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Memòria presentada per
JOSÉ MANUEL DE LOS REYES GONZÁLEZ
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INFORME DEL DIRECTOR

La tesis doctoral de José Manuel de los Reyes González, titulada "*Spatial ecology and migration of Calonectris shearwaters: new insights from Spanish populations revealed by biologging*" incluye seis capítulos relativos a la ecología espacial de dos especies de ave marina en base a datos obtenidos con instrumentos de seguimiento remoto. Como director de la tesis, doy constancia de que el doctorando contribuyó en todas o en la mayor parte de las tareas necesarias para el desarrollo de los capítulos, incluyendo el diseño, trabajo de campo, toma de muestras, análisis de datos y redacción científica.

Del mismo modo, doy constancia de que el capítulo titulado "*Sexual segregation in the foraging behaviour of a slightly dimorphic seabird: influence of environmental conditions and fishing activity*" fue realizado con igual grado de contribución por el autor de la presente tesis doctoral, Jose Manuel de los Reyes González, y por Fernanda Pereira de Felipe. Fernanda Pereira también realizó la tesis doctoral bajo mi dirección y la defendió en 2020 en la Universidad de Barcelona, dentro del mismo programa de Doctorado. El capítulo mencionado, incluído en ambas tesis, ha sido aceptado para su publicación en la revista Journal of Animal Ecology, compartiendo ambas personas la primera autoría. En relación a la contribución de cada autor en este trabajo, el doctorando José Manuel de los Reyes González desarrolló los diferentes análisis espaciales y estadísticos e implementó el código necesario en entorno de computación R. Fernanda Pereira de Felipe se encargó de la coordinación y el desarrollo del trabajo de campo, los análisis para el sexado molecular de las muestras en laboratorio y el análisis de isótopos estables. Ambos doctorandos redactaron conjuntamente el manuscrito presentado como capítulo de tesis.

Barcelona, 16 de diciembre de 2020

Dr. Jacob González Solís Bou

Nuestras horas son minutos cuando esperamos saber, y siglos cuando sabemos lo que se puede aprender.

Antonio Machado

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Deberíamos adquirir el coraje
de no ser como todo el mundo

Jean-Paul Sartre

Cada uno es mucha gente.
Para mi soy quien me pienso,
para otros - cada cual siente lo
que cree, y es yerro inmenso

Fernando Pessoa

Reconozco que muchas veces pensé que este día nunca llegaría. A veces da gusto equivocarse, por fortuna… Decía Fernando Pessoa que "cada uno es mucha gente". Y no puedo estar más de acuerdo. Después de este largo camino, es momento de hacer repaso por todos aquellos que han formado parte de esta etapa de mi vida, y que han contribuido a que yo sea quien soy. Vayan por delante mis disculpas a aquellos que olvidé mencionar, serán cosas de la edad. Siempre fui persona de pocas palabras, y quizá alguien que lea su nombre en las próximas líneas se sorprenda. Dicen que las pisadas no necesitan hacer ruido para dejar huella.

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Y nada más. Ahora ya sólo toca mirar al futuro, que es, como dice Woody Allen, el lugar en el que vamos a pasar el resto de nuestras vidas. Pasen y lean, si quieren.

ABSTRACT

The revolution in biologging and satellite telemetry technologies in the last two decades has led to a new era in seabird research. This thesis brings new insights into the spatial ecology and migration of the Cory's and the Scopoli's shearwaters (*Calonectris borealis* and *C. diomedea*, respectively), offering a comprehensive overview of these topics for the Spanish populations of these model species. In particular, the thesis provides new knowledge about the movement patterns, at-sea behaviour and the marine environment they inhabit year-round, through the use of GPS loggers and light-level geolocators.

Along the chapters of the thesis, I illustrate the potential and applications of *biologging* in seabird research and conservation. To do so, I address different questions aimed to evaluate the role of environmental features, fisheries, and breeding constraints in the foraging strategies and at-sea behaviour of tracked birds. We found that females of Scopoli's shearwater generally attended fisheries less than males, and both sexes associated less to fishing boats during unfavourable conditions. Sea surface temperature likely plays a role in individual decision-making: we found that birds may use this environmental feature to decide foraging trip destination. Moreover, we found variability in foraging trips at inter-annual scale, likely due to environmental fluctuations, but also at intra-annual scale, likely due to the different breeding constraints over the breeding period. We explored seabird behaviour from novel ways, deriving simple metrics that may enhance the use of seabirds as sentinel species. Last, we unveiled the role of individual differences in trophic ecology, and discussed the implications of such differences in the use of seabirds to monitor long term fluctuations in a complex upwelling ecosystem.

This thesis compiles and summarises the previous knowledge of the Spanish populations of Cory's and Scopoli's shearwaters, and extends it with novel insights. Moreover, in a transversal way, I discuss the role of seabirds as indicator species, particularly considering the use of biologging to enhance their suitability as ocean sentinels within the framework of ecosystem-based management.

RESUMEN

La reciente revolución en tecnologías de seguimiento remoto y biologging en las dos últimas décadas ha desembocado en una nueva era en la investigación con aves marinas. Esta tesis contribuye a un mejor conocimiento sobre de la ecología espacial y los patrones migratorios de la pardela cenicienta atlántica (*Calonectris borealis*) y de la pardela cenicienta mediterránea (*C. diomedea*), enfocándose en las poblaciones españolas de ambas especies. La tesis recopila y resume el conocimiento previo sobre ambas especies, y aporta nueva información relevante para su conservación. A lo largo de los diferentes capítulos, se ilustra el potencial uso y las aplicaciones de las técnicas de biologging en la investigación y conservación de las aves marinas, en particular el empleo de registradores GPS y de geolocalizadores por niveles de luz. Se abordan diferentes temas de interés, desgranando el papel que juegan la variabilidad ambiental, las pesquerías, o las restricciones asociadas al periodo reproductor, en los patrones de comportamiento y movimientos inferidos con los datos recogidos. En conjunto, la tesis aporta nueva información sobre los movimientos en el mar, el comportamiento y el uso del hábitat marino a lo largo del año. Finalmente, a lo largo del trabajo y de forma transversal, se resalta la utilidad de las aves marinas como especies centinela, particularmente teniendo en cuenta que la aplicación de técnicas de seguimiento remoto y de biologging amplían el potencial de estas especies como indicadoras en el marco del manejo del medio marino basado en un enfoque ecosistémico.

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General Introduction

GENERAL INTRODUCTION

Oceans are suffering impacts from human activities at unprecedented levels worldwide (Halpern et al., 2008). In historical times, marine resources were exploited by human beings in a sustainable manner on the whole (Jackson et al., 2001; Pitcher, 2001). However, the pace of exploitation changed drastically over the last century, leading to an extensive array of disturbances that have undermined the goods and services provided by the oceans (Coll et al., 2008; Jackson et al., 2001; McCauley et al., 2015). As a consequence, there is clear evidence of the severe impacts of human activity on marine ecosystems nowadays, including defaunation and biodiversity loss (Halpern et al. 2008; Worm et al., 2006). Unsustainable fishing, climate change, ocean warming, acidification, pollution, eutrophication, alteration of the coastline or settlement of invasive species are just a few of the many threats that are leading to a dramatic loss of biodiversity in the oceans (McCauley et al., 2015; Sala & Knowlton, 2006).

Conventional management actions developed in the second half of the past century, in search of solutions to curb these impacts on marine ecosystems, were proven ineffective (Curtin & Prellezo, 2010; Worm et al., 2006). A broad consensus among the research community, policy-makers and management practitioners on the need to improve management has led to two interlinked approaches: Ecosystem-Based Management (EBM) and Marine Spatial Planning (MSP) (Crowder & Norse, 2008). Unlike traditional management approaches, EBM is a more holistic approach, taking into account the interconnectedness and interdependent nature of ecosystem components, considering ecosystem structure and functioning, and reconciling social stakeholders in management decisions (Curtin & Prellezo, 2010). EBM is recognised as an iterative process that requires flexibility and adaptation since both natural systems and our knowledge of them change over time. This is why adaptive management, i.e., the process of formulating and testing hypotheses on the management actions in ways that incorporate uncertainty and enable learning, provides a suitable framework for EBM (Leslie & McLeod, 2007). Likewise, MSP is a tool to support sustainable development whilst implementing the EBM approach (Schaefer & Barale, 2011). MSP relies on supporting information systems for decision-making and governance of the marine systems from an integrated approach, reducing conflicts in the use of marine space and maintaining the delivery of ecosystem services (Foley et al., 2010). To be effective, both EBM and MSP need to understand the ecological dynamics of marine ecosystems, monitor these dynamics over time, and develop tools enabling adaptive management. Therefore, comprehensive monitoring of marine ecosystems becomes an essential requirement for implementing EBM, but it is challenging due to difficulties inherent in observing dynamic ocean environments at relevant time-scales (Leslie & McLeod, 2007).

In the context of EBM, the use of indicator species, also referred to as sentinel species, has been proposed as a tool for monitoring fluctuations in dynamic marine ecosystems (Levin & Möllmann, 2015;

Zacharias & Roff, 2001). Hazen et al. (2019) defined an ecosystem sentinel as a species that responds to changes and variability of ecosystems in a timely, measurable, and interpretable way. Useful ecosystem sentinel species must be conspicuous, easily accessible, and observable, and they should provide ecosystem information across different spatio-temporal scales (Burger, 2006; Fossi & Panti, 2015). Moreover, detailed knowledge on the biology of the indicator species is advisable to allow interpreting data recorded and temporal trends (Hilty & Merenlender, 2000). Mainly, ecosystem sentinels must be mechanistically linked to ecosystem components and response to changing environmental conditions, thus allowing for tracking unobserved components of the ecosystem (Hazen et al., 2019).

SEABIRDS AS INDICATOR SPECIES OF THE MARINE ENVIRONMENT

Marine top-predators are often proposed as sentinel species of the marine ecosystems, as their position at the top of the marine food webs makes them very sensitive to alterations in lower trophic levels (Bossart, 2006; Estes et al., 2016). Importantly, it is well known that top-predators react to environmental variability and respond to anthropogenic impacts on the ecosystems they inhabit (e.g., Hazen et al., 2019; Sergio et al., 2008; Sydeman et al., 2015). Among the marine top-predators, seabirds stand out as suitable sentinel species due to various of their particular life-history traits: (i) seabirds integrate ecological processes that occur at lower trophic levels, (ii) unlike other marine top predators, they are abundant, conspicuous and visible at sea, (iii) despite they spent the majority of time at sea to feed on marine prey, they breed colonially on land, where they are accessible, which eases sampling and monitoring (Durant et al., 2009). It is for these features that seabirds have been repeatedly proposed as ecosystem sentinels, and the scientific literature is plenty of examples (e.g., Burger & Gochfeld, 2002; Bost & Le Maho, 1993; Frederiksen et al., 2007; Furness & Camphuysen, 1997; Scopel et al., 2018).

Seabirds have evolved a set of particular adaptations to inhabit the oceans. Although oceans seem homogeneous to the human eye, they encompass highly dynamic ecosystems, thanks to the combination of physical and atmospheric features, which ultimately promote dynamism and variability in marine productivity levels (Kroeker et al., 2020). These adaptations allow seabirds to cope with the dynamism of the marine environment, including unpredictability and uneven distribution of resources, wind conditions or high seasonality, among others (Gaston, 2004; Schreiber & Burger, 2001). Many seabirds, especially the most pelagic species, have exceptional orientation capabilities to navigate the oceans and can fly over long distances, which allows them to wander vast extensions in search of prey, thereby integrating ecosystem information at several spatio-temporal scales (Schreiber & Burger, 2001). They prey on marine species, such as epipelagic fish, cephalopods, or crustaceans, which they catch near the sea surface or underwater through diving. Finally, regarding reproduction, seabirds have delayed sexual maturity (between 2 and 10 years of age) and long life spans, they reproduce annually or biannually, have small clutch sizes, and chick development is slow (Schreiber & Burger, 2001). Unfortunately, some of these features have led to a concerning conservation status of seabirds (Box 1).

Researchers have approached the use of seabirds as sentinels of the marine environments through monitoring five different features: life history, reproduction, demography, diet, and movement, each of them addressed through different proxies (Hazen et al., 2019). Except for movement, all have been traditionally measured at the breeding colonies, but they present some drawbacks. Demographic parameters, for instance, may exhibit a delayed response to fluctuations in the marine environment and could be determined by factors operating from both marine and land environments (Cury et al. 2011). Diet can be traced at different spatial and temporal scales through analysing easily sampled tissues (blood, plasma, feathers, eggs) and can inform about feeding resources, trophic relationships, or prey abundance (Ramos & González-Solís, 2012). However, it is difficult to discern the origin of resources consumed and reach conclusions without concurrent or previous spatial information (Ceia et al., 2018). Therefore, except movement, all these different features present a common weakness: they do not allow to link measurements with the marine habitat and areas used. This fact may be a significant drawback for using seabirds as ecosystem sentinels in the context of EBM and MSP, especially considering that they can fly over vast areas and use different habitats in short time windows. However, movement responds rapidly to changes in the environment, which would otherwise be difficult to observe (Parsons et al., 2008; Grémillet et al., 2010; Oswald & Arnold, 2012). Therefore, tracking movement and behaviour at sea enables to relate all seabird features measured with the actual environment exploited, which may enhance the use of seabirds as sentinel species of the oceans (Brisson-Curadeau et al., 2017).

Box 1. Seabirds under threat

The condition of most seabirds species as marine top-predators, together with their particular life-history traits, make this group of birds particularly prone to human-induced threats. Globally, seabirds represent the group of birds with the largest number of species with populations declining severely, and 30% of the species are listed as threatened (BirdLife International, 2008; Dias et al., 2019). Fishery-related threats are among the most harmful, including bycatch, overfishing, and dependence on discard scavenging (Anderson et al., 2011; Grémillet et al., 2008; Grémillet et al., 2018). In addition to this, there is growing evidence on changes in the distribution and abundance of feeding resources due to global warming (Brichetti et al. 2000; Gremillet & Boulinier 2009; Frederiksen et al. 2008; Jenouvrier et al. 2009). Besides, pollution, including heavy metals, oil spills, and plastic debris, causes damage and impacts on seabirds at different time-scale, from short- or mid-term due to internal organs injury or intoxication, to long-term due to bioaccumulation and fertility decline (e.g., Goutte et al., 2014; Moreno et al., 2011; Roman et al., 2019). Fishing activities such as longlining and oil spills cause the death of 160 000 - 320 000 seabirds each year globally (Croxall et al. 2012). Last, seabirds also suffer from invasive species, such as feral and domestic cats, rats, and mice, that predate on adults, chicks, and eggs, jeopardising individual survival and reproductive success in the breeding colonies in islands and islets (Towns et al., 2011). All together leads to the death of thousands of individuals annually and a decrease in reproductive success, causing negative global demographic trends (Dias et al., 2019).

BIOLOGGING: RECORDING BEHAVIOUR OF SEABIRDS TO ENHANCE THEIR ROLE AS ECOSYSTEM SENTINELS

The fast advances in tracking technologies in recent decades have allowed investigating animal movements in an unparalleled depth, leading to the emergence of a new scientific discipline, the movement ecology (Nathan et al., 2008). Seabird researchers have followed this path, and as a result, there has been a bloom of research articles addressing the at-sea ecology and behaviour of seabirds (Wilson et al., 2002; Burger & Shaffer, 2008; Wakefield et al., 2009). A full assortment of electronic devices are currently available. These devices can included different sensors to track the spatial location and behaviour of seabirds. Among them, for instance, GPS loggers and light-level geolocators have been widely used (Box 1; Box 2). In essence, tracking technologies provide an innovative and cost-effective tool that fosters the use of seabirds as ecosystem sentinels, allowing the assessment of ecosystem responses to environmental changes (Montevecchi et al., 2012; Lescroël et al., 2016).

Box 2. Light-level geolocators

In the context of seabird research, a remarkable milestone took place in 1992, when researchers interested in combining wildlife research with engineering developed the geolocators (Wilson et al., 1992). Geolocators were developed as a biologging solution to allow for tracking moving animals, meeting three requirements: reduced size, reduced weight, and low cost (Wilson et al., 1992). These loggers, also known as light-level geolocators or global location sensing loggers, take advantage of elementary mathematical and astrophysical methods, used by navigators since ancient times, to estimate the position of the tagged animals in the Earth (Weimerskirch & Wilson, 2000; Afanasyev, 2004). The method used to estimate geographical positions involves a considerable spatial error of about 200 km on average in latitude, which also increases close to the equinoxes (Phillips et al. 2004). However, it has several advantages, such as the aforementioned low cost and weight of the devices, and overall a long battery life that allows for long tagging periods. Because of their size, they can be attached to the leg mounted on a plastic ring, also enabling long-lasting deployment. Altogether makes geolocators the most suitable biologging devices to track movement and behaviour of seabirds over long periods, including migration and wandering in the wintering areas.

This revolution in tracking technologies has been accompanied by fast development in remote sensing techniques to gather environmental information from satellites. Combining data from animal-borne sensors with satellite-derived environmental information provides a perfect bypass to understand the role of the environment in the at-sea ecology of seabirds, including movements and behaviour (Burger & Shaffer, 2008). Moreover, intrinsic biological markers obtained from tissues easy to sample, such as blood or feathers, can inform about the trophic ecology of tagged individuals, which can further enhance the role of seabirds as ecosystem sentinels (Ramos & González-Solís, 2012).

Nevertheless, tracking movement and behaviour at sea was not possible neither easy until recent times. Back in the 1960s, researchers working with wild animals started to use the first devices to track birds' movements, the high-frequency radio transmitters (VHF) (Southern, 1964). These devices only provided, however, information of movements in the vicinities of the colony in a short-range, and with a short temporal and low spatial resolution (Wilson & Vandenabeele, 2012). Later on, the invention of satellite-telemetry devices, such as Platform Terminal Transmitters (PTT) based on the ARGOS satellites system, allowed to investigate at-sea movements of seabird species, first those with body mass large enough to accommodate the size of these first devices (Jouventin & Weimerskirch, 1990) and later with smaller species (Wilson et al., 2002).

The use of satellite-telemetry to track the movements and behaviour of seabirds used to have several drawbacks related to data transmission (Ropert-Coudert et al., 2005). In search of solutions, researchers and engineers started to developed tags able to record and store information, paving the way to what we call today *biologging* (Ropert-Coudert et al., 2005). The term *biologging* refers to the set of autonomous devices deployed on free-ranging animals to collect biological and physical information, although analytical techniques to handling and processing stored information start to be also included into this term (Fehlmann & King, 2016). Unlike satellite-telemetry, biologging relies on storing information in the devices and thus, it is mandatory to recapture the animal to download the information recorded by the animal-borne sensors, which may represent a challenge. Development of biologging devices has also straggled to enable tagging small-sized species, to avoid impacting on individuals' aero- and hydro-dynamic or to prevent corrosion by saltwater (Hull, 1997; Chiaradia et al., 2005; Gillies et al., 2020). Furthermore, thanks to technological advances, mostly related to the mobile phone industry, loggers are increasingly smaller, lighter and cheaper, allowing for tracking movement and behaviour from ever-smaller species and for ever-larger sample size (Wilson & Vandenabeele, 2012).

Lastly, in the last years, some manufacturers have started to combine biologging with remote downloading, making a mixture between satellite telemetry and biologging. This is done usually by taking advantage of the mobile phone network (e.g., GPS-GSM), base-station receptors (e.g., GPS-VHF), or ARGOS satellite system (e.g., GPS-PTT). However, this new technology requires that animals remain in the vicinities of receptors during a specific time to remotely downloading information, which needs to be long enough to allow retrieving the massive amount of data that sensors may record.

Box 3. GPS loggers

Conversely to free-range movements during migration and wintering, during the breeding period seabirds are central-place foragers, and thus they are forced to return to the colony frequently. This condition limits the extension of their foraging movements, and thus battery duration is not as much limiting, allowing to use different devices such as GPS loggers. These devices record the geographic location of tagged birds at high spatial and temporal resolution through the GPS-satellite network. These devices are typically attached on the back feathers or tail of the seabirds using a water-resistant adhesive tape, allowing for short-term deployments until recapture or until the device drops off.

CONSERVATION AND MANAGEMENT OF MARINE ECOSYSTEMS IN SPAIN

In the marine realm, the conservation and exploitation of resources is subject to important regulatory rules and directives, due to the many important good and services provided by the marine habitats and the difficulty in defining boundaries across states' jurisdictions. In Europe, the Marine Strategy Framework Directive aims to promote the integration of environmental considerations into all relevant policy areas and deliver the environmental pillar of the maritime policy for the European Union (UE Directive 2008/56/EC). Marine waters under the sovereignty and jurisdiction of the Member States of the European Union include waters in the Baltic Sea, the Black Sea, the Mediterranean Sea, and the North-east Atlantic Ocean, including the waters surrounding the Azores, Madeira and the Canary Islands.

Spain, located in the southwestern extremity of the European continent, holds a rich diversity of marine species —including a remarkable community of seabirds— and habitats, which are also threatened by human activities (Templado, 2011; Narayanaswamy et al., 2013; Navarro et al., 2015). Moreover, Spain hosts one of the most significant fishing fleets among the countries of the European Union (Anticamara et al., 2011). Therefore, Spain plays a critical role in the successful implementation of European policies aimed to achieve a good environmental status of the marine environment of the European Union. In this regards, several recently approved national Spanish regulations established a regulatory framework, providing management guidelines for the effective preservation of the marine ecosystems. Notably, the Law for the Protection of the Marine Environment (Spanish Law 41/2010, December 29th) incorporates the UE Directive 2008/56/EC into the Spanish legislation. It sets a comprehensive regulatory framework of human activities within the EBM framework to ensure the conservation of the marine ecosystems. This law states the use of indicators species to evaluate ecosystem functioning, even including the distribution and status of seabird species, albeit without mentioning any specific details (Annex I in Spanish Law 41/2010, December 29th). In this regard, the working report for the definition and implementation of the Marine Strategy in Spain - Group "Birds" (Arcos et al., 2012) remarked the role of seabirds as indicator species and highlighted the importance of remote tracking to evaluate the status of seabird populations in the context of the Marine Strategy Framework Directive; regarding tracking data, this text acknowledged the need to define quantifiable parameters to evaluate changes over time, even though not specifying any (Arcos et al., 2012). Other national regulations, including the Law on Natural Heritage and Biodiversity (Spanish Law 42/2007, December 13th), the List of Wild Species under Special Protection (art. 54, Spanish Law 42/2007, December 13th), and the Spanish Catalogue of Threatened Species (Royal ordinance 139/2011, February 4th), stress the importance of stopping the current rate of biodiversity loss and establishing specific protection measures for species in decline.

CORY'S & SCOPOLI'S SHEARWATERS AS OCEAN SENTINELS

The Cory's and the Scopoli's shearwaters are two of the most representative seabird species in temperate waters of southern Europe and northern Africa. Like other seabirds, they may work as sentinels of the functioning and health of marine ecosystems. Additionally, Cory's and Scopoli's shearwaters are charismatic species, which has led to use them as flagship species to promote media campaigns to arise public interest (Ducarme et al., 2013; Sergio et al., 2006). In Spain, SEO/BirdLife declared them as Bird of the Year in 2013, aiming to raise the attention of society on the conservation threats of the oceans and animals inhabiting them.

Spanish populations of both Cory's and Scopoli's shearwaters are facing population declines, although there is a more significant concern for the Scopoli's shearwater (Carboneras & Lorenzo, 2003; Sanz-Aguilar et al., 2016). In Spain, a population of 30 000 breeding pairs is estimated for the Cory's shearwater (Lorenzo, 2004; BirdLife International, 2016) and 10 000 pairs for the Scopoli's shearwater (Carboneras, 2004; BirdLife International, 2016).

Belonging to the order Procellariiformes, Cory's and Scopoli's shearwaters have been considered until recently as subspecies of a polytypic species that included the nominal form *Calonectris diomedea* subsp. *diomedea* (Scopoli 1769), which breeds on islands and islets in the Mediterranean Sea, and the Atlantic form *Calonectris diomedea* subsp. *borealis* (Cory 1881), which breeds mainly in the Macaronesia (Canary Islands, Azores, Madeira, and Selvagens; Marti & Del Moral, 2003). The Atlantic form also breeds in some islands and islets off the Atlantic coast of the Iberian and French regions (Granadeiro, 1991; Munilla et al., 2016), and even in small breeding colonies in the Alboran Sea, into the Mediterranean. Recent studies pointed out that genetic differences between the two subspecies are sufficient to consider them as separate species (Gómez-Díaz et al., 2006, 2009). However, other authors call for caution as they consider that the speciation process is still incipient, and some genetic flow still exists between the two taxa (Genovart et al., 2013). Although the debate is still open, the split as specific taxa has already been accepted by scientific organisations such as the British Ornithologist Union and BirdLife International (Sangster et al., 2012; Del Hoyo et al., 2014, 2016). In this thesis, we will treat them generally as different species: the Atlantic Cory's shearwater (*C. borealis*) and the Scopoli's shearwater (*C. diomedea*). Nevertheless, either considering them as subspecies or as separate species, both taxa should be treated as different conservation units. Therefore, in this work, they are treated as separate species for convenience.

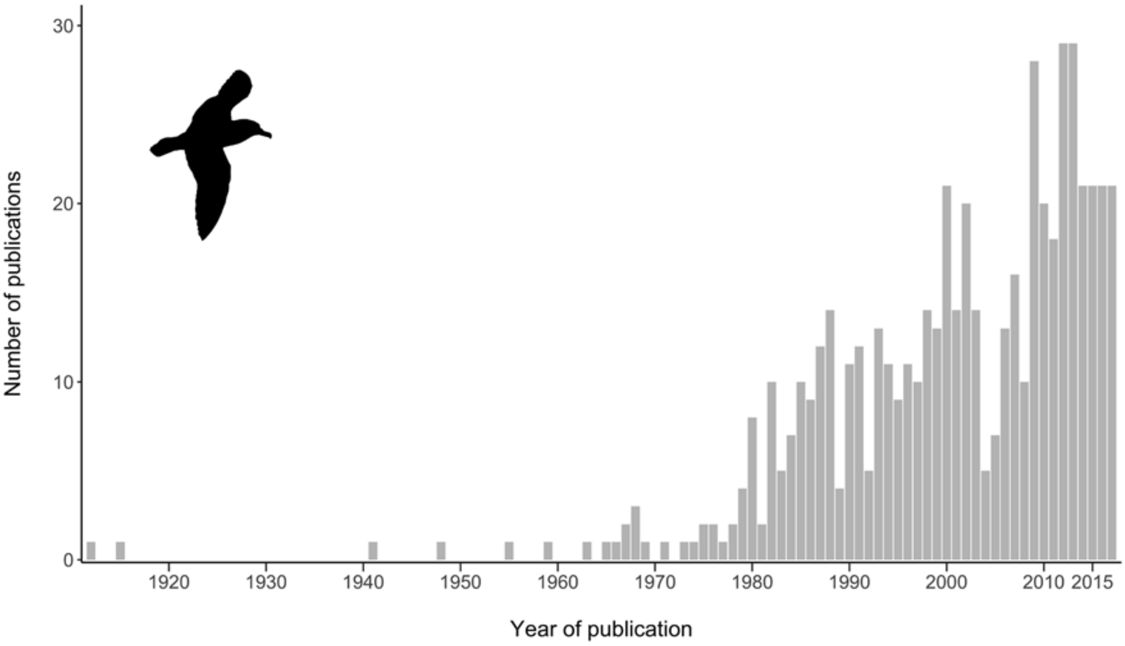

Figure 1 • Number of published research articles related to some extent with the Cory's and the Scopoli' shearwaters. Until 2017, 547 papers were published, which points out the appropriateness of these species as a study model. I performed a search in *ISI Web of Knowledge* (Web of Science, Thomson Reuters & Clarivate Analytics) and Zoological Record databases to look for articles published. The search contained the following topics: (("Calonectris") AND ("diomedea" OR "borealis" OR "diomedea borealis" OR "diomedea diomedea")) OR ("Cory's shearwater*") OR ("Scopoli's shearwater*"). After the search, I manually checked the output and excluded from the results all those not directly related to the study species.

The biology and natural history of these two species are well-known. To date, almost 550 research articles containing information on these species have been published, which probably places them among the most studied seabird species (Fig. 1). Their suitability as model species, together with the -still- significant size of their populations in Spain, and the possibility to track their movements at sea thanks to biologging, make these species as promising candidates for sentinel species for the EBM of the marine ecosystems in the Spanish maritime domain.

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OBJECTIVES AND STRUCTURE OF THE THESIS

This thesis generally aims to provide new ecological insights into the spatial ecology, movements and behaviour of seabirds, using the Cory's and Scopoli's shearwaters as model species, and biologging techniques as a research tool. In a transversal way, the thesis also attempts to illustrate how the combined use of biologging devices, and the application of state-of-the-art techniques to analyse behaviour, can altogether make up seabirds a suitable tool for the monitoring and management of marine ecosystems, therefore highlighting the potential use of these species as ecosystem sentinels. The thesis focuses on the Spanish populations in an attempt to foster the use of the aforementioned species as a management tool in Spain.

The specific objectives of the thesis are:

1. To compile and provide a comprehensive background summarising the natural history of the Cory's and Scopoli's shearwaters.
2. To extend our knowledge on the at-sea spatial ecology of the Spanish populations.
3. To provide new insights into the role of the environmental conditions in shaping the foraging strategies.
4. To evaluate the influence of fisheries on spatial ecology and foraging strategies.
5. To illustrate the use of these species as a tool for management in protected areas.
6. To provide new insights into short- and long- term monitoring of seabirds inhabiting dynamic marine ecosystems.

The work contained in this thesis is organised in the following six chapters:

In **Chapter 1**, we review more than two hundred scientific publications about the model species and summarise the current knowledge on their natural history. This chapter fulfils the objective 1.

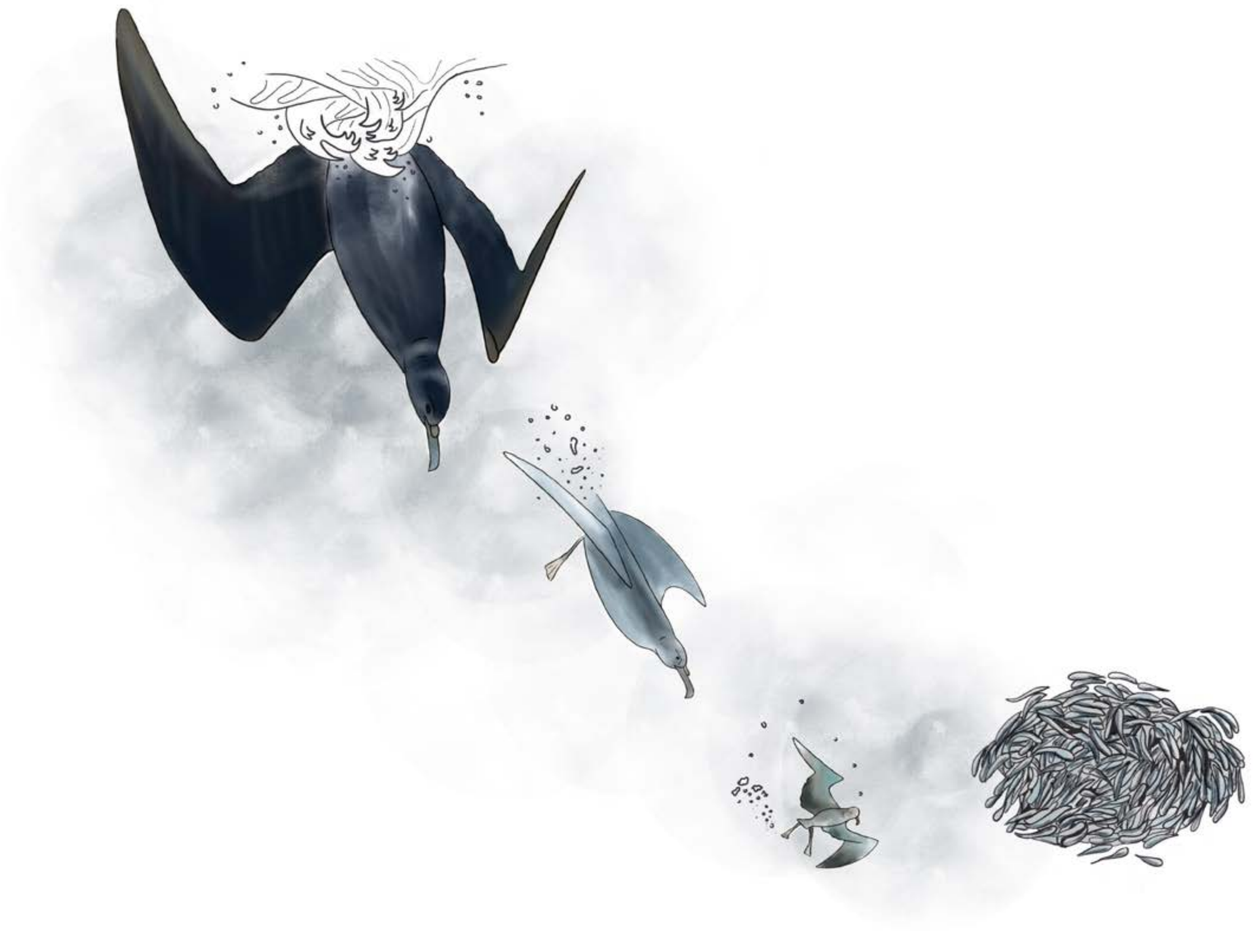
In **Chapter 2**, we compile and analyse a tracking dataset from 13 Spanish breeding colonies of the model species, providing an extensive and rigorous overview of the spatial ecology and migratory patterns of the Spanish populations of the model species. This chapter contributes to objectives 2 and 5.

In **Chapter 3**, we investigate the influence of the environment and fishery activity on the foraging behaviour of the Scopoli's shearwater, mainly focusing on sexual segregation. This chapter contributes to objectives 2, 3, 4, and 6.

In **Chapter 4**, we investigate the adjustment of foraging strategies over the breeding period, and the role of environmental features as foraging cues, in the Cory's shearwater. This chapter contributes to objectives 2 and 3.

In **Chapter 5**, we illustrate as a proof-of-concept the use of GPS tracking as a tool to inform management in the Spanish National Park Network. This chapter contributes to objectives 2, 5 and 6.

In **Chapter 6**, we combine tracking data with stable isotope analysis to evaluate long-term ecosystem trends in the Canary Current while accounting for the individual specialisation in the Cory's shearwater. This chapter contributes to objectives 3, 4, 5 and 6.



Chapter 1

Natural history of Cory’s & Scopoli’s shearwaters: a literature review

Chapter I is an English version of:

Reyes-González, J. M. & González-Solís, J. (2016). Cory's shearwater - *Calonectris borealis*. In: Enciclopedia Virtual de los Vertebrados Españoles. Salvador, A., Morales, M. B. (Eds.). Museo Nacional de Ciencias Naturales, Madrid. http://www.vertebradosibericos.org/
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Reyes-González, J. M. & González-Solís, J. (2016). Scopoli's shearwater - *Calonectris diomedea*. In: Enciclopedia Virtual de los Vertebrados Españoles. Salvador, A., Morales, M. B. (Eds.). Museo Nacional de Ciencias Naturales, Madrid. http://www.vertebradosibericos.org/
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NATURAL HISTORY OF CORY'S & SCOPOLI'S SHEARWATERS: A LITERATURE REVIEW

INTRODUCTION

This chapter introduces the species models of the thesis. I performed an extensive review of research papers and grey literature about these species published until 2016. The review did not aim to consider every research paper on the species but to provide a general overview of the main features of their natural history. Therefore, some research may not be cited.

CORY'S SHEARWATER (*CALONECTRIS BOREALIS*)

Description

The Cory's shearwater is a typical seabird, with long, slender wings adapted to take full advantage of the winds that frequently blow near the sea surface (González- Solís et al., 2009).

The Cory's shearwater is the largest of the shearwaters that can be found regularly in European waters, with an average wingspan of 126.30 ± 5.33 cm (sample size: 127; authors' data) and an average body mass of 785.80 ± 86.98 g (sample size: 771; authors' data). It is robust, with a rounded head, long wings and a short tail. Dull in colour, it has greyish-brown upperparts, which reach the lower part of the beak, while they are almost entirely white underneath, except for the outer edge of the wings, which is dark. The upper-tail coverts are white-spotted, often forming a narrow band separating the tail from the rump. The strong, long beak is yellowish with a blackish tip and conspicuous nostrils. Legs are pinkish. In some cases, pigmentary anomalies in the plumage have been reported. Bried et al. (2005) report three cases of individuals with aberrant colour, one of them melanic in the Canary Islands, as well as a case of melanism in the Azores Islands.

Compared with the Scopoli's shearwater *C. diomedea* (Thibault et al., 1997), Cory's shearwater is on average 46% heavier and its beak is more robust. The neck shows less contrast with the head and back in Cory's shearwater, giving the impression of being narrower than in the Scopoli's shearwater. The plumage of Cory's shearwaters is generally darker and more contrasted, in particular the underparts, where the dark wing ridge goes further inwards and defines a much more prominent margin than in Scopoli's shearwaters. In Cory's shearwater, the white area of the underwings is restricted to the covert feathers, which gives a rounded shape to this area. In contrast, in the Scopoli's shearwater, the proximal area of the outermost primaries is almost white, creating a wedge-shaped white panel effect, not just formed by the coverts, as in Cory's, but also by the primaries (Cramp & Simmons 1977; Gutiérrez 1998).

The flight of Cory's shearwaters is based on long gliding sequences alternated with active wing flapping, in which energy consumption increases significantly. As wind speed increases, the frequency and duration of flapping sequences decreases and the distance to the surface increases. Individuals always flight near the sea surface, although the flight altitude varies according to the wind speed (Paiva et al., 2010d).

Origin and evolution

The Cory's and the Scopoli's shearwater likely diverged by allopatry following the contraction of their distribution range during the Pleistocene. The Scopoli's shearwater is more closely related to the Cape Verde shearwater *Calonectris edwardsii*, a previously considered subspecies of *C. diomedea* (Gómez-Díaz et al., 2006). Recent gene flow has been reported between Cory's and Scopoli's shearwater, about 3% from the latter to the former, and about 10% from the former to the latter (Genovart et al., 2013b).

Haematological values

Hematocrit, leukocyte and thrombocyte values do not differ between the sexes. There is a positive correlation between the number of leukocytes and physical condition (Bried et al., 2011).

Biometrics

Table 1 includes biometric measurements from several breeding populations of Cory's shearwater.

Geographical distribution and variation

Cory's shearwater breeds in the archipelagos of Azores, Madeira, Selvagens and Canarias (Cramp & Simmons, 1977; Bauer & Glutz von Blotzheim, 1987). Besides, there are two colonies in the Western Mediterranean, one in Chafarinas Islands in North Africa, and a small one on the island of Terreros (Almería) (Gómez-Díaz et al., 2006). The populations of Berlenga, Azores, Salvagens and Canarias show genetic differentiation (Genovart et al., 2013b).

The species has expanded the breeding distribution to the north, with three new colonies located in Galicia in 2007-2008 (Cíes, Sisargas and Coelleira islands), about 500 km north from the nearest colonies in Portugal, the Berlengas Islands. Genetic analysis has suggested that the founding individuals came from various Atlantic colonies. A total of 4-7 chicks per year have been recorded between 2009 and 2013 (Munilla et al., 2016).

Moult

Moulting of rectrices is simple, starting in the centre of the tail and progressing towards the outer ones. It happens mostly in the wintering areas since in March-May the process is advanced but not finished. It is then apparently suspended until August when it is reactivated to be concluded before September in most birds (Monteiro & Furness, 1996). The moulting process and its overlap with the breeding season may be affected by the environmental stochasticity and individual breeding success: non-breeding adults and failed breeders advance the moulting process (Alonso et al., 2009).

Table 1 • Biometric measurements (in mm) of the Cory's shearwater. Numbers within brackets in the first column indicate sample size for males and females. Measurements indicate mean ± standard deviation.

Breeding colony	Tarsus		Wing		Head-bill length	
	♂	♀	♂	♀	♂	♀
Gran.Canaria- Canary Is. - Spain (81; 87)	57.82 ± 1.54	56.07 ± 1.20	367.78 ± 7.66	360.98 ± 6.86	114.43 ± 2.82	108.94 ± 2.37
Lanzarote - Canary Is - Spain (14; 11)	59.21 ± 1.37	56.77 ± 1.42	374.28 ± 9.77	366.91 ± 0.62	115.95 ± 2.69	111.72 ± 2.84
Tenerife - Canary Is - Spain (4; 5)	57.84 ± 1.21	55.97 ± 0.97	368.25 ± 12.76	360.40 ± 2.88	115.03 ± 1.44	109.35 ± 1.46
Almería - Spain (12; 16)	58.66 ± 1.85	56.19 ± 1.51	372.83 ± 6.51	366.00 ± 5.25	112.43 ± 4.37	109.28 ± 3.17
São Miguel- Azores Is. - Portugal (6;4)	59.70 ± 0.97	57.72 ± 1.75	373.50 ± 10.27	366.50 ± 3.87	117.44 ± 1.52	111.57 ± 0.86
Graciosa - Azores Is. - Portugal (13; 13)	59.66 ± 1.42	56.69 ± 1.23	375.85 ± 6.56	361.15 ± 5.81	116.88 ± 1.19	110.00 ± 2.45
Flores - Azores Is. - Portugal (5; 3)	60.42 ± 1.40	57.88 ± 2.24	376.80 ± 7.19	365.67 ± 4.04	118.22 ± 3.30	112.85 ± 1.51
Corvo - Azores Is. - Portugal (12; 10)	58.75 ± 1.28	56.64 ± 2.02	373.08 ± 6.58	364.30 ± 8.42	116.72 ± 2.82	111.48 ± 3.23
Faial- Azores Is. - Portugal (8; 5)	59.59 ± 1.24	56.65 ± 0.95	373.38 ± 6.70	361.60 ± 6.50	116.23 ± 3.02	111.52 ± 1.18
Madeira - Portugal (9; 17)	59.26 ± 1.74	56.92 ± 2.34	373.11 ± 7.23	362.71 ± 7.06	119.24 ± 1.98	111.48 ± 3.80
Berlengas - Portugal (12; 9)	59.33 ± 1.37	57.75 ± 1.97	375.58 ± 7.01	364.11 ± 6.17	116.88 ± 2.31	111.21 ± 2.12
Mean	58.70 ± 1.66	56.49 ± 1.50	371.04 ± 7.88	362.56 ± 7.28	115.89 ± 3.14	110.10 ± 2.67

Table I bis • Biometric measurements (in mm) of the Cory's shearwater. Numbers within brackets in the first column indicate sample size for males and females. Measurements indicate mean ± standard deviation.

Breeding colony	Bill length		Bill height		Bill height (including nostril)	
	♂	♀	♂	♀	♂	♀
Gran.Canaria- Canary Is. - Spain (81; 87)	55.43 ± 2.08	52.38 ± 1.69	21.34 ± 0.74	19.20 ± 1.17	15.56 ± 0.73	14.17 ± 0.74
Lanzarote - Canary Is - Spain (14; 11)	55.14 ± 1.91	53.35 ± 2.42	21.39 ± 0.99	19.79 ± 0.82	15.58 ± 1.04	14.23 ± 0.70
Tenerife - Canary Is - Spain (4; 5)	54.78 ± 0.63	51.65 ± 0.72	20.79 ± 0.97	18.98 ± 0.61	15.11 ± 0.81	13.50 ± 0.47
Almería - Spain (12; 16)	53.27 ± 2.50	51.40 ± 2.15	21.21 ± 1.47	19.05 ± 1.03	15.47 ± 1.19	14.10 ± 0.93
São Miguel- Azores Is. - Portugal (6;4)	56.39 ± 1.37	53.50 ± 1.21	21.88 ± 0.58	19.86 ± 0.86	16.40 ± 0.50	14.82 ± 0.62
Graciosa - Azores Is. - Portugal (13; 13)	55.59 ± 1.17	51.94 ± 1.77	21.14 ± 0.58	19.23 ± 0.39	15.56 ± 0.45	14.14 ± 0.49
Flores - Azores Is. - Portugal (5; 3)	57.50 ± 1.80	54.02 ± 0.73	21.07 ± 0.92	19.53 ± 0.78	15.52 ± 0.87	14.53 ± 0.70
Corvo - Azores Is. - Portugal (12; 10)	55.77 ± 2.09	53.34 ± 1.59	21.35 ± 0.90	18.93 ± 1.03	15.43 ± 0.84	13.98 ± 0.95
Faial- Azores Is. - Portugal (8; 5)	55.57 ± 2.47	52.98 ± 1.86	21.65 ± 0.37	21.21 ± 1.47	15.71 ± 0.49	14.33 ± 1.09
Madeira - Portugal (9; 17)	57.52 ± 1.42	52.86 ± 2.26	21.68 ± 0.58	19.45 ± 0.99	15.49 ± 0.85	14.08 ± 0.88
Berlengas - Portugal (12; 9)	56.83 ± 1.37	52.98 ± 1.85	21.94 ± 0.86	19.60 ± 0.86	16.01 ± 0.55	14.43 ± 0.71
Mean	55.79 ± 2.08	52.61 ± 1.79	21.49 ± 0.86	19.42 ± 1.02	15.74 ± 0.85	14.25 ± 0.76

Sexual dimorphism

There is a slight but clear sexual size dimorphism (Hughes, 1993; Bretagnolle & Thibault, 1995). Males are on average 10% heavier than females. In a sample from Gran Canaria Island, males had an average body mass of 789 g (sample size: 38) and females 709 g (sample size: 35) (Navarro et al., 2009c). Head and width of head and beak are the best discriminant features between sexes, being greater in males (Hughes, 1993). Likewise, the upper tip of the beak, the anterior end of the upper unguicorn (tip of the upper jaw), is more developed in males (Navarro et al., 2009c).

Voice

Individuals are often silent at sea, while noisy at the colony during the breeding season. The call of Cory's shearwaters has three syllables while that of the Scopoli's has two. The structure of calls is more severe in females (Bretagnolle & Lequette, 1990). They use acoustic signals in intra-sexual competition when males compete for nests and females for males (Bretagnolle & Lequette, 1990). Males respond to calls in recording experiments more from other males than to calls from females, suggesting the use of vocalizations as a nest defence behaviour (Bretagnolle & Lequette, 1990). Males and females respond more to their partner than to other individuals of the opposite sex, suggesting that they identify with each other (Bretagnolle & Lequette, 1990).

Activity and social behaviour

An essentially diurnal species, they move mostly during the day, while resting on the water most of the night (Passos et al., 2009; Catry et al., 2011). However, during periods such as migration or breeding, birds also show nocturnal activity. The eminently nocturnal activity in the colonies surely responds to an anti-depredatory strategy (Mougin et al., 2000a). Activity patterns vary across oceanographic regions, depending on water temperature and bathymetry, which are indirectly related to the type of prey that can be captured near the water surface. Shearwaters wintering in warm, shallow seas of the Benguela, Agulhas and Brazil currents are mostly diurnal while those that wintered in colder, deeper seas of the northwest Atlantic and central South Atlantic are more nocturnal (Dias et al., 2012b, Reyes-González, 2017). In their breeding colonies, their activity is entirely nocturnal, arriving and leaving the colony exclusively at night. Birds from Salvagens Islands are the only exception, as there the birds present both daylight and darkness activity (Dell'Ariccia & Bonadonna, 2013). Concerning their behaviour at sea, there are differences between ages likely related to individual immune status or to experience. Catry et al. (2011) indicate that older individuals (> 26 years) show lower levels of activity at sea compared to younger individuals (13 - 20 years), spending less time foraging and more time resting on the water. Missagia et al. (2015) found that experienced individuals fed more frequently in neritic waters, while inexperienced individuals tended to exploit more pelagic habitats.

Nesting habits

Individuals only visit land during the breeding season. It is a gregarious species, especially during breeding. Shearwaters breed colonially, on islands, islets and coastal cliffs, in areas originally free of terrestrial predators. Nests are located in burrows and crevices, often within limestone or volcanic caves, under debris, in small galleries, or even in burrows built by rabbits (Furness et al., 2000). In places with no or very low predation levels, such as in the Selvagens Islands archipelago, burrows may be short and even open, while in colonies with high predation rates, they are usually longer and narrower. At least in the Canary Islands, there is evidence that this species also breeds in abrupt areas inland (Martín & Lorenzo, 2001), a fact that must have been more common in the past, before the human occupation of the archipelago and the consequent hunting and introduction of foreign predators.

Foraging at sea

Cory's shearwaters forage in the open sea, in warm or temperate waters, in areas productive enough to supply their food requirements, mainly in neritic zones on the continental shelves but also in pelagic areas. The species is often associated with nutrient-rich areas such as oceanic fronts, upwellings, or continental shelves (Paiva et al., 2010a). During the breeding season, the marine habitat they exploit may vary. Due to the location of their colonies, adult breeders are forced to return to the nest to incubate or to feed the chick after spending several days at sea searching for food (a strategy known as central-place foraging). This factor determines the extent of the foraging movements during breeding. Birds from different breeding colonies can cope with this constraint using two different strategies, depending on the colony location. When resources in the neritic waters near the colony are scarce, shearwaters use a bimodal strategy during the chick-rearing phase, when feeding the highly demanding duty of feeding the offspring takes place. This bimodal strategy alternates short trips (less than 5 days) to waters near the colony to obtain food to feed the chick, with long self-maintenance trips in highly productive areas, often far away from the breeding colony (Paiva et al., 2010a). This is the case of Cory's shearwaters breeding in Azores and Selvagens (Paiva et al., 2010b, 2010c). However, other populations, such as those breeding in the Canary Islands, seem to not use this strategy, but instead engaging in fewer but longer trips, foraging always in the highly productive areas along the coast of Morocco and Western Sahara, relatively close to the Canary Islands (Navarro & González-Solís, 2009). Several studies have highlighted the strong dependence of populations from the Canary and Selvagens archipelagos on the Canary Current, one of the most important upwelling systems in Africa (Fig. 1) (Paiva et al., 2010b; Navarro & González-Solís, 2009, Ramos et al., 2013). Birds from Madeira, Selvagens and Canarias exploit the northwest African continental shelf, but with spatial segregation between colonies in the foraging grounds used along the Canary Current, although there is some overlap among them (Ramos et al., 2013).

In the western Mediterranean, in the colony of Chafarinas Islands, where Cory's and Scopoli's shearwaters breed, during incubation individuals from the former species forage mostly over the continental shelf, in waters surrounding the colony, overlapping with foraging grounds of the latter (Afán et al., 2014; Navarro et al. 2009b).

It is known that experience influences habitat use and migratory behaviour. Birds with more years of breeding success are less pelagic throughout the year (Haug et al., 2015), have less extensive migration routes, use fewer wintering areas and show higher isotopic nitrogen and carbon values than less experienced birds (Missagia et al., 2015).

Paiva et al., (2013) found that the decline in productivity occurred between 2007 and 2010 in areas near Berlengas Islands (Portugal) caused females breeding there to commute towards the Grand Banks of Newfoundland to forage during the pre-laying phase, almost 4 000 km away, which led to a decrease in body condition and hatching success.

Trophic ecology

The species feeds on epipelagic fish such as anchovies (*Engraulis encrasicholus*) and horse mackerel (*Trachurus trachurus*), as well as cephalopods and crustaceans to a lesser extent (Lipinski & Jackson, 1989; Xavier et al., 2011). Consumption of flying fish (family *Exocoetidae*) has also been reported (Moore, 1995). Xavier et al., (2011) pointed out inter-annual variability in diet composition related to changes in the annual availability of different prey species driven by changes in oceanographic conditions. Stomach washing in 959 individuals from the Azores pointed out that shifts in diet can occur between different areas, throughout the reproductive cycle and between years. 37 species of cephalopods and 33 species of fish were reported in the diet. *Trachurus picturatus* was the most abundant prey in some years but was not found in others (Neves et al., 2012). In a diet analysis in the Azores during the breeding season, Granadeiro et al. (1998b) found fish in about 90% of the stomach contents analysed, while cephalopods appeared in 25% and crustaceans in only about 5%. Den Hartog & Clarke (1996) in a sample of 26 birds from the Canary, Selvagens and Azores archipelagos, found a high frequency of consumption of cephalopods, highlighting the genera *Ommastrephes* and *Histioteuthis*. In Selvagens, according to a study based on prey items collected in 2018, the diet is mainly composed of fish and cephalopods. The most abundant fish was *Scomber colias*/sp. Other abundant fish in the diet were *Naucrates ductor*, *Sardina pilchardus* and flying fish (*Exocoetidae*). In total, the list of fish in the diet consisted of 33 species from 20 families. The most common cephalopods in the diet were *Ommastrephes bartramii* and *Histioteuthis arcturi*. Ten other species of cephalopods were found in the diet. Crustaceans of the order Isopoda and insects of the family *Halobatidae* were also found (Alonso et al., 2014). Analysis of stable nitrogen and carbon isotope ratios indicated the existence of trophic niche segregation between breeding adults and immatures and non-breeding adults in Selvagens. Active breeders would feed more on fish while non-breeding adults and immatures would feed more on cephalopods (Campioni et al., 2016). The degree of trophic segregation between adults and chicks, measured by isotope analysis, varies between colonies. In Selvagens, adults feed the chicks with a mix of pelagic and coastal prey, while adults exploit more coastal prey. In contrast, in the Berlengas, segregation is lower (Alonso et al., 2012). In the Azores, partial segregation in foraging areas between adult breeders from nearby colonies has been reported, although no differences were found in the type of habitat used or diet (Ceia et al., 2015). Cory's shearwater is also able to take advantage of fishing discards, although not in all populations (Bugoni et al., 2010).

Cory's shearwater can use smell to detect productive areas. Dell'Ariccia et al. (2014) showed with an experimental design that individuals can discriminate dimethyl sulphide, a gas produced by phytoplankton.

To capture their prey, they are able to dive by propelling themselves with the wings. In general, the diving bouts are short (in neritic zones: 3 s of average and maximum of 17 s; in oceanic zones: 4.9 s of average and maximum of 32 s), and shallow (in neritic zones: 1.3 m of average and maximum of 4.9 m; in oceanic zones: 2.6 m of average and maximum of 9.8 m) (Paiva et al., 2010b).

Migration

Cory's shearwaters engage in long-distance transequatorial migrations. The onset of the post-breeding migration takes place between mid and late October when the breeding season is over. Birds will remain away from the breeding areas for about 100 days on average, spending on average about 80 days in the wintering areas and migrating. The pre-breeding migration starts mostly in February, arriving at the breeding areas during February and March (Dias et al., 2012a).

Cory's shearwaters from Spanish populations migrate to different wintering areas. The Namibian coasts and the Benguela Current represent the main area (40.5%), followed by the Agulhas Current (21.5%), the confluence of the Agulhas and Benguela Currents (13.5%), the Canary Islands Current (11.5%), Brazilian waters (10%) and South Central Atlantic waters (3%). None of the Spanish colonies, in six years of study, visited the northwest Atlantic for wintering (Reyes-González et al., 2017). However, in the population breeding in the Salvagens Islands, 4% of the animals also use this last area (Dias et al., 2012a). During migration, they use one or two stopovers that last on average seven days (range of 1-31 days). Birds that do not use stopovers migrate faster than those that use them (535 km/day vs 428 km/day on average, respectively). Birds that leave the breeding colony later migrate faster than those that leave earlier. In total, the average speed in the post-breeding migration for birds from Salvagens was 429 km/day, and 644 km/day on the way back in the pre-breeding migration (Dias et al., 2012a). When they are on migration, they spend 50% of their time flying and do so much more during the day than at night. Moon phases affect migratory activity, flying more on full moon nights (Dias et al., 2012a).

The sense of smell plays an important role in orientation during navigation. In an experiment, individuals of Cory's shearwater breeding in Azores -where birds' activity is exclusively nocturnal- were temporarily deprived of their olfactory capacity and displaced 800 km from the colony. They were unable to homing (Gagliardo et al., 2013). In contrast, in a similar experiment with individuals from Selvagens, the unique population where birds are active in both day and night, birds were unable to return at night, and wait until the day for homing (Dell'Ariccia & Bonadonna 2013).

Fidelity to wintering areas is very high. In Spanish populations, about 77% of the animals, followed for up to six years, had only one wintering area. Only 22% presented two wintering areas, and just around 1% wintered in three different areas. On average, individuals from Spanish populations presented a spatial overlap of more than 60% between years in their wintering areas (Reyes-González et al., 2017). Birds from Selvagens Islands showed individual consistency between years in the flyway used during the post-breeding migration, between 10°N and 20°S, but not further south neither in the pre-breeding migration (Dias et al., 2010; Dias et al., 2013).

The species presents partial migration since a small number of individuals remain every winter in the area near the breeding colony. In the Spanish populations, 11.5% of the animals (sample size: 237) that breed in the Canary Islands remains in the Canary Current during the wintering months (Reyes-González et al., 2017). 8.1% of the individuals tracked from Selvagens (sample size: 172) remained in waters close to the colony, in the vicinities of the Canary Current (Pérez et al., 2014), being almost all of them males. Those males shifted their strategy over the years between remaining near to the breeding area and migrating to the southern. Males remaining near the breeding area occupied the nest earlier than those that migrated (Pérez et al., 2014).

The stress response, measured through levels of corticosterone in feathers, varies between sexes, years and migratory strategies. They were higher in males than in females and higher in males that migrated to wintering areas far from the colony compared to those they remained nearby. Also, birds that accumulated higher levels of corticosterone in winter were more successful in breeding (Perez et al., 2016).

The level of parental investment and conditions during a breeding season influences the subsequent migration, especially the timing, with effects extending to the next breeding season. Birds with lower breeding investment, i.e. those that failed at breeding, started both the postnuptial and the prenuptial migration earlier, returning to the breeding colony earlier in the following spring. A greater proportion of failed males remained closer to the breeding area for wintering, suggesting that partial migration is condition-dependent. The probability of nesting the following year was higher in birds that failed to breed (Catry et al., 2013).

The complete migratory trip from breeding to wintering areas and way back can range from 15000 and 35000 km and can follow several strategies. In essence, their journeys describe a loop over the Atlantic. Some wintering areas are shared with Scopoli's shearwaters, although in clearly different proportions (González-Solís et al., 2007).

The factors modulating individual decision-making on migratory strategies are still unclear, although wind seems to be the most influential feature governing the choice of route and migratory timing. Cory's shearwaters take advantage of prevailing winds to reduce energy costs despite these winds may lead to longer flyways. These prevailing winds also blow more intensively in specific time windows of the year, which likely explains the migratory flyway in 8-shape of Cory's shearwaters crossing the Atlantic Ocean twice a year to reach the Benguela and Agulhas currents in the South Atlantic (Felicísimo et al., 2008).

Dispersion

The species is highly philopatric. Nevertheless, its great migratory capacity and the mix of individuals from different breeding populations in the wintering areas suggest that some individuals could migrate and arrive in a colony different from that where they were born, leading to a small gene flow among populations (González-Solís et al., 2007). In this regard, the proportion of males that first reproduced on Selvagem Grande and were born there varied between years from 42.4% to 63.9% (Mougin et al., 2000c). There are numerous cases reported of Cory's shearwaters breeding in colonies of Scopoli's shearwaters (Lo Valvo & Massa, 1988; Granadeiro, 1991; Igual & Afán, 2005; Sánchez, 1997; Thibault & Bretagnolle, 1998; Gómez-Díaz et al., 2009). Genetic analyses suggest that 90 individuals from every generation would migrate from a Cory's to a Scopoli's shearwater colony, and 55 individuals would do it in the opposite direction (Genovart et al., 2013b).

Reproduction

After migration from the wintering areas, birds arrive at the breeding sites between late February and early March, when large groups of individuals start to aggregate in the vicinities of the colonies and visit them (Thibault et al., 1997). After arrival, the individuals start a physiological process degrading muscle tissue and increasing lipid reserves to recover and improve body condition eroded by migration and prepare for reproduction (Arizmendi-Mejía et al., 2013).

Cory's shearwater is a highly monogamous species, with pair bonds remaining for years. Extra-parental copulations are very rare (Rabouam et al., 2000), and when they happen, it is usually related to a lack of suitable nesting sites in the colony and males of low body size (Bried et al., 2010). In Selvagens, a divorce rate of 6% was recorded during the period 1980-1985 (Mougin et al., 1987). Between 1980 and 1998 an average divorce rate of 11.4% was recorded. However, notable individual differences were observed. For instance, one couple was observed breeding together for 18 consecutive years, while at the other extreme a bird was divorced twice and replaced its absent partner during nine seasons. (Mougin et al., 2000c). Additionally, the probability of divorce increase after a reproductive failure in the previous year (Mougin et al., 2000c). In early March, pairs are (re-) established and occupy the nesting sites (Granadeiro, 1990). Birds compete for nesting sites. Deeper nests have higher quality, and are more frequent in areas of higher density of breeding pairs in the colony (Ramos et al., 1997; Werner et al., 2014). According to Granadeiro et al. (1998a), the choice of partner and fidelity is not based on physical or behavioural traits, but on previous knowledge between individuals. However, a negative correlation has been found in bill height and length between paired males and females. Females with higher and longer bills are paired with males with lower and shorter bills (Nava et al., 2014). Mating is typically followed by a more or less massive exodus of all individuals from the colony. The colony is visited during this time always at night and especially by the male (except for Selvagens where this also occurs in the late afternoon; Hamer & Read, 1987; Mougin et al., 2002), who defend their burrows until the moment in which female lay the egg. From mating to egg-laying, females visit the nest less frequently than males, in some cases being at sea up to 20 days in the pre-laying phase, a period commonly referred to as pre-laying exodus (Jouanin et al., 2001). During the pre-laying phase, foraging trip time duration (1-19 days), areas used, distance travelled and trip sinuosity are greater in females than in males, mainly because males mostly engage in short trips near the colony to return to the nest every night and defend it from other males (Werner et al., 2014). Shearwaters can locate their nests in the dark of the night using their sense of smell (Bonadonna & Bretagnolle, 2002).

Egg-laying takes place in late May or early June, immediately after the female returns to the colony from the pre-laying exodus. Every female lays a single egg a year. Females do not lay a new egg in the case of lost clutch. Heavier females have a later laying date (Nava et al., 2014). Laying is highly synchronised between females in the same colony (Zino et al., 1987; Ramos et al., 2003; Giudici et al., 2010). According to Mougin (1998), the white egg has an average weight of 100 g (69.3-129.4 g) in the Selvagens Islands population, which represents 12% of the body mass of the females from that population. In addition, egg size correlates positively with both female size and breeding experience. In the Canary Islands, eggs have an average length of 74.72 mm and a width of 47.29 mm (Militão, T., Navarro, J. & González-Solís, J., unpublished data). In the case of the Canary Islands, incubation stints take 7-12 days, although in years with poor productivity, they can be exceptionally long, up to 20 days (Reyes- González, J. M., Militão, T., González-Solís, J., unpublished data). The foraging effort of adult breeders varies throughout the breeding season, increasing in the days before laying and during the chick-rearing (Navarro et al., 2007, Reyes-González et al., 2017). The breeding effort of the parents can affect the physiology of the chick. There is a correlation between corticosterone levels in the offspring and the duration and efficiency of foraging trips of the male, whereas such correlation in the case of females is lower (Fairhurst et al., 2012).

Hatching takes place in mid-July, although in later pairs it may be delayed until early August. Zino et al. (1987) recorded a hatching rate of 65.3% in Selvagens. In Veneguera (Gran Canaria) the breeding success (i.e., the number of pairs that successfully raised a chick related to the number of pairs that laid an egg), is 30-60%, and largely depend on the annual impact of rat predation on eggs and chicks (authors' data). The species is nidicolous and semi-altricial. The chick opens the eyes from the first day. It is homogeneously covered with greyish-brown down, except on the flanks where it is less thick. The chick is cared for by both parents during the first few days. The number of days the chick remains unattended varies depending on the time that parents need to obtain food (Catry et al., 2009). Chick feeding takes place only at night when parents return from the sea after foraging. As chick development advances, parent attendance shifts are spaced out and the chick remains increasingly more time alone at the nest.

Adult breeders need to return to the colony to feed the chick after foraging at sea for several days (i.e., central place foraging). This factor determines the extent of the foraging movements during the breeding period, and adult breeders from the different populations cope differently according to the location of their breeding colony. Two main strategies have been proposed in this sense. When resources in the neritic waters near the colony are scarce, individuals use a bimodal strategy, so they alternate short trips (less than 5 days) and long trips. During the short trips, birds forage in the waters close to the colony to obtain food for feeding the chick. The long trips are aimed at adult self-provisioning, commuting towards highly productive areas often far away from the breeding colony (Paiva et al., 2010a). This is the case of Cory's shearwaters breeding in Azores and Selvagens (Magalhaes et al., 2008; Paiva et al., 2010b, 2010c). In Selvagens, 79% of the chicks on average were fed every day (Hamer & Hill, 1993). In the Azores, for example, adults combined several short trips (up to 75 km from the nest) of 1 to 4 days that were followed by a long trip of 9 days on average (up to 1800 km from the nest), so that the chicks may spend up to 9 days without being attended (Magalhães et al., 2008). In the Canary Islands, long trips may be longer (Reyes-González et al., 2017). Chicks remain in the nest up to 90-99 days until fledging. During this time, the average rate of mass gain is 25 g per day (Klomp & Furness, 1992). According to Jones (1986), there is high synchronicity in the growth rate of chicks from nests located less than 3 m apart and in general from the same cohort. Adults return to the waters surrounding the colony at dusk, waiting the night to visit the nest and feed the chick. While waiting at sea birds form large rafting groups, with hundreds of individuals. These "rafts" also occur from the onset of the breeding period, the time before birds start to visit the nests. During full moon nights, parents decrease the frequency of visits to feed the chick or even delay them to further nights (Klomp & Furness, 1992). Fledging takes place in late October. During the previous weeks, the parents progressively reduce nest attending and chick caring and finally leave the chick alone. This moment entails the highest rate of chick mortality. According to Mougin et al. (2000b), the weight of fledglings when they leave the nest determines their survival probability, because greater fat reserves allow them to face the first migratory journey in better conditions.

As in other Procellariforms, adults of both sexes may take "sabbatical" years, i.e., years in which an adult do not attempt to breed (Mougin et al., 1997). Based on studies in the Canary Islands, Giudici et al. (2010) have suggested that fat stores and immune status may be the most important components in the individual decision to attempt breeding. The proportion of adults taking sabbatical years may be greater in Cory's shearwaters than in other related species. Mougin et al. (1996) quantified that every year 10% of a studied population from Selvagens do not engage in breeding, and estimated that this break lasts an average of 1.7 years, although in some individuals it can be as long as 7 years. When individuals attempt to breed after a sabbatical season, they usually pair with a new couple and use a different nest, as the previous is rarely available again, in particular, if the sabbatical period lasted more than one breeding season. Mougin et al. (1997) reported that 20.4% of males and 13.6% of females used their old same nest with their same couple when they again attempted to breed after a sabbatical season, but 30.8% of the males and 26.0% of the females changed couple or nest, and 48.8% of the males and 60.4% of the females changed both couple and nest. Other research indicates that these results cannot be generalised to all colonies. Giudici et al. (2010) recorded in the Canary Islands that 35% of birds ringed as breeders in the previous year were located in the surroundings of the colony but did not breed. Non-breeding floaters may have an important role in the population dynamics since they can replace the missing individuals.

Annual variations in breeding success are related to changes in marine productivity due to climate stochasticity (Paiva et al., 2013). In Selvagens, annual variations in breeding success were reported: the breeding success was 72% in 2009 (sample size: 313), 63% in 2011 (sample size: 290) and 73% in 2012 (sample size: 301) (Perez et al., 2016). In colonies where introduced predators such as rats or cats are present, their annual abundance may also influence overall breeding success of shearwaters.

Population structure and dynamics

Cory's shearwaters from Salvagens Islands start to breed for the first time at the age of 4-13 years (Jouanin et al., 1980; Mougin et al., 1986, 1992; 2000d). The mean age at the first breeding attempt is 8.9 years (Mougin et al., 2000c). Birds' life expectancy in that population was estimated at 22 years (Mougin et al., 1993). The annual survival rate in adults was 92.7%, but higher in females (93.5%) than in males (91.9%), and variable among years (from 84.1% to 98%) (Mougin et al., 1996, 2000c). Positive periods of the Southern Oscillation Index (SOI) may adversely affect the winter survival of Cory's shearwaters. During the breeding season, bycatch in longliners and the higher sea surface temperature may increase mortality rates; the effect of climatic variations on mortality seems to be greater than mortality from bycatch (Ramos et al., 2012).

Population size

Recent estimates point out about 251 100 - 251 300 couples in total (Derhé, 2011). In the Berlengas Islands, there are about 200-250 pairs. In the Azores archipelago about 180 000 pairs, in the Madeira archipelago between 16 500 and 25 000 pairs (BirdLife International, 2004) and in the Selvagens Islands about 30 000 pairs (Granadeiro et al., 2006).

n the Canary Islands, there is a breeding population of Cory's shearwaters estimated in 30 000 pairs (Carboneras & Lorenzo, 2003). In this region, the colonies located at the Chinijo Archipelago are the most important. The main breeding colony (8 000-10 000 pairs) is located on Alegranza Island. The islets of Montaña Clara, Lobos and Lanzarote are home to about 1 000 pairs each. In the Atlantic context but outside the Canary Islands, some incipient reproductive nuclei of small entity have been located recently in small islets off the coast of Galicia, although their viability is being seriously compromised due to the high mortality rate, both in adults and chicks, caused by introduced predators, including minks, rats and cats (Munilla & Velando, 2009).

Conservation status

IUCN global category (2015): Least Concern LC (BirdLife International, 2015). IUCN Spain category (2002): Vulnerable VU A3d+4d (Lorenzo, 2004).

In Spain, the species is included in the List of Wild Species under Special Protection (Real Decreto 139/2011), although the Scopoli's shearwater is also included in the Spanish Catalogue of Threatened Species under the category of "Vulnerable" (Real Decreto 139/2011). At the European level, the species is included in the category SPEC 2.

In general, the species presents from a regressive trend, despite the conservation measures carried out over the last two decades. This generalised regression is caused by different reasons.

Threats and conservation measures

Bycatch

Incidental bycatch, especially related to longlining, seems to be the main cause of unnatural mortality of the species, both in breeding and wintering areas (Cooper et al., 2003; ICES, 2009). As a long-lived species with one single chick per year, the mortality of adult breeders can cause serious decline in a short period, similarly to what has been shown in the Balearic shearwater (*Puffinus mauretanicus*) (Oro et al., 2004). During the wintering period in more southern waters, the species is also affected by fishing activity, although to a much lesser extent (Bugoni et al., 2008). The gradual implementation of techniques that reduce mortality has been proposed to minimize bycatch: night setting (Sánchez & Belda, 2003), scarecrow lines, and tinted bait, among others.

Overfishing

Overfishing can reduce resource availability, leading to a negative effect on seabird populations. However, this effect has not yet been confirmed on Cory's shearwater.

Alien species

Introduced species such as feral cats (*Felis catus*), rats (*Rattus* sp.) and mice (*Mus musculus*, *Apodemus sylvaticus*) on islands and islets have decreased population size and in some cases even led to the extinction of some colonies. Traveset et al. (2009) reported a reproductive failure rate of 53% in a set of 80 nests monitored in Gran Canaria, by direct predation of rats and mice. In Corvo Island (Azores), black rats (*Rattus rattus*) often supplement their diet by feeding on eggs and chicks of Cory's shearwater. Five out of six chicks recorded with cameras were predated by cats and one by a black rat (Hervias et al., 2014). In 2010, 23 adult deaths were recorded in the Sisargas Islands (Galicia, Spain), probably due to feral cats abandoned on the islands (Munilla et al., 2016). Control measures of alien predators have shown positive results on shearwater population dynamics (Donlan & Wilcox, 2008). In the Chafarinas Islands, where the density of rats was high, rat extermination was correlated with an increase in the productivity of the colony (Igual et al., 2006a, 2006b). Rabbits (*Oryctolagus cuniculus*), also introduced to some islands and islets, compete with Cory's shearwater for small galleries and burrows (Carboneras, 2004). On some islands, especially in the Canary Islands, competition with rabbits for nesting burrows has led to a decrease in the reproductive success of some colonies (Lorenzo, 2004). Active eradication measures have been taken to remove rabbits from some islands such as Montaña Clara (Lanzarote), where an important population of Cory's shearwater breeds (Martín et al., 2002). In Selvagens Islands, following the eradication of rabbits and mice in 2002, the number of chicks fledging successfully was 20-40% higher than in the thirteen breeding seasons before starting the control measures (Zino et al., 2008).

Light pollution

The increasing amount of artificial lights derived from new buildings on the coastline is a serious threat for shearwaters (Lorenzo, 2004; Rodríguez et al. 2012). In the Canary Islands, hundreds of fledglings are grounded by light pollution. As a consequence, they may end up colliding with buildings and electrical lines or be injured by dogs and cats. A 9-year long study indicated that about 9 000 fledglings of Cory's shearwaters were affected by this problem in Tenerife Island, and 95% of them were recovered and returned to the natural environment

(Rodríguez & Rodríguez, 2009). Mortality is higher in the colonies located in the interior of the islands (Rodríguez et al., 2015). Late fledglings are more susceptible to collisions (Rodríguez et al., 2012). Local organisations and the Government are tackling this problem by capturing and caring for grounded individuals while involving the citizens as volunteers in the process.

Marine pollution

In the wintering area of the Brazilian Current, plastic debris has been found in the stomach of 87% of analysed birds (Petry et al., 2009). Such accumulation of plastics in the stomach could cause negative effects on birds, although to date no studies have proved this fact. Moreover, pieces of plastic are transferred to chicks during the feeding. 83% of fledglings grounded by light pollution in the Canary Islands had an average of eight plastic fragments in their stomachs (Rodríguez et al., 2012).

As a top-predator, Cory's shearwater is susceptible to bioaccumulation of contaminants present in the marine environment. For example, Monteiro et al. (1998) demonstrated elevated mercury levels in blood in the population of Azores. Also in the Azores, Stewart et al. (1997) found comparatively higher levels of cadmium than those described in other seabirds. Renzoni et al. (1986) found lower levels of mercury, hexachlorobenzene, DDE and PCBs in Cory's than in Scopoli's shearwaters. Roscales et al. (2010) showed that the amount of organochlorine compounds in the blood is higher in Scopoli's than in Cory's shearwater.

Poaching

Poaching for human consumption is almost eradicated. However, this currently illegal practice has been traditionally very common in the islands (Martin & Lorenzo, 2001), at least since the time of the aborigines in the Canary Islands (Rando et al., 1997). The capture, mainly of chicks, was aimed at consumption but also to harvest oil and feathers. Martín & Lorenzo (2001) indicated around 6 000-8 000 shearwaters captures in Alegranza in the first half of the 20th century (7 500 chicks captured in 1926). Cases of occasional human consumption of chicks are still recorded in some localities of the Canary Islands.

Interactions with other species

At sea

Events of the spatio-temporal concurrence of Cory's shearwaters, dolphins and tunas during fishing episodes are likely to occur on a regular basin (Evans, 1986; Morgan, 1986; Martin, 1986). The phenomenon has been described in detail in the waters of the Azores archipelago (Steiner, 1995), although it has also been observed in other areas. During the summer, these productive waters hold large concentrations of fish. Usually, around the dawn and dusk, groups of common (*Delphinus delphis*), spotted (*Stenella frontalis*) and sometimes bottlenose dolphins (*Tursiops truncatus*), start strategic fishing, cornering from different fronts a large school of fish. The activity near the surface attracts numerous Cory's shearwaters, which congregate on the surface. The jumble triggers fish together until a compact shoal of hundreds to thousands of fish is formed near the surface. At some point, the dolphins begin to charge from down, while shearwaters start diving from the surface to catch fish. Often large tunas (*Thunnus thynnus*, *Thunnus albacares*, *Katsuwonus pelamis*) join the fishing action. Other seabirds can also join them, such as Great shearwaters (*Ardenna gravis*), Madeira's petrels (*Oceanodroma castro*), Bulwer's petrels (*Bulweria bulwerii*), terns or gulls. In a short lapse of time, most of the fish are consumed (Martin, 1986).

On land

The nests, especially when they are occupied, represent suitable habitat for numerous species of invertebrates. In Selvagem Grande, mites, spiders, pseudocorpions, crustaceans (*Oniscoidea*) and insects (Formicidae, Coleoptera, Diptera and Tisanura) have been reported in nests (Wheater, 1986).

The predation of eggs of Cory´s shearwater by reptiles and predation on newly hatched chicks by lizards (*Teira dugesii*) were reported in Selvagens (Thibault et al., 1997, Matias et al., 2009). Chick predation by buzzards (*Buteo buteo*) was observed in Azores (Ramos et al., 2003). Nevertheless, the strongest effect both on eggs and chicks, and overall reproductive success of shearwaters, is caused by introduced predators, such as rats and cats (Thibault, 1995; Igual et al., 2006a, 2006b).

In the Chafarinas Islands, the proportion of Cory's to Scopoli's shearwaters has increased from 6% to 23% from 2000 to 2010, and 14% of pairs monitored were mixed pairs (Genovart et al., 2013b).

Parasites and pathogens

The ectoparasite community of the species includes three species of lice (*Halipeurus abnormis* and *Saemundssonia peusi* (family *Philopteridae*), and *Austromenopon echinatum* (family *Menoponidae*)), and one flea species (*Xenopsylla gratiosa*, family *Pulicidae*) (Gómez-Díaz et al., 2007, 2008). Mites present in the species are *Microspalax brevipes*, *Microspalax ardennae*, *Zachvatkinia ovata*, *Rhinozachvatkinia calonectris*, *Promegninia calonectris* and *Ingrassia calonectris, Brephosceles puffini*, and a new species of genus Plicatalloptes (Stefan et al., 2015; Stefan, 2016), although the prevalence and abundance of each vary between individuals and colonies. Regarding endoparasites, the following species have been identified in birds from the Azores: nematodes (*Seuratia shipleyi*, *Contracaecum rudolphii*, *Thominx contorta*), cestodes (*Tetrabothrius minor*), trematodes (*Cardiocephalus physalis*), *Phthiraptera Ischnocera* (*Halipeurus abnormis*), *Phthiraptera Amblycera* (*Austromenopon echinatum*), Siphonaptera (*Xenopsylla graciosa*) and mites (*Ixodes ricinus*, *Haemaphysalis punctata*) (Hervias et al., 2013). Reproductive success decreases with predator activity and ectoparasite intensity (Hervias et al., 2013).

SCOPOLI'S SHEARWATER (*CALONECTRIS DIOMEDEA*)

Description

The Scopoli's shearwater looks very similar to Cory's shearwater, though on average it is slightly smaller and the beak is less robust. The neck shows more contrast with the head and back in Cory's shearwater, thus being apparently wider in the Scopoli's shearwater. The plumage is less contrasted than in Cory's shearwaters because particularly margin defined by the dark wing ridge is much less apparent than in Cory's shearwater. In contrast with the Cory's, in the Scopoli's shearwater, the proximal area of the outermost primaries is almost white, creating a wedge-shaped white panel effect, not just formed by the coverts, as in Cory's, but also by the primaries (Cramp & Simmons, 1977; Gutiérrez, 1998). Ristow & Witte (2004) reported two cases of partial albinism in tail and wing feathers, in both young and adult birds from the island of Crete. The flight strategy is similar to that of Cory's shearwater (Rosén & Hedenström, 2001). The species has an average wingspan of 121.7 ± 3.23 cm (sample size: 127, authors' data) and an average body mass of 646.7 ± 87.10 g (sample size: 199, authors' data).

Origin and evolution

See related content in the corresponding section in Cory's shearwater text.

Haematological values

See related content in the corresponding section in Cory's shearwater text.

Biometrics

Table 2 includes biometric measurements from several breeding populations of the Scopoli's shearwaters. See additional data from Menorca population in Triay & Capo (1996) and from Columbretes in Sánchez & Castilla (1996).

Geographical distribution and variation

The species is endemic to the Mediterranean Sea, where it is present during the breeding season. The populations have a poor genetic structure (Genovart et al., 2013b). A slight increase in body size along an east-west axis from Crete to Chafarinas has been described (Lapichino et al., 1983; Gómez-Díaz et al., 2006), although the populations in Corsica and Sardinia deviate from this pattern, being smaller than the other populations in the western Mediterranean (Massa & Lo Valvo, 1986).

Moult

Adult breeders undertake a complete moult every year. The moult greatly overlaps with the breeding period. The moulting sequence starts in the middle of the incubation period with the replacement of the breast body feathers and progress to the belly and flanks. The moult seems to follow the same pattern in the dorsal area of the body. Moulting the flight feathers lasts about 200 days, between August and March, starting during the chick-rearing phase. Moult of primaries is simple and descending, from the innermost (P1) to the outermost (P10) primary feather. The secondaries show a slightly more complex pattern, with three unsynchronized starting points: the initial focus occurs in the tertiary feathers (around S22), the second approximately in the fifth secondary (S5), and the third in the outermost secondary (S1) (Ramos et al., 2009). Moult of rectrices is simple, starting in the centre of the tail and advancing to the sides; it takes place mostly in wintering areas, but it is apparently suspended during the onset of the breeding season (March-May) and reactivated in August to conclude, in most birds, before September (Ramos et al., 2008, 2009).

Sexual dimorphism

Males of Scopoli's shearwater are slightly larger than females (Wink & Ristow, 1979; Gómez-Díaz & González-Solís, 2007; Lo Valvo, 2001). See related content in the corresponding section in Cory's shearwater text.

Voice

Generally quiet at open sea but noisy at the colony during the breeding season. Scopoli's shearwater has a complex system of vocalizations, with nasal tones in the call of the males, while in the females it is of guttural type (Cure et al., 2009). The call for the contact between the members of the pair is emitted both in flight over the colonies and on the ground and in the nest, although only at night, with some exceptions (Bretagnolle & Lequette, 1990). Females use higher diversity of acoustic parameters than males to vocally identify conspecifics (Cure et al., 2012, 2016). The pair call is disyllabic, whereas it has three syllables in Cory's shearwaters (Bretagnolle & Lequette, 1990).

Table 2 • Biometric measurements (in mm) of the Scopoli's shearwater. Numbers within brackets in the first column indicate sample size for males and females. Measurements indicate mean ± standard deviation. According to Gómez-Díaz & González-Solís (2007).

Breeding colony	Tarsus		Wing		Head-bill length	
	♂	♀	♂	♀	♂	♀
Islas Chafarinas - Spain (29; 30)	56.52 ± 2.02	54.67 ± 2.43	353.86 ± 8.08	347.52 ± 12.57	110.50 ± 3.59	106.65 ± 4.14
Murcia - Spain (9; 4)	57.18 ± 1.04	53.89 ± 1.03	353.67 ± 7.53	346.25 ± 4.19	111.36 ± 2.24	101.96 ± 1.27
Mallorca - Balearic Islands - Spain (24; 21)	54.60 ± 1.69	53.66 ± 2.09	352.79 ± 7.79	349.14 ± 6.05	107.70 ± 3.30	104.85 ± 3.57
Ibiza- Balearic Islands - Spain (23; 22)	55.61 ± 1.26	53.46 ± 1.11	360.04 ± 5.70	347.55 ± 5.84	109.08 ± 2.17	104.38 ± 1.53
Menorca - Balearic Islands - Spain (19; 23)	55.96 ± 1.43	53.29 ± 1.21	359.47 ± 7.22	350.26 ± 5.68	109.17 ± 1.01	103.88 ± 2.71
Crete - Greece (13; 4)	54.14 ± 1.35	52.03 ± 1.64	352.69 ± 6.03	336.25 ± 9.98	108.25 ± 1.40	102.98 ± 1.60
Mean	55.64 ± 1.81	53.77 ± 1.90	355.62 ± 7.73	347.97 ± 8.70	109.25 ± 3.15	104.88 ± 3.34

Table 2 bis • Biometric measurements (in mm) of the Scopoli's shearwater. Numbers within brackets in the first column indicate sample size for males and females. Measurements indicate mean ± standard deviation. According to Gómez-Díaz & González-Solís (2007).

Breeding colony	Bill length		Bill height		Bill height (including nostril)	
	♂	♀	♂	♀	♂	♀
Islas Chafarinas - Spain (29; 30)	52.93 ± 2.04	50.76 ± 3.37	20.38 ± 1.22	18.72 ± 1.29	15.08 ± 0.86	13.52 ± 0.99
Murcia - Spain (9; 4)	52.75 ± 0.73	47.79 ± 1.13	19.96 ± 1.16	17.56 ± 0.64	14.13 ± 0.92	12.14 ± 0.23
Mallorca - Balearic Islands - Spain (24; 21)	50.24 ± 2.14	48.52 ± 1.45	19.18 ± 2.20	17.59 ± 1.29	14.01 ± 0.74	12.86 ± 0.99
Ibiza- Balearic Islands - Spain (23; 22)	51.22 ± 1.70	48.40 ± 1.12	19.13 ± 0.69	17.57 ± 0.68	13.93 ± 0.71	12.80 ± 0.52
Menorca - Balearic Islands - Spain (19; 23)	51.58 ± 2.57	48.13 ± 1.77	19.00 ± 1.01	17.32 ± 0.77	13.91 ± 0.88	12.42 ± 0.56
Crete - Greece (13; 4)	51.63 ± 1.07	47.79 ± 1.08	18.59 ± 0.51	16.90 ± 0.27	13.18 ± 0.34	12.14 ± 0.48
Mean	51.67 ± 2.14	49.00 ± 2.43	19.44 ± 1.42	17.83 ± 1.17	14.16 ± 0.96	12.89 ± 0.89

Activity and social behaviour

During the breeding season, adults attend the nest at night. However, the attendance changes with the moon phase, when birds tend to visit the nest mostly during the moonlit nights (Rubolini et al., 2015). Adults group together in waters near the colony at dusk, showing a typical rafting behaviour; Rubolini et al. (2015) reported an average duration of 3.97 h. of these rafting groups. See further details in the corresponding section in Cory's shearwater text.

Nesting habits

See related content in the corresponding section in Cory's shearwater text.

Foraging at sea

Birds usually forage in neritic waters, both nearby the archipelagos where they breed or over the Mediterranean continental shelf. Birds breeding in Zembra Island (Tunisia) and equipped with remote tracking devices performed foraging trips of 0.7-8 days, with a total distance travelled of 51-1 919 km. The number of dives per trip ranged from 1 to 159, with a dive duration of 5.6-14 s and a depth of 0.7-5.4 m (Gremillet et al., 2014). Birds from Linosa (Italy) explore areas of higher primary productivity and shallow depth during the incubation phase, then at the beginning of chick-rearing, they decrease the distance to the colony in the foraging trips but again increase it later (Cecere et al., 2013). Birds from Linosa avoid areas close to other colonies (Cecere et al., 2015). Foraging trip duration increases with the growth in body mass of the chick (Cecere et al., 2014). Nocturnal foraging activity increases with the intensity of lunar illumination (Rubolini et al., 2015). Outside the breeding season, foraging areas of Scopoli's shearwater are distributed mostly over the Canary Current upwelling and the continental shelf of western Africa. For further details see related content in the corresponding section in Cory's shearwater text.

Trophic ecology

The diet of Scopoli's shearwater consists of fish, cephalopods, crustaceans and fishing discards (Sara, 1993). Shearwaters often follow fishing boats (Martínez-Abraín et al., 2002; Soriano-Redondo et al., 2016) and the fishing activity can influence the behaviour and movements of individuals (Bartumeus et al., 2010; Soriano-Redondo et al., 2016). For further details see the corresponding section in Cory's shearwater text.

Migration

Scopoli's shearwaters engage in long-distance migratory movements, exiting the Mediterranean in autumn when the breeding season is over and returning in spring. Individuals move to the Atlantic, distributing during the wintering period along the African continental shelf (Cramp & Simmons, 1977; Bauer & Glutz von Blotzheim, 1987). Males leave the colonies earlier than females and also return earlier in spring (Müller et al., 2014). Members of each pair migrate separately to the wintering area (Müller et al., 2015). There is individual consistency in the number of days spent in the wintering areas and the number of days in transit (Müller et al., 2014). On their post- and pre-breeding migration, birds cross the Strait of Gibraltar from the Atlantic to the Mediterranean (Telleria, 1980; Mateos, 2010). The crossing takes place between mid-October and late November in the post-breeding migration, and the return to the Mediterranean takes place between late February and early April (González-Solís et al., 2007; Reyes-

González et al., 2017). They mostly move along the African coast towards the shelf of Western Sahara, Mauritania, and Senegal. Some individuals continue further south while others shorten the flyway through the Gulf of Guinea to reach the Benguela Current near Namibia (González-Solís et al., 2007; Oro et al., 2008; Gremillet et al., 2015; Reyes-González et al., 2017). Shearwaters use olfactory and topographical clues but there is no evidence on the use of magnetic clues for navigation (Pollonara et al., 2015). The wind seems to be the most influential factor in the choice of route and migratory calendar, as shearwaters take advantage of the prevailing winds to reduce energy costs, even though it involves longer routes (Felicísimo et al., 2008; González-Solís et al., 2009). Juvenile individuals tagged with tracking devices in the colonies of the Mediterranean French islands (Gulf of Lion) showed less synchronisation in crossing the Strait of Gibraltar, slower migration, and longer daily distances travelled, compared to adults (Péron & Grémillet, 2013).

Dispersion

See related content in the corresponding section in Cory's shearwater text.

Reproduction

Birds return to the breeding locations between late February and early March when large groups of individuals start to aggregate in the vicinities of the colonies (Sánchez, 1997; Thibault et al., 1997). As in the case of Cory's shearwaters, this species is also highly monogamous, with reproductive links between both members of the pair remaining for years (Ristow et al., 1990). Extra-parental mating is almost inexistent (Swatschek et al., 1994; Rabouam et al., 2000). When a change in partner occurs, it is often related to either a low reproductive success over the previous season or the death of the partner (Swatschek et al., 1994). The occupation of the burrows usually begins early in March (Sánchez, 1997). The species shows high nest fidelity, with reoccupation rates year after year of 84.3% for males and 75.7% for females (Thibault, 1994). Changes in the burrow used for nesting are related to a breeding failure in the previous season, which usually leads to selecting a nearby burrow in the next breeding season (Thibault, 1994). Burrows measured at Rachgoun Island (Algeria) had an average length of 95.3 cm (Taibi et al., 2014). The member incubating can recognize its mate while flying over the colony through vocalization (Cure et al., 2009). As Cory's shearwaters, females lay a single egg at the end of May or early June, immediately after they return to the colony from the pre-laying exodus. There is a high synchronization among females of the same colony in the laying date (Sánchez, 1997; Giudici et al., 2010). In Columbretes, Sanchez (1997) recorded an average egg weight of 81.6 g at laying and 71.1 g at hatching, while its average length was 69.6 mm and width 45.8 mm. Incubation, carried out by both sexes, takes about 53 days, with an average of 15 incubation stint. The duration of each incubation stints depends on the length of the foraging trip of the partner at sea, so the distance to the foraging areas conditions the incubation shifts. After laying, it is frequently the female who takes the first incubation stint, in a short bout of about 3 days, although males could also take the first incubation stint, which usually lasts about 7 days (Sánchez, 1997).

Hatching takes place in early or mid-July. Hatching can take 2-6 days from the moment the eggshell begins to break until the chick is completely out of it (Sánchez, 1997). Sánchez (1997) reported a hatching rate in Columbretes of 91-100%. The species is nidicolous and semi-altricial. The chick opens the eyes from the first day. The physical condition of the parents does not affect the sex ratio of the offspring over the years (Genovart et al., 2005). The chick is cared for by both parents during the first days. Over the days the attendance bouts are spaced out. The chick can stay alone at the nest for 1-3 consecutive days. The chick is fed only at night when the parents return to the colony from the sea after foraging (Sanchez, 1997). The chicks can remain up to 90-99 days in the nest; during this time, the weight from hatching (40-80 g) to shortly before fledging (650-985 g) is increased by about 780 g (Sánchez, 1997). Chicks call intensively when parents are in the burrow. This call change over the chick development, allowing to determine individual sex (Bretagnolle & Thibault, 1995).

Fledging occurs at the end of October. Parents stop to attend the offspring some days before fledging. It is at this moment when the highest rates of juvenile mortality occur. In the Columbretes Islands, Sánchez (1997) recorded the following reproductive parameters over a 5-year study period: (i) hatching success: 91-100%, in the cases of failure, the causes were infertility, abandonment, embryo mortality, and egg disappearance; (ii) chick mortality: 3-28%, (iii) flight success: 72-97%, (iv) breeding success: 66-93%. The probabilities of future reproduction and fidelity to the burrow are lower in individuals temporarily absent from the colony, suggesting a lower quality of these individuals (Sanz-Aguilar et al., 2011). Costantini & Dell'Omo (2015) found that birds with higher levels of oxidative damage were less likely to be observed during the following seven years and raised a lower number of chicks. According to Ristow et al. (1992) birds in the Crete population do not take sabbatical years.

Population structure and dynamics

It is a long-lived species, with recorded cases of about 30 years of age (Rodriguez & McMinn, 2000), and with annual survival rates of about 95% when there is no human-related mortality (Rabouam et al., 1996; Ristow et al., 1990). The average survival rate after the first year of life is 52%. Individuals return to the natal colony or a close one after 5 years from fledging, although many of them do not attempt to breed until they are 6 to 9 years old (Jenouvrier et al., 2008).

Climatic variations in both the North Atlantic (NAO index) and South Atlantic (SOI index) affect the demography of the Scopoli's shearwater. NAO shapes both the variability in survival, explaining 66% of the variance, and the reproductive success, explaining 41% of the variance (Genovart et al., 2013a). The proportion of transients (i.e., breeders that do not settle) correlated with SOI, which may suggest a higher cost of the first breeding attempt (Genovart et al., 2013a).

However, in many colonies in the Mediterranean, the survival rate in recent years is lower than the previously reported. Igual et al. (2006b) calculated an adult survival rate of 87%. In other colonies in the western Mediterranean, annual adult survival estimates were also below 90% (Carboneras, 2004). These data suggest a regressive trend in the Mediterranean, with a progressive reduction of the population. A study carried out at Pantaleu islet (Mallorca) showed that the annual recruitment of immigrants represents 10-12% of the population size (Sanz-Aguilar et al., 2016a).

Population size

The total population of the species is estimated at 141 333 to 222 856 pairs, distributed among Spain: Murcia Islands (37-88 pairs), Balearic Islands (1801-6 946 pairs), Chafarinas Islands (624-780 pairs), Columbretes Islands (50 pairs); Algeria: Habibas Islands (350-500 pairs), Rachgoun Islands (100-150 pairs), West Coast Islands (90-130 pairs); Croatia: Lastovo Islands (140-175 pairs), Vis Islands (750-1 050 pairs); France: Corsica (338-440 pairs), Hyères Islands (182-367 pairs), Marseilles Islands (396 pairs); Greece: Aegean Islands (890-1 295 pairs), Crete (1 245-2 010 pairs), Cyclades Islands (760-1395 pairs), Dodecanese Islands (125-250 pairs), Evia (81-156 pairs), Ionian Islands (2 060-3 100 pairs), Sporades islands (30-80 pairs); Italy: Latium islands (220-345 pairs), Sardinia islands (1 921-5 245 pairs), Sicily islands (103-258 pairs), Sicily Channel islands (10 570-15 120 pairs), Tremiti islands (300-400 pairs), Tuscany islands (230-505 pairs). Malta: Comino island (20-25 pairs), Filfla island (200 pairs), Gozo island (2 300-2 350 pairs), Malta (1 550-2 000 pairs); Tunisia: La Galita islands (250-300 pairs). The size of the breeding population of Zembra Island (Tunisia) has recently been re-estimated at 141780 pairs, making it the largest colony of the species (Defos du Rau et al., 2015).

Conservation status

IUCN global category (2015): Least Concern LC (BirdLife International, 2015). IUCN Spain category (2002): Endangered EN A3cde (Carboneras, 2004).

In Spain, the species is included in the List of Wild Species under Special Protection (B. O. E., 2011), although *C. diomedea* (included as a subspecies) is also included in the Spanish Catalogue of Threatened Species under the category of "Vulnerable" (Real Decreto 139/2011). At the European level, it is included in category SPEC 2, and in the IUCN Red List (2010) it is listed as "Least Concern".

In general, the species presents a regressive trend, despite the conservation measures carried out in the last two decades. This generalised regression is due to different reasons.

Threats and conservation measures

Bycatch

Incidental bycatch, especially related to longlining, seems to be the main cause of unnatural mortality of the species (Sánchez & Belda, 2003; Cooper et al., 2003; Carboneras, 2004; ICES, 2009; Laneri et al., 2010). Particularly in the Spanish Mediterranean, there is an important fishing area where a large fishing fleet targeting pelagic and semi-pelagic fish operates. A large part of this fishing fleet captures mainly swordfish (*Xiphias gladius*) and two species of tuna (*Thunnus thynnus* and *Thunnus alalunga*) (García-Barcelona et al., 2010b). Belda & Sánchez (2001) estimated 650-3 000 birds were killed by the fishing gear around the Columbretes Islands, of which 66% were Scopoli's shearwaters, and the majority of them were adults. Valeiras & Camiñas (2003) and García-Barcelona et al. (2010a, 2010b) also cited the capture of Scopoli's shearwaters in Spanish Mediterranean waters. Some authors suggest a relatively low bycatch rate for this species in longliners in the Spanish Mediterranean, such as Baez et al. (2014), whose data indicated that after ten years of sampling (2000-2009) only 80 birds were caught in 30 fishing operations. However, Cortés et al. (2017) estimated an average of 683 birds that could be dying in the Balearic Sea (coast of Catalonia and Balearic Islands) in artisanal bottom longliners, so they encouraged the implementation of mitigation measures in these fleets to decrease the bycatch rate. Cortés et al. (2017) indicated that the type of fleet (artisanal or industrial), the fishing gear and bait used, the time of day when the line is set and the distance to the breeding colonies greatly influence the bycatch rate. Moreover, these catches usually occur in single episodes with massive catches (from tens to more than a thousand birds in a single fishing operation), which makes it difficult to record this type of event. As a long-lived species with only one chick per pair per year, the mortality of birds of breeding age can cause serious declines in a short time, similar to those detected in the Balearic shearwater (Oro et al., 2004). Sanz-Aguilar et al. (2016b) pointed out that the populations of the Balearic Islands have a high adult mortality rate, but are being able to remain more or less stable by integrating breeders from other Mediterranean colonies, presumably Zembra, the largest colony of this species.

Because Scopoli's shearwaters attend longliners when trawlers cannot operate, longline activity should be limited to working days (Soriano-Redondo et al., 2016). A ban for trawlers in October would greatly reduce Cory's shearwater catches (Báez et al., 2014). Also, the new European fisheries policy, which requires discards to be landed at harbour, may lead to the increased interaction of shearwaters with longliners, thus potentially increasing bycatch risk (Soriano-Redondo et al., 2016).

Overfishing

Overfishing can reduce resource availability, leading to a negative effect on seabird populations. However, this effect has not yet been confirmed on the Scopoli's shearwater.

Alien species

The introduction of anthropophilic predators such as feral cats (*Felis catus*), rats (*Rattus sp.*) and mice (*Mus musculus*, *Apodemus sylvaticus*) on the islands and islets where this and other seabird species breed, may lead to the disappearance of some colonies (Carboneras, 2004; Traveset et al., 2009). Scopoli's shearwaters can withstand some predation pressure from cats and rats (Ruffino et al., 2009; Igual et al., 2007). However, once introduced predators colonise an island or islet, the breeding success is affected (Thibault, 1995; Martin et al., 2000). In several cases, the species has disappeared from certain islets due to the action of these predators, as in the L'Imperial islet, in the archipelago of Cabrera close to Mallorca (Amengual & Aguilar, 1998). Eradication of invasive predator species seems to have very positive results (Donlan & Wilcox, 2008). In Chafarinas, where there was a high density of rats, rat eradication was followed by an increase in the productivity of the breeding colony (Igual et al., 2006a).

Coastal urbanization

The intensification of human uses along the coastline has progressively foreclosed suitable locations where colonies can be established (Coll et al., 2011). Since the 1960s, the accelerated urbanization of the coastline and the consequent intensification in touristic uses increased associated threats for seabirds such as disturbances, introduced predators, etc. This led to a decrease in the number of colonies. In this sense, declaring the main breeding colonies as Important Bird Areas (IBA) by SEO/BirdLife and the subsequent designation as Special Protected Areas for Birds should help to implement effective management measures for conservation (Arcos et al., 2009).

Light pollution

The artificial lighting disorients juveniles and draws them into the interior of the islands, where they can collide with buildings and expose themselves to introduced predators. During the period 1999-2013, a total of 304 fledglings of Scopoli's shearwater, Balearic shearwater *Puffinus mauretanicus* and European storm petrel *Hydrobates pelagicus* were rescued in the Balearic Islands, with a mortality rate of 8.5%. This proportion represents 0.13-0.56% of the juveniles produced annually (Rodríguez et al., 2015).

Marine pollution

The ever-present possibility of oil spills is a constant threat to all seabirds. In the case of the Scopoli's shearwater, the entire global population crosses the Strait of Gibraltar during its post-nuptial migration, so an oil spill at an unfortunate time could have strong negative consequences. On the other hand, Scopoli's shearwaters usually feed on plastics and floating debris: 94% of the adults examined had plastic in the stomach, with an average of 15 fragments of 3.4 mm in length per individual (Codina-García et al., 2013). Such accumulation in the stomach could cause negative effects, although to date no studies have clarified this issue.

As top-predators, Scopoli's shearwaters are susceptible to bioaccumulation of pollutants present in the marine environment. Renzoni et al. (1986) found higher levels of mercury, hexachlorobenzene, DDE and PCBs. Roscales et al. (2010) found a higher amount of organochlorine compounds in the blood of Scopoli's shearwaters than in Cory's shearwaters.

Poaching

In the Mediterranean, the species was traditionally caught for human consumption and also to be used as bait, but these practices seem to have disappeared (Carboneras, 2004).

Interactions with other species

At sea

Concurrence during foraging has been observed between Northern gannets (*Morus bassanus)* and Scopoli's shearwaters in the Mediterranean (Kennedy & Paterson, 1983). The concurrence of Scopoli's shearwaters with dolphins and tunas in fishing episodes is known to be common. Salvador García-Barcelona (personal communication) cited the observation of about 50 Scopoli's shearwaters catching fish pushed to the surface by bottlenose dolphins (*Tursiops truncatus*) very close to the coast of Malaga in 2010. The same author cited the direct observation of a group of Scopoli's shearwaters that followed his boat and suddenly changed bearing towards a large school of bluefin tuna (*Thunnus thynnus*) that appeared near the surface, in the vicinity of the Columbretes Islands, in 2002.

On land

In the Chafarinas Islands, the ratio of Cory's to Scopoli's shearwater has increased from 6% to 23% from 2000 to 2010, and 14% of the pairs monitored were mixed (Genovart et al., 2013b).

Regarding predators, introduced species such as rats and cats have a notable effect on the reproductive success of these birds, preying on both eggs and chicks (Thibault, 1995; Igual et al., 2006a).

Parasites and pathogens

The ectoparasite community of this species includes lice (*Halipeurus abnormis* and *Saemundssonia peusi*, Family *Philopteridae*), *Austromenopon longithoracium*, *Austromenopon echinatum*, Family *Menoponidae*), a species of flea (*Xenopsylla gratiosa*, Family *Pulicidae*), a species of tick (*Ornithodoros maritimus*, Family *Argasidae*) (Wink et al, 1979; Beaucornu & Alcover, 1993; Gómez-Díaz et al., 2007, 2008). Other mites are *Zachvatkinia ovata*, *Microspalax brevipes*, *Brephosceles puffini*, and a new species of genus Plicatalloptes (Stefan, 2016), although the prevalence and abundance of each vary between individuals and colonies. On the other hand, no blood parasites have been found in this species (González-Solís & Abella, 1997).

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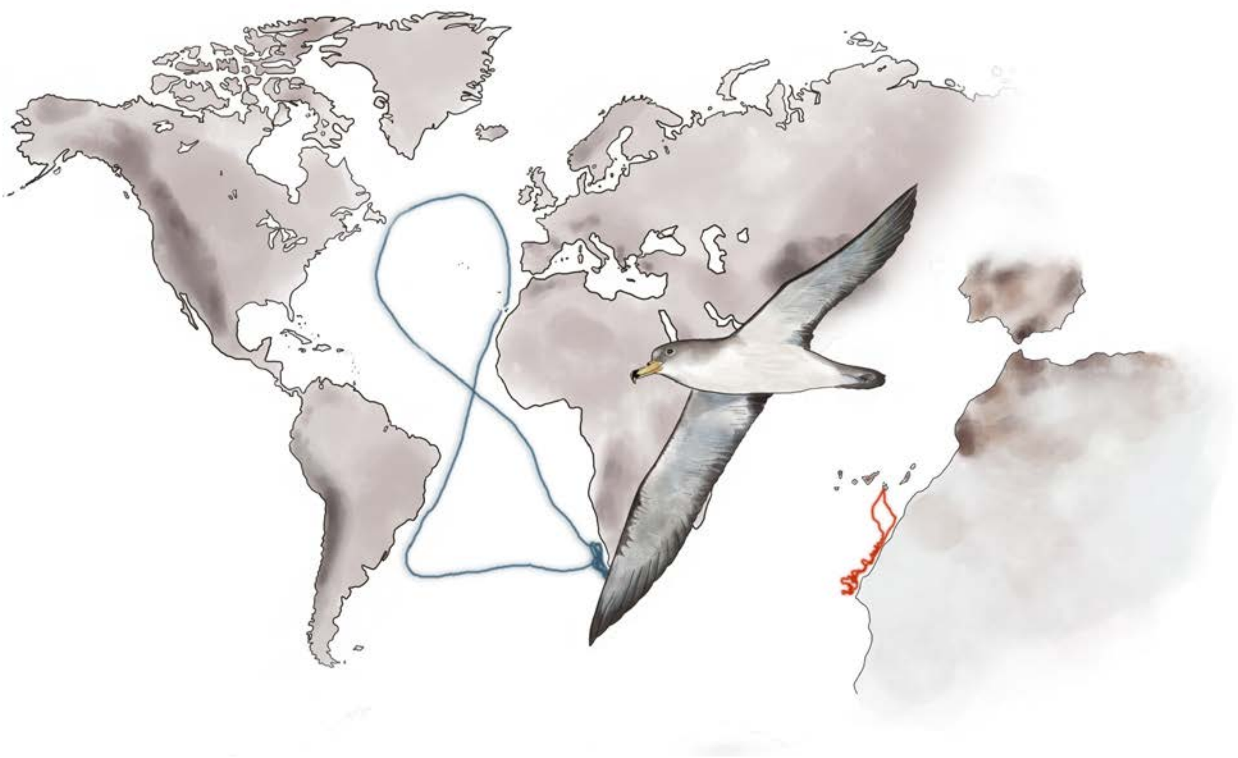

Chapter II

Spatial ecology and migration of Cory's and Scopoli's shearwaters breeding in Spain

Chapter II is an English version of the book:

Reyes-González, J. M., Zajková, Z., Morera-Pujol, V., De Felipe, F., Militão, T., Dell'Ariccia, G., Ramos, R., Igual, J. M., Arcos, J. M. & González-Solís, J. (2017) *Migración y ecología espacial de las poblaciones españolas de pardela cenicienta. Monografía n.º 3 del programa Migra*. 150 pp. SEO/BirdLife. Madrid. https://doi.org/10.31170/0056

SPATIAL ECOLOGY AND MIGRATION OF CORY'S AND SCOPOLI'S SHEARWATERS BREEDING IN SPAIN

ABSTRACT

Framework – This work addresses the at-sea ecology of Cory's and Scopoli's shearwaters breeding in Spain. Data gathered in the context of different independent projects allowed to compile a large dataset of remote tracking data for these species. Based on the number of individuals tracked, the representativeness of colonies studied, and the set of years considered, this study aimed to give a comprehensive, extensive yet rigorous overview of the at-sea ecology of these species, with the ultimate goal of providing tools to manage properly their populations and face effectively their threats.

Methodology – Data were recorded using different remote tracking systems according to aims and limitations. Fieldwork and deployments were carried out at 13 different breeding colonies distributed across different regions of Spain: Balearic Islands (Cala Morell, Aire Islet, Pantaleu, Cabrera), Castellón (Columbretes Islands), Murcia (Palomas Islet), Almería (Terreros Islet), Chafarinas Islands (Alborán Sea), and Canary Islands (Alegranza Islet, Montaña Clara Islet, Timanfaya and Veneguera). GPS loggers were used for tracking adults' movements during the breeding period, between 2007 and 2015, in the 13 different breeding colonies in Spain. Light-level geolocators were used to study year-round movements of birds from three colonies (Veneguera, Montaña Clara and Pantaleu), between 2007 and 2013.
State-of-the-art algorithms to classify behavioural modes from GPS data were used to quantify behaviour at varying temporal and spatial scales and to build up behavioural landscapes. Furthermore, salt-water immersion data from geolocators were used to characterize individuals' behaviour year-round, facilitating to compare performance and daily activity budgets among wintering areas. Migratory connectivity and site fidelity to wintering grounds were also evaluated. Overall, GPS analysis included a compiled dataset of 813 612 GPS locations and 1 546 foraging trips from 299 individuals. Geolocator analysis included data from 214 devices recovered, encompassing 203 427 locations in 309 tracks from 161 individuals. The results yielded a comprehensive overview of the year-round movements and at-sea behaviour of the Spanish populations of Cory's and Scopoli's shearwaters, providing insights about foraging strategies, foraging grounds, migratory patterns and phenology of the studied populations.

Results and discussion – During breeding, some differences were found between species regarding behaviour, movement range and areas visited. Both species, but particularly individuals breeding in colonies in the Atlantic, showed a clear preference for neritic waters far away from the colony, over the continental shelf near the mainland. However, individuals also used waters surrounding the colonies, suggesting the use of the dual foraging strategy during the chick-rearing phase. Regarding population from the Canary Islands, birds consistently foraged along the highly productive African shelf, performing

foraging trips of up to 1 000 km. Commuting flights were generally diurnal, whereas resting took place overnight. Birds were more active at sunrise and sunset, although they also foraged during the day. In the Mediterranean, birds foraged along the Iberian coast, from the Strait of Gibraltar up to the Gulf of Lyon during the long trips, with some degree of spatial segregation among individuals from different colonies. In the case of birds from Chafarinas, birds commuted to the near northern coast of Morocco, an area also used by birds from Palomas Islet in Murcia. Intensive foraging seemed to occur in similar proportion during darkness and daylight, both in the Mediterranean and in the Atlantic. Indeed, in the Atlantic, this behaviour seemed to be more important during darkness, which may relate to prey behaviour.

Cory's shearwaters breeding in Spain used six different wintering areas during the non-breeding period. Sorted by importance, they were: the Benguela Current off the coast of Namibia (from 10° S to 40° S), the Agulhas Current, the confluence between the Benguela and the Agulhas currents (around the parallel 40° S), the Canary Current (from 10° N to 25° N), the Brazil Current (from 15° S to 40° S), and the centre of the South Atlantic (around parallel 45° S and meridian 25° W). Birds were more active during daylight, especially at sunrise and sunset, except for the Canary Current where daylight and darkness activity were similar. Both species tended to be more active during darkness with an increasing depth and distance from the coast, suggesting population plasticity in the foraging strategies to adapt to the environmental conditions of each wintering area. This apparent population plasticity was likely related to a diversity of strategies across individuals since results indicate 75% of them used a single area repeatedly over several years and showed a high degree of intra-individual spatial overlap.

Scopoli's shearwaters breeding in Spain spent the non-breeding period in four main wintering areas. Sorted by importance, these areas were: the Canary Current (African shelf from 14° N to 23° N), offshore waters of Angola and Namibia (from the equator to the parallel 22° S), oceanic waters of Guinea (around parallel 8° N and meridian 20° W), and off the coast of Ghana (from the coast to the equator). Birds were more active during daylight across most of the wintering areas, with peaks of activity at sunrise and sunset. In the area of Guinea, however, birds were more active at night.

As the wintering areas used by the two species differ, so do the migratory flyways. Cory's shearwaters showed more complex migratory patterns than Scopoli's shearwaters. Overall, Cory's shearwaters completed migratory flyways - looking at the post- and pre-breeding migration together - drawing an 8-shaped loop across the Atlantic, likely taking advantage of the prevailing winds. Scopoli's shearwaters reached the wintering areas following the coastline during the post-breeding migration but entered into the pelagic areas of the North Atlantic during the pre-breeding migration on their way back to the breeding colonies. This detour was more common in individuals wintering in the southern areas. In both species, the pre-breeding migratory flyways were weaker and more spread than the post-breeding ones. Regarding phenology, the staging in the main wintering areas was slightly longer in Scopoli's shearwaters, while the breeding period was longer in the case of Cory's shearwaters.

Conclusions and future challenges – Overall, the results yielded helpful information to better address threats and implement conservation and management actions at sea, to guarantee the future of the Spanish populations of Cory's and Scopoli's shearwaters. The greatest upcoming challenge comes from social and political stakeholders involved in marine conservation since their willingness is necessary to incorporate data from cutting-edge technology into conservation strategies effectively.

INTRODUCTION

Movement is one of the most outstanding features of animals. Among different movements, migration is probably the one that most captivates the attention of many people towards birds. Many species perform periodic movements, remembering the passing of the seasons and thus fascinating humans since ancient times. Until the 18th century, singular explanations for this phenomenon were part of the popular imagination, such as the belief that swallows spent the winter at the bottom of lakes and ponds or that cuckoos transformed into sparrowhawks during winter (Newton, 2008).

Finding an accurate explanation for the concurrent and sudden disappearance of so many species did not come until the end of the 19th century. In Denmark, Hans Christian Cornelius Mortensen tagged for the first time birds with self-made rings, -using aluminium rings on European starlings-, a first step towards the bird ringing with scientific purposes (Newton, 2010). Well into the 20th century, individual tagging through ringing was the norm, allowing to decipher the migratory route of dozens of terrestrial and aquatic species, at least partially, thanks to the recapture of individuals in locations far from the place of ringing.

In the case of pelagic seabirds, however, ringing has yielded few insights about their migratory movements. Most of these species only land for breeding, when they congregate with conspecifics. Due to this behaviour, they are good model species because their gregarism in the breeding colonies makes them accessible in large numbers. By comparison, they are difficult to observe out of the breeding period when they are always at sea, i.e., during migration and wintering. Their pelagic habits keep them away from the coast, which greatly prevents both recapturing and reading of ring codes, therefore limiting our knowledge of their migratory movements. After more than 100 years of bird ringing, most ring recoveries of pelagic seabirds outside the breeding colonies correspond to individuals that died from different causes, including strong storms or oil spills, and were washed ashore by drift (García et al., 2003; Cadiou et al., 2004, 2008; Votier et al., 2008; Boano et al., 2010). A particular case of bird ringing that has yield more insights in this regard is the use of field-readable rings and other special tags, which allow for the identification of the tagged individuals from the distance thanks to a combination of colours and code used. These tags have helped to gather tons of information about the movement and behaviour of coastal species such as gulls, terns and cormorants. However, as pelagic seabirds are difficult to observe, these tags are not so helpful to study them.

In addition to bird ringing, direct observation has enormously contributed to the knowledge of movements and distribution of pelagic seabirds (Sage, 1968; Briggs et al., 1985; Mateos-Rodríguez et al., 2010, 2012). Both from the coastline and from vessels, hundreds of birders have helped to complete gradually the distribution map of many species. In the Iberian context, the study of seabird migration has been based traditionally on censuses from the coastline. Capes, arrows or artificial breakwaters break the straightness of the coastline and disrupt the migratory flow of flying seabirds. These locations have been the meeting points for enthusiastic and experienced seabird observers who have contributed enormously to the knowledge of the migratory phenomenon along our coasts (Tellería, 1981; De Juana & Garcia, 2015; Sandoval Rey, 2016). A noticeable example is this sense is the RAM programme (Red de observación de Aves & Mamíferos Marinos, http://redavesmarinas.blogspot.com.es), a citizen-science programme that coordinates volunteers to count seabirds from points along the Spanish and Portuguese coasts. The Migres Marinas programme carried out by the Migres Foundation is also another remarkable example of a dedicated programme to monitor the migration of seabirds through the Strait of Gibraltar. Thanks to this type of monitoring schedules from the coast, and in combination with surveys at sea (Arcos et al., 2009; Ramírez et al., 2009), the importance of Iberian waters as migratory flyways or stopover for many different species is well known nowadays. The strategic location in the western side of Europe, between the Atlantic Ocean and the Mediterranean Sea, promotes high diversity of seabird species. Some individuals of species breeding in the North West Atlantic enter the Mediterranean to wintering, such as puffins (*Fratercula artica*), razorbills (*Alca torda)*, gannets (*Morus bassanus*), or skuas (Tellería, 1981; Paterson, 1997; Mateos-Rodríguez, 2010). Moreover, some northern breeders migrate to the Atlantic coast of southern Europe and Africa to wintering, such as the vast majority of gannets (Fort et al., 2012), Sabine's gull (*Xema sabini*), the Arctic tern (*Sterna paradisaea)* or the great skua *(Catharacta skua*). On the other hand, some species that breed in the Mediterranean islands visit the Atlantic out of their breeding period, such as the Balearic shearwater (*Puffinus mauretanicus*; Le Mao & Yésou, 1993; Mouriño et al., 2003; Ruiz & Martí, 2004; Guilford et al., 2012). Finally, some other species such as the great shearwater (*Ardenna gravis*) or the sooty shearwater *(Ardenna grisea)*, breed at very distant remote locations of the southern Atlantic but perform long trans-equatorial migrations, approaching in some moments the Iberian coast (Valeiras, 2003; Louzao et al., 2015; Sandoval Rey, 2016).

Nevertheless, the study of movements and migration based on direct observation of pelagic seabirds has important limitations. On one hand, conditions often make it difficult to identify properly the species because of the distance, the waves, the weather and other factors (Louzao et al., 2015). Besides, the plumage and morphology of related species are difficult to distinguish, especially under poor observation conditions due to wind, rain or waves. On the other hand, these observations rarely make it possible to recognise the sex, age or breeding status of the individuals. The most important limitation though is the impossibility to be aware of the population of origin, which precludes knowing the sources of variability in movement patterns.

The advent of remote-tracking technologies over the last 15 years has completely moved forward this scenario, marking a tipping point in the study of birds' movement and migration. Our capacity to study seabirds at sea has rocketed, leading to a much deeper knowledge of the movements of seabird species than during the previous decades. A good example on this are the Cory's and the Scopoli's shearwaters (*Calonectris borealis and C. diomedea*), two subspecies recently upgraded to separated species (Sangster et al., 2012; Del Hoyo et al., 2014, 2016). Cory's and Scopoli's shearwaters have been widely studied (Reyes-González & González-Solís, 2016a, 2016b). However, detailed knowledge of the movements of individuals from the Spanish populations has remained largely unknown, at least to the public out of this research area. Like other seabird species, their natural-history traits makes them good indicators of the health of our seas. Furthermore, the charisma of these species makes them excellent flagship species. SEO/BirdLife chose them as "Bird of the Year" in 2013 to draw attention to the threats that our seas are facing. Over the last decade, both the *University of Barcelona* and SEO/BirdLife have worked extensively to get new insights into the ecology of these species, aiming to improve their conservation status. Many of these insights have remained unpublished or in grey literature.

This work combines a large dataset recorded through two kinds of remote tracking devices, GPS and light-level geolocators, to provide an extensive overview into the at-sea ecology of the Spanish populations of the Cory's and Scopoli's shearwaters. More specifically, in a simple yet rigorous way this work aimed to: (1) identify and characterise movement range, main foraging areas and behaviour during the breeding period, (2) identify main wintering areas and characterise winter ecology and behaviour, (3) identify the main migratory flyways connecting breeding and wintering areas, and (4) characterise annual phenology. Data compiled included a set of ~300 year-round tracks from more than 150 individuals tracked with a geolocator, and more than 1 500 foraging trips from about 300 individuals tracked with GPS, tagged at 13 breeding colonies.

MATERIAL & METHODS

Study species

Following recent phylogenetic studies and the British Ornithologists' Union Taxonomic Committee recommendations, the Atlantic and the Mediterranean taxa previously considered subspecies are now considered two different species: the Cory's shearwater (*Calonectris borealis*) and the Scopoli's shearwater (*C.diomedea*). This work follows this recommendation. This consideration is also based on behavioural differences between taxa, as shown in this work.

The Cory's shearwater is a medium-sized long-lived pelagic seabird, with breeding colonies located in the North-East Atlantic, in islands and islets of Azores and Madeira (Portugal), and Canarias (Spain). The species also breeds in islets close to the Iberian mainland (Berlengas Islands, in Portugal, and Cíes, Coelleira and Sisargas, in Galicia, Spain). Moreover, the breeding distribution also covers the Mediterranean Sea, as the species also breeds in Chafarinas Islands (Spain) and Terreros Islet (Almería, Spain) (Reyes-González & González-Solís, 2016a).

Scopoli's shearwater is very similar to Cory's shearwater, although a bit smaller in size (Reyes-González & González-Solís, 2016b). This species breeds in the Mediterranean Sea, in islands and islets from the Spanish coast to the Adriatic and Aegean Sea (Goméz-Díaz & González-Solís 2007).

Both species lay a single egg per year, egg-laying starts in mid to late May, and hatching starts in early to mid-July. Fledglings usually leave the colonies in October (Thibault et al. 1997, Telailia et al. 2014). Both species perform long-distance migrations. When the breeding period is over, birds leave the breeding areas and engage in migration towards the wintering areas in the south, where they spend several months.

At-sea observations, sightings from the coast, and the scarce recoveries of ringed birds led to a deficient knowledge of the global annual distribution of these species until the beginning of the 21st century (Figure 1). Populations from Portugal, particularly from Selvagens Islands, have been intensively studied in recent decades, and therefore their movements and behaviour are well known (e.g. Dias et al, 2011). Regarding Spanish populations, some publications have shed light in their year-round movements, although considering a small sample size (e.g. González-Solís et al., 2007, 2009).

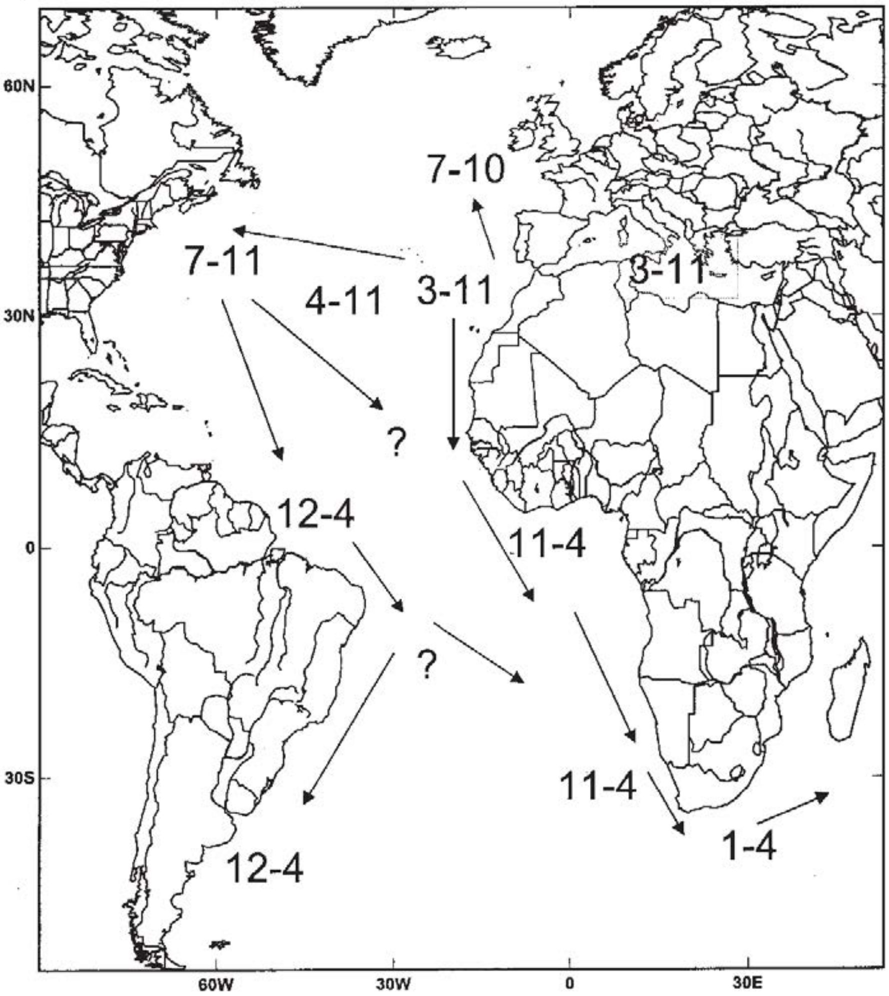

Figure 1 • Inferred migratory movements of Cory's and Scopoli's shearwaters until the beginnings of the 21st century, based on observations at sea and ring recoveries. Numbers represent the day and month of birds crossing the different regions during migration (synoptic representation from Camphuysen & Van der Meer, 2001). These two closely related species were considered subspecies until recently.

Study period & breeding colonies

This work took advantage of a large tracking dataset of Cory's and Scopoli's shearwaters tagged between 2007 and 2015 within the framework of different research projects, carried out by the *University of Barcelona* and SEO/BirdLife. The analysis included data from 13 different breeding colonies (Figure 2). GPS data came from birds tracked in the period 2007-2015. Geolocator data came from devices deployed between 2007 and 2012 and recovered between 2008 and 2013. As a whole, the dataset included an extensive representation of the Spanish breeding populations. Specifically, tracking devices were deployed at the following fieldwork locations:

1. Veneguera cliffs (Gran Canaria, Canary Islands). Included in the marine Important Bird Area (IBA) *ES395* and the ZEPA (special protected area for birds) *ES0000530 Espacio Marino de Mogán-La Aldea*. It holds an estimated breeding population of around 1 000 pairs of Cory's shearwaters. This work includes GPS data from the breeding period (pre-laying, incubation and chick-rearing phases) of 2012 and geolocator data from 2007-2013.

2. Montaña Clara Islet (Lanzarote, Canary Islands). Included in the marine IBA *ES327* and in the ZEPA *ES0000532 Espacio Marino de los islotes de Lanzarote,* together with the islets of La Graciosa, Roque del Este and Roque del Oeste. The IBA contains the largest group of colonies of Cory's shearwater in Spain, with more than 11 000 breeding pairs. This work includes GPS data from the breeding period of 2015 and geolocator data from 2011-2012.
3. Alegranza Islet (Lanzarote, Canary Islands). Also included in the marine IBA *ES327* and in the ZEPA *ES0000532 Espacio Marino de los islotes de Lanzarote*. A small islet of 10 km^2, it probably holds the most important breeding site for the Cory's shearwater in Spain, since more than 8 000 pairs breed here, and 11 000 pairs have been estimated for the whole IBA. This work includes GPS data from the breeding period of 2010.
4. Timanfaya National Park (Lanzarote, Canary Islands). The marine area adjacent to this National Park is included in the marine IBA *ES401* and the ZEPA *ES0000531 Espacio Marino de La Bocaina*. The estimated population of Cory's shearwater for the whole IBA is 1 350-1 450 pairs. This work includes GPS data from the breeding period of 2015.
5. Cíes Islands (Galicia). Included in the National Park of the Atlantic Islands of Galicia, in the marine IBA *ES402* and the ZEPA *ES0000499 Espacio Marino de las Rías Baixas de Galicia*. It is home to a small breeding colony of Cory's shearwater founded recently (2007) (Munilla et al., 2016). This work includes GPS data from the breeding period of 2015.
6. Chafarinas Islands. Included in the marine IBA *ES220* and the ZEPA *Islas Chafarinas ES0000036*. They have an estimated breeding population of 800-1 000 pairs of the Scopoli's shearwater, and 20-30 pairs of Cory's shearwater. Some pairs in this colony are mixed (Gómez-Díaz et al., 2009). This work includes GPS data from the breeding period of 2011.
7. Terreros Islet (Almería). Included in the marine IBA *ES170* and the ZEPA *ES0000507 Espacio Marino de los Islotes Marinos de Murcia y Almeria*. This islet currently has a small breeding population of barely a dozen pairs (authors, unpublished data). Together with Chafarinas, this is the unique colony where Cory's shearwater breeds in the Mediterranean Sea. Almost all the individuals present belong to this species, although Scopoli's shearwater can also breed here. This work includes GPS data from the breeding period of 2014.
8. Las Palomas Islet (Murcia). Included also in the marine IBA *ES170* and the ZEPA *ES0000507 Espacio Marino de los Islotes Marinos de Murcia y Almeria*. It holds an estimated breeding population of 37-88 pairs of Scopoli's shearwater. This work includes GPS data from the breeding period of 2014.
9. Columbretes Islands (Valencia). Located about 55 km off the coast of Castellón, they are included in the marine IBA *ES409* and the ZEPA *ES0000512 Espacio Marino del Delta de l'Ebre-Illes Columbretes Delta*. It holds an estimated breeding population of 63 pairs of Scopoli's shearwater. This work includes GPS data from the breeding period of 2012.
10. Cabrera Archipelago (Balearic Islands). The Maritime-Terrestrial National Park of Cabrera and adjacent waters are included in the marine IBA *ES324 Archipelago de Cabrera* and *ES415 Aguas al sur de Mallorca y Cabrera*. It holds an estimated breeding population of 356 pairs of Scopoli's shearwater. This work includes GPS data from the breeding period of 2015. Birds tracked were breeding in the islets of Na Pobra and Na Foradada.
11. Cala Morell cliffs (Menorca, Balearic Islands). These cliffs, included in the marine IBA *ES418* and the ZEPA *ES0000521 Espacio Marino del Norte y Oeste de Menorca*, are home to the largest breeding colony of

the Scopoli's shearwater in the Balearic Islands. The breeding population is estimated in 1 801 - 6 946 pairs (Arcos et al., 2009). This work includes GPS data from the whole breeding period (pre-laying, incubation and chick-rearing phases) of 2014.

12. Illa de l'Aire Islet (Menorca, Balearic Islands). This small islet is included in the marine IBA *ES419* and the ZEPA *ES0000522 Espacio Marino del Sureste de Menorca*. It holds an estimated breeding population of 50 pairs of Scopoli's shearwater. This work includes GPS data from the breeding period of 2007.
13. Illot d'Es Pantaleu (Mallorca, Balearic Islands). Included in the Natural Park of Sa Dragonera, and surrounded by the marine IBA *ES416* and the ZEPA *ES0000519 Espacio Marino del Poniente de Mallorca*. The estimated breeding population for the whole of the IBA is 210 pairs of Scopoli's shearwater. This work includes GPS data from the breeding period of 2007 and geolocator data from 2009-2013.

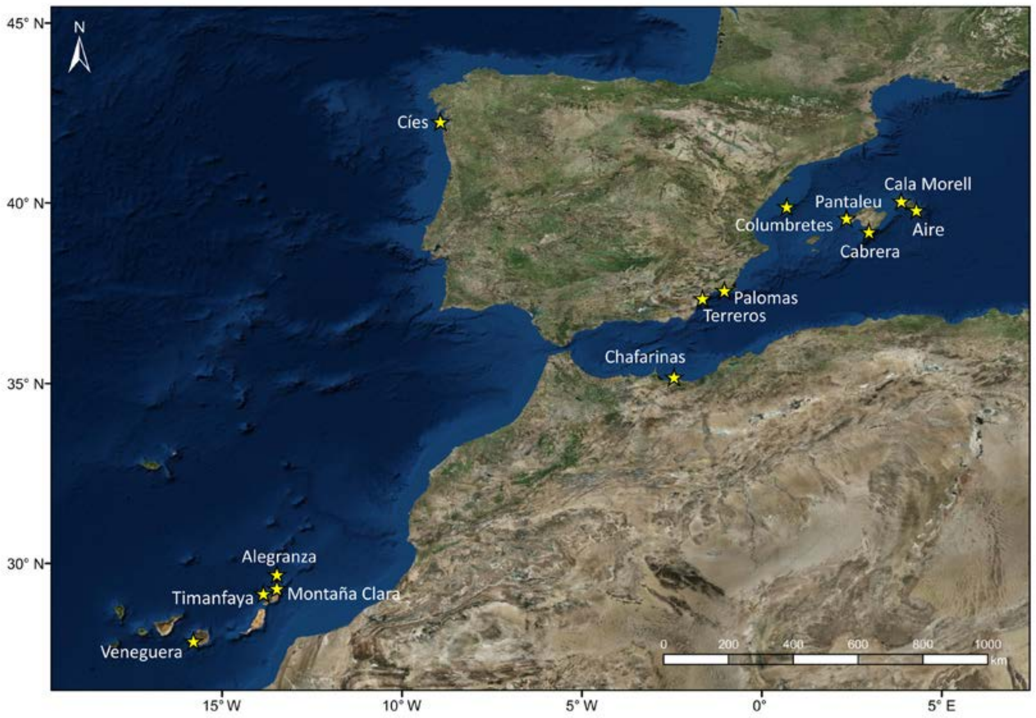

Figure 2 • Spatial location of breeding colonies of Cory's and Scopoli's shearwaters in Spain where tracking devices were deployed. From northeast to southwest, colonies are located in: Balearic archipelago (Cala Morell and Aire Islet, in Menorca, and Pantaleu Islet and Cabrera National Park, in Mallorca), Castellón offshore islets (Columbretes), southeast of Spain (Palomas and Terreros Islets), Alborán Sea (Chafarinas Islets), and Canary archipelago (Alegranza and Montaña Clara Islets, Timanfaya National Park in Lanzarote, and Veneguera in Gran Canaria). In all colonies birds were tracked with GPS loggers to reveal movement range and foraging areas during the breeding period. In the colonies of Veneguera, Montaña Clara and Pantaleu birds were also tracked using light-level geolocators to get insights into their wintering distribution, migratory flyways and year-round behaviour.

Tracking data

GPS

Movements during the breeding period were studied using small, light-weight GPS loggers (4.5 x 2 x 0.5 cm and 20-25 g - there was a slight variation depending on the manufacturer), with a square antenna to receive GPS signal, a Li-Po battery (320 to 750 mAh) and a storage memory. In GPS loggers, the geographic location is obtained by triangulation through the GPS satellite network, with an estimated accuracy of 5-25 m (Forin-Wiart et al., 2015). Geographic locations are stored in an internal memory along with the time stamp. These loggers require recapturing the bird to download the information recorded. The high resolution of these devices allows to determine the foraging areas in detail and to characterize individual movements during the breeding period. The battery life allows to record trips of 15 days at 1 fix/5 min or trips of 25 days at 1fix/15 min, ensuring the recording of complete foraging trips during the breeding period. These devices were attached to the feathers' bird back using a seawater-resistant TESA tape. The moulting period of body feathers overlaps with the breeding period in these species, easing the fall of the device after 2-3 weeks in case a bird is not recaptured (Figure 3).

This work included data recorded at a temporal resolution of 1 fix/5 min (Mediterranean colonies) and 1 fix/15 min (Atlantic colonies). This different resolution is due to the difference in the average duration of foraging trips, longer in the Atlantic colonies, which forces to decrease the GPS temporal resolution to record complete foraging trips without risk of battery depletion.

Figure 3 • Scopoli's shearwater from Cala Morell (Menorca) tracked with GPS. This individual was tagged in August 2013, and one month later, it was observed and photographed in the Gulf of Cádiz by the ornithologist Javier Elorriaga. Once the bird started the post-breeding migration, it left the Mediterranean Sea and visited the Atlantic area of the Gulf of Cádiz after crossing the Strait of Gibraltar. In this exceptional case, the device remained on its back at least four weeks after deployment. © Javier Elorriaga.

Light-level geolocators

To study migration and behaviour in the wintering areas, light-level geolocators manufactured by the British Antarctic Survey (BAS) and Biotrack LTd were used. These devices, sometimes called *GLS (Global Location Sensor),* measure and store two basic data: light intensity and timestamp. These devices must be recovered to download the data stored while they were placed on an animal. The basic components of the geolocators used in this study are:

- A battery. They are long-lasting and can work for long periods, from a few months up to 4 years, depending on the geolocator model.
- A photoelectric sensor. It measures the intensity of ambient light, on a scale from 0 to 64, and records it every 5 or 10 minutes, depending on the model. This information allows to later inferring the location of the animal.
- A clock, which records the date and time in the universal time since the activation moment.
- Metallic pins. A cathode and an anode serve as a connection to the computer, and in some models, they

record the electrical conductivity every few seconds, which allows knowing if the device is in contact with saltwater.

- A microprocessor, which evaluates and processes information in real-time to store aggregated data.
- An internal memory, which stores the information.

The method behind geolocation by light has been used by sailors for centuries. It is based on the change of day length according to latitude, and the change of midday time with longitude. By knowing sunrise and sunset times, it is possible to infer midday and midnight times for each day of data, and then to infer the geographical longitude. Besides, the date and length of the day (time between sunrise and sunset, which varies only with latitude), allow inferring the geographical latitude. However, close to the equinoxes, it is not possible to infer the latitude because during day and night length are the same throughout the Earth globe. This weakness entails the main source of error in geolocation by light (Hill, 1994). This error is not limited to the equinox period, but instead propagates over time and is variable according to the latitude at which the animal is located at any given moment (Lisovski et al., 2012). Equinoxes do not affect longitude, thus being more trustable all year-round. The average error for the geolocators used in pelagic seabird has been estimated in about 200 km (Phillips et al., 2004), being minimum at solstices and maximum at the equinoxes. Along with these weaknesses, geolocators often require a long processing time of the stored information to get geographic locations, far much longer than the time required to process GPS data. However, geolocators have clear advantages, like their lightweight (between 0.6 and 4 g, depending on the model), which allows for tagging a great number of species including small sized ones, and allows for long-lasting deployments without affecting individual welfare (Figure 4). Last, despite the large spatial error in latitude around equinoxes, the information provided is extremely valuable to study large-scale, long-distance migrations.

Geolocator data used in this study were processed using Bastrack© software, from the British Antarctic Survey research institute. Clock drift was corrected. Geolocators were calibrated before deployment. During the calibration period, geolocators were placed outdoors without light interference for a few days. The calibration period allowed to obtain a solar angle value, which is related to the threshold value further used to differentiate dawn and dusk. This solar angle value is used to infer location outside the calibration periods. Solar angle values obtained were between -2 and -6 degrees for the set of geolocators (considering civil twilight; Fox, 2010). Light curves were visually inspected to locate possible interferences at dawn and dusk that might cause erroneous estimates. When a twilight interference was located, it was manually corrected if there was an obvious correspondence in the time sequence of dawns and dusk before and after the twilight with interference. When this correction was not possible, twilights were labelled using an uncertainty scale depending on the time mismatch with the expected twilight moment. The previous process generated two locations per day, one for midday and one for midnight, as intermediate points between each sunrise and sunset. Location uncertainty was assigned by plotting locations on a map, and evaluating (i) distance from previous and next location, (ii) uncertainty assigned to previous twilights, and (iii) number of days until or from equinoxes. This credibility value was used to retain only the most credible locations. Last, a quadratic speed filter was then applied to every track, labelling and removing those locations with speed above the 95th percentile of the distribution of speed values (McConnell et al., 1992).

Migratory movements of Cory's and Scopoli's shearwaters overlap with the autumn and spring equinoxes. Currently, several researchers are working on developing state-of-the-art algorithms to reduce uncertainty related to equinox periods but also to reduce processing time (Gunnarsson et al., 2002; Ristic et al., 2004; Tremblay et al., 2009; Rakhimberdiev et al., 2015, 2016; Merkel et al., 2016). In this work, a modelling process was applied to locations obtained in the previous step (Tremblay et al., 2009). The animal movement can be interpreted as a temporal series of steps, where each step is characterized by a distance between locations, a speed, and an azimuth. The probabilistic distribution of the values of azimuth and speed in the time series determines the type of movement of an animal, which can be a simple straight line or a complex random movement. Accordingly, each possible step can be predicted with an associated probabilistic uncertainty by randomly selecting consecutive azimuth and speed values, and weighting them based on additional prior information (Tremblay et al., 2009). In the studied species, this additional information included the starting point of each trip (i.e., the breeding colony), every previous and subsequent locations, the longitude (which is not affected by the equinoxes), the speed, and a land mask as a constraint to force locations to be located over the sea. For each track resulting from the analysis of the light curves, 50 possible tracks were generated and averaged to get finally a track per individual and year, following Tremblay et al. (2009). Tracks obtained were used for further analyses.

Figure 4 • An individual of Scopoli's shearwater breeding colony in Pantaleu (Mallorca) and tracked with geolocator. The geolocator is visible in the left leg. This bird was photographed when it approached a touristic boat. © Maties Rebassa.

Sampling effort, sample size and study period

Regarding movements during the breeding period, the analysis included GPS data from 13 locations and 6 years (2007, 2010, 2011, 2012, 2014, 2015), 299 individuals, 813 602 locations and 1 546 foraging trips. To simplify the analyses only one year per colony was considered. For most of the colonies, only GPS data from the chick-rearing phase was included. The chick-rearing period is probably the most studied and therefore the most appropriate for making comparisons between colonies. In the case of Cala Morell (Menorca) and Veneguera (Gran Canaria), the analyses included GPS data from pre-laying, incubation and chick-rearing phases to explore the variability in foraging areas and behaviour over the breeding period.

Regarding geolocators, the analyses included data from 214 geolocators recovered, which on average were active for a year and a half, deployed in three different locations between 2007 and 2012, and recovered from 2008 to 2013. The unfiltered dataset contained 203 427 geographic locations, corresponding to 309 complete year-round trips from 161 individuals. 95 individuals and 207 trips from Veneguera, 20 individuals and 30 trips from Montaña Clara, and 46 individuals and 72 trips from Pantaleu. See Table 1 and 2 for further details.

TABLE 1 • Number of GPS locations, foraging trips, and individuals tracked using GPS devices, by species, colony, year and breeding phase (pre-laying, incubation and chick-rearing).

Breeding colony	Year	Breeding phase	GPS locations	Individuals	Trips
CORY'S SHEARWATER					
Alegranza	2010	Chick-rearing	33 044	27	27
Chafarinas	2011	Chick-rearing	1 332	1	2
Cíes	2015	Chick-rearing	8 358	3	16
Montaña Clara	2015	Chick-rearing	21 859	10	34
Terreros	2014	Chick-rearing	7 426	3	20
Timanfaya	2015	Chick-rearing	39 249	29	176
Veneguera	2012	Pre-laying	4 042	11	51
	2012	Incubation	24 035	21	39
	2012	Chick-rearing	21 280	19	45
SCOPOLI'S SHEARWATER					
Illa de l'Aire	2007	Chick-rearing	5 770	4	9
Cabrera	2015	Chick-rearing	82 730	32	219
Chafarinas	2011	Chick-rearing	16 019	8	40
Columbretes	2012	Chick-rearing	70 051	18	182
Cala Morell	2014	Pre-laying	277 246	51	400
	2014	Incubation	22 098	10	19
	2014	Chick-rearing	69 386	25	134

TABLE 2 • Number of trips per year and total number of individuals tracked by light-level geolocation at the breeding colonies of Veneguera and Montaña Clara (Gran Canaria and Lanzarote, Canary Islands, where the Cory's shearwaters breed), and Pantaleu (Mallorca, Balearic Islands, where the Scopoli's shearwaters breed).

	Cory's shearwater		Scopoli's shearwater
Breeding colony	**Veneguera**	**Montaña Clara**	**Pantaleu**
Individuals	**95**	**20**	**46**
Trips per wintering period			
2007-2008	25	-	-
2008-2009	26	-	-
2009-2010	26	-	20
2010-2011	44	-	24
2011-2012	58	18	22
2012-2013	28	12	6

Movements & behaviour

Foraging areas in the breeding period

GPS devices allow recording individual movements and distribution during the breeding period. Several descriptive parameters of the foraging trips were computed for every breeding colony (including median and 95% confidence interval): (1) total distance travelled, i.e., the total trip length; (2) total trip duration (in hours), and (3) maximum distance reached, i.e., the maximum distance from the colony to the furthest point reached during the trip. Confidence intervals were calculated using statistical bootstrapping techniques.

Main foraging areas were identified using data from chick-rearing, and also incubation in the case of Veneguera and Cala Morell. Bivariate Kernel Density Estimation (KDE) was used to delimit foraging areas (Fieberg & Kochanny, 2005; Kie et al., 2010; Lascelles et al., 2016). KDE estimates the probability of occurrence based on distribution and density of spatial locations, providing a continuous surface of presence probabilities. Smaller probability contours represent picks in the density distribution, i.e., congregating a greater number of location and therefore corresponding to areas of greater, intensive use. KDE is a method widely used in remote tracking studies of marine birds, including those aimed to design marine protected areas, as its results are easily interpreted (Arcos et al., 2012; Lascelles et al., 2016; Wood et al., 2000). KDE was computed using locations previously identified as intensive foraging through the Expected Maximization binary Clustering (EMbC, see details below). Apart from the foraging areas near the colonies, foraging areas used far from the breeding sites were also characterized. To avoid a bias in the representativeness imposed by a higher density of locations near the colonies, KDE was computed in successive steps, first excluding GPS locations inside a buffer of 100 km from the colony, then without excluding them, and finally, combining all the polygons into a single multi-polygon.

Migratory flyways

Flyways used during migration were characterised based on locations included between the onset of post-breeding migration and the arrival to the main wintering area, and between the onset of pre-breeding migration and the arrival to the breeding sites. Only fully recorded migratory trips were considered, thus excluding tracks with gaps. Movement-based Kernel Density Estimators (MKDE) were used to identify the post- and pre-breeding migratory flyways. MKDE were applied on year-round trips derived from modelling geolocator data, grouped by main wintering area. Unlike the KDE method, which considers independent locations and the probability of distribution in space according to a Gaussian function, the MKDE method takes into account the relationship between consecutive locations, thus incorporating into the classical concept of Kernel the intrinsic dependence of locations along trajectories (Benhamou & Cornélis, 2010; Benhamou, 2011; Benhamou & Riotte-Lambert, 2012).

Wintering areas: geographic location, migratory connectivity and site fidelity

Stationary areas used by the birds out of the breeding period were considered as wintering areas. These wintering areas excluded stopovers, i.e., areas were birds remained less than 5 days (Dias et al., 2011). When a bird used more than a single wintering area in the same non-breeding period, the main wintering area was defined as that area where the bird spent the greatest number of days. 50% contours of KDE were used to delimit main wintering areas at the population level. Individual KDE and the centroid of 50% probability contours were also computed.

Migratory connectivity is defined as the degree to which individuals or populations with the same origin tend to remain aggregated or, conversely, segregated, over the different non-breeding areas (Abel & Sander, 2014). The index proposed by Ambrosini et al. (2009) was calculated to quantify migratory connectivity. In addition, data was represented in a chord diagram to better visualize the connectivity (Gu et al., 2014). For this particular analysis and due to limitations in sample size (only three colonies tracked with geolocator: Pantaleu, Veneguera and Montaña Clara), both Cory's and Scopoli's shearwaters were considered together, without differentiating between species.

Wintering site fidelity was evaluated at intra-individual scale for birds tracked for more than a complete year-round, measuring the average overlap between every pair of wintering areas used while a bird was tracked. Birds were grouped attending to the number of years tracked (two to six years), and a value of overlap (mean and 95% confidence interval) was calculated by statistical resampling techniques.

Behavioural patterns in the breeding period

Behavioural annotation was applied on GPS tracks. To do so, the *Expectation-Maximization Binary Clustering* algorithm (EMbC) was applied on every foraging trip (Garriga et al. 2016). This is an unsupervised clustering method that provides a classification (and uncertainty) of every data point into an n-dimensional space, where n is the square of the number of input features used for classification. Unlike other clustering methods, the *EMbC* algorithm was developed specifically for behavioural annotation on tracking data. It provides simple semantics easily interpretable in a biological context. Using speed and turning angle as input features, every GPS location was classified into one out of four behavioural modes: resting (low speed and low turning angle), (2) intensive search (low speed and high turning angle), (3) extensive search (high speed and high turning angle), and (4) relocating (high speed and low turning angle) (Figure 5).

These four behavioural modes correspond to four putative basic behaviours of seabirds. Resting corresponds to drifting on the water, at low speed and in approximately straight line. Intensive search pinpoints foraging areas with a concentration of prey. Extensive search corresponds to search among prey patches. Relocation corresponds to long, direct flights between distant areas, mainly commuting (Figure 6).

Spatial and temporal distribution of behaviours throughout the breeding period was analysed for the colonies of Veneguera (Gran Canaria) and Cala Morell (Menorca). A behavioural landscape was built up for each breeding phase (pre-laying, incubation and chick-rearing) (Dean et al., 2012). To do so, firstly the EMbC was applied, and later every GPS data point was classified as day or night according to timestamp and geographic location. Next, extensive and intensive search were grouped into foraging behaviour. The total area used by the birds from each colony was rasterized into a grid with a cell size of 0.2 geographical degrees. For every cell, time spent in every behaviour by day and night was calculated. The main behaviour at each cell (i.e., with the greatest time) was scaled to the total time invested in that behaviour during the whole period. The process resulted in a behavioural landscape where the colour of each cell represents the most frequent behaviour, and the colour intensity indicates the importance of that cell for that particular behaviour across the distribution range.

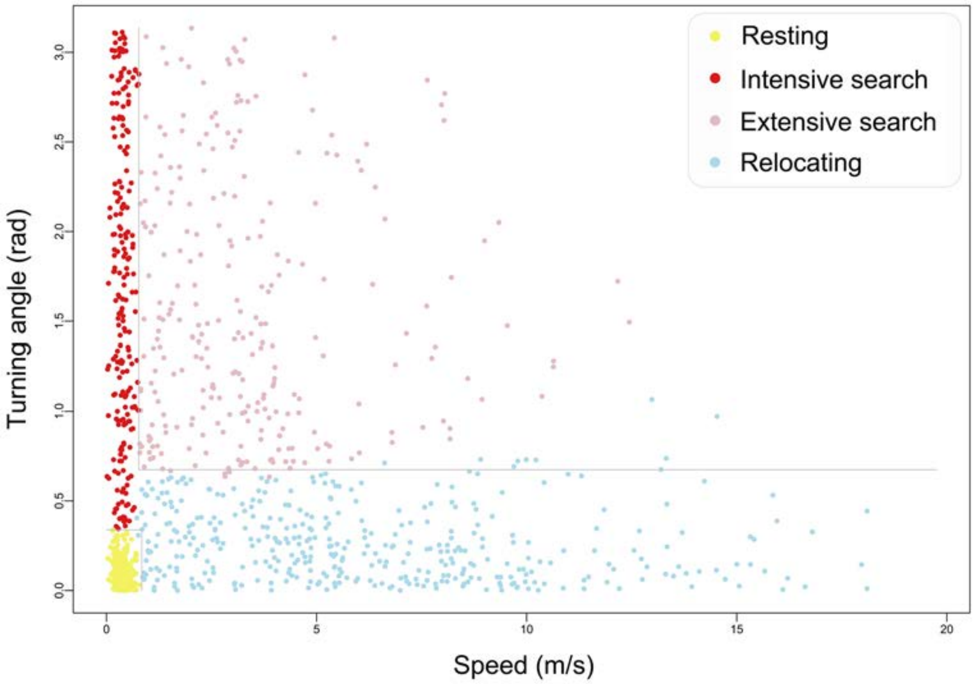

Figure 5 • Classification of GPS locations into behavioural modes after applying the Expectation-Maximization Binary Clustering algorithm (EMbC) developed by Garriga et al. (2016). Four possible putative behaviours are inferred: intensive search (red dots), extensive search (pink dots), resting (yellow dots) and relocating (blue dots).

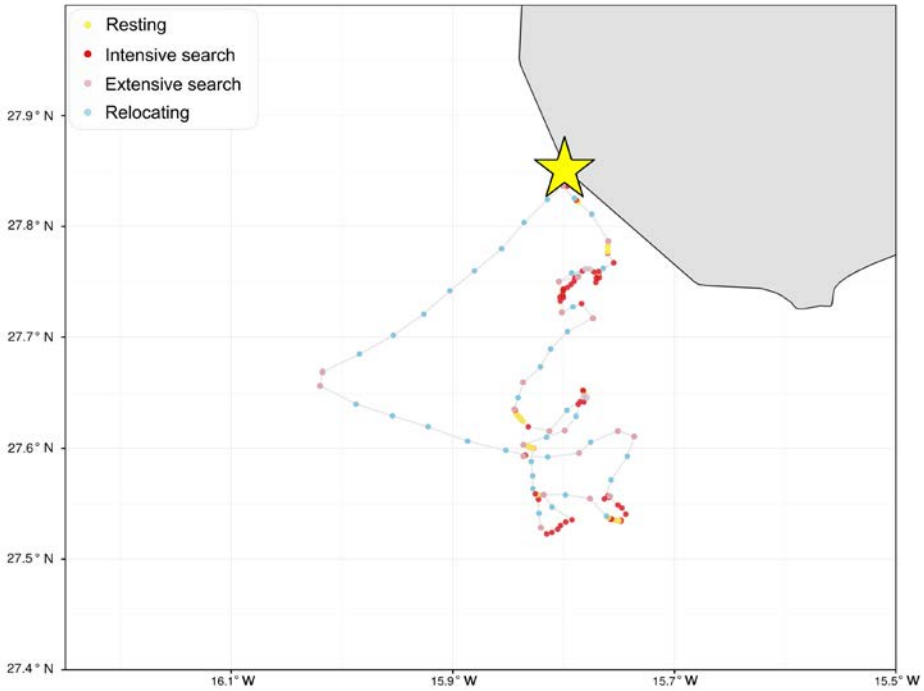

Figure 6 • Track of a Cory's shearwater tagged with a GPS logger in Veneguera (Gran Canaria). After applying the EMbC algorithm (Garriga et al., 2016), putative behaviour is assigned to each GPS location. The grey line represents the track. Red dots represent locations of intensive search (i.e. intensive foraging), pink dots represent extensive search locations, yellow dots represent resting episodes and blue dots correspond to relocating. The yellow star represents the breeding colony.

Behavioural patterns year-round

Geolocator models used in this study were sensitive to seawater salinity through conductivity between the metallic pins. These devices measured conductivity in a quasi-continuous mode (every 3 or 6 seconds, depending on the model). The number of positive records, i.e., records registering conductivity, registered at regular intervals (every 5 or 10 minutes, depending on the model) is stored in the memory, meaning about 50 000-100 000 records per geolocator in a year. This information indicates whether the device was in contact with salt water at any time, and therefore can be used as a proxy to infer when the bird was flying or resting on the water. The unique weakness is during the breeding period when it is not possible to differentiate between flying or being on land in the colony. Therefore, it is possible to infer daily activity patterns of birds throughout the year, unveil circadian rhythm, and relate them to environmental features. The high temporal resolution of this data source often leads to an early memory overload, driving to a lower sample size compared to positional data. Conductivity data were used to infer behaviour over the annual cycle of both Cory's and Scopoli's shearwater, and to compare the activity patterns according to the wintering area selected by the individuals.

Moreover, behavioural landscapes were built for the wintering areas based on the Night Flight Index (NFI, Dias et al., 2012a; Ramos et al., 2015). NFI represents the difference between the proportion of time spent flying during the daylight and darkness, divided by the higher of these two values. Thus, NFI ranges between -1, when flight activity is restricted exclusively to daytime hours, and +1, when flight activity occurs entirely during the night. This index was calculated on a grid of 2 geographic degrees cell size, according to the average spatial error of the geolocators.

Phenology

Individuals' phenology was inferred from geolocator tracking data. The onset of the post-breeding migration corresponded to a noticeable change in bearing and distance travelled, flying away from the previous core locations in the breeding area. After that, the first location where the bird showed a stationary behaviour, without evident directionality, was considered as the first location in a wintering area. Similarly, the last location within a stationary area before starting a clear, directional flight towards the breeding area was identified as the onset of the pre-breeding migration. The first day with stationary behaviour near the breeding colony was considered as the day of arrival to the breeding area. Arrival to the breeding area sometimes overlapped with the equinox period, preventing to infer the arrival date. When that happened, conductivity data was used to infer such date, considering the first night in an almost continuous dry state as the first night visiting the breeding colony.

Environmental information

Two environmental variables were measured within the distribution range of birds in the wintering period: chlorophyll *a* and bathymetry (Louzao et al., 2009, 2011). Chlorophyll-*a* is a pigment produced by phytoplankton. The concentration of chlorophyll-*a* on the sea surface can be inferred through satellite imagery (Carder et al., 2004), and it is frequently used as a proxy of productivity in the oceans, thus pointing out areas with an abundance of intermediate consumers (macro-zooplankton and small epipelagic fish) and ultimately top-predators such as seabirds. Values of chlorophyll *a* and bathymetry at every bird location in the wintering areas were extracted from layers of 30 days as temporal resolution and a spatial resolution of 4 km. Products downloaded corresponded to L3 processing and gathered by the AQUA MODIS sensor (*Moderate Resolution Imaging Spectroradiometer*) installed in the EOS PM-1 satellite. These products were downloaded from the NOAA ERDDAP platform system (http://coastwatch.pfeg.noaa.gov/erddap/index.html; Simons, 2011). The bathymetric information of the Atlantic comes from the ETOPO 1 model (Lover & Eakins, 2009).

Computing resources for data analysis

GPS and geolocator data were processed using custom-built functions in R (R Core Team, 2016). The environmental information was processed and analysed using the *raster* package (R.J. The & van Etten, 2012). Spatial analyses of locations were carried out using functions from the R packages *sp* (Bivand & Lewin-koh, 2016; Pebesma & Bivand, 2005; Bivand et al., 2013), *adehabitatHR* and *adehabitatLT* (Calenge, 2006, 2011). MKDE were computed using *Biased Random Bridges* (http://www.cefe.cnrs.fr/images/D_EE/eq_EC/simon_benhamou) in Pascal environment. Plots and visualizations were produced with the *R* package *ggplot2* (Wickham, 2009). Maps were produced in R (R Core Team, 2016) and ArcGIS 10.0 (ESRI, 2011).

RESULTS AND DISCUSSION

Foraging movements during the breeding period

During the breeding period, shearwaters and other Procellariiformes exhibit to a greater or lesser extent a particular foraging strategy during the chick-rearing phase, called dual foraging strategy. This strategy alternates much frequent short trips with less frequent long trips. During the former, birds exploit waters relatively close to the colony, where they obtain food to feed the chick frequently. During the latter, birds commute to distant but generally more productive areas, where they feed to replenish their body reserves eroded by the breeding duties (Weimerskirch et al., 1994; Magalhães et al., 2008; Shoji et al., 2015).

In this context, Cory's shearwaters, in particular those breeding in colonies of the Canary Islands, engaged in long trips towards the North-West African shelf (Western Sahara and southern Morocco off-shore; Figure 7). In this region, there is a highly productive upwelling system that provides important resources for seabirds (Navarro & González-Solís, 2009; Ramos et al., 2013; Grecian et al., 2016). Birds from these colonies exhibited a more evident dual foraging strategy, particularly in the case of individuals from Veneguera and Alegranza, which engaged in short trips of few days near the colonies but commuted towards distant foraging areas, travelling more than 1 000 km in a single trip (Table 3). Because of the proximity of Montaña Clara and Timanfaya to the African waters, the bimodal pattern was not clear for birds breeding in these islands, likely because of many short trips headed to these productive waters. Differences observed between Timanfaya and Montaña Clara respect to Alegranza may relate to annual differences in oceanographic conditions, given that fieldwork was carried out in different years. In the case of the small colony of Cory's shearwater in Galicia, birds intensively used the waters over the Galician and Portuguese continental shelf during the short trips, while entering the Atlantic during long ones.

In the case of the Scopoli's shearwater, birds made extensive use of waters on the Levantine shelf, in the eastern continental side of Spain, moving between the Straits of Gibraltar and the southern Gulf of

Table 3 • Descriptive parameters of Foraging trip performed during the chick-rearing period. Values show median and 95% Confidence Interval calculated by bootstrapping.

Breeding colony	Species	Trips	Year	Trip length (km)	Trip duration (h)	Maximum distance reached (km)
Atlantic Ocean						
Veneguera	Cory's sh.	45	2012	1 073.63 (548.32-1 506.27)	110.21 (45.14-139.64)	320.55 (48.56-389.04)
Montaña Clara	Cory's sh.	34	2015	508.08 (336.21-585.77)	39.12 (19.69-42.95)	173.60 (135.05-190.95)
Timanfaya	Cory's sh.	176	2015	273.83 (218.28-396.47)	21.60 (19.24-24.97)	109.48 (45.55-146.87)
Alegranza	Cory's sh.	27	2010	1 105.47 (582.11-1 676.04)	121.05 (44.12-140.88)	510.83 (230.50-547.1)
Cíes	Cory's sh.	16	2015	269.50 (199.36-701.02)	24.89 (17.59-67.16)	88.43 (53.90-168.89)
Mediterranean Sea						
Illa de l'Aire	Scopoli's sh.	9	2007	143.86 (97.97-998.82)	20.52 (17.52-74.05)	56.80 (37.37-310.57)
Cala Morell	Scopoli's sh.	145	2014	179.15 (162.34-217.67)	20.14 (18.13-21.98)	45.64 (36.90-51.59)
Cabrera	Scopoli's sh.	219	2015	142.29 (131.81-159.05)	22.00 (21.15-22.74)	32.36 (27.69-35.42)
Pantaleu	Scopoli's sh.	22	2007	292.82 (174.29-416.26)	23.00 (19.93-37.44)	73.17 (39.47-172.43)
Columbretes	Scopoli's sh.	182	2012	140.61 (119.96-157.37)	20.52 (18.58-21.73)	35.98 (32.75-37.72)
Palomas	Scopoli's sh.	111	2014	208.74 (179.75-231.45)	23.05 (21.51-40.12)	39.85 (33.14-44.06)
Terreros	Cory's sh.	20	2014	166.29 (111.08-247.19)	15.37 (14.7-15.97)	49.80 (28.01-101.73)
Chafarinas	Scopoli's sh.	40	2011	177.07 (132.28-208.72)	23.31 (21.2-27.32)	35.63 (23.11-47.54)
Chafarinas	Cory's sh.	2	2011	480.51 (2.35-480.51)	55.82 (0.67-55.82)	131.48 (1.13-131.48)

Lyon (Figure 8). This was observed in birds breeding in Columbretes, Palomas and Terreros, but also in the long trips of birds from the Balearic Islands. Indeed, regarding some colonies in the Balearic archipelago, a large number of birds commuted towards the Levantine shelf and slope, although many others made greater use of Balearic waters, especially in the case of the individuals from Cala Morell. The areas used along the eastern continental side of Spain are generally more productive than waters around the Balearic Islands (Coll et al., 2010). In the case of Chafarinas, birds made intense use of the waters in the southern side of the Mediterranean, as also did birds from Palomas. In general, the dual foraging strategy was not so much noticeable in birds from the Mediterranean colonies, maybe due to the limited extension of the Mediterranean basin, where distances between the most suitable areas for breeding and the most productive areas are relatively short for gliding seabirds. The trip length was lower than 300 km, maximum distance reached was about 70 km, and trip duration was about 24 hours (values corresponding to the median; see details in Table 3).

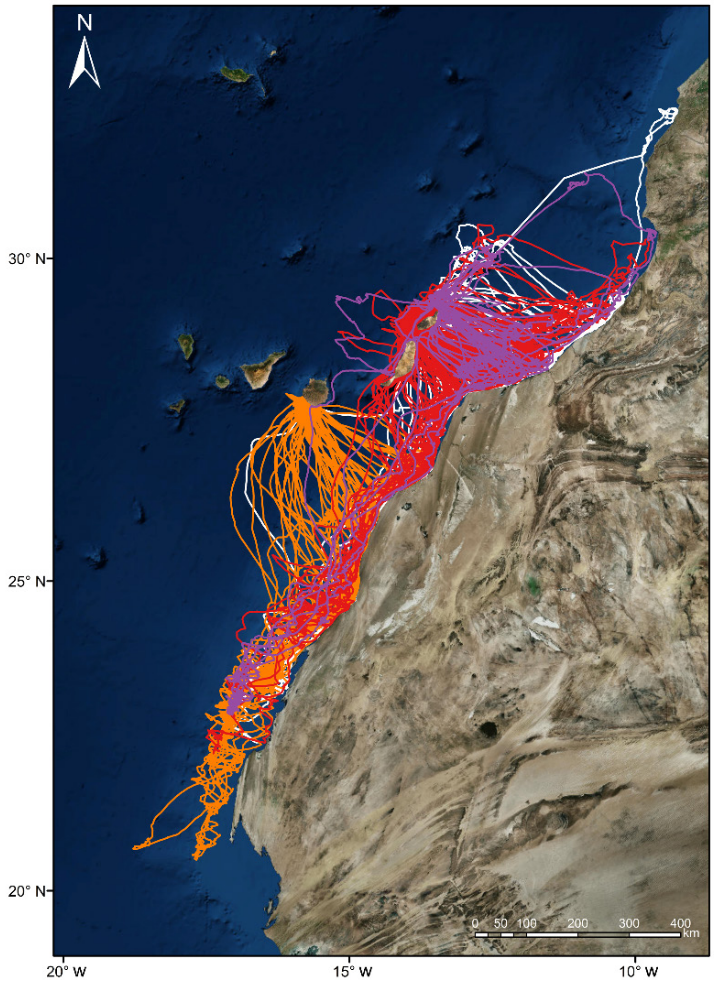

Figure 7 • A general overview of the foraging trips of Cory's shearwaters breeding in the Canary Islands. Lines represent trips from adult breeders tracked with GPS logger during the chick-rearing period. Each colour represents a colony: Alegranza (white), Montaña Clara (purple), Timanfaya (red) and Veneguera (orange). These birds made an extensive use of the African shelf.

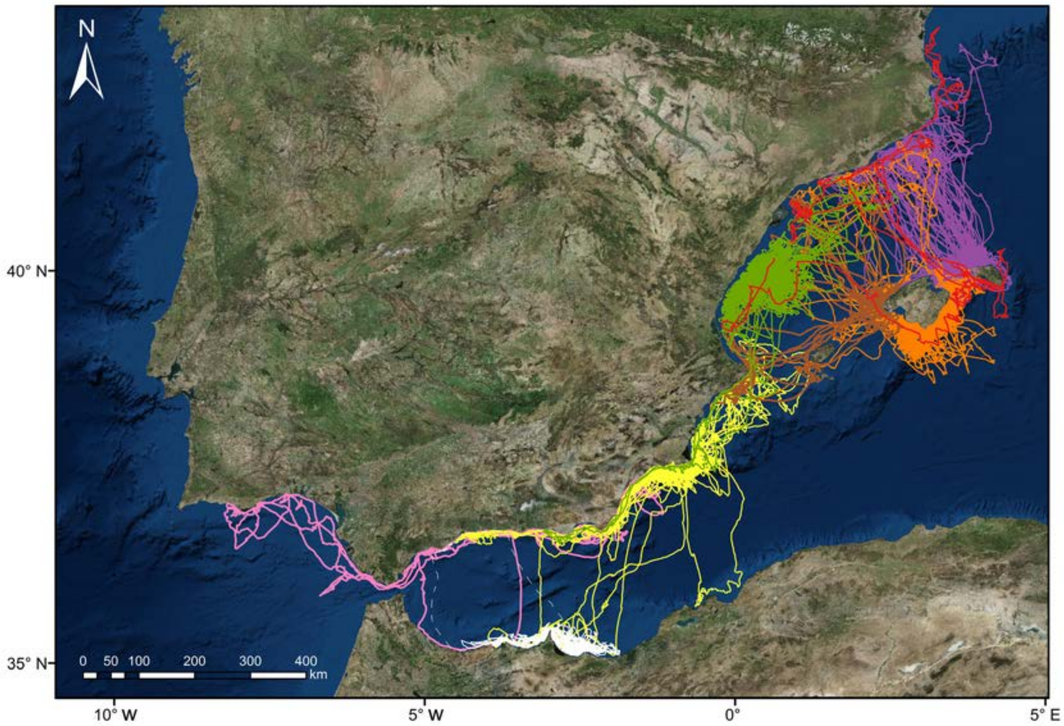

Figure 8 • A general overview of foraging trips of Scopoli's and Cory's shearwaters from Spanish colonies in the Mediterranean Sea. Each line represents a trip from an adult breeder tracked with GPS logger during the chick-rearing period. Aire islet (red), Cala Morell (purple), Cabrera (orange), Pantaleu (brown), Columbretes (green), Palomas (yellow), and Chafarinas (white solid lines) represent tracks from Scopoli's shearwater. Regarding the Cory's shearwater, white dashed lines correspond to individuals of this species from Chafarinas, where both species breed in sympatry. Lines in pink represent tracks of Cory's shearwaters from Terreros.

Colonies in the Atlantic Ocean

Individuals from colonies in the Canary Islands intensively foraged in the North West African shelf, over the so-called Saharan upwelling, within the Canary Current system (Figure 9). Off the Sahara and Mauritania, this system is particularly active during the summer, when the trade winds blow strongly from the northeast and cause the warmer surface water layers to shift towards the centre of the Atlantic. As a result, highly nutrient-rich cold waters rise from the bottom (Pérez & Barton, 2001; Davenport et al., 2002; Hernández-León et al., 2007). Thanks to this process, the area holds a rich community of top-predators, and it provides important fishing resources (Arístegui et al., 2006; Ramos et al., 2013; Scales et al., 2015; Grecian et al., 2016). Furthermore, the Canary Islands, just about 200 km from the African coast, are largely influenced by this upwelling system. In this archipelago, the convergence among trade winds and the topography of the islands promotes a local increase in marine productivity (Hernández-León, 1991).

Veneguera is the southernmost breeding colony included in this study. During the breeding period, birds from this colony foraged in waters off the southwest of Gran Canaria, while on their long trips they commuted further south than birds from any other colony, reaching Cabo Blanco, on the border of Western Sahara with Mauritania (Figure 9). None of the tracked birds ever moved further north of the island of Gran Canaria.

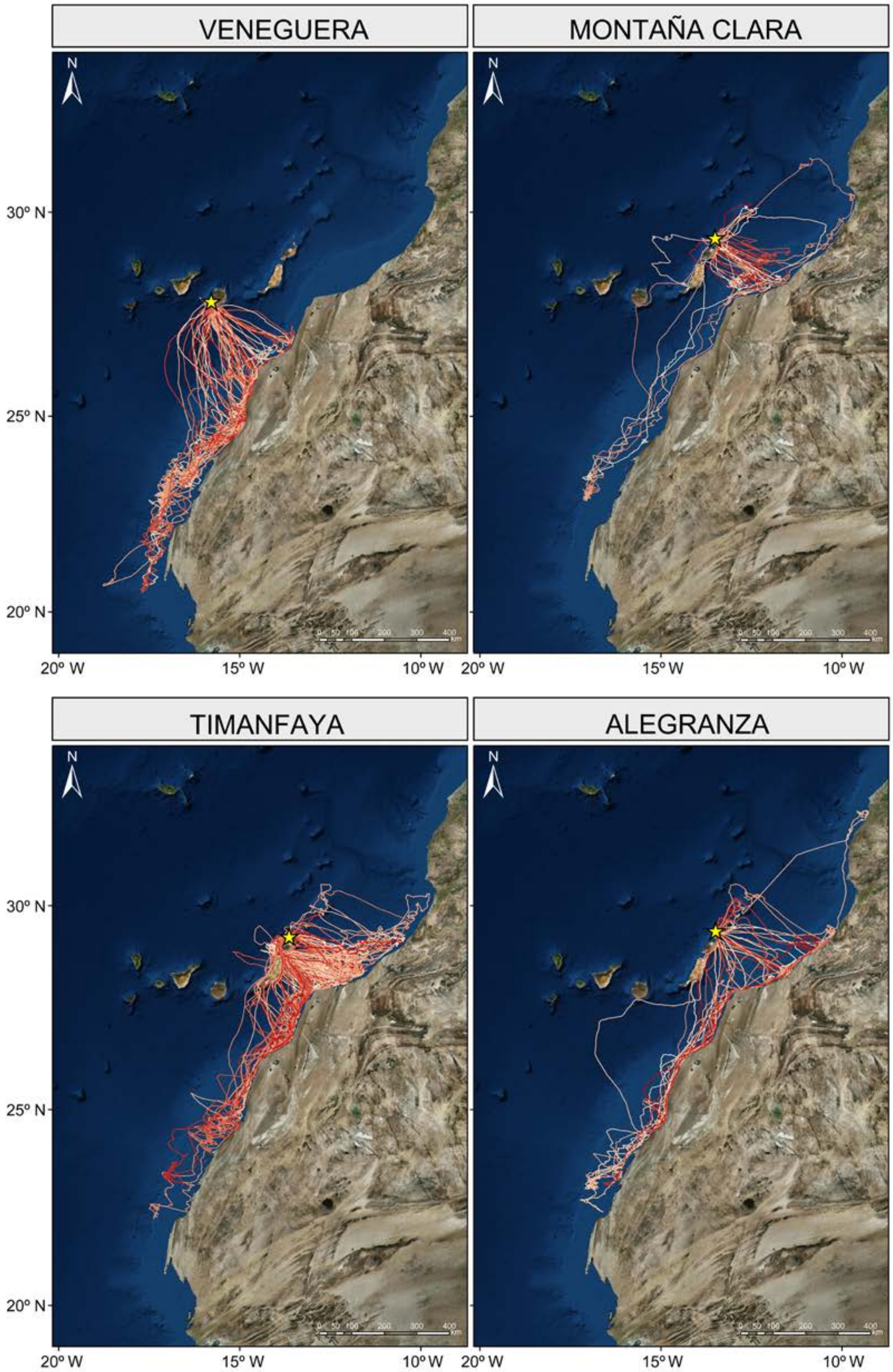

Figure 9 • Foraging trips of Cory's shearwaters from the breeding colonies in the Canary Islands. Each line represents a different trip. The stars indicate the location of the breeding colonies.

Birds from Montaña Clara, Timanfaya and Alegranza engaged in short trips in the waters around Lanzarote and Fuerteventura. They moved north to the Conception Bank and the Chinijo archipelago. On the African shelf, birds from both Montaña Clara and Timanfaya shared foraging areas, reaching Cabo Aguer in Morocco to the north and Cabo Dakhla to the south (Figure 9). Exceptionally, some individuals approached Cabo Blanco, although always staying further north compared to birds from Veneguera (Figure 9; Figure 10).

The few birds tracked from the small colony of Cíes, in Galicia, foraged in waters around the Rías Baixas area in their short trips. They also performed longer trips spreading widely over the continental shelf of Galicia and Portugal, reaching up to 200 km to the south. Besides, they made a few extraordinary long trips, headed towards northwest and west, up to about 500 km from the colony, in fully oceanic waters of the Atlantic (Figure 11).

Regarding trip duration, there were no common patterns but a different frequency by colony (Figure 12). Birds from Veneguera and Alegranza engaged in long trips more frequently than birds from Timanfaya, where birds mostly engaged in short trips.

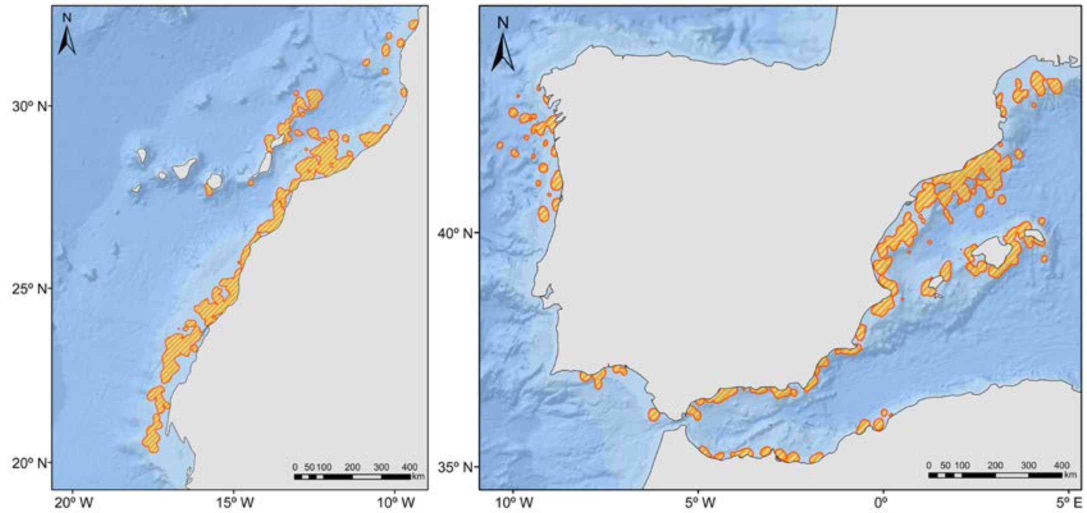

FIGURE 10 • Main foraging grounds of Cory's and Scopoli's shearwaters from breeding colonies in Spain. These areas were identified through Kernel Density Estimation (KDE, Fieberg & Kochanny, 2005). KDE was applied to locations previously identified as intensive search behaviour by the EMbC algorithm (Garriga et al., 2016).

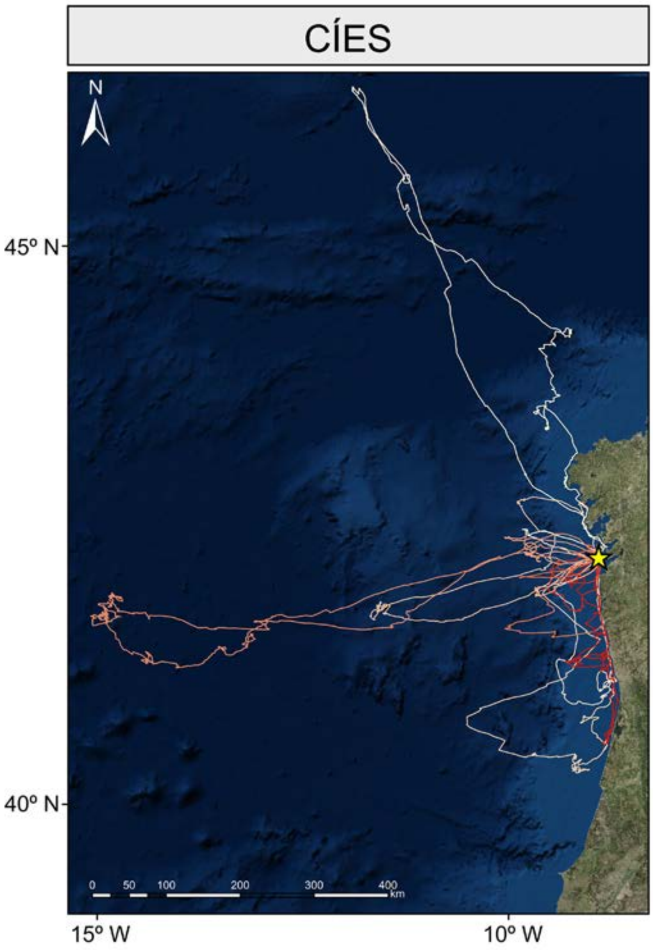

Figure 11 • Foraging trips of Cory's shearwaters from Cíes (Islas Atlánticas National Park, Galicia). Each line represents a different trip. The star indicates the location of the breeding colony.

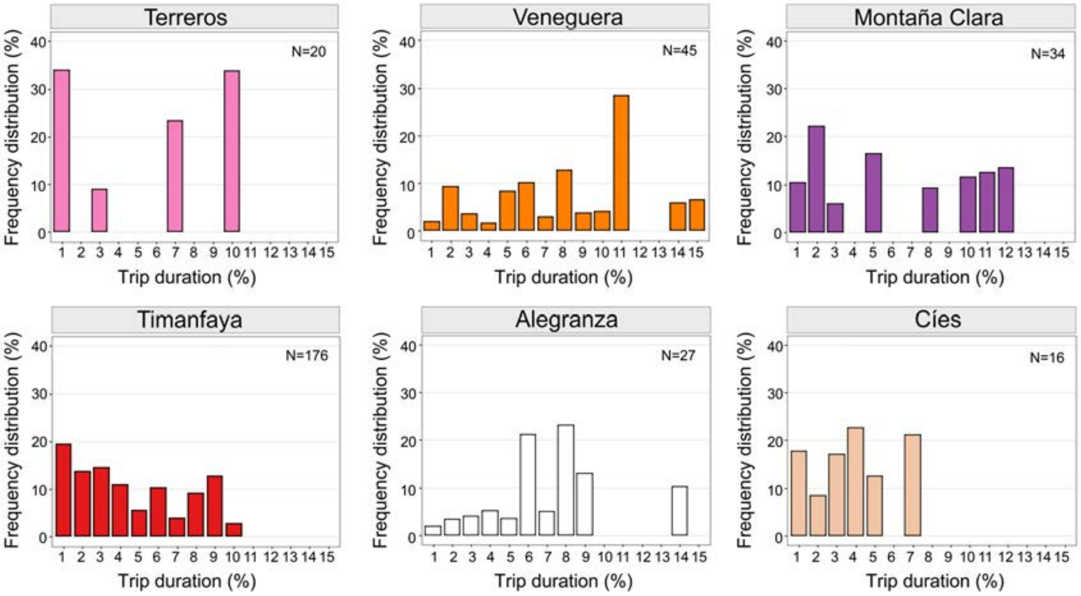

Figure 12 • Barplots showing the percentage frequency distribution of trip duration for Cory's shearwaters, from one to 15 days, during the chick-rearing period. Each facet represents a colony. Sample size, i.e., the number of trips, is indicated in the right upper corner. Unlike the colonies in the Mediterranean, there was no clear pattern for the colonies in the Atlantic.

Colonies in the Mediterranean Sea

Despite their geographical proximity, individuals from different Balearic colonies exploited very diverse areas. In general, there was apparent spatial segregation between the foraging areas used by individuals from different colonies during the chick-rearing (Figure 13). Nevertheless, these differences may also be caused by the annual environmental conditions, as birds from different colonies were tracked in different years.

Birds from Illa de l'Aire engaged in short trips along the coast of Menorca, while long trips headed towards the French coast of the Gulf of Lyon to the north, and the Gulf of Valencia to the south (Figure 13). Birds from Cala Morell foraged mainly in the Minorca channel during the short trips, between the islands of Mallorca and Menorca, while they commuted to the Catalan continental shelf during the long trips, from Cap de Salou to the south to Cap de Creus and Golf of Roses to the north. Interestingly, any individual from Cala Morell visited the nutrient-rich waters of the Ebro Delta or the Gulf of Valencia.

Birds from Cabrera mostly used the shallow waters between Cabrera and southern Mallorca, yet making some incursions to the deeper waters over the slope in the west of Balearic Islands. Moreover, they made some long trips to the mainland coast, from the Gulf of Valencia to the south to Barcelona to the north (Figure 13).

Birds from Pantaleu used the waters of the northwestern shelf of Mallorca on their short trips, whereas moved further south on their long trips, reaching the Cabo de la Nao to the south to the Ebro Delta to the north (Figure13).

Birds from Columbretes mostly exploited the Levantine shelf, around the Columbretes archipelago and the Valencia channel. However, they also moved towards Barcelona to the north and Almería and Granada to the south, reaching the Alboran Sea (Figure 14).

Birds from Palomas mainly used the shallow waters around Mazarrón and the shelf between Cabo de Palos and Cabo de la Nao during their short trips. On some occasions, they moved to the Balearic archipelago to forage around Ibiza and Formentera. On their long trip, they also flew south-west along the coast, entering the Alboran Sea. Most trips headed waters to the north of the Almería-Orán oceanic front, where Atlantic water on the sea surface loss relevance in the Mediterranean basin. Nevertheless, some individuals also moved to the west, visiting the coast of Malaga and Granada, as well as African waters in the south side of the Mediterranean, around the Bahía of Orán (Algeria) and Cabo Tres Forcas (Morocco; Figure 14).

In the case of Terreros, one of the only two colonies of Cory's shearwater in the Mediterranean, birds showed a clear different behaviour with regards to Scopoli's shearwaters, especially with individuals from the nearby colony of Palomas. Although some short trips also headed to the shallow waters of Mazarrón, most birds from Terreros moved to waters south of the Almería-Orán oceanic front, which are strongly influenced by the Atlantic, such as the coast of the Alborán Sea and the waters off the northern coast of Morocco. Some individuals even crossed the Strait of Gibraltar to reach the waters of the Gulf of Cadiz, which has not been observed in Scopoli's shearwaters (Figure 14).

In Chafarinas, both species breed sympatrically. All tracked Scopoli's shearwaters remained on the North African Mediterranean side, foraging in waters around the Bay of Alhucemas (Morocco), Cape Tres Forcas (Algeria) and the shallow waters around the Chafarinas archipelago (Figure 14). The only Cory's shearwater tracked engaged in a comparatively longer trip than those of Scopoli's shearwaters. On this long trip, the bird crossed the Alboran Sea to forage along the coast of the Iberian Peninsula, off the provinces of Malaga, Granada and Almería (Figure 14). These differences in behaviour when both species breed in sympatry have already been described in Chafarinas (Navarro et al., 2009; Afán et al., 2014).

Regarding trip duration, based on colonies with larger sample size, short trips of about one day were the most frequent, with a decreasing investment of time in longer trips. Birds from Illa de l'Aire, Pantaleu and Chafarinas did not show this pattern, likely due to low sample size (Figure 15).

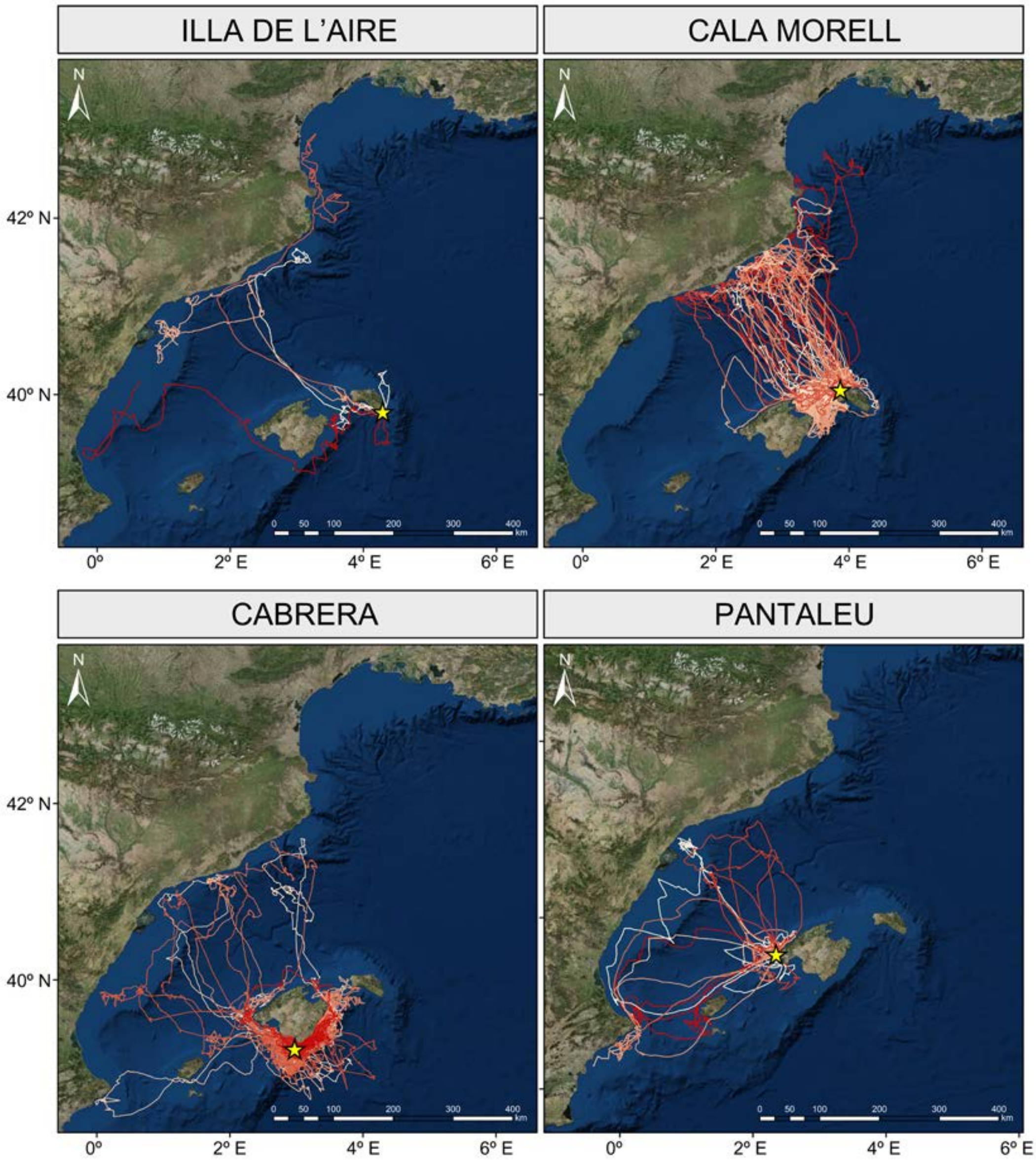

FIGURE 13 • Foraging trips of Scopoli's shearwaters from breeding colonies studied in the Balearic Islands. Each line represents a different trip. The stars indicate the location of the breeding colonies.

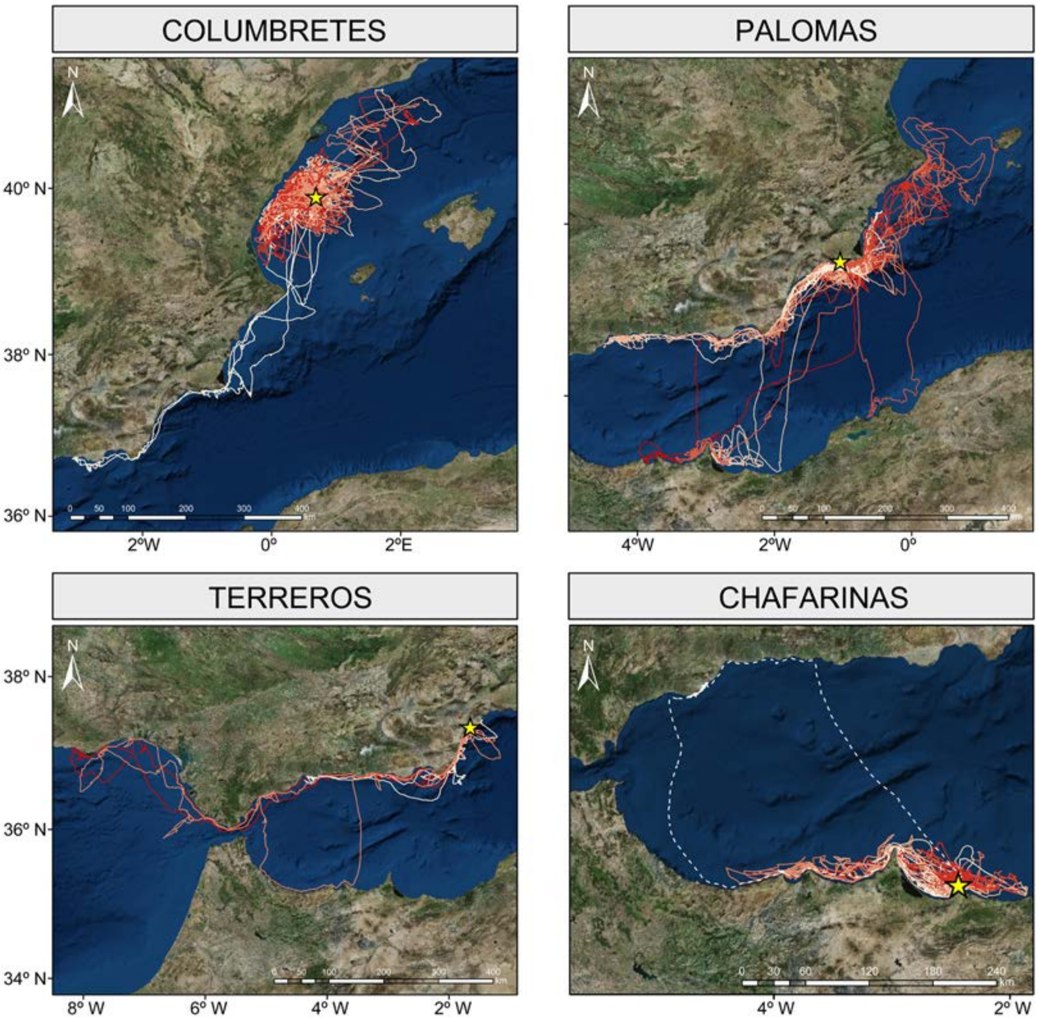

FIGURE 14 • Foraging trips of Scopoli's shearwaters breeding in Columbretes, Palomas and Chafarinas, and of Cory's shearwaters breeding in Terreros and Chafarinas. Each line represents a different trip. The stars indicate the location of the breeding colonies. In the map of Chafarinas, trips of Scopoli's shearwaters are represented by solid lines in different shades of red, and the trips of a Cory's shearwater are represented by white dashed lines (only one trip out of two recorded is noticeable in the map).

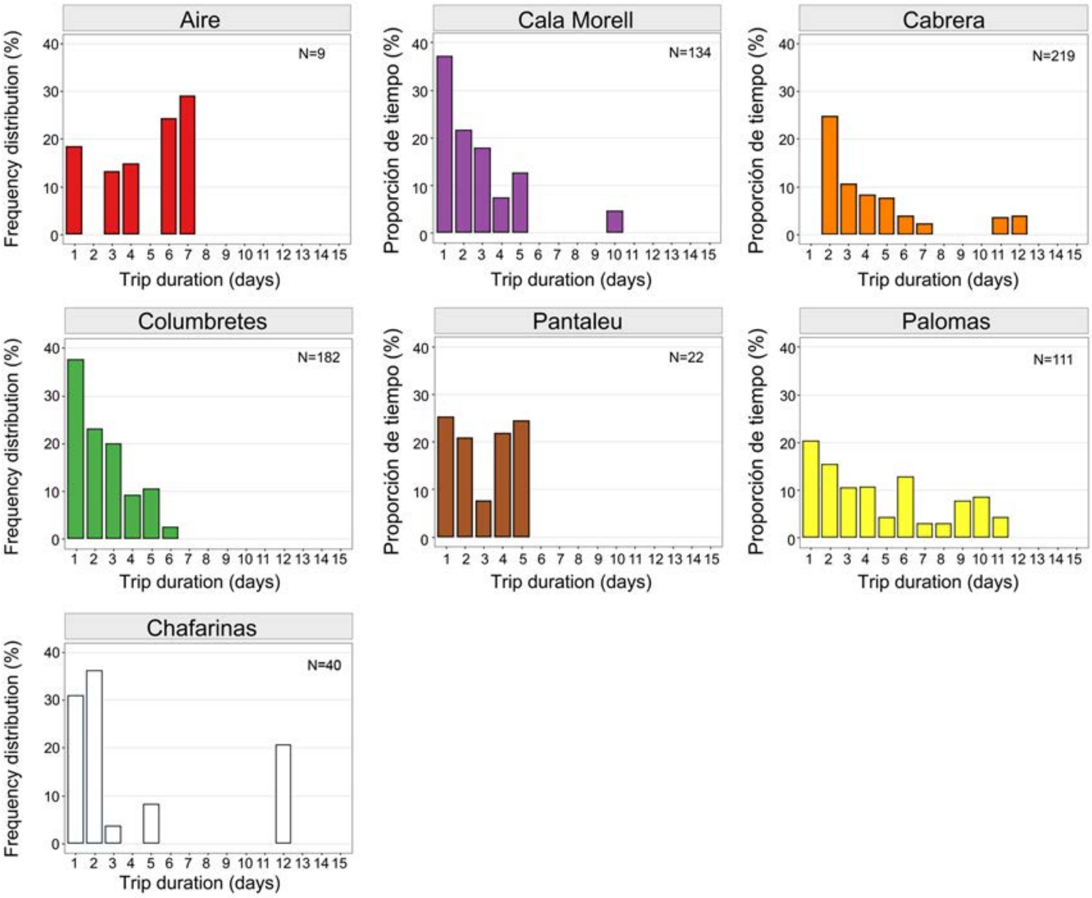

Figure 15 • Barplots showing the percentage frequency distribution of trip duration for Scopoli's shearwaters, from one to 15 days, during the chick-rearing period. Each facet represents a colony. Sample size, i.e., the number of trips, is indicated in the right upper corner. At least for colonies with representative sample size, foraging trips of one, two and three days were the most frequent, being the longer ones less frequent.

At-sea behaviour in the breeding period

A brief introduction

In late winter and early spring, Cory's shearwaters end pre-breeding migration after arriving at the breeding colony, setting the onset of the breeding period. This period entails almost 8 months, from February-March to October and November, when birds leave the breeding area and start post-breeding migration. During this period, three main phases can be distinguished: pre-laying, incubation and chick-rearing. Each one implies different behavioural constraints for the birds (Navarro et al., 2007).

During pre-laying, sexual differences in behaviour are more evident than during incubation and in the chick-rearing, because in the latter males and females share egg and chick caring (Paiva et al., 2010; Hedd et al., 2014; Phillips et al., 2017). The pre-laying phase can be split into sub-phases. The first begins after arriving at the breeding area, when the animals start to visit the colony, need to recover from migration, and prepare for reproduction (Arizmendi-Mejía et al., 2013). In a second sub-phase, the pairs are (re-) established, mating takes place, and males defend the nests (Werner et al., 2014). The third sub-phase is the pre-laying exodus, common to many Procellariiformes. After mating, females undertake a long trip that can last between two weeks and a month, visiting areas where they can find specific nutritional resources necessary for the egg formation (Jouanin et al., 2001; Navarro et al., 2007; Arizmendi-Mejía et al., 2013; Paiva et al., 2013b). Some authors pointed out that males could forage during this period in areas richer than those used by females, suggesting that females would search for areas not rich but able to provide some specific nutrients such as lipids and proteins, which do not necessarily coincide with the most productive areas (Werner et al., 2014). In any case, in this sub-phase males often return to the colony at night to defend the nest until the date when the female returns to lay the egg.

The incubation period begins with the female laying a single egg. Often, the female returns to the sea shortly after laying to feed and recover energy. As a result, the male frequently undertakes the first incubation bout. Both sex alternate in the incubation bouts to care the egg (Granadeiro et al., 1998a). The incubation bouts can last from less than a week up to 20 days (Reyes-González & González-Solís, 2016a), depending on the species, the colony, the distance to the areas with high productivity and the annual environmental conditions (Paiva et al., 2013a). While one of the members is foraging at sea, the other remains in the nest incubating, fasting. They often lose weight during this period, and thus they try to recover in their next foraging bout.

Hatching marks the onset of the chicken-rearing phase. During the first week, the brood-guarding, the chick is not able to regulate its own body temperature, so it needs to be under the parents to get warm. For this reason, parents' behaviour is similar to that shown during incubation, taking turns to care the chick, although shift more frequently at the nest (Catry et al., 2009). After a few days, the chick has developed more down and does not need to be warmed so frequently. Then, both parents start to leave the chick alone in the nest to search for food at sea. During this time, the parents visit the chick independently to fatten the chick, and may coincide or not at the nest. It is at this moment when the adult breeders perform the so-called dual foraging strategy previously explained. Finally, in late summer, once the chick has far more fat reserves than adults, the parents stop feeding it and no longer return to the nest. At the end of October, with plumage fully developed and fat reserves depleted, hungry fledglings leave the nest (Reyes-González & González-Solís, 2016a). With the first flight, they leave the colony, to which they will not return until three or four years as floaters, and will have the first breeding attempt at the age of 5 to 7 years old (Mougin et al., 2000; Jenouvrier et al., 2008).

Behavioural analysis of Cory's shearwater over the breeding period

Birds from Veneguera (Gran Canaria) were tracked over the three phases of the breeding period in 2012. However, only a few trips were recorded in pre-laying, in the second half of April, before the pre-laying exodus. Therefore, the observed behaviour cannot be generalised to the whole pre-laying phase. In the Canary Islands, plumes of productivity spreading from the African continental shelf largely determines the spatial ecology of Cory's shearwaters. Tracked birds (11 individuals, 51 trips) made intensive use of the waters to the southwest of Gran Canaria (Figure 16, top). Foraging took place mostly during the day (Figure 17, top). Some longer trip reached the African continental shelf, and foraging activity concentrated nearby the continental slope, both during day and night (Figure 17, top).

During the incubation phase, birds moved along the Saharan upwelling system, from the latitudes of the Canary Islands to the north to the northern edge of Mauritania to the south (Figure 16, centre). Behavioural

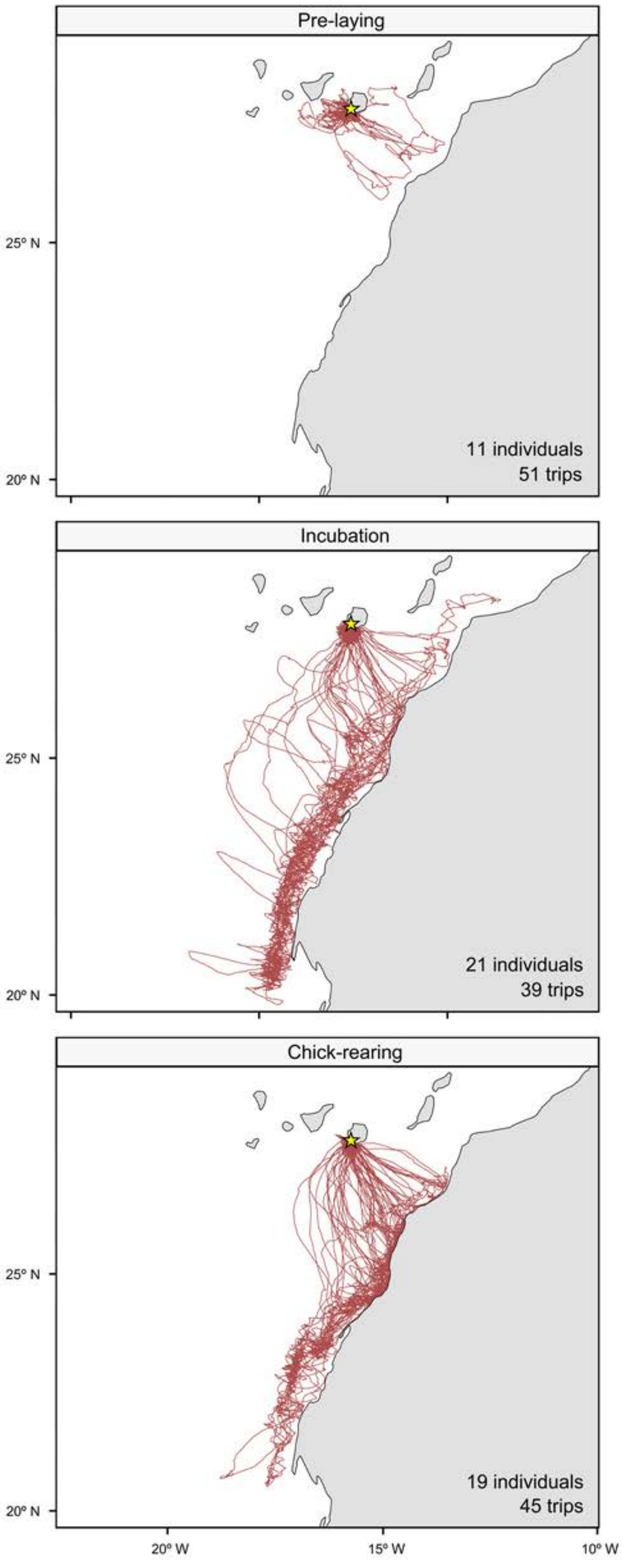

Figure 16 • Foraging trips of Cory's shearwaters breeding at Veneguera (Gran Canaria) in 2012. The map at the top shows the trips during the pre-laying phase (time window: April 15th - April 25th; 11 individuals, 51 trips; this period did not include the pre-laying exodus). The map in the centre shows trips of adult breeders in the first weeks after egg-laying, i.e., in the incubation phase (time window: June 16th - June 30th; 21 individuals, 39 trips). The map on the bottom shows the trips during the chick-rearing phase (time window: August 15th - September 11th; 19 individuals, 45 trips). Birds intensively used the waters surrounding the during the short trips, whereas birds commuted always and consistently to the African shelf during the long trips.

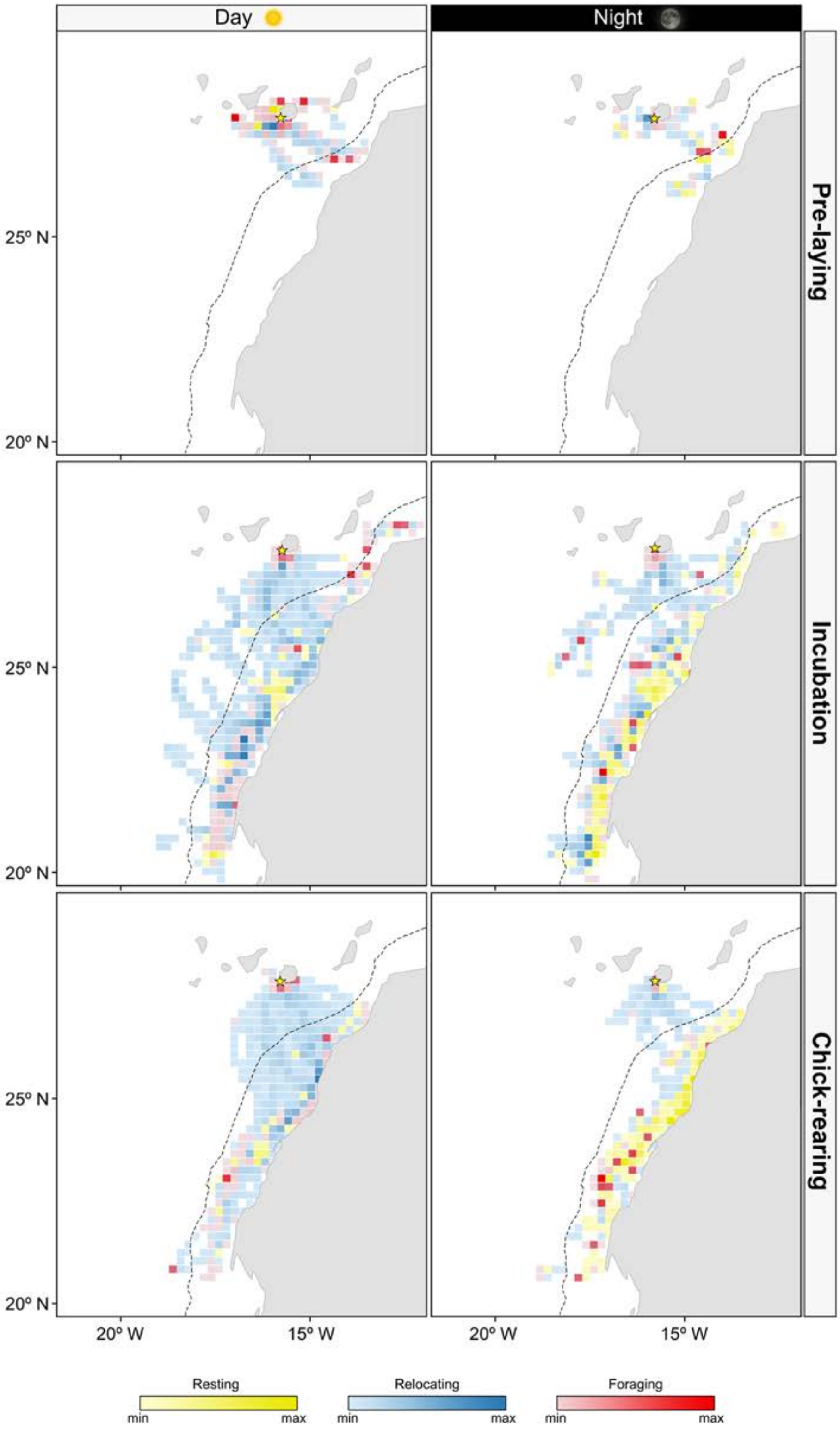

Figure 17 • Behavioural landscapes of Cory's shearwaters breeding in Veneguea (Gran Canaria) during 2012. Maps on the left represent diurnal behaviour and maps on the right represent nocturnal behaviour. For each cell, the colour identifies the most frequent behaviour, and its intensity represents the amount of time invested for that particular behaviour across the distribution range. Yellow colour represents resting, red colour represents foraging, and the blue colour represents relocating. The dashed line represents the edge of the continental African shelf.

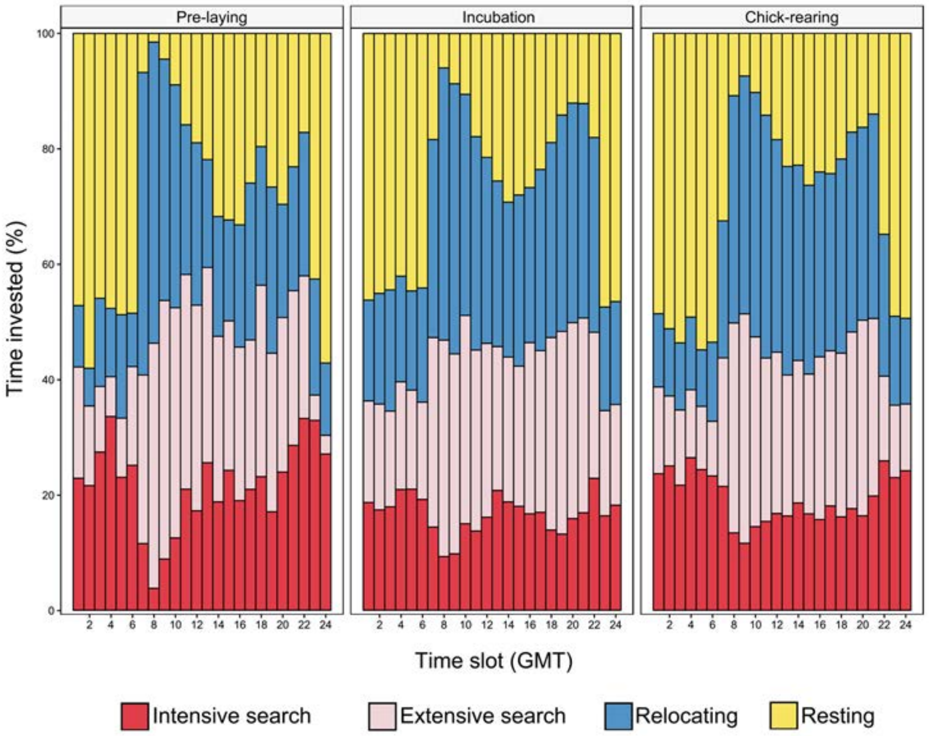

Figure 18 • Daily behavioural patterns of Cory's shearwater from Veneguera (Gran Canaria). Charts illustrate the proportion of time invested on each behaviour (Y-axis) per daily time slot (X-axis, from 0 to 24 h, GMT). Behaviours correspond to the behavioural states identified through the EMbC algorithm (Garriga et al., 2016). Colours represent: red - intensive search, pink - extensive search, blue - relocation, yellow - resting.

landscapes of the incubation phase pointed out that commuting between the breeding colony and the foraging areas in the African shelf occurred mainly during the day. Foraging behaviour near Gran Canaria took place during both day and night. On the African shelf, foraging took place more frequently during the day, although in some areas it was also the most frequent behaviour during the night. However, over the African shelf, resting was the most frequent behaviour during the night in most cells (Figure 17, centre).

During the chick-rearing phase, birds moved over the African shelf as during incubation (Figure 16, bottom). Commuting between the Canary Islands and the African shelf took place mainly during daylight hours (Figure 17, bottom). Resting was more frequent at night (Figure 17, bottom). Foraging was the most frequent behaviour during the day over the movement range. Interestingly, in some cells birds showed a very high engagement in foraging at night, suggesting that nocturnal foraging may be important in some specific areas (Figure 17, bottom; Figure 18).

The results of behavioural analysis in both species revealed differences between the different periods of the breeding period, both in the extent of movements and areas used and the temporal variation in behaviour. Overall, both species showed a high preference for neritic waters on the continental shelf or the oceanic slope, yet making also an intensive use of the waters around the islands where they breed. Movements to distant feeding grounds occurred mostly during the day, while resting occurs mostly at night. Foraging was also mostly concentrated in the daytime for both species, although it is remarkable that in the case of the

Atlantic species, in some specific areas on the African shelf there was a high investment of time in foraging at night. In this sense, likely both oceanic productivity values and the food requirements of each phase of the breeding period had an influence, and the moon phase might have influenced (Yamamoto et al., 2008; Dias et al., 2012a; Rubolini et al., 2015).

Behavioural analysis of the Scopoli's shearwater during the breeding period

Birds from Cala Morell (Menorca) were tracked over the three phases of the breeding period in 2014. In the pre-laying period, trips were recorded in April and May, so GPS data included the pre-laying exodus. The trips recorded showed how birds shift their behavioural strategies among phases. Continental shelf played an important role as foraging grounds over the breeding period, either around the Balearic Islands or over the eastern coast of the Iberian Peninsula and North Africa. Only occasionally, birds foraged beyond the continental slope. Oceanic waters worked mainly as flyway corridors, and only exceptionally as feeding areas.

During the pre-laying phase, the tracked birds (51 individuals, 400 trips) made intensive use of waters around the Balearic archipelago, as well as waters of the Catalan coast (Figure 19, top). On the other hand, several extraordinary long trips were recorded: some females moved east to the coast of Corsica, while some males moved south to the coast of Algeria. The limited extension of the Mediterranean basin might explain why females did not engage in longer trips than males. During pre-laying, much of the foraging activity occurred during daylight, mostly near the slope surrounding the Balearic Islands, and in the channel between Ibiza and Mallorca. Foraging episodes also occurred during darkness, although the most frequent behaviour was resting (Figure 20, top).

During incubation, the tracked birds (10 individuals, 19 trips) moved to different areas respect to the areas visited in pre-laying. Apart from using Balearic waters, they moved along the eastern coast of the Iberian Peninsula, from the Gulf of Lyon in France to Cabo de Palos in Murcia. They also visited the southern side of the Mediterranean, from Tetouan (Morocco) to the west to Algiers (Algeria) to the east (Figure 19, centre). In the areas where birds foraged more intensively, foraging took place mainly during the day (Figure 20, centre).

Finally, during the chick-rearing, the tracked birds (25 individuals, 134 trips) also used the waters surrounding the Balearic archipelago during the short trips. However, unlike in pre-laying and incubation, during the chick-rearing birds commuted almost exclusively to the coast of Catalonia during the long trips, more specifically to waters from the north of Tarragona to Cap de Creus (Figure 19, bottom). The greatest investment of time in foraging was recorded in the waters between Mallorca and Menorca, while on the Catalan coast the foraging was concentrated in areas corresponding to marine canyons (such as Blanes offshore), or waters near Barcelona. Foraging behaviour took place mainly during the day and resting behaviour during the night (Figure 20, bottom).

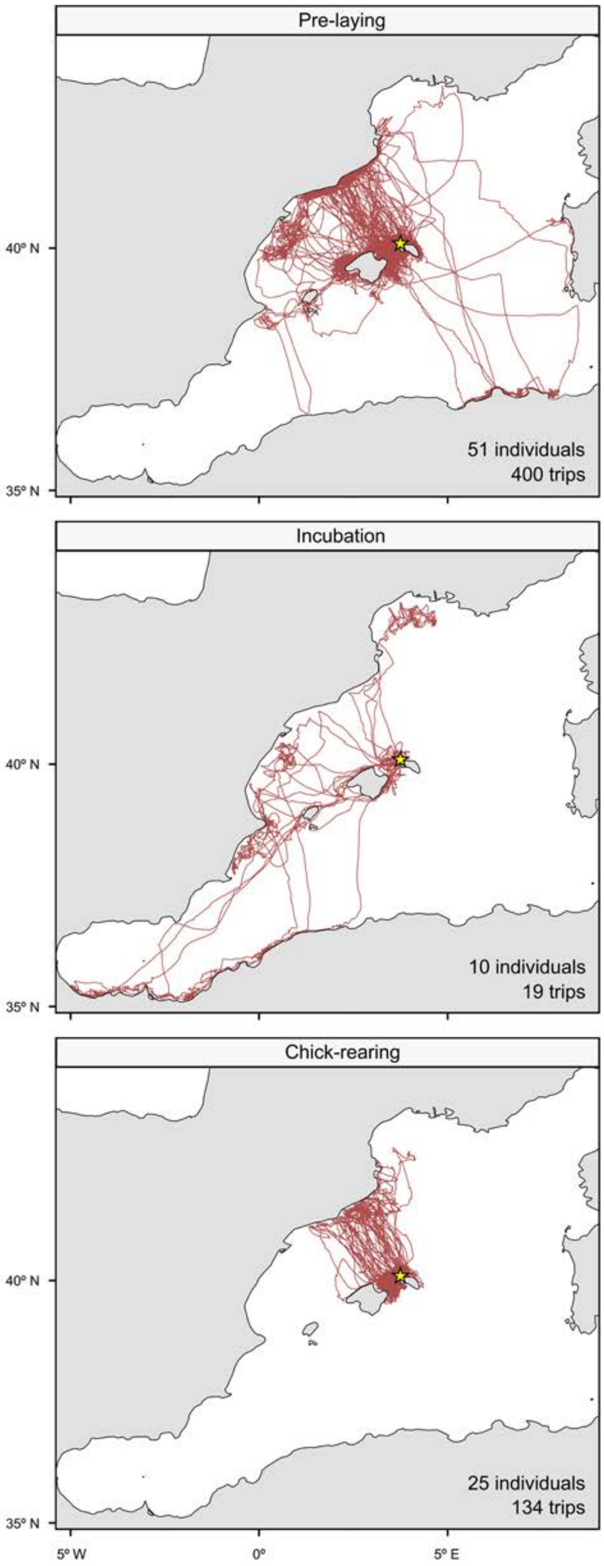

Figure 19 • Foraging trips of Scopoli's shearwaters breeding at Cala Morell (Menorca) during the breeding period of 2014. The map at the top shows the movements during the pre-laying (time window: April 17th - June 1st; 51 individuals, 400 trips). The map in the centre shows movements performed during the first weeks of incubation (time window: May 23rd - June 22nd; 10 individuals, 19 trips). The map on the bottom shows the movements during the chick-rearing phase (time window: July 22nd - September 12th; 25 individuals, 134 trips). Waters surrounding the Balearic archipelago were always important for short trips, whereas during the long trips birds visited different areas depending on the breeding phase.

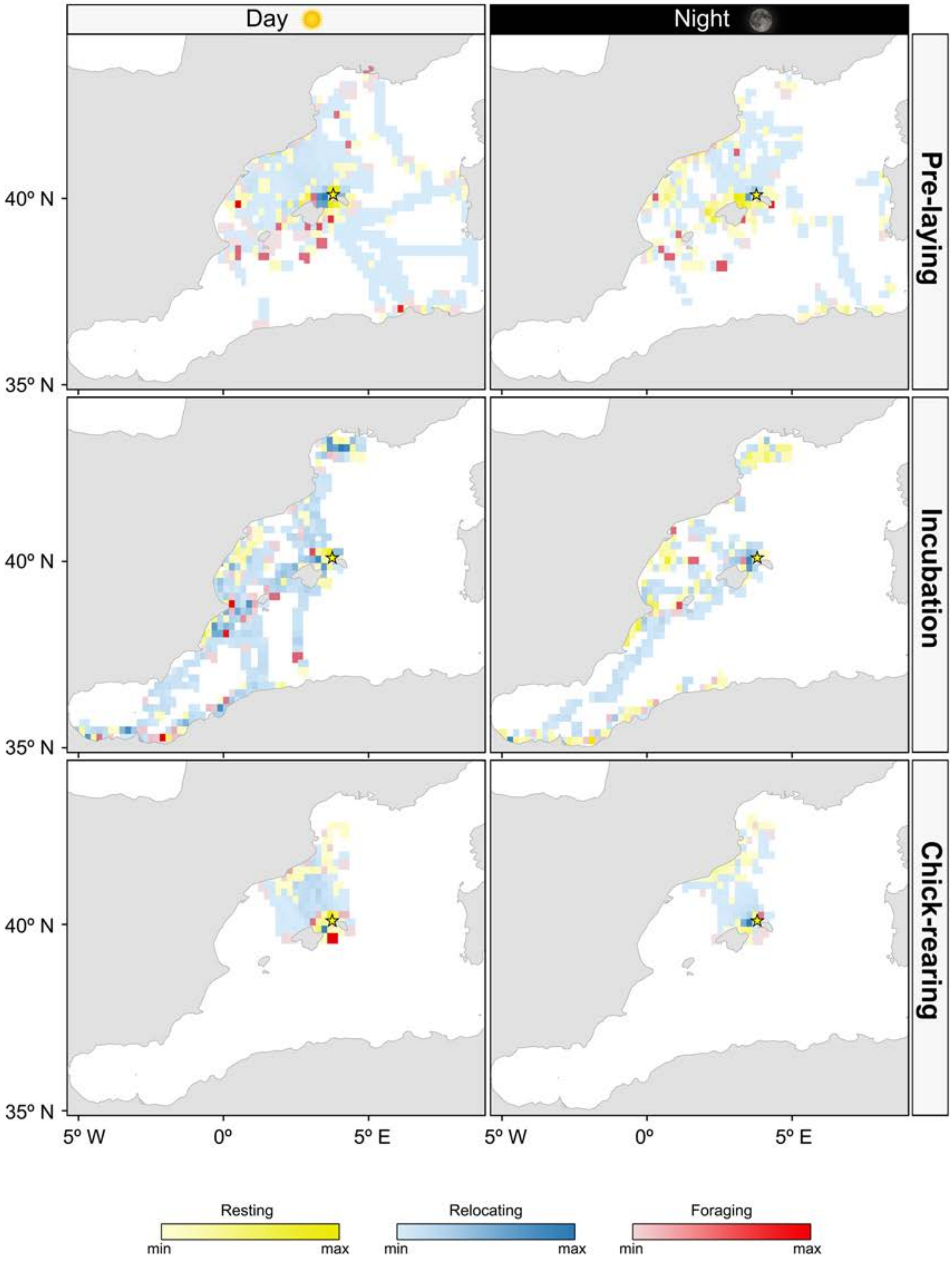

FIGURE 20 • Behavioural landscapes of the Scopoli's shearwaters breeding in Cala Morell (Menorca) during 2014. Maps on the left represent diurnal behaviour and maps on the right represent nocturnal behaviour. For each cell, the colour identifies the most frequent behaviour, and its intensity represents the amount of time invested for that particular behaviour across the distribution range. Yellow colour represents resting, red colour represents foraging, and the blue colour represents relocating.

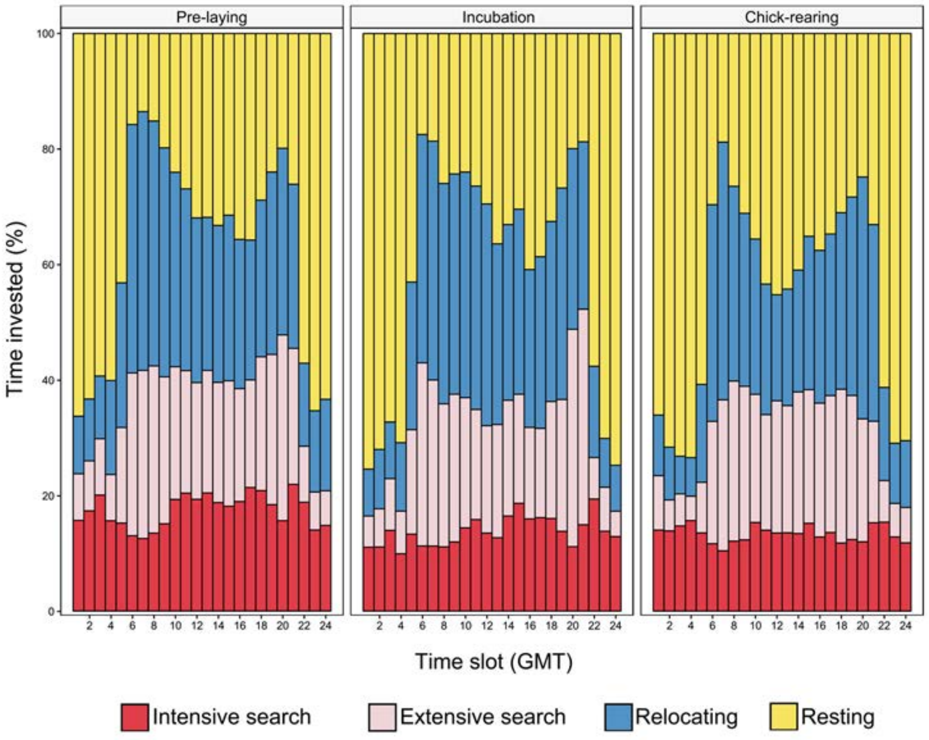

Figure 21 • Daily behavioural patterns of Scopoli's shearwater from Cala Morell (Menorca). Charts illustrate the proportion of time invested on each behaviour (Y-axis) per daily time slot (X-axis, from 0 to 24 h, GMT). Behaviours correspond to the behavioural modes identified through the EMbC algorithm (Garriga et al., 2016). Colours represent: red - intensive search, pink - extensive search, blue - relocation, yellow - resting.

Migration

Both species exhibit complex migratory patterns, with a diverse array of destinations over the Atlantic. In general, Cory's shearwaters used a greater number of wintering areas, with more complex migratory detours and less associated with the coastline to reach the wintering areas. It is known that wind patterns are key for migration in both Cory's and Scopoli's shearwaters (see Figure 22). Birds take advantage of the most favourable wind conditions, as they open "migration highways" to move among breeding and wintering areas (Felicísimo et al., 2008). Detours from apparent shorter paths are compensated by reducing the energetic coast of flying while flying with favourable winds. In the post-breeding migration, the windless belt associated with the inter-tropical convergence plays a relevant role. This belt seems to act as a barrier to migration between both hemispheres. Shearwaters do not cross it until such belt temporary disappears, which coincides with the end of the African monsoon and the entry of eastern winds, more favourable for birds to migrate south (Felicísimo et al., 2008; González-Solís et al., 2009).

Migratory flyways: Individual strategies

Cory's shearwater

Cory's shearwaters showed much more complex migratory patterns than Scopoli's shearwaters. Birds took advantage of prevailing winds in both the northern and southern hemispheres. All birds migrated following an 8-shaped loop, with the unique exception of the few individuals wintering in the Canary Current (González-Solís et al., 2007, 2009).

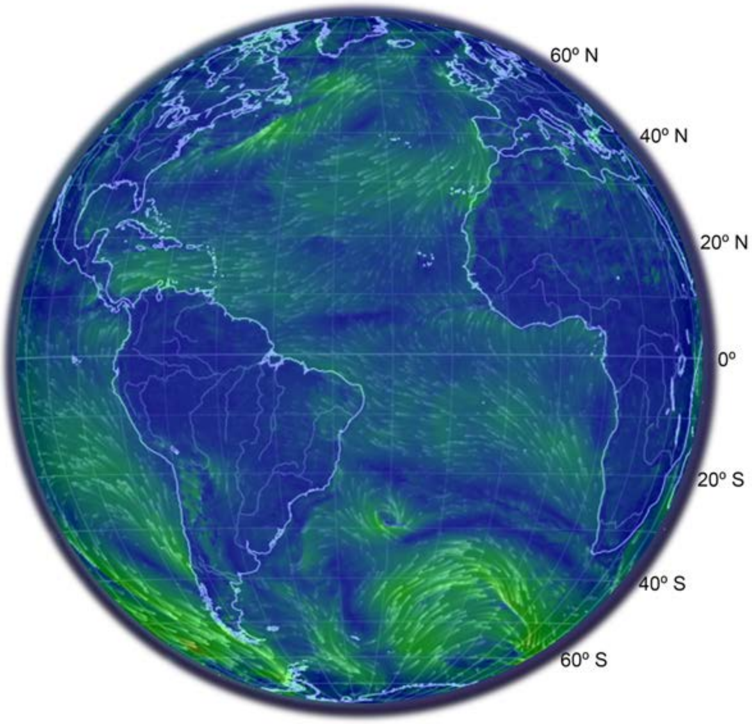

Figure 22 • Overview of the wind pattern in the Atlantic Ocean. Arrows illustrate the direction of the winds, and green intensity the wind intensity. Cory's and Scopoli's shearwaters take advantage of the wind to migrate across the Atlantic. During pre-breeding migration, birds follow the prevailing winds over the Atlantic in the northern hemisphere to reach the breeding colonies. After breeding, birds use again prevailing winds to reach their wintering areas in the southern hemisphere (Felicísimo et al., 2008). Image adapted from http://earth.nullschool.net (©Cameron Beccario).

Some birds wintered in Namibia offshore and the Benguela Current. They crossed the Atlantic from the Canary Islands towards the coast of Brazil, and after crossing the equator, they headed southwards taking advantage of the prevailing winds in the South Atlantic, which blow in an anti-clockwise direction. At the 35th parallel south, they turned east to head towards South Africa. On their pre-breeding migration, they used again favourable northbound winds, flying almost straight ahead from the wintering area to waters off Guinea, and then taking there the prevailing clockwise winds of the northern hemisphere to circumnavigate the North Atlantic until reaching the Canary Islands from the north (Figure 23). Like the Scopoli's shearwaters, some individuals of Cory's shearwater circumnavigated the entire North Atlantic during the pre-breeding migration before arriving at the colonies from the northwest. However, some birds cut their way back to the Canary archipelago from the south (Figure 24). This latter strategy may involve flying with headwinds, which is probably slower and demand more energy than circumnavigating the North Atlantic; however, the pre-breeding migration takes place in late winter or early spring, when the trade winds are not yet as strong as in summer. The decision to fly directly from the equator to the Canary Islands instead of circumnavigating the North Atlantic may relate to the opening of windless time windows, in line with the proposal of Felicísimo et al. (2008) and González-Solís et al. (2009) for the post-breeding migration to the south. Birds that wintered at the confluence of Benguela and Agulhas currents and in the Agulhas Current also showed an 8-shaped loop in their migration, yet truncated towards the east shortly after crossing the equator to avoid the complete circumnavigation of the Atlantic. In other words, their way back to the colonies headed towards the centre of the Atlantic and the coast of Brazil from the wintering area, and then they turned east towards the Cape Verde archipelago to reach the Canary Islands from the south (Figure 24).

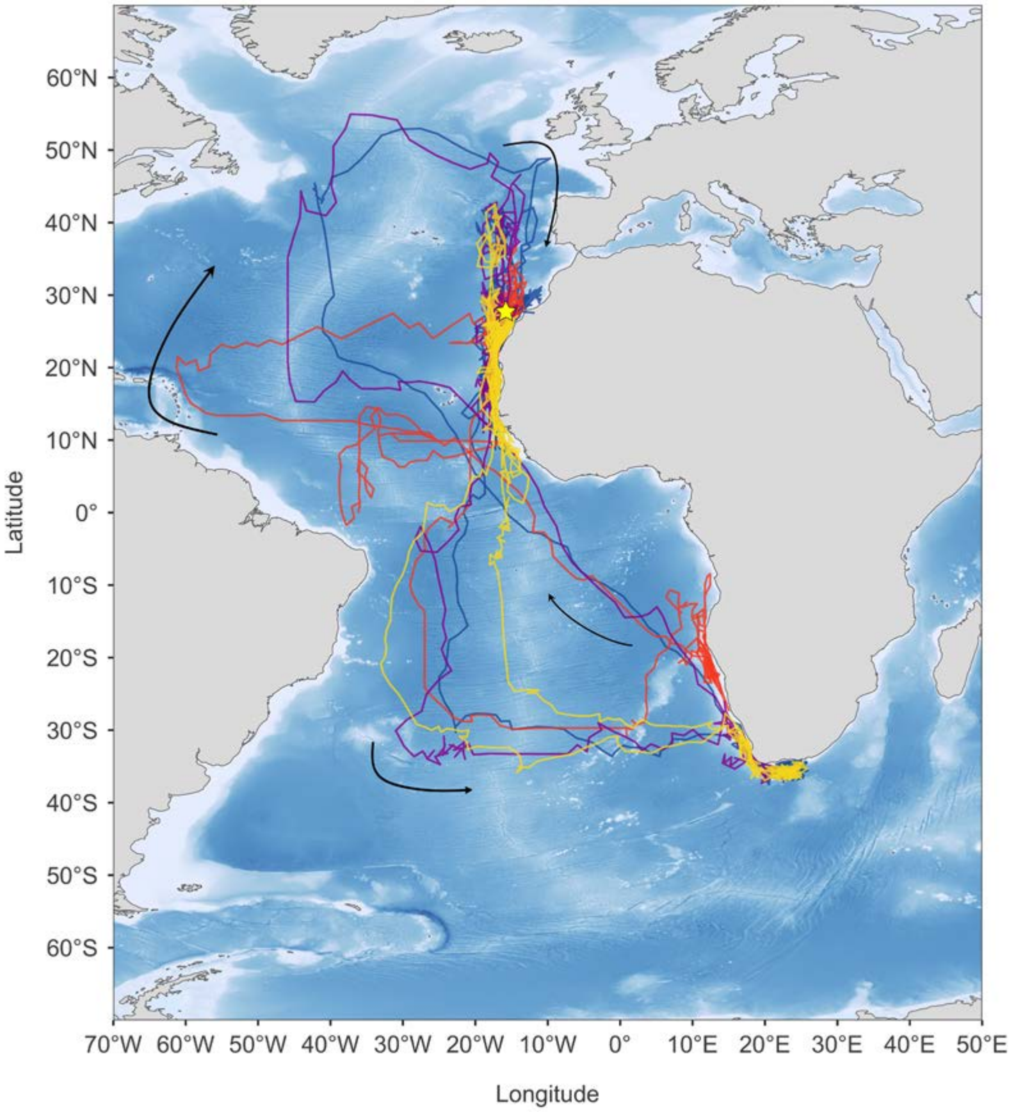

Figure 23 • Map showing a few migratory trips of Cory's shearwaters breeding in the Canary Islands and wintering in the Benguela Current, off Namibia and South Africa coast. Each coloured line represents an individual trip. Black arrows indicate the direction of the trip. The yellow star indicates the colony. Most individuals performed an 8-shaped loop across the Atlantic, taking advantage of the prevailing winds in both hemispheres, clockwise in the North Atlantic, and counter-clockwise in the South Atlantic, to reach the breeding colony and the wintering area.

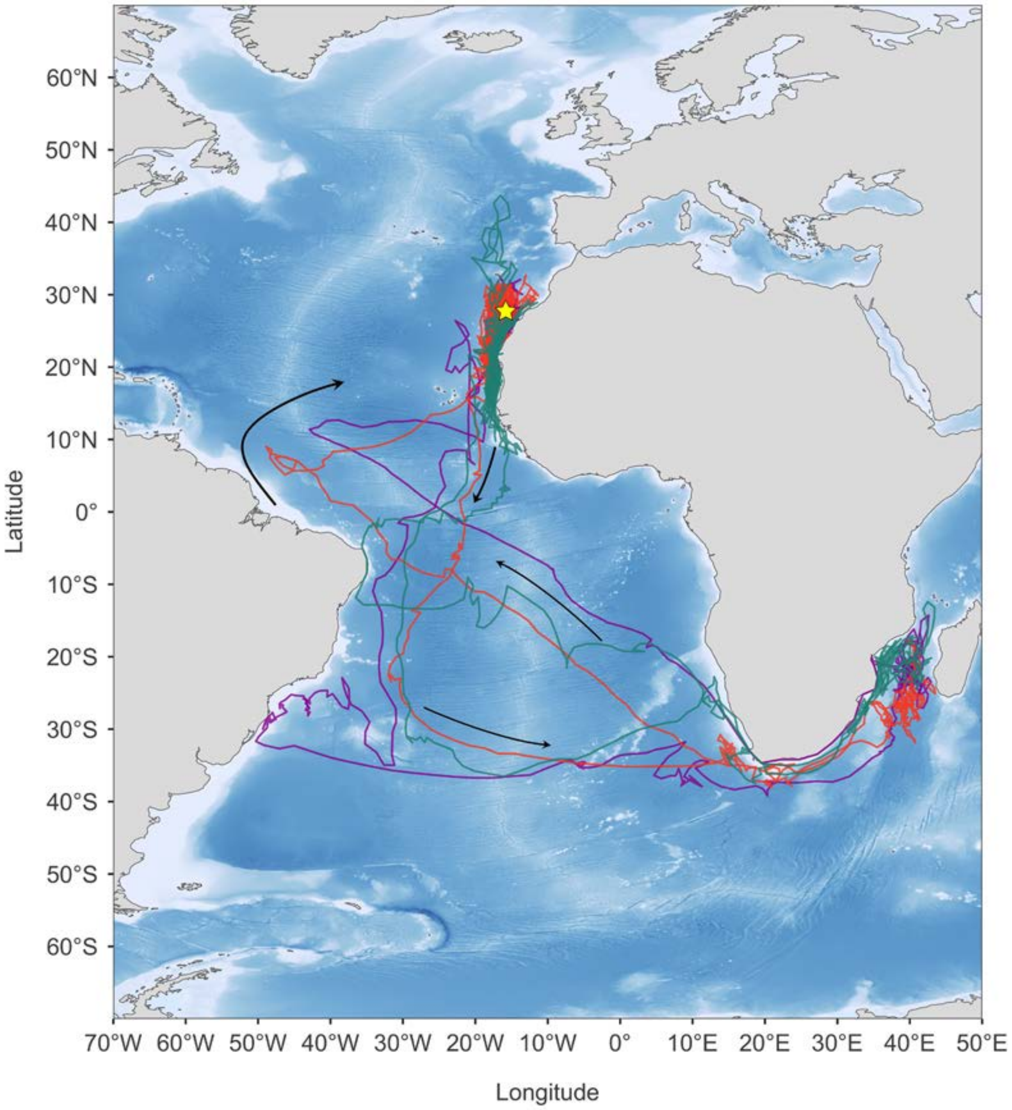

Figure 24 • Map showing a few migratory trips of Cory's shearwaters breeding in Canary Islands and wintering in the Agulhas Current. Each coloured line represents an individual trip. Black arrows indicate the direction of the trip. The yellow star indicates the colony. These birds performed a truncated 8-shaped loop, approaching to the African coast from Brazilian waters near the equator, instead of circumnavigating the North Atlantic.

Birds wintering in the Brazilian Current (Figure 25) and the centre of the South Atlantic also took advantage of the favourable winds in both hemispheres and drew an 8-shaped loop. However, they reached the wintering area by approaching the coast of Brazil from the parallel 10º S. They started the pre-breeding migration from the south, around the parallel 40º S, heading from there to the centre of the Atlantic in an easterly direction, and from there flying straight northwards until taking the prevailing winds of the North Atlantic, reaching the Canary Islands from the north.

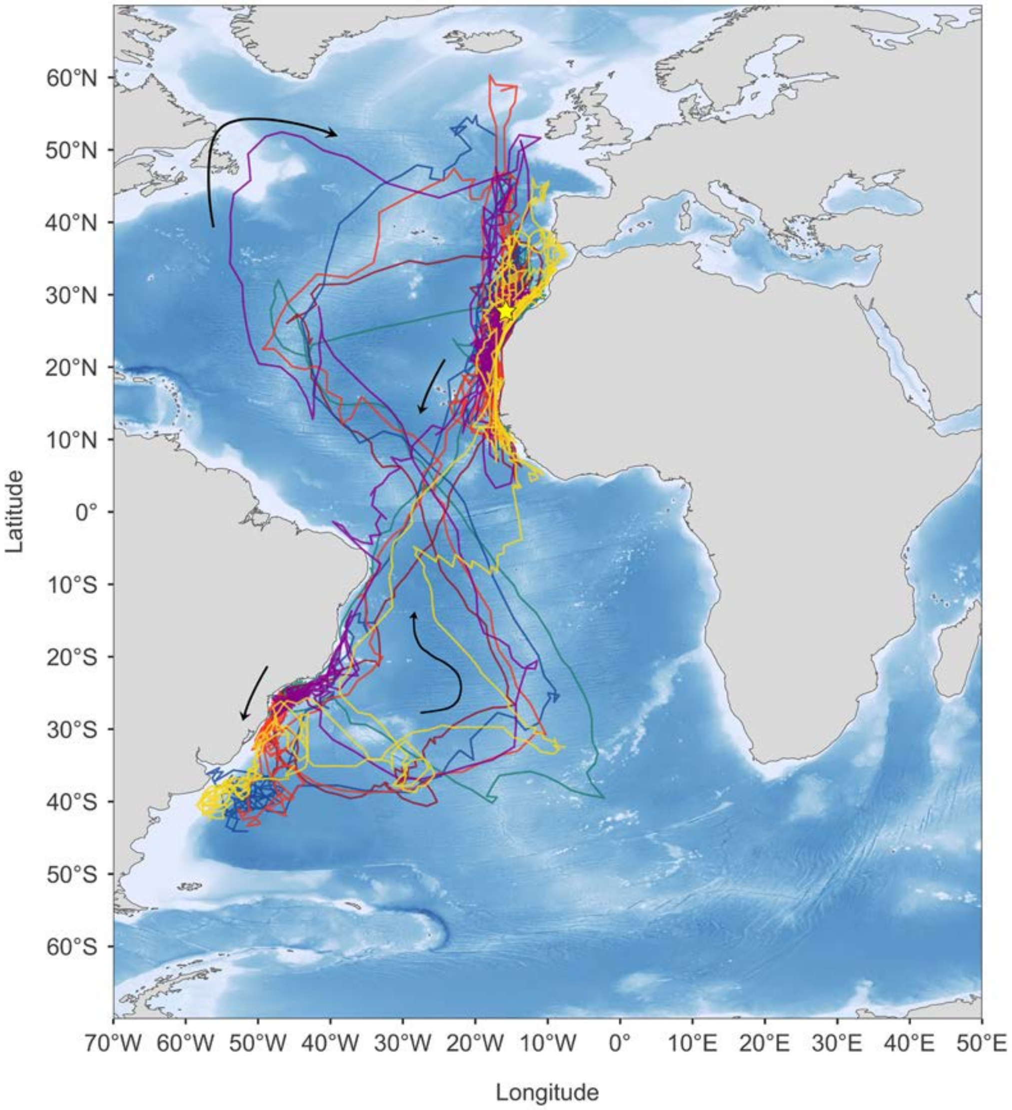

Figure 25 • Map showing a few migratory trips of Cory's shearwaters breeding in the Canary Islands and wintering along the coast of Brazil and Uruguay. Each coloured line represents an individual trip. Black arrows indicate the direction of the trip. The yellow star indicates the colony. These birds also performed an 8-shaped loop, but the post-breeding migration was straightforward, reaching fast South America. The pre-breeding migration completed the 8-shaped loop: from the wintering area birds headed east up to the centre of the South Atlantic and then made a turn left to fly north, following the Mid-Atlantic Ridge to circumnavigate the North Atlantic until approaching the Canary archipelago from the north.

Scopoli's shearwater

During their migratory movements, the Scopoli's shearwaters tracked with geolocators headed south after crossing the Strait of Gibraltar. As previously described, they followed the coastline towards the northern wintering area, the Canary Current, taking advantage of the trade winds blowing south and thus reducing energy expenditure during their trips (Felicísimo et al., 2008; González-Solís et al., 2007, 2009). Birds that migrated further south towards the Gulf of Guinea always moved along the African coast, even crossing regions where they did not find favourable tailwinds, which suggest that these individuals may use the coastline as a landmark to navigate. Some other individuals that spent the wintering period in waters off-shore Angola and Namibian did not use apparently the coastline as a landmark to navigate along the complete trip during post-breeding migration but instead flew away from the coastline one they crossed the equator. These individuals crossed the Gulf of Guinea also far away from the coastline in the pre-breeding migration (Figure 26). During the pre-breeding migration, tracked

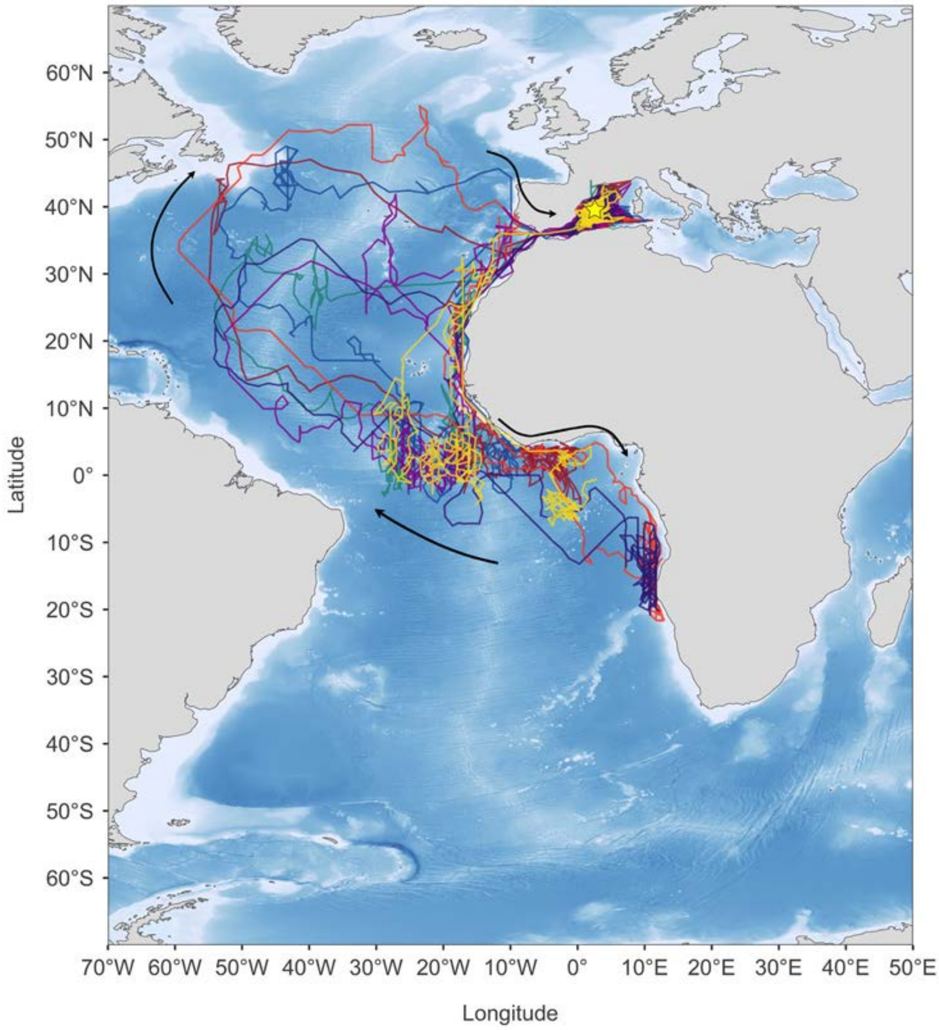

Figure 26 • Map showing a few migratory trips of Scopoli's shearwaters breeding in the Balearic Islands and wintering in the Gulf of Guinea, Angola and Namibia offshore. Each coloured line represents an individual trip. Black arrows indicate the direction of the trip. The yellow star indicates the colony. Most birds followed the clockwise prevailing winds of the North Atlantic. During the post-breeding migration, birds followed the coastline until reaching the wintering areas. In their way back to the breeding colonies, however, birds tended to cross the Mid-Atlantic Ridge and approached to the North American waters where they headed eastward towards Europe and the Strait of Gibraltar. Some individuals wintering in Angola and Namibia crossed the Gulf of Guinea during both pre- and post-breeding migration.

birds showed a greater diversity of flyways, which may be related to the temporal variability in wind patterns. Nevertheless, they followed a general pattern, drawing a loop from the south to northwest and from northwest to east. Individuals wintering in the Canary Current did not cross the mid-Atlantic. However, some individuals wintering in southern areas even exceeded the Mid-Atlantic Ridge in their way back to the breeding colonies, reaching the North American coast (Figure 27).

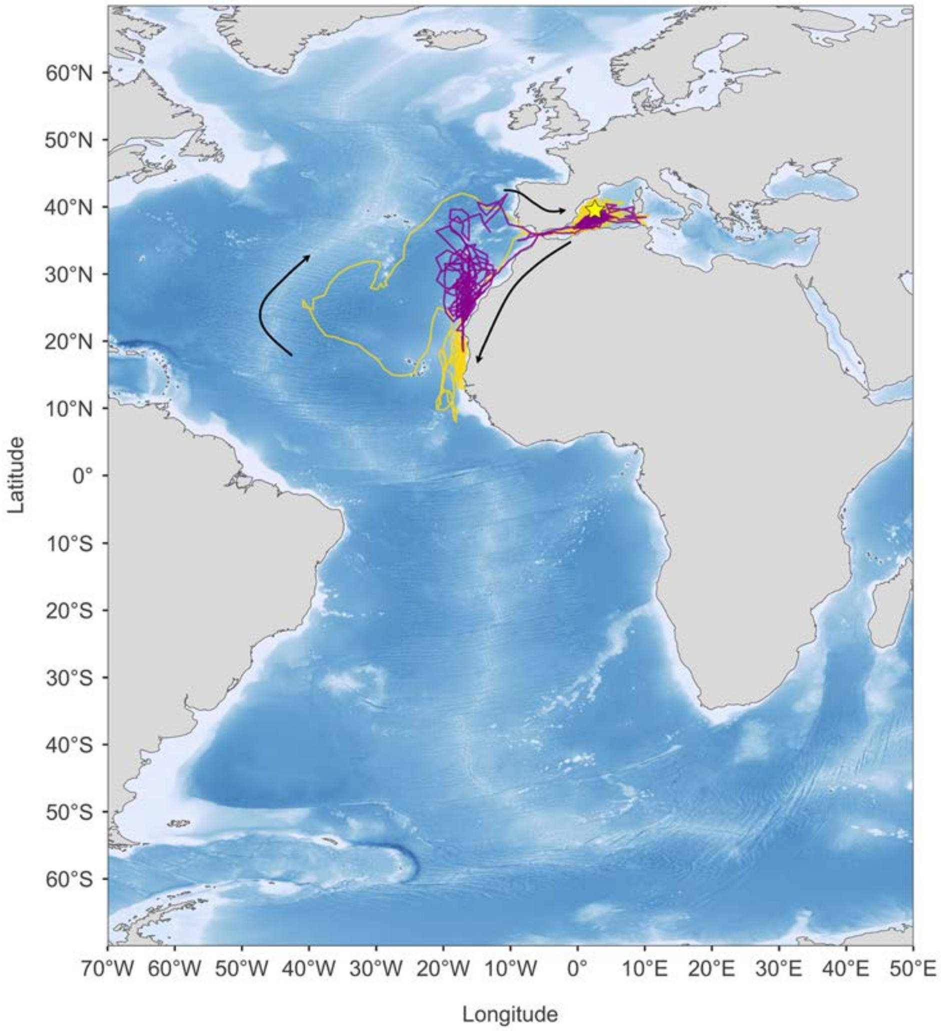

Figure 27 • Map showing a few migratory trips of Scopoli's shearwaters breeding in the Balearic Islands and wintering in the Canary Current. Each coloured line represents an individual trip. Black arrows indicate the direction of the trip. The yellow star indicates the colony. Birds wintering in this area also performed a clockwise migration but did not cross the Mid-Atlantic Ridge.

Migratory flyways: population patterns

A joint analysis of the individual flyways using MKDE allowed characterising and delimiting population migratory flyways. Regardless of the species and the wintering area, there was a clear difference between post-breeding migratory flyways and pre-breeding migratory flyways. The former were narrow and well defined, concentrating most birds during migration. The latter, however, were much fuzzier, being even difficult to define the flyways, because of great variability among individual strategies. Figures 28-33 show details of the migratory flyways.

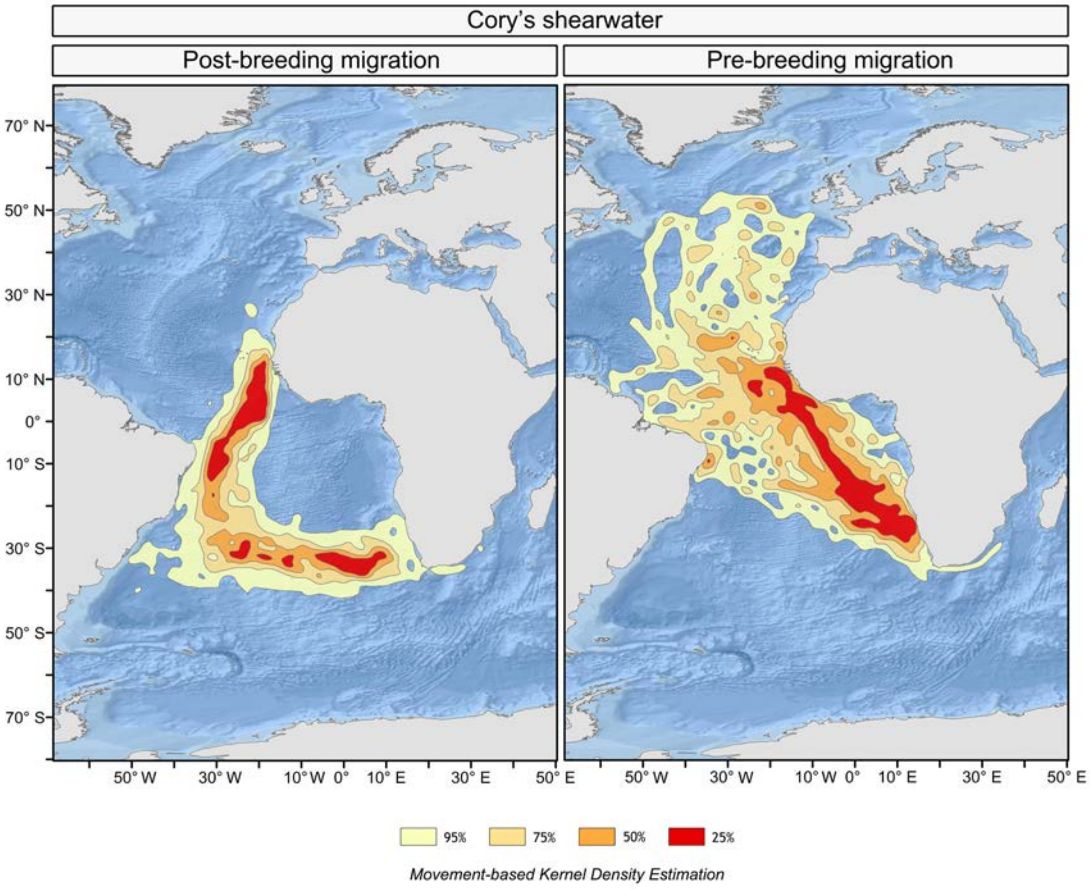

Figure 28 • Migratory flyways used by individuals of Cory's shearwaters breeding in the Canary Islands and wintering off Namibia, Benguela and Agulhas currents. Post-breeding migratory flyway crossed the equator approaching the coast of Brazil, turning then left towards the east, to head towards South Africa (map on the left). In contrast, pre-breeding migratory flyway was fuzzy and spread over a vast area of the Atlantic (map on the right). Migratory flyways modelled through applying Movement-based Kernel Density Estimators (MKDE, for details of the methodology, see: Benhamou & Cornélis, 2010; Benhamou, 2011; Benhamou & Riotte-Lambert, 2012) on migration locations gathered with light-level geolocators. Analysis performed by splitting pre- and post-breeding migration, considering 65 complete migratory trips from 47 individuals. Colour gradient, from yellow to red, depicts the importance at population scale. Thus, the red colour indicates the highest amount of birds during migration.

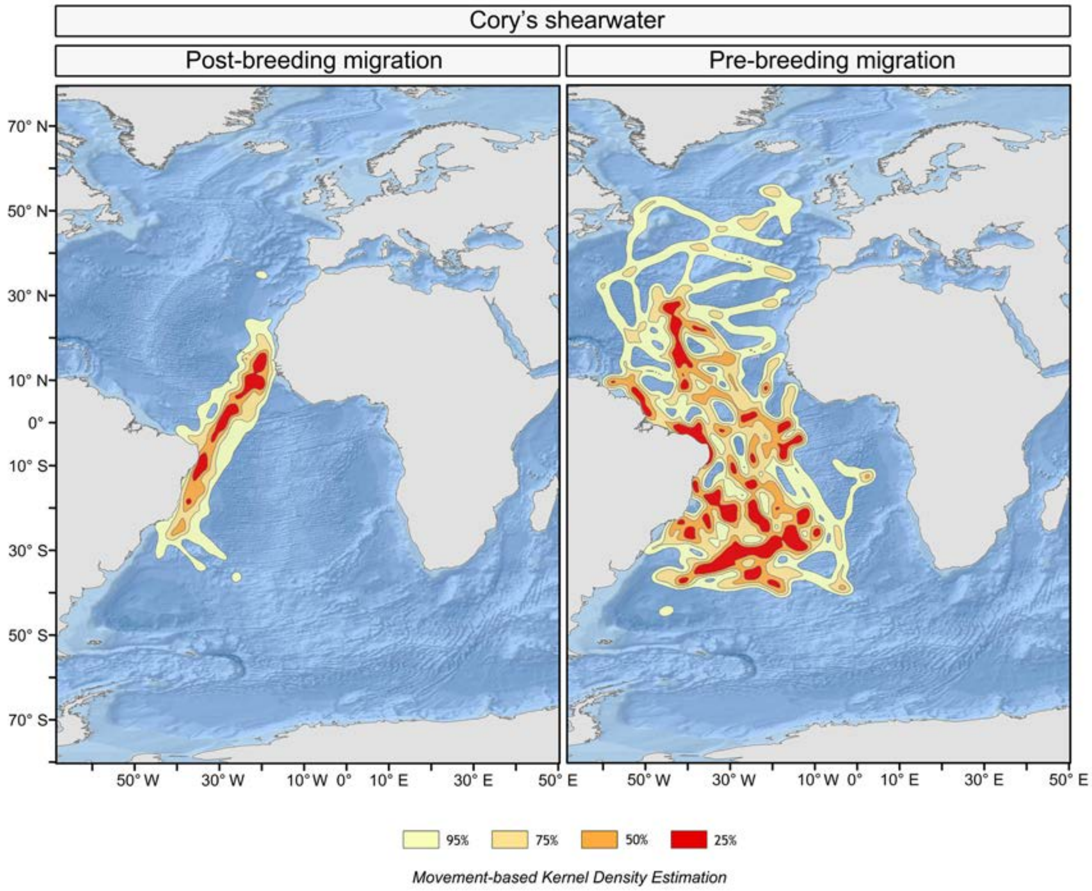

Figure 29 • Migratory flyways used by individuals of Cory's shearwaters breeding in the Canary Islands and wintering in waters off the Brazilian coast. Birds using this flyway reached the South American coast quickly, following the prevailing winds blowing southwest, which explains the narrow, well-defined shape of the post-breeding migratory flyway (map on the left). However, pre-breeding migratory flyway was fuzzy, spreading over the West Atlantic (map on the right). Migratory flyways modelled through applying Movement-based Kernel Density Estimators (MKDE, for details of the methodology, see: Benhamou & Cornélis, 2010; Benhamou, 2011; Benhamou & Riotte-Lambert, 2012) on migration locations gathered with light-level geolocators. Analysis performed by splitting pre- and post-breeding migration, considering 16 complete migratory trips from 13 individuals. Colour gradient, from yellow to red, depicts the importance at population scale. Thus, the red colour indicates the highest amount of birds during migration.

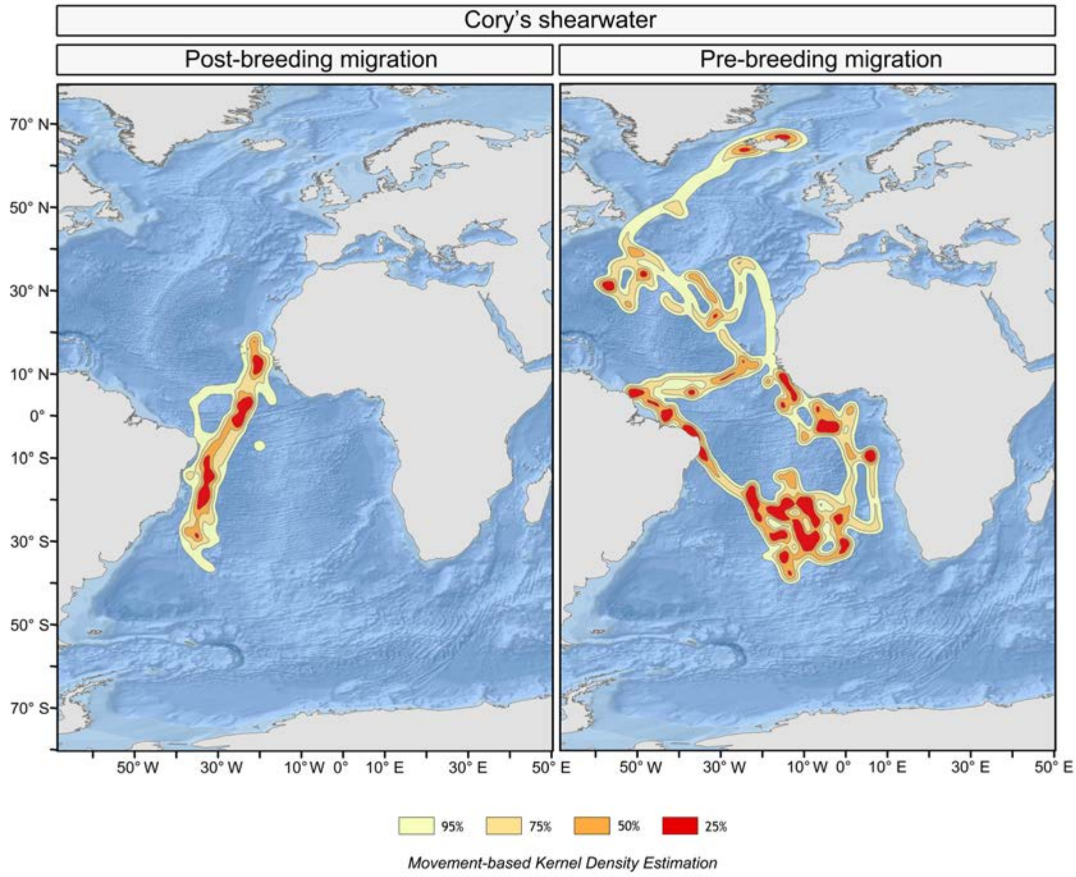

FIGURE 30 • Migratory flyways used by individuals of Cory's shearwaters breeding in the Canary Islands and wintering in the centre of the South Atlantic. This was the least visited area to winter. The few individuals wintering there arrived following a well-defined post-breeding flyway (map on the left). In the pre-breeding migration, some birds approached the Brazilian coast and some others approached the African coast up to the equator. The migratory flyway split there in two opposite flyways, one reaching the Canary Islands from the south and the other circumnavigating the Atlantic to reach the Canary Islands from the north (map on the right). Migratory flyways modelled through applying Movement-based Kernel Density Estimators (MKDE, for details of the methodology, see: Benhamou & Cornélis, 2010; Benhamou, 2011; Benhamou & Riotte-Lambert, 2012) on migration locations gathered with light-level geolocators. Analysis performed by splitting pre- and post-breeding migration, considering 6 complete migratory trips from 6 individuals. Colour gradient, from yellow to red, depicts the importance at population scale. Thus, the red colour indicates the highest amount of birds during migration.

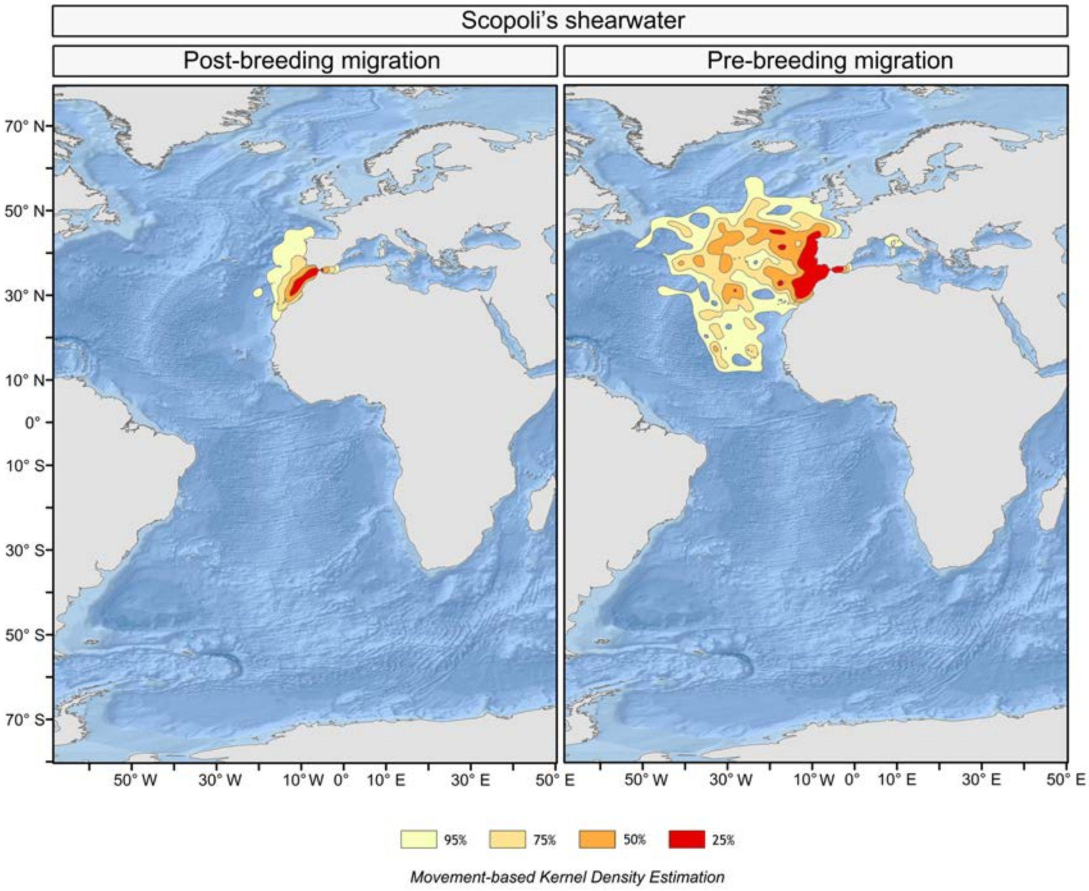

Figure 31 • Migratory flyways used by Scopoli's shearwaters breeding in the Balearic Islands and wintering in the Canary Current. Post-breeding migratory flyway was well defined (map on the left), but the pre-breeding one was fuzzy and widespread (map on the right). Migratory flyways modelled through applying Movement-based Kernel Density Estimators (MKDE, for details of the methodology, see: Benhamou & Cornélis, 2010; Benhamou, 2011; Benhamou & Riotte-Lambert, 2012) on migration locations gathered with light-level geolocators. Analysis performed by splitting pre- and post-breeding migration, considering 29 complete migratory trips from 19 individuals. Colour gradient, from yellow to red, depicts the importance at population scale. Thus, the red colour indicates the highest amount of birds during migration.

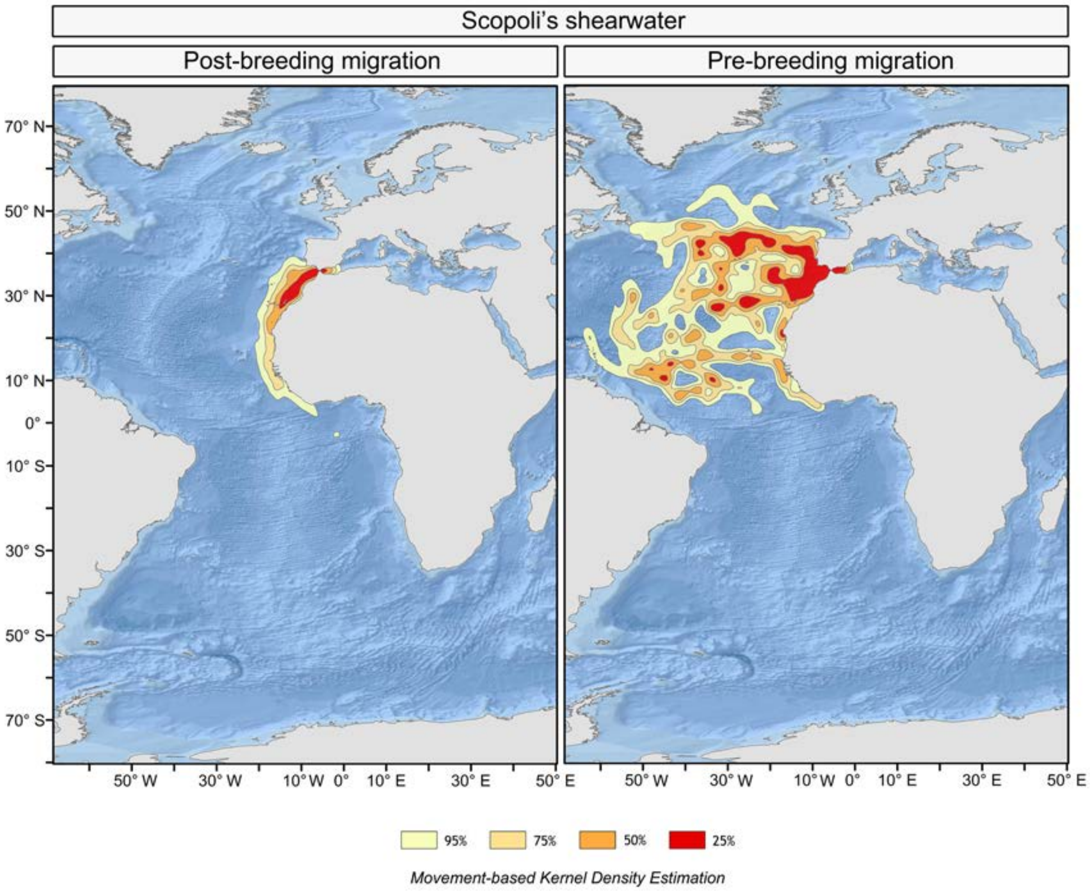

Figure 32 • Migratory flyways used by individuals of Scopoli's shearwaters breeding in the Balearic Islands and wintering off Guinea and Ghana. Post-breeding migratory flyway was well defined as a corridor along the coastline (map on the left). The pre-breeding migratory flyway, however, spread over the North Atlantic (map on the right). Migratory flyways modelled through applying Movement-based Kernel Density Estimators (MKDE, for details of the methodology, see: Benhamou & Cornélis, 2010; Benhamou, 2011; Benhamou & Riotte-Lambert, 2012) on migration locations gathered with light-level geolocators. Analysis performed by splitting pre- and post-breeding migration, considering 21 complete migratory trips from 15 individuals. Colour gradient, from yellow to red, depicts the importance at population scale. Thus, the red colour indicates the highest amount of birds during migration.

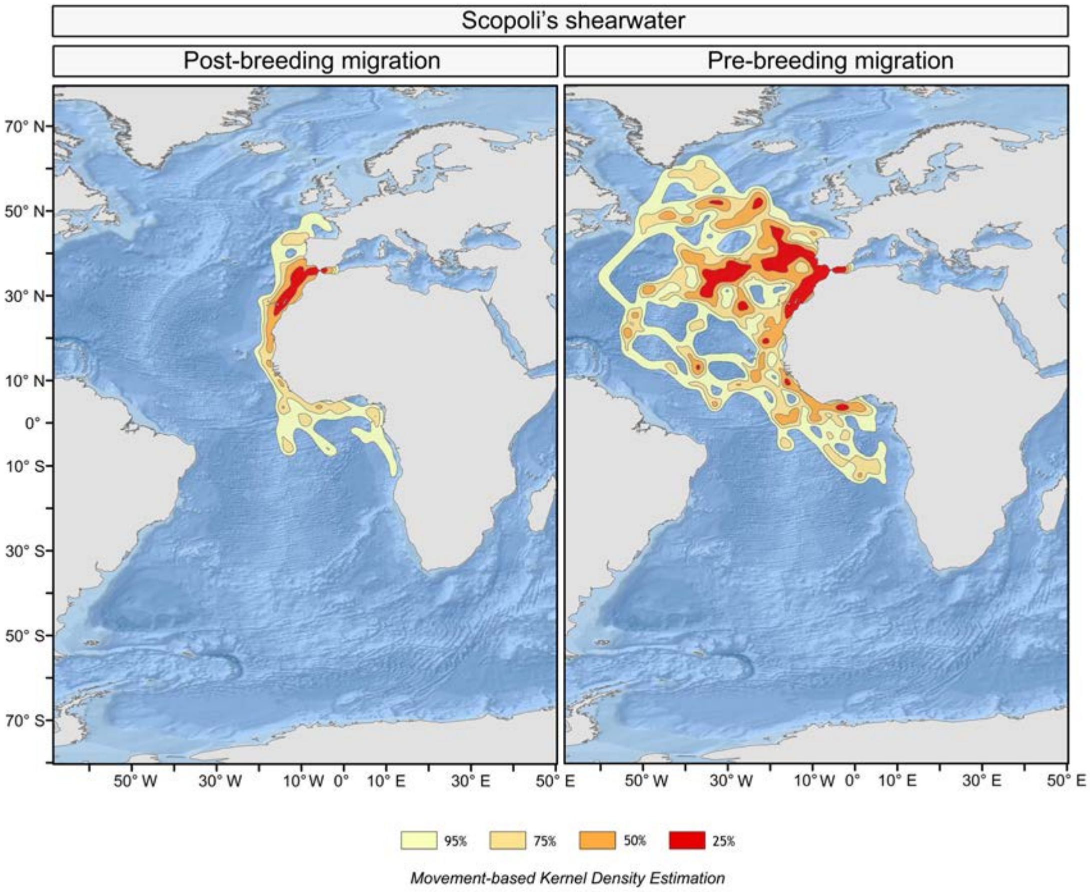

Figure 33 • Migratory flyways used by individuals of Scopoli's shearwaters breeding in the Balearic Islands and wintering off the coast of Angola and Namibia. Post-breeding migratory flyway was narrow and close to the African coastline (map on the left). The pre-breeding migratory flyway entered into the Gulf of Guinea, far from the coastline, and spread over the North Atlantic (map on the right). Migratory flyways modelled through applying Movement-based Kernel Density Estimators (MKDE, for details of the methodology, see: Benhamou & Cornélis, 2010; Benhamou, 2011; Benhamou & Riotte-Lambert, 2012) on migration locations gathered with light-level geolocators. Analysis performed by splitting pre- and post-breeding migration, considering 19 complete migratory trips from 15 individuals. Colour gradient, from yellow to red, depicts the importance at population scale. Thus, the red colour indicates the highest amount of birds during migration.

Wintering areas

The majority of individuals tracked spent the boreal winter in nutrient-rich areas of the Atlantic Ocean, between the tropic of Cancer and the temperate waters of the southern hemisphere. A few Cory's shearwaters even reached the Mozambique Channel in the Indian Ocean. In general, Cory's shearwaters used a higher number of wintering areas, at both sides of the Atlantic. Some wintering areas of Cory's shearwater were adjacent to or partially overlapped with some wintering areas of Scopoli's shearwaters.

Cory's shearwaters distributed during the wintering period in six large wintering areas located in the southern hemisphere, on both sides of the Atlantic (Figure 34). These areas were:

- The Canary Current, between parallels 10°N and 25°N, a few hundred kilometres south from the foraging areas used during the breeding period.
- The Benguela Current, between parallels 10°S and 40°S, including the coast of Namibia and South Africa.
- The confluence of Benguela and Agulhas currents, off the coast of South Africa, around the parallel 40°S.
- The Agulhas Current, from the coast of South Africa to the Mozambique Channel off Madagascar, in the Indian Ocean.
- The Brazil Current, from the parallel 15°S to parallel 40°S, in the mouth of Rio de la Plata, the area where this current meets the Malvinas Current.
- The centre of the South Atlantic, around the parallel 45°S and the meridian 25°W.

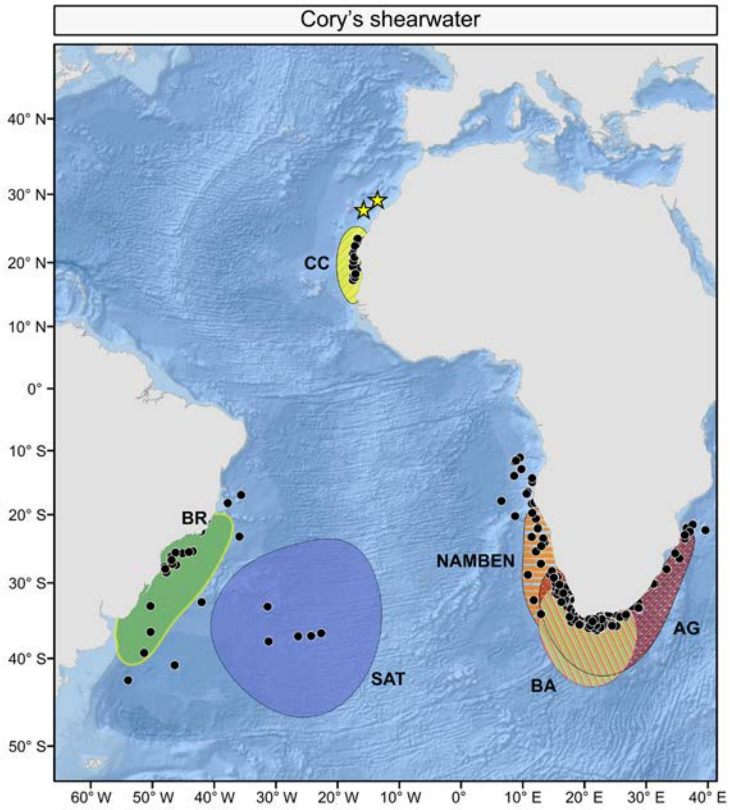

FIGURE 34 • Wintering areas of Cory's shearwaters that breed in Spain. Centroids of individual wintering areas, denoted with black dots, were clustered by proximity to define the main wintering areas, denoted by coloured polygons. The borders of the wintering areas correspond to the KDE 50% contour. CC = Canary Current, in yellow; NAMBEN = Benguela Current off the coast of Namibia, in orange; BA = Benguela-Agulhas Confluence, in green with crossed orange lines; AG = Agulhas Current, in brown; BR = Brazil Current, in green; SAT = centre of the South-Atlantic, in blue. KDE performed with data from 115 individuals and 237 trips. Yellow stars indicate the location of the breeding colonies, in Veneguera (Gran Canaria) and Montaña Clara islet (north of Lanzarote).

Scopoli's shearwaters distributed during the wintering period in four large areas, located exclusively along the western African side (Figure 35). These areas were:

- The Canary Current, approximately between parallels 14°N and 23°N.
- Guinea, around parallel 8°N and the meridian 20°W.
- Ghana, between the coast of Ghana and the equator, around the zero meridian.
- The coast of Angola and Namibia, approximately between the equator and the parallel 22ºS.
- Although some of the wintering areas around South Africa are close and partly overlap, each one has different oceanographic characteristics. This fact, together with the apparent spatial segregation between individuals selecting each of these areas, led to refuse to join them into a single wintering area.

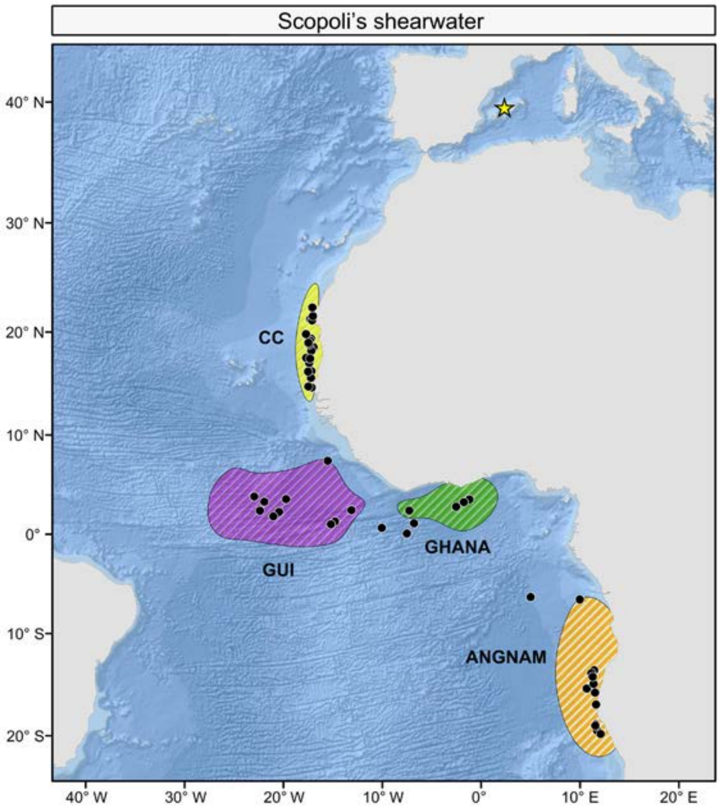

Figure 35 • Wintering areas of Scopoli's shearwaters that breed in Spain. Centroids of individual wintering areas, denoted with black dots, were clustered by proximity to define the main wintering areas, denoted by coloured polygons. The borders of the wintering areas correspond to the KDE 50% contour. CC = Canary Current, in yellow; GUI = oceanic waters of Guinea, in violet; GHANA = off the coast of Ghana, in green; ANGNAM = off the coast of Angola and Namibia, in orange. KDE performed with data from 46 individuals and 72 trips. Yellow star indicates the location of the breeding colony, in Pantaleu (Mallorca).

Relative importance of wintering areas

The relative importance of the wintering areas was calculated as the number of wintering events in each wintering area respect to the total number of wintering events recorded in the whole dataset. Therefore, the individual factor was not considered.

In the case of the Cory shearwater, the most important wintering area was the extreme south of Africa, off the coast of Namibia and the Benguela Current, which encompassed 40.5% of the wintering events. The second most important wintering area was the Agulhas Current, from the Mozambique Channel to the point where the Atlantic meets the Indian Oceans, which encompassed 21.5% of the events. The confluence of the Benguela and Agulhas currents accounted for 13.5% of the events, followed by the Brazilian Current, with 11.5%. At least for the populations studied, the area of the central South Atlantic had little importance, accounting only for 3.0% of the wintering events (Table 4, Figure 36). Surprisingly, none of the tracked birds wintered in the central North Atlantic, an important wintering area for Cory's shearwaters breeding in islands of Portugal (the Azores, Salvagens and Berlengas; González-Solís et al., 2007; Catry et al., 2011a; Dias et al., 2012b). Finally, a few individuals were resident year-round, because around 11% of the wintering events took place in the Canary Current. This last percentage is similar to that found for birds from Salvagens Islands. The individuals wintering in the Canary Current were probably different each year. The individual decision to remain in the breeding area to winter probably depends on intrinsic factors such as breeding success, the sex, or the individual experience. Males from the Selvagens Islands failing at breeding tend to remain year-round in the Canary Current (Catry et al., 2013). Perez et al. (2014) found a greater preference of males to remain in the Canary Current to winter. Missagia et al. (2015) found differences in wintering patterns according to individual experience.

In the case of the Scopoli's shearwater, the Canary Current is by far the main wintering area, with 41.7% of the trips, indicating the importance of the area for the Spanish population of this species. The waters off Angola and Namibia accumulated 27.8% of the wintering events. Waters off Guinea and Ghana had approximately the same importance, accounting for 16.7% and 13.9% of trips, respectively (Table 4, Figure 37). Other populations of Scopoli's shearwater from the central Mediterranean (Müller et al., 2014) also use these large wintering areas.

Table 4 • Relative importance of wintering areas according to the number of wintering events taking place there. Analysis based on 72 year-round tracks from 46 Scopoli's shearwaters and 237 year-round tracks from 115 Cory's shearwaters. Acronyms stand for: CC = Canary Current, ANGNAM = off the coast of Angola and Namibia, GUI = oceanic waters of Guinea, GHANA = off the coast of Ghana, NAMBEN = Benguela Current off the coast of Namibia, AG = Agulhas Current, BA = Benguela-Agulhas Confluence, BR = Brazil Current, SAT = centre of the South-Atlantic.

Species	Wintering area	Trips	Percentage
Cory's shearwater **Individuals = 115** **Trips = 237**	NAMBEN	96	40.5
	AG	51	21.5
	BA	32	13.5
	CC	27	11.5
	BR	24	10.0
	SAT	7	3.0
Scopoli's shearwater **Individuals = 46** **Trips = 72**	CC	30	41.7
	ANGNAM	20	27.8
	GUI	12	16.7
	GHANA	10	13.9

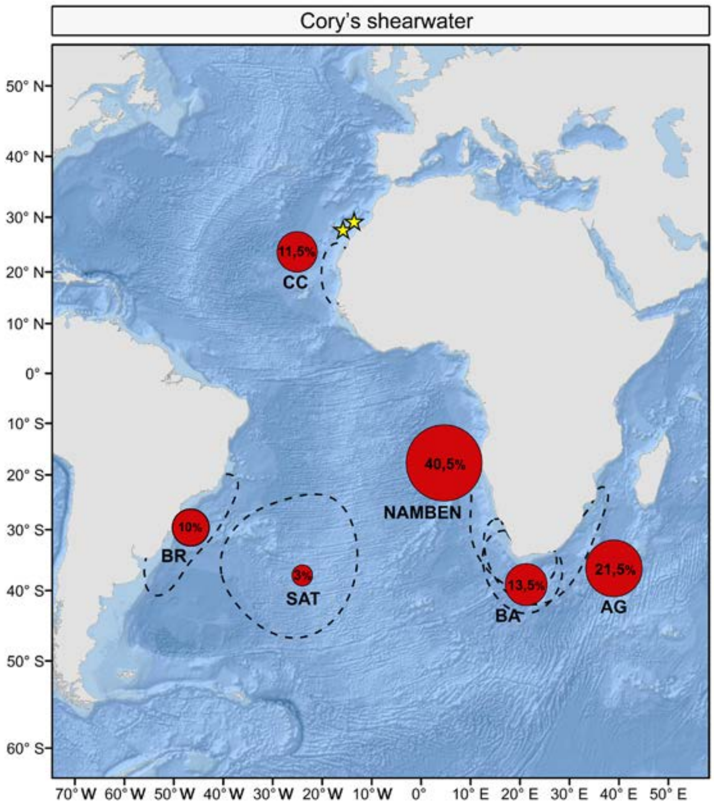

Figure 36 • Relative importance of the wintering areas used by Cory's shearwaters breeding in Spain. Dashed lines depict the KDE 50% contour of the wintering areas. Red bubble size corresponds to the percentage of wintering events that took place in each area. Analysis based on 237 year-round tracks from 115 Cory's shearwaters. Yellow stars indicate the location of the breeding colonies, in Veneguera (Gran Canaria) and Montaña Clara islet (north of Lanzarote). Acronyms stand for: CC = Canary Current, NAMBEN = Benguela Current off the coast of Namibia, BA = Benguela-Agulhas Confluence, AG = Agulhas Current, BR = Brazil Current, SAT = centre of the South-Atlantic.

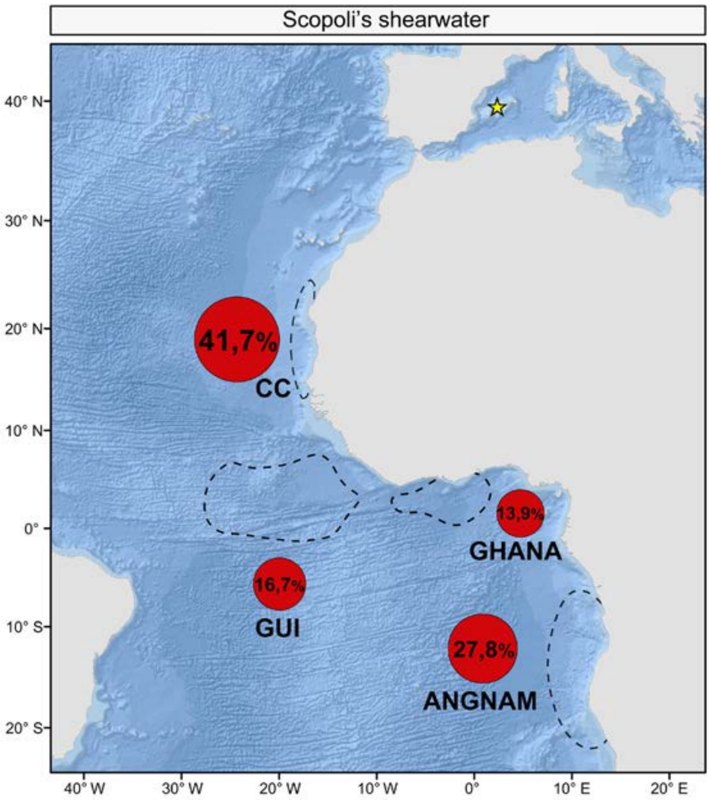

Figure 37 • Relative importance of the wintering areas used by Scopoli's shearwaters breeding in Spain. Dashed lines depict the KDE 50% contour of the wintering areas. Red bubble size corresponds to the percentage of wintering events that took place in each area. Analysis based on 72 year-round tracks from 46 Scopoli's shearwaters. Yellow star indicates the location of the breeding colony, in Pantaleu (Mallorca). Acronyms stand for: CC = Canary Current, GUI = oceanic waters of Guinea, GHANA = off the coast of Ghana, ANGNAM = off the coast of Angola and Namibia.

Wintering site fidelity

Measuring the site fidelity to the wintering areas is key to evaluate the variability of individual strategies and thus the plasticity of the population to face possible changes in the environment (Dingemanse et al., 2010; Sih et al., 2012). Furthermore, the variability in individual strategies may also determine the development and evolution of migratory strategies in a population (Cote et al., 2010).

The dataset compiled indicated that both Cory's and Scopoli's shearwaters present a high wintering site fidelity. An individual visited during the study period three different wintering areas at the most. However, considering all individuals followed for more than one year, 77% used only one area, while 23% visited different wintering areas in different years (Table 5). These results suggest a slightly higher wintering site fidelity than the reported for birds from Selvagens Islands, where 65% of the individuals followed for more than one year repeated the use of the same areas and 35% changed at least once (Dias et al., 2011). These differences may be due to smaller sample size (14 birds, 9 followed for more than one year) or to the number of years each individual was followed in that study. Also, factors such as age and experience can influence individual decision-making at the moment to decide the wintering destination (Catry et al., 2006, 2011b; Missagia et al., 2015). On the other hand, the likelihood of changing among wintering areas was higher in birds followed for four or more years. Despite this, wintering site fidelity of these birds was also relatively high: 55%, 80% and 50% of the birds followed for 4, 5 and 6 years, respectively, always visited the same area to spend the winter (Table 5).

Wintering site fidelity was also evaluated at intra-individual level measuring the overlap between areas used over the years. The values of this intra-individual overlap index also indicated that individuals from both Cory's and Scopoli's shearwaters showed high fidelity to specific regions at sea in successive winters, despite the vast marine areas visited and their huge movement range. All birds tracked for more than two years always showed a relatively high overlap, with average values between 60% and 80% in all cases and for both species (Figure 38).

TABLE 5 • Wintering site fidelity of Cory's and Scopoli's shearwaters breeding in Spain. Both species were considered together for this analysis, which included 224 year-round tracks from 78 individuals. Each row in the table corresponds to a different group of individuals, according to the number of years each individual was tracked (ranging from 2 to 6 years). The last row indicates the total percentage, without segregating by number of years of tracked. WA = Wintering area.

Years tracked	Individuals tracked	1 WA	2 WA	3 WA
2	44	83.7%	16.3%	-
3	14	71.4%	28.6%	0.0%
4	8	55.6%	33.3%	11.1%
5	10	80.0%	20.0%	0.0%
6	2	50.0%	50.0%	0.0%
Total	78	76.9%	21.8%	1.3%

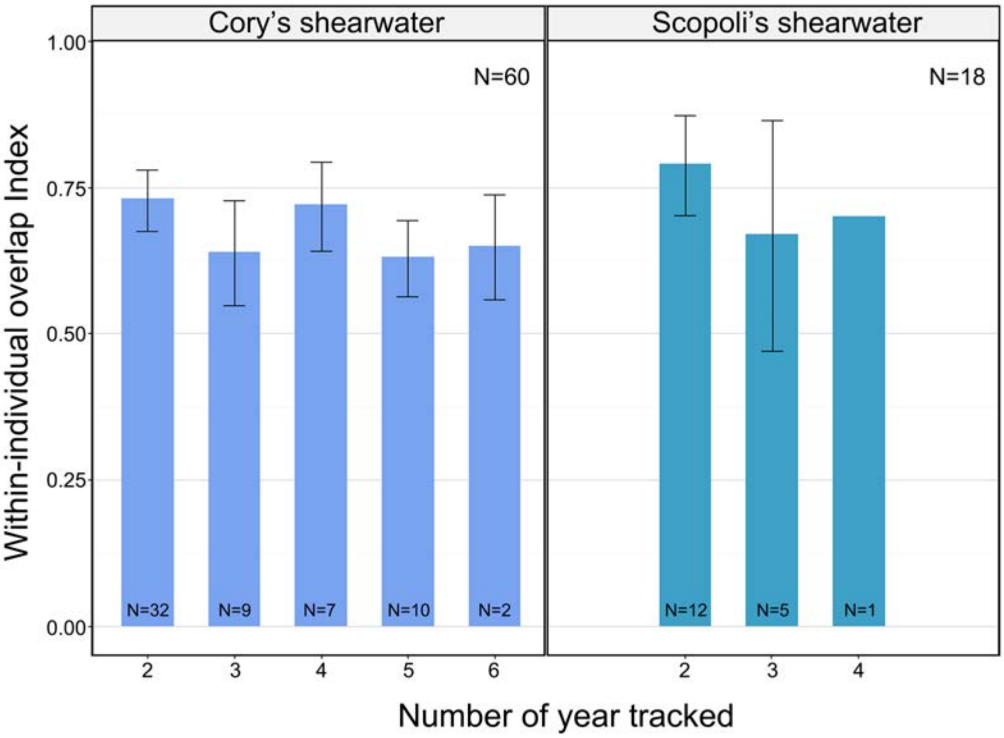

Figure 38 • Intra-individual overlap index, used as a proxy of wintering site fidelity. The index takes values from 0 to 1, 0 meaning no overlap and 1 complete overlap of one individual with itself when comparing its different wintering areas over the years. The X-axis of the plots aggregates the individuals according to the number of years that were tracked. Height of the bars corresponds to the average value of the index for each group of individuals, and the error bars depict the 95% confidence intervals calculated by bootstrapping. Total numbers of individuals considered for each species are presented in the upper right corners. The numbers of individuals in each group are presented at the bottom part of the bars. The analysis was based on Kernel overlap calculation performed in R with adehabitatHR package. Values calculated with data from 78 individuals and 224 year-round tracks.

Migratory connectivity

In species engaging in periodic movements between breeding and wintering areas, migratory connectivity describes the degree to which individuals from the same breeding locality migrate to a given wintering area (Esler, 2000; Webster et al., 2002). High connectivity indicates that all or a large proportion of individuals from the same breeding locality migrate to a single wintering area and do not mix with individuals from other breeding localities. On the contrary, low connectivity or its absence takes place when individuals from the same breeding locality equally distribute among different wintering areas and mix with individuals from other different breeding localities across the wintering areas (Webster et al., 2002; Ambrosini et al., 2009). Measuring migratory connectivity is important to assess the uneven impact that conditions in different wintering areas may have on the fitness of individuals, aspects that ultimately modulate population dynamics. On the other hand, from a conservation perspective, high migratory connectivity means a greater vulnerability for a species or a population, as all members will always be in the same geographical area, entailing a risk in the presence of threats (Webster et al., 2002).

In the case of long-distance migratory species, such as Cory's and Scopoli's shearwaters, individuals can face contrasting environmental conditions throughout the year and over the different areas visited. Therefore, knowing the proportion of individuals from a given breeding colony that use a particular wintering area can help to assess the impact of threats of natural or anthropogenic origin (e.g. storms, resource shortage, oil spills, interactions with fisheries, etc.), on the population dynamics. Similarly, the environmental conditions that birds experience in the wintering areas may explain part of the variability found in the breeding colonies, for instance, the number of individuals that attempt to breed in a given year (Harrison et al*.,* 2011). In this way, each period of the annual cycle can be shaped by the previous one and conditions the subsequent one (the so-called carry-over effects; Norris & Marra, 2007; Fayet et al*.,* 2016).

The migratory connectivity index (Ambrosini et al., 2009), which takes values from 0 to 1, represents the degree to which the spatial structure of the distances between individuals in the breeding areas is also maintained in the wintering areas. A value of 1 would indicate that the spatial structure is fully maintained and therefore individuals from each breeding colony would always migrate to a single destination, where they would not mix with individuals from other colonies. The value obtained considering the three colonies (Veneguera, Montaña Clara and Pantaleu) studied together was 0.82. This is a high value and is probably the result of the spatial segregation between both species in the wintering areas. Moreover, Cory's shearwaters also segregated at some extent during the winter, because birds from Montaña Clara rarely visited the Agulhas Current, and birds from Veneguera rarely visited the Brazilian Current. Data visualization using a chord diagram helped to interpret the importance of every wintering area for each breeding colony, as well as the mix of individuals from different colonies in the wintering areas (Figure 39). The Canary Current plays a major role for Scopoli's shearwaters from Pantaleu because it was the destination of almost as many migratory trips as those that headed to Guinea, Ghana, Angola and Namibia summed. The Canary Current was the wintering area where both species mixed the most, as a small number of Cory's shearwaters always remained in the area all the year-round. For both colonies of Cory's shearwater, Veneguera and Montaña Clara, the area of Namibia and Benguela were the most important. Cory's shearwaters overlapped partially with Scopoli's shearwaters in this wintering area. The confluence of Benguela and Agulhas also had similar importance for these two colonies, unlike the Brazilian Current, which seemed to be more important for birds from Montaña Clara. Finally, the Agulhas Current was only used by birds from Veneguera.

Ecology and behaviour in the wintering areas

Diversity in oceanographic conditions due to differences in weather, seabed and coastline topography, and other environmental features, promotes a high spatial heterogeneity in primary productivity. This heterogeneity forms the basis for the different marine food chains. The different areas occupied by the study species during winter are hundreds to thousands of km apart, and show differences in their environmental features, including depth, wind patterns, nutrient availability and seasonality, which altogether leads to differences in primary productivity (Figure 56), and subsequently, in structure, composition and dynamics of the marine food webs. Shearwaters, as top-predators, must face this heterogeneity by adapting their foraging strategies.

Briefly, areas used to winter by the tracked birds belong to the following marine regions: (1) the Canary Current, (2) the Guinea Current, (3) the Benguela Current, (4) the confluence of Benguela and Agulhas currents, (5) the Agulhas Current, (6) the Brazil Current and its confluence with the Malvinas Current, and (7) the subtropical convergence of the South Atlantic (Figure 40, Figure 41). The main characteristics of each system are summarised below (Longhurst, 1998):

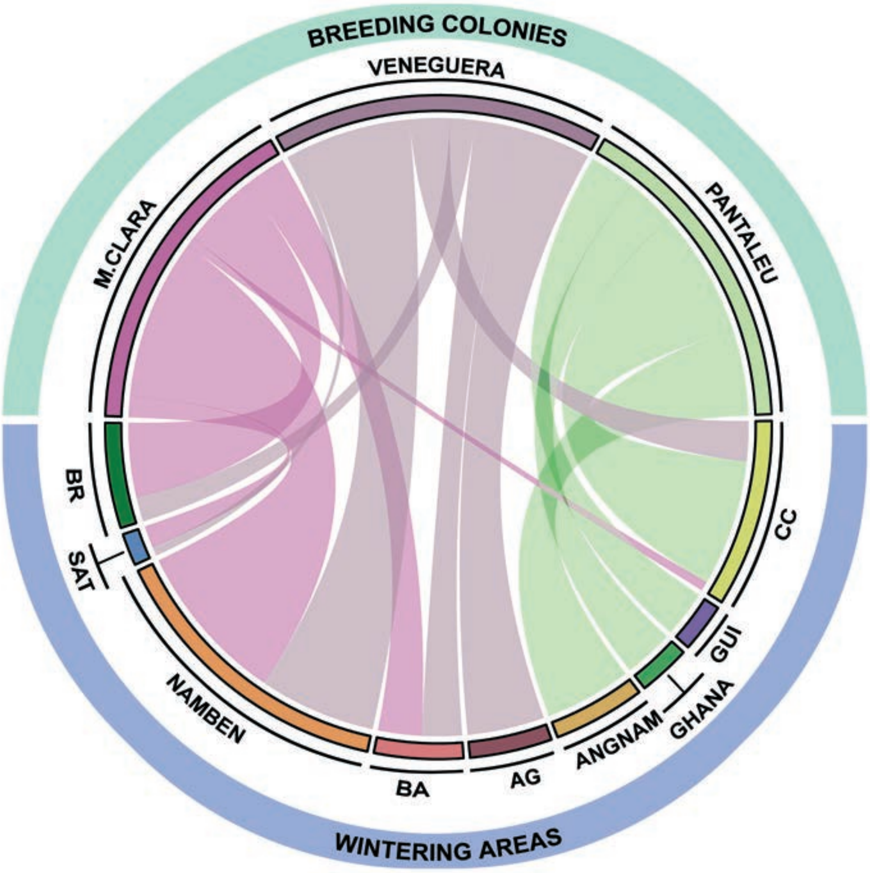

Figure 39 • Migratory connectivity of Cory's and Scopoli's shearwaters breeding in Spain. Analysis performed splitting by breeding colony but not by species, i.e., both Cory's and Scopoli's shearwaters were treated together. This chord diagram illustrates the migratory connectivity between the breeding colonies and the wintering areas. The upper divisions correspond to the breeding colonies where individuals were tagged with geolocators (Montaña Clara, Veneguera and Pantaleu). The lower divisions correspond to the wintering areas identified. The chords connect the breeding colonies to the wintering areas, and their thickness represents the magnitude of the migratory flow, that is, the proportion of trips from each colony that headed to each wintering area. Acronyms stand for: CC = Canary Current, ANGNAM = off the coast of Angola and Namibia, GUI = oceanic waters of Guinea, GHANA = off the coast of Ghana, NAMBEN = Benguela Current off the coast of Namibia, AG = Agulhas Current, BA = Benguela-Agulhas Confluence, BR = Brazil Current, SAT = centre of the South-Atlantic.

- The Canary and Benguela currents are located on the western side of Africa, along a coastline following the north-south direction. These are highly productive marine areas, mainly due to intensive upwelling processes that pump cold nutrient-rich waters up to the sea surface. Easterly winds blow strongly along the African coast and show a regular seasonal pattern over the year. These winds shape the upwelling intensity and its temporal pattern. Moreover, the steep continental shelf-slope also facilitates the rise of deep waters. All together enhances the primary productivity on the continental shelf, as phytoplankton take advantage of the nutrients to grow. Features such as plumes and eddies can further increase the productivity at the local and meso- scale.
- The Guinea Current, mostly located in the Gulf of Guinea, is east-west oriented, parallel to the equator. It is less productive than the previous ones. Here, the mix and displacement of water with different density -due to the Ekman effect caused by the Coriolis force-, determines the productivity.

- The Agulhas Current forms from the union of several smaller currents that flow from north to south on the southeastern side of Africa. These currents generate a convergence zone that causes surface waters to sink, promoting the rise of deep, nutrient-rich waters. The Agulhas Current is especially productive in the southern limit, where it converges in the west with the Benguela Current, and in the south, where it converges with the Antarctic Circumpolar Current. In the latter, the convergence causes the reversion of the current direction, known as the Agulhas retroflection.
- The Brazil Current is a system of warm waters flowing south along the Atlantic coast of South America, from the equator to the confluence with the Malvinas Current, which flows north and holds cold waters. The Brazilian Current flows over the continental shelf and the slope of South America, rising cold, nutrient-rich waters due to the Ekman effect.
- The subtropical convergence of the South Atlantic forms by the mixing of warm waters of the Brazilian Current with cold waters of the Malvinas Current, and then with the Antarctic Circumpolar Current. These mixed waters flow towards the southeast through the South Atlantic, moving away from the South American coast until meeting the Benguela Current.
- These oceanographic systems are predictable at large spatial and temporal scales, so top-predators, including seabirds, make intensive use of these areas (Bost et al., 2009; Block et al., 2011; Ramos et al., 2013; Scales et al., 2014; Grecian et al., 2016).

Cory's shearwater

Spatial distribution of Cory's shearwaters during wintering was largely neritic, using areas less than 500 m deep, except for the central South Atlantic (Figure 42). Birds from Veneguera and Montaña Clara showed no apparent differences in the wintering areas used, and therefore results are presented together for birds from the Canary Islands.

In the wintering areas of the Canary Current and Benguela Current off the coast of Namibia, chlorophyll-a values at birds locations were very high (1.2 mg/m^3). In the Brazilian, Agulhas and Benguela currents, most of the locations corresponded, however, to lower chlorophyll a values (0 to 0.4 mg/m^3; Figure 43). In the centre of the South Atlantic, between 2 000 and 6 000 m deep (Figure 42), chlorophyll-a values were always very low (near 0, with a maximum of around 0.4 mg/m^3). According to activity data and the Night Flight Index (NFI), birds invested more time in flight during the day across the wintering range. Peaks of activity took place at dawn and dusk (Figure 44, Figure 45), which suggests that birds were feeding on prey more accessible at the surface during the twilight, as is often the case of small pelagic fish species such as sardines and anchovies (Giannoulaki et al., 1999). Regarding the spatial pattern of the NFI over the whole wintering range, the more oceanic areas, such as the central area of the South Atlantic, showed a more nocturnal behaviour over a part of the grid (Figure 46). These results are similar to those reported for birds breeding in the Selvagens Islands (Dias et al., 2012a). Birds wintering in the centre of the South Atlantic, a very oceanic area, probably exploit more prey that performs diel vertical migration, therefore being more active (flying more) at night (Weimerskirch et al., 1997; Phalan et al., 2007; Dias et al., 2012a; Louzao et al., 2014).

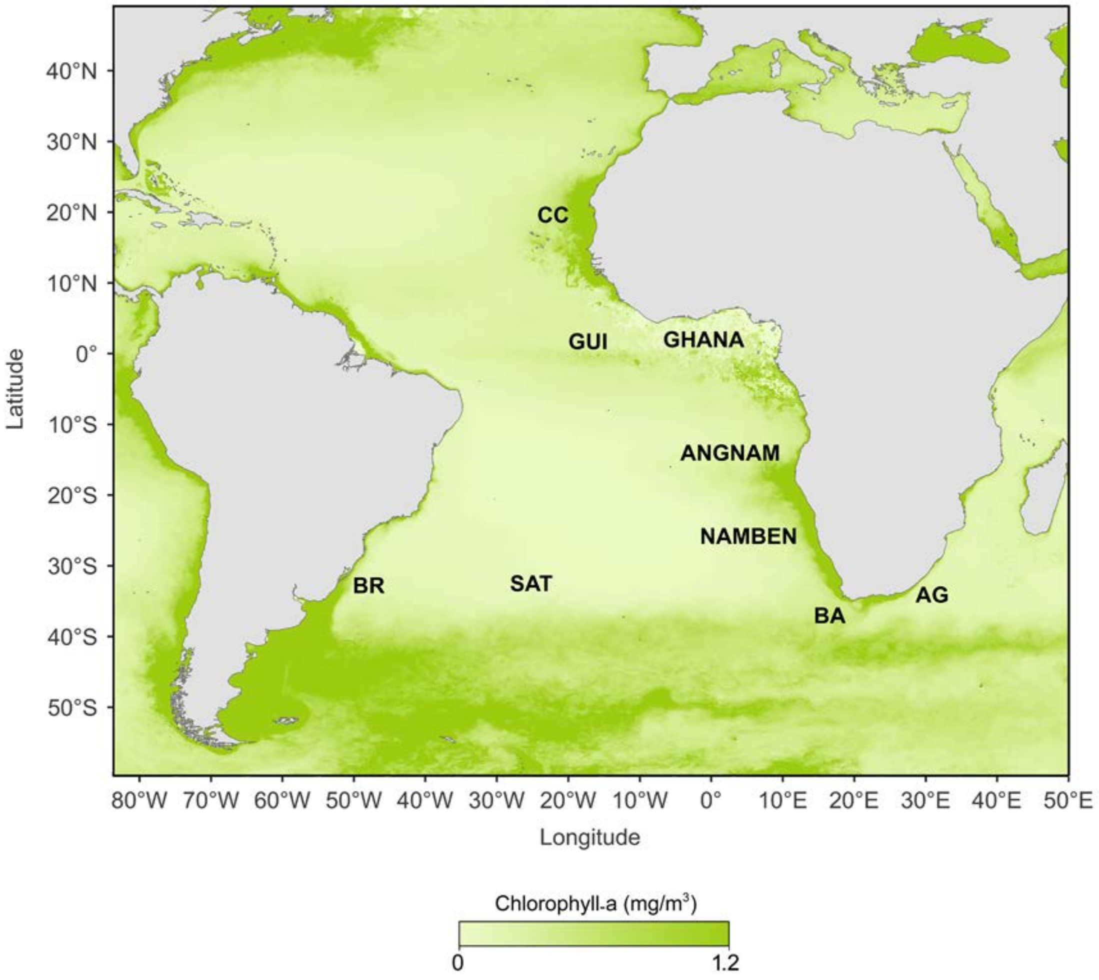

Figure 40 • Map illustrating the average value of chlorophyll-a in the Atlantic during the boreal winter (December to February) for the tracking period with geolocators (2006-2013). Phytoplankton is the base of the oceanic food web and produces a pigment called chlorophyll-a, frequently used as a proxy of ocean productivity. The intensity of the colour measured through sensors on satellites provides a value of abundance (in mg/m3) of chlorophyll-a. Most of the tracked shearwaters wintered in areas with high ocean productivity, such as the Canary Current and other upwelling systems. Acronyms stand for: CC = Canary Current, ANGNAM = off the coast of Angola and Namibia, GUI = oceanic waters of Guinea, GHANA = off the coast of Ghana, NAMBEN = Benguela Current off the coast of Namibia, AG = Agulhas Current, BA = Benguela-Agulhas Confluence, BR = Brazil Current, SAT = centre of the South-Atlantic.

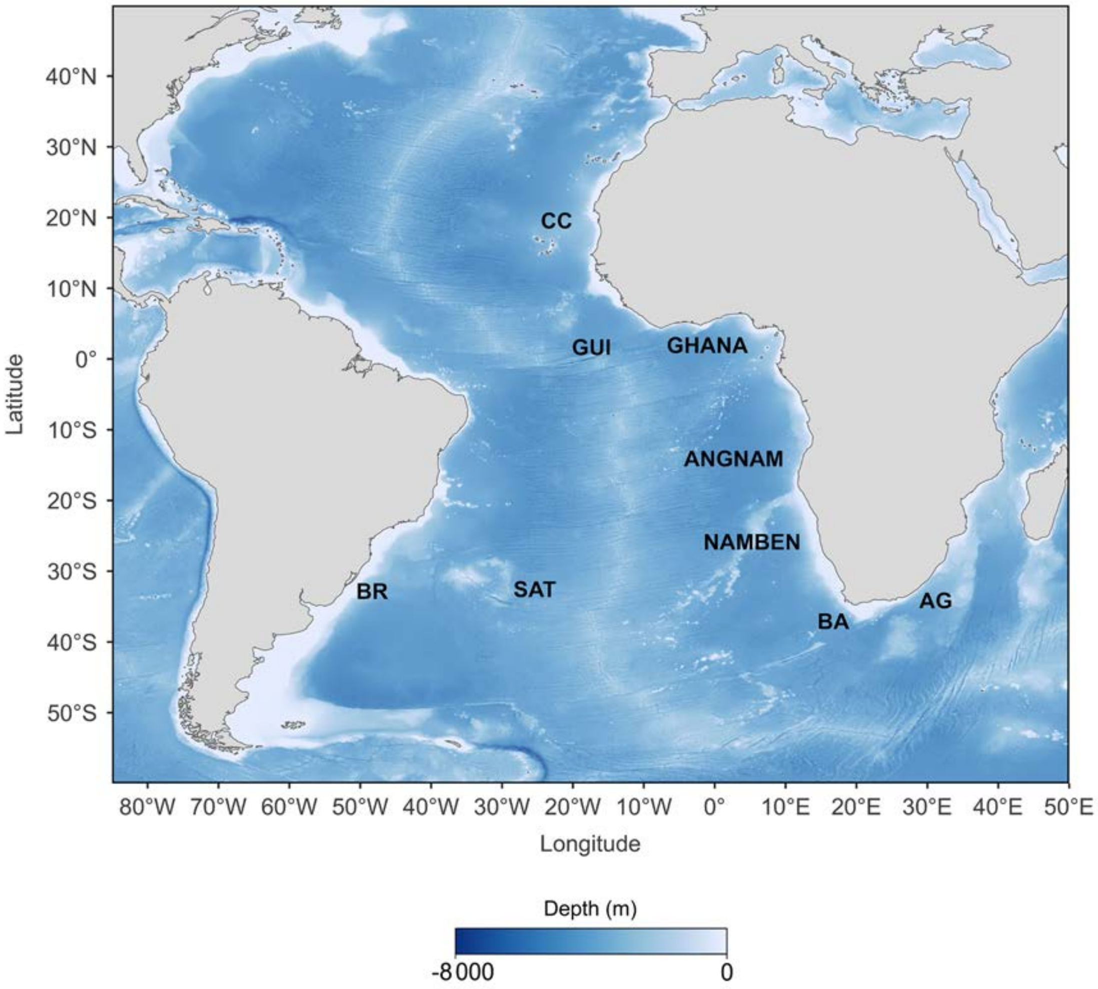

Figure 41 • Map illustrating the bathymetry of the Atlantic Ocean. Almost all the areas used by the tracked birds to winter corresponded to neritic areas, over the continental shelf and slope. Only two of them were oceanic, pelagic areas: Guinea and centre of the South-Atlantic. Depth ranges between -8000 and 0 m. Acronyms stand for: CC = Canary Current, ANGNAM = off the coast of Angola and Namibia, GUI = oceanic waters of Guinea, GHANA = off the coast of Ghana, NAMBEN = Benguela Current off the coast of Namibia, AG = Agulhas Current, BA = Benguela-Agulhas Confluence, BR = Brazil Current, SAT = centre of the South-Atlantic.

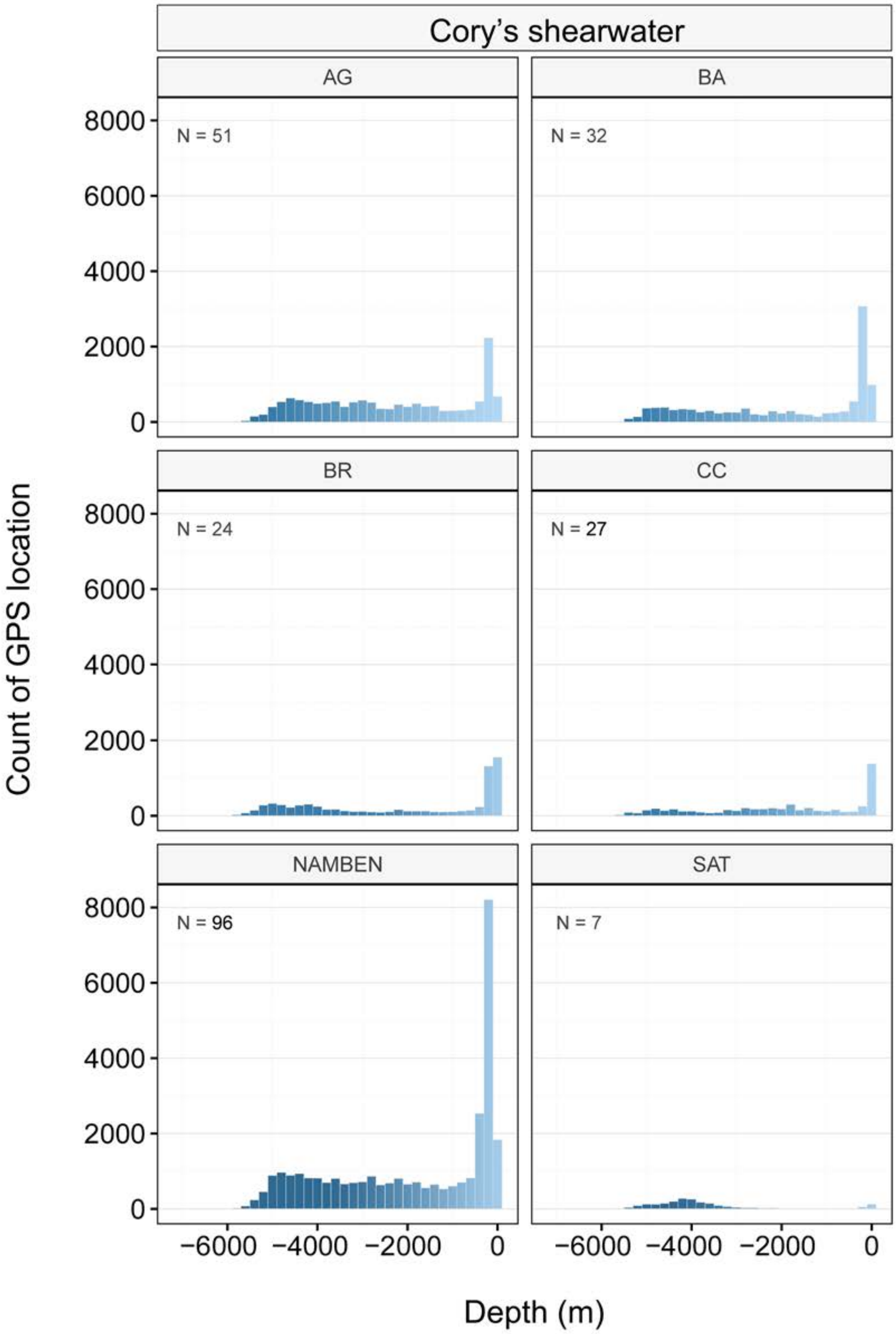

Figure 42 • Histograms of sea depth sampled at tracking locations of Cory's shearwaters. Each facet corresponds to a different wintering area. X-axis indicates depth (in m). Y-axis indicates the number of geolocator locations. The intensity of blue relates to depth, in accordance to the map in Figure 41. The tracked birds preferably selected more neritic waters, using regions with less than 500 m deep, except for the centre of the South Atlantic. Acronyms stand for: AG = Agulhas Current, BA = Benguela-Agulhas Confluence, BR = Brazil Current, CC = Canary Current, NAMBEN = Benguela Current off the coast of Namibia, SAT= centre of the South-Atlantic. Notation in the upper left corners indicates the number of individual wintering events at each area. Data sourced from geolocators equipped with salt-water conductivity sensor.

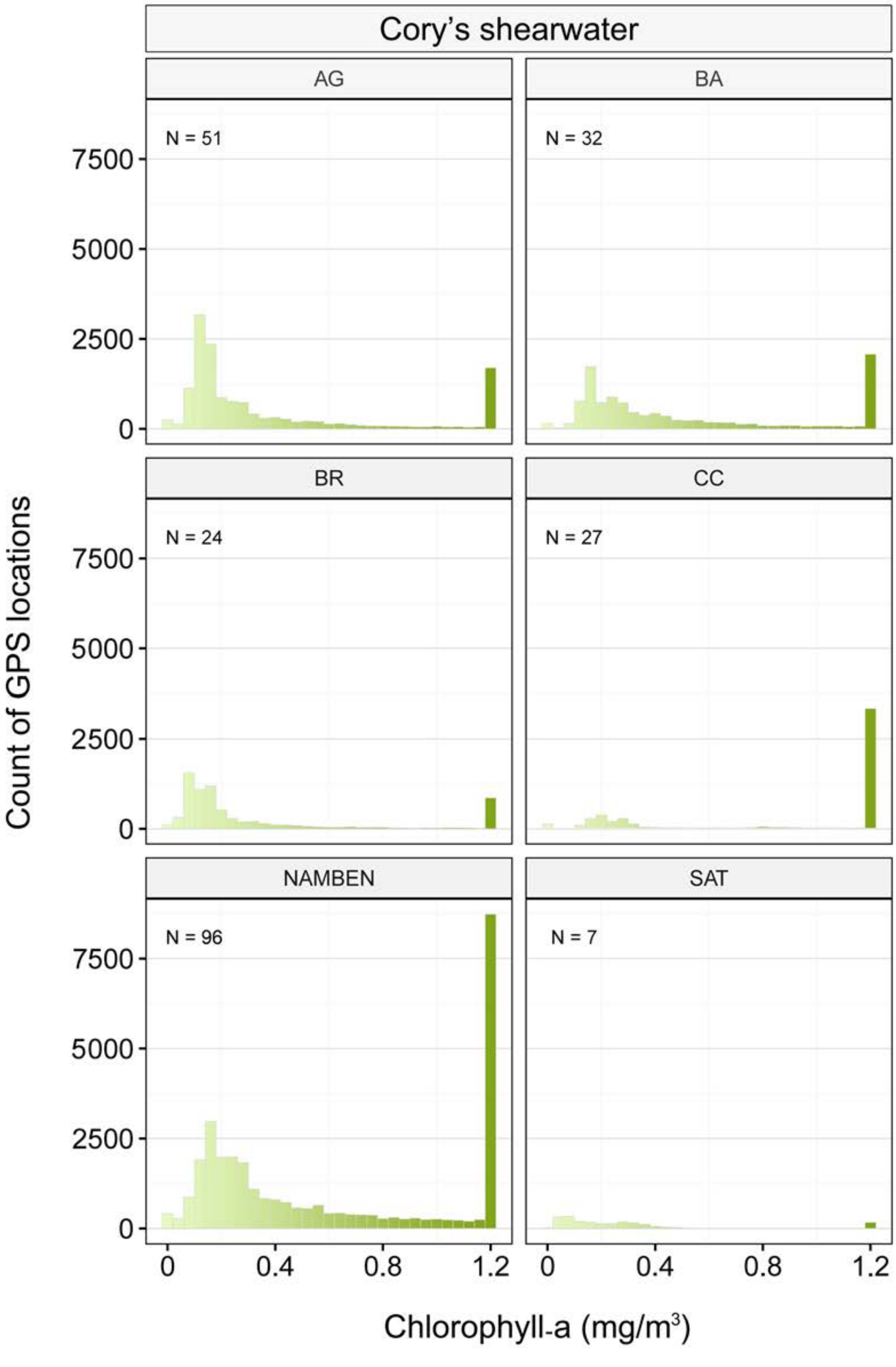

Figure 43 • Histograms of chlorophyll-a values sampled at tracking locations of Cory's shearwaters. Each facet corresponds to a different wintering area. X axis indicates chlorophyll-a value (in mg/m^3). Y-axis indicates the number of geolocator locations. The intensity of green relates to the abundance of chlorophyll as a proxy of marine productivity. The tracked birds preferably selected higher chlorophyll-a values in the Benguela Current off the coast of Namibia and in the Canary Current. Lowest chlorophyll-a values corresponded to the centre of the South-Atlantic, an oligotrophic region compared to the rest of wintering areas. Acronyms stand for: AG = Agulhas Current, BA = Benguela-Agulhas Confluence, BR = Brazil Current, CC = Canary Current, NAMBEN = Benguela Current off the coast of Namibia, SAT= centre of the South-Atlantic. Notation in the upper left corners indicates the number of individual wintering events at each area. Data sourced from geolocators equipped with salt-water conductivity sensor.

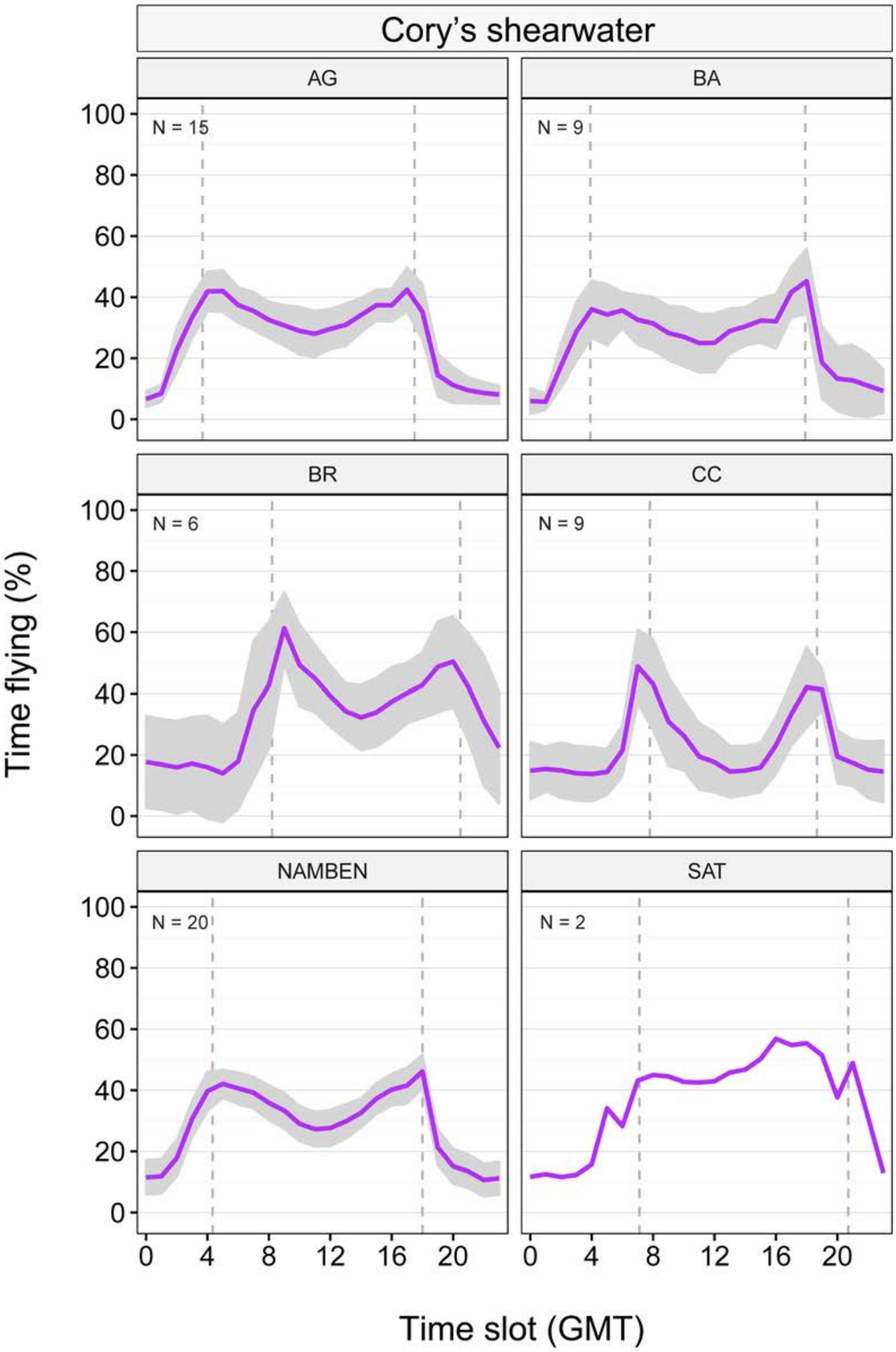

Figure 44 • Time flying per daily time slot of Cory's shearwaters. Each facet corresponds to a different wintering area. X-axis represents the time of the day (GMT). Y-axis represents the percentage of time flying. Violet lines represent the average value at every time slot. Grey shaded areas indicate the 95% confidence interval. Vertical dashed lines indicate the average time of sunrise (left) and sunset (right) from December to February when wintering take place. The tracked birds were more active (i.e. more time flying) during daylight hours, with remarkable peaks around the sunrise and sunset. Acronyms stand for: AG = Agulhas Current, BA = Benguela-Agulhas Confluence, BR = Brazil Current, CC = Canary Current, NAMBEN = Benguela Current off the coast of Namibia, SAT= centre of the South-Atlantic. Notation in the upper left corners indicates the number of individual wintering events at each area. Data sourced from geolocators equipped with salt-water conductivity sensor.

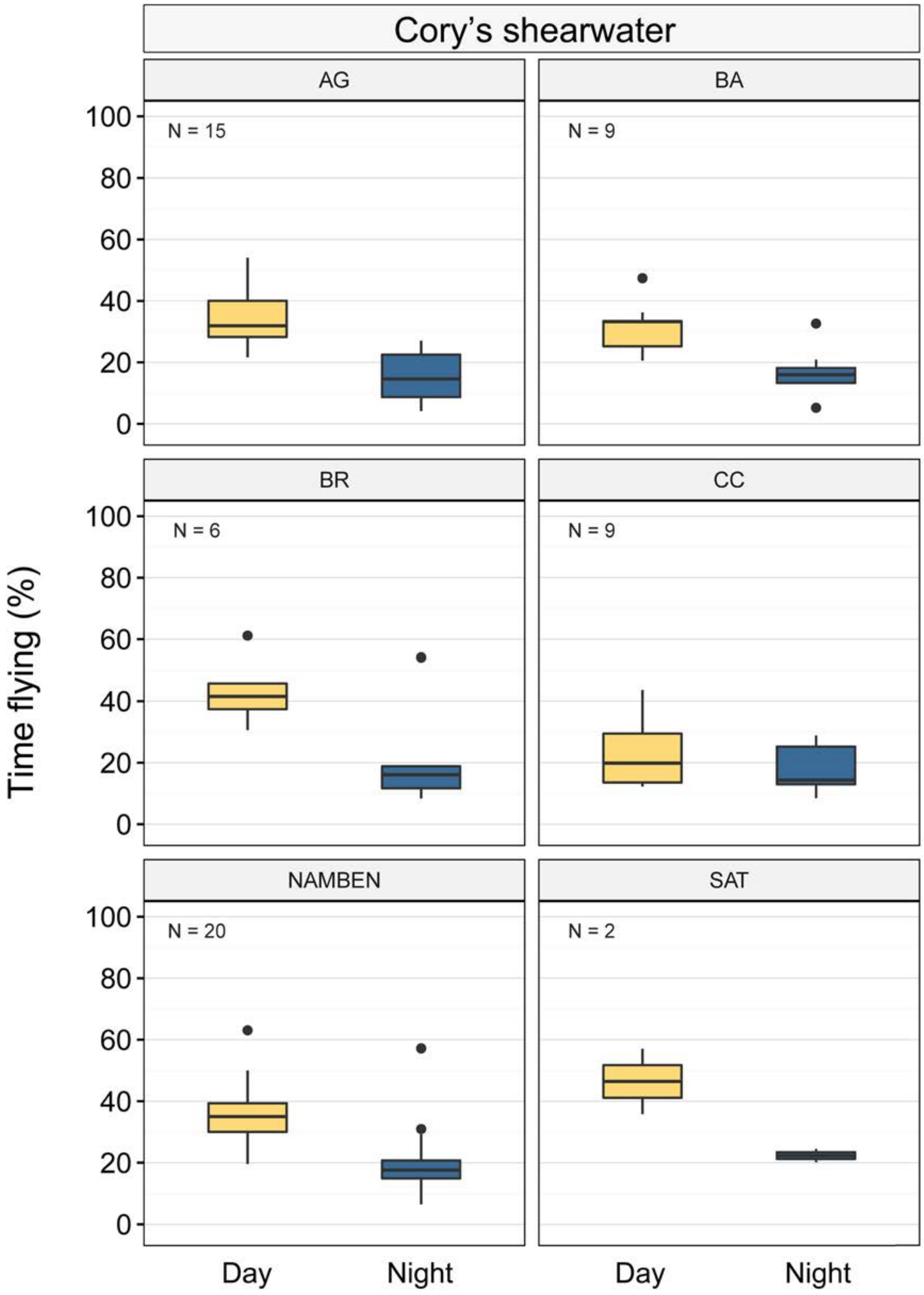

Figure 45 • Box plots showing the time flying by day and night by Cory's shearwaters in the wintering areas. Each facet corresponds to a different wintering area. X-axis identifies day and night (yellow and blue boxes, respectively). Y-axis represents the percentage of time flying. The tracked birds were more active (i.e. more time flying) during daylight across all the wintering areas, except for the Canary Current. Acronyms stand for: AG = Agulhas Current, BA = Benguela-Agulhas Confluence, BR = Brazil Current, CC = Canary Current, NAMBEN = Benguela Current off the coast of Namibia, SAT= centre of the South-Atlantic. Notation in the upper left corners indicates the number of individual wintering events at each area. Data sourced from geolocators equipped with salt-water conductivity sensor.

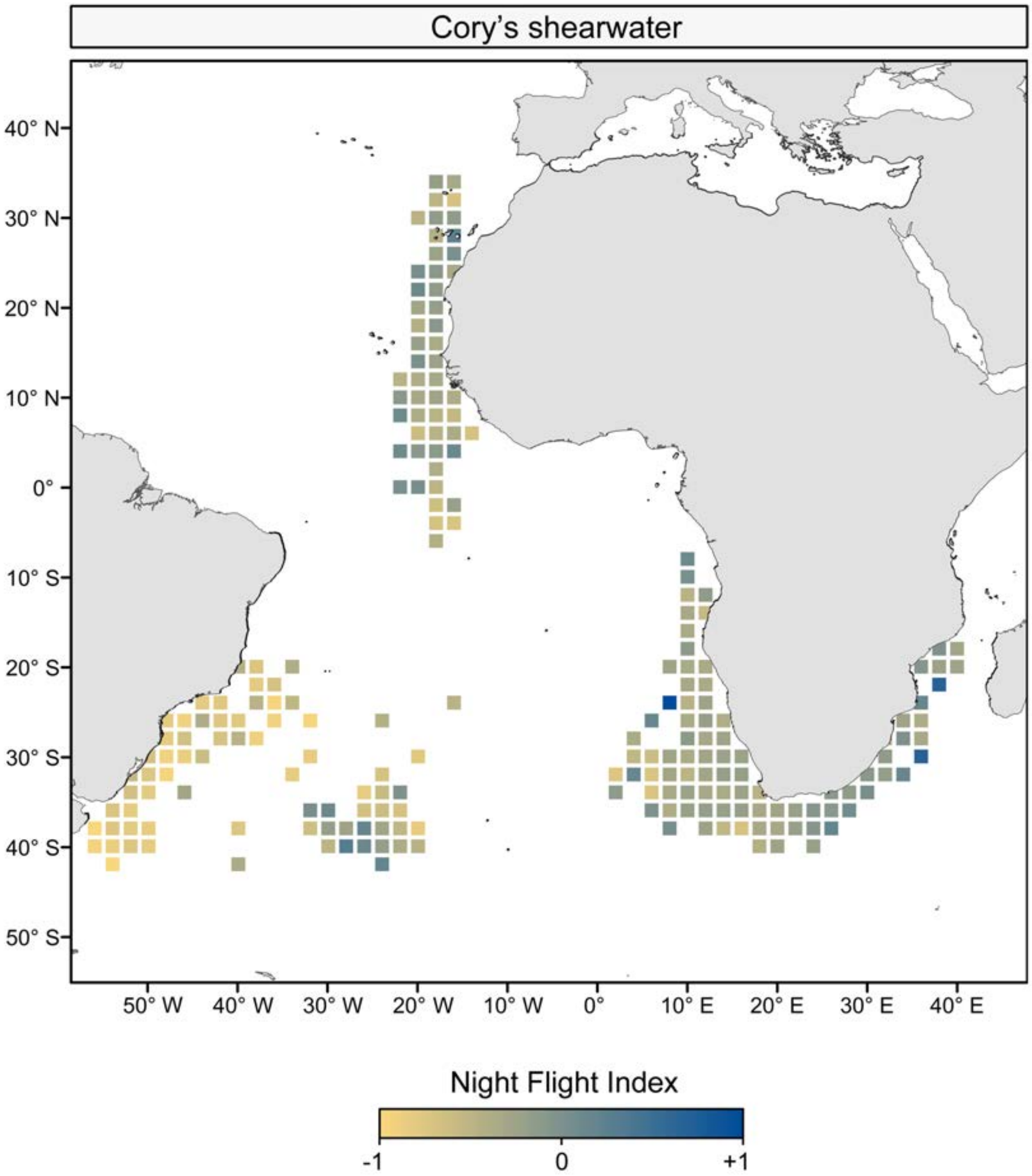

Figure 46 • Night Flight Index (NFI) mapped across the wintering range of Cory's shearwaters. NFI reflects the diurnal-nocturnal flying activity (see details on in: Dias et al., 2012a; Ramos et al., 2015). Colour gradient corresponds to NFI values, ranging from -1 (only diurnal flying, in yellow), to +1 (only nocturnal flying, in blue). Values around 0 (in grey) mean no preference for diurnal or nocturnal activity. Cell size was set to 2 geographic degrees. The tracked birds showed mostly diurnal flying in the wintering area of Brazil. There were no remarkable differences between diurnal and nocturnal activity in the rest of the areas, except a slight tendency towards being more active at night with an increasing depth and distance from the coast, which was also evident the centre of the South-Atlantic. Data sourced from geolocators equipped with salt-water conductivity sensor.

Scopoli's shearwater

Spatial distribution of Scopoli's shearwaters during wintering was largely neritic in the Canary Current and in the Benguela Current off the coast of Angola and Namibia, where a significant proportion of tracking locations were over the continental shelf and slope (Figure 47). Similarly, most locations in these two wintering areas were concentrated in areas with high or very high values of chlorophyll-*a* (Figure 48). In neritic areas of high primary productivity, small epipelagic fish such as sardines, mackerels, and small cephalopods constitute the diet of Cory's shearwaters (Granadeiro et al., 1998b). These prey species often approach the sea surface during twilight and at night, being then more accessible to aerial predators (Giannoulaki et al., 1999; Hays, 2003; Brierley, 2014). The increase in flying time before dawn and, in the case of Angola, also at dusk, may correspond to peaks of foraging activity during twilight preying on this kind of species (Figure 49). In the wintering area of Guinea, however, the tracked birds used more oceanic waters. Tracking locations corresponded to depths close to 5 000 m and with chlorophyll-a values below 0.4 mg/m^3 (Figure 47, Figure 48).

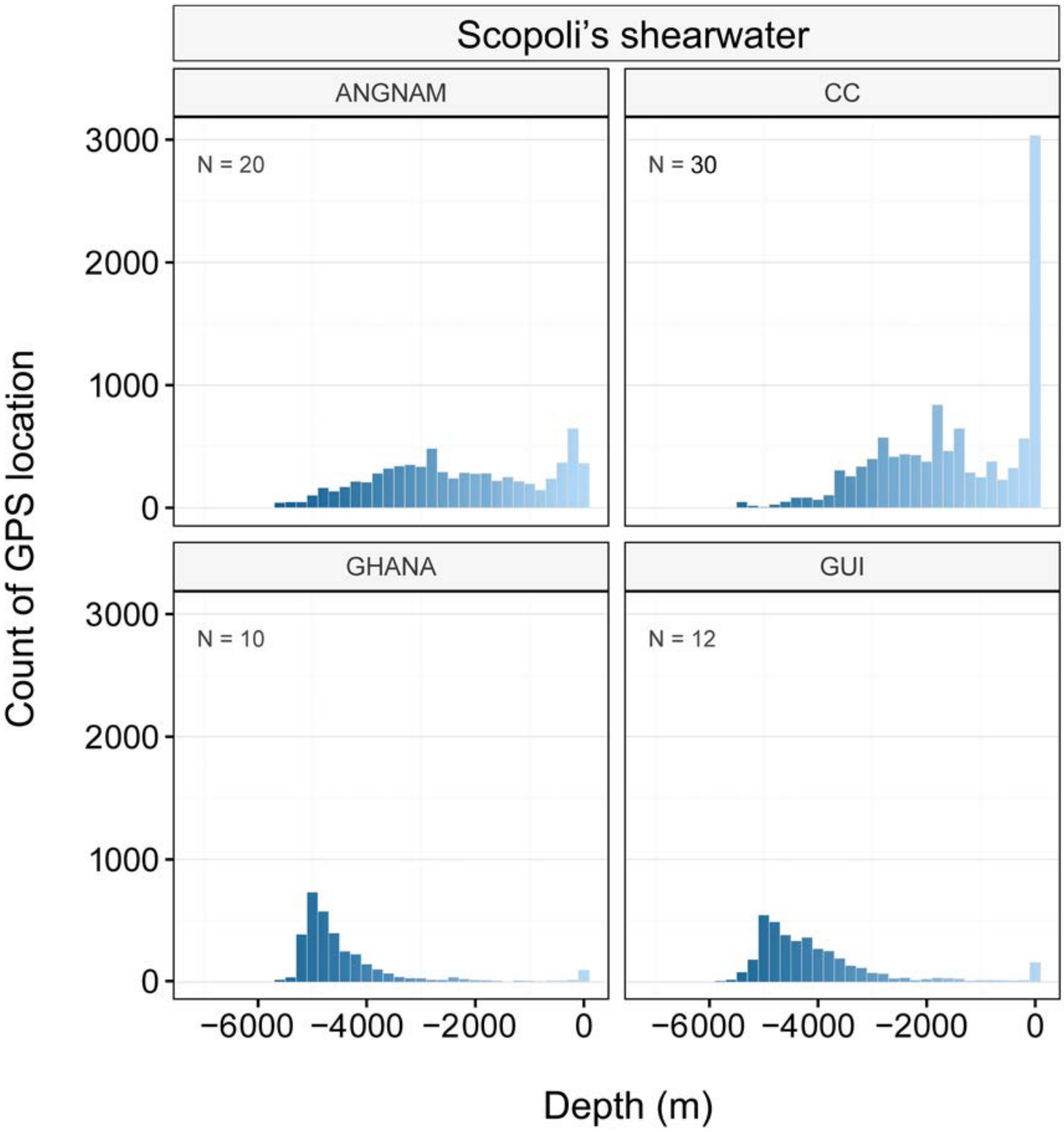

Figure 47 • Histograms of sea depth sampled at tracking locations of Scopoli's shearwaters. Each facet corresponds to a different wintering area. X-axis indicates depth (in m). Y-axis indicates the number of geolocator locations. Birds preferably selected deeper pelagic zones in the areas of Ghana and Guinea, whereas in the Canary Current and the coast of Angola and Namibia birds distributed across a gradient, especially over the neritic zones of the shelf. Acronyms stand for: ANGNAM = off the coast of Angola and Namibia, CC = Canary Current, GHANA = off the coast of Ghana, GUI = oceanic waters of Guinea. Notation in the upper left corners indicates the number of individual wintering events at each area. Data sourced from geolocators equipped with salt-water conductivity sensor.

Time flying in oceanic areas was lower than in neritic areas (Figure 49, Figure 50). Moreover, the NFI reflected larger zones (i.e., more cells in the grid) where night-time activity was more frequent (Figure 51). As for Cory's shearwaters wintering in the centre of the South Atlantic, the behaviour exhibited by Scopoli's shearwaters wintering in oceanic areas suggests they may exploit resources different from the small epipelagic fish that they captured in neritic areas. Some species of small cephalopods, crustaceans, and mesopelagic fish perform diel vertical migrations at night, becoming more accessible for seabirds, and such species have been reported in the of shearwaters from other populations (Angel & Pugh, 2000; Dias et al., 2012a; Granadeiro et al., 1998b; Hays, 2003; Imber, 1973).

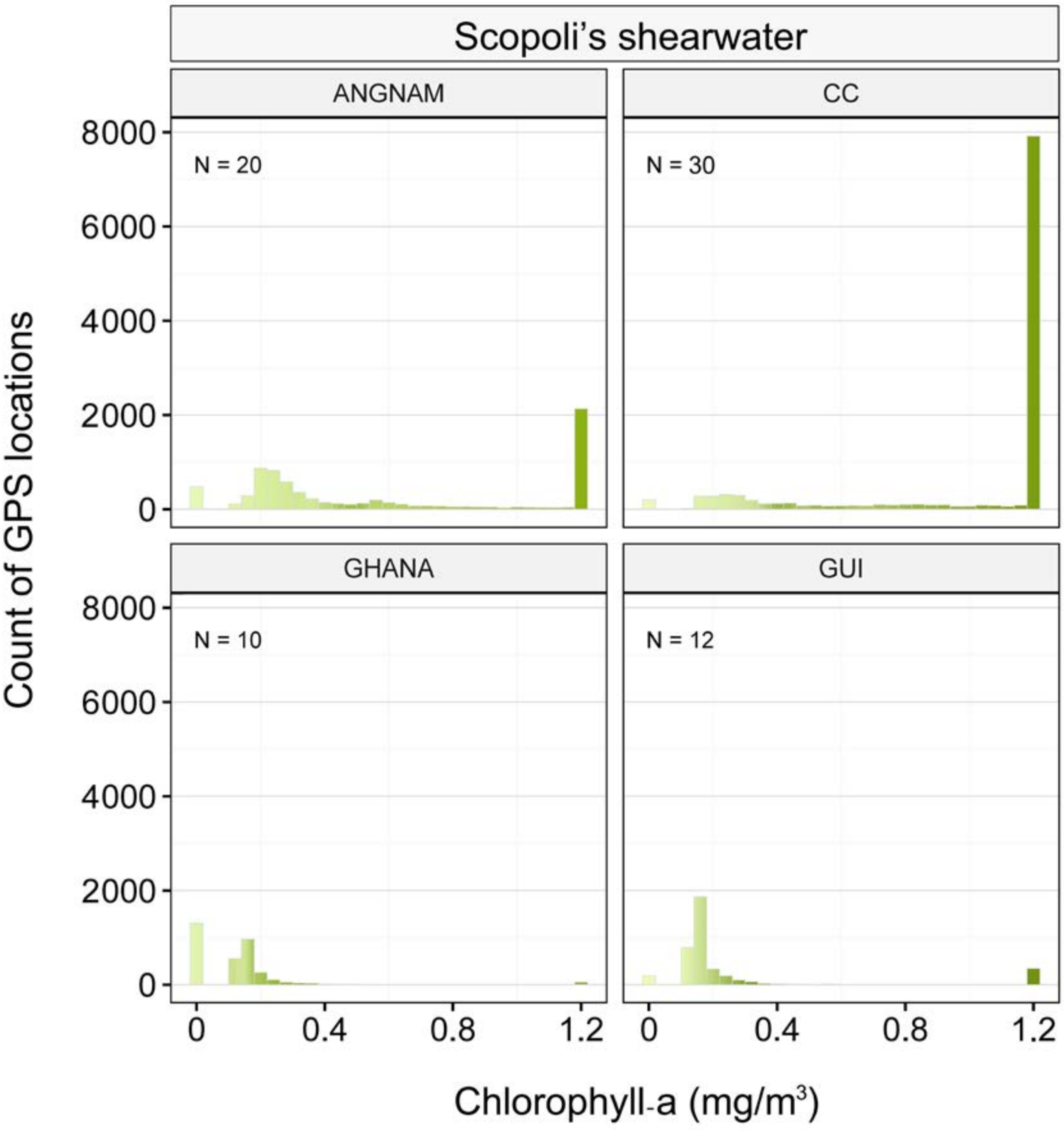

Figure 48 • Histograms of chlorophyll-a values sample at tracking locations of Scopoli's shearwaters. Each facet corresponds to a different wintering area. X-axis indicates chlorophyll-a value (in mg/m^3). Y-axis indicates the number of geolocator locations. The intensity of green relates to the abundance of chlorophyll as a proxy of marine productivity. Most tracking locations matched with high values of productivity, about 1 mg/m^3, in the areas of the Canary Current and the coast of Angola and Namibia, over the continental shelf. In more oceanic areas, such as Ghana and Guinea, chlorophyll-a values were lower. Acronyms stand for: ANGNAM = off the coast of Angola and Namibia, CC = Canary Current, GHANA = off the coast of Ghana, GUI = oceanic waters of Guinea. Notation in the upper left corners indicates the number of individual wintering events at each area. Data sourced from geolocators equipped with salt-water conductivity sensor.

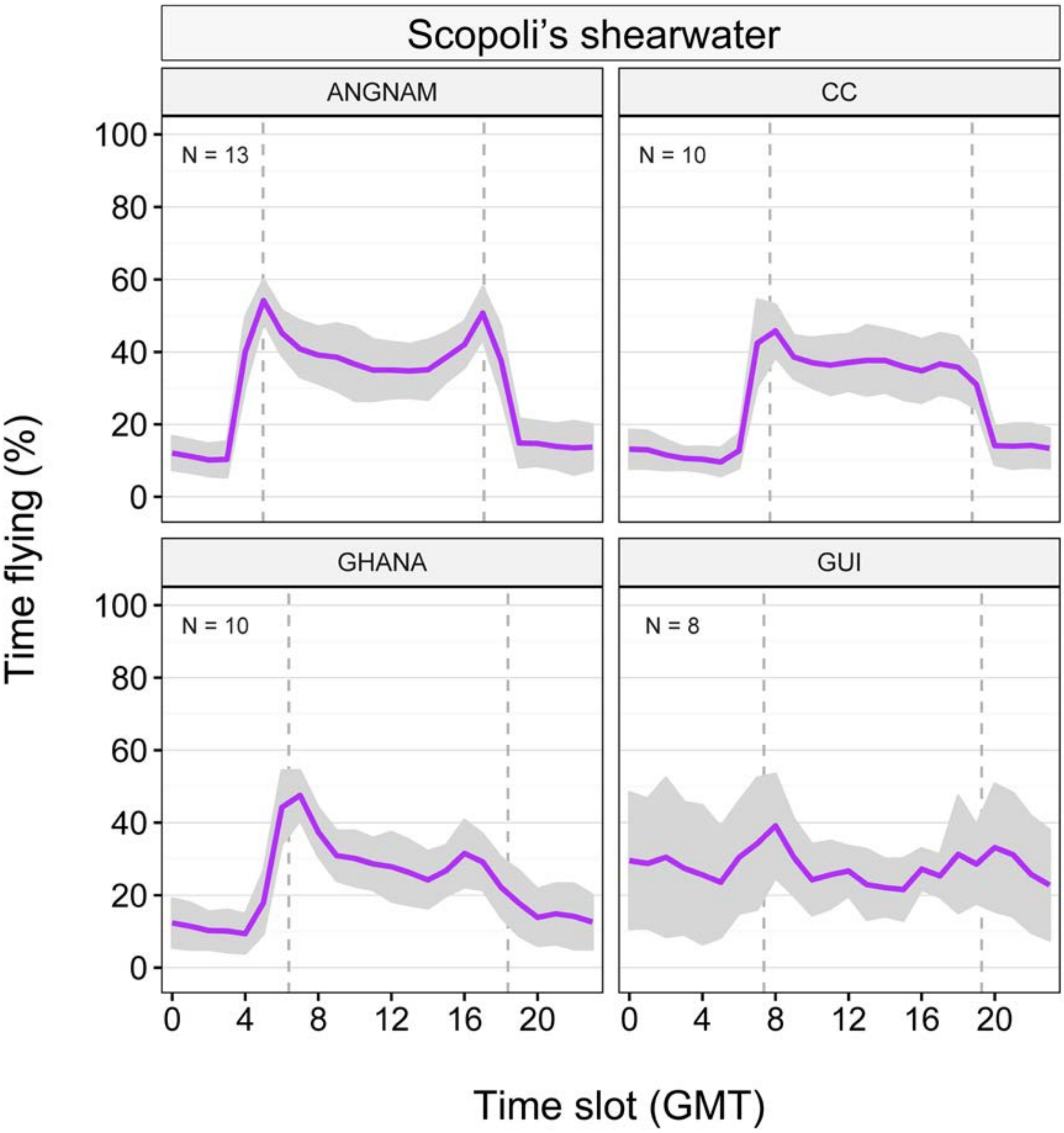

Figure 49 • Time flying per daily time slot of Scopoli's shearwaters. Each facet corresponds to a different wintering area. X-axis represents the time of the day (GMT). Y-axis represents the percentage of time flying. Violet lines represent the average value at every time slot. Grey shaded areas indicate the 95% confidence interval. Vertical dashed lines indicate the average time of sunrise (left) and sunset (right) from December to February when wintering take place. Birds were more active (i.e. more time flying) during daylight hours, with remarkable peaks around the sunrise and not so steep around the sunset. However, birds wintering in Guinea were equally active during day and night, with a weak peak around sunrise. Acronyms stand for: ANGNAM = off the coast of Angola and Namibia, CC = Canary Current, GHANA = off the coast of Ghana, GUI = oceanic waters of Guinea. Notation in the upper left corners indicates the number of individual wintering events at each area. Data sourced from geolocators equipped with salt-water conductivity sensor.

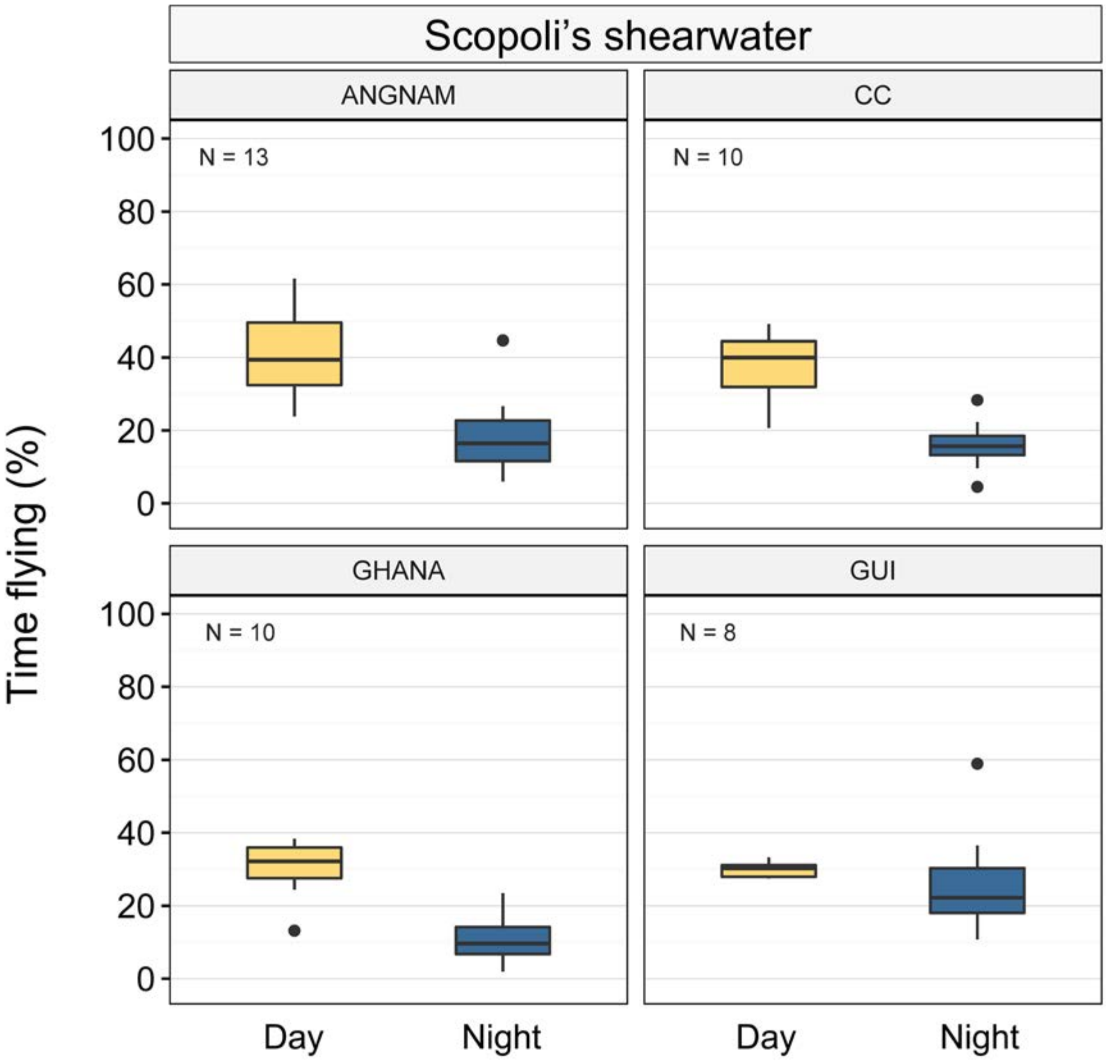

Figure 50 • Box plots showing the time flying by day and night by Scopoli's shearwaters in the wintering areas. Each facet corresponds to a different wintering area. X-axis identifies day and night (yellow and blue boxes, respectively). Y-axis represents the percentage of time flying. Birds were more active (i.e. more time flying) during daylight across all the wintering areas. They were more nocturnal in Guinea, suggesting birds were feeding at night in this area. Acronyms stand for: ANGNAM = off the coast of Angola and Namibia, CC = Canary Current, GHANA = off the coast of Ghana, GUI = oceanic waters of Guinea. Notation in the upper left corners indicates the number of individual wintering events at each area. Data sourced from geolocators equipped with salt-water conductivity sensor.

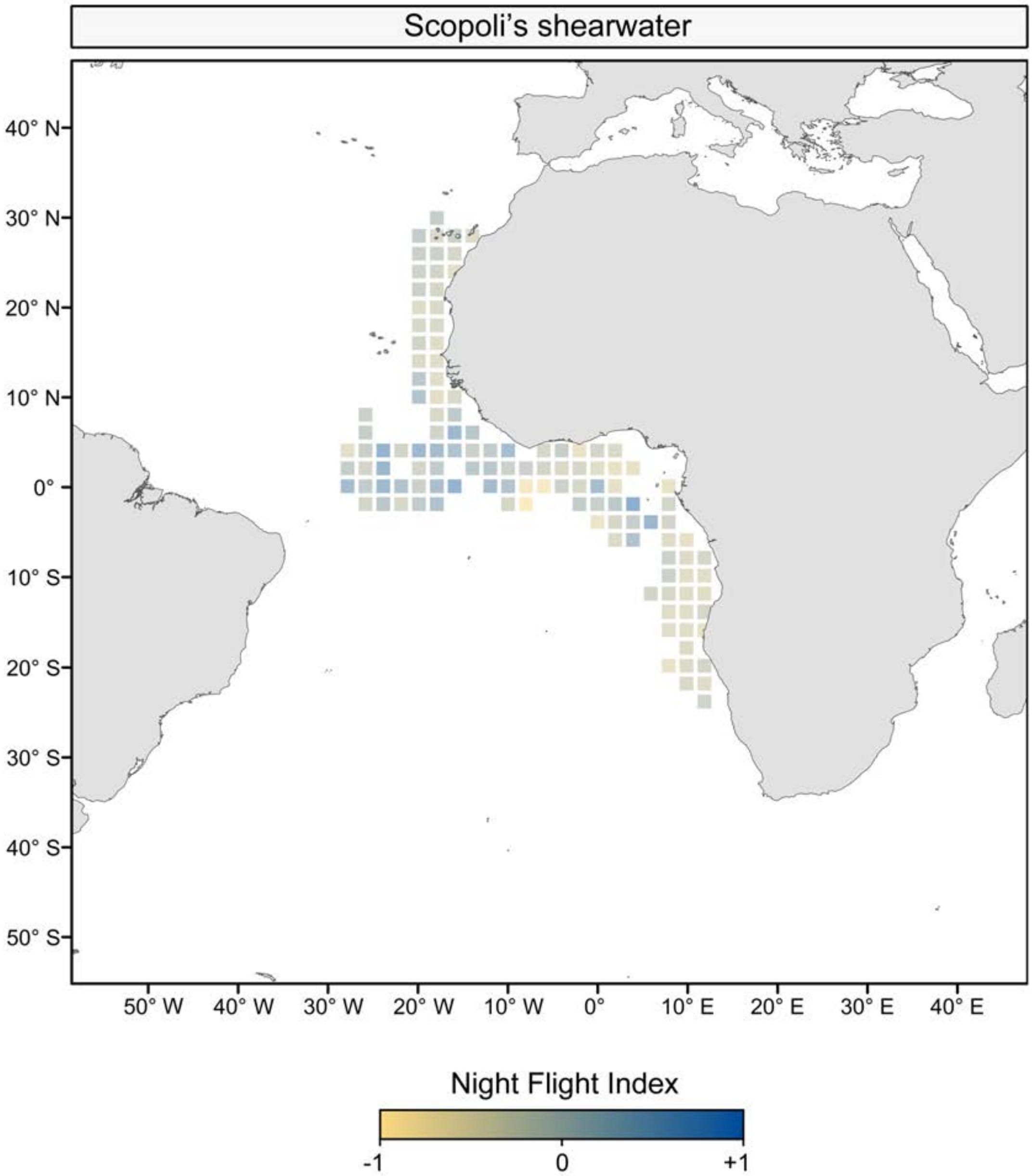

Figure 51 • Night Flight Index (NFI) mapped across the wintering range of Scopoli's shearwaters. NFI reflects the diurnal-nocturnal flying activity (see details on in: Dias et al., 2012a; Ramos et al., 2015). Colour gradient corresponds to NFI values, ranging from -1 (only diurnal flying, in yellow), to +1 (only nocturnal flying, in blue). Values around 0 (in grey) mean no preference for diurnal or nocturnal activity. Cell size was set to 2 geographic degrees. Scopoli's shearwaters were mostly diurnal over the entire wintering distribution, although showing a slight tendency towards being more active at night with increasing depth and distance from the coast. In this regard, the oceanic area of Guinea reflects more nocturnal activity, suggesting that birds in this area fed on nocturnal prey. Data sourced from geolocators equipped with salt-water conductivity sensor.

Phenology

Both species showed similar breeding phenology. Compared to other seabirds breeding in Spain, Cory's and Scopoli's shearwaters breeding phenology is a little more delayed. Only the breeding calendar of the Bulwer's petrel (*Bulweria bulwerii*) and the European storm-petrel (*Hydrobates pelagicus)* largely overlap, although fledglings of these species usually leave the nest a few weeks earlier than those of Cory's and Scopoli's shearwaters. Cory's shearwaters showed greater variability than Scopoli's shearwaters in the migratory calendar, likely due to the greater number of wintering areas in the former. Both the breeding colony and the area of destination to winter shape the variability in the onset of the post-breeding migration (Figure 52).

Table 6 • Migratory calendar of Cory's and Scopoli's shearwaters that breed in Spain. Dates correspond to the average value. The day of the year and the standard deviation in days are presented within brackets.

Species	Onset of post-breeding migration	Arrival to the main wintering area	Onset of pre-breeding migration	Arrival at the breeding colony
Cory's shearwater Trips = 237	November 13th (318 ± 28)	November 14th (319 ± 68)	February 14th (45 ± 13)	March 5th (66 ± 15)
Scopoli's shearwater Trips = 72	October 23rd (298 ± 6)	November 1st (306 ± 8)	February 18th (50 ± 10)	March 1st (62 ± 9)

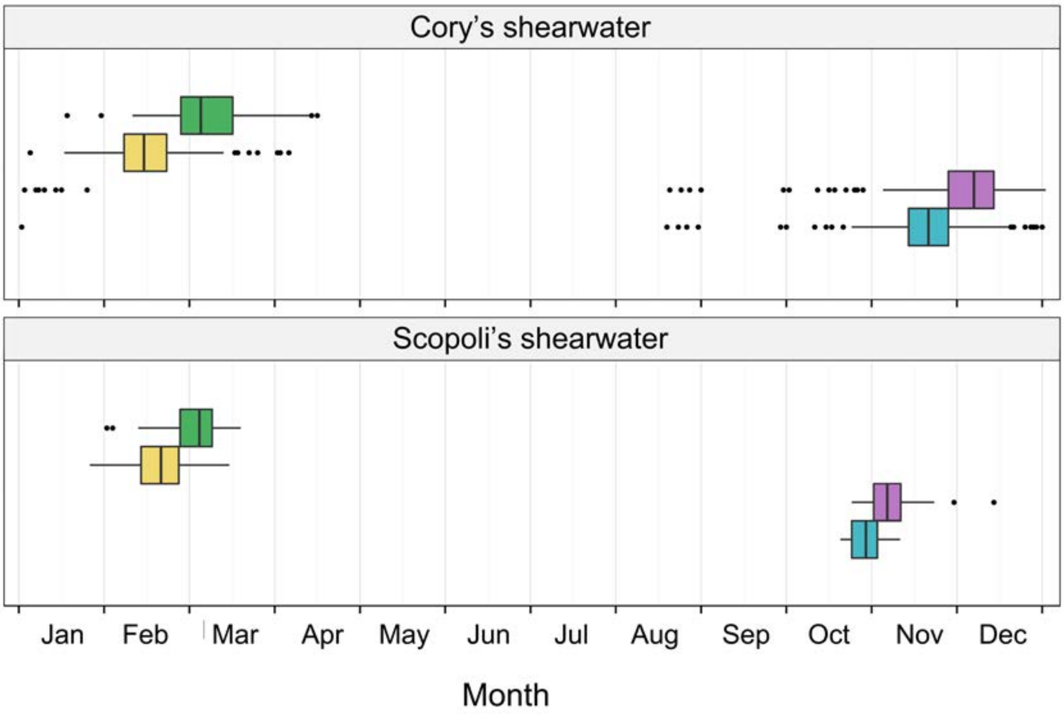

Figure 52 • Box plots showing median, interquartile range and extreme values (black dots) of the main phenological events of the migration. Yellow indicates the onset of the pre-breeding migration, green indicates the arrival at the breeding colony, blue indicates the onset of the post-breeding migration, and violet indicates the onset of the wintering period. The X-axis indicates months of the calendar year from left to right. Phenology between the two species differed in the onset of the post-breeding migration, thereby influencing the arrival to the wintering areas. Extreme values of post-breeding migration in August corresponded to failed breeders.

Cory's shearwaters spent about 15 days to cross the equatorial line to reach southern latitudes. Exceptionally, some individuals wandered over the South Atlantic for some months before settling in a wintering area. In the case of Scopoli's shearwaters, birds left the western Mediterranean in the second half of October. In barely 15 days they reached their wintering areas in the Atlantic, were remained for about 3.5 months. The onset of the pre-breeding migration was in mid-February, arriving after 10-15 days to the breeding colonies (Table 6, Figure 52, Figure 53). Comparing the two species, on average Scopoli's shearwaters started the post-breeding migration and arrived at their main wintering areas about two weeks before Cory's shearwaters did. The rest of the phenological events were more or less synchronized between species (Figure 53, Figure 54).

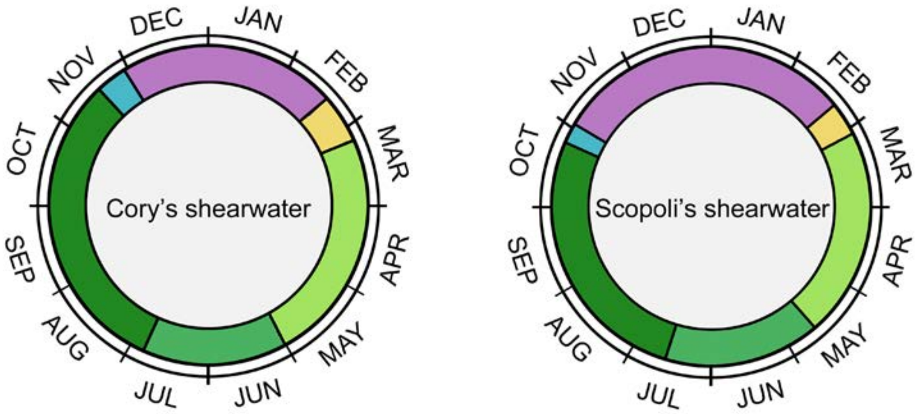

FIGURE 53 • Circular plot showing phenology year-round. In clockwise direction: violet indicates the wintering period, yellow the pre-breeding migration, light green the pre-laying period, green the incubation period, dark green the chick-rearing, and blue the post-breeding migration. Months are depicted outside the circles in a clockwise direction. The delimiter before each phase represents the average starting date of each phenological event.

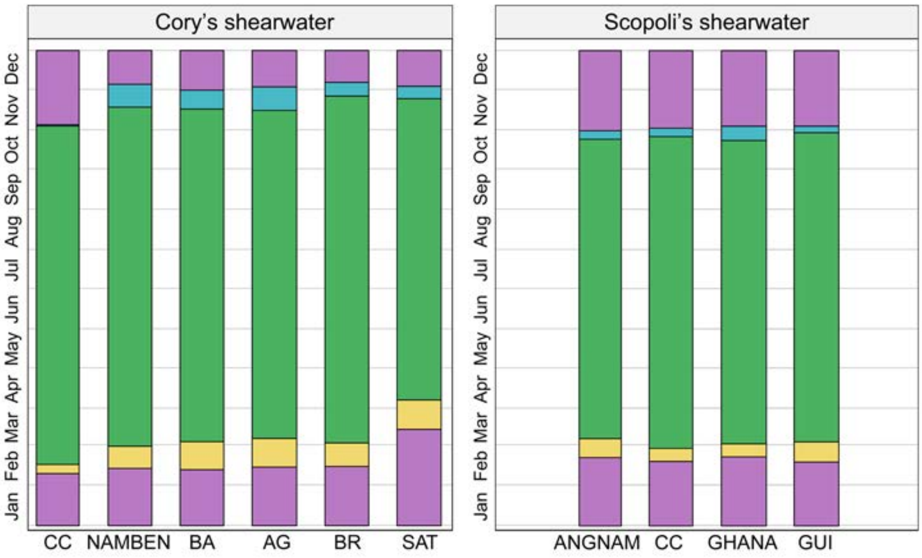

FIGURE 54 • Barplots showing the migratory phenology of Cory's (left) and Scopoli's shearwaters (right) by wintering area. Y-axis indicates months from the bottom to the top. Violet indicates the wintering period, yellow the pre-breeding migration, green the breeding period, and blue the post-breeding migration. X-axis indicates the wintering area. Acronyms in X-axes stand for: CC = Canary Current, NAMBEN = Benguela Current off the coast of Namibia, BA = Benguela-Agulhas Confluence, AG = Agulhas Current, BR = Brazil Current, SAT = centre of the South-Atlantic, ANGNAM = off the coast of Angola and Namibia, GHANA = off the coast of Ghana, GUI = oceanic waters of Guinea. Every delimiter between two sectors represents the average starting and ending date of the phenological event.

Moulting deserves a brief comment, as it is closely linked with phenology. Moulting schedule is sensitive to the external factor and the internal state. Particularly the breeding success has a great influence on the moulting calendar. The species have a complete moult that overlaps considerably with the breeding period. Adults that early fail to breed advance the moulting calendar (Alonso et al., 2009). During the pre-laying and early incubation phases, feather turnover is minimal. Well into the incubation phase, moult increases in breast feathers, progressing downwards and to the sides. The same happens in the dorsal parts of the body. The moult of flight feathers lasts about 200 days, from late August to March, thus starting during the chick-rearing. Moult of primary feathers is simple and descending, from the innermost (P1) to the outermost feather (P10). Secondary feathers show a more complex pattern, with three unsynchronized moult centres: the first in the innermost tertiary feathers (around S22), the second approximately in the fifth secondary (S5), and the third in the outermost secondary (S1, see Figure 55). Moult of rectrices is simple, starting in the tail centre and progressing towards the outer ones. Most rectrices are replaced in the wintering areas but in March-May their moult is advanced yet not finished, it is then apparently suspended until August, when it is reactivated to conclude, in most birds, before September (Monteiro and Furness, 1996, Ramos et al., 2009).

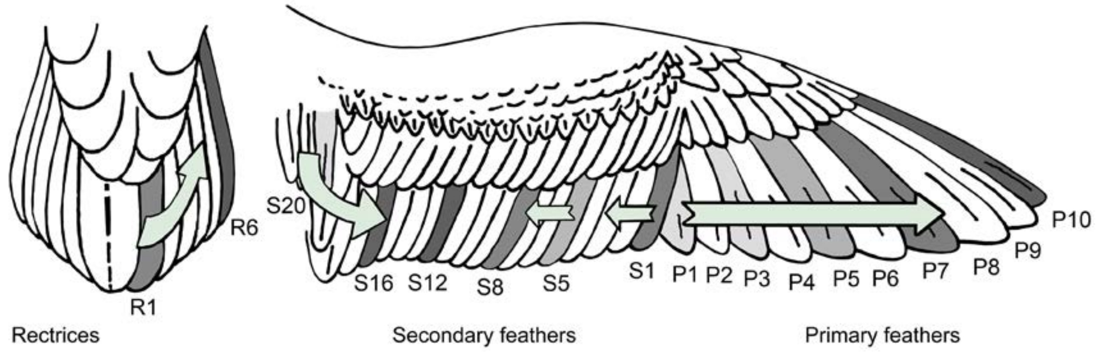

Figure 55 • In both the Cory's and the Scopoli's shearwaters, primary feathers are moulted according to a descendant pattern, from the inner-most primary P1) to the outer-most primary (P10). Secondary feathers show a more complex pattern with three non-synchronized moult centres: the first in the tertiary feathers (around S22), the second approximately in the fifth secondary feather (S5), and the third in the most external secondary one (S1; Monteiro & Furness, 1996, Ramos et al., 2009). Light grey indicates feather moulted at the breeding areas and dark grey those moulted at the wintering areas. Image adapted from Ramos et al. (2009).

Behavioural patterns year-round

By using conductivity data from geolocators, it is possible to discern between flight and diving/sitting on water behaviours unequivocally when looking out of the breeding period. However, during the breeding period, the dry state may reflect both flying and sitting in the colony, and thus interpreting behaviour is tricky. Time in the dry state has the maximum values during the breeding period, from March to November, due to the high investment in time searching for food to feed the chick and the time spent inside the burrow during the incubation stints. Long nest visits, including incubation stints, alternated with foraging bouts at sea are well reflected in the data as marked peaks and troughs between June and mid-July (Figure 56). Between December and February, dry time corresponds exclusively to flight episodes, and show comparatively much lower values. This likely reflects the lower investment in foraging during the wintering period, both because of the absence of the very demanding breeding duties and because of the decreased flight capabilities due to active moulting. On the other hand, the gradual increase in time flying from weeks before the onset of migration might be related to the migratory restlessness, the so-called *zugunruhe*, as described for other terrestrial bird species (Helm, 2006). Finally, unlike Scopoli's shearwaters, Cory's shearwaters flew over longer distances through the open sea to reach the wintering areas. These long flight bouts are reflected in the activity patters as a peak that matches the period of the post-breeding migration (Figure 56). The decrease in flight activity observed just before this peak may correspond to the moult of some flight feathers before the onset of migration (Ramos et al., 2009; Cherel et al., 2016).

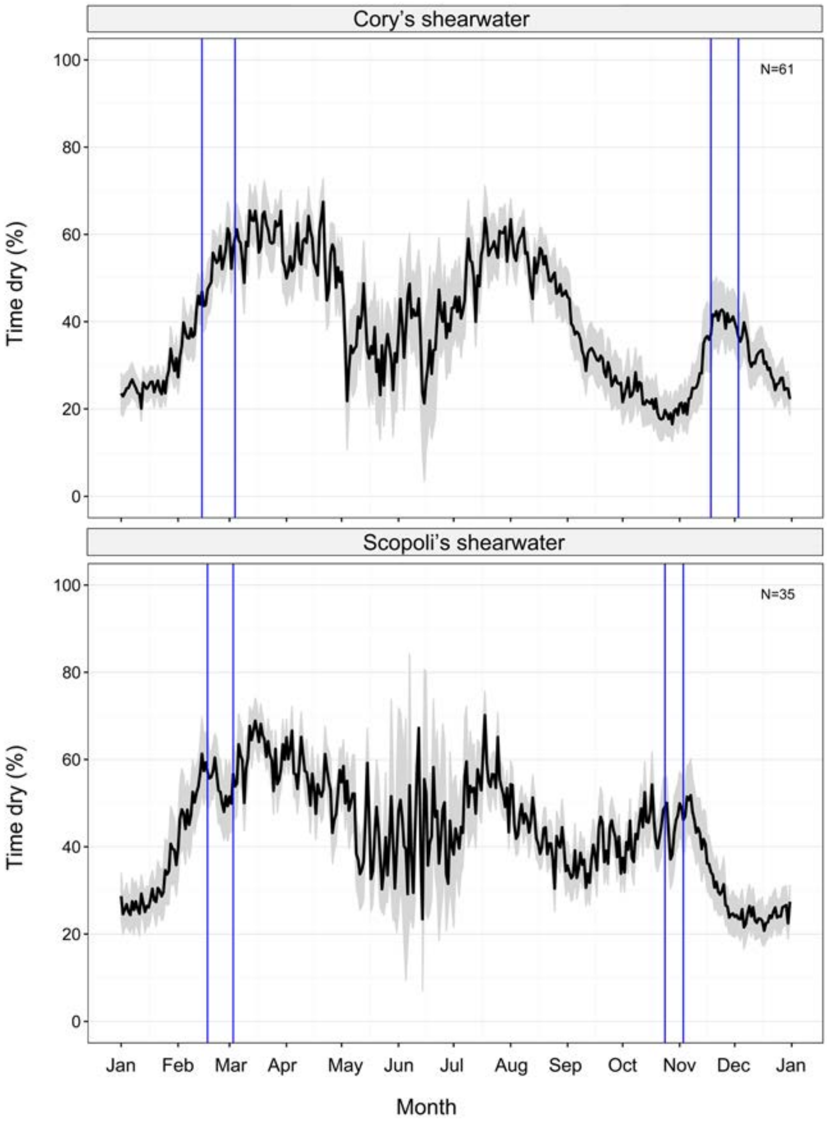

Figure 56 • Year-round activity patterns of Cory's and Scopoli's shearwaters from Spanish populations. The X-axis indicates the month. The Y-axis indicates the percentage of time dry, i.e., time out of the water. Vertical blue lines represent, from left to right, the average value for the onset of the pre-breeding migration, arrival to the breeding colony, the onset of the post-breeding migration and arrival to the wintering area. Black lines depict the daily average value of time dry for tracked individuals. Grey shaded areas indicate 95% confidence intervals. During the wintering, time dry certainly means flying. However, during the breeding period, time dry can also mean being at the colony. From December to February, during the wintering period, time dry is noticeably lower than during the breeding period. Note the peaks around April and August corresponds to activity during pre-laying and chick-rearing, whereas the valleys in June-July correspond mainly to the incubation period when birds alternate incubation stints with foraging bouts. Notation in the upper right corners indicates the sample size used for this particular analysis, expressed as the number of year-round individual tracks. Data sourced from geolocators equipped with salt-water conductivity sensor.

CONCLUSIONS AND FUTURE CHALLENGES

Nowadays, Cory's and Scopoli's shearwaters are probably among the best-known seabird species, thanks to the intensive use of remote tracking technology over the last decade. However, in the case of Spain, a large part of the tracking data had remained dispersed, largely unexplored or in the grey literature. This study provides an extensive analysis of the at-sea ecology of Cory's and Scopoli's shearwaters based on the compilation of a large tracking dataset that had remained largely unexplored so far. The results, obtained through combining modern remote-tracking techniques and state-of-the-art analytical methods, yield an opportunity to improve conservation strategies for these species at national and international level. However, there are still several challenges for the future.

At the national level, the results presented here support largely those areas identified by SEO/BirdLife as Marine Important Bird Areas (IBA) in Spain, which were later on included in Natura2000 network by the Spanish Government. The majority corresponds to areas used during the breeding period. However, there are still a few areas of importance for these species without legal protection. The results also reveal the great ubiquity of these species compared to other Procellariiformes. During the breeding period, Cory's shearwaters used intensively the African shelf, from southern Morocco to the north of Mauritania, and Scopoli's shearwaters used the entire Iberian and Balearic continental shelf. At the same time, however, some degree of spatial segregation tends to occur among birds from different colonies. Both aspects have strong implications for conservation. On one side, it is important to highlight that marine protected areas are useful to develop concrete site-specific conservation actions, but these local actions necessarily need to be complemented with more relaxed actions at regional or trans-boundary scales (both political and ecosystem). On the other side, spatial segregation of foraging grounds among colonies may allow linking impacts at sea with population trends of each breeding colony.

The information regarding wintering areas and migratory flyways is also helpful to forward conservation policies, because this knowledge is key to propose new marine IBAs on international waters, outside the jurisdiction of Spanish waters. In this sense, BirdLife International has already started a process in this line worldwide, including several specific areas of the Atlantic such as the Canary Current, the North Atlantic, or the Tristan da Cunha archipelago, for which data used in this work is playing a relevant role.

Regarding interactions with human activities, the better knowledge of spatio-temporal patterns of these populations may allow identifying overlap with potentially negative disturbances and threats, including fishing activities, oil spills, marine wind farms, etc., guiding the design and implementation of locally adapted management actions. Nevertheless, this will largely need combining the information obtained from remote tracking data with other complementary sources of information. In this way, proper conservation strategies and effective management plans would be possible in the context of marine spatial planning. For instance, carrying out censuses at sea to complement the information on distribution patterns (Louzao et al., 2009), addressing the trophic ecology using stable isotopes and other intrinsic markers (Ramos & González-Solís, 2012), tracking the fishing fleet activity, in particular concerning bycatch risk (García-Barcelona et al., 2013; Soriano-Redondo et al., 2016; Cortés et al., 2017), or identifying polluted areas, including plastic debris, within the foraging areas (Roscales et al., 2010; Rodríguez et al., 2012; Codina-García et al., 2014).

Nevertheless, there are still information gaps resulting from the limitations of technology. The improvement and diversification of remote tracking devices combined with other types of sensors, and the improvement of highly complex techniques for data analysis, can be expected to continue growing in coming years (López-López, 2016). In this study, insights on migration and wintering have been obtained through geolocation by light, as this is currently the only tracking device to study movement and behaviour of pelagic seabirds throughout the annual cycle while ensuring the welfare of the tagged individuals. The advance in the industry of remote tracking, including ever-smaller GPS recorders, combined with the technology for remote data downloading, seems to portend that it will be possible to get high-resolution data of seabirds movement year-round, notably improving the accuracy of current information. Likewise, it is expected that technological advances will lead to the increasingly widespread use of these technologies as a tool for conservation (Hays et al., 2016, Hooker et al., 2011; Allen & Singh, 2016; Hazen et al., 2016; Wedding et al., 2016). Therefore, the greatest upcoming challenge will come from social and political stakeholders involved in marine conservation, since their willingness is already necessary to incorporate data from cutting-edge technology into effective conservation strategies.

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Chapter III

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

Chapter III is a version of the research article:

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SEXUAL SEGREGATION IN THE FORAGING BEHAVIOUR OF A SLIGHTLY DIMORPHIC SEABIRD: INFLUENCE OF THE ENVIRONMENT AND FISHERY ACTIVITY

ABSTRACT

1. Sexual segregation in foraging strategies has been little studied in marine species with slight Sexual Size Dimorphism (SSD), particularly regarding the role of environmental conditions and fishery activities. Sexual differences in fishery attendance are of particular concern because uneven mortality associated with bycatch may exacerbate impacts in wildlife populations.

2. Using a seabird species with slight SSD, the Scopoli's shearwater (*Calonectris diomedea*), we assessed sexual differences in foraging strategies and evaluated whether annual environmental conditions and fishery activity shaped such differences.

3. We used a four-year dataset combining bird GPS tracking, stable isotope analysis, the North Atlantic Oscillation index (NAO, as a main proxy of the annual environmental conditions), and fishing vessel positioning data (Vessel Monitoring System, VMS) from the North-Western Mediterranean, a region under intense fishery pressure.

4. From 2012 to 2015, we tracked 635 foraging trips from 78 individuals. Females showed a greater foraging effort, a lower fishery attendance, a lower trophic level, and a narrower isotopic niche width than males. Moreover, in years with unfavourable environmental conditions, both sexes showed a lower fishery attendance and increased foraging effort compared to the year with most favourable conditions.

5. Our results revealed that environmental conditions influence space use, feeding resources, and fishery attendance differently in males and females, overall suggesting the competitive exclusion of females by males from main foraging areas and feeding resources, particularly in unfavourable environmental conditions. We highlight the importance of evaluating sexual segregation under disparate environmental conditions, particularly in species with slight SSD, since segregation may pass otherwise unnoticed if only years with similar environmental conditions are considered. The higher fishery attendance of males likely explains the male-biased bycatch ratio for this species. Thus, inter-sexual differences in foraging strategies can lead to an unbalanced exposure to relevant threats and have implications for the conservation of long-lived species.

Keywords

Diet • feeding ecology • North-Western Mediterranean • NAO •
seabird-fishery interactions • trophic ecology • VMS.

INTRODUCTION

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

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

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

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

In this work, we aimed to assess sexual differences in the foraging strategies of a seabird species with slight SSD, the Scopoli's shearwater (*Calonectris diomedea*), and to evaluate whether contrasting inter-annual environmental conditions and fishing fleet activity may play a role in shaping such differences. Using a four-year dataset combining bird GPS tracking, Stable Isotope Analysis (SIA), environmental data, and fisheries tracking data (Vessel Monitoring System, VMS), we investigated potential sexual segregation and its causes in Scopoli's shearwaters foraging in the North-Western Mediterranean (NWM), a region under intense fishing pressure. Some studies on the Cory's shearwater (*C. borealis*), a closely related species that moves across vast foraging areas in the North Atlantic, reported no sexual differences in foraging strategies during breeding (Magalhães, Santos, & Hamer, 2008; Navarro, Kaliontzopoulou, & González-Solís, 2009; Ramos, Granadeiro, Phillips, & Catry, 2009; see details in S1, Supporting Information). However, recent research on Cory's shearwater focusing on the role of environmental conditions within a multi-year approach found evidence of sexual segregation in years with poor environmental conditions (Paiva et al., 2017). We expected that our multi-year approach encompassing variable environmental conditions would allow us to detect any potential sexual differences in foraging strategies of Scopoli's shearwaters. Females, which are slightly smaller than males, could be outcompeted by males, and thus we expected that (1) females generally show greater foraging effort than males, and that (2) both males and females increase foraging effort during unfavourable environmental conditions, but females to a greater extent than males, owing to competitive exclusion exerted by males. Lastly, although we foresaw both sexes to associate with fisheries (Soriano-Redondo et al., 2016; Genovart et al., 2018), we expected (3) a lower fishery attendance of females, as the competitive exclusion of females by males should limit their access to this resource, particularly under low availability of discards.

MATERIAL AND METHODS

Model species and tracking data

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

Space use, foraging behaviour, and fishery attendance

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

Stable Isotope Analysis (SIA) of blood plasma

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

Environmental data

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

Statistical analyses

We evaluated sexual differences in space use and behavioural patterns, fishery attendance, and SIA using Linear (LMM) and Generalized Linear Mixed Models (GLMM; see details about response variables, predictors, and parametrization in S1, Supporting Information). We also used $\delta^{13}C$ and $\delta^{15}N$ to generate a bidimensional isotopic space for each year and assess Standard Ellipse Areas (SEA) for each sex as a proxy of Isotopic Niche Width (INW). We produced a Bayesian estimation of the SEA (SEAb) to compare the probability of a sex's ellipse to be smaller than the ellipse of the other sex for each year (Jackson et al., 2011).

RESULTS

Overall, we tracked 45 males and 34 females. Over the four years, 47 out of 79 individuals were tracked only one year, 23 for two years, 6 for three years, and 2 for four years. We recorded a total of 373 foraging trips from males and 262 trips from females (Table 1). Shearwaters consistently used two main foraging areas: the waters surrounding the Balearic Islands, especially the Menorca Channel, and the Catalan waters (Fig. 1; see details in S2, Supporting Information). We found females to perform on average longer trips than males, both in total distance covered (mean ± sd, males: 259.1 ± 254.3 km; females: 354.5 ± 356.1 km) and duration (mean ± sd, males: 1.3 ± 1.1 days; females: 1.8 ± 1.7 days; Table 1; Fig. 2A), whereas the difference in the maximum distance reached was marginally significant (Table 2). Both sexes performed short and long trips commuting towards Balearic and Catalan waters, respectively, defining a bimodal distribution in the maximum distance reached (Table 1; Fig. 1; Fig. S2 in S2, Supporting Information). The probability of performing long trips was twice as high for females as for males (Table 2; Fig. 2B). We found that females exploited larger foraging grounds than males in the Catalan shelf, but not in Balearic waters (Table 2; Fig. S3 in S2, Supporting Information). Time allocation to the different behavioural modes between males and females did not differ (Table 2). Regarding fisheries, birds interacted with fishing vessels in 26.46% of their trips (trawlers: 24.25%; purse-seiners: 7.24%; pelagic longliners: 3.46%). Fishery attendance was half as high for females than males (Table 2; Fig. S4 in S3, Supporting Information).

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

	2012		2013		2014		2015	
NAOw	1.04		-1.20		1.60		1.89	
Sex	Males	Females	Males	Females	Males	Females	Males	Females
Individuals (n)	24	20	12	11	14	10	17	12
Trip parameters								
Foraging trips (n)	76	60	117	103	81	52	99	47
Short trips	69	52	104	90	74	34	79	27
Long trips	7	8	13	13	7	18	20	20
Max. distance reached (km)								
Short trips	46.8 ± 21.0	52.1 ± 24.4	42.2 ± 20.5	43.9 ± 23.9	36.6 ± 17.4	38.7 ± 22.8	47.4 ± 21.9	51.1 ± 29.9
Long trips	237.3 ± 30.2	211.5 ± 30.1	198.0 ± 26.0	211.6 ± 25.1	200.0 ± 15.0	203.8 ± 39.0	200.7 ± 22.6	210.7 ± 24.9
Total distance covered (km)								
Short trips	207.8 ± 121.0	246.9 ± 130.0	175.1 ± 142.9	183.8 ± 129.4	154.5 ± 88.0	181.1 ± 122.4	185.5 ± 94.0	223.5 ± 128.2
Long trips	1 112.7 ± 450.8	1 055.0 ± 586.0	775.9 ± 263.5	783.1 ± 305.4	718.1 ± 209.5	666.3 ± 279.0	699.2 ± 203.7	1 010.0 ± 428.2
Duration (days)								
Short trips	1.3 ± 1.0	1.6 ± 1.0	1.1 ± 0.8	1.2 ± 0.8	0.9 ± 0.4	1.1 ± 0.7	0.9 ± 0.5	1.1 ± 0.7
Long trips	5.4 ± 2.0	4.8 ± 3.1	3.1 ± 0.9	3.7 ± 2.6	3.3 ± 1.2	2.7 ± 2.0	2.7 ± 1.2	4.6 ± 2.3
Foraging ground size (km^2)	736.8 ± 1319	1 073.6 ± 1732	1 109.9 ±2209	893.0 ±1541	571.1 ±1045	2 016 ±2519	1 316.3 ±2043	2 601.4 ±2810
Behaviour								
% of foraging	33.7 ± 8.1	33.0 ± 8.0	30.4 ± 8.7	32.2 ± 7.7	27.0 ± 7.8	29.8 ± 6.4	31.2 ± 9.2	27.8 ± 8.8
% of travelling	25.8 ± 8.5	23.4 ± 8.2	26.1 ± 9.9	25.5 ± 8.9	29.5 ± 12.4	28.2 ± 10.9	30.2 ± 12.4	31.3 ± 10.6
% of resting	40.2 ± 9.8	43.3 ± 10.7	42.9 ± 12.6	41.9 ± 10.7	43.1 ± 13.2	41.6 ± 10.6	38.1 ± 13.2	40.5 ± 13.2
Fishery attendance events								
Count	7 ± 1.3	3 ± 0.7	9 ± 1.6	21 ± 2.6	6 ± 1.3	4 ± 0.9	8 ± 1.6	10 ± 1.9
Time invested	11.3 ± 24.8	0.3.6 ± 10.8	10.7 ± 26.5	15.7 ± 43.1	8.3 ± 16.6	6.3 ± 18.2	9.9 ± 29.9	12.7 ± 28.8
Daily vessels operating	199.8 ± 115.3		214.7 ± 118.6		206.0 ± 119.2		199.7 ± 115.1	

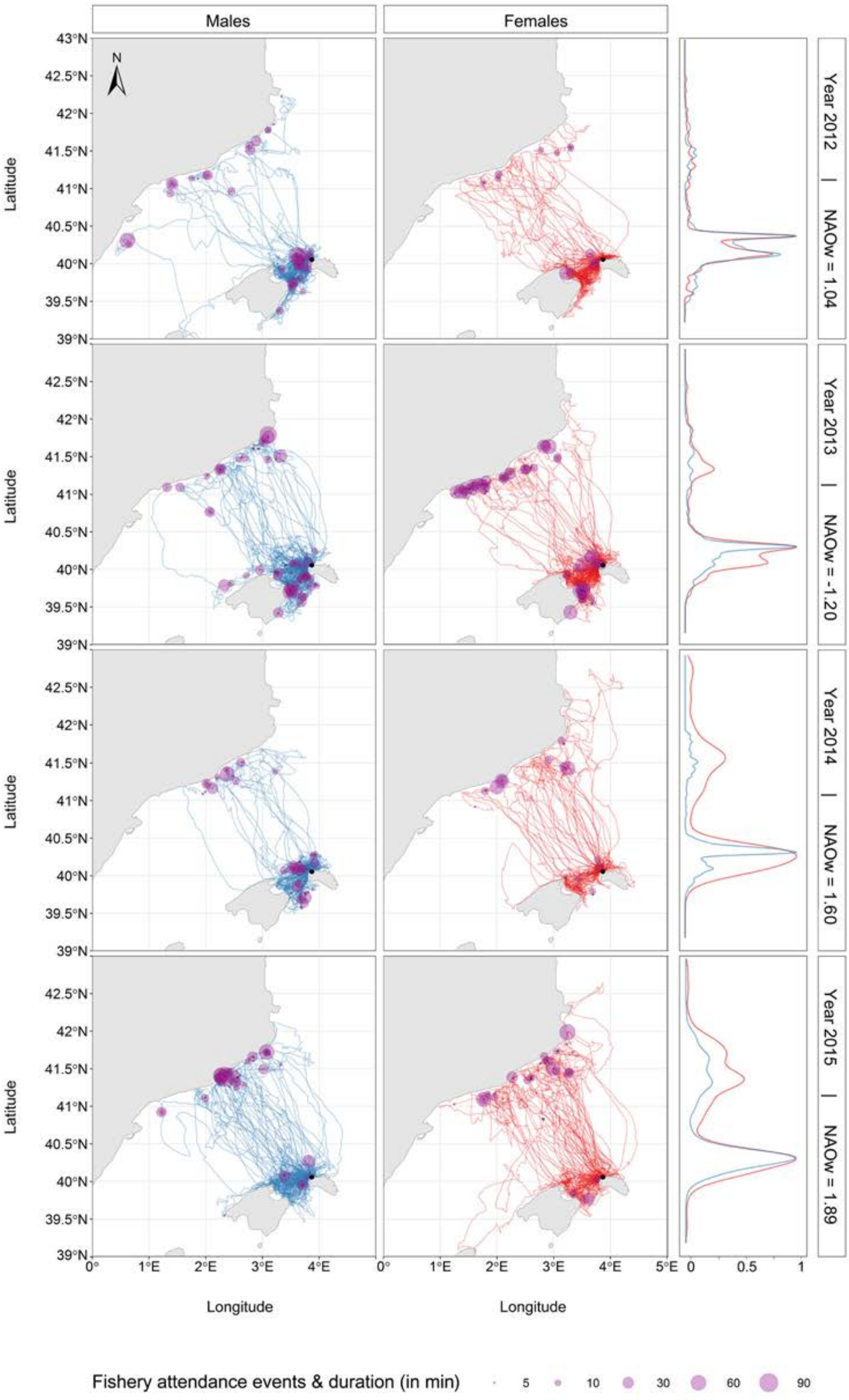

FIGURE 1 • Foraging trips and fishery attendance of males and females of Scopoli's shearwater breeding in Menorca during the chick-rearing period from 2012 to 2015. Purple circles represent fishery attendance events. The size of the circles is relative to the duration of the events (in minutes), and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

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

Model type	Response variable	Fixed effect	Estimate	95% CI	Statistic (t | z)	*p-value*
LMMlogT	Max. distance reached (km)	Intercept	54.97	47.0 – 64.3	50.0	**<0.001**
		Males	0.82	0.7 – 1.0	-1.9	0.053
		NAOw	1.10	1.0 – 1.2	2.5	**0.010**
LMMlogT	Total distance covered (km)	Intercept	229.76	198.9 – 265.4	73.8	**<0.001**
		Males	0.76	0.6 – 0.9	-2.9	**0.004**
		NAOw	1.11	1.0 – 1.2	3.3	**0.001**
nbGLMM	Duration (days)	Intercept	1.82	1.6 – 2.1	8.8	**<0.001**
		Males	0.72	0.6 – 0.8	-3.7	**<0.001**
		NAOw	1.06	1.0 – 1.1	1.7	0.087
LogitGLMM	Probability of long trip	Intercept	0.21	0.1 – 0.3	-6.4	**<0.001**
		Males	0.46	0.2 – 0.8	-2.5	**0.012**
		NAOw	1.37	1.1 – 1.7	2.7	**0.006**
LMM	Size of foraging ground	Intercept	530.36	500.2 – 620.5	18.3	**<0.001**
		Males	-1.94	-82.4 – 78.5	-0.1	0.962
		Main foraging area – CAT	908.00	788.4 – 1027.6	14.9	**<0.001**
		NAOw	11.17	-30.0 – 52.3	0.5	0.595
		Males * CAT	130.45	-35.1 – 296.0	1.5	0.122
		Males * NAOw	-11.44	-64.73 – 41.9	-0.4	0.674
		CAT * NAOw	95.48	17.2 – 173.8	2.4	**0.017**
		Males * CAT * NAOw	-212.61	-320 – -105.2	-3.4	**<0.001**
nbGLMM	% of foraging per trip	Intercept	0.31	0.3 – 0.3	-58.9	**<0.001**
		Males	1.00	1.0 – 1.1	0.1	0.957
		NAOw	0.98	1.0 – 1.0	-1.9	0.064

Table 2 • Continuation.

Model type	Response variable	Fixed effect	Estimate	95% CI	Statistic (t | z)	*p-value*
nbGLMM	% of travelling per trip	Intercept	0.26	0.3 – 0.3	-46.9	**<0.001**
		Males	1.04	1.0 – 1.1	1.1	0.253
		NAOw	1.04	1.0 – 1.1	2.9	**0.004**
nbGLMM	% of resting per trip	Intercept	0.42	0.4 – 0.4	-39.2	**<0.001**
		Males	0.97	0.9 – 1.0	-1.0	0.331
		NAOw	0.99	1.0 – 1.0	-1.2	0.244
nbGLMM	Fishery attendance events	Intercept	0.00	0.0 – 0.0	-32.9	**<0.001**
		Males	1.95	1.4 – 2.8	3.7	**<0.001**
		NAOw	0. 87	0.8 – 0.9	-2.3	**0.022**
		Average vessel availability	1.31	1.2 – 1.4	8.5	**<0.001**
LMM	δ^{13}C (‰)	Intercept	-18.24	-18.3 – -18.2	-404.3	**<0.001**
		Males	-0.00	-0.1 – 0.1	-0.1	0.939
		NAOw	-0.03	-0.1 – 0.0	-1.2	0.216
		Main foraging area – CAT	-0.09	-0.2 – 0.0	-1.5	0.146
		Time in fishery attendance	-0.04	-0.1 – 0.0	-1.3	0.211
LMM	δ^{15}N (‰)	Intercept	9.31	9.1 – 9.5	97.3	**<0.001**
		Males	0.42	0.2 – 0.6	3.9	**<0.001**
		NAOw	-0.09	-0.2 – -0.0	-2.0	**0.047**
		Main foraging area – CAT	0.30	0.0 – 0.1	2.2	**0.025**
		Time in fishery attendance	0.16	0.0 – 0.3	2.5	**0.012**

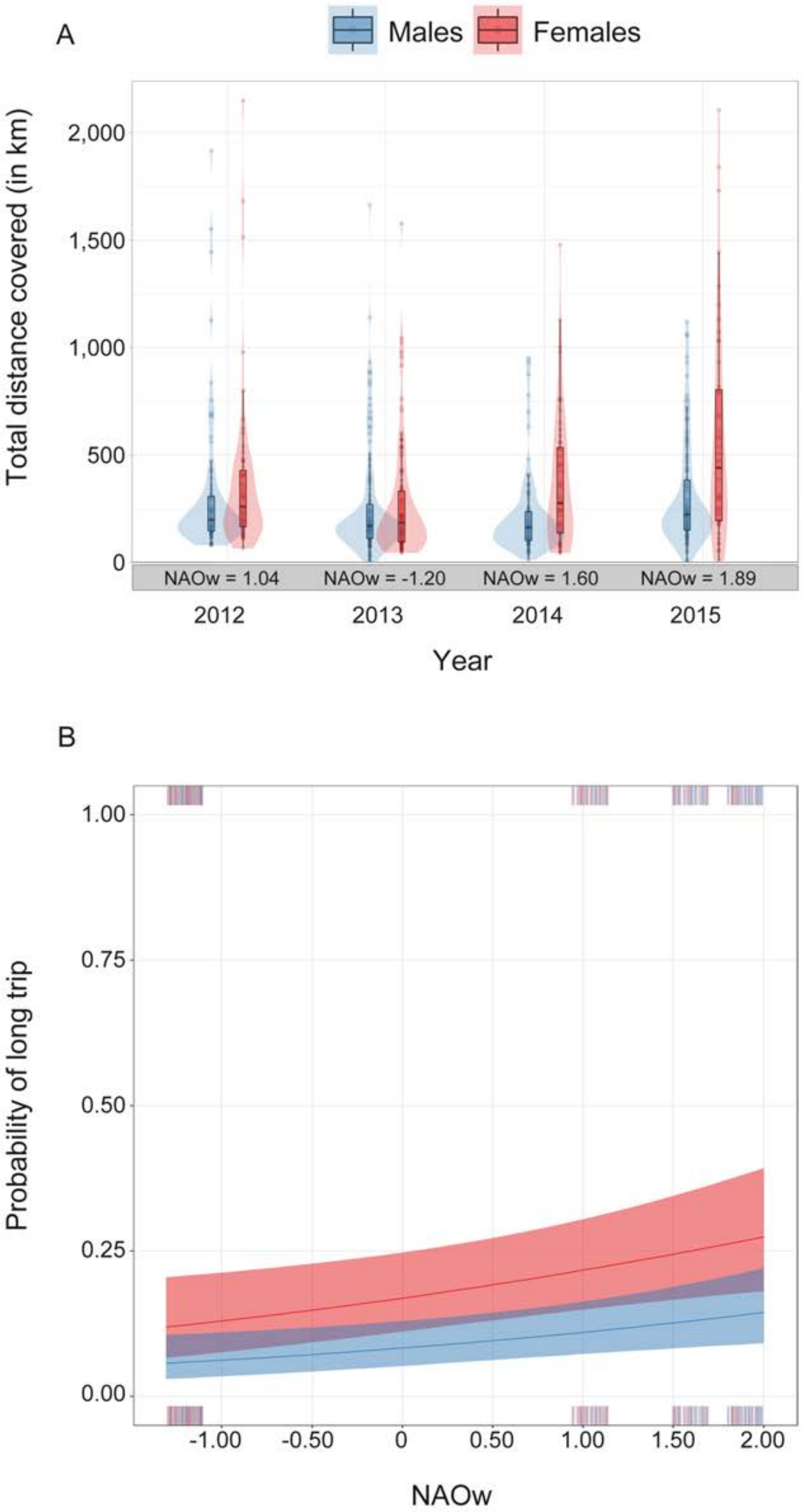

Figure 2 • (A) Observed values of distance covered grouped by sex and year. Each dot represents a single trip. Annual values of the extended winter North Atlantic Oscillation (NAOw) index are indicated at the bottom. Violins show the probability density of raw data. Black-contoured boxplots show the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

There were no sexual differences in $\delta^{13}C$ in plasma, but $\delta^{15}N$ was consistently lower in females than in males across the years (Table 3). $\delta^{13}C$ was higher and $\delta^{15}N$ lower in shearwaters foraging in Balearic waters than in those foraging in Catalan waters (Table 3; Fig. 4A). Time allocated to fishery attendance correlated significantly with an increase in $\delta^{15}N$ for both sexes (*p-value* = 0.032; Fig. 4B).

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

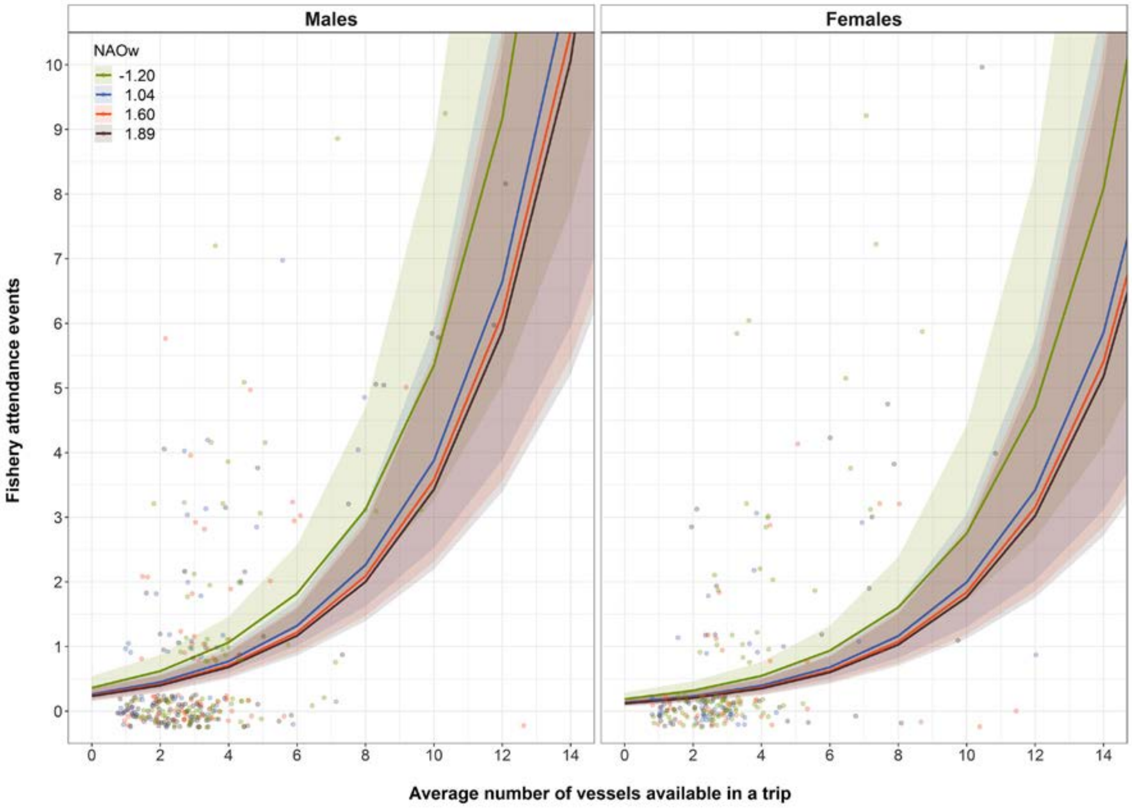

Figure 3 • Marginal estimates of fishery attendance events in relation to the average number of fishing vessels operating in the vicinities of birds during the foraging trips and annual values of NAOw. Shaded areas represent the associated 95% CI. Soft dots represent raw data. Some jittering was applied to dots to ease visualization.

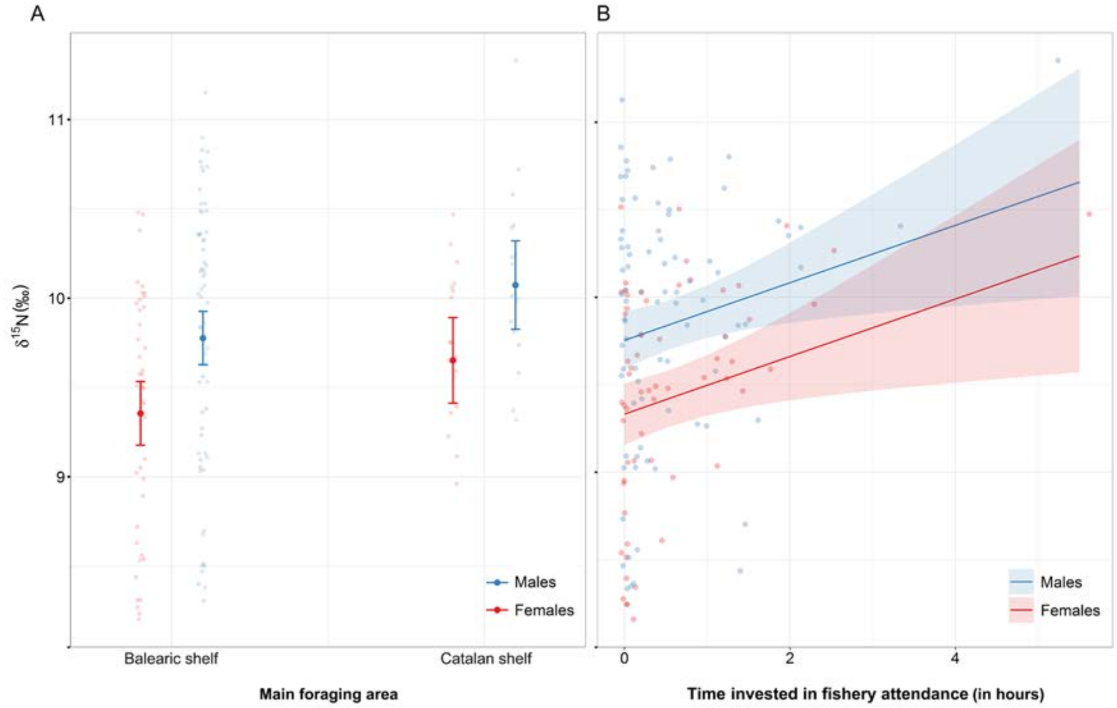

Figure 4 • (A) Marginal estimates of $\delta^{15}N$ in relation to the main foraging area used by birds within the 6-day window of plasma. Solid dots represent means and bars represent the associated 95% CI. Soft dots represent raw data with some jittering applied to ease visualization. (B) Marginal estimates of $\delta^{15}N$ in relation to time invested in fishery attendance within the 6-day window of blood plasma. Shaded areas represent the associated 95% CI. Soft dots represent raw data.

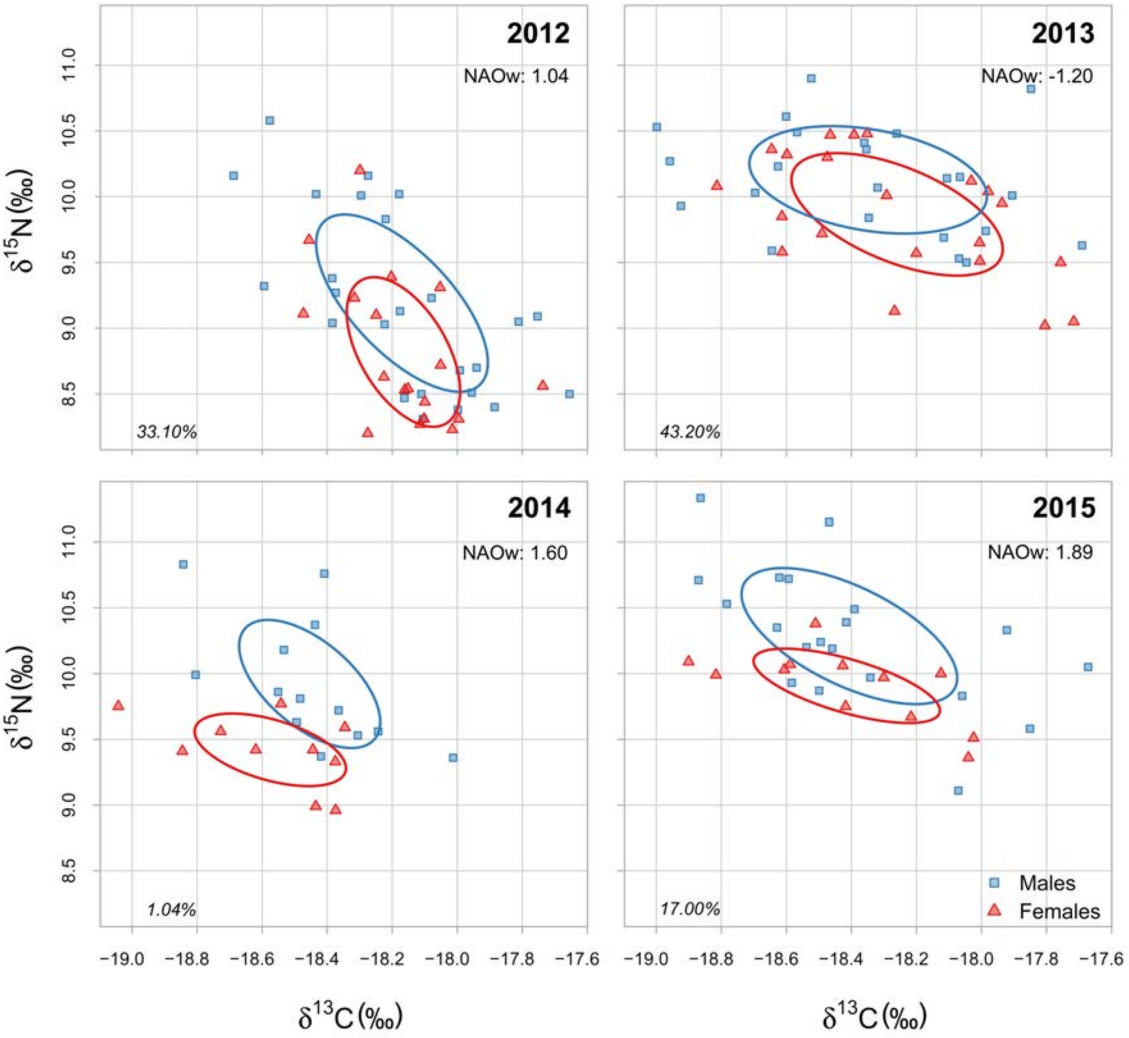

Figure 5 • Standard Ellipses by year, calculated in the bidimensional space of $\delta^{13}C$ and $\delta^{15}N$. The Standard Ellipse Area (SEA) represents the Isotopic Niche Width (INW). Values in italics in the lower-left corner of each panel represent the geometric overlap between males and females ellipses (i.e. the overlapped area as a proportion of the non-overlapping area of the two ellipses).

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

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

Discussion

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

Females consistently show greater foraging effort than males

As expected, we found relevant differences between males and females in their foraging strategies, indicating that males could be outcompeting females in the access to feeding resources, including discards, as previously suggested for various species both with slight and conspicuous SSD (Cianchetti-Benedetti, Dell'Omo, Russo, Catoni, & Quillfeldt, 2018; Collet, Patrick, & Weimerskirch, 2015). Our results support our first hypothesis, as females showed a greater foraging effort (longer foraging distances and duration) than males even though both sexes generally used similar foraging areas over the four years. The breeding colonies of the species in the Balearic Islands and the productive waters on the Catalan shelf are separated by ca. 200 km, an affordable distance for a gliding seabird species (Reyes-González et al., 2017). Thus, birds foraged in the Balearic waters during the short trips (~1-day) and commuted to Catalan waters during long trips (>3 days). This bimodal pattern during the chick-rearing may reflect the use of a dual foraging strategy, commonly used by many Procellariiformes (Phillips et al., 2017). Nevertheless, we found that the probability of performing long trips was nearly two times higher for females than for males, which also indicates a greater foraging effort by females when compared to males. Moreover, we found sexual differences in the interaction with fishing vessels, as females showed lower fishery attendance than males. Furthermore, according to $\delta^{15}N$, females seemed to have consumed fewer discards and showed narrower INW over the four years when compared to males, overall indicating relevant sexual differences in trophic ecology (Cherel et al., 2005). Our results contrast with previous research on the same species that did not find sexual differences in fishery attendance (Cecere et al., 2015), which may be due to the different approach used (distance from foraging grounds to harbours for evaluating fisheries influence). Conversely, our findings agree with results reported by Cianchetti-Benedetti et al. (2018) in the central Mediterranean that found females spent more energy than males when following vessels, making this behaviour a disadvantageous strategy for the smaller, less competitive sex.

Unfavourable environmental conditions may shape foraging behaviour and increase sexual segregation

During the chick-rearing period, when the need to frequently feed the chick compels parents to forage near the colony, unfavourable environmental conditions may result in local depletion of prey, forcing parents to increase foraging effort (Lewis et al., 2001). In our study, the increased competition for feeding resources near the colony in unfavourable environmental conditions likely forced Scopoli's shearwaters to increase foraging effort. Overall, both males and females spent more time searching for food, travelled longer distances, and engaged more on longer trips in unfavourable than in favourable environmental conditions. This is similar to results reported for other seabird species, including the closely related Cory's shearwater in the North-East Atlantic (Paiva et al., 2013, 2017). Yet, during unfavourable environmental conditions, the overlap of SEA between sexes decreased, suggesting sexual segregation in their trophic ecology likely due to increased competition. Moreover, sexes also segregated in space, as females had twice the probability to commute towards Catalan waters than males did in such unfavourable conditions. Females also tended to use larger foraging grounds than males in Catalan waters during unfavourable years. Therefore, according to our second expectation, females showed a greater increase in foraging effort than males in unfavourable conditions, most likely owing to competitive exclusion exerted by males, as found in many other species of petrels and albatrosses (Catry et al., 2005; Paiva et al., 2010; Phillips et al., 2011). Our work only includes a single year of favourable environmental conditions, which calls for caution because other factors not considered in this study may have promoted the observed differences between sexes. Future studies considering a larger set of years with disparate conditions regarding NAOw will contribute to solve this issue.

Variable fishery activity shapes fishery attendance

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

Conservation implications

Scopoli's shearwaters suffer the highest rate of bycatch among seabirds in the NWM (Valeiras & Camiñas, 2003; Cortés et al., 2017), thus being the major cause of mortality at sea and pushing adult survival to unsustainable levels (Genovart et al., 2018). We found that ~26% of the foraging trips presented at least one event of fishery attendance, and birds interacted with several vessels and gears in some events. Birds interacted with trawlers in 24% of the trips, in 7% with purse-seiners, and in 3% with pelagic longliners. Although this last rate may seem low, the risk of bycatch in any attendance event is high when associated with longliners and depends on the longlining fleet métier (Barcelona et al., 2010; Croxall et al., 2013; Báez et al., 2014). Moreover, recent studies point at artisanal demersal longliners, which are rarely equipped with

VMS, as being responsible for the majority of bycatch events at the NWM (Cortés et al., 2017). Trawlers and artisanal longliners frequently share fishing grounds (Cortés et al., 2017). As trawlers strongly attract seabirds and individuals can easily shift their attendance to other vessels in the vicinities, the rate of interaction with trawlers that we found should also raise concern in relation to bycatch risk (Abelló et al., 2003; Laneri et al., 2010; Soriano-Redondo et al., 2016). We found a higher fishery attendance in males, which supports previous findings showing that the bycatch rate of Scopoli's shearwaters is male-biased in the NWM (Cortés et al., 2018). This differential risk of bycatch must be considered for the effectiveness of conservation measures because a sexual unbalance in mortality at the population level could worsen population fecundity, viability, and dynamics (Durell et al., 2001; Mills & Ryan, 2005; Phillips et al., 2005).

Conclusions

Overall, we demonstrate the occurrence of sexual differences in foraging strategies, space and resource use, and fisheries attendance, suggesting males outcompete females from their main areas and feeding resources to a certain extent, in particular under unfavourable environmental conditions. These differences may pass unnoticed in studies carried out with data from very few years where conditions were similar, highlighting the importance of multi-year studies encompassing as much disparate environmental conditions as possible to ascertain sexual segregation and their implications, particularly in species with slight SSD. Thus, sexual segregation in foraging strategies can lead to an uneven exposure of males and females to human-induced threats. This impact is often neglected, but can reduce effective population size and compromise population viability of long-lived species and therefore should be appropriately considered even in species with slight SSD.

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Supporting Information

S1. Methods

Model species

Scopoli's shearwater *(Calonectris diomedea)* is a medium-sized, long-lived, pelagic seabird endemic to the Mediterranean. Females are slightly smaller and have smaller bills than males (Reyes-González & González-Solís, 2016; De Felipe et al., 2019). The species is present in the Mediterranean during boreal summer for breeding (Ramos, 2019). It breeds colonially in islands and islets all along the Mediterranean coast (Gómez-Díaz & González-Solís, 2007; Reyes-González & González-Solís, 2016). Laying starts in the second half of May, and hatching starts in mid-July. Fledgling usually occurs in the second half of October (Thibault et al., 1997; Telailia et al., 2014).

Several studies indicate a strong impact of fisheries on diverse populations of the species (Arcos et al., 2008; Genovart et al., 2018). Studies conducted on this species during the breeding period found that it feeds on a wide range of epi- and mesopelagic fish, such as sardines and anchovies (Afán et al., 2014; Grémillet et al., 2014). It is known that the fishing stocks of such species are currently depleted in the North-Western Mediterranean due to the combined effects of intense overfishing and climate change (Papaconstantinou & Farrugio, 2000; Coll et al., 2008; FAO, 2016). This may explain the use of alternative prey reported in some populations of Scopoli's shearwaters, such as discards from fisheries or krill (Arcos & Oro, 2002; Grémillet et al., 2014). Moreover, the species represents over 50% of all birds accidentally caught in longliners in the North-Western Mediterranean, with an estimated annual decrease of 4–6% of the local population (Belda & Sánchez, 2001; García-Barcelona et al., 2010; Genovart et al., 2018).

Previous studies in a related species

Some studies on a closely related species that moves across vast foraging areas in the North Atlantic, the Cory's shearwater (*C. borealis*), did not find evidence of sexual differences in foraging strategies during breeding. These papers analysed data from years with no contrasting environmental conditions (Magalhães et al., 2008; Navarro et al., 2009; Ramos et al., 2009). Although those studies did not focus specifically on testing inter-annual variability of environmental conditions as a driver of sexual differences -and thus they did not provide NAO values-, we checked for the years considered and calculated the standardised values of the extended annual winter NAO (NAOw, see below). These articles referred to the Cory's shearwater in the Atlantic, where NAO works in the opposite way to the Mediterranean, i.e. positive values tend to relate to favourable environmental conditions, and negative values to poor environmental conditions (Paiva et al., 2010). The study of Magalhães et al. (2008) included data from 3 years, all with unfavourable environmental conditions in the North Atlantic (2004: -0.68; 2005: -0.58; 2006: -0.86). Navarro & González-Solís (2009) included one year with unfavourable environmental conditions (2004: -0.68). Ramos et al. (2009) included data from two years, one of them with favourable environmental conditions (2006: -0.86, 2007: 0.46). In any case, individuals of Cory's shearwaters breeding in the Atlantic move vast distances over the North Atlantic in a much larger extent than Scopoli's shearwaters do in the Mediterranean, and thus it is likely that environmental factors may influence birds' behaviour differently.

Fieldwork location

The northern cliffs of Menorca Island hold the largest population of Scopoli's shearwater in the Balearic Islands, estimated at 1 801 - 6 946 pairs (Arcos et al., 2009). Fieldwork was conducted for four consecutive years (2012–2015) during the chick-rearing period (July-September) in Cala Morell (Latitude 40.055º, Longitude 3.869º) on breeders rearing a chick. Adults breeding in Menorca and other Balearic Islands usually forage over the Spanish Mediterranean waters, from the Strait of Gibraltar to Cap de Creus (Reyes-González et al., 2017).

Capturing, handling and GPS deployment

Birds were captured at night, using a looped pole or by hand when they landed at the colony or once inside the burrow. In order to minimise the possible impact on breeding success, we did not simultaneously tag both partners of the same couple. GPS loggers were encased in a heat-shrink tube for waterproofing and attached to mantle feathers with salt-water resistant Tesa® tape. The total mass of devices (~23 g) was below 4% of the adult body mass, as recommended by Phillips et al. (2003) and Passos et al., (2010). Loggers were recovered not earlier than four days and usually earlier than three weeks after deployment. Blood samples for molecular sexing and SIA were taken at GPS recovery. All animals were handled in strict accordance with guidelines for ethical research defined by the current European legislation and the University of Barcelona Local Ethical Review Procedures, and under licence approved by respective environmental agencies of Govern de les Illes Balears and Spanish Government.

Movements and behaviour

GPS temporal resolution

Most loggers (~90%) were set to record one position every five min, but the rest were set to 10 or 15 minutes. Prior to further analyses, we rediscretised the dataset to a common resolution of one position every five min (Calenge, 2006; Calenge et al., 2009).

Labelling trips as short or long

Many procellariform species perform the so-called dual foraging strategy: adults show bimodality in foraging trips, alternating short trips to waters surrounding the colony to feed the chick with less frequent long trips for self-provisioning (e.g. Magalhães, Santos, & Hamer, 2008). An exploratory analysis pointed out that most of the foraging occurred over two main areas: the Catalan and Balearic shelves, in accordance with the prevalent use of neritic waters by the species (Ramos et al., 2013; Reyes-González et al., 2017). To evaluate bimodality in the maximum distance reached objectively, we used the k-means algorithm (R Development Core Team 2019). We first ran a silhouette analysis to find the most appropriate number of clusters k, which tests how well every observation fits into the cluster it has been classified rather than the next nearest cluster. The number of clusters providing the largest average silhouette width indicates the optimal k (Marden, 2008). We applied the k-means algorithm on the maximum distance reached with k ranging from 2 to 5. $k=2$ provided the greatest average silhouette width, and thus we labelled every trip as short or long applying k-means with $k=2$.

Behavioural annotation of trajectories

We identified individual behaviour along every trip using unsupervised clustering based on the Expectation-Maximization algorithm. We applied the binary implementation of this algorithm provided by the R package *EMbC* (Garriga & Bartumeus, 2016), which provides a robust and fast statistical performance. EMbC also yields easily interpretable results in the context of animal behaviour and has already been successfully applied to study seabird movements (e.g. Afán et al., 2019; Louzao et al., 2014). Using speed and turning angle, each GPS location was classified into one out of four basic behavioural modes: resting (characterized by low velocity and low turning angle); intensive search (low velocity and high turning angle); extensive search (high velocity and high turning angle); and travelling (high velocity and low turning angle) (Garriga et al., 2016). We grouped intensive and extensive search into foraging behaviour for further analyses.

Fishery attendance

To characterize fishery attendance, we used data from the Vessel Monitoring System (VMS) tracking the Spanish fishing fleet operating in the North-Western Mediterranean. In European Union waters, fishing vessels over 12 m length are fitted with VMS that transmits the vessel position by satellite tracking devices installed on board, with a maximum interval of 2 h when outside the harbour (European Commission 2009). We first identified the spatio-temporal interactions between birds and fishing vessels following Soriano-Redondo et al. (2016). Briefly, a spatio-temporal interaction occurred when a GPS bird location was within 5 km and ± 1 h from a vessel location and the bird trajectory stayed within ± 30º from the bearing of the vessel. The spatio-temporal buffer of 5 km/h and ± 1 h corresponded to the average maximum speed of the vessels in this fleet and the positional recording schedule of 1 VMS fix every 2 h on average. We chose ± 30º because Soriano-Redondo et al. (2016) reported that in biological terms this was the most meaningful figure (see Soriano-Redondo et al., 2016 for further details). Once spatio-temporal interactions were identified, to avoid spurious interactions, we considered that a fishery attendance event occurred when at least two consecutive GPS bird locations labelled as foraging by the EMbC algorithm were involved in spatio-temporal interactions with fishing vessels. We finally quantified the amount of fishery attendance events for every bird trip and the total time attending vessels. Last, we were interested in measuring the number of vessels operating in the vicinity of every GPS bird position as a proxy of fishing vessel availability for the birds. To do so, we quantified the number of different vessels operating within a spatio-temporal buffer of 30 km (according to the visual distance some seabirds are able to react to fishing vessels, see Collet et al., 2015), and ± 1 h from every GPS bird position. We then calculated the average number of vessels available in the vicinity for every trip. VMS positions near to harbours (5 km) were not considered. Finally, for descriptive purposes, we calculated the percentage of trips interacting with fishing vessels disaggregated by fishing gear.

Identifying main foraging areas

After behavioural annotation of trajectories, we quantified for every trip the percentage of foraging at each of the main areas (Catalan and Balearic shelves) using the layer provided by Vion & Menot (2009) and accordingly identified the main foraging area used.

Identifying foraging grounds

We investigated foraging grounds computing the fixed Kernel Density Estimation (KDE) for every trip, taking only the locations previously identified as foraging through the EMbC algorithm. We used *kernelUD* function from the R package *adehabitatHR* and the ad-hoc method to choose a reasonable bandwidth (h) while avoiding convergence issues (Calenge, 2006). We then used the mean bandwidth value from the ad-hoc method (h = 7.5 km) to recompute all KDEs (Haug et al., 2015). We considered the 50% KDE volumes (K50) of every trip as the main foraging ground used and calculated their size in km^2. Locations were projected to a Lambert Azimuthal Equal Area projection centred in the breeding colony prior to KDE computation to ensure area comparability.

Molecular sexing from blood samples

Blood samples from individuals were collected from the tarsal vein of breeding adults after GPS recovery. From each sample, 0.5 ml were stored in absolute ethanol to identify the sex of the individual. Molecular sexing was done following Fridolfsson & Ellegren (1999) and based on the detection of the female-specific CHD1-W locus (diagnostic kit from Durviz, Valencia, Spain).

Stable Isotope Analysis (SIA) from blood samples

From every blood sample collected after GPS recoveries, we stored 1 ml of blood in a cold-preserved heparin-vial to be centrifuged within 12 h after collection. Next, we separated and froze plasma fractions at -20ºC to perform SIA. Once in the laboratory, plasma samples were lyophilized for 24 h at 0 mBar and -50°C prior to homogenization. Each sample was homogenized with an Eppendorf mortar. We weighed 0.25 mg of each sample to the nearest µg (microbalance Mettler Toledo MX5), placed each sample in a tin capsule, and crimpled them for combustion. Samples were oxidized in a Flash EA1112 coupled to a Delta-C isotope mass spectrometer through a Conflo III interface (Thermo Finnigan) to obtain $\delta^{13}C$ and $\delta^{15}N$ values. Isotope ratios are expressed as δ values in per mile (‰) related to the standard ratios (Viena Pee Dee Belemnite, VPDB for carbon and atmospheric nitrogen, AIR, for nitrogen). International standards (IAEA CH7, IAEA CH6 and USGS 40 for carbon and USGS 40, IAEA N1, IAEA NO3, IAEA N2 and IAEA 600 for nitrogen) were applied to calibrate and compensate for drift (Böhlke & Coplen, 1993; Böhlke et al., 2003; Qi et al., 2003; Coplen et al., 2006) (Table S1). Replicated assays of these standards indicated a precision (SD) of 0.20 for C and 0.15 for N. For complex organic compounds such as plasma, however, these values are probably underestimated. It is known that lipid concentrations in plasma can lead to depleted $\delta^{13}C$ values (DeNiro & Epstein, 1977; Cherel et al., 2005). Then, we calculated a correction value and applied to the $\delta^{13}C$ value of the samples. We randomly selected 20 previously analysed samples and performed lipid extraction to compare the $\delta^{13}C$ values. Plasma lipid extraction was performed by washing each sample with a solution of chloroform-methanol (2:1) (Bligh & Dyer, 1959). The process was repeated until the supernatant was transparent, indicating that lipid extraction was complete. Finally, the samples were dried at 60°C for 24 h and triturated with an Eppendorf mortar before weighing and laboratory analysing. With the values of C obtained after lipid extraction, we calculated a correlation between the relationship of the percentage of C and N with increasing $\delta^{13}C$. We corrected the values without lipid extraction according to the formula:

$$\delta^{13}C_{corrected} = -1.397 + 0.512 * C{:}N + \delta^{13}C,$$

where $\delta^{13}C_{corrected}$ is the corrected value after performing the lipid extraction, C:N ratio is the C and N relationship percentage, and $\delta^{13}C$ is the isotopic value of samples without lipid extraction. The relationship between the C:N ratio and $\delta^{13}C$ value is practically linear with a R^2 of about 0.2, a very low value which can increase $\delta^{13}C$ values in about 0.8-0.9‰. All the isotopic analyses were performed at the Isotopic Ratio Mass Spectrometry Facility of the University of Barcelona's Scientific and Technical Services.

Table S1 • Accepted and mean measured (± Standard Deviation, SD) of the standard material used in the stable isotope analysis performed in this study, as well as the mean, minimum (Min), and maximum (Max) values obtained. The "*n*" refers to the number of samples of standards materials used.

International standards	δ^{13}CVPDB (‰)							
	Reference value		Observed value					
	Mean	SD	n	Min	Max	Mean	SD	Mean diff.
IAEA CH6	-10.5	0.0	3	-10.9	-10.6	-10.8	0.2	0.3
IAEA CH7	-32.2	0.1	3	-32.3	-32.0	-32.2	0.1	0.0
IAEA 600	-27.8	0.0	3	-27.9	-27.3	-27.7	0.3	0.1
USGS 40	-26.2	0.1	3	-26.7	-26.5	-26.6	0.1	0.4
International standards	δ^{15}NAir (‰)							
	Reference value		Observed value					
	Mean	SD	n	Min	Max	Mean	SD	Mean diff.
IAEA CH6								
IAEA CH7								
IAEA 600	1.0	0.2	3	1.1	1.4	1.2	0.2	0.2
USGS 40	-4.5	0.1	3	-4.0	-3.9	-3.9	0.0	0.6
IAEA N1	0.4	0.1	3	0.3	1.0	0.7	0.4	0.3
IAEA N2	20.4	0.1	3	19.3	20.0	19.6	0.4	0.9
IAEA NO3	4.7	0.1	2	4.6	4.9	4.8	0.2	0.1

Environmental variables

We used different proxies to evaluate the effect of annual environmental variability. We considered the following satellite-derived environmental features: sea surface temperature (sst), sea surface temperature anomaly (sstA), chlorophyll-a concentration (chl), and net primary productivity (npp). We first calculated the convex hull polygon encompassing the full movement range of birds. Then we used functions from R package *rerddapXtracto* (Mendelssohn, 2019) to extracted 8-day composite raster data within the polygon for these environmental features matching the dates of the breeding period of tracked birds. We next calculated the mean value for each variable by year, so output represents the mean value of each variable for the whole breeding period of each year. We also download the daily values of the North Atlantic Oscillation Index (NAO) from NOAA website (www.cpc.ncep.noaa.gov) and calculated the extended annual winter NAO (NAOw) by averaging the winter values (December–March). We standardized NAOw values based on the whole time-series data (available since 1948 in www.cpc.ncep.noaa.gov), subtracting the mean and dividing by the standard deviation). We also scaled and centred all mean values of the rest of the variables and evaluated the correlation among them (see Fig. S1). As the annual mean values of all the variables were moderately to highly correlated among them, we finally decided to use only NAOw for parsimony. In all further models, we used scaled and centred values of NAOw. Values represented in all plots also correspond to scaled and centred values of NAOw.

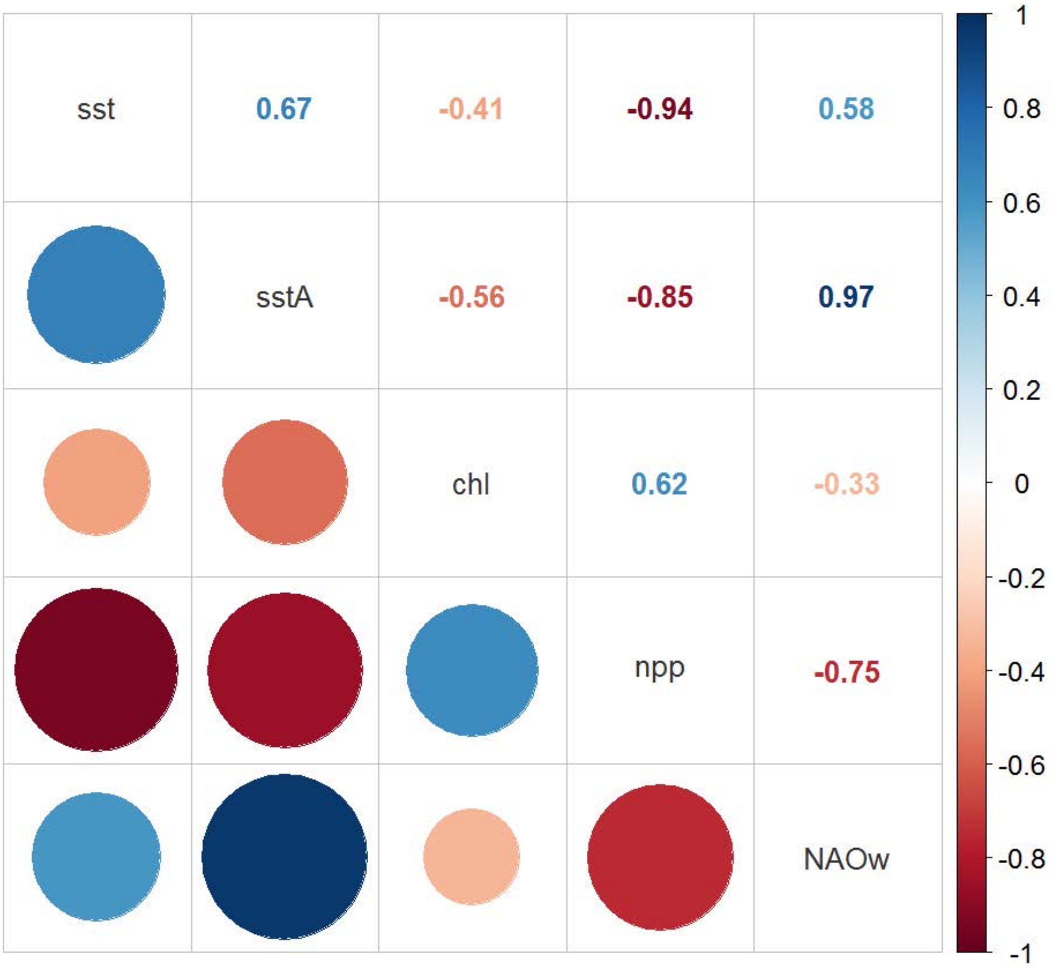

Figure S1 • Correlation matrix chart of annual mean values of the environmental variables measured within the movement range of tracked birds and initially considered: sea surface temperature (sst), mean of sea surface temperature Anomaly (sstA), mean of chlorophyll-a concentration (chl), mean of net primary production (npp), and the extended annual winter NAO (NAOw). Values in the upper triangular part of the matrix chart indicate the Pearson correlation coefficients for each combination of variables. Size and colour of circles in the lower triangular part of the matrix chart are relative to the strength and direction of the correlation coefficients, following the colour legend on the right side. Because of the moderate to high correlation values, we decided to only include NAOw in further models for parsimony.

Statistical procedures

We performed statistical data analyses using R (version 3.6.0., R Development Core Team., 2009).

We evaluated sexual differences in space use, behavioural patterns, fishery attendance, and SIA using regression modelling. We used Linear (LMM) or Generalized Linear Mixed Models (GLMM) as appropriate for each model (Harrison et al., 2018). We ensured the selection of the residual family that best fitted the data and avoided overdispersion, using functions provided by the R package *DHARMa* (Hartig, 2017). To test the significant effect of predictors in response variables, we used restricted maximum likelihood and likelihood ratio test for LMM and GLMM respectively. We used functions provided by R packages *lme4* (Bates et al., 2015), *lmerTest* (Kuznetsova et al., 2017), and *sjPlot* (Lüdecke, 2019). We set the significance level to 0.05 for all statistical tests. To test for sexual differences in space use and behavioural patterns, we included as the response variable in the models the maximum distance, the total distance covered, the trip duration, the foraging ground size (i.e. K50 size), the probability of performing long trips, and the amount of time invested in each behavioural mode. We included sex, NAOw, and the two-way interaction as predictors to test whether environmental variability differently affects individual performance according to sex, and bird identity as a random factor. The maximum and total distance were log-transformed before modelling with LMM. To model foraging ground size, we additionally included the main foraging area (Catalan or Balearic shelf) as a predictor, and its interaction with sex and NAOw. We used logistic binomial regression to model the probability of performing short or long trips and negative binomial GLMM to model trip duration. We also used negative binomial GLMM to model the amount of time invested in each behavioural mode, including the log of the number of locations of each trip as an offset to account for the different trip duration (Bates et al., 2015). To evaluate sexual differences in fishery attendance, we estimated the incidence rate ratio as the amount of fishing vessel attendance events related to the amount of foraging during a trip. We used negative binomial GLMM including sex, NAOw, and the average number of vessels available in the vicinity for every trip as predictors. We also included the three-way interaction because the three variables might interplay in the probability of fishery attendance. Bird identity was included as a random factor, and the log of the number of foraging locations was included as an offset in the model (Bates et al., 2015). Finally, regarding SIA, we used LMM to model δ^{13}C and δ^{15}N values, considering as predictors the sex, NAOw, main foraging area, and the time birds were foraging associated with fishing vessels within the 6-day window of plasma. We did not include interaction terms because we did not expect predictors to affect physiology (and thus isotopic values) of each sex differently. Bird identity was included as a random effect, and time invested in foraging within the 6-day window of plasma was included as weight in the model (Bates et al., 2015). When interactions between predictors were not significant, we ran again the final models excluding them for parsimony. Even though our dataset only considered four years, we included NAOw as a numeric predictor in the models since it is a numeric index of continuous nature. In doing so, we aimed to ease comparisons with other forthcoming studies including longer time series.

S2. Space use by sex and year

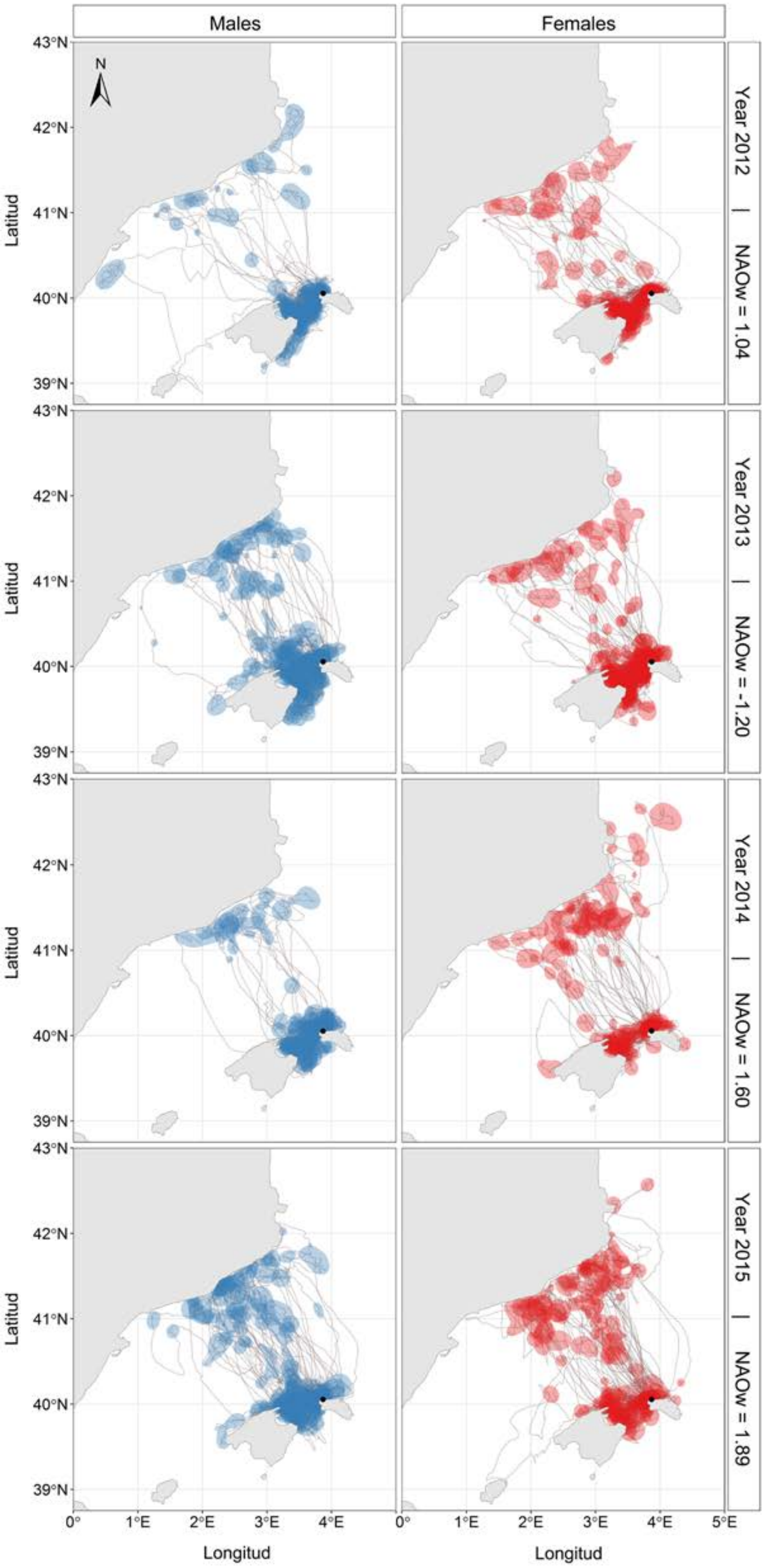

Figure S2 • Annual foraging grounds of male and female Scopoli's shearwaters breeding in Menorca during the chick-rearing period from 2012 to 2015. Birds trajectories recorded with GPS loggers are represented in soft brown. Individual foraging grounds identified along the trips (estimated 50% KDE volumes, k50) are shown in blue and red (males and females respectively). The colour intensity of foraging grounds indicates the number of foraging grounds overlapping. The black circle represents the colony. NAOw values are indicated on the right side.

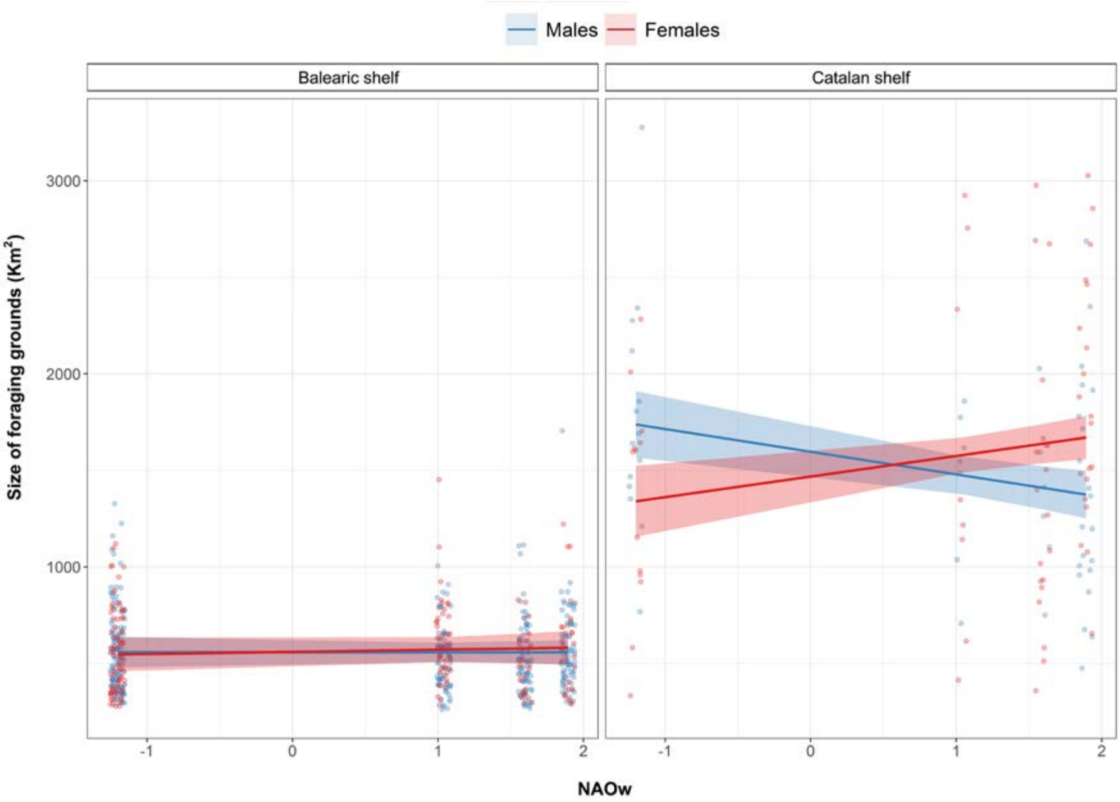

Figure S3 • Marginal estimates of the size of individual foraging grounds by trip in relation to NAOw. Shaded areas represent the associated 95% CI. Soft dots represent raw data. In the Catalan shelf, where birds commuted to forage from the breeding colony in Menorca, the worse the annual environmental conditions (i.e. the higher the NAOw), the larger the foraging grounds used by females and smaller those of males. This interaction did not occur in Balearic waters.

S3. Fisheries

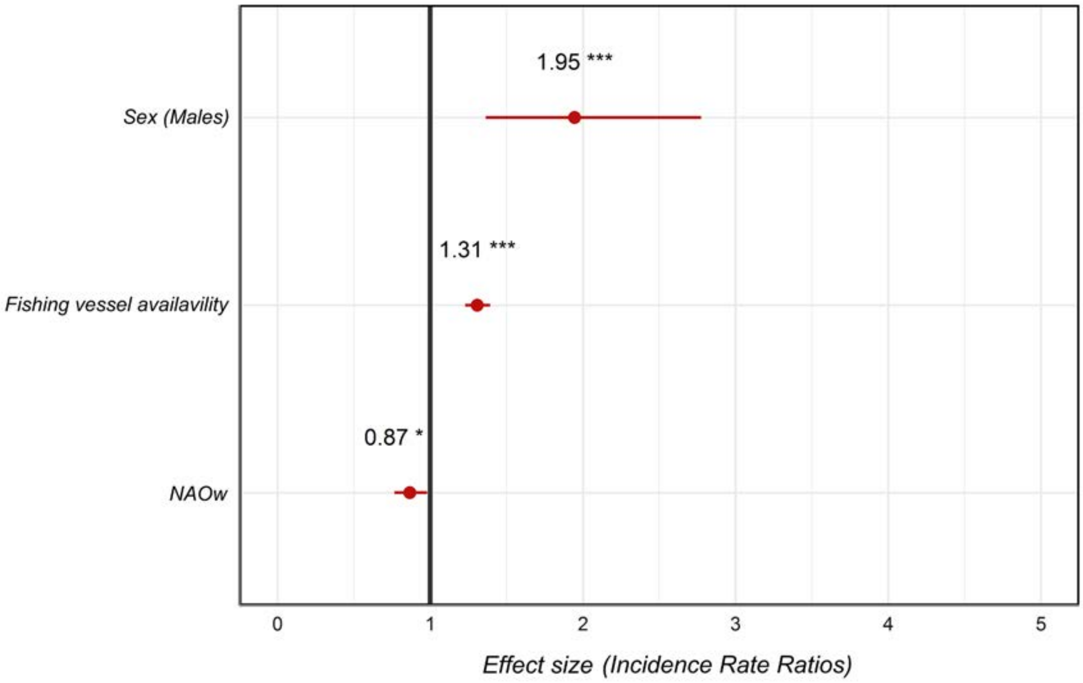

Figure S4 • Effect size of predictors in bird fishery attendance modelled through negative binomial GLMM. A vertical line in the value 1 in the X-axis represents the reference level (Females) at the mean value of numerical predictors. Horizontal red lines represent the confidence intervals of the estimates, being statistically significant when they do not cross 1. The probability of attendance was approximately double for males than for females. A high average number of fishing vessels operating in the vicinity of birds during the foraging trips increased the probability of attendance. NAOw had half as much influence as the average number of fishing vessels operating in the vicinity, although in the opposite direction (the higher the NAOw the lower the probability of attendance).

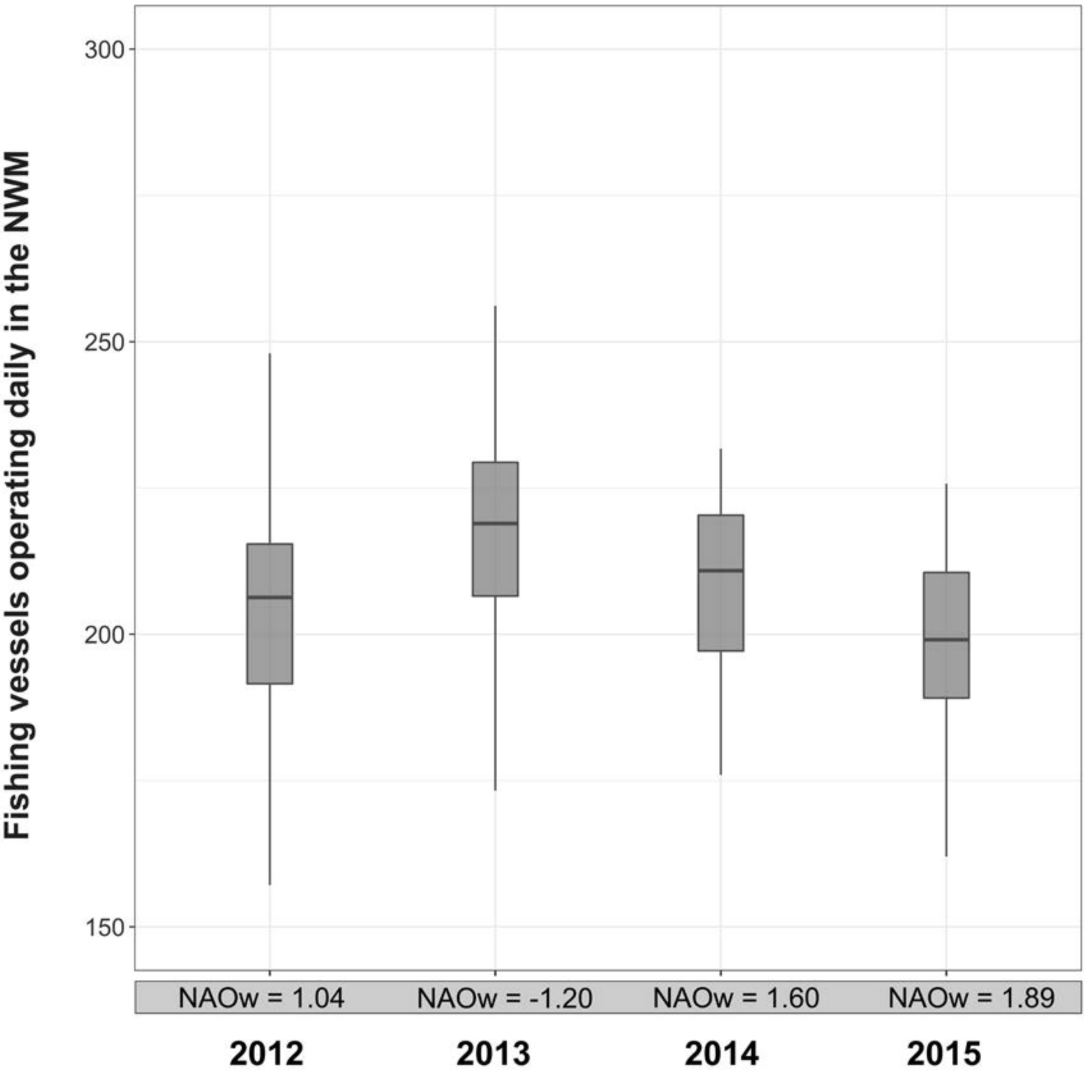

Figure S5 • Daily number of different fishing vessels from the Spanish fishing fleet operating within the full movement range of all the tracked birds over the study period (represented as the Minimum Convex Polygon from the whole dataset of GPS bird positions, Calenge 2006), which covers a large part of the North-Western Mediterranean (NWM). Black-contoured boxplots show the median (centreline) and quartiles (hinges corresponds to percentiles 25th and 75th); whiskers extend from hinges to the largest (and the smallest) value no further than 1.5 times the interquartile range. Fishing vessels positions were extracted from the Vessel Monitoring System (VMS). Positions closer than 5 km to harbours were not included. A running average of one week was applied to smooth daily values. Annual values of the extended annual winter North Atlantic Oscillation (NAOw) index are indicated at the bottom.

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Chapter IV

Revisiting the dual-foraging strategy: behavioural strategies of the Cory’s shearwater over the breeding period and the role of environmental features as foraging cues

REVISITING THE DUAL-FORAGING STRATEGY: BEHAVIOURAL STRATEGIES OF THE CORY'S SHEARWATER OVER THE BREEDING PERIOD AND THE ROLE OF ENVIRONMENTAL FEATURES AS FORAGING CUES

ABSTRACT

The breeding period in pelagic seabirds often takes several months, during which individuals need to maximise foraging, breeding success and survival. Therefore, foraging strategies may shift over time according to breeding stages, since reproductive constraints change over the breeding period. In this regard, to maximise foraging, seabirds may use proximate environmental features as a cue to decide foraging destination. In the last stage, the chick-rearing, the dual-foraging strategy has been proposed as a way to balance adult body condition and chick growth needs, shaping foraging destination and resources consumed, but no evidence of its use has been found for some species. In this work, we evaluate the role of the breeding stage (i.e., pre-laying, incubation, chick-rearing) and environmental features near the breeding colony in the foraging strategies of Cory's shearwaters breeding in Gran Canaria (Canary Is.) through GPS tracking. Besides, we evaluated the spatial origin of resources assimilated by parents and offspring analysing stable isotopes in whole blood from adults and chicks. Birds showed a shift in behavioural budgets according to the breeding stage, investing more time in foraging and less in resting with the advance of the breeding period, likely because of the demanding task of rearing the chick. Sea surface temperature in waters surrounding the colony had the most significant influence in trip destination, with lower temperatures promoting short trips. Last, trip destination, duration and distance, and stable isotope analysis, altogether gave support to the use of the dual-foraging strategy. Our findings point out the relevance of sea surface temperature as an important parameter for individual decision-making. This study recalls the need to study foraging strategies over the whole breeding period, as internal constraints and external conditions can shape individuals' behaviour and thus, general conclusions arising from single breeding stages can be misleading.

Keywords

Seabirds • SST • individual decision-making • behavioural budget • compositional data • conditional inference tree

Introduction

Resource availability in dynamic environments is ephemeral and often irregularly distributed, thus being rarely predictable at fine- or medium-scale for top-predators (Stewart, John, & Hutchings, 2000). That is the case of marine ecosystems, highly dynamic environments where prey is patchily distributed because of physical features such as seabed, coastline topography, currents or winds, but also ephemeral due to factors such as the weather, photoperiod and seasonality that influence the life-history traits of prey species (Stewart et al., 2000). In this scenario, top-predators might rely upon environmental features to inform individual decision-making, since the ability to read these cues would be advantageous to maximise foraging (Emlen, 1966; Stephens & Krebs, 1986).

Pelagic seabirds are highly mobile top-predators that forage at sea but are bound to a central place during the whole breeding period, the colony, usually located in oceanic islands (Gaston, 2004). Throughout the breeding period, events such as pair-bond (re-)establishment, mating, nest defence, incubation, brood-guarding or chick-feeding, could influence individual decision-making, behaviour and energy expenditure, in other words, these events may shape foraging strategies (Schreiber & Burger, 2001; Navarro et al., 2007; Phillips et al., 2017). The foraging strategies of pelagic seabirds have been extensively studied during the chick-rearing (e.g. Berlincourt & Arnould, 2015; Ochi et al., 2010; Regular et al., 2014), but comparatively less research has been carried out regarding the sequential adjustment of behaviour during all the stages of the breeding period (Navarro et al., 2007; Pinet et al., 2012; Shoji et al., 2016).

A particularly striking strategy exhibited during the chick-rearing by some seabird groups is the so-called dual-foraging strategy: adult breeders alternate frequent short foraging trips with less frequent long trips, resulting in a bimodal trip-length pattern (Weimerskirch, 1998; Weimerskirch & Cherel, 1998). During the chick-rearing, adult breeders are subjected to explicit central-place foraging, i.e. carrying food from feeding grounds to be delivered to the offspring at the nest (Orians & Pearson, 1979). The dual-foraging strategy would allow breeders to find an equilibrium between fulfilling chick growth needs —through foraging nearby the colony to deliver the meal to offspring regularly— and ameliorating adult body reserves eroded by chick-rearing duties —through foraging at more productive but distant areas—. Therefore, this strategy implicitly entails resource segregation between parents and offspring because of the different spatial origin of prey consumed by adults and chicks (Weimerskirch, 1998).

The use of the dual-foraging strategy has been widely reported in several seabird species, yet limited support to its use has been found for many other species, which has risen concerns about the assumption of the widespread use of this strategy (Phillips et al., 2009; Baduini & Hyrenback, 2003; Alonso et al., 2012). First, a bimodal trip-length pattern is often interpreted in the literature as the visible sign of a dual-foraging strategy (e.g., Welcker et al., 2009). However, such bimodal pattern could arise merely from a different use of disjunct foraging areas over time, without the need of a different origin of the feeding resources assimilated by parents and offspring (Baduini & Hyrenback, 2003; Phillips et al., 2009; Paiva et al., 2010). As pelagic seabirds can fly over long distances, they often encompass two disjunct foraging areas within their movement range over the breeding period, the oceanic waters surrounding the colony, and distant but often nutrient-richer waters over continental shelves, slopes or frontal zones (Congdon et al., 2005; Machu et al., 2009; Reese et al., 2011; Waugh & Weimerskirch, 2003). Second, some authors have pointed out that the dual-foraging strategy may be used on an optional basis depending on environmental conditions, that is, when prey resources near the colony are sufficient, birds would be more likely to exhibit a unimodal trip-length pattern, i.e., mostly short trips (Granadeiro et al., 1998). In this regard, it has been suggested that individuals may rely on cues from the proximate environment to decide whether engaging in short or long trips to optimise foraging performance (Berlincourt et al., 2015; Reed et al., 2010; Shoji et al., 2016). Last, the spatial origin of feeding resources consumed by parents and offspring have been rarely verified, despite being capital to attest the use of the dual-foraging strategy (Cherel et al., 2005; Bond et al., 2010; Granadeiro et al., 1998).

In this work, we analyse the foraging strategies over the different stages of the breeding period —namely pre-laying, incubation and chick-rearing— in the Cory's shearwater (*Calonectris borealis*), a pelagic seabird that breeds in oceanic islands and forages over the Northwest African shelf, in the highly dynamic Canary Current ecosystem (Ramos et al., 2013). Previous evidence from Cory's shearwaters breeding in Selvagens Islands (Portugal) and Veneguera (Gran Canaria, Canary Islands) did not find support to the dual-foraging strategy (Alonso et al. 2012; Navarro & González-Solís, 2009). Here, we revisit the foraging strategies of this species to explore their variability over the whole breeding period through combining GPS tracking, behavioural annotation, satellite-derived environmental data and stable isotope analysis. First, we explore temporal shifts in the behavioural budgets. Second, we aim to evaluate the use of environmental features as a cue to inform foraging decisions. Third, we assess whether an apparent dual-foraging strategy is supported by both a bimodal trip-length pattern and a different spatial origin of feeding resources consumed by parents and offspring. We hypothesise that (1) individual behavioural budgets will vary according to the breeding stage because of the change in breeding constraints, more specifically, foraging will be comparatively greater in chick-rearing —thus decreasing resting— and lower in pre-laying, and (2) individuals will rely upon proximate environmental features, that they may sense through sensorial capabilities, for the decision-making of performing short or long trips.

MATERIAL AND METHODS

Model species

The Cory's shearwater is a medium-sized, long-lived, pelagic seabird of the Procellariiformes order. The species breeds colonially in the Atlantic archipelagos of Azores, Madeira and Canary Islands (Ramos et al., 2013). It is present in the main breeding grounds from early March to October (Arizmendi et al., 2013; Navarro et al., 2008), starting then the migration to the wintering areas in the North, Central and South Atlantic (González-Solís et al., 2007; Dias et al., 2011). After arriving to the breeding grounds, birds prepare for reproduction: adult males occupy and defend the nests, couples are (re-)established and mating takes place. Females lay only one egg in late May and the incubation period takes around 60 days, during which both sexes alternate incubation stints and foraging bouts at sea. Hatching occurs around mid-late July, and both sexes undertake chick provisioning duties until fledging, in late October (Thibault et al., 1997). The species preys mainly on epipelagic fish (e.g. clupeiforms *Sardina* sp., *Sardinella* sp., *Engraulis* sp., scombrids *Scomber* sp.) and cephalopods (*Loligo* sp., *Todarodes* sp., *Ommastrephes* sp.), whose spatial and temporal abundance is strongly driven by seasonal dynamics in the Canary Current (Sánchez-Garrido et al., 2019).

Study area

The study was performed in the Veneguera cliffs (27° 50' 24" N, 15° 47' 24" W), in the southwest of Gran Canaria (Canary Islands). These cliffs hold an important breeding population of the species estimated in ca. 1 000 pairs (Arcos et al. 2009). The Canary Islands are located ~250 km away from the African coast, and they are under the influence of the Canary Current, a major coastal upwelling system along the Northwest African coast (Arístegui et al., 2009). The easterly winds in this area displace surface warm waters, promoting the rise of cool nutrient-rich subsurface waters over the shelf, which drives bottom-up nutrient cascades exploited by marine top-predators (Grecian et al., 2016; Hernández-León et al., 2007; Scales et al., 2015). As in other major upwelling systems, there is a strong coupling between atmospheric processes, ocean circulation and food web dynamics (Arístegui et al., 2009; Sambe et al., 2016). In accordance, seasonal variability in wind stress drives temporal changes in the abundance of phyto- and zooplankton, thus having a major impact on the ecosystem dynamics (Arístegui et al., 2006).

Fieldwork and sampling

Fieldwork was conducted in April, June - mid-July, and mid-August - September 2012, thus encompassing periods of the pre-laying, incubation and chick-rearing stages. At every stage, we captured several adults at night, using a looped pole or by hand, when they landed at the colony or once inside the burrow. In pre-laying, we captured birds that were accompanied by another individual of the opposite sex inside a burrow, which we interpreted as they were apparently in reproductive mode. In incubation and chick-rearing stages, we captured birds from nests where we verified the existence of an egg or a chick inside, respectively. Some individuals were captured in more than one stage. We equipped captured adults with GPS loggers (©Perthold Engineering LLC; median error of <10 m; Forin-Wiart et al., 2015; Morris & Conner, 2017) encased in a heat-shrink tube for waterproofing. We set the devices to record one location every 15 min and attached them to mantle feathers with salt-water resistant Tesa® tape. The total mass of the devices (~25 g) was below 4% of the adult body mass (Phillips et al., 2003; Passos et al., 2010). We recovered loggers between three days and three weeks after deployment. This could encompass one single trip during incubation but several trips in pre-laying and chick-rearing. We weighted the tracked birds at every GPS deployment and recovery.

Moreover, we took a blood sample after every GPS recovery from the tarsal vein of the bird to later perform Stable Isotopes Analysis (SIA, see below). We stored the blood samples, separated the plasma fractions after each fieldwork session, and froze them. During the chick-rearing period, we took 0.25 ml samples from chicks at 40 and 70 days after hatching. Chick blood samples were stored for further SIA.

We never tagged simultaneously both partners of the same couple. All animals were handled in strict accordance with guidelines for ethical research defined by the current European legislation and under a licence approved by the respective environmental agencies of the Spanish Government and Canary Islands Government.

Processing of GPS tracking data and behavioural annotation

We used custom-built functions in R to process GPS data (version 3.2.5, R Development Core Team 2016). We cleaned data and split recorded trajectories into separate trips considering as one trip the route travelled between nest departure and the subsequent arrival to the nest. We excluded incomplete trips from further analyses. Based on preliminary data exploration, we classified each trip as a short trip, when the bird remained in waters surrounding the Canary Islands, or as a long one, when the bird reached the Northwest African shelf.

To ensure the representativeness of data gathered, we evaluated whether the sample size of trips recorded at each breeding stage was sufficient. To this aim, we calculated the rate of increase in the maximum movement range in relation to the increase in the number of trips recorded (see a similar approach in Lascelles et al., 2016). We considered the 95% probability contour of Kernel Density Estimation (KDE95) as the maximum movement range; we calculated it with the function *kernelUD* from the R package *adehabitatHR* (Calenge, 2006).

To study the time that individuals allocated to basic behaviours at sea, i.e., behavioural budgets, we used the unsupervised clustering method provided by the R package *EMbC* for behavioural annotation of movement data (Garriga et al., 2018). The Expectation-Maximisation binary Clustering (EMbC) algorithm classifies every location into one out of four clusters based on the speed and turning angle. In the context of seabird behaviour, each cluster corresponds to a different basic behaviour: resting (low speed and low turning angle), intensive search (low speed and high turning angle), extensive search (high speed and high turning angle) and relocating (high speed and low turning angle). We grouped intensive and extensive search as foraging behaviour for further analysis (Wischnewski et al., 2019). For every trip, we calculated the behavioural budget, i.e., the proportion of time invested in each behaviour.

Environmental data

To investigate the role of environmental features in the proximate environment in individual decision-making to forage near the colony (short trips) or forage in the Northwest African shelf (long trips), we considered the following set of variables: chlorophyll-a concentration (CHL-a, units in mg m^{-3}), net primary productivity (NPP, units in g C m^{-2}), the Finite Size Lyapunov Exponents (FSLE, a proxy of (sub-) mesoscale features such as filaments, eddies and fronts, units in day^{-1}, De Monte et al., 2012), the Ekman transport (a proxy of coastal upwelling intensity, units in m^2 s^{-1}), the sea surface temperature (SST, in °C), the Charnock coefficient (an ocean surface roughness index), the ocean surface current (in m s^{-1}), wind speed (in m s^{-1}) and sea depth (in m) (Wakefield et al., 2009). Moreover, for SST we calculated the spatial gradient as a proxy of thermal fronts, using a 3-cell moving window. We considered the proximate environment as the area used by birds in the surroundings of the island of Gran Canaria, where the colony is located. First, we pooled together the trips previously labelled as short trips and used them to calculate the KDE95, using the function *kernelUD* from the R package *adehabitatHR* (Calenge, 2006). For most of the variables, we extracted the layers with environmental data in different raster formats within the bounding box defined by the KDE95 using the R package *rerddapXtracto* (Mendelssohn, 2019). For the case of FSLE, data was downloaded from AVISO+ service (www.aviso.altimetry.fr), and for the case of the Ekman transport, data was downloaded from Copernicus service (www.copernicus.eu). Layers were cropped with KDE95 to match the proximate environment. We extracted environmental data at the highest spatial resolution available. Regarding temporal resolution, we extracted environmental data at daily (~1 day) and weekly (~8 days) resolution, since daily data may have abundant spatial gaps due to cloud cover. For every trip (i.e., both short and long trips), we calculated the average and the maximum value of each environmental feature considering a time window encompassing from the first day of a trip until seven days back before the trip start. For FSLE and SST gradient, we calculated the rank between minimum and maximum to represent variability in the area within the time window. We evaluated the collinearity among the set of environmental features using the Variance Inflation Factor (VIF), setting a threshold of 10. We used the function *vifstep* from the R package *usdm* (Naimi et al., 2014). After it, six variables remained in the dataset for further analyses: mean CHL-a (8-day composite), mean SST (8-day composite), rank of SST gradient, mean of the Charnock coefficient, mean of ocean surface current and rank of FSLE.

Stable isotope analyses

Stable Isotope Analysis (SIA) are widely used to study the feeding ecology of top-predators (Ramos & González-Solís 2012). The isotope of Nitrogen ($\delta^{15}N$) is usually used to infer trophic position: $\delta^{15}N$ increases by 3 to 5‰ at every trophic level. The isotope of Carbon ($\delta^{13}C$) helps to infer the origin of the prey consumed, though it also increases to a lesser extent in accordance to the trophic level (by 0.5 to 1‰ at every trophic level). $\delta^{13}C$ is especially useful because it can reflect shifts in offshore-inshore feeding, i.e., a gradient from more pelagic to more shallow/neritic waters. To carry out SIA, we used whole blood because it integrates a temporal window of about four weeks (Ramos & González-Solís, 2012), which for chicks broadly corresponded to early chick-rearing (40 days samples) and mid to late chick-rearing (70 days samples). In the case of adults, as there was a gap of about one month between visits to the colony for fieldwork in the transition between breeding stages, we were confident that $\delta^{15}N$ and $\delta^{13}C$ values were not influenced by the preceding breeding stage. Moreover, we performed SIA on potential prey species to further delimit the spatial origin of feeding resources of adults and chicks. Local fishermen provided us with fish captured in July 2012, near the sea surface and up to eight km from the coastline to the south of Gran Canaria. In addition, we also performed SIA on potential prey species collected in an opportunistic sampling from a vessel operating over the Northwest African shelf (Cape Dakhla offshore), collected from 30 m up to 380 m depth in July 2012. We performed SIA on prey muscle.

Statistical analyses

We characterised foraging trips by calculating total distance travelled (km), maximum distance reached from the colony (km) and trip time duration (h). We used Linear Mixed Models (LMM) to assess differences between sexes and breeding stages in total distance travelled and maximum distance reached, including the sex and the breeding stage as fixed terms, i.e., predictors. Bird identity was included as a random effect to control for pseudo-replication, since several individuals were tracked more than once. Both total and maximum distance were log-transformed prior to modelling to achieve Gaussian error distribution. To model trip time duration, we used a negative binomial Generalised Linear Mixed Model (GLMM). We checked for Gaussian error distribution in the models using Q-Q plots. To test the significant effect of predictors in the response variables, we used restricted maximum likelihood and likelihood ratio test for LMM and GLMM respectively. We fitted the models using the R package *lme4* (Bates et al., 2015).

To characterise trip-length patterns and check for trip bimodality, we applied a clustering method. First, we assessed the clustering tendency to verify that data could be clustered by calculating the Hopkins statistic, using the R package *factoextra* (Kassambara & Mundt, 2017). Second, we applied a model-based agglomerative clustering method based on Gaussian finite mixture models (Austin et al., 2019). We used as input variables both the maximum distance reached and the trip time duration as they were not correlated, and ran the analysis separately for each breeding stage, using the R package *mclust* (Scrucca et al., 2016). *mclust* relies on the Expectation–Maximisation (EM) algorithm for maximum likelihood estimation, so the initialisation of EM is performed using the partitions obtained from agglomerative hierarchical clustering. We partitioned data into 1 up to 9 different clusters and selected the most plausible model based on the Bayesian Information Criterion (BIC; in *mclust,* the larger the value the stronger the support, Scrucca et al., 2016).

Next, we investigated shifts in the behavioural budgets according to the breeding stage. An individual behavioural budget displayed in a trip can be described as a composition of ratios (in our case, the proportion of time invested in foraging, resting and relocating in a trip), each bounded by the values of the others, and altogether adding up to the unity (Gupta et al., 2018). This type of constrained data is known as compositional data, and it is not suitable for standard multivariate analysis (Aitchison, 1986; Pawlowsky-Glahn & Egozcue, 2006). Following the rise of recent behavioural annotation algorithms (e.g., Garriga et al., 2016; Dean et al., 2013; Kane et al., 2020), a growing number of research articles have analysed behavioural budgets in seabirds, but the majorly has used statistical methods designed for unconstrained data, which may lead to inappropriate inferences (Pawlowsky-Glahn & Buccianti, 2011). In contrast, very few have considered this issue to properly address this kind of data (Regular et al., 2014). Therefore, to avoid inappropriate inferences, we analysed behavioural budgets as compositional data, treating simultaneously the different behaviours as part of a whole. We applied the isometric log-ratio (ilr-) transformation on behavioural budgets, using the R package *compositions* (van den Boogaart et al., 2018). The ilr-transformation maps compositional data into coordinates of orthogonal axes of the real space, preserving all metric properties and being therefore tractable in a multivariate analysis framework (Egozcue et al., 2003; van den Boogaart et al., 2018). Similarly to other transformations aiming to handle compositional data, ilr-transformation treats one of the ratios as the common denominator of the others, akin to a reference level (Pawlowsky-Glahn & Buccianti, 2011). We included ilr-transformed data of behavioural budgets as a multivariate response variable in a Multivariate Covariance Generalized Linear Model (MCGLM), using the R package *mcglm* (Bonat, 2018). We checked for normality in residuals of the model using Q-Q plots. Relocating behaviour was set as the common denominator. In addition to the breeding stage, we included as covariates the sex and the maximum distance reached. Bird identity was included as a random effect term. Males and pre-laying were set as reference levels (i.e., intercept). We calculated post-hoc pairwise comparisons with Bonferroni adjustment, using the R package *emmeans* (Lenth, 2020).

We later investigated the use of proximal environmental features in individual decision-making related to foraging near the colony (i.e., engagement in short trips) or flying towards the African shelf (i.e., engagement in long trips). To do so, we used two different approaches. First, we used a logistic regression by running a Generalised Linear Mixed Model (GLMM), including trip type (short or long) as a binomial response variable and the set of environmental variables free from multicollinearity as predictors. We also included breeding stage, sex, and bird body mass at the trip start as covariates, and bird identity as a random effect. We checked for normality in residuals using Q-Q plots. We fitted the global model using the R package *lme4* (Bates et al., 2015). Then, we generated a set of candidate models with combinations of fixed effect terms (i.e., predictors and covariates) and considered the most parsimonious models those with lowest value of AICc (corrected Akaike's Information Criterion) (Johnson & Omland 2004). Then, we calculated the relative importance of each variable by summing the Akaike weights over all the models that included each of the explanatory variables (Soriano-Redondo et al., 2016). We used the functions *dredge* and *importance* from the R package *MuMIn* (Barton, 2018). Nevertheless, although this kind of GLMM is often used to explore the role of explanatory variables in determining a binary outcome, it presents several caveats: (i) it makes several assumptions about the underlying data, (ii) it can hardly address complex non-linear relationships, and (iii) it is penalised by correlated variables. Moreover, relative variable importance based on Akaike model weigths, usually used after applying model comparisons and AICcc, has been called into question (Galipaud et al., 2014). Therefore, we additionally complemented the first approach by fitting a Conditional Inference Tree model (CIT). CIT is a kind of decision tree, i.e., an algorithm framework to create an explicit hierarchy of tests that ends up in a partitioning of the decision space (Hothorn et al., 2006). Machine learning non-parametric methods such as tree-based algorithms are getting more popular in ecology over the last years, including in seabird research (Jakubas et al., 2018; Valleta et al., 2017). In contrast with linear models such as GLMM, tree-based methods are more robust to problems such as over-fitting, collinearity and bias from predictor variables, and can deal with non-linear relationships with relative ease (Johnstone et al., 2014). Particularly, because tree-based methods are built upon permutation procedures, they are far less sensitive to correlation among predictors. When data contains correlated predictors, the truly influential predictors have a higher chance to be detected when conditional permutation is used (Strobl et al., 2008). CIT test the independence between a response variable and multiple explanatory variables through recursive partitioning. At each step, one explanatory variable is selected from all explanatory variables included in the model by maximising the association with the response variable through a permutation test (Hothorn et al., 2006). The split value that separates the values of the response variable into two homogeneous groups is estimated by a statistic test (i.e., split occurs when the p-value is smaller than a predefined α level) to maximise between-group variation and minimise within-group variation (Hothorn et al., 2006). The result is an inverted tree where each node represents a predictor, being at the top the most important one. The number of nodes in the tree corresponds to the number of explanatory variables having a significant effect on the response variable. Every node splits into two branches, and the terminal leaves are represented by bar plots at the bottom, which correspond to the final groups and indicate the proportion of observations included at each (Hothorn et al., 2015). We fitted the CIT model using the function *ctree* from the R package *party* (Hothorn et al., 2006). We used the same set of predictors than in the GLMM and set α to 0.05.

Last, we represented the isotopic niche space to evaluate segregation between feeding resources consumed by parents and offspring. We built up the isotopic niche space by fitting Bayesian ellipses in the bi-dimensional space defined by the values of $\delta^{13}C$ and $\delta^{15}N$ from parents and offspring. We also included values of $\delta^{13}C$ and $\delta^{15}N$ from potential prey to evaluate the possible spatial origin of resources consumed by the birds. We grouped samples according to age and spatial origin, i.e., adults at each breeding stage, chicks at 40-days and 70-days old, and prey (pelagic fish from Canarias, demersal fish from the African shelf, pelagic fish form the African shelf, and crustaceans and cephalopods from the African shelf). We used the R package *SIBER* to build up the Bayesian ellipses (Jackson et al., 2011).

RESULTS

We tracked a total of 41 birds that performed 135 trips: 51 trips during pre-laying, 39 during incubation and 45 during chick-rearing (see Supporting Information, Table S1). Representativeness analysis indicated that sample size was enough for the three breeding stages to capture population variability in foraging movements (see Supporting Information, Fig. S1). Birds predominantly used waters to the south of Canary Islands (i.e., short trips) and waters over the African shelf (i.e., long trips), whereas open waters between both areas were used as flight corridors (Fig. 1). Short trips were more frequent than long ones during pre-laying (48 short - 3 long), whereas during incubation both trip types had similar frequency (21 short - 18 long), and during the chick-rearing the long trips were the most frequent (16 short - 29 long) (Fig. 2).

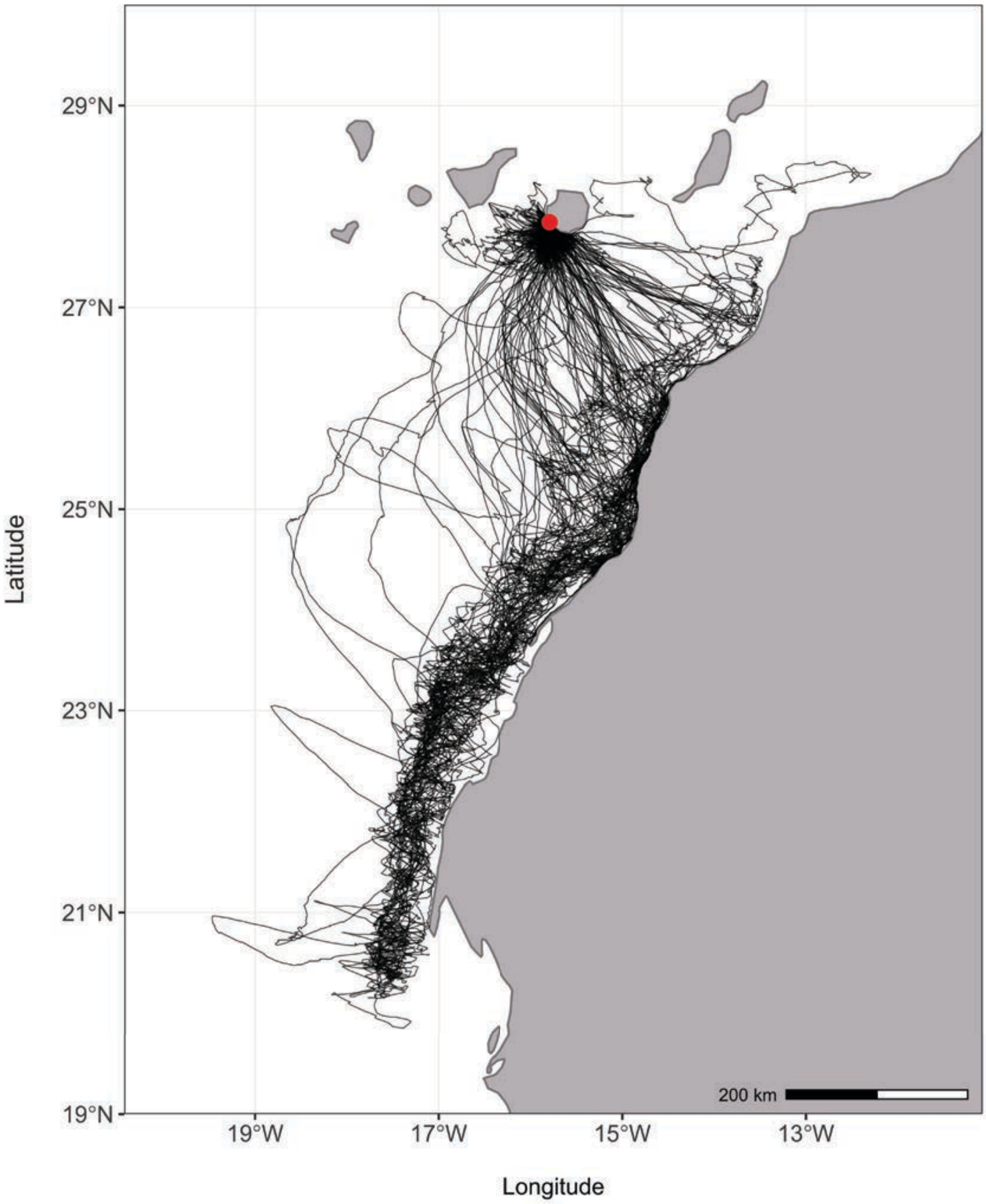

FIGURE 1 • General overview of foraging trips recorded through GPS tracking of Cory's shearwaters breeding in Veneguera (Gran Canaria, Canary Islands) during the breeding period of 2012 (135 trips, 41 individuals).

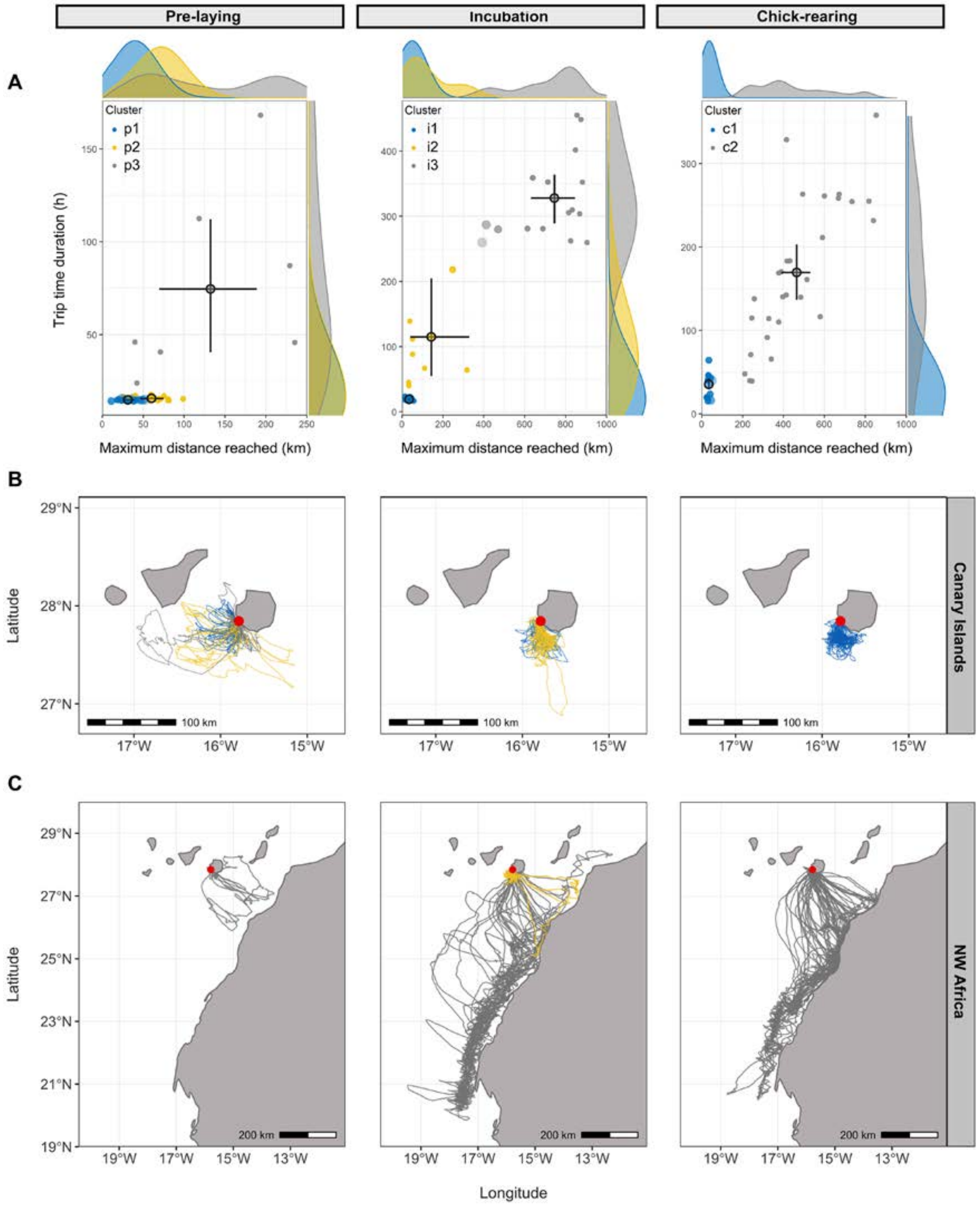

FIGURE 2 • (A) Expected-Maximization model-based clustering of individual foraging strategies over the three stages of the breeding period, based on both maximum distance reached and trip time duration simultaneously. Each column corresponds to a breeding stage. Each data point corresponds to a trip. Point colour identifies the cluster. Point size and colour transparency represent uncertainty (the larger the size and the higher the transparency, the higher the uncertainty). Black crosses represent the mean and its associated 95% confident interval for every cluster, calculated by bootstrapping. Marginal plots correspond to density plots of the clusters identified. Note the different scale in the X- and Y-axis in each plot. (B) Short trips (i.e., trips remaining in waters surrounding the Canary Islands) recorded at each breeding stage. (C) Long trips (i.e., trips reaching the Northwest African shelf) recorded at each breeding stage. Colours in (B) and (C) correspond to clusters showed in (A).

There was sexual differences in total distance travelled and trip time duration, being greater in females than males in the three breeding stages. Breeding stage also had influence on these two trip parameters: total distance travelled was longer during incubation and chick-rearing than during prelaying, and trip time duration was greater during incubation than during chick-rearing, and the lowest during pre-laying (see Supporting Information, Table S2, Fig. S2).

Data from the three breeding stages was significantly clustered (Hopkins statistic: 0.166 for pre-laying, 0.116 for incubation and 0.343 for chick-rearing, all < 0.5, Kassambara & Mundt, 2017). Model-based clustering indicated differences in foraging strategies among breeding stages in terms of distance reached and trip time duration. During pre-laying, the most plausible model indicated three groups of trips, with average maximum distance reached of 31.11, 60.27 and 132.25 km (Table 1). One cluster included both short and long trips (Fig. 2). During incubation, the most plausible model indicated also three groups, with average maximum distance reached of 34.50, 142.49 and 745.55 km, and again one of the clusters included both short and long trips (Table 1, Fig. 2). During chick-rearing, the most plausible model indicated two groups, with average maximum distance reached of 34.63 and 463.75 km (Table 1, Fig. 2). In the three stages, clusters with an average maximum distance lower than 100 km corresponds to trips remaining in the waters south of Canary Islands.

Table 1 • Trip parameters used to perform the model-based clustering of foraging strategies, and their values calculated from the trips belonging to each of the resulting clusters. Values represent mean and confidence intervals (CI95%) calculated through bootstrapping.

Breeding stage	Trips	Cluster	Maximum distance reached (km)	Trip time duration (h)
Pre-laying (11 individuals)	29	p1	31.11 (25.83 - 38.19)	14.90 (14.76 - 15.03)
	15	p2	60.27 (47.31 - 73.80)	15.75 (15.27 - 16.41)
	7	p3	132.25 (70.69 - 187.95)	74.66 (40.44 - 112.16)
	Global (n = 51)		55.24 (45.20-72.68)	23.44 (17.84 - 34.77)
Incubation (21 individuals)	15	i1	34.50 (28.89 - 40.25)	19.14 (17.99 - 20.42)
	8	i2	142.49 (40.42 - 328.22)	115.09 (54.68 - 204.77)
	16	i3	745.55 (630.47 - 846.38)	328.09 (288.97 - 364.18)
	Global (n = 39)		333.97 (220.61 - 450.48)	160.58 (117.95 - 207.39)
Chick-rearing (19 individuals)	16	c1	34.63 (31.17 - 37.79)	35.20 (28.85 - 42.57)
	29	c2	463.75 (389.27 - 531.24)	169.66 (136.55 - 203.13)
	Global (n = 45)		311.70 (237.92 - 386.54)	122.02 (96.89 - 150.41)

Multivariate analysis of behavioural budgets as compositional data (i.e., after applying the ilr-transformation) indicated that the breeding stage significantly influenced behavioural budgets (Table 2). The investment in foraging during chick-rearing was significantly greater than during pre-laying (p-value = 0.047) , and slightly greater than during incubation, though this difference was not significant (p-value = 0.902). The investment in foraging was also greater during incubation than during pre-laying (p-value = 0.022) (Table 2, Fig. 3). Time spent resting was significantly lower during chick-rearing than during pre-laying and incubation (Table 2, Fig. 3). There were no differences in behavioural budgets between sexes. The amount of resting decreased significantly with greater values of maximum distance reached from the colony (Table 2).

Table 2 • Summary of the Multivariate Covariance Generalized Linear Model evaluating the effect of sex, breeding stage and maximum distance reached on the behavioural budget of Cory's shearwaters tracked with GPS. Ratios of time invested in each behaviour per trip represent compositional data and thus they require specific statistical treatments. Isometric log-ratio (ilr-) transformation was applied to data before modelling to deal properly with such specificities. Intercept corresponds to males and relocating behaviour. α was set to 0.05. Terms statistically significant are highlighted in bold.

	Foraging behaviour				Resting behaviour			
Fixed term	Estimate	Std. error	Z value	p-value	Estimate	Std. error	Z value	p-value
(Intercept)	-0.403	0.064	-6.260	0.000	-0.596	0.182	-3.267	0.001
Females	0.098	0.078	1.252	0.210	0.064	0.222	0.288	0.773
Incubation	-0.283	0.100	-2.821	**0.004**	-0.017	0.284	-0.060	0.952
Chick-rearing	-0.240	0.096	-2.517	**0.011**	-0.829	0.271	-3.058	**0.002**
Maximum distance reached (km)	0.000	0.000	0.799	0.424	0.001	0.000	2.431	**0.015**

Pairwise differences of factor "Breeding stage" in foraging behaviour				
Contrast	Estimate	Std. error	t.ratio	p-value
Pre-laying vs Incubation	0.283	0.100	2.712	**0.022**
Pre-laying vs Chick-rearing	0.240	0.096	2.410	**0.047**
Incubation vs Chick-rearing	-0.042	0.098	-0.433	0.902

According to GLMM, the SST gradient in waters nearby the colony correlated positively with a greater probability of performing a short trip (Table 3). Relative importance of variables pointed out SST gradient followed by 8-day mean SST as the two most important features, followed far behind by all other explanatory variables (Fig 4; see Supporting Information, Table S3). CIT model pointed out that 8-day mean SST was the most (and unique) significantly influent environmental feature in the decision-making, with a split value slightly above 19 ºC, under which the likelihood of short trip were greater (Fig. 5). However, the prediction was more accurate for the node with SST under the split value (error rate = 6%) than for the node with SST above it (error rate = 44%) (Fig. 5).

Regarding the spatial origin of feeding resources, Bayesian ellipses performed on $\delta^{13}C$ and $\delta^{15}N$ of adults in pre-laying suggested that they fed on waters surrounding the Canary Islands, according to a more negative value of $\delta^{13}C$ and the proximity to the ellipse of fish from the islands. During incubation, adult birds exploited resources in a gradient of $\delta^{13}C$, from prey from the Canary Islands to prey from waters in the Northwest African shelf. Finally, during chick-rearing, adult birds exploited prey from the Northwest African waters, whereas chicks (both 40 and 70 days old) fed on resources from waters surrounding the Canary Islands (Fig. 6, Table 4; see also Supporting Information, Table S4).

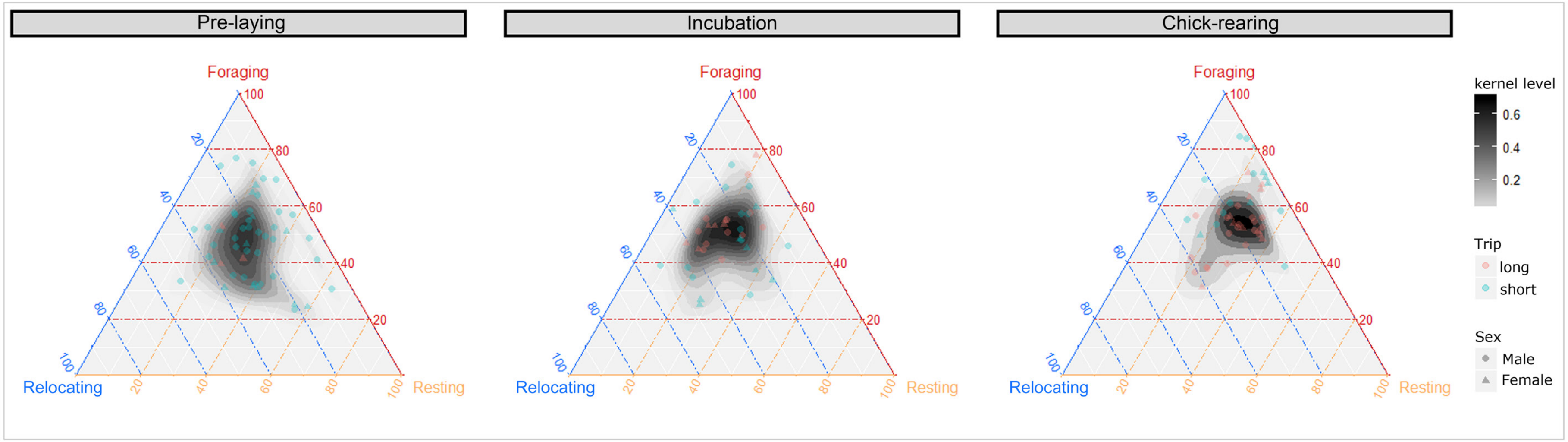

Figure 3 • Ternary plots showing behavioural budgets at the population level by breeding stage. Each data point corresponds to one trip, and its position along each of the three axes allows to visualise the investment per trip in each of the three behaviours simultaneously. Investment at the population level is represented by a density kernel distribution in greyscale.

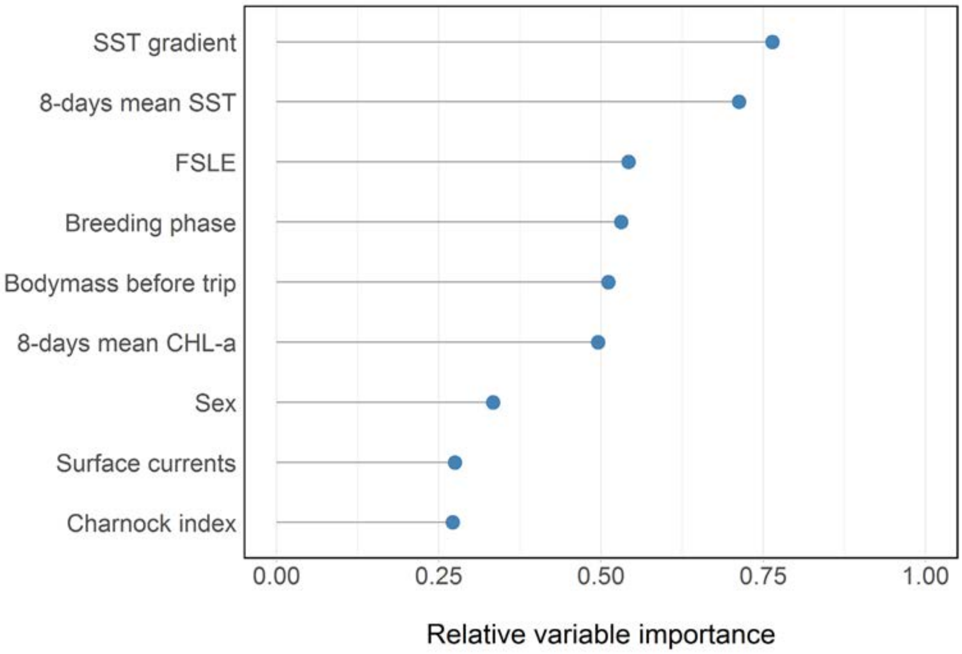

Figure 4 • Relative variable importance of explanatory variables used as input in the set of candidate Generalized Linear Mixed Models (GLMMs, logistic regression models with a binomial error distribution and logit link function) testing for the effect of proximate environmental features and the covariates sex, bodymass before the trip and breeding stage on the probability of performing a short trip instead of a long one. Relative variable importance was calculated by summing the Akaike weights over all GLMMs that included each of the explanatory variables (see methods for details).

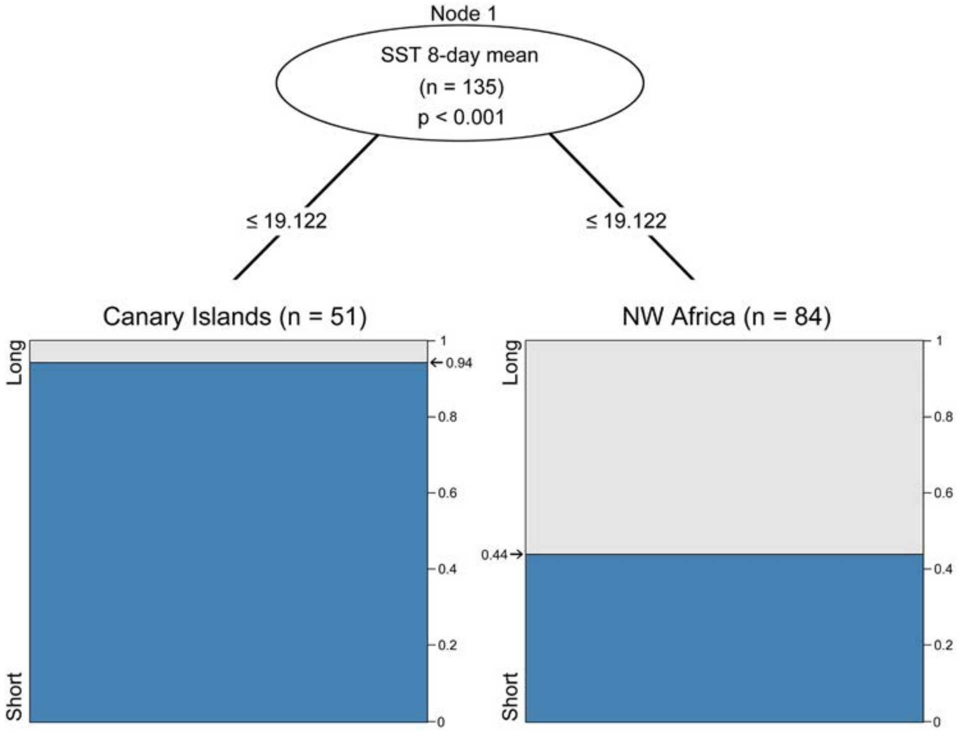

Figure 5 • The tree obtained from running a Conditional Inference Tree (CIT) model to test for the effect of proximate environmental features and the covariates sex, bodymass before the trip and breeding stage on the probability of performing a short or a long trip. Mean of sea surface temperature (SST) in waters nearby the south of Gran Canaria was the unique variable identified by the model as statistically significant in the individual decision-making of engaging in a short or a long trip.

Table 3 • Summary of the global Generalised Linear Mixed Model (logistic regression with a binomial error distribution and logit link function) aimed to evaluate the role of environmental predictors and the covariates breeding stage, sex and body mass in individual decision-making of Cory's shearwaters to engage in short or long trips. Intercept corresponds to males and pre-laying stage. α was set to 0.05. Terms statistically significant are highlighted in bold.

Fixed term	Estimate	Std. Error	z value	p-value
(Intercept)	-0.523	2.442	-0.214	0.830
Females	-0.346	0.775	-0.447	0.655
Incubation	-0.25	2.301	-0.109	0.913
Chick-rearing	4.986	5.651	0.882	0.377
Body mass before the trip	0.362	0.357	1.015	0.310
CHL-a	0.119	1.205	0.099	0.921
SST	-3.823	2.83	-1.351	0.176
SST gradient	0.968	0.346	2.798	**0.005**
Charnock index	-0.026	0.249	-0.106	0.915
Sea surface currents	-0.247	0.469	-0.526	0.598
FSLEs	1.534	0.797	1.924	0.054

Table 4 • Values of $\delta^{13}C$ and $\delta^{15}N$ of Cory's shearwaters sampled in the study. Values indicate mean ± standard deviation (‰). N indicates the number of individuals sampled.

Age - stage	N	$\delta^{13}C$	$\delta^{15}N$
Adults - Pre-laying	10	-19.6 ± 0.30	11.1 ± 0.23
Adults - Incubation	16	-18.7 ± 1.17	11.6 ± 0.36
Adults - Chick-rearing	17	-16.7 ± 0.58	11.5 ± 0.25
Chicks - 40 days old	7	-19.5 ± 0.32	10.9 ± 0.24
Chicks - 70 days old	7	-19.3 ± 0.27	11.0 ± 0.27

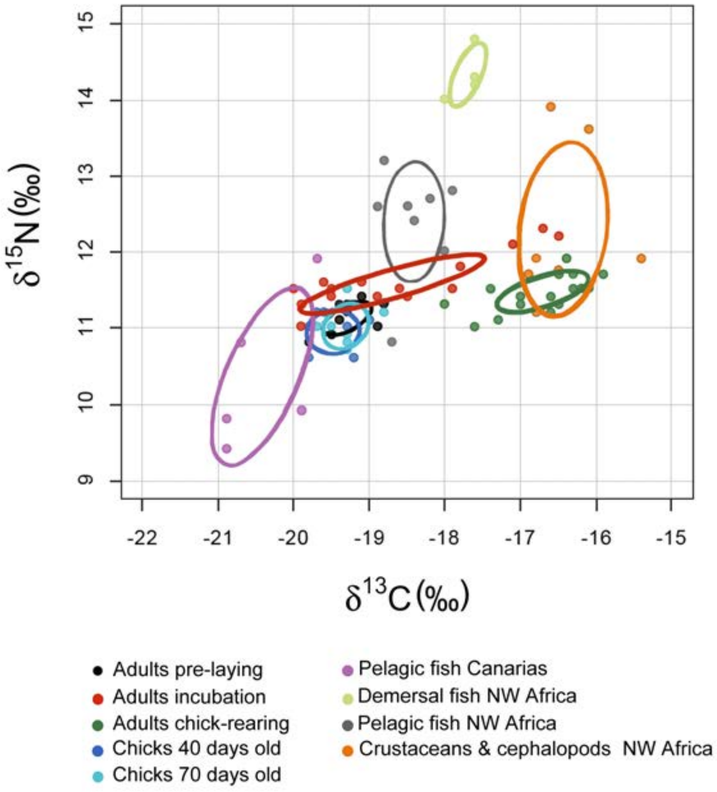

Figure 6 • Isotopic niche space of adult breeders and chicks of Cory's shearwaters from Veneguera (Gran Canaria, Canary Is.), and their potential prey. Each ellipse and colour represent a different group. Each ellipse contains 40% of the data of its corresponding group (SIBER, Jackson et al. 2011).

Discussion

This is a comprehensive study on behavioural patterns and foraging strategies of a pelagic seabird during the breeding period, evaluating simultaneously movement, behaviour and trophic ecology over the different breeding stages. We found evidence of shifts in foraging strategies among the different stages, with variation in trip time duration, distance, behavioural budgets and feeding resources used. Our findings suggest a key role of the sea surfate temperature in waters surrounding the colony in the probability of performing short or long trips. Lastly, our results support the use of the dual-foraging strategy: birds showed a clear bimodal pattern in trip distance and time duration during the chick-rearing, which was accompanied with a clear segregation in feeding resources assimilated by offspring and parents.

Breeding constraints shape behavioural budgets

Tracked birds presented flexible behavioural budgets across breeding stages. We found the breeding stage to influence behavioural budgets above other factors such as sex or maximum distance reached. During the breeding period, seabirds must cope with different constraints to maximise fitness and ensure survival while foraging efficiently in a dynamic environment (Navarro et al., 2007). Both the need to return to the central place after every foraging trip and the specific constraints of each breeding stage, impose variation in energy requirements over time, which is reflected in behavioural budgets (Regular et al., 2014). In accordance, tracked birds presented different investment in behaviours over the breeding period. Particularly regarding foraging, the investment was greater during incubation and chick-rearing than during pre-laying, pointing out the intense constraints of these stages.

After arriving from the distant wintering grounds, birds must prepare for the upcoming breeding season, which comes with strong physiological needs (Arizmendi-Mejía et al., 2013). During the pre-laying stage, both GPS data and SIA indicated that most of the trips were short, and the birds were feeding mainly in waters to the south of Gran Canaria. In this stage, males need to land every night to defend the nest. In contrast, females do not need to attend the colony every night and thus can remain at sea for longer periods, which may lead to sexual differences in the at-sea behaviour (Werner et al., 2014), However, we did not find differences between sexes in behavioural budgets, which suggest that males may modulate at-sea behaviour in some way to compensate the nest-attending constraint. Alternatively, the lack of sexual differences may be due to the annual environmental conditions. Werner et al. (2014) found sexual differences in the behaviour of Cory's shearwaters tracked during pre-laying in 2010, which was the poorest year in the North-East Atlantic in the last century in terms of productivity —using as a proxy the North Atlantic Oscillation index (NAO)— (Pereira et al., 2020). Our study was carried out in 2012, a year with NAO close to the average value of the NAO complete time series (Hurrell et al., 2003), so mild conditions could have reduced sexual differences in behavioural budgets. Last, regarding pre-laying, it is worth noting that our study did not include data from the pre-laying exodus, since we carried out GPS tracking well before birds performed it. Therefore, our results should not be extrapolated to the end part of the pre-laying stage. Nevertheless, our work is one of the few studies that have used electronic devices to study behaviour during pre-laying before the exodus takes place (Navarro et al., 2007; Werner et al., 2014).

Unlike pre-laying, during incubation the tracked birds engaged frequently in short and long trips to forage to the south of Gran Canaria and over the Northwest African shelf, respectively. Breeding constraints during this stage change drastically respect to pre-laying. During incubation, adult breeders of Cory's shearwater, both males and females, take long incubation stints at the nest while await to the mate relief to engage in the next foraging trip (Navarro et al., 2007). This likely explains our findings of greater investment in foraging compared to pre-laying, because birds need to recover their body condition eroded by severe starvation (Navarro et al., 2007). Investment in foraging was similar during incubation and chick-rearing, but birds spent less time resting at sea during chick-rearing. Compared to incubation, during chick-rearing adult breeders spent more time at sea, since they remain at the nest only for very short periods caring for the offspring (Catry et al., 2009). However, birds invested a great amount of time at sea foraging, as they needed to fulfil the chick requirements and at the same time maintain their own body conditions. This is probably the reason of the lower investment in resting behaviour during chick-rearing, which may entail greater physical wear compared to the other stages (Regular et al., 2014; Lewis et al., 2004).

Trip patterns and the use of the dual-foraging strategy

Our approach, based on the combination of different sources of data and statistical techniques, allowed us to underline the complexity of foraging strategies of Cory's shearwater during the breeding period. Although we recorded short and long trips in terms of distance over the three stages, we found foraging strategies composed of three different clusters during pre-laying, three different clusters in incubation and two different clusters in chick-rearing, each one characterised by a different combination of distance and time duration, together with differences in behavioural budgets and feeding resources used. Such complexity suggests that considering bimodality based solely on short or long trips may be over-simplistic since a variety of internal constraints and external conditions can lead to a diversity of foraging strategies. As model-based clustering pointed out, an apparent bimodal pattern may actually accommodate more than two clusters, i.e. foraging strategies. Therefore, using a single trip parameter alone to describe foraging strategies, or even worse, relying uniquely on data recorded at the colony, i.e., without using tracking devices, may lead to unsound assessment regarding foraging strategies.

Moreover, our approach took advantage of cutting-edge methodologies to revisit an important issue in the ecology of Procellariiformes, the dual-foraging strategy. Our results from model-based clustering and SIA point towards the same direction and give strong support to the use of the dual-foraging strategy in the terms defined by Weimerskirch (1998). Chick-rearing was the unique stage with two well-defined clusters, corresponding to short trips and long trips (in both time duration and distance). Also, SIBER indicated clear segregation between feeding resources used by parents and offspring, with adults consuming resources from the more distant African shelf, and chicks assimilating resources from the waters surrounding the Canary Islands. Previous evidence for the same species in a colony located at Selvagem Grande, an oceanic island ca. 250 km far from Gran Canaria, did not find support to the use of a dual-foraging strategy, contrary to authors' expectations (Alonso et al., 2012). They found that birds foraged in two contrasting areas (surroundings of the island and the Northwest African shelf) and that adults and chicks segregated along a gradient of oceanic-neritic waters defined by values of $\delta^{13}C$. However, they used only the trip time duration to evaluate the use of the dual-foraging strategy. Considering a multi-dimensional approach to evaluate the use of this strategy by the birds might have led to different conclusions, as discussed above.

Sea surface temperature as a cue for individual decision-making

SST has been shown to play a major role in seabird movement and distribution (e.g., Sommerfeld et al., 2015; Weeks et al., 2013). Our results, coming from different statistical approaches, agreed on the importance of SST (either temperature or gradient), highlighting the role of this environmental feature in individual decision-making in the context of foraging strategies. In contrast with warm waters, cold waters are often synonym of higher productivity and prey abundance in marine ecosystems, including prey species such as epipelagic fish (Arístegui et al., 1997; Sánchez-Garrido et al., 2019; Weeks et al. 2013). Diving seabirds, including shearwaters, have thermal adaptations to inhabit the marine environment (Oswald & Arnold, 2012; Birt-Friesenet al., 1989). Therefore, it may seem reasonable to expect that shearwaters can sense water temperature and use it as a cue of resource availability in the vicinities. In both terrestrial and marine birds, it has been shown that individuals can associate an environmental context with specific prey patterns, learning and maintaining over time the use of a contextual, environmental background cue with individual choices (Carroll et al., 2018; Hansen et al., 2010). Cory's shearwaters may learn and associate a range of sea surface temperatures with greater chances of foraging success, leading to engagement in short foraging trips when waters surrounding the islands are under a temperature threshold. Nevertheless, we acknowledge that other cues, such as olfactory clues, or social interactions, could also play an important role as has been shown for other seabird species (Abolaffio et al., 2018; Dell'Ariccia et al., 2014; Courbin et al., 2020; Jones et al., 2010). In this regard, other cues used by the birds likely covary with SST (Gawlik & Crozier, 2007).

Finally, we cannot rule out the fact that SST may increase over the breeding period simply because of higher solar heating as summer advances (Carton & Zhou, 2020). However, easterly winds blowing strongly during the summer in the Canary Islands likely contribute to blur the effect of solar heating in the sea surface (Azorín-Molina et al., 2018). Considering a multi-year framework to capture inter-annual variations in SST and winds may contribute to clarify this issue in further studies. In fact, our findings considered together with findings from previous studies suggest that the ratio of short vs long trips may vary according to annual conditions. The Canary Current is a dynamic ecosystem with high interannual variability (Navarro-Pérez & Barton, 2001). In years with strong easterly winds, nutrient-rich filaments and plumes of cold waters scape from the African shelf and reach the Canary archipelago, enhancing local productivity (Baltar et al., 2009; Moyano & Hernández-León, 2011; Sambe et al., 2016). This annual variability may support the use of the dual-foraging strategy on an optional basis, as argued by some authors (Granadeiro et al., 1998). If the annual conditions do not promote the arrival of cold waters to the islands, productivity in their vicinities will likely be lower and thus birds will tend to engage more in long trips. This fact may explain why Navarro & González-Solís (2009) did not record short trips of tracked birds during the chick-rearing stage in the same population that we studied, in contrast with our results.

Conclusions and implications for management

Understanding the drivers of individual decision-making in foraging strategies is important to advance our knowledge on the life-history of species living in dynamic environments (Becker et al., 2007). We used a multi-dimensional approach, not only regarding data source but also analytical techniques, to provide an in-depth analysis of foraging strategies used by a pelagic seabird over the different stages of the breeding period. Our results should also recall the need for addressing foraging strategies at different temporal scales, as internal constraints and external conditions can shape individuals' behaviour and therefore research performed by relying on single stages can be misleading. This is especially important in the context of identifying candidate at-sea areas for protection, a process that should rely on multi-temporal scales to encompass as much population variability as possible (Krüger et al., 2017; Oppel et al., 2018).

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SUPPORTING INFORMATION

TABLE S1 • Number of trips per bird registered with GPS in the study.

Bird identity	Sex	Pre-laying	Incubation	Chick-rearing	Total number of trips
6106934	♂	-	6	-	6
6106937	♂	-	1	-	1
6119927	♂	-	-	3	3
6119928	♀	-	-	1	1
6134549	♀	-	-	1	1
6134701	♂	-	4	-	4
6140488	♀	-	1	-	1
6140495	♀	-	1	3	4
6140719	♂	6	-	-	6
6140725	♂	5	1	6	12
6140754	♂	-	2	1	3
6140763	♀	-	-	4	4
6140785	♀	-	3	-	3
6140828	♂	-	2	-	2
6143020	♂	5	1	6	12
6143041	♂	-	1	4	5
6143080	♂	6	-	-	6
6175707	♂	-	1	-	1
6175725	♂	-	-	3	3
6175770	♀	-	2	-	2
6175776	♀	-	1	-	1
6175784	♂	-	1	-	1
6188615	♀	-	2	-	2
6195159	♂	7	3	1	11
6195171	♀	1	-	-	1
6198154	♀	6	-	-	6
6198157	♂	7	-	-	7
6198161	♂	-	1	-	1
6198253	♀	2	-	-	2
6198254	♀	3	-	2	5
6198255	♀	3	-	-	3
6198261	♀	-	1	-	1
6198263	♀	-	1	-	1
6198264	♀	-	3	-	3
6198272	♀	-	-	1	1
6198274	♂	-	-	1	1
6198276	♀	-	-	2	2
6198277	♂	-	-	1	1
6198280	♂	-	-	3	3
6198285	♂	-	-	1	1
6198300	♀	-	-	1	1
Total	**29 ♂♂ : 22 ♀♀**	**51**	**39**	**45**	**135**

Table S2 • Summary of the LMM and GLMM models to evaluate differences between sexes and breeding stages in the trip parameters. α was set to 0.05. Intercept corresponds to males in pre-laying. Model specifications are included.

Fixed-term	Estimate	Std. Error	Statistic	p-value
Response variable: Log (**Maximum distance reached** from the colony, in km)				
(Intercept)	3.701	0.199	18.614	<0.000
Females	0.274	0.234	1.173	0.251
Incubation	1.151	0.262	4.388	<0.000
Chick-rearing	1.374	0.249	5.523	<0.000
Model type: LMM				
Response variable: Log (**Total distance travelled**, in km)				
(Intercept)	4.976	0.167	29.819	<0.000
Females	0.456	0.200	2.276	0.033
Incubation	1.459	0.230	6.332	<0.000
Chick-rearing	1.64	0.220	7.448	<0.000
Model type: LMM				
Response variable: **Trip time duration** (h)				
(Intercept)	2.900	0.134	21.613	<0.000
Females	0.532	0.153	3.470	<0.000
Incubation	1.970	0.178	11.078	<0.000
Chick-rearing	1.740	0.172	10.076	<0.000
Model type: Negative binomial GLMM				

Table S3 • Rank of candidate Generalized Linear Mixed Models (GLMMs) testing for the effect of proximate environmental features and the covariates sex, bodymass before the trip and breeding stage on the probability of performing a short trip instead of a long one, sorted by corrected Akaike's Information Criterion (AICc). Explanatory variables were scaled before running the models. ΔAICc: AICc increments. Wgt: AICc weights. The best-supported models (i.e., ΔAICc ≤ 2) are shown in bold. Only models with Wgt > 0.015 are shown in this table. Relative variable importance based on Wgt indicated a greater relevance of SST gradient and 8-days mean SST (see Fig. 4 in the main text).

Intercept	SST gradient	8-days mean SST	FSLE	8-days mean CHL-a	Surface currents	Charnock index	Sex	Bodymass before trip	Breeding phase	df	logLik	AICc	ΔAICc	Wgt
0.928	**0.900**	**-1.186**	**0.741**	**1.404**				**0.481**		**7**	**-62.429**	**139.739**	**0.000**	**0.047**
-1.023	**0.893**	**-4.31**	**1.509**					**0.472**	+	**8**	**-61.791**	**140.726**	**0.986**	**0.029**
0.862	**0.798**	**-1.292**	**0.627**	**1.259**						**6**	**-64.289**	**141.235**	**1.496**	**0.022**
1.175	**0.818**	**-1.266**	**0.774**	**1.42**			+			**7**	**-63.232**	**141.346**	**1.607**	**0.021**
-0.35	**0.83**	**-4.134**	**1.534**				+		+	**8**	**-62.334**	**141.810**	**2.071**	**0.017**
0.997	0.895	-1.192	0.762	1.426			+	0.425		8	-62.39	141.922	2.183	0.016
0.924	0.912	-1.146	0.741	1.399				0.483	+	7	-63.551	141.983	2.244	0.015
0.932	0.913	-1.200	0.746	1.418	-0.056			0.486		8	-62.421	141.984	2.245	0.015
-0.339	0.797	-3.677	1.259			-0.031				8	-62.423	141.988	2.249	0.015
0.868	0.683	-1.388		0.519				0.399		6	-64.711	142.078	2.339	0.015

Table S4 • Values of $\delta^{13}C$ and $\delta^{15}N$ of specimens of potential prey species of the studied population of Cory's shearwater, collected in the Canary Islands and the Northwest African shelf. Mean values of prey grouped for SIBER are also shown. Values indicate mean ± standard deviation (‰). N indicates the number of individuals sampled.

Species	Habitat	N	$\delta^{13}C$	$\delta^{15}N$
Gran Canaria (GC)				
Fish				
Atherina presbyter	Demersal	1	-	9.9
Boops boops	Pelagic	5	-20.3 ± 0.2	8.4 ± 0.32
Engraulis encrasicolus	Pelagic	5	-20.5 ± 0.17	7.4 ± 0.19
Sardinella aurita	Pelagic	5	-20.5 ± 0.15	7.0 ± 0.21
Scomber colias	Pelagic	5	-19.5 ± 0.31	7.5 ± 0.22
Trachurus trachurus	Pelagic	5	-19.3 ± 0.29	9.5 ± 0.26
	Mean of the group - **Pelagic fish GC**		-20.0 ± 0.58	7.9 ± 1
Northwest African shelf (AF)				
Fish				
Anthias anthias	Demersal	5	-17.6 ± 0.25	11.6 ± 0.34
Dentex macrophthalmus	Demersal	5	-17.2 ± 0.2	11.8 ± 0.55
Dentex maroccanus	Demersal	5	-17.2 ± 1.11	11.9 ± 1.1
Cyttopsis rosea	Demersal	5	-18.3 ± 0.8	10.6 ± 0.7
Helicolenus dactylopterus	Demersal	5	-17.2 ± 0.4	12.4 ± 0.54
	Mean of the group - **Demersal fish AF**		-17.3 ± 0.21	11.9 ± 0.33
Macroramphosus gracilis	Pelagic	5	-17.6 ± 0.28	9.6 ± 0.26
Macroramphosus scolopax	Pelagic	5	-17.8 ± 0.8	10.3 ± 0.65
Merluccius merluccius	Pelagic	5	-18.1 ± 0.24	10.2 ± 0.4
Myctophidae	Pelagic	10	-18.0 ± 0.5	10.0 ± 0.5
Scomber colias	Pelagic	15	-18.3 ± 0.9	8.4 ± 0.35
Setarches guentheri	Pelagic	5	-18.4 ± 0.56	10.8 ± 0.48
Trachurus picturatus	Pelagic	15	-18.5 ± 0.59	10.2 ± 0.29
Trachurus trachurus	Pelagic	30	-17.5 ± 0.87	10.4 ± 0.45
	Mean of the group - **Pelagic fish AF**		-18 ± 0.38	10 ± 0.73
Crustaceans				
Macropipus rugosus	Nektobenthic	3	-16.2 ± 0.18	11.1 ± 0.65
Parapenaeopsis atlantica	Nektobenthic	5	-16.9 ± 0.64	9.4 ± 1
Parapenaeus longirostris	Nektobenthic	5	-17.0 ± 0.19	9.2 ± 0.31
Plesionika ensis	Nektobenthic	5	-16.9 ± 0.52	8.7 ± 0.82
Plesionika heterocarpus	Nektobenthic	5	-15.5 ± 0.53	9.4 ± 0.7
Cephalopods				
Abralia veranyi	Pelagic	5	-16.7 ± 0.14	11.4 ± 0.27
***Sepia* sp.**	Demersal	4	-16.6 ± 0.67	9.3 ± 0.66
	Mean of the group - **Crustaceans & Cephalopods AF**		-16.5 ± 0.52	9.8 ± 1.04

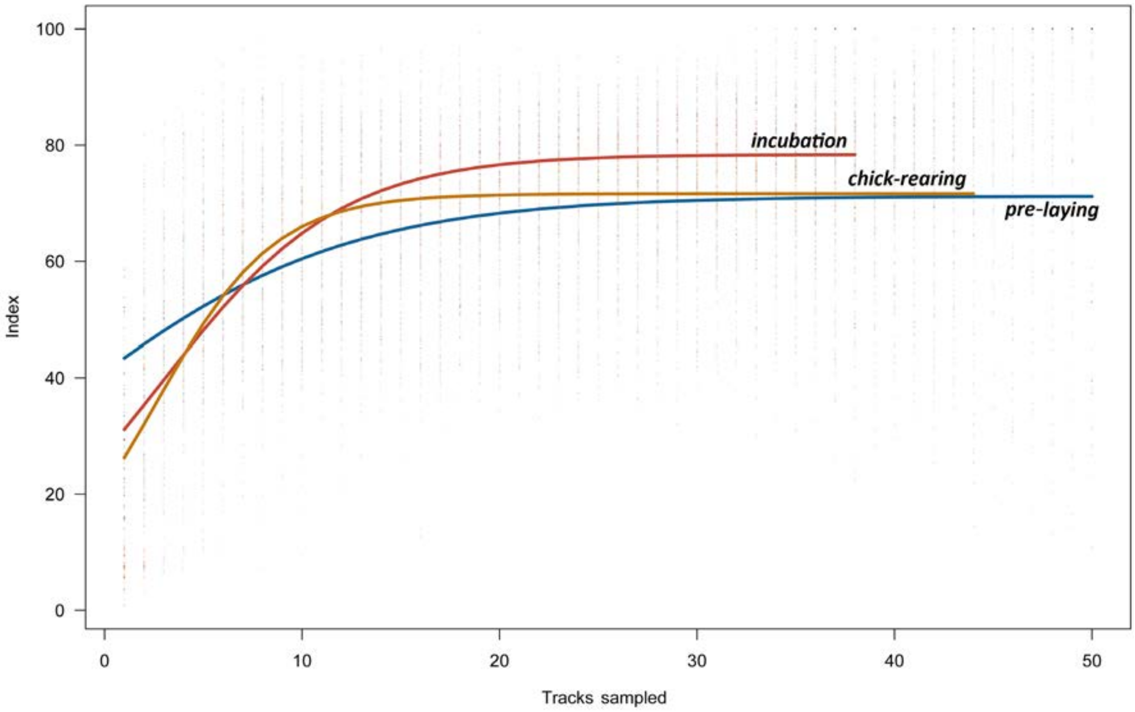

FIGURE S1 • Representativeness analysis of GPS tracking data. Data from all three breeding phases reached the asymptote, suggesting that the number of trips recorded was sufficient to capture population patterns.

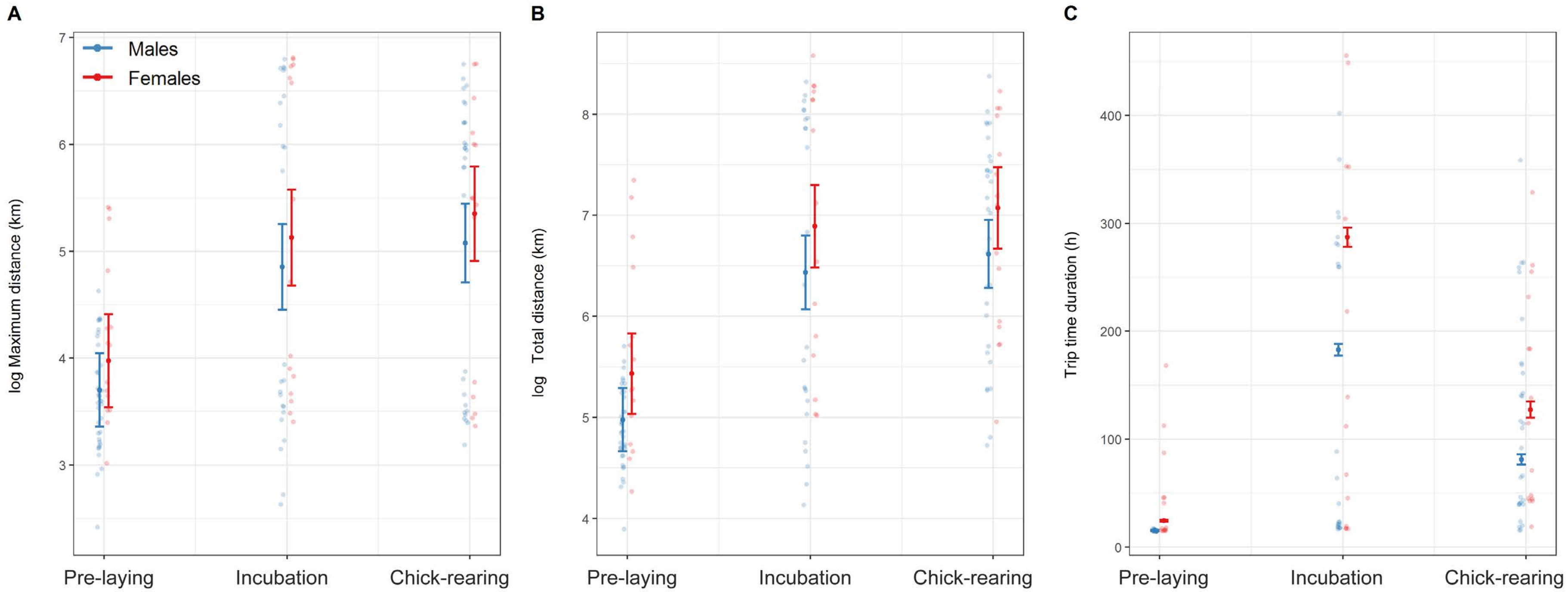

FIGURE S2 • Marginal estimates of trip parameters in relation to sex and breeding stage, estimated through Linear Mixed Models. (A) Maximum distance reached from the colony. (B) Total distance travelled. (C) Trip time duration. Solid dots represent means and bars represent the associated 95% CI. Soft dots represent raw data with some jittering applied to ease visualization.

Chapter V

Seabird remote-tracking as a tool for adaptive management in the Spanish National Park Network

Chapter V is an English version of the book chapter:

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SEABIRD REMOTE-TRACKING AS A TOOL FOR ADAPTIVE MANAGEMENT IN THE SPANISH NATIONAL PARK NETWORK

ABSTRACT

The footprint of human activities in the oceans is increasing. To reverse its negative effects, several laws and regulations have been established, both at European and State levels. This legislative framework advocates the need for adaptive management within an ecosystem-based framework to preserve important natural areas. In this regard, sentinel species have been proposed as a tool, as their long-term monitoring may help to assess management. Here we propose the use of the Cory's Shearwater *Calonectris borealis* and the Scopoli's Shearwater *C. diomedea* as sentinel species for the adaptive management in the Spanish National Park Network since their movements and behaviour can provide insights into the environmental status of marine ecosystems and within Marine Protected Areas. These species breed in three parks of the National Park Network: Cabrera, Timanfaya and Islas Atlánticas. We monitored adult breeders at the breeding colonies, recorded their movements through GPS tracking, and studied their trophic ecology using conventional and isotopic diet analyses. We found the individuals to intensively use waters within the boundaries of the protected areas and vicinities, both to rest and forage. Their movements also extended beyond the limits of these protected areas, reaching important nutrient-rich waters at a large ecosystem scale. We suggest the utility of seabird remote-tracking as a tool for the management of marine protected areas and provide the first data on movement and behaviour of pelagic seabird species breeding in the Spanish National Park Network as a required first step towards such goal.

Keywords

Sentinel species • GPS • Marine Protected Areas • stable isotopes analysis •
Cory's • Scopoli's shearwater.

INTRODUCTION

Mounting evidence currently shows a real impact of the human activities on marine ecosystems, modifying their physical functioning and altering ecological networks. Overfishing, pollution, eutrophication or coastal degradation are among the many activities with a significant negative impact on marine ecosystems and their biodiversity (Halpern et al., 2008; Halpern et al., 2015). At a European level, the Marine Strategy Framework Directive (EU, 2008; Sardá et al., 2017) aims to reverse this trend and recover the good environmental status of the marine environment. In Spain, the Law for the Protection of the Marine Environment (41/2010) transposes this regulation and establishes the guidelines for the management of the marine environment. This regulatory framework highlights in the article 4 the importance of the Adaptive Management and the ecosystem-based approach to guarantee the achievement of the good environmental status of the marine environment (B.O.E., 2010). Ecosystem-Based Management requires a thorough knowledge of ecosystems and the species that inhabit them (Pikitch et al., 2004; Leslie et al., 2007; Curtin et al., 2010; Sardá et al., 2017). Moreover, adaptive management requires efficient long-term monitoring programs, which implies taking high-quality data regularly over long periods, to periodically evaluate the effectiveness of the management measures applied and adapt them based on the pieces of evidence found (Salafsky et al., 2001).

Sentinel species, i.e. species that can function as early warning indicators of environmental changes, has been proposed as a tool to be integrated into the framework of the adaptive management (Dale & Beyeler, 2001; Constable & Doust, 2009). Monitoring sentinel species can assist in the design of conservation and management measures of the marine environment (Hooker & Gerber, 2004; Sergio et al., 2006). Top-predators stand out as sentinel species (Aguirre & Tabor, 2004; Sergio et al., 2008). Their position at the top of the food webs makes them highly sensitive to any alterations in the marine environment, no matter the natural or anthropogenic origin of such alterations (Heithaus et al., 2008; Piatt et al., 2007; Wanless et al., 2007; Einoder, 2009). Seabirds, as top-predators inhabiting marine ecosystems, are suitable as sentinel species due to some particular life-history traits: (i) they integrate ecological processes that occur at lower trophic levels, (ii) unlike other marine predators, they are conspicuous and visible out of the water, (iii) they feed at sea but are bounded to land for breeding, which facilitates monitoring, (iv) they breed colonially and are relatively easy to sample, and (v) their movements and behaviour respond rapidly to environmental changes in dynamic environments (Parsons et al., 2008; Grémillet, 2010; Oswald & Arnold, 2012; Elliot & Elliot, 2013).

Recent advances in remote tracking technologies allow nowadays to study the movements of different seabird species in an unprecedented way (López-López, 2016). Weight decrease and price drop in recent years in addition to an increase in spatial accuracy and temporal resolution have led altogether to blooming in animal movement research (Kays et al., 2015; Wilmers et al., 2015). Seabirds constitute one of the animal groups where this advance has been more noticeable (Burger & Shaffer, 2008, Wilson & Vandenabeele, 2012). Both the ability to know in detail their movement and behaviour and a good knowledge of their natural history have enhanced the suitability of seabirds as a tool for management and as sentinel species (Lescroël et al., 2016).

The use of seabirds as a tool to identify relevant marine areas to be protected, as well as to validate the effectiveness of boundaries, is a growing trend worldwide (Hyrenbach et al., 2000; Péron et al., 2013; Grémillet et al., 2014, Arcos et al., 2012). Moreover, seabirds are in a global decline, with 30% of species listed as threatened (Croxall et al., 2012), hence any new knowledge about their biology can contribute to inform or improve conservation measures. However, the use of seabirds as sentinel species is still rare within the set of monitoring tools in the context of management and planning of established protected areas, particularly in Spain. The Spanish National Park Network (SNPN) is a national agency aiming to protect and manage protected the areas with the highest level of protection level in Spain, the National Parks (NP), with exceptional value in terms of natural systems and biodiversity. Among the pelagic seabird species breeding in the SNPN, the Cory's Shearwater *Calonectris borealis* and the Scopoli's Shearwater *C. diomedea* are the best-represented species in the SNPN. As a first step to use seabird remote tracking data as a tool to inform management in the mid to long term, it is necessary to know the movements and behavioural patterns of the model species. However, this knowledge is almost inexistent within the SNPN (but see SEO/Birdlife, 2014).

The present study aims to fill this gap, providing detailed information on the distribution, movements, behavioural patterns and trophic ecology of Cory's and Scopoli's shearwaters breeding in the SNPN. Moreover, by providing maps and other visual tools within an analytical framework, we wanted to illustrate, as a proof-of-concept, the steps to boost a seabird tracking program that can serve as a tool to inform management actions in protected areas over time. More specifically, we aimed to: (i) characterise the spatial distribution, movement patterns and behavioural strategies of Cory's and Scopoli's shearwaters in the SNPN during the breeding season, (ii) evaluate the inter-annual consistency of the areas used, (iii) identify the environmental features modulating their at-sea distribution, and (iv) evaluate the trophic resources used during the breeding season.

MATERIAL & METHODS

Model species

The Cory's shearwater is a medium-sized, long-lived, pelagic seabird. The species feeds on small epipelagic fish and cephalopods. It forages mainly in neritic zones, although can also forage over oceanic waters. It breeds colonially in coastal cliffs in islands and islets. The breeding season takes place from May to October, when they raise only one chick per year, although adults do not attempt to breed every year. After the breeding season, all individuals migrate to the wintering areas spread over the Atlantic Ocean, some of them even reaching the Indian Ocean (González-Solís et al., 2007). The taxonomic status of the species has recently been modified. The previously considered subspecies taxa were split into two distinct species (Gómez-Díaz et al., 2006; Gómez-Díaz et al., 2009; Sangster et al. 2012): Cory's shearwater *Calonectris borealis* (CSH hereafter) and Scopoli's shearwater *C. diomedea* (SSH hereafter). CSH breeds mainly in the archipelagos of Azores, Madeira and Canarias, while SSH breeds in the Mediterranean archipelagos. See a review on the biology of these species in Reyes-González & González-Solís (2016a, 2016b). Spanish populations are considered in regression, although the decline is most noticeable in SSH (Sanz-aguilar et al., 2016; Genovart et al., 2017), which is listed as "Vulnerable" in the National Catalogue of Threatened Species (B.O.E., 2011) and "Endangered" in the Red Book of the Birds of Spain (Carboneras, 2004).

Study area

We carried out fieldwork in the three National Parks (NP) of the current SNPN that hold breeding colonies of the model species within their boundaries:

- Maritime-Terrestrial NP of the Cabrera Archipelago (hereafter CABR), which holds colonies of SSH. We tagged individuals from the colonies located on the islets of Na Pobra and Na Foradada. The most recent estimates indicate between 125 pairs (Mas & Muntaner, 2015) and 356 pairs (Arcos et al., 2009) in CABR.
- Timanfaya NP (hereafter TMFY), which holds colonies of CSH. We tagged individuals from the colony located in coastal cliffs of El Mojón. The colony was estimated in 650-750 breeding pairs (Arcos et al., 2009).
- Maritime-Terrestrial NP of the Atlantic Islands of Galicia (hereafter CIES), which holds a small breeding colony of CSH. This colony was established naturally in 2008 in the northern cliffs of Monteagudo Island. Between 2008 and 2013 less than 20 nests apparently occupied were located, and breeding was only confirmed in 2013 (Munilla et al., 2013; Munilla et al., 2016).

GPS tracking and blood sampling

We visited the breeding colonies in August and September in 2015 and 2016 (CIES only in 2015), during the chick-rearing period. We visited the colonies at night when the adults return from the sea to feed their chicks. Individuals were captured by hand or using tools designed for this purpose. All adult and chicks captured were ringed and measured. We tagged adult breeders in accessible nests. We used GPS tracking devices (Perthold Engineering ©, Germany) previously adapted for waterproofing. Devices were set to record a location every 5 min. We never tagged both members of the same couple simultaneously. The total weight of the devices used was ~25 g, below the weight threshold recommended for most seabird species (3-5%; Phillips et al., 2003). We attached devices to the mantle feathers on the bird's back, using a waterproof adhesive tape (TESA ©). This method allows the device to drop off after 2-3 weeks in case the bird is not recaptured. The minimum tracking time before recapture was 6 days. At every recapture, we recovered the device, weighed the bird, and took 2 ml of blood from the tarsal vein for further analysis. All fieldwork and instrumentation followed corresponding authorizations from the competent administrations and organisations. All the birds were processed following the guidelines of good practice for animal research of the European legislation.

GPS data processing

We performed the analyses with custom-built functions and specific libraries of the R programming environment (R Core Team, 2018). We split tracks recorded by GPS devices into separate foraging trips, i.e., considering a different trip the section of a track from the moment the bird left the colony to the moment it returned (Birdlife International, 2004). We carried out a representativeness analysis to evaluate whether the sample size of trips recorded for every colony each year was sufficient. To do so, we calculated the rate of increase in the maximum movement range reached at the population level (represented by the 95% probability contour of Kernel Density Estimation, K95) in relation to the increase in the number of sampled individuals (see a similar approach in Lascelles et al., 2016). We calculated the total distance travelled, the maximum distance reached from the colony, and the total duration as descriptive parameters of the trips. Given the multimodal nature of the foraging trips, we calculated median values and their respective 95% confidence intervals using bootstrapping techniques. To characterize the foraging strategy, we applied a hierarchical clustering method, using as input variables maximum distance reached from the colony and total trip duration because these two variables were not correlated. We used the EMbC algorithm to identify individual behaviours along every trip (Garriga et al., 2016). Briefly, this algorithm identifies and assigns to every GPS location one out of four basic behaviours, according to the values of speed and turning angle: resting, intensive search, extensive search and relocation. Intensive and extensive search correspond to foraging, while relocation corresponds to straight and sustained flight. To visually inspect the daily patterns of behaviours, we used General Additive Mixed Models (GAMM), which allow modelling non-linear effects (mgcv library in R, Wood & Augustin, 2002). To evaluate the relative importance of waters in the vicinities of the NP, we calculated for every colony and year the percentage of time invested in each behaviour in a circular grid of 100 km radius from the colony. To characterize and map bird distribution, we used bivariate Gaussian Kernel Density Estimations (KDE hereafter; Worton, 1989). We calculated KDE at the population level for every NP, behaviour and year, using the adehabitatHR library in R (Calenge, 2006). We set a bandwidth value of h=0.01. We characterised the commuting flight pathways between breeding colonies and foraging areas as trip sections where GPS locations labelled as relocation summed up a continuous duration of 60 minutes at the minimum. We evaluated inter-annual consistency in the areas used in TMFY and CABR. To do so, we used the Bhattacharyya affinity index, which can range between 0 (no spatial overlap) and 1 (complete overlap between both areas), using the kerneloverlap function in the adehabitatHR R package. We calculated the overlap for KDE contours of 50% and 95% (K50 and K95 respectively). As a required previous step to overlap calculations, we transformed K50 and K95 to the Lambert-Equal Area projection centred on the corresponding colony. To evaluate the relative contribution of environmental features influencing bird distribution, we modelled distribution using the maximum entropy algorithm MAXENT (Elith, 2011). The selection of geographical and environmental variables as input was based on previous literature highlighting their relevance in seabird distribution (Louzao et al., 2011). We used as static variables (1) the distance from the colony, (2) the bathymetry, and (3) the slope, and as dynamic variables (4) the primary productivity and (5) its gradient, (6) the sea surface temperature and (7) its gradient, and (8) the wind strength. Temperature and productivity gradients are indicators of areas of high productivity, such as oceanic gyres, upwellings and fronts. We calculated these gradients by measuring the proportional rate of change in a three-cell side moving window. We downloaded monthly average values of these variables from the ERDDAP platform website with a spatial cell resolution of 0.04º (https://coastwatch.pfeg.noaa.gov/erddap/). Before running MAXENT, we evaluated the correlation between the predictive variables using the Variance Inflation Factor (VIF) with a threshold value of 10 (vifstep function from the usdm R library; Naimi et al. 2014). We estimated the influence of all the variables on bird distribution in both linear and quadratic terms. We estimated the relative contribution of each variable using the Jackknife test. Our model species are central place foragers, that is, adult breeders need to return to the nest frequently to feed the chick during the breeding season. Adult breeders use short trips near the colony frequently, to provide food to their chick, whereas engage less frequently in long trips to reach more distant foraging grounds for self-feeding (Granadeiro et al., 1998). Therefore, including the distance from the colony as an input variable may bias model inference because of a higher set of GPS locations occurring in the vicinity of the colonies. To avoid this possible bias, we re-run the models without "distance from the colony" when this input variable had the highest relative contribution and evaluated whether the relative contribution of the other variables changed.

Trophic ecology

We investigated trophic ecology by conventional diet analysis and stable isotope analysis. During the fieldwork sampling, prey spontaneously regurgitated by the birds was collected and stored. These samples were preserved for later identification at the lab in the University of Barcelona, based in a reference collection of otoliths and scales from fish and cephalopod beaks. From the regurgitates, we evaluated the percentage of occurrence and frequency of each prey species identified. As a complementary technique, we used Stable Isotope Analysis (SIA), using Carbon (δ^{13}C) and Nitrogen (δ^{15}N) from the blood plasma of birds (Cherel et al., 2005). Plasma turnover rate integrates the diet of the 4-10 days before blood collection, which corresponds approximately to the average duration of a foraging trip. After each fieldwork session, we centrifuged blood samples collected to separate the blood plasma and froze them. Later, once in the lab, the plasma samples were freeze-dried for 24 hours at a pressure and temperature close to 0mBar and -50ºC. Once they were dry, we performed lipid extraction. We homogenized the lyophilized and lipid-free samples and weighed between 0.25 and 0.30 mg of each sample in a Mettler Toledo MX5 model microbalance. These samples were placed in tin capsules for combustion. Using a continuous flow mass spectrometry (CF-IRMS) we obtained the percentages of content and isotopic values of δ^{13}C and δ^{15}N. Isotope values are expressed in parts per million (‰) according to the following equation:

$$\delta X = (R_{sample}/R_{standard} - 1) * 1\,000$$

where δX corresponds to δ^{13}C or δ^{15}N, expressed in ‰ and R_{sample} corresponds to the ratio $\delta^{13}C/\ \delta^{12}C$ or $\delta^{15}N/\ \delta^{14}N$, related to the standard values (Subtract). The $R_{standard}$ values are the Vienna-Pee Dee Belemnite (V-PDB) and the atmospheric nitrogen (AIR) for carbon and nitrogen respectively. To calibrate the system and to compensate for any deviations over time, we inserted international standards in every previously weighed 12 samples. Replicated analyses of the standards indicated a sampling error of ± 0.1‰ for δ^{13}C and ± 0.2‰ for δ^{15}N, although these values are probably underestimated for complex organic compounds such as plasma (Roscales et al., 2016). During the fieldwork period, we also collected potential prey from fishermen at harbours of Mallorca (near CABR) and Lanzarote (near TMFY). From these prey, and from those obtained from regurgitates, we obtained the values of δ^{13}C and δ^{15}N in muscle, following the protocol described above. We grouped the different types of prey collected into functional groups representing the potential feeding sources for the shearwaters. The mean values and standard errors of the isotopic values for each functional group allow for the representation of the different potential prey sources in a two-dimensional isotopic space (namely isospace) of the two elements, δ^{13}C and δ^{15}N, together with the consumers. We were interested in estimating the relative contribution of each functional group of prey to the birds' diet using Bayesian isotope mixing models (simmr library of R; Parnell, 2016). For this approach it is mandatory a well-spread distribution of the isotopic values of potential prey in the isospace, that is, the set of potential feeding sources should form a well-defined polygon in the isospace, within which consumers should ideally be found. After exploratory analyses, we found that, according to the geometry obtained, our samples were not appropriate for a diet reconstruction of the shearwater populations studied. Hence, we limited the work to using δ^{13}C and δ^{15}N from the bird plasma to study trophic position and isotopic niche width. To do so, we calculated standard ellipses (the bivariate equivalent of the standard deviation) for each year in CABR and TMFY, and estimated their width and position in the isospace using the SIBER package in R (Jackson et al., 2011). The area of the standard ellipses, calculated by Bayesian methods, is related to the isotopic niche width, which can be used as an approximation of the isotopic niche of a population.

Results

Representativeness of the sampling

Overall, we carried out 215 nights of fieldwork in the two years. At CABR, we ringed and measured 62 and 43 adults of SSH in 2015 and 2016, respectively. Additionally, we also ringed 25 and 43 chicks, along with the recapture and reading of rings from 75 birds that were already ringed. We tagged 48 and 45 birds with GPS in 2015 and 2016, respectively, from which we recovered devices from 41 and 45 birds, respectively. In TMFY, we ringed 67 adults and 37 chicks between 2015 and 2016, in addition to locating 18 already ringed. We tagged 36 and 33 individuals in 2015 and 2016, from which we recovered devices from 29 and 33 individuals, respectively. At CIES, given the small population size and the logistical difficulties derived from its inaccessible location, topography, and local meteorology, fieldwork was only carried out during 2015. We handled a total of 12 individuals, from which five were already ringed birds. The presence of chicks was only confirmed in 11 nests. We tagged seven birds, and recovered four devices, although one of them did not record information. Overall, we recorded a total of 551 foraging trips in CABR, 347 in TMFY, and 16 in CIES, with a total of 359 751 GPS locations (Table 1). The analysis of representativeness indicated that representative sample size was achieved for CABR and TMFY, but not for CIES (Figure 1).

Table 1 • Sample size recorded for every breeding colony, i.e., National Park.

Breeding colony	Year	GPS locations	Individuals tracked	Trips recorded
CIES	2015	8 358	3	16
CABRERA	2015	82 730	32	219
	2016	112 041	45	332
TIMANFAYA	2015	39 249	29	176
	2016	117 373	33	171

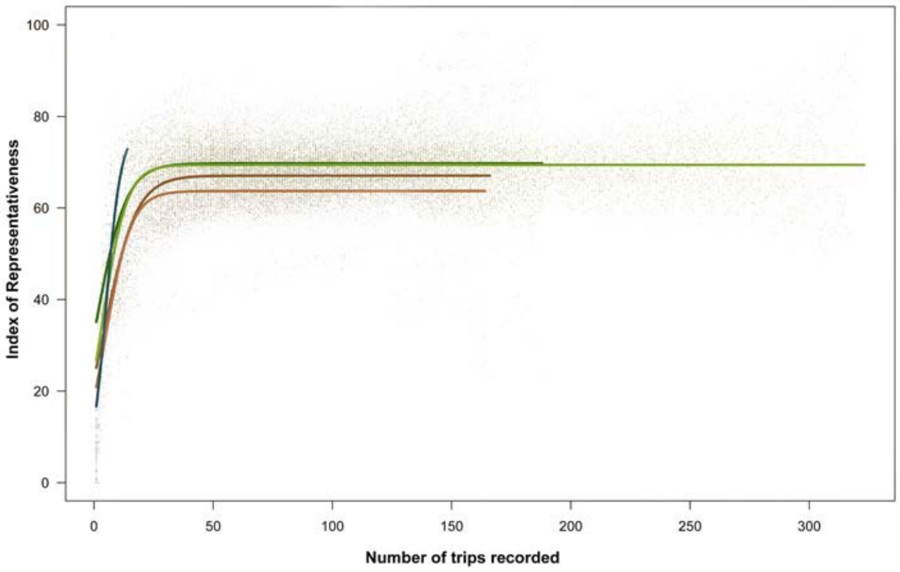


Figure 1 • Representativeness of the trips sampled in the study. Each colour identifies a different year and National Park: Cabrera 2015 (dark green), Cabrera 2016 (light green), Timanfaya 2015 (light brown), Timanfaya 2016 (dark brown) and Cíes (blue). Each curve represents the increment in maximum movement range for each group at a population level, as the sample size is increased sequentially. When the curves stabilise at a value in the Y-axis, indicates that the sample size is representative enough of the movement behaviour of the sampled population

Spatial distribution and behavioural patterns

The maximum distance from the colony was reached by birds from TMFY, followed by CIES and CABR, while the maximum trip duration was achieved by birds from CIES (Figure 2; Table 2; Table 3). In the three NP the birds exhibited a bimodal pattern in their foraging trips, performing sequences of several short trips with less frequent interspersed long trips (Figure 3). SSH from CABR intensively used the waters over the shelf to the south and west of Mallorca as foraging areas. Also, they engaged in long trips towards the Spanish mainland, from the coasts of Barcelona to the north, to the Gulf of Valencia to the south. Nevertheless, they mainly foraged off the coast of Garraf (Barcelona), and in the Ebro Delta shelf-slope (Figure 4). Some individuals travelled to the North African coast. In the vicinity of CABR (100 km radius), SSH exploited the area over the slope off the south-east of Mallorca (Figure 5). CSH from TMFY intensively exploited the waters around Lanzarote and Fuerteventura islands during their short foraging trips. They also travelled to the Conception Bank and the seamounts to the north of the Chinijo archipelago, in the north of the Canary Islands. Birds also performed longer foraging trips to the African shelf, reaching Cape Aguer in Morocco to the north and Cape Dakhla to the south (Figure 4). Within a radius of 100 km from the breeding colony, resting and foraging behaviours were concentrated near TMFY and to the north and west of Lanzarote (especially in 2015). CSH engaged more in relocation behaviour to the south ("Estrecho de la Bocaina") in 2015, and to the north in 2016 (Figure 5). Finally, CSH from the small colony in CIES moved mostly around the "Rías Baixas" area, over the continental shelf and slope off Galicia and Portugal coasts, reaching up to 200 km south from Vigo. Birds also performed long foraging trips up to 500 km from the colony, reaching oceanic waters to the north-west and west (Figure 4). Birds made intense use of the waters nearby the colony (Figure 5), although they did not make more intensive use of any particular area within 100 km radius around the colony (Figure 6).

Regarding daily behaviour, birds showed a similar pattern in all three NP, with no remarkable differences between years (Figure 7). Resting took place mostly at night and during the central hours of the day (the latter especially in CABR). Relocation behaviour took place mostly around sunset and sunrise. Greater investment in extensive search coincided with a lower investment in resting. Finally, the percentage of time invested in intensive search behaviour was generally similar along the day (Figure 7).

Inter-annual consistency and environmental drivers of distribution

The overlap between areas used at a population level was similar in 2015 and 2016 for both CABR and TMFY (~50% overlap for K50 and ~75% for K95) (Table 4). Regarding environmental features, the distance from the colony and the bathymetry had the highest contribution in explaining the distribution of birds from CABR in 2015, with a negative relationship (the greater the distance and depth, the lower the probability of occurrence). In 2016, however, wind strength also played an important role. When we removed the distance from the colony from the model, the relative contribution of wind strength became very relevant in the two years. The effect of winds strength was not linear, that is, intermediate values had a positive relationship whereas very low or very high values had a negative relationship. The contribution of wind strength was double in 2016 compared to 2015. In the case of TMFY, bathymetry had the highest contribution (highest probability of presence at lower depths), while the rest of the variables, including the distance from the colony, had negligible influence. Finally, in CIES, the distance from the colony had the highest contribution, although after removing this variable the depth gradient became the most important predictor, followed by sea surface temperature and wind strength (Table 5).

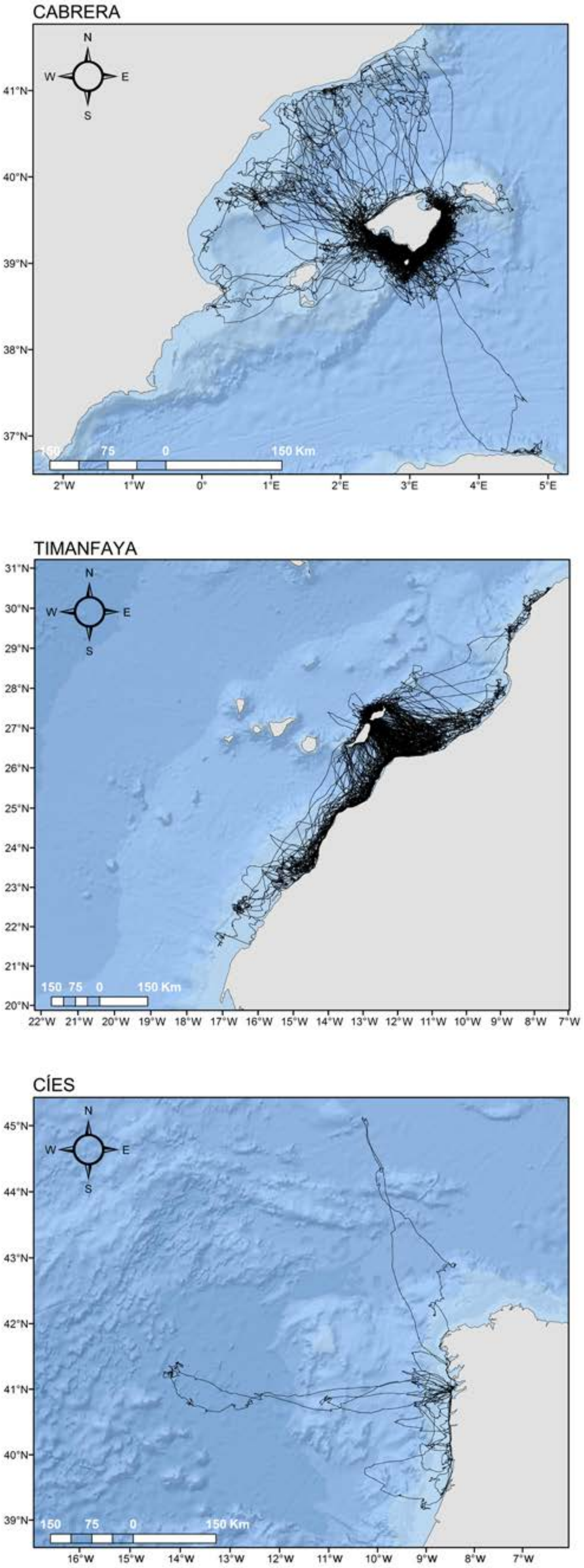


Figure 2 • General view of the recorded trajectories. From top to bottom: Cabrera, Timanfaya and Cíes.

TABLE 2 • Statistics (mean, median and confidence interval CI 95%) of trip parameters, estimated by bootstrapping.

Breeding colony	Year	Total distance travelled (km)	Maximum distance (km)	Total trip duration (h)
CIES	2015	570.41; 269.5 (199.7 - 701.0)	159.21; 88.43 (53.9 - 168.9)	51.39; 24.89 (17.6 - 67.2)
CABRERA	2015	215.91; 142.29 (131.8 - 159.6)	44.31; 32.36 (27.7 - 35.4)	35.45; 22 (21.1 - 22.7)
	2016	219.96; 153.75 (139.3 - 162.3)	56.78; 42.79 (36.7 - 47.1)	28.61; 19.43 (19.0 - 19.9)
TIMANFAYA	2015	507.77; 273.83 (216.0 - 381.8)	137.05; 109.48 (44.4 - 146.9)	47.93; 21.6 (19.2 - 24.8)
	2016	505.17; 336.7 (223.0 - 455.6)	143.99; 116.36 (63.3 - 149.4)	44.63; 21.34 (19.3 - 38.5)

TABLE 3 • Maximum values recorded in trip parameters.

Breeding colony	Year	Total distance travelled (km)	Maximum distance (km)	Total trip duration (h)
CIES	2015	1 731.08	514.25	165.49
CABRERA	2015	1 594.03	269.14	280.44
	2016	1 452.51	306.47	167.93
TIMANFAYA	2015	2 757.29	831.16	232.50
	2016	2 842.00	715.01	246.90

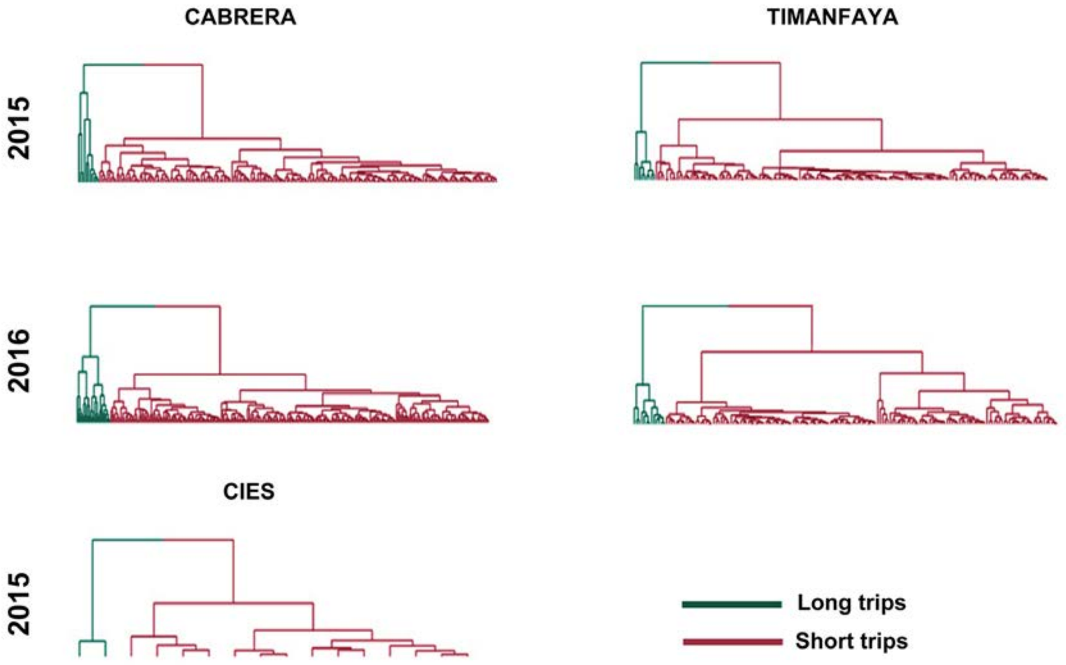
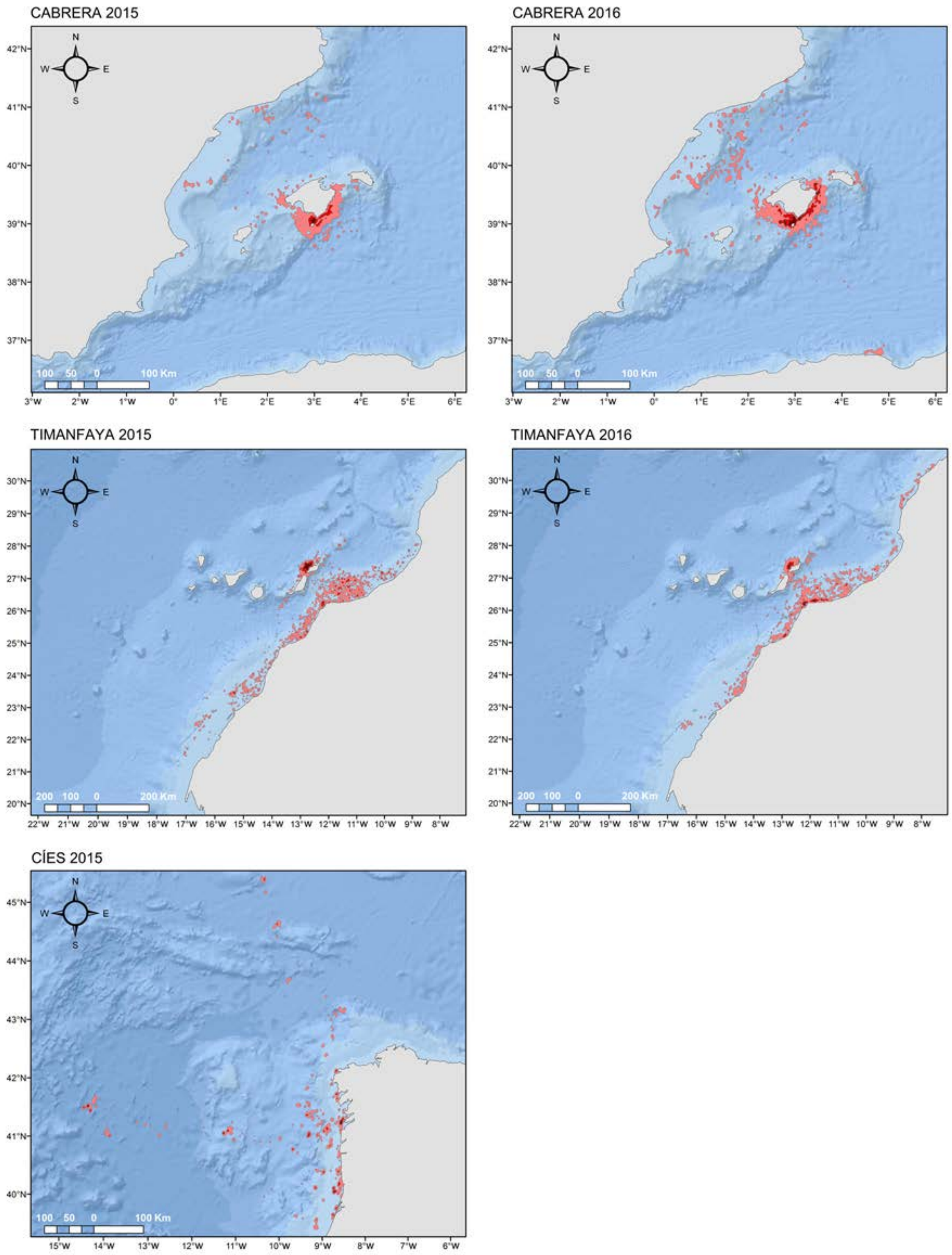


FIGURE 3 • Hierarchical classification dendrograms based on trip duration and maximum distance for each National Park and year. Each of the terminal branches represents a foraging trip. In all cases, the division in two types of trips was clear, indicating the existence of a bimodal pattern of frequent short trips and interspersed, less frequent long trips, which likely corresponded to a dual foraging strategy.



CABRERA 2015

CABRERA 2016

TIMANFAYA 2015

TIMANFAYA 2016

CÍES 2015

Figure 4 • Foraging areas, i.e. areas congregating search behaviour. Stronger to softer colour intensities correspond to 25%, 50% and 95% probability contours from the Kernel Density Estimations.

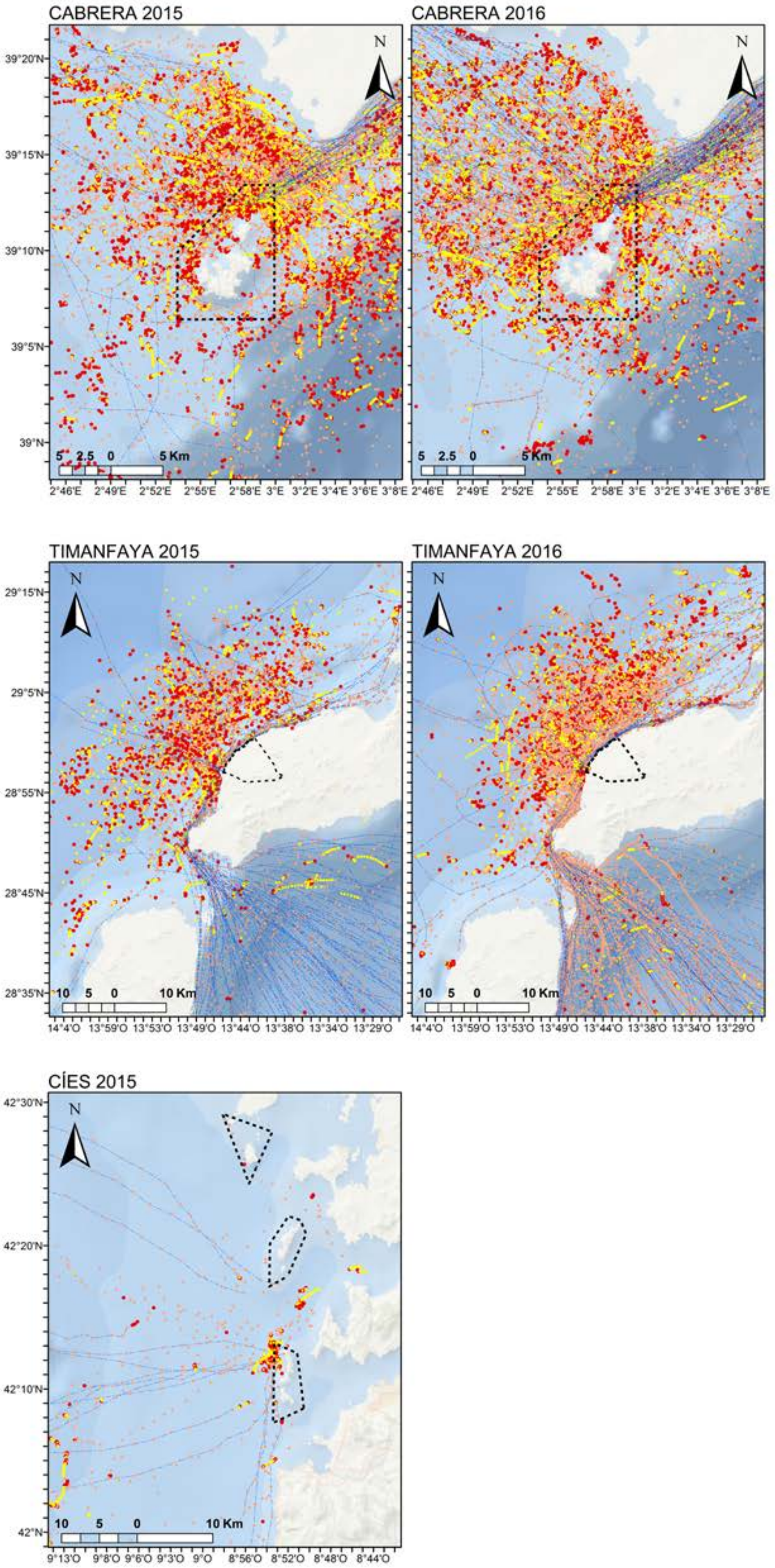


Figure 5 • GPS locations of shearwaters within the National Park boundaries or in waters nearby. Locations in yellow correspond to resting behaviour. Locations in red correspond to intensive search behaviour. Locations in pink correspond to extensive search. Dashed lines represent relocation. Black dashed lines represent the borders of the National Parks.

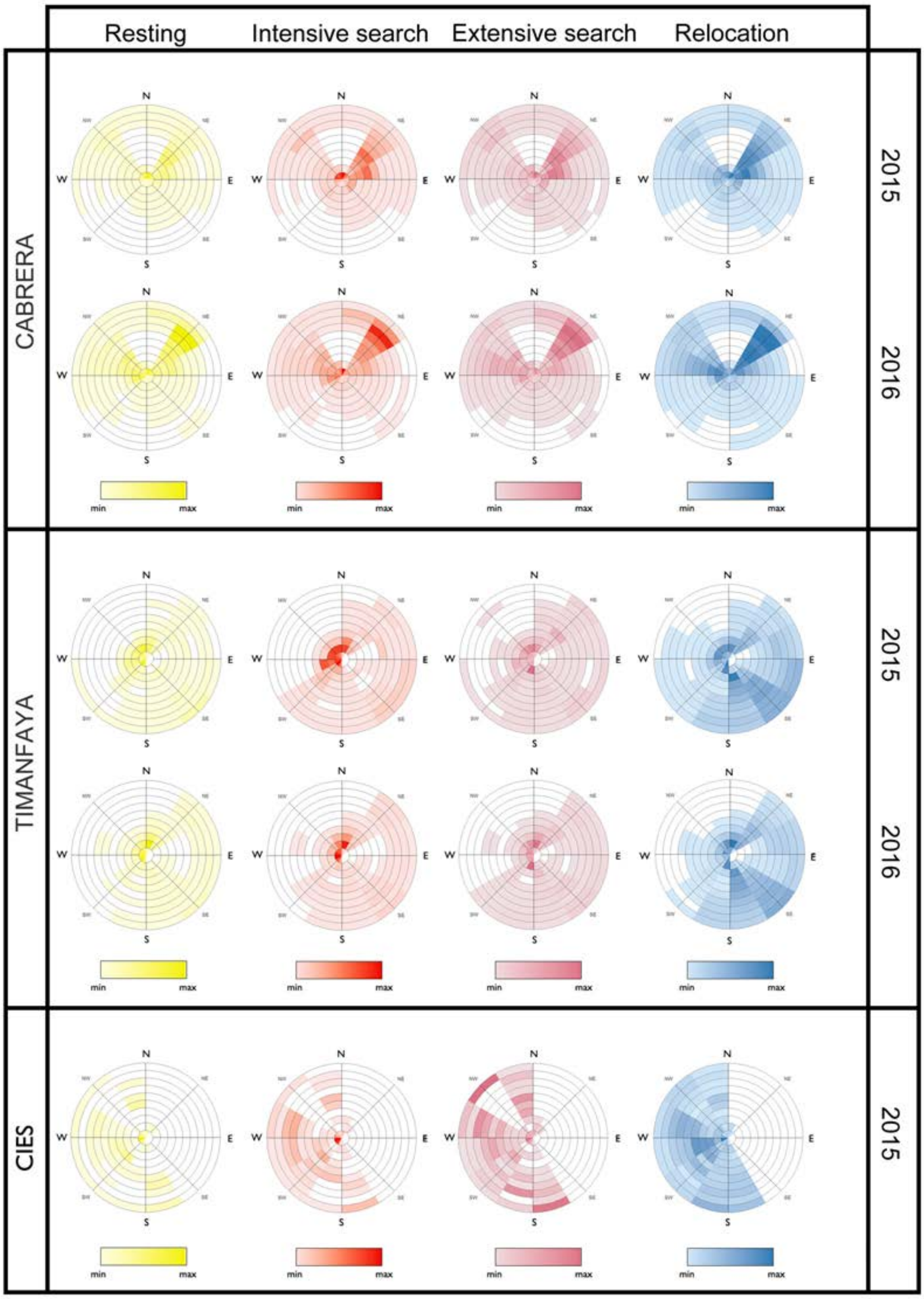


Figure 6 • Circular plots representing the relative importance of each sector for each of the behaviours obtained through the EMbC algorithm (Garriga et al., 2017) in a circular grid of 100 km radius of each National Park. Each colour represents one behaviour. A higher intensity in the colour gradient reflects a greater amount of time spent in a behaviour.

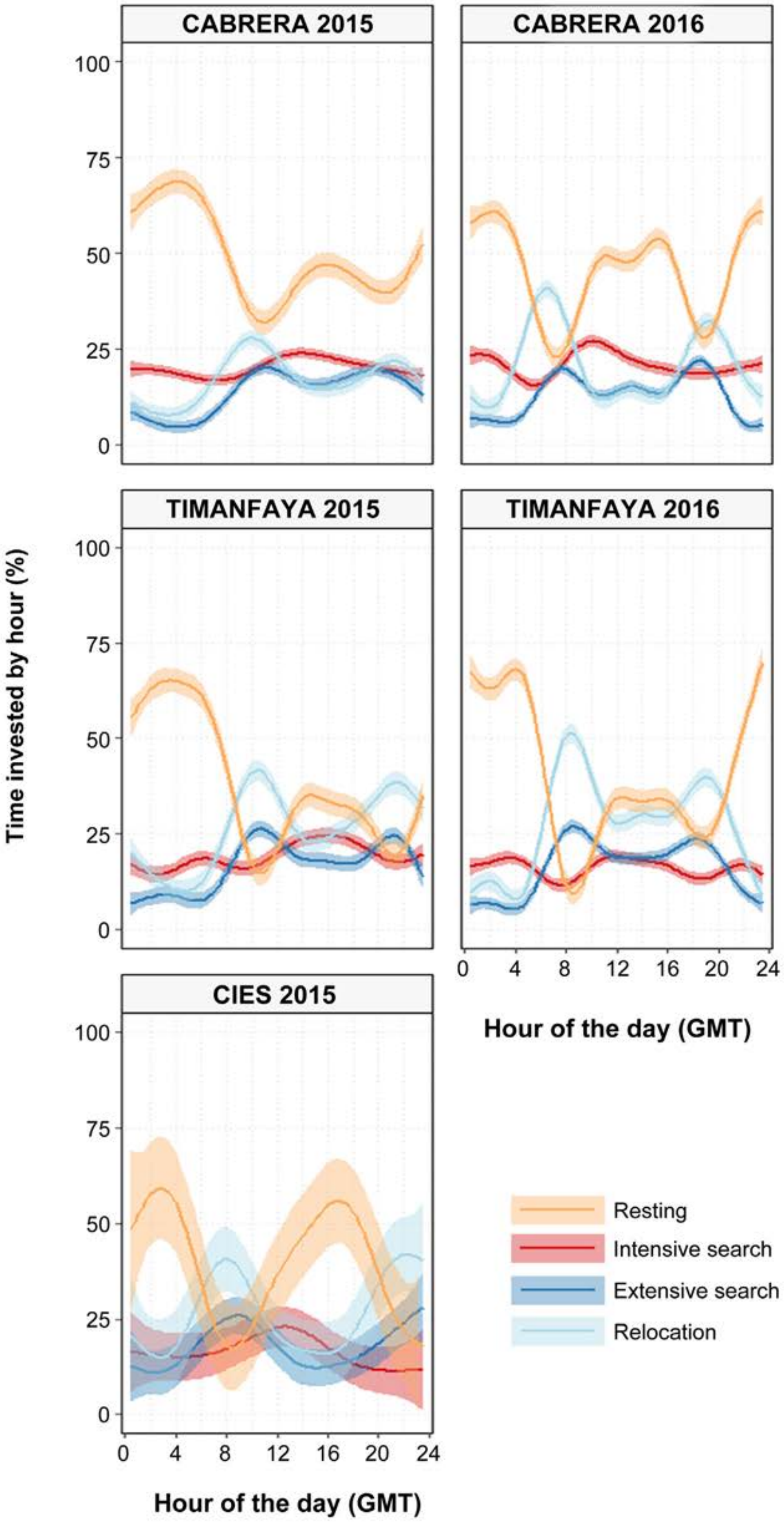


FIGURE 7 • GAMM illustrating the time invested in each of the 4 behaviours obtained through the EMbC algorithm (Garriga et al., 2017). Each box corresponds to a National Park and year, and each colour identifies a behaviour. Darker central lines represent the mean and shaded areas the 95% Confidence Intervals for each behaviour throughout the day. The smaller sample size in CIES caused wider confidence intervals.

Table 4 • Percentage of between-year overlap of used areas, estimated through the Bhattacharyya affinity index. CIES was not considered as we only had data from a single year. K50 and K95 mean the 50% and 95% probability contours of the Kernel Density Estimation (KDE). K50 R means K50 considering only resting locations to calculate KDE. K50 IS means K50 considering only intensive search locations to calculate KDE.

CABRERA		2015			
		K50	K95	K50 R	K50 IS
2016	K50	0.64	-	-	-
	K95	-	0.71	-	-
	K50 R	-	-	0.60	-
	K50 IS	-	-		0.57
TIMANFAYA		K50	K95	K50 R	K50 IS
2016	K50	0.53	-	-	-
	K95	-	0.74	-	-
	K50 R	-	-	0.48	-
	K50 IS	-	-	-	0.51

Table 5 • Relative contribution (in %) of environmental features considered on the shearwater distribution. For Cabrera and Cíes, we run models both considering and excluding distance from the colony as predictors to account for the possible bias imposed by the most frequent short trips on the importance of further areas. Columns shaded in dark grey correspond to model excluding distance to the colony as predictor.

	CABRERA				TIMANFAYA			CÍES
Environmental predictor	2015	2015	2016	2016	2015	2015	2016	2015
1. Distance from the colony	55.6	-	33.5	-	7.7	-	3.5	96.5
2. Depth	40.6	58.3	33.3	37.3	90.9	-	96	-
3. Depth gradient	2.1	4.3	0.9	0.4	0.3	64	0.2	2.5
4. Primary productivity (NP)	0	0	0	0	0	0	0	0
5. NP gradient	0	0	0.8	0.4	0.1	0.5	0	0
6. Sea Surface temperature (SST)	0	11.3	0.8	3.1	0.1	21.4	0.2	0.3
7. SST gradient	0	1.8	0	0	0	0.5	0	0
8. Wind strength	1.6	24.3	30.7	58.8	0.8	14.1	0	0.7

Trophic ecology

We identified about 50% of the items from the regurgitates. Fish with epipelagic habits were dominant in the samples (genera *Sardina* and *Trachurus* in CABR, and genus *Scomber* in TMNF, Table 6). A genus of a benthic fish, *Lepidotrigla sp.*, was identified in TMFY. Cephalopods appeared in low percentages (occurrence and frequency of less than 10%, Table 5). Results were similar in both years. Isotopic values for CABR were generally lower for both δ^{13}C and δ^{15}N (Figure 8). Values of standard ellipse width were similar between years in both CABR and TMFY, and larger in TMFY than in CABR (Table 7; Figure 9). Moreover, the standard ellipse positions were also similar in both years for the two NP, with greater overlap between years for CABR (Table 8; Figure 9).

TABLE 6 • Items identified from stomach contents.

	% Occurrence		% Frequency	
	CABRERA	TIMANFAYA	CABRERA	TIMANFAYA
Trachurus sp.	16.67	3.85	14.29	4.08
Scomber sp.	-	34.62	-	40.82
Sardina sp.	33.33	7.69	51.43	8.16
Lepidotrigla sp.	-	3.85	-	2.04
Otros peces	44.44	65.38	31.43	40.82
Cefalópodos	5.56	7.69	2.86	4.08

TABLE 7 • Isotopic values of Carbon (δ^{13}C) y Nitrogen (δ^{15}N) in blood plasma. Values represent the mean ± standard deviation.

	Year	Individuals	Samples	δ^{13}C	δ^{15}N
CABRERA	2015	46	69	-19.31 ± 0.30	9.65 ± 0.56
	2016	60	99	-19.57 ± 0.29	9.70 ± 0.63
TIMANFAYA	2015	30	33	-18.71 ± 0.95	12.35 ± 0.61
	2016	35	44	-18.59 ± 0.85	12.22 ± 0.44

TABLE 8 • Descriptive parameters of niche width according to isotopic values. SEAc stands for "Standard Ellipse Area corrected for small sample size". SEAb stands for "Bayesian estimates of the Standard Ellipse Areas".

	CABRERA		TIMANFAYA	
	2015	2016	2015	2016
SEAc	0.53	0.50	1.73	1.20
SEAb	0.42	0.55	1.40	1.29
SEAb CI95%	(0.33 - 0.53)	(0.45 - 0.67)	(1.00 - 2.02)	(0.96 - 1.75)

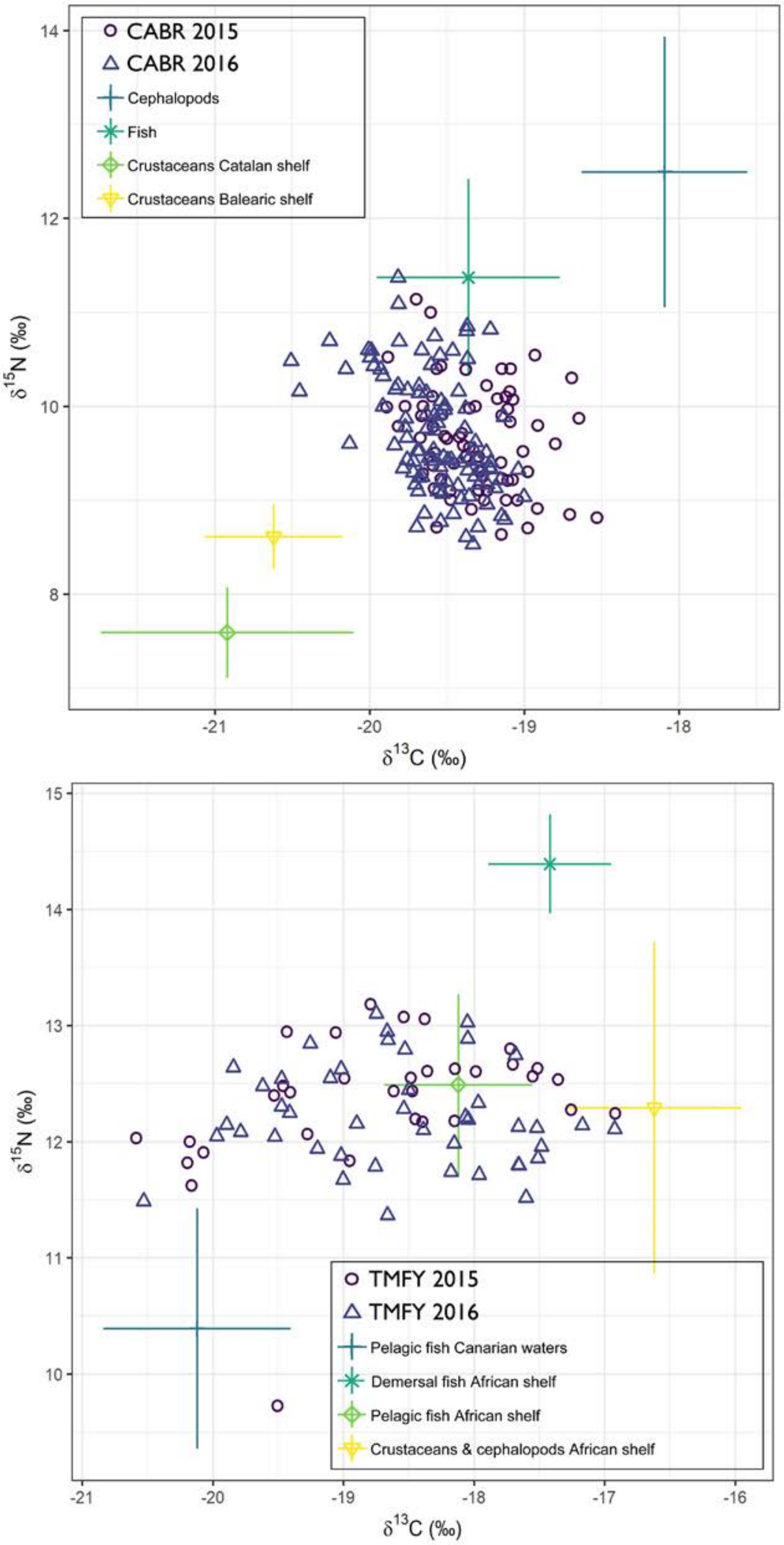


Figure 8 • Isotopic mean values (± SD) of potential prey, and values for each individual, of $\delta^{13}C$ and $\delta^{15}N$ for Cabrera (CABR) and Timanfaya (TMFY). The potential prey obtained from fisheries and those obtained from the regurgitates were grouped by functional groups and represented in the bidimensional space generated by the isotopic ratios of both elements. The geometry of the sources prevents us from running diet reconstruction models with enough confidence.

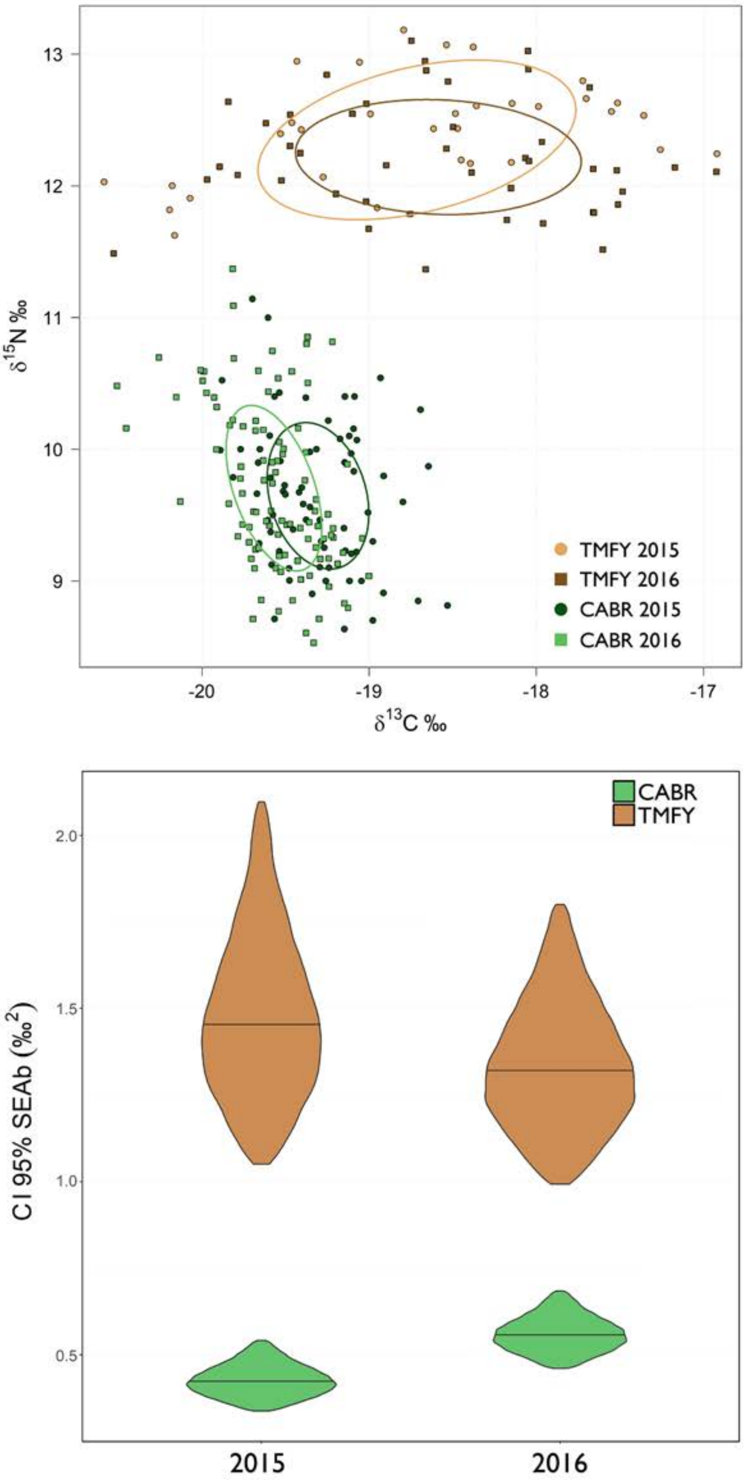


FIGURE 9 • (Top) $\delta^{13}C$ and $\delta^{15}N$ biplot of the plasma isotopic values for Cabrera (CABR) and Timanfaya (TMFY). Each point corresponds to a blood sample. The ellipses represent the Standard Ellipse Area, the bivariate equivalent to the standard deviation, which indicates their spread of data in the bidimensional space. They serve as a proxy of the niche width, and their overlap represents a measure of trophic consistency between years. (Bottom) Violin plots representing the posterior distribution of ellipse sizes, calculated using Bayesian methods (SEAb value in Table 8). The violins represent the 95% credibility intervals for each year, with the horizontal line representing the median value. Posterior distributions obtained through Markov chain-Monte Carlo procedures with 20 000 iterations. Similar values of the two violins from the same colony indicated consistency among years in the isotopic niche width.

Discussion

In this work, we present for the first time data on the movement, behaviour, and foraging strategies of the Cory's and Scopoli's shearwaters breeding in the SNPN. We outline an analytical framework to obtain tracking-derived parameters that might be monitored over the years, as a proof-of-concept of remote seabird tracking as a tool to be integrated within mid to long-term monitoring programs of marine protected areas. The number of individuals sampled at each colony was enough to consider the data representative and therefore to extrapolate the results to the population level in CABR and TMFY. In the case of CIES, a representative sample size was not achieved, even though the data obtained from 3 tagged individuals represent a third of the total number of breeding individuals in this incipient colony.

Spatial ecology and behaviour

CSH and SSH breeding in the SNPN behaved similarly to those from other previously studied colonies in Spain (Reyes-González et al., 2017). During the chick-rearing period, birds from all three NP performed frequent short trips to waters near the colony and less frequent long trips to more distant areas. This bimodal strategy may be the visible sign of the use of a dual foraging strategy, as described for other populations of these species and other Procellariforms (Weimerskirch et al., 1993; Phillips et al., 2017; Shoji et al., 2015). The Catalan coast, including the Ebro Delta shelf, is a highly productive area that SSH from CABR used on their long journeys. Both the distance to the colony and the depth determined the spatial distribution of the birds. They also used intensively the waters over the narrow continental shelf that surrounds the Balearic archipelago. Regarding CSH from TMFY, the colony is about 100 km apart from the African continental shelf. These waters correspond to the Saharan upwelling, a part of the important Canary Current, a major upwelling system extremely rich in nutrients that attracts seabirds and other top-predators (Arístegui et al., 2009; Scales et al., 2015; Grecian et al., 2016). The proximity of this upwelling likely led birds to forage in the area even during short trips lasting just a few days. When birds from TMFY performed long trips, they reached Cape Aguer, in Morocco, to the north, and Cape Boujdour and Cape Dakhla, to the south. They were probably exploiting different plumes of productivity generated from each of these capes, caused by the combined action of the coastal topography with the underwater currents and the trade winds (Nieto et al., 2012). SSH from CIES exploited the rich waters of the Galician coast, in the surroundings of the Rías Baixas, but also the Portuguese waters, more than 200 km to the South of the colony. These cold waters correspond to the northern section of the Canary Current, thus being also cold nutrient-rich waters. Besides, some individuals from CIES engaged in extraordinary long trips, visiting fully oceanic areas close to the central-Atlantic ridge. These areas seem to correspond to seamounts. Regarding inter-annual consistency, approximately half of the area used may change from year to year. We acknowledge that having only two years of data does not allow us to generalize this result, but if this figure is correct such amount of variability in distribution between years might have a noticeable impact on management strategies. A long-term tracking program would help to clarify this issue.

Trophic ecology

Birds from CABR and TMFY fed mostly on epipelagic fish during the chick-rearing period, according to regurgitates analysis, while exploiting cephalopods to a lesser extent, in agreement with previous studies (e.g. Granadeiro et al., 1998). The commercial interest of fisheries for these species may impact their population dynamic, given the generalised tendency towards over-exploitation of these fisheries resources

(Grémillet et al., 2018), particularly in the Mediterranean. The presence of a benthic fish genus, *Lepidotrigla sp*, suggests that the birds from TMFY likely fed on fishery discards since these fish species are not naturally accessible to shearwaters. We were not able to identify a high percentage of samples from regurgitates from both CABR and TMFY beyond the Class Actinopterygians (fish). This fact, together with the differential digestion of the hard remains of the consumed prey, led to a high degree of uncertainty in our results (Alonso et al., 2014). To complement the diet reconstruction, we studied the isotopic niche width of birds from CABR and TMFY. Baseline isotopic values in the Mediterranean and Atlantic differed for both $\delta^{13}C$ and $\delta^{15}N$ (Graham et al., 2010), which prevented us to compare trophic levels or diet origin between NP. Standard ellipses, however, allowed us to estimate the isotopic niche width for each year and population. Standard ellipse areas indicated a much broader isotopic niche of TMFY compared to CABR. This is consistent with the higher species diversity that we found in regurgitates and suggests that individuals from TMFY feed on a much diverse array of prey than individuals from CABR. Within each NP, isotopic niche width was similar in both years, suggesting consistency in the trophic ecology of both populations, at least between the two years analysed. The standard ellipses overlap between years was higher in CABR compared to TMFY. This finding supports a less diverse diet in birds from CABR, not only at the inter-individual level within the same year (which generates narrower isotopic niches) but also between years (which produce similar isotopic niche widths for both years).

Conclusions and applications for management

Within the context of the SNPN, birds used waters inside the boundaries of NP or neighbouring waters regularly, hence measures to ensure a good environmental status of the marine environment within and around the NP, especially in areas where shearwaters aggregated and rest at sea, would be beneficial for the these and likely for other co-existing species. Moreover, in case of further extension of marine protection boundaries, considering the areas used by the birds would likely cover other top-predators. Such boundaries extension would allow for appropriate management of human activities, including control of disturbance by recreational boats or the risk of interaction with fishing vessels. Temporal zoning, at least during the breeding season, might help in the same direction. Nevertheless, at least in CABR, we tracked birds from only two small breeding points located in the north of CABR, which calls for caution since birds breeding in other islets may use different areas within the boundaries of the NP. The full movement range of the tracked shearwaters goes far beyond the spatial scale of the SNPN. Their movements aimed to exploit dynamic resources on a medium to large scale, located far from the PN boundaries. This highlights the need for a larger scale ecosystem approach to their conservation, considering what happens beyond the limits of these protected areas. To guarantee the good status of these populations, the collaboration between the SNPN Agency and the other administrations involved in the governance of other protected areas would be required (Yorio, 2009). The government structure, availability of resources for management, and the degree of protection afforded by the SNPN provide a particularly useful scenario for promoting the implementation of long-term monitoring programs. Long-time series of seabird movement data would provide useful knowledge to improve management and conservation measures for these species and their habitats. This study proposes to integrate seabird remote-tracking as a tool for the adaptive management in the SNPN, and new data presented in this work can be considered as the first step in the process.

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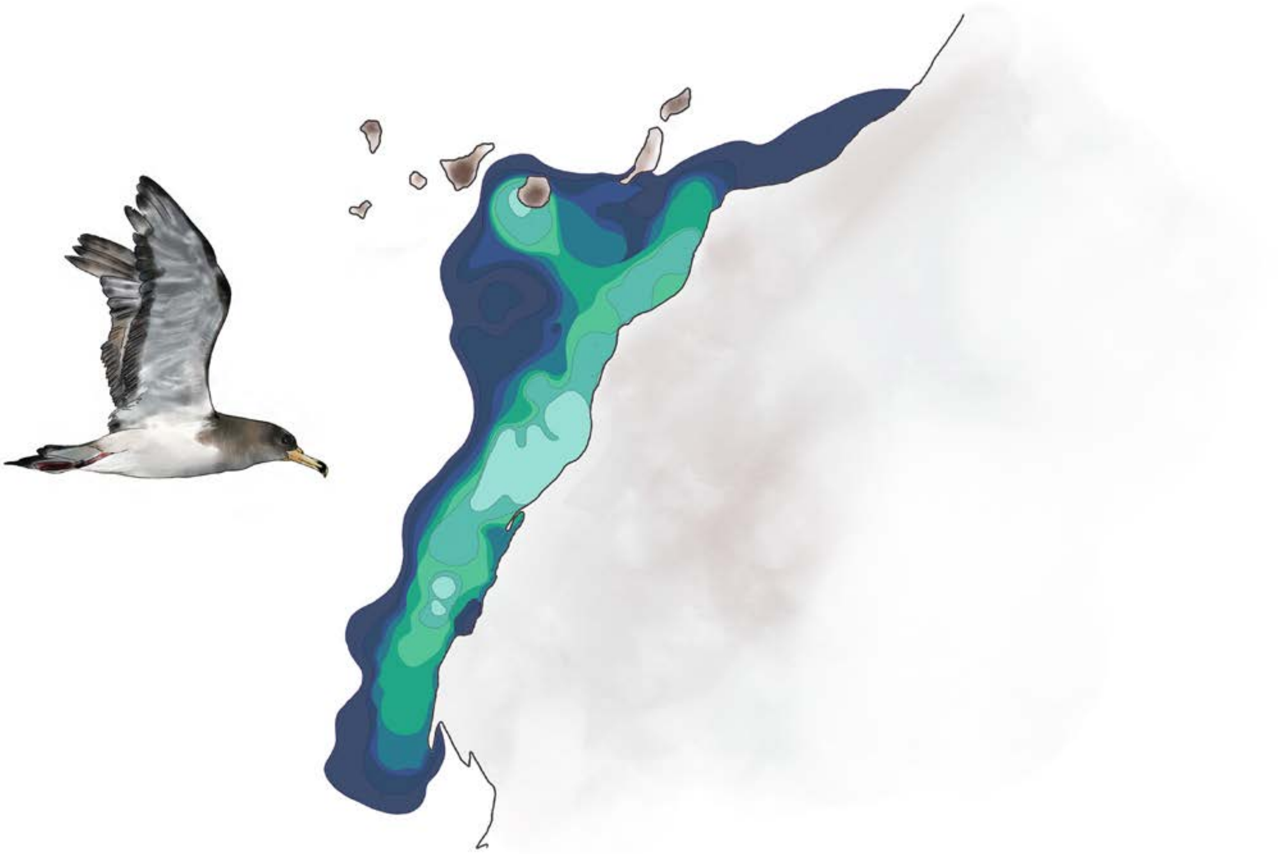

Chapter VI

Disentangling environmental from individual factors: a long-term study of a seabird species exploiting the Canary Current

Chapter VI is an amended version of the research article:

Ramos, R., Reyes-González, J. M., Morera-Pujol, V., Zajková, Z., Militão, T. & González-Solís, J. (2020) Disentangling environmental from individual factors in isotopic ecology: A 17-year longitudinal study in a long-lived seabird exploiting the Canary Current. *Ecological Indicators*, 111, 105963.

DISENTANGLING ENVIRONMENTAL FROM INDIVIDUAL FACTORS: A LONG-TERM STUDY OF A SEABIRD SPECIES EXPLOITING THE CANARY CURRENT

ABSTRACT

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

Keywords

Biomonitoring • Cory's shearwater • individual consistency • environmental variability • trophic specialization • stable isotope analysis.

INTRODUCTION

In marine ecosystems, trophic ecology of many predator species has been widely documented to correlate with oceanographic parameters (e.g., Gilles et al. 2016, Gagne et al. 2018, Byrne et al. 2019). These covariates usually focus either on fluctuations of marine environmental features at coarse-, meso- or local scale, such as chlorophyll-a concentration, salinity, temperature, or wind speed (Votier et al. 2010, Kurle & McWhorter 2017, Bird et al. 2018), or on large-scale climatic indexes, such as the North Atlantic Oscillation index (NAO; Moreno et al. 2013, Wallace et al. 2014, Fairhurst et al. 2015), which often capture complex associations between atmospheric and ecological processes better than local indexes (Hallett et al. 2004). Such environmental variables are often related to the recruitment and abundance of small pelagic fish (e.g. sardine) and cephalopods (Borges et al. 2003, Santos et al. 2005, Krüger et al. 2019), leading to complex changes in food availability for foraging predators (Barbraud & Weimerskirch 2001, Forcada et al. 2005, Saba et al. 2007). In addition, regional estimates of fishery catches have been suggested to be good proxies of ecosystem productivity and prey abundance (Paiva et al. 2013). Long term overexploitation of fisheries, however, can also alter the food web structure and ultimately affect prey availability and the trophic ecology of top predators (Gagne et al. 2018).

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

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

A reliable method to assess individual specialization in trophic ecology, alternative to those involving repeated conventional samplings (e.g. regurgitates or stomach contents), is the use of Stable Isotope Analysis (SIA; Ramos & González-Solís 2012). In marine ecosystems, stable isotope ratios of carbon ($\delta^{13}C$) experience little variation along the food chain and are mainly used to discriminate the source of primary production and the consumer's habitat type (increasing from pelagic to benthic or from oceanic to neritic; Hobson et al. 1994). In contrast, stable isotope ratios of nitrogen ($\delta^{15}N$) increase along the food chain and are typically used to infer consumer trophic positions (Hussey et al. 2014). Some studies have assessed the trophic specialization of the individuals over relatively short-time periods (i.e., from days to months) by performing SIA in different tissues with various turnover rates, which ultimately provides information on the feeding ecology of the individuals over different timescales (Bearhop et al. 2006, Ceia et al. 2014, Connan et al. 2014). Interestingly, other studies have performed SIA in regular subsamples of inert tissues with continuous growth (e.g., vibrissae, claws, etc), which has allowed them to infer the degree of long-term specialization of individual trophic ecology (i.e., over several years; Table 1). In any case, $\delta^{13}C$ has to be carefully evaluated, particularly in such multidecadal studies, as carbon ratios may decrease over time due to the increased burning of fossil fuels, which generate ^{13}C-depleted CO_2 (i.e., the Suess effect; Revelle & Suess 1957). In the marine environment, the strongest decreases occur in the subtropical regions of the Northern Hemisphere, such as the Canary Current upwelling ecosystem (hereafter CC) in the North Atlantic Ocean (where $\delta^{13}C$ could have decreased up to 0.9 ‰ since the industrial revolution; Eide et al. 2017). Finally, much research has been conducted on seabird trophic ecology using SIA over the last decades (Hobson et al. 1994, Inger & Bearhop 2008, Bond & Jones 2009). However, only very few attempts of characterising long-term individual specialization in foraging strategies and resource use of long-lived seabirds have been carried out (reviewed in Phillips et al. 2017), and to the best of our knowledge, none of them related this temporal variation at the individual level with environmental variability in a long temporal series.

Within this framework, we designed a longitudinal study to disentangle the relative importance of environmental variability as well as inter- (i.e., population) and intra-individual variation in the trophic ecology of a long-lived species. We used the Cory's shearwater (*Calonectris borealis*) breeding in the Canary Islands, which recurrently exploit the CC (Ramos et al. 2013), as model species. In this regard, the increasing exploitation of the CC by local and industrial fisheries (Ramos & Grémillet 2013, Sambe et al. 2016) calls for studying changes in the trophic web structure of such a relevant upwelling ecosystem. We performed SIA on the first primary feather (hereafter P1) of 99 individuals sampled repeatedly over a period of 17 years to determine changes in stable isotope values across years as well as to ascertain individual repeatability in the use of trophic resources. Specifically, we quantified $\delta^{13}C$ and $\delta^{15}N$ to assess repeatability at both population and individual level, in foraging habitats and consumer's trophic level, respectively, while also testing for

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

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

relevant environmental covariates and specific intrinsic factors (i.e., sex, bill morphology, and individual experience). Given the intense exploitation of the CC (Arístegui et al. 2006, Ramos & Grémillet 2013) and that most seabirds maximize foraging efficiency by responding opportunistically to prey availability (Pinaud & Weimerskirch 2005, Lyday et al. 2015), we expected to find a longitudinal change in the foraging habits of Cory's shearwater feeding more on discarded benthic prey, as well as a temporal decay of its trophic level in response to the increasing fishery pressure on small pelagic fish (e.g., Gagne et al. 2018).

METHODS

Model species

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

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

Sampling site and design

The present study and fieldwork experiments were conducted in a Cory's shearwater colony in Gran Canaria, Canary Archipelago, Spain (15°47'18" N; 27°50'41"W). During every early breeding season (i.e., April to June) of the period 2002-2018, we visited all known, accessible burrows of the colony, and sampled the entire emerged part of P1 of 99 adult shearwaters (n_{total} = 646 feathers; notice that every sampled P1 feather was grown the year before, therefore, the study period represented 2001-2017). The number of sampled feathers per individual varied between 3 and 14 years (in particular, one individual was sampled up to 14 times, one individual 13 times, and another two birds 12 times; Table 2). P1 feathers were cut at skin level (i.e., mid calamus) and were sampled alternatively on the right and left wings every year to avoid biases arising from a potential alteration on the moulting schedule of the feather after cutting it. Complimentarily, birds were sampled for specific morphometric measurements of the bill at the time of ringing by different researchers (see Supporting Information, Table S1). To evaluate the effect of bill size on the trophic ecology of the individuals, we performed a Principal Component Analysis (PCA) using *prcomp* function in R, version 3.3.2 (R Development Core Team 2017), with culmen, maximum bill depth, bill depth at nostril, and total head length (bill-head) as variables (see Supporting Information, Fig. S1). We took the first Principal

Component (PC1) from the PCA as an estimate of bill size for every individual bird. In addition, at the time of their first capture, all birds were sampled for 1.0 ml of blood taken from the tarsal vein using sterile syringes and needles. From these blood samples, all birds were sexed molecularly following Fridolfsson & Ellegren (1999), and based on the detection of a female-specific locus (CHD1-W; diagnostic kit from Durviz, Valencia, Spain). Finally, determining the exact age of birds can only be assessed by ringing the individuals as chicks but this is often impractical in long-lived species with delayed recruitment (such as the Cory's shearwater; Mougin et al. 2000). Since all individuals of this study were ringed as adults, we cannot assess their exact age at the time of sampling, and therefore we used "years since first sampling" as a proxy for experience (Exp), assuming that each year that passes, whatever the age at the first year of sampling, an individual has gained experience (e.g., Nichols et al. 1997, Crespin et al. 2006).

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

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

SIA procedures

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

±0.1 and ±0.2 ‰, for C and N, respectively, but these are likely underestimates of true measurement error for complex organic compounds like feathers.

Removing the marine Suess effect

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

Foraging areas and environmental variables

Shearwaters from the sampled population in Gran Canaria consistently exploit the CC throughout its breeding period (Ramos et al. 2013). To properly evaluate and extract the environmental variables that may condition trophic ecology of the individuals year after year, we first estimated foraging areas of the sampled population by tracking movements of 167 individuals during the late breeding period (July-August-September) of eight consecutive years (2011-2018). Birds were tracked using Global Positioning System loggers (GPS; CatTrack® Technologies and Perthold Industries Ltd.) attached to the back feathers of birds with Tesa® tape. Deployed loggers represented between 1.9 to 3.7% of bird body mass (depending on the battery size of GPSs and the weight of the bird, but always <4.0% of adult mass; Passos et al. 2010). We classified GPS at-sea positions into four possible behavioural modes, using the R-package EMbC (Garriga et al. 2016): intensive search, extensive search, resting and relocating. From the foraging positions only (i.e. intensive and extensive search), we calculated Kernel Density Estimations (KDEs; *kernelUD* function from the adehabitat v.1.8.7 package in R; Calenge 2006) for each trip, with a smoothing factor of h = 21 km (obtained from the mean of Area Restricted Search (ARS) radius; Lascelles et al. 2016). We calculated 50% KDE density contours (KDE50 hereafter) from each trip and, over a grid of 0.05º x 0.05º, we calculated the number of years that at least one KDE50 was present in each cell (Fig. 1). We used the resulting grid as a proxy of the yearly foraging consistency of the entire population during the chick-rearing period.

Second, and to determine the influence of the local environment on the trophic ecology of the population, we analyzed remote sensing data of key environmental variables in the area consistently used by foraging birds. We extracted environmental variables only from those areas used during the eight years of GPS tracking and over the African continental shelf (i.e. we excluded the area consistently used around the Canary archipelago where the breeding colony is located). We extracted monthly composites of the surface chlorophyll-a concentration (CHLa, mg m^{-3}), sea surface salinity (SAL, g of salt per kg of water), sea surface temperature (SST, °C) and wind speed (WIND, m s^{-1}) from global ocean physics reprocessed models (L4; www.marine.copernicus.eu, EU Copernicus Marine Service Information), with a grid resolution of 0.25° over the period 2001-2017. Monthly estimates were averaged over the aforementioned area. To consider the most influential period of each environmental variable on the isotopic ratios of P1 feathers, CHLa estimates were added from February to June, SAL and SST estimates were averaged for the same period, and WIND estimates were averaged from September to October within every year (see Supporting Information, Fig. S2).

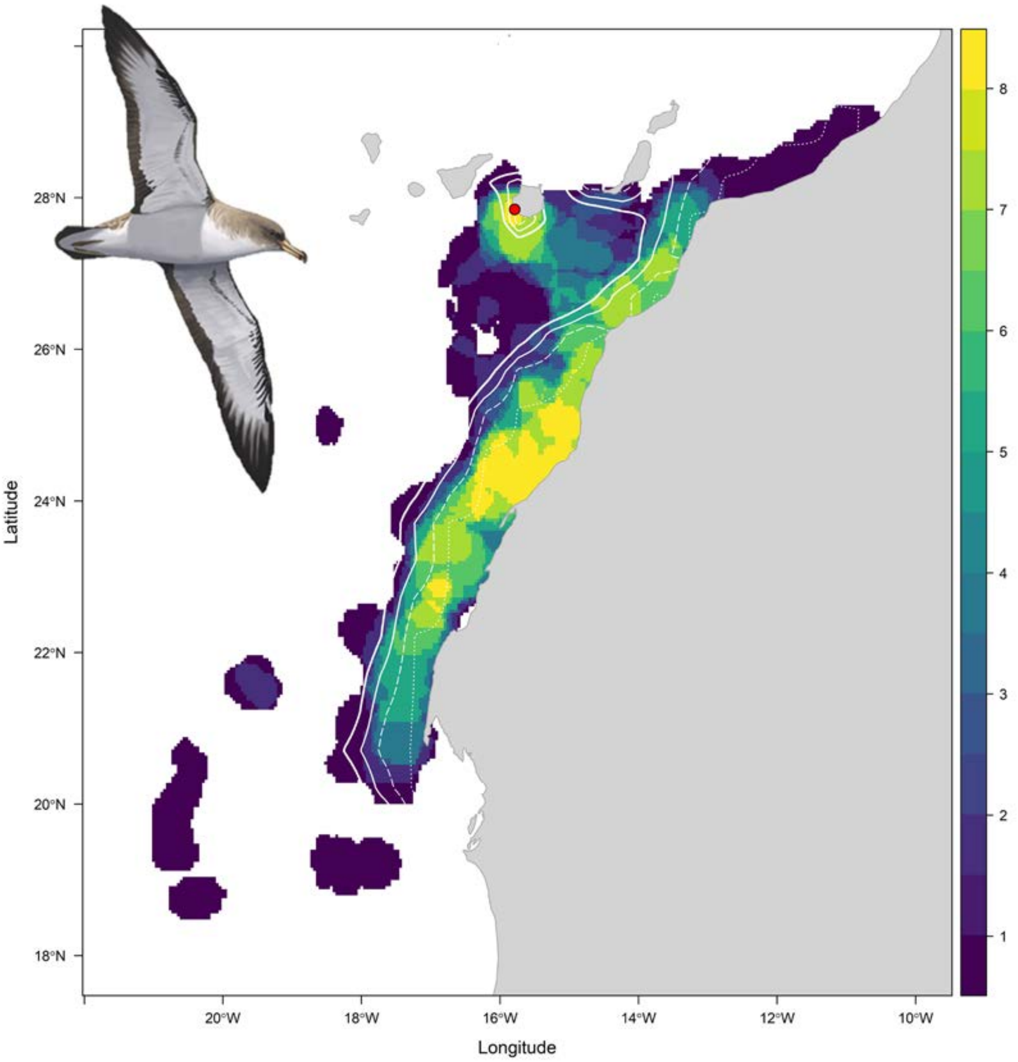

Figure 1 • Foraging areas of Cory's shearwater (*Calonectris borealis*) from Veneguera (Gran Canaria). The coloured background depicts the number of years that at least one individual KDE, calculated with foraging locations (see Methods for details), occurred within each cell during chick-rearing periods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

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

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

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

Statistical analysis, isotopic modelling, and repeatability assessments

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

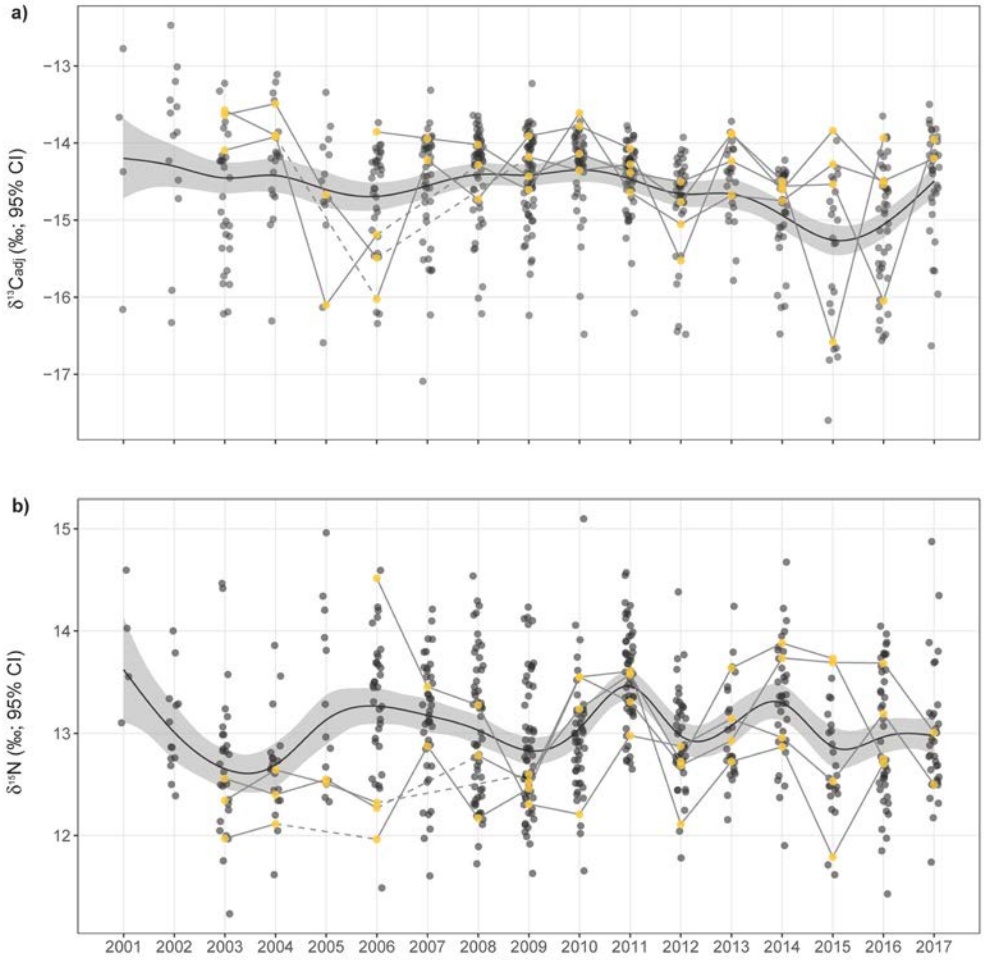

Figure 2 • Feather $\delta^{13}C_{adj}$ (a) and $\delta^{15}N$ (b) values of innermost primary feather (P1) of 99 Cory's shearwaters sampled throughout the 17-year study. The solid lines correspond to the mean estimated using Generalized Additive Mixed Models (GAMM), and the grey-coloured regions around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

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

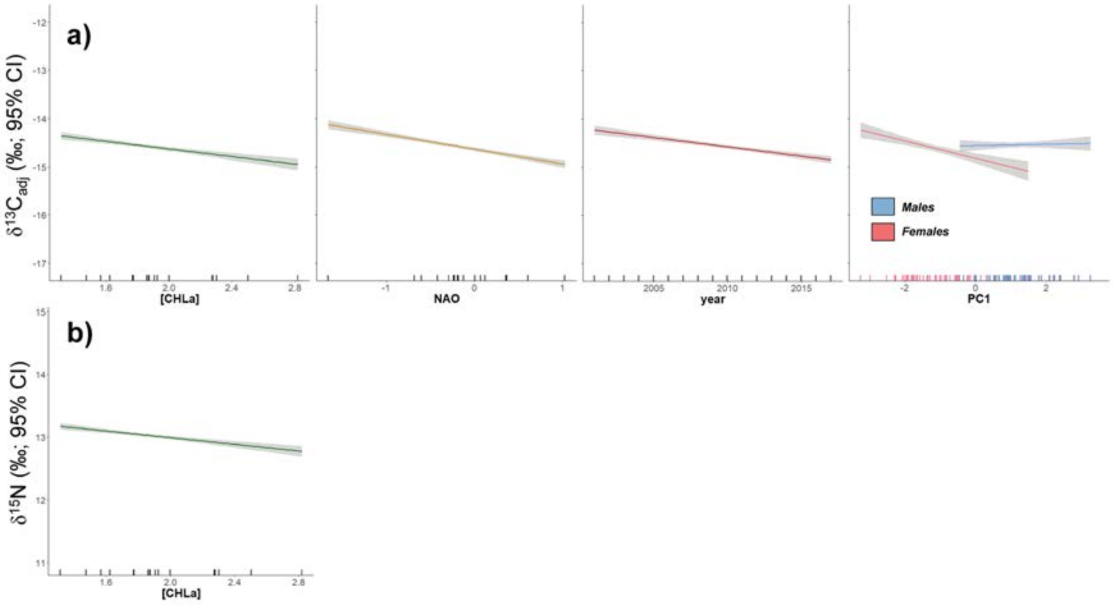

FIGURE 3 • Relationships of the surface chlorophyll-a concentration (CHLa, x100 000), the North Atlantic Oscillation Index (NAO), the longitudinal effect of year of sampling, and the bill size (PC1) linked to sex with $\delta^{13}C_{adj}$ trend (a) and the relationship of CHLa with $\delta^{15}N$ trend (b) throughout the 17-year study. Covariates relevance is quantified in Linear Mixed Models (LMM) detailed in Table 3.

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

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

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

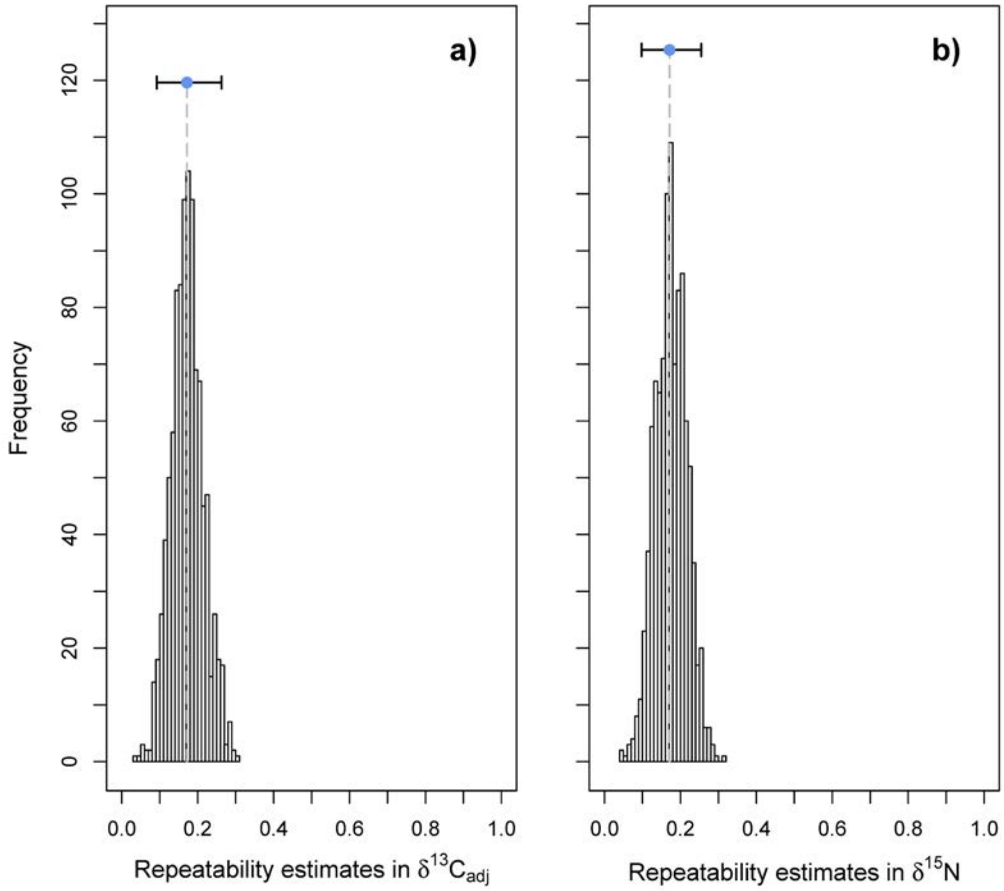

FIGURE 4 • Population-level repeatability estimates (R_{pop}) of the effect of bird identity extracted from LMMs of $\delta^{13}C_{adj}$ (a) and $\delta^{15}N$ (b; detailed in Table 3). Estimate frequencies were calculated using parametric bootstrapping procedures. The blue circle and grey, dashed line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

In order to assess individual specialisation in foraging habitats and trophic level, we further calculated repeatability of $\delta^{13}C_{adj}$ and $\delta^{15}N$ for each individual (individual-level repeatability, R_{ind}). We followed the approach of Potier et al. (2015) to separate the proportion of residual variance explained by each level of the random effect (i.e., the bird identities) from previous LMMs. Because we had a variety of sampling schedule among individuals, ranging from three to 14 years, we first performed linear regressions to evaluate possible biases imposed by the number of years sampled on the R_{ind} values (see Supporting Information, Fig. S4 & Fig. S5). Finally, we performed multiple linear regressions to evaluate simultaneously effects of R_{ind} and years sampled on $\delta^{13}C_{adj}$ and $\delta^{15}N$ ratios (Fig. 5).

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

		$\delta^{13}C_{adj}$ (‰)			$\delta^{15}N$ (‰)		
a)	df	AICc	ΔAICc	AICc Wgt	AICc	ΔAICc	AICc Wgt
Sex * PC1 + Exp + Chla + NAO + year	**10**	**1201.1**	**1.6**	**0.074**	1105.2	10.6	0.001
Sex * PC1 + CHLa + NAO + year	**9**	**1199.6**	**0.0**	**0.162**	1103.7	9.0	0.002
Sex * PC1 + Exp + CHLa + NAO	**9**	**1200.1**	**0.6**	**0.122**	1104.0	9.4	0.002
Sex + PC1 + Exp + CHLa + NAO + year	9	1203.4	3.8	0.024	1103.9	9.3	0.002
Sex + PC1 + CHLa + NAO + year	8	1201.6	2.0	0.058	1102.3	7.6	0.004
Sex + PC1 + Exp + CHLa + NAO	8	1202.8	3.2	0.032	1102.6	7.9	0.004
Sex + Exp + CHLa + NAO + year	8	1204.0	4.4	0.018	1101.9	7.2	0.005
Sex * PC1 + NAO + year	8	1203.7	4.1	0.021	1109.2	14.6	0.000
PC1 + Exp + CHLa + NAO + year	8	1204.2	4.7	0.016	1101.9	7.2	0.005
Sex * PC1 + Exp + NAO	8	1203.7	4.2	0.020	1110.7	16.0	0.000
Sex + CHLa + NAO + year	7	1202.2	2.6	0.044	1100.2	5.6	0.012
Exp + CHLa + NAO + year	7	1202.3	2.8	0.041	1099.9	5.2	0.014
PC1 + CHLa + NAO + year	7	1202.4	2.8	0.040	1100.3	5.6	0.011
Sex + Exp + CHLa + NAO	7	1203.4	3.9	0.023	1100.5	5.9	0.010
PC1 + Exp + CHLa + NAO	7	1203.9	4.3	0.019	1100.6	5.9	0.010
CHLa + NAO + year	**6**	**1200.5**	**1.0**	**0.101**	1098.3	3.6	0.031
Exp + CHLa + NAO	6	1202.0	2.4	0.049	1098.6	3.9	0.026
Exp + CHLa + year	6	1207.7	8.1	0.003	1098.1	3.4	0.034
Sex + CHLa + NAO	6	1209.5	10.0	0.001	1098.5	3.8	0.028
Sex + CHLa + year	6	1208.1	8.5	0.002	1098.6	3.9	0.027
PC1 + CHLa + NAO	6	1209.9	10.3	0.001	1098.5	3.9	0.027
PC1 + CHLa + year	6	1208.3	8.7	0.002	1098.6	3.9	0.026
Sex + Exp + CHLa	6	1210.1	10.5	0.001	1098.6	4.0	0.026

TABLE 3 • Continuation.

		$\delta^{13}C_{adj}$ (‰)			$\delta^{15}N$ (‰)		
	df	AICc	ΔAICc	AICc Wgt	AICc	ΔAICc	AICc Wgt
PC1 + Exp + CHLa	6	1210.7	11.1	0.001	1098.6	4.0	0.026
Sex + PC1 + CHLa	6	1233.0	33.4	0.000	1098.6	4.0	0.026
CHLa + year	5	1206.4	6.9	0.005	**1096.6**	**1.9**	**0.071**
CHLa + NAO	5	1208.0	8.4	0.002	**1096.6**	**1.9**	**0.073**
Sex + PC1 + Exp + CHLa + NAO	5	1233.9	34.4	0.000	**1096.6**	**1.9**	**0.071**
PC1 + CHLa	5	1234.5	34.9	0.000	**1096.6**	**1.9**	**0.071**
Exp + CHLa	5	1208.7	9.1	0.002	1096.7	2.0	0.068
CHLa	4	1232.5	33.0	0.000	**1094.7**	**0.0**	**0.188**
b)		Estimate ± SE (95% CI)	z value	*P*-value	Estimate ± SE (95% CI)	z value	*P*-value
Fixed effects							
Intercept		**-14.53 ± 0.11 (-14.75 | -14.31)**	**130.6**	**0.000**	**13.04 ± 0.04 (12.96 | 13.12)**	**325.1**	**0.000**
Sex(Female)		-0.26 ± 0.14 (-0.53 | 0.02)	1.9	0.065	0.02 ± 0.08 (-0.12 | 0.17)	0.3	0.754
PC1		0.03 ± 0.10 (-0.16 | 0.23)	0.3	0.743	-0.01 ± 0.04 (-0.08 | 0.06)	0.3	0.784
Exp		-0.02 ± 0.01 (-0.05 | 0.01)	1.4	0.149			
CHLa		**-0.08 ± 0.03 (-0.15 | -0.02)**	**2.5**	**0.014**	**-0.09 ± 0.03 (-0.14 | -0.04)**	**3.6**	**0.000**
NAO		**-0.11 ± 0.04 (-0.18 | -0.03)**	**2.8**	**0.005**	-0.01 ± 0.03 (-0.07 | 0.05)	0.4	0.718
year		**-0.10 ± 0.05 (-0.19 | -0.01)**	**2.1**	**0.037**	0.01 ± 0.03 (-0.05 | 0.06)	0.3	0.773
Females:PC1		**-0.29 ± 0.14 (-0.56 | -0.02)**	**2.1**	**0.036**			
Random effects		Variance ± SD			Variance ± SD		
Individual		0.09 ± 0.30			0.07 ± 0.26		
Residual		0.45 ± 0.67			0.35 ± 0.59		
c)		Estimate ± SE (95% CI)			Estimate ± SE (95% CI)		
Repeatability (R_{pop})							
Individual		0.167 ± 0.042 (0.087 | 0.255)			0.171 ± 0.040 (0.091 | 0.249)		

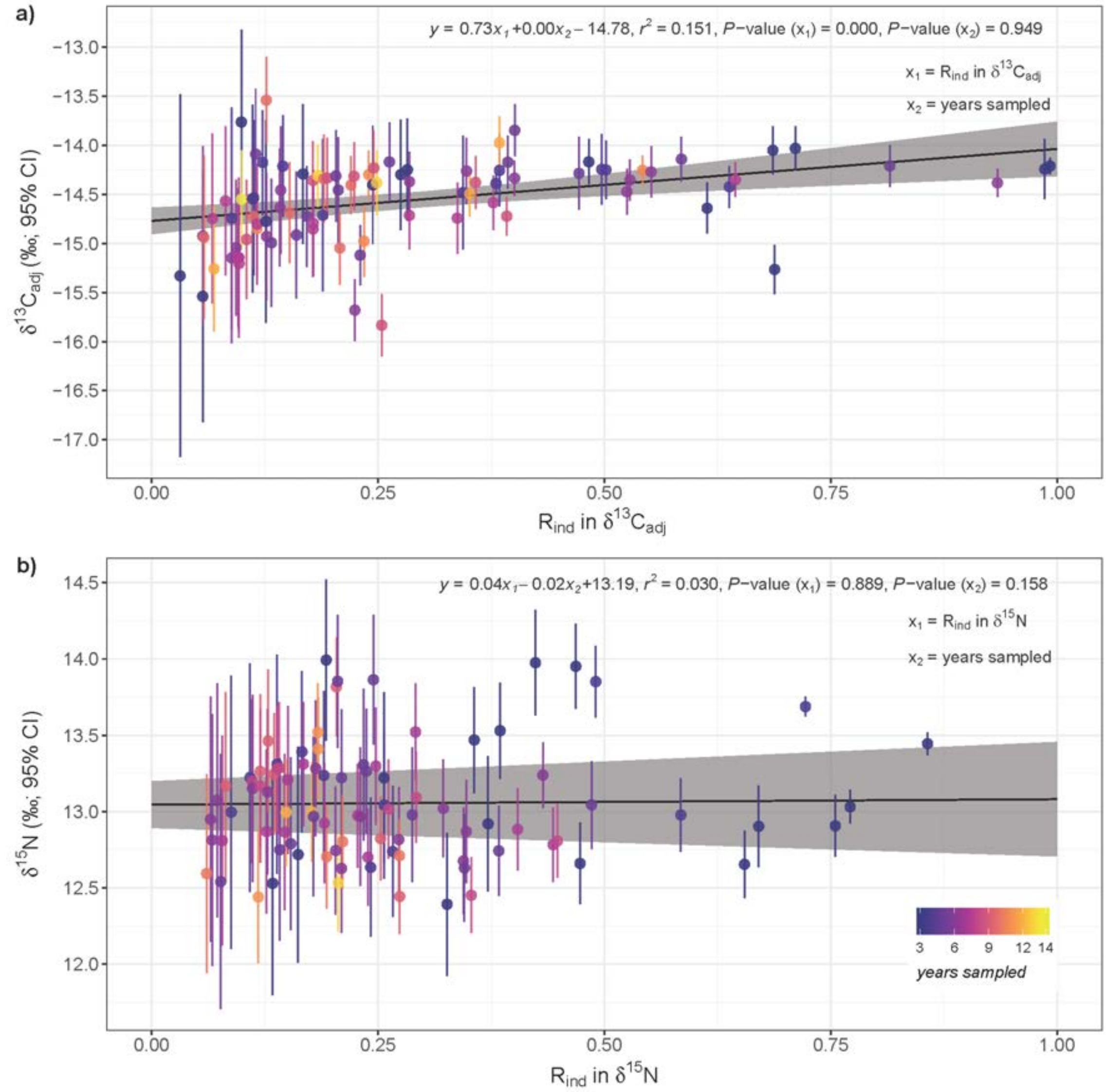

FIGURE 5 • Linear regression models between individual-level repeatability estimates (R_{ind}) with the individual mean ± 95% CI estimates of $\delta^{13}C_{adj}$ (a) and $\delta^{15}N$ (b). The colour gradient indicates the number of years an individual was sampled (99 individuals, sampled from three to 14 times). R_{ind} estimates were calculated from LMMs following Potier et al. (2015). Notice that equations refer to multiple linear regressions that evaluate simultaneously effects of R_{ind} and years sampled on $\delta^{13}C_{adj}$ and $\delta^{15}N$ ratios (see Methods section for details).

RESULTS

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

In general, $\delta^{13}C_{obs}$ experimented a slight, sustained decay over time (see Supporting Information, Table S2) that persisted even after correcting for the Suess effect (i.e., $\delta^{13}C_{adj}$; Fig. 2a). However, there was no perceivable long-term trend in the $\delta^{15}N$ values (Fig. 2b). On one hand, while examining the effect of extrinsic (environmental) variability on the trophic ecology of Cory's shearwaters, LMMs revealed that $\delta^{13}C_{adj}$ values were negatively related to CHLa and NAO values, in addition to a longitudinal, negative effect of year of sampling (Fig. 3), and that $\delta^{15}N$ values were also negatively related to CHLa (Table 3). On the other hand, LMMs also revealed that bill size (PC1) was a relevant factor in $\delta^{13}C_{adj}$ values of female individuals (Table 3 & Fig. 3). Finally, LMMs also revealed that bird identity accounted for a small proportion of the total variance in both isotopic ratios (Table 3). Accordingly, R_{pop} (i.e., population-level repeatabilities) were relatively low in both isotopic ratios (Table 3 & Fig. 4). Non-overlapping zero and relatively narrow 95% CI of both repeatabilities indicated, respectively, that they statistically differed from zero and that their estimations were precise (Wolak et al. 2012). Regarding R_{ind} (i.e., individual-level repeatabilities), most of the individuals had estimates around the mean value of R_{pop} (~0.2) for both $\delta^{13}C_{adj}$ and $\delta^{15}N$, although a few of them had higher R_{ind} values (out of 99 individuals, 16 for $\delta^{13}C_{adj}$ and seven for $\delta^{15}N$ had $R_{ind} > 0.5$; Fig. 5). We found statistically significant relationships between R_{ind} and the number of sampled years ($\delta^{13}C_{adj}$: $r^2 = 0.08$, P-value = 0.006; $\delta^{15}N$: $r^2 = 0.18$, P-value < 0.001; see Supporting Information, Fig. S4), suggesting slight but relevant biases on individual-level repeatabilities due to sampling effort. Finally, once we accounted for the effect of the sampling effort (i.e., using the residuals of linear regressions between R_{ind} and years sampled), we did not find a statistically significant correlation between R_{ind} of $\delta^{13}C_{adj}$ and R_{ind} of $\delta^{15}N$ ($r^2 = 0.00$; P-value= 0.990; see Supporting Information, Fig. S5).

DISCUSSION

In this study, SIA in feathers of about a hundred Cory's shearwaters repeatedly sampled for several years showed the influence of extrinsic (environmental) factors on the trophic ecology of this population for nearly two decades. Carbon isotopic ratios ($\delta^{13}C$) related negatively to local CHLa concentrations and to the global NAO index, both covariates related to upwelling intensity. Surprisingly, isotopic values of nitrogen ($\delta^{15}N$) remained relatively stable with no obvious temporal trend along the sampled years, and they did only relate, also negatively, to local CHLa concentrations. In addition, this sampling scheme allowed us to quantify the influence of intrinsic (individual) factors on the feeding ecology of the individuals, at group levels (sex) as well as at both, population and individual (bill size and experience) levels. These results pointed out the coexistence within our study population of individuals with different degree of specialization (from extremely flexible [generalists] to highly consistent individuals [specialists]), which ultimately have deep implications on how populations will cope with environmental changes.

Environmental variability on trophic ecology

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

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

In addition, $\delta^{13}C_{adj}$ maintained a negative correlation to local CHLa concentrations and to the global NAO index, both covariates related to upwelling intensity. In most large upwelling ecosystems, CHLa concentrations relate to nutrient fertilization by coastal upwelling, and they are often used as a proxy of marine primary productivity which is thus inherently linked to upwelling intensity (Thomas et al. 2004, Arístegui et al. 2006). The NAO index is associated with a range of climatic factors in the North Atlantic including temperature, precipitation, cloud cover and storms (Santos et al. 2005), which also condition coastal upwelling intensity. Many previous studies carried out specifically along the CC already suggested positive links between colder weather, NAO values, and the upwelling rate (Parsons & Lear 2001, Álvarez-Salgado et al. 2003, Borges et al. 2003, McGregor et al. 2007, Narayan et al. 2010). Upwelling intensity is certainly a major but complex phenomenon within the oceanic carbon cycle. Typically, deep waters are saturated in ^{12}C-enriched CO_2 due to the fact that photosynthesis reactions preferentially make use of isotopically lighter $^{12}CO_2$, and that ^{12}C-enriched phytoplankton sinks to the seafloor and it is mineralized at depth. Such deep waters with ^{12}C-enriched CO_2 are upwelled along continental coasts and act as a carbon source for primary producers (Sadler et al. 2012). Thus, upwelling intensity is often negatively related to $\delta^{13}C$ values of primary producers (Magozzi et al. 2017), and this relationship should be transferred up to the trophic web. This reasoning would explain the dual $\delta^{13}C$-CHLa and $\delta^{13}C$-NAO relationships we reported here, i.e., both higher CHLa and NAO values relate to higher upwelling intensity in the CC during the breeding period of Cory's shearwaters, which causes lower $\delta^{13}C$ values in the feathers of such top predators. This suggests that long-term changes in $\delta^{13}C$ values of predators should be tackled with caution, as they are not necessary linked to changes in feeding habits (e.g., Ceia et al. 2018, Ramos et al. 2018a), but they can result from changes in stable isotope baseline values in response to environmental conditions (Magozzi et al. 2017), and the propagation of these isotopic changes through the entire food web.

Surprisingly, $\delta^{15}N$ values remained relatively stable and did not show any temporal trend along the sampled years. The CC has been the fish basket of southern Europe since the mid-nineties, and Russia and China keep exploiting Exclusive Economic Zones of Morocco and Mauritania (Ramos & Grémillet 2013). We therefore expected to find changes in the trophic web structuring of this area over the last two decades as a consequence of fishery overexploitation (Sambe et al. 2016, Sánchez-Garrido et al. 2019). Indeed, previous longitudinal studies also based on isotopic data, but set on other oceanic basins, reported seabird shifts from higher- to lower-trophic level prey mostly due to increasing overexploitation of fisheries (e.g. Blight et al. 2015, Hobson et al. 2015, Gagne et al. 2018). Contrary to what we expected, our results showed that most

Cory's shearwaters did not change their trophic position over the last two decades, which could reflect the still relatively good health status of the trophic web in the CC. This unexpected result is of high conservation relevance, showing it is still possible to regulate fishing exploitation in the area before the entire food web structure is altered. It also highlights the potential of such a long-term study on marine top predators to monitor fishery impacts on the structure of marine trophic webs from an independent perspective of that from fishery metrics (e.g., commercial catches; Lyday et al. 2015). Often, the status of the marine ecosystems is estimated using fish catch data, which is obviously fishery-dependent, and therefore subject to inherent biases and limitations. Thus, longitudinal time series of predator tissues represent a promising method for fishery-independent assessments of marine ecosystem productivity and sustainability.

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

Individual specialization in trophic ecology

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

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

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

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

Conclusions & perspectives

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

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SUPPORTING INFORMATION

TABLE S1 • Four morphometric characteristics (mean ± Standard Deviation) of male (n=52) and female (n=47) Cory's shearwaters measured in the sampled breeding colony (Veneguera, Gran Canaria). In addition, the first Principal Component of the bill measurements PCA (PC1), explaining the 76.3% of the morphometric variability, is also included.

	Male	Female
Culmen length (mm)	54.9 ± 2.3	51.8 ± 1.6
Maximum bill depth (mm)	21.2 ± 0.9	19.1 ± 1.1
Bill depth at nostril (mm)	15.4 ± 0.8	14.1 ± 0.5
Total head length (mm)	113.7 ± 3.0	108.7 ± 2.4
PC1 (bill size)	1.1 ± 1.0	-1.3 ± 0.9

TABLE S2 • Carbon ($\delta^{13}C_{obs}$) and Nitrogen ($\delta^{15}N$) isotope values (mean ± Standard Deviation, SD, and 95% Confidence Intervals, 95% CI) of innermost primary feather (P1) of 99 Cory's shearwaters sampled throughout the 17 years of the study. Equal superscripts (i.e., letters) denote groups of years not significantly different in the isotopic ratios (based on posterior pair-wise comparisons between years made for each isotope ratio, using Hochberg's approach (Hochberg, 1988) to maintain the overall error type I at 0.05).

		$\delta^{13}C_{obs}$ (‰)	$\delta^{15}N$ (‰)
Year	n	mean ± SD (95% CI)	mean ± SD (95% CI)
2001	4	-13.8 ± 1.4 (-15.7|-12.4) ^{abcde}	13.8 ± 0.6 (13.1|14.6) ^{abc}
2002	13	-13.7 ± 1.1 (-15.9|-12.1) ^{a}	13.0 ± 0.5 (12.4|14.0) ^{abcd}
2003	31	-14.3 ± 0.9 (-15.8|-12.9) ^{abcd}	12.7 ± 0.7 (11.2|14.5) ^{d}
2004	22	-13.8 ± 0.7 (-16.0|-12.8) ^{ab}	12.6 ± 0.5 (11.6|13.9) ^{d}
2005	15	-14.4 ± 0.9 (-16.3|-13.0) ^{abcde}	13.2 ± 0.8 (12.3|15.0) ^{abcd}
2006	37	-14.4 ± 0.7 (-16.1|-13.4) ^{bcd}	13.3 ± 0.7 (11.5|14.6) ^{ab}
2007	43	-14.3 ± 0.8 (-16.8|-13.1) ^{abcd}	13.1 ± 0.6 (11.6|14.2) ^{abcd}
2008	58	-14.1 ± 0.6 (-16.0|-13.4) ^{ab}	13.0 ± 0.7 (11.7|14.5) ^{acd}
2009	66	-14.2 ± 0.6 (-16.0|-13.0) ^{abc}	12.8 ± 0.6 (11.6|14.2) ^{cd}
2010	50	-14.1 ± 0.5 (-16.3|-13.4) ^{ab}	13.0 ± 0.6 (11.7|15.1) ^{acd}
2011	57	-14.3 ± 0.4 (-16.0|-13.6) ^{abc}	13.5 ± 0.5 (12.7|14.6) ^{bc}
2012	46	-14.6 ± 0.6 (-16.4|-13.8) ^{cde}	12.9 ± 0.5 (11.8|14.4) ^{acd}
2013	27	-14.4 ± 0.5 (-15.7|-13.6) ^{abcd}	13.0 ± 0.5 (12.2|14.2) ^{acd}
2014	38	-14.8 ± 0.6 (-16.4|-14.1) ^{def}	13.3 ± 0.6 (11.9|14.7) ^{ab}
2015	26	-15.3 ± 1.0 (-17.5|-13.8) ^{f}	12.7 ± 0.6 (11.6|13.7) ^{cd}
2016	46	-15.0 ± 0.8 (-16.5|-13.6) ^{ef}	13.0 ± 0.7 (11.4|14.0) ^{acd}
2017	35	-14.5 ± 0.7 (-16.6|-13.5) ^{bcd}	13.0 ± 0.6 (11.7|14.9) ^{acd}

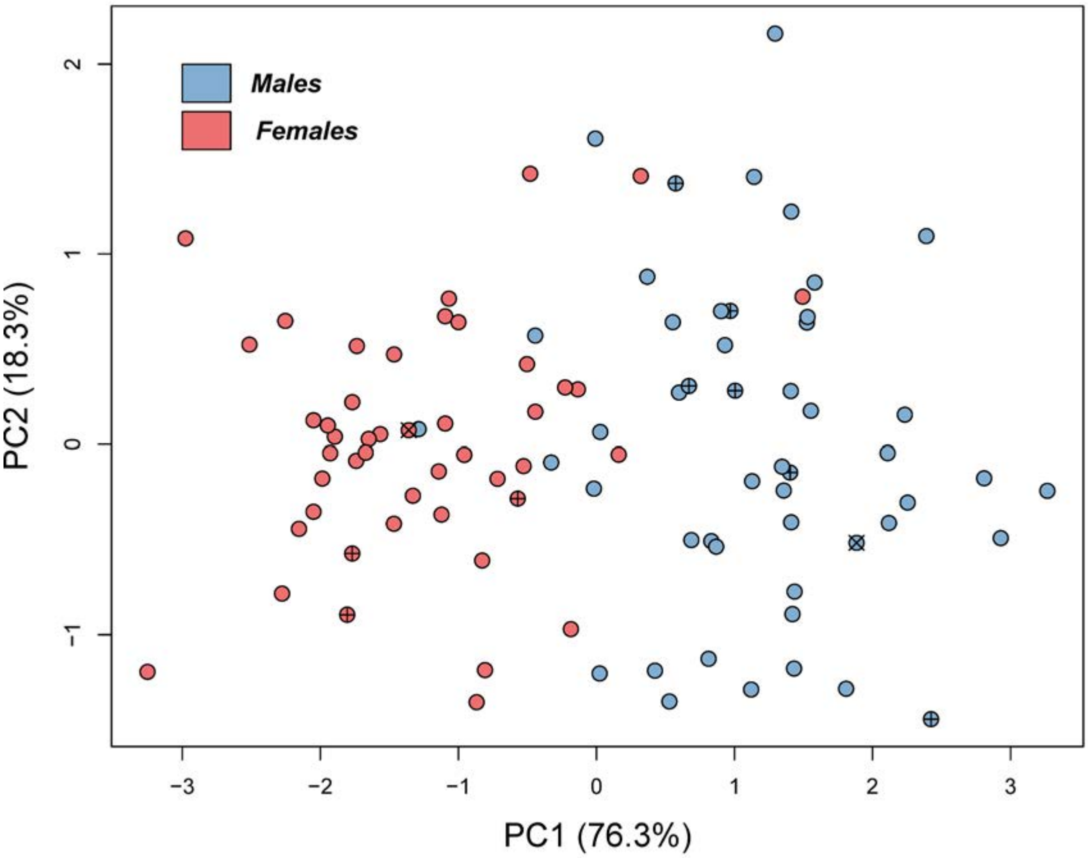


FIGURE S1 • Principal Component Analysis (PCA) of culmen, maximum bill depth, bill depth at nostril, and total head length (bill-head) used as variables to summarize the bill size of the individuals. Individual values of first and second Principal Components (PC1 and PC2, respectively) from the PCA are plotted according to the sex (blue for males and pink for females) and the isotopic repeatability ($R_{ind} > 0.4$ as circle plus for $\delta^{13}C_{adj}$ and as circle cross for $\delta^{15}N$) of every individual bird.

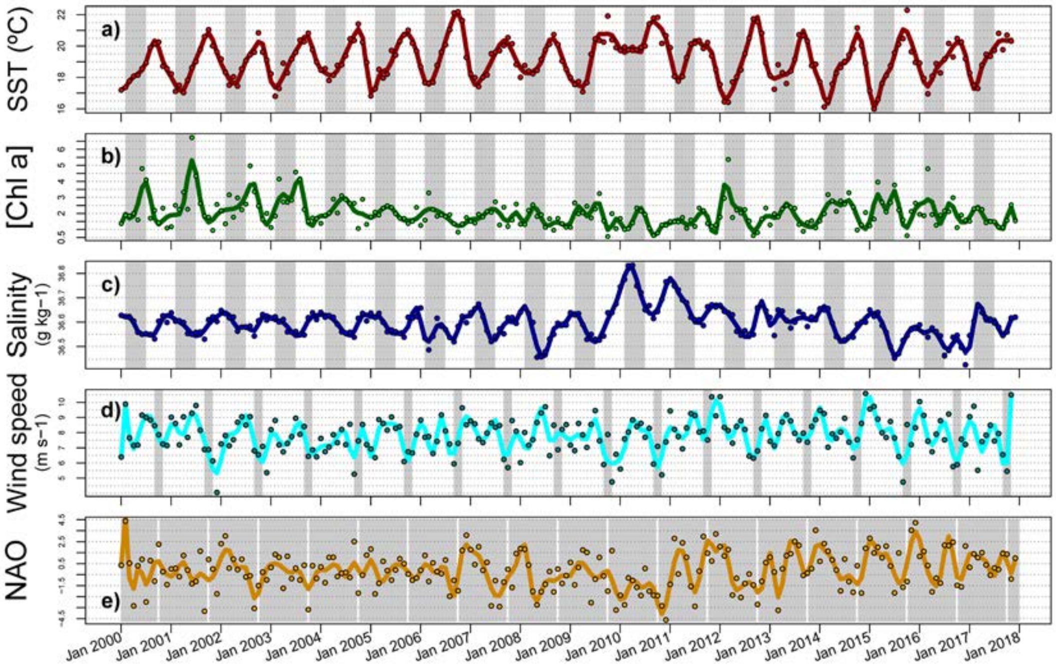


Figure S2 • Monthly estimates of environmental variables considered throughout this 17-year study, and to be correlated to the trophic ecology of Cory's shearwater. These included quantifications of the surface chlorophyll a concentration (CHLa, mg m^{-3}), sea surface salinity (SAL, g of salt per kg of water), sea surface temperature (SST, °C), wind speed (WIND, m s^{-1}), and the North Atlantic Oscillation index (NAO). Monthly estimates of the variable were extracted from https://www.marine.copernicus.eu (EU Copernicus Marine Service Information) and https://www.esrl.noaa.gov/psd/data/. Local environmental covariates were extracted only from those areas used during the eight years of GPS tracking and over the African continental shelf, defined as the main foraging area of the population (Fig. 1). While considering the most influential period of each environmental variable on the isotopic ratios of P1 feathers, we added CHLa estimates from February to June within every year to reflect the accumulated effect primary productivity of the CC, we averaged SAL and SST estimates for the same period to test for indirect trophic effects, we averaged WIND estimates from September to October to test direct manoeuvrability effects, and we averaged monthly estimates of NAO from October to September to account the environmental variability of every breeding cycle for the period 2000-2017. These specific influential periods are shown in grey (in the background) on each environmental variable plot.

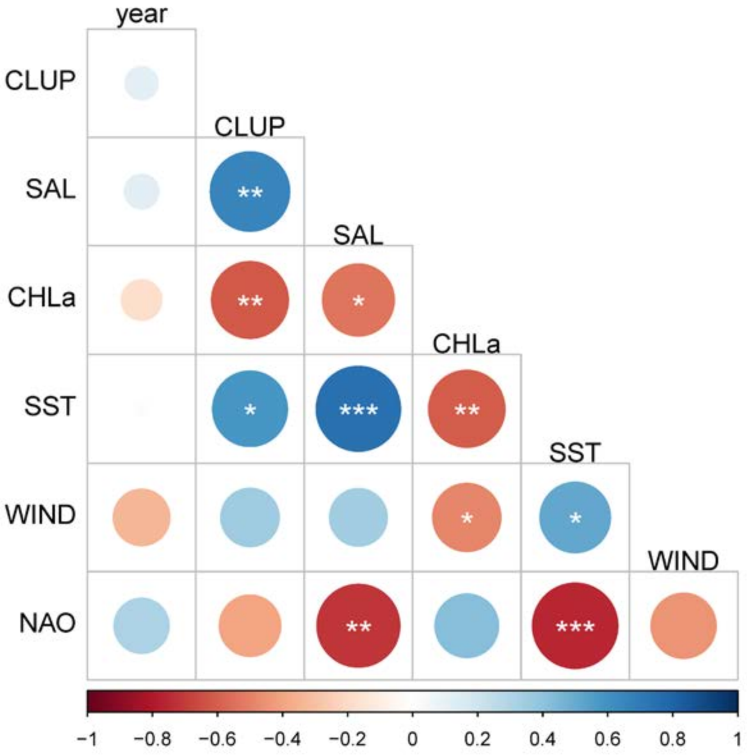


FIGURE S3 • Pairwise correlations among the six environmental explanatory covariates computed for their respective and most influential periods and year using Pearson's methodology. Pearson's coefficients are shown above the diagonal by coloured circles (from red for r= -1 to dark blue for r=1) as well as by circle size, and relevant significances are denoted by symbols: * for *P*-values < 0.05, ** for *P*-values < 0.01, *** for *P*-values < 0.001.

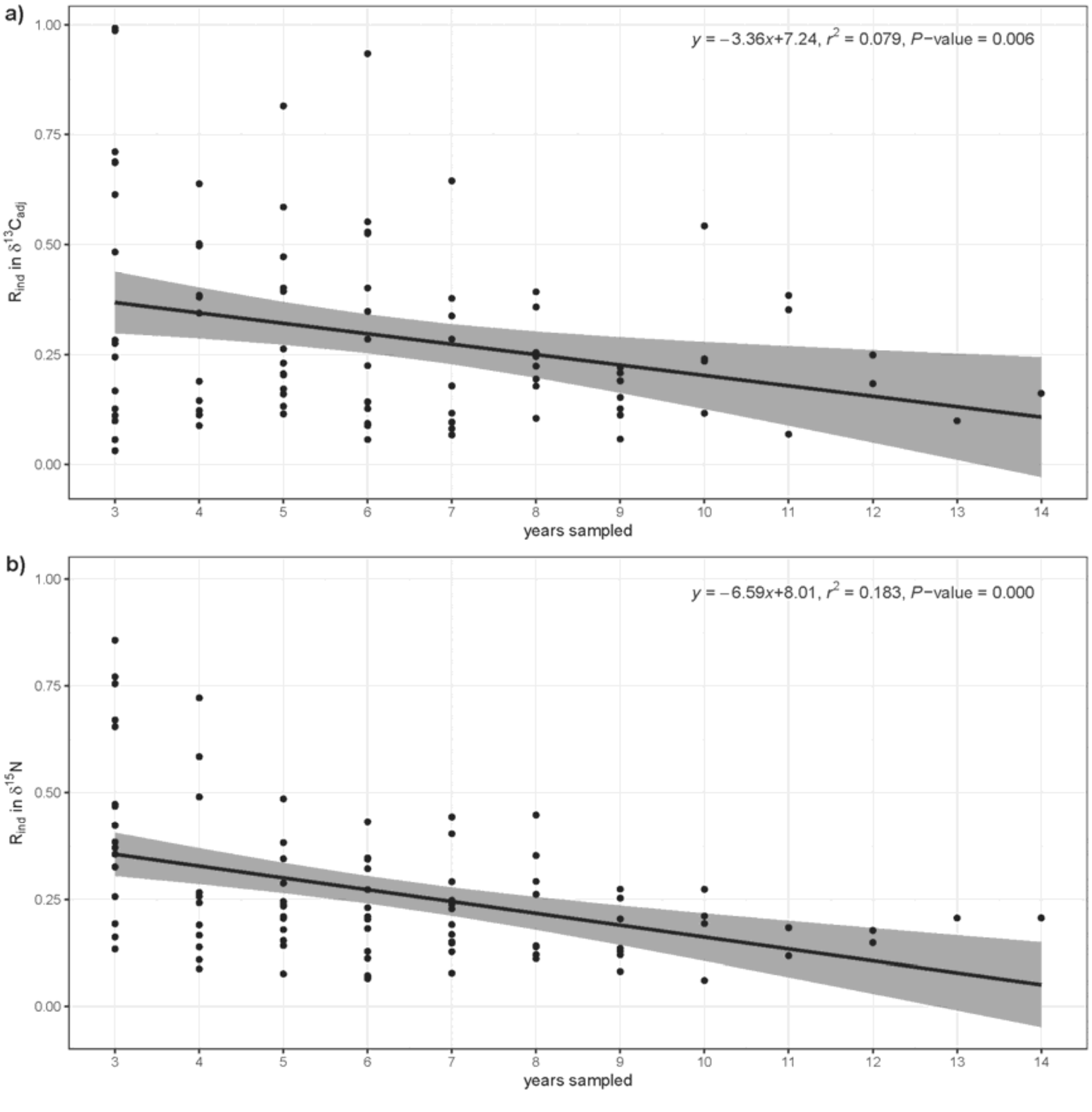


Figure S4 • Linear regression models between individual-level repeatability estimates (R_{ind}) of $\delta^{13}C_{adj}$ (a) and $\delta^{15}N$ (b) with the number of years an individual was sampled (99 individuals sampled from three to 14 times). Notice that both regression models are statistically significant.

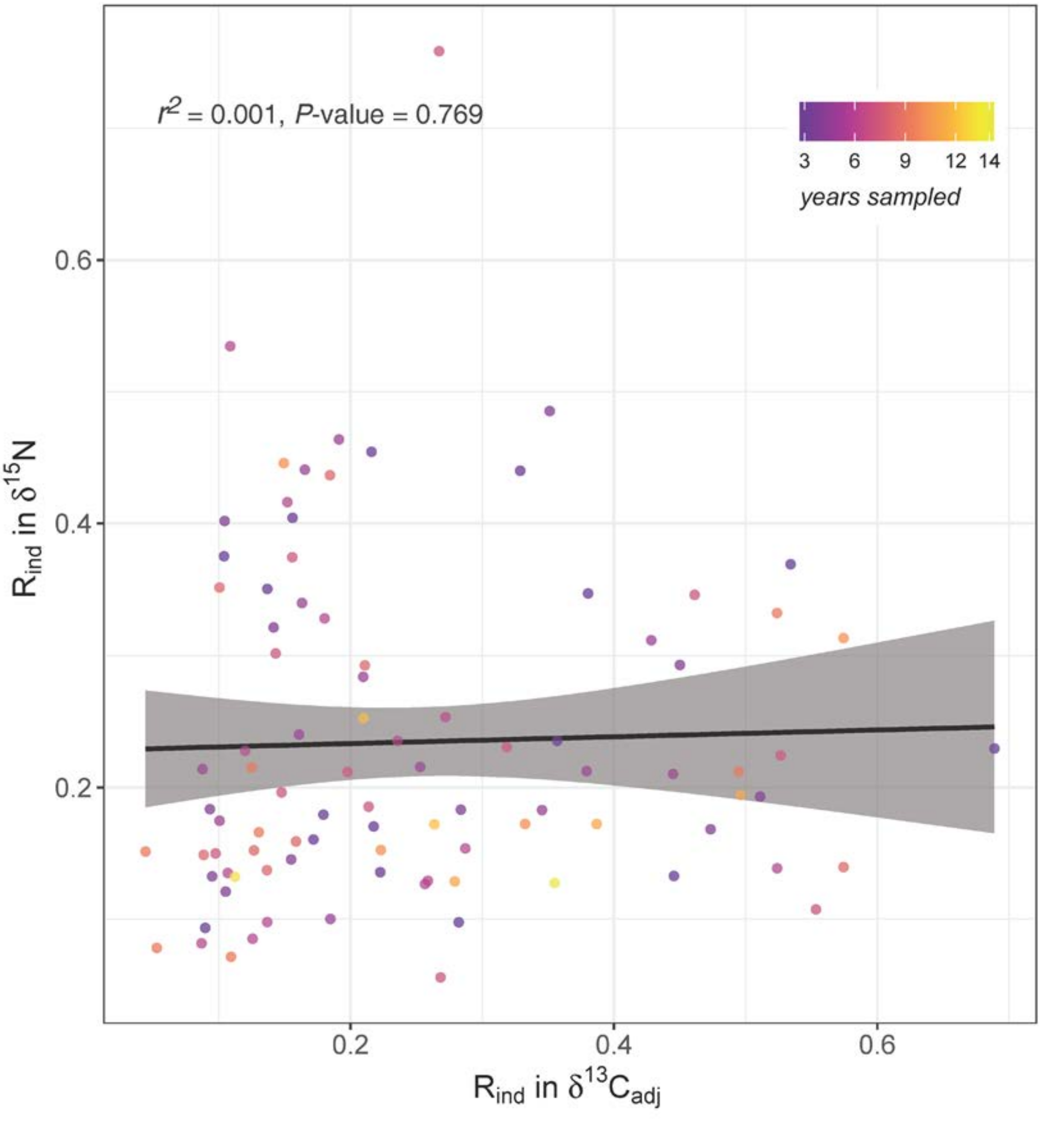


Figure S5 • Linear regression model between the residuals of those relationships of R_{ind} (of $\delta^{13}C_{adj}$ and $\delta^{15}N$) and the number of years an individual was sampled. Notice that the regression model is non-significant.

General Discussion

GENERAL DISCUSSION

The revolution in biologging and satellite telemetry technologies in the last two decades has led to a new era in seabird research, and has provided the knowledge needed to foster seabird conservation. Before the advent of such technology, researchers studied movements and distribution of seabirds at sea mainly through census from planes, vessels or the coastline. However, this approach is unaware of the origin of the birds observed, which mostly precludes the understanding of individual drivers —both internal and external— of their presence in the studied areas. Thanks to technology, it is now possible to fill this gap, addressing in unparalleled detail the life of seabirds at sea at multiple scales, from seconds to years, and from meters to thousands of km away from the breeding colonies where we tag them, thus allowing to know individual traits and their relation with the areas used at sea. In this way, we can study foraging movements and behaviour not only during the breeding period but also during the migration and at the wintering areas.

Along the six chapters of this thesis, I illustrate the potential and application of biologging in seabird research and conservation by providing a comprehensive overview of the spatial ecology of two pelagic seabird species, the Cory's and Scopoli's shearwaters. In particular, I provide new insights about their movement patterns, at-sea behaviour and the marine environment they inhabit throughout the year by the use of GPS loggers and light-level geolocators.

The results provided in this thesis extend our knowledge of the Spanish populations of two species of shearwaters, and support data-driven policies implemented to guarantee the conservation of these pelagic seabirds and their habitats. Significantly, the data presented here yield a better understanding of the ecology of seabirds from a behavioural perspective, which could improve hazard assessment and thus guide management actions. Finally, the thesis pinpoints the use of biologging devices and behavioural analysis as a way to enhance the role of seabirds as indicator species, thus fostering their performance as ocean sentinels for the management of marine ecosystems.

BASIC KNOWLEDGE OF A SPECIES AS A REQUIREMENT TO BECOME AN OCEAN SENTINEL

As explained in the Introduction of this thesis, Ecosystem-Based Management requires the use of indicator —sentinel— species to monitor fluctuations in the marine ecosystems (Hazen et al. 2019; Levin & Möllmann, 2015; Zacharias & Roff, 2001). When we intend to use certain species as sentinel, a solid knowledge of its biology is highly advisable (Hilty & Merenlender, 2000; Hyrenbach et al., 2000). To this aim, in **Chapter 1** we compiled a summary of previous research on Cory's and Scopoli's shearwaters published until 2017. This review covers most of the biological traits of the model species and represents the base-knowledge for interpreting the results of the following chapters. The amount of information gathered indicates that Cory's and Scopoli's shearwaters are probably among the most studied seabird species worldwide. However, under a closer look, we see that the amount of research in these species addressed using GPS loggers and geolocators represents only a small proportion of the total amount published (see **Box 4**). Therefore, despite being two well-studied species, there is still room for improving the knowledge in their spatial ecology using new technologies such as biologging.

AT SEA ECOLOGY: BOOSTING SEABIRD KNOWLEDGE AND CONSERVATION THROUGH BIOLOGGING

Seabirds depend on the oceans to live, but human activities are severely threatening the marine ecosystems (Field, Hempel & Summerhayes, 2013). To date, however, only 2.2% of the ocean is strongly protected (Gownaris et al., 2019). This lack of adequate protection at sea together with the threats at the breeding colonies have led to an accelerated decline of seabirds worldwide: ~50% of the species present declining population trends, and ~30% of the species are globally threatened (Croxall et al., 2012, Dias et al., 2019). Seabird populations breeding in Spain are no exception, and the Cory's and Scopoli's shearwaters are an example of the decline mentioned above (Carboneras, 2004; Lorenzo, 2004; Derhé, 2012; Sanz-Aguilar *et al*., 2016).

To curb this critical trend, we need to increase our knowledge of the spatial ecology of these species, to inform management actions and to take appropriate conservation measures. A better understanding of the spatio-temporal distribution of Cory's and Scopoli's shearwaters may enable the identification of areas overlapping with human activities, pointing out possible threats at sea (Montevicchi et al. 2012). In **Chapter 2,** we reveal the intensive use of the continental shelves by the tagged birds. Scopoli's shearwaters make intense use of the Levantine shelf, whereas Cory's sheawaters depend on the African shelf. Particularly in the case of Scopoli's shearwaters, the results also allow discerning the likely origin of birds that use the waters at the different maritime demarcations of Spain, which may assist and guide marine management. The great representativeness of the fieldwork sites during the breeding period, including 13 breeding colonies, strengths our findings. Also, the results reinforce the delimitation of areas identified by the *Sociedad Española de Ornitología* (SEO/BirdLife) as marine Important Bird Areas (IBA) in Spain and included in the Natura2000 network by the Spanish Government (Arcos et al., 2009). The NGOs SEO/BirdLife and the *Sociedade Portuguesa para o Estudo das Aves* (SPEA) were pioneers in the context of the European Union in addressing the identification of marine IBA in Spain and Portugal (Arcos et al., 2009). Such initiative was mostly based on biologging techniques, yet accompanied by data from census at sea (Arcos et al., 2009; Arcos et al., 2012; Lascelles et al., 2012).

The use of geolocators in seabird research has revealed that individuals from many species present a high fidelity to specific grounds at sea, despite the high dynamism of marine habitats (Patrick et al., 2014; Wakefield et al., 2015; Phillips et al. 2017; Yamamoto et al, 2014, Zango et al., 2019). In highly-mobile migratory seabirds spending a significant part of the year out of the breeding areas, our capacity to track their movements relies on long-lasting attachment using lightweight loggers. Almost 30 years after the invention of the light-level geolocators, these devices continue to be the most extended loggers used to track year-round movements of seabirds. Cost and weight, but also attachment methods, explain this fact. Because some seabird species, such as shearwaters and petrels, change body volume dramatically when dive, the use of a harness for long-lasting attachments of tracking devices is harmful and should be generally avoided (Mallory & Gilbert, 2008). Conversely, geolocators mounted on a plastic ring ensure the welfare of tagged individuals

Box 4

I performed a systematic literature review to evaluate the extent of scientific studies about the Cory´s and Scopoli´s shearwaters. In contrast to the review included in the Introduction, here I focused on more specific topic related to the use of seabirds as ocean sentinels, and extend the search until 2020.

First, I used *ISI Web of Knowledge* (Web of Science, Thomson Reuters & Clarivate Analytics) and Zoological Record databases to look for articles published. The search contained the following topic: *TOPIC: ((“Calonectris”) AND (“diomedea” OR “borealis” OR “diomedea borealis” OR “diomedea diomedea”)) OR (“Cory’s shearwater*”) OR (“Scopoli’s shearwater*”)*

After this search, I manually checked the output and excluded from the results all those not directly related to the study species. I performed the search over all years, however, I restricted the final visualisation only to years 1960 – 2020, as until 1960 only few articles were published. After the filtering, this search resulted in 597 published articles, seen as grey bars in the background in the Figure 1.

Additionally, I was interested in the number of published articles in specific areas of interest – topics. In relation to this thesis, I selected the following topics:

A) Biologging
In this topic I merged two searches conducted separately for GPS devices and geolocators.

GPS devices search:

> *TOPIC: ((“Calonectris”) and (“diomedea” or “borealis” or “diomedea borealis” or “diomedea diomedea”)) OR (“Cory’s shearwater*”) OR (“Scopoli’s shearwater*”)*
> *AND TOPIC: ((“GPS*” or “global positioning system”))*

Geolocators search:

> *TOPIC: ((“Calonectris”) and (“diomedea” or “borealis” or “diomedea borealis” or “diomedea diomedea”)) OR (“Cory’s shearwater*”) OR (“Scopoli’s shearwater*”)*
> *AND TOPIC: ((“geolocat*” or “gls*” or “light-level logger” or “global location sensing”))*

B) Ecosystem-Based Management (EBM) and Marine Spatial Planning (MSP)

> *TOPIC: ((“Calonectris”) and (“diomedea” or “borealis” or “diomedea borealis” or “diomedea diomedea”)) OR (“Cory’s shearwater*”) OR (“Scopoli’s shearwater*”)*
> *AND TOPIC: ((“marine spatial planning”) OR (“marine protected area*”) OR (“ecosystem-based management”))*

C) Fisheries

> *TOPIC: ((“Calonectris”) and (“diomedea” or “borealis” or “diomedea borealis” or “diomedea diomedea”)) OR (“Cory’s shearwater*”) OR (“Scopoli’s shearwater*”)*
> *AND TOPIC: (((“vessel*”) or (“fisher*”) or (“discard*”) or (“bycatch*”) or (“by-catch*”)))*

D) Bioindicator

> *TOPIC: ((“Calonectris”) and (“diomedea” or “borealis” or “diomedea borealis” or “diomedea diomedea”)) OR (“Cory’s shearwater*”) OR (“Scopoli’s shearwater*”)*
> *AND TOPIC: (“bioindicator*” OR “bio-indicator*” OR “ecological indicator*” OR “biomarker” OR “biomonitor*”)*

Results of each search were manually verified for the relation with the searched species and topic. The final number of articles considered within each topic is reflected in the Figure 1.

We can observe an increasing number of published articles on different aspects of biology and ecology of Cory's and Scopoli's shearwaters, in particular from the year 1980. However, the majority of articles published related to searched topics – and topics of this thesis– emerged mainly from the year 2010. Nevertheless, the articles specifically addressing topics in the framework of EBM and MSP are still scarce.

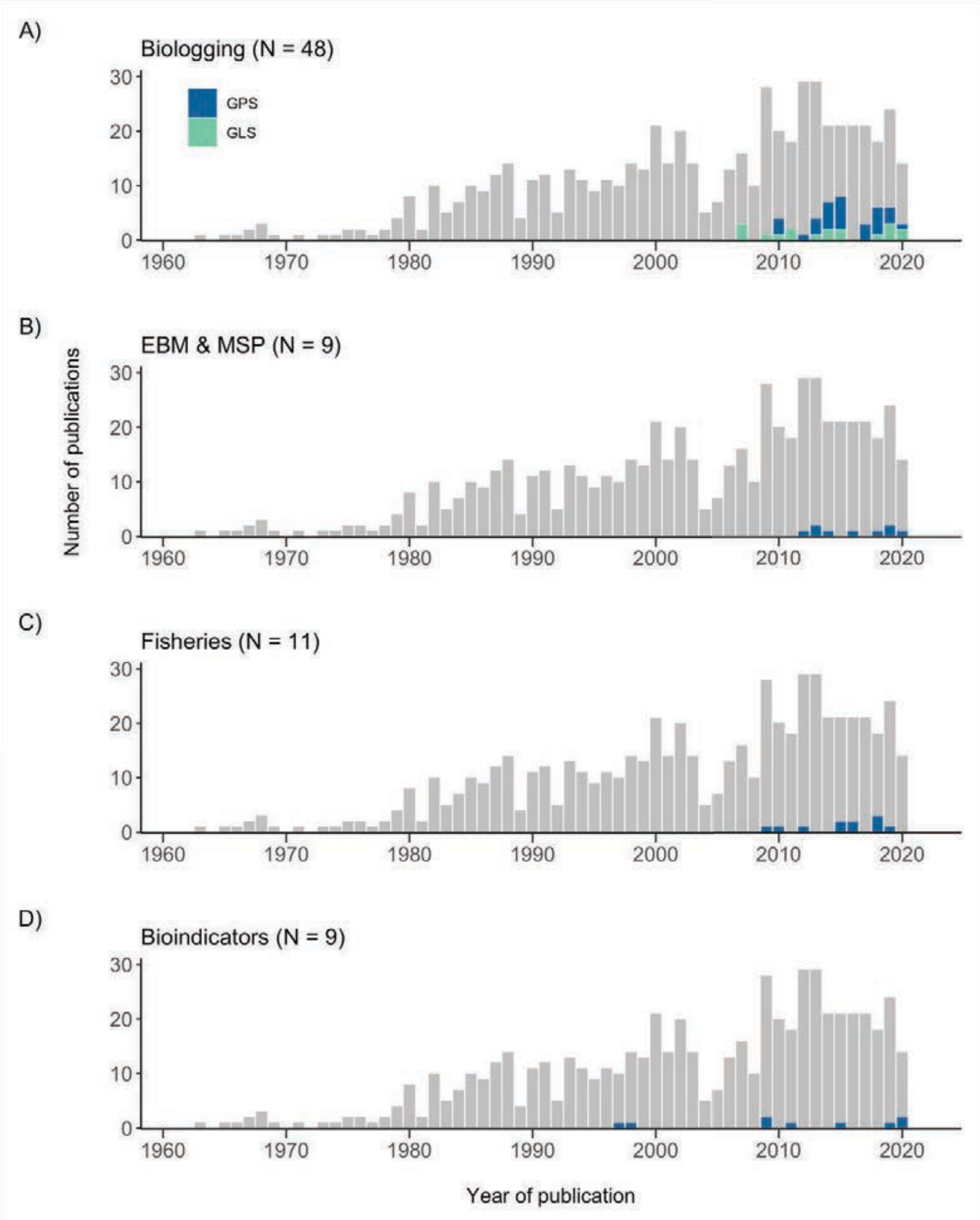


FIGURE 1 • Trend in the number of published research articles related to some extent with the Cory's and the Scopoli's shearwaters. The grey bars in the background refer to total number of articles considered in the timespan between 1960 – 2020 (N = 597 articles). Each facet highlights one of the searched topics of interest: A) Biologging (GPS devices and geolocators), B) Ecosystem-based management and Marine spatial planning, C) Fisheries and D) Bioindicators. See text in the Box 4 for more details regarding the search.

(Igual et al., 2005). In **Chapter 2,** we used geolocators to characterise year-round movements, including the identification of migratory corridors and the wintering areas of birds from different breeding colonies. The results show a diversity of behavioural strategies among individuals, not only in wintering destinations but also in at-sea behaviour. Such diversity likely allows birds to cope with the different environmental conditions they face at each of the different wintering areas, in order to maximise prey encounter (Dias et al., 2012; Zango et al., 2019). In addition, we found a high spatial consistency at the individual level over the years in the wintering areas used. Besides, looking at the population level, migratory connectivity was also high. Both results point in the same direction and have significant relevance in terms of conservation, indicating that threats, as well as management actions in the maritime domain of the wintering areas, may have a direct impact on specific breeding colonies in Spain (Dunn et al., 2019). These insights suggest that international collaboration is critical to improving the conservation status of pelagic seabird species (Dunn et al., 2019; Jodice & Suryan, 2010; Louzao et al., 2012). Also during the breeding period, birds from both species crossed boundaries and visited waters of different national jurisdictions, as shown by GPS data. In fact, the transboundary nature of pelagic seabirds is a great challenge for the conservation of pelagic, highly-mobile species, which at the same time reinforces the need for the ecosystem-based management approach (Jodice & Suryan, 2010). Results from **Chapter 2** also show that birds span both national waters and areas beyond national jurisdiction (i.e., within and outside Exclusive Economic Zones, respectively) not only during wintering but also during migration, which highlights the importance of the high seas for some populations (Dunn et al., 2019). These findings bring up the need of the involved states to reach international consensus and take responsibilities in the management of biodiversity in international waters (Beal et al., 2021; Hooker et al., 2011; Kark et al., 2015).

Finally, it is worth mentioning that **Chapter 2** places value on popular science. This chapter is a shortened version of a book originally published in Spanish by SEO/BirdLife, which aimed to get the message of ensuring the conservation of these species across the society. To grab people's attention, we reduced to the minimum the methodological content and instead included visually appealing content (such as figures and animations). As it was emphasised in the Introduction of this thesis, Cory's and Scopoli's shearwaters are charismatic species. Therefore, they provide an excellent path to show to society how science and technology can contribute to the conservation of biodiversity and marine habitats (Novacek, 2008).

THE ROLE OF FISHERIES IN SEABIRD FORAGING STRATEGIES

Fishing activity is one of the primary disturbances for marine ecosystems (Halpern et al., 2015). The behaviour of fishing fleets also relates to environmental conditions (Lloret et al., 2001). Fisheries can affect seabirds in different ways, including changes in behaviour and trophic ecology, yet little is known about the interplay between fisheries and environmental conditions on seabird behaviour (Wagner & Boersma, 2011). In **Chapter 3**, we show that individuals of Scopoli's shearwater modify foraging strategies according to annual environmental condition, attending fishing vessels more in favourable years. These results highlight the importance of multiyear analyses to evaluate the impact of fisheries at individual scale in top-predators. The interaction with the fishing fleet operating in the Northwestern Mediterranean was already reported in this species, though not at multiyear scale (Soriano-Redondo et al., 2016). Also, Genovart et al. (2018) provided evidence on the effects of fishing activity and bycatch on the individual survival and population trends of this species.

Our results extend the evidence on the association of seabirds with fisheries, which has been reported worldwide (Furness et al., 2003). It is known that this association can have deep consequences in seabird ecology, modifying foraging movements, diet or breeding success among others (Arcos et al. 2002; Arcos et al. 2008; Grémillet et al. 2008; Bartumeus et al. 2010). In the case of the Scopoli's shearwater in the Northwestern Mediterranean, in European waters, the ban of discards following the European Union regulation may represent a conservation concern, due to the unpredictable changes that discard ban could promote in seabird community (Bicknell et al. 2013; Real et al., 2018). However, according to our results, the population from Balearic Is. seems to be plastic enough to modify their attendance to the fishing fleet if discards are finally banned. Nevertheless, in front of this new scenario, the possible increase in attendance to longlining should be monitored (Soriano-Redondo et al., 2017). Indeed, an increase in bycatch rates could drive to a severe decline in this population, which not only would reduce adult survival but also would likely promote a high sexual unbalance, as **Chapter 3** suggests.

Such interaction between seabirds and fisheries could also allow evaluating fishery pressure using seabirds as indicator species (Einoder, 2019; Scopel et al., 2018). Long term overexploitation by fisheries can alter the food web structure of marine ecosystems, and thus, it may be detected using seabirds as a surrogate (Branch et al., 2018; Gagne et al. 2018). In **Chapter 6**, we study the trophic ecology of the Cory's shearwater foraging in the Canary Current ecosystem as a proxy of changes in the trophic food web due to fishing activity. From the analysis of a 17-year dataset of individual monitoring, we did not detect changes in the structure of the food web of the Canary Current marine ecosystem, despite the intense fishing exploitation that this ecosystem supports from local and industrial fisheries (Sambe et al. 2016, Sánchez-Garrido et al. 2019). This case illustrates how using seabirds as model species may advise the regulation of fisheries to prevent changes in the ecosystem before they become irreversible.

Regarding fisheries, this thesis sums up to the literature, which overall indicates a strong impact of the fishing activity on different life-history traits of seabirds (e.g., Bodey et al., 2014; Camphuysen & Garthe, 2000; Gagne et al., 2018; Patrick et al., 2015; Sherley et al., 2020;. Therefore, fishery management should consider seabird-fisheries interaction as a central issue within the framework of ecosystem-based management and marine spatial planning (Jennings & Kaiser, 1998; Norse, 2010; Rätz et al., 2010).

TEMPORAL SHIFTS IN FORAGING STRATEGIES RELATED TO ENVIRONMENTAL CONDITIONS, SEX AND BREEDING STAGE

Individual foraging strategies are inherently linked to the environment (MacArthur & Pianka, 1966). In **Chapter 3** and **Chapter 6** of this thesis, we evaluated the interannual variability of foraging patterns and the link with annual environmental conditions in the Northwestern Mediterranean and the Northwest African shelf, respectively. In marine habitats, resources patchily distributed yet aggregate at different scales, being overall more predictable at a coarse-scale and unpredictable at a fine-scale (Weimerskirch, 2007). At a coarse-scale, productivity is often more predictable in relation to oceanic physical features, such as upwellings, sea fronts, or river plumes (Cox et al., 2016; Daudt et al., 2019; Phillips et al., 2018; Scales et al., 2014). Nevertheless, the intensity of these predictable features (and thus resource abundance) depends on seasonality and atmospheric conditions (e.g., winds, rain), which ultimately depend on macro-scale clime processes (Narayan et al., 2010).

Some global scale index, such as the North Atlantic Oscillation index (NAO), perform well to point out interannual variability in environmental conditions. Indeed, the analysis of NAO has allowed tracking drastic changes at the interannual scale in upwelling regions and river plumes (deCastro et al., 2008; Trigo et al., 2011). In **Chapter 3**, we used NAO as a proxy of environmental conditions in the Northwestern Mediterranean. Despite using the same foraging areas overall, Scopoli's shearwaters increased foraging effort in years with unfavourable conditions, likely to cope with low resource availability. In **Chapter 6**, we also used NAO as a proxy of interannual variability in upwelling intensity and thus resource abundance in the Canary Current. In this case, we found that Cory's shearwaters reflected the upwelling interannual variability in their trophic ecology. The effect of interannual variability on seabirds has also been reported for other populations of the species, which pinpoints its plasticity to face changes in the environment, and the possibility of monitoring interannual fluctuations in the marine ecosystems through this species (Paiva et al., 2013; Pereira et al., 2020).

The role of environmental features in determining seabird foraging distribution has been widely studied (Tremblay et al., 2009). Going further, some researchers have suggested that seabirds might use environmental features as foraging cues, yet few have investigated this issue (Belincourt & Arnould, 2015; Shoji et al., 2016). Moreover, this issue has never been addressed from the point of view of individual decision-making. In **Chapter 4**, we wondered whether individuals might use the proximate environment to inform the trip destination. We used cutting-edge methods to evaluate a set of candidate environmental futures perceived by the birds. Among the variables considered, sea surface temperature was likely the most important in determining that birds decide to perform short or long trips. Water temperature in the marine environment plays a significant role in the ecology of marine vertebrates (McMahon & Hays, 2006). In a superb review recently published, Favilla & Costa (2020) precisely set up how marine habitats provide a significant thermoregulatory challenge for marine vertebrates. Morphological and physiological adaptations of seabirds likely allow them to perceive sea surface temperature at a fine scale and learn to relate temperature gradients with a likelihood of prey encounter. Since biologging provides sound devices to measure temperature, this issue clearly merits further attention by the biologging research community.

Looking at a within-year scale, during the breeding season, differences in foraging strategies are likely related to breeding constraints (Hedd et al. 2014, Quillfeldt et al. 2014; Shoji et al., 2016). In **Chapter 4**, we show how foraging strategies, particularly behavioural budgets, shift over the breeding period, as a result of the different breeding constraints at each breeding stage. Chick-rearing is the most demanding task, and therefore it is when adult breeders invest more time in foraging (Gaston, 2004). Results from Chapter 4 also suggest considering variability between breeding stages in tracking studies, especially in those aimed to identify candidate at-sea areas for protection, since focusing in a single stage may overlook areas notably relevant at the population level in other stages (Krüger et al., 2017; Oppel et al., 2018).

Individual traits, such as sex, also promote differences in foraging strategies (Phillips et al., 2011). In general, we found that females, which are slightly smaller than males, seems to be outcompeted by males. In Cory's shearwaters from Canarias, we found females to perform longer trips (both in time and duration), over the breeding period. In Scopoli's shearwaters from Balearic Is., we found the same pattern for the chick-rearing stage. Most of the research investigating sexual differences in foraging patterns focus on species with sexual size dimorphism (Phillips et al., 2004; Shaffer et al., 2003; Sztukowski et al., 2008), whereas differences in species with slight sexual size dimorphism may pass overlooked. Since sex can lead to different spatial patterns at sea, it would be advisable to consider sex as a relevant feature in tracking studies even when no differences in size between sex exist (De Felipe et al., 2019). In this regard, results from **Chapter 3** also highlight the value of individual tracking data to monitor annual fluctuations of ecosystem components. Even though birds generally showed consistency at population scale in the use of the foraging areas over the years (the Catalan shelf and the Minorca Channel), individual tracking data allowed to evince sexual spatial differences each year depending on the annual conditions. Individual traits, such as sex, are impossible to assess in these species when observed from a vessel (Blomdahl, 2003). Thus, species distribution models based on census data might systematically overlook this issue, leading to deceptive results, particularly when the scale of sexual differences in foraging patterns may vary between years, as shown in Chapter 3.

AT-SEA BEHAVIOUR AS A QUANTIFIABLE METRIC TO ENHANCE THE ROLE OF SEABIRDS AS OCEAN SENTINELS

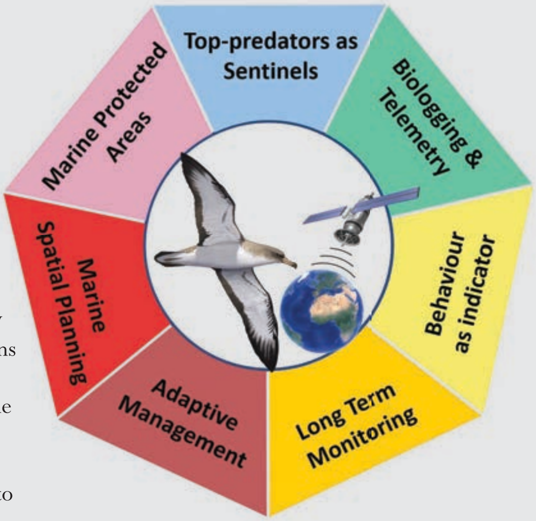
Advances in biologging and tracking technologies have been accompanied by intense development of machine-learning algorithms to infer behaviour (Bennison et al., 2018; Joo et al., 2020). Along this thesis, I took advantage of one of these methods, the *EMbC*, to infer behaviour and later on quantify behavioural metrics. These methods have paved the way for the use of behaviour as an indicator per se. Despite the species presence, abundance or distribution are frequently used as indicators to track ecosystem changes, there are many situations in which the animal behaviour may perform as an indicator even better than those mentioned before (Berger-Tal & Saltz, 2016). Changes in behaviour may provide an early warning expected from a good indicator. Behaviour can be related to the drivers of change (in our case, thanks to excellent knowledge of the model species). Moreover, it can provide a continuous assessment within long term tracking programmes. Furthermore, thanks to tracking devices and current analytic algorithms, the behaviour is easy and cost-effective to measure (Berger-Tal & Saltz, 2016). Therefore, tracking seabirds through biologging or remote telemetry, coupled with behavioural inference, can enhance the suitability of seabirds as ocean sentinels. In **Chapter 5**, we illustrate, as a proof of concept, a pilot study addressing this issue. Within the framework of the Spanish National Parks with a maritime domain, we tracked Cory's shearwaters with GPS, identified behaviour along the individual tracks, and calculated a variety of metrics to evaluate the behaviour exhibited by the birds in different areas and periods. Even though the project spanned only two years, the methodology developed could be incorporated in a long-term monitoring programme, using behaviour as an early warning indicator of fluctuations in the marine ecosystem (see Box 5).

LONG-TERM MONITORING

Long-term monitoring of the foraging behaviour of seabirds can help understand the medium- to long-term effects of environmental fluctuations in marine ecosystems (Paiva et al., 2013). In **Chapter 6**, we combined GPS tracking and Stable Isotope Analysis into a long-term monitoring programme, which allowed us to evaluate the changes in the trophic web structuring. Moreover, through this long-term approach we explored in-depth the relevance of individual specialisation, leading us to discern trophic specialist from generalist within the studied population (Pagani-Núñez et al., 2016). Grémillet and Charmantier (2010) argued the need to know the strength of the average plastic response of individuals in foraging preferences to use a seabird population as a long-term indicator. Our study, presented in Chapter 6, contributes to filling this gap, providing new insights into the individual long term monitoring and the use of seabirds as ocean sentinels.

Box 5: Conceptual framework about the combined use of seabirds and *biologging* as a tool for marine management

- Marine ecosystems are **highly dynamic**
- **Marine Spatial Planning** considers dynamism through an Adaptive Management approach
- To inform **Adaptive Management** strategies we need appropriate **Long Term Monitoring programmes** (LTM)
- LTDM need indicators to measure ecosystems dynamics
- **Top-predators** integrate ecosystem functioning, and they are also highly sensitive to ecosystem shifts and perturbations
- **Seabirds** are top-predators easy to track and respond to the dynamism of marine ecosystems
- **Seabird tracking** may provide a cost-effective approach to be incorporated within LTM and provides a tool for Marine Spatial Planning



UPCOMING CHALLENGES

The development of policies and strategies able to guarantee the good environmental status of marine ecosystems needs to take into account the dynamism of the marine environment. Conversely to the classical approach of static area-based management, a new approach aims to consider the dynamism of all the components in the marine realm (Oestreich et al., 2020). The dynamic management approach is built upon the adaptive management framework (Hobday et al., 2013). However, it goes further, proposing the use of near real-time data to feed supporting-decision systems (generally, well-trained predictive models), which will ultimately guide management actions (Lewison et al., 2015; Maxwell et al., 2015). This conceptual framework incorporates the particularities of highly mobile top predators across ocean basins, and thus approaches better the vision of ecosystem-based management (Hays et al., 2016). Dynamic management also increases the efficacy and efficiency of fisheries management over static approaches (Dunn et al., 2016). Biologging and remote tracking technologies can foster dynamic management, not only by providing the training data for tunning predicting models, but also to feed them with new data in near real-time to update prediction. Indeed, this approach is already working in important marine ecosystems such as the California Current, where it is used to manage marine traffic pathways in order to avoid collision with cetaceans (Hazen et al., 2017). In the case of seabirds, there is already a pilot study in which albatross were equipped with state-of-the-art loggers for monitoring fisheries and fight against illegal unreported and unregulated fishing (IUU) in remote areas (Weimerskirch et al., 2020). The incorporation of biologging and tracking technologies within the dynamic management framework is probably the most upcoming challenge in the use of seabirds as ocean sentinels.

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Conclusions

CONCLUSIONS

Regarding the spatial ecology and foraging patterns during the breeding period:

1. Both species showed a clear preference to forage in neritic areas. Cory's shearwaters from the Canary Islands consistently foraged along the highly productive African shelf, performing foraging trips of up to 1 000 km. In the Mediterranean, birds foraged along the Iberian coast, from the Strait of Gibraltar up to the Gulf of Lyon.

2. The analysis of behavioural budgets confirmed the importance of breeding constraints in shaping foraging strategies over the breeding period. Trip parameters, together with stable isotope analysis, indicate that Cory's shearwaters from the Canary Islands perform the dual-foraging strategy.

3. Females consistently show more significant effort than males in foraging parameters, both during the breeding period and at multi-year scale.

Regarding the migratory strategies and wintering distribution:

4. Both species exhibit complex migratory patterns, with a diverse array of wintering destinations over the Atlantic. Cory's shearwaters used a greater number of wintering areas than Scopoli's shearwaters, with more complex migratory detours.

5. Most individuals spent the boreal winter in nutrient-rich areas of the Atlantic Ocean. A few Cory's shearwaters reached the Mozambique Channel in the Indian Ocean.

6. The most important wintering area for the Cory's shearwater was the south of Africa, off the coast of Namibia and the Benguela Current, while the Canary Current was the main wintering area for the Scopoli's shearwater. Some of the wintering areas of the Cory's shearwater are adjacent or partially overlapped with the wintering areas of the Scopoli's shearwater. Both Cory's and Scopoli's shearwaters present high wintering site fidelity.

Regarding the interaction with fisheries:

7. A 17-year long-term study based on longitudinal data of monitored individuals did not show evidence of disturbance in trophic structuring in the Canary Current, despite the intense fishing pressure in this ecosystem.

8. The interactions with fisheries were higher in favourable environmental conditions, likely because of a greater availability of discards in such conditions.

9. The probability of fishery attendance was two times higher in males than females. This figure likely explains the higher rate of bycatch for males reported in this species.

Regarding the environmental conditions:

10. In unfavourable environmental conditions, the competitive exclusion of females by males likely increases. Females are more likely to perform longer trips than males.

11. Cory's shearwaters may use sea surface temperature in waters near the colony as a foraging cue. Individual engagement in short or long trips seems to depend on this environmental feature.

Regarding the use of seabirds as sentinel species:

12. Seabirds integrate ecosystem functioning and are highly sensitive to ecosystem shifts and perturbations. Moreover, they are easy to track using biologging devices, such as GPS loggers or geolocators by light. State-of-the-art methods allow to characterise and quantify behaviour, which may react faster than species distribution to changes in the environment.

13. A good knowledge of the natural history of a candidate species to be used as a sentinel is critical to support such use since it helps to interpret movement and behavioural patterns recorded with loggers.

14. Seabirds are suitable species to carry out long term monitoring programmes, which help to discern environmental from individual effects. This kind of programmes can help to evaluate temporal trends in complex marine ecosystems such as upwellings.

15. Seabirds are suitable and cost-effective species to be incorporated into management strategies. Tracking systems and behavioural analysis can enhance the performance and increase the reliability as ocean sentinels for the marine ecosystems.