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Relative abundance and distribution of fisheries influence risk of seabird bycatch

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Fisheries provide an abundant and predictable food source for many pelagic seabirds through discards, but also pose a major threat to them through bycatch, threatening their populations worldwide. The reform of the European Common Fisheries Policy (CFP), which intends to ban discards through the landing obligation of all catches, may force seabirds to seek alternative food sources, such as baited hooks from longlines, increasing bycatch rates. To test this hypothesis we performed a combined analysis of seabird-fishery interactions using as a model Scopoli's shearwaters *Calonectris diomedea* in the Mediterranean. Tracking data showed that the probability of shearwaters attending longliners increased exponentially with a decreasing density of trawlers. On-board observations and mortality events corroborated this result: the probability of birds attending longliners increased 4% per each trawler leaving the longliner proximity and bird mortality increased tenfold when trawlers were not operating. Therefore, the implementation of the landing obligation in EU waters will likely cause a substantial increase in bycatch rates in longliners, at least in the short-term, due to birds switching from trawlers to longliners. Thus the implementation of the landing obligation must be carefully monitored and counterbalanced with an urgent implementation of bycatch mitigation measures in the longline fleet.

Effects of fishing on marine megafauna are widespread and diverse, mainly due to overfishing, production of discards and bycatch[1–3]. Bycatch, the incidental capture of non-target species, is of particular concern for long-lived species with low reproductive rates and delayed sexual maturity, such as seabirds[1]. Baited hooks offer the opportunity for an easy meal, yet these entail a very high risk of birds being hooked and subsequently drowned. A recent global review estimated seabird bycatch by longlines in 160,000–320,000 birds per year[4]. In fact, for some species, the current rates of bycatch are unsustainable for their long-term viability[5–8].

On the other hand, fishery discards may also have profound impacts on the breeding biology, distribution and population dynamics of seabirds, by making available demersal and benthonic species otherwise naturally inaccessible[9–11]. Worldwide discards are estimated to be 8% of the total catch (i.e. around 7,000,000 tonnes discarded annually[2]). Ultimately, discards seem to be responsible for the increases in population sizes of several scavenging species over the last decades, such as large gulls[9,12].

Seabird-fishery interactions are of particular concern in the Mediterranean[13]; an enclosed and low-productive sea with a high degree of endemism[14]. Four seabird species are endemic to the basin and commonly caught by fishing gear, particularly in longlines: the Audouin's gull *Larus audouinii,* and the Scopoli's *Calonectris diomedea*, Yelkouan *Puffinus yelkouan* and Balearic shearwaters *Puffinus mauretanicus*[15,16]. Among these, the Yelkouan and Balearic shearwaters are globally threatened (Vulnerable and Critically Endangered, respectively[17]). According to conservative estimates, at least 5,000 birds could be killed annually in the region[18]. In particular, the bycatch of Scopoli's shearwaters represents over 50% of all birds caught in longlines in some areas of the Western Mediterranean, which would imply that 4–6% of the local population breeding in the Balearic Islands is killed every year[4,19,20]. For these species, bycatch by other gears appears to be far less relevant in the region[15,16].

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In the Mediterranean Sea, discards are estimated to be 18% of the catch (i.e. around 230,000 tonnes discarded annually), with trawlers being responsible for 15 to 65% of the discards[18]. Discard availability modifies the diet, foraging strategies and distribution of seabirds[21–24], with some species obtaining up to 75% of their energy needs from this resource[25,13].

To further complicate matters, interactions among different fisheries may lead to unexpected indirect effects on seabirds. Some recent studies in the Mediterranean provided evidence that the attendance of Scopoli's shearwaters to trawlers and longliners may depend on the relative activity schedules of these fleets[26–28]. When trawlers do not operate, shearwaters may seek alternatives to discards, such as baits used by longline fisheries, with a consequent increase in the risk of being hooked[27,28]. This possibility needs to be fully explored, since changes in fishery schedules or discard availability can occur at any time, and a proper management may minimize their negative impacts on seabird mortality. Indeed, the reform of the Common Fisheries Policy (CFP, http://ec.europa.eu/fisheries/cfp/) by the European Union (EU), among other measures, is implementing the elimination of discards through the so called *landing obligation*, with the aim of reducing the impact of fisheries on marine ecosystems. Therefore, there will be a gradual reduction in discards, from now to 2019, that could severely affect the Mediterranean seabird community, including the threatened shearwater species[13]. Thus, there is an urgent need to improve our understanding about the undesirable interactions among different fishery activities on seabird mortality.

To cast light on this problem, we studied the interaction between Scopoli's shearwater and fishing boats, and how different fishery schedules and vessel distribution patterns affect bycatch on the western Mediterranean Sea. Specifically, we used three different approaches: (1) individual GPS trajectories of Scopoli's shearwaters and Vessel Monitoring System (VMS) trajectories of fishing boats to study spatiotemporal dynamics, and establish whether vessel densities determine shearwaters choice between longliners and trawlers; (2) seabird counts on-board longliners to determine the main drivers influencing seabird attendance during longline settings, focusing particularly on the potential influence of trawler activity in the surrounding area; and (3) 13 complete years of bycatch data from one longline vessel to understand whether the rate of bycatch increases on days when trawlers do not operate.

Results

Spatiotemporal interactions. Overall, we tracked 65 shearwaters in two different years, 2010 and 2012, with 4 birds being tracked both years. We obtained trajectories from 90 GPS deployments, 30 trajectories corresponding to 38 foraging trips in 2010 and 60 trajectories corresponding to 145 foraging trips in 2012 (Fig. 1). Birds mainly foraged in the Catalan shelf and the Menorca channel, areas used by both trawlers and longliners (Fig. 1). We obtained 267 interaction events, where a bird followed a vessel, 246 interactions occurred with trawlers and 21 with pelagic longliners. From those, only 86 events corresponded to events in which at least one longliner and one trawler were fishing simultaneously in the same area (Fig. 1). From those interactions, 72 were with trawlers and 14 with longliners. Interactions with longliners mainly happened in the Menorca channel, close to the breeding areas, while interactions with trawlers happened both in the Catalan shelf and in the Menorca channel. We found no direct effect of the number of longliners in the area on the probability of interaction with either a trawler or a longliner. However, the probability of interacting with a longliner increased as the number of trawlers decreased ($P = 0.029$), from nearly 0% when 20 or more trawlers were in the area, to 40% probability of interaction when only 1 trawler was present (Fig. 2).

On-board censuses. We found that the number of attacks to the bait and the number of birds following a vessel was correlated ($r_s = 0.38$, $P = 0.004$). Since sample size for seabird attendance was greater than for bait attacks, we used seabird attendance as a proxy for bycatch risk on subsequent analyses, allowing us to study the ultimate factors that influence it. Analysis of relative importance showed that setting time was the main variable to account for shearwater presence and abundance behind longliners: shearwaters were more likely to occur in greater numbers at twilight (Tables 1 and 2). Bait type and longline type also had an important effect on bird attendance, birds being more likely to interact with longliners when they used mixed baits (fish and cephalopods, instead of only one of both) and when they targeted pelagic species (instead of demersal species) (Tables 1 and 2). The distance to the nearest breeding colony had a relatively high influence on shearwater abundance; the further away from colony areas the less likely it was to detect birds attending longliners (Tables 1 and 2). The number of hooks in each setting had a very low effect on the presence and abundance of birds attending longliners (Tables 1 and 2). The breeding stage of the birds (pre-laying, incubation or chick-rearing) and the meteorological conditions did not affect bird attendance to longliners (Tables 1 and 2). The probability of birds attending longliners increased 4% per each trawler leaving the longliner surroundings, but bird abundance was not affected by the number of trawlers (Tables 1 and 2).

Bycatch data. From 2003 to 2015, we collected all birds hooked in a longline boat from Vilanova i la Geltrú after arrival to the port. During this period, 67 Scopoli's shearwaters became entangled in the fishing gear and died. We found that the number of birds caught differed significantly among the days of the week; it was higher on Sundays and Mondays than on the remaining days ($\chi^2 = 17.63$, $p < 0.001$). In fact, 51% (34 individuals) of the birds were hooked on Sundays, when trawlers do not operate, and 28% (19 individuals) on Mondays, when longline vessels start operating before trawlers after the weekend rest. From Tuesday to Friday, only 14 birds were hooked across the 13 years covered. In addition, we found that the probability of a bycatch event (when one or several birds were hooked) followed the same pattern: events were more likely to occur on Sundays and on Mondays than on the rest of the week days (12 bycatch events occurred on a Sunday, 5 on a Monday and 6 from Tuesday to Friday; $\chi^2 = 4.9$, $p = 0.03$).

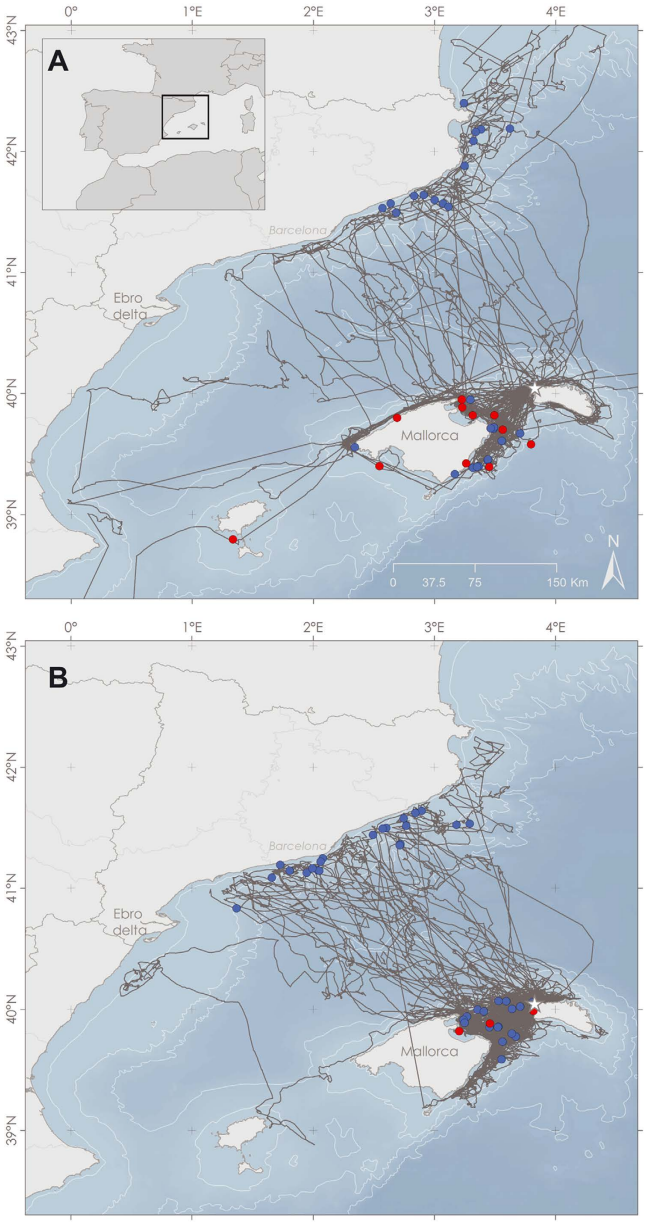


Figure 1. Shearwater GPS tracks (in grey) and concurrent interactions between shearwaters and fishing vessels (dots) inferred from the Vessel Monitoring System (VMS) in 2010 (**A**) and 2012 (**B**). Red dots correspond to interaction with longliners and blue dots to interactions with trawlers. Maps were generated with ArcGis version 10.3 (URL: https://www.arcgis.com).

Discussion

The concurrent analysis of GPS data from seabirds and vessels showed the importance of the spatiotemporal distribution of operating trawlers in determining the probability of seabirds interacting with longliners: the higher the density of trawlers, the less likely birds interacted with a longliner. On-board censuses of seabird attendance to longliners corroborated this result, showing that attendance, which can be taken as a proxy of bycatch risk, increased when trawlers were not operating in the longliner proximity. Finally, dead birds collected by fishermen showed that seabird catches were significantly and substantially greater on days when trawlers did not operate. Hence, results from these three different approaches point towards the same direction: seabird bycatch in longliners significantly increases when trawlers operate in low densities or do not operate.

In this regard, the reform of the CFP, which intends to substantially reduce or even eliminate fishery discards, might dramatically increase seabird bycatch risk, at least in the short term, by forcing seabirds to intensify their foraging efforts, including the search of an "easy meal", i.e. switching from trawler discards to longline baits. Our results show that, at present, trawlers are acting as a buffer of the seabird interactions with longliners, such that the probability of shearwaters interacting with a longliner decreases from 40% when only one trawler is present in the area to almost 0% when >20 trawlers are present (Fig. 2). The same pattern applies to the on-board

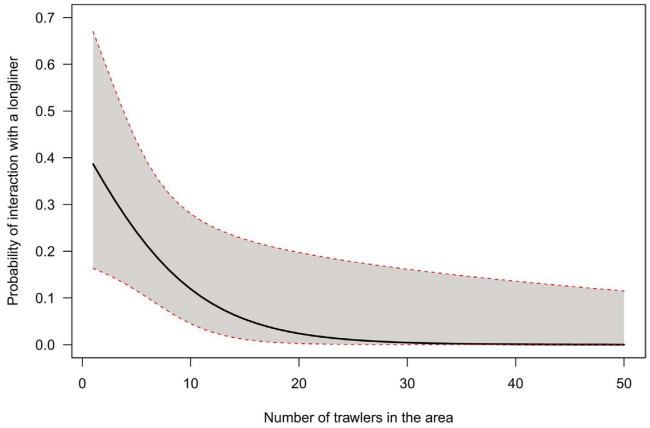


Figure 2. Probability of interaction between shearwaters and longliners as a function of the number of trawlers in the area. Black line represents the predicted values from the model and the grey area represents the 95% confidence intervals.

Variable	Value	Std. Error	RI
Presence - Zero part (Intercept)	−0.84	1.01	
Bait: Fish	1.75	1.11	0.93
Bait: Mixed	2.73	1.38	
LT: Pelagic	1.96	1.31	0.59
Time: Daytime	−1.39	0.79	0.90
Trawlers	−0.18	0.24	0.53
SDC	−0.27	0.45	042
Period: Incubation	0.11	0.47	0.35
Period: Prelaying	−0.41	0.74	
Wind: Windy	−0.07	0.34	0.24
SHS	0.02	0.16	0.24
Abundance – Count part (Intercept)	2.48	0.47	
LT: Pelagic	0.15	0.40	0.31
Time: Daytime	−0.53	0.46	0.76
Trawlers	−0.01	0.09	0.22
SDC	−0.15	0.19	0.55
Period: Incubation	0.01	0.07	0.05
Period: Prelaying	0.01	0.11	
Wind: Windy	−0.03	0.16	0.20
SHS	−0.08	0.14	0.39

Table 1. Coefficient, standard errors and relative importance (RI) of each variable for shearwaters attendance to longliners. See Table 2 for detailed explanation of the variables.

observations and bycatch rates. For each trawler leaving the surroundings of a longliner, the probability of seabirds following the longliner increases by 4%; and the rate of bycatch experiences a tenfold increase when trawlers do not operate. The reduction of discards is therefore likely to result in a substantial increase in bycatch rates of Scopoli's shearwaters, to a level that could be completely unsustainable for some western Mediterranean populations[29]. Moreover, our results can reasonably be extrapolated to other seabirds species targeting trawler discards in the Mediterranean which are also known to be caught in longlines, such as the Audouin's gull and the Yelkouan and Balearic shearwaters[23]. The latter is of particular concern given its sensitive conservation status, since bycatch appears to account for almost half the adult mortality estimated for the species[8].

Given the concern of bycatch for many Mediterranean seabirds, including the four endemic species, it is urgent to take into account this multi-fisheries interaction when designing fishing regulations, in order to minimise its potentially detrimental effect. As a first approach, our results suggest that precluding longline vessels (both demersal and pelagic) to set their lines when trawlers are not operating might substantially contribute to this aim. However, given that (trawling) discards will anyway be reduced in the short run, our results also call for an immediate enforcement of effective mitigation measures in longliners to reduce seabird bycatch. Since our results also point out that the strongest influence on seabird attendance to longliners was the time of setting, operational measures regulating the setting timing should contribute to minimise the problems. Indeed, seabirds were more prone to interact with longliners during sunset and sunrise. These results have also been observed in

Variable	Abbreviation	Type	Description
Breeding period	Period	Categorical	Pre-laying (March – 1st week June), incubation (until mid-July) or chick-rearing (until October)
Distance to colony	SDC	Continuous	Distance from the nearest colony (scaled km)
Wind	Wind	Categorical	Windy or still
Bait composition	Bait	Categorical	Fish, cephalopods or mixed (fish + cephalopods)
Setting time	Time	Categorical	1 h ± of the twilight or rest of the daytime
Longline type	LT	Categorical	Demersal or pelagic
Hooks setting	SHS	Continuous	Number of hooks setting (scaled)
Number of trawlers	Trawlers	Continuous	Number of trawler within 6 km from the longliner
Longliner ID		Random	Boat identifier

Table 2. Explanatory variables used in the analyses of Scopoli's shearwaters interaction with longliners.

other studies which showed that many diurnal seabirds have activity peaks at dawn and dusk[19,27,30]. Since most seabirds affected by longliners in the Mediterranean are basically diurnal, a promising mitigation measure to be applied in this region would be night setting, as previously suggested in other studies[19,30–34]. This measure could be easily implemented at low economic costs, and compliance could be monitored and enforced to some extent through the control of fishing schedules of longliners by harbour authorities, as it is currently done for other types of fisheries. However, fishermen could be reluctant because it would require a rearrangement of their schedules and it could also limit the number of setting operations, particularly during the relatively short summer nights. Therefore, further work is needed to assess the efficacy and viability of this measure as well as of other mitigation measures that have proven successful in other regions. Among them, the use of tori-lines, the increase of sinking rates of the line through configuration changes, or a combination of the above, might also contribute to minimise seabird bycatch in Mediterranean longliners[31,34–37].

In conclusion, our study highlights the importance of combining various sources of information to achieve robust and complementary results on the complex effects of fishing activities on seabird bycatch. In particular, three different approaches indicated that the risk of a seabird to be captured in longlines increases dramatically when trawlers are not present in the area where longliners operate. That is, when trawlers stop providing discards seabirds may switch from trawlers to longliners, and therefore the landing obligation being implemented by the CFP must be carefully monitored and counterbalanced with the urgent implementation of mitigation measures. In a more general sense, our results point out that to determine the best management practices of the different fishing fleets, we need to study unexpected impacts rising from the interactions among different types of fisheries. Therefore, impacts of changes on the discard availability must be carefully evaluated and monitored across the different fleets to avoid catastrophic effects on seabird populations as well as on other components of the marine ecosystem.

Methods

Spatiotemporal interactions. To establish the spatiotemporal interaction between tracked birds and fisheries, we obtained data from two main sources: GPS devices for tracking shearwaters and the VMS for tracking vessels. GPS-tracking of Scopoli's shearwaters was conducted in Cala Morell (Menorca, Balearic Islands, Spain; 40°3′N, 3°52′E), in two different years. In 2010, birds were tracked during the incubation period, from the 18th June to the 8th July; and in 2012 during the chick rearing period, from the 25th July to the 20th September. This area holds the largest Scopoli's shearwater colony of the Balearic Islands, tentatively estimated in 1,000–6,000 pairs[38,39]. Scopoli's shearwaters were captured at night by hand or using looped poles on the nest, when they flew back to the colony to feed their offspring or for incubation shifts. We used GPS loggers (Perthold Engineering LLC, weighing 20 g[40]) sealed to be waterproof and programmed to record bird position each 2.5 or 5 minutes. Loggers were attached to the back of the birds using Tesa© tape[41]. At deployment, birds were ringed, sexed (through biometric measures) and weighed. In an attempt to minimise adverse effects on the birds, total mass of the device did not exceed 3% of the birds body mass[42]. At recovery, GPS devices were detached and birds were weighed. On average, we found a 25 g decrease on bird weight after tag retrieval (Paired t-test, $t = 4.4138$, $df = 83$, $p < 0.001$), that we do not expect to have relevant effects on the foraging behaviour of the birds[43]. In 2010, we deployed 30 GPS tags in 25 individuals, whereas in 2012, 79 GPS loggers were deployed on 56 individuals. In order to minimise the possible impact of tagging birds on their breeding success, only one adult bird per nest was tagged. Birds carried loggers from 3 to 17 days before retrieval, recording from 1 to 9 foraging trips. These protocols were approved by *Servei de Protecció d'Espècies*, from the Balearic Islands Government. The methods were carried out in accordance with the relevant guidelines and bird handling and tagging protocols.

The Vessel Monitoring System (VMS) is a satellite-based monitoring system, implemented by the European Union, that provides data on the location, course and speed of fishing vessels over 12 m long[44]. In the Spanish Mediterranean, 90% of trawlers and 60% of pelagic longliners use this localization system, although only a few demersal longliners and artisanal (polyvalent) vessels use it[45]. The default frequency of VMS locations is one fix every two hours. Consequently, the spatiotemporal combination of VMS and GPS data was obscured by the uncertainty about the position of each vessel in the two hour gap between two consecutive locations. Taking into account this limitation, to cover the potential interactions between birds and vessels throughout the entire vessel trip, we identified all bird locations within a ±1 h interval and within a 5 km buffer from a vessel location (as maximum speeds of vessels are around 5 km/h). Next, we applied a second filter selecting bird trajectories where

the bird bearing diverged in less than ±30° from the vessel bearing (estimated from consecutive locations). This bird bearing was considered the mean bearing for all locations inside each buffer of spatiotemporal coincidence. We chose ±30° because after some trials this angle emerged as the most biologically meaningful figure. For each bird-vessel interaction location, we assessed the number of vessels within a ±1 h interval and a 30 km radius. We chose 30 km as it has been shown that some procellariforms can detect food resources up to 30 km away[46,47]. We focused our research in two types of fisheries, trawling and pelagic longlining, since shearwaters tend to associate with them in search of food. Demersal longliners, including artisanal (polyvalent) vessels were excluded from this analysis, despite also attracting (and catching) seabirds, since most of them are too small to carry the VMS system (see above). Moreover, we only selected the interaction events where at least one trawler and one longliner were present in the area to control for the fisheries different regime and ensure that when birds interacted with a trawler they had also the option to interact with a longliner and vice versa.

We used a generalized lineal mixed model that included year as a random effect, number of trawlers and number of longliners as fixed effects and a binomial response, either the bird interacted with a longliner or it interacted with a trawler. We calculated the AIC values of all candidate models and selected the model with the lowest AIC value as the best model for explaining bird interaction with fisheries.

On-board censuses. At-sea surveys were carried out during 3 consecutive years (2011–2013) covering the main fishing grounds of longline fisheries in the Catalan shelf and Balearic Islands, during the period where the species was present in the Mediterranean (March–October). The counts were conducted during 102 longline settings from 20 small-scale vessels operating in the NW Mediterranean (16 demersal and 4 pelagic longliners). Here we only considered the maximum number of Scopoli's shearwaters following the vessels at the end of each 10-min counts in each setting operation, as well as the number of attacks to the bait and the number of birds incidentally captured. The number of birds hooked (26 birds in nine events) was too low to perform reliable statistical analyses. Fishing habits, detailed description of fishing gear used and meteorological data were noted in each fishing trip (Table 2). The number of trawlers in a 6 km radius around the longliner was also recorded in each 10-min survey.

Bycatch events are relatively rare and patchy, thus being difficult to monitor through low-effort observer programmes. We evaluated seabird attendance to longliners as a proxy of seabird attacks, which are more closely related to seabird bycatch and therefore mortality. Generalized lineal mixed models (GLMMs) were used to identify the main factors influencing Scopoli's shearwater interaction with longliners. Abundance data is characterized by having a high proportion of zero values and a skewed distribution of non-zero positive values caused by large counts of individuals (flocking behaviour)[48]. Hurdle models are a suitable method for modelling this type of distributions, which is characterized by treating the data in two parts: (1) presence/absence of the species (Zero part) and (2) the abundance when the species is present (Count part)[48–51]. We analysed the relationship between the number and presence of Scopoli's shearwaters and temporal, spatial and operational variables (Table 2). Trawler presence in the surrounding area was also considered to assess their influence on seabird attraction to longliners. Longliner identity was used as a random effect. We used "glmmadmb" function from the "glmmADMB" R package (R version 3.1.2). Zero hurdle part was modelled with the assumption of a binomial error structure (logit link function), while in the Count part a truncated version of the Negative Binomial distribution was considered (log link function). We checked collinearity between predictors and removed redundant ones. Then, we used the variance inflation factor (VIF) to verify the independence of each variable on the estimate of the regression coefficients of the model[52].

Relative importance analysis was carried out with the model-averaging approach. This approach is useful when there is a large uncertainty about a set of models[53]. In this way, we obtained model-averaged parameter estimates that were directly comparable to each other[53]. We estimated the parameters from the set of all models for which the sum of Akaike weights reached >0.95.

Bycatch records. From 2003 to 2015 fishermen from a single demersal longline vessel fishing off the Catalan coast recorded and handed over Scopoli's shearwater carcasses accidentally caught in their longline. To establish temporal bycatch patterns, we analysed whether the number of birds hooked and the number of capture events differed among the days of the week by using a Pearson's Chi-squared Test for Count Data with Bonferroni correction.

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Author Contributions

A.S.R. collected and analysed the data and wrote the paper; V.C. collected and analysed data and made comments in the manuscript; J.M.R.G. and S.G. provided advice in analytic and ecological issues and logistic support throughout all the stages of the study and discussed drafts of the manuscript; J.B., B.R. and J.M.A. collected the data and made comments on the manuscript and J.G.S. conceived the study and wrote the paper.

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RESEARCH ARTICLE

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Double-tagging scores of seabirds reveals that light-level geolocator accuracy is limited by species idiosyncrasies and equatorial solar profiles

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Abstract

1. Light-level geolocators are popular bio-logging tools, with advantageous sizes, longevity and affordability. Biologists tracking seabirds often presume geolocator spatial accuracies between 186 and 202 km from previously innovative, yet taxonomically, spatially and computationally limited, studies. Using recently developed methods, we investigated whether assumed uncertainty norms held across a larger-scale, multispecies study.
2. We field-tested geolocator spatial accuracy by synchronously deploying these with GPS loggers on scores of seabirds across five species and 11 Mediterranean Sea, east Atlantic and south Pacific breeding colonies. We first interpolated geolocations using the geolocation package `FLightR` without prior knowledge of GPS tracked routes. We likewise applied another package, `probGLS`, additionally testing whether sea-surface temperatures could improve route accuracy.
3. Geolocator spatial accuracy was lower than the ~200 km often assumed. `probGLS` produced the best accuracy (mean ± *SD* = 304 ± 413 km, *n* = 185 deployments) with 84.5% of GPS-derived latitudes and 88.8% of longitudes falling within resulting uncertainty estimates. `FLightR` produced lower spatial accuracy (408 ± 473 km, *n* = 171 deployments) with 38.6% of GPS-derived latitudes and 23.7% of longitudes within package-specific uncertainty estimates. Expected inter-twilight period (from GPS position and date) was the strongest predictor of accuracy, with increasingly equatorial solar profiles (i.e. closer temporally to equinoxes and/or spatially to the Equator) inducing more error. Individuals, species and geolocator model also significantly affected accuracy, while the impact of distance travelled between successive twilights depended on the geolocation package.
4. Geolocation accuracy is not uniform among seabird species and can be considerably lower than assumed. Individual idiosyncrasies and spatiotemporal dynamics (i.e. shallower inter-twilight shifts by date and latitude) mean that practitioners

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should exercise greater caution in interpreting geolocator data and avoid universal uncertainty estimates. We provide a function capable of estimating relative accuracy of positions based on geolocator-observed inter-twilight period.

KEYWORDS

animal tracking, archival tags, bio-logging, FLightR, probGLS, sea-surface temperature, solar geolocation

1 | INTRODUCTION

Light-level geolocators ('geolocators') are one of the most popular and practical tools available to study animal movement, with well-established, open access standards and techniques available to guide analyses of geolocation data (see Lisovski et al., 2020). However, there can be considerable uncertainty associated with the accuracy of location estimates derived from light-level data. Geolocators are small (i.e. ~0.3–3.3 g) archival data loggers that measure and record solar intensity at regular intervals, some with the capability of measuring and archiving other information such as water temperature, wet/dry events and barometric pressure. When geolocators are retrieved, light-level data are downloaded and directed into astronomical equations that estimate spatial locations based on the timing of twilight events (i.e. sunrises and sunsets). Geolocator data can be interpolated into one or two positions per day with latitude estimated by day length, and longitude estimated by the timing of local midday or midnight relative to Greenwich Mean Time and Julian day (Hill, 1994).

Geolocators were first applied to tracking the movements of marine vertebrates including elephant seals (Delong et al., 1992), fish (Block et al., 1998), seabirds (Croxall et al., 2005; Egevang et al., 2010; González-Solís et al., 2007; Guilford et al., 2009; Phillips et al., 2006; Shaffer et al., 2006; Tuck et al., 1999) and sea turtles (Fuller et al., 2008). Recently, geolocators have undergone considerable miniaturisation and improvements to onboard storage capacity, which has stimulated an increase in studies that use light-level data to infer spatial information about both marine and terrestrial species that were otherwise too small to be burdened with tracking devices (Bridge et al., 2011). The number of ecologists using geolocators to study seabird movements has increased in tandem with these sensor improvements and newly designed geolocation methods implemented in several R packages for processing and analysing light-level data (e.g. Merkel et al., 2016; Rakhimberdiev et al., 2017; Sumner et al., 2009).

Despite the growing volume of geolocator data, the spatial accuracy of geolocators used on seabirds has to-date been empirically tested relative to more precise technologies only on three species of albatross with limited latitudinal breadth (Phillips et al., 2004; Shaffer et al., 2005). These studies employed older geolocator sensors that recorded light levels more infrequently and previous threshold method geolocation software that, unlike modern methods, did not incorporate movement models or probabilistic algorithms. These studies measured the distances of satellite Platform Terminal Transmitter (PTT) locations to corresponding geolocation estimates and assessed mean accuracies ± standard deviation (*SD*) of 186 ± 114 km (Phillips et al., 2004) to 202 ± 171 km (Shaffer et al., 2005). These estimations of geolocation accuracy are coarse relative to those obtained from satellite loggers that fix positions from orbiting Advanced Research and Global Observation Satellites (ARGOS), which have a typical 1–3 km accuracy (Burger & Shaffer, 2008) or the Global Positioning System (GPS), which regularly has average location accuracies of less than 10 m (Hulbert & French, 2001) to ~15 m (Forin-Wiart et al., 2015). However, tracking instruments that use satellites tend to be too large for many species and may be prohibitively expensive. Satellite tracking instruments typically have limited power capacity and on-board memory storage, and depending on the species, can place unreasonable burdens on birds in terms of wing-loading and hydrodynamic drag (Phillips et al., 2004; Shaffer et al., 2005). Furthermore, attaching satellite instruments to feathers for long-term deployments is not suitable for most seabirds because they periodically moult. For many seabird species the use of harness attachment to remedy this constraint is not recommended (Phillips et al., 2003) and may increase mortality and device-induced behaviours (Barron et al., 2010). Light-level geolocation has therefore offered an attractive year-round alternative to satellite tracking that tackles many of the constraints associated with using larger, more spatially accurate technology.

Light-level geolocation is inherently prone to coarse spatial accuracy, particularly for estimates of latitude which are generally considered to become less accurate under increasingly 'equatorial' solar profiles; that is, either nearer the Equator (spatial variation) or solar equinox (temporal variation) where and when day length changes more shallowly with latitude (Ekstrom, 2004; Hill, 1994; Lisovski et al., 2020). The inherent accuracy of latitudinal geolocations fluctuates by date, even if the amount of sensor shading remains constant (Lisovski et al., 2012). Weather (e.g. cloud cover) and behavioural patterns such as roosting at twilight periods can induce errors in estimates of day or night length and are thus thought to affect accuracy in geolocation (Lisovski et al., 2012). In addition, light-level data collected during breeding stages are often thought to have reduced spatial accuracy due to specific behaviours that

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might affect light curves (Lisovski et al., 2012, 2020). For example, some species roost on the ground (Corre & Jouventin, 1997; Schreiber & Chovan, 1986), brood their young at twilights (Howell & Bartholomew, 1969) which can shade sensors, or nest underground in burrows (Shaffer et al., 2006). Geolocators fitted on birds that go to roost before last light or depart nest sites after first light could therefore exhibit abnormal transitions between light and dark at twilight times in light curve data (Gow, 2016).

Another typical behaviour of seabirds is wide-ranging movement that can occur within a single day or night (Clay et al., 2018; McDuie et al., 2015). Such large-scale movement between twilights can impact interpolations of longitude by shifting the solar noon, or latitude by compressing or elongating day length, all depending on the speed and direction of travel and time of year (Lisovski et al., 2012). Furthermore, data collected by geolocators fitted to wide-ranging seabirds, generally on leg rings, are likely to have idiosyncratic differences relative to being collected at a stationary location (Lisovski et al., 2012; Welch & Eveson, 1999). Accordingly, it has been suggested that the performance of geolocators might be species dependent (Shaffer et al., 2005) and that the choice of geolocation algorithm might affect the accuracy of position estimates (Musyl et al., 2001).

Despite the well-known and hypothesised limitations of light-level geolocation, geolocators have generally been considered satisfactory for studying foraging ranges (Phillips et al., 2004), and habitat preferences and distributions of pelagic seabirds (Egevang et al., 2010; González-Solís et al., 2007; Guilford et al., 2009; Halpin et al., 2018; Lascelles et al., 2016; McDuie & Congdon, 2016; Pollet et al., 2014; Quillfeldt et al., 2017; Shaffer et al., 2006). Here, we sought to evaluate for the first time the accuracy of modern geolocation algorithms on a large and diverse sample of free-flying seabirds and assess whether accuracy is affected by the species being tracked and movement behaviours. Past studies of geolocation accuracy have used older technology and/or geolocation algorithms (e.g. Phillips et al. 2004; Shaffer et al. 2005), evaluated static deployments of tags either carried by resident birds or fixed in the environment (e.g. Fudickar et al., 2012), or been carried out on single species with sample sizes that are likely too small to have adequate statistical power to disentangle patterns in accuracy (e.g. Rakhimberdiev et al., 2016).

Our objectives were to (a) investigate if the spatial accuracy typically reported in geolocation studies of seabirds is applicable in the context of a large-scale, multi-species study; (b) test uncertainty estimates of more advanced geolocation models; (c) test whether sea-surface temperature (SST) interpolation improved average accuracy in these new methods and d) model which situational factors most affected geolocator spatial accuracy. To address these aims, we conducted a field test using synchronous deployments of GPS loggers and geolocators fitted to individual seabirds from around the world. We measured the spatial accuracy of geolocator-interpolated routes from GPS tracks, tested for effects of species and individuals, and whether the inter-twilight distances travelled by birds affected the spatial accuracy of geolocation.

2 | MATERIALS AND METHODS

2.1 | Study species & locations

We analysed synchronous location data from 151 chick-provisioning individual seabirds that were tracked concurrently with GPS and light-level geolocator loggers (i.e. 'double tagged') using the geolocation packages, `FlightR` (Rakhimberdiev et al., 2017) and `prob-GLS` (Merkel et al., 2016). Tracking data represent 200 deployments across five species from 11 separate seabird colonies between 2011 and 2019 (Table 1). We originally had access to 278 double-tagged deployments (some individuals were tagged more than once within and between years), but we reduced the dataset to 200 deployments after excluding those with insufficient data to produce stationary calibrations, or where light curve transitions were poor. Breeding colonies were located in several marine regions including in Southern Europe (Mediterranean Sea), West Africa (east Atlantic Ocean) and Australia (south Pacific Ocean). In the northern hemisphere, we analysed double-tagged deployments from Cape Verde Shearwaters (*Calonectris edwardsii*, $n = 11$; 2014 and 2018), Cory's Shearwaters (*C. borealis*, $n = 100$; 2011 and 2013–2018), Scopoli's Shearwaters (*C. diomedea*, $n = 61$; 2014–2018) and Red-billed Tropicbirds (*Phaethon aethereus*, $n = 7$; 2017–2018) on 10 breeding colonies between latitudes 15°N–40°N. In the southern hemisphere, we analysed double-tagged deployments from White-necked Petrels *(Pterodroma cervicalis*, $n = 21$; 2018 and 2019) on a single colony at latitude 29°S.

2.2 | Double tagging

We fitted birds with one of five light-level geolocator immersion sensors: BAS_MK19 (British Antarctic Survey) or Biotrack_MK3005 [formerly BAS_MK19] (Biotrack Ltd), which sample light intensity every minute and record the maximum value every 5 min with water temperature recorded when the sensor is immersed continuously for 25 min; and Intigeo-C330, Intigeo-C250 or C65-SUPER (Migrate Technology Ltd), which sample light intensity every minute, storing the maximum value every 5 min and record water temperature when the sensor is immersed continuously for 20 min. The conductivity (wet/dry) sensor sampling rate was 6 s for all models. Devices were leg mounted and fitted to the tarsus by mounting to either a darvic or metallic ring using a plastic cable tie, or a Velcro© (38 mm; Paskal) hook-and-loop harness. GPS loggers were fitted to birds using Tesa© tape (4651; Tesa Tape Inc.) by taping either to contour feathers between scapulae, or at the base of the two to four central rectrices on shearwaters and petrels and six rectrices on tropicbirds.

2.3 | Data preparation and analysis

All data were processed in the statistical software environment R, version 3.5.1 (R Core Team, 2020), and spatial measurements were

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TABLE 1 The species, individuals, regions and respective colonies where seabirds were tracked synchronously with light-level geolocators and GPS loggers. The sample size of geolocation estimates used in analyses of each geolocation algorithm isprovided

Colony name	Latitude	Country	Marine Region	Species (no. individuals)	Number of geolocations[a]	
					FLightR	probGLS
Cala Morell (Menorca)	40.1°N	Spain	Mediterranean	Scopoli's Shearwater (52)	574	626
Islas Columbretes	39.9°N	Spain	Mediterranean	Scopoli's Shearwater (4)	73	77
Isla de Cabrera	39.2°N	Spain	Mediterranean	Scopoli's Shearwater (2)	24	26
Isla de las Palomas	37.6°N	Spain	East Atlantic	Scopoli's Shearwater (3)	41	44
Islote de Montaña Clara	29.3°N	Spain	East Atlantic	Cory's Shearwater (32)	441	501
Timanfaya (Lanzarote)	29.0°N	Spain	East Atlantic	Cory's Shearwater (6)	92	43
Veneguera (Gran Canaria)	27.8°N	Spain	East Atlantic	Cory's Shearwater (62)	598	1,206
Ilhéu Raso	16.6°N	Cabo Verde	East Atlantic	Red-billed Tropicbird (2)	8	10
Ilha Boa Vista	16.2°N	Cabo Verde	East Atlantic	Red-billed Tropicbird (5)	48	52
Ilhéu de Curral Velho	15.9°N	Cabo Verde	East Atlantic	Cape Verde Shearwater (11)	189	199
Phillip Island (Norfolk Island)	29.1°S	Australia	South Pacific	White-necked Petrel (21)	993	410

[a]The number of geolocations per package (i.e. `FLightR` or `probGLS`) differs depending on the suitability of the data for analysis in a given package. For example, whether the geolocator recorded water temperature exclusively when immersed, and calibration data from a stationary location.

calculated on the World Geodetic System (WGS 1984) ellipsoid. The processing of geolocation data was carried out by an analyst who had no knowledge of the spatial attributes of the paired GPS tracking data so that decisions about parameterising geolocation algorithms were not influenced by prior knowledge of the birds' underlying movements. This was done to ensure that geolocation positions in our study would be comparable to those of other geolocation studies for which practitioners typically have no knowledge of where the bird travelled. GPS tracks were standardised using the package `adehabitatLT` (Calenge, 2006) by resampling all GPS locations to an equal 10 min interval because the GPS sample rates varied among species and colonies. We gap-filled GPS tracks except when periods of more than 1 hr occurred between fixes. To account for erroneous positions that may have been caused by poor satellite reception, we applied a standard maximum allowable flight velocity of 27.8 m/s (100 km/hr) between consecutive locations for all seabird taxa. We considered this to be a maximum realistic speed for wide-ranging seabirds (Lascelles et al., 2016).

Depending on the brand of geolocator, we first imported raw light-level data using the functions `readMTlux` in the package `TwGeos` (Wotherspoon et al., 2016) or `ligTrans` in the package `GeoLight` (Lisovski & Hahn, 2012). We then automated twilight event (i.e. sunrises and sunsets) annotation in raw light-level data using the function `preprocessLight` in the package `TwGeos` (Wotherspoon et al., 2016) with a threshold level of 1, which presented as a suitable level above which to differentiate twilights from night time noise in log-transformed data. Following guidelines in Lisovski et al. (2020), we visually reviewed raw light data to identify any areas of the time series affected by shading and manually inspected each twilight event, subsequently deleting such events that we deemed to be falsely annotated in the automated procedure, or those with poor transitions between dark and light. Indistinguishable or unclear transitions between dark and light can occur due to the light sensors becoming shaded by weather, individual bird behaviours or bird plumage. This procedure resulted in an average rate of transition exclusion of 33.6% for Cape Verde Shearwaters, 29.1% for Cory's Shearwaters, 33.9% for Red-billed Tropicbirds, 32% for Scopoli's Shearwaters and 14% for White-necked Petrels. We expected to see a greater proportion of twilights excluded in these data because birds were in their breeding phase. Contrary to non-breeding, migratory seabirds, those in their breeding phase regularly visit nests, or raft on the water before visiting nests which can cause obscured light curves at twilight times.

We used two geolocation analysis packages to estimate the spatial locations of tracked seabirds: `FlightR` and `probGLS`. Using the annotated twilight data, we produced 'TAGS' files using the `TwGeos2TAGS` function in the `FLightR` package in preparation for light-level analyses. We analysed light-level data from 171 deployments in `FLightR` and 185 deployments in `probGLS`, which included 156 of the same datasets used in `FLightR` (15 deployments analysed in `FLightR` were excluded from `probGLS` because they did not collect SST data exclusively when the device was immersed in water). Data from sensors that recorded light and temperature, but did not have light data recorded from a stationary location were included in `probGLS` but excluded from `FLightR` analyses. While on-bird geolocator calibration is possible for some centrally placed species (see Rakhimberdiev et al., 2017), we considered that it may not be suitable for seabirds due to the large distances travelled during foraging. Calibrations were therefore conducted as 'rooftop calibrations' (see Lisovski et al., 2012). All species reported were included in analyses by both geolocation packages.

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2.4 | Estimating spatial locations from light-level data

We parameterised both geolocation algorithms (FlightR and probGLS) to calculate seabird locations within a bounding box extending from the breeding colony by 35° of longitude in each direction, and 25° of latitude in the direction of the nearest pole and 50° of latitude in the direction of the Equator.

The geolocation analysis package, FLightR was used first to estimate the spatial likelihood of locations from annotated light-level data. To model movements, FLightR uses a hidden Markov model with the true location as the unobserved state. Inference is performed using a particle filter, with a template-fit method to allow the algorithm to use all available light measurements around annotated twilight events (Rakhimberdiev et al., 2017). FLightR also incorporates biologically relevant behavioural parameters to improve location estimates. To function, FLightR requires calibration data from each geolocator with which it measures the relationship between observed light levels (i.e. calibration data) and theoretical light levels estimated from current solar elevation angles (Ekstrom, 2004; Rakhimberdiev et al., 2017). When executing the FLightR algorithm, we included only data from geolocators that were calibrated by measuring light levels at a stationary location prior to deployment on a seabird. Analyses in FLightR were run with and without spatial masks to explore how land masking affected accuracy. We set the algorithm to allow maximum daily flight distances of 1,500 km on a 50 km grid. To estimate locations, we ran the FLightR particle filter with 1 million particles and used the median of the posterior probability distribution as the estimates of daily seabird relocations.

For light-level data from geolocators that also recorded SST, we analysed the same annotated twilights with the package, probGLS (Merkel et al., 2016), to investigate whether SST interpolation improved the spatial accuracy of geolocations. The probGLS algorithm estimates locations using an iterative forward step selection process, computing a weighted probability cloud of potential locations (10,000 particles for each point cloud) and producing the most likely movement path with 200 iterations for each track (Merkel et al., 2016). We included flight speed parameters for when the loggers were dry (probable maximum and *SD* (m/s), see supplementary metadata) based on Spear and Ainley (1997) and a maximum allowable dry-logger flight speed of 27.8 m/s, thus matching the speed used to filter GPS relocations; and wet speed parameters to allow for modest drift on the ocean if the bird was roosting on the water for long periods (fastest most likely = 1 m/s, *SD* = 1.3 m/s, maximum = 5 m/s). Geolocations were estimated using probGLS with a land mask to prevent the algorithm from estimating locations more than 1 km inland of coasts. We also used the daily median SST encountered by each bird, which was computed from that recorded by geolocators every 4 hr (Merkel et al., 2016) and matched this to satellite-derived SST (0.25° × 0.25°, NOAA OI SST V2 High-Resolution Dataset). We also ran probGLS both with and without SST matching and spatial masks.

2.5 | Measuring and modelling spatial accuracy

To measure the spatial discrepancy between geolocations and GPS positions, we calculated the distance between the geographic mean of all GPS fixes that occurred within ±30 min, respectively, of a given pair of twilights (i.e. sunset–sunrise or vice versa) and the geolocator-estimated solar noon/midnight position for that same period. This measure of accuracy is expressed as the great-circle distance in kilometres from an individual's GPS location to its corresponding geolocation for a given set of twilight events. To investigate the potentially nonlinear effects of predictor variables on the spatial accuracy of geolocation estimates, we constructed generalised additive mixed-effects models (GAMM) with a gamma distribution and a log link function. We separately modelled geolocation accuracy in position estimates computed by both the FLightR and probGLS analysis packages. We considered two predictors of geolocation accuracy: spatial displacement as the great-circle distance (kilometres) between successive twilight locations (from GPS) for individuals, and the expected inter-twilight period as the expected duration of day or night calculated from day of year and GPS latitude using the daylength function in the package geosphere (Hijmans, 2019). We modelled these as nonlinear effects using univariate thin-plate regression splines. We initially considered two other potential predictors of geolocation error: latitudinal position and closeness in time to the March and September equinoxes; but we could not consider these as independent variables due to strong concurvity with the inter-twilight period predictor, which we considered an equatorial solar profile index and the more proximate mechanism governing geolocation accuracy. We included the model of geolocator as a fixed effect. To account for potential effects of species and individuals, we also included the identity of each tracked individual nested under species type as random effects in the model.

Both geolocation packages contain spatial mask functions to avoid the algorithms estimating positions over land. In our data, this would likely have masked the effects of modelled covariates on spatial error, particularly for birds restricted to the relatively small Mediterranean Sea. Therefore, we modelled the effects of covariates on geolocation accuracy only on the position estimates produced without a land mask (both packages), SST (probGLS) or inbuilt outlier detection (FLightR). We used a correlogram to examine for residual autocorrelation in the time series of geolocations. Some evidence of autocorrelation was evident at the first time lag, but thinning the dataset to include only every second or third observation had no effect on the overall model results. Thus, we did not thin time series of geolocations.

We fitted the models by restricted maximum likelihood using the package mgcv (Wood, 2011). We used the inbuilt checks of the mgcv package to ensure that the models converged and that the basis dimension was sufficiently large (using a permutation test for the presence of a residual pattern along predictors). The residuals of the fitted models were inspected to ensure that residuals followed the gamma distribution assumption and that there was no

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evident structure or heterogeneity of variances against candidate predictors.

3 | RESULTS

Our initial geolocation results were implemented without applying land masks or SST interpolation and produced mean spatial accuracy (±*SD*) of 432 ± 460 and 372 ± 290 km for `FLightR` and `probGLS`, respectively (Table 2). When we applied land masks (for both analysis packages), and SST (`probGLS` only) mean accuracies were improved to 408 ± 473 and 304 ± 413 km, for `FLightR` and `probGLS` respectively (Table 2). As an additional test to investigate the effect of equinoxes on location accuracy, when we excluded from accuracy measurements the locations within 3 weeks (21 days) of the March or September equinoxes the mean spatial accuracies (km ± *SD*) were reduced to 227 ± 250 and 290 ± 369 for `FLightR` and `probGLS` respectively (Table 2).

GPS-derived latitude was within package-specific geolocation uncertainty estimates 38.6% and 84.5% of the time for `FLightR` (parameter set 4, see Table 2) and `probGLS` (parameter set 3, see Table 2), respectively, and GPS-derived longitude fell within uncertainty estimates for 23.7% and 88.8% of geolocations, for `FLightR` and `probGLS` respectively. Estimated uncertainties derived from package functions for each geolocation produced by each method are provided as supplementary material. We also provide as supplementary material the spatial accuracies for individual species within (i.e. ≤21 days) and outside (i.e. ≥21 days) of equinox periods. Results outputs with different parameters from the geolocation analyses are also provided as Supporting Information.

We found strong evidence of a bell-shaped effect of expected inter-twilight period on the spatial accuracy of geolocations (Figure 1a, `FLightR`: $F_{6.47} = 993$, $p < 0.001$; Figure 2a, `probGLS`: $F_{7.1} = 718$, $p < 0.001$). Results demonstrated that spatial accuracy in both `FLightR` and `probGLS` drastically declines as expected inter-twilight periods approach 12 hr (i.e. closer to an equinox or the Equator) and best at approximately 9 and 15 hr (Figures 1a and 2a). Mean spatial accuracy (±*SD*) calculated on geolocation results associated with inter-twilight periods ≤10 and ≥14 hr was reduced to 243 ± 232 and 202 ± 239 km (±*SD*) for `probGLS` (with spatial land mask and SST) and `FLightR` (with spatial land mask and outlier detection) respectively.

We found significant effects of differences among species and individuals on the spatial accuracy of geolocations when individuals were fitted as random effects nested within their respective species type (Figure 1c, `FLightR`: $F_{154.7} = 25.7$, $p < 0.001$; Figure 2c, `probGLS`: $F_{158.2} = 11.8$, $p < 0.001$). The model of geolocator used also affected the accuracy (Figure 1d, `FLightR`: $F_{4.0} = 5$, $p < 0.001$; Figure 2d, `probGLS`: $F_{4.0} = 16.8$, $p < 0.001$). We found that there was an effect of an individual's spatial displacement within expected inter-twilight periods on the accuracy of geolocations when using `FLightR` (Figure 1b, $F_{2.3} = 40.3$, $p < 0.001$), but not for `probGLS` (Figure 2b, $F_{0.5} = 0.35$, $p = 0.111$).

TABLE 2 Spatial accuracy for each geolocation algorithm with specified package parameters. Accuracy is expressed as the great-circle distance between the GPS position and corresponding geolocator-derived position for a given twilight. GPS position was defined as the geographic mean of all GPS positions recorded within ±30 min of the given twilight

Geolocation package	Parameter set	Number of deployments included	Land mask[a]	SST[b]	Outlier detection[c]	Mean absolute latitudinal accuracy ± *SD* (°)	Mean absolute longitudinal accuracy ± *SD* (°)	Mean great-circle accuracy (km ± *SD*)		
								All data	Equinox periods (<21 days)	Non-equinox periods (>21 days)
`FLightR`	1	171	No	N/A	No	2.9 ± 3.7	2.1 ± 3.1	432 ± 460	670 ± 564	286 ± 300
	2	171	Yes	N/A	No	2.9 ± 4.1	2.1 ± 3.2	430 ± 508	707 ± 635	260 ± 305
	3	171	No	N/A	Yes	2.7 ± 3.8	2.2 ± 3.2	416 ± 474	659 ± 576	267 ± 318
	4	171	Yes	N/A	Yes	2.7 ± 3.7	2.3 ± 3.2	408 ± 473	702 ± 587	227 ± 250
`probGLS`	1	185	No	No	N/A	3.0 ± 2.6	1.2 ± 1.3	372 ± 290	484 ± 388	344 ± 253
	2	185	Yes	No	N/A	3.7 ± 3.5	1.3 ± 1.3	449 ± 381	713 ± 465	384 ± 325
	3	185	Yes	Yes	N/A	2.4 ± 3.7	1.1 ± 1.5	304 ± 413	364 ± 554	290 ± 369

[a]Spatial mask restricting estimation of locations >1 km inland;
[b]Sea-surface temperature (not currently available in `FLightR`);
[c]Inbuilt outlier detection is not currently a function in `probGLS`.

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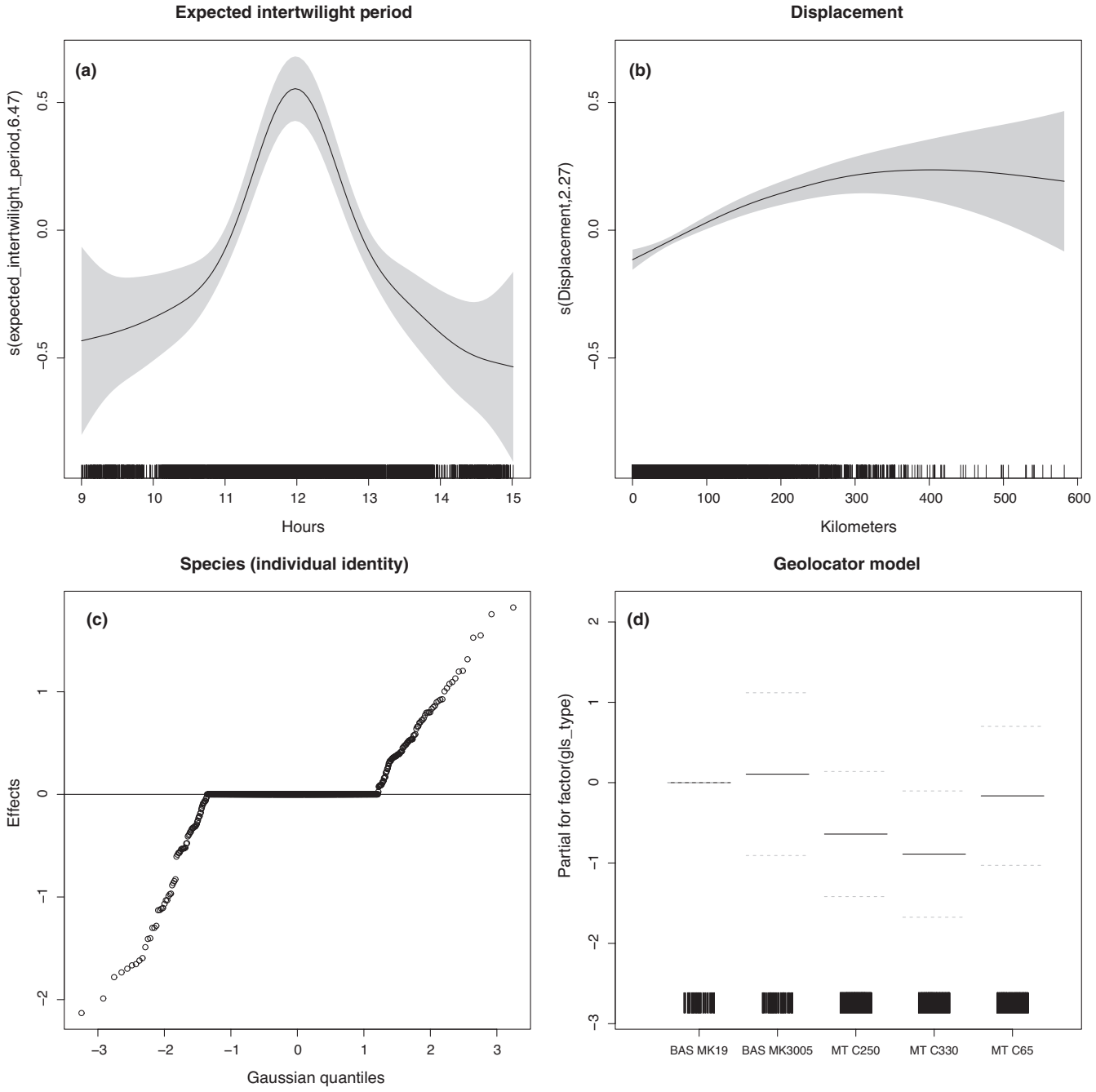


FIGURE 1 Response curves for spatial accuracy in `FLightR` geolocations as a function of expected inter-twilight period (a) and spatial displacement (b) with individual identity nested within species (c) and geolocator model as a fixed effect (d). Tick marks on the horizontal axis of the expected inter-twilight period (a) and displacement (b) plots are observed datapoints. For each predictor with a smooth term (a and b), the effect on spatial accuracy is shown on the *y*-axis and represented as a spline (s) of the predictor variable with the estimated degrees of freedom. Shaded grey areas in the expected inter-twilight period (a) and displacement (b) plots indicate 95% confidence intervals

The average spatial accuracy differed depending on species and geolocation package (Figure 3), with Red-billed Tropicbirds producing the poorest accuracy between GPS and corresponding geolocator positions in the `probGLS` results, whereas White-necked Petrel geolocations had the poorest accuracy in the `FLightR` results. Scopoli's Shearwater geolocations had consistently better spatial accuracy relative to other species (Figure 3) in all model runs of both geolocation packages, including when SST and spatial land masks were not applied.

4 | DISCUSSION

We provide the first large-scale assessment of the spatial accuracy of modern geolocation algorithms under field conditions. The advance in understanding our findings provide contextualises the results and hypotheses of past tests of geolocation accuracy that have until now been limited in field testing (e.g. static tags, small sample sizes, single species studies and outdated methods). Our results

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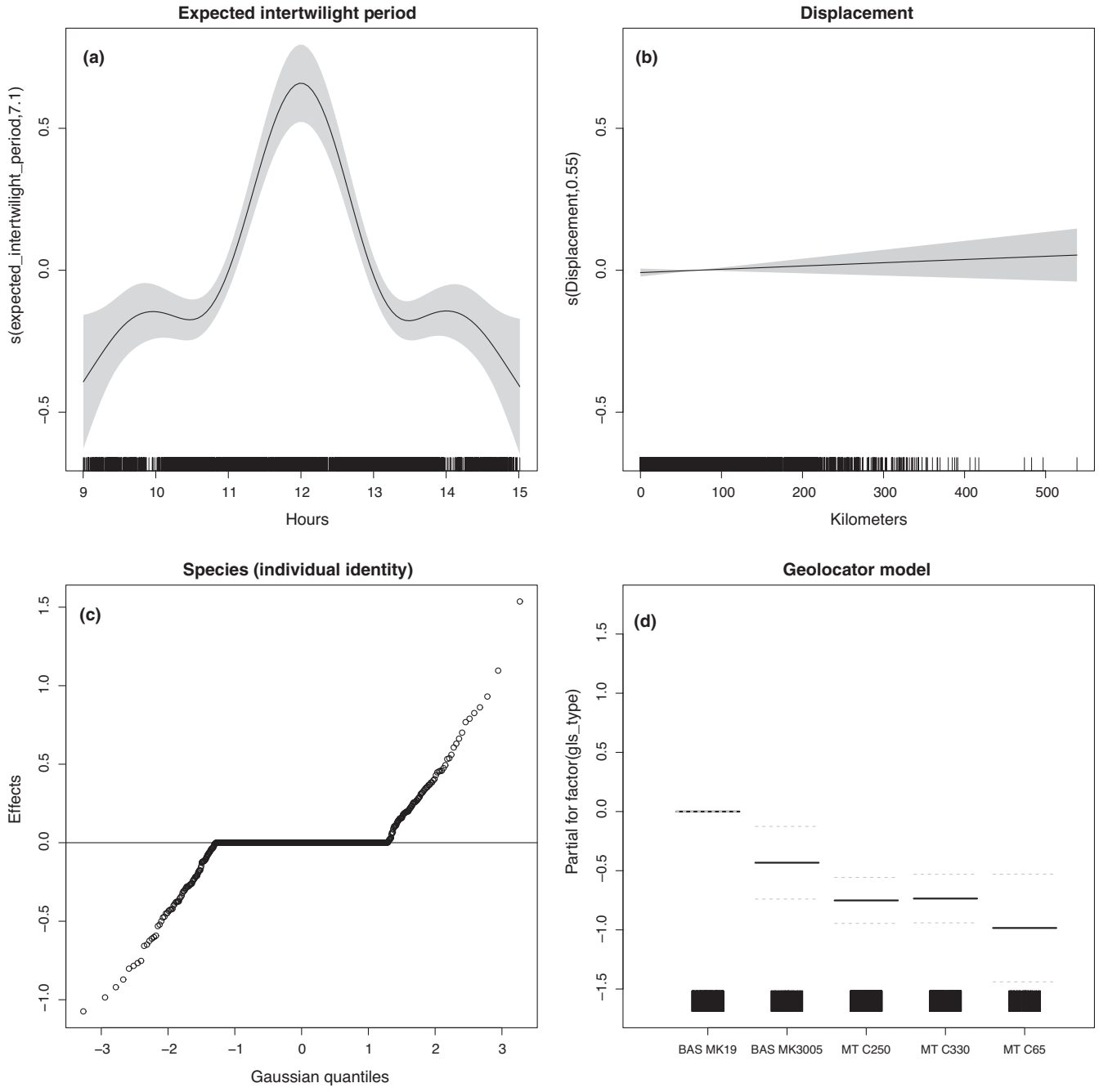


FIGURE 2 Response curves for spatial accuracy in probGLS geolocations as a function of expected inter-twilight period (a) and spatial displacement (b) with individual identity nested within species (c) and geolocator model as a fixed effect (d). Tick marks on the horizontal axis of the expected inter-twilight period (a) and displacement (b) plots are observed datapoints. For each predictor with a smooth term (a and b), the effect on spatial accuracy is shown on the *y*-axis and represented as a spline (s) of the predictor variable with the estimated degrees of freedom. Shaded grey areas in the expected inter-twilight period (a) and displacement (b) plots indicate 95% confidence intervals

emphasise the need for practitioners to account for species and spatiotemporal effects on geolocation accuracy by considering both when (i.e. temporal effects) and where (i.e. equatorial effects) they might expect a species to travel. If the former is either a wandering, circuitous or tropical path, the practitioner should be adequately aware of what scale their data could be analysed. This is particularly true of land birds, which do not have the luxury of using SST to enhance the accuracy of interpolation. We observed lower mean spatial accuracy in light-level geolocation of seabirds than what is typically reported as the expected accuracy in studies that use this tracking method. Moreover, the true location of a seabird was often outside of package-specific uncertainty estimates (as much as 76.3% of the time for `FLightR` and 15.5% of the time for `probGLS`). We also observed that the spatial accuracy in light-level geolocation of seabirds varies among species. As previously suggested by Lisovski et al. (2020) and Shaffer et al. (2005), it is likely that inconsistent

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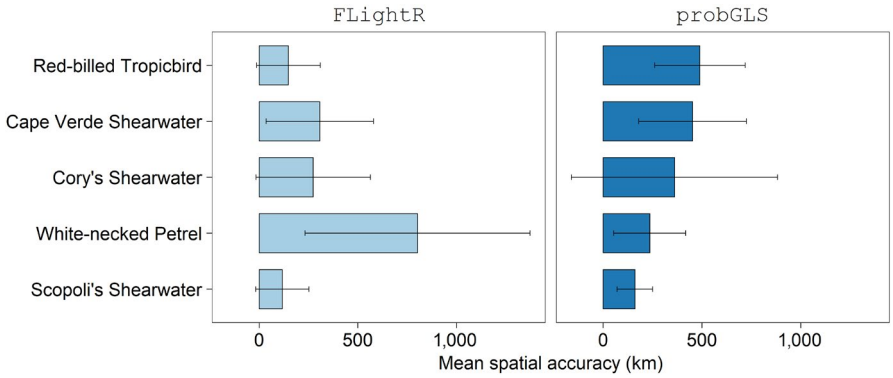


FIGURE 3 Mean spatial accuracy for each double-tagged seabird species as derived from the `FLightR` package (left) with a spatial land mask applied (parameter set 4, see Table 2) and `probGLS` package (right) using SST correction and a spatial land mask (parameter set 3, see Table 2). Accuracy is expressed as the great-circle distance between the GPS position and corresponding geolocator-derived position for a given twilight. GPS position was defined as the geographic mean of all GPS positions recorded within ±30 min of the given twilight. Distances were measured on the WGS 1984 ellipsoid. Error bars represent the standard deviation

accuracy is the result of species-dependent geolocator performance, which relates to the way in which the geolocator light sensors are affected by a combination of species-specific behaviour, morphology, plumage and habitat use. It is possible that smaller geolocator models are more prone to sensor shading than larger models, but we could not reliably test this hypothesis due to the confounding effects of species and individuals.

The method and quality of calibration can influence geolocation accuracy (see Lisovski et al., 2012 for a detailed discussion), so it is important that geolocation practitioners carefully consider calibration when planning their study. In particular, the calibration period should capture the complete variability in twilight transitions and care must be taken to ensure that the calibration method is suitable for the focal species (Lisovski et al., 2012). It is possible that calibration effects contributed to the poor accuracy seen in the `FLightR` results of some of the species we tracked—particularly in the case of White-necked Petrels due to their very long distance, looping trips away from the colony whence the geolocators were calibrated. However, we used standard 'rooftop' calibration methods that are commonly used by seabird biologists. Therefore, we expect our geolocation accuracies to be directly comparable to those obtained by seabird biologists in other geolocation studies.

Our modelling results showed that differences in species and individuals affected how accurate geolocations were. For example, in `probGLS` geolocation, Red-billed Tropicbirds had the poorest mean spatial accuracy. This could be explained by the species' morphology (i.e. extremely short tarsi) and nesting habits, which often include returning to the nest before or during sunset and sunrise, affecting geolocator performance. Conversely, White-necked Petrels had the poorest mean spatial accuracy in `FLightR` geolocation, which our models suggest is explained by their wide-ranging movement habits and large spatial displacement between twilights. The vastly different performance between `FLightR` and `probGLS` for this species supports the assertion that using SST correction is important for geolocation of wide-ranging marine species (Shaffer et al., 2005).

Mean spatial accuracy in Scopoli's Shearwater geolocations was good relative to other species possibly due to the species being restricted to a relatively small marine area (i.e. the Mediterranean Sea) compared to the other open ocean-foraging species that we tracked in this study. Spatial displacement of individuals between sunrises and sunsets affected the accuracy of geolocations produced by both packages, but was strongest in `FLightR`. Scopoli's Shearwaters made short-range movements within a small marine basin, and hence displacement did little to diminish their geolocation accuracy in either package. In the case of `probGLS`, the application of a land mask will have forced the algorithm to produce these geolocations within a small marine area, thus improving the latitudinal accuracy when using a spatial land mask. However, the species still had the highest mean spatial accuracy when a land mask was not applied. The spatial displacement of individuals between sunrises and sunsets appeared to be weakest in its effect on accuracy of geolocations estimated by the `probGLS` package, which suggests that the accuracies we observed for this package are not only applicable to breeding seabirds that exhibit central place foraging behaviour, but also for non-breeding or migratory seabirds. For these reasons, researchers working on coastal-foraging seabirds or seabirds in small marine basins will likely achieve useful results using either the `FLightR` or `probGLS` packages, whereas `probGLS` seems most suitable for researchers working on open ocean-foraging seabirds.

The `FLightR` package sometimes did not produce uncertainty estimates at the start of deployments, or for short-term deployments. This may have occurred because, for a given geolocation, `FLightR` determined low probability of movement between twilights (Rakhimberdiev et al., 2017). It is important to recognise that `FLightR` was designed to track migratory paths, therefore the algorithm may not calculate a probability of movement away from a capture location when tracking duration is short and when the tracked individual is in a state of central place foraging.

Our results suggest that the effect of spatial displacement on `FLightR` geolocations was driven by White-necked Petrels, which

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had the largest mean spatial displacement between twilights (more than double that of all other included species). This effect was likely due to the inbuilt Bayesian priors of the movement model incorporated by the `FLightR` algorithm. For geolocation of marine species, the `FLightR` package may benefit from the inclusion of SST as an optional model prior.

We found that the strongest predictor of accuracy was the duration of day or night between twilight events, with this pattern broadly consistent between expected day or night length (i.e. expected inter-twilight period calculated from GPS latitude) contrasted with the empirical geolocator-observed duration of day or night (i.e. calculated from raw light-level data). Our results empirically demonstrate why those using light-level geolocators should not only expect spatial accuracy to be lower during periods of solar equinox when day and night length is similar across the globe, but also as tracked animals move nearer the Equator where day and night length changes ever more shallowly per degree of latitude (Ekstrom, 2004; Hill, 1994; Lisovski et al., 2012).

Our results imply that practitioners should adopt variable spatial uncertainties by estimating a relative spatial accuracy based on observed inter-twilight period calculated from geolocator data, rather than by excluding data from an arbitrary duration either side of the March and September equinox dates, as is done in many geolocation studies (e.g. Van Bemmelen et al., 2017; Fayet et al., 2016; Jones et al., 2020). This approach not only tackles the issue of reduced spatial accuracy during solar equinoxes, but also of equatorial solar profiles and is a particularly important advance for geolocation of animals that migrate to, or reside on or near the Equator. The spatial accuracy of geolocation differs between species and inference method, but the relationship between geolocator-observed inter-twilight period and relative accuracy is consistent between periods of 9 and 15 hr, and closely follows a Gaussian function. We can therefore provide a rule-of-thumb for estimating the relative spatial accuracy of geolocations depending on the apparent inter-twilight period, which can be computed directly from geolocator data. The equation:

$$\exp\left(-0.5\left(\frac{d-12}{1.2}\right)^2\right)$$

where d is the duration in hours between the first and second twilight, gives the spatial accuracy in an estimate, relative to the accuracy with a duration of 12 hr. For example, when $d = 12$ the relative accuracy is 1, but at $d = 9$ or $d = 15$, the relative accuracy is 0.044, a 95.6% improvement in accuracy relative to when the duration of an inter-twilight period is 12 hr and accuracy is at its worst. When $d > 15$ or $d < 9$, this rule is not generalisable.

Our results present mean spatial accuracies that are within the order of magnitude of the reported average spatial errors (94–1,043 km) in studies of other marine vertebrates (Beck et al., 2002; Delong et al., 1992; Hull, 1999; Teo et al., 2004), but, in some species, are considerably larger than those that have previously measured accuracy in geolocation of pelagic seabirds (186–202 km; Merkel et al., 2016; Phillips et al., 2004; Shaffer et al., 2005). Based on our results, and considering previous studies that improved geolocations with SST (Delong et al., 1992; Gunn et al., 1994; Hill, 1994; Le Boeuf et al., 2000; Shaffer et al., 2005; Teo et al., 2004), we suggest that for pelagic seabirds, using SST as a prior in geolocation models might be essential to achieve better results and to increase spatial accuracy in light-level geolocation. Furthermore, the variation we observed between geolocation packages and geolocator types, and among outputs resulting from differently parametrised geolocation analyses (e.g. use of a land mask, SST interpolation etc.) validate the recommendations of Lisovski et al. (2020) concerning reporting of study parameters. Specifically, practitioners should clearly and unambiguously report assumptions and package-specific model parameters used to compute geolocations along with estimates of uncertainty associated with the data.

Light-level geolocation and geolocators are unquestionably important tools for studying the movement ecology and behaviour of marine organisms, and in many cases are the only available options to track small or sensitive species. Based on our results, we urge greater caution and consideration of the limitations of light-level geolocation when using geolocator data to draw inferences about regional spatial use and behaviour of wide-ranging marine species. Light-level geolocation is not an exact science and different combinations of geolocation packages, parameterisation, study species and data quality can yield different results and uncertainties. The key message in this study is not a criticism of light-level geolocation due to its inherent spatial uncertainty, but a demonstration that this can be reduced if practitioners adopt a dynamic approach to estimating uncertainty using duration of the inter-twilight period. While the spatial accuracy of geolocation may vary between packages, species and the quality of calibration data, the influence of the inter-twilight period on relative accuracy will be valid irrespective of the geolocation package chosen, or the species tracked. In particular, practitioners should make use of dynamic uncertainty estimates based on equatorial solar profiles and be aware that the average accuracy that one can expect will vary by species and might be greater than what is typically reported in seabird geolocation studies. This is especially important in the context of using geolocator-derived tracking data when precise, spatially explicit conservation or management actions are to be implemented.

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work. Pacific tracking data were collected under Monash University Animal Ethics Permit BSCI/2017/42 and Parks Australia wildlife research approvals. Tracking data from the Atlantic and Mediterranean were gathered with valuable help from many students and volunteers to whom we are enormously grateful. These data were collected under the following permits: Cabildo de Lanzarote num. I-15-16-T, Cabildo Gran Canaria num. 1169, Excmo. Cabildo de Lanzarote 2107, Excmo. Cabildo de Lanzarote num. 1948, Excmo. Cabildo de Lanzarote num. 2018/2290, Generalitat Valenciana num. 249-18 SGENP, Gobierno de Canarias num. 2011/0795, Gobierno de Canarias num. 2015/1170 & 2016/9887, Gobierno de Canarias num. 2018/6432, Govern Balear num. ANE-02/2017, Govern Balear num. ANE-05/2016, Govern Balear num. CEP-24/2015, Govern Balear num. CEP-30/2016, Govern Balear num. CEP-31/2014, Parque Nacional num. 160/15, Parque Nacional num. RES-AUT I03/2015, Región de Murcia num. AUF20140056.

CONFLICT OF INTEREST

The authors declare no conflict of interest.

AUTHORS' CONTRIBUTIONS

L.R.H. and J.D.R. conceived the project idea and co-designed the research; L.R.H. acquired funding and scientific permits, collected Pacific data, analysed the data and led the writing of the manuscript; J.D.R. generated positions of geolocator data, performed data analysis and contributed to writing the manuscript; R.M. helped with data analysis and contributed to project development and writing the manuscript; N.C. contributed to project development and ideas, permit acquisition and funding and assisted with Pacific data collection and writing the manuscript; N.G. helped with data analysis and contributed to writing the manuscript; R.R. was responsible for collating the Atlantic and Mediterranean tracking data; R.R. and J.G.-S. acquired funding and scientific permits, collected Atlantic and Mediterranean data, and assisted with writing the manuscript; J.M.R.-G., T.M., Z.Z., M.C.-F., S.S., V.M.-P., and L.Z. collected Atlantic data; F.D.F. and L.N.-H. collected Mediterranean data; R.H.C. contributed to project development, acquisition of scientific permits and funding and assisted with Pacific data collection and writing the manuscript. All authors contributed critically to manuscript drafts and gave final approval for publication.

DATA AVAILABILITY STATEMENT

Data and code used in these analyses are archived on the Dryad Digital Repository https://doi.org/10.5061/dryad.gb5mkkwpf (Halpin et al., 2021).

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SUPPORTING INFORMATION

Additional Supporting Information may be found online in the Supporting Information section.

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METHOD

Methods to detect spatial biases in tracking studies caused by differential representativeness of individuals, populations and time

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Abstract

Aim: Over the last decades, the study of movement through tracking data has grown exceeding the expectations of movement ecologists. This has posed new challenges, specifically when using individual tracking data to infer higher-level distributions (e.g. population and species). Sources of variability such as individual site fidelity (ISF), environmental stochasticity over time, and space-use variability across species ranges must be considered, and their effects identified and corrected, to produce accurate estimates of spatial distribution using tracking data.

Innovation: We developed R functions to detect the effect of these sources of variability in the distribution of animal groups when inferred from individual tracking data. These procedures can be adapted for their use in most tracking datasets and tracking techniques. We demonstrated our procedures with simulated datasets and showed their applicability on a real-world dataset containing 1346 year-round migratory trips from 805 individuals of three closely related seabird species breeding in 34 colonies in the Mediterranean Sea and the Atlantic Ocean, spanning 10 years. We detected an effect of ISF in one of the colonies, but no effect of the environmental stochasticity on the distribution of birds for any of the species. We also identified among-colony variability in nonbreeding space use for one species, with significant effects of population size and longitude.

Main conclusions: This work provides a useful, much-needed tool for researchers using animal tracking data to model species distributions or establish conservation measures. This methodology may be applied in studies using individual tracking data to accurately infer the distribution of a population or species and support the delineation of important areas for conservation based on tracking data. This step, designed to precede any analysis, has become increasingly relevant with the proliferation of studies using large tracking datasets that has accompanied the globalization process in science driving collaborations and tracking data sharing initiatives.

KEYWORDS
animal movement, environmental stochasticity, metapopulation study, site fidelity, species distribution

1 | INTRODUCTION

Although movement is a widespread characteristic in the animal kingdom, the study of movement ecology has been hampered by the scarcity of, and difficulty in obtaining, individual tracking data (Dingle, 1996). Since the 90s, the technological advances in animal tracking have facilitated the acquisition of large amounts of individual movement data with increasing precision (Wilmers et al., 2015). This boosted the development of long-term (Klaassen et al., 2014), metapopulation (Ferreras, 2001) and even ecosystem-wide (Courbin et al., 2018) tracking studies. The miniaturization and increasing precision of tracking devices has overtaken the development of tools to prepare and analyse tracking data (Gupte et al., 2022) and has revealed sources of variability in the estimation of higher-level ecological groups' spatial distributions (e.g. colony, population and species) from individual movement data that are yet to be properly addressed (Gutowsky et al., 2015).

Among the most important sources of variability when using methods to scale up from individual tracks to the space use of higher-level ecological groups, we can find the following: the presence of individual site fidelity (ISF; Spiegel et al., 2017), the variation in space use according to changing environmental conditions at a range of temporal scales (Paiva et al., 2013) and the heterogeneous use of space by distant populations (Frederiksen et al., 2012; Matthiopoulos, 2003).

Firstly, fidelity to a geographic area is a well-documented phenomenon, present in a wide range of animal species (Switzer, 1993), and can be related to breeding or foraging behaviour, and to social

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interactions (Giuggioli & Bartumeus, 2012; Torney et al., 2018). An individual shows fidelity to a site when, based on previous experience, it returns to the same area where it had bred successfully or found a favourable environment for foraging (Schmidt, 2004). Although ISF usually refers to the individuals returning to the same breeding area (Schumm et al., 2021; Shimada et al., 2021), fidelity also occurs independently of the breeding period, to foraging areas or nonbreeding areas (Léandri-Breton et al., 2021; Robillard et al., 2018). Regardless, its effect must be considered when individual tracking data are used to infer the distribution of a population, as it can bias results towards areas preferred by the animals with better data coverage (Giuggioli & Bartumeus, 2012; Lascelles et al., 2012).

Secondly, temporal changes in environmental conditions also play an important role in populations' distributions. Despite being based on individual decisions, an animal's use of space is linked to the optimal use of resources, and therefore, affected by environmental dynamism (Wolf & Trillmich, 2007). For instance, herds of nomadic herbivores move following peaks in productivity of grasslands (Aikens et al., 2017), migratory bird species change their distributions along the year or specific route characteristics and nonbreeding areas of migratory birds are linked to changing environmental conditions (Dias et al., 2011).

Lastly, failing to consider the entire distribution of a species when it spans a heterogeneous environment leads to underestimating its space use. Individuals from different parts of this distribution will be exposed to different environmental conditions and ecological pressures and will thus exhibit a differential use of space (Jeltsch et al., 2013). In fact, it has been shown that the size of the home ranges calculated using tracking data can be correlated with the size of the study area (Nekolny et al., 2017). Thus, maximizing not only the number of animals tracked, but also the geographical area where they are tracked from, seems necessary to obtain precise space-use estimates (Börger et al., 2006). In addition, in species with spatially structured distributions, or in migratory species with nonoverlapping nonbreeding distributions among populations, tracking individuals from only a few breeding populations could lead to an erroneous estimation of their nonbreeding areas (Webster et al., 2002).

Behind all these sources of variability there are specific ecological drivers, mentioned in previous paragraphs which, although of great interest, do not represent the goal of the current study. Here, we focus on presenting a method to detect (1) how individuals having different spatial preferences and uneven sampling intensities can affect the higher-level distribution when pooling all individual data without weighting or correcting; (2) how different sampling efforts across time can bias the results, if spatial preferences of the study species vary along time; (3) how different sampling efforts across space can bias the results, if there is a spatial structure in the space use of the target species. The set of functions we developed here, once applied to the tracking data prior to their use in any analyses answering ecological questions, can help to detect the presence of these three sources of variability. Correcting for the detected sources of variability, and then using the corrected data in the ensuing analyses, will guarantee more accurate distribution maps, protected area delimitations and space-use studies.

Marine top predators are a particularly useful group to study the effect of these sources of variability in tracking data since they show geographically widespread distributions and diverse movement and migratory patterns (Yurkowski et al., 2018). In addition, (1) they are often faithful to foraging and wintering areas (Chapman et al., 2009; Léandri-Breton et al., 2021; Wege et al., 2016); (2) their movements and distributions are affected by the dynamism of the marine environment (Albert et al., 2021; Patterson et al., 2021); and (3) they may display space-partitioning among populations (Wakefield et al., 2013). Lastly, they have, in recent years, been subject to a plethora of tracking studies, and although some start to acknowledge the need to account for these and other biases (Fauchald et al., 2021; O'Toole et al., 2020), a unified framework to detect these three main sources of bias would be beneficial particularly for multiyear and multicolony studies.

Among marine top predators, *Calonectris* shearwaters are medium-sized Procellariforms that engage on year-round, long-distance and often trans-equatorial migrations (González-Solís et al., 2007) and show remarkable philopatry to the natal colony (Thibault, 1994). Three of the four extant species breed on the Mediterranean and Atlantic coasts, and their nonbreeding distributions are composed of discrete pelagic areas over the Atlantic and Indian Oceans (Dias et al., 2011; González-Solís et al., 2007). All these characteristics make them a suitable study group to investigate the effects of the sources of variability listed above.

In this work, we aim to provide a set of tools to understand the effects that (a) ISF, (b) environmental stochasticity over time and (c) the geographic extent of sampling effort, have on the distributions of mobile species tracked using animal-borne devices, regardless of tracking method, or habitat and characteristics of the study species, and to demonstrate their applicability to a real set of tracking data. To do so, we first tested the performance of the method with artificial datasets simulating different degrees of ISF, as well as different sampling regimes and efforts, and then demonstrated its applicability to real data by collating, for the first time, a dataset of 1346 year-round trips from 805 individuals of three *Calonectris* shearwater species breeding in 34 colonies. This constitutes a robust and diverse dataset and provides a relevant example to demonstrate the applicability of the method. Finally, we provide examples of the direct application of these methods by (1) calculating the nonbreeding distribution of each of the species and (2) evaluating the representativeness of each colony on the entire species based on their geographic location and centrality to the species breeding distribution.

2 | METHODS

We describe here the procedures developed to detect instances in which the methodology used to obtain population- or species-level space-use measures from individual tracking data can introduce biases. In particular, we aim to test the effects of ISF and temporal and

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spatial variation in a tracking dataset, applicable to most sets of animal tracking data, as long as it can be split into discrete bouts such as foraging trips, migratory cycles, or even days, weeks or years (bouts, hereafter). We first demonstrate the efficiency of the procedures in simulated datasets and then illustrate the use of these methods using the nonbreeding distributions of *Calonectris* shearwaters tracked with Global Location Sensors (GLS, Wilson et al., 1992). In our worked example, the bouts were clearly defined as a migratory trip. In other types of data and species, bouts might be less evident and need to be carefully decided based on the research question and spatial ecology of the study species.

2.1 | Testing for ISF

To detect the bias caused by individuals with larger sample sizes preferring certain areas, we propose a method that consists of obtaining an estimate of space use for each bout and then comparing the similarities of bouts from the same individual to those of bouts from different individuals. If ISF exists within the sample being evaluated, space use of bouts from the same individual should be, on average, more similar among them than that of bouts of different individuals of the same sample. We estimate the space use of each individual with the autocorrelated kernel density estimate method (AKDE; Fleming & Calabrese, 2017) provided by the package "ctmm" (Fleming & Calabrese, 2021). This method models the movement of the animal, from the relocations obtained with the tracking device, as a continuous-time stochastic process, which separates the discrete observation process (a relocation every few minutes or hours depending on the device) from the continuous-time process which is the movement of the animal (the animal has continued to move between relocations, even if our observation process does not have information on where the animal has been in that time). From these models, an unbiased measure of space use can be estimated that considers the existing autocorrelation in tracking data with high spatiotemporal resolution (Fleming et al., 2015).

We developed a function, *indEffectTest*, in the R programming language, that computes, for every possible pair of bouts regardless of the individual that performs them, the similarity (i.e. spatial overlap) between their utilization distributions (UD). To assess this similarity, we used the Bhattacharyya affinity (BA), which is based on the comparison of two UD (p_1 and p_2, evaluated at locations determined by x and y) to their joint distribution, and ranges from 0 (completely disjunct UD) to 1 (identical UD):

$$\mathrm{BA} = \int_{-\infty}^{+\infty}\int_{-\infty}^{+\infty}\sqrt{p_1(x,y)p_2(x,y)}\,\mathrm{d}x\,\mathrm{d}y$$

In the BA version provided in the overlap function from the "ctmm" package, the calculation of the BA is corrected for small sample bias (Winner et al., 2018) which, in addition to the modelling of autocorrelation in the AKDE, provides a fairly unbiased measure of overlap, and a distribution to draw confidence intervals (CI) from,

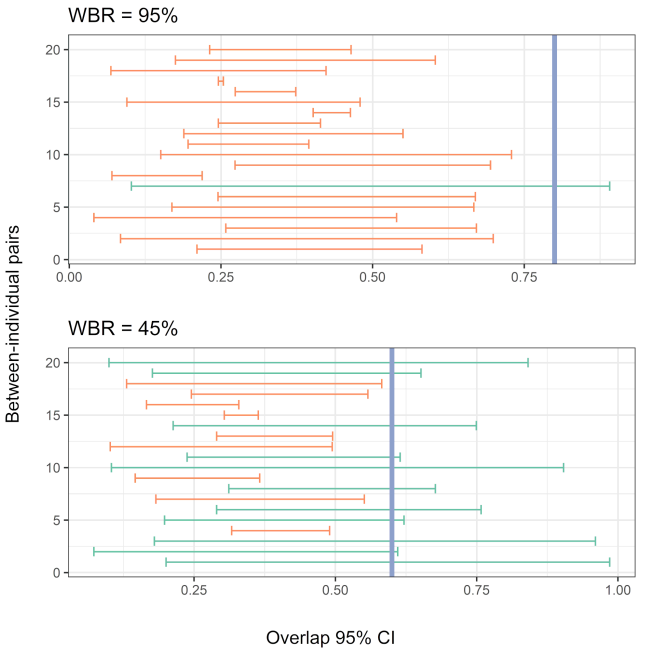


FIGURE 1 Example results of the individual site fidelity (ISF) function. On the top panel, a simulated dataset with high ISF, with a WBR of 95%, and on the bottom panel a simulated dataset without ISF, with a WBR of 45%. The vertical blue line represents de median within-individual overlap, while the horizontal lines represent the 95% CI of each between-individual overlap. The CI represented in orange does not contain the median within-individual overlap, while those represented in green do. High proportion of orange intervals indicates high levels of ISF.

thanks to the propagation of error from the uncertainties generated around the UD estimates. The mean and 95% CI of pairwise overlaps between all bouts are stored in an array of square matrices. The *indEffectTest* function provides the density plots of the within-individual and between-individual median overlaps to visualize differences in their distribution. In addition, it calculates the median of all within-individual median overlaps as a point estimate of within-individual overlap and provides the number of times in which this point estimate falls above each of the between-individual overlap CI (as a proportion of the total number of between-individual pairings). This value (within–between ratio, WBR hereafter) is a population-level measure of how similar the within-individual and between-individual overlaps are in that population's sample. Thus, if a large proportion of the between-individual overlap CI contains the within-individual overlap median, this would indicate that the within-individual and between-individual overlaps are similar, suggesting no effect of the ISF in the spatial distribution at a population level. Conversely, if the median of the within-individual overlaps falls above the majority of the between-individual CI, this would indicate higher overlaps within individuals than between individuals, a clear indication of the presence of ISF (Figure 1).

To demonstrate the function's ability to detect the effect of ISF, we performed practical examples by generating datasets that simulated 10 different degrees of fidelity (one dataset for each scenario).

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To simulate ISF, we generated the bouts over a resistance surface with a "hole" of null resistance inside. We set high resistance outside the "hole" to simulate maximum levels of fidelity and to simulate sequentially decreasing levels of fidelity, we sequentially decreased the value of resistance.

We performed additional tests on simulated datasets to analyse the performance of the function under different sample sizes for each individual, as well as for different sampling rates. The code for simulating the trips and running the different tests can be found at the GitHub repository specified in Appendix S1.

2.2 | Testing for temporal variability

The aim of this test was to explore the existence of changes in distribution over time and not to understand why or how these changes occur. In the example with empirical data, we tested variability among years, but the user may select any other temporal unit. When testing differences in nonbreeding distributions of migratory species, for instance, or differences in foraging distributions of central place foragers such as colonial animals, the temporal unit is obvious: nonbreeding season and foraging trip, respectively. For species with nomadic movement or with less evident temporal units, the selection of this unit is not as straightforward. The user is advised to carefully consider the biological meaning of defining a unit, the aim of the analysis and the hypotheses being tested to select an appropriate time unit to split the data. In general, larger temporal units will allow larger within-group variabilities, and thus less possibility of finding significant differences when compared to between-group variability.

The existence of temporal variability can be detected with an approach that mimics the method used to test the effect of ISF (see Section 2.1): the aim is to check whether variability in space use within a unit of time is the same as between units. The function is the same as above, but instead of the individual, the temporal unit is the grouping variable. Thus, we ignore the individual identity for this and compare overlaps of trips within and between temporal units. The "between-group" values are overlaps of all pairs of trips from the different temporal units (regardless of the individual identity), while the "within-group" values are overlaps of all pairs of trips from the same temporal unit. Thus, a large WBR indicates that the overlap values within temporal units are similar to the overlap values between temporal units, which suggests a lack of effect of the time in the spatial distribution at a population level.

In the case of individuals tracked repeatedly each year, and then for consecutive years, the ISF effect and year effect can be confounded: in case there is an effect of the year (i.e. distributions shift from year to year), testing the effect of ISF using the dataset containing all years of tracking might cause an underestimation of within-individual overlap, thus underestimating in turn the WBR for the individual effect test. In this case, we suggest testing first for the temporal effect and, if the test shows no differences among years, calculating the effect of ISF for the entire dataset. In case a temporal effect is detected, we recommend testing the effect of ISF year by year instead of for all the data pooled together.

2.3 | Testing for spatial variability

We propose a method to test the representativeness of each spatial unit with respect to the entire species (i.e. how well the distribution of a unit represents the distribution of the entire species) in spatially structured populations with large spatial ranges. In our example, since the study species is colonial, we used breeding colonies (from now on *colonies*) as spatial units. However, depending on the species studied, this choice might not be obvious. The user should decide then, based on the spatial ecology and distribution of the study species, and the spatial scope of their research question, if spatial variability is an issue and at which scale it should be tested.

This method works in two steps schematically described in Figure 2a–g. The first step is aimed at obtaining unbiased species distributions and can be accomplished with the *simulateDistribution* function (Appendix S2: Table S1). Empirical tracking data collected at different colonies have biases related to different sampling efforts and population sizes in all sampled colonies (i.e. the larger colonies will not necessarily be the ones with a larger sample). To correct these biases, we first simulate distributions for each colony by pooling all trips of each colony together and calculating colony-level space use (Figure 1a,b). In this instance, we are going to estimate space use using independent and identically distributed (IID) kernel density estimation (KDE) provided by the functions in package "adehabitatHR" (Calenge, 2006), since the AKDE method uses individual movement models that are not applicable to population-level space-use estimates. The user should be aware that, for tracking data with high temporal resolution and for small sample sizes, this method, which does not consider autocorrelation of tracking data, can underestimate space use (Fleming et al., 2015). The effects that the choice of smoothing parameter has on the resulting distribution should also be considered, a parameter that can be controlled by the scale argument in the *simulateDistribution* function (Lascelles et al., 2016). Colony-level space use is represented by the obtained KDE surface, and a number of locations that is proportional to the colony size can be generated with a distribution proportional to the density surface (Figure 2c). Once we have locations simulating each population's distribution, in a number proportional to each population's size, we pool the simulated locations from all populations to generate a simulated distribution that mimics that of the entire species, but unbiased by different sample sizes of each population, and faithful to the real population sizes (Figure 2c,d).

The drawback of this process is that it requires a good knowledge of the population distribution to generate a simulated location dataset against which researchers can compare their real location data. In our worked example, we have used our own data, since the dataset includes a good representation of the entire breeding distribution of the species. If such a comprehensive dataset is not available, users can skip the *simulateDistribution* step, and simply

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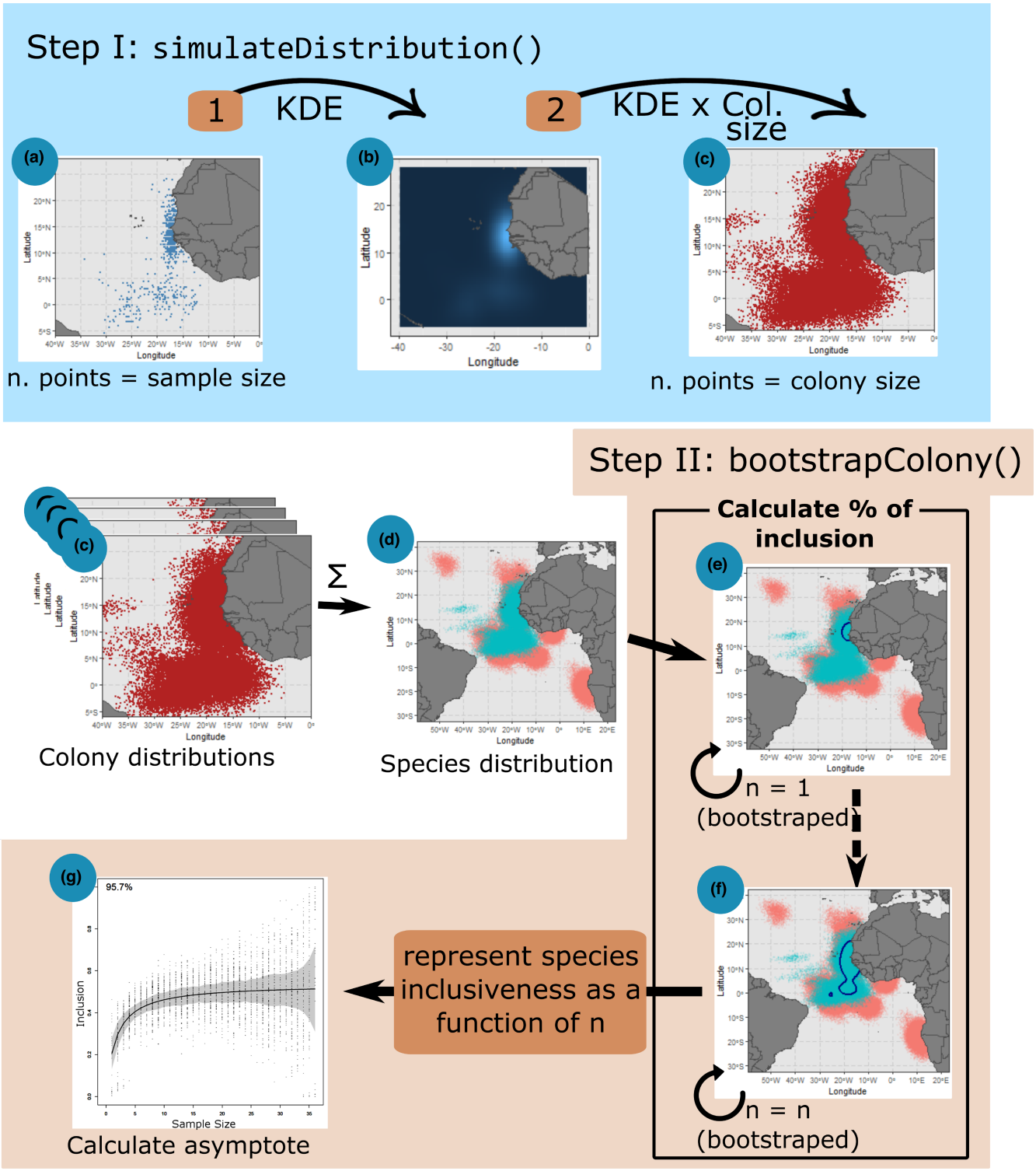


FIGURE 2 Schematic representation of the two-step process developed to test the effect the spatial variability in the use of space.

generate random points within a known distribution of the species (e.g. those provided by the BirdLife database for birds, or the International Union for Conservation of Nature, IUCN, website for species with a red list assessment), thus starting the process at step II in Figure 2. Although this second procedure simplifies the process, it has the drawback that the relative abundances within different regions of the distribution will not be correctly represented, and thus, the representativeness of each subpopulation will not be accurately represented.

Once we have a set of spatial locations representing the distribution of the species, we calculate how well each colony represents it, based on inclusion with the *bootstrapColony* function (Figure 2e,f). For each colony, it iteratively subsamples individual tracks from the full colony sample and calculates a pooled UD

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from which the desired outline polygon (usually a core area, 50% UD) is obtained. The inclusion value is calculated as the number of locations from the simulated species distribution (created on the previous step) included in this subsample core area. This inclusion value is estimated sequentially from $n = 1$ trip until $n =$ total of trips and for a user-defined number of iterations at each step. If the subsample is correctly representing the population distribution, the inclusion value should approximate the quantile for the UD (in this case 50%). As the number of randomly selected trips increases, the inclusion value increases as well, until it stabilizes at a point (an asymptote) when adding more trips to the dataset no longer increases the inclusion value. To calculate the asymptote, a nonlinear least squares model (*nls* function in R) is fitted, with the formula:

$$\text{Inclusion mean} \sim \frac{a \times \text{Sample size}}{1 + b \times \text{Sample size}}$$

where a and b are given start values of 1 and 0.1, respectively, and Inclusion mean is the mean inclusion value at each sample size. Through this model, we calculate the value for the Inclusion mean at which continuing to increase sample size will not increase inclusion further (i.e. the asymptote; Figure 2g). We regard this value as the maximum inclusion value (MIV) possible for that colony. Because MIV is calculated based on 50% UD, they range between 0 and 0.5 (i.e. even if a sample represents the entire species perfectly, its 50% UD will only include around 50% of the simulated locations). However, values higher than the UD percentage (in this case 50%) can occasionally occur, as the UD is calculated based on the locations of the colony, but the inclusion is calculated from the simulated locations of the entire species. In addition, users must exercise caution when comparing the representativity of colonies with vastly different sample sizes, as the biases introduced by the violation of the IID assumption and the bootstrapping of the KDE have a larger effect in small sample sizes. The function then multiplies the MIV obtained by 100, producing the value of "species inclusiveness," defined as the percentage of points of the entire species that falls within the 50% UD of the sampled colony.

2.4 | Empirical application

To demonstrate the use of these functions, we put together a dataset containing year-round trips from Cory's (*Calonectris borealis*), Scopoli's (*C. diomedea*) and Cape Verde (*C. edwardsii*) shearwaters obtained between the summers of 2007 and 2016, from 34 breeding colonies (Table 1). Locations were obtained from GLS (Wilson et al., 1992), which register ambient light and derive longitude from the time of twilight and latitude from the length of the light period, obtaining low spatial accuracy positions with a temporal resolution of one or two positions per day (Halpin et al., 2021). The dataset contains individuals tracked for up to eight consecutive years, which allows us to also test the effect of ISF. Details of GLS deployment for each of the colonies can be found in Appendix S2: Table S2.

2.4.1 | Data preparation

The twilight events were calculated from the raw light measurements (obtained from the GLS) and visually inspected and adjusted when necessary. The locations were obtained using either Intiproc® (Migrate Technology, 2012) or Biotrack® (BiotrackLtd) software, or the "GeoLight" package in R (Lisovski & Hahn, 2012). We discarded position data from 20 days before and after each equinox, as latitudes cannot be correctly inferred from day length during these periods (Ekstrom, 2004), and applied a quadratic speed filter following McConnell et al. (1992) to remove other highly inaccurate locations. Phenological states (migrating, breeding, wintering or staging) were assigned using custom-made R routines and confirmed by visual inspection: the first two consecutive days of directional commuting movement were assigned as the beginning of migration, and the first two consecutive days without a fixed direction were considered as the beginning of a stationary period (either breeding, wintering or staging). Only the nonbreeding stationary periods (i.e. wintering and staging) were selected for the analyses.

2.4.2 | Individual site fidelity

To test the effect of ISF on nonbreeding distributions, we selected, for each species, all the colonies where individuals had been tracked more than once (Appendix S2: Table S3). We ran the *indEffectTest* function for each colony, using individual as the grouping variable, to obtain a WBR value based on debiased estimates of within- and between-individual overlaps. High WBR values are indicative of an effect of the ISF in the studied colony.

2.4.3 | Temporal differences

Since in our dataset each of the trips corresponded to a year, and to avoid confounding interannual differences with ISF, we used a subset of the original data containing only one trip per individual, randomly selected but ensuring a similar sample size for each year (through a stepwise custom-made R function that randomly selected trips per year, without selecting two trips from the same individual, but weighted the selection at every step to ensure all years had the same number of trips, whenever possible). With the resulting dataset (Appendix S2: Table S4), we ran the *indEffectTest* test for each colony, using year as the grouping variable.

2.4.4 | Spatial differences

Before proceeding with the analysis, we calculated the representativeness of our sample at each of the colonies, using the *repAssess* function from the package "track2kba" (Beal et al., 2020; Beal, Oppel, et al., 2021). This function performs a representativity test to estimate how many trips would be necessary to accurately represent

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TABLE 1 Number of trips obtained each year at the 13 colonies of Cory's shearwaters, 19 colonies of Scopoli's shearwaters and two colonies of Cape Verde shearwaters

Species	Breeding population	Breeding colony	2007	2008	2009	2010	2011	2012	2013	2014	2015	2016	Total
Cory's shearwater	East Azores	Vila			15	9	30	8	3		4	3	72
	Central Azores	Faial			8	5	10						23
		Graciosa			8	7	10						25
		Pico					15						15
	West Azores	Corvo			6	2	2						10
	Iberian coast	Berlenga	10					14				13	37
		Sisargas										2	2
	Alboran Sea	Chafarinas			5			4	2		5		16
		Terreros									1	1	2
	Canary and Savage Islands	Selvagem Grande	30	28	40	50	43	28					219
		Montaña Clara						18	12	15	11		56
		Timanfaya										15	15
		Veneguera		27	28	27	44	61	31	18	44	29	309
Scopoli's shearwater	Alboran Sea	Palomas									18	8	26
		Chafarinas			3			4	3		4	2	16
	Balearic Islands	Cala Morell									10	13	23
		Na Foradada										6	6
		Na Pobra										9	9
		Pantaleu				28	26	24	6	9	10		103
	French coast	Porquerolles						7					7
		Riou						27					27
		Frioul						8					8
	Corsica and Sardinia	Giraglia						24					24
		Lavezzi						18					18
	Sicilian Channel	Filfla							5	7			12
		Malta					1			3		9	13
		Gozo					1		1	2			4
		Linosa				22	27	11	7	17	6		90
		Zembra									13	13	26
	Middle Adriatic	Tremiti						7	1				8
	Ionian Sea	Strofades				3	2		2	2			9
	Aegean Sea	Paximada									8	8	16

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TABLE 1 (Continued)

Species	Breeding population	Breeding colony	2007	2008	2009	2010	2011	2012	2013	2014	2015	2016	Total
Cape Verde shearwater	Cabo Verde	Curral Velho	13	8	11	9	10	5	3	2	10		71
		Raso	13	9	5	2							29
		Total	66	72	129	164	221	268	76	75	144	131	1346

Note: The bottom row contains the total number of trips per year and the end column the total number of trips per colony.

the distribution of the entire colony, and how far away the current sample size is from that number. This approach is akin to that of species discovery curves and calculates a value of representativity that ranges between 0 and 100.

After calculating the colonies representativeness, we selected only those with a representativeness >80% (Table 2). From those colonies, we simulated the distribution of each species using the *simulatedDistribution* function, with a multiplication factor of 1 (i.e. one location at sea was generated for every individual in the colony). We obtained a set of simulated locations for each species (Table 2), which was used in the following step. Finally, we ran the *bootstrapColony* function (see Section 2.3 of this section and Appendix S2: Table S1), which calculated, for each colony, a value of species inclusiveness, a measure of how well space use by individuals of that colony represents space use by the entire species.

2.4.5 | Examples of applicability of the developed methods

To further demonstrate the applicability of these methods, we used them in two different types of analyses, which exemplify possible uses. First, we calculated the nonbreeding distribution of each species, and to ensure these distributions were unbiased by different population and sample sizes from each colony, and due to different colony sizes, we used the following procedure: we first selected the colonies with a sample size larger than five individuals and a local representativeness >80%. Then, for each of those colonies, we selected the full dataset (if ISF has not been detected) or one track per individual (if ISF has been detected), and with the resulting dataset we followed the workflow of the package "track2kba" (Beal et al., 2020) to obtain rasterized abundance maps proportional to the colony sizes. We obtained 21 raster layers, seven for Cory's shearwater colonies, 12 for Scopoli's shearwater colonies and two for Cape Verde shearwater colonies. Finally, for each species, we added the colony-level raster layers to produce a more accurate, unbiased representation of the distribution of the species.

Second, we used generalized linear models to model the obtained colony inclusiveness value, that is, how well they represent species nonbreeding distribution in relation to several variables that could be of interest to disentangle ecological from methodological drivers of differences in inclusiveness: geographic location, centrality in the breeding distribution and colony and sample size. We ran these models for Cory's and Scopoli's shearwaters (data from Cape Verde were excluded since we had data from only two colonies). The sampling unit for these models were the sampled colonies, and to use as response variables, we calculated two values: (1) the distance of each colony to the geographic centroid of the species' spatial distribution and (2) the distance of each colony to the centre of the species' spatial distribution accounting for population sizes of each colony. For the distance to the geographic centroid (1), we calculated a KDE of all known breeding locations

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TABLE 2 Sample size, within-between range (WBR) for the individual site fidelity (ISF) (in %) for the colonies with repeated samples, WBR for the year effect (in %) for the colonies sampled more than 1 year, local representativeness (in %), number of simulated locations and species inclusiveness (in %) for each colony.

Species	Population	Colony	Sample size	WBR (ISF)	WBR (year)	Local representativeness	n simulated locations	Species inclusiveness
Cory's shearwater	East Azores	Vila	71	30.1	15.8	92.3	800	52.2
	Central Azores	Faial	22	19.2	13.2	89.2	11,426	37.0
		Graciosa	*12*	*36.0*	*7.3*	*68.6*		
		Pico	*14*	–	–	*71.8*		
	West Azores	*Corvo*	*9*	*20.5*	–	*68.1*		
	Iberian coast	Berlenga	36	–	6.2	95.6	620	44.1
		Sisargas	*2*	–	–			
	Alboran Sea	Chafarinas	10	11.3	8.2	80.6		
		Terreros	*2*	–				
	Canary and Savage Islands	Selvagem Grande	211	31.9	6.9	98.6	59,080	47.8
		Montaña Clara	55	28.1	12.2	95.1	2000	40.4
		Timanfaya	14	–		84.1	700	27.4
		Veneguera	301	29.5	21.5	98.9	4000	35.1
Scopoli's shearwater	Alboran Sea	Palomas	25	17.8	0.0	91.8	134	38.4
		Chafarinas	*5*	*9.7*	*2.5*	*56.1*		
	Balearic Islands	Cala Morell	22	28.2	0.0	91.4	2000	42.0
		Na Foradada	*5*	–	–	*38.5*		
		Na Pobra	*8*	–	–	*61.8*		
		Pantaleu	101	24.0	0.0	97.6	400	47.9
	French coast	*Porquerolles*	*6*	–	–	*55.2*		
		Riou	26	–	–	95.0	560	28.7
		Frioul	7	–	–	82.3	140	39.7
	Corsica and Sardinia	Giraglia	23	–	–	96.6	76	24.8
		Lavezzi	17	–	–	93.7	600	22.6
	Sicilian Channel	*Filfla*	*9*	*53.1*	*0.0*	*74.2*		
		Malta	12	–	0.0	85.0	3100	31.1
		Gozo	*3*	–	–			
		Linosa	89	20.7	0.0	97.5	10,000	47.6
		Zembra	25	19.5	0.0	93.9	227,440	53.4

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TABLE 2 (Continued)

Species	Population	Colony	Sample size	WBR (ISF)	WBR (year)	Local representativeness	n simulated locations	Species inclusiveness
	Middle Adriatic	*Tremiti*	7	*14.8*	-	*74.6*		
	Ionian Sea	Strofades	8	0.0	0.0	89.1	11,000	17.6
	Aegean Sea	Paximada	15	17.8	0.0	96.7	1420	29.9
Cape Verde shearwater	East Cabo Verde	Curral Velho	70	18.3	0.0	99.4	66	49.4
	West Cabo Verde	Raso	28	8.7	0.0	97.9	13,000	50.8

Note: Colonies with a sample size <5 or local representativeness <80.0% (in italics) were considered nonrepresentative, and species inclusiveness was not calculated.

for each species (Appendix S2: Table S5), obtained the centroid of the 95% contour of that kernel and calculated the straight-line distance of each colony to that centroid. To calculate the centre of the species accounting for population sizes (2), we repeated the same process but weighing each colony by their population size and calculating the KDE of those weighed locations. The centroid of that distribution was taken as the species centre of mass (*species centre*, hereafter), and we calculated the straight-line distance of each colony to this species centre. These two distances were included as predictors in the model, as a measure of how centric each colony is within the species breeding range, both geographically and taking into account breeding population distribution. For Scopoli's shearwaters, we modelled the inclusiveness value against colony latitude and longitude (and their interaction), distance to the species centre, geographic centre, sample size and colony size. Since sample size and colony size had a few extreme values, these variables were log-transformed before being entered into the model. For Cory's shearwaters, we could not include all variables in the full model since the number of colonies was smaller than the number of predictors (we are only using the colonies with representativeness >80%), so we ran the full model without the interaction between latitude and longitude, and without the distance to the geographic centre (since it was strongly correlated with the distance to the species centre). For both species, we used Variance Inflated Factor (VIF; Dormann et al., 2013) values of the predictor variables and diagnostic plots to sequentially remove variables in order to obtain the most parsimonious model. To compensate for the small sample size in these models, particularly for Cory's shearwaters, we used a robust method to estimate standard errors, provided by the package "jtools" (Long, 2019), which is more stable to the effects of highly leveraged points than the ordinary least squares (OLS) method provided by the *lm* function (Cribari-Neto et al., 2007).

All analyses were performed in R (R Core Team, 2021) versions from 3.4.4 to 4.0.2. All the developed functions and their arguments are defined and explained in the supplementary material (Appendix S2: Table S1). The code for all the functions and performance tests can be found at https://github.com/VirginiaMorera/Tracking_data_analysis

3 | RESULTS

3.1 | Results of ISF test on the simulated dataset

We ran the ISF test in data simulating a situation where the tracked animals were not colonial (e.g. a residential species where all trips from the same individual had a common origin but trips from different individuals had different origins). Within that paradigm, we tested the function in 10 simulated datasets of decreasing site fidelity (Figure 3). At null resistance (i.e. simulating the absence of ISF), WBR value was 4.8%, increasing up to 85.8% at maximum resistance (Table 3).

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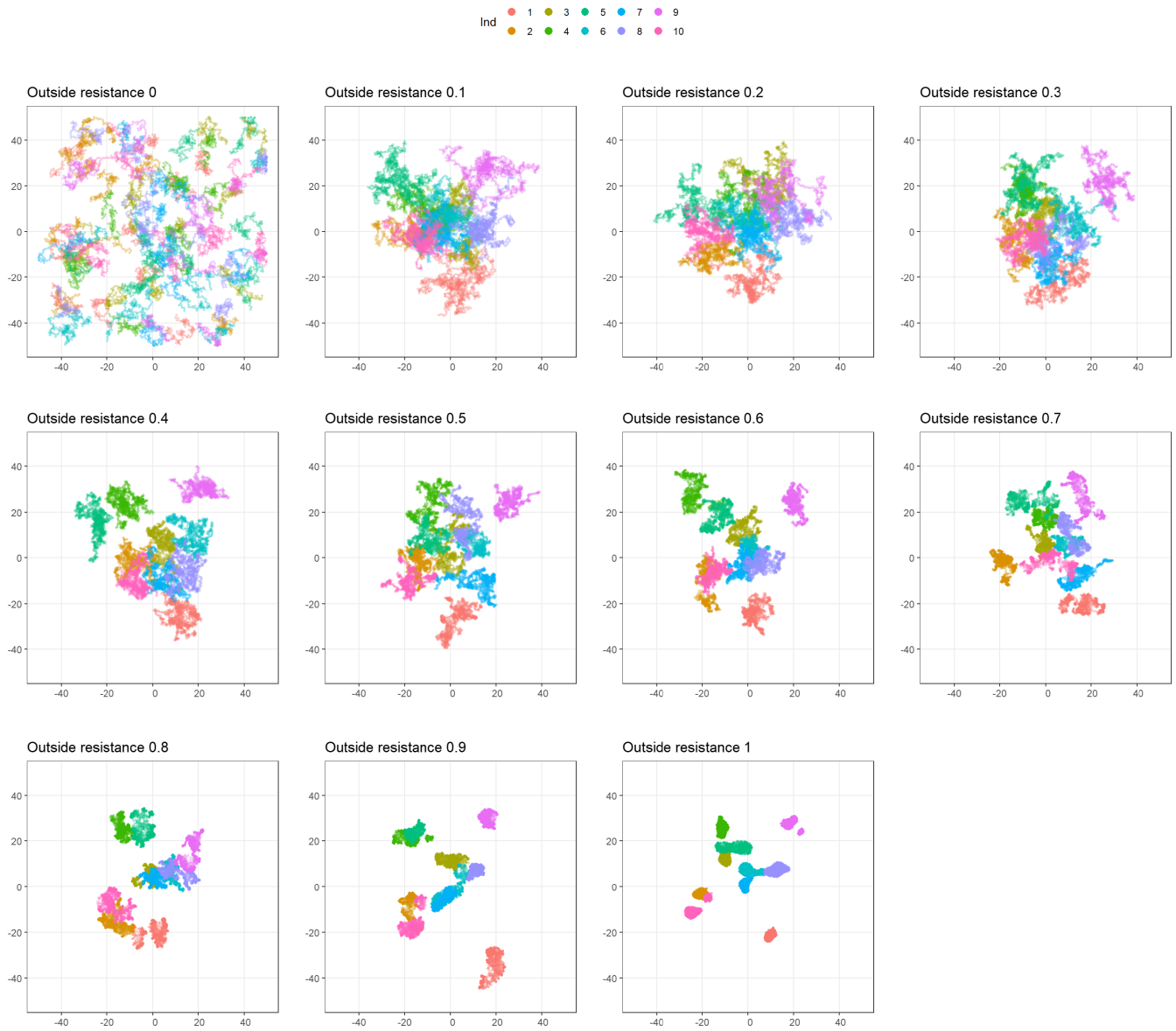


FIGURE 3 Simulated datasets created to test the ISF function. The datasets consist of 10 trips of 100 positions each for each of the 10 animals simulated (in different colours). From left to right and top to bottom, ISF has been increased by increasing the resistance of the surface outside the *allowed* area (see Section 2) from 0 to 1.

3.2 | Results of the empirical application

3.2.1 | ISF effect

Values of WBR (with high values indicative of an effect of ISF) were on average higher for Cory's shearwater than for the other two species, ranging between 11.3% (Chafarinas) and 36.0% (La Graciosa) for Cory's shearwater, between 0.0% (Strofades) and 53.1% (Filfla) for Scopoli's shearwater and between 8.7% (Raso) and 18.3% (Curral Velho) for Cape Verde shearwater (Table 2).

3.2.2 | Interannual differences in distribution

Values of WBR were much lower in testing for interannual differences (evidencing no differences among years) than in the test for ISF and again higher for Cory's shearwaters than for the other two species. Values ranged between 6.2% (Berlenga) and 21.5% (Veneguera) for Cory's shearwaters, and the only nonzero value for the other two species was for the Scopoli's shearwaters of Chafarinas (2.5%).

3.2.3 | Spatial differences in species representativeness

Before the analyses, we excluded three of the 34 sampled colonies, which had less than five trips. From the 31 remaining colonies, we selected one trip per individual for Flifla (Scopoli's shearwater) since a WBR higher than 50% suggested an effect of ISF. With the resulting dataset, we obtained values of local representativeness >80% in 22 of them (Table 2). With these, we proceeded to test their species inclusiveness.

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We simulated nonbreeding distributions from each of those breeding colonies using the *simulateDistribution* function and obtained a dataset that contained more than 78,000 locations for Cory's shearwaters, more than 250,000 for Scopoli's shearwaters and more than 10,000 for Cape Verde shearwaters (Table 2).

Values of species inclusiveness for Cory's shearwater colonies ranged between 27.4% (Timanfaya) and 52.2% (Vila); for Scopoli's shearwater colonies from 17.6% (Strofades) to 53.4% (Zembra); and for Cape Verde shearwaters from 49.4% (Curral Velho) to 50.8% (Raso; Table 2).

TABLE 3 Results of the ISF test on simulated datasets

Within–between ratio (WBR, %)	
Resistance	**Noncolonial**
0.0	4.8
0.1	6.3
0.2	4.3
0.3	8.3
0.4	12.2
0.5	12.9
0.6	23.4
0.7	21.6
0.8	30.7
0.9	54.7
1.0	85.8

Note: For resistances outside the *allowed* polygon from 0 to 1, simulating ISF from low to high (see Section 2), we calculated how many within-individual overlap values fell below, inside and above the 95% CI of the between-individual overlap, for datasets simulating both a noncolonial and a colonial species.

For Cory's shearwaters, after running the full model we found none of the predictors had a significant effect on the species inclusiveness value. We performed stepwise selection on the full model and found that none of the models improved the intercept-only model, with all effects being nonsignificant despite an R^2 of .57 (Table 4). After running the full linear model for the Scopoli's shearwater data, we found high VIF values for distance to geographic centre and distance to population centre. We removed distance to geographic centre and latitude, until we obtained a model with low VIF values indicating no correlation among variables. From the final model, longitude had a negative effect on species inclusiveness and population size had a positive effect on it, while distance to the population centre and sample size had no significant effect (Table 4; Appendix S2: Figure S1).

3.2.4 | Nonbreeding distributions of three species of *Calonectris* shearwaters

After selecting one track per individual for the colony of Filfla, for which we found an effect of ISF, and since tests for temporal variability were not able to detect any effect in our data, we used data from all years together to plot the nonbreeding distribution of each species. We also plotted, for each species, the nonbreeding distribution of each of the main breeding areas, to compare them to the distribution of the entire species. For Cory's shearwaters globally, the main nonbreeding area was off the coast of South Africa, at the confluence between the Agulhas and Benguela currents and the Agulhas current retroflection (Figure 4a; Appendix S2: Figure S2). In single-area distributions, however, we observed that the main nonbreeding area for animals breeding in the Azores was the Agulhas retroflection, with secondary areas in the North and South central Atlantic (Figure 4b); for colonies in the Atlantic Iberian coast, the main nonbreeding area was the confluence between the Agulhas

TABLE 4 Main parameters from the models obtained from the selected linear models testing representativeness for Cory's and Scopoli's shearwaters.

Species	Effect	Estimate	*p* Value	95% CI
Cory's shearwater	**Intercept**	**41.27**	**.006**	**27.63, 54.91**
	Latitude	5.82	.199	−7.41, 19.06
	Distance to population centre	2.67	.643	−18.59, 23.94
	Population size	−2.36	.669	−22.79, 18.08
	Sample size	7.47	.261	−13.20, 28.05
	Adjusted R^2	.57		
Scopoli's shearwater	**Intercept**	**36.02**	**.000**	**31.33, 40.70**
	Longitude	**−7.93**	**.039**	**−15.35, −0.52**
	Distance to population centre	3.43	.259	−3.08, 9.94
	Population size	**7.87**	**.004**	**3.34, 12.40**
	Sample size	4.13	.061	−0.23, 8.50
	Adjusted R^2	.51		

Note: Continuous predictors are mean-centred and scaled by 1 standard deviation. Effects with a *p* value <.05 and/or a CI not overlapping 0 are considered significant and highlighted in bold. A parameter of the goodness of fit (adjusted R^2) is also shown.

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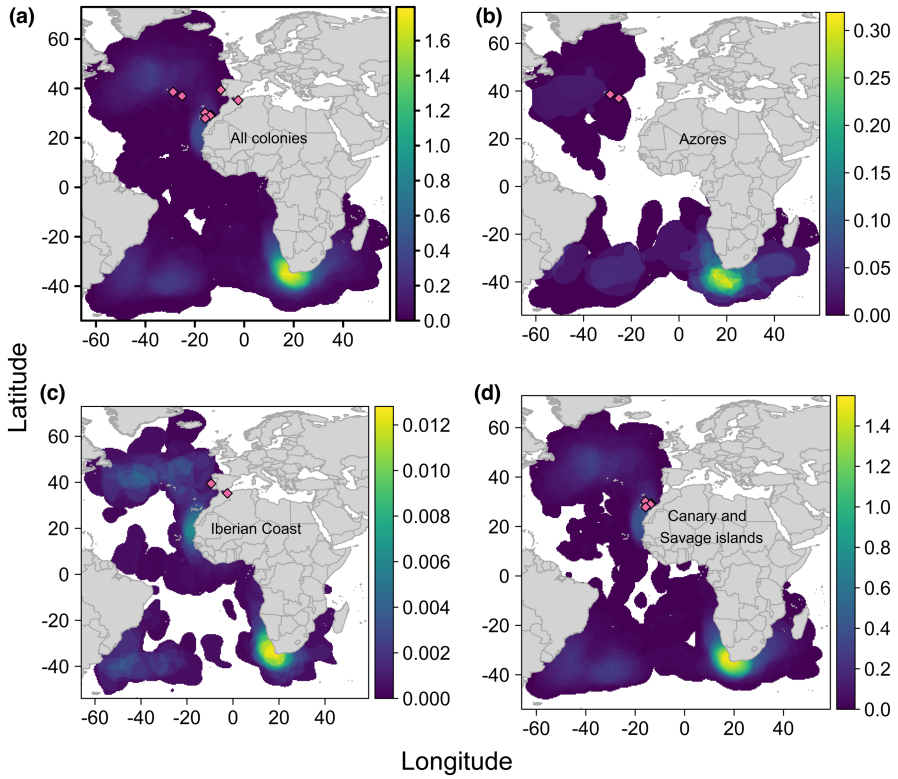


FIGURE 4 Nonbreeding distributions of Cory's shearwaters corrected for sample effort and weighted by population size. Using data from all representative colonies pooled together to represent the species' nonbreeding distribution (a), and using data only from the representative colonies in (b) Azores, (c) the Iberian coast and (d) Canary and Savage islands. Pink diamonds in (a) show the location of all sampled colonies. In (b–d), pink diamonds show representative colonies for each population. Scales show the number of individuals per 0.1 × 0.1° cell.

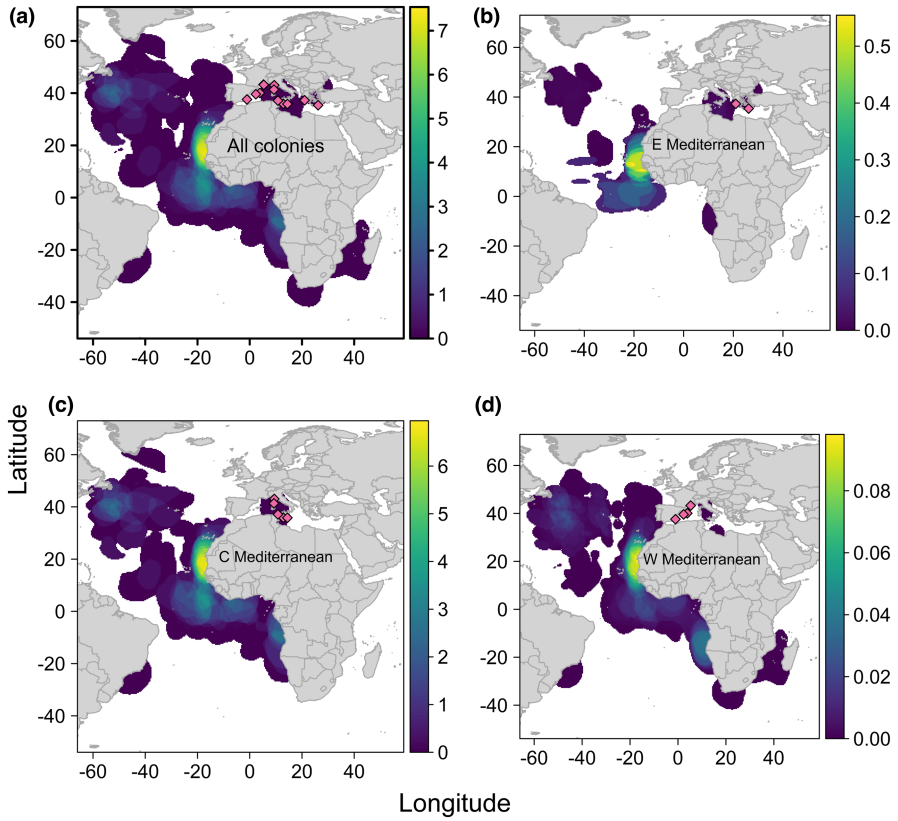


FIGURE 5 Nonbreeding distributions of Scopoli's shearwaters corrected for sample effort and weighted by population size. Using data from all representative colonies pooled together to represent the species' nonbreeding distribution (a), and using data only from the representative colonies in (b) the Eastern Mediterranean, (c) Central Mediterranean and (d) the Western Mediterranean. Pink diamonds in (a) show the location of all sampled colonies. In (b–d), pink diamonds show representative colonies for each population. Scales show the number of individuals per 0.1 × 0.1° cell.

and Benguela currents (Figure 4c); and for animals from the Canary and Savages Islands, the main nonbreeding area was the southern Benguela current, with the Canary current, off the coast of Western Sahara and Senegal, as a secondary area (Figure 4d).

For Scopoli's shearwaters, the main nonbreeding area was the Canary current (Figure 5a), but the distribution of nonbreeding birds changed if we considered only animals from the eastern, central or western colonies, with animals from the westernmost colonies using

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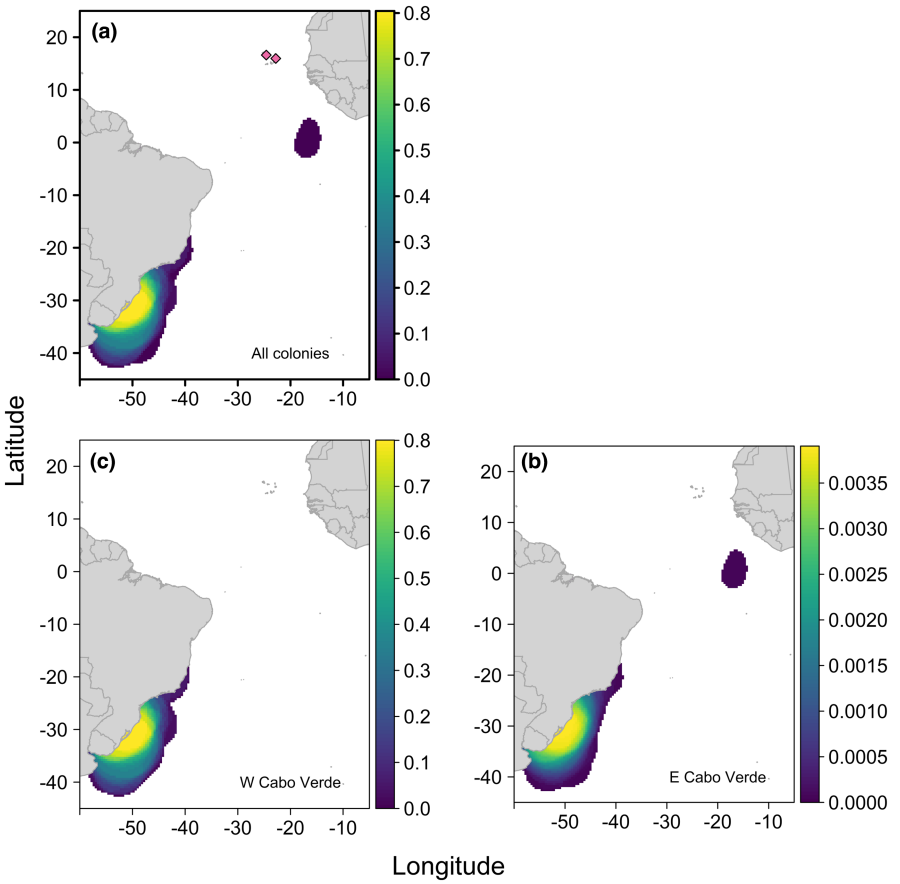


FIGURE 6 Nonbreeding distributions of Cape Verde shearwaters corrected for sample effort and weighted by population size. Using data from all representative colonies pooled together to represent the species' nonbreeding distribution (a), and using data only from the representative colonies in (b) eastern Cabo Verde and (c) western Cabo Verde. Pink diamonds in (a) show the location of all sampled colonies. In (b) and (c), pink diamonds show representative colonies for each population. Scales show the number of individuals per 0.1 × 0.1° cell.

more southern nonbreeding areas, and animals from the eastern Mediterranean colonies spending the nonbreeding period mainly in the Northern hemisphere (Figure 5b–d). The only nonbreeding area of Cape Verde shearwaters was off the southern coast of Brazil and Uruguay (Figure 6).

4 | DISCUSSION

In this study, we provide a workflow to test the effect of three major sources of variability in spatial studies at the species level (ISF, temporal variability and spatial variability), potentially applicable to a wide variety of tracking datasets. In a context of increasingly sophisticated, miniaturized, and inexpensive animal tracking devices, studies using individual tracking data are proliferating, with ever larger extents both spatially and temporally. This emphasizes the need to account for the biases described here when studying space use at a population or species level, that is, before putting all tracks together towards generating a single measure of space use that does not consider potential differences in individual behaviour.

The ISF test is useful for datasets with uneven amounts of data for each individual. It detects instances when trips from the same individual are more similar than trips from different individuals, which causes the areas preferred by the more represented individual to be overrepresented in the distribution at a population level, and it can help designing future tracking studies to avoid this effect. The solution will largely depend on the type of data, size of the dataset, the type of analysis to develop and the aims of each particular study. In general, researchers should aim to (a) subset the data so the sampling effort is evenly distributed among all individuals, for example, sequentially removing one random track from the repeatedly sampled individuals and testing for the effect of ISF again until the effect is no longer detected or (b) apply different weights to each track, with larger weights applied to trips of underrepresented individuals.

The test for interannual differences gives a measure of how spatial distribution varies among years at the population level. We would expect this test to find a significant effect of temporal variability in adaptable species that live in dynamic but predictable environments. On the contrary, species less able to track environmental conditions, or those that live in relatively constant environments, would have the same distributions year after year, resulting in nonsignificant effects of temporal variability on the distributions. Practically, what to do with a dataset that exhibits temporal variability will depend on the type of analysis planned. As an example, if the goal is to model species distributions based on environmental variables (a species distribution model), the effect of year should be considered by either modelling the tracks of each year separately and with the corresponding values for the environmental variables, or using a spatiotemporal model that will account for temporal as well as spatial autocorrelation (e.g. Martínez-Minaya et al., 2018). Conversely, if no temporal variability has been detected, a possible

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course of action could be to average the values of the environmental variables during the whole tracking period, to capture general trends rather than detailed conditions, and use it in a species distribution model with all tracked positions to obtain general large-scale environmental preferences of the species.

The spatial variability test calculates how well a population represents the entire species distribution. In spatially structured populations, we would expect the inclusiveness value to be low for any of the sub-populations tested. Conversely, in unstructured populations, or in migratory species with very low migratory connectivity (i.e. that mix in common nonbreeding areas; Marra et al., 2019), we would expect the inclusiveness to be relatively high and similar for the majority of populations. Researchers aiming to represent the space use or environmental preferences of a species should take care in not using individual populations to represent the whole species when the representativeness is low. Instead, the different population sizes should be considered when combining data from all tracked populations, so the weight of each population in the species distribution is proportional to its size (Beal, Dias, et al., 2021; Beal, Oppel, et al., 2021; Carneiro et al., 2020; Davies et al., 2021).

In our simulated datasets, the *indEffectTest* was able to detect the effect of ISF as intended, as the WBR value increased with increasing simulated ISF. These datasets were simulated as noncolonial but central place forager individuals (i.e. each individual had a different starting position, but all trips from one individual started in the same location). These particular settings are just an example of the conditions under which tracking data may be collected, but users can use the code provided (see Section 2) and modify it to but simulate trips with characteristics similar to their real data (duration, number of positions and step length), in order to know the ability of the function to detect ISF in a dataset of those particular characteristics.

Applied to our GLS dataset of nonbreeding distributions of Cory's, Scopoli's and Cape Verde shearwaters, the proposed method detected an effect of the ISF in the distributions of two out of the 31 colonies tested. It did not detect an effect of temporal variability for any of the colonies, and there was spatial variability in species among the 21 colonies that were representative enough to enter the analysis. For most of the sampled colonies, the WBR value was high. For the colony of Filfla (Scopoli's shearwater), where the function detected a WBR of 53.1% (i.e. the median within-individual overlap is above the majority of between-individual overlap values) indicating an effect of ISF in the population-level space use, the correct course of action to take was to select one single trip per individual. For the rest of the colonies, no effect of the ISF was found, and we did not take any action on them.

The general lack of ISF found in our shearwater dataset agrees with published evidence suggesting a lack of individual consistency in the use of foraging areas during breeding and in several migratory and nonbreeding parameters for both Cory's and Scopoli's shearwaters (Courbin et al., 2018; Dias et al., 2011; Müller et al., 2014; Zango et al., 2019). At a population level, there are studies reporting interannual consistency in nonbreeding distribution and migration phenology of seabirds (Bogdanova et al., 2014; Legrand et al., 2016), and our results agreed with these findings, showing that within-individual overlaps were mainly inside the 95% CI of between-individual overlaps for the three species.

In our example with these three phylogenetically close species that share nonbreeding areas, we found that the Cape Verde shearwater, the species with the most restricted breeding and nonbreeding distributions, had consistently higher inclusiveness values, while Cory's and Scopoli's shearwaters, with widespread breeding distributions, and several discrete nonbreeding areas had more diverse values of inclusiveness, as high as around 50% (maximum inclusiveness) but as low as 17.6% in the case of Strofades (one of the easternmost colonies of Scopoli's shearwaters). As expected, these highly spatially structured populations exhibited low values of species inclusiveness in each of their populations, that is, they poorly represented the distribution of the entire species, which has implications for study design and interpretation of results of single-population studies.

When trying to understand which factors affected the inclusiveness values, we found that for Cory's shearwaters, neither population or sample size, nor any geographical or population structure (represented in the distances to the geographic and population centre of the species) had an effect in such values. Since in six out of the 13 colonies we had sampled the sample size was not enough to achieve an 80% of representativeness, only seven colonies were used for the inclusiveness analysis. This small sample, and the fact that we did not have a good representation of the species to simulate the distribution, might have affected our ability to detect the effects of the geographic structure in the inclusiveness values. For Scopoli's shearwaters, however, we found that inclusiveness was positively affected by sample size and population size. These results indicate that larger colonies would better represent the entire distribution of the species, which particularly in the case of Scopoli's shearwaters seems logical since its largest colony, Zembra, represents about 80% of the entire species population, and, thus, getting a representative sample from that colony means obtaining a representative sample of the majority of the species. The model was not able to predict large differences in inclusiveness with increasing values of sample size. The relationship with longitude, although not significant, might suggest a west-to-east decline in inclusiveness values. Birds breeding in the easternmost colonies of the Mediterranean used the northernmost nonbreeding areas preferentially (Ramos, 2019), which made their use of the southernmost nonbreeding locations less likely. Thus, they were not good in representing the entire nonbreeding distribution of the species, although necessary for the complete knowledge of the wintering grounds of the species. As with the results detailed above, the representativeness of each colony or population can offer insights into their migratory connectivity: in species with low migratory connectivity, all populations will present higher values of representativeness, while in species with high connectivity, each population will have a low level of representativeness.

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The findings obtained from our shearwater dataset are a clear example of the implications of this work for conservation studies. When the aim is to identify areas where the study species is more abundant, it would be more convenient to concentrate sampling efforts in colonies or breeding areas with larger populations. However, when the aim is to define the entire range of a given species, that is, any region in which an individual from the study species can be found, a sampling strategy including spread colonies or areas throughout the range of the species would be more appropriate. In addition, these methods could help decide when the data already collected are representative enough to extract conclusions relevant for conservation, thus avoiding the collection of more superfluous data and making the most of the data already collected. This work will serve as an example of the importance of taking these issues into consideration, as well as providing the tools to do so.

Collaborative datasets, metapopulation studies and their applications to predicting distributions of animals from unsampled areas (Péron et al., 2018; Wakefield et al., 2017) and to informing conservation and management policies (Hays et al., 2019) are becoming common-place in the current scientific context, although they do not always account for the sources of variability explored here (but see Beal, Dias, et al., 2021). The proposed method provides an objective protocol for the detection of three of the main sources of variability (ISF, interannual variability and spatial variability). This is a first step in the building of more accurate spatial and spatiotemporal models of movement and species distribution that can be used by movement ecologists working with a wide diversity of tracking data types.

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CONFLICT OF INTEREST

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

The novel code developed for this manuscript, and to recreate the simulated datasets used to demonstrate the functions, can be found at https://github.com/VirginiaMorera/Tracking_data_analysis. The animal tracking data used to demonstrate the real-life application of the functions developed are archived in the University of Barcelona data repository under DOI https://doi.org/10.34810/data232

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BIOSKETCH

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SUPPORTING INFORMATION

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PRIMARY RESEARCH ARTICLE

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

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Abstract

Marine megafauna, including seabirds, are critically affected by fisheries bycatch. However, bycatch risk may differ on temporal and spatial scales due to the uneven distribution and effort of fleets operating different fishing gear, and to focal species distribution and foraging behavior. Scopoli's shearwater *Calonectris diomedea* is a long-lived seabird that experiences high bycatch rates in longline fisheries and strong population-level impacts due to this type of anthropogenic mortality. Analyzing a long-term dataset on individual monitoring, we compared adult survival (by means of multi-event capture–recapture models) among three close predator-free Mediterranean colonies of the species. Unexpectedly for a long-lived organism, adult survival varied among colonies. We explored potential causes of this differential survival by (1) measuring egg volume as a proxy of food availability and parental condition; (2) building a specific longline bycatch risk map for the species; and (3) assessing the distribution patterns of breeding birds from the three study colonies via GPS tracking. Egg volume was very similar between colonies over time, suggesting that environmental variability related to habitat foraging suitability was not the main cause of differential survival. On the other hand, differences in foraging movements among individuals from the three colonies expose them to differential mortality risk, which likely influenced the observed differences in adult survival. The overlap of information obtained by the generation of specific bycatch risk maps, the quantification of population demographic parameters, and the foraging spatial analysis should inform managers about differential sensitivity to the anthropogenic impact at mesoscale level and guide decisions depending on the spatial configuration of local populations. The approach would apply and should be considered in any species where foraging distribution is colony-specific and mortality risk varies spatially.

KEYWORDS
adult survival, *Calonectris diomedea*, capture–recapture, climatic index, demography, fisheries bycatch, Mediterranean, remote tracking, risk map

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1 | INTRODUCTION

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

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

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

The degree of overlap between bycatch risk and seabird preferences for oceanic habitat influences their vulnerability (Hyrenbach, Fernandez, & Anderson, 2002; Inchausti & Weimerskirch, 2002). For any given species, the greater the overlap of risky longline fisheries and species distribution, at both temporal and spatial scales, the higher the mortality risks. In this regard, some species may show spatial foraging segregation among populations (Grémillet et al., 2004; Louzao et al., 2011; Wakefield et al., 2013), with possible consequences at the level of bycatch probability. Tracking technology presently offers the opportunity to accurately assess this segregation and to obtain information about foraging grounds and range in highly vagile marine species, information that is otherwise difficult, if not impossible, to obtain (BirdLife International, 2004; Wilson et al., 2002). While cross-taxa and cross-gear bycatch assessment is necessary for good global fisheries management schemes, for both a better understanding and the successful management of most species, it is also extremely useful to cross information on specific maps of bycatch risk and species foraging distribution. The generation of spatially explicit risk maps for anthropogenic impacts related to global change is a useful tool for prioritizing conservation actions targeting threatened populations, species, and communities (Bradbury et al., 2014; Brown et al., 2015; Certain, Jørgensen, Christel, Planque, & Bretagnolle, 2015; Jaiswal, Mukherjee, Raju, & Saxena, 2002; Lewison, Soykan, & Franklin, 2009; Venette et al., 2010).

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

Here, we take advantage of the long-term monitoring of three rat- and carnivore-free colonies of Scopoli's shearwater and a 17-year individual mark-recapture dataset to jointly analyze potential spatio-temporal variation in vital rates and assess factors affecting these differences. We also build the first detailed longline bycatch risk map in the western Mediterranean for this species, gathering and analyzing detailed information on longline fisheries (i.e., type of longline, power, temporal and spatial vessel distribution, fishing

effort, number of hooks). Furthermore, this information is useful not only for other seabird species, but also for other megafauna affected by longline bycatch in the study area. We additionally analyzed data on GPS-tracking of 75 breeding adults from the three colonies, to assess both their foraging distribution pattern during the breeding period and the longline bycatch risk depending on the colony. The present study specifically aims to (1) rigorously estimate adult survival and breeding performance at three western Mediterranean colonies of Scopoli's shearwater; (2) build a longline bycatch risk map for this species for the western Mediterranean; (3) assess the foraging range and spatial segregation of the individuals from the three different study colonies; and (4) assess longline bycatch risk of individuals breeding at each colony. In the absence of any anthropogenic impact, we would expect survival to be almost constant in this long-lived species, especially when individuals breed in predatory-free colonies and inhabit the same geographical area. If spatial variation appears, we expect this to be linked to differential bycatch mortality risk among colonies.

2 | MATERIALS AND METHODS

2.1 | Study species

Scopoli's shearwater is a long-lived Procellariiform that breeds at colonies on the Mediterranean islands. It was recently split from the closely related Atlantic form, Cory's shearwater *Calonectris (d.) borealis* (Sangster et al., 2012; but see Genovart, Thibault, et al., 2013). This Mediterranean form carries out long-distance migrations to Sub-tropical and South Atlantic waters, with most individuals arriving in the Mediterranean by early March and breeding from May to October (Cramp & Simmons, 1977; Reyes-González & González-Solís, 2016; Karris, 2014). The species lays one egg and is characterized by biparental care during incubation and chick-feeding (Cramp & Simmons, 1977; del Hoyo, Elliott, & Sargatal, 1992; Sánchez & Castilla, 1997). The species feeds mostly on fish, squid, and crustaceans, but also exploits fishing discards and experiences high mortality in longlines (Báez et al., 2014; García-Barcelona et al., 2010; Genovart et al., 2017; Karris, Ketsilis-Rinis, Kalogeropoulou, Xirouchakis, & Machias, 2015).

2.2 | Bycatch risk map

Longline fishing is an extensive fishing practice in the Spanish Mediterranean, with substantial variability in configuration and practices. Overall, we can define three major types of longline, all of them contributing to seabird bycatch: (1) small-scale demersal; (2) medium-scale demersal; and (3) pelagic (Cortés et al., 2017; García-Barcelona et al., 2010). Vessels conducting pelagic longline are the largest (12–27 m) and tend to operate at larger scales. The two classes of demersal longliners defined here are quite heterogeneous, with vessels ranging from 6 to 18 m, but medium-scale vessels are specifically licensed for demersal longlining and tend to be slightly larger, whereas small-scale vessels are polyvalent and can alternate between different gears.

We built a longline bycatch risk map for Scopoli's shearwater covering the Spanish Mediterranean waters from the coastline off to 2,800 m depth, and from the French border and slightly beyond in the NE (42.8°N) to almost Gibraltar in the SW (36.3°N) (Figure 1). To that aim, we used a grid of 0.1° × 0.1°, a spatial resolution that allows to correctly grouping the information of the vessel monitoring system (VMS) data, but without losing spatial detail. For each grid cell, a bycatch risk index was estimated, taking in consideration fishing effort and the likelihood to capture birds according to the period and the type of bycatch. Each type of bycatch was first considered separately, and then values were averaged taking into account the relative risk of each type of bycatch for the Scopoli's shearwaters (i.e., according to bycatch rates; Cortés et al., 2017; García-Barcelona et al., 2010; Laneri et al., 2010).

Fishing effort was estimated as the relative abundance of vessels on any given cell across time (for each month during the 4 years of study), and also taking into account the maximum number of hooks potentially set by each type of longline vessel (BOE, 2012) (Table 1). To assess vessel distribution, whenever possible we used VMS data, provided by the Spanish Government (Centro de Seguimiento de Pesca, Ministerio de Agricultura y Pesca, Alimentación y Medio Ambiente—MAPAMA) for the period 2008–2012. However, VMS only applies to vessels over 12 m long, so it was mostly appropriate to assess pelagic longliners distribution (as about 60% of the fleet overpasses that length; Bécares & Cama, 2013). However, for the demersal longliners most vessels are small and lack VMS data. In this case, we relied on the fleet statistics also provided by the Spanish Government (Subdirección General de la Flota Pesquera, MAPAMA). This provided the number of vessels per port, and from that we inferred their abundance at sea considering a radius of action of 75 km (and 500 m depth) for the medium-scale demersal longliners and 50 km (and 200 m depth) for the small-scale vessels, based on the available data from studies with observers onboard and questionnaires (Cortés et al., 2017; Laneri et al., 2010; Tarzia et al., 2017). In the case of the small-scale vessels, taking into account information from questionnaires (SEO/BirdLife, 2014), we assumed that about 20% of them used demersal longline at some point, and that one-third of their time was devoted to longline. This assumption is rough and subject to strong variability, but fishing statistics do not provide this type of information and hence available data did not allow making a more refined assessment. In the case of the Balearic Islands, however, the bulk of the small-scale fleet concentrates in the fishing of lobsters (with nets and traps) from April to August, so we disregarded small-scale vessels for that period.

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

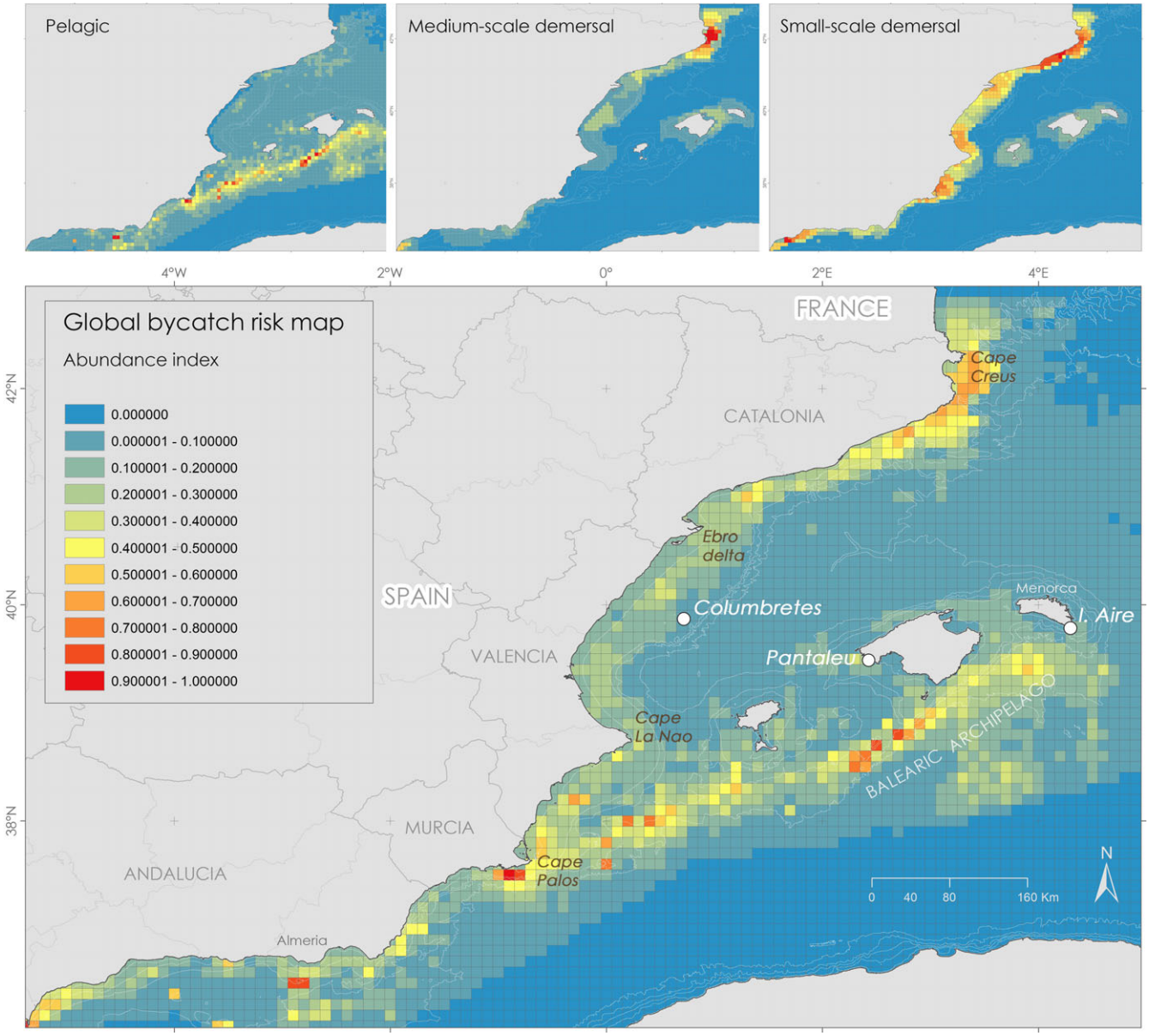


FIGURE 1 Map of longline risk bycatch in western Mediterranean waters for Scopoli's shearwater. In the upper panels, we show the risk for different longline modalities, and in the lower panel we show a global longline risk map for the area and the location of the three study colonies

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

Fishing gear	Number of boats in the study area (2008)[a]	Maximum hooks per boat	% of boats longline fishing	Time dedicated to longline fishing	Weight
Small-scale longline	1,052	2,000	20%	33%	0.20
Bottom longline	59	3,000	100%	100%	0.25
Pelagic longline	79	5,000	100%	100%	0.55

[a]Data given by "Subdirección General de la Flota Pesquera" (MAPAMA).

2.3 | Study colonies and field methods

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

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

2.4 | Remote tracking of Scopoli's shearwaters

To analyze the overlap between longline fishing activity and shearwater distribution at sea, we used GPS tracking data obtained between 2007 and 2012 during the late incubation and chick-rearing periods. Birds were equipped with CatTrack GPS loggers (Perthold, 2011), sealed using a rubber shrink tube to ensure waterproof. Loggers were programmed to collect locations every 5 min, which allowed for a battery life of 10–15 days. The weight of the sealed devices was approximately 20 g, roughly representing 3%–5% of the bird's body mass (Phillips, Xavier, & Croxall, 2003; Wilson et al., 2002). We used data from Mallorca (6 individuals from Pantaleu monitored in 2007), Menorca (4 individuals from Aire monitored in 2007 and 34 individuals from Cala Morell monitored in 2007 and 2010), and Columbretes (31 individuals monitored in 2011 and 2012). Data from the two colonies in Menorca (Cala Morell and Aire) were pooled together to obtain a larger sample size and based on the fact that birds from both colonies forage at the same fishing grounds, as determined by GPS tracking (see Figure S1).

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

2.5 | Egg volume

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

Egg volume (in cm^3) was calculated as follows: $V = 0.00051 \times$ egg length (in cm) $\times$ (egg width [in cm])^2 (Hoyt, 1979; Mougin, 1998). We then estimated the annual mean egg volume for each colony and assessed which factors affected its spatio-temporal variability. We tested for the influence of the North Atlantic Oscillation (NAO) Index, as the NAO affects water column hydrodynamics and may drive the production, distribution and abundance of the organisms upon which birds feed (Gordo, Barriocanal, & Robson, 2011; Stenseth, 2004). To test the NAO effect, we selected the extended annual winter NAO (i.e., December–March) with positive values related to windy and warmer conditions, and negative values to colder air and wetter conditions in the Mediterranean (http://www.cgd.ucar.edu/cas/jhurrell/indices.html) (Hurrell, 1995). To do this, we carried out generalized linear models in R, with egg volume as the response variable, colony and year as explanatory factors, and NAO as a covariate. Additionally, to complementarily assess the amount of variation explained by the NAO index, we also performed an analysis of deviance test (ANODEV) (Skalski, Hoffman, & Smith, 1993). The percentage of variation that was explained by the NAO (r^2) was estimated as:

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

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

2.6 | Analysis of survival

We jointly analyzed adult survival at the three colonies. To assess the fit of our models, we first carried out a goodness-of-fit (GOF) test using U-care (Choquet, Lebreton, Gimenez, Reboulet, & Pradel, 2009). To estimate annual survival probability, we used multi-event capture–recapture modeling and models were fitted in the program E-SURGE (Choquet, Rouan, & Pradel, 2009; Pradel, 2005). These models hold two levels in capture–recapture data: field observations, called "events," encoded in the capture histories, and "states" defined to match the biologic questions and which can only be inferred. Individuals were classified into three groups based on their breeding colony and only adults were included in the analysis. To correct for trap heterogeneity (see Results), we differentiated individuals depending on whether they had been previously observed (Aware) or not (Unaware) (Pradel & Sanz-Aguilar, 2012). Thus, our models included three biologic states: individual alive aware (AA); individual alive unaware (AU); and dead (D). The latter state was non-observable. The initial state in our models was always AA. Transitions between states were modeled in a two-step approach: survival and recapture probability (conditional on survival). On each capture–recapture occasion ("t"), we considered two possible events: individual not seen (noted 0); and individual seen alive (noted 1). Details on the multi-event models can be found in Appendix S1. As we found a strong transient effect (see Results below), we included one different survival for individuals captured for the first time and another for those captured more than once. Based on previous results (Genovart, Sanz-Aguilar, et al., 2013), we tested for a time variant survival, and for an effect of the Southern Oscillation Index (SOI) (http://www.cru.uea.ac.uk/cru/data/soi/soi.dat), in an additive

and interaction manner with colony. As an exploratory model, we also ran a model to estimate mean adult survival, including transients and residents. Given the different capture–recapture efforts made annually in the three colonies, we kept the recapture probability time variant and colony dependent. Model selection relied on QAICc (i.e., the Akaike Information Criterion duly corrected for overdispersion and small sample size) (Burnham & Anderson, 2002).

3 | RESULTS

3.1 | Bycatch risk and foraging patterns

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

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

When assessing the risk of longline bycatch for individuals at the three colonies, we observed that individuals from Pantaleu had a higher probability of longline bycatch due to a greater overlap between areas of high bycatch risk and foraging (Figure 2). Both individuals from Columbretes (post-hoc pairwise permutation test; p-value = .0316), and especially those from Menorca (p-value = .00067), showed a lower risk of longline bycatch than those from Pantaleu Islet in Mallorca. Individuals from Menorca also showed a lower risk of longline bycatch than those from Columbretes (p-value = .0267, Figure 2).

3.2 | Egg volume

We measured 123 and 789, eggs at Aire and Pantaleu, respectively. Egg volume varied annually and in a similar way between Pantaleu

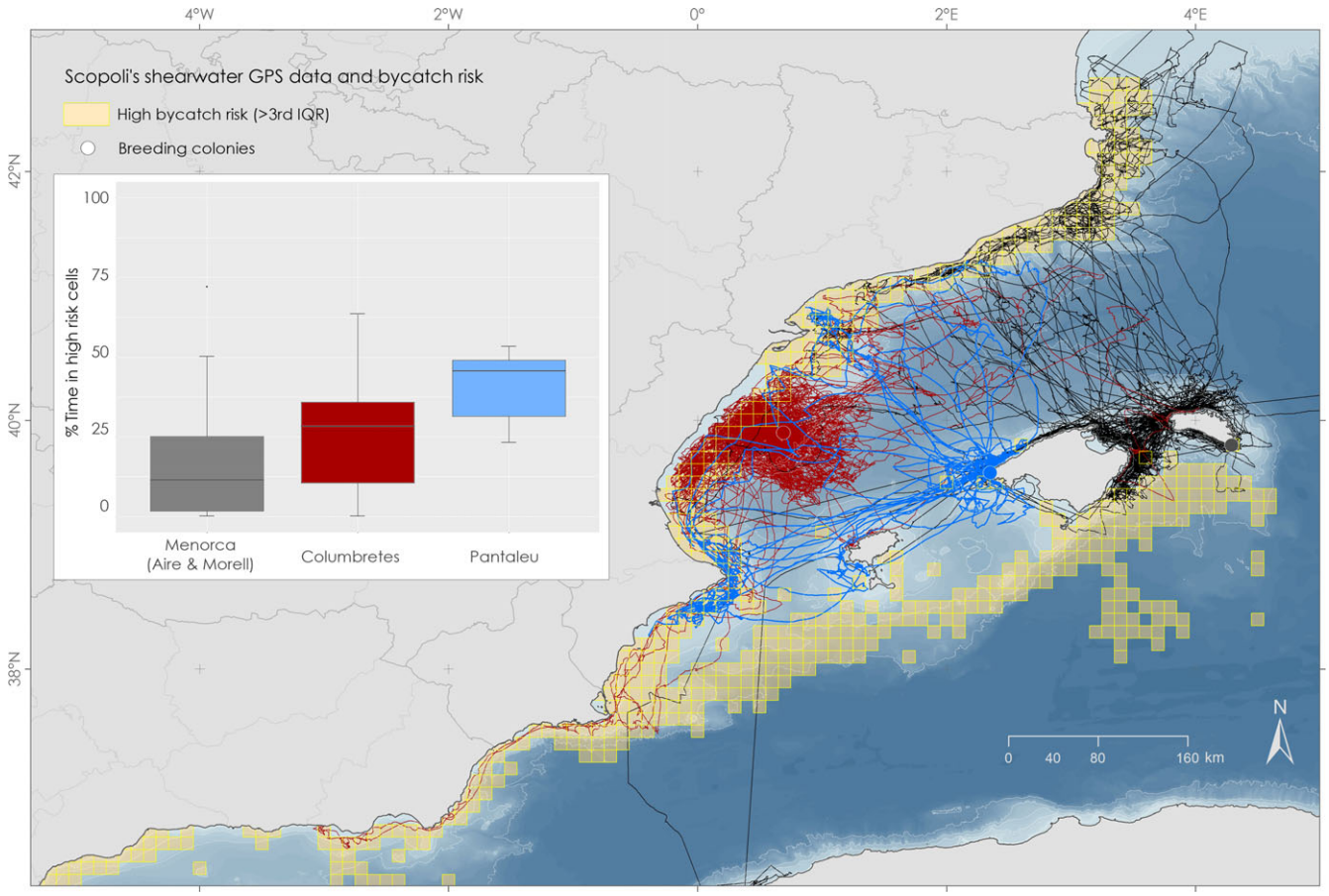


FIGURE 2 Map showing the foraging patterns of individuals from the three colonies obtained from GPS remote sensing and areas of high longline bycatch risk. Trajectories from each colony are shown in different colors: black for individuals from Menorca, red for individuals from Columbretes, and blue for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

TABLE 2 Model selection for assessing factors affecting egg volume variation between colonies of Scopoli's shearwater. Data are from Aire Island and Pantaleu Islet, during 2009–2016

Model	Deviance	np	AICc	ΔAIC	w_i
Constant	2,877.982	2	5,759.963	27.134	0.00
Year	2,858.245	9	5,734.489	1.660	0.18
Colony	2,877.351	3	5,760.702	27.873	0.00
NAO	**2,863.415**	**3**	**5,732.829**	**0**	**0.42**
Colony + Year	2,857.828	10	5,735.656	2.827	0.10
Colony × Year	2,855.897	16	5,743.793	10.964	0.00
NAO + Colony	2,863.216	4	5,734.432	1.603	0.19
NAO × Colony	2,862.855	5	5,735.711	2.882	0.10

np, number of parameters; QAICc, AIC value corrected for overdispersion; ΔAIC, AIC difference points from the best model; w_i, weight of model *i* from all the models tested.
Best model is shown in bold. "×" and "+" show interaction and additive effect between factors, respectively.

and Aire; annual differences were influenced in both colonies by the NAO index (Table 2 and Figure 3), with smaller volumes when higher NAO index values. The ANODEV test performed revealed a relevant effect of the NAO index, explaining a significant 74% of the annual egg volume variation ($F_{1,7} = 19.72$, $p < .005$).

3.3 | Analysis of survival

We analyzed 1,561 individual capture–recapture histories from the three colonies; 231 from Aire, 876 from Pantaleu, and 454 from Columbretes. When analyzing the complete dataset, the GOF for the Cormack–Jolly–Seber model was poor ($\hat{c} = 2.76$) mainly due to both the presence of transients and trap-heterogeneity. All of our models included two ages to correct for transience and a trap effect and we corrected for remaining overdispersion with a lower inflation factor ($\hat{c} = 1.42$).

The most parsimonious model indicated that adult survival differed between colonies and also depended on the annual SOI value (model 1, Table 3). The SOI globally explained about 21% of the variance in annual survival ($F_{1,16} = 4.38$, $p = .05$). Adult survival probability was highest for breeders from Aire and lowest for individuals from Pantaleu, whereas shearwaters from Columbretes showed an intermediate annual survival probability (Table 4). When not correcting for a transient effect and thus assuming equal survival probability for those individuals seen for the first time and those residents (model 9, Table 3), mean adult survival probability (and 95% confidence intervals) for individuals breeding at Aire, Pantaleu, and Columbretes were 0.877 (0.846–0.902), 0.819 (0.802–0.834), and 0.860 (0.826–0.887), respectively, again showing the same pattern of differences among colonies.

4 | DISCUSSION

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

Wakefield et al. (2013) provide strong evidence that seabirds in neighboring colonies avoid direct food competition by segregating in largely mutually exclusive areas. In agreement with this and other previous studies (Corman, Mendel, Voigt, & Garthe, 2016; Grémillet et al., 2004; Wiley et al., 2012), we show such a foraging segregation between relatively close colonies (140–250 km apart) despite the fact that Procellariforms are highly vagile. In our study case, the spatial foraging segregation between colonies differently affected the risk of mortality due to longline bycatch. This was due to the heterogeneous distribution of fishing effort within the study region, related to topographical and oceanographic features, as well as differences in longline modalities and practices across the region, as well as an uneven distribution of the longline fleet across ports. As a result, non-negligible spatial differences in survival may occur even at a small scale, and this should be taken into account when assessing species bycatch risk and its impact on different populations, even at relatively close distances or even when assessing global species status. More research should be done to determine spatial bycatch risk in the wintering areas to assess if there is also differential bycatch mortality during the wintering phase (González-Solís, Croxall, Oro, & Ruiz, 2007; Rayner et al., 2011; Thiebot, Cherel, Trathan, & Bost, 2011).

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

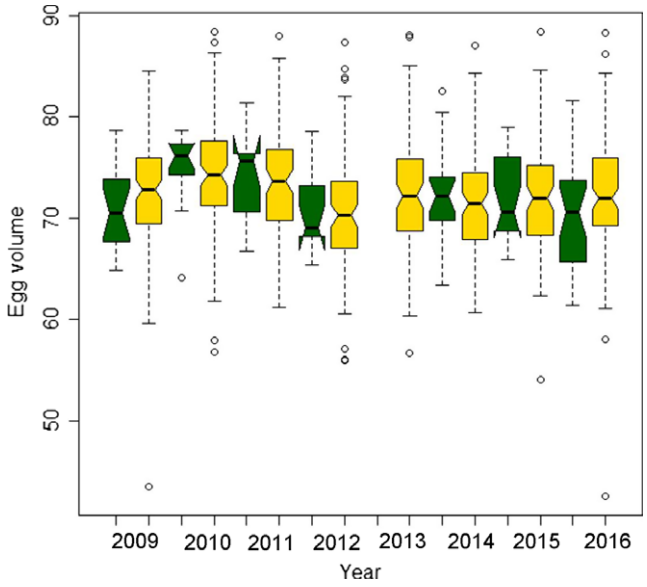


FIGURE 3 Boxplot of the annual mean egg volume (in cm^3, from 2009 to 2016) of Scopoli's shearwater breeding at Aire Island (green boxes) and Pantaleu Islet (yellow boxes). Outliers are also plotted as individual points

We also show that global climatic indices play an important role in the population dynamics of this long-lived seabird species. Apart from the differential mortality between colonies due to anthropogenic effects, we confirm that El Niño-Southern Oscillation is driving adult survival in all the colonies, with lower survival in years with low SOI values. It has been previously suggested that SOI affects adult survival in this species via annual differences in the intensity and frequency of hurricanes in the wintering season (Bricchetti, Foscolo, & Boano, 2000; Genovart, Sanz-Aguilar, et al., 2013). While an indirect effect of the SOI on survival via changes in food availability cannot be ruled out, long-lived organisms mostly maintain a constant adult survival rate despite temporal environmental variability (Lescroël, Dugger, Ballard, & Ainley, 2009); thus, we would only expect a decrease when facing very drastic disturbances and extended to a very large area. On the other hand, egg volume seems to be partially driven by the NAO index, which probably influences food availability prior to and during the egg-laying period (see also Michel, Ollason, Grosbois, & Thompson, 2003).

The demographic buffering process allows populations to persist in the face of environmental change by favoring traits that buffer most sensitive vital rates from temporal environmental variation (Gaillard et al., 2000; Pfister, 1998). Thus, adult survival in long-lived species population dynamics is often high and shows little temporal and spatial variation (Stearns, 1992; i.e. Altwegg et al., 2007 and Baker & Thompson, 2007). However, if global change agents act, as bycatch does in this species, strongly decreasing adult survival, and especially if this effect is prolonged over time, it may compromise population and species persistence (see Genovart et al., 2017). In two of the three colonies, survival is critically low, compromising populations and perhaps species' persistence (see Genovart et al., 2017). Foraging segregation between colonies may desynchronize population growth rates and thus confer some resilience to the species (Heino, Kaitala, Ranta, & Lindström, 1997; Royama, 1992). This may be especially true because Menorca, where bycatch impact was low, actually holds one of the largest Scopoli's shearwater numbers in the western Mediterranean. The spatio-temporal heterogeneity for the intensity of anthropogenic impacts may also alter source-sink

TABLE 3 Model selection (see Methods) for estimating survival in Scopoli's shearwater in three western Mediterranean colonies. All models assumed a time variant and colony-specific recapture probability

Model	Survival	Np	Deviance	QAICc	ΔQAICc	w_i
1	**(T/R) × colony + SOI**	**57**	**9452.72**	**6867.364**	**0**	**0.73**
2	(T/R) + colony + SOI	55	9463.05	6870.65	3.28	0.14
3	(T/R) × colony	56	9461.18	6871.36	3.99	0.10
4	(T/R) × colony. SOI	62	9448.10	6874.33	6.96	0.02
5	(T/R) × colony + t	72	9421.81	6876.13	8.77	0.01
6	(T/R) + SOI	53	9478.59	6877.65	10.29	0.00
7	(T/R) + colony + t	70	9430.26	6878.04	10.68	0.00
8	(T/R) + t	68	9447.18	6883.98	16.62	0.00
9	(T/R) × colony	*56*	*9481.09*	*6885.58*	*18.21*	*0.00*
10	Colony + SOI	54	9490.27	6888.04	20.68	0.00
11	Colony	53	9495.24	6889.55	22.18	0.00
12	Colony + t	69	9454.73	6893.46	26.10	0.00
13	(T/R) × t + colony	84	9413.46	6894.99	27.63	0.00
14	(T/R) × t	82	9429.57	6902.35	34.99	0.00
15	Colony × t	96	9416.00	6921.75	54.39	0.00
16	(T/R) × colony × t	141	9335.45	6958.95	91.59	0.00

T/R: two ages, transients and residents. Best model is shown in bold and the model for estimating annual mean survival at each colony is shown in italics. "+" indicates additivity between factors and "×" interaction.

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

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

[a]First encounter.

dynamics and the rescue effect potentially provided by source populations (Sanz-Aguilar, Igual, Tavecchia, et al., 2016). However, given the survival estimates obtained and the bycatch rates estimated for the species (Belda & Sanchez, 2001; Laneri et al., 2010; Soriano-Redondo et al., 2016), urgent bycatch mitigation actions should be taken to reduce anthropogenic adult mortality. Finally, selection pressure over individuals more prone to bycatch-related mortality may exert evolutionary rescues in impacted populations (Barbraud et al., 2013; Carlson, Cunningham, & Westley, 2014).

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

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SUPPORTING INFORMATION

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

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LETTER

Multispecies tracking reveals a major seabird hotspot in the North Atlantic

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Abstract

The conservation of migratory marine species, including pelagic seabirds, is challenging because their movements span vast distances frequently beyond national jurisdictions. Here, we aim to identify important aggregations of seabirds in the North Atlantic to inform ongoing regional conservation efforts. Using tracking, phenology, and population data, we mapped the abundance and diversity of 21 seabird species. This revealed a major hotspot associated with a discrete area of the subpolar frontal zone, used annually by 2.9–5 million seabirds from ≥56 colonies in the Atlantic: the first time this magnitude of seabird concentrations has been documented in the high seas. The hotspot is temporally stable and amenable to site-based conservation and is under consideration as a marine protected area by the OSPAR Commission. Protection could help mitigate current and future threats facing species in the area. Overall, our approach provides an exemplar data-driven pathway for future conservation efforts on the high seas.

KEYWORDS

area beyond national jurisdiction, Atlantic, biologging, conservation, high seas, marine protected area, regional seas convention

1 | INTRODUCTION

Many seabird species are wide-ranging, traveling thousands of kilometers across jurisdictional and international waters, only returning to land to breed (Harrison et al., 2018). Such migratory species are increasingly exposed to the expanding cumulative human impacts in the oceans (Halpern et al., 2019). Consequently, seabirds are one of the most threatened groups of vertebrates, with almost half of all species (47%) experiencing population declines (Dias et al., 2019).

As higher predators, seabirds play key roles in marine ecosystems making their conservation critical (Grémillet et al., 2018). However, their high mobility makes this challenging, particularly because seabirds rely on multiple, often geographically distant ecosystems, all of which need some form of protection for successful conservation (Dunn et al., 2019). For highly pelagic species, this is further complicated by the lack of an effective governance mechanism for areas beyond national jurisdictions (De Santo et al., 2019), and often incomplete knowledge of their distribution throughout all life-history stages (Carneiro et al., 2020).

Identifying important areas at-sea has been facilitated through advances in biologging technology (Lascelles et al., 2016). Individual-based tracking, using animal-attached devices, is becoming an indispensable tool for guiding conservation efforts through the identification of areas of high species diversity and abundance (hereafter, "hotspots") that are critical for species survival (e.g., molting or foraging areas) (Hays et al., 2019). Recent animal tracking studies have demonstrated that many pelagic seabird species consistently occur at predictable times and places at the macroscale (Frederiksen et al., 2016), often in association with particular habitats or migratory corridors (Dias et al., 2013). This presents an opportunity for area-based conservation for migratory species, particularly because many oceanic hotspots (i.e., areas beyond continental shelves) are often associated with persistent features, such as major frontal and upwelling systems (Block et al., 2011).

The North Atlantic is a priority area for seabird conservation because over the last decade many species in this region have experienced pronounced population declines, including Atlantic Puffin (*Fratercula arctica*), Black-legged Kittiwake (*Rissa tridactyla*), Common Guillemot (*Uria aalge*), and Northern Fulmar (*Fulmarus glacialis*) (Dias et al., 2019). While colonies in the Northeast Atlantic are generally afforded good protection, their foraging areas remain poorly known and protected (Ramirez et al., 2017). Moreover, many seabird species in the North Atlantic, such as shearwaters and auks, are impacted by marine-based threats (e.g., bycatch, pollution, and overfishing; Dias et al., 2019), indicating an urgent need to identify and protect important marine areas to address the recent declines of threatened seabird species.

The Oslo-Paris-Convention on the protection of the North-East Atlantic (OSPAR) is one of two regional seas

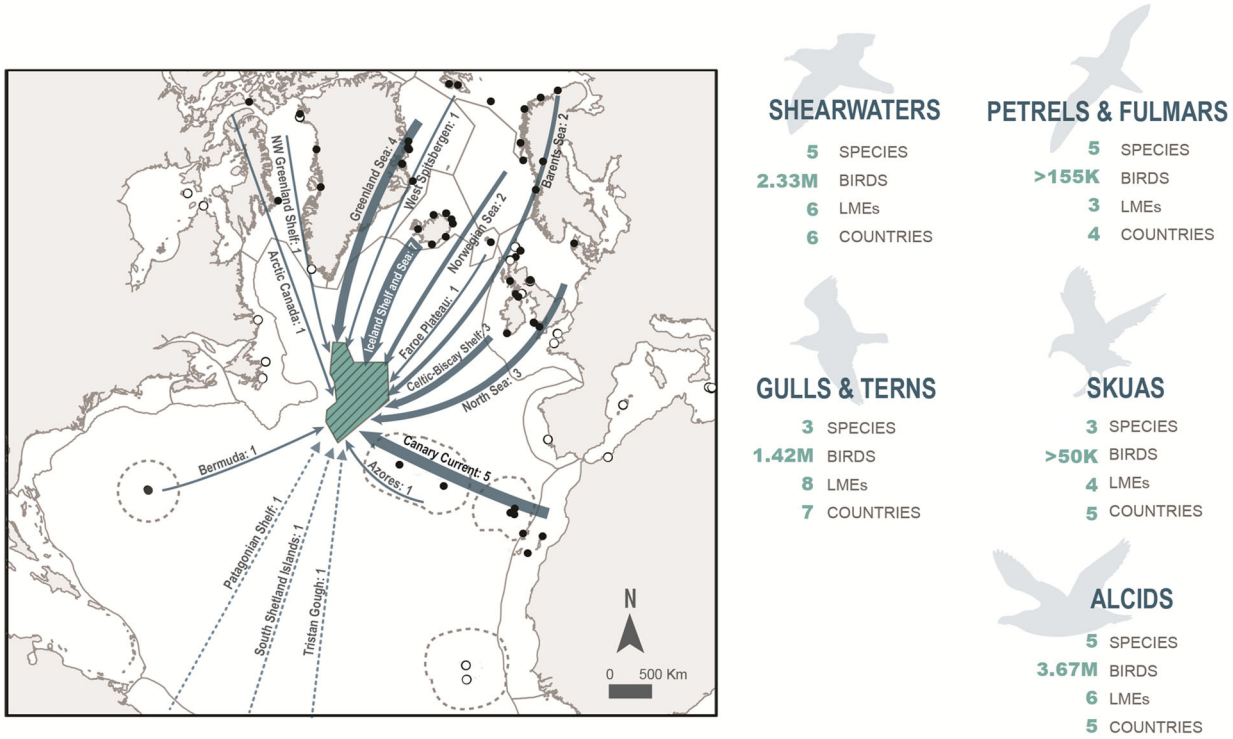


FIGURE 1 Location of identified hotspot in the middle of North Atlantic (green) and summary information of species groups at the site. Arrows indicate the LMEs the birds are traveling from to the site, labeled with LME name and number of species. Dashed arrows are from LMEs in the South Atlantic (not visible on the map). LMEs are shown by a solid gray line, with a dashed gray line for adapted LMEs (Azores, Bermuda, Cabo Verde, Madeira; the latter analyzed with the Canary Current LME). Colonies are shown in circles (black = data used in analysis, white = data considered but not included in final analysis). Figure prepared by Terra Communications

conventions (the other being the Commission for the Conservation of Antarctic Marine Living Resources) that have initiated actions within their remit in Areas Beyond National Jurisdiction (ABNJ), providing a unique opportunity for conservation action in ABNJ. OSPAR have established a number of marine protected areas (MPAs) in ABNJ and are working toward improving the ecological coherence of this network––including addressing an identified gap for seabirds, alongside achieving 10% protection of the OSPAR Maritime Area (Aichi Target 11) (Johnson et al., 2014; OSPAR, 2019). At-sea surveys (Bennison & Jessopp, 2015; Boertmann, 2011) and single species tracking studies (e.g., Dias et al., 2012; Egevang et al., 2010; Fayet et al., 2017) indicate that important seabird concentrations may occur around the Mid-Atlantic Ridge (MAR), and suggesting a community-level assessment of available tracking data is needed, and could help guide current policy and practice.

Here, we combine tracking, phenology, and population data on 21 Atlantic seabird species to quantify their distribution, density, and diversity in the ABNJ of OSPAR Region V. We reveal an important hotspot of unexpected extent and temporal stability. We suggest how our findings could guide conservation management, and provide an exemplar for the use of multispecies tracking to identify sites suitable for protection in ABNJ.

2 | METHODS

2.1 | Study area

Our study area is defined as ABNJ within OSPAR Region V (www.ospar.org/convention/the-north-east-atlantic). This encompasses the deeper waters of the North Atlantic, between 35 and 62°N and from 10 to 42°W west of Iberia/France and west of the 200 m depth contour off the British Isles (Figure 1).

2.2 | Tracking data

We downloaded all available seabird tracking data that overlapped OSPAR Region V from the BirdLife Seabird Tracking Database (www.seabirdtracking.org) in 2016. These data comprised 2188 tracks of 23 species, from 105 colonies within 16 countries and 25 large marine ecosystems (LME), located in both the North and South Atlantic

(Figure S1). We excluded all tracks from colonies that had less than 2% overlap with the study area, unless other colonies in the same LME had higher overlap. The final analyses included 1524 tracked birds of 21 species, from 56 colonies, across 17 LMEs and 16 countries/jurisdictions (Table 1). Phenology and population data for each species and colony were obtained from the literature and verified by experts (Table S1, Figure S2). Following advice from the scientific community, and in line with other studies (e.g., Frederiksen et al., 2016; Frederiksen et al., 2012), colonies of the same species located in the same LME were combined and considered to represent unique populations. Our data were representative of the species distributions in the Atlantic (Table S2).

2.3 | Identification of marine Important Bird and Biodiversity Areas

We analyzed tracking data in combination with objective site selection criteria following the method developed to delineate marine Important Bird and Biodiversity Areas (IBAs) (Lascelles et al., 2016) and Key Biodiversity Areas ("track2kba" R package; Beal et al., 2020). This is a well-established, standardized approach to identify important hotspots for foraging seabirds based on kernel density analysis of tracking data, in combination with abundance estimates of the colonies of origin. The hotspots identified through this method are key sites for the persistence of species by regularly holding important numbers of a globally threatened species, or supporting > 1% of the global or biogeographic population (Lascelles et al., 2016). This method has been applied in all oceans, with many resultant sites informing conservation action (e.g., Hays et al., 2019; Waliczky et al., 2018). We checked tracked birds of nonthreatened species against the IBA criteria: 1% threshold (i.e., LME represents ≥ 1% of the global [for species breeding outside Europe] or biogeographic population [EU number of individuals for European species]). Population sizes refer to the number of mature individuals.

We conducted all analyses in R, as detailed in the Supporting Methods. In brief, we first grouped tracking data by species, LME, and breeding stage (i.e., breeding, nonbreeding, migration, e.g., Black-legged Kittiwake, Iceland Shelf and Sea LME, nonbreeding; Figure S3). We followed the Lascelles et al. (2016) methodology for each group. We estimated the "core use area" of each bird in each group, defined by the 50% utilization distribution contour. We then calculated the proportion of core use areas occurring in each cell in a 0.2×0.2 degree grid (Lascelles et al., 2016). We then estimated the number of birds in each cell by multiplying the proportion of the tracked population in each grid cell by the size of the LME population (Table S1) to generate one *density map/group*.

2.4 | Species richness and abundance hotspot identification

To identify areas that are important for multiple species at the same time of year, we aggregated the density maps in calendar seasons (Supporting Methods), defined as: Q1: January–March, Q2: April–June, Q3: July–September, and Q4: October–December. We weighted each *density map/group* by the average number of half months in each season spent in each breeding stage, based on the species' phenology (Carneiro et al., 2020) to generate one *density map/species-LME-season*.

We combined all *density maps/species-LME-season* to produce: (1) *density maps/species-season*; (2) *density maps for all species combined/season*; and (3) *overall density map* (all species and seasons) (Figure S3). We also estimated species richness by binary coding presence/absence raster density maps and summing across species for each season. Finally, we combined the richness and density maps and used the 15% highest values to delimit the most important hotspot within the study area. We then excluded areas within extended shelf claims to facilitate the uptake of conservation measures (Ramirez et al., 2017), so the final area is located solely within ABNJ.

2.5 | Interannual consistency of area use

To assess the consistency in area use, we conducted additional analysis within groups with relatively large sample sizes (> 20 birds) in multiple years (Supporting Methods, Figure S4). We conducted an analysis of similarity (ANOSIM, a measure of relative within-group dissimilarity based on a bootstrap randomization; Oksanen et al., 2013) to test for differences in the distribution within and between-years using two metrics of distribution overlap (Bhattacharyya's affinity and HR indexes; Fieberg & Kochanny, 2005).

3 | RESULTS

Our analysis revealed an extensive (~595,000 km^2) hotspot of seabird diversity and abundance near the western boundary of OSPAR Region V (Figure 1), extending from ~41 to 53°N and 32 to 42°W. The area is bounded in the north by the Charlie–Gibbs Fracture Zone, to the west by the Flemish Cap and the Grand Banks of Newfoundland,

TABLE 1 Summary of the final seabird tracking data used in the analyses

Species	IUCN status	No. colonies	No. birds	Tracking years (*N*)	Locations of colonies birds tracked from	
					Large marine ecosystem	Country/jurisdiction
Cory's Shearwater, *Calonectris borealis*	LC	6	349	2002–2015 (14)	Azores	Spain, Portugal
					Canary Current	
Manx Shearwater, *Puffinus puffinus*	LC	6	181	1999–2014 (11)	Celtic-Biscay Shelf	United Kingdom, Iceland
					Iceland Shelf and Sea	
Audubon's Shearwater,*Puffinus lherminieri*	LC	2	23	2010–2014 (5)	Canary Current	Portugal
Great Shearwater, *Ardenna gravis*	LC	2	72	2006–2012 (6)	Tristan Gough*	Saint Helena, Ascension and Tristan da Cunha
Sooty Shearwater, *Ardenna grisea*	NT	1	18	2007–2009 (3)	Patagonian Shelf	Falkland Islands (Malvinas)
Northern Fulmar, *Fulmarus glacialis*	LC	1	72	2006–2013 (8)	North Sea	United Kingdom
Desertas Petrel, *Pterodroma deserta*	VU	1	39	2008–2013 (6)	Canary Current*	Portugal
Zino's Petrel, *Pterodroma madeira*	EN	1	12	2007–2010 (4)	Canary Current*	Portugal
Bermuda Petrel, *Pterodroma cahow*	EN	1	11	2009–2010 (2)	Bermuda*	Bermuda
Bulwer's Petrel, *Bulweria bulwerii*	LC	2	48	2009–2013 (5)	Canary Current	Portugal, Spain
Black-legged Kittiwake,*Rissa tridactyla*	VU	16	275	2007–2011 (5)	Barents Sea	Russian Federation, United Kingdom, Faroe Islands, Iceland, Denmark, Norway
					North Sea	
					Celtic-Biscay Shelf	
					Faroe Plateau	
					Iceland Shelf and Sea	
					Norwegian Sea	
					West Spitsbergen	
Sabine's Gull,*Xema sabini*	LC	1	8	2007–2008 (2)	Greenland Sea	Greenland
Arctic Tern, *Sterna paradisaea*	LC	1	9	2007–2008 (2)	Greenland Sea	Greenland
Great Skua, *Catharacta skua*	LC	1	11	2008–2009 (2)	Iceland Shelf and Sea	Iceland
South Polar Skua, *Catharacta maccormicki*	LC	1	32	2007–2010 (4)	South Shetland Islands	Antarctica
Long-tailed Jaeger, *Stercorarius longicaudus*	LC	6	42	2006–2015 (8)	Greenland Sea	Greenland, Norway, Sweden
Norwegian Sea + Barents Sea						

(Continues)

TABLE 1 (Continued)

Species	IUCN status	No. colonies	No. birds	Tracking years (*N*)	Locations of colonies birds tracked from	
					Large marine ecosystem	Country/jurisdiction
Atlantic Puffin, *Fratercula arctica*	VU	8	146	2007–2015 (9)	Celtic-Biscay Shelf	Ireland, Iceland,United Kingdom
					Iceland Shelf and Sea	
					North Sea	
Common Murre,*Uria aalge*	LC	3	20	2013–2014 (2)	Iceland Shelf and Sea	Iceland
Thick-billed Murre, *Uria lomvia*	LC	9	151	2007–2014 (7)	Arctic Canada	Canada, Greenland, Iceland
					NW Greenland Shelf	
					Iceland Shelf and Sea	
Razorbill,*Alca torda*	NT	3	20	2013–2015 (3)	Iceland Shelf and Sea	Iceland
Little Auk,*Alle alle*	LC	1	18	2010–2011 (2)	Greenland Sea	Greenland

Note: Tracking years show the overall year range, with the max number of years held per LME in brackets. * Species endemic to an LME. For further details on population (Table S1) and phenology (Figure S3).

to the east by the MAR and to the south by the Azores (Figure 1).

All 21 species used the identified hotspot, including five globally threatened species (endangered Bermuda Petrel [*Pterodroma cahow*], Zino's Petrel [*Pterodroma madeira*], and vulnerable Desertas Petrel [*Pterodroma deserta*], Black-legged Kittiwake and Atlantic Puffin; Table 1). We estimated that 2.9–5 million birds use the area throughout the year (Table 2) traveling from 56 colonies within 16 countries (Figure 1).

The highest abundance (ca. 4.4–5 million individuals) occurred during the boreal winter (October–March; Q4–Q1, Table 2). The highest number of species ($n = 21$) occurred in spring–summer (April–September), when ca. 2.9–3.3 million birds were present (Q2–Q3, Table 2). Consistency in area use was demonstrated for all nine species with multiyear data, with the ANOSIM index [*R* value] always lower than 0.12 (Supporting Methods, Figure S4).

The most abundant (2.3 million) species using the area was the Little Auk (*Alle alle*) during nonbreeding (January–March), followed by wintering Great Shearwater (*Ardenna gravis;* 1.8 million, July–September; Table 2), a migrant species breeding in Tristan da Cunha archipelago, South Atlantic. We found three species with more than 50% of their global population using the area as a winter or staging ground: South Polar Skua (*Catharacta maccormicki*; 64.8–68.4%, April–September), Long-tailed Jaeger (*Stercorarius longicaudus*; 63.3%, July–September), and Sooty Shearwater (*Ardenna grisea;* 61%, April–June; Figure 2). Almost 50% of the endangered Bermuda Petrel (45.8%) use the area during July–September.

Most seabirds used the area during their nonbreeding stage. This included three species of southern hemisphere breeders that winter in the area (Great Shearwater, Sooty Shearwater, and South Polar Skua), as well as Long-tailed Jaeger and Arctic Tern (*Sterna paradisaea*) that use the area as a staging ground for 1–4 weeks during their outward and return migrations. Seven species used the area throughout the year: Zino's Petrel, Great Skua (*Catharacta skua*; peak July–December), and the following species showing a peak in numbers October–March: Cory's Shearwater (*Calonectris borealis*), Northern Fulmar, Black-legged Kittiwake, Atlantic Puffin, and Thick-billed Murre (*Uria lomvia*). Four species also used the area while breeding (Manx Shearwater [*Puffinus puffinus*], Cory's Shearwater, Desertas Petrel, and Bulwer's Petrel [*Bulweria bulwerii*]).

4 | DISCUSSION

Our analysis revealed a major hotspot for foraging seabirds in the North Atlantic, used by 21 species totaling up to an

TABLE 2 Estimated maximum number of adults from tracked populations using the site per year quarter

Species name	Biogeographic population (max mature birds)	Q1 Jan–Mar (max ind)	Q2 Apr–Jun (max ind)	Q3 Jul–Sept (max ind)	Q4 Oct–Dec (max ind)
Cory's Shearwater	503,430	69,685	20,358	40,085	59,442
Manx Shearwater	982,510		71,827	167	
Audubon's Shearwater	4084		62	743	278
Great Shearwater	8,000,000		1,564,472	1,819,681	
Sooty Shearwater	600,000		368,627	338,562	
Northern Fulmar	756,210	154,024	70,506	86,893	154,024
Desertas Petrel	340		12	53	13
Zino's Petrel	160	15	21	21	15
Bermuda Petrel	142			65	22
Bulwer's Petrel	100,000			1418	
Black-legged Kittiwake	3,822,882	1,347,050	63,650	664,577	1,366,342
Sabine's Gull	3000		375		
Arctic Tern	165,000			65,529	
Great Skua	10,800	1964	1309	2618	2945
South Polar Skua	1542		999	1054	
Long-tailed Jaeger	72,856		34,765	46,131	
Atlantic Puffin	5,121,612	936,713	506,057	257,030	1,079,091
Common Murre	1,392,408		71,406	35,703	
Thick-billed Murre	2,589,888	161,184	50,625	13,619	144,309
Razorbill	626,944		26,123		
Little Auk	7,000,000	2,333,333	129,630		1,555,556
Total number of birds		5,003,968	2,980,824	3,373,949	4,362,037
Total number of species		8	18	18	11

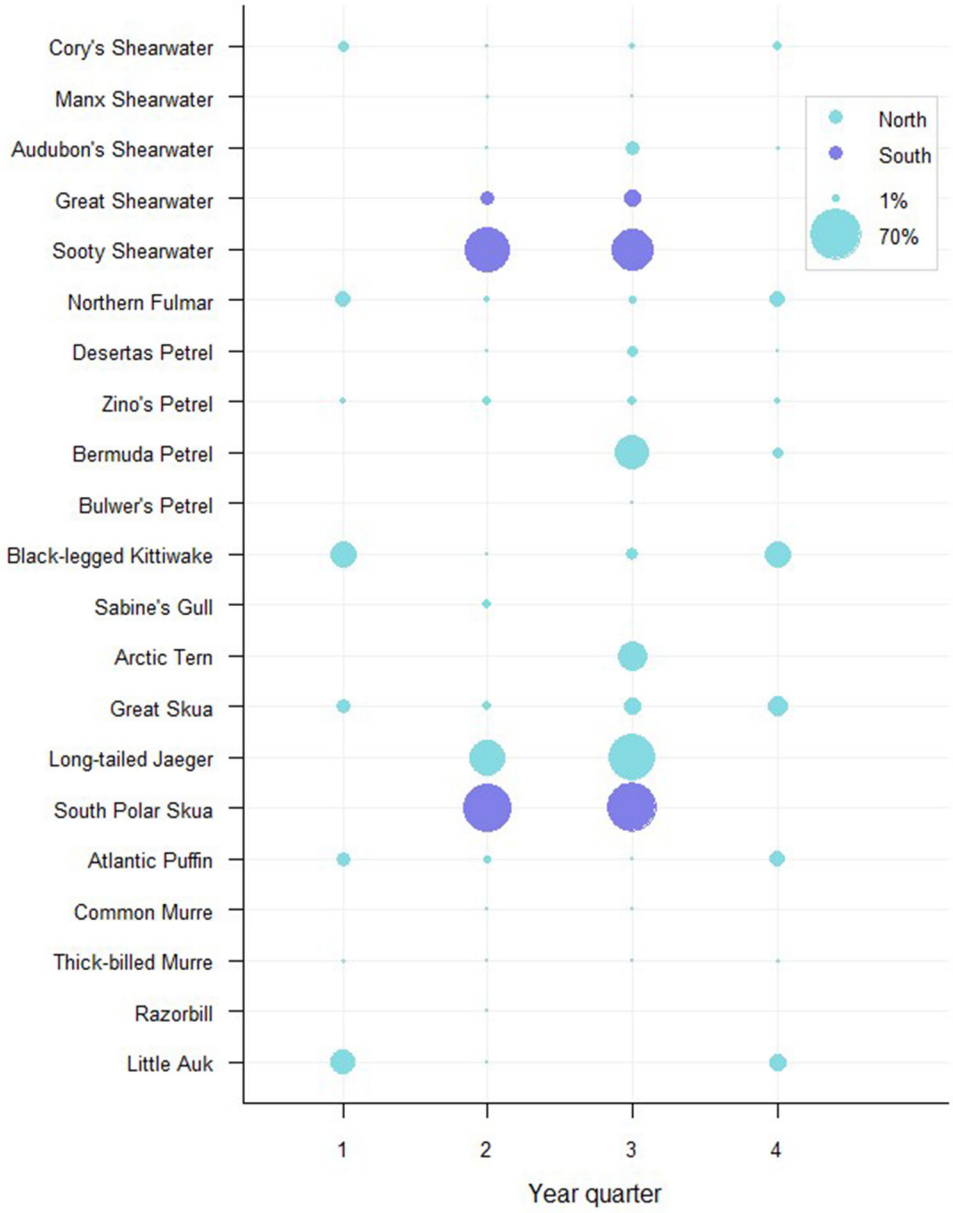


FIGURE 2 Percentage of biogeographic population of each species estimated to be using the hotspot for each year quarter. Colors indicate if the species breeds in the northern or southern hemisphere

estimated 5 million adults. At-sea surveys previously indicated that relative abundance peaked in this area, but this is the first time that a seabird aggregation of this absolute abundance has been robustly quantified anywhere in the high seas. The hotspot qualifies as an IBA and can be considered the most important oceanic foraging grounds for the community of seabirds in the OSPAR maritime high seas area and one of the most important concentrations of migratory seabirds in the Atlantic. Seabirds using this hotspot originated from a minimum of 56 colonies in 16 different countries. Many of these species traveled great distances to use the area, with some using it year-round, suggesting that food availability in the area is consistently high. Boreal breeders, such as Arctic Terns, Long-tailed Jaegers, Sabine's Gulls, Manx Shearwaters, and Cory's Shearwaters, use the area as a staging area to fuel trans-equatorial migrations (Egevang et al., 2010; Guilford et al., 2009; Sittler et al., 2011), or to fuel the last migration leg to the breeding areas (Egevang et al., 2010; van Bemmelen et al., 2017) sometimes making detours of > 5000 km to do so (Dias et al., 2013). Southern Hemisphere breeders, such as South Polar Skuas, Sooty Shearwaters, and Great Shearwaters, migrate up to 13,000 km to spend some of the austral winter in the area (Hedd et al., 2012; Kopp et al., 2011).

Our analysis included tracking data from major colonies of each species in the Atlantic, including those that

represent more than 90% of the global or Atlantic population for many species (e.g., Cory's Shearwater, Sooty Shearwater, Great Shearwater; all gadfly petrels, genus *Pterodroma*). We only used tracks of adults, because relatively few juvenile and immature birds have so far been tracked, which can have an influence on the overall distribution of seabirds (Carneiro et al., 2020). Indeed, a recent study also found the area to be used by immature Cory's Shearwaters (Campioni et al., 2020). Thus, our estimates should be considered a minimum. Population estimates for each colony are subject to natural variation and recording error, and the number of birds using the area should ideally be updated regularly.

4.1 | Biodiversity hotspot

Recent studies have found additional seabird species use the area, including Leach's Storm-Petrel (*Oceanodroma leucorhoa*) (Pollet et al., 2019), Wilson's Storm-Petrel (*Oceanites oceanicus*), Great Black-backed Gull (*Larus marinus*), Arctic Jaeger (*Stercorarius parasiticus*), Pomarine Jaeger (*S. pomarinus*), and Northern Gannet (*Morus bassanus*) (Boertmann, 2011; Wakefield, 2018). Tracking studies also demonstrate that the area is used by many nonavian, wide-ranging species, including Blue Shark (*Prionace glauca*), Shortfin Mako Shark (*Isurus oxyrinchus*) (Queiroz et al., 2016), Basking Shark (*Cetorhinus maximus*) (Gore et al., 2008), Atlantic Bluefin Tuna (*Thunnus thynnus*) (Walli et al., 2009), Sei Whale (*Balaenoptera borealis*) (Prieto *et al*. 2014), and Leatherback Turtle (*Dermochelys coriacea*) (Fossette et al., 2014). At-sea surveys in the area have also found many cetacean species, including Blue Whale (*Balaenoptera musculus*), various beaked whales, Common and Spotted dolphins (Wakefield, 2018). Further work is needed to understand how these species use and interact in the area, and the role of oceanographic drivers in the region.

4.2 | Potential drivers of abundance and diversity

The hotspot is located in an area of complex oceanography, dominated by the North-Atlantic Current (NAC) and the associated Subpolar Frontal system (Belkin & Levitus 1996). These oceanographic drivers are both more intense and spatially stable due to bathymetric steering by the continental slope/Grand Banks to the West and Charlie-Gibbs Fracture Zone in the East (Rossby, 1996). The associated mesoscale turbulence creates high rates of primary production (Longhurst, 2010), and it is likely the combination of high primary production and spatiotemporal predictability that allows the area to support large numbers of higher predators. Studies indicate that prey, such as zooplankton (e.g., calanoid copepods) and mesopelagic fish (e.g., myctophids; Fort et al., 2010; Hudson et al., 2014), are abundant in the area, with the availability to seabirds further enhanced through both mesoscale turbulence (McGillicuddy, 2016) and the diel vertical migration of mesopelagic prey (Dias et al., 2012). See Supporting Information—Oceanography.

4.3 | Conservation implications

Most seabirds used the multispecies hotspot during their nonbreeding stage––a period of their lifecycle that is currently poorly protected (Ramirez et al., 2017). Conditions during nonbreeding can directly affect subsequent breeding productivity via carryover effects (Fayet et al., 2017). This stage includes the mid-winter period, when adverse weather, food, and light conditions may account for the highest mortality of some Atlantic seabirds (Mesquita et al., 2015). Many of the studied seabird species use the hotspot while molting (Hedd et al., 2012; Wakefield, 2018). Molt is a critical time for seabirds because it is energetically demanding and can compromise flight efficiency, potentially increasing the susceptibility to natural and anthropogenic threats (Grissot et al., 2019).

We contend that the identified hotspot deserves year-round protection as an MPA, given the regular use by a large number of birds and spatiotemporal stability of the area (likely caused by stable physical drivers). Seventeen of the 21 species using the area are impacted by marine-based threats, including bycatch (65%), overfishing (29%), energy production and mining (18%), climate change (71%), pollution (including light pollution; 59%), and are undergoing population declines (Dias et al., 2019). Except for climate change, these threats can be reduced via area-based management (Game et al., 2009) and given that many breeding colonies are already protected, there is an urgent need for marine spatial protections. Although there is a debate about the utility of MPAs to protect migratory species (Game et al., 2009), there are an increasing number of studies showing their importance, particularly during spatially limited and vulnerable life-history stages (Péron et al., 2013; White et al., 2017; Young et al., 2015), and there have been demonstrated successes for seabirds when management measures have preserved their prey base (Croxall, 2008; Pichegru et al., 2010). MPAs can help reduce the likelihood of mortality, and even though the MPA may only represent a small portion of a seabirds' migratory range, they can serve a vital role in species conservation (Hooker et al., 2011; Péron et al., 2013). Given that many migratory species have limited protection at sea, even small

reductions in mortality rates can have decisive demographic benefits, especially for rare and endangered species (Caswell et al., 1999; Péron et al., 2013).

The identified hotspot is currently being discussed by the OSPAR Commission as the North Atlantic Current and Evlanov Seamount (NACES) MPA. Protection of this proposed MPA would address an identified gap in the OSPAR MPA network for seabirds (Johnson et al., 2014), and improve the coverage of nonbreeding areas more broadly (Game et al., 2009; Ramirez et al., 2017). Present threats to seabirds in the area are not fully understood: shipping lanes are predominantly in the southern part of the area (risk of disturbance, oil, and light pollution), some, limited long-line fishing occurs (bycatch risk), and recent oil exploration west of the hotspot (oil pollution and light pollution) (Impact Assessment Agency of Canada, 2020). Understanding the threats in the area, alongside the relevant contribution of other threats––both at breeding sites and across the rest of their migratory journeys––that are driving population declines should be evaluated. Understanding the relative contributions of different threats, both terrestrial and marine, that are driving population trends could help direct conservation priorities. However, it is also important to consider protection of remote areas before they become heavily exploited (McCauley et al., 2013) and to mitigate against future threats, particularly because impacts are increasing across the high seas (Halpern et al., 2019; O'Leary et al., 2020). MPAs are not a panacea for conserving marine biodiversity, and their capacity to reduce threats differs depending on their management and level of enforcement (Zupan et al., 2018). However, MPAs can contribute to biodiversity conservation where effectively managed, and the proposed NACES MPA should include measures to mitigate current and prevent future threats to seabirds. A research and monitoring plan should be adopted alongside the managed MPA, to understand more about the features supporting seabirds and other taxa, to monitor the effectiveness of the MPA, and to inform additional management measures if required. There are also increasing opportunities for monitoring remote areas using satellite and biologging technologies that could be explored (Harcourt et al., 2019; Sutherland et al., 2016). The current ABNJ MPAs under OSPAR are managed through a "Collective Arrangement" (NEAFC & OSPAR, 2015), and a collaborative approach to management would also be needed for this proposed MPA.

Overall, our analysis has demonstrated that multispecies tracking data can identify important sites in ABNJ that are suitable for protection. The ongoing work of the OSPAR Commission presents a unique opportunity for this study to inform policy and practice to benefit seabird conservation on the high seas. Once the new UN Treaty for the high seas has been adopted, replicating this approach for different regions and taxa could provide a data-driven pathway for marine conservation in ABNJ.

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AUTHORS' CONTRIBUTIONS

Study conception: B.L., M.T., M.P. D., J.H., and B.C.; Methods workshop: M.T., A.P.B.C., M.P.D., B.C., C.H., J.H., H.A., J.D., E.D., M.F., J.P.G., T.G., E.S.H., B.M., V.H.P., Th.L.Th., and E.W.; Data collection/processing: T.A-N., R.T.B., M.B., L.B., T.B., P.C., F.R.C., O.C., S.C-D., M.C-F., J.D., F.D., M.P.D., C.E., A.I.F., A.L.F., J.F., M.F., R.W.F., O.G., J.G-S., J.P.G., D.G., T.G., E.S.H., S.A.H., M.P.H., A.H., N.P.H., M.J., Y.K., J.K., J.L., J.F.L., S-H.L., J.M., E.M., M.L.M., L.Mc.T., F.R.M., T.M., B.M., W.A.M., V.M-P., A.M., V.N., M.A.N., B.O., V.H.P., H-U.P., A.P., R.A.P., I.R., J.A.R., R.R., R.A.R., P.G.R., N.M.S., I.A.S., B.S., H.Ste., I.J.S., H.Str., G.H.R.S., P.T., Th.L.Th., R.S.A.Vb., S.W., and F.Z.; Data analysis; A.P.B.C. led the analysis, with support from M.P.D., T.E.D., M.T., and E.W.; Writing: T.E.D. led the writing of the manuscript with significant contributions from all coauthors. All authors reviewed and approved the final version for submission.

ETHICS STATEMENT

The authors adhered to all relevant laws, regulations, and protocols in conducting this research.

DATA ACCESSIBILITY STATEMENT

The data are deposited on BirdLife International's Seabird Tracking Database http://www.seabirdtracking.org/

CONFLICT OF INTEREST

The authors declare no conflict of interest.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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APPLIED ECOLOGY

Global political responsibility for the conservation of albatrosses and large petrels

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Migratory marine species cross political borders and enter the high seas, where the lack of an effective global management framework for biodiversity leaves them vulnerable to threats. Here, we combine 10,108 tracks from 5775 individual birds at 87 sites with data on breeding population sizes to estimate the relative year-round importance of national jurisdictions and high seas areas for 39 species of albatrosses and large petrels. Populations from every country made extensive use of the high seas, indicating the stake each country has in the management of biodiversity in international waters. We quantified the links among national populations of these threatened seabirds and the regional fisheries management organizations (RFMOs) which regulate fishing in the high seas. This work makes explicit the relative responsibilities that each country and RFMO has for the management of shared biodiversity, providing invaluable information for the conservation and management of migratory species in the marine realm.

INTRODUCTION

The marine environment is characterized by high connectivity, which helps structure ecosystems and has important consequences for biodiversity conservation and human welfare (*1*, *2*). Distant waters are connected through the migrations of megafauna, including sea turtles, pelagic fish, marine mammals, and seabirds, as well as by ocean currents which drive the dispersal of fish larvae and other planktonic life forms (*3*–*5*). In addition to connecting natural systems, these processes also connect countries, which depend on shared biodiversity elements as resources for consumption, cultural identity, and associated ecosystem services but differ in their commitment to sustainable exploitation and conservation (*5*, *6*). During their seasonal movements, migratory marine animals visit areas under different legal and management regimes, including Exclusive Economic Zones (EEZs; up to 200 nautical miles from shore) where countries have resource rights, and areas beyond national jurisdiction (hereafter, the "high seas") that are a global commons. Identifying the set of national jurisdictions and high seas areas visited by species across their seasonal cycles is vital, as strong management policy in one region may be nullified by unmitigated threats in another (*7*).

International cooperation and collaboration is key to the conservation of migratory species (*8*). On a global scale, countries can sign and actively engage in multilateral environmental agreements (MEAs), such as the Convention on Biological Diversity and the Convention on Migratory Species (CMS), and thereby contribute to international conservation by establishing common regulatory and guidance frameworks and setting global goals (*9*). Under CMS, there are a number of subsidiary agreements, such as the Agreement on the Conservation of Albatrosses and Petrels (ACAP), through which countries can share knowledge and promote policy measures relevant to specific elements of biodiversity (*10*). However, the degree to which these MEAs apply to the high seas is debated, as the obligations of signatory countries are restricted to areas and vessels under their jurisdiction (*11*). The primary global legal framework for maritime activities, the United Nations Convention on the Law of the Sea (UNCLOS), calls on countries to cooperate to preserve the marine environment both within national jurisdictions and in the high seas. However, explicit processes for enacting conservation and management measures for biodiversity in the high seas are lacking under UNCLOS, leaving a gap in legal responsibility (*12*).

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The high seas have been documented as important habitat for an increasing number of migratory marine megafauna, yet, regardless, the footprint of human activities in the high seas continues to grow (*13*, *14*). Governance in the high seas is currently fragmented among institutional arrangements with sector-specific and/or regional mandates (*12*). The International Maritime Organization regulates shipping, for example, while regional fisheries management organizations (RFMOs) have mandates to regulate fishing. Fishing represents one of the largest industries operating in the high seas (*15*), and despite the formal commitment of RFMOs to ensure sustainable harvests and minimize broader ecosystem impacts, fisheries continue to represent a profound threat to high seas biodiversity (*16*).

To address the existing governance gap in the high seas, the United Nations have agreed to develop an international legally binding instrument under UNCLOS on the conservation and sustainable use of marine biological diversity of areas beyond national jurisdiction (aka "BBNJ treaty"). Core to the BBNJ treaty are provisions for protecting biodiversity through area-based management tools [e.g., marine protected areas (MPAs)] and the biodiversity-inclusive management of the wider ocean space, such as through the implementation of strategic environmental assessments and environmental impact assessments for planned activities (*11*, *17*). However, it remains unclear how existing management organizations and bodies will interact with the future processes adopted under the BBNJ treaty (*18*). For countries to be able to negotiate for, and ultimately implement, effective conservation and management measures under the new treaty and within the existing frameworks of MEAs and RFMOs, information is needed on the ways in which migratory species depend on and connect national jurisdictions and the high seas.

Tracking data from animals fitted with electronic devices have been used previously to estimate the proportion of time spent in different national jurisdictions and high seas areas and hence their relative importance to megafauna such as seabirds, sea turtles, tuna, sharks, and marine mammals (*13*, *19*–*21*). Tracking data can be integrated with population sizes to better quantify the importance of areas at sea, as sample-derived patterns can be contextualized with respect to the large-scale or regional distribution of each species (*22*, *23*). Population estimates are unreliable for many marine megafauna species because of their low detectability and wide distributions; yet, for seabirds, which assemble at predictable sites on land to breed, reasonably accurate estimations of population size can be used to weight estimates of space use at sea (*24*).

Albatrosses and large petrels have wide annual ranges spanning all major ocean basins. They are considered among the most threatened of all bird groups and are subject to several anthropogenic threats at sea, especially incidental mortality in fishing gear (termed "bycatch")

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and competition with fisheries caused by overfishing, as well as pollution and climate-related changes to ecosystems (*25*, *26*). Using a unique tracking dataset assembled from across the global distributions of 39 species of albatrosses and large petrels, we estimate the importance of national jurisdictions and high seas areas across the annual cycle. First, we calculate species richness for each national jurisdiction (including the dependent territories under each sovereign country) and the high seas as a whole, distinguishing between breeding and visiting species (i.e., breeding in another country). Next, we estimate the amount of time, year-round, that each breeding population spends in each of these political areas, again discriminating between time spent in breeding-origin countries and other visited areas. Then, we attribute annual time spent in the high seas to the areas of competence of RFMOs. Last, we construct networks to reveal the geopolitical connections most important to the populations of each breeding-origin country and to the global community of albatrosses and large petrels. These detailed quantitative estimates of interconnectivity will inform countries on which jurisdictions their biodiversity depends and how to prioritize their engagement with the BBNJ treaty and other instruments and agreements.

RESULTS

Standalone importance of countries and the high seas

All 39 species of albatrosses and large petrels visited the high seas during their annual cycles, and except for the shy albatross *Thalassarche cauta*, all species visited the areas of jurisdiction of at least one country outside their breeding origin (Table 1, Fig. 1, and data S1). France had the highest total species richness (n = 28) and visiting-species richness (n = 26), while Argentina and Brazil had the highest number of species visiting that do not also breed in areas under their jurisdiction (n = 23 and n = 19, respectively; Fig. 1A). New Zealand had the highest number of breeding species (n = 15), and the United Kingdom had the highest richness of species that both breed in areas under their jurisdiction and visit from elsewhere (n = 10; Fig. 1B and data S1). In general, countries hosting a high diversity of breeding species also hosted a high number of visiting species, and countries with larger territories had higher richness (Fig. 1B and fig. S4). Brazil, Uruguay, Namibia, and Peru were each visited by ≥10 species although they have no breeding populations, and Antarctica (areas south of 60°S) was visited by 20 species (Fig. 1A and data file S1).

These species richness values were estimated directly from available tracking data; for several species, the sampled sites are not comprehensive of all breeding sites, and therefore, reported richness values are underestimates for certain countries. Breeding richness estimated from the tracking data was on average one species (mean, SD ±1.4) fewer than true breeding richness as calculated from the literature. Estimated richness was equal to true richness for 9 of the 22 countries that are known to have at least one breeding species of albatross or large petrel (data file S1). In most cases, missed breeding populations are relatively small in global terms, because our data included most of the global breeding population of each species (Table 1).

The high seas as a whole hosted the greatest amount of time spent by albatrosses and large petrels across the year, including 16 million of the total 41.3 million (39%) estimated bird-years (Fig. 1C). Among national jurisdictions, Australia had the highest annual time spent (i.e., by both visiting and breeding birds), with 4.0 million (9.6%) bird-years. Russia and the United States hosted the most time spent by visiting birds, representing an annual 3.9 million (9.4%) and 2.7 million (6.5%) bird-years, respectively (Fig. 1C and data S1). Australia and New Zealand each hosted the highest annual time spent by their own breeding populations, with a respective 3.9 million (9.4%) and 2.9 million (7.0%) bird-years (Fig. 1C and data S1). Static maps of annual species richness and time spent revealed contrasting patterns of albatross and large petrel diversity across the world (Fig. 2). The spatial pattern of time spent per month varied within a year, reflecting the dynamic seasonal distributions of albatrosses and large petrels (movie S1).

Geopolitical connectivity

In terms of annual time spent, the high seas as a whole represent a "top connection" (i.e., one of the top five most visited areas) for the albatross and large petrel communities of all breeding-origin countries (Fig. 3A). At the global level, the breeding communities of the United Kingdom, France, and New Zealand have the strongest links to the high seas, indicated by the time spent there by the large breeding populations in these countries (i.e., proportions of all adult birds of each species), as well as the number of species making the connection. South Africa and Brazil were top connections for four separate breeding-origin countries (South Africa: France, Portugal, Spain, and United Kingdom; Brazil: Argentina, Cabo Verde, Portugal, and United Kingdom), and France, Peru, Mauritania, Russia, and the United States were among the top connections for populations breeding in three different countries (Fig. 3A and data S2A).

All high seas areas under the legal competence of RFMOs hosted a top connection (i.e., one of the top three most visited areas) with at least one breeding-origin country, with the exception of the smallest RFMOs (the North Atlantic Fisheries Organization and the Convention on the Conservation and Management of Pollock Resources in the Central Bering Sea; Fig. 3B). The International Commission for the Conservation of Atlantic Tunas (ICCAT), the Western and Central Pacific Fisheries Commission (WCPFC), and the South Pacific Regional Fisheries Management Organisation (SPRFMO) represented the most important high seas areas, in terms of the number of top connections with breeding-origin countries and the strength of connection (Fig. 3B and data S2B). The competence areas of ICCAT, WCPFC, and SPRFMO are among the largest in the world, and the size of RFMO areas was positively related to the total strength of their connections with breeding-origin countries (i.e., the sum of all connections per RFMO; Fig. 3B; R^2 = 0.6, P < 0.001, df = 12; fig. S4).

DISCUSSION

Migratory species cover immense distances on their seasonal movements, connecting numerous areas both within and beyond national jurisdiction and making their conservation a challenging task. By analyzing a comprehensive tracking dataset and accounting for the size of each breeding population relative to the global total, our study provides the first global estimation of the relative importance of political areas to a group of highly threatened migratory megafauna, the albatrosses and large petrels. We estimated the standalone importance of national jurisdictions and the connectivity between them, providing a potential road map for international collaboration. We also quantified the connections between breeding-origin countries and areas of legal competence of RFMOs in the high seas, providing a useful scoping tool for identifying which national populations of albatrosses and large petrels may be affected by management decisions in international fisheries. Our results showed that the high seas are

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Table 1. Tracking data coverage of the global breeding population and annual cycle of 39 species of albatrosses and large petrels. "$N_{species}$" is the estimated size (individuals) of the global breeding population. "n_{sites}" is the number of breeding populations tracked per species. "n_{birds}" is the number of unique birds tracked. "% Species pop." is the percentage of the global breeding population made up by the sites tracked herein. "% Species year known" is the percentage of the annual cycle of the global breeding population estimated by our tracking data. "% Species year unknown" is the percentage of the annual cycle not estimated by our tracking data (i.e., months or populations without tracking data).

Common name	Scientific name	$N_{species}$	n_{sites}	n_{birds}	% Species pop.	% Species year known	% Species year unknown
Amsterdam albatross	*Diomedea amsterdamensis*	90	1	74	100	100	0
Antipodean albatross	*Diomedea antipodensis*	14,864	2	211	100	100	0
Tristan albatross	*Diomedea dabbenena*	2,218	1	52	100	100	0
Wandering albatross	*Diomedea exulans*	18,568	5	977	100	100	0
Northern royal albatross	*Diomedea sanfordi*	10,270	2	75	100	92	8
Short-tailed albatross	*Phoebastria albatrus*	2,600	1	32	78	52	48
Laysan albatross	*Phoebastria immutabilis*	1,333,316	1	208	100	100	0
Waved albatross	*Phoebastria irrorata*	16,942	1	54	100	42	58
Black-footed albatross	*Phoebastria nigripes*	140,072	1	160	96	96	4
Sooty albatross	*Phoebetria fusca*	24,192	4	121	100	100	0
Light-mantled albatross	*Phoebetria palpebrata*	41,046	5	73	65	58	42
Buller's albatross	*Thalassarche bulleri*	65,402	1	115	44	44	56
Indian yellow-nosed albatross	*Thalassarche carteri*	64,414	2	184	87	63	37
Shy albatross	*Thalassarche cauta*	29,368	1	143	100	83	17
Atlantic yellow-nosed albatross	*Thalassarche chlororhynchos*	67,300	1	45	100	92	8
Gray-headed albatross	*Thalassarche chrysostoma*	165,854	5	232	85	57	43
Chatham albatross	*Thalassarche eremita*	10,592	1	50	100	92	8
Campbell albatross	*Thalassarche impavida*	43,296	1	81	100	92	8
Black-browed albatross	*Thalassarche melanophris*	1,374,890	5	803	88	86	14
Salvin's albatross	*Thalassarche salvini*	82,426	1	22	3	3	97
White-capped albatross	*Thalassarche steadi*	191,834	1	38	100	100	0
Buller's shearwater	*Ardenna bulleri*	700,000	1	8	100	100	0
Flesh-footed shearwater	*Ardenna carneipes*	148,000	2	91	48	41	59
Pink-footed shearwater	*Ardenna creatopus*	67,040	1	102	100	92	8
Great shearwater	*Ardenna gravis*	5,000,000	1	72	100	100	0
Sooty shearwater	*Ardenna grisea*	20,000,000	2	54	46	45	55
Wedge-tailed shearwater	*Ardenna pacifica*	5,200,000	4	56	58	49	51

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Common name	Scientific name	$N_{species}$	n_{sites}	n_{birds}	% Species pop.	% Species year known	% Species year unknown
Short-tailed shearwater	*Ardenna tenuirostris*	23,000,000	1	16	78	72	28
Cory's shearwater	*Calonectris borealis*	423,672	4	514	98	90	10
Scopoli's shearwater	*Calonectris diomedea*	327,250	4	228	95	80	20
Cape Verde shearwater	*Calonectris edwardsii*	26,228	1	19	100	83	17
Streaked shearwater	*Calonectris leucomelas*	3,000,000	2	104	59	54	46
Southern giant petrel	*Macronectes giganteus*	95,406	5	243	25	19	81
Northern giant petrel	*Macronectes halli*	21,382	5	227	81	59	41
White-chinned petrel	*Procellaria aequinoctialis*	2,405,136	4	133	80	68	32
Gray petrel	*Procellaria cinerea*	151,132	4	61	98	89	11
Spectacled petrel	*Procellaria conspicillata*	28,800	1	8	100	50	50
Black petrel	*Procellaria parkinsoni*	3,000	1	61	100	92	8
Westland petrel	*Procellaria westlandica*	5,654	1	28	100	92	8
		64,302,254	87	5775	84.9	75.0	25.0

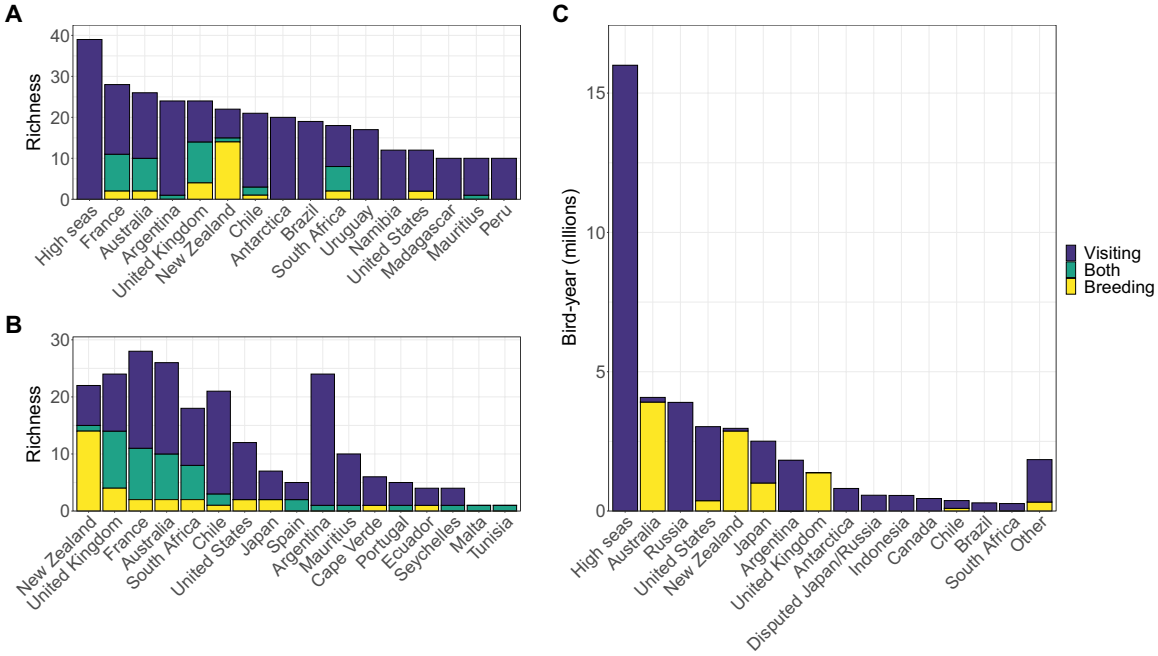


Fig. 1. Standalone importance of countries and the high seas for albatrosses and large petrels. (**A** and **B**) Species richness within national jurisdictions and the high seas. For each political area, richness is divided into three categories: species that breed in the country ("Breeding"), species that visit the area but do not breed ("Visiting"), and species that both breed locally and visit from elsewhere ("Both"). (A) Top 15 areas in terms of total species richness. (B) Species richness of countries that host breeding populations, ordered by breeding richness. (**C**) Most important areas in terms of annual time spent, an index of abundance, by adult albatrosses and large petrels split into visiting and breeding bird components. Areas shown host more than 0.1% of annual time spent, with all others summed into the category "Other." National jurisdictions refer to the aggregated EEZs (up to 200 nautical miles from shore) of each country, and high seas refers to all areas beyond national jurisdiction.

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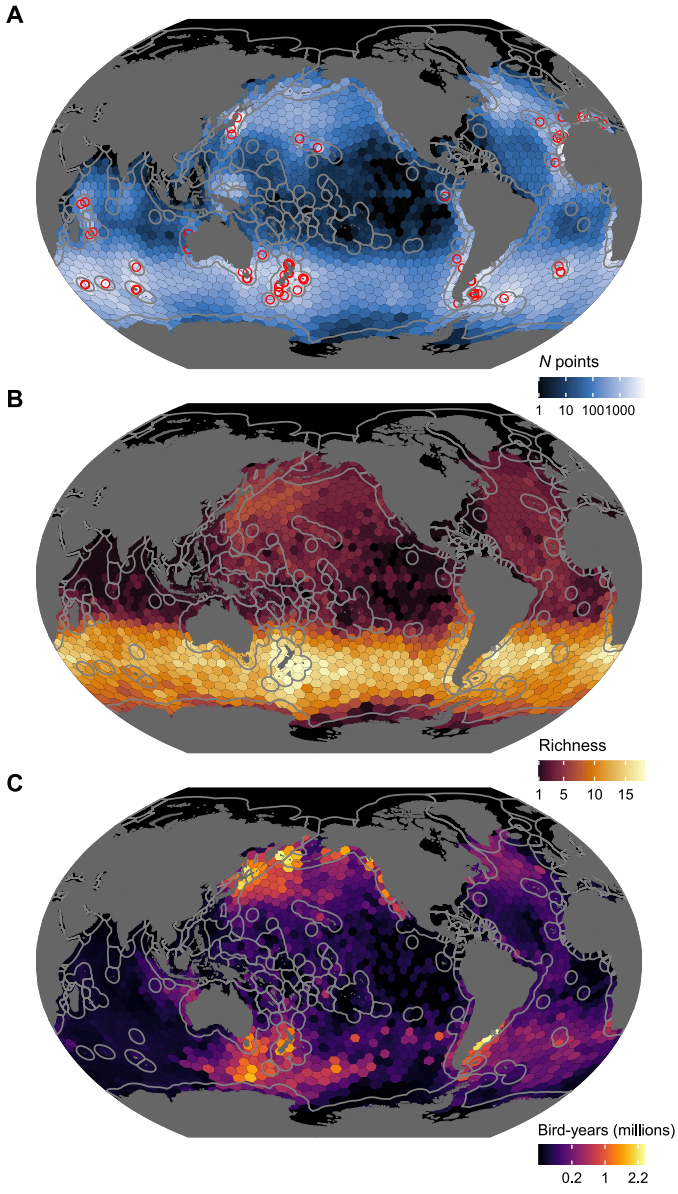


Fig. 2. Tracking data and year-round distributions of albatrosses and large petrels. (**A**) Study sites (open red circles) and the number of daily positions derived from tracked birds. (**B**) Species richness of adult birds in a breeding year. (**C**) Time spent during a breeding year. Cells indicate the total amount of time spent by the global breeding population of albatrosses and large petrels in a year. Gray lines at sea represent borders of national EEZs.

important to albatrosses and large petrels from every country and in every ocean basin, indicating that effective management of international waters is of common, global interest.

By identifying the specific set of countries visited by albatrosses and large petrels originating in different countries, our findings provide support for existing bilateral and multilateral agreements and reveal additional connections of importance for these species. Our network confirms the connections, in terms of their albatross and petrel populations, among signatories of the CMS daughter agreement ACAP (which lists 29 of the 39 species studied herein) (*10*) and shows that bilateral agreements, such as the Japan-Australia Migratory Bird Agreement (http://www.austlii.edu.au/au/other/dfat/treaties/1981/6.html) or the New Zealand–Chile arrangement to protect seabirds (https://www.doc.govt.nz/news/media-releases/2018/chile-and-nz-arrangement-to-protect-seabirds/) including those affected by fisheries, have measurable importance. However, our results also reveal important gaps; for example, many birds from both Australia and Japan use Russian waters, yet there are no treaties or agreements between these countries that reflect this relationship. South Africa and Brazil host large numbers of birds from breeding populations across the Atlantic Ocean, and despite the engagement of these countries in CMS instruments, the most numerous species (i.e., *Calonectris* and *Ardenna* shearwaters) that contribute to these connections are not listed in CMS appendices and are therefore at risk of being omitted from international policy developments concerning migratory marine animals. To minimize gaps in protection, we suggest that any international conservation efforts for albatrosses and large petrels would benefit by considering the relative importance of countries for these species as identified herein.

Our maps of species richness and annual time spent reveal contrasting patterns in these two measures of biodiversity and identify hotspots both within and beyond national jurisdictions. Areas of high species richness were concentrated in the Southern Ocean, whereas areas of high annual time spent were generally distributed in the productive waters of continental shelf or upwelling regions, like the Patagonian Shelf in the South Atlantic Ocean and the Kuril Trench in the North Pacific Ocean. Notably, some areas of high annual time spent occurred in specific regions in the high seas, such as the Southern Ocean south of Tasmania, the northwest Pacific Ocean, and north-central Atlantic Ocean. The identified hotspots largely reflect the distributions of several species that are highly abundant trans-equatorial migrants, which number in the millions in the Atlantic (great shearwater *Ardenna gravis*) and Pacific Oceans (sooty *Ardenna grisea* and short-tailed shearwaters *Ardenna tenuirostris*). Our synthesis provides global snapshots of albatross and large petrel diversity, which have markedly seasonal distributions (see supplementary animation). The extensive and dynamic ranges of migratory marine megafauna, such as albatrosses and large petrels, indicate that static, area-based conservation measures alone, like MPAs, are not sufficient to address threats (*27*, *28*). Very large MPAs or those with dynamic management, with boundaries that shift across space and time, can be effective during the breeding season for certain species (*29*). However, during the nonbreeding season, when the movements of seabirds are less restricted, process-oriented and ecosystem-based management across the wider seascape is required (*27*). Regardless of the spatiotemporal scale of the approach, for any at-sea area-based protection to have positive outcomes for albatross and large petrel conservation, the implementation of effective fisheries measures is vital.

The high seas constitute the most important at-sea area for albatrosses and large petrels globally. Our estimates provide countries with tangible, quantitative indicators of the relative importance of the high seas for their respective communities of breeding seabirds, which are highly pertinent for countries involved in the ongoing discussions on the BBNJ treaty. The treaty objective is the conservation and sustainable use of high seas biodiversity; however, on the basis of the precondition of "not undermining" preexisting management organizations and bodies, fisheries have been excluded from treaty discussions (*18*). As the major, immediate at-sea threats to albatrosses and large petrels relate largely to fisheries (*25*), this exclusion may represent a missed opportunity to improve fisheries governance. Nevertheless, the BBNJ treaty could still influence RFMOs to the

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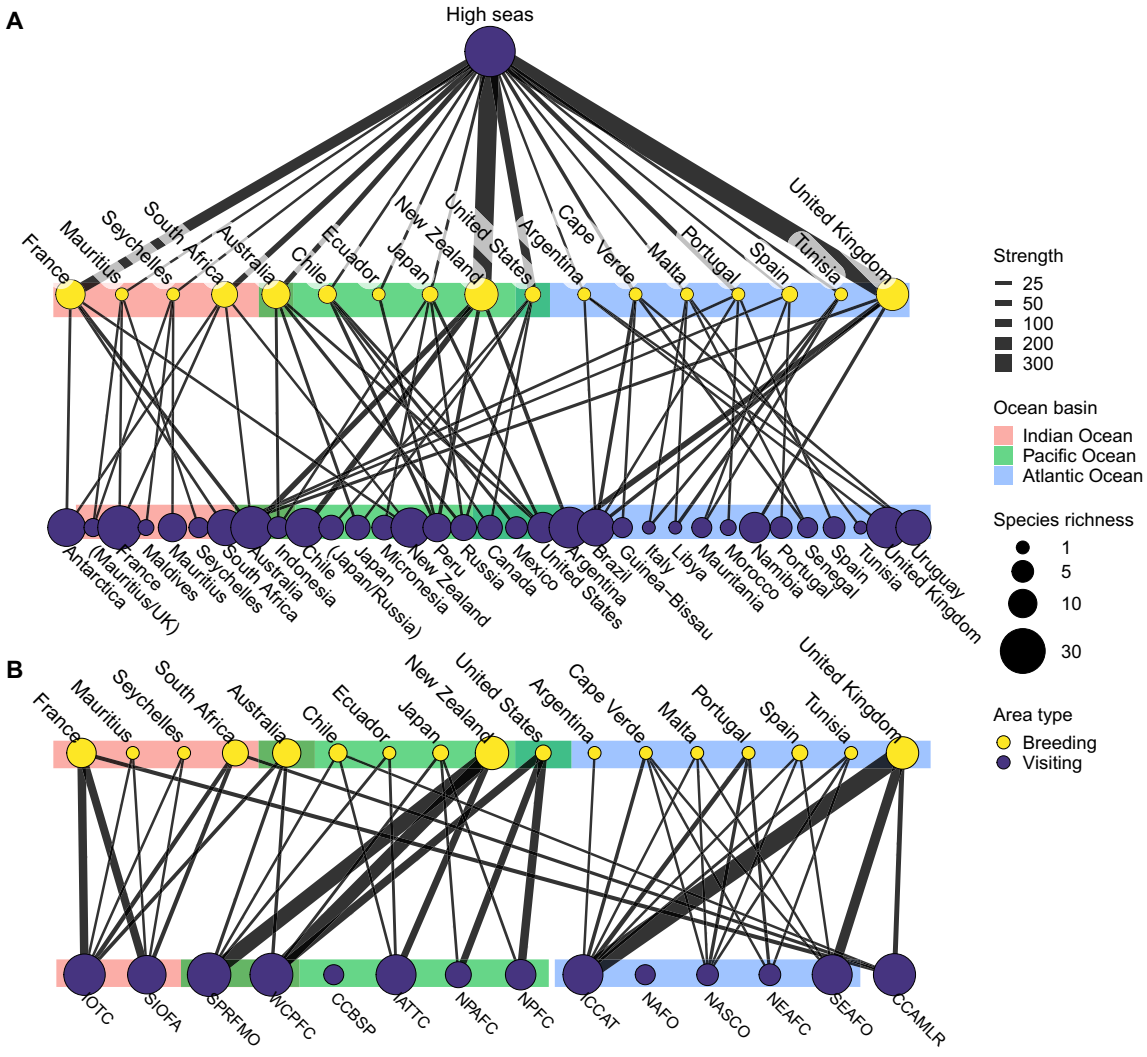


Fig. 3. The most important geopolitical connections for albatrosses and large petrels. Connections are between breeding-origin countries (yellow dots) and visited national jurisdictions or high seas areas (purple dots), with dot size respectively representing the breeding and visiting richness in each and the link width signifying the strength of the connection. Connection strength is quantified as the percentage of annual time spent in the visited area, summed across the species making the connection. Annual time spent is calculated for each breeding population and weighted by the size of the population relative to global total of each species. (**A**) Top five connections between each breeding-origin country and the other areas visited throughout the annual cycle. (**B**) Top three connections between breeding-origin countries and the areas of competence of RFMOs in the high seas. Colored boxes represent the ocean basin in which most of the jurisdictional waters of each country or RFMO are located. RFMO abbreviations correspond to the following (left to right): Indian Ocean Tuna Commission, Southern Indian Ocean Fisheries Agreement, South Pacific Regional Fisheries Management Organisation, Western and Central Pacific Fisheries Commission, Convention on the Conservation and Management of Pollock Resources in the Central Bering Sea, Inter-American Tropical Tuna Commission, North Pacific Anadromous Fish Commission, North Pacific Fisheries Commission, International Commission for the Conservation of Atlantic Tunas, Northwest Atlantic Fisheries Organization, North Atlantic Salmon Conservation Organisation, North East Atlantic Fisheries Commission, South East Atlantic Fisheries Organisation, and Convention on the Conservation of Antarctic Living Marine Resources.

benefit of albatrosses and large petrels (*18*) in a number of ways—by formalizing a global process for establishing area-based management tools with appropriate regulations regarding bycatch and overfishing, by improving transparency and information sharing (particularly related to bycatch) via the establishment of an independent scientific committee, and by setting specific thresholds of impact that trigger the need for fisheries (or any other industry) to implement environmental impact assessments (*18*, *30*).

Our results also provide information to breeding-origin countries about the RFMO management areas in the high seas that are most important to each of their seabird populations. Despite being important because of their ocean-basin scale, the tuna RFMOs [ICCAT, WCPFC, Indian Ocean Tuna Commission (IOTC), and Inter-American Tropical Tuna Commission (IATTC)] are particularly relevant to albatross and large petrel conservation as industry practices have frequently been linked with overfishing and high bycatch rates (*16*, *31*). Fishing fleets operating in the high seas are under the jurisdiction of their flag states (*32*); therefore, despite not hosting albatrosses and large petrels within their national jurisdictions, some countries still affect them through poor fishing practices (*33*). The effectiveness of regulatory measures ultimately depends on the attitude of each country in terms of implementation and monitoring of compliance; however,

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as RFMOs operate on a consensus basis, it is the countries with a will to protect nontarget biodiversity that must push for effective regulation. Our results confirm that national measures for albatrosses and large petrels if coupled with coordinated, international efforts would successfully mitigate threats occurring across the ranges of these species. For example, while many species of conservation concern breeding on South African, French, United Kingdom, and Australian islands benefit from national action plans for reducing bycatch within national waters and fleets (*34*), birds are still at risk from longline effort in the high seas of the Indian Ocean, where they spend a considerable part of the year (Fig. 3B). Despite this, these countries have not advocated for the improvement of bycatch mitigation measures at the IOTC since 2012.

The tracking dataset used herein spanned the global ranges and annual cycles for most of our focal group, the albatrosses and large petrels, providing a uniquely representative picture of their global distribution (mean coverage of 85 and 75%, respectively; Table 1). Nevertheless, gaps remain in terms of untracked populations and unsampled months of the year. Using knowledge of known breeding sites and population sizes, we quantified these sampling limitations (Table 1) and thereby identified gaps at the species level where future work may be focused (*35*, *36*). Tracking and population data were only analyzed for breeding adults, and therefore, our results pertain to the global breeding populations of each species in a given year. A substantial proportion of the global population is made up of juveniles, immatures, and deferring breeders (particularly for biennial species), which may have different annual distributions and hence geopolitical connectivity (*37*, *38*). These are important gaps to fill in terms of tracking and monitoring effort; however, as these data accumulate, syntheses across ranges, taxonomic groups, and life stages can become standard practice (*24*).

Here, we stress that, when possible, population delineations and size estimates should be incorporated when identifying areas that are important for migratory species (*23*, *39*) or subject to particular threats (*40*, *41*). Our results show how such analyses can quantify political responsibility and reveal unexpected linkages, providing opportunities for improving the conservation of migratory species. The high seas are a global commons, where there is a lack of effective legal processes for ensuring the conservation and sustainable use of biodiversity. We show that migratory seabirds across the world connect numerous countries and the high seas, thereby contributing to the connectivity of the global ocean. As human endeavor in the marine environment expands, it becomes more important than ever that our systems of management and protection reflect this interconnected reality.

MATERIALS AND METHODS

Study taxa

For the purposes of this study, the term "albatrosses and large petrels" refers to all species in the albatross family Diomedeidae, and the genera *Macronectes*, *Ardenna*, *Calonectris*, and *Procellaria* of the family Procellariidae. This grouping was selected for the following reasons: 21 of these 40 species are listed as vulnerable, endangered, or critically endangered under the International Union for Conservation of Nature (IUCN) Red List Criteria and an additional 11 as near threatened (*42*); 29 are listed by ACAP (*10*), a high proportion face at-sea threats, namely incidental mortality in association with fishing, as well as direct competition with fisheries; last, these species are highly mobile and are relatively well studied across their ranges, and hence, the necessary tracking and population data are available for a global synthesis (*10*, *24*, *25*).

Data assembly

Tracking data were obtained from the BirdLife International Seabird Tracking Database (www.seabirdtracking.org) and directly from collaborators. Data were sought from all the breeding aggregations for each species, with the goal of maximizing coverage of the global breeding population (Table 1 and data S3). Each "breeding population" was defined according to criteria adopted by ACAP as individuals of each species found breeding at each "island group"; the latter correspond with major archipelagos and reflects current biogeographic and political separation (*10*). For each breeding population with tracking data, we maximized coverage of the annual cycle (Table 1) by using data from light-level geolocation (Global Location Sensor or GLS), Platform Terminal Transmitters (PTTs), and Global Positioning System (GPS) devices. We obtained island group and global breeding population size estimates from the ACAP database (https://data.acap.aq/) and from the literature (data S4). We assembled requisite data for 39 of the 40 species of albatrosses and large petrels, with only the southern royal albatross *Diomedea epomophora* lacking the necessary data for analysis.

Filtering and standardization

Because time intervals between locations differed among device types and datasets, we used a single location per day (i.e., the lowest common interval) from each individual track, nearest to local noon, for analysis. GLS, PTT, and GPS devices provide positions in different ways, resulting in different levels of spatial accuracy. Data from GLS devices are used to estimate location based on day length and the relative timing of local noon and have the highest spatial error, of around SD ±186 km (*43*). We applied a series of filters to GLS datasets in addition to those used by data contributors. We also performed a resampling procedure to test the sensitivity of our measures of the importance of political areas to spatial error and concluded that the effects on estimated richness and time spent were very small and had no substantial effects on the results (see Supplementary Materials and Methods for details and fig. S3 for results). Nine species (all *Diomedea* and *Phoebetria* spp. and gray-headed albatross *Thalassarche chrysostoma*) breed biennially, and because tracking data coverage during the nonbreeding year is generally poor, we retained only data from the first 365 days following logger attachment for each individual track. Hence, all results pertain to the distribution of adult birds during a breeding year.

After filtering, there were a total of 842,527 tracking days available for analysis from 5775 individual birds (Fig. 2A, fig. S1, and data S4). These data represent movements sampled between 1989 and 2017, across 87 breeding populations from 39 of the 40 species of albatrosses and large petrels (Table 1 and data S3). These populations represent a total of 44 million of the estimated 58 million breeding albatrosses and large petrels worldwide and a mean of 85% (range, 3 to 100%) of the global breeding population per species (Table 1). We identified the national jurisdictions and high seas areas visited by each breeding population for each month of the year (see the "Analysis" section); we considered months with fewer than 10 unique tracking days to be unrepresentative and removed them from the analysis. To test the sensitivity of this threshold, we reran the analysis with a more conservative threshold of at least 10 tracking days across five different individuals. This did not alter any

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major patterns or conclusions but excluded valuable data for several important populations from which few birds have been tracked; therefore, we opted to use the less conservative threshold (see data S5, A and B, and S6, A and B). Combined tracking samples for each population spanned a mean of 300 days (SD ±56) of the annual cycle (Table 1). After filtering unrepresentative months, tracking data allowed for the calculation of the national jurisdictions and high seas areas visited during a total of 94% of the annual cycle of 44 million albatrosses and large petrels and a mean of 76% (range, 3 to 100%) of the annual cycle per species (Table 1). Therefore, our results pertain to 41.3 million of a possible total of 58 million (71%) bird-years.

Analysis

Each daily location estimate was assigned to a maritime zone (herein used when simultaneously referring to the following areas: EEZs, the high seas as a whole, and the areas of legal competence of RFMOs in the high seas). First, this was done for national jurisdictions and the high seas as a whole, using a spatial union between country land borders and EEZs (VLIZ 2020, available at http://marineregions.org). We considered national jurisdictions to be the aggregated area of EEZs (and territorial waters) under a single country, including therein any overseas dependencies. Then, the analysis was run again, attributing points in the high seas to the areas of competence of the RFMOs, available at http://fao.org/geonetwork/ (fig. S2). Areas with overlapping territorial claims were left named with all claimant countries listed (e.g., "disputed – Russia/Japan"), unless they had breeding colonies with tracking data, which was only the case for the Falklands/Malvinas, South Georgia/Georgias del Sur, and the Chafarinas/Zafarin Islands. For these cases, the analysis was run twice with breeding populations alternately assigned to each disputing country (see alternate results in data S5, C and D, and S6, C and D).

Species richness

Species richness was calculated for each national jurisdiction and the high seas as a whole based on tracking data occurrence and reflects the number of (i) breeding species, (ii) visiting species, and (iii) species that both breed locally and visit from elsewhere. To visualize this pattern in space, maps were constructed by binning total richness on a global hexagonal grid of with cell-center spacing of 495 km (SD ±30) which is a grid resolution large enough to encompass the average error of GLS devices (*43*). Calculations of breeding species richness for each country reflect only the breeding populations with available tracking data to ensure a valid comparison with the number of visiting species; therefore, this will be an underestimate of true breeding richness in certain cases. Using information on all known breeding countries for each species, we calculated the degree of underestimation in our calculations of breeding richness per country.

Time spent estimation

To reflect the relative abundances of albatrosses and large petrels in each maritime zone, we estimated the amount of time spent by each breeding population in a year. Time spent was first calculated for each month to account for uneven sample sizes and shifting seasonal distributions and then summed and expressed in "bird-years." Each daily location within a maritime zone was considered one bird-day spent therein. The total amount of time spent (T_{spme}; in bird-months) by the breeding population p of species s in maritime zone e was calculated as

$$T_{spme} = \frac{\sum_{i=1}^{i_{max}} \left(\frac{D_{ime}}{D_{im}}\right)}{n_m} * N_p \quad (1)$$

where D_{ime} represents the number of days an individual i spent in maritime zone e in month m, and D_{im} represents the total number of days individual i was tracked in month m. This proportion of days spent in each maritime zone was then averaged across all tracked individuals (i_1 to i_{max}) by dividing the sum of proportions by the number of tracked individuals for a species and population n_m in month m. The average proportion of monthly time spent per tracked individual was then multiplied by the breeding population size N_p to extrapolate to the total amount of time (in bird-months) that breeding population p of species s spends in maritime zone e in month m.

For example, an individual (i) Cory's shearwater *Calonectris borealis* (s) from the breeding population in Madeira (p) spent 10 of a total of 31 tracking days (32% of the time) in the high seas $\left(\frac{D_{ime}}{D_{im}}\right)$ during January (m). In this way, we calculated the proportion of days spent in the high seas for each of the 72 tracked individuals (n_m) of the same species and population. Next, we calculated the mean proportion of time spent across these 72 individuals, estimating that these birds spent, on average, 17% of January in the high seas. Multiplying this mean proportion by the breeding population size of 66,080 individuals (N_p) results in a monthly total of 11,284 bird-months spent in the high seas in January (T_{spme}).

Annual time spent

We then summarized the monthly time spent across all months to estimate the standalone importance of maritime zones e in terms of the total amount of time spent in a year (T_e; in bird-years) by the global community of albatrosses and large petrels

$$T_e = \sum_{p=1}^{p_{max}} \frac{\sum_{m=1}^{m_{max}} (T_{spme})}{12} \quad (2)$$

where the total time spent within each month (T_{spme}) was summed across the months for which tracking data were available (m_{max}) and divided by 12 to convert the unit from bird-months to bird-years. The number of bird-years per population was then summed across all populations in maritime zone e to give an estimate of the total annual time spent there by all species.

Continuing our example of Cory's shearwaters from Madeira, the total monthly time spent in the high seas (T_{spme}) was calculated for the 11 months of the year where tracking data existed (m_1 *to* m_{max}) and then divided by the full 12 months of the year to convert the unit from bird-months to bird-years. To put this species- and population-specific pattern in the global context, we added the resulting total amount of time spent by Cory's shearwaters to the values of all other breeding populations visiting the high seas (p_1 *to* p_{max}), giving the total amount of time spent in the high seas in a year by the global community of albatrosses and large petrels (T_e).

Since tracking data were unavailable for some months of the year for certain populations, T_e was underestimated in these cases because the unit conversion still divided the sum of all tracking months by 12 rather than the number of months for which tracking data were available; however, we preferred this conservative approach because calculating over the full year avoided extrapolating occurrence patterns into unsampled periods. The sum of T_e across all maritime zones therefore equals the population size of all breeding populations with tracking data minus the untracked portions of the year for each population (i.e., 41.3 million bird-years estimated for 44 million birds; see the "Filtering and standardization" section). To visualize the time spent pattern in space, we aggregated the annual time spent over a hexagonal grid with cell-center spacing of 495 km (SD ±30) using the same equation (i.e., where e signified grid cells).

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Network analysis

To estimate the strength of connection between breeding-origin countries and other visited maritime zones, we developed an index based on the percentage of annual time spent per maritime zone by populations of different breeding origins. The proportion of annual time spent G_{soe} in maritime zone e by species s breeding under the jurisdiction of origin country o was calculated as

$$G_{\mathrm{soe}} = \frac{\sum_{p=1}^{x}\sum_{m=1}^{m_{\max}}(T_{spme})}{N_s * 12} \quad (3)$$

where the total within-month time spent (T_{spme}) was summed across all months and all tracked populations x of a given species breeding in country o and converted from bird-months to bird-years by dividing by 12. This annual time spent value was then divided by the global population size N_s of that species to calculate the proportion of annual time spent in each maritime zone by all individuals of said species.

In our example of Cory's shearwaters from Madeira, we first added the total amount of time spent in the high seas in each month (T_{spme}) across all tracking months of the year, resulting in 115,844 bird-months. Similarly, we calculated 1,988,600 bird-months spent in the high seas across the year for Cory's shearwaters from the Azores and 4771 bird-months for the Berlengas population, which resulted in a total of 2,109,215 bird-months or 175,768 bird-years for all breeding populations of Cory's shearwater falling under the jurisdiction of Portugal. We then divided the latter value by the global population size of 423,672 individuals of that species to estimate that the proportion of time spent (G_{soe}) in the high seas (e) attributable to Cory's shearwaters (s) of Portuguese breeding origin (o) was 41.5% of the annual time for the species.

Then, the strength of connection between each breeding-origin country and visited maritime zones was calculated as the percentage of annual time spent in each zone summed across all the species breeding in each country

$$G_{\mathrm{oe}} = \sum_{s=1}^{s_{\max}} G_{\mathrm{soe}} * 100 \quad (4)$$

where G_{oe} indicates the strength of the connection between breeding-origin country o and visited maritime zone e with respect to the global breeding population for each species and to the breeding community in each country. The connections were ranked by strength (G_{oe}), and the strongest links were then plotted in a network diagram. We represented the top connections per breeding-origin country in the network as (i) the top five links in the country-to-country and the high seas analysis and (ii) the top three links in the country-to-RFMO competence area analysis (see tables S6 and S8 for the full set of connections). A virtual application is available at https://birdlifeseabirds.shinyapps.io/seabird-connections/ to facilitate viewing the specific connections albatrosses and large petrels create between different national jurisdictions and high seas areas, including RFMOs. All analyses were run using the R statistical computing environment; maps were made using the R packages "dggridR," "ggplot2," and "sf," and networks were constructed using "ggraph" (*44*–*48*). Analysis scripts are available at https://github.com/MartinBeal/political_connectivity.

SUPPLEMENTARY MATERIALS

Supplementary material for this article is available at http://advances.sciencemag.org/cgi/content/full/7/10/eabd7225/DC1

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Assessing the location and stability of foraging hotspots for pelagic seabirds: An approach to identify marine Important Bird Areas (IBAs) in Spain

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Storm-petrel

ABSTRACT

Protected areas play a key role in the preservation of biodiversity, but their implementation at sea is lagged behind terrestrial environments, especially in offshore areas. Here we describe the identification of foraging hotspots off the Mediterranean Iberian coast using three Procellariiform species as examples, and assess the stability of these sites. Then, we show how these foraging hotspots contributed to the delimitation of marine Important Bird Areas (IBAs). The whole process consisted of: (1) seabird data collection (extensive boat-based surveys and seabird tracking, conducted in 1999–2010) and compilation of relevant spatial descriptors of the marine environment; (2) species distribution modeling (SDM) aimed at identifying areas with high habitat quality for the different seabird species (3); identification and delineation of the main seabird hotspots, based on models, supported by direct seabird data, and mediated by expert opinion; (4) application of BirdLife International IBA criteria for hotspot validation; and (5) combination of hotspots from different species to set the final limits of the marine IBAs. This approach allowed to identify a series of hotspots for pelagic species in the study area, and provided nice examples of stability assessment, which slightly differed in performance between seabird species. They contributed to the Spanish marine IBA inventory, which is in the process of receiving legal protection. Future work should be directed at confirming the stability of the marine IBAs in the long term, and to address the development of management plans to make effective the protection of these sites.

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1. Introduction

Protected areas are recognized as key tools for biodiversity conservation (Lovejoy, 2006). However, the marine environment has received little attention relative to terrestrial areas, and less than 1% of the ocean's surface is included in marine protected areas (MPAs) (Wood et al., 2008). Moreover, most MPAs are small, coastal sites, focusing on benthic habitats (e.g. coral reefs, sea-grass prairies), whereas the dynamic open sea and its related biota have been largely neglected (Game et al., 2009).

In line with this general pattern, seabirds have received protection in many of their breeding colonies, but few sites have been protected at sea for these top predators (Grémillet and Boulinier, 2009). Moreover, the few MPA initiatives regarding seabirds have been primarily directed at protecting the marine areas surrounding seabird colonies (e.g. Airamé et al., 2003; McSorley et al., 2003; Yorio, 2009) and, to a lesser extent, distinct coastal and/or shallow areas hosting non-breeding congregations of highly gregarious species such as sea-duck (McSorley et al., 2005; O'Brien et al., this issue; Skov et al., 2007). Far less attention has been placed on offshore areas, although these include key foraging sites for several seabird species (Hyrenbach et al., 2006; Harris et al., 2007; Louzao et al., 2006; Nur et al., 2011). The dynamic nature of the marine environment, the lack of obvious boundaries and the requirement of large extensions for effective protection of wide ranging megafauna have been among the major concerns regarding the identification of such areas (Alpine and Hobday, 2007; Game et al., 2009; Hyrenbach et al., 2000). In addition, the difficulties to carry out studies at sea have contributed to the scarcity of MPA proposals in offshore areas (Lascelles et al., this issue).

New efforts are directed at addressing this gap, brought about by the increasing awareness of the threats facing the marine environment worldwide, including seabirds (BirdLife International, 2011; Butchart et al., 2004), and also the increasing facilities to study and monitor seabirds at sea (extensive long-term surveys and the upsurge of tracking technologies and analytical tools; e.g. Camphuysen et al., this issue; Le Corre et al., this issue; Louzao et al., 2009, 2011; Montevecchi et al., this issue; Oppel et al., this issue). These efforts are supported by increasing political willingness and commitment, backed by the Convention on Biological Diversity (CBD) target of protecting at least 10% of the World

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ocean's surface by 2020 (Lascelles et al., this issue). In accordance, BirdLife International has set among its priorities the extension of its Important Bird Area (IBA) Programme to the marine environment, with the aim of guiding the designation of MPAs for seabirds worldwide (BirdLife International, 2004, 2010a).

Within this frame, one of the first comprehensive initiatives to identify marine IBAs at national level was conducted in Spain (Arcos et al., 2009). Based on this initiative, we report here on the most novel contribution of the Spanish marine IBA inventory, the identification of hotspots for pelagic species in the open sea, which primarily represent important foraging grounds. The main aims of this paper are to: (1) depict the process to identify, assess the stability and delimit seabird foraging hotspots for pelagic species; and (2) describe the remaining steps from hotspot identification to IBA delimitation.

2. Material and methods

2.1. Study area

The present study is framed within the initiative of marine IBAs identification in Spain (Arcos et al., 2009). Here we focus on the Iberian Mediterranean shelf and the adjacent pelagic waters, from Almeria in the SW to the Spanish–French border in the NE (Fig. 1). Previous work in this region (Abelló et al., 2003; Arcos and Oro, 2002; Louzao et al., 2006) allowed to use longer datasets here than elsewhere in Spain, thus providing the best conditions to exemplify both the identification of seabird foraging hotspots and the assessment of their stability. The continental shelf is very narrow (ca. 3 km) in the south (Vera Gulf) and widens towards the centre of the region, reaching a width of up to 70 km off the Ebro Delta area; in the northernmost area the shelf becomes relatively narrow again, and is indented by submarine canyons (Salat, 1996). Ocean productivity is notoriously heterogeneous in the region, being influenced by marine currents (Atlantic waters flowing northwards in the SW and Mediterranean waters flowing southwards in the NE) and the input of freshwater run-off, which deliver large amounts of nutrients and fertilize the coastal waters (Arnau et al., 2004).

The Iberian Mediterranean marine region is of particular seabird conservation concern, as several sensitive species regularly occur there in high numbers, including Mediterranean endemic taxa: Cory's (Scopoli's) shearwater *Calonectris diomedea diomedea*, Balearic shearwater *Puffinus mauretanicus*, yelkouan shearwater *Puffinus*

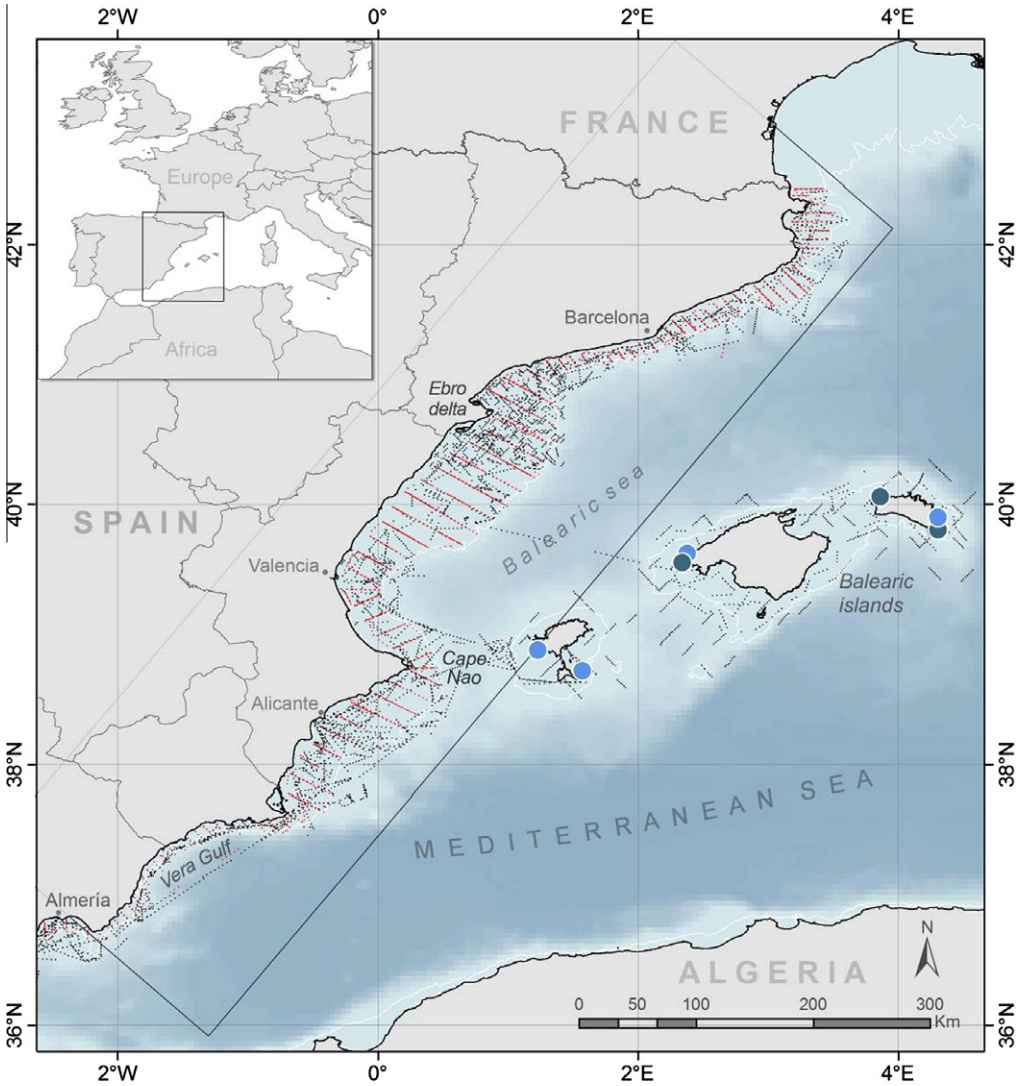


Fig. 1. Map of the study area (diagonal rectangle) and adjacent waters in the western Mediterranean. Boat-based transect locations (mid-position for the 10-min count units) are represented by small dots (black for the breeding and red for the non-breeding seasons), and the circles correspond to shearwater colonies where tracking was conducted (light for Balearic shearwaters, dark for Cory's shearwaters). Finally, the 200-m isobaths is also shown (white line). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

yelkouan, European (Mediterranean) storm-petrel *Hydrobates pelagicus melitensis*, European (Mediterranean) shag *Phalacrocorax aristotelis desmarestii*, and Audouin's gull *Larus audouinii* (BirdLife International, 2011; Zotier et al.,1999). Here we selected as examples three species of Procellariiforms, as representatives of the seabird "pelagic" community: Cory's and the Balearic shearwaters, and the European storm-petrel. Cory's shearwater and the European storm-petrel are summer visitors (March–October, breeding May–October), whereas the Balearic shearwater is present most of the year, mainly from October to June (breeding March–June).

2.2. Overview of the marine IBA identification process

For the identification of marine IBAs, four types of sites were considered, depending on the ecological reason for seabirds to use them (BirdLife International, 2010a): (1) non-breeding (coastal) concentrations; (2) areas for pelagic species; (3) seaward extensions to breeding colonies; and (4) migration bottlenecks. These sites could be eventually combined into a single IBA (see Section 2.7), but followed slightly different approaches to their identification. For the foraging hotspots for pelagic species (type 2), which are the focus of this paper, the process is described in full length in the following Sections 2.3–2.7, and is also outlined in Fig. 2.

2.3. Data collection

Fieldwork was focused on two main approaches, boat-based seabird counts and remote tracking of tagged individuals. The compilation of remote sensing data was also key to produce habitat species distribution models (SDMs hereafter; see Section 2.4).

2.3.1. Boat-based surveys

Within the study area we relied on information from two annual oceanographic surveys organized by the Spanish Institute of Oceanography (IEO), the MEDITS bottom trawl survey (late Spring, 4 years) and the ECOMED acoustic survey (late Autumn, 5 years), as well as a specific seabird survey around the Ebro Delta in Spring–Summer (3 years), within the period 2000–2007 (Table 1). Additional data from another 5 MEDITS cruises within the period 1999–2010 were also compiled and included in the validation of SDMs (Section 2.4), and as supporting information for hotspot delimitation (Section 2.5).

Seabird surveys followed the methodology proposed by Tasker et al. (1984): birds were counted within a 300 m strip transect band, at one or two sides ahead of the vessel depending on census conditions; snap-shot counts were used to count flying birds. Seabird observations were summed up into 10 min survey units, for which species density values were estimated (birds/km^2). Birds outside the transect band were also considered for presence/absence information. During the oceanographic surveys, stern counts of seabirds attending the vessel in experimental trawling operations were also recorded following Abelló et al. (2003), to complement transect data.

2.3.2. Individual remote tracking

Individual remote tracking relevant to the study area included breeding Cory's shearwaters from three colonies of the Balearic islands, using either Platform Terminal Transmitters (PTTs, 2005–2006) or Global Positioning System loggers (GPS, 2007), attached to the back feathers with TESA tape (Arcos et al., 2009; Louzao et al., 2009). PTT tracking data of Balearic shearwaters were also

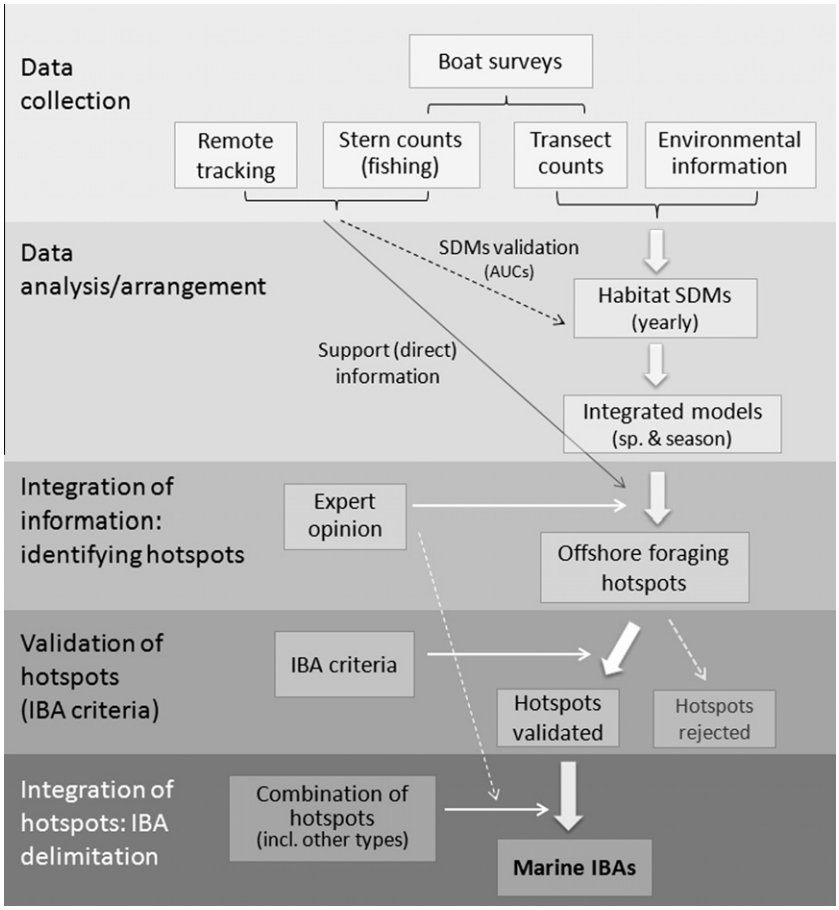


Fig. 2. Outline of the process of IBA identification, focusing on the foraging hotspots. See text for more details (Sections 2.3 through 2.7).

Table 1
Boat surveys effort for the three cruises conducted within the study area: number of transect units (10-min counts), number of experimental trawling operations for which stern seabird counts were conducted (for IEO cruises), and distance and area surveyed (during transects). For the MEDITS cruise, information from years for which species distribution models (SDMs) were not built (i.e. supporting/validating data) is presented separately.

Cruise	10-min counts	stern counts	Distance (km)	Area (km^2)	Period	
					Month	Years
ECOMED (IEO)	2256	30	7003.3	2897.8	Nov–Dec	2003–2007
MEDITS (IEO) – core years	1792	432	5167.9	2619.2	May–Jun	2000, 2002, 2006–2007
MEDITS (IEO) – support years	1341	278	3772.0	1885.2	May–Jun	1999, 2004–2005, 2008, 2010
Ebro Delta surveys	708	–	1186.7	629.3	May–Jun	2005–2007
TOTAL	6097	740	17 129.9	8031.4		1999–2010

used, taking advantage of previous work in the region by SEO/BirdLife (1999–2001; Ruiz and Martí, 2004). These tracking data are summarized in Table 2.

2.3.3. Environmental variables

Information on habitat features was compiled and used to build SDMs (see Section 2.4). Habitat variables were selected on the basis of data availability and potential biological relevance, after bibliographical revision and preliminary modeling trials. The selected variables included both static and dynamic features (Table 3), the latter being behind the variability that characterizes the marine environment.

Static features consisted of a set of measures related both to the topography of the marine environment (depth, slope, distance to coast and distance to shelf-break) and to the location of breeding colonies. These variables were calculated from ETOPOv2 bathymetric data (NGDC and NOAA, 2006) and GSHHS shoreline (Wessel and Smith, 1996) (Table 3).

Dynamic features were derived from time series of remote sensing data, in particular seasonal and monthly Terra MODIS SST (Sea Surface Temperature 11 μ daytime) and Aqua MODIS Chl-a (Chlorophyll-a concentration) imagery from Ocean Color Web (Feldman and McClain, 2007) (Table 3). We also introduced the distance to oceanic fronts as a surrogate of food availability (Louzao et al., 2006; Valavanis et al., 2005). Oceanic fronts were computed on the basis of monthly Terra MODIS SST imagery using a Sobel edge detection filter (Praca and Gannier, 2008). From the resulting temperature gradients, oceanic fronts were identified as the areas with more pronounced gradients, here defined as areas above the 95 percentile values. Once identified, distance to the fronts was calculated by means of Cost Distance methodology implemented in ESRI Spatial Analyst. The temporal definition of this set of variables was necessarily linked to the timing of the oceanographic surveys. Thus, we selected (1) eight seasonal variables, related to SST and Chl-a for the four (3-month) seasons previous to the surveys, assuming that the overall productivity of the environment is conditioned by SST and Chl-a values during the previous year; and (2) three monthly variables related to SST, Chl-a and distance to oceanic fronts which coincided with the month with the highest frequency of surveys, assuming that areas where food is concentrated are related to productivity phenomena that determine species' short-term distributions.

2.4. Data analysis

This step of the process was focused on the production of SDMs, as they allowed capturing the relationship between seabirds and their habitat and to assess the temporal variability of such habitat. This reduced the biases related to direct seabird data, which represent snap-shots in time and space. However, boat-based and remote tracking data were also arranged to help their visualization and support the identification of seabird foraging hotspots.

2.4.1. Model construction

SDMs were based on transect count data, and were built for each species, for the two most ecologically relevant seasons (breeding and/or non-breeding) on a yearly basis, according to the availability of oceanographic surveys (Table 1). The modeled area included the Balearic Islands, though here we report on the results for the study area as defined in Fig. 1. We used a modeling method based on maximum entropy implemented in the software MAXENT (Phillips et al., 2006), because of its flexibility when handling different kind of species data and responses. The basic principle of the statistical approach implemented in MAXENT is the estimation of the probability of a distribution with maximum entropy (that is, the most spread out or the most uniform distribution) given a set of conditions (the environmental characteristics of the site where the species is detected) that shows our incomplete information regarding the distribution of the species (Phillips et al., 2006). This approach based on presence but not absence data seems particularly appropriate in the seascape, where a low encounter probability for many species is to be expected and consequently many false negatives occur (Péron et al., 2010).

The general approach of MAXENT also offers great adaptability and allows incorporating information related to observed seabird numbers to give greater importance to areas where a species is more abundant (Herrando et al., 2011). Preliminary tests showed that abundance improved the predictive strength of the SDMs. Hence, models were developed from quantitative data in which relative abundance categories were used leading to an increasing number of presences. Six abundance categories were defined: 1 for a single individual and for observations from outside the transect band, 2 for 2–5 individuals, 3 for 6–10 individuals, 4 for 11–25 individuals, 5 for 26–100 individuals, and 6 for more than 100 individuals. These intervals were defined considering the existing

Table 2
Remote tracking survey effort for Cory's *Calonectris diomedea* and Balearic shearwaters *Puffinus mauretanicus*. These birds were tagged in their breeding colonies at the Balearic Islands, but foraged extensively within the study area. See Section 2.3.2 for details.

Species	Device	Colonies (*n*)	Birds tracked (*n*)	Tagging locations (*n*)	Period	
					Month	Years
Calonectris diomedea	PTT	2	18	196	Aug–Sep	2005–2006
	GPS	3	29	22 422	Aug–Sep	2007
Puffinus mauretanicus	PTT	4	18	573	Jun–Jul	1999–2001
Total		7	65	23 191	Jun–Sep	1999–2007

Table 3
Habitat variables used to produce species distribution models. To build the models, all data sources were adjusted to a resolution of 2.5' (≈4.5 km) pixels, which was the standard format for most variables. See Section 2.3.3 for details.

Variable	Spatial resolution	Temporal resolution	Source
Sea depth	2′	Constant	ETOPO (http://www.ngdc.noaa.gov)
Slope	2′	Constant	Derived from ETOPO
Distance to coast	2.5′	Constant	Derived from GHSS *shoreline* (http://www.ngdc.noaa.gov)
Distance to shelf-break	2.5′	Constant	Derived from ETOPO
Distance to breeding colonies	2.5′	Constant	Method CostDistance (GIS). Data from Martí and Del Moral (2003)
Sea surface temperature (SST)	2.5′	Monthly & Seasonal	SST (Terra MODIS; http://oceancolor.gsfc.nasa.gov/)
Chlorophyll concentration (Chl-a)	2.5′	Monthly & Seasonal	Chlorophyll (Aqua Modis; http://oceancolor.gsfc.nasa.gov/)
Distance to productivity fronts	2.5′	Monthly	Derived from monthly Terra MODIS SST, using Sobel filter and Cost Distance

dataset (with a high proportion of the observations including few birds, and a few counts accounting for large groups), and taking into account expert opinion.

SDMs were run on the 100% of training data taking advantage of relative abundance data to provide the best estimates of the species potential distribution. Outputs were projected to the resolution fixed by environmental information, which usually was 2.5 minutes of arc ('), i.e. about 4.5 km pixels (Table 3). Default parameterization of MAXENT was used to develop the SDMs, limiting the response to environmental variables to linear and quadratic functions. All available environmental variables (5 static + 11 dynamic) were included, except distance to colonies, which was only considered for the breeding season, when these sites exert their main influence on seabird distribution patterns (Orians and Pearson, 1979). Seasonal and monthly Chl-a and seasonal SST were not available for 2000 and 2002, hence the corresponding breeding season SDMs included only two dynamic variables (i.e. monthly SST and distance to oceanic fronts). For 1999 only static variables were available, and models have not been included here. Finally, MEDITS data for 2004 and 2005 were not modeled as were provided by an external observer for complementation, and only stern counts were available for MEDITS 2008 and 2010.

2.4.2. Model evaluation

The predictive reliability of the models was assessed in two ways. First, model performance was estimated with the AUC (Area Under the Curve) generated between the SDMs predictions and presence/absence data from surveys used for model building. The AUC of the ROC curve (Receiver Operating Characteristics) provides a measure of the models predictive capability ranging between 0.5 (no predictive power) and 1 (a perfect model) (Boyce et al., 2002). This metrics was complemented measuring the strength of linear dependence between predictions and relative abundance categories (1–6) based on the Pearson product-moment correlation coefficient (PCC) (Phillips et al., 2009). Second, we used the AUC to test to what extent predictions produced by SDMs matched with data derived from surveys available from other years, as a measure of hotspot stability over time. Thus, seasonal SDMs from a given year were assessed with presence/absence data derived from transect and stern counts (breeding season) conducted on surveys from other years, including years for which models were not available (Table 1). Computations were made with "PresenceAbsence" and "Hmisc" libraries implemented in R software.

2.4.3. Models integration

Hierarchically prioritized maps were created from SDMs to highlight the best seabird areas (for each species, season and year), using two simple and effective approaches with strong ecological components. Firstly, we defined as presence areas (in terms of prevalence of the data used in the model development) those with habitat suitability values above the lowest 10% percentile. Secondly, within the presence areas three scores of habitat suitability were used (1, 2, and 3, from low to high quality), defined by the following thresholds: (1) the average mean of the suitable values within the areas of presence; and (2) the average mean of the values above the previous threshold (Herrando et al., 2011).

For each species and season we combined the models of different years, by averaging the scores defined above. We then defined three categories of habitat quality over time: (1) moderate (averaged score from >1.5 to 2); good (>2–2.5); and (3) optimal (>2.5–3). This way we combined habitat suitability and stability, as any area above score 2 (which was used as a guiding baseline for the identification of hotspots, see Section 2.5) would be the result of repeated years of moderate to high annual scores.

2.4.4. Arrangement of direct seabird information

Direct information on seabird distribution patterns, as obtained from boat surveys and remote tracking, were arranged in a way that helped their visualization, thus optimizing their contribution to the integration of data sources (Section 2.5). BirdLife International (2010a) recommendations were taken into account. Boat-based data were represented selecting the upper 95% percentile of the positive values (i.e. presence data), as well as values above the mean of positive values, to reduce the confusion created by a large number of observations (Table 1) when plotted in a map. This way the areas of highest densities were highlighted. For tracking data, 25%, 50% and 75% kernels were used to highlight the most used areas. As the aim was to use this information just for support, the smoothing factor was selected arbitrarily at $h = 0.1$ for PTTs and $h = 0.05$ for GPSs, taking in consideration the adequacy of the results to the raw data. Kernels were produced independently for every year, colony and species.

2.5. Integration of data sources (intra-specific): identification of hotspots

Once all available spatial information had been arranged, hotspots for each seabird species (and relevant season) were identified and delimited. This process was primarily guided by the integrated SDMs, for which optimal areas were almost always selected and good areas most often helped to delimit the hotspots (i.e. averaged scores above 2 were prioritized). However, direct seabird information (i.e. boat-based and tracking data) did also play a role, so that: (1) hotspots revealed by SDMs were only considered if direct data supported their relevance and (2) direct data independent of the SDMs (i.e. not used for modeling) were also used to set the limits, allowing for deviations from the models when obvious hotspots were highlighted and appeared relevant. Moreover, exceptionally a hotspot was identified based on the overlap of two or more independent layers clearly highlighting the site, even if SDMs did not provide relevant support. Thus the identification and delimitation of hotspots was partly subjective. To maximize the rigor of this process, however, it was guided by expert opinion. This culminated in a small workshop with over 10 people with experience on

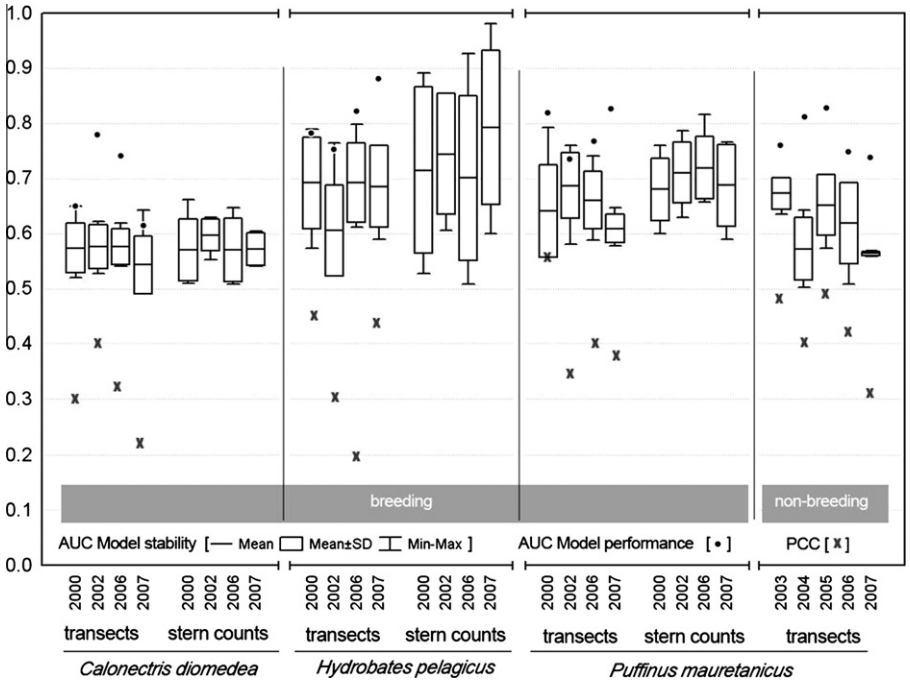


Fig. 3. Habitat species distribution models (SDMs) validation for Cory's shearwater and the European storm-petrel (breeding period), and the Balearic shearwater (breeding and non-breeding periods), on a year basis. Dots correspond to the AUC values resulting of validating models with the data used to build them (i.e. transect data for the same year), and are used to determine model performance. Box plots correspond to the AUC values obtained when validating models with independent data (transect counts from other years, and stern counts during trawling operations), which provide a measure of model stability across years. Finally, Pearson correlation coefficient (PCC) values indicate the relationship between predictions and relative abundance (range: −1 to 1). See Section 2.4.2 for details.

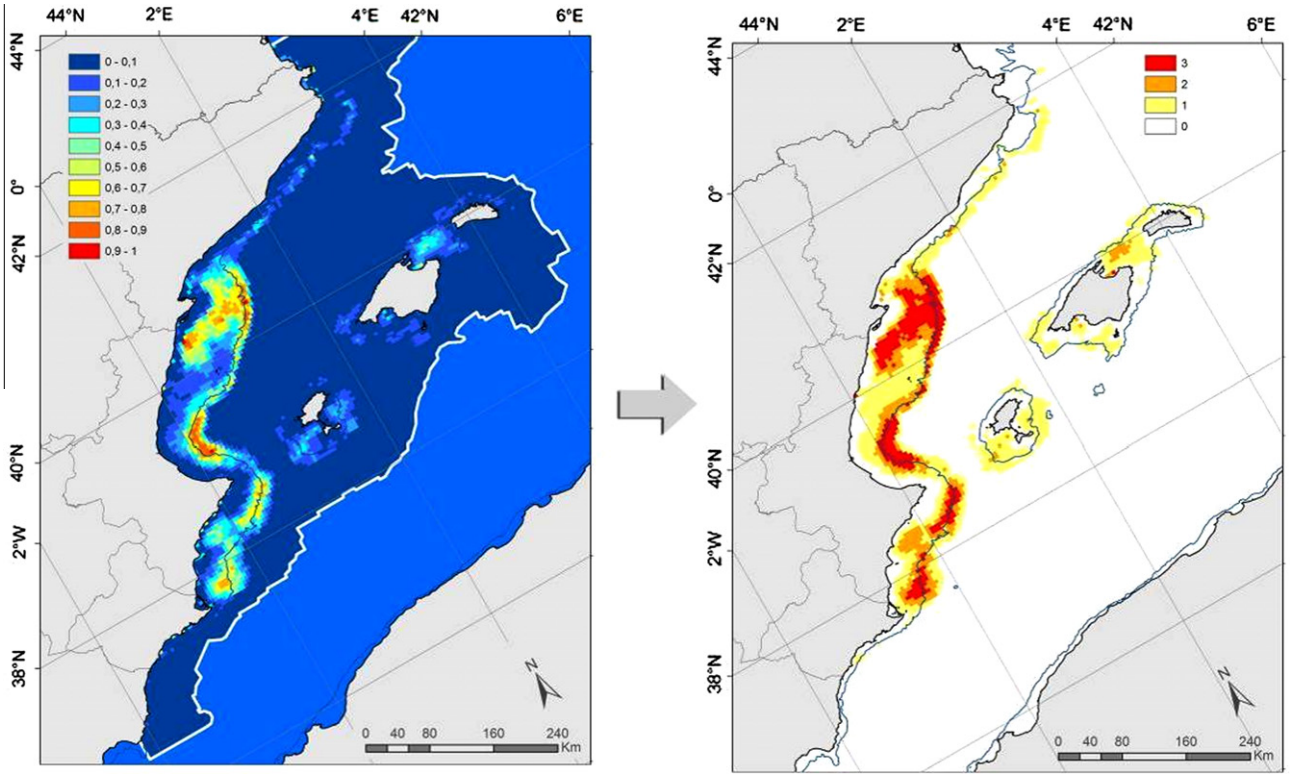


Fig. 4. Categorization of an annual model, taking as example the European storm-petrel (breeding season, 2007). The left figure shows habitat suitability values on a continuum from 0 (low) to 1 (optimal). On the right figure these values have been converted into in four categories, from 0 ("no presence") to 3 (highly suitable areas). Only categories 1 (yellow), 2 (orange), and 3 (red) are represented. See Section 2.4.3 for details. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

diverse relevant issues: the local seabird community and marine environment, habitat modeling, IBA criteria, BirdLife International strategy, and similar projects in other parts of the world.

2.6. Application of BirdLife International IBA criteria to validate the seabird hotspots

To qualify as an IBA, a given area requires meeting one or more of a series of objective, numerical criteria established by BirdLife International (Heath and Evans, 2000). These criteria allow assessing the ornithological importance of the area in an international context, thus ensuring that sites are comparable throughout the globe. In simple terms, a site meets IBA criteria if it regularly holds over 1% of the global (A), regional (B, Europe) or sub-regional (C, European Union) population of a given species. Species of special conservation concern can also validate IBAs with lower numbers.

The IBA criteria were used to validate or reject the hotspots identified following the previous steps. If a hotspot regularly held a significant number of individuals of a given seabird species (according to the thresholds set by the corresponding IBA criteria), it was validated as meriting IBA consideration. Otherwise, the hotspot was disregarded.

To assess seabird numbers in a hotspot, density values were averaged from all boat transect-counts within the hotspot (per species and season) and these estimates were projected to the whole hotspot area, provided that these counts were representative in number and coverage. Bootstrap resampling was used to assess confidence intervals (Quinn and Keough, 2002). This provided a figure of total birds using the area 'simultaneously'. These figures should be regarded as conservative, as turnover rates were not considered.

2.7. Integration of seabird hotspots (inter-species) and final delimitation of marine IBAs

Once all foraging hotspots had been identified and validated for each species and season, we set the final boundaries of the marine IBAs. This process incorporated other types of seabird hotspots (e.g. seaward extensions to breeding colonies), and all the species for which relevant sites had been identified and validated. If different seabird hotspots partly overlapped, they were combined to form a single IBA, provided that it made biological sense (i.e. the relevant habitat features were continuous, as well as the overall seabird distribution pattern observed). The final boundaries of marine IBAs consisted of straight lines to facilitate their recognition by marine stakeholders, key to their effective management once protected. When different hotspots were combined to form a larger IBA, seabird numbers occurring there were re-estimated taking into account the new area coverage, and IBA criteria were re-assessed accordingly.

3. Results

The identification of seabird foraging hotspots within the study area was based on a relatively large dataset of boat-based counts and tracking studies over a period of 11 years, including the data used for validation. In total we used boat data from 6097 transect units (10 min counts) and 740 stern-counts along 17 cruises, counting across 17,130 km and covering over 8000 km^2 (Table 1). Of these, 12 cruises contributed to build the SDMs. Tracking data were obtained for Cory's shearwaters (three colonies, 47 individuals including PTTs and GPSs), and PTT data from another 18 Balearic shearwaters were also used (Table 2). Habitat variables were compiled for 2000–2007 (Table 3).

For each of the three study species 4 annual SDMs were generated for the breeding season, whereas a further 5 annual SDMs were built for the Balearic shearwater in the non-breeding season (Table 1). SMD performance (i.e. evaluation based on data used to build the models) was reasonably good, with all SMDs achieving AUC values above 0.7 (i.e. reasonable discrimination power), with the exception of Cory's shearwater in 2000 and 2007 (Fig. 3). As for SMD stability (i.e. evaluation from independent data), AUC values were slightly lower, as expected , but still quite good (Fig. 3). In both cases AUCs were consistent between years and sources of validating information, but showed slight differences between species, with Cory's shearwaters displaying the lowest values and European storm-petrels the highest (Fig. 3). Regarding the strength

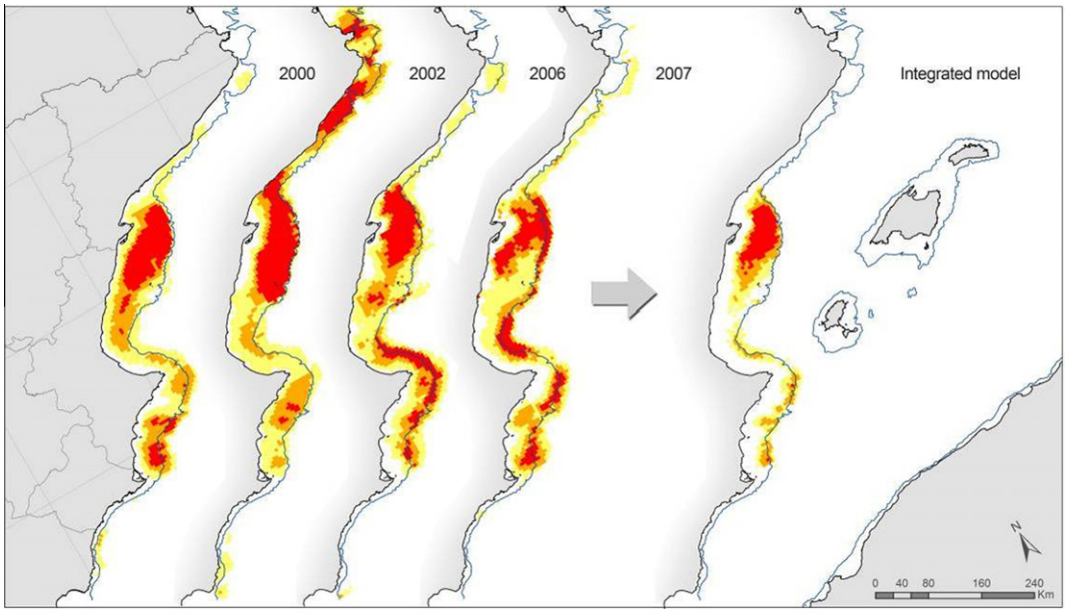


Fig. 5. Integration of models across different years, taking as example the European storm-petrel (breeding season). Categorized models for different years were averaged, and resulted in an integrated model that showed moderate areas (yellow, averaged score from >1.5 to 2); good (orange, >2–2.5); and optimal (red, >2.5–3). Note that this is a conservative approach that only enhances those areas that are good or optimal on a regular basis (i.e. stable); for instance, optimal areas in an unusual year such as 2002 are not reflected in the final map. See Section 2.4.3 for details. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

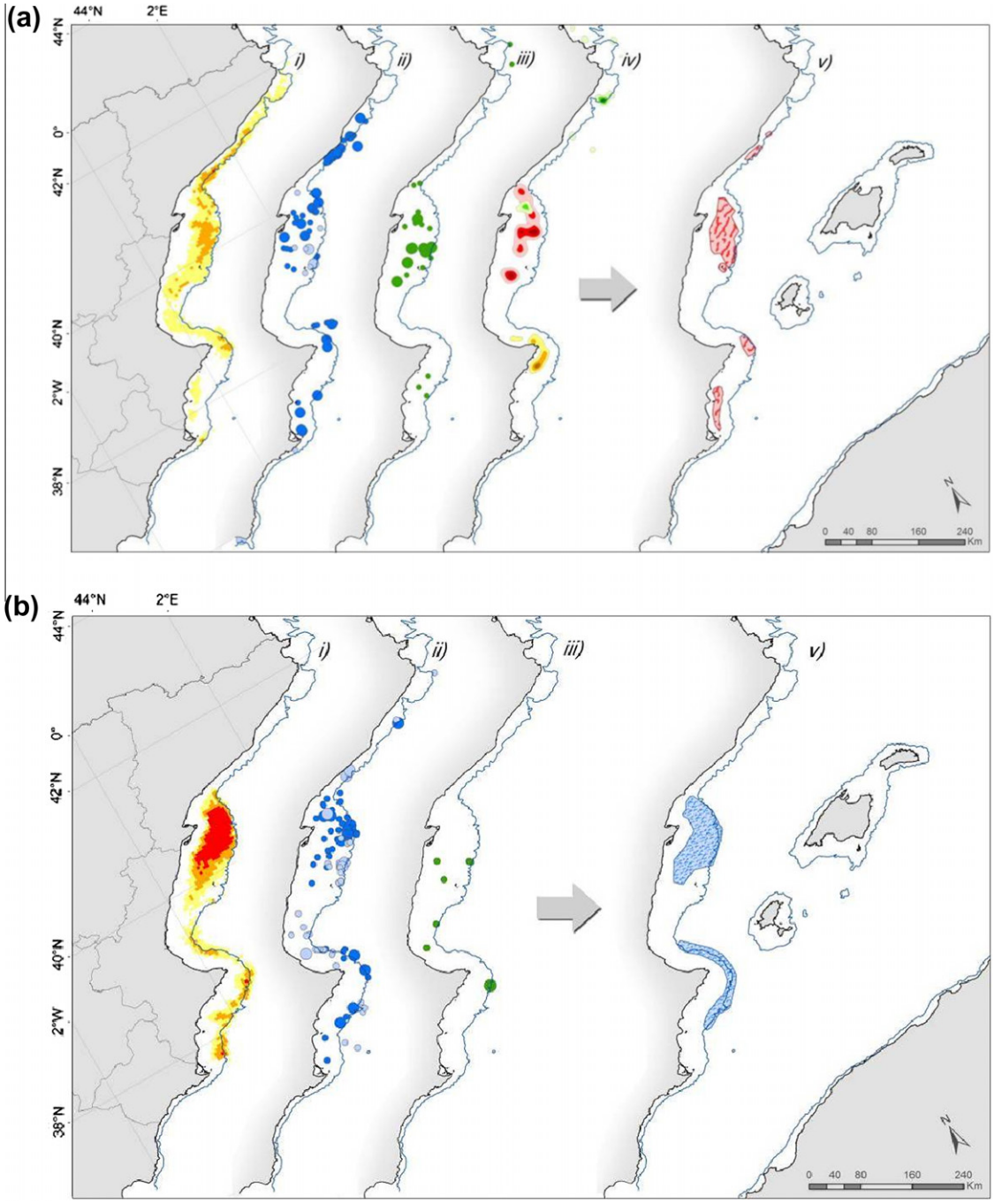


Fig. 6. Integration of information to identify and delimitate foraging hotspots for the three study species: (a) Cory's shearwater, breeding; (b) European storm-petrel, breeding; (c) Balearic shearwater, breeding; and (d) Balearic shearwater, non-breeding. The process starts with the integrated habitat models ("i"), and incorporates any available direct data to refine the identification and delimitation of the final hotspots ("v"), being mediated by expert opinion. Circles ("ii" and "iii") correspond to boat-based count data, and represent the density/abundance values above the 95% percentile (large circles) and above the mean (small circles) of positive values; "ii" correspond to transect data (dark dots, data used to build the models; light dots, data from years not used for modeling), and "iii" to stern counts during trawling operations. Tracking data is represented by kernels ("iv"; dark color, 25%; medium, 50%; light 75%). See Section 2.5 for details. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

of relation between predictions and relative abundance, for all models there was a moderate linear dependence as measured by the PCC (Fig. 3), with a high level of statistical significance in all cases ($p < 0.001$).

The categorization of SDMs and the subsequent integration of different years are shown taking as example the European storm-petrel (Figs. 4 and 5, respectively). Once integrated, models usually showed consistency with both related data (i.e. transects used to build the models) and independent data (non-related boat counts, tracking locations), allowing to easily identify and delimit the key foraging hotspots (Fig. 6). Some sites, however, were not so obvious and expert opinion had a major role on their delimitation (see Section 2.5; Fig. 6).

In total 13 foraging hotspots were identified for the three study species (Table 4, Figs. 6 and 7). These hotspots ranged from strictly coastal areas (for Balearic shearwaters in Autumn–Winter) to outer

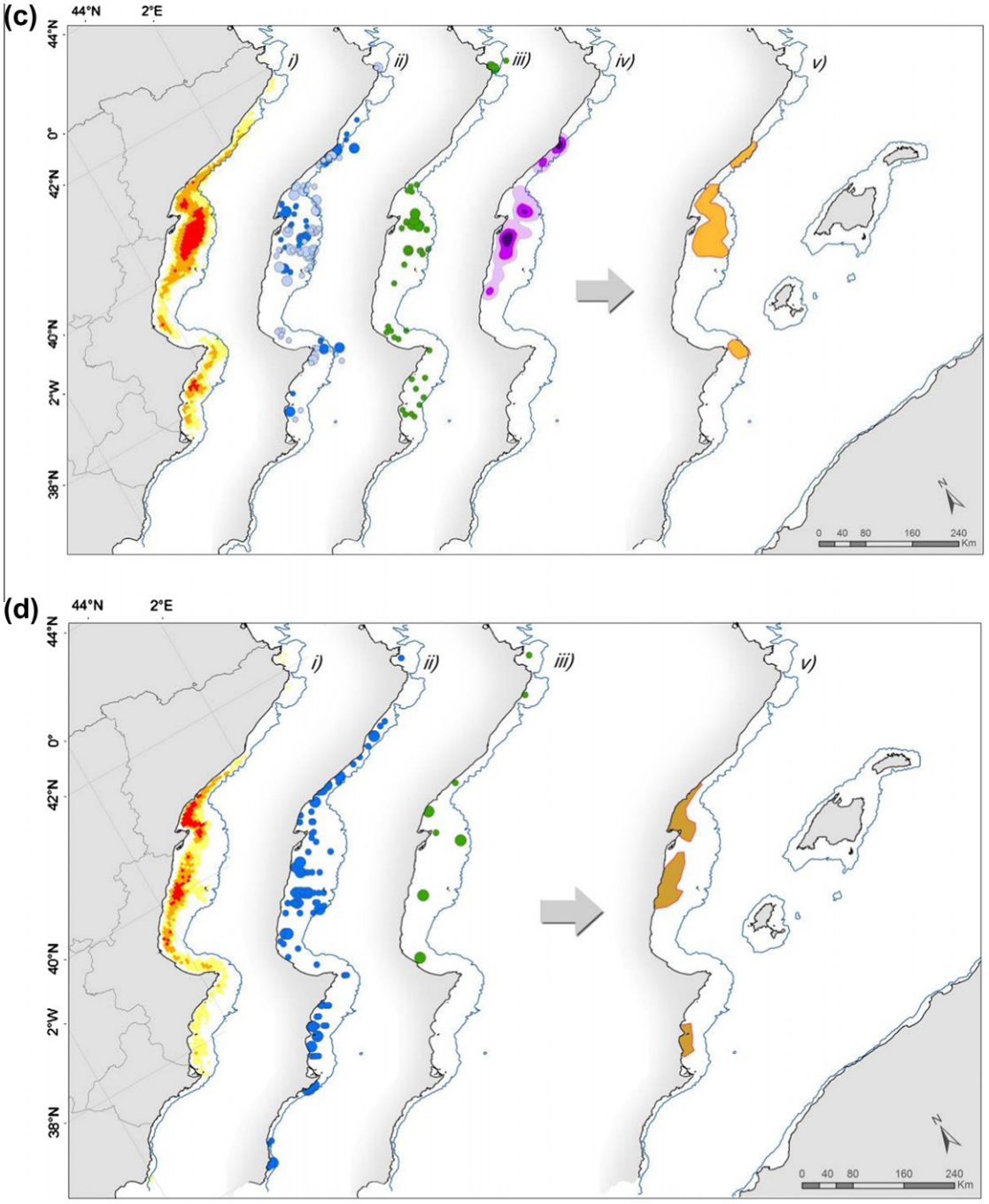


Fig. 6 (*continued*)

shelf and continental slope areas (especially for the European storm-petrel). Three hotspots were disregarded following IBA criteria, all of them corresponding to Cory's shearwater (Table 4). The remaining 10 sites were combined with seaward extensions for Cory's shearwater and the European storm-petrel, as well as with hotspots of any type (see Section 2.2) for other eight seabird species, and altogether contributed to set the limits of four out of eight marine IBAs identified in the study area, representing over 90% of them in terms of surface (Fig. 7). Only one of these IBAs, once all the hotspots were integrated, was disconnected from the coastline. The remaining four IBAs were primarily identified as seaward extensions to colonies, except one that included a foraging hotspot for the yelkouan shearwater.

4. Discussion

4.1. Location and stability of offshore seabird hotspots

The establishment of MPAs for pelagic seabirds faces several difficulties including the wide-ranging nature of these organisms (that makes necessary protecting relatively large areas to be effective), the dynamic nature of the marine environment (which poses a challenge regarding the stability of the protected sites), the lack of obvious boundaries to set MPA limits, and the difficulties to carry out extensive studies in the open sea (Alpine and Hobday, 2007; Game et al., 2009; Hyrenbach et al., 2000; Lascelles et al., this issue). These constrains have often led to suggest that the

offshore MPA approach is not appropriate to ensure seabird conservation (Boersma and Parrish, 1999). However, this view has started to change in recent years, due to the increasing perception of the threats that seabirds face in the open oceans, and also the increasing facilities to address the identification of offshore hotspots, as well as to assess their stability over time (Game et al., 2009; Lascelles et al., this issue). For instance, areas that could merit MPA designation in the Southern Ocean have been proposed using long-term datasets of boat-based seabird counts (Harris et al., 2007), and the compilation of tracking data has helped to identify seabird hotspots in the open seas (BirdLife International, 2004). Boat-count and tracking data are subject to potentially strong biases, as they just represent snap-shots in time and space, but they can be regarded as complementary, and their combined

Table 4
Hotspots identified for the breeding (all three study specie) and non-breeding seasons (Balearic shearwater). For each hotspot the area and the mean number of birds estimated to be present "simultaneously" are presented, as well as the corresponding 95% Confidence Intervals, within brackets. The necessary thresholds to meet IBA criteria are also shown (both global, A, and regional, B). Finally, last column shows if hotspots were validated or not by IBA criteria, also indicating if their value was global or regional.

Species	Season	Hotspot location	Area (km^2)	Averaged bird numbers	IBA threshold	Validated by IBA criteria
Cory's shearwater	Breeding	Barcelona-N	52.0	111 (34–190)	A: 8700	No
		Barcelona-S	1474.8	1189 (542–2068)	B: 1090	Yes (B)
		Ebro Delta	2883.7	1600 (897–2439)		Yes (B)
		Cape Nao	456.5	458 (107–1008)		No
		Alicante-S	665.4	257 (43–589)		No
European storm-petrel	Breeding	Ebro Delta	4375.8	3783 (2574–5330)	A: 15,000	Yes (B)
		Cape Nao	2271.3	1899 (1185–2691)	B: 300	Yes (B)
Balearic shearwater	Breeding	Barcelona	551.3	2230 (691–4161)	A & B: 66	Yes (A)
		Ebro Delta	3872.9	4940 (3219–7174)		Yes (A)
		Cape Nao	643.4	896 (289–1904)		Yes (A)
	Non-breeding	Ebro Delta-N	1355.7	6682 (2064–12 807)		Yes (A)
		Ebro Delta-S	1865.8	5307 (3151–8083)		Yes (A)
		Alicante-S	666.2	1926 (927–3180)		Yes (A)

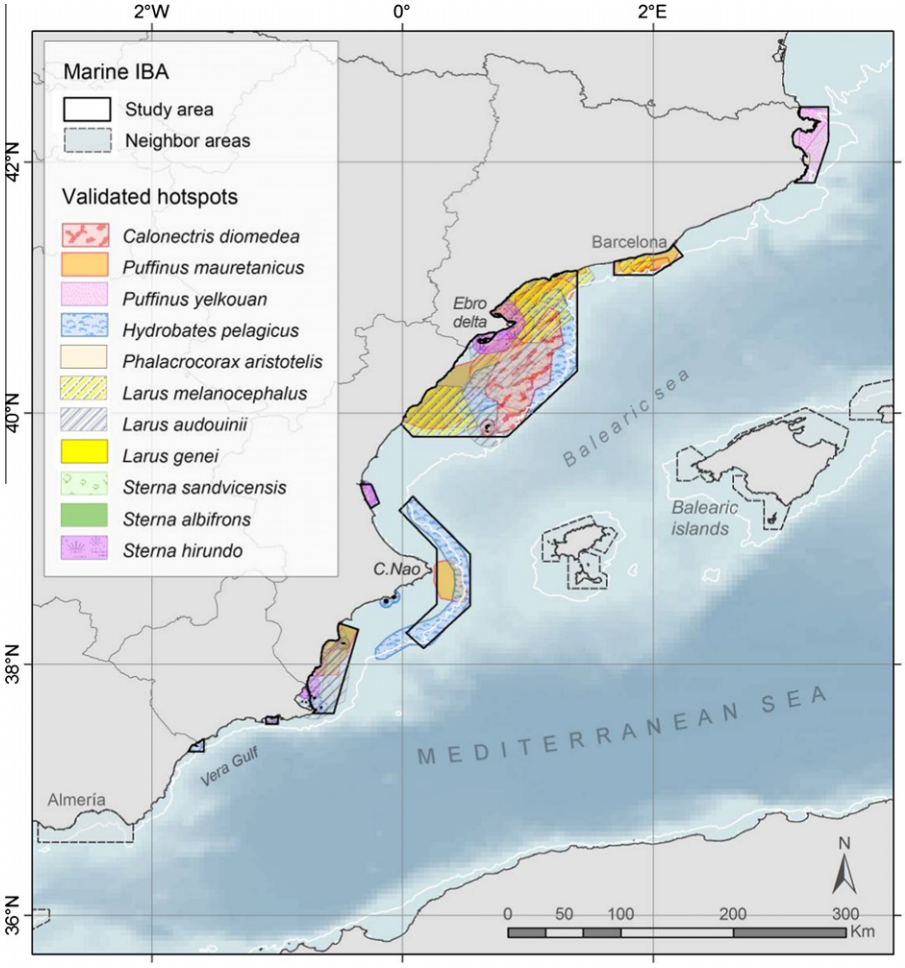


Fig. 7. Marine IBA delimitation process. Validated foraging hotspots for the three study species were combined with other types of hotspots (seaward extensions to colonies), as well as hotspots identified for other species (both foraging areas and colony extensions). The limits of the marine IBAs were set to encompass the hotspots the best possible way using straight lines to simplify future management. All the hotspots shown in the figure accomplished the required IBA criteria. See Section 2.7 for details.

use has been a step forward for the identification of offshore MPAs (e.g. Hyrenbach et al., 2006). A further and significant step has been the development of species distribution modeling techniques incorporating habitat descriptors, which allow capturing the relationship between seabirds and their habitat and to assess the temporal variability of such habitat, thus contributing to reduce data bias and provide more accurate MPA proposals (e.g. Le Corre et al., this issue; Louzao et al., 2006, 2011; Oppel et al., this issue; Nur et al., 2011).

The present study integrates all these approaches and represents a sound example of hotspot identification for pelagic seabirds. Indeed, the study is based on reasonably large datasets of both boat-based counts and tracking information over a wide area, thus allowing combining complementary data to identify hotspots and, to some degree, assess their stability at relatively large spatial and temporal scales. The process was objectively structured so that objective, reproducible information could be generated through the use of innovative methodologies. SDMs played a fundamental role here, largely contributing to the identification and delimitation of seabird foraging hotspots. The SDMs integration process was a particularly good example of how models allow assessing hotspot stability, and to disregard areas that are subject to strong inter-year variability, a process supported by the direct seabird information (i.e. boat-count and tracking data). Expert opinion was also a key piece, allowing supervising the process of hotspot delimitation, which necessarily had to incorporate a subjective component when combining several data sources to set limits in a dynamic and roughly continuous habitat. Finally, for hotspots to be considered as meriting IBA consideration, they had to meet BirdLife International IBA criteria, as a last validation step. It is worth to note that this study was integrated into a larger project that ended up with an inventory of marine IBAs for the whole of Spanish waters, now firmly proposed to become MPAs (see Section 4.2).

In spite of these achievements, the study had also some limitations worth to be mentioned. Firstly, all the hotspots highlighted here were located over the continental shelf and slope, coinciding with areas of high productivity and high prey availability (Arnau et al., 2004; Bellido et al., 2008; Salat, 1996). These areas are related to features direct or indirectly influenced by topography, such as river plumes and oceanic fronts, which explains their value for seabirds (Ballance, 2007; Louzao et al., 2006; Nur et al., 2011). Therefore, the identification of truly oceanic areas, unrelated to obvious topographical features, still poses a challenge to the identification of seabird foraging hotspots. This is particularly so for the most unpredictable tropical and sub-tropical areas (Weimerskirch, 2007), which might require flexible approaches to MPAs (Hyrenbach et al., 2000; Game et al., 2009; Lascelles et al., this issue). Secondly, even in the case of sites coinciding with topographical features, we cannot guarantee their stability in the long term under the current scenario of rapid environmental change, though this could also apply to protected sites inland (Hannah et al., 2007). Thirdly, behavioral information from boat observations was collected but not analyzed, and tracking devices did not include additional recorders of activity, and therefore there is no sound proof that the hotspots identified were actually foraging areas. However, behavioral information derived from GPS movements (Louzao et al, 2009) and expert opinion input (including experience from the boat observers) were consistent at pointing the identified hotspots as foraging areas. Fourthly, the usefulness of the MPA approach could differ between species, as suggested by the different performance of the models presented here (AUC values), probably linked to the particular ecological requirements of each species (McPherson and Jetz, 2007). Cory's shearwater presented the most ubiquitous distribution, and is also the most widespread of the three study species (BirdLife International, 2011), suggesting that MPA designation for this Procellariiform would not be so effective as for the Balearic shearwater and the European storm-petrel, which showed higher predictability. Other species for which foraging hotspots were identified within the study area are the yelkouan shearwater, the Mediterranean gull *Larus melanocephalus* and Audouin's gull. Finally, when considering the whole inventory of Spanish marine IBAs, other areas and/or species counted with more limited datasets, and it was not always possible to count with robust SDMs to guide the process of hotspot identification.

4.2. Implications for conservation

The present study was part of a more ambitious project to identify marine IBAs in Spain, which was conducted in parallel to a sister project in Portugal (Ramírez et al., 2008). There was strong feed-back between both projects, which jointly contributed substantially to the "marine IBA toolkit" (BirdLife International, 2010a), a living document that is intended to provide guidance to any new initiative on marine IBA identification worldwide.

The Spanish marine IBA inventory produced a total of 44 marine IBAs, covering altogether over 50,000 km^2 (i.e. more than 5% of the Spanish waters). These areas have been recently acknowledged and proposed as Special Protection Areas (SPAs) by the Spanish Government, within the Natura 2000 network framework (BirdLife International, 2010b; European Commission, 2007), and once approved will represent the first complete national inventory of SPAs/MPAs for seabirds worldwide. These sites, along with the colonies that already enjoy some degree of protection, will provide a coherent network of protected areas combining the needs of seabirds throughout their life cycle, provided that these are undertaken within Spanish waters. International cooperation will be essential to extend the protection needs of these birds to other countries and international waters, given the large-scale movements of many seabird species (Croxall, 2008).

Along with the designation of MPAs/SPAs, it will be necessary to develop and implement appropriate management plans to gain effective protection for the seabirds and their habitats (Hooker and Gerber, 2004; Norse et al., 2005). This will require a detailed diagnosis of the threats to seabirds on a site by site basis, and the development of management tools that mitigate them. Of the serious threats that seabirds face in the marine environment (Boersma et al., 2002), some will likely be difficult to address on a site-by-site basis, such as diffuse pollution and climate change. But other serious threats can be handled more easily, particularly seabird bycatch (Anderson et al., 2011; Karpouzi et al., 2007). MPAs placed near the coast, as those proposed here, could also address issues related with pollution (especially point-source events), recreational activities, and industrial development (e.g. windfarms) (Pedersen et al., 2009; Pichegru et al., 2010; Ronconi et al., 2002; Velando and Munilla, 2011). Finally, it is also very important to complement these site-based conservation efforts with other regulations at the wider scale, an issue for which Marine Spatial Planning brings new opportunities (Ehler and Douvere, 2009).

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Combined Spatio-Temporal Impacts of Climate and Longline Fisheries on the Survival of a Trans-Equatorial Marine Migrant

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Abstract

Predicting the impact of human activities and their derivable consequences, such as global warming or direct wildlife mortality, is increasingly relevant in our changing world. Due to their particular life history traits, long-lived migrants are amongst the most endangered and sensitive group of animals to these harming effects. Our ability to identify and quantify such anthropogenic threats in both breeding and wintering grounds is, therefore, of key importance in the field of conservation biology. Using long-term capture-recapture data (34 years, 4557 individuals) and year-round tracking data (4 years, 100 individuals) of a trans-equatorial migrant, the Cory's shearwater (*Calonectris diomedea*), we investigated the impact of longline fisheries and climatic variables in both breeding and wintering areas on the most important demographic trait of this seabird, i.e. adult survival. Annual adult survival probability was estimated at 0.914 ± 0.022 on average, declining throughout 1978–1999 but recovering during the last decade (2005–2011). Our results suggest that both the incidental bycatch associated with longline fisheries and high sea surface temperatures (indirectly linked to food availability; SST) increased mortality rates during the long breeding season (March-October). Shearwater survival was also negatively affected during the short non-breeding season (December-February) by positive episodes of the Southern Oscillation Index (SOI). Indirect negative effects of climate at both breeding (SST) and wintering grounds (SOI) had a greater impact on survival than longliner activity, and indeed these climatic factors are those which are expected to present more unfavourable trends in the future. Our work underlines the importance of considering both breeding and wintering habitats as well as precise schedules/phenology when assessing the global role of the local impacts on the dynamics of migratory species.

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Introduction

Understanding population dynamics of long-lived marine vertebrates is essential to identify relevant human impacts for the sustainability of our oceans [1,2]. Due to the complexity of their annual cycles, this knowledge is particularly important for long-distance migrants as these anthropogenic threats might impact them over a larger geographical range, while breeding, migrating or at their wintering grounds [3,4].

We have now clear evidences that human activities and resulting global changes are strongly impacting marine ecosystems [2,5,6]. A major threat for marine top predators is the increasing industrial fisheries occurring in most of our oceans [7,8]. Effects of these fisheries on apical species may be negative, increasing incidental mortality [9–11], impoverishing food webs and reducing fish stocks [12], but also positive either directly through discards which provide additional food [13,14] or indirectly by removing larger predatory fish (i.e. competitors). From the conservation point of view, fishery sustainability represents a sensitive, socio-economic issue and data regarding these collateral effects on marine top predators is scarce and poorly reported by the competent authorities [15–17], generating a poor knowledge on the real impact of commercial fisheries on marine megafauna. Global warming is also inducing changes in the distribution and abundance of marine prey and will therefore affect the dynamics of their predators [18–21]. Several long-term studies have documented links between climate and population dynamics through both local fluctuations in oceanographic parameters (e.g. sea surface temperature, SST; [22]) and large-scale cyclic patterns (e.g. Southern Oscillation Index, SOI; [23,24]). The fact that the increasing global warming especially impacts polar environments [25,26], might bias the bulk of climate-induced demography research towards Arctic and Antarctic species. In this sense, little is known about the potential

effects of local and large-scale climatic phenomena on the productivity of temperate to tropical oceanic water masses.

Assessing the precise interactions between these changes and marine predator dynamics will therefore be critical for effective conservation management. In this sense, long-lived predator species are rather the most endangered and sensitive group of animals to environmental perturbation due to their extreme life history traits (e.g. high survival, low fecundity and an usually considerable degree of specialization; [9,27]). Moreover, migratory predators, inhabiting very different water masses throughout their annual cycles, are particularly challenging in this respect (e.g. [28]). For instance, environmental conditions could have a strong impact on these migratory species not only at the breeding grounds but also along their migration routes or at their wintering grounds, when individuals from a variety of breeding origins congregate into common migratory corridors and wintering areas. Hence, the ability to identify and quantify the respective roles of climate and human activities in both breeding and wintering grounds of these long-lived top predators is important in the field of marine biological conservation.

The sophistication of statistical modelling techniques and the increasing availability of environmental data makes possible to integrate both climate and human effects on powerful demographic models to ultimately build realistic scenarios of the impact of future environmental changes on populations of marine organisms (e.g. [29,30]). Spatio-temporal impacts of harmful processes on population dynamics have been studied in large marine species (e.g. albatrosses and marine mammals), but this has seldom been done in smaller migratory predators despite the fact they might be highly relevant in explaining energy flow and food web structuring in marine environments [31–33]. In addition, precise movements and foraging locations for these highly mobile predators are often unknown, notably in winter when many of these species remain unavailable to most researchers very far from their breeding colonies. In this sense, the Cory's shearwater (*Calonectris diomedea*) represents a good model species as (1) it is a medium-sized long-lived marine top predator, (2) it breeds colonially at temperate to sub-tropical latitudes, (3) it carries out an annual trans-equatorial migration, (4) its survival is known to be affected by climate [34–37], and (5) several of its populations may be threatened by longline fisheries [38]. We took advantage of a capture-recapture monitoring carried out on the world's largest colony of Cory's shearwater over 34 years (from 1978 to 2011, with an in-between four-years gap), (a) to model its adult survival and (b) to assess the potential effects of fishery activity and (c) climate fluctuations on this long-lived migratory predator. More novelty, in order to select the most appropriate environmental variables that should be tested as candidate predictors of survival, detailed information on spatial and temporal distribution of the study population was obtained along four years by tracking 100 of their long-distance migrations.

Methods

Study Site and Data Collection

The island of Selvagem Grande (30°09′N, 15°52′W; Fig. 1) holds the largest known breeding colony of Cory's shearwater in the world [39]. There are some historical records of its exploitation at this remote location, with Cory's shearwater eggs and chicks being intensively exploited for food, oil and feathers through the first two thirds of the 20th century [40]. Constant harvests of chicks but also a few severe killings of adults in the 1970's, reduced this population from *ca.* 100,000 breeding pairs (crude estimations at the beginning of the 20th century) to only 5,000 pairs in 1977 [41]. Since then, and due to the establishment of the Selvagens Islands Nature Reserve and a permanent vigilance, the shearwater population has increased and was estimated at *ca.* 29,540 breeding pairs in 2005 (Fig. 2; [39]). During the breeding season (March-October), Cory's shearwaters from Selvagem Grande forage to a large extent in the Canary Current, along the Moroccan and Western Sahara coast where productivity is high, owing to the enrichment of the surface waters by a strong upwelling [42,43]. Most of these trans-equatorial migratory shearwaters congregate in the South Atlantic Ocean during the non-breeding season (November-February), the Benguela Current being one of the most used wintering sites [44,45].

Each year since the 1978 breeding season, new individuals found nesting at study sites within the colony and all their chicks were ringed with a monel band. The presence/absence of each ringed individual in the colony was recorded annually from 1978 by consecutive burrow visits during early incubation (early June). The analysed dataset is composed by (1) a continuous period of 22 years monitoring data (from 1978 to 1999) from a sample of *ca.* 500 individually numbered nests (3,227 individuals), and, (2) a period of eight years (from 2004 to 2011) coming from a different sample of 358 numbered nests (1,330 individuals), with no data collected in-between.

Tracking Data

Additionally, to choose the most appropriate and relevant environmental predictors for Cory's shearwater survival, we first characterized the phenology and annual distribution of birds breeding at Selvagem Grande Island. We tracked their trans-equatorial migrations by deploying leg-mounted 3.6-g geolocators (mk7 model, developed by British Antarctic Survey, [46]) at the end of breeding seasons 2006, 2007, 2008 and 2009 (August/September). In the beginning of the following breeding seasons (April/June), we recovered complete data from 100 geolocators. Geolocators provide two positions per day based on light levels (one at local midday and other at local midnight), with an accuracy of approximately 186±114 km [47]. Data were analysed using TransEdit (to check for integrity of light curves and to fit dawn and dusk times; [46]) and Birdtrack software (to estimate the latitude from day length and longitude from the time of local midday relative to Greenwich Mean; [46]). We assumed a sun elevation angle of −4.5 degrees, based on known positions obtained during ground-truthing of loggers carried out before and after deployment. Unrealistic positions (those resulting from interference of light curves at dawn or dusk, or around equinox periods) were removed from the analyses.

Environmental and Fishery Data

We chose a series of climatic and fishery-related indices with biological interest for Cory's shearwaters to explore their relationship with adult survival (Table 1). We extracted monthly values of all indices specifically for the Canary Current (20°–35°N, 10°–20°W) to evaluate their effect on the breeding ground, and for the Benguela (15°–40°S, 5°–25°E) and Agulhas (15°–40°S, 25°–45°E) Currents to assess their impact on the non-breeding grounds as described by tracking data (Fig. 1 and Appendix S1). In order to integrate the breeding and non-breeding periods separately, we averaged monthly data over April-September and December-February, respectively.

In most cases, fishery-related indices are expected to affect directly adult survival, with longlining affecting negatively seabirds through incidental bycatch (e.g. [48,49]). In particular, foraging areas exploited by Cory's shearwater both in breeding and wintering periods are thought to largely overlap with areas

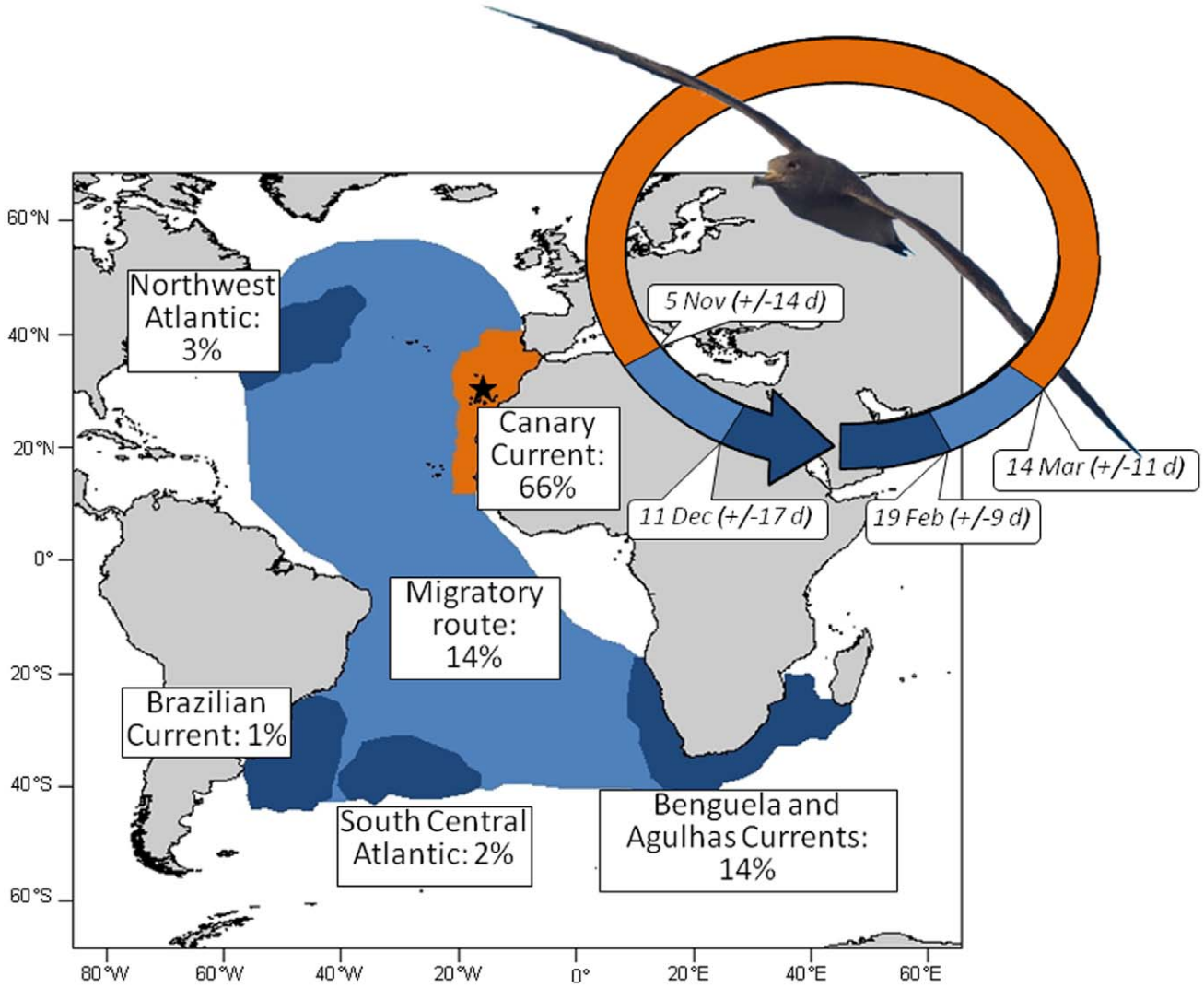


Figure 1. Distribution of Cory's shearwaters from Selvagem Grande Island (star) throughout the annual cycle. Schematic annual phenology (starting 1st January) and annual distribution of 100 Cory's shearwaters tracked with geolocators between 2006 and 2009. Coloured areas encompass bird positions during the breeding and wintering seasons (in orange and dark blue, respectively) and the overall distribution during the migration periods (i.e., when commuting between breeding and wintering areas; in light blue). The main wintering areas were associated with Benguela and Agulhas Currents (n = 72 individuals), central South Atlantic (n = 11), Brazil-Malvinas confluence region (n = 8), northwest Atlantic (n = 4) and Canary Current (n = 5). Estimated proportion of time spent in each area by the whole adult population is shown in white panels. Note that the Canary Current includes all breeding positions as well as the few wintering ones. Photo credit R. Ramos.
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frequented by longlining fishery vessels [38,50,51]. Thus, we tested the effect of longlining effort (LL) by extracting the number of hooks used by tuna longliners in specific areas and seasons (Appendix S1). Longlining data was obtained from International Commission for the Conservation of Atlantic Tunas (ICCAT) website (http://www.iccat.es/en/accesingdb.htm), which offers small scale ($5^\circ \times 5^\circ$ squares) monthly catch and fishing effort indices.

Climatic fluctuations are also suspected to affect seabird mortality either directly through storminess (e.g. [34]), or after a temporal lag through an indirect mechanism (e.g. [52]), where climate first affects primary production, and then integrates along the trophic web up to top predators [53]. Firstly, we explored potential effects of the Southern Oscillation Index (SOI, available at http://www.esrl.noaa.gov/psd/data/correlation/soi.data), which reflects El Niño/La Niña large-scale oscillations through changes in sea level pressure between the south-eastern and south-western Pacific waters. Although the effect of the SOI is most pronounced in the south-eastern Pacific Ocean, other southern marine ecosystems such as the Southern Atlantic where most Cory's shearwaters winter seem also affected by sustained positive SOI values (i.e. La Niña episodes; [54]). Secondly, we tested a local index, the Sea Surface Temperature (SST, available at http://badc.nerc.ac.uk/view/badc.nerc.ac.uk_ATOM_dataent_hadisst, at 1° spatial resolution, HadISST 1.1; Hadley Centre, British Atmospheric Data Centre), which provides information on oceanographic conditions on a finer geographical scale and which may ultimately structure the trophic web. Finally, we considered both SOI and SST variables lagged one (breeding to non-breeding, or vice versa), two (i.e. one entire year), three or even four seasons (see Appendix S1 for details). By these means, we investigated the potential long-lasting effects of

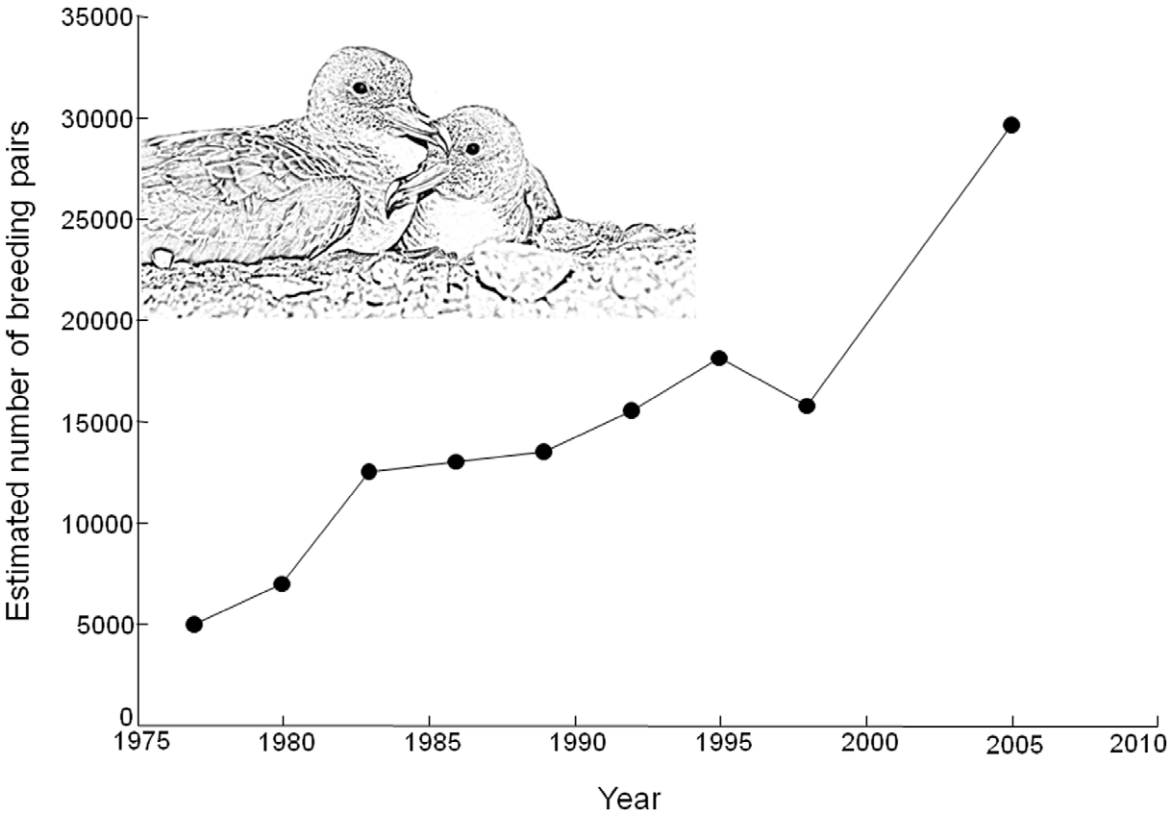


Figure 2. Estimated breeding population of Cory's shearwaters at Selvagem Grande Island along the sampled period. Data from Mougin et al. 2000 and Granadeiro et al. 2006. Photo credit R. Ramos.
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these environmental variables through the whole trophic web on survival.

To reduce the number of explanatory variable and avoid spurious relationships (errors of type I, [55]), we either combined correlated variables of the same nature (i.e. units) by averaging all respective months (e.g. SST in the breeding ground for four consecutive seasons and SOI for the non-breeding and the previous breeding seasons) or we performed a Principal Component Analyses (PCA) when the correlated variables were of a different nature (e.g. LL with all SST in the non-breeding grounds). We retained the first and second PCs for that last synthetic covariate (denoted by PC1LLSST and PC2LLSST, respectively) which accounted for 47.7% and 28.8% of the variation of the four original covariates, respectively. This reduced set of six variables is detailed in Appendix S1.

Demographic Modelling

Demographic parameters were estimated with capture-mark-recapture (CMR; [56]) models, using M-Surge version 1.8 [57] and a total of 4,555 adult capture-recapture histories, over the 1978–2011 period. We started with the Cormarck-Jolly-Seber (CJS) model where survival (Φ, probability that a shearwater alive at year t survives at year t+1) and capture (p, probability that a shearwater alive and present at the breeding colony at year t is caught during the year t) were time (t) and group (sex) dependent. The fit of the general model to the data was investigated with goodness-of-fit (GOF) tests for each period (1978–99 and 2004–11) and sex using program U-Care version 2.2 [58]. Model selection was done using the Akaike Information Criterion corrected for small sample size and overdispersion (QAICc; [59]). When comparing two models, if ΔQAICc >2, the preferred model is

Table 1. Questions addressed concerning the impact of fisheries and climate on Cory's shearwater survival.

Question of interest	Covariate response in the breeding ground	Covariate response in wintering grounds	Potential effect on survival
Are longline fisheries having an impact on survival?	LL_{CC}	LL_{BA}	Direct, negative
Is SST affecting shearwater survival?	SST_{CC}	SST_{BA}	Indirect, positive or negative
Does SOI have an impact on its survival?	–	SOI	Direct or indirect, negative

LL longlining effort; SST Sea Surface Temperature; SOI Southern Oscillation Index; subindex $_{CC}$ Canary Current; subindex $_{BA}$: Benguela and Agulhas Currents.
Note that specific covariate responses (longlining activity: LL, sea surface temperature: SST, and Southern Oscillation Index: SOI) in breeding and wintering grounds were tested. Potential effects of these covariates on survival were also predicted as direct when the covariate in itself influences survival, indirect when it is though a trophic cascade effect for instance, positive when the effect of the covariate increases survival probability, and negative when that effect damages survivorship.
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the one with the smallest QAICc value (i.e. the most parsimonious model in terms of the number of parameters and model deviance; [56]). Along the modelling, capture probability was fixed to zero for the period 2000–2003 in all the individuals, and for the period 2004–2011 in those individuals sampled during the first period (i.e. 1978–1999) to account for changes in the monitoring protocol over the course of the study. To test and evaluate the impact of (uncorrelated) climate and fishery covariates on adult survival, we progressively built models from the best time dependent model including one covariate at a time. We started testing the potential linear effect of longline fisheries (direct mortality) on survival and we then tested for linear and non-linear (quadratic) effects of the climate on seabird demography. We also tested whether the impact of each of these covariates was constant over the entire period 1978–2011 (one slope) or whether it differed between 1978–1999 and 2004–2011 periods (two slopes). By doing so, we aimed to disentangle whether these variables had changed their potential effect between the two considered periods. The ability of each covariate to describe significant variation in survival was assessed using analysis of deviance tests (ANODEV: *F*-test statistic with n_{cov} and n-n_{cov}-1degrees of freedom, where n_{cov} represented the number of covariates included and n was the number of parameters of the time dependent model; [60]) and the effects of these covariates were quantified using an approximated R^2statistic [61]: $R^2 = \mathrm{DEV}(M_{cst})\text{-}\mathrm{DEV}(M_{cov})/[\mathrm{DEV}(M_{cst})\text{-}\mathrm{DEV}(M_t)]$, where $\mathrm{DEV}(M_{cst})$, $\mathrm{DEV}(M_{cov})$ and $\mathrm{DEV}(M_t)$ are the respective deviances for the models constant, with covariate(s) and time dependent. While modelling the effect of the covariates, M_{cst} were selected according to the aim of the test (see Table 3 for details).

Results

Annual Phenology and Distribution Gathered from Geolocator Data

Movements of tracked Cory's shearwaters were easily classified into frequent foraging trips around the breeding colony (including the Canary Current), rapid, long-distance migratory movements, and persistent presence in a well defined non-breeding ground, by combining location data and date. Most birds wintered in five broad areas (Fig. 1), associated with the Benguela and Agulhas Currents (72% of the individuals), central South Atlantic (11%), the Brazilian Current (8%), northwest Atlantic (4%) and the Canary Current (5%). On average, they left the colony the first fortnight of November (mean departure date: 5 November+/−14 days), and took 36 days to reach their major destination (mean arrival date: 11 December+/−17 days). Birds left their non-breeding areas around mid-February (19 February+/−9 days) and arrived at Selvagem Grande three weeks later (14 March+/−11 days). Overall, Cory's shearwaters from Selvagem Island spend 66.3% of their annual time in the breeding grounds, only 13.8% of the time migrating and 19.9% in one of their non-breeding areas, mainly in the South Atlantic Ocean (Fig. 1). Later, these dates, time expenditure and precise locations along the year allowed us defining precise spatio-temporal delimitations of several environmental indices which were likely to affect Cory's shearwater survival.

Goodness of Fit Test

The GOF test indicated a severe lack of fit of the umbrella model ($\chi^2_{316} = 1783.7$, $P<0.0001$), coming from the presence of both transient and trap dependence effects [62]. The first effect suggested the presence of transients, i.e. prospecting or inexperienced animals from other locations, in both periods and sexes (test 3.SR in Table 2). Transience violates the CJS model assumption of equal survival between newly and previously marked individuals. In the case of high capture probabilities, transient individuals can be efficiently deleted by suppressing the first recapture of all animals [63,64]. After doing so, test 3.SR was not significant anymore for any of the periods or sexes (Table 2). The positive trap-dependent effect (test 2.CT in Table 2), which indicates that individuals captured on one occasion were more likely to be captured on the following occasion than others was accounted by splitting capture-recapture histories (using U-Care software) and implementing a trap-dependence model (where capture probability results from a Markovian dependence on previous capture, denoted by m; [65]). Finally, our modelling based on $\Phi_{sex*t}\ p_{m*sex*t}$ was also corrected with a variance inflation factor *c-hat* to take into account the remaining lack of fit ($\chi^2_{203} = 354.7$, $P<0.0001$), calculated as the χ^2 statistic over its number of degrees of freedom (*c-hat* = 1.746; [56]).

Estimating Demographic Parameters through the 1978–2011 Period

We started testing in the umbrella model ($\Phi_{sex*t}\ p_{m*sex*t}$) whether survival and capture probabilities varied with sex and/or time (Table 3). The lowest QAICc was obtained for a model with an additive effect of time on trap-dependence categories (additive trap effect) for capture probability and time-dependent survival (model 7; Fig. 3a). Survival probability was estimated as $\Phi = 0.915$ (SE = 0.037, range = 0.909–0.921) from the constant model (model 8). We then assessed the effect of covariates using the model structure of that selected time-dependent model as a starting point (model 7; Table 3). Searching for direct causes of mortality (models 9–14), we detected a significant negative effect of the longlining effort on the Canary Current during the breeding period on survival (LL_{CC}br, model 9, ANODEV = 5.772, $P_{ANODEV} = 0.024$), explaining 20.8% of the variation. We then tested for potential additive effects of climatic parameters on Cory's shearwater survival (models 15–26): in model 15, we noted a significant negative impact of SST in the Canary Current on survival estimates (SST_{CC}2yr, ANODEV = 6.623, $P_{ANODEV} = 0.005$) although in model 18, a more significant negative effect of annual SOI was found impacting on survival parameters (SOIyr, ANODEV = 7.937, $P_{ANODEV} = 0.002$, $R^2 = 0.425$). In model 24, additively to LL_{CC}br and SOIyr, the integrative covariate of SST of the Canary Current was still affecting seabird demography (SST_{CC}2yr, ANODEV = 3.984, $P_{ANODEV} = 0.021$, $R^2 = 0.498$; Fig. 3). The relevance of both climatic variables was more apparent when they were considered in a linear trend, suggesting therefore weak non-linear effects of climate on Cory's shearwater survival (models 16, 19 and 25). In addition, none of the models including different slopes for 1980–1999 and 2005–2011 periods were preferred when tested against the model with a single slope (although models 10 and 20 were close to), suggesting similar effects of the covariates along the two periods. Finally, none of the confidence intervals of the selected covariates included zero, suggesting that all three covariates, i.e. LL_{CC}br, SOIyr and SST_{CC}2yr contributed negatively and significantly (-0.104 ± 0.040, -0.212 ± 0.081, -0.137 ± 0.058, respectively) to year-to-year variations in survival throughout the period 1980–2011 (Fig. 4).

Discussion

The present study revealed that combined effects of climate and fishery activities in both breeding and non-breeding areas impacted negatively on the survival of a long-lived migratory seabird. Interestingly, tracking data of a hundred individuals

Table 2. Results of goodness-of-fit (GOF) tests of CJS model (Φ_t p_t), for each period (1978–99 and 2004–11) and sex. individual was removed to account for transience.

		Test 3SR			Test 3SM			Test 2CT			Test 2CL			Sum of Tests		
		df	χ^2	*P*	df	χ^2	*P*	df	χ^2	*P*	df	χ^2	*P*	df	χ^2	*P*
Complete data set																
1978–1999	males	20	36.3	0.014	42	138.3	0.000	19	360.5	0.000	52	101.5	0.000	133	636.7	0.000
	females	20	71.1	0.000	39	113.3	0.000	19	516.2	0.000	54	101.0	0.000	132	801.6	0.000
2004–2011	males	6	41.1	0.000	8	36.3	0.000	5	61.2	0.000	6	33.6	0.000	25	172.1	0.000
	females	6	18.7	0.005	8	38.9	0.000	5	102.4	0.000	7	13.3	0.066	26	173.3	0.000
After removing first encounter																
1979–1999	males	19	15.8	0.674	32	53.2	0.011	18	259.8	0.000	35	64.7	0.002	104	393.4	0.000
	females	19	20.7	0.352	33	83.1	0.000	18	378.7	0.000	37	73.2	0.000	107	555.7	0.000
2005–2011	males	5	9.0	0.110	5	8.3	0.143	4	35.0	0.000	3	8.7	0.034	17	60.9	0.001
	females	5	3.4	0.646	6	5.5	0.482	4	60.5	0.000	4	9.1	0.058	19	78.4	0.000

Two different datasets are used: a complete dataset with all the encounters and a reduced dataset where the first recapture of every.
Tests 3 (3SR and 3SM) check the homogeneity of recapture histories while tests 2 (2CT and 2CL) examine the independence between last release and next recapture (Burnham & Anderson 1998); df degrees of freedom; χ^2 Pearson's chi-squared statistic; *P* significance of the χ^2 test.
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allowed us to estimate that Cory's shearwaters breeding at Selvagens Islands spend two thirds of the year mainly feeding in the Canary Current while breeding, and the other third migrating toward very restricted areas of the Southern Atlantic Ocean (Fig. 1). These precise spatio-temporal schedules along the entire year achieved by tracking devices became clue in selecting and delimiting specific environmental variables and potential anthropogenic threats, and ultimately allowed us to relate these precise covariates to the demography of this highly pelagic seabird.

Modelling Demography of a Long-lived Migratory Seabird

Marine top predators, such as the Cory's shearwater, are considered extreme K-selected species, which means that their specific life history traits, long life expectancy, delayed maturity and low reproductive rates are unavoidably linked to high adult survival [27]. Using CMR analysis we found that estimated adult survival of this mid-sized Procellariiform seabird (0.915 ± 0.037 on average, from the model Φ. p_{m+t}) was low compared with other Atlantic colonies (>0.93; [34,66]), but higher than in Mediterranean populations (ranging from 0.82 to 0.90; [34,36,37,67]). Survival of Cory's shearwaters breeding at Selvagens Islands was negatively affected by a combined effect of environmental variables and fishery effort at different points of their annual life cycle. Our models reported evidence that greater longlining activity and La Niña events increased shearwater mortality in breeding and non-breeding grounds, respectively (Fig. 4). Temperature variation in the Canary Current apparently also affected negatively shearwater survival probability, although likely through an indirect effect mediated through the trophic web on which the birds depend.

Longlining has a harmful effect on the entire marine ecosystem, with significant implication for the non-targeted top predators [9–11]. During line setting of thousands of baited hooks, seabirds (among other marine top predators) are particularly prone to be accidentally caught while scavenging on bait, being dragged under water afterwards and finally drowned. In the Mediterranean, longlining activity is thought to be responsible for large population declines of Cory's shearwaters at several breeding colonies [68,69], while in the Southern Atlantic (and for extension in the entire Atlantic) Cory's shearwater incidental bycatch was thought to occur very scarcely [50,66,70–72]. However, our results suggested that incidental mortality may have been overlooked in Atlantic waters, i.e. that longlining activity might have not only affected Mediterranean birds, but also have affected the survival of Atlantic Cory's shearwaters (see also [51]). We suggest that the short time spent by this migratory seabird outside its breeding areas decreases the probability to be caught (as well as observed) in the Southern Atlantic Ocean, where most bycatch research has been done. Thus, Cory's shearwater may be threatened by commercial fisheries all along its distribution, although higher impacts probably occurred at the breeding grounds [38,73], where shearwaters spend two thirds of their annual cycle (Fig. 1).

Adult survival of Cory's shearwaters was also negatively affected by SOI (Fig. 4b). Typically, local manifestations of the Southern Oscillation are expected to influence Cory's shearwater wintering grounds in the Southern Atlantic, where birds spend the short non-breeding season (Fig. 1). Sustained positive values of the SOI are characterized by tropical storms and hurricanes in the Atlantic (i.e. extreme La Niña events; [23]) which have long been related to several mass mortalities and breeding failures of many marine top predators in the Southern Ocean [20,54,74], including seabirds in the Benguela upwelling system [75]. Indeed, our results corroborated the findings of others, which suggested that during La Niña years the greater storminess of the Southern Atlantic may cause a decrease in Cory's shearwater survivorship [34–37]. Although most of these studies considered that these climate effects acted directly on winter mortality, indirect effects of SOI on wintering grounds through a trophic cascade cannot be ruled out.

In addition to longliner activity, warm sea surface temperatures around the Canary Current during the current year and the year before a given breeding period also predicted low adult survival (Fig. 4c) during the long breeding season. Although high SST has been previously found affecting negatively several seabird populations (e.g. [76–78]), the fact that this effect is lagged supports the idea that it is not temperature *per se*, but a mediated effect, presumably through the food web, which might trigger seabird mortality [12,79]. Indeed, some evidence of delayed effects of SST on the trophic web of the Canary Current have been previously reported at lower trophic levels (e.g. the 6 months delay between

Table 3. Modelling capture (p) and survival (ϕ) probabilities in the Cory's shearwater breeding at Selvagem Grande Island and the effects of covariates on survival.

n°	Model	np	DEV	QAICc	ΔQAICc	P_{ANODEV}	M_{cst}
Modelling capture probability (p)							
1	ϕ (*sex*t*) p (*m*sex*t*)	148	28296.6	16502.5	120.3		
2	ϕ (*sex*t*) p (*m*t*)	100	28353.1	16438.9	56.7		
3	ϕ (*sex*t*) p (*m*)	56	29609.1	17070.3	688.0		
4	ϕ (*sex*t*) p (*m1(·) m2(t)*)	77	28601.5	16535.2	153.0		
5	ϕ (*sex*t*) p (*m1(t) m2(·)*)	74	29437.2	17007.8	625.6		
6	**ϕ (*sex*t*) p (*m+t*)**	**79**	**28383.6**	**16414.4**	**32.1**		
Modelling survival probability (ϕ)							
7	**ϕ (*t*) p (*m+t*)**	**53**	**28418.3**	**16382.2**	**0.0**		
8	ϕ (·) p (*m+t*)	29	28553.4	16411.6	29.4		
Modelling covariates in survival							
Direct mortality							
9	**ϕ ($LL_{CC}br_{1980–2011}$) p (*m+t*)**	**31**	**28525.5**	**16399.6**		**0.024**	**8**
10	ϕ ($LL_{CC}br_{1980–99+2005–11}$) p (*m+t*)	32	28512.0	16393.9		0.068	9
11	ϕ (PC1$LLSST_{BA1980–2011}$) p (*m+t*)	31	28553.1	16415.5		0.795	8
12	ϕ (PC1$LLSST_{BA1980–99+2005–11}$) p (*m+t*)	32	28552.8	16417.2		0.943	11
13	ϕ (PC2$LLSST_{BA1980–2011}$) p (*m+t*)	31	28553.5	16415.6		0.896	8
14	ϕ (PC2$LLSST_{BA1980–99+2005–11}$) p (*m+t*)	32	28553.2	16417.5		0.969	13
Indirect climate effects							
15	ϕ ($LL_{CC}br_{1980–2011}$+ $SST_{CC}2yr_{1980–2011}$) p (*m+t*)	32	28499.7	16386.9		0.005	9
16	ϕ ($LL_{CC}br_{1980–2011}$+ $[SST_{CC}2yr_{1980–2011}]^2$) p (*m+t*)	33	28487.3	16381.8		0.044	15
17	ϕ ($LL_{CC}br_{1980–2011}$+ $SST_{CC}2yr_{1980–99+2005–11}$) p (*m+t*)	33	28496.6	16387.1		0.498	15
18	**ϕ ($LL_{CC}br_{1980–2011}$+ $SOIyr_{1980–2011}$) p (*m+t*)**	**32**	**28496.1**	**16384.8**		**0.002**	**9**
19	ϕ ($LL_{CC}br_{1980–2011}$+ $[SOIyr_{1980–2011}]^2$) p (*m+t*)	33	28485.3	16380.6		0.058	18
20	ϕ ($LL_{CC}br_{1980–2011}$+ $SOIyr_{1980–99+2005–11}$) p (*m+t*)	33	28486.3	16381.2		0.060	18
21	ϕ ($LL_{CC}br_{1980–2011}$+ $SOIw\text{-}1_{1980–2011}$) p (*m+t*)	32	28525.4	16401.6		0.994	9
22	ϕ ($LL_{CC}br_{1980–2011}$+ $[SOIw\text{-}1_{1980–2011}]^2$) p (*m+t*)	33	28524.1	16402.8		0.778	21
23	ϕ ($LL_{CC}br_{1980–2011}$+ $SOIw\text{-}1_{1980–99+2005–11}$) p (*m+t*)	33	28521.1	16401.1		0.483	21
Modelling three covariates in survival							
24	**ϕ ($LL_{CC}br$ + $SOIyr$ + $SST_{CC}2yr_{1980–2011}$) p (*m+t*)**	**33**	**28486.2**	**16381.1**		**0.021**	**18**
25	ϕ ($LL_{CC}br$ + $SOIyr$ + $[SST_{CC}2yr_{1980–2011}]^2$) p (*m+t*)	34	28476.8	16377.7		0.051	24
26	ϕ ($LL_{CC}br$ + $SOIyr$ + $SST_{CC}2yr_{1980–99+2005–11}$) p (*m+t*)	34	28484.2	16382.0		0.678	24

np number of parameters estimated; DEV deviance; QAICc quasi-likelihood Akaike's information criterion values; ΔQAIC difference between the current and the lowest QAICc model; P_{ANODEV} P-value of the ANODEV test on covariates; M_{cst} model considered as constant model when evaluating P_{ANODEV}; t time; (·) constant; *m* two states of trap dependence; * interaction; + additive effect. Covariate codes are defined in Appendix S1; subindex $_{1980–2011}$ accounts for a single period/slope while $_{1980–99+2005–11}$ accounts for two periods/slopes; [*covariate*]^2 denoted a covariate in a quadratic trend; in bold characters denoted the models considered.

plankton and sardine recruitment [80,81]). Several oceanographic factors, such as positive SST values negatively influence the abundance of plankton, which in turn plays a key role in fish recruitment [82–84]. Thus, a reduction in productivity would decrease fish abundance, constraining the foraging opportunities of birds, and therefore increasing Cory's shearwater mortality rate (e.g. [12,79,85]).

The Selvagem's Perspective

Cory's shearwaters of Macaronesian Islands were exploited by indigenous inhabitants from prehistoric times (e.g. [86,87]). More recently, regular chick harvest, with likely increasing intensity during most of the 20th century, plus severe episodes of adult killings reduced dramatically the population of Selvagem Island [41]. Fortunately, after enhanced protection since the late 1970's, the number of breeding birds built up rapidly, at *ca.* 30% per year in the early 1980's, mainly due to the progressive recruitment of large numbers of non-breeding individuals that survived the 1975 and 1976 culls (Fig. 2; [41]). Survival estimates for that period remained relatively high and rather stable (i.e. 0.92 ± 0.01 in 1980–1986, see Fig. 3a), which contributed to the rapid recovery of the nesting numbers. From 1987 to 1995, survival rates oscillated year-to-year, and the population growth stabilized at an average rate of 5% per year, with an estimated population of 18,100 breeding pairs in 1995 [88]. However, from that point and at least until the end of the century (i.e., 1999), survival estimates dropped to 0.86 ± 0.02 on average, and in 1998 the numbers apparently reduced to 15,750 breeding pairs (Fig. 2; [89]), a reduction of over

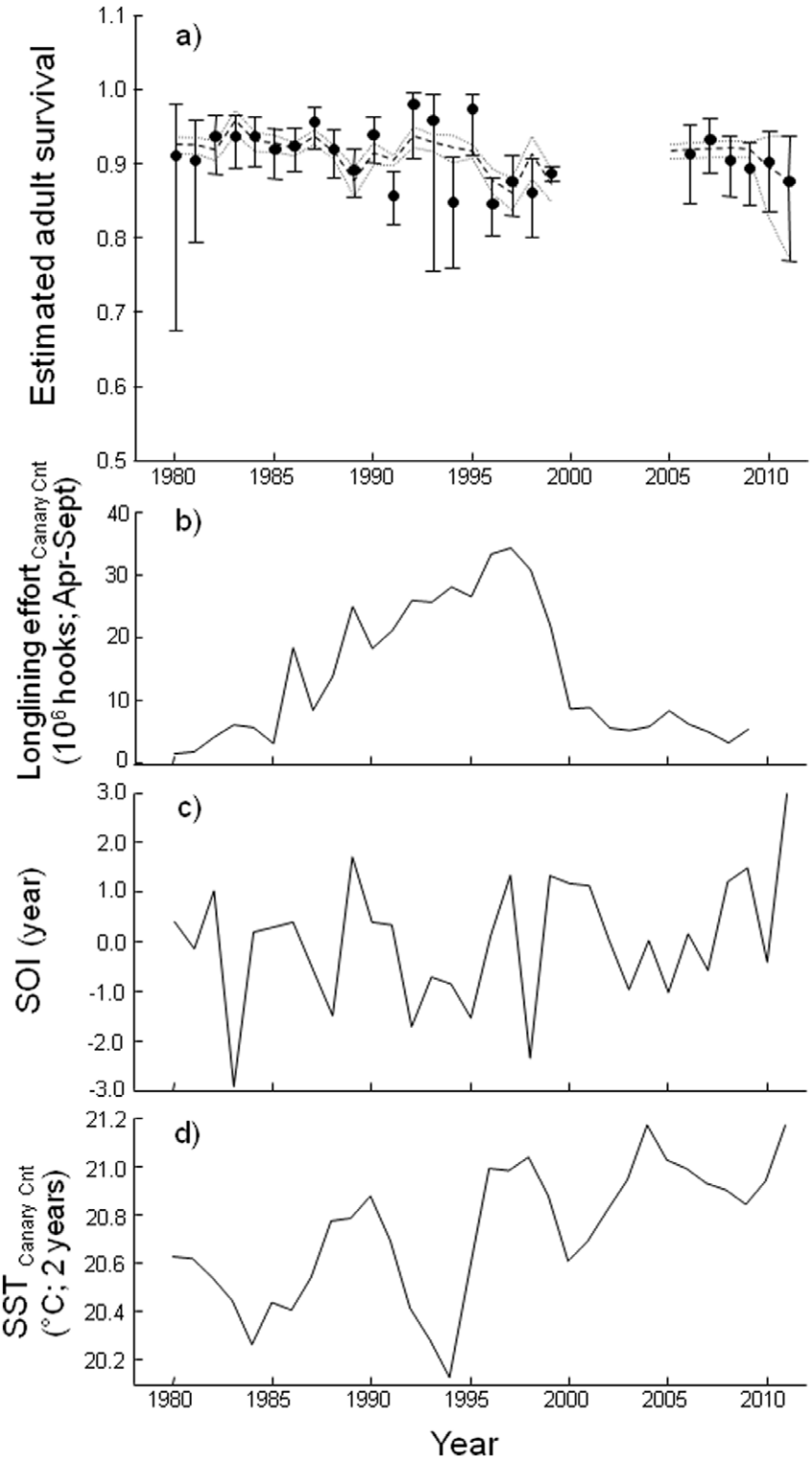


Figure 3. Annual variation of adult survival probabilities and the selected covariates for the period 1980–2011. Variation in survival rates of adults (a) and the selected covariates: (b) longlining effort in the Canary Current during the breeding, (c) annual SOI and (d) SST in the Canary Current (2 years averaged) are shown separately. Survival estimates come from the time-dependent model (Φ_t p_{m+t}; in black dots and CI in solid bars) and from the selected model with the covariates ($\Phi_{LLccbr+SOIyr+SSTcc2yr}$ p_{m+t}; in dense dashed line and CI in light dashed lines).
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13% in three years. The decrease in survival probability along this period coincides with an elevated number of hooks used by longliners in the Canary Current (Fig. 3b), which could be contributing to the significance of this covariate in our modelling. After an unknown gap of four years, Cory's shearwater survival rates for 2005–2011 somewhat recovered (0.91±0.02) and the

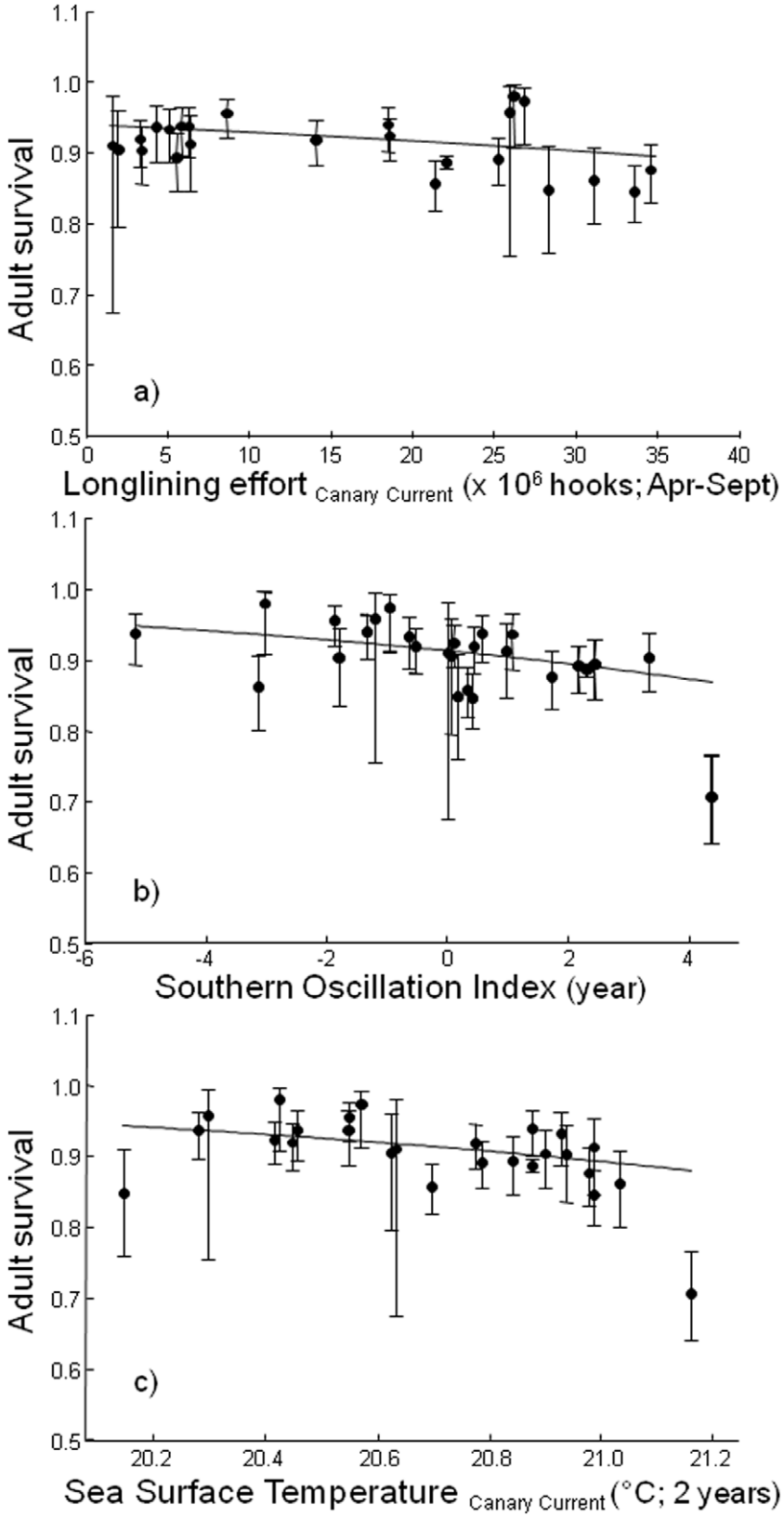


Figure 4. Relationship between annual adult survival probabilities and the selected covariates from the best CMR model. (a) Longlining effort in the Canary Current during the breeding, (b) annual SOI and (c) SST in the Canary Current (2 years averaged) are depicted against survival estimates (mean in black dots and asymmetric CI in solid bars estimated from the model Φ_t p_{m+t}). Regression lines estimated from model 24 in Table 3.

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population apparently resumed its growth, reaching up to around 30,000 breeding pairs in 2005 (Fig. 2; [39]), and making Selvagem Grande the largest world colony of Cory's shearwaters. Furthermore, the longliner activity in the Canary Current region seems to have decreased considerably during the last decade (Fig 3b), which may have positively contributed to the recovery of the population throughout this last period. Hence, though the Cory's shearwater population from the Selvagens is still far from its presumed size at the beginning of the 20th century, the evidence of a recovery process is very clear. However, predicted climate change and the resulting global warming could still have a negative impact both in breeding and non-breeding grounds, and continued monitoring of the dynamics of this population may be relevant to understand future trends.

Conclusions

High adult survival and low fecundity are typical of long-lived species, and even small reductions in survival can have dramatic effects on population trends. Although survival rates reported for Cory's shearwaters breeding at Selvagem Grande were generally higher and more stable than in most other colonies, particularly those in the Mediterranean, the amount of variation in survival explained by climatic and human-related variables was high (49.8%), considering the long period analysed. The survival of this species was moderately influenced by longlining activity and more markedly by climatic factors. Although it was encouraging that tuna longlining fishing effort declined over the last decade in the Canary Current, our results highlight the need for more research on fisheries impact on sea life in the subtropical Northeast Atlantic, where very few studies have been conducted. The results of this study also warn to the negative effects of climate at both breeding (SST) and non-breeding grounds (SOI), and it is clear that these could be aggravated in the near future, given that inter-annual variation in SST and the virulence of El Niño/La Niña events are expected to further increase [26].

From the conservation point of view, the negative impact of both longline fisheries and raised SST in the Canary Current possibly does not only concern locally breeding Cory's shearwaters, but also wintering shearwaters from both Atlantic and Mediterranean populations that use this Current [44,45,90–92], as well as many other species inhabiting this restricted upwelling area of the subtropical Atlantic [93–96]. However, in terms of magnitude, the storminess generated by El Niño/La Niña phenomena in the Southern Atlantic Ocean seems to have a higher impact in the survival of Cory's shearwaters than the effects occurring in the Canary Current. In fact, although it only represents 20% of their annual cycle, events occurring during the non-breeding period may be highly relevant for the population dynamics of Cory's shearwaters. Overall, our results contributed to highlight the importance of considering not only breeding grounds, but also precise schedules and places visited while non-breeding for the appropriate understanding of impacts of the environment on the population dynamics of long-distance migratory species.

Ethics Statement

All animals were handled in strict accordance with good animal practice as defined by the current European legislation. The deployment of MK7 loggers (see details above) did not take more than 10 minutes and on no occasion did it interfere with reproduction or have visible deleterious effects on study animals [97]. All work was approved by Instituto da Conservação da Natureza e da Biodiversidade and Serviço do Parque Natural da Madeira, where Selvagens Islands Nature Reserve belongs to (research permits 107/2006, 116/2007, 333/2007/CAPT).

Supporting Information

Appendix S1 Correlations among the explanatory covariates. Pearson's coefficients are placed below the diagonal and *P*-values of a *t*-test above the diagonal. Shaded areas highlight three sets of correlated covariates: a) sea surface temperatures (SST) in the breeding ground (4 consecutive periods averaged, $SST_{CC}2yr$), b) longlining effort (LL) and SST (3 consecutive periods) in the non-breeding grounds (first and second principal components (PC) explaining respectively 47.7 and 28.8% of covariate variability), and c) Southern Oscillation Index (SOI) in two consecutive periods (current non-breeding and previous breeding periods, SOIyr). Bold type highlights the covariates retained for the analysis of survival and the correlations among them.
(DOC)

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Author Contributions

Conceived and designed the experiments: RR JPG PC. Performed the experiments: RR JPG JLM MPD PC. Analyzed the data: RR JPG MN MPD PC. Contributed reagents/materials/analysis tools: JPG PC. Wrote the paper: RR JPG MN MPD PC.

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Original Articles

Disentangling environmental from individual factors in isotopic ecology: A 17-year longitudinal study in a long-lived seabird exploiting the Canary Current

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ABSTRACT

Despite its importance for ecology and conservation, we are still far from understanding how environmental variability interacts with intrinsic factors and individual specialization to determine trophic strategies of long-lived taxa, mostly due to difficulties in studying the same animals over extended periods. Here, by yearly consistently sampling the first primary feather of 99 Cory's shearwaters (*Calonectris borealis*) foraging in the Canary Current (CC) upwelling ecosystem, we provide robust evidence on the individual changes of isotopic ratios of carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) over 17 years. We reported a slight longitudinal decline of $\delta^{13}C$ values throughout 2001–2017, even after being adjusted for the marine Suess effect (linked to the increasing CO_2 emissions). Although CC is often considered to be overexploited by industrial fisheries, we could not detect a decline in Cory's shearwater trophic level indicating a change in the trophic web structuring, as revealed by $\delta^{15}N$. We found negative correlations of $\delta^{13}C$ and $\delta^{15}N$ with the CC upwelling intensity, indicating annual variability in baseline isotopic levels propagates through the food chain and it integrates in predators' tissues. Low individual repeatabilities among years at population level indicates low long-term specialization, suggesting long-lived individuals foraging on highly productive areas can adjust their foraging strategies and diet according to environmental variability. However, individual-level repeatabilities in isotopic values showed a range of individual specialization within the population, indicating most individuals are generalist and a few of them highly specialized. First, although we found a clear influence of the upwelling intensity on the trophic ecology of birds, we could not detect any temporal trend in the trophic level of the Cory's shearwater population, suggesting a stability in the structure of the pelagic food web of the CC over the last two decades despite the fishing pressure. Second, the existence of individual specialization highlights the importance of considering the repeated sampling of individuals to detect small changes in the trophic ecology of a population. Finally, the coexistence of individuals with different degree of specialization (from extremely flexible [generalists] to highly consistent individuals [specialists]) within a population can have deep implications on the capacity of populations to cope with environmental change.

1. Introduction

In marine ecosystems, trophic ecology of many predator species has been widely documented to correlate with oceanographic parameters (e.g., Gilles et al., 2016; Gagne et al., 2018; Byrne et al., 2019). These covariates usually focus either on fluctuations of marine environmental features at coarse-, meso- or local scale, such as chlorophyll *a* concentration, salinity, temperature, or wind speed (Votier et al., 2010; Kurle and McWhorter, 2017; Bird et al., 2018), or on large-scale climatic indexes, such as the North Atlantic Oscillation index (NAO; Moreno et al., 2013; Wallace et al., 2014; Fairhurst et al., 2015), which often capture complex associations between atmospheric and ecological processes better than local indexes (Hallett et al., 2004). Such environmental variables are often related to the recruitment and abundance of small pelagic fish (e.g. sardine) and cephalopods (Borges et al., 2003; Santos et al., 2005; Krüger et al., 2019), leading to complex

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Table 1
A selection of studies that used diverse animal tissues to assess the trophic ecology of the individuals throughout long time periods (from months to years). Individuals in all studies were sampled only once, and information on their trophic ecology was assessed by subsampling sequentially small amounts of specific tissues.

Organism	Species	Location, study area	Tissue	Study period	Sample size	Biogeochemical tracer	Reference
Squids	Jumbo squid (*Dosidicus gigas*)	Northern Peru	Gladius	8–9 months	5	$\delta^{13}C$, $\delta^{15}N$	Lorrain et al. (2011)
Seaturtles	Loggerhead sea turtle (*Caretta caretta*)	Cape Canaveral, Florida, USA	Carapace scutes	12 years	15 females	$\delta^{13}C$, $\delta^{15}N$	Vander Zanden et al. (2010)
Whales	Killer whale (*Orcinus orca*)	Northeast Pacific Ocean	Tooth dentin	2–4 years	11 males, 2 females	$\delta^{13}C$, $\delta^{15}N$	Newsome et al. (2009)
	North Atlantic minke whale (*Balaenaptera acutorostrina*)	West Greenland	Baleen plates	ca. 12 months	12 females	$\delta^{13}C$, $\delta^{15}N$, Hg	Hobson et al. (2004)
	Gray whale (*Eschrichtius robustus*)	Eastern Pacific Ocean	Baleen plates	ca. 12 months	7 females	$\delta^{13}C$	Caraveo-Patiño and Soto (2005)
Seals	Southern elephant seal (*Mirounga leonina*)	Kerguelen Archipelago, Southern Indian Ocean	Tooth dentin	11 years	8 males, 6 females	$\delta^{13}C$, $\delta^{15}N$	Martin et al. (2011)
	Antarctic fur seal (*Arctocephalus gazella*)	Kerguelen Archipelago, Southern Indian Ocean	Vibrissae	7 years	5 males, 7 females	$\delta^{13}C$, $\delta^{15}N$	Kernaléguen et al. (2016)
	Antarctic fur seal (*Arctocephalus gazella*)	Crozet Islands, Southern Indian Ocean	Vibrissae	7 years	10 males	$\delta^{13}C$, $\delta^{15}N$	Cherel et al. (2009)
	Ringed seal (*Pusa hispida*)	Arviat, Nunavut, Canada	Claws	5 years	1 male	$\delta^{13}C$, $\delta^{15}N$, Hg	Ferreira et al. (2010)
Seaotters	Southern sea otter (*Enhydra lutris nereis*)	Monterey Bay, California, USA	Vibrissae	1–4 years	15 males, 16 females	$\delta^{13}C$, $\delta^{15}N$	Newsome et al. (2009)
Elephants	African bush elephant (*Loxodonta africana*)	Samburu National Reserve, Northern Kenya	Tail hair	6 years	4 females	$\delta^{13}C$, $\delta^{15}N$, $\delta^{2}H$	Cerling et al. (2009)
Humans		Belfast, Northern Ireland	Hair, Nails	8 months	4 males, 4 females	$\delta^{13}C$, $\delta^{15}N$, $\delta^{2}H$, $\delta^{18}O$	Fraser et al. (2006)

changes in food availability for foraging predators (Barbraud and Weimerskirch, 2001; Forcada et al., 2005; Saba et al., 2007). In addition, regional estimates of fishery catches have been suggested to be good proxies of ecosystem productivity and prey abundance (Paiva et al., 2013). Long term overexploitation of fisheries, however, can also alter the food web structure and ultimately affect prey availability and the trophic ecology of top predators (Gagne et al., 2018).

In addition to environmental variability, trophic ecology of top predators is also driven by many individual traits, such as sex, morphology, age, experience, natal locality or even breeding stage (Svanbäck and Bolnick, 2005; Bolnick et al., 2011; Phillips et al., 2017). For instance, sexes often segregate as a result of social dominance and competitive exclusion (usually between smaller females and larger males; Catry et al., 2005). Individuals differing in body sizes or morphologies may also specialize in different trophic niches (even within the same sex; French et al., 2018). Age might relate to experience and this to foraging capabilities of individuals and therefore to their success (e.g., Lucifora et al., 2009; Haug et al., 2015). Additionally, different individual strategies in resource use within a population and their individual consistency over a long time-scale in relation to differences among individuals, can reveal the presence of specialists even within a generalist population (Bolnick et al., 2003; Araújo et al., 2011). Specialist individuals consistently exploit a narrower specific portion of all the resources available to the population, thus presenting low within individual variability (Araújo et al., 2011). Therefore, trophic assessments at the individual level while maintaining the view on the population are essential for understanding niche use and resource partitioning processes (Araújo et al., 2011; Pagani-Núñez et al., 2016). Nevertheless, little is known about the variability in the degree of specialization among individuals of the same population (but see Edelaar and Bolnick, 2019).

Thus, a fundamental question for ecologists and population biologists is the relative influence of the environment (extrinsic) and the individual (intrinsic) characteristics on the trophic ecology of top predators through time. However, in spite of its importance, understanding and quantifying how environmental variability interacts with intrinsic effects driving trophic ecology is still poorly known in animal ecology (Pires et al., 2011; Sutherland et al., 2013). To properly assess this issue in long-lived predators, the time scale over which we record the individual use of resources is a crucial factor to consider. The individual specialisation in the use of resources can vary through time (Ceia and Ramos, 2015; Carneiro et al., 2017). The drivers of this variation can be either medium-term processes, such as stochasticity and predictability in dynamic environments, or long-term effects such as ontogenetic variations related to morphology, experience and breeding traits (Riotte-Lambert and Weimerskirch, 2013; Grecian et al., 2018). Many studies have investigated individual specialization following individuals over weeks, months, or even a few years (Bolnick et al., 2003; Fraser et al., 2006; Yamamoto et al., 2014; Potier et al., 2015). Such short-term studies, however, are likely to artificially increase the apparent individual specialisation of a given population, particularly in the case of long-lived species (Clutton-Brock and Sheldon, 2010). Long-term longitudinal studies investigating inter- and intra-individual variability in resource use of long-lived species require repeated capture and sampling of the same individuals over more than a decade, which means these are scarce, although badly needed.

A reliable method to assess individual specialization in trophic ecology, alternative to those involving repeated conventional samplings (e.g. regurgitates or stomach contents), is the use of Stable Isotope Analysis (SIA; Ramos and González-Solís, 2012). In marine ecosystems, stable isotope ratios of carbon ($\delta^{13}C$) experience little variation along the food chain and are mainly used to discriminate the source of primary production and the consumer's habitat type (increasing from pelagic to benthic or from oceanic to neritic; Hobson et al., 1994). In contrast, stable isotope ratios of nitrogen ($\delta^{15}N$) increase along the food chain and are typically used to infer consumer trophic positions

(Hussey et al., 2014). Some studies have assessed the trophic specialization of the individuals over relatively short-time periods (i.e., from days to months) by performing SIA in different tissues with various turnover rates, which ultimately provides information on the feeding ecology of the individuals over different timescales (Bearhop et al., 2006; Ceia et al., 2014; Connan et al., 2014). Interestingly, other studies have performed SIA in regular subsamples of inert tissues with continuous growth (e.g., vibrissae, claws, etc.), which has allowed them to infer the degree of long-term specialization of individual trophic ecology (i.e., over several years; Table 1). In any case, $\delta^{13}C$ has to be carefully evaluated, particularly in such multidecadal studies, as carbon ratios may decrease over time due to the increased burning of fossil fuels, which generate ^{13}C-depleted CO_2 (i.e., the Suess effect; Revelle and Suess, 1957). In the marine environment, the strongest decreases occur in the subtropical regions of the Northern Hemisphere, such as the Canary Current upwelling ecosystem (hereafter CC) in the North Atlantic Ocean (where $\delta^{13}C$ could have decreased up to 0.9‰ since the industrial revolution; Eide et al., 2017). Finally, much research has been conducted on seabird trophic ecology using SIA over the last decades (Hobson et al., 1994; Inger and Bearhop, 2008; Bond and Jones, 2009). However, only very few attempts of characterising long-term individual specialization in foraging strategies and resource use of long-lived seabirds have been carried out (reviewed in Phillips et al., 2017), and to the best of our knowledge, none of them related this temporal variation at individual level with environmental variability in a long temporal series.

Within this framework, we designed a longitudinal study to disentangle the relative importance of environmental variability as well as inter- (i.e., population) and intra-individual variation in the trophic ecology of a long-lived species. We used the Cory's shearwater (*Calonectris borealis*) breeding in the Canary Islands, which recurrently exploit the CC (Ramos et al., 2013), as model species. In this regard, the increasing exploitation of the CC by local and industrial fisheries (Ramos and Grémillet, 2013; Sambe et al., 2016) calls for studying changes in the trophic web structure of such a relevant upwelling ecosystem. We performed SIA on the first primary feather (hereafter P1) of 99 individuals sampled repeatedly over a period of 17 years to determine changes in stable isotope values across years as well as to ascertain individual repeatability in the use of trophic resources. Specifically, we quantified $\delta^{13}C$ and $\delta^{15}N$ to assess repeatability at both population and individual level, in foraging habitats and consumer's trophic level, respectively, while also testing for relevant environmental covariates and specific intrinsic factors (i.e., sex, bill morphology, and individual experience). Given the intense exploitation of the CC (Arístegui et al., 2006; Ramos and Grémillet, 2013) and that most seabirds maximize foraging efficiency by responding opportunistically to prey availability (Pinaud and Weimerskirch, 2005; Lyday et al., 2015), we expected to find a longitudinal change in the foraging habits of Cory's shearwater feeding more on discarded benthic prey, as well as a temporal decay of its trophic level in response to the increasing fishery pressure on small pelagic fish (e.g., Gagne et al., 2018).

2. Methods

2.1. Model species

Cory's shearwater is a medium-sized Procellariiform species with a long lifespan of over 30 years (Ramos et al., 2012). The species is a colonial pelagic shearwater, highly monogamous, with strong philopatry and interannual breeding burrow fidelity. It breeds annually, mostly in remote islets and islands across Macaronesia (Thibault et al., 1997). Adults arrive at the colony in late February or early March, where females lay a single egg in early June. Both mates share incubation duties, and chicks hatch in mid-late July and fledge in late October (Thibault et al., 1997). In general, these shearwaters undertake long and rapid transoceanic migrations from their Macaronesian breeding grounds to their wintering areas in the North, Central and South Atlantic Ocean, even reaching the Indian Ocean (González-Solís et al., 2007).

Primary feather renewal of the Cory's shearwater occurs at the end of the breeding period. Moult is simple and descending from the most proximal primary feather (the first primary, P1), moulted at the end of the breeding period, towards the most distal feather (the tenth primary, P10), moulted at the end of the non-breeding period, and in a fairly synchronous way between wings (Alonso et al., 2009). Alonso et al. (2009) reported that 81% of the Cory's shearwaters they captured in early October had P1 feathers moulted and regrown. In addition, recent moult results on the species, based on SIA, revealed that the innermost primaries (i.e., from P1 to P3) of all individuals were moulted and regrown at the breeding grounds, regardless of their breeding success (Ramos et al., 2018b).

2.2. Sampling site and design

The present study and fieldwork experiments were conducted in a Cory's shearwater colony in Gran Canaria, Canary Archipelago, Spain (15°47′18″ N; 27°50′41″ W). During every early breeding season (i.e., April to June) of the period 2002–2018, we visited all known, accessible burrows of the colony, and sampled the entire emerged part of the P1 of 99 adult shearwaters (n_{total} = 646 feathers; notice that every sampled P1 feather was grown the year before, therefore, the study period represented 2001–2017). The number of sampled feathers per individual varied between 3 and 14 years (in particular, one individual was sampled up to 14 times, one individual 13 times, and another two birds 12 times; Table 2). P1 feathers were cut at skin level (i.e., mid calamus) and were sampled alternatively on the right and left wings every year to avoid biases arising from a potential alteration on the moulting schedule of the feather after cutting it. Complimentarily, birds were sampled for specific morphometric measurements of the bill at the time of ringing by different researchers (Appendix S1: Table S1). To evaluate effect of bill size on the trophic ecology of the individuals, we performed a Principal Component Analysis (PCA) using *prcomp* function in R, version 3.3.2 (R Core Team, 2018), with culmen, maximum bill depth, bill depth at nostril, and total head length (bill-head) as variables (Appendix S1: Fig. S1). We took the first Principal Component (PC1) from the PCA as an estimate of bill size for every individual bird. In addition, at the time of their first capture, all birds were sampled for 1.0 ml of blood taken from the tarsal vein using sterile syringes and needles. From these blood samples, all birds were sexed molecularly following Fridolfsson and Ellegren (1999), and based on the detection of a female-specific locus (CHD1-W; diagnostic kit from Durviz, Valencia, Spain). Finally, determining exact age of birds can only be

Table 2
Summary of individual Cory's shearwaters (*Calonectris borealis*) included in the study (n = 99 birds), and the repeated samplings of the innermost primary feather (P1) of every bird (n = 646 feathers).

Years of sampling	Number of individuals
3	19
4	12
5	13
6	14
7	13
8	9
9	7
10	5
11	3
12	2
13	1
14	1
Total	99

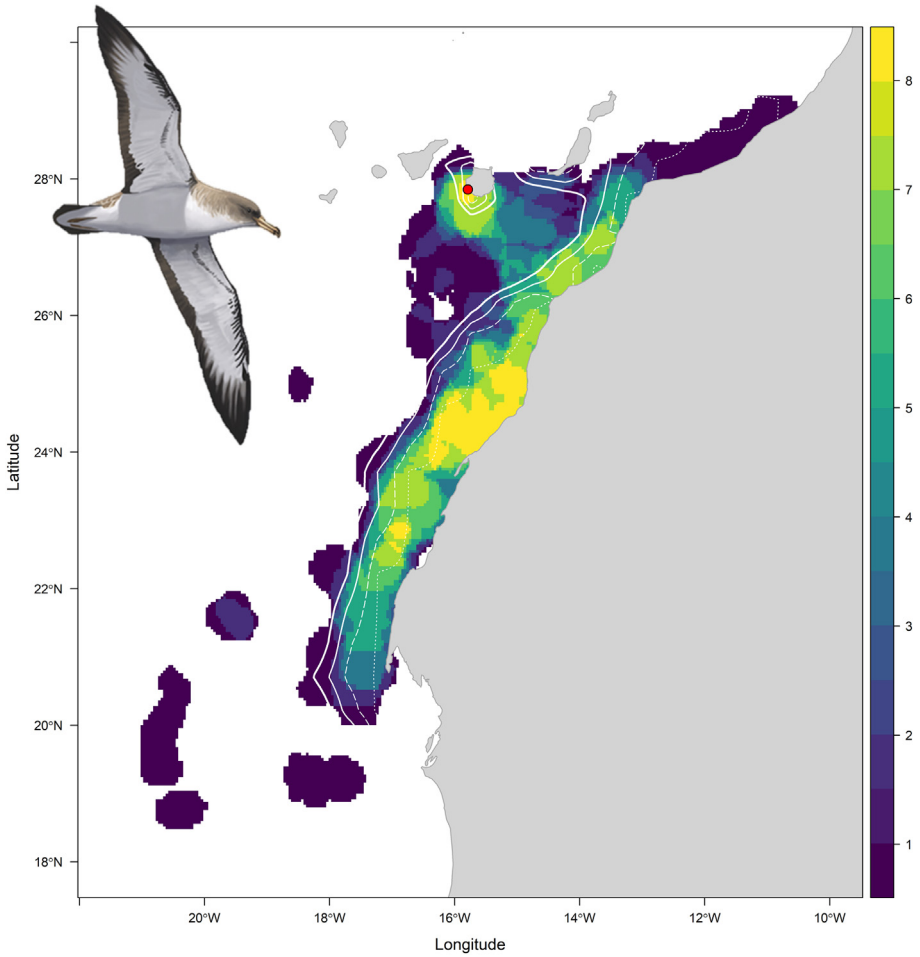


Fig. 1. Foraging areas of Cory's shearwater (*Calonectris borealis*) from Veneguera (Gran Canaria). The coloured background depicts the number of years that at least one individual KDE, calculated with foraging locations (see Methods for details), occurred within each cell during chick-rearing periods (July-August-September) of eight consecutive years (2011–2018). The red circle shows the location of the breeding colony (Gran Canaria). White contours indicate bathymetry curves (dotted = 100 m, dashed = 500 m, continuous = 1,000 m, thick continuous = 1,500 m). The bird silhouette is courtesy of Martí Franch.

assessed by ringing the individuals as chicks but this is often impractical in long-lived species with delayed recruitment (such as the Cory's shearwater; Mougin et al., 2000). Since all individuals of this study were ringed as adults, we cannot assess their exact age at the time of sampling, and we used therefore "years since first sampling" as a proxy for experience (Exp), assuming that each year that passes, whatever the age at the first year of sampling, an individual has gained experience (e.g., Nichols et al., 1997; Crespin et al., 2006; R Core Team, 2018).

2.3. SIA procedures

We first washed P1 feathers in a 0.25 M sodium hydroxide solution (NaOH), rinsed twice thoroughly in distilled water to remove any surface contamination and dried to constant mass in an oven at 40 °C. Second, we grounded them to a fine powder in a cryogenic impact grinder (Freezer mill Spex Certiprep 6750; Spex Industries). Finally, we weighed subsamples of powdered feathers to the nearest μg, placed in tin capsules and crimped for combustion for C and N isotope determinations. SIA was carried out at the Serveis Científico-Tècnics of the Universitat de Barcelona (SCT-UB; Spain) by means of elemental analysis-isotope ratio mass spectrometry using a ThermoFinnigan Flash 1112 (CE Elantech, Lakewood, NJ, USA) elemental analyser coupled to a Delta-C isotope ratio mass spectrometer via a CONFLOIII interface (ThermoFinnigan MAT, Bremen, Germany). Stable isotope ratios were expressed in the standard δ-notation (‰) relative to Vienna Pee Dee Belemnite (VPDB; $\delta^{13}C$), and atmospheric N_2 (AIR; $\delta^{15}N$). The isotopic ratio mass spectrometry facility at the SCT-UB applies international inorganic standards (IAEA CH_7, IAEA CH_6 and USGS-24 for C, and IAEA N_1, IAEA N_2 and IAEA NO_3 for N) inserted every 12 samples to calibrate the system and compensate for any drift over time. Replicate assays of standard materials indicated measurement errors of ± 0.1 and ± 0.2‰, for C and N, respectively, but these are likely underestimates of true measurement error for complex organic compounds like feathers.

2.4. Removing the marine Suess effect

Prior to evaluating temporal trends in $\delta^{13}C$ records in individual and population parameters, it was necessary to remove variability associated with the marine Suess effect, because this reflects changing atmospheric $\delta^{13}C$ ratios rather than climate variability (Eide et al., 2017). The marine Suess effect is typically characterized by a negative trend in $\delta^{13}C$ values over the last ~150 years, which for the latter half of the 20th century has been estimated as (Körtzinger et al., 2003): $\delta^{13}C_{adj} = \delta^{13}C_{obs} - 0.026*(2017 - t_i)$, where t_i is the year assigned to each $\delta^{13}C_{obs}$ value and $\delta^{13}C_{adj}$ are values adjusted for the Suess effect.

2.5. Foraging areas and environmental variables

Shearwaters from the sampled population in Gran Canaria consistently exploit the CC throughout its breeding period (Ramos et al., 2013). To properly evaluate and extract the environmental variables that may condition trophic ecology of the individuals year after year,

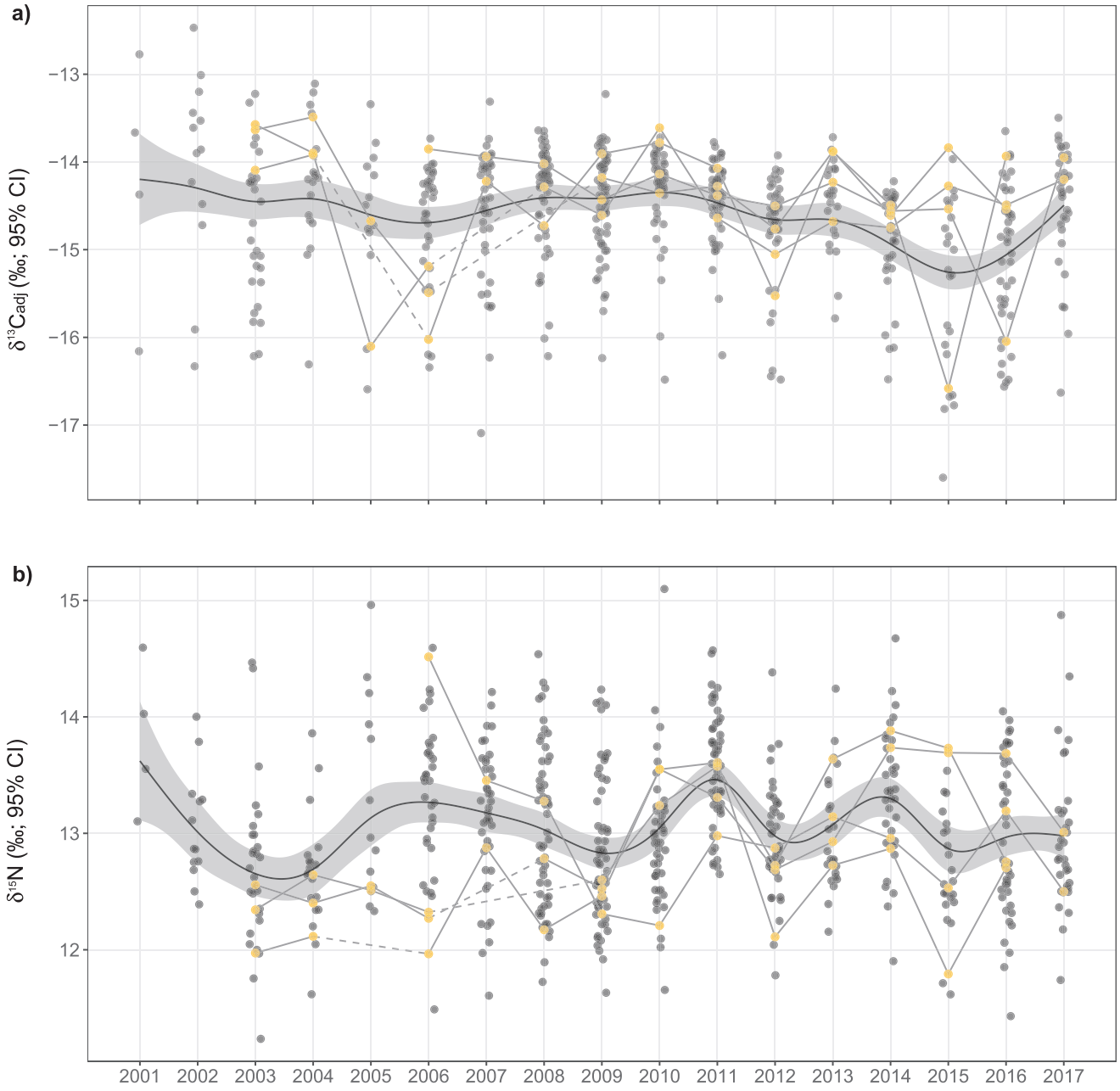


Fig. 2. Feather $\delta^{13}C_{adj}$ (a) and $\delta^{15}N$ (b) values of innermost primary feather (P1) of 99 Cory's shearwaters sampled throughout the 17-year study. The solid lines correspond to the mean estimated using Generalized Additive Mixed Models (GAMM), and the grey-coloured regions around the means represent the associated 95% Confidence Intervals (95% CI) of the slopes. Additionally, we depict four individuals sampled for 12, 13 and 14 years with line-connected yellow circles, dashed lines connect years with missing sampling (see Table 2 for details of sample sizes).

we first estimated foraging areas of the sampled population by tracking movements of 167 individuals during the late breeding period (July-August-September) of eight consecutive years (2011–2018). Birds were tracked using Global Positioning System loggers (GPS; CatTrack® Technologies and Perthold Industries Ltd.) attached to the back feathers of birds with Tesa® tape. Deployed loggers represented between 1.9 and 3.7% of bird body mass (depending on the battery size of GPSs and the weight of the bird, but always < 4.0% of adult mass; Passos et al., 2010). We classified GPS at-sea positions into four possible behavioural modes, using the R-package EMbC (Garriga et al., 2016): intensive search, extensive search, resting and relocating. From the foraging positions only (i.e. intensive and extensive search), we calculated Kernel Density Estimations (KDEs; *kernelUD* function from the adehabitat v.1.8.7 package in R; Calenge, 2006) for each trip, with a smoothing factor of $h = 21$ km (obtained from the mean of Area Restricted Search (ARS) radius; Lascelles et al., 2016). We calculated 50% KDE density contours (KDE50 hereafter) from each trip and, over a grid of 0.05° x 0.05°, we calculated the number of years that at least one KDE50 was present in each cell (Fig. 1). We used the resulting grid as a proxy of the yearly foraging consistency of the entire population during the chick-rearing period.

Second, and to determine the influence of the local environment on the trophic ecology of the population, we analyzed remote sensing data of key environmental variables in the area consistently used by foraging birds. We extracted environmental variables only from those areas used during the eight years of GPS tracking and over the African continental

shelf (i.e. we excluded the area consistently used around the Canary archipelago where breeding colony is located). We extracted monthly composites of the surface chlorophyll *a* concentration (CHLa, mg m^{-3}), sea surface salinity (SAL, g of salt per kg of water), sea surface temperature (SST, °C) and wind speed (WIND, m s^{-1}) from global ocean physics reprocessed models (L4; www.marine.copernicus.eu, EU Copernicus Marine Service Information), with a grid resolution of 0.25° over the period 2001–2017. Monthly estimates were averaged over the aforementioned area. To consider the most influential period of each environmental variable on the isotopic ratios of P1 feathers, CHLa estimates were added from February to June, SAL and SST estimates were averaged for the same period, and WIND estimates were averaged from September to October within every year (see details in Appendix S1: Fig. S2).

Third, we also wanted to explore potential effects of large-scale climatic indexes, such as NAO, on the trophic ecology of the individuals/population, as these global indexes often capture the complex associations between atmospheric and ecological processes better than local indexes (Hallett et al., 2004). NAO index, defined as the normalized sea level pressure difference measured in meteorological stations located at Gibraltar and Iceland (Jones et al., 1997), is often a good indicator of environmental conditions in the North Atlantic. Positive values of NAO lead to windy and warmer conditions in the North Atlantic, and thus positively affect upwelling intensity in the CC (Santos et al., 2005). In this regard, the recruitment and abundance of small pelagic fish (e.g., sardine) and cephalopods in the area is known to be positively influenced by upwelling intensity (Borges et al., 2003; Santos et al., 2005). Therefore, we extracted monthly estimates of NAO for the period 2000–2017, available at https://www.esrl.noaa.gov/psd/data/, and we averaged them from October to September to account the environmental variability of every annual cycle (Appendix S1: Fig. S2).

Forth, we also estimated the productivity of the CC by obtaining annual fishery catches (i.e., landings in tonnes, excluding quantities discarded after catching) from the FAO online query panel of the Eastern Central Atlantic (CECAF) Capture Production 1970–2016 (http://www.fao.org/fishery/statistics/cecaf-capture-production/query/en). Specifically, we extracted data for Clupeiforms (herrings, sardines, anchovies; hereafter CLUP), for the Saharan coast, and for the period 2001–2016.

Finally, to exclude redundant covariables for the modelling, we evaluated pairwise and cross correlations among the six environmental variables (CHLa, SAL, SST, WIND, NAO, and CLUP) computed for the most influential time periods using Pearson's methodology (Appendix S1: Fig. S3).

2.6. Statistical analysis, isotopic modelling, and repeatability assessments

To illustrate isotopic changes through time, we modelled both $\delta^{13}C_{adj}$ and $\delta^{15}N$, using Generalized Additive Mixed Models (GAMM), including year as a smooth term and bird identity as a random term (Fig. 2). We used the package *mgcv* in R, and penalized regression splines and generalized cross-validation to select the appropriate smoothing parameters (Wood and Augustin, 2002).

We built a set of competing Linear Mixed Models (LMM) to evaluate the relationships of $\delta^{13}C_{adj}$ and $\delta^{15}N$ with extrinsic (environmental) determinants and the influence intrinsic (sex, bill size, and experience) factors in the trophic ecology of birds. Specifically, we considered sex as fixed effect, PC1 (from bill measurements), Exp, CHLa, NAO, and year as covariates, and bird identity as a random effect (Table 3 and Fig. 3). Notice that we excluded SAL and SST from the modelling as they were highly correlated with NAO; and WIND and CLUP because they were correlated with CHLa (Appendix S1: Fig. S3). The full model only included interaction between sex and PC1, because we foresee differential effect of bill size depending on the sex (Catry et al., 2005; Navarro et al., 2009). We selected the most parsimonious models based on corrected Akaike's information criterion (AICc hereafter) values. When ΔAICc among the best models was lower than 2 (Johnson and Omland, 2004), we performed model averaging of the selected models using the function *model.avg* (Bartoń, 2017) to obtain average statistical estimates. For final $\delta^{13}C_{adj}$ and $\delta^{15}N$ models, we assessed the normality of residuals through Q-Q plots and Shapiro-Wilk tests. LMMs were conducted in R (version 3.2.5, R Development Core Team, 2016) with additional functions provided by the R packages *lme4* (lmer; Bates et al., 2008), *MuMIn* (Bartoń, 2017), and *lmerTest* (Kuznetsova et al., 2017).

We quantified population-level repeatability (R_{pop}; also known as intra-class correlation coefficient) of both $\delta^{13}C_{adj}$ and $\delta^{15}N$ ratios. *R* is defined as the relative partitioning of variance into within-group and between-group sources of variance (Nakagawa and Schielzeth, 2010):

$$R_{pop} = \frac{\sigma_\alpha^2}{\sigma_\alpha^2 + \sigma_\varepsilon^2}$$

In the context of individual variation, σ_α^2 corresponds to the between-individual variance, σ_ε^2 is the within-individual variance, and the sum of both σ_α^2 and σ_ε^2represents the global population variance. R_{pop} value can range from 0 (no repeatability) to 1 (high repeatability). However, low values can arise because of high within-individual variation but also because of low between-individual variation. We assessed R_{pop} using the framework of the most parsimonious LMMs. Note that as we controlled for confounding effects in the fixed part of LMMs, the resulting estimates should be considered as adjusted repeatabilities (Nakagawa and Schielzeth, 2010). R_{pop} was calculated for each isotope ratio using the *rpt* function from *rptR* package in R (Stoffel et al., 2017); we ran 999 permutations to get 95% Confidence Intervals (95% CI) from bootstrapping procedures (Fig. 4).

In order to assess individual specialisation in foraging habitats and trophic level, we further calculated repeatability of $\delta^{13}C_{adj}$ and $\delta^{15}N$ for each individual (individual-level repeatability, R_{ind}). We followed the approach of Potier et al. (2015) to separate the proportion of residual variance explained by each level of the random effect (i.e., the bird identities) from previous LMMs. Because we had a variety of sampling schedule among individuals, ranging from three to 14 years, we performed a linear regression to evaluate a possible bias imposed by the number of years sampled on the R_{ind} values (Fig. 5 and Appendix S1: Fig. S4).

3. Results

As expected, the foraging grounds during the chick-rearing period of Cory's shearwaters breeding in Gran Canaria are closely linked to CC ecosystem (Fig. 1). Based on tracking data of eight consecutive years, we showed that shearwaters foraged mainly in the nearby highly productive waters over the African continental shelf (at < 80 km from the African coast and in shallow waters < 100 m in depth).

In general, $\delta^{13}C_{obs}$ experimented a slight, sustained decay over time (Appendix S1: Table S2) that persisted even after correcting for the Suess effect (i.e., $\delta^{13}C_{adj}$; Fig. 2a). However, there was no perceivable long-term trend in the $\delta^{15}N$ values (Fig. 2b). On one hand, while examining the effect of extrinsic (environmental) variability on the trophic ecology of Cory's shearwaters, LMMs revealed that $\delta^{13}C_{adj}$ values were negatively related to CHLa and NAO values, in addition to a longitudinal, negative effect of year of sampling (Fig. 3), and that $\delta^{15}N$ values were also negatively related to CHLa (Table 3). On the other hand, LMMs also revealed that bill size (PC1) was a relevant factor in $\delta^{13}C_{adj}$ values of female individuals (Table 3 and Fig. 3). Finally, LMMs also revealed that bird identity accounted for a small proportion of the total variance in both isotopic ratios (Table 3). Accordingly, R_{pop} (i.e., population-level repeatabilities) were relatively low in both isotopic ratios (Table 3 and Fig. 4). Non-overlapping zero and relatively narrow 95% CI of both repeatabilities indicated, respectively, that they statistically differed from zero and that their estimations were precise (Wolak et al., 2012). Regarding R_{ind} (i.e., individual-level

Table 3
Linear Mixed Models (LMM) testing for the effect of sex, bill size, bird experience (years since the first sampling) and environmental covariates on $\delta^{13}C_{adj}$ and $\delta^{15}N$ values of 99 Cory's shearwaters analysed repeatedly for the period 2001–2017. To properly quantify within-individual effects, between-individual effects and environmental variability, all models included bird identity as a random factor. (a) Candidate models evaluated to fit the data corresponding to both isotopic ratios (in ‰) and their associated measures of information (AICc: corrected Akaike's Information Criterion; ΔAICc: AICc increments and AICc Wgt: AICc weights). The most complete model included the sex, the first Principal Component of the bill measurements PCA (PC1), as well as their interaction (Sex:PC1), every? bird experience (Exp), the surface chlorophyll *a* concentration (CHLa), the large-scale North Atlantic Oscillation index (NAO), and the effect of year. Only models with AICc Wgt > 0.015 for any of the isotopic ratios are shown in this table. As AICc values of the best-supported models did not differ in 2.0 units, we performed model averaging to obtain statistical estimates of the variables. The best-supported models are shown in bold. (b) Estimates of fixed effects and covariates (± Standard Error, SE) from the averaged models, and the estimated variance of each random term (± Standard Deviation, SD). (c) Repeatability (R_{pop}) measurements (± SE) of individual effects calculated from random-effect variance estimates (see Methods section for details), and their associated uncertainty (as 95% Confidence Intervals, 95% CI) calculated via parametric bootstrapping.

a)		$\delta^{13}C_{adj}$ (‰)			$\delta^{15}N$ (‰)		
	df	AICc	ΔAICc	AICc Wgt	AICc	ΔAICc	AICc Wgt
Sex * PC1 + Exp + Chla + NAO + year	10	**1201.1**	**1.6**	**0.074**	1105.2	10.6	0.001
Sex * PC1 + CHLa + NAO + year	9	**1199.6**	**0.0**	**0.162**	1103.7	9.0	0.002
Sex * PC1 + Exp + CHLa + NAO	9	**1200.1**	**0.6**	**0.122**	1104.0	9.4	0.002
Sex + PC1 + Exp + CHLa + NAO + year	9	1203.4	3.8	0.024	1103.9	9.3	0.002
Sex + PC1 + CHLa + NAO + year	8	1201.6	2.0	0.058	1102.3	7.6	0.004
Sex + PC1 + Exp + CHLa + NAO	8	1202.8	3.2	0.032	1102.6	7.9	0.004
Sex + Exp + CHLa + NAO + year	8	1204.0	4.4	0.018	1101.9	7.2	0.005
Sex * PC1 + NAO + year	8	1203.7	4.1	0.021	1109.2	14.6	0.000
PC1 + Exp + CHLa + NAO + year	8	1204.2	4.7	0.016	1101.9	7.2	0.005
Sex * PC1 + Exp + NAO	8	1203.7	4.2	0.020	1110.7	16.0	0.000
Sex + CHLa + NAO + year	7	1202.2	2.6	0.044	1100.2	5.6	0.012
Exp + CHLa + NAO + year	7	1202.3	2.8	0.041	1099.9	5.2	0.014
PC1 + CHLa + NAO + year	7	1202.4	2.8	0.040	1100.3	5.6	0.011
Sex + Exp + CHLa + NAO	7	1203.4	3.9	0.023	1100.5	5.9	0.010
PC1 + Exp + CHLa + NAO	7	1203.9	4.3	0.019	1100.6	5.9	0.010
CHLa + NAO + year	6	**1200.5**	**1.0**	**0.101**	1098.3	3.6	0.031
Exp + CHLa + NAO	6	1202.0	2.4	0.049	1098.6	3.9	0.026
Exp + CHLa + year	6	1207.7	8.1	0.003	1098.1	3.4	0.034
Sex + CHLa + NAO	6	1209.5	10.0	0.001	1098.5	3.8	0.028
Sex + CHLa + year	6	1208.1	8.5	0.002	1098.6	3.9	0.027
PC1 + CHLa + NAO	6	1209.9	10.3	0.001	1098.5	3.9	0.027
PC1 + CHLa + year	6	1208.3	8.7	0.002	1098.6	3.9	0.026
Sex + Exp + CHLa	6	1210.1	10.5	0.001	1098.6	4.0	0.026
PC1 + Exp + CHLa	6	1210.7	11.1	0.001	1098.6	4.0	0.026
Sex + PC1 + CHLa	6	1233.0	33.4	0.000	1098.6	4.0	0.026
CHLa + year	5	1206.4	6.9	0.005	**1096.6**	**1.9**	**0.071**
CHLa + NAO	5	1208.0	8.4	0.002	**1096.6**	**1.9**	**0.073**
Sex + PC1 + Exp + CHLa + NAO	5	1233.9	34.4	0.000	**1096.6**	**1.9**	**0.071**
PC1 + CHLa	5	1234.5	34.9	0.000	**1096.6**	**1.9**	**0.071**
Exp + CHLa	5	1208.7	9.1	0.002	1096.7	2.0	0.068
CHLa	4	1232.5	33.0	0.000	**1094.7**	**0.0**	**0.188**
b)							
Fixed effects	Estimate ± SE (95% CI)			z value	*P*-value	Estimate ± SE (95% CI)	z value	*P*-value
Intercept	**−14.53 ± 0.11 (-14.75|-14.31)**			**130.6**	**0.000**	**13.04 ± 0.04 (12.96|13.12)**	**325.1**	**0.000**
Sex(Female)	−0.26 ± 0.14 (-0.53|0.02)			1.9	0.065	0.02 ± 0.08 (-0.12|0.17)	0.3	0.754
PC1	0.03 ± 0.10 (-0.16|0.23)			0.3	0.743	−0.01 ± 0.04 (-0.08|0.06)	0.3	0.784
Exp	−0.02 ± 0.01 (-0.05|0.01)			1.4	0.149			
CHLa	**−0.08 ± 0.03 (-0.15|-0.02)**			**2.5**	**0.014**	**−0.09 ± 0.03 (-0.14|-0.04)**	**3.6**	**0.000**
NAO	**−0.11 ± 0.04 (-0.18|-0.03)**			**2.8**	**0.005**	−0.01 ± 0.03 (-0.07|0.05)	0.4	0.718
year	**−0.10 ± 0.05 (-0.19|-0.01)**			**2.1**	**0.037**	0.01 ± 0.03 (-0.05|0.06)	0.3	0.773
Females:PC1	**−0.29 ± 0.14 (-0.56|-0.02)**			**2.1**	**0.036**			
Random effects	Variance ± SD					Variance ± SD		
Individual	0.09 ± 0.30					0.07 ± 0.26		
Residual	0.45 ± 0.67					0.35 ± 0.59		
c)								
Repeatability (R_{pop})	Estimate ± SE (95% CI)					Estimate ± SE (95% CI)		
Individual	0.167 ± 0.042 (0.087|0.255)					0.171 ± 0.040 (0.091|0.249)		

repeatabilities), most of the individuals had estimates around the mean value of R_{pop} (~0.2) for both $\delta^{13}C_{adj}$ and $\delta^{15}N$, although a few of them had higher R_{ind} values (out of 99 individuals, nine for $\delta^{13}C_{adj}$ and two for $\delta^{15}N$ had $R_{ind} > 0.5$; Fig. 5). We did not find any relationship between R_{ind} and the number of sampled years ($\delta^{13}C_{adj}$: $r^2 = 0.003$, *P*-value = 0.585; $\delta^{15}N$: $r^2 = 0.000$, *P*-value = 0.873), discarding any possible bias due to sampling effort. Finally, we did not find a statistically significant correlation between R_{ind} of $\delta^{13}C_{adj}$ and $\delta^{15}N$ ($r^2 = 0.001$; *P*-value = 0.769; Appendix S1: Fig. S4).

4. Discussion

In this study, SIA in feathers of about a hundred Cory's shearwaters repeatedly sampled for several years showed the influence of extrinsic (environmental) factors on the trophic ecology of this population for nearly two decades. Carbon isotopic ratios ($\delta^{13}C$) related negatively to local CHLa concentrations and to the global NAO index, both covariates related to upwelling intensity. Surprisingly, isotopic values of nitrogen ($\delta^{15}N$) remained relatively stable with no obvious temporal trend along the sampled years, and they did only relate, also negatively, to local CHLa concentrations. In addition, this sampling scheme allowed us to

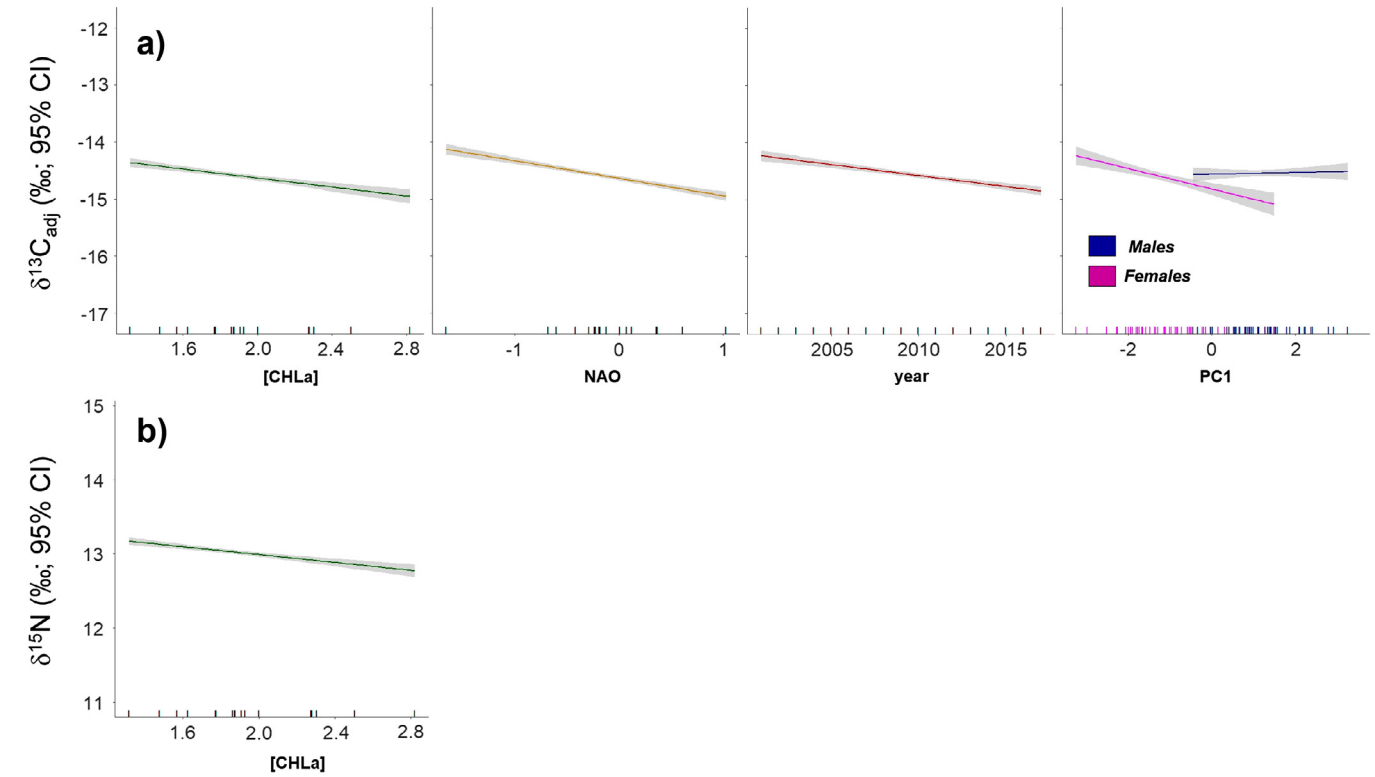


Fig. 3. Relationships of the surface chlorophyll *a* concentration (CHLa, ×100,000), the North Atlantic Oscillation Index (NAO), the longitudinal effect of year of sampling, and the bill size (PC1) linked to sex with $\delta^{13}C_{adj}$ trend (a) and the relationship of CHLa with $\delta^{15}N$ trend (b) throughout the 17-year study. Covariates relevance is quantified in Linear Mixed Models (LMM) detailed in Table 3.

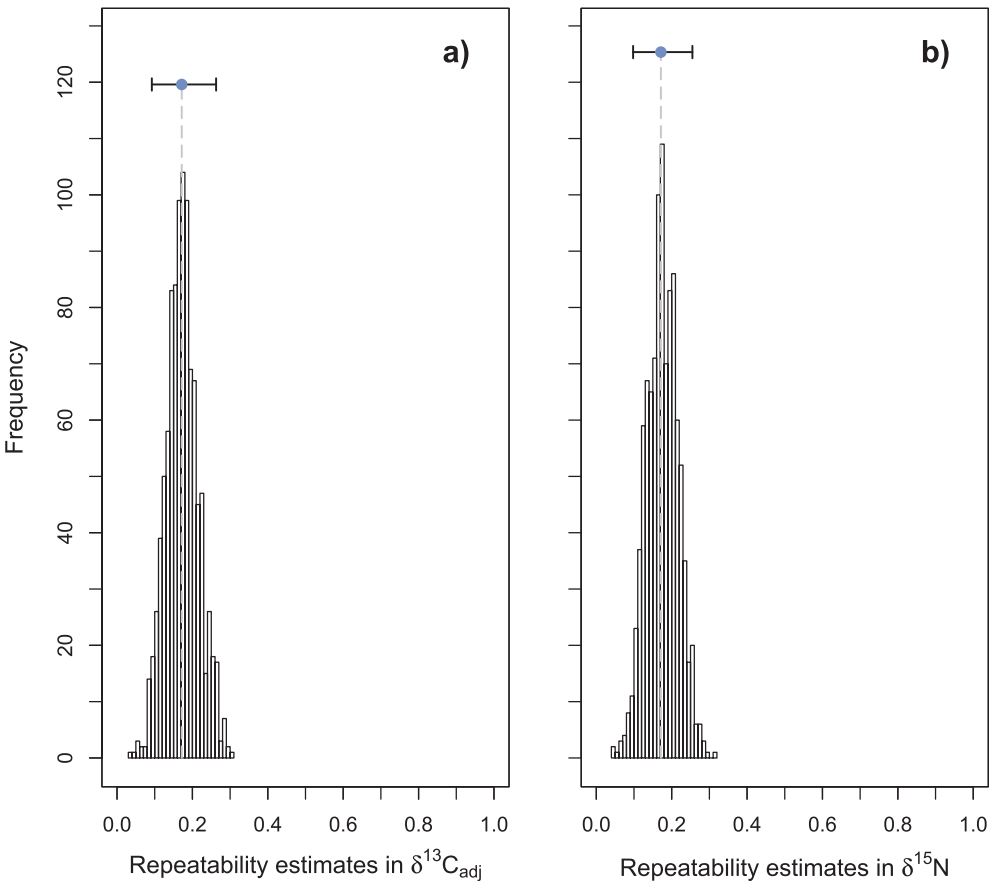


Fig. 4. Population-level repeatability estimates (R_{pop}) of the effect of bird identity extracted from LMMs of $\delta^{13}C_{adj}$ (a) and $\delta^{15}N$ (b; detailed in Table 3). Estimate frequencies were calculated using parametric bootstrapping procedures. The blue circle and grey, dashed line indicate the median and the whiskers indicate the 95% CI.

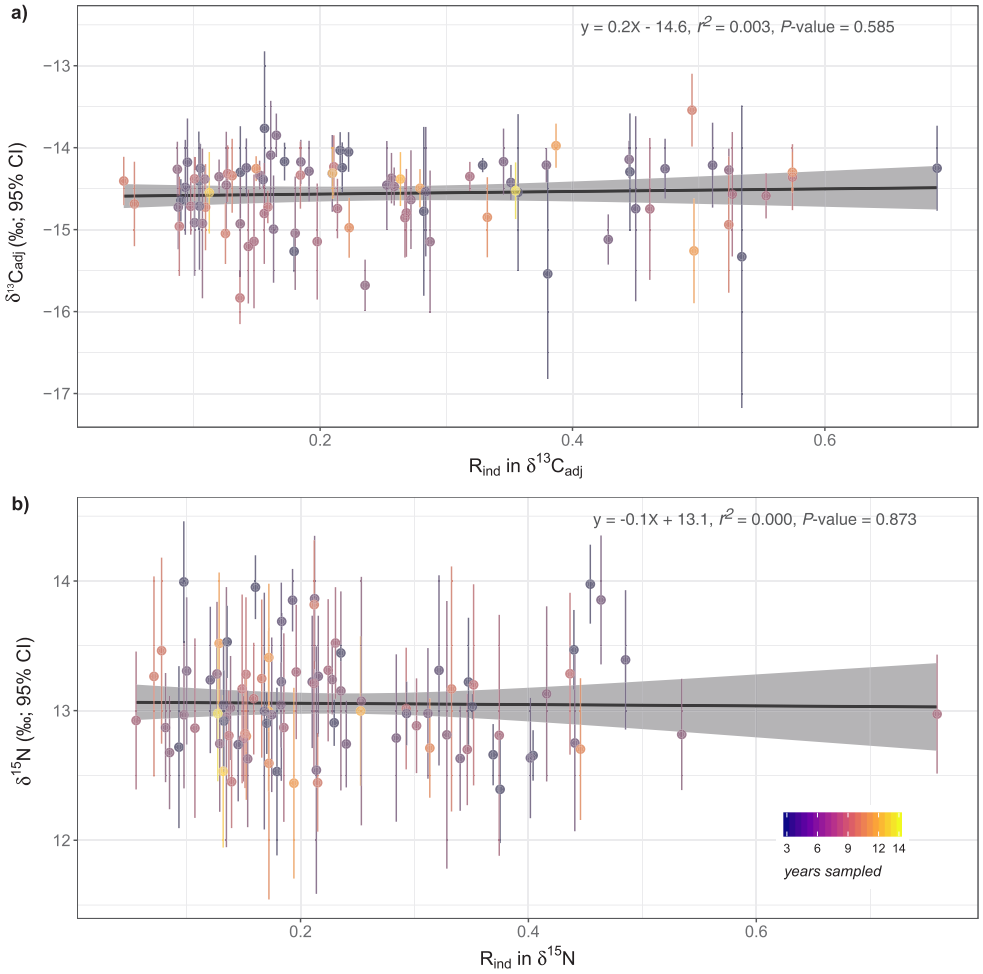


Fig. 5. Linear regression models between individual-level repeatability estimates (R_{ind}) with the individual mean ± 95% CI estimates of $\delta^{13}C_{adj}$ (a) and $\delta^{15}N$ (b). The colour gradient indicates the number of years an individual was sampled (99 individuals, sampled from three to 14 times). R_{ind} estimates were calculated from LMMs following Potier et al. (2015). Notice that both regression models are non-significant.

quantify the influence of intrinsic (individual) factors on the feeding ecology of the individuals, at group levels (sex) as well as at both, population and individual (bill size and experience) levels. These results pointed out the coexistence within our study population of individuals with different degree of specialization (from extremely flexible [generalists] to highly consistent individuals [specialists]), which ultimately have deep implications on how populations will cope with environmental changes.

4.1. Environmental variability on trophic ecology

As previously reported, our study confirmed that foraging strategies of Cory's shearwaters breeding in the Canary Islands are closely linked to the CC ecosystem during the late chick-rearing period (Ramos et al., 2013). This link is rather obvious over the Western African continental shelf, but particularly acute over one core foraging ground located at ~25°N (Fig. 1). This area geographically matches a peak in primary productivity, with strong trade winds from North-north-east and complex sea current systems, and it is known to be one of the areas with the coldest nutrient-enriched waters within the CC upwelling ecosystem (Machu et al., 2009). Nutrient-rich cold waters enhance primary and secondary productivity, and support high abundances of epipelagic fish and cephalopod species (Arístegui et al., 2009; Sambe et al., 2016) which are known to be important prey of Cory's shearwaters (Paiva et al., 2010; Alonso et al., 2018). Since the P1 feather is known to be grown at the end of the breeding period, it is reasonable to assume most elements and their isotopes incorporated in P1 originate in this region of the CC.

The carbon isotopic values ($\delta^{13}C_{obs}$) in feathers sampled throughout the period 2001–2017 showed a slight long-term decay. This trend is consistent with the reported Suess effect in marine environments, which is ultimately caused by the sequestration of isotopically light carbon (^{12}C of CO_2) derived from the increasing burning of fossil fuels (Körtzinger et al., 2003; Eide et al., 2017). Such an effect on $\delta^{13}C_{obs}$ was already reported in the CC upwelling ecosystem (McGregor et al., 2007). However, even after correcting for the marine Suess effect, our values of $\delta^{13}C_{adj}$ kept such negative long-term trend along the sampled years. This finding reveals the correction proposed by Körtzinger et al. (2003) might not be lineal and that the marine Suess effect could have accentuated in our study area in the most recent years. Further research is certainly needed in this regard, as our finding could reflect even larger effects of human impacts at large-scale ecosystem level than previously thought (McGregor et al., 2007; Ramos et al., 2012).

In addition, $\delta^{13}C_{adj}$ maintained a negative correlation to local CHLa concentrations and to the global NAO index, both covariates related to upwelling intensity. In most large upwelling ecosystems, CHLa concentrations relate to nutrient fertilization by coastal upwelling, and they are often used as a proxy of marine primary productivity which is thus inherently linked to upwelling intensity (Thomas et al., 2004; Arístegui et al., 2006). The NAO index is associated with a range of climatic factors in the North Atlantic including temperature, precipitation, cloud cover and storms (Santos et al., 2005), which also

condition coastal upwelling intensity. Many previous studies carried out specifically along the CC already suggested positive links between colder weather, NAO values, and the upwelling rate (Parsons and Lear, 2001; Álvarez-Salgado et al., 2003; Borges et al., 2003; McGregor et al., 2007; Narayan et al., 2010). Upwelling is certainly a major but complex phenomenon within the oceanic carbon cycle. Typically, deep waters are saturated in ^{12}C-enriched CO_2 due to the fact that photosynthesis reactions preferentially make use of isotopically lighter $^{12}CO_2$, and that ^{12}C-enriched phytoplankton sinks to the seafloor and it is mineralized at depth. Such deep waters with ^{12}C-enriched CO_2 are upwelled along continental coasts and act as a carbon source for primary producers (McMahon et al., 2013). Thus, upwelling intensity is often negatively related to δ^{13}C values of primary producers (Sadler et al., 2012), and this relationship should be transferred up to the trophic web. This reasoning would explain the dual δ^{13}C-CHLa and δ^{13}C-NAO relationships we reported here, i.e., both higher CHLa and NAO values relate to higher upwelling intensity in the CC during the breeding period of Cory's shearwaters, which causes lower δ^{13}C values in the feathers of such top predators. This suggests that long-term changes in δ^{13}C values of predators should be tackled with caution, as they are not necessary linked to changes in feeding habits (e.g., Ceia et al., 2018; Ramos et al., 2018a), but they can result from changes in stable isotope baseline values in response to environmental conditions (Magozzi et al., 2017), and the propagation of these isotopic changes through the entire food web.

Surprisingly, δ^{15}N values remained relatively stable and did not show any temporal trend along the sampled years. The CC has been the fish basket of southern Europe since the mid-nineties, and Russia and China keep exploiting Exclusive Economic Zones of Morocco and Mauritania (Ramos and Grémillet, 2013). We therefore expected to find changes in the trophic web structuring of this area over the last two decades as a consequence of fishery overexploitation (Sambe et al., 2016; Sánchez-Garrido et al., 2019). Indeed, previous long-term studies also based on isotopic data, but set on other oceanic basins, reported seabird shifts from higher- to lower-trophic level prey mostly due to an increasing overexploitation of fisheries (e.g. Blight et al., 2015; Hobson et al., 2015; Gagne et al., 2018). Contrary to what we expected, our results showed that most Cory's shearwaters did not change their trophic position over the last two decades, which could reflect the still relatively good health status of the trophic web in the CC. This unexpected result is of high conservation relevance, showing it is still possible to regulate fishing exploitation in the area before the entire food web structure is altered. It also highlights the potential of such a long-term studies on marine top predators to monitor fishery impacts on the structure of marine trophic webs from an independent perspective of that from fishery metrics (e.g., commercial catches; Lyday et al., 2015). Often, the status of the marine ecosystems is estimated using fish catch data, which is obviously fishery-dependent, and therefore subject to inherent biases and limitations. Thus, long time series of predator tissues represent a promising method for fishery-independent assessments of marine ecosystem productivity and sustainability.

Isotopic values of nitrogen (δ^{15}N) did only relate, negatively, to local CHLa concentrations. Because δ^{15}N values are more sensitive to diet variation (i.e. prey type) than δ^{13}C values (Newsome et al., 2007), δ^{15}N-CHLa and δ^{13}C-CHLa relationships are not fully equivalent. As stated above, high CHLa concentrations are related to marine primary productivity due to coastal upwelling intensity (Thomas et al., 2004; Arístegui et al., 2006). Annual differences in marine productivity of CC produce differences in prey availability and prey types consumed by Cory's shearwaters between years (Paiva et al., 2013, 2017; Alonso et al., 2014), which could certainly affect δ^{15}N values measured in feathers. Although we do not have yearly data on diet, it is known that Cory's shearwaters change foraging tactics and diet among years (Alonso et al., 2014). Therefore, our results point out that years with more intense upwelling activity in the CC could possible relate to a slight change of diet at lower trophic positions.

4.2. Individual specialization in trophic ecology

Long-term individual specialization in trophic ecology has rarely been evaluated in long-lived taxa due to difficulties in sampling the same individuals over long time periods (Layman et al., 2012). Here, by yearly sampling the same primary feather of approximately a hundred individuals of Cory's shearwaters (up to 14 times per individual), we provide robust evidence on the repeatability of the isotopic ratios, and thus on the trophic ecology of a given population through time. The relatively wide population range in both $\delta^{13}C_{adj}$ and δ^{15}N values (i.e., 5.4 and 4.3‰, respectively; Fig. 2) indicated that our population might be feeding on different trophic webs, and over one or two trophic levels of the CC throughout the sampling period (Post, 2002). Interestingly, and contrarily to what we expected, δ^{15}N values were related neither to the sex nor to bill size of shearwaters. However, δ^{13}C values were influenced by sex, and, particularly, by the bill size of female shearwaters. This result suggests that smaller and medium-sized females could share the habitat with conspecific males along shallow waters in the CC where they could forage on different prey sizes, while the few larger females (with larger bills) are likely being competitively excluded by males with similar sized-bills and thus use more pelagic waters which is reflected in lower $\delta^{13}C_{adj}$ (Fig. 3). Finally, the experience of birds was related neither to $\delta^{13}C_{adj}$ nor δ^{15}N values, suggesting that aging *per se* should not intrinsically affect the stable isotope ratios of adults of long-lived species (Jaeger et al., 2014). However, our sampling design did not allow to properly test for the effect of aging on the trophic ecology of such a long-lived predator. Future studies focussing only on birds ringed as chicks should be more conclusive about this topic (Pelletier et al., 2014).

The low individual repeatabilities at a population level (i.e., R_{pop}) in isotopic ratios of both elements along the 17 years of sampling largely agreed with those computed at an individual level (i.e., R_{ind}). These consistent results revealed that our population of Cory's shearwaters is mostly composed by generalist individuals (Pagani-Núñez et al., 2016). This was unexpected and contrary to what others reported for both short-lived (Hjernquist et al., 2009) and long-lived bird species (Woo et al., 2008), but also for other long-lived marine predators (Newsome et al., 2009; Vander Zanden et al., 2010). Here, we argue that, although predictably productive at large temporal scale, foraging grounds of these shearwaters at small to mid-scale might be rather unpredictable from year to year within the CC, and, thus, most of the individuals could select a generalist strategy while foraging to ensure long-term success. This result suggested that long-lived individuals from populations inhabiting highly productive areas might learn and adjust their foraging and trophic ecology according to the environmental variability.

However, some individuals (nine for δ^{13}C and two for δ^{15}N out of 99) showed high repeatabilities in one isotopic ratio. Although we acknowledge that consumption of different prey combinations may eventually result in similar averaged isotopic values (e.g., Vander Zanden et al., 2010), we believe these few individuals sampled repeatedly could be identified as trophic specialists, in contrast to most of their conspecifics, which acted as generalists. This result shows not only that a generalist population may indeed be composed by specialist individuals, but that different degrees of specialisation among individuals of the same population may occur (Pagani-Núñez et al., 2016). The coexistence of such contrasting foraging strategies within a population is often neglected in literature (but see Vander Zanden et al., 2010; Toscano et al., 2016). Our results highlighted the need to consider different degrees of specialization among individuals of the same population. This variety of foraging strategies along the generalist-specialist gradient emphasise that natural selection might balance the array of trophic strategies of individuals facing environmental stochasticity to ultimately ensure long-term population viability.

Interestingly, the number of measurements on each individual (in our case, sampled years) did not influence our repeatability estimates for either of the isotopic ratios we evaluated. The result has importance not only in the present study, to discard biases due to sampling effort and ensure robustness, but also in the context of the studies on individual specialization, since there is no consensus on the period that should be considered for analysing it. In any case, this highlights the need of testing such potential influences of sample sizes in any longitudinal study evaluating inter- and intra-individual variabilities. Certainly, sample sizes of longitudinal studies should not refer only to the number of individuals, but also to the number of measurements on each individual, and the effect of such sample sizes when estimating repeatability is still a fundamental question in animal ecology and behaviour (Bonett, 2002; Wolak et al., 2012; Cleasby et al., 2015).

5. Conclusions and perspectives

By combining isotopic, morphometric and tracking data of Cory's shearwaters together with environmental data, we not only provided insights into the most influential oceanographic variables determining the trophic ecology of the study population, but also unveiled the diversity in the degree of individual specialization of the sampled individuals. First, we found clear, negative relationships of $\delta^{13}C$ and $\delta^{15}N$ values with the upwelling intensity (through NAO index and CHLa concentrations). Second, we reported a longitudinal decline of $\delta^{13}C$ values, even when values were adjusted for the marine Suess effect, suggesting a non-linear exacerbation of the Suess effect in this area of the North Atlantic. Third, we did not find any temporal trend in the trophic web structuring of the CC (through $\delta^{15}N$), despite often considered to be overexploited by industrial fisheries (Sambe et al., 2016; Sánchez-Garrido et al., 2019), suggesting a prompt regulation of fisheries may still prevent irreversible changes in this ecosystem. Fourth, our long-term sampling design also enabled us to evaluate with confidence the repeatability in the isotope ratios of individual Cory's shearwaters, revealing the coexistence of contrasting degrees of individual specialization in resource use, from highly generalist to highly specialised individuals. Finally, the latter result calls for further research focussing on understanding what defines the degree of specialization among individuals from the same population and the factors driving it in long-lived species (e.g., genetics, stages of life histories, or other intrinsic factors rather than sex and size).

Credit authorship contribution statement

Raül Ramos: Conceptualization, Formal analysis, Writing - original draft. **José Manuel Reyes-González:** Formal analysis, Writing - review & editing. **Virginia Morera-Pujol:** Formal analysis, Writing - review & editing. **Zuzana Zajková:** Formal analysis, Writing - review & editing. **Teresa Militao:** Writing - review & editing. **Jacob González-Solís:** Conceptualization, Funding acquisition, Writing - review & editing.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ecolind.2019.105963.

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RESEARCH ARTICLE

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Sexual segregation in the foraging behaviour of a slightly dimorphic seabird: Influence of the environment and fishery activity

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Abstract

1. Sexual segregation in foraging strategies has been little studied in marine species with slight sexual size dimorphism (SSD), particularly regarding the role of environmental conditions and fishery activities. Sexual differences in fishery attendance are of particular concern because uneven mortality associated with bycatch may exacerbate impacts in wildlife populations.
2. Using a seabird species with slight SSD, the Scopoli's shearwater *Calonectris diomedea*, we assessed sexual differences in foraging strategies and evaluated whether annual environmental conditions and fishery activity shaped such differences.
3. We used a 4-year dataset combining bird GPS tracking, stable isotope analysis, the North Atlantic Oscillation index (NAO, as main proxy of the annual environmental conditions), and fishing vessel positioning data (Vessel Monitoring System, VMS) from the North Western Mediterranean, a region under intense fishery pressure.
4. From 2012 to 2015, we tracked 635 foraging trips from 78 individuals. Females showed a greater foraging effort, a lower fishery attendance, a lower trophic level, and a narrower isotopic niche width than males. Moreover, in years with unfavourable environmental conditions, both sexes showed a lower fishery attendance and increased foraging effort compared to the year with most favourable conditions.
5. Our results revealed that environmental conditions influence space use, feeding resources and fishery attendance differently in males and females, overall suggesting competitive exclusion of females by males from main foraging areas and feeding resources, particularly in unfavourable environmental conditions. We highlight the importance of evaluating sexual segregation under disparate environmental conditions, particularly in species with slight SSD, since segregation may pass otherwise unnoticed if only years with similar environmental conditions are considered. The higher fishery attendance of males likely explains the male-biased bycatch ratio for this species. Thus, inter-sexual differences in foraging strategies can lead to an unbalanced exposure to relevant threats and have implications for the conservation of long-lived species.

José Manuel Reyes-González and Fernanda De Felipe contributed equally and share first coauthorship.

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KEYWORDS
diet, feeding ecology, North Atlantic Oscillation, North Western Mediterranean, seabird–fishery interactions, trophic ecology, vessel monitoring system

1 | INTRODUCTION

Sexual segregation in foraging strategies can work as a mechanism to endure or even avoid competition between males and females (Catry et al., 2005). In species with conspicuous sexual size dimorphism (SSD), the dominant sex —usually the larger one— gains priority of access to preferred resources when these are limited (Ruckstuhl & Neuhaus, 2005). This competitive exclusion usually forces the smaller sex to shift foraging strategies, which may lead to sexual segregation in space and/or feeding resource use (Ruckstuhl & Neuhaus, 2005). SSD may imply different body size but also different size in specific structures associated with prey handling, such as the bill in birds, allowing each sex to exploit different prey type due to variation in foraging abilities, thus allowing sexual segregation in the trophic niche by resource partitioning (Catry et al., 2005; Lewis et al., 2005).

The mechanisms underlying sexual segregation have been often explored in species with conspicuous SSD (e.g. González-Solís et al., 2000; Phillips et al., 2004), yet less attention has been paid to species with slight SSD in which differences in foraging strategies may not be solely mediated by body size (Lewis et al., 2002; Phillips et al., 2011). Instead, previous findings suggest that in slightly dimorphic species, sexual differences in foraging strategies are driven by the interaction at different extent among SSD, habitat selection, and environmental conditions (Cleasby et al., 2015; Paiva et al., 2017; Soldatini et al., 2019).

In the marine environment, feeding resources are patchily distributed, but they are often predictable at large spatial scales (Stewart et al., 2000). During the breeding period, colonial breeders engage in intense foraging on the feeding grounds around the colony, causing local depletion of feeding resources —the so-called Ashmole halo—, which can increase the inter-sexual competition (Ashmole, 1963; Orians & Pearson, 1979). Additionally, variability in environmental conditions, such as that driven by the North Atlantic Oscillation (NAO) phenomenon, usually modifies resource abundance (Paiva et al., 2013). In favourable environmental conditions, when prey are more abundant, competition is likely to be relaxed (Lloret et al., 2001). Conversely, when unfavourable environmental conditions lead to prey scarcity, competition may be intensified (Oro et al., 2004; Paiva et al., 2013). It is expected that, with increasing inter-sexual competition, individuals of the subordinate sex will be outcompeted and end up paying higher costs by increasing foraging effort, either by expanding their foraging areas (i.e. foraging over longer distances and for longer periods) or shifting to different feeding resources from those of the dominant sex (Gauthreaux, 1978).

Anthropogenic resources also modify food availability through commercial fishing (Montevecchi, 2002). Some fisheries, most notably trawlers and, to a lesser extent, purse seiners, provide discards, a feeding resource that is easily accessible and rather predictable for seabirds (Montevecchi, 2002; Votier et al., 2010). Many seabird species associate with fisheries to exploit this resource, which has profound consequences in their biology, for instance in modifying their foraging movements, diet, or breeding success (Arcos et al., 2008; Bartumeus et al., 2010; Grémillet et al., 2008; Laneri et al., 2010). As mentioned before, in favourable environmental conditions prey becomes more abundant/available. In accordance, fishery activity usually increases and therefore discards are more abundant (Gamito et al., 2015). Under this scenario, competition may decrease and the between-sex overlap of trophic niches may increase (González-Solís et al., 1997; Oro et al., 2013). In contrast, in conditions of discard shortage (as when the activity of the fishing fleet is reduced), competition for feeding resources increases, leading less competitive individuals to reduce fishery attendance and exploit natural prey more (Oro et al., 2013; Paiva et al., 2017). In addition, seabirds also attend longliners to try catching the baited hooks, which often leads to bycatch, a major threat for seabirds (Bicknell et al., 2013; Rodríguez et al., 2019). Concerning longliners, a sex-related bias in bycatch mortality has been found for several species (Gianuca et al., 2017). Since seabirds are socially and mostly sexually monogamous, sex-biased adult mortality is of great conservation concern because it entails pair-disruption and breeding failure, causing a severe reduction of effective population size (Mills & Ryan, 2005; Rodríguez et al., 2019; Weimerskirch et al., 2005).

In this work, we aimed to assess sexual differences in the foraging strategies of a seabird species with slight SSD, the Scopoli's shearwater *Calonectris diomedea*, and to evaluate whether contrasting inter-annual environmental conditions and fishing fleet activity may play a role in shaping such differences. Using a 4-year dataset combining bird GPS tracking, stable isotope analysis (SIA), environmental data, and fisheries tracking data (Vessel Monitoring System, VMS), we investigated potential sexual segregation and its causes in Scopoli's shearwaters foraging in the North Western Mediterranean (NWM), a region under intense fishing pressure. Some studies on the Cory's shearwater *C. borealis*, a closely related species that moves across vast foraging areas in the North Atlantic, reported no sexual differences in foraging strategies during breeding (Magalhães et al., 2008; Navarro et al., 2009; Ramos et al., 2009; see details in Appendix S1). However, recent research on Cory's shearwater focusing on the role of environmental conditions within a multi-year approach found evidence of sexual segregation in years with poor environmental conditions (Paiva et al., 2017). We expected that our multi-year approach encompassing variable environmental conditions would allow us to detect any potential sexual differences in foraging strategies of Scopoli's shearwaters. Females, which are slightly smaller than males, could be outcompeted by males, and thus we expected that (a) females generally show greater foraging effort than males, and that (b) both males and females increase foraging effort during unfavourable environmental conditions, but females to

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a greater extent than males, owing to competitive exclusion exerted by males. Lastly, although we foresaw both sexes to associate with fisheries (Genovart et al., 2018; Soriano-Redondo et al., 2016), we expected (c) a lower fishery attendance of females, as competitive exclusion of females by males should limit their access to this resource, particularly under low availability of discards.

2 | MATERIALS AND METHODS

2.1 | Model species and tracking data

The Scopoli's shearwater is a slightly dimorphic, medium-sized, long-lived, pelagic seabird endemic to the Mediterranean (De Felipe et al., 2019; Reyes-González & González-Solís, 2016). We tagged adults breeding in Cala Morell (Menorca, Balearic Islands) in four consecutive years (2012–2015) during the chick-rearing period with GPS loggers (©Perthold Engineering LLC, USA; median error of <10 m; Forin-Wiart et al., 2015). Most devices were set to record one location every 5 min, except the <10% that were set to 10 or 15 min. For further explanations about the model species, the breeding colony and fieldwork, see details in Appendix S1.

2.2 | Space use, foraging behaviour, and fishery attendance

We characterized the foraging behaviour, space and resource use and fishery attendance of males and females over the four consecutive breeding seasons using GPS tracking data. We processed data using custom-built functions in R (version 3.6.0, R Development Core Team, 2009). We first re-sampled GPS locations to one fix every 5 min (Calenge, 2006; Calenge et al., 2009; see details in Appendix S1). Then we split tracks into separate trips, considering as one foraging trip the route travelled between nest departure and the subsequent arrival to the nest. Only complete trips were considered for further analyses. For every trip, we calculated the total distance covered (in km), maximum distance reached from the colony (in km) and duration (number of days at sea). We also classified each trip as long or short (see details in Appendix S1). We applied behavioural annotation on trajectories using the EMbC algorithm to label each GPS location as foraging, resting and travelling (Garriga et al., 2016; see details in Appendix S1), and calculated the proportion of time invested on each behaviour for every trip. We identified whether birds in every trip were mainly foraging over the Balearic or Catalan waters, the two main foraging areas used (see details in Appendix S1). We characterized foraging grounds computing the fixed kernel density estimation (KDE) for every trip (see details in Appendix S1), taking only the locations previously identified as foraging. We considered 50% KDE contours (K50) to represent the main foraging ground of every single trip and estimated their size in km^2. Next, to assess the role of fisheries, we quantified for every trip the number of attendance events to fishing vessels. To do so, we used VMS data from the Spanish fishing fleet operating in the NWM. We considered that a fishery attendance event occurred when at least two consecutive GPS locations previously labelled as foraging were involved in a spatio-temporal interaction with a fishing vessel. These spatio-temporal interactions with fishing vessels were identified following Soriano-Redondo et al. (2016) (see details in Appendix S1). We also calculated the average number of vessels available in the vicinity of the birds for every trip as a proxy of fishing vessel availability (see details in Appendix S1). Lastly, for descriptive purposes, we calculated the percentage of trips presenting fishery attendance disaggregated by fishing gear.

2.3 | Stable Isotope Analysis (SIA) of blood plasma

In marine ecosystems, the ratio of the stable isotopes of carbon ($\delta^{13}C$) provides spatial information on latitudinal distribution and can help differentiate benthic and pelagic food webs. Therefore, $\delta^{13}C$ are often used to infer the origin of food sources (Ramos & González-Solís, 2012). Moreover, the ratio of the stable isotopes of nitrogen ($\delta^{15}N$) is often used to assess the trophic positions of consumers, since higher $\delta^{15}N$ correspond to a higher trophic position (Ramos & González-Solís, 2012). Thus, we performed stable isotope analysis (SIA) of both $\delta^{13}C$ and $\delta^{15}N$ to explore resource use and trophic position during the foraging trips. We collected blood at every GPS recovery and performed SIA of blood plasma, as the turnover rate of this tissue is about a week (Votier et al., 2010), which is similar to the average duration of shearwater trips (see details in Appendix S1). Every sample of plasma was linked to GPS locations in a 6-day window before each blood collection. To assign the main foraging area of such time window, we quantified the percentage of time invested in foraging both within Balearic and Catalan waters. We also quantified fishery attendance within the 6-day window before GPS recovery and blood collection.

2.4 | Environmental data

Inter-annual variability in NAO is linked to annual changes in wind patterns, sea surface temperature and rainfall in the North Atlantic, impacting ecosystem dynamics, marine productivity and distribution of prey species (Báez & Real, 2011; Durant et al., 2004). Conversely to its effects in the North Atlantic and Western Europe, in the Mediterranean basin, negative values of NAO promote an overall increase in the productivity and abundance of marine organisms from lower to upper trophic levels, whereas positive values of NAO lead to resource scarcity (Genovart et al., 2013; Hurrell, 1995). In addition to NAO, we evaluated several satellite-derived environmental features as proxies of environmental conditions, but only included NAO in further analyses because it is an integrated regional index representative of annual environmental conditions (see details in Appendix S1). We used the extended annual winter NAO (NAOw) by averaging the winter monthly values (December–March) since it is known to better correlate with resource availability in subsequent months (Paiva et al., 2013). We standardized NAOw values

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(i.e. subtracting the mean of the whole time-series data and dividing by the standard deviation) to ease interpretability of further models. Despite having only four values of NAOw (one per year), we included NAOw as a numeric variable in all models because it is a numeric index of continuous nature (see details in Appendix S1).

2.5 | Statistical analyses

We evaluated sexual differences in space use and behavioural patterns, fishery attendance, and SIA using linear (LMM) and generalized linear mixed models (GLMM; see details about response variables, predictors, and parametrization in Appendix S1). We also used $\delta^{13}C$ and $\delta^{15}N$ to generate a bidimensional isotopic space for each year and assess standard ellipse areas (SEA) for each sex as a proxy of isotopic niche width (INW). We produced a Bayesian estimation of the SEA (SEAb) to compare the probability of a sex's ellipse to be smaller than the ellipse of the other sex for each year (Jackson et al., 2011).

3 | RESULTS

Overall, we tracked 45 males and 34 females. Over the 4 years, 47 of 79 individuals were tracked only 1 year, 23 for 2 years, 6

TABLE 1 Sexual differences in trip parameters. Regional environmental conditions (as indicated by the extended annual winter North Atlantic Oscillation (NAOw) index standardized), sample size and observed annual values of the trip parameters and related metrics from males and females of Scopoli's shearwaters sampled at Cala Morell (Menorca, Balearic Islands, Spain) between 2012 and 2015. Daily vessel operating indicates the total amount of different vessels from the Spanish fishing fleet operating in the North Western Mediterranean during the breeding period of the birds. All values correspond to the mean ± Standard Deviation

	2012		2013		2014		2015	
NAOw	**1.04**		**−1.20**		**1.60**		**1.89**	
Sex	**Males**	**Females**	**Males**	**Females**	**Males**	**Females**	**Males**	**Females**
Individuals (*n*)	**24**	**20**	**12**	**11**	**14**	**10**	**17**	**12**
Trip parameters								
Foraging trips (*n*)	76	60	117	103	81	52	99	47
Short trips	69	52	104	90	74	34	79	27
Long trips	7	8	13	13	7	18	20	20
Max. distance reached (km)								
Short trips	46.8 ± 21.0	52.1 ± 24.4	42.2 ± 20.5	43.9 ± 23.9	36.6 ± 17.4	38.7 ± 22.8	47.4 ± 21.9	51.1 ± 29.9
Long trips	237.3 ± 30.2	211.5 ± 30.1	198.0 ± 26.0	211.6 ± 25.1	200.0 ± 15.0	203.8 ± 39.0	200.7 ± 22.6	210.7 ± 24.9
Total distance covered (km)								
Short trips	207.8 ± 121.0	246.9 ± 130.0	175.1 ± 142.9	183.8 ± 129.4	154.5 ± 88.0	181.1 ± 122.4	185.5 ± 94.0	223.5 ± 128.2
Long trips	1,112.7 ± 450.8	1,055.0 ± 586.0	775.9 ± 263.5	783.1 ± 305.4	718.1 ± 209.5	666.3 ± 279.0	699.2 ± 203.7	1,010.0 ± 428.2
Duration (days)								
Short trips	1.3 ± 1.0	1.6 ± 1.0	1.1 ± 0.8	1.2 ± 0.8	0.9 ± 0.4	1.1 ± 0.7	0.9 ± 0.5	1.1 ± 0.7
Long trips	5.4 ± 2.0	4.8 ± 3.1	3.1 ± 0.9	3.7 ± 2.6	3.3 ± 1.2	2.7 ± 2.0	2.7 ± 1.2	4.6 ± 2.3
Foraging ground size (km^2)	736.8 ± 1,319	1,073.6 ± 1,732	1,109.9 ± 2,209	893.0 ± 1,541	571.1 ± 1,045	2,016 ± 2,519	1,316.3 ± 2,043	2,601.4 ± 2,810
Behaviour								
% of foraging	33.7 ± 8.1	33.0 ± 8.0	30.4 ± 8.7	32.2 ± 7.7	27.0 ± 7.8	29.8 ± 6.4	31.2 ± 9.2	27.8 ± 8.8
% of travelling	25.8 ± 8.5	23.4 ± 8.2	26.1 ± 9.9	25.5 ± 8.9	29.5 ± 12.4	28.2 ± 10.9	30.2 ± 12.4	31.3 ± 10.6
% of resting	40.2 ± 9.8	43.3 ± 10.7	42.9 ± 12.6	41.9 ± 10.7	43.1 ± 13.2	41.6 ± 10.6	38.1 ± 13.2	40.5 ± 13.2
Fishery attendance events								
Count	7 ± 1.3	3 ± 0.7	9 ± 1.6	21 ± 2.6	6 ± 1.3	4 ± 0.9	8 ± 1.6	10 ± 1.9
Time invested	11.3 ± 24.8	0.3.6 ± 10.8	10.7 ± 26.5	15.7 ± 43.1	8.3 ± 16.6	6.3 ± 18.2	9.9 ± 29.9	12.7 ± 28.8
Daily vessel operating	199.8 ± 115.3		214.7 ± 118.6		206.0 ± 119.2		199.7 ± 115.1	

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for 3 years, and 2 for 4 years. We recorded a total of 373 foraging trips from males and 262 trips from females (Table 1). Shearwaters consistently used two main foraging areas: the waters surrounding the Balearic Islands, especially the Menorca Channel, and the Catalan waters (Figure 1; see details in Appendix S1). We found females to perform on average longer trips than males, both in total distance covered ($M \pm SD$, males: 259.1 ± 254.3 km; females: 354.5 ± 356.1 km) and duration ($M \pm SD$, males: 1.3 ± 1.1 days; females: 1.8 ± 1.7 days; Table 1; Figure 2a), whereas the difference in the maximum distance reached was marginally significant (Table 2). Both sexes performed short and long trips commuting towards Balearic and Catalan waters, respectively, defining a bimodal distribution in the maximum distance reached (Table 1; Figure 1; Figure S2 in Appendix S1). The probability of performing long trips was twice as high for females as for males (Table 2; Figure 2b). We found that females exploited larger foraging grounds than males in the Catalan shelf, but not in Balearic waters (Table 2; Figure S3 in Appendix S1). Time allocation to the different behavioural modes between males and females did not differ (Table 2). Regarding fisheries, birds interacted with fishing vessels in 26.46% of their

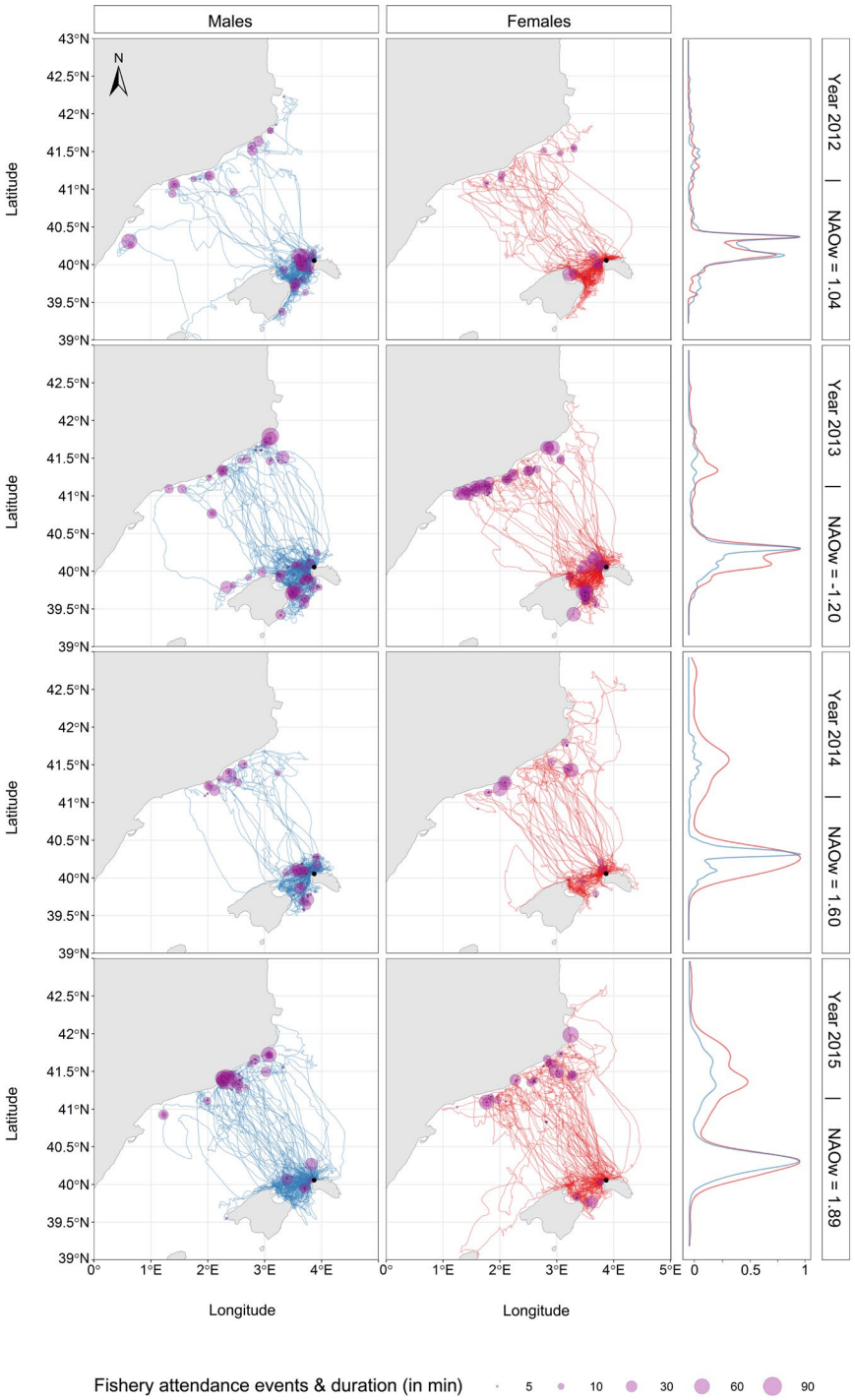


FIGURE 1 Foraging trips and fishery attendance of males and females of Scopoli's shearwater breeding in Menorca during the chick-rearing period from 2012 to 2015. Purple circles represent fishery attendance events. The size of the circles is relative to the duration of the events (in minutes), and the black spot in their centre corresponds to the centroid of the events. The black circle represents the colony, located in Cala Morell (Menorca, Balearic Islands). Density plots in the right side represent the relative amount of GPS positions by latitude, pointing out the bimodal strategy of birds that perform short trips to waters nearby the colony and long trips towards Catalan waters. The number of long trips varied annually, especially in females, likely due to inter-annual variability in the environmental conditions. NAOw values of each year are indicated on the right side

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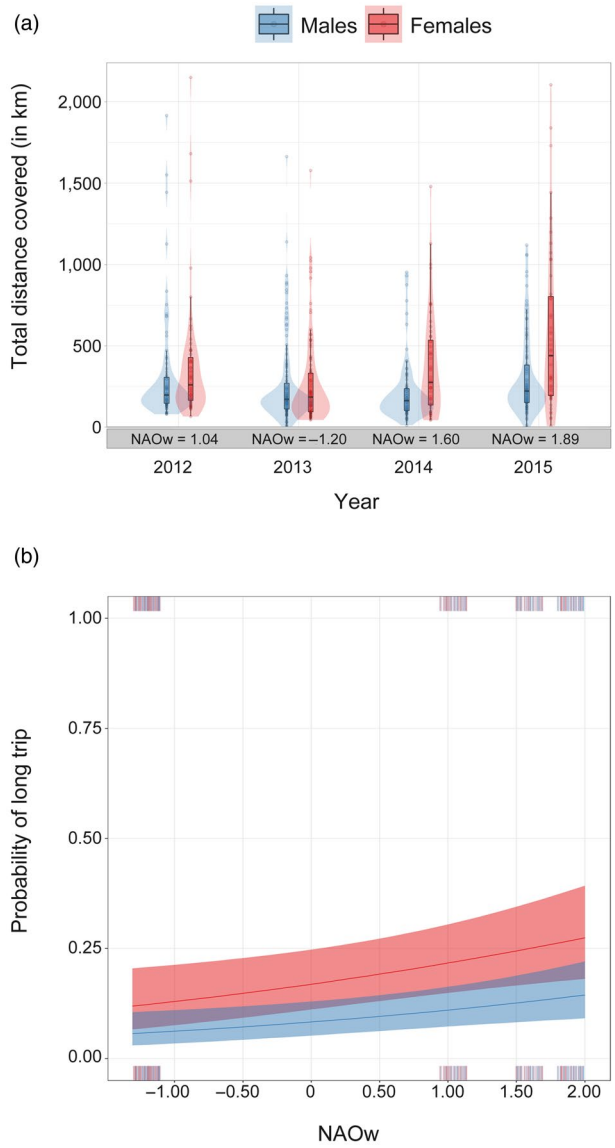


FIGURE 2 (a) Observed values of distance covered grouped by sex and year. Each dot represents a single trip. Annual values of the extended winter North Atlantic Oscillation (NAOw) index are indicated at the bottom. Violins show the probability density of raw data. Black-contoured boxplots show the median (centreline) and quartiles (hinges corresponds to percentiles 25th and 75th); whiskers extend from hinges to the largest (and the smallest) value no further than 1.5 times the interquartile range. Soft dots represent raw data. (b) Predicted probability of performing trips towards Catalan waters from the binomial logistic generalized linear mixed model. Shaded areas represent the associated 95% CI. Some jittering was applied in rugs of *X*-axis to ease visualization

trips (trawlers: 24.25%; purse seiners: 7.24%; pelagic longliners: 3.46%). Fishery attendance was half as high for females than males (Table 2; Figure S4 in Appendix S1).

There were no sexual differences in $\delta^{13}C$ in plasma, but $\delta^{15}N$ was consistently lower in females than in males across the years (Table 3). $\delta^{13}C$ was higher and $\delta^{15}N$ lower in shearwaters foraging in Balearic waters than in those foraging in Catalan waters (Table 3; Figure 3a). Time allocated to fishery attendance correlated significantly with an increase in $\delta^{15}N$ for both sexes (p-value = 0.032; Figure 3b).

Regarding environmental conditions, NAOw showed contrasting values over the four years, oscillating between −1.20 and 1.89, with positive values (i.e. likely unfavourable environmental conditions) in 2012, 2014 and 2015 and negative values (i.e. likely favourable environmental conditions) in 2013 (Table 1). An increase in the distance and duration of trips, as well as a greater probability of performing long trips towards Catalan waters correlated with higher values of NAOw. This correlation also occurred with the amount of travelling (Table 2). An enlargement of foraging grounds of females in Catalan waters correlated with higher values of NAOw. Conversely, males' foraging grounds shrunk with higher values of NAOw (Table 2; Figure S3 in Appendix S1). Fishery attendance increased with lower values of NAOw and correlated positively with the number of fishing vessels available in the vicinities (Table 2; Figure 4; Figure S4 in Appendix S1). LMM also indicated that $\delta^{15}N$ negatively correlated with NAOw (Table 2). Furthermore, females showed a smaller SEA in years with positive values of NAOw compared to males. The SEA overlap between sexes was lower in years with positive values of NAOw (Table 3; Figure 5).

4 | DISCUSSION

Despite the slight SSD of Scopoli's shearwaters (De Felipe et al., 2019), we found consistent differences in space and resource use and fishery attendance between males and females, indicating sexual segregation in their foraging strategies. Females seemed to be outcompeted by males and forced to increase their foraging effort, particularly in unfavourable environmental conditions. Moreover, males interacted more with fishing vessels than females did, profiting more from discards, and thus likely exposing themselves to a higher risk of bycatch.

4.1 | Females consistently show greater foraging effort than males

As expected, we found relevant differences between males and females in their foraging strategies, indicating that males could be outcompeting females in the access to feeding resources, including discards, as previously suggested for various species both with slight and conspicuous SSD (Cianchetti-Benedetti et al., 2018; Collet et al., 2015). Our results support our first hypothesis, as females showed a greater foraging effort (longer foraging distances and duration) than males even though both sexes generally used similar foraging areas over the 4 years. The breeding colonies of the species in the Balearic Islands and the productive waters on the Catalan shelf are separated by *c*. 200 km, an affordable distance for a gliding seabird species (Reyes-González et al., 2017). Thus, birds foraged in the Balearic waters during the short trips (~1-day) and commuted to Catalan waters during long trips (>3 days). This bimodal pattern during the chick-rearing may reflect the use of a dual foraging strategy, commonly used by many Procellariiformes (Phillips

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TABLE 2 Summary of linear (LMM) and generalized linear mixed models (GLMM). We performed several models to test for the effect of the predictors sex, extended winter North Atlantic Oscillation (NAOw) index standardized, main foraging area and fishery attendance on response variables related to space use, behaviour and trophic ecology ($\delta^{13}C$ and $\delta^{15}N$) of Scopoli's shearwaters breeding in Cala Morell (see details in Appendix S1). We included NAOw as a numeric predictor in the models since it is a numeric index of continuous nature. LMMlogT = LMM with response variable log-transformed; nbGLMM = Negative binomial GLMM; LogitGLMM = Logistic binomial regression. CAT = Catalan waters. Please note that estimates correspond to odds ratios in the case of LogitGLMM and to incidence rate ratios in the case of nbGLMM. Females in Balearic waters was set as the reference level. Statistically significant results are highlighted in bold. Also note that in nbGLMM and LogitGLMM, 95% confidence interval (95% CI) not crossing 1 indicates statistical significance

Model type	Response variable	Fixed effect	Estimate	95% CI	Statistic (t|z)	p-value
LMMlogT	Max. distance reached (km)	Intercept	54.97	47.0 to 64.3	50.0	**<0.001**
		Males	0.82	0.7 to 1.0	−1.9	0.053
		NAOw	1.10	1.0 to 1.2	2.5	**0.010**
LMMlogT	Total distance covered (km)	Intercept	229.76	198.9 to 265.4	73.8	**<0.001**
		Males	0.76	0.6 to 0.9	−2.9	**0.004**
		NAOw	1.11	1.0 to 1.2	3.3	**0.001**
nbGLMM	Duration (days)	Intercept	1.82	1.6 to 2.1	8.8	**<0.001**
		Males	0.72	0.6 to 0.8	−3.7	**<0.001**
		NAOw	1.06	1.0 to 1.1	1.7	0.087
LogitGLMM	Probability of long trip	Intercept	0.21	0.1 to 0.3	−6.4	**<0.001**
		Males	0.46	0.2 to 0.8	−2.5	**0.012**
		NAOw	1.37	1.1 to 1.7	2.7	**0.006**
LMM	Size of foraging ground	Intercept	530.36	500.2 to 620.5	18.3	**<0.001**
		Males	−1.94	−82.4 to 78.5	−0.1	0.962
		Main foraging area—CAT	908.00	788.4 to 1,027.6	14.9	**<0.001**
		NAOw	11.17	−30.0 to 52.3	0.5	0.595
		Males × CAT	130.45	−35.1 to 296.0	1.5	0.122
		Males × NAOw	−11.44	−64.73 to 41.9	−0.4	0.674
		CAT × NAOw	95.48	17.2 to 173.8	2.4	**0.017**
		Males × CAT × NAOw	−212.61	−320 to −105.2	−3.4	**<0.001**
nbGLMM	% of foraging per trip	Intercept	0.31	0.3 to 0.3	−58.9	**<0.001**
		Males	1.00	1.0 to 1.1	0.1	0.957
		NAOw	0.98	1.0 to 1.0	−1.9	0.064
nbGLMM	% of travelling per trip	Intercept	0.26	0.3 to 0.3	−46.9	**<0.001**
		Males	1.04	1.0 to 1.1	1.1	0.253
		NAOw	1.04	1.0 to 1.1	2.9	**0.004**
nbGLMM	% of resting per trip	Intercept	0.42	0.4 to 0.4	−39.2	**<0.001**
		Males	0.97	0.9 to 1.0	−1.0	0.331
		NAOw	0.99	1.0 to 1.0	−1.2	0.244
nbGLMM	Fishery attendance events	Intercept	0.00	0.0 to 0.0	−32.9	**<0.001**
		Males	1.95	1.4 to 2.8	3.7	**<0.001**
		NAOw	0. 87	0.8 to 0.9	−2.3	**0.022**
		Average vessel availability	1.31	1.2 to 1.4	8.5	**<0.001**
LMM	$\delta^{13}C$ (‰)	Intercept	−18.24	−18.3 to −18.2	−404.3	**<0.001**
		Males	−0.00	−0.1 to 0.1	−0.1	0.939
		NAOw	−0.03	−0.1 to 0.0	−1.2	0.216
		Main foraging area—CAT	−0.09	−0.2 to 0.0	−1.5	0.146
		Time in fishery attendance	−0.04	−0.1 to 0.0	−1.3	0.211

(Continues)

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TABLE 2 (Continued)

Model type	Response variable	Fixed effect	Estimate	95% CI	Statistic (*t*|*z*)	*p*-value
LMM	δ^{15}N (‰)	Intercept	9.31	9.1 to 9.5	97.3	**<0.001**
		Males	0.42	0.2 to 0.6	3.9	**<0.001**
		NAOw	−0.09	−0.2 to −0.0	−2.0	**0.047**
		Main foraging area—CAT	0.30	0.0 to 0.1	2.2	**0.025**
		Time in fishery attendance	0.16	0.0 to 0.3	2.5	**0.012**

TABLE 3 Sexual differences in trophic ecology. Regional environmental conditions, sample sizes, observed annual means of δ^{13}C and δ^{15}N (±*SD*), Bayesian estimates of the standard ellipse areas (SEAb, mean and 95% Credibility interval, Bayesian overlap (i.e. the overlapped area as a proportion of the non-overlapping area) between male and female isotopic niches ($Overlap_B$, mean and 95% CI) and geometric overlap (OverlapG) of standard ellipse areas from the blood plasma of males and females of Scopoli's shearwaters sampled at Cala Morell between 2012 and 2015. NAOw represents the extended annual winter North Atlantic Oscillation index standardized. BAL = Balearic waters, CAT = Catalan waters

	2012		2013		2014		2015	
NAOw	**1.04**		**−1.20**		**1.60**		**1.89**	
Sex	**Males**	**Females**	**Males**	**Females**	**Males**	**Females**	**Males**	**Females**
Individuals (*n*)	**23**	**16**	**12**	**10**	**12**	**9**	**16**	**9**
δ^{13}C (‰)	−18.2 ± 0.3	−18.2 ± 0.2	−18.3 ± 0.4	−18.3 ± 0.4	−18.5 ± 0.2	−18.6 ± 0.2	−18.4 ± 0.3	−18.4 ± 0.3
BAL	−18.1 ± 0.3	−18.1 ± 0.1	−18.3 ± 0.4	−18.3 ± 0.4	−18.4 ± 0.2	−18.4 ± 0.0	−18.3 ± 0.4	−18.3 ± 0.0
CAT	−18.3 ± 0.2	−18.3 ± 0.1	−18.4 ± 0.3	−18.3 ± 0.3	−18.5 ± 0.2	−18.6 ± 0.2	−18.5 ± 0.3	−18.4 ± 0.3
δ^{15}N (‰)	+9.2 ± 0.7	+8.8 ± 0.6	+10.1 ± 0.4	+9.9 ± 0.5	+9.9 ± 0.5	+9.4 ± 0.3	+10.3 ± 0.5	+9.9 ± 0.3
BAL	+8.9 ± 0.5	+8.5 ± 0.3	+10.1 ± 0.5	+9.8 ± 0.5	+9.9 ± 0.5	+9.0 ± 0.0	+10.2 ± 0.6	+10.0 ± 0.0
CAT	+9.9 ± 0.5	+9.5 ± 0.4	+10.1 ± 0.3	+9.9 ± 0.4	+10.0 ± 0.6	+9.5 ± 0.2	+10.4 ± 0.5	+9.9 ± 0.3
SEAb	0.4 (0.3–0.6)	0.3 (0.2–0.4)	0.4 (0.3–0.7)	0.4 (0.3–0.6)	0.3 (0.2–0.5)	0.2 (0.1–0.3)	0.4 (0.3–0.7)	0.2 (0.1–0.4)
$Overlap_B$ (%)	15.4 (0–52.5)		19.4 (0–63.2)		4.9 (0–37.9)		10.1 (0–43.5)	
$Overlap_G$ (%)	33.1		43.2		1.4		17.0	

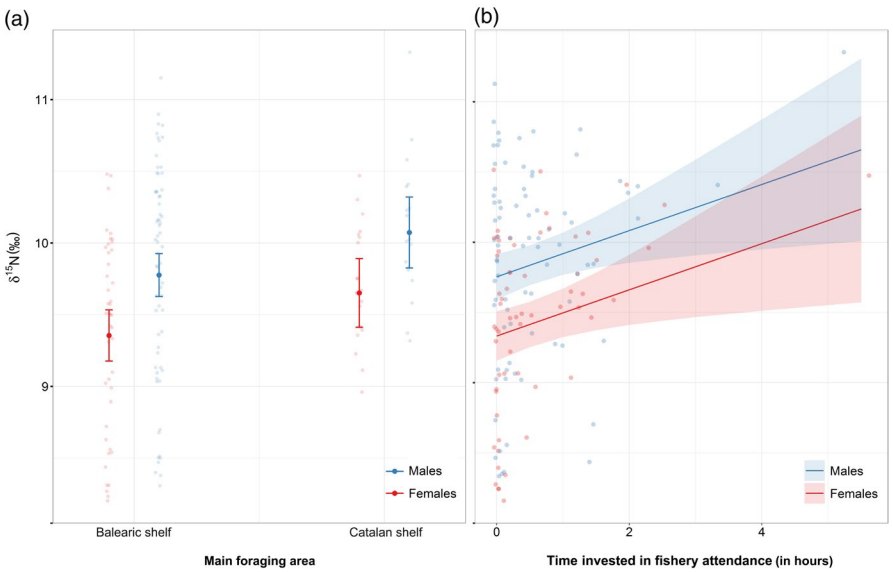


FIGURE 3 (a) Marginal estimates of δ^{15}N in relation to the main foraging area used by birds within the 6-day window of blood plasma. Solid dots represent means and bars represent the associated 95% CI. Soft dots represent raw data with some jittering applied to ease visualization. (b) Marginal estimates of δ^{15}N in relation to time invested in fishery attendance within the 6-day window of blood plasma. Shaded areas represent the associated 95% CI. Soft dots represent raw data

et al., 2017). Nevertheless, we found that the probability of performing long trips was nearly two times higher for females than for males, which also indicates a greater foraging effort by females when compared to males. Moreover, we found sexual differences in the interaction with fishing vessels, as females showed lower fishery attendance than males. Furthermore, according to δ^{15}N, females seemed to have consumed fewer discards and showed narrower INW over the 4 years when compared to males, overall indicating relevant sexual differences in

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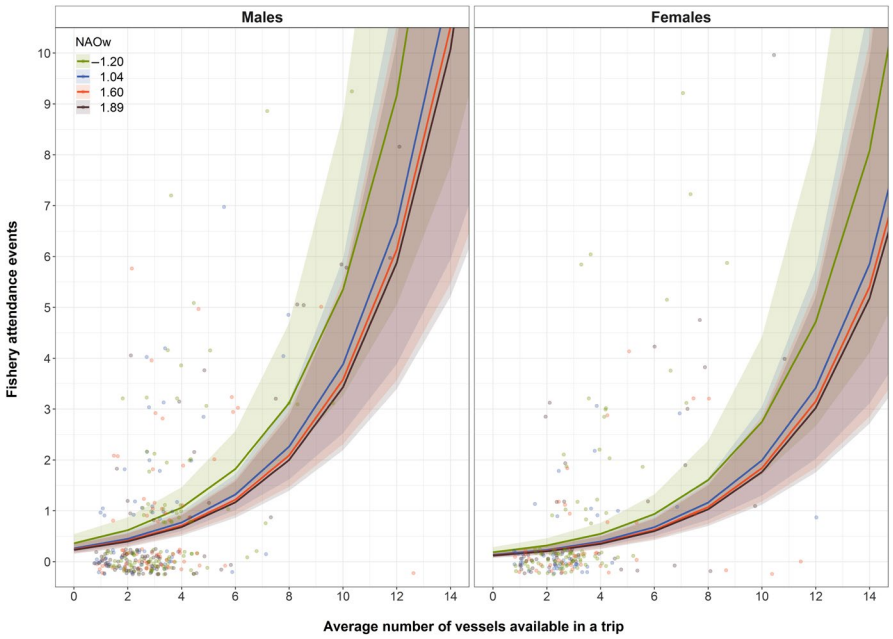


FIGURE 4 Marginal estimates of fishery attendance events in relation to the average number of fishing vessels operating in the vicinities of birds during the foraging trips and annual values of NAOw. Shaded areas represent the associated 95% CI. Soft dots represent raw data. Some jittering was applied to dots to ease visualization

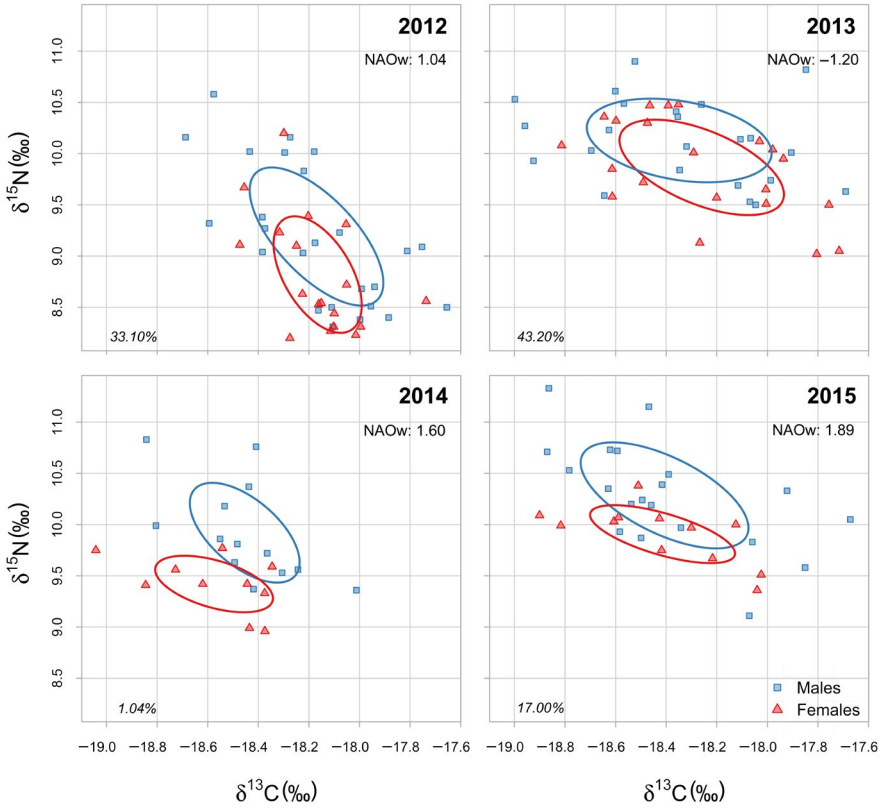


FIGURE 5 Standard ellipses by year, calculated in the bidimensional space of $\delta^{13}C$ and $\delta^{15}N$. The standard ellipse area (SEA) represents the isotopic niche width (INW). Values in italics in the lower-left corner of each panel represent the geometric overlap between males and females ellipses (i.e. the overlapped area as a proportion of the non-overlapping area of the two ellipses)

trophic ecology (Cherel et al., 2005). Our results contrast with previous research on the same species that did not find sexual differences in fishery attendance (Cecere et al., 2015), which may be due to the different approach used (distance from foraging grounds to harbours for evaluating fisheries influence). Conversely, our findings agree with results reported by Cianchetti-Benedetti et al. (2018) in the central Mediterranean that found females spent more energy than males when following vessels, making this behaviour a disadvantageous strategy for the smaller, less competitive sex.

4.2 | Unfavourable environmental conditions may shape foraging behaviour and increase sexual segregation

During the chick-rearing period, when the need to frequently feed the chick compels parents to forage near the colony, unfavourable environmental conditions may result in local depletion of prey, forcing parents to increase foraging effort (Lewis et al., 2001). In our study, the increased competition for feeding resources near

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the colony in unfavourable environmental conditions likely forced Scopoli's shearwaters to increase foraging effort. Overall, both males and females spent more time searching for food, travelled longer distances and engaged more on longer trips in unfavourable than in favourable environmental conditions. This is similar to results reported for other seabird species, including the closely related Cory's shearwater in the North East Atlantic (Paiva et al., 2013, 2017). Yet, during unfavourable environmental conditions, the overlap of SEA between sexes decreased, suggesting sexual segregation in their trophic ecology likely due to increased competition. Moreover, sexes also segregated in space, as females had twice the probability to commute towards Catalan waters than males did in such unfavourable conditions. Females also tended to use larger foraging grounds than males in Catalan waters during unfavourable years. Therefore, according to our second expectation, females showed a greater increase in foraging effort than males in unfavourable conditions, most likely owing to competitive exclusion exerted by males, as found in many other species of petrels and albatrosses (Catry et al., 2005; Paiva, Geraldes, et al., 2010; Paiva, Xavier, et al., 2010; Phillips et al., 2011). Our work only includes a single year of favourable environmental conditions, which calls for caution because other factors not considered in this study may have promoted the observed differences between sexes. Future studies considering a larger set of years with disparate conditions regarding NAOw will contribute to solving this issue.

4.3 | Variable fishery activity shapes fishery attendance

In agreement with previous studies, we found Scopoli's shearwaters to interact with fishing vessels operating in both Balearic and Catalan waters (Genovart et al., 2018; Soriano-Redondo et al., 2016). We also found that high numbers of fishing vessels operating in the vicinity of birds can promote bird attendance (Cianchetti-Benedetti et al., 2018). It is known that fishery activity increases in years with favourable environmental conditions (Lloret et al., 2001). From the 4 years of the study, 2013, the year with most favourable environmental conditions, presented the highest number of different vessels from the Spanish fishing fleet operating in the NWM (Figure S5, Appendix S1). This could indicate that discards were more abundant on that year (Louzao et al., 2011). In favourable conditions (i.e. the year 2013), both sexes increased fishery attendance, suggesting greater use of discards. This is also reflected in an increase in INW when comparing years with contrasting environmental conditions (Table 3; Figure 5). That is, scavenging on discards typically results in a higher INW due to the consumption of a diverse array of demersal and inshore benthonic species (Votier et al., 2010). We also found sexual differences regarding interaction with fisheries. Females consistently showed lower fishery attendance, as well as lower use of discards than males according to INW. Moreover, in years with a lower fishery activity, the INW of females shrunk and the overlap of SEA between males and females decreased. The observed sexual differences in trophic ecology may partly emerge from differential fishery attendance and consumption of discards between males and females. Altogether, these results suggest that males could limit the access of females to this anthropogenic resource, in line with our third expectation of competitive exclusion exerted by the larger sex. Nevertheless, differences observed in relation to fisheries, particularly regarding 2013, may be also due to factors not considered in this study, which calls for future research addressing interaction with fisheries in the context of disparate environmental conditions.

4.4 | Conservation implications

Scopoli's shearwaters suffer the highest rate of bycatch among seabirds in the NWM (Cortés et al., 2017; Valeiras & Camiñas, 2003), thus being the major cause of mortality at sea and pushing adult survival to unsustainable levels (Genovart et al., 2018). We found that ~26% of the foraging trips presented at least one event of fishery attendance, and birds interacted with several vessels and gears in some events. Birds interacted with trawlers in 24% of the trips, in 7% with purse seiners, and in 3% with pelagic longliners. Although this last rate may seem low, the risk of bycatch in any attendance event is high when associated with longliners and depends on the longlining fleet métier (Báez et al., 2014; Barcelona et al., 2010; Croxall et al., 2013). Moreover, recent studies point at artisanal demersal longliners, which are rarely equipped with VMS, as being responsible for the majority of bycatch events at the NWM (Cortés et al., 2017). Trawlers and artisanal longliners frequently share fishing grounds (Cortés et al., 2017). As trawlers strongly attract seabirds and individuals can easily shift their attendance to other vessels in the vicinities, the rate of interaction with trawlers that we found should also raise concern in relation to bycatch risk (Abelló et al., 2003; Laneri et al., 2010; Soriano-Redondo et al., 2016). We found a higher fishery attendance in males, which supports previous findings showing that the bycatch rate of Scopoli's shearwaters is male-biased in the NWM (Cortés et al., 2018). This differential risk of bycatch must be considered for the effectiveness of conservation measures because a sexual unbalance in mortality at the population level could worsen population fecundity, viability and dynamics (Durell et al., 2001; Mills & Ryan, 2005; Phillips et al., 2005).

5 | CONCLUSIONS

Overall, we demonstrate the occurrence of sexual differences in foraging strategies, space and resource use and fishery attendance, suggesting males outcompete females from their main areas and feeding resources to a certain extent, in particular under unfavourable environmental conditions. These differences may pass unnoticed in studies carried out with data from very few years where conditions were similar, highlighting the importance of multi-year studies encompassing as much disparate environmental conditions

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as possible to ascertain sexual segregation and their implications, particularly in species with slight SSD. Thus, sexual segregation in foraging strategies can lead to an uneven exposure of males and females to human-induced threats. This impact is often neglected, but can reduce effective population size and compromise population viability of long-lived species and therefore should be appropriately considered even in species with slight SSD.

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AUTHORS' CONTRIBUTIONS

F.D.F., J.M.R.-G., R.R. and J.G.-S. conceptualized the work with contributions of the rest of the authors; J.M.R.-G. devised data analysis pipelines, performed spatial and statistical analyses and wrote the manuscript; F.D.F. led the fieldwork, performed molecular sexing, stable isotope analysis and wrote the manuscript; V.M.-P. contributed to the stable isotope analysis; A.S.-R. led the fieldwork and contributed to VMS data analysis; L.N.-H. contributed to stable isotope and VMS data analyses; L.Z. led the fieldwork; S.G.-B. contributed to VMS data analysis; J.G.-S. supervised the work. All authors contributed to reviewing different versions of the manuscript.

DATA AVAILABILITY STATEMENT

GPS tracking dataset is hosted at the Seabird Tracking Database of BirdLife International http://seabirdtracking.org with the following IDs: 870, 871, 1618, 1619, 1622, 1623, 1624. GPS tracks used are indicated in Appendix S1. Stable isotope data are available at the Digital Repository of the University of Barcelona (http://hdl.handle.net/2445/171750). VMS data are under restricted use provided by the Ministry of Agriculture, Fisheries and Food of the Spanish Government, and should be formally requested to the Secretaría General de Pesca (C/Velázquez, 144, C.P. 28071, Madrid, Spain; sgpesca (a) mapa.es).

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SUPPORTING INFORMATION

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Year-round individual specialization in the feeding ecology of a long-lived seabird

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Many generalist species are composed of individuals varying in the size of their realized niches within a population. To understand the underlying causes and implications of this phenomenon, repeated samplings on the same individuals subjected to different environmental conditions are needed. Here, we studied individual specialization of feeding strategies in breeding and non-breeding grounds of Cory's shearwaters (*Calonectris borealis*) for 2–8 years, and its relationship with fitness. Individuals were relatively flexible in non-breeding destinations, but specialized in diet, habitat use and daily activity across years. Daily activity was also consistent throughout the year for the same individual, suggesting that it is driven by individual constraints, whereas individual diet and habitat use changed between breeding and non-breeding grounds, indicating that these specializations may be learned at each area. Moreover, individuals that were intermediate specialized in their diet tended to show higher breeding success than those with weakly and highly specialized diets, suggesting stabilizing selection. Overall, this study suggests that the development of individual specialization is more flexible than previously thought, i.e. it emerges under specific environmental conditions and can develop differently when environmental conditions vary. However, once established, individual specialization may compromise the ability of individuals to cope with environmental stochasticity.

In ecology, it has been traditionally assumed that individuals of the same population are ecologically equivalent[1]. However, populations of many apparently generalist species are in fact composed of individuals with different degrees of specialization, varying in their realized niches within a population[2,3]. This means that individuals consistently exploit a subset of resources, although resources are potentially available for all individuals in the population. These differences may not be attributable to specific classes, such as sex, age or morphotypes, but to differences among individuals, known as individual specialization[4]. Although initially referred to as trophic specialization, individuals have been reported to specialize in different habitats[5], in more nocturnal/diurnal behaviour or in migration and foraging patterns in terms of timing, routes or areas exploited[6–8].

The fact that individuals of the same species consistently differ in their biological traits has broad implications in ecology, evolution and conservation[4,9]. Ecologically, individual differences in biological traits may have broad consequences on individual fitness. Individual differences in habitat use or diet can influence breeding success. For example, neritic foragers showed better reproductive performance than oceanic ones in the loggerhead sea turtle (*Caretta caretta*)[10], whereas western gulls (*Larus occidentalis*) specialized in exploiting human waste showed significantly lower long-term reproductive success than those specialized in fish[11]. Individual specialization is also key in evolutionary processes, since differences in resource exploitation among individuals may reduce intraspecific competition and promote ecological segregation[12]. Moreover, long-term individual specialization may limit behavioural plasticity and thus responses to changes in the environment[13]. That is, responses to a changing environment may occur within a generation if individuals are plastic or flexible in their strategies, whereas in populations composed of a majority of highly specialized individuals, adaptation will occur via natural selection[4]. From a conservation point of view and in the context of anthropogenic changes, behavioural plasticity at both the individual and population levels is therefore key because adaptation via natural selection is normally too slow for responding to rapid and extensive human-induced changes[14].

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Despite its implications, few studies have focussed on understanding the degree of individual specialization in several dimensions of the ecological niche simultaneously, precluding more general conclusions about its population consequences. This may be due to the difficulty of gathering long-term time series of individual longitudinal data[15], which is often complicated for wild species. Although individual specialization has been broadly studied in past decades, many studies on wild-living animals are short-term, only including observations within the same season or for up to 2–4 years[4,6,7,16–18] (but see some exceptions[19,20]). Although there is no consensus on the length of the period needed to study individual specialization, short-term studies may not capture the entire individual repertoire of the traits considered[21], leading to a gross overestimation of individual specialization.

Little is known about the processes underlying individual specialization. Differences among individuals in resource use reflect a complex interaction between an individual's phenotype, i.e. morphological, behavioural, or physiological variability, and external constraints, such as resource abundance and availability or environmental heterogeneity[4]. In this context, long-distance migrants are a good model to explore the processes driving individual specialization. If individual specialization is maintained year-round, this would suggest that intrinsic constraints exist, such as cognitive processes, memory, physiological abilities, etc., which are part of individuals' traits. On the contrary, specialization maintained only during a particular period of time would indicate a temporal adaptive response related to specific constraints or specific environmental conditions of that given period, such as energetic constraints related to breeding duties or disparate environmental predictability in breeding and non-breeding grounds. In this context, seabirds constitute an ideal model for studying the incidence and consequences of individual specialization, since many of these birds perform complex and long-distance migrations, exposing them to different environmental conditions in breeding and non-breeding grounds. Moreover, their long life span allows an exploration of consistency in different dimensions of the ecological niche over extended periods.

We aim to quantify the extent of individual specialization and its fitness implications in a long-distance migrant, the Cory's shearwater (*Calonectris borealis*), using 74 adult individuals tracked for two to eight years both in breeding and non-breeding grounds and sampled in two breeding colonies of the Canary Islands. Specifically, we explore individual specialization in four dimensions of the ecological niche: non-breeding site fidelity, diet, habitat preference and daily activity (diurnal/nocturnal foraging) evaluated in breeding and non-breeding grounds. Non-breeding site fidelity was evaluated using global location sensors (GLS) devices, combined with stable isotope analyses (SIA) on feathers moulted in breeding and non-breeding grounds to infer seabirds' diet. Habitat preference was inferred with sea surface temperature (SST) recorded by GLS devices. This variable can indicate habitat preferences within the upwellings, since many seabirds forage in upwelling systems, where the motion of deep cold waters towards the surface creates a contrasting gradient in temperature values from highly productive colder areas to oligotrophic warmer waters. Finally, daily activity was inferred using conductivity measured by GLS devices. Daily activity is a key component of seabirds' foraging ecology, as the type of prey and its availability may change during the day and night[22].

Cory's shearwaters migrate to distinct areas throughout the Atlantic, and are subjected to different environmental conditions, types of prey and prey availability[20,23]. We thus hypothesize that individuals will show non-breeding site fidelity, as we expect it to be more beneficial to winter in a specific non-breeding area rather than adapting to different conditions every year. Indeed, non-breeding site fidelity has been previously found in Cory's shearwaters from other colonies[20]. We also hypothesize that individual specialization will not be maintained year-round, as non-breeding areas are distantly located areas with different environmental conditions than those encountered at the breeding ground[23]. However, within breeding and non-breeding grounds, we expect individuals to be specialized in their diet, habitat preference and daily activity across years as a strategy to improve eficciency in resource explotation and to reduce intraspecific competition[4]. We also expect some individual trait preferences to have an impact on the reproductive success of individuals, as any biological trait with variability can potentially promote differences in fitness among individuals. Finally, we hypothesize that intermediate specialized individuals will show higher fitness, as highly specialized individuals will be less adapted to cope with environmental stochasticity and weakly specialized individuals will be less efficient in resource exploitation[4,24].

Results

Non-breeding site fidelity. We obtained GLS data of 59 individuals: 32 tracked for two years, 10 for three years, seven for four years, six for five years and four for six years, comprising a total of 176 year-round trips. At a population level, we found that Cory's shearwaters spent the non-breeding period in eight different areas (Fig. 1): Benguela Current (63.1% of migration events), Canary Current (14.2%), Agulhas Current (10.2%), Brazil Current (6.8%), Angola Current (2.3%), confluence of Brazil-Falklands/Malvinas Currents (1.7%), south central Atlantic (1.1%) and Equatorial Guinea Current (0.6%). We found that 21 of 59 individuals changed their areas at least once over the seven years of the study (i.e. 35.6%): 15 animals changed their non-breeding area once, five changed twice and one three times. Overall, we recorded 28 changes of non-breeding area from one year to the next in a total of 176 migration events (i.e. 15.9%). This corresponded to a Krippendorff's alpha coefficient of 0.55 (95% CI: 0.37–0.69).

Repeatability across years and year-round consistency. We found repeatability to some extent in almost all proxies in all dimensions of the ecological niche, both in breeding and non-breeding grounds, namely isotopic diet (proxies $\delta^{13}C$ and $\delta^{15}N$ measured in two specific feathers: thirteenth secondary, hereafter S13, and the first innermost primary feather, hereafter P1), habitat preference (SST as a proxy) and daily activity (night flight index [NFI] as a proxy) (Table 1). Estimates of adjusted population repeatability values were statistically significant and thus trustworthy (95% confidence interval, CI, did not include 0), with the only exception being SST during breeding (Table 1). However, we did not find a correlation between breeding and non-breeding in $\delta^{13}C$, $\delta^{15}N$ and SST values at an individual level, with the exception of SST in resident animals staying in the Canary

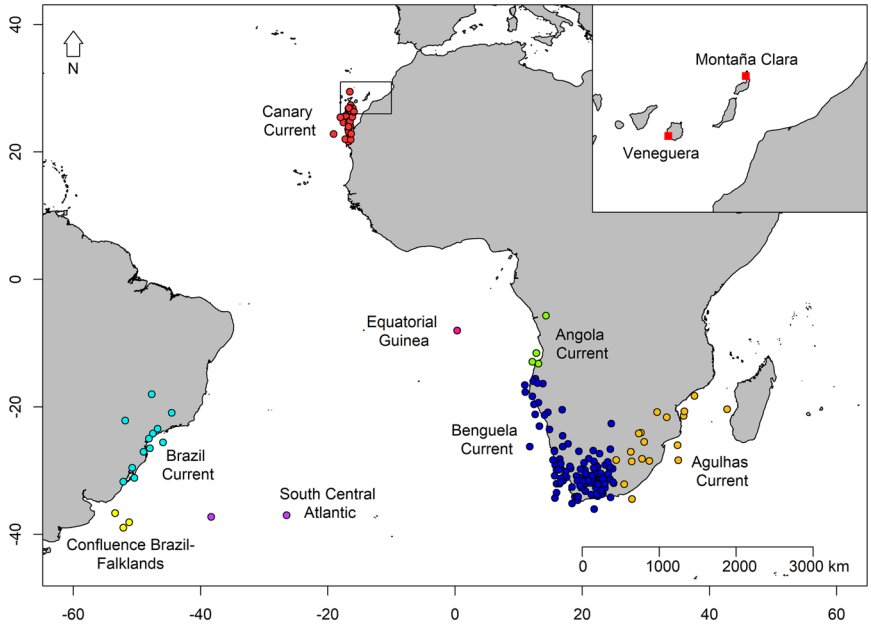


Figure 1. Non-breeding areas (points) and breeding colonies (red squares in the enlarged map, upper right-hand panel) of Cory's shearwater from this study. Each point in non-breeding areas is the centroid of the non-breeding distribution of one individual in one year ($N_{ind} = 59$, $N_{trips} = 176$). Note that centroids over land are due to the intrinsic spatial error associated with light-level geolocation, since positions on land were not removed as they are subject to the same rate of error as positions at sea.

Dimension of the ecological niche	Proxy	Period	N_{total} ($N_{ind.}$)	r^2c	Adjusted population repeatability (*R*) across years (95% CI)	Year-round consistency (correlation breeding/non-breeding)
Diet	$\delta^{13}C$	Breeding (P1)	300 (74)	0.22	0.14 (0.04–0.28)	$\chi^2_{(1)} = 1.2$; $p = 0.231$
		Non-breeding (S13)	130 (43)	0.71	0.25 (0.06–0.52)	
	$\delta^{15}N$	Breeding (P1)	300 (74)	0.36	0.18 (0.08–0.32)	$\chi^2_{(1)} = 0.3$; $p = 0.673$
		Non-breeding (S13)	130 (43)	0.84	0.50 (0.34–0.70)	
Daily activity	NFI	Breeding	187 (61)	0.44	0.38 (0.23–0.56)	$\chi^2_{(1)} = 13.0$; **$p < 0.001$**
		Non-breeding	160 (54)	0.44	0.19 (0.03–0.41)	
Habitat	SST	Breeding	101 (36)	0.44	0.18 (0–0.44)	Benguela Current ($N = 44$): $\chi^2_{(1)} = 0.02$; $p = 0.652$ Canary Current ($N = 12$): $\chi^2_{(1)} = 8.9$; **$p = 0.003$**
		Non-breeding	64 (25)	0.72	0.45 (0.22-0.74)	

Table 1. Summary of parameters for each dimension of the ecological niche. Significant breeding/non-breeding correlation are shown in bold. NFI is the night flight index, SST is sea surface temperature (°C) recorded by GLS devices and r^2c is conditional r square of linear mixed models, i.e. the variability explained by the model including both fixed and random factors. Breeding/non-breeding correlations were performed only with animals spending the non-breeding season in the Benguela Current, except for SST which was also performed for animals wintering in the Canary Current. Note that adjusted population repeatability values obtained for all traits in both breeding and non-breeding grounds were statistically significant (i.e. 95% confidence interval $CI > 0$) and thus trustworthy, except for SST breeding. Note that sample size (N) is not the same in all cases because input data came from different sources of information (stable isotope analyses, immersion data from GLS devices and temperature data from GLS devices).

Current year-round (Fig. 2). We found a significant positive correlation between breeding and non-breeding NFI values at an individual level (Table 1, Fig. 3). Moreover, in order to characterize habitat use in the context of available habitat, we looked at the range of SST in both breeding and in non-breeding grounds (for non-breeding only in Benguela due to the low sample size of the other areas). The range of SST values in the breeding ground ($N = 101$) was 6.0 °C (18.2–24.2 °C), whereas in the non-breeding ground ($N = 44$), the range of SST was 5.7 °C (17.0–22.7 °C).

Influence of individual trait preferences and degree of specialization on fitness. We found different impacts of trait preferences and the degree of specialization on individual fitness, as inferred by fledging success. Regarding $\delta^{13}C$ and $\delta^{15}N$, we found a general tendency of intermediate specialized individuals showing higher fledging success than those weakly or highly specialized (Fig. 4A–D). However, this pattern was only significant in

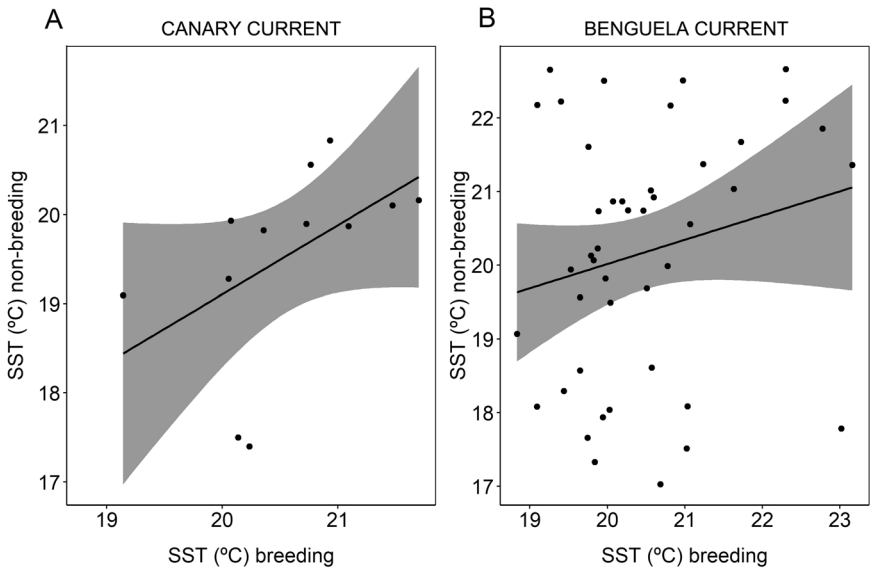


Figure 2. Relationship between sea surface temperature (SST) values during breeding and non-breeding periods of individuals spending the non-breeding period in the Canary Current (**A**; N = 12 values from six individuals, $\chi^2_{(1)} = 8.9$; $p = 0.003$, $r^2 = 0.50$) and the Benguela Current (**B**; N = 44 values from 20 individuals, $\chi^2_{(1)} = 0.02$; $p = 0.652$, $r^2 = 0.04$). Black lines correspond to the mean of the relationship and the grey shades are the associated 95% CI. Each point represents one individual per year.

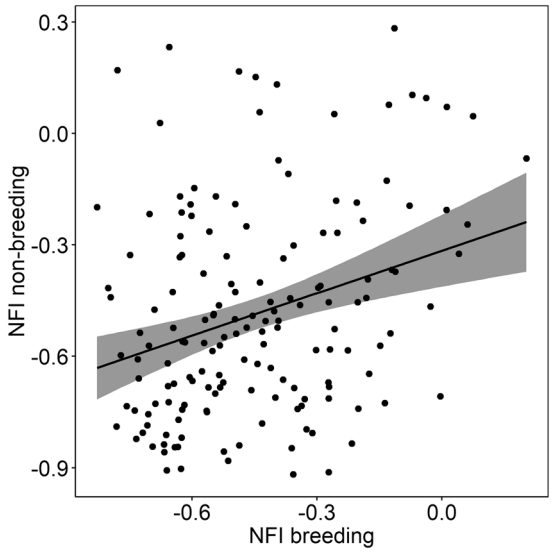


Figure 3. Relationships between night flight index (NFI) values during breeding and non-breeding periods (N = 158 from 53 individuals; $\chi^2(1) = 13.00$, $p < 0.001$, $r^2 = 0.15$) only for birds spending the non-breeding period at the Benguela Current. The black line corresponds to the mean of the relationship and the grey shade is the associated 95% CI. Each point represents one individual per year.

two cases: intermediate specialized individuals showed higher fledging success than weakly specialized individuals in $\delta^{13}C$ values during breeding (Odds Ratio, OR = 1.96, 95% CI 1.02–3.75, $N_{intermediate} = 22$, $N_{weak} = 37$, $p = 0.044$, Fig. 4A) and in $\delta^{15}N$ during non-breeding (OR = 4.89, 95% CI 1.72–13.94, $N_{intermediate} = 10$, $N_{weak} = 10$, $p < 0.001$, Fig. 4D). Nevertheless, the mean level of $\delta^{13}C$ and $\delta^{15}N$ was not related to fledging success. In regards to NFI, during non-breeding there was a tendency for individuals with higher specialization in NFI to have higher fledging success, although the difference was only significant between weakly and highly specialized individuals (OR = 17.93, 95% CI 2.73–117.95, $N_{intermediate} = 5$, $N_{high} = 2$, $p < 0.001$, Fig. 4F). However, we did not find statistical evidence of an influence on the degree of NFI specialization during breeding (Fig. 4E). On the other hand, the more nocturnal that individuals were during breeding (higher NFI values), the higher their fledging success (OR = 1.85, 95% CI 1.06–3.21, N = 27, $p = 0.030$, Fig. 5), although we did not find any pattern during non-breeding. Regarding SST, we found that neither trait preferences nor the degree of individual specialization were related to fledging success.

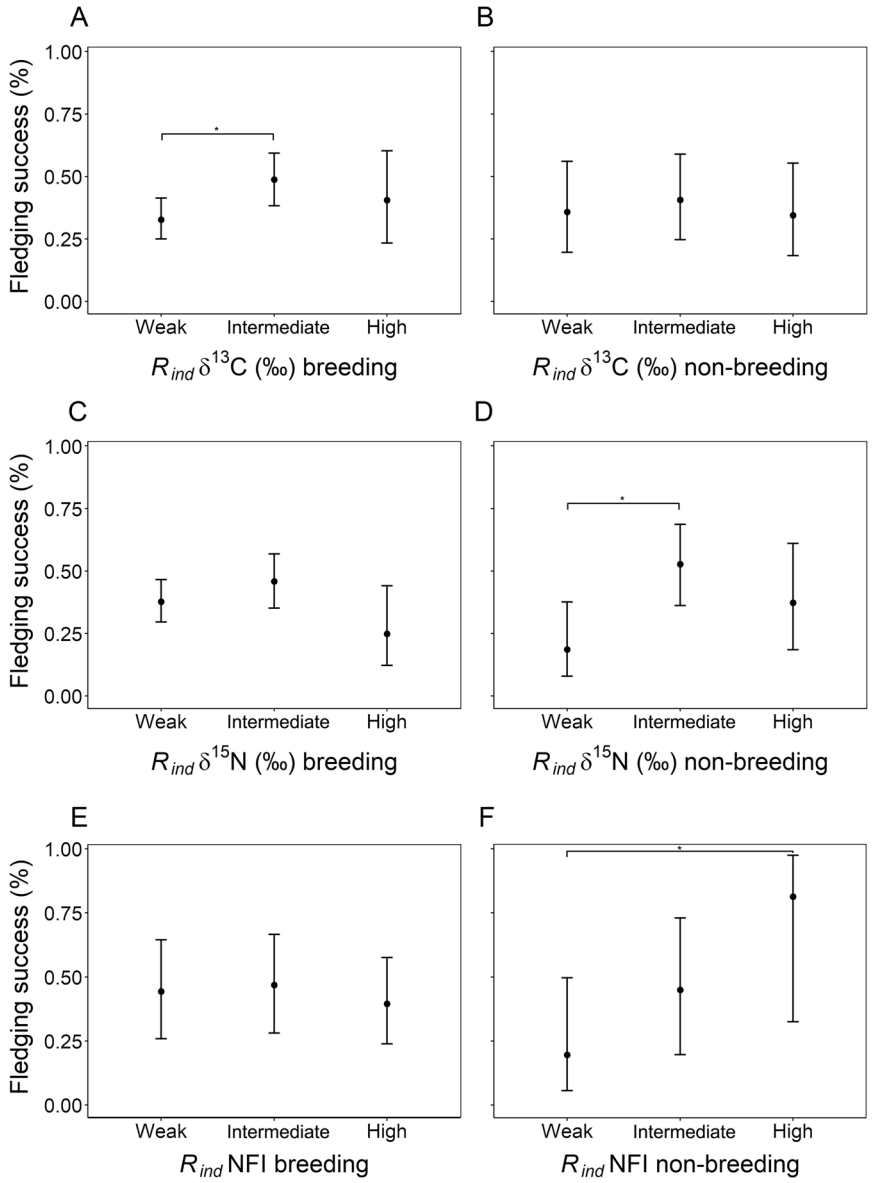


Figure 4. Probability of fledging success ± 95% CI depending on the degree of individual specialization estimated at the individual level (R_{ind}) in $\delta^{13}C$ (**A**,**B**), $\delta^{15}N$ (**C**,**D**) and night flight index, NFI (**E**,**F**), during breeding (**A**,**C**,**E**) and non-breeding periods (**B**,**D**,**F**). Probability of fledging is calculated as the average fledging success (ranging from 0 to 1) for all years of each individual. Significant differences are shown with (*). Note than with $\delta^{13}C$ and $\delta^{15}N$, intermediate specialized individuals tend to have higher mean fledging success than those weakly and highly specialized, although this difference is only significant between intermediate and weakly specialized in $\delta^{13}C$ during breeding (Odds Ratio, OR = 1.96, 95% CI 1.02–3.75, $N_{intermediate} = 22$, $N_{weak} = 37$, $p = 0.044$) and in $\delta^{15}N$ during non-breeding (OR = 4.89, 95% CI 1.72–13.94, $N_{intermediate} = 10$, $N_{weak} = 10$, $p < 0.001$). Note that with NFI during non-breeding, the higher the specialization, the higher the fledging success tends to be, although it is only significant between weakly and highly specialized individuals (OR = 17.93, 95% CI 2.73–117.95, $N_{intermediate} = 5$, $N_{high} = 2$, $p < 0.001$).

Discussion

In this study, we addressed inter-annual individual specialization in different aspects of the ecological niche and including the different conditions to which individuals are exposed, by studying several traits of the feeding ecology of Cory's shearwaters in breeding and non-breeding grounds. In general, we found evidence of individual specialization in feeding strategies across years in both breeding and non-breeding grounds, although these individual strategies differed between grounds, suggesting the capacity of individuals to develop disparate strategies when environmental conditions differ. Moreover, the degree of individual dietary specialization seemed to influence fledging success, thus highlighting the importance of individual strategies on fitness.

Individual non-breeding site fidelity has been reported in many seabird species, such as skuas, puffins or albatrosses[6]. The first studies on Cory's shearwaters suggested that individuals are plastic in their non-breeding

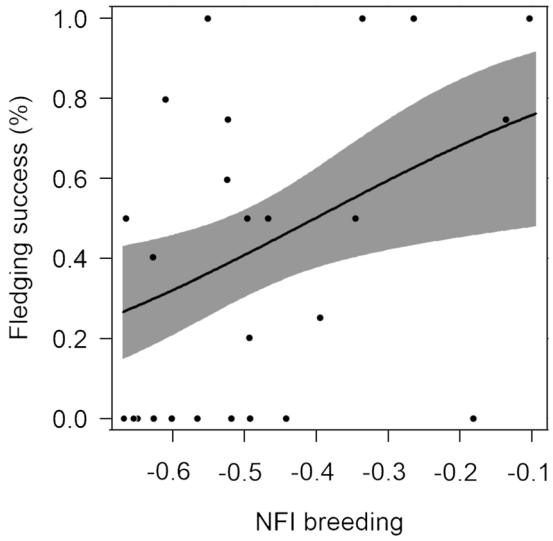


Figure 5. Probability of fledging success ± 95% CI in relation to individual mean values of night flight index (NFI) during breeding. Probability of fledging is the average fledging success (value ranging from 0 to 1) for all years of each individual. Note that during breeding, the higher the NFI values, the higher the fledging success (OR = 1.85, 95% CI 1.06–3.21, N = 27, p = 0.030).

destinations, with 36% of the individuals changing their non-breeding grounds from year to year, although this study was performed on only 13 individuals tracked for two years and one tracked for three years[23]. A more recent study with 51 individuals tracked for up to six years suggests that Cory's shearwaters are less plastic than previously shown[20]. They found that 31% of individuals changed their non-breeding destination at least once during the study period, but that only 16% of individuals changed between consecutive migration events if we take into account all possible changes in all individuals and years[20]. In our study, we tracked 59 individuals for two to six years and found an overall strikingly similar result, with 36% of individuals changing non-breeding destinations and 16% of changes between consecutive migration events. Previous studies on shearwater species showed substantially higher non-breeding site fidelities than Cory's shearwaters, including the streaked shearwaters (*Calonectris leucomelas*), in which just 2% of the individuals changed their grounds with 39 individuals tracked for two years and seven for three years[25], and Scopoli's shearwaters (*Calonectris diomedea*), which showed 0.46 repeatability in the distance travelled to non-breeding destinations with 10 individuals tracked for two years and two for three years[26]. These differences may emerge from a less complex migration system in these species, with both streaked and Scopoli's shearwaters only having three different non-breeding destinations[25,27], but may also be due to small sample sizes and fewer years considered in those studies. Overall, in this study Cory's shearwaters used seven non-breeding areas across the Atlantic and Indian Oceans and some animals remained as residents in the Canary Current year-round, thus making its migration system more complex than the others. However, we should note that one of the non-breeding areas defined for streaked shearwaters was larger (3.4 million km^2 approximately)[25] than those defined in our study (up to 2.3 million km^2 approximately). If this large non-breeding area of streaked shearwater was divided into smaller areas, as we did in our study, the percentage of change may have been greater.

Despite showing some flexibility in their non-breeding destination, Cory's shearwaters showed specialization across years in the habitat exploited in non-breeding locations, as inferred from the high repeatability values ($R = 0.45$) in SST recorded by GLS. These values implies that individuals specialize in exploiting different foraging grounds within each non-breeding area, ranging from strictly neritic to the shelf slope waters or beyond.

Although shearwaters showed habitat specialization across years in non-breeding grounds, habitat specialization was not maintained all year-round. That is, the SST of the waters used during breeding and non-breeding were unrelated at the individual level, meaning that individuals changed their preferences when moving from breeding to non-breeding grounds. Indeed, there was no individual specialization in SST during breeding. Given that the range of SST was similar within breeding and non-breeding grounds, we can dismiss that these differences in specialization arose from a different range of available habitats in both areas. Ruling out differences in availability, different habitat specializations in breeding and non-breeding grounds could imply that such specializations are not driven by behavioural or physiological constrains, but are likely learned and fixed by experience early in life[28,29]. This process may occur independently in breeding and non-breeding areas, where environmental conditions are probably different, thus leading to different habitat use in each area. Indeed, only resident animals, spending the breeding and non-breeding periods in the same area (the Canary Current), showed a significant association between the SST used in the two periods, thus indicating changes in specialization between breeding and non-breeding period does not arise from the change in the period but from a change in the area.

Flexible preferences in environmental traits between breeding and non-breeding periods contrast with a year-round maintenance of individual strategies regarding daily activity, as observed by a significant positive correlation between breeding and non-breeding NFI values at an individual level. This implies, for instance, that

birds that are more diurnal during breeding are also more diurnal during the non-breeding period. This suggests that daily behavioural specialization, once it is fixed, may have some returns regardless of the conditions in breeding and non-breeding grounds, such as an increased ability and efficiency in exploiting specific resources. However, this individual specialization maintained year-round may also imply some constraints on the foraging behaviour of individuals that could lead to sub-optimal foraging. Although NFI values showed that shearwaters are mainly diurnal animals, i.e. flight mainly occurs during daylight hours, there may be some individuals that are specialized in taking advantage of crepuscular hours to forage[30]. Diurnal individuals probably rely on pelagic fish[30], whereas crepuscular birds probably depend on prey performing diel vertical migrations, as was previously found in other seabirds[22,31]. Indeed, the targeted prey of Cory's shearwater includes prey that perform diel vertical migrations, such as Myctophidae species[32]. Individual specialization in daily activity has also been previously reported in seabirds. Similarly to the studied shearwaters, white-chinned petrel (*Procellaria aequinoctialis*) individuals specialized in their nocturnal activity[33] and European shags (*Phalacrocorax aristotelis*) showed individual consistency in foraging either during morning or afternoon in daylight hours[34].

Individual specialization in habitat and daily activity can lead to specialization in diet. Accordingly, we found that Cory's shearwater individuals specialized in diet across years, as inferred by $\delta^{13}C$ and, especially by $\delta^{15}N$ values. $\delta^{13}C$ values of a predator' tissue are widely acknowledged to be good proxies of its food and habitat type[35], while $\delta^{15}N$ values indicate its trophic level[35]. It is known that Cory's shearwaters mainly feed on epipelagic fish, although some birds can also rely on krill and cephalopods to some extent[32]. Since these prey show different $\delta^{15}N$ values according to their trophic level, our results suggest that some individuals specialize on prey at low trophic levels, e.g. incorporating more krill, whereas others mainly feed on prey at mid-trophic levels, such as pelagic fish. Alternatively, higher $\delta^{15}N$ values may also result from individuals scavenging on demersal fish discarded by trawlers, which typically has greater $\delta^{15}N$ values than pelagic fish[36]. This may imply that some individuals specialize in naturally obtained pelagic prey, whereas others specialize on fishery discards to some extent. Indeed, fishery discard specialization has been reported in other seabirds, such as northern gannets (*Morus bassanus*)[37], great skuas (*Catharacta skua*)[38] or lesser black-backed gulls (*Larus fuscus*)[39], although high flexibility regarding fishery waste utilization was also observed in black-browed albatross (*Thalassarche melanophrys*)[40].

Although shearwaters showed diet specialization across years both, in breeding and non-breeding grounds, we did not find a correlation in the isotopic values between these two periods. This implies, for instance, that individuals with a high trophic level during breeding do not necessarily hold a high trophic level during non-breeding. Similar to the habitat inferred from SST, this result suggests that diet specialization may change between areas. Area-dependent dietary specialization may originate from changes in prey type between breeding and non-breeding areas. Indeed, target species of breeding Cory's shearwaters are not necessarily found in non-breeding grounds. Namely, Atlantic horse mackerel (*Trachurus trachurus*) and European anchovy (*Engraulis encrasicolus)* are only present on the east coast of the Atlantic to northern Namibia, and are thus inaccessible to birds spending the non-breeding period in the west and central Atlantic and southern east African coast. Alternatively, different prey preferences depending on the area may originate from the observed differences in habitat preferences in each area, with neritic and oceanic habitats allocating different prey[41]. Accessibility to different prey can also explain the lack of correlation observed between breeding and non-breeding isotopic values of resident animals staying in the Canary Current year-round. Even when staying in the same area and habitat, prey accessibility can change due to seasonal movements, which occurs with sardines and horse mackerels performing seasonally latitudinal migrations in the Canary Current[42].

The observed individual specialization in the different dimensions of the ecological niche may have consequences on individual fitness. We found some interesting tendencies regarding the implications of individual specialization on fitness, as indicated by fledging success. In the case of the diet, $\delta^{13}C$ and $\delta^{15}N$ values did not relate to fitness, but the degree of individual dietary specialization seems related to fledging success. Low and highly specialized individuals tended to exhibit lower fledging success than those medium specialized, although paired comparisons were only significant between intermediate and weakly specialized in $\delta^{13}C$ during breeding and in $\delta^{15}N$ during non-breeding. Higher fitness in intermediate individuals suggests stabilizing selection. This stabilizing selection, which crops the extremes and holds the intermediate phenotypes, is typical in stable environments with little variability[43]. Upwelling systems could be considered stable environments with high prey availability and spatiotemporal predictability. For instance, Benguela and Canary Current, were most individuals forage in the non-breeding and breeding period respectively[44], are amongst the most important upwelling systems of the Atlantic[45]. In addition, shearwaters with a weak specialization in diet could be less efficient in resource exploitation than intermediate or highly specialized individuals, which may lead to lower breeding success[4,24,46]. Indeed, foraging specialization has been shown to increase breeding success in herring Gulls (*Larus argentatus*)[46]. Alternatively, a low breeding success in weakly specialized individuals may be related to the use of fishery discards. This resource is widely used by many seabird species, including shearwaters[47], and it is also available in both, breeding and non-breeding grounds, of the studied shearwaters[48]. The exploitation of discards could be considered a specialized strategy, but the offered prey is variable in their isotopic values, which may lead to an apparently weakly specialized diet. Individuals exploiting discards may be less experienced and less efficient foragers and may also be those provisioning their chicks with suboptimal prey items from discards[49]. Highly specialized individuals showed similar or slightly lower breeding success than intermediate specialized ones, thus suggesting a limitation to positive effects of specialization, possibly related to a lower capability to cope with environmental stochasticity. Alternatively, the degree of specialization may just respond to different dietary strategies not necessarily related to fitness. Further research with higher sample sizes should ideally be undertaken to actually understand the influence of the degree of individual dietary specialization on the breeding success in long-lived species.

Contrarily, specialization in daily activity during non-breeding seemed to increase subsequent breeding success. However, taking into account the small sample size, with five weakly specialized, five intermediate

specialized and two highly specialized individuals, these results should be interpreted with caution. Individual specialization in other aspects of the foraging strategies has been previously shown to be adaptive in other seabirds. For instance, successful breeders of black-browed albatross showed a substantially lower spatial niche than failed ones[50], whereas repeatability in diving behaviour was related to foraging efficiency in great cormorants (*Phalacrocorax carbo*)[51]. Other studies with larger sample sizes are needed to understand the fitness implications of more nocturnal/diurnal behaviour on shearwaters.

In addition, we found more nocturnal animals during breeding to show higher concurrent breeding success. An increased fitness of more nocturnal animals could be related to the extensive fisheries operating on the Saharan coast of the Canary Current where shearwaters forage during breeding, which is clearly dominated by fisheries targeting epipelagic fish, such as sardines[52]. These type of fisheries are mainly active during crepuscule and night, when high concentrations of epipelagic fish are attracted to the surface by purse seine vessels using powerful lights. In this context, more nocturnal individuals may have large amount of their preferred prey available, thus increasing their body condition and ultimately their breeding performance.

Conclusions

Overall, in this study we found that Cory's shearwaters specialized in diet, daily activity and habitat from year to year. Additionally, daily activity behaviour was individually repeatable across seasons, independently of the areas visited by the individuals. Both results (i.e., repeatability between years and seasons) suggest that these animals may have a limited plasticity in their ecology and behaviour. Global changes, such as the forecasted increase of SST worldwide[53], will not only alter the environmental conditions of the habitat itself, but may also alter abundance and distribution of prey[54]. In this scenario, low plasticity of predators could eventually compromise their ability to cope with environmental stochasticity and limit adaptive responses to global changes[55].

Nevertheless, our study also showed Cory's shearwaters are relatively flexible in their non-breeding destinations and are able to independently develop different habitat and dietary specializations under different environmental conditions. This suggests that individual specialization is not driven by individual constraints but can be acquired independently in different areas, suggesting the specialization process is more plastic than previously thought. Therefore, our study highlights the need to understand the underlying causes of individual specialization, in particular the need to distinguish between the specialization driven by permanent intrinsic traits of the individuals versus that promoted by temporal extrinsic factors, such as the stability or predictability of environmental conditions.

Materials and Methods

Fieldwork. Fieldwork was conducted from 2007 to 2015 in two colonies of Cory's shearwaters (see Supplementary Material for basic information on the species): Veneguera (27°50′39.98″N, 15°47′19″E) and Montaña Clara (29°17′29″N, 13°31′57″E), both located in the Canary Islands. We deployed and re-deployed GLS loggers (global location sensor, models MK4, MK9, MK13, MK18-H and MK19 from British Antarctic Survey and MK3005 from Biotrack) on the same individuals whenever possible. GLS were recovered mainly after one year of deployment (but some of them after up to three years), thus reducing a potential bias of device id on anual measurements. The recovery rate was 93.7% (194 recoveries from 207 deployments). Of those recovered, 8.8% failed and had no light data during the non-breeding period to infer positions, thus resulting in 176 year-round tracks. GLS devices were attached to the leg of the animal with a PVC ring. We only included in this study birds tracked from two to eight years. At the time of recovering each GLS, we sampled S13 and P1 feathers, known to be moulted at the non-breeding and breeding grounds, respectively[56,57]. To link the specialization and strategies adopted by individuals to their fitness, we recorded fledging success by evaluating whether the chick from every monitored nest was alive around mid-October every year, when they are close to leaving the nest; this data was available for Veneguera but not for Montaña Clara.

Assessing individual specialization. We analysed different dimensions of the ecological niche: non-breeding site fidelity, isotopic diet, daily activity behaviour and habitat preference. As explained below in detail, every dimension was analysed using a different source of information, which means that sample size and number of individuals will vary among them (see Table 1 for sample sizes).

We used the locations obtained from GLS devices to address non-breeding site fidelity. After processing raw GLS data, it is possible to infer two locations per day with an error of $\pm$200 km[58] based on timings of sunrise and sunset. We used TransEdit software to inspect light curves and to define dawn and dusk times daily. To filter erroneous locations, we removed the 30 days around the equinoxes and applied velocity filters by removing speed values higher than the 95th percentile. Since shearwaters normally perform some stopovers and occasionally spend the non-breeding period in more than one area, we selected the main non-breeding area of each individual/year as the area where each animal spent the most days. For each individual and year, we calculated the kernel utilization distribution (UD) using positions within the main non-breeding area. To do so we used the function "kernelUD" from the package "adehabitatHR"[59] and a smoothing parameter equivalent to ~2° to account for the spatial error in geolocation. Each centroid of the 5% kernel UD contour per individual and year was then assigned to one out of ten main non-breeding areas known to be used by the species, following the limits of the areas proposed by Militão *et al.* (2018)[60].

To examine individual specialization in diet, we analysed stable isotope values of $\delta^{13}C$ and $\delta^{15}N$ for S13 and P1 feathers (see Supplementary Material for details on these analyses). To link trophic with the spatial information of the non-breeding period, each S13 feather sample was related to a non-breeding area inferred from GLS devices previous to the year of feather sampling, when that feather was moulted. P1 feathers were also linked to the previous year of sampling, as it was also the year of moult. To increase sample size during breeding, we included P1 feathers of animals not necessarily tracked with GLS devices.

Daily activity was assessed using the variation of behaviours (flying, resting) exhibited by individuals throughout the day and that are detected by GLS immersion data. GLS devices equipped with immersion sensor measure conductivity every three seconds and can provide information about two elemental states: wet, which means the animal was in contact with water and thus likely sitting on the sea surface, and dry, meaning the animal was flying and likely foraging. To address consistency in the daily activity, we calculated the NFI[23]. This index was calculated as the difference between the proportion of time spent in flight during darkness and during daylight, divided by the highest of these two values. Values of NFI range from −1, flight exclusively restricted to daylight, to 1, flight restricted to night. We defined day and night using the time of sunrise and sunset generated during the analysis of the light data from GLS devices. Per each individual and year, we calculated the mean of the daily values of NFI in the breeding and the main non-breeding area. Dry records in conductivity occur when birds are flying but also during nest attendance. To avoid misleading results, we selected a period of ~30 consecutive days just preceding the onset of post-nuptial migration to calculate NFI, since in this period animals were still at the breeding area but did not frequently visit the nest. We also selected a period of ~30 consecutive days in the middle of the period spent in the main non-breeding area, in order to avoid interferences of moonlight activity, which influence shearwaters at-sea behaviour[61].

To understand habitat specialization, we used as a proxy the SST (°C) recorded by GLS devices, which is measured every 20 minutes after a minimum of 20 minutes of continuous contact with salt water. We calculated the mean SST per individual and year in breeding and non-breeding stages using the same 30-day window as with NFI. Cory's shearwater are in contact with salt water when drafting and diving, and maximum diving depth is 6–7 meters[62]. Therefore, GLS-recorded temperatures can be considered as SST.

Statistical analyses. All statistical analyses were carried out using R 3.4.3[63]. Prior to statistical analyses, we checked for normality of $\delta^{13}C$, $\delta^{15}N$, NFI and SST values using Kolmogorov-Smirnov tests and Q-Q plots. As no severe deviations from normality were found, we used parametric tests throughout. Significant levels in all analyses were set to 0.05. To disregard the possibility that GLS id inflated repeatability values of GLS measurements (SST and NFI), we first included GLS id in the models and in all cases was not significant.

We used Krippendorff's alpha coefficient to estimate how repeatable individuals were in the selection of a specific non-breeding area, i.e. non-breeding site fidelity. This index can be calculated with several years of data and multiple individuals, allowing missing data for some individuals in some years and also taking into account the number of possible non-breeding areas to which individuals can go. This index ranges from 0, meaning the same individual constantly changes its non-breeding area, to 1, meaning the same individual always selects the same non-breeding area. We calculated it using "krip.alpha" function in the "irr" R package[64] and performed bootstrapping with 10,000 iterations to obtain the 95% CI of the estimate[65].

Repeatability is a commonly used statistic in behavioural studies to address individual specialization[16]. For the traits $\delta^{13}C$, $\delta^{15}N$, NFI and SST, we addressed individual specialization by calculating repeatability (R), Eq. (1):

$$R = \frac{s_A^2}{s_W^2 + s_A^2} \quad (1)$$

where R is repeatability, s_A^2 is the variance among individuals and s_W^2 is the variance within individuals, with $s_W^2 + s_A^2$ being the total variation in the sampled population. The value of R ranges from 0 to 1, 0 meaning the trait has no repeatability and the majority of individuals do not show specialization (i.e. population is mainly composed of generalists) and 1 meaning that trait is highly repeatable and individual specialization is at a maximum in a given population (i.e. most individuals of the population do show specialization). Note that in order to be repeatable, a trait must be consistent within individuals but different among individuals[66]. Among and within individual variances can be directly estimated from residuals of Linear Mixed-Effects Models, LMM[15,66]. Moreover, LMM allow the control of possible effects of confounding factors by including them as fixed factors or covariates, thus providing an adjusted repeatability[15,66]. We estimated adjusted repeatability (R hereafter) through LMM using the "rpt" function in the "rptR" package, which returns the mean value of R in the population and its 95% confidence interval (CI) calculated by parametric bootstrapping[67]. A 95% CI that does not include 0 means the value of R is statistically significant. We calculated R for the traits $\delta^{13}C$, $\delta^{15}N$, NFI and SST, separately for breeding and non-breeding. Each LMM included "year" (the year of moult in the case of isotopic values from feathers), "sex" and "non-breeding area" (the latter only in non-breeding models) as fixed factors and "individual" as a random factor. The factor "colony" (either Veneguera or Montaña Clara) was also added for all models except $\delta^{13}C$ and $\delta^{15}N$ during breeding, since we do not have P1 from Montaña Clara. We ran 10,000 iterations for each model to obtain the 95% CI. We included year as a fixed factor to keep the possible effects of annual variability out of the residual variance of the models. Animals were sexed either with molecular sexing (68% of individuals) or using discriminant functions (32%) from fieldwork bill measurements. For those models related to non-breeding, we only considered non-breeding areas with a sample size larger than five individuals/year.

To explore the consistency of traits throughout the annual cycle, we performed LMM with the same structure explained previously but also including as a covariate the parameters calculated during breeding, in order to explain the same trait during the following non-breeding season. As an example, NFI during breeding was used as covariate to explain NFI during non-breeding. We used the "lmer" function in the "lme4" package[68] to run the models. Significance of the non-breeding covariate was estimated using the "mixed" function in the "afex"[69] package with the likelihood ratio test.

To address the effect of individual strategies on fitness, we explored the influence of individual trait preferences and degree of specialization on the probability of fledging success. Considering each individual and year for which the nest was monitored at the time of fledging (mid-October), we proceeded as follows. First, we calculated the average fledging success (value ranging from 0 to 1) for all years of each individual. We later calculated the

average value of each trait ($\delta^{13}C$, $\delta^{15}N$, NFI and SST) for all years of each individual. From the previous LMM performed to calculate *R*, we extracted the individual repeatability value (R_{ind} hereafter) associated with each trait, following previous approaches[51]. We considered individuals to be weakly, intermediate or highly specialized according to their R_{ind} value. To classify them objectively, we used the k-means algorithm for clustering R_{ind} values into three groups (note that mean and size of each group varies depending on the range of R_{ind} values in each trait, see summary in Table 1 of Supplementary Material). Finally, we fitted logistic regression models (Generalised Linear Models, GLM, with logit-link function and binomial error distribution) to model the probability of fledging success, including the number of years fledging was recorded as a weight into the models. We included as predictors the R_{ind} group (fixed factor) and the mean value of its associated trait (covariate). The weakly specialized group was set as a reference level. To ensure model suitability, we tested uniformity of residuals and accounted for overdispersion for every GLM using functions provided by the "DHARMa" package[70]. To evaluate the effect of predictors, both the p-value and 95% CI of coefficient estimates were calculated. Pairwise comparisons among levels were calculated based on estimated marginal means and adjusted using post-hoc Tukey correction[71]. Regarding mean values of traits, in the cases of $\delta^{13}C$ and $\delta^{15}N$, we used the fledging success following the year of moult in the case of non-breeding variables and of the year of moult in the case of breeding variables. Similarly, for NFI and SST we used the fledging success following the non-breeding period in the case of non-breeding variables and of the concurrent breeding attempt in the case of breeding variables. Regarding non-breeding, we only performed GLM with individuals spending the non-breeding period in the Benguela system, because it was the only area with $N > 5$.

Ethics. All experiments were performed in accordance with relevant guidelines and regulations and all protocols were approved by Gobierno de Canarias (permits: 84/2007, 2011/0795, 2015/1170).

Data Availability

Data will be available at Universitat de Barcelona archive.

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Author Contributions

L.Z. analysed the data and wrote the paper; J.M.R.-G. led the fieldwork, analysed geolocator data, performed statistical analyses and contributed on writing the manuscript; T.M. analysed S.I.A., led the fieldwork, analysed geolocator data and commented on drafts of the manuscript; Z.Z. led the fieldwork, analysed geolocator data and commented on drafts of the manuscript; E.A. participated in fieldwork and commented on drafts of the manuscript; R.R. obtained funding, participated in fieldwork and commented on drafts of the manuscript; J.G.-S. conceived the study, obtained funding, participated in fieldwork and wrote the paper.

Additional Information

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