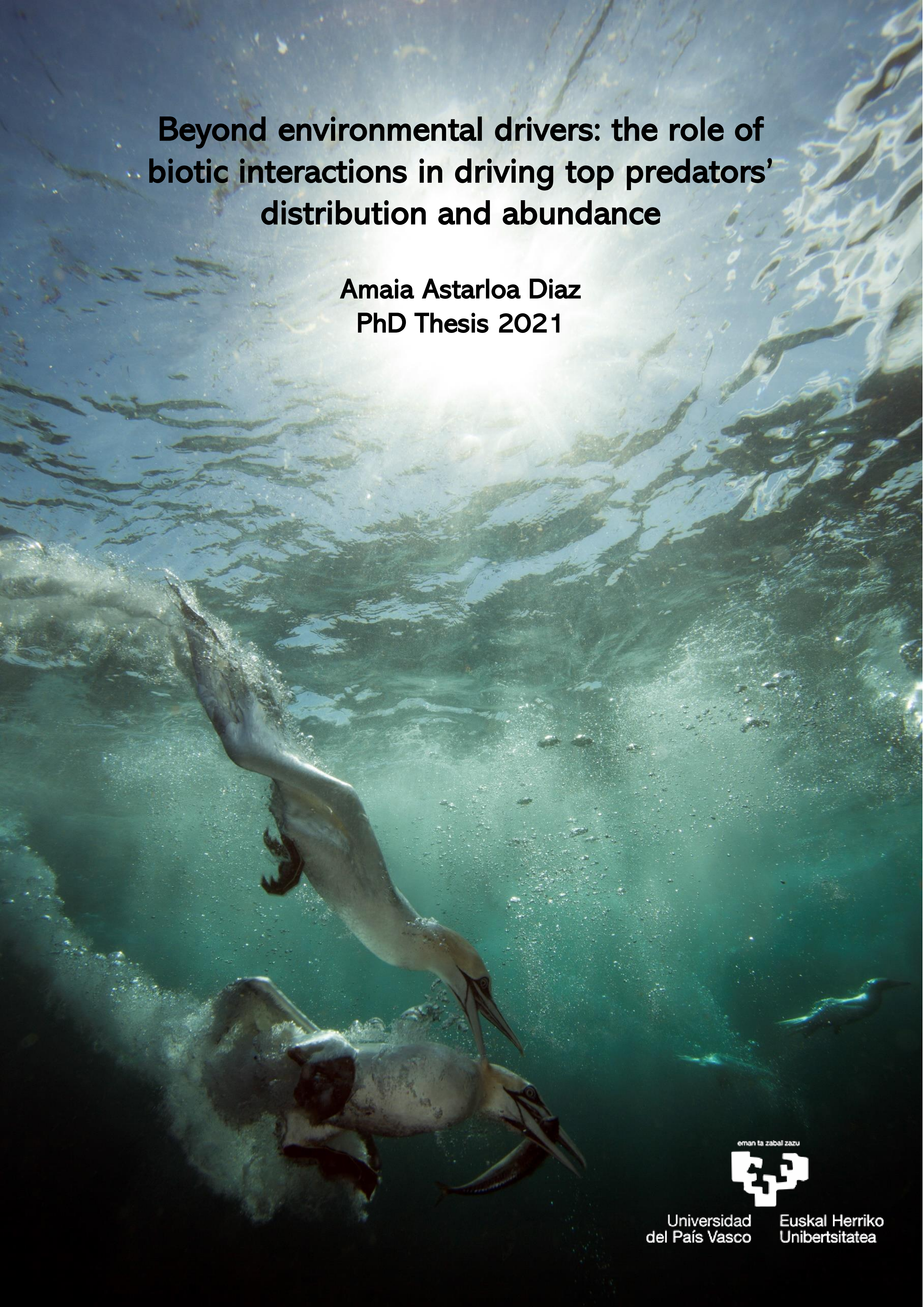
Beyond environmental drivers: the role of biotic interactions in driving top predators' distribution and abundance

Amaia Astarloa Diaz
PhD Thesis 2021



eman ta zabal zazu

Universidad
del País Vasco

Euskal Herriko
Unibertsitatea

Beyond environmental drivers: the role of biotic interactions in driving top predators' distribution and abundance

Presented by

Amaia Astarloa Diaz

A thesis submitted to the University of the Basque Country for the degree of

DOCTOR OF PHILOSOPHY

Thesis Directors

Dr. Maite Louzao Arsuaga (AZTI)

Dr. Guillem Chust Peters (AZTI)

Department

Zoology and Animal Cell Biology

Doctoral programme

Marine Environment and Resources

University of the Basque Country

May 2021

MEMBER OF
BASQUE RESEARCH
& TECHNOLOGY ALLIANCE

eman ta zabal zazu

Universidad del País Vasco
Euskal Herriko Unibertsitatea

This PhD thesis was funded by the Education Department of the Basque Government [PRE_2016_1_0134] and supported by JUVENA, CHALLENGES, CLIPES, ECOPES, EPELECO, H2020 Mission Atlantic, and LIFE-IP URBAN KLIMA 2050 projects.

It was presented under the international mention from the University of Basque Country and reviewed by two scientific experts from non-Spanish research institutions:

- Dr. **Vitor Hugo Rodrigues Paiva**, from the Marine and Environmental Sciences Centre, University of Coimbra (Coimbra, Portugal).
- Dr. **James J. Waggitt**, from the School of Ocean Sciences, Bangor University (Anglesey, UK).

Recommended citation:

Astarloa A. (2021) Beyond environmental drivers: the role of biotic interactions in driving top predators' distribution and abundance. PhD Thesis. Department of Zoology and Animal Cell Biology, University of the Basque Country, 213 pp.

CONTENTS

ACKNOWLEDGEMENTS

First of all, I would like to thank my supervisors Maite Louzao and Guillem Chust for their valuable guidance, opinions and patience. I really appreciate the time and effort you put into this thesis along these four years.

I would also like to thank the Education Department of the Basque Government for awarding me with the Doctoral Fellowship [PRE_2016_1_0134], and of course, to AZTI, to the "Marine Ecosystem Functioning" area and to all the projects I have been involved in and that have economically supported conferences and research stays: JUVENA, CHALLENGES, CLIPES, ECOPES, EPELECO, H2020 Mission Atlantic and LIFE-IP URBAN KLIMA 2050 project.

Thanks as well to the University of St Andrews, the CREEM research centre, the University of Bangor and Rutgers University for hosting academic exchanges and naturally, to the University of Basque Country for the academic support and funding. Also, to the researchers that guided me while I was there (Len Thomas, Richard Glennie, James Waggitt, Peter Evans, Malin Pinsky, James Thorson) and to all the people I met and stayed with me during those months abroad.

I also appreciate the efforts made by the two external reviewers, James Waggitt and Vitor Paiva, so this thesis could receive the international mention awarded by the University of Basque Country as well as the support and help provided by Manu Soto along these years.

Special thanks are given to the crew on board R/V Emma Bardán and R/V Ramón Margalef and all the AZTI and Spanish Institute of Oceanography (IEO) staff who participated in JUVENA and PELACUS surveys for their excellent job, collaborative support and unforgettable experiences. Many thanks to all the friends and colleges from AZTI that have made this period easier and worthwhile and to the A8 team, who made the long journeys from home to work more entertaining. And last but not least, to my parents, family, friends, mate for always being there.

SCIENTIFIC PRODUCTION AND FORMATION

The scientific and technical material produced, and the scientific formation acquired during the period of this doctoral thesis (January 2017- May 2021) are detailed in this section:

1. Peer-Reviewed Publications

First author publications

Astarloa, A., Louzao, M., Andrade, J., Babey, L., Berrow. S, Boisseau, O. Brereton, T., Dorémus, G., Evans P.G.H., Hodgins, N.K., Lewis, M., Martinez-Cedeira, J., Pinsky, M., Ridoux, V., Saavedra, C., Santos, M.B., Thorson, J., Waggitt J.J., Wall D., Chust, G. (Under review). The role of climate, oceanography, and prey in driving decadal spatio-temporal patterns of a highly mobile top predator. *Frontiers in Marine Science.*

Astarloa, A., Glennie, R., Chust, G., García-Barón, I., Boyra G., Martínez, U, Rubio, A., & Louzao, M. (2021). Niche segregation mechanisms in marine apex predators inhabiting dynamic environments. *Diversity and Distributions*. https: //doi.org /10.1111/ddi.13229.

Astarloa, A., Louzao, M., Boyra, G., Martínez, U., Rubio, A., Irigoien, X., Hui, F.K.C. & Chust, G. (2019). Identifying main interactions in marine predator-prey networks of the Bay of Biscay. ICES Journal of Marine Science, 76(7), 2247-2259. https://doi.org/10.1093/icesj ms/fsz140.

Other

Gaspar, C., Giménez, J., Andonegi, E., **Astarloa, A.**, Chouvelon, T., Franco, J., Goñi, N., Corrales, X., Spitz J., Bustamante, P. & Louzao M. (Submitted). Trophic ecology of northern gannets and niche segregation within the apex predator community in the Bay of Biscay. *Marine Progress in Marine Science*.

García-Barón, I., Santos, M.B., Saavedra, C., **Astarloa, A.**, Valeiras, J., Barcelona, S.G., Louzao, M. (2020). Essential dynamic ocean variables shape the environmental envelopes of marine megafauna diversity. *Ecological Indicators*. 117, 106504. DOI: 10.1016/j.ecolind.2020.106504

2. Conference Papers

Oral communications

Astarloa, A., Louzao, Chust, G. (2020). *The role of environment and prey in driving marine predators' distribution in the Bay of Biscay*. In 14th International Postgraduate Course Research in Marine Environment & Resources 2019. Donostia-San Sebastián (Spain).

Astarloa, A., Glennie, R., Chust, G., García-Barón, I., Boyra G., Martínez, U, Rubio, A., & Louzao, M. (2019). *Evidence of niche differentiation in co-occurring birds.* In British Ecological Society Annual Meeting. Belfast (UK)

Louzao, M, **Astarloa, A.**, García-Barón, I., Martínez U., Uranga, J., Rubio, A., Chust, G., Boyra, G. (2019). *Marine mammals seeking for prey in tridimensional environments.* In World Marine Mammals Conference. Barcelona (Spain).

Astarloa, A., Louzao, M., Martínez, U., Boyra G., Rubio, A., Irigoien, X., Chust, G. (2019). *Understanding predator-prey networks structure from co-occurrence patterns.* In 1st Meeting of the Iberian Ecological Society & XIV AEET Meeting. Barcelona (Spain).

Astarloa, A., Louzao, Chust, G. (2019). *The role of environment and prey in driving marine predators' distribution in the Bay of Biscay*. In 13th International Postgraduate Course Research in Marine Environment & Resources 2019. Donostia-San Sebastián (Spain).

Louzao, M., **Astarloa, A.**, García-Barón, I., Chust, G., Martínez, U., Uranga, J., Rubio, A., Boyra, G. (2018) *Superposición espacial de mamíferos marinos y presas pelágicas en el golfo de Bizkaia.* In XI Spanish Society of Cetaceans. Bilbao (Spain).

Astarloa, A., Louzao, M., Martínez, U., Boyra G., Chust, G. (2018). *Disentangling the co-occurrence patterns of marine top predators and prey in the Bay of Biscay: environment versus species interactions.* In XVIth International Symposium on Oceanography of the Bay of Biscay (ISOBAY 16). Anglet (France).

Astarloa, A., Louzao, M., Martínez, U., Boyra G., Chust, G. (2017). *Interacción espacial de la comunidad de aves, mamíferos marinos y presas pelágicas a partir de campañas oceanográficas.* In XXIII Spanish Ornithology Conference. Badajoz (Spain).

Posters

Astarloa, A., Louzao, M., Martínez, U., Boyra G., Rubio, A., Irigoien, X., Chust, G. (2018). *Comunidad de cetáceos del golfo de Bizkaia: ausencia de coocurrencia entre especies como consecuencia de la competencia interespecífica*. In XI Spanish Society of Cetaceans Congress. Bilbao (Spain).

Astarloa A., Louzao, M., Martínez, U., Boyra G., Chust, G. (2017). *Understanding pelagic community's assembly from multidisciplinary oceanographic cruises.* In COAST. Bordeaux (France).

Louzao, M., García-Barón, I., Martínez, U., Saavedra, C., **Astarloa, A**., Santos, M.B., Pierce, G., Boyra, G. (2017). *Uso de las campañas oceanográficas anuales para monitorear los mamíferos marinos.* In X Spanish Society of Cetaceans Congress. Valencia (Spain).

3. Scientific Reports

Astarloa, A., Vázquez, J.A., Predajas, A. & Louzao, M. Predators observation in JUVENA 2019. *In* ICES. 2020. Working Group on Acoustic and Egg Surveys for Sardine and Anchovy in ICES areas 7, 8 and 9 (WGACEGG; outputs from 2019 meeting). ICES Scientific Reports. 2:44. 490 pp.

García-Barón, I., **Astarloa, A**., Vázquez, J.A., Bidegain, G., Urtizberea, I., Basterretxea, M. and Louzao, M. Predators observation in JUVENA 2018. *In* ICES. 2018. Report of the Working Group on Acoustic and Egg Surveys for Sardine and Anchovy in ICES Areas 7, 8 and 9 (WGACEGG). 19-23 November. Nantes, France. ICES CM 2018/EOSG:03. 355pp.

García-Barón, I., **Astarloa, A**., Vázquez, J.A., Bidegain, G., Urtizberea, I., Basterretxea, M. and Louzao, M. Predators observation in JUVENA 2017. *In* ICES. 2018. Working Group on Acoustic and Egg Surveys for Sardine and Anchovy in ICES Areas 7, 8 and 9 (WGACEGG). ICES WGACEGG REPORT 2017 3-17 November 2017. pp. 388.

4. Projects

LIFE-IP URBAN KLIMA 2050: project for the systemic implementation of the climate change action in the Basque Country for increased urban resilience as full territory enabler. Funded by the European Union through LIFE programme (Grant agreement n°: LIFE18 IPC/ES/000001)

MISSION ATLANTIC: project for evaluating and ensuring a sustainable development of Atlantic Ocean. Funded by Horizon 2020 programme of the European Commission (Contract No. 862428).

EPELECO: project for evaluating the pelagic realm from an integrated ecosystem-based perspective in a changing world: insights from the NE Atlantic (RTI2018-101591- B- I00). Funded by "Ministerio de Ciencia, Innovación y Universidades (MCIU)", "Agencia Estatal de Investigación (AEI)" and "Fondo Europeo de Desarrollo Regional (FEDER)".

ECOPES: project for applying an ecosystem-based approach to the fisheries research. Funded by "Departamento de Desarrollo Económico e Infraestructuras – Vice. de Agricultura, Pesca y Política Alimentaria, Dirección de Pesca y Acuicultura" of the Basque Government.

CLIPES: project for predicting and anticipating the effects of variability in oceanographic conditions and global climate change on Basque fleet fisheries. Funded by "Departamento de Desarrollo Económico e Infraestructuras, Vice. de Agricultura, Pesca y Política Alimentaria, Dirección de Pesca y Acuicultura" of the Basque Government.

CHALLENGES: project for advancing conservation efforts in southern European waters: Pelagic changing ecosystems from predators' perspective (CTM2013-47032- R). Funded by "Ministerio de Economía y Competitividad" of the Spanish Government.

JUVENA: project for evaluating and estimating the abundance of juvenile anchovy in the Bay of Biscay. Funded by the 'Viceconsejería de Agricultura, Pesca y Políticas Alimentarias - Departamento de Desarrollo Económico y Sostenibilidad y Medio Ambiente' of the Basque Government, the 'Secretaría General de Pesca, Ministerio de Agricultura, Alimentación y Medio Ambiente' of the Spanish Government and by the Spanish Institute of Oceanography (IEO).

5. Oceanographic Surveys

JUVENA 2019 - Acoustic survey providing a synoptic overview on the autumn distribution of small pelagic species and of their environment. AZTI. R/V Ramón Margalef. 3rd September – 23rd September. From the north Iberian coast in the south to the Celtic Sea in the north.

JUVENA 2018 - Acoustic survey providing a synoptic overview on the autumn distribution of small pelagic species and of their environment. AZTI. R/V Ramón Margalef. 1st September - 30th September. From the north Iberian coast in the south to the Celtic Sea in the north.

JUVENA 2017 - Acoustic survey providing a synoptic overview on the autumn distribution of small pelagic species and of their environment. AZTI. R/V Ramón Margalef. 31st August – 2nd October. From the north Iberian coast in the south to the Celtic Sea in the north.

PELACUS 2017 – Acoustic survey for the assessment of pelagic resources. IEO. R/V Miguel Oliver. 14th March - 16th April. Galician shell - Spanish national waters.

6. Research stays

Centre for Research into Ecological and Environmental Modelling (CREEM), St Andrews, UK (May-July 2018). Supervisors: Richard Glennie and Len Thomas

Rutgers University - Department of Ecology, Evolution and Natural Resources, New Brunswick, USA (May-July 2019). Supervisor: Malin Pinsky

SUMMARY

Over the past 10 years, Species Distribution Models (SDMs) have become commonplace in the studies of biogeography, ecology, conservation biology, and climate change. However, most studies applying SDMs mainly quantify species-environment relationships, being related to the Grinnellian niche concept, which describes the response of the species to a given set of non-interactive variables. As a result, the Eltonian niche –focused on the functional roles of species, biotic interactions and resource-consumer dynamics– has been largely omitted in the field of SDMs, although it is well known that species distribution and abundance patterns not only depend on species individual responses to the abiotic environment, but also on their interactions.

For a long time, biotic interactions have been believed to affect ecological processes mainly at local scales, preventing researchers working at large biogeographical scales from addressing them. In contrast, recent evidence suggest that biotic interactions can shape species distributions from local to regional and continental scales, and even improve the explanatory power and predictive accuracy of the models.

Inferring biotic interactions, however, is not an easy task, as it requires a good knowledge on species behaviour or a direct observation of interactions. When direct information about biotic interactions is not available, proxies such as geographical data can help obtain insights about them, by asking if some species co-occur more or less often than what could be expected by random, or by computing and visualizing the spatial overlap in species distributions.

In dynamic environments such as ocean, acquiring such information requires big efforts, due to the size and complexity of the marine realm and the relative difficulty of taking measurements in there. Integrated ecosystem surveys, directed to monitor the biological (e.g., plankton, fishes, megafauna) and the physical (hydrography) component of the ecosystem, provide an excellent opportunity, as they offer a simultaneous framework in which the different components of the ecosystem can be analysed together at the same spatio-temporal scale. By this means, synoptical relationship can be explored between the species and their environment, following the traditional SDM approach, or between species, aiming to advance towards a better knowledge of biotic interactions.

In southern European waters, several institutions perform multidisciplinary surveys to monitor the widely diverse community of plankton, fish and megafauna inhabiting the area. The JUVENA survey is such an example, which monitors the marine environment of the Bay of Biscay in autumn, coinciding with the period in which numerous top predator species use the area as a migration corridor.

Top predators such as seabirds and cetaceans have been long considered good ecological indicators, as they face numerous impacts and respond to different ecosystem changes while moving across their vast distributional ranges. They are, in addition, protected under different international agreements, such as the Bird Directive (Council Directive 2009/147/EC) or the Habitat Directive (Council Directive 92/43/EEC), which aim to promote and maintain biological diversity through the conservation of natural habitats and biodiversity in the European Union territory. But despite the conservation efforts, seabirds are one of the most threatened groups, while many cetacean species are still intentionally killed or indirectly impacted by commercial fisheries.

Effective conservation and management measures require the identification of variables shaping the niche of species (both the Eltonian and the Grinnellian niche) and that is why this thesis aimed to advance in the understanding of how biotic and abiotic factors shape species distribution and abundance by using the community of top predators of the Bay of Biscay as case study. To address this overall objective, we carried out three different studies that were displayed as independent chapters and that aimed to answer specific research questions.

Chapter I, for example, aimed to identify interspecific associations occurring within the predator-prey network of the Bay of Biscay as well as their potential drivers. For that, we applied the Joint Species Distribution Modelling approach, JSDM, to the co-occurrence (presence/absence) patterns of both prey and top predator communities (11 and 17 species, respectively) obtained from JUVENA surveys during 2013–2016. JSDM, unlike conventional approaches, allows distinguishing between biotic interactions and dis-/similar environmental preferences. In fact, a positive (or negative) spatial association between two species does not necessarily signify a biotic interaction, and it can result, instead, from the species having similar (or dissimilar) habitat requirement. By this means, we found that the co-occurrence patterns of top predators and prey were driven by a combination of environmental factors (dis-/similar environmental preferences) and biotic interactions, among which we identified schooling in prey (e.g., anchovy–sardine), local enhancement/facilitation in predators (e.g., Cory's shearwater–fin whale), and predation between predator–prey species (e.g., northern gannet–horse mackerel). These results suggest that analysing species co-occurrence patterns with tools such as JSDM can help identify, up to a certain point, interspecific interactions, which in turn, may be useful to obtain insights on the functioning of ecological network. However, the identification of biotic interactions with JSDM, like with all statistical approaches aimed at attributing sources of species covariation, is very sensitive to the choice of environmental covariates, and this is why a careful and reflective interpretation of resulting interactions is recommended.

A conceptually simpler but technically more challenging alternative would be to derive interactions from abundance (count) data while including interacting species (e.g., prey) as predictor variables in SDMs. Although inferring ecological interactions from the easiest data to acquire (presence-absence data) holds a great appeal, count data carry more information that could be used to make more refined inferences on why species occur at a specific location and how the biotic predictors affect their distribution and abundance patterns.

In this line, Chapter II modelled the sightings (counts) of five phylogenetically related seabird species collected during 2013-2017 in JUVENA surveys with the aim of understanding how co-occurring top predators shared the environmental and trophic niche. To address this objective, we a) identified the biologically meaningful vertical range affecting seabird species, b) modelled their environmental and trophic niches, c) estimated an environmental and trophic overlap index for each pair-wise species, and d) developed a conceptual framework with the most plausible segregation hypotheses. The application of the conceptual framework revealed that in this particular area, pelagic birds coexist through environmental and trophic niche partitioning and potentially through vertical segregation, based on the different biologically meaningful vertical ranges we identified for each species. Indeed, some species responded to prey and oceanographic conditions on the surface (10 m), while others responded to the conditions on deeper waters (above the depth of maximum temperature gradient). Considering all the dimensions of the niche is therefore essential to fully understand how diving seabirds coexist in dynamic systems and in addition, provides insights on species' 3D niches that may help advance into their management.

Both Chapter I and Chapter II, however, were restricted to autumn (i.e., JUVENA survey), which despite being one of the most diverse seasons in terms of top predators, only provides information for a given period of time.

Chapter III managed to solve the temporal scale issue by analysing the spatio-temporal patterns of one of the most abundant cetaceans in the area with data collected throughout the year and over 24 years. In this case, we tested the effect of three sets of potential drivers (climate indices, oceanographic conditions, and prey biomasses) on the common dolphin abundance and distribution with a Vector Autoregressive Spatio Temporal (VAST) model that accounts for changes in sampling effort resulting from the combination of multiple datasets. Our results showed that the common dolphin significantly increased in abundance in the Bay of Biscay during the study period. These changes were best explained by the North Atlantic Oscillation (NAO) climatic index and by prey species biomass, while oceanographic variables such as chlorophyll *a* concentration and temperature were less useful or not related. In addition, we found high variability in the geographic centre of gravity of the species within the study region, with shifts between the inner (southeast) and the outer (northwest) part of the bay, although the majority of this variability could not be attributed to the drivers considered in the study. Overall, these findings indicate that at relatively small scales and within the core of the species range, as in the Bay of Biscay, temperature may not be such an important driver for explaining the abundance and distribution patterns of common dolphin and instead, suggest important influences from prey and regional climate indices that integrate multiple ecological influences.

The results obtained in this thesis have therefore shown that the incorporation of biotic drivers to the traditionally used Species Distribution Modelling approach allow the identification of biotic interactions (e.g., facilitation, competition or predation), trophic preferences and trophic segregation processes, providing new information on the coexistence, food web structure and spatio-temporal patterns of the top predators of the Bay of Biscay.

However, the incorporation of biotic drivers, and specially the use of prey variables, has also revealed a lower contribution and/or smaller explanatory power of such drivers in comparison to environmental variables, which can be related to 1) methodological constraints in the acoustic detection of prey, 2) mismatches between predator and prey distribution linked to the resolution of the scale or 3) the use of inadequate predictors of predators-prey relationships.

These results reaffirm the difficulty of capturing significant spatio-temporal relationships between mobile marine top predators and prey and suggest that environmental variables are generally better predictors of marine top predator distributions than prey abundance.

Even so, we consider that given the valuable information provided by biotic drivers, it is worth keeping investigating on the identification of suitable scales and meaningful prey characteristics that could help us obtain more accurate and representative relationships of the ecosystem functioning.

RESUMEN

Durante los últimos 10 años, los modelos de distribución de especies (*Species Distribution Models*; SDM) se han convertido en herramienta indispensable de los estudios de biogeografía, ecología, biología de la conservación y cambio climático. Sin embargo, la mayoría de los estudios que aplican SDM cuantifican principalmente las relaciones especie-ambiente, estando relacionados con el concepto del nicho grinnelliano, que describe la respuesta de la especie a un conjunto de variables no interactivas. De este modo, el nicho eltoniano, centrado en los roles funcionales de las especies y las interacciones bióticas, es generalmente omitido en el desarrollo de los SDM, a pesar de ser bien sabido que los patrones de distribución y abundancia de las especies no solo dependen de sus respuestas al ambiente abiótico, sino también de sus interacciones.

Durante mucho tiempo, sin embargo, las interacciones bióticas han sido consideradas relevantes únicamente a la hora de estudiar procesos ecológicos a escalas locales, haciendo que los investigadores que trabajaban a grandes escalas biogeográficas no las abordasen. Recientemente, en cambio, se ha demostrado que las interacciones bióticas pueden influir en la distribución de las especies desde escalas locales a regionales y continentales, e incluso mejorar el poder explicativo y la precisión predictiva de los modelos.

Inferir interacciones bióticas, no obstante, no es una tarea sencilla, ya que requiere un buen conocimiento del comportamiento de las especies o una observación directa de las interacciones. Cuando no se dispone de información directa sobre las interacciones bióticas, los datos georreferenciados de ocurrencia de las especies pueden ayudar a obtener información sobre las mismas, analizando si algunas especies coexisten con más o menos frecuencia de lo que podría esperarse al azar, o estimando la superposición espacial en la distribución de las especies.

En ambientes dinámicos como el océano, la adquisición de dicha información requiere de grandes esfuerzos, debido al tamaño y la complejidad del medio marino y la relativa dificultad de tomar medidas en él. Las campañas oceanográficas multidisciplinares, destinadas a monitorear el componente biológico (p. ej., plancton, peces, megafauna) y el físico (hidrografía) del ecosistema, brindan una excelente oportunidad, ya que ofrecen un marco simultáneo en el que los diferentes componentes del ecosistema pueden ser analizados conjuntamente en la misma escala espaciotemporal. De esta manera, se puede explorar la relación entre la

especie y su entorno, siguiendo el enfoque tradicional de los SDM, o entre las propias especies, con el objetivo de avanzar hacia un mejor conocimiento de las interacciones bióticas.

En aguas del sur de Europa, varias instituciones realizan programas de monitoreo multidisciplinares con el fin de estudiar la amplia y diversa comunidad de plancton, peces y megafauna que habita la zona. La campaña oceanográfica JUVENA representa uno de esos programas, en el cual se realiza un seguimiento del medio marino del golfo de Vizcaya en otoño, coincidiendo con el período en el que numerosas especies de depredadores utilizan la zona como corredor migratorio.

Los depredadores apicales como las aves marinas y los cetáceos se han considerado desde hace mucho tiempo buenos indicadores ecológicos, ya que enfrentan numerosos impactos y responden a diversos cambios en los ecosistemas mientras se desplazan a lo largo de sus amplios rangos de distribución. Además, están protegidos por diferentes acuerdos internacionales, como la Directiva Aves (Directiva 2009/147 / CE del Consejo) o la Directiva Hábitat (Directiva 92/43 / CEE del Consejo), que tienen como objetivo promover y mantener la diversidad biológica a través de la conservación de los hábitats naturales y la biodiversidad en el territorio de la Unión Europea. Pero a pesar de los esfuerzos de conservación, las aves marinas constituyen uno de los grupos más amenazados mientras que muchas especies de cetáceos mueren todavía intencional o indirectamente por la pesca comercial.

Frente a esa situación, es necesario desarrollar medidas efectivas de conservación y gestión, que a su vez requieren un profundo conocimiento de las variables que configuran el nicho de las especies (tanto el nicho eltoniano como el grinnelliano). Por ese motivo, esta tesis tiene como objetivo avanzar en la comprensión de cómo los factores bióticos y abióticos contribuyen a moldear la distribución y abundancia de las especies utilizando como caso de estudio la comunidad de depredadores del golfo de Vizcaya. Para abordar este objetivo general, llevamos a cabo tres diferentes estudios que se presentan en esta tesis como capítulos y que buscan responder preguntas de investigación específicas.

El Capítulo I tuvo como objetivo identificar las principales asociaciones ambientales y bióticas que ocurren dentro de la red depredador-presa del golfo de Vizcaya. Para eso, aplicamos un método relativamente nuevo llamado Modelización Conjunta de Distribución de Especies (*Joint Species Distribution Modelling*, JSDM) a los patrones de coocurrencia (presencia/ausencia) de las comunidades de presas y depredadores (11 y 17 especies, respectivamente) obtenidos durante las campañas

JUVENA 2013-2016. Los JSDM, a diferencia de los enfoques convencionales, permiten distinguir entre interacciones bióticas y preferencias ambientales, ya que una asociación espacial positiva (o negativa) entre dos especies no significa necesariamente una interacción biótica, sino que también puede ser resultado de compartir requisitos ambientales similares (o diferentes). De esta manera, encontramos que los patrones de coocurrencia de los depredadores y presas del golfo de Vizcaya ocurren por la combinación de factores ambientales (preferencias ambientales similares/diferentes) e interacciones bióticas, entre las cuales identificamos principalmente interacciones del tipo mutualista (por ejemplo, anchoa-sardina, pardela cenicienta-rorcual común), y depredación (por ejemplo, alcatraz-jurel). Estos resultados sugieren que el análisis de patrones de coocurrencia con herramientas como JSDM pueden ayudar a identificar, hasta cierto punto, interacciones interespecíficas, que a su vez, pueden ser útiles para obtener información sobre el funcionamiento de los ecosistemas. Sin embargo, la identificación de interacciones bióticas con JSDM, al igual que con la mayoría de los análisis estadísticos destinados a atribuir fuentes de covariación entre especies, resulta muy sensible a la elección de las variables ambientales, por lo que se recomienda una interpretación cuidadosa y reflexiva de las interacciones resultantes.

Una alternativa conceptualmente más simple pero técnicamente más compleja consistiría en inferir las interacciones bióticas a partir de datos de abundancia (contaje) mientras se incluyen las especies interactivas (por ejemplo, las presas) como variables predictoras en los SDM. Aunque inferir interacciones ecológicas a partir de los datos de presencia-ausencia resulta atractivo por su menor complejidad, los datos de contaje posibilitan hacer inferencias más refinadas sobre por qué las especies ocurren en un lugar específico y sobre cómo los predictores bióticos afectan a sus patrones de distribución y abundancia.

En esta línea, el Capítulo II modeló la distribución de cinco especies de aves marinas relacionadas filogenéticamente a partir de los avistamientos (contajes) recogidos durante 2013-2017 en las campañas JUVENA. En este caso, el objetivo era comprender cómo los depredadores del golfo de Vizcaya compartían el nicho ambiental y trófico. Para ello, a) identificamos el rango vertical biológicamente significativo de cada una de las aves marinas, b) modelamos sus nichos ambientales y tróficos, c) estimamos un índice de superposición ambiental y trófico para cada pareja de especie, y d) desarrollamos un marco conceptual con las hipótesis de segregación más plausibles. La aplicación del marco conceptual reveló que, en esta área en particular, las aves pelágicas coexisten a través de la partición del nicho ambiental y trófico y potencialmente a través de la segregación vertical, ya que algunas especies respondieron a las condiciones ambientales y tróficas asociadas a la superficie del mar (10 m), mientras que otras respondieron a las condiciones asociadas a aguas más profundas (por encima de la profundidad del gradiente máximo de temperatura). Considerar todas las dimensiones del nicho es, por tanto, esencial para comprender más profundamente cómo las aves marinas coexisten en sistemas dinámicos y permite, a su vez, obtener información relevante que puede ayudar a avanzar en su gestión.

Tanto el Capítulo I como el Capítulo II, sin embargo, se restringieron al otoño (campaña JUVENA), que a pesar de ser una de las estaciones más diversas en cuanto a número de depredadores, solo proporciona información para un período de tiempo determinado.

El Capítulo III logró resolver el problema de la escala temporal mediante la compilación de datos recolectados a lo largo del año y durante 24 años en el golfo de Vizcaya. En este caso, analizamos el efecto de tres grupos de variables (índices climáticos, condiciones oceanográficas y biomasas de presas) en la abundancia y distribución del delfín común con un modelo Vector Autorregresivo Espacio Temporal (*Vector Autoregressive Spatio Temporal,* VAST) que tiene en cuenta los cambios que puedan ocurrir en el esfuerzo de muestreo como consecuencia de combinar múltiples fuentes de datos. Nuestros resultados mostraron que el delfín común aumentó significativamente su abundancia en el golfo de Vizcaya durante el período de estudio. Estos cambios se explicaron mejor por índices climáticos como la Oscilación del Atlántico Norte (NAO) y por la biomasa de las presas. Las variables oceanográficas como la concentración de clorofila *a* y la temperatura explicaron una menor proporción de la variabilidad o directamente no estuvieron relacionadas. Además, encontramos una alta variabilidad en el centro de gravedad geográfico de la especie dentro del área de estudio, aunque la mayoría de esta variabilidad no pudo ser atribuida a las variables consideradas en el estudio. En general, estos hallazgos indican que, a escalas relativamente pequeñas y dentro del núcleo de distribución de la especie, como es el golfo de Vizcaya, la temperatura puede no ser un factor tan importante a la hora de explicar los patrones de abundancia y distribución y que, en su lugar, las presas y los índices climáticos pueden contribuir en mayor medida a explicar la variabilidad observada en esta área.

Los resultados obtenidos en esta tesis han demostrado, por tanto, que la incorporación de variables bióticas en el Modelado de Distribución de Especies permite la identificación de interacciones bióticas (como, por ejemplo, la facilitación, la competencia o la depredación), preferencias tróficas y procesos de segregación, proporcionando nueva información sobre la coexistencia, red trófica y patrones espaciotemporales de los principales depredadores del golfo de Vizcaya.

Sin embargo, la incorporación de variables bióticas, y especialmente el uso de las presas, también ha revelado una menor contribución y/o menor poder explicativo de dichas variables en comparación con las variables ambientales, lo que puede estar relacionado con: 1) limitaciones metodológicas en la detección acústica de las presas, 2) desajustes espaciales entre la distribución de depredadores y presas vinculados a la resolución de la escala, o 3) el uso de predictores inadecuados para el estudio de las relaciones depredador-presa. Estos resultados reafirman la dificultad de capturar relaciones espaciotemporales significativas entre los depredadores móviles y las presas y sugieren que las variables ambientales son generalmente mejores predictores de la distribución de los depredadores apicales que la propia abundancia de presas.

Aun así, consideramos que dada la valiosa información que brindan las variables bióticas, vale la pena seguir investigando hacia la identificación de las escalas adecuadas y características significativas de las presas que podrían ayudarnos a obtener relaciones más precisas y representativas del funcionamiento del ecosistema.

LABURPENA

Azken 10 urteetan, espezieen banaketa-ereduak (*Species Distribution Models*; SDM) ezinbesteko tresna bihurtu dira biogeografia, ekologia, kontserbazioaren biologia eta klima-aldaketa aztertzeko, besteak beste. Hala ere, SDM aplikatzen duten ikerketa gehienek espeziearen eta ingurunearen arteko harremanak neurtzen dituzte nagusiki, eta hortaz, loturik daude Grinnell-ek definituriko nitxoaren kontzeptuarekin, hau da, nitxo grinnelliarrarekin, zeinak espezie eta aldagai ez-interaktiboen arteko erlazioak deskribatzen dituen. Ostera, nitxo eltoniarra, espezieen rol funtzionalak eta elkarrekintza biotikoak aztertzen dituena, gutxitan hausnartzen da SDMen esparruan, nahiz eta ondo jakin espezieen banaketa eta ugaritasun-patroiak espezien elkarrekintzen mende ere badaudela.

Denbora luze batez, interakzio biotikoek eskala txikiko prozesu ekologikoei soilik eragiten zietela uste izan da, eta ondorioz, eskala biogeografiko handietan lan egiten zuten ikertzaileek elkarrekintza horiek alde batera utzi dituzte. Duela gutxi, ordea, elkarrekintza biotikoek eskala handiagoetan ere eragina izan dezaketela frogatu da, bai espezien banaketa bera azaltzen bai banaketa-ereduen azalpen-ahalmena eta aurreikuspen-zehaztasuna hobetzen.

Hala ere, interakzio biotikoak ondorioztatzea ez da lan erraza, espezieen portaera ondo ezagutzea edota interakzioak zuzenean behatzea eskatzen baitu. Elkarrekintza biotikoei buruzko zuzeneko informaziorik ez dagoenean, espezieen banaketari buruzko datu geoerreferentziatuak lagungarri izan daitezke interakzioak ondorioztatzeko, espezie batzuk ausaz espero litzatekeena baino maiztasun handiagoz edo txikiagoz elkarrekin existitzen diren aztertuz, edo espezieen banaketa eremuen gainjartze espaziala estimatuz.

Itsasoa bezalako ingurune dinamikoetan, aipatutako informazioa eskuratzeko ahalegin handiak egin behar dira, bai itsasoaren tamaina eta konplexutasunagatik, bai bertan lagintzeak dituen zailtasunengatik ere. Diziplina anitzeko kanpaina ozeanografikoek, ekosistemaren osagai biologikoa (planktona, arrainak, megafauna) eta fisikoa (hidrografia) aztertzera bideratuta daude eta hortaz, aukera paregabea eskaintzen dute ekosistemaren osagai desberdinak eskala tenporal eta espazial berean aztertzeko. Horrela, espeziearen eta bere ingurunearen arteko harreman sinoptikoa azter daiteke, SDMen ikuspegi tradizionalari jarraituz, edota espezieen artekoa, interakzio biotikoak hobeto ezagutze aldera.

Europa hegoaldeko uretan, hainbat erakundek diziplina anitzeko laginketa-programak burutzen dituzte zonaldean bizi den plankton, arrain eta megafauna komunitate zabal eta aberatsa aztertzeko. JUVENA kanpaina ozeanografikoa laginketa-programa horietako bat da. Bertan, Bizkaiko golkoko itsas ingurunea aztertzen da udazkenean, harrapakari espezie askok eremua korridore migratzaile gisa erabiltzen duten garaiarekin bat etorriz.

Harrapakari apikalak, hala nola, itsas hegaztiak eta zetazeoak, aspalditik hartu dira adierazle ekologiko ontzat; izan ere, ekosistemetan gertatzen diren aldaketa eta inpaktu ugariri erantzun behar izaten diete itsaso zabalean zehar mugitzen diren bitartean. Gainera, nazioarteko hainbat akordiok babesten dituzte, hala nola Hegaztien Zuzentarauak (Kontseiluaren 2009/147/EE Zuzentaraua) edota Habitatei buruzko Zuzentarauak (Kontseiluaren 92/43/EEE Zuzentaraua). Baina kontserbatzeko ahaleginak egiten badira ere, itsas hegazti askok larriki mehatxatuta egoten jarraitzen dute eta zetazeo-espezie asko oraindik ere nahita edo zeharka hiltzen dira arrantza komertzialaren ondorioz.

Egoera horri aurre egiteko, kontserbazio eta kudeaketa neurri eraginkorrak garatu behar dira, baina horretarako, espezieen nitxoa (bai eltoniar nitxoa, bai grinnelliarra) osatzen duten aldagaiak ondo ezagutu behar dira. Horregatik, tesi honen helburua faktore biotiko eta abiotikoek espezieen banaketa eta ugaritasuna nola moldatzen duten ulertzea da, azterketa-kasu gisa Bizkaiko golkoko harrapakarien komunitatea erabiliz. Helburu orokor horri heltzeko, hiru azterlan burutu ditugu, tesi honetan kapitulu independente gisa aurkezten direnak.

I. kapituluan, esaterako, Bizkaiko golkoko harrapakari-harrapakin komunitatearen baitan gertatzen diren harreman nagusiak (bai inguruneari lotuak zein biotikoak) identifikatu genituen. Horretarako, Espezieen Banaketarako Modelizazio Bateratua (Joint Species Distribution Modelling, JSDM) izeneko metodoa aplikatu genien JUVENA 2013-2016 kanpainetan lortutako harrapakin eta harrapakarien (11 eta 17 espezie, hurrenez hurren) banaketa datuei (presentzia/ausentzia). JSDMek, ikuspegi konbentzionalek ez bezala, elkarrekintza biotikoak eta inguruneari lotutakoak bereiztea ahalbidetzen dute; izan ere, bi espezieren arteko harreman espazial positibo (edo negatibo) batek ez du nahitaez elkarrekintza biotiko baten seinale izan behar, eta ostera espezieek antzeko ingurumen-betekizunak (edo desberdinak) partekatzen dituztela adieraz dezake. Horrela, Bizkaiko golkoko harraparien eta harrapakinen arteko harremanak ingurumen-faktoreen (antzeko ingurumenlehentasunak/desberdinak) eta elkarrekintza biotikoen konbinazioagatik gertatzen direla ikusi genuen. Azken hauen artean, batez ere harrapakaritza (adibidez, zanga eta txitxarroa artekoa) eta mutualista motako elkarrekintzak (adibidez, antxoa eta sardina artean, edota gabai arrea-zere arrunta artean) identifikatu genituen. Emaitza hauek, beraz, JSDM bezalako tresnek elkarrekintza inter-espezifikoak identifikatzeko balio dutela adierazten dute, ekosistemen funtzionamenduari buruzko informazioa eskuratzeko baliagarriak izan daitezkeelarik. Hala ere, JSDMren bitartez eginiko ondorioztapenak oso sentikorrak dira erabilitako ingurumen-aldagaiekiko eta, hori dela eta, identifikatutako interakzioak arretaz eta arduraz interpretatzea gomendatzen da.

Interakzio biotikoak aztertzeko aukera sinpleagoa baina teknikoki konplexuagoa abundantzia (kontaketak) datuetan oinarritzean datza, elkarrekintzan parte hartzen duten espeziak (adibidez, harrapakinak) SDMetan aldagai iragarle gisa erabiltzen diren bitartean. Presentzia/absentzia datuetatik abiatuz interakzio ekologikoak ondorioztatzea erakargarria bada ere, eskaintzen duten konplexutasun txikiagoagatik, kontaketak dituzten datuek informazio zehatzagoa ematen dute espezieak leku jakin batean zergatik agertzen diren edota iragarle biotikoek euren banaketa- eta ugaritasun-patroiei nola eragiten dieten jakiterako orduan.

Ildo horretan, II. kapituluan, filogenetikoki harremandutako bost itsas-hegazti espezieren banaketa aztertu genuen 2013-2017 bitarteko JUVENA kanpainetan jasotako behaketetatik (kontaketak) abiatuta. Kasu honetan, helburua Bizkaiko golkoko harrapakariek nitxoa (bai ingurune fisikoari lotutakoa, zein trofikoa) nola partekatzen zuten ulertzea zen. Horretarako, a) itsas hegazti-espezie bakoitzaren eremu bertikal biologikoki esanguratsua identifikatu genuen, b) haien nitxoak modelatu, c) espezie-bikote bakoitzarentzat nitxoaren gainjartze-indize bat kalkulatu, eta d) segregazio-hipotesi onargarrienak dituen grafika kontzeptuala garatu genuen. Grafika kontzeptualaren aplikazioak agerian utzi zuen, eremu honetarako behintzat, hegazti pelagikoek ingurumen-nitxoa eta nitxo trofikoa partekatzen dituztela eta horri esker, bost espeziak elkarrekin bizitzeko gai direla eremu berean. Horrez gain, nitxoaren bereizketa dimentsio bertikalean ere gerta zitekeela aurkitu genuen; izan ere espezie batzuk itsaso gainazalari lotutako ingurumen-baldintzei eta baldintza trofikoei (10 m) erantzun zieten, eta beste batzuk ur sakonagoei lotutako baldintzei (tenperaturaren gehieneko gradientearen sakoneraren gainetik). Honela, emaitza hauek nitxoaren dimentsio guztiak kontuan hartzea funtsezkoa dela erakusten dute, bai itsas hegaztiak sistema dinamikoetan nola existitzen diren sakonago ulertzeko baita haien kudeaketan aurrera egiteko ere.

Hala eta guztiz ere, I. eta II. kapituluak, udazkenera mugatu ziren (hau da, JUVENA kanpainara), eta nahiz eta, harrapakarien kopuruari dagokionez, urtaro aberatsenetako bat izan, onartu beharra dago, ikerketa biek denbora-tarte jakin baterako informazioa baino ez dutela ematen.

III. kapituluak denbora-eskalaren arazoa konpontzea lortu zuen, urtean zehar eta 24 urtez bildutako datuak erabili baitziren gure zonaldean oso ugaria den zetazeo baten aldaketa espazio-tenporalak aztertzeko. Kasu honetan, hiru aldagai-multzok (klimaren indizeak, baldintza ozeanografikoak eta harrapakinen biomasak) izurde arruntaren ugaritasunean eta banaketan duten eragina aztertu genuen. Horretarako, Vector Autoregressive Spatio Temporal (VAST) izeneko eredua aplikatu genuen, datu-iturri ugari konbinatzearen ondorioz gerta daitezkeen aldaketak kontuan hartzen baititu. Horrela, Bizkaiko golkoan izurde arruntak nabarmen egin duela gora aurkitu genuen, aldaketa horiek batez ere Ipar Atlantikoko Oszilazioa (*North Atlantic Oscillation*, NAO) izeneko indize klimatikoak eta harrapakinen biomasak azaltzen zituztelarik. Klorofila *a*-ren kontzentrazioa eta tenperatura bezalako aldagai ozeanografikoek aurkitutako aldaketak azaltzeko ahalmen gutxiago erakutsi zuten edo zuzenean ez ziren erlazionatuta ageri. Espeziearen banaketari dagokiola, grabitate zentroa izeneko metrikak aldakortasun handia erakutsi zuen azterketa-eremuaren barruan, nahiz eta aldakortasun horren gehiengoa ezin izan zen azaldu azterlanean aztertutako aldagaiekin. Aurkikuntza hauetan oinarriturik, beraz, ondoriozta dezakegu, Bizkaiko golkoan, tenperatura ez dela uste bezain faktore garrantzitsua izurdearen ugaritasun- eta banaketa-patroiak azaltzeko eta aldiz, harrapakinak eta klima-indizeak baliagarriagoak izan daitezkeela.

Tesi honetan lortutako emaitzek, beraz, frogatu dute Espezieen Banaketa Ereduetan aldagai biotikoak sartzeak interakzio biotikoak (adibidez, mutualismoa edo edo harrapakaritza), dieta preferentziak eta segregazio prozesuak identifikatzea ahalbidetzen duela, Bizkaiko golkoko harrapakarien koexistentziari, elikadura-sare trofikoaren egiturari eta aldaketa espazio-tenporalei buruzko informazio berria emanez. Hala ere, aldagai biotikoak gehitzeak, eta, bereziki, harrapakinak erabiltzeak, agerian utzi du aldagai horien ekarpen txikiagoa eta/edo azalpen ahalmen txikiagoa ingurumen-aldagaien aldean, zeinak zerikusia izan dezake 1) harrapakinak estimatzeko erabiltzen den metodologia akustikoaren mugekin, 2) harrapakarien eta harrapakinen banaketa espazialen arteko desorekarekin edo 3) harrapakari-harrapakinen arteko erlazioak aztertzeko erabiltzen diren iragarle motekin. Oro har, emaitza horiek harrapakari eta harrapakinen arteko harreman esanguratsuak identifikatzea zaila dela berresten dute, eta iradokitzen dute inguruneko aldagaiak harrapakari apikalen banaketaren iragarle hobeak direla harrapakinen ugaritasuna bera baino. Hala ere, aldagai biotikoek ematen duten informazio baliotsua kontuan izanik, merezi du ekosistemaren funtzionamenduaren erlazio zehatzagoak eta adierazgarriagoak lortzen lagun diezaguketen eskala egokien eta harrapakinen ezaugarri esanguratsuen identifikazioari buruz ikertzen jarraitzea.

GENERAL INTRODUCTION

The ecological niche of species

The niche concept has always been central to ecology (Hutchinson 1957, Chase & Leibold 2003). However, a renewed interest has emerged in recent years as a consequence of the computational and technological advances that have allowed scientists to estimate species distribution patterns through new modelling techniques (Soberon 2007, Holt 2009, Soberon & Nakamura 2009, Peterson et al. 2011, Pocheville 2015).

Over the past 10 years, Species Distribution Models (SDM; Guisan & Zimmermann 2000) have become commonplace in the studies of biogeography, ecology, conservation biology, and climate change (Broennimann et al. 2011, Ballard et al. 2012, Erauskin-Extramiana et al. 2019b, Waggitt et al. 2020). But still, there are conflicting views about what the models truly represent. Despite several authors have attempted to clarify the relationship between SDMs and the concept of ecological niche (Guisan & Thuiller 2005, Araújo & Guisan 2006, Kearney 2006, Soberon & Nakamura 2009), the debate is still open and opposes authors who think that SDMs provide an approximation to the species' fundamental niche (Soberón & Peterson 2005), with others that consider them a spatial representation of the realized niche (Pearson & Dawson 2003, Araújo & Pearson 2005) on the grounds that the observed species' spatial distributions are already constrained by non-climatic factors.

What is clear is that most modelling approaches developed for predicting species distributions (and abundances) have their roots in quantifying species-environment relationships (Guisan & Thuiller 2005) and so, they are based on the Grinnellian niche concept (Grinnell 1917), which describes the response of the species to a given set of non-interactive variables (termed scenopoetic variables or conditions). However, species also depend on their intra- and interspecific interactions and therefore, species distribution and abundance patterns will be hardly understood by studying exclusively their individual responses to the abiotic environment (Wisz et al. 2013).

The role of biotic interactions, together with resource-consumer dynamics, are defined in the Eltonian niche (Elton 1927), but unlike the increasingly available scenopoetic variables (Turner et al. 2003), biotic interactions (or bionomic variables) remain difficult to measure (Araújo et al. 2011). As a result, little is known about the types of interactions that exist among species and the importance of such interactions for the generation and maintenance of biodiversity on Earth (Bascompte 2009, Morales-Castilla et al. 2015).

This lack of knowledge regarding intra- and interspecific interactions is called the Eltonian shortfall (Figure 1) (Peterson et al. 2011) and one reason why it is so prevalent in the field of SDMs is that, for a long time, biotic interactions were believed to affect ecological processes mainly at local scales (Pearson & Dawson 2003). In contrast, recent evidence suggest that biotic interactions can shape species distributions from local to regional and continental scales (Araújo & Luoto 2007, Gotelli et al. 2010, Wisz et al. 2013), improve the explanatory power and predictive accuracy of the models (Heikkinen et al. 2007), and even assess the impacts of climate change prediction in species distributions (Araújo et al. 2011).

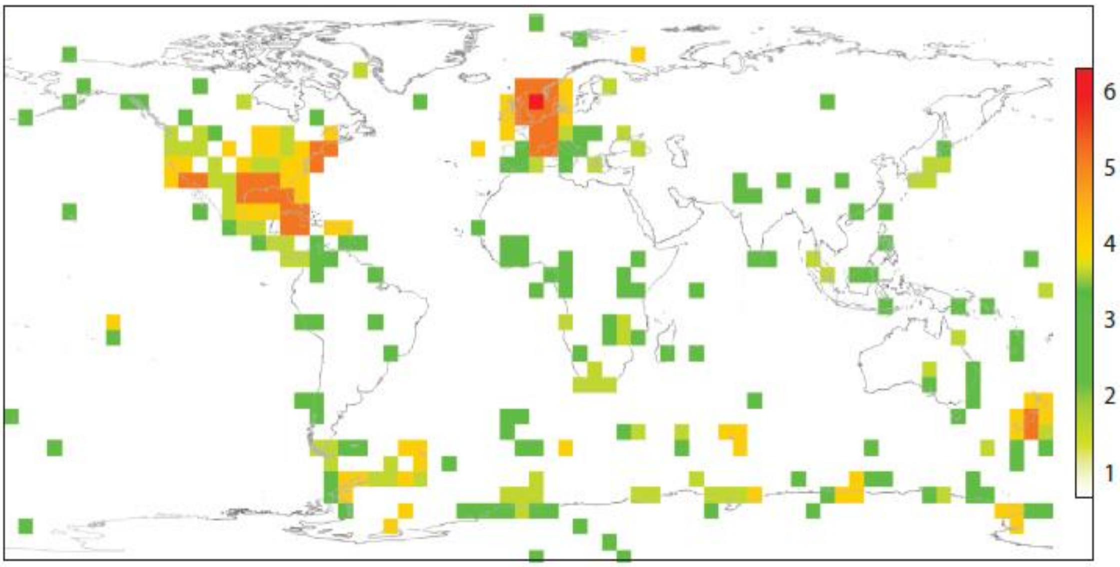


***Figure 1**. Global distribution of the number of recorded interactions (5°x5° grid cell resolution). Adapted from Hortal et al. (2015).*

Thus, one key aim of modern community ecology is to gain an integrative understanding of how biotic and abiotic factors structure local species pool at different spatio-temporal scales (Ovaskainen et al. 2017). However, fulfilling this objective in the marine realm is harder than in land, where the three dimensionality of the habitat and its inherent complexity have often lagged its understanding behind that of terrestrial environment (Carr et al. 2003). As a result, information on species distribution, abundance and diversity patterns is poorer in marine ecosystems than in terrestrials (Carr et al. 2003), and so is our knowledge about biotic interactions (Hortal et al. 2015).

Biotic interactions

There are many ways to describe a biotic interaction, including the type (e.g., negative or positive, direct or indirect), the strength (e.g., weak or strong), and the symmetry (e.g., symmetric or asymmetric). Interactions can be also defined based on whether the net effect of the interaction on each interacting species is detrimental (competition, -/-) or beneficial for both (mutualism, +/+), positive for one species and negative for the other (predation or parasitism, -/+), positive for one species and indifferent for the other (commensalism, +/0), or detrimental for one and indifferent for the other (amensalism, -/0).

Although the quantification of the prevalence of each interaction in nature is still lacking, those concerning competition and predation have been the focus of more than three quarters of all published studies on biotic interactions (Figure 2) (Morales-Castilla et al. 2015). Competition, in particular, has attracted ~50% of all citations in the biotic interaction's literature in the past decades (Figure 2), believed to be one of the most important processes determining the structure of natural communities (Tilman 1982, Chase et al. 2002). In the last few years, in contrast, positive interactions

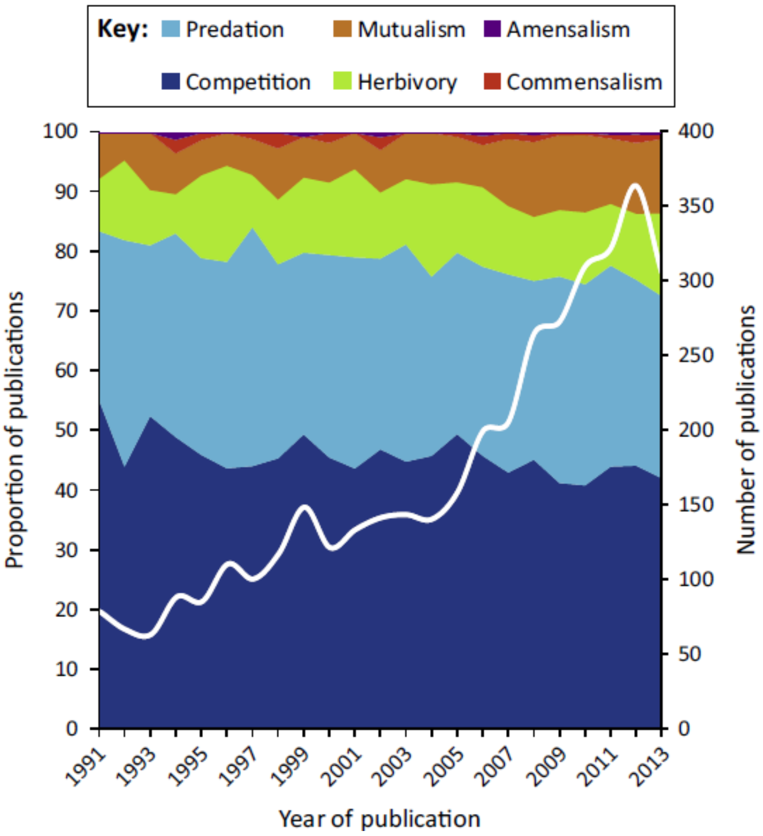


***Figure 2**. Published studies on biotic interactions from 1991 to 2013. From Morales-Castilla et al. (2015).*

such as mutualism have become increasingly popular, with numerous studies indicating that they can be as important as negative interactions for species survival, conservation and diversification (Callaway et al. 2002, Aizen et al. 2012, Veit & Harrison 2017, Bascompte 2019).

Inferring biotic interactions, however, is not an easy task, as it requires a good knowledge on species behaviour or a direct observation of interactions (Clua & Grosvalet 2001, Camphuysen et al. 2007). When direct information about biotic interactions is unavailable, proxies such as geographical data, traits, or phylogenies can help obtain insights about them while offering a starting point for predicting the general properties of the interaction network (Morales-Castilla et al. 2015).

Geographical data, for example, provide co-occurrence patterns from which signals of species interactions can be inferred by asking if some species co-occur more or less often than what could be expected by random (Gotelli & Ulrich 2010, Veech 2013). Species assemblages, however, are affected by environmental conditions and a multitude of direct and indirect interactions, and hence, it is difficult to conclusively infer the causal links from observational data by this means (Sebastian-Gonzalez et al. 2010). In fact, a positive (or negative) association between two species does not necessarily signify a direct or indirect interaction, and it can result, instead, from the species having similar (or dissimilar) habitat requirements (Ovaskainen et al. 2010).

Within that context, traits —defined as morphological, physiological and/or phenological characteristics of species that directly impact on their fitness (Violle et al. 2007)— can help simplify the interacting groups of species, by determining if a given interaction is probable or possible. In marine predator-prey relationships, for example, traits such as prey body size or predators' diving capability determine prey selection (Spitz et al. 2014, Lambert et al. 2018) and hence, can be used to discard "impossible" trophic relationships, assuming that predators cannot capture prey species that are bigger than what they can swallow or that occur at depths that cannot reach. Finally, phylogenies measuring evolutionary relationship can also be used when information on traits is not available or incomplete, under the assumption that phylogenetically related species are ecologically similar (Losos 2008).

Lately, substantial advances have been made to improve the accuracy of biotic interactions inferences. New approaches enable now distinguishing between biotic interactions and similar environmental preferences while combining the information given by traits and phylogenies (Figure 3) (Hui 2016, Morueta-Holme et al. 2016, Ovaskainen et al. 2017).

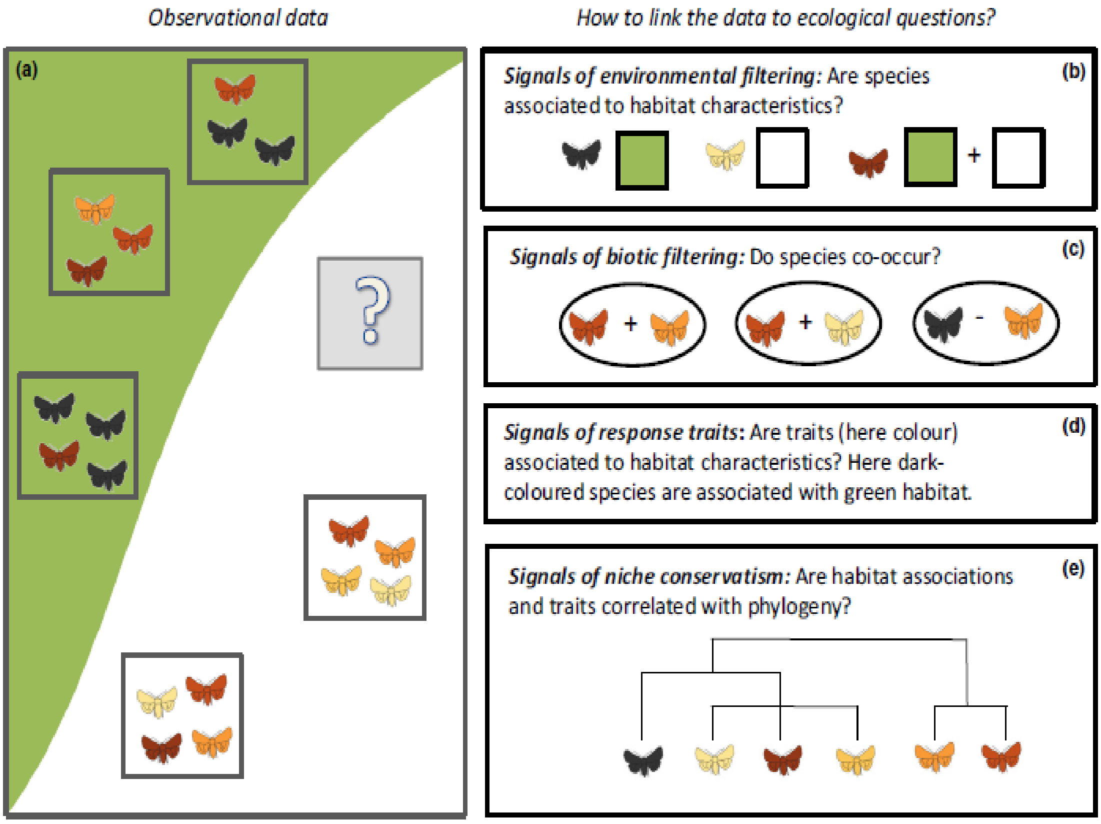


***Figure 3**. A conceptual illustration of how data can be linked to community ecology. The green and white colours represent differences in the environmental conditions, the butterflies with different colours represent different species, and the small boxes represent sampling units. From Ovaskainen et al. (2017).*

Such developments have led to the application of network statistics, which based on the number of species' interactions or links provide insights about species role and species centrality. Having more positive than negative associations, for example, makes a species an aggregator (or a segregator, if otherwise), while a high centrality score (e.g., a high number of links) means that the species is important for the network structure and stability (Martín González et al. 2010, Morueta-Holme et al. 2016). The simply mapping of interactions can also tell us about the properties of the community network (Figure 4); we can know, for example, how resilient the community is (complex communities are on average more resistant to species loss) or how the loss of a given species will affect the remaining interacting species (the loss of highly connected species triggers on average the largest number of secondary extinctions) (Eklof & Ebenman 2006).

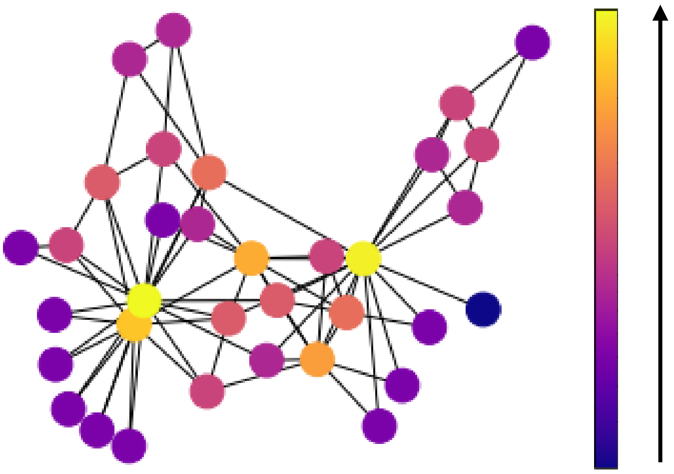


Figure 4. *Illustration of a network's nodes and links. Nodes with many links have a higher centrality and are shown with light colours. From https://aksakalli.github.io*

Network theory provides, therefore, a suitable and powerful framework to address the complexity of the network functioning, and hence, bigger effort should be directed to account for interdependencies between species, especially when anthropogenic impacts such as climate change or overfishing are expected to keep altering the properties and functioning of communities (Myers et al. 2007, Doney et al. 2012, Chust et al. 2014a).

Changing environment

Over the past 50 years, the global mean surface temperature has increased on average about 0.7° C (Stocker et al. 2013). Such warming, however, has not been uniform and has led to heterogenous patterns across Earth. Ocean surface waters, for example, have warmed three times slower than air temperatures (Solomon et al. 2007). Isotherms, in contrast, have shifted faster at the ocean surface than over land (Burrows et al. 2011), and as a result, the rates of observed shifts in species distribution are comparable to or greater than those for terrestrial systems (Poloczanska et al. 2013). Such rapid change, summed to an increase in acidification, a decrease in oxygen and an alteration in primary production has led the Intergovernmental Panel on Climate Change (IPCC) to highlight in their Special Report on the Ocean and Cryosphere in a Changing Climate (IPCC 2019) an ocean transition to unprecedented conditions, impelling an universal redistribution of life on Earth (Pecl et al. 2017).

It is therefore not surprising that climate change was identified as the primary anthropogenic force impacting marine ecosystems (Halpern et al. 2008), affecting not only the distribution, but also demography, abundance, phenology and calcification of species (Poloczanska et al. 2016). However, long-term studies of climate change on marine ecosystems are less numerous by comparing to those on land, partly due to the size and complexity of the ocean and the relative difficulty of taking measurements in marine environments (Hoegh-Guldberg & Bruno 2010). In addition, the multiple factors that influence a species' ability to track climate change make predictions challenging, being necessary the implementation of quantitative tools able to distinguish climate impacts from other drivers (Brown et al. 2011).

Spatio-temporal models considering the effect of explanatory variables such as latitude, longitude and time have been described as promising methods beyond those traditionally used (i.e., correlation and linear regression) (Brown et al. 2011). But even with robust tools, several weakness have been detected when trying to understand climate change impacts, such as marginalizing other important non-climate drivers of change, ignoring temporal and spatial autocorrelation, or not accounting for uneven sampling effort (Brown et al. 2011, Thorson et al. 2016, Erauskin-Extramiana et al. 2020).

Despite the challenges, the biological trends detected up to now seem to match with global warming predictions, including poleward shifts, warm water species increase and earlier spring events (Figure 5), among others (Parmesan & Yohe 2003, Poloczanska et al. 2013, Poloczanska et al. 2016). Most taxonomic groups have also

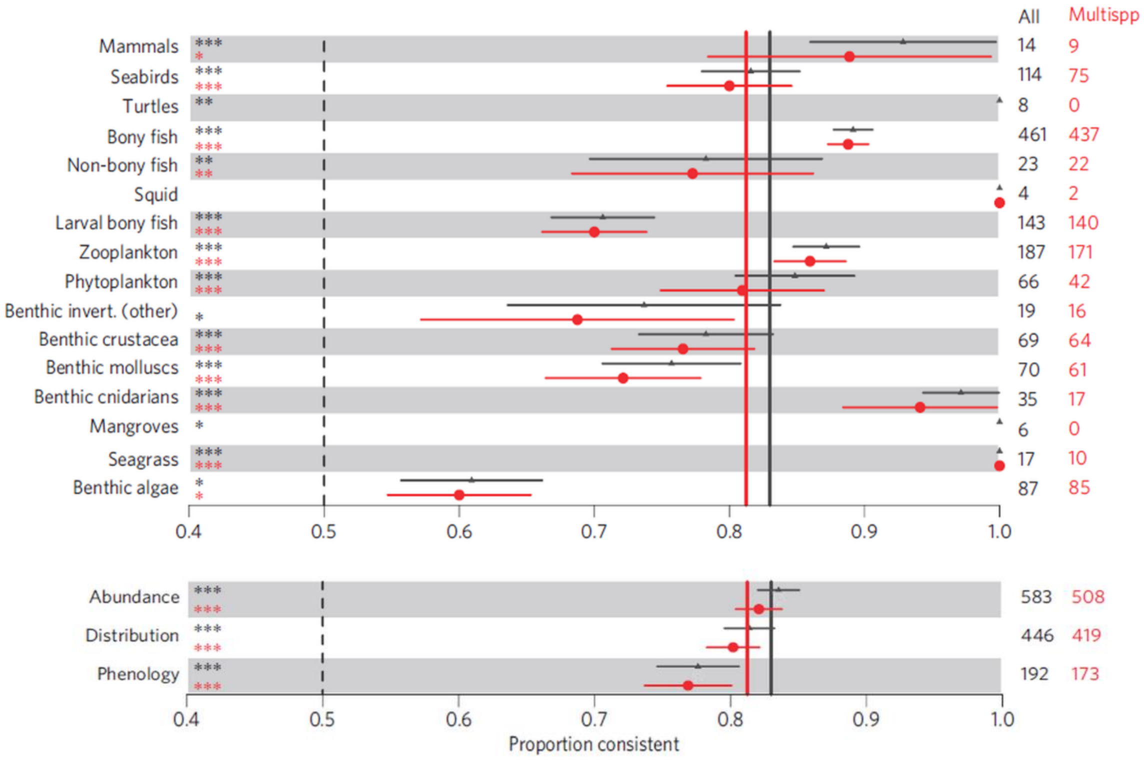


***Figure 5**. Proportion of marine observations consistent with global climate change predictions by taxonomic group and response type. Adapted from Poloczanska et al. (2013)*

shown consistent responses (Poloczanska et al. 2013), including endothermic animals (e.g., marine mammals and seabirds), in which physiological functions are not directly impacted by changes in ambient temperatures or other environmental variables (Sydeman et al. 2015, Poloczanska et al. 2016).

At regional scales, in contrast, climate change effects may be more difficult to detect, given the high degree of both spatial and temporal variability and the relative importance of other variables besides temperature, such as vertical mixing, salinity, rainfall, fresh water run off or nutrients supply (Anker-Nilssen et al. 2008). In addition, climate change effects at these scales may be combined with the existing regional pressures, such as overfishing or bycatch, leading to complex and sometimes synergistic interactions (Doney et al. 2012). Indeed, both climate change and overfishing (and also bycatch) have the potential to modify ecosystem properties such as trophic structure and food web dynamics by altering biotic interactions (Estes et al. 2011, Doney et al. 2012).

Trophic cascades, largely attributed to overfishing, constitute such an example, as they are now being described in the context of climate change too. In some cases, they occur by the combined effect of climate change and overfishing, as in Australia, where the removal of predators and increasing temperatures have led to the expansion of sea urchin, with the subsequent kelp deforestation and loss of biodiversity (Ling et al. 2009).

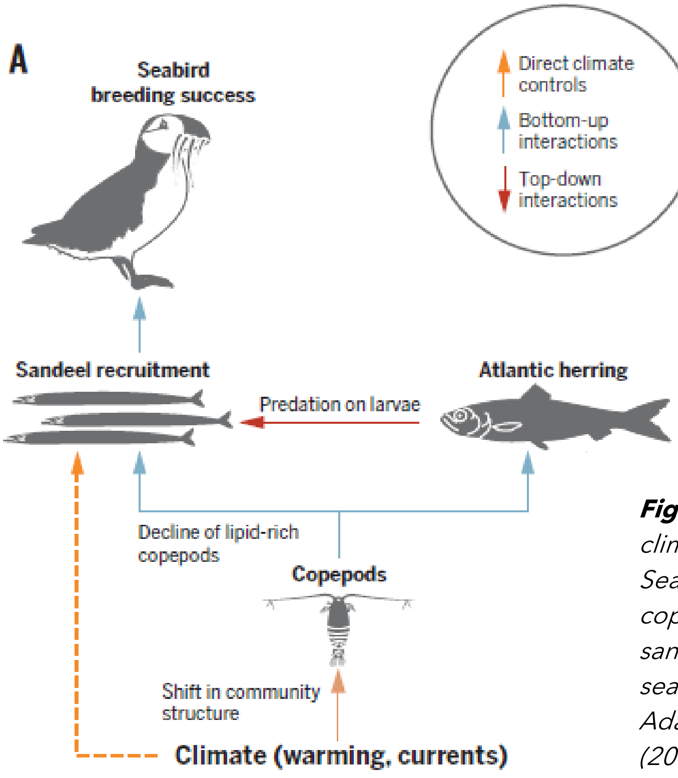


Figure 6. *Bottom-up effects of climate change in the North Sea. The reduction in lipid-rich copepods results in declines in sandeel recruitment and poor seabird breeding success Adapted from Sydeman et al. (2015).*

In other cases, in contrast, detected cascading effects are purely attributed to climate change. In the North Sea, for example, shifts in the abundance and distribution of the dominant copepod have caused a decline in sandeel recruitment and poor seabird breeding success (Figure 6) (Frederiksen et al. 2013), whereas in the California Current, changes in basic oceanographic processes such as upwelling have reduced the productivity of the zooplankton, forage fish and seabirds (Sydeman et al. 2009).

Such profound changes at ecosystem level show that focusing on single species is not sufficient and highlight the importance of considering other factors besides temperature (e.g., prey, productivity) in a more comprehensive, multispecies- to ecosystem-level assessment context.

Ecosystem-based approach

The collapse of numerous fish stocks together with the depletion of vulnerable populations caught incidentally over the last years revealed the incapability of traditional approaches to sustainably manage marine resources (Jackson et al. 2001, Myers & Worm 2003). The main reason given to explain such failure was the focus on single species and single sector (Leslie & McLeod 2007, Curtin & Prellezo 2010). In fact, by doing so, it was ignored the role that ecological interactions play in the resilience and health of coastal and ocean systems (Hughes et al. 2005) and the pressure exerted by all the activities and threatens (shipping, fisheries, tourism, climate change) taking place in or around seas (Curtin & Prellezo 2010).

Ecosystem based management (EBM) was developed to address such gaps, which means that it considers the interactions among ecosystem components and the cumulative impacts of multiple activities and pressures (Leslie & McLeod 2007, Curtin & Prellezo 2010). It represents, therefore, a new and more holistic way of understanding ecosystem functioning (Curtin & Prellezo 2010), which aims to protect and manage ecosystem structure, function and key processes while acknowledging their social and economic features (Arkema et al. 2006, Leslie & McLeod 2007).

Although scientists have been contemplating EBM to land management since the early 1950s, EBM in the ocean is a relatively new approach (Christensen et al. 1996, Arkema et al. 2006), and by now, only few cases exist in which large parts of the marine ecosystem are being managed (Ruckelshaus et al. 2008). One of such cases is illustrated by the krill fishery in the Southern Ocean, where the rates of krill removal are determined considering its importance to predators, with the result that the recommended rates of removal are 25% lower than if predators were not considered (CCAMLR 2006, Ruckelshaus et al. 2008).

At European level, the Marine Strategy Framework Directive (MSFD; Directive 2008/56/EC) approved in 2008 is considered the first concerted attempt by the EU to apply an ecosystem-based approach to the management of human activities affecting the marine environment and ecological systems (Long 2015). In fact, it established a framework that required Member States to assess the environmental status of species and ecosystems based on 11 high level criteria or descriptors, that included, among others, biological diversity, food webs, invasive and overexploited species, and anthropogenic impacts.

Achieving a good knowledge of all those descriptors in marine environments, however, is challenging, and requires long term, scientifically oriented and ecosystem-based monitoring programmes. Integrated ecosystem surveys meet all those criteria and thus, provide an excellent opportunity to advance towards a more comprehensive EBM while providing simultaneous information on different ecosystems components.

Integrated ecosystem surveys

As with resources management, monitoring programmes have also evolved from single species assessment, typically oriented to fisheries management, to a more comprehensive and holistic multispecies approach focused on sampling the biological (plankton, fishes, megafauna) and the physical (hydrography) components of the ecosystem (Doray et al. 2018). Such integrated assessment is usually conducted in four differentiated areas, consisting in acoustic sampling and mid-water trawls for fish estimation (Figure 7, step 1,2,3), hydrological sampling and CTD casts (Figure 7, step 4 & 6), megafauna observation (Figure 7, step 5), and meso-zooplankton collection (Figure 7, step 7).

By this means, multidisciplinary surveys provide a simultaneous framework in which the different components of the ecosystem can be analysed together at the same spatio-temporal scale. As a result, synoptical relationship can be explored between species-environment (Boyra et al. 2016, Louzao et al. 2019a, García-Barón et al. 2020), predator-prey (Certain et al. 2011, Lambert et al. 2018, Waggitt et al. 2018, Louzao et al. 2019a), or predator-predator (Louzao et al. 2019b) using the data collected in situ either as a response variable or as a predictor.

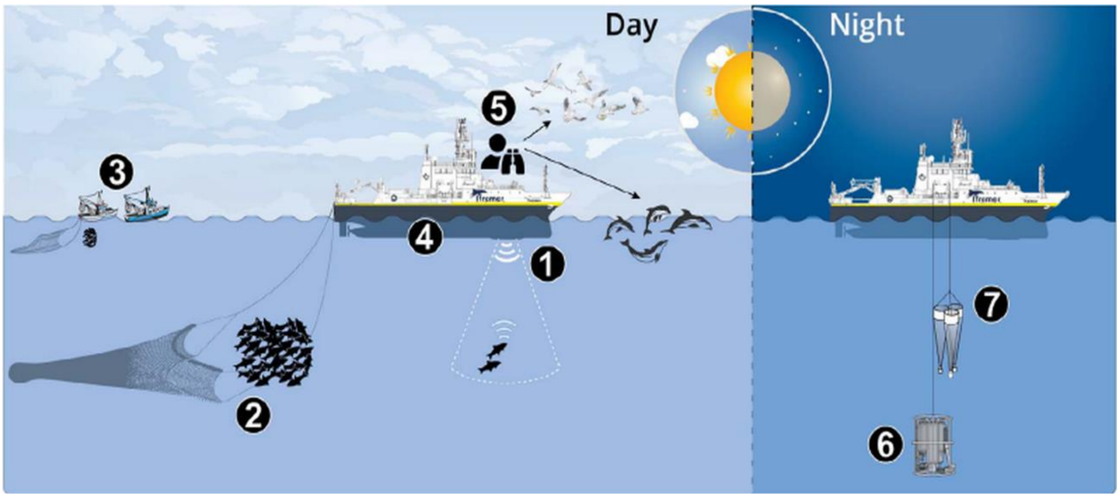


***Figure 7**. Example of how data is collected in an integrated ecosystem monitoring programme. During daytime: 1) Fisheries acoustics, 2) Midwater trawling, 3) Support of pair trawlers fishing vessels, 4) Hull-mounted thermosalinometer, 5) Megafauna sightings. During night-time, at fixed stations: 6) Sonde-based hydrobiological sampling, 7) Meso-zooplankton nets. Source: Doray et al. (2018).*

In southern European waters, several institutions perform multidisciplinary surveys (e.g., BIOMAN, PELGAS, PELACUS, JUVENA) to monitor the widely diverse community of plankton, fish and megafauna inhabiting the area (Lavin et al. 2006, Doray et al. 2018). Such diversity becomes specially high in summer-autumn months, coinciding with JUVENA survey, as it is when many top predator species use the Bay of Biscay as a migration corridor (Lezama-Ochoa et al. 2010, Louzao et al. 2015a, García-Barón et al. 2019). Both the Bay of Biscay and the JUVENA survey constitute therefore an excellent opportunity to analyse the abundance, distribution and coexistence patterns of many top predators while addressing some of the descriptors defined by the MSFD, such as biodiversity and food webs.

Relying on annual surveys, however, has its own limitations too, as they only provide a snapshot of a particular period. Under such circumstances, efforts have been recently directed to cover longer and wider spatio-temporal scales through compiling different survey data (Waggitt et al. 2020), although important components of the ecosystem still need to be incorporated.

Case study: the top predators of the Bay of Biscay

The Bay of Biscay (BoB, hereafter) is a well-differentiated geomorphological unit in the Northeast Atlantic that comprises the waters between Cape Ortegal in Spain (43°46′N 7°52′W) and Penmarch Point in France (47°48′N 4°22′W). It falls within the North Atlantic demarcation defined by the MSFD and forms the transitional region between the cold boreal waters and the warm waters of the temperate biogeographical province (Lavin et al. 2006), which results in a higher biodiversity in comparison to adjacent areas. It is limited in the south by the North-Iberian margin, where water temperature is warmer and continental shelf narrower, and by the Aquitaine and Armorican margin in the eastern part, characterized by a large French continental shelf and colder waters (Figure 8) (Koutsikopoulos & Le Cann 1996, Mulder et al. 2012).

In the oceanic area, the general circulation is weak and generally variable, with a frequent presence of cyclonic and anticyclonic eddies. In the slope, a consistent poleward flow can be detected while in the shelf, the residual currents are principally governed by the wind, tides and water density (Figure 8) (Koutsikopoulos & Le Cann 1996).

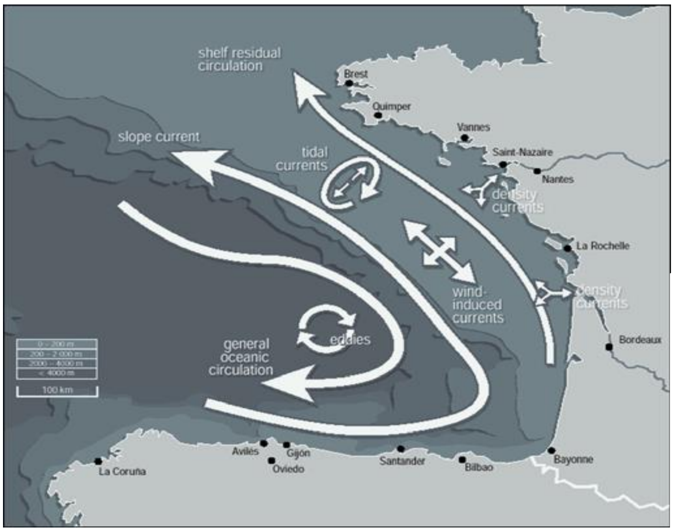


***Figure 8**. General water circulation in the Bay of Biscay according to Koutsikopoulos and Le Cann (1996) and modified by OSPAR (2000).*

Following the typical pattern of a temperate sea, the primary production is governed by the alternation between mixing and stratification of the water column, and shows two phytoplanktonic peaks, a primary one in spring and a secondary one in autumn (Bode et al. 1996, Varela 1996). Despite being considered moderate (Aquarone et al. 2008), the primary production of the BoB is seasonally and locally enhanced by mesoscale features, such as coastal run-offs, river plumes, coastal upwelling and internal waves, which have long allowed the development of important fisheries (Lavin et al. 2006).

Upper in the trophic level, this moderately productive bay also maintains a highly diverse and abundant community of top predators. Some of these are resident species, while others only visit the BoB during their feeding migrations in summer-autumn months, coinciding with JUVENA survey. The BoB is therefore an important feeding ground, that congregates a wide variety of taxa (e.g., seabirds, cetaceans, tuna, sharks, sunfish, turtles), although seabirds and cetaceans represent the most diverse groups (Lorance et al. 2000, Sims et al. 2009, Goñi & Arrizabalaga 2010, Doherty et al. 2017, Laran et al. 2017, Pettex et al. 2017, Avens & Amico 2018).

Among seabirds, resident species (those that breed in the BoB) include yellow-legged gull *Larus michahellis*, the lesser black-backed gull *L. fuscus*, the European herring gull *L. argentatus*, the European shag *Phalacrocorax aristotelis*, the European storm-petrel *Hydrobates pelagicus*, the black-legged kittiwake *Rissa tridactyla*, the sandwich tern *Thalasseus sandvicensis*, the common tern *Sterna hirundo* and the Cory's shearwater *Calonectris borealis*. Wintering/migrants species, on the other hand, comprise the northern gannet *Morus bassanus*, the great skua *Stercorarius skua*, the artic jaeger *S. parasiticus*, the pomarine jaeger *S. pomarine*, the Black-headed gull *Chroicocephalus ridibundus*, the Sabine's gull *Xema sabini*, the Mediterranean gull

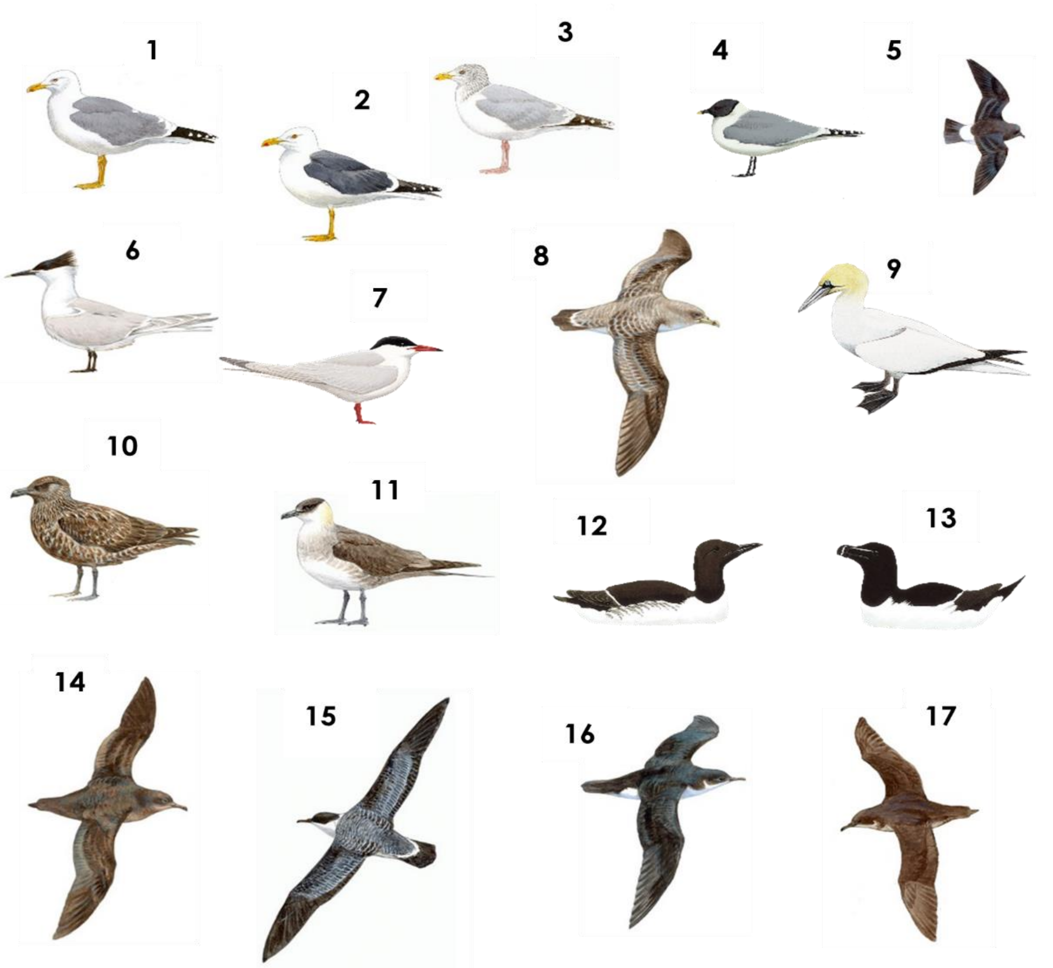


Figure 9. *Some of the most frequently observed seabird species during JUVENA survey. (1) yellow-legged gull, (2) lesser black-backed gull, (3) European herring gull, (4) Sabine's gull, (5) European storm-petrel, (6) sandwich tern, (7) common tern, (7) Cory's shearwater, (9) northern gannet, (10) great skua, (11) Arctic jaeger, (12) common guillemot, (13) razorbill, (14) sooty shearwater, (15) great shearwater, (16) Manx shearwater, (17) Balearic shearwater. Images have been compiled from www.seo.org and birdguides.com.*

Ichthyaetus melanocephalus, the common guillemot *Uria aalge*, the razorbill *Alca torda*, the sooty and great shearwaters *Ardenna grisea* and *A. gravis*, and the Balearic and Manx shearwaters *Puffinus mauretanicus* and *P. puffinus* (Figure 9).

Among cetaceans, the fin whale *Balaenoptera physalus* represents the most commonly reported baleen whale, known to visit the BoB during the sping-autumn period (García-Barón et al. 2019). The vast majority of remaining species are small toothed-cetaceans that include the common dophin *Delphinus delphis*, the striped dolphin *Stenella coeruleoalba*, the bottlenose dolphin *Tursiops truncatus*, the harbour porpoise *Phocoena phocoena*, the long-finned pilot whale *Globicephala melas* and the Risso's dolphin *Grampus griseus*, although some deep diving cetacean species can be also found, such as the sperm whale *Physeter macrocephalus* and the Cuvier' beaked whale *Ziphius cavirostris* (Figure 10).

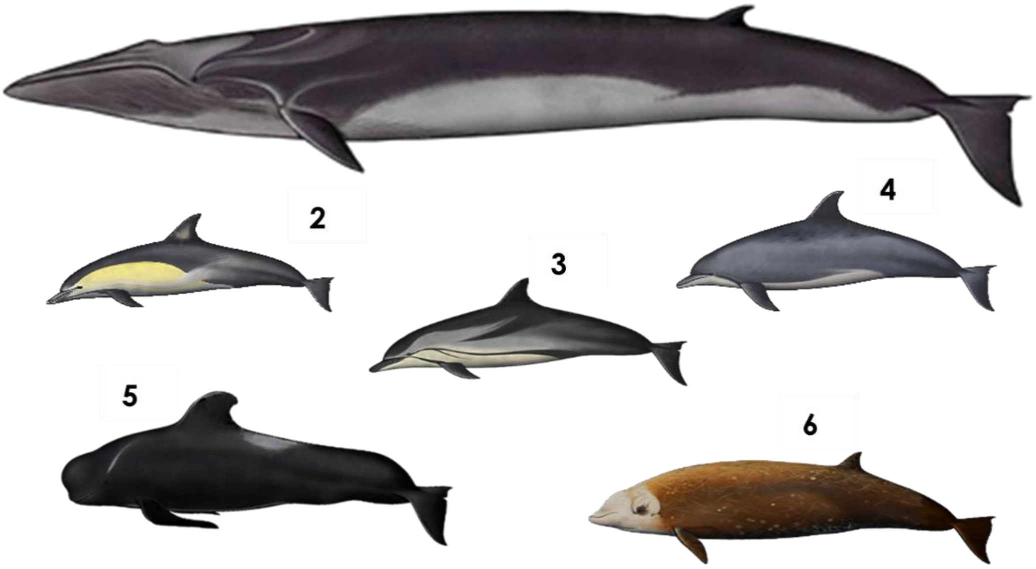


Figure 10. *Some of the most frequently observed cetacean species during JUVENA survey. (1) fin whale, (2) common dolphin, (3) stripped dolphin, (4) bottlenose dolphin, (5) long-finned pilot whale, (6) Cuvier's beaked whale. Image courtesy of Joshua G. Herranz (Marine Life Project).*

Such productivity and diversity, however, might be altered by climate change in a near future, as raising temperatures are expected to increase ocean stratification and reduce primary production and zooplankton biomass (Chust et al. 2014a). In the last years, a significant warming has been detected in the BoB (Costoya et al. 2015), together with losses in fisheries production (Free et al. 2019), and changes in the composition, distribution and abundance of both fish and top predators species (Blanchard & Vandermeirsch 2005, Hemery et al. 2007, Authier et al. 2018, Baudron et al. 2020).

Overexploitation episodes (Lazkano et al. 2013), oil spills events (Ridoux et al. 2004) and unsustainable bycatch rates (ICES 2020) have been also reported in the last decades in the BoB, which overall, threaten the stability and health of the ecosystem and put in risk the conservation and viability of many top predators that are either protected, endangered or threatened.

The rationale of the study

Seabirds and cetaceans have been long considered good ecological indicators, as they face numerous impacts and respond to different ecosystem changes while moving across their vast distributional ranges (Piatt & Sydeman 2007, Hazen et al. 2012). They are in addition protected under different international agreements, such as the Bird Directive (Council Directive 2009/147/EC) and the Habitat Directive (Council Directive 92/43/EEC), which aim to promote and maintain biological diversity through the conservation of natural habitats and biodiversity in the European Union territory. But despite the conservation efforts, seabirds are one of the most threatened groups (Croxall et al. 2012, Dias et al. 2019), while many cetacean species are still intentionally killed or indirectly impacted by commercial fisheries (Allen 2014).

The BoB comprises some of these protected, endangered, and threatened (PET) species, whose study is now systematically possible thanks to the development of integrated ecosystem surveys. Given the nature of the observations recorded in research vessels, species' abundance and distribution patterns are the most commonly addressed topics. However, and despite the large variety of species comprised in on-board-collected data, many studies mostly focus on the individualistic responses of top predators to environmental conditions, omitting the potential interactions with species from the same guild or other trophic levels.

Recent examples have shown that not accounting for biotic interactions limits the understanding of underlying patters when studying species distribution (Wisz et al. 2013) and hence, effective conservation and management measures should require the identification of variables shaping both the Eltonian and Grinnellian niche of species.

For that reason, the present study has aimed to incorporate both biotic and abiotic factors in the study of top predators' community of the BoB, for which we have set the following hypothesis and objectives. By this means, we intended to obtain a more comprehensive understanding of the drivers governing the assemblage of top predators and a better knowledge of the ecosystem functioning of the BoB.

Hypothesis and objectives

The working hypothesis is a ”provisional, working means of advancing investigation” that acts as a guide for the explanatory research (Dewey 1999, Shields & Tajalli 2006), and as such, it has been constructed as follows:

”The distribution and abundance of top predators are driven by environmental factors and biotic interactions, and thus, the consideration of both components should provide us with new information on species interactions while contributing to improve our understanding of the assembly rules governing species coexistence, food web structure and spatio-temporal patterns”.

In order to test the working hypothesis, four specific research objectives were established. Three of them were tackled in each specific chapter, while the last one was addressed along the whole thesis:

1. To uncover the underlying mechanisms of predator-prey co-occurrence patterns by identifying interspecific associations and their main drivers (Chapter I).
2. To understand how co-occurring top predators share the environmental and trophic niche (Chapter II).
3. To define the role of prey, climatic and oceanographic variables in driving the spatio-temporal patterns of a highly mobile top predator (Chapter III).
4. To determine the relative importance of biotic and environmental drivers in explaining the abundance and distribution of top predators (Chapter I, II, III).

Structure of the thesis

Beyond this general introduction in the topic, which aimed to provide some insights on the concepts that will be discussed later on, the main body of the thesis is structured in three chapters, followed by a general discussion acknowledging the main limitations and major findings and a final section resuming main conclusions. Although the three chapters are related and directed to test the hypothesis of this dissertation, the specific questions and methodologies addressed in each of them led us to present the chapters as individual scientific papers with their own introduction, material and methods, results, and discussion. The development of the three chapters allowed us to address the first three objectives, while the conjunction of all of them provided us with an additional conclusion that served to answer a widely discussed topic in the field. The main subjects of each chapter are described below:

- In chapter I, we explored the main drivers governing the assemblage of the pelagic predator–prey community by analysing their co-occurrence patterns with a Joint Species Distribution Modelling approach (JSDM), that unlike conventional approaches, allows distinguishing between biotic interactions and similar environmental preferences.
- In chapter II, we aimed to disentangle how co-occurring top predators share the environmental and trophic niches by identifying the main segregation mechanisms with a spatial modelling approach.
- In chapter III, we analysed the spatio-temporal changes and the effect of biotic and abiotic drivers in the abundance and distribution of a highly mobile top predator by means of a spatio-temporal model (VAST) that accounts for changes in sampling effort resulting from the combination of multiple datasets.

CHAPTER 1

Identifying drivers of interspecific associations in the marine predator-prey network of the Bay of Biscay

ABSTRACT

Identifying the role that environmental factors and biotic interactions play in species distribution can be essential to better understand and predict how ecosystems will respond to changing environmental conditions. Within that context, this study aimed to disentangle the assemblage of the pelagic predator–prey community by identifying interspecific associations and their main drivers. For this purpose, we applied the Joint Species Distribution Modelling approach, JSDM, to the co-occurrence patterns of both prey and top predator communities obtained from JUVENA surveys during 2013–2016 in the Bay of Biscay. Results showed that the co-occurrence patterns of top predators and prey were driven by a combination of environmental and biotic factors, which highlighted the importance of considering both components to fully understand the community structure. In addition, results also revealed that many biotic interactions, such as schooling in prey (e.g., anchovy–sardine), local enhancement/facilitation in predators (e.g., Cory's shearwater–fin whale), and predation between predator–prey species (e.g., northern gannet–horse mackerel), were led by positive associations, although predator avoidance behaviour was also suggested between negatively associated species (e.g., striped dolphin–blue whiting). The identification of interspecific associations can therefore provide insights on the functioning of predators–prey network that might be used for the conservation of endangered species or for developing a sustainable management of exploited species based on their predators and competitors. By this means, approaches such as JSDM can help advance towards an ecosystem-based management, although contrasting the results with additional data source is recommended to discern true interactions.

Published as:

Astarloa, A., Louzao, M., Boyra, G., Martinez, U., Rubio, A., Irigoien, X., Hui, F. K. C. & Chust, G. (2019). Identifying main interactions in marine predator–prey networks of the Bay of Biscay. *ICES Journal of Marine Science*, 76 (7), 2247-2259.

1. Introduction

Climate change has been identified as a major future threat for marine ecosystems (Collins et al. 2013) and it has triggered shifts in the abundance, phenology and distribution of organisms (Doney et al. 2012, Poloczanska et al. 2013). The assessment of these changes has been typically conducted considering only climatic factors, based on the assumption that biotic interactions might play a minor role in governing species distribution at regional to global scales (Pearson & Dawson 2003). However, it is now generally accepted that interspecific interactions can strongly affect the biogeography of species beyond local extents (Araújo & Luoto 2007, Wisz et al. 2013). Therefore, it is essential to understand the interplay between environmental factors and biotic interactions to better anticipate how ecosystems will respond (Gilman et al. 2010, Blois et al. 2013).

Biotic interactions are known to affect species spatial patterns via several mechanism such as predation, competition, parasitism, mutualism and facilitation (Wisz et al. 2013). Identifying such associations has long been a subject of ecological research, that has been tackled by studying species co-occurrence patterns and specifically by comparing observed occurrences with null models to detect non-random patterns (for approaches based on randomized null models see Gotelli & Ulrich 2010, for analytical null models see Veech 2013). These conventional approaches, however, do not allow to distinguish whether the resulting associations derive from the species having (dis-) similar habitat requirements or from a biotic relationship. In fact, a positive association may be caused by biotic interactions (e.g. facilitation) or by shared environmental requirements (e.g. similar habitat affinities), whereas negative associations may be driven by biotic interactions (e.g. competition) or reflect different habitat preferences (Ovaskainen et al. 2010).

Lately, new approaches including niche associations and network theory have been developed to infer species associations (Morueta-Holme et al. 2016). In parallel, other methods consisting in incorporating species co-occurrence data into the classical species distribution model (SDM) framework have emerged (Clark et al. 2014, Pollock et al. 2014, Warton et al. 2015, Hui 2016). By combining both components, Joint Species Distribution Models (JSDMs hereafter) allow the analysis of correlation patterns across taxa at the same time as studying environmental response (Warton et al. 2015); as a result, species co-occurrence patterns can be decomposed into environmental responses and residual correlation not explained by the measured predictors (Hui 2016). A key step consists then in attributing this residual correlation to biotic interactions, as there could also be non-biological explanations such as missing environmental variables or poor model fit (Zurell et al. 2018). Some authors, however, have already succeed in identifying biotic interactions, including codominance in trees (Pollock et al. 2014) and heterospecific attraction in river birds (Royan et al. 2016). In contrast, the implementation of JSDMs on predator-prey co-occurrence patterns has been scarcely explored (Zurell et al. 2018) and hence, the potential to detect ecological processes such as predation needs further investigation.

In the Bay of Biscay (BoB hereafter), the upwelling occurring mainly over the Iberian Shelf section and the river run-offs of the French shelf (Aquarone et al. 2008) favour the occurrence of a rich community of small pelagic fishes, including European sardine *Sardina pilchardus*, European anchovy *Engraulis encrasicolus*, Atlantic mackerel *Scomber scombrus* and Atlantic horse mackerel *Trachurus trachurus* (ICES 2008). Additionally, the BoB also holds a rich cetacean fauna (Kiszka et al. 2007, Spitz et al. 2011) and a highly diverse seabird population (Pettex et al. 2017), including some endangered species such as the fin whale *Balaenoptera physalus* (García-Barón et al. 2019) and the Balearic shearwater *Puffinus mauretanicus* (Pérez-Roda et al. 2017) that make the identification of interspecific associations essential to advance towards an ecosystem based management (Veit & Harrison 2017). Acquiring simultaneous data for both predator and prey, however, is challenging and as a result, predator-prey interactions involving cetaceans and seabirds remain poorly understood in the area (but see Certain et al. 2011, Lambert et al. 2018).

Within this context, this work aims to better understand the mechanisms underlying the assemblage of the pelagic predator-prey community of the BoB by identifying interspecific associations and their main drivers. For this purpose, we fitted JSDMs by combining the environmental conditions and the co-occurrence patterns of top predators and prey obtained from JUVENA surveys over the 2013-2016 period. By this means, we addressed the following specific questions:

1. Are species interactions, such as predator-prey, triggering the observed co-occurrence patterns?
2. Or, in contrast, are environmental factors the main explanatory features of species co-occurrence?

By answering to these questions, this study intends to provide relevant insights about the functioning of predators and prey communities that may help the conservation of endangered species and the sustainable management of exploited species to advance ecosystem-based monitoring (Louzao et al. 2019a).

2. Material and Methods

2.1. Multidisciplinary surveys

JUVENA oceanographic survey takes place every September with the aim of evaluating the population of European anchovy and monitoring the abundance of other pelagic species in the BoB (Figure 1.1) (Boyra et al. 2013). The sampling strategy is based on parallel transects arranged perpendicular to the coast, spaced at 15 nautical miles (nmi) and carried out by two oceanographic research vessels, Ramon Margalef and Emma Bardan (R/V RM and R/V EB, hereafter), surveying transects from the coast (20 m bottom depth) to beyond the shelf break (Figure 1.1). Data from plankton to predators, as well as environmental information is also collected in order to obtain an overall assessment of the marine ecosystem (Louzao et al. 2019a) (for a schematic flowchart of the entire Material and Methods section see Figure 1.2).

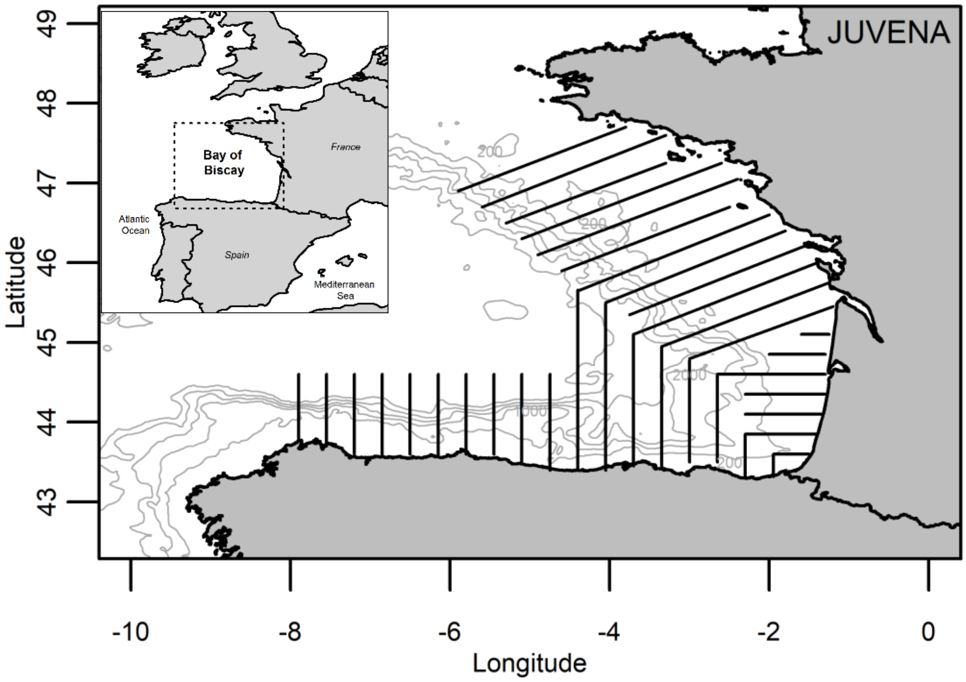
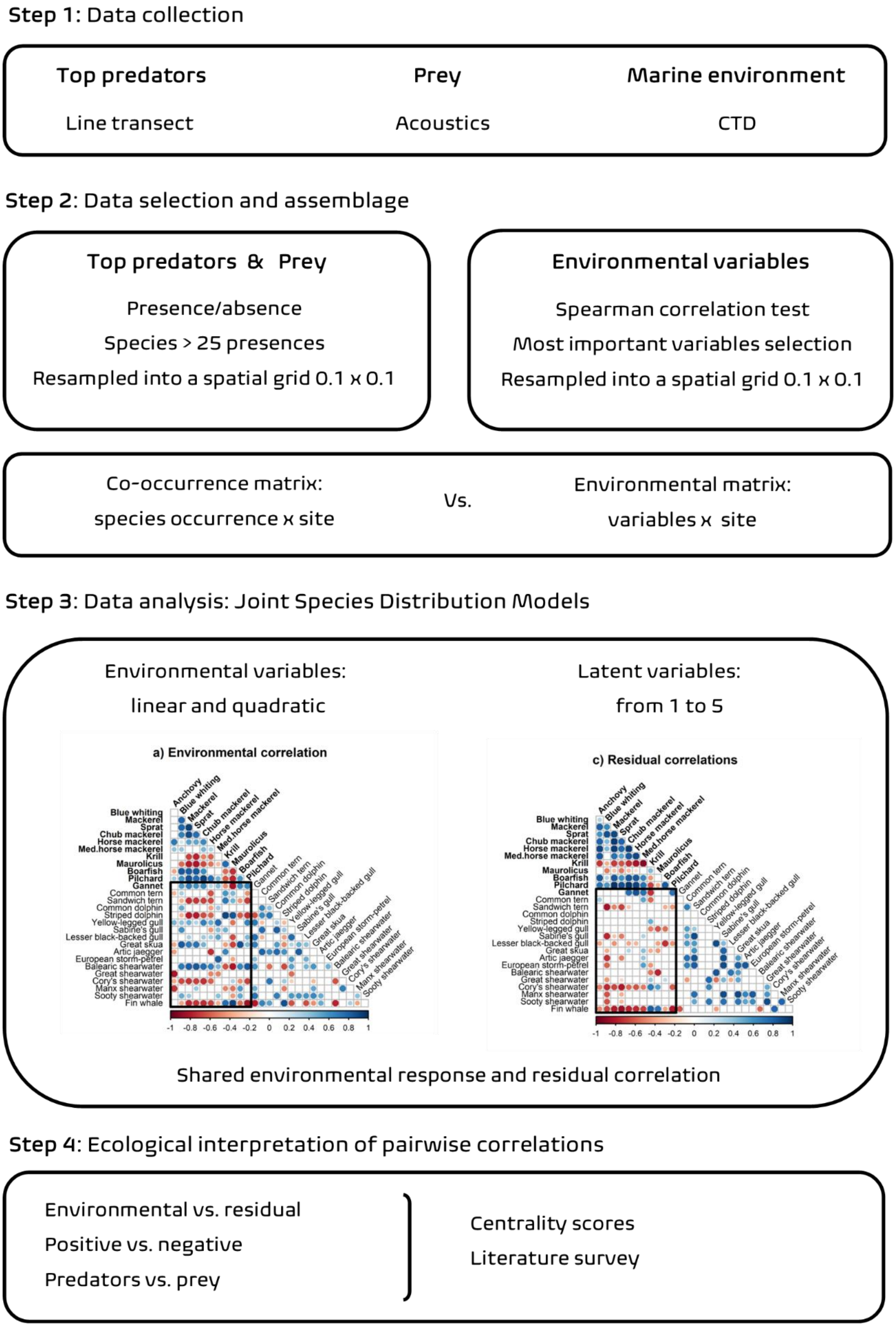


Figure 1.1. Overview of the study area and the sampling design of JUVENA survey. Isobaths of 200 m, 1000 m and 2000 m are indicated.



Step 1: Data collection

Top predators — Line transect

Prey — Acoustics

Marine environment — CTD

Step 2: Data selection and assemblage

Top predators & Prey

Presence/absence

Species > 25 presences

Resampled into a spatial grid 0.1 x 0.1

Environmental variables

Spearman correlation test

Most important variables selection

Resampled into a spatial grid 0.1 x 0.1

Co-occurrence matrix:
species occurrence x site

Vs.

Environmental matrix:
variables x site

Step 3: Data analysis: Joint Species Distribution Models

Environmental variables:
linear and quadratic

Latent variables:
from 1 to 5

Shared environmental response and residual correlation

Step 4: Ecological interpretation of pairwise correlations

Environmental vs. residual

Positive vs. negative

Predators vs. prey

Centrality scores

Literature survey

Figure 1.2. *Workflow showing the steps taken throughout the study, including data collection, data selection and assemblage, data analysis and data interpretation.*

Sightings of top predators

Since 2013 sightings of top predators have been recorded aboard R/V RM by a team of three experienced observers. By following the Distance sampling methodology (Buckland et al. 2001), observers (2 at a time) searched for cetaceans and seabirds ahead of the bow within an angle of 180° and from a single observation platform located at 7.5 m above the sea level. For each observation, the radial distance to animal clusters (individual birds or groups of animals of the same species) and the angle of the cluster sighting with respect to the trackline were estimated based on a range finding stick (Heinemann 1981) and an angle metre. Sightings were made with naked eye, except for the identification of species and counting of individuals, which was aided by 10 x 42 Swarovski binoculars. Time of observation, species composition, group size, movement direction, and behaviour (e.g., displacing, foraging, attracted) were also noted. In addition, environmental conditions affecting the detectability of species such as Beaufort sea-state, swell height, wind speed, visibility, or glare intensity were recorded at the beginning of each observation period (i.e. every hour) or whenever observation conditions changed. Sampling effort was performed only during daytime, at a constant speed and under sea-state conditions ≤6 and it was geographically located based on the vessel GPS which logs the coordinates of the vessel every 1 min.

Biomass estimates of pelagic prey species

Biomass of pelagic species (fish and crustaceans, prey hereafter) were estimated by means of acoustic methods and pelagic trawls for the 2013–2016 period to match in time with the available data of predators. The acoustic equipment used for that consisted on Simrad EK60 split-beam echosounders (Kongsberg Simrad AS, Kongsberg, Norway) located on both vessels that sampled the water column to depths of 200-300 m during daytime (Boyra et al. 2013). Sampling started on the northern Spanish coast, from west to east, where each R/V monitored the pelagic ecosystem simultaneously over different transects. Then, both R/V moved to the north to sample French waters where the smaller R/V EB sampled the inner section of the transects, while the larger R/V RM sampled the outer sector. The acoustic data collected by both vessels were then processed together: abundance estimates were obtained processing the collected acoustic data in the positive strata by layer echo integration and using an ESDU (Echo integration Sampling Distance Unit) of 0.1 nmi, whereas identification of organisms and population size structure was determined using net sampling and echo trace characteristics. Finally, abundance in number of individuals was multiplied by the mean weight, obtaining biomass estimates per age, and length class for each ESDU [more details can be found in Boyra et al. (2013)].

Oceanographic characterization of the pelagic realm

During the survey, oceanographic data were also collected using a CTD profiler. For each transect, a minimum of three profiles were performed (coastal, continental shelf, and oceanic waters) measuring the water column from the surface to 200 m depth. Temperature, salinity, and water density were directly inferred from CTD casts. The depth of the maximum temperature gradient (as a proxy of the mixing layer depth) and geostrophic velocities were derived from temperature and density data following Rubio et al. (2009) and Caballero et al. (2016), respectively. Horizontal fields of these variables were obtained using Optimal Statistical Interpolation scheme described in Gomis et al. (2001) over a spatial grid with regular node distances of 0.15 x 0.15° latitude–longitude. To obtain 3D matrix fields, horizontal analyses were performed independently at 5 dbar intervals from 10 to 200 m. In this way, we obtained temperature, salinity, and geostrophic velocities values for the surface (Ts, SALs, and GVs) and for the water column up to 200 m by estimating the median value (T_{200}, SAL_{200}, GV_{200}), making them suitable for the study of seabirds and cetaceans. For the depth of maximum temperature gradient (DTG), no additional estimates were made since it is a two-dimensional field. Finally, distance to the coast (DCO) and depth values (DEP) were extracted from NOAA database using the marmap R package V.: 1.0.2 (Pante & Simon-Bouhet 2013) and added to the analysis (Table 1.1).

Table 1.1. *Summary of the environmental variables used in the study. Dynamic variables were estimated from oceanographic data collected on board, whereas static variables were extracted from NOAA (ETOPO1 database).*

Variables	**Acronym**	**Type**	**Dimension**
Temperature (°C)	T	Dynamic	3D
Salinity (psu)	SAL	Dynamic	3D
Geostrophic velocity (m s^{-1})	GV	Dynamic	3D
Depth of maximum temperature gradient (m)	DTG	Dynamic	2D
Depth (m)	DEP	Static	2D
Distance to coast (km)	DCO	Static	2D

2.2. Data selection and assemblage

Top predator's data were filtered by including only those sightings where the identification was made at species level and by removing sightings considered to be attracted by the vessel (i.e., those individuals coming directly to the boat). In the case of prey, all species for which a biomass estimate was available were selected. Predator and prey data (i.e., number of sightings and biomasses) were then transformed to presence-absence and overlaid per year over a standard grid covering the study area (latitudinal range: 43.2-48°N; longitudinal range: 1-9°W) with a cell size of 0.1° spatial resolution. At this point, a second filter was applied, selecting only those prey and predator data with common sampling effort within the same year. In addition, species with less than 25 presences over the total survey period were removed with the aim of avoiding problems related to small sample size (Wisz et al. 2008, Authier et al. 2018). As a whole, 28 species were chosen, 17 top predators and 11 prey (Table 1.2) that were arranged as a community matrix where columns were species and rows were each cell of the standard grid by year (sites hereafter). As it can be seen, some species within the prey group could be also acting as predators over other prey species, e.g. mackerel-blue whiting (Olaso et al. 2005). However, to avoid misunderstandings, predators and prey in this study will only refer to those species defined as such in Table 1.2. Finally, environmental variables were resampled with the *raster* package V.: 2.9.5 (Hijmans et al. 2017) to match the standard grid of predators and prey and arranged in a matrix of environmental variables (columns) vs. sites (rows).

Table 1.2. *List containing the family, scientific name, common name and acronym of the selected species of pelagic prey and top predators. Acronym for prey refers to FAO code, whereas acronym for predator holds the abbreviation, widely used by observers, of the scientific name.*

	Family	**Scientific name**	**Common name**	**Acronym**
PREY	***Caproidae***	*Capros aper*	Boarfish	BOC
	Carangidae	*Trachurus mediterraneus* *Trachurus trachurus*	Mediterranean horse mackerel Atlantic horse mackerel	HMM HOM
	Clupeidae	*Sardina pilchardus* *Sprattus sprattus*	European pilchard European sprat	PIL SPR
	Engraulidae	*Engraulis encrasicolus*	European anchovy	ANE
	Euphausiidae	*Euphasia spp.*	Krill	KRX
	Gadidae	*Micromesistius poutassou*	Blue whiting	WHB
	Scombridae	*Scomber scombrus* *Scomber japonicus*	Atlantic mackerel Pacific chub mackerel	MAC MAS
	Sternoptychidae	*Maurolicus muelleri*	Mueller's pearlside	MAV

PREDATORS	***Balaenopteridae***	*Balaenoptera physalus*	Fin whale	BALPHY
	Delphinidae	*Delphinus delphis*	Common dolphin	DELDEL
		Stenella coeruleoalba	Striped dolphin	STECOE
	Hydrobatidae	*Hydrobates pelagicus*	European storm-petrel	HYDPEL
	Laridae	*Larus michahellis*	Yellow-legged gull	LARMIC
		Larus fuscus	Lesser black-backed gull	LARFUS
		Xema sabini	Sabine's gull	XEMSAB
	Procellariidae	*Ardenna gravis*	Great shearwater	ARDGRA
		Ardenna grisea	Sooty shearwater	ARDGRI
		Calonectris borealis	Cory's shearwater	CALBOR
		Puffinus mauretanicus	Balearic shearwater	PUFMAU
		Puffinus puffinus	Manx shearwater	PUFPUF
	Stercorariidae	*Stercorarius parasiticus*	Arctic jaeger	STEPAR
		Stercorarius skua	Great skua	STESKU
	Sternidae	*Sterna hirundo*	Common tern	STEHIR
		Thalasseus sandvicensis	Sandwich tern	THASAN
	Sulidae	*Morus bassanus*	Northern gannet	MORBAS

2.3. Predator-prey networks

In order to uncover the community structure behind predator-prey networks and identify interspecific associations, we fitted a series of JSDMs using the *boral* package V.: 1.7 (Hui 2018). JSDMs are extensions of the Generalised Linear Modelling (GLMs, McCullagh and Nelder, 1989) framework, which is widely used for modelling species distribution data (Guisan et al. 2002). A key feature of JSDMs is that they comprise both environmental variables and latent variables, where the latter can be understood as a set of unobserved predictors that induce correlation between species. Latent variables, similarly to ordination axes, aim to represent the main axes of covariation across taxa and that is why they are used as a tool for estimating the underlying causes of covariation as well as for studying the factors driving co-occurrence (Warton et al. 2015). We refer the reader to Warton et al. (2015, 2016) or to Ovaskainen et al. (2017), among others, for more comprehensive overviews of latent variables aimed at ecologists.

Latent variables

A critical issue when fitting JSDMs is the choice of the number of latent variables: a small number of latent variables means a simpler model, but risks a potentially too poor approximation of the true correlation structure, while more latent variables means an inherently more complex model (Wilkinson et al. 2018). Previous literature suggests that a small number (less than five) of latent variables is often enough for a good approximation to the species correlation structure (Warton et al. 2015), so in order to obtain the best model, we fitted a series of JSDMs using from 1 to 5 latent variables.

Environmental covariates

Species distribution modelling is fundamental to understand the ecological niche of species, which theoretically assumes a symmetric Gaussian-shaped response (Austin 2007). When fitting GLMs for each species via the *boral* package, fitting a quadratic polynomial function can be a possible solution in the absence of more sophisticated non-linear methods (Jamil & Ter Braak 2013). However, adding quadratic terms to the already available covariates could potentially lead to model overfitting (Harris 2015). To overcome this problem, we identified the most important variables by using two complementary approaches (based on the Multi-Model Inference Approach and the JSDM approach) and limited the selection to five variables at most to avoid excessive complexity (D'Amen et al. 2018) (for detailed variable selection approach see Appendix A1).

Model fit

Five JSDMs ranging from 1 to 5 latent variables were fitted to the species co-occurrence matrix, assuming the binomial error distribution with a probit-link function and the aforementioned five environmental covariates as explanatory predictors. All environmental covariates were standardized to have a mean of zero and a standard deviation of one (Zuur et al. 2007) before entering them as both linear and quadratic terms in the model. Additionally, a random row effect for both site and year was also included in order to account for spatial and temporal correlation. To address the issue of non-convergence due to complete separation in binary variables, we used an informative prior on the regression coefficients (Ghosh et al. 2018), specifically $\beta \sim N(0, 1)$, as recommended by Wilkinson *et al.* (2018). We adopted the default Markov Chain Monte Carlo (MCMC) configuration in *boral*, that is, running Bayesian MCMC sampler with 40000 iteration, with the first 10000 discarded as burn in and the remaining thinned by a factor of 30 (Hui 2018). For checking MCMC convergence, a combination of trace plots and the Geweke diagnostic (Geweke 1992) was used. Finally, estimated residual correlations, their uncertainty (defined as the width of their corresponding 95% credible interval) and a variation partitioning was obtained for each JSDM to assess the best model in terms of the number of latent variables required (Appendix A2).

Ecological interpretation

Significant environmental and residual correlations (those whose 95% credible interval does not contain zero) resulting from the best model were first analysed at the community level and then separately in predator, prey and predator-prey assemblies. To uncover the community structure behind each assembly, pair-wise correlations were ecologically interpreted following D'Amen *et al.* (2018) approach (Table 1.3). To identify species with a high number of associations, degree centrality —defined as the number of species a given species interacts with— was assessed for each group using both positive and negative associations. For this purpose, the *igraph* package V.: 1.2.4.1 (Csardi & Nepusz 2006) was used, which enabled the visualization of all associations and in addition, assigned a larger weight to those species with higher number of positive or negative associations.

Table 1.3. *The ecological interpretation given to pair-wise associations based on their environmental and residual response (inspired by D'Amen et al. 2018).*

Environmental correlation	**Residual correlation**	**Ecological interpretation of pair-wise associations**
0	+	Positive interactions causing aggregation
-	+	Positive interactions despite of habitat differentiation
+	+	Positive interactions and similar env. preferences causing aggregation
+	0	Similar habitat preferences
0	-	Negative interactions causing segregation
-	-	Negative interactions and habitat filtering causing segregation
+	-	Negative interactions despite shared environmental preferences
-	0	Habitat differentiation
0	0	Random pair

Additionally, a literature survey was conducted with the aim of contrasting results and to discern biotic interactions from those associations driven by missing predictors. Specifically, scientific papers focusing primarily in the North Atlantic and describing species diet and feeding behaviour were searched in order to support predator-prey interactions, mutualistic relationships or interspecific competition. Nevertheless, the difficulty to assign mutualistic or competition evidences to pair-wise species lead us to only quantify trophic evidences.

3. Results

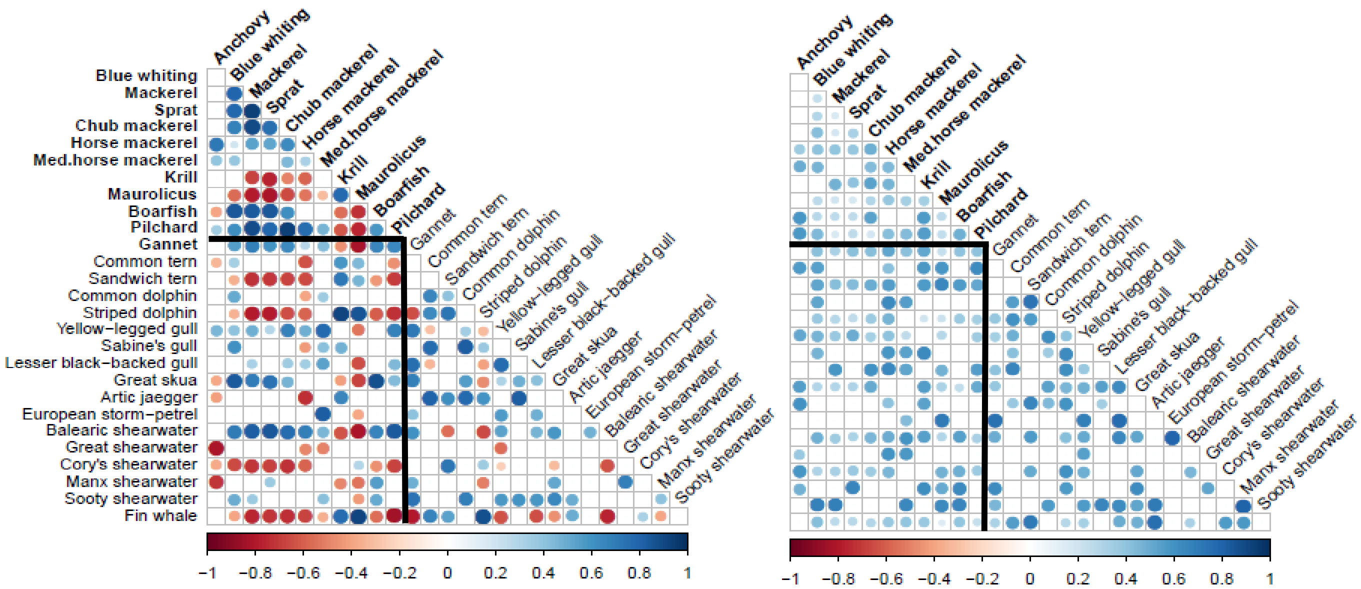
3.1. Predator-prey network structure

The comparison among the five JSDM candidates (where the number of latent variables varied from 1 to 5) showed that the models tended to stabilize in terms of their residual correlations from three latent variables onwards. We decided in the end to select the JSDM with four latent variables, given that the model with three latent variables showed small evidence (based on the Geweke diagnostic) that the MCMC sampling algorithm had failed to converge within the current sampling configuration (to compare the different JSDMs see Appendix A2).

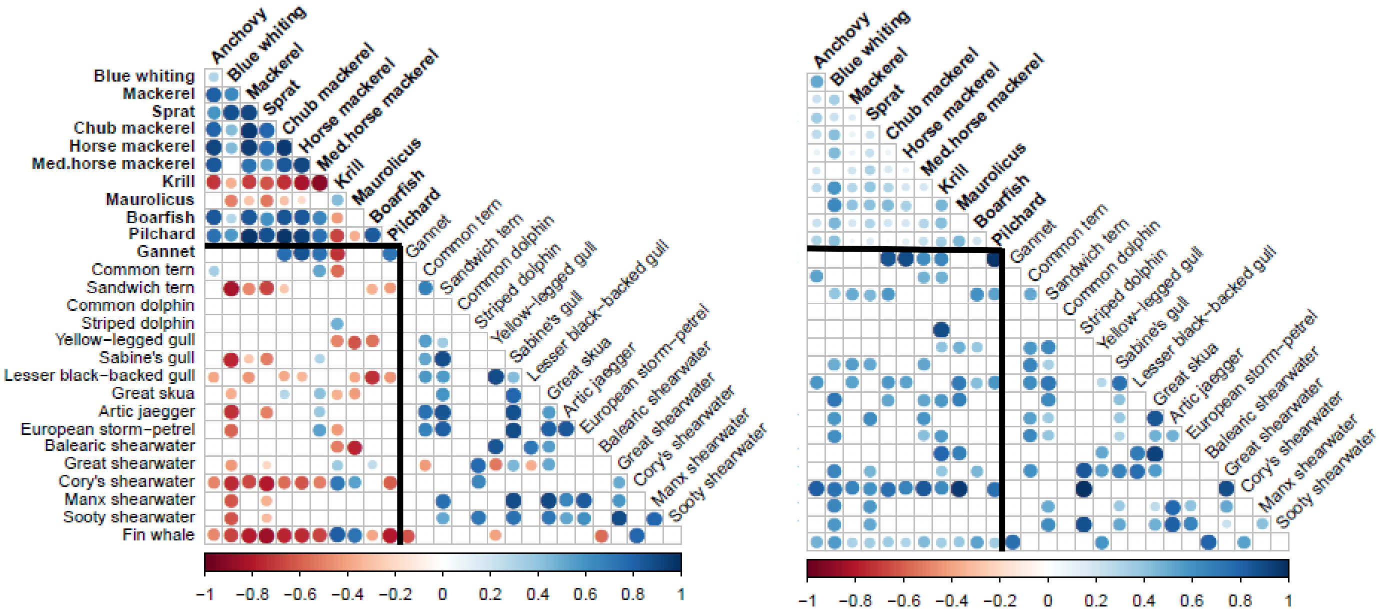
At the community level, the significant environmental correlations (58%) resulting from the selected model showed a relatively homogeneous distribution of positive and negative correlations (Figure 1.3a), followed by a homogenous distribution of their uncertainty (Figure 1.3b) and a percentage of accounted variance ranging from 8% (lesser black-backed gull) to 70% (blue whiting) (Appendix A3). By contrast, the significant residual correlations (45%) showed that positive correlations mainly occurred between pair-wise species of prey or predators whilst negative correlations especially happened among predator-prey species (Figure 1.3c). Estimates of residual uncertainty also showed unbalanced results, pointing out some species, e.g., northern gannet *Morus bassanus,* striped dolphin *Stenella coeruleoalba* or Cory's shearwater *Calonectris borealis,* with high uncertainty (Figure 1.3d) and low percentage of variance accounted for the latent variables (Appendix A3).

A similar pattern was found when environmental and residual correlations between species pairs were compared: positive responses were mainly detected in prey and predators' guilds separately, while negative responses mainly occurred within predator-prey group (Figure 1.4a-c). This last group showed the most diverse response while the prey guild showed a clear two-fold pattern that corresponded to neritic-oceanic species pairs (Figure 1.4c, a).

More detailed information was obtained when attributing an ecological meaning to every pair-wise correlation (Figure 1.5). The two-fold pattern seen in prey (Figure 1.4a), for instance, was found to be mainly driven by the combined effect of positive interactions and similar environmental preferences (49%) and by the combination of negative interactions and habitat differentiation (22%). Predator guild, although in a minor extent, also showed a high number of positive correlations (54%), attributed mainly to similar habitat preferences (22%) and positive interactions (18%).


a) Environmental correlation

b) Environmental correlation uncertainty


c) Residual correlations

d) Residual correlation uncertainty

***Figure 1.3**. Environmental and residual correlations and their corresponding uncertainty (defined as the width of their 95% credible interval) for each species-pair. Positive associations are indicated in blue and negatives in red. The rectangle defined under the black lines corresponds to correlations among predator-prey species.*

Negative correlations, in contrast, were very low (14%) and in most of the cases were caused by different environmental preferences (10%). In the predator-prey group, positive correlations were less abundant (30%) and mainly driven by similar habitat preferences (20%), whereas the proportion of negative correlations was higher (42%) and more diverse. Although no specific driver was detected in this group, for first time all possible negative associations were described here, including those classified as negative interactions despite shared environmental preferences.

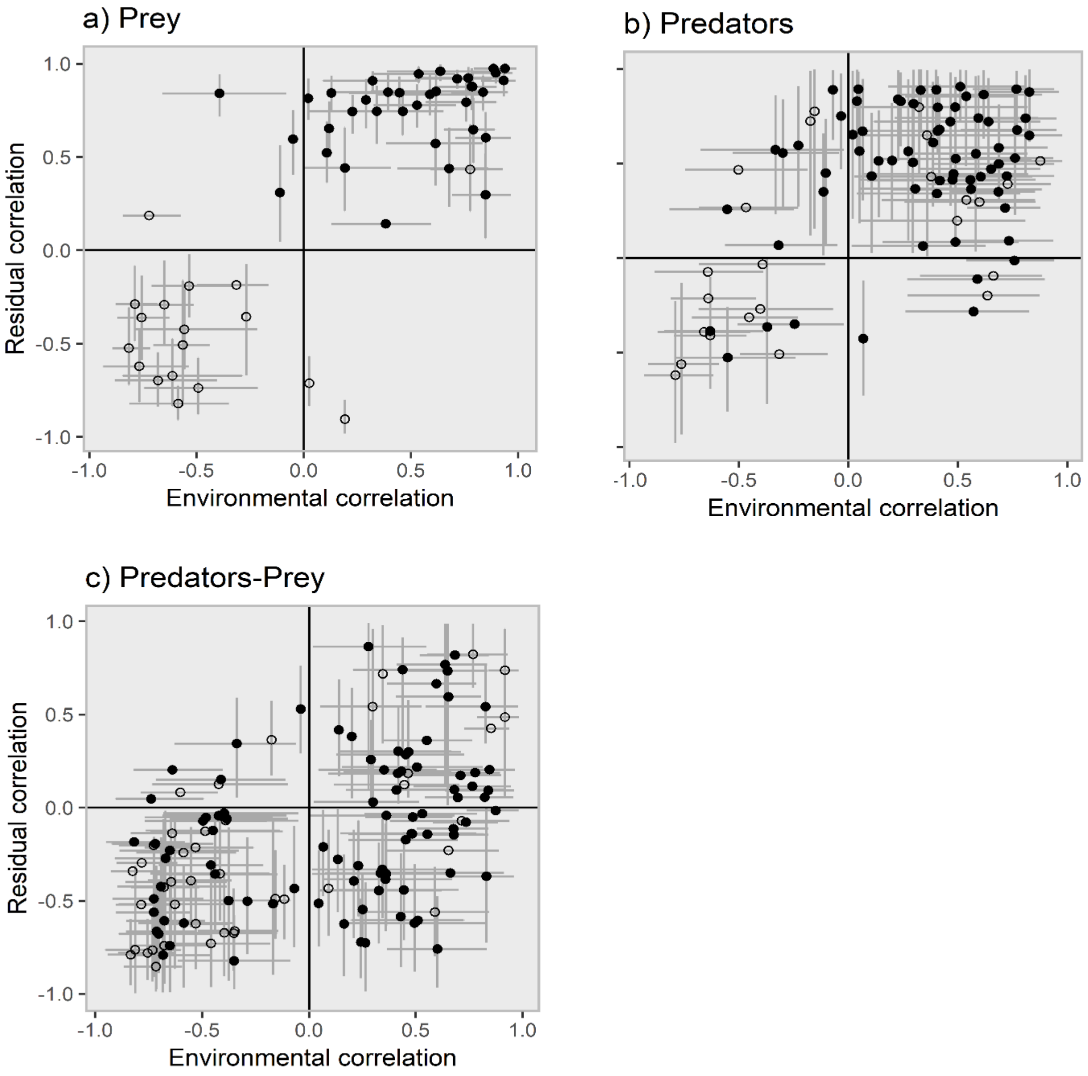


Figure 1.4. *Significant environmental and residual correlations (those whose 95% credible interval does not contain zero) between pairs of prey, predators, and predator-prey species. The error bars represent 95% credible intervals. White circles indicate neritic-oceanic species pairs, while black points represent either neritic-neritic or oceanic-oceanic species pairs.*

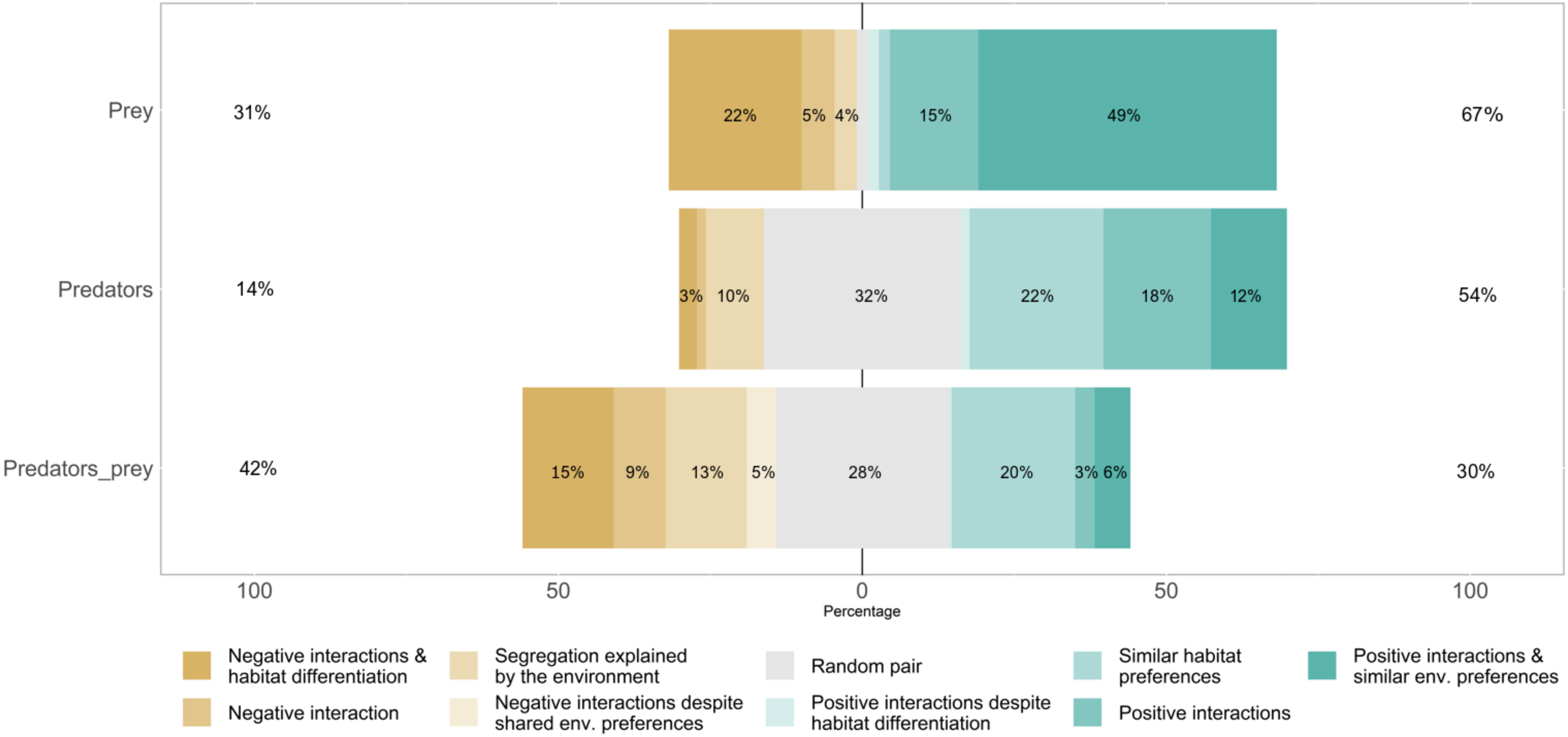


Figure 1.5. *Ecologically interpreted associations (explained in Table 1.3) displayed in each of the groups with their corresponding proportion (percentages smaller than 3% are not shown). Blue colours refer to positive associations and brown colours to negatives. Grey colour refers only to random associations.*

3.2. Predator-prey network associations

The attribution of ecological associations to each pair-wise species enabled us to identify species individual role and assess species degree centrality. This led to the identification of many central species within the prey guild that interacted similarly in terms of positive associations (Figure 1.6a). Krill and Mueller's pearlside *Maurolicus muelleri* were the exception and accounted for the highest number of negative associations (Figure 1.6d).

Among predators, many interacting species were found too, with sandwich tern *Thalasseus sandivicensis*, great skua *Stercorarius skua* and sooty shearwater *Ardenna grisea* as main central species. Among species with the lowest number of positive associations, fin whale and Cory's shearwater were identified, followed by the endangered Balearic shearwater (Figure 1.6b). These species were also found to have negative associations, although the species with the highest proportion of negative associations were fin whale and striped dolphin (Figure 1.6e).

Among predators-prey group, northern gannet, Balearic shearwater and yellow-legged gull *Larus michahellis* seabirds together with Mediterranean horse-mackerel *T. mediterraneus* were identified as central species, followed in a minor extent by krill *Euphasia spp.* (Figure 1.6c). In the opposite side, species previously found to have negative associations such as Cory's shearwater, fin whale, striped dolphin or lesser black-backed gull *L.fuscus* were identified, accompanied by blue whiting *Micromesistius poutassou*, horse mackerel *T.trachurus* and sprat *Spratus sprattus* (Figure 1.6f). In this case (Figure 1.6f), a new association not previously described in the other guilds came out, i.e., negative interactions despite shared environmental preferences.

On the other hand, the literature survey based on 36 scientific papers focusing on all the predator-prey associations (those represented in Figure 1.6c, f) revealed that evidences of predation (mainly based on regurgitates, pellets and stomach content) tended to be found more often between positively associated predator-prey species (59%) than between negatively associated pairs (27%) (Figure 1.7 and Appendix A4).

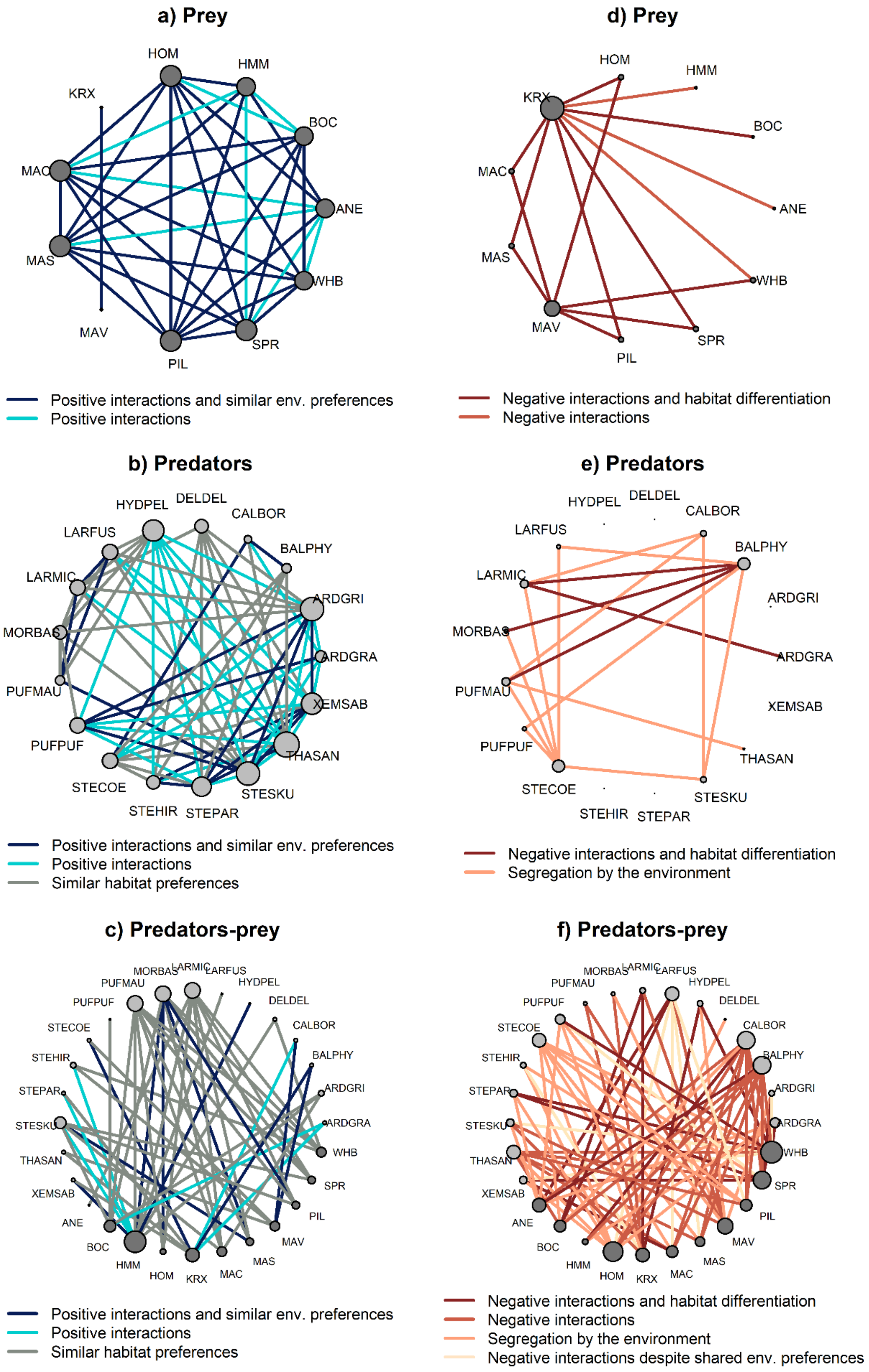


***Figure 1.6**. Networks graphs showing the ecologically interpreted associations in prey, predators, and predators-prey groups (associations occurring two times or less are not shown in order to simplify the visualization). First column refers to positive associations, second column to negatives and the size of the circle represents species degree centrality. Acronyms can be found in Table 1.2.*

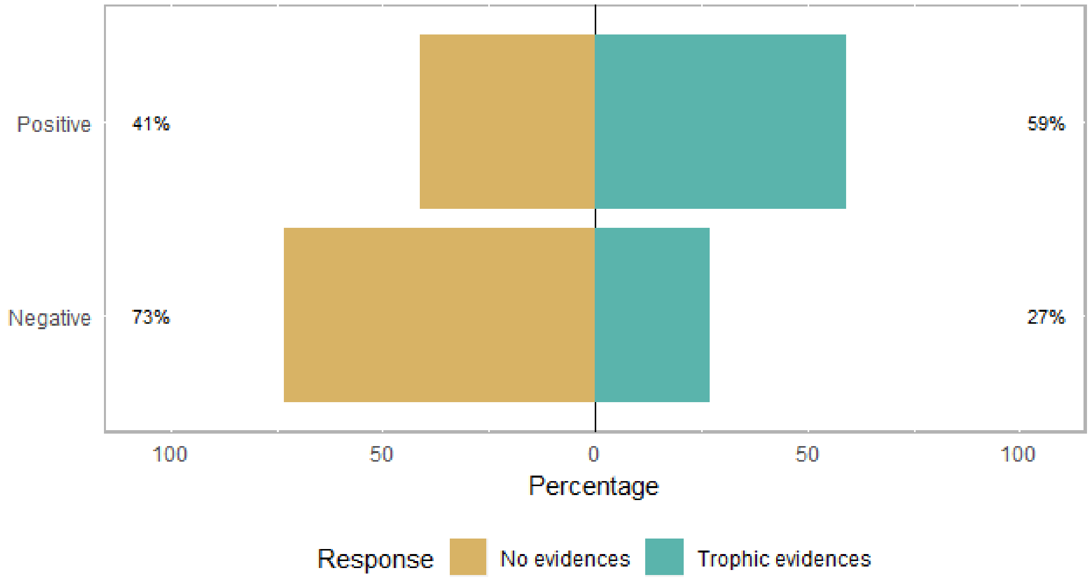


Figure 1.7. *Proportion of trophic evidences (and no evidences) found in the literature for all the positive and negative associations occurring within predators-prey group.*

4. Discussion

4.1. Environmental factors vs biotic interactions

The significant associations resulting from the JSDM at the community level showed a slightly larger proportion of correlations due to (dis)similarity in environmental preferences (58% of environmental correlations vs. 45% of residual correlations), which may indicate a higher weight of the environmental conditions in driving the co-occurrence patterns of the overall predator-prey network. Similar results were also found by Royan et al. (2016) in river bird communities, who concluded that species interactions were of secondary importance in comparison to habitat structure. In this work, however, the proportion of residual correlations did not greatly differ from the former, meaning that biotic interactions might also be an important driver. It is important to keep in mind that in the JSDM, like with all statistical approaches aimed at attributing sources of species covariation, the identification of biotic interactions is sensitive to the choice of environmental covariates (D'Amen et al. 2018). Unexplained deviance due to missing predictors could result in the effect of biotic interactions (Hui 2016), and hence, contrasting the results with an additional source of information, such as literature, is recommended. In our case, the literature survey conducted, despite referring only to predator-prey group, could indicate that some of the residual correlations do not correspond to a truly biotic interaction. Otherwise, a higher percentage of agreement would have been found between literature and predator-prey associations. Nevertheless, it must be considered that obtaining information on predators' diet may have some limitations too. Indeed, most of the top predators of this study are protected under different Conservation Agreements, while most of the seabird species observed do not breed in the BoB, which does not make possible colony-based field studies that would contribute to the collection of trophic evidences. Diet studies, therefore, are limited to the analysis of stomach contents of opportunistically stranded or bycaught animals (Spitz et al. 2006, Pusineri et al. 2007) or to the application of indirect methods such as stable isotope analysis, genetics or fatty acids (Navarro et al. 2009, Käkelä et al. 2010). Consequently, the information used to contrast the results can be incomplete, leading to an underestimation.

4.2. Ecological interpretation of associations

While acknowledging its limitations, the JSDM approach has successfully identified general patterns of species co-occurrence such as environmental filtering (D'Amen et al. 2018), competition (Zurell et al. 2018) or mutualism (Royan et al. 2016). In our case, the mutualistic associations derived from the aggregation behaviour of both prey and predators could also explain a large proportion of positive interactions. Among pelagic fishes, for instance, schooling behaviour has been long described, including mixed schools among engraulids, clupeids, carangids and scombroids (Pitcher 1986). In the BoB, Boyra *et al.* (2013) reported that European anchovy could be found mixed with European sardine, Atlantic horse-mackerel, Atlantic mackerel and European sprat, explaining up to some extent the positive interactions detected in this study.

Similarly, the positive interactions found in seabirds, which are known to heavily rely on other seabirds and cetaceans to locate prey and increase fishing success (Fauchald 2009), could also indicate mutualistic associations such as local enhancement or facilitative mechanisms. Among predator-prey group, positive interactions could indicate predation, based on the trophic evidences found in the literature. In contrast, negative interactions could be related to the aggregation behavior of prey and predators described above, which may induce local peaks in predators' densities, leaving other zones free of predators and leading to spatial mismatches between predators and prey (Ballance et al. 2001, Fauchald 2009).

Alternatively, a second reason could be a predator avoidance behaviour, described by Lambert *et al.* (2018) for the cetaceans-prey of the BoB and suggested by Logerwell and Hargreaves (1996) for seabirds-prey species. In our case, the smaller percentage of trophic evidences found among negative interactions might indicate that predation leads positive spatio-temporal associations, but also might support the avoidance behaviour hypothesis, since several predator-prey pairs have been identified.

Among prey, the negative interactions in krill could also indicate some kind of avoidance, since most of the neritic species targeted in this study could feed on euphausiids (Bachiller & Irigoien 2015). However, the effect of habitat segregation cannot be omitted, since the highest number of negative interactions was found in oceanic species (krill and Mueller's pearlside). Habitat differentiation was also found to be the main driver among predators, where the fin whale and striped dolphin (oceanic species) accounted for the highest proportion of negative associations. Competition, in contrast, might not be occurring (e.g., due to a non-limiting resource) or might be hidden by indirect effects; in fact, if two competing species share a positive relationship to the same resource, their occurrence could be positively correlated, when the true effect should be negative (Morueta-Holme et al. 2016). Despite being difficult to test with the current method, this possibility cannot be discarded given the high diet overlap that some prey (Bachiller & Irigoien 2015) and some top predator species have within their own guilds (Appendix A4).

Besides that, it must be taken into account that biotic interactions overall are scale dependent. Positive interactions (e.g. mutualism), for instance, can be manifested across scales, whereas negative interactions (e.g. competition) are unlikely to be discernible beyond local and regional scales (Araújo & Rozenfeld 2013). Many studies focusing on predator-prey relationships have found that spatial correlations increase with increasing scales. At large scales, prey may be aggregated on predictable areas linked to mesoscale oceanographic features, leading to positive correlations, whilst at smaller scales, prey may be further congregated in dense and unpredictable schools to avoid predation, inducing negative correlations (Rose & Leggett 1990, Fauchald et al. 2000). In this work, we have characterized mesoscale processes (phenomenon of spatial scales between ~10 and ~100 km and timescales from several days up to 1 month) as a result of analysing synoptically the data of this regional survey (Louzao et al. 2019a). However, the analysis of spatial associations at finer scales is still possible using the same dataset but different approaches (see Lambert et al. 2018).

4.3. Main association components

In graph theory, indicators of centrality are used to identify the most important vertices within a graph. During the last decades, a growing number of studies have applied these measures in species co-occurrence networks in order to assess the species contribution to network robustness (Araújo et al. 2011) or to identify keystone species (Martín González et al. 2010, Berry & Widder 2014). The analyses conducted in this study did not enable the identification of keystone species (sensu Paine 1969) but pointed out those species with an important role within their own community (Morueta-Holme et al. 2016). In the predator's guild, for instance, the high centrality shown by the sandwich tern, sooty shearwater and great skua may be related to their role within the flock as catalysts (species that initiate the flock and attract other seabirds with their presence; Camphuysen et al. 2007), facilitators (species that drive prey to surface and make available to others; Veit & Harrison 2017) and kleptoparasites (species that steal prey from other seabirds; Camphuysen et al. 2007), respectively. However, these roles are not limited to these three species; instead, they can be found widespread along the top predator community. Fin whale and striped dolphins for instance, can act as facilitators too, leading to some positive interactions previously described by other authors, e.g. fin whale - Cory's shearwater (Veit & Harrison 2017) or striped dolphin - great shearwater - Cory's shearwater (Clua & Grosvalet 2001) and also found in this study. Due to their limited ability to dive, species such as terns and storm-petrels also tend to interact with cetaceans or shearwaters; it is the case, for instance, of the interaction between the storm petrel and the Manx shearwater detected in this study and also described by Skov et al. (1995). Similarly, the lower centrality showed by other species such as the northern gannet, could be also a consequence of their role as suppressors (species whose presence decreases the availability of prey to other predators), since they take over the surface-feeding opportunities from smaller species (Camphuysen et al. 2007).

In the prey guild, the degree centrality measure did not reveal any outstanding species but reflected species spatial distribution, making difference between neritic and oceanic species. In predator-prey guild, the analysis detected highly interacting species but did not identify most predatory species or most consumed prey since predation evidences were spread into both positive and negative interactions. But we could identify, based on the literature, some predator-prey associations potentially occurring in the BoB. Some of them were accurately identified by the model as biotic interaction, such as the northern gannet predating upon the horse mackerel (Lewis et al. 2003, Hamer et al. 2007, Certain et al. 2011), the striped dolphin feeding on krill (Hassani et al. 1997) and the fin whale feeding upon krill and Mueller's pearlside (Bravo Rebolledo et al. 2016). In other cases, in contrast, potential trophic relationships described by the literature were classified as environmental association by the model. Northern gannet, for example, is known to feed on mackerel, but here we only found a positive association indicating similar habitat preferences. Same happened with the Balearic shearwater, which only showed similar habitat preferences with species that are known to be part of its diet, such as sardine, mackerel, horse mackerel or blue whiting (Yésou 2003, Navarro et al. 2009, Käkelä et al. 2010, Meier et al. 2017).

The JSDMs can therefore detect predator-prey associations, although complementary information such as trophic evidence is necessary to contrast the results. The incorporation of ancillary information such as traits or phylogeny may be also helpful to complement the analysis and discern true interactions and thus, their inclusion should be considered in further analysis (Ovaskainen et al. 2017, Hui 2018). Meanwhile, a cautious application of JSDM in predator-prey networks can be useful to obtain proxies of ecosystem functioning and community structure that may contribute to advance towards an ecosystem based-management. Indeed, some of the detected interactions can be used for the conservation of top predators, as suggested by Veit and Harrison (2017) or for a sustainable management of exploited and potentially exploited species (St John et al. 2016) based on their predators and competitors (CCAMLR 2006, Ruckelshaus et al. 2008).

The combination of biotic and environmental drivers found in this study, on the other hand, suggests that co-occurrence patterns of these species may be vulnerable to climate change variability, and hence, to the potential modification of the network's link, being necessary further research to project how species networks will respond under changing conditions.

CHAPTER 2

Niche segregation mechanisms in marine apex predators inhabiting dynamic environments

ABSTRACT

Understanding the mechanisms that allow the coexistence of species is key to preserve full ecosystem functioning. In dynamic environments, the study of ecological niches faces the complexity associated to the three dimensionality of the habitat and requires information that reflects such heterogeneity. Within this context, this study intends to identify the segregation mechanisms behind the co-occurrence of five phylogenetically related pelagic birds by applying a functional perspective based on seabirds' vertical ranges and prey availability features such as depth and body size. Based on the hypothesis that niche differentiation may occur in any of the three dimensions of the marine environment, we a) identified the biologically meaningful vertical range affecting seabird species, b) modelled their environmental and trophic niches, c) estimated an environmental and trophic overlap index for each pair-wise species, and d) developed a conceptual framework with the most plausible segregation hypotheses. The application of the conceptual framework revealed that in this particular area, pelagic birds coexist through environmental and trophic niche partitioning, and potentially through vertical segregation, based on the different biologically meaningful vertical ranges we identified for each species. Indeed, some species responded to prey and oceanographic conditions on the surface (10 m), while others responded to the conditions on deeper waters (above the depth of maximum temperature gradient). These different responses could be interpreted as an additional mechanism to reduce competition, although seabirds diving records would be needed to contrast this hypothesis. Considering all the dimensions of the niche is therefore essential to fully understand how diving seabirds coexist in dynamic systems and additionally provides insights on species' 3D niches that may help advance into their management.

Published as:

Astarloa, A., Glennie, R., Chust, G., García-Barón, I., Boyra G., Martinez, U, Rubio, A., & Louzao, M. (2021). Niche segregation mechanisms in marine apex predators inhabiting dynamic environments. *Diversity and Distributions.* https: //doi.org /10.1111/ddi.13229

1. Introduction

The niche concept has been a major theme in ecology, mostly influenced by the definition stated by Hutchinson (1957), who described it as a "n-dimensional hypervolume of environmental states within which a species is able to survive". However, even the classical definition may create a dichotomy that affects the way in which the entire concept is approached (Chase & Leibold 2003). In fact, much of the confusion surrounding the term results because no distinction is made between the responses of organisms to their environment and the effect of organisms on their environment (Chase & Leibold 2003, Peterson et al. 2011). Under such circumstances, two different niches should be discerned: the Grinnellian and the Eltonian niches (Soberon 2007, Devictor et al. 2010). The Grinnellian niche (Grinnell 1917) describes the response of the species to a given set of non-interactive variables, while the Eltonian niche (Elton 1927) describes the biotic interactions and resource-consumer dynamics trough trophic variables. Despite the attempts at synthesis and unification (Chase & Leibold 2003), the complementary concepts of the environmental niche (sensu Grinnell 1917) and trophic niche (sensu Elton 1927) serve as basis to assess the ecological and biogeographical dis-/similarities of species and contribute to the understanding of their distribution and diversity (Soberon 2007, Broennimann et al. 2011). Indeed, some of the main segregation mechanisms driving species coexistence are known to occur either by means of trophic (MacArthur 1968, Tilman 1982) or environmental niche partitioning (Chesson 2000). The spit up of the niche provides, therefore, an excellent opportunity to advance in the identification of segregation mechanisms, which is specially poorly understood in complex and dynamic environments such as marine ecosystems.

In such ecosystems, the study of environmental niches faces the difficulties inherent in understanding the three-dimensionality of the habitat, where physical and ecological processes occurring below the surface layer, such as subsurface thermal structure or subsurface primary production, have been found to be highly important (Kuhn 2010, Scott et al. 2013). On the other hand, trophic niche analyses require the consideration of complex predator-prey interactions, that result from the trade-off between the energetic cost of seeking prey and the foraging profitability obtained from successful events (MacArthur & Pianka 1966, Pyke 1984). Traditionally, predator-prey interactions have been studied using a predominantly taxonomic approach (species-species perspective), although functional characteristics related to the species' role, such as biological traits, have been proved to affect predator-prey interactions (Spitz et al. 2014). In 3D dynamic environments, addressing community ecology from functional traits perspective may be specially relevant, since prey depth (i.e. the depth at which prey is available), together with body size or energy density, can be key to understand predators' prey preferences (Boyd et al. 2017, Lambert et al. 2018, Spitz et al. 2018, Waggitt et al. 2018). Similarly, predators' physiology and morphology may also play an essential role in the foraging process by defining the metabolic cost of living or the diving capabilities of species (Spitz et al. 2012, 2014).

Among marine top predators exploiting dynamic environments, seabirds are considered one of the most diverse taxa, with several evidences indicating niche differentiation among its members (Phillips et al. 2011). Most studies, however, have been conducted during the breeding season, when the competition for resources is particularly intense and segregation mechanisms are more likely to arise (Navarro et al. 2013, Mancini et al. 2014). As a result, limited knowledge exists about the potential segregation mechanisms outside the breeding season (Thiebot et al. 2012), despite being the period in which animals migrate or disperse to favourable foraging areas, aggregating in highly productive regions and coinciding with a high number of migratory species (Grecian et al. 2016). Investigating and explaining niche segregation outside the breeding season could help complement management strategies involving all life stages, and thus, bigger efforts should be made in studying the non-breeding areas of seabirds.

The Bay of Biscay (BoB hereafter) represents such an example, as numerous seabird species stopover there during their feeding migrations attracted by a highly diverse and abundant community of small pelagic fishes (Pettex et al. 2017). It conforms, therefore, an exceptional biogeographical area to test segregation hypothesis and provides an incomparable opportunity to understand the mechanisms that allow the coexistence of protected species. In fact, many pelagic birds visiting the BoB are protected under different international agreements, such as the Bird Directive (Council Directive 2009/147/EC) and the Convention for the Protection of the Marine Environment of the Northeast Atlantic (OSPAR Convention), among others. Despite the conservation efforts, seabirds are still one of the most threatened groups, comprising rapid declining populations and critically endangered species (Croxall et al. 2012, Dias et al. 2019). Effective conservation and management measures require the identification of variables shaping species' niches (García-Barón et al. 2019, 2020) and that is why, understanding the role that prey and environment play in species distribution turns so necessary. Within that context, the present study focused on disentangling the assembly rules of pelagic birds by addressing the following research questions:

1) Does niche segregation occur among wide-ranging species during their feeding migrations?
2) Does this niche segregation occur in the environmental niche or in the trophic niche?
3) Do prey and environmental conditions on the vertical dimension influence the trophic and environmental niche of species?

To answer these questions, we modelled species environmental and trophic niches and developed a conceptual framework with the most plausible segregation hypotheses (Figure 2.1). This way, we aim to contribute to the understanding of protected and endangered species coexistence and provide insights on the 3D niches of species that may help advance into their management and conservation.

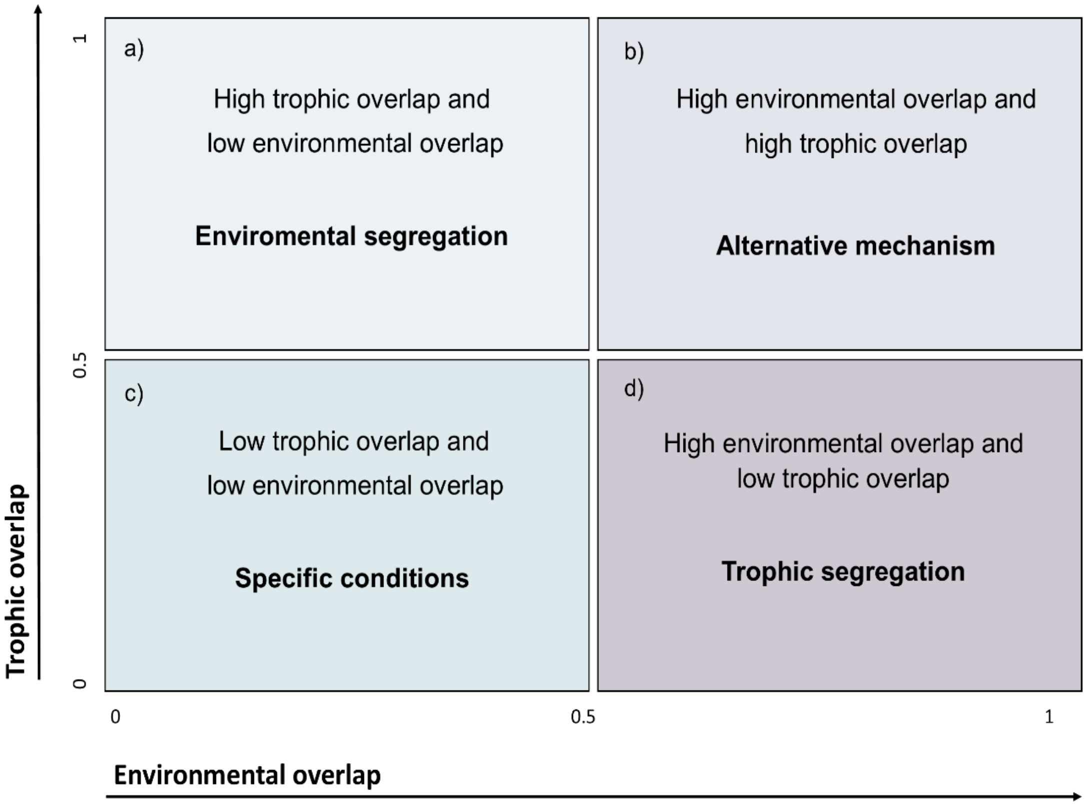


***Figure 2.1**. Conceptual framework displaying the plausible segregation hypotheses that arise from the pairwise comparison of environmental and trophic overlap. Main hypotheses comprise: a) environmental segregation, b) alternative mechanisms, c) specific conditions and d) trophic segregation.*

2. Material and methods

2.1. Data collection: integrated monitoring schemes

Data on pelagic birds, prey species and environmental predictors were collected through the multidisciplinary oceanographic survey JUVENA, which takes place every September in the BoB by means of two different research vessels, *Ramon Margalef* and *Enma Bardan* (R/V RM and R/V EB, hereafter). Since 2013, different components of the pelagic environment (i.e., plankton, fish, megafauna, physical oceanography, marine litter) are monitored, although its main aim is to assess the population of juvenile European anchovy *Engraulis encrasicolus*. The sampling strategy is based on parallel transects perpendicularly arranged to the coast and spaced at 15 nautical miles, whose offshore and along-coast extension changes from year to year depending on the distribution of the European anchovy (see details in Boyra et al. 2013, Louzao et al. 2019a). A schematic workflow of the entire analytical process is described in Figure 2.2.

Pelagic birds

Five phylogenetically related shearwaters were selected based on their conservation status and their high diversity and abundant records: the Cory's shearwater *Calonectris borealis*, the great shearwater *Ardenna gravis*, the near threatened sooty shearwater *A. grisea*, the Manx shearwater *Puffinus puffinus* and the critically endangered Balearic shearwater *P. mauretanicus*. Sightings of these species were recorded aboard R/V RM by a team of three experienced observers (2 at a time) that followed the line-transect methodology (Buckland et al. 2001). This methodology is conducted within the Distance Sampling framework to estimate seabirds' densities and requires the collection in-the-field of at least the radial distance of each observation (Heinemann 1981), the angle of the cluster sighting with respect to the trackline (estimated with an angle meter), time of observation, species composition and group size. In addition, the behaviour of observed species (e.g., attraction) as well as environmental descriptors affecting the detectability of species (e.g., Beaufort sea-state, visibility, glare intensity or observation conditions) were collected in order to account for response bias (when animals react to the presence of the platform) and perception bias (when observer miss animals because their visibility is compromised), respectively. Sampling effort was performed during daytime, at a constant speed and under Beaufort sea-state conditions ≤ 6 and it was geographically located every minute with the vessel GPS (Figure 2.3).

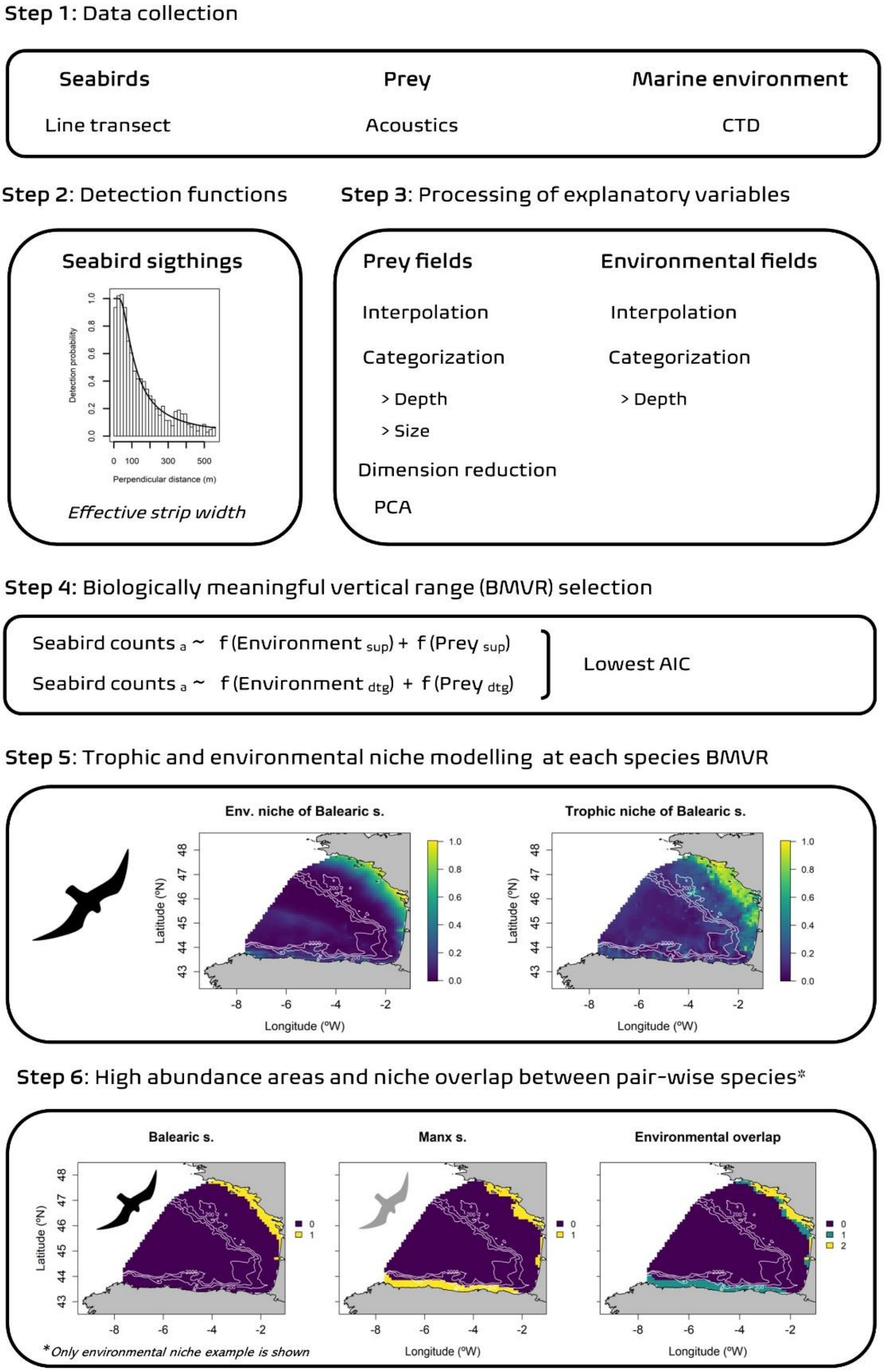


Figure 2.2. *Schematic overview of the main steps conducted to identify segregation mechanisms in pelagic apex predators.*

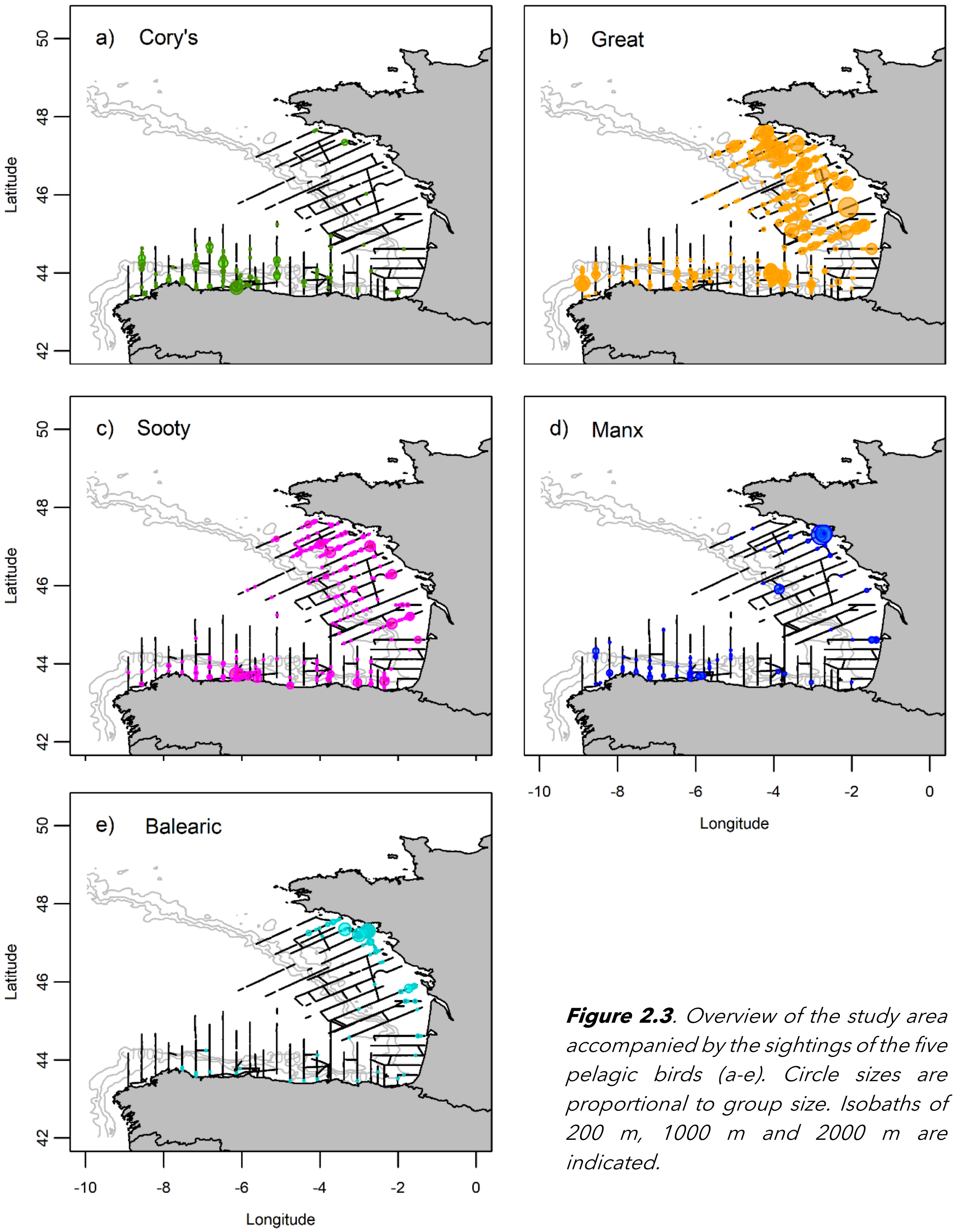


Figure 2.3*. Overview of the study area accompanied by the sightings of the five pelagic birds (a-e). Circle sizes are proportional to group size. Isobaths of 200 m, 1000 m and 2000 m are indicated.*

Pelagic prey

Acoustically-based biomasses were included in the analysis only for those fish species that were considered, based on bibliography, part of the diet of the seabirds (see Appendix B1: Table B1.1): European anchovy (juveniles and adults were treated separately due to their different spatial distribution), European sardine *Sardina pilchardus*, European sprat *Sprattus sprattus*, Atlantic mackerel *Scomber scombrus*, Atlantic horse mackerel *Trachurus trachurus* and Mueller's pearlside *Maurolicus muelleri*. Acoustic data were collected on R/V RM and R/V EB (Figure 2.4) by means of Simrad EK60 split-beam echosounders (Kongsberg Simrad AS, Kongsberg, Norway), that sampled the water column during daytime from the surface (5 m) to depths that ranged from 200 to 400 m depending on the year (Appendix B1: Table B1.2). The collected acoustic data by both vessels were processed in the positive strata by layer echo integration using an ESDU (Echo integration Sampling Distance Unit) of 0.1 nmi and categorized into ten depth layers (Appendix B1: Table B1.2). In parallel, mid-water trawls were performed to assign the eco-traces to species (identification purposes) and to obtain the necessary biological data (length, weight and age) to convert the acoustic back-scattered energy to fish abundance. Finally, abundance in number of individuals was multiplied by the mean weight, obtaining biomass estimates (tonnes) per age, length and depth interval (Boyra et al. 2013).

Oceanographic and geographic environment

Oceanographic data were collected in both vessels using a CTD profiler. For each transect, a minimum of three profiles were performed (coastal, continental shelf and oceanic waters) measuring the water column from the surface (10 m, first available data) up to 200 m depth (Figure 2.4). Temperature (T), salinity (SAL) and density data were directly inferred from CTD casts. Horizontal fields of these three variables were estimated every 5db from the vertical profiles using Optimal Statistical Interpolation scheme (Gomis et al. 2001) on a spatial grid with regular node distances of 0.15 x 0.15° latitude–longitude covering all the study area (see details in Appendix B2). Then, geostrophic velocities (GV) were derived from the interpolated density fields following Rubio et al. (2009). Secondarily, the depth of the maximum temperature gradient (DTG, as a proxy of ocean mixed layer depth and water column stability indicator), the maximum temperature gradient (MTG, as a proxy of the strength of the water column stratification) and the sea surface temperature gradient (SSTG, as an important predictor for seabirds distributions) were estimated from temperature fields as described in Louzao et al. (2019a).

In order to characterize the geographic environment, depth (DEP) was extracted from NOAA at a resolution of 0.016° (marmap package, Pante & Simon-Bouhet 2013) and posteriorly modified to obtain the distance to the coast (DCO) and the distance to the shelf break (DSHEL), defined by the isobath of 200 m. The spatial gradient in depth (DEPG) was also estimated (Table 2.1); in fact, areas of strong spatial

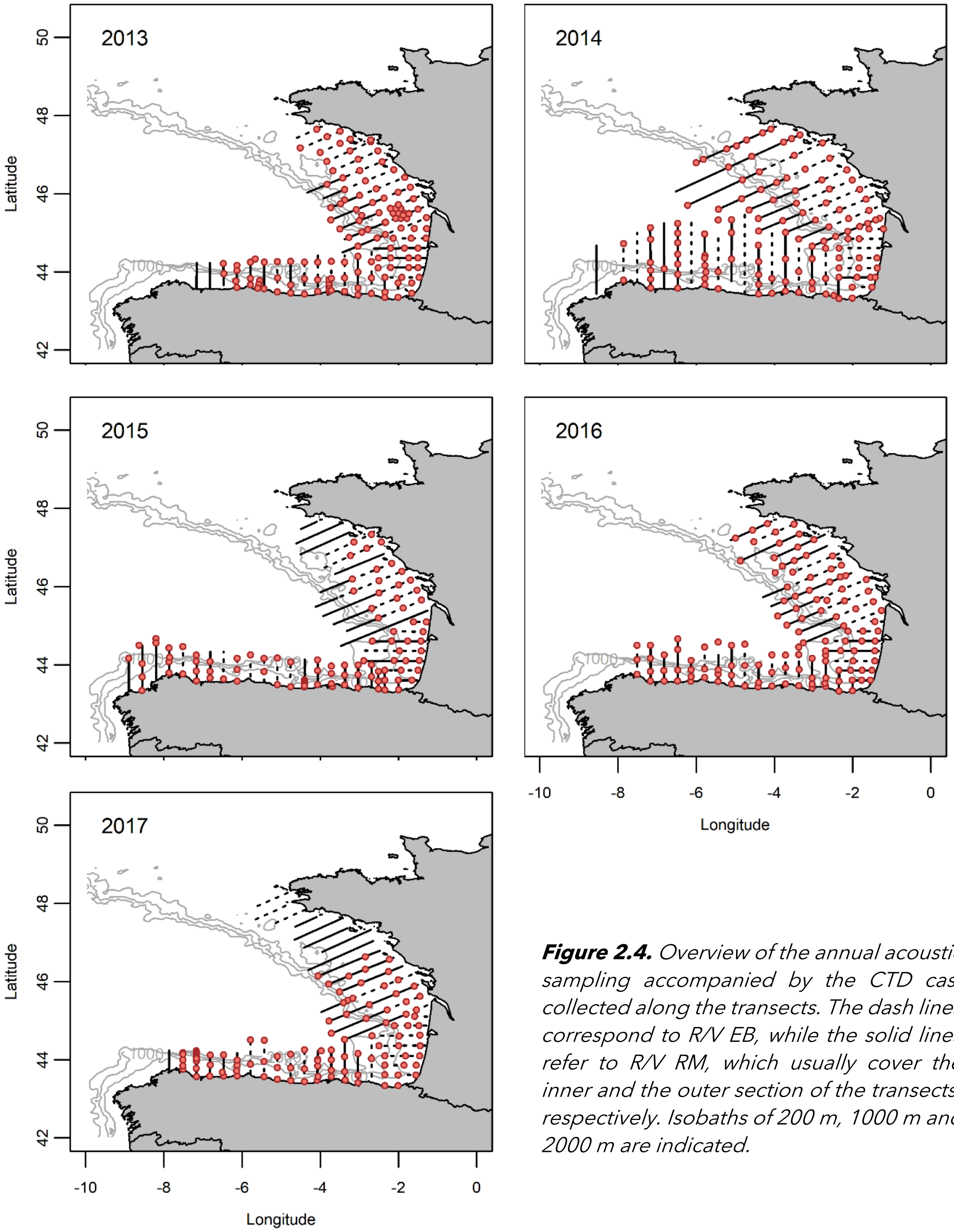


Figure 2.4. *Overview of the annual acoustic sampling accompanied by the CTD cast collected along the transects. The dash lines correspond to R/V EB, while the solid lines refer to R/V RM, which usually cover the inner and the outer section of the transects, respectively. Isobaths of 200 m, 1000 m and 2000 m are indicated.*

gradient may correspond to areas where internal waves generate, which can promote an increase in primary production and small preys' availability according to Scott et al. (2010). For that, a spatial window of 3 x 3 cells was used in which the spatial differences in bathymetric values were calculated and scaled to the maximum value [(maximum value - minimum value)/maximum value] (Louzao et al. 2019a).

***Table 2.1**. Summary of the environmental variables used in the study. Dynamic variables were estimated from oceanographic data collected on board, whereas static variables were extracted from NOAA (ETOPO1 database).*

Variables	Acronym	Type	Dimension
Temperature (°C)	T	Dynamic	3D
Salinity (psu)	SAL	Dynamic	3D
Geostrophic velocity (m s^{-1})	GV	Dynamic	3D
Depth of maximum temperature gradient (m)	DTG	Dynamic	2D
Maximum temperature gradient (°C m^{-1})	MTG	Dynamic	2D
Sea surface temperature gradient	SSTG	Dynamic	2D
Depth (m)	DEP	Static	2D
Depth gradient	DEPG	Static	2D
Distance to coast (km)	DCO	Static	2D
Distance to shelf break (km)	DSHEL	Static	2D

2.2. Detection functions of seabirds' sightings

In line transects, it is assumed that the likelihood of detecting animals becomes smaller as the distance to the observer increases. To account for that bias, distance sampling analyses were applied, which mainly consist on fitting a detection function to the observed distances in order to estimate the proportions of animals missed by the observer (Thomas et al. 2002). To do so, sightings of seabirds were first filtered (by removing sightings with attraction behaviour) to avoid the response bias generated when animals react to the presence of the platform; in fact, fisheries discards can attract large feeding flocks and lead to misunderstand the distribution and abundance of seabirds (Valeiras 2003). Due to the low number of sightings per year of some species (Buckland et al. 2001), small (Balearic and Manx shearwaters) and large species (Cory's, great and sooty shearwaters) were grouped together based on their size (see Appendix B3). Once we defined the groups, the 5% of the sightings detected at the largest distances were truncated to delete outliers (i.e. by setting the truncation distance, *w*) (Buckland et al. 2001) and analysed using Multiple Covariate Distance Sampling (Marques & Buckland 2004). Hazard rate and half normal functions with no adjustments were then fitted in each of the groups using the *ds* function from the *Distance* package (Miller 2020). As covariates, only those descriptors related to the effort were considered, *i.e.* Beaufort sea-state, visibility, cloudiness, glare intensity, observation conditions and year (see details in Appendix B4: Table B4.1), which were introduced in the detection function as factor and selected by means of forward selection (Appendix B4: Table B4.2) until the lowest Akaike information criterion (AIC hereafter) was obtained (Sakamoto et al. 1986, Guisan & Zimmermann 2000). From here, the probability of detecting an animal (Pa) was estimated, which multiplied by the truncation distance (w) provided the effective strip half width (ESW= Pa*w). ESW can be defined as the perpendicular distance in which the missing detections equal the recorded detections and serves to estimate the area effectively covered, when considering both observation sides and transect length (A= ESW*2*L). In such estimations, seabirds' behaviour (on flight vs. on water) can be an important aspect to be considered, since flying individuals can lead to overestimation of densities when they move faster than the observation platform (Buckland et al. 2001). In our case, most seabirds were recorded on flight (90%– 95% of individuals in all species), and hence, little bias was expected between areas with flying and sitting individuals; overall overestimation, on the other hand, was considered negligible, since obtaining absolute abundances was out of our scope.

2.3. Processing of explanatory variables

In order to understand the ecological niches of seabirds in the BoB, environmental and trophic relationships were modelled. However, the differences in the sampling coverage of seabirds, prey and environmental data did not allow for a homogenous prediction. To solve that, prey and environmental data were first processed to obtain continuous fields of explanatory variables covering the study area and then categorized by depth and size to address the multidimensionality and functionality of the environmental and trophic niches (Figure 2.2; step 3).

Prey fields

Since prey selection may be also conditioned by other factors related to prey availability such as body size or depth at which prey is available, the original biomasses (tonnes) of the seven prey species were categorized using 10 cm length classes (Lambert et al. 2018): <10 cm, 10-20 cm and 20-30 cm. The resulting biomass categories were then log-transformed and interpolated using universal kriging (Appendix B2) over a standard grid covering the study area (latitudinal range: 43.2-48°N; longitudinal range: 1-8°W) with a cell size of 0.1° spatial resolution. Secondarily, all species biomasses but Mueller's pearlside (see below) were split into two main vertical layers (Appendix B5) following Louzao et al. (2019a): 1) the surface layer, and 2) the deep layer, limited by the depth of the maximum temperature gradient (DTG), a dynamic feature that approximates the depth of the ocean mixed layer and that usually comprises the first 40 m of the water column (for the interannual variability of DTG see Appendix B6). For the surface layer, the biomasses of each prey species and each size class comprised in the shallowest depth layer were selected (between 5 and 15 m); for the deep layer, the same was done but summing the biomasses from the surface up to the DTG. As a result, we obtained the biomasses for a total of 18 prey categories (Table 2.2), that were afterwards introduced in a PCA (Principal Component Analysis) to understand how prey fields were spatially and functionally structured.

Table 2.2. *Prey species categorized by size and depth. The biomasses of all these species categories, excepting the Mueller's pearlside, were split into surface (~10 m) and deep layers (above the depth of maximum temperature gradient).*

Species categories	**Scientific name**	**Size (cm)**	**Depth categories**	**Depth layers**
Anchovy adult	*Engraulis encrasicolus*	10-20	2	Surface and deep
Anchovy juvenile	*Engraulis encrasicolus*	0-10	2	Surface and deep
Anchovy juvenile	*Engraulis encrasicolus*	10-20	2	Surface and deep
Sardine	*Sardina pilchardus*	10-20	2	Surface and deep
Horse mackerel	*Trachurus trachurus*	0-10	2	Surface and deep
Horse mackerel	*Trachurus trachurus*	10-20	2	Surface and deep
Mackerel	*Scomber scombrus*	10-20	2	Surface and deep
Mackerel	*Scomber scombrus*	20-30	2	Surface and deep
Sprat	*Sprattus sprattus*	0-10	2	Surface and deep
Mueller's pearlside	*Maurolicus muelleri*	0-10	1	Surface-200m

In the case of the mesopelagic Mueller's pearlside*,* it was not classified into two layers, as it spends the daytime between ~50 and 200 m (Kaartvedt et al. 1998, Sobradillo et al. 2019); that is, in greater depths than the ones considered in this study (i.e. surface and above the DTG). It is known, however, that it is an important resource among procellariids (Watanuki & Thiebot 2018), so in order to test its relevance in our seabird community, we included as predictor the biomass of the Mueller's pearlside comprised between the surface and 200 m depth (Table 2.2). Although seabirds are not able to dive so deep, this estimation was used as a proxy of the biomass available at dusk and dawn, that it is when the pearlside migrates close to the surface and aggregates at about 20 to 40 m (Kaartvedt et al. 1998), becoming available to seabirds.

Environmental fields

As with prey fields, those environmental variables collected at different depths (i.e. T, SAL and GV) were also vertically analysed and classified into surface and deep layers (Louzao et al. 2019a). For the surface layer, the shallowest values were selected (10 m); for the deep layer, in contrast, the median values between surface and the DTG were estimated. Remaining environmental variables (DTG, MTG, SSTG, DEP, DEPG, DCO, DSHEL) were 2D variables (Table 2.1), so no vertical analysis was performed with them. Finally, all variables were resampled with the *raster* package (Hijmans et al. 2017) to match with the standard grid of prey (latitudinal range: 43.2-48°N; longitudinal range: 1-8°W, 0.1° spatial resolution).

2.4. Biologically meaningful vertical range selection

Since pelagic birds show different diving abilities, the vertical range they exploit may also differ. Without obtaining in-situ diving records, we cannot test that hypothesis, but we can determine the vertical range that best explains seabirds' density patterns (biologically meaningful vertical range, hereafter). For that, two models per species were fitted: one using the conditions given by the environmental and prey variables in the surface layer, and the other, using the conditions given by the same variables but in the deep layer (Fig 2.2, step 4). Since this step required 3D data, the environmental variables comprised T, SAL and GV (Table 2.1), whilst the prey data included the first three axes of the PCA analysis (explaining the 70% of the variability; Appendix B7). In all cases, individual density surface models were fitted from the previous detection function analyses using the *dsm* package (Miller et al. 2019). The number of individuals per unit effort was fitted by means of Generalized Additive Models (GAM), assuming a negative binomial distribution with a probit link function. Degrees of smoothness were limited to fit unimodal response curves and restricted to three (Bruge et al. 2016) to avoid overfitting (Burnham & Anderson 2003). All variables were standardized to have a mean of zero and a standard deviation of one (Zuur et al., 2007). The most plausible model was selected based on the lowest AIC (Sakamoto et al. 1986, Guisan & Zimmermann 2000).

In addition, a literature survey was conducted to contrast the obtained results. For that, we focused on published biologging studies providing the average diving depth reached by the species, as it refers to the vertical range more regularly exploited (Appendix B8: Table B8.1). This way, obtained results could be compared with expected results based on the average diving depths measured for each of the target species by different time dive recorders.

2.5. Identification of segregation mechanisms

To identify niche differentiation mechanisms within the pelagic bird community, we modelled separately the environmental and trophic niche of species by integrating the data at their biologically meaningful vertical range (Figure 2.2, step 5), estimated an environmental and trophic overlap index for each pair-wise species (Figure 2.2, step 6) and developed a conceptual framework with the most plausible segregation hypotheses (Figure 2.1).

Environmental and trophic niche modelling

For the environmental niche, models combining environmental variables (both 3D and 2D, Table 2.1) were fitted in the biologically meaningful vertical range of each species, according to the results obtained in the previous section. For the trophic niche, the first three axes of the PCA (explaining the 70% of the variability; Appendix B7) and the biomass of the Mueller's pearlside were used.

In both cases, individual density surface models were fitted from the previous detection function analyses using the *dsm* package (Miller et al. 2019). For each species, the number of individuals per unit effort was fitted by means of GAMs, assuming a negative binomial distribution with a probit link function. Degrees of smoothness were limited to fit unimodal response curves and restricted to three (Bruge et al. 2016) to avoid overfitting (Burnham & Anderson 2003). All variables were standardized to have a mean of zero and a standard deviation of one (Zuur et al., 2007) and subsequently analysed by means of Spearman's Rank correlation coefficient to identify highly correlated ($|r| \geq 0.6$) pair-wise predictors (Thiers et al. 2014). The most plausible model was selected based on the lowest AIC (Sakamoto et al. 1986, Guisan & Zimmermann 2000). When models were within 2 units of AIC ($\Delta AIC \leq 2$), they were considered statistically equivalent and the one with a smaller number of variables was chosen following the parsimony principle (Arnold, 2010). Once the most plausible "environmental" and "trophic" niche models were defined, seabirds' densities were predicted per year over the standard grid (latitudinal range: 43.2-48°N; longitudinal range: 1-8°W, 0.1° spatial resolution) (Figure 2.5a, b).

Environmental and trophic niche overlap

In order to assess the degree of environmental and trophic niche segregation, an overlap index was calculated between pair-wise species based on Ballard et al. (2012). In the case of environmental niche overlap, we first estimated the mean density for the 2013-2017 period based on the predictions obtained from the environmental niche modelling and selected only those cells containing the highest 95% of the mean density in order to avoid very low values (Figure 2.5c, d). After that, we assessed the degree of environmental overlap (Figure 2.5e) by dividing the number of cells where both species were present (i.e. cells containing both species) by the total number of cells where either species was present (i.e. cells containing one species or both) (Ballard et al. 2012).This led to a total number of 10 overlap values, derived from the pair-wise combination of 5 species ($C_{5,2} = \binom{5}{2}$), that were posteriorly standardized so that values ranged between 0 and 1. To estimate the degree of trophic niche overlap the same procedure was followed based on trophic niche modelling results.

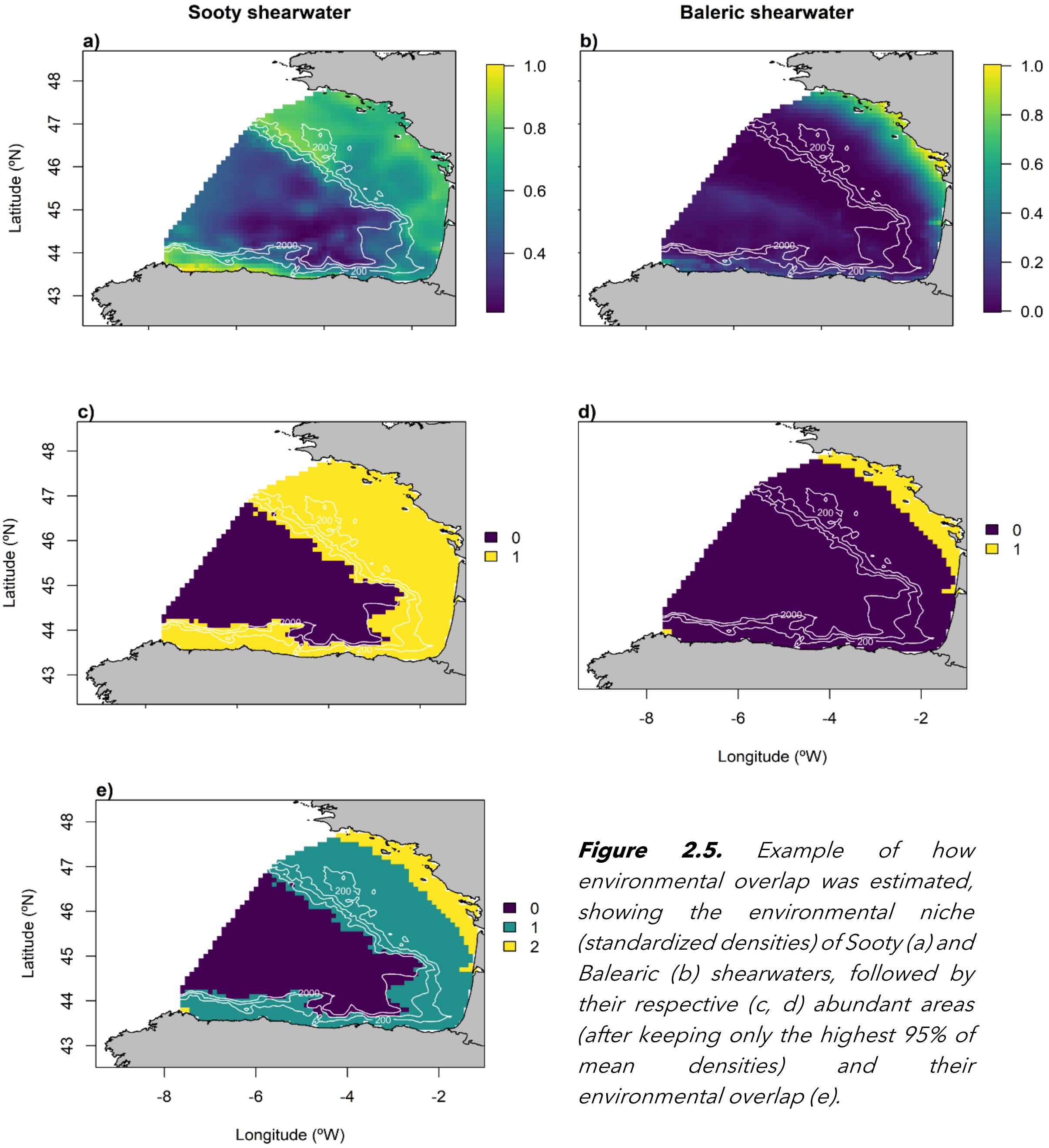


Figure 2.5. *Example of how environmental overlap was estimated, showing the environmental niche (standardized densities) of Sooty (a) and Balearic (b) shearwaters, followed by their respective (c, d) abundant areas (after keeping only the highest 95% of mean densities) and their environmental overlap (e).*

Finally, the conceptual framework displayed in Figure 2.1 was developed. In brief, this conceptual framework describes the plausible hypothesis that may arise from the pair-wise comparison of environmental and trophic overlap indices. These main hypotheses comprise two clear segregation mechanisms, defined as environmental segregation (high trophic overlap but low environmental overlap) and trophic segregation (high environmental overlap but low trophic overlap), and two additional situations described as specific conditions (low trophic and low environmental overlap) and alternative mechanisms (high trophic and high environmental overlap). Specific conditions would refer to any situation explaining why the pair-wise species found in that section do not overlap (e.g., isolation, breeding, specialization), whereas alternative mechanism hypothesis would try to find out how those species can coexist in a situation of both high trophic and environmental overlap.

3. Results

3.1. Sightings and detectability of seabirds

The most frequently observed species was the great shearwater (944 sightings), followed by the sooty (293 sightings), the Cory's (165 sightings), the Balearic (124 sightings) and the Manx shearwater (115 sightings). These sightings were relatively equally distributed over the BoB for great, sooty and in a lesser extent, for Manx shearwaters (Figure 2.3b, c, d), while sightings of Cory's and Balearic shearwaters were mainly recorded in the Spanish and French side of the study area, respectively (Figure 3a, e). When grouping these species, detection functions showed that same detectability could be assumed for Balearic and Manx shearwaters (i.e., small shearwaters) and for Cory's and great shearwaters (Appendix B3).

Table 2.3. *Summary of the features used in the detection function of each group of shearwaters. Number of sightings refers to the final number obtained after having removed the 5% of the data detected at the largest distances.*

Species	Truncation distance (m)	Num. of sightings	Detection function	Selected covariates	Average detection probability	Goodness of fit
Balearic & Manx	362	227	Half normal	Year Beaufort General conditions	0.44	p>0.05
Cory's & Great	561	1053	Hazard rate	Year	0.31	p>0.05
Sooty	479	278	Half normal	Year	0.39	p>0.05

Sooty shearwater was the most different species in terms of detectability so, it was analysed separately (Appendix B3), resulting in three different detection functions (Table 2.3 and Appendix B9: Figure B9.1).

3.2. Biologically meaningful vertical range

According to the test conducted to identify each species' biologically meaningful vertical range, we found that the density patterns of Cory's, great and Manx shearwaters were better explained by the explanatory variables of the surface layer (10 m), while the density patterns of sooty and Balearic shearwaters were better explained by the explanatory variables integrated over the deep layer (above DTG) (Table 2.4). Obtained results were in agreement with the results expected from the literature review (Appendix B8: Table B8.2), in which the average diving depth records indicated a surface diving behaviour for Cory's, great and Manx shearwaters (with an average depth of 1.7, 3.2 and 5.7 m, respectively) and a subsurface diving performance for sooty shearwater (average depth 12.3 m). The only exception was the Balearic shearwater, as the average diving depth found in the literature did not agree with the obtained results from the modelling of the biologically meaningful vertical range (Appendix B8: Table B8.2).

Table 2.4. *Summary of the vertical segregation test conducted for each shearwater species using conditions in the surface (first row) and conditions in the deep layer (second row). Biologically meaningful vertical range is shown in bold.*

Species	Models	AIC	Δ AIC
Cory's shearwater	**$T_{S\,+} SAL_{S\,+} GV_{S+} PCA1_{S\,+} PCA2_{S}, PCA3_{S}$**	**1419.71**	**0**
	$T_{D\,+} SAL_{D\,+} GV_{D+} PCA1_{D\,+} PCA2_{D}, PCA3_{D}$	1440.11	20.4
Great shearwater	**$T_{S\,+} SAL_{S\,+} GV_{S+} PCA1_{S\,+} PCA2_{S}, PCA3_{S}$**	**6764.13**	**0**
	$T_{D\,+} SAL_{D\,+} GV_{D+} PCA1_{D\,+} PCA2_{D}, PCA3_{D}$	6846.45	82.32
Sooty shearwater	$T_{S\,+} SAL_{S\,+} GV_{S+} PCA1_{S\,+} PCA2_{S}, PCA3_{S}$	2928.49	3.19
	$T_{D\,+} SAL_{D\,+} GV_{D+} PCA1_{D\,+} PCA2_{D}, PCA3_{D}$	**2925.30**	**0**
Balearic shearwater	$T_{S\ UP+} SAL_{S\,+} GV_{S+} PCA1_{S\,+} PCA2_{S}, PCA3_{S}$	1348.09	52.26
	$T_{D\,+} SAL_{D\,+} GV_{D+} PCA1_{D\,+} PCA2_{D}, PCA3_{D}$	**1292.83**	**0**
Manx shearwater	**$T_{S\,+} SAL_{S\ UP+} GV_{S+} PCA1_{S\,+} PCA2_{S}, PCA3_{S}$**	**1187.58**	**0**
	$T_{D\,+} SAL_{D\,+} GV_{D+} PCA1_{D\,+} PCA2_{D}, PCA3_{D}$	1190.32	2.73

3.3. Environmental and trophic drivers

Trophic niche models showed a high preference for PCA1 (small-medium fish species) in Balearic and Manx shearwaters, for PCA3 (big fish species) in Cory's and for the Mueller's pearlside in great and sooty shearwaters, highlighting three main groups (Figure 2.6). Environmental models, although more diverse, showed a more homogenous pattern in terms of variables' importance, suggesting a more balanced contribution of the environmental variables (Figure 2.6). Nevertheless, some similarities could be found too; large shearwaters (Cory's, great and sooty), for instance, were found to rely moderately on salinity (SAL) and depth (DEP), whereas small shearwaters preferred those variables linked to land or shelf-break closeness (DCO and DHSEL). Temperature (T), although present in most of the models, was found to be of low importance for all the species (Fig 2.6). In general, environmental niche models provided higher percentages of deviance explained, that ranged between 15-71%, while trophic niche models showed a deviance explained between 5-59% (see Appendix B10).

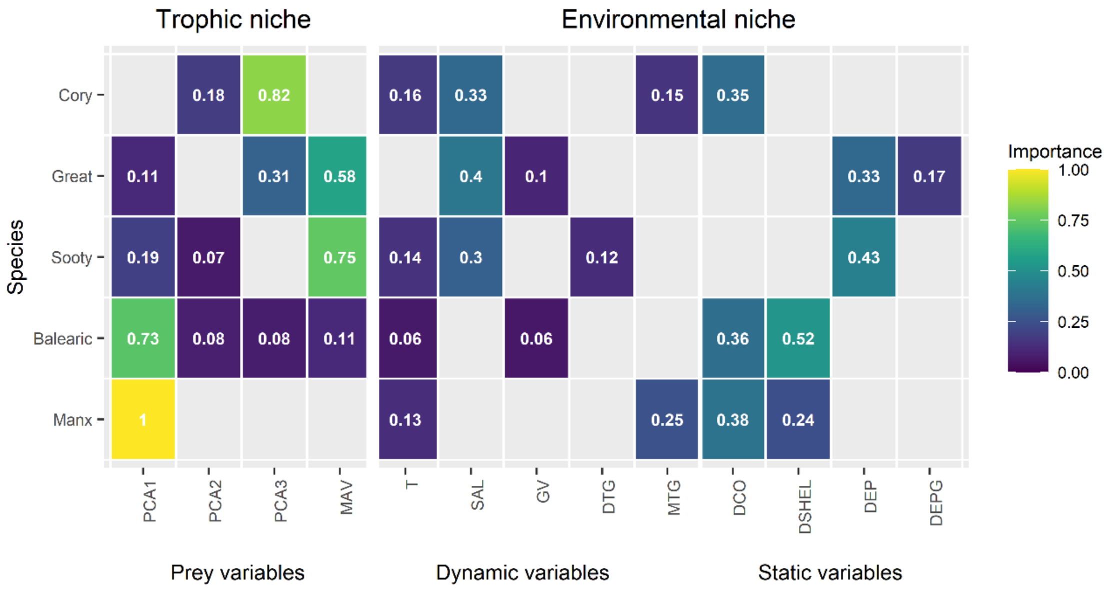


***Figure 2.6**. Relative importance of the variables included in the environmental and prey-based models, integrated at the biologically meaningful vertical range of each species.*

Prey variables: the main three axes of the PCA analysis (PCA1, PCA2, PCA3) plus Mueller's pearlside (MAV). Environmental variables: temperature (T), salinity (SAL), geostrophic velocity (GV), depth of the maximum temperature gradient (DTG), maximum temperature gradient (MTG), distance to coast (DCO), distance to shelf break (DSHEL), depth (DEP) and depth gradient (DEPG).

3.4. Niche differentiation mechanisms

Overlap indices obtained from previous environmental and trophic niche models were displayed following Figure 2.1 in order to assign the main four segregation hypotheses to each pair-wise species (Figure 2.7). In this way, the pairs composed by Balearic-Great, Manx-Great and Balearic-Sooty were assumed to segregate environmentally (Figure 2.7a, 2.1a), while Manx-Cory's shearwaters were presumed to segregate through trophic niche partitioning (Figure 2.7d, 2.1d). The category classified as specific conditions (Figure 2.1c) was assigned to the Cory's shearwater, as it was present in all pair-wise combinations showing low trophic and low environmental overlap, including Cory's-Balearic, Cory's-Sooty and Cory's-Great pairs (Figure 2.7c). On the other hand, Manx-Balearic, Manx-Sooty and Sooty-Great pairs showed the opposite pattern, suggesting that these pair-wise species coexist through an alternative mechanism in conditions of high environmental and high trophic overlap (Figure 2.7b, 2.1b).

Figure 2.7. *Comparison of trophic vs. environmental overlap indexes that display pair-wise species in sections of a) high trophic overlap but low environmental overlap, b) high trophic and high environmental overlap, c) low trophic and low environmental overlap and d) high environmental overlap but low trophic overlap. The most plausible segregation hypothesis explaining each section can be found in Figure 2.1.*

4. Discussion

Unlike other marine predators, air breathing seabirds are limited in prey accessibility due to their anatomy and their diving capabilities. Thus, considering the processes that concentrate prey close to the surface, prey size or depth at which seabirds can fish is essential. In this study, the incorporation of such elements has enabled us to conclude that 1) wide ranging species coexist through environmental and trophic niche partitioning, 2) species respond differently to prey and oceanographic conditions on the vertical dimension (potential vertical segregation) and 3) phylogenetically and morphologically closer species (e.g., Sooty-Great or Manx-Balearic) show more similarities in their trophic and environmental niches.

These major findings were mainly extracted from the conceptual diagram, resulting from the modelling of environmental and trophic niches. Previous co-occurrence analyses conducted in the area already described some of the results found here, such as the environmental overlap between Manx-Sooty or the environmental dissimilarity in Cory's-Balearic shearwaters (Chapter I). However, the way in which this approach was addressed (i.e., by considering both environmental and trophic niches, prey depth and size, conditions on the vertical dimension) provided more detailed information on species assemblage and revealed four different scenarios resulting from niche overlap patterns that could not have been identified otherwise.

The two clearest scenarios were the environmental and trophic segregation (Figure 2.1a-2.7a and 2.1d-2.7d, respectively). The former, detected in Balearic-Great, Manx-Great and Balearic-Sooty pairs, can be understood with the spatial distribution described for these species. In fact, Balearic and Manx shearwaters are known to occupy primarily coastal waters (Authier et al. 2018), whereas sooty and great shearwaters show preference for shelf and oceanic waters, respectively (Louzao et al. 2019a). When they stopover in the BoB, Balearic and Manx stay closer to the coast, while great and sooty shearwaters exploit offshore areas, leading to a non-overlap pattern in their environmental niche.

On the other hand, trophic segregation was only identified in the case of Manx-Cory's pair-wise species. This segregation mechanism can be explained by the results given by diet-based studies, that suggest that Cory's shearwater feeds on Atlantic mackerel and horse mackerel (Paiva et al. 2010b), while the Manx shearwater mainly relies on clupeids (e.g. herring, sprat) (Thompson 1987). This single association also indicated that overall, the community of pelagic birds in the BoB was characterised by a low trophic segregation, which can be due to the generalist behaviour of most species, known to take advantage of available pelagic feeding resources (Bicknell et al. 2013). In fact, even the critically endangered Balearic shearwater, with a potentially more restricted foraging range compared to the remaining wide ranging pelagic birds, feeds on the main pelagic resources of the BoB (e.g. mackerel, horse mackerel, anchovy, sardine) (Meier et al. 2017). However, it must be mentioned that, despite not having found strong evidence of trophic segregation in the conceptual diagram, the modelling of trophic niches already revealed some differences in the seabird community. Indeed, great and sooty shearwaters were associated to Mueller's pearlside, Balearic and Manx shearwaters to small-medium fish species (PCA1), and Cory's shearwaters to big fish species (PCA3), meaning that clustering prey species based on functional characteristics can help uncover subtle differences on the trophic preferences of species (Lambert et al. 2018).

The remaining two scenarios (Figure 2.1b, 2.1c) could not be explained by environmental and trophic requirements and instead, further information on the biology of the species was required to be untangled. Low patterns of both trophic and environmental overlap, for instance, were related to the reproductive behaviour of the Cory's shearwater (involved in all associations with low overlap). In fact, it was the only species that was breeding (they breed in the north west of the Iberian Peninsula) at the time the study was conducted (Munilla et al. 2016). During this period, seabirds acts as central place foragers (Orians & Pearson 1979), which means they have to make a balance between selecting productive areas (to obtain enough food supplies for their chicks and themselves) and performing not too long trips (to come back to the colony to feed the chicks). The limited foraging trips of the species, as a result of its reproductive status, could therefore be the responsible of such different pattern.

High environmental and trophic overlap patterns, in contrast, were hypothesized to be linked to a potential vertical segregation, as all the pairs showing highly overlapped patterns had opposite biologically meaningful vertical ranges: Manx-Balearic (surface vs. deep), Manx-sooty (surface vs. deep) and sooty-great (deep vs surface). If so, this could mean that vertical segregation occurs when species share similar environmental and trophic requirements and would agree with previous studies conducted with sympatric species in which vertical segregation has been found (Mori & Boyd 2004, Navarro et al. 2013). In addition, our results also seem to indicate that vertical segregation mainly occurs between closely related species, such as the sooty and great shearwaters (*Ardenna* genus) or the Manx and Balearic shearwaters (*Puffinus* genus). Phylogenetically related species are expected to be ecologically similar (Losos 2008), so we could additionally suggest that under very similar niche conditions segregating in the vertical dimension is the only way to reduce competition.

Vertical segregation hypothesis, however, cannot be confirmed without diving depth records, although it seems plausible based on the high agreement found between the biologically meaningful vertical ranges defined here and the average depths recorded by data loggers (see Appendix B8). Indeed, the only exception in which the average depth recorded in previous studies was not in agreement with our results was the case of the Balearic shearwater (see Appendix B8). This may be due to the low sample size (only diving data from one individual was obtained in Aguilar et al. (2003), but see Meier et al. (2015) or due to the contrasting oceanographic and prey conditions between the Mediterranean Sea and the Atlantic Ocean (i.e. oligotrophic versus eutrophic conditions, respectively). However, with the available data, no significant conclusion can be made, and we can only acknowledge that further research is needed to elucidate the diving behaviour and the vertical range of the Balearic shearwater.

Advancing in the understanding of protected, endangered, and threatened species (PET) is critical. The pelagic bird community of the BoB, characterised by a highly migratory behaviour, is protected under multiple international agreements. By combining data collected from integrated ecosystem surveys and habitat modelling, we have proved that studying seabirds outside their breeding areas can also provide useful results regarding species niche. Indeed, we have contributed to understand the underlying environmental and trophic drivers of both environmental and trophic niches, which are necessary to identify critical feeding grounds and high biodiversity areas in the context of marine spatial planning. Assessing the degree of overlap between such areas and anthropogenic pressures (e.g., fishing bycatch) could be for instance, a potentially useful step to conduct in the near future that will undoubtedly help advance in the conservation of these species.

CHAPTER 3

The role of climate, oceanography, and prey in driving decadal spatio-temporal patterns of a highly mobile top predator

ABSTRACT

Marine mammals have been proposed as ecosystem sentinels due to their conspicuous nature, wide ranging distribution, and capacity to respond to changes in ecosystem structure and functioning. In southern European Atlantic waters, their response to climate variability has been little explored, partly because of the inherent difficulty of investigating higher trophic levels and long lifespan animals. Here, we analysed spatio-temporal patterns from 1994 to 2017 of one of the most abundant cetaceans in the area, the common dolphin *Delphinus delphis*, in order to explore changes in its abundance and distribution and identify the underlying drivers. For that, we estimated the density of the species and the centre of gravity of its distribution in the Bay of Biscay (BoB) and tested the effect of three sets of potential drivers (climate indices, oceanographic conditions, and prey biomasses) with a Vector Autoregressive Spatio Temporal (VAST) model that accounts for changes in sampling effort resulting from the combination of multiple datasets. Our results showed that the common dolphin significantly increased in abundance in the BoB during the study period. These changes were best explained by climate indices such as the North Atlantic Oscillation (NAO) and by prey species biomass. Oceanographic variables such as chlorophyll *a* concentration and temperature were less useful or not related. In addition, we found high variability in the geographic centre of gravity of the species within the study region, with shifts between the inner (southeast) and the outer (northwest) part of the BoB, although the majority of this variability could not be attributed to the drivers considered in the study. Overall, these findings indicate that considering temperature alone for projecting spatio-temporal patterns of highly mobile predators is insufficient and suggest important influences from prey and climate indices that integrate multiple ecological influences. Accurate projections into the future should therefore integrate existing observational datasets in order to understand first the causes of past shifts.

Under review as:

Astarloa, A., Louzao, M., Andrade, J., Babey, L., Berrow, S., Boisseau, O., Brereton, T., Dorémus, G., Evans, P. G.H., Hodgins, N. K., Lewis M., Martinez-Cedeira, J., Pinsky, M., Ridoux, V., Saavedra, C., Santos, M.G., Thorson J., Waggitt, J.J., Wall, D., Chust, G. The role of climate, oceanography, and prey in driving decadal spatio-temporal patterns of a highly mobile top predator. *Frontiers in Marine Science.*

1. Introduction

Over the past 50 years, the global mean surface temperature has increased by approximately 0.7° C (Stocker et al. 2013), triggering shifts in the abundance, phenology and distribution of organisms worldwide (Parmesan & Yohe 2003, Poloczanska et al. 2013). Marine ecosystems, despite having experienced a slower warming, show comparable or even greater shift rates and vulnerability than terrestrial systems (Burrows et al. 2011, Poloczanska et al. 2013, Pinsky et al. 2019), with seagrasses, corals, cephalopods and marine mammals exhibiting the most abrupt changes (Trisos et al. 2020).

Marine mammals, as wide ranging top predators, amplify trophic information across multiple spatio-temporal scales and can therefore act as sentinels of ecosystems' responses to climate variability and change (Hazen et al. 2019). However, the potential impact of climate change on marine mammals has been little explored in southern European Atlantic waters, partly because of the inherent difficulty of investigating higher trophic levels and long lifespan animals, for which relationships to climate may be nonlinear and affected by time lags (Simmonds & Isaac 2007). Even so, most of the studies conducted up to now in the area suggest that future increases in water temperature will drive marine mammals to track those water temperatures that define their thermal niche (MacLeod 2009, Lambert et al. 2014), although indirect effects through changes in prey availability may also be expected (Simmonds & Isaac 2007, Thorson et al. 2021). Indeed, predicted range shifts in the ocean often deviate from simple expectations of poleward migration, and hence, uniform responses across global oceans should not be anticipated (Burrows et al. 2011).

Understanding past reactions of species to environmental variability is crucial to be able to predict future responses and implement effective management and conservation strategies. This process often requires a combination of data from multiple sampling programmes (Waggitt et al. 2020, Maureaud et al. 2021) that increases the intrinsic variability related to observers' skills, sampling design and sampling effort, and which may result in confounding species range shifts with variations in the distribution and intensity of the sampling effort (Thorson et al. 2016). As a result, separating the observation process from the true underlying spatial distribution is essential to accurately identify range shifts over time (Chust et al. 2014b) and to identify their potential drivers (Erauskin-Extramiana et al. 2020). Recently, a species distribution function (SDF) able to distinguish between sampling variation and true geographic variability has been developed (Thorson et al. 2016). Unlike conventional estimators such as the abundance-weighted average (AWA), the SDF is applied through a Vector Autoregressive Spatio-Temporal (VAST) model that allows the estimation of species distribution over predicted locations rather than sampled locations, while also estimating a standard error that allows one to distinguish between sampling variation and significant interannual variability (Thorson et al. 2016). Until now, this estimator has been mainly applied to commercially important fish stocks (Godefroid et al. 2019, Perretti & Thorson 2019, Xu et al. 2019), although the fragmented and methodologically variable nature of marine mammal observations suggest the method could be highly useful for analysing the spatio-temporal patterns of marine megafauna too.

Within that context, the Bay of Biscay (BoB hereafter) represents an interesting study area as 1) numerous marine mammals species cohabit there attracted by a highly diverse and abundant community of pelagic fish species (Laran et al. 2017), 2) it is already warming (Chust et al. 2011, Costoya et al. 2015), and 3) it falls within the North Atlantic demarcation defined by the European Marine strategy Framework Directive (MSFD; Directive 2008/56/EC), whose main aim is to assess the environmental status of species and ecosystems. Although both abundance and distribution are considered key criteria by the MSFD, most studies conducted on marine mammals in the BoB have focused on determining changes in abundance rather than in distributional range (Hemery et al. 2007, Castège et al. 2013, Authier et al. 2018). Advancing in the understanding of spatiotemporal patterns at regional scale is therefore necessary, especially when projections of climate change impacts mainly consider global scales (MacLeod 2009). In fact, assumptions at such large scales may sometimes differ from regional-scale patterns. The distributional area of blue whales *Balaenoptera musculus* in the eastern North Pacific, for instance, is expected to be reduced in the future (Hazen et al. 2013), despite no changes were predicted at global scale (MacLeod 2009). Similarly, warm-water cetaceans were also predicted to expand poleward in the Northeast Atlantic (MacLeod 2009, Lambert et al. 2011, Lambert et al. 2014), although the south-eastward shift detected for some Northeast Atlantic fish species in the BoB could indicate an alternative pattern in this area (Baudron et al. 2020). Indeed, some of the fish species (e.g., horse mackerel *Trachurus trachurus*, anchovy *Engraulis encrasicolus* and sprat *Sprattus sprattus*) analysed by Baudron et al. (2020) constitute an important food resource for many cetaceans in the BoB (Meynier et al. 2008, Spitz et al. 2018), which may have driven the distribution of cetaceans in this region.

The hypothesis that climate change may affect top predators through climate influences on their ectothermic prey has been often suggested (Robinson et al. 2005, Simmonds & Isaac 2007, Evans & Waggitt 2020). Most studies, however, examine environmental characteristics as proxies of prey distribution rather than studying prey data directly (Torres et al. 2008), which can lead to a poor understanding of their real contribution in the context of climate change. Similarly, many studies aimed at understanding multidecadal shifts in species distribution typically focus on exploring the effects of local environmental conditions such as temperature (Hazen et al. 2012, Chust et al. 2014b), while omitting the potential effect that regional climate indices may have in explaining climate-related variation in ecological patterns and processes (Hallett et al. 2004, Stenseth & Mysterud 2005).

With the aim of understanding the role of multiple drivers in the distribution and abundance of cetaceans, we analysed the spatio-temporal patterns of one of the most abundant species in the BoB, the common dolphin *Delphinus delphis* while testing the effects of prey biomasses, regional climate indices and locally estimated oceanographic conditions on a 24-year-long temporal series (1994-2017). We used the Vector Autoregressive Spatio-Temporal (VAST) model (Thorson & Barnett 2017) and the spatio-temporal species data compiled by Waggitt et al. (2020) to address two main research questions:

1) Has the abundance or the distribution of the common dolphin in the BoB experienced significant changes over the last two decades?
2) If so, are changes best explained by climatic, oceanographic, or prey variables measured locally and/or regionally?

By answering these questions, this study intends to provide insights that will help understand past and future trends in the distribution and abundance of the common dolphin in the BoB and contribute to the management strategies for this species through the development of MSFD criteria in the context of climate change.

2. Material and Methods

2.1. Data collection and standardization

Cetacean observations analysed in this study belong to a large compilation made by Waggitt et al. (2020) that included data collected on aerial and vessel surveys conducted in the Northeast Atlantic between 1980-2018. Although here we only focus on the BoB and on the 1994-2017 period (data providers in Appendix C1), the dataset we analysed derived from the collation and standardization undertaken by Waggitt et al. (2020) to the whole data set, in which they 1) assessed differences in protocols by grouping data according to a) the survey transect design (line transects, strip transects, and an intermediate method called ESAS, *European Seabirds At Sea*) and b) the platform-type (vessel vs. aircraft) and 2) fitted detection functions using platform height and Beaufort sea-state as explanatory variables to estimate the proportion of animals missed by the observers (Marques & Buckland 2004). They also assessed response bias (when animals react to the presence of the platform) through double-platform surveys that enabled the detection of animals before responsive movements. This correction was applicable to vessel surveys and is particularly relevant to common dolphins, which typically show a positive response to vessels (Cañadas et al. 2004). Finally, they calculated the effective strip half width (ESW), which considers the decline in the detection probability as a function of distance and covariates and serves to estimate the area effectively covered [A= ESW *s*L] when including the number of observation sides (s) and transect length (L). Full details can be found in Waggitt et al. (2020) while a schematic overview of the entire Material and methods section can be seen Figure 3.1.

2.2. Spatio-temporal pattern detection

Sampling effort

In order to match with the spatial resolution of the environmental data that we examined in later steps (see *Identification of main drivers* section), we divided larger transects into 10 km segments (García-Barón et al. 2019). Then, we checked whether compiling data had led to a non-uniform distribution of sampling in space and time by analysing with a linear regression latitudinal and longitudinal changes on sampled segments as a function of year.

Baseline* spatio-*temporal model

Observations of common dolphin were analysed by means of a spatio-temporal delta-generalised linear mixed model (delta-GLMM), referred to here as VAST model (Thorson & Barnett 2017), which is a flexible variant of the classical delta models that decompose density into two components (Stefánsson 1996): 1) the probability of encountering the species at a given location and time and 2) the expected density of the species when encountered. This two-part approach, also known as a hurdle model, helps combat statistical problems with zero-inflation and overdispersion in the original data (Martin et al. 2005) and is therefore suitable for use with cetacean survey data that are known to have patchy distributions (Waggitt et al. 2020).

Another feature of the VAST model is that it can include an intercept, spatial and spatio-temporal variation, temporal correlation, habitat covariates (i.e., those affecting density) and detectability covariates (i.e., those affecting detectability). In this case, we included in both components (probability of presence and expected density) 1) spatial variation to account for spatial autocorrelation, 2) spatio-temporal variation to account for correlation that changes among years and locations, and 3) temporal autocorrelation on spatio-temporal components to estimate whether hotspots in populations density persist from one year to the next (Thorson 2019a). Year was treated as a fixed effect (default VATS setting), whereas spatial and spatio-temporal variation were modelled with random effects to help account for multidimensional factors that are not included directly in the model but that can affect the density and distribution of the modelled species. Since Beaufort sea-state and platform height were included in Waggitt et al. (2020), detectability covariates were assumed to be already accounted for and were not considered here. Habitat covariates were also omitted for our initial investigation of trends (but see *Identification of main drivers* section). As a response variable, the density of common dolphin was analysed (Waggitt et al. 2020), after truncating the highest 5% to control outliers (Buckland et al. 2001). Model was fitted assuming a lognormal error distribution, while model parameters were estimated, for computational reasons, for 200 locations (knots) that were equally distributed within the spatial domain with a "2D mesh" smoother with geometric anisotropy (Thorson, 2019a). Species density was predicted at each knot by multiplying the predicted probability of occurrence by the predicted density (Thorson 2019a). Density estimates for each knot were then interpolated to a standard grid of 0.1 ° spatial resolution (latitudinal range: 43 °–49 °N; longitudinal range: 1 °–10 °W) to match with the spatial resolution of the environmental data (see *Identification of main drivers* section) and multiplied by the area of the grid cell to create annual surfaces of common dolphin abundances across the BoB.

Predicted abundance per year was then analysed by means of a linear regression to identify significant temporal trends and compared with an observed abundance index to assess the validity of the predicted values (model validation). The observed abundance index was based on the encounter rate (individuals/km) of common dolphin estimated from a constant effort-based systematic sampling scheme, i.e., the Pride of Bilbao ferry. This survey consistently crosses the BoB using the same route every year (Louzao et al. 2015) and, hence, the comparison of observed (ferry) and predicted (VAST) abundance indices can help determine whether the model predictions have been affected by bias in the effort.

An additional analysis with predicted abundances was also conducted to identify areas in which significant spatio-temporal changes occurred over the study period. For that, predicted abundances per grid cell were analysed as a function of year by means of a linear regression. The slope and the p-value obtained in each cell, as indicators of change rate and its significance, were then plotted over the standard grid covering the study area.

Distribution shift metrics

Shifts in distribution were summarized by calculating the centroid of the distribution for a given year (termed centre of gravity, CoG) after having predicted the density associated with every knot and year in the previous step. By means of the SDF estimator implemented in the VAST model, the CoG was calculated for the BoB population domain and standardized by the total abundance predicted for the study area, so that our analysis focused on changes in distribution after controlling for changes in total abundance (Thorson et al. 2016). Shifts in CoG were displayed in terms of "Eastings" and "Northings", meaning km from the most western point of the study area and km from the Equator, respectively. Significant trends were identified using a linear regression against year.

2.3. Identification of main drivers

To understand spatio-temporal patterns, three main groups of drivers were analysed (Table 3.1), classified into local and regional covariates (a local covariate varies across space while a regional covariate is a univariate time series representing the covariate over the entire study area):

1) Local oceanographic conditions integrated at 100 m depth, specifically temperature and chlorophyll *a* concentration (Chl-a), based on their direct relationship with climate change and their importance for predicting top predators distribution (Hazen et al. 2012, García-Barón et al. 2020).

2) Regional climate indices, specifically North Atlantic Oscillation (NAO), East Atlantic Pattern (EA) and Atlantic Multidecadal Oscillation (AMO) (details in Table 3.1), due to their ability to extract the leading pattern in weather and climate variability over the North Atlantic and their relationship to cetacean and prey populations (Simmonds & Isaac 2007, Borja et al. 2008, Evans et al. 2010, Evans & Waggitt 2020).

3) Regional biomasses of potential prey species, based on the assumption that climate change will affect the distribution of cetaceans through changes in their prey (Robinson et al. 2005, Simmonds & Isaac 2007, Evans & Waggitt 2020).

Temperature and Chl-a values were sourced from the Iberian Biscay Irish Ocean Reanalysis Model available at the Marine Environmental Monitoring Systems (www.marine.copernicus.eu), providing values at 0.08° and 1-month resolution and 27 depth intervals. To test their effect on the annual estimates predicted by the baseline spatio-temporal model, the annual mean of both temperature and Chl-a was estimated integrating the data available in the first 100 m of the water column and then resampled with the *raster* package (Hijmans et al. 2017) at 0.1° (~10km) resolution (Waggitt et al. 2020). The three climate indices were downloaded from NOAA (the National Oceanic and Atmospheric Administration) at a monthly scale and averaged to obtain annual values (www.ncdc.noaa.gov), while the biomass of prey species was acquired from the ICES (International Council for The Exploration of Seas) website at annual scale (https://standardgraphs.ices.dk/).

We selected prey species based on their relative importance in the common dolphin's diet in the BoB (Meynier et al. 2008, Santos et al. 2013) as well as data availability and suitability because not every potential prey species (e.g., sprat, myctophids) was available for the spatio-temporal scale defined in this study. European anchovy *Engraulis encrasicolus* was the only prey species whose biomass had been estimated exclusively for the BoB. Horse mackerel *Trachurus trachurus* estimates were for the Northeast Atlantic, Atlantic mackerel *Scomber scombrus* and blue whiting *Micromesistius poutassou* for the Northeast Atlantic and adjacent waters and sardine *Sardina pilchardus* estimates for the Cantabrian-Atlantic Iberian waters (for information on the extent of stocks see Table 3.1). Although there is an assessment for the sardine stock of the BoB, data were only available from 2000 onwards (ICES 2019c), so we decided to use the biomass estimations from the Cantabrian sea and Atlantic Iberian waters instead after having checked that both indices were highly correlated (r=0.87) and followed similar trends (Appendix C2). Finally, the biomasses of all species were summed and used as a proxy for total prey biomass available in the BoB.

For modelling purposes, local temperature and Chl-a variables were included as quadratic forms in the model to allow for nonlinear responses (Perretti & Thorson 2019). Regional climate indices were included as "spatially varying coefficients" as in

Table 3.1. *Summary of the local oceanographic, regional climatic and regional prey variables used in this study accompanied by a little description and the source from which they were obtained.*

	Variable	***Measure***	***Description***	***Source***
Local oceanographic	Temperature	°C	Mean annual temperature between 0 and 100 m depth	The Iberian Biscay Irish Ocean Reanalysis Model
	Chlorophyll *a*	Mg/m^3	Mean annual chlorophyll between 0 and 100 m depth	
Regional climatic	NAO	-	Both NAO and EA are estimated from the difference of atmospheric pressure at sea level between the Icelandic Low and Azores High, but the anomaly centres of the EA pattern are displaced southeastward to the approximate nodal lines of the NAO pattern	NOAA (National Oceanic and Atmospheric Administration)
	EA	-		
	AMO	-	Average anomalies of sea surface temperatures	
Regional prey	Anchovy	Tonnes	Mean spawning stock biomass in subarea 8 (Bay of Biscay)	ICES (International Council for The Exploration of Seas)
	Sardine	Tonnes	Mean spawning stock biomass in division 8.c and 9.a (Cantabrian Sea and Atlantic Iberian waters)	
	Mackerel	Tonnes	Mean spawning stock in subareas 1-8 and 14, and in Division 9.a (the Northeast Atlantic and adjacent waters)	
	Horse mackerel	Tonnes	Mean spawning stock biomass in Subarea 8 and divisions 2.a, 4.a, 5.b, 6.a, 7.a-c., and 7.e-k (the Northeast Atlantic)	
	Blue whiting	Tonnes	Mean spawning stock biomass in subareas 1-9, 12, and 14 (Northeast Atlantic and adjacent waters)	

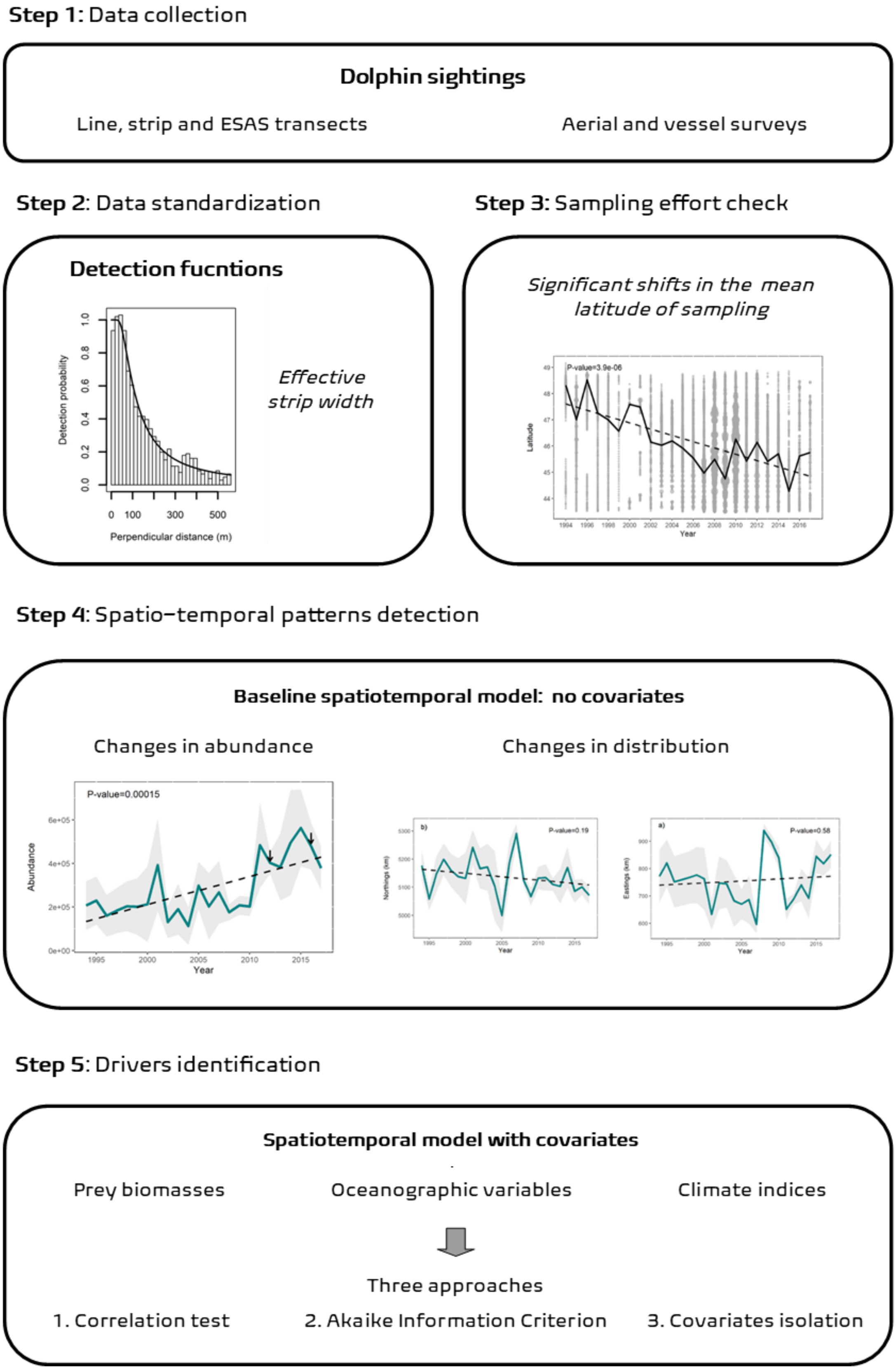


Figure 3.1. *Schematic overview of the main steps conducted to identify the spatio-temporal patterns in common dolphin.*

Thorson (2019b), which means that instead of estimating a single slope parameter presenting the effect of a climate index on density, the model estimates a separate slope parameter for every modelled location (every knot). The biomass of each prey species, as well as the total biomass index, were first log transformed and then included as spatially varying coefficients because they were also available as a single regional time-series.

As a preliminary analysis, potential drivers were correlated with the abundance and CoG of common dolphin obtained in the previous baseline spatio-temporal model. Then, covariates-based modelling was performed in two different ways to identify the most parsimonious drivers and to uncover the relative contribution of covariates (Figure 3.1):

1) Univariate spatio-temporal models were fitted for each variable using the same configuration as in the baseline spatio-temporal model. Univariate models were then compared with the baseline model by means of the AIC (Sakamoto et al. 1986). Only a decrease in the AIC > 2 in relation to the baseline spatio-temporal model was considered an improvement. When models were within 2 units of AIC (ΔAIC ≤ 2), they were considered statistically equivalent (Arnold, 2010). The way in which covariates were related to the spatio-temporal patterns of common dolphin was also explored by plotting the functional relationships from the model parameters.

2) Univariate models were fitted for each variable after setting the spatio-temporal variation (i.e., spatio-temporal random effects) to 0. This was done to remove the contribution of random effects and isolate the effect of the covariates since in VAST, random fields can also account for changes in distribution over time by capturing the residual spatial patterns that cannot be attributed to the fixed effect (Thorson et al. 2017). The abundances and CoG obtained from these models were then compared with those from the baseline spatio-temporal model to determine the amount of variation attributable to covariates.

3. Results

3.1. Spatio-temporal patterns

Sampling effort

A total of 1494 sightings of common dolphin from 21 different surveys were analysed (Figure 3.2, Appendix C1). Those surveys mainly covered spring-summer months and showed a peak of maximum effort between the 2007-2012 period (Appendix C3).

The mean latitude of sampling also varied and shifted significantly south over time, while no significant change was observed in the mean longitude of sampling (Figure 3.3a, b).

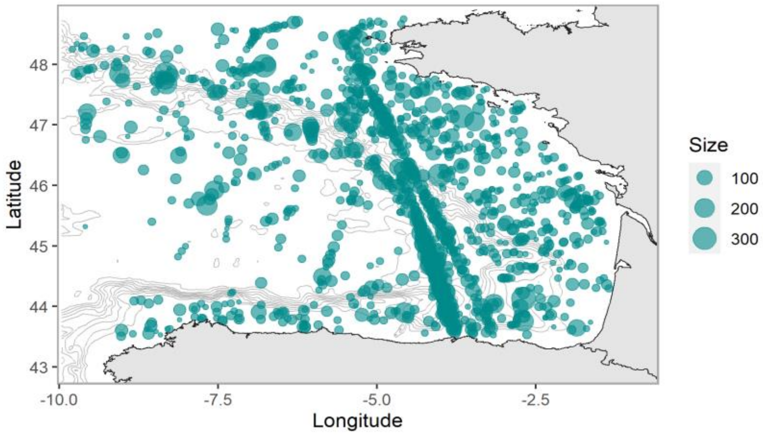


Figure 3.2. *Sightings of common dolphins displayed over the study area. Circle sizes are proportional to group size, while solid grey lines indicate the isobaths.*

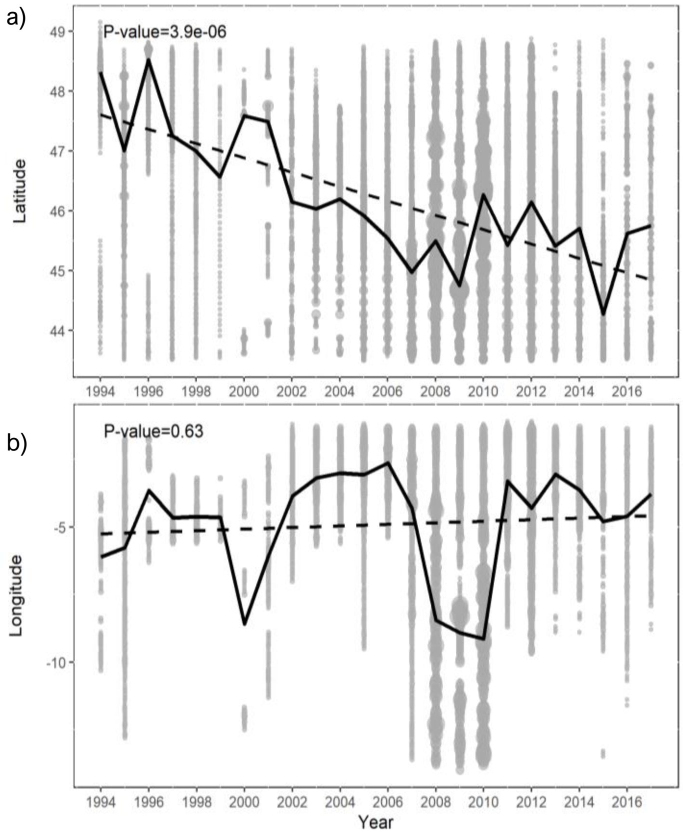


***Figure 3.3**. Sampling effort (number of segments) as a function of year and latitude (a), and year and longitude (b). In both (a) and (b) the size of the circle is proportional to the sampling effort; the black line indicates the mean value and the dotted line the linear temporal trend.*

Common dolphin

The abundance of common dolphin estimated by the baseline spatio-temporal model showed a significant increase throughout the study period accompanied by a high variability (Figure 3.4, Appendix C4). This increase was most pronounced over the more recent years (2011-2017), just after a period of low abundance (2002-2010), and mainly occurred in the southeast corner of the BoB (Figure 3.5a, b). These results agreed with the ferry data, which also showed an increasing trend and a significant correlation with the predicted abundances (Appendix C5).

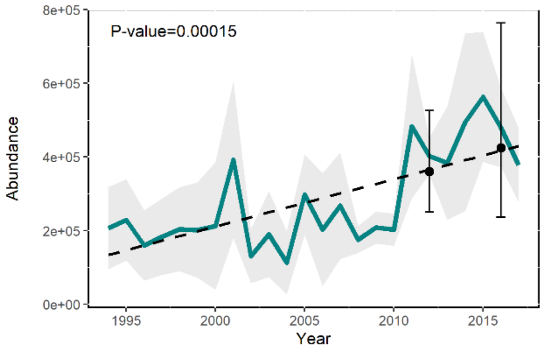


Figure 3.4. *Abundance of common dolphin in the BoB predicted by the baseline spatio-temporal model with standard deviation (shaded area), the linear trend, and its significance. Black dots in 2012 and 2016 represent independent abundance estimates (and their confidence intervals) predicted by other studies.*

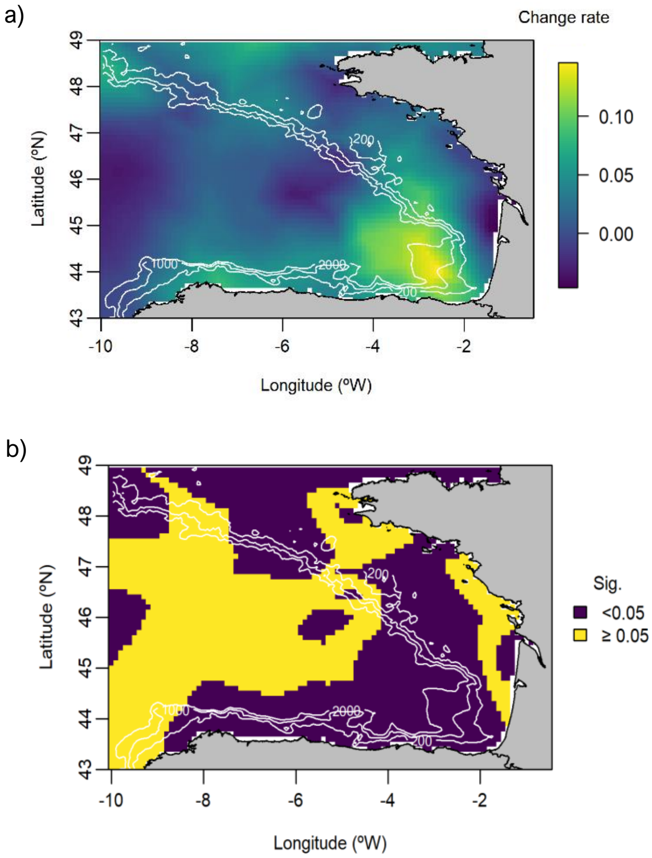


Figure 3.5. *Spatio-temporal changes in the predicted abundance of common dolphin illustrated by means of (a) the change rate (the slope of the linear regression) and (b) its statistical significance (p-value).*

The CoG also showed a high interannual variability, but no significant trend was found over time in either of the two axes (Figure 3.6a, b). In contrast, the correlation between eastings and northings indicated that the common dolphin generally shifted either to the inner (southeast) or to the outer part (northwest) of the BoB (Figure 3.6c).

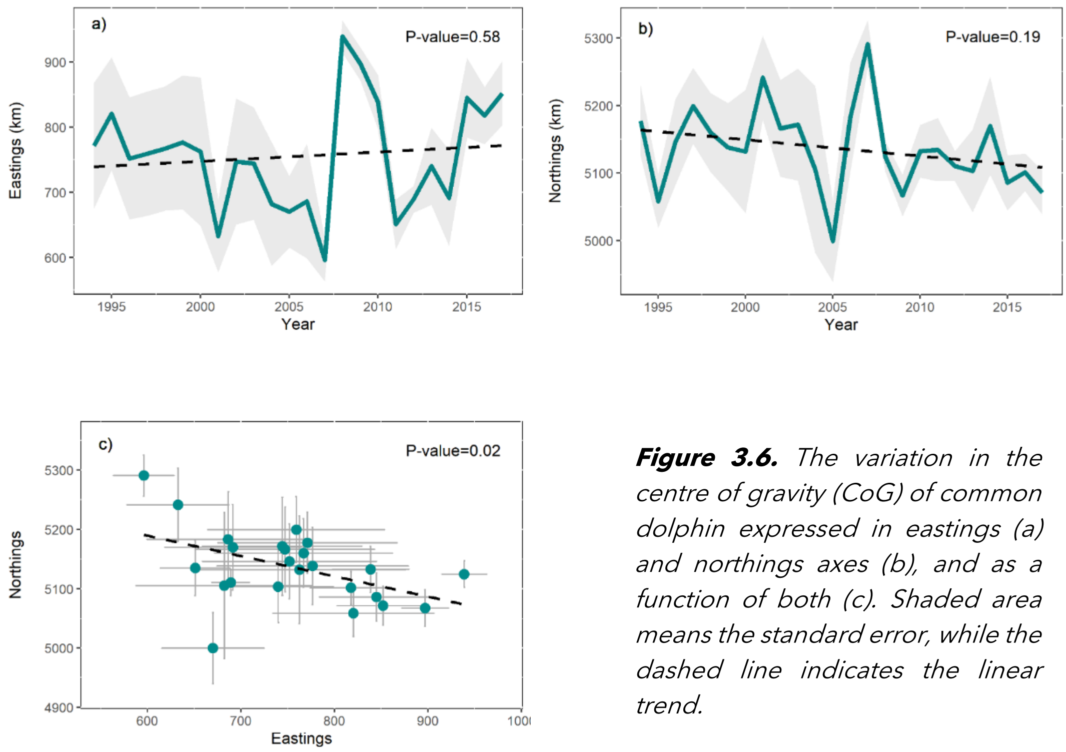


Figure 3.6. *The variation in the centre of gravity (CoG) of common dolphin expressed in eastings (a) and northings axes (b), and as a function of both (c). Shaded area means the standard error, while the dashed line indicates the linear trend.*

3.2. Drivers and covariate contributions

Neither the annual temperature nor the Chl-a concentration integrated at 100 m depth revealed a significant temporal trend across the full BoB (Appendix C6). The climate index AMO has remained in a positive phase since 1997, whereas NAO and EA indices have shown a higher variability with alternation between positive and negative phases (Appendix C6). Both anchovy and mackerel biomasses showed a substantial recovery after a period of low abundance, while sardine and horse mackerel underwent a severe decline. In contrast, blue whiting did not show any significant temporal trend. The prey biomass index, on the other hand, exhibited a significant increase, despite the large variability (Appendix C6).

The correlation between the potential drivers and the CoG (easting and northings) of common dolphin only showed weak relationships. In contrast, predicted abundance revealed several strong relationships (r>0.5) with prey species, specifically mackerel and anchovy (positive correlation), and sardine and horse mackerel (negative correlation) (Figure 3.7). After prey species, only EA and NAO climate indices showed a moderate correlation with abundance (r=0.49 and r=0.48, respectively). Blue whiting was not significant, while temperature, Chl-a, AMO and the prey biomass index showed weak relationships (r<0.35) (Figure 3.7).

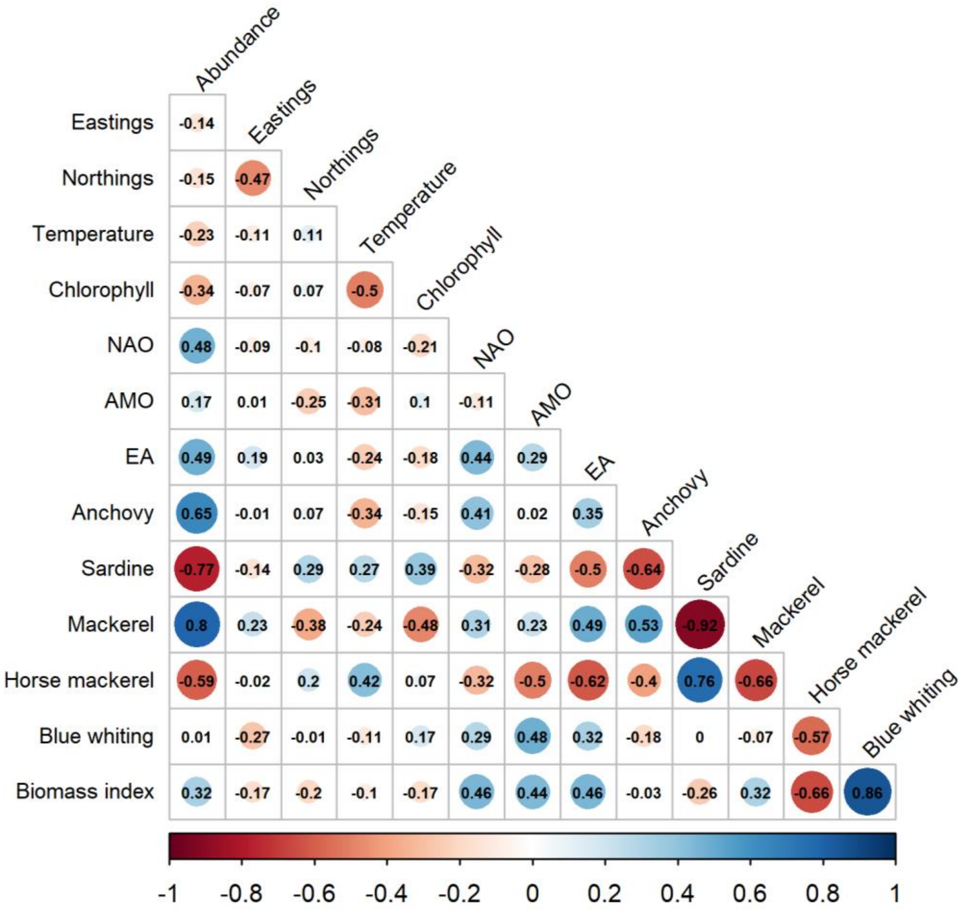


Figure 3.7. *Pearson correlation among the common dolphin's predicted abundance, CoG and potential drivers. Circle sizes are proportional to the correlation coefficient, which is indicated inside the circles. Non-significant correlations (p>0.05) are shown without a circle.*

For covariates-based models, the AIC score showed that the most substantial decrease was for the NAO index while regional prey species biomasses (especially anchovy and prey biomass index) were considered the second most important drivers. Local Chl-a concentration and regional EA only contributed slightly, while temperature and AMO index were not relevant in terms of AIC (Table 3.2). Functional relationships of those important drivers revealed positive responses for NAO, anchovy, mackerel, and prey biomass index and negative for Chl-a, EA, horse mackerel and sardine (Appendix C7).

Table 3.2. *Model terms. Second column refers to the AIC score of each model, while the third column refers to the difference in the AIC (ΔAIC) resulting from the comparison of each univariate model with the spatio-temporal model (reference model). Positive values mean that higher AIC were obtained relative to the spatio-temporal models while negative values mean that lower AIC scores were achieved. Numbers in bold mean improvement in model fitting (ΔAIC < -2) and hence, substantial contribution of the given variable.*

	Model	***AIC***	***ΔAIC***
Baseline spatio-temporal	No covariates	23873.56	0
Local oceanographic conditions	Temperature	23875.31	1.75
	Chlorophyll *a*	23870.2	**-3.36**
Regional climate indices	NAO	23865.28	**-8.28**
	EA	23871.41	**-2.15**
	AMO	23875.22	1.66
Regional prey biomasses	Anchovy	23866.44	**-7.12**
	Sardine	23869.68	**-3.88**
	Mackerel	23870.29	**-3.27**
	Horse mackerel	23868.49	**-5.07**
	Blue whiting	23873.64	0.08
	Biomass index	23867.51	**-6.05**

Similarly, covariate-only models (with no random effects) showed that the NAO and EA indices and prey species biomasses were able to explain the increase in the abundance of common dolphin (Figure 3.8). Chl-a concentration and the prey biomass index, despite having showed a decrease in AIC score (Table 3.2), did not contribute to explain the relative abundance (Figure 3.8), and neither did temperature, AMO index, or blue whiting (Appendix C8). In contrast, only Chl-a and temperature contributed to explain the observed variability in the CoG and, even then, only in a very small proportion (Figure 3.9). In fact, the variation in the CoG explained by these variables only accounted for about 10-20 km (Appendix C9), while the spatio-temporal model suggested variation of 100-300 km.

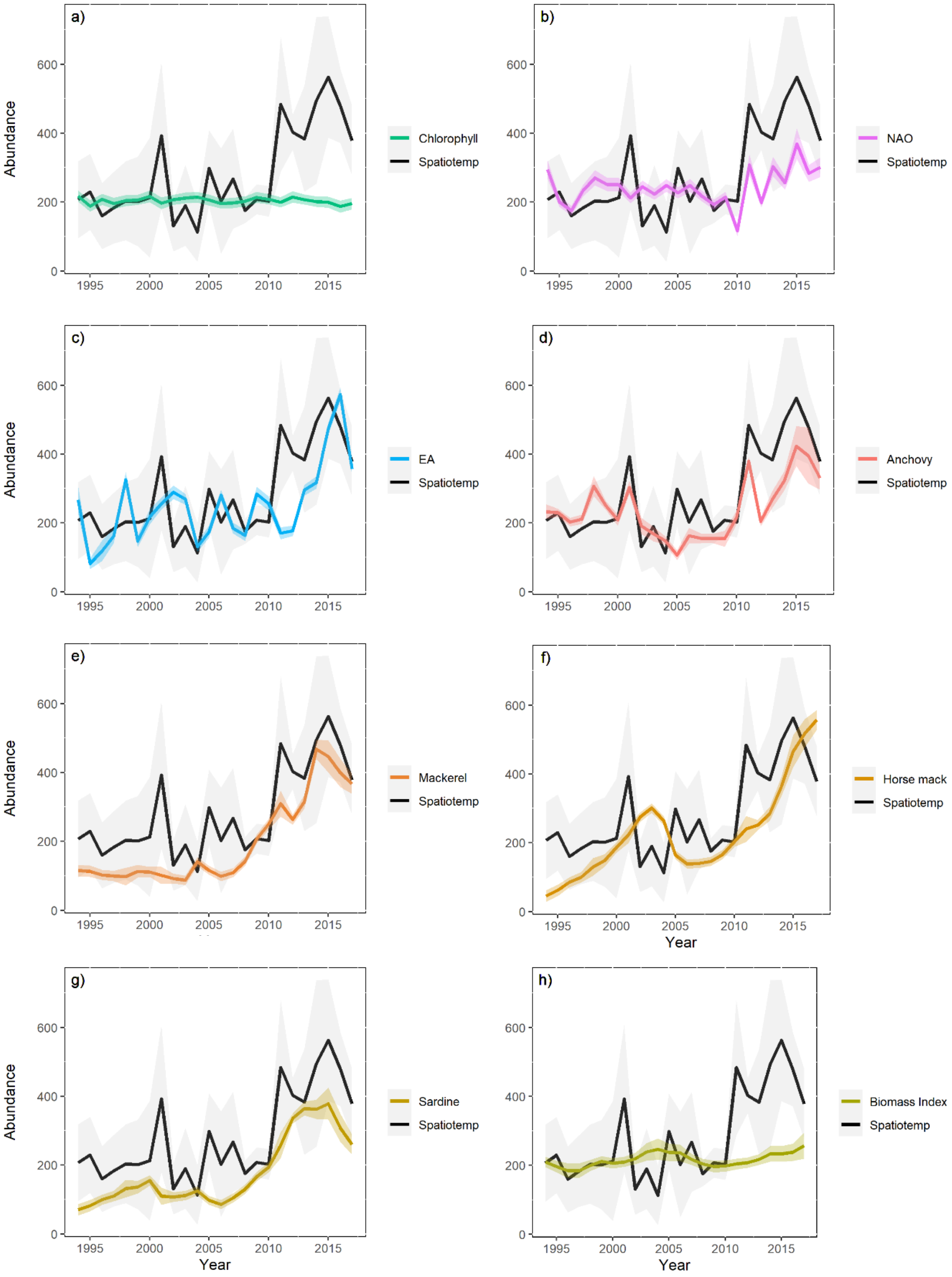


Figure 3.8. *Abundance estimates predicted by the baseline spatio-temporal model and by the covariates-based model (with no random effects) so that the contribution made by each variable can be visualized. Only drivers identified as relevant by AIC score are shown.*

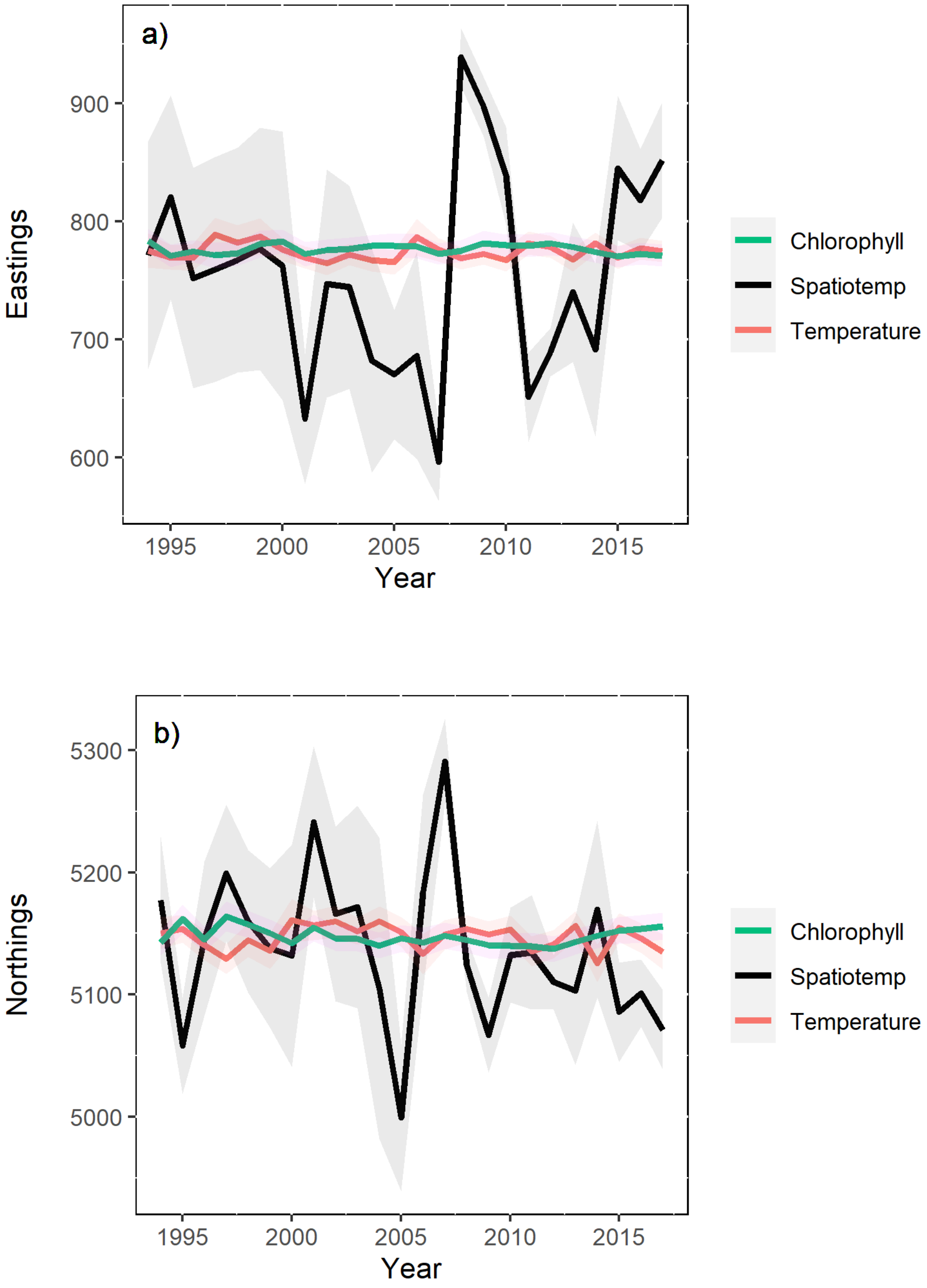


Figure 3.9. *Centre of gravity estimates predicted by the baseline spatio-temporal model and by the temperature and chlorophyll-based models (with no random effects), expressed in easting (a) and northings (b) axes*

4. Discussion

Although the common dolphin community studied here belongs to a wide-ranging population inhabiting the Northeast Atlantic waters, the BoB represents the core habitat of the species as it comprises the largest part of the population (Hammond et al. 2017). It conforms, in addition, one of the marine sub-regions included in the MSFD and hence, the evaluation of the spatio-temporal patterns of common dolphin in this area agrees with the MSFD criteria aiming to assess the abundance and distribution of species. Surveys providing information on species distribution and abundance at this scale, however, have shown significant shifts in the spatial distribution of observations, being necessary the application of methods such as VAST to account for uneven spatial coverage.

4.1. Spatio-temporal trends in common dolphin abundance

The modelling of common dolphin sightings revealed a significant increase in abundance, which is in agreement with previous studies conducted in the BoB (Hemery et al. 2007, Authier et al. 2018, Saavedra et al. 2018) and in the wider Northeast Atlantic (Hammond et al. 2017, Evans & Waggitt 2020) that also reported an increasing abundance of this species. In addition, data from ferry surveys, known to perform the same route every year, showed the same pattern and confirmed that the results were not biased by the detected latitudinal shifts in effort.

In addition, the predicted abundance estimates were found to be quite coherent with those obtained in previous surveys conducted in summer 2012 in the BoB (Laran et al. 2017) and in summer 2016 in the Northeast Atlantic (ICES 2020) in which 490,000 (95% CI: 340,000-720,000) small delphinids (common and striped dolphins) and 634,000 (95% CI: 353,000-1,140,000) common dolphins were estimated, respectively. Although it is not possible to make a direct comparison with our predictions, the ratios for common/striped dolphins and Northeast Atlantic/BoB estimated from Hammond et al. (2017) would lead to an approximate abundance of 360,000 (95% CI: 250,000-526,000) and 425,000 (95% CI: 237,000-764,000) individuals of common dolphin in the BoB for 2012 and 2016, respectively. These numbers, although slightly lower than ours, were similar in magnitude to and within confidence intervals for our predictions in those years (400,000 ± 50,200 and 480,000 ± 107,300 individuals, respectively; Appendix C4), and would indicate, that overall, abundance estimates from VAST were consistent with previous studies.

Given the heterogeneity of the data used in this study, that comprised 21 datasets, the concordance with previous estimates is remarkable and emphasizes the importance of applying methods that are robust to shifts in sampling effort.

The increasing trend in abundance found in this study, however, does not necessarily imply an overall population increase, and instead, could be due to the arrival of individuals from unsampled areas. That is why, the results found in this study should be treated with caution, and never be used to downplay the effects of incidental capture on common dolphin, especially when recent estimates suggest that the bycatch in the BoB is unsustainable for the population as a whole (ICES 2020).

4.2. Regional vs. locally estimated environmental variables

The NAO large-scale climate index is the dominant mode of climate variability over the North Atlantic (Hurrell & Deser 2009), and it can exert a strong influence on several marine organisms through changes in ocean temperature and salinity, as well as vertical mixing and circulation patterns (Drinkwater et al. 2003, Hurrell & Deser 2009).

In the BoB, however, the EA pattern has been identified as a more important driver than NAO (Borja et al. 2008) given that the anomaly centre of EA is located closer to the BoB, and hence, the effects of the NAO have often been assumed to be weaker (Planque et al. 2003). In this study, both EA and NAO showed a moderate correlation with the abundance of common dolphin, although the NAO index was found to be more correlated according to AIC score. One reason why NAO outperformed EA in the BoB could be the wide distribution range of common dolphin, which includes not only the BoB, but also the whole Northeast Atlantic. At such scales, the NAO is the dominant mode of climate variability, which would also explain why the NAO was identified as the main driver of two transatlantic migratory seabirds present in the BoB (Louzao et al. 2015a).

Similarly, common dolphin abundance in the BoB was associated to the South Biscay Climatic (SBC) index, a regional index estimated from oceanic and atmospheric variables and significantly correlated with NAO (Hemery et al. 2007). These findings would support our results and would indicate that climate indices are often better predictors of ecological processes in comparison to local environmental variables (Hallett et al. 2004). Indeed, by holding information about several environmental factors, they act as an integrated measure of weather at any time of the year that likely explains more of the variability of the system than just, for example, ocean temperature (Hurrell & Deser 2009, Thorson et al. 2021). This reasoning matches with the low contribution made by local temperature in this study and suggests that within the core of the species range temperature may not be such an important variable for explaining the abundance and distribution patterns of common dolphin.

4.3. The role of prey

In marine organisms of low trophic level such as phytoplankton or zooplankton, responses to climate indices such as NAO are mediated by changes in the physical or chemical characteristics of the water, while in the case of top predators, such responses are likely to occur through the influence of the climate indices on food resources (Drinkwater et al. 2003). In this study, prey species were the second most important driver, and although we did not model each of the prey biomasses in response to NAO, a significant and positive correlation was found between them (Figure 6). We could therefore hypothesize a potential bottom-up process, in which NAO affects common dolphins through its influence on prey. In fact, bottom-up control has been suggested for the continental shelf food web of the BoB, where a highly diverse and abundant community of forage fishes regulates higher trophic levels (Lassalle et al. 2011).

Accordingly, common dolphins feed on a wide variety of species, although a preference for energy-rich species (>5-6 kJ g-1), such as the anchovy, sardine, mackerel and horse mackerel investigated in this study, has been suggested (Meynier et al. 2008). Atlantic mackerel, however, is only present in large quantities during the first half of the year in the BoB, coinciding with its spawning period (Uriarte & Lucio 2001), while Atlantic horse mackerel and the Iberian sardine are currently in serious decline (ICES 2018, 2019b). European anchovy, in contrast, has been at a sustainable level since 2010, with an overall increasing trend that reached its maximum in 2019 (ICES 2019a). The importance of prey species in common dolphin diet has been found to be related to their availability in terms of abundance (Santos et al. 2004, Meynier et al. 2008), which could explain the negative responses shown by species with low abundances (e.g., Iberian sardine and Atlantic horse mackerel) and the positive and larger contribution in terms of AIC made by those species with higher abundance (i.e., European anchovy and the prey biomass index representing the total biomass available). Blue whiting, on the other hand, did not seem to be relevant in explaining the variability of common dolphin over the study period, despite being more abundant than, for example, anchovy or mackerel. Evidence of blue whiting in the diet of the common dolphin was found in the BoB in the 1980s (Desportes 1985), which could mean that it was important in the past but less so now, or that it is only important, given its poorer energetic condition (4.4 kJ g^{-1}), in the absence of other remarkable prey species (Santos et al. 2013).

Besides, it must be mentioned that not all potential prey species were included and that differences in the distribution of stocks may have also affected the results. In fact, only anchovy's biomass had been estimated exclusively for the BoB. Remaining species biomasses were either estimated using adjacent areas (i.e., Iberian sardine) or distribution areas that extended considerably the observations range of common dolphin (i.e., blue whiting, mackerel and in a lesser extent horse mackerel), which could have contributed, for example, to the higher prominence of anchovy detected in this study.

4.4. Distributional shifts

The common dolphin is considered a warm-temperate species, and accordingly, its range is expected to expand in response to increasing water temperature (MacLeod 2009). This northward expansion seems to be already happening, at least at the northern limit of the species range, as evidenced by a higher frequency of strandings and sightings in northern Britain and southern Scandinavia (MacLeod et al. 2005, Evans & Waggitt 2020). The BoB, however, does not constitute a range edge within common dolphin's distribution, which can explain why we did not find a northward shift in its CoG, but instead, switches between the inner (i.e., southeast) and the outer (i.e., northwest) part of the BoB. This pattern has also been detected when forecasting the future distribution of anchovy's egg density in the BoB (Erauskin-Extramiana et al. 2019a) and was associated to the contraction (southeast) and expansion (northwest) of anchovy population (Motos et al. 1996). A prey driven distribution was already suggested for albacore tuna in the area (Lezama-Ochoa et al. 2010), so we could hypothesize that the distributional shifts of common dolphins in the BoB are also driven by the distribution of their main prey. Similarly, the increase in common dolphin abundance detected in the southeast corner of the BoB could be also related to a higher prey availability. Indeed, other important prey species of the diet of common dolphin (e.g., horse mackerel, sprat) also shifted to the southeast of the BoB in the past 30 years (Baudron et al. 2020), a spot that is considered a refuge basin for the maintenance of species such as anchovy (Motos et al. 1996).

The prey variables considered in this study, however, could not explain much of the observed spatio-temporal variability of the CoG as a result of being introduced as a biomass index that changed across time but not across space. Whether top predator abundance and distribution is driven by the environment or prey is a much debated question in ecology (Grinnell 1917, Elton 1927, Torres et al. 2008). However, acquiring co-occurring top predator and prey data in space and time to test these hypotheses is challenging. In this study, we have taken advantage of a large spatio-temporal compilation of top predator sightings, but in contrast, we have only been able to incorporate annual, non-spatial biomass indices of prey. Future work, therefore, should focus on improving prey data inputs to better understand top predator distributional shifts in the BoB, a question that remains open. Climate indices, as for prey biomasses, were regional time-series rather than spatio-temporal datasets (i.e., changed across time but not across space), so their effect on the CoG is also difficult to understand. Local oceanographic variables did account for spatio-temporal changes, but even so, only explained a very small proportion of spatial shifts, which means that most of the distributional shifts occurred due to unidentified sources. This inability to attribute a source to distributional shifts was also found in previous studies with fishes (Thorson et al. 2017, Perretti & Thorson 2019), and suggests that more effort must be made to understand when distributional shifts can be attributed to covariates in spatial random effects models (Hodges & Reich 2010).

Given the increasingly feasible possibility for combining surveys across areas and regions provided by methods such as those used here, future research should also focus on comprising the whole distribution range of common dolphin. This way, we could address important knowledge gaps that have not been solved here, as for example, if the increasing trend found in abundance is due to the arrival of new individuals or it is the result of an overall population growth. Answering to this question will undoubtedly help understand population dynamics and bycatch implications, but meanwhile, we reiterate our call for caution when interpreting the abundance patterns predicted in this study.

GENERAL DISCUSSION

Since biotic interactions were found to impact beyond local scales, they have received considerable attention, leading to the development of many statistical analyses of species co-distribution in few years (Gotelli & Ulrich 2010, Veech 2013, Pollock et al. 2014, Morueta-Holme et al. 2016, Ovaskainen et al. 2016). Approaches such as JSDM managed to deal with one of the biggest challenges in co-occurrence data analysis, i.e., environmental filtering, and for that reason they were considered robust enough to infer biotic interactions (Dormann et al. 2018, Blanchet et al. 2020).

Recently, however, several uncertainties regarding co-occurrence analyses have arisen, not related to the statistical method as such, but to the interpretation of results. Indeed, many studies state now the difficulty of interpreting biotic interactions from co-occurrence data, arguing that not accounting for some key factors, such as those described below, can lead to false conclusions (Cazelles et al. 2015, Dormann et al. 2018, Blanchet et al. 2020).

1. Missing predictors: the failure to include an important environmental predictor for a target species may result in an apparent biotic interaction if other species can indicate the missing environmental information (type I error). In such case, species with similar habitat requirements will appear to interact positively, whereas species that have contrasting requirements will appear to interact negatively (Warton et al. 2015, Harris 2016).
2. Indirect effects: if two competing species share a positive relationship to the same resource, their occurrence could be positively correlated, when the true effect should be negative (Morueta-Holme et al. 2016).
3. Asymmetric associations: predators usually prefer locations with high prey densities, whereas prey should prefer areas with lower predation risk. Depending on the outcome of this space race, their joint space use can indicate either a positive association (prey tracking) or a negative association (predator avoidance) (Thurman et al. 2019, Blanchet et al. 2020).

Although every statistical approach has its own limitations, some of the findings of Chapter II and Chapter III could indicate some inaccuracies in our JSDM results and interpretations due to the aforementioned reasons. For instance, shearwater species were found to positively interact in JSDM analysis, which we tended to interpret as mutualistic associations linked to local enhancement. Findings from Chapter II, in contrast, suggested strong competition between some of its members, e.g., sooty and great shearwaters, and hence, the positive interactions found among them could be instead the result of an indirect effect derived from sharing the same resources.

In this line, the JSDM did not find any significant biotic interaction between the common dolphin and prey species, whilst the detailed study in Chapter III suggested a potential relationship between common dolphin and energy rich species such as anchovy or mackerel. While this could be due to the smaller data set analysed in Chapter I (only four years of data in contrast to 24 years in Chapter III), it could be also related to the limitations of JSDM in detecting asymmetric associations. In fact, the final outcome of predator-prey associations has been linked to species prevalence: when prevalence is low in both species, co-occurrence tends to be higher than the null expectation (+), when at least one species in the predator-prey relationships is more common, then co-occurrence is lower than expected (-), and when the two are widespread species (or both are rare), then the probabilistic model will likely classify them as random (Veech 2013, Zurell et al. 2018).

This is why a careful and reflective interpretation of resulting interactions is recommended, ideally complemented by and compared with experimental evidence or independent data sets (Dormann et al. 2018). But this is not always possible; empirical evidence of species interactions is usually lacking while trophic evidence may be inadequate or insufficient depending on the target species or the study area. Most of the seabird species of this study, for example, do not breed in the BoB, not being possible colony-based field studies that could contribute to the collection of trophic evidence. In addition, most of the top predators studied here are protected under different Conservation Agreements, and so, diet studies are limited to the analysis of stomach contents of opportunistically stranded or bycaught animals (Spitz et al. 2006, Pusineri et al. 2007) or to the application of indirect methods such as stable isotope analysis, genetics or fatty acids (Navarro et al. 2009, Käkelä et al. 2010).

Under such circumstances, co-occurrence analysis could be used, while acknowledging its limitations, as an additional indirect method to advance in the understanding of ecological networks rather than as a direct interaction detector. Periodical JSDM analysis, for instance, could help find significant changes over time, such as the emergence of new species or the disappearance of links/species, being adequate as hypothesis generating tools (e.g., for identifying an association that should be further investigated) or as evidence for alterations in ecological interactions (Araújo et al. 2011, Clark et al. 2014, Dormann et al. 2018, Blanchet et al. 2020).

A conceptually simpler but technically more challenging alternative would be to derive interactions from abundance (count) data (Blanchet et al. 2020) while including interacting species as predictor variables in SDMs (Meier et al. 2010, Godsoe et al. 2017). Although inferring ecological interactions from the easiest data to acquire (presence-absence data) holds a great appeal, count data carry more information that could be used to make more refined inferences on why species occur at a specific location and how the biotic predictors affect their distribution and abundance patterns (Blanchet et al. 2020).

Accordingly, count data was modelled in the following chapters (Chapter II and Chapter III) but restricting the potential biotic predictors to prey variables. This led us to identify potential trophic interactions not identified previously with the JSDM, such as those involving common dolphin (Chapter III), but also to infer the segregation mechanisms that allow species coexistence by computing and visualizing the spatial overlap in their niches (Chapter II). Indeed, a necessary condition for detecting an effect of species B on species A is that within the range of A there exist regions without B (Dormann et al. 2018).

Overlap metrics and analyses have long been used to quantify niche dis/-similarities (Warren et al. 2008, Broennimann et al. 2011) and more recently to identify biotic interactions (Araújo & Rozenfeld 2013, D'Amen et al. 2018). However, a conceptual diagram such as the one developed in Chapter II had not been previously addressed. In fact, by means of this diagram, we were able to describe up to four different scenarios based on spatially explicit overlap analyses, including breeding-driven isolation, environmental and trophic niche partitioning, and a potential vertical segregation. Although these results did not represent any biotic interactions *per se*, they suggested a competition driven scenario in which shearwaters must share the environmental space or the trophic resources to coexist.

Nevertheless, both Chapter I and Chapter II were restricted to autumn (i.e., JUVENA survey), which despite being one of the most diverse seasons in terms of top predators, only provides information for a given period of time. Chapter III managed to solve the temporal scale issue by compiling data collected throughout the year and over 24 years, and additionally revealed the usefulness of climatic indices not previously used. But failed to answer some key questions regarding the distribution and abundance of a highly mobile top predator such as common dolphin by focusing purely on the BoB.

Each approach used in thesis had therefore its own weakness and strengthens. They were in addition, aimed to answer specific question and hence, they should not be directly compared. However, all of them shared a common feature: they allowed the identification of biotic interactions/processes while acknowledging a greater contribution of environmental drivers, either through a higher number of environmental correlations (Chapter I), a larger deviance explained (Chapter II) or a better model fit (Chapter III).

As stated before, in JSDM approach, missing predictors can lead to biotic interactions, so focusing on the number of environmental and residual correlations may not be the most adequate proxy to measure their relative contribution. However, many other studies using JSDM, and thus, with the same potential problems, have also identified environmentally driven associations as the primary driver of species co-occurrence (Pollock et al. 2014, Royan et al. 2016, D'Amen et al. 2018). This finding would therefore agree with other studies in which species interactions were considered of secondary importance in comparison to habitat structure. Nevertheless, heterospecific attraction processes such as local enhancement cannot be omitted in seabird communities, where the occurrence of congeners can be essential to locate prey in patchy environments such as oceans (Fauchald et al. 2000, Fauchald 2009, Tremblay et al. 2014, Veit & Harrison 2017).

In the two approaches used in Chapter II and III, prey species were incorporated as predictors and in such case, several reasons can explain the lower explanatory power of prey variables:

1. The fisheries acoustic equipment used to assess prey abundance does not capture fish abundance in the top 8 m of the water column (Boyra et al. 2013). It excludes, therefore, the main foraging depth of surface feeders, which may result in weaker associations (Phillips et al. 2021).
2. Predator and prey distributions may be mismatched at fine scales. Many studies focusing on predator-prey relationships found that spatial correlations increase with increasing scales. At large scales, prey may be aggregated on predictable areas linked to mesoscale oceanographic features, leading to positive correlations, whilst at smaller scales, prey may be further congregated in dense and unpredictable schools to avoid predation, inducing negative correlations (Rose & Leggett 1990, Fauchald et al. 2000, Fauchald 2009).

3. At large spatio-temporal scales, prey biomasses may be only available as annual indices that often belong to adjacent areas or that extend considerably the observations range of the target predator species, potentially reducing the association strength or significance (Santos et al. 2013).
4. Most common measures to quantify prey distributions such as abundance or density may be inadequate predictors of predators-prey relationships; instead, prey patch characteristics such as depth and local density within spatial aggregations may be more suitable (Benoit-Bird et al. 2013, Boyd et al. 2017). In Chapter II, we attempted a trait-based approach using prey species depth and size, but further investigation may be still needed to find more meaningful characteristics.

The lower contribution and/or the smaller explanatory power of prey variables found along the chapters reaffirm the difficulty of capturing significant spatio-temporal relationships between mobile marine top predators and prey. This is in agreement with previous findings (Fauchald 2009, Lambert et al. 2018) and overall, suggests that environmental variables are generally better predictors of marine top predator distributions than prey abundance (Torres et al. 2008, Phillips et al. 2021). However, the incorporation of prey variables also enabled to disentangle segregation mechanisms in shearwaters, confirmed their low trophic segregation and led to explain a greater part of the common dolphin's spatio-temporal variability in comparison to other widely used variables such as temperature.

We therefore consider that it is worth keeping investigating on the identification of suitable scales and meaningful prey characteristics in order to obtain more accurate results. Indeed, one way to advance towards an ecosystem-based management is to account for the effects that both predators and prey exert on each other. Fish removal rates, for example, can be determined by considering the feeding requirements of predators, as in the Southern Ocean (Ruckelshaus et al. 2008), but for that, a profound knowledge on food web is required. The final aim of this thesis, however, was not to approach an ecosystem-based management but to achieve a more holistic perspective on the assembly rules that govern top predators' community by including environmental variables and biotic interactions that could contribute to the understanding of ecosystem functioning. The following conclusions and thesis suggest that such objective has been fulfilled.

CONCLUSIONS

The studies carried out in this PhD thesis have contributed to answer the four specific objectives stated initially, resulting in the following conclusions:

Objective 1: To uncover the underlying mechanisms of predator-prey co-occurrence patterns by identifying interspecific associations and their main drivers (Chapter I). The main conclusions in relation to this objective are:

1. Co-occurrence patterns of top predators and prey were driven by a combination of environmental factors (dis-/similar environmental preferences) and biotic interactions, although the later were found to be of secondary importance relative to habitat structure.
2. Among biotic interactions, we identified schooling in prey (e.g., anchovy–sardine), local enhancement/facilitation in predators (e.g., Cory's shearwater–fin whale), and predation between predator–prey species (e.g., northern gannet–horse mackerel), all of them led by positive associations.
3. The identification of interspecific association can therefore provide insights on the functioning of predators–prey network, although given the sensitivity of the analysis to several factors, a careful and reflective interpretation of resulting interactions is recommended.

Objective 2: to identify how co-occurring species share the environmental and trophic niche (Chapter II). The main conclusions from this objective are:

4. Niche differentiation does occur among the shearwater community of the BoB and is primarily driven by environmental niche partitioning and only slightly by trophic segregation, which agrees with the generalist and opportunistic behaviour of the species.
5. According to their different biologically meaningful vertical ranges, vertical segregation is possibly the third segregation mechanism used by these species, although diving depth records would be needed to confirm this hypothesis.
6. Including trophic variables, as well as vertical dimension, in the study of ecological niches provides new information and turns useful to fully understand how species exploit the physical environment and the biotic resources. However, models with only environmental models perform better, which requires further investigation on why this may happen and how can be improved.

Objective 3: to define the role of prey, climatic and oceanographic variables in driving the spatio-temporal patterns of a highly mobile top predator (Chapter III). The main conclusions are:

7. Oceanographic variables such as chlorophyll *a* concentration and sea temperature hardly contributed to explain the abundance patters of common dolphin, while regional climatic indices such as NAO and prey species biomasses were the most important drivers.
8. The centre of gravity (CoG) of the species distribution showed a high variability, but no significant shift, and could not be explained by the variables considered. Additional research is therefore required to identify the drivers that govern the distribution of a highly mobile species in the BoB.
9. Overall, the role of sea temperature in explaining common dolphin spatiotemporal patterns in this region was found to be small and thus, climate change projections based on sea temperature increase should consider the species' whole distribution range.

Objective 4: to determine the relative importance of biotic and environmental drivers in explaining the abundance and distribution of top predators (Chapter I, II and III). Main conclusions in relation to this objective are:

10. All the approaches used in this thesis, despite allowing the identification of biotic interactions, showed a greater contribution of environmental drivers, either through a higher number of environmental correlations, a larger deviance explained or a better model fit.
11. This is in agreement with previous findings and overall, supports suggestions that environmental variables are generally better predictors of marine top predator distributions than direct measurements of prey abundance.
12. However, the incorporation of biotic variables provided valuable information that could not have been possible otherwise, being their inclusion necessary, useful, and worthy.

Additionally, the consecution of these objectives has allowed working towards the validation of the enunciated working hypothesis, being the **thesis** that:

"The incorporation of biotic drivers to the traditional Species Distribution Modelling approach allowed the identification of biotic interactions (e.g., facilitation, competition or predation), trophic preferences and trophic segregation processes, providing new information on the coexistence, food web structure and spatio-temporal patterns of the top predators of the Bay of Biscay. Despite the valuable information provided by biotic drivers, environmental variables still appeared as better predictors of top predators' abundance and distribution, being necessary to keep working in the identification of right spatio-temporal scales and meaningful prey characteristics that could provide more accurate and representative relationships of the entire ecosystem functioning".

APPENDICES

CHAPTER 1 – APPENDIX A

Appendix A1. Selecting most important variables

The nine environmental variables were first standardized to have a mean of zero and a standard deviation of one (Zuur et al. 2007) and then analyzed using Spearman correlation coefficients (r) to assess the degree of co-linearity between them. Those variables with a |r| ≥ |0.6| were removed (only one per pair) and as a result, only Ts, T_{200}, SALs, SAL_{200}, GVs, GV_{200}, DTG, DEP were included in the model (Table A1.1).

Table A1.1. *Spearman rank correlation coefficients between pairwise variables. Correlation higher than |0.6| are in bold.*

	DCO	***DEP***	***Ts***	***T_{200}***	***SALs***	***SAL_{200}***	***GVs***	***GV_{200}***	***DTG***
DCO	1,00	-**0,66**	0,10	-0,34	0,16	0,26	-0,09	-0,38	0,35
DEP	**-0,66**	1,00	-0,41	0,40	-0,16	-0,52	-0,05	0,37	-0,37
Ts	0,10	-0,41	1,00	-0,03	-0,40	0,38	0,37	-0,03	-0,20
T_{200}	-0,34	0,40	-0,03	1,00	-0,16	-0,36	0,14	0,48	-0,06
SALs	0,16	-0,16	-0,40	-0,16	1,00	0,13	-0,22	-0,08	0,50
SAL_{200}	0,26	-0,52	0,38	-0,36	0,13	1,00	0,24	-0,36	0,09
GVs	-0,09	-0,05	0,37	0,14	-0,22	0,24	1,00	0,32	-0,22
GV_{200}	-0,38	0,37	-0,03	0,48	-0,08	-0,36	0,32	1,00	-0,14
DTG	0,35	-0,37	-0,20	-0,06	0,50	0,09	-0,22	-0,14	1,00

With the selected environmental variables, generalized linear models (GLMs, McCullagh & Nelder 1989) were then fitted to each species, using the species occurrence as the response variable and assuming the binomial error distribution as the probit-link function. By using MuMIn package (Barton 2016) we ranked the models based on the lowest AICc values (second-order Akaike Information Criterion) and the Akaike weights (Sakamoto et al. 1986, Guisan & Zimmermann 2000) and selected those for which the cumulative sum of Akaike weight was ≥ 0.95 (Burnham & Anderson 2003). Finally, we measured for each species the relative variable importance by summing the Akaike weights of all the models containing the specific predictor (Burnham & Anderson 2003). Variable selection was then limited to five variables at most to avoid excessive complexity and model overfitting (Table A1.2) (D'Amen et al. 2018).

Table A1.2. *Variables' importance based on AIC and Akaike weights. Only first five species have been included as example. The final sum corresponds to that obtained by summing all variables importance in the 28 species.*

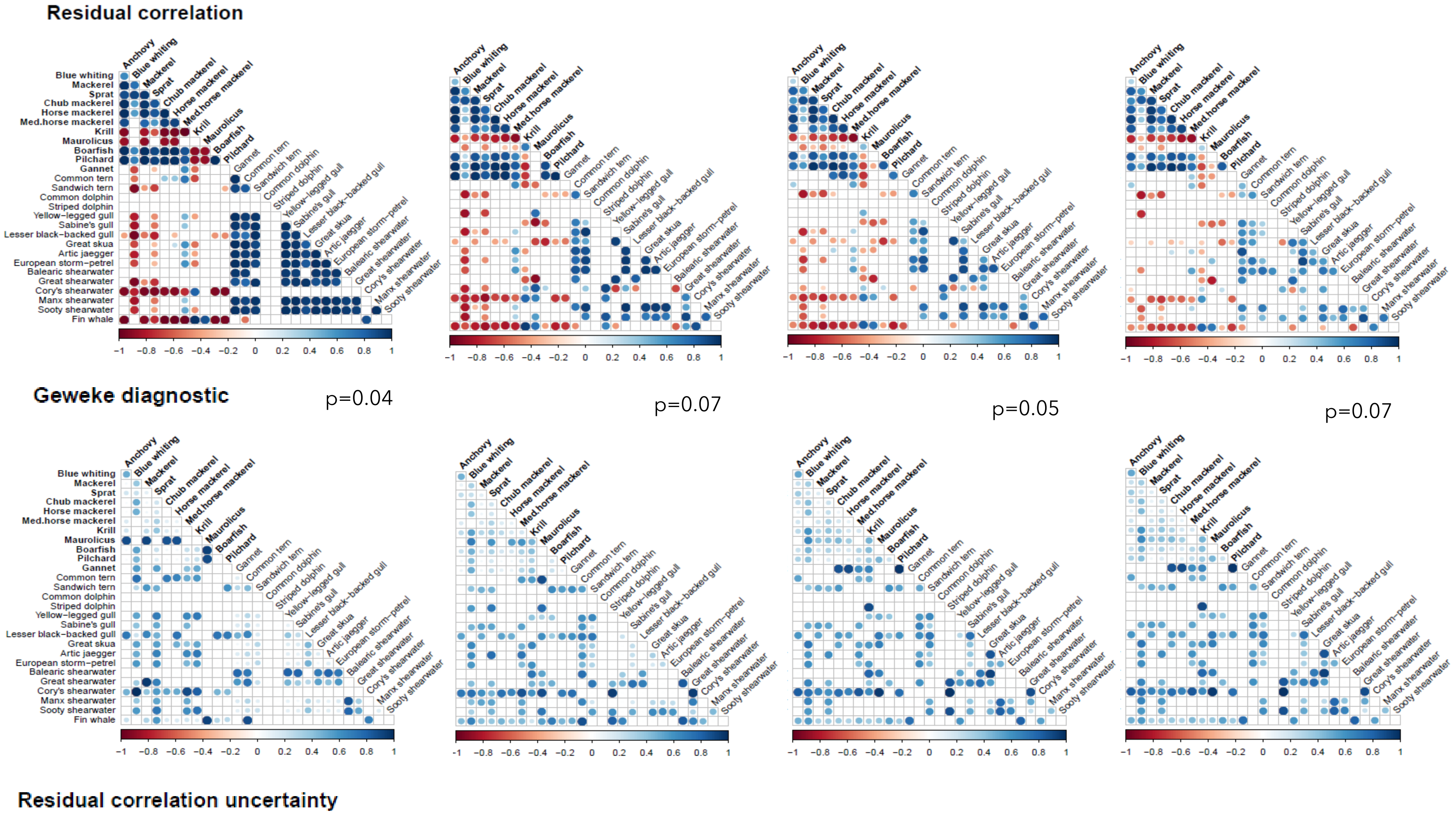
	Northern gannet	**Anchovy**	**Blue whiting**	**Common tern**	**Horse mackerel**		**Sum**
DEP	1,00	0,95	1,00	1,00	0,96	**…**	**22,93**
SAL_{200}	0,26	0,51	0,29	0,91	1,00	**…**	**19,75**
SALs	0,70	1,00	1,00	0,43	1,00	**…**	**19,13**
T_{200}	0,99	0,37	1,00	1,00	0,35	**…**	**18,72**
Ts	0,34	0,28	1,00	0,89	0,67	**…**	**17,57**
DTG	0,28	0,27	1,00	1,00	0,43	**…**	16,70
GVs	0,34	0,27	0,20	0,40	0,48	**…**	15,90
GV_{200}	0,44	0,28	0,61	0,57	0,89	**…**	14,24

Alternatively, stochastic search variable selection, SSVS (George & McCulloch 1993) available in the *boral* package was used to assess covariates importance and compare the results with the previous approach. Similar to the previous approach, a GLM was fitted to each species with all the environmental covariates included and the species co-occurrence matrix used as the response (again assuming the binomial error distribution and the probit-link function). SSVS was then applied to each coefficient separately. We included random effects for every site and every year, an informative prior on the regression coefficients, $\beta \sim N(0, 1)$, as recommended by Wilkinson et al. (2018) and the default configurations in *boral* otherwise. By limiting variable selection to a maximum of five variables, as we did before, results based on the highest mean posterior probability chose DEP, Ts, T_{200}, SALs, SAL_{200} as the most important predictors. This agreed exactly with the results provided by the Akaike weights approach (Table A1.3).

Table A1.3. *Summary of the coefficients obtained for every predictor after having applied SSVS on each coefficient separately. To select most important variables the mean of the posterior probability was used (in bold).*

	DEP	**T_S**	**T_{200}**	**SAL_S**	**SAL_{200}**	**GV_S**	**GV_{200}**	**DTG**
Min	0.07	0.05	0.05	0.08	0.08	0.04	0.06	0.05
1st Qu. :	0.34	0.1050	0.17	0.15	0.12	0.08	0.11	0.07
Median	0.97	0.275	0.38	0.38	0.642	0.16	0.23	0.17
Mean	**0.69**	**0.4546**	**0.49**	**0.49**	**0.57**	0.35	0.31	0.40
3rd Qu.:	1.00	0.9233	0.9	0.93	0.97	0.50	0.48	0.86
Max:	1.00	1.0000	1.00	1.00	1.00	1.00	0.91	1.00

Appendix A2. Estimated residual correlations, their uncertainty (defined as the width of their corresponding 95% credible interval) and the proportion of Geweke diagnostic statistics that were deemed to be significant (without no adjustment for multiple comparisons) for each of the four candidate JSDMs fitted with 2 to 5 latent variables. The JSDM with one latent is not shown as the correlations by definition can only take values 1 or -1.



Appendix A3. Proportion of accounted deviance by the environmental covariates and latent variables in the selected model, accompanied by the number of presences, absences and number of observations for each species (prey species in bold).

Species	***Pres***	***Abs***	***Nobs***	***Accounted deviance (%)***	
				Env.	***Latents***
European anchovy	673	338	1011	11%	69%
Mueller's pearlside	503	508	1011	42%	23%
Atlantic horse mackerel	479	532	1011	13%	83%
Northern gannet	364	647	1011	15%	7%
Lesser black-backed gull	220	791	1011	8%	18%
Atlantic mackerel	198	813	1011	61%	35%
Great shearwater	195	816	1011	9%	52%
Med. horse mackerel	141	870	1011	30%	64%
Krill	134	877	1011	17%	62%
Great skua	131	880	1011	24%	23%
Sooty shearwater	125	886	1011	9%	33%
Yellow-legged gull	124	887	1011	34%	33%
Sabine's gull	115	896	1011	19%	24%
European sprat	108	903	1011	50%	42%
Blue whiting	90	921	1011	70%	18%
European pilchard	84	927	1011	43%	50%
Fin whale	75	936	1011	51%	27%
Boarfish	70	941	1011	37%	53%
Common dolphin	69	942	1011	23%	5%
Pacific chub mackerel	69	942	1011	34%	59%
Cory's shearwater	64	947	1011	35%	11%
Arctic jaeger	58	953	1011	29%	20%
Common tern	51	960	1011	44%	27%
Striped dolphin	47	964	1011	65%	7%
European storm-petrel	41	970	1011	11%	38%
Manx shearwater	41	970	1011	16%	41%
Balearic shearwater	31	980	1011	37%	20%
Sandwich tern	27	984	1011	27%	47%

Appendix A4. Summary of the literature survey conducted for the pair-wise associations (both positive and negative) found within predator-prey group.

Predator	Prey	Ecological meaning of pair-wise association	Trophic evidence	Reference for trophic evidence and comments	Location	Methodology
Positive associations						
Arctic jaeger	Med. Horse mackerel	Positive interactions causing aggregation	0	No evidence in Jones et al. (2010). Relies heavily on kleptoparasitism.	NE Atlantic	Pellets
Arctic jaeger	Krill	Similar habitat preferences	0	No evidence in Jones *et al.* (2010). Relies heavily on kleptoparasitism.	NE Atlantic	Pellets
Balearic shearwater	Boarfish	Similar habitat preferences	0	No evidence in Arcos *et al.* (2000), Navarro *et al.* (2009) and Meier *et al.* (2015)	NE Atlantic and Mediterranean Sea	Experimental discards and stable isotopes
Balearic shearwater	Med. Horse mackerel	Similar habitat preferences	1	Evidence in Arcos *et al.* (2000) and Meier *et al.* (2015). Considered equal to horse mackerel.	NE Atlantic and Mediterranean Sea	Experimental discards and stable isotopes
Balearic shearwater	Horse mackerel	Similar habitat preferences	1	Evidence in Arcos *et al.* (2000) and Meier *et al.* (2015)	NE Atlantic and Mediterranean Sea	Experimental discards and stable isotopes
Balearic shearwater	Atlantic mackerel	Similar habitat preferences	1	Evidence in Meier et al. (2015)	NE Atlantic	Stable isotopes
Balearic shearwater	Chub mackerel	Similar habitat preferences	1	Evidence in Meier et al. (2015). Considered equal to Atlantic mackerel	NE Atlantic	Stable isotopes

Balearic shearwater	European pilchard	Similar habitat preferences	1	Evidence in Navarro *et al*. (2009) and Meier *et al*. (2015)	NE Atlantic and Mediterranean Sea	Stable isotopes
Balearic shearwater	European sprat	Similar habitat preferences	0	No evidence in Arcos et al. (2000), Navarro *et al*. (2009) and Meier *et al*. (2015)	NE Atlantic and Mediterranean Sea	Experimental discards and stable isotopes
Balearic shearwater	Blue whiting	Similar habitat preferences	1	Evidence in Navarro *et al*. (2009) and Meier *et al*. (2015)	NE Atlantic and Mediterranean Sea	Stable isotopes
Common dolphin	Med. Horse mackerel	Similar habitat preferences	1	Evidence for *Trachurus spp*. in Meynier et al. (2008)	NE Atlantic	Stomach content of stranded animals
Common dolphin	Blue whiting	Similar habitat preferences	1	Evidence in Meynier et al. (2008) and Pusineri et al. (2007) in a minor extent	NE Atlantic	Stomach content of stranded and by caught animals
Common tern	European anchovy	Positive interactions despite of habitat differentiation	0	No evidence but very similar to sprat documented in Robertson et al. (2016)	NE Atlantic	Nest observations
Common tern	Med. Horse mackerel	Positive interactions causing aggregation	1	Evidence in Monteiro *et al*. (1998) and Granadeiro *et al*. (2002). Considered equal to *T.picturatus*.	NE Atlantic	Regurgitations and pellets
Common tern	Mueller's pearlside	Similar habitat preferences	1	Evidence in Granadeiro *et al*. (2002)	NE Atlantic	Pellets
Common tern	Blue whiting	Similar habitat preferences	0	No evidence in Monteiro *et al*. (1998), Granadeiro *et al*. (2002) or Robertson et al. (2016)	NE Atlantic	Nest observations, regurgitations and pellets
Cory's shearwater	Krill	Positive interactions causing aggregation	0	No evidence in Granadeiro et al. (1998), Paiva et al. (2010) or Neves et al. (2012).	NE Atlantic	Regurgitates and stable isotopes

Cory's shearwater	Mueller's pearlside	Positive interactions and similar env preferences	1	Evidence in Neves et al. (2012)	NE Atlantic	Regurgitates
European storm-petrel	Med. Horse mackerel	Positive interactions and similar env preferences	0	No evidence in D'Elbee and Hemery (1998) or Thomas et al. (2006).	NE Atlantic	Regurgitates
Fin whale	Krill	Positive interactions and similar env preferences	1	Evidence in Víkingsson (1997) and Bravo Rebolledo *et al.* (2016)	NE Atlantic	Stomach and intestinal content
Fin whale	Mueller's pearlside	Positive interactions and similar env preferences	1	Evidence in Bravo Rebolledo *et al.* (2016)	NE Atlantic	Stomach and intestinal content
Great shearwater	Boarfish	Positive interactions causing aggregation	0	No evidence in Ronconi et al. (2010a)	NW Atlantic	Stable isotopes and fatty acids signatures
Great shearwater	Krill	Positive interactions causing aggregation	1	Evidence in Ronconi et al. (2010a)	NW Atlantic	Stable isotopes and fatty acids signatures
Great skua	Boarfish	Similar habitat preferences	0	No evidence in Bearhop *et al.* (2001) ,Votier *et al.* (2003), Käkelä *et al.* (2006) or Votier *et al.* (2007).	NE Atlantic	Stable isotopes, pellets, regurgitates and fatty acids signatures

Great skua	Med. Horse mackerel	Positive interactions causing aggregation	0	No evidence in Bearhop *et al.* (2001) ,Votier *et al.* (2003), Käkelä *et al.* (2006) or Votier *et al.* (2007)	NE Atlantic	Stable isotopes, pellets, regurgitates and fatty acids signatures
Great skua	Atlantic mackerel	Similar habitat preferences	1	Evidence in Bearhop *et al.* (2001) ,Votier *et al.* (2003), Käkelä *et al.* (2006) and Votier *et al.* (2007).	NE Atlantic	Stable isotopes, pellets, regurgitates and fatty acids signatures
Great skua	Chub mackerel	Positive interactions and similar env preferences	1	Evidence in Bearhop *et al.* (2001) ,Votier *et al.* (2003), Käkelä *et al.* (2006) and Votier *et al.* (2007). Considered equal to Atlantic mackerel.	NE Atlantic	Stable isotopes, pellets, regurgitates and fatty acids signatures
Great skua	European pilchard	Similar habitat preferences	0	No evidence but very similar to sprat documented in Votier *et al.* (2007)	NE Atlantic	Pellets
Great skua	European sprat	Similar habitat preferences	1	Evidence in Votier *et al.* (2007)	NE Atlantic	Pellets
Lesser black-backed gull	Med. Horse mackerel	Similar habitat preferences	1	Evidence in Kubetzki and Garthe (2003). Considered equal to Atlantic horse mackerel	NE Atlantic	Pellets and faecal samples

Manx shearwater	Boarfish	Similar habitat preferences	0	No evidence in Thompson (1987) or Gray and Hamer (2001)	NE Atlantic	Radiotracking, regurgitates and stomach contents of corpses.
Northern gannet	Boarfish	Similar habitat preferences	0	No evidence in Hamer *et al*. (2000), Lewis *et al*. (2003) or Hamer *et al*. (2007)	NE Atlantic	Regurgitates
Northern gannet	Med. Horse mackerel	Positive interactions and similar env preferences	1	Evidence in Lewis *et al*. (2003) and Hamer *et al*. (2007). Considered equal to Atlantic horse mackerel.	NE Atlantic	Regurgitates
Northern gannet	Horse mackerel	Positive interactions and similar env preferences	1	Evidence in Lewis *et al*. (2003) and Hamer *et al*. (2007).	NE Atlantic	Regurgitates
Northern gannet	Atlantic mackerel	Similar habitat preferences	1	Evidence in Hamer *et al*. (2000), Lewis *et al*. (2003) and Hamer *et al*. (2007).	NE Atlantic	Regurgitates
Northern gannet	Chub mackerel	Positive interactions and similar env preferences	1	Evidence in Hamer *et al*. (2000), Lewis *et al*. (2003) and Hamer *et al*. (2007). Considered equal to Atlantic mackerel.	NE Atlantic	Regurgitates
Northern gannet	European pilchard	Positive interactions and similar env preferences	0	No evidence although other clupeids have been documented in Hamer *et al*. (2000), Lewis *et al*. (2003) and Hamer *et al*. (2007)	NE Atlantic	Regurgitates

Northern gannet	European sprat	Similar habitat preferences	1	Evidence in Hamer *et al*. (2000), Lewis *et al*. (2003) and Hamer *et al*. (2007).	NE Atlantic	Regurgitates
Northern gannet	Blue whiting	Similar habitat preferences	0	Although other gadoids have been documented in Lewis *et al*. (2003) and Hamer *et al*. (2007).	NE Atlantic	Regurgitates
Sabine's gull	Med. Horse mackerel	Positive interactions and similar env preferences	0	No specific evidence was found in Blomqvist and Elander (1981). Only references to small fish.	Arctic	General review
Sabine's gull	Krill	Similar habitat preferences	0	No specific evidence was found in Blomqvist and Elander (1981). Only references to small fish.	Arctic	General review
Sandwich tern	Krill	Similar habitat preferences	0	No evidence in Stienen et al. (2000)	NE Atlantic	Continuous observation on food provisioning
Sandwich tern	Mueller's pearlside	Similar habitat preferences	0	No evidence in Stienen et al. (2000)	NE Atlantic	Continuous observation on food provisioning
Sooty shearwater	Boarfish	Similar habitat preferences	0	No evidence in Ronconi et al. (2010a)	NW Atlantic	Stable isotopes and fatty acids signatures
Sooty shearwater	Med. Horse mackerel	Similar habitat preferences	0	No evidence in Ronconi et al. (2010a)	NW Atlantic	Stable isotopes and fatty acids signatures

Sooty shearwater	Atlantic mackerel	Similar habitat preferences	1	Evidence in Ronconi et al. (2010a)	NW Atlantic	Stable isotopes and fatty acids signatures
Striped dolphin	Krill	Positive interactions and similar env preferences	1	Evidence in Hassani *et al.* (1997) and Ringelstein *et al.* (2006)	NE Atlantic	Stomach contents of caught animals
Striped dolphin	Mueller's pearlside	Similar habitat preferences	1	Evidence in Ringelstein *et al.* (2006) and Spitz *et al.* (2006).	NE Atlantic	Stomachs of caught and stranded animals
Yellow-legged gull	European anchovy	Similar habitat preferences	1	Evidence. in Calado *et al.* (2018).	NE Atlantic	Pellets and stable isotopes
Yellow-legged gull	Med. Horse mackerel	Similar habitat preferences	1	Evidence for *Trachurus spp.* Calado *et al.* (2018).	NE Atlantic	Pellets and stable isotopes
Yellow-legged gull	Horse mackerel	Similar habitat preferences	1	Evidence in Alonso *et al.* (2015) and Calado *et al.* (2018).	NE Atlantic	Regurgitates, pellets and stable isotopes
Yellow-legged gull	Atlantic mackerel	Similar habitat preferences	1	Evidence for *Scomber spp.* in Alonso *et al.* (2015) and Calado *et al.* (2018).	NE Atlantic	Regurgitates, pellets and stable isotopes
Yellow-legged gull	Chub mackerel	Similar habitat preferences	1	Evidence in Pedro *et al.* (2013)	NE Atlantic	Regurgitates, pellets and stable isotopes
Yellow-legged gull	European pilchard	Similar habitat preferences	1	Evidence in Alonso *et al.* (2015) Calado *et al.* (2018).	NE Atlantic	Regurgitates, pellets and stable isotopes

Yellow-legged gull	European sprat	Similar habitat preferences	0	No evidence in Pedro *et al*. (2013), Alonso *et al*. (2015) or Calado *et al*. (2018).	NE Atlantic	Regurgitates, pellets and stable isotopes
Yellow-legged gull	Blue whiting	Similar habitat preferences	1	Evidence in Alonso *et al*. (2015)	NE Atlantic	Regurgitates and pellets
Negative associations						
Great shearwater	European sprat	Negative interaction causing segregation	0	No evidence in Ronconi et al. (2010a) but evidence for another clupeid (herring).	NW Atlantic	Stable isotopes and fatty acids signatures
Great shearwater	Blue whiting	Negative interaction causing segregation	0	No evidence in Ronconi et al. (2010a)	NW Atlantic	Stable isotopes and fatty acids signatures
Sooty shearwater	European sprat	Negative interaction causing segregation	0	No evidence in Ronconi et al. (2010a) but evidence for another clupeid (herring).	NW Atlantic	Stable isotopes and fatty acids signatures
Sooty shearwater	Blue whiting	Negative interactions despite shared env preferences	0	No evidence in Ronconi et al. (2010a)	NW Atlantic	Stable isotopes and fatty acids signatures
Fin whale	European sprat	Negative interactions and habitat filtering causing segregation	0	No evidence in Víkingsson (1997) or Bravo Rebolledo *et al*. (2016) but very similar to herring documented in Aguilar and García-Vernet (2018)	NE Atlantic, worldwide	Stomach and intestinal content; general review

Fin whale	European anchovy	Negative interaction causing segregation	0	No evidence in Víkingsson (1997) and Bravo Rebolledo *et al.* (2016) but suggested by García-Barón et al. (2019)	NE Atlantic	Stomach and intestinal content
Fin whale	Horse mackerel	Negative interactions and habitat filtering causing segregation	0	No evidence in Víkingsson (1997), Bravo Rebolledo *et al.* (2016) or Aguilar and García-Vernet (2018)	NE Atlantic, worldwide	Stomach and intestinal content; general review
Fin whale	Med. horse mackerel	Negative interactions and habitat filtering causing segregation	0	No evidence in Víkingsson (1997), Bravo Rebolledo *et al.* (2016) or Aguilar and García-Vernet (2018)	NE Atlantic, worldwide	Stomach and intestinal content; general review
Fin whale	Atlantic mackerel	Negative interactions and habitat filtering causing segregation	1	Evidence in Aguilar and García-Vernet (2018)	Worldwide	General review
Fin whale	Boarfish	Negative interactions and habitat filtering causing segregation	0	No evidence in Víkingsson (1997), Bravo Rebolledo *et al.* (2016) or Aguilar and García-Vernet (2018)	NE Atlantic. worldwide	Stomach and intestinal content; general review
Fin whale	Blue whiting	Negative interactions and habitat filtering causing segregation	1	Evidence in Aguilar and García-Vernet (2018)	Worldwide	General review
Fin whale	Chub mackerel	Negative interactions and habitat filtering causing segregation	1	Evidence in Aguilar and García-Vernet (2018)	Worldwide	General review
Fin whale	European pilchard	Negative interactions and habitat filtering causing segregation	0	No evidence in Víkingsson (1997), Bravo Rebolledo *et al.* (2016) or Aguilar and García-Vernet (2018)	NE Atlantic Worldwide	Stomach and intestinal content; general review

Cory's shearwater	Chub mackerel	Negative interactions and habitat filtering causing segregation	1	Evidence in Granadeiro *et al*. (1998) and for *Scomber sp*. in Paiva et al. (2010b)	NE Atlantic	Regurgitates and stable isotopes
Cory's shearwater	Horse mackerel	Negative interactions and habitat filtering causing segregation	1	Evidence in Paiva et al. (2010b)	NE Atlantic	Stable isotopes
Cory's shearwater	Med. horse mackerel	Negative interaction causing segregation	1	Evidence in Paiva et al. (2010b). Considered equal to Atlantic horse mackerel.	NE Atlantic	Stable isotopes
Cory's shearwater	European sprat	Negative interactions and habitat filtering causing segregation	0	No evidence in Granadeiro *et al*. (1998), Paiva *et al*. (2010) or Neves et al. (2012).	NE Atlantic	Regurgitates and stable isotopes
Cory's shearwater	European anchovy	Negative interactions and habitat filtering causing segregation	0	No evidence in Granadeiro *et al*. (1998), Paiva *et al*. (2010) or Neves et al. (2012).	NE Atlantic	Regurgitates and stable isotopes
Cory's shearwater	Atlantic mackerel	Negative interactions and habitat filtering causing segregation	1	Evidence for *Scomber sp*. in Paiva et al. (2010b)	NE Atlantic	Stable isotopes
Cory's shearwater	Blue whiting	Negative interactions and habitat filtering causing segregation	0	No evidence in Granadeiro *et al*. (1998), Paiva *et al*. (2010) or Neves et al. (2012).	NE Atlantic	Regurgitates and stable isotopes
Cory's shearwater	European pilchard	Negative interactions and habitat filtering causing segregation	1	Evidence in Paiva et al. (2010b)	NE Atlantic	Stable isotopes
European storm-petrel	Krill	Negative interaction causing segregation	1	Evidence for *euphasiacea* in D'Elbee and Hemery (1998)	NE Atlantic	Regurgitates

European storm-petrel	Blue whiting	Negative interaction causing segregation	0	No evidence in D'Elbee and Hemery (1998) or Thomas et al. (2006)	NE Atlantic	Regurgitates
Lesser black-backed gull	European anchovy	Negative interaction causing segregation	1	Evidence for clupeids in Kubetzki and Garthe (2003)	NE Atlantic	Pellets and faecal samples
Lesser black-backed gull	Chub mackerel	Negative interaction despite shared env preferences	0	No evidence for clupeids in Kubetzki and Garthe (2003)	NE Atlantic	Pellets and faecal samples
Lesser black-backed gull	Atlantic mackerel	Negative interaction despite shared env preferences	0	No evidence for clupeids in Kubetzki and Garthe (2003)	NE Atlantic	Pellets and faecal samples
Lesser black-backed gull	Horse mackerel	Negative interaction despite shared env preferences	1	Evidence for clupeids in Kubetzki and Garthe (2003)	NE Atlantic	Pellets and faecal samples
Lesser black-backed gull	Mueller's pearlside	Negative interactions and habitat filtering causing segregation	0	No evidence for clupeids in Kubetzki and Garthe (2003)	NE Atlantic	Pellets and faecal samples
Lesser black-backed gull	Boarfish	Negative interaction causing segregation	0	No evidence for clupeids in Kubetzki and Garthe (2003)	NE Atlantic	Pellets and faecal samples
Lesser black-backed gull	European pilchard	Negative interactiosn despite shared env preferences	1	Evidence for clupeids in Kubetzki and Garthe (2003)	NE Atlantic	Pellets and faecal samples
Yellow-legged gull	Krill	Negative interaction causing segregation	0	No evidence in Pedro *et al.* (2013), Alonso *et al.* (2015) and Calado *et al.* (2018).	NE Atlantic	Pellets and faecal samples

Yellow-legged gull	Mueller's pearlside	Negative interactions and habitat filtering causing segregation	0	No evidence in Pedro *et al.* (2013), Alonso *et al.* (2015) and Calado *et al.* (2018).	NE Atlantic	Pellets and faecal samples
Yellow-legged gull	Boarfish	Negative interaction causing segregation	1	Evidence in Pedro *et al.* (2013), Alonso *et al.* (2015) and Calado *et al.* (2018).	NE Atlantic	Pellets and faecal samples
Northern gannet	Krill	Negative interactions and habitat filtering causing segregation	0	No evidence in Hamer *et al.* (2000), Lewis *et al.* (2003) or Hamer *et al.* (2007).	NE Atlantic	Regurgitates
Balearic shearwater	Krill	Negative interactions and habitat filtering causing segregation	1	Evidence in Louzao et al. (2015b)	Mediterranean Sea	Regurgitation
Balearic shearwater	Mueller's pearlside	Negative interactions and habitat filtering causing segregation	0	No evidence in Arcos *et al.* (2000), Navarro *et al.* (2009), Louzao et al. (2015b) or Meier *et al.* (2015)	NE Atlantic and Mediterranean Sea	Experimental discards and stable isotopes
Manx shearwater	European sprat	Negative interactiosn despite shared env preferences	1	Evidence in Thompson (1987)	NE Atlantic	Regurgitates and stomach contents of corpses.
Manx shearwater	Blue whiting	Negative interaction causing segregation	0	No evidence in Thompson (1987) or Gray and Hamer (2001)	NE Atlantic	Radiotracking, regurgitates and stomach contents of corpses.
Common tern	Krill	Negative interactiosn despite shared env preferences	0	No evidence in Monteiro et al. (1998), Granadeiro et al. (2002) or Robertson et al. (2016)	NE Atlantic	Nest observations, regurgitations and pellets

Arctic jaeger	European sprat	Negative interaction causing segregation	0	No evidence in Jones et al. (2010). Relies heavily on kleptoparasitism.	NE Atlantic	Pellets
Arctic jaeger	Blue whiting	Negative interaction causing segregation	0	No evidence in Jones et al. (2010). Relies heavily on kleptoparasitism.	NE Atlantic	Pellets
Great skua	Krill	Negative interactions and habitat filtering causing segregation	0	No evidence in Bearhop *et al.* (2001) ,Votier *et al.* (2003), Käkelä *et al.* (2006) or Votier *et al.* (2007).	NE Atlantic	Stable isotopes, pellets, regurgitates and fatty acids signatures
Great skua	Blue whiting	Negative interactiosn despite shared env preferences	1	Evidence Votier *et al.* (2003) and Käkelä *et al.* (2006)	NE Atlantic	Stable isotopes, pellets, regurgitates and fatty acids signatures
Great skua	Mueller's pearlside	Negative interactions and habitat filtering causing segregation	0	No evidence in Bearhop *et al.* (2001) ,Votier *et al.* (2003), Käkelä *et al.* (2006) or Votier *et al.* (2007).	NE Atlantic	Stable isotopes, pellets, regurgitates and fatty acids signatures
Sandwich tern	Atlantic mackerel	Negative interactions and habitat filtering causing segregation	0	No evidence in Stienen et al. (2000)	NE Atlantic	Continuous observation on food provisioning
Sandwich tern	Blue whiting	Negative interactions and habitat filtering causing segregation	0	No evidence but others gadoids have been documented in Stienen et al. (2000)	NE Atlantic	Continuous observation on food provisioning

Sandwich tern	European sprat	Negative interactions and habitat filtering causing segregation	1	Evidence in Stienen et al. (2000)	NE Atlantic	Continuous observation on food provisioning
Sandwich tern	Chub mackerel	Negative interactions and habitat filtering causing segregation	0	No evidence in Stienen et al. (2000)	NE Atlantic	Continuous observation on food provisioning
Sandwich tern	Boarfish	Negative interactions and habitat filtering causing segregation	0	No evidence in Stienen et al. (2000)	NE Atlantic	Continuous observation on food provisioning
Sandwich tern	European pilchard	Negative interactions and habitat filtering causing segregation	0	No evidence but very similar to sprat documented in Stienen et al. (2000)	NE Atlantic	Continuous observation on food provisioning
Sabine's gull	Atlantic mackerel	Negative interaction causing segregation	0	No specific evidence was found in Blomqvist and Elander (1981). Only references to small fish. But suggested by Stenhouse et al. (2012).	Atlantic & Arctic	Tracking; general review
Sabine's gull	European sprat	Negative interaction causing segregation	0	No specific evidence was found in Blomqvist and Elander (1981). Only references to small fish. But very similar to anchovy suggested by Stenhouse et al. (2012).	Atlantic & Arctic	Tracking; general review
Sabine's gull	Blue whiting	negative interactiosn despite shared env preferences	0	No specific evidence was found in Blomqvist and Elander (1981). Only references to small fish.	Arctic	general review

Great shearwater	Med. horse mackerel	segregation explained by the environment	0	No evidence in Ronconi et al. (2010a)	NW Atlantic	Stable isotopes and fatty acids signatures
Great shearwater	Horse mackerel	segregation explained by the environment	0	No evidence in Ronconi et al. (2010a)	NW Atlantic	Stable isotopes and fatty acids signatures
Great shearwater	European anchovy	segregation explained by the environment	0	No evidence but very similar to herring documented in Ronconi et al. (2010a)	NW Atlantic	Stable isotopes and fatty acids signatures
Sooty shearwater	Mueller’s pearlside	segregation explained by the environment	0	No evidence in Ronconi et al. (2010a)	NW Atlantic	Stable isotopes and fatty acids signatures
Cory’s shearwater	Boarfish	segregation explained by the environment	1	Evidence in Granadeiro *et al.* (1998), Paiva *et al.* (2010)	NE Atlantic	Regurgitates and stable isotopes
Common dolphin	Horse mackerel	segregation explained by the environment	1	Evidence for *Trachurus spp*. in Meynier et al. (2008)	NE Atlantic	Stomach content of stranded animals
European storm-petrel	Mueller’s pearlside	segregation explained by the environment	0	No evidence for Mueller’s pearlside but for myctophids in D'Elbee and Hemery (1998)	NE Atlantic	Regurgitates
Northern gannet	Mueller’s pearlside	segregation explained by the environment	0	No evidence in Hamer *et al.* (2000), Lewis *et al.* (2003) or Hamer *et al.* (2007).	NE Atlantic	Regurgitates
Manx shearwater	Krill	segregation explained by the environment	0	No evidence in Thompson (1987) or Gray and Hamer (2001)	NE Atlantic	Radiotracking, regurgitates and stomach contents of corpses.

Manx shearwater	Mueller's pearlside	segregation explained by the environment	0	No evidence in Thompson (1987) or Gray and Hamer (2001)	NE Atlantic	Radiotracking, regurgitates and stomach contents of corpses.
Manx shearwater	European anchovy	segregation explained by the environment	0	No evidence but very similar to sprat documented in Thompson (1987)	NE Atlantic	Regurgitates and stomach contents of corpses.
Striped dolphin	Atlantic mackerel	segregation explained by the environment	0	No evidence in Hassani *et al.* (1997), Ringelstein *et al.* (2006) or Spitz *et al.* (2006).	NE Atlantic	Stomach content of caught and stranded animals
Striped dolphin	Blue whiting	segregation explained by the environment	1	Evidence in Spitz *et al.* (2006).	NE Atlantic	Stomach content of stranded animals
Striped dolphin	European sprat	segregation explained by the environment	0	No evidence in Hassani *et al.* (1997), Ringelstein et al. (2006) or Spitz et al. (2006)	NE Atlantic	Stomach content of caught and stranded animals
Striped dolphin	Chub mackerel	segregation explained by the environment	0	No evidence in Hassani *et al.* (1997), Ringelstein *et al.* (2006) or Spitz et al. (2006)	NE Atlantic	Stomach content of caught and stranded animals
Striped dolphin	Horse mackerel	segregation explained by the environment	0	No evidence in Hassani *et al.* (1997), Ringelstein *et al.* (2006) or Spitz et al. (2006)	NE Atlantic	Stomach content of caught and stranded animals
Striped dolphin	Boarfish	segregation explained by the environment	0	No evidence in Hassani *et al.* (1997), Ringelstein *et al.* (2006) or Spitz et al. (2006)	NE Atlantic	Stomach content of caught and stranded animals

Striped dolphin	European pilchard	segregation explained by the environment	0	No evidence in Hassani *et al.* (1997), Ringelstein *et al.* (2006) or Spitz et al. (2006)	NE Atlantic	Stomach content of caught and stranded animals
Common tern	Horse mackerel	segregation explained by the environment	1	Evidence for *T.picturatus* in Monteiro et al. (1998) and Granadeiro et al. (2002).	NE Atlantic	Regurgitations and pellets
Common tern	European pilchard	segregation explained by the environment	0	No evidence but very similar to sprat documented in Robertson et al. (2016)	NE Atlantic	Nest observations
Arctic jaeger	European anchovy	segregation explained by the environment	0	No evidence in Jones et al. (2010). Relies heavily on kleptoparasitism.	NE Atlantic	Pellets
Arctic jaeger	Horse mackerel	segregation explained by the environment	0	No evidence in Jones et al. (2010). Relies heavily on kleptoparasitism.	NE Atlantic	Pellets
Great skua	European anchovy	segregation explained by the environment	0	No evidence in Bearhop *et al.* (2001) ,Votier *et al.* (2003) or Votier *et al.* (2007) but suggested by Käkelä *et al.* (2006)	NE Atlantic	Fatty acid signatures and regurgitates
Sandwich tern	Horse mackerel	segregation explained by the environment	0	No evidence but very similar to sprat documented in Stienen et al. (2000)	NE Atlantic	Continuous observation on food provisioning
Sabine's gull	Horse mackerel	segregation explained by the environment	0	No specific evidence was found in Blomqvist and Elander (1981). Only references to small fish.	Arctic	General review

CHAPTER 2 – APPENDIX B

Appendix B1. Pelagic prey

Table B1.1. Potential prey species for each seabird based on trophic evidences (stomach content and stable isotopes) found in the literature. For each relationship, the bibliographic reference is cited.

	Mackerel	*Sardine*	*Horse mackerel*	*Anchovy*	*Sprat*	*Mueller's pearlside*
Cory's	Paiva et al. (2010b)	Paiva et al. (2010b)	Paiva et al. (2010b)			Neves et al. (2012)
Great	Ronconi et al. (2010a)					
Sooty	Ronconi et al. (2010a)					
Manx					Thompson (1987)	
Balearic	Meier et al. (2017)	Meier et al. (2017)	Meier et al. (2017)	Meier et al. (2017)		

Table B1.2. Depth intervals (m) used to group the prey acoustic data each year. Depths refer to the distance from the transducer face, which are located at 3 m and 6.5 m from sea surface in R/V EB and RM, respectively. But in the latter, a lateral-looking transducer and higher frequency transducers of 200 kHz (with a near field of about 1 m) are used to increase the coverage at the upper layers of the water column and monitor shallow fish aggregations. This way we achieve a coverage from around 7-8 m depth from sea surface in both vessels.

	2013	***2014***	***2015***	***2016***	***2017***
Depth intervals	5-7	-15	5-10	5-15	5-15
	7-9	15-25	10-25	15-25	15-25
	9-11	25-35	25-40	25-35	25-35
	11-15	35-50	40-50	35-50	35-50
	15-25	50-75	50-75	50-75	50-75
	25-35	75-100	75-100	75-100	75-100
	35-45	100-125	100-125	100-125	100-125
	45-70	125-150	125-150	125-150	125-150
	70-100	150-175	150-175	150-200	150-200
	100-200	175-200	175-300	200-300	200-400

Appendix B2. Interpolation of the explanatory variables

Oceanographic data: Optimal Statistical Interpolation

Variables such as temperature (T), salinity (SAL) or density can be directly inferred from CTD samples collected on oceanographic surveys. However, due to the CTD sampling coverage, interpolation is needed to obtain horizontal fields of these variables. In our case, we used the Optimal Statistical Interpolation (OSI) scheme described in Gomis et al. (2001) in a regular 33 × 54 grid, covering all the study area with regular node distances of 0.15 × 0.15°. A Gaussian function for the correlation model between observations (assuming 2D isotropy) was set up, with a correlation length scale of 25-km, chosen according to the dynamic heights profiles (DYN; derived from density values) correlation statistics obtained at different depths. The noise-to-signal (NTS) variance ratio used for the analysis of SST, SAL and DYN were: 0.005, 0.05, and 0.01, respectively. This ratio was defined as the variance of the observational error divided by the variance of the interpolated field (the latter referring to the deviations between observations and the mean field). This parameter allows the inclusion in the analysis of an estimation of the observational error and adjustments of the weight of the observations on the analysis (the larger the NTS parameter, the smaller the influence of the observation). Then, after the interpolation, all fields were spatially smoothed, with an additional low-pass filter with a cut-off length scale of 30 km to avoid aliasing errors due to unresolved structures (due to the limited resolution enabled by the CTD sampling).

Several methods can be used for interpolating oceanographic data, although OSI has been proved to be advantageous over traditional distance-weighting methods (Gomis et al. 2001). Its main characteristics are:

1) It takes into account the correlation between nearby observations, instead of considering all observations independent
2) The weights used are chosen so that the expected error of the estimate is a minimum in the least squares sense, and the estimate itself is unbiased
3) The output field is smoothed according to a given measure of observational errors.

As a result, the OSI scheme is a good option to obtain an accurate linear unbiased estimate of a field from a set of arbitrarily distributed observations (Gomis et al. 2001) and it is, therefore, suitable to deal with CTD data from JUVENA oceanographic surveys.

Prey data: Universal kriging

In the echo-integration method, samples are taken continuously along the ship's sailing track, so that the sample locations are serially correlated (Petitgas 1993). As a result, they are rarely adaptable to the random sampling theory (which would allow for direct estimation from the samples) and instead, require modelling the spatial correlation through a model of spatial covariance (Petitgas 2001). Geostatistics is based on the possibility that a spatial structure can be inferred and that is why it constitutes a relevant tool for providing abundance estimates of fish stocks (Petitgas 1993).

Within geostatistics, the density surface sampled at a certain number of locations is interpreted as one outcome of a stochastic spatial process, while kriging is the mathematical algorithm that estimates the values of that process by performing a weighted average of the sampled values. The weight assigned to the data are appropriately determined according to the structure and sampling configuration so that the estimates are unbiased, and the estimation of variance is minimised. In this way, kriging techniques allow to reconstruct the process at unsampled locations without bias, and with minimum variance (Petitgas 1996, 2009).

Kriging techniques, therefore, can provide reliable estimates of fish abundance in surveys performed along parallel transect, such as ours, and that is why they are widely used between fisheries acousticians (Petitgas 1997, Simard et al. 2002, Doray et al. 2008). Universal kriging is just an extension of Ordinary kriging used when the data has a strong trend or drift. Such drift can result from the response of fish concentration to explanatory environmental parameters (e.g., a gradient in fish density from coast to off-shore depending on bottom depth) (Petitgas 2009) and it was already explored in the Bay of Biscay by Petitgas (1997).

For that reason, we applied universal kriging to the biomasses of our prey species. We first categorized the original biomasses (tonnes) of the seven prey species using 10 cm length classes and then log-transformed the resulting biomass categories. This way, we obtained more homogenously distributed data ("Gaussian like" distributions), that prevent us from dealing with the alternance of high abundance peaks and very low abundances of the raw data. Finally, we interpolated the prey data using universal kriging in *automap* package (Hiemstra et al. 2009) over a standard grid covering the study area (latitudinal range: 43.2-48°N; longitudinal range: 1-8°W) with a cell size of 0.1° spatial resolution.

Appendix B3. Grouping seabird species

To determine whether seabirds could be analysed in groups instead of individually, we made a simple test grouping large (Cory, great and sooty) and small (Balearic and Manx) species. For each group, we fitted 1) two separate detection functions for each species, whose AIC scores were summed, 2) a joint detection function combining both species and 3) a joint detection function combining both species and including species as covariate. Hazard rate and half normal functions with no adjustments were fitted in each of the groups using *Distance* package (Miller 2020). Best function was selected based on the lowest AIC (Sakamoto et al. 1986, Guisan & Zimmermann 2000) (Table S3.1 and Table S3.2). When functions were within 2 points of AIC (ΔAIC<2), they were considered statistically equivalent and the function with the smaller number of parameters was chosen instead based on parsimony principle (Arnold 2010).

Table B3.1. *Comparison between the individually performed detection functions and the joint ones for small shearwaters. Selected function is indicated in bold.*

	Truncation distance (m)	*Num. sightings*	*Detection function*	*AIC*	*ΔAIC*	*Num. parameters*
Balearic and Manx shearwaters separately	362	227	Half normal	2571,014	1,435	2
Balearic and Manx shearwaters together	**362**	**227**	**Half normal**	**2569,579**	**0**	**1**
Balearic and Manx shearwaters together + species as covariate	362	227	Half normal	2571,014	1,435	2

Table B3.2. *Comparison between the individual detection functions and the joint ones for large shearwaters. Selected function is indicated in bold.*

	Truncation distance (m)	*Num. sightings*	*Detection function*	*AIC*	*ΔAIC*	*Num. parameters*
Great, sooty and Cory's shearwaters separately	**543**	**1332**	**Hazard rate**	**15727,19**	**0**	**6**
Great, sooty and Cory's shearwaters together	543	1332	Hazard rate	15730,56	3,37	2
Great, sooty and Cory's shearwaters + species as covariate	543	1332	Hazard rate	15731,11	3,92	3

In the case of small shearwaters, results showed that there were not significant differences among the three detections functions in terms of AIC score. However, small shearwaters were decided to group together based on the smaller number of parameters of the second detection function (Table S3.1). In the case of large shearwaters, in contrast, the AIC score did not support the joint approach (Table S3.2). A second aggrupation composed only by two large shearwater species (Great-Cory, Great-Sooty, Cory-Sooty) was then tried following the same approach. Only the function formed by the Great and the Cory's shearwaters enabled their analysis together based on the parsimony principle (Table S3.3). So, in the end we had Balearic-Manx and Great-Cory's shearwaters together and the sooty shearwater alone.

Table B3.3. *Comparison between the individual detection functions and the joint ones for great and Cory's shearwaters. Selected function is indicated in bold.*

	Truncation distance (m)	*Num. sightings*	*Detection function*	*AIC*	*ΔAIC*	*Num. parameters*
Great and Cory's shearwaters separately	561	1053	Hazard rate	12502,816	0,696	4
Great and Cory's shearwaters together	**561**	**1053**	**Hazard rate**	**12502,99**	**0,87**	**2**
Great and Cory's shearwaters together + species as covariate	561	1053	Hazard rate	12502,12	0	3

Appendix B4. Fitting detection functions

Table B4.1. Main properties of the environmental descriptors included as covariates in the detection functions.

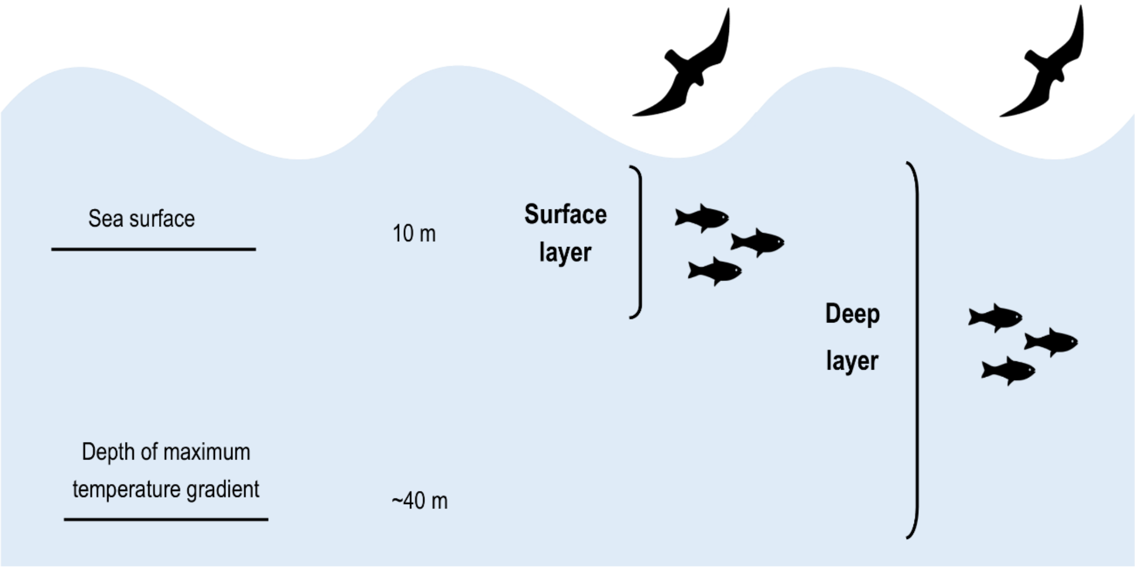
Variable	***Range***	***Meaning***
Beaufort sea-state	0-8	**0:** less than 1 knot; **1:** 1-3 knots; **2:** 4-6 knots; **3:**7-10 knots; **4:**11-16 knots; **5:**17-21 knots, **6:** 22-27 knots.
Visibility	1-4	**1:** 5-10 miles; **2:** 2-5miles; **3:** 1-2 miles; **4:** <1mile
Cloudiness	1-8	**1:** sky completely clear; **8:** sky completely overcast
Glare intensity	1-4	**1:** none**; 2:** faint; **3:** medium**; 4** strong
Observation conditions	Excellent, good, medium, bad	**1:** excellent; **2:** good**; 3:** medium; **4** bad

Table B4.2. Example of how forward selection was performed for each detection function. In all cases, covariates were introduced in the detection function until the lowest AIC was obtained. When functions were within 2 points of AIC (ΔAIC<2), they were considered statistically equivalent and the function with the smaller number of parameters was chosen instead based on parsimony principle (Arnold 2010).

	Key functions	*Truncation distance*	*Covariates*	*AIC*	*ΔAIC*	*Num. parameters*
Balearic & Manx shearwaters	Half normal	362	No covariates	2569.58	19.06	1
			Beaufort	2562.65	12.13	2
			Beaufort + Year	2555.29	4.7	3
			Beaufort + Year + general conditions	**2550.59**	**0.07**	**4**
			Beaufort + Year + general conditions + glare	2550.52	0	5
Great & Cory's shearwaters	Hazard rate	561	No covariates	12503	111.8	2
			Year	**12392.10**	**0.9**	**3**
			Year + Glare	12391.20	0	4
Sooty shearwater	Half normal	479	No covariates	3201.27	2.58	1
			Year	**3198.69**	**0**	**2**
			Year + general conditions	3200.51	1.82	3

Appendix B5. Surface and deep layers

Figure B5.1. Graphic description of the two vertical layers used in this study to integrate predators diving capacity, prey availability and environmental variability. The depth of maximum temperature gradient shown here (DTG ~ 40 m) refers to an approximate value; real values of DTG can be seen in Appendix B6.

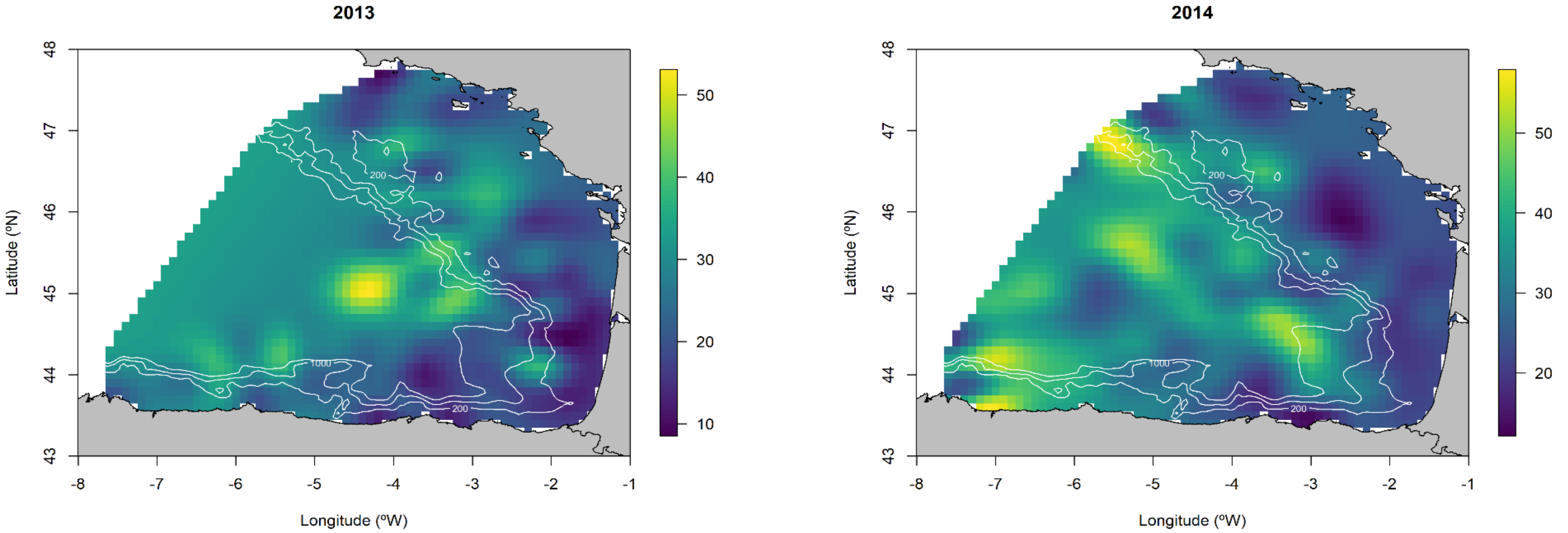


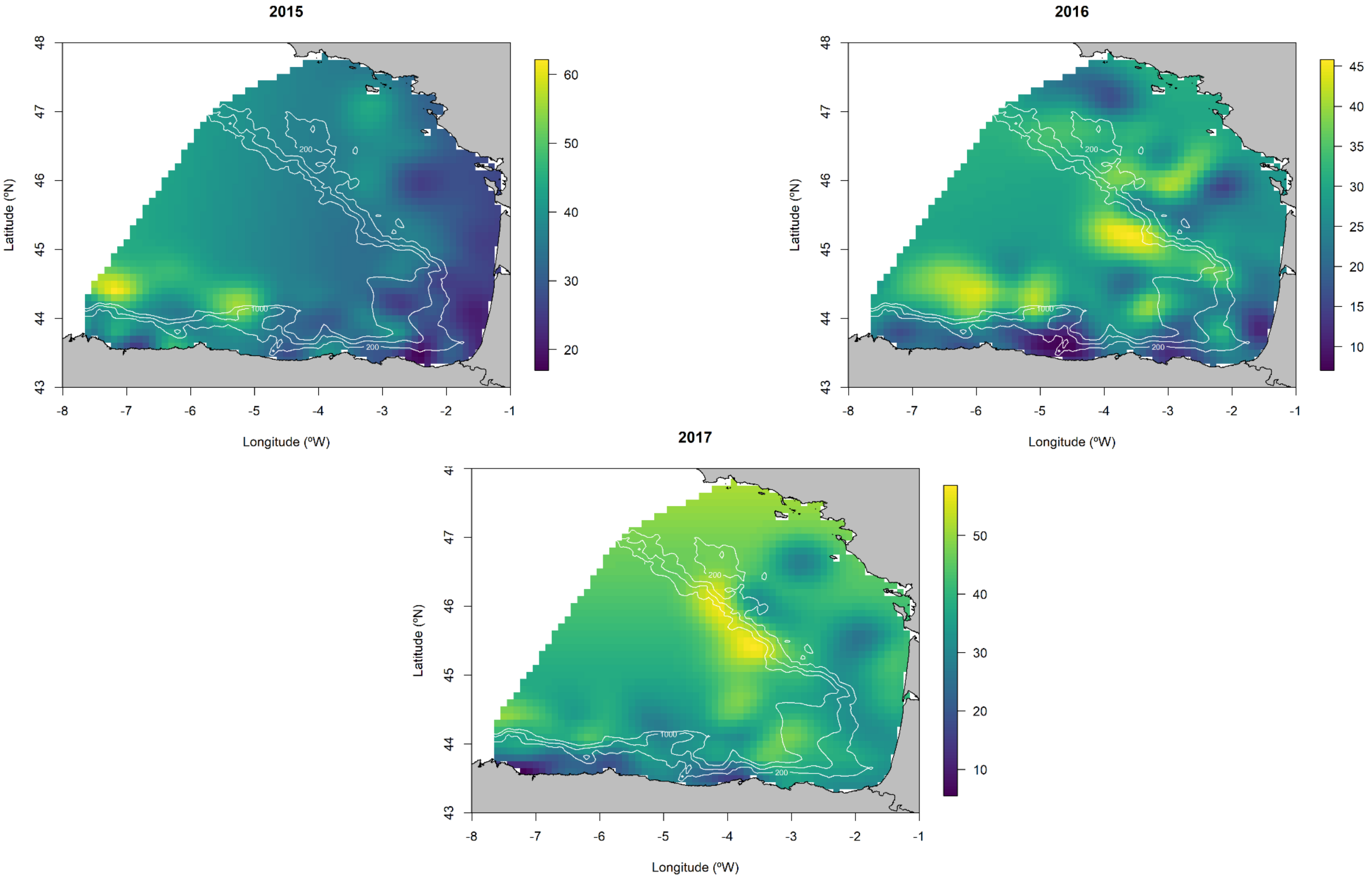
Appendix B6. Interannual variability of the depth of maximum temperature gradient (DTG)

Table B6.1. Minimum, maximum, mean and median values of the DTG along the study period.

Years	*Min. depth (m)*	*Max. depth (m)*	*Mean depth (m)*	*Median depth (m)*
2013	8,71	53,66	29,40	30,46
2014	12,20	58,94	33,83	34,99
2015	17,21	87,33	39,08	38,55
2016	6,38	46,26	29,04	30,02
2017	4,88	59,27	41,61	42,28

Figure B6.1. Spatial variability of the DTG along years.




2015
2016
2017
Latitude (ºN)
Longitude (ºW)
43
44
45
46
47
48
-8
-7
-6
-5
-4
-3
-2
-1
200
1000
20
30
40
50
60
10
15
20
25
30
35
40
45
10
20
30
40
50

Appendix B7. PCA results

The first three axes of the PCA were selected as main explanatory axes for both surface and deep layers since they explained the 70% of the variability (Figure B7.1). Both in surface and deep conditions, the first axis comprised a negative relationship with small-medium sardine, sprat, mackerel and anchovy (adult and juvenile) distributed along the north-east part of the French coast, i.e. from the Gironde estuary (~45°) to Belle-Ille (~47°) (Fig B7.2 and B7.3). The second axis also showed a negative relation, but with small horse mackerel and juvenile of anchovy that were mainly located in the shelf breaks of the southern and south-eastern part of the BoB. The third axis, in contrast, was positively related with medium-big horse mackerel and mackerel and associated to the Gironde estuary area (Fig B7.2 and B7.3).

Figure B7.1. The percentage of explained variances for all the dimensions found by the PCA analysis in a) surface layer and b) deep layer.

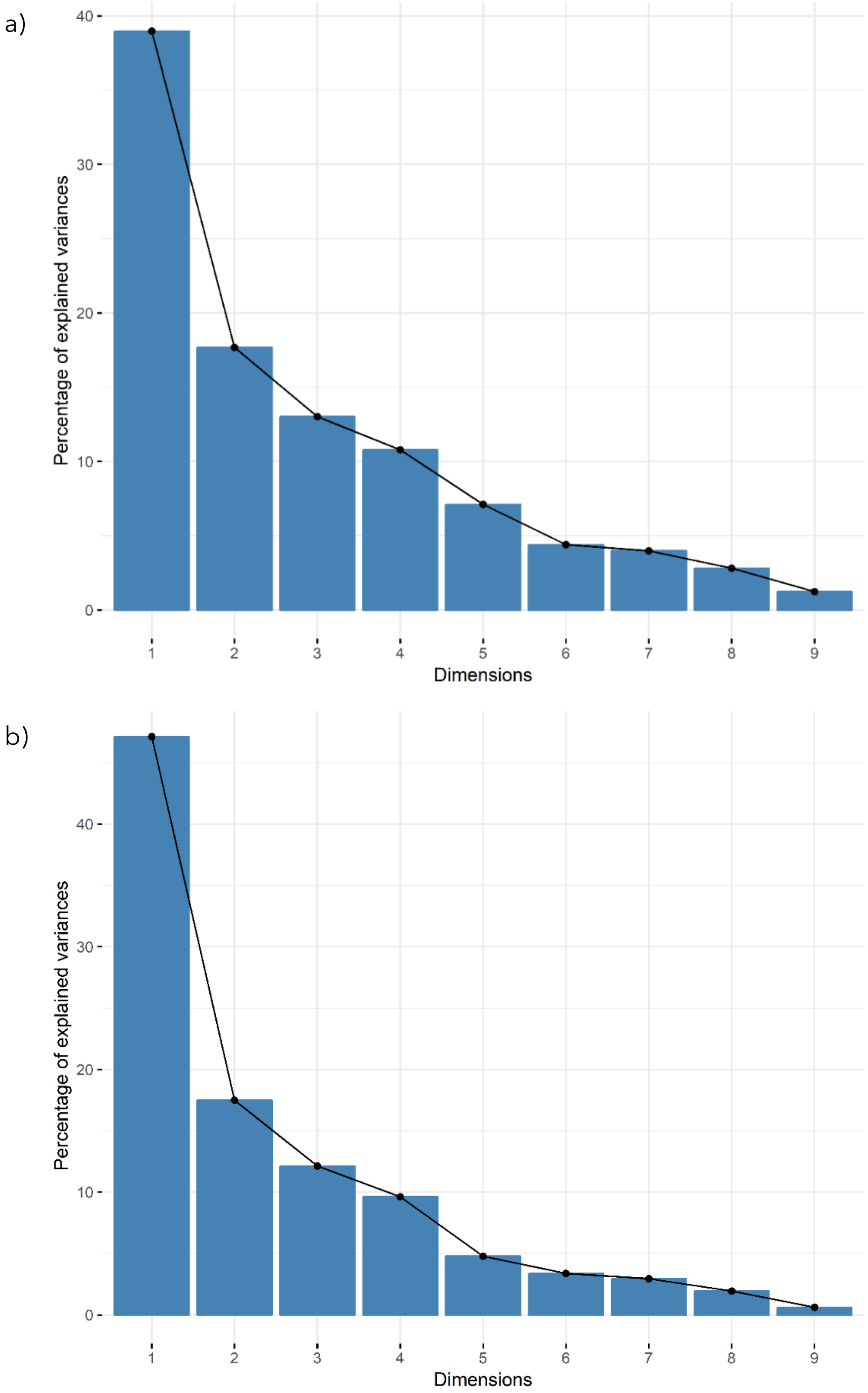


Figure B7.2. PCA results for the a) surface layer and b) deep layer showing the same main three groups: 1) small-medium sardine, mackerel, sprat and anchovy (both adults and juveniles), 2) small horse mackerel and anchovy juvenile and 3) medium-big horse mackerel and mackerel.

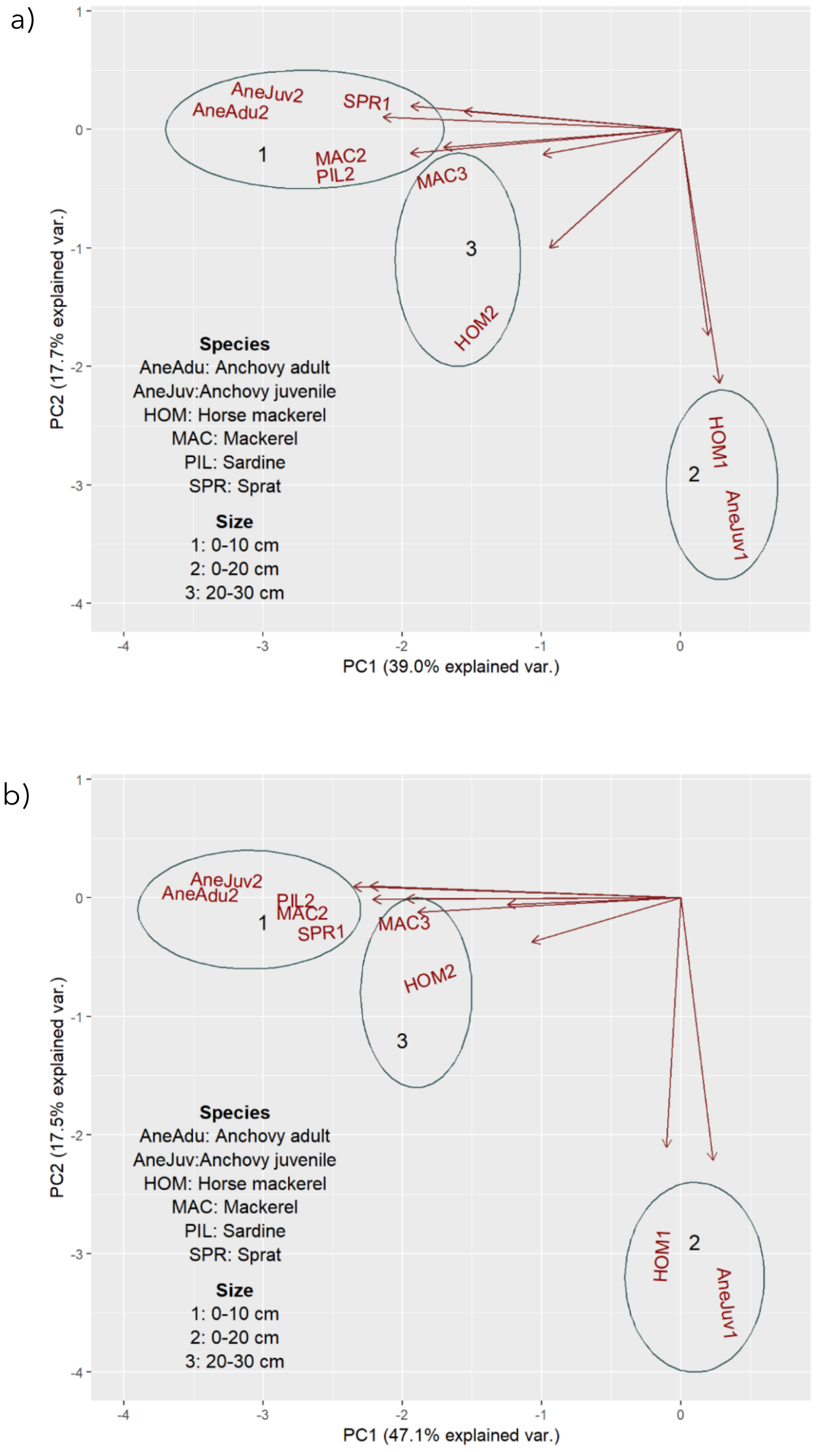
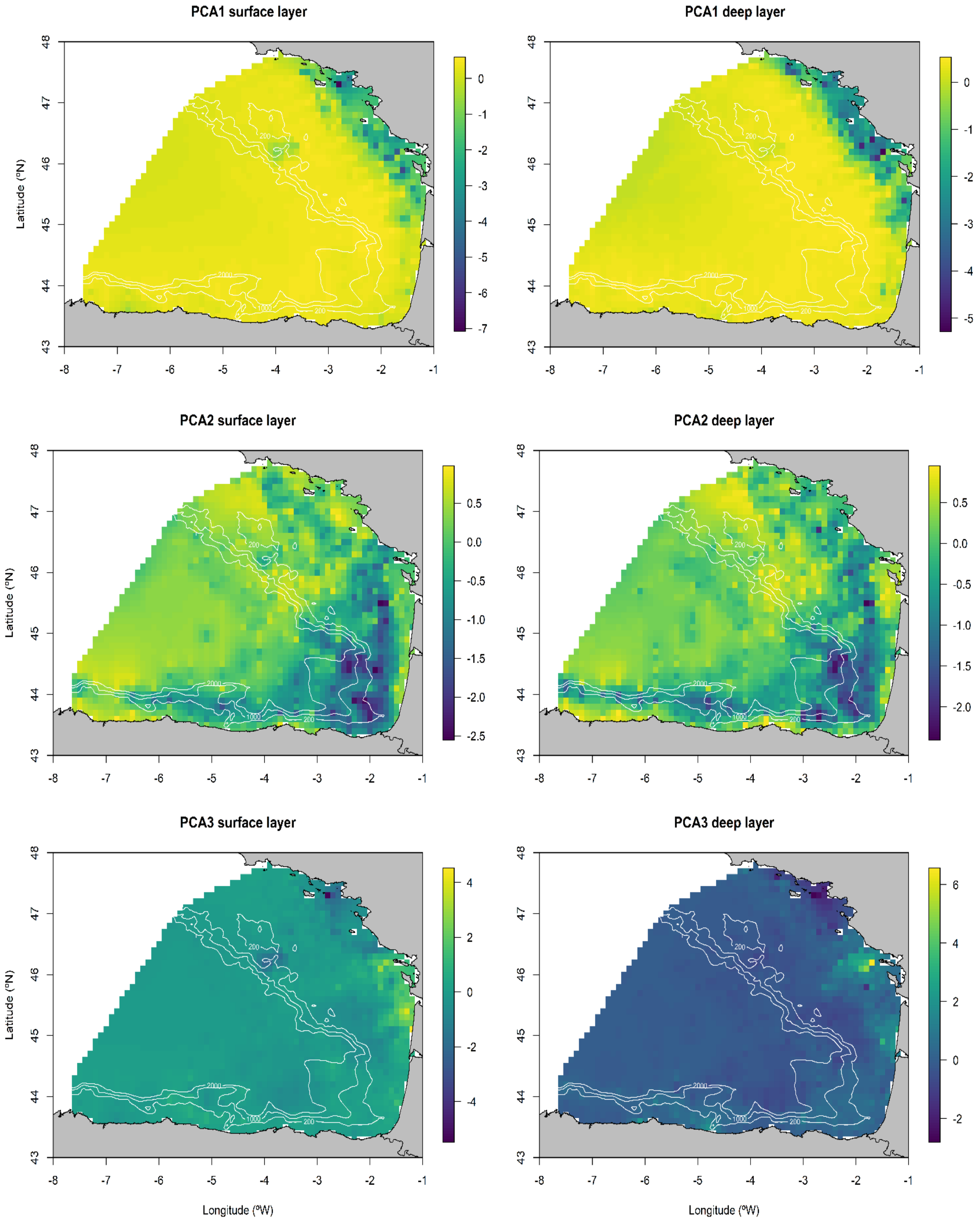


Figure B7.3. Spatial distribution of the three main axes obtained from the PCA analysis in the surface and deep layer (must be remembered, that axis 1 and 2 were negatively associated, while axis 3 was positively related).



Appendix B8. Literature survey on species' diving depths

Table B8.1. Summary of seabirds' average depth records compiled from published biologging studies. Only studies providing number of dives, average depth and standard deviation were included. When multiple data were available, mean and variance were combined (fishmethods package, Nelson 2014).

	Cory's	*Great*	*Sooty*	*Balearic*	*Manx*
Average depth (m)	1.7 ± 0.8	3.2 ± 3.5	12.3 ±9.4	5.6 ± 4.1	5.7 ± 1.5
Num. individuals	22	2	20	1	33
Num. dives	22	930	6377	165	7417
Location	Portuguese archipelago	South Atlantic	New Zeeland	Mediterranean	Wales, UK
Reproductive phase	Chick-rearing	Breeding	Breeding	Chick rearing	Chick rearing
Source	Paiva et al. (2010a)	Ronconi et al. (2010b)	Shaffer et al. (2006), Shaffer et al. (2009)	Aguilar et al. (2003)*	Dean (2012)

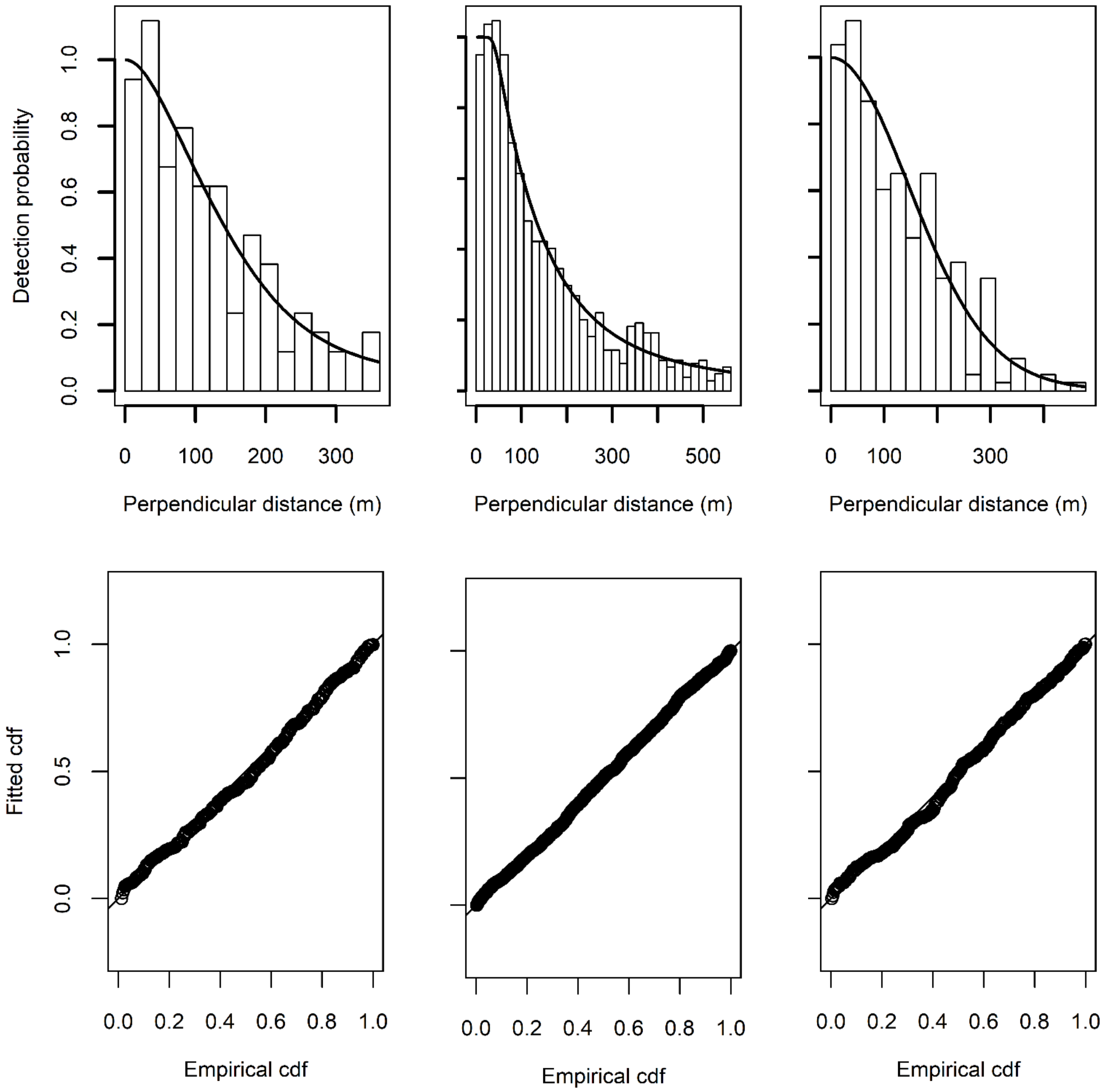
***Meier et al. (2015) also analysed the diving patterns of Balearic shearwater in the Mediterranean, using 19 individuals. However, they did not provide an average depth and that is why their results (proportion of dives per trip <4 m = 0.63–0.93) have not been included.

Table B8.2. Comparison between the expected results based on other authors’ records and the results obtained in this study. As it can be seen, only one species (i.e. Balearic shearwater) was not in agreement with what we expected.

	Cory’s	*Great*	*Sooty*	*Balearic*	*Manx*
Average depth (m)	1.7 ± 0.8	3.2 ± 3.5	12.3 ±9.4	5.6 ± 4.1	5.7 ± 1.5
Expected results	Surface	Surface	Deep	Surface	Surface
Obtained results	Surface	Surface	Deep	Deep	Surface

Appendix B9. Fitted detection functions

Figures B9.1. Detection functions (first row) and goodness of fit (second row) for a) Balearic and Manx shearwaters, b) Cory's and Great shearwaters and c) Sooty shearwater.



Appendix B10. Niche models' outputs

Table B10.1. Output of the individual environmental models, showing the selected environmental variables and the deviance explained (DE).

	Variables	*DE (%)*
Cory's	SSTsup, SALTsup, DIST, MTG,	38,2
Great	BATG, SALTsup, BATHY, GEOsup,	20.6
Sooty	SSTdtg, SALTdtg, BATHY, DTG	14.9
Balearic	SSTdtg, DSHEL, DIST, GEOdtg	71.4
Manx	SSTsup, DSHEL, DIST, MTG,	49

Table B10.2. Output of the individual trophic models, showing the selected prey variables and the deviance explained (DE).

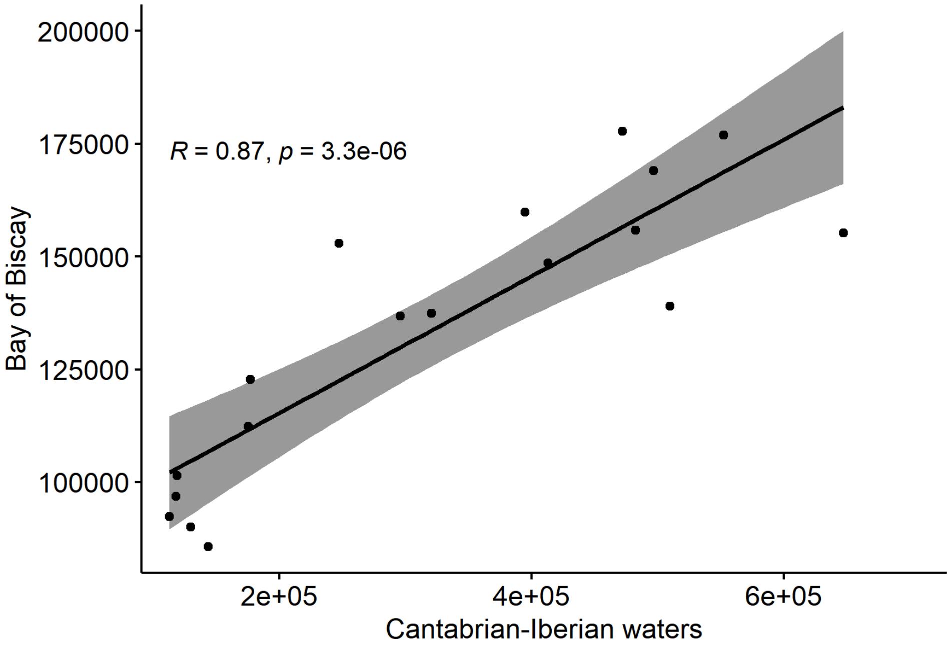
	Variables	*DE (%)*
Cory's	PCA2sup, PCA3sup	14.7
Great	PCA1sup, PCA3sup, MAV	8.83
Sooty	PCA1dtg, PCA2dtg, MAV	5.49
Balearic	PCA1dtg, PCA2dtg, PCA3dtg, MAV	58.5
Manx	PCA1sup	29.4

CHAPTER 3 – APPENDIX C

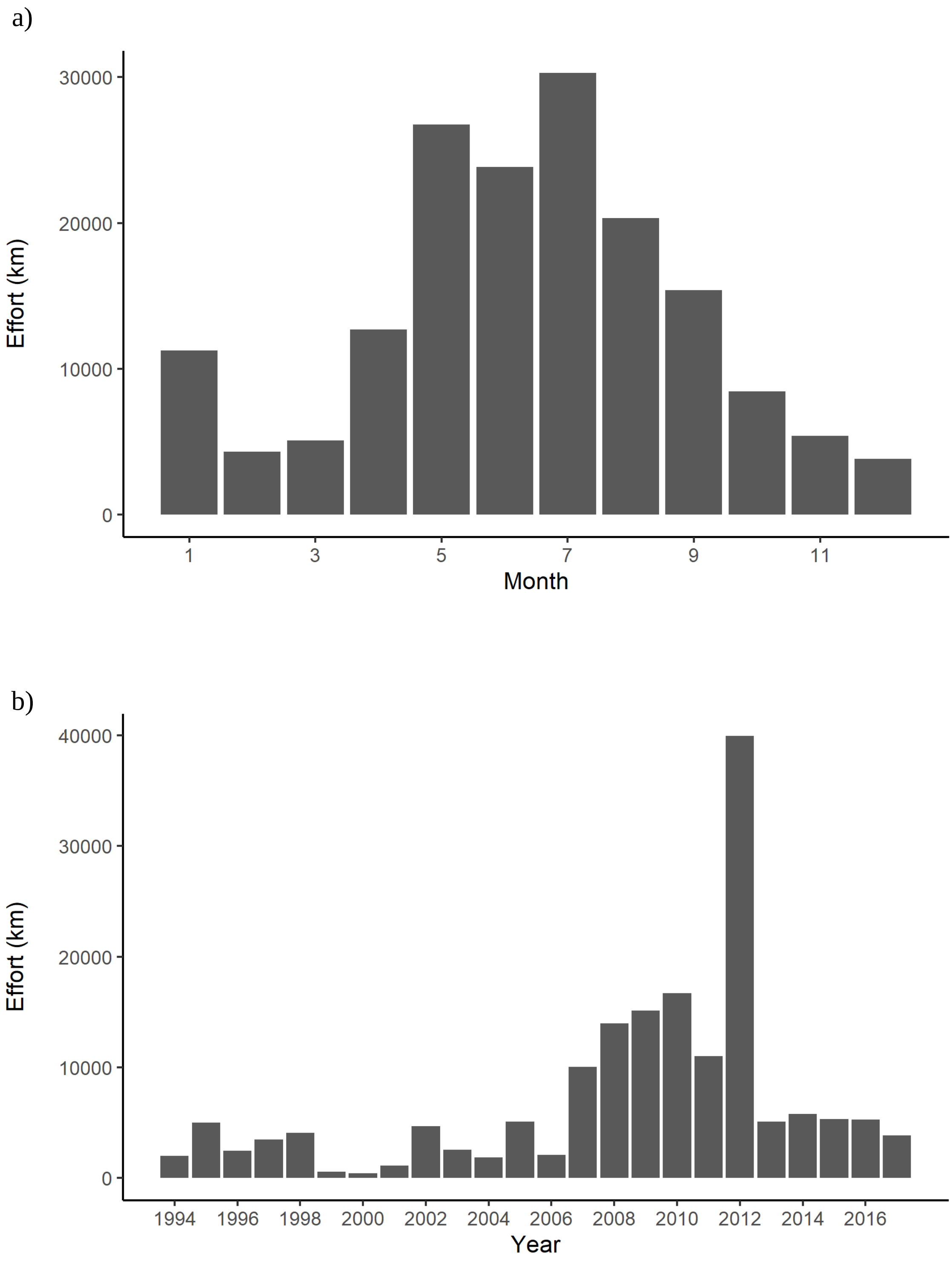
Appendix C1. List of data providers

Survey/Dataset	***Institution***	***Responsible***
ATLANCET	La Rochelle Université	Vincent Ridoux Ghislain Dorémus
BIOMAN	AZTI	Maite Louzao
CEMMA	Coordinadora Para O Estudo Dos Mamíferos Mariños	Jose Martinez Cedeira
CODA	University of St Andrews	Philip Hammond
ESAS	European Seabirds-At-Sea	Mark Lewis
EVHOE	IFREMER	Vincent Ridoux Ghislain Dorémus
IBTS	IFREMER	Vincent Ridoux Ghislain Dorémus
IFAW	Marine Conservation Research	Oliver Boisseau
IWDG	Irish Whale and Dolphin Group	Dave Wall Simon Berrow
JUVENA	AZTI	Maite Louzao
KOSMOS	University College Cork	Mark Jessopp
MARINELIFE	MARINElife	Tom Brereton
ORCA	Organisation Cetacea	Lucy Babey
PELACUS	Instituto Español de Oceanografía	Camilo Saavedra M. Begoña Santos
PELGAS	IFREMER	Vincent Ridoux Ghislain Dorémus
SAMM	La Rochelle Université	Vincent Ridoux Ghislain Dorémus
SCANS1	University of St Andrews	Philip Hammond
SCANS2	University of St Andrews	Philip Hammond
SPEA	Sociedade Portuguesa Para o Estudo das Aves	Joana Andrade
SWF	Sea Watch Foundation	Peter Evans
WDC	Whale and Dolphin Conservation	Nicola Hodgins

Appendix C2. Pearson correlation between the biomass estimates of the sardine inhabiting the Bay of Biscay (only available since 2000) and the biomasses of sardine from Cantabrian and Iberian waters (available since 1978) for the 2000-2017 period.



Appendix C3. Overall survey effort per month (a) and year (b) in the Bay of Biscay for the study period.



Appendix C4. The abundance estimates and the standard deviation predicted by the baseline spatio-temporal model per year.

Year	Estimated abundance	Standard Deviation
1994	206866.89	111642.44
1995	229253.95	110072.50
1996	159744.79	95702.34
1997	183166.86	103573.55
1998	203589.75	114249.34
1999	201689.14	129590.19
2000	212661.06	172835.84
2001	392603.31	213376.33
2002	130557.34	73239.62
2003	190112.70	116537.44
2004	112637.14	85430.82
2005	298342.69	109221.05
2006	202624.87	152671.49
2007	267381.52	144414.13
2008	175733.80	36693.53
2009	207971.19	43106.12
2010	202232.27	43980.45
2011	483434.50	195652.75
2012	402481.24	50214.63
2013	383484.50	153190.08
2014	495112.07	242008.83
2015	562790.30	176209.07
2016	479303.84	107265.16
2017	378133.58	100998.02

Appendix C5. Model validation test.

Figure C.5.1. Common dolphin's observed abundance index (encounter rate) estimated from ferry data. Green line indicates the annual mean, while the grey bar shows the standard error.

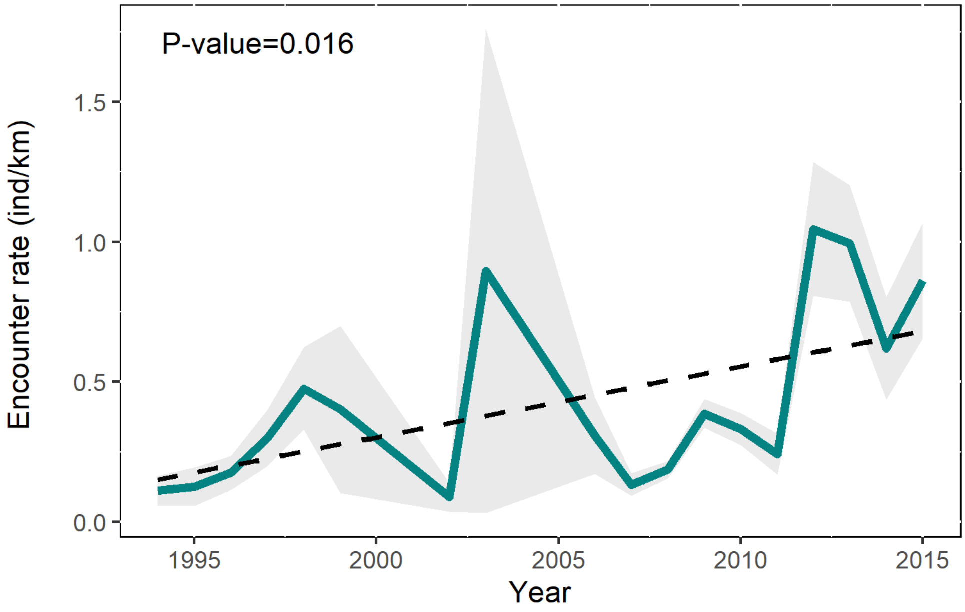
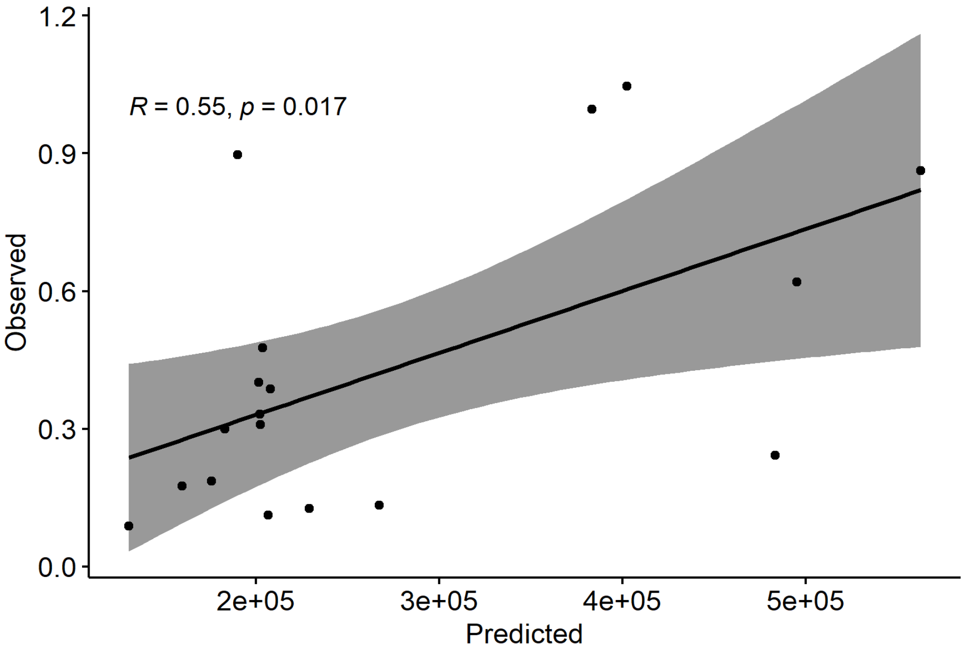


Figure C.5.2. Pearson correlation between observed abundance index (above) and predicted abundance index from the baseline spatio-temporal model.



Appendix C6. Environmental variables used in the study

Figure C6.1 The annual mean of temperature and chorophyll *a* integrated at 100m depth along the study period, accompanied by the standard error, the linear trend and its significance.

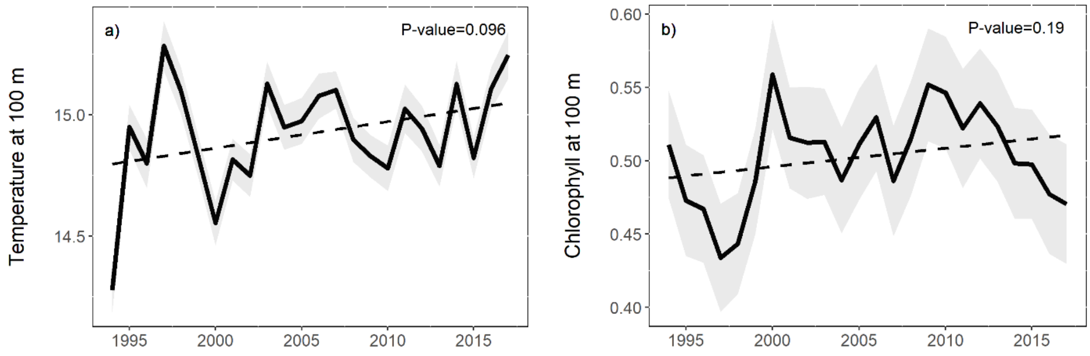


Figure C6.2. The annual mean of NAO, AMO and EA climatic indeces over the study period. Red and blue colors indicate the positive and negative phases of the indices, respectively.

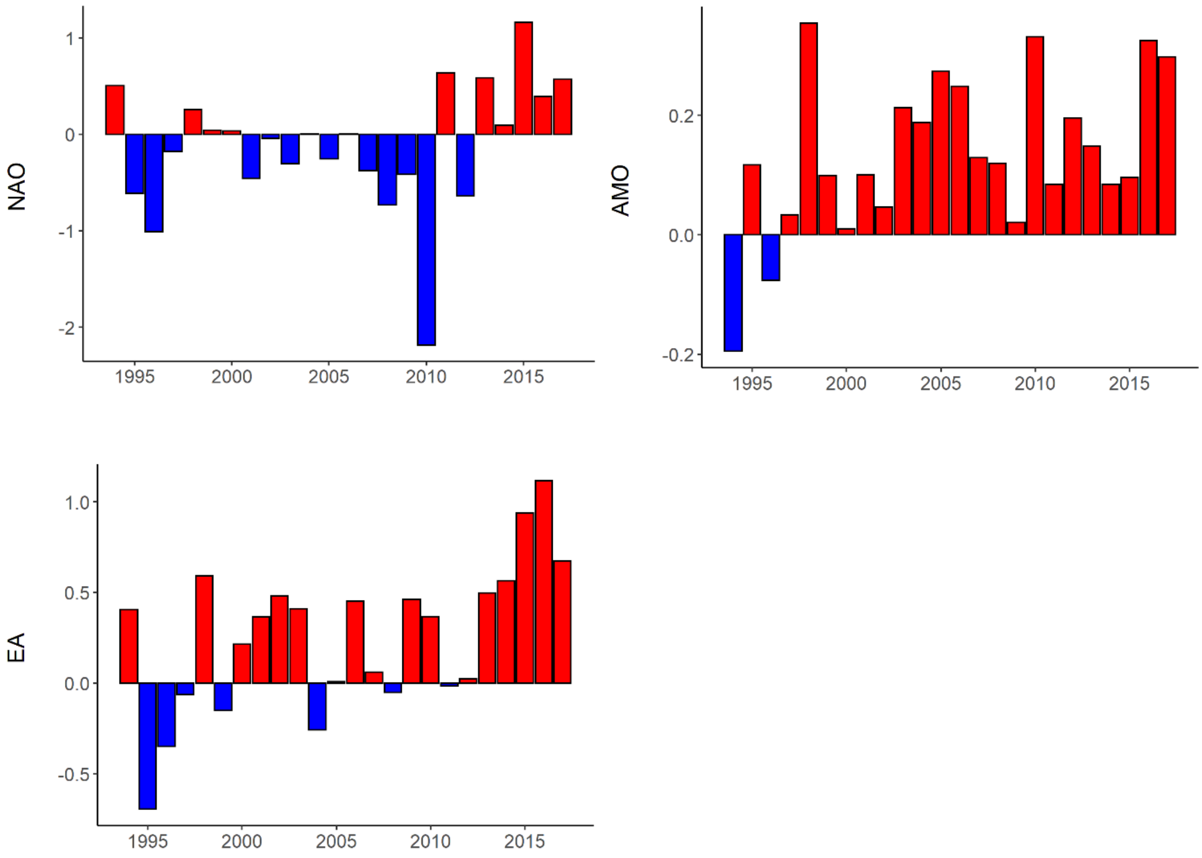
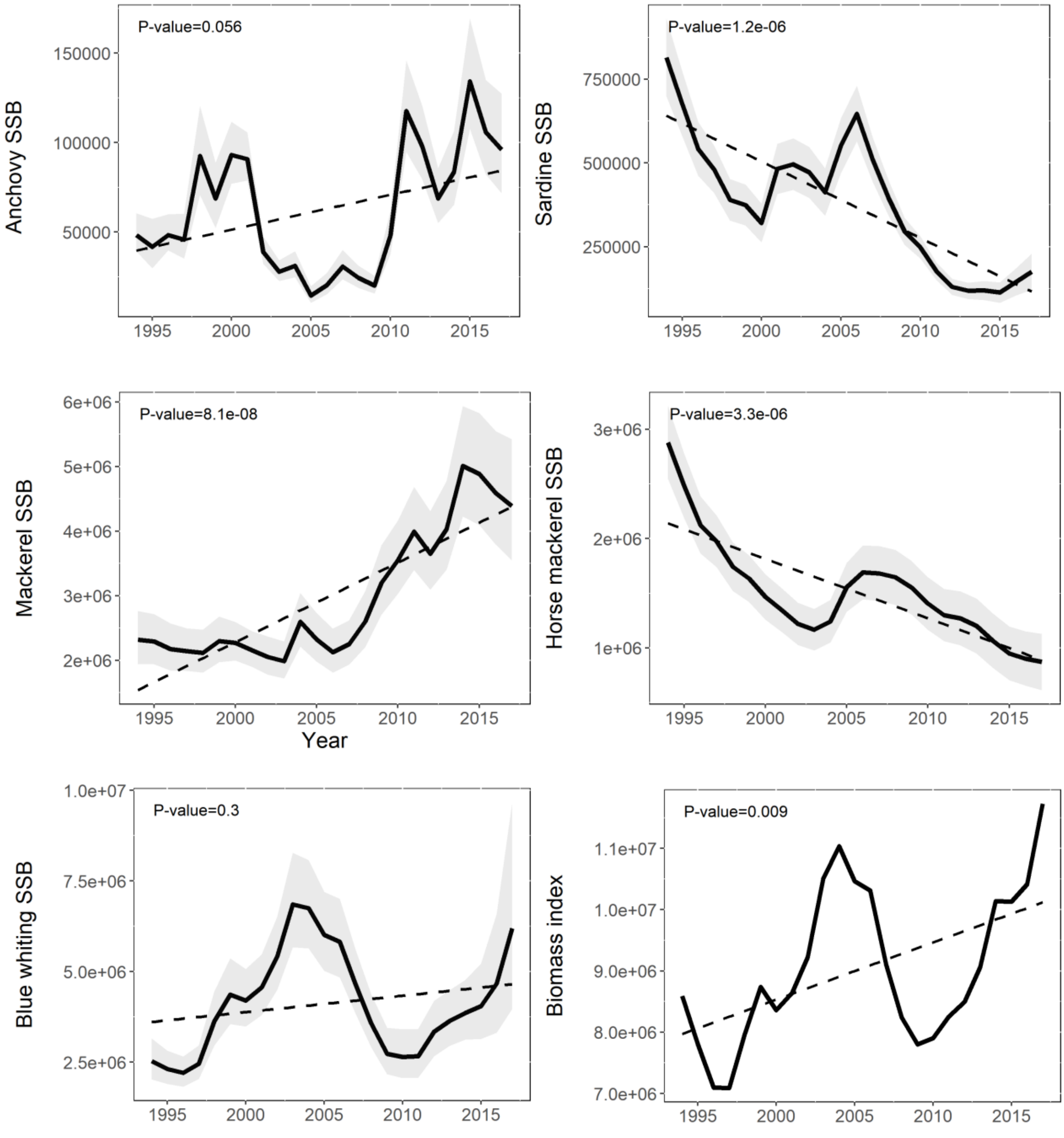
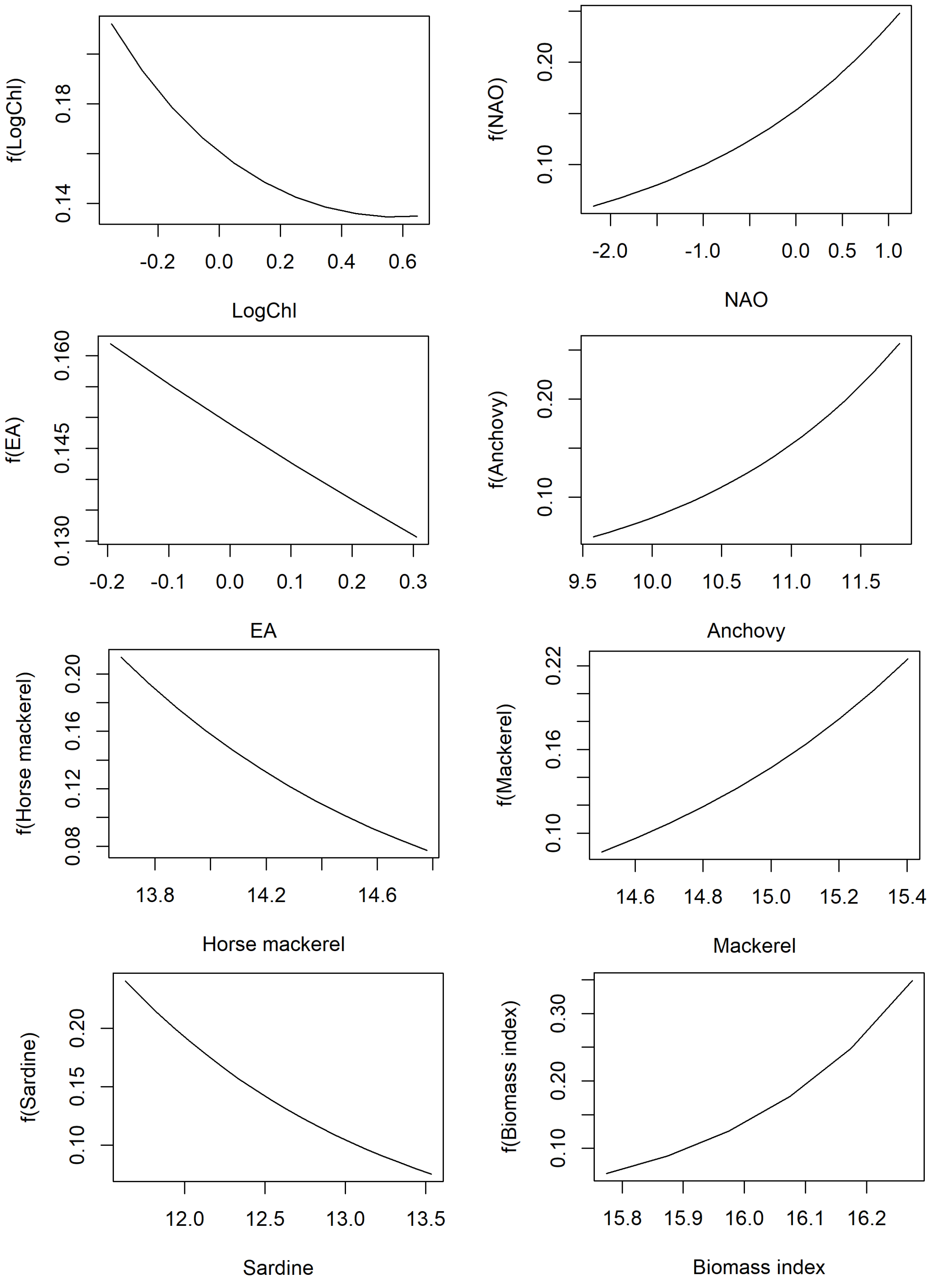


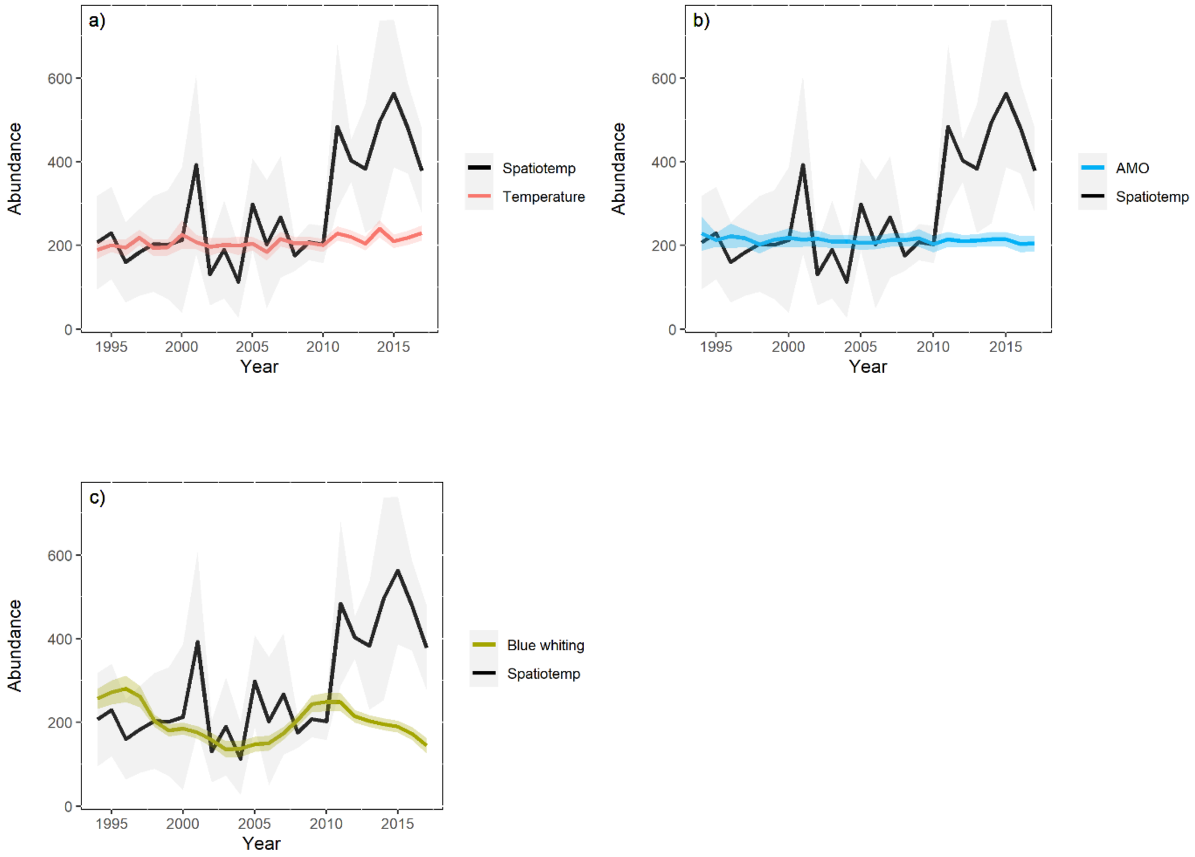
Figure C6.3. Spawning stock biomass of anchovy, sardine, mackerel, horse mackerel and blue whiting (a-e), accompanied by the higher and lower boundaries (95% CI), the linear trend and its significance. Biomass index (f) represents the sum of all previous species.



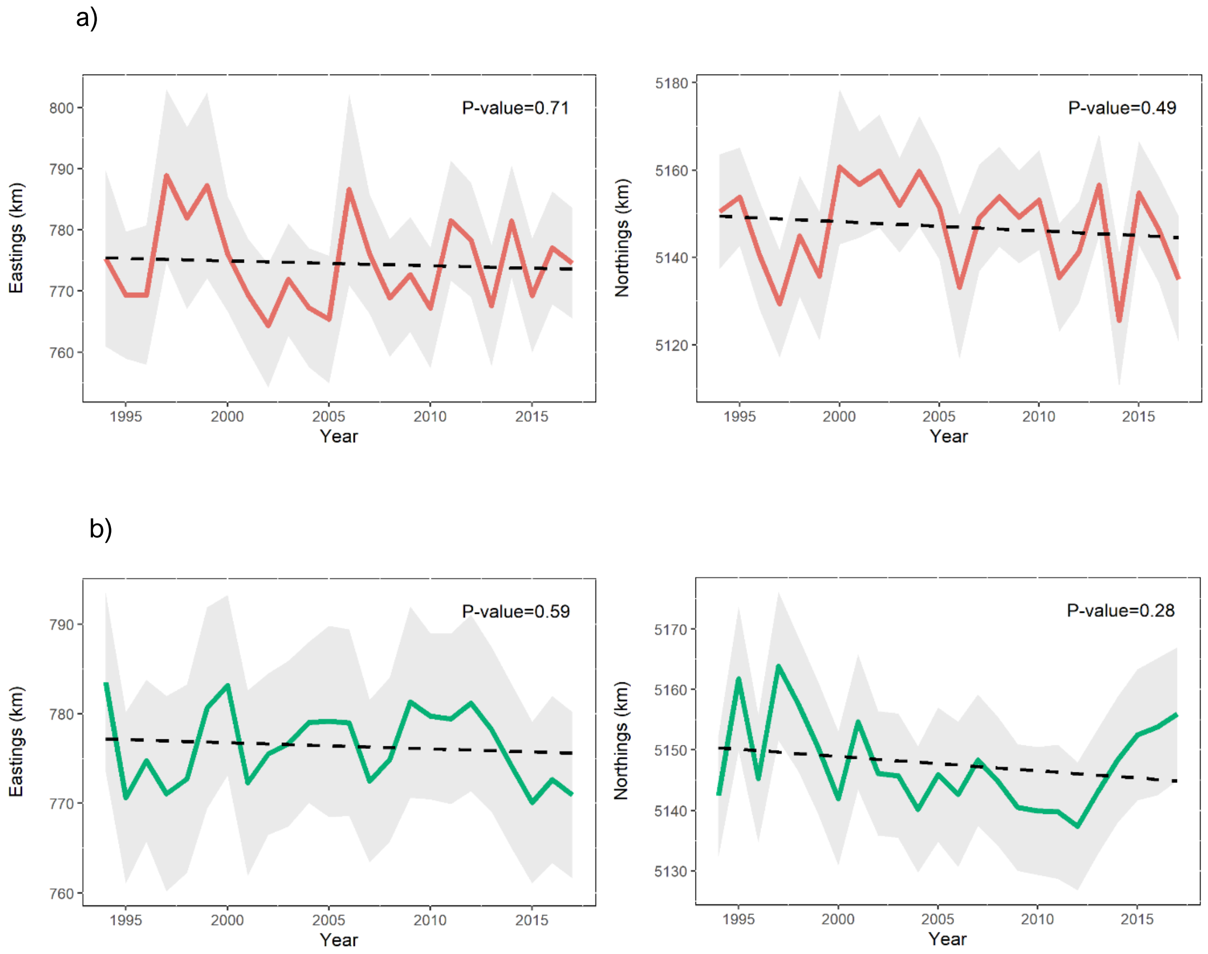
Appendix C7. Functional relationships estimated from the parameters (intercepts and coefficients) given by the model only for those variables considered important in terms of AIC. Confidence interval could not be estimated with the parameters provided.



Appendix C8. Abundance estimates predicted by the spatio-temporal model and by the covariates-based model, in which the contribution made by AMO, temperature and blue whiting (those drivers not considered relevant by AIC score) can be visualized**.**



Appendix C9. Isolated contribution of temperature (a) and chlorophyll *a* (b) variables to the centre of gravity predicted by covariate-based models with no random effects (same as Figure 8 but with y-axis zoomed). Shaded area means the standard error, while the dashed line indicates the linear trend.



REFERENCES

Aguilar A, García-Vernet R (2018). Fin whale, *Balaenoptera physalus*. *In*: W. Perrin, B. Würsig, & J. Thewissen (Eds.), Encyclopedia of marine mammals (pp.433–437). Academic Press , Amsterdam, The Netherlands.

Aguilar JS, Benvenuti S, Dall'Antonia L, McMinn-Grivé M, Mayol-Serra J (2003). Preliminary results on the foraging ecology of Balearic shearwaters (*Puffinus mauretanicus*) from bird-borne data loggers. Scientia Marina 67:129-134.

Aizen MA, Sabatino M, Tylianakis JM (2012). Specialization and rarity predict nonrandom loss of interactions from mutualist networks. Science 335:1486-1489.

Alonso H, Almeida A, Granadeiro JP, Catry P (2015). Temporal and age-related dietary variations in a large population of yellow-legged gulls *Larus michahellis*: implications for management and conservation. European Journal of Wildlife Research 61:819-829.

Allen SJ (2014). From exploitation to adoration. *In*: J. Higham, L. Bejder, & R. Williams (Eds.), Whale-watching: Sustainable Tourism and Ecological Management (pp. 31-47). Cambridge University Press, Cambridge, UK.

Anker-Nilssen T, Fátima Borges Md, Brander K, Duplisea D, Frederiksen M, Gallego A, Gislason A, Van Hal R, Heath M, Hofstedte RT (2008). The effect of climate change on the distribution and abundance of marine species in the OSPAR Maritime Area. ICES Cooperative Research Report No. 293. 45 pp.

Aquarone M, Adams S, Valdés L (2008). Celtic-Biscay Shelf. *In*: K. Sherman and G. Hempel (Eds), The UNEP Large Marine Ecosystem Report: A Perspective on Changing Conditions in LMEs of the World's Regional Seas (pp. 527-534). United Nations Environment Programme. Nairobi, Kenya.

Araújo MB, Guisan A (2006). Five (or so) challenges for species distribution modelling. Journal of Biogeography 33:1677-1688.

Araújo MB, Luoto M (2007). The importance of biotic interactions for modelling species distributions under climate change. Global Ecology and Biogeography 16:743-753.

Araújo MB, Pearson RG (2005). Equilibrium of species' distributions with climate. Ecography 28:693-695.

Araújo MB, Rozenfeld A (2013). The geographic scaling of biotic interactions. Ecography37:406-215.

Araújo MB, Rozenfeld A, Rahbek C, Marquet PA (2011). Using species co-occurrence networks to assess the impacts of climate change. Ecography 34:897-908

Arcos JM, Massutí E, Abelló P, Oro D (2000). Fish associated with floating drifting objects as a feeding resource for Balearic Shearwaters *Puffinus mauretanicus* during the breeding season. Ornis Fennica 77: 177-182.

Arkema KK, Abramson SC, Dewsbury BM (2006). Marine ecosystem-based management: from characterization to implementation. Frontiers in Ecology and the Environment 4:525-532.

Arnold TW (2010). Uninformative Parameters and Model Selection Using Akaike's Information Criterion. Journal of Wildlife Management 74:1175-1178.

Austin M (2007). Species distribution models and ecological theory: A critical assessment and some possible new approaches. Ecological Modelling 200:1-19.

Authier M, Dorémus G, Van Canneyt O, Boubert J-J, Gautier G, Doray M, Duhamel E, Massé J, Petitgas P, Ridoux V, Spitz J (2018). Exploring change in the relative abundance of marine megafauna in the Bay of Biscay, 2004–2016. Progress in Oceanography 166:159-167.

Avens L, Amico FD (2018). Evaluating viability of sea turtle foraging populations at high latitudes: age and growth of juveniles along the French Atlantic coast. Endangered Species Research 37:25-36.

Bachiller E, Irigoien X (2015). Trophodynamics and diet overlap of small pelagic fish species in the Bay of Biscay. Marine Ecology Progress Series 534:179-198.

Ballance LT, Ainley DG, Hunt GL (2001). Seabird Foraging Ecology. *In*: J.H. Steele, S.A. Thorpe and K.K. Turekian (Eds.) Encyclopedia of Ocean Sciences, vol. 5 (pp. 2636-2644). Academic Press, London, UK.

Ballard G, Jongsomjit D, Veloz SD, Ainley DG (2012). Coexistence of mesopredators in an intact polar ocean ecosystem: The basis for defining a Ross Sea marine protected area. Biological Conservation 156:72-82

Barton K (2016) MuMIn: Multi-Model Inference. R package.

Bascompte J (2009). Disentangling the web of life. Science 325:416-419

Bascompte J (2019). Mutualism and biodiversity. Current Biology 29:467-470

Baudron AR, Brunel T, Blanchet MA, Hidalgo M, Chust G, Brown EJ, Kleisner KM, Millar C, MacKenzie BR, Nikolioudakis N, Fernandes JA, Fernandes PG (2020). Changing fish distributions challenge the effective management of European fisheries. Ecography 43:494-505.

Bearhop S, Thompson DR, Phillips RA, Waldron S, Hamer KC, Gray CM, Votier SC, Ross BP, Furness RW (2001). Annual variation in great skua diets: the importance of commercial fisheries and predation on seabirds revealed by combining dietary analyses. The Condor 103:802-809.

Benoit-Bird KJ, Battaile BC, Heppell SA, Hoover B, Irons D, Jones N, Kuletz KJ, Nordstrom CA, Paredes R, Suryan RM, Waluk CM, Trites AW (2013) .Prey patch patterns predict habitat use by top marine predators with diverse foraging strategies. PLoS ONE 8:1-12.

Berry D, Widder S (2014). Deciphering microbial interactions and detecting keystone species with co-occurrence networks. Frontiers in Microbiology 5:1-14.

Bicknell AWJ, Oro D, Camphuysen KCJ, Votier SC, Blanchard J (2013). Potential consequences of discard reform for seabird communities. Journal of Applied Ecology 50:649-658.

Blanchard F, Vandermeirsch F (2005). Warming and exponential abundance increase of the subtropical fish Capros aper in the Bay of Biscay (1973–2002). Comptes Rendus Biologies 328:505-509.

Blanchet FG, Cazelles K, Gravel D (2020). Co-occurrence is not evidence of ecological interactions. Ecological Letters 23:1050-1063.

Blois JL, Zarnetske PL, Fitzpatrick MC, Finnegan S (2013). Climate change and the past, present, and future of biotic interactions. Science 341:499-504.

Blomqvist S, Elander M (1981). Sabine's Gull (*Xema sabini)*, Ross's Gull (*Rhodostethia rosea*) and Ivory Gull (*Pagophila eburnea*) Gulls in the Arctic: A Review. Arctic:122-132.

Bode A, Casas B, Fernández E, Marañón E, Serret P, Varela M (1996). Phytoplankton biomass and production in shelf waters off NW Spain: spatial and seasonal variability in relation to upwelling. Hydrobiologia 341:225-234.

Borja A, Fontán A, Sáenz Jon, Valencia V (2008). Climate, oceanography, and recruitment: the case of the Bay of Biscay anchovy (*Engraulis encrasicolus*). Fisheries Oceanography 17:477-493.

Boyd C, Grünbaum D, Hunt GL, Punt AE, Weimerskirch H, Bertrand S, Votier S (2017). Effects of variation in the abundance and distribution of prey on the foraging success of central place foragers. Journal of Applied Ecology 54:1362-1372.

Boyra G, Martinez U, Cotano U, Santos M, Irigoien X, Uriarte A (2013). Acoustic surveys for juvenile anchovy in the Bay of Biscay: abundance estimate as an indicator of the next year's recruitment and spatial distribution patterns. ICES Journal of Marine Science 70:1354-1368.

Boyra G, Peña M, Cotano U, Irigoien X, Rubio A, Nogueira E (2016). Spatial dynamics of juvenile anchovy in the Bay of Biscay. Fisheries Oceanography 25:529-543.

Bravo Rebolledo EL, Ijsseldijk LL, Solé L, Begeman L, de Vries S, van den Boom L, Camalich Carpizo J, Leopold MF (2016). Unorthodox Sampling of a Fin Whale's (Balaenoptera physalus) Diet Yields Several New Mesopelagic Prey Species. Aquatic Mammals 42:417-420.

Broennimann O, Fitzpatrick MC, Pearman PB, Petitpierre B, Pellissier L, Yoccoz NG, Thuiller W, Fortin M-J, Randin C, Zimmermann NE, Graham CH, Guisan A (2011). Measuring ecological niche overlap from occurrence and spatial environmental data. Global Ecology and Biogeography 21:481-497

Brown CJ, Schoeman DS, Sydeman WJ, Brander K, Buckley LB, Burrows M, Duarte CM, Moore PJ, Pandolfi JM, Poloczanska E, Venables W, Richardson AJ (2011). Quantitative approaches in climate change ecology. Global Change Biology 17:3697-3713.

Bruge A, Alvarez P, Fontán A, Cotano U, Chust G (2016). Thermal niche tracking and future distribution of Atlantic mackerel spawning in response to ocean warming. Frontiers in Marine Science 3:1-13.

Buckland ST, Anderson D, Burnham K, Laake J, Thomas L, Borchers D (2001). Introduction to distance sampling: estimating abundance of biological populations. Vol 335. Oxford university press, Oxford, UK.

Burnham KP, Anderson DR (2003). Model selection and multimodel inference: a practical information-theoretic approach. Springer Science & Business Media, New York, USA.

Burrows MT, Schoeman DS, Buckley LB, Moore P, Poloczanska ES, Brander KM, Brown C, Bruno JF, Duarte CM, Halpern BS, Holding J, Kappel CV, Kiessling W, O'Connor MI, Pandolfi JM, Parmesan C, Schwing FB, Sydeman WJ, Richardson AJ (2011). The pace of shifting climate in marine and terrestrial ecosystems. Science 334:652-655

Caballero A, Rubio A, Ruiz S, Le Cann B, Testor P, Mader J, Hernandez C (2016). South-Eastern Bay of Biscay eddy-induced anomalies and their effect on chlorophyll distribution. Journal of Marine Systems 162:57-72.

Calado JG, Matos DM, Ramos JA, Moniz F, Ceia FR, Granadeiro JP, Paiva VH (2018). Seasonal and annual differences in the foraging ecology of two gull species breeding in sympatry and their use of fishery discards. Journal of Avian Biology 49:1-12.

Callaway RM, Brooker RW, Choler P, Kikvidze Z, Lortie CJ, Michalet R, Paolini L, Pugnaire FI, Newingham B, Aschehoug ET, Armas C, Kikodze D, Cook BJ (2002). Positive interactions among alpine plants increase with stress. Nature 417:844-848

Camphuysen C, Scott B, Wanless S (2007). Distribution and foraging interactions of seabirds and marine mammals in the North Sea: multispecies foraging assemblages and habitat-specific feeding strategies. *In*: I.L. Boyd, S. Wanless & C.J. Camphuysen (Eds.) Top Predators in Marine Ecosystems: Their Role in Monitoring and Management (pp. 82–97). Cambridge University Press, Cambridge, UK.

Cañadas A, Desportes G, Borchers D (2004). The estimation of the detection function and g (0) for short-beaked common dolphins (*Delphinus delphis*), using double-platform data collected during the NASS-95 Faroese survey. Journal of Cetacean Research and Management 6:191-198.

Carr MH, Neigel JE, Estes JA, Andelman S, Warner RR, Largier JL (2003). Comparing marine and terrestrial ecosystems: implications for the design of coastal marine reserves. Ecological Applications 13:90-107.

Castège I, Soulier L, Hémery G, Mouchès C, Lalanne Y, Dewez A, Pautrizel F, d'Elbée J, D'Amico F (2013). Exploring cetacean stranding pattern in light of variation in at-sea encounter rate and fishing activity: Lessons from time surveys in the south Bay of Biscay (East-Atlantic; France). Journal of Marine Systems 109-110:284-292.

Cazelles K, Araújo MB, Mouquet N, Gravel D (2015). A theory for species co-occurrence in interaction networks. Theoretical Ecology 9:39-48.

CCAMLR (2006). Commission for the Conservation of Antarctic Marine Living Resources.Report of the Workshop on Management Procedures,Walvis Bay, Namibia.

Certain G, Masse J, Van Canneyt O, Petitgas P, Doremus G, Santos M, Ridoux V (2011). Investigating the coupling between small pelagic fish and marine top predators using data collected from ecosystem-based surveys. Marine Ecology Progress Series 422:23-39.

Clark JS, Gelfand AE, Woodall CW, Zhu K (2014). More than the sum of the parts: forest climate response from joint species distribution models. Ecological Applications 24:990-999.

Clua É, Grosvalet F (2001). Mixed-species feeding aggregation of dolphins, large tunas and seabirds in the Azores. Aquatic Living Resources 14:11-18.

Collins M, R. Knutti, J. Arblaster, J.-L. Dufresne, T. Fichefet, P. Friedlingstein, X. Gao, W.J. Gutowski, T. Johns, G. Krinner, M. Shongwe, C. Tebaldi, A.J. Weaver and M. Wehner (2013). Long-term Climate Change: Projections, Commitments and Irreversibility. *In*: Stocker, T.F., D. Qin, G.-K.Plattner, M. Tignor, S.K. Allen, J. Boschung, A. Nauels, Y. Xia, V. Bex and P.M. Midgley (Eds.), Climate Change 2013: The Physical Science Basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge, UK and New York, USA.

Costoya X, deCastro M, Gómez-Gesteira M, Santos F (2015). Changes in sea surface temperature seasonality in the Bay of Biscay over the last decades (1982–2014). Journal of Marine Systems 150:91-101.

Croxall JP, Butchart SHM, Lascelles BEN, Stattersfield AJ, Sullivan BEN, Symes A, Taylor P (2012). Seabird conservation status, threats and priority actions: a global assessment. Bird Conservation International 22:1-34.

Csardi G, Nepusz T (2006). The igraph software package for complex network research. InterJournal, Complex Systems 1695:1-9.

Curtin R, Prellezo R (2010). Understanding marine ecosystem based management: A literature review. Marine Policy 34:821-830.

Chase JM, Abrams PA, Grover JP, Diehl S, Chesson P, Holt RD, Richards SA, Nisbet RM, Case TJ (2002). The interaction between predation and competition: a review and synthesis. Ecology letters 5:302-315.

Chase JM, Leibold MA (2003). Ecological niches: linking classical and contemporary approaches. University of Chicago Press, Chicago, USA.

Chesson P (2000). General theory of competitive coexistence in spatially-varying environments. Theoretical population biology 58:211-237.

Christensen NL, Bartuska AM, Brown JH, Carpenter S, D'Antonio C, Francis R, Franklin JF, MacMahon JA, Noss RF, Parsons DJ (1996). The report of the Ecological

Society of America committee on the scientific basis for ecosystem management. Ecological applications 6:665-691.

Chust G, Allen JI, Bopp L, Schrum C, Holt J, Tsiaras K, Zavatarelli M, Chifflet M, Cannaby H, Dadou I, Daewel U, Wakelin SL, Machu E, Pushpadas D, Butenschon M, Artioli Y, Petihakis G, Smith C, Garcon V, Goubanova K, Le Vu B, Fach BA, Salihoglu B, Clementi E, Irigoien X (2014a). Biomass changes and trophic amplification of plankton in a warmer ocean. Global Change Biology 20:2124-2139.

Chust G, Borja Á, Caballero A, Irigoien X, Sáenz J, Moncho R, Marcos M, Liria P, Hidalgo J, Valle M, Valencia V (2011). Climate change impacts on coastal and pelagic environments in the southeastern Bay of Biscay. Climate Research 48:307-332.

Chust G, Castellani C, Licandro P, Ibaibarriaga L, Sagarminaga Y, Irigoien X (2014b). Are Calanus spp. shifting poleward in the North Atlantic? A habitat modelling approach. ICES Journal of Marine Science 71:241-253.

D'Amen M, Mod HK, Gotelli NJ, Guisan A (2018). Disentangling biotic interactions, environmental filters, and dispersal limitation as drivers of species co-occurrence. Ecography 41:1233-1244.

D'Elbee J, Hemery G (1998). Diet and foraging behaviour of the British Storm Petrel Hydrobates pelagicus in the Bay of Biscay during summer. Ardea 86:1-10.

Dean B (2012). The at-sea behaviour of the Manx Shearwater. Oxford University, UK.

Desportes G (1985). La nutrition des Odontocètes en Atlantique Nord-Est (côtes Françaises-îles Feroë). PhD dissertation, Université de Poitiers. France.

Devictor V, Clavel J, Julliard R, Lavergne S, Mouillot D, Thuiller W, Venail P, Villéger S, Mouquet N (2010). Defining and measuring ecological specialization. Journal of Applied Ecology 47:15-25.

Dewey J (1999) Logic: The Theory of Inquiry, 1938. Holt, Rinehart & Winston, New York, USA.

Dias MP, Martin R, Pearmain EJ, Burfield IJ, Small C, Phillips RA, Yates O, Lascelles B, Borboroglu PG, Croxall JP (2019). Threats to seabirds: A global assessment. Biological Conservation 237:525-537.

Doherty P, Baxter J, Gell F, Godley B, Graham R, Hall G, Hall J, Hawkes L, Henderson S, Johnson L (2017). Long-term satellite tracking reveals variable seasonal migration strategies of basking sharks in the north-east Atlantic. Scientific reports 7:1-10.

Doney SC, Ruckelshaus M, Duffy JE, Barry JP, Chan F, English CA, Galindo HM, Grebmeier JM, Hollowed AB, Knowlton N, Polovina J, Rabalais NN, Sydeman WJ, Talley LD (2012). Climate change impacts on marine ecosystems. Annual Review of Marine Science 4:11-37.

Doray M, Petitgas P, Josse E (2008). A geostatistical method for assessing biomassof tuna aggregations around moored fish aggregating devices with star acoustic surveys. Canadian Journal of Fisheries and Aquatic Sciences 65:1193-1205.

Doray M, Petitgas P, Romagnan JB, Huret M, Duhamel E, Dupuy C, Spitz J, Authier M, Sanchez F, Berger L, Dorémus G, Bourriau P, Grellier P, Massé J (2018). The PELGAS survey: Ship-based integrated monitoring of the Bay of Biscay pelagic ecosystem. Progress in Oceanography 166:15-29.

Dormann CF, Bobrowski M, Dehling DM, Harris DJ, Hartig F, Lischke H, Moretti MD, Pagel J, Pinkert S, Schleuning M, Schmidt SI, Sheppard CS, Steinbauer MJ, Zeuss D, Kraan C (2018). Biotic interactions in species distribution modelling: 10 questions to guide interpretation and avoid false conclusions. Global Ecology and Biogeography 27:1004-1016.

Drinkwater KF, Belgrano A, Borja A, Conversi A, Edwards M, Greene CH, Ottersen G, Pershing AJ, Walker H (2003). The response of marine ecosystems to climate variability associated with the North Atlantic Oscillation. Geophysical Monograph 134:211-234.

Eklof A, Ebenman B (2006). Species loss and secondary extinctions in simple and complex model communities. Journal of Animal Ecology 75:239-246.

Elton C (1927) Animal Ecology. Sedgwick & Jackson Ltd., London, UK.

Erauskin-Extramiana M, Alvarez P, Arrizabalaga H, Ibaibarriaga L, Uriarte A, Cotano U, Santos M, Ferrer L, Cabré A, Irigoien X, Chust G (2019a). Historical trends and future distribution of anchovy spawning in the Bay of Biscay. Deep Sea Research Part II: Topical Studies in Oceanography 159:169-182.

Erauskin-Extramiana M, Arrizabalaga H, Cabré A, Coelho R, Rosa D, Ibaibarriaga L, Chust G (2020). Are shifts in species distribution triggered by climate change? A swordfish case study. Deep Sea Research Part II: Topical Studies in Oceanography 175:1-11.

Erauskin-Extramiana M, Arrizabalaga H, Hobday AJ, Cabre A, Ibaibarriaga L, Arregui I, Murua H, Chust G (2019b). Large-scale distribution of tuna species in a warming ocean. Global Change Biology 25:2043-2060

Estes JA, Terborgh J, Brashares JS, Power ME, Berger J, Bond WJ, Carpenter SR, Essington TE, Holt RD, Jackson JB (2011). Trophic downgrading of planet Earth. Science 333:301-306.

Evans P, Waggitt J (2020). Impacts of climate change on marine mammals, relevant to the coastal and marine environment around the UK. MCCIP Science Review 2020:421-455.

Evans PGH, Pierce GJ, Panigada S (2010). Climate change and marine mammals. Journal of the Marine Biological Association of the UK 90:1483-1487.

Fauchald P (2009). Spatial interaction between seabirds and prey: review and synthesis. Marine Ecology Progress Series 391:139-151.

Fauchald P, Erikstad KE, Skarsfjord H (2000). Scale-dependent predator–prey interactions: the hierarchical spatial distribution of seabirds and prey. Ecology 81:773-783.

Frederiksen M, Anker-Nilssen T, Beaugrand G, Wanless S (2013). Climate, copepods and seabirds in the boreal Northeast Atlantic - current state and future outlook. Global Change Biology 19:364-372.

Free CM, Thorson JT, Pinsky ML, Oken KL, Wiedenmann J, Jensen OP (2019). Impacts of historical warming on marine fisheries production. Science 363:979-983.

García-Barón I, Authier M, Caballero A, Vázquez JA, Santos MB, Murcia JL, Louzao M, Treml E (2019). Modelling the spatial abundance of a migratory predator: A call for transboundary marine protected areas. Diversity and Distributions 25:346-360.

García-Barón I, Santos MB, Saavedra C, Astarloa A, Valeiras J, García Barcelona S, Louzao M (2020). Essential ocean variables and high value biodiversity areas: Targets for the conservation of marine megafauna. Ecological Indicators 117:1-12.

George EI, McCulloch RE (1993). Variable selection via Gibbs sampling. Journal of the American Statistical Association 88:881-889.

Geweke J (1992). Evaluating the accuracy of sampling-based approaches to the calculations of posterior moments. Bayesian statistics 4:641-649.

Ghosh J, Li Y, Mitra R (2018). On the Use of Cauchy Prior Distributions for Bayesian Logistic Regression. Bayesian Analysis 13:359-383.

Gilman SE, Urban MC, Tewksbury J, Gilchrist GW, Holt RD (2010). A framework for community interactions under climate change. Trends in Ecology and Evolution 25:325-331.

Godefroid M, Boldt JL, Thorson JT, Forrest R, Gauthier S, Flostrand L, Ian Perry R, Ross ARS, Galbraith M (2019). Spatio-temporal models provide new insights on the biotic and abiotic drivers shaping Pacific Herring (*Clupea pallasi*) distribution. Progress in Oceanography 178:1-17.

Godsoe W, Franklin J, Blanchet FG (2017). Effects of biotic interactions on modeled species' distribution can be masked by environmental gradients. Ecology and Evolution 7:654-664.

Gomis D, Ruiz S, Pedder M (2001). Diagnostic analysis of the 3D ageostrophic circulation from a multivariate spatial interpolation of CTD and ADCP data. Deep Sea Research Part I: Oceanographic Research Papers 48:269-295.

Goñi N, Arrizabalaga H (2010). Seasonal and interannual variability of fat content of juvenile albacore (*Thunnus alalunga*) and bluefin (*Thunnus thynnus*) tunas during their feeding migration to the Bay of Biscay. Progress in Oceanography 86:115-123.

Gotelli NJ, Graves GR, Rahbek C (2010). Macroecological signals of species interactions in the Danish avifauna. PNAS 107:5030-5035.

Gotelli NJ, Ulrich W (2010). The empirical Bayes approach as a tool to identify non-random species associations. Oecologia 162:463-477.

Granadeiro JP, Monteiro LR, Furness RW (1998). Diet and feeding ecology of Cory\'s shearwater *Calonectris diomedea* in the Azores, north-east Atlantic. Marine Ecology Progress Series 166:267-276.

Granadeiro JP, Monteiro LR, Silva MC, Furness RW (2002). Diet of common terns in the Azores, Northeast Atlantic. Waterbirds 25:149-155.

Gravel D, Poisot T, Albouy C, Velez L, Mouillot D, Freckleton R (2013). Inferring food web structure from predator-prey body size relationships. Methods in Ecology and Evolution 4:1083-1090.

Gray CM, Hamer KC (2001). Food-provisioning behaviour of male and female Manx shearwaters, Puffinus puffinus. Animal Behaviour 62:117-121.

Grecian WJ, Witt MJ, Attrill MJ, Bearhop S, Becker PH, Egevang C, Furness RW, Godley BJ, González-Solís J, Grémillet D (2016). Seabird diversity hotspot linked to ocean productivity in the Canary Current Large Marine Ecosystem. Biology letters 12:1-5.

Grinnell J (1917). The niche-relationships of the California Thrasher. The Auk 34:427-433.

Guisan A, Edwards Jr TC, Hastie T (2002). Generalized linear and generalized additive models in studies of species distributions: setting the scene. Ecological modelling 157:89-100.

Guisan A, Thuiller W (2005). Predicting species distribution: offering more than simple habitat models. Ecology letters 8:993-1009.

Guisan A, Zimmermann NE (2000). Predictive habitat distribution models in ecology. Ecological Modelling 135:147-186.

Halpern BS, Walbridge S, Selkoe KA, Kappel CV, Micheli F, D'Agrosa C, Bruno JF, Casey KS, Ebert C, Fox HE, Fujita R, Heinemann D, Lenihan HS, Madin EM, Perry MT, Selig ER, Spalding M, Steneck R, Watson R (2008). A global map of human impact on marine ecosystems. Science 319:948-952.

Hallett T, Coulson T, Pilkington J, Clutton-Brock T, Pemberton J, Grenfell B (2004). Why large-scale climate indices seem to predict ecological processes better than local weather. Nature 430:71-75.

Hamer K, Humphreys E, Garthe S, Hennicke J, Peters G, Grémillet D, Phillips R, Harris M, Wanless S (2007). Annual variation in diets, feeding locations and foraging behaviour of gannets in the North Sea: flexibility, consistency and constraint. Marine Ecology Progress Series 338:295-305.

Hamer K, Phillips R, Wanless S, Harris M, Wood A (2000). Foraging ranges, diets and feeding locations of gannets Morus bassanus in the North Sea: evidence from satellite telemetry. Marine ecology progress series 200:257-264.

Hammond P, Lacey C, Gilles A, Viquerat S, Boerjesson P, Herr H, Macleod K, Ridoux V, Santos M, Scheidat M (2017). Estimates of cetacean abundance in European Atlantic waters in summer 2016 from the SCANS-III aerial and shipboard surveys. Sea Mammal Research Unit, University of St Andrews, Scotland.

Harris DJ (2015). Generating realistic assemblages with a joint species distribution model. Methods in Ecology and Evolution 6:465-473.

Harris DJ (2016). Inferring species interactions from co-occurrence data with Markov networks. Ecology 97:3308-3314.

Hassani S, Antoine L, Ridoux V (1997). Diets of albacore, *Thunnus alalunga*, and dolphins, *Delphinus delphis* and S*tenella coerulaeoalba*, caught in the northeast Atlantic albacore drift-net fishery: a progress report. Journal of Northwest Atlantic Fishery Science 22:119-123.

Hazen EL, Abrahms B, Brodie S, Carroll G, Jacox MG, Savoca MS, Scales KL, Sydeman WJ, Bograd SJ (2019). Marine top predators as climate and ecosystem sentinels. Frontiers in Ecology and the Environment 17:565-574.

Hazen EL, Jorgensen S, Rykaczewski RR, Bograd SJ, Foley DG, Jonsen ID, Shaffer SA, Dunne JP, Costa DP, Crowder LB (2013). Predicted habitat shifts of Pacific top predators in a changing climate. Nature Climate Change 3:234-238.

Hazen EL, Jorgensen S, Rykaczewski RR, Bograd SJ, Foley DG, Jonsen ID, Shaffer SA, Dunne JP, Costa DP, Crowder LB, Block BA (2012). Predicted habitat shifts of Pacific top predators in a changing climate. Nature Climate Change 3:234-238.

Heikkinen RK, Luoto M, Virkkala R, Pearson RG, Körber J-H (2007). Biotic interactions improve prediction of boreal bird distributions at macro-scales. Global Ecology and Biogeography 16:754-763.

Heinemann D (1981). A range finder for pelagic bird censusing. The Journal of Wildlife Management 45:489-493.

Hemery G, D'Amico F, Castege I, Dupont B, D'Elbee J, Lalanne Y, Mouches C (2007). Detecting the impact of oceano-climatic changes on marine ecosystems using a multivariate index: The case of the Bay of Biscay (North Atlantic-European Ocean). Global Change Biology 14: 1-12.

Hiemstra PH, Pebesma EJ, Twenhöfel CJ, Heuvelink GB (2009). Real-time automatic interpolation of ambient gamma dose rates from the Dutch radioactivity monitoring network. Computers & Geosciences 35:1711-1721.

Hijmans RJ, van Etten J, Cheng J, Mattiuzzi M, Sumner M, Greenberg JA, Lamigueiro OP, Bevan A, Racine EB, Shortridge A (2017). Package 'raster'. R package.

Hodges JS, Reich BJ (2010). Adding Spatially-Correlated Errors Can Mess Up the Fixed Effect You Love. The American Statistician 64:325-334.

Hoegh-Guldberg O, Bruno JF (2010). The impact of climate change on the world's marine ecosystems. Science 328:1523-1528.

Holt RD (2009). Bringing the Hutchinsonian niche into the 21st century: ecological and evolutionary perspectives. PNAS 106 Suppl 2:19659-19665.

Hortal J, de Bello F, Diniz-Filho JAF, Lewinsohn TM, Lobo JM, Ladle RJ (2015). Seven Shortfalls that Beset Large-Scale Knowledge of Biodiversity. Annual Review of Ecology, Evolution, and Systematics 46:523-549.

Hughes TP, Bellwood DR, Folke C, Steneck RS, Wilson J (2005). New paradigms for supporting the resilience of marine ecosystems. Trends in Ecology and Evolution 20:380-386.

Hui FK (2016). boral–Bayesian ordination and regression analysis of multivariate abundance data in R. Methods in Ecology and Evolution 7:744-750.

Hui FK (2018) boral: Bayesian ordination and regression Analysis. R package.

Hurrell JW, Deser C (2009). North Atlantic climate variability: The role of the North Atlantic Oscillation. Journal of Marine Systems 78:28-41.

Hutchinson GE (1957). Concluding remarks. Cold Spring Harbor Symposia on Quantitative Biology 22:415-427.

ICES (2008). ICES. 2008. Report of the ICES Advisory Committee, 2008. ICES Advice, 2008. Book 7, 122 pp.

ICES (2018). Sardine (*Sardina pilchardus*) in divisions 8.c and 9.a (Cantabrian Sea and Atlantic Iberian waters) advice sheet. In Report of the ICES Advisory Commitee, 2018.

ICES (2019a). Anchovy (*Engraulis encrasicolus*) in Subarea 8 (Bay of Biscay) advice sheet. In Report of the ICES Advisory Commitee, 2019.

ICES (2019b). Horse mackerel (*Trachurus trachurus)* in Subarea 8 and divisions 2.a,4.a,5.b,6.a,7.a-c,e-k (the Northeast Atlantic) advice sheet. In Report of the ICES Advisory Commitee, 2019.

ICES (2019c). Sardine (*Sardina pilchardus*) in divisions 8.a-b and 8.d (Bay of Biscay) advice sheet. In Report of the ICES Advisory Commitee, 2019.

ICES (2020). Workshop on fisheries Emergency Measures to minimize Bycatch of short-beaked common dolphins in the Bay of Biscay and harbour porpoise in the Baltic Sea (WKEMBYC). ICES Scientific Reports, 2 (43), 354 pp.

IPCC (2019). Technical Summary. *In*: H.O. Pörtner DCR, V. Masson-Delmotte, P. Zhai, E. Poloczanska, K. Mintenbeck, M. Tignor, A. Alegría, M. Nicolai, A. Okem, J. Petzold, B. Rama, N.M. Weyer (Eds.), IPCC Special Report on the Ocean and Cryosphere in a Changing Climate, In press.

Jackson JB, Kirby MX, Berger WH, Bjorndal KA, Botsford LW, Bourque BJ, Bradbury RH, Cooke R, Erlandson J, Estes JA (2001). Historical overfishing and the recent collapse of coastal ecosystems. Science 293:629-637.

Jamil T, Ter Braak CJ (2013). Generalized linear mixed models can detect unimodal species-environment relationships. PeerJ 1:1-14

Jones T, Smith C, Williams E, Ramsay A (2010). Breeding performance and diet of Great Skuas *Stercorarius skua* and Parasitic Jaegers (Arctic Skuas) *S. parasiticus* on the west coast of Scotland. Bird Study 55:257-266.

Kaartvedt S, Knutsen T, Holst JC (1998). Schooling of the vertically migrating mesopelagic fish *Maurolicus muelleri* in light summer nights. Marine Ecology Progress Series 170:287-290.

Käkelä A, Crane J, Votier SC, Furness RW, Käkelä R (2006). Fatty acid signatures as indicators of diet in great skuas Stercorarius skua, Shetland. Marine Ecology Progress Series 319:297-310.

Käkelä R, Käkelä A, Martínez-Abraín A, Sarzo B, Louzao M, Gerique C, Villuendas E, Strandberg U, Furness RW, Oro D (2010). Fatty acid signature analysis confirms foraging resources of a globally endangered Mediterranean seabird species: calibration test and application to the wild. Marine Ecology Progress Series 398:245-258.

Kearney M (2006). Habitat, environment and niche: what are we modelling? Oikos 115:186-191.

Kiszka J, Macleod K, Van Canneyt O, Walker D, Ridoux V (2007). Distribution, encounter rates, and habitat characteristics of toothed cetaceans in the Bay of

Biscay and adjacent waters from platform-of-opportunity data. ICES Journal of Marine Science 64:1033-1043.

Koutsikopoulos C, Le Cann B (1996). Physical processes and hydrological structures related to the Bay of Biscay anchovy. Scientia Marina 60:9-19.

Kubetzki U, Garthe S (2003). Distribution, diet and habitat selection by four sympatrically breeding gull species in the south-eastern North Sea. Marine Biology 143:199-207.

Kuhn CE (2010). The influence of subsurface thermal structure on the diving behavior of northern fur seals (*Callorhinus ursinus*) during the breeding season. Marine Biology 158:649-663.

Lambert C, Authier M, Doray M, Dorémus G, Spitz J, Ridoux V (2018). Hide and seek in the Bay of Biscay—a functional investigation of marine megafauna and small pelagic fish interactions. ICES Journal of Marine Science 76: 113-123.

Lambert E, MacLeod CD, Hall K, Brereton T, Dunn TE, Wall D, Jepson PD, Deaville R, Pierce GJ (2011) Quantifying likely cetacean range shifts in response to global climatic change: implications for conservation strategies in a changing world. Endangered Species Research 15:205-222.

Lambert E, Pierce GJ, Hall K, Brereton T, Dunn TE, Wall D, Jepson PD, Deaville R, MacLeod CD (2014) Cetacean range and climate in the eastern North Atlantic: future predictions and implications for conservation. Global Change Biology 20:1782-1793.

Laran S, Authier M, Blanck A, Doremus G, Falchetto H, Monestiez P, Pettex E, Stephan E, Van Canneyt O, Ridoux V (2017). Seasonal distribution and abundance of cetaceans within French waters- Part II: The Bay of Biscay and the English Channel. Deep Sea Research Part II: Topical Studies in Oceanography 141:31-40.

Lassalle G, Lobry J, Le Loc'h F, Bustamante P, Certain G, Delmas D, Dupuy C, Hily C, Labry C, Le Pape O, Marquis E, Petitgas P, Pusineri C, Ridoux V, Spitz J, Niquil N (2011). Lower trophic levels and detrital biomass control the Bay of Biscay continental shelf food web: Implications for ecosystem management. Progress in Oceanography 91:561-575.

Lavin A, Valdes L, Sanchez F, Abaunza P, Forest A, Boucher J, Lazure P, Jegou A-M (2006). The Bay of Biscay: the encountering of the Ocean and the Shelf. *In*: Robinson, A, Brink, K. (Eds.), The Sea, Volume 14, Part B: The Global Coastal Ocean: Interdisciplinary Regional Studies and Syntheisis. Harvard University Press, Harvard, USA.

Lazkano I, Nøstbakken L, Prellezo R (2013). Past and future management of a collapsed fishery: The Bay of Biscay anchovy. Natural Resource Modeling 26:281-304.

Leslie HM, McLeod KL (2007). Confronting the challenges of implementing marine ecosystem-based management. Frontiers in Ecology and the Environment 5:540-548.

Lewis S, Sherratt TN, Hamer KC, Harris MP, Wanless S (2003). Contrasting diet quality of northern gannets *Morus bassanus* at two colonies. Ardea 91:167-176.

Lezama-Ochoa A, Boyra G, Goñi N, Arrizabalaga H, Bertrand A (2010). Investigating relationships between albacore tuna (*Thunnus alalunga*) CPUE and prey distribution in the Bay of Biscay. Progress in Oceanography 86:105-114.

Ling SD, Johnson CR, Frusher SD, Ridgway KR (2009). Overfishing reduces resilience of kelp beds to climate-driven catastrophic phase shift. PNAS 106:22341-22345.

Logerwell EA, Hargreaves NB (1996). The distribution of sea birds relative to their fish prey off Vancouver Island: opposing results at large and small spatial scales. Fisheries Oceanography 5:163-175.

Lorance P, Latrouite D, Seret B (2000). Observations of chondrichthyan fishes (sharks, rays and chimaeras) in the Bay of Biscay (North-eastern Atlantic) from submersibles. Proc. 3rd European Elasmobranch Association Meeting, Boulogne-sur-Mer, France.

Losos JB (2008). Phylogenetic niche conservatism, phylogenetic signal and the relationship between phylogenetic relatedness and ecological similarity among species. Ecology Letters 11:995-1003.

Louzao M, Afán I, Santos M, Brereton T (2015a). The role of climate and food availability on driving decadal abundance patterns of highly migratory pelagic predators in the Bay of Biscay. Frontiers in Ecology and Evolution 3: 1-12.

Louzao M, García-Barón I, Rubio A, Martínez U, Vázquez JA, Murcia JL, Nogueira E, Boyra G (2019a). Understanding the 3D environment of pelagic predators from multidisciplinary oceanographic surveys to advance ecosystem-based monitoring. Marine Ecology Progress Series 617-618:199-219.

Louzao M, García D, Rodríguez B, Abelló P (2015b). Evidence of krill in the diet of Balearic shearwaters *Puffinus mauretanicus*. Marine Ornithology 43:49-51.

Louzao M, Valeiras J, García-Barcelona S, González-Quirós R, Nogueira E, Iglesias M, Bode A, Vázquez JA, Murcia JL, Saavedra C, Pierce GJ, Fernández R, García-Barón I, Santos MB (2019b). Marine megafauna niche coexistence and hotspot areas in a temperate ecosystem. Continental Shelf Research 186:77-87.

MacArthur R (1968). The thoery of the niche. *In*: Lewontin KC (Eds.), Population Biology and Evolution. Syracuse University Press, Syracuse, USA.

MacArthur R, Pianka ER (1966). On optimal use of a patchy environment. The American Naturalist 100:603-609.

MacLeod CD (2009). Global climate change, range changes and potential implications for the conservation of marine cetaceans: a review and synthesis. Endangered Species Research 7:125-136.

MacLeod CD, Bannon SM, Pierce GJ, Schweder C, Learmonth JA, Herman JS, Reid RJ (2005). Climate change and the cetacean community of north-west Scotland. Biological Conservation 124:477-483.

Mancini PL, Hobson KA, Bugoni L (2014). Role of body size in shaping the trophic structure of tropical seabird communities. Marine Ecology Progress Series 497:243-257.

Marques F, Buckland S (2004). Covariate models for the detection function. *In*: S.T. Buckland, D.R. Anderson, K.P. Burnham, J.L. Laake, D.L. Borchers and L. Thomas (Eds.), Advanced Distance Sampling (pp. 31–47). Oxford Univeristy Press, Oxford, UK.

Martín González AM, Dalsgaard B, Olesen JM (2010). Centrality measures and the importance of generalist species in pollination networks. Ecological Complexity 7:36-43.

Martin TG, Wintle BA, Rhodes JR, Kuhnert PM, Field SA, Low-Choy SJ, Tyre AJ, Possingham HP (2005). Zero tolerance ecology: improving ecological inference by modelling the source of zero observations. Ecology Letters 8:1235-1246.

Maureaud AA, Frelat R, Pecuchet L, Shackell N, Merigot B, Pinsky ML, Amador K, Anderson SC, Arkhipkin A, Auber A, Barri I, Bell RJ, Belmaker J, Beukhof E, Camara ML, Guevara-Carrasco R, Choi J, Christensen HT, Conner J, Cubillos LA, Diadhiou HD, Edelist D, Emblemsvag M, Ernst B, Fairweather TP, Fock HO, Friedland KD, Garcia CB, Gascuel D, Gislason H, Goren M, Guitton J, Jouffre D, Hattab T, Hidalgo M, Kathena JN, Knuckey I, Kide SO, Koen-Alonso M, Koopman M, Kulik V, Leon JP, Levitt-Barmats Y, Lindegren M, Llope M, Massiot-Granier F, Masski H, McLean M, Meissa B, Merillet L, Mihneva V, Nunoo FKE, O'Driscoll R, O'Leary CA, Petrova E, Ramos JE, Refes W, Roman-Marcote E, Siegstad H, Sobrino I, Solmundsson J, Sonin O, Spies I, Steingrund P, Stephenson F, Stern N, Tserkova F, Tserpes G, Tzanatos E, van Rijn I, van Zwieten PAM, Vasilakopoulos P, Yepsen DV, Ziegler P, J TT (2021). Are we ready to track climate-driven shifts in marine species across international boundaries? - A global survey of scientific bottom trawl data. Global Change Biology 27:220-236.

McCullagh P, Nelder JA (1989). Generalized linear models, Vol 37. Chapman and Hall, London, UK.

Meier ES, Kienast F, Pearman PB, Svenning J-C, Thuiller W, Araújo MB, Guisan A, Zimmermann NE (2010). Biotic and abiotic variables show little redundancy in explaining tree species distributions. Ecography 33:1038-1048.

Meier RE, Votier SC, Wynn RB, Guilford T, McMinn Grivé M, Rodríguez A, Newton J, Maurice L, Chouvelon T, Dessier A, Trueman CN, Wiersma Y (2017). Tracking, feather moult and stable isotopes reveal foraging behaviour of a critically endangered seabird during the non-breeding season. Diversity and Distributions 23:130-145.

Meier RE, Wynn RB, Votier SC, McMinn Grivé M, Rodríguez A, Maurice L, van Loon EE, Jones AR, Suberg L, Arcos JM, Morgan G, Josey SA, Guilford T (2015). Consistent foraging areas and commuting corridors of the critically endangered Balearic shearwater *Puffinus mauretanicus* in the northwestern Mediterranean. Biological Conservation 190:87-97.

Meynier L, Pusineri C, Spitz J, Santos MB, Pierce GJ, Ridoux V (2008). Intraspecific dietary variation in the short-beaked common dolphin *Delphinus delphis* in the Bay of Biscay: importance of fat fish. Marine Ecology Progress Series 354:277-287.

Miller DL (2020). Package 'Distance'. R package.

Miller DL, Rexstad E, Burt L, Bravington MV, Hedley S, Model A (2019) Package 'dsm'.R.package.

Monteiro L, Granadeiro J, Furness R (1998). Relationship between mercury levels and diet in Azores seabirds. Marine Ecology Progress Series 166:259-265.

Morales-Castilla I, Matias MG, Gravel D, Araujo MB (2015). Inferring biotic interactions from proxies. Trends in Ecology and Evolution 30:347-356.

Mori Y, Boyd IL (2004). Segregation of foraging between two sympatric penguin species: does rate maximisation make the difference? Marine Ecology Progress Series 275:241-249.

Morueta-Holme N, Blonder B, Sandel B, McGill BJ, Peet RK, Ott JE, Violle C, Enquist BJ, Jørgensen PM, Svenning J-C (2016). A network approach for inferring species associations from co-occurrence data. Ecography 39:1139-1150.

Motos L, Uriarte A, Valencia V (1996). The spawning environment of the Bay of Biscay anchovy (Engraulis encrasicolus L.). Scientia Marina 60:117-140.

Mulder T, Zaragosi S, Garlan T, Mavel J, Cremer M, Sottolichio A, Sénéchal N, Schmidt S (2012). Present deep-submarine canyons activity in the Bay of Biscay (NE Atlantic). Marine Geology 295-298:113-127.

Munilla I, Genovart M, Paiva VH, Velando A (2016). Colony foundation in an oceanic seabird. PLoS ONE 11: 1-24.

Myers RA, Baum JK, Shepherd TD, Powers SP, Peterson CH (2007). Cascading effects of the loss of apex predatory sharks from a coastal ocean. Science 315:1846-1850.

Myers RA, Worm B (2003). Rapid worldwide depletion of predatory fish communities. Nature 423:280-283.

Navarro J, Louzao M, Igual JM, Oro D, Delgado A, Arcos JM, Genovart M, Hobson KA, Forero MG (2009). Seasonal changes in the diet of a critically endangered seabird and the importance of trawling discards. Marine Biology 156:2571-2578.

Navarro J, Votier SC, Aguzzi J, Chiesa JJ, Forero MG, Phillips RA (2013). Ecological segregation in space, time and trophic niche of sympatric planktivorous petrels. PLoS ONE 8: 1-12.

Nelson GA (2014) fishmethods: fishery science methods and models in R. R package.

Neves V, Nolf D, Clarke M (2012). Spatio-temporal variation in the diet of Cory's shearwater Calonectris diomedea in the Azores archipelago, northeast Atlantic. Deep Sea Research Part I: Oceanographic Research Papers 70:1-13.

Olaso I, Gutiérrez JL, Villamor B, Carrera P, Valdés L, Abaunza P (2005). Seasonal changes in the north-eastern Atlantic mackerel diet (Scomber scombrus) in the north of Spain (ICES Division VIIIc). Journal of the Marine Biological Association of the UK 85:415-418.

Orians GH, Pearson NE (1979). On the theory of central place foraging. *In*: Horn DJ, Mitchell RD, Stairs GR (Eds.), Analysis of ecological systems. Ohio State University Press, Columbus, USA.

OSPAR (2000). Quality Status Report 2000: Region IV: Bay of Biscay and Iberian Coast. OSPAR Commission, London, UK.

Ovaskainen O, Abrego N, Halme P, Dunson D, Warton D (2016). Using latent variable models to identify large networks of species-to-species associations at different spatial scales. Methods in Ecology and Evolution 7:549-555.

Ovaskainen O, Hottola J, Siitonen J (2010). Modeling species co-occurrence by multivariate logistic regression generates new hypotheses on fungal interactions. Ecology 91:2514-2521.

Ovaskainen O, Tikhonov G, Norberg A, Guillaume Blanchet F, Duan L, Dunson D, Roslin T, Abrego N (2017). How to make more out of community data? A conceptual framework and its implementation as models and software. Ecology Letters 20:561-576.

Paine RT (1969). A Note on Trophic Complexity and Community Stability. The American Naturalist 103:91-93.

Paiva VH, Geraldes P, Ramírez I, Meirinho A, Garthe S, Ramos JA (2010a). Foraging plasticity in a pelagic seabird species along a marine productivity gradient. Marine Ecology Progress Series 398:259-274.

Paiva VH, Xavier J, Geraldes P, Ramirez I, Garthe S, Ramos JA (2010b). Foraging ecology of Cory's shearwaters in different oceanic environments of the North Atlantic. Marine Ecology Progress Series 410:257-268.

Pante E, Simon-Bouhet B (2013). marmap: a package for importing, plotting and analyzing bathymetric and topographic data in R. PLoS ONE 8:1-4.

Parmesan C, Yohe G (2003). A globally coherent fingerprint of climate change impacts across natural systems. Nature 421:37-42.

Pearson RG, Dawson TP (2003). Predicting the impacts of climate change on the distribution of species: are bioclimate envelope models useful? Global Ecology and Biogeography 12:361-371.

Pecl GT, Araújo MB, Bell JD, Blanchard J, Bonebrake TC, Chen I-C, Clark TD, Colwell RK, Danielsen F, Evengård B (2017). Biodiversity redistribution under climate change: Impacts on ecosystems and human well-being. Science 355: 1-9.

Pedro PI, Ramos JA, Neves VC, Paiva VH (2013). Past and present trophic position and decadal changes in diet of Yellow-legged Gull in the Azores Archipelago, NE Atlantic. European Journal of Wildlife Research 59:833-845

Pérez-Roda A, Delord K, Boué A, Arcos JM, García D, Micol T, Weimerskirch H, Pinaud D, Louzao M (2017). Identifying Important Atlantic Areas for the conservation of Balearic shearwaters: Spatial overlap with conservation areas. Deep Sea Research Part II: Topical Studies in Oceanography 141:285-293

Perretti CT, Thorson JT (2019). Spatio-temporal dynamics of summer flounder (*Paralichthys dentatus*) on the Northeast US shelf. Fisheries Research 215:62-68.

Peterson AT, Soberón J, Pearson RG, Anderson RP, Martínez-Meyer E, Nakamura M, Araújo MB (2011). Ecological niches and geographic distributions (MPB-49), Vol 49. Princeton University Press, Princeton, USA.

Petitgas P (1993). Geostatistics for fish stock assessments: a review and an acoustic application. ICES Journal of Marine Science 50:285-298.

Petitgas P (1996). Geostatistics and their applications to fisheries survey data. *In*: Megrey B.A., Moksness E. (Eds.), Computers in Fisheries Research. Springer, Dordrecht, The Netherlands.

Petitgas P (1997). Sole egg distributions in space and time characterised by a geostatistical model and its estimation variance. ICES Journal of Marine Science 54:213-225.

Petitgas P (2001). Geostatistics in fisheries survey design and stock assessment: models, variances and applications. Fish and Fisheries 2:231-249.

Petitgas P (2009). Geostatistics and their applications to fisheries survey data: a history of ideas, 1990–2007. *In*: Megrey B.A., Moksness E. (Eds.) Computers in Fisheries Research. Springer, Dordrecht. The Netehrlands.

Pettex E, Laran S, Authier M, Blanck A, Dorémus G, Falchetto H, Lambert C, Monestiez P, Stéfan E, Van Canneyt O, Ridoux V (2017). Using large scale surveys to investigate seasonal variations in seabird distribution and abundance. Part II: The Bay of Biscay and the English Channel. Deep Sea Research Part II: Topical Studies in Oceanography 141:86-101.

Phillips JA, Banks AN, Bolton M, Brereton T, Cazenave P, Gillies N, Padget O, van der Kooij J, Waggitt J, Guilford T (2021). Consistent concentrations of critically endangered Balearic shearwaters in UK waters revealed by at-sea surveys. Ecology and Evolution, 11: 1544-1557.

Phillips RA, McGill RAR, Dawson DA, Bearhop S (2011). Sexual segregation in distribution, diet and trophic level of seabirds: insights from stable isotope analysis. Marine Biology 158:2199-2208.

Piatt IJF, Sydeman WJ (2007). Seabirds as indicators of marine ecosystems. Marine Ecology Progress Series 352:199-204.

Pinsky ML, Eikeset AM, McCauley DJ, Payne JL, Sunday JM (2019). Greater vulnerability to warming of marine versus terrestrial ectotherms. Nature 569:108-111.

Pitcher TJ (1986). Functions of shoaling behaviour in teleosts. *In*: T.J. Pitcher (Ed.), The behaviour of teleost fishes (pp. 291-227). Springer, USA.

Planque B, Beillois P, Jégou A-M, Lazure P, Petitgas P, Puillat (2003). Large-scale hydroclimatic variability in the Bay of Biscay: the 1990s in the context of interdecadal changes. Proc ICES Marine Science Symposia, 219: 61-70.

Pocheville A (2015). The Ecological Niche: History and Recent Controversies. *In*: T. Heams et al., (Eds.), Handbook of Evolutionary Thinking in the Sciences (547-586). Springer, Dordrecht, The Netherlands.

Poloczanska ES, Brown CJ, Sydeman WJ, Kiessling W, Schoeman DS, Moore PJ, Brander K, Bruno JF, Buckley LB, Burrows MT (2013). Global imprint of climate change on marine life. Nature Climate Change 3:1-7.

Poloczanska ES, Burrows MT, Brown CJ, García Molinos J, Halpern BS, Hoegh-Guldberg O, Kappel CV, Moore PJ, Richardson AJ, Schoeman DS, Sydeman WJ (2016). Responses of Marine Organisms to Climate Change across Oceans. Frontiers in Marine Science 3:1-21.

Pollock LJ, Tingley R, Morris WK, Golding N, O'Hara RB, Parris KM, Vesk PA, McCarthy MA, McPherson J (2014). Understanding co-occurrence by modelling species simultaneously with a Joint Species Distribution Model (JSDM). Methods in Ecology and Evolution 5:397-406.

Pusineri C, Magnin V, Meynier L, Spitz J, Hassani S, Ridoux V (2007). Food and feeding ecology of the common dolphin (*Delphinus delphis*) in the oceanic Northeast Atlantic and comparison with its diet in neritic areas. Marine Mammal Science 23:30-47.

Pyke GH (1984). Optimal foraging theory: a critical review. Annual review of ecology and systematics 15:523-575.

Ridoux V, Lafontaine L, Bustamante P, Caurant F, Dabin W, Delcroix C, Hassani S, Meynier L, Vasco Pereira da S, Simonin S, Robert M, Spitz J, Van Canneyt O (2004). The impact of the "Erika" oil spill on pelagic and coastal marine mammals: Combining demographic, ecological, trace metals and biomarker evidences. Aquatic Living Resources 17:379-387.

Ringelstein J, Pusineri C, Hassani S, Meynier L, Nicolas R, Ridoux V (2006). Food and feeding ecology of the striped dolphin, Stenella coeruleoalba, in the oceanic waters of the north-east Atlantic. Journal of the Marine Biological Association of the UK 86:909-918.

Robertson GS, Bolton M, Monaghan P (2016). Influence of diet and foraging strategy on reproductive success in two morphologically similar sympatric seabirds. Bird Study 63:319-329.

Robinson RA, Learmonth JA, Hutson AM, Macleod CD, Sparks TH, Leech DI, Pierce GJ, Rehfisch MM, Crick HQ (2005). Climate change and migratory species. Departmentfor Environment, Food and Rural Affairs, London, UK.

Ronconi RA, Koopman HN, McKinstry CAE, Wong SNP, Westgate AJ (2010a). Inter-annual variability in diet of non-breeding pelagic seabirds Puffinus spp. at migratory staging areas: evidence from stable isotopes and fatty acids. Marine Ecology Progress Series 419:267-282.

Ronconi RA, Ryan PG, Ropert-Coudert Y (2010b). Diving of great shearwaters (*Puffinus gravis*) in cold and warm water regions of the South Atlantic Ocean. PLoS ONE 5:1-7.

Rose GA, Leggett WC (1990). The importance of scale to predator-prey spatial correlations: an example of Atlantic fishes. Ecology 71:33-43.

Royan A, Reynolds SJ, Hannah DM, Prudhomme C, Noble DG, Sadler JP (2016). Shared environmental responses drive co-occurrence patterns in river bird communities. Ecography 39:733-742.

Rubio A, Gomis D, Jordà G, Espino M (2009). Estimating geostrophic and total velocities from CTD and ADCP data: Intercomparison of different methods. Journal of Marine Systems 77:61-76.

Ruckelshaus M, Klinger T, Knowlton N, DeMaster DP (2008). Marine ecosystem-based management in practice: scientific and governance challenges. BioScience 58:53-63.

Saavedra C, Gerrodette T, Louzao M, Valeiras J, García S, Cerviño S, Pierce GJ, Santos MB (2018). Assessing the environmental status of the short-beaked common dolphin (Delphinus delphis) in North-western Spanish waters using abundance trends and safe removal limits. Progress in Oceanography 166:66-75.

Sakamoto Y, Ishiguro M, Kitagawa G (1986). Akaike information criterion statistics. D Reidel, Dordrecht, The Netherlands.

Santos M, Pierce G, López A, Martínez J, Fernández M, Ieno E, Mente E, Porteiro C, Carrera P, Meixide M (2004). Variability in the diet of common dolphins (*Delphinus delphis*) in Galician waters 1991–2003 and relationship with prey abundance. ICES Theme Session: Recent Advances in the Oceanography and Biology of the Iberian Waters and Adjacent Shelf Seas: Results from Integrated Multidisciplinary Projects.

Santos MB, German I, Correia D, Read FL, Cedeira JM, Caldas M, López A, Velasco F, Pierce GJ (2013). Long-term variation in common dolphin diet in relation to prey abundance. Marine Ecology Progress Series 481:249-268.

Scott BE, Sharples J, Ross ON, Wang J, Pierce GJ, Camphuysen CJ (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.

Scott BE, Webb A, Palmer MR, Embling CB, Sharples J (2013). Fine scale bio-physical oceanographic characteristics predict the foraging occurrence of contrasting seabird species; Gannet (*Morus bassanu*s) and storm petrel (*Hydrobates pelagicus*). Progress in Oceanography 117:118-129.

Sebastian-Gonzalez E, Sanchez-Zapata JA, Botella F, Ovaskainen O (2010). Testing the heterospecific attraction hypothesis with time-series data on species co-occurrence. Proceeding of theRoyal Society B 277:2983-2990.

Shaffer SA, Tremblay Y, Weimerskirch H, Scott D, Thompson DR, Sagar PM, Moller H, Taylor GA, Foley DG, Block BA, Costa DP (2006). Migratory shearwaters integrate oceanic resources across the Pacific Ocean in an endless summer. PNAS 103:12799-12802.

Shaffer SA, Weimerskirch H, Scott D, Pinaud D, Thompson DR, Sagar PM, Moller H, Taylor GA, Foley DG, Tremblay Y, Costa DP (2009). Spatiotemporal habitat use by breeding sooty shearwaters Puffinus griseus. Marine Ecology Progress Series 391:209-220.

Shields PM, Tajalli H (2006). Intermediate theory: The missing link in successful student scholarship. Journal of public affairs education 12:313-334.

Simard Y, Lavoie D, Saucier FJ (2002). Channel head dynamics: capelin (Mallotus villosus) aggregation in the tidally driven upwelling system of the Saguenay - St. Lawrence Marine Park's whale feeding ground. Canadian Journal of Fisheries and Aquatic Sciences 59:197-210.

Simmonds MP, Isaac SJ (2007). The impacts of climate change on marine mammals: early signs of significant problems. Oryx 41:19-26.

Sims DW, Queiroz N, Doyle TK, Houghton JD, Hays GC (2009). Satellite tracking of the World's largest bony fish, the ocean sunfish (Mola mola L.) in the North East Atlantic. Journal of Experimental Marine Biology and Ecology 370:127-133.

Skov H, Durinck J, Danielsen F, Bloch D (1995). Co-occurrence of cetaceans and seabirds in the northeast Atlantic. Journal of Biogeography:71-88.

Soberon J (2007). Grinnellian and Eltonian niches and geographic distributions of species. Ecology Letters 10:1115-1123.

Soberon J, Nakamura M (2009). Niches and distributional areas: concepts, methods, and assumptions. PNAS 106 Suppl 2:19644-19650.

Soberón J, Peterson AT (2005). Interpretation of models of fundamental ecological niches and species' distributional areas. Biodiveristy Informatics, 2:1-10.

Sobradillo B, Boyra G, Martinez U, Carrera P, Peña M, Irigoien X (2019). Target Strength and swimbladder morphology of Mueller's pearlside (Maurolicus muelleri). Scientific Reports 9:1-14.

Solomon S, Manning M, Marquis M, Qin D (2007). Climate change 2007: the physical science basis. Working group I contribution to the fourth assessment report of the IPCC, Vol 4. Cambridge university press, Cambridge,UK.

Spitz J, Cherel Y, Bertin S, Kiszka J, Dewez A, Ridoux V (2011). Prey preferences among the community of deep-diving odontocetes from the Bay of Biscay, Northeast Atlantic. Deep Sea Research Part I: Oceanographic Research Papers 58:273-282.

Spitz J, Richard E, Meynier L, Pusineri C, Ridoux V (2006). Dietary plasticity of the oceanic striped dolphin, Stenella coeruleoalba, in the neritic waters of the Bay of Biscay. Journal of Sea Research 55:309-320.

Spitz J, Ridoux V, Brind'Amour A (2014). Let's go beyond taxonomy in diet description: testing a trait-based approach to prey–predator relationships. Journal of Animal Ecology 83:1137-1148.

Spitz J, Ridoux V, Trites AW, Laran S, Authier M (2018). Prey consumption by cetaceans reveals the importance of energy-rich food webs in the Bay of Biscay. Progress in Oceanography 166:148-158.

Spitz J, Trites AW, Becquet V, Brind'Amour A, Cherel Y, Galois R, Ridoux V (2012). Cost of Living Dictates what Whales, Dolphins and Porpoises Eat: The Importance of Prey Quality on Predator Foraging Strategies. PLoS ONE 7:1-7.

St John MA, Borja A, Chust G, Heath M, Grigorov I, Mariani P, Martin AP, Santos RS (2016). A dark hole in our understanding of marine ecosystems and their services: perspectives from the mesopelagic community. Frontiers in Marine Science 3:1-6.

Stefánsson G (1996). Analysis of groundfish survey abundance data: combining the GLM and delta approaches. ICES Journal of Marine Science 53:577-588.

Stenhouse IJ, Egevang C, Phillips RA (2012). Trans-equatorial migration, staging sites and wintering area of Sabine's Gulls Larus sabini in the Atlantic Ocean. Ibis 154:42-51.

Stenseth NC, Mysterud A (2005). Weather packages: finding the right scale and composition of climate in ecology. Journal of Animal Ecology 74:1195-1198.

Stienen EW, Van Beers PW, Brenninkmeijer A, Habraken J, Raaijmakers M, Van Tienen PG (2000). Reflections of a specialist: patterns in food provisioning and foraging conditions in Sandwich Terns Sterna sandvicensis. Ardea 88:33-49.

Stocker TF, Qin D, Plattner G-K, Tignor M, Allen SK, Boschung J, Nauels A, Xia Y, Bex V, Midgley PM (2013). Climate change 2013: The physical science basis. Contribution of working group I to the fifth assessment report of the intergovernmental panel on climate change. 1535 pp. Cambridge University Press, Cambridge, UK and New York, USA.

Sydeman WJ, Mills KL, Santora JA, Thompson SA, Bertram DF, Morgan KH, Hipfner JM, Wells BK, Wolf SG (2009). Seabirds and climate in the California Current—a synthesis of change. CalCOFI Reports 50:82-104.

Sydeman WJ, Poloczanska E, Reed TE, Thompson SA (2015). Climate change and marine vertebrates. Science 350:772-777.

Thiebot J-B, Cherel Y, Trathan PN, Bost C-A (2012). Coexistence of oceanic predators on wintering areas explained by population-scale foraging segregation in space or time. Ecology 93:122-130.

Thiers L, Louzao M, Ridoux V, Le Corre M, Jaquemet S, Weimerskirch H (2014). Combining methods to describe important marine habitats for top predators: application to identify biological hotspots in tropical waters. PLoS ONE 9:1-23.

Thomas L, Buckland ST, Burnham KP, Anderson DR, Laake JL, L BD, S. S (2002). Distance sampling. *In*: A.H. E-S, W.W. P (Eds.) Encyclopedia of Environmetrics. John Wiley & Sons, Chichester, UK.

Thomas RJ, Medeiros RJ, Pollard AL (2006). Evidence for nocturnal inter-tidal foraging by European Storm-petrels Hydrobates pelagicus during migration. Atlantic seabirds 8:87-96

Thompson KR (1987). The ecology of the Manx shearwater Puffinus puffinus on Rhum, West Scotland. University of Glasgow, Scotland.

Thorson JT (2019a). Guidance for decisions using the Vector Autoregressive Spatio-Temporal (VAST) package in stock, ecosystem, habitat and climate assessments. Fisheries Research 210:143-161.

Thorson JT (2019b). Measuring the impact of oceanographic indices on species distribution shifts: The spatially varying effect of cold-pool extent in the eastern Bering Sea. Limnology and Oceanography 64:2632-2645.

Thorson JT, Arimitsu ML, Barnett LAK, Cheng W, Eisner LB, Haynie AC, Hermann AJ, Holsman K, Kimmel DG, Lomas MW, Richar J, Siddon EC (2021). Forecasting community reassembly using climate-linked spatio-temporal ecosystem models. Ecography 44:612-625.

Thorson JT, Barnett LAK (2017). Comparing estimates of abundance trends and distribution shifts using single- and multispecies models of fishes and biogenic habitat. ICES Journal of Marine Science 74:1311-1321.

Thorson JT, Ianelli JN, Kotwicki S (2017). The relative influence of temperature and size-structure on fish distribution shifts: A case-study on Walleye pollock in the Bering Sea. Fish and Fisheries 18:1073-1084.

Thorson JT, Pinsky ML, Ward EJ, Gimenez O (2016). Model-based inference for estimating shifts in species distribution, area occupied and centre of gravity. Methods in Ecology and Evolution 7:990-1002.

Thurman LL, Barner AK, Garcia TS, Chestnut T (2019) .Testing the link between species interactions and species co-occurrence in a trophic network. Ecography 42:1658-1670.

Tilman D (1982). Resource competition and community structure. Princeton university press, Princeton, USA.

Torres LG, Read AJ, Halpin P (2008). Fine-scale habitat modeling of a top marine predator: Do prey data improve predictive capacity. Ecological Applications 18:1702-1717.

Tremblay Y, Thiebault A, Mullers R, Pistorius P (2014). Bird-borne video-cameras show that seabird movement patterns relate to previously unrevealed proximate environment, not prey. PLoS ONE 9:1-6.

Trisos CH, Merow C, Pigot AL (2020). The projected timing of abrupt ecological disruption from climate change. Nature 580:496-501.

Turner W, Spector S, Gardiner N, Fladeland M, Sterling E, Steininger M (2003). Remote sensing for biodiversity science and conservation. Trends in Ecology & Evolution 18:306-314.

Uriarte A, Lucio P (2001). Migration of adult mackerel along the Atlantic European shelf edge from a tagging experiment in the south of the Bay of Biscay in 1994. Fisheries Research 50:129-139.

Valeiras J (2003). Attendance of scavenging seabirds at trawler discards off Galicia, Spain. Scientia Marina 67:77-82.

Varela M (1996) Phytoplankton ecology in the Bay of Biscay. Scientia Marina 60:45-53

Veech JA (2013). A probabilistic model for analysing species co-occurrence. Global Ecology and Biogeography 22:252-260.

Veit RR, Harrison NM (2017). Positive Interactions among Foraging Seabirds, Marine Mammals and Fishes and Implications for Their Conservation. Frontiers in Ecology and Evolution 5:1-8.

Víkingsson GA (1997). Feeding of fin whales (Balaenoptera physalus) off Iceland–diurnal and seasonal variation and possible rates. Journal of Northwest Atlantic Fishery Science 22:77-89

Violle C, Navas M-L, Vile D, Kazakou E, Fortunel C, Hummel I, Garnier E (2007). Let the concept of trait be functional! Oikos 116:882-892.

Votier SC, Bearhop S, Crane JE, Manuel Arcos J, Furness RW (2007). Seabird predation by great skuas Stercorarius skua–intra-specific competition for food? Journal of Avian Biology 38:234-246.

Votier SC, Bearhop S, MacCormick A, Ratcliffe N, Furness RW (2003). Assessing the diet of great skuas, Catharacta skua, using five different techniques. Polar Biology 26:20-26.

Waggitt JJ, Cazenave PW, Howarth LM, Evans PG, van der Kooij J, Hiddink JG (2018). Combined measurements of prey availability explain habitat selection in foraging seabirds. Biology letters 14:1-5.

Waggitt JJ, Evans PGH, Andrade J, Banks AN, Boisseau O, Bolton M, Bradbury G, Brereton T, Camphuysen CJ, Durinck J, Felce T, Fijn RC, Garcia-Baron I, Garthe S, Geelhoed SCV, Gilles A, Goodall M, Haelters J, Hamilton S, Hartny-Mills L, Hodgins N, James K, Jessopp M, Kavanagh AS, Leopold M, Lohrengel K, Louzao M, Markones N, Martínez-Cedeira J, Ó Cadhla O, Perry SL, Pierce GJ, Ridoux V, Robinson KP, Santos MB, Saavedra C, Skov H, Stienen EWM, Sveegaard S, Thompson P, Vanermen N, Wall D, Webb A, Wilson J, Wanless S, Hiddink JG, Punt A (2020). Distribution maps of cetacean and seabird populations in the North-East Atlantic. Journal of Applied Ecology 57:253-269.

Warren DL, Glor RE, Turelli M (2008). Environmental niche equivalency versus conservatism: quantitative approaches to niche evolution. Evolution 62:2868-2883.

Warton DI, Blanchet FG, O'Hara RB, Ovaskainen O, Taskinen S, Walker SC, Hui FKC (2015). So Many Variables: Joint Modeling in Community Ecology. Trends in Ecology and Evolution 30:766-779.

Warton DI, Blanchet FG, O’Hara R, Ovaskainen O, Taskinen S, Walker SC, Hui FK (2016). Extending Joint Models in Community Ecology: A Response to Beissinger et al. Trends in Ecology & Evolution 31:737-738.

Watanuki Y, Thiebot J-B (2018). Factors affecting the importance of myctophids in the diet of the world’s seabirds. Marine Biology 165: 1-14.

Wilkinson DP, Golding N, Guillera-Arroita G, Tingley R, McCarthy MA, Peres-Neto P (2018). A comparison of joint species distribution models for presence-absence data. Methods in Ecology and Evolution 10: 198-211.

Wisz MS, Hijmans RJ, Li J, Peterson AT, Graham CH, Guisan A (2008). Effects of sample size on the performance of species distribution models. Diversity and Distributions 14:763-773.

Wisz MS, Pottier J, Kissling WD, Pellissier L, Lenoir J, Damgaard CF, Dormann CF, Forchhammer MC, Grytnes JA, Guisan A, Heikkinen RK, Hoye TT, Kuhn I, Luoto M, Maiorano L, Nilsson MC, Normand S, Ockinger E, Schmidt NM, Termansen M, Timmermann A, Wardle DA, Aastrup P, Svenning JC (2013). The role of biotic interactions in shaping distributions and realised assemblages of species: implications for species distribution modelling. Biol Rev Camb Philos Soc 88:15-30.

Xu H, Lennert-Cody CE, Maunder MN, Minte-Vera CV (2019). Spatiotemporal dynamics of the dolphin-associated purse-seine fishery for yellowfin tuna (*Thunnus albacares*) in the eastern Pacific Ocean. Fisheries Research 213:121-131.

Yésou P (2003). Recent changes in the summer distribution of the Balearic shearwater *Puffinus mauretanicus* off western France. Scientia Marina 67:143-148.

Zurell D, Pollock LJ, Thuiller W (2018). Do joint species distribution models reliably detect interspecific interactions from co-occurrence data in homogenous environments? Ecography 41:1812-1819.

Zuur A, Ieno EN, Smith GM (2007). Analyzing ecological data. Springer Science & Business Media, New York, USA.