

Non-breeding distribution and at-sea activity patterns of the smallest European seabird, the European Storm Petrel (*Hydrobates pelagicus*)

TERESA MILITÃO,*¹  ANA SANZ-AGUILAR,^{2,3}  ANDREU ROTGER²  & RAÛL RAMOS¹ 

¹Departament de Biologia Evolutiva, Ecologia i Ciències Ambientals – Facultat de Biologia, Institut de Recerca de la Biodiversitat (IRBio), Universitat de Barcelona (UB), Av. Diagonal 643, Barcelona, 08028, Spain

²Animal Demography and Ecology Group, Institut Mediterrani d'Estudis Avançats (IMEDEA), C/ Miquel Marquès 21, Esporles, Illes Balears, 07020, Spain

³Applied Zoology and Conservation Group, Universitat de les Illes Balears (UIB), Carretera de Valldemossa km 7.5, Palma, Illes Balears, 07122, Spain

Determining the non-breeding distribution and activity patterns of migratory animals is essential to understand the trade-offs across breeding, moulting and migratory periods and to evaluate the differential levels of exposure of these animals to threats throughout the year. By taking advantage of the current miniaturization of geolocators, during the breeding season of 2019, we deployed geolocators on 10 European Storm Petrels *Hydrobates pelagicus* breeding on Benidorm Island, Western Mediterranean, to determine the distribution and activity patterns of this small seabird species. Of the eight individuals that were recaptured with usable geolocation data, all individuals migrated to the North Atlantic Ocean, ranging between the Canary Islands and south of Iceland. They possibly take advantage of the more productive waters in the North Atlantic areas explored during the non-breeding period compared with the Western Mediterranean areas explored during the breeding period. This migratory pattern contrasted with the partial migration described for individuals breeding in the Central Mediterranean. Tracked individuals were more synchronous in their prenuptial than in their postnuptial migratory phenology, probably due to a higher probability of breeding success related to earlier arrival to the breeding area. At-sea activity data indicated that individuals spent more time on the water at night (and especially on those nights around the new moon) during the first half of the non-breeding period (matching the dates of the moulting period of the species). Although birds may begin to moult their feathers while breeding, some seemed to overlap the moulting period with the postnuptial migration. Our results show that multi-colony studies are needed to understand the drivers of distinct migratory patterns at intra- and inter-population levels and how small migratory species trade-off the overlap of moult with other energetically demanding activities such as breeding or migrating.

Keywords: at-sea behaviour, global location sensor, *Hydrobates pelagicus melitensis*, marine primary production, Mediterranean Storm Petrel, Procellariiformes.

INTRODUCTION

Migratory animals move among areas to take advantage of the spatial and/or temporal variation

of resources, avoid predators or find the most suitable habitats for each stage of their life cycle (Dingle 1996, Greenberg & Marra 2005, Newton 2008). Migration is thus a component of the animal's life history that helps them improve their fitness. Although animals can benefit from migrating, high levels of mortality can occur during the non-breeding period (Klaassen *et al.* 2014, Lok

*Corresponding author.
Email: tnetomilitao@ub.edu
Twitter: @TeMilitao

et al. 2015, Sanz-Aguilar *et al.* 2015), as they must cope with the energetic costs of long-distance movements in addition to the exposure to threats while migrating and/or in the non-breeding area (Alerstam *et al.* 2003, Newton 2008, Møller & Szép 2011). As migratory movements may differ at intra- and inter-population levels, it is essential to identify at both levels which migratory routes and non-breeding areas are used, as they may be associated with distinct threats and/or mortality risks (Sanz-Aguilar *et al.* 2012, Klaassen *et al.* 2014, Lok *et al.* 2015, Flack *et al.* 2016).

In addition to coping with the energetic costs of breeding and migrating, migratory birds must deal with the costs of feather moult (Hemborg *et al.* 1998, Echeverry-Galvis & Hau 2013). Besides the resource costs of synthesizing new feathers, moult may compromise flight ability and thermal insulation (Murphy 1996, Cyr *et al.* 2008). Gaps in the wings and/or tail during moulting can reduce flight efficiency and manoeuvrability, which ultimately affects the aerodynamic performance of birds, and increases the cost of flying and the risk of predation (Hedenström & Sunada 1999, Swaddle *et al.* 1999). In many bird species, to avoid the overlap with other demanding energetic activities, moult is not expected to occur when migrating or breeding (Ginn & Melville 1983).

Knowledge about the non-breeding distribution and the moulting-breeding and moulting-migration temporal overlaps is relevant to understanding the trade-offs between these life-history events. In seabirds, the complexity and duration of moult are positively related to the size of their wings, and the probability of overlap between breeding and moulting seems to be higher in non-migratory species (Bridge 2006). Nevertheless, without knowledge of the non-breeding distribution, this result may be biased. For example, Bridge (2006) assigned Scopoli's Shearwater *Calonectris diomedea* as a non-migratory species, but nowadays we know that this is an obligate migratory species with several individuals performing trans-equatorial migration (Müller *et al.* 2014, De Felipe *et al.* 2019). Furthermore, the non-breeding distribution and temporal overlap between energetically demanding events are still unknown in many pelagic seabird species because they are only accessible to researchers during the breeding period. Outside the breeding period, pelagic seabirds are particularly challenging to study, as they are somewhere

out at sea. But this is also an important period of their life cycle, as it is when they migrate and usually moult their feathers.

Information on seabirds' migratory movements and non-breeding distributions can be revealed by the deployment of bio-logging devices (e.g. Egevang *et al.* 2010, Frederiksen *et al.* 2012, Péron & Grémillet 2013, Weimerskirch *et al.* 2017, Ramos *et al.* 2021). Light-level geolocators (hereafter geolocators) are small bio-logging devices that record and store solar irradiance (ambient light), allowing the inference of movements of the tracked individuals (Lisovski *et al.* 2012). The light data registered by the geolocators are used to determine the day length and the time of solar noon, allowing an estimation of the latitude and longitude of the bird's location, respectively, with an average error of between 200 and 400 km (Phillips *et al.* 2004, Shaffer *et al.* 2005, Halpin *et al.* 2021). By deploying geolocators with two gold contact pins on the leg of the bird, it is possible to record conductivity, which is useful to infer when the individual was in contact with saltwater, as saltwater is a good conductor of electricity. This information allows us to determine when a tracked individual was out of the water (flying/searching for food) or on the water (resting/feeding) during the non-breeding period, being a powerful tool to infer at-sea activity and moulting periods of the tracked individuals (Cherel *et al.* 2016).

Until recently these bio-logging devices were still too heavy to be deployed in small species, restricting the assessment of the impacts of threats at-sea that they are exposed to (Dias *et al.* 2019). Due to the current miniaturization of these devices, it is now possible to track one of the smallest seabird species in the world, the European Storm Petrel *Hydrobates pelagicus* (about 28 g, Warham 1990). There are two recognized sub-species, the Mediterranean *H. p. melitensis* and the Atlantic sub-species *H. p. pelagicus* of the European Storm Petrel, which differ morphologically (Lalanne *et al.* 2001) and genetically (Cagnon *et al.* 2004), and may also differ in migratory behaviours. Individuals from the Atlantic sub-species can engage in trans-equatorial migrations as far as the southern tip of Africa (Matović *et al.* 2017, Ausems *et al.* 2021); however, to our knowledge, no tracking studies have been published on the Atlantic sub-species. In contrast, most individuals of the Mediterranean sub-species are thought to remain year-round in the Mediterranean basin

(Martínez *et al.* 2019), with only a small proportion of the population migrating to the Atlantic (Lago *et al.* 2019). Nevertheless, the migratory patterns and non-breeding distribution of this subspecies are based only on stable isotope analyses of feathers of birds not tracked with geolocator (Martínez *et al.* 2019) and geolocation data from a single population at Filfla Islet, Malta (Lago *et al.* 2019).

Therefore, in our study, we aim to determine the migratory phenology and non-breeding distribution of European Storm Petrels breeding in the Western Mediterranean, which will allow us to evaluate possible inter-population differences in the non-breeding distribution and phenology by comparing our results to those of Lago *et al.* (2019). Additionally, as the breeding phenology of this species is related to the peak of abundance of their main prey, the ichthyoplankton (D'Elbée & Hémery 1998, Albores-Barajas *et al.* 2011), which in turn is related to the peak of marine primary productivity (Ramírez *et al.* 2016), we also aim to assess the year-round monthly variation of marine primary productivity in the Mediterranean breeding area and in the main Atlantic non-breeding areas explored by this species to determine whether productivity also influences their migratory phenology. We hypothesize that European Storm Petrels migrate to areas that are more productive than the breeding area during the non-breeding season. Finally, we also aim to unravel their at-sea activity patterns during the non-breeding period. More specifically, we want to verify whether European Storm Petrels are a nocturnal species during the non-breeding period, as this could have conservation implications such as a higher susceptibility of being threatened by at-sea light pollution and to evaluate whether at-sea activity patterns change throughout the non-breeding period, especially during moult compared with the non-moulting period, as in other seabird species the proportion of time on the water is higher while birds are moulting their feathers (Cherel *et al.* 2016, Ramos *et al.* 2018). This information could be useful to identify the moulting period at individual level and how these patterns are shaped by the moon cycle, as moonlight is known to influence the at-sea activity patterns in many seabird species (e.g. Dias *et al.* 2012). We hypothesize that European Storm Petrels will be more active (less time on the water and more time flying searching for prey) during the night than

during the day, as nocturnal foraging has already been detected during migratory and breeding periods (Thomas *et al.* 2006, Albores-Barajas *et al.* 2011). Furthermore, as they rely mainly on ichthyoplankton prey (Sanz-Aguilar *et al.* 2019), many of which perform diel vertical migrations, i.e. at night they are closer to the sea surface than during the day (Prihartato *et al.* 2016), European Storm Petrels will probably be more active in those nights around the full moon when the intense moon illumination may facilitate the detection of their prey, as has been reported in other seabird species (Pinet *et al.* 2011, Dias *et al.* 2016). Given that European Storm Petrels start moulting during breeding and continue to moult into the non-breeding period (Martínez *et al.* 2019), we hypothesize that they will spend more time on the water during the first part of the non-breeding period.

METHODS

Study species and area

The European Storm Petrel breeds in the Mediterranean and the northeast Atlantic Ocean. On a global scale, its conservation status is categorized as Least Concern by IUCN (BirdLife International 2018), but the Mediterranean sub-species is of greater conservation concern (Massa & Borg 2018). The species begins to moult its primary and body feathers during the breeding period, usually overlapping with the end of incubation or the early chick-rearing period, although there is some variation among populations (Ginn & Melville 1983, Arroyo *et al.* 2004). Secondary and tail feathers usually begin to moult 1 month after the onset of the primary feather moult (Arroyo *et al.* 2004). The end of the moulting period is more difficult to define, as individuals finish moulting during the non-breeding period, probably in November or December (Martínez *et al.* 2019).

This study was conducted in one of the most important colonies of European Storm Petrels in the Western Mediterranean, on Benidorm Island (38.50°N, 0.13°W). In this colony, European Storm Petrels breed inside a cave, where artificial nests were set, and a long-term individual-based study has been carried out since 1993. The species has some variability in its breeding phenology both within and between geographical areas (Cadiou 2001, Sultana & Borg 2012, Sanz-Aguilar *et al.*

2019). In the Mediterranean, European Storm Petrels usually begin to visit the colonies at the end of March (Mínguez 1994), females lay a single egg between May and early July (Sanz-Aguilar *et al.* 2019) and chicks usually fledge in August–September (Sanz-Aguilar *et al.* 2019) after the chick-rearing period, which ranges from 56 to 86 days (Brooke 2004).

Geolocation deployment and data processing

On 26 July 2019, we deployed 10 geolocators (Intigeo-W30A9-SEA, Migrate Technology, Cambridge, UK, ~ 0.45 g, 15 × 5 × 4 mm) on 10 breeding adults of European Storm Petrels rearing well-developed chicks (from 27 to 45 days old). Birds were captured at night by hand when entering the colony and walking to their nests. The geolocators were deployed on the tibia attached to a metal ring using stainless steel cable ties (Fig. S1), totalling an average weight of 0.80 g ± 0.01 (average ± standard deviation (sd)), which corresponded to 2.64% of the weight of tracked individuals (30.3 g ± 1.9). Each geocator was calibrated before its deployment and after its recovery on top of a high building of known coordinates and far from lit areas. To check for possible deleterious effects associated with the deployment and carrying of the geocator, we compared the return rates and breeding success (number of fledged chicks per number of eggs laid) in 2020 of the tracked birds ($n = 10$) and of control birds ($n = 85$) with *a priori* similar characteristics, i.e. birds that were captured in 2019 as experienced breeders that reproduced successfully and were not equipped with a geocator. Partners of the tracked birds were excluded from the control group. Note that we can only provide a return rate, which is a combination of both survival and recapture probabilities, because to estimate survival probabilities separately we would have needed one additional monitoring year (Sandercock 2020).

All geolocation data processing was carried out using R 3.6.2 (R Core Team 2021). We used the *preprocessLight* function of the 'BAStag' package (Wotherspoon *et al.* 2016) to process the light data registered by the geolocators every 5 min and using a light threshold value of 2 lux. This threshold allowed us to define the beginning of sunrise and sunset, which occur when the light values

exceed or fall below this threshold, respectively. With this function, we estimated the hour of sunrise and sunset, inspected the integrity of the light curve of each day and manually adjusted the time of sunrise or sunset where we suspected the time was incorrect by comparing it with the observed light profile of preceding and following days. These incorrect times occurred possibly due to interference of feathers covering the light sensor. We usually manually adjusted the incorrect time of twilight to the mean time between the previous and the following days, except in those cases when there was a small peak of light (below the light threshold we defined) before (or after, in the case of sunset) the twilight time assigned automatically; in those cases, we moved the transition to this small peak of light. Subsequently, we used the 'Solar/Satellite Geolocation for Animal Tracking (SGAT)' package (Sumner *et al.* 2009, Lisovski & Hahn 2012, Lisovski *et al.* 2019), which applies Markov chain Monte Carlo (MCMC) simulations to estimate and refine the locations of the tracked individuals. For this analysis, we first calculated the zenith angle and the error distribution around the twilights based on the calibration period of each geocator at a known location, using a threshold value of 2 lux and assuming a gamma distribution. We also generated a gamma distribution of flight speeds between 0 and 20 km/h based on the average values known for the species (Rotger *et al.* 2021). We used the *thresholdPath* function to obtain the initial path of each bird, which is needed to begin the MCMC simulations. Furthermore, we generated a spatial mask to avoid locations over land or over sea-areas outside the known distribution of the species (Flood & Fisher 2013) and out of the range of the raw data of the geolocators. All previous information was included in the MCMC simulations to obtain the estimated locations of each bird. This analysis allows us to obtain better estimations of the location of the individuals, especially around the equinoxes, when latitude is unreliable due to low variation in the daylight length (Lisovski *et al.* 2012); nevertheless, some uncertainty may still exist and the accuracy of the positions during the equinox periods will still be lower than outside these periods (Halpin *et al.* 2021).

Every 6 s, geolocators also registered conductivity as a binary variable, with 1 when the bird was in contact with saltwater and 0 if there was no conductivity, i.e. the bird was either flying or on

land. These saltwater immersion occasions were then summed up in blocks of 5-min intervals. Therefore, conductivity ranged from 0, if the individual was not on the water during a 5-min interval, to 50 (i.e. the sum of the 50 blocks of 6-s periods with conductivity 1) if the bird was continuously in contact with saltwater for 5 min.

Migratory phenology

To determine when European Storm Petrels were staging or moving between staging areas, we used the residence in space and time approach (<https://github.com/raorben/RST>; hereafter RST, Torres *et al.* 2017). This approach is usually used with GPS data and allows the location of an animal to be associated with the behavioural states of travelling, resting or foraging activity (area restricted search, ARS) based on the distance travelled and time spent within a specific radius. This specific radius was calculated using the diagnostic tool provided in the RST approach by testing several potential radii, from 15 to 100 km (in 5-km intervals) and from 110 to 800 km (in 10-km intervals). We assumed that European Storm Petrels were staging when the RST approach assigned a specific position as resting or ARS, and moving between staging areas when the geographical position was assigned as travelling.

The migratory phenology was then defined based on the RST assignment and conductivity data of the individuals (see also the schematic diagram in Fig. S2). The breeding period was considered to be finished on the last night the bird continuously spent more than 2 h ($2.7 \text{ h} \pm 0.3$, average \pm sd) on dry land at night (approximately the average time breeders spent at the colony when rearing chicks; García, 2009). The onset of postnuptial migration was defined as the first day after the deployment of the geolocator that a given bird was travelling for at least 3 days. The end of the non-breeding period was defined as the first night the bird continuously spent more than 5 h ($12.0 \text{ h} \pm 10.5$) on land at night after the end of prenuptial migration. The onset of prenuptial migration was defined as the first day of a period of at least 3 days a bird spent travelling before the first day in the colony. The first day in the colony was determined as the first day without light or conductivity detected (because the bird was inside the nest cavity) by the geolocator during the daylight period.

The Strait of Gibraltar is an important landmark for migratory animals not only because it defines the limits between the Atlantic Ocean and the Mediterranean Sea, but also because it is frequently used to study the migratory passage and phenology of seabirds (Ramos 2019), including European Storm Petrels (Hashmi & Fliege 1994). Some of the tracked European Storm Petrels passed through the Strait of Gibraltar more than once at the beginning and/or at the end of the non-breeding period. We assigned the period in the Strait of Gibraltar as the time between the first and last days that birds passed through the Strait on postnuptial and prenuptial migration. Furthermore, we considered that European Storm Petrels were in the Atlantic after the last day they passed through the Strait of Gibraltar towards the Atlantic until the first day they passed through it towards the Mediterranean. We considered the non-breeding period to span from the day after the last night in the colony until the day before the first night in the colony. All positions of the birds that were assigned as resting or ARS by the RST approach (described above) were considered non-breeding staging areas. The geographical region of each non-breeding staging area was defined whenever possible based on the main subdivisions of the Mediterranean Sea and Atlantic Ocean (International Hydrographic Organization, 2002).

Statistical analysis

All statistical analyses were carried out using R 3.6.2 (R Core Team 2021), and we assumed a critical p -value of 0.05.

To identify the main areas used during the non-breeding period, we calculated the utilization distribution (UD) from kernel density estimations at a population level based on the non-breeding staging positions of all individuals together using *kernelUD* [with a smoothing factor of 1.82° as recommended by Lascelles *et al.* (2016), an extent of 0.5 and a grid of 1000] and *getverticeshr* functions of the 'adehabitatHR' package (Calenge 2006). To characterize inter-individual variability in migratory phenology and non-breeding distribution, we calculated the 50 % UD contour of each individual per month (using the same function and parameters described previously, except by an extent value of 25).

The breeding phenology of the European Storm Petrels is timed to coincide with the peak of

relative abundance of ichthyoplankton, one of the main prey of this species (D'Elbée & Hémerly 1998, Albores-Barajas *et al.* 2011). This peak occurs on average 110 days after the peak of marine primary productivity in the Western Mediterranean (Ramírez *et al.* 2016). To understand whether the timing of migration of European Storm Petrels (i.e. the onset of the migratory movements) could be influenced by the variation of the marine primary productivity throughout the year, we compared the monthly variation of this environmental variable in the Mediterranean areas used during the breeding period with the Atlantic areas used during non-breeding periods. Assuming that a temporal lag (of several months) between a peak of primary producers and a peak in the abundance of European Storm Petrel prey exists, we expect the mean migratory movement towards the Atlantic areas to occur several months after a drop in the primary productivity values in the Mediterranean breeding area, and vice versa regarding the migratory movement from the Atlantic non-breeding areas towards the Mediterranean. The monthly net primary production of biomass (mg/m^3) data from May 2019 to April 2020 were obtained from <https://resources.marine.copernicus.eu/> at 0.25° resolution. We extracted the values of the monthly net primary production of biomass (primary productivity hereafter) for each cell of the 50% UD contour kernel (using the same function and parameters previously described) of areas each individual explored during its the breeding period (before the last night in the colony and after the first night in the colony) and during the period each individual was in the Atlantic Ocean (between the last outbound and first inbound crossing of the Strait of Gibraltar). Subsequently, for each individual we calculated the mean primary productivity of each kernel. We performed a set of generalized additive mixed models (GAMMs) with the logarithm of base 10 of an individual's mean primary productivity of each kernel as a response variable. The GAMMs were fitted using the *gamm* function of the 'mgcv' package (Wood 2011) and Gaussian distribution as family. In these models, we included area (Mediterranean breeding vs. Atlantic non-breeding area) as a fixed factor and month as a smoothing factor with interaction with area. Furthermore, in all models, we included individual as a random factor.

The amount of time a migratory seabird spends on saltwater or flying may change throughout the

year due to different constraints such as breeding duties, moulting and/or migration, as well as due to the moon cycle. We used GAMMs to determine whether European Storm Petrels are a nocturnal species during the non-breeding period and to evaluate whether their at-sea activity patterns change throughout the non-breeding period (especially during vs. outside the moulting period) and whether they are influenced by moonlight intensity. The night and the daylight periods were defined based on the hour of sunrise and sunset at each bird location using the *getSunlightTimes* function of the package 'suncalc' (Thieurmel & Elmarhraoui 2019). We calculated the daily proportion of time each bird spent on the water during the night and the daylight periods, separately, as a previous study revealed that, during the moulting period, some seabird species may decrease their time foraging (i.e. out of the water) during the day or during the night depending on diurnal or nocturnal foraging mode (Cherel *et al.* 2016). We constructed a set of candidate models using the *bam* function of the 'mgcv' package (Wood 2011), in which we included the proportion of time on the water as a response variable. As the response variable was a proportion that varied from 0 to 1, we fitted our models using a beta distribution as a family and logit as a link function. Furthermore, in all models, we included individual as a random factor. We also included as fixed factors the variables day/night and moulting vs. non-moulting periods. The moulting period was defined, based on the literature, from 25 June to 30 November (Ginn & Melville 1983, Arroyo *et al.* 2004, Sultana & Borg 2012, Martínez *et al.* 2019). As smoothing factors, we included day of the year and moon illumination (obtained from the *moonAngle* function of the 'oce' package; Kelley & Richards 2020). We used a likelihood ratio test (function *lrtest* from the packaged 'lmtree'; Zeileis & Hothorn 2002) to assess the importance of the interaction between day of the year and the day/night variable and between moon illumination and moulting vs. non-moulting period because, during moult, seabirds may spend more time on the water (Cherel *et al.* 2016, Ramos *et al.* 2018). These interactions were only included in the final set of candidate models if the likelihood ratio tests were significant. The most parsimonious model was selected as the one with the lowest Akaike information criterion (AIC) value.

RESULTS

Nine of the 10 deployed geolocators were recovered in the subsequent breeding season between 30 April and 1 July. The return rate for tracked and control birds was 0.90 ($n = 9/10$) and 0.47 ($n = 40/85$), respectively. Breeding success during the 2020 breeding season was 0.56 ($n = 5/9$) for tracked birds and 0.78 for control birds ($n = 31/40$). Two of the geolocators stopped collecting data before recovery; one (BU458001) had an almost complete year-round trip (viable light data until 22 February 2020), whereas the other was excluded from the analyses as it stopped working 2 months after being deployed. The geolocation data processed with SGAT provided better estimations of the locations of the birds, although latitude tended to have constant values throughout the equinox period (Fig. 1, Fig. S3).

Phenology and spatial distribution

European Storm Petrels spent the last night in the colony in mid-August, 1 month before the onset of post-nuptial migration (Table 1). All individuals migrated to the North Atlantic Ocean (Fig. S4). The date of the outbound passage through the Strait of Gibraltar varied between the end of August and the end of December. Three individuals passed through the Strait of Gibraltar several times, with an interval of 26–57 days between the first and the last passage (Fig. 2, Fig. S5). Of the eight tracked individuals (with viable geolocation data), only one migrated to the east of Tunisia (Central Mediterranean), subsequently to the Balearic Sea, and only then migrated to the Atlantic Ocean (Figs S4 and S5). Between 25 December and 15 February, all individuals were in the Atlantic Ocean but using different non-breeding areas. The non-breeding period of the tracked individuals lasted on average 220 days, with 75–197 days spent in the Atlantic Ocean (Table 1). Individuals spread from waters as far south as around the Canary Islands (one individual) to waters to the south of Iceland (one individual); the remaining birds were located off Morocco and the Gulf of Cádiz to the Irish and Celtic Seas (Fig. 3, Figs S4 and S5). Two of the three individuals that passed through the Strait of Gibraltar several times on their way to the Atlantic Ocean showed the same behaviour on the outbound and inbound passages, with an interval of 12–29 days between the first

and last inbound passage (Fig. 2, Fig. S5). Birds spent the first night at the colony on average on 25 March, ranging from 25 February to 13 April (Table 1).

Year-round variation in primary productivity in breeding and non-breeding areas

The most parsimonious GAMM of the primary productivity was the one including both fixed factors, month and area (the areas used in this analysis are represented in Fig. S6), as well as their interaction (Table 2). In general, in the Mediterranean breeding area, primary productivity remained low and stable from May until late September, followed by a rapid increase in October, and high values from the end of November until April. In contrast, in the Atlantic non-breeding areas, primary productivity decreased from May until the end of December, when it began to increase until April. However, more importantly, we found that primary productivity varied differently between months in the two areas (Fig. 4, Table 2), being higher in the Atlantic non-breeding areas than in the Mediterranean breeding area from May to September, whereas from November to the end of February, primary productivity was higher in the Mediterranean breeding area than in the Atlantic non-breeding areas.

At-sea activity patterns

The likelihood ratio tests pointed to the importance of both interactions between day of the year and day/night periods ($\chi^2 = 178.1$, $df = 5.4$, $p < 0.001$) and between moon illumination and moulting vs. non-moulting period ($\chi^2 = 9.5$, $df = 2.7$, $p = 0.002$), and therefore we retained them in the analysis. The most parsimonious GAMM of the proportion of time on the water was the one including the fixed factors day/night and moulting vs. non-moulting period and the two previously mentioned interactions. Based on the individual activity patterns and the GAMM, during the non-breeding period, European Storm Petrels spent more time on the water during daylight than at night (Fig. 5, Table 3, Fig. S7) and during the moulting period than outside it (Table 3). The proportion of time on the water during the night varied significantly throughout the non-breeding

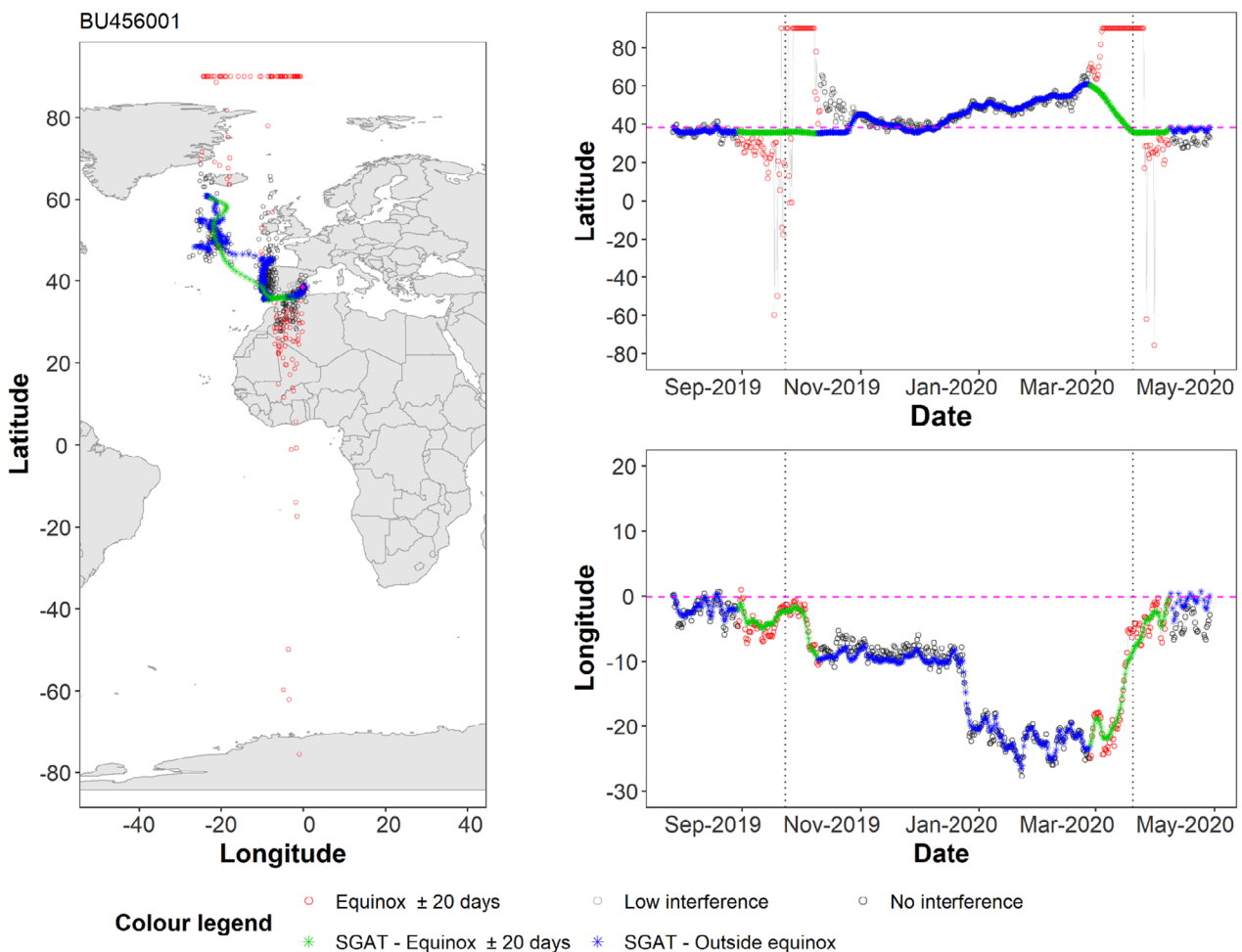


Figure 1. Example of comparison between original geolocation positions (in circles) and those obtained after the geolocation data processing with the ‘Solar/Satellite Geolocation for Animal Tracking (SGAT)’ package of R (in stars). On the left is the map with the positions with both types of trips and on the right the same information but more detailed and segregated by latitude and longitude. Original data are represented in light or dark grey circles whenever the twilights showed low or no interference, respectively; the red circles represent those twilights 20 days before and after the equinoxes. The positions obtained from SGAT are represented as dark blue stars, except during the 20 days before and after the equinoxes, which are represented in light green stars. The pink diamond (in the map) and horizontal dashed lines represent the colony coordinates, while the vertical dotted lines represent the dates of the equinoxes [Color figure can be viewed at [wileyonlinelibrary.com](https://onlinelibrary.wiley.com/terms-and-conditions)]

period (Table 3). It was higher from September to the end of December, with a peak around mid-October (Fig. 5a). During daylight, the proportion of time on the water also varied throughout the non-breeding period (Table 3), showing a bell-shaped curve, with higher values from November to January. The moon illumination only influenced the activity patterns of European Storm Petrels during the moulting period (Table 3), showing a linear trend, with birds spending less time on the water on nights with higher levels of moon illumination (Fig. 5b).

DISCUSSION

This study improves our knowledge of the European Storm Petrel’s migratory phenology and reveals the importance of the North Atlantic Ocean as a major non-breeding area for the western population of the Mediterranean sub-species. It also emphasizes the variability of areas used throughout the non-breeding period, with each individual using between two and four different areas in the North Atlantic Ocean. Moreover, our results suggest that the seasonal variation in

Table 1. Migratory phenology of European Storm Petrels from Benidorm Island (Spain) tracked with geolocators in 2019–2020. The duration of the non-breeding period was calculated as the difference between the day after the last night and the day before the first night in the colony. The duration of the Atlantic staging was calculated as the difference between the last outbound and the first inbound crossing the Strait of Gibraltar of each bird. *n* represents the sample size and sd the standard deviation

Phenological parameter	<i>n</i>	Average ± sd	Range
Last night in the colony	8	18 Aug ± 6.9	10 Aug–30 Aug
Beginning of postnuptial migration	8	17 Sep ± 46.0	15 Aug–23 Dec
Last outbound crossing of the Strait of Gibraltar	8	15 Oct ± 45.3	18 Aug–24 Dec
Beginning of prenuptial migration	7 ^a	24 Feb ± 18.7	21 Jan–26 Mar
Last inbound crossing of the Strait of Gibraltar crossing	7 ^a	13 Mar ± 12.2	29 Feb–3 Apr
First night in the colony	8	25 Mar ± 15.9	25 Feb–13 Apr
First day in the colony	7 ^a	11 Apr ± 10.5	30 Mar–27 Apr
Duration of the non-breeding period	8	219.8 days ± 19.0	191–247 days
Duration of the Atlantic staging	7 ^a	155.6 days ± 42.0	75–197 days

^aOne individual was excluded from these estimations as the light data were unreliable due to battery problems, although the saltwater immersion data registered correctly.

primary productivity differs between the Mediterranean breeding and Atlantic non-breeding areas, which may drive the migration behaviour of this species. Based on the at-sea activity patterns, we confirmed that the European Storm Petrel is a nocturnal species during the non-breeding period, although during moulting it spends more time on the water than after the moulting period. Furthermore, our results showed that the at-sea activity patterns of this species were only slightly influenced by moonlight during the moulting period.

We believe the deployment of small geolocators on European Storm Petrels did not present a relevant impact on the tracked birds, at least on their survival, as the 90% return rate matches the survival rate of this species in the study colony (range 0.85–0.90; Sanz-Aguilar *et al.* 2019). However, it may have had an effect on the breeding success in the following year, although due to our small number of tracked birds, we cannot conclude whether there was a real difference in breeding success due to the potential tag effect. Therefore, we recommend that future studies deploying large numbers of geolocators on European Storm Petrels should also include a control group to evaluate the potential impact of these devices on survival, body condition, breeding success and phenology (Bodey *et al.* 2018, Kürten *et al.* 2019, Cleasby *et al.* 2021).

Due to their small size, it is difficult to detect European Storm Petrels at sea and, when detected, it is impossible to distinguish which sub-species or colony they belong to. By combining the information from light levels and conductivity obtained

from geolocators, we were able to describe in detail the migratory phenology of European Storm Petrels at an individual level, improving previous phenological knowledge inferred from boat and on-land sightings. In general, our results agree with the sightings from boat surveys at the Strait of Gibraltar in which European Storm Petrels were observed passing through from August to November with a peak in October–November (Hashmi & Fliege 1994). However, one of the tracked individuals passed through the Strait at the end of December on a similar date as the only individual tracked from Malta that also migrated to the Atlantic Ocean (Lago *et al.* 2019). This suggests that there are still some migratory movements in December, although no European Storm Petrels were observed from boats in this month in the Strait of Gibraltar, which could be due to a lower observation effort in this month compared with the previous ones (Hashmi & Fliege 1994). Our results also concur with the on-land sightings of this species from August to December in the Gulf of Cádiz (Arcos *et al.* 2009) and from October to January on the west coast of Portugal (Ramirez *et al.* 2008). Some tracked individuals also made a small stopover in the Gulf of Cádiz and off the western coast of Morocco in February or March before returning to the Mediterranean Sea. The small differences between the phenologies obtained from sightings and geolocators are probably caused by the distance birds pass from the observation points (boats or land) and by weather and sea conditions, which may preclude the observation of such small birds. As tracked individuals

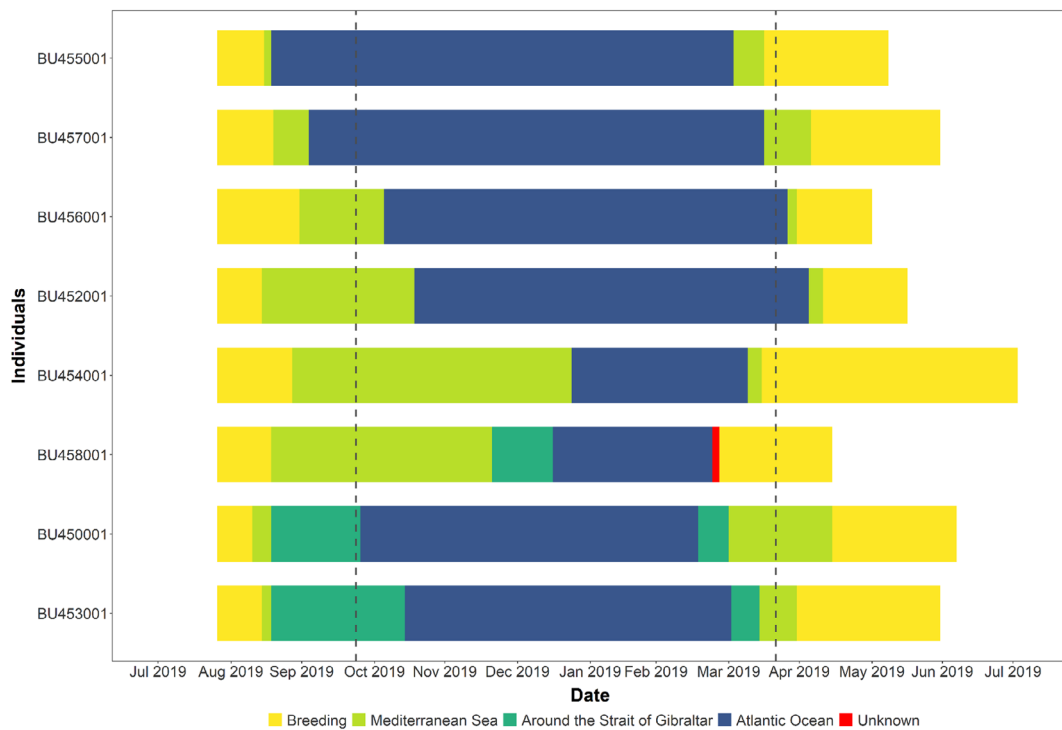


Figure 2. Migratory phenology of the European Storm Petrels based on the geographical location and activity data obtained from geolocators. Each horizontal bar represents the tracking period of each bird. Yellow represents the breeding period, which was defined as the period from the deployment of the geolocator until the last night in the colony prior to postnuptial migration and the period from the first night in the colony after prenuptial migration until the recovery date of the geolocator. Light green represents the period between the last night in the colony and the first day the bird passed through the Strait of Gibraltar towards the Atlantic Ocean or the period between the last passage of the Strait of Gibraltar towards the Mediterranean and the first night in the colony. Dark green represents the period between the first and last passage of the Strait of Gibraltar towards the Atlantic or after returning from it. Dark blue represents the period during which birds were exclusively in the Atlantic Ocean, i.e. between the last passage of the Strait of Gibraltar towards the Atlantic and the first passage of that strait towards the Mediterranean Sea. Red represents the period in which the light data were not correctly collected by the geolocator. The dashed vertical lines represent the dates of the equinoxes of September 2019 and March 2020 [Color figure can be viewed at [wileyonlinelibrary.com](https://onlinelibrary.wiley.com/terms-and-conditions)]

flew more during the night than during the day, we cannot exclude the possibility that European Storm Petrels might also migrate by night, making it harder to detect them by boat- or land-based censuses. Regarding the return from migration, the average first day spent in the colony was similar to those of tracked individuals from Malta (4 April, $n = 3$; Lago *et al.* 2019). We found a higher variability in the timing of the beginning of post-nuptial migration and of the last outbound passage through the Strait of Gibraltar than in the remaining phenological variables. In waders (especially those breeding in the polar or sub-polar areas), the higher consistency in the phenology of spring migration compared with autumn migration is common (Conklin *et al.* 2013, Åkesson *et al.* 2017, Carneiro *et al.* 2019) and is explained by a

restricted period suitable for breeding. In contrast, at end of the breeding period, there are fewer constraints, and the differences found in the phenology were explained by the accumulation of individual circumstances (timing of nest initiation, breeding success, variation in laying dates, etc.; Åkesson *et al.* 2017, Carneiro *et al.* 2019). A higher variability in the post-nuptial than in the pre-nuptial migration phenology has also been detected in some seabird species (Phillips *et al.* 2006, Ramos *et al.* 2018, Pastor-Prieto *et al.* 2019). Competition for breeding opportunities or access to better nests seem to be the reason given for high synchrony in pre-nuptial migration (Phillips *et al.* 2006), while the main reason pointed out for the greater variability in the timing of post-nuptial migration has been breeding success,

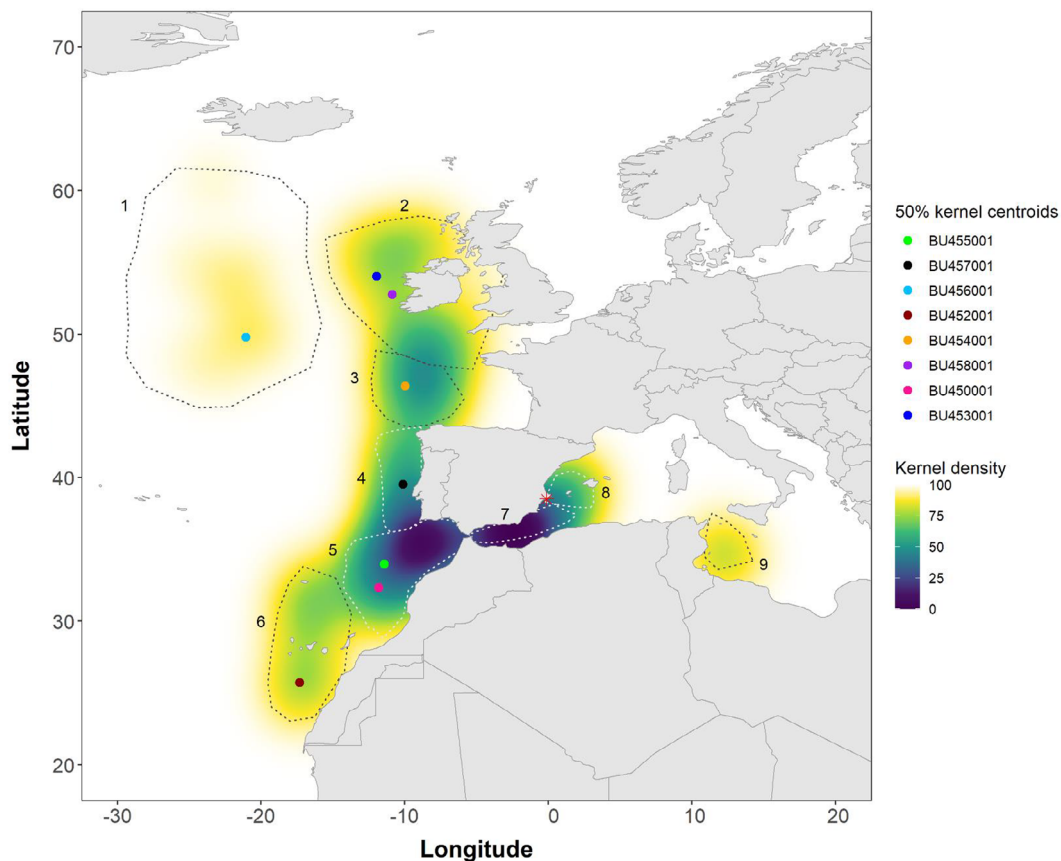


Figure 3. Non-breeding distribution (excluding the migratory movements) of the eight European Storm Petrels tracked with a geolocator. The colour gradient of the background represents the percentage of utilization distribution (UD) contours from the kernel density estimation. Colour dots represent the centroids of the 50% UD contour of each individual during the period in which all of them were simultaneously in the Atlantic Ocean. The red star indicates the location of the breeding colony of the tracked birds, Benidorm Island. The numbers and dotted lines represent the staging areas used by the tracked individuals: 1 – south of Iceland, 2 – Celtic and Irish seas, 3 – west of the Bay of Biscay, 4 – western coast of the Iberian Peninsula, 5 – Gulf of Cádiz and western coast of Morocco, 6 – Canary Islands, 7 – Alborán Sea and Algerian Basin, 8 – Balearic Sea, and 9 – Central Mediterranean. [Color figure can be viewed at [wileyonlinelibrary.com](https://onlinelibrary.wiley.com/terms-and-conditions)]

as failed breeders usually migrate earlier than successful breeders (Bogdanova *et al.* 2011, Catry *et al.* 2013, Desprez *et al.* 2018, Pastor-Prieto *et al.* 2019). In our study, at geolocator deployment, all tracked individuals already had a well-developed chick (from 27 to 45 days old), so the differences in breeding success cannot explain the pattern we observed. Other studies have found differences in the post-nuptial phenology between ages (Campioni *et al.* 2019), but mainly between immature individuals and adult breeders, which also does not apply to our study, as all individuals were already breeders. Other intrinsic factors, such as sex (Medeiros *et al.* 2012) or age (Péron & Grémillet 2013), may also influence the synchrony in the migratory phenology of a species; however,

more studies and data are required to explore these and other possibilities, such as the body condition of adults and/or the development of moulting at end of the breeding period.

Until recently, the information available has suggested that most individuals of the Mediterranean sub-species of European Storm Petrels remain within the Mediterranean Sea basin during the non-breeding period (Lago *et al.* 2019, Martínez *et al.* 2019). During post-nuptial migration, sightings from boats at the Strait of Gibraltar were mainly of individuals moving east entering the Mediterranean, with only < 20 % leaving it (Hashmi & Fliege 1994). Additionally, isotopic differences in the feathers of individuals from both sub-species suggest that those from the

Table 2. (A) Results of the generalized additive mixed models (GAMMs) performed on the monthly net primary production of biomass (mg/m^3) around the Mediterranean breeding area and in the non-breeding areas of the Atlantic Ocean used by European Storm Petrels (see main text for the definition of breeding and non-breeding areas). All models included individual as a random factor. $s()$ denotes the smoothing factor and 'by' refers to the interaction between variables. AIC refers to the Akaike information criterion and ΔAIC to the difference of AIC value of each model in relation to the AIC value of the best model, i.e. the most parsimonious, which is shown in bold type. The models are organized from lower to higher AIC values. (B) Estimate \pm standard error (se) of the fixed factor included in the best model and their statistical significance. (C) Effective degrees of freedom (edf) and statistical significance of the smoothing factors of the best model

A – Formula	AIC	ΔAIC	R^2 adjusted
s(month by area) + area	12.3	0	0.49
s(month) + area	60.9	48.6	0.29
area	69.3	57.0	0.23
s(month by area)	89.5	77.2	0.25
s(month)	116.8	104.5	0.06
null	120.5	108.2	0

B – Fixed factor	Estimate \pm se	t (edf)	p
Atlantic (intercept) vs. Mediterranean area	0.32 \pm 0.03	10.0 (1)	<0.001

C – Smoothing factors	edf	F	p
month in the Atlantic non-breeding area	4.66	14.9	<0.001
month in the Mediterranean breeding area	4.65	10.1	<0.001

Mediterranean sub-species remained in the Mediterranean Sea basin, at least during the moulting period (Martínez *et al.* 2019). Also, the low number of individuals ringed in the Mediterranean Sea basin and recaptured/recovered in areas throughout the Atlantic Ocean (Matović *et al.* 2017, Lago *et al.* 2019, Sanz-Aguilar *et al.* 2019) may indicate that only a small number of individuals of the Mediterranean sub-species leave the Mediterranean Sea during the non-breeding season. This was confirmed by the first tracking study of European Storm Petrels breeding in Malta, in which only one out of the seven tracked individuals migrated to the Atlantic, while two migrated to the Western Mediterranean and four remained around the breeding grounds (Lago *et al.* 2019). However, in our study all the tracked individuals spent at least part of the non-breeding period in

the Atlantic Ocean, indicating that this ocean is a non-breeding area far more relevant than previously thought, at least for the European Storm Petrels breeding in the Western Mediterranean. Therefore, our results contrast with the partial migration strategy described for individuals from Malta. The different inter-population proportion of resident vs. migratory individuals also occurs in other seabird species (Fayet *et al.* 2017), including the Yelkouan Shearwater *Puffinus yelkouan*, which also breeds along the Mediterranean Sea (Péron *et al.* 2013, Raine *et al.* 2013). Interestingly, both geolocation studies on European Storm Petrels showed that the tracked individuals explored different staging areas throughout their non-breeding period (Lago *et al.* 2019, present study). This is not uncommon in seabirds (Guilford *et al.* 2009, Egevang *et al.* 2010, Dias *et al.* 2012, Seyer *et al.* 2021) and has already been detected in other storm petrel species (Pollet *et al.* 2019). Exploring several areas throughout the non-breeding period may preclude the identification and protection of the main areas explored by European Storm Petrels and may expose these individuals to different threats at sea in each of those areas. At the same time, however, this may reflect an adaptation to explore different habitats, which may help this species to adapt to future environmental changes (Webster *et al.* 2002). Furthermore, an acute threat in a single staging area may not have drastic consequences at the population level, as it may only affect part of the population. During the non-breeding period, our tracked individuals moved close to some of the breeding areas of the Atlantic sub-species (Canary Islands, north of Spain, Ireland, UK and south of Iceland), whereas the individuals from the latter sub-species are thought to migrate to the South Atlantic (Matović *et al.* 2017, Aulsems *et al.* 2021). The differences in resource availability in the breeding vs. non-breeding foraging areas and/or differences in habitat preferences may lead to distinct migratory strategies among colonies (Ramos *et al.* 2015, Fayet *et al.* 2017) and/or sub-species. It is also still unknown why Mediterranean European Storm Petrels do not migrate to more productive upwelling areas off the West African coast as the Atlantic sub-species does (Matović *et al.* 2017, Aulsems *et al.* 2021). More tracking studies throughout the Atlantic and Mediterranean sub-species breeding ranges of European Storm Petrels are needed, together with other sources of information

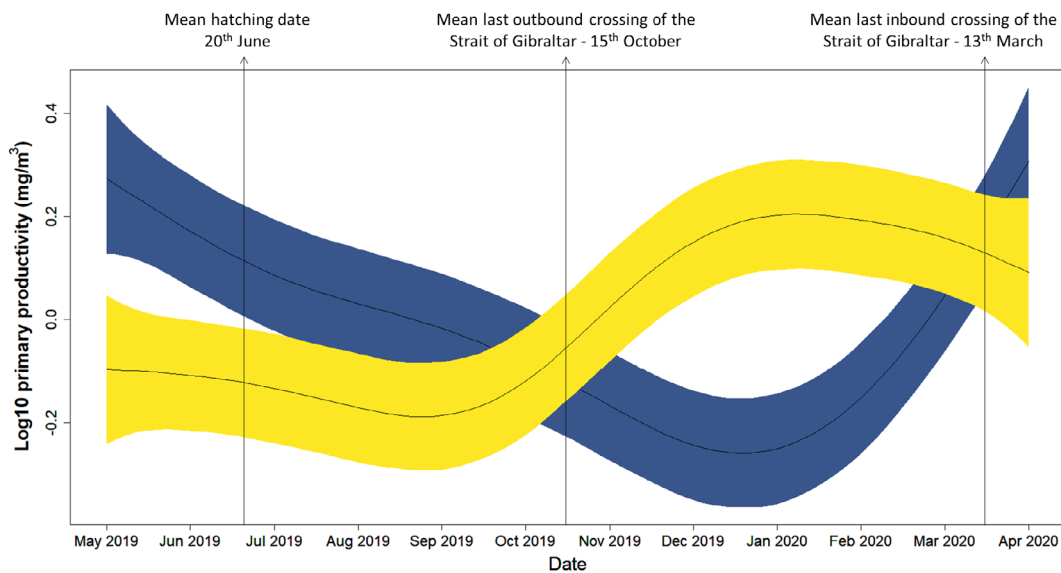


Figure 4. Output of the generalized additive mixed model (GAMM) of the monthly variation of the logarithm of base 10 of the monthly net primary production of biomass (mg/m^3) at the Mediterranean breeding area (in yellow) vs. at the Atlantic non-breeding areas (in dark blue) used by European Storm Petrels. Vertical lines indicate important mean phenological dates: hatching date of the chicks of the tracked individuals, last outbound crossing of the Strait of Gibraltar towards the Atlantic Ocean, and last inbound crossing of the Strait of Gibraltar towards the Mediterranean Sea [Color figure can be viewed at [wileyonlinelibrary.com](https://onlinelibrary.wiley.com/doi/10.1111/1365-3113.13068)]

(breeding performance, body condition, age, sex, etc.) to understand the drivers of the distinct migratory strategies among colonies and subspecies and to evaluate potential annual differences in migratory movements.

In this study, we assessed the monthly variation of primary productivity in the Mediterranean breeding areas and in the Atlantic non-breeding areas explored by the tracked individuals to understand its potential effect on the migratory phenology of European Storm Petrels. In this species, the peak of the hatching period is timed to coincide with the peak of relative abundance of ichthyoplankton prey, which occurs on average 110 days after the peak of primary productivity in the Western Mediterranean (Ramírez *et al.* 2016). The mean hatching date of the tracked individuals' chicks was on 20 June (± 7 days sd), matching a period of high primary productivity values in the Mediterranean breeding areas in the preceding 3–5 months (from January to March). Assuming that a drop in primary productivity will also be followed by a drop in the abundance of European Storm Petrel prey several months later, we expect that the tracked individuals migrated after a period of several months of low primary productivity. In fact, the mean crossing date of the Strait of

Gibraltar towards the Atlantic occurred after several months (from May to September) of low primary productivity values in the Mediterranean breeding area and high primary productivity in their Atlantic non-breeding areas. Similarly, the mean crossing date of the Strait of Gibraltar towards the breeding area occurred after several months (from November to February) of low primary productivity in their Atlantic non-breeding areas and high primary productivity values in the Mediterranean breeding areas. These results suggest that the migratory phenology of European Storm Petrels from the Western Mediterranean may be mediated by the spatial variation in peak primary productivity (i.e. through its lag effects on the abundance of ichthyoplankton) between breeding and non-breeding areas; however, multi-year tracking data are needed to confirm this potential relationship.

Regarding the at-sea activity patterns, our results confirm that the European Storm Petrel is a nocturnal species (Warham 1990), also during the non-breeding period, spending most of the daylight time on the water and flying mainly during the night. Interestingly, after the end of the breeding period until the beginning of December, we detected that most tracked individuals spent

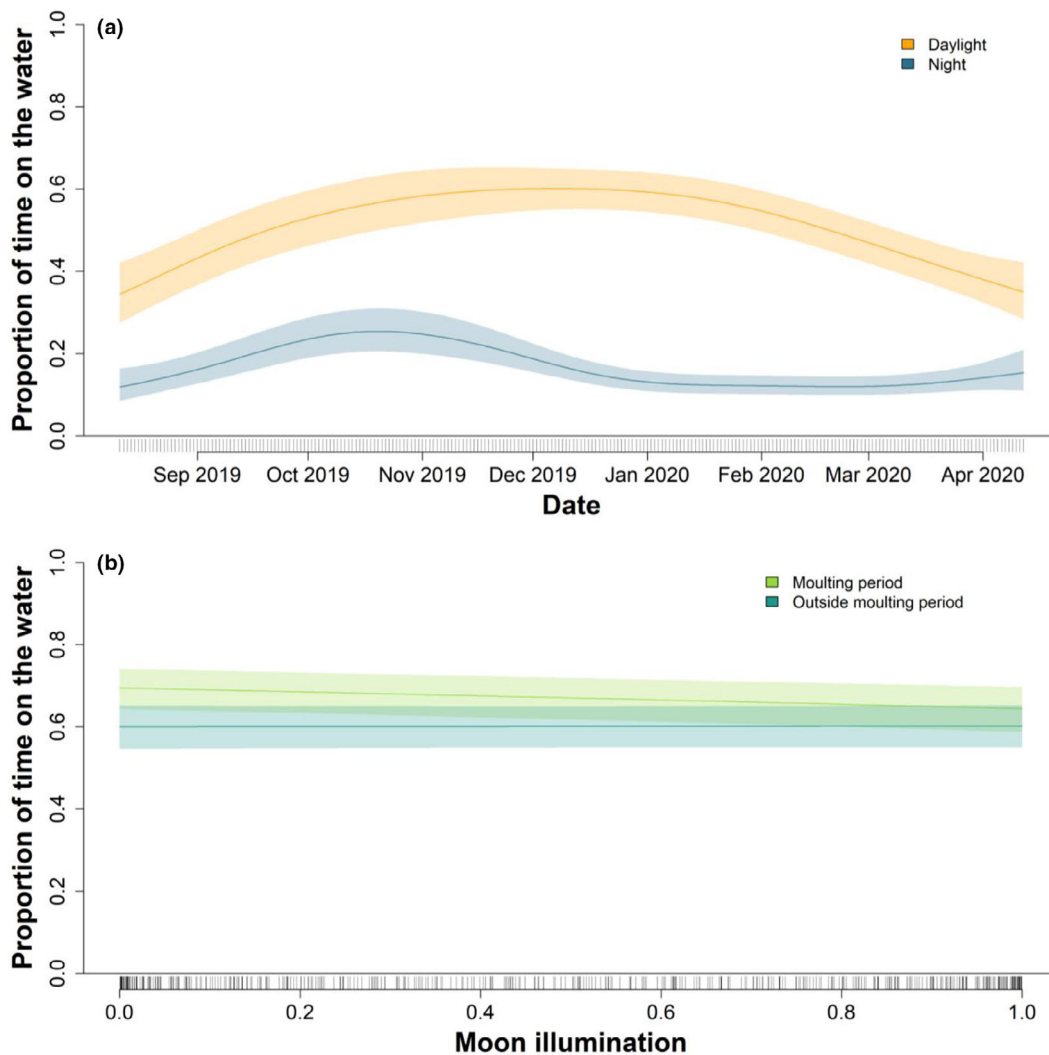


Figure 5. Relationships obtained from the generalized additive mixed model (GAMM) between the daily proportion of time on the water during the non-breeding period and (a) day of the year, segregated by daylight (yellow) and night (blue) periods, and (b) moon illumination segregated by moulting (light green) and non-moulting (dark green) periods. [Color figure can be viewed at [wileyonlinelibrary.com](https://onlinelibrary.wiley.com/terms-and-conditions)]

more time on the water during the night than in the rest of the non-breeding period. This increase in time spent on the water at the end of the year could indicate that birds are possibly still moulting some of their flight feathers (Cherel *et al.* 2016), giving support to the timing of the end of moulting inferred from the literature. This would mean that, in this species, the moulting period may not only overlap with breeding duties (Arroyo *et al.* 2004, Sultana & Borg 2012) but also with migratory movements in most individuals (if individuals do not suspend the moult while migrating). European Storm Petrels moult their primary feathers

from the innermost to the outermost feathers (Arroyo *et al.* 2004). This may allow European Storm Petrels to migrate at the end of the moulting period, as feather gaps would probably be closer to the tip of the wing, and flight costs and efficiency are less affected than when gaps occur in the middle of the wing (Hedenström & Sunada 1999). However, how European Storm Petrels are able to trade-off such high energy-demanding activities simultaneously (i.e. breeding-moulting and moulting-migration) remains unknown. A previous study on isotopic values on feathers stated that European Storm Petrels breeding in the

Table 3. (A) Results of the generalized additive mixed models (GAMMs) performed on the daily proportion of time on the water during the non-breeding period. All models included individual as a random factor. The variables day/night and moulting are categorical variables to test for differences in the proportion of time on the water between the daylight and night periods and between moulting and non-moulting periods, respectively. $s()$ denotes the smoothing factor and 'by' refers to the interaction between variables. AIC refers to the Akaike information criterion and Δ AIC to the difference of AIC value of each model in relation to the AIC value of the best model, i.e. the most parsimonious one, which is shown in bold type. The models are organized from lower to higher AIC values. (B) Estimates \pm standard error (se) of each of the fixed factors included in the best model and their statistical significance. (C) Effective degrees of freedom (edf) and statistical significance of the smoothing and random factors of the best model. Note that an edf value near 1 indicates a linear relationship between the response and explanatory variable

A – Formula	AIC	Δ AIC	R^2 adjusted
day/night + s(day of the year, by = day/night) + moulting + s(moon illumination, by = moulting)	-3825.0	0.0	0.63
day/night + s(day of the year, by = day/night) + s(moon illumination, by = moulting)	-3821.0	4.1	0.63
day/night + s(day of the year, by = day/night)	-3811.5	13.5	0.63
day/night + s(day of the year, by = day/night) + moulting + s(moon illumination, by = moulting)	-3804.0	21.0	0.63
day/night + moulting + s(moon illumination, by = moulting)	-3422.5	402.5	0.58
day/night + moulting	-3410.7	414.3	0.58
day/night + moulting + s(moon illumination, by = moulting)	-3109.4	715.6	0.54
day/night	-3102.3	722.7	0.54
s(day of the year, by = day/night) + moulting + s(moon illumination, by = moulting)	-1178.8	2646.2	0.12
s(day of the year, by = day/night) + s(moon illumination, by = moulting)	-1176.1	2648.9	0.12
s(day of the year, by = day/night) + moulting	-1174.1	2650.9	0.12
s(day of the year, by = day/night)	-1169.1	2655.9	0.12
moulting + s(moon illumination, by = moulting)	-1011.9	2813.1	0.07
moulting	-1006.9	2818.1	0.07
s(moon illumination, by = moulting)	-811.7	3013.3	0.03
null	-808.2	3016.8	0.03

B – Fixed factors	Estimate \pm se	t (edf)	p
daylight (intercept) vs. night periods	-1.74 \pm 0.03	-63.6 (1)	<0.001
moulting (intercept) vs. outside moulting periods	-0.30 \pm 0.09	-3.3 (1)	0.001

C – Smoothing factors	edf	F	p
days since deployment during daylight	4.90	38.8	<0.001
days since deployment during the night	6.15	15.5	<0.001
moon illumination during the moulting period	1.04	16.4	<0.001
moon illumination outside the moulting period	1.00	0.0	0.891
individual (random factor)	6.86	48.8	<0.001

Mediterranean moulted all their primary and secondary feathers in the Mediterranean Sea basin (Martínez *et al.* 2019). However, our activity data suggest that six of the eight tracked individuals were still actively moulting during their staging in the Atlantic, more specifically in the Gulf of Cádiz and western coast of Morocco area (Fig. S8). The apparent incongruence between Martínez *et al.*'s (2019) study on the same breeding population and our results may derive from similar isotopic values at baseline levels between the Atlantic area of the Gulf of Cádiz and the western coast of Morocco area and Mediterranean area of the Alborán Sea and Algerian basins

(McMahon *et al.* 2013), both used throughout the moulting period. Future studies determining stable isotope values in feathers of European Storm Petrels tracked with geolocators are needed to infer where and when specific feathers are moulted to help confirm this hypothesis, as well as to assess the potential effects of breeding success and annual variability in moulting patterns. During the moulting period, we detected a negative relationship between the time spent on the water and the moon illumination. During avian moult, flight efficiency is often affected by feather gaps on wings and tail, which increases the energetic cost of flying and reduces foraging success (Hedenström &

Sunada 1999). Therefore, individuals in active moult may minimize flight activity and synchronize their foraging activity with higher levels of moon illumination to increase their probability of foraging success. At night, European Storm Petrels rely on prey that conduct diel vertical migrations (Sanz-Aguilar *et al.* 2019). These prey are not as abundant near the surface during moonlit nights as during those nights without moonlight (Prihar-tato *et al.* 2016), but higher moon illumination will probably increase the prey detectability for European Storm Petrels. In sum, immersion data from geolocators allowed us to confirm both hypotheses tested, i.e. that European Storm Petrels fly more at night than during the day, as they rely mainly on prey that are closer to the sea surface during the night, and that they spend more time on the water during moult than outside the moulting period, probably due to the energetic constraints associated with feather moult.

CONCLUSIONS

This study confirms that geocator data are crucial to improving our knowledge about the phenology, distribution, migration and at-sea activity patterns of small seabird species, such as storm petrels. European Storm Petrels present high variability in migratory patterns at individual, population and sub-species levels (present study, Matović *et al.* 2017, Lago *et al.* 2019, Ausems *et al.* 2021), which may expose them to different threats at sea. Meta-population studies of species using geolocators are needed to unravel the drivers of distinct migratory patterns as well as to reveal the non-breeding distribution of the Atlantic sub-species. This is also relevant in terms of conservation, as environmental conditions during the non-breeding period can influence the adult survival rate of this species (Soldatini *et al.* 2014, Matović *et al.* 2017). Finally, although the overlap between breeding and moult is more common in large non-migratory seabird species (Bridge 2006), European Storm Petrels are a small migratory species that moult their feathers from the end of their breeding period to almost the first half of their non-breeding period, possibly overlapping moult with their migratory movements. We do not yet understand how these small birds trade-off moulting, breeding and migration periods and their associated resources. Therefore, there is also an urgent need for multi-colony studies that provide eco-

evolutionary insights into the balance of such life-history events in small avian species.

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ETHICS STATEMENT

All birds were handled for short periods (< 5 min) and in strict accordance with good animal practices as defined by the current European legislation (Directive 2010/63/EU; European Union 2010). The permit (Exp 324/19 SGENP) to work with European Storm Petrels in Benidorm Island was granted by the *Generalitat Valenciana*.

AUTHOR CONTRIBUTIONS

Teresa Militão: Data curation (lead); formal analysis (lead); investigation (equal); methodology (equal); visualization (lead); writing – original draft (lead); writing – review and editing (lead). **Ana Sanz-Aguilar:** Conceptualization (equal); data curation (equal); funding acquisition (equal); project administration (equal); resources (equal); writing – review and editing (equal). **Andreu Rotger:**

Data curation (equal); writing – review and editing (equal). Raúl Ramos: Conceptualization (equal); data curation (equal); funding acquisition (equal); methodology (equal); project administration (equal); resources (equal); supervision (equal); writing – review and editing (equal).

Data Availability Statement

The raw geographical coordinates of all the trips obtained from the geolocators used in this article are available at Seabird Tracking Database <http://www.seabirdtracking.org/> upon request (ID database 1848).

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Supplementary Material