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Ecological response of marine predators to environmental heterogeneity and spatio-temporal variability in resource availability

Isabel Afán Asencio

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Estación Biológica Doñana CSIC

Ecological response of marine predators to environmental heterogeneity and spatio-temporal variability in resource availability

Resposta ecològica de depredadors marins a l'heterogeneïtat ambiental i a la variabilitat espai-temporal en la disponibilitat de recursos

Memòria presentada per **Isabel Afán Asencio** per optar al grau de **Doctora** per la **Universitat de Barcelona**

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A mis padres
A mi hermana

Acts in what Hutchinson (1965) has called the 'ecological theatre' are played out on various scales of space and time to understand the drama, we must view it on the appropriate scale

(Wiens 1989)

TABLE OF CONTENTS

ABSTRACT

Seabirds have evolved within an open and dynamic environment, the ocean. As meso-top predators, seabirds are greatly influenced by the oceanographic conditions driving marine productivity, and therefore, distribution of their prey. Consequently, seabirds' behaviour and, ultimately, life-history traits are greatly influenced by the ever-changing oceanographic conditions. However, oceanographic conditions are currently changing at ever-increasing rates due to global warming and human harvest impacting marine ecosystems. Thus, seabirds have become particularly vulnerable to these changes. Accordingly, in this thesis, we investigated the ecological responses of seabirds, in terms of foraging and breeding performance, to the spatio-temporal variability of environmental conditions imposed by oceans and exacerbated by climate and human stressors. In particular, we (i) identified the climate and human stressors impacting the world's ocean, (ii) investigated the actual scale at which seabirds interact with their environment, (iii) assessed how seabirds respond to oceanographic variability by changing their foraging and reproductive strategies and (iv) proposed an integrative tool for the design of marine reserves protecting seabirds and their environment.

The objectives of this thesis were accomplished through advanced procedures in the fields of satellite remote sensing and animal tracking. Our results confirmed the unprecedented changes experienced by oceans in the last decades. However, we were able to provide deepest insights on the uneven distribution of climate and human driven environmental changes. When investigating the link between such environmental variability and seabirds' behaviour, we found that dynamic processes as ocean currents were key factors determining the scale at which seabirds interact with their environment. Environmental features driving the spatiotemporal distribution of prey (e.g. sea surface temperature, chlorophyll-a, sea fronts and persistent areas of productivity) along with industrial fisheries played a fundamental role in determining the foraging distribution of seabirds. However, seabirds' foraging strategies were largely constrained by limitations imposed by their central-place foraging behaviour and by dynamic factors such as prevalent winds, which influenced individual decision-making in heading directions when foraging. Intra and interspecific competition for resources also modulated foraging distributions, avoiding conspecifics or segregating foraging areas among sympatric species in appropriate stages. In general, we have provided a complete picture of environmental processes affecting seabirds. We argue that this information would be extremely useful for designing suitable management and conservation strategies. Thus, we finally proposed an adaptive framework for delimitation of more meaningful marine reserves that maximises conservation targets for seabirds, while accounting for human activities, environmental and biological factors largely driven seabird performance and, remarkably, the dynamism inherent to marine systems.

Keywords: seabirds, foraging strategies, remote sensing, oceanographic features, tracking, chlorophyll-a, sea surface temperature, scales.

INTRODUCTION

» Recent changes in marine ecosystems

The world's ocean, covering about 70% of the Earth's surface, plays a major role in the Earth's climate. The ocean accomplishes a key role in the transfer of heat energy across the globe, and stores large amounts of carbon, buffering surface warming (Wu, L. et al., 2012). Oceans also provide humans with a wide variety of services, including food. Nevertheless, human activities have been the cause of profound disturbances on marine ecosystems, particularly during last decades (Halpern, B.S. et al., 2015; Halpern, B.S. et al., 2008). In particular, environmental changes caused by both climate and human stressors have imposed novel challenges for marine ecosystems.

Climate stressors

The exponential rise of greenhouse gases in the atmosphere has been the major driver of surface warming and accordingly, upper layers of the ocean have absorbed most of this extra heat, increasing their average global temperature by 0.2ºC per decade over the past 30 years (Hansen, J. et al., 2006; Hoegh-Guldberg, O. & J.F. Bruno, 2010). The warming of the oceans has disturbed their physical parameters and dynamic, promoting greater stratification in upper-ocean layers (Shackell, N.L. et al., 2009), which influence oxygen and nutrient availability and, hence, primary production. These patterns are correlated with changes in ocean circulation influencing coastal upwelling world areas of enhanced productivity (Sydeman, W.J. et al., 2014). Responses to current drifts may have consequences in terms of population dynamics, survival and recruitment of diverse marine populations, such as plankton and fishes (Fossette, S. et al., 2015). As a consequence, marine productivity has experienced local increases or decreases in an uneven way across the globe, but with no significant overall trends (Behrenfeld, M.J. et al., 2006; Keeling, R.F. et al., 2010).

As a result, marine ecosystems have been affected in their structure (biodiversity distribution; Cheung, W.W.L. et al., 2013; Dulvy, N.K. et al., 2008; García Molinos, J. et al., 2015) and function (nutrient cycling; Boyce, D.G. et al., 2014; Doney, S.C., 2010). Climate change disrupts marine ecosystem productivity and trophic pathways from primary producers to upper-trophic levels, propagating changes throughout ecosystems in both bottom-up and top-down directions (Grémillet, D. & T. Boulinier, 2009; Paiva, V.H. et al., 2013).

Human stressors

Together with climate change, other human activities as fishing may also cause food web disturbance in marine ecosystems. Since 1950, when data on fishing activity have been recorded (Pulvenis, J.-F., 2014), global fishing intensity has been growing continuously with an average increase of 10-fold, although catches slowly declined from the late 1980s (Pauly, D. et al., 2002; Watson, R.A. et al., 2013). At the present time, almost 50% of world fish stocks have been depleted and nearly 30% are overfished (Einoder, L., 2009), with 35% of the productivity of the oceanic shelf intended for human consumption (Sanderson, E.W. et al., 2002). Intense fishing pressure has also modified drastically the top-down control of marine ecosystems (Shackell, N.L. et al., 2009). Overfishing has induced changes not only in composition and abundance of species (Myers, R.A. & B. Worm, 2003), but has also affected local food-web persistence, decreasing their capacity to withstand further environmental degradation (Gilarranz, L.J. et al., 2016), with far-reaching consequences on ecosystem functioning (Anderson, C.N.K. et al., 2008). Moreover, fisheries activities have ecological impacts on species with no commercial value that become hooked accidentally by fishing gear. Incidental take, or bycatch, affect many vulnerable predator species as sea turtles, seabirds or marine mammals, with mortality levels proportional to intensifying fishing effort (Lewison, R. et al., 2004).

» Marine predators facing sea change: under the umbrella of seabirds

Marine predators, like all animals, require food in order to survive and leave offspring. While taking upper trophic levels of food webs, marine predators incorporate the processes and trophic interactions of the entire food web below them. Therefore, food web disruptions due to climate change are expected to have a profound bottom up impact upon these organisms (Grémillet, D. & T. Boulinier, 2009; Paiva, V.H. et al., 2013). There is also no doubt that negative interactions with fisheries, as bycatch, are among the current threats to marine predators, especially for seabirds (Phillips, R.A., 2013). Accordingly, marine predators such as seabirds are excellent models of study of the integrated ecological impacts of climate and human stressors on the marine environment.

Seabirds are important mid-top predators in marine ecosystem food webs. As reflection of the underlying state of oceanic systems, marine predators, particularly seabirds, play pivotal roles in assessments of marine ecosystem health (Croxall, J.P. et al., 2012; Sydeman, W.J. et al., 2015): they occur worldwide and are relatively easy to observe, they operate at the apex of marine food webs, and are likely integrating ecological processes occurring across lower trophic levels (Grémillet, D. & A. Charmantier, 2010). For this reason, they could act as sentinels, i.e., allowing early warning signals about changes in ocean environment and alerting in case of unknown pollution or food supply

problems (Frederiksen, M. et al., 2007; Furness, R.W. & K.C. Camphuysen, 1997).

Seabirds are exceptionally well-studied compared with other groups of marine predators. Decades of seabird research have strengthened the role of seabirds in marine ecological processes (Schreiber, E.A. & J. Burger, 2001). But in recent years, novel conceptual and technological advances have revolutionized our ability to remotely observe both, the oceanographic environment (remote sensing data, Box 1) and seabirds (tracking devices). This has meant a breakthrough on understanding the interplay between spatio-temporal variability of the environment and the behavioral responses of populations, embracing one of the main gaps in seabird research priorities (Lewison, R. et al., 2012).

» The sea: a complex, dynamic and endless environment

In marine systems, wide-ranging seabirds operate in a vast, ever-changing and three-dimensional environment (Croxall, J.P., 1987). In this highly complex habitat, seabirds must actively locate sparsely and moreover unpredictable prey patches (Weimerskirch, H. et al., 2005). Physical processes causing aggregations of prey are not static, and seabirds must adapt to continuous changes in the physical structure of the ocean (Shealer, D.A. et al., 2002). Besides, factors that determine prey and predators distribution and abundances are scale-dependent, from global circulation patterns to mesoscale eddies or local upwellings (Bertrand, A. et al., 2014; Hunt Jr, G. & D. Schneider, 1987) without forgetting ecological interactions such as intra or interspecific competition (Ashmole, N.P. & M.J. Ashmole, 1967; Forero, M.G. et al., 2004). Therefore, the formation and propagation of foraging habitats is a function of complex oceanographic and dynamic processes. Consequently, habitat in the marine context does not always refer to fixed geographical space, but preferentially to dynamic areas that may shift while energy flows from primary to higher trophic levels throughout marine food webs (Boersma, P.D. et al., 2009; Scales, Kylie L. et al., 2014). The study of the ecological interactions that take place in the ocean has to deal not only with this habitat complexity, but also with the inherent difficulty of taking measurements in the marine environment (Hoegh-Guldberg, O. & J.F. Bruno, 2010; Stommel, H., 1963).

The understanding of how particular organisms behave and respond to their environment is also hampered by the need of delimitate the study area in this endless habitat. Particularly, relationships between marine predator behavior and foraging performance with the bio-physical properties of the ocean environment requires the assessment of the appropriate spatial and temporal resolution at which relationships succeed (Adrian, R. et al., 2012; Bradshaw, C. et al., 2002). Furthermore, the influence of physical properties of the ocean surface on top predators behavior are poorly understood largely due to the unknown lag times between productivity characterization of surface waters, lower trophic organisms occurrence and predator-prey interactions (Grémillet, D. et al., 2008; Oro, D., 2014).

But this is not just a matter of methodological constraints or sufficiently detailed data in space or time (Ramírez, F. et al., 2016). In the interfacing of physical and biological phenomena the observer imposes its perceptual bias to perceive the system. To understand how physical features determine biological events and adaptation of organisms, problems must be addressed on the appropriate spatio-temporal scale, since different patterns emerge at different scales of investigation (Wiens, J.A., 1989).

» New remote techniques promote science advance

Ocean from space: satellite remote sensing

Satellite remote sensing systems as platforms for ocean-viewing sensors has the unique capacity to sample detailed spatial distribution of ocean variables from hundreds to thousands of kilometers over all the entire globe. These measurements regularly repeated for the last three decades, give a key role in measuring ocean variability spatial and temporally (Rose, R.A. et al., 2015; Yang, J. et al., 2013).

Important shortcoming in seabirds' foraging studies is the lack of direct assessments of prey availability at matching spatio-temporal scales with seabirds' distribution (Scales, K. L. et al., 2014). Studies sustained by abundance and spatial distribution of preys based on plankton traps, ship transects or echo-sounding techniques (Grémillet, D. et al., 2008; Moseley, C. et al., 2012; Tew Kai, E. et al., 2013) are in a minority compared to the studies that uses indirect remote sensing proxies for productivity (Catry, T. et al., 2013; Louzao, M. et al., 2012b; Tremblay, Y. et al., 2009). Satellite images provide a reliable basis for estimating the concentrations of chlorophyll-a associated with the phytoplankton of the upper ocean, and have been the most practical and extensively used surrogate of marine productivity in the last decades (Behrenfeld, M.J. et al., 2006; Boyd, C. et al., 2015). However, marine predators usually feed in higher trophic levels up the food chain, so correlations with seabird distribution can consequently be quite misleading and time lagged between real prey availability and productivity data (Grémillet, D. & T. Boulinier, 2009; Ramírez, F. et al., 2016). Satellite data has also become an important tool for monitoring environmental parameters associated with biodiversity distribution, providing a reliable basis for estimating physical conditions that drive foraging habitat selection (Boersma, P.D. et al., 2009; Cimino, M.A. et al., 2013; Turner, W. et al., 2015). Seabirds should show a strong affinity to areas with specific oceanographic properties, such as frontal areas delineating different water masses, or inshore waters, characterized by physical properties that enhance or accumulate resources available to their prey (Bost, C.A. et al., 2009; Fauchald, P., 2009). The spatial and temporal variability of these oceanographic properties and structures (i.e. sea surface temperature, fronts, currents or productivity) can be characterized from instantaneous snapshots from a specific date, to trends or persistency in oceanographic features by means of summarized images describing decadal of oceanographic processes (Cottin, M. et al., 2012; Grémillet, D. et al., 2008).

Following fingerprints: animal tracking

One step further in the study of seabirds' ecology and environmental variability in the last recent years is the development of small and lightweight devices that can readily record animal movements, behavior and even some environmental variables, thus providing an integrated view of the animal and its environment (Hays, G.C. et al., 2016; Kays, R. et al., 2015; Ropert-Coudert, Y. & R.P. Wilson, 2005). Devices have been developed in a wide range of tracking systems to address individual movements, and allow choosing the best option in weight and data recovery for each case, offering results at different spatial and temporal resolutions (Ponchon, A. et al., 2013).

Tracking studies have soared in recent years, revolutionizing our understanding of the at-sea distribution movements of marine species (Hays, G.C. et al., 2016). Biotelemetry studies combined with satellite images offers an integrative understanding of the response of marine predators to environmental variability at different scales (De Monte, S. et al., 2012; González-Solís, J. et al., 2007). Through this data, information on inter and intra-specific relationships such as competitive dynamics in the use of space can be also obtained (Navarro, J. et al., 2015; Wakefield, E.D. et al., 2013), thus providing useful information for conservation management (Arcos, J.M. et al., 2012).

» Environmental variability affects seabirds foraging ecology and reproductive cycles

Seabirds foraging studies have been highlighted substantially with the advent of tracking technologies (Louzao, M. et al., 2012b; Paiva, V.H. et al., 2010c; Quillfeldt, P. et al., 2015). Effective foraging theory predicts that animals should minimize energy expenditure with respect to energy acquisition, maximizing their net rate of energy gain, and involves a set of processes that implies individual experience and decision-making processes regarding the effort invested in foraging (Pyke, G.H. et al., 1977). During the breeding period, most seabirds are central-place foragers, and become spatially constrained by the location of their breeding grounds, which are ultimately limited by food resource availability. In order to fully cover their energetic requirements for reproduction seabirds have therefore to adapt their searching movements and foraging strategies to environmental conditions. Individual decision-making can be constrained by predictable oceanographic structures where they can find prey more efficiently (i.e. eddies and fronts; Cotté, C. et al., 2007; Fauchald, P. et al., 2000) and forcing factors such as winds (Amélineau, F. et al., 2014; Raymond, B. et al., 2010).

Box: Satellite oceanography

Satellite remote sensing systems have the unique capacity to sample detailed spatial distribution of ocean variables from hundreds to thousands of kilometers over the entire globe. Satellite images have been carried out regularly over the last three decades, which gives them a key role in measuring ocean variability and changes over time (Rose, R.A. et al., 2015; Yang, J. et al., 2013), compared with other oceanographic sampling techniques. A remote sensing image, unlike the "snapshots" obtained from cameras, consists of millions of measurements built up over a short length of time from a regular sampling pattern over the ground. Ocean color sensors are aboard polar platforms that can potentially cover the whole Earth in a single day, and obtain a total coverage of the Earth in several days (Robinson, I.S., 2010). So, time series of satellite observation inform us about the temporal variability of the ocean. Sensors employed on ocean-observing satellites exploit different regions of the electromagnetic spectrum to derived oceanographic products describing world sea surface. The most well-known ocean color derived products (cholorophyll, suspended particulates and bathymetry) derive from visible and near infrared wavebands sensors. Thermal region of electromagnetic radiation allows measurements of sea surface temperature parameters and microwaves wavebands are utilized by active radar and microwave sensors to final generate surface winds, wave height or sea surface and geostrophic currents (Robinson, I.S., 2010). While satellite data have been used for over 25 years, the most significant advances in measurement methods have come in the last 10 years. First reliable long-term operational platform was the SeaWiFS (Sea-viewing Wide Field-of-view Sensor), launched in 1997. Previous sensors as CZCS (Coastal Zone Color Scanner) operated from 1978 to 1986, but with unparalleled gaps in data collection in relation to most recent sensors (i.e. MODIS, Moderate Resolution Imaging Spectroradiometer), which offers data from 2002. Processed products are increasingly widely affordable, aided by new data policies promoting free access to government satellite imagery (Turner, W. et al., 2015). Every remote-sensing instrument has a particular space-time sampling capabilities, offering products with different spatial and temporal coverage and composites images. Some international programs have aid to the widespread use of satellite imagery, offering images and re-analysis products regularly updated. This is the case of the Ocean Biology Processing Group (OBPG) which supports the NASA Ocean Color Web (http://oceancolor.gsfc.nasa.gov/cms) or the major space European programme Copernicus for Earth Observation and Monitoring which provides products and services for all marine application (http://marine.copernicus.eu).

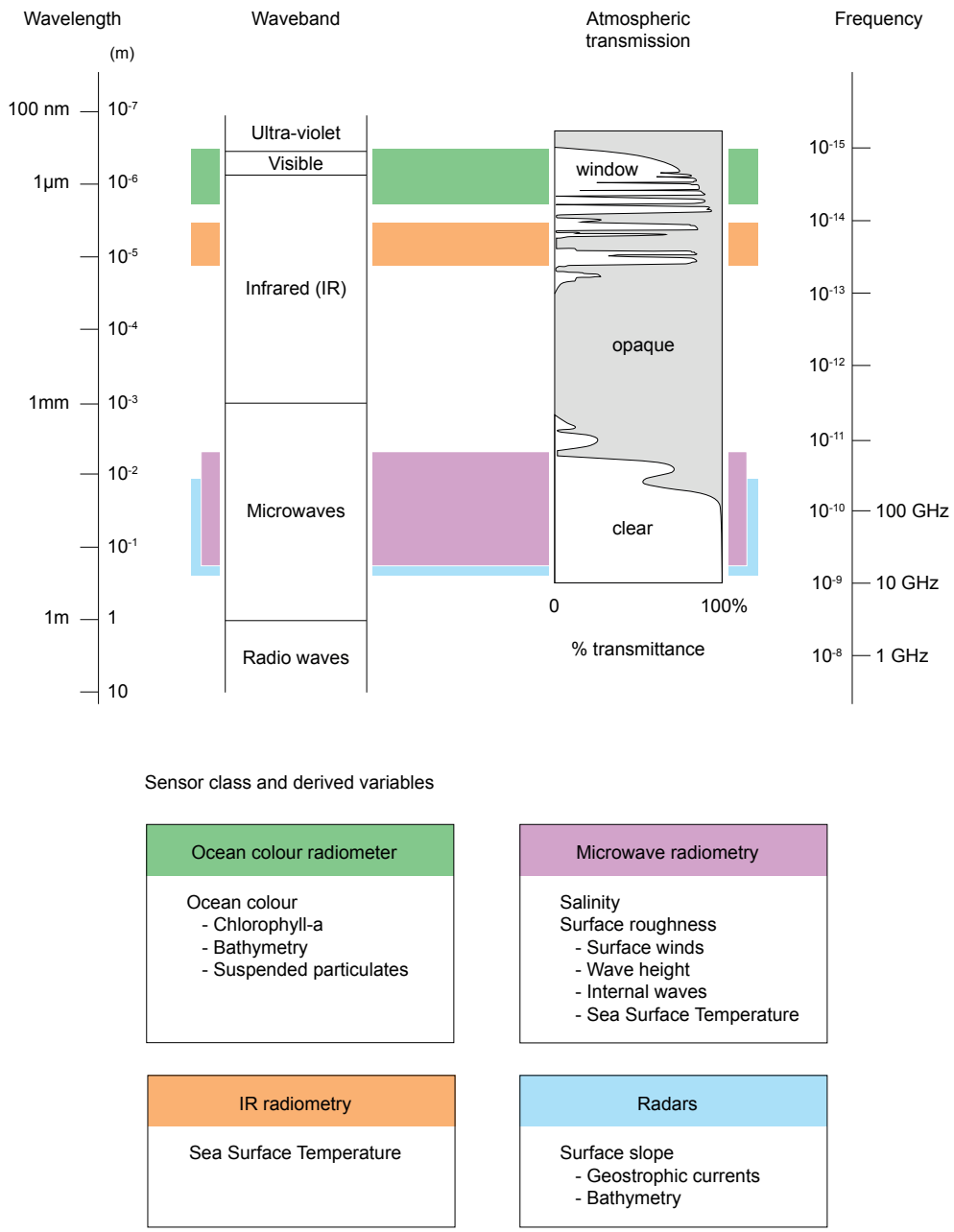

Figure 1: Scheme of the different remote sensing sensors used in satellite oceanography, along with their applications. The figure shows the electromagnetic spectrum and the transmittance of the atmosphere for each wavelength. The atmosphere is opaque for much of the spectrum and therefore unusable for remote sensing but there are a number of windows regions where most of the radiation gets through and remote sensing sensors can operate. Bands used for the four broad classes of satellite sensors used for viewing the ocean are showed in colours. (Adapted from Robinson I.S. 2010).

Distribution, behavior and reproductive performance of seabirds have been proven to be linked to several ocean features, which ultimately drives food availability: ocean color (Louzao, M. et al., 2012b; Paiva, V.H. et al., 2010a), sea surface temperature (Awkerman, J.A. et al., 2005; Guinet, C. et al., 1998; Sandvik, H. et al., 2008), currents (Suthers, I.M. et al., 2011), frontal zones (Bost, C.A. et al., 2009; Scales, K. L. et al., 2014), eddies and gyres (Cotté, C. et al., 2007; Hyrenbach, K.D. et al., 2006), thermocline (Pelletier, L. et al., 2012; Scott, B. et al., 2010), sea-ice extent (Barbraud, C. et al.; Grémillet, D. et al., 2015), and bathymetry and seamounts (Austin, D. et al., 2006; Conners, M.G. et al., 2015; Paiva, V.H. et al., 2010b). Higher predators such as seabirds are reported to actively use most of these particular oceanic features to travel and search efficiently for their food supply.

Environmental variability goes beyond foraging strategies, having major consequences on seabirds' life-history traits (Ramírez, F. et al., 2016; Ricklefs, R.E., 1990; Weimerskirch, H., 2007). Climate influences seabird demography and population dynamics, generally by affecting food availability (Jenouvrier, S. et al., 2005; Oro, D., 2014). Most studies have correlated population trends and reproductive traits with variability in environmental factors of the marine environment (Descamps, S. et al., 2015; Doney, S.C., 2006; Genovart, M. et al., 2012; Russell, D.J.F. et al., 2015). Organism' annual cycles presumably evolved in response to predictable seasonal patterns of environmental features driving food availability (Mackas, D.L. et al., 2012). This is especially true in temperate and polar climates, where only a short period of the year is suitable for reproduction (Frederiksen, M. et al., 2004; Wassmann, P., 2011) and breeding success depends on the ability to adjust reproductive timing to seasonal patterns of food availability (Ramírez, F. et al., 2016). However, environmental changes are likely causing phenological shifts at a different rate in the various levels of the food webs, leading to mistiming in seasonal activities between different levels and disrupting tight trophic interactions between predator and prey (Durant, J.M. et al., 2005; Visser, M.E. & C. Both, 2005). Addressing this issue has to overcome the appropriate scale each species experiences the environment, responding to its variability and predictability (Levin, S.A., 1992).

» Seabird conservation

Despite all progress, seabirds are nonetheless one of the most threatened group of birds worldwide (Butchart, S.H.M. et al., 2004), with strong evidence of dramatic declines in many geographic areas (Lewison, R. et al., 2012). Current anthropogenic threats to seabird populations include fisheries bycatch, pollution, human disturbance, artificial lighting, introduced predators and global climate change (Phillips, R.A., 2013; Rodriguez, A. et al., 2015; Trathan, P.N. et al., 2015).

Overfishing poses a great threat to fish stocks upon which seabirds prey. Coexistence

of foraging seabirds and operating fisheries may result in negative interactions such as prey depletion when birds and man compete for the same prey resources (Bertrand, S. et al., 2012) or increase of mortality due to fishery bycatch (Lewison, R. et al., 2004). Fisheries may also have a positive effect, providing new feeding opportunities when seabirds take advantage of discarded preys that would otherwise be unavailable (Karpouzi, V.S. et al., 2007; Montevecchi, W.A., 2002; Oro, D. et al., 2004). But the upcoming law reforms of the European Union fisheries policy are expected to limit discards, which could trigger negative effects on scavenging seabirds (Bicknell, A.W.J. et al., 2013).

Within this context, an important current challenge is to maintain seabirds in a favorable conservation status (Croxall, J.P. et al., 2012). Effective design of management and conservation strategies for these species requires knowledge on both the distribution of the species during the overall annual cycle, along with the environment they inhabit (Hyrenbach, K.D. et al., 2000). The understanding of the factors governing the dynamics of marine ecosystems is, therefore, paramount to implement effective management strategies for marine ecosystems (Boyce, D.G. et al., 2015). The utility of tracking and remote sensing data as tools for marine conservation planning is essential to facilitate detailed investigations of the spatial overlap of species and their threats, such as fisheries (Lascelles, B.G. et al., 2016). But concurrently, the long time series of biological data of seabird populations are crucial to unravel trends and ecological effects related to changes in the marine environment. In this sense, interdisciplinary studies combining state-of-the-art remote sensing technologies with long time series data on life-history traits are key to the maintenance of seabirds and their changing environment.

AIMS

The overall aim of this thesis is to investigate the influence of the spatio-temporal variability of environmental conditions on the foraging strategies and reproductive traits of seabirds, and the assessment of conservation strategies for seabirds facing changes in the oceanographic environment.

To achieve this overall goal, the following specific objectives were pursued:

1. To describe the spatial distribution of climate and human stressors impacting the world's oceans and, therefore, seabirds.
2. To determine the spatio-temporal scale at which seabirds interact with their environment. Such scale may prompt life-history traits in response to environmental variability.
3. To investigate whether varying oceanographic conditions, fishing activities and biological interactions (competition) affect foraging habitat selection in seabirds
4. To investigate how varying oceanographic conditions affect reproductive performance
5. To propose spatially explicit management strategies for seabirds based on scientific knowledge encompassing biological data, anthropogenic threats and environmental variability

These aims were developed in six chapters presented as scientific papers, addressing oceanographic environmental variability from local to global scale, and analysing the ecological responses of different species of seabirds to the foraging and reproductive constraints imposed by this variability.

THESIS OUTLINE

» Study sites and species

Study sites of this thesis covered a wide geographical range, from the entire world ocean to three specific areas located fully or partially at Mediterranean climates. The first of these areas include the south western regions of our Mediterranean Sea, the largest and deepest enclosed sea on earth (Coll, M. et al., 2012), rightfully referred by Lejeusne (2010) as a highly diverse but highly impacted miniature ocean, which holds unprecedented anthropic pressure on marine ecosystems (i.e. pollution, overfishing). The Bass Strait, a broad shallow region of mixed boundary currents between Tasmania and the Australian mainland (Gibbs, C. et al., 1986), and the Patagonian Sea (Argentina), one of the highly and most predictable productive area of the southern hemisphere (Foro para la conservación del Mar Patagónico y áreas de influencia, 2008), comprise the two other marine scenarios. All the mentioned study sites are characterized by highly mixed waters and complex and strong seasonal circulations. The great dynamism of these areas offer interesting seascapes where studying ecological responses of seabirds.

We selected five different seabird species as study models (three shearwaters and two penguin species, which will be introduced in the overview of each chapter presented below). The selection of these model species was made according to suitability of each species for accomplishing the particular aims of each chapter and the availability of biological data for addressing the ecological questions.

» Environmental variability at a global scale (Chapter I)

This thesis starts with the exploration of the oceanographic environmental variability at a global scale**.** Seabirds have evolved within the conditions imposed by one of the most heterogeneous habitats of the world, oceans, to the challenge of obtaining food (Ashmole, N.P., 1971). Nevertheless, clear evidences point out that global changes are exerting considerable stress on marine ecosystems (Halpern, B.S. et al., 2008), and particularly on seabird species and communities, that have to adapt their foraging and reproductive behaviour to disturbed environments (Grémillet, D. & T. Boulinier, 2009). Chapter I addresses climate and fishing impacts on the world global ocean, introducing the main environmental changes that marine predators have to face with, and stresses the need to consider together climate and human features as promoters of environmental variability.

» Variability in patterns and scales (Chapter II)

Ecological interactions between species and the environment take place at various scales of space and time (Wiens, J.A., 1989). This chapter explores the relevance of selecting a correct scale of study to integrate environmental variability since predictability of organisms responses to environmental patterns may only emerge when studying the system at the appropriate scale.

The ability of seabirds to successfully reproduce in the unpredictable food supply scenario imposed by oceans has emerged as an adaptive response to adjust their breeding decision to match the peak of food availability during rearing (Durant, J.M. et al., 2004). Studies on phenology are of great interest in this respect because climate change is causing variation in the peak and seasonality of primary production in the oceans (Sydeman, W.J. et al., 2015). In Chapter II we analyse the temporal matching patterns between Little penguin *Eudyptula minor* (Fig. 2) laying date and the productivity peak extracted from a dynamic scale. This scale is based on the temporal and spatial variability on ocean circulation around the foraging areas at the Bass Strait, Australia. The Little penguin is a good model species to study environmental pressures experienced by central place foragers. First of all, the availability of one of the longest time series of reproductive timing data provided generously by Phillip Island Nature Park was essential to address meaningful linkages between environmental and biological patterns. Furthermore, Little penguin is a resident species with very small foraging ranges that forage in a highly unpredictable and heterogeneous environment (Chiaradia, A. et al., 2016). For all these reasons, we predicted that this species would be particularly sensitive to environmental variability and physical breeding cues in the surroundings of their colony.

» Foraging strategies facing environmental variability (Chapters III, IV, V)

From this point on, the thesis reaches its central core, exploring the ecological responses of model species to environmental variability in terms of acquisition of resources (Chapters II, IV, V) and demographic effects (Chapter V).

Shearwaters breeding in the south western Mediterranean Sea were used as a study model in tracking studies developed in Chapter III and Chapter IV. The aim of these chapters was to relate seabirds' movements to the spatio-temporal heterogeneity of the environment in their breeding and foraging areas. A multi-year (2011-2014) tracking study of the endangered Balearic shearwater *Puffinus mauretanicus* (Fig. 3) from Eivissa (Balearic Islands, Spain) allowed us to study the role of between year differences in oceanic winds and productivity patterns on foraging habitat selection. In Chapter IV, the study included tracking data for only one year (2011), but divided in two breeding stages (incubation and chick-rearing period), of two different –yet closely related – species of shearwaters (Scopoli's shearwater *Calonectris diomedea* and Cory's shearwater *C.*

borealis, Fig. 4) breeding in sympatry in Chafarinas Islands (Spain). This colony is one of the few location all over the world where this ecologically similar species coexists, providing a unique scenario to investigate competition constraints in the selection of foraging areas between different breeding stages. In Chapter V, Magellanic penguin *Spheniscus magellanicus (*fig. 5) breeding in Chubut province (Argentina) was the model species for investigating their foraging habitat preferences in a highly, man-modified environment. This chapter focuses on the effects that spatio-temporal environmental variations have on high quality prey availability, and their ultimate consequences on breeding parameters.

» Gaining conservational strategies integrating environmental variability (Chapter VI)

Finally, we conclude this thesis with an applied study regarding the design of marine reserves. Oceanographic changes are a challenge for management and conservation, but conservation efforts in marine systems follow the path of terrestrial conservation initiatives. Therefore, there is an important and immediate need for delineating representative Marine Protected Areas (Lescroël, A. et al., 2016; Ronconi, R.A. et al., 2012). Seabirds has been widely recognized as excellent indicators of marine ecosystem health and used as umbrella species in global ocean conservation purposes (Lascelles, B.G. et al., 2012). But marine protected areas should be designated not only for the conservation of the species, but also for preserving their biophysical environment (Lubchenco, J. et al., 2003), including the physical mechanisms that influence the formation and persistence of important habitats for the species (Hyrenbach, K.D. et al., 2000). Following these guidelines and integrating relevant knowledge acquired in previous chapters, we explore a tool to define marine protected areas integrating biological, socio-economic and environmental factors in the Patagonian seabird community (Argentina). Any effort to conserve seabirds needs to start with a determination and understanding of the major threats facing these species (Boersma, P.D. et al., 2002). In Chapter I, we gave an overview of some of these major threats to seabirds, regarding environmental and fishing challenges. Methodological approaches developed in Chapters II, III and V (connectivity analysis, delimitation of persistent productive features and predicted at-sea projections from colony-based data, respectively) were incorporated to define potential areas of conservation of seabirds also incorporating the environmental variability to the identification of ecologically relevant areas.

Figure 2: Group of Little penguins (*Eudyptula minor*), returning to their nests at the final of the day, in their breeding colony of Phillip Island (Australia). Little penguins are the smallest penguin in the world at only 33cm and are only found in southern Australia and New Zealand. They breed on land in burrows, providing them protection from predators and extreme heat. During breeding, they regularly return to land to incubate the eggs and feed their chicks. When returning to land after feeding at sea, Little penguins only cross the beach at sunset.

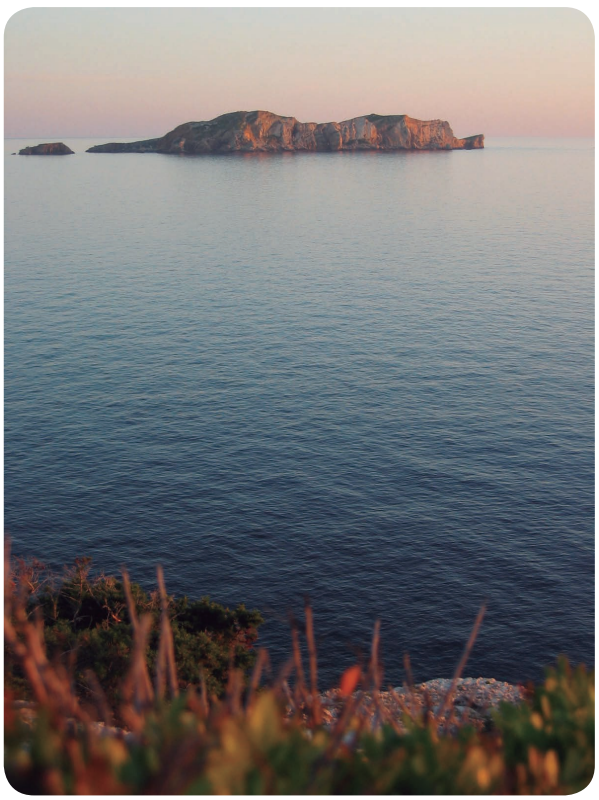

Figure 3: Balearic shearwater (*Puffius mauretanicus*), in their breeding colony in Conillera, Eivissa, Balearic Islands. This species breeds only in the Balearic Islands, Spain. Its small population (estimated at 3,200 pairs) affected by particular threats as predation by introduced mammals at breeding colonies and mortality caused by fisheries by-catch. Balearic shearwater is categorized as Critically Endangered by the IUCN.

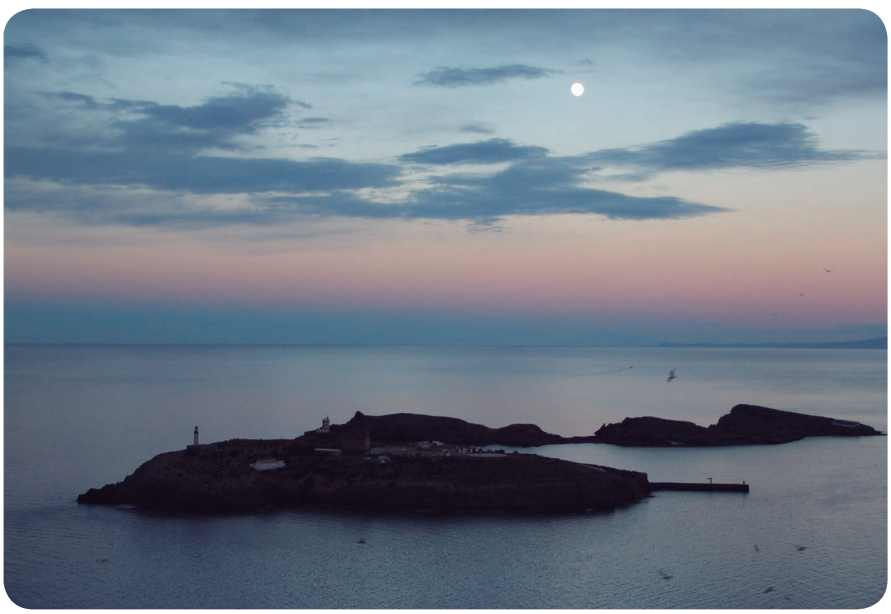

Figure 4: Scopoli's shearwater (*Calonectris diomedea*) and Cory's shearwater (*C. borealis*) are related species (actually in consideration as different species or subspecies) that breeds sympatrically only in the colony of Chafarinas Islands, an Spanish archipelago close to north Morocco coasts, and Terreros Islands (Almería). Scopoli's shearwater breeds on islands of the Mediterranean Sea, whereas Cory's shearwaters distributes for breeding in north Atlantic islands, mainly Madeira and Azores. Both shearwaters perform long-distance winter migrations in the Atlantic.

Figure 5: Magellanic penguin (*Spheniscus magellanicus*) is list as Near Threatened by the IUCN Red List. This species breeds on the Atlantic and Pacific coasts of South America. Despite its large world population, Magellanic penguins has been seriously threatened by the expanding Argentinian anchovy fishery, competing with their main feeding resource, and also having additional effect on populations as by-catch. Predation by mammals in their breeding sites and oil pollution are also mentioned as threats to the species, as well as to other seabirds' species.

SUPERVISORS' REPORT

Dr. Francisco José Ramírez Benítez and Dra. Manuela González Forero, co-supervisors of the Doctoral thesis entitled *Ecological response of marine predators to spatio-temporal environmental variability in resource availability* certify that the dissertation presented here has been carried out by Isabel Afán Asencio in its totality and grants her the right to defend her thesis in front of a scientific committee.

As supervisors, we have participated in designing, guiding and correcting earlier drafts of the chapters and manuscripts written by the Doctoral candidate. We also certify that none of the manuscripts included in this Doctoral thesis has been used as a part of another PhD thesis. The contribution of the Doctoral candidate to each manuscript is detailed below:

- Chapter I: *Climate and fishing impacts on global hotspots of marine biodiversity*

  F. Ramírez, **I. Afán**, L.S. Davis and A. Chiaradia (2016)
  Science Advances (2016): under review. Impact factor (2015): recently founded journal, without impact factor yet
  The PhD candidate IA has contributed in the data analysis and writing

- Chapter II: *A novel spatio-temporal scale based on ocean currents unravels environmental drivers of reproductive timing in a marine predator*

  I. Afán, A. Chiaradia, M.G. Forero, P. Dann, F. Ramírez
  Proceedings of the Royal Society B: Biological Sciences (2015) 282: 20150721.
  Impact factor (2015): 5.051
  The PhD candidate IA has contributed in the study design, data analysis and scientific writing

- Chapter III: *Where to head? Investigating the role of wind and productivity patterns in driving the foraging destinations in a central-place forager*

  I. Afán, J.M. Arcos, F. Ramírez, D. García, B. Rodríguez, K. Delord, A. Boué,

  T. Micol, H. Weimerskirch, M. Louzao
  Submitted to Scientific Reports (2016)
  The PhD candidate IA has contributed in the in the study design, data analysis and scientific writing

- Chapter IV: *Foraging movements and habitat niche of two closely related seabirds breeding in sympatry*
  I. Afán, J. Navarro, L. Cardador, F. Ramírez, A. Kato, B. Rodríguez, Y. Ropert-Coudert, M.G. Forero
  Marine Biology (2014) 161: 657-668. Impact factor (2015): 2.391
  The PhD candidate IA has contributed in the study design, field work, data analysis and scientific writing

- Chapter V: *Natural and anthropogenic factors affecting the feeding ecology of a top marine predator, the Magellanic penguin*
  F. Ramírez, **I. Afán**, K.A. Hobson, M. Bertellotti, G. Blanco, M.G. Forero
  Ecosphere (2014) 5: art38. Impact factor (2015): 2.255
  The PhD candidate IA has contributed in the study design, data analysis and scientific writing

- Chapter VI: *An integrated method for identifying marine areas of highest conservation priority: a case study at the Argentinean Patagonia coast*
  I. Afán, M.G. Forero, F. Ramírez
  Diversity and Distributions (2016): under review. Impact factor (2015): 3.667
  The PhD candidate IA has contributed in the study design, data analysis and scientific writing

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CHAPTER I

Climate and fishing impacts on global hotspots of marine biodiversity.

Ramírez F., Afán I., Davis L.S., Chiaradia A. (2016)
Science Advances, under review

Climate and fishing impacts on global hotspots of marine biodiversity

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Abstract

Human activities are driving environmental changes at scales that could potentially cause ecosystem collapses in the marine environment. We combined information on marine biodiversity with spatial assessments of the impacts of climate change and industrial fisheries to identify the key areas to prioritise for the conservation of global marine biodiversity. This process identified six marine regions of exceptional biodiversity based upon global distributions of 1,729 species of fish, 124 marine mammals and 330 seabirds. Overall, these hotspots of marine biodiversity coincide with areas most severely impacted by global warming and fishing pressure. In particular, these marine hotspots have undergone local to regional increasing water temperatures, slowing current circulation, decreasing primary productivity and increasing fishing pressure. In light of these findings, we offer an adaptive framework for effectively depicting those local to regional areas of special concern for the conservation of marine biodiversity; along with a suitable tool for the spatial management of global fisheries if the aggravating effect of fishing on climate change impacts is to be minimized.

INTRODUCTION

The exponential rise of atmospheric greenhouse gas concentrations over the past 30 years has increased the average global temperature by 0.2°C per decade (*1*). Most of this extra heat is being absorbed by the world's oceans, particularly by its upper layers (*2*), with the mean global sea-surface temperature (SST) increasing by approximately 0.4°C since 1950s (*3*). The warming of the oceans drives greater stratification of the water column, thereby reducing mixing in some parts of the ocean, which affects oxygen (*4*) and nutrient availability (*5*) and, hence, primary production (*2*, *6*, *7*) and the ecophysiology of water-breathing organisms (*8*). The increase in water temperatures is, however, unevenly distributed spatially (*9*, *10*) and, together with increased meltwater and discharged ice from terrestrial glaciers and ice sheets, is influencing the behaviour of ocean currents, which play critical roles in the dynamics, local climates, and biology of the ocean (*11*, *12*). Coincidentally with these environmental changes, industrial fisheries have resulted in the overexploitation and decimation of about 70% of world fish stocks (*13*), resulting in changes to fish communities and marine ecosystems since the second world war (*14*, *15*). Both climate and human pressures can lead to shifts in the size, structure, spatial range, and seasonal abundance of populations (*9*, *16–18*), which in turn may alter trophic pathways from primary producers to upper-trophic levels, propagating changes throughout ecosystems in both bottom-up and top-down directions (*8*, *18–20*). Accordingly, climate and fishing impacts should not be treated in isolation from each other when it comes to conservation of marine biodiversity (*21*).

Despite the scale of these perturbations, our understanding of how environmental variability, driven by climate change and human activities, is affecting marine ecosystems has lagged far behind our knowledge of their impacts in terrestrial ecosystems (*22*). In part, this is because there is considerable uncertainty regarding the spatial and temporal details of such impacts in marine environments (*23*, *24*). Satellite remote-sensing records have emerged as important tools for studying the most recent (up to three decades) and striking trends and patterns in both environmental (e.g. SST or ocean currents) and biological (marine productivity) variables in the world's oceans at an unprecedented spatio-temporal resolution (*7*, *10*, *25*). Additionally, worldwide fishing records (e.g., annual landings) are available from the 1950s onwards (see http://www.fao.org/fishery/en), providing important information on a major human harvest that impacts marine ecosystems (*13*, *15*, *26*). Together, these data provide the most detailed insights, so far, on the spatio-temporal distribution of environmental and human stressors threatening marine communities.

However, few studies to data have analysed the data on a fine enough scale to identify the specific marine areas globally that are most at risk from climate change (*9*, *10*) and exploitation from fisheries (*26*); and none of them have combined such measurements on climate and human impacts with those for species

distribution globally in order to identify hotspots of marine diversity that can be targeted for conservation at the local, regional and global scale.

Here, by overlapping spatially-explicit measurements available of marine biodiversity globally and fishing pressure with the finest-scale measurements for the cumulative impacts from climate change, we aimed to identify the areas of highest conservation priority within our planet's marine estate. In particular, (i) we compiled a species-level database recording the global distribution of 2183 marine species in order to identify hotspots of marine biodiversity; (ii) we derived spatially-explicit information on the cumulative impact of climate change by combining more than three-decades worth of information on SST, oceans currents and marine productivity (i.e., chlorophyll-a concentration, CHL); (iii) we evaluated changes in fishing captures over the last sixty years to examine temporal trends in the exploitation of marine resources worldwide. We also identified those countries that have contributed the most to fishing pressure at marine hotspots over the last decade.

RESULTS AND DISCUSSION

Temporal trends for SST, CHL and ocean currents (Table S1) were explored through least-square liner regressions of annual information on a 1-degree pixel basis covering the world's oceans (Fig. S1). Absolute values for the obtained slopes (a proxy to the magnitude of environmental changes occurring on a pixel basis) were combined to produce an index of cumulative impacts of equally-weighted changes in targeted oceanographic features (hereafter Cumulative Impact Index) with values ranging from 0 (no change) to 1 (maximum change). Overall, our Cumulative Impact Index reveals indisputably the uneven distribution of environmental changes in the Earth's oceans, with the most striking changes occurring at the poles and the tropics (Fig. 1). In northern regions, the main changes concern the North Sea, but also those areas connected by the cold waters of the Labrador Current flowing southward along the eastern coast of Greenland and North America. These changes are largely driven by an increase in SST (Fig. S1), likely caused by the increasing temperatures of the northward flowing Atlantic waters arriving in the Arctic (*27*). As expected for warmer waters with increased vertical stratification and lower nutrient supply (*7*), we observed a general reduction in CHL values (Fig. S1); a trend that may be exacerbated in the polar region by an increased influx of freshwater from melting sea-ice (*2*, *28*, *29*), but see (*24*). Similarly, large areas enclosing coastal waters of the North-Pacific Ocean Basin from the Bering to the East China Seas have also recorded large increases in SST with consequent decreases in CHL (Fig. S1, see also (*7*, *29*)). Overall, the South Atlantic Basin has apparently experienced a gradual decline in marine productivity (*29*). However, we detect a large degree of spatial variability mainly as a consequence of the high rate of increase in CHL observed for the south-eastern and south-western Atlantic (Fig. S1), patterns that might

be associated with seafronts prevalent at these areas (*7*, *30*). Spatial heterogeneity is also apparent with regard to changes in SST of this ocean basin. Water temperature has experienced a positive, but marginal, change in temperate regions. Southernmost seawater has become slightly colder, particularly in areas close to Tierra del Fuego and the Antarctic continent (*31*). Increasing water temperatures have also been very acute around the Australian continent (*32*); a trend that is probably driven by changes in the Eastern Australian Current transporting hot water southward from the tropics to mid-latitudes (Fig. S1).

Overall, observed changes in ocean circulation are in agreement with the slowing of the global thermohaline circulation, resulting from the disproportionate heating at the Earth's polar regions: this encompasses all ocean basins and is likely influencing global climate (*23*) and marine productivity (*7*, *11*, *28*, *33*). Accordingly, with a reorganization of the Atlantic Meridional Overturning Circulation (*34*), the substantial decrease in water speed (both for the eastern and northern components) that we detected for the Labrador Current (Fig. S1) may contribute to the observed decline in marine productivity in the North Atlantic (*28*). Further, we detected a deceleration in the South Atlantic Gyre that affects both sides of the South Atlantic Ocean Basing (i.e., the Brazil and the Benguela Currents) and flows anti-clockwise between the 15ºS and the 40ºS latitudes. The Malvinas Current that flows northward from Cape Horn along the Patagonian coast of Argentina has also decelerated, as has also occurred for the Antarctic Circumpolar Current flowing eastward ca. 40ºS throughout the South Atlantic and the Indian Oceans. In the tropics, there have also been striking changes to ocean circulation, with increasing water speeds for the eastward Equatorial Countercurrent and with reversed trends for the North and South Equatorial Currents flowing westward ca. 10ºN and 10ºS latitudes, respectively (Fig. S1).

Similarly to the observed changes in oceanographic features, marine species are heterogeneously distributed (*35–38*). This begs the question: are environmental stressors affecting key marine areas of enhanced biodiversity? Based on the worldwide distribution (presence within an area) of 1729 species of fish, 124 marine mammals and 330 seabirds, we produced a dimensionless index of biodiversity based on the equally-weighted distribution of species richness for targeted taxa. This index allowed us to identify up to six different hotspots of marine biodiversity that concentrate in the Southern Hemisphere and include marine areas in temperate and tropical regions of the Atlantic, Indian and Pacific Oceans (Fig. 1). The westernmost includes the central-western Pacific waters of Peru and the Galápagos Archipelago. In the south-western Atlantic Ocean, a marine hotspot occurs in the Patagonian waters of Argentina and Uruguay. The coasts of South Africa, Mozambique, Tanzania, Kenya and Madagascar were included in a hotspot at the western side of the Indian Ocean. In the central-western Pacific Ocean, a large area including

water masses surrounding Indonesia, Malaysia, Philippines, Papua New Guinea, Taiwan and the south of Japan was grouped into one single hotspot. Waters surrounding New Zealand and Eastern and Southern Australia were considered the fifth hotspot at the south-western Pacific Ocean, whereas the sixth hotspot included disperse marine areas in Oceania and the Central Pacific Ocean. Overall, all these areas have experienced environmental perturbations. However, we detected a large degree of spatial variability in observed environmental impacts at the local and the meso-scales (Fig. 2 and Fig. S1). The most striking changes have occurred in the central-western Pacific and the south-western Atlantic hotspots as a consequence of significant changes in SST and CHL (Fig. 2). Whereas the first hotspot has largely undergone local to regional increases in both SST and CHL, the latter one have been characterized by a huge decrease in SST over the last three decades (Fig. 2 and Fig. S1), which may be partially driven by natural modes of climate variability, i.e., El Niño/Southern Oscillation (ENSO, *7*, *39*, *40*). In general, most other hotspots for marine biodiversity have experienced similar rising trends in SST, but remain quite stable in terms of CHL or ocean circulation (Fig. 2).

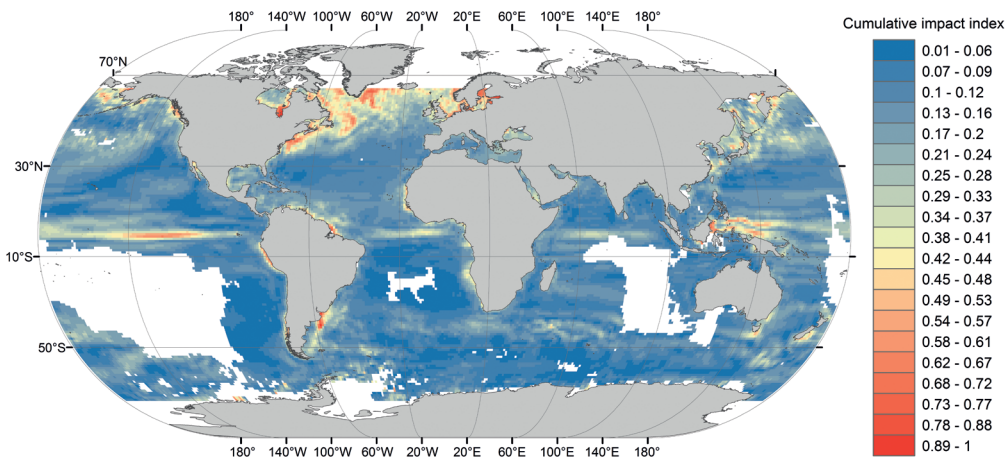

Figure 1. Global distribution of cumulative environmental impacts. Index of cumulative impact of equally-weighted changes in sea surface temperature, chlorophyll-a concentration (a proxy to primary productivity) and ocean currents. Colours represent a dimensionless index of global impact (Cumulative Impact Index) ranging from 0 (no change) to 1 (maximum change), providing a measure of spatial heterogeneity in the magnitude of environmental changes and highlighting those marine areas that have undergone the largest changes in their environmental conditions.

All these environmental stressors likely interact in a number of ways, but little is known about the potential for synergetic or antagonistic interactions that may exacerbate or counteract deleterious effects on marine communities inhabiting at these hotspots of marine biodiversity (*41*). Marine species may also respond differentially to changes in environmental conditions (*42–44*). Whereas some species may benefit from shifts towards environmental conditions outside the normal range of variability (*45*), in most cases, however, such environmental changes will prove suboptimal and this will made apparent through changes to populations and communities (*2*).

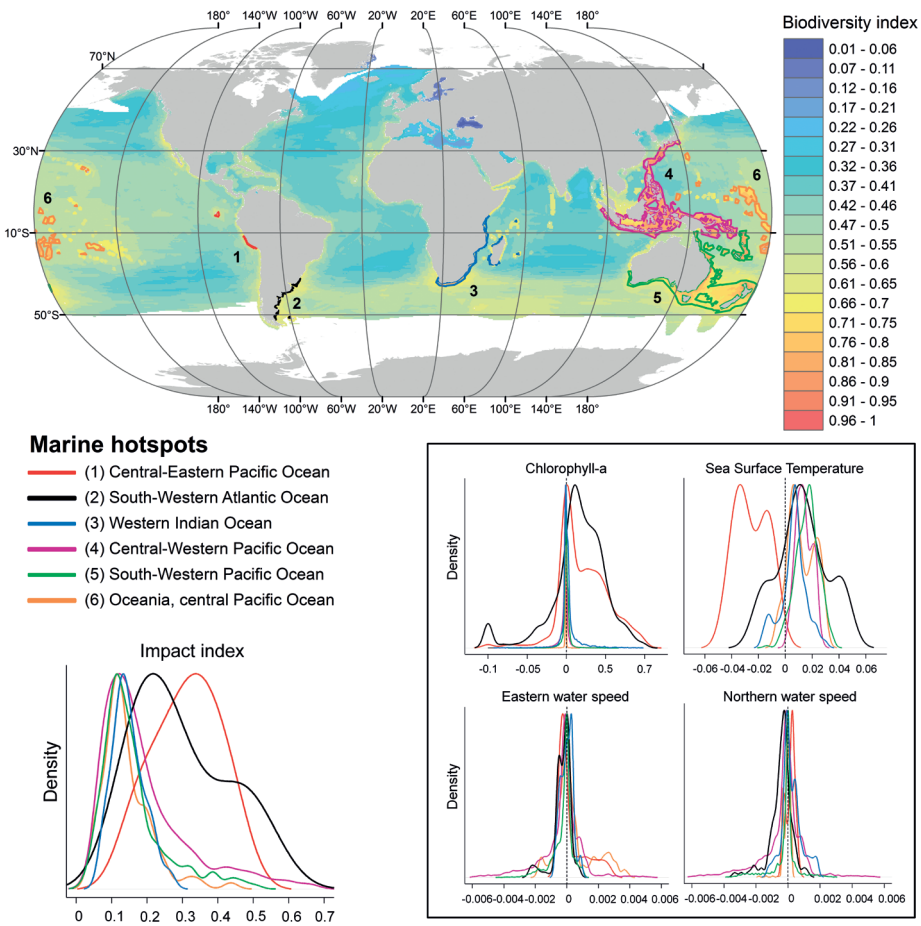

Figure 2. Environmental stressors impacting hotspots of marine biodiversity. Marine hotspots (upper figure) were identified based on the spatially-explicit information on the equally-weighted distribution of fish (1,729), marine mammal (124) and seabird (330) species. Colours represent a dimensionless index of biodiversity ranging from 0 (absence of species) to 1 (maximum species richness). Hotspots enclose 0.5 degree pixels with values of biodiversity over the upper 95 percentile. Density plots represent the distribution of environmental changes occurring within marine biodiversity hotspots and the derived Cumulative Impact Index.

In particular, there is overwhelming evidence that ocean warming in temperate regions such as the south-western Pacific or the western Indian Oceans can affect marine species through a reduction in primary productivity (*4–6*), and also through trophic disruptions due to shifts in species distributions (*18*, *46–48*) and changes in the timing of ecosystem-level processes (*17*, *49*, *50*). Small changes in water temperature and pH may also result in coral bleaching (*51*) and a severe simplification of tropical communities from the central-western Pacific Ocean and Oceania (*52*, *53*). Changes in ocean circulation, that largely control marine patterns of productivity and food availability (*54*), may also have important consequences for biological communities globally. Climate impacts on marine communities might vary spatially from the local to the regional scales according to the heterogeneous distribution of environmental stressors, so that we should expect that consequences of changing climatic variables will be species- and even site-specific. Fine-scale, spatially-explicit measurements on the distribution of environmental stressors, such as those provided in this study, are therefore crucial for effectively depicting those local to regional areas of special concern for the conservation of marine biodiversity in the face of climate change.

Industrial fisheries may pose another serious threat for the conservation of species inhabiting marine biodiversity hotspots when those areas overlap with areas of intense human fishing activity (*19*, *55*, *56*). Based on FAO fisheries statistics, we evaluated changes in landings of fish over the last sixty years to look for temporal trends in the exploitation of marine resources. While fishing has been practised for centuries, the fishing pressure has intensified during recent decades (*15*, *57*) as a consequence of technical developments in fishing techniques and this has led to the over-exploitation and, even, collapse of many fish stocks (*21*). Indeed, the world's marine fisheries resources are under enormous pressure, with global fishing effort estimated to exceed the optimum by a factor of three to four (*57*). Observed trends showing a yearly increase in fishing captures (Fig. 3) suggest this harvest pressure will continue and further exacerbate well into the future (*21*, *58*).

Fishing activities are particularly intense at Major Fishing Areas (MFA, according to their FAO categorization) that overlap with marine biodiversity hotspots (Fig. 3). This is particularly true for the tropical regions of the Indian and the Western Pacific Oceans, where the highest increasing rates in fishing pressure have been recorded both at the regional (Fig. 3) and the local scales (*26*). Although biodiversity conservation is an issue of global concern, fishing policies are most commonly derived from national decisions, particularly with regard to those occurring within Exclusive Economic Zones (EEZ, Fig. 3), where bordering sovereign states have special rights regarding the use of marine resources (United Nations Convention on the Law of the Sea, 1982). Fishing pressure differs among countries. China and Peru contribute most to global captures (ca. 20%) and are likely to continue to do

so according to the observed trends in fishing captures (Fig. 3). However, many other countries also contribute substantially to fishing captures within MFAs that overlap with marine hotspots (Fig. 3 and S3). We identified 30 different coastal countries that collectively account for 80.5% of fishing captures in the areas of high biodiversity (Fig. S2). All of them have sovereign EEZs overlapping marine hotspots, with the exception of Spain, which currently maintains huge distant fishing fleets in both the Indian and the South-Western Atlantic Oceans (Fig. S2).

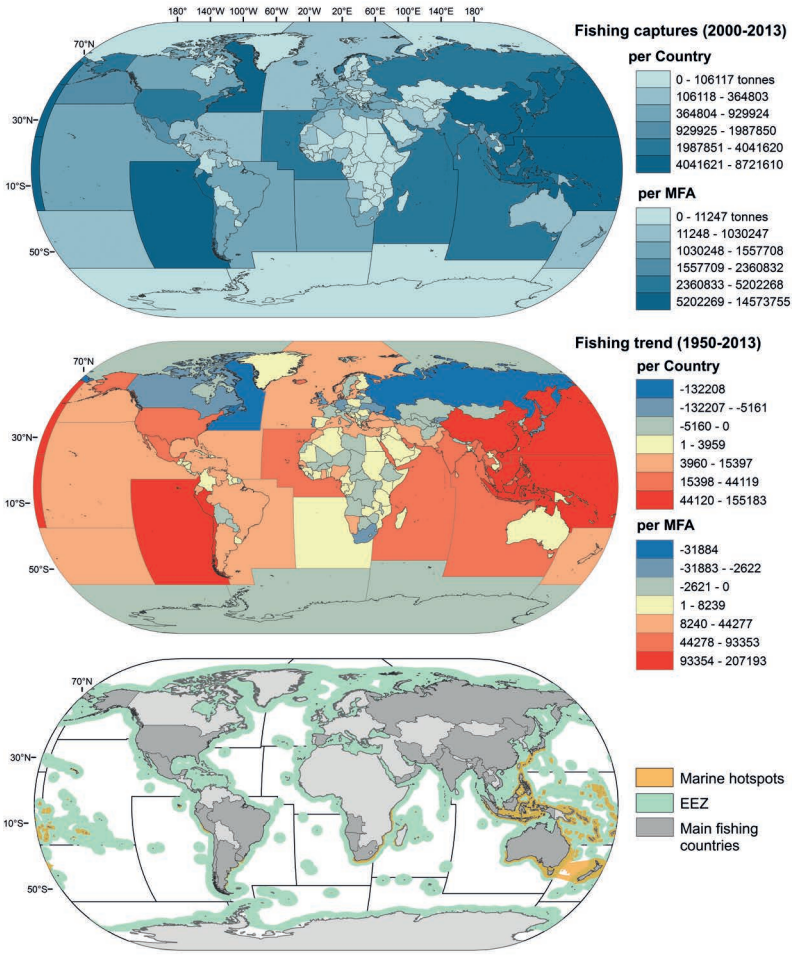

Figure 3. Fishing impact on the marine environment. Average fishing captures (in tonnes) for the 2000-2013 period are represented per country and Major Fishing Area (MFA) (upper figure). Trends in fishing captures (slope of the linear trend for the 1950-2013 period) are also represented per country and MFA (central figure). Those countries contributing most to fishing captures at those MFA that overlap to a large extent with marine biodiversity hotspots are highlighted in dark grey (lower figure). All of them have sovereign Exclusive Economic Zones (EEZ) overlapping marine hotspots, with the exception of Spain.

Fishing policies that promote sustainable fishing practices are required if the aggravating effect of fishing intensity on climate change impacts is to be minimized. Our results can be used to assess whether, or how, fishing activities can be spatially managed to reduce their negative impacts on ecosystems, for example, by shifting fishing zones to decrease impacts in regions of high biodiversity that are being affected by climate change-driven environmental variability (*55*, *59*).

Uncertainty will always be a factor in research on marine organisms and their open environment. The challenge is to use the available data to produce timely and scientifically sound approaches to identify issues of marine conservation now (*60*). Our analyses provide a framework that allows the evaluation of environmental and human impacts on marine communities at the local, regional and global scales. Further, this adaptive framework can be continuously updated and enhanced by incorporating additional information on human stressors (*55*, *61*) or finer scale data on oceanographic features and fishing captures whenever these become available. What is clear from our current analyses is that the world's areas of highest marine biodiversity are threatened by the impacts from both global warming and human fishing pressure. It behoves the international community, then, to find solutions that go beyond the interests and borders of sovereign states if we are to conserve the biodiversity in these marine hotspots, in a similar way to which the world must tackle the associated causes of climate change itself.

MATERIALS AND METHODS

Experimental Design

We used the longest time-series available of remote-sensing records on SST (1980-2014), CHL (1979-2014) and marine currents (1980-2014) to provide finest-scale measurements available of the impacts of climate change in the marine environment globally (Table S1). We then observed and described such environmental changes within hotspots of marine biodiversity determined from the world distributions of more the 2,000 species of seabirds, marine mammals and fish.

Furthermore, the overall picture of human-related impacts on the marine environment would be incomplete without consideration of industrial fisheries. Using FAO data over the last 60 years, we investigated spatiotemporal variation in fishing captures and identified those countries contributing the most to fishing pressure within these marine hotspots.

Statistical Analysis

Pixel basis, least-square liner regression of annual information from SST, CHL and the Eastern and Northern components of water speed was used for deriving the significance of temporal trends (p-value < 0.05) and its magnitudes (slopes; i.e. annual changes in target features) over the past three decades (Fig. S1). These magnitudes were combined to obtain our spatially-explicit

Cumulative Impact Index. Different layers were first resampled following a bilinear interpolation procedure to match the spatial resolution of the coarsest SST product (i.e., one-degree grid). Absolute values for the slopes of obtained trends (a proxy to the magnitude of environmental changes) were then standardized to the maximum value to make all variables comparable. These relative values were subsequently added on a pixel basis and standardized again to the maximum value. In this way, we obtained a dimensionless index ranging from 0 (no change) to 1 (maximum change), thereby providing information about spatial heterogeneity in the magnitude of environmental changes and highlighting those marine areas that have undergone the largest changes in their environmental conditions (Fig. 1).

We used information on the distribution of 2183 species of vertebrates comprised of 1729 fish, 124 marine mammals and 330 seabirds to derive spatially-explicit information on species richness (number of species) and to identify hotspots of marine biodiversity. The worldwide distribution of species was sourced online from IUCN (http://www.iucnredlist.org/) and BirdLife International (http://www.birdlife.org) as ESRI supported geodatabases including spatial information on species-specific occurrences (presence/absence).
Occurrence shapefiles were transformed to 0.5 degree, dichotomous grid features with 1 denoting presence and 0 indicating absences. Obtained grid features for different fish, marine mammal and seabird species were added to obtain three maps indicating the number of species per group occurring in each pixel. Each map was standardized by the total number of species per group in order to obtain a relative measure of the spatial distribution of fish, marine mammal and seabird species richness. These relative values were subsequently added on a pixel basis and standardized again to the maximum value to obtain a dimensionless index ranging from 0 (absence of species) to 1 (maximum species richness), providing information about the spatial heterogeneity in species richness and highlighting hotspots of marine biodiversity without biases towards those groups (e.g., fish) with a larger number of species (Fig. 2). We considered hotspots of marine biodiversity to be those marine areas enclosing pixels with values of species richness over the upper 95 percentile, which was a threshold that identified relatively small and compact marine areas of special concern within the main ocean basins (i.e. Pacific, Indic and Atlantic Oceans, Fig. S3).

Finally, we evaluated changes in landings of fish over the last sixty years to look for temporal trends in the exploitation of marine resources. Further, we identified those countries that have contributed the most to fishing captures in general and, in particular, at the derived hotspots of marine diversity during the last decade. Long-term information (1950-2013) on marine fishing captures (tonnes) where sourced from FAO throughout the FishStatJ software. Captures were restricted to marine fish (1,149 species) and grouped per year, country and Major Fishing Area (according to FAO categories).

Least-square liner regressions of annual information on fish landing were used for deriving the temporal trend per country and Major Fishing Area (Fig. 3).

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REFERENCES

1. J. Hansen *et al.*, Global temperature change. *Proc. Natl. Acad. Sci.* **103**, 14288–14293 (2006).
2. S. C. Doney *et al.*, Climate change impacts on marine ecosystems. *Annu. Rev. Mar. Sci.* **4**, 11–37 (2012).
3. S. Levitus *et al.*, Global ocean heat content 1955–2008 in light of recently revealed instrumentation problems. *Geophys. Res. Lett.* **36**, L07608 (2009).
4. R. F. Keeling, A. Körtzinger, N. Gruber, Ocean deoxygenation in a warming world. *Annu. Rev. Mar. Sci.* **2**, 199–229 (2010).
5. J. J. Polovina, E. A. Howell, M. Abecassis, Ocean's least productive waters are expanding. *Geophys. Res. Lett.* **35**, L03618 (2008).
6. W. W. Gregg, M. E. Conkright, P. Ginoux, J. E. O'Reilly, N. W. Casey, Ocean primary production and climate: Global decadal changes. *Geophys. Res. Lett.* **30**, 1809 (2003).
7. M. J. Behrenfeld *et al.*, Climate-driven trends in contemporary ocean productivity. *Nature*. **444**, 752–755 (2006).
8. W. W. L. Cheung *et al.*, Shrinking of fishes exacerbates impacts of global ocean changes on marine ecosystems. *Nat. Clim. Change*. **3**, 254–258 (2013).
9. M. T. Burrows *et al.*, The pace of shifting climate in marine and terrestrial ecosystems. *Science*. **334**, 652–655 (2011).
10. W. W. L. Cheung, R. Watson, D. Pauly, Signature of ocean warming in global fisheries catch. *Nature*. **497**, 365–368 (2013).
11. M. Winton, S. M. Griffies, B. L. Samuels, J. L. Sarmiento, T. L. Frölicher, Connecting changing ocean circulation with changing climate. *J. Clim.* **26**, 2268–2278 (2012).
12. J. Alheit, A. Bakun, Population synchronies within and between ocean basins: Apparent teleconnections and implications as to physical–biological linkage mechanisms. *J. Mar. Syst.* **79**, 267–285 (2010).
13. FAO, *State of the World's Fisheries and Aquaculture 2008* (Food and Agriculture Organization of the United Nations, Rome, 2009).
14. B. Worm *et al.*, Impacts of biodiversity loss on ocean ecosystem services. *Science*. **314**, 787–790 (2006).
15. J. A. Anticamara, R. Watson, A. Gelchu, D. Pauly, Global fishing effort (1950–2010): Trends, gaps, and implications. *Fish. Res.* **107**, 131–136 (2011).
16. J. M. Durant *et al.*, Timing and abundance as key mechanisms affecting trophic interactions in variable environments. *Ecol. Lett.* **8**, 952–958 (2005).

17. J. Hipfner, Matches and mismatches: ocean climate, prey phenology and breeding success in a zooplanktivorous seabird. *Mar. Ecol. Prog. Ser.* **368**, 295–304 (2008).
18. J. García Molinos *et al.*, Climate velocity and the future global redistribution of marine biodiversity. *Nat. Clim. Change*. **advance online publication** (2015), doi:10.1038/nclimate2769.
19. P. M. Cury *et al.*, Global seabird response to forage fish depletion—One-third for the birds. *Science*. **334**, 1703–1706 (2011).
20. J. K. Baum, B. Worm, Cascading top-down effects of changing oceanic predator abundances. *J. Anim. Ecol.* **78**, 699–714 (2009).
21. K. M. Brander, Global fish production and climate change. *Proc. Natl. Acad. Sci.* **104**, 19709–19714 (2007).
22. C. Rosenzweig *et al.*, Attributing physical and biological impacts to anthropogenic climate change. *Nature*. **453**, 353–357 (2008).
23. O. Hoegh-Guldberg, J. F. Bruno, The impact of climate change on the world's marine ecosystems. *Science*. **328**, 1523–1528 (2010).
24. A. McQuatters-Gollop *et al.*, Is there a decline in marine phytoplankton? *Nature*. **472**, E6–E7 (2011).
25. C. R. McClain, A decade of satellite ocean color observations. *Annu. Rev. Mar. Sci.* **1**, 19–42 (2009).
26. R. Watson, A. Kitchingman, A. Gelchu, D. Pauly, Mapping global fisheries: sharpening our focus. *Fish Fish.* **5**, 168–177 (2004).
27. R. F. Spielhagen *et al.*, Enhanced modern heat transfer to the arctic by warm Atlantic water. *Science*. **331**, 450–453 (2011).
28. A. Schmittner, Decline of the marine ecosystem caused by a reduction in the Atlantic overturning circulation. *Nature*. **434**, 628–633 (2005).
29. D. G. Boyce, M. R. Lewis, B. Worm, Global phytoplankton decline over the past century. *Nature*. **466**, 591–596 (2010).
30. E. M. Acha, H. W. Mianzan, R. A. Guerrero, M. Favero, J. Bava, Marine fronts at the continental shelves of austral South America: Physical and ecological processes. *J. Mar. Syst.* **44**, 83–105 (2004).
31. C. Deser, A. S. Phillips, M. A. Alexander, Twentieth century tropical sea surface temperature trends revisited. *Geophys. Res. Lett.* **37**, L10701 (2010).
32. L. Wu *et al.*, Enhanced warming over the global subtropical western boundary currents. *Nat. Clim. Change*. **2**, 161–166 (2012).
33. S. C. Doney, Oceanography: Plankton in a warmer world. *Nature*. **444**, 695–696 (2006).
34. C. A. Boulton, L. C. Allison, T. M. Lenton, Early warning signals of Atlantic Meridional Overturning Circulation collapse in a fully coupled climate model. *Nat. Commun.* **5**, 5752 (2014).
35. V. S. Karpouzi, R. Watson, D. Pauly, Modelling and mapping resource overlap between seabirds and fisheries on a global scale: a preliminary assessment. *Mar. Ecol. Prog. Ser.* **343**, 87–99 (2007).
36. D. P. Tittensor *et al.*, Global patterns and predictors of marine biodiversity across taxa. *Nature*. **466**, 1098–1101 (2010).
37. S. Pompa, P. R. Ehrlich, G. Ceballos, Global distribution and conservation of marine mammals. *Proc. Natl. Acad. Sci.* **108**, 13600–13605 (2011).
38. A. D. Davidson *et al.*, Drivers and

hotspots of extinction risk in marine mammals. *Proc. Natl. Acad. Sci.* **109**, 3395–3400 (2012).

39. G. Beaugrand, M. Edwards, V. Raybaud, E. Goberville, R. R. Kirby, Future vulnerability of marine biodiversity compared with contemporary and past changes. *Nat. Clim. Change*. **5**, 695–701 (2015).
40. R. T. Barber, F. P. Chavez, Biological Consequences of El Niño. *Science*. **222**, 1203–1210 (1983).
41. E. S. Darling, I. M. Côté, Quantifying the evidence for ecological synergies. *Ecol. Lett.* **11**, 1278–1286 (2008).
42. L. Gangoso, R. Márquez-Ferrando, F. Ramírez, I. Gomez-Mestre, J. Figuerola, Understanding phenotypic responses to global change. *BioEssays*. **35**, 491–495 (2013).
43. Y. Loya *et al.*, Coral bleaching: the winners and the losers. *Ecol. Lett.* **4**, 122–131 (2001).
44. E. A. Fulton, Interesting times: winners, losers, and system shifts under climate change around Australia. *ICES J. Mar. Sci.* **68**, 1329–1342 (2011).
45. H. Weimerskirch, M. Louzao, S. de Grissac, K. Delord, Changes in wind pattern alter albatross distribution and life-history traits. *Science*. **335**, 211–214 (2012).
46. F. J. Mueter, M. A. Litzow, Sea ice retreat alters the biogeography of the bering sea continental shelf. *Ecol. Appl.* **18**, 309–320 (2008).
47. P. D. Spencer, Density-independent and density-dependent factors affecting temporal changes in spatial distributions of eastern Bering Sea flatfish. *Fish. Oceanogr.* **17**, 396–410 (2008).
48. J. A. Hare, M. A. Alexander, M. J. Fogarty, E. H. Williams, J. D. Scott, Forecasting the dynamics of a coastal fishery species using a coupled climate–population model. *Ecol. Appl.* **20**, 452–464 (2010).
49. J. M. Durant, D. Hjermann, G. Ottersen, N. C. Stenseth, Climate and the match or mismatch between predator requirements and resource availability. *Clim. Res.* **33**, 271–283 (2007).
50. F. Ramírez *et al.*, Oceanographic drivers and mistiming processes shape breeding success in a seabird. *Proc R Soc B*. **283**, 20152287 (2016).
51. O. Hoegh-Guldberg *et al.*, Coral reefs under rapid climate change and ocean acidification. *Science*. **318**, 1737–1742 (2007).
52. G. P. Jones, M. I. McCormick, M. Srinivasan, J. V. Eagle, Coral decline threatens fish biodiversity in marine reserves. *Proc. Natl. Acad. Sci. U. S. A.* **101**, 8251–8253 (2004).
53. J. A. Idjadi, P. J. Edmunds, Scleractinian corals as facilitators for other invertebrates on a Caribbean reef. *Mar. Ecol. Prog. Ser.* **319**, 117–127 (2006).
54. I. Afán, A. Chiaradia, M. G. Forero, P. Dann, F. Ramírez, A novel spatio-temporal scale based on ocean currents unravels environmental drivers of reproductive timing in a marine predator. *Proc R Soc B*. **282**, 20150721 (2015).
55. B. S. Halpern *et al.*, A global map of human impact on marine ecosystems. *Science*. **319**, 948–952 (2008).
56. F. Ramírez *et al.*, Natural and anthropogenic factors affecting the feeding ecology of a top marine predator, the Magellanic penguin. *Ecosphere*. **5**, art38 (2014).
57. D. Pauly *et al.*, Towards sustainability in world fisheries. *Nature*. **418**, 689–695

(2002).
58. W. W. L. Cheung *et al.*, Large-scale redistribution of maximum fisheries catch potential in the global ocean under climate change. *Glob. Change Biol.* **16**, 24–35 (2010).
59. D. Witherell, C. Pautzke, D. Fluharty, An ecosystem-based approach for Alaska groundfish fisheries. *ICES J. Mar. Sci. J. Cons.* **57**, 771–777 (2000).
60. R. L. Lewison, L. B. Crowder, A. J. Read, S. A. Freeman, Understanding impacts of fisheries bycatch on marine megafauna. *Trends Ecol. Evol.* **19**, 598–604 (2004).
61. B. S. Halpern *et al.*, Spatial and temporal changes in cumulative human impacts on the world/'s ocean. *Nat. Commun.* **6** (2015), doi:10.1038/ncomms8615.

Supplementary Material

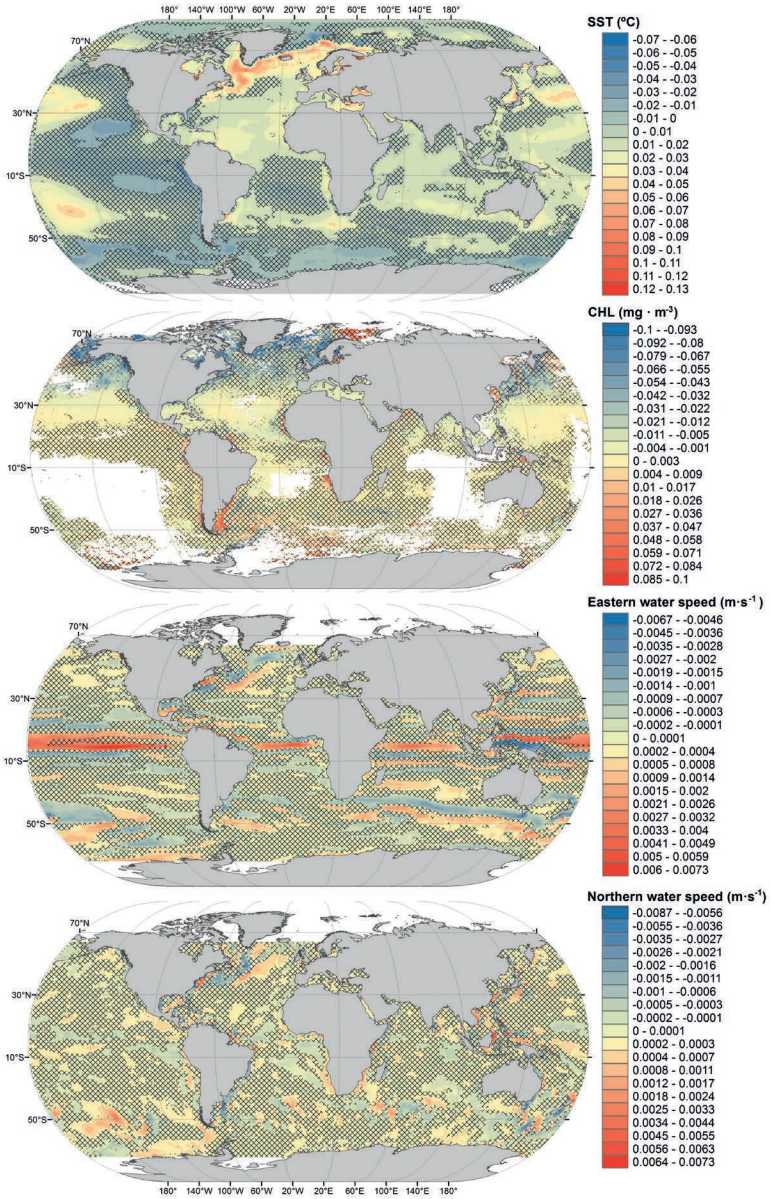

Figure S1. Significances and magnitudes of observed environmental changes. Long term trends in sea surface temperature (SST, 1983-2014), chlorophyll-a concentration (CHL, 1979-2014) and the Eastern and Northern component of water speed (1980-2014). Colors represent the slope of derived linear regressions for each single pixel; white pixels indicate no data and gridded areas include those water masses in which observed trends were not significant (p-value > 0.05).

	Country	Fishing captures (tonnes)	Cumulative %
Pacific, Eastern Central MFA 77	Mexico	962723.4	61.8
	Panama	155137.3	71.8
	USA	136875.9	80.6
	Others	302971.3	100
Pacific, Southwest MFA 81	New Zealand	418192.8	73.7
	Australia	62201	84.7
	Others	87087.6	100
Pacific, Southeast MFA 87	Perú	7013396.1	62.8
	Chile	3344109.1	92.7
	Ecuador	418287.8	96.4
	Others	398236.9	100
Atlantic, Southwest MFA 41	Argentina	615552.6	47.1
	Brazil	458650.1	82.2
	Uruguay	86813.6	88.9
	Spain	71457.3	94.4
	Others	73593	100
Atlantic, Southeast MFA 47	Soth Africa	658576.5	45.1
	Namibia	491099.5	78.7
	Angola	239899.6	95.1
	Others	71151.1	100
Indian Ocean, Western MFA 51	India	1688476.4	44.3
	Pakistan	331067.3	53
	Iran	329393.9	61.6
	Yemen	174535.9	66.2
	Spain	150252.6	70.2
	Oman	146678.7	74
	Maldives	141404.5	77.7
	Others	849019.8	100
Indian Ocean, Eastern MFA 57	Myanmar	1521985.4	29.3
	Indonesia	1090430.3	50.2
	India	859186.2	66.7
	Thailand	560752.5	77.5
	Malaysia	499108.9	87.1
	Others	670804.8	100
Pacific, Northwest MFA 61	China	8532664.1	58.5
	Japan	2658153.5	76.8
	Russia	1855706.7	89.5
	Others	1527230.7	100
Pacific, Western Central MFA 71	Indonesia	2951187.8	30.5
	Philipines	1983863.3	50.9
	Vietnam,	1445675.4	65.9
	Thailand	1233662.9	78.6
	Malaysia	632644.1	85.1
	Others	1440805.1	100

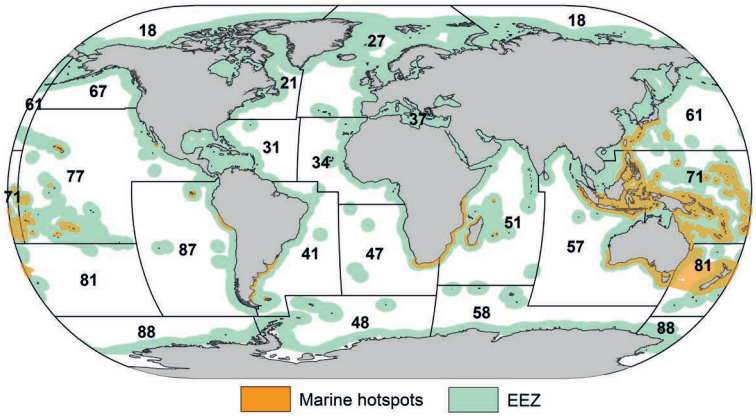

Figure S2. Major contributors to fishing pressure. Top-ranked countries mostly contributing to fishing captures within Major Fishing Areas (MFA, according to FAO categorization) enclosing hotspots of marine biodiversity. The upper map shows the spatial distribution of the world's MFA, the Exclusive Economic Zones (EEZ) and the hotspots of marine biodiversity. The left Table provides detailed information on the average fishing captures (raw values and the percentage of accumulated captures with respect total captures) for those countries (sorted as a function of fishing captures) that mainly contribute to human fisheries within MFAs with high biodiversity.

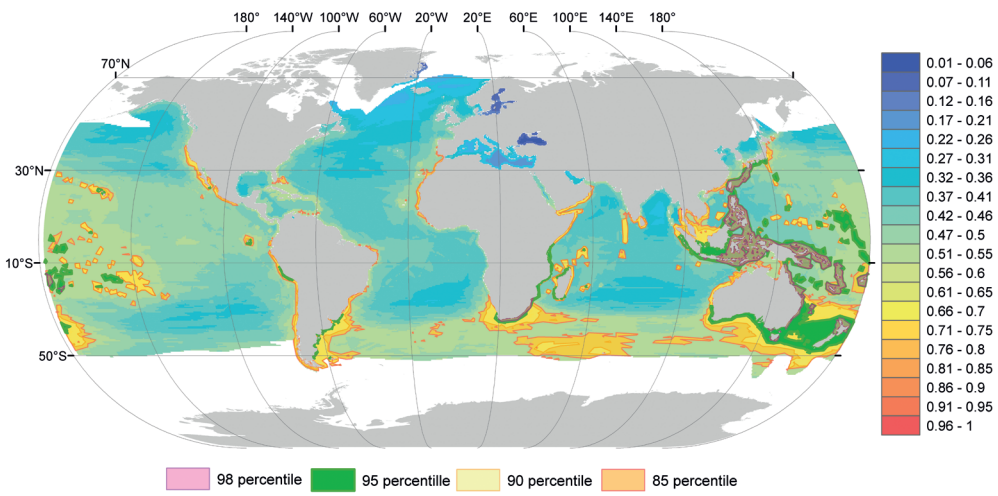

Figure S3. Identifying hotspots of marine biodiversity. Marine areas encompassing 0.5 degree pixels with values of species richness over the upper 85, 90, 95 and 98 percentiles. The upper 95 percentile include marine hotspots from main ocean basins (Indian, Pacific and Atlantic Oceans) while minimizing their extend (surface), thus providing a more realistic picture of potential areas to be protected. Background represents a represent a dimensionless index of biodiversity ranging from 0 (absence of species) to 1 (maximum species richness).

Table S1. Long-term, remote sensing records of oceanographic features. Oceanographic features used for tracing the impact of global change on the marine ecosystems, accessed on 2015/04/20.

	Coverage		Resolution	
	Spatial	Temporal	Spatial (^{0})	Temporal
Chlorophyll-a concentration				
Coastal Zone Color Scanner (CZCS)[1]	90N - 90S, 0E - 360E	1979-1986	0.08333	annual
SeaWiFS[1]	90N - 90S, 0E - 360E	1997-2001	0.08333	annual
MODIS[1]	90N - 90S, 0E - 360E	2002-2014	0.08333	annual
Sea Surface Temperature				
NOAA Optimum Interpolation (OI) Sea Surface Temperature (SST) V2[2]	89.5N - 89.5S, 0.5E - 359.5E	1982-2014	1	monthly
Marine currents				
NCEP Global Ocean Data Assimilation System (GODAS)[2]	74.5S - 64.5N, 0.5E - 359.5E	1980-2014	0.333 lat x 1 lon	monthly

[2]NOAA: http://www.esrl.noaa.gov/psd/data/gridded/data.noaa.oisst.v2.html

[1]OceanColor: http://oceancolor.gsfc.nasa.gov/cms/

CHAPTER II

A novel spatio-temporal scale based on ocean currents unravels environmental drivers of reproductive timing in a marine predator.

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A novel spatio-temporal scale based on ocean currents unravels environmental drivers of reproductive timing in a marine predator.

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Abstract

Life-history strategies have evolved in response to predictable patterns of environmental features. In practice, linking life-history strategies and changes in environmental conditions requires comparable space–time scales between both processes, a difficult match in most marine system studies. We propose a novel spatio-temporal and dynamic scale to explore marine productivity patterns probably driving reproductive timing in the inshore little penguin (*Eudyptula minor*), based on monthly data on ocean circulation in the Southern Ocean, Australia. In contrast to what occurred when considering any other fixed scales, little penguin's highly variable laying date always occurred within the annual peak of ocean productivity that emerged from our newly defined dynamic scale. Additionally, local sea surface temperature seems to have triggered the onset of reproduction, acting as an environmental cue informing on marine productivity patterns at our dynamic scale. Chlorophyll-*a* patterns extracted from this scale revealed that environment factors in marine ecosystems affecting breeding decisions are related to a much wider region than foraging areas that are commonly used in current studies investigating the link between animals' life history and their environment. We suggest that marine productivity patterns may be more predictable than previously thought when environmental and biological data are examined at appropriate scales.

CHAPTER III

Where to head? Investigating the role of wind and productivity patterns in driving the foraging destinations in a central-place forager

Afán I., Arcos J.M., Ramírez F., García D., Rodríguez B., Delord K., Boué A., Micol T., Weimerskirch H., Louzao M. (2016) *Scientific Reports*, submitted

Where to head? Investigating the role of wind and productivity patterns in driving the foraging destinations in a central-place forager

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Abstract

Foraging opportunities for seabirds are largely driven by heterogeneous distribution of prey availability and forcing factors influencing individual decision-making, such as winds. This is particularly true during the breeding period, when their movements are constrained by the location of their breeding grounds (central-place foragers). Here, we assessed the role of oceanic winds and productivity patterns in driving the foraging destinations of a critically endangered seabird, the Balearic shearwater *Puffinus mauretanicus*, during its breeding period. We used GPS data-loggers and Argos PTTs to track the foraging flights of Balearic shearwaters during the chick-rearing period of 2011-2014 in the Balearic Islands (Western Mediterranean). We identified at-sea hotspots, characterized their productivity patterns, and estimated flying costs to reach them from the colony, accounting for the temporal and spatial variability of wind forces. Closest areas on the Iberian shelf were used on a regular basis every year, whereas areas farther away were only used occasionally, coinciding with short time windows when winds were favourable to reach them. Our study provides an energetic understanding of individual foraging destinations and highlights the importance of studying the energetic ecology of wide-ranging seabird

INTRODUCTION

Animals are expected to find an optimal balance between food intake (energy gain) and foraging costs (energy expenditure), in order to maximize their foraging efficiency[1]. In the case of wide-ranging marine top predators, the optimal energetic balance requires a good choice of where and when to move, to exploit sparsely and often elusively distributed prey in heterogeneous and dynamic oceans[2,3]. This is especially true for breeding seabirds, which are spatially constrained by the location of their colonies (central-place foragers). Therefore, seabird foraging patterns would be largely driven by the energetic trade-off between resource acquisition and the cost of travel throughout environmentally suitable seascapes[4,5]. During breeding, the location of the foraging grounds of seabirds might be determined by several intrinsic traits, such as internal state or previous experience, and extrinsic factors such as intra-specific competition[6], information sharing[7] or environmental conditions[8].

One challenge in understanding animal foraging decisions is determining the factors shaping the habitat choice of wide ranging species[9]. A way of addressing this question is to analyse the combine effect of resource distribution and forcing factors. In marine ecosystems, the main gap is the lack of direct information on prey distribution, but remotely sensed data on oceanographic environment offer suitable surrogates of marine productivity (e.g. chlorophyll *a*), which in turn can be taken as a surrogate of prey availability[10,11].

But increased understanding of the influence of marine productivity patterns in habitat choice has not yet answered the question of why seabirds choose to forage within specific locations at specific times[9]. Furthermore, the main forcing factor for flying seabirds is the wind, which may be either an opposing or an assisting force to the movement, depending on its relative direction to the bird trajectory [12,13]. Seabirds are able to reduce flying energy expenditure by using wind in an optimal way, spending little energy when searching for prey following favourable winds[14,15]. The study of efficiency in movement strategies must be examined in relation to the environment that is being traversed[16]. Therefore modelling the cost of transport through different routes or times of travel might be of paramount relevance to advance our understanding of foraging destinations.

Recent studies have modelled energy landscapes, predicting the fine-scale energetic costs of moving in a given environment[16,17] providing valuable information about animals' distribution in the space. Marine ecosystems differ from terrestrial landscapes in their higher variability in environmental conditions, shaping dynamics and continuously changing seascapes. Accordingly, the study of wind conditions as a trigger of animal behavioural responses (e.g. search movement, decision-making) ideally needs high temporal and spatial resolution data to be able to reflect the dynamic character of the environment[18,19].

In the present study, we focused on the most threatened seabird in Europe, the Balearic shearwater *Puffinus mauretanicus*, which breeds only in the Balearic Islands in the western Mediterranean Sea[20]. Previous studies have provided important insights into the spatial distribution and the at-sea ecology of the species, which forages in waters along the Iberian continental shelf during the breeding period[21-24]. Despite such attention, this species has been the focus of relatively few tracking studies[25-28]. We performed a multi-year tracking study with the aim of unravelling the influence of environmental factors in the spatial and temporal variability in foraging destinations (i.e., heading decision). Selected environmental variables were (1) marine productivity patterns at foraging grounds and (2) the flying costs associated to reach overall foraging grounds considering windscapes[29]. We hypothesized that seabird decision making might be related with a trade-off between selecting higher productive areas and minimizing flying costs while commuting between breeding and foraging grounds.

RESULTS

We obtained tracking information from 21 GPS-devices and 5 PTTs during the chick-rearing period. After discarding one incomplete trip and two failed breeders which performed consecutive trips without returning to the colony, we accounted for a total of 21,873 locations, grouped in 31 foraging trips of 15 different individuals (7 females and 8 males) (Table 1, Supplementary Fig. S1). Mean maximum distances from the colony averaged 214 ± 142 km (range 20 – 616 km, see Table 1). Trips lasted in average 70 ± 53 hours (range 18 – 167) and covered 775 ± 557 km (range 102 – 2196).

Females tended to perform shorter trips, both on time and distance, and had shorter trip ranges than males (Table 1), but these differences were not statistically significant, and did not show any year-effect for the GPS tracks (2012-2014) (linear mixed models, all $p > 0.05$). Commuting trips between the colony and the hotspots (Supplementary Fig. S2) represent 13% of total fixes. Commuting sections measured in average 109 ± 87 km and lasted in average 5 ± 4 hours. Trips described straight-line paths (mean relative angle between consecutive fixes, 1 ± 6 degrees) with an average westward direction (261 ± 52 degrees).

At-sea hotspots

We identified nine hotspots for southern Balearic shearwaters for the chick-rearing periods of 2011-2014 (Fig. 1), which encompassed 70 % of the total bird fixes. These areas were located within the Iberian and north-African continental shelves (65 ± 30 % of total area placed in waters within the 200 m isobaths, which represents the limits of the continental shelf). The most utilized area was located in the Gulf of Valencia (area 3), accounting for 20 ± 16% of total fixes. Major areas (areas 2 to 6, encompassed by the 25% kernel contours) were concentrated between 41-38º N, and located 125 ± 78

Tracking season	Individuals (n)	Trips (n)	Trip duration (h)	Total distance (km)	Trip range (km)
2012 (25 May-3 Jun)					
all	4	5	64.1 ± 60.5	708.1 ± 513.0	209.4 ± 124.5
♂	3	3	78.2 ± 77.5	814.6 ± 657.4	231.5 ± 163.1
♀	1	2	42.8 ± 34.0	548.4 ± 321.4	176.3 ± 71.3
2013 (23-30 May)					
all	7	10	65.0 ± 5.3	704.2 ± 464.4	188.1 ± 78.7
♂	3	4	73.6 ± 42.7	759.3 ± 406.8	206.7 ± 80.3
♀	3	5	57.9 ± 62.1	667.1 ± 596.7	176.0 ± 92.4
2014 (27 May-7 Jun)					
all	8	12	77.2 ± 55.9	860.7 ± 668.7	238.5 ± 188.5
♂	2	3	75.6 ± 76.5	752.5 ± 803.2	227.4 ± 220.3
♀	3	4	70.7 ± 36.6	690.8 ± 371.5	154.9 ± 15.5

Table 1. Foraging trip characteristics of Balearic shearwaters tracked with GPS devices during the chick-rearing stage from Conillera, Eivissa Island between 2012 and 2014. Values for trip duration, total distance and trip range show mean ± SD.

km from the colony (range: 7-202 km; distance calculated from the colony to the centroid of each polygon). Areas 1, 7 and 8 were defined by the 50% contours, whereas the furthermost area 9 in Morocco (more than 600 km from the colony) was encompassed by the 75% contour. Regarding temporal patterns, we detected annual differences in the visiting patterns (Fig. 2). While the closest areas to the colony (hotspots 3, 4, 5) were visited all four years, the farthest areas received individuals only in one or two years of the study. Moreover, northern and southern areas were visited in alternate years: northern areas (hotspots 1 and 2) were visited during 2012 and 2013 whereas southern Algerian (hotspot 7) was visited during 2011 and 2014 years. Farthest areas (hotspots 8 and 9 in the Alboran Sea) were only visited during 2014.

Outward flights always passed through area 4 (which enclosed the surroundings of the colony), though usually traded other areas further away (only 7% of trips had area 4 as their final destination). After area 4, most trips reached first hotspot 3 (48%) and 5 (38%), while other areas were usually accessed travelling through inshore trips following the eastern Spanish coastline rather than commuting directly from the colony.

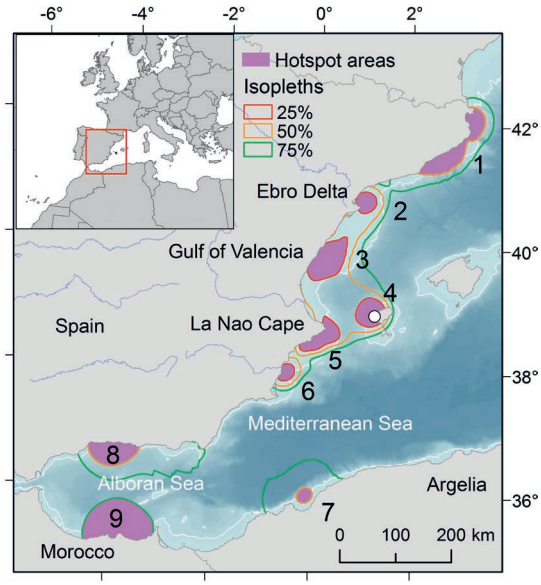

Figure 1. At-sea hotspot areas derived from PTT satellite transmitter and GPS tracking during the chick-rearing period of 2011 to 2014 from southern breeding population of Balearic shearwaters (Conillera Island colony location indicated by a white dot). Volume contours (isopleths) resulting from utilization distribution averaged across marked individuals from 2011 to 2014 are represented in red, orange and green lines for the 75%, 50% and 25% percentages respectively. At-sea hotspot areas are identified in violet polygons. Bathymetry is shown in the background. White line indicates the 200 m isobath.

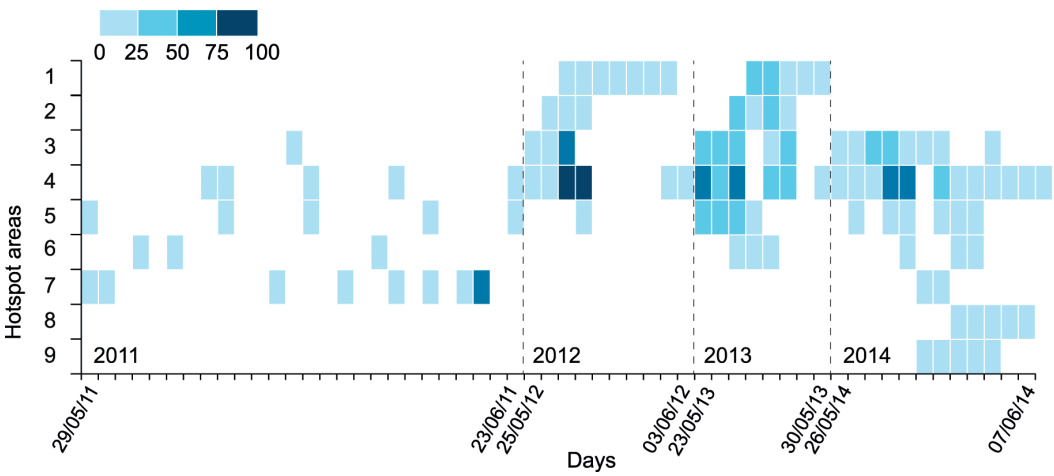

Figure 2. Timeline of visits to the hotspot areas during the study (2011-2014 chick-rearing stage). Colours show percentage of tracked individuals from the corresponding year visiting daily each area. Vertical dotted lines divide each study year.

Productivity patterns at hotspots areas

CHL maximum annual peak typically occurred during the end of winter and the beginning of spring, from January to April (Figs. 3a and S4). Afterwards, because of the formation of a sub-surface CHL maximum layer, surface CHL values drop drastically in all areas. CHL values during maximum annual peak significantly varied between the hotspot areas (ANOVA, $F_{8,27}$= 9.103, $p < 0.001$), but no year effect of the year was found (ANOVA, $F_{3,32}$= 1.091, $p = 0.367$). Higher values of CHL (averaged for the January-April peak) were found throughout all years in area 8 (1.45 ± 0.3 mg m^{-3}), and in the surroundings of the Ebro Delta in area 2 (mean ± SD: 1.0 ± 0.3 mg m^{-3}). These areas also showed the greatest variability between years (Fig. 3a).

At-sea activity patterns

Resting, take-off, flight and landings represented 42 ± 15, 9 ± 3, 39 ± 12 and 10 ± 7 % (mean ± SD) of total time trips, respectively. Landings, which could be considered as a proxy of foraging effort, were spatially concentrated inside the hotspot areas, which accounted for 74% of total landings. This supports the idea that hotspot areas are mainly used to forage. Percentage of landings inside UDs areas relative to total trip landings (Fig. 4) were higher in the areas farther from colony (areas 1, 2, 8 and 9 showed percentages above 60%) and lower in the areas closest to the colony (areas 4, 5, 6) and area 7 in Algeria (below 20%). Predominant activity outside the continental shelf was flight (75.2% of time during out shelf journeys).

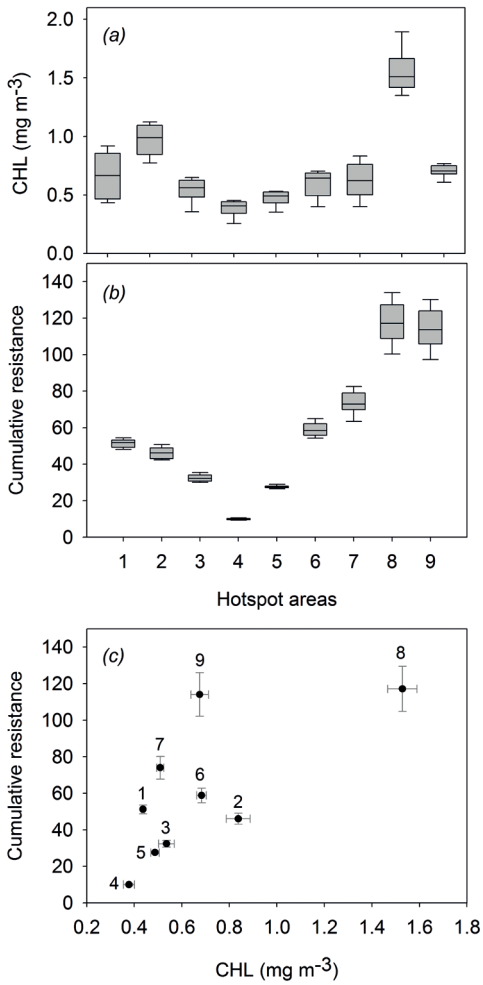

Figure 3. (a) Chlorophyll a (CHL) values for each hotspot area of Balearic shearwater during the 2011-2014 period. Values for each area were averaged for the maximum annual peak period (January to April). Median is shown by horizontal line within each box. Upper and lower limit of each box define the upper and lower quartile respectively. Ends of the whiskers represent the minimum and maximum values excluding outlayers (b) Cumulative resistances values for each hotspot area obtained from the pairwise model with Circuitscape analysis. (c) Biplot of CHL and cumulative resistance from the colony to each hotspot (referred in numbers above dots) area obtained from the connectivity analysis. Higher values of cumulative resistance show less connectivity between areas.

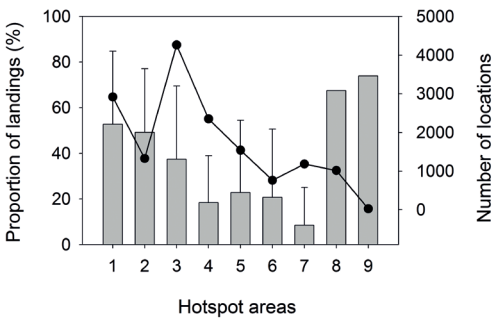

Figure 4. Percentage of landings inside each hotspot area regarding total trip landings. Black points show number of total fixes inside each area computed during the 2011-2014 study period.

Seascape flying costs

Main mean annual winds (Supplementary Fig. S3) during the study period blew south-eastwards from the colony (average direction for blowing winds: 143 ± 57 degrees), creating favourable conditions for reaching the closest shelf waters of eastern Iberia every year. There were no significant differences between years in neither wind direction (circular ANOVA, $F_{2,10}$=1.15, p=0.354) nor outward trip direction (circular ANOVA, $F_{2,10}$=0.79, p=0.476). Despite no differences were found in the mean direction of winds, daily cost maps showing the resistance to fly from the colony to each pixel showed great variability between days (see Fig. 5, Supplementary S4 and S5). The continental shelf areas of Algeria (area 7) were reached when environmental conditions provided lower flying costs to reach those southern areas (Fig. 5, Supplementary S5 and S6) and the flying costs occasionally increased for commuting to frequently exploited central areas. Linear models show that heading taken by birds during out shelf journeys was mainly affected by cost computed during these trips (t=3.903, p < 0.001), and also, but in a lesser degree, by CHL peak values for the first area achieved (t=4.685, p=0.013).

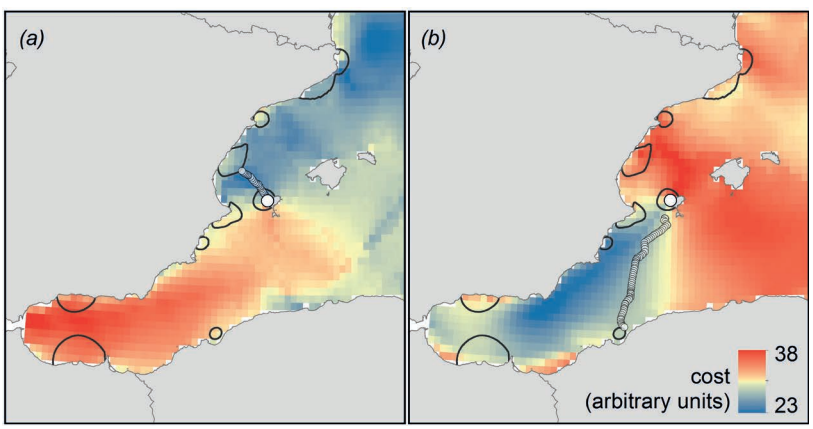

Figure 5. Examples of cost seascapes for (a) 26/05/2014 and (b) 31/05/2014. Surface costs were calculated as the relative effort required to traverse a pixel following the direction from the colony to each cell, and based on the cost flight function developed by Louzao et al. (2014). For each day, mean flying costs were calculated for the time range (in hours) with tracked individuals, considering straight flights from the colony to each cell. Arbitrary cost units are graded in ramp colours. Polygons (black lines) represent the limits of the hotspot areas.

Results from Circuitscape analysis show higher resistance values and variability as getting away from the colony (Fig. 3b), as costs were cumulative and possible paths increased with distance. Hotspots 4 and 5, the less productive ones and the closest to the colony, resulted as the most predicable (less variability) and with a lower cumulative resistance values for arriving, followed by area 3. Farther from these areas, only area 7 was achieved directly only during two outward trips, despite its higher cumulative resistance cost. Combination of productivity and connectivity information (Fig. 3c) show that a greater effort would be needed to achieve farther areas of enhanced productivity.

DISCUSSION

Based on a multi-year tracking study, we tried to unravel the main factors influencing individual foraging decision-making of a central-place forager. Particularly, we assessed how windscapes and marine productivity interact to influence foraging destinations in Balearic shearwaters. We found that the proximity to the colony and windscapes were the main factors influencing the selection of foraging destinations, whereas productivity patterns played a secondary role. This is the first study providing an energetic understanding of the movement ecology of this critically endangered species.

Southern Balearic shearwaters did select the closest continental shelf productive areas, based on the facility to reach them (less costly outward trips). Indeed, the most frequently visited areas were located in the Gulf of Valencia (latitudinal range: 41-38º N) in an average range of 125 km from the colony. Prevailing winds blow from south-east (143 ± 57º) during trips, favouring trips to these areas. Flights toward hotspot areas were accomplished by using commuting movements[30], maintaining a particular bearing during the 100 km length (in average) of these flights. After leaving the colony, the arrival to the first destination was facilitated by favourable winds during the outward stages of trips, coinciding with lesser cumulative flight costs and higher stability in cumulative resistances values from the colony. While hotspots in the Gulf of Valencia were visited every year, areas farther north and south within the distribution range were less frequently visited. From those areas, only southern distant areas in the northern African coast (the west of Algeria and east of Morocco) and the Alboran Sea were directly reached from the colony. We also found that heading taken by birds was more affected by cost computed during outward trips than by productivity patterns of the first visited foraging grounds.

Birds can save energy when flying across-wind, and can also gain substantial speed by flying with the wind[15,31,32]. The construction of geographic information system type cost seascapes offers an excellent framework to study spatio-temporal variability in physical properties of the environment in which variation in animal movements can be understood[16]. Seascapes flying costs show

high spatial and temporal variability in costs computed from the colony, which highlights the importance of using the best spatial and temporal resolution environmental models available. The use of winds as environmental driver provides support for trips toward closest areas to the colony (areas 3, 4 and 5). Nevertheless, Algerian coasts are also directly accessed from the colony under certain conditions, specifically when favourable winds towards the Algerian coasts minimize travel costs there, at the same time the costs of reaching the closest foraging areas in the Iberian shelf increase. However, reaching these areas suppose in average a threefold effort than arriving to closer and most visited areas.

Balearic shearwaters forage consistently in shallow shelf and coastal waters, as confirmed by previous studies[21,25,28]. Although the Mediterranean Sea is globally considered oligotrophic, hydrographic features linked to shelf areas contribute to increase its productivity, especially in the western sub-basin, as coastal upwelling and rivers runoff[33]. Another enrichment mechanism includes shelf-slope fronts along the continental and insular coasts. Shelf areas used by Balearic shearwaters present a clear seasonal cycle in CHL patterns typical of the Mediterranean Sea[34], with maximum annual peaks of CHL occurring at the end of winter and the beginning of spring. Outstanding values in CHL characterized the Ebro Delta and especially the northern Alboran Sea areas, which are considered the most productive areas in the Mediterranean Sea[34]. While mesoscale oceanographic features such as the Ebro River runoff enhanced marine productivity in the area 2[35], a costal upwelling induced by the anticyclonic gyres of the Alboran Sea provides high CHL values in area 8[36]. Differences in productivity values were reflected in activity patterns, which were not equally distributed within all areas, with higher rates of landings in farther but also in more productive areas, as in the Ebro Delta. This might be also related to the need to offset the higher cost of reaching these areas.

A recent study performed in central populations of Balearic shearwater (located in Mallorca island, 120 km northeast from Eivissa), during the incubation period of 2011-2014, identified that this population undertake direct commuting flights to foraging areas off the north-eastern coasts of Spain[28]. Those areas largely coincided with area 1 of our study, and marginally with areas 2 and 3. But overall, despite a partial overlap off the Ebro Delta, the Gulf of Valencia and La Nao Cape were basically visited by southern population individuals, despite being within the foraging range of both populations. Therefore, the hypothesis raised by Louzao et al.[22] suggesting a spatial segregation of foraging grounds, supported by stable isotope signatures and habitat models, among Balearic shearwater populations have been partially contrasted by tracking information of both central and southern populations. Further studies describing the foraging distribution of northern populations of Balearic shearwaters are required to complete the overall foraging distribution of the species. This seems to be a common

situation for seabirds e.g.,[37,38,39], and might be the result of density-dependence competition (i.e., birds would minimize intra-specific competition of adjacent colonies by increasing foraging ranges as a result of prey depletion or disturbance until their home ranges overlap). But in small populations such as Balearic shearwaters, other factors such as individual experience or windscapes seem also a plausible hypothesis.

Our results indicate that the main foraging grounds of the Balearic shearwater seems stable over time, coinciding with previous studies[28]. The high site fidelity of foraging grounds makes feasible the designation of Marine Protected Areas for the species, where conservation efforts might be focused. Particular attention deserves the implementation of mitigation measures for fishing bycatch, which is regarded as the main threat at sea for the species[40]. The main foraging areas identified off the Iberian coast largely coincide with the Important Bird Areas (IBAs) proposed by SEO/BirdLife[23] and recently designated as Special Protection Areas (SPAs) under the EU Natura 2000 network. Management plans are pending of implementation, but these might well contribute to the conservation of this critically endangered seabird. However, our results show that Balearic shearwaters also make substantial use of areas off the African coast, which also merit protection. Further studies are required to refine these areas, as well as other potentially new foraging grounds, and properly complement the whole picture including data from northern, central and southern populations of the Balearic shearwater. The inclusion of the areas already identified here as marine IBAs would be a first step to reach their final conservation[41]. Afterwards, these could be achieved by designating them as Specially Protected Areas and Biological Diversity in the Mediterranean (SPAMI) under the Barcelona Convention[42].

METHODS

Study site and field methods

The tracking study was carried out during the chick-rearing periods (May-June; see details in Table 1) of 2011-2014 in Conillera islet (off west Eivissa, southern Balearic Islands, western Mediterranean; 38.98ºN, 1.21ºE, Fig. 1), hosting a population of about 180 breeding pairs[43]. In 2011, six breeding adults were tagged with solar panel PTTs (Platform Terminal Transmitters; Microwave Telemetry, Columbia: three 5 g and three 9 g devices) with a duty-cycle of 48-hour off period, with 10-hour on period see more details in[25]. From 2012 to 2014, 31 breeding adults were tagged with i-gotU GPS loggers (CatTraQ™, Catnip Technologies, USA, modified GT-120: 11.2-15.4 g). The initial package was removed and put in a heat-shrink tube for water proofing. GPS devices were set to record one fix every 5 minutes. Tracking devices were attached on the back feathers using solely Tesa TapeH®[44]. The total weight of combined GPS bio-loggers and attachments (12.8-17 g), representing 2.0-3.8% of the bird body mass for GPS and 0.8-1.9% for PTT (i.e., within the 3-5% limit recommended by most authors;[45]. To reduce potential

detrimental effects to the birds, devices were deployed for the duration of one foraging trip (average 2.9 ± 2.2 days) and, upon return to the nest, the birds were recaptured and the devices removed. Whenever birds evaded recapture, two or more trips were recorded by a single individual. Sex was determined from 12 of the 15 individuals with successful data retrieval by molecular discrimination from DNA extracted from blood collected during device recovery (n=8), but a species-specific discriminant function based on biometry measurements was used otherwise (n=7)[46].

Data processing

Argos PTT locations were filtered using the algorithm described in Freitas et al.[47] using a speed-distance-angle filter ("SDA filter" function with maximum threshold speed at 70 km h^{-1}) and default settings for distance and turning angles from the *Argosfilter* package[48] in the statistical program R[49] . For GPS data, fixes with speed higher than 70 km·h^{-1} were discarded (0.2% of total fixes)[25]. Bird activity at each location (resting, take-off, flying, landing) was estimated on the basis of speed between successive positions. Threshold limit of resting positions was fixed on 2 km h^{-1} after visual inspection of speed trip histograms (Supplementary Fig. S7a). After discriminating resting and flying locations, landing was assigned to the last flying position before resting and take-off to the last resting position before flying (Supplementary Fig. S7b). Trips were divided into outward and return phases, defined according to the maximum range distance reached from the colony. For the outward phase, locations covering the areas out of the shelf from the colony to the first destination in the Iberian or African shelf were classified as out shelf journeys. We hypothesised that this phase of the trips would be the most influenced by wind conditions in the decision-making process to select a foraging destination, on the basis of minimizing energy expenditure.

For all complete trips, total travelling distance (geodetic distance in m), trip range (maximum distance from the breeding colony in km), trip duration (days), speed (km h^{-1}), bearing (degrees) and distance (m) between successive raw positions were computed. Differences in foraging trip parameters (trip range, trip duration and total distance) were tested by using generalized linear mixed models. Sex and year (2012-2014, excluding 2011 data from PTTs) were included as fixed factors in the models. Individual identity was also included as a random factor to account for the dependence among different foraging trips from the same GPS-tracked individual. Normality (Shapiro–Wilk test) and homoscedasticity (Levene's test) of the data were verified before statistical analysis. Both trip distance and trip range were log transformed and trip duration was squared root transformed. All statistical analyses were performed using the R environment[49].

Identification of at-sea hotspots

At-sea hotspots were identified by the probability utilization distribution

defining the space use of southern population of Balearic shearwaters, calculating the population mean kernel density with the R package *adehabitatHR*[50]. Because individuals were tracked for different years, with different devices, and trips differed in duration, we estimated kernel density for each individual[6], selecting the smoothing parameter *h* best describing the individual's distribution by the default *ad hoc* method, on a 3 km UTM ETRS89 31N grid To avoid overweight due to the different systems used, each individual kernel was standardized to a range of values within 0 to 1, before averaging. To characterize all areas, including those scarcely used, and categorize them according to their use frequency, we chose the isopleth with the minimum volume contour that covers each separate area (25% in the nearby of the colony and most frequently visited from the eastern Spanish continental shelf, 50% for the Algerian area and northern and southern areas of the Spanish shelf, and 75% for the less visited area in the north east Moroccan coast). This choice might introduce some bias in the different size of the surfaces selected but assure the incorporation of all potential destinations.

Environmental variables were selected considering the hypothesis we formulated in relation to the choice of foraging destinations, depending on drivers such as chlorophyll a as a proxy of productivity[21] and the cost of flight (wind speed and direction to calculate flying costs). Both variables were obtained at higher temporal and spatial resolution available from remote sensing data and developed meteorological wind models.

Marine productivity patterns

We derived CHL data (mg m^{-3}) as a proxy to marine productivity from the MODIS sensor on board the Aqua satellite. Weekly data for 2011-2014 was retrieved from the NASA Ocean Color website (http://oceancolor.gsfc.nasa.gov/), as level 3 Hierarchical Data Format (HDF) at a spatial resolution of 9 km. Data was processed and converted from HDF files to raster images using the Marine Geospatial Ecology Tools for ArcGIS10.2 (ESRI, Redland, USA)[51]. Weekly CHL was averaged for each hotspot and daily interpolated using a non-parametric locally smoothing function (loess) to remove noise in the original signal of weekly data[52]. Time series of CHL values for each area showed a seasonal peak from January to April (Supplementary Fig. S8). After these months, CHL detected by remote sensors drops drastically, according with the stratification period in the Mediterranean, which cause the formation of a sub-surface CHL maximum layer, harder to detect in satellite images[2,53].

For comparative purpose between areas, CHL values were yearly averaged for each hotspot area for the maximum annual peak of CHL (January to April). Differences in CHL were tested for years and areas using analysis of variance (ANOVA) previous to log transforming the variable to account for normality.

Flying costs across the seascape

Based on high spatial and temporal resolution wind fields, we generated daily spatial cost seascapes during the days when trips were recorded to estimate the most easily connected hotspot area with the breeding site. This analysis took into account both distance and travel facilitation provided by winds.

Wind speed (m s^{-1}) and wind direction (degrees) at 10 m above sea level were obtained from the prediction system of the sea state (WANA) that the Spanish Ports Authority (www.puertos.es) has developed in collaboration with the AEMET (Spanish State Meteorological Agency, www.aemet.es). Nevertheless, these data are not predictions but they are analysis or diagnosis data, and they are consistent with observations realized from a buoyancy network points in the Mediterranean Sea. AEMET uses the HIRLAM (HIgh Resolution Limited Area Model) wind model to generate wind fields. Original data was provided as individual files for each node of a regular network of 0.167º (approximately 15 km) spatial resolution and temporal resolution of 6 hours for 2011 and hourly for the years 2012-2014, and subsequently were aggregated in a netCDF file.

Following methods from Afán et al.[52], we constructed daily cost maps representing the relative effort required to traverse a pixel on a map moving out from the breeding colony, reflecting variability in the seascape. Cost maps were estimated for the range of hours at which outward trips took place using wind speed and direction at the original spatial resolution of 0.167º covering the areas in a radius of 600 km around the colony. We used cost flight function developed by Louzao et al.[14] based on the effect of wind speed and the angle between flight and wind direction based on Weimerskirch et al.[15] and González-Solís et al.[32]:

$$c = 30 + 2.381e\text{-}09 * \theta + -9.667e\text{-}01 * w + 1.093e\text{-}02 * \theta * w$$

where c is the flying cost (*i.e.*, energy expenditure with arbitrary cost units), w represents the wind speed and θ is the angle between flight and wind direction. This function is based on the effect of wind speed w and the angle between flight and wind direction θ based on Weimerskirch et al.[15] and González-Solís et al.[32]. In our case, θ was replaced by the angle between wind direction and the departure direction from the colony in Eivissa to each raster cell of the seascape, resulting in lower values when flight and wind direction match.

Connectivity measures between breeding sites and foraging grounds were calculated with the free software Circuitscape[54], which is based on circuit theory to quantify connectivity incorporating both the minimum movement distance or cost and the availability of alternative pathways. Therefore, the lesser connectivity is assigned to areas with multiple possible pathways. As resistance seascape for Circuitscape we used cost seascapes maps. Effective distances separating each area from the colony were obtained from the matrix of cumulative resistances derived

with the pairwise mode when running Circuitscape.

Analyzing seabirds directionality towards at-sea hotspots

We estimated the heading angle (i.e., bird directionality) as the mean flight direction taken by birds during the straight flights between shelves from the colony and the first hotspot area achieved (commuting flights), averaging the bearing of all trip locations. The estimation of the heading angle to the first foraging destination was based only on the locations outside the continental shelf (depth > 200 m), where birds performed straight flights[28]. Bird directionality while travelling to hotspot areas (out shelf journeys) was evaluated using circular statistics. In order to avoid pseudo-replication, we randomly selected one trip per individual. A circular analysis of variance was performed to test differences in wind direction and heading angles between years. Variables were previously tested for their uniform distribution with the Rayleigh test[55]. A linear regression analysis[56] was performed to examine the relationship between the mean flight direction during out shelf journeys and productivity (CHL) and spatial flying costs. Marine productivity was characterized by the average value of the maximum annual peak of CHL at the locations of the first foraging ground visited by each bird. The flying cost was summarised as the cumulative cost of the out shelf journeys. Angular variables were treated with the *circular* R package[57].

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REFERENCES

Parker, G. A. & Smith, J. M. Optimality theory in evolutionary biology. *Nature* **348**, 27-33 (1990).

Scales, K. L. *et al.* Mesoscale fronts as foraging habitats: composite front mapping reveals oceanographic drivers of habitat use for a pelagic seabird. *J. R. Soc. Interface* **11**, 20140679 (2014).

Fauchald, P. Spatial interaction between seabirds and prey: review and synthesis. *Mar. Ecol. Prog. Ser.* **391**, 139-151 (2009).

Tomlinson, S. *et al.* Applications and implications of ecological energetics. *Trends Ecol. Evol.* **29**, 280-290 (2014).

Weimerskirch, H., Louzao, M., de Grissa, S. & Delord, K. Change in wind pattern alter

albatross distribution and life-history traits. *Science* **335**, 211-214 (2012).

Wakefield, E. D. *et al.* Space partitioning without territoriality in gannets. *Science* **341**, 68-70 (2013).

Weimerskirch, H., Bertrand, S., Silva, J., Marques, J. C. & Goya, E. Use of social information in seabirds: compass rafts indicate the heading of food patches. *PLOS ONE* **5**, e9928 (2010).

Paiva, V. H. *et al.* The foraging ecology of the endangered Cape Verde shearwater, a sentinel species for marine conservation off West Africa. *PLOS ONE* **10**, e0139390 (2015).

Scott, B. E., Webb, A., Palmer, M. R., Embling, C. B. & Sharples, J. Fine scale bio-physical oceanographic characteristics predict the foraging occurrence of contrasting seabird species; Gannet (*Morus bassanus*) and storm petrel (*Hydrobates pelagicus*). *Prog. Oceanogr.* **117**, 118-129 (2013).

Copello, S., Dogliotti, A. I., Gagliardini, D. A. & Quintana, F. Oceanographic and biological landscapes used by the Southern Giant Petrel during the breeding season at the Patagonian Shelf. *Mar. Biol.* **158**, 1247-1257 (2011).

Coppini, G. *et al.* The use of ocean-colour data to estimate chl-a trends in European seas. *Int. J. Geosci.* **4**, 927-949 (2013).

Chapman, J. W. *et al.* Animal orientation strategies for movement in flows. *Curr. Biol.* **21**, R861-R870 (2011).

Felicísimo, A. M., Munoz, J. & González-Solis, J. Ocean surface winds drive dynamics of transoceanic aerial movements.*PLOS ONE* **3**, e2928 (2008).

Louzao, M., Wiegand, T., Bartumeus, F. & Weimerskirch, H. Coupling instantaneous energy-budget models and behavioural mode analysis to estimate optimal foraging strategy: an example with wandering albatrosses. *Mov. Ecol.* **2**, 8 (2014).

Weimerskirch, H., Guionnet, T., Martin, J., Shaffer, S. A. & Costa, D. Fast and fuel efficient? Optimal use of wind by flying albatrosses. *Proc. R. Soc. B* **267**, 1869-1874 (2000).

Shepard, E. L. C. *et al.* Energy landscapes shape animal movement ecology. *The American Naturalist* **182**, 298-312 (2013).

Wilson, R. P., Quintana, F. & Hobson, V. J. Construction of energy landscapes can clarify the movement and distribution of foraging animals. *Proc. R. Soc. B* **279**, 975-980 (2012).

Giuggioli, L. & Bartumeus, F. Animal movement, search strategies and behavioural ecology: a cross-disciplinary way forward. *J. Anim. Ecol.* **79**, 906-909 (2010).

Mueller, T. *et al.* How landscape dynamics link individual- to population-level movement patterns: a multispecies comparison of ungulate relocation data. *Glob. Ecol. Biogeogr.* **20**, 683-694 (2011).

BirdLife International. Species factsheet: *Puffinus mauretanicus*. (2016).

Louzao, M. *et al.* Oceanographic habitat of an endangered mediterranean procellariiform: Implications for marine protected areas. *Ecol. Appl.* **16**, 1683-1695 (2006).

Louzao, M. *et al.* Exploiting the closest productive area: geographical segregation of foraging grounds in a critically endangered seabird. *Mar. Ecol. Prog. Ser.* **429**, 291-301 (2011).

Arcos, J. M. *et al.* Assessing the location and stability of foraging hotspots for pelagic seabirds: An approach to identify marine Important Bird Areas (IBAs) in Spain.

Biol. Conserv. **156**, 30-42 (2012).

Arcos, J. M. & Oro, D. Significance of fisheries discards for a threatened Mediterranean seabird, the Balearic shearwater *Puffinus mauretanicus*. *Mar. Ecol. Prog. Ser.* **239**, 209-220 (2002).

Louzao, M., Delord, K., Garcia, D., Boue, A. & Weimerskirch, H. Protecting persistent dynamic oceanographic features: transboundary conservation efforts are needed for the critically endangered balearic shearwater. *PLOS ONE* **7**, e35728 (2012).

Bartumeus, F. *et al.* Fishery discards impact on seabird movement patterns at regional scales. *Curr. Biol.* **20**, 215-222 (2010).

Ruiz, A., Martí, R. & Mayol, J. *La pardela balear*. (SEO/Bird Life - Conselleria de Medi Ambient del Govern de les Illes Balears, 2004).

Meier, R. E. *et al.* Consistent foraging areas and commuting corridors of the critically endangered Balearic shearwater Puffinus mauretanicus in the northwestern Mediterranean. *Biol. Conserv.* **190**, 87-97 (2015).

Ellis, H. I. & Gabrielsen, G. W. in *Biology of marine birds* (eds E. A. Schreiber & J. Burger) 359-408 (CRC Press, 2001).

Weimerskirch, H. Are seabirds foraging for unpredictable resources? *Deep-Sea Res. Pt. II* **54**, 211-223 (2007).

Amélineau, F. *et al.* Windscape and tortuosity shape the flight costs of northern gannets. *J. Env. Biol.* **217**, 876-885 (2014).

González-Solís, J. *et al.* Influence of sea surface winds on shearwater migration detours. *Mar. Ecol. Prog. Ser.* **391**, 221-230 (2009).

Estrada, M. Primary production in the northwestern Mediterranean. *Sci. Mar.* **60**, 55-64 (1996).

Lazzari, P. *et al.* Seasonal and inter-annual variability of plankton chlorophyll and primary production in the Mediterranean Sea: a modelling approach. *Biogeosciences* **9**, 217-233 (2012).

Olivar, M. P., Salat, J. & Palomera, I. Comparative study of spatial distribution patterns of the early stages of anchovy and pilchard in the NW Mediterranean Sea. *Mar. Ecol. Prog. Ser.* **217**, 111-120 (2001).

Oguz, T., Macias, D., Renault, L., Ruiz, J. & Tintore, J. Controls of plankton production by pelagic fish predation and resource availability in the Alboran and Balearic Seas. *Prog. Oceanogr.* **112**, 1-14 (2013).

Ceia, F. R. *et al.* Spatial foraging segregation by close neighbours in a wide-ranging seabird. *Oecologia* **177**, 431-440 (2015).

Cecere, J. G. *et al.* Commercial fisheries, inter-colony competition and sea depth affect foraging location of breeding Scopoli's Shearwaters *Calonectris diomedea*. *Ibis* **157**, 284-298 (2015).

Grémillet, D. *et al.* Offshore diplomacy, or how seabirds mitigate intra-specific competition: a case study based on GPS tracking of Cape gannets from neighbouring colonies. *Mar. Ecol. Prog. Ser.* **268**, 265-279 (2004).

Genovart, M. *et al.* Demography of the critically endangered Balearic shearwater: the impact of fisheries and time to extinction. *J. Appl. Ecol.*, doi: 10.1111/1365-2664.12622 (2016).

Lascelles, B. G., Langham, G. M., Ronconi, R. A. & Reid, J. B. From hotspots to site protection: Identifying Marine Protected Areas for seabirds around the globe. *Biol. Conserv.* **156**, 5-14 (2012).

Abdulla, A., Gomei, M., Maison, E. & Piante, C. *Status of marine protected areas in*

the Mediterranean Sea. (UICN, Málaga (España) WWF, París (Francia), 2008).

Louzao, M., García, D. & Arcos, J. M. (SEO/BirdLife, IEO, AZTI-tecnalia & IRBI. Informe de actualización 2013-2015, 2016).

Wilson, R. P. *et al.* Long-term attachment of transmitting and recording devices to penguins and other seabirds. *Wildlife Society Bulletin (1973-2006)* **25**, 101-106 (1997).

Phillips, R. A., Xavier, J. C. & Croxall, J. P. Effects of satellite transmitters on albatrosses and petrels. *The Auk* **120**, 1082-1090 (2003).

Genovart, M., McMinn, M. & Bowler, D. A discriminant function for predicting sex in the Balearic Shearwater. *Waterbirds* **26**, 72-76 (2003).

Freitas, C., Lydersen, C., Fedak, M. A. & Kovacs, K. M. A simple new algorithm to filter marine mammal Argos locations. *Mar. Mamm. Sci.* **24**, 315-325 (2008).

Argosfilter: Argos locations filter. R package version 0.63 (http://CRAN.R-project.org/package=argosfilter, 2012).

R: A language and environment for statistical computing (R Foundation for Statistical Computing, Vienna, Austria. http://www.R-project.org/, 2015).

Calenge, C. The package "adehabitat" for the R software: A tool for the analysis of space and habitat use by animals. *Ecol. Model.* **197**, 516-519 (2006).

Roberts, J. J., Best, B. D., Dunn, D. C., Treml, E. A. & Halpin, P. N. Marine Geospatial Ecology Tools: An integrated framework for ecological geoprocessing with ArcGIS, Python, R, MATLAB, and C++. *Environ. Modell. Softw.* **25**, 1197-1207 (2010).

Afán, I., Chiaradia, A., Forero, M. G., Dann, P. & Ramírez, F. A novel spatio-temporal scale based on ocean currents unravels environmental drivers of reproductive timing in a marine predator. *Proc. R. Soc. B* **282**, 20150721 (2015).

Ramírez, F. *et al.* Oceanographic drivers and mistiming processes shape breeding success in a seabird. *Proc. R. Soc. B* **283**, 20152287 (2016).

McRae, B. H., Dickson, B. G., Keitt, T. H. & Shah, V. B. Circuit theory to model connectivity in ecology, evolution, and conservation. *Ecology* **89**, 2712-2724 (2008).

Fisher, N. & Lee, A. Regression models for an angular response. *Biometrics* **48**, 665-677 (1992).

Lund, U., Agostinelli, C. & Agostinelli, M. C. Package 'circular'. (2013).

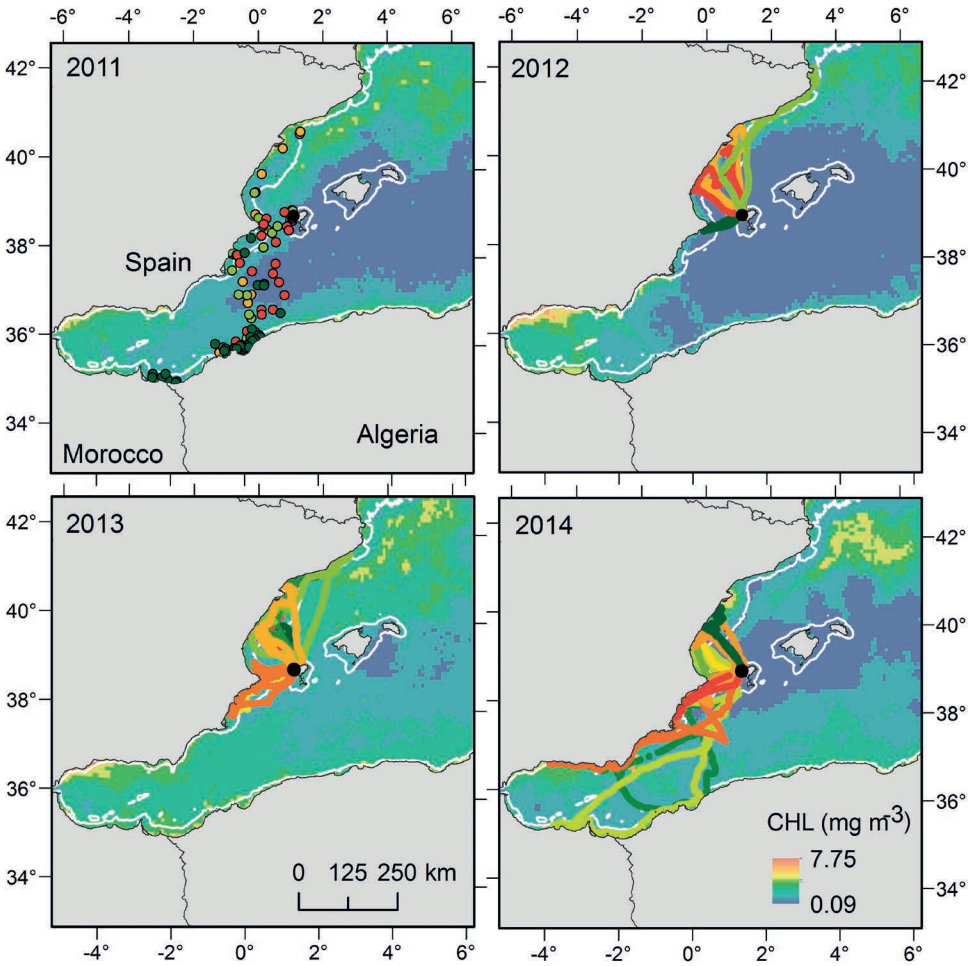

Figure S1. Balearic shearwater foraging trips tracked during chick-rearing periods in 2011 (n=4), 2012 (n=4), 2013 (n=7) and 2014 (n=8). Individuals are coloured in unique colors within each year and only complete trips are displayed. Background shows averaged Chlorophyll a values (CHL) for the maximum annual peak (January-April) for each year. Colony location is indicated with a black dot. White line indicates the 200 m isobath.

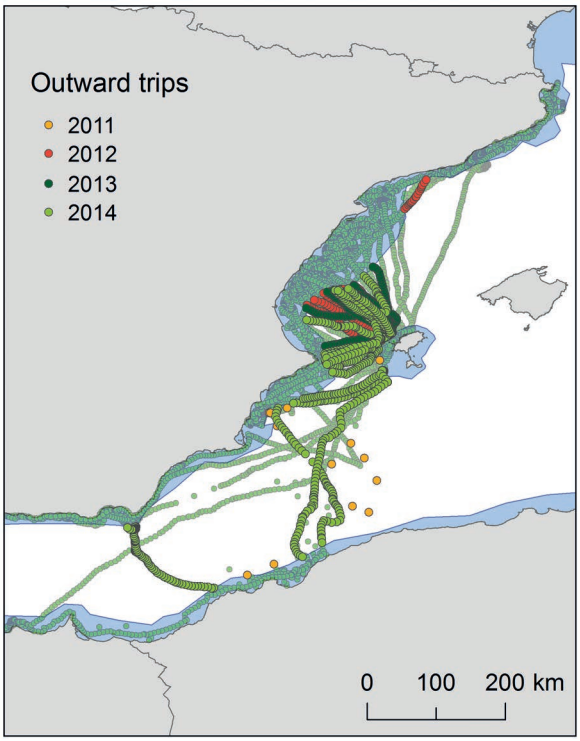

Figure S2. Out shelf journeys: displacements from the colony until the hotspot areas between costal shelves (blue areas). Commuting trips of the Balearic shearwater during the study period (2011-2014). Displacements between costal shelves areas (blue zones) are colour highlighted.

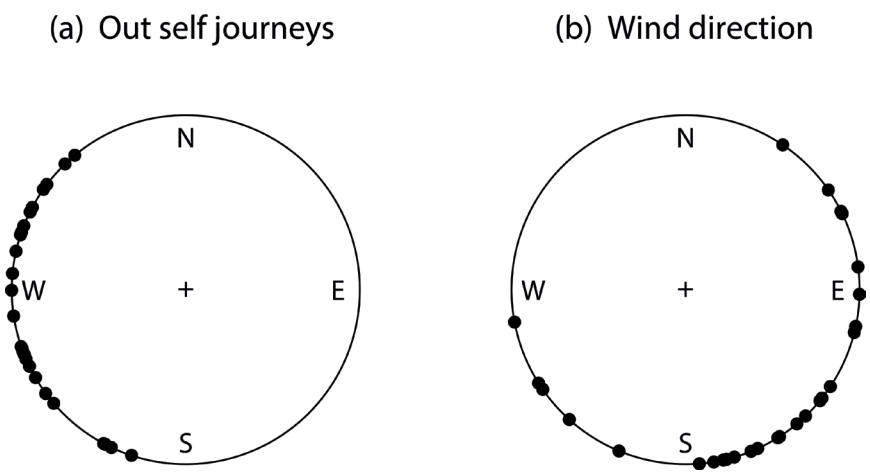

Figure S3. Circular plots of directions taking by tracked adult individuals during (a) out shelf journeys and (b) direction of wind blowing during these trips. Plots include data for all the study years.

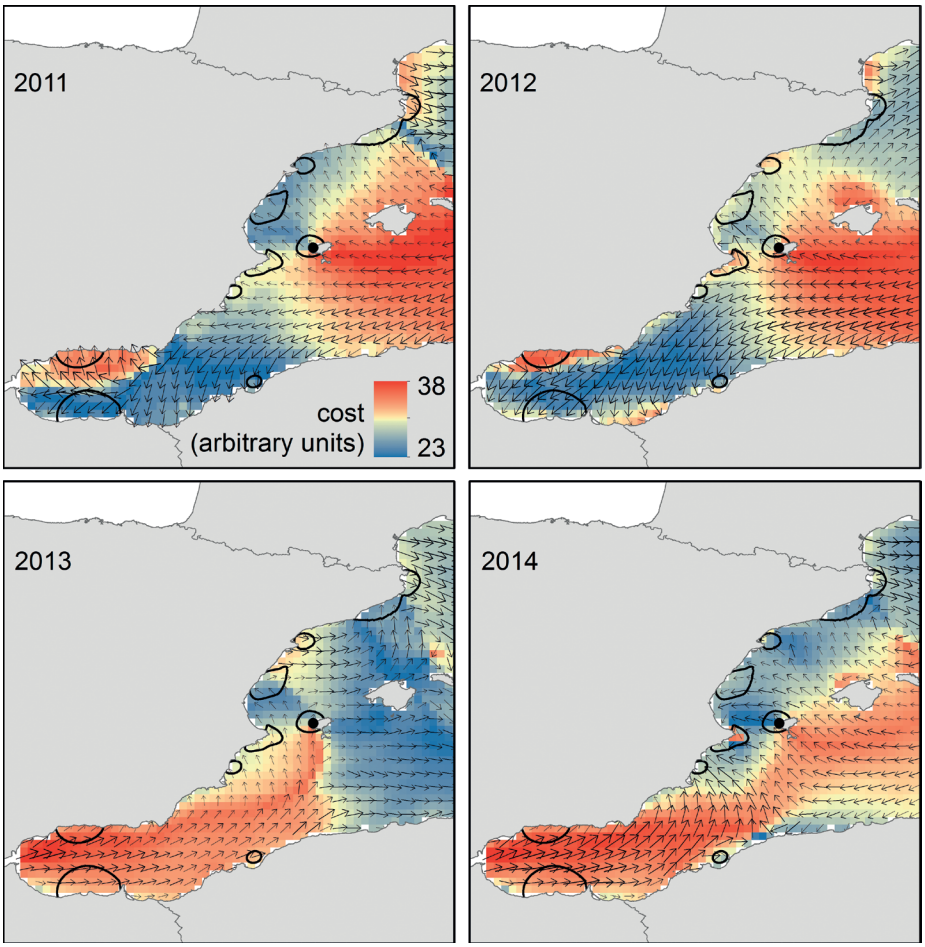

Figure S4. Mean annual cost surfaces. For each year, mean costs were calculated for the time range with tracked individuals, considering straight flights from the colony to each cell. Time ranges addresses 29 May to 1 June for 2011, 25 to 28 May for 2012, 23 to 28 May for 2013 and 26 May to 6 June for 2014. Cost arbitrary units are graded in ramp colors. Arrows direction and size show wind direction and speed. Colony location is indicated with a black dot. At-sea hotspot areas for Balearic shearwaters are enclosed within the black lines.

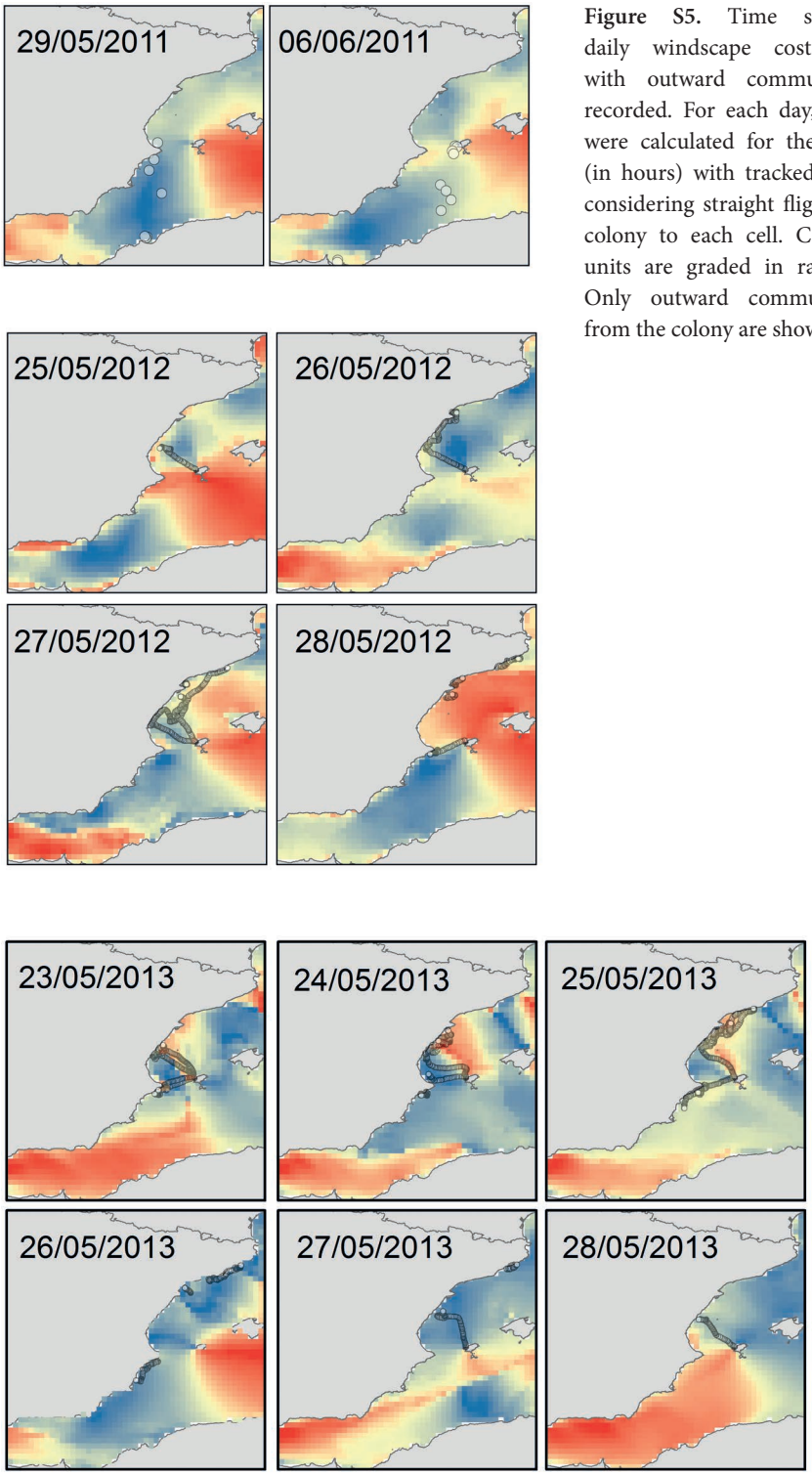

Figure S5. Time sequence of daily windscape costs for days with outward commuting flights recorded. For each day, mean costs were calculated for the time range (in hours) with tracked individuals, considering straight flights from the colony to each cell. Cost arbitrary units are graded in ramp colours. Only outward commuting flights from the colony are shown.

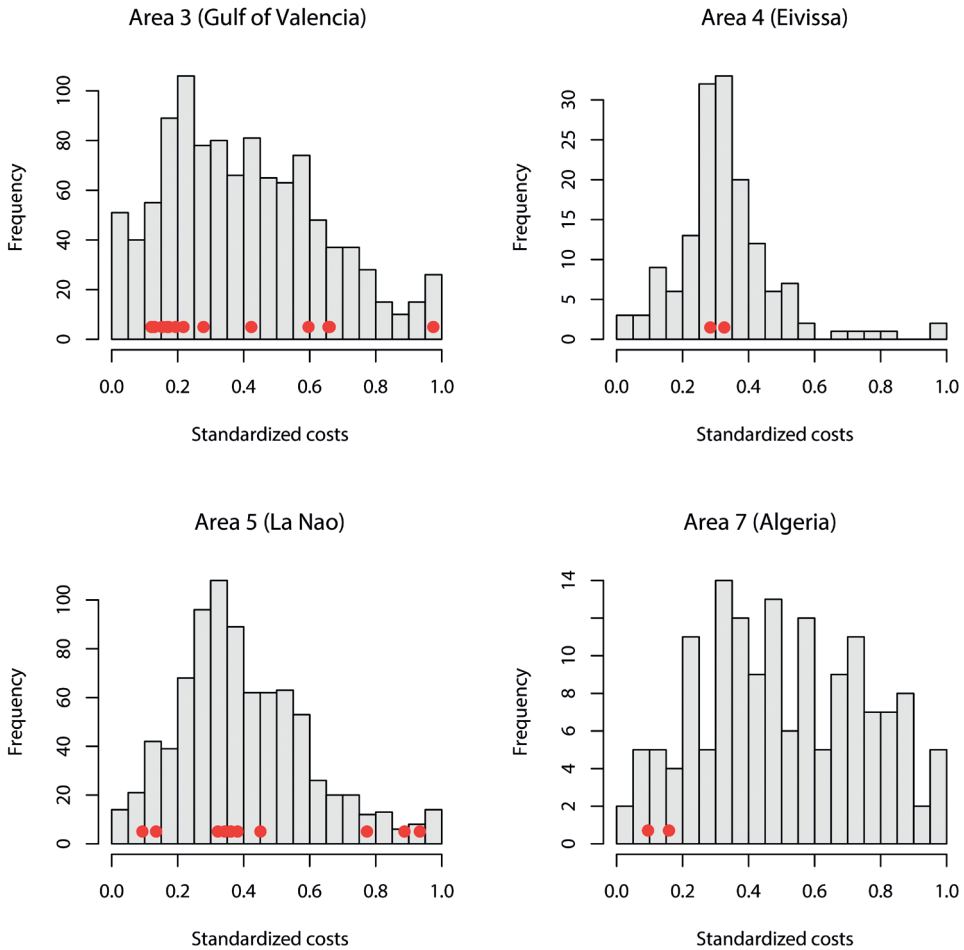

Figure S6. Histograms of costs calculated for all outward trips recorded during the four years of study (2011-2014) arriving as at first destination to each one of the hotspot areas: 3, 4, 5 or 7. Histogram results from the potential data trips costs for all the range of days of the study with tracking birds. Red points show the real cost computed when outward trips were actually realized.

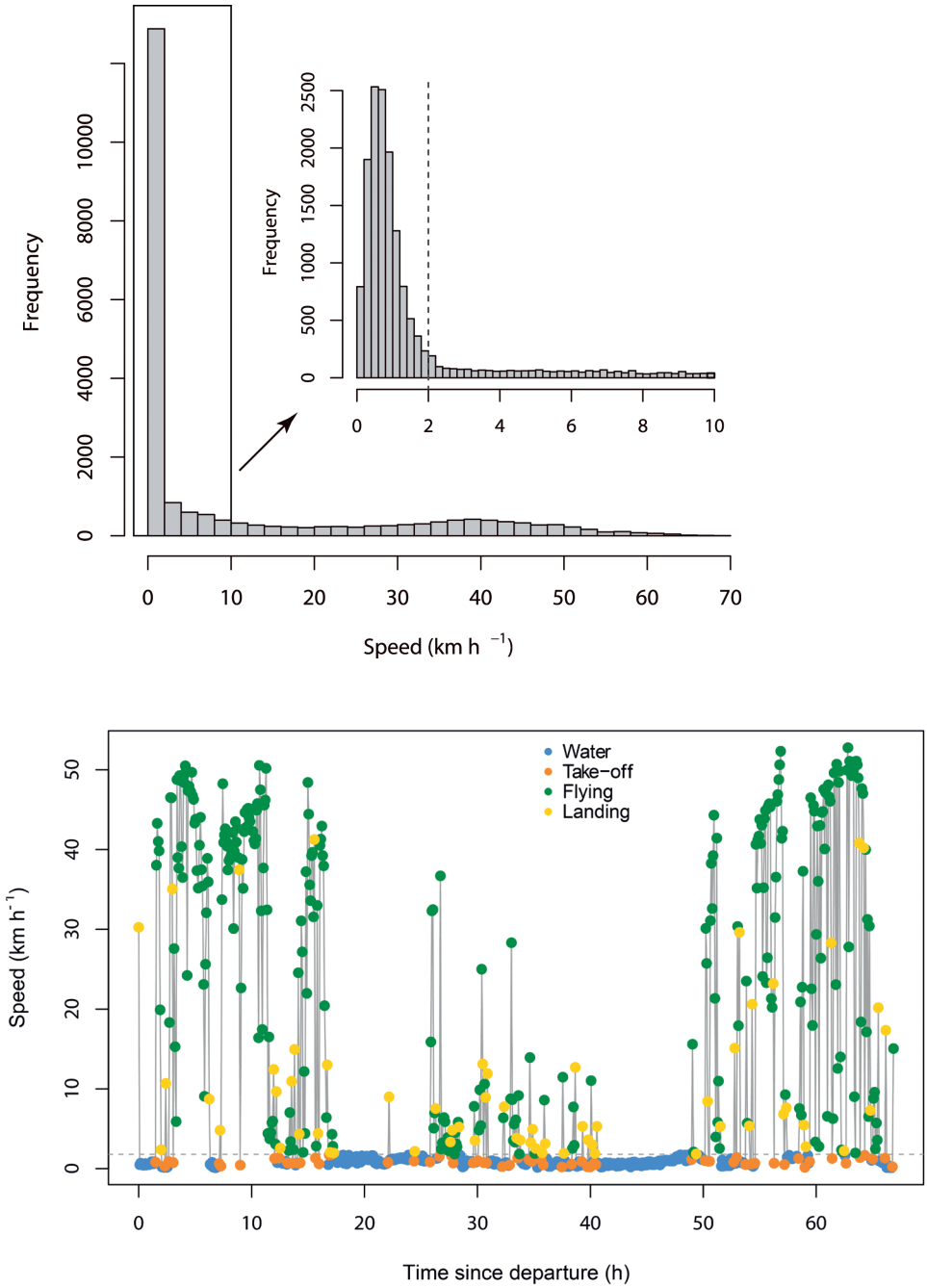

Figure S7. Characterization of activity patterns. (a) Histogram of mean speed (km h-1) for all GPS tracked trips. Threshold at 1.8 km h-1 was established to classify resting from flying locations. (b) Example of sequential activity pattern of one individual of Balearic shearwater along its foraging trip. The black dashed line indicates the threshold of 2 km h-1.

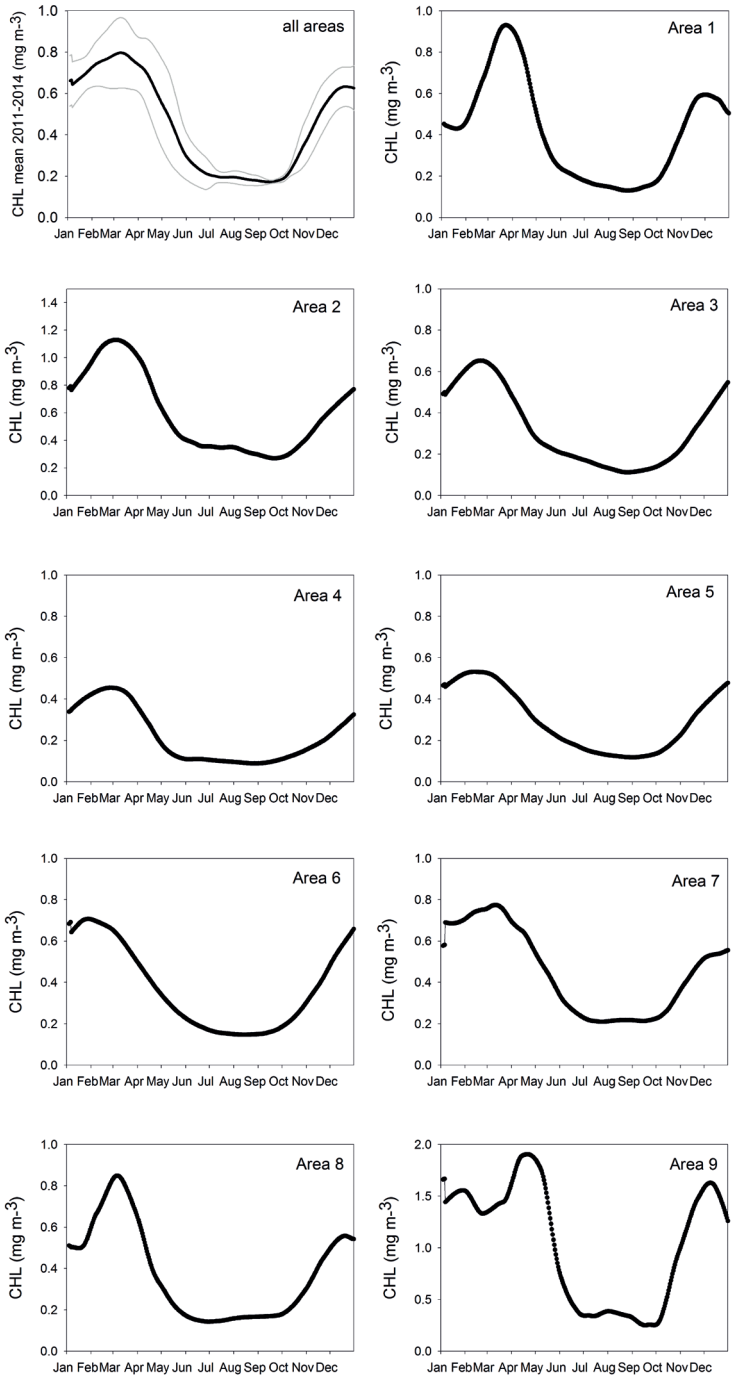

Figure S8. Seasonal patterns of Chlorophyll a (CHL, mg m-3) in the hotspot areas of southern Balearic shearwaters (see Figure 1 for the location of each area). Black line shows the average values for all areas, and grey lines standard deviation values.

CHAPTER IV

Foraging movements and habitat niche of two closely related seabirds breeding in sympatry

Afán I., Navarro J., Cardador L., Ramírez F., Kato A., Rodríguez B., Ropert-Coudert Y., Forero M.G. (2014) *Marine Biology* 161: 657-668

http://link.springer.com/article/10.1007%2Fs00227-013-2368-4

An integrated method for identifying marine areas of highest conservation priority: a case study at the Argentinean Patagonia coast

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Abstract

As central place foragers, pelagic seabirds are constrained by spatiotemporal heterogeneity to find productive marine areas and compete for prey. We analyzed 97 foraging trips to study the movement and oceanographic characteristics of foraging habitats of two different – yet closely related – species of shearwaters (Scopoli's shearwater *Calonectris diomedea* and Cory's shearwater *C. borealis*) breeding in sympatry in the Mediterranean. We combined various methodological approaches (GPS tracking, species distribution modeling and stable isotope analysis) to explore the foraging strategies of these two species. Isotopic results suggested that trophic habits of both shearwater species were similar, mainly based on pelagic fish consumption. Foraging areas of both species were characterized by shallow waters near the colony. Both shearwater species exploited persistent productive marine areas. The foraging areas of the two species broadly overlapped during the incubation period, but during chick-rearing period Scopoli's shearwaters apparently foraged in different areas than Cory's shearwaters.

CHAPTER V

Natural and anthropogenic factors affecting the feeding ecology of a top marine predator, the Magellanic penguin

Ramírez F., Afán I., Hobson K.A., Bertellotti M., Blanco G., Forero M.G. (2014) *Ecosphere* 5: art 38

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Natural and anthropogenic factors affecting the feeding ecology of a top marine predator, the Magellanic penguin

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Abstract

Understanding how top predators respond to natural and anthropogenically induced changes in their environment is a major conservation challenge especially in marine environments. We used a multidisciplinary approach to explore the mechanisms through which a typical central-place forager, the Magellanic penguin (*Spheniscus magellanicus*) from the Chubut province of Argentina, responds to variations in oceanic conditions and prey resources. We combined habitat and species distribution modeling with isotopic dietary reconstructions based on blood $\delta^{13}C$ and $\delta^{15}N$ values to quantify the role of bathymetry, sea-surface temperature and chlorophyll-a concentration, abundance of conspecifics, and extent of fisheries activities in explaining the foraging and feeding ecology of individuals breeding at different colonies. The at-sea distribution of penguins was tightly coupled with the spatial distribution of their staple prey species, anchovies (*Engraulis anchoita*), especially in areas over the continental shelf (200 m depth), with relatively warm water (from 16º to 21ºC), and moderate abundances of conspecifics (from 50 to 250 individuals). Competition with conspecifics and human fisheries were also identified as important factors explaining penguin diet with decreasing relative contributions of anchovies with increasing abundance of conspecifics and fishing activity. Our multifactorial approach allowed us to simultaneously explore different physical, biological and anthropogenic features likely affecting marine resource availability, and, consequently, driving the feeding and foraging ecology of this central-place forager. Our approach can be extended to a large suite of central-place foragers, thus providing important advances in the way we investigate how to effectively conserve and manage these species.

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Natural and anthropogenic factors affecting the feeding ecology of a top marine predator, the Magellanic penguin

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Abstract. Understanding how top predators respond to natural and anthropogenically induced changes in their environment is a major conservation challenge especially in marine environments. We used a multidisciplinary approach to explore the mechanisms through which a typical central-place forager, the Magellanic penguin (*Spheniscus magellanicus*) from the Chubut province of Argentina, responds to variations in oceanic conditions and prey resources. We combined habitat and species distribution modeling with isotopic dietary reconstructions based on blood $\delta^{13}C$ and $\delta^{15}N$ values to quantify the role of bathymetry, sea-surface temperature and chlorophyll-*a* concentration, abundance of conspecifics, and extent of fisheries activities in explaining the foraging and feeding ecology of individuals breeding at different colonies. The at-sea distribution of penguins was tightly coupled with the spatial distribution of their staple prey species, anchovies (*Engraulis anchoita*), especially in areas over the continental shelf (>200 m depth), with relatively warm water (from 16° to 21°C), and moderate abundances of conspecifics (from 50 to 250 individuals). Competition with conspecifics and human fisheries were also identified as important factors explaining penguin diet with decreasing relative contributions of anchovies with increasing abundance of conspecifics and fishing activity. Our multifactorial approach allowed us to simultaneously explore different physical, biological and anthropogenic features likely affecting marine resource availability, and, consequently, driving the feeding and foraging ecology of this central-place forager. Our approach can be extended to a large suite of central-place foragers, thus providing important advances in the way we investigate how to effectively conserve and manage these species.

Key words: Argentinean Patagonia; breeding performance; carbon-13; competition; feeding ecology; fisheries; foraging distribution; indicator species; nitrogen-15; Magellanic penguin; *Spheniscus magellanicus*; stable isotopes.

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Introduction

Top-predators integrate sources of nutrients and trophic interactions throughout entire food webs and so can be ideal indicators of overall ecosystem functioning (Frederiksen et al. 2006, Fauchald 2009). The utility of such indicators would be enhanced if variation in key environmental features could be linked with subsequent changes in predator feeding ecology. Such information would also increase our understanding of ecosystem responses to natural or human-induced environmental changes. In marine systems, top predators are confronted by highly dynamic and spatially heterogeneous prey resources and so are forced to fine-tune their diet and foraging distribution in response to variations in food resource availability both in space and time. Thus, marine top predators may be particularly appropriate for investigating the consequences of changes to food-web composition and function (Furness and Camphuysen 1997).

Marine productivity is patchily distributed, and marine predators that are also central-place foragers tend to distribute themselves according to oceanographic features (e.g., frontal systems, shelf edges or upwellings) surrounding their breeding sites where their prey aggregates (Hunt et al. 1992, Weimerskirch et al. 2005). Moreover, strong breeding and foraging site fidelity exhibited by these predators indicates that experienced individuals are able to consistently locate adequate food to raise young and the occurrence of predictable food resources or seasonally productive areas are important cues for selecting foraging areas (Weimerskirch 2007, Cama et al. 2012, Louzao et al. 2012). In addition to these oceanographic features, human fisheries or the abundance and distribution of conspecifics are known to affect the diet and foraging behavior of marine predators in a variety of ways, including facilitation (Henkel 2009, Bartumeus et al. 2010, Cama et al. 2012) or competition for resources (Crawford 2007, Weimerskirch et al. 2009, Masello et al. 2010, Bertrand et al. 2012). Understanding how top predators respond to variations in such physical, biological and anthropogenic features is a major conservation challenge in marine environments.

Recent advances in the fields of modeling habitat and species' distributions (Louzao et al. 2011*a*, Louzao et al. 2012), animal tracking (Hobson and Wassenaar 2008, Boersma et al. 2009, Navarro et al. 2009) and the use of endogenous tracers of diet including fatty acids and stable isotopes (Navarro et al. 2009, Ramos et al. 2011, Karnovsky et al. 2012) offer a unique opportunity to investigate the feeding response of central-place foragers to spatiotemporal variations in the availability of marine food resources. In particular, remote sensing data on oceanographic features for the last decades are now available (e.g., Acha et al. 2004, Boersma et al. 2009, Louzao et al. 2012), thus providing valuable information on marine productivity patterns at large spatial and temporal scales. In addition, spatially explicit information derived from monitoring programs of fishing vessels provides a unique opportunity to investigate the interaction between marine predators and fishing activities (Yorio et al. 2010, Bertrand et al. 2012). Furthermore, the recent development and widespread application of bio-logging techniques have revolutionized our knowledge on the movement ecology and spatial distribution of marine predators (Weimerskirch et al. 2009, Masello et al. 2010, Louzao et al. 2012). Based on this previous information, predictive modeling of species' distribution has provided a popular analytical framework for relating geo-located observations of occurrence to environmental variables that contribute to a species distribution (Monk et al. 2012).

We evaluated the role of several environmental factors, including physical, biological and anthropogenic features, likely driving the availability of marine food that in turn constrains the feeding behavior and reproductive performance of a typical central-place forager, the Magellanic penguin (*Spheniscus magellanicus*), breeding at the Chubut province of Argentinean Patagonia. This species has been studied extensively because it constitutes 84% of the breeding seabird community in this region (Yorio et al. 1998), is near threatened (IUCN 2012; IUCN Red List of Threatened Species; Version 2012.2. www.iucnredlist.org; accessed on December 2012), and interacts with humans through fisheries and ecotourism (Yorio et al. 2001, 2010, Villanueva et al. 2012). Magellanic penguins have been the subject of several studies aimed at investi-

gating the link between prey availability and diet (e.g., Forero et al. 2002*a*, 2004, Wilson et al. 2005), spatial distribution of conspecifics (e.g., Wilson et al. 2005, Boersma et al. 2009, Yorio et al. 2010) and reproductive performance (e.g., Tella et al. 2001, Forero et al. 2002*a*). However, most previous studies have not addressed large-scale ecological mechanisms in an integrative way. We combined and reanalyzed previous information in light of recent advances in habitat and species distribution modeling and Bayesian isotopic approaches to diet reconstructions in order to quantify the importance of several factors influencing the foraging ecology and reproductive success of Magellanic penguins. Our approach was based on key predictions associated with the expected effects of environmental and anthropogenic factors on penguin foraging movements and diet and ultimately on reproductive performance. Our proposed approach could be also extended to a large suite of central-place foragers, thus providing important advances in the way we tackle investigations into the feeding ecology of these organisms.

Materials and Methods

General approach

Diet and foraging distribution of Magellanic penguins were expected to be coupled with the abundance and spatial distribution of the richest and most predictable prey patches available within their foraging range. In addition, the abundance and distribution of conspecifics and fishing vessels were expected to influence the diet and foraging distribution of penguins through a density-dependent depletion of optimal (i.e., high-protein) prey types (Tella et al. 2001, Forero et al. 2002*a*). We used remote sensing and geographic information systems (GIS) to derive several explanatory variables likely informing marine productivity patterns (Acha et al. 2004), fishing pressure (Skewgar et al. 2007, Yorio et al. 2010), and intra-specific competition (Tella et al. 2001, Forero et al. 2002*a*). A species distribution model was used to quantitatively infer the role of different environmental features in explaining the at-sea distribution of penguins and general linear models were used to evaluate the effect of food availability on different dietary metrics (inferred from penguin blood $\delta^{13}C$ and $\delta^{15}N$ values). Given that food quality and availability is positively correlated with animal reproductive output, inter-colony dietary differences were finally expected to influence penguin reproductive performance, with penguins feeding on suboptimal prey likely showing poorer reproductive output (Tella et al. 2001, Forero et al. 2002*a*). Accordingly, we finally investigated the relationship between inferred dietary estimates and penguin breeding success.

Magellanic penguins in Chubut province

Magellanic penguins occur at Argentinean Patagonia in 29 colonies on the mainland and islands from about 42° S to almost 55° S (Yorio et al. 1998, Wilson et al. 2005). Our study area extended along ~1000 km of the coast of Chubut province (from 42° S to 46° S latitude; Fig. 1). Colony size is highly variable (Yorio et al. 1998) and adjacent marine areas exhibit considerable heterogeneity in marine productivity at the meso-scale, mostly driven by the spatial distribution of frontal systems (Acha et al. 2004). In particular, marine areas surrounding southern colonies (those located near the Golfo de San Jorge; see Fig. 1) are strongly influenced by the cold and low salinity water of the northward flowing Patagonian current that reaches the southern boundary of the Golfo de San Jorge during austral summers producing a highly productive extension of waters north (Acha et al. 2004, Boersma et al. 2009). North of Golfo de San Jorge, tidal mixing fronts dominate the coastal oceanography, being visible along the coast from Cabo dos Bahías to Península Valdés. Finally, the cooler and more saline waters of the Malvinas Current meet the sub Antarctic shelf waters in the offshore along the continental shelf-break, resulting in a thermohaline front where nutrients from the Malvinas Current reach the euphotic zone and enhance marine productivity (Acha et al. 2004).

Previous dietary investigations of breeding Magellanic penguins at our study area indicated that diet remained stable across years (Wilson et al. 2005). However, inter-colony dietary differences were also reported and these differences followed a latitudinal gradient (Scolaro et al. 1999, Wilson et al. 2005, Boersma et al. 2009) related to the abundance of anchovy (*Engraulis anchoita*; Scolaro et al. 1999, Hansen et al. 2001,

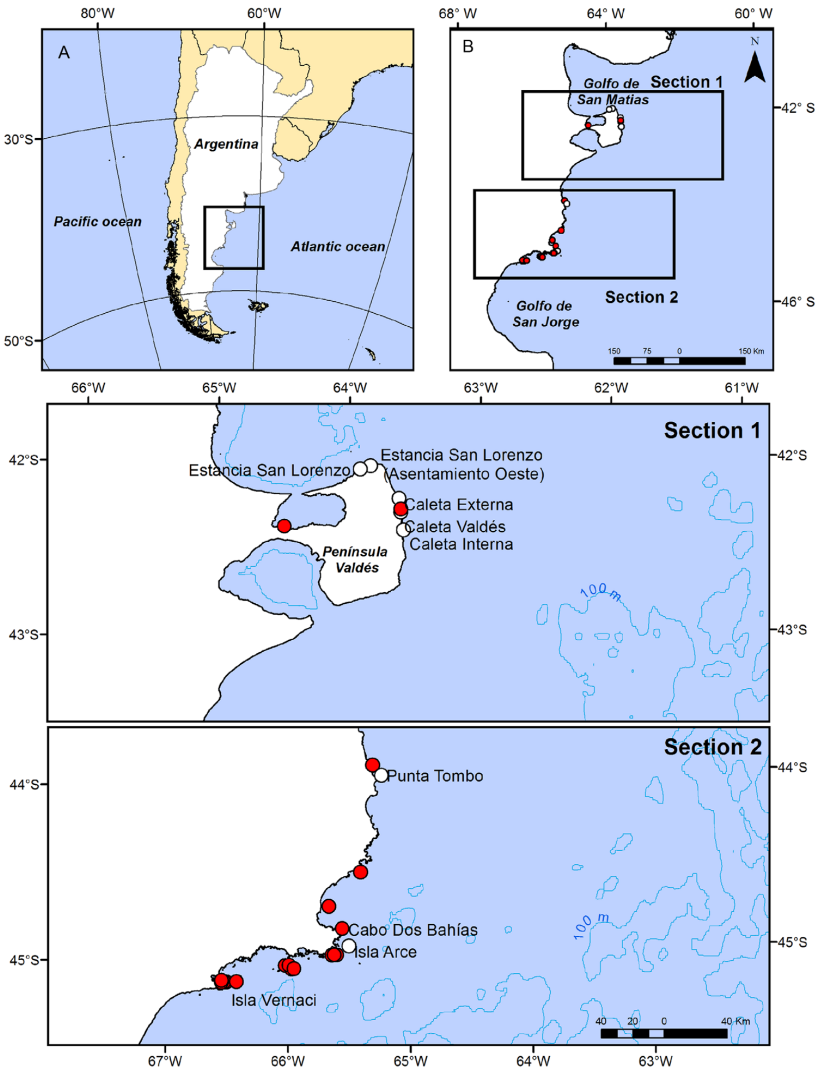

Fig. 1. Geographical location of the study area and breeding colonies of Magellanic penguins (dots). White dots represent penguin colonies that were sampled for stable isotope determinations (white dots for Cabo dos Bahías and Isla Vernaci are not visualized as they are hidden by red dots of neighboring colonies).

Wilson et al. 2005, Boersma et al. 2009). At northern colonies penguins consume anchovy almost exclusively, whereas squid (*Loligo* spp. and *Illex* spp.) or hake (*Merluccius hubbsi*) become much more important in penguin diet at southern colonies (i.e., North Puerto Deseado; Scolaro et al. 1999, Forero et al. 2002*b*, Wilson et al. 2005).

In addition to natural variability in food supplies, inter-colony dietary differences could also be explained by a density-dependent reduction in food resource availability due to a heterogeneous distribution in the abundance of

conspecifics (Tella et al. 2001, Forero et al. 2002*a*) and fishing pressure (see Skewgar et al. 2007, Yorio et al. 2010). Indeed, increasing densities of conspecifics may increase competition for common resources among penguins and deplete more optimal prey types such as anchovy (Tella et al. 2001, Forero et al. 2002*a*). Competition may contribute to observed inter-colony differences in diet, but also result in poorer reproductive performance at those colonies experiencing high levels of competition (Tella et al. 2001, Forero et al. 2002*a*). Similarly, fishing activities may also affect diet, distribution and, ultimately, penguin reproductive performance since anchovy, hake and squid are important target species for commercial fisheries in the area (Argentinean "Ministerio de Agricultura, Ganadería y Pesca," www.minagri.gob.ar; accessed on September 2012), suggesting high competition between fisheries and penguins (see Skewgar et al. 2007, Yorio et al. 2010).

Penguins breeding at the Chubut province typically forage up to 450 km from their colonies (Wilson et al. 2005, Boersma et al. 2009, Yorio et al. 2010). Foraging trips typically show a commuting pattern (sensu Weimerskirch 2007) where individuals depart the colony and meander toward their foraging area where they stay before swimming rapidly and directly back to colony. However, individuals from the northern and central colonies spend most of their time within 150 km from the focal colonies, with a peak in abundance at ca. 120 km (Wilson et al. 2005).

Identifying features driving penguin feeding locations

Information on foraging distribution of penguins breeding at the Chubut province was extracted from Boersma et al. (2009) who, during the 2003–2004 breeding season, placed 37 satellite transmitters (Platform Transmitter Terminals, PTT) on individuals from six colonies spanning most of the latitudinal range of the species in Argentina, and including three colonies enclosed within our study area (i.e., La Ernestina, 42°07′ S, 63°43′ W; Punta Tombo, 44°02′ S, 65°12′ W; and Cabo dos Bahías, 44°51′ S, 65°32′ W). Boersma et al. (2009) used a fixed-kernel analysis on foraging locations (once excluded commuting locations) to show main foraging areas. We considered previously defined areas encompassing 50% isopleths (i.e., 50% kernel contours; Boersma et al. 2009: Fig. 5) as main foraging grounds for Magellanic penguins (see Seaman and Powell 1996). We randomly drew ten different points within each of the 12 defined foraging areas to extract potential foraging locations for individuals breeding at colonies located within the Chubut province (see below for the appropriateness of considered sample size).

Environmental predictors

1. Marine productivity.—Among different oceanographic features commonly used for identifying highly productive hotspots, chlorophyll-*a* concentrations (mg/m^3), sea-surface temperature (°C) and bathymetry (m) are widely considered as the most biologically relevant and readily measured. In particular, chlorophyll-*a* can be considered a reliable surrogate of marine productivity and, consequently, of prey abundance, whereas sea-surface temperature and bathymetry may provide relevant information on physical processes or oceanographic features driving prey distribution (Acha et al. 2004, Yen et al. 2004, Pinaud et al. 2005, Louzao et al. 2011*b*, Louzao et al. 2012). Here, we used Aqua MODIS (4×4 km resolution) derived winter composites (i.e., austral summers) to extract information on chlorophyll-*a* and sea-surface temperature for the area and breeding season (2003–2004) of interest. Bathymetry was downloaded from the ETOPO web site (http://www.ngdc.noaa.gov/mgg/global/global.htm), as a binary product at a spatial resolution of 0.01° (approximately 1 km). For analysis purposes, bathymetry was adjusted to match the spatial resolution for the Aqua MODIS imagery data by averaging depth values for pixels enclosed within a 4×4 km cell grid.

Key marine areas associated with sea fronts were identified by exploring the spatiotemporal component of sea-surface temperature gradients. In particular, we used the longest time series (2002–2012) of Aqua MODIS sea-surface temperature derived winter seasonal composites. For each one of these composites, and following Louzao et al. (2012), we estimated a dimensionless metric Proportional Change (PC) expressing the magnitude of change in sea-surface temperature, within a moving window of a 3×3 cells and following the equation: PC = [(maximum

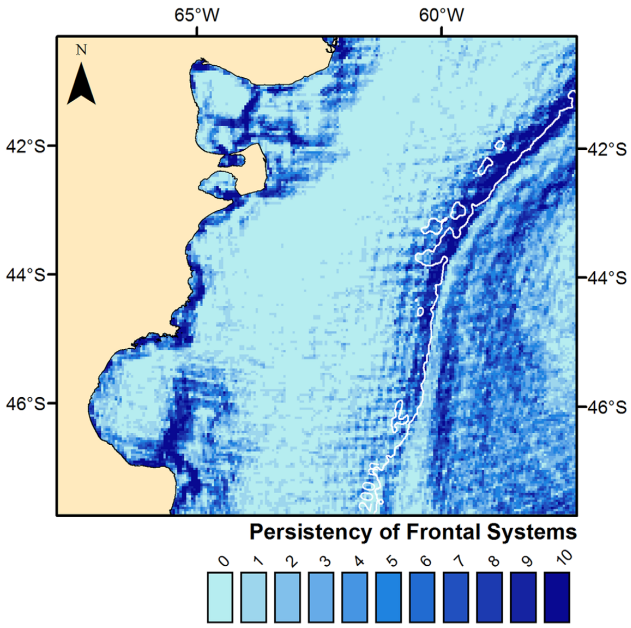

Fig. 2. Spatiotemporal heterogeneity of key marine areas associated with sea fronts at the marine area surrounding the Chubut province and based on sea-surface temperature gradients. Colors represent the persistency of such key marine areas according to the number of years in which each pixel was defined as frontal system (see *Materials and Methods* for information on criteria used to define each pixel as frontal system). Values range from 0 (minimum persistence) to 10 (maximum persistence), according to the time period for which imagery data on sea surface temperature is available, i.e., 10 years (2002–2003 to 2011–2012). White line represents the 200 m isobaths.

value − minimum value) × 100]/(maximum value). Frontal systems were identified as areas with PC values within the 75th percentile, whereas the persistence of these areas was quantified by counting in how many years each cell was identified as a frontal system (values ranged from 0 to 10 corresponding to the sea-surface temperature time series; Fig. 2).

2. *Penguin abundance.*—Following Grecian et al. (2012), we combined available information on colony sizes and locations (Yorio et al. 1998), and frequencies of foraging distances (Wilson et al. 2005), to generate a predicted distribution of penguins in the marine area around the Chubut province. In particular, the penguin abundance distribution (Fig. 3) was generated by uniformly distributing the total number of individuals reported at each colony within their foraging range (i.e., 450 km from the focal colony; Wilson et al. 2005, Yorio et al. 2010), based on calculations of the Euclidean distances from each colony, and on the average frequency of distances provided by Wilson et al. (2005) for the northern and central colonies (Fig. 3).

3. *Fishing pressure.*—The spatial distribution of fishing vessels operating within our study area for the 2001–2005 period were grouped as cold store and freezer vessels differing in their main target species and fishing areas based on the On-board Observer Program of Chubut Province (Secretaría de Pesca de la Provincia de Chubut; Fig. 4). In addition, long-term (1999–2010) fish landing data obtained from the Argentinean "Ministerio de Agricultura, Ganadería y Pesca" (www.minagri.gob.ar; accessed in November 2012) was used to estimate the relative contribution of main fishing fleets to total landing of anchovies. Extraction of environmental variables

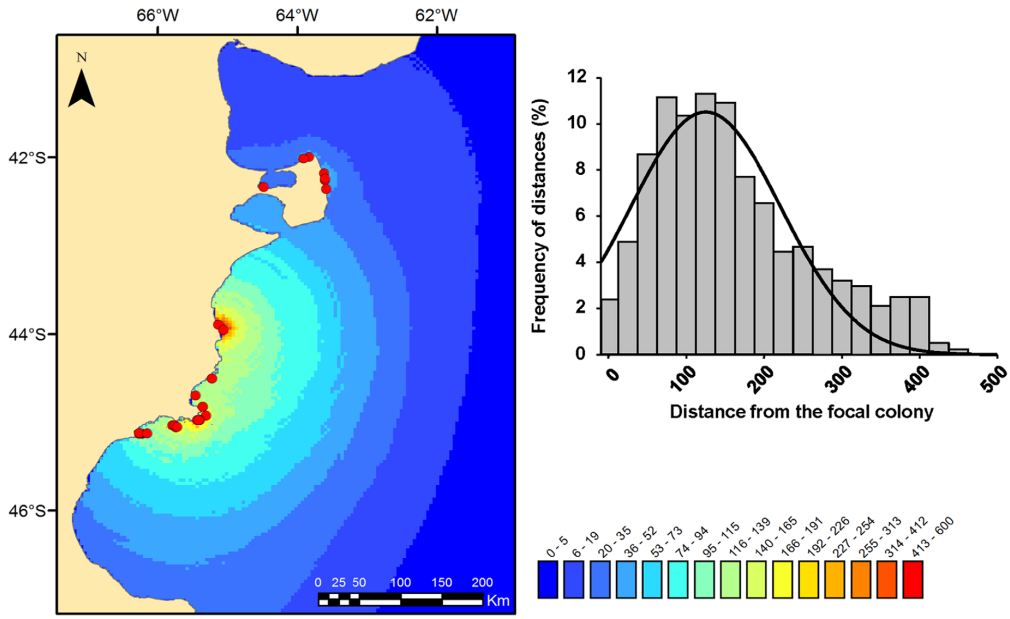

Fig. 3. Spatial distribution of abundances of Magellanic penguins within the marine area surrounding the Chubut province (left side). Individuals from each colony (information on colony sizes were obtained from Yorio et al. 1998) were uniformly distributed within their home range (i.e., 450 km; Wilson et al. 2005), based on calculations of the Euclidean distances from the focal colonies, and on the average frequency of distances provided by Wilson et al. (2005) (right side).

and spatial analyses were performed with ArcGis 10 (Environmental Systems Research Institute [ESRI], Redlands, California, USA).

Species distribution modeling

Penguin distribution (Fig. 5) was performed using Maximum Entropy (MaxEnt) modeling (version 3.3.3; http://www.cs.princeton.edu/~schapire/maxent/) based on presence data obtained from Boersma et al. (2009), and the above-mentioned explanatory variables. Among different modeling methods, MaxEnt has been proposed as the strongest because it remains fairly stable in both prediction accuracy and the total area predicted present across all sample size categories (Hernandez et al. 2006, Pearson et al. 2007). Thus, we considered that ten randomly chosen points within previously defined foraging areas (Boersma et al. 2009) would provide us with an appropriate representation of the spatial distribution of penguins while foraging. Regarding explanatory variables, we considered chlorophyll-*a* and sea-surface temperature for the 2003–2004 winter season, along with bathymetry as integrative measures of marine productivity and physical features driving prey distribution. The persistence of frontal systems was considered as a proxy for the predictability of prey patches. Penguin abundance distribution was also considered to account for the degree of intra-specific competition for food. Finally, distribution of cold store and freezer vessels were used to account for potential interaction between penguins and human fisheries.

MaxEnt procedure was used to estimate relationships between estimated probability of presence of penguins and the above-mentioned explanatory variables. Although MaxEnt can fit complex relationships between estimated probabilities of presence and different environmental variables, we exclusively fitted linear and quadratic relationships due to the difficulty of

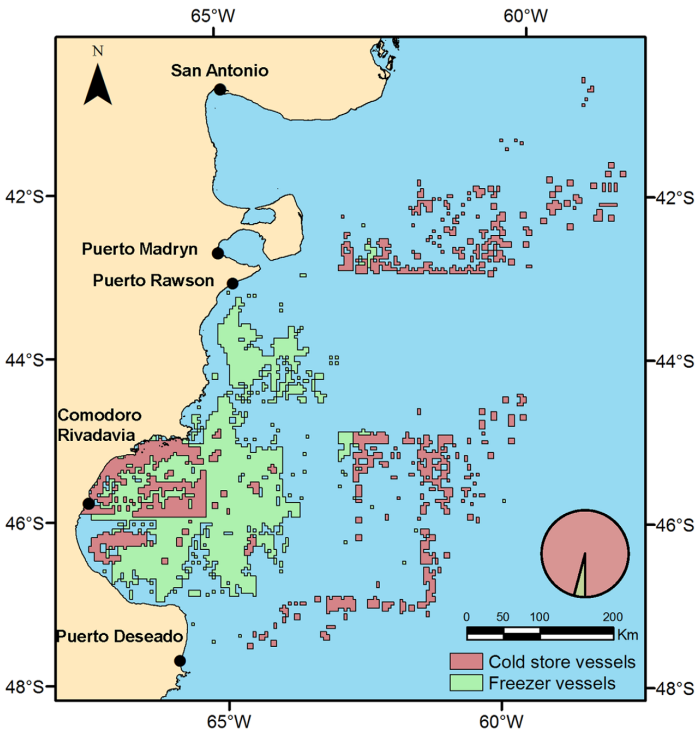

Fig. 4. Spatial distribution of main fishing vessels (grouped in cold store and freezer vessels) for the 2001–2005 period obtained from the On-board Observed Program of Chubut Province (Secretaría de Pesca de la Provincia de Chubut). Black dots represent main fishing ports at the area. The relative contribution of main fishing fleets (i.e., cold store and freezer vessels) to total landing of anchovies are represented by a pie chart.

interpreting other more complex associations. For internal validation, obtained models were tested using 30% of potential foraging locations randomly selected. One hundred replicates of the model were run to obtain an average prediction and a coefficient of variation for predictions. To assess the predictive performance of our model, we evaluated each MaxEnt prediction using the Area Under the Receiver Operating Characteristic (ROC) Curve (hereafter AUC; ranging from 1, perfect predictive performance, to 0, perfect reversed predictive performance, and with 0.5 values denoting null predictive ability; Fielding and Bell 1997). AUC values were also used to evaluate the predictive performance of each explanatory variable when used in isolation. Finally, we tested for spatial autocorrelation in model residuals by calculating the Moran's *I* values (ranging from −1, perfect dispersion, to +1, perfect autocorrelation, with zero values denoting random spatial distribution) for 20 equal-distance classes, and using the Spatial Analysis in Macroecology (SAM, v.4.0) software (Rangel et al. 2010). We used this test because significant spatial patterning in the residuals might reflect missing environmental effects that are geographically patchy or reflect the effect of disturbance-related processes that are independent of environment (Barry and Elith 2006).

Features affecting penguin feeding habits

Dietary metrics.—Dietary information was based on stable isotope measurements extracted from Forero et al. (2004). These authors provided blood $\delta^{13}C$ and $\delta^{15}N$ values for penguins ($n = 246$ and 153 for adults and fledglings, respectively)

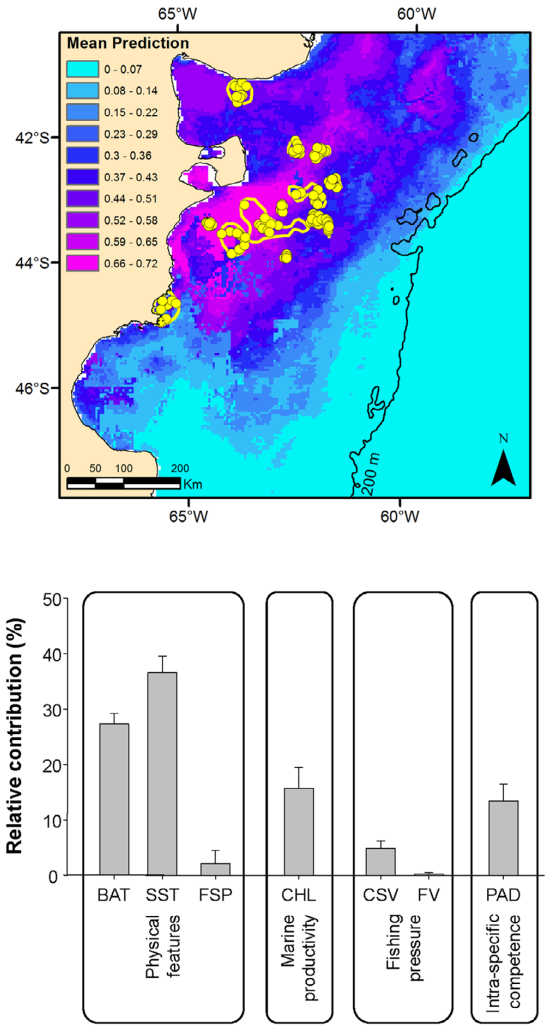

Fig. 5. Species distribution modeling output for Magellanic penguins (top). Potential foraging locations were extracted by randomly drawing 10 different points (yellow dots) within main foraging areas (50% contours from a fixed-kernel analysis, yellow lines) defined by Boersma et al. 2009. Explanatory variables considered and their relative contributions to the MaxEnt model (mean ± SD) have been also represented (bottom). Explanatory variables have been grouped according to their ecological significance. In particular, bathymetry (BAT), sea surface temperature (SST) and the persistence of frontal systems (FSP) were included as physical features likely driving prey distribution and their persistence/predictability. Chlorophyll-*a* concentrations for the 2003–2004 (CHL) winter period were included as a surrogate of marine productivity. Spatial distributions of cold store (CSV) and freezer vessels (FV) for the 2001–2005 period (On-board Observed Program of Chubut Province, Secretaría de Pesca de la Provincia de Chubut) were included as a proxy to fishing pressure. Estimated distribution of penguin abundances (PAD) was also incorporated to account for the degree of intra-specific competence for food.

Table 1. Isotopic composition ($\delta^{13}C$ and $\delta^{15}N$, mean ± SD) of Magellanic penguins breeding at different colonies at the Chubut province (Argentinean Patagonia). Based on isotopic variability ascribed to different colonies, and the recent isotopic Bayesian framework developed for R (Parnell et al. 2008), we generated multivariate ellipse-based metrics (SEA.B; median, and low and high 95% Bayesian credibility interval [95% BCI]) which were taken as a reliable proxy to trophic niche width. Localities are listed from north to south.

Locality	$\delta^{13}C$ (‰) (mean ± SD)	$\delta^{15}N$ (‰) (mean ± SD)	SEA.B (‰^{2})	
			95% BCI	Median
Estancia San Lorenzo	−17.16 ± 0.48	18.84 ± 0.26	0.38–0.58	0.47
Estancia San Lorenzo†	−17.22 ± 0.33	19.08 ± 0.24	0.28–0.48	0.37
Caleta Externa	−16.58 ± 0.17	18.65 ± 0.32	0.43–1.65	0.91
Caleta Valdés	−16.49 ± 0.37	18.85 ± 0.51	0.55–1.21	0.84
Caleta Interna	−16.62 ± 0.36	18.97 ± 0.46	0.43–0.76	0.59
Punta Tombo	−16.48 ± 0.48	18.51 ± 0.41	0.52–0.84	0.67
Cabo dos Bahías	−16.36 ± 0.61	18.76 ± 0.6	0.88–1.34	1.09
Isla Arce	−17.01 ± 0.44	18.43 ± 0.45	0.52–1.11	0.79
Islas Vernaci	−16.13 ± 0.36	19.16 ± 0.23	0.45–1.58	0.9

† Asentamiento Oeste.

sampled during three consecutive breeding seasons (from 1999 to 2001) and at nine different breeding colonies distributed across the Chubut province (Table 1 and Fig. 1). Bird diet was reconstructed using dual-isotope ($\delta^{13}C$ and $\delta^{15}N$) Bayesian mixing models (SIAR; Parnell et al. 2008). Dietary endpoints included in these models were isotopically clustered (mean ± SD) by grouping main potential prey species defined by previous dietary reports at this area (i.e., anchovy, hake and squid), and adjusted to account for diet-blood isotopic discrimination factors (ΔX) linking diet with consumers' tissues ($\Delta^{13}C$: 1.1‰; $\Delta^{15}N$: 2.9‰; see Caut et al. 2009). The robustness of derived inter-colony dietary estimates was tested through sensitivity analysis in which different diet to blood discrimination factors ($\Delta^{13}C$: ranging from 0.7‰ to 1.5‰; $\Delta^{15}N$: ranging from 2.5‰ to 3.3‰) and error terms (SD ranging from 0.1‰ to 0.6‰) were incorporated in our multisource isotope mixing models.

We also used isotopic variability ascribed to different colonies, and the recent isotopic Bayesian framework, to generate multivariate ellipse-based metrics (area of the multivariate ellipses, hereafter referred as SEA.B, expressed as ‰^{2}; Table 1) following methods from Jackson et al. (2011) and the R package SIAR (Parnell et al. 2008). These metrics were taken as a reliable proxy to trophic niche width for each colony (Bearhop et al. 2004, Jackson et al. 2011).

Linking dietary metrics with environmental features.—General linear models (GLM) with normal error and identity link functions of PROC GENMOD in SAS (SAS Institute, Cary, North Carolina, USA) were used to explore the effect of derived explanatory variables on median percentages of anchovy and median values for SEA.B for each sampled colony. Marine productivity and fishing pressure associated with a given colony was estimated by adding chlorophyll-*a* concentrations and presences of cold store and freezer vessels (i.e., 4 × 4 km pixels in which fishing activity was reported) respectively for the marine area enclosed within penguin foraging range (450 km; Wilson et al. 2005). As estimates of intra-specific competition, we considered the total number of penguins within different buffer areas from the focal colonies. In particular, we extracted, from the predicted distribution of penguins, the total number of individuals within buffers of 150, 300 and 450 km from the focal colonies, to account for areas in which penguins spend ~50%, 90% and 100% of their time (Wilson et al. 2005). Each explanatory variable and their potential interactions were tested following a forward-step procedure to finally obtain a set of models that only retained variables with significant (or nearly significant) effects. Model parsimony was evaluated based on the Akaike information criterion corrected for small sample sizes (AIC_C; Johnson and Omland 2004) and the corresponding AIC_C weights. All tests were two tailed. QQplot and a scatterplot of the residuals plotted against fitted values indicated no obvious deviations from the assumptions of normally distributed and homogeneous residuals.

Diet and penguin reproductive performance

Reproductive performance was based on average brood size and fledgling body condition. Brood size was measured as part of a previous study (1999–2000) at six of the sampled colonies (Forero et al. 2002*a*) and was based on the average number of siblings at fledging time in nests located within a transect (2 m wide) perpendicular from each focal nest to the sea (n = 3220, range = 204–1138 nests per colony). Empty nests were excluded from analysis because of the impossibility of distinguishing unoccupied nests from those resulting from breeding failure. Chicks were measured (flipper length ±1 mm) and weighed (±10 g) during the 1999–2000 and 2000–2001 breeding seasons at seven different colonies where blood samples were taken (Forero et al. 2002*a*, *b*). Here, we used these morphometrics to estimate fledgling body condition by averaging residuals from the linear regression between flipper length and body mass ($F_{1,213} = 84.98$, $p < 0.001$). Season was included in the model as a fixed factor to account for observed differences in fledglings' body conditions among breeding events ($F_{2,213} = 18.27$, $p < 0.001$).

The effect of diet on penguin reproductive performance was explored through Pearson correlation tests between estimated relative median contribution of anchovy to the diet of penguins from different colonies and the corresponding mean values of brood size and fledgling body condition. For this latter relationship, we exclusively considered fledglings' isotopic data when applying Bayesian mixing models for dietary reconstructions. Our predictions of the influence of anchovy to reproductive success were directional and so one-tailed tests were used. Statistical analyses were done using SAS (SAS Institute, Cary, North Carolina, USA) and SPSS 18.0 software (SPSS, Chicago, Illinois, USA).

Results

Spatiotemporal heterogeneity in marine productivity, fishing pressure and penguin abundance

Long-term information on sea-surface temperature was used to explore the spatiotemporal distribution of key marine areas surrounding the Chubut province (Fig. 2). This approach revealed several highly productive marine areas that occurred consistently along the coast and following the continental shelf-break (200 m isobath). The at-sea distribution of main fishing vessels in this area suggested that fishing pressure was particularly high within the Golfo de San Jorge. However, fishing activity was also detected in the nearshore between Cabo dos Bahías and Península Valdés and following the continental shelf-break. Freezer vessels aggregated in the nearshore, whereas cold stores were clearly associated to the continental shelf-break where they were responsible of more than 90% of anchovy captures (Fig. 3).

Penguin abundance, and consequently the assumed degree of intra-specific competition for food, was higher in areas close to Punta Tombo where the largest colony occurred, but also in the northern part of Golfo de San Jorge and Peninsula Valdés, where a number of smaller colonies aggregate in relatively small coastal areas. In contrast, northern and southern inshore areas (i.e., marine areas within the Golfo de San Jorge and Golfo de San Matías), and offshore marine areas (nearby the continental shelf-break) had the lowest penguin densities.

Physical, biological and anthropogenic features driving penguin feeding ecology

Penguin distribution.—The distribution model for penguins performed reasonably (mean AUC ± SD = 0.84 ± 0.02, for the model and the internal validation), with model residuals showing a moderate but non-significant spatial autocorrelation at any distance class (mean Moran's I ± SD = 0.35 ± 0.23; $p > 0.0025$ once adjusted through Bonferroni procedure). Penguins were more likely to forage in the nearshore between Cabo dos Bahías and Península Valdés thus overlapping with key marine areas associated with tidal mixing fronts. In contrast, key marine areas located at the southern boundary of the Golfo de San Jorge and over the continental shelf-break were not considered as suitable foraging areas. Penguin distribution was best explained by sea-surface temperature and bathymetry, with a moderate contribution of chlorophyll-*a* concentration and penguin abundance (Fig. 5). However, sea-surface temperature, the distribution of penguin abundance and bathymetry were the best predictive variables when considered indi-

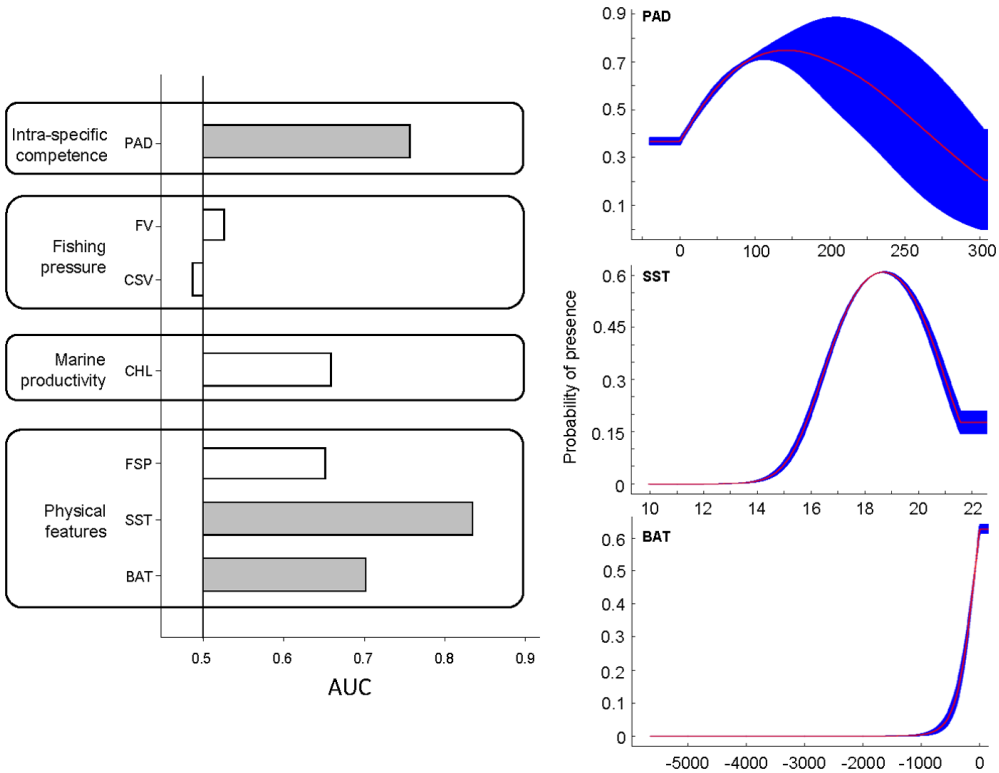

Fig. 6. Predictive performance of single explanatory variables (see Fig. 5 for acronyms) as indicated by the Area Under the ROC (Receiver Operating Characteristic) Curve (AUC, right side). AUC values range from 1, perfect predictive performance, to 0, perfect reversed predictive performance, and 0.5 values denote null predictive ability). Best predictive variables (AUC > 0.7) are shown in grey. Response curves illustrating the relationship between best predictive variables and the probability of presences for penguins are also shown (left side).

vidually (AUC = 0.83 ± 0.02, 0.75 ± 0.02 and 0.7 ± 0.03, respectively, see Fig. 6). Based on obtained response curves for best predictors (Fig. 6), penguins were more likely to forage over the continental shelf (>200 m depth) and in areas of relatively warm water (sea surface temperature values ranging from 16° to 21°C) and with moderate penguin abundances (abundances ranging from 50 to 250 individuals).

Penguin diet.—Overall, isotopic analysis of penguin diet indicated it was mainly composed of anchovy, followed by hake and squid. However, diet composition differed slightly among colonies (see Table 2), with inter-colony dietary differences quite consistent regardless of variations in considered discrimination factors (Fig. 7 and 8). In particular, Northern colonies were characterized by a greater contribution of anchovy to penguin diet (ranging from 46% in Caleta Externa to 73% in Estancia San Lorenzo-Asentamiento W). In contrast, hake (ranging from 19% to 48%) and squid (ranging from 10% to 33%) became more prevalent at central colonies (North of Golfo de San Jorge; Fig. 1, Section 2). Indeed, inferred dietary estimates suggested that hake was the most consumed prey type for penguins breeding at Cabo dos Bahías, with an average relative contribution of 48%, followed by anchovy (27%) and squid (25%). Derived dietary estimates from our multisource isotope mixing

Table 2. Relative contribution (%, median, and low and high 95% Bayesian credibility interval [95% BCI]) of main food resources (anchovy, hake and squid) to penguin diet. Dietary reconstructions were performed through a double isotope ($\delta^{13}C$ and $\delta^{15}N$) Bayesian mixing model (Stable Isotope Analysis for R [SIAR]; Parnell et al. 2008). Localities are listed from north to south.

	Anchovy (%)		Hake (%)		Squid (%)	
Locality	95% BCI	Median	95% BCI	Median	95% BCI	Median
Estancia San Lorenzo	55.13–75.66	65.4	3.37–18.5	11.0	19.92–27.46	23.6
Estancia San Lorenzo†	60.85–83.53	72.5	0.75–17.21	9.1	13.91–23.04	18.4
Caleta Externa	22.49–74.67	46.9	7.85–46.84	28.4	12.47–36.79	24.7
Caleta Valdés	29.2–70.08	48.7	16.44–46.04	32.1	10.89–27.36	19.3
Caleta Interna	44.02–74	59.0	13.58–35.31	24.5	11.03–22.02	16.5
Punta Tombo	24.45–49.03	36.5	23.78–43.68	34.0	24.84–34.11	29.4
Cabo dos Bahías	14.86–39.22	26.9	38.01–56.78	47.7	20.72–30.34	25.4
Isla Arce	29.38–68.11	48.0	3.75–32.78	18.6	26.26–40.44	33.4
Islas Vernaci	27.65–80.07	52.9	15.58–56.24	336.9	0.08–20.57	10.2

† Asentamiento Oeste.

model were most useful in a comparative sense (since we lacked diet-tissue discrimination factors specific for Magellanic penguins) and only considered as an approximation of the actual diet.

When investigating the effect of environmental variables driving food resource availability on inferred contribution of anchovies to the diet of penguins, the best supported model (see Table 3) included a negative effect of fishing pressure by cold store vessels (explaining up to 67.9% of original deviance). However, penguin diet was also affected by the number of conspecifics feeding near the colony, as indicated by penguin abundance within 150 (explaining up to 61.4% of original deviance) and 300 km (explaining up to 53.5% of original deviance) buffer areas, with decreasing relative contributions of anchovies to penguins' diet as the abundance of conspecifics increased. Regarding isotopic niches (SEA.B), the null model (including intercept) was best supported (Table 4). However, the model including penguin abundance within a 450 km buffer also showed good support (AIC_C increments, $\Delta AIC_C = 0.8$; explaining up to 35.9% of original deviance) with wider isotopic niches as the number of conspecifics within penguins' foraging ranges increased.

Dietary constraints on penguin reproductive performance

A positive relationship was found between the relative contribution of anchovy to fledgling diet and their body condition (Pearson's $r = 0.685$, $p = 0.045$, $n = 7$; Fig. 9A). Similarly, we found a positive, but non-significant, relationship between estimated relative contribution of anchovy to penguins' diet and brood size (Pearson's $r = 0.652$, $p = 0.8$, $n = 6$; Fig. 9B). Just one colony, Caleta Interna, strayed from this general trend, showing smaller brood sizes relative to estimated dietary consumption of anchovy and fledglings' body condition (Fig. 9C).

Discussion

Seabirds forage in diverse and stochastic environments that are influenced strongly by natural and anthropogenic processes (Zimmer et al. 2011). The complexity of these systems has seriously limited our ability to understand how these central-place foragers respond to such processes and especially how they adapt their foraging strategies to cope with their environments spatially and temporally. However, through the combined use of several analytical tools, it is now possible to model responses of predators to variation in food availability at various scales. Here, we combined remote sensing, animal tracking, species distribution modeling and isotopic dietary reconstructions to provide deeper insights into the mechanisms through which these top predators adapt to variation in critical resources. As expected, penguin foraging distributions were tightly coupled to the spatial distribution of their staple prey species (driven, in turn, by oceanographic features) but other biological and anthropogenic features, such as the abundance of conspecifics or the presence of fishing vessels, also played an

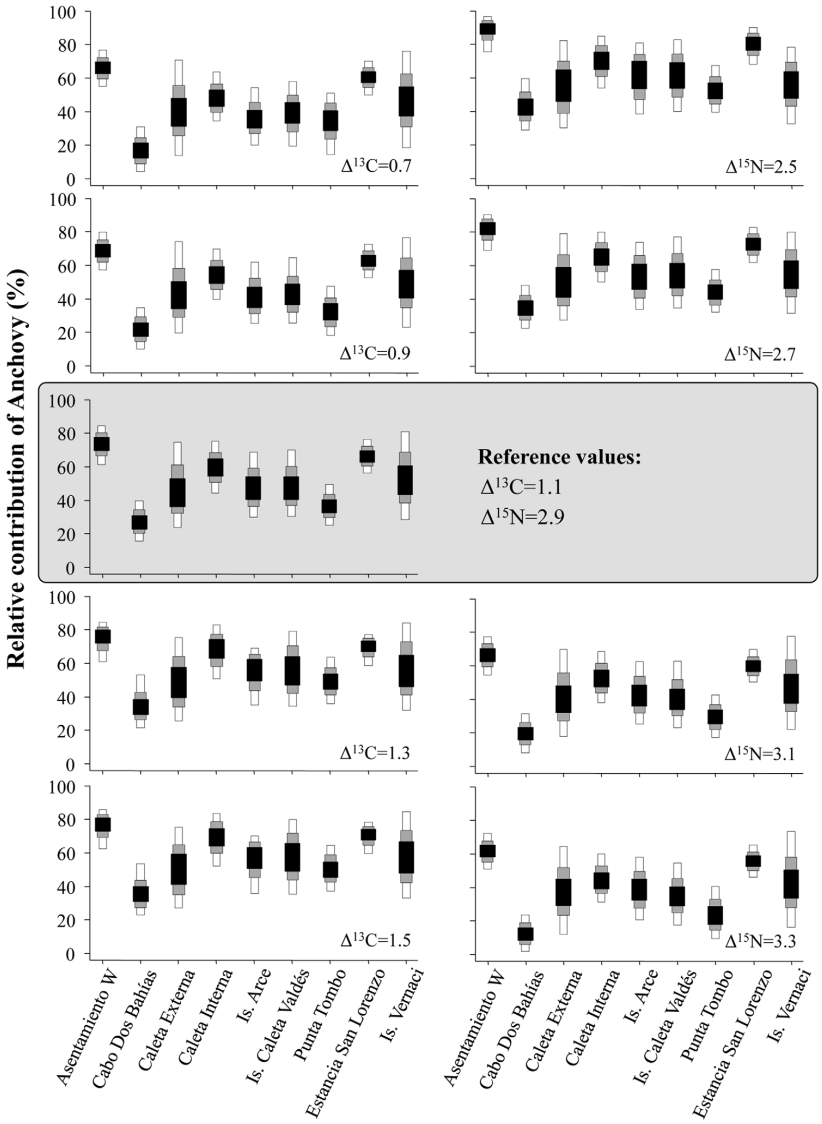

Fig. 7. Sensitivity analysis for estimated contributions of anchovy to penguin diet. Isotopic discrimination factor for $\delta^{13}C$ ($\Delta^{13}C$) ranged from 0.7‰ to 1.5‰, whereas that one for $\delta^{15}N$ ($\Delta^{15}N$) ranged from 2.5‰ to 3.3‰ (while the other factor was kept constant).

important role in explaining the foraging and feeding preferences of Magellanic penguins. Given the observed relationship between penguin diet and reproductive output, such physical, biological and anthropogenic features should be considered as important drivers of Magellanic penguin breeding parameters and population dynamics.

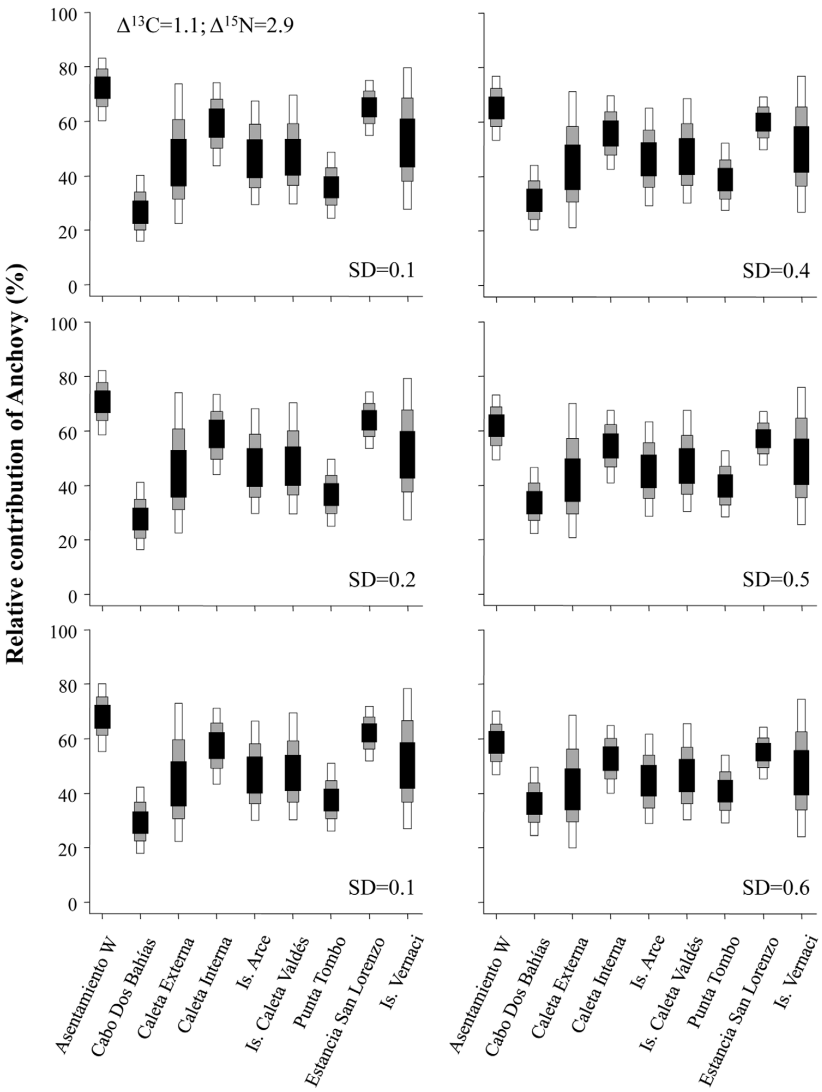

Fig. 8. Sensitivity analysis for estimated contributions of anchovy to penguin diet. The error term for considered discrimination factors ($\Delta^{13}C = 1.1‰$ and $\Delta^{15}N = 2.9‰$) ranged from 0.1 to 0.6.

Features driving the at-sea distribution of penguins

As expected, Magellanic penguins concentrated their foraging effort in highly productive marine areas, commonly characterized by high chlorophyll-*a* concentrations and sea-surface temperature and bathymetry gradients (Acha et al. 2004), where prey species also tend to aggregate (see Boersma et al. 2009). However, their foraging range was restricted to areas surrounding breeding colonies and this constraint resulted in many prey patches being out

Table 3. Set of models that retained variables with significant (or nearly significant) effects to fit the data corresponding to estimated relative contributions of anchovy (%) to the diet of Magellanic penguins from different colonies. Associated measures of information (corrected AIC [AIC_C]; AIC_C increments [ΔAIC_C]; and AIC_C weights [AIC_C Wgt]) are shown to evaluate their parsimony. Best supported models (i.e., the most parsimonious) appear in boldface.

Models	Residual deviance	AIC_C	ΔAIC_C	AIC_C Wgt	df	χ^2	*p*
Null model	0.156	−4.966	5.423	0.033	8		
Marine productivity							
Chlorophyll-a	0.073	−7.025	3.364	0.094	7	6.86	0.0088
Fishing pressure							
Cold store vessels	**0.05**	**−10.389**	**0**	**0.503**	**7**	**10.22**	**0.0014**
Freezer vessels	0.076	−6.642	3.747	0.077	7	6.48	0.0109
Intra-specific competence							
Penguin abundance at 150 km	0.06	−7.869	2.52	0.143	7	7.7	0.0055
Penguin abundance at 300 km	0.072	−7.057	3.332	0.095	7	6.89	0.0087
Penguin abundance at 450 km	0.082	−5.933	4.457	0.054	7	5.77	0.0163

of reach (see Hunt et al. 1992). Penguins in our study area tended to forage on tidal mixing fronts occurring consistently near the shore and between Cabo dos Bahías and Península Valdés (see also Boersma et al. 2009), whereas other key marine areas, such as those associated with the continental shelf-break front, were likely out of their foraging range (see Figs. 2 and 5).

Despite the spatial linkage between productivity and foraging distribution of penguins, our results suggested that the at-sea distribution of penguins was primarily a reflection of physical oceanographic features driving the distribution of their staple prey species. In particular, sea-surface temperature and bathymetry were the most important explanatory variables within our species' distribution model. Indeed, individuals preferentially selected foraging habitats within a 16–21°C sea-surface temperature range over shallower waters. These attributes also described the distribution of penguin prey such as anchovies, hake and squid (Acha et al. 2004, Hansen et al. 2001).

Penguins distributed themselves in areas with moderate abundance of conspecifics. As in many other colonial seabirds, intra-specific competition for food resources can be strong for Magellanic penguins due to a lack of dietary segregation (Masello et al. 2010). Ecological theory predicts that animals with similar feeding strategies should not coexist without segregating either in space, time or diet. Indeed, intra-specific competition for food can drive the neighboring populations of the same species to spatial segregation of foraging areas (e.g., Boersma et al. 2009, Masello et al. 2010), but also can lead to segregation of foraging areas by sex, foraging periods, dive depth, or prey choice (Weimer-

Table 4. Set of models that retained variables with significant (or nearly significant) effects to fit the data corresponding to the multivariate ellipse-based metrics (SEA.B), which were taken as a reliable proxy to trophic niche width. Associated measures of information (corrected AIC [AIC_C]; AIC_C increments [ΔAIC_C]; and AIC_C weights [AIC_C Wgt]) are shown to evaluate their parsimony. Best supported models (i.e., the most parsimonious) appear in boldface.

Models	Residual deviance	AIC_C	ΔAIC_C	AIC_C Wgt	df	χ^2	*p*
Null model	**0.427**	**4.099**	**0**	**0.261**	**8**		
Marine productivity							
Chlorophyll-a	0.292	5.477	1.378	0.131	7	3.42	0.0643
Fishing pressure							
Cold store vessels	0.348	7.056	2.957	0.06	7	1.89	0.1746
Freezer vessels	0.287	5.324	1.225	0.142	7	3.57	0.0587
Intra-specific competence							
Penguin abundance at 150 km	0.301	5.759	1.66	0.114	7	3.14	0.0764
Penguin abundance at 300 km	0.299	5.7	1.601	0.117	7	3.2	0.0737
Penguin abundance at 450 km	**0.273**	**4.899**	**0.8**	**0.175**	**7**	**4**	**0.0455**

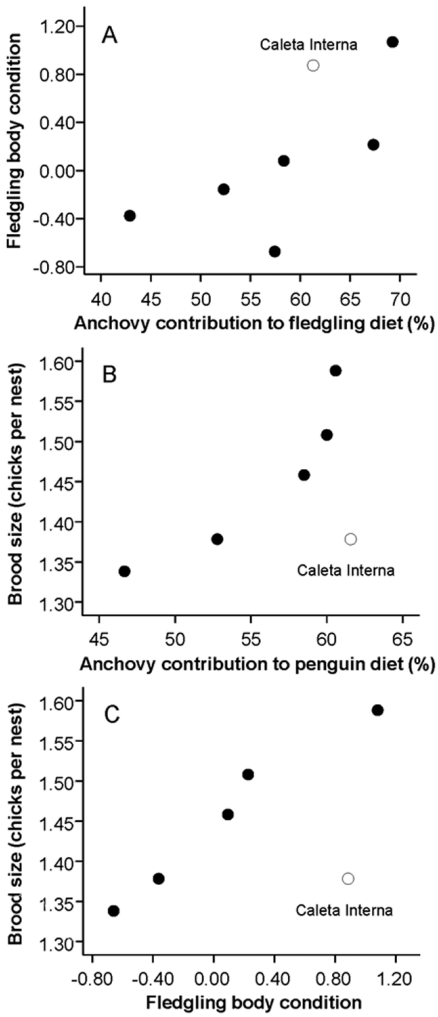

Fig. 9. Observed relationship between (A) estimated relative contribution of anchovies to the diet of fledglings (in %) and their body condition (residuals of the relationship between body size and weight); (B) estimated relative contribution of anchovies to the diet of penguins and their brood size (average number of chicks per nest); and (C) estimated body condition and brood size.

skirch et al. 2009, Navarro et al. 2010). Individual penguins may reduce the degree of intra-specific competition by avoiding areas with higher densities of conspecifics. However, deleterious effects of interference competition for food must be traded against the benefits of feeding in flocks (Henkel 2009). Thus, penguins may preferably concentrate at areas with moderate penguin abundances, where the benefits of flock-foraging likely outweighed any cost of competition.

Features driving penguin dietary composition and trophic niche breadth

In agreement with previous dietary reports for Magellanic penguins breeding in Argentinean Patagonia (e.g., Scolaro et al. 1999, Forero et al. 2002*b*, Wilson et al. 2005, Boersma et al. 2009), our isotope approach reveled a latitudinal dietary segregation which could reflect the abundance and distribution of anchovies, which are widespread North of 43° S latitude (Hansen, Martos and Madirolas 2001, Wilson et al. 2005, Boersma et al. 2009). However, interactions with human fisheries may also affect penguin diet. Localized depletions of prey by fisheries, even if occurring at reasonably large scales, may affect seabird feeding strategies due to local prey depletions (Bertrand et al. 2012). Our models suggested that the occurrence of cold store vessels, which are responsible for the vast majority of anchovy captures, within penguins' foraging ranges negatively affected the consumption of anchovies by penguins. Finally, inter-colony dietary differences could also be explained by food depletion mechanisms mediated through intra-specific competition (Tella et al. 2001, Forero et al. 2002*a*). Consistent with this latter hypothesis, our models suggested that the abundance of conspecifics feeding near the focal colonies (up to 300 km, where penguins spend up to 90% of their time; Wilson et al. 2005) was negatively correlated with the relative contribution of anchovies to individual diet. In addition to this effect, higher densities of conspecifics within penguins' foraging ranges also resulted in wider trophic niches (i.e., SEA.B median values), suggesting certain intra-specific segregation in prey choice likely directed to reduce the degree of competition among conspecifics. However, it is necessary to be aware of the several assumptions and limitations associated with the use of isotopic variability as a proxy to dietary niche width. Isotopic variability not only depends on inter-individual trophic segregation, but also on

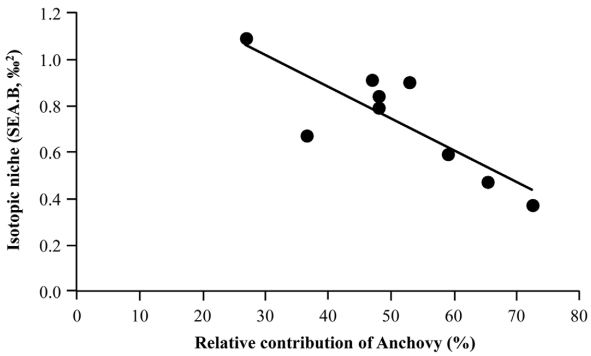

Fig. 10. Observed relationship between the relative contribution on anchovy to penguin diet and derived metrics for isotopic niche breadth (SEA.B, ‰^{2}).

the amount of isotopic variation among different food sources (Newsome et al. 2007). This may hamper the use of isotopic approaches for comparisons of dietary niche width between species or populations exploiting isotopically different food resources (Newsome et al. 2007). Alternatively, total isotopic variability can be composed of among- and within-individual components (Carrasco et al. 2010). Here, we compared isotopic variability among neighboring colonies of the same species which are expected to share foraging areas and trophic resources, thus minimizing potential biases in observed inter-colony differences in estimated isotopic niche breadths. Further, and provided there are only three main prey species for Magellanic penguins (anchovy, hake and squid), the observed negative relationship between the contribution of anchovy to penguin diet and derived SEA.B values supported the use of this metric as a reliable proxy to penguins' trophic niche breadth since the less diverse diets resulted in the narrower isotopic niches (Fig. 10).

Effect of diet on reproductive performance

Previous studies have suggested that depletion of high-protein prey may result in poorer reproductive performance of Magellanic penguins (Tella et al. 2001, Forero et al. 2002*a*). Our isotopic models support this idea since those colonies relying mainly on anchovies showed higher brood sizes and raised fledglings with better body condition (see Fig. 9). Just one colony, Caleta Interna, strayed from this general trend. That colony showed smaller mean brood size than predicted based on estimated consumption of anchovy and fledgling body condition. Possibly the high levels of human disturbances and more frequent predation episodes noted at this colony could be factors causing higher breeding failure (Yorio et al. 2001). In general, marine productivity patterns, along with spatiotemporal variations in fishing pressure and intra-specific competition constrain the availability and accessibility of optimal prey types for Magellanic penguins during the breeding period, modulating breeding parameters and population dynamics.

Concluding remarks and future considerations

Previous approaches to investigating responses of marine predators to spatiotemporal variations in marine productivity patterns have focused on feeding responses of key top predators (e.g., Pinaud et al. 2005, Weimerskirch 2007, Boersma et al. 2009, Louzao et al. 2012). However, for penguins, few have considered other effects on foraging such as social or competitive interactions among conspecifics (Forero et al. 2002*a*) or with fishing activities (Bartumeus et al. 2010, Yorio et al. 2010, Cama et al. 2012). Ours is the first to explore simultaneously the role of these different physical, biological and anthropogenic features likely affecting marine resources availability, and, consequently, driving the feeding and foraging ecology of this central-place forager. Accordingly, we provide a useful framework for evaluating

and predicting the potential impact of currently undergoing fishing policies such those aimed at developing a trawler fishery for anchovy as an alternative to the overfished hake (Skewgar et al. 2007 and references therein) on Magellanic penguin populations. Consequently, this work supposes an important advance in the way we tackle the management and conservation of this species. However, further investigation should additionally contemplate other potential explanatory variables likely affecting the feeding ecology of this central-place forager, such as the at-sea distribution of competitive species (e.g., South American sea lion, *Otaria flavescens*; Koen-Alonso and Yodzis 2005, Drago et al. 2010) and predators (e.g., the killer whale, *Orcinus orca*; Guinet 1992), or additional geographic features, such as marine currents, that can directionally impede or facilitate animal movements, thus affecting their distribution (Elith and Leathwick 2009).

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Literature Cited

Acha, E. M., H. W. Mianzan, R. A. Guerrero, M. Favero, and J. Bava. 2004. Marine fronts at the continental shelves of Austral South America: Physical and ecological processes. Journal of Marine Systems 44:83–105.

Barry, S., and J. Elith. 2006. Error and uncertainty in habitat models. Journal of Applied Ecology 43:413–423.

Bartumeus, F., L. Giuggioli, M. Louzao, V. Bretagnolle, D. Oro, and S. A. Levin. 2010. Fishery discards impact on seabird movement patterns at regional scales. Current Biology 20:215–222.

Bearhop, S., C. E. Adams, S. Waldron, R. A. Fuller, and H. Macleod. 2004. Determining trophic niche width: A novel approach using stable isotope analysis. Journal Animal Ecology 73:1007–1012.

Bertrand, S., R. Joo, C. A. Smet, Y. Tremblay, C. Barbraud, and H. Weimerskirch. 2012. Local depletion by a fishery can affect seabird foraging. Journal of Applied Ecology 49:1168–1177.

Boersma, P. D., G. A. Rebstock, E. Frere, and S. E. Moore. 2009. Following the fish: Penguins and productivity in the South Atlantic. Ecological Monographs 79:59–76.

Cama, A., R. Abellana, I. Christel, X. Ferrer, and R. Vieites. 2012. Living on predictability: Modelling the density distribution of efficient foraging seabirds. Ecography 35:912–921.

Carrasco, J. L., C. Sanpera, M. García-Tarrasón, F. Ramírez, K. Skaltsa, and L. Jover. 2010. Distinguishability, isotopic variance and niche width. VII International Conference on Applications of Stable Isotope Techniques to Ecological Studies (IsoEcol), Fairbanks, Alaska, USA, August 9–13.

Caut, S., E. Angulo, and F. Courchamp. 2009. Variation in discrimination factors (delta N-15 and delta C-13): The effect of diet isotopic values and applications for diet reconstruction. Journal of Applied Ecology 46:443–453.

Crawford, R. J. M. 2007. Food, fishing and seabirds in the Benguela upwelling system. Journal of Ornithology 148:S253–S260.

Drago, M., L. Cardona, A. Aguilar, E. A. Crespo, S. Ameghino, and N. García. 2010. Diet of lactating South American sea lions, as inferred from stable isotopes, influences pup growth. Marine Mammal Science 26:309–323.

Elith, J. and J. R. Leathwick. 2009. Species distribution models: Ecological explanation and prediction across space and time. Annual Review of Ecology, Evolution, and Systematics 40:677–697.

Fauchald, P. 2009. Spatial interaction between seabirds and prey: Review and synthesis. Marine Ecology Progress Series 391:139–151.

Fielding, A. H., and J. F. Bell. 1997. A review of methods for the assessment of prediction errors in conservation presence/absence models. Environmental Conservation 24:38–49.

Forero, M. G., J. L. Tella, K. A. Hobson, M. Bertellotti, and G. Blanco. 2002*a*. Conspecific food competition explains variability in colony size: A test in Magellanic penguins. Ecology 83:3466–3475.

Forero, M. G., K. A. Hobson, G. R. Bortolotti, J. A.

Donázar, M. Bertellotti, and G. Blanco. 2002*b*. Food resource utilisation by the Magellanic penguin evaluated through stable-isotope analysis: Segregation by sex and age and influence on offspring quality. Marine Ecology Progress Series 234:289–299.

Forero, M. G., G. R. Bortolotti, K. A. Hobson, J. A. Donazar, M. Bertelloti, and G. Blanco. 2004. High trophic overlap within the seabird community of Argentinean Patagonia: A multiscale approach. Journal of Animal Ecology 73:789–801.

Frederiksen, M., M. Edwards, A. J. Richardson, N. C. Halliday, and S. Wanless. 2006. From plankton to top predators: Bottom-up control of a marine food web across four trophic levels. Journal of Animal Ecology 75:1259–1268.

Furness, R. W., and C. J. Camphuysen. 1997. Seabirds as monitors of the marine environment. ICES Journal of Marine Science 54:726–737.

Grecian, W. J., M. J. Witt, M. J. Attrill, S. Bearhop, B. J. Godley, D. Grémillet, K. C. Hamer, and S. Votier. 2012. A novel projection technique to identify important at-sea areas for seabird conservation: An example using Northern Gannets breeding in the North East Atlantic. Biological Conservation 156:43–52.

Guinet, C. 1992. Comportement de chasse des orques (*Orcinus orca*) autour des îles Crozet. Canadian Journal of Zoology 70:1656–1667.

Hansen, J. E., P. Martos, and A. Madirolas. 2001. Relationship between spatial distribution of the Patagonian stock of Argentine anchovy, *Engraulis anchoita*, and sea temperatures during late spring to early summer. Fisheries Oceanography 10:193–206.

Henkel, L. A. 2009. Co-occurrence and aggregation of marine birds and mammals in Monterey Bay, California, USA. Marine Ecology Progress Series 387:295–303.

Hernandez, P. A., C. H. Graham, L. L. Master, and D. L. Albert. 2006. The effect of sample size and species characteristics on performance of different species distribution modelling methods. Ecography 29:773–785.

Hobson, K. A., and L. I. Wassenaar. 2008. Tracking animal migration with stable isotopes. Elsevier, Amsterdam, The Netherlands.

Hunt, G. L., J. Priddle, M. J. Whitehouse, R. R. Veit, and R. B. Heywood. 1992. Changes in seabird species abundance near South Georgia during a period of rapid change in sea-surface temperature. Antarctic Science 4:15–22.

Jackson, A. L., R. Inger, A. C. Parnell, and S. Bearhop. 2011. Comparing isotopic niche widths among and within communities: SIBER—Stable Isotope Bayesian Ellipses in R. Journal of Animal Ecology 80:595–602.

Johnson, J. B., and K. S. Omland. 2004. Model selection in ecology and evolution. Trends in Ecology and Evolution 19:101–108.

Karnovsky, N. J., K. A. Hobson, and S. J. Iverson. 2012. From lavage to lipids: Estimating diets of seabirds. Marine Ecology Progress Series 451:263–284.

Koen-Alonso, M., and P. Yodzis. 2005. Multispecies modelling of some components of the marine community of northern and central Patagonia, Argentina. Canadian Journal of Fisheries and Aquatic Sciences 62:1490–1512.

Louzao, M., K. Delord, D. García, A. Boué, and H. Weimerskirch. 2012. Protecting persistent dynamic oceanographic features: Transboundary conservation efforts are needed for the critically endangered Balearic shearwater. PLoS ONE 7:e35728.

Louzao, M., D. Pinaud, C. Perón, K. Delord, T. Wiegand, and H. Weimerskirch. 2011*a*. Conserving pelagic habitats: Seascape modelling of an oceanic top predator. Journal of Applied Ecology 48:121–131.

Louzao, M., J. Navarro, M. G. Forero, J. M. Igual, M. Genovart, K. A. Hobson, and D. Oro. 2011*b*. Exploiting the closest productive area: Geographical segregation of foraging grounds in a critically endangered seabird. Marine Ecology Progress Series 429:291–301.

Masello, J. F., R. Mundry, M. Poisbleau, L. Demongin, C. C. Voigt, M. Wikelski, and P. Quillfeldt. 2010. Diving seabirds share foraging space and time within and among species. Ecosphere 1:19.

Monk, J., D. Ierodiaconou, E. Harvey, A. Rattray, and V. L. Versace. 2012. Are we predicting the actual or apparent distribution of temperate marine fishes? PLoS ONE 7:e34558.

Navarro, J., D. Oro, A. Bertolero, M. Genovart, A. Delgado, and M. G. Forero. 2010. Age and sexual differences in the exploitation of two anthropogenic food resources for an opportunistic seabird. Marine Biology 157:2453–2459.

Navarro, J., M. G. Forero, J. González-Solís, J. M. Igual, J. Bécares, and K. A. Hobson. 2009. Foraging segregation between two closely related shearwaters breeding in sympatry. Biology Letters 5:545–548.

Newsome, S. D., C. M. del Rio, S. Bearhop, and D. L. Phillips. 2007. A niche for isotopic ecology. Frontiers in Ecology and Environment 5:429–436.

Parnell, A., R. Inger, S. Bearhop, and A. L. Jackson. 2008. Stable isotope analysis in R (SIAR). http://cran.r-project.org/web/packages/siar/index.html

Pearson, R. G., C. J. Raxworthy, M. Nakamura, and A. T. Peterson. 2007. Predicting species distributions from small numbers of occurrence records: a test case using cryptic geckos in Madagascar. Journal of Biogeography 34:102–107.

Pinaud, D., Y. Cherel, and H. Weimerskirch. 2005. Effect of environmental variability on habitat

selection, diet, provisioning behaviour and chick growth in Yellow-nosed albatrosses. Marine Ecology Progress Series 298:295–304.

Ramos, R., F. Ramírez, J. L. Carrasco, and L. Jover. 2011. Insights into the spatiotemporal component of feeding ecology: An isotopic approach for conservation management sciences. Diversity and Distributions 17:338–349.

Rangel, T. F., J. A. F. Diniz-Filho, and L. M. Bini. 2010. SAM: A comprehensive application for spatial analysis in macroecology. Ecography 33:46–50.

Scolaro, J. A., R. P. Wilson, S. Laurenti, M. Kierspel, H. Gallelli, and J. A. Upton. 1999. Feeding preferences of the Magellanic penguin over its breeding range in Argentina. Waterbirds 22:104–110.

Seaman, D. E., and R. A. Powell. 1996. An evaluation of the accuracy of kernel density estimators for home range analysis. Ecology 77:1197–1207.

Skewgar, E., P. D. Boersma, G. Harris, and G. Caille. 2007. Anchovy fishery threat to Patagonian ecosystem. Science 315:45.

Tella, J. L., M. G. Forero, M. Bertellotti, J. A. Donázar, G. Blanco, and O. Ceballos. 2001. Offspring body condition and immunocompetence are negatively affected by high breeding densities in a colonial seabird: A multiscale approach. Proceedings of the Royal Society B 268:1455–1461.

Villanueva, C., B. G. Walker, and M. Bertellotti. 2012. A matter of history: Effects of tourism on physiology, behaviour and breeding parameters in Magellanic penguins at two colonies in Argentina. Journal of Ornithology 153:219–228.

Weimerskirch, H. 2007. Are seabirds foraging for unpredictable resources? Deep-Sea Research Part II 54:211–223.

Weimerskirch, H., M. Le Corre, S. Jaquemet, and F. Marsac. 2005. Foraging strategy of a tropical seabird, the red-footed booby, in a dynamic marine environment. Marine Ecology Progress Series 288:251–261.

Weimerskirch, H., S. A. Shaffer, Y. Tremblay, D. P. Costa, H. Gadenne, A. Kato, Y. Ropert-Coudert, K. Sato, and D. Aurioles. 2009. Species and sex specific differences in foraging behaviour and foraging zones in Blue-footed and Brown boobies in the Gulf of California. Marine Ecology Progress Series 391:267–278.

Wilson, R. P., et al. 2005. How do Magellanic penguins cope with variability in their access to prey? Ecological Monographs 75:379–401.

Yen, P. P. W., W. J. Sydeman, and K. D. Hyrenbach. 2004. Marine bird and cetacean associations with bathymetric habitats and shallow-water topographies: Implications for trophic transfer and conservation. Journal of Marine Systems 50:79–99.

Yorio, P., F. Quintana, P. Dell'arciprete, and D. González-Zevallos. 2010. Spatial overlap between foraging seabirds and trawl fisheries: Implications for the effectiveness of a marine protected area at Golfo San Jorge, Argentina. Bird Conservation International 20:320–334.

Yorio, P., E. Frere, P. Gandini, and A. Schiavini. 2001. Tourism and recreation at seabird breeding sites in Patagonia, Argentina: Current concerns and future prospects. Bird Conservation International 11:231–245.

Yorio, P., E. Frere, P. Gandini, and G. Harris. 1998. Atlas De La Distribución Reproductiva De Aves Marinas En El Litoral Patagónico Argentino. Fundación Patagonia Natural, Puerto Madryn, Argentina.

Zimmer, I., Y. Ropert-Coudert, N. Poulin, A. Kato, and A. Chiaradia. 2011. Evaluating the relative importance of intrinsic and extrinsic factors on the foraging activity of top predators: A case study on female Little penguins. Marine Biology 158:715–722.

CHAPTER VI

An integrated method for identifying marine areas of highest conservation priority: a case study at the Argentinean Patagonia coast

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Diversity and Distributions, under review.

An integrated method for identifying marine areas of highest conservation priority: a case study at the Argentinean Patagonia coast

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Abstract

Aim: Identifying priority areas for conservation of biodiversity is particularly challenging in the marine environment due to the high mobility of species and the open and dynamic nature of the ocean. Here, we used the case study of the Argentinean seabird breeding community to propose an integrated method for delimiting key areas for marine conservation following the "core-buffer" zonation model.

Location: Argentinean Patagonia

Methods: Main core areas for conservation were defined through a free decision-support tool (Marxan) that considered a predicted at-sea distribution of seabirds and the economic costs of potential restrictions in fishing practices. Buffer regions were delimited by considering favorable oceanographic features for seabirds (oceanographic drivers of marine productivity), along with possible threats (i.e., risk of pollutant spills) potentially influencing the corresponding core areas through water inflows.

Results: We propose up to ten potential priority areas for conservation of this seabird community during breeding. Along the 3,000 km of Patagonian coastline, around 25 % (more than 800 km) contains core areas. Four main buffer areas were selected around core areas with a total area nearly double that of core areas.

Main conclusions: This methodology allows the whole breeding community to be considered for conservation purposes and could be periodically updated with changes in population dynamics, human activities or alterations in the ocean environment.

Ending: This methodology may be exportable to other regions or marine communities where information on the at-sea distribution of species is lacking.

INTRODUCTION

Human activities have extensively impacted the marine environment in recent decades, causing a loss of marine biodiversity and extensively affecting the structure and functioning of marine ecosystems globally (Lewison *et al.*, 2004; Cury *et al.*, 2011). Accordingly, marine conservation addresses issues of social, political and scientific concern, important worldwide. The conservation of our marine environment is, however, particularly challenging as it requires the delimitation of protected marine areas in an open and continuous system (Pérez-Jorge *et al.*, 2015), where the dynamisms of both physical (e.g. mesoscale features responsible of marine productivity patterns) and biological processes (e.g. changes in species distribution and population dynamics) are key to the effective design of marine reserves (Game *et al.*, 2009). Further, the effectiveness of marine reserves necessarily requires a balance between marine conservation targets and the sustainability of industrial fisheries, a major harvest activity that impacts marine ecosystems (Agardy *et al.*, 2003; Bennett & Dearden, 2014). At the same time, this industry benefits from conservation measures aimed at regenerating and protecting suitable refuges for target species (Gell & Roberts, 2003).

Marine top-meso predators, such as seabirds, have been frequently used as biodiversity surrogates and sentinel species of marine ecosystem (Grémillet & Charmantier, 2010). These species are sensitive to environmental changes that affect the distribution and abundance of their prey, thus integrating into many aspects of their life history those processes occurring at the lower trophic levels (Raymond *et al.*, 2014). Additionally, most seabirds are recognized as flagship species that can potentially be used to leverage support for biodiversity conservation. Seabirds distribute themselves according to oceanographic features (e.g., frontal systems, shelf edges or upwellings) where their prey aggregate (Hyrenbach *et al.*, 2006; Cotté *et al.*, 2007). However, these features vary spatially and temporary and marine protected areas would ideally (although difficult to enforce) require dynamic boundaries encompassing persistent and predictable prey patches along with habitat refuges from human and environmental stressors (Hyrenbach *et al.*, 2000; IUCN, 2015).

In turn, the delimitation of effective marine reserves for seabird conservation depends on our accurate understanding of their foraging distribution and interaction with human fisheries (Karpouzi *et al.*, 2007; Cury *et al.*, 2011). This insight has been enhanced in recent years with methodologies such as tracking devices for both seabirds (GPS, PTTs) and fishing vessels (VMS, Vessel Monitoring System), advancing toward the estimation of concurrent spatial patterns of at-sea distribution of foraging seabirds and fisheries practices (Votier *et al.*, 2010).

Based on a "core-buffer" zonation model, whereby each area adopts distinct functional roles and levels of protection (Hyrenbach *et al.*, 2000), we herein provide a new approach in which data on the

spatial distribution of breeding seabirds and human fisheries are combined with information on environmental features and human threats to identify key marine reserves. Main core areas were delimited via a free decision-support tool (Marxan) that considered the predicted at-sea distribution of seabirds and the economic costs of potential restrictions in fishing practices within protected areas. Mesoscale oceanographic features derived from ocean circulation and marine productivity patterns were also characterized spatially in an attempt to delimit effective buffer regions from a conservation perspective. Indeed, proposed buffer areas considered simultaneously oceanographic drivers of marine productivity (i.e., frontal systems and areas of enhanced chlorophyll-a concentration) and possible threats (i.e., risk of pollutant spills) potentially reaching each core area through water inflows. This proposed multidisciplinary method integrates the predicted spatial distribution of seabirds with that of key oceanographic features and explicit threats (pollutant spills and fisheries) for the determination of areas of highest conservation priority.

METHODS

Core areas zoning

Predicted spatial distribution of seabirds

The study area comprises the entire seabird community breeding on the Argentinean Patagonia coast from Península Valdés to Tierra del Fuego (41.5-55.5ºS, Fig. 1). Only species distribution during the breeding season was considered for this theoretical exercise. The recent miniaturization of tracking devices has largely improved our comprehension of at-sea seabird distribution while foraging (Ropert-Coudert & Wilson, 2005). However, this information is difficult to obtain for a whole breeding community over large areas and multiple breeding species. In an alternative approach, we combined existing data from censuses and biotelemetry to predict the at-sea distribution of breeding Patagonian seabirds (Grecian *et al.*, 2012; Ramírez *et al.*, 2014). Breeding pairs were extracted from Yorio *et al.* (1998) based on colony counts. Maximum foraging ranges were collected from previous tracking studies on the Magellanic penguin (*Spheniscus magellanicus*), South American tern (*Sterna hirundinacea*), southern giant petrel (*Macronectes giganteus*), Olrog's gull (*Larus atlanticus*) and king cormorant (*Phalacrocorax atriceps*) (Bugoni & Vooren, 2005; Wilson *et al.*, 2005; Boersma *et al.*, 2009; Copello *et al.*, 2011; Suárez *et al.*, 2012; Wilson *et al.*, 2012). These maximum ranges were averaged for inshore (n=3 species) and offshore feeders (n= 2 species), establishing a maximum foraging range of ca. 60 km for inshore and 500 km for offshore species. Following Ramírez et al. (2014), individuals from each species and colony were uniformly distributed within their potential foraging range using a modified version of an isolation function (Hanski, 1998; Afán *et al.*, 2014) $F_i = \sum \exp(-d_{ij} \cdot B_j) \cdot P_j$, where d_{ij} is the distance from each grid cell i to the colony j, and P_j is the number of breeding pairs of colony j. B_j is the inverse

of the minimum Euclidean distance from each colony to the maximum foraging range (Fig. S1). This methodology enables the prediction of the distribution of all species and colonies involved in the study when tracking data were not available for all of them.

Fishing pressure

Socio-economic activities, such as fisheries, were treated to minimize the potential threat of incidental capture of seabirds and the economic costs associated with limiting anthropogenic activities in protected areas, which is crucial for successful implementation. Information on fishing pressure was extracted and georeferenced from Copello and Quintanta (2009), who obtained data on distributions and total catches for the main fishing fleets operating on the Patagonian Shelf (trawlers, jiggers and longliners) from National Fishing reports provided by the National Institute of Fisheries Research and Development (INIDEP). As a proxy for fishing effort, these authors used monthly catch values for the austral summer months (January, February and March) of years 1999, 2000, 2002 and 2004. Considering the great variability among fisheries in the total captures, catch data were classified into three categories considering the same intervals as Copello and Quintana (2009): low (<60 ton), medium (60 - 200 ton) and high (>200 ton) for trawlers; low (<900 ton), medium (900 – 2 500 ton) and high (>2 500 ton) for jiggers, and low (<4 ton), medium (4 - 9 ton) and high (>9 ton) for longliners.

Core areas selection

The projected at-sea distribution of the Patagonian breeding seabird community, along with that of industrial fisheries operating in this region, were used to identify potential areas for conservation of breeding seabird diversity along the Patagonian coast. We used the most commonly used free decision-support tool for conservation reserve network design, Marxan v1.8.10, University of Queensland (Ball *et al.*, 2009; http://www.uq.edu.au/marxan/). This algorithm relies on distribution patterns of biodiversity to select candidate sites for protected areas. Marxan enables the combination of biological, economic and social criteria (Fraschetti *et al.*, 2009) addressing quantitative conservation objectives, qualitative design criteria, patterns of threat and competing demands for resource use (Game *et al.*, 2009). This algorithm begins with a random set of grid cells, and swaps units in and out of that set in each iteration, in order to maximize the ratio between conservation targets and costs ascribed to marine area protection. The study area was divided into 14,948 planning units, 8x8 km in size, inside the 200 m depth contour of the predicted at-sea distribution map of Patagonian breeding seabirds. Conservation features included potential seabird distribution maps, prioritizing vulnerable and near threatened species with a conservation target of 40% (three species) over 20% for the least concern IUCN status species (Table 1). Our goal was to maximize our conservation targets while minimizing the economic impact on fishery activities, in order to

enhance the efficacy of protection. The distribution pattern of fishing activity within the region is a socio-economic and environmental aspect that may generate use-protection conflict (Alpine & Hobday, 2007). Thus, this parameter was used as a penalty factor imposed on the overall reserve cost, i.e. costs associated with potential restrictions in fishing practices within protected areas. Fishing costs were assigned to three gradual and proportional categories according to the landings intervals described above. Areas included within the upper quartile of summed selection frequency solution over 100 simulations were used as output reserves. Selection frequency represents the number of times each planning unit is selected in each simulation.

Buffer areas zoning

Environmental variables (productive areas and ocean currents) and anthropogenic threats (oil pollution) were selected to evaluate extensive zones contributing to the maintenance of healthy and biodiverse conditions around core areas (so-called buffer areas).

Drivers of marine productivity

Among different oceanographic features commonly used for identifying productive hotspots, chlorophyll-*a* concentrations (CHL, mg m^{-3}) and sea surface temperature (SST, ºC) are widely considered as the most biologically relevant. In particular, CHL can be considered a reliable surrogate of marine productivity and, consequently, of prey abundance. SST may provide relevant information on physical processes or oceanographic features, such as sea fronts, driving prey distribution (Acha *et al.*, 2004; Behrenfeld *et al.*, 2006). We used time series of CHL (1998-2012) and SST (2003-2012) to spatially and temporally evaluate the predictability of productive areas over time, and consequently expected to be recurrently visited by marine predators (Ramírez *et al.*, 2014). Data was obtained from SeaWifs and MODIS sensors (spatial resolution 0.08333º, ca 9 km), for the austral summer seasonal composites (NASA Ocean Color Service (http://oceancolor.gsfc.nasa.gov/). Highly productive areas were identified through two different approaches. Firstly, we defined high-productive pixels for each summer season as those with CHL values within the upper quartile (75th percentile, Q4) (Afán *et al.*, 2014). Secondly, high-productive areas associated with sea fronts were identified by exploring spatial gradients in SST. We calculate the magnitude of change in SST with a dimensionless metric applied within a moving window of 3x3 cells as follows: Proportional Change = [(maximum value - minimum value)*100]/(maximum value) (Louzao *et al.*, 2012; Ramírez *et al.*, 2014). Frontal systems were identified as areas with proportional change values within Q4. Following Louzao *et al.* (2012), the persistency of ocean features was subsequently quantified by counting in how many years each pixel was assigned to the high-productive category (values ranging from 0 to 15 years corresponding to the CHL time series and from 0 to 10 years in the case of the SST time series).

Anthropogenic threats

Oil pollution is considered a major potential threat for the marine ecosystem in general, and seabirds in particular (Grémillet & Boulinier, 2009). Information on the potential impact of pollution in our study area was downloaded from Halpern et al. (2008) global data sets of anthropogenic drivers of ecological change (http://www.nceas.ucsb.edu/globalmarine/impacts). This serves as an ocean pollution index that informs on the occurrence of commercial ships and port activities at a particular location. This index has been used previously as a proxy to the amount of pollution produced by these human activities (via fuel leaks, oil discharge, waste disposal, etc.).

Ocean currents

Water masses drifted by ocean currents may present enhanced local production and increased pollution risks derived from ship traffic or pollutant leaks. They also favor biomass drifts as energy flows through food chains (e.g. from larvae production to spawning aggregations). Ocean currents should therefore be considered for creating reliable buffer areas aimed at favoring food availability for seabirds, while minimizing potential risks from human activities (e.g. fuel leaks or oil spills). We retrieved sea surface currents data from the Global Ocean Physics Reanalysis Models Glorys2V3 1993-2012 (www.myocean.eu, Copernicus: Marine environment monitoring service). Models are provided in netCDF format at a 0.25º horizontal resolution and -5500 to 0 m vertical coverage and contain monthly average patterns of the main ocean currents as meridional and zonal components of water speed vectors. These variables were converted to monthly mean rasters of water speed and direction in the upper layer (first 14 m of depth). Finally, mean water speed and direction for the 1993-2012 breeding months (from September to February) was calculated.

Ocean currents were used to estimate areas with potentially water inflows to selected core areas. We used a connectivity-modelling approach using circuit theory to estimate probabilities of water masses to flow from source nodes of a grid of 0.25º over the entire study area to each core area derived from Marxan (sink areas) (Afán *et al.*, 2015). Circuitscape is a free software that couples graph theory with electrical circuit theory and measures habitat connectivity by calculating the cumulative current that flows through each cell of a resistance map (McRae, 2006). Mean ocean currents were used to generate a resistance surface as input for Circuitscape. For this purpose, we generated a direction raster representing azimuth angles between each raster cell and each core area. Then, we estimated the absolute differences (Δ angle) between mean sea surface current azimuths and the angle obtained from the direction raster for each cell and core area. Δ angles were transformed into a measure of resistance by the function $y = 0.6184 x - 0.0984 x2$ (y=resistance, x= Δ angle, in radians). Parameters were estimated from calculated angles to obtain a [0, 1] range of values. This function assumes a resistance quadratic function, assigning

minimum resistance values to angles pointing to the core areas, and increasing gradually for opposite directions. The final measure of resistance was obtained multiplying the results by water speed (Afán *et al.*, 2015). Connectivity final pixel value was obtained as the sum of connectivity values (in volts) from each pixel derived from the analysis for each core area.

Buffer areas selection

Buffer areas were depicted based on the equally-weighted spatial distribution of key marine productive areas and frontal systems (as defined by CHL persistency and spatial gradients in SST), oil pollution threats and ocean currents. In this way, we aimed to define buffer regions encompassing water masses potentially affecting core areas through water inflows. To avoid biases towards certain oceanographic features or human threats, all variables were standardized by dividing each cell by the maximum value of the respective grid. We then calculated a pixel-basis index of spatial overlap between targeted features following the equation: Overlap index = (Connectivity value)* (CHL + SST + Threats), where connectivity value refers to the output of our ocean current analysis, and CHL, SST and threats indicate the sum of standardized values for marine productivity, frontal systems and pollutant threats, respectively. In order to establish a conservative delimitation of buffer areas, a limit was selected enclosing the 98th quartile values of the overlap index. All the analyses were performed in R (R Core Team, 2013).

RESULTS

Study system description: environmental and anthropogenic features

The estimated distribution of seabirds along the Patagonian shelf (Fig. 1) showed that the highest densities occur north of Golfo de San Jorge, where the most abundant species (Magellanic penguin and kelp gull *Larus dominicanus*) coexist (Fig. S2).

Three species (Magellanic penguin, king cormorant and red-legged cormorant *Phalacrocorax gaimardi*) were distributed in a large latitudinal range (Fig. S2), whereas remaining species showed a localized colony distribution along the coast. Only one species was listed as vulnerable (VU) in the IUCN conservation status, the near endemic Olrog's gull, and two species were categorized as near threatened (NT), the Magellanic penguin and the red-legged cormorant (Table 1). The latter two species had an accordingly increased weight in the Marxan core area selection.

The at-sea distribution of the main fishing vessels suggested that fishing pressure was broadly distributed throughout the Patagonian shelf (Fig. 2). Trawlers and jiggers were primarily responsible for close coastal fishing pressure and were also distributed in the middle shelf, whereas longline vessels operate in northern and southern waters in the middle and external shelf.

Table 1. Breeding species of the Argentinean Patagonian coast used in this study to generate a predicted at-sea distribution map for the entire seabird community. For each species, population size extracted from Yorio et al (1998) and IUCN conservation status are shown (LC: least concern, VU: vulnerable NC: threatened).

	Scientific name	Conservation status (IUCN)	Population size
Inshore feeders			
Laridae			
Olrog's gull	*Larus atlanticus*	VU	186
Dolphin gull	*Leucophaeus scoresbii*	LC	1,248
Kelp gull	*Larus dominicanus*	LC	138,482
Sternidae			
Cayenne tern	*Thalasseus eurygnatha*	LC	4,272
Royal tern	*Thalasseus maximus*	LC	1,542
South American tern	*Sterna hirundinacea*	LC	28,132
Phalacrocoracidae			
Rock shag	*Phalacrocorax magellanicus*	LC	15,072
King cormorant	*Phalacrocorax atriceps*	LC	97,872
Neotropic cormorant	*Phalacrocorax olivaceus*	LC	3,024
Red-legged cormorant	*Phalacrocorax gaimardi*	NT	2,182
Stercorariidae			
Brown skua	*Stercorarius antarcticus*	LC	974
Chilean Skua	*Stercorarius chilensis*	LC	86
Offshore feeders			
Spheniscidae			
Magellanic penguin	*Spheniscus magellanicus*	NT	1,927,760
Procellariidae			
Southern giant petrel	*Macronectes giganteus*	LC	4,624

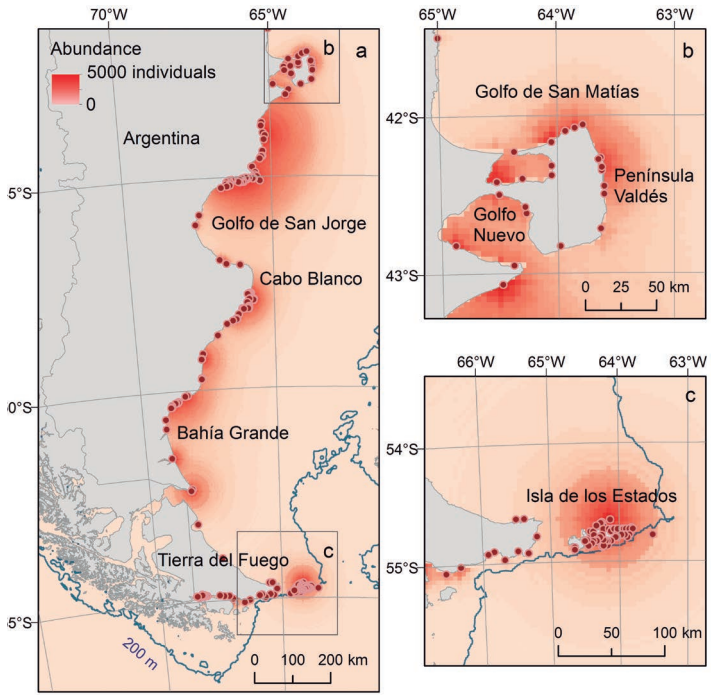

Figure 1. Geographic location of the study area. Red points show seabird colonies where information from breeding pairs has been used as a basis for the projected at-sea distribution of individuals. Color gradient reflects the predicted spatial distribution of all seabird species (in number of individuals) based on breeding pair colony censuses.

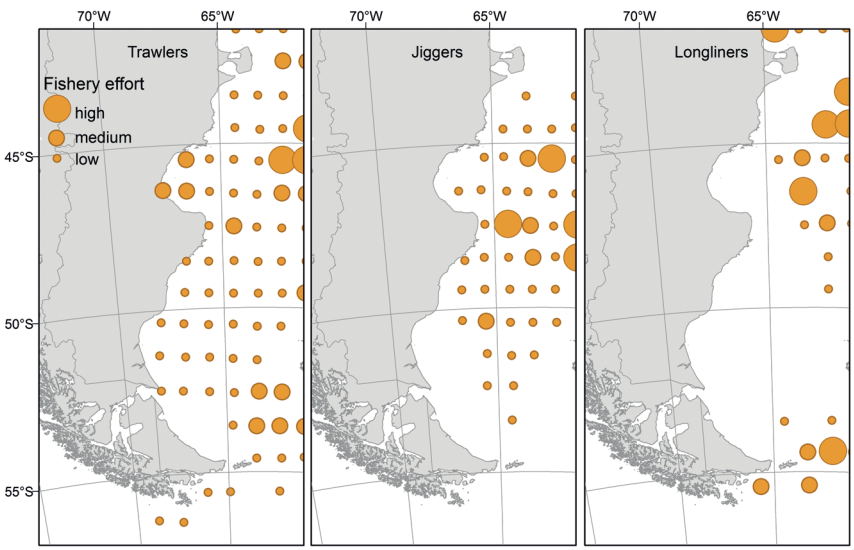

Figure 2. Spatial distribution of total fisheries catches from the Argentinean Sea grouped as trawlers, jiggers and longliners, differing in their main target species and fishing areas. For trawlers, total captures were classified as follows: low (<60 ton), medium (between 60 and 200 ton) and high (>200 ton); for jiggers: low (<900 ton), medium (between 900 and 2 500 ton) and high (>2 500 ton); and for longliners: low (<4 ton), medium (between 4 and 9 ton) and high (>9 ton). Information was extracted from Capello and Quintana (2009) based on monthly catch values for the summer months (January, February and March) of 1999, 2000, 2002 and 2004.

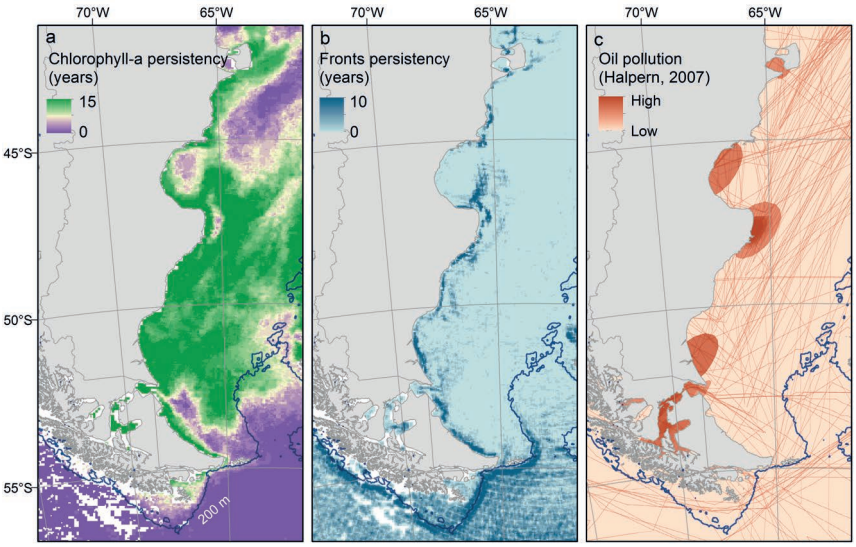

Figure 3. Spatiotemporal heterogeneity of marine areas associated with productivity (chlorophyll-a) (a) and front systems (b). Graduated colors represent values ranging from 0 (minimum persistence) to 10 (maximum persistence) in productivity (2002-2012) and from 0 to 15 years in fronts (1998-2012). c) Ocean-based pollution derived from commercial and recreational ship activity (Halpern et al. 2008). The shipping data provide an estimate of the occurrence of ships at a particular location, and therefore an estimate of the amount of pollution they produce (via fuel leaks, oil discharge, waste disposal, etc.). Blue line represents the 200 m isobaths.

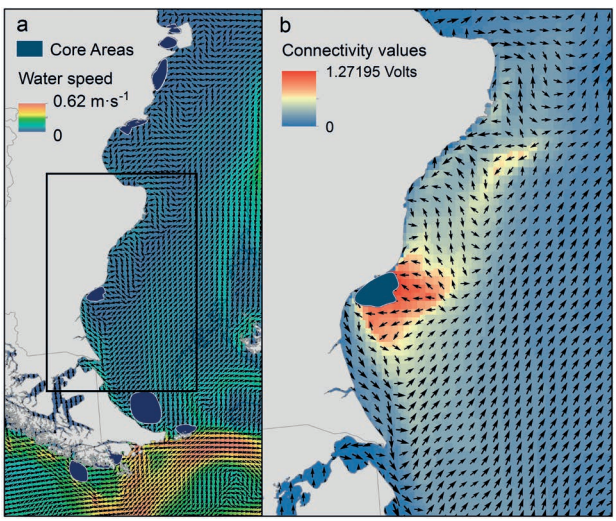

Figure 4. (a) Mean ocean currents on the Patagonian shelf. Water speed is graded in color. Arrows show current direction. (b) Example of output from connectivity analysis. Graduated colors display connectivity (in volts). Connectivity maps should be interpreted as a probability of ways to arrive to the sink. Higher values indicate areas more likely to arriving at the core area (in blue). White line represents the 200 m isobaths.

Highly productive areas occurred consistently from coastal waters to the shelf break, covering great areas up to 200 m isobaths. Low productivity values were found only inside Golfo de San Jorge and in two great water tongues parallel to the coast in the middle shelf of Tierra del Fuego and south of Península Valdés (Fig. 3a). Greater persistence occurred on the middle Patagonian shelf. Distribution of persistent front summer systems is far more restricted to nearer narrow areas along the entire coast, with a very narrow and persistent front maximum that closely follows the 200 m isobath (Fig. 3b).

The main Patagonian ocean circulation for the breeding period involves two opposing flows: a northeast flow in the middle and outer shelf and a southward but slow current prevailing parallel to the coast (Fig. 4a). A significant change occurs below 55º latitude, with higher water speed and prevailing strong eastward water movements. In this region, an inflow tongue of southern waters between Tierra del Fuego and Isla de los Estados could clearly be observed (Fig. 4a). Areas delimited by the connectivity analysis from ocean currents (Fig. 4b) suggest that core areas in southern Tierra del Fuego are safe from potential anthropogenic threats around them. Speedy water flow move away from this part of the Patagonian coast, which is, furthermore, less exposed to oil pollution. The remaining core areas present a radius of approximately 50 km with waters with potential inflows into the core areas.

Oil pollution, selected as a potential anthropogenic threat, was particularly high in Golfo de San Jorge, Golfo Nuevo (southern Península Valdés), Bahía Grande, areas surrounding Cabo Blanco and waters between Patagonia and Tierra del Fuego (Fig. 3c).

Marine reserves: core and buffer areas

The areas covered in the solution by Marxan (incorporating seabird distribution and fishing pressure, Fig. 5b) encompass ten potential marine reserves, four in the north, five in the south (areas 6 to 10), around Tierra del Fuego and only one area in the middle latitudes (Bahía Grande, area 5). Area 6 is the largest, concurring with the near-threatened red-legged cormorant breeding area Fig. S2) and a free fishing zone (Fig. 2). All other areas present higher fishing activities in the surrounding waters with the subsequent reduction of the protected core area. The majority of cells with a high selection frequency protect areas of overlapping species distribution, heightening threatened species according to the specific targets proposed. Along the 3,000 km of Patagonian coastline, around 25 % (more than 800 km) contains core areas. The mean extent of core areas is 27,771.6 ± 25,651.9 km^2, whereas the maximum depth varies from 174 m in the northern areas, 102 m in the only protected area in the center and 260 m in southern areas.

The overlap index encompassing potential protected zones, key oceanographic areas, potential threats and waters connected by ocean circulation to the core areas, suggest four main buffer

areas with a sizeable extension (Fig. 5): an area ranging from Península Valdés to Cabo Blanco along the coast, an area surrounding the core area north of Bahía Grande, a tongue around 120 km in length that extends from the core area of Tierra del Fuego to the northeast, and an area south from Tierra del Fuego. These areas amount to 54,998 km^2 of waters, with an area nearly double that of core areas.

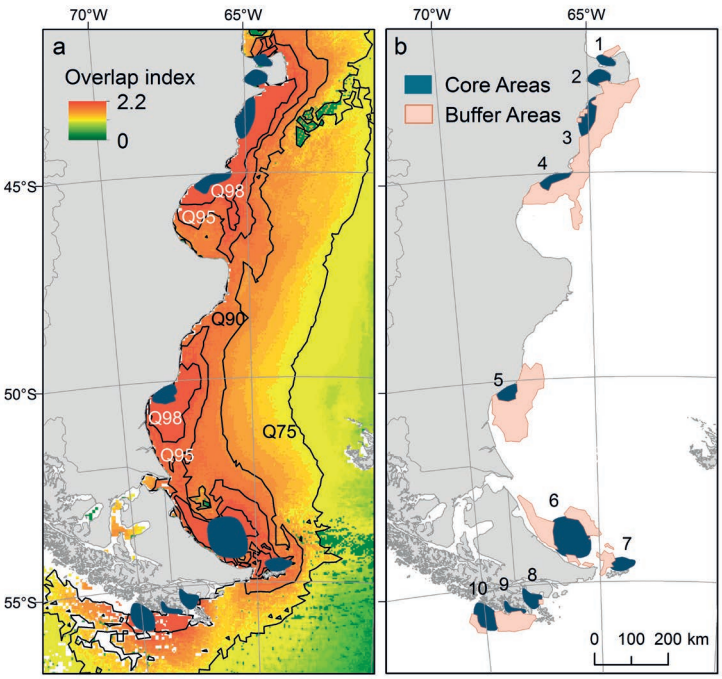

Figure 5. Final proposal of prioritized marine areas for protection (core areas) derived from Marxan over 100 simulations (dark blue). Conservation objectives were adjusted to 40% for near threatened species and 20% for least concern species. Fishery effort, as measured by tons of landings, was used as a penalty factor imposed on the overall reserve cost. Graduated colors (a) display the overlap index considering key oceanographic features (spatial distribution of higher productivity and front systems persistent in time), pollution threats and areas with waters with a higher probability of arriving at the reserves, drifted by oceanic currents. Limit of quantiles 75th to 98th are represented in black lines. Buffer areas (b) result from the consideration of the 98th quantile (Q98) from the overlap index. White line represents the 200 m isobaths.

DISCUSSION

The establishment of marine protected areas faces several constraints in dynamic, open and extensive systems such as oceans. One of them, and probably the most insurmountable, is obtaining sufficient habitat use information for the species considered. Another common challenge for oceanic conservation is the dynamism in space and time of physical processes that could enhance productivity and therefore, lead species distribution (Game *et al.*, 2009). This requires dynamic processes to be incorporated into reserve design (Welch *et al.*, 2015). Finally, conservation policies must ensure biodiversity conservation and the sustainability of fishing practices, both for sustaining these important socio-economic activities and for avoiding the depletion of resources and the collapse of fish stocks (Bennett & Dearden, 2014). Within this scenario, we hereby propose an integrated method for identifying marine areas of highest conservation priority by considering seabirds as flagship species informing on the structure and functioning of the whole marine system, along with relevant oceanographic features and anthropogenic threats affecting biodiversity conservation. In particular, we have identified up to ten priority areas for conservation of the Patagonian seabird breeding community, encompassing ca. 28,000 km^2 of ocean areas close to the mainland.

Core areas were delimited based on a trade-off between seabird species conservation thresholds and fishery sustainability. We used a free planning tool (Marxan) that allows an adaptive management application taking into account different conservation statuses of species or socio-economic objectives, allowing different solutions based on the specific goals and conditions needed for the the non-fixed status of the marine reserves (Agardy *et al.*, 2003). Marxan has been used extensively in marine (Ban *et al.*, 2009; Klein *et al.*, 2009) and terrestrial habitats (Becker *et al.*, 2010) for conservation purposes. Seabird foraging distribution in marine habitats does not adhere to fixed geographical areas. These preferentially used areas are spatially structured by dynamic oceanographic conditions (Scales *et al.*, 2014). In particular, the degree to which habitat features recur, the amount of time they persist, and how much their location and extent vary in time and space will determine the feasibility of marine reserves (Hyrenbach *et al.*, 2000). Recent works have highlighted the need to include ocean features that are dynamic in space and time, and the value of advances in satellite technology to facilitate the incorporation of remote sensing data in conservation planning (Game *et al.*, 2009). Therefore, in order to delimit buffer areas, we combined the dynamic water properties of the area in a spatio-temporal study identifying those areas that encompass higher levels of surrogates of productivity (CHL and SST fronts) during the breeding season over the last decade (Grémillet *et al.*, 2008). By incorporating key oceanographic features persistent in time into these buffer areas, we aimed to ensure the protection of oceanographic features with a high degree of spatial and temporal predictability

(Game *et al.*, 2009; Grecian *et al.*, 2012) that could improve the productivity of areas localized in convergence zones, such as fronts (Bost *et al.*, 2009).

Other physical processes, such as oceanic currents, could modify the limits of marine reserves. Perturbations such as dumpings and pollution events (Ruoppolo *et al.*, 2012; Marinho *et al.*, 2013) would expose the protected areas to external threats if water masses are highly connected. Distances covered by oils and contaminants facilitated by wind and sea-currents could easily reach hundreds of miles (González *et al.*, 2006), with catastrophic and delayed consequences for marine life and ecosystem recovery (Peterson *et al.*, 2003). In a similar way, high productivity areas adjacent to core protected areas can play an important role, enhancing prey supply in the core areas by animal movement and drifts. Our study is novel in its attempt to combine conservation needs with dynamic oceanographic features, such as currents, which influence water mass quality and system performance in an area depending on the direction and speed of the water masses surrounding them (Afán *et al.*, 2015).

Our approach incorporates into the buffer areas those waters potentially influencing the core areas through water inflows derived from oceanic currents. The determination of these areas differs from simpler solutions such as concentric and fixed radius areas around the core areas (Fig. 5) and reduces unnecessary protection areas. Although the main conservation targets are seabird species, protection against anthropogenic threats and environmental features affecting productivity, positively impacts not only the distribution of these top predators, but promotes the health of whole ecosystem functioning, a great challenge in conservation policies.

Birdlife International has proposed 28 candidate marine IBAs (BirdLife Important Bird and Biodiversity Area), considering coastal and marine areas. Great effort has been made to address the reduction of bycatch in longline fisheries, oil pollution and interactions with shipping vessels in the marine counterpart. This proposal is still under consideration for potential new sites (BirdLife International, 2015). The proposal envisages several coastal protected areas and only two zones of marine IBAs near the coastline: one north of the Golfo de San Jorge, which is also covered by our study, and other areas in southern Tierra del Fuego and surrounding Isla de los Estados (Fig. S3). While the IBAs and core areas proposed do not overlap entirely, these two areas were also considered in our study. The remaining IBAs proposed cover great ocean areas near the 200 m isobaths, and much more distant from the coast than our study area. These differences may be a result of the different phenological stage considered (in our case, only breeding time).

The integrated framework presented indicates the limitations of modelling the at-sea distribution of species instead of using real tracking data. However, it allows the effective integration of the entire

seabird population of a coastal area in the early stages of conservation planning. This could be subsequently revisited and enhanced with additional information on the distribution of other groups (e.g. marine mammals) or breeding colonies (e.g. those occurring in nearby areas such as the Falkland/Malvinas Islands), along with finer-scale information on seabird distribution or updated data on colony sizes when these become available. Our approach is useful only for the breeding period, the only time of year when central-place foragers are restricted to foraging zones near the breeding colony, and consequently, particularly sensitive to environmental changes in the zone. Complete protection would require uneven protected areas for each season, focusing on foraging aggregations during winter. Marine protected areas should be designated to enhance the conservation of geographical areas, including targeted and non-targeted species, marine resources and their biophysical environment (Lubchenco *et al.*, 2003). Our approach addresses quantitative conservation objectives and qualitative design criteria, along with the dynamism and quality of the oceanographic habitat.

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REFERENCES

Acha, E.M., Mianzan, H.W., Guerrero, R.A., Favero, M. & Bava, J. (2004) Marine fronts at the continental shelves of austral South America. *Journal of Marine Systems*, **44**, 83-105.

Afán, I., Chiaradia, A., Forero, M.G., Dann, P. & Ramírez, F. (2015) A novel spatio-temporal scale based on ocean currents unravels environmental drivers of reproductive timing in a marine predator. *Proceedings of the Royal Society B*, **282**, 20150721.

Afán, I., Navarro, J., Cardador, L., Ramírez, F., Kato, A., Rodríguez, B., Ropert-Coudert, Y. & Forero, M.G. (2014) Foraging movements and habitat niche of two closely related seabirds breeding in sympatry. *Marine Biology*, **161**, 657-668.

Agardy, T., Bridgewater, P., Crosby, M.P., Day, J., Dayton, P.K., Kenchington, R., Laffoley, D., McConney, P., Murray, P.A., Parks, J.E. & Peau, L. (2003) Dangerous targets? Unresolved issues and ideological clashes around marine protected areas. *Aquatic Conservation-Marine and Freshwater Ecosystems*, **13**, 353-367.

Alpine, J. & Hobday, A. (2007) Area requirements and pelagic protected areas: is size an impediment to implementation? *Marine and Freshwater Research*, **58**, 558-569.

Ball, I.R., Possingham, H.P. & Watts, M. (2009) Marxan and relatives: Software for spatial conservation prioritisation. *Spatial conservation prioritisation: Quantitative methods and computational tools* (ed. by A. Moilanen, A.J. Wilson and H.P. Possingham), pp. 185-195. Oxford University Press, Oxford, UK.

Ban, N.C., Picard, C.R. & Vincent, A.C.J.

(2009) Comparing and integrating community-based and science-based approaches to prioritizing marine areas for protection. *Conservation Biology*, **23**, 899-910.

Becker, C., Loyola, R., Haddad, C. & Zamudio, K. (2010) Integrating species life-history traits and patterns of deforestation in amphibian conservation planning. *Diversity and Distributions*, **16**, 10-19.

Behrenfeld, M.J., O/'Malley, R.T., Siegel, D.A., McClain, C.R., Sarmiento, J.L., Feldman, G.C., Milligan, A.J., Falkowski, P.G., Letelier, R.M. & Boss, E.S. (2006) Climate-driven trends in contemporary ocean productivity. *Nature*, **444**, 752-755.

Bennett, N.J. & Dearden, P. (2014) From measuring outcomes to providing inputs: Governance, management, and local development for more effective marine protected areas. *Marine Policy*, **50**, 96-110.

BirdLife International (2015) Country profile: Argentina. In, Available at http://www.birdlife.org/datazone/country/argentina. Checked: 2015-12-16.

Boersma, P.D., Rebstock, G.A., Frere, E. & Moore, S.E. (2009) Following the fish: penguins and productivity in the South Atlantic. *Ecological Monographs*, **79**, 59-76.

Bost, C.A., Cotté, C., Bailleul, F., Cherel, Y., Charrassin, J.B., Guinet, C., Ainley, D.G. & Weimerskirch, H. (2009) The importance of oceanographic fronts to marine birds and mammals of the southern oceans. *Journal of Marine Systems*, **78**, 363-376.

Bugoni, L. & Vooren, C.M. (2005) Distribution and abundance of six tern species in southern brazil. *Waterbirds*, **28**, 110-119.

Copello, S. & Quintana, F. (2009) Spatio-temporal overlap between the at-sea distribution of Southern Giant Petrels and fisheries at the Patagonian Shelf. *Polar Biology*, **32**, 1211-1220.

Copello, S., Dogliotti, A.I., Gagliardini, D.A. & Quintana, F. (2011) Oceanographic and biological landscapes used by the Southern Giant Petrel during the breeding season at the Patagonian Shelf. *Marine Biology*, **158**, 1247-1257.

Cotté, C., Park, Y.-H., Guinet, C. & Bost, C.-A. (2007) Movements of foraging king penguins through marine mesoscale eddies. *Proceedings of the Royal Society B*, **274**, 2385-2391.

Cury, P.M., Boyd, I.L., Bonhommeau, S., Anker-Nilssen, T., Crawford, R.J., Furness, R.W., Mills, J.A., Murphy, E.J., Österblom, H. & Paleczny, M. (2011) Global seabird response to forage fish depletion—one-third for the birds. *Science*, **334**, 1703-1706.

Fraschetti, S., D'Ambrosio, P., Micheli, F., Pizzolante, F., Bussotti, S. & Terlizzi, A. (2009) Design of marine protected areas in a human-dominated seascape. *Marine Ecology Progress Series*, **375**, 13-24.

Game, E.T., Grantham, H.S., Hobday, A.J., Pressey, R.L., Lombard, A.T., Beckley, L.E., Gjerde, K., Bustamante, R., Possingham, H.P. & Richardson, A.J. (2009) Pelagic protected areas: the missing dimension in ocean conservation. *Trends in Ecology & Evolution*, **24**, 360-369.

Gell, F.R. & Roberts, C.M. (2003) Benefits beyond boundaries: the fishery effects of marine reserves. *Trends in Ecology & Evolution*, **18**, 448-455.

González, J.J., Viñas, L., Franco, M.A., Fumega, J., Soriano, J.A., Grueiro, G., Muniategui, S., López-Mahía, P., Prada, D., Bayona, J.M., Alzaga, R. & Albaigés, J. (2006) Spatial and temporal distribution

of dissolved/dispersed aromatic hydrocarbons in seawater in the area affected by the Prestige oil spill. *Marine Pollution Bulletin*, **53**, 250-259.

Grecian, W.J., Witt, M.J., Attrill, M.J., Bearhop, S., Godley, B.J., Grémillet, D., Hamer, K.C. & Votier, S.C. (2012) A novel projection technique to identify important at-sea areas for seabird conservation: An example using Northern gannets breeding in the North East Atlantic. *Biological Conservation*, **156**, 43-52.

Grémillet, D. & Boulinier, T. (2009) Spatial ecology and conservation of seabirds facing global climate change: a review. *Marine Ecology Progress Series*, **391**, 121-137.

Grémillet, D. & Charmantier, A. (2010) Shifts in phenotypic plasticity constrain the value of seabirds as ecological indicators of marine ecosystems. *Ecological Applications*, **20**, 1498-1503.

Grémillet, D., Lewis, S., Drapeau, L., Van Der Lingen, C.D., Huggett, J.A., Coetzee, J.C., Verheye, H.M., Daunt, F., Wanless, S. & Ryan, P.G. (2008) Spatial match–mismatch in the Benguela upwelling zone: should we expect chlorophyll and sea-surface temperature to predict marine predator distributions? *Journal of Applied Ecology*, **45**, 610-621.

Halpern, B.S., Walbridge, S., Selkoe, K.A., Kappel, C.V., Micheli, F., D'Agrosa, C., Bruno, J.F., Casey, K.S., Ebert, C., Fox, H.E., Fujita, R., Heinemann, D., Lenihan, H.S., Madin, E.M., Perry, M.T., Selig, E.R., Spalding, M., Steneck, R. & Watson, R. (2008) A global map of human impact on marine ecosystems. *Science*, **319**, 948-952.

Hanski, I. (1998) Metapopulation dynamics. *Nature*, **396**, 41-49.

Hyrenbach, K.D., Forney, K.A. & Dayton, P.K. (2000) Marine protected areas and ocean basin management. *Aquatic Conservation-Marine and Freshwater Ecosystems*, **10**, 437-458.

Hyrenbach, K.D., Veit, R.R., Weimerskirch, H. & Hunt, G.L. (2006) Seabird associations with mesoscale eddies: the subtropical Indian Ocean. *Marine Ecology Progress Series*, **324**, 271-279.

IUCN (2015) IUCN Standard for the Identification of Key Biodiversity Areas, Version 1.0. In, p. 22, Gland, Switzerland.

Karpouzi, V.S., Watson, R. & Pauly, D. (2007) Modelling and mapping resource overlap between seabirds and fisheries on a global scale: a preliminary assessment. *Marine Ecology Progress Series*, **343**, 87-99.

Klein, C.J., Steinback, C., Watts, M., Scholz, A.J. & Possingham, H.P. (2009) Spatial marine zoning for fisheries and conservation. *Frontiers in Ecology and the Environment*, **8**, 349-353.

Lewison, R.L., Crowder, L.B., Read, A.J. & Freeman, S.A. (2004) Understanding impacts of fisheries bycatch on marine megafauna. *Trends in Ecology & Evolution*, **19**, 598-604.

Louzao, M., Delord, K., Garcia, D., Boue, A. & Weimerskirch, H. (2012) Protecting persistent dynamic oceanographic features: transboundary conservation efforts are needed for the critically endangered balearic shearwater. *PLOS ONE*, **7**, e35728.

Lubchenco, J., Palumbi, S.R., Gaines, S.D. & Andelman, S. (2003) Plugging a hole in the ocean: the emerging science of marine reserves. *Ecological applications*, **13**, 3-7.

Marinho, C.H., Gil, M.N. & Esteves, J.L. (2013) Distribution and origin of trace metals in sediments of a marine park (Northern

San Jorge Gulf) from Argentina. *Marine Pollution Bulletin*, **72**, 260-263.

McRae, B.H. (2006) Isolation by resistance. *Evolution*,

Pérez-Jorge, S., Pereira, T., Corne, C., Wijtten, Z., Omar, M., Katello, J., Kinyua, M., Oro, D. & Louzao, M. (2015) Can static habitat protection encompass critical areas for highly mobile marine top predators? Insights from coastal East Africa. *PLOS ONE*, **10**, e0133265.

Peterson, C.H., Rice, S.D., Short, J.W., Esler, D., Bodkin, J.L., Ballachey, B.E. & Irons, D.B. (2003) Long-term ecosystem response to the Exxon Valdez oil spill. *Science*, **302**, 2082-2086.

R Core Team (2013) *R: A language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, Austria.

Ramírez, F., Afán, I., Hobson, K.A., Bertellotti, M., Blanco, G. & Forero, M.G. (2014) Natural and anthropogenic factors affecting the feeding ecology of a top marine predator, the Magellanic penguin. *Ecosphere*, **5**, art38.

Raymond, B., Lea, M.-A., Patterson, T., Andrews-Goff, V., Sharples, R., Charrassin, J.-B., Cottin, M., Emmerson, L., Gales, N., Gales, R., Goldsworthy, S.D., Harcourt, R., Kato, A., Kirkwood, R., Lawton, K., Ropert-Coudert, Y., Southwell, C., van den Hoff, J., Wienecke, B., Woehler, E.J., Wotherspoon, S. & Hindell, M.A. (2014) Important marine habitat off east Antarctica revealed by two decades of multi-species predator tracking. *Ecography*, **38**, 121-129.

Ropert-Coudert, Y. & Wilson, R.P. (2005) Trends and perspectives in animal-attached remote sensing. *Frontiers in Ecology and the Environment*, **3**, 437-444.

Ruoppolo, V., Vanstreels, R.E.T., Woehler, E.J., Heredia, S.A.R., Adornes, A.C., da Silva-Filho, R.P., Matus, R., Poleschi, C., Griot, K., Kolesnikovas, C.K.M. & Serafini, P. (2012) Survival and movements of Magellanic penguins rehabilitated from oil fouling along the coast of South America, 2000-2010. *Marine Pollution Bulletin*, **64**, 1309-1317.

Scales, K.L., Miller, P.I., Hawkes, L.A., Ingram, S.N., Sims, D.W., Votier, S.C. & Punt, A. (2014) On the Front Line: frontal zones as priority at-sea conservation areas for mobile marine vertebrates. *Journal of Applied Ecology*, **51**, 1575-1583.

Suárez, N., Retana, M.V. & Yorio, P. (2012) Spatial patterns in the use of foraging areas and its relationship with prey resources in the threatened Olrog's Gull (*Larus atlanticus*). *Journal of Ornithology*, **153**, 861-871.

Votier, S.C., Bearhop, S., Witt, M.J., Inger, R., Thompson, D. & Newton, J. (2010) Individual responses of seabirds to commercial fisheries revealed using GPS tracking, stable isotopes and vessel monitoring systems. *Journal of Applied Ecology*, **47**, 487-497.

Welch, H., Pressey, R.L., Heron, S.F., Ceccarelli, D.M. & Hobday, A.J. (2015) Regimes of chlorophyll-a in the Coral Sea: implications for evaluating adequacy of marine protected areas. *Ecography*, **38**, 1-16.

Wilson, R.P., Quintana, F. & Hobson, V.J. (2012) Construction of energy landscapes can clarify the movement and distribution of foraging animals. *Proceedings of the Royal Society B*, **279**, 975-980.

Wilson, R.P., Scolaro, J.A., Grémillet, D., Kierspel, M.A.M., Laurenti, S., Upton, J., Gallelli, H., Quintana, F., Frere, E.,

Müller, G., Straten, M.T. & Zimmer, I. (2005) How do magellanic penguins cope with variability in their access to prey? *Ecological Monographs*, **75**, 379-401.

Yorio, P., Frere, E., Gandini, P. & Harris, G. (1998) *Atlas de la distribución reproductiva de aves marinas en el litoral patagónico argentino*. Fundación Patagonia Natural, Puerto Madryn.

Supplementary Material

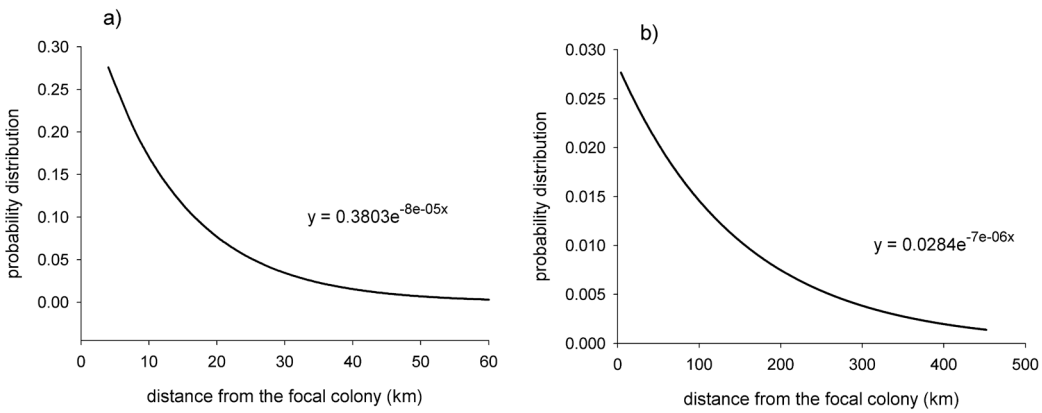

Figure S1. Probability distributions for inshore (a) and offshore (b) feeders extracted from previous tracking studies in the study area.

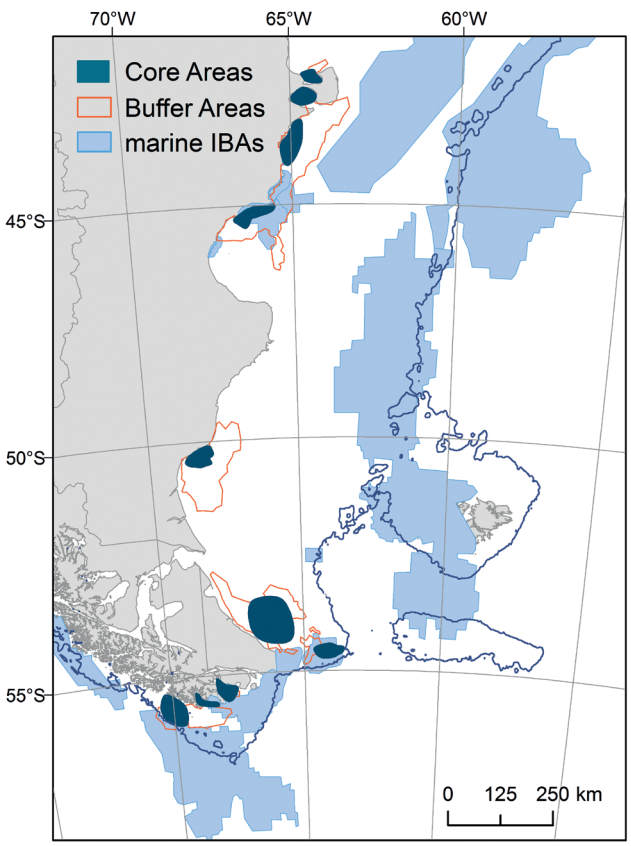

Figure S2. Projected at-sea distribution for the 14 species considered, classified into inshore and offshore feeders.

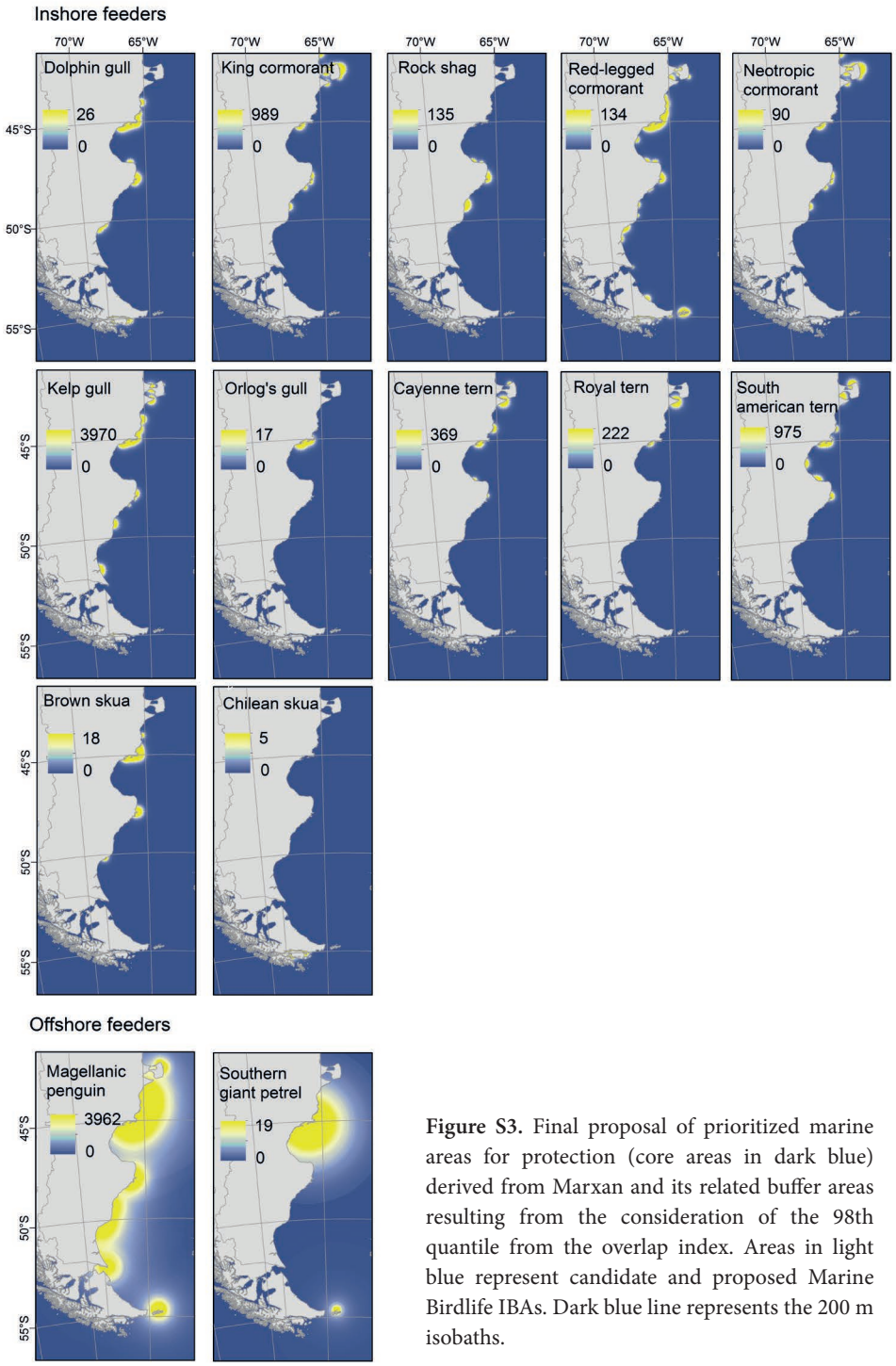

Figure S3. Final proposal of prioritized marine areas for protection (core areas in dark blue) derived from Marxan and its related buffer areas resulting from the consideration of the 98th quantile from the overlap index. Areas in light blue represent candidate and proposed Marine Birdlife IBAs. Dark blue line represents the 200 m isobaths.

DISCUSSION

Seabirds have adapted to essentially all latitudes on the earth, spending on average more than 80% of their time in the ocean. Obtaining the necessary food resources for survival and reproduction in this highly complex, dynamic and heterogeneous environment constitute a severe challenge, and has thereby played an important role in shaping the behaviour, ecology and life-history traits of seabirds (Schreiber, E.A. & J. Burger, 2001). As marine predators, seabirds are constrained by the distribution and dynamics of their prey, and consequently, are greatly influenced by the oceanographic conditions and climate regimes controlling marine productivity (Hunt Jr, G. & D. Schneider, 1987; Oro, D., 2014; Parmesan, C., 2006; Ramírez, F. et al., 2016).

Over the last decades, many studies have addressed the role of environmental variability in shaping seabirds' life-history traits (Lewison, R. et al., 2012; Louzao, M. et al., 2012a; Weimerskirch, H. et al., 2012; White, T.C.R., 2008). Specifically, these studies have provided great insights into the environmental determinants of seabirds' distributions and foraging strategies. However, few studies have deepened on the role played by environmental changes at fine-enough spatial and temporal scales in our understanding of movement patters and long-term responses to environmental variability (Paiva, V.H. et al., 2013; Pinaud, D. & H. Weimerskirch, 2005). Within this context, in this thesis we have explored how seabirds respond to spatio-temporal variability in oceanographic conditions by changing their foraging strategies (Chapters II, IV and V) and life history traits such as breeding phenology and reproductive success (Chapters II and V), while highlighting the key role of environmental variability in conservation and management (Chapters I and VI). To achieve these overall goals, we have benefited from recent technological innovations. Firstly, satellite remote sensing data provide nowadays readily accessible information at sufficiently large spatial and ecologically relevant time scales (Hunsaker, C.T. et al., 2013). This is particularly important for long-lived organisms which move over extensive areas such as seabirds. Secondly, the advent of small, reliable devices that can track animal movements at a level of detail unthinkable until recently has led to address and respond new questions regarding movement ecology (Hays, G.C. et al., 2016). When possible, we have combined both techniques to explore how environmental variability affects seabirds' ecology and behaviour.

» Facing changes in environmental conditions

Seabirds constitute a good study model to investigate the adaptation of long-lived organisms to extreme and highly variable environments. Ocean variability have modulated seabirds' life-history traits during millennia (Ricklefs, R.E., 1990; Weimerkirch, H., 2002), but human activities such as fisheries and pollution are threatening the world's marine ecosystems in an unprecedented way, causing changes in species abundance and distribution that alter ecosystem structure, function and resilience (Burrows, M.T. et al., 2014; Paleczny, M. et al., 2015). If we want to understand if seabirds are able to cope with the consequences of climate change, we first need to identify the factors affecting seabird distribution, foraging strategies and life-history traits (Grémillet, D. & T. Boulinier, 2009).

In the introductory Chapter I, we attempt to explore the spatial distribution of climate and human impacts on the world's oceans, with a particular focus on those areas holding most of the marine biodiversity. We have generated a cumulative impact index that accounts for changes in sea surface temperature, marine productivity and ocean currents over the last three decades. This index reveals the uneven distribution of climate driven environmental changes in oceans. Global areas of exceptional biodiversity coincide with severely impacted areas by raising sea surface temperature and decreasing primary productivity, along with higher rates of fishing pressure. Remarkably, areas of special concern are the sea around the Australian continent, the western Mediterranean and the southern Atlantic around the Argentinean Patagonian, where most of our works on seabirds have been conducted. Our results agree with other previous studies that have stated the unevenly spatially distribution of increasing water temperature (Hansen, J. et al., 2006; Winton, M. et al., 2013) and global chlorophyll-a (Boyce, D.G. et al., 2014). However, the novelty and main contribution of our work is the combination of stressors derived from fishery and environmental data along with biodiversity information to create a sort of index, as the ones proposed in recent works by Halpern (2008) and Maxwell (2013), that may be used to identify areas of highest conservation priority within our marine world heritage.

One important limitation affecting this work and when modelling spatial distribution of shearwaters in Chapter IV and Magellanic penguins in Chapter V is the availability of information on the spatial distribution of fishing effort at high spatial resolution. As has been evidenced (Scales, K.L. et al., 2016), the spatial resolution of data layers are key in modelling the determinants of habitat selection. But first high-resolution map of fishing intensity covering all EU waters are becoming available only recently. Recent imposed ship control regulation systems, as Vessel Monitoring System (VMS) and Automatic Identification System (AIS) (Natale, F. et al., 2015; Witt, M.J. & B.J. Godley, 2007), compulsory in the European Union from 2014, may provide detailed information on the vessel tracks. In Chapters IV and V, we have solved this constraint by generating a synoptic index of fishery effort at the resolution required from bibliography and data coming from fishing ports.

» Environmental drivers of breeding phenology and optimal decision-making

Chapter I evidences changes in oceanographic conditions over the last decades, especially since 1980, as a result of climate warming. This period is coincident with the beginning of satellite oceanography and so there is an important record of satellite observations about climate variables and their evolution (García-Soto, C. et al., 2012). This long-term environmental information, when used together with long time-series of biological data, becomes a powerful tool to evaluate responses of seabirds to contrasting environmental conditions (Oro, D., 2014; Ramírez, F. et al., 2016; Reed, T.E. et al., 2009). However, investigating the role of trends and patterns in environmental conditions as determinants of seabirds' life-history traits requires the selection of ecologically relevant spatio-temporal scales.

Evolutive pressures have shaped the long-term average of annual optima breeding time, selecting strategies that succeed reasonably well in most years. Successful reproduction implies a future forecast of resource availability, in response to predictable patterns of environmental features (Mackas, D.L. et al., 2012; McNamara, J.M. et al., 2011). In this sense, in temperate and polar climates, and especially in terrestrial ecosystems, many studies have proved that breeding phenology has evolved so as to couple reproductive timing and the annual peak of prey abundance (McNamara, J.M. et al., 2011; Visser, M.E. & C. Both, 2005). In marine ecosystems, due to the difficulty in obtaining direct measures or prey distribution, correlations with proxies of marine productivity have been often used. For example, correlations have been found between breeding phenology of some seabirds species and large-scale climate indexes such as North Atlantic Oscillation (NAO) or the Southern Annular Mode (SAM) in the case of migratory seabirds (Durant, J.M. et al., 2004; Frederiksen, M. et al., 2004), or with local conditions such as sea surface temperature values for resident species (Brommer, J.E. et al., 2008). In these latter species, most previous studies correlated phenological timing with environmental variables extracted from the species' foraging ranges and at different time-lags (from weeks to months) before the breeding onset. However, in the open and dynamic marine environment, biomass drifts both temporally and spatially as energy flows up through the food change. Extremely fine temporal information on oceanographic features extracted from dynamic areas that account for the movement of water masses (i.e. ocean currents) are necessary, therefore, to properly investigate the ability of species for coupling phenological processes with productivity patterns.

In Chapter II, we investigated the phenological responses of a marine predator, the Australian Little penguin, to the environmental variability at different spatio-temporal scales. Here, we demonstrate that productivity patterns in areas beyond foraging ranges and including water masses largely connected with foraging grounds through ocean circulation determine the reproductive timing in one population of this inshore seabird. Sea surface temperature has been identified as a factor triggering reproduction by many

other marine studies, from zooplankton and fishes to marine predators (Frederiksen, M. et al., 2004; Greve, W. et al., 2001; Hipfner, J.M., 2008; Sidhu, L.A. et al., 2012). Our work agrees with this previous research by pointing out the potential role of sea surface temperature as a local trigger for the onset of reproduction.

» Environmental, biological and anthropogenic drivers of the at-sea distribution of seabirds

As stated in the former sections, seabirds depend heavily on the distribution of resources. Furthermore, they are undeniably the most mobile of all marine predators. Tracking studies based on Global Positioning System (GPS) data of shearwaters (Chapters III and IV), and in penguins predicted distribution (Chapter V) aim to provide deeper insights into the study of the complex drivers of seabird distribution and foraging movements. These works provide an overall picture of the exploitation of three different marine environments, and try to unravel the role of main factors (oceanographic conditions, fishing activities and biological interactions) in the selection of foraging habitats by seabirds.

Summarizing the main findings of these chapters, we found that all species studied forage in shallow shelf-productive waters close to their breeding grounds. Foraging areas match with historical, highly predictable productive areas in space and time (Chapters IV and V). Sea surface temperature and chlorophyll-a offered a clear predictive performance in characterising foraging destinations, as shown in previous research (Catry, T. et al., 2013; Grémillet, D. et al., 2008; Ramos, J.A. et al., 2013). Foraging areas also reflect the physical oceanographic features driving prey distribution (Chapter V), affecting the reproductive output, and ultimately, population dynamics. Unlike terrestrial habitats, characterizing foraging habitats and factors promoting foraging decisions in marine habitats present the additional difficulty of incorporating the rapid environmental changes occurring in the ocean in both space and time. In this sense, recent works have highlighted the role of dynamic features as thermal fronts for identifying foraging hotspots of pelagic species (Scales, K. L. et al., 2014), although we have obtained little explanatory power when trying to associate key marine areas of offshore feeders with sea fronts in Chapter V. In line with the integration of dynamic variables in foraging habitat selection, in the study of searching movements of seabirds is important considering not only the aquatic fraction of the environment, but also forcing dynamic factors constraining individual decision-making, such as winds (Amélineau, F. et al., 2014; Louzao, M. et al., 2014; Weimerskirch, H. et al., 2000). Furthermore, movement strategies might be examined in relation to the environment that is being traversed (Shepard, E.L.C. et al., 2013). This was the objective of Chapter III, where we explore the role of oceanic winds and productivity patterns in driving foraging destinations from Balearic shearwaters' breeding sites.

Previous studies alert about the lack of precision of data obtained by satellite imagery regarding wind data due to the coarse spatial and temporal resolution compared with GPS bird data (Amélineau, F. et al., 2014; Raymond, B. et al., 2010; Scales, K.L. et al., 2016). Following this recommendation, we employed high spatial and temporal resolution meteorological models to generate seascapes of wind fields, with the aim of calculating energetic costs of moving both to selected and discarded destinies. Our results suggest that environmental conditions affecting flight performance change daily, influencing foraging decisions at certain times, although proximity to foraging ranges, aided by wind facilitation, explains the main foraging destinies. One interesting point of further research is the real rate of energy expenditure during foraging trips. Recently, most GPS devices incorporate also accelerometers, which allow the direct conversion of de overall dynamic body acceleration into a measure of the rate at which an animal expends energy during a specific life-history event (Amélineau, F. et al., 2014). This is of particular concern during reproductive time, the energetically most demanding stage, offering new study possibilities.

Biotic interactions affecting foraging strategies have been addressed, on the one hand, comparing foraging distribution of related species breeding in sympatry (in Scopoli's and Cory's shearwaters, Chapter IV) and, on the other hand, considering the effects on foraging distribution of interactions among conspecifics (in Magellanic penguins, Chapter V). Ecological theory predicts that animals with similar feeding strategies should not coexist without segregating either in space, time or diet, and recent works have highlighted that spatial segregation contributes to minimize intra-specific competition between adjacent colonies (Cecere, J.G. et al., 2015; Ceia, F.R. et al., 2015; Wakefield, E.D. et al., 2013).

Few distribution models explicitly include biotic interactions (Cunningham, H.R. et al., 2009), such as the presence of conspecific, as descriptors, thus hampering the relative importance of biotic predictors (Elith, J. & J.R. Leathwick, 2009). In Chapter V we modelled the spatial distribution of Magellanic penguins combining environmental and biological variables, as the predicted Magellanic penguins abundance at-sea. At an intraspecific level, we have found that Magellanic penguins forage in waters with moderate abundances of conspecifics, likely as a trade-off between reducing competition for food with conspecifics and not losing the benefits of flock-foraging. In Chapter IV, interactions were addressed at an interspecific level, resulting in a broadly overlap of foraging areas of two species of shearwaters during the incubation period but showing a spatial segregation during chick-rearing.

Anthropogenic activities like fisheries might affect seabird distribution in opposite ways. They may locally enhance prey availability for seabirds by discards, which represent highly abundant and predictable food resources (Bartumeus, F. et al., 2010; Bugoni, L. et al., 2009), but also entail competition with seabirds for common target species, as is the case of the anchovy for the Magellanic penguin (Skewgar, E. et al., 2007). We

have shown here that the distribution of fisheries largely overlaps with the foraging distribution of shearwaters and Magellanic penguins (Chapters IV and V). In Chapter V, our results indicate that fisheries are negatively affecting the consumption of preys by penguins, whereas in Chapter IV fishing activity was proven to have a relatively high explanatory power for predicting the foraging distribution of two species of shearwaters during the incubation period.

» Relevance of research results in the spatial management planning for seabirds

The oceans are rapidly changing as a result of human activities and global climate change, and seabird populations are declining as a result (Paleczny, M. et al., 2015). To date, a large body of research has recognized that seabirds are excellent surrogates for biodiversity hotspots in marine spatial planning and potential indicators of the health of the marine environment both regionally and globally (Lascelles, B.G. et al., 2016; Le Corre, M. et al., 2012; Piatt, I.J.F. et al., 2007; Ronconi, R.A. et al., 2012). The concluding Chapter VI pursues the important goal of the spatial management of seabirds and marine habitats, trying to encompass both the species and their environment in marine planning (Turner, W. et al., 2015). Analytical approaches developed in previous chapters have been used in Chapter VI to define marine protected areas integrating biological, socio-economic and environmental factors. Even though it is best to employ tracking data as unparalleled information on the distribution of marine birds, there are also known shortcomings in biotelemetry monitoring of seabirds, such as between-colony differences in habitat use strategies, tracking deployments constrained by logistic (e.g. seasonal accessibility to breeding sites), and huge costs of devices (Raymond, B. et al., 2014). These reasons prompted us to work with simulated data from breeding pair censuses to infer seabird distribution at-sea (Grecian, W.J. et al., 2012). Putting our results in a conservation context, we verify that the identification of key marine areas for conservation needs from the understanding of the physical features that drives the formation and persistence of prey availability (Scales, Kylie L. et al., 2014), and requires of dynamic boundaries and extensive buffers (Hyrenbach, K.D. et al., 2000) potentially influencing the core areas. Our work also concurs with recent works that highlight a shift towards dynamic ocean management (Game, E.T. et al., 2009; Maxwell, S.M. et al., 2015), since stationary boundaries are not the most effective marine management strategy to protect mobile marine features and animals. Innovation technologies and analytical approaches will provide new opportunities to investigate the factors that determine reproductive and movement patterns of seabirds regarding their dynamic environment. Conservation managements can benefit in turn from all new ecological insights.

CONCLUSIONS

1 Climate and human driven environmental changes have greatly affected marine ecosystems in the last decades. We detected local to regional changes in sea surface temperature, productivity and ocean currents in all oceans, with most significant changes occurring in polar and tropical regions. Ocean areas with higher impact did overlap with areas of enhanced marine biodiversity and fishing pressure.

2 The environmental variability along with the complexity of open marine systems cannot be neglected when investigating the link between marine animals and their environment. The long-term series of environmental and biological data we have used revealed clear patterns on the role of environmental variability as a determinant of ecological processes.

3 Inshore seabirds, such as the Australian little penguins, may set the optimal-time window for reproduction through the use of local cues such as sea surface temperature to inform on marine productivity patterns that emerge from a regional and dynamic scale. This regional scale integrates temporal and spatial changing productivity patterns influencing foraging habitat. This study showed the importance of selecting appropriate temporal and spatial scales for investigating how environmental variability affects life-history strategies. Large-scale productivity patterns might be also important determinants of the foraging strategies of offshore feeders, such as shearwaters, which main foraging grounds were largely restricted to productive continental shelf areas nearby the breeding colony.

4 Energy constraints imposed by central-place foraging during breeding might be also an important factor affecting foraging strategies of seabirds. This constrain was particularly clear for offshore-feeders such as Cory, Scopoli's and Balearic shearwaters that forage over huge areas but must return to land periodically during breeding. In these species, favourable winds might largely determine the heading direction during the outward stages of their foraging trips. Indeed, we showed that windscapes played a major role in determining heading decisions by Balearic shearwaters.

5 Intra and interspecific competition for limited resources were also revealed as important drivers of seabirds' foraging strategies. For instance, the sympatric Cory and Scopoli's shearwaters tended to segregate their foraging areas during the high energy demanding period of the chick rearing, whereas a high degree of overlap occurred during incubation. Further, we showed that the competition for resources among conspecifics was also an important driver of the at-sea distribution of the Argentinean Magellanic penguin during the breeding period. In this species, individuals tended to avoid areas with high densities of conspecifics.

6 Human activities affecting resources availability such as fisheries, affected Cory and Scopoli's shearwater foraging distribution and Magellanic penguins diet during breeding. We inferred a negative pressure for Magellanic penguins population over time by consumption of the same target species, i.e. the anchovy.

7 Climate and human factors impacting wild populations must be considered together for conservation and management decisions. Conservation planning must take into account the heterogeneity in space and time of animal distribution, marine features driving the abundance and dynamic of dietary resources as well as impacts of anthropogenic and economic activities both in the distribution of seabirds or in the distribution of their preys.

RESUM EN CATALÀ

RESUM

Els ocells marins han evolucionat en un ambient molt dinàmic i sense fronteres fàcilment apreciables, l'oceà. Com a predadors meso-superiors, els ocells marins estan molt influenciats per les condicions oceanogràfiques responsables de la productivitat marina, de la que es deriva la distribució de les seves preses. Per tant, el comportament dels ocells marins, i en darrera instància, els seus trets de vida, es troben molt influenciats per la dinàmica de les condicions marines. No obstant, en l'actualitat, les condicions oceanogràfiques estan canviant a un ritme sense precedents, degut a l'escalfament global i a l'explotació dels recursos pesquers per part nostre, provocant greus impactes sobre els ecosistemes marins. Com a conseqüència de l'acceleració d'aquests canvis, els ocells marins han resultat particularment amenaçats. És per això, que en aquesta tesi, investigo les respostes ecològiques dels ocells marins, en termes d'estratègies d'alimentació i comportament reproductor, a la variabilitat espaciotemporal en les condicions ambientals imposades pels oceans i exacerbades per factors climàtics i antròpics. En particular, (i) identifiquem els factors estressants climàtics i antròpics que estan impactant en el món dels oceans, (ii) investiguem l'escala apropiada a la que els ocells marins interaccionen amb el seu ambient, (iii) avaluem com els ocells marins responen a la variabilitat oceanogràfiques canviant les seves estratègies d'alimentació i reproducció i (iv) proposem una eina integradora per al disseny de reserves marines, amb l'objectiu de protegir tant els ocells marins com el seu ambient.

Els objectius d'aquesta tesi s'han acomplert mitjançant procediments dels camps de la teledetecció per satèl·lit i el seguiment remot d'animals. Els nostres resultats confirmen els canvis sense precedents experimentats pels oceans a les darreres dècades. A més, hem aprofundit en la descripció de la distribució heterogènia d'aquests canvies provocats tant pel clima com per activitats antròpiques com la pesca. Quan vam investigar els vincles entre aquesta variabilitat ambiental i el comportament dels ocells marins, vam trobar que la dinàmica de processos oceanogràfics com les corrents marines, van ser factors claus per a la determinació de l'escala a la qual els ocells marins interaccionen amb el seu ambient. Les característiques marines responsables de la distribució espaciotemporal de les preses (per ex., la temperatura superficial del mar, la clorofil·la-a, els fronts marins o les àrees productivament persistents), juntament amb la indústria pesquera juguen un paper fonamental en la distribució de les àrees d'alimentació dels ocells marins. No obstant, les estratègies d'alimentació dels ocells marins estan molt constretes per les limitacions imposades per la necessitat de retornar freqüentment al niu durant la cria, i per factors dinàmics com els vents, que influencien les decisions individuals sobre les direccions a prendre durant els viatges d'alimentació. La competència intra i

interespecífica pels recursos també modula les distribucions durant l'alimentació, amb comportaments per evitar els individus de la mateixa espècie o mitjançant la segregació d'àrees d'alimentació entre espècies simpàtriques durant les èpoques adequades. En general, hem proporcionat una visió global dels processos ambientals que afecten als ocells marins. Creiem que aquesta informació podria ser extremadament útil per dissenyar estratègies de gestió i conservació adequades. En aquest sentit proposem finalment un marc de treball adaptable per a la delimitació de reserves marines que maximitzin els objectius de conservació per als ocells marins, a la vegada que considera les activitats humanes, i els factors ambientals i biològics responsables del comportament dels ocells marins, i de manera molt important, el dinamisme ambiental inherent als sistemes marins.

Paraules clau: ocells marins, estratègies d'alimentació, característiques oceanogràfiques, seguiment remot, clorofil·la-a, temperatura superficial del mar, escales.

INTRODUCCIÓ

» Canvis recents en els ecosistemes marins

Els oceans cobreixen al voltant del 70% de la superfície de la Terra i juguen un important paper en la regulació del clima del planeta. Els oceans són peces clau en la transferència d'energia calòrica cap a l'atmosfera, a més d'actuar com a magatzems de grans quantitats de carbó, suavitzant així l'escalfament de la superfície de la Terra (Wu, L. et al., 2012). Els oceans també ens proveeixen d'una àmplia varietat de serveis, entre els que s'inclou el que sigui una font de provisió d'aliments per als humans. No obstant, i particularment durant les darreres dècades, les activitats humanes han sigut la causa de profundes alteracions dels ecosistemes marins (Halpern, B.S. et al., 2015; Halpern, B.S. et al., 2008). En particular, els canvis ambientals causats tant per factors ambientals com antròpics, han suposat nous desafiaments per aquests ecosistemes.

Factors climàtics

L'augment exponencial dels gasos d'efecte hivernacle a l'atmosfera ha sigut el principal factor responsable de l'escalfament global i com a conseqüència, les capes superficials dels oceans han absorbit gran part d'aquest calor extra, augmentant la seva temperatura mitjana global en 0.2ºC per dècada durant els darrers 30 anys (Hansen, J. et al., 2006; Hoegh-Guldberg, O. & J.F. Bruno, 2010). L'escalfament dels oceans ha alterat tant els paràmetres físics com la dinàmica d'aquest medi, provocant una major estratificació de les capes més superficials de l'oceà (Shackell, N.L. et al., 2009), afectant a la disponibilitat d'oxigen i de nutrients, i per tant, a la producció primària. Aquests patrons estan correlacionats amb canvis en la circulació oceànica que afecten a zones claus d'elevada productivitat com són els afloraments costers mundials (Sydeman, W.J. et al., 2014). Els canvis en aquests patrons poden tenir conseqüències en termes de dinàmica de poblacions, supervivència i reclutament de diverses poblacions d'espècies marines, com el plàncton i els peixos (Fossette, S. et al., 2015). Com a conseqüència, la productivitat marina ha experimentat increments i disminucions de manera desigual per tot el globus, però sense un patró general i significatiu (Behrenfeld, M.J. et al., 2006; Keeling, R.F. et al., 2010).

Com a resultat, els ecosistemes marins s'han vist afectats en la seva estructura (distribució de la biodiversitat; Cheung, W.W.L. et al., 2013; Dulvy, N.K. et al., 2008; García Molinos, J. et al., 2015) i en les seves funcions (cicles dels nutrients; Boyce, D.G. et al., 2014; Doney, S.C., 2010). El canvi climàtic pertorba la productivitat dels ecosistemes marins i les rutes tròfiques que van des dels productors primaris fins als nivells més alts

de la xarxa tròfica, propagant les alteracions a través de tot l'ecosistema en ambdues direccions, tant des dels nivells més baixos cap a dalt, com des dels nivells més alts de la cadena cap als més baixos (Grémillet, D. & T. Boulinier, 2009; Paiva, V.H. et al., 2013).

Factors humans

Juntament amb el canvi climàtic, d'altres activitats humanes com la pesca poden ser també causa d'alteracions en les xarxes tròfiques dels ecosistemes marins. Des de 1950, quan comença el registre de les activitats pesqueres (Pulvenis, J.-F., 2014), la intensitat de la pesca a nivell global ha continuat creixent de manera contínua, amb un augment mitjà de 10 vegades, encara que les captures hagin disminuït poc a poc des de finals de 1980 (Pauly, D. et al., 2002; Watson, R.A. et al., 2013). A l'actualitat, quasi el 50% de les reserves mundials de peixos han sigut exhaurits i gairebé el 30% estan sobreexplotats (Einoder, L., 2009), amb el 35% de la productivitat de la plataforma continental destinada al consum humà (Sanderson, E.W. et al., 2002). Les intenses pressions pesqueres també han modificat dràsticament el control de les xarxes tròfiques des dels esglaons més alts als més baixos dels ecosistemes marins (Shackell, N.L. et al., 2009). La sobreexplotació pesquera ha provocat canvis no només en l'abundància i la composició de les espècies (Myers, R.A. & B. Worm, 2003), sinó que també ha afectat a la persistència de les xarxes tròfiques locals, disminuint la seva capacitat de resistir a futures degradacions ambientals (Gilarranz, L.J. et al., 2016), amb greus conseqüències per al funcionament dels ecosistemes (Anderson, C.N.K. et al., 2008). A més, les activitats pesqueres poden impactar negativament inclús a les espècies sense valor comercial que accidentalment esdevenen enganxades pels aparells de pesca. Aquestes captures accidentals afecten a moltes espècies depredadores i vulnerables, com les tortugues, ocells marins o mamífers, amb nivells de mortalitat proporcionals a l'esforç de l'activitat pesquera (Lewison, R. et al., 2004).

» El depredadores marins davant els canvis en els oceans: sota el paraigües dels ocells marins

El depredadors marins, com tots els animals, requereixen aliment per tal de sobreviure i deixar descendència. Degut a la seva posició en els esglaons més alts de l'escala tròfica, els depredadors marins incorporen els processos i les interaccions tròfiques de tota la xarxa tròfica situada per sota d'ells. En conseqüència, és esperable que les alteracions provocades pel canvi climàtic a les xarxes tròfiques tinguin un profund impacte des dels nivells més baixos fins arribar a aquests organismes (Grémillet, D. & T. Boulinier, 2009; Paiva, V.H. et al., 2013). És indiscutible que les interaccions negatives amb les pesqueries, com les captures accidentals, es troben entre els actuals perills que aguaiten els depredadors marins, i especialment als ocells marins (Phillips, R.A., 2013). Per tot això, els depredadors marins com els ocells, són un excel·lent model integrador per a l'estudi dels impactes que els factors climàtics i antròpics provoquen en els ambients marins.

Els ocells marins són importants depredadors apicals dintre de les xarxes tròfiques dels ecosistemes marins. Com a reflex de les condicions subjacents en els sistemes oceànics, els depredadors marins, i particularment els ocells marins, juguen un paper primordial en l'avaluació de la salut d'aquests ecosistemes (Croxall, J.P. et al., 2012; Sydeman, W.J. et al., 2015): aquests grups d'aus es distribueixen a nivell mundial, i són relativament fàcils d'observar; operen a les posicions més altes de les xarxes tròfiques, i probablement integren els processos ecològics que tenen lloc al llarg de tots els nivells tròfics (Grémillet, D. & A. Charmantier, 2010). Per aquesta raó poden actual com a sentinelles, avisant de manera precoç de les primeres senyals sobre canvis en l'ambient marí i alertant en el cas d'impactes desconeguts de pol·lució o problemes de subministrament d'aliments (Frederiksen, M. et al., 2007; Furness, R.W. & K.C. Camphuysen, 1997).

Els ocells marins són un grup excepcionalment ben estudiat comparat amb d'altres grups de depredadors marins. Dècades d'investigació han posat de manifest el rol dels ocells marins en els processos ecològics dels ambients marins (Schreiber, E.A. & J. Burger, 2001). Però en els darrers anys, nous avenços, tant conceptuals com tecnològics, han revolucionat la nostra capacitat remota d'observació tant de l'ambient oceanogràfic (dades de teledetecció, Requadre 1) com dels ocells marins (dispositius de posicionament). Això ha suposat un gran avanç en el coneixement de les relacions entre la variabilitat espaciotemporal de l'ambient i les respostes comportamentals cap a elles de les poblacions d'ocells marins, cobrint així un dels buits en la recerca d'aquest grup d'ocells (Lewison, R. et al., 2012).

» El mar: un ambient complex, dinàmic i sense fronteres

Als sistemes oceànics, els ocells marins interactuen amb un ambient sempre canviant, ampli i tridimensional (Croxall, J.P., 1987). En aquest hàbitat altament complex, els ocells marins han de cercar activament les zones discontínues i a més impredictibles on es troben les seves preses (Weimerskirch, H. et al., 2005). Els processos físics que provoquen l'agregació de les preses no són estàtics, i els ocells marins han d'adaptar-se als continus canvis en l'estructura física dels oceans (Shealer, D.A. et al., 2002). A més, els factors que determinen la distribució i l'abundància tant de preses com de depredadors són dependents de l'escala, i abasten des de patrons de circulació a escala global fins a remolins a la meso-escala o afloraments a escala local (Bertrand, A. et al., 2014; Hunt Jr, G. & D. Schneider, 1987). Tot això sense oblidar els factors ecològics que també intervenen, com la competència a nivell intra o interespecífica (Ashmole, N.P. & M.J. Ashmole, 1967; Forero, M.G. et al., 2004). Per tant, la formació i propagació dels hàbitats d'alimentació es dóna en funció de complexos i dinàmics processos oceanogràfics. En conseqüència, els hàbitats en el context marí no sempre es refereixen a localitzacions geogràfiques fixes, sinó que preferentment fan al·lusió a àrees dinàmiques que poden variar en les seves característiques mentre l'energia flueix des dels nivells tròfics més

baixos fins els superior a través de les xarxes tròfiques (Boersma, P.D. et al., 2009; Scales, Kylie L. et al., 2014). L'estudi de les interaccions ecològiques que tenen lloc als oceans té la dificultat afegida no només de la complexitat de l'hàbitat, sinó també de la inherent dificultat de prendre mesures en aquests ambients marins (Hoegh-Guldberg, O. & J.F. Bruno, 2010; Stommel, H., 1963).

El coneixement de com organismes particulars es comporten i responen al seu ambient es veu també obstaculitzat per la necessitat de delimitar un àrea d'estudi en aquest ambient sense fronteres. En particular, les relacions entre el comportament d'alimentació dels depredadors marins i les propietats bio-físiques de l'ambient oceànic requereix de l'avaluació de l'escala correcta, tant espacial com temporal, on es donen aquestes relaciones (Adrian, R. et al., 2012; Bradshaw, C. et al., 2002). A més, la influència de les propietats físiques de la superfície dels oceans en el comportament dels predadors superiors no són del tot conegudes, degut en gran part al desconeixement dels intervals de temps entre diferents processos, com els que van des de la caracterització de la productivitat a les aigües superficials, a la ocurrència dels organismes dels nivells tròfics inferiors i a les interaccions predador-presa (Grémillet, D. et al., 2008; Oro, D., 2014).

Però l'estudi de les relacions entre els ocells marins i el seu ambient no presenta només limitacions metodològiques o de disponibilitat de dades de la suficient resolució espacial i temporal (Ramírez, F. et al., 2016). En aquesta relació entre els fenòmens físics i biològics l'observador imposa el seu particular biaix en la percepció del sistema. Per entendre qüestions sobre com els fenòmens físics determinen els fenòmens biològics i l'adaptació dels organismes, aquestes deuen ser abordades en una escala espaciotemporal adequada, ja que podem trobar que diferents patrons emergeixen a diferentes escales d'investigació (Wiens, J.A., 1989).

» Noves tècniques promouen l'avanç de la ciència

L'oceà des de l'espai: la teledetecció des de satèl·lit

Els sistemes de teledetecció per satèl·lit, com les plataformes amb sensors específics per a l'observació dels oceans, tenen la capacitat única de mostrejar de manera detallada la distribució espacial de les variables oceanogràfiques des de centenars a milers de kilòmetres per sobre tot el globus. Aquestes mesures repetides regularment durant les darreres tres dècades, els hi confereixen un paper clau en la mesura tant espacial com temporal de la variabilitat de l'oceà (Rose, R.A. et al., 2015; Yang, J. et al., 2013).

Una limitació molt important en els estudis d'ecologia tròfica dels ocells marins és la falta de dades directes sobre disponibilitat de preses que coincideixin amb l'escala adequada espaciotemporal de distribució dels ocells marines (Scales, K. L. et al., 2014). Els estudis que es basen en l'abundància i distribució espacial de preses mitjançant tècniques com les trampes de plàncton, els transsectes en vaixell o les tècniques d'eco-

sondeig (Grémillet, D. et al., 2008; Moseley, C. et al., 2012; Tew Kai, E. et al., 2013) són minoritaris comparats amb els estudis que utilitzen aproximacions indirectes a la productivitat marina com las que ofereix la teledetecció (Catry, T. et al., 2013; Louzao, M. et al., 2012; Tremblay, Y. et al., 2009). Les imatges de satèl·lit proporcionen una base fiable per a l'estimació de les concentracions de clorofil·la-a associades al fitoplàncton de les capes més superficials, i han estat els indicadors indirectes de productivitat més pràctics i extensivament utilitzats en les darreres dècades (Behrenfeld, M.J. et al., 2006; Boyd, C. et al., 2015). No obstant, com els predadors marins habitualment s'alimenten de nivells superiors de la xarxa tròfica, les correlacions de les mesures per satèl·lit de la productivitat amb la distribució dels ocells poden portar a resultats confusos ja que pot existir un desfàs temporal entre la disponibilitat real de preses i les dades de productivitat (Grémillet, D. & T. Boulinier, 2009; Ramírez, F. et al., 2016). Les dades de satèl·lit també han esdevingut una eina molt important per monitoritzar paràmetres ambientals associats a la distribució de la biodiversitat, proporcionant una base sòlida per estimar les condicions físiques que determinen la distribució dels hàbitats d'alimentació (Boersma, P.D. et al., 2009; Cimino, M.A. et al., 2013; Turner, W. et al., 2015). Els ocells marins poden mostrar una forta afinitat a àrees amb unes propietats oceanogràfiques específiques, com a les àrees amb fronts que delimiten diferents masses d'aigua, o a les aigües costeres, caracteritzades per propietats físiques que augmenten la disponibilitat de recursos a les preses (Bost, C.A. et al., 2009; Fauchald, P., 2009). La variabilitat espacial i temporal d'aquestes propietats i formacions oceanogràfiques (temperatura superficial del mar, fronts, corrents o productivitat) poden ser caracteritzades des d'imatges instantànies en una data determinada, fins a la caracterització de tendències o persistències d'aquestes formacions oceanogràfiques mitjançant l'acumulació d'imatges de sèries temporals llargues que descriuen dècades de processos oceanogràfics (Cottin, M. et al., 2012; Grémillet, D. et al., 2008).

Perseguint rastres: el seguiment remot animal

Un pas endavant en l'estudi de l'ecologia dels ocells marins i de la variabilitat ambiental en els darrers anys és el desenvolupament de dispositius cada cop més lleugers capaços d'enregistrar els moviments animals, el seu comportament i inclús algunes variables ambientals, proporcionant així una visió integradora dels animals i el seu ambient (Hays, G.C. et al., 2016; Kays, R. et al., 2015; Ropert-Coudert, Y. & R.P. Wilson, 2005). Recentment, s'han desenvolupat una àmplia gama de dispositius de seguiment per tal d'abordar els moviments individuals, que ofereixen dades a diferentes resolucions temporals i espacials (Ponchon, A. et al., 2013).

REQUADRE: L'OCEANOGRAFIA PER SATÈL·LIT

Els sistemes de teledetecció via satèl·lit presenten la capacitat única de mostrejar de manera detallada la distribució espacial de les variables oceàniques des de centenars a milers de kilòmetres sobre tota la Terra. Les imatges de satèl·lit s'han vingut recollint de manera regular durant les darreres tres dècades, la qual cosa els hi confereix un paper clau en la mesura de la variabilitat oceànica i dels canvis al llarg del temps (Rose, R.A. et al., 2015; Yang, J. et al., 2013), si les comparem amb altres tècniques presencials de mostreig oceanogràfic. Una imatge de teledetecció, a diferència de les imatges instantànies obtingudes amb les càmeres fotogràfiques, consisteix en milions de mesures obtingudes en un curt període de temps sobre un patró regular de mostreig sobre la superfície terrestre. Els sensors de color oceànic viatge a bord de plataformes polars que potencialment poden recórrer la Terra en un sol dia, i així obtenir una cobertura de tota la superfície en uns quants dies (Robinson, I.S., 2010). És per això que les series històriques d'observacions de satèl·lit ens informen sobre la variabilitat temporal dels oceans. Els sensors emprats en la observació per satèl·lit dels oceans aprofiten diferents regions de l'espectre electromagnètic per derivar productes oceanogràfics que descriuen la superfície dels oceans. Els productes de color oceànic més coneguts (clorofil·la, partícules en suspensió i batimetria) deriven de sensor que recullin la informació de les longitud d'ona del visible i de l'infraroig proper. La regió tèrmica de l'espectre electromagnètic permet fer mesures de la temperatura superficial del mar i la regió de la longitud d'ona de les microones les utilitzen els sensors actius com els radars per a la generació de la informació de vents de superfície, altura de les ones, o corrents marines superficials o geostròfiques (Robinson, I.S., 2010). Les dades de satèl·lit han estat utilitzades des de fa més de 25 anys, però els avenços més significatius s'han produït en els darrers 10 anys. La primera plataforma operacional a llarg termini va ser el SeaWiFS (Sea-viewing Wide Field-of-view Sensor), llançat en 1997. Altres sensor previs com el CZCS (Coastal Zone Color Scanner) havien operat entre 1978 i 1986, però amb buits d'informació en les dades recollides que res a veure tenen amb la qualitat dels sensors més recents (per ex., MODIS, Moderate Resolution Imaging Spectroradiometer), que recull dades de la superfície de la Terra des de 2002. Els productes processats són cada cop més fàcilment accessibles, gràcies a les noves polítiques que promouen l'accés lliure a les imatges de satèl·lit propietat dels governs (Turner, W. et al., 2015). Cadascú dels instrument de teledetecció té una capacitat particular de mostreig amb una resolució espai-temporal, oferint productes amb diferents cobertures en espai i en temps i en combinacions temporals d'imatges. Els programes internacionals han ajudat a la difusió de l'ús de les imatges de satèl·lit, oferint imatges i productes de reanàlisi actualitzats periòdicament. Aquest és el cas del Ocean Biology Processing Group (OBPG), al que dóna suport la NASA Ocean Color Web (http://oceancolor.gsfc.nasa.gov/cms) o el principal programa europeu per a la observació i seguiment de la Terra, Copernicus, que proporciona productes i serveis per aplicacions marines (http://marine.copernicus.eu).

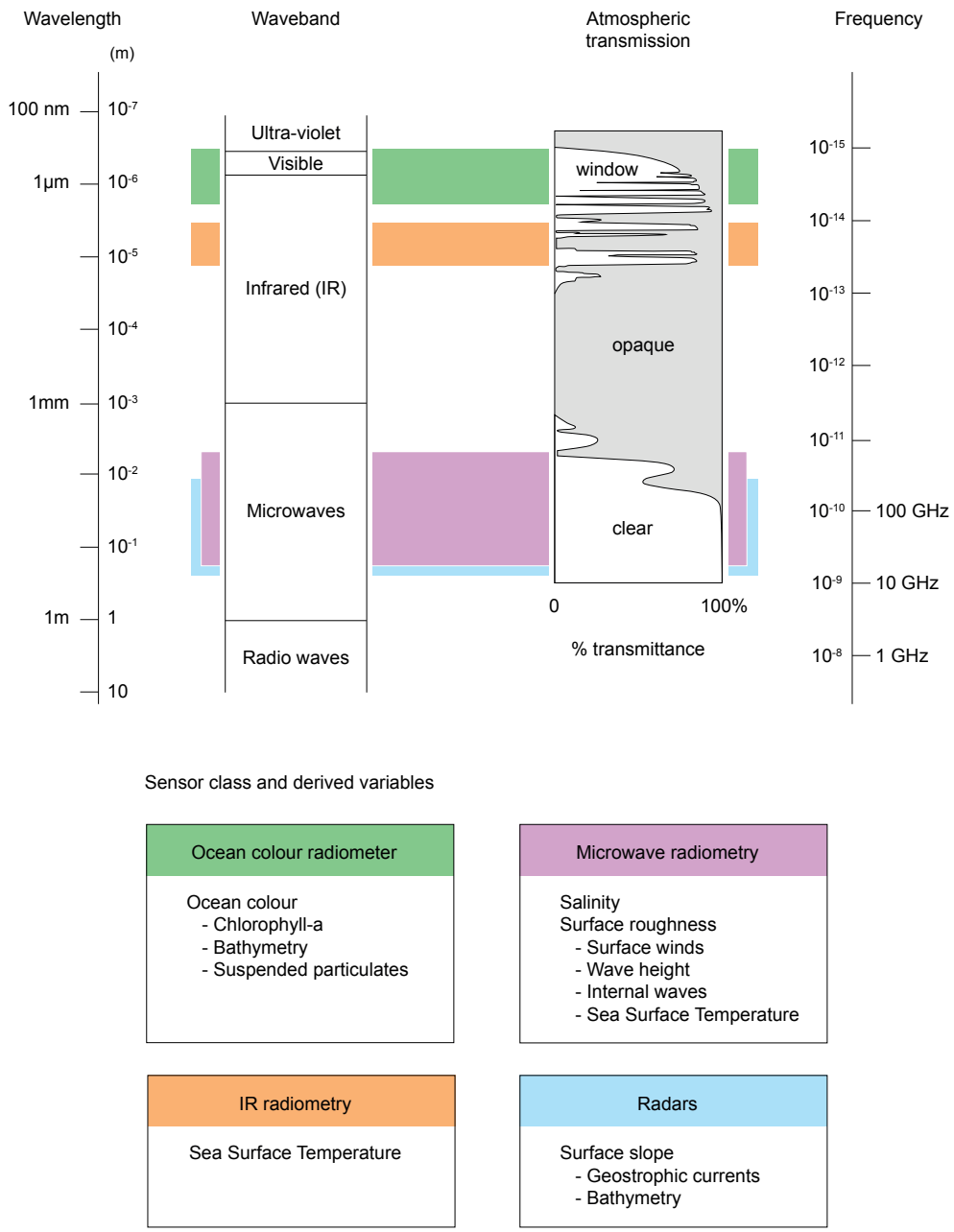

Figura 1: Esquema dels diferents sensors de teledetecció utilitzats en la oceanografia per satèl·lit, amb les aplicacions de cada sensor. La figura mostra l'espectre electromagnètic i la transmitància de l'atmosfera per a cada longitud d'ona. L'atmosfera és opaca a la majoria de l'espectre, i per tant en aquestes zones no pot ser utilitzada per la teledetecció. Però existeixen una sèrie de "finestres" que permeten el pas de la radiació i on els sensors de teledetecció poden opera. Les bandes utilitzades per les quatre classes principals de sensors utilitzats per l'observació de l'oceà es mostren en colors. (Adaptat de Robinson I.S. 2010). SST: temperatura superficial del mar.

Els estudis de seguiment de localitzacions s'han disparat en els darrers anys, revolucionant el nostre coneixement dels moviments i de la distribució al mar de les espècies marines (Hays, G.C. et al., 2016). Els estudis de biotelemetria, combinats amb les imatges per satèl·lit, ofereixen una visió integradora de les respostes dels predadors marins a la variabilitat ambiental a diferentes escales (De Monte, S. et al., 2012; González-Solís, J. et al., 2007). A través d'aquestes dades, es pot obtenir informació tan valuosa com la de les relacions intra o inter-específiques i la dinàmica de competició en l'ús de l'espai (Navarro, J. et al., 2015; Wakefield, E.D. et al., 2013), la qual cosa proporciona una informació molt valuosa per als programes de conservació (Arcos, J.M. et al., 2012).

» La variabilitat ambiental afecta a l'ecologia tròfica dels ocells marins i als seus cicles reproductius

Els estudis d'ecologia tròfica dels ocells marins s'han vist beneficiats de manera important amb l'aparició de les tecnologies de seguiment remot (Louzao, M. et al., 2012; Paiva, V.H. et al., 2010c; Quillfeldt, P. et al., 2015). Per portar a terme una cerca d'aliment de manera eficaç, els animals deuen minimitzar la despesa respecte a l'adquisició d'energia, maximitzant així la taxa neta de guany energètic. En aquest procés es veuen implicats tota una sèrie de processos que van des de l'experiència individual a la presa de decisions en relació a l'esforç que s'inverteix durant els processos de cerca d'aliment (Pyke, G.H. et al., 1977). Durant el període de reproducció, molts ocells marins necessiten tornar regularment al niu després d'alimentar-se, i per això estan espacialment restringits per la localització de les seves àrees de cria, les quals estan limitades, en última instància, per la disponibilitat de recursos tròfics. Per tal de cobrir els requeriments energètics per a la reproducció, els ocells marins han d'adaptar els seus moviments i estratègies en la cerca d'aliment a les condicions ambientals. La presa de decisions individual pot estar restringida espacialment per fenòmens oceanogràfics que facilitin que a determinades àrees les preses es puguin trobar més eficientment (per ex. remolins i fronts; Cotté, C. et al., 2007; Fauchald, P. et al., 2000) i forces impulsores del moviment com els vents (Amélineau, F. et al., 2014; Raymond, B. et al., 2010).

Està demostrat que els fenòmens oceanogràfics, que en última instància són responsables de la disponibilitat d'aliment, estan vinculats a la distribució, comportament i paràmetres reproductius dels ocells marins: color oceànic (Louzao, M. et al., 2012; Paiva, V.H. et al., 2010a), temperatura superficial del mar (Awkerman, J.A. et al., 2005; Guinet, C. et al., 1998; Sandvik, H. et al., 2008), corrents (Suthers, I.M. et al., 2011), zones frontals (Bost, C.A. et al., 2009; Scales, K. L. et al., 2014), remolins i girs (Cotté, C. et al., 2007; Hyrenbach, K.D. et al., 2006), termoclina (Pelletier, L. et al., 2012; Scott, B. et al., 2010), extensió del gel (Barbraud, C. et al.; Grémillet, D. et al., 2015), i batimetria i monts submarins (Austin, D. et al., 2006; Conners, M.G. et al., 2015; Paiva, V.H. et al., 2010b). Els predadors apicals, com els ocells marins, utilitzen activament molts d'aquests fenòmens oceanogràfics per viatjar i cercar de manera eficient els seu aliment.

La variabilitat ambiental afecta més enllà de les estratègies d'alimentació, i té conseqüències fins i tot en les estratègies de vida dels ocells marins (Ramírez, F. et al., 2016; Ricklefs, R.E., 1990; Weimerskirch, H., 2007). El clima influeix en la demografia dels ocells marins i la seva dinàmica de poblacions, generalment afectant a la disponibilitat de recursos (Jenouvrier, S. et al., 2005; Oro, D., 2014). Molts estudis han correlacionat les tendències poblacionals i els paràmetres reproductius amb la variabilitat en els factors ambientals de l'ambient marí (Descamps, S. et al., 2015; Doney, S.C., 2006; Genovart, M. et al., 2012; Russell, D.J.F. et al., 2015). Els cicles anuals del organismes van evolucionar presumptament com a resposta als patrons estacionals predictibles dels fenòmens ambientals que afavoreixen la disponibilitat d'aliments (Mackas, D.L. et al., 2012). Això és especialment cert en els climes temperats i polars, on només hi ha un curt període a l'any adequat per a la reproducció (Frederiksen, M. et al., 2004; Wassmann, P., 2011) i l'èxit reproductor depèn de l'habilitat per ajustar el moment de la reproducció als patrons estacionals de la disponibilitat d'aliments (Ramírez, F. et al., 2016). No obstant, els canvis ambientals estan probablement causant també canvis en diversos nivells de les xarxes tròfiques i a diferents velocitats, provocant un desacoblament temporal entre els diferents nivells i pertorbant les ajustades interaccions tròfiques entre els predadors i les seves preses (Durant, J.M. et al., 2005; Visser, M.E. & C. Both, 2005). Per tal d'abordar adequadament aquest tema s'ha d'avaluar quina és l'escala a la que cada espècie experimenta el seu ambient, responent així tant a la variabilitat com a la predictibilitat de l'ambient (Levin, S.A., 1992).

» Conservació dels ocells marins

Malgrat tots els progressos, els ocells marins són un dels grups més amenaçats d'ocells en tot el món (Butchart, S.H.M. et al., 2004), amb fortes evidències d'una reducció dramàtica en moltes àrees geogràfiques (Lewison, R. et al., 2012). Les amenaces per part de factors antròpics a les poblacions d'ocells marins inclouen les captures accidentals per arts de pesca, la pol·lució, les molèsties directes humanes, les llums artificials, la introducció de predadors i el canvi climàtic global (Phillips, R.A., 2013; Rodriguez, A. et al., 2015; Trathan, P.N. et al., 2015).

La sobreexplotació pesquera suposa un gran risc per a les reserves de peixos sobre els que depreden els ocells marins. La coexistència de pesqueries i ocells a les zones d'alimentació poden suposar interaccions negatives com la deguda a l'esgotament de les preses quan tots dos competeixen pel mateix recurs (Bertrand, S. et al., 2012) o a l'increment de la mortalitat dels ocells degut a les captures accidentals (Lewison, R. et al., 2004). Les pesqueries poden tenir també efectes positius, proporcionant noves oportunitats d'alimentació quan els ocells marins es beneficien de les preses descartades que d'una altra manera haguessin esdevingut inaccessibles (Karpouzi, V.S. et al., 2007; Montevecchi, W.A., 2002; Oro, D. et al., 2004). Però els descarts es veuran limitats per la imminent reforma de la llei de la Unió Europea en quant a la política pesquera, amb la

qual cosa s'esperen efectes negatius en aquestes espècies depredadores (Bicknell, A.W.J. et al., 2013).

En aquest context, un important repte actual és mantenir els ocells marins en un favorable estat de conservació (Croxall, J.P. et al., 2012). El disseny efectiu d'estratègies de conservació i gestió per a aquestes espècies requereix del coneixement tant de la distribució de les espècies durant tot el seu cicle anual, com dels factors ambientals que determinen aquesta distribució (Hyrenbach, K.D. et al., 2000). Per tant, el coneixement dels factors que governen la dinàmica dels ecosistemes marins és imprescindible per tal d'implementar estratègies efectives de gestió als ecosistemes marins (Boyce, D.G. et al., 2015). La utilitat de les dades provinents de sistemes de seguiment de les localitzacions així com de teledetecció com a eines per als plans de conservació és essencial per tal d'obtenir investigacions detallades de la coincidència espacial de les espècies i dels seus perills, com les pesqueries (Lascelles, B.G. et al., 2016). Simultàniament, les series temporals llargues de dades biològiques de poblacions d'ocells marins són crucials per descobrir tendències i efectes ecològics relacionats amb els canvis en els ambients marins. En aquest sentit, els estudis interdisciplinaris combinant tecnologies punteres com la teledetecció amb sèries llargues de dades de paràmetres reproductius són clau pel manteniment dels ocells marins i el seu ambient.

OBJECTIUS

El principal objectiu d'aquesta tesi és investigar la influència de la variabilitat espaciotemporal en les condicions ambientals de les estratègies d'alimentació i els paràmetres reproductius dels ocells marins, i l'avaluació de les estratègies de conservació dels ocells marins per tal d'afrontar els canvis en l'ambient oceanogràfic.

Per aconseguir aquest objectiu principal, es van definir els següents objectius específics:

1. Descriure la distribució espacial dels factors climàtics i antropogènics que afecten negativament als oceans a escala global, i en conseqüència, als ocells marins.
2. Determinar la escala espaciotemporal a la qual els ocells marins interaccionen amb el seu ambient. A aquesta escala es relacionen paràmetres de reproducció en resposta a la variabilitat ambiental.
3. Investigar si les condicions oceanogràfiques canviants, les activitats pesqueres o les interaccions biològiques (competència) afecten a la selecció dels hàbitats d'alimentació dels ocells marins.
4. Investigar com les variacions en les condicions oceanogràfiques afecten als paràmetres reproductius
5. Proposar estratègies de gestió espacialment explícites per als ocells marins, basades en el coneixement científic englobant dades biològiques, perills d'origen antròpic i variabilitat ambiental.

Aquests objectius s'han desenvolupat en sis capítols presentats com a articles científics, que aborden la variabilitat de l'hàbitat oceanogràfic des de l'escala global a l'escala local, i analitzant les respostes ecològiques de diferents espècies d'ocells marins a les limitacions que aquesta variabilitat imposa a les estratègies d'alimentació i de reproducció.

ESTRUCTURA DE LA TESI

» Localització i espècies de l'estudi

Les localitzacions d'estudi d'aquesta tesi cobreixen un ampli rang geogràfic, des de l'oceà mundial de manera global fins a tres àrees específiques localitzades total o parcialment a climes mediterranis. La primera d'aquestes àrees inclou la regió sud-oest del mar Mediterrani, el més gran i profund dels mars tancats (Coll, M. et al., 2012), i al que Lejeusne (2010) es va referir de manera encertada com a un oceà en miniatura, altament divers i a la vegada altament impactat, que suporta una pressió antròpica sense precedents (pol·lució, sobreexplotació pesquera). Els altres dos escenaris són el Bass Strait, una regió somera i àmplia entre Tasmània i el continent australià, que fa de límit i de zona de barreja de vàries corrents marines (Gibbs, C. et al., 1986), i el mar Patagònic (Argentina), una de les àrees més productives de l'hemisferi sud (Foro para la conservación del Mar Patagónico y áreas de influencia, 2008). Tots els llocs d'estudi mencionats es caracteritzen per ser zones amb una elevada barreja d'aigües i per una complexa i pronunciada circulació estacional. El gran dinamisme d'aquestes àrees ofereix interesants escenaris on estudiar les respostes ecològiques dels ocells marins.

Es van seleccionar cinc espècies diferents d'ocells marins com a model d'estudi (tres baldrigues y dos espècies de pingüins, que s'introduiran en el breu resum de cada capítol que s'exposarà a continuació). La selecció d'aquestes espècies model es va fer tenint en compte la idoneïtat de cada espècie per acomplir els objectius particulars de cada capítol, i la disponibilitat de dades biològiques necessàries per tractar les qüestions ecològiques plantejades a cada capítol.

» Variabilitat ambiental a escala global (Capítol I)

Aquesta tesi comença amb l'exploració de la variabilitat ambiental oceanogràfica a escala global. Els ocells marins han evolucionat amb les condicions imposades per un dels hàbitats més heterogenis del món, els oceans, i amb el gran repte d'obtenir aliment d'ell (Ashmole, N.P., 1971). Però existeixen evidències clares que senyalen que s'estan produint canvis globals que estan exercint un estrès considerable sobre els ecosistemes marins (Halpern, B.S. et al., 2008), i particularment sobre les espècies i comunitats d'ocells marins, que han d'adaptar els seus comportaments d'alimentació i reproductors a aquests ambients pertorbats (Grémillet, D. & T. Boulinier, 2009). El Capítol I tracta dels impactes climàtics i els deguts a les pesqueries que s'estan produint a nivell mundial, introduint els principals canvis ambientals amb els que s'han d'enfrontar

els depredadors marins, i emfatitza la necessitat de considerar conjuntament els factors climàtics i antròpics com a promotors de la variabilitat ambiental.

» Variabilitat en patrons i escales (Capítol II)

Les interaccions ecològiques entre espècies i el seu ambient tenen lloc a diverses escales d'espai i temps (Wiens, J.A., 1989). Aquest capítol explora la rellevància de seleccionar una correcta escala d'estudi que integri la variabilitat ambiental, ja que la predictibilitat de les respostes dels organismes als patrons ambientals només poden emergir quan s'estudien els sistemes a l'escala correcta.

L'habilitat dels ocells marins de reproduir-se de manera exitosa a l'escenari impredictible envers el subministrament d'aliment que imposen els oceans, ha emergit com una resposta adaptativa per tal d'ajustar el moment de la reproducció al pic de disponibilitat d'aliment durant la criança dels polls (Durant, J.M. et al., 2004). Els estudis sobre fenologia són d'un gran interès actualment, ja que el canvi climàtic està provocant variacions en el pic i l'estacionalitat de la producció primària dels oceans (Sydeman, W.J. et al., 2015). Al Capítol II analitzem l'ajust temporal dels patrons entre la data de posta del pingüí petit australià *Eudyptula minor* i el pic de productivitat extret d'una escala dinàmica. Aquesta escala està basada en la variabilitat espacial i temporal de la circulació oceànica al voltant de les àrees d'alimentació del Bass Strait, a Austràlia. El pingüí petit és una bona espècie model per estudiar les pressions ambientals experimentades pels ocells marins que necessiten tornar regularment al niu després d'alimentar-se (*central-place foragers*): en primer lloc, per la disponibilitat d'una de les sèries temporals de dades més llargues sobre el moment reproductiu que generosament ens va proporcionar Phillip Island Nature Park, i que va ser essencial per poder estudiar vincles significatius entre l'ambient i els patrons biològics. A més, el pingüí petit australià és una espècie resident amb unes àrees d'alimentació molt restringides, caracteritzades per una elevada impredictibilitat i per situar-se en un ambient molt heterogeni (Chiaradia, A. et al., 2016). Per totes aquestes raons, nosaltres preveiem que aquesta espècie podria ser particularment sensible a la variabilitat ambiental i a les senyals físiques del medi al voltant de la colònia per iniciar la reproducció.

» Estratègies d'alimentació per fer front a la variabilitat ambiental (Capítols III, IV, V)

Des d'aquest punt i cap endavant, la tesis arriba al seu nucli central, on s'exploren les respostes ecològiques de les espècies model a la variabilitat ambiental en termes d'adquisició de recursos (Capítol II, IV, V) i efectes sobre la demografia de les espècies (Capítol V).

Com a model d'estudi als Capítols III i IV vam seleccionar tres espècies de baldrigues

que crien al sud-oest del mar Mediterrani. Aquests capítols mostren dos estudis realitzats amb ocells marcats amb dispositius de seguiment remot. L'objectiu d'aquests capítols va ser el de relacionar els moviments d'aquestes aus marines amb la heterogeneïtat espaciotemporal de l'ambient de les seves àrees de cria i d'alimentació.

Un dels estudis es va realitzar durant quatre anys (2011-2014) mitjançant el seguiment dels moviments d'alimentació de l'amenaçada baldriga balear *Puffinus mauretanicus* de la colònia d'Eivissa (Illes Balears, Espanya). Aquest seguiment ens va permetre analitzar el paper del vent i els patrons de productivitat en la selecció dels hàbitats d'alimentació i avaluar les diferències entre anys. Al Capítol IV, l'estudi inclou dades de només un any d'estudi (2011), però s'analitzen per separat dos períodes de cria (la incubació i la criança dels polls), de dos espècies diferents, tot i que molt properes, de baldrigues cendroses (*Calonectris diomedea* i *C. borealis*), que crien de manera simpàtrica a les Illes Chafarinas (Espanya). Aquesta colònia, una de les poques localització a tot el món on coexisteixen aquestes espècies ecològicament molt similars, és un escenari únic per investigar les limitacions que imposa la competència en la selecció de les àrees d'alimentació en diferents moments reproductius. Al Capítol V, l'espècie escollida com a model d'estudi va ser el pingüí de Magallanes *Spheniscus magellanicus*, concretament les poblacions que crien a la província de Chubut (Argentina). En aquest Capítol s'investiguen les preferències en quant a la selecció d'hàbitat d'aquesta espècie en un ambient altament modificat per la pressió antròpica. El Capítol estudia els efectes de les variacions espaciotemporals en la disponibilitat de preses d'elevada qualitat, i les conseqüències d'aquesta disponibilitat en els paràmetres reproductors de l'espècie.

» La integració de la variabilitat ambiental beneficia les estratègies de conservació (Capítol VI)

Finalment, concloem aquesta tesi amb un estudi aplicat sobre el disseny de reserves marines. Els canvis oceanogràfics són un repte per als gestors i per a la conservació, però els esforços en temes de conservació en sistemes marins segueixen el camí per darrera de les iniciatives a nivell terrestre. Per tant, existeix una important e immediata necessitat per delinear Àrees Marines Protegides representatives (Lescroël, A. et al., 2016; Ronconi, R.A. et al., 2012). Els ocells marins han estat àmpliament reconeguts com a excel·lents indicadors de la salut dels ecosistemes marins i s'han utilitzat com a espècies paraigües (*umbrella especies*) amb finalitats de conservació en tots els oceans (Lascelles, B.G. et al., 2012). Però les àrees marines protegides deurien ser designades no només per a la conservació de les espècies, sinó també per preservar el seu ambient biofísic (Lubchenco, J. et al., 2003), incloent els mecanismes físics que influencien la formació i persistència d'importants hàbitats per a les espècies i les seves preses (Hyrenbach, K.D. et al., 2000). Seguint aquestes directrius, i integrant els coneixements rellevants adquirits en capítols previs, explorem en aquest Capítol VI una eina per definir àrees marines protegides, integrant factors biològics, sòcio-econòmics i ambientals, en la comunitat

d'ocells marins de la Patagònia argentina. Qualsevol esforç per tal de conservar els ocells marins necessita plantejar amb determinació la necessitat de conèixer els majors perills als que s'enfronten aquestes espècies (Boersma, P.D. et al., 2002). Al Capítol I, vam oferir una perspectiva general dels majors perills que afecten als ocells marins, en relació als riscos ambientals i les activitats pesqueres. Els plantejaments metodològics desenvolupats als Capítols II, III i V (anàlisi de connectivitats, delimitació de formacions d'elevada productivitat i persistència i projeccions de distribució d'individus al mar a partir de dades basades en el censos en colònies, respectivament) es van incorporar amb l'objectiu final de definir àrees potencials de conservació per als ocells marins, mitjançant la identificació d'àrees ecològicament rellevants.

DISCUSSIÓ

Els ocells marins s'han adaptat a totes les latituds de la Terra, on passen de mitjana més del 80% del seu temps a l'oceà. Obtenir els recursos tròfics necessaris per sobreviure i reproduir-se en aquest ambient summament complex, dinàmic i heterogeni suposa un repte important, i que per tant, ha jugat un paper important modelant el comportament, l'ecologia i les estratègies de vida dels ocells marins (Schreiber, E.A. & J. Burger, 2001). Com a depredadors marins, els ocells marins estan limitats per la distribució i la dinàmica de les seves preses, i en conseqüència, estan enormement influenciats per les condicions oceanogràfiques i els règims climàtics que controlen la productivitat marina (Hunt Jr, G. & D. Schneider, 1987; Oro, D., 2014; Parmesan, C., 2006; Ramírez, F. et al., 2016).

Durant les darreres dècades, molts estudis han investigat el paper de la variabilitat ambiental en la modulació dels trets de vida dels ocells marins . Específicament, aquests estudis han proporcionat grans coneixements sobre els determinants ambientals de la distribució i les estratègies d'alimentació dels ocells marins. No obstant, pocs estudis han profunditzat en el coneixement del paper que juguen els canvis ambientals a escales espacials i temporals prou fines com per afectar als patrons de moviment o a les respostes a llarg termini a la variabilitat ambiental (Paiva, V.H. et al., 2013; Pinaud, D. & H. Weimerskirch, 2005). Dintre d'aquest context, en aquesta tesi hem explorat com els ocells marins responen a la variabilitat espaciotemporal en les condiciones oceanogràfiques canviant les seves estratègies d'alimentació (Capítols II, IV i V) i les seves estratègies de vida, com la fenologia i l'èxit reproductor (Capítols II i V), ressaltant el paper clau que pot tenir el coneixement de la variabilitat ambiental en la conservació i la gestió (Capítols I i VI). Per aconseguir tots aquests objectius, ens hem beneficiat de recents innovacions tecnològiques. Primer de tot, la teledetecció per satèl·lit és actualment una font d'informació fàcilment accessible a resolucions espacials suficientment grans i a escales temporals rellevants ecològicament (Hunsaker, C.T. et al., 2013). Això és particularment important per organismes de vida llarga i que es mouen sobre extenses àrees com els ocells marins. En segon lloc, l'aparició de dispositius cada cop més miniaturitzats i fiables que poden enregistrar el moviment animal a un nivell de detall impensable recentment, ha facilitat la investigació i la resposta a noves qüestions referents a l'ecologia del moviment (Hays, G.C. et al., 2016). Quan ha sigut possible, hem combinat ambdues tècniques per explorar com la variabilitat ambiental afecta a l'ecologia dels ocells marins i els seu comportament.

» Fer front als canvis en les condicions ambientals

Els ocells marins constitueixen un bon model per investigar les adaptacions d'organismes de vida llarga als ambients extrems i molt variables. La variabilitat oceànica ha modulat els trets de vida dels ocells marins durant mil·lennis (Ricklefs, R.E., 1990; Weimerkirch, H., 2002), però les activitats humanes com la pesca i la pol·lució estan amenaçant els ecosistemes marins de tot el món d'una forma sense precedents, causant canvis en l'abundància i distribució de les espècies, i alterant l'estructura, funcionalitat i resiliència dels ecosistemes (Burrows, M.T. et al., 2014; Paleczny, M. et al., 2015). Si volem entendre si els ocells marins són capaços de fer front a les conseqüències del canvi climàtic, primer de tot necessitem identificar els factors que afecten la distribució, estratègies d'alimentació i trets de vida d'aquestes espècies (Grémillet, D. & T. Boulinier, 2009).

Al Capítol I introductori, vam intentar explorar la distribució espacial dels impactes climàtics i antropogènics en els oceans mundials, amb un interès particular en aquelles àrees que acullen una part important de la biodiversitat marina. Vam generar un índex d'impactes acumulat que considerava els canvis en les últimes tres dècades en la temperatura superficial del mar, la productivitat marina i les corrents oceanogràfiques. Aquest índex ens va revelar la distribució heterogènia als oceans dels canvis impulsats pel clima. A més, les àrees a nivell global d'una excepcional biodiversitat coincideixen amb les àrees més severament impactades per l'augment de la temperatura del mar o el descens de la productivitat primària, i són les que presenten també unes elevades taxes de pressió pesquera. Cal remarcar que les àrees d'especial preocupació són la del mar al voltant del continent Australià, l'oest del Mediterrani i l'Atlàntic sud al voltant de la Patagònia Argentina, on molts dels nostres treballs s'han desenvolupat. Els nostres resultats coincideixen amb estudis previs que havien posat de manifest la distribució espacial heterogènia de l'augment de la temperatura de l'aigua (Hansen, J. et al., 2006; Winton, M. et al., 2013) i de la clorofil·la-a (Boyce, D.G. et al., 2014). No obstant, la novetat i principal contribució del nostre treball és la combinació dels factors amenaçadors derivats de la pesca i l'ambient, i que conjuntament amb informació sobre la biodiversitat, ens ha permès generar un índex com el proposat en treballs recents (Halpern, B.S. et al., 2008; Maxwell, S.M. et al., 2013), perquè pugui ser utilitzat en la identificació d'àrees amb una urgent prioritat de conservació dintre del patrimoni marí del nostre planeta.

Una limitació important que afecta al nostre treball i que vam trobar també quan modelàvem la distribució espacial de les baldrigues al Capítol IV i del pingüí de Magallanes al Capítol V, és la disponibilitat d'informació sobre la distribució, a resolució espacial elevada, de l'esforç pesquer. Com s'ha posat de manifest recentment (Scales, K.L. et al., 2016), la resolució espacial de les capes d'informació espacial és clau per modelar els determinants que actuen en la selecció d'hàbitat de les espècies. Però els primers mapes amb detallada resolució d'intensitat de pesca cobrint totes les aigües

de la Unió Europea estan esdevenint disponibles des de molt recentment. Sistemes de regulació de control dels vaixells de pesca imposats fa pocs anys, com el Sistema de Seguiment d'Embarcacions (*Vessel Monitoring System*, VMS) o el Sistema Automàtic d'Identificació (*Automatic Identification System*, AIS) (Natale, F. et al., 2015; Witt, M.J. & B.J. Godley, 2007), obligatoris a la Unió Europea des de 2014, poden proporcionar informació detallada i molt valuosa sobre els circuits recorreguts per les embarcacions. Als Capítols IV i V, vam resoldre aquesta limitació generant un índex sinòptic d'esforç pesquer a la resolució requerida, a partir de dades de ports pesques o publicades anteriorment.

» Senyals ambientals impulsors de la fenologia de cria i presa de decisions òptima

El Capítol I demostra els canvis en les condicions oceanogràfiques ocorreguts durant les darreres dècades, especialment des de 1980, com a resultat del canvi climàtic. Aquest període coincideix amb els inicis de la oceanografia per satèl·lit i per tant existeix des de llavors un important registre d'observacions de satèl·lit sobre variables climàtiques i la seva evolució (García-Soto, C. et al., 2012). Aquesta informació ambiental a llarg termini, quan s'utilitza juntament amb sèries temporals llargues de dades biològiques, es converteix en una valuosa eina per investigar les respostes dels ocells marins a condicions ambientals contrastades (Oro, D., 2014; Ramírez, F. et al., 2016; Reed, T.E. et al., 2009). No obstant això, avaluar el paper dels patrons i les tendències de les condicions ambientals com a determinants dels trets de vida dels ocells marins requereix de la selecció d'una escala espaciotemporal ecològicament rellevant.

Les pressions evolutives han modelat a llarg termini el moment òptim per a la reproducció, seleccionant estratègies que acabin raonablement amb èxit la majoria dels anys. Una reproducció exitosa implica fer un pronòstic futur de la disponibilitat de recursos, en resposta als patrons predictibles que indiquen els fenòmens ambientals (Mackas, D.L. et al., 2012; McNamara, J.M. et al., 2011). En aquest sentit, als climes temperats i polars, i especialment als ecosistemes terrestres, molts estudis han demostrat que la fenologia de reproducció ha evolucionat per fer coincidir el temps de la reproducció amb el pic anual d'abundància de preses (McNamara, J.M. et al., 2011; Visser, M.E. & C. Both, 2005). Als ecosistemes marins, degut a la dificultat per obtenir mesures directes de distribució de preses, les correlacions es fan habitualment amb variables indirectes (*proxies*) indicadores de la productivitat marina. Per exemple, s'han trobat correlacions entre la fenologia de reproducció d'algunes espècies d'ocells marins i índexs climàtics a gran escala com l'Oscil·lació de l'Atlàntic Nord (NAO), o el Mode Anular del Sud (SAM) en el cas d'ocells migratoris (Durant, J.M. et al., 2004; Frederiksen, M. et al., 2004), o amb condicions locals com la temperatura superficial del mar per espècies residents (Brommer, J.E. et al., 2008). En aquestes darreres espècies, molts estudis previs han correlacionat el temps fenològic amb les variables ambientals

extretes de les àrees d'alimentació de les espècies a diferents desfasaments temporals (des de setmanes fins a mesos) abans del moment d'inici de la reproducció. Tanmateix, en ambients tan oberts i dinàmics com els marins, la biomassa es mou temporal i espacialment mentre l'energia passa d'un esglaó a un altre de la xarxa tròfica. És per això que la informació sobre fenòmens oceanogràfics a resolució espacial extremadament fina extreta d'àrees dinàmiques que tenen en compte el moviment de les masses d'aigua (corrents oceàniques), és important per a investigar la habilitat de les espècies per acoblar els seus processo fenològics amb els patrons de productivitat marina.

Al Capítol II, vam investigar les respostes fenològiques d'un depredador marí, el pingüí petit australià, a la variabilitat ambiental a diferents escales espaciotemporals. En aquest treball hem demostrat que els patrons de productivitat a les àrees més enllà de les zones d'alimentació però amb masses d'aigua connectades amb les primeres a través de la circulació oceànica, determinen el moment de la reproducció en una població d'aquest ocell marí coster. La temperatura superficial del mar ha estat identificada com a factor desencadenant de la reproducció en molts estudis de diversos grups, des del zooplàncton i els peixos fins els depredadors marins (Frederiksen, M. et al., 2004; Greve, W. et al., 2001; Hipfner, J.M., 2008; Sidhu, L.A. et al., 2012). El nostre treball coincideix amb aquestes investigacions prèvies senyalant el paper potencial de la temperatura superficial del mar com a desencadenant local de l'inici de la reproducció al pingüí petit australià.

» Factors ambientals, biològics i antropogènics responsables de la distribució al mar dels ocells marins

Tal i com s'ha explicat a seccions anteriors, els ocells marins depenen enormement de la distribució dels recursos. Indubtablement, a més, són els animals més mòbils de tots els predadors marins. Els estudis de seguiment de la localització amb dispositius de posicionament global (GPS) a les baldrigues (Capítols III i IV), i l'estudi sobre la distribució potencial dels pingüins (Capítol V) pretenen aprofundir en els coneixements sobre la complexitat dels factors responsables de la distribució dels ocells marins i dels seus moviments d'alimentació. Aquests treballs ofereixen una visió general de l'explotació de tres ambients marins diferents, i intenten investigar el paper de factors com les condicions oceanogràfiques, les activitats pesqueres i les interaccions biològiques, en la selecció dels hàbitats d'alimentació per part dels ocells marins.

Resumint els principals resultats d'aquests capítols, hem trobat que totes les espècies estudiades s'alimenten a aigües someres i productives de la plataforma continental, i properes a les seves zones de cria. Les àrees d'alimentació es corresponen amb àrees que històricament han estat àrees productivament molt predictibles tant a l'espai com al temps (Capítols IV i V). La temperatura superficial del mar i la clorofil·la-a ofereixen una clara capacitat predictiva per a caracteritzar els destins d'alimentació, tal i com

s'ha vist en treballs anteriors (Catry, T. et al., 2013; Grémillet, D. et al., 2008; Ramos, J.A. et al., 2013). Les àrees d'alimentació també són un reflex de les formacions físiques oceanogràfiques responsables de la distribució de les preses (Capítol V), i que per tant afecten a l'èxit reproductor i, en última instància, a la dinàmica de les poblacions. A diferència dels hàbitats terrestres, la caracterització dels hàbitats d'alimentació i dels factors que promouen les decisions sobre estratègies d'alimentació als hàbitats marins, presenten la dificultat addicional d'haver d'incorporar els ràpids canvis ambientals que es produeixen als oceans tant en temps com en espai. En aquest sentit, treballs recents han posat de manifest el paper de les formacions dinàmiques i els fronts tèrmics per a la identificació de zones importants d'alimentació per a espècies pelàgiques (Scales, K. L. et al., 2014), tot i que al nostre cas vam obtenir una baixa capacitat explicativa dels fronts marines vers les àrees marines clau d'espècies pelàgiques (Capítol V). En relació amb la integració de les variables dinàmiques en la selecció dels hàbitats d'alimentació, als estudis de moviments de cerca d'alimentació dels ocells marins és important tenir en compte, no només la fracció aquàtica de l'ambient, sinó també els factors dinàmics que limiten les decisions individuals, com els vents (Amélineau, F. et al., 2014; Louzao, M. et al., 2014; Weimerskirch, H. et al., 2000). A més, les estratègies de moviment és important examinar-les en relació amb l'ambient que es travessa (Shepard, E.L.C. et al., 2013). Aquest ha sigut l'objectiu del Capítol III, on explorem el paper dels vents oceànics i els patrons de productivitat en l'elecció dels destins d'alimentació escollits per la baldriga balear.

Estudis previs han alertat sobre la manca de precisió de les dades obtingudes per imatges de satèl·lit en relació als vents, degut a la grossera resolució espacial i temporal d'aquestes dades comparades amb les dades dels GPS dels ocells (Amélineau, F. et al., 2014; Raymond, B. et al., 2010; Scales, K.L. et al., 2016). Seguint aquestes recomanacions, nosaltres vam emprar models meteorològics d'una elevada resolució espacial i temporal per generar paisatges marins de camps de vents, amb l'objectiu de calcular els costos energètics de moure's tant als destins seleccionats com als descartats. Els nostres resultats suggereixen que les condicions ambientals que afecten al rendiment del vol canvien diàriament, i que influencien les decisions sobre les zones d'alimentació a explotar a determinats moments, tot i que la proximitat de les zones d'alimentació, facilitada per l'acció dels vents, explica la gran majoria dels destins d'alimentació. Un punt interessant d'investigació futura seria el càlcul de la despesa real d'energia durant els viatges d'alimentació. Recentment, molts dispositius GPS incorporen també acceleròmetres, que permeten la conversió directa de l'acceleració dinàmica del cos a mesures de les taxes a les quals un animal gasta l'energia durant un esdeveniment específic de la seva vida (Amélineau, F. et al., 2014). Això és de particular importància i ofereix noves oportunitats d'estudi del moviment durant el període reproductiu, el moment anual de més demanda energètica per a les espècies.

Les interaccions biòtiques que afecten a les estratègies d'alimentació s'han abordat, d'una banda, comparant les distribucions d'alimentació d'espècies relacionades que crien en simpatria (baldrigues cendroses, Capítol IV) i, d'altra banda, considerant els efectes que les interaccions entre individus de la mateixa espècie tenen en les distribucions d'alimentació dels pingüins de Magallanes (Capítol V). La teoria ecològica prediu que els animals amb estratègies d'alimentació similars no poden coexistir sense segregació o bé en l'espai, el temps o la dieta, i treballs recents han destacat que la segregació espacial contribueix a minimitzar la competència intra-específica entre colònies adjacents (Cecere, J.G. et al., 2015; Ceia, F.R. et al., 2015; Wakefield, E.D. et al., 2013).

Pocs treballs inclouen explícitament interaccions biòtiques als models de distribució d'espècies (Cunningham, H.R. et al., 2009), com la presència d'individus de la mateixa espècie com a descriptors, afectant així a la importància relativa dels predictors biòtics (Elith, J. & J.R. Leathwick, 2009). Al Capítol V hem modelat la distribució espacial dels pingüins de Magallanes, combinant variables ambientals i biològiques, com l'abundància modelada al mar dels pingüins. A nivell intra-específic, hem trobat que els pingüins de Magallanes s'alimenten a aigües amb una abundància moderada d'altres individus de la seva espècie, probablement en un compromís entre reduir la competència per l'aliment però sense perdre els beneficis de la caça en grup. Al Capítol IV, les interaccions es van avaluar a nivell inter-específic, i com a resultat vam trobar un ampli solapament de les àrees d'alimentació de les dues baldrigues cendroses objecte d'estudi durant la incubació, però van mostrar segregació espacial durant la criança dels polls.

Les activitats antròpiques com les pesqueries poden afectar la distribució dels ocells marins de manera contraposada. Per una banda podem augmentar localment la disponibilitat de preses pels ocells marins mitjançant els descarts, que representen un font força abundant i predictible de recursos (Bartumeus, F. et al., 2010; Bugoni, L. et al., 2009), però també poden suposar la competència amb els ocells marins per espècies comunes, com és el cas de l'anxova per als pingüins de Magallanes (Skewgar, E. et al., 2007). Als capítols IV i V hem demostrat que la distribució de les pesqueries es solapa en gran part amb les àrees d'alimentació de les baldrigues i dels pingüins de Magallanes. Al Capítol V, els nostres resultats indiquen que les pesqueries afecten negativament al consum de preses dels pingüins, mentre que al Capítol IV, l'activitat pesquera sembla tenir una importància explicativa relativament alta en la predicció de la distribució de les zones d'alimentació durant la incubació de les dos espècies de baldrigues estudiades.

» La rellevància dels resultats de la recerca en els plans de gestió espacials per als ocells marins

Els oceans estan canviant ràpidament com a resultat de les activitats humanes i del canvi global, i paral·lelament estan declinant les poblacions d'ocells marins (Paleczny, M. et al., 2015). Fins ara, un grup important d'estudis ha reconegut als ocells marins com

a excel·lents espècies subrogades per a la planificació espacial de les zones importants de biodiversitat marina i com a potencials indicadors de la salut de l'ambient marí, tan regional com globalment (Lascelles, B.G. et al., 2016; Le Corre, M. et al., 2012; Piatt, I.J.F. et al., 2007; Ronconi, R.A. et al., 2012). El darrer Capítol VI tracta de la importància d'abordar correctament l'important objectiu de la gestió i conservació dels ocells i els hàbitats marins, intentant abastar tant les espècies com el seu ambient en els plans de conservació (Turner, W. et al., 2015). Les aproximacions analítiques desenvolupades en capítols previs s'han utilitzat en aquest Capítol VI per tal de definir àrees marines de protecció per a la conservació, integrant factors biològics, sòcio-econòmics i ambientals. Encara que la utilització de dades remotes de posicionament és una eina òptima que ofereix una informació sense precedents sobre la distribució dels ocells marins, també existeixen deficiències en la biotelemetria, com les diferències que poden donar-se entre estratègies d'ús d'hàbitat entre colònies, limitacions logístiques en la instal·lació dels dispositius (per ex., accessibilitat només estacional a les colònies de cria) i sobre tot l'elevat cost dels aparells (Raymond, B. et al., 2014). Aquestes raons ens van impulsar a treballar amb dades simulades a partir de dades de censos de parelles reproductores (Grecian, W.J. et al., 2012) per inferir la distribució de tota la comunitat d'ocells marins al mar Patagònic. Posant els nostres resultats en un context de conservació, hem verificat que la identificació d'àrees marines clau per a la conservació necessita de la interpretació dels fenòmens físics responsables de la formació i persistència de la disponibilitat de preses (Scales, Kylie L. et al., 2014), i requereix també de límits dinàmics i buffers extensius (Hyrenbach, K.D. et al., 2000) de zones que potencialment puguin influir a les àrees clau. El nostre treball també coincideix amb treballs recents que destaquen el canvi cap a una gestió dinàmica de l'oceà (Game, E.T. et al., 2009; Maxwell, S.M. et al., 2015), ja que les fronteres estacionàries no són les estratègies marines més efectives per protegir a fenòmens tan mòbils com els fenòmens o els animals marins. La innovació en les tecnologies i les noves aproximacions analítiques oferiran noves oportunitats per investigar els factors que determinen els patrons reproductius i de moviment dels ocells marins en relació amb el seu ambient dinàmic i els programes de conservació es podran beneficiar de tots aquests nous coneixements ecològics.

CONCLUSIONS

1 Els ecosistemes marins s'han vist afectats dràsticament en els darrers anys per canvis provocats tant per factors climàtics com antropogènics. Hem detectat canvis tant a escala local com regional en la temperatura superficial del mar, la productivitat i les corrents marines en tots els oceans, encara que el canvis més significatius han tingut lloc a les regions polars i tropicals. Les àrees oceàniques que han sofert major impacte coincideixen amb àrees amb una elevada biodiversitat i que presenten també una forta pressió pesquera.

2 La investigació de les relacions entre els animals marins i el seu ambient ha d'incloure tant la variabilitat ambiental així com la complexitat dels ecosistemes marins. Degut a l'elevada variabilitat d'aquests sistemes tan complexos, les sèries temporals llargues de dades que hem utilitzat, tant biològiques com ambientals, ens han revelat clars patrons de com la variabilitat ambiental és determinant en els processos ecològics.

3 Els ocells marins costers, com els pingüins petits australians, són capaços d'ajustar el moment òptim per a la reproducció mitjançant l'ús de senyals locals com la temperatura superficial del mar, que els aporta informació sobre els patrons de productivitat que emergeixen a escala regional. Aquesta escala regional integra canvis tant temporals com espacials en els patrons de productivitat que afecten les zones d'alimentació del pingüí petit. Aquest estudi mostra la importància d'escollir una correcta escala temporal i espacial que determini com la variabilitat ambiental afecta a les estratègies de vida. Els patrons de productivitat a grans escales poden ser també importants determinants de les estratègies d'alimentació en ocells pelàgics, com les baldrigues, que presenten àrees d'alimentació restringides en gran part per la proximitat a les àrees de cria de zones productives de la plataforma continental.

4 Les restriccions energètiques durant la reproducció que suposa el haver de retornar periòdicament a la colònia (central-place foraging), pot ser un condicionant important de les estratègies d'alimentació dels ocells marins. Vam trobar aquest limitant especialment evident en espècies com la baldriga cendrosa i la baldriga balear que s'alimenten a àrees allunyades de la colònia de cria però que han de retornar periòdicament a terra durant la reproducció. En aquestes espècies, els vents favorables poden determinar en gran part la direcció de sortida de la colònia durant els viatges d'alimentació. Hem demostrat que els vents juguen un paper important en l'elecció de la direcció d'anada cap a les zones d'alimentació de la baldriga balear.

5 Un altre factor determinant en les estratègies d'alimentació dels ocells marins que hem examinat durant aquest estudi ha sigut la competència pels recursos entre espècies amb requeriments ecològics similars o entre individus de la mateixa espècies. Per exemple, les baldrigues cendroses Calonectris diomedea i C. borealis que crien de manera simpàtrica, tendeixen a segregar les àrees d'alimentació al període de més exigència energètica durant la criança dels polls. Tanmateix, durant el període previ de la incubació, mostren un alt grau de superposició en les seves àrees d'alimentació. La competència pels recursos ha sigut un factor explicatiu molt important en la distribució dels pingüins de Magallanes, ja que hem trobat que aquesta espècie tendeix a evitar les àrees amb elevada densitat d'individus de la seva mateixa espècie a les zones del mar on acudeixen per alimentar-se.

6 Les activitats antròpiques que afecten a la disponibilitat de recursos, com les pesqueries, afecten a la distribució de les àrees d'alimentació durant la cria de les dues espècies de baldrigues cendroses estudiades i també a la dels pingüins de Magallanes. En aquest darrer cas, a més, hem trobat una influència negativa de les pesqueries sobre la població d'aquests pingüins degut a la competència pel consum de la mateixa espècie, l'anxova, clau en l'alimentació dels pingüins de Magallanes.

7 Les decisions relatives a la gestió i conservació dels ocells marines han de considerar tant els factors ambientals con els antropogènics que estan afectant aquest grup d'ocells. Els plans de conservació han de tenir en compte l'heterogeneïtat de la distribució de les espècies tant en el temps com en l'espai, els processos físics de l'oceà que afecten l'abundància i la dinàmica dels recursos tròfics d'aquestes espècies, així com l'impacte de les activitats antròpiques i econòmiques tant en els ocells marins com en les seves preses.

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REFERENCES

ADRIAN, R., GERTEN, D., HUBER, V., WAGNER, C., & SCHMIDT, S. R. (2012). Windows of change: temporal scale of analysis is decisive to detect ecosystem responses to climate change. Marine Biology, 159 (11), 2533-2542.

AMÉLINEAU, F., PÉRON, C., LESCROËL, A., AUTHIER, M., PROVOST, P., & GRÉMILLET, D. (2014). Windscape and tortuosity shape the flight costs of northern gannets. The Journal of Experimental Biology, 217 (6), 876-885.

ANDERSON, C. N. K., HSIEH, C.-H., SANDIN, S. A., HEWITT, R., HOLLOWED, A., BEDDINGTON, J., MAY, R. M., & SUGIHARA, G. (2008). Why fishing magnifies fluctuations in fish abundance. Nature, 452 (7189), 835-839.

ARCOS, J. M., BÉCARES, J., VILLERO, D., BROTONS, L., RODRÍGUEZ, B., & RUIZ, A. (2012). Assessing the location and stability of foraging hotspots for pelagic seabirds: An approach to identify marine Important Bird Areas (IBAs) in Spain. Biological Conservation, 156, 30-42.

ASHMOLE, N. P. (1971). Seabird ecology and the marine environment. In D. S. Farner & J. R. King (Eds.), *Avian biology* (Vol. 1, pp. 223-286). New York: Academic Press.

ASHMOLE, N. P., & ASHMOLE, M. J. (1967). *Comparative feeding ecology of sea birds of a tropical oceanic island*: Peabody Museum of Natural History, Yale University.

AUSTIN, D., DON BOWEN, W., MCMILLAN, J. I., & IVERSON, S. J. (2006). Linking movement, diving, and habitat to foraging sucesss in a large marine predator. Ecology, 87 (12), 3095-3108.

AWKERMAN, J. A., FUKUDA, A., HIGUCHI, H., & ANDERSON, D. J. (2005). Foraging activity and submesoscale habitat use of waved albatrosses Phoebastria irrorata during chick-brooding period. Marine Ecology Progress Series, 291, 289-300.

BARBRAUD, C., WEIMERSKIRCH, H., GUINET, C., & JOUVENTIN, P. Effect of sea-ice extent on adult survival of an Antarctic top predator: the snow petrel *Pagodroma nivea*. Oecologia, 125 (4), 483-488.

BARTUMEUS, F., GIUGGIOLI, L., LOUZAO, M., BRETAGNOLLE, V., ORO, D., & LEVIN, S. A. (2010). Fishery discards impact on seabird movement patterns at regional scales. Current Biology, 20 (3), 215-222.

BEHRENFELD, M. J., O'MALLEY, R. T., SIEGEL, D. A., MCCLAIN, C. R., SARMIENTO, J. L., FELDMAN, G. C., MILLIGAN, A. J., FALKOWSKI, P. G., et al. (2006). Climate-driven trends in contemporary ocean productivity. Nature, 444 (7120), 752-755.

BERTRAND, A., GRADOS, D., COLAS, F., BERTRAND, S., CAPET, X., CHAIGNEAU, A., VARGAS, G., MOUSSEIGNE, A., et al. (2014). Broad impacts of fine-

scale dynamics on seascape structure from zooplankton to seabirds. Nature Communications, 5, 5239.

BERTRAND, S., JOO, R., SMET, C. A., TREMBLAY, Y., BARBRAUD, C., & WEIMERSKIRCH, H. (2012). Local depletion by a fishery can affect seabird foraging. Journal of Applied Ecology, 49 (5), 1168-1177.

BICKNELL, A. W. J., ORO, D., CAMPHUYSEN, K. C. J., VOTIER, S. C., & BLANCHARD, J. (2013). Potential consequences of discard reform for seabird communities. Journal of Applied Ecology, 50 (3), 649-658.

BOERSMA, P. D., CLARK, J. A., & HILLGARTH, N. (2002). Seabird conservation. In J. Burger & E. A. Schreiber (Eds.), *Biology of marine birds* (pp. 217-261). Boca Raton: CRC Press.

BOERSMA, P. D., REBSTOCK, G. A., FRERE, E., & MOORE, S. E. (2009). Following the fish: penguins and productivity in the South Atlantic. Ecological Monographs, 79 (1), 59-76.

BOST, C. A., COTTÉ, C., BAILLEUL, F., CHEREL, Y., CHARRASSIN, J. B., GUINET, C., AINLEY, D. G., & WEIMERSKIRCH, H. (2009). The importance of oceanographic fronts to marine birds and mammals of the southern oceans. Journal of Marine Systems, 78 (3), 363-376.

BOYCE, D. G., DOWD, M., LEWIS, M. R., & WORM, B. (2014). Estimating global chlorophyll changes over the past century. Progress in Oceanography, 122, 163-173.

BOYCE, D. G., FRANK, K. T., WORM, B., & LEGGETT, W. C. (2015). Spatial patterns and predictors of trophic control in marine ecosystems. Ecology Letters, 18 (10), 1001-1011.

BOYD, C., CASTILLO, R., HUNT, G. L., JR., PUNT, A. E., VANBLARICOM, G. R., WEIMERSKIRCH, H., & BERTRAND, S. (2015). Predictive modelling of habitat selection by marine predators with respect to the abundance and depth distribution of pelagic prey. Journal of Animal Ecology, 84 (6), 1575-1588.

BRADSHAW, C., HINDELL, M. A., MICHAEL, K. J., & SUMNER, M. D. (2002). The optimal spatial scale for the analysis of elephant seal foraging as determined by geo-location in relation to sea surface temperatures. ICES Journal of Marine Science, 59 (4), 770-781.

BROMMER, J. E., RATTISTE, K., & WILSON, A. J. (2008). Exploring plasticity in the wild: laying date-temperature reaction norms in the common gull *Larus canus*. Proceedings of the Royal Society B: Biological Sciences, 275 (1635), 687-693.

BUGONI, L., D'ALBA, L., & FURNESS, R. W. (2009). Marine habitat use of wintering spectacled petrels *Procellaria conspicillata*, and overlap with longline fishery. Marine Ecology Progress Series, 374, 273-285.

BURROWS, M. T., SCHOEMAN, D. S., RICHARDSON, A. J., MOLINOS, J. G., HOFFMANN, A., BUCKLEY, L. B., MOORE, P. J., BROWN, C. J., et al. (2014). Geographical limits to species-range shifts are suggested by climate velocity. Nature, 507 (7493), 492-495.

BUTCHART, S. H. M., STATTERSFIELD, A. J., BENNUN, L. A., SHUTES, S. M., AKÇAKAYA, H. R., BAILLIE, J. E. M., STUART, S. N., HILTON-TAYLOR, C., et al. (2004). Measuring global trends in the status of biodiversity: Red list indices for birds. PLoS Biology, 2 (12), e383.

CATRY, T., RAMOS, J. A., CATRY, I., MONTICELLI, D., & GRANADEIRO, J. P. (2013). Inter-annual variability in the breeding performance of six tropical seabird species: influence of life-history traits and relationship with oceanographic parameters. Marine Biology, 160 (5), 1189-1201.

CECERE, J. G., CATONI, C., GAIBANI, G., GERALDES, P., CELADA, C., & IMPERIO, S. (2015). Commercial fisheries, inter-colony competition and sea depth affect foraging location of breeding Scopoli's Shearwaters *Calonectris diomedea*. Ibis, 157 (2), 284-298.

CEIA, F. R., PAIVA, V. H., CEIA, R. S., HERVÍAS, S., GARTHE, S., MARQUES, J. C., & RAMOS, J. A. (2015). Spatial foraging segregation by close neighbours in a wide-ranging seabird. Oecologia, 177 (2), 431-440.

CHEUNG, W. W. L., SARMIENTO, J. L., DUNNE, J., FROLICHER, T. L., LAM, V. W. Y., DENG PALOMARES, M. L., WATSON, R., & PAULY, D. (2013). Shrinking of fishes exacerbates impacts of global ocean changes on marine ecosystems. Nature Climate Change, 3 (3), 254-258.

CHIARADIA, A., RAMÍREZ, F., FORERO, M. G., & HOBSON, K. A. (2016). Stable Isotopes (δ13C, δ15N) Combined with Conventional Dietary Approaches Reveal Plasticity in Central-Place Foraging Behavior of Little Penguins *Eudyptula minor*. Frontiers in Ecology and Evolution, 3 (art. 154).

CIMINO, M. A., FRASER, W. R., IRWIN, A. J., & OLIVER, M. J. (2013). Satellite data identify decadal trends in the quality of Pygoscelis penguin chick-rearing habitat. Global Change Biology, 19 (1), 136-148.

COLL, M., PIRODDI, C., ALBOUY, C., LASRAM, F. B. R., CHEUNG, W. W. L., CHRISTENSEN, V., KARPOUZI, V. S., GUILHAUMON, F., et al. (2012). The Mediterranean Sea under siege: spatial overlap between marine biodiversity, cumulative threats and marine reserves. Global Ecology and Biogeography, 21 (4), 465-480.

CONNERS, M. G., HAZEN, E. L., COSTA, D. P., & SHAFFER, S. A. (2015). Shadowed by scale: subtle behavioral niche partitioning in two sympatric, tropical breeding albatross species. Movement ecology, 3 (1), 28.

COTTÉ, C., PARK, Y.-H., GUINET, C., & BOST, C.-A. (2007). Movements of foraging king penguins through marine mesoscale eddies. Proceedings of the Royal Society B: Biological Sciences, 274 (1624), 2385-2391.

COTTIN, M., RAYMOND, B., KATO, A., AMÉLINEAU, F., MAHO, Y., RACLOT, T., GALTON-FENZI, B., MEIJERS, A., et al. (2012). Foraging strategies of male Adélie penguins during their first incubation trip in relation to environmental conditions. Marine Biology, 159 (8), 1843-1852.

CROXALL, J. P. (1987). *Seabirds: feeding ecology and role in marine ecosystems* (J. P.

Croxall Ed.). Great Britain: Cambridge University Press.
CROXALL, J. P., BUTCHART, S. H., LASCELLES, B., STATTERSFIELD, A. J., SULLIVAN, B., SYMES, A., & TAYLOR, P. (2012). Seabird conservation status, threats and priority actions: a global assessment. Bird Conservation International, 22 (01), 1-34.
CUNNINGHAM, H. R., RISSLER, L. J., & APODACA, J. J. (2009). Competition at the range boundary in the slimy salamander: using reciprocal transplants for studies on the role of biotic interactions in spatial distributions. Journal of Animal Ecology, 78 (1), 52-62.
DE MONTE, S., COTTÉ, C., D'OVIDIO, F., LEVY, M., LE CORRE, M., & WEIMERSKIRCH, H. (2012). Frigatebird behaviour at the ocean-atmosphere interface: integrating animal behaviour with multi-satellite data. Journal of the Royal Society Interface, 9 (77), 3351-3358.
DESCAMPS, S., TARROUX, A., LORENTSEN, S.-H., LOVE, O. P., VARPE, Ø., & YOCCOZ, N. G. (2015). Large-scale oceanographic fluctuations drive Antarctic petrel survival and reproduction. Ecography, 38, 1-10.
DONEY, S. C. (2006). Oceanography: Plankton in a warmer world. Nature, 444 (7120), 695-696.
DONEY, S. C. (2010). The growing human footprint on coastal and open-ocean biogeochemistry. Science, 328 (5985), 1512-1516.
DULVY, N. K., ROGERS, S. I., JENNINGS, S., STELZENMÜLLER, V., DYE, S. R., & SKJOLDAL, H. R. (2008). Climate change and deepening of the North Sea fish assemblage: a biotic indicator of warming seas. Journal of Applied Ecology, 45 (4), 1029-1039.
DURANT, J. M., ANKER-NILSSEN, T., HJERMANN, D. Ø., & STENSETH, N. C. (2004). Regime shifts in the breeding of an Atlantic puffin population. Ecology Letters, 7 (5), 388-394.
DURANT, J. M., HJERMANN, D. O., ANKER-NILSSEN, T., BEAUGRAND, G., MYSTERUD, A., PETTORELLI, N., & STENSETH, N. C. (2005). Timing and abundance as key mechanisms affecting trophic interactions in variable environments. Ecology Letters, 8 (9), 952-958.
EINODER, L. (2009). A review of the use of seabirds as indicators in fisheries and ecosystem management. Fisheries Research, 95 (1), 6-13.
ELITH, J., & LEATHWICK, J. R. (2009). Species Distribution Models: Ecological Explanation and Prediction Across Space and Time. Annual Review of Ecology Evolution and Systematics, 40 (1), 677-697.
FAUCHALD, P. (2009). Spatial interaction between seabirds and prey: review and synthesis. Marine Ecology Progress Series, 391, 139-151.
FAUCHALD, P., ERIKSTAD, K. E., & SKARSFJORD, H. (2000). Scale-dependent predator–prey interactions: the hierarchical spatial distribution of seabirds and prey. Ecology, 81 (3), 773-783.
FORERO, M. G., BORTOLOTTI, G. R., HOBSON, K. A., DONÁZAR, J. A.,

BERTELLOTI, M., & BLANCO, G. (2004). High trophic overlap within the seabird community of Argentinean Patagonia: a multiscale approach. Journal of Animal Ecology, 73 (4), 789-801.

FORO PARA LA CONSERVACIÓN DEL MAR PATAGÓNICO Y ÁREAS DE INFLUENCIA. (2008). *Síntesis del estado de conservación del mar Patagonico y áreas de influencia*. Puerto Madryn, Argentina: Edición del Foro.

FOSSETTE, S., GLEISS, A. C., CHALUMEAU, J., BASTIAN, T., ARMSTRONG, C. D., VANDENABEELE, S., KARPYTCHEV, M., & HAYS, G. C. (2015). Current-oriented swimming by jellyfish and its role in bloom maintenance. Current Biology, 25 (3), 342-347.

FREDERIKSEN, M., HARRIS, P. M., DAUNT, F., ROTHERY, P., & WANLESS, S. (2004). Scale-dependent climate signals drive breeding phenology of three seabird species. Global Change Biology, 10, 1214-1221.

FREDERIKSEN, M., MAVOR, R. A., & WANLESS, S. (2007). Seabirds as environmental indicators: the advantages of combining data sets. Marine Ecology Progress Series, 352, 205-211.

FURNESS, R. W., & CAMPHUYSEN, K. C. (1997). Seabirds as monitors of the marine environment. ICES Journal of Marine Science, 54 (4), 726-737.

GAME, E. T., GRANTHAM, H. S., HOBDAY, A. J., PRESSEY, R. L., LOMBARD, A. T., BECKLEY, L. E., GJERDE, K., BUSTAMANTE, R., et al. (2009). Pelagic protected areas: the missing dimension in ocean conservation. Trends in Ecology & Evolution, 24 (7), 360-369.

GARCÍA-SOTO, C., VÁZQUEZ-CUERVO, J., CLEMENTE-COLÓN, P., & HERNÁNDEZ, F. (2012). Satellite oceanography and climate change. Deep Sea Research Part II: Topical Studies in Oceanography, 77-80, 1-9.

GARCÍA MOLINOS, J., HALPERN, B. S., SCHOEMAN, D. S., BROWN, C. J., KIESSLING, W., MOORE, P. J., PANDOLFI, J. M., POLOCZANSKA, E. S., et al. (2015). Climate velocity and the future global redistribution of marine biodiversity. Nature Climate Change, advance online publication.

GENOVART, M., SANZ-AGUILAR, A., FERNÁNDEZ-CHACÓN, A., IGUAL, J. M., PRADEL, R., FORERO, M. G., & ORO, D. (2012). Contrasting effects of climatic variability on the demography of a trans-equatorial migratory seabird. Journal of Animal Ecology, 82 (1), 121-130.

GIBBS, C., TOMCZAK JR, M., & LONGMORE, A. (1986). The nutrient regime of Bass Strait. Marine and Freshwater Research, 37 (4), 451-466.

GILARRANZ, L. J., MORA, C., & BASCOMPTE, J. (2016). Anthropogenic effects are associated with a lower persistence of marine food webs. Nature Communications, 7, 10737.

GONZÁLEZ-SOLÍS, J., CROXALL, J. P., ORO, D., & RUIZ, X. (2007). Trans-equatorial migration and mixing in the wintering areas of a pelagic seabird. Frontiers in Ecology and the Environment, 5 (6), 297-301.

GRECIAN, W. J., WITT, M. J., ATTRILL, M. J., BEARHOP, S., GODLEY, B. J.,

GRÉMILLET, D., HAMER, K. C., & VOTIER, S. C. (2012). A novel projection technique to identify important at-sea areas for seabird conservation: An example using Northern gannets breeding in the North East Atlantic. Biological Conservation, 156, 43-52.

GRÉMILLET, D., & BOULINIER, T. (2009). Spatial ecology and conservation of seabirds facing global climate change: a review. Marine Ecology Progress Series, 391, 121-137.

GRÉMILLET, D., & CHARMANTIER, A. (2010). Shifts in phenotypic plasticity constrain the value of seabirds as ecological indicators of marine ecosystems. Ecological Applications, 20 (6), 1498-1503.

GRÉMILLET, D., FORT, J., AMÉLINEAU, F., ZAKHAROVA, E., LE BOT, T., SALA, E., & GAVRILO, M. (2015). Arctic warming: nonlinear impacts of sea-ice and glacier melt on seabird foraging. Global Change Biology, 21 (3), 1116-1123.

GRÉMILLET, D., LEWIS, S., DRAPEAU, L., VAN DER LINGEN, C. D., HUGGETT, J. A., COETZEE, J. C., VERHEYE, H. M., DAUNT, F., et al. (2008). Spatial match–mismatch in the Benguela upwelling zone: should we expect chlorophyll and sea-surface temperature to predict marine predator distributions? Journal of Applied Ecology, 45 (2), 610-621.

GREVE, W., LANGE, U., REINERS, F., & NAST, J. (2001). Predicting the seasonality of North Sea zooplankton. Senckenbergiana Maritima, 31 (2), 263-268.

GUINET, C., CHASTEL, O., KOUDIL, M., DURBEC, J. P., & JOUVENTIN, P. (1998). Effects of warm sea–surface temperature anomalies on the blue petrel at the Kerguelen Islands. Proceedings of the Royal Society B: Biological Sciences, 265 (1400), 1001-1006.

HALPERN, B. S., FRAZIER, M., POTAPENKO, J., CASEY, K. S., KOENIG, K., LONGO, C., LOWNDES, J. S., ROCKWOOD, R. C., et al. (2015). Spatial and temporal changes in cumulative human impacts on the world's ocean. Nature Communications, 6, 7615.

HALPERN, B. S., WALBRIDGE, S., SELKOE, K. A., KAPPEL, C. V., MICHELI, F., D'AGROSA, C., BRUNO, J. F., CASEY, K. S., et al. (2008). A global map of human impact on marine ecosystems. Science, 319 (5865), 948-952.

HANSEN, J., SATO, M., RUEDY, R., LO, K., LEA, D. W., & MEDINA-ELIZADE, M. (2006). Global temperature change. Proceedings of the National Academy of Sciences, 103 (39), 14288-14293.

HAYS, G. C., FERREIRA, L. C., SEQUEIRA, A. M. M., MEEKAN, M. G., DUARTE, C. M., BAILEY, H., BAILLEUL, F., BOWEN, W. D., et al. (2016). Key questions in marine megafauna movement ecology. Trends in Ecology & Evolution, 2076.

HIPFNER, J. M. (2008). Matches and mismatches: ocean climate, prey phenology and breeding success in a zooplanktivorous seabird. Marine Ecology Progress Series, 368, 295-304.

HOEGH-GULDBERG, O., & BRUNO, J. F. (2010). The impact of climate change on the world's marine ecosystems. Science, 328 (5985), 1523-1528.

HUNSAKER, C. T., GOODCHILD, M. F., FRIEDL, M. A., & CASE, T. J. (2013). *Spatial uncertainty in ecology: implications for remote sensing and GIS applications*: Springer-Verlag.

HUNT JR, G., & SCHNEIDER, D. (1987). Scale-dependent processes in the physical and biological environment of marine birds. In J. P. Croxall (Ed.), *Seabirds: feeding ecology and role in marine ecosystems* (pp. 7-41). Great Britain: Cambridge University Press.

HYRENBACH, K. D., FORNEY, K. A., & DAYTON, P. K. (2000). Marine protected areas and ocean basin management. Aquatic conservation: marine and freshwater ecosystems, 10 (6), 437-458.

HYRENBACH, K. D., VEIT, R. R., WEIMERSKIRCH, H., & HUNT, G. L. (2006). Seabird associations with mesoscale eddies: the subtropical Indian Ocean. Marine Ecology Progress Series, 324, 271-279.

JENOUVRIER, S., WEIMERSKIRCH, H., BARBRAUD, C., PARK, Y. H., & CAZELLES, B. (2005). Evidence of a shift in the cyclicity of Antarctic seabird dynamics linked to climate. Proceedings of the Royal Society B: Biological Sciences, 272 (1566), 887-895.

KARPOUZI, V. S., WATSON, R., & PAULY, D. (2007). Modelling and mapping resource overlap between seabirds and fisheries on a global scale: a preliminary assessment. Marine Ecology Progress Series, 343, 87-99.

KAYS, R., CROFOOT, M. C., JETZ, W., & WIKELSKI, M. (2015). Terrestrial animal tracking as an eye on life and planet. Science, 348 (6240), aaa2478.

KEELING, R. F., KÖRTZINGER, A., & GRUBER, N. (2010). Ocean deoxygenation in a warming world. Annual review of marine science, 2, 199-229.

LASCELLES, B. G., LANGHAM, G. M., RONCONI, R. A., & REID, J. B. (2012). From hotspots to site protection: Identifying Marine Protected Areas for seabirds around the globe. Biological Conservation, 156, 5-14.

LASCELLES, B. G., TAYLOR, P. R., MILLER, M. G. R., DIAS, M. P., OPPEL, S., TORRES, L., HEDD, A., LE CORRE, M., et al. (2016). Applying global criteria to tracking data to define important areas for marine conservation. Diversity and Distributions, 22 (4), 422-431.

LE CORRE, M., JAEGER, A., PINET, P., KAPPES, M. A., WEIMERSKIRCH, H., CATRY, T., RAMOS, J. A., RUSSELL, J. C., et al. (2012). Tracking seabirds to identify potential Marine Protected Areas in the tropical western Indian Ocean. Biological Conservation, 156, 83-93.

LEJEUSNE, C., CHEVALDONNE, P., PERGENT-MARTINI, C., BOUDOURESQUE, C. F., & PEREZ, T. (2010). Climate change effects on a miniature ocean: the highly diverse, highly impacted Mediterranean Sea. Trends in Ecology & Evolution, 25 (4), 250-260.

LESCROËL, A., MATHEVET, R., PÉRON, C., AUTHIER, M., PROVOST, P., TAKAHASHI, A., & GRÉMILLET, D. (2016). Seeing the ocean through the eyes of seabirds: A new path for marine conservation? Marine Policy, 68, 212-

220.
LEVIN, S. A. (1992). The problem of pattern and scale in ecology: the Robert H. MacArthur award lecture. Ecology, 73 (6), 1943-1967.
LEWISON, R., CROWDER, L., READ, A., & FREEMAN, S. (2004). Understanding impacts of fisheries bycatch on marine megafauna. Trends in Ecology & Evolution, 19 (11), 598-604.
LEWISON, R., ORO, D., GODLEY, B., UNDERHILL, L., BEARHOP, S., WILSON, R., AINLEY, D., ARCOS, J., et al. (2012). Research priorities for seabirds: improving conservation and management in the 21st century. Endangered Species Research, 17 (2), 93-121.
LOUZAO, M., AUMONT, O., HOTHORN, T., WIEGAND, T., & WEIMERSKIRCH, H. (2012a). Foraging in a changing environment: habitat shifts of an oceanic predator over the last half century. Ecography, 35, 1-11.
LOUZAO, M., DELORD, K., GARCIA, D., BOUE, A., & WEIMERSKIRCH, H. (2012b). Protecting persistent dynamic oceanographic features: transboundary conservation efforts are needed for the critically endangered balearic shearwater. PLOS ONE, 7 (5), e35728.
LOUZAO, M., WIEGAND, T., BARTUMEUS, F., & WEIMERSKIRCH, H. (2014). Coupling instantaneous energy-budget models and behavioural mode analysis to estimate optimal foraging strategy: an example with wandering albatrosses. Movement ecology, 2 (1), 8.
LUBCHENCO, J., PALUMBI, S. R., GAINES, S. D., & ANDELMAN, S. (2003). Plugging a hole in the ocean: the emerging science of marine reserves. Ecological Applications, 13 (sp1), 3-7.
MACKAS, D. L., GREVE, W., EDWARDS, M., CHIBA, S., TADOKORO, K., ELOIRE, D., MAZZOCCHI, M. G., BATTEN, S., et al. (2012). Changing zooplankton seasonality in a changing ocean: comparing time series of zooplankton phenology. Progress in Oceanography, 97-100, 31-62.
MAXWELL, S. M., HAZEN, E. L., BOGRAD, S. J., HALPERN, B. S., BREED, G. A., NICKEL, B., TEUTSCHEL, N. M., CROWDER, L. B., et al. (2013). Cumulative human impacts on marine predators. Nature Communications, 4, 2688.
MAXWELL, S. M., HAZEN, E. L., LEWISON, R. L., DUNN, D. C., BAILEY, H., BOGRAD, S. J., BRISCOE, D. K., FOSSETTE, S., et al. (2015). Dynamic ocean management: defining and conceptualizing real-time management of the ocean. Marine Policy, 58, 42-50.
MCNAMARA, J. M., BARTA, Z., KLAASSEN, M., & BAUER, S. (2011). Cues and the optimal timing of activities under environmental changes. Ecology Letters, 14 (12), 1183-1190.
MONTEVECCHI, W. A. (2002). Interactions between fisheries and seabirds. In E. A. Schreiber & J. Burger (Eds.), *Biology of marine birds* (pp. 527-557). United States of America: CRC Press.
MOSELEY, C., GRÉMILLET, D., CONNAN, M., RYAN, P. G., MULLERS, R. H. E., VAN

DER LINGEN, C. D., MILLER, T. W., COETZEE, J. C., et al. (2012). Foraging ecology and ecophysiology of Cape gannets from colonies in contrasting feeding environments. Journal of Experimental Marine Biology and Ecology, 422-423, 29-38.

MYERS, R. A., & WORM, B. (2003). Rapid worldwide depletion of predatory fish communities. Nature, 423 (6937), 280-283.

NATALE, F., GIBIN, M., ALESSANDRINI, A., VESPE, M., & PAULRUD, A. (2015). Mapping fishing effort through AIS data. PLOS ONE, 10 (6), e0130746.

NAVARRO, J., CARDADOR, L., BROWN, R., & PHILLIPS, R. A. (2015). Spatial distribution and ecological niches of non-breeding planktivorous petrels. Scientific Reports, 5, 12164.

ORO, D. (2014). Seabirds and climate: knowledge, pitfalls and opportunities. Frontiers in Ecology and Evolution, 2, 79.

ORO, D., CAM, E., PRADEL, R., & MARTÍNEZ-ABRAÍN, A. (2004). Influence of food availability on demography and local population dynamics in a long-lived seabird. Proceedings of the Royal Society B: Biological Sciences, 271 (1537), 387-396.

PAIVA, V. H., GERALDES, P., MARQUES, V., RODRIGUEZ, R., GARTHE, S., & RAMOS, J. A. (2013). Effects of environmental variability on different trophic levels of the North Atlantic food web. Marine Ecology Progress Series, 477, 15-28.

PAIVA, V. H., GERALDES, P., RAMIREZ, I., MEIRINHO, A., GARTHE, S., & RAMOS, J. A. (2010a). Foraging plasticity in a pelagic seabird species along a marine productivity gradient. Marine Ecology Progress Series, 398, 259-274.

PAIVA, V. H., GERALDES, P., RAMÍREZ, I., MEIRINHO, A., GARTHE, S., & RAMOS, J. A. (2010b). Oceanographic characteristics of areas used by Cory's shearwaters during short and long foraging trips in the North Atlantic. Marine Biology, 157 (6), 1385-1399.

PAIVA, V. H., GUILFORD, T., MEADE, J., GERALDES, P., RAMOS, J. A., & GARTHE, S. (2010c). Flight dynamics of Cory's shearwater foraging in a coastal environment. Zoology (Jena), 113 (1), 47-56.

PALECZNY, M., HAMMILL, E., KARPOUZI, V., & PAULY, D. (2015). Population trend of the world's monitored seabirds, 1950-2010. PLOS ONE, 10 (6), e0129342.

PARMESAN, C. (2006). Ecological and evolutionary responses to recent climate change. Annual Review of Ecology, Evolution, and Systematics, 37, 637-639.

PAULY, D., CHRISTENSEN, V., GUÉNETTE, S., PITCHER, T. J., SUMAILA, U. R., WALTERS, C. J., WATSON, R., & ZELLER, D. (2002). Towards sustainability in world fisheries. Nature, 418 (6898), 689-695.

PELLETIER, L., KATO, A., CHIARADIA, A., & ROPERT-COUDERT, Y. (2012). Can thermoclines be a cue to prey distribution for marine top predators? A case study with little penguins. PLOS ONE, 7 (4), e31768.

PHILLIPS, R. A. (2013). Requisite improvements to the estimation of seabird by-catch

in pelagic longline fisheries. Animal Conservation, 16 (2), 157-158.
PIATT, I. J. F., SYDEMAN, W. J., & WIESE, F. (2007). Introduction: seabirds as indicators of marine ecosystems. Marine Ecology Progress Series, 352, 199-204.
PINAUD, D., & WEIMERSKIRCH, H. (2005). Scale-dependent habitat use in a long-ranging central place predator. Journal of Animal Ecology, 74 (5), 852-863.
PONCHON, A., GRÉMILLET, D., DOLIGEZ, B., CHAMBERT, T., TVERAA, T., GONZÁLEZ-SOLÍS, J., BOULINIER, T., & RANDS, S. (2013). Tracking prospecting movements involved in breeding habitat selection: insights, pitfalls and perspectives. Methods in Ecology and Evolution, 4 (2), 143-150.
PULVENIS, J.-F. (2014). Fisheries and Aquaculture topics. The State of World Fisheries and Aquaculture (SOFIA). In FAO (Ed.), FAO Fisheries and Aquaculture Department. Rome.
PYKE, G. H., PULLIAM, H. R., & CHARNOV, E. L. (1977). Optimal foraging: a selective review of theory and tests. Quarterly Review of Biology, 137-154.
QUILLFELDT, P., CHEREL, Y., DELORD, K., & WEIMERKIRCH, H. (2015). Cool, cold or colder? Spatial segregation of prions and blue petrels is explained by differences in preferred sea surface temperatures. Biology Letters, 11 (4), 20141090.
RAMÍREZ, F., AFÁN, I., TAVECCHIA, G., CATALÁN, I. A., ORO, D., & SANZ-AGUILAR, A. (2016). Oceanographic drivers and mistiming processes shape breeding success in a seabird. Proceedings of the Royal Society B: Biological Sciences, 283 (1826), 20152287.
RAMOS, J. A., GRANADEIRO, J. P., RODRIGUEZ, B., NAVARRO, J., PAIVA, V., BÉCARES, J., REYES-GONZÁLEZ, J., FAGUNDES, I., et al. (2013). Meta-population feeding grounds of Cory's shearwater in the subtropical Atlantic Ocean: implications for the definition of Marine Protected Areas based on tracking studies. Diversity and Distributions, In press.
RAYMOND, B., LEA, M.-A., PATTERSON, T., ANDREWS-GOFF, V., SHARPLES, R., CHARRASSIN, J.-B., COTTIN, M., EMMERSON, L., et al. (2014). Important marine habitat off east Antarctica revealed by two decades of multi-species predator tracking. Ecography, 38 (2), 121-129.
RAYMOND, B., SHAFFER, S. A., SOKOLOV, S., WOEHLER, E. J., COSTA, D. P., EINODER, L., HINDELL, M., HOSIE, G., et al. (2010). Shearwater foraging in the Southern Ocean: the roles of prey availability and winds. PLOS ONE, 5 (6), e10960.
REED, T. E., WARZYBOK, P., WILSON, A. J., BRADLEY, R. W., WANLESS, S., & SYDEMAN, W. J. (2009). Timing is everything: flexible phenology and shifting selection in a colonial seabird. Journal of Animal Ecology, 78 (2), 376-387.
RICKLEFS, R. E. (1990). Seabird life histories and the marine environment: some speculations. Colonial Waterbirds, 13 (1), 1-6.
ROBINSON, I. S. (2010). *Discovering the Ocean from Space: The unique applications of satellite oceanography* (Vol. 4110): Springer.

RODRIGUEZ, A., RODRIGUEZ, B., & NEGRO, J. J. (2015). GPS tracking for mapping seabird mortality induced by light pollution. Scientific Reports, 5, 10670.

RONCONI, R. A., LASCELLES, B. G., LANGHAM, G. M., REID, J. B., & ORO, D. (2012). The role of seabirds in Marine Protected Area identification, delineation, and monitoring: Introduction and synthesis. Biological Conservation, 156, 1-4.

ROPERT-COUDERT, Y., & WILSON, R. P. (2005). Trends and perspectives in animal-attached remote sensing. Frontiers in Ecology and the Environment, 3, 437-444.

ROSE, R. A., BYLER, D., EASTMAN, J. R., FLEISHMAN, E., GELLER, G., GOETZ, S., GUILD, L., HAMILTON, H., et al. (2015). Ten ways remote sensing can contribute to conservation. Conservation Biology, 29 (2), 350-359.

RUSSELL, D. J. F., WANLESS, S., COLLINGHAM, Y. C., ANDERSON, B. J., BEALE, C., REID, J. B., HUNTLEY, B., & HAMER, K. C. (2015). Beyond climate envelopes: bio-climate modelling accords with observed 25-year changes in seabird populations of the British Isles. Diversity and Distributions, 21 (2), 211-222.

SANDERSON, E. W., JAITEH, M., LEVY, M. A., REDFORD, K. H., WANNEBO, A. V., & WOOLMER, G. (2002). The human footprint and the last of the wild. Bioscience, 52 (10), 891-904.

SANDVIK, H., COULSON, T. I. M., & SÆTHER, B.-E. (2008). A latitudinal gradient in climate effects on seabird demography: results from interspecific analyses. Global Change Biology, 14 (4), 703-713.

SCALES, K. L., HAZEN, E. L., JACOX, M. G., EDWARDS, C. A., BOUSTANY, A. M., OLIVER, M. J., & BOGRAD, S. J. (2016). Scale of inference: on the sensitivity of habitat models for wide-ranging marine predators to the resolution of environmental data. Ecography, advance online publication.

SCALES, K. L., MILLER, P. I., EMBLING, C. B., INGRAM, S. N., PIROTTA, E., & VOTIER, S. C. (2014). Mesoscale fronts as foraging habitats: composite front mapping reveals oceanographic drivers of habitat use for a pelagic seabird. Journal of the Royal Society Interface, 11 (100), 20140679.

SCALES, K. L., MILLER, P. I., HAWKES, L. A., INGRAM, S. N., SIMS, D. W., VOTIER, S. C., & PUNT, A. (2014). On the Front Line: frontal zones as priority at-sea conservation areas for mobile marine vertebrates. Journal of Applied Ecology, 51 (6), 1575-1583.

SCHREIBER, E. A., & BURGER, J. (2001). *Biology of marine birds*. United States of America: CRC Press.

SCOTT, B., SHARPLES, J., ROSS, O. N., WANG, J., PIERCE, G., & CAMPHUYSEN, C. (2010). Sub-surface hotspots in shallow seas: fine-scale limited locations of top predator foraging habitat indicated by tidal mixing and sub-surface chlorophyll. Marine Ecology Progress Series, 408, 207-226.

SHACKELL, N. L., FRANK, K. T., FISHER, J. A., PETRIE, B., & LEGGETT, W. C. (2009). Decline in top predator body size and changing climate alter trophic structure in an oceanic ecosystem. Proceedings of the Royal Society B: Biological Sciences,

rspb20091020.
SHEALER, D. A., SCHREIBER, E., & BURGER, J. (2002). Foraging behavior and food of seabirds. In J. Burger & E. A. Schreiber (Eds.), *Biology of marine birds* (pp. 137-177). Boca Raton: CRC Press.
SHEPARD, E. L. C., WILSON, R. P., REES, W. G., GRUNDY, E., LAMBERTUCCI, S. A., VOSPER, S. B., ASSOCIATE EDITOR: ROBERT, D., & EDITOR: JUDITH, L. B. (2013). Energy landscapes shape animal movement ecology. The American Naturalist, 182 (3), 298-312.
SIDHU, L. A., DANN, P., CHAMBERS, L., & CATCHPOLE, E. A. (2012). Seasonal ocean temperature and the survival of first-year little penguins Eudyptula minor in south-eastern Australia. Marine Ecology Progress Series, 454, 263-272.
SKEWGAR, E., BOERSMA, P. D., HARRIS, G., & CAILLE, G. (2007). Sustainability. Anchovy fishery threat to Patagonian ecosystem. Science, 315 (5808), 45.
STOMMEL, H. (1963). Varieties of oceanographic experience. Science, 139 (3555), 572-576.
SUTHERS, I. M., YOUNG, J. W., BAIRD, M. E., ROUGHAN, M., EVERETT, J. D., BRASSINGTON, G. B., BYRNE, M., CONDIE, S. A., et al. (2011). The strengthening East Australian Current, its eddies and biological effects — an introduction and overview. Deep Sea Research Part II: Topical Studies in Oceanography, 58 (5), 538-546.
SYDEMAN, W. J., GARCÍA-REYES, M., SCHOEMAN, D. S., RYKACZEWSKI, R. R., THOMPSON, S. A., BLACK, B. A., & BOGRAD, S. J. (2014). Climate change and wind intensification in coastal upwelling ecosystems. Science, 345 (6192), 77-80.
SYDEMAN, W. J., POLOCZANSKA, E., REED, T. E., & THOMPSON, S. A. (2015). Climate change and marine vertebrates. Science, 350 (6262), 772-777.
TEW KAI, E., BENHAMOU, S., VAN DER LINGEN, C. D., COETZEE, J. C., PICHEGRU, L., RYAN, P. G., & GRÉMILLET, D. (2013). Are Cape gannets dependent upon fishery waste? A multi-scale analysis using seabird GPS-tracking, hydro-acoustic surveys of pelagic fish and vessel monitoring systems. Journal of Applied Ecology, 50 (3), 659-670.
TRATHAN, P. N., GARCÍA-BORBOROGLU, P., BOERSMA, D., BOST, C.-A., CRAWFORD, R. J. M., CROSSIN, G. T., CUTHBERT, R. J., DANN, P., et al. (2015). Pollution, habitat loss, fishing, and climate change as critical threats to penguins. Conservation Biology, 29 (1), 31-41.
TREMBLAY, Y., BERTRAND, S., HENRY, R. W., KAPPES, M. A., COSTA, D. P., & SHAFFER, S. A. (2009). Analytical approaches to investigating seabird–environment interactions: a review. Marine Ecology Progress Series, 391, 153-163.
TURNER, W., RONDININI, C., PETTORELLI, N., MORA, B., LEIDNER, A. K., SZANTOI, Z., BUCHANAN, G., DECH, S., et al. (2015). Free and open-access satellite data are key to biodiversity conservation. Biological Conservation, 182,

173-176.

VISSER, M. E., & BOTH, C. (2005). Shifts in phenology due to global climate change: the need for a yardstick. Proceedings of the Royal Society B: Biological Sciences, 272 (1581), 2561-2569.

WAKEFIELD, E. D., BODEY, T. W., BEARHOP, S., BLACKBURN, J., COLHOUN, K., DAVIES, R., DWYER, R. G., GREEN, J. A., et al. (2013). Space partitioning without territoriality in gannets. Science, 341 (6141), 68-70.

WASSMANN, P. (2011). Arctic marine ecosystems in an era of rapid climate change. Progress in Oceanography, 90 (1–4), 1-17.

WATSON, R. A., CHEUNG, W. W. L., ANTICAMARA, J. A., SUMAILA, R. U., ZELLER, D., & PAULY, D. (2013). Global marine yield halved as fishing intensity redoubles. Fish and Fisheries, 14 (4), 493-503.

WEIMERKIRCH, H. (2002). Seabird conservation. In J. Burger & E. A. Schreiber (Eds.), *Biology of marine birds* (pp. 115-135). Boca Raton: CRC Press.

WEIMERSKIRCH, H. (2007). Are seabirds foraging for unpredictable resources? Deep Sea Research Part II: Topical Studies in Oceanography, 54 (3-4), 211-223.

WEIMERSKIRCH, H., GAULT, A., & CHEREL, Y. (2005). Prey distribution and patchiness: factors in foraging success and efficiency of wandering albatrosses. Ecology, 86 (10), 2611-2622.

WEIMERSKIRCH, H., GUIONNET, T., MARTIN, J., SHAFFER, S. A., & COSTA, D. (2000). Fast and fuel efficient? Optimal use of wind by flying albatrosses. Proceedings of the Royal Society B: Biological Sciences, 267 (1455), 1869-1874.

WEIMERSKIRCH, H., LOUZAO, M., DE GRISSA, S., & DELORD, K. (2012). Change in wind pattern alter albatross distribution and life-history traits. Science, 335, 211-214.

WHITE, T. C. R. (2008). The role of food, weather and climate in limiting the abundance of animals. Biological Reviews, 83 (3), 227-248.

WIENS, J. A. (1989). Spatial Scaling in Ecology. Functional Ecology, 3, 385-397.

WINTON, M., GRIFFIES, S. M., SAMUELS, B. L., SARMIENTO, J. L., & FRÖLICHER, T. L. (2013). Connecting changing ocean circulation with changing climate. Journal of Climate, 26 (7), 2268-2278.

WITT, M. J., & GODLEY, B. J. (2007). A step towards seascape scale conservation: using vessel monitoring systems (VMS) to map fishing activity. PLOS ONE (10), e1111.

WU, L., CAI, W., ZHANG, L., NAKAMURA, H., TIMMERMANN, A., JOYCE, T., MCPHADEN, M. J., ALEXANDER, M., et al. (2012). Enhanced warming over the global subtropical western boundary currents. Nature Climate Change, 2, 161-166.

YANG, J., GONG, P., FU, R., ZHANG, M., CHEN, J., LIANG, S., XU, B., SHI, J., et al. (2013). The role of satellite remote sensing in climate change studies. Nature Climate Change, 3 (10), 875-883.