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INFERRING THE WINTERING DISTRIBUTION OF THE MEDITERRANEAN POPULATIONS OF EUROPEAN STORM-PETRELS *HYDROBATES PELAGICUS MELITENSIS* FROM STABLE ISOTOPE ANALYSIS AND OBSERVATIONAL FIELD DATA

INFIRIENDO LA DISTRIBUCIÓN INVERNAL DE LAS POBLACIONES MEDITERRÁNEAS DE PAÍÑO EUROPEO *HYDROBATES PELAGICUS MELITENSIS* A PARTIR DE ANÁLISIS DE ISÓTOPOS ESTABLES Y DATOS OBSERVACIONALES DE CAMPO

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SUMMARY.—Bird migration studies have been given added impetus recently thanks to the miniaturisation of tracking devices. However, tracking methodologies have remained impractical for the smallest pelagic species and so important gaps in knowledge still exist. In the case of the European Storm-petrel *Hydrobates pelagicus*, while Atlantic populations are thought to overwinter along the south-western African coast, the winter quarters of Mediterranean birds remain more enigmatic. We performed stable isotope analysis (SIA) of C and N on P1, S8 and P10 feathers from 33 adult birds captured in three Atlantic colonies and 156 adult birds in seven western Mediterranean colonies to infer their wintering areas. In addition, we collated all observational field data, both from peer-reviewed publications and the wider literature, to complement our inferences from SIA. Within the Atlantic, isotopic profiles of feathers moulted at the breeding grounds (P1) differed between birds captured at northern Atlantic and Canary Islands colonies, but were similar for feathers moulted in winter quarters

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(S8 and P10), indicating low migratory connectivity. Isotopic values of feathers from western Mediterranean birds differed from those of Atlantic birds and showed Mediterranean values for all feathers, indicating that the former overwinter in Mediterranean waters. Variance in the isotopic values was greater in winter than in breeding season feathers, suggesting that birds disperse over larger areas in winter. Isotopic values of feathers moulted during the non-breeding period could match a post-breeding movement towards the southern and eastern Mediterranean. This inference matches the distribution of the few winter reports, which are mainly concentrated in the south-central Mediterranean, mostly in the Tunisian Platform. Our results suggest that this region is the principal wintering area of Mediterranean Storm-petrels. —Martínez, C., Roscales, J.L., Sanz-Aguilar, A. & González-Solís, J. (2019). Inferring the wintering distribution of the Mediterranean populations of European Storm-petrels *Hydrobates pelagicus melitensis* from stable isotope analysis and observational field data. *Ardeola*, 66: 13-32.

Key words: Atlantic Ocean, isotopic seascapes, Mediterranean Sea, pelagic Birds.

Resumen.—Los estudios sobre la migración de las aves se han incrementado recientemente gracias a la miniaturización de los dispositivos de seguimiento. Sin embargo, para las especies pelágicas más pequeñas, los métodos de seguimiento han permanecido poco prácticos y, por tanto, continúan existiendo importantes lagunas de información. En el caso del paíño europeo *Hydrobates pelagicus*, mientras se considera que las poblaciones atlánticas invernan a lo largo de la costa sudoeste africana, continúa sabiéndose muy poco sobre las zonas de invernada de las aves mediterráneas. Realizamos un análisis de isótopos estables (AIE) de C y N en las plumas P1, S8 and P10 de 33 aves adultas capturadas en tres colonias atlánticas y 156 aves adultas en siete colonias en el Mediterráneo occidental para inferir sus áreas de invernada. Además, recogimos los datos de observaciones de campo, tanto de publicaciones con revisión como de literatura gris, para complementar nuestras inferencias a partir del AIE. En el caso del Atlántico, los perfiles isotópicos de las plumas mudadas en las áreas reproductivas difirieron entre las aves capturadas en las colonias del Atlántico Norte y en las islas Canarias, pero fueron similares para plumas mudadas en áreas de invernada, indicando una baja conectividad migratoria. Los valores isotópicos de las plumas de las aves del Mediterráneo occidental difirieron de las del Atlántico y mostraron valores mediterráneos para todas las plumas, indicando que las aves permanecen en aguas mediterráneas durante el invierno. La variancia de los valores isotópicos fue mayor en las plumas mudadas durante el invierno que durante la reproducción, indicando que las aves se dispersan por áreas más extensas. Los valores isotópicos de las plumas mudadas durante el invierno son compatibles con un movimiento posreproductivo hacia el sur y tal vez hacia el este dentro del Mediterráneo. Esta inferencia es coherente con la distribución de los pocos registros invernales existentes, que se concentran sobre todo en el centro-sur del Mediterráneo, principalmente en la Plataforma Tunecina. Nuestros resultados apuntan a esta región como la principal área de invierno del paíño europeo Mediterráneo. —Martínez, C., Roscales, J. L. Sanz-Aguilar, A. y González-Solís, J. (2019). Infiriendo la distribución invernal de las poblaciones mediterráneas de paíño europeo *Hydrobates pelagicus melitensis* a partir de análisis de isótopos estables y datos observacionales de campo. *Ardeola*, 66: 13-32.

Palabras clave: aves pelágicas, mar Mediterráneo, océano Atlántico, paisajes marinos isotópicos.

Introduction

Studying bird migration is very important to the design and development of conservation policies, both along migration routes and in non-breeding areas, as well to understanding the mechanisms driving migration processes. Migration patterns are extremely variable, not only among species, but also among populations and individuals within populations (Newton, 2008; Rappole, 2013). The complex movement patterns of pelagic seabirds are influenced by food abundance and distribution, but also by winds and marine habitat features (e.g. Sanz-Aguilar *et al.*, 2012). Traditional methods to study bird migration, such as ringing, have revealed that European Storm-petrels are highly philopatric to their breeding areas (e.g. Sanz-Aguilar *et al.*, 2009), but have provided little insight into migration routes and wintering areas, as rings are rarely recovered at sea.

During the last few decades, tracking technologies have been developed as the most reliable alternative to ringing in the study of bird migration. Studies involving extrinsic markers, such as PTTs (Platform Terminal Transmitters) and geolocators, are increasingly common (e.g. Kays *et al.*, 2015). These devices have seen a continuous process of miniaturisation, allowing the tracking of smaller-sized animals. However, to date no studies using geolocators have involved the smallest pelagic species, such as small Storm-petrels (<30g).

Alternatively, intrinsic markers, such as stable isotope analysis (SIA) of H, C and N (δD, δ^{13}C and δ^{15}N), can be used to study large scale movements in a wide range of animals (Rubenstein & Hobson, 2004). More specifically, values of δ^{13}C and δ^{15}N have been primarily used to study the trophic structure of animal communities, since these levels are incorporated from prey into the tissues of their predators in a predictable manner (Hobson & Welch, 1992; Roscales *et al.*, 2011). Nevertheless, assuming diet among individuals and populations is fairly homogeneous and given that differences in isotopic baseline levels between distant geographical areas are often very large, SIA of C and N has recently been applied to the study of the spatiotemporal movements of birds using information on geographical and temporal isotopic variation, i.e. isoscapes both in terrestrial (Hobson & Wassenaar, 2008) and marine environments (Cherel *et al.*, 2016; Polito *et al.*, 2017). Consumer tissues incorporate, via the diet, the isotopic baseline indicating the time and place of origin of food sources (Cherel & Hobson, 2007). In particular, feathers are a valuable tissue for studying migration using SIA because they remain chemically inert after their formation. In the ocean, isotope baselines among marine food webs are known to vary geographically as a consequence of differences in nutrient cycles at the base of the food web (Graham *et al.*, 2010; McMahon *et al.*, 2013). For example, δ^{15}N values in feathers of Scopoli's Shearwaters *Calonectris diomedea* increased from an average value of 10.37‰ in the first primary feather moulted in the Mediterranean to 13.44‰ in the 10th primary feather moulted in the Atlantic (Ramos *et al.*, 2009b). This change cannot easily be attributed to changes in diet, since it would mean a change of one trophic level, but to differences in baseline levels between some areas of the two basins (e.g. McMahon *et al.*, 2013). The first isotopic geographic gradients have been recently described (Graham *et al.*, 2010; Ramos & González-Solís, 2012; McMahon *et al.*, 2013) and the first studies using this variability to reveal seabird movements are starting to emerge (Jaeger *et al.*, 2010; Militão *et al.*, 2013). However, the spatial resolution of this approach is still limited and, consequently, the conclusions drawn from SIA would require some additional support, which currently can only be obtained (pending the availability of data from tracking devices) from field observations and ring recoveries.

The foraging areas and migration movements of the smallest pelagic seabirds, the Storm-petrels (Hydrobatidae), are unknown for most species due to their small size and the negative impacts that current tracking devices may cause, even after short-term handling (Kim *et al.*, 2014). Although some Hydrobatidae (e.g. Leach's Storm-petrel *Oceanodroma leucorhoa*) have been tracked with geolocators (Pollet *et al.*, 2014), devices have yet to produce reliable results for one of the smallest seabirds in the world, the European Storm-petrel *Hydrobates pelagicus*.

Here we collated all available information using traditional methodologies, such as field observation and ringing data, together with SIA from several Atlantic and Mediterranean colonies of European Storm-petrels to elucidate their winter distribution.

We gave particular emphasis to Mediterranean colonies because the breeding and non-breeding distributions, as well as the migration patterns, of Mediterranean Storm-petrels are still poorly known (Soldatini *et al*., 2014; Matović *et al*., 2017). It has been suggested that *H. p. melitensis* is partly sedentary, but there is little data supporting these general statements (e.g. Cramp & Simmons, 1977; Carboneras *et al*., 2018). In the Western Mediterranean, the species almost disappears in winter, the latest observations in coastal areas being in late November (e.g. Arcos *et al*., 2012; Rodríguez *et al*., 2012; F. Aguado and J.M. Arcos, pers. coms.). Whether these birds overwinter in the Mediterranean Sea or in the Atlantic Ocean remains unknown.

We also collected feather samples from three Atlantic colonies in order to compare their isotopic profiles with those from the Mediterranean colonies and, in particular, to identify whether winter quarters of Mediterranean Storm-petrels are located in Atlantic waters. In such a case, we would expect a higher proportion of ^{15}N relative to ^{14}N (i.e. an increase in δ^{15}N values) in feathers moulted in the Atlantic due to baseline differences in δ^{15}N between these two basins, as found in Scopoli's and Balearic *Puffinus mauretanicus* shearwaters (Ramos *et al*., 2009b; Militão *et al*., 2013). Changes in δ^{13}C values would be more uncertain, since they would largely depend on the areas used by storm-petrels within the Atlantic, but assuming Mediterranean populations have a winter distribution similar to the Atlantic populations, mainly off South Africa and Namibia (Carboneras *et al*., 2018), we would also expect an increase in δ^{13}C values of at least 2‰ (Ramos *et al*., 2009a; McMahon *et al*., 2013).

Materials and methods

Study species, area and field methods

The European Storm-petrel has two subspecies, the nominate *H. p. pelagicus* (Linnaeus, 1758), nesting in the Atlantic and *H. p. melitensis* (Schembri, 1843), breeding in the Mediterranean Sea. The Mediterranean subspecies was described in the 19th century and, based on genetic studies, has been recognised as a separate taxon (Cagnon *et al*., 2004). Indeed, some authors have proposed splitting them into two species (Sangster *et al*., 2012). European Storm-petrels are pelagic seabirds, occurring in coastal waters to a greater extent during the breeding season than during the rest of the year (Cramp & Simmons, 1977). In the Mediterranean, they return to their breeding colonies in March, lay their single egg between April and June and chicks mainly fledge in late August (Mínguez, 1994). In the Atlantic, reproduction occurs about a month later than in the Mediterranean (Davis, 1957; Mínguez *et al*., 1992). Adults from both basins moult primary feathers annually, beginning during the breeding season and continuing for several months in winter. Adults start with the innermost primary feather (P1), which is moulted by the end of the incubation period and the beginning of chick rearing (Arroyo *et al*., 2004), continuing outwards to P10 (the outermost). Moult in secondaries progresses from three loci, and S8 is one of the last feathers to be moulted, by the end of October. Precise moulting dates of P10 feathers are not well known but in most birds it has not yet occurred when S8 has been moulted. This would indicate that it does not occur before November or December (Arroyo *et al*., 2004; Roscales *et al*., 2011; F. Aguado, pers. Com; see Appendix I).

From 2001 to 2005, we collected the entire P1 and S8 feathers from 99 adult birds; 33 captured at three Atlantic colonies and 66 at six Mediterranean colonies (Table 1). The

TABLE 1

Number of European Storm-petrel individuals sampled by site, basin (either Atlantic or Mediterranean), year and feather. Sites: A1, Ellidaey, Iceland. A2, Copeland, North Ireland. A3, Lanzarote, Canary Is. M1, Benidorm islet, south-eastern Iberian Peninsula. M2, Terreros islet, Almería, south-eastern Iberian Peninsula. M3, S'Espardell, Ibiza, Balearic Is. M4, S'Espartar, Ibiza, Balearic Is. M5, Palomas islet, Murcia, south-eastern Iberian Peninsula. M6, Toro islet, Majorca, Balearic Is. M7, de l'Aire islet, Minorca, Balearic Is.

[Número de individuos de paíño europeo muestreados por localidad, cuenca (atlántica o mediterránea), año y pluma. Leyenda: A1, Ellidaey, Islandia. A2, Copeland, Irlanda del Norte. A3, Lanzarote, Is. Canarias, M1, isla de Benidorm, sudeste de la península Ibérica. M2, isla Terreros, Almería, sudeste de la península Ibérica. M3, S'Espardell, Ibiza, Is. Baleares. M4, S'Espartar, Ibiza, Is. Baleares. M5, isla Palomas, Murcia, sudeste de la península Ibérica. M6, illa Toro, Mallorca, Is. Baleares. M7, illa de l'Aire, Menorca, Is. Baleares.]

SITE	BASIN	YEAR(S)	FEATHERS SAMPLED	n
A1	Atl.	2001-2005	P1+S8	8
A2	Atl.	2001-2005	P1+S8	14
A3	Atl.	2001-2005	P1+S8	11
M1	Med.	2014	P1+P10	71
M2	Med.	2001-2005	P1+S8	20
M3	Med.	2001-2005	P1+S8	12
M4	Med.	2001-2005	P1+S8	18
M4	Med.	2014	P1+P10	19
M5	Med.	2001-2005	P1+S8	5
M6	Med.	2001-2005	P1+S8	8
M7	Med.	2001-2005	P1+S8	3

Atlantic colonies were: Ellidaey (Iceland), 63°27'55"N, 20°10'50"W, Copeland (Northern Ireland), 54°40'32"N, 5°32'34"W and Montaña Clara (Lanzarote, Canary Archipelago), 29°18'15"N, 13°32'04"W. The Mediterranean colonies were: Terreros (Almería), 37°20'51"N, 1°39'06"W, and Palomas (Murcia), 37°34'14"N, 1°02'29"W, islets (both on the South-eastern Mediterranean coast of Spain), S'Espardell, 38°47'57"N, 1°28'45"E, and S'Espartar, 38°57'34"N, 1°11'55"E islets (both along the Ibiza coast), Toro islet (Majorca), 39°27'46"N, 2°28'18"E, and de l'Aire islet (Minorca), 39°48'05"N, 4°17'44"E. The last four sites are in the Balearic Archipelago. These feathers were used to compare breeding and non-breeding isotope profiles. The initial analyses of P1 and S8 feathers collected during the first sampling period indicated that Mediterranean birds showed similar patterns for P1 and S8. Consequently, and only for Mediterranean birds, we sampled P10 feathers, which are moulted later than S8. Thus, in 2014 we sampled P1 and P10 feathers from 90 breeding birds from Benidorm (South-

Eastern Mediterranean Spain), 38°30’09”N, 0°7’45”W, and again, the S’Espartar colony in Ibiza, both in Mediterranean waters (Table 1). In this case, only the 5mm tip was cut from the body of the feather in order to reduce any interference with flying ability, since P10 is especially important for flight. Birds were captured in their nesting burrows (in 2014 only) or at their breeding colonies using mist nets (in 2001-2005). All field procedures at every study site were approved by the relevant government agencies.

Isotope analysis

We cleaned all feathers in 0.25M sodium hydroxide (NaOH) solution and oven-dried them at 60º. Each feather (and P10 tips) was finely chopped up with stainless steel surgical scissors. Weighed feather sub-samples (0.26-0.36mg) were placed into tin cups and crimped for combustion. Isotope analysis was carried out by elemental analysis-isotope ratio mass spectrometry (EA-IRMS) using a ThermoFinnigan Flash 1112 elemental analyser coupled to a Delta isotope ratio mass spectrometer via a CONFLOIII interface (Serveis Científico-Tècnics, University of Barcelona) (Roscales *et al*., 2011). Stable isotope ratios were expressed in conventional notation as parts per thousand (‰) relative to standards: Vienna Peedee Belemnite (VPDB) for $\delta^{13}C$ and atmospheric nitrogen (AIR) for $\delta^{15}N$. Three reference materials (International Atomic Energy Agency, IAEA) were analysed every 12 samples to correct potential shifts over time. Precision and accuracy for $\delta^{13}C$ measurements was ≤ 0.1‰ and for $\delta^{15}N$ it was ≤ 0.3‰.

Data analysis

Statistical analyses were performed with IBM-SPSS 23. Normality of data was checked by visually inspecting Q-Q plots. We compared general isotopic results between basins using a Student’s t-test. A General Linear Mixed Model (GLMM) was built using the bird as the subject and the feather as the repeated measure. ‘Capture locality’, ‘feather’ and the interaction ‘feather*locality’ were introduced as fixed factors and ‘subject’ as random. The factor year was not included in the analyses, as only one site (S’Espartar) was sampled in two different years, and only for one feather (P1). Pairwise comparisons with sequential Bonferroni procedures were also conducted within factor levels ($\alpha = 0.05$).

Geographic patterns in stable isotope values were also explored, in order to find eventual relationships between the isotopic values and the geographical distribution of the birds during the seasons when each feather was moulted. First, we explored the relationship between $\delta^{13}C$ and $\delta^{15}N$ and latitude and longitude of petrels’ colonies using Pearson’s correlation analysis, specifically within the Mediterranean basins. Then, we tested the relationship between $\delta^{13}C$ and $\delta^{15}N$ values and the latitude and longitude of the sampled colonies using a linear regression, where R^2 measured the variability explained by the resulting function. This part of the study was performed using only P1 feathers, moulted during the breeding season.

Observational field data

We collected observational field data from several literature sources and from individuals with local expertise. The relevant literature included reports from the MIGRES Foundation on migration through the Gibraltar Strait (Arroyo & Cuenca, 2004); ringing recoveries reported in the Migration Atlases of Spain (SEO/BirdLife, 2012), Italy (Spina & Volponi, 2008) and France (http://www.atlas-ornitho.fr/index.php?m_id=1415&y=-10&speciesFilter=&frmSpecies=17&frmDisplay=Affichez) and non peer-reviewed sources (ornithological society annual reports, unpublished reports, unpublished theses, reviews, etc.). The individuals consulted were Felipe Aguado, José Manuel Arcos, Eduardo de Juana, Andrés de la Cruz, Jakob Fric, Carlos Gutiérrez, Benjamin Metzger). We also examined photographs, both of birds in the hand and in flight, of known date and locality, in which plumage (moult stage) could be observed (see Appendix I), as well as data from ship sightings and other ring recoveries. Observational data were collected only for the Mediterranean Sea and the neighbouring Atlantic waters of the Gulf of Cadiz.

We mapped the winter distribution of European Storm-petrels across the Mediterranean based on winter reports of the species from December to February. Following Coll *et al*. (2010), we divided the whole Mediterranean Basin into fourteen regions and then classified each region according to the frequency of winter reports for the species, from the highest (A) to the lowest (D). Frequency was based on how many independent sources we found reporting the species in winter, and how many of them reported it as regular. The resulting classification was: A: Regions where we found three independent sources (published material or personal comments) reporting the species in winter, and at least two of them reporting it as regular. B: Regions where we found two independent sources reporting the species in winter, and one of them reporting it as regular. C: Regions where we found only one source reporting the species in winter. In category C, all the sources reported the species as occasional, except for the Tyrrhenian Sea, where it was reported as regular by the only source we found. D: Regions where we found no winter reports for the species (Figure 1). We did not take into account general reviews, citing other sources, unless they reported unpublished data. In addition, we plotted on the map the sites where the species was reported by any source as regular in winter (Figure 1).

Results

Differences in $\delta^{13}C$ *and* $\delta^{15}N$ *values between the two basins*

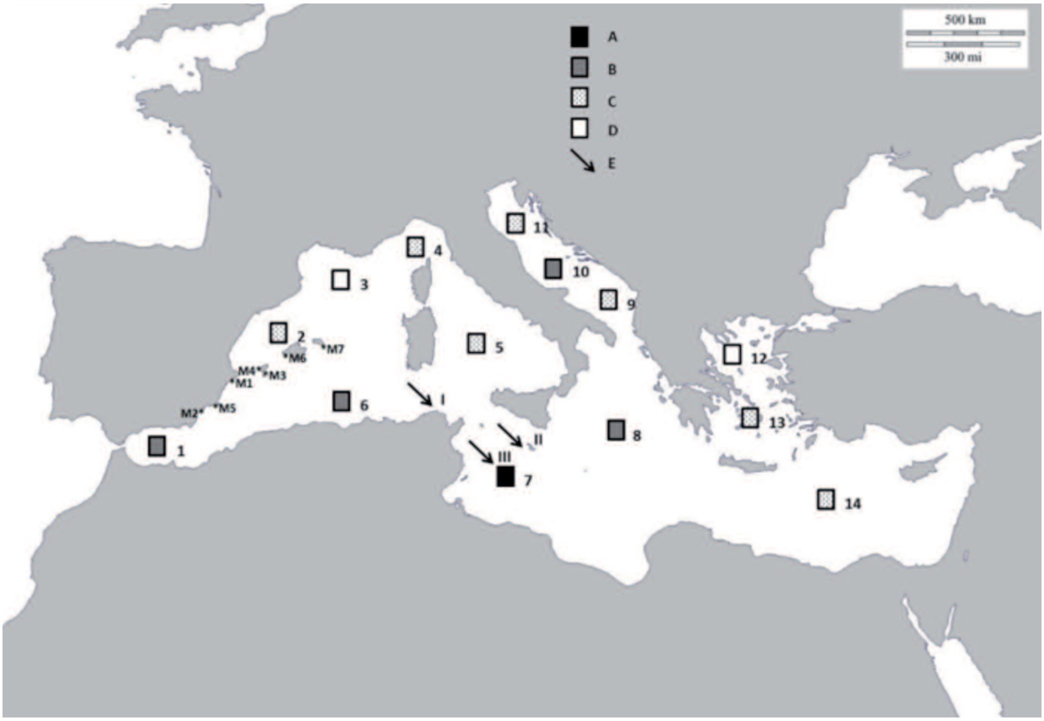
Stable isotope values in the studied feathers showed little or no overlap among basins which probably reflects marked differences in baseline values between Atlantic and Mediterranean waters. Atlantic colonies showed significantly greater δ^{13}C and δ^{15}N values than those from the Mediterranean in P1 feathers sampled during 2001-2005 (Student t-test; δ^{13}C, $t = -10.92$, $p < 0.001$; δ^{15}N, $t = -6.57$, $p < 0.001$), since this feather is moulted during the breeding period. Similarly, isotope values in S8, moulted after breeding, were significantly greater in the Atlantic birds (Student t-test; δ^{13}C, $t = -10.54$, $p < 0.001$; δ^{15}N, $t = -7.17$, $p < 0.001$) (Figure 2).

Variation in $\delta^{13}C$ *and* $\delta^{15}N$ *values within each basin*

For the Mediterranean Basin, GLMM results showed significant differences for both chemical elements, among feathers, localities and their interactions, except for feather effect for δ^{15}N. Case by case, there were significant differences between colonies in the isotopic values of some feathers (Table 2) and, in some cases, those isotopic values had a geographic pattern (Figure 3).

In the Atlantic Basin, GLMM results showed significant differences for δ^{15}N among localities but also a significant interaction between locality and feather effects. There were significant differences between P1 and S8 within localities, in Ireland for δ^{13}C, and in Lanzarote for δ^{15}N. Between sites, only Lanzarote showed significant differences in δ^{15}N values, between Lanzarote and the remaining two sites (Table 2).

In Mediterranean birds, P1 and either S8 or P10 feather values roughly showed a simi-



Area	1	2	3	4	5	6	7	8	9	10	11	12	13	14
References	d, e	e	j	c	c	e, f	b, c, i	a, c	c	c, g	c	a	a	h

Site	I	II	III
References	f	c, i	c

FIG. 1.—Top: Probable distribution of European Storm-petrels in the Mediterranean Sea in winter. A: Regions where we found three independent sources (published material or personal communications) reporting the species in winter, with at least two sources reporting occurrence as regular. B: Regions where we found two independent sources reporting the species in winter, with one of them reporting it as regular. C: Regions where we found only one original source reporting the species in winter. All of these cases reported the species as occasional, except for the Tyrrhenian Sea, where it was reported as regular by the sole source found. D: Regions where we found no winter reports for the species. E: Specific sites where we found at least one source reporting the species as regular in winter. 1: Alboran Sea. 2: Balearic Sea. 3: Gulf of Lion. 4: Ligurian Sea. 5: Tyrrhenian Sea. 6: Algerian and Northern Tunisian Waters. 7: Tunisian Platform. 8: Ionian Sea. 9: Southern Adriatic Sea. 10: Central Adriatic Sea. 11: Northern Adriatic Sea. 12: Northern Aegean Sea. 13: Southern Aegean Sea. 14: Levantine Sea. I: Galite Islands. II: Maltese Islands. III: Pelagie Islands. Asterisks: location of studied colonies. M1, Benidorm islet, south-eastern Iberian Peninsula. M2, Terreros islet, Almería, south-eastern Iberian Peninsula. M3, S'Espardell, Ibiza, Balearic Is. M4, S'Espartar, Ibiza, Balearic Is.

lar pattern across localities. That is, SIA data showed $\delta^{15}N$ values did not change from P1 to S8/P10 feathers, whereas $\delta^{13}C$ values slightly increased in both S8 and P10 feathers. Differences were not significant at most sites (except S'Espartar and S'Espardell) for P1-S8 feathers (Figure 2), but were clearly significant in the two sites where we sampled P1 and P10, the latter being moulted later than S8 (Figure 2). Within the Atlantic birds, SIA analyses showed that P1 values from Northern Ireland and Iceland grouped closely whereas those from Lanzarote showed significantly lower $\delta^{15}N$ values (Table 2; Figure 2). Regarding S8 values, however, birds from the three sites grouped together (Figure 2).

When comparing between basins, it can be seen that feathers from Atlantic and Mediterranean birds clearly grouped by basin. While there were significant differences by season within basins in all cases, these differences were much smaller than those found between basins.

Both $\delta^{13}C$ and $\delta^{15}N$ values increased significantly towards the east across the Western Mediterranean ($\delta^{13}C$, $R^2 = 0.103$, $P < 0.001$, $\delta^{15}N$, $R^2 = 0.196$, $P < 0.001$). $\delta^{13}C$ values also increased towards the south ($R^2 = 0.241$, $P < 0,001$), while $\delta^{15}N$ did not significantly change with latitude ($R^2 = 0.005$, $P = 0.573$) (Figure 3).

Observational Field Data and local reports

Numbers of Storm-petrels passing through the Gibraltar Strait seem to be low, and the few birds observed during post-breeding migration seem to move into the Mediterranean rather than out of it (Mínguez, 1995; Arroyo

M5, Palomas islet, Murcia, south-eastern Iberian Peninsula. M6, Toro islet, Majorca, Balearic Is. M7, de l'Aire islet, Minorca, Balearic Is. Bottom: Area Category References: a: Akriotis & Handrinos, 1986. b: Bannerman & Vella-Gaffiero, 1976. c: Brichetti, 1980. d: de Juana, 1986. e: de Juana & Garcia, 2015. f: Hamrouni, 2015. g: Kralij & Barišić, 2013. h: Massa & Sultana, 1993. i: B. Metzger (pers. com.). j: http://www.atlas-ornitho.fr/index.php?m_id=1415&y=-10&speciesFilter=&frmSpecies=17&frmDisplay=Affichez.

[Arriba: Distribución probable del paíño europeo en el mar Mediterráneo en invierno. A: Regiones donde encontramos tres fuentes independientes (material publicado o comunicaciones personales) registrando la especie en invierno, con al menos dos de ellas registrando su incidencia como regular. B: Regiones donde encontramos dos fuentes independientes registrando la especie en invierno, con una de ellas registrándola como regular. C: Regiones donde encontramos sólo una fuente registrando la especie en invierno. Todos estos casos registraron la especie como ocasional, excepto para el mar Tirreno, donde fue registrada como regular por la única fuente que encontramos. D: Regiones donde no encontramos registros invernales para la especie. E: Localidades específicas donde encontramos por lo menos una fuente registrando la especie como regular en invierno. 1: Mar de Alborán. 2: Mar Balear. 3: Golfo de León. 4: Mar Ligur. 5: Mar Tirreno. 6: Aguas Argelinas y Norte Tunecinas. 7: Plataforma Tunecina. 8: Mar Jónico. 9: Sur del mar Adriático. 10: Centro del mar Adriático. 11: Norte del mar Adriático. 12: Norte del mar Egeo. 13: Sur del mar Egeo. 14: Mar Levantino. I: Islas Galite. II: Islas Maltesas. III: Islas Pelagias. Asteriscos: localización de las colonias estudiadas. M1, isla de Benidorm, sudeste de la península Ibérica. M2, isla Terreros, Almería, sudeste de la península Ibérica. M3, S'Espardell, Ibiza, Is. Baleares. M4, S'Espartar, Ibiza, Is. Baleares. M5, isla Palomas, Murcia, sudeste de la península Ibérica. M6, Illa Toro, Mallorca, Is. Baleares. M7, illa de l'Aire, Menorca, Is. Baleares. Abajo: Referencias de las categorías de las áreas: a: Akriotis & Handrinos, 1986. b: Bannerman & Vella-Gaffiero, 1976. c: Brichetti, 1980. d: de Juana, 1986. e: de Juana & Garcia, 2015. f: Hamrouni, 2015. g: Kralij & Barišić, 2013. h: Massa & Sultana, 1993. i: B. Metzger (pers. com.). j: http://www.atlas-ornitho.fr/index.php?m_id=1415&y=-10&speciesFilter=&frmSpecies=17&frmDisplay=Affichez.]

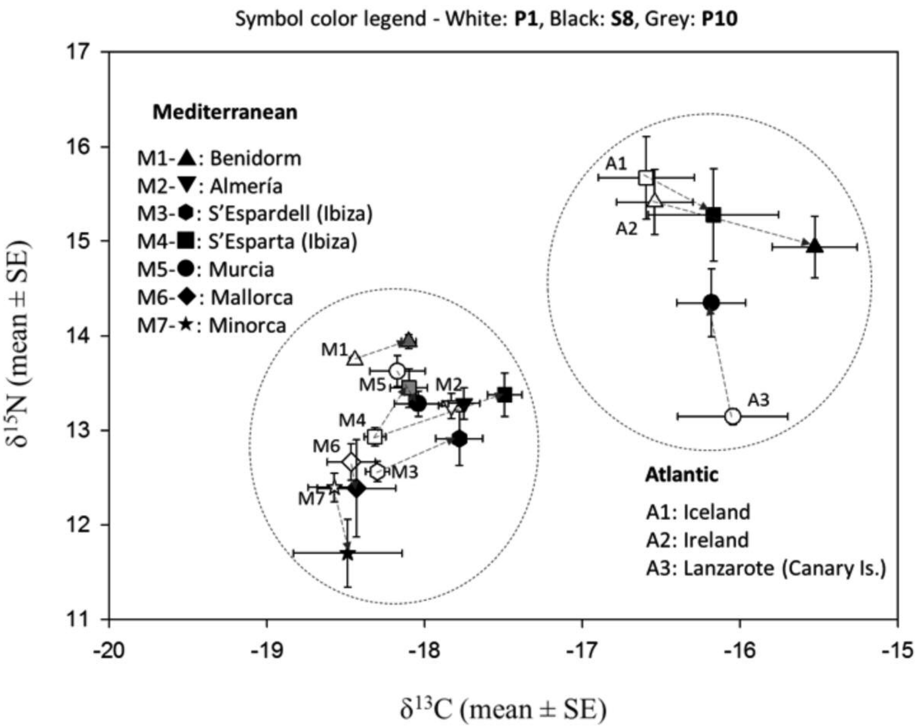


FIG. 2.—Mean values for $\delta^{13}C$ and $\delta^{15}N$ for P1 (white), S8 (black) and P10 (grey) at three Atlantic and six Mediterranean colonies in feathers of European Storm-petrels from 2001 to 2005 (pairs P1-S8), and at two Mediterranean colonies in 2014 (pairs P1-P10).
[Valores medios para $\delta^{13}C$ y $\delta^{15}N$ para P1 (blanco), S8 (negro) y P10 (gris) en tres colonias atlánticas y seis mediterráneas en plumas de paíño europeo de 2001 a 2005 (pares P1-S8), y dos colonias mediterráneas en 2014 (pares P1-P10).]

& Cuenca, 2004; Rodríguez *et al*., 2012). Furthermore, only a few unsystematic nocturnal samplings were attempted in the Strait of Gibraltar, and no birds were found (A. de la Cruz, pers. com.). In the Gulf of Cadiz, up to several tens of thousands have been counted in December (Arcos *et al*., 2009; SEO/BirdLife, 2009; J.M. Arcos, C. Gutiérrez, pers. com.). However, the Gibraltar data suggest that most of these birds come from Atlantic colonies.

The review of Mediterranean winter reports showed that from the 14 different regions defined by Coll *et al*. (2010), only one (the Tunisian Platform) was included in category A (three sources reporting the species in winter, two as regular). While not located on the Tunisian Platform, an additional report from neighbouring waters in Northern Tunisia noted regular winter occurrence (Hamrouni, 2015) (Figure 1).

Four regions were included in category B (two sources reporting the species in winter, one as regular): the Alboran Sea; Algerian and Northern Tunisian coast; Central Adriatic Sea; and the Ionian Sea (Figure 1). In the case of the Alboran basin no sources reported the species as regular but Soldatini *et al*., 2014 indicate why we include this area in category B.

TABLE 2

Results of General Linear Mixed Model (GLMM) for $\delta^{13}C$ and $\delta^{15}N$ in Storm-petrel feathers according to marine basin. The model was built using 'bird' as a subject and 'feather' as a repeated measure. 'Breeding locality', 'feather' and the interaction 'feather*locality' were introduced as fixed factors and 'subject' as random. Significant fixed effects are indicated in bold ($p < 0.05$). Pairwise comparisons with sequential Bonferroni procedure were also conducted within factor levels.
[Resultados de un Modelo Lineal Generalizado Mixto (GLMM) para $\delta^{13}C$ y $\delta^{15}N$ en plumas de paíño europeo según la cuenca marina. El modelo fue construido utilizando el individuo como sujeto y las plumas como medida repetida. La localidad de cría, pluma y su interacción se consideraron como factores fijos y el individuo como factor aleatorio. Los efectos estadísticamente signifcativos se indican en negrita (p < 0,05). Las comparaciones dos a dos se realizaron para cada factor usando la corrección secuencial de Bonferroni.]

	AIC	Model	Fixed effects	Significant pairwise comparisons between feathers within localities	Significant pairwise comparisons for P1 among localities	Significant pairwise comparisons for S8 among localities	Significant pairwise comparisons for P10 among localities
Atlantic (n = 64)							
$\delta^{15}N$	201.0	$F = 7.44$, $p < 0.001$	**Locality**: $F = 12.5$, $p < 0.001$ Feather: $F = 0.14$, $p = 0.70$ **Loc*feather**: $F = 3.53$, $p < 0.05$	Lanzarote[a] ($p < 0.05$)	Lanzarote*Iceland ($p < 0.001$) Lanzarote*Ireland ($p < 0.001$)	None	–
$\delta^{13}C$	180.7	$F = 2.45$, $p < 0.05$	Loc: $F = 0.68$, $p = 0.51$ Feather: $F = 3.09$, $p = 0.08$ Loc*feather: $F = 2.10$, $p = 0.13$	Ireland[a] ($p < 0.01$)	None	None	–
Mediterranean (n = 132)							
					Murcia*Majorca ($p < 0.05$) Murcia*Minorca ($p < 0.01$)		

TABLE 2 (cont.)

	AIC	Model	Fixed effects	Significant pairwise comparisons between feathers within localities	Significant pairwise comparisons for P1 among localities	Significant pairwise comparisons for S8 among localities	Significant pairwise comparisons for P10 among localities
Mediterranean (n = 132) [cont.]							
δ^{15}N	561.03	F = 4.36; p < 0.001	**Locality**: F = 14.7, p < 0.001 Feather: F = 1.03, p = 0.36 **Loc*feather**: F = 2.81, p = 0.05	S'Espartar[a] (p < 0.001) S'Espartar[b] (p < 0.01) S'Espartar[c] (p < 0.01) Benidorm[b] (p < 0.001)	Murcia*S'Espartar (p < 0.01) Murcia*S'Espardell (p < 0.01) Almería*Majorca (p < 0.05) Almería*Minorca (p < 0.05) Almería*S'Espartar (p < 0.01) Almería*S'Espardell (p < 0.01) Benidorm*Majorca (p < 0.001) Benidorm*Minorca (p < 0.001) Benidorm*S'Espartar (p < 0.001) Benidorm*S'Espardell (p < 0.001)	S'Espartar*Minorca (p < 0.05)	None
δ^{13}C	307.9	F = 10.3; p < 0.001	**Locality**: F = 7.06, p < 0.001 **Feather**: F = 7.90, p < 0.001 **Loc*feather**: F = 3.62, p < 0.05	S'Espardell[a] (p < 0.001) S'Espartar[a] (p < 0.001) S'Espartar[b] (p < 0.01) S'Espartar[c] (p < 0.01) Benidorm[b] (p < 0.05)	Murcia*Minorca (p < 0.05) Almería*Majorca (p < 0.001) Almería*Minorca (p < 0.01) Almería*S'Espardell (p < 0.01) Almería*S'Espartar (p < 0.001) Benidorm*Almería (p < 0.01)	Almería*Majorca (p < 0.05) S'Espartar*Majorca (p < 0.001) S'Espartar*Minorca (p < 0.05) S'Espardell*Minorca (p < 0.05)	S'Espartar*Benidorm (p < 0.05)

[a] -Feather P1 *vs*. S8; [b] -Feather P1 *vs*. P10; [c] -Feather P10 *vs*. S8.

Seven regions were included in category C (one source reporting the species in the winter): the Balearic Sea; Ligurian Sea; Tyrrhenian Sea; Northern Adriatic Sea; Southern Adriatic Sea; Southern Aegean Sea; and Levantine Sea (Figure 1). In the case of the Balearics some personal communications indicate rare occurrence in winter but we retain this region in category C since the species was considered rare in winter in Spanish Mediterranean waters after an extensive sampling effort, (SEO/BirdLife, 2012).

Finally, in the Gulf of Lion and the northern Aegean Sea, we found no winter reports for the species and these areas were categorised as D (Figure 1).

In addition, we found reports of regular occurrence in winter for three specific sites, which could then be plotted on a map: the Maltese, Pelagie and Galite Islands. The Mal-

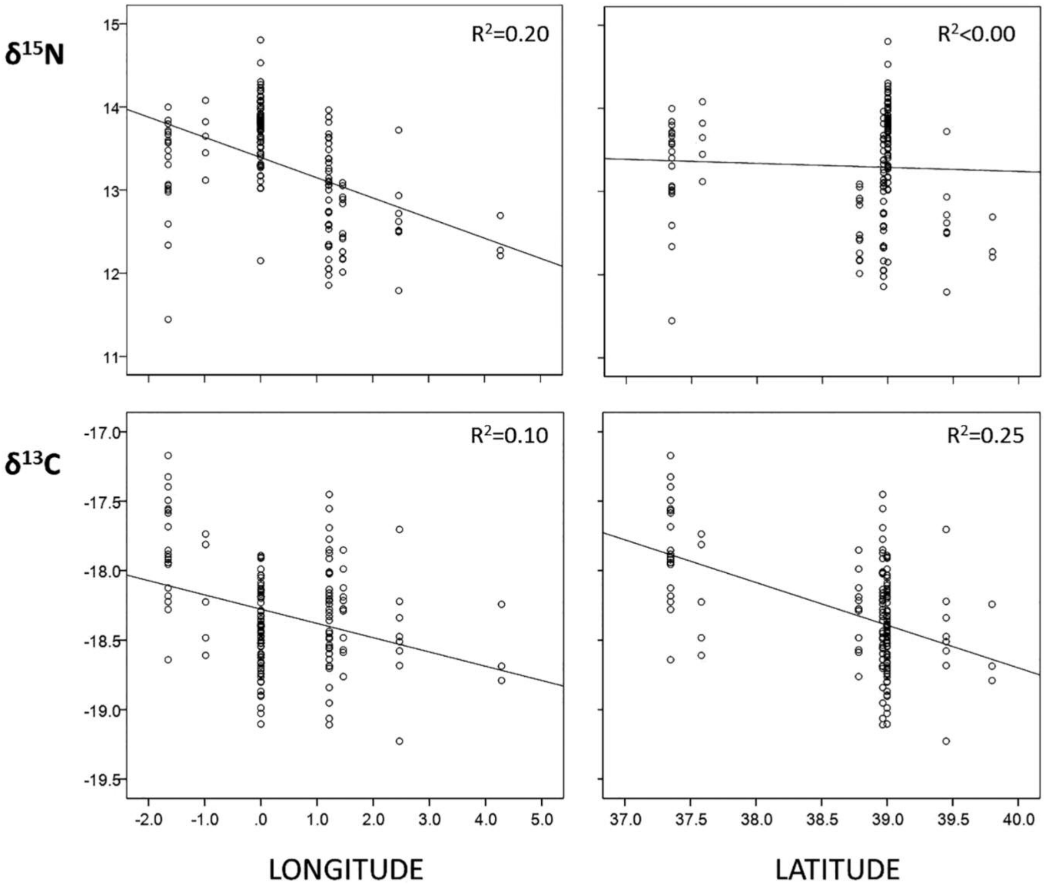


FIG. 3.—Relationship between δ^{15}N and δ^{13}C values in P1 feathers of European Storm-petrels and latitude and longitude of their respective breeding sites across the Western Mediterranean. Both relationships with δ^{13}C, and longitude with δ^{15}N, were significant.

[Relación entre los valores de δ^{15}N y δ^{13}C en plumas P1 de paíño europeo, y la latitud y longitud de sus respectivas localidades reproductivas a lo largo del Mediterráneo Occidental. Ambas relaciones con δ^{13}C, y la longitud con δ^{15}N, son significativas.]

tese and Pelagie Islands are on the Tunisian Platform while the Galite Islands are off the northern Tunisian Coast (Figure 1).

Discussion

Our results indicate that the winter quarters of Atlantic and western Mediterranean European Storm-petrels are completely different. Atlantic Storm-petrels captured at widely distant colonies over the NE Atlantic differed in isotopic values of feathers grown during the breeding season. However, feathers grown during the non-breeding season showed similar isotopic values, suggesting the existence of common winter quarters. On the other hand, western Mediterranean Storm-petrels presented similar isotopic values in all feathers with little or no overlap with those from the Atlantic. Thus, our results suggest that this subspecies may stay in the Mediterranean year-round, which is in agreement with field observations.

By remaining within the Mediterranean basin throughout the year, Mediterranean Storm-petrels may experience lower migration costs than Atlantic long-distance migrants (Matović *et al*., 2017). In fact, when wintering conditions at the breeding areas are favourable, residency can represent an advantageous fitness strategy (Sanz-Aguilar *et al*., 2012, 2015; Rotics *et al*., 2017). For instance, survival analyses indicate that Mediterranean Storm-petrels breeding at Benidorm Island (Spain) face lower winter mortality than Atlantic Storm-petrels breeding at Enez Kreiz island (Atlantic France), which are affected by oceanographic conditions within the Angola-Benguela upwelling and by La Niña conditions (e.g. hurricanes) during migration (Matović *et al*., 2017).

Adults moult their innermost primary feathers (P1) around a month before the end of the breeding season, which occurs about one month earlier in the Mediterranean than in the Atlantic (Arroyo *et al*., 2004). In Atlantic birds, both SIA and observational field data suggest the existence of a continuous moulting process starting on the breeding grounds and ending in winter quarters. Birds captured in Icelandic and Northern Ireland colonies showed significantly greater δ^{15}N values in P1 than those captured in the Canary Islands. These differences may result from baseline isotopic differences in δ^{15}N between cold and subtropical northern Atlantic waters (Roscales *et al.,* 2011; McMahon, 2013). In contrast, isotopic values of the eighth secondary feather (S8), probably moulted at wintering sites, were similar for individuals captured at the three breeding colonies. This result agrees with previous evidence indicating that the vast majority of Atlantic birds overwinter in the southern Atlantic, mainly in the Angola and Benguela currents (e.g. Cramp & Simmons, 1977; Mínguez, 2006; Carboneras *et al*., 2018; Matović *et al*., 2017).

Recoveries and field sightings of Mediterranean Storm-petrels during winter are very scarce (Spina & Volponi, 2008; SEO/BirdLife, 2012; Matović *et al*., 2017; http://www.atlas-ornitho.fr/index.php?m_id=1415&y=-10&speciesFilter=&frmSpecies=17&frmDisplay=Affichez), making it difficult to identify wintering areas (Soldatini *et al*., 2014; Matović *et al*., 2017). Our study showed that, at least, the westernmost Mediterranean Storm-petrels present similar isotopic values for P1 feathers, moulted during the breeding season, and for S8 and P10 feathers, moulted after the breeding season, showing in all cases Mediterranean signatures. The Mediterranean values found for S8 and P10 feathers could be explained by three alternative hypotheses: a) birds interrupt their moult, winter in the Atlantic and reactivate the moult upon returning to the Mediterranean in spring; b) birds migrate to the Atlantic but the moult is completed before the end of the season spent in the Mediterranean, or; c) birds remain in the Mediterranean year-round.

Although Demongin (2016) described suspended moult in the European Storm-petrel, we believe that the moult suspension hypothesis is very unlikely for our Mediterranean study populations, as the most advanced Mediterranean Storm-petrels have been observed with moults up to P7 and P8 feathers at the end of the breeding season (Appendix I, F. Aguado, pers. com., A. Sanz-Aguilar, pers. obs.). Moreover, Mediterranean breeders captured during long-term studies presented very worn S8 and P10 feathers at the beginning of the breeding season (own data, Appendix I). Regarding the second hypothesis, that birds migrate to the Atlantic after moulting, field evidence indicates that only a few birds migrate from the Mediterranean to the Atlantic through the Gibraltar Strait and that this movement is concentrated in October-November (Arroyo & Cuenca, 2004; Rodríguez *et al*., 2012). Also, recoveries of Mediterranean birds in Atlantic waters are extremely rare. In that case, migration timing could be consistent with complete moult (including P10) only for the most advanced birds but is highly unlikely for the entire population. The alternative and most plausible hypothesis is that Mediterranean Storm-petrels breeding in the westernmost colonies remain in the Mediterranean during the winter. Indeed, recent demographic long-term studies show that survival of Mediterranean Storm-petrels is related to winter environmental conditions in the Mediterranean (Soldatini *et al*., 2014; Matović *et al*., 2017). Soldatini *et al*. (2014) found that survival of Storm-petrels breeding in Marettimo (Italy) is related to the winter sea surface temperature (SST) in the Alboran Sea. Matović *et al*. (2017) found that survival of Storm-petrels breeding in Benidorm (Spain) is related to the Western Mediterranean Oscillation Index. Although wintering records of Storm-petrels in the Mediterranean are scarce, some available data place them in the Southern Mediterranean (Alboran Sea, Northwestern Africa; de Juana 1986; de Juana & Garcia, 2015) and Eastern Mediterranean (Akriotis & Handrinos, 1986; Massa & Sultana, 1993; J. Fric pers. com.), but mostly (by far) in the South-central Mediterranean (Figure 3, Ionian Sea, Tunisian Platform, Northern Tunisian waters; Bannerman & Vella-Gaffiero, 1976; Brichetti, 1980; Akriotis & Handrinos, 1986; Hamrouni, 2015; B. Metzger, pers. com.).

Our SIA results show slightly higher $\delta^{13}C$ values but similar $\delta^{15}N$ values in S8/P10 compared to P1, and are in agreement with these observations, suggesting a southward wintering migration of Mediterranean Storm-petrels, i.e. to the Alboran Sea and Northwestern Africa. In our study, $\delta^{13}C$ values in P1 of birds captured at different Mediterranean colonies decreased significantly from south to north and from west to east, with the relationship with latitude being twice as strong as that with longitude. However, two comments must be made. First, some birds captured with mist nets were probably prospecting non-breeders visiting several colonies during the breeding season (Sanz-Aguilar *et al*., 2010). Since prospectors move between colonies, they should present more homogeneous isotopic values than breeders. Thus, the differences we found could be related to differences of isotopic values of breeders, which are also captured by mist nets (Sanz-Aguilar *et al*., 2010). In such a case, the real differences between colonies could be more robust that shown. Also, and most remarkably, while our Mediterranean results could point to a slightly western component in winter quarters, it should be taken into account that we sampled a restricted range of longitudes in Western Mediterranean. On the other hand, Gómez-Díaz & González-Solís (2007) showed that $\delta^{15}N$ values in P1 feathers of Mediterranean Scopoli's shearwaters *Calonectris diomedea* decreased from 10ºW to 30ºE, sampling a much wider longitudinal range. Hence, if the $\delta^{15}N$ gradient found for Scopoli's shearwaters also applies to Storm-petrels, a southeastwards migration could also match our SIA results. Furthermore, most winter reports come from the Tunisian Platform and Northern Tunisian waters. We thus consider that Mediterranean Storm-petrels may winter in Tunisian waters, where resource availability in winter is high. In spring, the most highly productive spots in the Mediterranean are the Gulf of Lion and the Balearic Sea, but from December to February the most productive area is precisely the Tunisian Platform (Bosc *et al*., 2004; Siokou-Frangou *et al*., 2010; Lazzari *et al*., 2012; Volpe *et al*., 2012).

It will be possible to study European Storm-petrel migration using geolocation in the near future. Until then, we consider that conservation policies for Mediterranean Storm-petrel should regard Tunisian waters as the most important wintering area of this taxon.

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Author's contributions.—All authors formulated the questions; J.L.R., A.S.-A. and J.G.-S. collected data; all authors supervised research; J.L.R. and J.G.-S. designed methods; C.M. and J.L.R. analyzed the data; C.M. led the writing of the article. All authors contributed to the drafts and gave final approval for publication.

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Supplementary Electronic Material

Addtitonal supporting information may be found in the on-line version of this paper. See volumen 66(1) on www.ardeola.org.

Appendix 1. European Storm-petrel pictures.

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