two survivals, suggesting that either we had no power to detect this difference in survival between individuals of two years and that of older birds, or that survival was almost equal for these age categories. The selected model (model 1, Table 4b) also showed that immature individuals had higher probability of dying in bycatch events. The models including survival changes over time in interaction with age had higher QAICc value (Models 5 and 9, Table S2). The model suggesting equal bycatch probability for immature and adult birds (Model 8, Table S2) was poorer. The model with recapture probabilities varying over time (Model 10, Table S2) performed worse, suggesting that recapture probability was very constant during the study period. Probability of incidental capture in fishing gears for immature birds was estimated at 0.096 (SE: 0.039) (Table 7). The annual probability of dying in fishing gears for juveniles was about 3.5% (Table S7). Local immature survival without incidental capture was then estimated at 0.679 (SE: 0.044). Given the limited data on bycatch events, and that no adults were found dying on gillnets, we could not estimate the bycatch probability for adults; while not estimable, it is clear that this probability is much lower than that estimated for immature birds.

Deterministic $\lambda$ under current conditions was estimated as 1.03, reflecting an annual growth of about 2.5% in population size, and a generation time of 5.6 years. The stable stage distribution for the species showed that more than half of the population was formed by breeders and ca. 5% by adults in sabbatical (Table S9). Taking into account the estimated total population size of 4000 individuals, we estimated the actual breeding population at ca. 2028 breeding pairs. Sensitivity and elasticity analysis showed that changes in survival of breeding adults had the largest effect on the population growth rate.
k scenario with no bycatch impact on juveniles, (95% CI: 0.9492 - 1.1134; Table 6, Fig. 6) suggesting an equilibrium stronger effect of longline fishing, whose impact strongly decreased on fishing gear and the age of individuals (Tables 4c and S3). The model detected sharply different bycatch probabilities depending on fishing gear and the age of individuals (Tables 4c and S3). The fit of the general model was poor and we then performed a separate GOF test for each cohort and then summed all the test results. We detected a significant trap-dependence effect and a significant transient effect. After accounting for trap dependence and transience in our models, we also accounted for remaining overdispersion applying a c-value of 1.42 to all models constructed in E-SURGE.

Our best model showed three different survivals for individuals 1, 2 and more than 2 years old and that survival changes over time; this model detected sharply different bycatch probabilities depending on fishing gear and the age of individuals (Tables 4c and S3). The probability of dying in longline fishing was much larger than the probability of dying by sport trolling, but the impact on each age class was different for each fishing gear (Tables 8 and S7). Sport trolling fishing had a low impact in the total annual mortality, with adults more prone to die in this gear than juveniles (ca. 0.1% and 0.02%, respectively; Table S7). On the contrary, we found a much stronger effect of longline fishing, whose impact strongly decreased with age: the percentage of individuals dying annually in longlines was 34%, 16% and 2.5% for juveniles, immatures and adults,

### TABLE 4
Model selection (see Methods) for estimating survival and the probability of dying in fishing gears, both by age (juveniles or immature, and adults) in (a) Scopoli's shearwater (b) Mediterranean shag (c) Audouin's gull. All models assumed a constant recovery probability different for bycatch and other causes of death. 2p: two periods with different recapture probability. Best models are shown in bold and selected model for estimating annual mean survival is shown in italics.

<table>
<thead>
<tr>
<th>Model</th>
<th>Survival</th>
<th>Bycatch</th>
<th>$p$</th>
<th>Deviance</th>
<th>QAICc</th>
<th>$\Delta$QAICc</th>
<th>$w_i$</th>
</tr>
</thead>
<tbody>
<tr>
<td>(a)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>1</td>
<td>Two ages (1 year/ad)+transients</td>
<td>Two ages (1–3/ad)</td>
<td>2p</td>
<td>10</td>
<td>8558.424</td>
<td>2798.752</td>
<td>0</td>
</tr>
<tr>
<td>2</td>
<td>Two ages (1 year/ad)+transients</td>
<td>Two ages (1–2/ad)</td>
<td>2p</td>
<td>10</td>
<td>8559.391</td>
<td>2799.066</td>
<td>0.314</td>
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<tr>
<td>3</td>
<td>Two ages (1 year/ad)+transients</td>
<td>Two ages (1/ad)</td>
<td>2p</td>
<td>10</td>
<td>8560.407</td>
<td>2799.396</td>
<td>0.6441</td>
</tr>
<tr>
<td>4</td>
<td>Two ages (1 year/ad)+transients</td>
<td>ctant</td>
<td>2p</td>
<td>8</td>
<td>8574.502</td>
<td>2799.957</td>
<td>1.2056</td>
</tr>
<tr>
<td>5</td>
<td>Two ages (1–3 year/ad)</td>
<td>Two ages (1–3/ad)</td>
<td>2p</td>
<td>10</td>
<td>8566.422</td>
<td>2801.348</td>
<td>2.5968</td>
</tr>
<tr>
<td>(b)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>1</td>
<td>Two age + time</td>
<td>Two age</td>
<td>One p/two r</td>
<td>15</td>
<td>1271.27</td>
<td>878.36</td>
<td>0.00</td>
</tr>
<tr>
<td>2</td>
<td>Three age + time</td>
<td>Two age</td>
<td>One p/two r</td>
<td>16</td>
<td>1269.86</td>
<td>879.54</td>
<td>1.18</td>
</tr>
<tr>
<td>3</td>
<td>Two age</td>
<td>Two age</td>
<td>One p/two r</td>
<td>7</td>
<td>1308.14</td>
<td>886.29</td>
<td>7.93</td>
</tr>
<tr>
<td>(c)</td>
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<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>1</td>
<td>Three age * time</td>
<td>Two age &amp; gear</td>
<td>5a</td>
<td>rl+rs+ro* two ages Imm/Ad</td>
<td>174</td>
<td>105565</td>
<td>74711</td>
</tr>
<tr>
<td>2</td>
<td>Three age * time</td>
<td>Three age * time &amp; gear</td>
<td>5a</td>
<td>r1+two ages +r2+ro* two ages</td>
<td>175</td>
<td>105565</td>
<td>74693</td>
</tr>
<tr>
<td>3</td>
<td>Four age * time</td>
<td>Three age * time &amp; gear</td>
<td>5a</td>
<td>rl+rs+ro*two ages</td>
<td>191</td>
<td>105545</td>
<td>74807</td>
</tr>
<tr>
<td>11</td>
<td>Three age * time * gear</td>
<td>5a</td>
<td>r1+rs+ro*two ages</td>
<td>121</td>
<td>106270</td>
<td>75081</td>
<td>390.15</td>
</tr>
</tbody>
</table>

---

### TABLE 5
Estimates of demographic parameters from the selected model for Scopoli’s shearwaters at Pantaleu islet (model 1, except "Mean Bycatch probability" from model 4) (standard errors in brackets).

<table>
<thead>
<tr>
<th>Demographic parameter</th>
<th>Mean (SE)</th>
<th>95% CI</th>
</tr>
</thead>
<tbody>
<tr>
<td>Juvenile survival (1 year)</td>
<td>0.2945 (0.0247)</td>
<td>0.2485–0.3451</td>
</tr>
<tr>
<td>First encounter adult survival</td>
<td>0.7741 (0.0244)</td>
<td>0.7227–0.8183</td>
</tr>
<tr>
<td>Adult survival</td>
<td>0.8786 (0.0058)</td>
<td>0.8667–0.8896</td>
</tr>
<tr>
<td>Bycatch probability in juveniles and immatures (1–3 year)</td>
<td>0.0165 (0.0249)</td>
<td>0.0008–0.2530</td>
</tr>
<tr>
<td>Bycatch probability in adult birds (&gt;3 year)</td>
<td>0.2815 (0.3029)</td>
<td>0.0204–0.8806</td>
</tr>
<tr>
<td>Mean Bycatch probability</td>
<td>0.5001 (0.0320)</td>
<td>0.4387–0.5633</td>
</tr>
<tr>
<td>Recapture probability 1985–2001</td>
<td>0.0641 (0.0049)</td>
<td>0.0552–0.0744</td>
</tr>
<tr>
<td>Unaware</td>
<td>0.2076 (0.0163)</td>
<td>0.1775–0.2414</td>
</tr>
<tr>
<td>Aware</td>
<td>0.7678 (0.0117)</td>
<td>0.7408–0.7898</td>
</tr>
<tr>
<td>Recovery rate bycatch</td>
<td>0.0419 (0.0465)</td>
<td>0.0045–0.2972</td>
</tr>
</tbody>
</table>

(Table S9). When adding environmental stochasticity under current conditions, the mean growth rate for the population $\lambda_k$ was 1.0337 (95% CI: 0.9492–1.1134; Table 6, Fig. 6) suggesting an equilibrium or a very slight population increase. As expected, when projecting a scenario with no bycatch impact on juveniles, $\lambda_k$ was even higher (Table 6, Fig. 6). In this species relatively low adult survival may be theoretically compensated with high values of fertility (Fig. 5b).

#### 3.3 | Audouin’s gull

During 1992–2012 a total of 21679 individuals were captured and banded as chicks at the study colony. We had a total of 25071 recaptures. We obtained 511 recoveries, 40 dead from sport trolling bycatch, 15 from longline bycatch, 372 from other nonbycatch causes and 84 from unknown causes.

The fit of the general model was poor and we then performed a separate GOF test for each cohort and then summed all the test results. We detected a significant trap-dependence effect and a significant transient effect. After accounting for trap dependence and transience in our models, we also accounted for remaining overdispersion applying a c-value of 1.42 to all models constructed in E-SURGE.

Our best model showed three different survivals for individuals 1, 2 and more than 2 years old and that survival changes over time; this model detected sharply different bycatch probabilities depending on fishing gear and the age of individuals (Tables 4c and S3). The probability of dying in longline fishing was much larger than the probability of dying by sport trolling, but the impact on each age class was different for each fishing gear (Tables 8 and S7). Sport trolling fishing had a low impact in the total annual mortality, with adults more prone to die in this gear than juveniles (ca. 0.1% and 0.02%, respectively; Table S7). On the contrary, we found a much stronger effect of longline fishing, whose impact strongly decreased with age: the percentage of individuals dying annually in longlines was 34%, 16% and 2.5% for juveniles, immatures and adults,
TABLE 6  Mean stochastic population growth rate $\lambda_s$ and 95% confidence intervals, probability of extinction, and mean time to extinction resulting from each scenario projected for Scopoli’s shearwaters, Mediterranean shag and Audouin’s gull

<table>
<thead>
<tr>
<th>Scenario</th>
<th>Scopoli’s shearwater</th>
<th>Mediterranean shag</th>
<th>Audouin’s gull</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>current 1</td>
<td>current 2</td>
<td>no bycatch 1</td>
</tr>
<tr>
<td>$\lambda_s$</td>
<td>0.9287</td>
<td>0.9297</td>
<td>1.0285</td>
</tr>
<tr>
<td>$\lambda_s$ lower 95% CI</td>
<td>0.9151</td>
<td>0.9159</td>
<td>1.0147</td>
</tr>
<tr>
<td>$\lambda_s$ upper 95% CI</td>
<td>0.9417</td>
<td>0.9431</td>
<td>1.0414</td>
</tr>
<tr>
<td>Extinction probability</td>
<td>0.9798</td>
<td>0.9598</td>
<td>0.0014</td>
</tr>
</tbody>
</table>

Mean time to extinction in years 81 82 101 100.99 - - 99.640 100.4886

respectively (Table S7). Local survival without incidental capture was then estimated at 0.7108 (SE: 0.0386) for juveniles, 0.8638 (SE: 0.0507) for immatures and 0.9173 (SE: 0.0027) for adult birds. We detected a different recapture probability for the first 5 age classes (Tables 4c and S3).

The estimated deterministic $\lambda_s$ under current conditions was 0.9944, reflecting almost equilibrium in population size, and a generation time of 12.43 years. The stable stage distribution for the species showed that about 68% of females were breeders (Table S10). Sensitivity and elasticity analysis showed that changes in survival of breeding adults had the largest effect on the population growth rate (Table S10).

When adding environmental stochasticity under current conditions, the mean growth rate for the population $\lambda_s$ was 0.9724 (95% CI: 0.8914–1.0640) (Table 6), showing that the population under current conditions will suffer an annual mean decrease of about 3%. The mean time to extinction was estimated at 99 years and the probability of extinction in 100 years was low (0.11). The scenario with increased survival resulting from an absence of longline bycatch predicted a stable population over time (Table 6, Fig. 7).

This species shows a theoretical capability to compensate adult mortality via increased fertility that is intermediate compared to the Mediterranean shag and the Scopoli’s shearwater (Fig. 5c).

4 | DISCUSSION

To assess the effect of fisheries bycatch is crucial for developing careful, ecosystem-based approaches to sustainable fisheries management. Limited recovery data present a large challenge in the accurate quantification of bycatch mortality rates in seabirds and in marine megafauna. Despite these constraints, we demonstrate here that the bycatch impact on three seabird species in the Mediterranean with very different life histories and foraging skills is significant. Moreover our study reinforces the idea that fisheries bycatch is a serious global threat for long-lived marine taxa (Dulvy et al., 2014; Lewison et al., 2014; Wallace et al., 2013), and we show that the demographic impact may strongly depend on the species and the fishing gear.

Perhaps our most general finding is a clear documentation that bycatch mortality varies enormously between types of fishing gear, the species of seabird, and even the ages of individuals. Longlines in particular are responsible for the highest mortality, whereas the effects of gillnets and sport fishing are estimated to be relatively low in our study. However, the low effect of these other fishing gears should be taken with caution. First, more detailed research should be carried out to assess whether the estimated lower bycatch rates of these gears are related to the fact that they are intrinsically less harmful gears, or to the fishing effort of each fleet using specific gears (e.g., number of boats, power, and number of setting operations). Second, some recoveries could be erroneously assigned to death in longline, in particular deaths caused by sport fishing, since in both cases the animal may be found with a fishing line. Even within the same fishing gear, differences in setting and specific gear operation may cause differences in bycatch rates; for instance, Ryan, Keith, and Kroese (2002) reported different incidental seabird mortality between longliners from different countries operating in the same area.

We also document that for some species young individuals were more susceptible to die in fishing gears whereas in other species, adults were the most affected age class. Specifically, first-year-old shags were strongly affected by bycatch in gillnets whereas no bycaught adults have been recovered. On the other side, in Scopoli’s shearwaters, even with high estimate uncertainty due to the small sample sizes, adults were much more affected by fishing gears than immatures. These differences in bycatch rates among age classes may be related to different foraging ranges and areas between age classes that would overlap differently with fishing vessels (Daunt, Afanasyev, Adam, Croxall, & Wanless, 2007; Votier, Grecian, Patrick, & Newton, 2010). For instance, Navarro et al. (2010) showed that the attendance of Audouin’s gull to fishing vessels decreased with age, likely because more experienced birds were more able to obtain food without relying on fisheries. For shearwaters, our estimates of 3.4% and 6% of annual percentage of adults dying in longlines at Western Mediterranean would also agree with those of 4.7–8.6% previously estimated based on bycatch observations (du Rau et al., 2015).

4.1 | Spatial and temporal heterogeneity in bycatch rates

Previous studies indicate that bycatch rates are highly variable in space and time at different scales, even for the same fishing gear and species. For instance, temporal changes in bycatch may occur at
the scale of the day, monthly, seasonal and interannual (e.g. Jiménez, Domingo, & Brazeiro, 2008; Klaer & Polacheck, 1997; Weimerskirch, Capdeville, & Duhamel, 2000) and this variability is especially high in Mediterranean artisanal fisheries. In the long term there are also temporal trends influenced by socio-economic factors. For instance a decrease of fishing yield followed by an increase of fishing effort by the artisanal fleet has occurred over the last decades in the Mediterranean (Colloca, Crespi, Cerasi, & Coppola, 2004), and the number of anglers practicing sport trolling has doubled in the Balearic Islands in the last 10 years (Cerdà, Alós, Palmer, Grau, & Riera, 2010). Thus the potential bycatch impact on some species (particularly Audouin’s gull and Scopoli’s shearwaters) may increase over time.

Bycatch rates may also differ spatially, due to the fishing distribution and effort and to the species distribution range both during breeding and wintering (e.g. Báez et al., 2014; Clusa et al., 2016; Trebilco et al., 2010). In general there is high spatial overlap between the density of birds foraging and the number of fishing boats operating in highly productive marine areas (Croxall et al., 2012), but differences in bycatch impact may occur depending on the fishing fleet and the targeted commercial fish. The Mediterranean Sea has been previously proposed as a bycatch hotspot for many species of marine megafauna (Lewison et al., 2014). The Western Mediterranean, our study area for two of the three species, may be particularly risky for seabirds, because the fishing fleet (both commercial and sport) is large compared to other Mediterranean areas, and the size and number of seabird colonies also make this an area of concentrated seabird use (Arcos et al., 2012; Zotier et al., 1999) even if central Mediterranean also holds

![Figure 4](image-url)
important seabird colonies (Karris et al., 2013). On the other hand, our study population of Mediterranean shags is located in the Adriatic, an area with lower fishing effort, thus in other shag populations the demographic impact may be stronger. The use of different wintering grounds may also account for some differences in the bycatch rate for some species and populations (González-Solis, Croxall, Oro, & Ruiz, 2007; Klaer, 2012). All these spatial differences in bycatch rate may cause colony-specific impact intensity that may be important from a demographic point of view. For instance, colonies less affected by bycatch may become demographic sources from which a temporary rescue effect via emigration may act in some population sinks more impacted by fisheries (Sanz-Aguilar, Igual, Tavecchia, Genovart, & Oro, 2016). However in species with a very restricted distribution and small populations all affected similarly by fishing bycatch, this compensatory demographic mechanism cannot operate (Genovart et al., 2016). Thus, we advise to set or continue with demographic studies, especially

**FIGURE 5** Hypothetical lambda estimates for different survival and fertility values in the three species: (a) Scopoli’s shearwater, (b) Mediterranean shag and (c) Audouin’s gull. In the three species “Survival” indicates adult survival, and juvenile survival take values proportional to adult survival. For all other demographic parameters we assume the actual estimates and are kept constant for all survival and fertility values. Lambda = 1 indicates population stability

**TABLE 7** Estimates of demographic parameters in best model with constant survivals for Mediterranean shags (model 2) (standard errors in brackets)

<table>
<thead>
<tr>
<th>Demographic parameter</th>
<th>Estimate (SE)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Juvenile survival (1 year)</td>
<td>0.645 (0.051)</td>
</tr>
<tr>
<td>Adult survival (&gt;1 year)</td>
<td>0.762 (0.037)</td>
</tr>
<tr>
<td>Bycatch probability for juvenile birds</td>
<td>0.096 (0.039)</td>
</tr>
<tr>
<td>Recapture probability</td>
<td>0.491 (0.039)</td>
</tr>
<tr>
<td>Recovery rate unknown cause</td>
<td>0.104 (0.028)</td>
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</tbody>
</table>

**FIGURE 6** Stochastic projections of Mediterranean shag population at Northern Adriatic Sea population over 100 years under different scenarios proposed. Each graph shows 20 randomly chosen trajectories from the 1000 population trajectories run in our Monte Carlo simulations. Scenario 1: current survival estimates and a very conservative estimate of sabbatical probability. Scenario 2: no bycatch impact on juveniles. Recruitment and sex ratios estimates were common for all scenarios and kept constant (see Methods and Table 4 for details)
in large seabird colonies which may host thousands of breeding pairs, to obtain estimates of bycatch mortality rates and assess the impact of fisheries also in these colonies.

### TABLE 8

<table>
<thead>
<tr>
<th>Demographic parameter</th>
<th>Mean (95% CI)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Juvenile survival (1 year)</td>
<td>0.6221 (0.5441–0.6943)</td>
</tr>
<tr>
<td>Two-year survival (2 year)</td>
<td>0.8219 (0.7006–0.9011)</td>
</tr>
<tr>
<td>Adult survival (≥3 year)</td>
<td>0.8919 (0.8866–0.8970)</td>
</tr>
<tr>
<td>Sport fishing bycatch in juveniles and</td>
<td>0.0005 (0.0001–0.0017)</td>
</tr>
<tr>
<td>immatures (1–2 year)</td>
<td></td>
</tr>
<tr>
<td>Sport fishing bycatch in adults (&gt;2 year)</td>
<td>0.0094 (0.0057–0.0155)</td>
</tr>
<tr>
<td>Longline bycatch in juveniles and</td>
<td>0.8996 (0.8611–0.9283)</td>
</tr>
<tr>
<td>immatures (1–2 year)</td>
<td></td>
</tr>
<tr>
<td>Longline bycatch in adults (&gt;2 year)</td>
<td>0.2349 (0.0180–0.8372)</td>
</tr>
<tr>
<td>Mean recapture probability for age 1</td>
<td>0.0043 (0.0033–0.0056)</td>
</tr>
<tr>
<td>Mean recapture probability for age 2</td>
<td>0.3249 (0.3070–0.3434)</td>
</tr>
<tr>
<td>Mean recapture probability for age 3</td>
<td>0.6798 (0.6643–0.6949)</td>
</tr>
<tr>
<td>Mean recapture probability for age 4</td>
<td>0.6809 (0.6664–0.6951)</td>
</tr>
<tr>
<td>Mean recapture probability for age 5</td>
<td>0.6270 (0.6171–0.6367)</td>
</tr>
<tr>
<td>Recovery rate sport trolling bycatch</td>
<td>0.6628 (0.4453–0.8279)</td>
</tr>
<tr>
<td>Recovery rate longline bycatch</td>
<td>0.0015 (0.0007–0.0028)</td>
</tr>
<tr>
<td>Recovery rate other causes juveniles and immatures</td>
<td>0.9961 (0.0168–0.9999)</td>
</tr>
<tr>
<td>Recovery rate other causes adults</td>
<td>0.0107 (0.0051–0.0211)</td>
</tr>
<tr>
<td>Recovery rate as unknown causes adults</td>
<td>0.0164 (0.0083–0.0328)</td>
</tr>
</tbody>
</table>

### 4.2 Other sources of variability in bycatch impact

Some evidence suggests that the majority of bycatch may occur during specific events, with dozens to hundreds of individuals killed, whereas many fishing line setting operations cause no bycatch (Laneri et al., 2010; Oliveira et al., 2015). For instance, up to 500 Yelkouan shearwaters (*Puffinus yelkouan*) were reported caught in a single drift net in Greece (Zydelis et al., 2013) whereas other studies assessing seabird bycatch on the same gear recorded no incidents (Tudela et al. 2005). It is crucial to assess why these events occur and what are the environmental drivers that influence such mass mortality events. For instance, some species are more gregarious than others while foraging, thus increasing the potential occurrence of mass mortalities. Gulls and shearwaters may in particular incur mass bycatch losses because large flocks may concentrate behind fishing vessels when baits become available during fishing setting lines operations, whereas shags are more solitary or forage in small groups, at least in some regions of their distribution. Nevertheless, these mass mortality events are difficult to detect through observer programmes with limited coverage (Besson 1973; Arcos, Louzao & Oro 2008; ICES 2008; Louzao et al. 2011) and are not included in our data set or estimated bycatch rate nor in the PVA analyses.

It is known that when trawlers do not operate, discards from this fleet are not available and seabirds increase their attendance to longliners and in turn the number of incidental captures rises (Garcia-Barcelona et al., 2010; Laneri et al., 2010). There is actually an incoming reform of the EU Common Fisheries Policy (CFP; http://ec.europa.eu/fisheries/reform/) that makes a ban on all fishing discards a management goal. This Reform of the EU fishing policies is essential for attaining sustainable fisheries, and thus desirable, but seabirds that heavily exploit discards are likely to suffer strong negative effects due to reduced food and elevated bycatch rate in other

### FIGURE 7

Stochastic projections of Audouin’s gull population over 100 years under current situation with longline bycatch (scenario 1), and without bycatch mortality (scenario 2). Each graph shows 20 randomly chosen trajectories from the 1000 population trajectories run in our Monte Carlo simulations.
fisheries, as recorded in some species during trawling moratoria periods. It has been also suggested that decreasing ocean productivity observed in recent years in the central north Pacific may have predisposed birds to the attend vessels and thus contributed to the increasing trend in a seabird catch rate (Gilman, Chaloupka, Peschon, & Ellgen, 2016).

4.3 Demographic features of seabird bycatch rates

Apart from the source-sink dynamics that fishing bycatch may generate at population level (see above) there are other demographic aspects of importance when evaluating the effect of bycatch mortality. First, this mortality may be additive, compensatory or partially compensatory to natural mortality (Péron, 2013). If mortality is compensatory, no effects may be expected at population level, as those individuals dying by anthropogenic causes would have died from other causes. Since juveniles of seabirds are less experienced individuals and are more exposed to natural mortality (e.g. predation, starvation), some compensatory mortality may be especially important for these ages. Nevertheless, the extremely low survival found in the present study, especially for immature Scopoli’s shearwaters, suggests that anthropogenic mortality will be largely additive. Secondly, some bias may occur if the sample of individuals dying in fishing gears is not random but biased, that is birds having higher or lower survival rate than the average (Barbraud, Tuck, Thomson, Delord, & Weimerskirch, 2013). However a recent study did not find a link between different personalities and the overlap with fisheries (Patrick & Weimerskirch, 2014). Thirdly, the observed effects of the anthropogenic mortality at population level will be also driven by the capability of the species to compensate or buffer this additional mortality (Péron, 2013; Servanty et al., 2010). This mortality may be compensated by increasing subsequent survival, increasing fertility and advancing age of first reproduction, for example via density dependence. Related to this point, generation time has been proposed as a strong predictor of compensation rate via increased fertility (Niel & Lebreton, 2005), with populations of long-lived species showing lower ability to compensate than short-lived species. Additionally, mortality in younger age classes is expected to be compensate better than in older classes (Forslund & Pärt, 1995). As expected, our projections show a stronger bycatch effect in the Scopoli’s shearwater, the longest lived species in the present study and the one most affected by bycatch of older bird. In the same vein, even if the bycatch rate observed in Audouin’s gull juveniles is much larger than the one observed in Scopoli’s shearwater, projections show a much stronger bycatch effect in the Scopoli’s shearwater. Although detailed data are still lacking, reviews of bycatch rates on seabirds at global level actually suggest that the species more affected are petrels and albatrosses, the group with slower life-history strategies (i.e. lower fertilities and higher survival rates) (Croxall et al., 2012; Lewison et al., 2014).

Seabirds are among the most threatened of predator taxa (Croxall et al., 2012), and it is now clear that bycatch is an important threat to their populations. However, as our results show, the effects of bycatch vary dramatically across species and fishing methods. There is a crucial and urgent need to implement mitigation actions to reduce bycatch (Lokkeborg, 2011) if we want to avoid extinction of some seabird populations and even species. At the same time, given the spatial and temporal heterogeneity in bycatch rates, and the different species vulnerability, we also advise setting up or continuing current demographic studies, to allow researchers to diagnose the species status, assess with reliability the effectiveness of management actions and guide future management.

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REFERENCES


SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

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