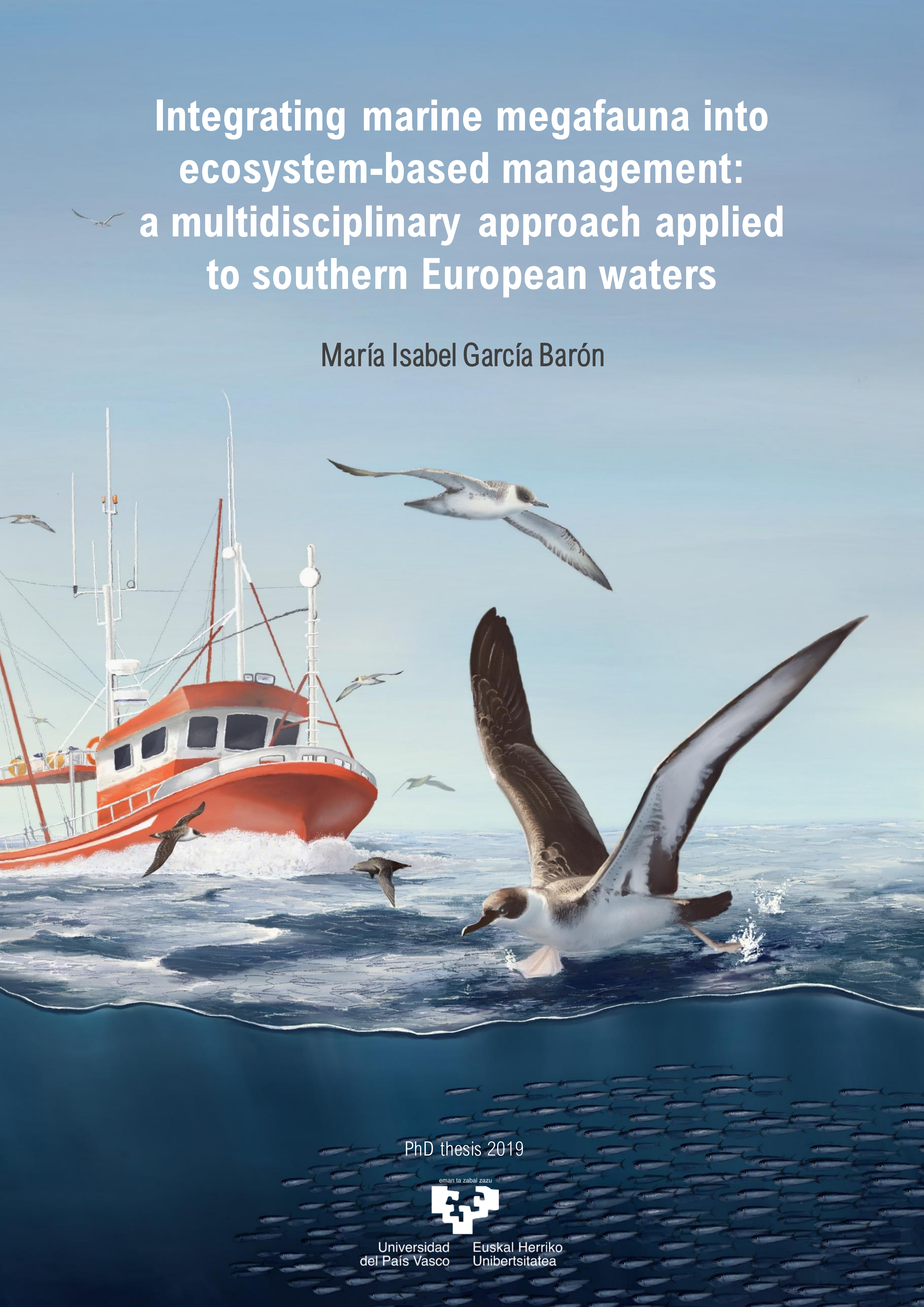

Integrating marine megafauna into ecosystem-based management: a multidisciplinary approach applied to southern European waters

María Isabel García Barón

PhD thesis 2019

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Integrating marine megafauna into ecosystem-based management: a multidisciplinary approach applied to southern European waters

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A mis padres y mi hermana

"Even if you never have the chance to see or touch the ocean,
it touches you with every breath you take, every drop of water you drink,
every bite you consume. Everyone, everywhere is inextricably connected to
and utterly dependent upon the existence of the sea."

Sylvia Earle

"It is a curious situation that the sea, from which life first arose,
should now be threatened by the activities of one form of that life.
But the sea, though changed in a sinister way,
will continue to exist: the threat is rather to life itself."

Rachel Carson

CONTENTS

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SCIENTIFIC PRODUCTION AND FORMATION

The scientific and technical material produced, and the scientific formation acquired during the period of this doctoral thesis (March 2015 - October 2019) are detailed in this section:

1. Peer-Reviewed Publications

First author publications

García-Barón, I., Giakoumi, S., Santos, M.B., Granado, I., Louzao, M. (Submitted) *The value of time series data for conservation planning.* Journal of Applied Ecology.

García-Barón, I., Santos, M.B., Saavedra, C., Astarloa, A., Valeiras, J., Barcelona, S.G., Louzao, M. (Under review) *Essential dynamic ocean variables shape the environmental envelopes of marine megafauna diversity.* Ecological Indicators.

García-Barón, I., Santos, M.B., Uriarte, A., Inchausti, J.I., Escribano, J.M., Albisu, J., Fayos, M., Pis-Millán, J.A., Oleaga, Á., Alonso, F.E., Hernández, O., Moreno, O., Louzao, M., 2019. *Which are the main threats affecting the marine megafauna in the Bay of Biscay?* Continental Shelf Research 186, 1–12.

García-Barón, I., Authier, M., Caballero, A., Vázquez, J.A., Santos, M.B., Louzao, M., 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., Cortés-Avizanda, A., Verburg, P.H., Marques, T.A., Moreno-Opo, R., Pereira, H.M., Donázar, J.A., 2018. *How to fit the distribution of apex scavengers into land-abandonment scenarios? The Cinereous vulture in the Mediterranean biome.* Diversity and Distributions 24, 1018–1031.

Other

Waggitt, J.J., Evans P.G.H., Hiddink, J.G., Geert, J., Kavanagh, A., Banks, A., Gilles, A., Santos, M.B., Saavedra, C., Wall, D., Stienan, E.W.M., Bradbury, G., Pierce, G.J., Skov, H., Garcia-Barón, I., Haelters, J., Wilson, J., Andrade, J., Martinez-Cedeira, J., James, K., Lohrengel, K., Bolton, M., Jessopp, M., Markones, M., Hodgins, N., Vanermen, N., O'Cadhla, O., Thompson, P., Fijn, R.C., Hamilton, S., Perry, S.L., Wanless, S., Sveegaard, S., Garthe, S., Geelhoed, S., Brereton, T., Felce, T. (In press) *Distribution maps of cetacean and seabird populations in the North-East Atlantic.* Journal of Applied Ecology.

Louzao, M., Valeiras, J., Garcia-Barcelona, S., González-Quirós, R., Nogueira, E., Iglesias, M., Bode, A., Vázquez, J.A., Murcia, J.L., Saavedra, C., Pierce, G.J., Fernández, R., García-Barón, I., Santos, M.B., 2019. *Marine megafauna niche coexistence and hotspot areas in a temperate ecosystem.* Continental Shelf Research 186, 77–87.

Franco, J., Fort, J., García-Barón, I., Loubat, P., Louzao, M., del Puerto, O., Zorita, I., 2019. *Incidence of plastic ingestion in seabirds from the Bay of Biscay (Southwestern Europe).* Marine Pollution Bulletin 146, 387-392.

Louzao, M., García-Barón, I., Rubio, A., Martínez, U., Vázquez, J.A., Murcia, J.L., Nogueira, E., Boyra, G., 2019. *Understanding the 3D environment of pelagic seabirds from multidisciplinary oceanographic surveys, to advance ecosystem-based monitoring.* Marine Ecology Progress Series 617–618, 199–219.

Virgili, A., Authier, M., Boisseau, O., Cañadas, A., Claridge, D., Cole, T., Corkeron, P., Dorémus, G., David, L., Di-Méglio, N., Dunn, C., Dunn, T.E., García-Barón, I., Laran, S., Lauriano, G., Lewis, M., Louzao, M., Mannocci, L., Martínez-Cedeira, J., Palka, D., Panigada, S., Pettex, E., Roberts, J.J., Ruiz, L., Saavedra, C., Santos, M.B., Van Canneyt, O., Vázquez Bonales, J.A., Monestiez, P., Ridoux, V., 2019. *Combining multiple visual surveys to model the habitat of deep-diving cetaceans at the basin scale.* Global Ecology and Biogeography 28(3), 300-314.

Louzao, M., Gallagher, R., García-Barón, I., Chust, G., Intxausti, I., Albisu, J., Brereton, T., Fontán, A., 2019. *Threshold responses in bird mortality driven by extreme wind events.* Ecological Indicators 99, 183–192.

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Giménez, J., Marçalo, A., García-Polo, M., García-Barón, I., Castillo, J.J., Fernández-Maldonado, C., Saavedra, C., Santos, M.B., de Stephanis, R., 2018. *Feeding ecology of Mediterranean Common dolphins: The importance of mesopelagic fish in the diet of an endangered subpopulation.* Marine Mammal Science 34, 136–154.

2. Conference Papers

Oral communications

García-Barón, I., Franco, J., Fort, J., Loubat, P., Louzao, M., Zorita, I. (2019). *Primeros datos sobre la ingestión de desechos plásticos por aves marinas en el Golfo de Bizkaia*. In II Ornithological Congress of Euskadi. Vitoria-Gasteiz (Spain).

García-Barón, I., Giakoumi, S., Santos, M.B., Saavedra, C., Granado, I., Louzao, M. (2019). *Identifying high priority areas for marine top predators in southern Europe.* In 1st Meeting of the Iberian Ecological Society & XIV AEET Meeting. Barcelona (Spain).

García-Barón, I., Santos, B., Saavedra, C., Valeiras, X., García, S., Louzao, M. (2018) *Estimas de abundancia de depredadores apicales para determinar áreas clave en el sur del Golfo de Bizkaia*. In XI Spanish Society of Cetaceans Congress. Bilbao (Spain).

García-Barón, I., Authier, M., Caballero, A., Vázquez, J.A., Santos, M.B., Murcia, J.L., Louzao, M. (2018). *Modelling the relative abundance of an endangered baleen whale to identify missing critical conservation areas*. In 12th International Postgraduate Course Research in Marine Environment & Resources 2018. Donostia-San Sebastián (Spain).

García-Barón, I., Louzao, M., Santos M.B. (2017). *Pelagic changing ecosystems from predators' perspective: advancing conservation efforts in southern European waters.* In 11th International Postgraduate Course Research in Marine Environment & Resources 2017. Donostia-San Sebastián (Spain).

García-Barón, I., Authier, M., Caballero, A., Vázquez, J.A., Santos, M.B., Murcia, J.L., Louzao, M. (2016). *Modelado espacial de la abundancia relativa de rorcual común en la Bahía de Bizkaia.* In IX Spanish Society of Cetaceans Congress. Las Palmas de Gran Canaria (Spain).

García-Barón, I., Louzao, M., Intxausti, I., Albisu, J. (2016). *¿A qué presiones se enfrentan las aves marinas en el Cantábrico oriental?: una aproximación desde el punto de vista de los centros de recuperación.* In I Ornithological Congress of Euskadi. Busturia (Spain).

Franco, J., Fort, J., García-Barón, I., Loubat, P., Louzao, M., Zorita, I. (2018) *First data on plastic litter ingested by seabirds in the Bay of Biscay.* In MICRO 2018, Fate and Impact of Microplastics: Knowledge, Actions and Solutions. Lanzarote (Spain).

Louzao, M., García-Barón, I., Astarloa, A., 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).

Louzao, M., Valeiras, S., García-Barcelona, S., González-Quirós, R., Nogueira, E., Iglesias, M., Bode, A., Vázquez, J.A., Murcia, J.L., Saavedra, C., Pierce, G.J., Fernández, R., García-Barón, I., Santos, M.B. (2018). *Co-occurrence of marine predators in the northern Iberian Peninsula inferred from spatial modelling.* In XVIth International Symposium on Oceanography of the Bay of Biscay (ISOBAY 16). Anglet (France).

Virgili, A., Authier, M., Boisseau, O., Cañadas, A., Claridge, D., Cole, T., Corkeron, P., Dorémus, G., David, L., Di-Méglio, N., Dunn, C., Dunn, T., García-Barón, I., Laran, S., Lauriano, G., Lewis, M., Louzao, M., Mannocci, L., Martínez-Cedeira, J., Palka, D., Panigada, S., Pettex, E., Roberts, J., Ruiz, L., Saavedra, C., Santos, M.B., Van-Canneyt, O., Vázquez Bonales, J.A., Monestiez, P., Ridoux, V. (2018). *Would habitat models for deep-diving cetaceans be improved if prey distributions were included?* In 32nd European Cetacean Society Conference. La Spezia (Italy).

Virgili, A., Authier, M., Boisseau, O., Cañadas, A., Claridge, D., Cole, T., Corkeron, P., Dorémus, G., David, L., Di-Méglio, N., Dunn, C., Dunn, T., García-Barón, I., Laran, S., Lauriano, G., Lewis, M., Louzao, M., Mannocci, L., Martínez-Cedeira, J., Palka, D., Panigada, S., Pettex, E., Roberts, J., Ruiz, L., Saavedra, C., Santos, M.B., Van-Canneyt, O., Vázquez Bonales, J.A., Monestiez, P., Ridoux, V. (2017). *Large scale distribution of deep-diving cetaceans in the North Atlantic Ocean and the Mediterranean Sea.* In 22nd Society for Marine Mammal Conference. Halifax, Nova Scotia (Canada).

Louzao, M., Boyra, G., García-Barón, I., Rubio, A., Martínez, U., Vázquez, J.A., Murcia, J.L., Krug, I., Oyarzabal, I., Basterretxea, M. (2017). *Understanding pelagic seabird 3D environment from multidisciplinary oceanographic cruises.* In Symposium on Drivers of dynamics of small pelagic fish resources. Victoria, BC (Canada).

Louzao, M., García-Barón, I., Rubio, A., Martínez, U., Vázquez, J.A., Murcia, J.L., Krug, I., Oyarzabal, I., Basterretxea, M., Boyra, G. (2016). *Understanding pelagic seabird 3D environment from multidisciplinary oceanographic cruises.* In 6th International Albatross and Petrel Conference. Barcelona (Spain).

Louzao, M., Boyra, G., García-Barón, I., Rubio, A., Martínez, U., Vázquez, J.A., Murcia, J.L., Krug, I., Oyarzabal, I., Basterretxea, M. Franco, J., Cotano, U. (2016). *Algo más que avistar aves marinas: cómo pueden contribuir los programas de observadores a los planes seguimiento.* In I Ornithological Congress of Euskadi. Busturia (Spain).

Louzao, M., Boyra, G., Rubio, A., Martínez, U., García-Barón, I., Vázquez, J.A., Murcia, J.L., Cotano, U. (2015). *Disentangling the effects of environmental conditions and pelagic prey availability in* *driving the spatial patterns of highly migratory seabirds while refueling.* In 2nd World Seabird Conference. Cape Town (South Africa).

Louzao, M., Valeiras, J., García-Barcelona, S., González-Quirós, R., Nogueira, E., Iglesias, M., Bode, A., Vázquez, J.A., Murcia, J.L., Saavedra, C., Pierce, G.J., García-Barón, I., Santos, M.B. (2015). *Modelización espacial de la distribución de cetáceos en el norte de la Península Ibérica: la importancia de incluir información de sus presas.* In VIII Spanish Society of Cetaceans Congress. Vigo (Spain).

Giménez, J., Marçalo, A., Garcia Polo, M., García-Barón, I., Castillo, J.J., Fernández Maldonado, C., Santos, M.B., de Stephanis, R. (2015). *Ecología trófica de los delfines comunes del Mar de Alborán (Mar Mediterráneo).* In VIII Spanish Society of Cetaceans Congress. Vigo (Spain).

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García-Barón, I., Intxausti, I., Albisu, J., Fayos, M., Oleaga, A., Santos, M.B., Louzao, M. (2018). *Pressures facing marine top predators in the Bay of Biscay: insights from rehabilitation centres.* In XVIth International Symposium on Oceanography of the Bay of Biscay (ISOBAY 16). Anglet (France).

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LIST OF ACRONYMS

Acronym	Definition
2D	2-dimensional
3D	3-dimensional
ACAP	Agreement on the Conservation of Albatrosses and Petrels
ACCOBAMS	Agreement on the Conservation of Cetaceans of the Black Seas, Mediterranean and Contiguous Atlantic Area
ASCOBANS	Agreement on the Conservation of Small Cetaceans of the Baltic, North East Atlantic, Irish and North Seas
AIC	Akaike information criterion
AICc	Corrected Akaike Information Criterion
ALCTOR	*Alca torda*
ANEJ	Juvenile European anchovy (*Engraulis encrasicolus*)
$ANEJ_{10}$	Juvenile European anchovy between 5 and 15 m depth
$ANEJ_{70}$	Juvenile European anchovy between 5 and 70 m depth
$ANEJ_{DTG}$	Juvenile European anchovy from the surface up to the depth of maximum temperature gradient
ANEA	Adult European anchovy
$ANEA_{10}$	Adult European anchovy between 5 and 15 m depth
$ANEA_{70}$	Adult European anchovy between 5 and 70 m depth
$ANEA_{DTG}$	Adult European anchovy from the surface up to the depth of maximum temperature gradient
BAT	Bathymetry
BATG	Spatial gradient of the bathymetry
BD	Birds Directive (79/409/EEC)
BoB	Bay of Biscay
BLM	Boundary length modifier
BRI	Biodiversity richness index
CBD	Convention on Biological Diversity
CC	Central Cantabrian Sea
CDS	Conventional Distance Sampling
Chl-a	Chlorophyll-a concentration
Chl-a_g	Spatial gradient of the chlorophyll-a concentration
CI	Confidence interval
CITES	Convention on International Trade in Endangered Species of Wild Fauna and Flora
CMS	Convention on the Conservation of Migratory Species of Wild Animals
CODA	Cetacean Offshore Distribution and Abundance in the European Atlantic

Acronym	Definition
CR	Critically endangered
CV	Coefficient of variation
DCO	Distance to the coastline
DD	Data deficient
DELDEL	*Delphinus delphis*
DistCO	Closest distance to the coast
DisCO	Closest distance to the coast
DistSB	Closest distance to the shelf-break
DisSB	Closest distance to the shelf-break
DSB	Distance to the shelf-break
DSM	Density Surface Model
DTG	Depth of maximum temperature gradient
DYN	Dynamic height
EB	Emma Bardán
EBM	Ecosystem-Based Management
EBSA	Ecologically or Biologically Significant Marine Area
EC	Eastern Cantabrian Sea
ED	Explained Deviance
EEZ	Economic Exclusive Zone
EKE	Eddy Kinetic Energy
EN	Endangered
EOV	Essential Ocean Variable
ESW	Effective strip half-width
EU	European Union
FOO	Framework for Ocean Observing
GAM	Generalized Additive Model
GEO	Geostrophic velocity
GEO_{10}	Geostrophic velocity at 10 m
GEO_{70}	Median value of geostrophic velocity from the surface to 70 m depth
GEO_{DTG}	Median value of geostrophic velocity from the surface up to the depth of maximum temperature gradient
GES	Good Environmental Status
GLOMEL	*Globicephala melas*
GOOS	Global Ocean Observing System
GPS	Global Positioning System
GRSH	Great shearwater (*Ardenna gravis*)
HD	Habitats Directive (92/43/EEC)
HVBA	High-value biodiversity areas

Acronym	Definition
IAC	Inter-American Convention
IATTC	Inter-American Tropical Tuna Commission
IBA	Important Bird Area
ICCAT	International Commission for the Conservation of Atlantic Tunas
ICES	International Council for the Exploration of the Sea
ICHMEL	*Ichthyaetus melanocephalus*
ICG-COBAM	Intersessional Correspondence Group on the Coordination of Biodiversity Assessment and Monitoring
IEO	Spanish Institute of Oceanography
IMMA	Important Marine Mammal Areas
IUCN	International Union for Conservation of Nature
IWC	International Whaling Commission
JWGBIRD	Joint Working Group on Seabirds
L	Length of the segment in km
LARMIC	*Larus michahellis*
LARFUS	*Larus fuscus*
LC	Least concern
logBAT	Logarithm of bathymetry
MCDS	Multiple-Covariate Distance Sampling
MMPATF	Marine Mammal Protected Areas Task Force
MO	Miguel Oliver
MORBAS	*Morus bassanus*
MPA	Marine Protected Area
MS	Member States
MSFD	Marine Strategy Framework Directive
MSPD	Maritime Spatial Planning Directive
MTG	Maximum temperature gradient
N	Relative abundance
NA	North Atlantic
NAO	North Atlantic Oscillation
NG	North Galicia
nMDS	Non-metric multidimensional scaling
NOAA	National Oceanic and Atmospheric Administration (USA)
Np	Number of parameters
NT	Near threatened
NW	North-western
OECM	Other effective area-based conservation measure
OSI	Optimal statistical interpolation

Acronym	Definition
OSPAR	The Convention for the Protection of the Marine Environment of the North-East Atlantic
PA	Protected area
PCB	Polychlorinated biphenyl
PIL	European pilchard (*Sardina pilchardus*)
PIL_{10}	European pilchard between 5 and 15 m depth
PIL_{70}	European pilchard between 5 and 70 m depth
PIL_{DTG}	European pilchard from the surface up to the depth of maximum temperature gradient
PU	Planning unit
PUFMAU	*Puffinus mauretanicus*
PUFPUF	*Puffinus*
r	Spearman correlation coefficient
R/V	Research vessel
RM	Ramón Margalef
SAAM	Suivi Aérien de la Megafaune Marine
SAC	Special Area of Conservation
SAL	Salinity
SAL_{10}	Salinity at 10 m
SAL_{70}	Median value of salinity from the surface to 70 m depth
SAL_{DTG}	Median value of salinity from the surface up to the depth of maximum temperature gradient
SCANS	Small Cetacean Abundance in the North Sea and Adjacent waters
SCP	Systematic conservation planning
SDM	Species distribution model
SE-BoB	South-eastern Bay of Biscay
SG	South Galicia
SOSH	Sooty shearwater (*Ardenna grisea*)
SLA	Sea Level Anomalie
SLOPE	Slope
SPA	Special Protection Area
SST	Sea surface temperature
SSTG	Sea surface temperature gradient
SST_g	Sea surface temperature gradient
STESKU	*Stercorarius skua*
TEM	Temperature
TEM_{10}	Temperature at 10 m
TEM_{70}	Median value of temperature from the surface to 70 m depth

Acronym	Definition
TEM_{DTG}	Median value of temperature from the surface up to the depth of maximum temperature gradient
TH	Thalassa
THASAN	*Thalasseus sandvicensis*
TURTRU	*Tursiops truncatus*
URIAAL	*Uria aalge*
VMS	Vessel Monitoring System
VU	Vulnerable
w	Modulus of the Geostrophic currents
WC	Western Cantabrian Sea
WDPA	World Database of Protected Areas
WFD	Water Framework Directive
WGMME	Working Group on Marine Mammal Ecology
WOCE	World Ocean Circulation Experiment
WRC	Wildlife Rehabilitation Centre
ω_i	Akaike weight

LIST OF TABLES

LIST OF FIGURES

RESUMEN

Los ecosistemas marinos se ven amenazados por múltiples actividades humanas que afectan su sostenibilidad y resiliencia, causando una disminución de la biodiversidad marina y afectando a su funcionamiento. Las especies de mayor tamaño, la megafauna marina, presentan un alto riesgo de extinción en todo el mundo, lo que aumenta la necesidad de priorizar estrategias de conservación para garantizar su protección. Para revertir esta situación, se necesita urgentemente información sobre los patrones espacio-temporales de las presiones que afectan al medio marino y una evaluación de su severidad para proporcionar información para la conservación de la biodiversidad y de los hábitats, diseñar las medidas de mitigación apropiadas y asesorar en los procesos de toma de decisiones en materia de ordenación territorial.

La megafauna marina juega un papel esencial en los ecosistemas marinos y, debido a su intrínseca vulnerabilidad cuando está expuesta a presiones antropogénicas, actúa como centinela de la variabilidad y reorganización que se está produciendo en el ecosistema marino. En este contexto, se han promulgado leyes nacionales e internacionales y convenios internacionales para proteger a este grupo de especies. Dentro de la Unión Europea (UE), la Directiva Hábitats y la Directiva Aves tienen por objeto promover medidas de conservación y mantener la diversidad biológica y obliga a los Estados Miembros a que adopten medidas para alcanzar o mantener el estado de conservación favorable de los hábitats naturales y las especies. Además, la Directiva Marco sobre la Estrategia Marina (DMEM) incorpora el Enfoque Ecosistémico y el Principio de Precaución, con el fin de lograr y mantener el Buen Estado Ambiental (BEA) de las aguas de la UE para 2020. Además, la DMEM hace referencia de manera específica a la biodiversidad marina y refuerza la protección que ofrecen la Directiva Hábitats y la Directiva Aves. Por último, la Directiva para la Ordenación del Espacio Marítimo promueve también el desarrollo y la utilización sostenible de los recursos marinos y costeros desde una perspectiva holística.

Para anticipar la respuesta de los ecosistemas frente a las crecientes presiones a las que se ven sometidos, se requiere un enfoque holístico para su gestión con una visión integral del ecosistema (enfoque incluido en Directivas como la DMEM o la Directiva para la Ordenación del Espacio Marítimo). Un enfoque de gestión basada en el ecosistema (EBM) requiere conocimientos sobre los aspectos ecológicos, económicos y sociales del

ecosistema y sus interacciones para lograr su objetivo de un uso sostenible de los mismos. La implementación de un EBM requiere la recolección multidisciplinar de datos, el seguimiento del estado del sistema, su comportamiento y funcionamiento, la elaboración de métodos para organizar, mostrar e ilustrar las relaciones entre los componentes del ecosistema y avances metodológicos de carácter transdisciplinario para sintetizar datos, polivalentes e integradores, con el fin de asesorar en la adopción de medidas de gestión.

El Golfo de Vizcaya (en adelante 'GdV') y la costa norte y noroeste de la península ibérica, donde se ha centrado esta tesis, están situados en el Atlántico noreste. El GdV se caracteriza por una plataforma continental amplia en la zona occidental de Francia y estrecha en la costa norte de la Península Ibérica, donde un complejo patrón de circulación oceánica influenciado por diferentes corrientes genera fenómenos oceanográficos de mesoescala. En el GdV se producen dos afloramientos de fitoplancton, uno en primavera y otro en otoño, mientras que en la costa ibérica se producen durante el verano y principios de otoño. El GdV es un ecosistema pelágico muy dinámico y biológicamente rico con una comunidad de megafauna marina muy diversa que incluye varios grupos taxonómicos. Esta área representa además un importante corredor migratorio de aves y es una zona clave para aquellas especies que realizan migraciones estacionales en busca de áreas de alimentación.

La megafauna marina del GdV está sufriendo crecientes amenazas debido a diferentes presiones antropogénicas, tales como actividades extractivas (por ejemplo, la pesca o la acuicultura), las actividades industriales contaminantes, el transporte marítimo, que conlleva riesgo de derrames de petróleo o mareas negras y de colisiones con embarcaciones, en el caso de mamíferos marinos, y la introducción de especies alóctonas. Además, hay pruebas de los impactos, cada vez mayores, del cambio climático (como son los fenómenos meteorológicos extremos). Actualmente, las medidas de gestión implementadas para proteger la biodiversidad marina del GdV se centran en la designación, bajo diferentes legislaciones ambientales o sectoriales, de Áreas Marinas Protegidas (AMPs) tales como Zonas de Especial Conservación (ZEC), Zonas de Especial Protección para las Aves (ZEPA) o Biotopos Protegidos, entre otras. Todas estas áreas de conservación abarcan una amplia gama de diversidad de especies y hábitats y pueden constituir una red de AMPs cuyo objetivo es el revertir los impactos negativos causados por las actividades antropogénicas.

En este contexto, el objetivo de esta tesis fue evaluar los impactos de las actividades antropogénicas sobre la megafauna marina mediante la integración de su ecología espacial en el EBM. Al centrarse en las aves marinas y los cetáceos que habitan en el GdV, esta tesis desarrolla un marco ecológico integrador basado en enfoques multidisciplinares para identificar amenazas, desarrollar indicadores ambientales, establecer valores de referencia, obtener estimas de abundancia espacio-temporales, evaluar la coherencia de la actual red de AMPs y, además, examinar el valor de las series temporales de datos para una designación robusta de AMPs. Para lograr este objetivo, la tesis ha sido dividida en cinco capítulos.

Con el fin de recopilar información con relación a la susceptibilidad de la comunidad de megafauna del GdV a amenazas, tales como la captura incidental y, así contribuir a la evaluación del BEA dentro de la DMEM, en el **Capítulo 1**, se evaluó el impacto de las principales amenazas que afectan a las aves marinas y a los cetáceos en el GdV. En primer lugar, se realizó una evaluación cuantitativa basada en la causa de ingreso de aves marinas en los Centros de Recuperación de Fauna Silvestre de la costa cantábrica durante un periodo de 13 años. En segundo lugar, se llevó a cabo una evaluación cualitativa para identificar las principales amenazas que afectan directa o indirectamente a las especies de cetáceos y aves marinas del GdV. Además, sintetizamos la información de ambas evaluaciones para identificar aquellas amenazas que necesitan ser gestionadas con urgencia. Las principales amenazas identificadas para las aves marinas fueron la caquexia, la exposición a hidrocarburos y la interacción con artes de pesca, siendo las principales especies afectadas el arao común, la gaviota patiamarilla, el alcatraz atlántico, el cormorán grande y el alca. La evaluación cualitativa mostró que los cetáceos son especialmente vulnerables a la captura accidental, la colisión con buques y a aquellas amenazas relacionadas con la contaminación, mientras que las aves marinas son particularmente sensibles a los derrames de petróleo, la captura accidental y a la basura marina. Este tipo de estudios de evaluación de amenazas puede ayudar a identificar áreas y/o especies prioritarias para la aplicación de medidas de gestión para asegurar que el objetivo final de la DMEM, la conservación sostenible del medio marino, se alcanza.

Los programas de seguimiento, como son las campañas oceanográficas multidisciplinares, se están convirtiendo en sistemas de integración de datos que proporcionan información de múltiples componentes del sistema dentro del mismo esquema de seguimiento. En el **Capítulo 2**, se muestra un ejemplo de los resultados de un análisis combinando múltiples componentes pelágicos que proporciona una evaluación integral para avanzar en el seguimiento a nivel del ecosistema. En este capítulo desarrollamos un enfoque metodológico para identificar aquellos predictores oceanográficos y de abundancia de presas (*preyscapes*) biológicamente apropiados para considerar conjuntamente la dimensión espacial y vertical de los hábitats oceanográficos y que puede ser aplicado a cualquier especie marina. El objetivo de este trabajo fue comprender el entorno tridimensional de las aves marinas pelágicas mediante la evaluación de la importancia de la distribución espacial de la abundancia de sus presas y de las características oceanográficas a nivel de mesoescala que condicionan los patrones espaciales de abundancia de las pardelas sombría *Ardenna grisea* y capirotada *A. gravis* en el GdV. Estos patrones fueron explicados tanto por las condiciones oceanográficas como por la accesibilidad de las presas, ambas integradas por encima de la profundidad del gradiente máximo de temperatura en el caso de la pardela sombría e integradas a nivel de superficie en el caso de la pardela capirotada, lo que conduce a una segregación de las especies en el uso del hábitat vertical. De la misma manera, ambas especies mostraron una segregación espacial en la preferencia de hábitat, en zonas de plataforma continental (preferidas por la pardela sombría, que se asocia a zonas de afloramiento y desembocaduras de ríos) frente a zonas oceánicas (preferidas por la pardela capirotada). Además, en este trabajo se presentan las primeras estimas de abundancia de las pardelas sombría y capirotada durante el mes de septiembre en el GdV.

La medición de parámetros tales como las variables oceánicas esenciales (VOEs) es necesaria para evaluar el estado, la variabilidad y el cambio en los ecosistemas marinos, además de para la toma de decisión hacia una gestión sostenible de la diversidad biológica y los bienes y servicios de los ecosistemas. Las VOEs conforman la envolvente ambiental de una especie (es decir, las condiciones ambientales que una determinada especie encuentra idóneas para vivir). En consecuencia, su identificación es necesaria para detectar cambios en la distribución y abundancia de la megafauna marina. Asimismo, la ubicación de áreas importantes donde se agregan individuos o comunidades, como las Áreas con Alto Valor de Biodiversidad (AAVBs), se convierte en un importante objeto de estudio debido a las consecuencias que los cambios en las comunidades de megafauna marina pueden tener sobre la dinámica de los ecosistemas. Además, tanto las VOEs como las AAVBs pueden ayudar a anticipar la vulnerabilidad de las especies y los ecosistemas frente a amenazas como el cambio climático. En el **Capítulo 3**, identificamos las VOEs que conforman la envolvente ambiental de la comunidad de aves marinas y cetáceos del norte y noroeste peninsular y delineamos sus AAVBs utilizando los avistamientos recogidos durante campañas oceanográficas anuales. Para delimitar las AAVBs y encontrar las VOEs para la comunidad, empleamos un enfoque de modelado espacio-temporal utilizando Modelos Aditivos Generalizados. Identificamos la temperatura superficial del agua y la concentración de clorofila como VOEs ya que fueron las variables dinámicas con mayor importancia predictiva relativa. Estas VOEs delimitan la envolvente ambiental y dan forma a las AAVBs. Las AAVBs se localizaron principalmente en aguas del noroeste peninsular, con una menor presencia hacia el interior del GdV y permaneciendo espacialmente estables durante el periodo de estudio. El uso de esta información puede facilitar el establecimiento de valores de referencia para predecir y detectar el efecto de múltiples amenazas sobre las AAVBs, así como para satisfacer la necesidad emergente de información espacial sólida que apoye la aplicación de la planificación espacial marina.

En su origen, las AMPs no se diseñaron con el fin de proteger especies altamente móviles, sin embargo, su utilidad como medida de gestión para proteger a este tipo de especies se ha reconocido a pesar de la extensión de sus hábitats y su comportamiento migratorio. La identificación de áreas críticas para especies altamente móviles puede informar la designación de AMPs que, además, pueden ofrecer protección a otras especies. En este contexto, el **Capítulo 4** aborda la dificultad de proteger especies que por su alta movilidad cruzan múltiples límites jurisdiccionales y AMPs no específicas, con el ejemplo de los rorcuales comunes *Balaenoptera physalus*, una especie altamente migratoria. Para ello, se analizaron los datos de avistamiento recogidos durante campañas oceanográficos anuales utilizando la metodología de Muestreo de Distancia (*Distance Sampling*) y Modelos Aditivos Generalizados para predecir la abundancia relativa de esta especie e identificar sus áreas críticas en el GdV a finales del verano. Con esta información, evaluamos si la red actual de AMPs designada en el área ofrece protección a la especie. La principal área crítica para los rorcuales comunes se localizó en la parte sureste del GdV, un área que actualmente está marginalmente cubierta por tres AMPs. En base a estos resultados proponemos la creación de un AMP transfronteriza para esta especie en el GdV, que además beneficiaría a otras especies de megafauna que habitan el área.

La Planificación Sistemática para la Conservación ha sido reconocida como el enfoque más robusto y transparente para diseñar redes de AMPs que tiene en cuenta los posibles conflictos entre los factores ecológicos, sociales y económicos. El proceso de Planificación Sistemática para la Conservación necesita información de múltiples fuentes, siendo la cantidad y calidad de los datos disponibles el principal factor responsable de la exactitud de los resultados, ya que la falta de datos puede introducir incertidumbre en el proceso de priorización espacial. En el **Capítulo 5** se evaluó el valor de las series temporales de datos explorando si las áreas prioritarias para la conservación de las especies de megafauna son consistentes, independientemente del período de tiempo (es decir, el número de años) considerado en el proceso de priorización. Para ello utilizamos los resultados de abundancia espacial derivados del Capítulo 3 y la herramienta de apoyo a la toma de decisiones Marxan para desarrollar y comparar varios planes de conservación. Para cada plan de conservación, utilizamos datos de abundancia de megafauna marina y esfuerzo pesquero que engloban diferentes años del período 2007-2016. Se incluyó el esfuerzo pesquero como un indicador de las interacciones entre depredadores y pesquerías. De esta manera proporcionamos un método para calcular el número mínimo de años de monitoreo requeridos para establecer una red efectiva de AMPs, método que recomendamos para la priorización espacial futura de AMPs enfocadas a la gestión y conservación de especies altamente móviles. Además, estos resultados pueden tener especial relevancia para la configuración de redes de AMPs en alta mar.

Los capítulos incluidos en esta tesis comparten un objetivo práctico, ya que se centran en los aspectos relacionados con la biodiversidad y la conservación de los ecosistemas del EBM, el cual requiere de estudios multidisciplinarios que implican diferentes enfoques y técnicas de estudio. Con el objetivo de hacer operativo el EBM dentro de la legislación europea actual, los resultados de esta tesis pretenden integrar nuevos componentes del ecosistema en este enfoque, como la megafauna marina, con el fin de que sirva para informar las medidas de conservación y gestión en el contexto del objetivo general de la DMEM, posibilitar el uso sostenible de los bienes y servicios marinos.

SUMMARY

Marine ecosystems are under threat by multiple human activities which are affecting their sustainability and resilience, causing a decline in marine biodiversity and impacting ecosystem functioning. The largest species, *i.e.* marine megafauna, show high risk of extinction worldwide, raising awareness of the need of priority conservation strategies to ensure their protection. To reverse this situation, information on the spatio-temporal patterns of the pressures that affect the marine environment and an assessment of their severity are urgently needed to inform biodiversity and habitats conservation, devise appropriate mitigation measures and advise spatial planning decision processes.

Marine megafauna plays an essential role in marine ecosystems and due to their intrinsic vulnerability when exposed to anthropogenic pressures, acts as sentinels of the variability and reorganization that are taking place in the marine ecosystem. In this context, national and international legislation and international conventions have been enacted to protect marine megafauna. Within the European Union (EU), the Habitats and the Birds Directives aim to promote and maintain biological diversity with Member States required to take measures to reach or maintain the favourable conservation status of natural habitats and species. In addition, the Marine Strategy Framework Directive (MSFD), incorporates the Ecosystem Approach and the Precautionary Principle, by aiming at achieving and maintaining the Good Environmental Status (GES) of EU waters by 2020. The MSFD refers specifically to marine biodiversity and reinforces the protection offered by the Habitats and the Birds Directives. Finally, the Maritime Spatial Planning Directive (MSPD) promotes a sustainable development and use of the marine and coastal resources also from a holistic perspective.

To anticipate the response of the ecosystems in the face of growing pressures, a holistic management approach with an integral vision of the ecosystem is required (an approach included in Directives such as the MSFD or the MSPD). An integrated Ecosystem-Based Management (EBM) approach requires knowledge on the ecologic, economic and social aspects of the ecosystem and their interactions aiming at their sustainable management. Implementing the EBM approach requires multidisciplinary data collection, monitoring of the system state, behaviour, and functioning, development of methods to organize, display, and illustrate the relationships of ecosystem components and

methodological developments of transdisciplinary nature to synthesis data, multipurpose and integrative in order to inform management measures.

The Bay of Biscay (hereafter 'BoB') and the North and North-western Iberian coast, where this thesis dissertation has focused, are situated in the eastern North Atlantic Ocean. The BoB is characterized by a wide shelf in the Western area of France and a narrow shelf on the Northern Iberian coast, while a complex circulation pattern is present influenced by different currents resulting in different mesoscale oceanographic events. Two phytoplankton blooms take place in the BoB, one in spring and one in autumn, whilst two upwelling events take place during summer and early autumn over the Iberian coast. The BoB is a dynamic and biologically rich pelagic ecosystem with a highly diverse marine megafauna community that include several taxonomic groups. This area represents a migration corridor and a key seasonal feeding ground for those species undertaking seasonal feeding migrations into the area.

The marine megafauna of the BoB is suffering increasing disturbances due to anthropogenic pressures, such as extractive activities (*e.g.* fishing or aquaculture), polluting industrial activities, maritime transport with the risk of oil spills and marine mammals' collisions or introduction of non-native species. Furthermore, there is evidence of the increasing impacts of climate change (*e.g.* extreme weather events). Currently, the management measures implemented to protect the marine biodiversity of the BoB are mainly focused in the designation, under different environmental legislation or sectoral laws, of Marine Protected Areas (MPAs) such as Special Areas of Conservation (SAC), Special Protection Areas (SPA) or Protected biotopes among others. All these conservation areas encompass a broad range of species diversity and habitats and would constitute a network of MPAs aiming at reversing the negative impacts of human impacts/stressors.

Within this context, the aim of this thesis was to assess the impacts of human activities on marine megafauna by integrating their spatial ecology into EBM. By focusing on seabirds and cetaceans inhabiting the BoB, we developed an integrative ecological framework based on multidisciplinary approaches to identify threats, develop environmental indicators, establish baseline values, obtain estimates of spatio-temporal abundance, assess the coherence of MPAs networks and in addition, examine the value of long-term series for MPA robustness. To achieve this aim, the thesis has been divided into five chapters.

In order to collect information about the status of the megafauna community and the mortality caused by several threats, such as bycatch, and contribute to the assessment of the GES within the MSFD, in **Chapter 1**, the impact of the main threats affecting seabirds and cetaceans in the BoB was assessed. Firstly, a quantitative assessment was performed based on seabirds' cause of admissions data collected from Wildlife Recovery Centres along the Cantabrian coast during a 13 years period. Secondly, a qualitative assessment was carried out to identify the main pressures affecting directly or indirectly cetacean and seabird species of the BoB. We synthesized the information from both assessments to identify those threats that need to be urgently managed. The main marine threats for seabirds were cachexia, exposure to crude oil and interaction with fishing gears and the main affected species were the Common guillemot, the Yellow-legged gull, the Northern gannet, the Great cormorant and the Razorbill. The qualitative assessment showed that cetaceans are especially vulnerable to bycatch, vessel collision, and pollution-related threats, whilst seabirds are particularly sensitive to oil spills, bycatch and marine litter. This type of assessment studies can aid in the identification of priority areas and/or species where management measures should be applied to ensure that the goal of the MSFD, sustainable conservation of the marine environment, is reached.

Monitoring schemes, such as multidisciplinary oceanographic surveys, are becoming data integration systems by providing information from multiple system components in the same overall monitoring scheme. Within the **Chapter 2**, an example of the combination of multiple pelagic components is shown to provide an integral assessment to advance ecosystem-based monitoring. We developed a methodological approach to identify biologically appropriate oceanographic and preyscape predictors to jointly consider both the spatial and vertical dimensions of oceanographic habitats, which can be applied to any marine species. The aim of this work was to understand the 3D environment of pelagic seabirds by assessing the importance of prey fields and mesoscale oceanographic features in driving sooty shearwaters *Ardenna grisea* and great shearwater *A. gravis* abundance patterns in the BoB. Abundance patterns were influenced by oceanographic conditions and prey accessibility integrated above the depth of maximum temperature gradient for Sooty shearwaters and at the surface for Great shearwaters, leading to a vertical segregation. Similarly, both species showed a spatial segregation in relation to shelf areas (preferred by Sooty shearwaters associated with upwelling and river discharge) versus oceanic areas (preferred by Great shearwaters). The first abundance estimates for the Sooty and the Great shearwaters during September in the BoB are provided.

The measurement of parameters, such as the Essential Ocean Variables (EOVs), is needed to assess the status, variability and change in marine ecosystems and to inform management decisions for sustainable management of biodiversity, ecosystem goods and services. EOVs shape the environmental envelope of a species (*i.e.* the environmental conditions that a given species may find suitable for living). Consequently, their identification is needed to detect changes in marine megafauna distribution and abundance. Likewise, the location of important areas where individuals or communities aggregate, such as high-value biodiversity areas (HVBAs) becomes an important study subject due to the consequences that changes in the marine megafauna communities can have on ecosystem dynamics. Furthermore, both EOVs and HVBAs can help to anticipate the vulnerability of species and ecosystems in the face of threats, such as climate change. In **Chapter 3,** we identified the EOVs that shape the environmental envelope of the North and North-western Spanish seabird and cetacean's community and delineate their HVBAs taking advantage of the sightings collected during annual oceanographic surveys. To delimitate the HVBAs and find the EOVs of the community, we used a spatio-temporal modelling approach using Generalized Additive Models. The sea surface temperature and the chlorophyll-a concentration were identified as EOVs due to their highest relative predictor importance, driving the environmental envelope and shaping the HVBAs. HVBAs were located mainly over the North-western Spanish waters and decreased towards the inner BoB remaining spatially stable over the study period. The use of this information can facilitate the establishment of baseline values to predict and detect the effect of multiple threats on HVBAs, as well as to fulfil the emergent need for sound spatial information to support the implementation of marine spatial planning.

MPAs were not originally designed for highly mobile species, however, their usefulness as management measures to protect highly mobile species is well-established, even though the extension of their suitable habitats and their migration behaviour. The identification of critical areas can inform the establishment of MPAs for these highly mobile species, which may also offer protection to other species. Within this context, **Chapter 4** addresses the difficulty of protecting highly mobile species that cross multiple jurisdictional boundaries and multiple non-specific MPAs, applied to the highly migratory fin whale *Balaenoptera physalus*. Sighting data collected during annual oceanographic surveys was analysed using Distance Sampling and Generalized Additive Models to predict Fin whale relative abundance and to identify critical areas for the species in the BoB during late summer. With this information, we assessed whether the current MPAs network in the area offers protection to the species. The main critical area for Fin whale was located over the

South-eastern part of the BoB, an area that is currently only marginally covered by three MPAs. Based on these results, we proposed a transboundary MPA for this species in the BoB, a MPA which would benefit other megafauna species inhabiting the area.

Systematic Conservation Planning has been recognized as the most robust and transparent approach to design MPAs networks that takes into account the possible conflicts between the ecological, social and economic factors. A Systematic Conservation Planning process needs input information from multiple sources, being the quantity and quality of data available the main factor responsible for the accuracy of conservation planning outcomes since the lack of data can introduce uncertainty into the spatial prioritization process. In **Chapter 5**, the value of time-series was assessed by exploring whether priority areas for the conservation of megafauna species remain consistent regardless of the time period (*i.e.* number of years) considered. We used the spatial abundance results derived from Chapter 3 and the decision-support tool *Marxan* in order to develop and compare several conservation plans. For each conservation plan, we used marine megafauna abundance and fishing effort data that covered different years between the period 2007-2016. Fishing effort was included as a proxy for predator-fishery interactions. We provided a method for calculating the minimum number of monitoring years required to establish an effective MPA network, which we recommend for future spatial prioritization for highly mobile species. Furthermore, our results may have special relevance for the configuration of MPA networks in high seas.

The chapters included in this thesis dissertation share a practical goal as they focus on the biodiversity and ecosystem conservation aspects of the EBM, which needs multidisciplinary studies involving different approaches and study techniques. With the aim of operationalising the EBM within the current European legislation, the results of this thesis intend to integrate new ecosystem components such as marine megafauna into EBM to inform conservation and management measures in the context of the MSFD overall aim, which is to enable sustainable use of marine goods and services.

GENERAL INTRODUCTION

1. Status of marine ecosystems

The world's oceans cover about 71% of the Earth's surface and 90% of the Earth's biosphere (Costello et al., 2010). Marine ecosystems provide essential services to society such as food and energy and play a major role in economic activities. For centuries, it was assumed that marine ecosystems were limitless and immune to human impacts. For example, Huxley wrote in 1884 that several of the most important fisheries in the Northeast Atlantic at the time were "inexhaustible", arguing that the amount of fish caught was insignificant in relation to the number of individual fish and that fishing mortality was unimportant, when compared with the natural mortality suffered by the commercially exploited species. Less than one hundred fifty years later, the most recent studies based on indicators of ecosystem health and on biodiversity trends have evidenced a different picture (IPBES, 2019) with both ecosystem health and biodiversity showing rapid declines due to growing human activities and global change. Anthropogenic activities are impacting the sustainability and resilience of marine environments (Boonstra et al., 2015; Dulvy et al., 2003; Sala and Knowlton, 2006) leading to the loss of unique biota, as well as impacting ecosystem functioning and the provision of services, which are essential for human wellbeing (Cardinale et al., 2012; Millennium Ecosystem Assessment, 2005).

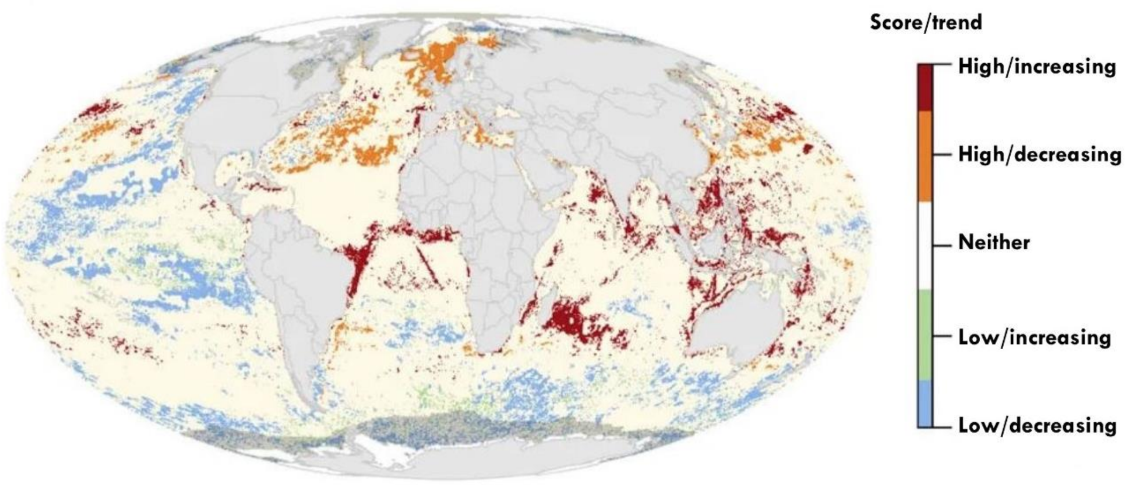

Figure 1. Map of the change in human impacts to marine ecosystems from 2008 to 2013 showing that nearly 66% of the ocean experienced increasing impacts. Adapted from Halpern et al., 2015.

Human exploitation of marine ecosystems has been taking place worldwide for many centuries, but its negative impacts have been especially severe over the past 50 years, when human population doubled, the global economy grew nearly 4-fold and global trade increased 10-fold (Figure 1; Halpern et al., 2015; IPBES, 2019). Main impacts are due to overfishing (Jackson et al., 2001); pollution (with growing concern about plastic and acoustic contamination; Eriksen et al., 2014; Hildebrand, 2009) and habitat degradation and destruction, especially in coastal areas (Airoldi et al., 2008). Furthermore, climate change-driven processes, such as increasing water temperature, acidification or extreme weather events (Harley, 2011; Harley et al., 2006; Vaughan et al., 2001) are adversely affecting marine ecosystems. To reverse this situation, information on the spatio-temporal patterns of the pressures that affect the marine environment and an assessment of their severity is urgently needed to inform biodiversity and habitats conservation, devise appropriate mitigation measures and advise spatial planning decision processes (Halpern et al., 2015, 2007; Tulloch et al., 2015).

Anthropogenic pressures are causing declines in marine biodiversity and species abundance (Selig et al., 2014), with 23% of marine taxa classified as threatened with extinction (IUCN, 2012). Moreover, extinctions and threats to marine species may have been underestimated (Costello, 2015) and the real figure of threatened marine taxa may be even higher. It has been well established that the largest species are at a higher risk of extinction worldwide (Cardillo et al., 2005; Fisher and Owens, 2004; Gaston and Blackburn, 1995), referring to marine megafauna (namely marine mammals, large teleosts, elasmobranchs, seals, turtles and seabirds) in marine ecosystems (Heithaus et al., 2008). Global assessments of human impacts on marine ecosystems suggest that coastal wildlife and habitats have been more influenced than deep-water or pelagic ecosystems (Halpern et al., 2008). However, marine megafauna inhabits the shelf and oceanic ecosystems where they are becoming subject to an ever-increasing diversity of threats (O'Hara et al., 2019), raising awareness of the need of priority conservation strategies to help ensure their protection (Figure 2).

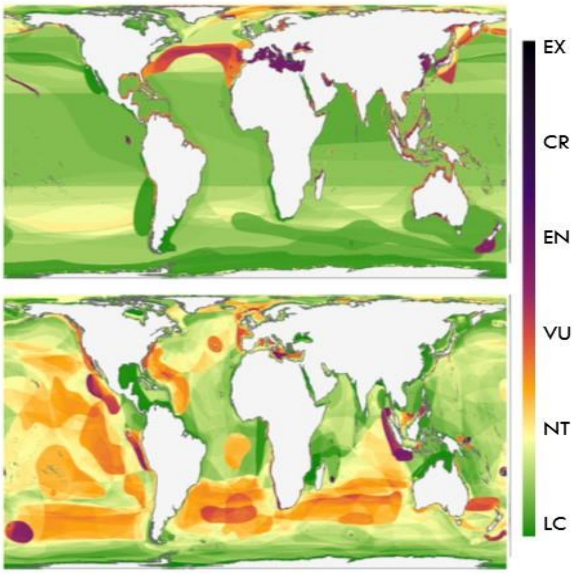

Figure 2. Biodiversity risk (i.e., conservation status by the IUCN) of marine mammals (upper map) and seabirds (lower map). Adapted from O'Hara et al., 2019.

2. Marine megafauna and their role in the ecosystem

Marine megafauna plays an important role in the marine ecosystem as predators, prey, sources of detritus, and nutrient vectors (Estes et al., 2016). As predators, marine megafauna affects the life history strategies and population dynamics of their prey, as well as those organisms of other trophic levels that with which their prey interact, through top-down processes (Atwood et al., 2015; Pinnegar et al., 2000). Marine megafauna is also involved in other ecosystem pathways, such as bottom-up processes (Roman et al., 2014). These bottom-up processes may occur through the redistribution of nutrients by marine megafauna and they are of particular relevance due to the diversity of reallocation actions involved. These actions can relocate nutrients from: (a) the deep ocean to the surface (*i.e.,* when marine megafauna feeds at or near the thermocline and makes part of these nutrients available at or near the surface via their faeces which are produced when surfacing), (b) offshore into nearshore waters where some species rest, (c) high latitudes to oligotrophic tropical systems through marine megafauna migration between both (see Figure 3), (d) surface to the deep-sea (*i.e.,* when marine megafauna carcasses sink) or (e) sea to land by seabirds or seals (Estes et al., 2016; Malhi et al., 2016; Norris and Dohl, 1980; Roman et al., 2014; Wenny et al., 2011).

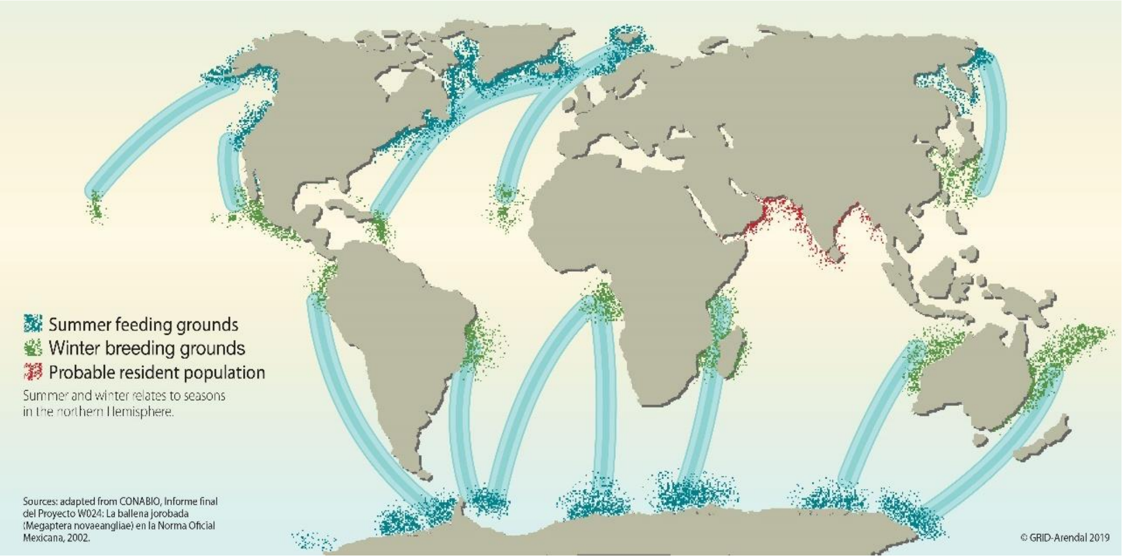

Figure 3. *Distribution of humpback whales Megaptera novaeangliae in the world. The map shows the migratory connections between summer feeding grounds (blue) and winter breeding grounds (green) as an example of the redistribution of nutrients by marine megafauna from high latitudes to oligotrophic tropical systems. Adapted from GRID-Arendal (www.grida.no).*

Marine megafauna plays also a role within the marine megafauna community itself as competitors by the same resources (Ainley et al., 2006) or through mutualistic associations, such as local enhancement or facilitative mechanisms between different megafauna functional groups. For instance, seabirds are known to rely on other seabirds and sub-surface predators (*e.g.* cetaceans and tunas) to locate prey and increase fishing success when they push prey towards the surface (Dill et al., 2003; Fauchald, 2009; Kiszka et al., 2015). Finally, other processes such as the hosting of a variety of commensal or parasitic species, sometimes completely dependent on megafauna through all life stages or using them as definitive hosts, are also important (*e.g. Anisakis*; Kuhn et al., 2016).

When considering fisheries as apex predators of marine ecosystems, marine megafauna may interact with them due to resources overlap (Goetz et al., 2015; Santos et al., 2014), influencing prey availability by direct exploitation with an implicit competition between fisheries and megafauna for forage fish (pelagic fish, crustaceans, and cephalopods) (Cury et al., 2011; Furness, 2006; Grémillet et al., 2018). Prey scarcity can affect marine megafauna life-history traits such as breeding success (Bourgeois and Vidal, 2008; Sommer et al., 2009) and species' survival since low food availability may increase attraction to vessels, and thus, increase bycatch (Laneri et al., 2010; Soriano-Redondo et al., 2016). Fishing activities can also alter interactions within the marine megafauna community by reducing sub-surface predators and therefore reducing the abovementioned foraging facilitation (Rodríguez et al., 2019). In summary, this competition acts as a stressor upon the marine megafauna due to resource scarcity or risk of bycatch rather than being a pressure over fisheries (Breen et al., 2016; Grémillet et al., 2018; Lassalle et al., 2012). Consequently, decreases in marine megafauna richness or abundance is ultimately affecting species composition and abundance at lower trophic levels (Baum and Worm, 2009; Essington et al., 2002) causing a top-down trophic cascade, that could even diminished fisheries target species. Kaschner and Pauly (2005) exemplified the latter with the reduction of toothed whales and other high-level predators. These species feed on desirable fish species but also on various squids, which in turn feed on juvenile groundfish. Therefore, predator abundance decreased has contributed indirectly, through an increase of cephalopod consumption of juvenile fish, to the inhibition of fin fish population recovery. Furthermore, the decline of marine megafauna can threaten ecosystem services such as nutrient cycling, and can reduce overall ecosystem stability and resilience (Selig et al., 2014).

Marine megafauna species must adapt to physical and biological changes integrating the environmental heterogeneity of the habitats they occupy, acting as sentinels of the variability and reorganization of ecosystems (Moore et al., 2014). Moreover, the study of their ecology may help us to understand and track ecosystem changes (Xavier et al., 2013). For that reason, this group of species have been often proposed as indicators of the status of the marine environment (*e.g.* Einoder, 2009; Santos and Pierce, 2015) and they are considered as a key element for the implementation of conservation strategies due to their intrinsic vulnerability when exposed to anthropogenic pressures due to their large size, high trophic level, slow growth and low fecundity (Ridoux et al., 2010).

3. Conservation of marine megafauna

Marine megafauna is protected by national and international legislation and international conventions such as the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES), the Convention on the Conservation of Migratory Species of Wild Animals (CMS), the Convention for the Protection of the Marine Environment of the North-East Atlantic (OSPAR), the Bern Convention on the Conservation of European Wildlife and Natural Habitats or the Convention on Biological Diversity (CBD) which aims to conserve and enhance these species through the creation of Ecologically or Biologically Significant Marine Areas (EBSAs). Concerning marine mammals, the Marine Mammal Protected Areas Task Force (MMPATF) aims to protect these species through the designation of Important Marine Mammal Areas (IMMAs). Regarding seabirds, BirdLife International has developed the Important Birds Areas (IBAs) programme to identify the most relevant areas for bird conservation (Arcos et al., 2007; Donald et al., 2019). The identification of IBAs does not guarantee legal protection, but they are intended to guide legal conservation action afterwards. Furthermore, the Agreement on the Conservation of Albatrosses and Petrels (ACAP) provides a comprehensive framework to achieve and maintain favourable conservation status for albatrosses and petrels through research, monitoring or reduction of incidental mortality in fisheries among other measures (ACAP Interim Secretariat, 2001). Other specific administrative tools to protect marine megafauna species are international shark finning bans and policies adopted by the United Nations General Assembly and most of the Regional Fisheries Management Organizations [*e.g.* International Commission for the Conservation of Atlantic Tunas (ICCAT), Inter-American Tropical Tuna Commission (IATTC)] in the case of shark species or the Inter-American Convention (IAC) for the Protection and Conservation of Sea Turtles in the case of sea turtles.

Within the European Union (EU), the Habitats and the Birds Directives (HD 92/43/EEC and BD 79/409/EEC, respectively) aims to promote and maintain biological diversity through the conservation of natural habitats and biodiversity in the EU territory, including the most threatened seabirds, turtles and cetaceans. The HD requires Member States to take measures to reach or maintain the favourable conservation status of natural habitats and species of wild plants and animals. The HD includes marine mammal species (*e.g.* cetaceans and seals) and sea turtles which must be protected through Special Areas of Conservation (SACs), whilst the BD includes seabird species to be protected through Special Protection Areas (SPAs). Many Member States have designed SPAs on the basis of national IBAs (BirdLife, 2014). The synergy between both, the Habitats and the Birds Directives, constitutes the Natura 2000 network which has become the largest coordinated network of protected areas in the world, covering approximately 11% of the EU's marine territory (European Commission, 2019a). In addition, the Marine Strategy Framework Directive (MSFD; 2008/56/EC) aiming at achieving and maintaining the Good Environmental Status (GES) of the EU marine ecosystems by 2020 is the first EU marine legislation that specifically refers to marine biodiversity and reinforces the protection offered by the HD and BD. The MSFD offers a comprehensive and integrated approach to the protection of all EU coasts and marine waters and is a key instrument for marine conservation in EU waters (Santos and Pierce, 2015).

Nowadays, the MSFD has acquired relevance by moving forward from a species-centred and pressure-by-pressure approach to a holistic approach, *i.e.* an ecosystem-based approach (Armsworth et al., 2007; Authier et al., 2018). Within the MSFD, marine megafauna species have been chosen as relevant groups which monitoring and assessment is needed to determine GES of the EU waters (Machado et al., 2019; Santos and Pierce, 2015). In addition, specific agreements adopted under the auspicious of the CMS such as the Agreement on the Conservation of Cetaceans of the Black Seas, Mediterranean and Contiguous Atlantic Area (ACCOBAMS) and the Agreement on the Conservation of Small Cetaceans of the Baltic, North East Atlantic, Irish and North Seas (ASCOBANS) promote close cooperation between EU countries with a view to achieving and maintaining a favourable conservation status for cetaceans.

4. Ecosystem-based management

Conventional approaches for natural resource management may not be able to anticipate the response that is required in the face of exponentially growing pressures. It can be argued that traditional management approaches have indeed failed to achieve sustainable management of natural resources. Faced with this situation, holistic approaches (where an integral vision to understand ecosystem functioning is considered) have emerged. One such an example is the Ecosystem-Based Management (EBM; Arkema et al., 2006; Curtin and Prellezo, 2010). The EBM involves the integrated management of species, natural resources, and humans as components of the larger ecosystem (Christensen et al., 1996;

Grumbine, 1994; Larkin, 1996). The main aim of the EBM is to maintain ecosystems in a healthy, clean, productive and resilient condition, so that they can continue to provide humans with services and benefits (McLeod and Leslie, 2009). Thereby, the concept of EBM covers the ecologic, economic, and social aspects of the ecosystem, acknowledging their interaction and aiming at their sustainable management (Figure 4; Laurila-Pant et al., 2015).

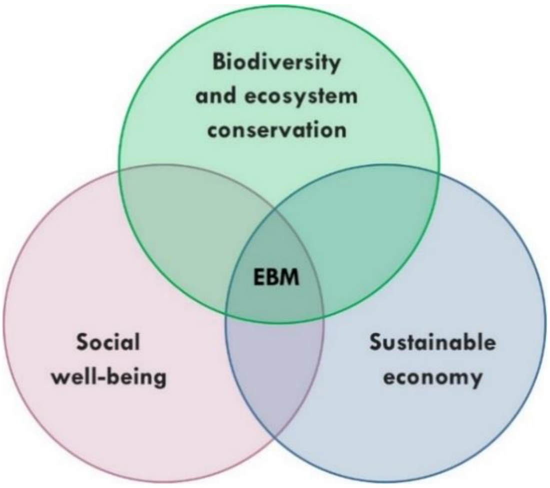

Figure 4. *Interactions of the different components covered by the concept of ecosystem-based management (EBM), adapted from Laurila-Pant et al. (2015).*

Implementing the EBM approach requires: (a) multidisciplinary data collection, including monitoring of the system state, behaviour, and functioning, (b) methods to organize, display, and illustrate the relationships of data collected, such as statistical models and (c) methods of transdisciplinary synthesis of data, multipurpose and integrative, such as integrative targets or indicators in order to implement management measures (Slocombe, 1993). Thus, EBM is made adaptable through monitoring and research based on our best understanding of ecological interactions and processes necessary to sustain ecosystem composition, structure and function (Christensen et al., 1996). The identification of management objectives and indicators is essential to operationalize EBM, and this is recognised in the emphasis put by international policies on the need to develop sustainable strategies for implementing the principles of EBM.

4.1. Tracking ecosystem changes

During the 1980s and 1990s, the World Ocean Circulation Experiment (WOCE) established the largest internationally coordinated oceanographic monitoring programme with the primary goal of obtaining an understanding of the large-scale circulation of the ocean, its time variablity and its impact on climate (Siedler et al., 2001). Nowadays, The Framework for Ocean Observing (FOO; Lindstrom et al., 2012), as one of its major heirs embraces the Global Ocean Observing System (GOOS) which provides estimates of physical and chemical changes in the ocean by developing an international framework for coordinating, enhancing and supplementing existing monitoring and research programs. This framework is organized around Essential Ocean Variables (EOVs, *i.e.* priority variables for monitoring), rather than any specific observing system, platform, program, or region highlighting the importance of monitoring EOVs to assess the status, variability and change in marine ecosystems, parameters needed to inform management decisions for sustainable management of biodiversity, ecosystem goods and services (Muller-Karger et al., 2018).

The identification of EOVs for each species or community and the establishment of baseline values are needed to detect changes in marine megafauna distribution and abundance. The description and subsequent monitoring of EOVs is important to identify areas of persistent oceanographic processes of particular ecological importance for the species, such as upwelling or transition zones (Louzao et al., 2012), as well as to identify or forecast environmental changes which may affect the distribution or even survival of the species under study (Soldatini et al., 2016). Changes in EOVs values may result in a redistribution of populations or species persistence, as species can move to maintain existing physiological associations with particular environmental conditions, therefore mantaining its ecological niche (Alcaraz-Segura et al., 2017). In this context, the identification of EOVs is crucial in the face of threats such as climate change for scientists and managers to effectively predict spatio-temporal patterns of change to anticipate the vulnerability of species and ecosystems (Dawson et al., 2011). Similarly, changes in EOVs may affect distribution patterns either by changes that affect the species´ environmental envelope directly (*i.e.,* the environmental conditions that a given species may find suitable for living, Wiens and Graham, 2005) or through changes in the environmental envelopes of their prey (Goldbogen et al., 2015). The relationship between the environmental conditions shaping the environmental envelope of the species could be further displayed and illustrated using statisticals tools. This information is needed to establish baseline values useful for biodiversity trend interpretation (Constable et al., 2016).

4.2. Identification of important areas

The identification of the EOVs driving the most suitable environmental conditions for a species enables us to understand the habitat requirements of the species and identify its spatio-temporal changes in distribution and/or abundance. However, marine megafauna is highly mobile with complex habitat requirements making difficult the evaluation of the conservation value of any particular location in isolation (Martin et al., 2007). The identification of important or critical areas is needed to inform management in areas of conservation interest, however, protecting highly mobile species presents a conservation challenge because their distribution and abundance is influenced by geographically separated events, that can even occur during different periods of the year (Edwards et al., 2015; Lambert et al., 2017a; Webster et al., 2002).

The identification of important areas can focus on the location of species-specific or community important areas. Species-specific important or critical areas (Cañadas and Vázquez, 2014; García-Barón et al., 2019a; Hedd et al., 2012) can be classified as essential habitats for the survival of the species (Heupel et al., 2007) or where individuals aggregate either during breeding or foraging (Louzao et al., 2006). These critical areas become a priority when planning any species-specific conservation and management measure (Harwood, 2001). Conversely, High-Value Biodivesiy Areas (HVBAs), where several species can be found (Kuletz et al., 2015; McClellan et al., 2014), becomes an important study subject due to the far-reaching and unexpected consequences that changes in the marine megafauna communities can cause on ecosystem dynamics (Casini et al., 2009; Rey Benayas and De La Montaña, 2003; Trites et al., 2007).

4.3. Spatially-explicit management measures

Marine megafauna has traditionally been used as flagship species for conservation efforts since protection of their large and diverse habitats can also help protect other species (Zacharias and Roff, 2001). EBM has emphasided the need to use ecosystems, communities, and assemblages as the basis for the implementation of conservation measures. This is why marine megafauna has been identified as a key element of spatial management within the EBM framework for which the understanding of species distribution and spatially explicit threats impact is fundamental. In this regard, the implementation of spatial management measures has the potential of implementing this type of holistic approach to provide protection both to the species of concern and to the entire ecosystem, facilitating a mechanism for managing anthropogenic impacts on ecosystems (Hooker and Gerber, 2004).

The most common spatial management measure implemented in the marine environment is the establishment of MPAs. A MPA is defined by the International Union for the Conservation of Nature (IUCN) as '*any area of intertidal or sub-tidal terrain, together with its overlying water and associated flora, fauna, historical and cultural features, which* *has been reserved by law or other effective means to protect part or all of the enclosed environment'* (Kelleher, 1999). MPAs were originally designated to regulate and manage food resources (*e.g.* closing of fishing grounds or crabbing areas) (Johannes, 1978). During the First World Conference on National Parks, held in 1962 in Seattle (Washington, USA), Carlenton Ray presented the only paper on MPAs which included the recommendation to the Governments of all the countries with marine frontiers of urgently examining the possibility of creating marine parks or reserves to defend underwater areas of special significance from all forms of human interference (Ray, 1962). The Ray's appeal resulted in the organization of the Symposium on Marine Parks, organized in 1966 (Committee on Marine Parks, 1966) which triggered many of the global and national initiatives which are underway today (Wells et al., 2016). The next two decades saw the beginning of global programmes, reflecting an increasing awareness of threats to ocean and marine biodiversity. In 1979, the BD came into force in Europe, which requires the creation of SPAs for areas of critical importance for listed birds. This was followed in 1992 by the HD, which requires the establishment of SACs for habitats and species of European importance, both Directives shaping the Natura 2000 network (see section 3).

After decades of global initiatives and designation of protected areas, the Parties to the CBD agreed to adopt the Strategic Plan for Biodiversity 2011–2020 in 2010 and developped the Aichi Biodiversity Targets (CBD, 2010a). Among these targets, the Aichi Target 11 requires that, by 2020, at least '*10% of coastal and marine areas, especially areas of particular importance for biodiversity and ecosystem services, are conserved through effectively and equitably managed, ecologically representative and well-connected systems of protected areas and other effective area-based conservation measures*' (CBD, 2010a). However, nowadays only the 8% of the ocean is covered by MPAs (Figure 5; UNEP-WCMC and IUCN, 2019) and new targets are needed for a post-2020 protected framework. In this sense, CBD Parties pledged to protect at least 30% of the Earth by 2030 by well-connected systems of protected areas and other effective area-based conservation measures (OECMs) covering sites such as Key Biodiversity Areas (CBD, 2019).

Throughout history, the objective sought with the establishment of MPAs has shifted from the protection of food supplies to the protection of threatened species and ecosystems, conservation of biodiversity and re-establishment of ecosystem integrity, following the holistic view of the EBM. In Europe, the implementation of the Directive 2014/89/EU establishing a framework for marine spatial planning requires the use of an EBM approach that contributes to promote the sustainable development and growth of marine economies and sustainable use of marine and coastal resources while accounting for the conservation of marine ecosystems (European Commission, 2014).

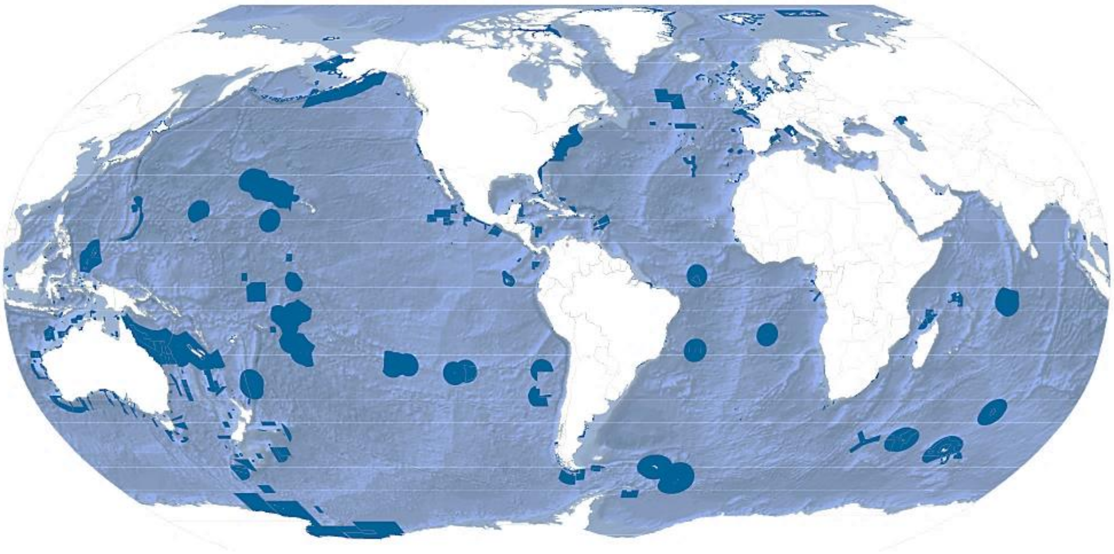

Figure 5. Official Marine Protected Areas (MPAs) map showing the 7.78% of the global ocean covered by MPAs. National waters represent 39% of the global ocean and 18% of these waters are designated as MPAs at present. In contrast, only 1% of areas beyond national jurisdiction, which makes up the remaining 61% of the global ocean, has been established as MPAs. Adapted from: UNEP-WCMC and IUCN (2019).

The protection of the marine megafauna, is challenging due to the extension of their suitable habitats and their migration behaviour, with individuals sometimes migrating thousands of kilometers twice a year between feeding or breeding areas (*e.g.,* Edwards et al., 2015; Egevang et al., 2010). MPAs were not originally designed for highly mobile species, but nowadays their usefulness as management measures to protect also these highly mobile species is well-established (Daly et al., 2018; Gormley et al., 2012; Hooker et al., 2011; Lascelles et al., 2012; Young et al., 2015). In this regard, areas of high abundance or HVBAs for marine megafauna enable the establishment of MPAs (Bastari et al., 2016; Gaines et al., 2010; O'Leary et al., 2018) as well as critical areas (Cañadas and Vázquez, 2014; Carlucci et al., 2017) which allow to protect complementary species (Bailey and Thompson, 2009; Gaston and Rodrigues, 2003; Reyers et al., 2000).

5. Marine ecosystem-based management in practice

New international policies emphasize the need to develop sustainable strategies for implementing the principles of EBM. In Europe, three main Directives focus on the protection, conservation or enhancement of marine ecosystems: the Water Framework Directive (WFD, 2000/60/EC; European Commission, 2000) covering transitional and coastal waters up to 1 nm from the continental baseline, the MSFD encompassing all marine waters up to the limit of the Exclusive Economic Zone (EEZ) and extended continental shelf and, the recent Maritime Spatial Planning Directive (MSPD, 2014/89/EU; European Commission, 2014) covering marine and coastal resources within the maritime boundaries and jurisdiction of the Member States.

Both the WFD and the MSFD Directives aim at ensuring marine uses compatible with the conservation of ecosystems and the maintenance of the good status of waters, habitats and resources. However, the WFD aims to achieve Good Ecological Status (GEcS) in transitional and coastal waters and focuses mainly on the ecological structure of ecological components (*e.g.,* presence, abundance, cover), referred to as *biological quality elements* (Heiskanen et al., 2004). Whilst the MSFD aims to achieve Good Environmental Status (GES) in marine waters and focuses on the structure, function and processes of marine ecosystems, gathering physical, chemical, physiographic, geographic and climatic factors, and integrates these conditions with anthropogenic impacts and activities carried out in the area of concern (European Commision, 2008). Hence, the MSFD uses the EBM as its framework of reference and describes GES on the basis of eleven descriptors including biological, physico-chemical and pressure indicators (Borja et al., 2013; Santos and Pierce, 2015). Within these descriptors, Descriptors 1 '*Biological diversity*' and 4 '*Food webs*' refer to marine megafauna and their role within the ecosystem functioning, respectively (European Commission, 2010). The type of spatial protection measures for the marine environment predefined under the MSFD are subject of the MSPD. The Directive, defines marine spatial planning '*as a process by which the relevant Member State's authorities analyze and organize human activities in marine areas to achieve ecological, economic and social objectives*' (European Commission, 2014). Thus, the MSPD is perceived as a tool to support a sustainable use of resources whilst implementing the EBM approach, and achieving the GES required as a part of the MSFD (Fernandes et al., 2018).

5.1. Marine ecosystem monitoring

The first step to implement an EBM approach is the collection of data from the system, which can be operationalised through monitoring programmes. As an EBM approach, the MSFD requires the implementation of monitoring programmes to evaluate and assess the performance of the management measures implemented to achieve GES. Monitoring can be defined as '*the systematic measurement of biotic and abiotic parameters of the marine environment, with predefined spatial and temporal schedule, having the purpose to produce* *datasets that can be used for application of assessment methods and derive credible conclusions on whether the desired state is achieved or not and on the trend of changes for the marine area concerned*' (Zampoukas et al., 2013). Thus, the primary question underlying monitoring schemes is to assess the actual status of the monitored system and whether they are changing over time and/or space, and if so, the rate of change (Balmford et al., 2005).

Monitoring schemes are essential to inform management and to assess whether the decisions of policymakers and the instruments developed to implement their decisions are effective to achieve the dessired objectives (Schmeller, 2008; Yoccoz et al., 2001). The integration of data monitoring is an essential step in the progress towards a unified, appropriately scaled, adaptive EBM, such as the MSFD (Henry et al., 2008; Laurila-Pant et al., 2015). EBM requires that a large number of ecosystem components are monitored simultaneously in order to disentangle their relationships (Hindell et al., 2003) to obtain a holistic view of the ecosystem. Furthermore, given the connection between marine ecosystems and human communities that depend on them, monitoring and evaluation of socio-economic variables is also needed in this context (McLeod and Leslie, 2009).

Monitoring schemes must ensure that the geographic and temporal coverage of the target components are sufficient and constant over time and should be cost-effective (Ondei et al., 2018). This trade-off between spatial and temporal coverage should ensure that the effects of spatiotemporal variability on the measured components are captured in order to be able to detect changes and to interpret the mechanisms that lead to these changes (Couvet et al., 2011; Dobson, 2005).

5.2. *Multidisciplinary oceanographic surveys*

Nowadays, monitoring schemes are becoming data integration systems by providing information from multiple system components in the same overall monitoring scheme. This is the case of multidisciplinary oceanographic suveys which, as mobile sampling platforms, significantly reduce barriers for collecting high-quality data on the ocean (Doray et al., 2018; Frolov et al., 2014), allowing the synoptical collection of data on different oceanographic and biological components (Figure 6; Doray et al., 2018; Frolov et al., 2014). Data on several trophic levels such as plankton (*i.e.* phyto and zooplankton), pelagic fish species and megafauna (*i.e.* seabird, cetacean, tuna or shark species) can be collected simultaneously (Louzao et al., 2019a). Oceanographic data, such as conductivity, temperature or salinity can be also sampled to characterize in-situ oceanographic

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1 https://www.nature.com/subjects/ecological-modelling

conditions (Bachiller et al., 2013). Thus, multidisciplinary oceanographic surveys enable the development of integrative studies to better understand the oceanographic conditions to which biological descriptors are related (Louzao et al., 2019a). Furthermore, biological data collected within these monitoring schemes are useful to disentangle the mechanisms underlying the assemblage of the pelagic predator-prey community (Benoit-Bird et al., 2013; Lawrence et al., 2016) describing the community structure and type of associations (Astarloa et al., 2019).

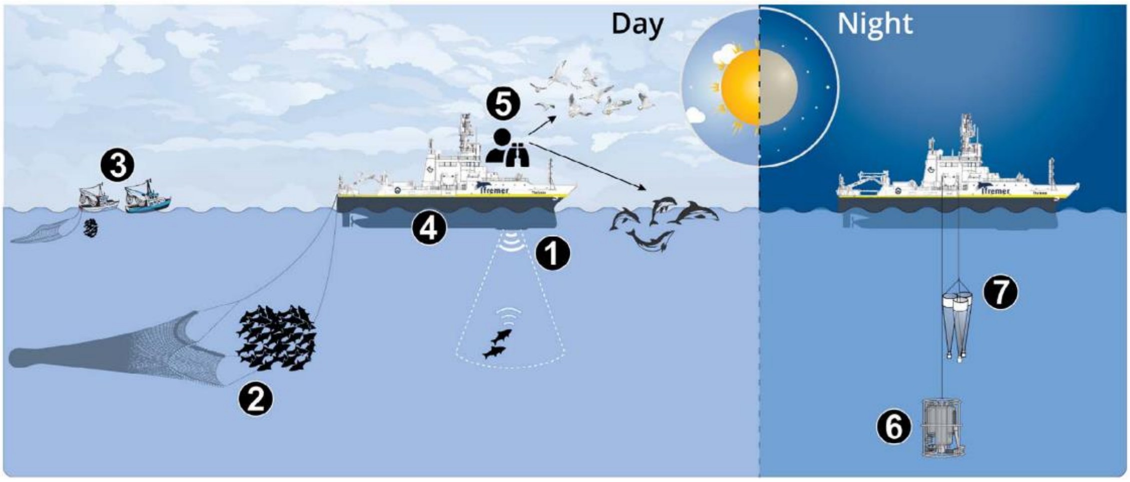

Figure 6. Example of an ecosystem data collection from a multidisciplinary oceanographic survey monitoring the pelagic realm. 1. Fisheries acoustics, 2. Midwater trawl fishing, 3. Support of pair trawlers fishing vessels, 4. Hull-mounted thermosalinometer, 5. Megafauna sightings (e.g. seabirds and cetaceans), 6. Sonde-based hydrobiological sampling, 7. Meso-zooplankton nets. Adapted from Doray et al., 2018.

5.3. Ecological modelling for ecosystem assessment

Ecological modelling has been described as '*the construction and analysis of mathematical models of ecological processes, including both purely biological and combined biophysical models*'[1]. Ecological modelling is widely used when there is a need to understand the functioning of complex system such as ecosystems (Jørgensen and Bendoricchio, 2001). Ecological modelling is very useful for simulating and analysing long-term dynamics, describing elements and properties of the stability of ecological systems and predicting spatio-temporal changes. Furthermore, it allows the integration of information from different sources. This is particularly important in the context of biodiversity preservation and ecosystem functioning in the face of growing human pressures and changing environmental conditions (Attorre et al., 2013; Rodríguez et al., 2007).

Within the EBM, it is essential to identify the main factors driving species distribution and the functional relationships with the environment to conserve and manage species and ecosystems. In this context, the ecological niche concept is particularly important. Hutchinson (1957) defined the ecological niche as a series of independent environmental variables with simple ranges of suitable conditions defining an '*n*-dimensional hyperspace' within which a species can survive and reproduce. Thus, the ecological niche considers all of the interactions between a species and both biotic (*i.e.* living organisms) and abiotic (*i.e.* non-living physical and chemical elements such as temperature, salinity, ocean currents) environments (Polechová and Storch, 2008).

The spatial distribution of species, as well as their abundances, are often determined by the breadth and position of their ecological niches. Species Distribution Models (SDMs), also named as habitat suitability models or ecological niche models, are statistical tools that can help identify a species' ecological niche (Elith and Leathwick, 2009). Elith and Leathwick (2009) defined a SDM as a model that relates species distribution data (presence or abundance at known locations) with information on the environmental and/or spatial characteristics of those locations. Thus, SDMs can be used not only to understand which biotic or abiotic factors explain the distribution and abundance of a species, but also to predict species distribution and abundance by estimating the similarity of the conditions at any site to the conditions where the species was sighted (Franklin, 2010) (Figure 7).

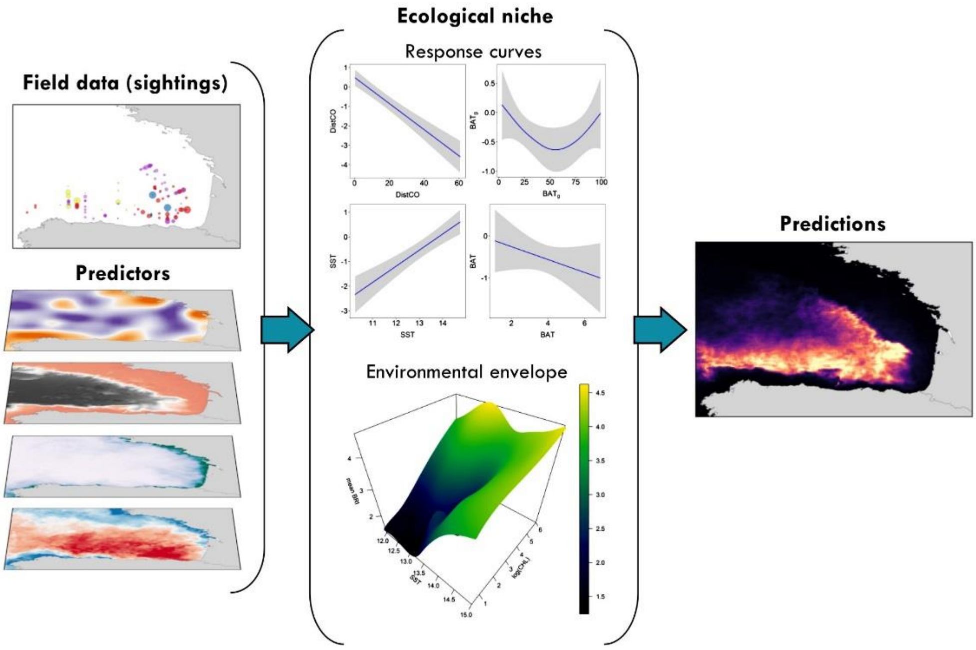

Figure 7. The concept behind Species Distribution Models (SDMs) is to use environmental information (predictors) either collected in-situ or from satellite imagery and species data to identify species ecological niche, i.e. environmental variables driving suitable conditions for species (illustrated through response curves or environmental envelopes in the case of one or two predictors, respectively). After the ecological niche has been identified, SDMs can be used to predict the spatial distribution and abundance of the species.

SDMs have been used to model the spatial variability in species distribution and abundance, but they usually generate estimates of the probability of ocurrence of a species that use relative or unit-less scales (*e.g.* ranging from 0 to 1) regardless of the effort (*i.e.,* sampled area) or the detectability of the species (Roberts et al., 2016). To consider animal counts, the development of Density Surface Models (DSMs) allows to obtain abundance estimations by relating sampled density to spatially explicit environmental covariates while accounting for the effort and species detectability (Hedley and Buckland, 2004; Miller et al., 2013). Species count data used to develop DSMs can be obtained from dedicated surveys, such as multidisciplinary oceanographic surveys (Section 5.2). These surveys are design-based schemes (*i.e.* the design is predefined) where the presence of the animals is visually detected, allowing to infer the relative spatial density/abundance of individuals (Buckland et al., 2001; Redfern et al., 2006).

The selection of relevant descriptors to be used in DSMs is helped by prior knowledge on potential biophysical processes driving species distribution and abundance. These descriptors can be classified into distal and proximal, being proximal descriptors those variables to which the species is assumed to react more directly than distal descriptors, which usually are those variables describing the environment (Austin, 2007; Guisan and Zimmermann, 2000). It is reasonable to assume that for marine megafauna, as predator species, trophic variables [*e.g.,* related to lower-trophic (phyto and zooplankton) or mid-trophic levels (forage fish)] could act as proximal descriptors as principal and direct drivers of their distribution (Friedlaender et al., 2006; Laidre et al., 2010; Louzao et al., 2019a; Paiva et al., 2008). Conversely, physiographic variables related to bathymetry (*e.g.* depth, slope, distance to the coast) or oceanographic variables related with water masses (*e.g.* geostrophic velocity, eddy kinetic ennergy, salinity, sea surface temperature, chlorophyll concentration) could act as distal descriptors, indirectly influencing species' distribution and/or abundance. However, this classification could be more complex when variables considered as distal could act as proximal (*e.g.,* oceanographic fronts as foraging hotspots for marine megafauna; Queiroz et al., 2012; Scales et al., 2015, 2014).

Values of distal descriptors can be obtained in-situ during multidisciplinary oceanographic surveys or from high-resolution satellite imagery (Ferreira et al., 2019; Lehodey et al., 2010; Pettorelli et al., 2016). Proximal descriptors can be also obtained in-situ from multidisciplinary oceanographic surveys (*e.g.* prey biomass or preyscapes; (Astarloa et al., 2019; Lehodey et al., 2010; Louzao et al., 2019). However, their sampling in the marine environment is challenging and the use of distal variables instead, as proxies of important ecological processes, could overcome these limiatations (*e.g.* chlorophyll concentration as a proxy of primary productivity) (Druon et al., 2012; García-Barón et al., 2019a).

5.4. Systematic conservation planning

Systematic Conservation Planning (SCP) has been recognized as the most robust and transparent approach to design MPAs networks while taking into account the possible conflicts between the ecological, social and economic factors (Haupt et al., 2017; Margules and Pressey, 2000; Metcalfe et al., 2013). Thus, the SCP framework allows to examine whether the basic requirements for conservation are meet while allowing for a sustainable management of the resources (Pressey and Bottrill, 2009). SCP has several distinctive characteristics such as the need to choose features to be used directly or as surrogates for overall biodiversity in the planning process; it is based on explicit goals, preferably translated into quantitative targets; it recognizes the extent to which conservation goals are met in the priority areas for conservation and it is able to locate and design new priority areas to complement the existing ones (Margules and Pressey, 2000).

A SCP process includes a wide variety of input information from multiple sources, incorporated within a transparent and inclusive process (Pressey and Bottrill, 2009). Nowadays, this information (*i.e.* wildlife abundance distribution and spatially-explicit data on marine human activities) is usually available allowing to conduct a spatial prioritization (B.S. Halpern et al., 2008; Kroodsma et al., 2018; Lee et al., 2010). However, the data often used in the SCP process are those which are readily available, being in many cases, incomplete. Therefore, features indicative of resource hotspots as well as the factors controlling the distributions of threatened and rare species are likely to be missed (Noss, 2004). This can affect the accuracy of conservation planning outcomes and introduce uncertainty into the spatial prioritization process (Rondinini et al., 2006). For that reason, fine-scale and/or long-term data must be a priority in the SCP process, both for the conservation features and the socio-economic data.

Long-term data measuring changes through time are essential. On the one hand, the lack of information on ecological systems, such as background values or rates of changes, can make it difficult to detect anthropogenic impacts (Magurran et al., 2010). On the other hand, insufficient data on socio-economic activities may limit our ability to determine their spatial distribution, frequency, or seasonality. The benefits of long-term monitoring have been well documented (Cheney et al., 2014; Heupel, 2005; Lowerre-

Barbieri et al., 2019; Ojeda-Martinez et al., 2007) and can contribute towards an effective spatial prioritization process, as well as provide wildlife managers and stakeholders with mechanism for optimizing action plans and reduced costs. However, obtaining long-term datasets is expensive and time-consuming (Magurran et al., 2010), highlighting the need for studies to assess the amount of data required to determine spatial and temporal changes in the SCP processes.

6. Rationale for the study

The MSFD and the MSPD required the use of an EBM approach to protect marine ecosystems by managing human activities. Within the MSFD, two main taxonomic groups of marine megafauna (marine mammals and seabirds covered by the HB and BD, respectively) are included for the assessment and reporting under the Descriptor 1 '*Biological Diversity*' (European Commission, 2014). This Descriptor provides a definition of the Good Environmental Status in relation to biological diversity, stating that there should not be further loss of diversity, the deteriorated attributes of biological diversity are restored and the use of the marine environment is sustainable (European Commission, 2014). The assessment of the state is required at three main ecological levels: species, habitats and ecosystems. Some of the criteria included in the Descriptor 1 are related with the population abundance and distributional range of the species, the conditions of the biodiversity habitats and the anthropogenic pressures which may adversely affect the biodiversity considered (European Commission, 2014).

In this context, the North-East Atlantic Ocean is one of the four marine regions considered in the MSFD, and is further divided into ecologically coherent sub-regions, one of which is the 'Bay of Biscay and the Iberian Coast' (Authier et al., 2018) that includes waters under the juridiction of three Member States: Spain, France and Portugal. As part of their obligations under the MSFD, the three countries have described actions related to the creation or expansion of MPAs such as 'spatial protection measures for the marine environment', where Spain included the proposal for the creation of new MPAs and a number of specific regulations to manage human activities (Cavallo, 2018).

6.1. The Bay of Biscay and the Iberian Coast

The Bay of Biscay (hereafter 'BoB') is an open oceanic bay situated in the eastern North Atlantic limited in the south by the West-East oriented Spanish coast and in the eastern part by the French coast with a South-North orientation (Figure 8). The southern sector (*i.e.* the Cantabrian Sea) is characterized by the narrow Northern Iberian continental shelf, which extends to 15-20 nm (Borja and Collins, 2004; Prego and Vergara, 1998). The French coast, on the contrary is characterized by a wider shelf (reaching its widest points in the Armorica and Aquitaine regions) that extend from 30 to 80 nm increasing in width northwards. The southern part of the Bay of Biscay includes several submarine canyons (*e.g.* Capbreton, Cap-Ferret) with the deepest waters in the area (2000-5000 m; Borja and Collins, 2004; Mulder et al., 2012). Large river discharge is the main source of freshwater into the BoB resulting in a low-salinity gradient from coastal to oceanic waters, occurring mainly in the Northern BoB (Mason et al., 2006).

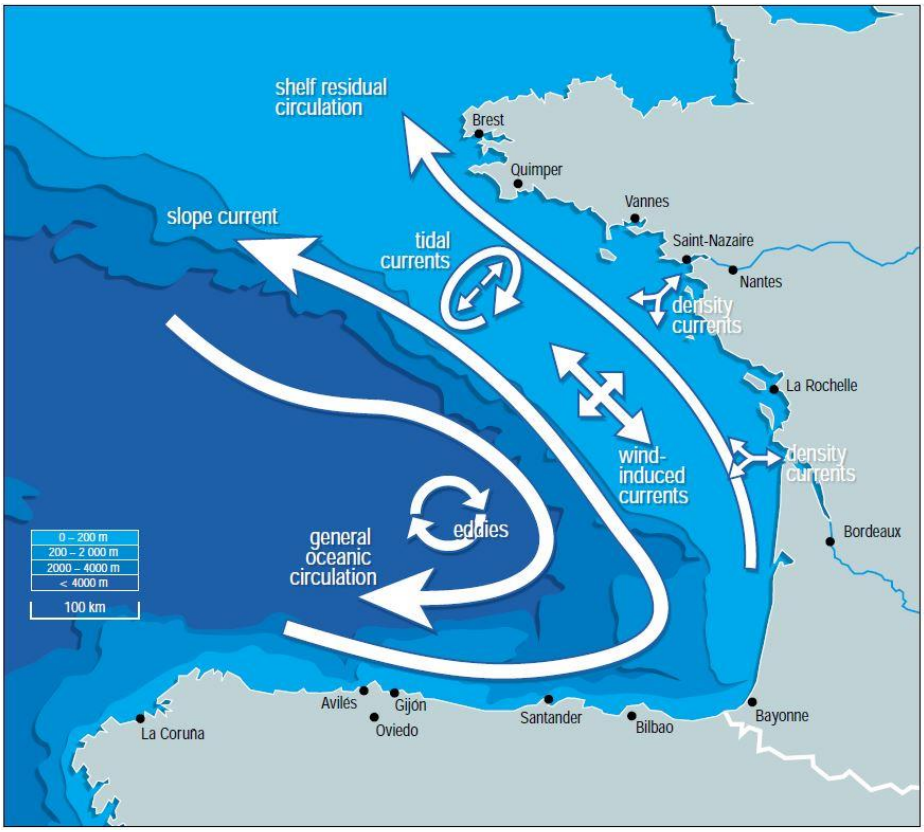

Figure 8. The main hydrographic features in the Bay of Biscay. Source: reproduced from Koutsikopoulos and Le Cann (1996) and modified by OSPAR Commission (2000).

The circulation in the BoB is complex and depends on bathymetry, tides, density-driven currents, and wind. There is a weak oceanic circulation flowing southward originating from the North-Atlantic Gyre and a stronger slope current that flows northward along the shelf break (Koutsikopoulos and Le Cann, 1996; Pingree and Garcia-Soto, 2014). The confluence of these opposite flows frequently results in mesoscale eddies that persist in time (Caballero et al., 2014; Pingree and Le Cann, 1992). The sea surface temperature shows a latitudinal gradient in the summer period, being the south-eastern part of the BoB the warmest area (Koutsikopoulos et al., 1998), while the warming of the southern BoB waters can occur in winter due to the *Navidad* current (Borja et al., 2018). Two phytoplankton blooms take place in the Bay of Biscay, one in spring and one in autumn (Pingree and Garcia-Soto, 2014; Varela, 1996). During summer and early autumn the coastal areas of the southern shelf are characterized by the presence of local upwelling events, persistent through the thermal stratification (Botas et al., 1990; Koutsikopoulos and Le Cann, 1996).

Due to the industrialization and urban development of the coastal margin of the BoB over the past 50 years (Borja et al., 2018), the marine environment has suffered increased disturbance triggered by the input of chemical substances, physical perturbation, and direct impacts on biological communities and species (Valdés and Lavín, 2002). These pressures include: (a) extractive activities such as fishing, aquaculture, and farming which can have a direct impact on marine megafauna (*e.g.* bycatch, entanglement, prey depletion) (Lassalle et al., 2012; Mannocci et al., 2012); (b) polluting industrial activities (*e.g.* paper milling, petroleum refining); (d) the introduction of non-native species via ballast waters (Butrón et al., 2011; ICES, 2015) and (e) maritime transport with the risk of oil spills, since the BoB is located on the main route of tankers transporting oil from the Middle East and Africa to European harbours (Lavín et al., 2006), also having a high likelihood of collisions with marine mammals. In relation to global change, some studies suggest that the BoB is under a meridionalization process with the establishment of warm-water native species previously restricted to southernmost areas (Punzón et al., 2016). Moreover, there are robust indications of the increase of the intensity and frequency of extreme weather events over the recent decades due to climate change (Cai et al., 2014; Ummenhofer and Meehl, 2017) that can impact on marine biodiversity.

6.2. Marine megafauna within the Bay of Biscay

The marine megafauna community of the BoB is highly diverse, and includes boreal and subtropical species of several taxonomic groups (elasmobranchs, large teleosts, marine mammals, seabirds and seaturtles). The BoB is a dynamic and biologically rich pelagic ecosystem that represents an important seasonal key feeding ground for those species that undertake seasonal feeding migrations into the area (García-Barón et al., 2019a; Lambert et al., 2017a; Lezama-Ochoa et al., 2010). Seabirds (Boué et al., 2013; Fort et al., 2012; Louzao et al., 2015; Stenhouse et al., 2012), cetaceans (Edwards et al., 2015), sharks (Doherty et al., 2017), tuna (Chust et al., 2019), turtles (Avens and Dell'Amico, 2018), sunfish (Sims et al., 2009) use the BoB as a migration corridor, while during spring and summer, various species of seabirds breed in colonies spread along the French coasts of the Northern BoB (Bilan et al., 2006; Cadiou et al., 2010; Cadiou and Monnat, 1996).

Within the megafauna community, this thesis is focused on marine mammals and seabirds. In the BoB, representatives of three very different groups of marine mammals can be found, baleen whales (the most common being the Fin whale *Balaenoptera physalus*), small toothed-cetaceans (the Short-beaked common *Delphinus delphis*, the Risso's *Grampus griseus*, the Striped *Stenella coeruleoalba* and the Bottlenose dolphins *Tursiops truncatus*, the Long-finned pilot whale *Globicephala melas* and the Harbour porpoise *Phocoena phocoena*) and deep-diving cetaceans (with the most common being the Sperm whale *Physeter macrocephalus* but with other species, such as the Cuvier's beaked whale *Ziphius cavirostris* also present).

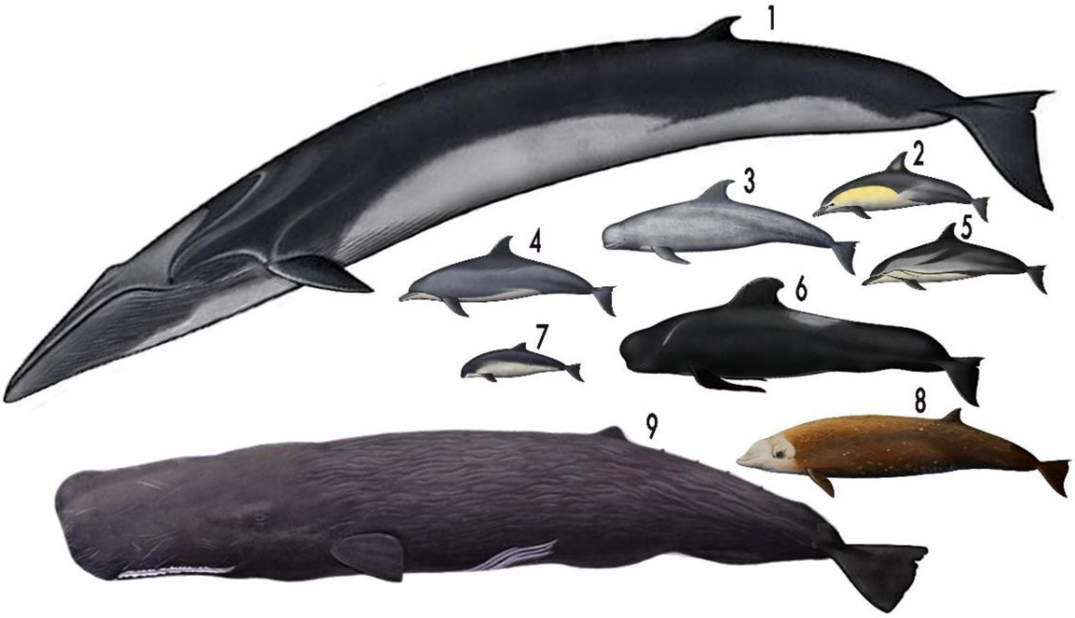

Figure 9. *Most common species of marine mammals inhabiting the Bay of Biscay: (1) Fin whale, (2) Short-beaked common, (3) Risso's dolphin, (4) Bottlenose dolphin, (5) Stripped dolphin, (6) Long-finned pilot whale, (7) Harbour porpoise, (8) Cuvier's beaked whale and (9) Sperm whale. Image courtesy of Joshua G. Herranz (Marine Life Project).*

Concerning seabirds, species can be classified depending on the habitat usage being resident (those that breed in the BoB, with the most common being the Yellow-legged *Larus michahellis*, the Lesser black-backed *L. fuscus* and the European herring gulls *L. argentatus*, the European shag *Phalacrocorax aristotelis*, the European storm-petrel *Hydrobates pelagicus*, the Black-legged kittiwake *Rissa tridactyla*, both the Sandwich *Thalasseus sandvicensis* and the Common tern *Sterna hirundo* and the Cory's shearwaters *Calonectris diomedea*) and wintering/migrants (those seabirds not breeding in the BoB, with the most common being the Northern gannet *Morus bassanus,* the Great skua *Stercorarius skua*, the Black-headed *Chroicocephalus ridibundus*, the Sabine's *Xema sabini* and the Mediterranean gulls *Ichthyaetus melanocephalus*, the Common guillemot *Uria aalge*, the

Razorbill *Alca torda*, the Sooty *Ardenna grisea*, the Balearic *Puffinus mauretanicus*, the Manx *P. puffinus* and the Great shearwaters *A. gravis*).

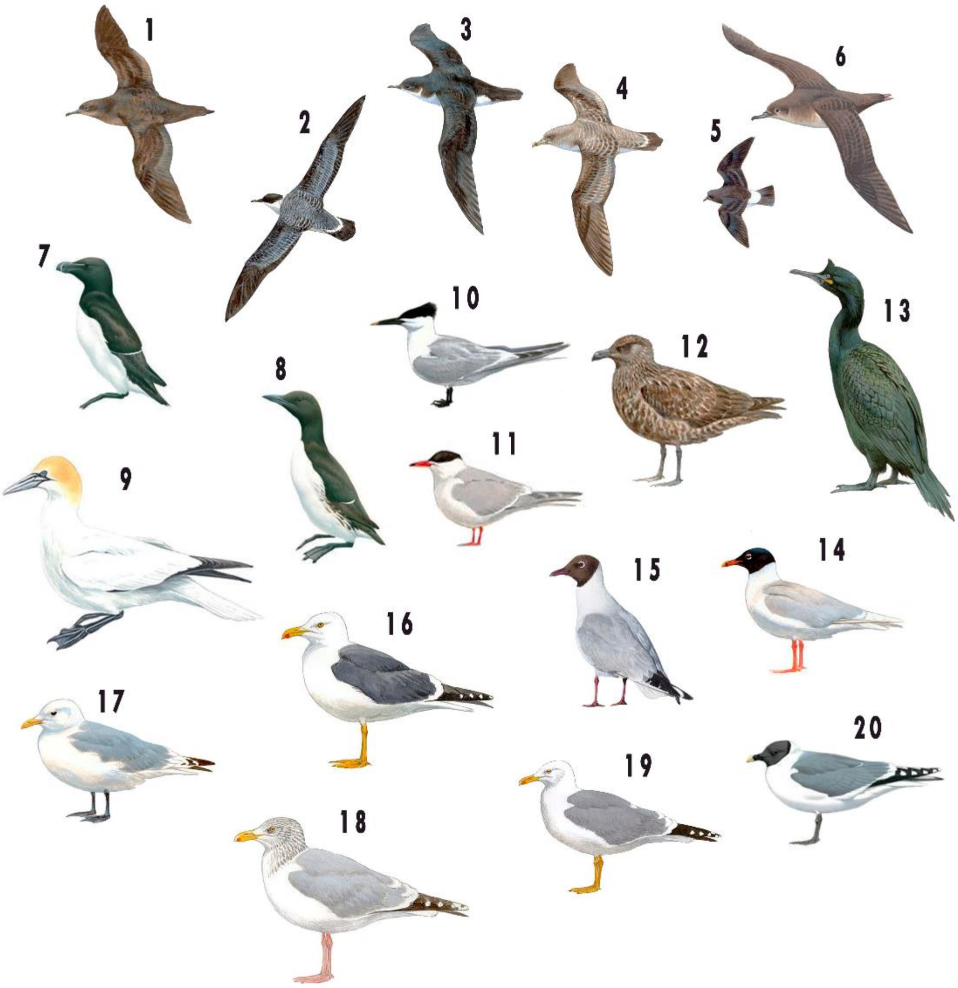

Figure 10. Most common seabird species inhabiting the Bay of Biscay: (1) Sooty shearwater, (2) Great shearwater, (3) Manx shearwater, (4) Cory's shearwater, (5) European storm-petrel, (6) Balearic shearwater, (7) Razorbill, (8) Common guillemot, (9) Northern gannet, (10) Sandwich tern, (11) Common tern, (12) Great skua, (13) European shag, (14) Mediterranean gull, (15) Black-headed gull, (16) Lesser black-backed gull, (17) Black-legged kittiwake, (18) European herring gull, (19) Yellow-legged gull and (20) Sabine's gull. Images have been compiled from www.seo.org and www.hbw.com and edited by Joshua G. Herranz (Marine Life Project).

6.3. Marine protected areas in the Bay of Biscay

In the BoB, the designation and establishment of MPAs is required by national and international (EU) legislation (see Section 3). In Spain, the HD and BD requirements have been transposed into the national legislation with the Ley 42/2007 del Patrimonio Natural y de la. Biodiversidad (in english "Law on the Spanish Natural Heritage and Biodiversity", partially modified in 2015 by the Law 33/2015). This law created the basic legal regime for the conservation, sustainable use, enhancement and restoration of the natural heritage and biodiversity. Moreover, it incorporates the concept of MPA and the creation of the MPAs networks, in line with EU guidelines, as well as the possibility of creating transboundary protected natural spaces. The law 42/2007 determines that the MPAs will be integrated into the Spanish Marine Protected Areas Network (RAMPE in its Spanish acronym). The RAMPE is regulated under Law 41/2010 on the protection of the marine environment which establishes its objectives, the natural areas that make it up and the mechanisms for its designation and management. This law is the legal instrument which transposed the MSFD requirements to the national territory. In the case of France, the process has been similar with the creation of the Agence des Aires Marines Protégées (in english "Marine Protected Areas Agency") under the Law of 14 April 2006, with the aim of supporting public policy for the creation and management of MPAs across all french public maritime domain and coordinate and manage MPAs network.

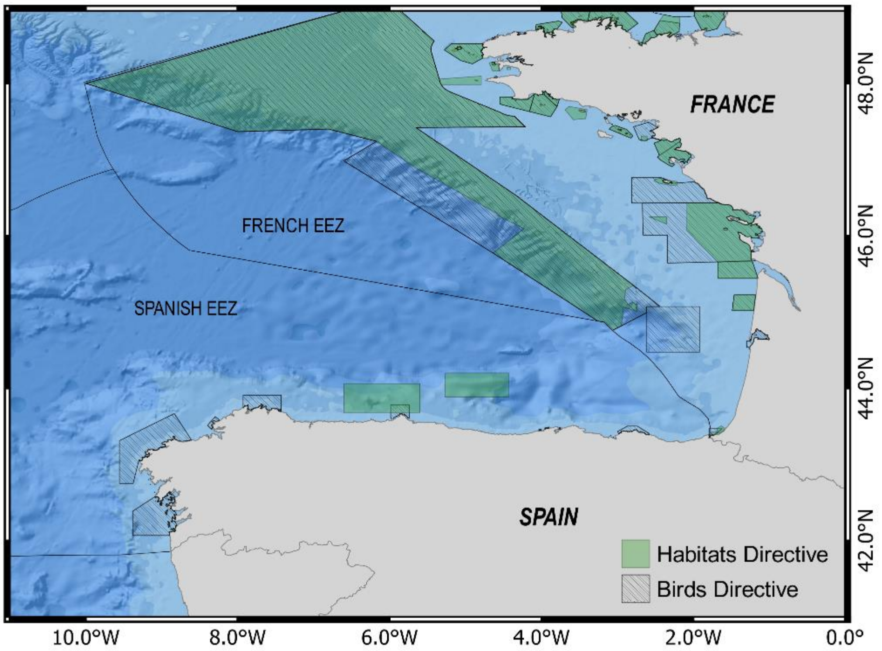

Figure 11. *Marine Protected Areas (MPAs) designated under the Birds or the Habitats Directive (2009/147/EC and 92/43/EEC, respectively) within the Bay of Biscay.*

The BoB is characterized by a broad range of MPAs categories, *e.g.* SACs, SPAs, Protected biotopes, Marine Natural Parks and National Nature Reserves. They have been created as a result of multiple governamental initiatives at local, regional and national levels and under different environmental legislation or sectoral laws. Overall, 71 MPAs are designated integrally in the marine environment (with no territory on land) of wich 16 belong to the Spanish Exclusive Economic Zone (EEZ) and 55 to the French EEZ (UNEP-WCMC and IUCN, 2019). Under the HD, the SACs were designated *inter alia* to protect cetacean species listed in Appendix II of the HD and their habitats (European Commission, 2007), oftern overlapping with SPAs sites (BD) (Figure 11). The only cetacean species listed in HD's Appendix II are the Harbour porpoise and the Bottlenose dolphin. Regarding SPAs designated under the BD, these MPAs aim to protect all the species listed in Annex I, which do not include all the species occurring in the BoB. However, the BD requires to take similar measures for regularly occurring migratory species not listed in Annex I (European Commission, 2009). As a network, these sites represent a broad range of species diversity, habitats, and ecological regimes in the marine environment of the BoB aiming at reversing the negative impacts of human impacts/stressors.

7. Hypothesis, aim and objectives

7.1. Working hypothesis

The working hypothesis is a "provisional, working means of advancing investigation" which could lead to the discovery of unforeseen, but relevant facts during the progress of the research (Dewey, 1938; Shields and Tajalli, 2006). As such, the working hypothesis has helped to establish the connection between the questions posed for the research and the evidence observed, and it can be constructed as follows:

"The highly diverse marine megafauna community of the Bay of Biscay face several anthropogenic threats, that requires increasing our understanding on their spatio-temporal abundance patterns to develop spatially explicit measures such as the identification of high biodiversity areas, assessment of the coherence of MPA network and estimation of the long-term robustness of MPAs."

7.2. Aim and objectives

The overarching aim of this thesis is to assess the impacts of human activities on marine megafauna in southern European waters by integrating the spatial ecology of this ecosystem component into ecosystem-based management. By focusing on marine megafauna species (*i.e.* seabirds and cetaceans) inhabiting the BoB, we developed an integrative ecological framework based on multidisciplinary approaches to identify threats, develop environmental indicators, establish baseline values, obtain estimates of spatio-temporal abundance, assess the coherence of MPAs networks and in addition, examine the value of long-term series for MPA robustness.

In order to fulfil the general aim, specific research objectives have been defined and summarized below:

1. To assess the main threats affecting the marine megafauna community in the Bay of Biscay providing a qualitative and, when possible quantitative, assessment to identify the main pressures affecting directly or indirectly the cetacean and seabird species inhabiting the area. (**Chapter 1**)
2. To develop a methodological approach, applicable to other species, to identify biologically appropriate predictors to jointly consider both the spatial and vertical dimensions of oceanographic habitats. (**Chapter 2**)

3. To locate ecologically meaningful areas for the marine megafauna community through the identification of Essential Ocean Variables shaping their environmental envelopes and driving their spatio-temporal trends. (**Chapter 3**)
4. To identify critical areas for marine megafauna and to assess whether the current Marine Protected Areas network offers protection for species for which it has not been designated. (**Chapter 4**)
5. To explore the temporal stability of spatial prioritization for marine megafauna by assessing the number of years needed to ensure a robust MPA network. (**Chapter 5**)

All these objectives share a practical goal as they focus on the 'biodiversity and ecosystem conservation' aspect of the EBM which should be supported by multidisciplinary studies involving different approaches and study techniques. With the aim of operationalising the EBM within the current European legislation, this thesis intends to inform conservation and management measures in the context of the MSFD overall aim, which is to enable sustainable use of marine goods and services.

8. Structure of the thesis

The nature of this work and the disparity of the questions and methodologies addressed during the thesis led to the presentation of different research themes separately in different chapters. Each chapter is therefore presented as an individual scientific paper with its own introduction, material and methods, results, and discussion. In this manner, some redundant information has perhaps been inevitably included in the introduction and materials and methods sections.

Chapter 1

Which are the main threats affecting the marine megafauna in the Bay of Biscay?

ABSTRACT

The marine environment faces an increasing number of threats, mainly driven by anthropogenic activities, that are causing growing impacts on marine species and processes. In Europe, the EU Marine Strategy Framework Directive (MSFD) aims to achieve or maintain Good Environmental Status (GES) of the European waters by 2020. The Directive specifically refers to biodiversity with the first of the eleven qualitative descriptors (proposed to help describe what GES should look like) being Biodiversity is maintained. For this descriptor, the status of several functional groups, including marine megafauna species, need to be assessed using criteria such as population size and condition and mortality due to bycatch in fishing gear that compare current values against agreed thresholds. To contribute to this process, we performed an assessment of the threats affecting the marine megafauna community (*i.e.,* seabirds and marine cetaceans) in the Bay of Biscay synthesizing the available evidences and identifying the main threats affecting the marine megafauna to help prioritise the required management and conservation actions. We analysed 4,023 admissions of seabirds recorded during 2004-2016 from four Wildlife Rehabilitation Centres (WRCs) to obtain an initial quantitative assessment of the pressures exerted on seabirds. The main marine threats identified in the Spanish North Atlantic sub-region were cachexia (52.3%), exposure to crude oil (10%) and interaction with fishing gears (5.3%). When considering all threats together, the Common guillemot, the Yellow-legged gull, the Northern gannet, the Great cormorant and the Razorbill were the main affected species. In addition, we summarised the available information to perform an updated qualitative assessment of the severity of the threats faced by seabirds and cetaceans. The qualitative assessment showed that cetaceans are especially vulnerable to bycatch, vessel collision, and pollution-related threats, whilst seabirds are particularly sensitive to oil spills, bycatch and marine litter. This type of assessment studies can aid in the identification of priority areas and/or species where management measures should be applied to ensure that the ultimate goal of the MSFD, sustainable conservation of the marine environment, is reached.

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1. Introduction

The marine environment faces an increasing number of threats that are causing growing impacts on marine species and processes; with over a third of the world's oceans estimated to suffer high or very high impacts (Halpern et al., 2008). These threats are mostly driven by anthropogenic activities, such as overexploitation of marine resources, pollution and habitat degradation and destruction (Dulvy et al., 2003; Halpern et al., 2007; IPBES, 2019). In addition, climate change-driven processes such as extreme weather events, increasing temperature and acidification are having serious effects on marine habitats (Descamps et al., 2015; Harley et al., 2006; Vaughan et al., 2001). These threats could have a cumulative effect and therefore the assessment of their spatio-temporal patterns could be of crucial importance (Halpern et al., 2015; Maxwell et al., 2013). In a recent assessment (IPBES, 2019), over 40% of marine ecosystems were highly impacted by climate-driven anthropogenic threats and 66% experienced cumulative impacts.

In Europe, the Marine Strategy Framework Directive (MSFD; 2008/56/EC) aims to provide the legal framework to achieve the sustainable use of marine goods and services of European waters by effectively managing human activities and pressures through an ecosystem-based approach. The MSFD requires Member States (MS) to follow a series of steps with the aim of achieving (or maintaining) *Good Environmental Status* (GES) of their waters by 2020 (see Santos and Pierce, 2015). One of the requirements of the Directive is that MS should define what GES means for their waters, in terms of the eleven qualitative descriptors provided. The Directive defines that GES will be reached when "*the overall state of the environment in marine waters provides ecologically diverse and dynamic oceans and seas which are healthy and productive*". MS are also required to set environmental targets and develop criteria (with associated thresholds) to reach GES, and to monitor the progress towards GES. The first descriptor of Biodiversity states that GES will be achieved when "*Biological diversity is maintained. The quality and occurrence of habitats and the distribution and abundance of species are in line with prevailing physiographic, geographic and climatic conditions".* For this descriptor, the guidance provided by the European Commission (Cochrane et al., 2010) suggests a focus at the level of "functional group" (defined as "*an ecologically relevant set of species*") for assessment and reporting. Highly mobile groups of species such as cetaceans and seabirds are included as two of these functional groups. Cetaceans and seabirds ('marine megafauna' hereafter) have key roles in marine ecosystem functioning, with changes in their abundance and distribution impacting ecosystem structure, function and resilience (Baum and Worm, 2009; Estes et al., 2011).

The BoB hosts numerous seabird and cetacean species of high conservation value. In the case of seabirds, many species breed in Northern Europe but spend the non-breeding period in this area (Pettex et al., 2017). Among seabirds, there are species classified as "Critically Endangered" (Balearic shearwater *Puffinus mauretanicus*), "Endangered" (Atlantic puffin *Fratercula arctica*), "Vulnerable" (black-legged kittiwake *Rissa tridactyla*) and "Near threatened" (Razorbill *Alca torda*) (IUCN, 2018). Of the common cetacean species, the Fin whale *Balaenoptera physalus* is classified as "Near threatened" and both the sperm whale *Physeter macrocephalus* and the Harbour porpoise *Phocoena* as "Vulnerable" in Europe (IUCN, 2018). At the Spanish level, ten cetacean and four seabird species are listed as "Threatened" in the Royal Decree for the Development of the List of Wild Species in Regime of Special Protection and the Spanish Catalogue of Endangered Species (RD139/2011).

There is an overall lack of knowledge on the severity of the impact of different threats (*e.g.,* climate change, pollution, fishing, habitat-related changes) on seabirds and cetaceans in the BoB. This information is valuable in the context of the MSFD to develop criteria and their associated thresholds to determine if GES is reached. Within this context, we provided the first assessment of the impact of different threats on the marine megafauna community of the BoB based on two complementary approaches. Firstly, we evaluated the quantitative information gathered for seabirds at Wildlife Rehabilitation Centres (WRCs) to provide the basis for an initial assessment. Secondly, we carried out a literature review to (1) identify the main threats affecting both seabird and cetacean species occurring in the BoB and (2) evaluate their potential impact on both taxonomic groups. Both approaches were compared to provide a full assessment of their potential impact on the marine megafauna in the BoB.

2. Material and Methods

2.1. Selection of species

The species considered were those listed as present in the North Atlantic sub-region of the Spanish initial evaluation document for the MSFD (MAGRAMA, 2012a, 2012b). The conservation status of the species listed was obtained at the global, European and national level. For global and European level, we used the International Union for Conservation of Nature criteria (IUCN) and checked whether the species was listed in the Annex I of the Birds Directive (BD; Council Directive 79/409/EEC) and/or in the Annex II of the Habitats

Directive (HD; Council Directive 92/43/EEC). At the national level, we used for seabirds the Red Book of the Birds of Spain (Madroño et al., 2004) and for cetaceans the Red Book of Spanish vertebrates (Blanco and González, 1992) and the RD139/2011.

The marine megafauna list was composed by 35 seabird species belonging to nine families (Anatidae, Gaviidae, Procellariidae, Hydrobatidae, Sulidae, Phalacrocoracidae, Stercorariidae, Laridae and Alcidae) and 24 cetacean species belonging to five families (Balaenopteridae, Balaenidae, Delphinidae, Physeteridae and Ziphiidae) (Appendix A, see Table A-1.1 and A-1.2, respectively). Based on the IUCN criteria, six seabird and five cetacean species at the global level and eight seabird and six cetacean species at the European level were identified as *threatened* (*i.e.,* vulnerable, endangered or critically endangered). Furthermore, 33 seabird species were included in the Annex I of the BD and two cetacean species were included in the Annex II of the HD. At the national level, nine seabird and eleven cetacean species were listed as *threatened* by the RD139/2011.

2.2. Threats considered

An increasing number of threats could affect seabirds and cetaceans. We grouped the threats into different categories depending on their source: (a) *climate change*; (b) *pollution* which groups together all the threats associated with contamination; (c) *fishing* that includes direct (*e.g.,* bycatch) and indirect (*e.g.,* prey depletion) interactions of megafauna with fishing activities; (d) *habitat-related changes* that includes threats related with habitat degradation, loss and destruction and (e) *others* that include a variety of marine threats such as vessel collision or disturbance due to tourism.

2.3. Impact assessment

a) Quantitative approach

Ethical statement: The rehabilitation programmes of the WRCs were conducted under the authorization of the appropriate departments of each regional government and were consistent with good veterinary practices.

Information of the admissions of marine megafauna species to WRCs were only available for seabirds in the southern BoB (Figure 1.1). Information was gathered for a 13-year period (2004-2016) from the four existing WRCs in the southern BoB located in Gipuzkoa (Arrano Etxea WRC, 2004-2016), Bizkaia (Bizkaia WRC, 2004-2016), Cantabria (Cantabria WRC, 2010-2016) and Asturias (SERIDA, 2009-2016).

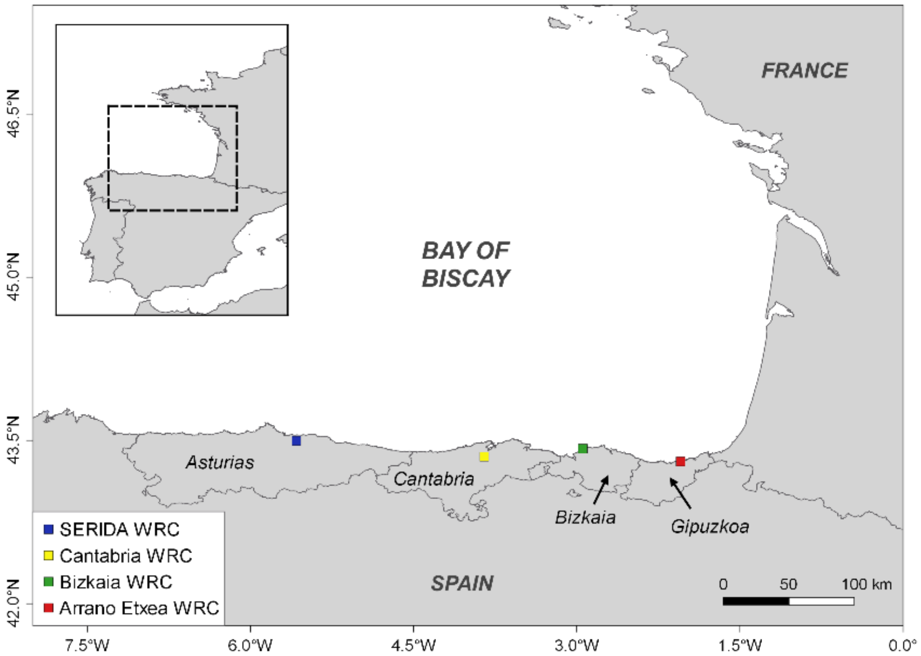

Figure 1.1. Locations of the four Wildlife Rehabilitation Centres (WRC) along the southern Bay of Biscay.

The WRCs' protocol (Figure 1.2) involves recording the location, date of collection and admission, cause of admission, clinical evolution, date of release or death and, in the latter case, cause of death for each animal arriving at the WRCs. We coded the causes of admission into four different categories of threats, with a special focus on marine-related threats. *Cachexia* (*i.e.,* extreme weight loss and muscle wasting) was included into climate change since this cause of admission has been related to extreme climatic events in the study area (Louzao et al. 2019). Similarly, *interaction with fishing gear* and *exposure to crude oil* were included into fishing and pollution, respectively. The remaining causes of admissions were included into the category *others*: *traumas* (subdivided into *car impact*, *gunshot*, *electrocution* and *undefined trauma*), *disease* (subdivided into *parasitic/infectious disease* and *others*), *orphaned*, *intraspecific interaction*, *without apparent lesions, other causes* (including *forfeited, poisoning* and *autolytic*) and *undetermined*.

We further analysed the causes of admissions by identifying the main affected seabird families/species and the temporal evolution of the number of individuals affected by each threat, both seasonally and inter-annually, testing whether there were statistically significant differences in seabird families/species and causes of admission using Chi-square tests. Furthermore, we explored the associated variability [*i.e.,* coefficient of variation (CV)] of the percentage of admissions per year and species.

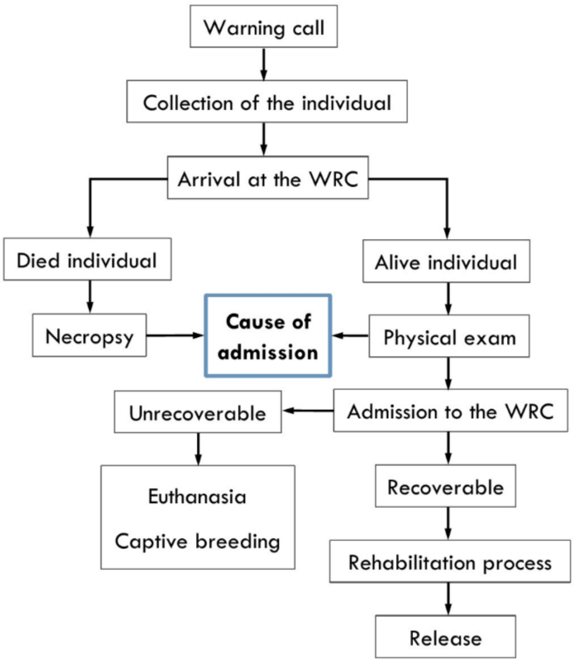

Figure 1.2. The protocol implemented in the Wildlife Rehabilitation Centres (WRCs). The blue box shows the data used to perform the quantitative assessment.

b) *Qualitative approach*

We carried out a literature review to (a) determine the main threats affecting directly or indirectly the cetacean and seabird species and (b) gather evidence (based on published data) on the likelihood of the impact of different threats. The scoring was based on a categorical codification of low, medium and high impact following the criteria used by the Working Group on Marine Mammal Ecology (WGMME) of the International Council for the Exploration of the Sea (ICES) (ICES, 2015). A *high* score was given when "there were evidences of negative population effects, mediated through effects on individual mortality, health and/or reproduction"; a *medium* score was given when "there were evidences or strong likelihood of impact at individual level on survival, health or reproduction, but population effects were not clear" and finally *low* score was given when there were "possible negative impacts on individuals, but weak evidence and/or infrequent occurrence". Finally, the text "*No evidence of threat to date in the area*" was used for cases where there was no evidence of the impact of the threat in the BoB or it was not considered relevant for the species. The literature review was conducted on the ISI Web of Knowledge using the following key words: *cetacean*, *marine mammal*, *seabird*, *threat*, *pressure*, *East Atlantic* and *Bay of Biscay*. In addition, relevant reports and publications were accessed including the initial MSFD evaluations of Spain and France, the ICES reports of the Joint Working Group on Seabirds (JWGBIRD) and WGMME, the reports of the Intersessional Correspondence

Group on the Coordination of Biodiversity Assessment and Monitoring (OSPAR ICG-COBAM) expert group and the reports of the International Whaling Commission (IWC) Scientific Committee. Based on the review, we created a matrix of species and marine threats categories.

c) Quantitative versus qualitative assessments

The comparison of the quantitative and qualitative assessments was only possible for seabird species. We compared the number of admissions due to cachexia, exposure to crude oil and interaction with fishing gears in the quantitative assessment with the scoring obtained in the qualitative assessment of extreme weathers events, oil spills and bycatch, respectively. This comparative analysis was based on 26 seabird species included in both assessments. We transformed the number of admissions into impact scores for each species and threat by scoring as *low* when the percentage of the number of admissions for a given threat was <33%. Similarly, scores of *medium* and *high* were assigned when the percentage of the number of admissions for a given threat ranged between 33% and 66% and >66%, respectively. Then, we compared both sets of scores by threat.

3. Results

3.1. Quantitative impact assessment

a) Overall description

Data from a total of 4,023 admissions were available divided between WRCs as follows: 1,616 (40.2%; 2014-2016 period) from the Gipuzkoa WRC, 1,854 (46.1%; 2014-2016 period) from the Bizkaia WRC, 227 (5.6%; 2010-2016 period) from the Cantabria WRC and 326 (8.1%; 2009-2016 period) from the Asturias WRC. The admissions included 29 species belonging to nine families (see Figure 1.3a): Alcidae (41.2% of the total number of admissions), Laridae (38.9%), Sulidae (13.3%), Phalacrocoracidae (3.7%), Procellariidae (0.6%), Anatidae (0.4%), Gaviidae (0.2%) and Stercorariidae (0.07%). The Common guillemot *Uria aalge* was the species most frequently admitted (36.3%, n=1,459), followed by the Yellow-legged gull *Larus michahellis* (26.8%, n=1,078), the Northern gannet *Morus bassanus* (13.3%, n=536), the Black-headed gull *Chroicocephalus ridibundus* (4.87%, n=196), the Geat cormorant *Phalacrocorax carbo* and the Razorbill (both 3%, n=124).

The number of cases and the frequency distribution by cause of admission (summarised in 8 categories as previously explained) is shown in Table A-2.1. The most frequent cause of admission was *cachexia* (51.2%, n=2,061), followed by *exposure to crude* *oil* (9.9%, n=397) and *interaction with fishing gears* (5.2%, n=207). The category *others* included 33.8% of the admissions of which *undefined trauma* (12.9%, n=511) and *orphaned* (5.7%, n=224) were the main contributors to the number of admissions (Figure 1.3b).

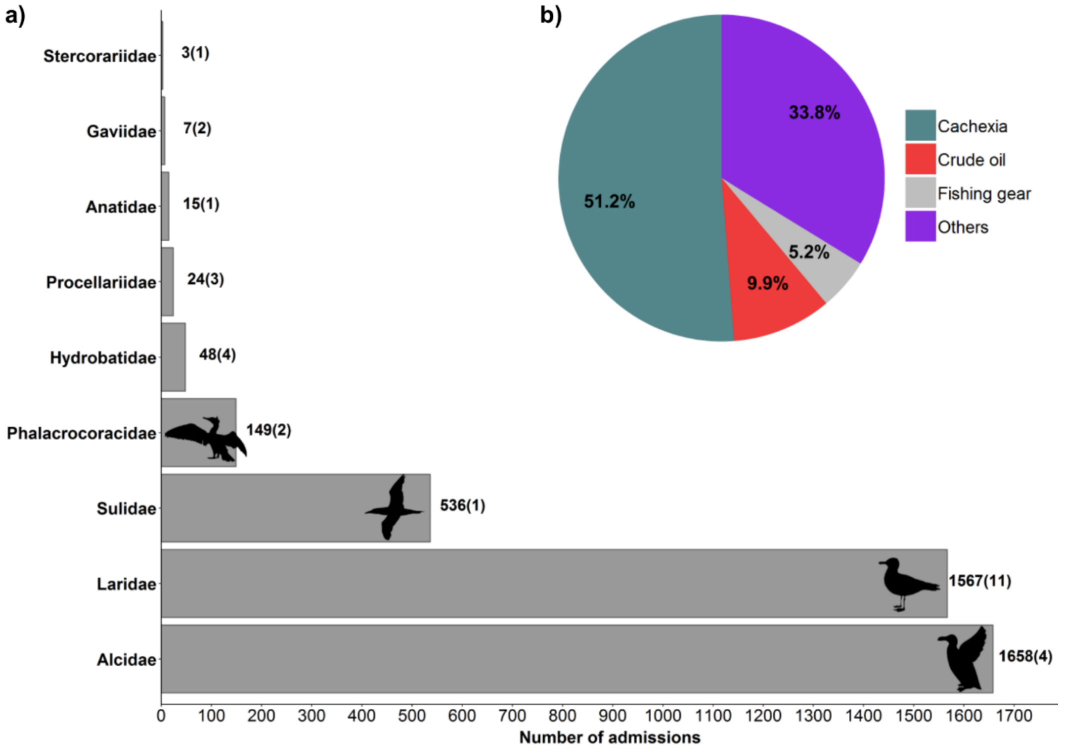

Figure 1.3. a) Number of admissions at the Wildlife Rehabilitation Centres located in the southern Bay of Biscay (2004-2016) categorized by taxonomic family. The numbers to the right of the bars indicate the number of admissions and the number of species belonging to each family is given between brackets. b) Pie chart of the number of admissions by threats expressed as the percentage of the total number of admissions.

b) Temporal variation of admissions

The most frequently recorded species (see details above) were registered every year, in contrast to those species which were less commonly recorded. Overall inter-annual variability (CV) of the most frequently recorded species ranged between 0.33 (Great cormorants) and 0.66 (Razorbills) (Table A-2.2). By year, the Alcidae family was mainly recorded in 2004 and 2014, whilst the admissions of individuals of the families Laridae, Sulidae and Phalacrocoracidae remained almost constant during the study period (Figure 1.4a). The highest numbers of admissions related to *cachexia* (the most prevalent cause of admission) were recorded in 2007, 2014 and 2016 (χ^2=1449.5, df = 12, p<0.0001; Figure 1.4b). The most affected families were Alcidae (58.5%), Laridae (22.5%) and Sulidae (13.2%). Significant higher numbers of admissions due to *exposure to crude oil* took place in 2004 and 2007 (χ^2=1062, df = 12, p<0.0001; Figure 1.4b). The most affected families were Alcidae (85.1%), Sulidae (8,4%) and Laridae (4.8%). For both threats, the most affected species was the Common guillemot with 51.3% and 77.3% of the total admissions (considering all species together) corresponding to *cachexia* and *exposure to crude oil*, respectively. The number of admissions related to interaction with fishing gears remained almost stable over time (Figure 1.4b). The most affected species were Northern gannets (28.7%), Yellow-legged gulls (8.6%), Great cormorants (4.6%) and Common guillemots (2.7%).

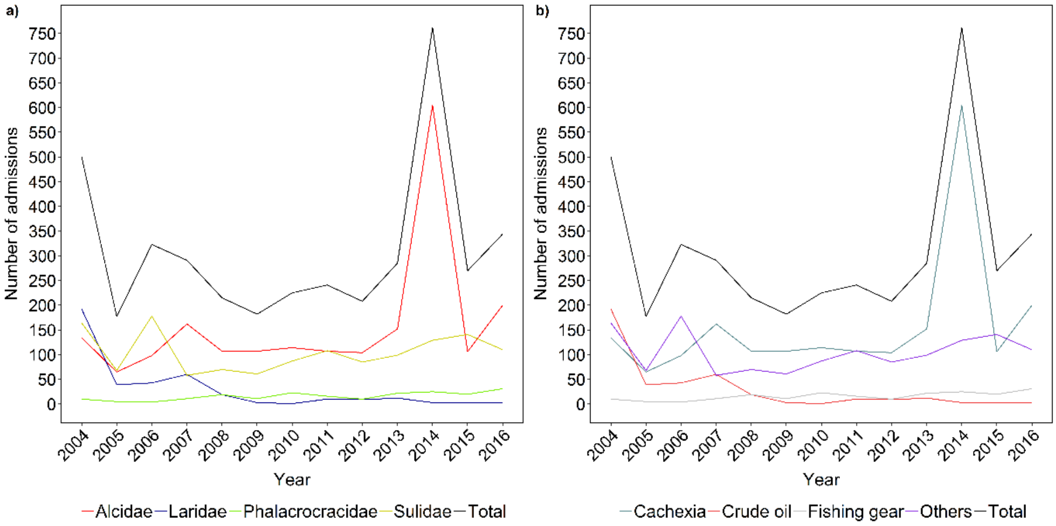

Figure 1.4. Annual admissions of a) the four most frequently admitted seabird families and b) the main marine threats and others recorded at the Wildlife Rehabilitation Centres in the southern Bay of Biscay (2004-2016).

The highest percentage of admissions was recorded in winter (31.4%, n=1,264), followed by spring (23.2%, n=935), summer (23.2%, n=935) and fall (22.1%, n=889). Seasonal admissions of the main families are shown in Figure 5a. The family Alcidae showed more significant admissions in winter and spring (χ^2=1095.5, df=3, p<0.0001), whereas the family Laridae was the main family admitted in summer and fall (χ^2=399.89, df=3, p<0.0001). The families Sulidae and Phalacrocoracidae were significantly most frequently admitted in fall than the rest of the year (χ^2=133.1, df=3, p<0.0001; χ^2=45.497, df=3, p<0.0001, respectively). The most frequent causes of admission varied among seasons (Figure 1.5b). We detected significant differences in the number of admissions between seasons for all threats, except for the *interaction with fishing gear*s (χ^2=8.16, df=3, p=0.06). In the case of *cachexia* and *exposure to crude oil* (χ^2=384.04, df=3, p<0.0001; χ^2=240.99, df=3, p<0.0001, respectively), the highest number of admissions were recorded in winter and during both winter and spring, respectively. Admissions due to *undefined traumas* and *orphaned* ($\chi^2=121.38$, df=3, $p<0.0001$; $\chi^2=388.75$, df=3, $p<0.0001$, respectively) were more numerous in summer and fall.

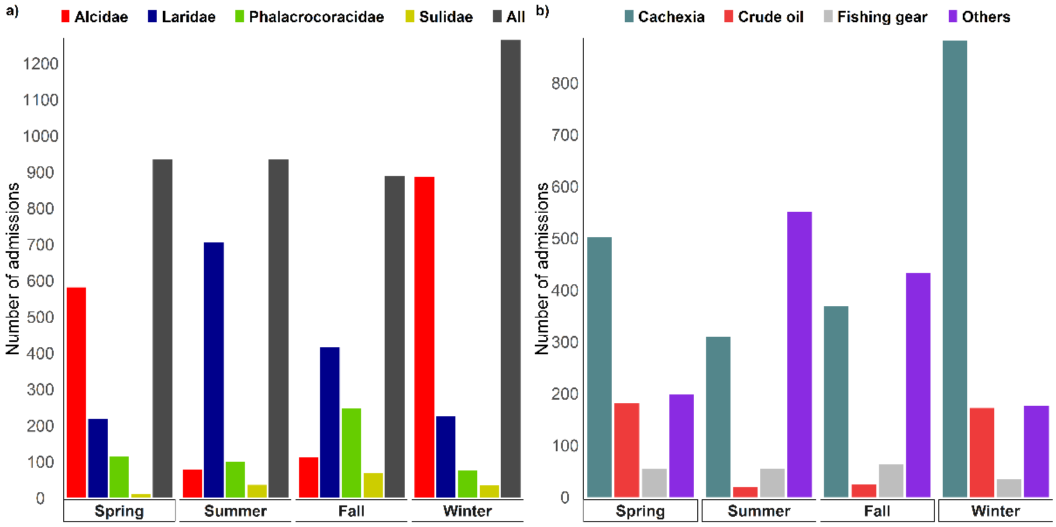

Figure 1.5. Seasonal admissions of a) the four most frequently admitted seabird families and all the admissions and b) the main threats and other causes of admission at Wildlife Rehabilitation Centres of the southern Bay of Biscay (2004-2016).

3.2. Qualitative impact assessment

a) Cetaceans

Threats related to climate change were scored as *low* for most of the selected species (31.8%). However, the increase in water temperature was scored as a *medium* for 31.8% of the species (Table 1.1). In relation to pollution, 27.1% of the species scored *high* or *medium* due to the potential effect of persistent organic pollutants (*e.g.,* PCBs), considered to be especially dangerous for the Long-finned pilot whale *Globicephala melas*, the Killer whale *Orcinus orca*, the Bottlenose dolphin *Tursiops truncatus* and the Harbour porpoise. Almost 23% of the species scored *medium* for the impact of marine litter (*e.g.,* plastics), whilst ghost fishing scored *medium* for 13.6% of the species. Sixty-eight percent of the species scored *medium* (40.9%) or *high* (27.2%) for acoustic pollution (*e.g.*, seismic surveys or mining). Finally, all the species scored *low* for oil spills. In relation to fishing, bycatch was identified as particularly dangerous for 54.5% of the species (13.6% *medium* and 40.9% *high*) while overfishing scored *low* for all the species. Habitat related threats scored *low* for all species, except the Harbour porpoise. This species scored *medium* for impact of coastal urbanization. Regarding other threats, introduction of pathogens scored *low* for all the species, while the impact of vessel collision was *high* and *medium* for the 40.9% and 13.6% of the species, respectively. Finally, tourism scored *medium* for the Bottlenose dolphin and *low* for the remaining species.

Table 1.1. Threat matrix for cetaceans in the Bay of Biscay. This matrix is an updated version derived from the one developed by the Working Group on Marine Mammal Ecology (WGMME; ICES, 2015) and it is based on the literature reviewed in this chapter. (*) indicates that the evaluation was obtained from the WGMME report; (†) indicates that the threat is referenced for the same species but in another area. Numbers in superscript indicate the reference used to evaluate the effect (references are included in the Appendix C). Colours highlight the effect of the threats as L: low (green), M: medium (yellow) and H: high (red).

		Minke whale	Sei whale	Blue whale	Fin whale	Humpback whale	Common dolphin	Long-finned pilot whale	Short-finned pilot whale	Risso's dolphin	Killer whale	False killer whale	Striped dolphin
Climate change	Elevated temperatures	M^{2}	L^{1}	L^{1}	L^{1}	L^{1}	M^{3,5}	L^{2}	L^{1}	L^{1}	L^{2}	L^{1}	L^{1,2}
	Ocean acidification	L^{4}	L^{4}	L^{4}	L^{4}	L^{4}	L	L	L	L	L	L	L
	Sea level rise	L	L	L	L	L	L	L	L	L	L	L	L
	Extreme weather events	L	L	L	L	L	L	L	L^{5}	L	L	L	L
	Shifts in ocean current patterns	L	L	L	L	L	L	L	L	L	L	L	L
Pollution	Chemical contamination (e.g. PCB, DDT)	L^{5}	L^{†,8}	L	L^{*,5}	L	M^{*,12}	H^{*,5}	L^{5}	L*	H^{*,15}	L	M*
	Marine litter (e.g. plastics, microplastics)	M^{*,5}	L	L^{†,24}	L^{*,5}	L^{5}	M^{5}	L^{*,5}	L^{5}	L^{*,5}	L^{*,5}	L^{5}	L*
	Ghost fishing	M^{5,7}	L	L	L^{*,5}	L^{†,25,26}	L*	L*	L	L*	L*	L	L*
	Eutrophication	L	L	L	L	L	L	L	L	L	L	L	L
	Acoustic pollution (e.g. sonar, seismic surveys)	M^{*,5,6}	L^{†,8}	L	M*	M^{6}	H^{5,6}	L*	L	M*	L^{5}	L	M*
	Light pollution	No evidence of threat to date in the area											
	Oil spills	L^{5,14}	L	L	L^{5}	L	L^{5,17}	L^{5,14}	L	L^{14}	L^{14}	L	L
Fishing	Overfishing	L^{6}	L	L	L^{6}	L^{6}	L^{11}	L^{6}	L	L*	L^{*,5}	L	L^{*,11}
	Bycatch	M^{23}	L	L	L*	M^{5}	H^{*,5,7,9,10}	H^{†,5,22,23}	H^{5}	H^{5,23}	L*	L	M^{*†,5,22,23}
Habitat-related changes	Habitat los	L	L	L	L*	L	L*	L*	L	L*	L*	L	L*
	Habitat degradation	L	L	L	L*	L	L*	L*	L	L*	L*	L	L*
	Invasive species	L	L	L	L	L	L	L	L	L	L	L	L
	Coastal urbanization	L	L	L	L	L	L	L	L	L	L	L	L
Others	Introduction of pathogens (ballast waters)	L^{5}	L^{5}	L	L	L	L^{*,5}	L*	L	L*	L*	L	L*
	Vessel collision	M^{*,5,6}	H^{†,8}	L	H^{5}	H^{5,6}	M^{5}	H^{5}	H^{5}	L*	L*	L	L*
	Tourism (e.g. whale/birdwatching)	L*	L	L	L*	L	L*	L^{*,5}	L^{5}	L*	L*	L	L*

Table 1.1. Continuation

		Bottlenose dolphin	White-beaked dolphin	Harbour porpoise	Pigmy sperm whale	Sperm whale	North Atlantic bottlenose whale	Blainville's beaked whale	True's beaked whale	Sowerby's Beaked whale	Cuviers's beaked whale
Climate change	Elevated temperatures	L[1]	M[1,2]	M[1]	L[1]	L[1,5]	M[1,2]	L[1]	M[1]	M[1]	L[1]
	Ocean acidification	L	L	L	L	L	L	L	L	L	L
	Sea level rise	L	L	L[6]	L	L	L	L	L	L	L
	Extreme weather events	L	L	L	L	L[5]	L[5]	L	L	L	L
	Shifts in ocean current patterns	L	L	L	L	L	L	L	L	L	L
Pollution	Chemical contamination (e.g. PCB, DDT)	H[*,12]	L[5]	H[*,12]	L	L[*,5]	L[*]	L[5]	L	L[*]	L[5]
	Marine litter (e.g. plastics)	L[*]	L[5]	L[*,5]	L[5]	M[*,5]	M[*]	L[5]	L[5]	L [†,27]	M[*,16]
	Ghost fishing	L[*]	L	L[*]	L	L[*,5]	M[*]	L	L	L	M[*]
	Eutrophication	L	L	L	L	L	L	L	L	L	L
	Acoustic pollution (e.g. sonar, seismic surveys)	H [†,6]	M[5,6]	H [†,5,6]	L	M[*]	M[*]	H [†,5,13]	H [†,13]	M[*] [†,13]	H[*,5,13]
	Light pollution	No evidence of threat to date in the area									
	Oil spills	L[14]	L	L[14]	L	L	L	L	L	L	L
Fishing	Overfishing	L[11,19]	L[6]	L[11]	L	L[6]	L[*]	L	L	L[*]	L[*]
	Bycatch	H[*,5,6,15,21,23]	H[5]	H[*,5,6,11,15,20]	H[5]	L[*,23]	L[*]	L	L	L[*]	H[5]
Habitat-related changes	Habitat loss	L[*]	L	L[*]	L	L[*]	L[*]	L	L	L[*]	L[*]
	Habitat degradation	L[*]	L	L[*]	L	L[*]	L[*]	L	L	L[*]	L[*]
	Invasive species	L	L	L	L	L	L	L	L	L	L
	Coastal urbanization	L	L	M[6]	L	L	L	L	L	L	L
Others	Introduction of pathogens (ballast waters)	L[*]	L	L[*]	L	L	L[*]	L	L	L[*]	L[*]
	Vessel collision	L	L	H[5]	H[5]	H[*]	M [†,28]	L	L	L[*]	H[5]
	Tourism (e.g. whale/birdwatching)	M[*]	L	L[*]	L	L[*]	L[*]	L	L	L[*]	L[*]

b) Seabirds

Concerning climate change, 2.7% of the species scored *high* impact due to the increase of water temperature and 11.1% scored *medium* due to the occurrence of extreme weather events (both especially importantfor the European storm-petrel *Hydrobates pelagicus*). The remaining threats related to climate change scored *low* for all the species. In relation to pollution, persistent organic pollutants scored *medium* for 13.8% of the species and *low* for the remaining species. Impact of marine litter scored *medium* for 16.6% of the species, *high* for 11.1% and *low* for the remaining 71.3% of the species. Impact of ghost fishing scored *medium* for the Northern gannet and the Great cormorant and *low* for the remaining species. All the species showed a *low* impact due to eutrophication. Light pollution scored *medium* for 11.1% of the species, being especially relevant for the family Procellariidae, and impact of oil spills scored *medium* and *high* for 47.2% and 16.6% of the species, respectively. Regarding the interaction with fishing, overfishing scored *low* for all the species, whilst 13.8% and 19.4% of the species scored *high* or *medium* due to bycatch. For threats associated with habitat change, 5.5% of the species scored *medium* due to habitat loss and *high* due to invasive species. However, 5.4% of the species showed a *medium* or *high* score due to habitat loss or habitat degradation, respectively. Impact of tourism scored *medium* or *high* for only 8.3% and 2.7% of the species, respectively (Table 1.2).

3.3. Quantitative versus qualitative assessments

The comparison of the assessments (Figure 1.6) between the admissions caused by cachexia and the occurrence of extreme weather events showed that the quantitative assessment rated a higher number of species as experiencing *medium* or *high* impact . In the case of the admissions related to the exposure to crude oil (caused mainly by oil spills), the qualitative approach classified the effect of this threat as *low*, *medium* and *high* depending of the species. However, the quantitative approach scored this threat as *low* for all the species. Concerning the interaction with fishing gear, the quantitative approach scored *low* for most of the species, while a small percentage of species scored *medium*. Regarding the bycactch in the qualitative approach, the majority of species scored *low*, while the remaining species scored *medium* or *high*.

Table 1.2. Threat matrix based on the literature reviewed in this chapter for seabirds in the Bay of Biscay. (†) indicates that the threat is referenced for the same species but in another area. Numbers in superscript indicate the reference used to evaluate the effect (references are included in the Appendix C). Colours highlight the effect of the threats as L: low (green), M: medium (yellow) and H: high (red).

		Black scoter	**Red-breasted merganser**	**Red-throated loon**	**Black-throated loon**	**Common loon**	**Cory's shearwater**	**Manx shearwater**	**Great shearwater**	**Sooty shearwater**	**Balearic shearwater**	**Northern fulmar**	**European-storm petrel**
Climate change	Elevated temperatures	L	L	L	L	L	L	L	L	L[†,46,47]	L[29,31]	L	H[30]
	Ocean acidification	L	L	L	L	L	L	L	L	L	L	L	L
	Sea level rise	L	L	L	L	L	L	L	L	L	L	L	L
	Extreme weather events	L	L	L	L	L	L	L	L	L	L	L[68]	H[32]
	Shifts in ocean current patterns	L	L	L	L	L	L	L	L	L	L	L	L
Pollution	Chemical contamination (e.g. PCB, DDT)	L[†,54]	L	L	L	L	L[†,50,56,79]	L[†,79]	M[†,78]	L[†,80]	M[35]	L	L
	Marine litter (e.g. plastics)	L	L	L[†,86]	L[†,88]	L	M[†,95]	M[†,90]	L[77]	L[†,89]	L[77]	L[77,81,82,83]	L[†,91]
	Ghost fishing	L	L	L[†,87]	L[†,87]	L[†,87]	L	L	L	L	L	L	L
	Eutrophication	L	L	L	L	L	L	L	L	L	L	L	L
	Acoustic pollution (e.g. sonar, seismic surveys)	No evidence of threat to date in the area											
	Light pollution	L	L	L	L	L	M[†,58,72,73]	L[†,72]	M	M[†,76]	L[†,75]	L	L[†,72,74,75]
	Oil spills	M[36,104]	M[36]	M[36]	M[36]	M[36,104,106]	L[36]	L[36]	L[36,104]	L[36]	L[36]	L[106]	H[43,104]
Fishing	Overfishing	L	L	L	L	L	L	L	L	L	L	L	L
	Bycatch	L[†,98]	L[†,85]	L[†,85]	L	L[†,86]	L[†,100,101]	M[23]	M[†,65]	H[†,63,65]	M[23]	M[23,65]	L
Habitat-related changes	Habitat loss	L	L	L	L	L	L	L	L	L	M[103]	L	M[102]
	Habitat degradation	L	L	L	L	L	L	L	L	L	M[103]	L	L
	Invasive species	L	L	L	L	L	H[†,99]	L	L	L	L	L	L
	Coastal urbanization	L	L	L	L	L	L	L	L	M[†,76]	L	L	L
Others	Introduction of pathogens (ballast waters)	L	L	L	L	L	L	L	L	L	L	L	L
	Vessel collision	L	L	L	L	L	L	L	L	L	L	L	L
	Tourism (e.g. whale/birdwatching)	L	L	L	L	L	L	L	L	L	L	L	L

Table 1.2. Continuation

		Leach's storm-petrel	Band-rumped storm-petrel	Northern gannet	Great cormorant	European shag	Pomarine jaeger	Arctic jaeger	Great skua	Mediterranean gull	Little gull	Sabine's gull	Black-headed gull
Climate change	Elevated temperatures	L	L	L	L	L	L	L	L	L	L	L	L
	Ocean acidification	L	L	L	L	L	L	L	L	L	L	L	L
	Sea level rise	L	L	L	L	L	L	L	L	L	L	L	L
	Extreme weather events	L	L	M^{68}	L^{68}	L^{68}	L	L	L	L	L	L	L^{68}
	Shifts in ocean current patterns	L	L	L	L	L	L	L	L	L	L	L	L
Pollution	Chemical contamination (e.g. PCB, DDT)	L	L	L^{39}	L^{†,51}	L	L	L	L$^{\dagger, 79}$	L	L	L	L^{†,52}
	Marine litter (e.g. plastics)	L^{†,92}	L	H^{77}	M^{77}	L^{77}	L$^{\dagger, 93}$	L	L$^{\dagger, 84,95}$	L^{77}	L	L^{†,93}	M^{77}
	Ghost fishing	L	L	M^{59}	M^{†,65}	L	L	L	L	L	L	L	L
	Eutrophication	L	L	L	L	L	L	L	L	L	L	L	L
	Acoustic pollution (e.g. sonar, seismic surveys)	No evidence of threat to date in the area											
	Light pollution	L^{†,70}	L	L	L	L	L	L	L	L	L	L	L
	Oil spills	L	L	H^{36,40}	L^{36}	H^{36,40,42,44}	L	L	L^{104}	M^{36}	M^{36}	M^{36}	M^{36,104}
Fishing	Overfishing	L	L	L^{†,48}	L	L	L^{†,48}	L^{†,48}	L^{†,48}	L	L	L	L
	Bycatch	L	L	M^{23}	L^{†,85}	H^{109}	L	L	L	L	L	L	L^{†,85,88}
Habitat-related changes	Habitat loss	L	L	L	L	L	L	L	L	L	L	L	L
	Habitat degradation	L	L	L	L	L	L	L	L	L	L	L	L
	Invasive species	L	L	L	L	H^{109}	L	L	L	L	L	L	L
	Coastal urbanization	L	L	L	L	L	L	L	L	L	L	L	L
Others	Introduction of pathogens (ballast waters)	L	L	L	L	L	L	L	L	L	L	L	L
	Vessel collision	L	L	L	L	L	L	L	L	L	L	L	L
	Tourism (e.g. whale/birdwatching)	L	L	L	L	M^{107}	L	L	L	L	L	L	L

Table 1.2. Continuation

		Common gull	Lesser black-backed gull	Yellow-legged gull	Great black-backed gull	Kittiwake	Sandwich tern	Common tern	Arctic tern	Little tern	Common guillemot	Razorbill	Atlantic puffin
Climate change	Elevated temperatures	L	L	L	L	L	L	L	L	L	L[†,71]	L	L
	Ocean acidification	L	L	L	L	L	L	L	L	L	L	L	L
	Sea level rise	L	L	L	L	L	L	L	L	L	L	L	L
	Extreme weather events	L	L[68]	L	L[68]	M[68]	L	L	L	L	H[67,68]	M[68]	M[68,68]
	Shifts in ocean current patterns	L	L	L	L	L	L	L	L	L	L[†,66]	L	L
Pollution	Chemical contamination (e.g. PCB, DDT)	L	L	M[34]	L	L	L	M[†,53,57,79]	L	L	L[†,54]	M[33]	L[†, 79]
	Marine litter (e.g. plastics)	L	L[†,85,97]	M[†,95,97]	L	M[77]	L[77]	L[77]	L	L[†,96]	H[77]	H[77]	H[77]
	Ghost fishing	L	L	L	L	L	L	L	L	L	L[†,87]	L	L
	Eutrophication	L	L	L	L	L	L	L	L	L	L	L	L
	Acoustic pollution (e.g. sonar, seismic surveys)	No evidence of threat to date in the area											
	Light pollution	L	L	L	L	L	L	L	L	L	L	L	M[†,110]
	Oil spills	M[36]	M[36]	M[36,41,45]	M[36]	M[36,104]	L[36]	M[36]	M[36]	M[36]	H[36,38,40,104]	H[36,37,38]	H[36,38,40]
Fishing	Overfishing	L	L	L	L	L[†,45,69]	L	L	L	L	L	L	L[†,55]
	Bycatch	L	L[†,94]	L	L	L[†,85]	L[†,94]	L	L	L[†,96]	H[†,60,61,62]	M[†,65]	M[23]
Habitat-related changes	Habitat loss	L	L	L	L	L	L	L	L	L	L	L	L
	Habitat degradation	L	L	L	L	L	L	L	L	L	L	L	L
	Invasive species	L	L	L	L	L	L	L	L	L	L	L	L
	Coastal urbanization	L	L	L	L	L	L	L	L	L	L	L	L
Others	Introduction of pathogens (ballast waters)	L	L	L	L	L	L	L	L	L	L	L	L
	Vessel collision	L	L	L	L	L	L	L	L	L	L	L	L
	Tourism (e.g. whale/birdwatching)	L	L[106]	L	L	M[†,108]	L[106]	L[106]	L	L	M[†,108]	L	L

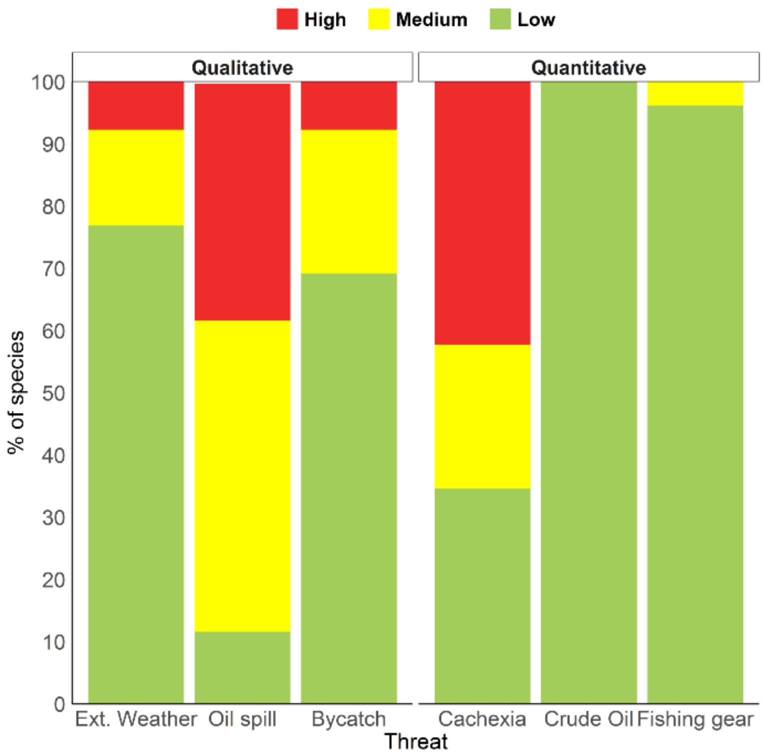

Figure 1.6. Comparison between the impacts of the threats scored in the qualitative and quantitative assessments (left and right panels, respectively).

4. Discussion

The lack of knowledge on the impact that different threats could have on seabird and cetacean individuals and populations hampers the development of suitable mitigation measures despite the efforts of several expert groups in summarising the existing evidence and categorising these threats. The present study advances our knowledge on the main threats faced by the marine megafauna community in the BoB by providing new (quantitative) evidence of their impact on seabird species (based on WRCs records) and updating the information (qualitative) in relation to the severity of these threats on cetacean species.

4.1. Evaluating threat impacts based on monitoring schemes

The causes of admission to WRCs can be used to evaluate the impact of multiple threats on seabird populations (Sleeman and Clark, 2003). However, long-term studies of seabird admissions to WRCs covering more than a decade are scarce (Haman et al., 2013; Montesdeoca et al., 2017). We compiled data spanning 13 years (from 2004-2016) that corresponds to the longest time series analysed in the study area.

Potential biases in the WRCs data are related to possible differences in the probability (1) of arrival to the coast, (2) of being encountered and (3) of being delivered to

WRCs (M Louzao et al., 2019). However, we considered that these datasets can provide useful information on the prevalence of certain threats, as it is the case of cetacean strandings.

When considering all threats together, the Common guillemot, the Yellow-legged gull, the Northern gannet, the Black-headed gull, the Great cormorant and the Razorbill were the most affected species, since they are the most abundant species in the North Atlantic subregion (MAGRAMA, 2012b). Although cachexia was the main cause of admission for all the above-mentioned species, exposure to crude oil for Common guillemots and Razorbills, and the interaction with fishing gear for northern gannets were the second main causes of admission. However, the second main cause of admission for the Yellow-legged gull was orphaned, for the Black-headed gull undefined trauma and for the Great cormorant gunshot. In the case of the Yellow-legged gull, the location of the breeding grounds and their low dispersion rate along the northern Iberian coast favoured the collection of orphaned individuals (Arizaga et al., 2014, 2010). Regarding the Great cormorants, the admission of individuals with gunshots may be due to the well-known existing conflict of the species with river fishermen (Carss and Marzano, 2005), as Great cormorants are perceived as competitors.

Admitted cachectic individuals, mainly Common guillemots, suffered extreme weakness and starvation in the winters of 2006/2007 and 2013/2014 (present study; Louzao et al., 2019), coinciding with a succession of extreme and persistent weather events in the study area (Morley et al., 2016). Extreme wind conditions, as prolonged stormy weather, can reduce the flight capacity and, consequently, increase the foraging costs for seabirds (Finney et al., 1999; Fort et al., 2009). In the case of exposure to crude oil, the highest number of admissions was reached during late winter - early spring of 2004 and 2007. Crude oil can suffocate seabirds by ingestion and cause the loss of water-proofing, thermal insulation and buoyancy by preventing them from diving or flying and eventually leading to starvation (Troisi et al., 2016). Finally, although the interaction with fishing gears (*e.g.,* bycatch) is considered the most important threat to seabirds (Croxall et al., 2012), this threat represented only 5.3% of the total admissions to WRCs. This could be explained by the low probability of arrival of bycaught seabird carcasses to the coast. However, the higher bycatch incidence among those species known to interact with fisheries (*e.g.,* northern gannet, Yellow-legged gull and Great cormorant) (ICES, 2017; Votier et al., 2013) is well reflected.

4.2. Overall threats to marine megafauna

a) Climate change

It is expected that climate change will impact directly on the populations of cetaceans and seabirds by modifying the physical and chemical characteristics of their environment and indirectly by affecting the distribution, availability and accessibility to their prey (Hemery et al., 2007; Simmonds, 2016). Among the different processes characterising climate change, ocean warming is believed to be forcing range shifts due to the changes in the location of thermal niches (Edwards and Richardson, 2004; Gregory et al., 2009), altering food web dynamics (Hays et al., 2005) and producing a northerly shift of marine megafauna species (Hemery et al., 2007; Macleod, 2009). While ocean acidification could produce trophic cascades (Lassalle et al., 2012; Sydeman et al., 2012) due to changes in primary production (Duarte et al., 2013), the sea level rise could reduce breeding grounds (Croxall et al., 2012). Extreme weather events have increased in frequency and severity (Cai et al., 2014; Ummenhofer and Meehl, 2017) causing seabird mortality events due to starvation, exhaustion and drowning (*i.e.,* cachexia) (Morley et al., 2016), lower breeding success (Zuberogoitia et al., 2016) and more cetacean stranding due to the increased incidence of rough conditions (Simmonds, 2017). This is well reflected on the quantitative assessment, where cachexia was the main cause of seabirds' admissions to WRCs, specially for the Common guillemot and the razorbill.

b) Pollution

There are still high concentrations of organic pollutants in the marine environment that can affect cetacean and seabird reproduction, immunosuppression and increase susceptibility to disease [*i.e.,* polychlorinated biphenyl (PCBs)] (Jepson et al., 2016; Romero-Romero et al., 2017). Increasing levels of chemical pollutants such as nitrogen or phosphorus derived from plant fertilizers can cause harmful and increasingly frequent phytoplankton blooms and eutrophication (Anderson et al., 2012; McCauley et al., 2015). Marine litter has become a concern with increased evidence of the impact of plastics, microplastics and abandoned fishing gears on the marine ecosystems (Gall and Thompson, 2015; OSPAR Commission, 2000). Few studies have examined to what extent seabirds and cetaceans are affected by plastic and microplastics in the BoB. Hernandez-Gonzalez et al. (2017) found microplastics in 100% of the stomachs of Short-beaked common dolphin analysed, while Franco et al. (2019) found microplastics in 12%, 18%, 27% and 33% of the stomachs of Common guillemots, northern gannets, Atlantic puffins and Black-headed gulls, respectively. Discarded nets and lines (ghost fishing), which can continue to fish, it is becoming a growing problem as new gear materials (particularly synthetic fibers) do not decay and continue to catch non-target species (Macfadyen et al., 2009). Cetaceans are more affected (Stelfox et al., 2016), but seabirds are also impacted when scavenging in the lost gears (Žydelis et al., 2013), as is the case of the Northern gannets, for which Rodríguez et al. (2013) reported a 0.36% entanglement incidence over the Cantabrian and Galician coasts. Noise pollution is produced by vessel traffic, sonars and seismic exploitation among others (Evans, 2006) mainly affecting cetaceans by altering their acoustic communication, distributions patterns, provoking stress responses and impacting foraging behaviours by masking the sound produced by prey movement (Blair et al., 2016; Gomez et al., 2016). Light pollution, mostly affecting seabird species, can originate from both terrestrial (*e.g.,* coastal anthropogenic transformation) or marine (*e.g.,* vessels and offshore oil and gas platforms) sources, inducing attraction and disorientation (Rodríguez et al., 2015b, 2017, 2019) provoking strikes (Merkel and Johansen, 2011; Rodríguez et al., 2015a). Cory's and Balearic shearwaters, Atlantic puffin and Storm-petrels have been reported as the main affected species (Fontaine et al., 2011; Rodríguez et al., 2017, 2015a; Rodríguez and Rodríguez, 2009; Wilhelm et al., 2013).

Finally, the BoB is an area at high-risk of oil spills, in fact, more than 70% of the total oil consumed in the EU is transported through the English Channel (Lavín et al., 2006) with two big oil spills taking place in the BoB in recent years, the "Erika" in 1999, and the "Prestige" in 2002 (Lorance et al., 2009). Seabird populations are particularly vulnerable to oil spill events due to their distribution and foraging behaviour, as is the case of auks, which perform migrations during winter into areas where they are highly vulnerable to these events (Le Rest et al., 2016), such as the BoB. As the results of the quantitative assessment showed, the presence of crude oil represents an importante threat to the seabirds inhabiting the BoB.

c) *Fishing*

Overfishing, the main cause of declining fish stocks, reduces the resources available for higher-trophic level species (Blyth et al., 2004) and has been linked to declines in predator populations (Lassalle et al., 2012; McCauley et al., 2015). Bycatch can also directly affect seabird and cetacean species causing mortality (Peltier et al., 2016). Gillnets and trawls are the gears where most cetacean bycatch is reported to take place, whilst long-lines represent a bigger threat for seabirds (Bellido et al., 2011). In the BoB, the Short-beaked common dolphin is the most reported bycatch cetacean species (Peltier et al., 2014; Spitz et al., 2013) although many of the other commonly present species are also affected (Goetz et al., 2015). In the case of seabids, there is no robust data to assess bycatch levels in the area due to low observation effort (ICES, 2017).

d) Habitat-related changes

There are many habitat-related changes taking place in the marine environment, such as habitat loss or degradation (Airoldi et al., 2008). Structurally complex habitats are becoming rarer across temperate marine environments such as the BoB (Lotze et al., 2006) due to habitat degradation (*e.g.,* developing of the coastline, dredging, vessel traffic, seismic surveys or military sonar; Butterworth, 2017) which leads to a biodiversity loss by deacreasing abundances and species richness (Airoldi et al., 2008). Likewise, although there are still unknown consequences of biodiversity loss (Worm et al., 2006), it may lead to a decrease in the foraging success of seabirds and cetaceans by modifying their intra and interspecific interactions difficulting their foraging success (*e.g.,* cetaceans are important for foraging seabirds since they use the presence of hunting individuals to detect prey patches; Henkel, 2009; Veit and Harrison, 2017).

Habitat-related changes may also be associated with the rapid growth of the worlds' population. In many areas, as well as in the BoB, overpopulation has resulted in the development and urbanization of beaches and shores for recreational uses. This has produced an impact upon several cetacean species such as Bottlenose and Short-beaked common dolphins and Harbour porpoises (Gibson, 2005) as well as coastal seabird species such as Yellow-legged and Mediterranean gulls, Great cormorant or European shag (Croxall et al., 2012).

e) Others

Other threats posing a risk to marine megafauna in the BoB are related with the rising demand for tourist activities at sea (*e.g.,* whale- and bird-watching) that can disturb and change the behaviour of cetacean and seabird species with associated temporal or permanent habitat exclusion (Avila et al., 2018). Furthermore, the requirements caused by the growing human population have increased shipping, boosting the likelihood of collisions (particularly affecting baleen whales and large odontocetes such as sperm and Fin whales; ICES, 2015). Shipping is also the cause of a growing threat, the introduction of non-native species through their transport in the ballast waters which can in turn transmit new pathogens to the indigenous species of the BoB (Butrón et al., 2011).

5. Conclusions

The marine megafauna of the BoB faces several threats with species scoring differently under different threats depending on their biology and habitat use. The information collected and summarised in the present chapter can help identify conservation priorities (combination of threats and species requiting the most urgent management measures), work needed in the context of MSFD and other relevant legislation. Our complementary assessment is of special relevance for threatened species inhabiting the BoB for which there are many conservation actions underway or proposed, both in Europe and in the BoB, such as the identification of Important Bird Areas (IBAs; BirdLife International) and Special Protection Areas (SPAs; EU Natura 2000 network), particularly in offshore regions. However, additional management measures are needed and these should include a decrease in the use of artificial lighting, the management of coastal and inland development surrounding important seabird breeding areas, development of rapid and trans-boundary response plans to oil spills, establishment of observer programmes on gillnet fisheries and improvement of the current observer programs in other fisheries to assess bycatch, assessment of resources overexploitation and establishment of long-term research programs to assess population trends regarding climate change and severe weather events (ICES, 2016; IUCN, 2018; Rodríguez et al., 2019). The creation of a coordinated networks between the administration and WRCs to forecast the massive arrival of individuals to the coasts should also be considered.

Chapter 2

Understanding the 3D environment of pelagic seabirds from multidisciplinary oceanographic surveys to advance ecosystem-based monitoring

ABSTRACT

Marine predators move through the seascape searching for foraging resources. Prey configuration and oceanographic processes could therefore shape their 3-dimensional (3D) oceanographic habitats. Taking advantage of multidisciplinary oceanographic surveys targeting biomass estimation of pelagic fishes (*i.e.,* JUVENA surveys), observations of 2 highly migratory pelagic seabirds were collected during line-transects: Sooty shearwaters (SOSHs) *Ardenna grisea* and Great shearwater (GRSHs) *A. gravis*. Every autumn these species visit the pelagic ecosystem of the BoB. We developed generalised additive models to disentangle the effects of the 3D ocean environment and preyscapes at different depth ranges, in addition to static variables, on driving the spatial abundance of these predators. The species differed in their vertical habitat use, with SOSHs and GRSHs influenced by habitat conditions above the depth of the maximum temperature gradient and at the surface, respectively. SOSHs were more abundant in deeper shelf areas with localised hotspots associated with upwelling and river discharges. In contrast, GRSHs were more abundant in shallow slope areas in the outer BoB sectors, followed by less dense areas with intermediate levels of juvenile anchovy biomass. Therefore, both species integrate marine resources at different vertical and spatial dimensions, influenced by topographic features, oceanographic conditions and preyscapes. Relative abundance estimations provided mean values of 3203 SOSHs (95% CI: 1753−5748) and 12 380 GRSHs (95% CI: 5797−28152) in the BoB during their annual migration; these numbers varied slightly inter-annually. This study provides an example of the combination of multiple pelagic components as a means to provide an integral assessment to advance ecosystem-based monitoring.

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1. Introduction

Marine predators move through the seascape searching for prey that vary spatially across different water masses/regions and vertically through the water column. During migration, predators make stopovers in certain marine regions to refill their energetic reserves in order to complete their annual migratory journey (Stenhouse et al., 2012). These marine regions are frequently characterized by productive waters, where the vertical and horizontal distribution of prey resources is governed by diverse oceanographic processes, and which can be visited recurrently year after year (Block et al., 2011; Louzao et al., 2015; Nur et al., 2011). Therefore, prey configuration and oceanographic processes may shape the 3-dimensional (3D) oceanographic habitats of highly migratory predators, which can be very predictable (Block et al., 2011). The effect of fisheries on the availability of prey for top predators is a long-standing issue (Bertrand et al., 2012; Cury et al., 2011; Sydeman et al., 2017) and critical foraging grounds should be identified to advance their conservation and management to potentially secure prey availability in these areas (Boyd et al., 2015). When critical areas of highly migratory predators are persistent over time the implementation of spatially explicit conservation initiatives is more feasible (Lascelles et al., 2014).

The BoB represents an important non-breeding foraging ground for numerous predators during certain periods of the year (Doherty et al., 2017; Fossette et al., 2010; García-Barón et al., 2019a; Lambert et al., 2017a; Lezama-Ochoa et al., 2010; Pérez-Roda et al., 2016). The seabird population of the BoB is highly diverse due to the visits of different trans-equatorial migrating species (Louzao et al., 2015; Stenhouse et al., 2012). Moreover, the BoB represents both a major flyway for north European breeding seabirds during migration periods and an important wintering ground (Arcos et al., 2009; Fort et al., 2012; Pettex et al., 2017). In this biogeographic area, there is evidence that the spatiotemporal distribution of some fish predators (*e.g.,* Albacore tuna *Thunnus alalunga)* is driven by early stages (corresponding to young-of-the-year) of the European anchovy *Engraulis encrasicolus* (Lezama-Ochoa et al., 2010). However, there is no evidence whether other pelagic predators, such as seabirds, exploit similar foraging resources and, therefore, whether their oceanographic habitats could be shaped by early stages (juveniles) of different fish species. The importance of early stages of fish as prey for seabirds has been largely evidenced in other geographic areas such as the North Sea (Daunt et al., 2008), the Barents Sea (Barrett, 2002) and the Bering Sea (Hatch and Sanger, 1992), among others. In the BoB, few studies have related the distribution and abundance of marine predators to that of their prey (but see Certain et al., 2011), given the difficulty in obtaining simultaneous data on both prey and predator distributions. In addition, the relatively low number of seabird breeding colonies in the BoB hinders the study of their foraging ecology.

Annual multidisciplinary oceanographic surveys directed to assessing the stock of commercial pelagic resources provide an ideal platform to simultaneously monitor annual changes of different components of the pelagic ecosystem (Authier et al., 2018; Certain et al., 2011; Irigoien et al., 2009; Santos et al., 2013). In the BoB, the JUVENA oceanographic survey is conducted every year in late summer and has collected concurrent information on pelagic fishes since 2003 (Boyra et al., 2013) and on plankton and marine megafauna observations since 2012 (García-Barón et al., 2019a). These surveys provide information on inter-annual variation in the patterns of spatial distribution and biomass of small pelagic fish (Boyra et al., 2013) as indicators of food availability for pelagic predators (Lezama-Ochoa et al., 2010). Surveys specifically dedicated to the estimation of predator abundance need to cover large areas within the distribution range of predators (*e.g.,* Hammond et al., 2013; Pettex et al., 2017), so are rarely run on an annual basis. In contrast, annual monitoring surveys cover smaller areas (*e.g.,* regions), but at higher frequency. Therefore, large spatial coverage surveys conducted at a lower frequency and regional coverage surveys conducted every year provide complementary approaches (Saavedra et al., 2018).

One of the main advantages of multidisciplinary surveys is the possibility of considering the joint effect of the 3D preyscapes and ocean dynamic environments on driving abundance patterns of highly migratory seabirds. Prey availability depends on abundance, predictability, degree of aggregation, accessibility and depth range (Boyd et al., 2015; Regular et al., 2013; Thaxter et al., 2013). For air-breathing predators such as seabirds, prey availability at shallow depths is particularly important in identifying important foraging grounds (Boyd et al., 2015), since seabirds might be limited by their maximum diving depth. Most studies assessing their oceanographic habitats have been based on surface oceanographic conditions and integrating the vertical range of prey (Boyd et al., 2015), but sub-surface oceanographic processes can be crucial in understanding seabird distribution patterns (Scott et al., 2010). Defining biologically meaningful depth ranges (*e.g.,* considering prey accessibility) to describe 3D preyscape and oceanography can be a critical step in understanding seabird abundance patterns (Cox et al., 2013; Thackeray et al., 2010).

Two highly migratory seabird species, the Sooty shearwater (SOSH) *Ardenna grisea* and the Great shearwater (GRSH) *A. gravis*, visit the BoB during the autumn during their annual migratory journey. Both species reproduce on remote islands of the South Atlantic

Ocean and migrate to the North Atlantic Ocean during the non-breeding period. Millions of individuals visit the productive North-western Atlantic waters from June to August (Hedd et al., 2012). Afterwards, they cross to the eastern North Atlantic following prevailing wind patterns at middle latitudes (Hedd et al., 2012). Breeding individuals will continue their migratory journey to their breeding quarters, but many non-breeding individuals will arrive at the BoB between August and October (Hobbs et al., 2003). Their stopover in the BoB depends on climate variability at long timescales (*i.e.,* North Atlantic Oscillation), adjusted by optimal flying conditions and foraging grounds during migration (Louzao et al., 2015). Both species shape their arrival at the BoB by periods of potential minimum flying costs (Louzao et al., 2015). There is a lack of knowledge of pelagic seabird movements and the oceanographic processes driving their abundance at potentially important stopovers such as the BoB. Within this context, we aimed at understanding the pelagic seabird 3D environment from multidisciplinary oceanographic surveys. Specifically, our objectives were to assess the importance of (1) prey fields (preyscapes) and (2) mesoscale oceanographic features in driving SOSH and GRSH abundance patterns, with the ultimate aim of (3) obtaining spatial abundance predictions of these highly pelagic predator species in the BoB. We developed generalized additive models (GAMs) to disentangle the effect of the 3D preyscape, 3D ocean dynamic environment, 2-dimensional (2D) oceanographic predictors and static variables on driving the spatial abundance patterns of these highly migratory predators. We validated the development of 3D predictors that integrate the outputs of ecosystem-based surveys by identifying the biologically meaningful depth ranges linked to the ecology of the predators.

2. Material and Methods

2.1. Multidisciplinary surveys

JUVENA surveys cover the shelf-slope areas of the BoB every September (Figure 2.1). The sampling strategy is designed to monitor European anchovy and other small pelagic fish over both Spanish and French continental shelf and slope waters (Boyra et al., 2013). The semi-adaptive sampling scheme is based on across-shelf transect lines from the coast (20 m bottom depth) to beyond the shelf-break. Transects are parallel, regularly spaced and perpendicular to the coast with an inter-transect distance of 15 nautical miles (nmi) (Boyra et al., 2013). The offshore and along-coast extension of transects are conditioned by the distribution of the European anchovy positive area encountered. Two vessels (R/V 'Ramón Margalef' and R/V 'Emma Bardán', hereafter R/V RM and R/V EB, respectively) are used simultaneously to cover the extensive area potentially occupied by the European anchovy.

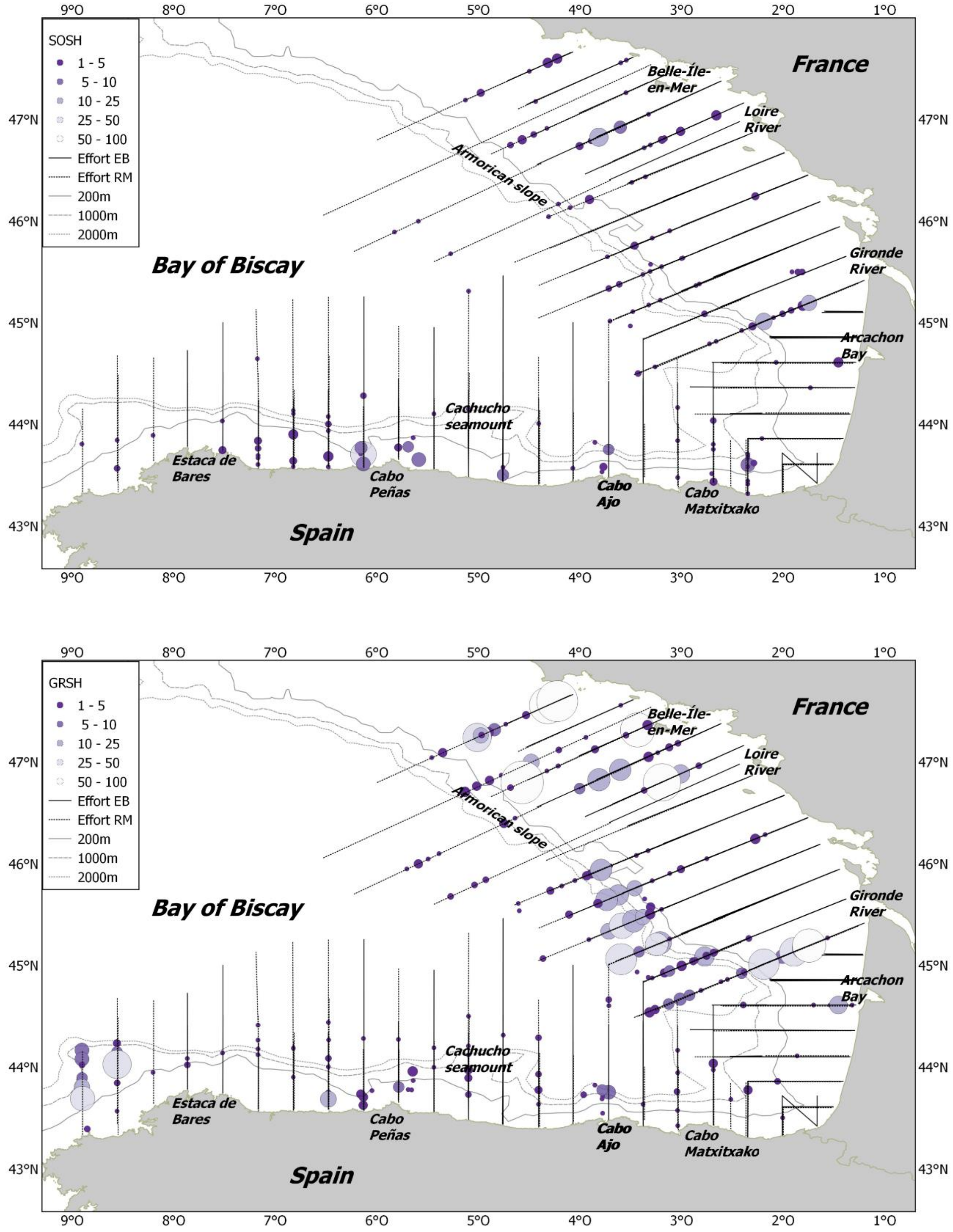

Figure 2.1. Sooty shearwater (SOSH) and Great shearwater (GRSH) observations during the JUVENA surveys. Circle sizes are proportional to the group size. Survey effort is represented separately for the 2 oceanographic research vessels (EB: 'Emma Bardán'; RM: 'Ramón Margalef'). Isobaths of 200 m (i.e., representing the shelf-break), 1000 m and 2000 m are indicated. Geographical references mentioned in the text are shown.

a) *Seabird observations*

Line-transect surveys were conducted every September between 2013 and 2016 by a team of 3 experienced observers (2 at a time), who were placed at a height of 7.5 m on board R/V RM. At the beginning of each observation period, observers recorded the meteorological and sea-state conditions that could affect sightings (*i.e.,* wind speed and direction, Beaufort sea-state [a categorical scale that relates wind speed to observed conditions at sea], swell height, glare intensity and visibility). The port observer scanned the water to the front of the boat covering the area from 270–10° on the port side and the starboard observer from 350–90° on the starboard side. In this way, the transect line was well covered while the vessel was navigating at a constant heading and speed during daytime. Observations were performed with the naked eye, while the identification of species and the number of individuals was aided by 10 × 42 Swarovski binoculars. For each observation, the radial distance to bird clusters (individual birds or groups of birds of the same species; Ronconi and Burger, 2009) and the angle of the cluster sighting with respect to the track-line at first detection were estimated. Distance was recorded using a stick based on the Heinemann (1981) method and the angle based on an angle meter. Additional data collected from each sighting included species, group size (*i.e.,* number of birds), movement direction, behaviour, etc. Observation effort was located geographically based on the vessel GPS, which logged geographic coordinates every 1 minute.

b) *3D preyscapes*

Pelagic fish represent 37 and 46% of the average diet of SOSHs and GRSHs during the non-breeding season, respectively (Ronconi et al., 2010a) (Table B-1.1 in Appendix B). Therefore, we obtained 3D spatial biomass patterns of juvenile and adult European anchovy (hereafter as ANEJ and ANEA, respectively) and European pilchard (hereafter as PIL) from both R/V RM and R/V EB, based on trawl-acoustic methodology (Simmonds and MacLennan, 2005). Data on similar prey species have been used to model shearwater abundance in other temperate latitudes (Phillips et al., 2017). The acoustic equipment included Simrad EK60 splitbeam echosounders (Kongsberg Simrad) of 38, 120 and 200 kHz (Boyra et al., 2013). Catches from the fishing hauls and echo-trace characteristics were used to identify fish species and to determine the population size structure. The location of the trawls was selected based on the aggregation structure of the echograms: each time the fish aggregations changed, the acoustic sampling and observations were interrupted to make a trawl. Afterwards, echograms were examined visually with the aid of the species composition of the catch.

For estimation of spatial abundance patterns, the 38 kHz acoustic data were processed by layer echo integration with the Movies+software (Ifremer), using an elementary sampling distance unit of 0.1 nmi. Echoes were thresholded to −60 dB and integrated into appropriate depth layers (of ~10−50 m depth; and of ~50 m below that depth). More details related to pelagic prey abundance estimation is given in Boyra et al. (2013).

Depths down to 200 m were sampled in 2013 and 2014, and down to 300 m in 2015 and 2016, and the different depth intervals were integrated. The 200 m range limit is typical of small pelagic acoustic surveys and is assumed to contain 100% of the European anchovy and European pilchard biomass (*e.g.,* Boyra et al., 2016, 2013; Massé, 1996; Petitgas et al., 2006). Thus, the increase of depth limit to 300 m after 2015 (changed to include information of some mesopelagic species not considered in this chapter) should not have introduced any bias for the prey species considered here. Original biomass values (in tonnes) per 0.1 nmi were laid over a standard grid in the study area (latitudinal range: 43.2−47.7° N; longitudinal range: 1.3− 7.7° W) consisting of a regular grid with a cell size of 0.1 × 0.1° (see Figure 2.2). Original biomasses corresponding to each cell were totalled. A combination of universal kriging and an automatic variogram fitting procedure was applied to obtain small pelagic fish biomass estimations based on the '*automap*' package in R (Hiemstra et al., 2009).

c) 3D oceanographic seascapes

Here, we focused on mesoscale oceanography (referring to physical processes of spatial scales between ~10 and ~100 km and timescales from several days up to 1 month) since these are the scales that can be solved using physical data gathered during the JUVENA surveys. We used 2D and 3D descriptors to characterise the oceanographic habitat of seabirds (Table 2.1). The 3D oceanographic predictors were temperature (TEM; °C), salinity (SAL; psu) and geostrophic velocity (GEO; $m\ s^{-1}$), whereas the 2D oceanographic predictors corresponded to depth of maximum temperature gradient (DTG; m), maximum temperature gradient (MTG; $°C\ m^{-1}$) and sea surface temperature gradient (SSTG).

CTD casts (using a SBE25 and a SBE911 on the R/V EB and RM, respectively) were used to obtain vertical depth profiles of TEM and SAL at selected stations along transects. Based on these vertical profiles, density values (or specific volume) were obtained and integrated over depth to obtain the dynamic height (DYN). Based on Rubio et al. (2009), DYN was computed relative to the next vertical level and not to a common reference level.

Once DYN was interpolated over the study area, GEO values were obtained (further methodological details below).

To characterise water column stability, we estimated DTG, computed by adjusting the vertical profiles of TEM to a logistic function (following methodology used in Caballero et al., 2016). The inflexion point of the logistic function (determined using the maximum of its first derivative) marks out the mean depth of the most intense gradient within the thermocline. MTG was obtained using linear differences in the points adjacent to the DTG, which is an indicator of the strength of the water column stratification.

To obtain horizontal fields of TEM, SAL, DYN, DTG and MTG, 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° (further methodological details in Appendix B – Section 2).

From DYN interpolated fields, GEO was obtained by the first derivative between adjacent grid nodes. To obtain 3D matrix fields, horizontal analyses were performed independently at 5 dbar intervals (except for DTG and MTG, which are 2D fields) from 10 to 200 m (below this level, the information available was poor and did not allow obtaining consistent horizontal fields). The horizontal interpolated fields of all the variables were finally re-sampled with the '*raster*' R-package (Hijmans and van Etten, 2014) to match the standard grid.

Furthermore, we considered an additional variable to describe horizontal TEM changes as a coarse indicator of the presence of oceanographic fronts (Table 2.1). The shallowest TEM interpolated field was used to derive the spatial gradient of sea surface temperature (SSTG) by means of a spatial moving window within an area of 3 × 3 cells (0.3 × 0.3°). This 2D predictor has previously been identified as an important variable to explain seabird distribution patterns (Louzao et al., 2009). More details about the computation of spatial gradients appear in the following section.

d) Static variables

Four different static variables were obtained to define seabird oceanographic habitats: bathymetry (BAT; m) and its spatial gradient (BATG; dimensionless), distance to the coastline (DCO; km) and distance to the shelf-break (DSB; km) (Table 2.1 and Figure B-3.1). Bathymetry was obtained from the topographic data ETOPO1 at 0.016° after removing the land topographic data (Amante and Eakins, 2009). The coastline was obtained from the Coastline Extractor hosted by the NOAA/National Geophysical Data Center (www.ngdc.noaa.gov/mgg_shorelines/) Static variables were obtained at the spatial scale of the standard grid. Original bathymetric data were overlaid over the standard grid; those values occurring in the same cell size were averaged. Then, a spatial moving window was used to estimate the spatial differences in bathymetric values (*i.e.,* bathymetric spatial gradient [SG]) within an area of 3 × 3 cells (0.3 × 0.3°) as follows:

$$\mathrm{SG} = \frac{\text{maximum value-minimum value}}{\text{maximum value}} \times 100$$

This dimensionless metric expresses the magnitude of change in bathymetric values, scaled to the maximum value (Louzao et al., 2006). An increased variation in the depth in offshore waters (higher bathymetric gradients in slope areas; Figure B-3.1b) can be considered a proxy of the areas where internal waves generate (Scott et al., 2010). In addition to a steep sea-floor slope, strong barotropic tidal forcing and strong stratification gradients are needed for enhanced internal tide formation. In the BoB, maximum internal tide ranges are located over the Armorican slope, where the barotropic tidal forcing is very energetic (Le Cann, 1990; Pairaud et al., 2010; Serpette and Mazé, 1989).

The distances between the centre of each cell and both DCO and DSB (*i.e.,* defined by the isobath of 200 m depth) were estimated based on the '*fields*' R-package (Nychka et al., 2017).

Table 2.1. Predictors obtained from annual JUVENA oceanographic surveys and additional static variables. Sea surface temperature gradient is derived from interpolated temperature fields at 10 m depth (i.e., temperature at the shallowest depth; TEM$_{10}$).

Predictor	Acronym	Dimensions	Source
Prey environment			
Biomass of juveniles of European anchovy (tonnes)	ANEJ	3D	Acoustic and pelagic trawls
Biomass of adults of European anchovy (tonnes)	ANEA	3D	Acoustic and pelagic trawls
Biomass of European pilchard (tonnes)	PIL	3D	Acoustic and pelagic trawls
Ocean dynamic environment			
Salinity (psu)	SAL	3D	CTD casts
Temperature (°C)	TEM	3D	CTD casts
Geostrophic velocity (m s^{-1})	GEO	3D	CTD casts
Depth of maximum temperature gradient (m)	DTG	2D	CTD casts
Maximum temperature gradient (°C m^{-1})	MTG	2D	CTD casts
Sea surface temperature gradient	SSTG	2D	Derived from TEM$_{10}$
Static variables			
Bathymetry (m)	BAT	2D	ETOPO 1
Bathymetric spatial gradient	BATG	2D	Derived from ETOPO 1
Distance to shelf-break (km)	DSB	2D	Derived from Coastline Extractor
Distance to coast (km)	DCO	2D	Derived from Coastline Extractor

2.2. *Characterising the vertical domain*

To consider the 3D pelagic environment, we adapted the collected biological and physical information to 3 different depth criteria: (1) surface conditions and integrated conditions limited by (2) the diving capability of the deep diver SOSH and (3) the accessibility of pelagic prey. In the first case, the depth range was set by the shallowest depth layer available in the data set considered, which matches with the diving capabilities of the GRSH (maximum diving depth of 18.9 m; Ronconi et al., 2010b). In the second, the depth limit was set at 70 m given the maximum diving depth of the SOSH (Shaffer et al., 2009), which has been similarly applied in previous work (Phillips et al., 2017). In the third case, the vertical depth was limited by DTG, as the main potential prey (ANEJ) are commonly found above the thermocline (above 50 m depth) (Boyra et al., 2016, 2013). In this way, we summarised oceanographic and prey scape data considering the vertical structure of the water column.

To accommodate ecological predictors of the different vertical criteria, preyscapes were represented by the shallowest biomass between 5 and 15 m depth (indicated by $ANEJ_{10}$, $ANEA_{10}$ and PIL_{10}), the sum of biomass from 5 to 70 m depth (indicated by $ANEJ_{70}$, $ANEA_{70}$ and PIL_{70}) or the sum of biomass from the surface up to the DTG estimated for each cell and year (indicated by $ANEJ_{DTG}$, $ANEA_{DTG}$ and PIL_{DTG}). Similarly, oceanographic conditions were described by the shallowest depth (10 m; indicated by SAL_{10}, TEM_{10} and GEO_{10}) and integrated values conditioned by the 2 depth limits: the median value of SAL, TEM and GEO from the surface to 70 m depth (indicated by SAL_{70}, TEM_{70} and GEO_{70},) or the DTG limit (indicated by SAL_{DTG}, TEM_{DTG} and GEO_{DTG}). The 2D oceanographic variables (SSTG, DTG and MTG) and static variables were not modified by any vertical criteria.

To characterise the vertical domain, we explored the relationship between surface environmental conditions (both preyscape and oceanography) and integrated conditions above the DTG and down to 70 m depth. We calculated the non-parametric Spearman rank correlation coefficient between pairwise predictors.

2.3. *Seabird detection functions*

We applied multiple covariate distance sampling (Marques and Buckland, 2004) to consider the effects of different observational (environmental) conditions affecting seabird detection probability. We developed detection functions based on both SOSH and GRSH sightings for the period 2013 to 2016 in good environmental conditions (*i.e.,* Beaufort sea-state ≤5, wave height ≤2 m and overall medium and good conditions; García-Barón et al., 2019). Truncation distances for SOSHs and GRSHs were set to 400 and 600 m, respectively, to eliminate outliers and improve model fitting (Buckland et al., 2001). The elimination of the 5 to 10% of the most distant observations is a common procedure during the exploratory phase (Buckland et al., 1993). For each species, hazard-rate and half-normal models were fitted to perpendicular distances (Laura Mannocci et al., 2014). We assessed the effect of different environmental conditions that could affect the detection probability (group size as a continuous variable, and year, Beaufort sea-state, wave height and cloud cover as factor variables; García-Barón et al., 2019). We selected the detection function that provided the lowest Akaike information criterion (AIC) value, informed by the p-value of the Cramér von Mises goodness-of-fit test (García-Barón et al., 2019a). Then, the effective strip half-width (ESW) was calculated as the perpendicular distance in which the missing detections at lower distances were equal to the recorded detections at greater distances. ESW was used to estimate the effective sampled area ($L \times 2 \times$ ESW, where L is the length of the segment in km and ESW is in m). These analyses were conducted with the '*distance*' R-package (Miller, 2017).

2.4. Spatial abundance models

We developed seabird spatial abundance models to explore the effects of the 3D preyscapes (ANEJ, ANEA and PIL), the 3D (SAL, TEM and GEO) and 2D (DTG, MTG and SSTG) ocean dynamic environment and different static environmental variables (BAT, BATG, DSB and DCO) (Table 2.1).

a) Data processing

Before model development, each period of observation was divided into 10 km length segments of the same observation conditions (Lambert et al., 2017a). The geographic position of the centroid of the segment was used to extract both dynamic preyscape and oceanographic conditions, as well as static variables.

b) General modelling framework

We used GAMs developed within the information theoretic approach using the '*mgcv*' R-package (Wood, 2011). The response variable (no. of seabirds·segment^{-1}) was fitted following a negative binomial distribution (the over-dispersion parameter close to 1). The effective sampled area was included as an offset. The smoothing splines were limited to a maximum of 3 degrees of freedom to capture non-linear associations without increasing the complexity of the functions towards unrealistic conclusions (Pérez-Jorge et al., 2015). Seabird observations were fitted to environmental data year by year, and not by combining all years.

c) Selecting the biologically meaningful depth range

We ran different set of GAMs including only preyscapes (ANEA, ANEJ and PIL), only 3D oceanographic predictors (SAL, TEM and GEO), and both together, at different depth ranges for each species. All sets of GAMs were compared based on AIC and explained deviance (ED). When models were within 2 points of AIC ($AIC < 2$), they were considered statistically equivalent (Williams et al., 2002). Models were first ordered by their AIC value, and between equivalent models the best model was chosen as the one with the highest ED.

d) Identifying non-collinear variables

Explanatory variables at selected depth ranges were standardised, and highly collinear pairwise predictors were identified (Spearman rank correlation coefficient, $rS \geq 0.5$) (Louzao et al., 2011). To keep the most explicative predictors, we compared the AIC values of the GAMs run with each predictor and selected the predictor yielding a model with a lower AIC value.

e) Model-averaging approach

GAMs were developed for a maximum of 4 predictors (Lambert et al., 2017a) to avoid excessive complexity. Afterwards, models were developed for all possible combinations of predictors, and were ranked based on their AIC values and the Akaike weights using the '*MuMIn*' R-package (Barton, 2016). We obtained averaged coefficients and variance estimators from the models included in the 95% confidence set (*i.e.,* including models in which the cumulative sum of Akaike weights was ≥ 0.95; Burnham and Anderson, 2002). The relative importance of predictors was measured by summing the Akaike weights for all models containing a specific predictor (Burnham and Anderson, 2002). The ED of the model with the lowest AIC value was used to assess the explanatory power (Pérez-Jorge et al., 2015).

f) Mapping predictions

We mapped the most likely abundance predictions of pelagic seabirds over the standard grid. Whereas static variables were extracted once, dynamic variables were extracted for each year (*i.e.,* every September survey). Averaged models were applied to descriptor grids to obtain spatial predictions of SOSH and GRSH densities (birds·km^{-2}) every year.

Pelagic seabird abundance was calculated for each survey by summing the values resulting from multiplying the predicted density for each cell by the cell area (García-Barón et al., 2019a). Furthermore, the 95% confidence interval was calculated assuming a positively skewed distribution of the predicted density (Buckland et al., 2001). Estimated abundances were relative (*i.e.,* uncorrected) due to the absence of available data to correct for perception and availability bias for studied species or from alternative similar studies in the BoB.

3. Results

3.1. Characterization of the vertical domain

We analysed the correlation between preyscapes and oceanography between surface and depth integrated conditions. ANEJ, ANEA and PIL were highly correlated at different depths, but correlations between surface and conditions above the DTG were higher for ANEA and PIL compared to those between the surface and conditions above 70 m depth (Table B-4.1). Correlations between biomasses integrated between the surface and DTG or 70 m depth were high. Likewise, the correlation between oceanographic conditions at the surface and depth-integrated above the DTG or above 70 m depth yielded similar results (Table B-4.2). Globally, shallower oceanographic conditions were more correlated with integrated oceanographic conditions above the DTG than above 70 m depth, even if the correlation was also high for SAL and GEO. In addition, correlations between both integrated oceanographic conditions at different vertical ranges were high. Due to the high correlation between each predictor estimated at different depth ranges, overall preyscape and oceanographic conditions were further described by conditions above the DTG (see Figures 2.2 and 2.3).

3.2. 3D preyscapes

The spatial patterns of biomass of European anchovy showed a clear age-mediated spatial segregation, independent of the year. ANEJ were concentrated in the slope (both Spanish and French areas) and oceanic areas of the inner BoB, as well as over the French continental shelf (Figure 2.2a–d). ANEA occupied a narrow band over the northern coastal French area (south of Brittany), the southern extension of which varied from year to year (Figure 2.2e–h). The spatial extension of the main aggregation areas for the species and ages differed depending on the year considered. While ANEJ extended their distribution to the whole BoB in 2014 (including the oceanic area), ANEA were concentrated in specific hotspots over the French continental shelf in 2015, coinciding with the maximum total biomass.

In the case of PIL, the main aggregation areas overlapped with ANEA along a narrow band on the French coast (Figure 2.2i–l). Biomasses of ANEA and PIL were highly correlated at all depth ranges considered (Table B-4.1).

3.3. 3D oceanographic environment

The 3D oceanographic predictors showed important inter-annual variability. SAL_{DTG} showed a positive gradient from east to west, with lower values east of 4–5° W. The lowest SAL_{DTG} gradients were found in 2015, with higher values east of 4–5° W compared to the remaining years (Figure 2.3a–d). TEM_{DTG} showed a positive gradient from north to south, with higher values south of 45° N, especially in the southeast corner of the BoB (Figure 2.3e–h). Colder waters were also observed near the coast along the Spanish and French shelves, indicating the occurrence of upwelling events. However, inter-annual variability was reflected in lower overall TEM_{DTG} values in 2015 compared to the remaining years (Figure 2.3e–h). In 2013 and 2016, a warm longitudinal band was identified over the Spanish slope, from 6–7° W to the French coast (Figure 2.3e and h, respectively). Regarding GEO_{DTG}, density fields depicted an anticyclonic tendency (data not shown), with currents intensified over the shelf and slope (Figure 2.3i–l). Different mesoscale structures were observed in each survey and the position and sizes of the eddy-like features were highly variable. 2015 was again the year showing a singular picture, with the less intense GEO_{DTG} values (Figure 2.3k).

Regarding the 2D oceanographic variables, the DTG patterns observed were different between the analysed years (Figure 2.4a–d). The lowest values for the DTG (values over the shelf and slope between 10 and 35 m) and MTG (values over the shelf and slope around 0.28°C m−1) were observed in 2013 and 2016 (Figure 2.4e–h), suggesting the weakest stratification. DTG was significantly deeper in 2015 (values between 20 and 50 m) and MTG was stronger compared to the remaining years (values over the shelf and slope around 0.36°C m−1), although the surface heating of shelf waters at the SE of the domain was less intense (Figure 2.3g). The highest SSTG values were located in shelf-break areas, especially in the southern BoB, which were especially high in 2013 (Figure 2.4i–l).

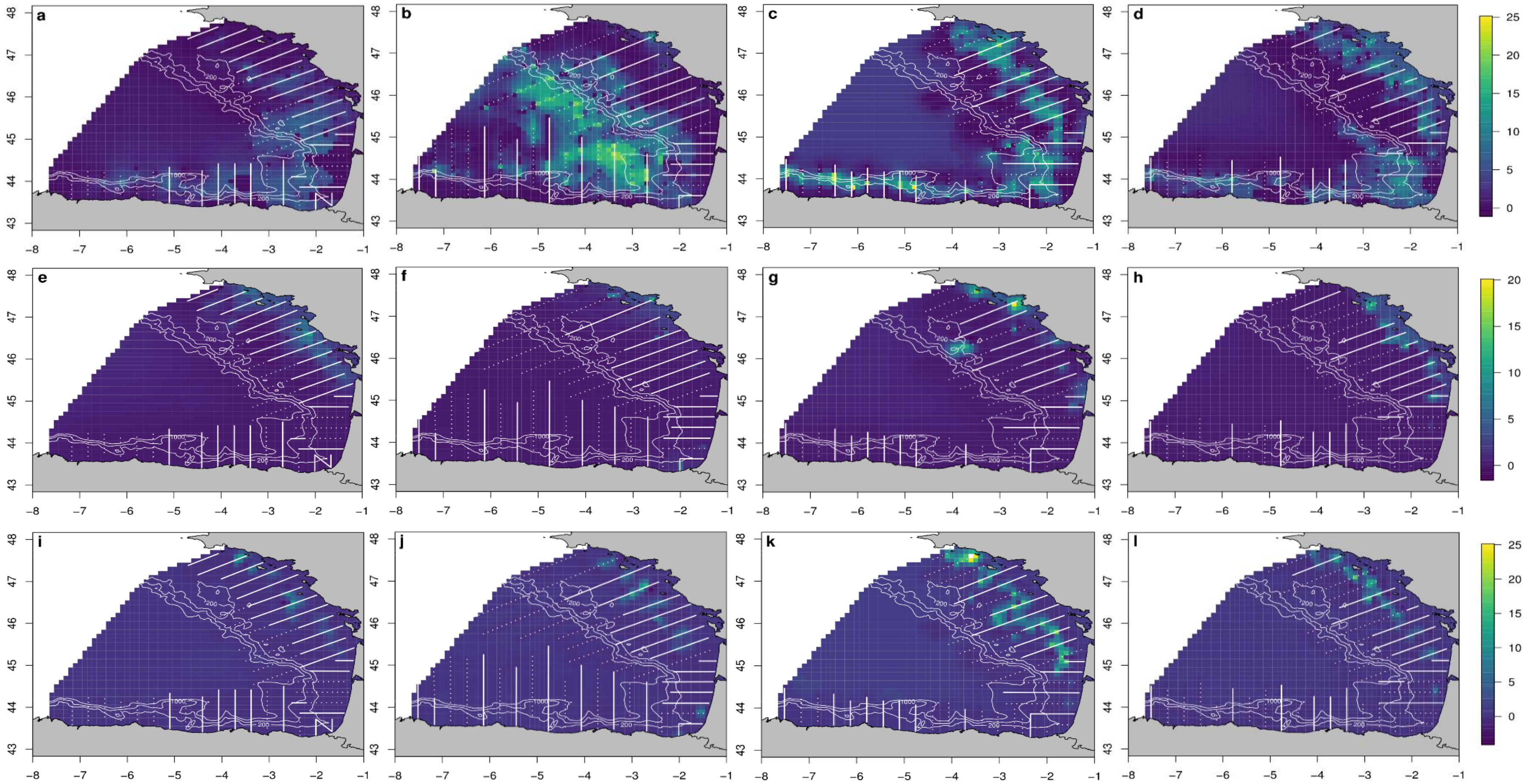

Figure 2.2. *The 3D preyscape represented by the spatial patterns of log-transformed biomass (tonnes) of (a–d) juveniles (ANEJ$_{\text{DTG}}$), and (e–h) adults of European anchovy (ANEA$_{\text{DTG}}$), as well as (i–l) European pilchard (PIL$_{\text{DTG}}$) summed from 5 m depth to the depth of maximum temperature gradient (DTG) during 2013–2016. White solid and dashed lines: annual effort coverage corresponding to the R/Vs 'Emma Bardán' and 'Ramón Margalef', respectively. Isobaths of 200, 1000 and 2000 m are outlined. Geographic references are indicated in Figure 2.1.*

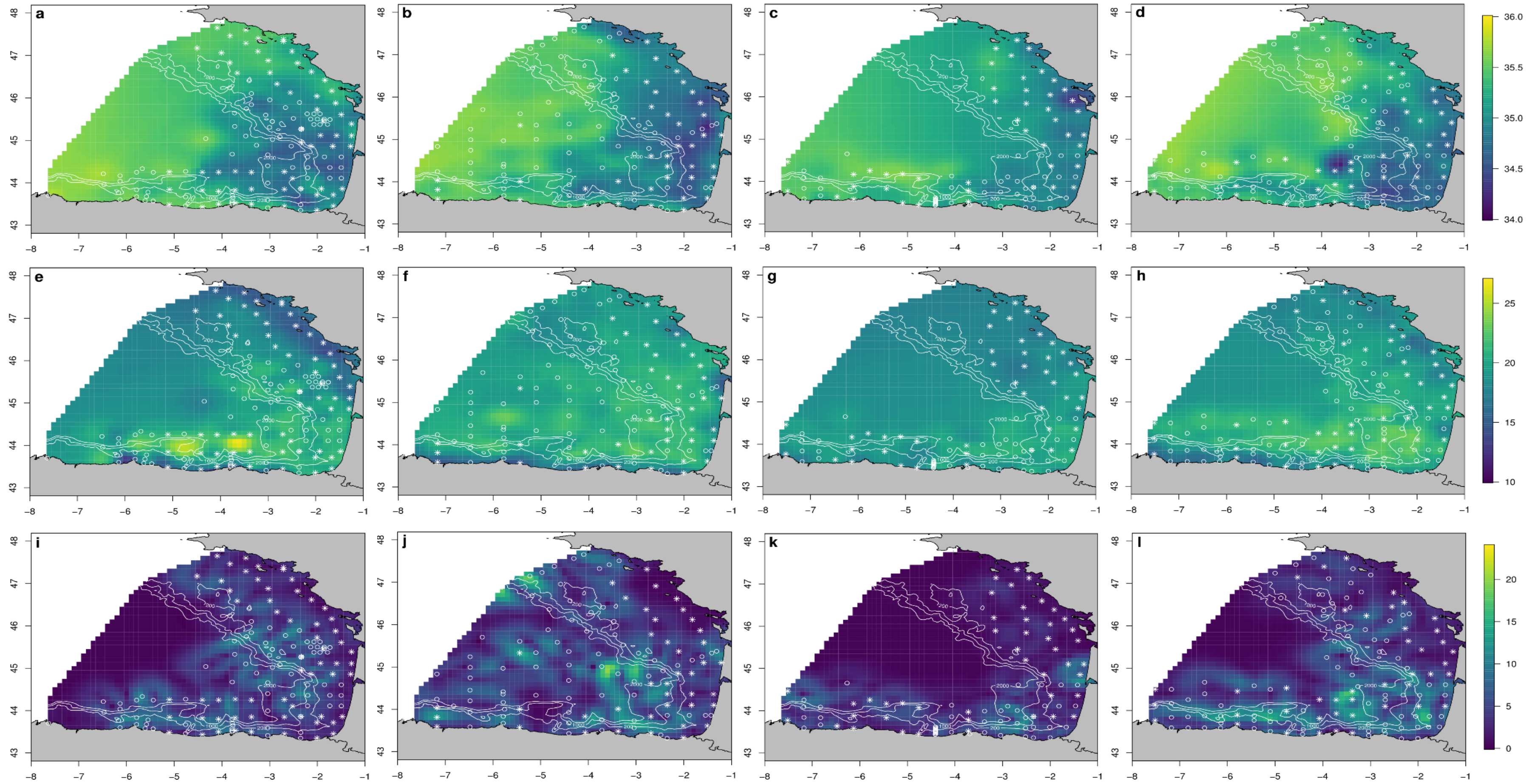

Figure 2.3. The 3D oceanographic environment represented by median values of (a–d) salinity (SAL_{DTG}; values in psu), (e–h) temperature (TEM_{DTG}; values in °C) and (i–l) geostrophic velocity module (GEO_{DTG}; values in $m\ s^{-1}$) integrated between 10 m depth and the depth of maximum temperature gradient (DTG) during 2013–2016. Dots and stars: CTD casts performed by R/Vs 'Emma Bardán' and 'Ramón Margalef', respectively. Isobaths of 200, 1000 and 2000 m are outlined. Geographic references are indicated in Figure 2.1.

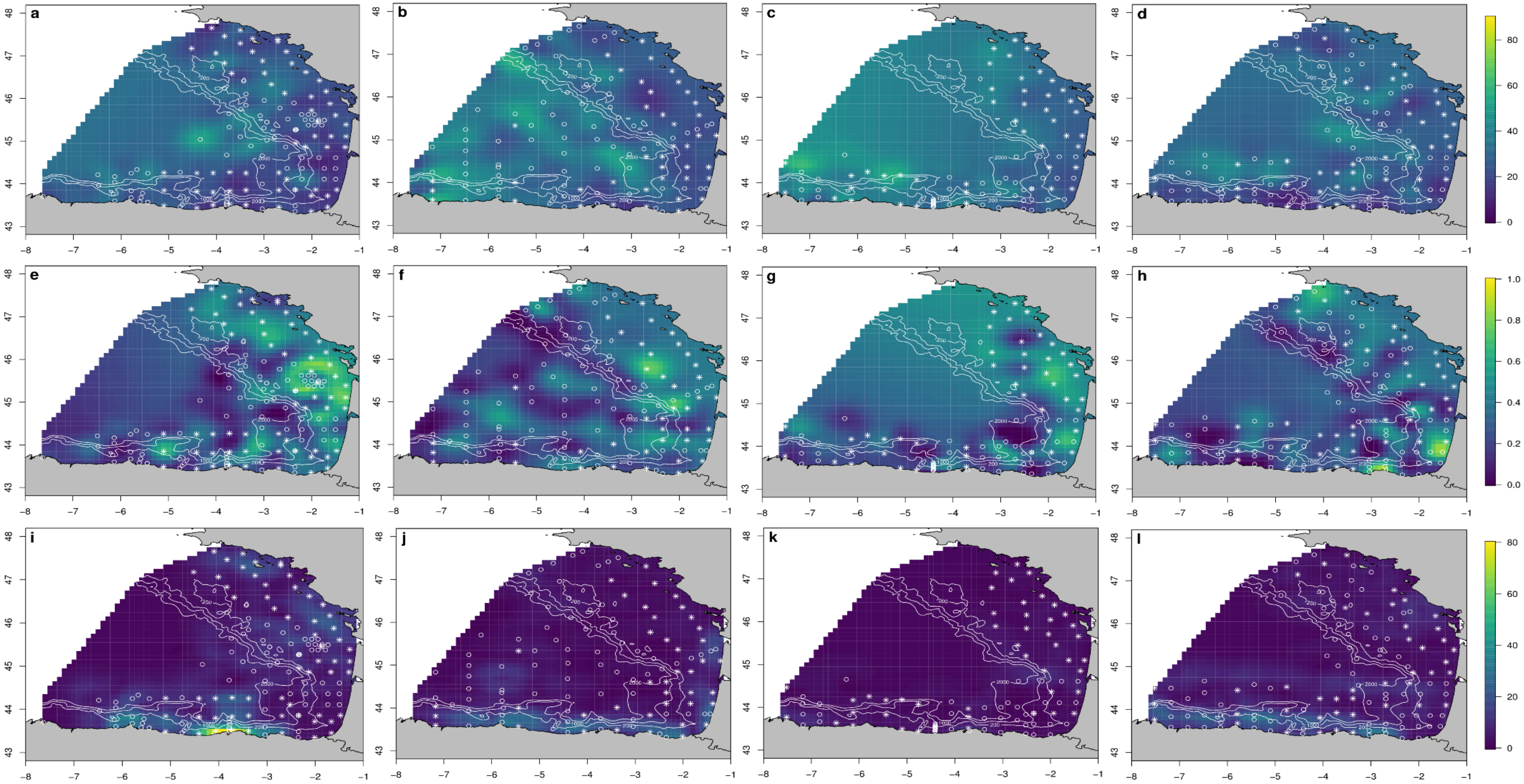

Figure 2.4. The 2D oceanographic environment represented by (a–d) depth of maximum temperature gradient (DTG; values in m), (e–h) maximum temperature gradient (MTG; values in °C m^{-1}) and (i–l) sea surface temperature gradient (SSTG; non-dimensional) during 2013–2016. Dots and stars: CTD casts performed by R/Vs 'Emma Bardán' and 'Ramón Margalef', respectively. Isobaths of 200, 1000 and 2000 m are outlined. Geographic references are indicated in Figure 2.1.

3.4. *Seabird sightings and detection function*

We observed a total of 360 SOSHs in 206 sightings (mean ± SD group size = 1.75 ± 2.74), while 1708 GRSHs were observed in 615 sightings (group size = 2.77 ± 6.52) for the period 2013 to 2016 (Figure 2.1). After selecting data collected in 'good environmental conditions', we retained 183 and 552 sightings of SOSH and GRSH, respectively. After setting the truncation distance to 400 and 600 m, sightings were reduced to 171 and 523 (truncating at 6 and 5% of observations), respectively. For SOSHs, the detection function with the lowest AIC was the half normal with no covariates and it showed a non-significant Cramér von Mises goodness-of-fit test (Table B-5.1, Figure B-5.1a,b). This detection function estimated an ESW of 195.45 m. For GRSHs, the hazard-rate detection model was selected with Beaufort sea-state as a covariate (Table B-5.2, Figure B-5.1c,d). We estimated the corresponding ESW for GRSH at Beaufort sea-state 0, 1, 2, 3, 4 and 5 as 198, 278, 245, 332, 232 and 51 m, respectively.

3.5. *Biologically meaningful vertical domain*

Environmental conditions above the DTG and surface conditions led to models with lower AIC values for SOSHs and GRSHs, respectively (Table 2.2). Environmental conditions characterising the depth range 10–70 m were within the models with higher AIC values. Therefore, abundance patterns of each species were better explained by integrating preyscape and oceanographic conditions at different depth ranges.

3.6. *Pelagic seabird 3D oceanographic habitat and abundance predictions*

Among highly correlated predictors for SOSHs (Table B-6.1), $\mathrm{ANEA_{DTG}}$, $\mathrm{SAL_{DTG}}$, BATG and DCO were the least explicative variables (results not shown) and they were not further considered. The 95% confidence set included 76 out of a total of 255 models. The model with the lowest AIC showed an ED of 16.7%. The main variables influencing SOSH abundance were BAT, SSTG, DTG and $\mathrm{PIL_{DTG}}$ (Figure 2.5a). BAT influenced SOSH abundance negatively, with a decreasing negative trend up to 3000 m depth (Figure 2.6a), followed by SSTG with an increasingly positively relationship (Figure 2.6b). SOSH abundance showed a weak quadratic relationship with DTG, with higher abundances at approximately 35 m depth over both the Spanish and French shelves (Figure 2.6c). Finally, SOSHs showed a slightly increasing relationship with increasing values of $\mathrm{PIL_{DTG}}$ (Figure 2.6d). Globally, SOSH abundance was higher in shallow bathymetric ranges (*i.e.,* over the continental shelf; Figure S3.1a), in areas of higher spatial gradients of sea surface temperature *(i.e.,* in the southern slope of the BoB; Figure 2.4i–l), as well as in areas associated with medium DTG values (over shelf areas; Figure 2.4a–d) of high PIL_{DTG} biomass (French coastal areas; Figure 2.2i–l).

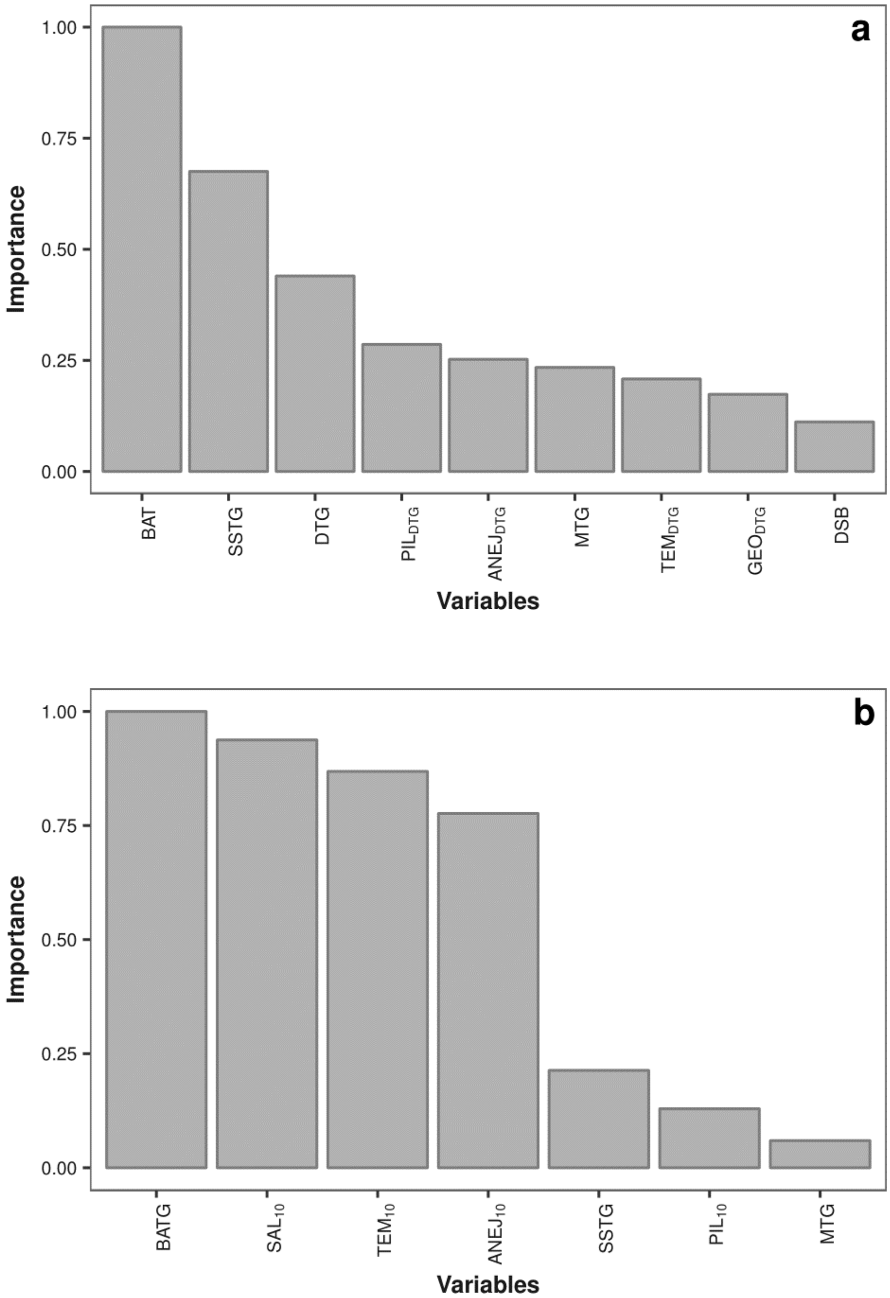

Figure 2.5. Predictor importance in explaining (a) Sooty and (b) Great shearwater spatial abundance patterns. See Table 2.1 for acronyms.

Table 2.2. Generalized additive model output showing the ranking of candidate models based on their Akaike's information criterion (AIC) value by species (SOSH: Sooty shearwater; GRSH: Great shearwater), variable type (preyscape, oceanography or both types) and depth range considered (DTG: depth of maximum temperature gradient). Models are first ordered by the AIC value, and among equivalent models (i.e., AIC < 2) the best model is the one with the highest explained deviance (ED). Np: number of parameters. Selected models are in bold. See Table 2.1 for acronyms.

Species	Data type	Depth range	Variables	Np	AIC	ED	ΔAIC
SOSH	**Preyscape + oceanography**	**Above DTG**	**$ANEJ_{DTG}$ + $ANEJ_{DTG}$ + PIL_{DTG} + SAL_{DTG} + TEM_{DTG} + GEO_{DTG}**	**7**	**1239.323**	**0.127**	**1.007**
	Oceanography	Above DTG	SAL_{DTG} + TEM_{DTG} + GEO_{DTG}	4	1238.316	0.112	0
	Oceanography	Surface	SAL_{10} + TEM_{10} + GEO_{10}	4	1243.127	0.102	4.811
	Preyscape + oceanography	Surface	$ANEJ_{10}$ + $ANEJ_{10}$ + PIL_{10} + SAL_{10} + TEM_{10} + GEO_{10}	7	1246.042	0.109	7.726
	Preyscape + oceanography	10–70 m	$ANEJ_{70}$ + $ANEJ_{70}$ + PIL_{70} + SAL_{70} + TEM_{70} + GEO_{70}	7	1246.303	0.118	7.987
	Oceanography	10–70 m	SAL_{70} + TEM_{70} + GEO_{70}	4	1254.377	0.072	16.061
	Preyscape	10–70 m	$ANEJ_{70}$ + $ANEJ_{70}$ + PIL_{70}	4	1258.349	0.057	20.033
	Preyscape	Above DTG	$ANEJ_{DTG}$ + $ANEJ_{DTG}$ + PIL_{DTG}	4	1261.321	0.054	23.005
	Preyscape	Surface	$ANEJ_{10}$ + $ANEJ_{10}$ + PIL_{10}	4	1265.063	0.044	26.747
GRSH	**Preyscape + oceanography**	**Surface**	**$ANEJ_{10}$ + $ANEJ_{10}$ + PIL_{10} + SAL_{10} + TEM_{10} + GEO_{10}**	**7**	**2154.028**	**0.122**	**0**
	Oceanography	Surface	SAL_{10} + TEM_{10} + GEO_{10}	4	2162.617	0.088	8.589
	Preyscape + oceanography	Above DTG	$ANEJ_{DTG}$ + $ANEJ_{DTG}$ + PIL_{DTG} + SAL_{DTG} + TEM_{DTG} + GEO_{DTG}	7	2164.189	0.101	10.161
	Oceanography	Above DTG	SAL_{DTG} + TEM_{DTG} + GEO_{DTG}	4	2166.962	0.079	12.934
	Preyscape	Surface	$ANEJ_{10}$ + $ANEJ_{10}$ + PIL_{10}	4	2189.718	0.033	35.69
	Preyscape + oceanography	10–70 m	$ANEJ_{70}$ + $ANEJ_{70}$ + PIL_{70} + SAL_{70} + TEM_{70} + GEO_{70}	7	2194.988	0.037	40.96
	Preyscape	10–70 m	$ANEJ_{70}$ + $ANEJ_{70}$ + PIL_{70}	4	2195.769	0.018	41.741
	Preyscape	Above DTG	$ANEJ_{DTG}$ + $ANEJ_{DTG}$ + PIL_{DTG}	4	2196.342	0.017	42.314
	Oceanography	10–70 m	SAL_{70} + TEM_{70} + GEO_{70}	4	2198.689	0.013	44.661

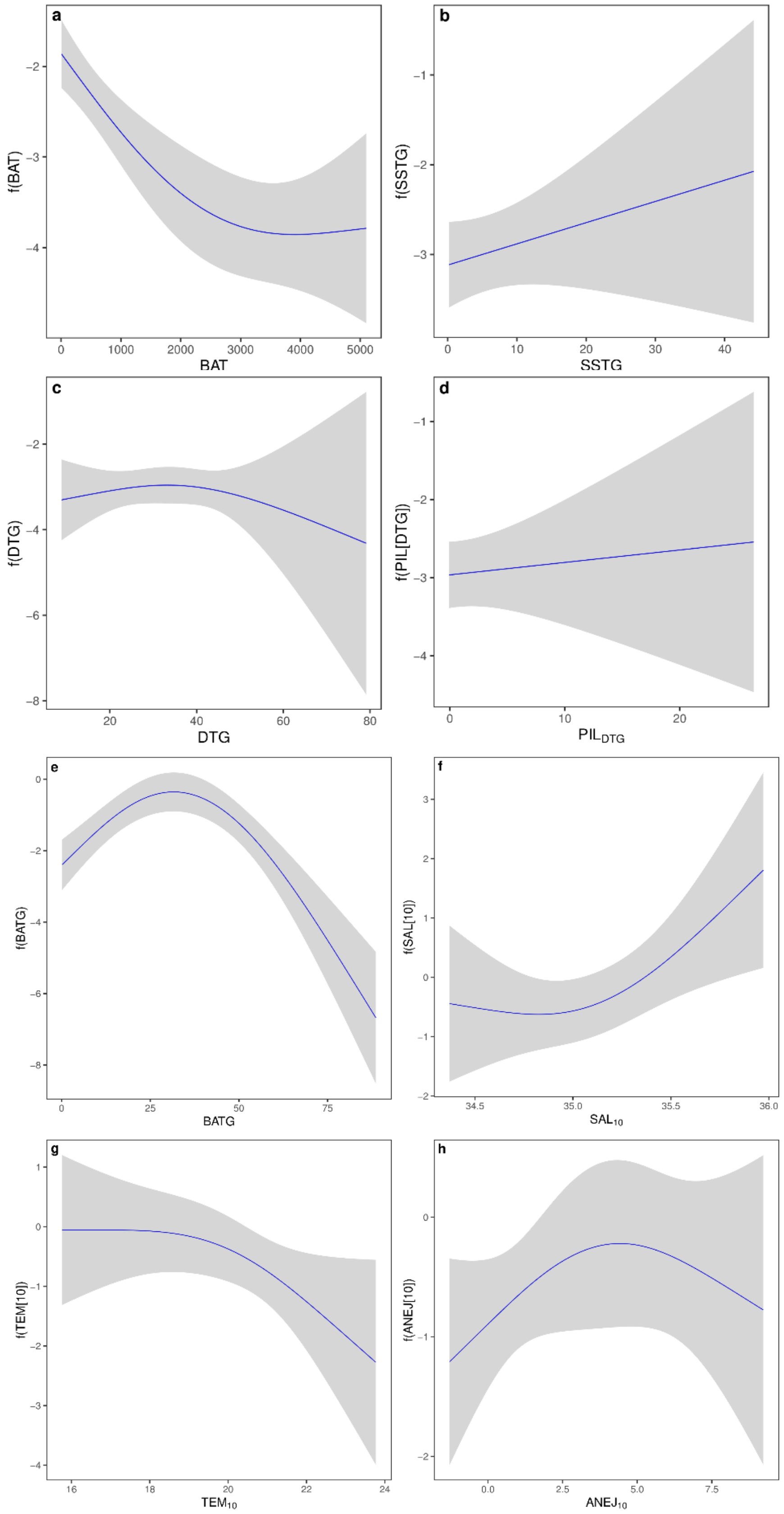

Figure 2.6. *Response plots showing the mean relationship (blue line) between the most influential environmental variables and the predicted spatial abundance of (a–d) Sooty and (e–h) Great shearwaters, considering all models within the 95% confidence set (grey shading). For acronyms see Table 2.1.*

Among highly correlated predictors for GRSHs (Table B-6.2), $ANEA_{10}$, BAT, DCO and DSB were the least explicative variables (results not shown) and they were removed. The 95% confidence set comprised 15 models out of a total of 255. The model with the lowest AIC showed an ED of 17.8%. The main variables driving the spatial abundance patterns of GRSHs were BATG, SAL_{10}, TEM_{10} and ANEJ10 (Figure 2.5b). Abundance of GRSHs showed a quadratic relationship with BATG, with maximum values at approximately 35% of BATG (Figure 2.6e). SAL_{10} (ranging between 34 and 36 psu) and TEM_{10} (ranging between 16 and 24°C) influenced GRSH abundance positively (Figure 2.6f) and negatively (Figure 2.6g), respectively. Finally, intermediate $ANEJ_{10}$ values were related to higher GRSH abundance (Figure 2.6h). In particular, GRSH abundance was higher at intermediate BATG values (*i.e.,* corresponding to coastal and slope areas; Figure B-3.1b), in areas of higher SAL10 values (*i.e.,* located in the southwestern shelf, slope and oceanic areas; Figure B-7.2a–d). In addition, GRSH abundance was higher in colder TEM_{10} occurring in the northern French continental shelf (Figure B-7.2e–h) and associated with areas of intermediate $ANEJ_{10}$ values (Figure B-7.1a–d).

Spatial abundance predictions showed the highest densities of SOSHs over both the Spanish and French continental shelves (Figure 2.7a–d). Overall, higher densities were highlighted within specific marine areas around the main capes of the Spanish continental shelf (*i.e.,* Estaca de Bares, Cabo Peñas, Cabo Ajo and Cabo Matxitxako, from west to east) and in specific coastal areas of the French continental shelf (*e.g.,* the marine area surrounding the Belle-Îleen-Mer in south Brittany, and the area of influence of the Loire and Gironde rivers and the Arcachon Bay, from north to south). However, these areas showed high interannual variability and high-density areas were spread over both continental shelves. The lowest predicted relative densities were identified recurrently every year over the oceanic area of the BoB. Regarding GRSHs, spatial density predictions highlighted important areas in the French and Spanish continental slopes. These areas showed a high inter-annual variability over the Armorican slope (especially high in 2014 and 2016), and over the Cachucho area, an elongated near-shelf seamount (especially high in 2015). Less dense areas were located over the northern sector of the French continental shelf (Figure 2.7e–h).

Predictions of relative density and abundance estimated that SOSHs were less abundant than GRSHs, showing an annual average of 3203 (95% CI: 1753– 5748) and 12 380 (95% CI: 5797–28 152) birds, respectively (Table 2.3). Therefore, the SOSH:GRSH abundance ratio was almost 1:4. Averaged values of predicted relative densities yielded lower estimates for SOSHs compared to GRSHs (0.09 vs. 0.38 birds km^{-2}). Maximum density values were approximately 0.6 and 3.5 birds km^{-2} for SOSH and GRSH, respectively (Figure 2.7).

Table 2.3. Abundance estimations of Sooty (SOSH) and Great shearwaters (GRSH) during JUVENA surveys for the 2013–2016 period. Animal density (D in ind. km^{-2}) and its coefficient of variation (CV_D), estimated abundance (N), its 95% confidence interval (95% CI_N) and its coefficient of variation (CV_N).

Species	Year	*D*	CV_D	N	95% CI_N	CV_N
SOSH	2013	0.09	0.3	3200	1810–5658	0.3
	2014	0.10	0.3	3250	1837–5748	0.3
	2015	0.09	0.3	3202	1785–5743	0.3
	2016	0.09	0.31	3162	1753–5702	0.31
GRSH	2013	0.35	0.35	11263	5797–21881	0.35
	2014	0.37	0.37	12160	6043–24466	0.37
	2015	0.39	0.42	12830	5847–28152	0.42
	2016	0.41	0.36	13269	6681–26354	0.36

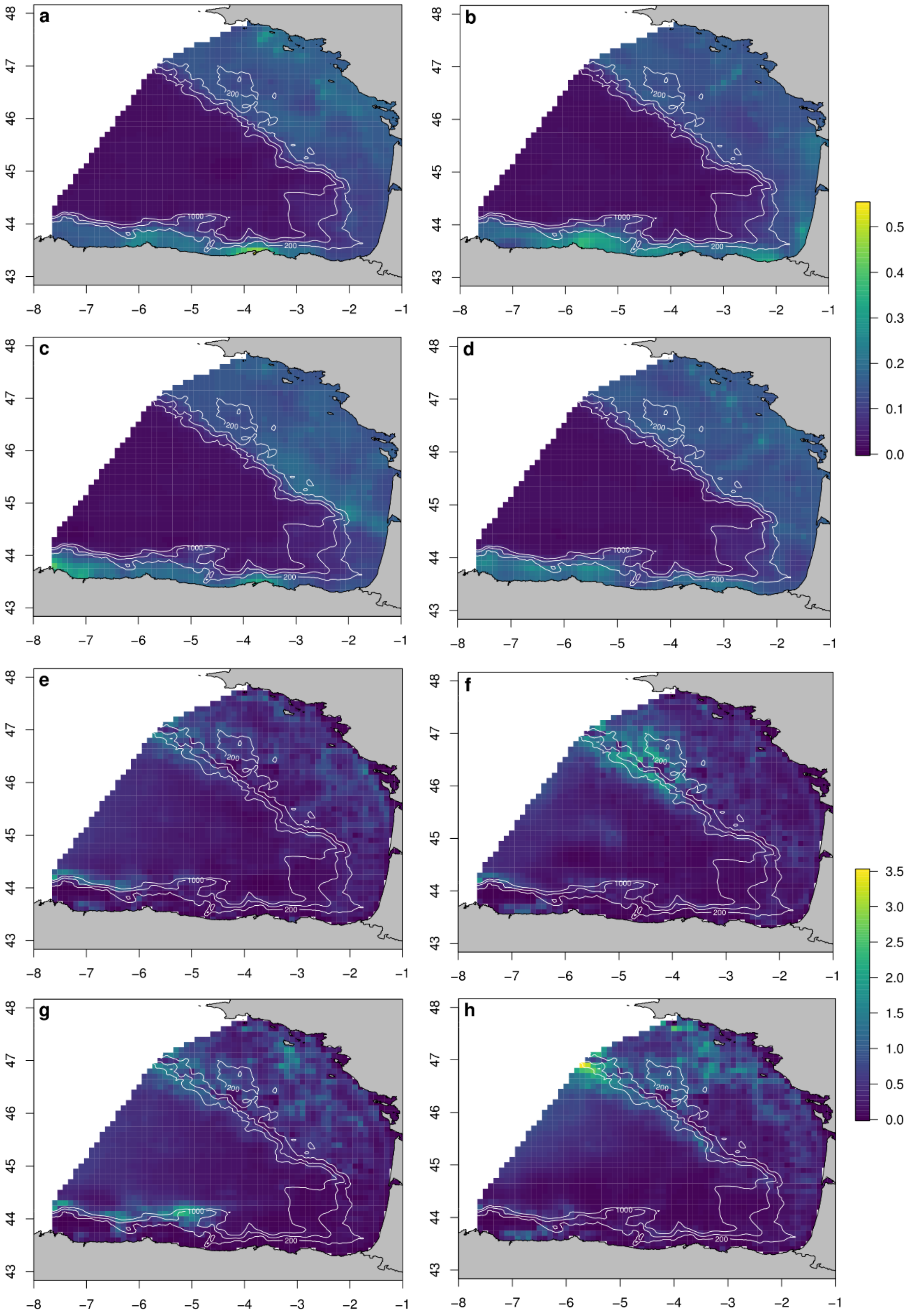

Figure 2.7. Predicted spatial density of (a–d) Sooty shearwaters and (e–h) Great shearwaters for the 2013–2016 period during the JUVENA surveys. Predicted bird densities are represented in the colour scale bar; values range between 0–0.6 and 0–3.5 birds km^{-2} for both Sooty and Great shearwaters, respectively. Geographic references are indicated in Figure 2.1.

4. Discussion

This study illustrates the integration of predator observations, preyscapes and mesoscale oceanographic fields to assess the importance of foraging grounds for highly migratory pelagic predators. Determining migratory pathways of marine predators can have important implications for conservation strategies and climate change studies. Based on data collected during multidisciplinary oceanographic surveys, we characterised the 3D environment (preyscape plus oceanography) to explain abundance patterns of 2 highly migratory seabirds during their stage in the BoB. The JUVENA survey is featured by being a unique ecosystem-based survey that covers the oceanic area of the BoB. Based on our spatial modelling approach, we provide the first density and abundance values for SOSHs and GRSHs in the BoB.

Defining the 3D oceanographic habitats of marine species is challenging, owing to the difficulty in defining biologically meaningful spatial and vertical ranges at which they are able to integrate marine resources through the seascape. Here, we considered 3 different depth ranges, taking into account (1) surface conditions, (2) diving range (*i.e.,* down to 70 m depth; Shaffer et al., 2009) and (3) accessibility of pelagic prey (Boyra et al., 2016, 2013). Our results highlighted species-specific biologically meaningful vertical domains. Whereas environmental conditions (both oceanography and preyscape) influencing prey accessibility (above the DTG) better explained SOSH observed abundance patterns, surface environmental conditions were better predictors of GRSH abundance patterns. Thus, each pelagic seabird species exploits the vertical habitat that they are able to reach: 70 and 20 m depth for SOSH and GRSH, respectively (Ronconi et al., 2010b; Shaffer et al., 2009). This is especially important for air-breathing predators (Benoit-Bird et al., 2013), since oceanographic covariates should characterise the vertical accessibility of forage fish to seabirds (Passuni et al., 2018). Therefore, both species integrate marine resources in different ways, even if prey and oceanographic conditions were highly correlated between the surface and above both the DTG and 70 m depth.

The 3D environments of both species were primarily influenced by different static, oceanographic and preyscape predictors, shaping a major 3D segregation. Overall, SOSHs were more abundant over the Northern and Southern continental shelves of the BoB, where this species could be regularly observed. Over the Spanish shelf, dense aggregations were located in areas of high SSTG (close to the main capes), probably influenced by summer coastal upwelling (Koutsikopoulos and Le Cann, 1996). Over the French shelf, hotspots of the species were located in areas of low salinity associated with the discharge of the main rivers. The lowest densities were identified recurrently every year over the oceanic area of the BoB. In contrast, GRSH densities were higher in slope waters of the French (Armorican slope) and Spanish (southwestern slope) sectors, followed by less dense areas over the Northern sector of the French continental shelf. Thus, this species could regularly be observed in the outer slope areas, characterized by high values of both bathymetric gradient and surface salinity. Over the Armorican slope, the generation of energetic internal waves has been reported (Le Cann, 1990; Pairaud et al., 2010; Serpette and Mazé, 1989). An increased variation in depth, which is also related to the generation of internal waves, has been linked to the higher probability of presence and abundance of 7 different species of seabirds and marine mammals in the North Sea (Scott et al., 2010). The formation of internal waves in those slope areas might promote an increase in primary production and aggregation of smaller prey items (Scott et al., 2010). Furthermore, internal waves may influence biological activity (plankton and small pelagic fish) at the sub-mesoscale level (100s of m to km), at a finer spatial scale than the JUVENA mesoscale survey (Bertrand et al., 2008; Grados et al., 2016). The effect of internal waves on mixing and the associated impact on seabirds in other areas of the BoB needs to be quantified and deserves further research.

Concerning preyscapes, abundance patterns of SOSHs and GRSHs were driven, to a certain extent, by the biomass of PIL and ANEJ, respectively. While PIL were located mainly over the French coastal area, intermediate values of ANEJ biomass were located in the southern BoB and in the central French continental shelf (Boyra et al., 2013). The vertical distribution of the biomass of ANEJ show common depth ranges around 14 m depth (Boyra et al., 2013), shallower than the common depth of the PIL (*e.g.,* Zwolinski et al., 2007). Depth ranges for these 2 small pelagic fishes are within the maximum diving depth recorded for the deep SOSH and shallow GRSH divers (Ronconi et al., 2010b; Shaffer et al., 2009). Therefore, this is the first study showing that early life stages of a small pelagic fish can drive the distribution patterns of seabirds in the BoB. However, the most important predictors were not the preyscapes, but the oceanographic ones (Torres et al., 2008). This could be related to (1) the wide spectrum of prey eaten by both species during the non-breeding period (krill, squid, sand lance and fishing discards) (Ronconi et al., 2010a), (2) the need to develop prey patch predictors (*e.g.,* depth and local density of prey patches) in addition to prey biomass (Benoit-Bird et al., 2013), (3) the importance of considering the scale-dependence of predator–prey relationships (Fauchald et al., 2000; Rose and Leggett, 1990) and (4) the problem of sampling scale in relation to ecosystem-process scales.

Spatial habitat segregation could be a mechanism to avoid inter-specific competition between 2 closely related species (Brown et al., 1981) that perform long-distance trans-equatorial migrations between the Northern and Southern Hemispheres (Hedd et al., 2012; Huettmann and Diamond, 2000; Shaffer et al., 2006). This has been evidenced not only in the BoB (NE Atlantic), but also in their main non-breeding quarters in the NW Atlantic (Brown et al., 1981). In addition, observed spatial segregation could be partially explained by differences in forage fish depth distribution. In slope areas, where GRSHs concentrated, ANEJ are more abundant at shallower depths than in shelf areas, where they show a deeper vertical range (Boyra et al., 2016). Ultimately, both species differ in their foraging abilities, associated with bill morphology and underwater swimming adaptation (Brown et al., 1981). GRSHs might be adapted to obtain larger and tougher bodied prey such as squid (*Illex* spp.) and mackerel, whereas SOSHs feed preferentially upon euphausiids *Meganyctiphanes norvegica* and soft-bodied fish such as Herring *Clupea harengus* (Brown et al., 1981).

The present study provides the first specific abundance values for both SOSH and GRSH in the BoB during September: 3203 SOSHs (95% CI: 1753−5748) and 12 380 GRSHs (95% CI: 5797−28 152), which vary slightly inter-annually. There are no alternative specific abundance values for SOSHs and GRSHs separately, but a large-sized shearwater group (pooling SOSH, GRSH and Cory's shearwaters) showed an abundance value of 31 980 individuals (95% CI: 21 324−48 776) for summer (mid-May to mid-August) (Pettex et al., 2017). Both studies (Pettex et al., 2017 and this study) provided similar figures and orders of magnitude, but differed in multiple factors such as different platforms (aerial vs. vessel-based surveys), methodologies (strip-transect vs. line-transect), surveyed months (mid-May to mid-August vs. September) and the time period considered (2012 vs. 2013−2016). Coastal counts during migration in the southwestern sector of the study area (Estaca de Bares) yielded an estimation of 54 501 SOSHs (range: 26 652−69 096) and 5898 GRSHs (range: 560−11 867) mainly in September-October in the northwestern tip of the Iberian Peninsula (Arcos et al., 2009; Sandoval et al., 2010). However, the arrival of these species is highly variable (Arcos et al., 2009), influenced by different climatic conditions leading the species into the BoB (Louzao et al., 2015). However, Louzao et al. (2015) provided higher numbers of GRSHs compared to SOSHs based on monthly at-sea surveys in the inner BoB, and the proportion of GRSHs to SOSHs was higher in the main stopover in the NW Atlantic Ocean (Huettmann and Diamond, 2000). The ratio GRSH:SOSH of approximately 4:1 estimated in the present study falls within the observed ratio in the NW Atlantic, ranging from 3:1 to 30:1 (Huettmann and Diamond, 2000).

Understanding the abundance patterns of highly migratory species and the underlying environmental drivers will assist in advancing current efforts to identify conservation targets in the pelagic realm (Game et al., 2009). We found inter-annual variability in both shearwater species' spatial abundance patterns, driven by annual oceanography and preyscapes. In the California Current system, SOSHs show an inter-annual variability in distribution and aggregation patterns within the shelf-slope area (Adams et al., 2012). However, persistent shearwater hotspots can be found, influenced by mesoscale oceanographic features (*e.g.,* river plumes, oceanographic fronts or upwelling areas), since these areas support a large biomass of small pelagic fish (Adams et al., 2012). Within the non-breeding North Atlantic distribution, SOSHs wintering on the Newfoundland continental shelf are associated with persistent small pelagic fish hotspots (Davoren, 2013). In the BoB, some of the oceanographic features influencing abundance patterns of both shearwater species are predictable (*e.g.,* coastal upwelling, area of influence of river plumes), occurring in similar spatial locations year after year (Llope et al., 2006). In addition, concentrations of small pelagic fish occur in the same overall areas every September (Boyra et al., 2013). Therefore, shearwater foraging locations could be spatially limited to guide conservation actions in the BoB.

The main objective of the JUVENA annual surveys is the assessment of ANEJ for predicting the strength of their recruitment to the adult stock the following year in the BoB (Boyra et al., 2013). Monitoring and management progress have recently been made due to the need for holistic management. Based on requirements established by frameworks such as the Marine Strategy Framework Directive (European Commision, 2008), the JUVENA survey has widened its objectives to provide an integrative assessment of the BoB. The present study is a good example of such an effort by integrating not only other pelagic fish species but also marine megafauna monitoring and oceanographic characterisation in annual oceanographic surveys (Authier et al., 2018; Certain et al., 2011; García-Barón et al., 2019a; Saavedra et al., 2018), in order to guide ecosystem-based management and conservation efforts. The spatial coverage of the JUVENA surveys (*e.g.,* extended to the oceanic domain) is greater than any other monitoring scheme in the BoB (ICES, 2018), but there are certain limitations caused by the use of 2 different research vessels. Predator observers are placed on only one of the vessels, and therefore a spatial modelling approach is necessary to obtain abundance estimations over the entire study area. In addition, a validation process is necessary to merge the data recorded from 2 different CTDs to obtain the oceanographic conditions of the survey. Despite these limitations, the present study illustrates the capabilities of annual oceanographic surveys in simultaneously characterising the 3D environment of different pelagic species, from plankton to marine predators (*e.g.,* Certain et al., 2011).

In the present study, we have developed a methodological approach to identify biologically appropriate oceanographic and preyscape predictors to jointly consider both the spatial and vertical dimensions of oceanographic habitats, that can be applied to any marine species. Further research is necessary to develop integrative studies to understand the foraging strategies developed by predators in relation to prey patches (Benoit-Bird et al., 2013; Boyd et al., 2015). Fine-scale dedicated surveys would help understanding fine-scale interactions of marine megafauna with bio-physical variables, such as sub-surface chlorophyll and internal waves, by repeatedly surveying specific important marine areas (Scott et al., 2013). Other technologies, such as tracking devices, provide a complementary alternative to identify important marine areas for pelagic predators by providing continuous timescale information to evaluate seasonal, non-restricted at-sea distributions (Adams et al., 2012; Hedd et al., 2012; Pérez-Roda et al., 2016). The combination of at-sea surveys and tracking technologies provides complementary perspectives of the spatial ecology of pelagic predators (*e.g.,* Louzao et al., 2009).

CHAPTER 3

Essential dynamic ocean variables shape the environmental envelopes of marine megafauna diversity

ABSTRACT

Effective conservation and management measures are needed to face the unprecedent changes that marine ecosystems, and particularly marine megafauna are suffering. These measures require the identification of high-value biodiversity areas (HVBAs) which in turn require the identification of the essential ocean variables (EOVs) that shape the environmental envelope of communities (*i.e.,* space defined by a set of environmental variables), such as those composed by seabirds and cetaceans. The aim of this study was to delineate and characterize the HVBAs for the North and North-western Spanish seabird and cetacean's community taking advantage of the sightings collected during the annual oceanographic surveys PELACUS (2007-2016). Firstly, we used distance sampling methodology to analyse the species detectability based on environmental conditions. Then, we explored the relationship between the effective strip width and biometry measurements of seabirds, finding an overall positive relationship between both parameters. Finally, to delimitate the HVBAs and find the EOVs defining the environmental envelope of the community we used a spatio-temporal modelling approach using Generalized Additive Models. Overall, the main environmental variables driving species abundance were the sea surface temperature (SST), the distance to the shelf-break and the chlorophyll-a concentration (Chl-a). The SST and Chl-a were identified as the dynamic EOVs due to their highest relative predictor importance, driving the environmental envelope and shaping areas of higher density. HVBAs were located mainly over the North-western Spanish waters and decreased towards the inner Bay of Biscay remaining spatially stable over the study period. By identifying community-level HVBAs, the underlying ecological and oceanographic processes driving the spatio-temporal patterns of biological communities, can be understood. This information would allow the establishment of baseline values to predict and detect the effect of anthropogenic or climate change threats on HVBAs. In addition, the location of HVBAs can help to fulfil the emergent need for sound spatial information to support the implementation of marine spatial planning.

Under review as:

García-Barón, I., Santos, M.B., Saavedra, C., Astarloa, A., Valeiras, J., Barcelona, S.G., Louzao, M. *Essential dynamic ocean variables shape the environmental envelopes of marine megafauna diversity.* Ecological Indicators.

1. Introduction

The accelerated loss of biodiversity that marine ecosystems are suffering is a global concern (IPBES, 2019). Human impacts such as overexploitation, pollution or coastal development (Dulvy et al., 2003; Halpern et al., 2008; IPBES, 2019) and also climate change (IPBES, 2019; Simmonds and Smith, 2009; Sydeman et al., 2012) are causing unprecedented changes at global level. In fact, only 3% of the global ocean was described as free from human pressures in 2014 (IPBES, 2019). Among marine fauna, apex predators are particularly vulnerable to human-related threats (Lascelles et al., 2014) due to their life history characteristics and position at the top of the marine food web. Furthermore, a large proportion of marine megafauna, such as seabirds and cetaceans, seem to have consistent migration pathways (Horton et al., 2017) that difficult their adaptation to bottom-up effects caused by changes in the distribution of their prey (Evans and Bjørge, 2013; Luczak et al., 2011) and to shifts in environmental conditions (Macleod, 2009; Soldatini et al., 2016). Therefore, the provision of the spatial patterns of species distribution to identify their essential habitats is a key factor for guiding conservation and management strategies of these species (Evans and Hammond, 2004; Louzao et al., 2010).

Species-specific oceanographic habitats reflect environmental envelopes (*i.e.,* space defined by a set of environmental variables) critical for the species' survival resulting from their adaptation to a highly variable system where feeding resources vary at multiple spatial and temporal scales (Lambert et al., 2018). When information on preyscapes (*i.e.,* ecological features describing spatial patterns of prey biomass; Louzao et al., 2019) of marine megafauna is not available, environmental predictors have been used as proxies of prey distribution. To do this, habitat modelling techniques can be used to identify areas of high probability of presence and/or abundance of individuals by identifying the environmental conditions driving their ecological niche (Holt, 2009; Redfern et al., 2006). Furthermore, habitat modelling techniques can serve to define the environmental conditions or essential ocean variables (EOVs) that shape the environmental envelope of marine megafauna.

Ideally, habitat modelling would be based on accurate presence data at a range of temporal and spatial scales (Redfern et al., 2006). Marine megafauna monitoring requires dedicated surveys over large areas; however, due to the logistics and costs involved, these large scale surveys have been taking place once every 10 years (Evans and Hammond, 2004), leading to few studies showing the consistency of high-value biodiversity areas (HVBAs) over time (*e.g.,* Kuletz et al., 2015; McClellan et al., 2014). The information provided by annual surveys is essential to address habitat preferences over time and can complement the less frequent European dedicated at-sea surveys which are not carried out yearly (SCANS surveys, Hammond et al., 2017; SAMM surveys, Laran et al., 2017).

Since 2007, the PELACUS annual oceanographic survey, which is carried out every spring by the Spanish Institute of Oceanography (IEO) covering the North and NW Spanish continental shelf, collects data on a broad community of seabirds and cetaceans which exploits the coastal and shelf waters of the BoB (Saavedra et al., 2018). For numerous seabird species, the BoB represents a key feeding area during certain periods of the year, when they undertake seasonal feeding migrations into the area (Arcos et al., 2009). In the same way, the resource availability and the combination of diverse physiographic characteristics of the environment make the BoB a suitable habitat for several species of cetaceans (Laran et al., 2017). Although several studies have described the oceanographic habitats of cetacean and seabird species along the French waters of the BoB (Authier et al., 2018; Lambert et al., 2018, 2017a; Laran et al., 2017; Pettex et al., 2017), very few studies have been carried out in the North-western (NW) and Northern Iberian shelf waters (Arcos et al., 2009; Louzao et al., 2019b), none of which has characterized the marine megafauna HVBAs.

This chapter aims to better understand the spatio-temporal trends of the marine megafauna community (*i.e.,* seabirds and cetaceans) of the southern BoB in relation to ecosystem dynamic over the last decade (2007-2016). We used a threefold approach: (i) a spatio-temporal modelling of megafauna spatial density, (ii) an identification of HVBAs and, finally, (iii) the characterization of the environmental envelope driving megafauna diversity in our study area. The workflow of the present study is described in Figure 3.1. Our results can serve as a first step to identify ecologically meaningful areas in the southern BoB at the marine megafauna community level, providing the knowledge needed to support management decisions and conservation measures in a marine spatial planning context.

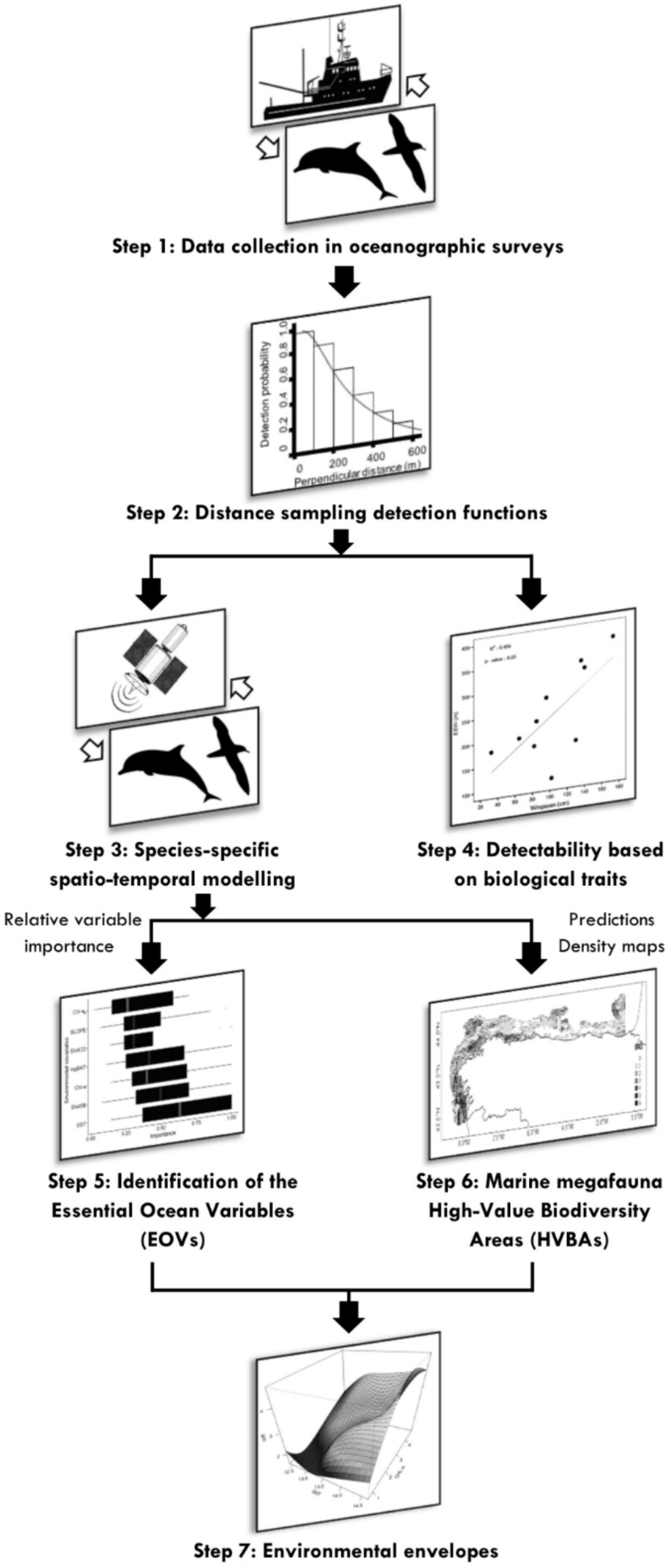

Figure 3.1. Graphical representation of the methodological steps used in this study.

2. Material and Methods

2.1. Oceanographic survey and data collection

Since 2007, the IEO has included a standardised observer program for marine megafauna data collection following single platform visual line-transect protocols (Buckland et al., 2001) in its multidisciplinary oceanographic acoustic surveys PELACUS. PELACUS surveys last one month and take place annually in spring (March-April). The study area encompassed the North and Northwest Spanish continental shelf waters covering an area of ≈ 42800 km^2 (Figure 3.2).

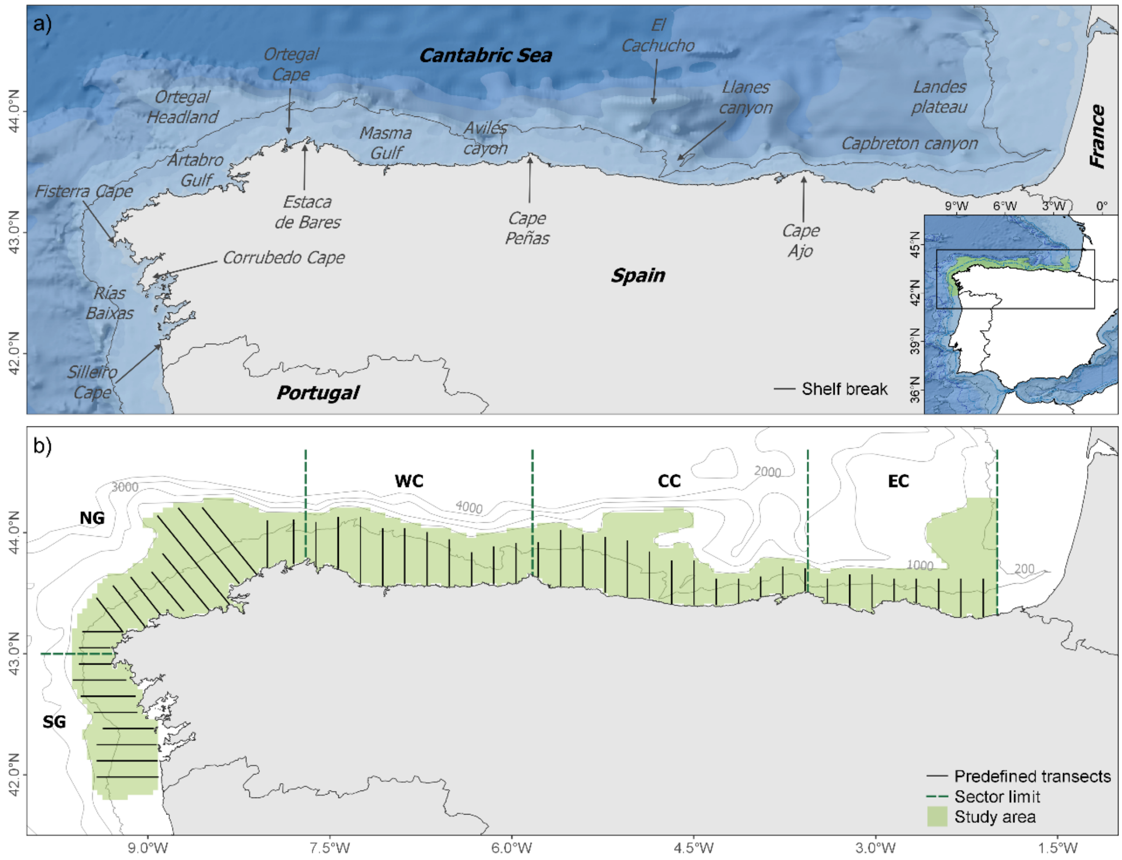

Figure 3.2. Map of the study area showing a) the geographic references mentioned in the text; b) the predefined transects followed during the PELACUS oceanographic acoustic surveys (2007-2016); the sectors in which we have subdivided the study area: south Galicia (SG), north Galicia (NG), western Cantabrian Sea (WC), central Cantabrian Sea (CC) and eastern Cantabrian Sea (EC) based on Santos et al. (2013).

At-sea observations were collected during the period 2007-2012 on board the *R/V Thalassa* (TH) and from 2013-2016 on board the *R/V Miguel Oliver* (MO). The sampling protocol consisted on equidistant parallel transects perpendicular to the coastline separated by 8 nautical miles. Data on megafauna sightings were collected by a team of three trained observers working in turns of two and placed on the highest accessible point of the vessel.

This height corresponded approximately to 16 m and 12 m on the TH and MO, respectively. Observers scanned a 180° sector ahead of the vessel (from 270º to 10º on the port side and from 350º to 90º on the starboard side). Observers searched with naked eyes, and binoculars (10x42) were only used to aid species identification and to record the group size and/or animals' behaviour (Saavedra et al., 2018). Observers collect data along transects while the vessel is navigating at constant heading and speed (≈ 10 knots) during daytime. Navigation routes between predefined transects that follow a fixed course and constant 10 knots speed were also sampled when possible. Observation effort was georeferenced every minute with the vessel GPS. Surveyed transects were split into observation periods of identical detection conditions (*legs*). For each *leg*, observers recorded data on vessel speed, heading, Beaufort sea-state, swell height and direction, wind speed and direction, cloud coverage, visibility, sun glare on each side of the vessel (port or starboard) and an overall subjective assessment of detection conditions of the sightings (good, moderate or bad relative to the detections). For each sighting, observers recorded the time, the species, the group size, the detection distance [using a stick based on the Heinemann (1981) method] and its angle with respect to the track line (using an angle meter). Additional data recorded for each sighting included the animal heading relative to the ship, the behaviour and the presence of calves.

2.2. Species detectability based on environmental conditions and biological traits

We explored the detectability of the marine megafauna community with two different approaches based on the effect of: (1) environmental conditions by modelling the detection function obtaining the effective strip half-width (ESW), and (2) biological traits of each species by exploring the relationship between the ESW and biometry measurements.

a) Detectability based on environmental conditions

Detection functions were estimated independently for each species pooling together the sightings from ten years (2007-2016). Only sightings with wave height ≤ 2 m, Beaufort sea-state ≤ 5 and overall medium and good visibility conditions were used following the García-Barón et al. (2019) approach. To avoid overestimation of the density, sightings of animals attracted to the ship or associated with human activities (*i.e.,* individuals following the R/V or scavenging on fishing discards) were systematically excluded from further analyses as Authier et al., (2018) suggested. Finally, ten seabird: Northern gannet *Morus bassanus*, Lesser black-backed *Larus fuscus*, Yellow-legged *L. michahellis and* Mediterranean gulls *Ichthyaetus melanocephalus*, Great skua *Stercorarius skua*, Sandwich tern *Thalasseus* *sandvicensis*, Razorbill *Alca Torda*, Common guillemot *Uria aalge*, Balearic *Puffinus mauretanicus* and Manx shearwaters *P. puffinus* and three cetacean species: Short-beaked common *Delphinus delphis* and Bottlenose dolphins *Tursiops truncatus* and Long-finned pilot whale *Globicephala melas* with at least 15 sightings over the study period were included in the analysis (Authier et al., 2018).

Detection functions were modelled using both Conventional and a Multiple-Covariate Distance Sampling approaches (CDS and MCDS; Buckland et al., 2001; Marques and Buckland, 2004), with the '*mrds'* R-package (Laake, J. et al., 2015) including the effect of detection covariates in the case of the MCDS, in addition to distance, on the detection probability. Covariates tested with the MCDS methodology included Beaufort sea-state, glare intensity, categorized swell height, cloud coverage, visibility, overall detection condition and year. Beaufort sea-state, glare intensity, cloud coverage and visibility were included raw and as categorical covariates in the analyses (Appendix B). MCDS detection functions were fitted using forward stepwise model building based on Akaike's Information Criterion (AIC) selection, as well as by inspection of Q-Q plots and Kolmogorov-Smirnov and Cramer-von Mises goodness of fit tests (Thomas et al., 2010). The initial model was fitted without any covariate (*i.e.,* CDS). Then, univariate models were fitted with each covariate on its own (*i.e.,* MCDS). If the addition of a covariate provided a smaller AIC score (difference > 2), models of increasing complexity were built by comparing the score obtained by the addition of each covariate to the previous best model (Mannocci et al., 2015). Then, the process was repeated with the new best model until the addition of a new covariate did not improve the AIC (Barlow et al., 2001). Final detection function selection was made on parsimony grounds (*i.e.,* similar explicative power but less parameters; Arnold, 2010) when the two best detection functions did not show a difference in AIC > 2 (*i.e.,* ΔAIC < 2). After selecting the best detection function, the ESW was calculated. In the case of the models with covariates, the ESW was calculated for each level of the covariate.

b) *Detectability based on biological traits*

Since the size of the species might influence the ability of observers to detect them, we assessed the potential relationships between the ESW and data on species' biometry based on linear regression models. Due to the small number of cetacean species used in this study, we selected only seabird species for this analysis, using the wingspan and bird size as explanatory variables. Size and wingspan data were obtained from "The Handbook of the Birds of the World Alive" (del Hoyo et al., 2019).

2.3. *Spatio-temporal modelling of megafauna abundance*

Surveyed *legs* were subdivided into segments of an average of 10 km of homogeneous conditions, so the variability in environmental characteristics was limited within segments (García-Barón et al., 2019a; Virgili et al., 2017). Density surface models were then obtained for the best quality data (*i.e.,* wave height ≤ 2 m, Beaufort sea-state < 5 and overall medium and good visibility conditions). Segments with length ≤ 5 km and segments associated with a depth > 1000 m were removed from the analysis.

Environmental covariates were selected based on biological relevance and data availability (Table C-2.1 in Appendix C). We used four physiographic predictors: logarithm of depth (logBAT), slope (SLOPE), the closest distance to the coast (DistCO) and to the shelf-break (measured as the distance to the 200 m-isobath; DistSB); and three oceanographic predictors: sea surface temperature (SST), logarithm of Chlorophyll *a* concentration (Chl-*a*) as a proxy for phytoplankton biomass and its spatial gradient (Chl-a_g). We estimated the Chl-a_g by estimating its proportional change within a surrounding 3×3 cell grid following the Louzao et al. (2009) methodology. All oceanographic predictors were calculated by averaging the values over the period surveyed each year (March-April mean value). To eliminate the effect of varying measurements scales, all variables were standardized to a mean of 0 and a standard deviation of 1 before fitting the model (Zuur et al., 2007). We investigated the co-linearity between predictors by calculating the pairwise Spearman correlation coefficients (r). When variables showed high correlation (above $r = |0.7|$) they were not used together in the same model (Dormann et al., 2013). None of the pairs of variables tested in our analysis showed high correlation.

Density surface models were fitted independently for each species by applying Generalized Additive Models (GAMs) to identify the most important environmental covariates explaining the distribution of species abundance (*i.e.,* to relate the number of individuals per segment to environmental predictors). We selected a negative binomial distribution and log-link function to account for overdispersion. We used flexible smoothing splines to model the nonlinear functional relationship between the response variable and the covariates and the logarithm of the effective sampled area as an offset. The sampled area associated to each segment was calculated as the length of the segment multiplied by twice the corresponding ESW for each species.

GAMs were implemented following the Information-Theoretic framework to evaluate the competing models by assessing their relative support based on the AIC value corrected for small sample sizes (AICc) and Akaike weight (ω_i) (Burnham and Anderson, 2002). Models were constructed with all possible combinations of covariates and ranked based on their AICc. When the ω_i of the model with lowest AICc was below 0.90, a model averaging procedure was used to account for all models and parameters uncertainty (Burnham and Anderson, 2002; Thiers et al., 2014). To obtain averaged coefficients and variance estimator, we identified the 95% confidence set of models where the cumulative sum of ω_i was ≥ 0.95, starting with the model with the highest ω_i (Johnson and Omland, 2004). The ω_i were used for the assessment of the relative importance of predictor variables (Burnham and Anderson, 2002; Louzao et al., 2016) and the response plots of the explanatory variables were constructed based on averaged coefficient of the 95% confidence set. Finally, we calculated the spatial-density predictions for each species and year on a 0.04° x 0.04° resolution grid of covariates using the averaged model developed. This procedure provides maps of density per year for each species analysed. GAMs were conducted in R version 3.4.4 (R Core Team, 2018) using the *'mgcv'* R-package (Wood, 2011) with additional functions provided by the R-package *'MuMIn'* (functions *dredge* and *model.avg*; Barton, 2016). Finally, we used a relative quantitative index to validate the models based on the relationship between the number of individuals sightings by means of the encounter rate (*i.e.,* number of individuals sighted per 100 km surveyed) and the predicted density for each species.

2.4. High-value biodiversity areas

High-value biodiversity areas (HVBAs) for the studied megafauna were identified based on a biodiversity richness index (BRI) relying on the marine areas of highest predicted abundance. Areas of highest predicted abundance were calculated for each species and year following the Cañadas and Vázquez (2014) methodology also applied by García-Barón et al. (2019). Firstly, the estimated abundance per cell was calculated by multiplying the predicted density of each cell by the cell area. Then, all the cells were sorted by their estimated abundance in decreasing order classifying them by steps of 10% of the total estimated abundance in the study area. Values > 40% were selected for each species and year layer to delimitate the areas of highest predicted abundance.

In order to find the HVBAs, the number of species areas of highest predicted abundance overlapping each cell was summed up to calculate the BRI, thus we obtained the number of species for which each cell represents the highest predicted abundance area. The HVBAs were mapped separately for seabird and cetacean species and jointly to illustrate the megafauna community HVBAs. Hence, we obtained three layers per year and three layers for the whole study period (2007-2016).

2.5. Environmental envelopes driving megafauna diversity

EOVs were defined by the dynamic variables that showed the highest relative predictor importance within the megafauna community (Constable et al., 2016; Lindstrom et al., 2012). At the community level, the combination of dynamic EOVs would help define the environmental envelope (Wiens and Graham, 2005) that could help describe the characteristics of the HVBAs. However, this would suggest that the underlying oceanographic conditions should differ among geographical areas, at least in relation to the variables we have tested. Therefore, we firstly explored whether baseline oceanographic conditions differ among geographical areas. For that, we divided our study area into five geographical sectors based on Santos et al. (2013): south Galicia (SG), from Portugal to Cape Finisterre; North Galicia (NG) from Cape Fisterra to Cape Estaca de Bares; western Cantabrian Sea (WC) from Cape Estaca de Bares to Cape Peñas; central Cantabrian Sea (CC) from Cape Peñas to Cape Ajo; and eastern Cantabrian Sea (EC) from Cape Ajo to the eastern end of the study area (see Figure 3.2b).

Abundance of HVBAs were determined by calculating the percentage of cells by sector with high predicted abundance. This analysis was two-fold, by year and by species. To assess geographical patterns in quantitative HVBAs, we used two different approaches: (1) an exploration of the differences in quantitative HVBAs by sector based on dissimilarities calculated using the Bray-Curtis dissimilarity distance using the *metaMDS* function in '*vegan*' R-package (Oksanen et al., 2018) (the examination on a non-metric multidimensional scaling (nMDS) plot of the differences between sectors was assessed using the function *envfit* ('*vegan*' R-package) with 1000 permutations), (2) an analysis of latitudinal gradients in the quantitative HVBAs by sector fitting linear models, using the slope and R^2.

Finally, to explore whether differences in dynamic environmental envelopes could explain the differences in megafauna richness in the study area we calculated the averaged values of the EOVs (*i.e.,* those dynamic variables that showed the highest relative predictor importance) and the BRI per year and sector. We also plotted the convex hull of the set of mean BRI values per sector. Furthermore, to describe the response of the BRI as function of dynamic environmental envelopes a GAM was fitted with the determined EOVs. Tensor product splines were used for *n*-dimensional effects, depending on the *n* variables considered as EOVs (Chen et al., 2012).

3. Results

3.1. Oceanographic survey data

A total of 20,942 km were surveyed over the ten years of data analysed in this study (2007-2016). After filtering the effort to remove those observations taken under less optimal conditions, 15,003 km remained, representing ≈ 72% of the total available effort (Table 3.1). Filtered survey effort ranged from a minimum of 597 km in 2013 to a maximum of 1494 km in 2007 (annual mean ± standard deviation: 1231 ± 318 km). A total of 16,820 individuals were recorded during this period (13,730 seabirds and 3,103 cetaceans). The most often sighted seabird species were the Northern gannet followed by the Yellow-legged and the Lesser black-backed gulls and the Great skua, all of them sighted over the whole study area. The Razorbill, the Sandwich tern, the Mediterranean gull and the Balearic shearwater were sighted mainly over the western and south-western sector of the study area. The least sighted species were the Common guillemot (sighted sparsely over the study area) and the Manx shearwater for which the sightings were mainly concentrated over the western sector. The most often sighted cetacean species was the Short-beaked common and the Bottlenose dolphins followed by the Long-finned pilot whale. These three species were sighted over the whole study area, with the Short-beaked common dolphin being found specially over the western sector and the Bottlenose dolphin mainly over the eastern sector (see figures in Appendix C-Section 1).

Table 3.1. *Total effort, effort on good visibility conditions (Beaufort sea-state ≤ 5, wave height ≤ 2 m and medium to good general conditions), effort after removing segments of length ≤ 5 km and effort after removing segments with a depth > 1000 m for each year of the PELACUS survey.*

Year	Effort (km)	Filtering visibility conditions (km)	Filtering segments < 5 km (km)	Filtering depth > 1000 m (km)	Segments
2007	1695.91	1608.62	1522.95	1494.61	150
2008	2250.15	1506.56	1429.26	1387.16	145
2009	2908.02	2665.37	1786.83	1716.17	189
2010	3286.61	1784.68	977.26	903.29	98
2011	1338.21	1198.50	1153.20	1153.20	121
2012	2063.06	1124.70	1087.53	1087.54	108
2013	1835.80	1036.57	597.93	597.94	61
2014	1836.52	1387.51	1428.43	1397.24	145
2015	1857.08	1427.00	1367.69	1367.69	141
2016	1871.11	1263.52	1217.14	1207.52	130
Total	20942.47	15003.03	12583.24	12312.36	1288

3.2. Species detectability

Detections functions were estimated based on the sightings that remained after filtered for weather conditions. The best model for 4 species did not included any covariate (CDS) and included at least one covariate for 9 species (MCDS). The most selected covariates in the latter models were visibility (n=4) and Beaufort sea-state (n=4) either raw or categorized. Wave height was the next most selected covariate (n=3) followed by year (n=1) and general conditions (n=1) (Table 3.2). The average ESW was 240 m (CV=0.36) for seabird species and 550 m (CV=0.34) for cetacean species (Table 3.2).

The detectability based on biological traits assessed by analysing the relationships between the ESW and the biometry of the species showed a positive correlation between the increase of the ESW and the increase of the two variables tested, wingspan (p-value = 0.03, $R^2 = 0.45$) and bird size (p-value = 0.01, $R^2 = 0.55$) (Figure 3.3).

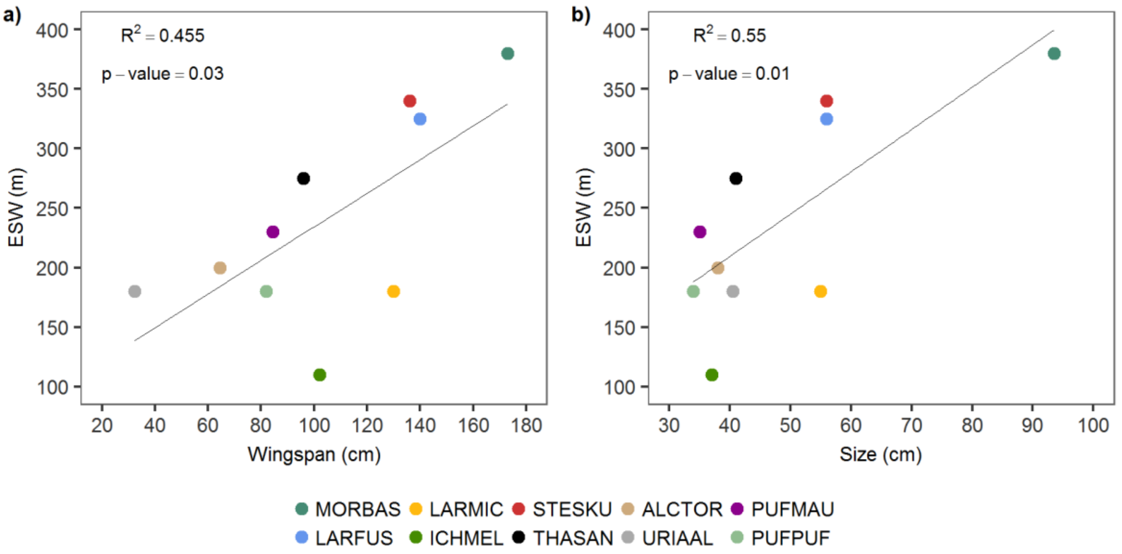

Figure 3.3. *Relationships between the effective strip-width (ESW) and seabird species' biometry data a) wingspan and b) bird size. The plots show the result of the linear regression models fitted for each explanatory variable. Acronyms of species are defined in Table 3.2.*

Table 3.2. Results of the best fitted detection functions for each species: Sightings (number of sightings used to fit the detection function); Model (type of model used to fit the detection function, MCDS: Multiple-Covariate Distance Sampling or CDS: Conventional Distance Sampling); Key (type of detection function, hr: hazard-rate or hn: half-normal); Detection covariate (environmental covariates used to fit the detection function); w (m) (truncation distance in meters); Pa (averaged detection probability); SE Pa (standard error of the detection probability); Mean ESW (averaged effective strip half-width obtained from the detection function) and CV ESW (coefficient of variation of the ESW).

	Family	Scientific name	Code	Sightings	Model	Key	Covariate	w (m)	Pa	SE Pa	Mean ESW (m)	CV ESW
Seabird	Sulidae	*Morus bassanus*	MORBAS	6440	MCDS	hr	visibility categorized general conditions	1000	0.37	0.01	380	0.21
	Laridae	*Larus fuscus*	LARFUS	1213	MCDS	hr	year visibility	1000	0.20	0.007	325	0.74
		Larus michahellis	LARMIC	1626	MCDS	hr	visibility	500	0.29	0.02	180	0.33
		Ichthyaetus melanocephalus	ICHMEL	45	MCDS	hn	wave height categorized	500	0.53	0.08	340	0.37
	Stercorariidae	*Stercorarius skua*	STESKU	334	MCDS	hr	Beaufort wave height categorized	600	0.41	0.04	275	0.19
	Sternidae	*Thalasseus sandvicensis*	THASAN	118	MCDS	hr	Beaufort categorized	800	0.20	0.05	200	0.34
	Alcidae	*Alca torda*	ALCTOR	128	CDS	hr		500	0.36	0.03	180	-
		Uria aalge	URIAAL	78	CDS	hr		300	0.35	0.09	110	-
	Procellariidae	*Puffinus mauretanicus*	PUFMAU	96	MCDS	hn	visibility categorized	500	0.44	0.04	230	0.18
		Puffinus	PUFPUF	66	CDS	hn		350	0.50	0.04	180	-
Cetacean	Delphinidae	*Delphinus delphis*	DELDEL	74	CDS	hr		1000	0.34	0.07	340	-
		Tursiops truncatus	TURTRU	93	MCDS	hn	Beaufort categorized wave height categorized	1300	0.40	0.07	700	0.34
		Globicephala melas	GLOMEL	69	MCDS	hn	Beaufort categorized	1500	0.30	0.07	620	0.13

3.3. *Spatio-temporal modelling of marine megafauna*

After filtering the effort and excluding segments < 5 km and segments with a depth > 1000 m, a total of 1288 segments were used to fit the density surface models (see Table 3.1). The number of models combined to achieve ≥ 0.95 of the cumulative sum of ω_i, starting with the model with the highest ω_i, ranged from 4 to 78 out of a total of 98. The most important predictors (*i.e.,* environmental covariates with importance > 50% for at least 5 species) describing the spatial abundances of the species were SST (n=7), DistSB (n=5), Chl-*a* (n=5) and logBAT (n=5) (Figure 3.4 and C-4.1). Those predictors that appear in all the models selected for the modelled species (*i.e.,* 100% importance) were SST (n=4), DistSB (n=2), Chl-*a* (n=1), logBAT (n=1) and DistCO (n=2). For seabird species, the most important variables describing their spatial abundance were SST, DistSB, logBAT and Chl-*a*, whilst in the case of cetaceans the main variables were SST, Chl-*a*, SLOPE and DistSB (Figure C-4.1). The Yellow-legged gull, the Razorbill, the Manx and the Balearic shearwaters showed preference for a strictly coastal habitat whilst the Lesser black-backed gull, the Mediterranean gull and the Great skua (mainly sighted preying on discards or kleptoparasiting other seabirds) showed preference for shelf and slope areas. Other species, such as the Sandwich tern, the Common guillemot, the Northern gannet and the Short-beaked common dolphin were classified as ubiquitous as they were widely dispersed over the whole study area. The Bottlenose dolphin and the Long-finned pilot whale were associated with the slope. Overall, the result of the relative quantitative index used to validate the models showed that the encounter rate and the predicted density were positive related (Figure C-4.2).

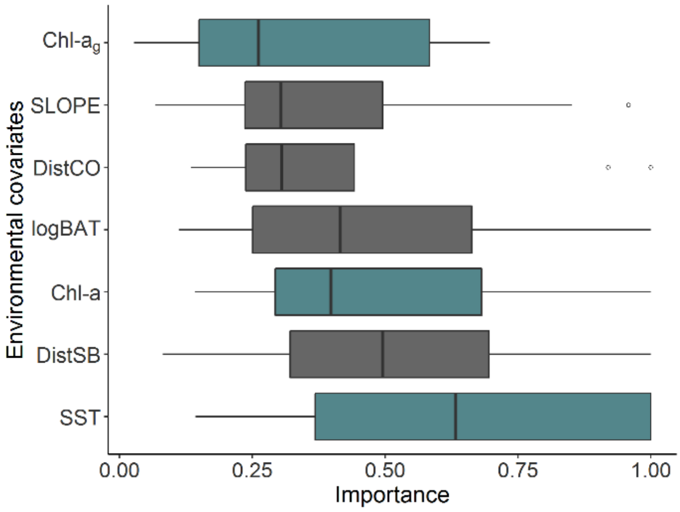

Figure 3.4. *Boxplot of the relative variable importance for each group of species. Dynamic variables (in green): sea surface temperature (SST), logarithm of Chlorophyll a concentration (Chl-a) and its spatial gradient (Chl-a$_g$) and static variables (in grey): closest distance to the shelf-break (DistSB), closest distance to the coast (DistCO), slope (SLOPE) and logarithm of depth (logBAT).*

3.4. *High-value biodiversity areas*

We identified the HVBAs based on the BRI calculated from the highest 40% of the species predicted abundance (Appendix C-Section 5). For cetaceans, the HVBAs (BRI = 3, *i.e.,* all the cetacean species analysed) were located over the western and NW shelf-break, Avilés and Capbreton canyons (Figure C-5.1). In the case of seabirds, the HVBAs were located over the Rías Baixas, NW coast, Ortegal headland, the Masma Gulf, El Cachucho and Landes Plateau. The seabirds' HVBA with the maximum value of BRI (BRI = 7, *i.e.,* 70% of the seabird species analysed) was located over the Rías Baixas (Figure C-5.2). For the megafauna community (cetacean and seabird species), the HVBAs with the maximum value of BRI (BRI = 8, *i.e.,* 61% of the species analysed) were located over the Rías Baixas and the western and NW shelf-break (Figure C-5.3). The HVBAs were stable over the whole time-series analysed (Figure 3.5) showing that the main habitats for cetaceans were located in the western and NW shelf-break (Figure 3.5a) whilst seabirds, were mainly concentrated on the Rías Baixas, the Ártabro and Masma Gulfs (Figure 3.5b). The HVBAs of the whole community (seabirds and cetaceans) were located over the western and NW Spanish waters and the Masma Gulf (Figure 3.5c).

3.5. *Environmental envelope*

The assessment of the geographical patterns in quantitative HVBAs by means of a nMDS plot (Figure C-5.4) showed three well differentiated groupings: (1) the sectors located on the eastern part of the study area, EC and CC; (2) sectors WC and NG, located on the centre and the NW part of the study area; and (c) sector SG, located on the south-western part of the study area. Results of the linear models showed a negative slope for 9 of the 13 analysed species indicating that quantitative HVBAs decreased from the SG towards the EC sectors.

The spatio-temporal modelling was used to discriminate which dynamic predictors could help explain the variability in biodiversity and could be considered as EOVs. Therefore, we defined as dynamic EOVs for the megafauna community analysed the SST and the Chl-*a* (*i.e.,* relative importance > 50% for at least 5 modelled species). Thus, plotting the mean BRI per sector and year as a function of the EOVs SST and Chl-*a* gave us an overall pattern (see Figure 6a) where higher SST and Chl-*a* corresponded to higher mean BRI. The highest values of mean BRI shaped the convex hull of the SG sector. The other four sectors (NG, WC, EC and CC) and their respective convex hulls revealed a similar pattern and were located together but separated from the SG sector. These four sectors showed less variability in the SST and Chl-*a* values among years; thus, their convex hulls were smaller than the convex hull defined by the SG sector.

Finally, a GAM was fitted using a tensor-product smooth function of the EOVs identified, *i.e.,* SST and Chl-*a*. The BRI was used as the response variable with a Gaussian link function. The model explained 72.3% of the deviance (approximate significance of smooth terms: edf = 10.8 and p-value < 0.001; AIC 42.5 units lower than the null model). The 3D smoothers obtained (Figure 3.6b) showed that maximum BRI corresponded to higher SST and Chl-*a* values The BRI was lower at mean values of SST and Chl-*a*.

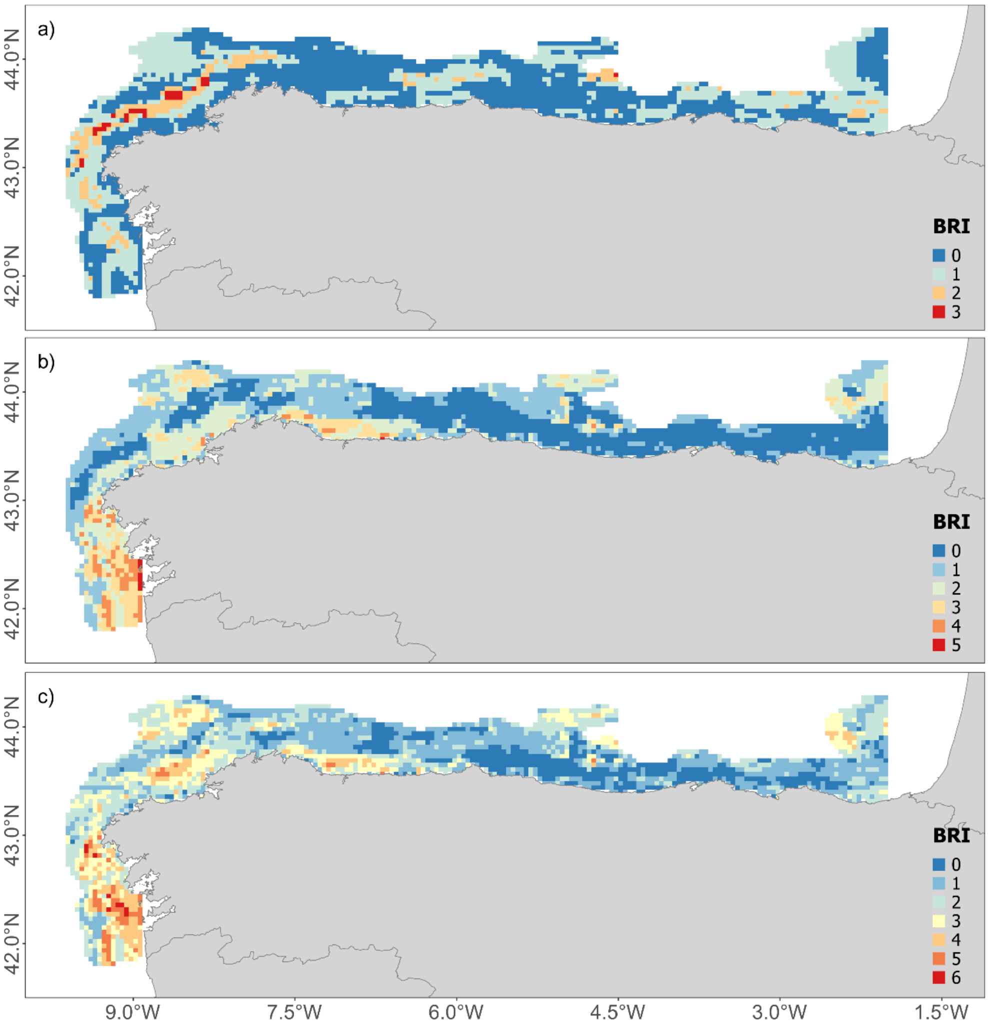

Figure 3.5. Maps showing the high-value biodiversity areas based on the mean biodiversity richness index (BRI) from the time-series 2007-2016 for a) cetaceans, b) seabirds and c) all the species together.

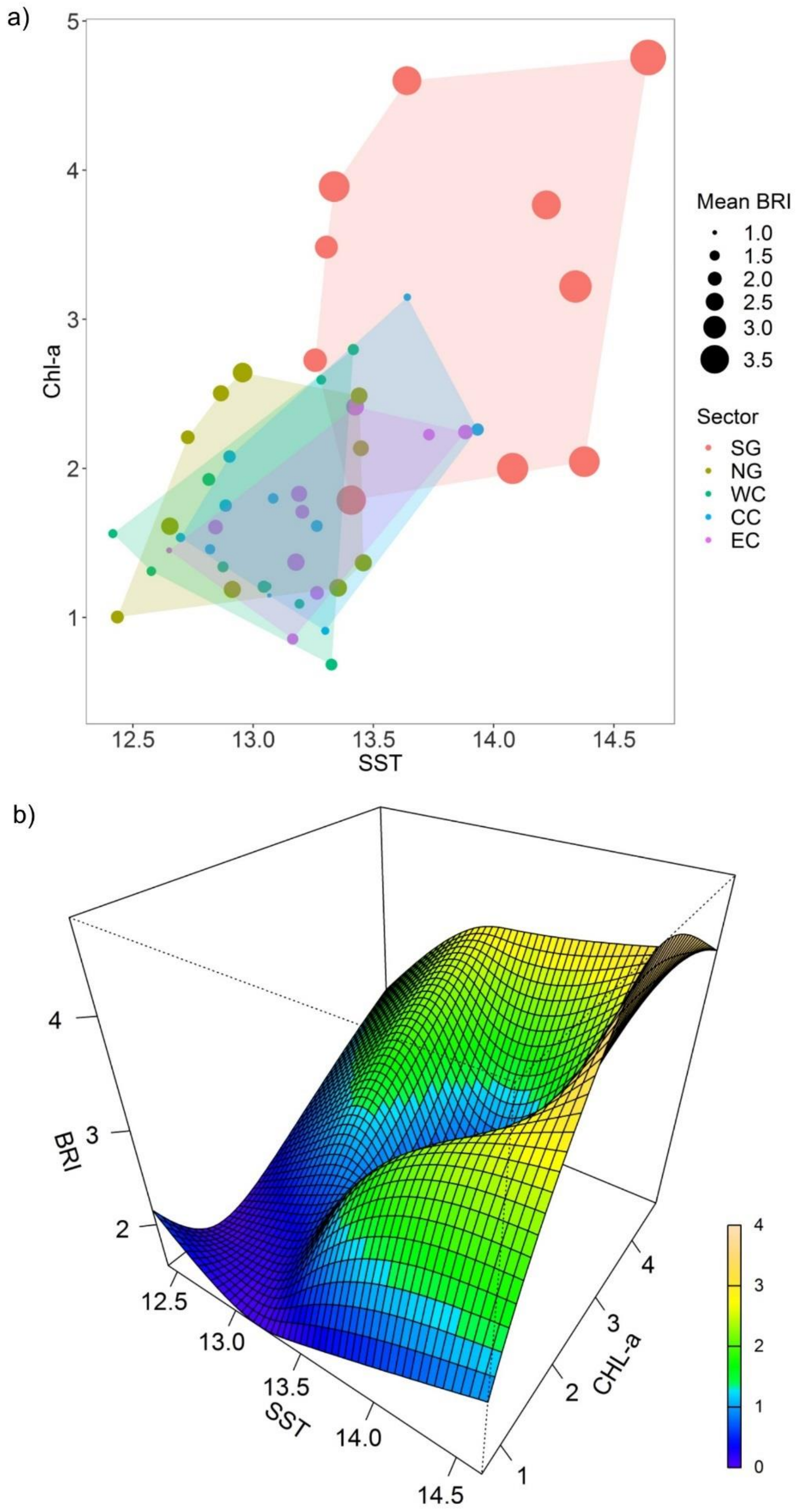

Figure 3.6. *Environmental envelope showing: a) mean biodiversity richness index (BRI) per sector and year according to the averaged values of SST and Chl-a per sector and year and b) three-dimensional Generalized Additive Model graphic output with the BRI as a function of SST and Chl-a.*

4. Discussion

We have described the spatial and temporal changes of high-value biodiversity areas for the seabird and cetacean community of the Northern and NW Iberian waters. By defining high diversity areas of marine megafauna, we have identified the EOVs shaping their environmental envelopes. This is one of the first studies that develop such an approach in this area, with other long-term studies documenting only the relative abundance of top predators (Authier et al., 2018) or describing their species-specific habitat preferences (Lambert et al., 2018).

4.1. Marine megafauna community and detectability

The Northern and NW Iberian waters are transition waters located between the boreal and subtropical environments where species of different biogeographic range converge (Andonegi et al., 2015; Valdés and Lavín, 2002). This region is a diversity hotspot area for multiple functional groups (Borja et al., 2018). In terms of the megafauna community composition, we considered the most sighted species, which included ten seabird species (ranging from the smaller Manx shearwater to the larger Northern gannet) and three cetacean species (the Short-beaked common dolphin, the Bottlenose dolphin and the Long-fined pilot whale). Our spatio-temporal modelling approach applied to marine megafauna abundance was based on the distance sampling methodology that allows to quantify detectability and measure the proportion of individuals that may be missed during line transects (Buckland et al., 2001). Although distance sampling analyses assume that all animals are detected on the transect line, at their initial location and that angle and radial distance are measured without error (Buckland et al., 2015), perfect detection on the transect line is unlikely due to perception, attraction and/or availability bias (*e.g.,* presence of animals below the surface) causing a possible measurement error of the radial distance and the angle (Authier et al., 2018). Additionally, other factors also influence animal detectability, such as the distance from the observer, the environmental conditions (*e.g.,* glare intensity, swell height), the time of day, the year (Gottschalk and Huettmann, 2011; Ronconi and Burger, 2009), the colour or the size of the species (Tasker et al., 1984; Van Der Meer and Camphuysen, 1996), etc. Species-specific detection functions allow us to capture the influence of species-specific biological traits on detection probability (Buckland et al., 2001). Few studies have quantified the relationship between species' biometry and effective sampling area (Barbraud and Thiebot, 2009). Although our models were not corrected for the abovementioned biases (*i.e.,* perception, attraction or availability bias) due to the absence of correction factors in the area (Certain et al., 2008; Virgili et al., 2018), our results suggest that there was an overall positive relationship between ESW and either the wingspan or the body size of the seabird species considered. Therefore, larger species such as the Northern gannet could be detected within a wider effective sampling area (and during a longer period), while smaller species such as the Manx and Balearic shearwaters, Mediterranean gulls, Razorbills and Common guillemots could only be detected within a smaller effective sampling area (and for a shorter period).

4.2. Environmental envelopes

Defining EOVs for a community implies identifying the most important overall predictors of distribution and abundance of the species that form that community. In our case, both physiographic and oceanographic descriptors were important drivers of the distribution patterns of the species considered. Specifically, the SST and the Chl-*a* concentration were the most important dynamic covariates, while the distance to the shelf-break was the most important physiographic descriptor. The importance of SST and Chl-*a* driving marine ecosystem functioning can be explained because they indicate the provision of nutrient-rich deep waters to the surface (*i.e.,* upwelling systems), planktonic productivity and phytoplankton blooms (Bode et al., 2009; Friedland et al., 2012). Variation in the SST and the Chl-*a* concentration are likely associated with prey retention, highlighting dense prey patches available to predators (Yen et al., 2004). Thus, these EOVs can shape the marine ecosystem from plankton, to mid-trophic level fish, up to apex predators such as seabirds and cetaceans (Lehodey et al., 2010). The response of the organisms to these EOVs differs across trophic levels, whilst lower-trophic levels (plankton) may be directly influenced by the SST and the Chl-*a* concentration, mid- and upper-trophic levels (from small pelagic fishes to apex predators) may respond to changes in prey caused by changes in the EOVs. Hence, the SST and the Chl-*a* concentration were highlighted as EOVs in line with results from other studies which have shown their importance in driving the large-scale patterns of marine megafauna (Grémillet et al., 2008; Whitehead et al., 2008).

Overall, marine megafauna abundance was positively influenced by both dynamic variables which define the environmental envelope shaping areas of higher density. Thus, HVBAs were associated with higher values of SST and Chl-*a* concentration shaping the specific environmental envelopes for the study period. These HVBAs were mainly located in the Western and NW area (SG and NG sectors) and decreased towards the inner BoB (from SG to EC sectors). The waters of the SG sector are highly productive due to a large phytoplankton bloom that develops over the shelf between March–April, starting gradually in coastal waters and progressively extending to the outer shelf and oceanic regions (Bode et al., 2003; Figueiras et al., 2002) caused by persistent northerly wind forcing. In addition, the strongest rivers runoffs that transport inland nutrients further offshore coincide with the onset of these northerly winds (Picado et al., 2016; Teles-Machado et al., 2016) increasing the Chl-a concentration over the area and creating a highly attractive and temporally stable oceanographic feature. Over our study period these areas showed a highly diverse marine megafauna community. Although upwelling areas are characterized by colder waters, the SST values of our study period (March-April) reached the highest values in the SG sector and decreased towards the eastern BoB (WC, CC and EC sectors). This phenomenon may be explained by the influence of the "Navidad" current, a prolongation of the poleward current, which inflows into the BoB around Cape Fisterra supplying warm waters along the NW shelf and slope. The influence of the "Navidad" current is evident until April (Pingree, 1994; Sánchez and Gil, 2000; Torres, 2003).

Secondly, HVBAs also extend into the NG sector over the shelf-break. This result is in line with previous studies which indicated that continental shelf-breaks appear to be highly productive habitats, which frequently support high densities of marine predators (Certain et al., 2008; Lambert et al., 2017a). Due to the site-specific oceanographic features over these areas, zooplankton often aggregates close to the surface making prey available to diving predators (Certain et al., 2008; Croll et al., 1998). Both, the SG and NG sectors showed higher values of biodiversity concurring with the fishing grounds of a large bottom-trawling fleet operating in the shelf and upper slopes (Valeiras, 2003). This fishing activity provides also food for many seabird species (Depestele et al., 2016; Valeiras, 2003).

4.3. Implications of the EOVs for the conservation of the HVBAs

The underlying relationship between EOVs and specific biological communities could justify the long-term monitoring of EOVs (Constable et al., 2016). Analysis of temporal and spatial variability in EOVs could help identify areas of persistent dynamic oceanographic features (Louzao et al., 2012) that create relatively stable habitat associations of upper-trophic marine predators and serve to locate HVBAs (Lambert et al., 2018). Monitoring EOVs will therefore support spatially dynamic ocean management (Hobday et al., 2014).

An additional advantage of the monitoring of EOVs would be the detection of changes resulting from specific anthropogenic pressures (Constable et al., 2016) or the forecasting of the response of the species or communities in the face of climate change. In fact, the location of the primary HVBAs matches with the area which has the highest number of fishing vessels (≈ 4200 to date; https://www.pescadegalicia.gal/rexbuque/) and where the highest amount of their catches is landed, making the area one of the main fishing regions at European and worldwide scales (Vázquez-Rowe et al., 2011). Most of the fishing gears used in this area, such as pelagic or bottom trawl nets, gillnets or longlines, pose a risk of bycatch for large marine vertebrates, such as seabirds and cetaceans (Goetz et al., 2015; Rodríguez et al., 2013; Saavedra et al., 2018). HVBAs could help identify areas with the highest risks of interactions guiding where to concentrate management and conservation efforts especially aimed at marine megafauna.

This study provides an example of the monitoring of EOVs and the biodiversity of marine megafauna communities along with the extent of HVBAs. Studies like ours will assist scientists, managers and policy makers forecast and prepare for a possible redistribution of species due to climate change or other pressures and its ecological, social and economic consequences (Miloslavich et al., 2018). In addition, the identification of a quantitative index such as the HVBAs is crucial in order to quantify gaps in the coverage of the present protected areas network as recent works has demonstrated (García-Barón et al., 2019a; Lambert et al., 2017b). HVBAs may help to identify whether the current network of protected areas (*e.g.,* Natura 2000 network) need to be expanded, particularly in the context of climate change. These types of studies are important to fulfil the emergent need on sound spatial information to support marine spatial planning approaches and are needed to improve the management and conservation of the marine megafauna species and/or communities at their key areas (IPBES, 2019).

CHAPTER 4

Modelling the spatial abundance of a migratory predator: a call for transboundary marine protected areas

ABSTRACT

During their migration, highly mobile species cross multiple jurisdictional boundaries and multiple not-specific marine protected areas (MPAs). When identifying the critical habitats where individuals aggregate, these areas can be ideal candidates for MPAs. This study was focused on the endangered Fin whale (*Balaenoptera physalus*) for which there is little knowledge on its distribution and abundance in non-breeding temperate latitudes. Firstly, we modelled the relative abundance of Fin whales in the Bay of Biscay by means of generalized additive models (GAMs) using data collected on the PELACUS (2007–2008) and JUVENA (2013–2016) oceanographic surveys during late summer. Secondly, we evaluated the reliability of the predictions by distinguishing environmental extrapolations and interpolations. Finally, we identified critical areas of highest predicted abundance and we assessed whether existing MPAs comprised within the Natura 2000 network and designated for other species offer protection to Fin whales in the Bay of Biscay. Fin whales were especially abundant in deep offshore waters, mainly associated with intermediate temperature water values in the inner part of the Bay of Biscay. The years with the highest relative predicted abundances (an average of 1,500 whales) matched with years when warmer sea surface temperature extended into larger areas. In colder years, the average predicted abundance dropped to 400 whales. The main critical area for Fin whales (defined by the highest 40% of abundance) was common for both surveys, and it was located in the south-eastern part of the Bay of Biscay. Our study contributes to the identification of important concentration areas of Fin whales during late summer, based on reliable spatial predictions. The assessment of the current Natura 2000 network highlights the fact that only three MPAs marginally covered the critical area we have identified for Fin whales. We propose a transboundary potential MPA to aid the conservation of the species in the Bay of Biscay.

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1. Introduction

Wide-ranging animals perform annual migratory movements in search of foraging areas to overcome energetic limitation during certain periods of the year (Edwards et al., 2015; Silva et al., 2013). Migratory species use environmental cues to locate prey fields, and inter-annual differences in distribution and abundance patterns are a consequence of environmental variability (Stern, 2009). The marine environment is a highly dynamic system where different oceanographic processes influence the distribution of prey and their predators (Mann and Lazier, 2013; Sims et al., 2008). Specifically, mesoscale oceanographic features such as fronts, eddies and upwelling events are important processes that can drive the foraging locations of highly migratory oceanic species (*e.g.,* Bost et al., 2009).

The management and conservation of highly migratory species faces particular challenges since animals cross multiple jurisdictional boundaries (Lascelles et al., 2014). One initial step to advance in their conservation and management would be to delineate candidate protected marine areas for highly migratory species, by identifying high abundance areas that are visited every year (Lascelles et al., 2014). Statistical tools such as habitat modelling can help identify areas with the highest presence probability or higher abundance of a species during critical periods (Maite Louzao et al., 2011; Pérez-Jorge et al., 2015). The dynamic nature of the marine environment needs to be considered when designing and implementing Marine Protected Areas (MPAs): understanding how oceanographic processes influence marine vertebrate distribution is essential for effective conservation (Hooker et al., 2011). MPAs delimited by fixed geographical boundaries might not have the capacity to cover the habitat requirements of the species (Lascelles et al., 2012), and consequently a flexible design approach adapted to overlap the life history traits of the species and the pelagic environment will require implementing dynamic MPAs (Hooker et al., 2011).

Among highly migratory species, baleen whales are of special conservation and management interest since they were commercially hunted until almost forty years ago (Stoett, 2011). For instance, Fin whale *Balaenoptera physalus* populations were reduced by 70% during the commercial whaling era (Brownell and Yablokov, 2009; Buckland et al., 1992). Since the International Whaling Commission's (IWC) moratorium on commercial whaling (Stoett, 2011), Fin whale populations have increased (Víkingsson et al., 2009). However, they remain classified as Endangered (IUCN, 2013) in need of appropriate management measures to ensure the recovery of the populations (Edwards et al., 2015).

In Europe, the Habitats Directive (HD, Council Directive 92/43/EEC) requires that each Member State set up Special Areas of Conservation (SACs) for those species listed under Annex II which for cetaceans includes only Harbour porpoise, *Phoconea phocoena* and the Bottlenose dolphin *Tursiops truncatus*. Together, these areas, will constitute a network of protected sites across the European Union (EU), called the Natura 2000 network (Trouwborst, 2011). However, the HD Annex II is insufficiently representative of marine species in need of conservation (Trouwborst and Dotinga, 2011). The Marine Strategy Framework Directive (MSFD, 2008/56/EC), which aims at achieving and maintaining the Good Environmental Status (GES) of EU marine ecosystems by 2020, addresses some shortcomings of the HD (Trouwborst and Dotinga, 2011). MSFD requires Member States to monitor progress towards GES and set up appropriate measures to restore GES if needed. Such measures may include setting up MPAs for species not listed under the HD Annex II (Trouwborst and Dotinga, 2011), such as the Fin whale which is endangered (IUCN, 2013) worldwide and have been listed in the Annex IV of the HD as species of Community interest. Besides, Fin whales are listed in the Appendix I of the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES[1]), Appendix I and II of the Convention on the Conservation of Migratory Species of Wild Animals (CMS[2]) Appendix II of the Bern Convention and they are recognized by the Ecologically or Biologically Significant Marine Areas (EBSAs[3]) under the criteria of threatened, endangered or declining species. Since Fin whales requires strict protection, the designation of MPAs that include appropriate management measures to minimise/eliminate the anthropogenic threats whales are facing is required although the species is not specifically listed in the Annex II of the HD.

Fin whales are widely distributed in the North Atlantic (NA), spending the summer in high-latitude feeding grounds and breeding in middle and low-latitudes during winter (Edwards et al., 2015). Their migratory patterns remain unclear and not all individuals migrate seasonally: some individuals remain in higher latitudes during colder months and in lower latitudes during warmer months (Edwards et al., 2015). Lack of detailed knowledge about their migratory patterns partly stems from most research taking place in non-breeding high latitudes areas, while temperate latitudes have been less studied (Mizroch et al., 2009). Fin whale population structure in the NA is similarly poorly known, though recent studies suggest the existence of two subpopulations (Vighi et al., 2015). Fin whales present in the BoB are part of the British Isles-Spain-Portugal subpopulation, with an estimated abundance of 17,400 individuals in Aguilar and García-Vernet, 2017. Presumably, Fin whales occupy the

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1 https://www.cites.org/eng/app/index.php
2 https://www.cms.int/en/page/appendix-i-ii-cms
3 https://www.cbd.int/ebsa

BoB during the spring-autumn period, but only sparse information is available on their distribution and abundance in this temperate biogeographic area.

Given the oceanic habitat of the species, dedicated surveys are costly and logistically difficult to organise; thus, their periodicity to date has been decadal (*e.g.*, SCANS; Hammond et al., 2017 and CODA; Hammond et al., 2009). Marine mammal sightings can also be obtained from other non-dedicated monitoring schemes, such as oceanographic surveys directed at assessing the status of the stocks of commercial fish species, which cover the same geographic area every year with standardised methodology (Lambert et al., 2018; Saavedra et al., 2018). Within this framework, we took advantage of JUVENA (Boyra et al., 2013) and PELACUS (ICES, 2009) annual multidisciplinary oceanographic surveys that every September monitor the pelagic environment of the BoB.

The main objective of the present chapter was to obtain relative spatial abundance estimates of the endangered Fin whale to assess critical conservation areas in the BoB. Specifically, (1) we explored the oceanographic and physiographic features explaining the observed patterns of Fin whale abundance, (2) we obtained spatial predictions of Fin whale density, (3) we identified critical areas within the 6-years study period and (4) we assessed the relevance of the Natura 2000 network for Fin whales of both Spanish and French waters. Our spatial modelling approach relies on Generalized Additive Models to predict marine mammal spatial abundance and on Model Averaging to account for model uncertainty, a rarely used method to model marine mammal spatial abundance. In addition, we assessed the reliability of predictions by carefully distinguishing environmental extrapolations and interpolations. The present study exemplifies a methodological approach to obtain spatial abundance estimates of marine animals sampled following non-dedicated line-transect surveys and provides an assessment of the importance of existing MPAs for the protection of an endangered highly migratory predator.

2. Material and Methods

2.1. Data collection

At-sea observations were collected during PELACUS and JUVENA multidisciplinary surveys that took place in the BoB yearly during late summer (September) in 2007-2008 on board *R/V Thalassa* (TH) and 2013-2016 on board *R/V Ramón Margalef* (RM), respectively (Figure 4.1). Visual line-transect protocols (Buckland et al., 2001) were followed during all surveys. For each sighting, top predator observers recorded detection distance using a stick based on the Heinemann (1981) method and the angle based on an angle meter and measured with respect to the track line. Additional data recorded for each sighting was the time, species, group size, animal heading relative to the ship, behaviour and the presence of calves. The surveys' protocol and a schematic workflow of the entire analytical process are included in the Appendix D-Section 1 and 2, respectively.

2.2. Detection function modelling

Detection functions were estimated pooling Fin whale sightings from the six years. Only sightings with a Beaufort sea-state ≤ 5, wave height ≤ 2 m and overall medium and good visibility conditions were used. Perpendicular distances were truncated to exclude sightings beyond 4000 m (around 5% of the individuals detected at the longest distances; Buckland et al., 2001). We used Conventional Distance Sampling (CDS) and Multiple-Covariate Distance Sampling (MCDS; Marques and Buckland, 2004) using the '*mrds*' R-package (Laake et al., 2015). Covariates tested in the MCDS analyses included group size as continuous variable and Beaufort sea-state, cloud cover, year, wave height and type of vessel as factor variables. The long period that Fin whales remain at the surface and the high visibility of their blows make them easily detectable. This fact justifies the assumption that detection on the track line is close to 100%, *i.e.,* $g(0) = 1$ (Hammond et al., 2017) however, we have not formally corrected for availability and perception bias and consequently the abundance estimates should be considered relative. We selected the model specification that resulted in the smallest value of the Akaike Information Criterion (AIC) and by comparing the p-value of the Cramér-von Mises goodness of fit test statistics (Thomas et al., 2010). Detection function selection was made on parsimony grounds (*i.e.,* similar explicative power but less parameters; Arnold, 2010) when the two best detection functions remained within a difference of AIC of 2 (ΔAIC < 2). Once the best detection function was selected, the effective strip half-width (ESW) was calculated for each level of the covariate as the perpendicular distance in which the missing detections at lower distances were equal to the recorded detections at higher distances.

2.3. Data processing

Surveyed transects were split into legs of identical detection conditions, then each leg was subdivided in 10 km-long segments, so the variability in environmental characteristics was limited within segments (Mannocci et al., 2014; Virgili et al., 2017). To fit the models on the best quality data, we kept only segments with a Beaufort sea-state ≤ 5, wave height ≤ 2 m and overall medium and good visibility conditions. For every segment we summed up the group size of each Fin whale sightings (Table 4.1). The mid-point of each segment was used to assign the environmental data to the segments.

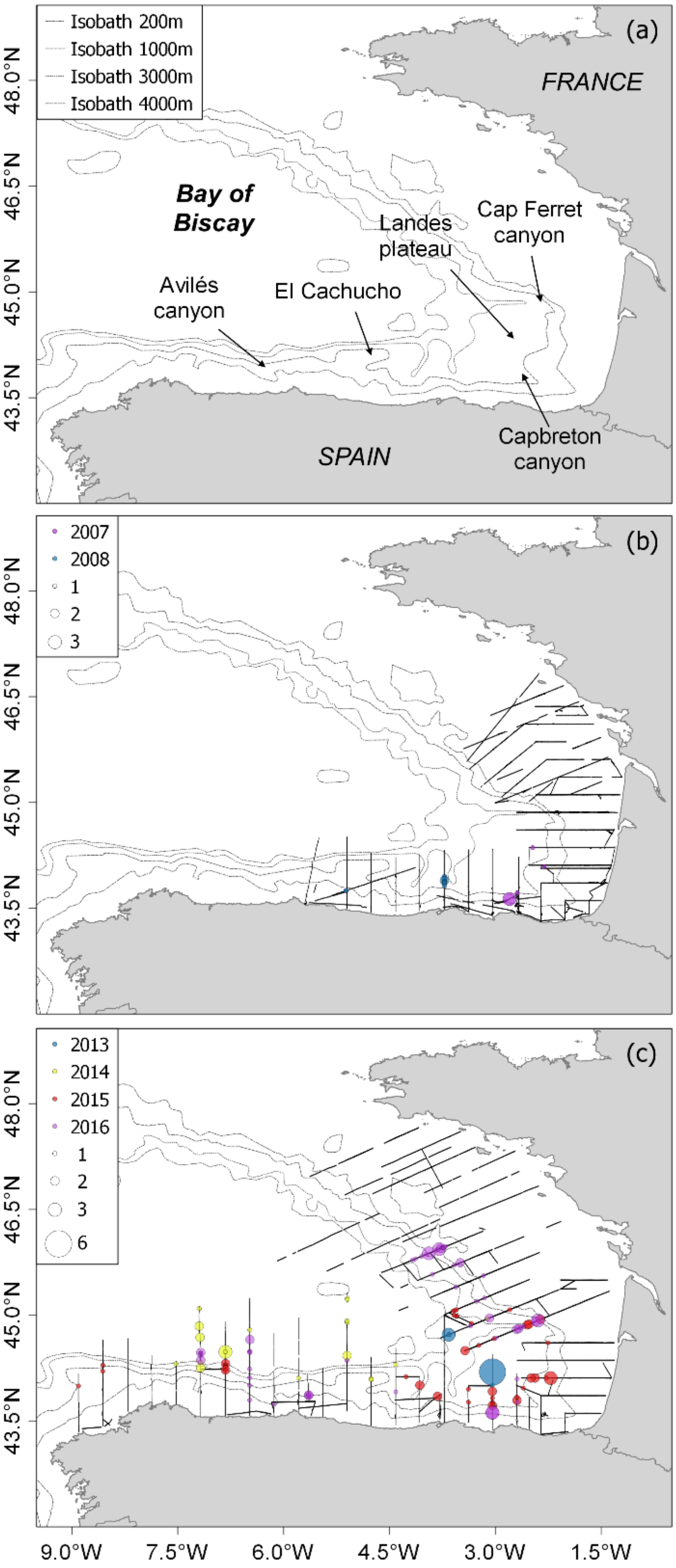

Figure 4.1. Map of the study area showing (a) geographical names and line-transect surveys (grey lines) with Fin whale sightings by size and year during (b) PELACUS and (c) JUVENA surveys.

Table 4.1. *Effort, filtered effort (Beaufort sea-state ≤5, wave height ≤2 m and medium to good general conditions), number of sightings, number of individuals, mean group size and coefficient of variation, encounter rate, total number of segments and number of segments with sightings of Fin whales for each survey and year.*

Survey	Year	Effort (km)	Filtered effort (km)	Sightings	Individuals	Mean group size (CV)	Encounter rate ($ind \cdot km^{-1}$)	Segments	Sightings' segments
PELACUS	2007	3315	2310	11	12	1.09 (27%)	0.005	396	8
	2008	2265	1560	4	6	1.50 (66%)	0.004		
JUVENA	2013	2166	1555	4	11	2.75 (86%)	0.007	962	78
	2014	2630	1845	19	25	1.32 (44%)	0.010		
	2015	2550	2261	44	59	1.34 (40%)	0.020		
	2016	2286	2170	55	74	1.37 (47%)	0.025		

2.4. Density surface models

Density surface models were fitted using Generalized Additive Models (GAMs) to identify the most important environmental variables explaining Fin whale abundance patterns (*i.e.,* to relate the number of Fin whales per segment to environmental covariates; Table 4.2). To account for overdispersion in the data, we selected a negative binomial distribution. The logarithm of the effective sampled area (L*2*ESW where L is the length of the segment in km) was included as an offset. To limit the scope for over-fitting the data, smoothers in the models were constrained to a maximum of 3 degrees of freedom (k=4) and a maximum number of four covariates was used (Lambert et al., 2017a). Prior to modelling, all variables were standardized to have a mean of 0 and a standard deviation of 1 due to differing ranges of variables (Zuur et al., 2007). To avoid co-linearity problems, we calculated pairwise Spearman correlation coefficients (r) between all pairs of variables and did not include variables with $|r| > |0.7|$ (Dormann et al., 2013). We selected the 'non-correlated' predictors using the lowest Akaike Information Criteria (AIC) from univariate models of the two predictor variables. This analysis led to the removal of the closest distance to the 1000 m-isobath and the modulus of the geostrophic currents (w), correlated to 2000 m-isobath and Eddy Kinetic Energy (EKE), respectively (Table D5.1).

GAMs were implemented following the Information-Theoretic framework using the *dredge* command of the *'MuMIn'* R-package (Barton, 2016). We then ranked the models using their AIC value corrected for small sample sizes (AICc) and we calculated the Akaike weight (ω_i) for each model (Burnham and Anderson, 2002). Incorporating all possible explanatory variables produce a large number of models: if no clear top model was identified (*i.e.,* $\omega_i > 0.90$) a model averaging procedure was used instead to account for all models and parameters uncertainty (Burnham and Anderson, 2002). Therefore, to obtain averaged coefficients and variance estimator, we used a model averaging approach from the top set of models where the cumulative sum of ω_i was ≥ 0.95, starting with the model with the highest ω_i (Johnson and Omland, 2004). Finally, we measured the relative variable importance as the sum of the ω_i of the models in which the predictor was included (Burnham and Anderson, 2002). We used the resulting averaged model to compute the spatial predictions for each year on a 0.04° x 0.04° resolution grid of covariates. This procedure provided maps of Fin whale density per year.

Overall Fin whale relative abundance (N) was calculated for each year by summing the values resulting of multiplying the predicted density for each cell ($\widehat{D}$) by the cell area (A) over the whole study area (Eq. 1). Furthermore, 95% confidence interval was calculated assuming a positively skewed distribution of $\hat{D}$ following the equations 2, 3 and 4.

$$N = \sum_i^n \hat{D}_i A_i \qquad \text{(Eq. 1)}$$

$$\left(\hat{D}/C \, , \, \hat{D} \cdot C \right) \qquad \text{(Eq. 2)}$$

$$\text{where: } C = \exp\left[1.96 \cdot \sqrt{\widehat{var}\left(\log_e \hat{D}\right)}\right] \qquad \text{(Eq. 3)}$$

$$\text{and: } \widehat{var}\left(\log_e \hat{D}\right) = \log_e \left[1 + \frac{\widehat{var}(\hat{D})}{\hat{D}^2}\right] \qquad \text{(Eq. 4)}$$

Table 4.2. Environmental covariates used for spatial density modelling of Fin whales in the Bay of Biscay, their units, resolution and source. ETOPO1 (Amante and Eakins, 2009, https://www.ngdc.noaa.gov/) was used to compute all the physiographic variables. Aqua MODIS satellite products from the web source ERDDAP (Simons, 2016) were used to compute SST and Chl-a and their gradients. The AVISO product from Copernicus Marine Environment Monitoring Service (http://marine.copernicus.eu/) was used to compute the Geostrophic current modulus, Eddy Kinetic Energy and Sea Level Anomalies.

Type	Environmental covariate	Units	Acronyms	Resolution	Source
Physiographic	Depth	m	BAT	0.04°	ETOPO1
	Slope	degrees	BAT_g		
	Closest distance to the coast	m	DisCO		
	Closest distance to the self-break	m	DisSB		
	Closest distance to the 1000 m-isobath	m	Dist1		
	Closest distance to the 2000 m-isobath	m	Dist2		
Oceanographic	Mean SST	°C	SST	0.04°	Aqua MODIS
	Mean gradient SST	°C	SST_g	0.04°	Aqua MODIS
	Modulus of the Geostrophic currents	cm/s	w	0.25°	AVISO
	Eddy Kinetic Energy	cm^2/s^2	EKE	0.25°	AVISO
	Sea Level Anomalies	m	SLA	0.25°	AVISO
	Mean Chlorophyll a	mg/m^3	Chl-a	0.04°	Aqua MODIS
	Chlorophyll a mean gradient	mg/m^3	$Chl\text{-}a_g$	0.04°	Aqua MODIS

2.5. Spatial prediction reliability

We assessed spatial prediction reliability by quantifying whether a prediction was an inter- or an extrapolation in environmental space, which amounts to testing whether the combination of environmental variable values associated with the prediction lies inside or outside the smallest convex hull defined by the environmental variables used when calibrating (*i.e.,* estimating) the model (Authier et al., 2017; King and Zeng, 2006). Importantly, assessing convex hulls does not require any model fitting: the definition of an environmental extrapolation is thus model independent. In the simple case of two environmental variables, a convex hull is the polygon with vertices at the extreme points of the data (see Appendix S6). When a prediction falls outside the convex hull, it is an extrapolation *stricto sensu*, but can be still informed by any data point lying within a given radius of the prediction here chosen as one geometric mean Gower's distance of all pairs of available data points (King and Zeng, 2007).

Since we used model averaging, extrapolation was estimated as the average frequency across models included the 95% confidence set with which each prediction was an extrapolation *stricto sensu*. For each prediction, its neighbourhood (in percentage) was estimated as the average proportion of calibration data points in environmental space lying within one geometric mean Gower's distance (Gower, 1971; King and Zeng, 2007). Reliable predictions (less model-dependent) were defined by a low percentage of extrapolation and a high percentage of neighbourhood (defined as the percentage of calibration data used to inform neighbouring cells), whilst a high percentage of extrapolation and a low percentage of neighbourhood indicate that predictions are less trustworthy. Reliability thus defined reflects how much a prediction is informed by actual data versus modelled inferences. Thus, place more confidence in a prediction that is informed by a lot of data than in a prediction that is not, although both may turn out to be correct if the model used for the prediction captures accurately the underlying relationships between the covariates and the response variable (whale abundance in our case). We used the R-package '*WhatIf*' (Stoll et al., 2014) to calculate the convex hull and Gower`s distances.

2.6. Critical areas of Fin whales in the Bay of Biscay

Since this species requires strict protection, we assessed whether existing MPAs within the Natura 2000 network could be relevant to aid in their conservation in the BoB. MPA designation should be accompanied by the implementation of appropriate management measures that minimise/eliminate the anthropogenic threats faced by the species in the area, but to carry out this exercise, we followed the thresholds proposed by the European Commission (Hab. 97/2 rev. 4 18/11/97): a site was considered relevant if encompasses more than 1% of the national population. Whether a national protected area network contains less than 20% of the national population (*i.e.,* individuals belonging to the focal species present within the national territory) is considered *inadequate*, whilst a network which covers more than 60% of the national population would be considered *sufficient*. Lastly, a network that covers between 20% and 60% of the national population is considered *adequate,* although they are to be subjected to further expert judgement (European Commission, 2007). Although, our study area only covers the Northern Spanish and Western French waters of the BoB, we still used the term 'national population' because it is the one used by the European Commission to apply the thresholds to assess the Natura 2000 network. Furthermore, this term does not consider the importance of biogeographical populations or conservations units as it is the case of our study area which includes the British Isles-Spain-Portugal Fin whale subpopulation (IWC, 2007). Therefore, the term 'national population' of the present study refers separately to Spanish and French sectors of the BoB.

We first identified marine areas of highest predicted abundance estimates as critical areas. Areas of highest abundances were calculated based on the averaged abundance values predicted for each survey and, therefore, different years were considered (PELACUS: 2007-2008 and JUVENA 2013-2016). For each survey, we sorted all grid cells by their decreasing estimate of mean abundance. We then transformed the numerical estimated averaged abundance in a relative index of abundance in terms of percentage by steps of 10%, ranging from the minimum value (0) to the maximum value over the study period (100%) over the whole study area (Cañadas and Vázquez, 2014). Critical areas comprising the highest abundance were defined by the highest 40% of predicted abundance. Secondly, we overlapped the average Fin whale abundance per survey with the location of existing MPAs included in both Spanish and French Special Areas of Conservation. The location of current MPAs was obtained from the World Database on Protected Areas (UNEP-WCMC and IUCN, 2017). We identified an additional Large Off-shore Sector belonging to the French Economic Exclusive Zone (EEZ), which at the time of conducting this study was under designation process (Agence des Aires Marines Protégées, 2016).

3. Results

3.1. Detection function modelling

We estimated detection functions based on 137 Fin whale sightings after filtering for weather conditions. The hazard-rate function with no adjustment terms and vessel identity as covariate was selected as the best-fitting detection function (Figure D-6.1). Although this was not the model with the lowest AIC value (all the models tested are shown in Table D-6.1), it remained within a difference of AIC of 2 (ΔAIC < 2) and it was preferred on parsimony grounds. From the detection function selected, we calculated the corresponding effective strip half-widths (ESW) for Fin whales as 2050 m (CV=7%) for the RM (JUVENA) and 2680 m (CV=13%) for the TH (PELACUS).

3.2. Density surface models

After excluding segments with missing environmental predictors, a total of 1 252 segments of which 85 segments included 183 individual Fin whales were used to fit density surface models (Table 4.1). The number of models combined to achieve the 95% confidence set was 26 out of a total of 561 (Table D-7.1.). Explained deviances ranged between 32.3 and 37.4%. Effective degrees of freedom of smooth terms in the confidence set of models show that the relationship between the explanatory variables and the Fin whale density were nonlinear (estimated degrees of freedom > 1). BAT, SST, SLA and Chl-a_g were the most important variables describing the spatial abundance of Fin whales and those included in the top ranked GAM as explanatory variables (Figure 4.2a). Densities of Fin whale increased at depths (BAT) higher than 1000 m with maximum values around 2000 m depth, that is beyond the continental shelf (Figure 4.2b). The SST ranged between 16ºC and 24ºC, showing the highest densities around 20ºC, whereas densities increased within a positive SLA range (Figure 4.2b). Chl-a_g values showed a negative effect, since Fin whale densities decreased as the Chl-a_g values increased (Figure 4.2b).

Estimated relative density predictions were higher in the south-eastern part of the BoB (SE-BoB) within the Capbreton and Cap-Ferret canyons, and off the French and Spanish continental slopes associated with deeper waters (Figure 4.3). Whilst in 2013, 2014 and 2016 the highest relative densities of Fin whales were found in the abyssal plain, in 2007, 2008 and 2015 the highest densities were concentrated in the SE-BoB. The lowest predicted relative densities were identified recurrently every year over both the French and Spanish continental shelves.

The averaged relative estimated density varied from $7 \cdot 10^{-4}$ to $4 \cdot 10^{-3}$ Fin whales·km^{-2}, with total predicted relative abundances ranging from 291 to 1735 Fin whales. Annual density and abundance estimates are shown in Table 4.3. When the predicted high abundance habitats included the abyssal plain (2013, 2014 and 2016), relative abundance values were higher than 1200 whales (1241 - 1600). The remaining years the abundance values were much lower, ranging between 291 and 610 animals.

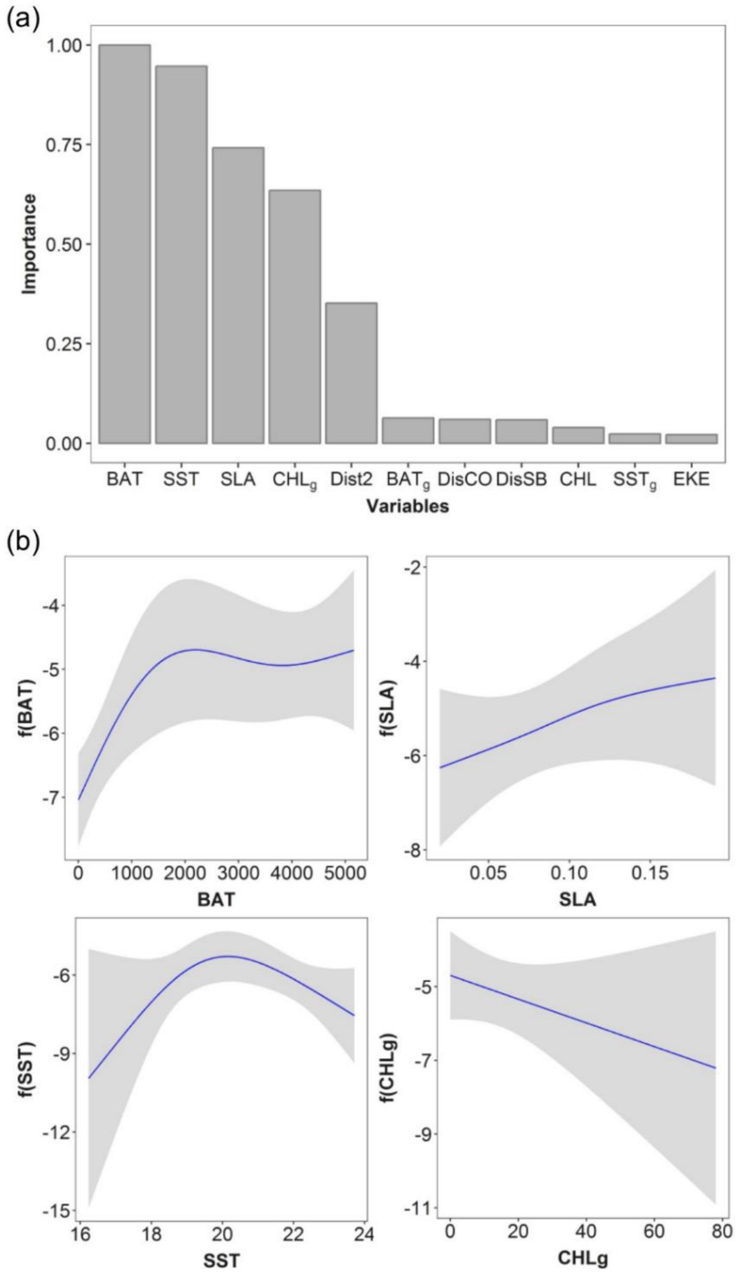

Figure 4.2. Main environmental variables driving Fin whale abundance patterns characterized by means of (a) relative variable importance and (b) smoothed fits of the main covariates. The x-axis shows the predictor variable values. The y-axis represents the centred smooth term contribution to the model on the scale of the linear predictor. Grey shaded area indicates approximate 95% confidence bounds. See Table 4.2 for variable description.

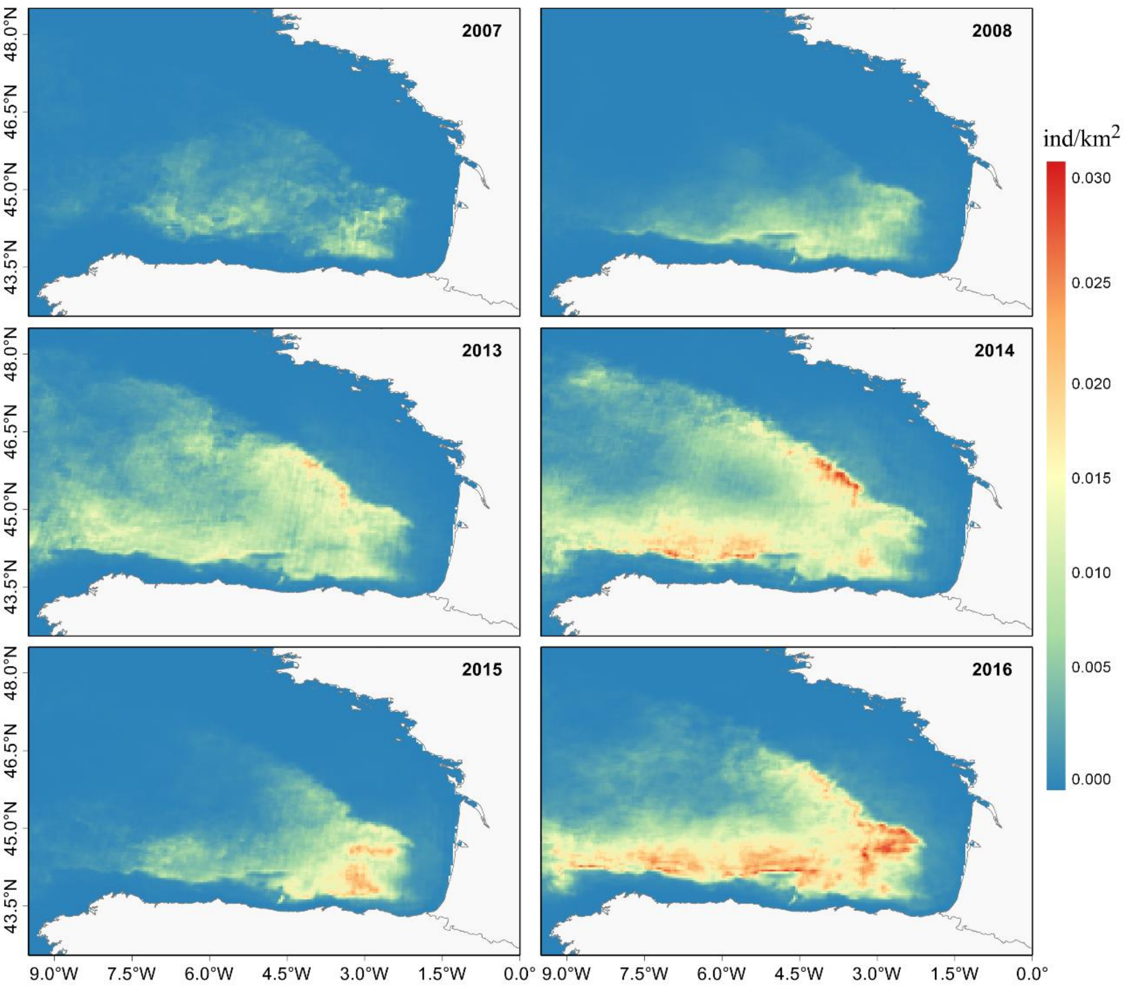

Figure 4.3. Fin whale spatial density predictions in the Bay of Biscay during PELACUS (2007–2008) and JUVENA (2013–2016) surveys. Geographical references are located in Figure 4.1.

Table 4.3. Abundance estimates for Fin whales in the Bay of Biscay for the 6-years study period. Averaged animal density (D, individuals·km^{-2}) and its coefficient of variation (CV_D), estimated abundance (N) and its 95% Confidence Interval (95% CI_N).

Year	D	CV_D	N	95% CI_N
2007	0.0007	0.89	291	65 – 1,310
2008	0.0010	0.66	387	118 – 1,267
2013	0.0030	0.63	1,241	395 – 3,901
2014	0.0045	0.54	1,735	638 – 4,718
2015	0.0010	0.61	610	201 – 1,853
2016	0.0040	0.58	1,600	551 – 4,641

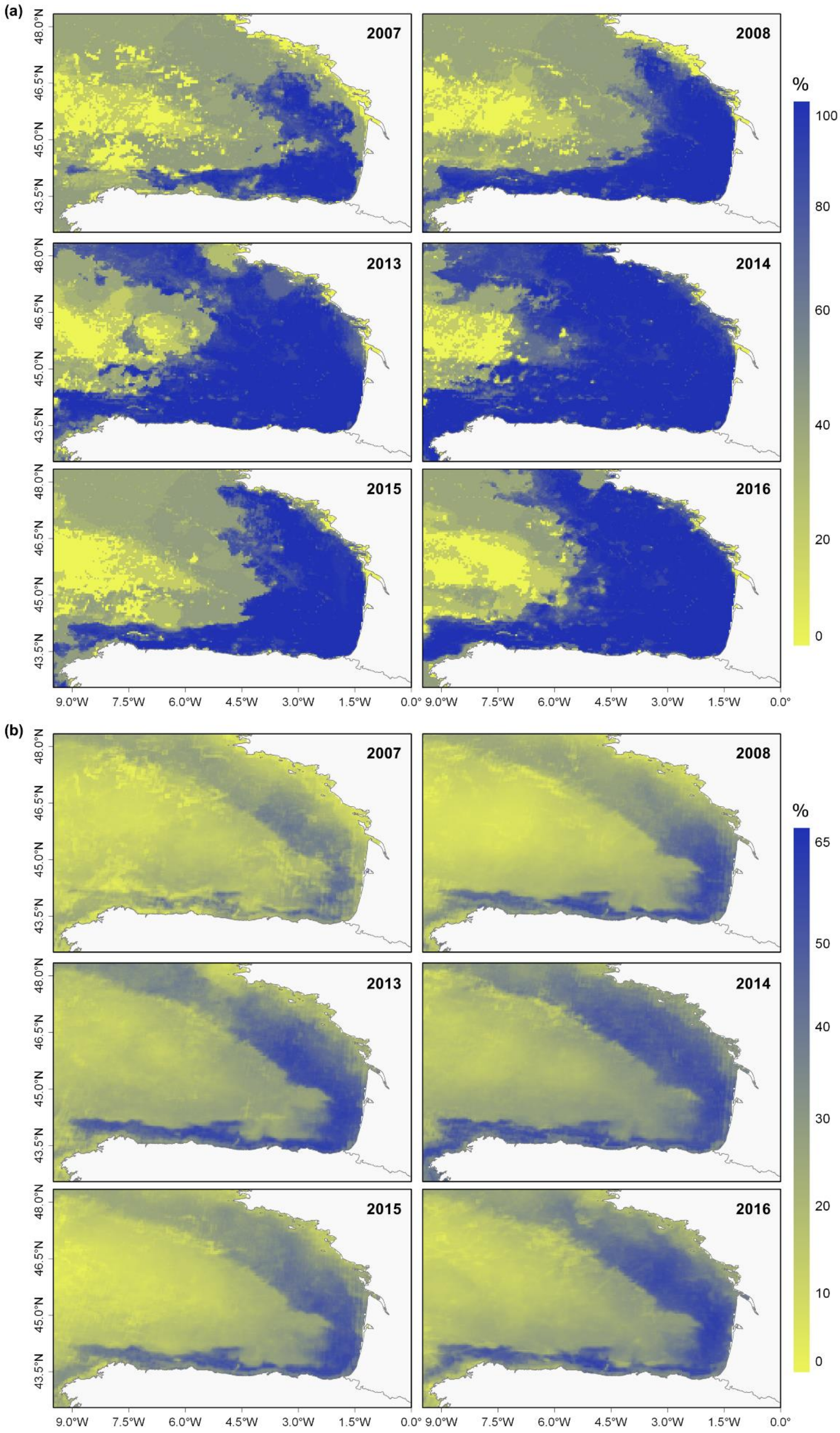

Figure 4.4. Extrapolation analysis using Gower's distance (Gower, 1971). The extra-interpolation maps (a) show the (model-averaged) cases when a prediction was an environmental extrapolation (0%) or interpolation (100%). The neighbourhood maps (b) show the (model averaged) percentage of environmental data that inform a prediction.

3.3. Spatial predictions reliability

Environmental extrapolation and neighbourhood maps showed that across years, predictions were reliable (that it is less model-dependent) on the continental shelf, and partially covering the oceanic area. Predicted Fin whale abundances on the shelf and shelf-break areas of the BoB were informed by at least 30% of the calibration data (Figure 4.4b): these areas of high neighbourhood percentages were located mainly over Spanish and French continental shelves and extended to deeper waters in the former case.

3.4. Suitability of Marine Protected Areas in the Bay of Biscay for Fin whales

By overlapping the spatial location of existing and projected MPAs under the Natura 2000 network with the averaged abundance for each survey (Figure 4.5 and 4.6), we observed that only the French MPAs were *adequate* (*i.e.,* covering > 20% but less than 60% of the national population) by covering the 39.3% and 41.1% of the French population for PELACUS and JUVENA surveys. When considering only the Large off-shore sector the 25.7% and 35.1% of the French Fin whale population for PELACUS and JUVENA surveys respectively would be protected. However, the Spanish MPAs did not achieve the threshold to consider a network as *adequate* covering only the 4.8% and 3.3% of the Spanish Fin whale population (Figure 4.6).

The area comprising the highest 40% of the fin wale abundance in the study area was selected as critical area for each survey. This selection was done after exploring the highest 30% to 60%. The highest 40% was selected to incorporate most of the sightings and based on the approximate limit of the 4000 m-isobath. The critical areas had an average density of 0.006 animals/km^2 (CV = 0.21) and 0.010 animals/km^2 (CV = 0.13) for the PELACUS and JUVENA survey respectively. These critical areas (Figure 4.5) included Capbreton and Cap-Ferret canyons in both surveys. Furthermore, the critical area was smaller and located off the central Spanish continental slope for PELACUS, whereas the JUVENA critical area covered also the area off the southern French continental slope.

By delimiting the common critical area (we define critical areas as the areas of highest predicted abundance which comprise the highest 40% of the predicted abundance), for Fin whales based on the results from both surveys, we identified an important marine area for the conservation of a highly migratory predator in the BoB (Figure 4.5). This area, located in the SE-BoB, was delimited following the 1000-m isobath in the south and eastern part and until the 4000-m isobath to define the Northern boundary and represents an area of 4090 nmi^2. In summer, this marine area encompasses 31.4% and

20.2% of Spanish national population of Fin whales based on the PELACUS and JUVENA estimations, respectively. Regarding the French EEZ, this marine area would comprise 7% and 3.4% of the French Fin whale population estimated based on PELACUS and JUVENA surveys respectively. Regarding the whole network along with this important marine area, 36.2% and 23.5% of the Spanish Fin whale population for PELACUS and JUVENA respectively would be protected implying the Spanish network is *adequate*, whilst in the case of French population the network would cover 46.3% and 44.5% and would continue to be *adequate* (Figure 4.6).

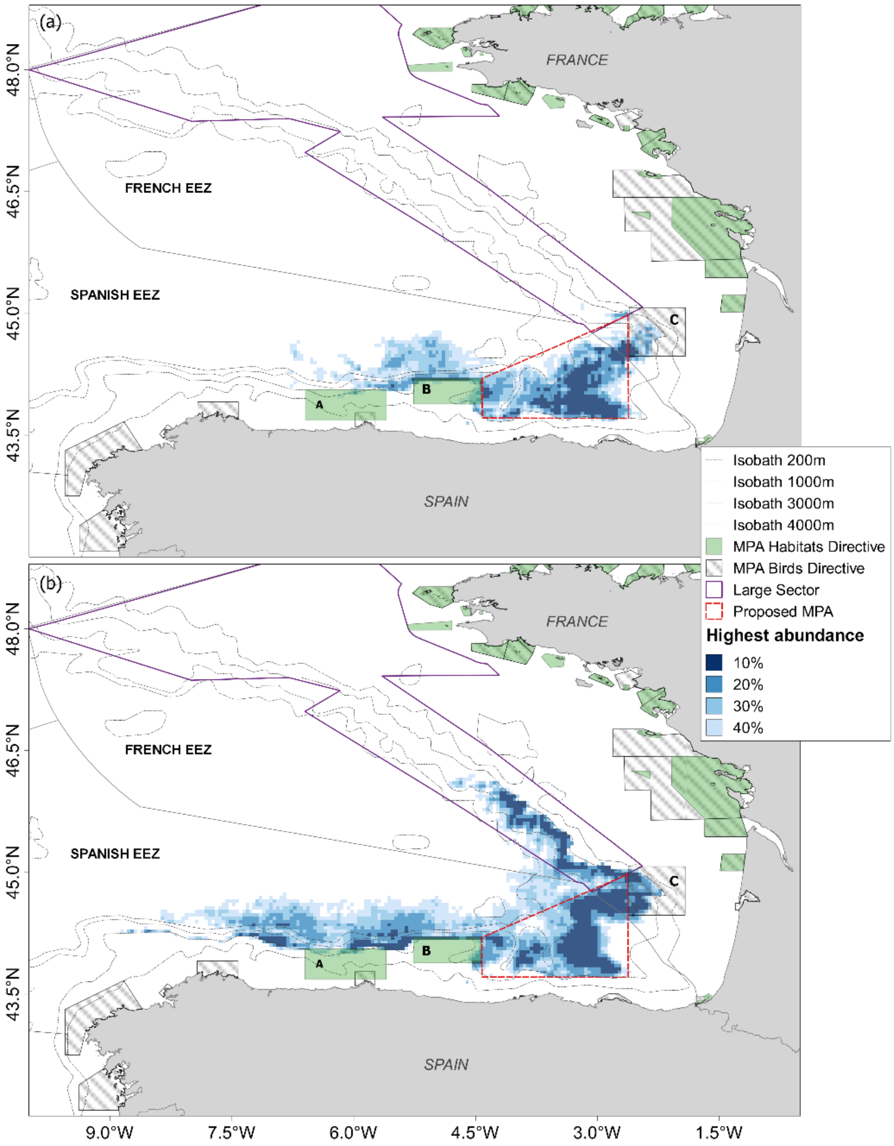

Figure 4.5. Map showing the different areas covered by the highest percentages of abundance for (a) PELACUS and (b) JUVENA critical areas (created by selecting the highest 40% of the averaged predicted abundance for each survey). Existing relevant MPAs are (A) Sistema de cañones submarinos de Avilés, (B) El Cachucho and (C) Tête de Canyon Du Cap Ferret. A projected MPA is included within the Large Sector. The dashed line shows the location of the potential MPA based on the results for this study. Geographical references are located in Figure 4.1.

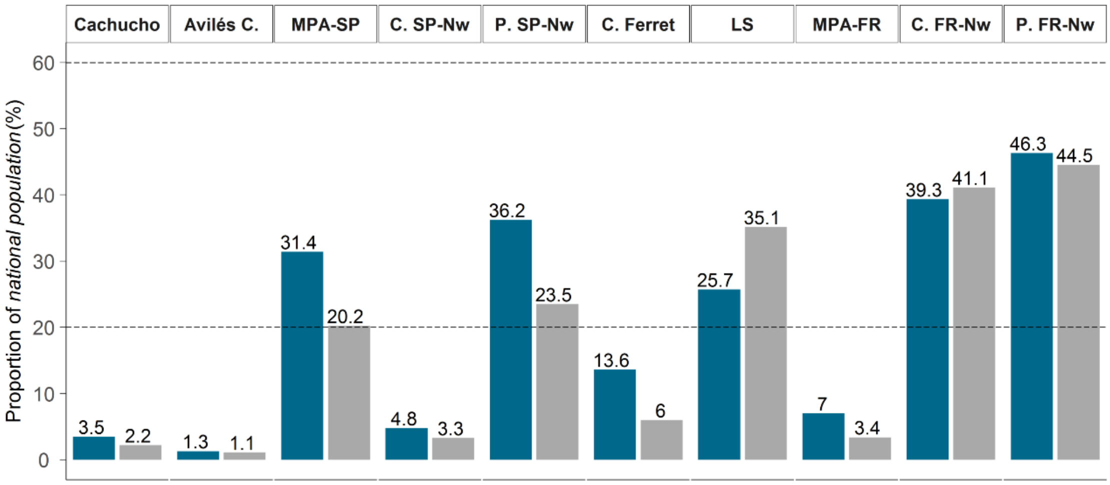

Figure 4.6. Proportion of the Fin whales' national predicted population (i.e., all individuals present within the national territory) for each survey (PELACUS in blue and JUVENA in grey) covered by those MPAs belonging to the Natura 2000 Network which include at least some proportion of the national populations. The Spanish network comprises El Cachucho (Cachucho) and Sistema de cañones submarinos de Avilés (Avilés C.), while the French network comprises Tête de Canyon Du Cap Ferret (C. Ferret) and a projected MPA included within the Large offshore Sector (LS). MPA-SP and MPA-FR refer to the Spanish and French proportion of the Fin whales' population included in the potential MPA. C. SP-Nw and C. FR-Nw refer to the current Natura 2000 network in Spain and France, respectively, while P. SP-Nw and P. FR-Nw refer to the current Natura 2000 network MPAs in addition with the potential MPA for Spain and France, respectively. The dashed lines set the levels of adequacy: less than 20% inadequate, between 20% and 60% adequate and more than 60% sufficient.

4. Discussion

The protection of highly migratory species faces multiple challenges due to the difficulty of data collection and the implementation of effective conservation measures, among others, mainly due to the range of pressures they encounter during their extensive movements (Lascelles et al., 2014). Despite the recovery of baleen whale populations after the IWC's moratorium on commercial whaling, Fin whales are still classified as Endangered by the IUCN (2013). The present study advances the conservation of Fin whales by providing relative abundance estimates in a temperate non-breeding area. We also assessed the adequacy of the existing and projected network of MPAs for Fin whale conservation and concluded the need to include an additional marine area to encompass the identified Fin whale critical areas in the BoB.

4.1. Spatial abundance of Fin whales in the Bay of Biscay

Within their annual migratory journey, North Atlantic Fin whales visit high-latitude areas for foraging (Edwards et al., 2015). The BoB is presumably one of the foraging grounds exploited by the British Isles-Spain-Portugal subpopulation outside polar and subpolar feeding grounds, as it is the case of other areas (*e.g.,* Azores; Silva et al., 2013). Here, our effective strip half-width results were consistent to those previously reported for Fin whales (Barlow and Forney, 2007; Moore and Barlow, 2011). Within the BoB, Fin whale abundance was driven by both physiography and oceanography. Depth was the most important physiographic parameter as Fin whales were found predominantly in deep off-shore waters of the BoB at depths beyond 1000 m, in accordance with previous studies (*e.g.,* Laran et al., 2017). Additionally, SST had an important role with preferred Fin whale habitat occupying intermediate temperature waters (20 °C). Despite the inter-annual variability in SST spatial patterns, Fin whale abundance was better explained by the spatial distribution of SST values, which were intermediate and concentrated over the abyssal plain of the SE-BoB, shaping Fin whale abundance patterns. Densities increased with SLA, being highest around 15-20 cm: these values coincide with those near the core of anticyclonic eddies typical of off-shore areas of the SE-BoB during this period (*e.g.,* Caballero et al., 2014). As has been reported by other studies, we found a negative relationship between the spatial patterns of Fin whales abundance and Chl-a_g (Cotté et al., 2009; Panigada et al., 2008). In the BoB the highest values of Chl-a were found near the coast (Figure D.4.2.f) due to the presence of local upwelling events (Koutsikopoulos and Le Cann, 1996) which explains why the highest Chl-a_g were also located in these areas (Figure D.4.2.g). This oceanographic feature would explain the negative relationship between the whale predicted densities and the Chl-a_g as the highest whale densities were found predominantly in off-shore waters where the lowest Chl-a_g values are found.

This marked Fin whale off-shore distribution and abundance may be driven by food resources. There are no studies on Fin whale diet in the inner part of the BoB, but their diet off North-western Spanish waters is constituted by krill (mainly euphausiids) and small pelagic fish (Aguilar, 2009). Fin whales are reported to rely on krill when available and to prey on small pelagic fish otherwise (Vighi et al., 2015). In the BoB, plankton blooms take place in spring and late autumn, whereas in summer and winter this area reaches minimum plankton biomass (Pingree and Garcia-Soto, 2014). In this area, higher Fin whale abundances could occur with a time lag of some months after the onset of the spring phytoplankton bloom as suggest by Visser et al. (2011). These authors found that baleen whale peak abundance in the Azores archipelago occurred three months later than the onset of the spring phytoplankton bloom. Although a study conducted during our survey period confirmed that the zooplankton detected in the area was predominantly composed by euphausiids (Lezama-Ochoa et al., 2010), the absence of high biomass of zooplankton support the hypothesis that Fin whales feed mainly on small pelagic fish during the late summer in the BoB. In fact, from early August onwards, off-shore French waters support a high biomass of age 0 fish (*i.e.,* juveniles) of the European anchovy *Engraulis encrasicolus* (Boyra et al., 2016, 2013). This small pelagic fish could constitute the main food resource for Fin whales during this period in the BoB as has been demonstrated for other areas such as the Celtic Sea, where Fin whales feed on age 0 Sprat *Sprattus* and Herring *Clupea harengus* (Vighi et al., 2015).

Abundance predictions produced by our spatial models should be carefully considered, since they are relative abundances due to the absence of available data to correct for perception and availability bias for ship-based surveys in the BoB (Certain et al., 2008). However, the environmental extrapolation analysis showed that the main predicted areas of the highest Fin whale abundance were interpolations *stricto sensu* (inside the convex hull) and they were informed by at least (on average) 25% of the data. Relative abundance estimates for Fin whales were shaped by SST patterns during the study period. Estimates were higher (> 1,200 individuals) in those years when warmer SST extended over the oceanic areas of the BoB. On the contrary, in years when temperate SST values were restricted to the inner part of the BoB the predicted relative abundances were lower (< 600 individuals). Our abundance estimates are consistent with previous studies carried out in summer in the BoB such as CODA (Hammond et al., 2009) and SAMM (Suivi Aérien de la Megafaune Marine 2012; Laran et al., 2017), despite the different extension of the sampling areas.

4.2. Critical areas for oceanic species

Under the United Nation Convention on Biological Diversity, the EU has committed to ensure the conservation of 10% of its coastal and marine areas by 2020 following the 11th Aichi Biodiversity Target of the Convention (CBD, 2010b). Usually, marine zoning strategies are based on geographically fixed features to define the extent of the (MPAs) contours (Louzao et al., 2006). However, oceanographic habitats are highly dynamic and many pelagic species (*e.g.,* cetaceans) are highly migratory covering extensive areas annually (*e.g.,* Silva et al., 2013) with the location of their aggregations and migratory routes depending on oceanographic features. For these reasons, the efficiency of static MPAs to conserve highly mobile species are still discussed (Wilson, 2016) but the need to develop dynamic MPAs that can be adapted to deal with this variability within and between years is gaining momentum (Game et al., 2009). Despite the large-scale movements of many pelagic predators, the protection of specific zones where individuals aggregate either during breeding or foraging (Louzao et al., 2006) or during their migration routes (Víkingsson and

Heide-Jørgensen, 2015) can help their conservation if appropriate management and conservation measures are in place to ensure that the anthropogenic threats are reduced/eliminated (*i.e.,* overfishing causing food resources depletion or maritime traffic increasing the probability of collision of cetacean species; Avila et al., 2018). Detailed information on the distribution and abundance of cetaceans is paramount to assess critical areas of conservation interest. However, obtaining these data for oceanic cetaceans is a difficult task due to the costs and logistics involved in developing dedicated surveys. Additionally, platforms of opportunity such as ecosystem-based surveys usually do not cover oceanic areas (*e.g.,* Authier et al., 2018). The oceanic sampling of JUVENA and PELACUS surveys is exceptional in this respect. It is therefore important to take advantage of the non-dedicated monitoring programs already in place to conduct long-term monitoring studies of cetacean populations.

In the BoB, multiple MPAs are designated under the provision of the HD and Birds Directive (Council Directive 79/409/EEC) either in the French or Spanish EEZs. Even though the Natura 2000 network was not designated specifically for most marine mammal species (which are not listed under HD Annex II), it is well known that the implementation of ecologically and economically sustainable management practices can benefit these species if accompanied by appropriate management measures. As Lambert et al. (2017b) suggests for the French network in the case of most of the cetacean species inhabiting the BoB (Bottlenose, Short-beaked common *Delphinus delphis* and Striped *Stenella coeruleoalba* dolphins, Long-finned pilot whale *Globicephala melas* and Risso's dolphin *Grampus griseus)*, the current Spanish MPA network does not reach the less stringent threshold proposed by the European Commission (2007) and is inadequate (*i.e.,* encompassing less than 20% of the national population of interest). The Large off-shore Sector (still in the process of designation) is the most important area for Fin whales due to their location in off-shore waters where the predicted abundance is higher. This result was in line with Lambert et al. (2017b) who demonstrated that this area is highly relevant for cetaceans in summer. Thus, even if Fin whales and other cetacean species are not considered under the Annex II of the HD and therefore they are not candidates for SACs within the Natura 2000 network at the European level, additional legislation (*e.g.,* CITES, CMS, EBSAs) specifically recognises the need to account for threatened species in need of management measures to recover or maintain their population. Therefore, Fin whales as an endangered species should be the focus of specific protection and management measures.

The main critical area for Fin whales was common for both surveys, located in the SE-BoB. Previous studies showed that this area is also important for other cetacean species such as Long-finned pilot whales, Risso's, Short-beaked common and Striped dolphins (Lambert et al., 2017a). Based on the critical areas defined by this study, we propose a potential MPA in the area of the Capbreton and Cap Ferret canyons and the Landes plateau. Although the French area covered by the potential MPA has a small contribution it is important to include this area inside the French EEZ to ensure that all the critical area for Fin whales are included to ensure MPAs connectivity, which improves the protection of such an important area for cetaceans in the BoB. This potential MPA would be similar in spirit to the Pelagos Sanctuary in the Mediterranean Sea (Notarbartolo-Di-Sciara et al., 2008) in that it would involve transboundary collaboration between neighbouring countries to agree on conservation measures that would benefit the marine species inhabiting this MPA.

Furthermore, as many other cetacean species, Fin whales are facing many threats which disregard for jurisdictional boundaries (di Sciara et al., 2016) such as climate change, underwater noise and other forms of pollution (*e.g.,* litter consisting of plastics or derived from fishing activities; Butterworth, 2017). Besides, it is well known that the BoB supports a significantly high level of maritime traffic and fishing activity (OSPAR, 2000) increasing the possibility of ship strikes and entanglement in fishing gears which along with the vulnerability of this species to seismic surveys (ICES, 2015) contribute to the importance of taking appropriate management measures for the protection of this species, such as the creation of transboundary MPAs (Edwards et al., 2015; Lascelles et al., 2014). Thus, this potential MPA would not only cover critical areas for Fin whales in summer, but also it could be useful for the conservation of many other cetacean species.

4.3. Futures perspectives

Not all Fin whales perform seasonal migrations (Edwards et al., 2015) and the migration routes from the summer to the wintering grounds in the NA are poorly known (Vighi et al., 2015). Likewise, it is unknown whether the BoB corresponds to a stop-over site or hosts a resident population of Fin whales. Tracking studies, such as those performed in middle latitudes of the NA (Silva et al., 2013), as well as the development of habitat and abundance models for the whole year are necessary to assess the importance of the BoB for Fin whales. For that purpose, additional dedicated surveys as well as expanding the sampling area of the existing non-dedicated surveys are necessary to monitor cetacean oceanic species in the BoB; dedicating surveys covering off-shore waters are currently only carried out every ten years (Hammond et al., 2017).

The analysis of critical areas along with the assessment of the adequacy of existent MPAs reveals that further studies are necessary to improve the management and conservation of oceanic populations at their key areas. Furthermore, as we show in the present chapter, critical areas can encompass more than one EEZ, hence transboundary collaboration and agreements between governments are necessary to implement and manage new high seas MPAs (Chin et al., 2017; Kark et al., 2015). In the case of the EU, the MSFD encourages transboundary initiatives through existing conservation instruments, such as Regional Sea Conventions; but leaves much discretion to Member States. Although it is the responsibility of individual EU Member States to develop and implement the MSFD in the waters under their jurisdiction, the success of monitoring strategies and conservation measures at broad scales will require policy coordination at a regional level to facilitate and guide the cooperation between EU Member States, a role led by OSPAR for the Northeast Atlantic through the “OSPAR Regional Implementation Framework for the MSFD”.

Chapter 5

The value of time-series for conservation planning

ABSTRACT

Protected areas (PAs) are increasingly been used worldwide for the conservation and management of wildlife. Systematic conservation planning (SCP) aims at ensuring species persistence while minimizing the threats faced by the species and the economic costs related to protection. To account for spatio-temporal interactions between species and human threats, spatial prioritization of mobile wildlife requires the long-term monitoring of both system components, a process that is costly and technically challenging. Therefore, assessments of the number of years needed to ensure a cost-effective PAs network are crucial. We demonstrated with this chapter the value of time-series in conservation planning by implementing SCP to identify priority conservation areas for highly mobile marine megafauna in relation to their main threat: fishing activity. Ten reserve-design scenarios were run in Marxan following two different approaches forcing the inclusion or not of current MPAs in the planning solutions. Then, planning scenarios were statistically compared using the Cohen`s Kappa test. Furthermore, we assessed differences in spatial similarity among and within scenarios using the Wilcoxon non-parametric test and a hierarchical cluster analysis, respectively. Our study highlights the importance of time-series on species abundance and human activities for the robust selection of conservation areas. Spatially explicit conservation plans based on a period equal or greater than three years provided similar marine reserve configurations, showing analogous areas of high irreplaceability and spatial prioritization. We provided a method for calculating the minimum number of years of monitoring required to establish an effective PAs network, which we recommend for future spatial prioritizations for highly mobile species. Our results may have special relevance for the configuration of a Marine PAs network in high seas where many species of conservation interest present high mobility.

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1. Introduction

As the pressures to biodiversity increase and more species become threatened, the need for an effective management of species and habitats increases (Lascelles et al., 2014; Le Saout et al., 2013). Progress has been made in implementing policy responses and actions to conserve biodiversity, but not enough to stem the direct and indirect factors causing nature deterioration (IPBES, 2019). It is recognized that protected areas (PAs) are a cornerstone of the efforts to ameliorate the negative impacts and to effectively manage and conserve habitats and biodiversity (Chape et al., 2008; Gray et al., 2016). The Convention on Biological Diversity (CBD) is committed to increase the area under protection by 2020 (Aichi Target 11; CBD, 2010) and the view for the post 2020 framework propose to protect at least 30% of the Earth by 2030 by well-connected systems of PAs and other effective area-based conservation measures (OECMs) (CBD, 2019). In the European Union (EU), the Natura 2000 network is the largest coordinated network of PAs in the world covering approximately 18% and 11% of the EU's terrestrial and marine territories (European Commission, 2019a, 2018). However, many threatened species are not effectively covered by this large network due to planning inefficiencies (*e.g.*, Giakoumi et al., 2019; Hermoso, Clavero et al., 2017).

Systematic conservation planning (SCP) has been used extensively as a robust and transparent approach for spatial planning to improve conservation benefits and outcomes (Margules and Pressey, 2000). Within this approach, species-level information could be incorporated to prioritize areas for protection that meet conservation objectives (Pressey and Bottrill, 2009), including both spatial and temporal abundance patterns of species and communities. However, the assessment of temporal patterns of biodiversity for SCP have received much less attention than spatial approaches (Magurran et al., 2010) even though the importance of long-term monitoring schemes to account for temporal changes in biodiversity (Proença et al., 2017). Time-series are particularly important since many ecological processes operate on a broad time scale, as in the case of trend detection related to climate change (Parr et al., 2002). Furthermore, time-series become essential for conservation planning in the marine environment due to the highly mobile nature of many marine species and the high dynamism of oceanographic processes (Hoyt, 2018; McClellan et al., 2014).

Although Marine PA (MPA) networks have been frequently focused on sessile and sedentary organisms and their utility for the protection of highly mobile species has been questioned (Breen et al., 2015; Game et al., 2009), recently the designation of MPAs has been attempted also for highly mobile marine megafauna such as seabirds or cetaceans (Gormley et al., 2012; Young et al., 2015) mainly due to the availability of data from ongoing long-term monitoring programmes.

Monitoring of threats is needed to evaluate the trade-offs between human uses and protection of the ecosystems (Halpern et al., 2008; Tulloch et al., 2015). SCP must also consider the spatial and temporal distribution of threats so that possible conflicts can be minimised while conservation goals are meet (Rondinini et al., 2005). In the marine environment, fishing activity is one the main threats to marine megafauna (Clay et al., 2019; Dias et al., 2019) which requires accounting for its spatial distribution, frequency, or seasonality to include it in SCP

Data requirements on spatial prioritization will depend on features such as the reserve objectives and the scale of management as well as the availability of data. Several studies have demonstrated the implications of using data of different resolution and type (*e.g.,* Ban, 2009; Peckett et al., 2014; Stevens et al., 2007). However, there has been limited assessment of the sensitivity of conservation planning outcomes to the temporal extent considered for spatial prioritization. Thus, the aim of this chapter was to explore the value of time-series (and thus long-term monitoring) in conservation planning by exploring the temporal stability of spatial prioritization for marine megafauna (for which conservation targets were set) by assessing the number of years needed to ensure a consistently cost-effective PAs network. More specifically, we produced ten conservation plan scenarios that covered different time periods (from one up to ten years of monitoring) and examined whether there was a threshold above which the planning solutions (or conservation plans) would not change significantly. Our results can contribute toward an effective management of monitoring schemes and provide wildlife managers and stakeholders with mechanism for optimizing action plans, reducing their costs.

2. Material and Methods

2.1. Protected areas and conservation features

The study area was situated in the North and North-western Spanish continental shelf and comprised a total surface of approximately 42800 km^2 (Figure1). We divided the study area into a standard grid of 2770 planning units (PUs) of 4x4 km each. Currently, the study area includes 11 MPAs, ten of which belong to the Natura 2000 network and were designated under the EU Habitats Directive (92/43/EEC) and Birds Directive (79/409/EEC) (Figure 1).

The remaining MPA was designated under regional legislation as a Protected Biotype (Decree 34/2009).

We identified as conservation features, *i.e.,* species of conservation interest, ten seabird and three cetacean species whose populations are listed as protected under national and international legislation (García-Barón et al., 2019b). The seabird species included: the Yellow-legged *Larus michahellis*, the Lesser black-backed *L. fuscus* and the Mediterranean gulls *Ichthyaetus melanocephalus*, the Sandwich tern *Thalasseus sandvicensis*, the Balearic *Puffinus mauretanicus* and the Manx shearwaters *P. puffinus*, the Razorbill *Alca torda*, the Common guillemot *Uria aalge*, the Great skua *Stercorarius skua* and the Northern gannet *Morus bassanus*. The cetacean species were the c *Delphinus delphis* and the Bottlenose dolphins *Tursiops truncatus,* as well as the Long-finned pilot whale *Globicephala melas*. Not all our conservation features were included as target species for the designation of the current MPAs. However, most of them are referenced in the conservation objectives and management guidelines of the MPAs benefiting from the protection provided by current MPA network (Figure 5.1).

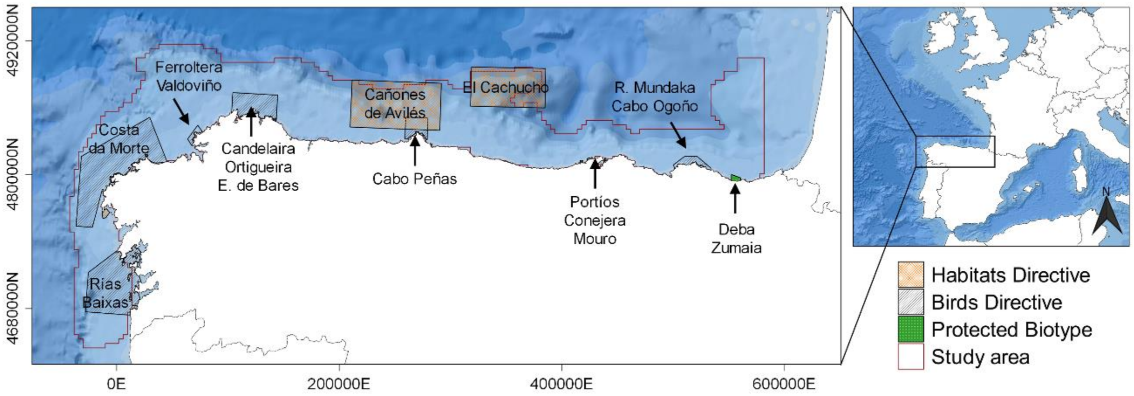

Figure 5.1. Map of the North and North-western Spanish continental shelf showing the study area delimited by a red polygon and the MPAs within the study area either designated under the EU Habitats Directive (orange polygons), the Birds Directive (grey polygons) or under the regional legislation as a Protected Biotype (green polygon).

Species spatial distribution and abundance over a ten-year period (2007-2016) were obtained from the chapter 3. In this previous chapter, we estimated the yearly spatial density during spring (March-April) based on sightings data (PELACUS monitoring platform; Saavedra et al., 2018). Species data were analysed by means of Generalized Additive Models following the Information-Theoretic framework for the identification of the most important dynamic and static variables explaining the spatio-temporal patterns of the density of marine megafauna species (Chapter 3). In the present chapter, the spatial density predictions were re-projected into the WGS84/UTM zone 30N coordinate system and resampled from their original spatial resolutions to the resolution of the PUs. Finally, the abundance value of each conservation feature per PU was obtained by multiplying the area of the PU and the predicted density of each species in each PU (Appendix E-Section 1).

We set conservation targets for the 13 conservation features based on European guidelines (as in Giakoumi et al., 2013) and considering the conservation status of the species according to the International Union for the Conservation of Nature (IUCN) Red List of Threatened Species in Europe (IUCN, 2018), as well as the level of occurrence of the species in the study area (MAGRAMA, 2012b, 2012a). Thus, the conservation targets varied between 20% for species categorized as of “least concern” and with an “abundant” level of occurrence to 60% for species categorized as “critically endangered” and with an “abundant” level of occurrence (Table 1 and E-2.1).

Table 5.1. Conservation targets set for each species. The table shows the IUCN category in Europe for each species (DD: data deficient; LC: Least concern; NT: Near threatened; VU: Vulnerable; EN: Endangered and CR: Critically Endangered), the level of occurrence in the area (MAGRAMA, 2012a, 2012b) and the final conservation target selected.

Group	Species	IUCN	Occurrence	Conservation target (%)
Seabirds	Yellow-legged gull	LC	Abundant	20
	Lesser black-backed gull	LC	Abundant	20
	Mediterranean gull	LC	Common	30
	Sandwich tern	LC	Common	30
	Balearic shearwater	CR	Abundant	60
	Manx shearwater	LC	Abundant	20
	Razorbill	NT	Common	40
	Common guillemot	NT	Common	40
	Great skua	LC	Common	30
	Northern gannet	LC	Abundant	20
Cetaceans	Short-beaked common dolphin	DD	Common	50
	Bottlenose dolphin	DD	Common	50
	Long-finned pilot whale	DD	Common	50

2.2. Threat spatio-temporal distribution

Trawl and gillnet fishing were considered the most important threats for our conservation features in the area due to bycatch (Goetz et al., 2015; Peltier et al., 2012). Due to the importance of considering such activities when planning for the conservation of seabirds and cetaceans in the area, we used Vessel Monitoring System (VMS) to obtain spatial quantitative descriptors of the fishing pressure exerted by trawl and gillnet fisheries in the study area (as in Giakoumi et al., 2012). The VMS satellite-based positional tracking system is currently used successfully to monitor the distribution and intensity of the fishing activity providing a long time-series of data to inform the design of MPAs (Game et al., 2009). VMS data provide information on the identity, position, speed, and heading of the vessels over 12 m (European Commission, 2011) and were obtained from the *Spanish Secretary-General for Fisheries* for the period 2007-2016.

We used the spatio-temporal distribution of trawl and gillnet fishing as a proxy for the level of pressure posed by these activities on our conservation features assuming that the pressure is higher where the fishing activity is greater. Thereby, the threat level was estimated as the intensity of fishing activity (measured in hours) per PU. We processed the VMS data using the '*vmstools*' R-package (Hintzen et al., 2017). Firstly, we removed duplicated or pseudo-duplicated data (we considered pseudo-duplicated data those records for which interval time was < 5 minutes), records located on land or in ports, and records associated with high unusual speeds for fishing vessels (> 20 knots). Secondly, we used a vessel speed range to discriminate between fishing and non-fishing activity (*i.e.,* when the vessel was only on route). The range set for trawlers was 2-4 knots and for gillnets 0-3 knots (Fernandes et al., 2018). All the records with speeds included within the speed ranges were considered fishing activity and were included to compute the threat layer. Finally, the fishing intensity (*i.e.,* threat level) per year was mapped by summing the fishing effort per PU of both trawling and gillnet and rescaled on a scale from 0-100 (Figure 5.2).

2.3. Conservation planning scenarios

We used Marxan software (Ball et al., 2009) to produce alternative conservation plans depending on the temporal scale (*i.e.,* number of years) considered. Marxan uses a simulated annealing algorithm to find a range of near-optimal solutions to achieve the predetermined conservation targets minimizing the cost (Possingham et al.,2000). Here, we tried to achieve the targets set for our conservation features minimizing the risk posed by fishing.

We followed two approaches to identify potential areas for conservation under ten plausible planning scenarios to investigate the value of new spatial information to meet our conservation targets: a) *Approach 1*: the selection of PUs included in the existing PAs was forced in the Marxan solutions (*i.e.,* the existing MPAs remain in the reserve network throughout the analysis and in the final solution) and b) *Approach 2*: the selection of PUs included in existing PAs is free, so these PUs may be not included, partially included or totally included in Marxan solutions.

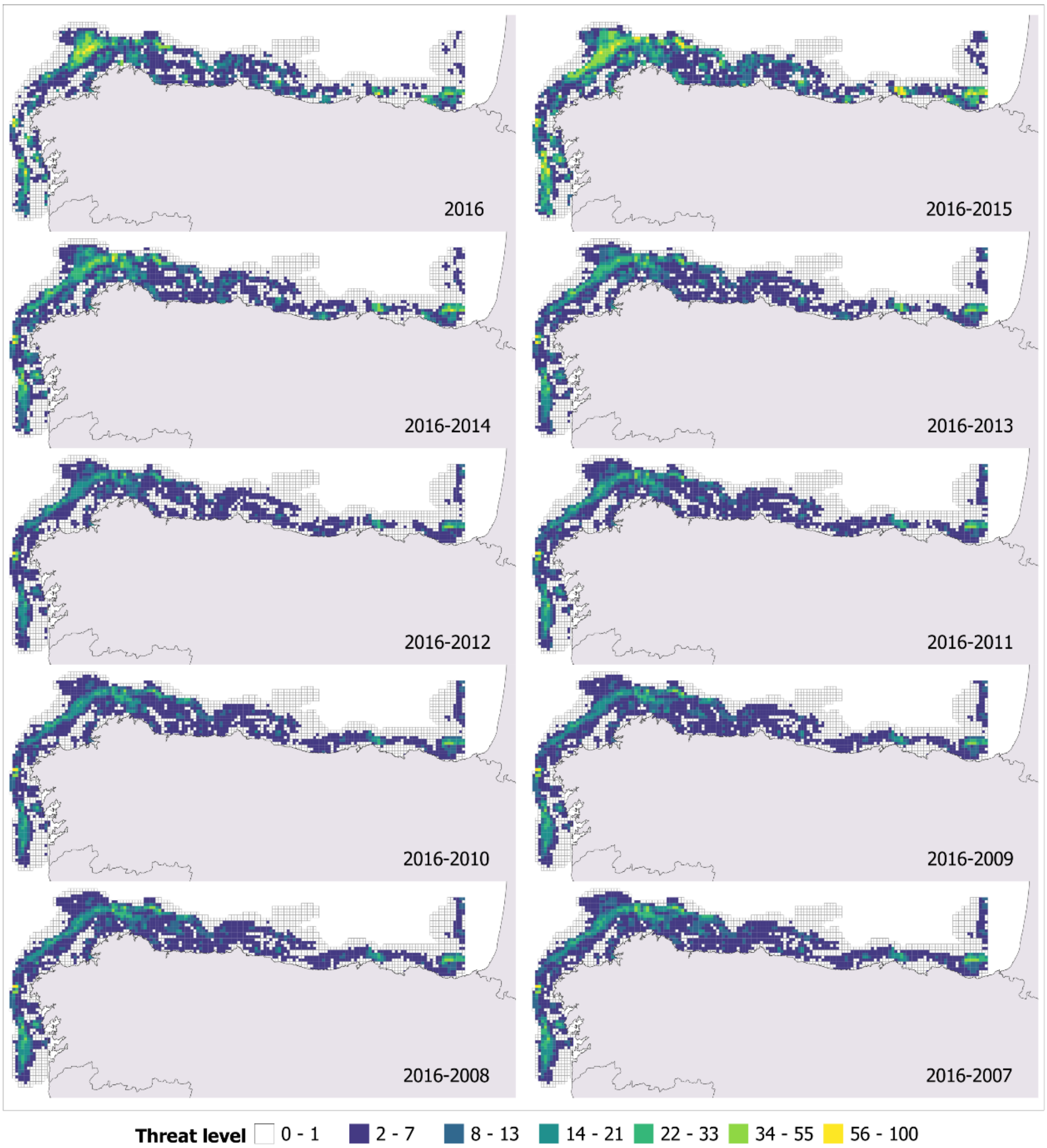

Figure 5.2. Maps of threat level for the ten planning scenarios. The threat level was calculated by summing the fishing effort (in hours) per planning unit obtained from the analysis of the Vessel Monitoring System data of trawl and gillnet fisheries and rescaled from 0-100.

Within each approach, we run ten different scenarios integrating different amount of data from the time-series:

- *Scenario2016*: created using the conservation features and the threat data of the year 2016;
- *Scenario2016-2015*: created by calculating the mean abundance per cell of each conservation feature and the mean threat level per cell for the years 2015 and 2016;
- *Scenario2016-2014*: as the previous scenario but integrating information for the years 2014, 2015 and 2016;
- *Scenarios 2016-2013*, *2016-2012*, *2016-2011*, *2016-2010*, *2016-2009*, *2016-2008* were similarly obtained;
- *Scenario2016-2007*: included the whole time-series of data (from 2007 to 2016).

To evaluate the influence of the longitude of the time-series (*i.e.,* the number of years) on the conservation solutions, we kept constant the number of iterations (100 runs) and the Boundary Length Modifier (BLM) was set to zero. The BLM parameter is used to set the desired level of compactness of the MPA network. Here, we did not adjust this parameter because the aim of our study was not to produce an MPA network, but to investigate changes in conservation priorities depending on the longitude of the time series (see Mazor et al., 2014 for similar approach). Thus, we obtained a near-optimal solution, referred to as *best solution* hereafter, which is the solution with the lowest cost (Ball et al., 2009) and a summed solution, referred to as *selection frequency* hereafter, which is the number of times that a planning unit is selected as part of a near-optimal solution (with values ranging from 0 to 100) (Ball et al., 2009). The resulting spatial conservation priorities were illustrated by mapping the *best solution* and the *selection frequency* of each scenario and approach. Finally, to test the sensitivity of our results to the level of conservation targets set, we produced conservation plans where all the targets were set to 20%. In this case the selection of PUs included in the existing MPAs was free.

2.4. Comparison of planning scenarios

The planning scenarios were compared in three ways: (1) we used the Cohen`s Kappa statistic (K; Fielding and Bell, 1997) to make pairwise comparisons of the best solution of each scenario; (2) we assessed differences in overlap of selection frequency between scenarios calculating the Wilcoxon non-parametric pair-difference test (Ferrari et al., 2018); and (3) we compared the spatial similarity among and within scenarios by means of an hierarchical cluster analysis using the *hclust* function using all solutions as samples (100 samples per scenario) following Harris et al., (2014) methodology. This analysis was based on a Jaccard resemblance matrix built using the *vegdist* function (‘*vegan’* R-package; Oksanen et al., 2018). To complement the hierarchical analysis, we also displayed a non-metric multidimensional scaling plot (nMDS) of the solutions set per scenario using the *metaMDS* function (‘*vegan’* R-package), based on the Jaccard resemblance matrix. For all analyses, the *Scenario2016-2007* was used as the baseline against which the alternative scenarios were compared to.

3. Results

All analyses performed showed similar results regardless of the approach used. Overall, our results showed that conservation plans based on data covering a period equal to or greater than three years provided similar spatial prioritization results. More specifically, the Cohen’s Kappa pairwise comparisons between the best solution of each scenario and the *Scenario2016-2007* (which includes all the time-series data, Figure 5.3a) showed that with three years of monitoring (*i.e.,* from the *Scenario2016-2013* onwards) the best solutions had a statistically almost perfect agreement in the case of *Approach 1* ($K > 0.8$; $p\text{-value} < 2.2e\text{-}16$), whilst the *Approach 2* showed an almost perfect agreement on best solutions after including at least four years of monitoring.

The Wilcoxon-test between the selection frequency of each scenario and the *Scenario2016-2007* (Figure 5.3b) found no significant differences from the scenario with three or more years of monitoring in both approaches (*Approach 1:* W-range = 3802643-3849175, p-value-range = 0.53-1; *Approach 1:* W-range = 3804757-3836450, p-value-range = 0.55-1; Table S3.1).

The hierarchical cluster analysis of the full set of solutions per scenario showed three major splits both in the *Approach 1* or *2* (Figure 5.4a and Figure 5.4c, respectively). The first cluster was composed by *Scenario2016* and *Scenario2016-2015* which were the most dissimilar compared to the remaining scenarios. Furthermore, note that in the *Approach 2*, all the solutions of the abovementioned scenarios were identical as the nMDS plot, where a unique point can be distinguished within each scenario (Figure 5.4d). The second cluster was composed by *Scenario2016-2014*, *Scenario2016-2013* and *Scenario2016-2012* and the third cluster included *Scenario2016-2011, Scenario2016-2010*, *Scenario2016-2009*, *Scenario2016-2008,* and *Scenario2016-2007.* The nMSD plot of the *Approach 1* (Figure 4b) showed a clear grouping of all the scenarios but the *Scenario2016* and *Scenario2016-2015*, a pattern less clear in the case of the *Approach 2* (Figure 4d). Both nMDS plots showed how similarity increases as more years are added to the scenarios. Similar results were obtained when we lowered the targets for all conservation features to 20% (Appendix E-Section 4).

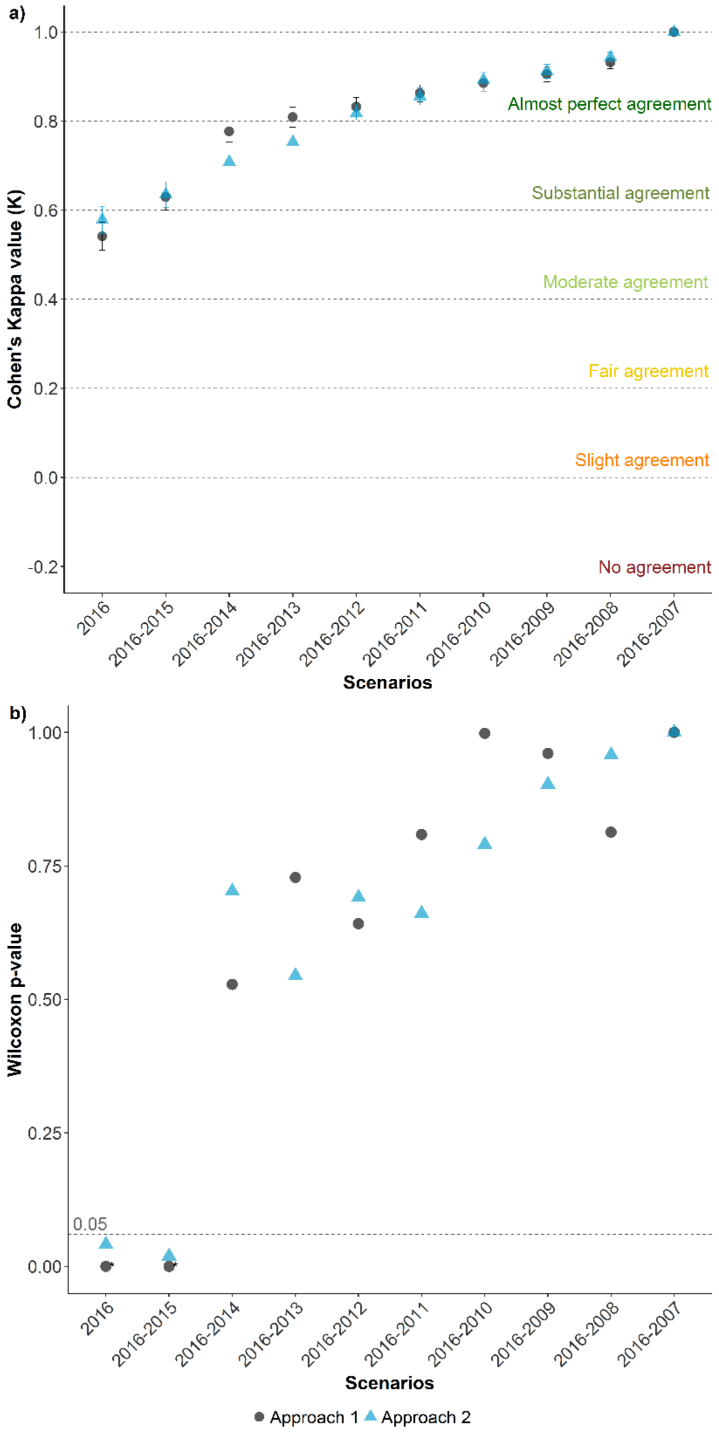

*Figure 5.3. (a) Pairwise comparison of planning scenarios using the Cohen`s Kappa statistics (K) for the Marxan best solution of each scenario and approach. For each comparison it is represented the value of K with their confidence interval. Colours highlighting the judgement for K about the extent of agreement in a < 0 - 1 scale (from red to green; Landis and Koch, 1977); (b) Wilcoxon rank sum tests to assess differences in percentage of overlap of selection frequency of each scenario and approach. Dotted line shows the limit of significance for the test (p-value = 0.05) and * indicate p-value < 2.2e-16; Both analyses were based on the Scenario 2016-2007.*

For both approaches, similar areas of high irreplaceability (*i.e.,* high percentage of selection frequency) become apparent as the number of years included in each scenario increased (Figure 5.5). The same applies to the resulting conservation priorities areas that showed similar best solutions as the years of monitoring included in the scenario increased (Figure 5.6). Furthermore, the spatial prioritization identified as best solutions met all the conservation targets of all the conservation features considered.

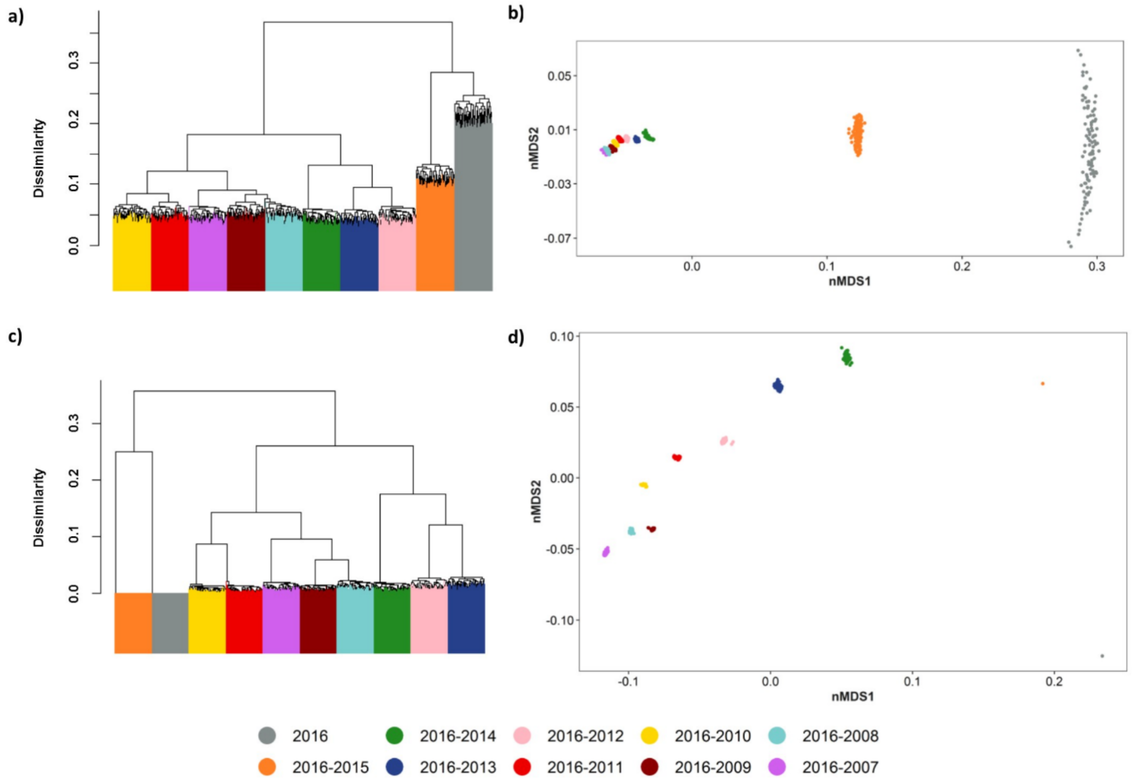

Figure 5.4. Relationships among solutions of the ten scenarios of the Approach 1 (top panels) and Approach 2 (bottom panels). Left panels (a-c) show the dendrograms from a complete hierarchical cluster analysis and right panels (b-d) the nMDS plots based on a Jaccard resemblance matrix.

The hierarchical cluster analysis of the full set of solutions per scenario showed three major splits both in the *Approach 1* or *2* (Figure 5.4a and Figure 5.4c, respectively). The first cluster was composed by *Scenario2016* and *Scenario2016-2015* which were the most dissimilar compared to the remaining scenarios. Furthermore, note that in the *Approach 2*, all the solutions of the abovementioned scenarios were identical as the nMDS plot, where a unique point can be distinguished within each scenario (Figure 5.4d). The second cluster was composed by *Scenario2016-2014*, *Scenario2016-2013* and *Scenario2016-2012* and the third cluster included *Scenario2016-2011, Scenario2016-2010*, *Scenario2016-2009*, *Scenario2016-2008,* and *Scenario2016-2007.* The nMSD plot of the *Approach 1* (Figure 4b) showed a clear grouping of all the scenarios but the *Scenario2016* and *Scenario2016-*

2015, a pattern less clear in the case of the *Approach 2* (Figure 4d). Both nMDS plots showed how similarity increases as more years are added to the scenarios. Similar results were obtained when we lowered the targets for all conservation features to 20% (Appendix E-Section 4).

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4. Discussion

This study highlights the value of time-series in the spatial planning of PA networks for highly mobile species reducing the risk of exposure to threats. We present a method to assess the minimum temporal monitoring (*i.e.,* number of years) required for the spatial planning of a consistent network of PAs. Our results showed that after the incorporation of a minimum of three years, within either of the two different approaches applied, the selection of PUs was robust enough for the planning of an MPA network. We obtained similar results using different statistical analyses demonstrating the robustness of our results. Besides, setting all conservation targets to 20% and obtaining similar results proved that changes in conservation targets had minor influence in the results being the temporal coverage of the monitoring included in the scenarios the driver of the spatial prioritization result.

The method we are presenting, that allows the determination of the required temporal coverage for the spatial planning of a consistent network of MPAs, can be developed into a useful tool for conservation management, usually hampered by limited resources (Palareti et al., 2016). Managers must decide between further investment in surveys to improve spatial prioritization versus investment in the maintenance and management of planned areas which have been selected based on the best data available. Determining the temporal coverage of monitoring influencing on the prioritization outcomes will ensure an informed investment in spatial conservation planning. Our results show that relying on a few years entails the risk of determining priority conservation areas that are too restricted or inappropriate for the conservation of the species. In our example, this was the case for planning scenarios that integrated only one or two years of marine megafauna sightings. Once three or more years of monitoring were added, the resulting spatial planning

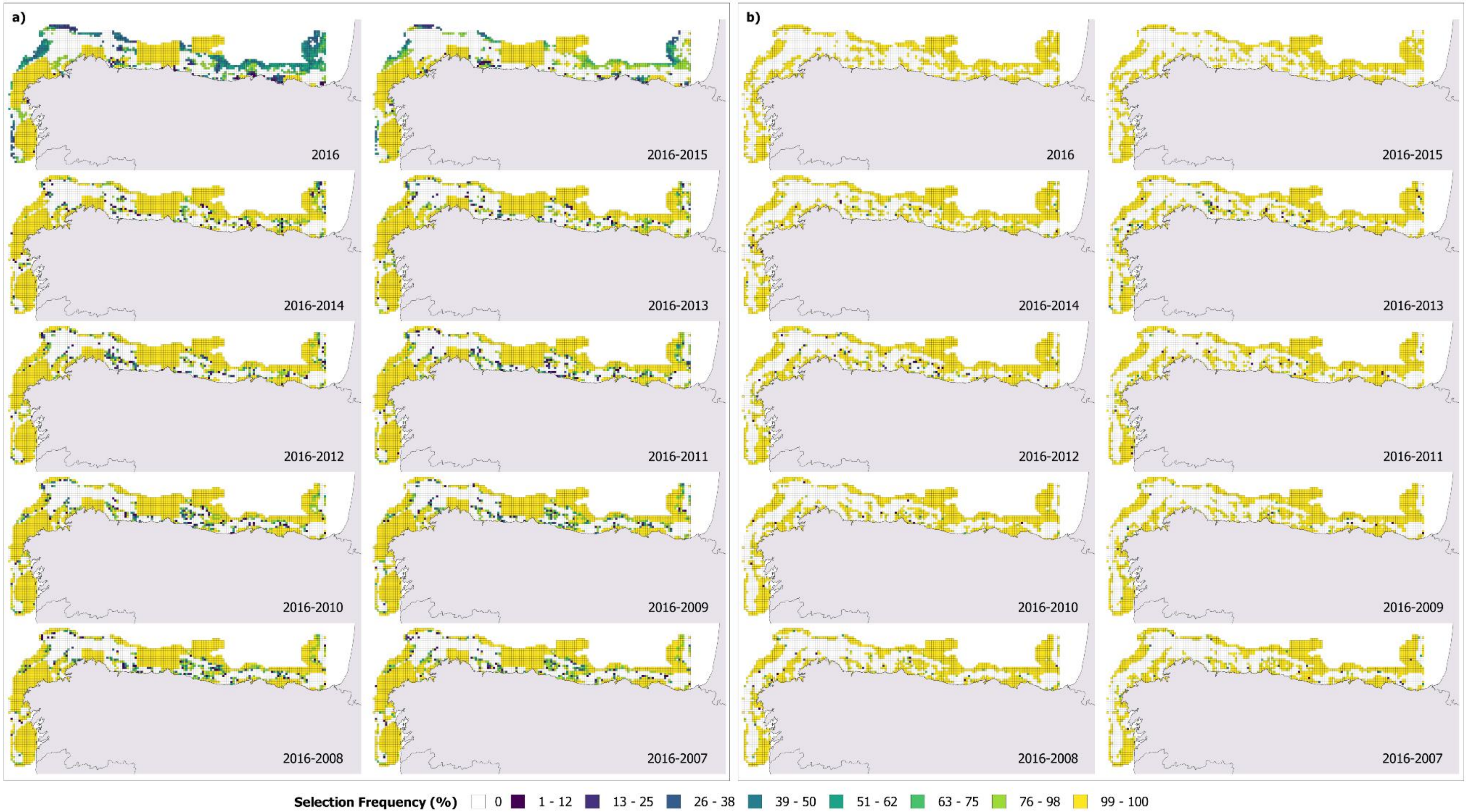

Figure 5.5. Maps of the ten planning scenarios showing the selection frequency of the planning units (PUs) (the percentage of times a PU was selected when run in Marxan 100 times) for the (a) Approach 1 (the selection of PUs included in the existing PAs was forced in the Marxan solutions and (b) Approach 2 (the selection of PUs included in existing PAs is free in the Marxan solutions).

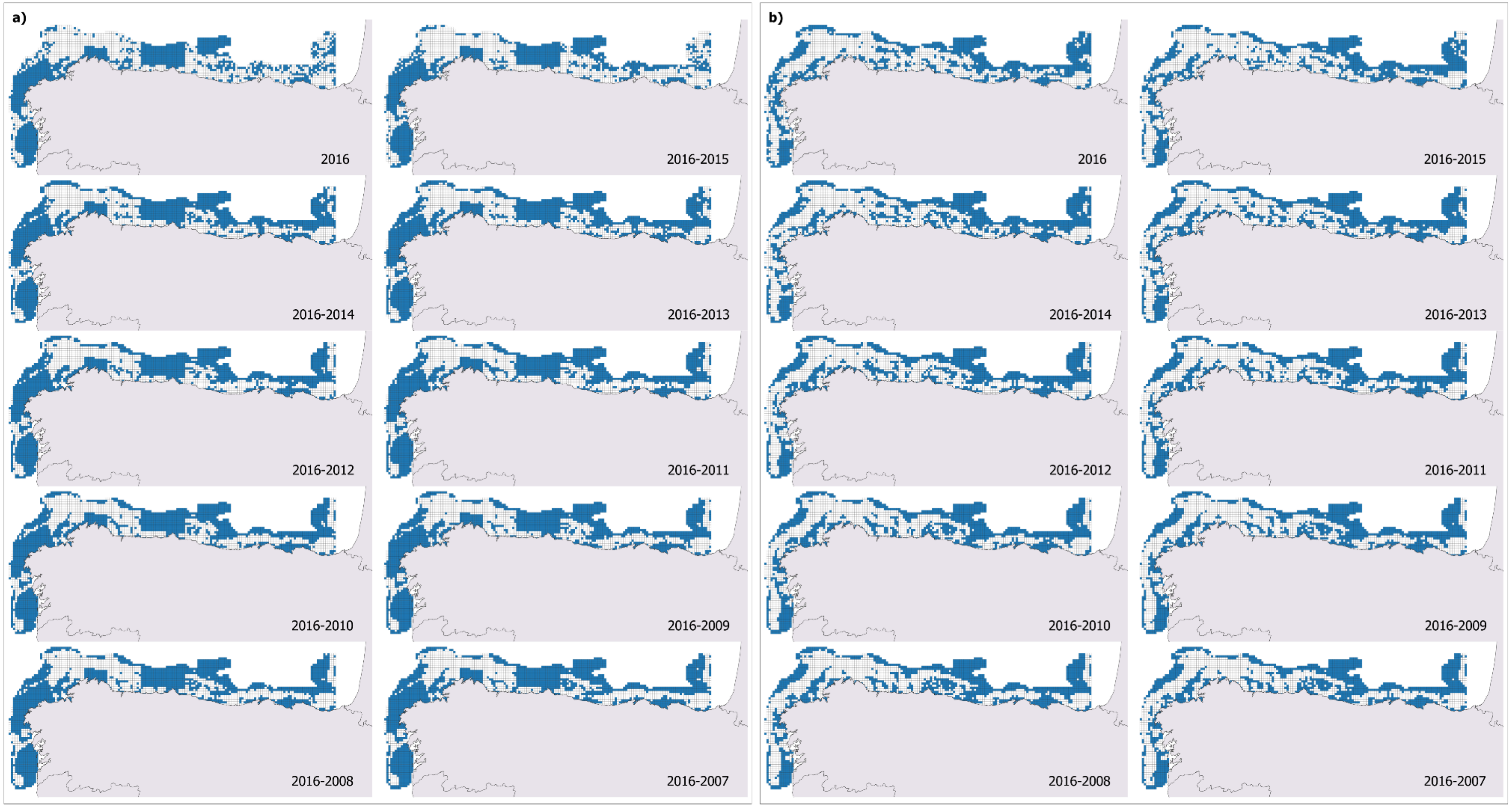

Figure 5.6. Maps of the ten planning scenarios showing the Marxan best solution (the reserve configuration that best reduces risk of threat and meets biodiversity targets from 100 Marxan runs) for the (a) Approach 1 (the selection of planning units (PUs) included in the existing PAs was forced in the Marxan solutions and (b) Approach 2 (the selection of PUs included in existing PAs is free in the Marxan solutions). Blue shaded PUs represent the best solution.

solutions identified priority conservation areas that were missed in the scenarios run with shorter temporal coverage.

This study highlights not only the value of time series of conservation features, but also of threats. However, gathering information on both system components requires setting up appropriate long-term monitoring schemes. Monitoring schemes must ensure that the geographic coverage of target biodiversity components is sufficient and constant over time. However most current monitoring programmes do not meet these requirements, with geographic coverage usually being insufficient and uneven (Pereira et al., 2010). In fact, the most important gaps identified by systematic conservation planning is the insufficient geographic coverage of most threatened high-biodiversity areas (Álvarez-Romero et al., 2018) and the lack of good distributional data (Giakoumi et al., 2013). These shortcomings prevent more sophisticated analyses, such as modelling habitat suitability or identification of key areas at large scales (Kaschner et al., 2006).

Besides incomplete spatial coverage, another major shortcoming is the lack of adequate temporal coverage. Long-term programs of biodiversity monitoring are needed to establish baseline values for applied research such as to identify changes through time and to distinguish between the influence of both anthropogenic and natural factors on community turnover (Magurran et al., 2010; Ondei et al., 2018). Thus, designing and implementing a long-term monitoring scheme is a trade-off between the geographic and the temporal coverage, with few existing time-series meeting both criteria due to lack of funding (Mascia et al., 2014). Owing to the widespread under-funding of conservation science, conservation managers and planners must decide where the investment is needed, whether in the biodiversity monitoring or the enforcement of the actual management measures. In this sense, we demonstrated that time-series data are required in SCP but also recommended test for robustness in the spatial prioritization regarding the number of years of monitoring included to decide where to cost-effectively invest.

In addition to species distribution data, time series of socio-economic and/or threats-related data are also needed. Failing to integrate this information in the spatial prioritization can cause the implementation of conservation plans to be ineffective and the failure of conservation strategies (Polasky, 2008). As Bode et al. (2008) showed, conservation priorities are more sensitive to variation in the degree of threats the area is facing than to changes in how biodiversity data is measured. Relatively little effort has been devoted to improve threats or costs maps in contrast with the large amount of effort spent in improving statistical tools to obtain more accurate species data (Armsworth, 2014). Poor quality threat or cost data could be problematic, especially if they are used in spatial prioritisation (Bode et al., 2008). For example, one of the limitations of VMS data is related to the fishing fleet covered. In Europe, VMS is only mandatory for fishing vessels with an overall length > 12 m, however 85% of the fishing vessels are not larger than 12 m long (European Commission, 2019b). Moreover, VMS is not mandatory for vessels with an overall length between 12 and 15 m, if the fishing activity occurs only in EEZ areas or the fishing trips duration is less than 24h (EC 1224/2009). This might lead to underestimating the level of threat posed by fishing and misidentification of the areas with the highest fishing pressure.

In this study, we have focused on fisheries, being identified as one of the main threats to the conservation of cetacean and seabirds in Europe. Including data on fishing effort is an essential factor for the design of MPA networks to minimize the negative impacts on both biodiversity and fisheries themselves (Klein et al., 2008). The spatial resolution of fishing pressure has to be fine enough to differentiate areas to be used in spatial prioritization (Ban and Klein, 2009), but must also have a minimum temporal coverage to take into account their dynamics and long-term spatial changes (Giakoumi et al., 2015). Our results confirmed the importance of including time-series VMS data in spatial planning to track the spatial and temporal changes of fishing and identify more accurately priority areas for conservation (*e.g.,* Bertrand et al., 2008; Gloaguen et al., 2015; Walker and Bez, 2010).

The high dynamism of the marine ecosystem and the related high mobility of the marine megafauna, as well as the spatio-temporal dynamic of human activities require long-term monitoring schemes to inform effective marine spatial conservation planning. Further methodological improvements should consider applying our approach to larger areas and/or oceanographically more dynamic to test the robustness and general applicability of our method to assess the cost-effectivity of stable MPA networks. Our findings may have special relevance in high seas where the establishment and continuation of long-term monitoring is difficult because such programs require international agreement and cooperation, as the established by the Convention on the Conservation of Migratory Species of Wild Animals (CMS) or the International Whaling Commission (IWC), which is also needed to designate and implement effective MPAs for migratory species.

CONCLUSIONS

The first objective of this thesis was: "*to provide a qualitative and, when possible quantitative, assessment of the main threats affecting the marine megafauna community in the Bay of Biscay*" (**Chapter 1**). The main conclusions in relation to this objective are:

1. The quantitative assessment for seabirds, the first long time-series (13 years) analysis of the causes of admission to rehabilitation centers in the area, showed that cachexia, exposure to crude oil and interaction with fishing gear were the most common treats faced by seabirds. Of all the seabird community, individuals from the families Alcidae, Laridae, Sulidae and Phalacrocoracidae were the most affected.
2. The qualitative assessment showed that the risks faced by cetaceans and seabirds depend on the biology and habitat use of the species. Particularly dangerous threats for cetaceans were those related with pollution (*e.g.* organic pollutants, plastics, acoustic pollution), bycatch and vessel collision, whilst for seabirds main threats were oil spills, bycatch, and those also related with pollution such as the presence of plastics or ghost fishing.
3. Both types of assessments are of special relevance for threatened species and provide useful information on the prevalence of certain threats, which can help to identify conservation priorities and inform management measures needed in the context of the Marine Strategy Framework Directive and other relevant legislation.

The second objective was: "*to develop a methodological approach, applicable to other species, to identify biologically appropriate predictors to jointly consider both the spatial and vertical dimensions of oceanographic habitats*" (**Chapter 2**). The main conclusions from this objective are:

4. The methodological approach developed allows the identification of oceanographic and preyscape predictors to jointly consider the spatial and vertical dimensions of oceanographic habitats and it is applicable to any marine species. This approach revealed the importance of integrating monitoring of pelagic fish, oceanographic descriptors and marine megafauna species during fine-scale integrated oceanographic surveys to guide ecosystem-based management and conservation efforts.
5. Abundance patterns of pelagic seabirds were influenced by oceanographic conditions and prey accessibility (*i.e.* sardine and juvenile anchovy biomass) integrated above the depth of maximum temperature gradient for Sooty shearwaters and at the surface for Great shearwaters, leading to a vertical segregation. Similarly,

both species showed a spatial segregation in relation to shelf (preferred by Sooty shearwaters associated with upwelling and river discharge) versus oceanic areas (preferred by Great shearwaters).

6. The first abundance estimates are provided for Sooty (3,203 individuals; 95% CI: 1753−5748) and Great shearwaters (12,380 individuals; 95% CI: 5797−28 152) in September for the Bay of Biscay.

The third objective was: "*to locate ecologically meaningful areas for the marine megafauna community through the identification of Essential Ocean Variables shaping their environmental envelopes and driving their spatio-temporal trends*" (**Chapter 3**). The main conclusions from this chapter are:

7. Sea surface temperature and chlorophyll-a concentration were the Essential Ocean Variables (EOVs) driving the spatial patterns of the megafauna community. Higher values of both EOVs shape the High-Value Biodiversity Areas (HVBAs), which were mainly located in the Western and North-western Iberian coast. The location of HVBAs (associated to higher productivity) overlaps with fishing grounds, increasing the risk of by-catch for both seabirds and cetaceans.
8. These results highlight the importance of EOVs monitoring to detect changes resulting from specific anthropogenic pressures and/or climate change and to forecast the response of the species or communities.
9. This study contributes to the provision of sound spatial information needed to support marine spatial planning approaches and to improve the management and conservation of the marine megafauna species and/or communities in the context of the Marine Strategy Framework Directive and the Maritime Spatial Planning Directive.

From the fourth objective, "*to identify critical areas for marine megafauna and to assess whether the current Marine Protected Areas network offers protection for species for which it has not been designated*" (**Chapter 4**), the main conclusions are:

10. Density surface models developed for the highly migratory endangered Fin whale revealed that the species was especially abundant in deep offshore waters of the inner Bay of Biscay, when warmer sea surface temperature extended into larger areas.
11. The main critical area determined for the species, located in the South eastern Bay of Biscay, is not included within the current Natura 2000 network. Thereby, we

propose a new MPA, which would require transboundary collaboration between Spain and France to ensure connectivity across the network, while improving the protection for Fin whales and other megafauna species.

12. Additional dedicated surveys, as well as expanding the sampling area of the existing non-dedicated surveys, are necessary to monitor oceanic megafauna species in the Bay of Biscay to inform measures for their management and conservation at critical areas.

The fifth objective was: "*to explore the temporal stability of spatial prioritization for marine megafauna by assessing the number of years needed to ensure a robust MPA network*" (**Chapter 5**). The main conclusions from this chapter are:

13. We demonstrated the value of time-series in spatial conservation prioritization by implementing systematic conservation planning to identify the minimum number of years required to establish an effective and robust MPA network, applied to highly mobile marine megafauna in relation to their main threat: fishing activity.
14. Spatially explicit conservation plans based on a period equal or greater than three years provide similar MPAs configurations, showing analogous areas of high irreplaceability and spatial prioritization.
15. We recommend the use of this method for future spatial prioritizations for highly mobile species, in particular for the configuration of MPAs in high seas, an area of special interest for many highly mobile species of conservation interest.

Thesis

The specific results obtained on this thesis dissertation allowed working towards the validation of the enunciated working hypothesis, being the thesis that:

"The distribution and abundance of the multiple species conforming the marine megafauna assemblage of the Bay of Biscay are affected by human threats, as well as by environmental variability independently of the years and geographic coverage considered. Long-term time series of both, megafauna distribution and abundance and threats need to be considered for the development of spatially explicit measures. In addition, the ecological coherence of the current Marine Protected Area network needs to be assessed to ascertain whether the critical areas of marine megafauna are included, as we have shown is not the case for some species. These actions are needed in order to inform the management and conservation of the marine megafauna species in the context of the Marine Strategy Framework Directive and other relevant legislation"

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APPENDICES

CHAPTER 1 – APPENDIX A

Which are the main threats affecting the marine megafauna in the Bay of Biscay?

Appendix A – Section 1: Species data

Table A-1.1. Species of seabirds listed in the Bay of Biscay (North Atlantic demarcation) and frequency of occurrence. Adapted from MAGRAMA, 2012a. The table also shows the status of the species at global and European scale given by the IUCN, the status in Spain based on the Red Book of the Birds of Spain (Madroño et al., 2004) and the Royal Decree 139/2011 for The Development Of The List Of Wild Species In Regime Of Special Protection And The Spanish Catalogue Of Endangered Species (RD 139/2011). DD: data deficient; LC: Least concern; NT: Near threatened; VU: Vulnerable; EN: Endangered; CR: Critically Endangered; EX?: not sure if is Extinct; NE: not evaluated.

FAMILY	SPECIES	COMMON NAME	OCCURENCE	IUCN GLOBAL	IUCN EUROPE	RED BOOK SPAIN	RD 139/2011
Anatidae	*Melanitta nigra*	Black scoter	Common	NE	NE	NE	*
	Mergus serrator	Red-breasted merganser	Rare	LC	NT	NE	*
Gaviidae	*Gavia stellata*	Red-throated loon	Rare	LC	LC	NE	*
	Gavia arctica	Black-throated loon	Rare	LC	LC	NE	*
	Gavia immer	Common loon	Rare	LC	VU	VU	*
Procellariidae	*Calonectris diomedea*	Cory's shearwater	Abundant	LC	LC	VU	VU*
	Puffinus	Manx shearwater	Common	LC	LC	EN	VU*
	Ardenna gravis	Great Shearwater	Abundant	LC	NE		
	Ardenna grisea	Sooty shearwater	Abundant	NT	NE		*
	Puffinus mauretanicus	Balearic shearwater	Abundant	CR	CR	CR	CR*
Hydrobatidae	*Hydrobates pelagicus*	European storm-petrel	Abundant	LC	LC	VU	*
	Oceanodroma leucorhoa	Leach's storm-petrel	Rare	VU	LC		*
	Oceanodroma castro	Band-rumped storm-petrel	Rare	LC	LC	EN	VU*
Sulidae	*Morus bassanus*	Northern gannet	Abundant	LC	LC	NE	*
Phalacrocoracidae	*Phalacrocorax carbo*	Great cormorant	Abundant	LC	LC	NE	*
	Phalacrocorax aristotelis	European shag	Abundant	LC	LC	EN	*
Stercorariidae	*Stercorarius pomarinus*	Pomarine jaeger	Common	LC	LC	NE	*
	Stercorarius parasiticus	Arctic jaeger	Common	LC	LC	NE	*
	Stercorarius skua	Great skua	Common	LC	LC	NE	*

* Species for which Special Protection Areas (SPAs) should be considered under the Birds Directive (Annex I and migratory species).

Table A-1.1. Continuation

FAMILY	SPECIES	COMMON NAME	OCCURENCE	IUCN GLOBAL	IUCN EUROPE	RED BOOK SPAIN	RD 139/2011
Laridae	*Ichthyaetus melanocephalus*	Mediterranean gull	Common	NE	NE	NE	*
	Hydrocoloeus minutus	Little gull	Rare	LC	NT	NE	*
	Larus sabini	Sabine's gull	Common	LC	LC		
	Chroicocephalus ridibundus	Black-headed gull	Common	LC	LC	NE	*
	Larus canus	Common gull	Rare	LC	LC	NE	*
	Larus fuscus	Lesser black-backed gull	Abundant	LC	LC	LC	*
	Larus michahellis	Yellow-legged gull	Abundant	LC	LC	NE	*
	Larus marinus	Great black-backed Gull	Rare	LC	LC	NE	*
	Rissa tridactyla	Kittiwake	Common	VU	VU	VU	*
	Thalasseus sandvicensis	Sandwich tern	Common	LC	LC	NT	*
	Sterna hirundo	Common tern	Common	LC	LC	NT	*
	Sterna paradisaea	Arctic tern	Common	LC	LC	NE	*
	Sternula albifrons	Little tern	Common	LC	LC	NT	*
Alcidae	*Uria aalge*	Common guillemot	Common	LC	NT	CR	*
	Alca torda	Razorbill	Common	NT	NT	NE	*
	Fratercula arctica	Atlantic puffin	Rare	VU	EN	NE	*

* Species for which Special Protection Areas (SPAs) should be considered under the Birds Directive (Annex I and migratory species).

Table A-1.2. Species of marine mammals listed in the Bay of Biscay (North Atlantic demarcation) and frequency of occurrence. Adapted from MAGRAMA, 2012b. The table also shows the status of the species at global and European scale given by the IUCN, the status in Spain based on the categories of the Red Book of Spanish vertebrates (Blanco and González, 1992) and the Royal Decree 139/2011 for The Development Of The List Of Wild Species In Regime Of Special Protection And The Spanish Catalogue Of Endangered Species (RD 139/2011). DD: data deficient; LC: Least concern; NT: Near threatened; VU: Vulnerable; EN: Endangered; CR: Critically Endangered; EX?: not sure if is Extinct; NE: not evaluated.

FAMILY	SPECIES	COMMON NAME	OCCURENCE	IUCN GLOBAL	IUCN EUROPE	RED BOOK SPAIN	RD 139/2011
Balaenopteridae	*Balaenoptera acutorostrata*	Minke whale	Occasional	LC	LC	VU	VU
	Balaenoptera borealis	Sei whale	Occasional	EN	EN	VU	VU
	Balaenoptera musculus	Blue whale	Rare	EN	EN	EN	VU
	Balaenoptera physalus	Fin whale	Common	EN	NT	VU	VU
	Megaptera novaeangliae	Humpback whale	Occasional	LC	LC	EN	VU
Balaenidae	*Eubalaena glacialis*	North Atlantic right whale	Extinct?	EN	CR	EX?	CR
Delphinidae	*Delphinus delphis*	Common dolphin	Common	LC	DD	DD	SP
	Globicephala melas	Long-finned pilot whale	Common	DD	DD	DD	SP
	Globicephala macrorhynchus	Short-finned Pilot Whale	Rare	DD	NE	NE	VU
	Grampus griseus	Risso's dolphin	Common	LC	DD	NE	SP
	Orcinus orca	Killer whale	Rare	DD	DD	DD	SP
	Pseudorca crassidens	False killer whale	Rare	DD	NE	NE	SP
	Stenella coeruleoalba	Striped dolphin	Common	LC	DD	DD	SP
	Tursiops truncatus	Bottlenose dolphin	Common	LC	DD	DD	VU**
	Lagenorhynchus albirostris	White-beaked dolphin	Rare	LC	LC	NE	SP*
	Lagenorhynchus acutus	Atlantic white-sided dolphin	Rare	LC	LC	NE	SP*
Phocoenidae	*Phocoena*	Harbour porpoise	Common	LC	VU	VU	VU**

* Species not included, by default it means that the category is SP.

** Species included in the Annex II of the Habitats Directive which it is required the establishment of Special Areas of conservation (SACs).

Table A-1.2. Continuation

FAMILY	SPECIES	COMMON NAME	OCCURENCE	IUCN GLOBAL	IUCN EUROPE	RED BOOK SPAIN	RD 139/2011
Physeteridae	*Kogia breviceps*	Pygmy sperm whale	Occasional	DD	NE	NT	SP
	Physeter macrocephalus	Sperm whale	Common	VU	VU	VU	VU
Ziphiidae	*Hyperoodon ampullatus*	North Atlantic bottlenose whale	Rare	DD	DD	NE	SP
	Mesoplodon densirostris	Blainville's beaked whale	Rare	DD	DD	NT	SP
	Mesoplodon mirus	True's beaked whale	Rare	DD	DD	NT	SP
	Mesoplodon bidens	Sowerby's beaked whale	Rare	DD	DD	NT	SP*
	Ziphius cavirostris	Cuvier's beaked whale	Occasional	LC	DD	NE	SP

* Species not included, by default it means that the category is SP.

** Species included in the Annex II of the Habitats Directive which it is required the establishment of Special Areas of conservation (SACs).

Appendix A – Section 2: Seabird admissions

Table A-2.1. Seabird causes of admission (n=4,023) to the Wildlife Rehabilitation Centres of the Cantabrian coast during the years 2004-2016.

GROUP	CAUSE OF ADMISSION	FAMILY ALCIDAE				FAMILY LARIDAE											
		Alca torda	*Alle alle*	*Fratercula arctica*	*Uria aalge*	*Chroicocephalus ridibundus*	*Hydrocoloeus minutus*	*Larus argentatus*	*Larus cachinnans*	*Larus canus*	*Larus fuscus*	*Larus michahellis*	*Larus sp.*	*Rissa tridactyla*	*Sterna hirundo*	*Sterna paradisaea*	*Thalasseus sandvicensis*
CLIMATE CHANGE	**Cachexia**	89	4	55	1057	103	1	27	39	2	6	254	5	12	6	0	9
FISHING	**Fishing gear interaction**	4	0	0	11	10	0	5	2	0	0	34	0	1	0	0	0
POLLUTION	**Crude oil**	21	0	10	307	2	1	0	1	0	1	11	0	0	3	0	0
OTHERS	**Traumas:**																
	Car impact	0	0	0	0	0	0	0	0	0	0	10	1	1	0	0	0
	Gunshot	0	0	0	0	5	0	4	5	0	1	33	3	0	1	0	0
	Electrocution	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	Undefined Trauma	2	0	1	10	53	1	6	32	0	6	318	21	2	2	0	0
	Forfeited	0	0	0	0	2	0	0	0	0	0	2	0	0	0	0	0
	Poisoning	3	0	3	8	0	1	0	5	0	0	25	2	0	1	0	0
	Autolytic	0	0	1	4	1	0	0	0	0	2	5	0	0	0	0	0
	Orphaned	0	0	0	0	4	0	0	5	0	0	182	19	0	0	0	0
	Intraspecific interaction	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0
	Disease:																
	Parasitic/Infectious disease	0	0	0	0	4	0	0	1	0	0	21	22	0	0	0	0
	Others	0	0	0	0	4	0	0	0	0	0	12	4	0	0	0	0
	Other causes:																
	Without apparent lesions	4	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0
	Undetermined	1	0	1	62	6	0	0	1	0	3	47	2	0	3	1	0
	Others	0	0	0	0	5	0	0	2	0	3	123	3	0	0	0	0
	Total	124	4	72	1459	196	4	43	91	2	19	955	79	16	16	1	9
	%	3.08	0.10	1.79	36.27	4.87	0.10	1.07	2.26	0.05	0.47	23.74	1.96	0.40	0.40	0.02	0.22

Table A-2.1. Continuation

GROUP	CAUSE OF ADMISSION	FAMILY SULIDAE	FAMILY PHALACROCORACIDAE		FAMILY HIDROBATIDAE		FAMILY PROCELLARIDAE				FAMILY GAVIIDAE	
		Morus bassanus	*Phalacrocorax aristotelis*	*Phalacrocorax carbo*	*Hydrobates pelagicus*	*Oceanodroma leucorhoa*	*Calonectris diomedea*	*Fulmarus glacialis*	*Puffinus mauretanicus*	*Puffinus puffinus*	*Gavia arctica*	*Gavia immer*
CLIMATE CHANGE	**Cachexia**	273	10	38	34	9	1	17	1	1	0	1
FISHING	**Fishing gear interaction**	114	6	18	0	0	0	0	0	0	1	1
POLLUTION	**Crude oil**	33	0	3	0	0	0	1	0	0	0	0
OTHERS	**Traumas:**											
	Car impact	1	0	0	0	0	0	0	0	0	0	0
	Gunshot	1	0	19	0	0	0	0	0	0	0	0
	Electrocution	2	0	0	0	0	0	0	0	0	0	0
	Undefined Trauma	34	2	15	2	0	0	1	0	0	1	1
	Forfeited	2	0	0	0	0	0	0	0	0	0	0
	Poisoning	2	0	4	0	0	0	0	0	0	0	1
	Autolytic	0	1	1	0	0	0	0	0	0	0	0
	Orphaned	11	2	1	0	0	0	0	0	0	0	0
	Intraspecific interaction	0	0	0	0	0	0	0	0	0	0	0
	Disease:											
	Parasitic/Infectious disease	2	4	3	1	0	0	0	0	0	0	0
	Others	4	0	0	0	0	0	0	0	0	0	0
	Other causes:											
	Without apparent lesions	42	9	0	0	0	1	0	0	0	0	1
	Undetermined	11	4	22	0	0	0	0	0	0	0	0
	Others	4	2	1	1	0	1	0	0	1	0	0
	Total	532	38	124	37	9	2	19	1	1	2	5
	%	13.22	0.94	3.08	0.92	0.22	0.05	0.47	0.02	0.02	0.05	0.12

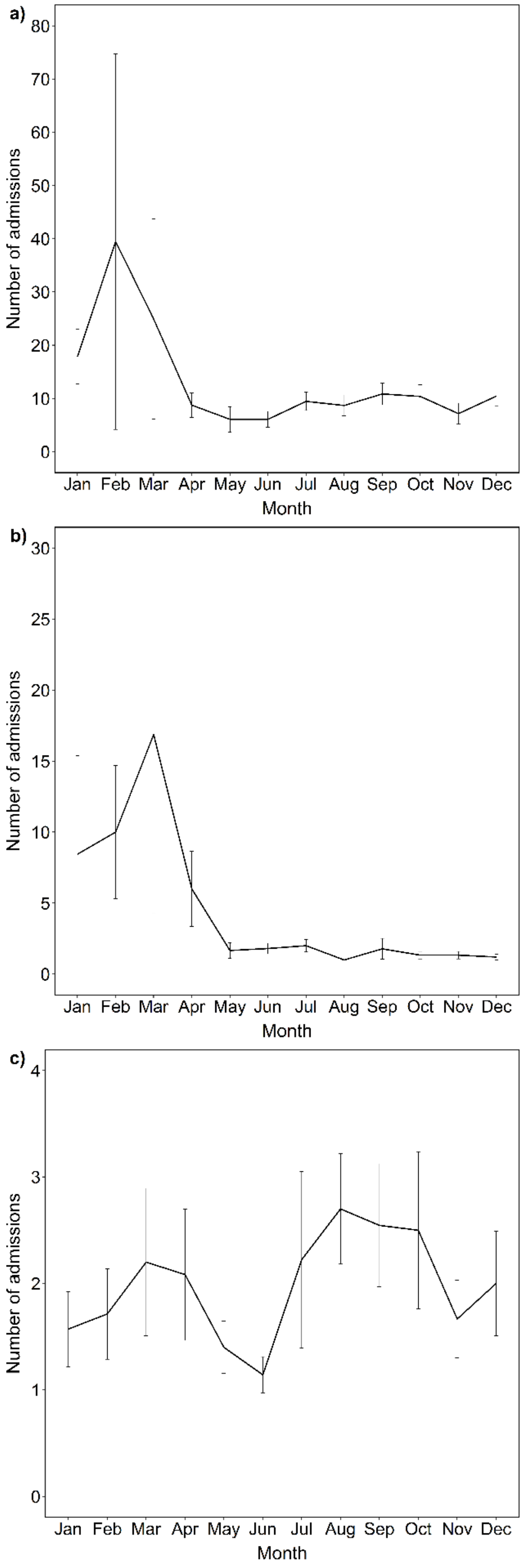
Table A-2.1. Continuation

GROUP	CAUSE OF ADMISSION	FAMILY ANATIDAE	FAMILY STERCORARIIDAE		
		Melanitta nigra	*Catharacta skua*	*Total*	%
CLIMATE CHANGE	**Cachexia**	5	2	2061	51.3
FISHING	**Fishing gear interaction**	0	0	207	5.15
POLLUTION	**Crude oil**	3	0	397	9.87
OTHERS	**Traumas:**				
	Car impact	0	0	13	0.32
	Gunshot	0	0	72	1.79
	Electrocution	0	0	2	0.05
	Undefined Trauma	1	0	511	12.8
	Forfeited	0	0	6	0.15
	Poisoning	1	1	57	1.42
	Autolytic	0	0	15	0.37
	Orphaned	0	0	224	5.57
	Intraspecific interaction	0	0	2	0.05
	Disease:				
	Parasitic/Infectious disease	0	0	58	1.44
	Others	0	0	24	0.60
	Other causes:				
	Without apparent lesions	2	0	62	1.54
	Undetermined	3	0	167	4.15
	Others	0	0	146	3.63
	Total	15	3	4,023	
	%	0.37	0.07		

Table A-2.2. Number of seabird admissions per year (expressed as percentage of the total number of admissions) to the Wildlife Rehabilitation Centres of the Cantabrian coast during the years 2004-2016. The table also shows the overall inter-annual variability (CV) of the admissions per species.

	% admissions /year													
Species	**2004**	**2005**	**2006**	**2007**	**2008**	**2009**	**2010**	**2011**	**2012**	**2013**	**2014**	**2015**	**2016**	**CV**
Alca torda	2.60	1.69	0.62	7.22	0.93	1.10	3.56	2.49	4.81	3.86	2.76	1.85	5.81	0.66
Alle					0.47	1.65								2.86
Calonectris diomedea												0.74	0.29	2.70
Catharacta skua							0.44		0.48		0.13			2.13
Fratercula arctica	1.20	1.13	0.31	0.34		1.10	2.67	7.47	0.48	1.40	3.15	1.11	0.87	1.20
Fulmarus glacialis	0.20	1.13		1.03	2.79	0.55		0.41	0.96				0.87	1.29
Gavia arctica													0.58	3.61
Gavia immer					0.47	0.55		0.83			0.13			1.83
Hydrocoloeus minutus						1.65			0.48					2.84
Hydrobates pelagicus	0.40	0.56	3.72	1.37	2.33	1.65	1.33	0.83			0.13	1.85		1.02
Larus argentatus	1.60	2.26	0.93	5.84		3.30		1.24		0.70				1.42
Larus cachinnans	0.40	1.69	7.12	3.78			2.67	2.07	4.81	6.67	1.84			1.06
Larus canus				0.69										3.61
Larus fuscus			2.17			0.55	0.44	1.24	0.48	1.75	0.13	1.11		1.22
Larus michahellis	32.00	26.55	20.74	19.59	23.26	31.32	36.44	25.31	24.52	25.61	12.60	52.59	39.24	0.36
Chroicocephalus ridibundus	2.00	6.21	4.95	3.78	7.91	8.24	6.67	6.64	6.73	6.67	3.67	5.93	3.78	0.33
Larus sp.					12.56	4.95	3.56	7.88	8.65	0.35				1.47
Melanita nigra	0.20	2.82	0.31		0.47	0.55		1.24			0.26		0.29	1.66
Oceanodroma leucorhoa						0.55	0.89	0.41		0.70		0.74	0.29	1.24
Phalacrocorax aristotelis	0.20				0.93	0.55	2.67	2.90	1.92	0.35	1.44	1.11	1.16	0.97
Phalacrocorax carbo	2.40	3.95	3.72	2.06	4.65	7.14	6.22	3.32	4.33	4.91	0.92	2.22	2.03	0.48
Puffinus mauretanicus						0.55								3.61
Puffinus							0.44							2.50
Rissa tridactyla						4.95				0.35	0.13	0.37	1.16	2.55
Sterna hirundo	0.40	2.26	1.55	0.69	0.47						0.13		0.29	1.57
Sterna paradisaea		0.56												3.61
Sterna sandvicensis	1.20			0.34			0.89							2.12
Morus bassanus	5.40	14.12	4.33	12.71	15.35	15.38	20.00	24.48	21.15	22.46	6.43	20.00	16.57	0.43
Uria aalge	49.80	35.03	49.54	40.55	27.44	13.74	11.11	11.20	20.19	24.21	66.14	10.37	26.45	0.59

Figure A-2.1. Total number of seabird admissions by month to the Wildlife Rehabilitation Centres of the Cantabrian coast during the years 2004-2016 diagnosed as a) cachexia, b) presence of crude oil and c) interaction with fishing.



Appendix A – Section 3: List of references

Table A-3.1. List of references used to create the threat matrix both, for marine mammals and seabirds (Tables 1.1 and 1.2 of the Chapter 1 respectively).

Code	Reference
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Chapter 2 – Appendix B

Understanding the 3D environment of pelagic seabirds from multidisciplinary oceanographic surveys to advance ecosystem-based monitoring

Appendix B – Section 1: Non-breeding diet of pelagic seabirds

Table B-1.1. Non-breeding diet of highly pelagic seabirds in the Northwest Atlantic Ocean extracted from Ronconi et al. (2010).

Species	n	Krill	Herring	Squid	Mackerel	Sandlance	Pollock livers
Great shearwater	231	0.19	0.36	0.135	0.105	0.125	0.08
Sooty shearwater	22	0.265	0.305	0.17	0.065	0.13	0.05

Appendix B – Section 2: Horizontal fields of oceanographic descriptors

To obtain horizontal fields of temperature (TEM, ºC), salinity (SAL, p.s.u.), dynamic height (DYN), depth of maximum temperature gradient (DTG, m) and maximum temperature gradient (MTG, ºC m^{-1}), 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 0.15º × 0.15º. Since this scheme analyses observation increments (Gomis et al., 2001), we used a local 1st order degree polynomial least-square fit to the observations to estimate a background field and to compute the anomalies. Then, 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 DYN profiles correlation statistics obtained at different depths. The noise-to-signal (NTS) variance ratio used for the analysis of TEM, 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 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). Finally, all fields were spatially smoothed, with an additional low-pass filter with a cut-off length scale of 30 km, in order to avoid aliasing errors due to unresolved structures.

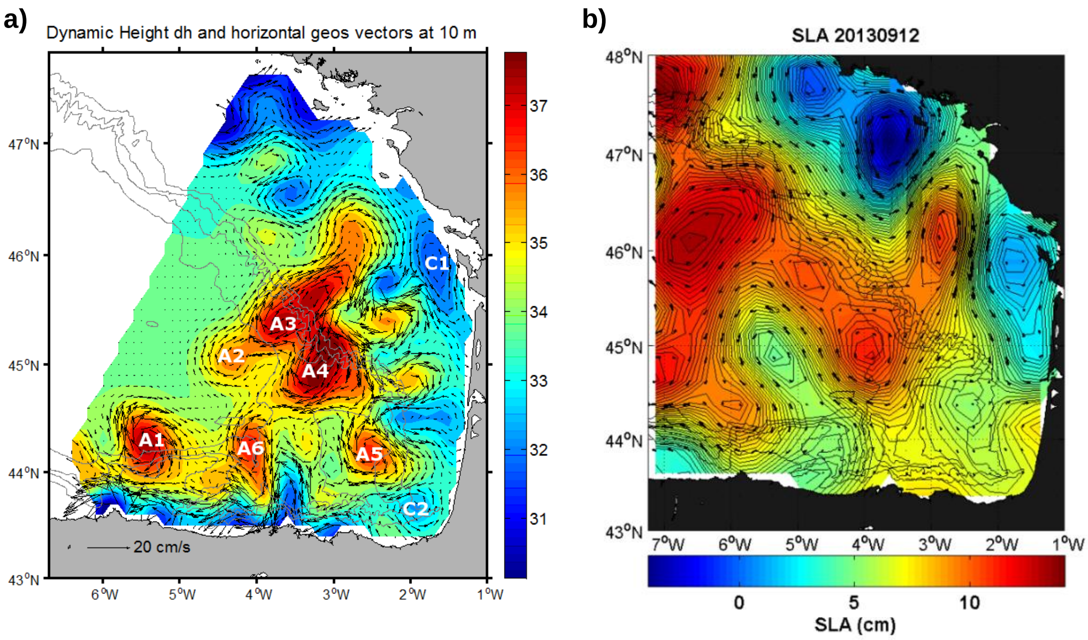
After station DYN data were interpolated onto the grid, all levels were referred to the lowest one by adding the contributions of all the levels below. This method allows profiles obtained at shallow stations take part in the recovery of the dynamic height field and has been previously tested over the continental shelf (*e.g.,* Rubio et al., 2009). Then, geostrophic velocities (GEO, m s^{-1}) were obtained by the first derivative between adjacent grid nodes of the DYN interpolated fields.

The used of in situ CTD data can be challenging and different methodological steps are necessary to undertake to assure the validity of the oceanographic outcomes used to describe the regional of oceanography. Among them, the OSI is a robust methodology to obtain interpolated fields from uneven spaced data (Cotroneo et al., 2016; León et al., 2015; Torres et al., 2011). In the schema used here, too additional parameters control the scales that are resolved and permit to filter out small structures that could emerge from the interpolation and that are not resolved by the original data. Those are the correlation length scale (which avoids spurious structures between observational points that are too far away) and the cut-off length scale which smooths the resulting interpolated fields to avoid structures under a given scale which are not resolved by the original observations. The first parameter is fixed taking into account the empirical correlation scales computed using the original data. The second one is fixed taking into account the mean distance between CTD stations.

In addition to using a robust methodology, we carefully processed the CTD data to avoid salinity spikes (and the associated density), bias in temperature or conductivity between the profiles of the two ships, low synoptic measurements in a given area, among others. Moreover, resulting OSI fields have been validated individually by comparison with satellite imagery (SST, IR) and Sea Level Anomaly (SLA) maps, and even with the fields from Copernicus CMEMS GLORYS reanalyses.

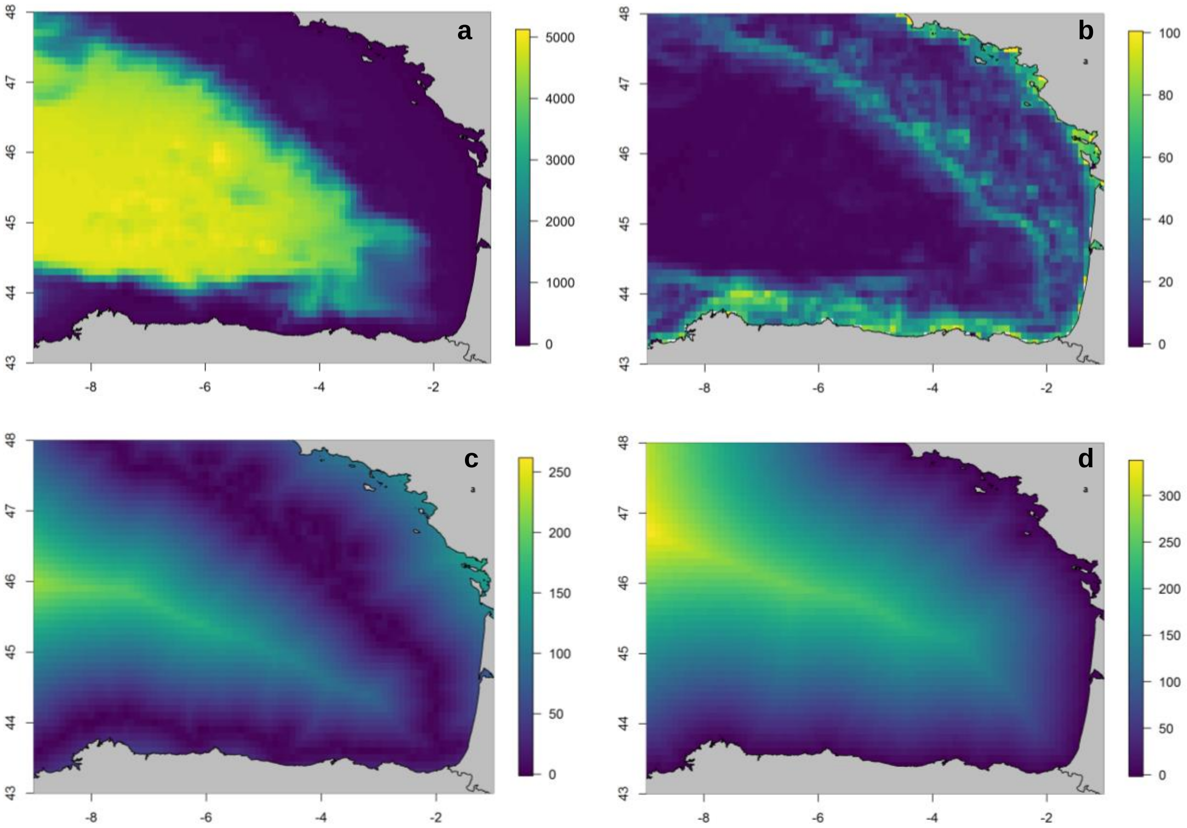
An example is given in Figure B-2.1 where there is an agreement in the area covered by CTD measurements of the in-situ dynamic heights with the corresponding SLA fields. Satellite SLA fields offer much lower spatial resolution. Satellite SLA can be used as an alternative to obtain dynamic heights in an area where there is no in-situ observational data. SLA mapped fields consist in an optimal interpolation (similar methodology to the one used in this study) of along-track SLA data obtained from a constellation of altimeters onboard satellites measuring the global sea level with a revisit period higher than a week and a track distance around tens of kilometres. Thus, even if the along-track resolution is classically of around 7 km the resulting interpolated (and smoothed) SLA maps and the derived geostrophic currents are of much less spatio-temporal resolution (see for instance Dussurget et al. 2011) that the one obtained from the analysis of in-situ observations, following the methodology used in this study. Moreover, satellite SLA fields present specific problems in the coastal area, where the sea level measurements have lower quality than in the open ocean.

Figure B-2.1. (a) Interpolated fields of dynamic height (values in dynamic meters indicated by the respective colour bars) and geostrophic vectors at 10 m obtained from JUVENA 2013 CTD data. (b) Interpolated fields of satellite sea level anomalies (SLA) in cm and geostrophic vectors during 12th September 2013.



Appendix B – Section 3: Static variables

Figure B-3.1. Static variables such as (a) bathymetry (BAT, m) and (b) its spatial gradient (BATG), (c) distance to the shelf-break (DSB, km) and distance to the coast (DCO, km).



Appendix B – Section 4: Characterising the vertical domain

Table B-4.1. Summary of pair-wise correlation analysis of preyscapes at different depth ranges by means of Spearman rank correlation coefficients and corresponding significance levels (lower and upper diagonal, respectively). Significance levels were set at <0.05, <0.01 and <0.001; NS: not significant. Strongly correlated (|rs| > 0.5) descriptors are marked in bold. See Table 1 for abbreviations.

	ANEJ$_{10}$	**ANEA$_{10}$**	**PIL$_{10}$**	**ANEJ$_{DTG}$**	**ANEA$_{DTG}$**	**PIL$_{DTG}$**	**ANEJ$_{70}$**	**ANEA$_{70}$**	**PIL$_{70}$**
ANEJ$_{10}$	NA	0.01	0.01	0.001	0.05	0.01	0.001	0.001	NS
ANEA$_{10}$	0.082	NA	0.001	NS	0.001	0.001	NS	0.001	0.001
PIL$_{10}$	0.094	**0.614**	NA	NS	0.001	0.001	NS	0.001	0.001
ANEJ$_{DTG}$	**0.680**	-0.011	0.05	NA	NS	0.05	0.001	0.01	NS
ANEA$_{DTG}$	0.069	**0.763**	**0.751**	0.038	NA	0.001	NS	0.001	0.001
PIL$_{DTG}$	0.086	**0.568**	**0.984**	0.066	**0.758**	NA	NS	0.001	0.001
ANEJ$_{70}$	**0.630**	-0.051	-0.029	**0.829**	-0.047	-0.029	NA	NS	NS
ANEA$_{70}$	0.128	**0.541**	**0.826**	0.081	**0.672**	**0.805**	0.040	NA	0.001
PIL$_{70}$	0.038	**0.537**	**0.727**	0.020	**0.687**	**0.702**	-0.030	**0.746**	NA

Table B-4.2. Summary of pair-wise correlation analysis of oceanographic variables at different depth ranges by means of Spearman rank correlation coefficients and corresponding significance levels (lower and upper diagonal, respectively). Significance levels were set at <0.05, <0.01 and <0.001; NS: not significant. Strongly correlated (|rs| > 0.5) descriptors are marked in bold. See Table 1 for abbreviations.

	SAL$_{10}$	**TEM$_{10}$**	**GEO$_{10}$**	**SAL$_{DTG}$**	**TEM$_{DTG}$**	**GEO$_{DTG}$**	**SAL$_{70}$**	**TEM$_{70}$**	**GEO$_{70}$**
SAL$_{10}$	NA	0.01	0.01	0.01	0.01	0.01	0.01	0.01	NS
TEM$_{10}$	-0.409	NA	0.01	0.01	0.01	0.01	0.001	0.01	0.01
GEO$_{10}$	-0.212	0.303	NA	0.01	0.01	0.01	0.001	0.05	0.01
SAL$_{DTG}$	**0.973**	-0.334	-0.206	NA	0.01	0.01	0.01	0.01	0.01
TEM$_{DTG}$	-0.394	**0.904**	0.254	-0.355	NA	0.01	0.001	0.01	0.01
GEO$_{DTG}$	-0.261	0.346	**0.973**	-0.258	0.311	NA	0.001	0.01	0.01
SAL$_{70}$	**0.627**	-0.019	0.051	**0.643**	-0.020	0.022	NA	0.001	0.01
TEM$_{70}$	0.361	0.101	-0.088	0.430	0.121	-0.109	0.004	NA	0.01
GEO$_{70}$	0.066	0.325	**0.630**	0.101	0.288	**0.679**	0.145	0.296	NA

Appendix B – Section 5: Seabird detection functions

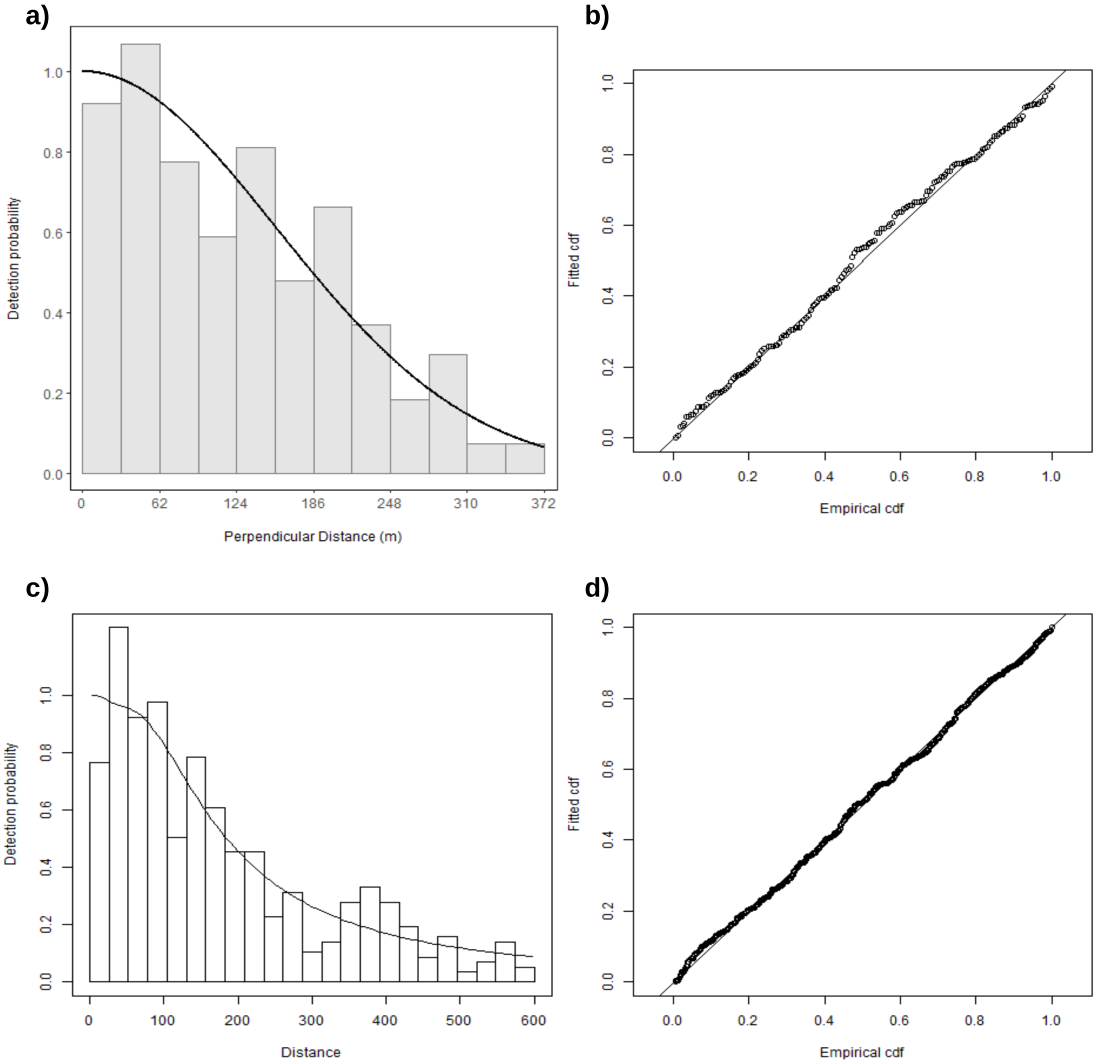
Table B-5.1. Modelling the detection function for Sooty shearwaters during the JUVENA surveys. Hn: half-normal. Hr: hazard-rate. Beaufort: sea state. waveH: wave height. Cloud: cloud cover.

Model	**Key function**	**Formula**	**AIC**	**Cramér-von Mises p-value**	**Pa**	**se (Pa)**	**ΔAIC**
hn	hn	~1	1963.132	0.738	0.489	0.032	0.000
hn.year	hn	~as.factor(Year)	1965.102	0.629	0.482	0.032	1.971
hn.size	hn	~group size	1965.119	0.720	0.489	0.036	1.988
hr	hr	~1	1965.999	0.358	0.603	0.032	2.868
hr.year	hr	~as.factor(Year)	1966.427	0.282	0.604	0.031	3.295
hr.size	hr	~size	1967.638	0.285	0.611	0.032	4.506
hn.beaufort	hn	~as.factor(Beaufort)	1969.324	0.657	0.486	0.033	6.192
hr.beaufort	hr	~as.factor(Beaufort)	1970.053	0.520	0.598	0.032	6.922
hn.waveH	hn	~as.factor(waveH)	1972.434	0.794	0.480	0.033	9.303
hn.cloud	hn	~as.factor(cloud)	1973.665	0.702	0.483	0.033	10.533
hr.waveH	hr	~as.factor(waveH)	1974.887	0.954	0.530	0.045	11.755
hr.cloud	hr	~as.factor(cloud)	1975.842	0.245	0.613	0.030	12.710

Table B-5.2. Modelling the detection function for great shearwaters during the JUVENA surveys. Hn: half-normal. Hr: hazard-rate. Beaufort: sea state. waveH: wave height. Cloud: cloud cover.

Model	**Key function**	**Formula**	**AIC**	**Cramér-von Mises p-value**	**Pa**	**se (Pa)**	**ΔAIC**
hr.beaufort	hr	~as.factor(Beaufort)	6394.602	0.837	0.397	0.027	0.000
hr.year	hr	~as.factor(year)	6396.791	0.841	0.401	0.026	2.189
hr.size	hr	~ group size	6398.656	0.779	0.399	0.027	4.054
hr	hr	~1	6399.875	0.746	0.404	0.026	5.273
hr.waveH	hr	~as.factor(waveH)	6405.030	0.796	0.402	5.239	10.428
hr.cloud	hr	~as.factor(cloud)	6408.496	0.790	0.398	0.026	13.894
hn.beaufort	hn	~as.factor(Beaufort)	6413.327	0.002	0.469	0.017	18.725
hn.year	hn	~as.factor(year)	6415.097	0.002	0.481	0.015	20.495
hn.waveH	hn	~as.factor(waveH)	6417.314	0.005	0.470	5.675	22.712
hn	hn	~1	6422.534	0.001	0.488	0.015	27.932
hn.size	hn	~size	6423.510	0.001	0.487	0.015	28.908
hn.cloud	hn	~as.factor(cloud)	6426.154	0.002	0.482	0.015	31.552

Figure B-5.1. Modelling the detection function for great shearwaters during the JUVENA surveys. Hn: half-normal. Hr: hazard-rate. Beaufort: sea state. waveH: wave height. Cloud: cloud cover.



Appendix B – Section 6: Correlation between descriptors

Table B-6.1. Pair-wise Spearman-rank correlation coefficient and corresponding significance levels (lower and upper diagonal, respectively) between 3D environmental descriptors integrated over the depth of maximum temperature gradient (DTG), 2D environmental descriptors and static descriptors. Significance levels were set at <0.05, <0.01 and <0.001; NS: not significant. Strongly correlated (|rs| > 0.5) descriptors are marked in bold. See Table 2.1 for abbreviations.

	ANEJ$_{DTG}$	**ANEA$_{DTG}$**	**PIL$_{DTG}$**	**SAL$_{DTG}$**	**TEM$_{DTG}$**	**GEO$_{DTG}$**	**DTG**	**MTG**	**SSTG**	**BAT**	**BATG**	**DCO**	**distSB**
ANEJ$_{DTG}$	NA	NS	0.05	0.001	0.001	0.001	NS	NS	0.05	0.01	NS	NS	NS
ANEA$_{DTG}$	0.038	NA	0.001	0.05	0.001	NS	NS	NS	0.01	0.001	0.001	0.001	NS
PIL$_{DTG}$	0.066	**0.758**	NA	0.05	0.001	0.001	NS	NS	NS	0.001	0.001	0.001	0.01
SAL$_{DTG}$	-0.195	0.078	0.07	NA	0.001	0.001	0.001	0.001	0.01	0.001	NS	NS	NS
TEM$_{DTG}$	0.131	-0.227	-0.244	-0.354	NA	0.001	0.001	NS	NS	0.001	0.001	0.001	NS
GEO$_{DTG}$	0.142	-0.056	-0.117	-0.259	0.312	NA	0.001	0.001	0.001	0.05	0.001	NS	0.001
DTG	-0.004	-0.017	-0.010	**0.541**	-0.173	-0.275	NA	0.001	0.001	0.001	0.001	0.001	0.001
MTG	0.013	-0.032	0.037	-0.264	-0.032	-0.131	-0.169	NA	NS	0.001	0.01	NS	0.001
SSTG	-0.064	0.081	-0.009	-0.088	0.013	0.364	-0.365	-0.05	NA	0.001	0.001	0.001	0.001
BAT	0.082	-0.238	-0.267	0.198	0.476	0.074	0.361	-0.199	-0.263	NA	0.001	0.001	0.001
BATG	-0.053	0.158	0.110	-0.035	-0.209	0.129	-0.235	-0.09	0.397	**-0.586**	NA	0.001	0.001
DCO	0.012	-0.239	-0.234	0.054	0.243	-0.029	0.292	-0.053	-0.349	**0.656**	**-0.524**	NA	0.001
DSB	0.045	0.049	0.093	0.051	0.033	-0.181	0.112	0.143	-0.249	0.266	**-0.688**	0.235	NA

Table B-6.2. Pair-wise Spearman-rank correlation coefficient and corresponding significance levels (lower and upper diagonal, respectively) between surface 3D environmental descriptors, 2D environmental descriptors and static descriptors. Significance level set at <0.05, <0.01 and <0.001; NS: not significant. Strongly correlated (|rs| > 0.5) descriptors are marked in bold. See Table 2.1 for abbreviations.

	ANEJ$_{10}$	**ANEA$_{10}$**	**PIL$_{10}$**	**SAL$_{10}$**	**TEM$_{10}$**	**GEO$_{10}$**	**DTG**	**MTG**	**SSTG**	**BAT**	**BATG**	**DCO**	**DSB**
ANEJ$_{10}$	NA	0.01	0.01	0.001	0.001	0.001	0.001	0.05	0.001	0.01	NS	NS	NS
ANEA$_{10}$	0.082	NA	0.001	NS	0.001	NS	0.001	NS	0.001	0.001	0.001	0.001	NS
PIL$_{10}$	0.094	**0.614**	NA	NS	0.001	0.01	NS	NS	NS	0.001	0.001	0.001	0.001
SAL$_{10}$	-0.399	-0.021	0.059	NA	0.001	0.001	0.001	0.001	0.05	0.001	NS	NS	NS
TEM$_{10}$	0.228	-0.171	-0.236	-0.408	NA	0.001	0.001	0.01	NS	0.001	0.001	0.001	NS
GEO$_{10}$	0.224	0.025	-0.094	-0.213	0.305	NA	0.001	0.001	0.001	NS	0.001	0.01	0.001
DTG	-0.376	-0.161	-0.055	0.486	-0.193	-0.225	NA	0.001	0.001	0.001	0.001	0.001	0.001
MTG	0.063	0.031	0.048	-0.251	-0.083	-0.166	-0.169	NA	NS	0.001	0.01	NS	0.001
SSTG	0.237	0.166	0.016	-0.065	0.032	0.406	-0.365	-0.05	NA	0.001	0.001	0.001	0.001
BAT	-0.083	-0.292	-0.295	0.139	0.456	0.039	0.361	-0.199	-0.263	NA	0.001	0.001	0.001
BATG	0.026	0.203	0.122	-0.015	-0.166	0.173	-0.235	-0.090	0.397	**-0.586**	NA	0.001	0.001
DCO	-0.029	-0.255	-0.261	0.056	0.176	-0.090	0.292	-0.053	-0.349	**0.656**	**-0.524**	NA	0.001
DSB	0.026	0.018	0.101	0.031	0.023	-0.213	0.112	0.143	-0.249	0.266	**-0.688**	0.235	NA

Appendix B – Section 7: Surface environmental conditions

Figure B-7.1. 3D preycapes represented by the spatial patterns of log-transformed biomass (tonnes) of juveniles (ANEJ$_{10}$) (a-d) and adults (ANEA$_{10}$) (e-h) of European anchovy and European pilchard (ANEJ$_{10}$) (i-l) at 10 m depth during the 2013-2016 period. White solid and dashed lines depict the annual effort coverage corresponding to the R/V Emma Bardán and R/V Ramón Margalef, respectively. Isobaths of 200 m, 1000 m and 2000 m are outlined. Geographic references are indicated in Figure 2.1.

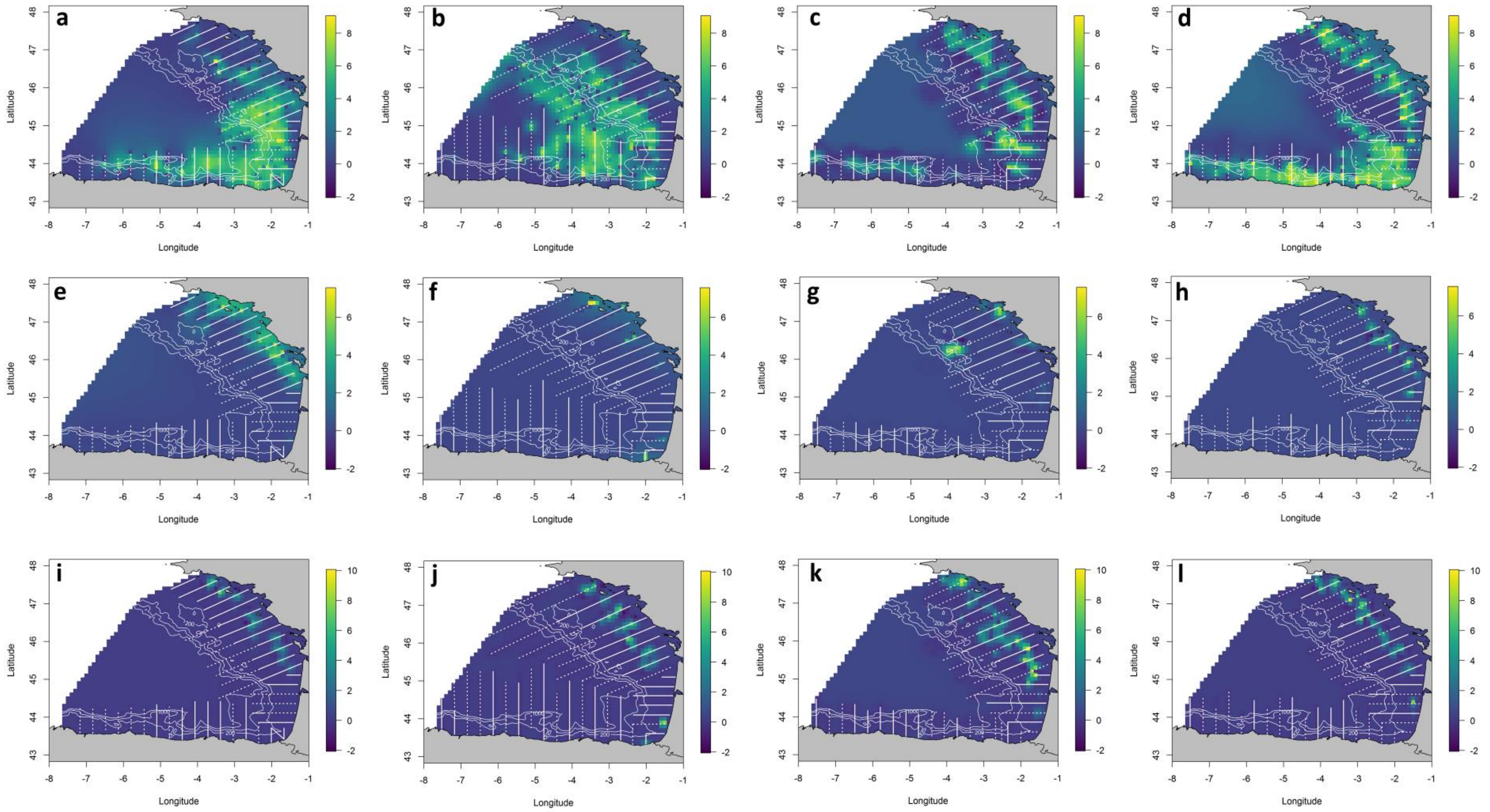
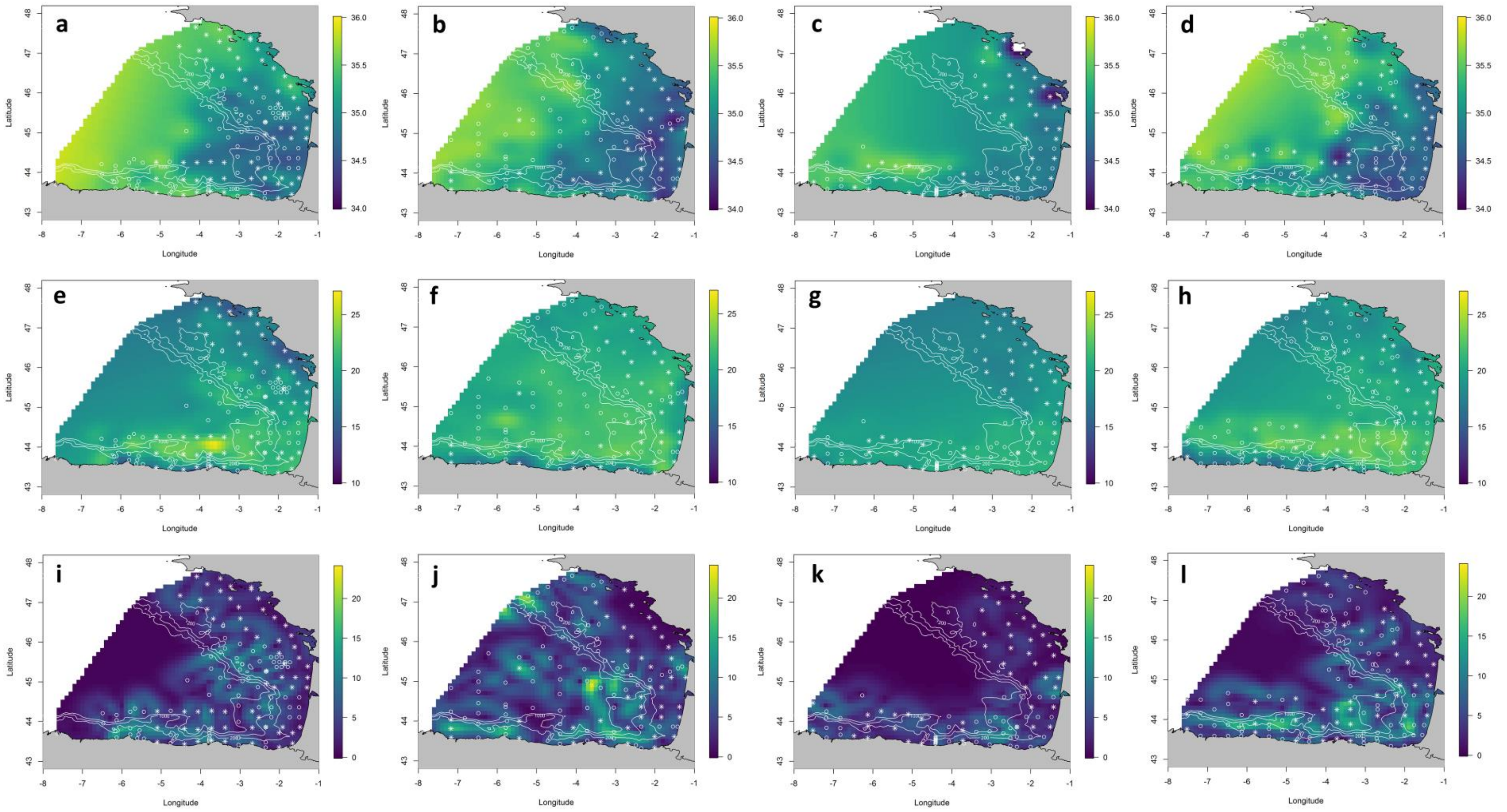


Figure B-7.2. 3D oceanographic environment represented by median values of (a-d) salinity (values in p.s.u., SAL_{10}), (e-h) temperature (values in ºC, TEM_{10}) and (i-l) geostrophic velocity module (values in ms^{-1}, GEO_{10}) at 10-m depth during the 2013-2016 period. Dots and stars represent CTD cats performed by Emma Bardán and Ramón Margalef RVs, respectively. Isobaths of 200 m, 1000 m and 2000 m are outlined. Geographic references are indicated in Figure 2.1.



CHAPTER 3 – APPENDIX C

Essential dynamic ocean variables shape the environmental envelopes of marine megafauna diversity

Appendix C – Section 1: Species data

Figure C-1.1. Northern gannet (*Morus bassanus*) data from the PELACUS surveys 2007-2016. a) Number of sightings collected and individuals sighted each year and b) map of sightings and number of individuals per sighting.

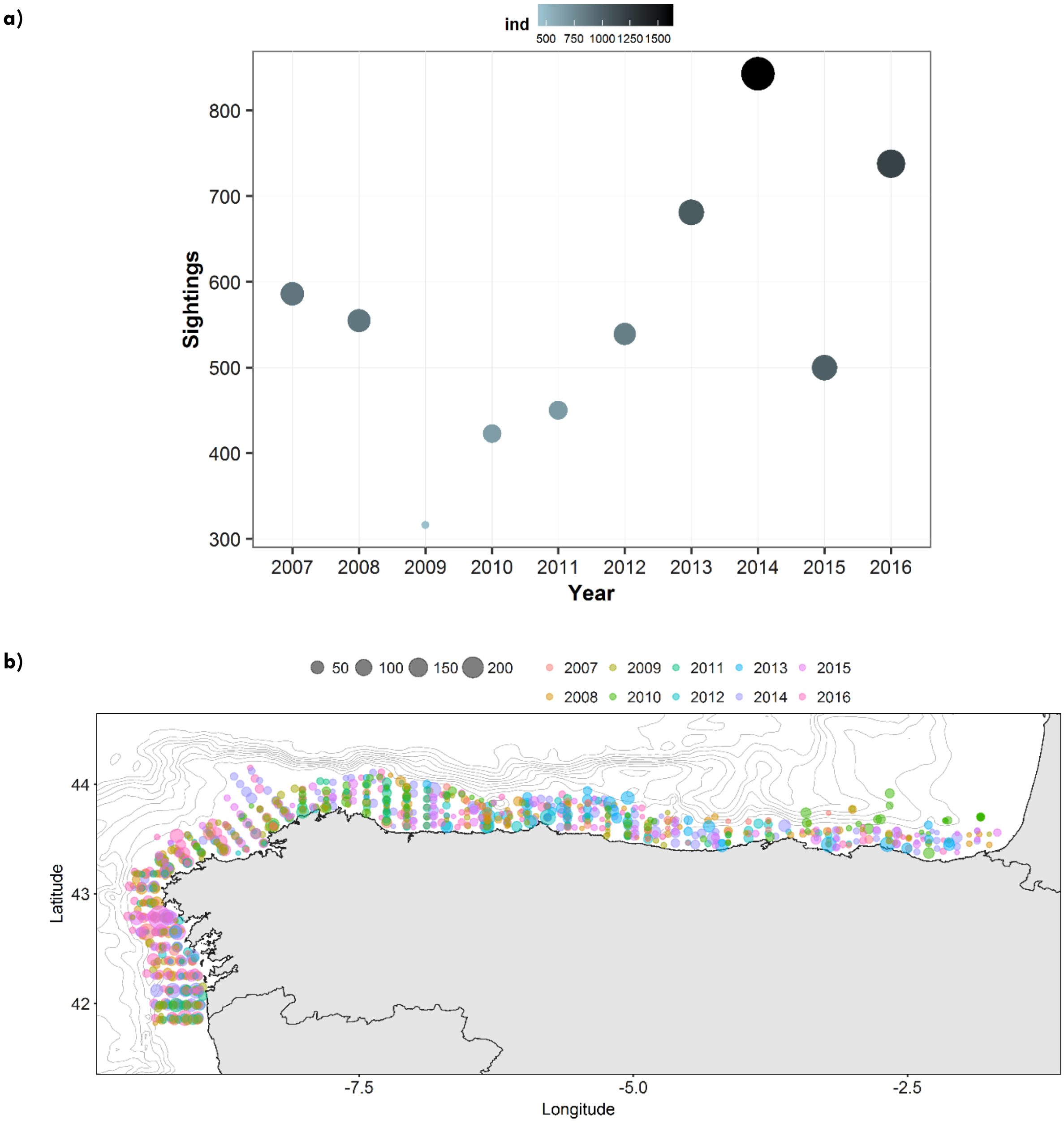


Figure C-1.2. Lesser black-backed gull (*Larus fuscus*) data from the PELACUS surveys 2007-2016. a) Number of sightings collected and individuals sighted each year and b) map of sightings and number of individuals per sighting.

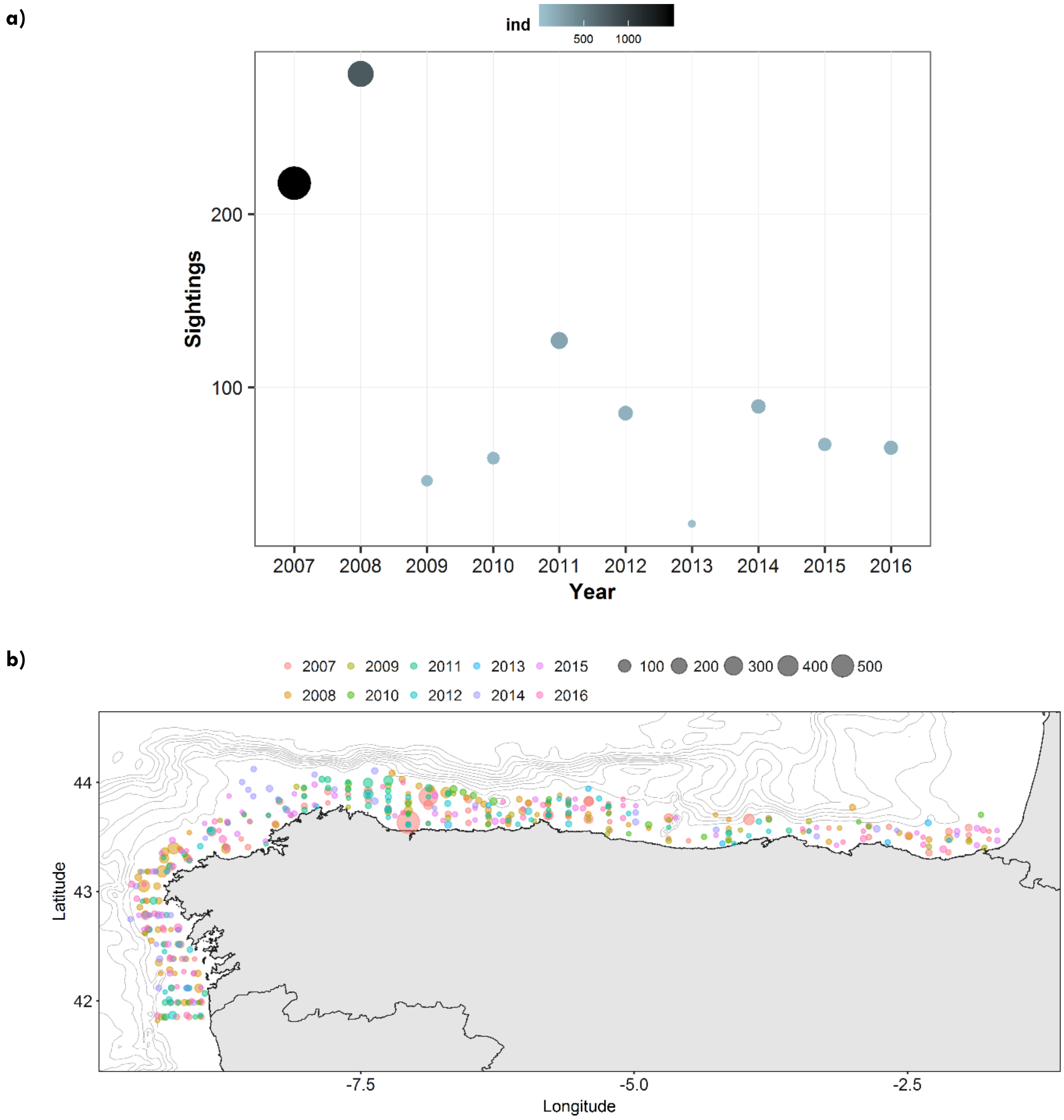


Figure C-1.3. Yellow-legged gull (*Larus michahellis*) data from the PELACUS surveys 2007-2016. a) Number of sightings collected and individuals sighted each year and b) map of sightings and number of individuals per sighting.

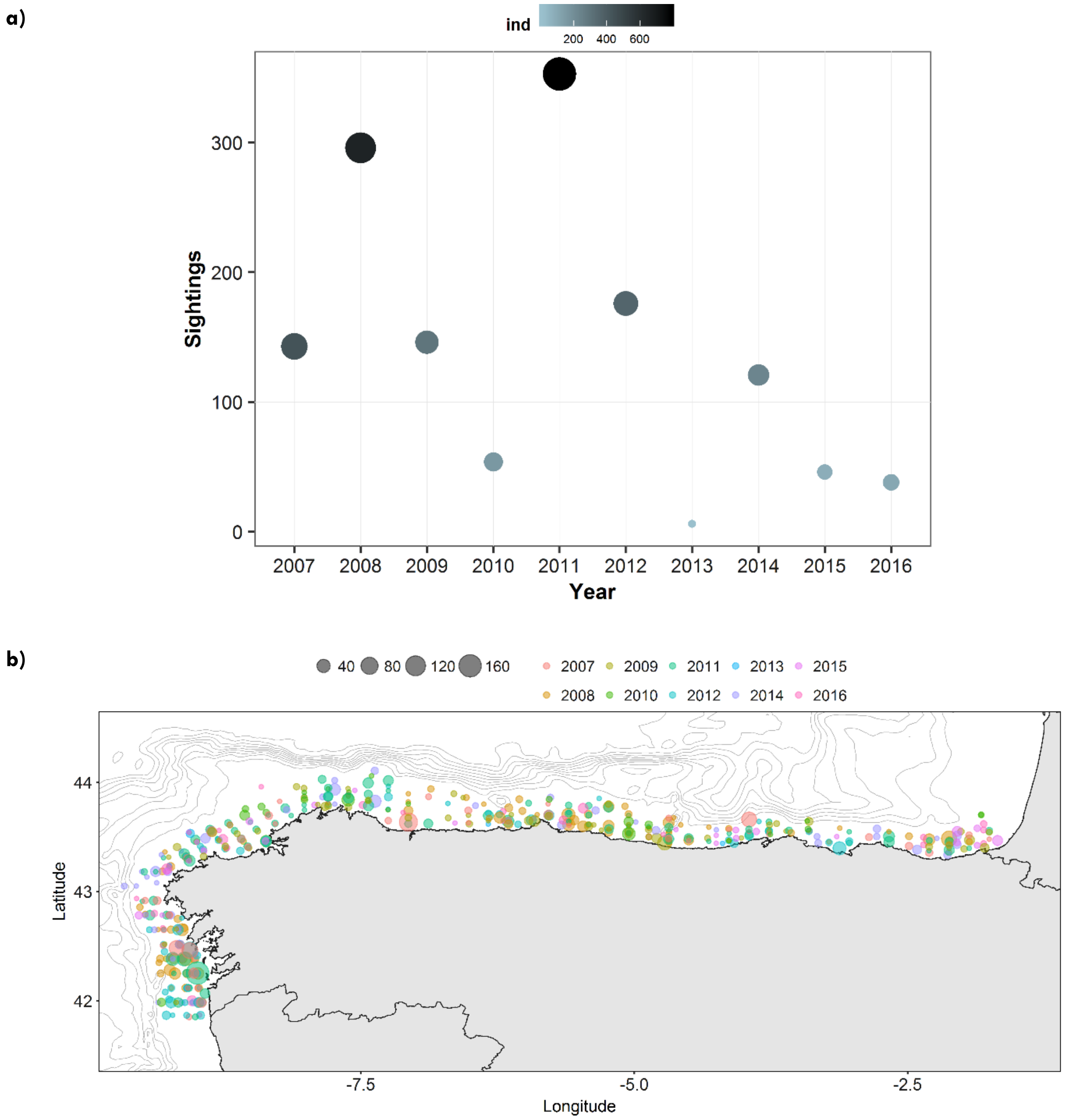
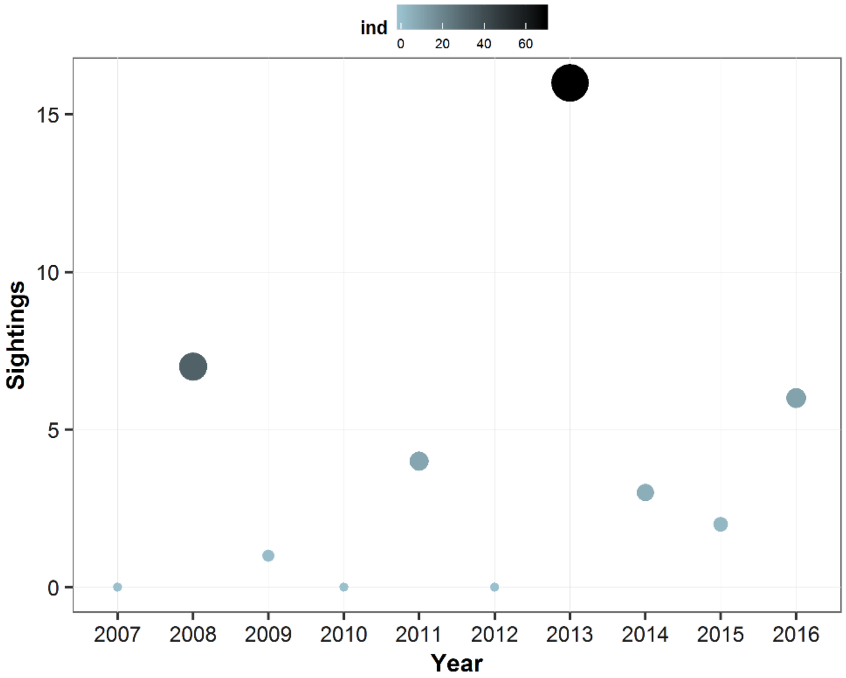


Figure C-1.4. Mediterranean gull (*Ichthyaetus melanocephalus*) data from the PELACUS surveys 2007-2016. a) Number of sightings collected and individuals sighted each year and b) map of sightings and number of individuals per sighting.

a)



b)

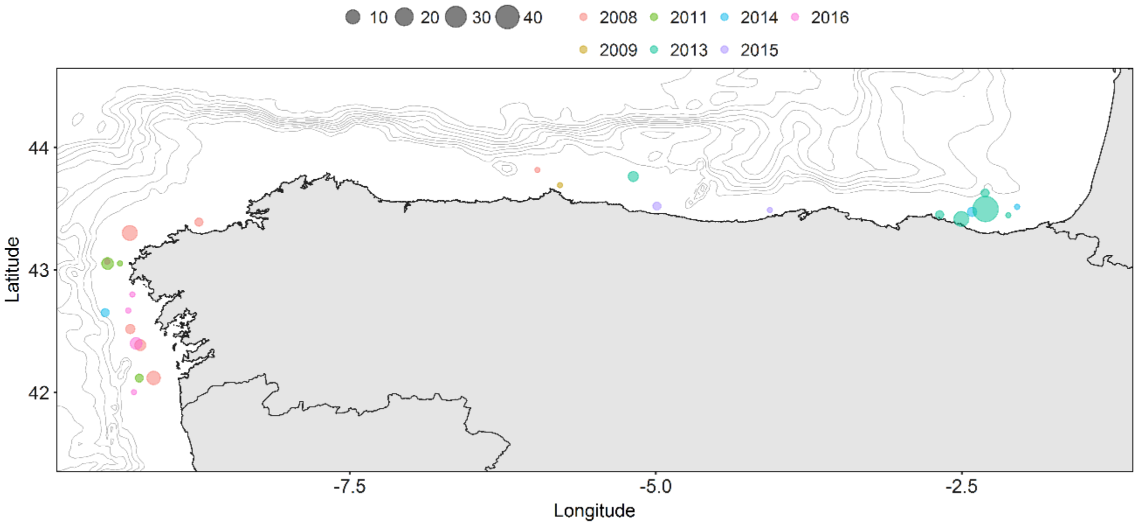


Figure C-1.5. Great skua (*Stercorarius skua*) data from the PELACUS surveys 2007-2016. a) Number of sightings collected and individuals sighted each year and b) map of sightings and number of individuals per sighting.

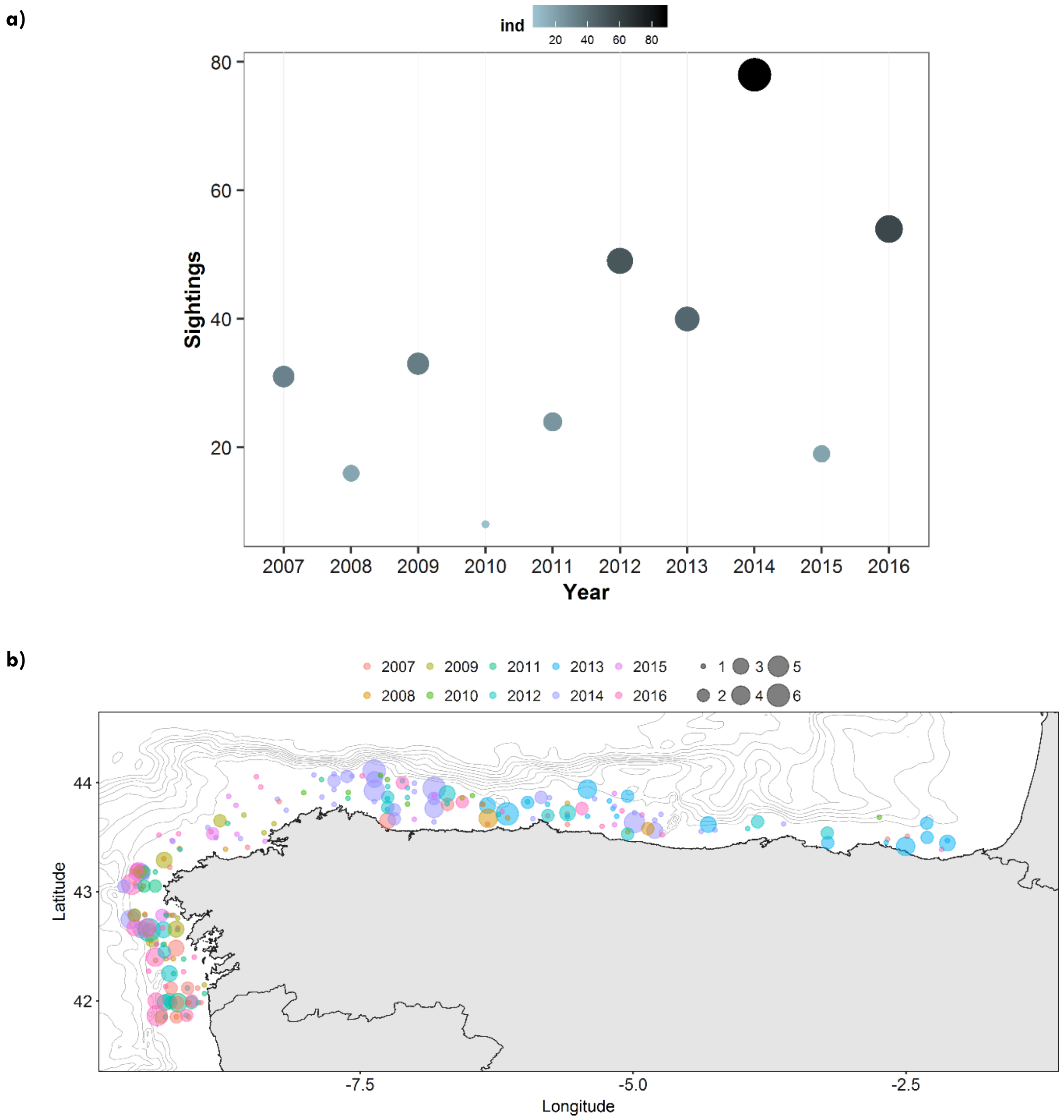
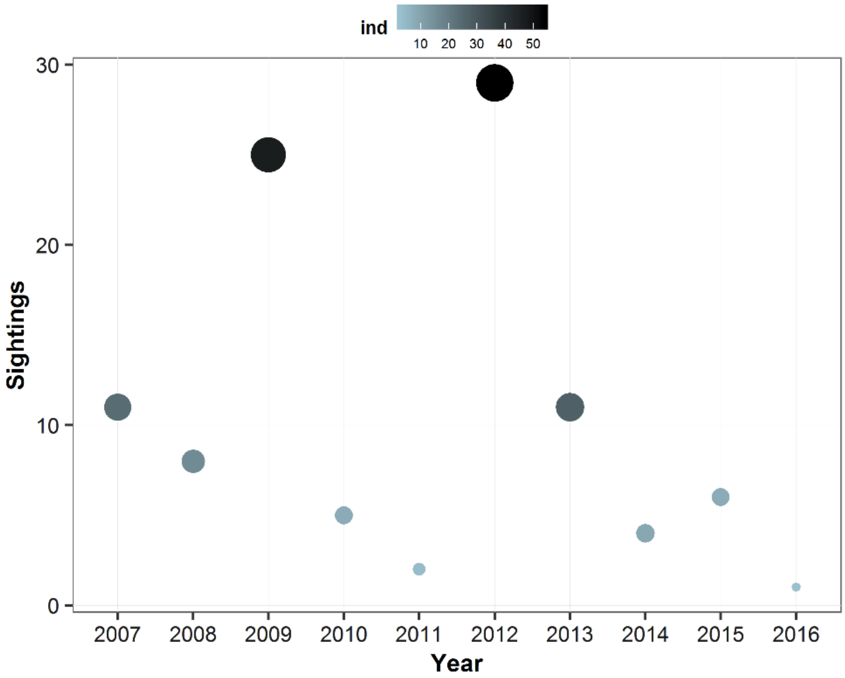


Figure C-1.6. Sandwich tern (*Thalasseus sandvicensis*) data from the PELACUS surveys 2007-2016. a) Number of sightings collected and individuals sighted each year and b) map of sightings and number of individuals per sighting.

a)



b)

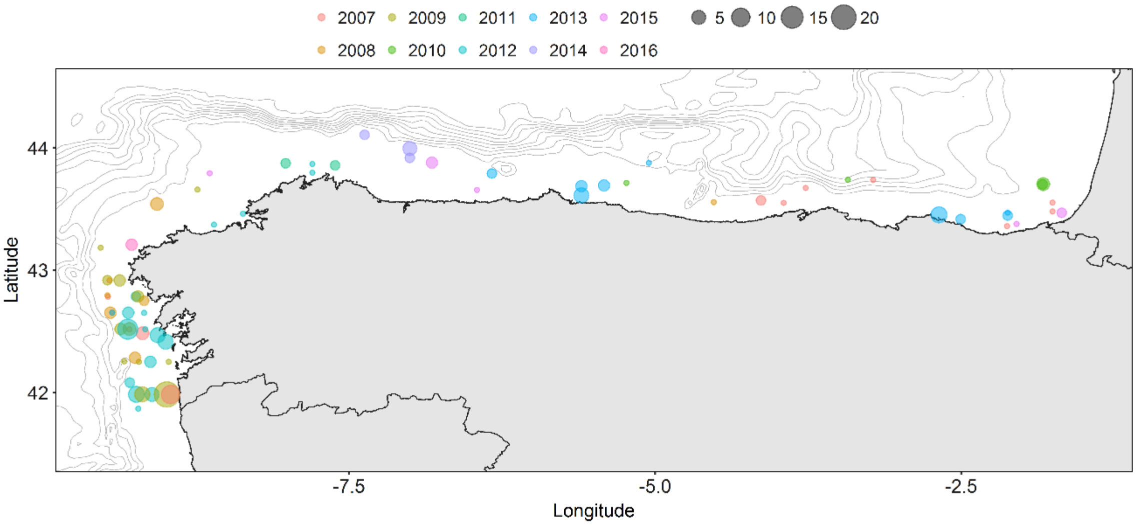


Figure C-1.7. Razorbill (*Alca torda*) data from the PELACUS surveys 2007-2016. a) Number of sightings collected and individuals sighted each year and b) map of sightings and number of individuals per sighting.

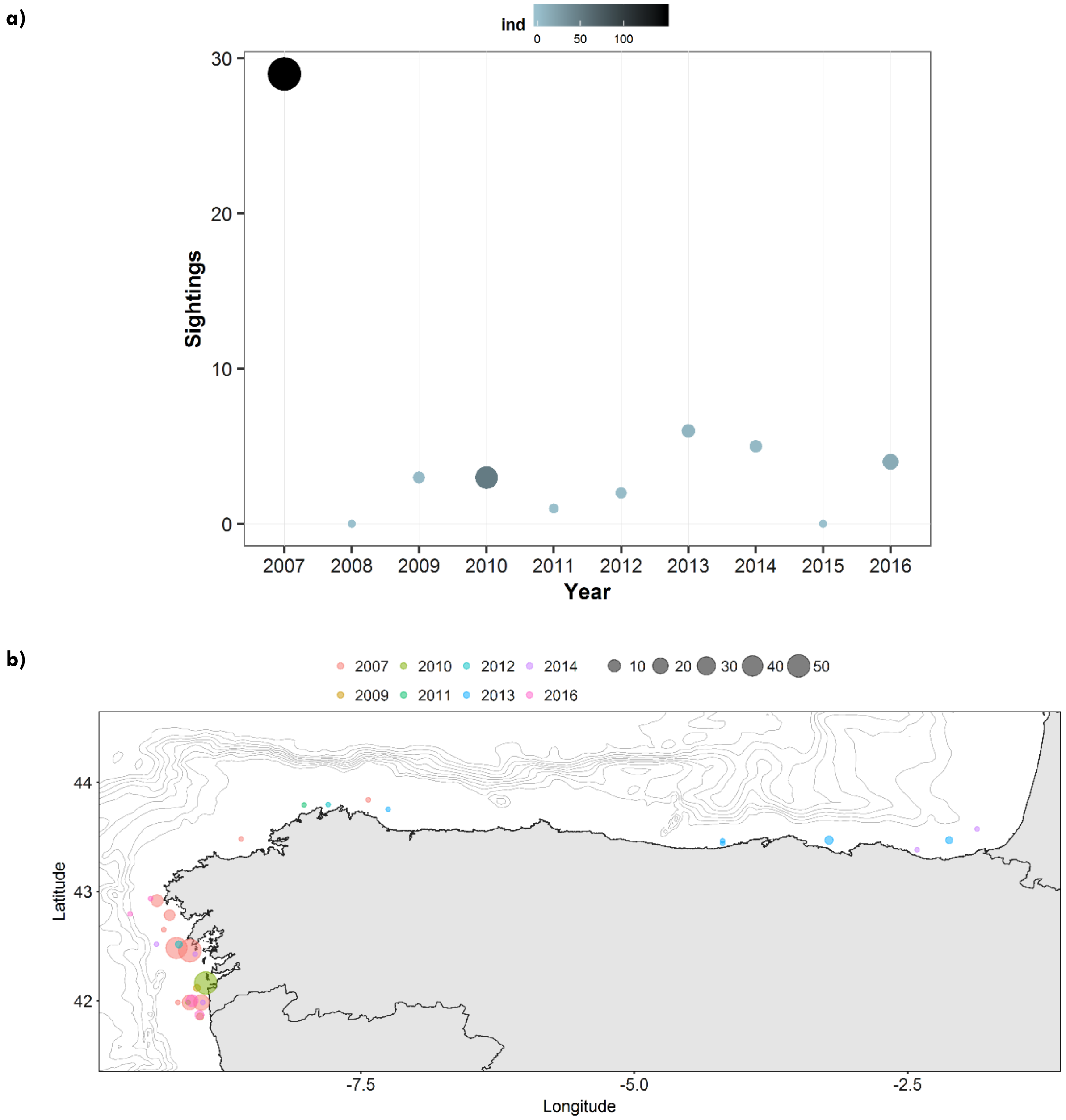
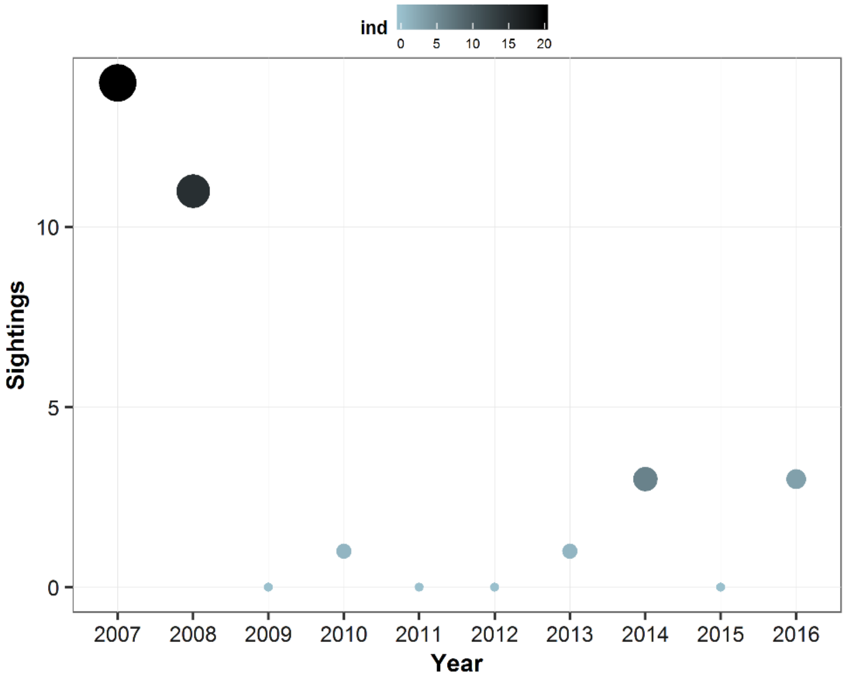


Figure C-1.8. Common guillemot (*Uria aalge*) data from the PELACUS surveys 2007-2016. a) Number of sightings collected and individuals sighted each year and b) map of sightings and number of individuals per sighting.

a)



b)

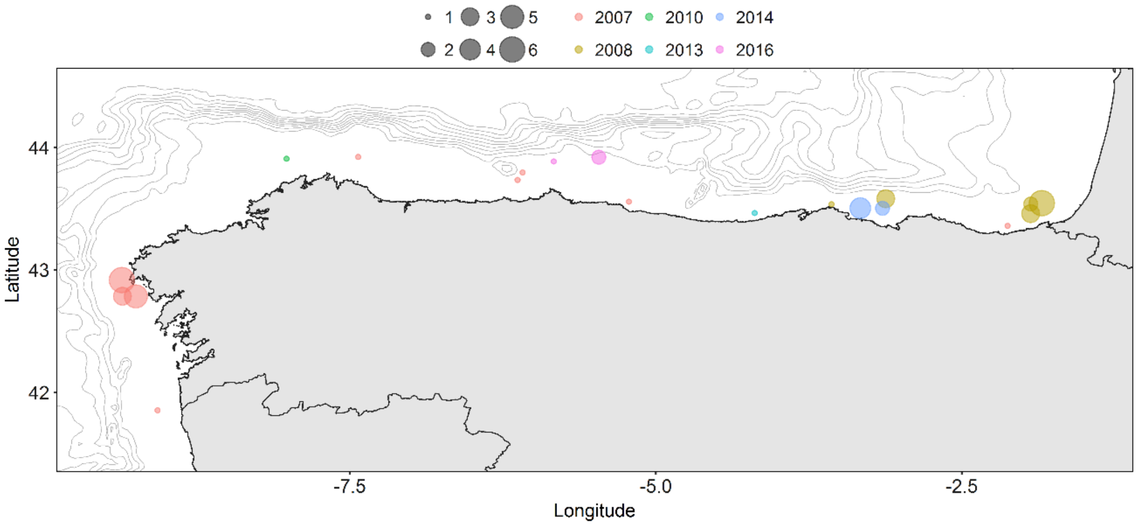


Figure C-1.9. Balearic shearwater (*Puffinus mauretanicus*) data from the PELACUS surveys 2007-2016. a) Number of sightings collected and individuals sighted each year and b) map of sightings and number of individuals per sighting.

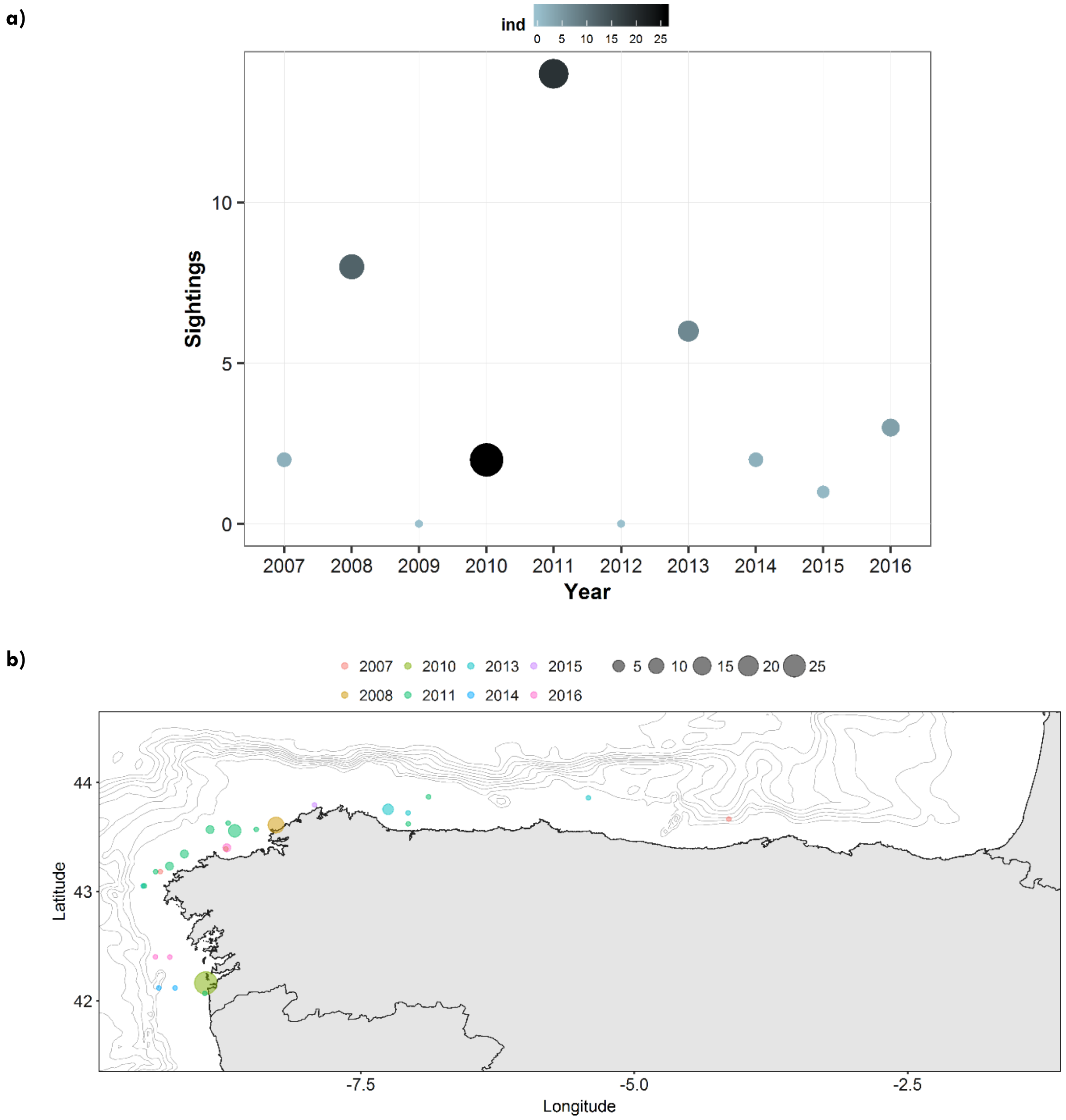


Figure C-1.10. Manx shearwater (*Puffinus puffinus*) data from the PELACUS surveys 2007-2016. a) Number of sightings collected and individuals sighted each year and b) map of sightings and number of individuals per sighting.

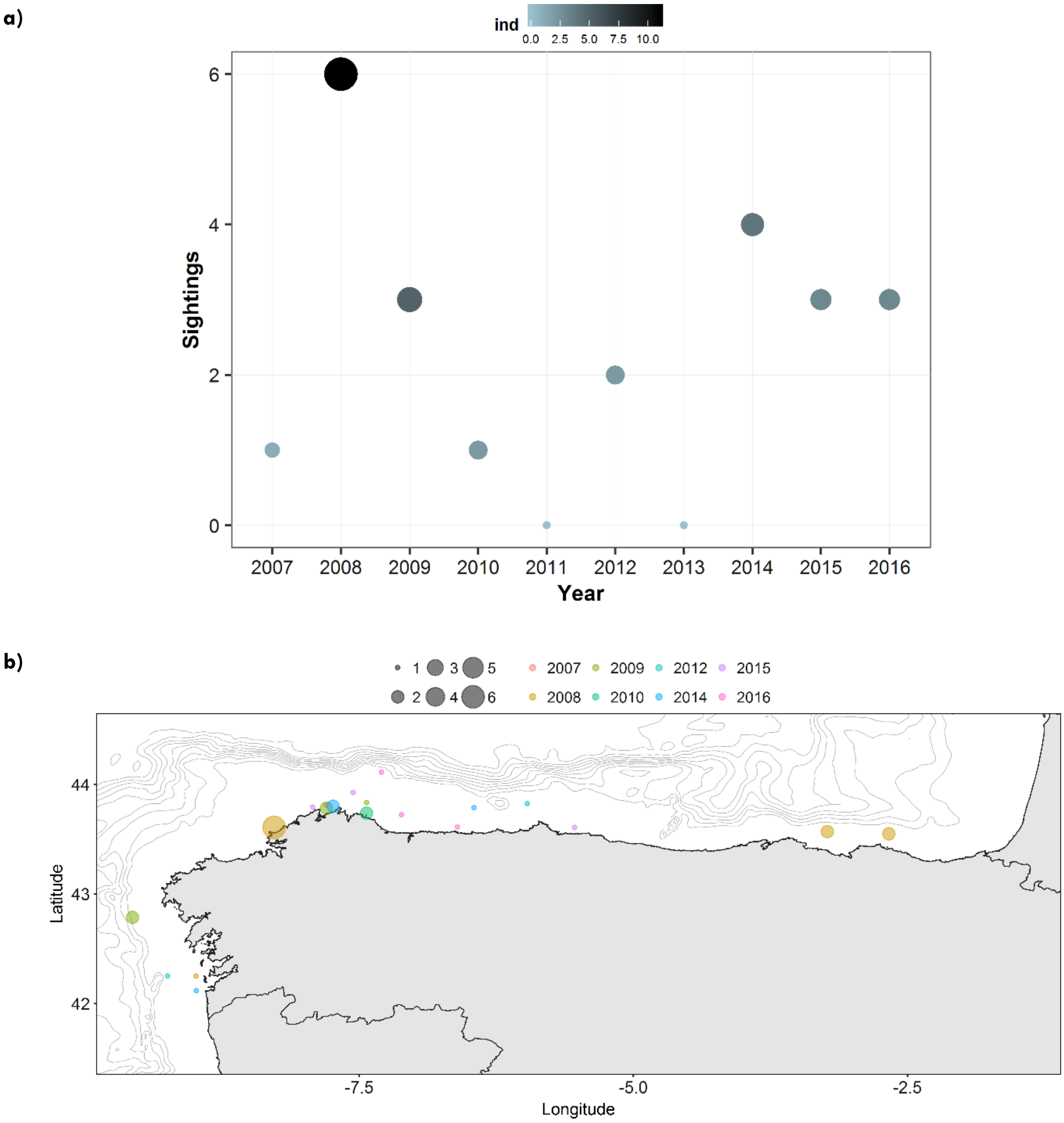


Figure C-1.11. Common dolphin (*Delphinus delphis*) data from the PELACUS surveys 2007-2016. a) Number of sightings collected and individuals sighted each year and b) map of sightings and number of individuals per sighting.

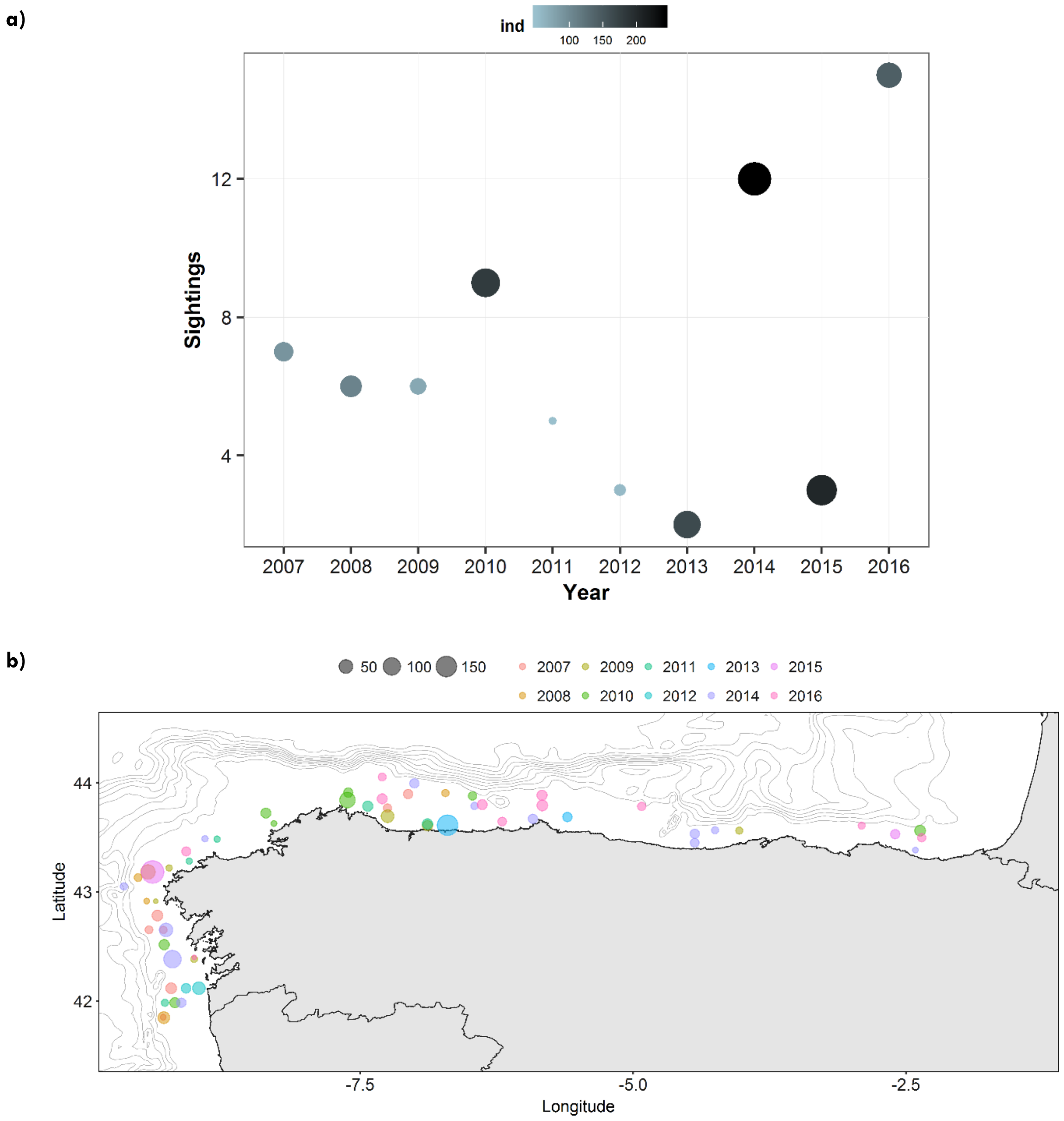


Figure C-1.12. Bottlenose dolphin (*Tursiops truncatus*) data from the PELACUS surveys 2007-2016. a) Number of sightings collected and individuals sighted each year and b) map of sightings and number of individuals per sighting.

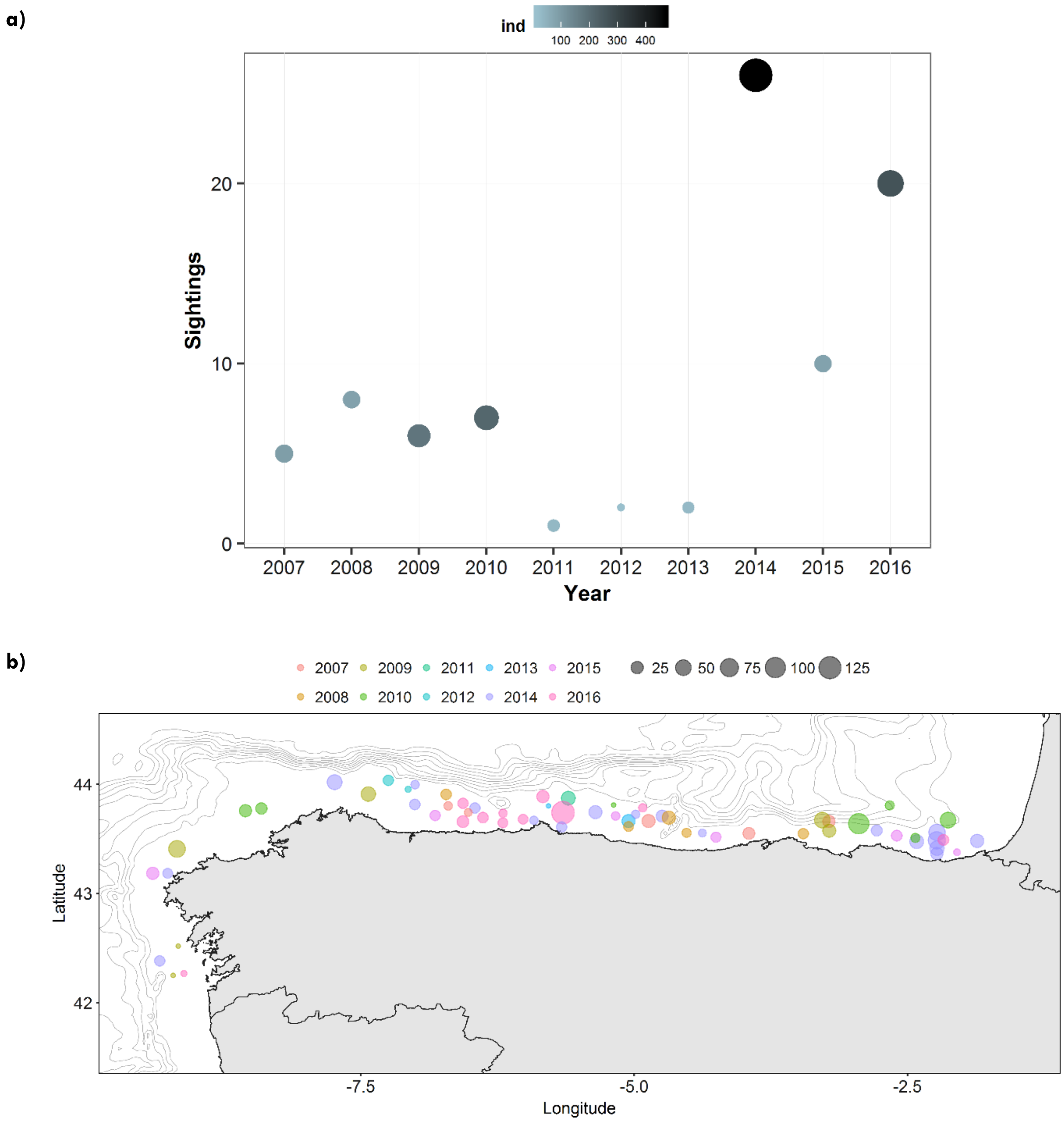
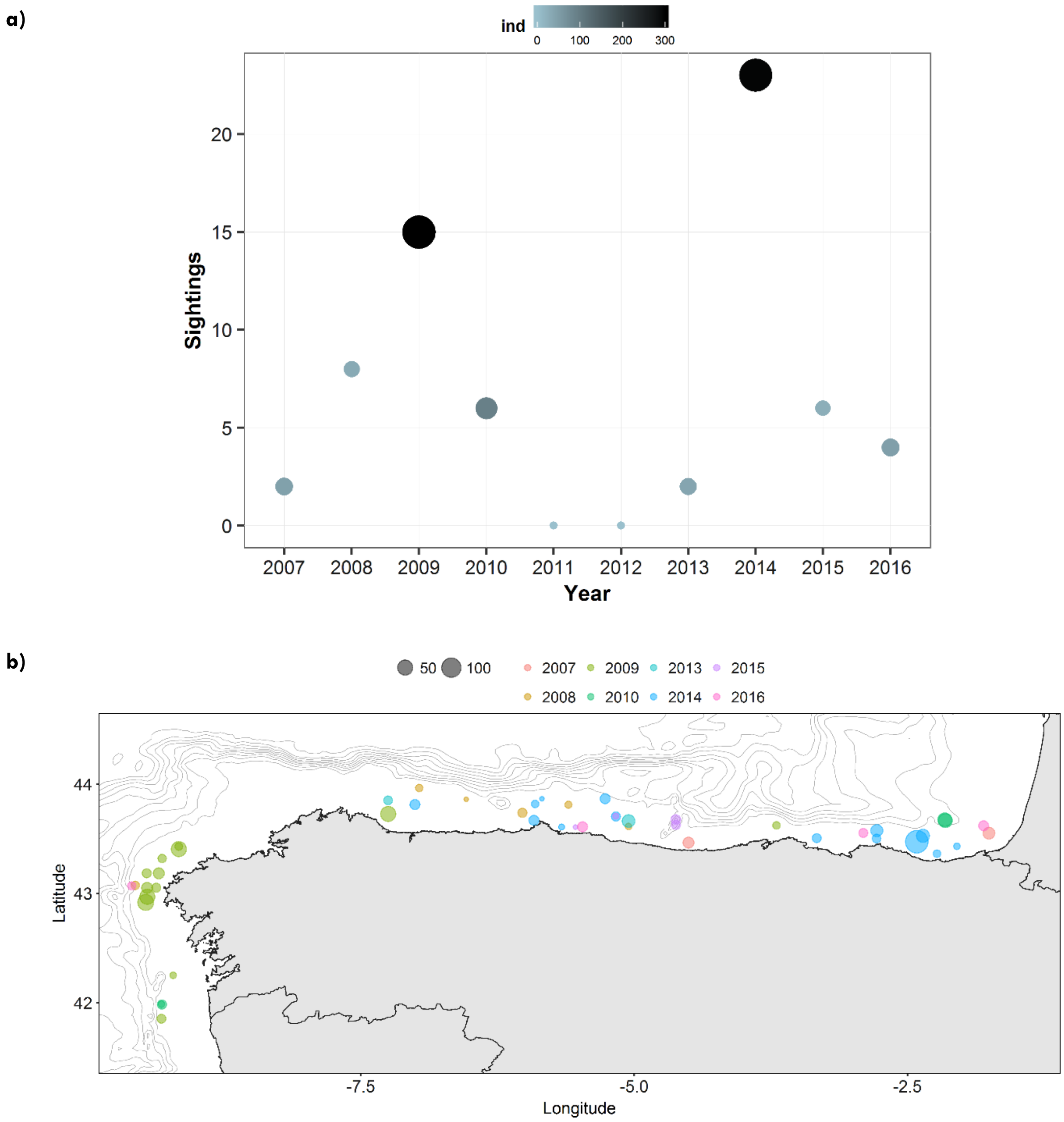


Figure C-1.13. Long-finned pilot whale (*Globicephala melas*) data from the PELACUS surveys 2007-2016. a) Number of sightings collected and individuals sighted each year and b) map of sightings and number of individuals per sighting.



Appendix C – Section 2: Distance Sampling Analysis

Table C-2.1. Covariates tested in the Multi Covariate Distance Sampling analyses.

Covariate	**Levels**
Beaufort sea-state	1 - 6
Beaufort sea-state categorized	1 → 1, 2 2 → 3, 4 3 → 5, 6
Glare intensity	None Faint Medium Strong Total
Glare intensity categorized	None_Faint → None, Faint Medium → Medium Strong_Total → Strong, Total
Swell height categorized	1 → ≤ 0.50 2 → ≥ 0.60 ≤ 1.0 3 → ≥ 1.2 ≤ 1.5 4 → ≥ 1.7 ≤ 2.0
Cloud coverage	0 - 8
Cloud coverage categorized	1 → 0, 1, 2 2 → 3, 4 3 → 5, 6 4 → 7, 8
Visibility	0 - 8
Visibility categorized	1 → 0, 1, 2 2 → 3, 4 3 → 5, 6 4 → 7, 8
Overall detection conditions	Bad Medium Good Excellent
Year	2007 - 2016

Figure C-2.1. Northern gannet hazard-rate detection function showing histogram of perpendicular distance data for the sightings and the fitted detection probability (black line) predicted by the model. Perpendicular distance was truncated at 1000 m.

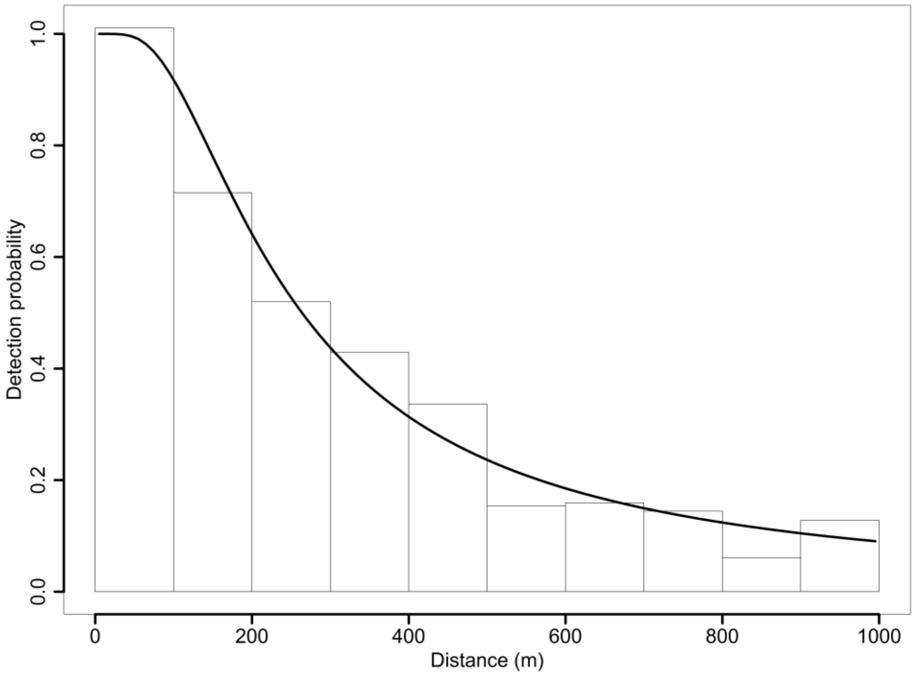


Figure C-2.2. Lesser black-backed gull hazard-rate detection function showing histogram of perpendicular distance data for the sightings and the fitted detection probability (black line) predicted by the model. Perpendicular distance was truncated at 1000 m.

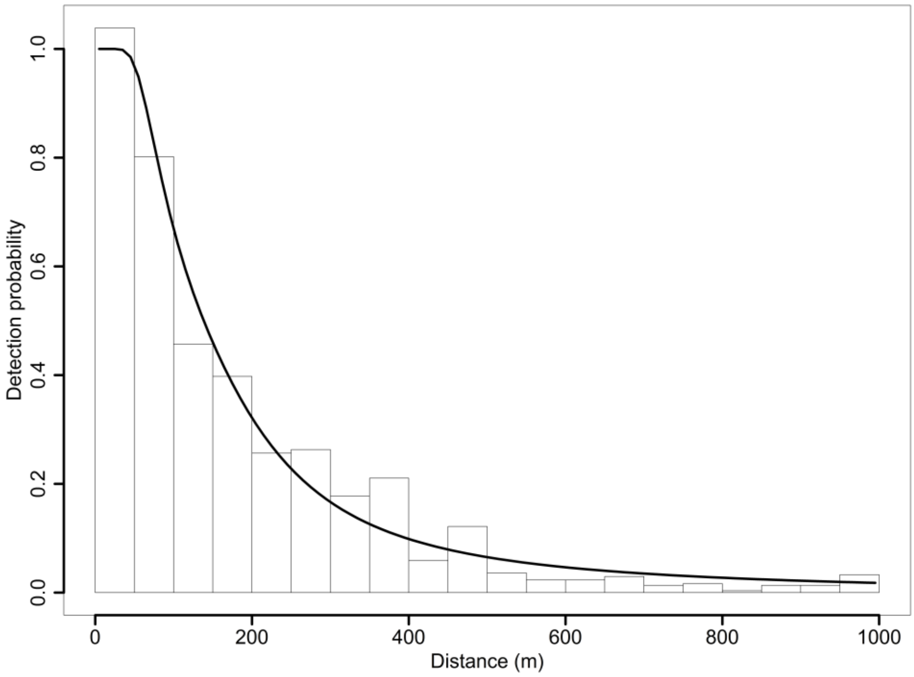


Figure C-2.3. Yellow-legged gull hazard-rate detection function showing histogram of perpendicular distance data for the sightings and the fitted detection probability (black line) predicted by the model. Perpendicular distance was truncated at 500 m.

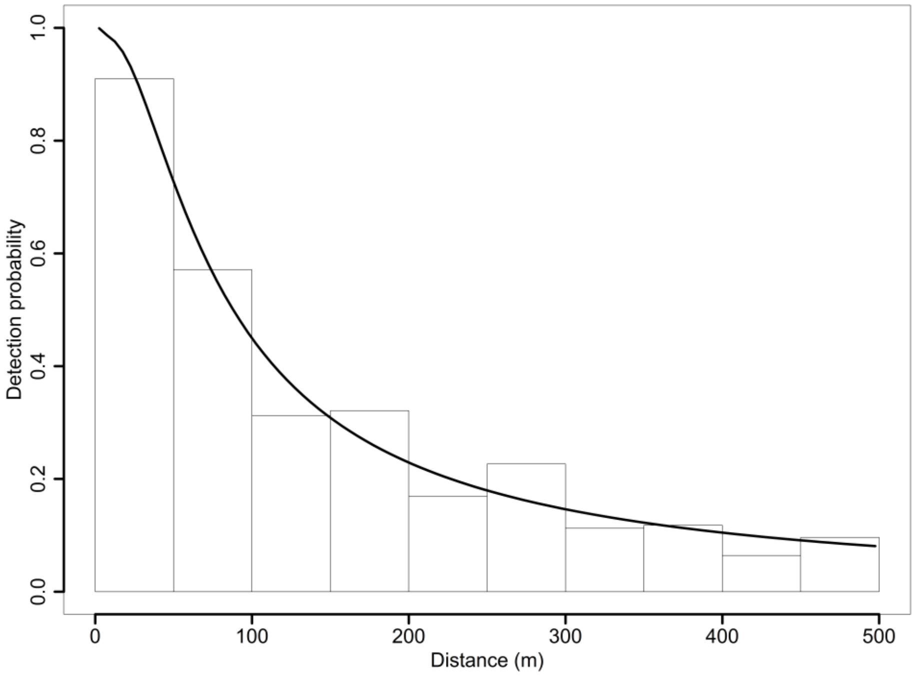


Figure C-2.4. Mediterranean gull half-normal detection function showing histogram of perpendicular distance data for the sightings and the fitted detection probability (black line) predicted by the model. Perpendicular distance was truncated at 500 m.

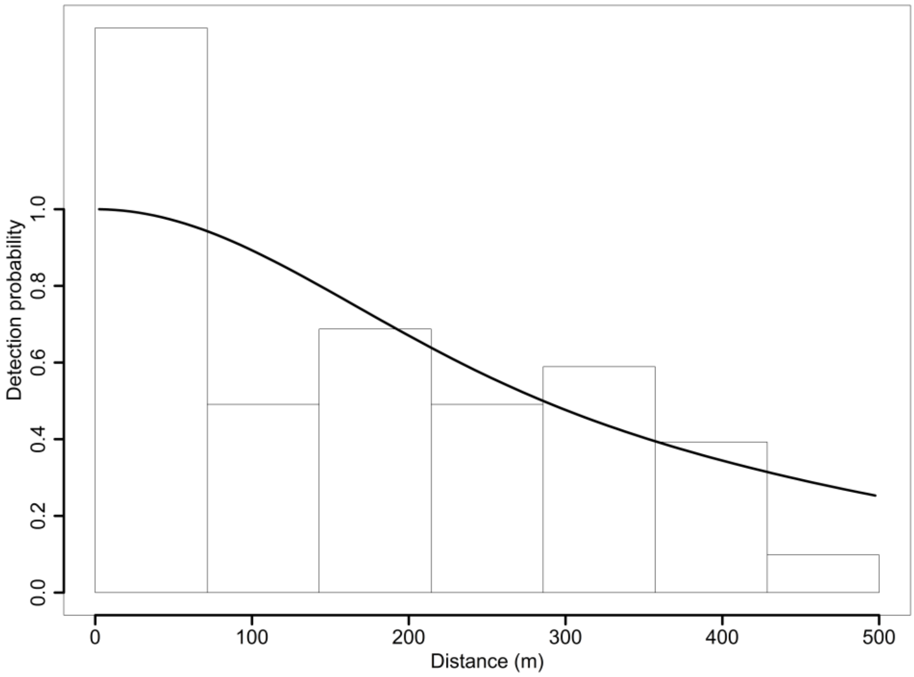


Figure C-2.5. Great skua hazard-rate detection function showing histogram of perpendicular distance data for the sightings and the fitted detection probability (black line) predicted by the model. Perpendicular distance was truncated at 600 m.

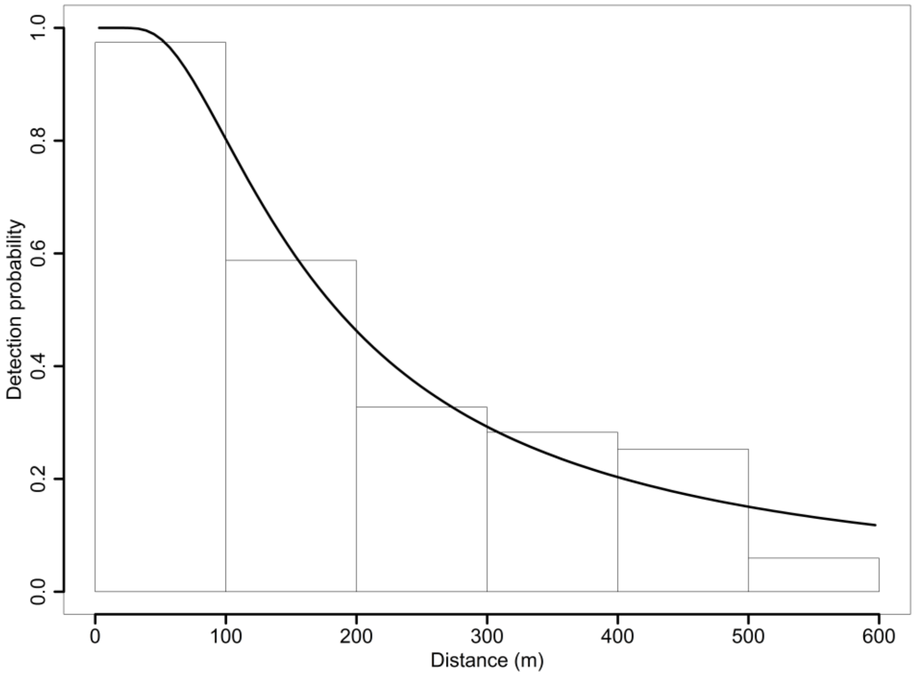


Figure C-2.6. Sandwich tern hazard-rate detection function showing histogram of perpendicular distance data for the sightings and the fitted detection probability (black line) predicted by the model. Perpendicular distance was truncated at 800 m.

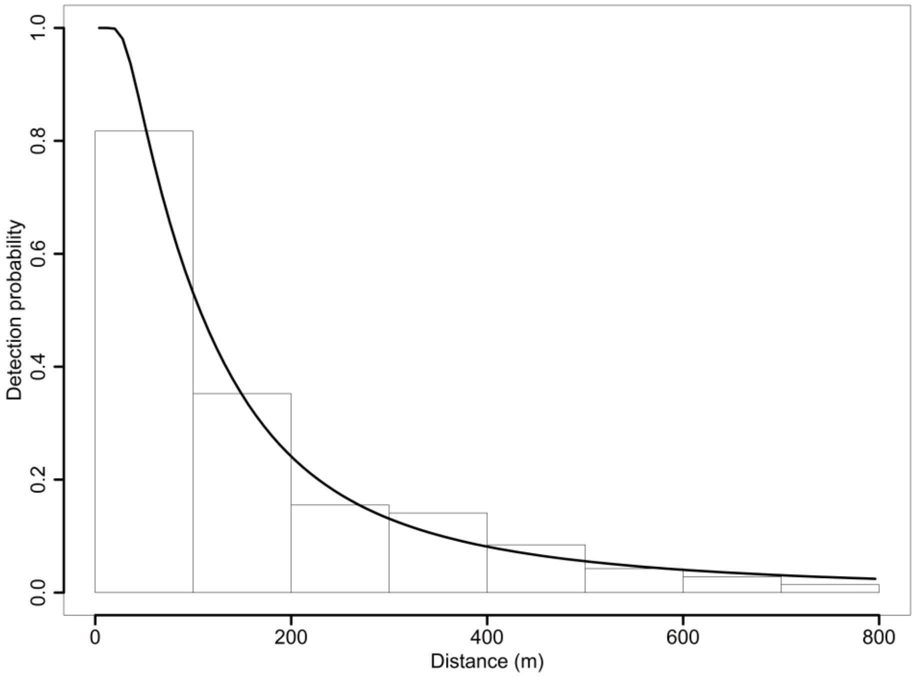


Figure C-2.7. Razorbill hazard-rate detection function showing histogram of perpendicular distance data for the sightings and the fitted detection probability (black line) predicted by the model. Perpendicular distance was truncated at 500 m.

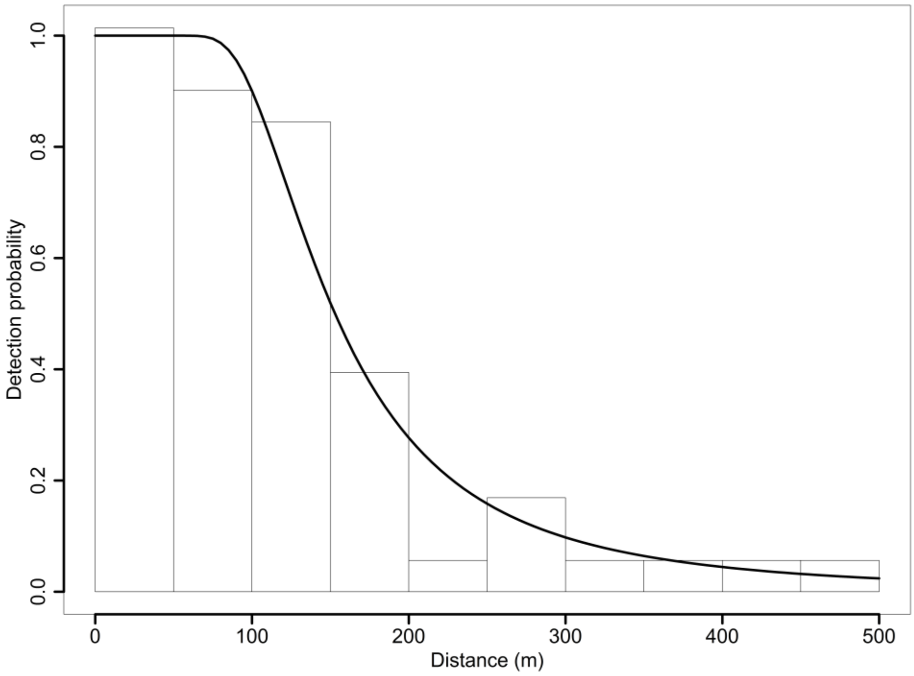


Figure C-2.8. Common guillemot hazard-rate detection function showing histogram of perpendicular distance data for the sightings and the fitted detection probability (black line) predicted by the model. Perpendicular distance was truncated at 300 m.

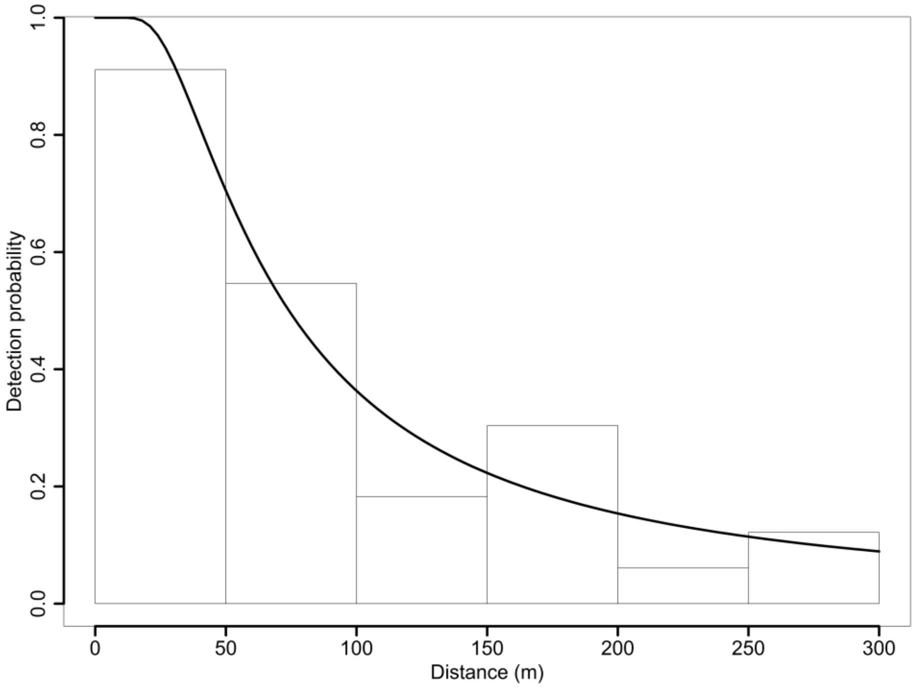


Figure C-2.9. Balearic shearwater half-normal detection function showing histogram of perpendicular distance data for the sightings and the fitted detection probability (black line) predicted by the model. Perpendicular distance was truncated at 500 m.

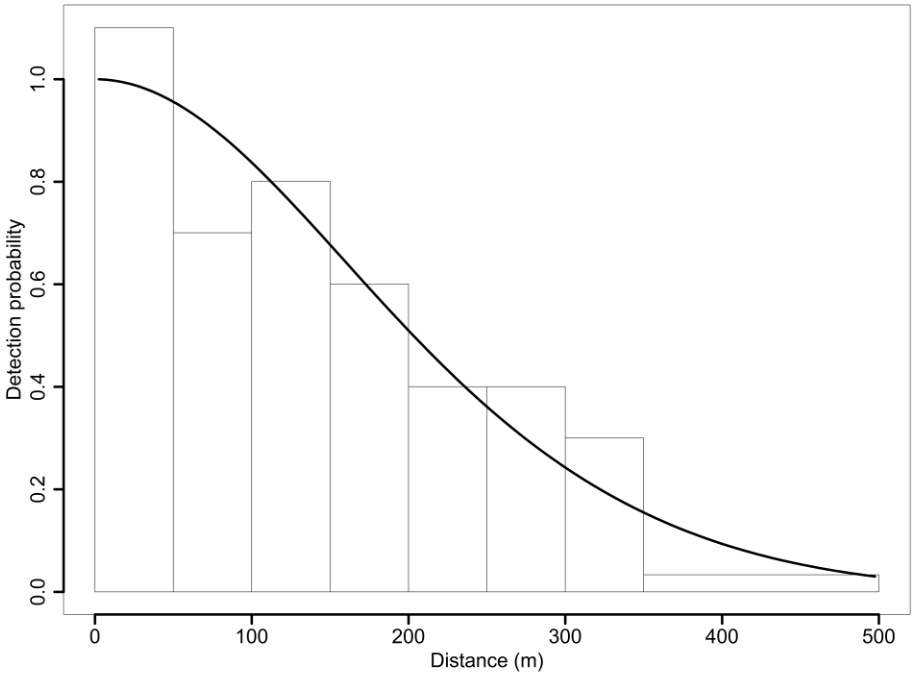


Figure C-2.10. Manx shearwater hazard-rate detection function showing histogram of perpendicular distance data for the sightings and the fitted detection probability (black line) predicted by the model. Perpendicular distance was truncated at 350 m.

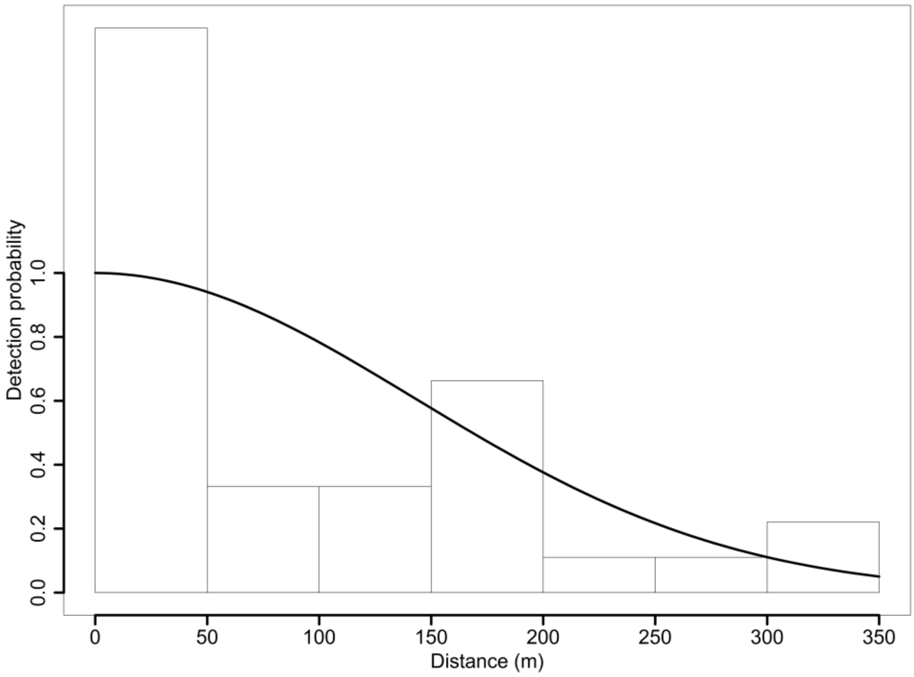


Figure C-2.11. Common dolphin hazard-rate detection function showing histogram of perpendicular distance data for the sightings and the fitted detection probability (black line) predicted by the model. Perpendicular distance was truncated at 1000 m.

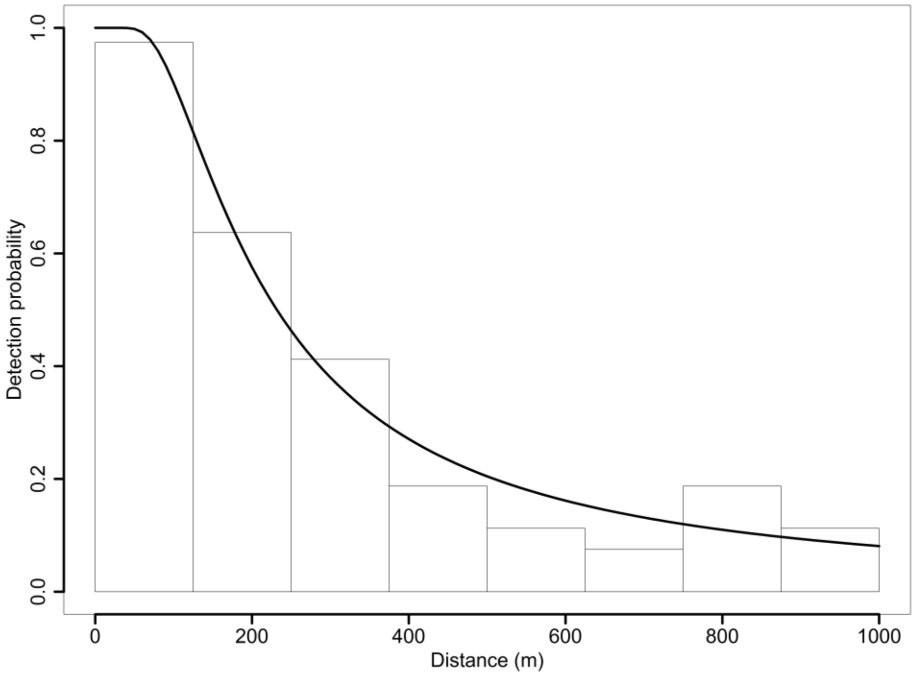


Figure C-2.12. Bottlenose dolphin half-normal detection function showing histogram of perpendicular distance data for the sightings and the fitted detection probability (black line) predicted by the model. Perpendicular distance was truncated at 1300 m.

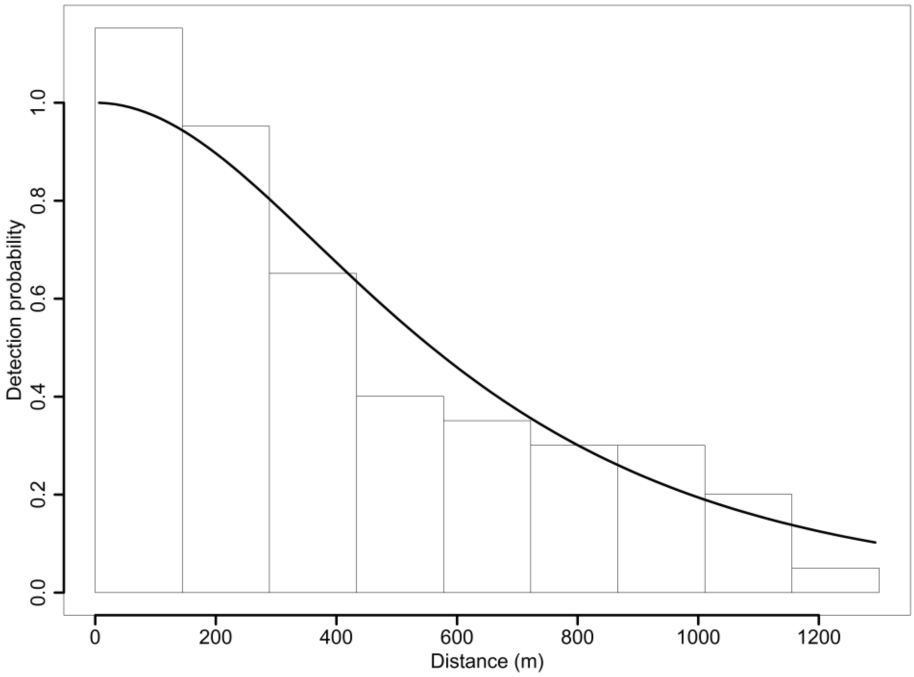
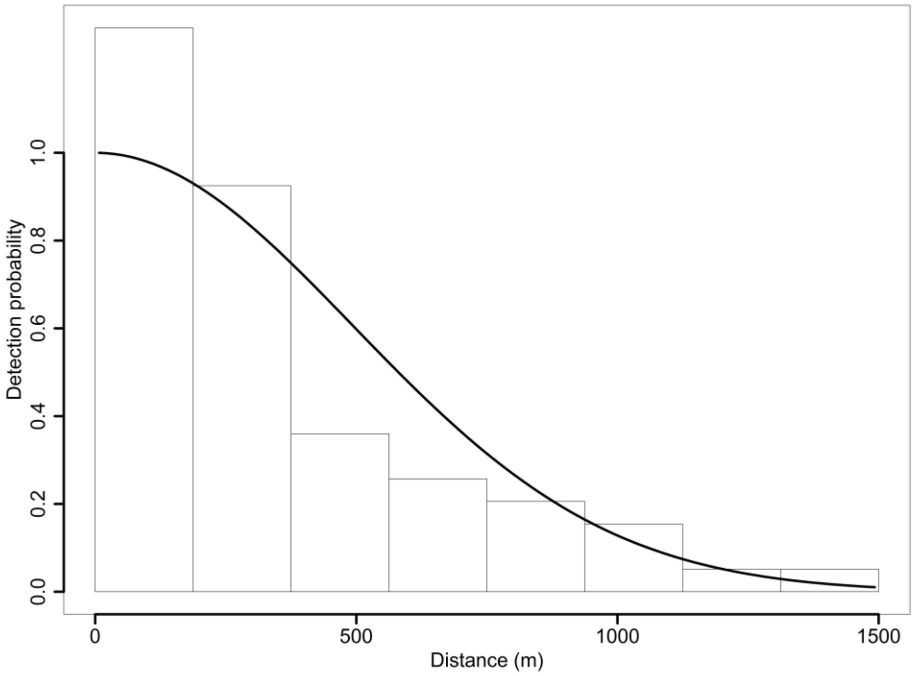


Figure C-2.13. Long-finned pilot whale half-normal detection function showing histogram of perpendicular distance data for the sightings and the fitted detection probability (black line) predicted by the model. Perpendicular distance was truncated at 1500 m.



Appendix C – Section 3: Environmental covariates

Table C-3.1. Environmental covariates used for spatial density modelling of the species, their units, resolution and source. ETOPO1 (Amante and Eakins, 2009, https://www.ngdc.noaa.gov/) was used to compute all the physiographic variables. Aqua MODIS satellite products from the web source ERDDAP (Simons, 2016) were used to compute SST, Chl-a and its gradient.

Type	Environmental covariate	Acronyms	Resolution	Source
Physiographic	Logarithm of the depth (m)	logBAT	0.04°	ETOPO1
	Slope (degrees)	SLOPE		
	Closest distance to the coast (km)	DisCO		
	Closest distance to the self-break (km)	DisSB		
Oceanographic	Mean SST (°C)	SST	0.04°	Aqua MODIS
	Logarithm of the mean Chlorophyll a (mg/m^3)	Chl-a	0.04°	Aqua MODIS
	Chlorophyll a mean gradient	Chl-a$_g$	0.04°	Aqua MODIS

Figure C-3.2. Pair-wise correlation between predictor variables by means of Spearman-rank correlation coefficient. See Table C-3.1 for explanation of the abbreviations.

	log(BAT)	SLOPE	DistSB	DistCO	SST	Chl-a	Chl-a$_g$
log(BAT)	1	-0.501	-0.601	0.474	0.130	-0.043	-0.235
SLOPE	-0.501	1	0.042	-0.177	-0.170	-0.152	0.020
DistSB	-0.601	0.042	1	-0.540	-0.002	0.174	0.284
DistCO	0.474	-0.177	-0.540	1	0.136	-0.239	-0.389
SST	0.130	-0.170	-0.002	0.136	1	-0.033	-0.122
log(Chl-a)	-0.043	-0.152	0.174	-0.239	-0.033	1	0.351
Chl-a$_g$	-0.235	0.020	0.284	-0.389	-0.122	0.351	1

Figure C-3.1. Physiographic variables: (a) depth, (b) slope, (c) distance to the coast, (d) distance to the shelf-break.

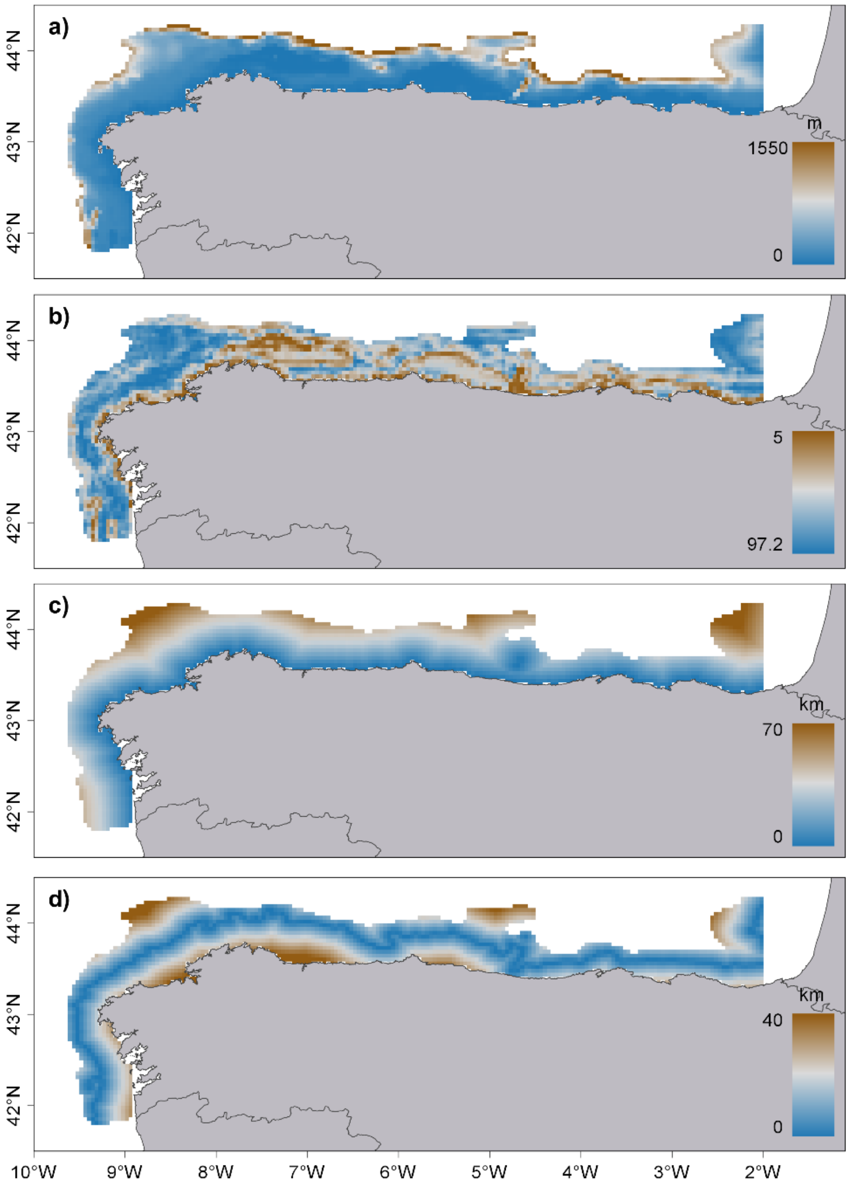


Figure C-3.2. Sea surface temperature (SST) over the time-series 2007-2016.

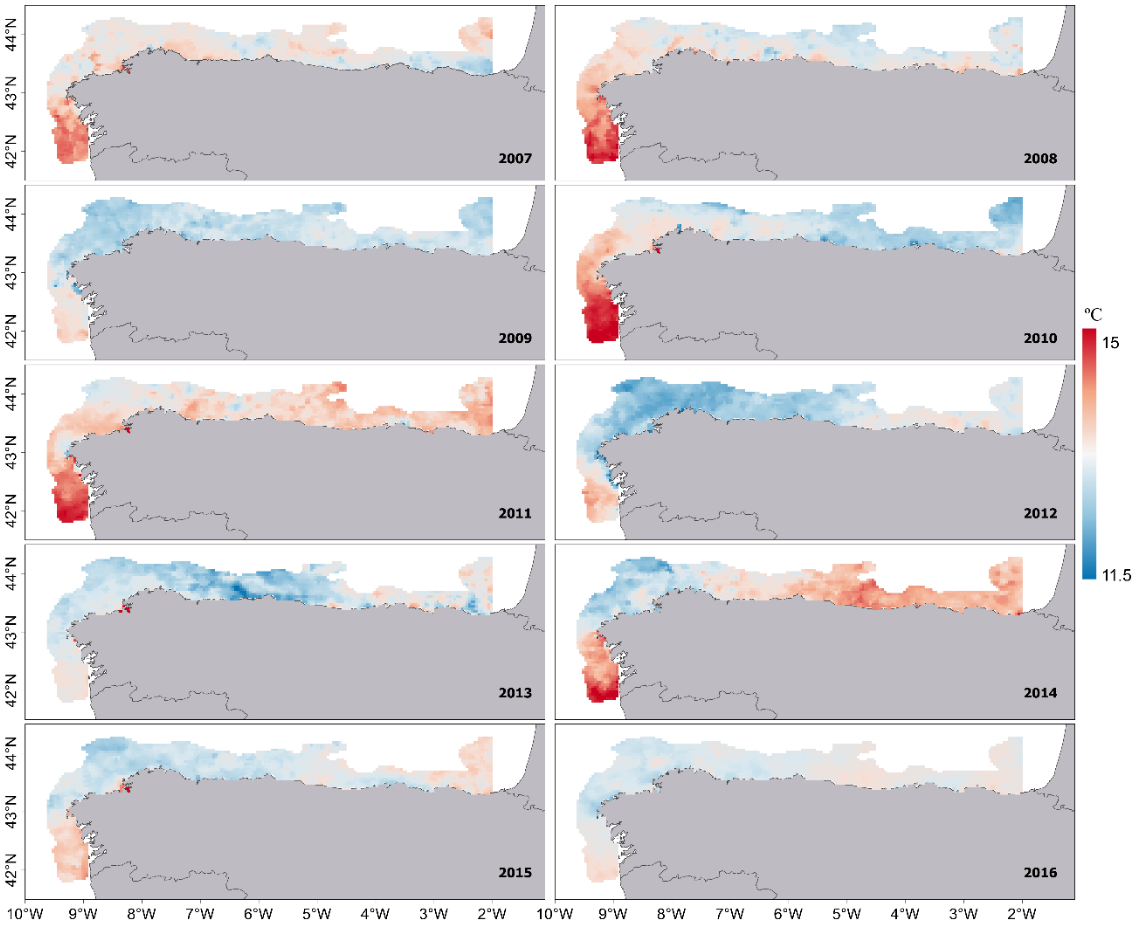


Figure C-3.3. Mean Chlorophyll a (Chl-a) over the time-series 2007-2016.

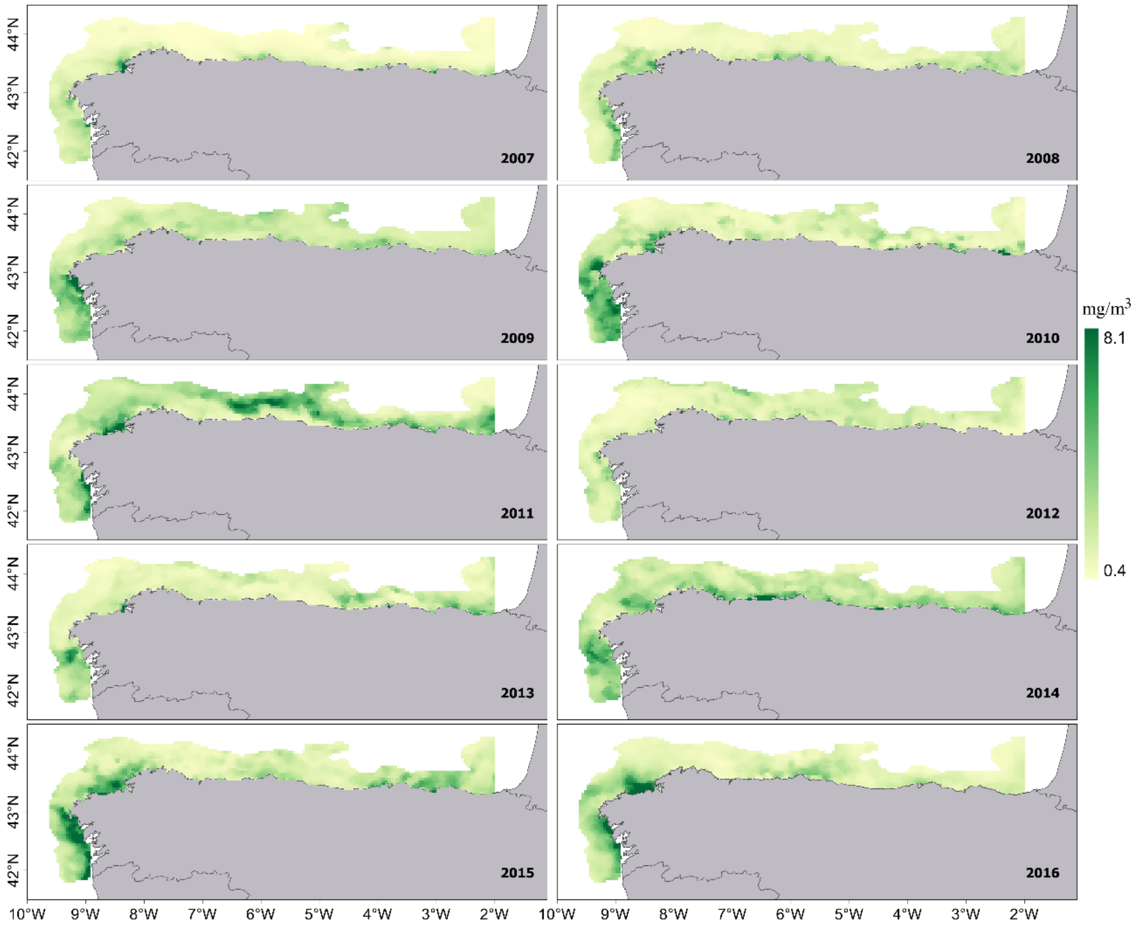
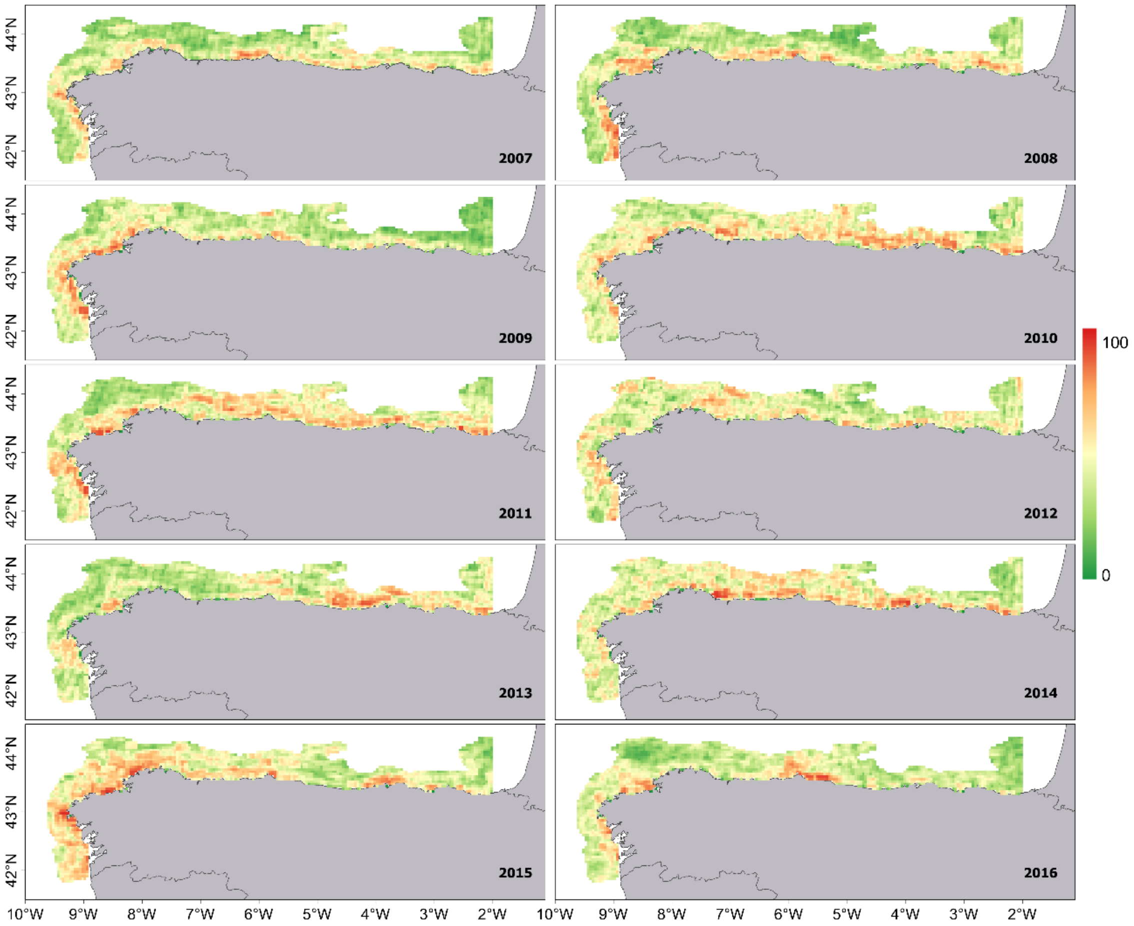
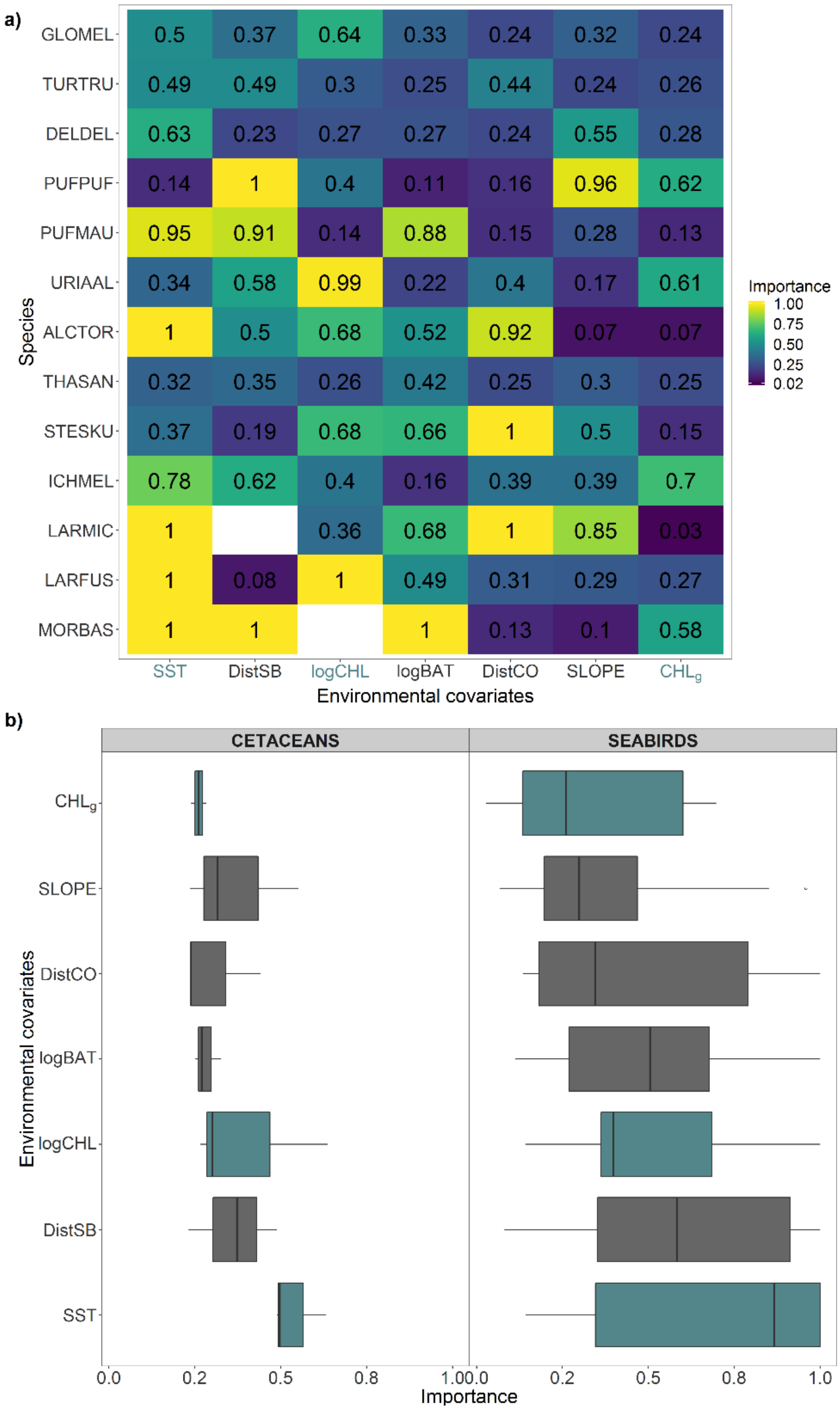


Figure C-3.4. Chlorophyll a mean gradient (Chl-a_g) over the time-series 2007-2016.



Appendix C – Section 4: Density surface models

Figure C-4.1. a) Environmental variables driving species abundance patterns characterized by means of relative variable importance (white colour indicates that the variable was not selected in the models) and b) boxplot of the relative variable importance for each group of species. Green colour indicates dynamic variables and grey colour indicate static variables. Acronyms of species are defined in Table 1 of the main text of the manuscript.



a)

Species	SST	DistSB	logCHL	logBAT	DistCO	SLOPE	CHL_g
GLOMEL	0.5	0.37	0.64	0.33	0.24	0.32	0.24
TURTRU	0.49	0.49	0.3	0.25	0.44	0.24	0.26
DELDEL	0.63	0.23	0.27	0.27	0.24	0.55	0.28
PUFPUF	0.14	1	0.4	0.11	0.16	0.96	0.62
PUFMAU	0.95	0.91	0.14	0.88	0.15	0.28	0.13
URIAAL	0.34	0.58	0.99	0.22	0.4	0.17	0.61
ALCTOR	1	0.5	0.68	0.52	0.92	0.07	0.07
THASAN	0.32	0.35	0.26	0.42	0.25	0.3	0.25
STESKU	0.37	0.19	0.68	0.66	1	0.5	0.15
ICHMEL	0.78	0.62	0.4	0.16	0.39	0.39	0.7
LARMIC	1		0.36	0.68	1	0.85	0.03
LARFUS	1	0.08	1	0.49	0.31	0.29	0.27
MORBAS	1	1		1	0.13	0.1	0.58

Figure C-4.2. Relationship between the average encounter rate (number of individuals sighted per 100 km of effort) of all species during the PELACUS surveys (2007-2016) and the average relative densities predicted in the study area. Densities were first averaged over the study area every year between 2007-2016. Acronyms of species are defined in Table 2 of the main text of the manuscript.

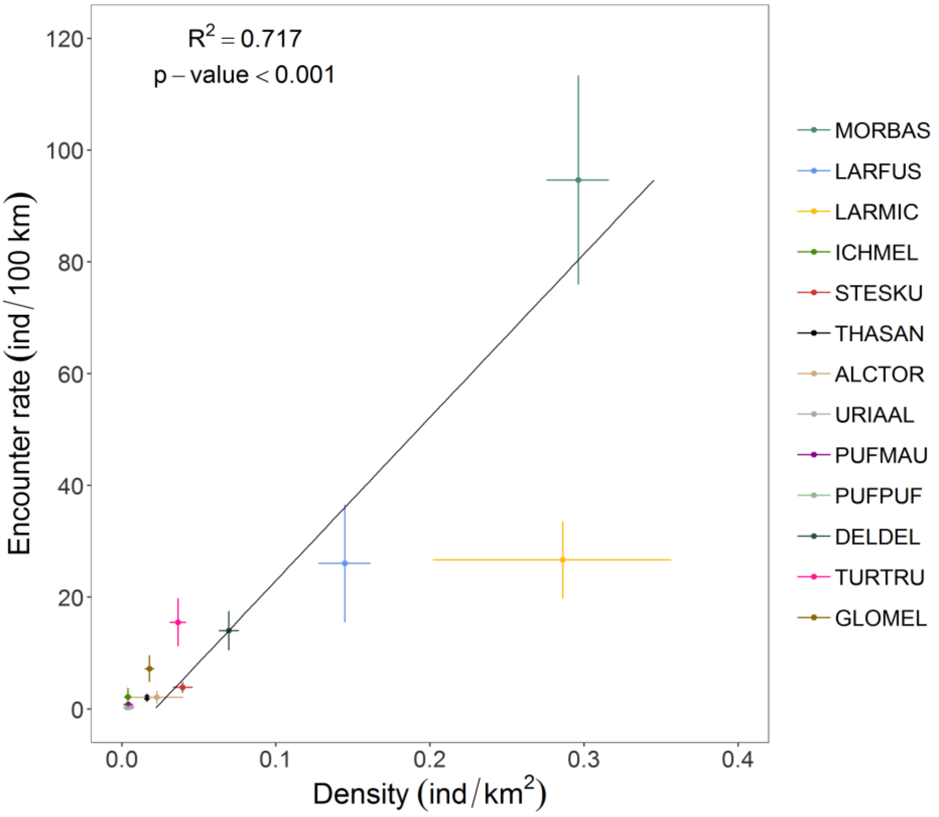


Figure C-4.3. Northern gannet spatial density predictions during PELACUS (2007–2016) oceanographic acoustic surveys.

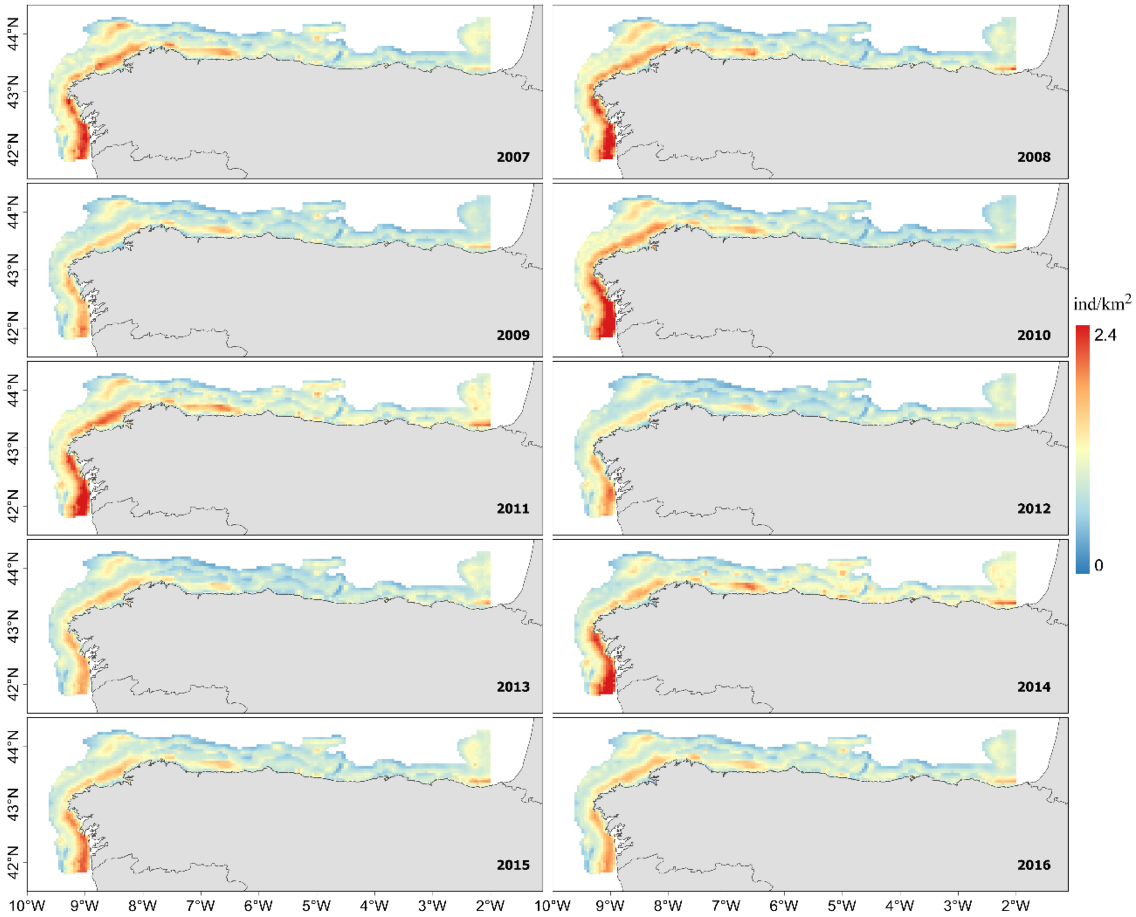


Figure C-4.4. Lesser black-backed gull spatial density predictions during PELACUS (2007–2016) oceanographic acoustic surveys.

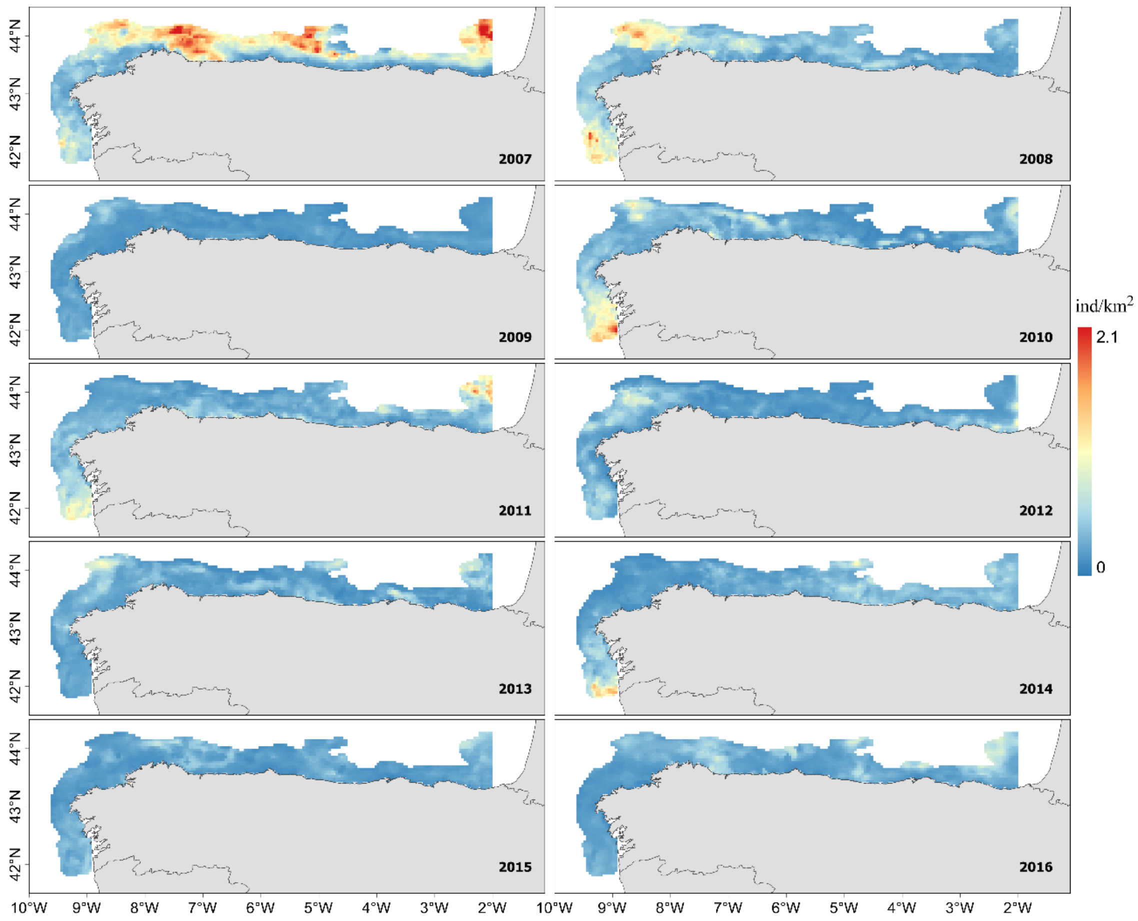


Figure C-4.5. Yellow-legged gull spatial density predictions during PELACUS (2007–2016) oceanographic acoustic surveys.

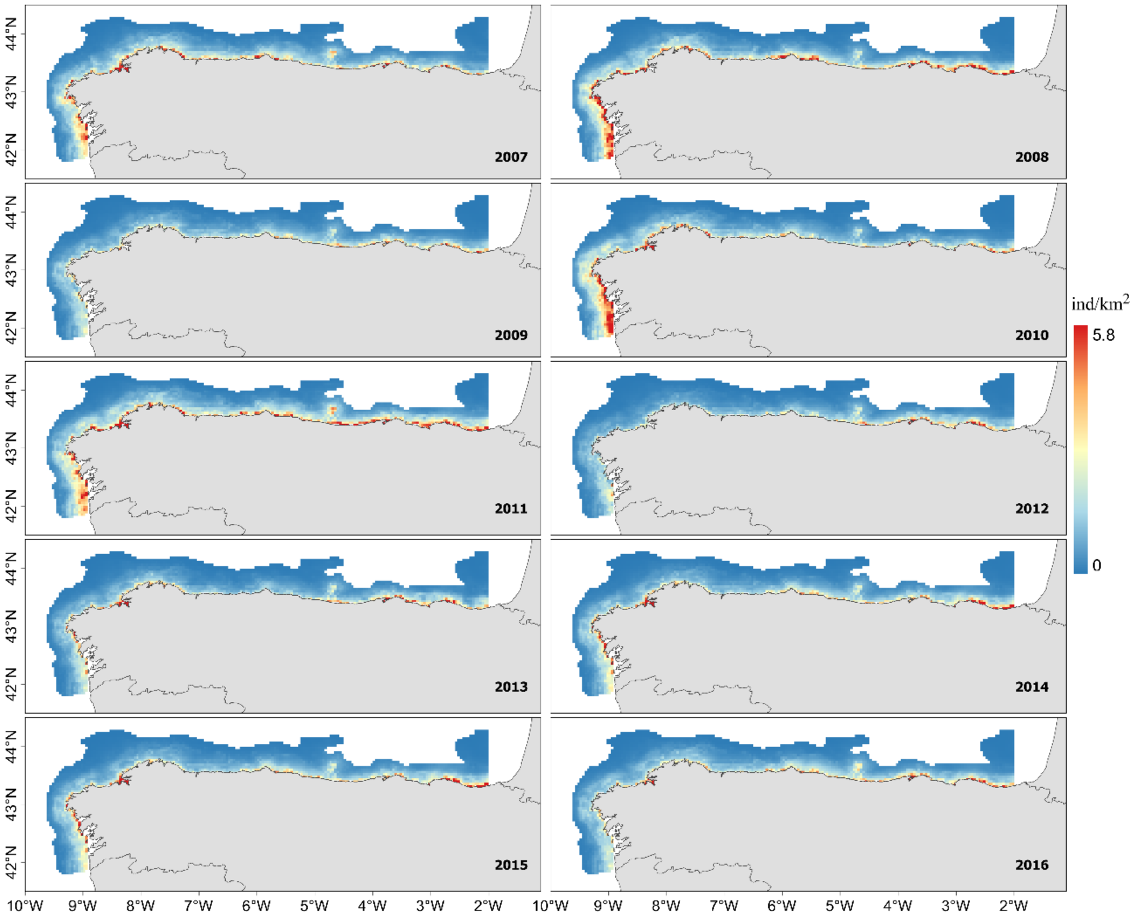


Figure C-4.6. Mediterranean gull spatial density predictions during PELACUS (2007–2016) oceanographic acoustic surveys.

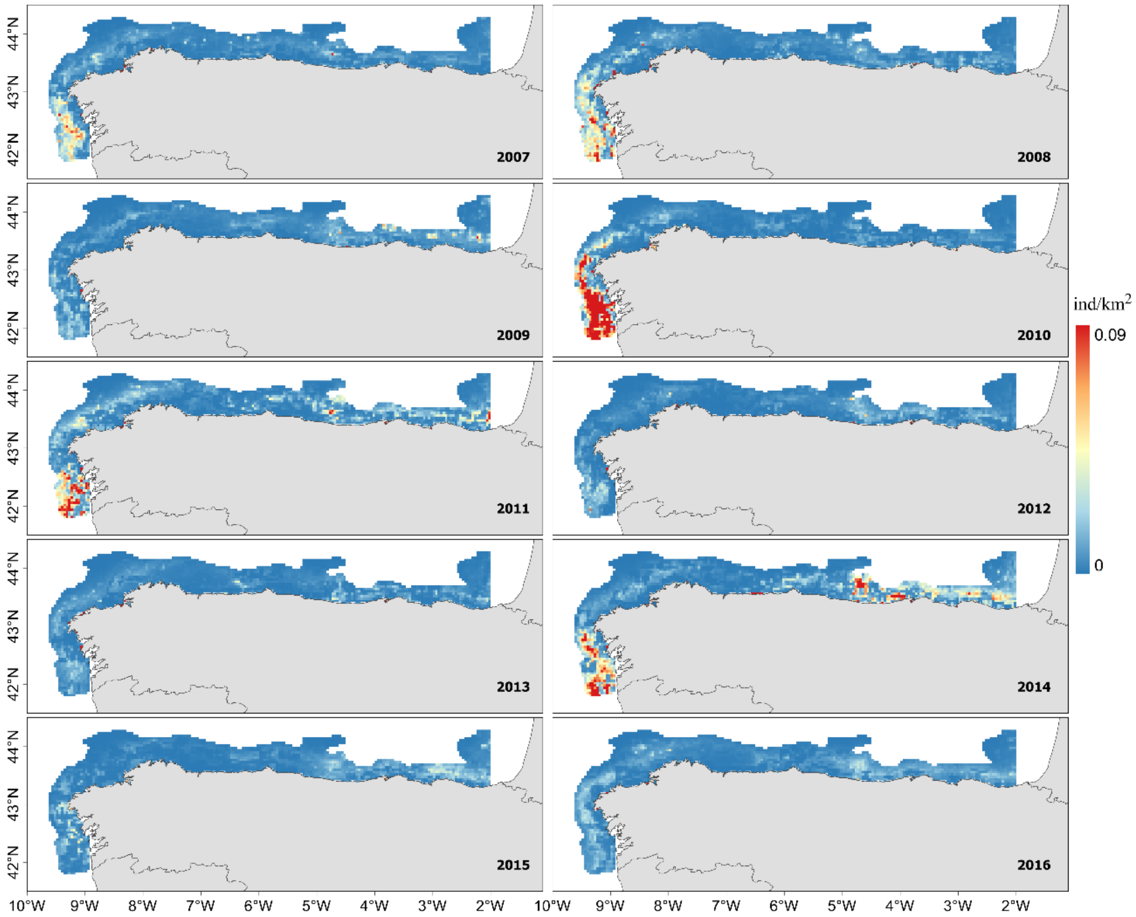


Figure C-4.7. Great skua spatial density predictions during PELACUS (2007–2016) oceanographic acoustic surveys.

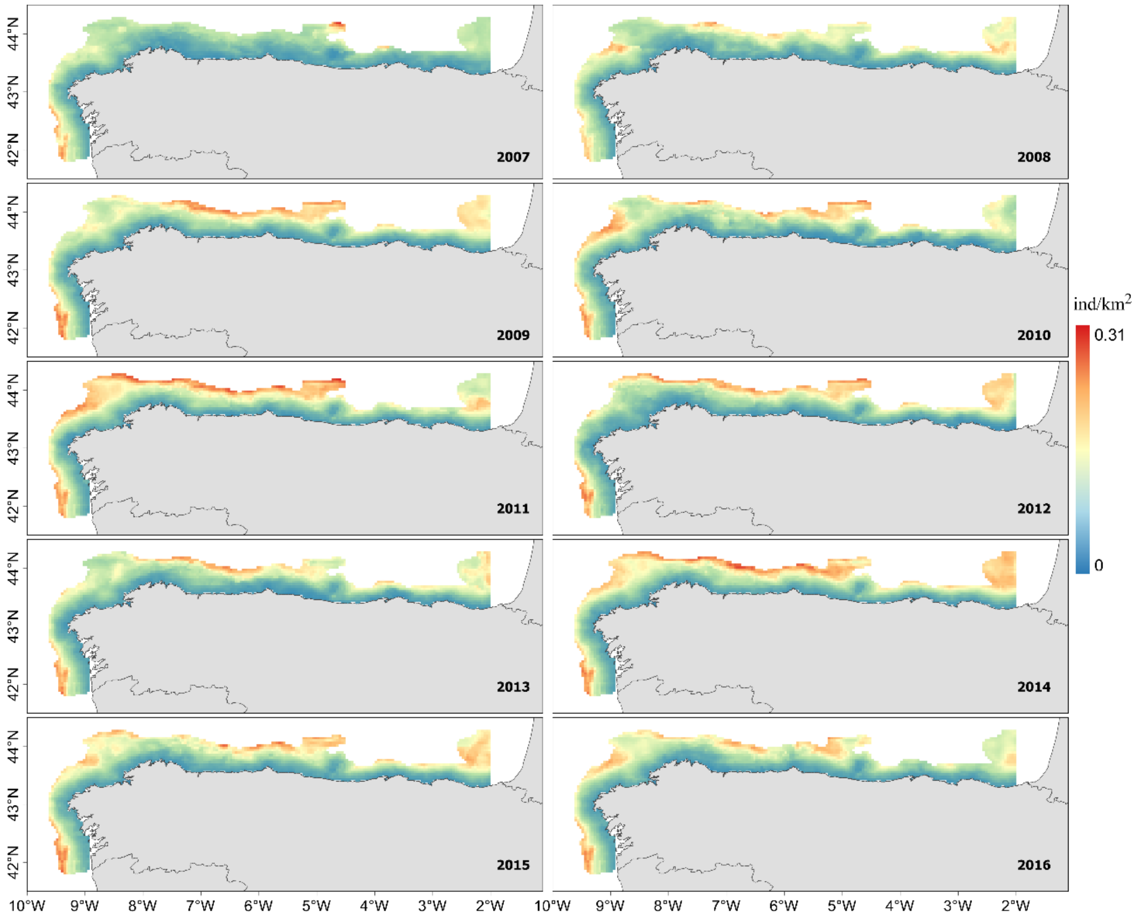


Figure C-4.8. Sandwich tern spatial density predictions during PELACUS (2007–2016) oceanographic acoustic surveys.

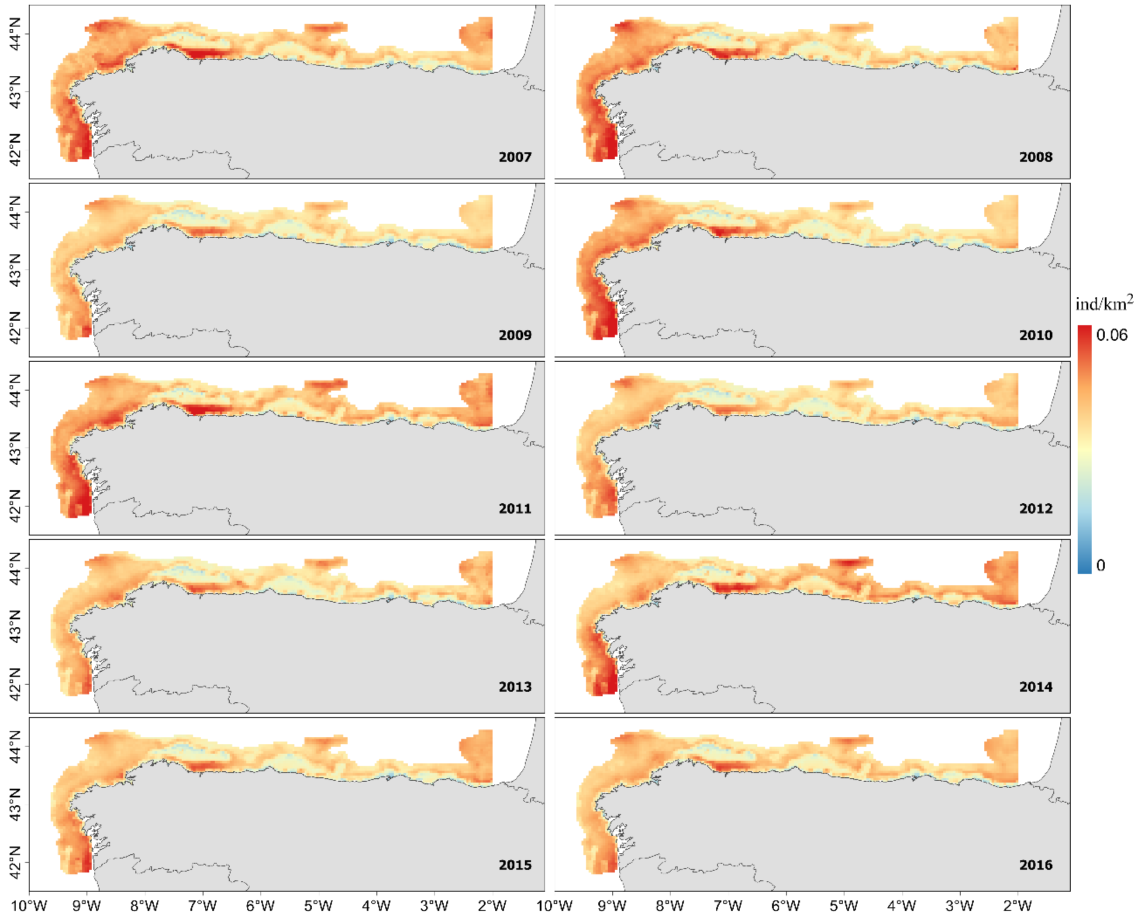


Figure C-4.9. Razorbill spatial density predictions during PELACUS (2007–2016) oceanographic acoustic surveys.

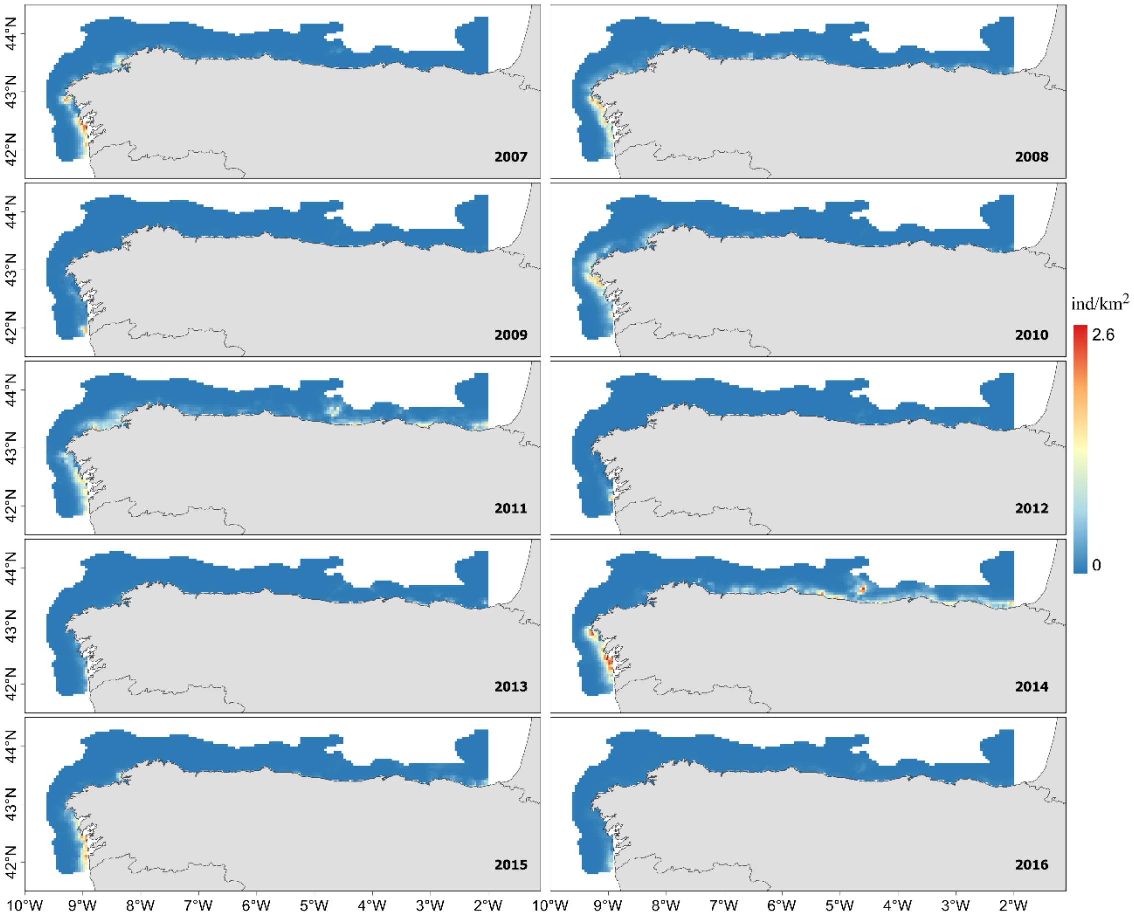


Figure C-4.10. Common guillemot spatial density predictions during PELACUS (2007–2016) oceanographic acoustic surveys.

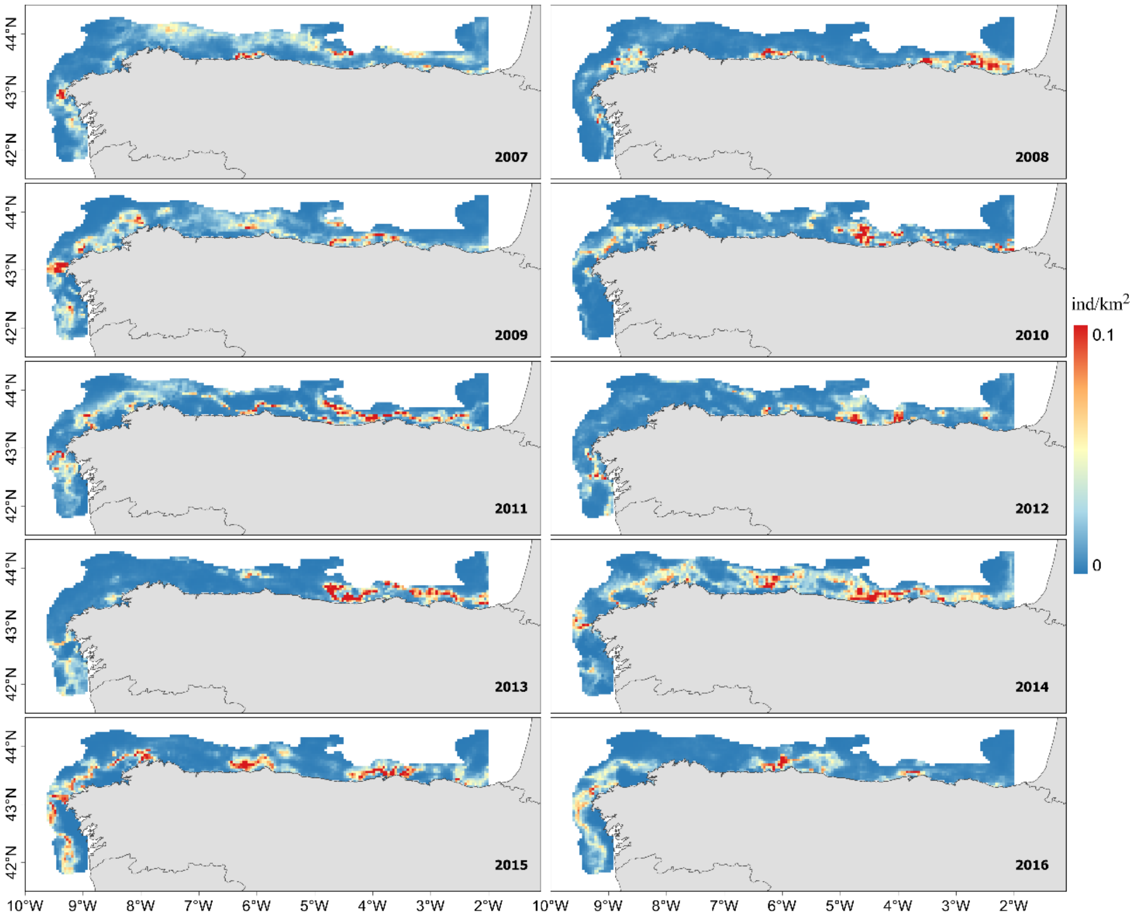


Figure C-4.11. Balearic shearwater spatial density predictions during PELACUS (2007–2016) oceanographic acoustic surveys.

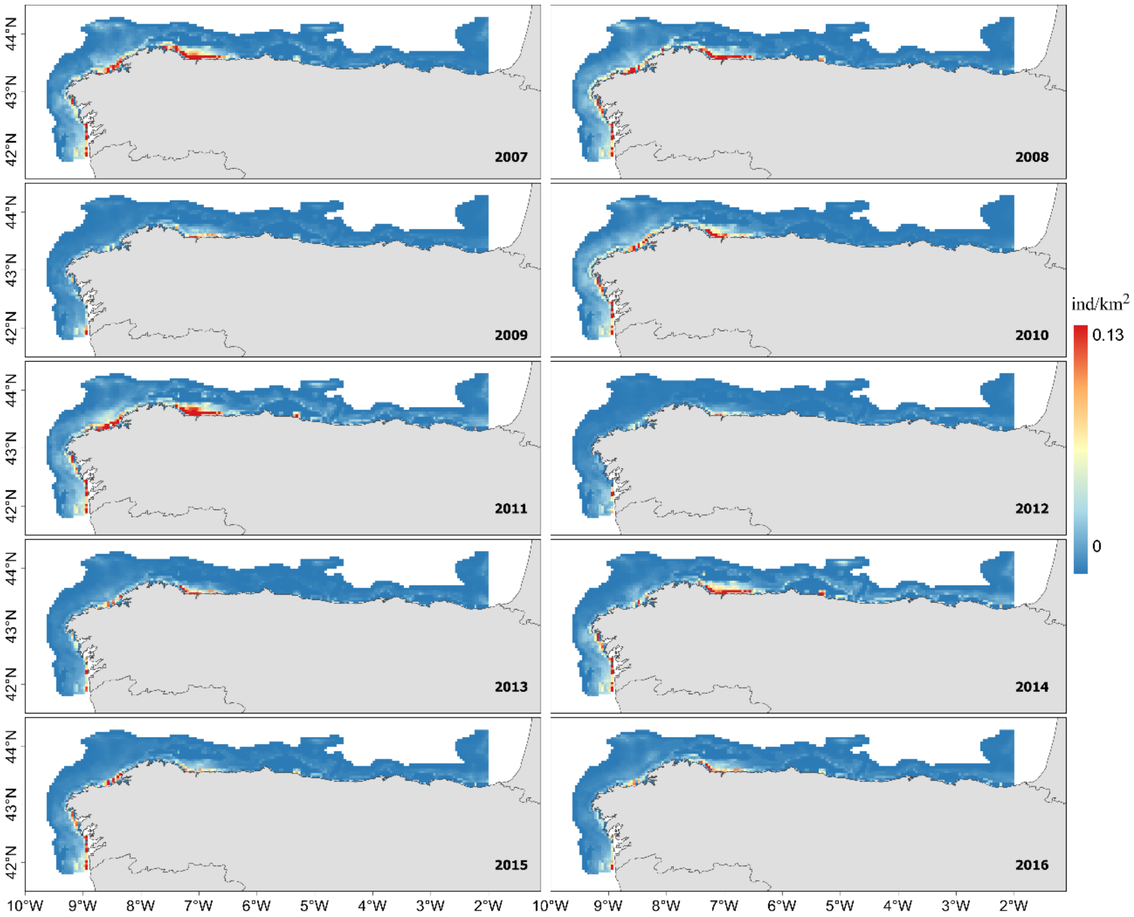


Figure C-4.12. Manx shearwater spatial density predictions during PELACUS (2007–2016) oceanographic acoustic surveys.

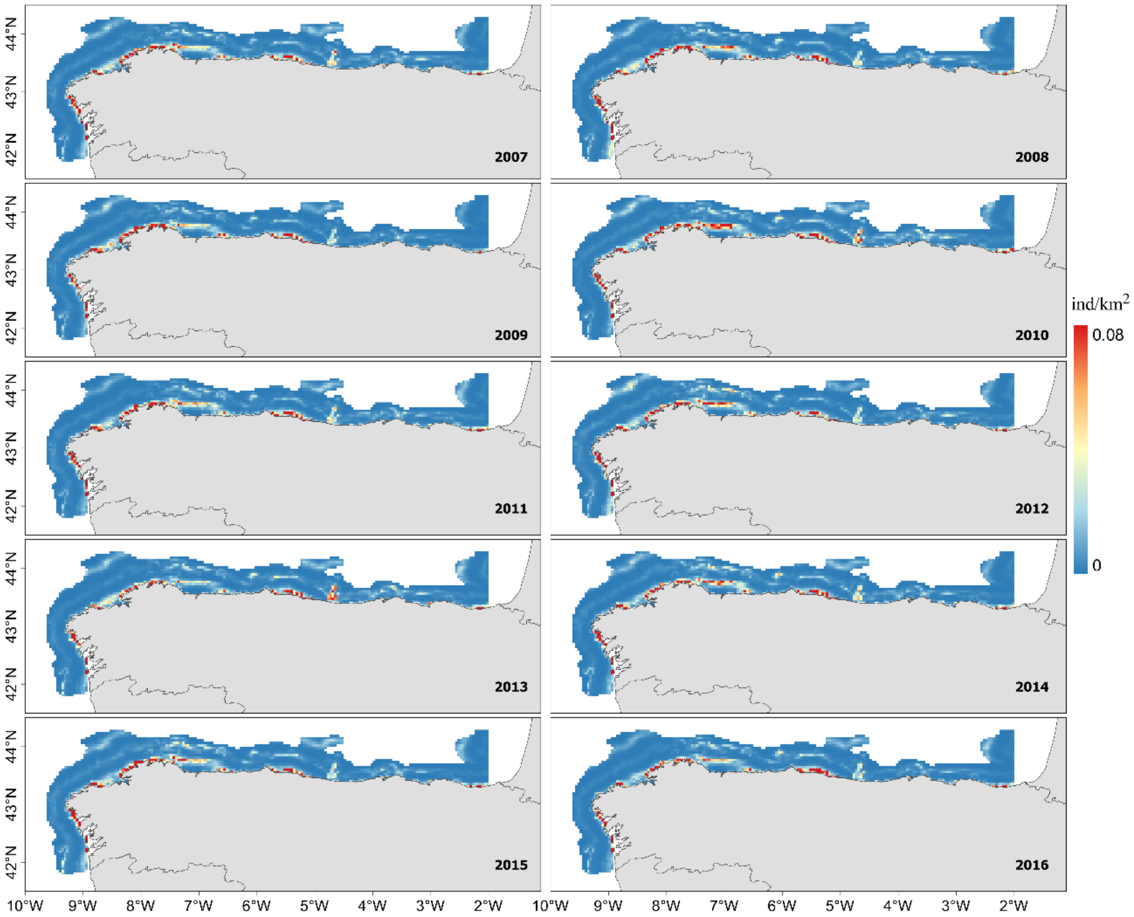


Figure C-4.13. Common dolphin spatial density predictions during PELACUS (2007–2016) oceanographic acoustic surveys.

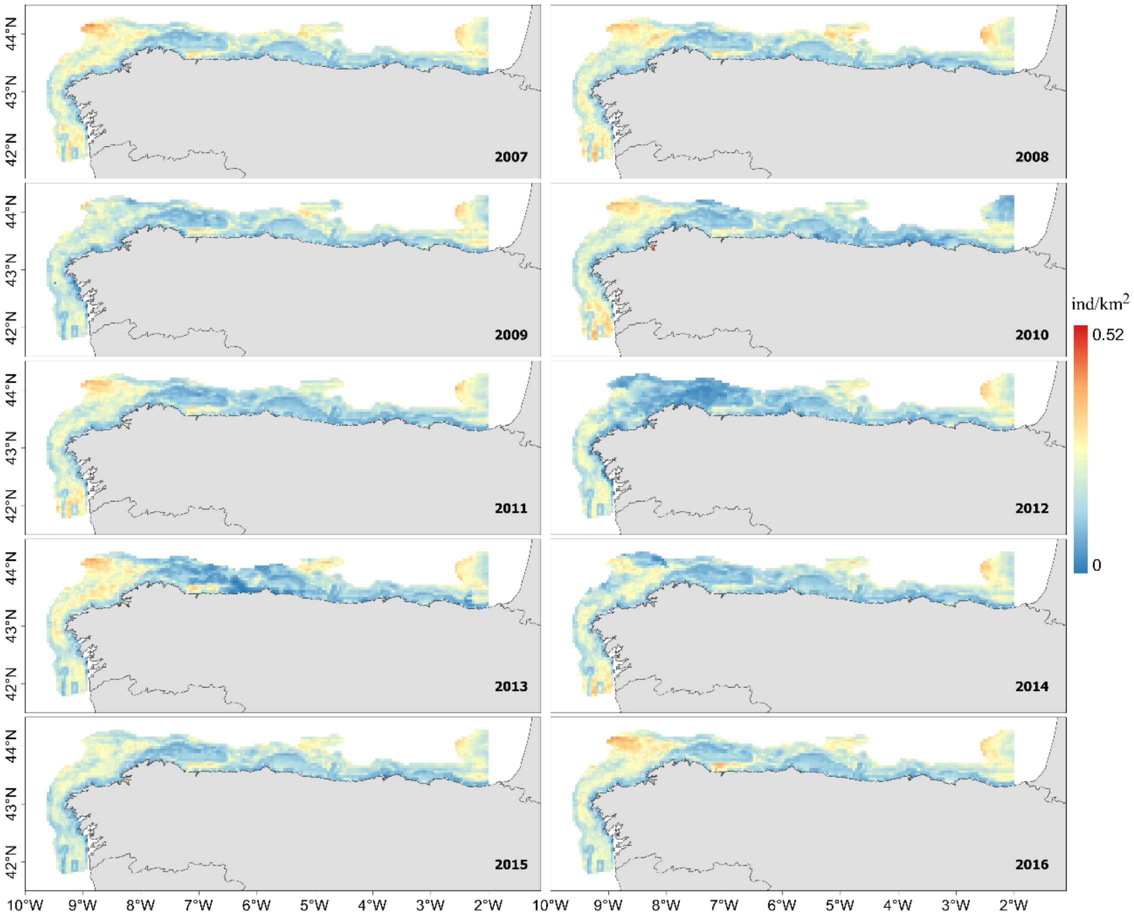


Figure C-4.14. Bottlenose dolphin spatial density predictions during PELACUS (2007–2016) oceanographic acoustic surveys.

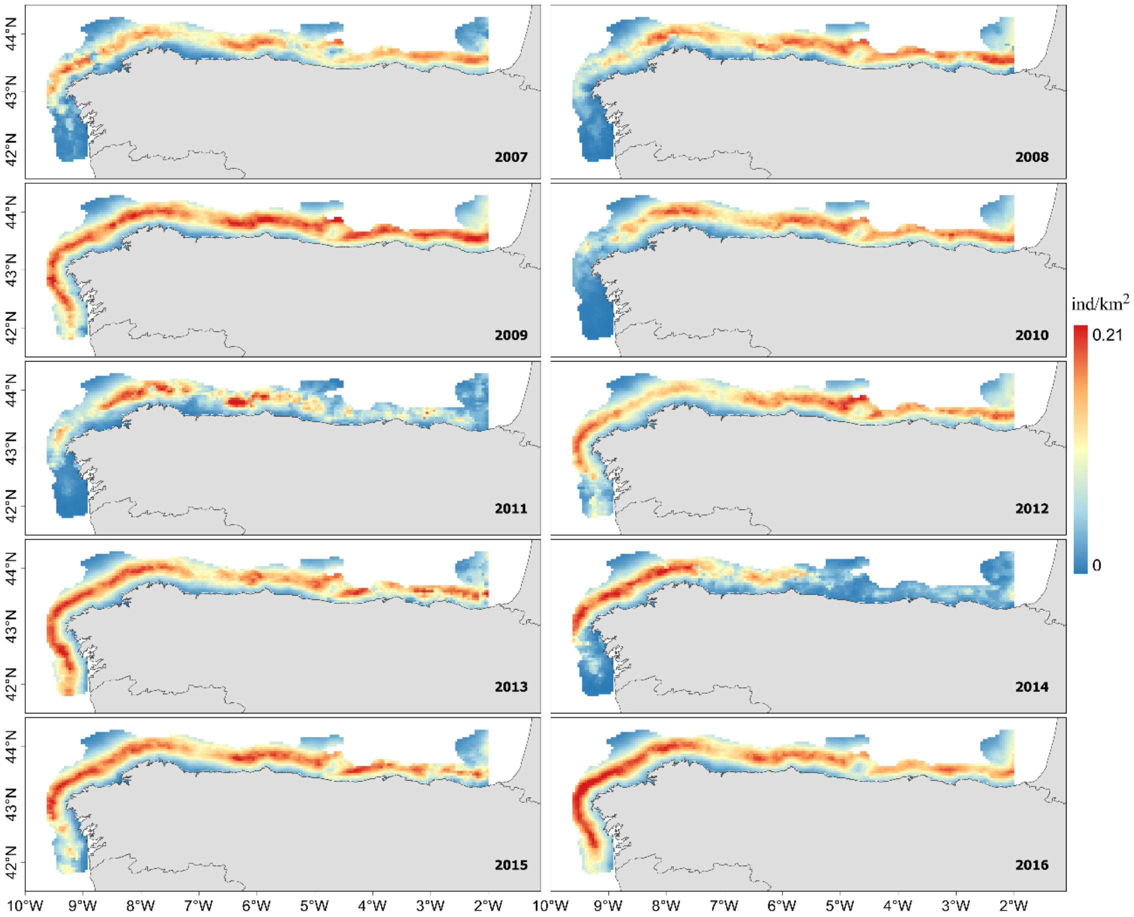
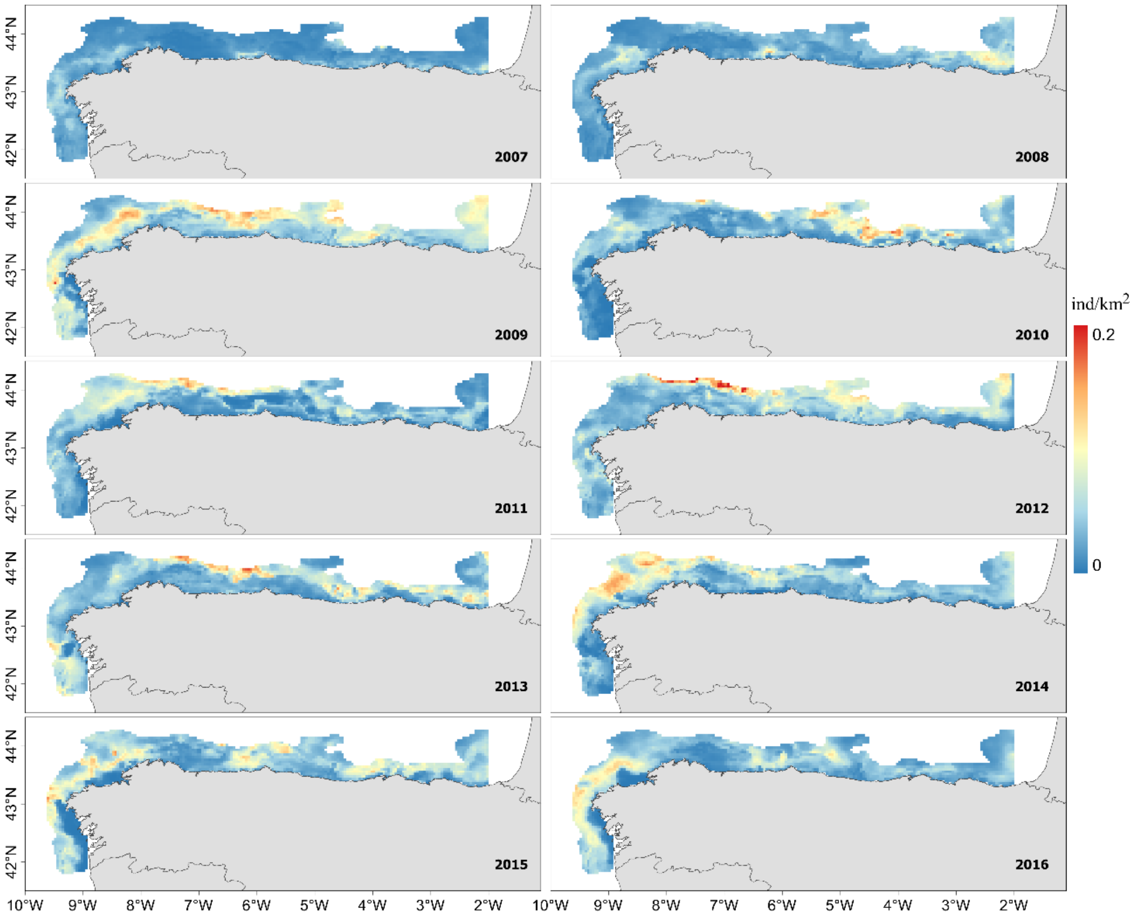


Figure C-4.15. Long-finned pilot whale spatial density predictions during PELACUS (2007–2016) oceanographic acoustic surveys.



Appendix C – Section 5: High-value biodiversity areas

Figure C-5.1. Maps showing the high-value biodiversity areas for the time-series 2007-2016 based on the biodiversity richness index (BRI) calculated for three cetacean species.

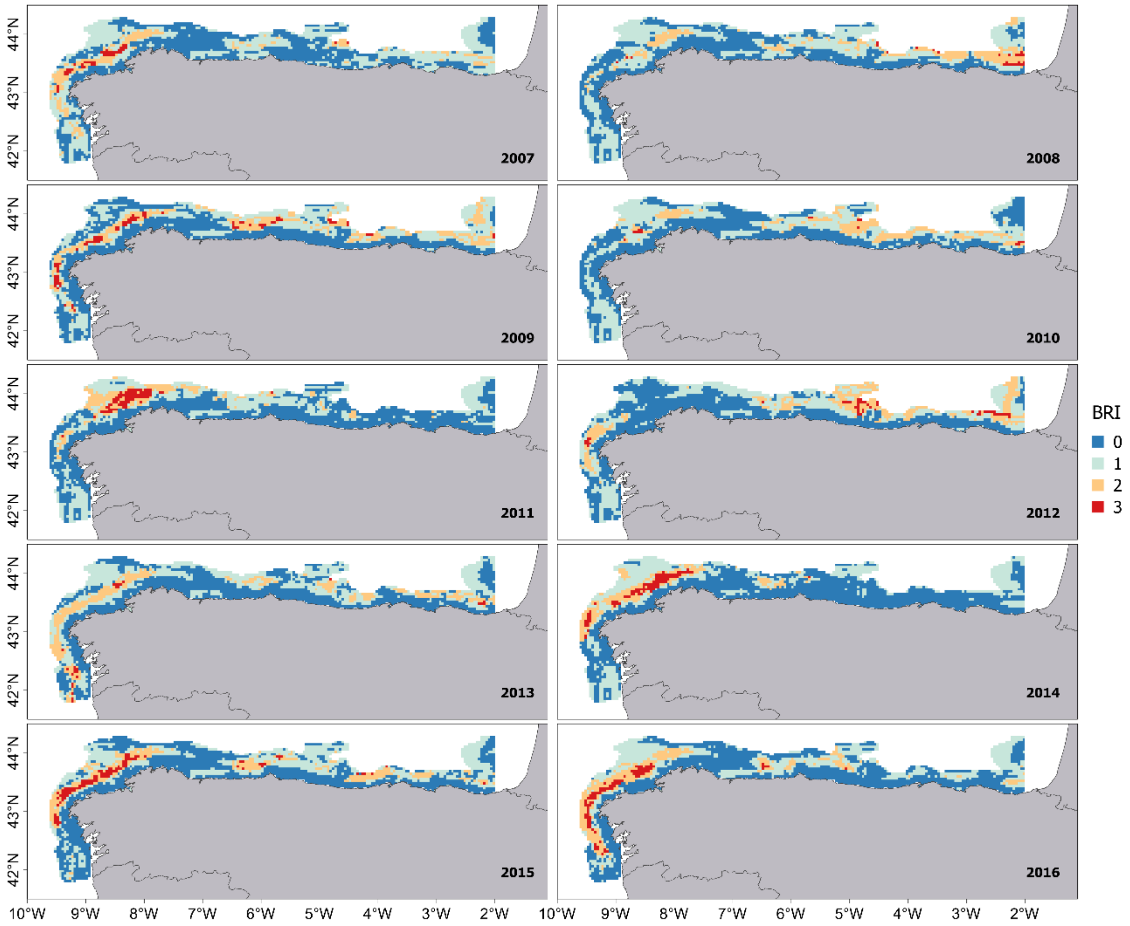


Figure C-5.2. Maps showing the high-value biodiversity areas for the time-series 2007-2016 based on the biodiversity richness index (BRI) calculated for ten seabird species.

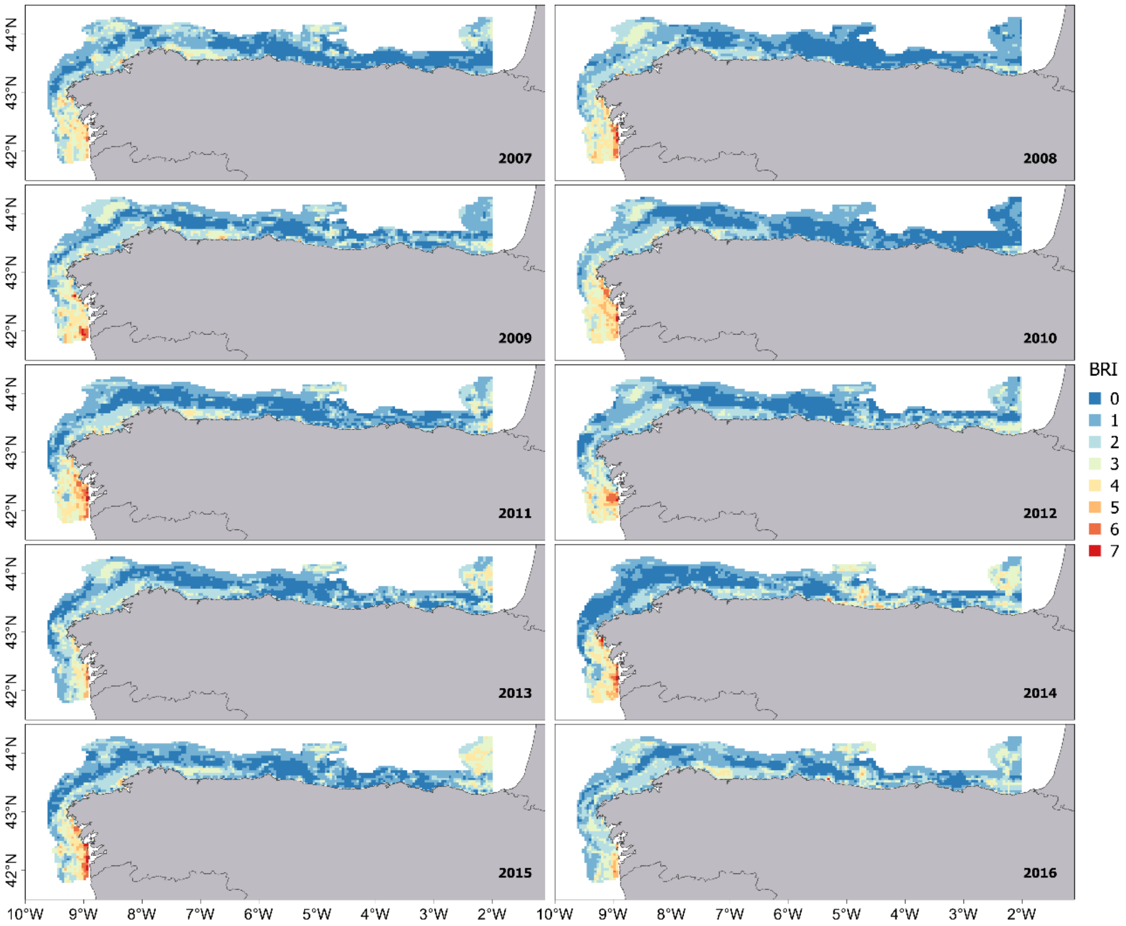


Figure C-5.3. Maps showing the high-value biodiversity areas for each year of the time-series 2007-2016 based on the biodiversity richness index (BRI) calculated for all the species analysed (three cetacean and ten seabird species).

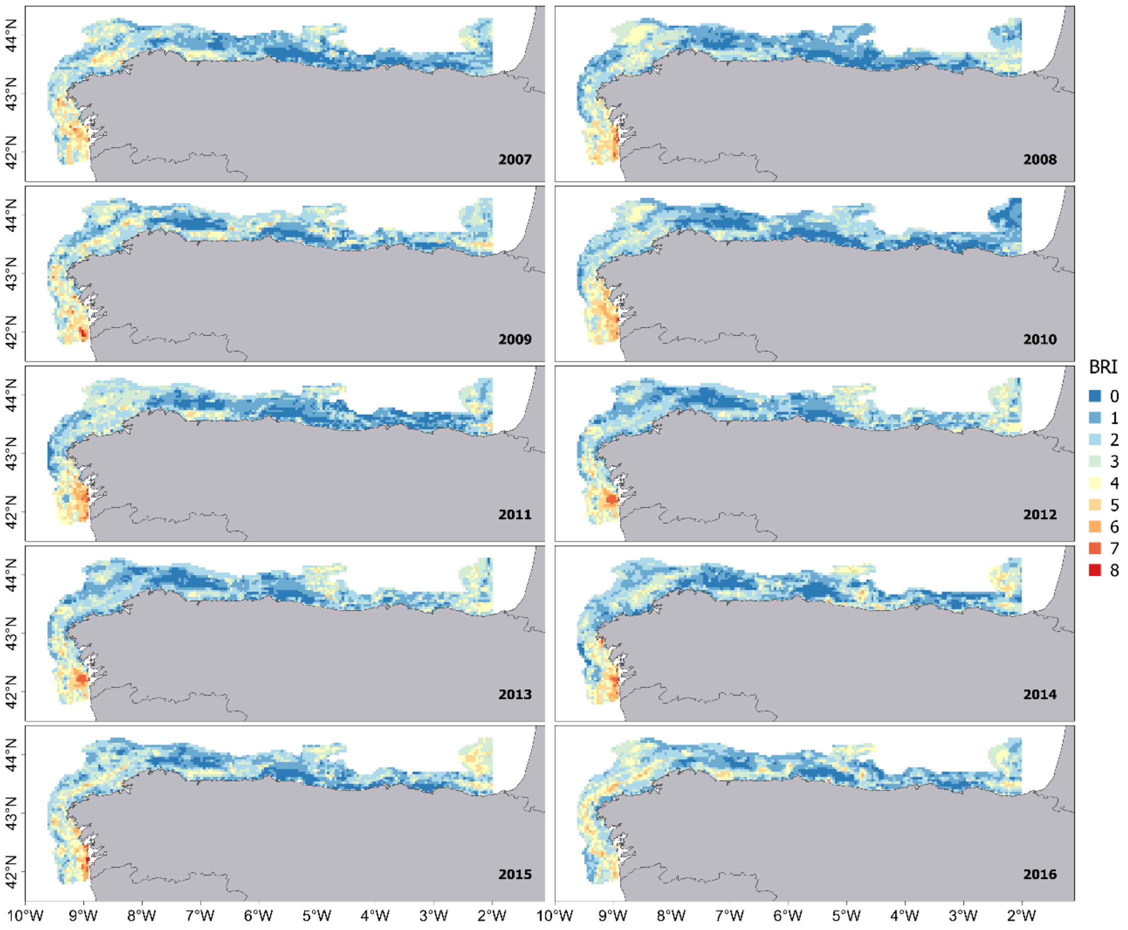
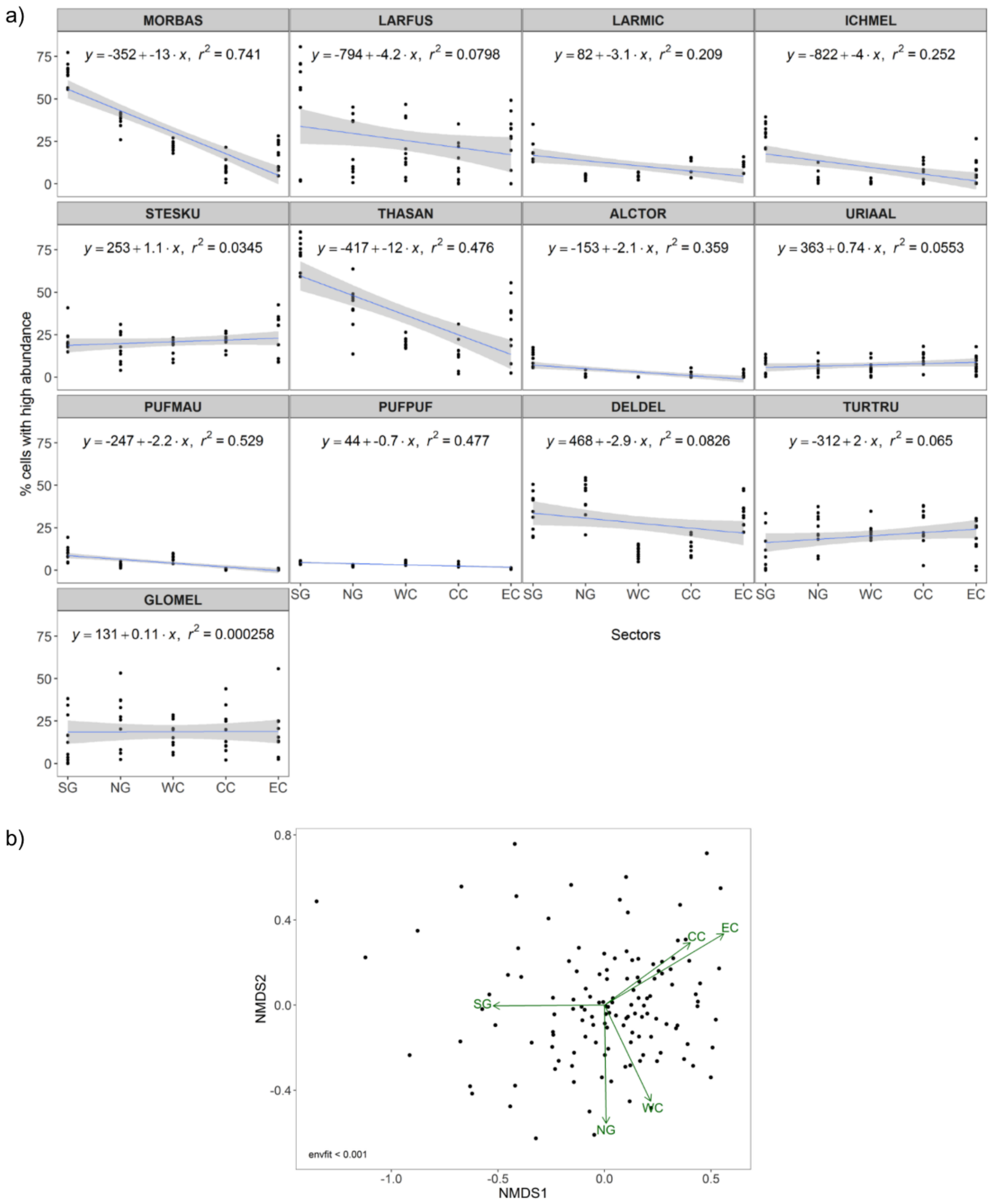


Figure C-5.4. Assessment of the geographical patterns in quantitative high-value biodiversity areas: a) linear models fitted for the percentage of cells with high abundance areas per sector, year and species. The solid blue line in each plot is the smooth function estimate and the shaded regions refer to the approximate 95% confidence intervals (the formula is showed in each plot). b) nMDS biplot based on a Bray Curtis dissimilarity distance showing the sectors correlating with the data as determined by *envfit* analysis (green arrows; *vegan* R-package (Oksanen et al., 2018)).



CHAPTER 4 – APPENDIX D

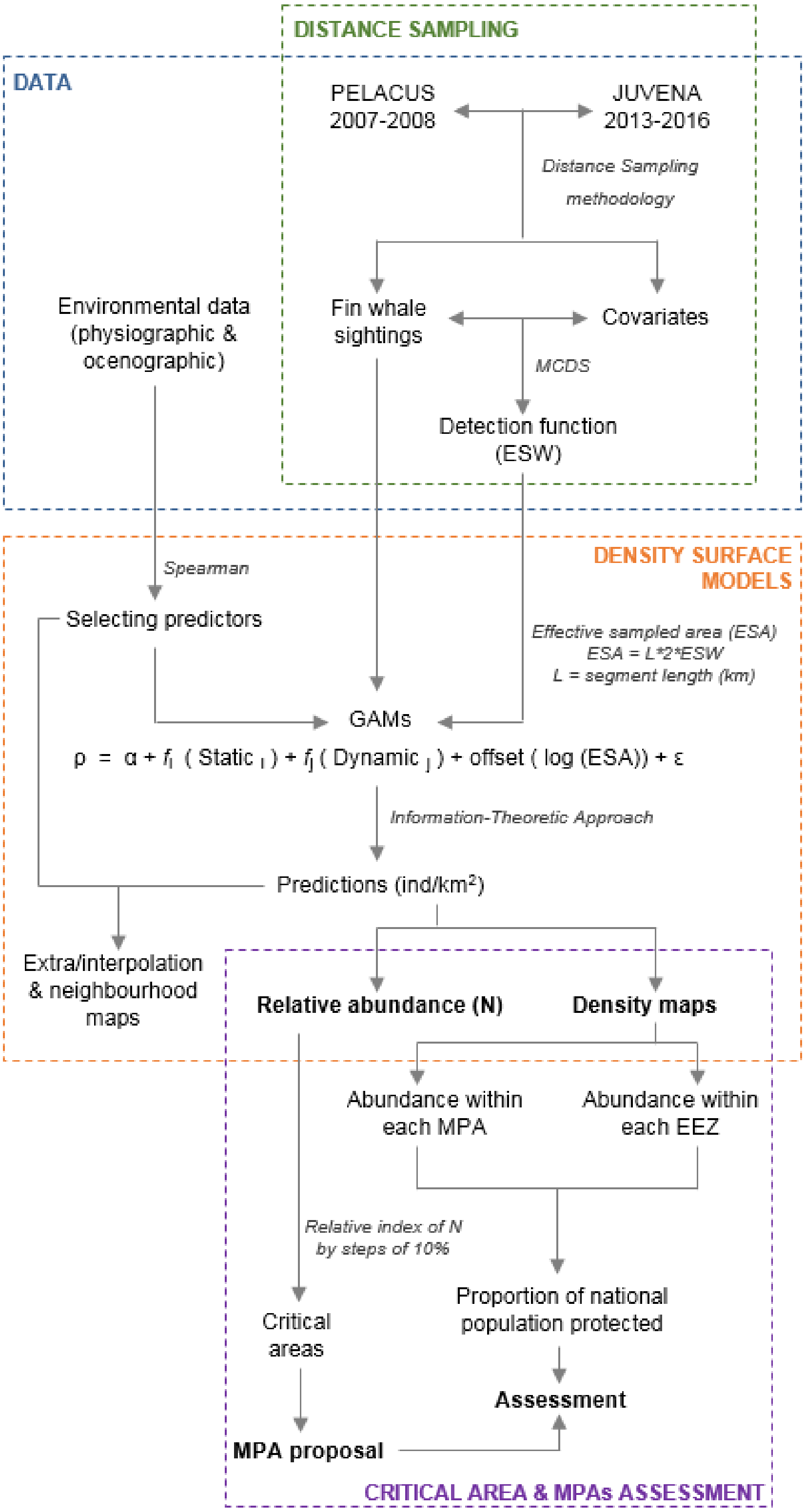
Modelling the spatial abundance of a migratory predator: a call for transboundary marine protected areas

Appendix D – Section 1: Survey's protocol

Visual line-transect protocols (Buckland et al., 2001) were followed during all surveys by a team of 3 observers working in turns of two and placed on the highest accessible point of the vessel, such that eye height was approximately 12 m and 7.5 m onboard *R/V Thalassa* and *R/V Ramón Margalef*, respectively. Observers scanned for marine mammals and seabirds a 180° sector ahead of the vessel. The port observer scanned the water to the front of the boat covering from 270º to 10º on the port side and the starboard observer from 350º to 90º on the starboard side, to ensure a good coverage of the track-line. Observers searched with naked eyes, and binoculars (10x42) were only used to aid species identification and to record the animals' behaviour. Observers collected data only along acoustic transects and, therefore, the vessel was navigating at constant heading and speed (around 10 knots) during daytime. Observation effort was geographically located thanks to the vessel GPS, which logs the coordinates of the vessel every 1 minute. For each observation period (i.e., leg), observers recorded data on vessel speed, heading, Beaufort sea-state, swell height and direction, wind speed and direction, cloud coverage, visibility, sun glare on each side of the vessel (port or starboard) and an overall subjective assessment of detection conditions of the sightings (good, moderate or bad relative to the detections).

Appendix D – Section 2: Workflow of the entire analytical process

Figure D.3.1. Workflow of the methods from the data collection to the Natura 2000 network assessment. MCDS: Multiple-Covariate Distance Sampling, GAMs: Generalized Additive Models; MPA: Marine Protected Area; EEZ: Exclusive Economic Zone.



Appendix D – Section 3: Environmental covariates

Figure D.4.1. Physiographic variables: (a) Depth, (b) Slope, (c) distance to the coast, (d) distance to the shelf-break, (e) distance to the 1000 m-isobath, (f) distance to the 2000 m-isobath.

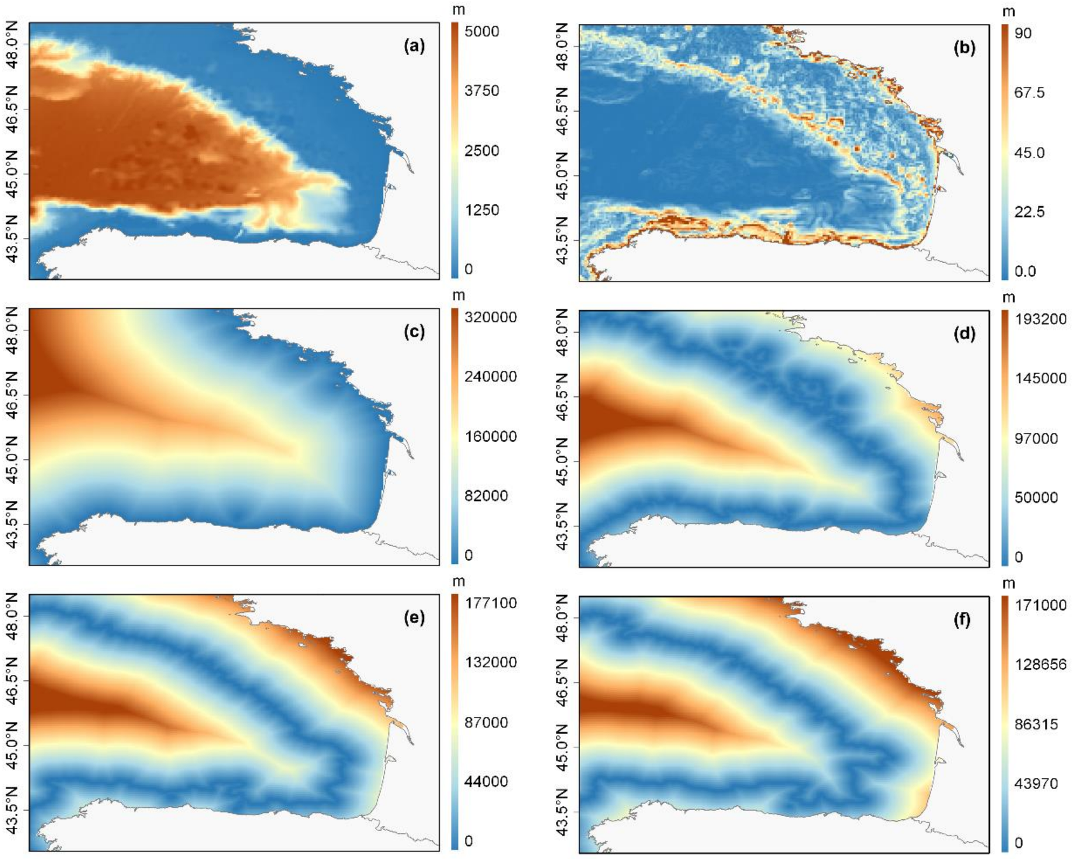
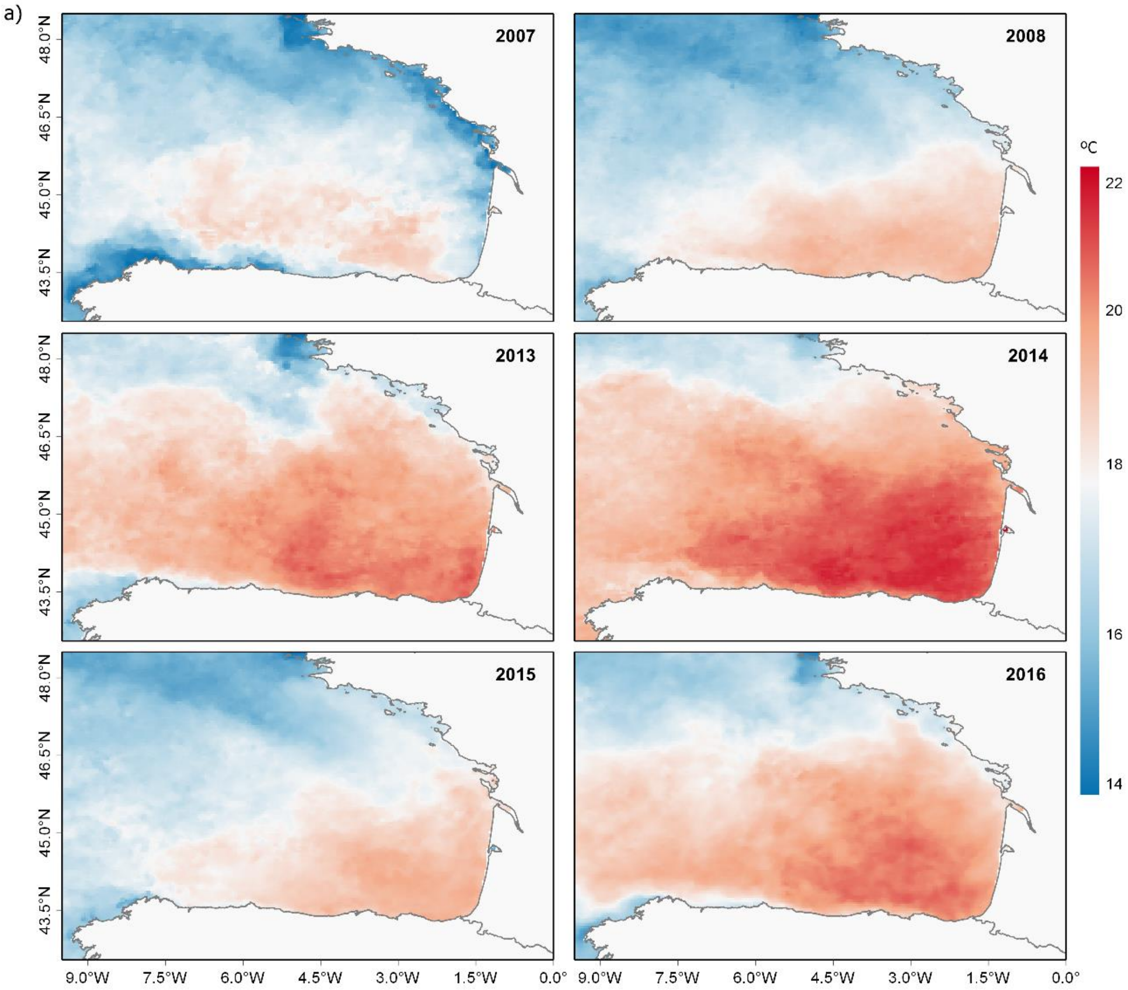
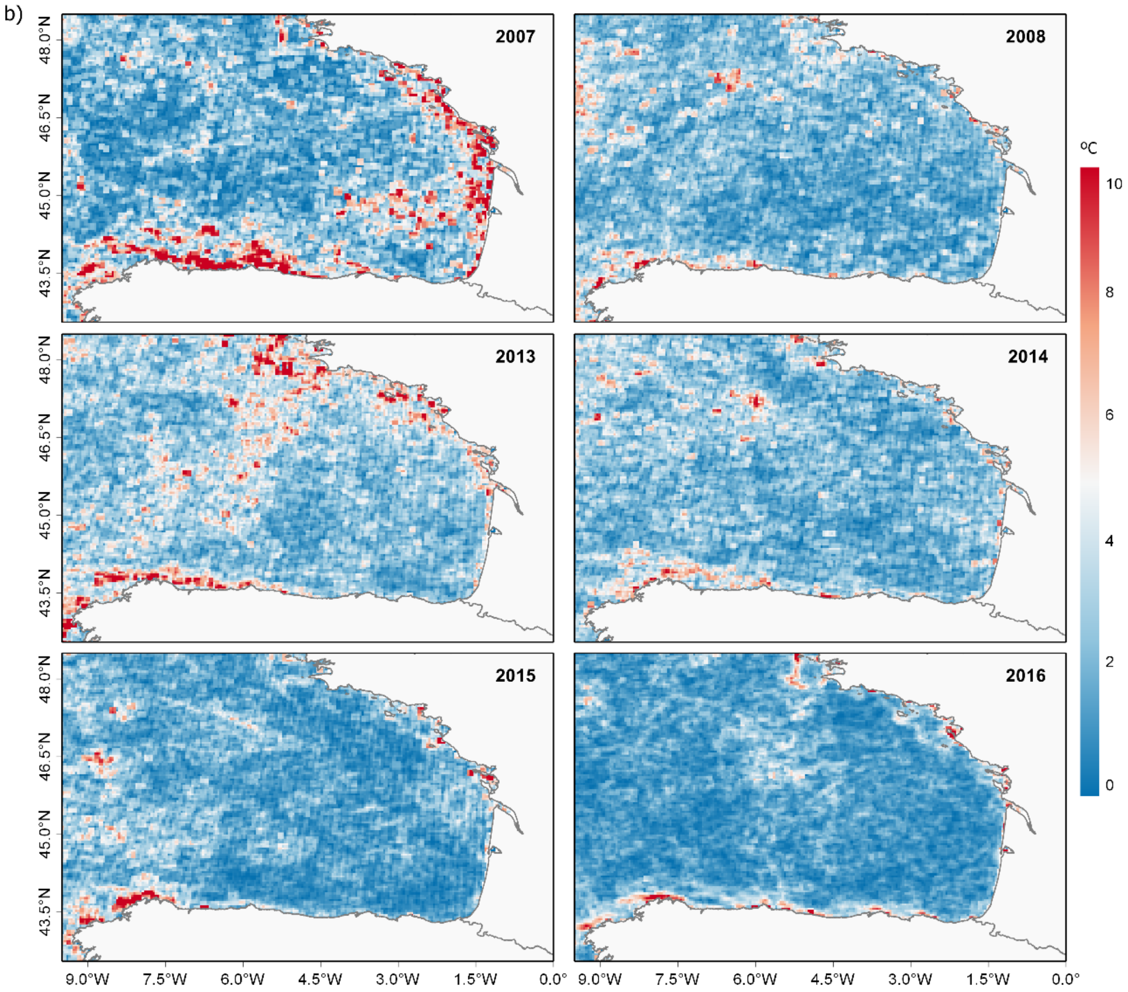
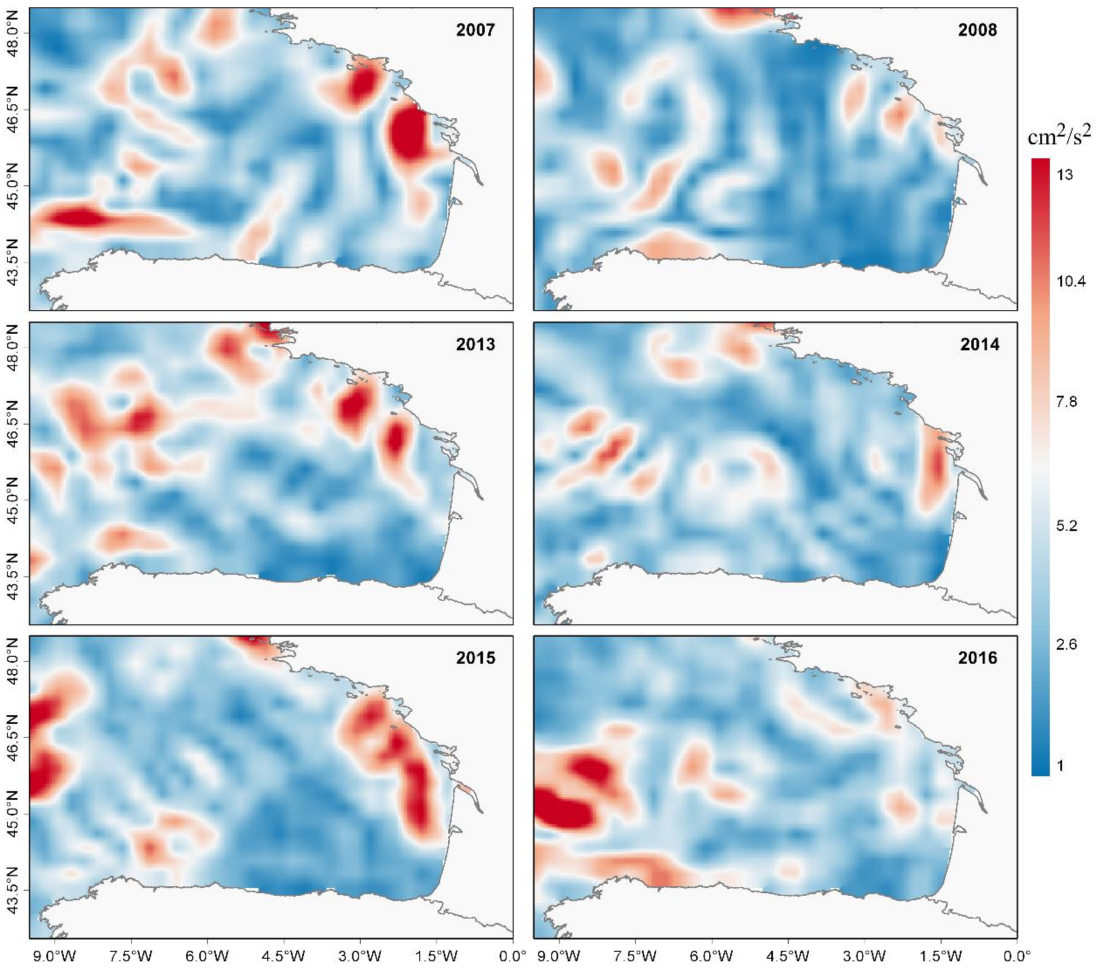


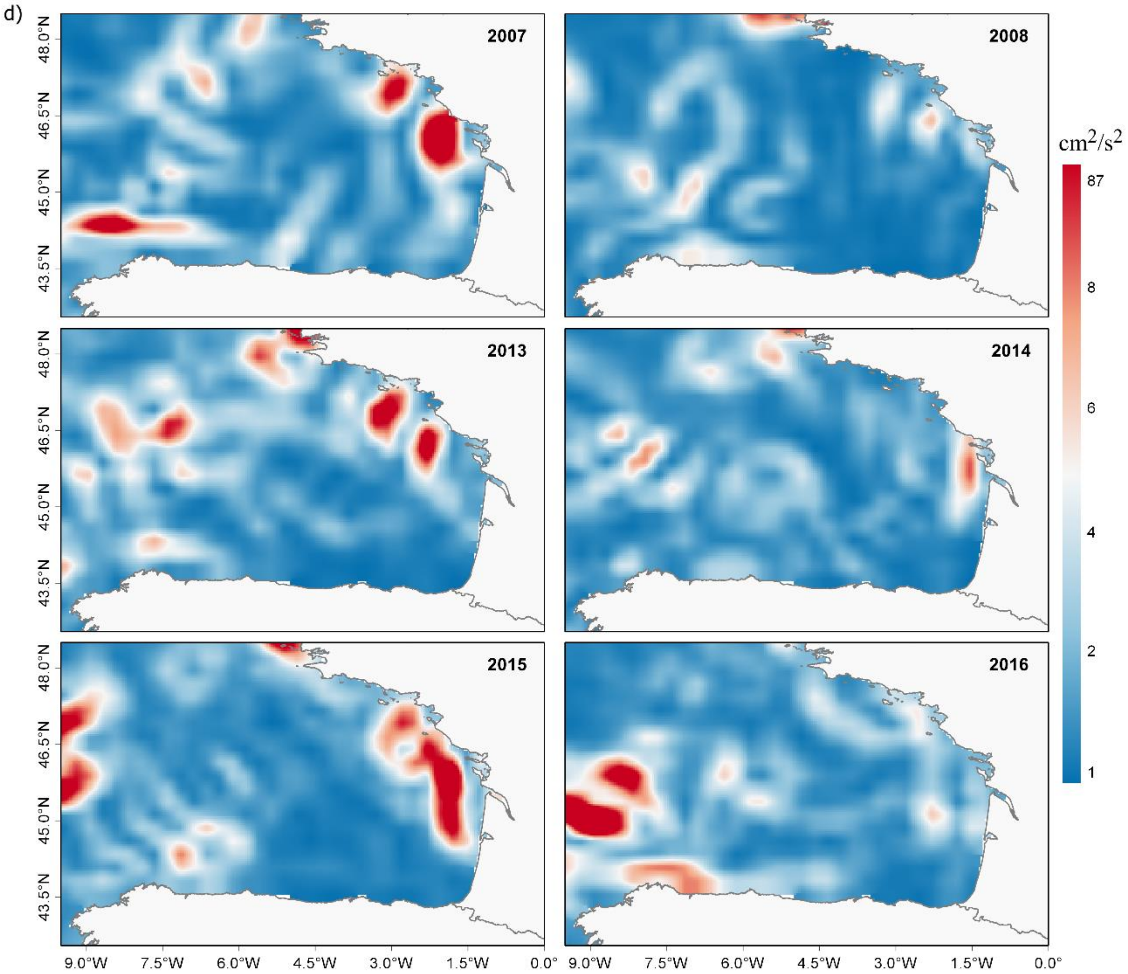
Figure D.4.2. Oceanographic variables over the study years. a) SST; b) SST_g; c) w; d) EKE; e) SLA; f) Chl-a; g) $Chl\text{-}a_g$.

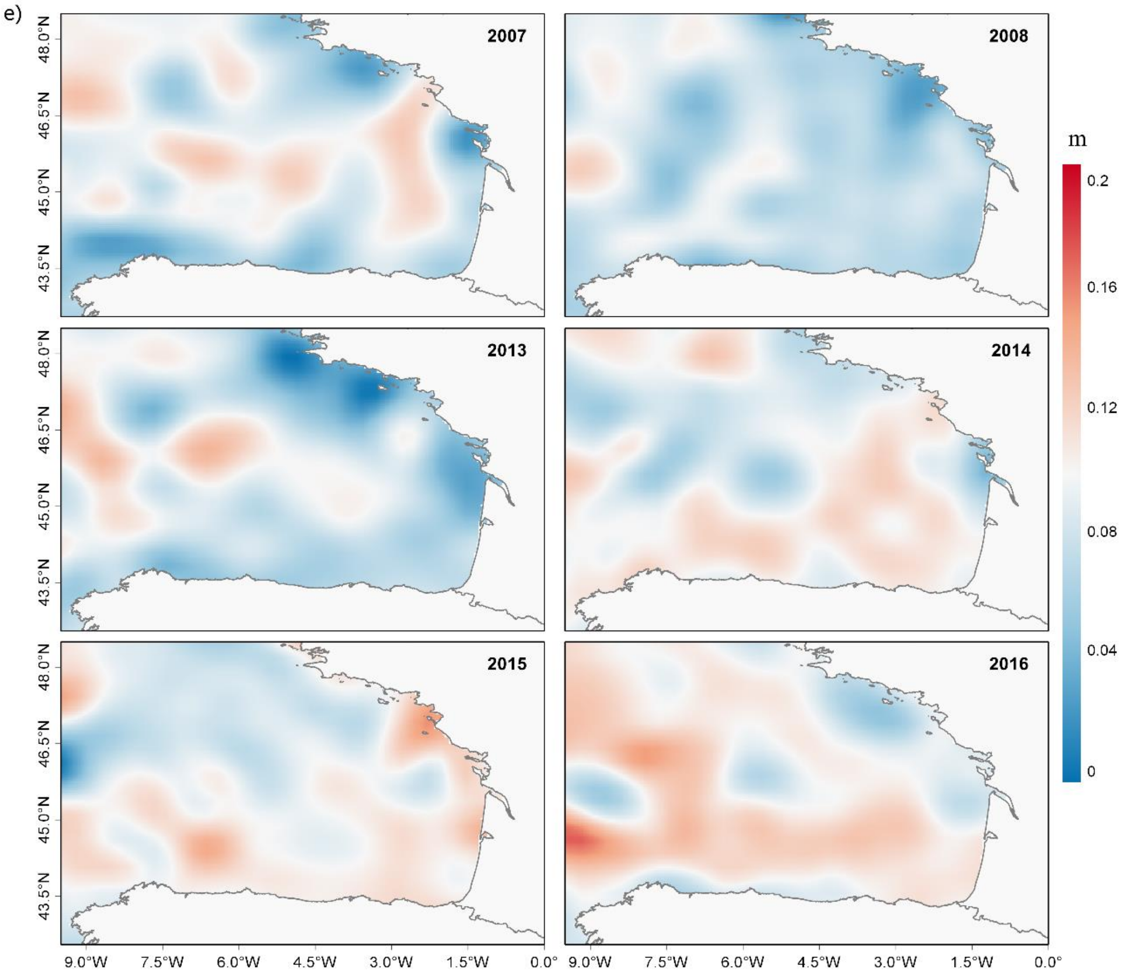



b)
2007
2008
2013
2014
2015
2016
48.0°N
46.5°N
45.0°N
43.5°N
9.0°W
7.5°W
6.0°W
4.5°W
3.0°W
1.5°W
0.0°
ºC
10
8
6
4
2
0

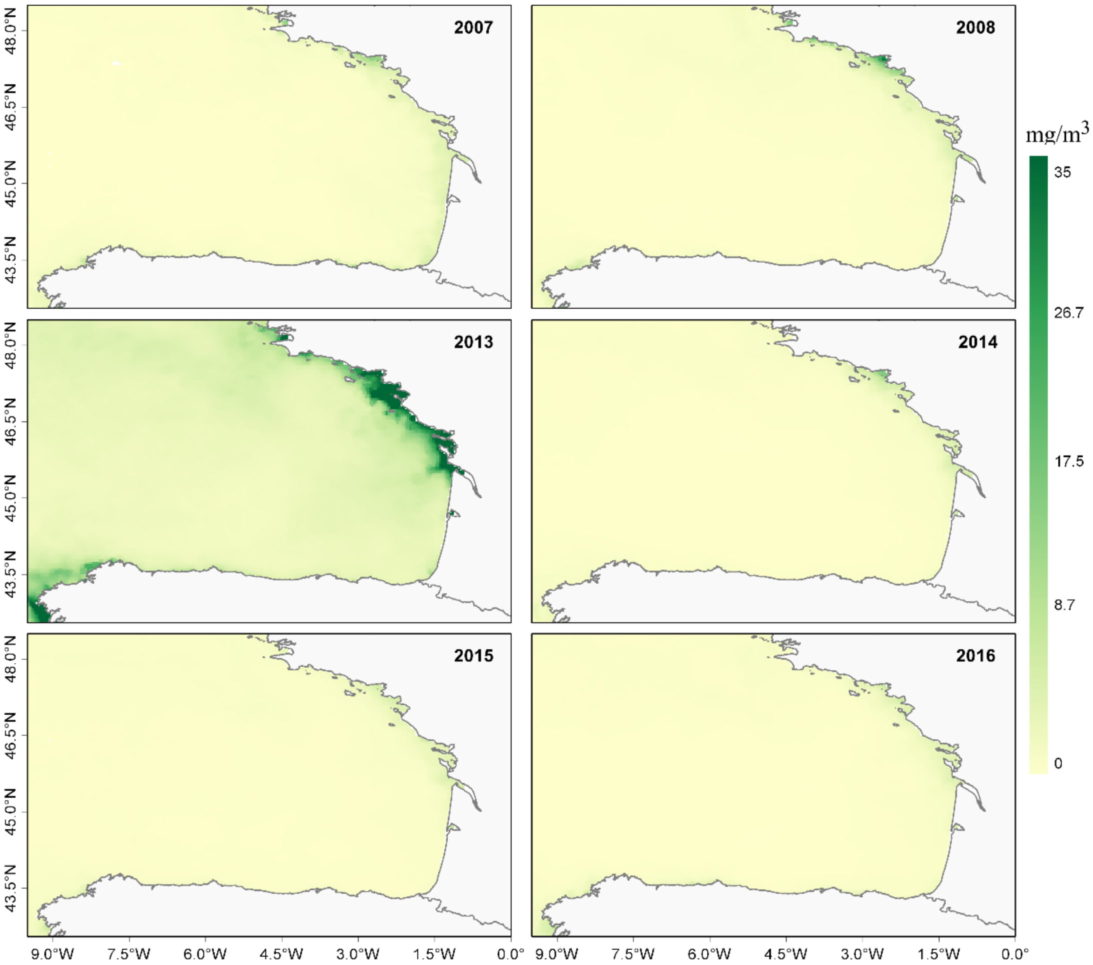
c)

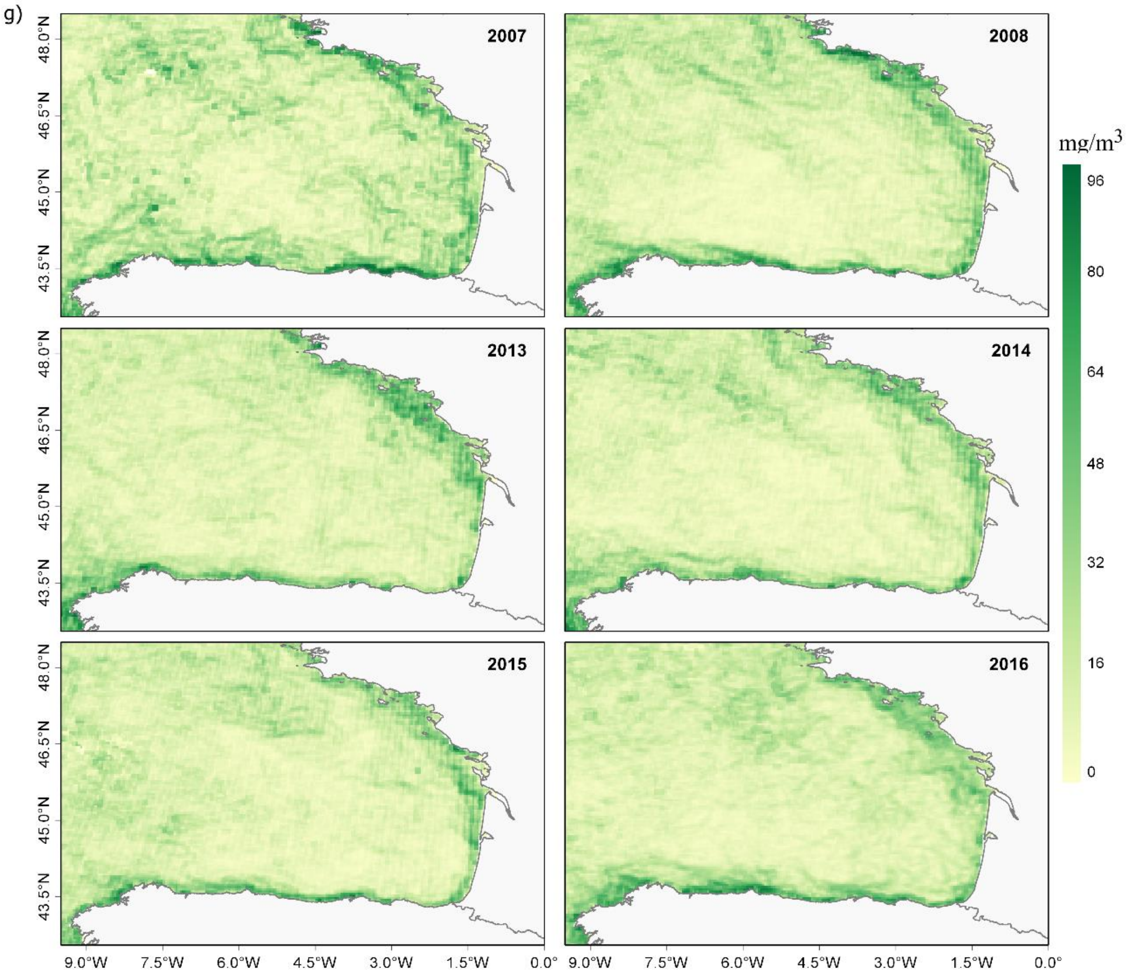

2007
2008
2013
2014
2015
2016
48.0°N
46.5°N
45.0°N
43.5°N
9.0°W
7.5°W
6.0°W
4.5°W
3.0°W
1.5°W
0.0°
cm^2/s^2
13
10.4
7.8
5.2
2.6
1


d)
2007
2008
2013
2014
2015
2016
48.0°N
46.5°N
45.0°N
43.5°N
9.0°W
7.5°W
6.0°W
4.5°W
3.0°W
1.5°W
0.0°
cm^2/s^2
87
8
6
4
2
1


e)
2007
2008
2013
2014
2015
2016
m
0.2
0.16
0.12
0.08
0.04
0
48.0°N
46.5°N
45.0°N
43.5°N
9.0°W
7.5°W
6.0°W
4.5°W
3.0°W
1.5°W
0.0°

f)


2007
2008
2013
2014
2015
2016
48.0°N
46.5°N
45.0°N
43.5°N
9.0°W
7.5°W
6.0°W
4.5°W
3.0°W
1.5°W
0.0°
mg/m^3
35
26.7
17.5
8.7
0


g)
2007
2008
2013
2014
2015
2016
48.0°N
46.5°N
45.0°N
43.5°N
9.0°W
7.5°W
6.0°W
4.5°W
3.0°W
1.5°W
0.0°
mg/m³
96
80
64
48
32
16
0

Appendix D – Section 4: Spearman-rank correlation coefficients

Table D.5.1. Pair-wise correlation between predictor variables by means of Spearman-rank correlation coefficient. Correlation higher than |0.7| are in bold. See Table 4.2 for abbreviations.

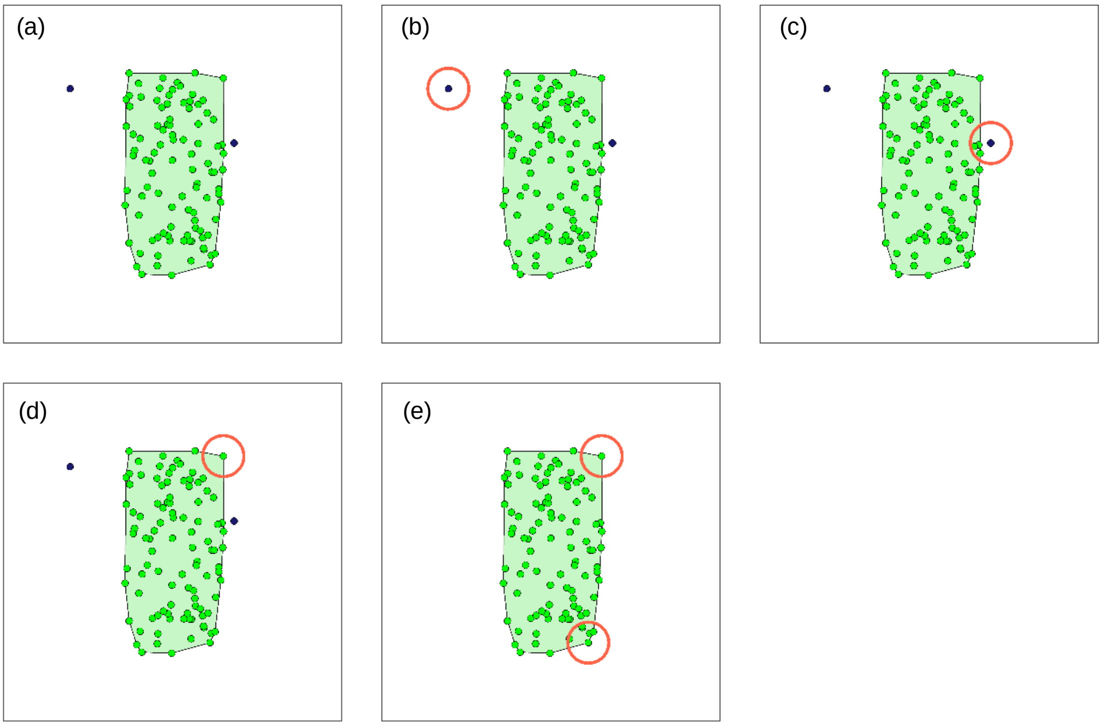
	CHL	CHL$_g$	SST	SST$_g$	w	EKE	SLA	BAT	BAT$_g$	DisSB	Dist1	Dist2	DisCO
CHL	1	0.505	-0.401	0.158	0.005	0.017	-0.133	-0.563	0.125	0.082	0.337	0.481	-0.336
CHL$_g$	0.505	1	-0.181	0.319	-0.038	-0.032	-0.248	-0.464	0.192	0.018	0.217	0.324	-0.439
SST	-0.401	-0.181	1	-0.052	-0.271	-0.286	0.174	0.378	0.039	-0.190	-0.425	-0.414	0.031
SST$_g$	0.158	0.319	-0.052	1	0.113	0.118	-0.105	-0.233	0.106	0.009	0.098	0.118	-0.177
w	0.005	-0.038	-0.271	0.113	1	0.998	0.011	-0.010	-0.156	0.237	0.176	0.092	0.158
EKE	0.017	-0.032	-0.286	0.118	0.998	1	-0.001	-0.020	-0.154	0.239	0.183	0.103	0.152
SLA	-0.133	-0.248	0.174	-0.105	0.011	-0.001	1	0.353	-0.161	-0.020	-0.141	-0.246	0.358
BAT	-0.563	-0.464	0.378	-0.233	-0.010	-0.020	0.353	1	-0.466	0.009	-0.379	-0.577	0.656
BAT$_g$	0.125	0.192	0.039	0.106	-0.156	-0.154	-0.161	-0.466	1	-0.566	-0.389	-0.132	-0.471
DisSB	0.082	0.018	-0.190	0.009	0.237	0.239	-0.020	0.009	-0.566	1	0.687	0.380	0.160
Dist1	0.337	0.217	-0.425	0.098	0.176	0.183	-0.141	-0.379	-0.389	0.687	1	0.823	-0.068
Dist2	0.481	0.324	-0.414	0.118	0.092	0.103	-0.246	-0.577	-0.132	0.380	0.823	1	-0.312
DisCO	-0.336	-0.439	0.031	-0.177	0.158	0.152	0.358	0.656	-0.471	0.160	-0.068	-0.312	1

Appendix D – Section 5: Spatial prediction reliability

We developed an example of interpolation versus extrapolation from simulated data: the light green polygon simulates the convex hull, *i.e.,* the smallest convex polygon containing the environmental variable values used as calibration data when estimating the models (Figure D.6.1). Likewise, derived from a simulated prediction dataset we represent those points (*i.e.,* predictions) which fall inside the convex hull and are interpolations (in green) and those which are outside the convex hull and are extrapolations (in blue).

This example is intended to show the importance of not only considering a prediction as an extrapolation but also taking into account the calibration data which is informing this prediction. In the Figure D.6.1b, c, d and e the red circles indicate the neighbourhood of some predictions. The Figure D.6.1b shows the neighbourhood of an extrapolation which is not informed by any calibration data, whilst the Figure D.6.1c shows that even if a prediction falls outside the convex hull (*i.e.,* even if it's an extrapolation), it can be still informed by calibration data lying in its neighbourhood, and we can argue that is “less of an extrapolation” (King and Zeng, 2007). However, as the Figure D.6.1d shows, an interpolation may not have calibration data lying in its neighbourhood and be less reliable than a “pure” extrapolation. Finally, the bottom red circle in the Figure D.6.1e shows the “ideal” prediction, in this case this prediction can be considered as interpolation since it falls inside the convex hull and its informed by calibration data lying in its neighbourhood.

Figure D.6.1. Example of interpolation versus extrapolation from simulated data.



Appendix D – Section 6: Distance Sampling Analysis

Figure D-6.1. Fin whale hazard-rate detection function based on JUVENA and PELACUS surveys showing histogram of perpendicular distance data for the sightings and the fitted detection probability (line) predicted by the model. Perpendicular distance was truncated at 4000 m.

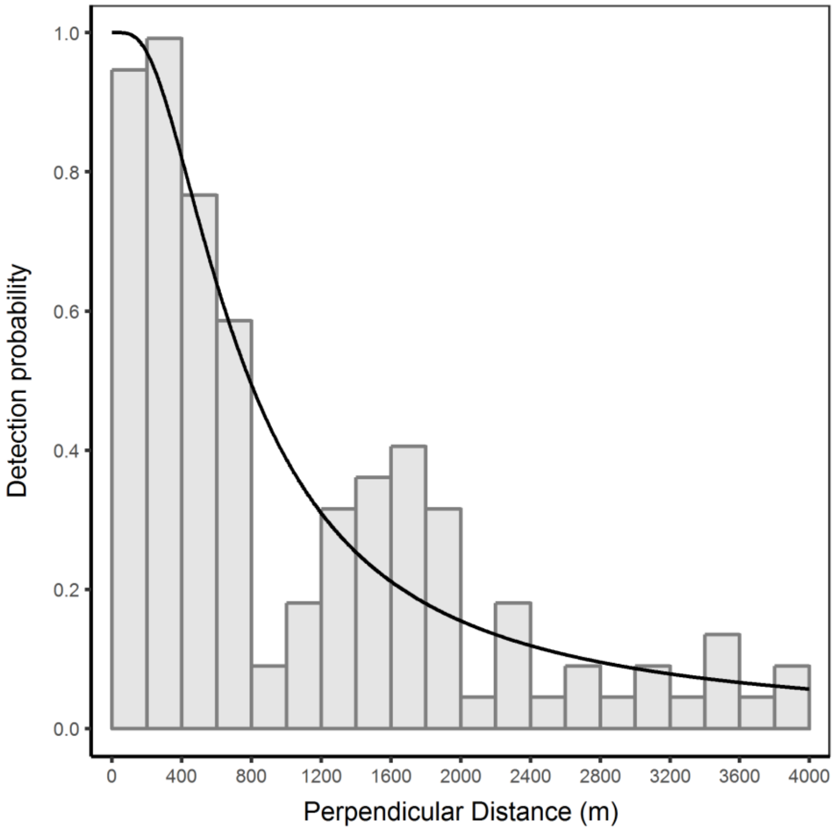


Table D-6.1. Results of the best fitted detection functions, table show the following data: Key: type of detection function, Detection covariate: environmental covariates sued to perform MCDS (Multiple-Covariate Distance Sampling) analysis, Cov.1: levels of the covariate 1 used to perform the MCDS analysis, Cov2: if used, levels of the covariate 2 used to perform the MCDS analysis, ESW: effective strip half-width in meters, AIC: Akaike Information Criteria, ∆ AIC: delta AIC, Param: number of parameters included in the detection function, Ks Dn: Kolmogorov-Smirnov goodness-of-fit statistics, Ks pvalue: p-value of Kolmogorov-Smirnov, CvM: Cramer-von Mises goodness-of-fit statistics, CvM pvalue: p-value of Cramer-von Mises goodness-of-fit statistics, Pa: averaged detection probability, SE Pa: standard error of detection probability, CV Pa: coefficient of variation of detection probability.

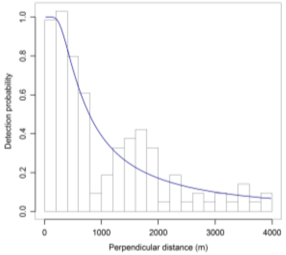
Key	Detection covariate	Cov. 1	Cov. 2	ESW (m)	AIC	∆ AIC	Param	Ks Dn	Ks pvalue	CvM	CvM pvalue	Pa	SE Pa	CV Pa	Fitted detection function
HR	R/V + cluster size	TH	1	2760.96	674.10	0.00	4	0.09	0.26	0.10	0.61	0.30	0.05	0.16	
			2	3299.854											
			3	3712.013											
		RM	1	1011.133											
			2	1377.985											
			3	1835.753											
			6	3447.211											

Table D-6.1. Continuation

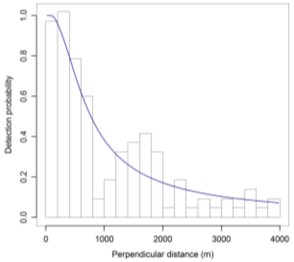
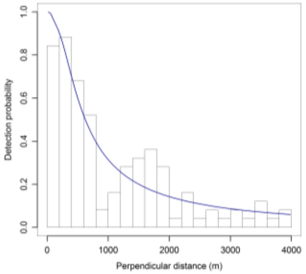
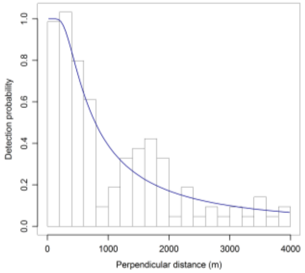
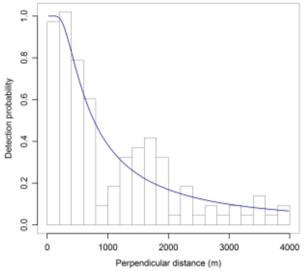
Key	Detection covariate	Cov. 1	Cov. 2	ESW (m)	AIC	∆ AIC	Param	Ks Dn	Ks pvalue	CvM	CvM pvalue	Pa	SE Pa	CV Pa	Fitted detection function
HR	R/V + Beaufort	TH	0,1,2,3	3255.67	674.22	0.13	4	0.08	0.32	0.11	0.54	0.30	0.05	0.17	
			4,5	3946.1726											
		RM	0,1,2,3	636.3327											
			4,5	1302.4449											
HR	Year	2007		3256.51	674.77	0.67	7	0.08	0.35	0.11	0.55	0.26	0.06	0.22	
		2008		281.81											
		2013		663.11											
		2014		1291.45											
		2015		1187.91											
		2016		950.59											

Table D-6.1. Continuation

Key	Detection covariate	Cov. 1	Cov. 2	ESW (m)	AIC	∆ AIC	Param	Ks Dn	Ks pvalue	CvM	CvM pvalue	Pa	SE Pa	CV Pa	Fitted detection function
HR	R/V	TH		2047.8	674.95	0.85	3	0.09	0.21	0.15	0.39	0.30	0.05	0.16	
		RM		2683.85											
HR	R/V + Cloud cover	TH	0 to 4	2681.23	676.79	2.69	4	0.07	0.53	0.11	0.52	0.30	0.05	0.16	
			5 to 8	-											
		RM	0 to 4	1078.31											
			5 to 8	1231.27											

Appendix D – Section 7: Results of spatial abundance modelling procedure

Table D-7.1. Detailed results of spatial abundance modelling procedure based on the Information-Theoretic approach. '+' signs indicate variables included in the model. Int: intercept, k: number of knots, AIC_c: corrected Akaike Information Criteria, Δ AICc: $(AIC_c)_i - (AIC_c)_{min}$, ω_i: Akaike weights, Dev (%): Percentage of deviance explained, see Table 4.2 for predictors abbreviations.

Model	**Int**	**BAT**	**SST**	**EKE**	**SLA**	**CHL_g**	**DisCO**	**Dist2**	**DisSB**	**SST_g**	**BAT_g**	**CHL**	**k**	**AIC_c**	**Δ AIC_c**	**ω_i**	**Dev (%)**
1	-6.779	+	+	+	+								4	775.627	0	0.340	37.42
2	-6.707	+	+	+		+							4	776.998	1.371	0.171	36.63
3	-6.842	+	+		+	+							4	777.895	2.268	0.109	36.21
4	-6.657	+	+	+			+						4	780.421	4.794	0.031	36.59
5	-6.626	+	+	+									4	780.520	4.893	0.029	35.98
6	-6.725	+	+	+						+			4	780.619	4.992	0.028	36.03
7	-6.752	+	+		+			+					4	780.687	5.060	0.027	36.42
8	-6.643	+	+	+					+				4	780.863	5.236	0.025	36.14
9	-6.690	+		+	+	+							4	780.880	5.253	0.025	34.12
10	-6.766	+	+		+				+				4	781.252	5.625	0.020	35.87
11	-6.758	+	+		+		+						4	781.753	6.126	0.016	36.03
12	-6.700	+	+		+								4	781.773	6.146	0.016	34.84
13	-6.623	+	+	+								+	4	781.893	6.266	0.015	35.53

Table D-7.1. Continuation

Model	Int	BAT	SST	EKE	SLA	CHL_g	DisCO	Dist2	DisSB	SST_g	BAT_g	CHL	k	AIC_c	Δ AIC_c	ω_i	Dev (%)
14	-6.741	+	+			+		+					4	782.320	6.693	0.012	35.89
15	-6.721	+	+		+						+		4	782.420	6.793	0.011	35.25
16	-6.628	+	+	+							+		4	782.491	6.864	0.011	36.04
17	-6.721	+		+	+				+				4	782.536	6.909	0.011	35.06
18	-6.639	+	+	+				+					4	782.856	7.229	0.009	36.51
19	-6.674	+		+	+		+						4	783.085	7.458	0.008	34.99
20	-6.730	+	+		+					+			4	783.637	8.010	0.006	34.89
21	-6.663	+	+			+							4	783.705	8.078	0.006	34.44
22	-6.701	+	+		+							+	4	783.831	8.204	0.006	34.84
23	-6.671	+	+				+	+					4	784.003	8.376	0.005	36.25
24	-6.657	+			+	+							4	784.738	9.111	0.004	32.28
25	-6.696	+			+	+		+					4	784.777	9.150	0.004	33.53
26	-6.737	+	+			+				+			4	785.048	9.421	0.003	34.62

CHAPTER 5 – APPENDIX E

The value of time-series for conservation planning

Appendix E – Section 1: Conservation features

Figure E.1.1. Map of the study area representing the abundance per planning unit of the Yellow-legged gull (*Larus michahellis*).

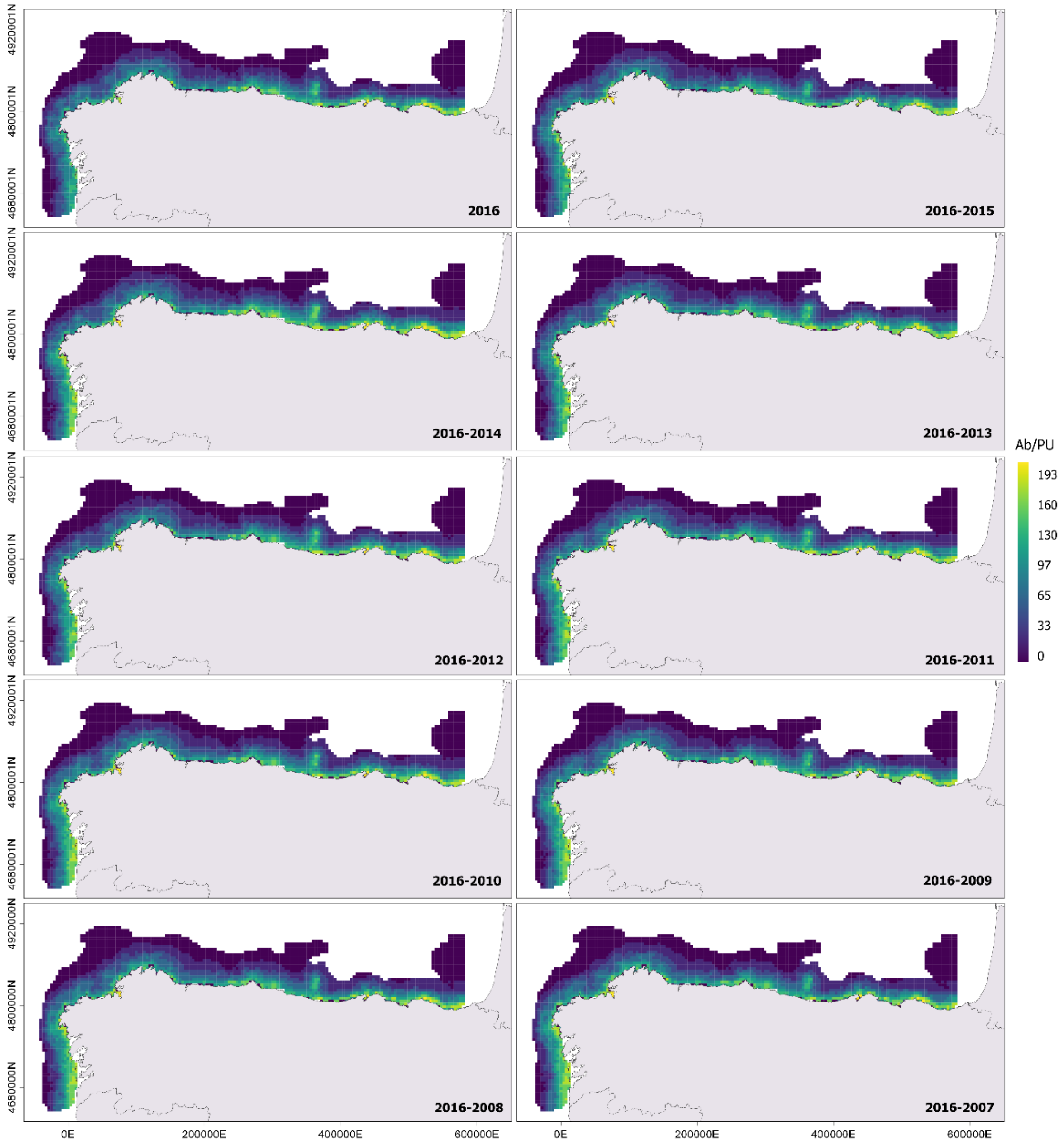


Figure E1.2. Map of the study area representing the abundance per planning unit of the Lesser black-backed gull (*Larus fuscus*).

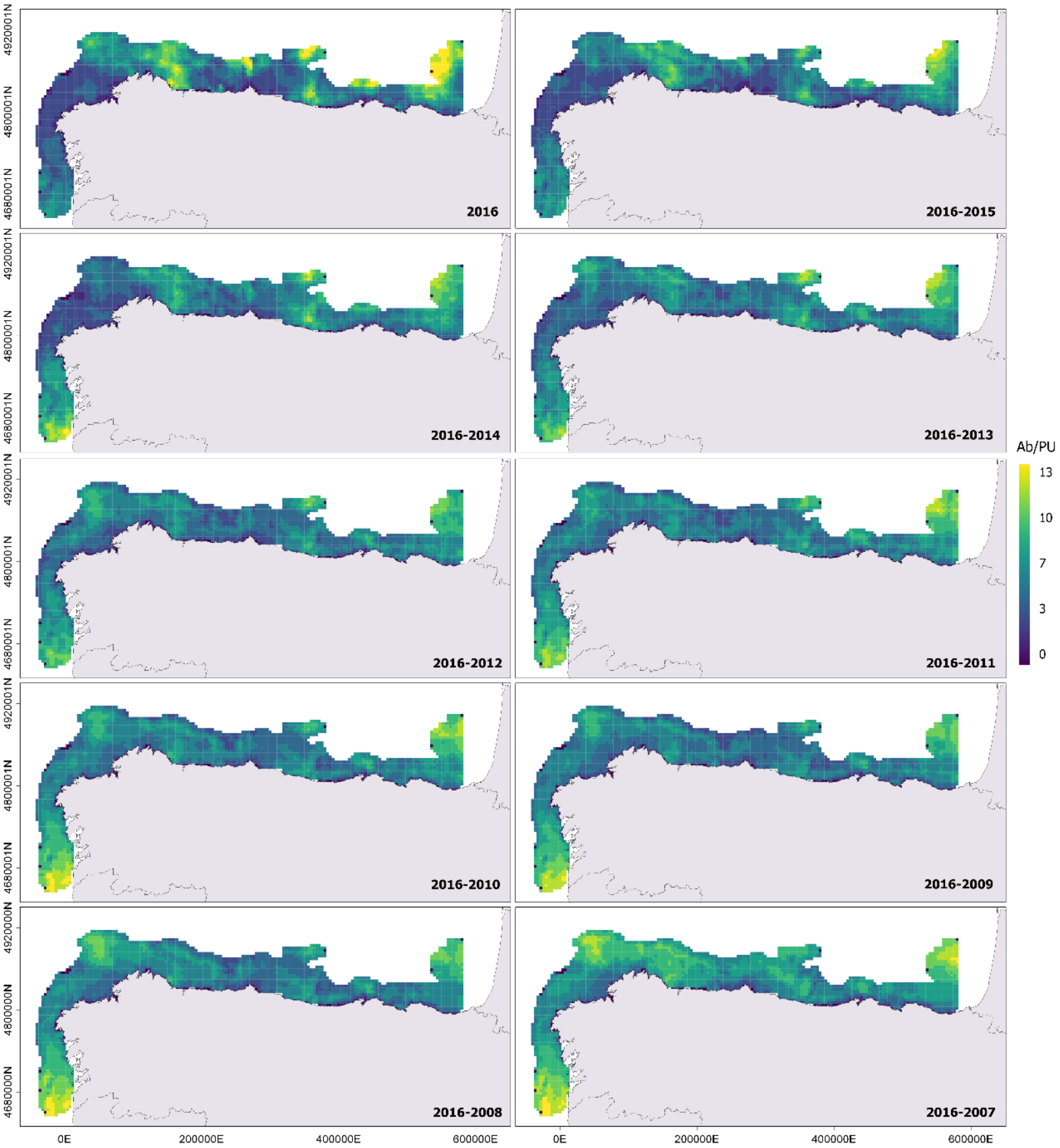


Figure E1.3. Map of the study area representing the abundance per planning unit of the Mediterranean gull (*Ichthyaetus melanocephalus*).

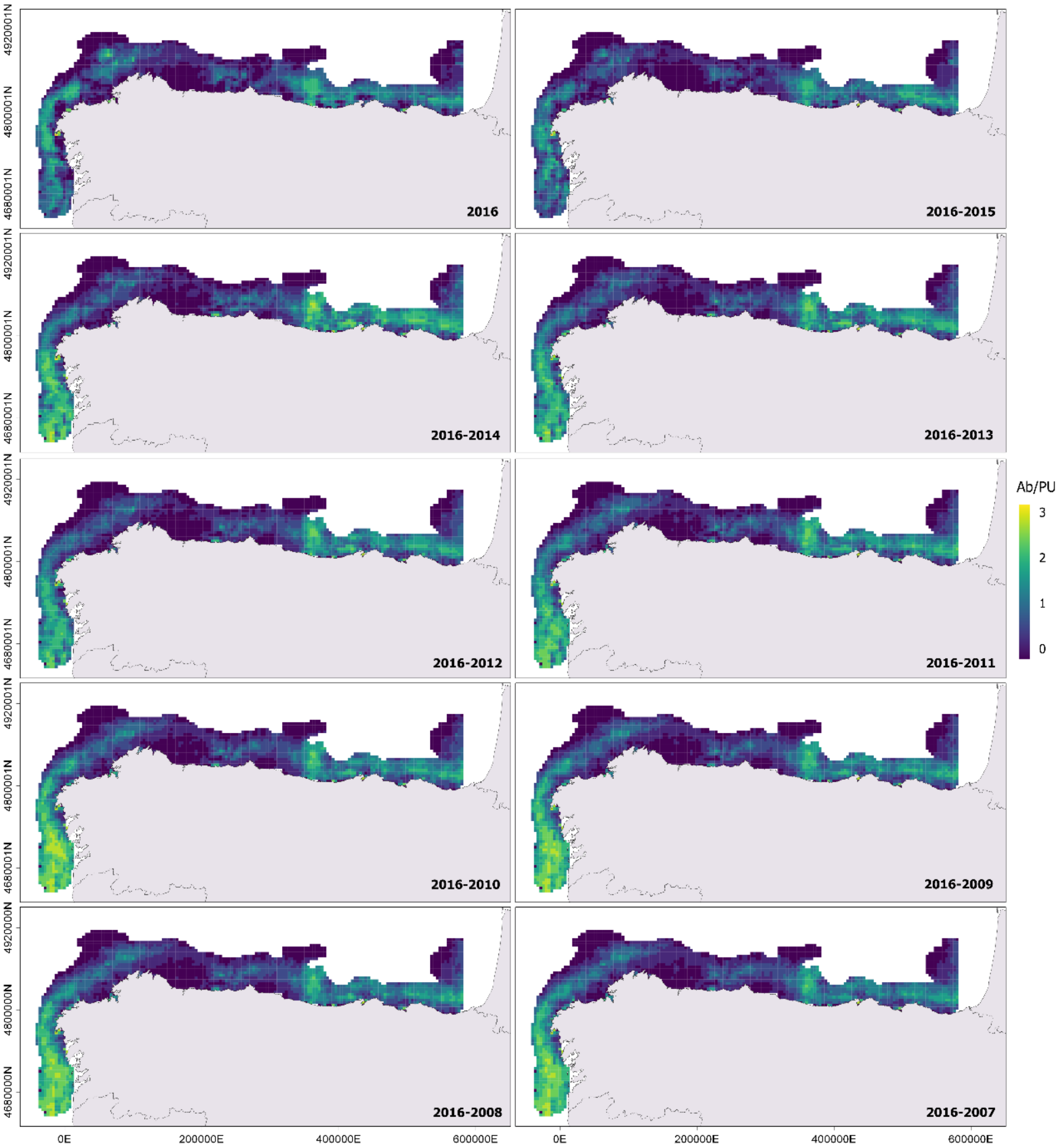


Figure E1.4. Map of the study area representing the abundance per planning unit of the Sandwich tern (*Thalasseus sandvicensis*).

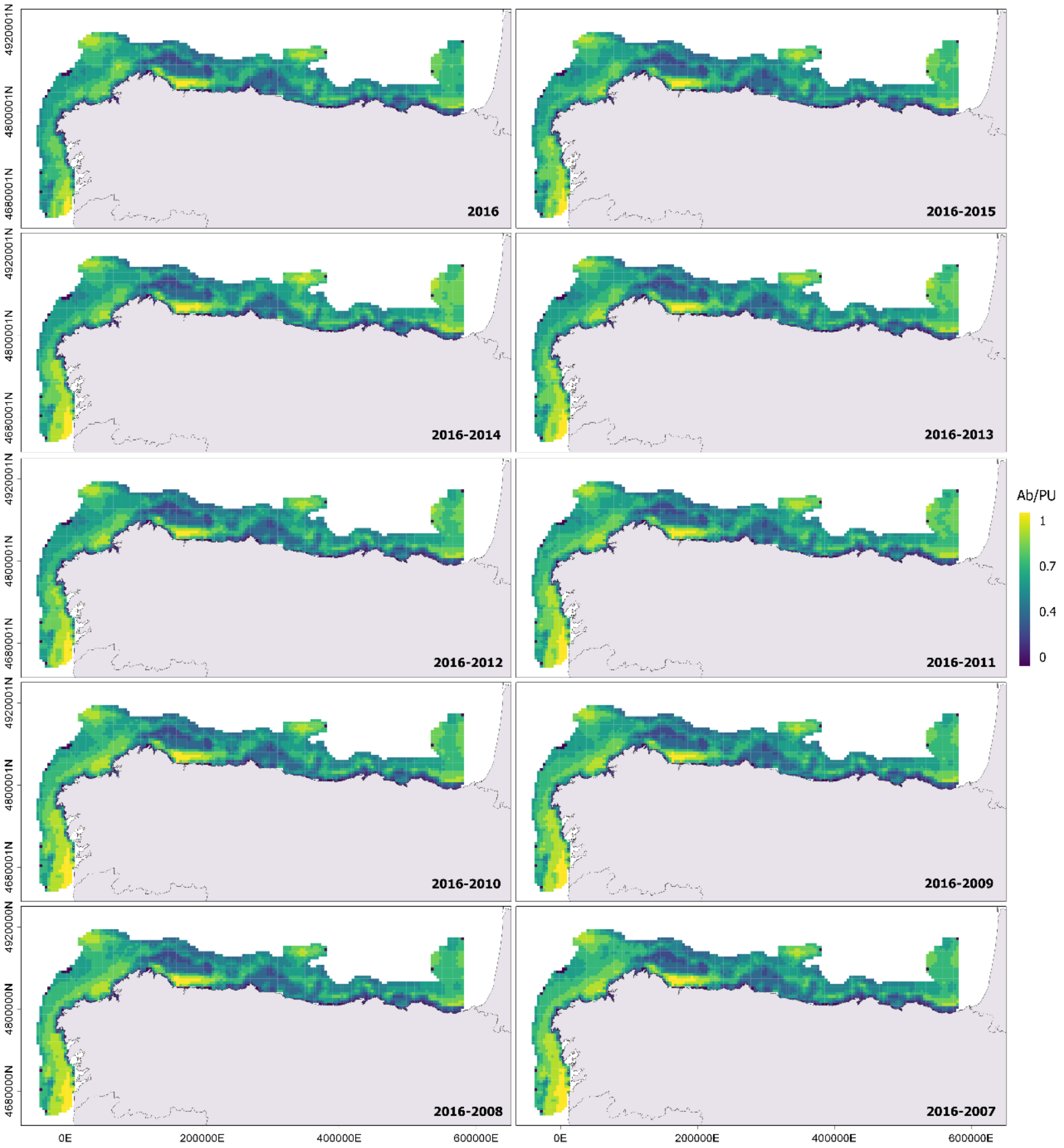


Figure E1.5. Map of the study area representing the abundance per planning unit of the Razorbill (*Alca torda*).

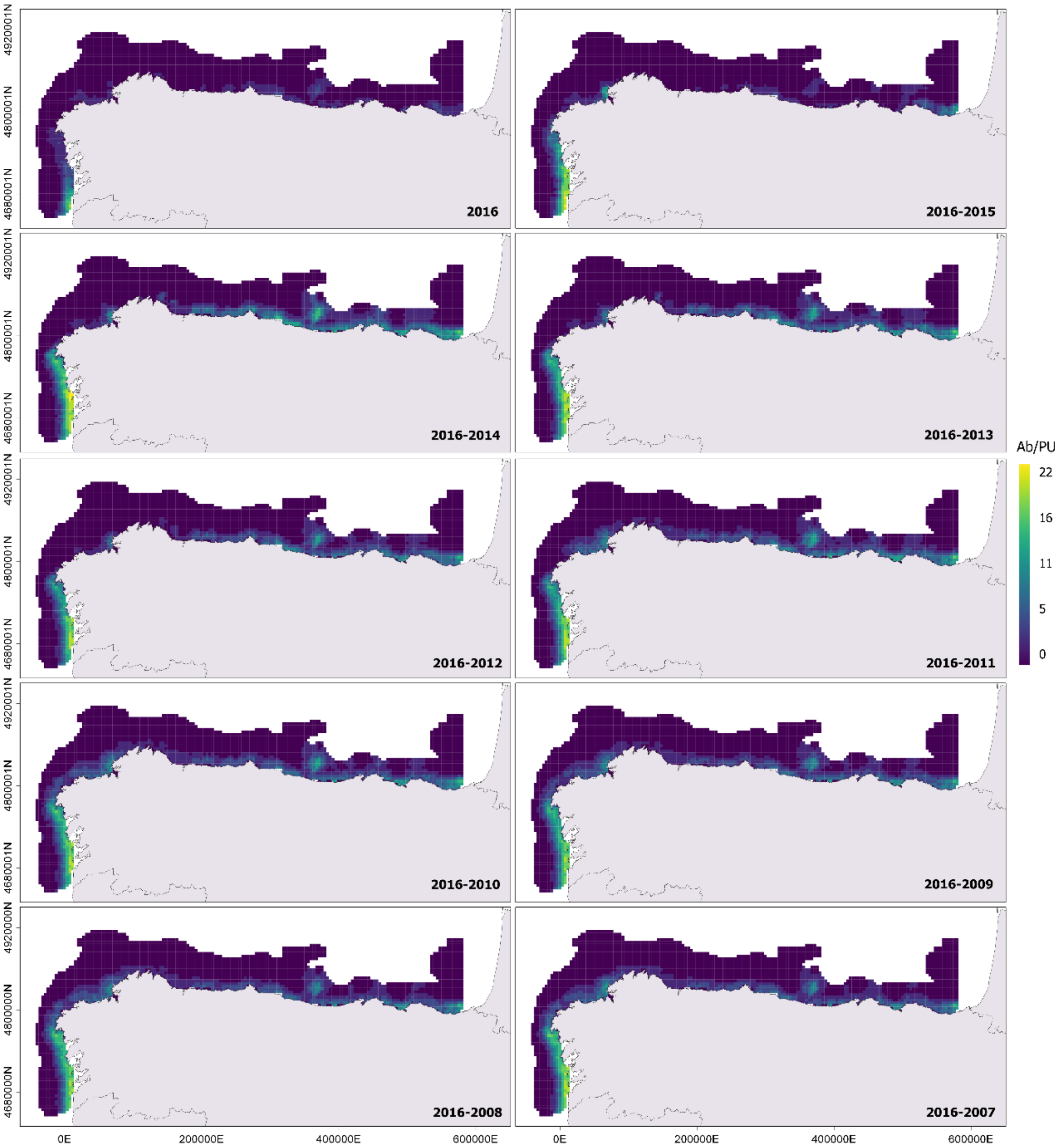


Figure E1.6. Map of the study area representing the abundance per planning unit of the Common guillemot (*Uria aalge*).

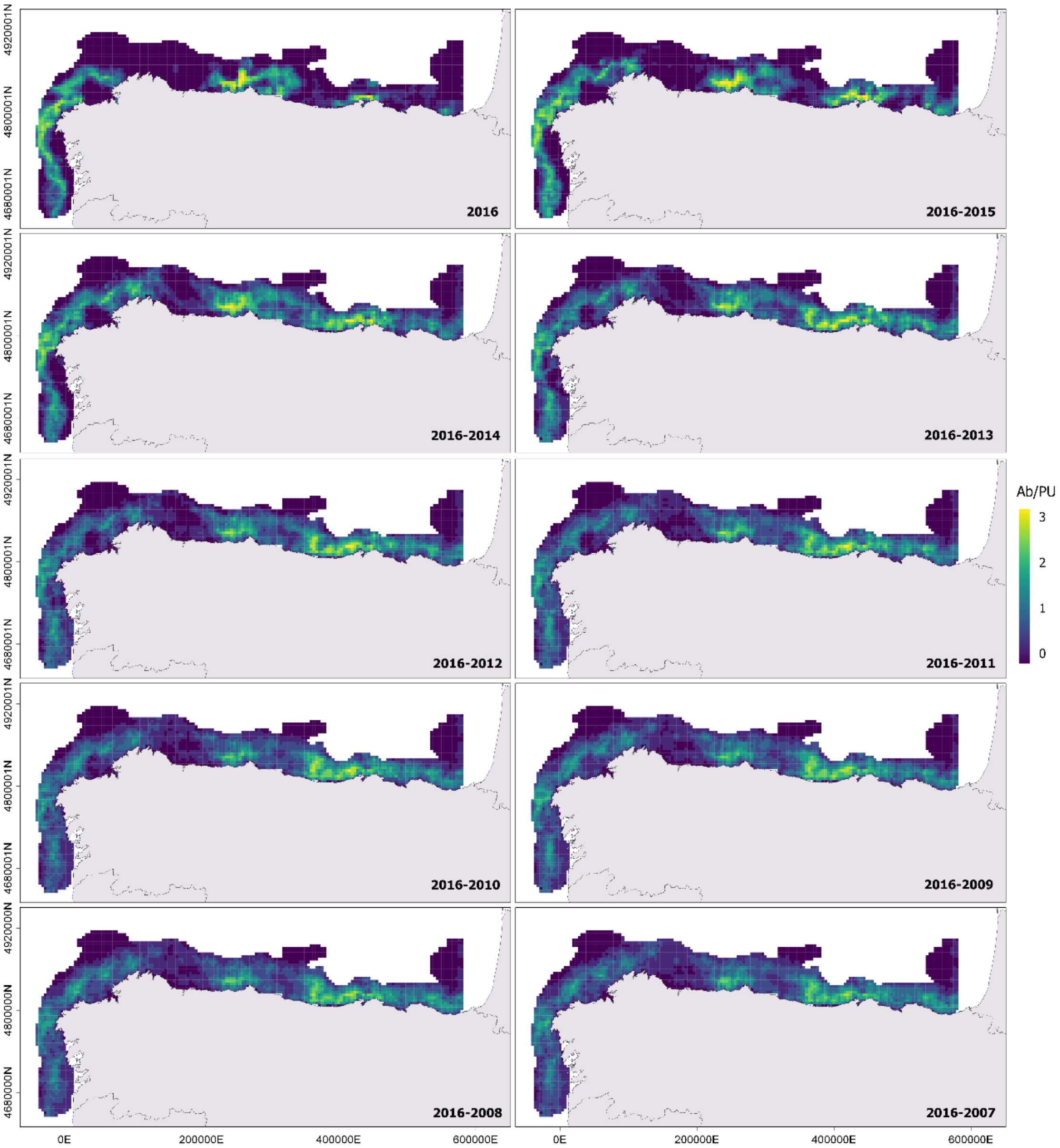


Figure E1.7. Map of the study area representing the abundance per planning unit of the Balearic shearwater (*Puffinus mauretanicus*).

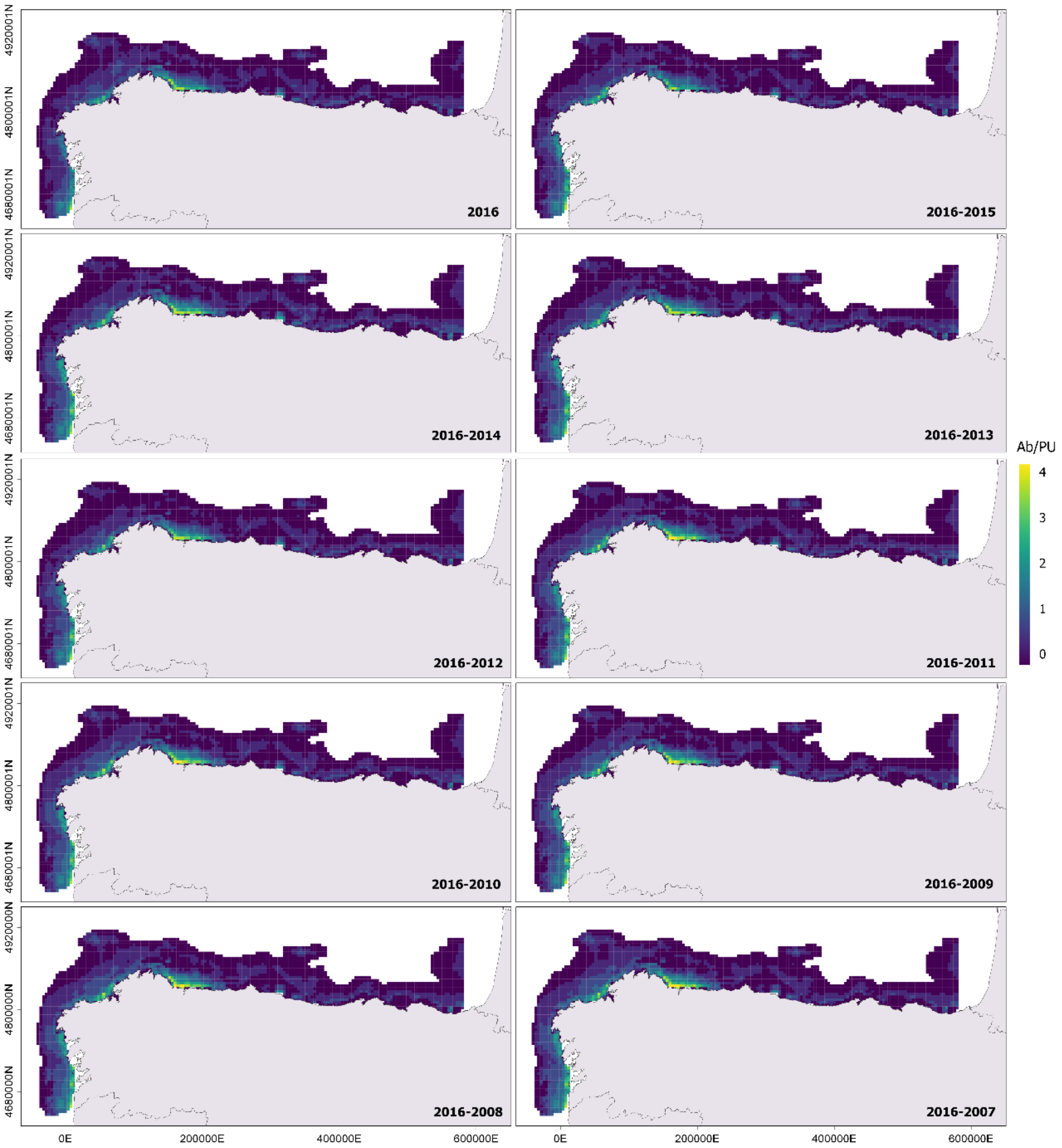


Figure E1.8. Map of the study area representing the abundance per planning unit of the Manx shearwater (*Puffinus puffinus*).

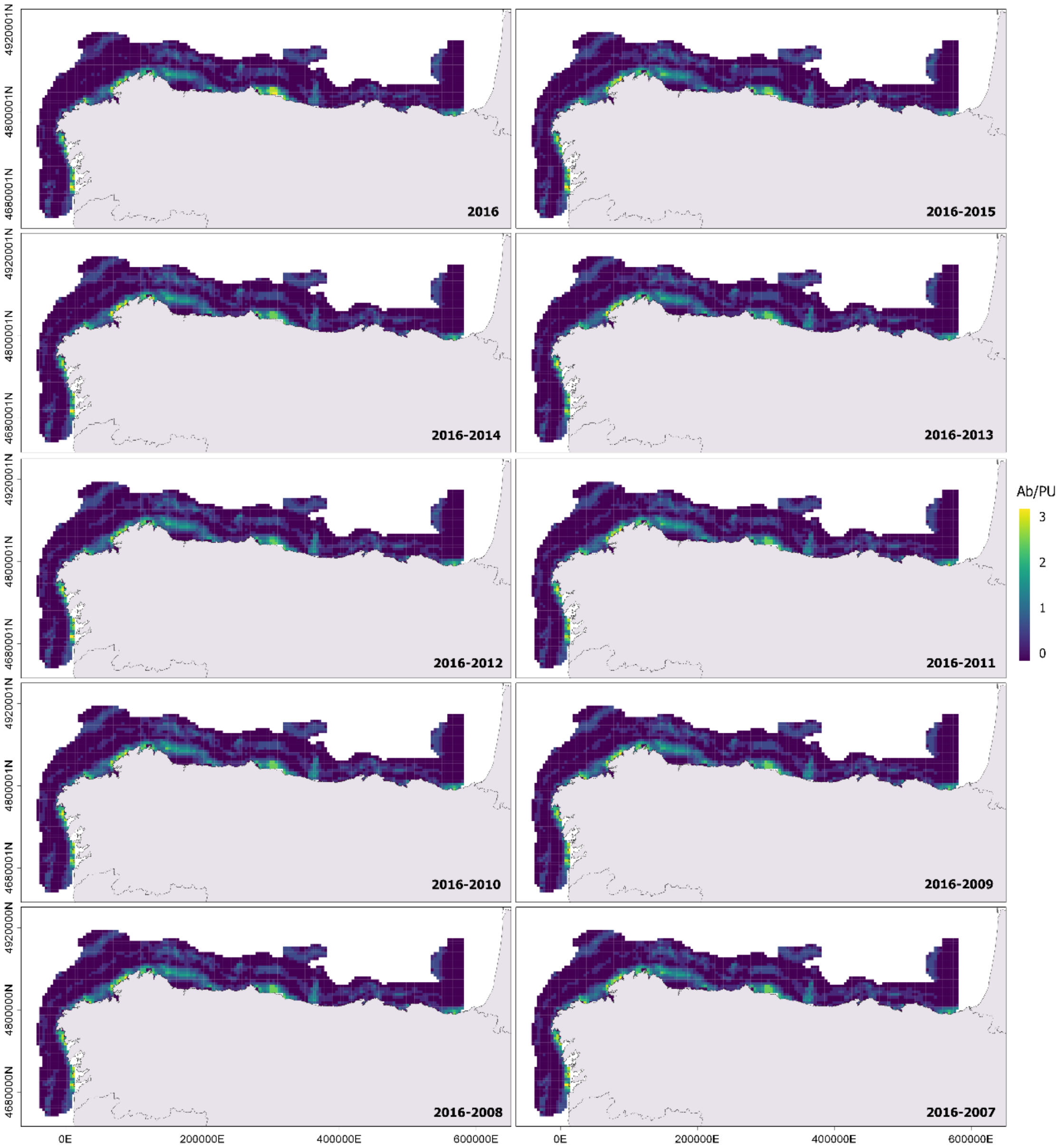


Figure E1.9. Map of the study area representing the abundance per planning unit of the Great skua (*Stercorarius skua*).

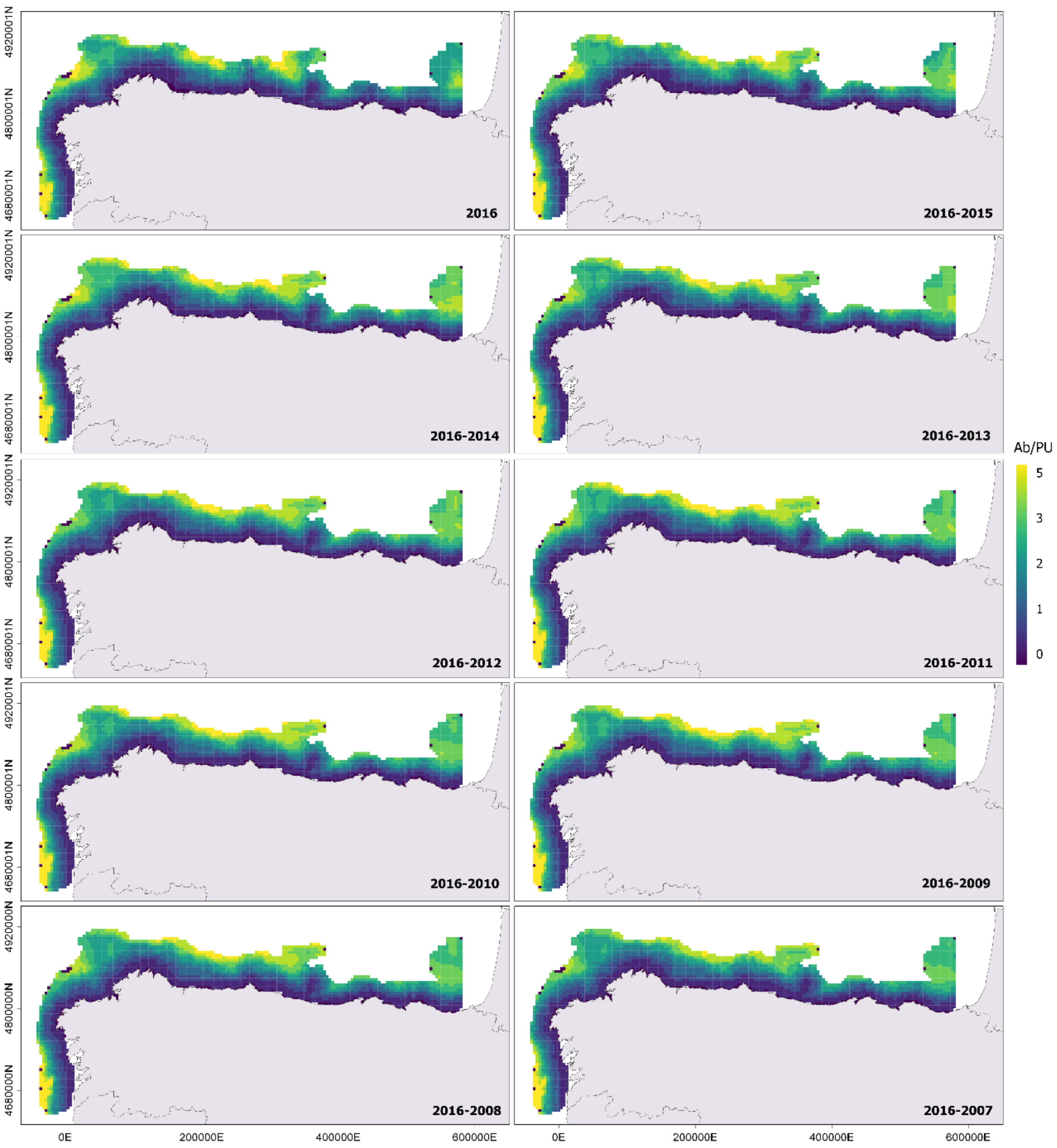


Figure E1.10. Map of the study area representing the abundance per planning unit of the Northern gannet (*Morus bassanus*).

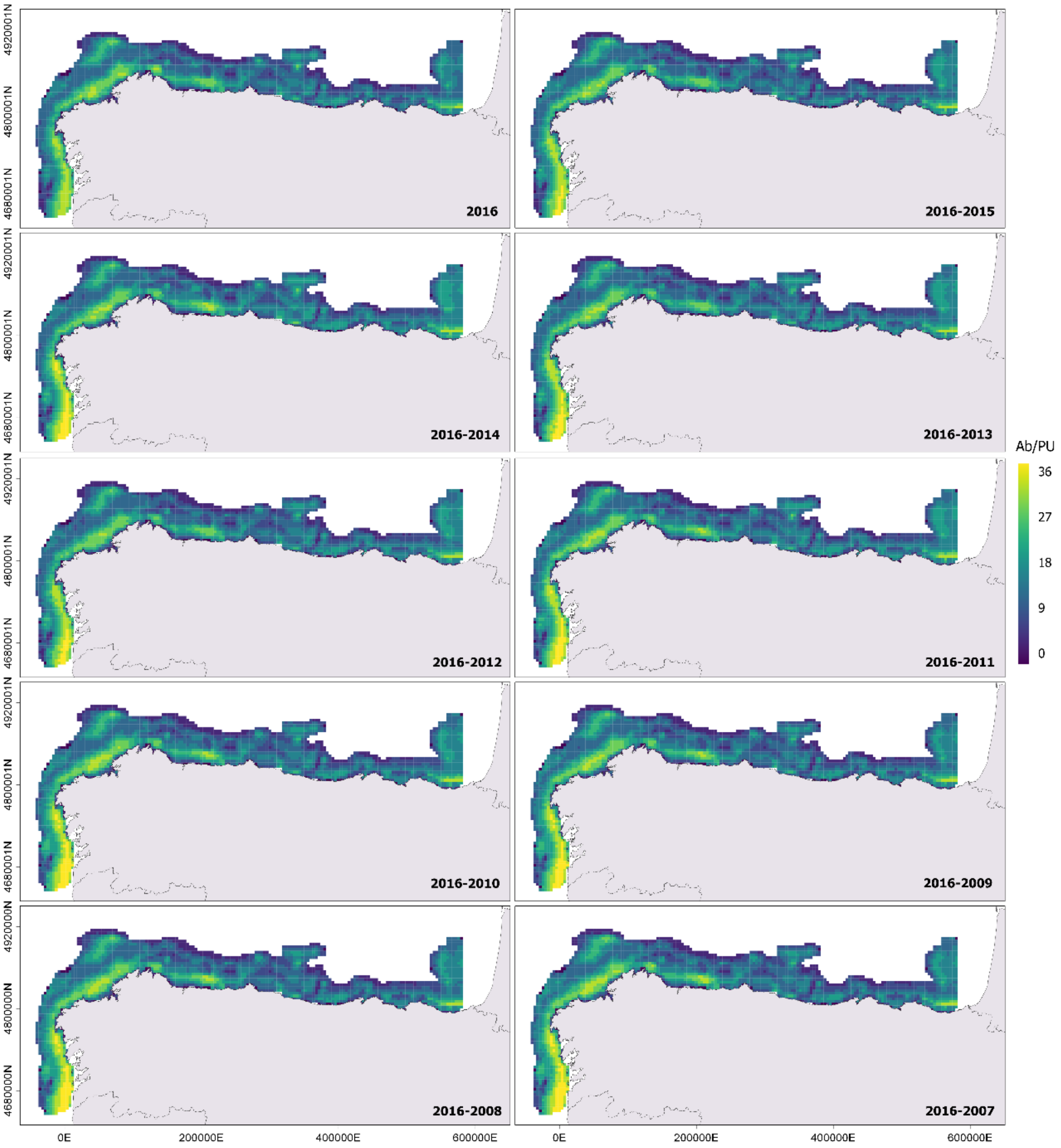


Figure E1.11. Map of the study area representing the abundance per planning unit of the Common dolphin (*Delphinus delphis*).

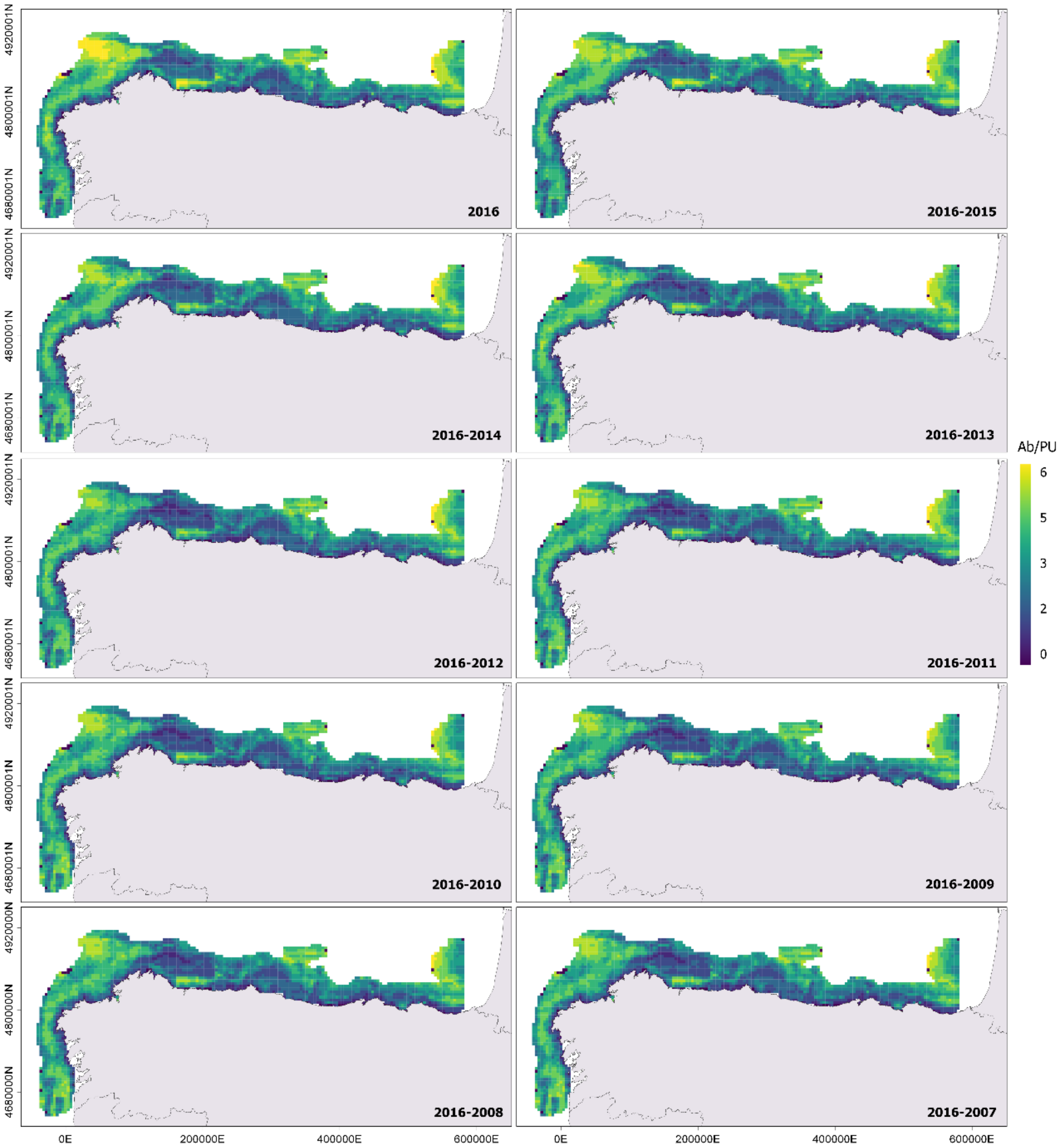


Figure E1.12. Map of the study area representing the abundance per planning unit of the Bottlenose dolphin (*Tursiops truncatus*).

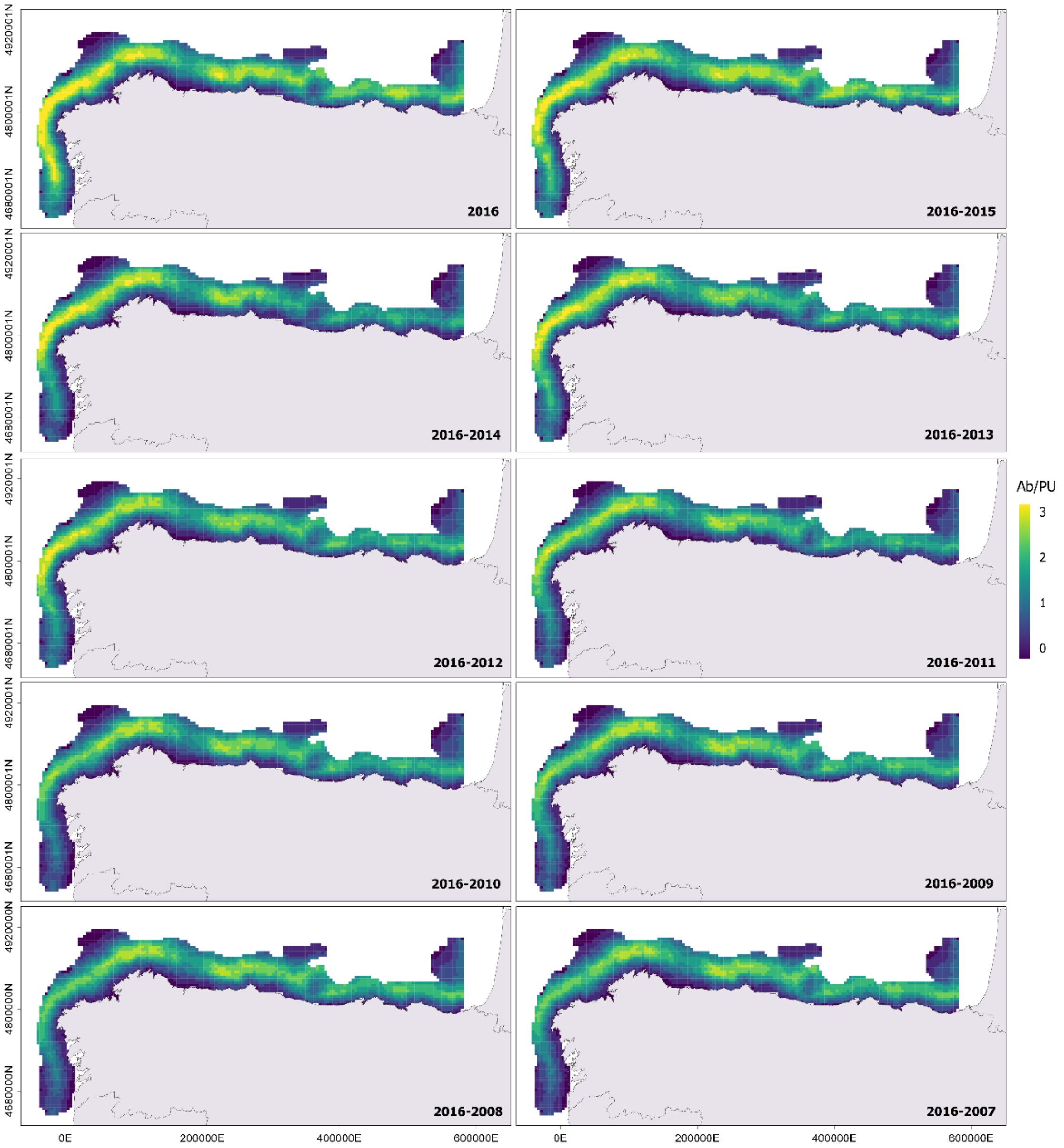
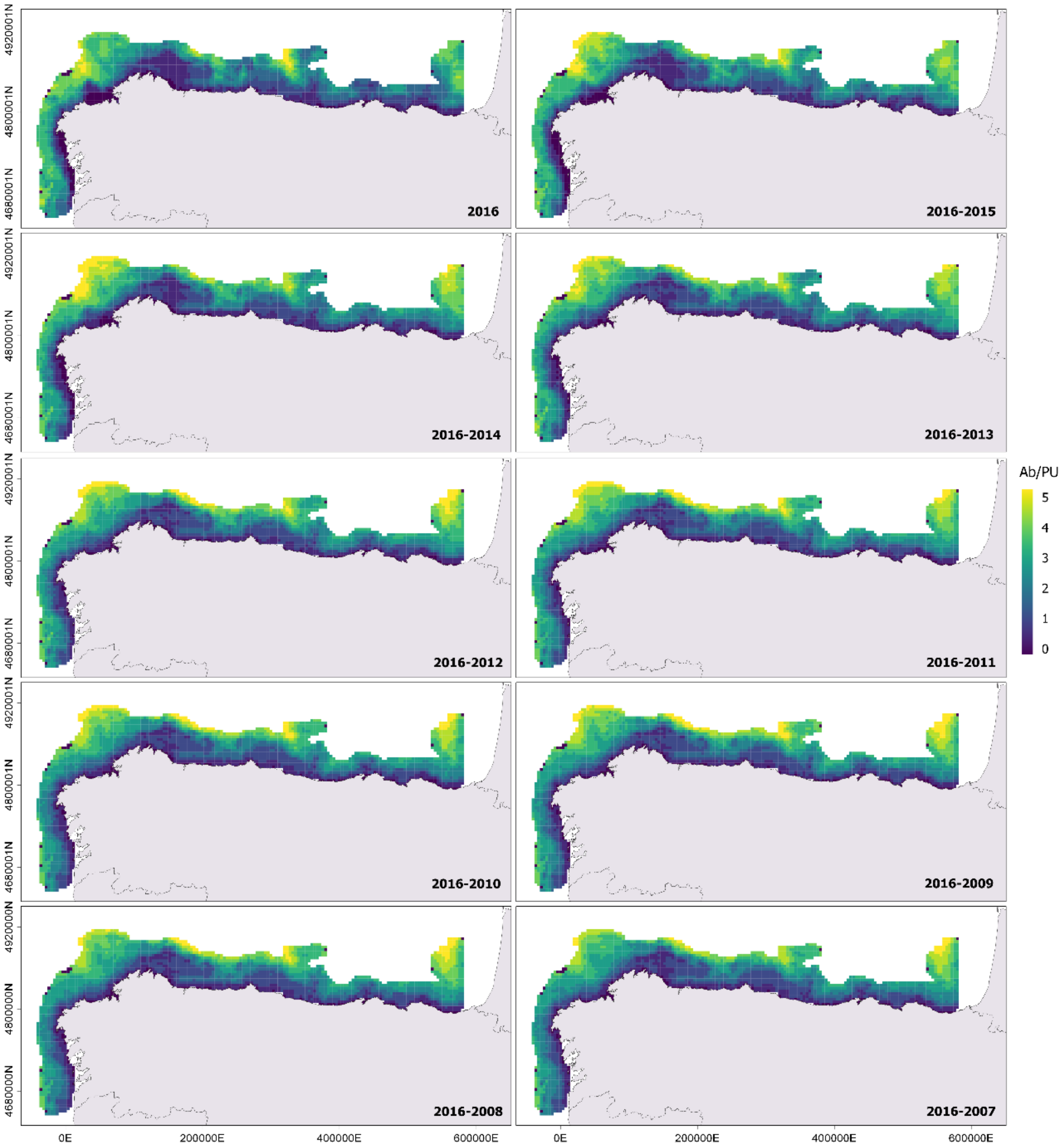


Figure E1.13. Map of the study area representing the abundance per planning unit of the Long-finned pilot whale (*Globicephala melas*).



Appendix E – Section 2: Conservation targets

Table E2.1. Conceptual decision framework showing the conservation targets (%) based on the categories of the International Union for the Conservation of Nature (IUCN) Red List of Threatened Species in Europe and the level of occurrence of the species in the area (MAGRAMA, 2012a, 2012b). The categories of the IUCN are DD: data deficient; LC: Least concern; NT: Near threatened; VU: Vulnerable; EN: Endangered and CR: Critically Endangered. To set the conservation target of the species categorized as DD we consider the same criteria as the species categorized as VU.

	DD	LC	NT	VU	EN	CR
Common	50	30	40	50	60	70
Abundant	40	20	30	40	50	60

Appendix E – Section 3: Approach 1 and Approach 2 results

Table E3.1. Results of Wilcoxon rank sum tests to assess differences in percentage overlap of selection frequency for the approaches 1 and 2. Significant results are shown in blue.

Approach	**Scenario comparison**	**W**	**p value**
Approach 1	Scenario2016	4403875	< 2.2e-16
	Scenario2016-2015	4407625	< 2.2e-16
	Scenario2016-2014	3802643	0.528
	Scenario2016-2013	3817852	0.728
	Scenario2016-2012	3811503	0.642
	Scenario2016-2011	3823452	0.809
	Scenario2016-2010	3836589	0.998
	Scenario2016-2009	3839091	0.961
	Scenario2016-2008	3849175	0.813
	Scenario2016-2007	3836450	1.000
Approach 2	Scenario2016	3942480	0.041
	Scenario2016-2015	3958084	0.019
	Scenario2016-2014	3816540	0.703
	Scenario2016-2013	3804757	0.544
	Scenario2016-2012	3815665	0.691
	Scenario2016-2011	3813579	0.661
	Scenario2016-2010	3822565	0.790
	Scenario2016-2009	3830083	0.903
	Scenario2016-2008	3833689	0.958
	Scenario2016-2007	3836450	1.000

Appendix E – Section 4: Approach 3 results

Table E4.1. Pairwise comparison of planning scenarios using the Cohen`s Kappa for the Marxan's best solution of each scenario. All the scenarios comparisons were based on the Scenario2016-2007. For each comparison it is represented the value of the Cohen`s Kappa statistics (K) with their confidence interval. Colours highlighting the judgement for K about the extent of agreement in a < 0 - 1 scale (from red to green; Landis & Koch, 1977).

Approach	**Scenarios comparison**	**K**	**L-CI**	**U-CI**	**Judgement**
3	Scenario2016	0.541	0.510	0.573	Moderate agreement
	Scenario2016-2015	0.630	0.601	0.658	Substantial agreement
	Scenario2016-2014	0.777	0.753	0.801	Substantial agreement
	Scenario2016-2013	0.809	0.786	0.831	Almost perfect agreement
	Scenario2016-2012	0.832	0.811	0.853	Almost perfect agreement
	Scenario2016-2011	0.862	0.843	0.882	Almost perfect agreement
	Scenario2016-2010	0.885	0.867	0.903	Almost perfect agreement
	Scenario2016-2009	0.905	0.889	0.921	Almost perfect agreement
	Scenario2016-2008	0.932	0.918	0.946	Almost perfect agreement

All K values were significant at p-value < 2.2e-16

Figure E4.1. Relationships among solutions of the 10 scenarios of the approach 3. Left panel shows the dendrogram from a complete hierarchical cluster analysis and right panel the nMDS plots based on a Jaccard resemblance matrix.

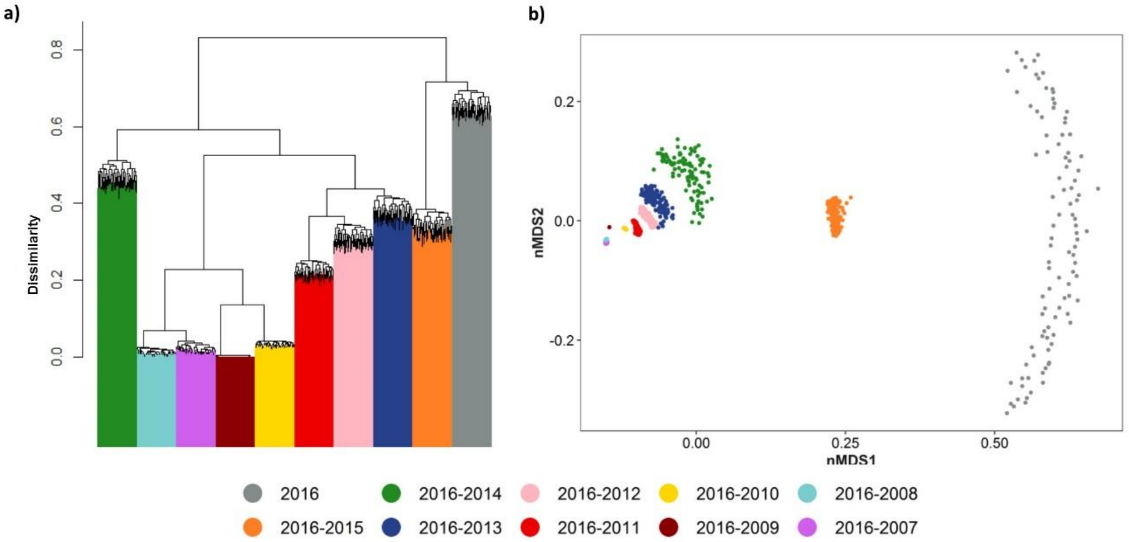
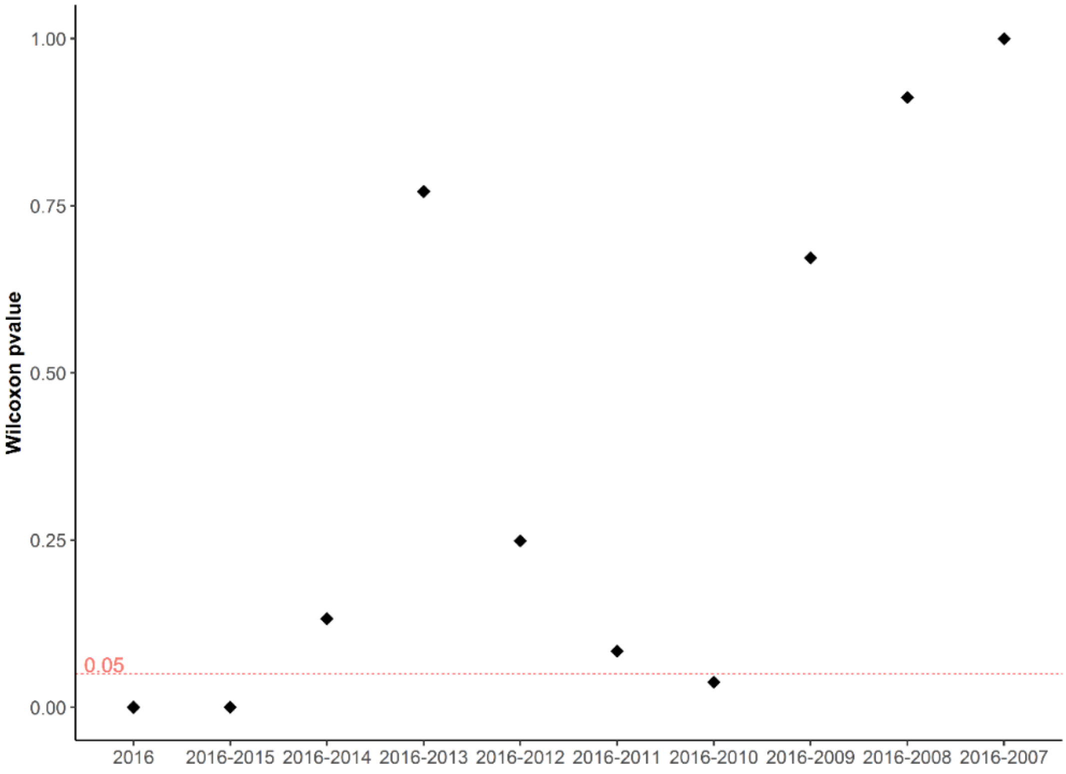


Figure E4.2. Results of Wilcoxon rank sum tests to assess differences in percentage overlap of selection frequency for the approach 3. All the scenarios comparisons were based on the Scenario2016-2007. Dotted line shows the limit of significance for the test (p value = 0.05).



“All we have to decide is what to do with the time that is given us.”

J.R.R. Tolkien, The Fellowship of the Ring