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Project Deliverable Report

Charismatic species model projections. Projections of the impacts of scenarios of CC and NBS2 policies on charismatic species.

Dissemination level:	**Public, after approval**
Type of deliverable:	Other
Due date:	Project month 30 [28.02.2023]

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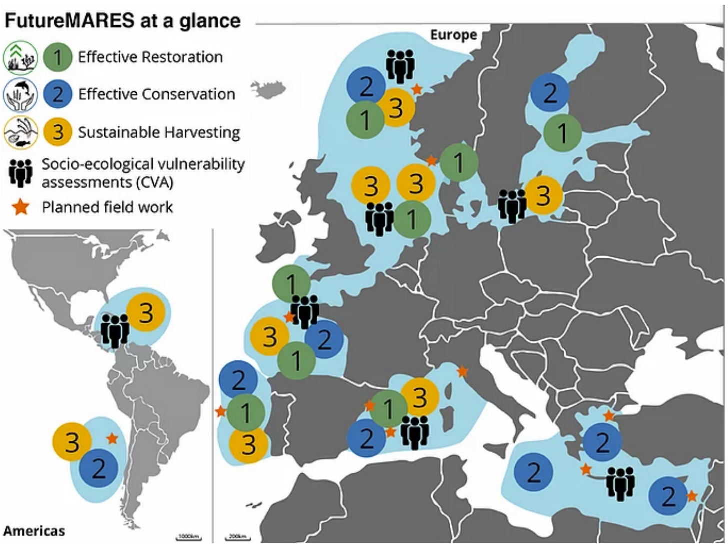
FutureMARES Project

FutureMARES - Climate Change and Future Marine Ecosystem Services and Biodiversity is an EU-funded research project examining the relations between climate change, marine biodiversity, and ecosystem services. Our activities are designed around two Nature-based Solutions (NBS) and nature-inclusive (sustainable) harvesting of marine resources (NIH):

Effective Restoration (NBS1)

Effective Conservation (NBS2)

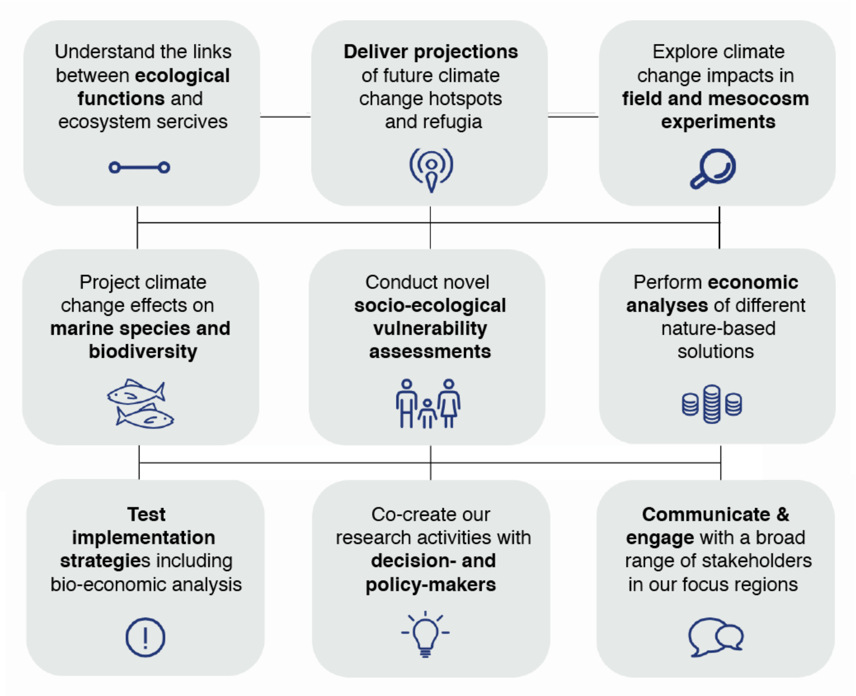
Nature-inclusive Harvesting (NIH)



We are conducting our research and cooperating with marine organisations and the public in Case Study Regions across Europe and Central and South America. Our goal is to provide science-based policy advice on how best to use NBS to protect future biodiversity and ecosystem services in a future climate.

FutureMARES provides socially and economically viable actions and strategies in support of nature-based solutions for climate change adaptation and mitigation. We develop these solutions to safeguard future biodiversity and ecosystem functions to maximise natural capital and its delivery of services from marine and transitional ecosystems.

To achieve this, the objectives of FutureMARES defined following goals:


Understand the links between **ecological functions** and ecosystem sercives
Deliver projections of future climate change hotspots and refugia
Explore climate change impacts in **field and mesocosm experiments**
Project climate change effects on **marine species and biodiversity**
Conduct novel **socio-ecological vulnerability assessments**
Perform **economic analyses** of different nature-based solutions
Test implementation strategies including bio-economic analysis
Co-create our research activities with **decision- and policy-makers**
Communicate & engage with a broad range of stakeholders in our focus regions

Deliverable data	
Work Package(s) / Task(s):	WP4 – Mechanistic projections for species, food webs and habitats, Task 4.2 – Charismatic species
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Involved partners

Partners involved in workshops, discussions and/or performing work reported in this deliverable: AUTH, AZTI, CIIMAR, CMCC, NIOZ, NIVA and PML

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Contents

List of symbols, abbreviations, and a glossary

CC	Climate change
Tn.x	Task – a sub-component of a work package where “n” is a number of the work package and “x” is a number of the task within this work package
WP	Work Package
DEB	Dynamic Energy Budget
SDM	Species Distribution Model
PET	Protected, Endangered and Threatened Species
IAS	Invasive Alien Species
OPO	Platforms of Opportunity
MMO	Marine Mammals Observer
SCL	Straight Carapace Length
CCL	Curved Carapace Length
KDE	Kernel Density Estimate
CDS	Conventional Distance Sampling
MCDS	Multiple-Covariate Distance Sampling
AIC	Akaike’s Information Criterion
AUC	Area Under the Curve
TSS	True Skill Statistics
LCP	Least-cost Path
RSP	Randomized Shortest Path
PCA	Principal Component Analysis

ESW	Effective Strip Half-width

Executive Summary

This report summarizes the work performed to fulfill Task 4.2 of WP4 of the EU funded FutureMARES project.

A growing number of evidence is unveiling an emerging marine biodiversity crisis. Models projecting CC impacts in marine biodiversity further suggest that by the year 2100 numerous species will face an increasing risk of extinction, with the majority of species subjected to shrinkage of their suitable habitats. Yet, the first step in order to conserve marine biodiversity is to delineate the spatial distribution of at-risk species and exposure they dynamic habitat features (e.g. indirect effects of CC on prey), allowing to estimate their vulnerability to pronounced current and future threats.

For emblematic, marine megafauna information about species distributions and their interactions with host environment are often based on fragmented information. Here, we focus on a number of marine megafauna organisms, used as ideal models on how to establish analytical frameworks to examine the distributional patterns and interaction with dynamic ocean under a changing climate.

To contribute to this scientific and conservation challenges, in task 4.2 we develop, test and apply spatially based tools, focusing on life histories, energy budget, spatial and temporal dimensions of habitat utilization, movement, behavior and population dynamics of marine megafauna species towards improving the understanding of key habitat use. We develop and optimize widely used statistical (non mechanistic) distribution models to be applied in cases of lack of extensive empirical datasets and further develop novel mechanistic distribution models for charismatic marine species, towards providing insights into potential climate-driven changes in the distribution of highly migratory species. We further advance the state-of-the-art in megafauna modelling, by delivering a new framework for mechanistic (non statistical) species distribution modelling, that accounts for species response to environmental change as CC unfolds.

A total of nine case studies is presented here with the first three exploring how alternative types of data, tools and monitoring protocols could be used to deliver critical information for delineating spatial distribution of marine megafauna. For the next six case studies different modelling approaches for delineating habitat use of charismatic marine species (including traditional approaches employing statistically estimated distribution, and novel mechanistic and, food web interaction modelling), gradually exploring how climate change leads to spatial shifts of critical habitats, possibly changes species migration phenology and migration routes, affects megafauna (seabirds, cetaceans and sea turtle species) and prey species interactions, and, ultimately, the response of species to environmental change.

The Deliverable's case studies highlighted the importance and usefulness of opportunistically collected data (chapter 2.1), independent field data (chapter 2.2) and bycatch data (chapter 2.3) as a complementary source of information to systematic monitoring protocols and validation of species distribution modelling outputs, given the multiple challenges to adequately and systematically monitor marine megafauna species. CC modelling approaches based on statistical species distribution technics revealed a possible future westward shift in part of the foraging areas of loggerhead sea turtles in the Mediterean Sea (chapter 3.1). A 3D climatic niche framework applied for the charismatic sea turtles further revealed key habitats at the regional scale, filling gaps to our current knowledge and conservation capacity at a regionally scale (chapter 3.2). Aiming to provide a modeling framework which could capture interactions between marine and prey species, in chapter 3.3, large functional groups for seabird and cetacean species were used as surrogates feeding ecosystem-based models for the Bay of Biscay; the outputs of this analysis highlighted the potential resilience of these groups of

marine megafauna to climate change, as the results did not project large changes or differences among the CC scenarios applied. In the same line, a rather optimistic message was produced for Balearic shearwater, with a GAM modeling framework predicts a decreasing trend until the end of 2070s, with a potential recovery by the end of century (chapter 3.4). Moving from a statistical modelling approaches to mechanistic frameworks, in chapter 3.5, we developed and parametrized a mechanistic models based on outputs of graph theory-based models, to explore the possible CC impacts of sea currents patterns on sea turtles' migration movements, with main results suggesting that CC is expected to minimally alter the species migration routes in the future. A novel mechanistic distribution model was further developed in chapter 3.6. This model was based on the DBEM framework, allowing to properly integrate process-based information and assess population dynamic responses to climate change for cetaceans and sea turtles' species at the regional scale.

Defining the challenge

Marine ecosystems have undergone severe biodiversity loss worldwide, with one-third of the highly migratory marine megafauna being currently at risk of extinction (Pimiento et al. 2020). These charismatic marine organisms, which serve key roles in ecosystem functioning (Estes et al. 2016), have broad distributions inhabiting various sites even within their annual life cycle. These life history characteristics allow them to have access to different resources (Learmonth et al. 2006). Yet, the migratory nature of marine megafauna could lead to increased exposure to multiple human-induced pressures (e.g., fisheries, overfishing, pollution, habitat degradation, noise pollution and climate change), threatening their persistence (Albouy et al. 2017). Indeed, many species of marine megafauna are included among the most vulnerable organisms, making the implementation of targeted and flexible management actions an imperative task (Lascelles et al. 2014).

For an efficient management of the marine ecosystems towards biodiversity conservation, the knowledge on the species distribution patterns is essential. However, the vast majority of the oceanic systems still lacks basic data on species occurrence, or have insufficient biodiversity data for an adequate analysis of distribution in space and time (Kaschner et al. 2012; Mannocci et al. 2018). Knowledge and population management of marine megafauna, including pelagic predators, obtained through monitoring efforts, has been key for the conservation and management of marine areas since such organisms play key roles for the overall health, structure, and functioning of marine ecosystems (Sergio et al. 2006 & 2008). Lastly, projecting the response of these species to climate change, without which we cannot create climate-resilient conservation measures, requires the development of species distribution modelling tools that are built not just on the current response of species to environmental drivers but their physiological response to combinations of ocean drivers not currently observed at present (Kerney and Porter 2009).

By and large, species distribution models currently used for megafauna are statistical (i.e. based on current distributions) and, therefore, lack the robust predictive ability required to support the design of climate-resilient conservation measures for these species, especially for long-term efficacy (Silber et al. 2017). A key development needed to improve model capability is the ability to understand how marine megafauna use habitats. Such information is also critical in order to provide accurate climate change impacts assessments at local or regional levels. However, surveying of marine megafauna is a very challenging task. Most species spend the majority of their time submerged, having wide and heterogeneous distributions. They inhabit different marine ecosystems at different life stages, perform seasonal movements and their presence depends on synergistic environmental and anthropogenic parameters (Evans and Hammond 2004). To respond to these challenges, a variety of tools and monitoring protocols have recently been developed and used including satellite tracking, drone overflights in the areas of interest, unmanned aircraft systems, and visual and acoustic sampling Regardless of practical difficulties for comprehensive research campaigns (e.g. being expensive and logistically complex; Alves et al. 2018; Tobeña et al. 2016), species occurrence datasets are becoming available to researchers and conservation managers. Still, before these datasets can be translated into a wealth of information for conservation and policy development, data collected based on different observation protocols should be validated, and the most accurate tools and approaches that permit transforming and extrapolating point data into spatially-explicit information regarding species presence and habitat suitability should be highlighted. These approaches are also critically needed to project potential changes triggered by the ongoing climatic change.

Different types of challenges are, thus, encountered when surveying CC impacts on the marine megafauna regarding: 1) the type of data, tools and monitoring protocols to be used. 2) the modelling approaches varying from statistical links of species occurrence and environmental factors, to more mechanistic modelling approaches (Figures 1&2).

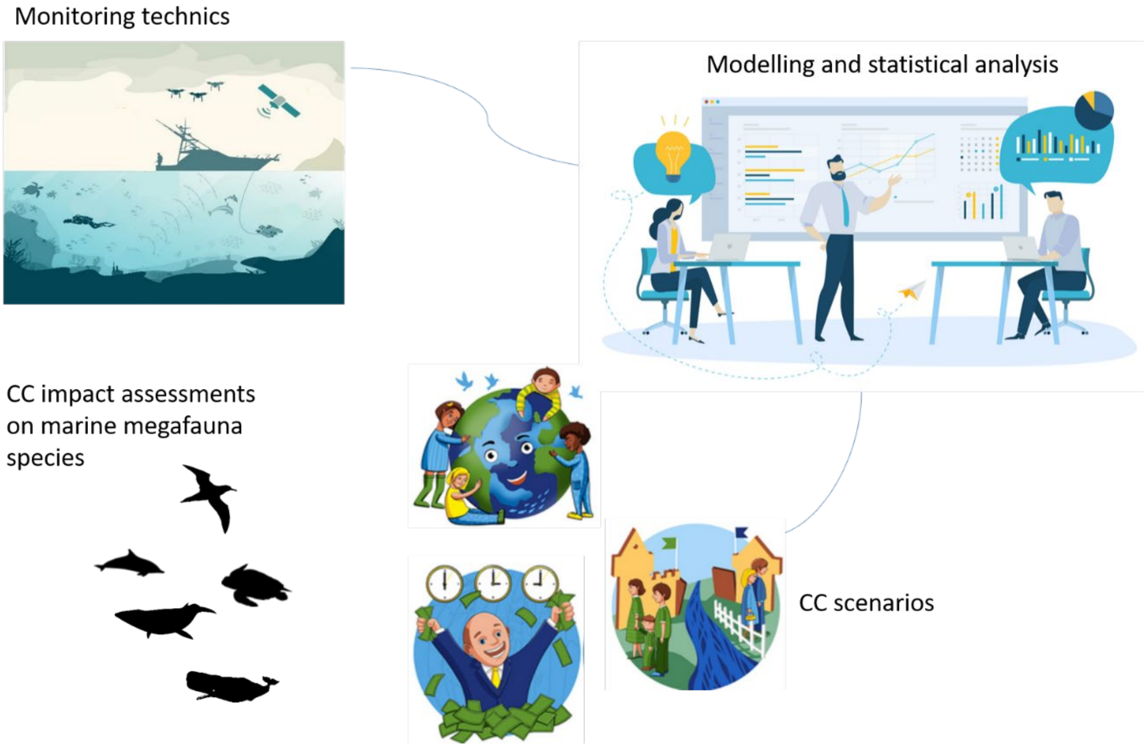

Figure 1. Important components of CC impact assessments on marine megafauna regarding the type of monitoring technics, the modelling approaches and the climate change scenarios.

The first aim of task 4.2 was to assemble, integrate, and improve the mechanistic approaches for distribution modeling for charismatic marine species, into a comprehensive framework that consists of a set of methodological tools, databases and background information. In task 4.2 we develop, test and apply spatialy based tools, focusing on life histories, energy budget, spatial and temporal dimensions of habitat utilization, movement, behavior and population dynamics of marine megafanua species to improve the understanding of species habitat use. We developed and optimized widely used statistical (non-mechanistic) distribution models applied in cases lacking existing, extensive empirical datasets and further developed novel mechanistic distribution models for charismatic marine species, towards providing insights into potential climate-driven changes in the distribution of highly migratory species. We further propose new approaches and solutions for the monitoring and conservation of the marine megafauna. A legacy database was compiled that will be made publicly available concerning sea turtle, seabird and cetacean species. The second aim of Task 4.2 was to advance the state-of-the-art in megafuana modelling, by delivering a new framework for mechanistic (not statistical) species distribution modelling that accounts for the responses of species to environmental drivers as climate change unfolds, and not just for current ocean habitat changes (Kerney and Porter 2009).

Approach

This report is structured in 9 case studies (Figure 2) aiming to advance our understanding of habitat use and advance modelling capability by marine megafauna species. These 9 case studies illustrate: 1) different types of data and monitoring protocols used for assessing marine megafauna, 2) different modelling approaches for delineating habitat use of charismatic marine species (including traditional approaches employing statistically estimated distribution, and novel mechanistic and, food web interaction modelling), gradually exploring how climate change leads to spatial shifts of critical habitats, possibly changes species migration phenology and migration routes, affects megafauna (seabirds, cetaceans and sea turtle species) and prey species interactions, and, ultimately, the response of species to environmental change. These tools are developed to inform the next generation of climate-smart conservation measures for these species.

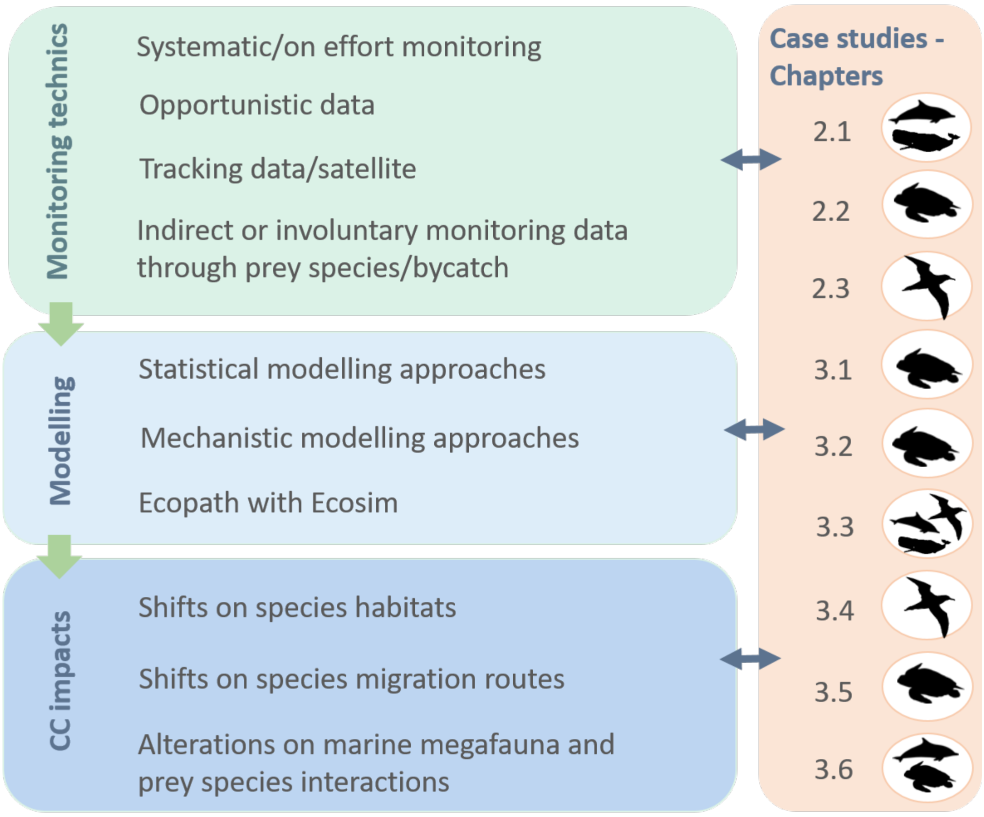

Figure 2. Deliverable 4.2 structure moving from monitoring technics and challenges, to modelling approaches, to the quantification of CC impacts on marine megafauna. The model species/taxa used to illustrate each case study are shown on the right, together with the number of the corresponding chapter.

Contribution to the project

This task aimed to deliver new generation mechanistic species distribution models for charismatic megafauna to help the EU addresses climate-driven changes in the distribution of these species. To that end, we have taken strides to create the infrastructure needed to support that model development, with particular focus on monitoring and methodological improvements that can facilitate biodiversity surveys of charismatic megafauna in the future. We then undertook specific applications of existing models and developed a new mechanistic species distribution modelling framework, to feed into activities in project Storylines, and WP6. Modelling work presented in this report uses as in inputs, among other sources, outputs of Task 2.1 on Ensemble hindcasts & climate change projections, regarding the Mediterranean Sea (chapter 3.5) and the Bay of Biscay (chapter 3.3). The outcomes of this report will feed into Tasks 4.4 using food-web projection models and Tasks 6.1 and 6.3. Task 4.2 also contributes to WP7 and WP8, enhancing outreach and policy dialogue on the conservation of marine megafauna under climate change. Information from this deliverable report also provided input and data to Task 5.1 where Ecological Climate Risk assessments are conducted. Storylines that contributed to or will benefit from this report are #2, #12, #22, #23 #26, #27, #31, #32, #36, #39.

Dissemination and Exploitation

The work undertaken within Task 4.2 and presented in this deliverable has contributed to 4 published papers, 1 article in preparation and 1 presentation to international congresses. Work done in this task was also presented at the European Maritime Day 2021 (Den Helder), Euromarine Science Day 2023, and the ICES working group on marine planning and coastal zone management (2021-2023). The mechanistic model developed within FutureMARES will also be deposited in the ZENODO open source repository when validated.

Published articles:

1. Petsas, P., Tzivanopoulou M., Doxa, A., Sailley, S.F, Mazaris, A.D. 2023. Climate change on sea currents is not expected to alter contemporary migration routes of loggerhead sea turtles. *Ecological Modeling*, 475, 110220
2. García-Barón I., Granado I., Astarloa A., Boyra G., Rubio A., Fernandes-Salvador J.A., Zarauz L., Onandia I., Mugerza E., Louzao M., 2022. Ecological risk assessment of a pelagic seabird species in artisanal tuna fisheries, *ICES Journal of Marine Science*, 2022; fsac136, https://doi.org/10.1093/icesjms/fsac136
3. Almpanidou, V., Tsapalou, V., Chatzimentor, A., Cardona, L., Claro F., Hostettere, P., Kaska, Y., Liuh, W., Mansuii, J., Miliou, A., Pietroluongoe, G., Sacchi, J., Sezging, Ç., Sözbileng, D., Mazaris, A.D. 2021. Foraging grounds of adult loggerhead sea turtles across the Mediterranean Sea: key sites and hotspots of risk. Biodiversity and Conservation, *31, 143–160.*
4. Chatzimentor, A., Almpanidou, V., Doxa, A., Dimitriadis, C., Mazaris, A.D. 2021. Projected redistribution of sea turtle foraging areas reveals important sites for conservation. *Climate Change Ecology, 2, 100038.*

Articles in preparation:

1. Chatzimentor, A., Doxa, A., Mazaris, A.D. Projected 3D climatically suitable foraging areas for sea turtles reveal marine conservation challenges.

Presentations to international congresses:

1. Queirós, Ana. Session I: Maritime Spatial Planning & the EU Green Deal An Ecological Perspective. Workshop: Maritime Spatial Planning: EU offshore (wind) energy and biodiversity ambitions. European Maritime Day 2021. 20th May 2021, Den Helder. (invited keynote talk).
2. García-Barón I., Granado I., Astarloa A., Boyra G., Rubio A., Gondra, J., Uriarte, A., Fernandes-Salvador J.A., Zarauz L., Onandia I., Mugerza E., Louzao M. Are predator critical areas overlapping with important fishing grounds? ICES conference. 6–10 September 2021. Virtual.
3. Queirós, Ana. Nature-based solutions for climate change adaptation & mitigation in Mediterranean coastal ecosystems. United Nations Framekwork Convention on Cliamte Change, COP27, Blue Zone. Sharm-el-Sheik. 9th November 2022.
4. Queirós, Ana. Nature-based Solutions for the Ocean under Climate Change. Euromarine Open Science Day 2023. 23rd January 2023.

1. Introduction

Marine megafauna comprises large charismatic species, such as marine mammals, sea turtles and seabirds which perform an important ecological role on the structure and functions of the ocean environment (Estes et al. 2016). These highly mobile organisms have been long considered as ecological indicators, often serving as keystone and flagship species. The charismatic marine megafauna occupies diverse habitats that often span large distances and, thus, are exposed to several threats that can negatively impact the ability of their populations to persist (Pimiento et al. 2020; McCauley et al. 2015). Many representatives of marine megafauna are listed in the Bird Directive 2009/147/EC and the Habitat Directive 92/43/EEC (e.g., bottlenose dolphin *Tursiops truncatus,* fin whale *Balaenoptera physalus,* Cory's shearwater *Calonectris diomedea*), which aim to promote and maintain biological diversity through the conservation of natural habitats and biodiversity in the European Union territory. In addition, the need for protection of these unique organisms is also highlighted and supported by a number of additional international agreements and strategies (e.g. Convention on the Conservation of Migratory Species of Wild Animals, Bern Convention, Bonn Convention, the Convention on International Trade in Endangered Species of Wild Fauna and Flora).

Figure 3. Bottlenose dolphins at the Iberian Atlantic coasts.

Nevertheless, despite the international attention and the fact that marine megafauna include many Protected, Endangered and Threatened (PET) species, there is increasing evidence that these species are subjected to major threats and often suffer from significant population declines. For example, many cetacean species are still intentionally killed or indirectly impacted by commercial fisheries (e.g, common dolphin *Delphinus delphis*), while seabirds are still one of the most threatened groups with some critically endangered species (e.g., Balearic shearwater *Puffinus mauretanicus*) (Croxall et al. 2012; Allen 2014; Diaset al. 2019*)*. Indeed, about one-third of marine megafauna are threatened with extinction (Pimiento et al. 2020; Lascelles et al. 2014).

Climate change (CC) is affecting the physical and biochemical characteristics of the oceans (Harley et al. 2006) triggering major ecological responses, often threatening the viability of species (Poloczanska et al. 2009) and our ability to deliver effective conservation mechanisms (Queiros et al. 2021). While CC impacts on the physiology and robustness of marine species, marine megafauna are often faced with additional impacts. A changing climate is driving spatiotemporal shifts in environmental parameters (e.g., sea currents, local productivity) that are modifying migration routes, constrain existing migratory corridors or even favor previously unsuitable routes (Robinson et al. 2009; Tulloch et al. 2019). These cumulative, and often indirect, pressures include changes in prey availability affecting distribution, abundance and migration patterns, community structure, susceptibility to disease and contaminants. Ultimately, such changes could alter the reproductive success and survival of the charismatic marine megafauna. Indeed, the distribution and migration of marine megafauna largely depends on food availability patterns. The migration of charismatic species like cetaceans, large fishes and seabirds, is largely influenced for instance by the dynamics of pelagic fishes, such as the European anchovy *Engraulis encrasicolus* (García-Barón et al. 2019a; Louzao et al. 2019b). Thus biotic interactions between marine megafauna and pelagic prey can have synergetic impacts on species, amplifying CC impacts, both in cases of positive associations such as schooling in prey (e.g., anchovy–sardine), local enhancement/facilitation in predators (e.g., Cory's shearwater–fin whale), and predation between predator–prey species (e.g., northern gannet–horse mackerel) as well as in negative associations, for instance in predator avoidance behaviours (e.g., striped dolphin–blue whiting) (Astarloa et al. 2019). The climate-driven redistrubution of prey species, and the new conditions (i.e. climatic, biochemical, ecological) within key habitats of current range of marine megafauna could force them to dynamically track their climatic niche in space (Tulloch et al. 2019; Vedor et al. 2021).

Several uncertainties still exist on where and how climate change could affect such highly migratory species and the different areas these species inhabit during their life cycle (Albouy et al. 2020; Payne et al. 2016). Surveying, understanding and delineating conservation priority areas for migratory marine megafauna is challenging since integrated knowledge on habitat use and, thus, relative exposure to threats can be particularly complex and information still remains rather scarce (Hays et al. 2019). The existing gaps in the spatial extent and location of critical habitat areas of marine megafauna, further jeopardize our ability to project future distribution shifts. It therefore becomes apparent that, as a first key step towards improving our conservation capacity for charismatic marine megafauna, it is important to spatialy deliniate and project the potential redistribution of their important areas. Furthermore, current modelling capability for these species is mainly based on statistical approaches, focused on current species habitat ranges, which do not perform well in long-term forecasting and ignore links to prey distributions (Silber et al. 2017). A mechanistic approach to modelling megafauna distribution could offer additional inisghts, as available for many other types of marine species, which performs better and is able to deliver more robust conservation advice that can enable climate-resilient spatial management mechanisms.

Objectives

This task aims to develop and apply novel distribution models for emblematic and vulnerable species of sea turtles, marine mammals and seabirds of the Mediterranean Sea, the Bay of Biscay and the Iberian Atlantic coast waters, including a new framework for megafuana mechanistic species deistribution modelling. The specific aims are:

1. to compile unique empirical movement datasets and projections and assess the impact of CC on species distribution, habitats and migration routes,
2. to develop and optimize widely used statistical distribution models in cases of lack of extensive empirical datasets, like for several marine mammals and seabirds,
3. to investigate possible links between habitat suitability and prey distributions, by developing and applying innovating process-based modelling,

4. to develop novel mechanistic distribution models for charismatic marine species, based on the DBEM framework, shedding light on essential dynamic habitat features (e.g. indirect effects of CC on prey) to be considered in conservation strategies.

Study area and CC context

The **Mediterranean Sea**, the largest semi-enclosed sea on the planet, represents a worldwide marine biodiversity hotspot but also a CC hotspot. Covering less than 1% of the global ocean surface and containing 4-18% of the identified marine species, the Mediterranean Sea contains some of the fastest-warming marine ecoregions, with future projections suggesting temperatures increases at a higher rate compared to the global average (25% more than the global mean) (Lionello et al. 2018). Projections conducted within FutureMARES suggest that mean sea surface temperatures within the Mediterranean Sea basin will increase by more than 4 degrees Celsius under the SSP5-85 scenario by the end of century (Figure 4).

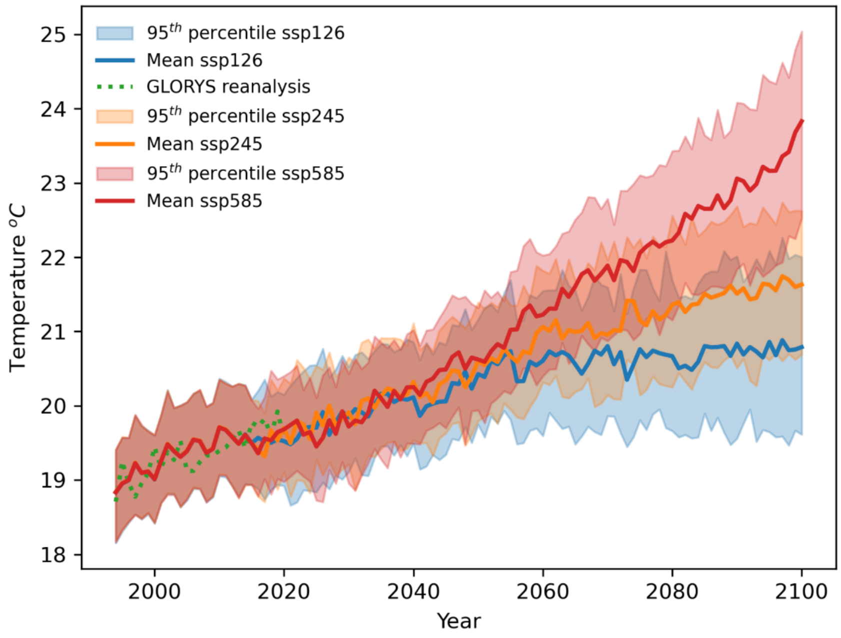

Figure 4. Temperature (C) across the Mediterranean Sea for three scenarios SSP1-2.6, SSP2-4.5, and SSP5-8.5, as resulted from Task 2.1. of FutureMARES. The 95th percentiles are shaded around the mean values (thicker lines). Green lines indicate the GLORYS reanalysis for the historical period 1993-2019.

Over the last three decades, the western basin suffered from two extreme heat waves causing mass mortalities of sessile invertebrates. Towards the end of the 21st century, the intensity and the severity of marine heatwaves are projected to increase by 4 and 42 times, respectively, with at least one long-lasting event (up to three months longer) being projected every year (Darmaraki et al. 2019). Biodiversity has also been exposed to extensive anthropogenic stressors acting in synergy with CC (Coll et al. 2012), with reported widespread impacts due to land-borne pollution, over-exploitation and invasive alien species (IAS). Synergies between CC and other stressors have caused many shallow reefs to shift to urchin-dominated barrens and IAS, mainly macroalgae, to outcompete native benthic species. The eastern basin is also rapidly warming and multiple harvested and non-harvested species have collapsed and/or have been largely replaced by thermophilic IAS, especially in the SE corner – the Levant (Edelistet et al. 2013). Northern coasts of the Mediterranean Sea act as a barrier, a “cul de sac” for colder water species, with an estimated 25 fish species that would qualify for the IUCN Red list of threatened species (Ben Rais Lasram et al. 2010). Climate change impacts pose serious and multi-faceted challenges to the conservation of the Mediterranean marine biodiversity.

The **Bay of Biscay** and **Iberian Coast** contain a high degree of geomorphological diversity with rocky reefs, sedimentary habitats, and mixed rock and sediment seascapes. The area is rich in transitional waters that contribute to the high biological productivity and diversity with important ecosystem engineers such as seagrass beds of Zostera noltei. The coast has a long history of fisheries (purse seiners, trawlers and artisanal fisheries, recreation) and tourism. A prominent feature of the coast is the Bay of Biscay, a wide shelf extending west of France and a narrow shelf in the north of Spain. Summer upwelling events along the Spanish and French coastline sustain a highly productive and diverse fish community. In the Basque region, there are two coastal protected areas and two larger proposed Marine Protected Areas (MPAs). The most recent decade has witnessed a large upsurge in renewable and traditional (oil and gas) energy production as well as offshore aquaculture initiatives. A variety of marine mammal species are present in the Bay of Biscay. The seabird community is of relevance during certain periods of the year through an important migratory flyway and more than 700 species of fishes have been reported. Mammals are vulnerable to fishing bycatch, vessel collision, and pollution-related threats, whilst seabirds are particularly sensitive to oil spills, fishing bycatch and marine litter (García-Barón et al. 2019b).

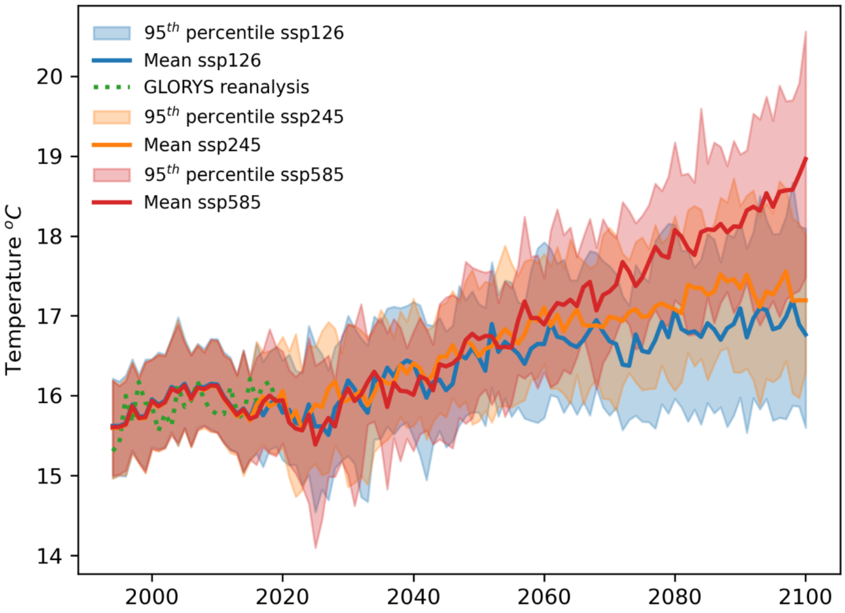

Figure 5. Temperature (C) across the Bay of Biscay region for three scenarios SSP1-2.6, SSP2-4.5, and SSP5-8.5, as resulted from Task 2.1. of FutureMARES. The 95th percentiles are shaded around the mean values (thicker lines). Green lines indicate the GLORYS reanalysis for the historical period 1993-2019.

FutureMARES climate change projections suggest that mean sea surface temperatures will increase up to 3 degrees Celsius under the SSP5-85 scenario by the end of century in the Bay of Biscay region (Figure 5).

Work form WP1 shows that, in the last four decades, there have been four groups of climate regime shifts (Chust et al. 2022): 1) A gradual shift associated with CC starting in the 1980s, with a warming of the sea surface down to 100 m depth in the bay (0.10-0.25 °C per decade) and an increase in air temperature and insolation. This warming may have impacted on benthic community redistribution in the Basque coast, favouring warm-water species relative to cold-water species. Weight-at-age for European anchovy and sardine decreased in the last two decades. 2) Deepening of the winter mixed layer depth in the south-eastern bay that probably led to increases in nutrients, surface oxygen, and chlorophyll concentration. Current increases on chlorophyll and zooplankton (i.e., copepods) biomass are contrary to those expected under CC scenarios in the region. 3) Sea-level rise (1.5-3.5 cm per decade since 1990s), associated with CC. 4) Increase of extreme wave height events of 16.8 cm per decade in the south-eastern bay, probably related to stormy conditions in the last decade, with impacts on beach erosion. Estimating accurate rates of sea warming, sea-level rise, extreme events, and foreseeing the future pathways of marine productivity, are key to define the best adaptation measures to minimize negative CC impacts in the region. For more details, please see deliverable D1.3.

2. Validating species detectability technics

2.1 Comparing dedicated and opportunistically collected data to study diversity, distribution and habitat

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2.1.1 Context and case study

Monitoring from platforms of opportunity (OPOs) has been widely used to collect cetacean occurrence data, allowing sampling of areas far from the coast and for long periods of time. This monitoring methodology relies on existing resources, activities or structures that were not originally designed with the objective of studying cetaceans (e.g., cargo ships, seismic survey vessels, oil platforms, rafts, touristic activities, incidental catches in fishing gear, opportunistic stranding records), and is often carried out by volunteer observers at a decreased cost (Figure 6). Although this methodology presents limitations (e.g., heterogeneous effort, monitoring area conditioned to the route taken by the OPO), it enables the collection of valuable data on cetacean distribution and abundance, that would otherwise be unlikely to be collected, over a large spatial and temporal framework (Correia et al. 2021; Oliveira-Rodrigues et al. 2022; Correia et al. 2020; Correia et al. 2019a; Alves et al. 2018; Tobeña et al. 2016; Aïssi et al. 2015; Correia et al. 2015; Hupman et al. 2014; Viddi et al. 2010; Kiszka et al. 2007). In the OPOs, it is possible to collect data through dedicated effort or opportunistically. As opposed to opportunistic observation, that does not allow an assessment of the sampling effort and limits the analyses possible to perform, dedicated observation is performed by observers who are in the OPO exclusively to collect cetacean occurrence data and who record the sampling effort, as well as other relevant data (among others: animal behaviour, exact position of the sighting, meteorology, maritime traffic) (Correia et al. 2015; Evans and Hammons 2004).

Figure 6. Marine Mammal Observer in Navy vessel

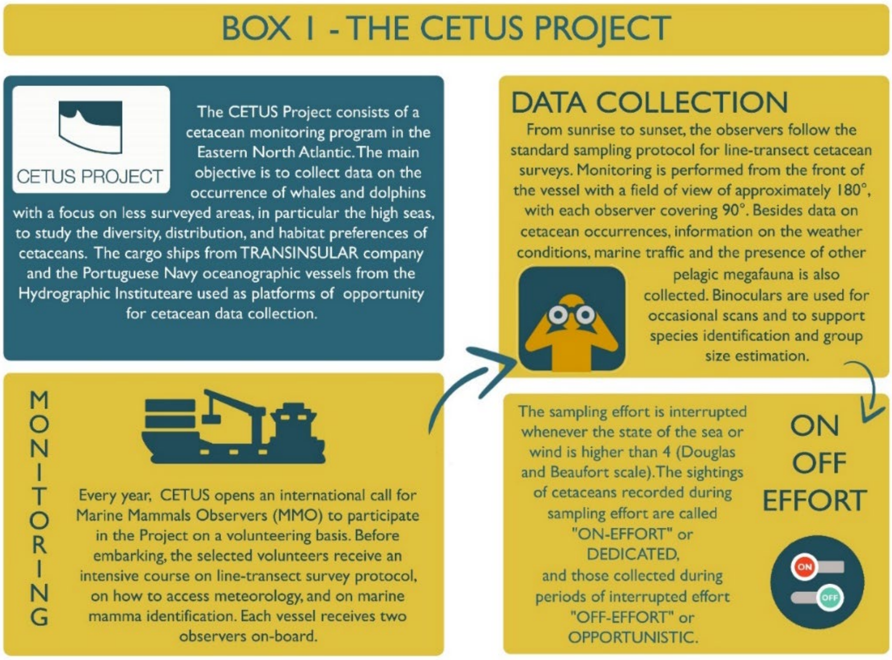
Since 2012, the CETUS Project, led by the Interdisciplinary Centre of Marine and Environmental Research (CIIMAR), has been monitoring the occurrence of cetacean species in the Eastern North Atlantic, within the area between Mainland Iberia, the Northwestern Africa, and the archipelagos of Madeira, Azores, Canaries, and Cape Verde. Data collection is dedicated, carried out by observers trained in the detection and identification of cetaceans. In addition, the data collected are associated with the sampling effort, which is crucial to provide reliable relative abundances, especially when the effort is highly heterogeneous (Correia et al. 2015; Correia et al. 2019a; Correia et al. 2019b). When weather, or activities in the vessels, impede dedicated monitoring (i.e., poor conditions for cetacean detection or no access to the observation standouts), opportunistic data on cetacean occurrence is still registered opportunistically (Correia et al. 2019a). Such records have been rarely used in data analysis for the lack of associated information on survey effort, largely conditioning interpretation of results (except for Correia et al. 2021, where all occurrence data was used for MAXENT presence-only ecological niche models).

Considering the large amount of cetacean occurrence data collected opportunistically in the CETUS dataset (Correia et al. 2022), it is important to evaluate the possibility to use such records to study cetacean diversity, distribution and abundance trends over large areas. This is especially relevant when accounting for the number of monitoring networks operating with OPOs, with data covering large spatial and temporal frameworks (CETUS, ORCA, FLT Network). Data from monitoring programmes, increasingly available in open repositories (OBIS, EMODnet, GBIF), is fundamental for regional and worldwide assessments on biodiversity loss, distribution shifts, and habitat degradation, in response to anthropogenic pressures and trajectories of climate change.

2.1.2 Methodology

Cetacean Occurrence Data

Every year, CETUS opens an international call for Marine Mammals Observers (MMO). Monitoring campaigns are carried out mostly during the summer (~ 4 months/year), and each MMO participates in the data collection for about two months/year, on a volunteering basis (Box 1).



BOX 1 - THE CETUS PROJECT

The CETUS Project consists of a cetacean monitoring program in the Eastern North Atlantic. The main objective is to collect data on the occurrence of whales and dolphins with a focus on less surveyed areas, in particular the high seas, to study the diversity, distribution, and habitat preferences of cetaceans. The cargo ships from TRANSINSULAR company and the Portuguese Navy oceanographic vessels from the Hydrographic Instituteare used as platforms of opportunity for cetacean data collection.

DATA COLLECTION

From sunrise to sunset, the observers follow the standard sampling protocol for line-transect cetacean surveys. Monitoring is performed from the front of the vessel with a field of view of approximately 180°, with each observer covering 90°. Besides data on cetacean occurrences, information on the weather conditions, marine traffic and the presence of other pelagic megafauna is also collected. Binoculars are used for occasional scans and to support species identification and group size estimation.

MONITORING

Every year, CETUS opens an international call for Marine Mammals Observers (MMO) to participate in the Project on a volunteering basis. Before embarking, the selected volunteers receive an intensive course on line-transect survey protocol, on how to access meteorology, and on marine mamma identification. Each vessel receives two observers on-board.

ON OFF EFFORT

The sampling effort is interrupted whenever the state of the sea or wind is higher than 4 (Douglas and Beaufort scale). The sightings of cetaceans recorded during sampling effort are called "ON-EFFORT" or DEDICATED, and those collected during periods of interrupted effort "OFF-EFFORT" or OPPORTUNISTIC.

Before embarking, the selected volunteers receive an intensive course on the line-transect survey protocol, on how to assess weather conditions, and on marine mammal identification (Correia et al. 2015; Correia et al. 2019a). Ideally, each vessel receives two observers on-board, and rarely only one observer embarks (only in the case where there are not two volunteers available for a specific campaign). The observers are, ideally, located in the exterior, in the wings of the navigation bridge, one on each side, and perform the sampling protocol from sunrise to sunset. The observation standouts are at between 13 and 16 metres height. Each observer monitors an area of 90º (port or starboard), resulting in a total of 180º field of view from the bow of the ship, in the direction of the route. To avoid fatigue, observers switch observation sides every hour and rest in shifts: one hour at each meal (lunch and dinner) and, optionally, for periods of approximately 40 minutes (usually, for each observer, once in the morning and once in the afternoon). During these periods, the lone observer covers the entire 180º. Each vessel is annually equipped with a marine mammal species identification guide, two binoculars (7x5) with compass and scale, two walkie-talkie radios for communication between the observers, sunglasses with polarized lenses, two digital wristwatches, a tablet with integrated GPS to record the trips and data collected and, when possible, a camera with a long-range lens. Monitoring is carried out with the naked eye and with the support of binoculars to occasionally scan the area and facilitate the data collection (e.g., number of vessels, animal counts, species identification). The survey effort is interrupted whenever sea or wind conditions are above 4 (on the Douglas and Beaufort scale, respectively), or else due to heavy rain, visibility below 1 km, or when observers are not allowed to remain at the observation post (e.g. during safety drills, manoeuvres, deck cleaning). During these periods of interrupted effort, cetacean occurrence data are recorded opportunistically. Weather conditions are recorded at the start and end of sampling, and whenever they change significantly. Information on maritime traffic (number of boats) is collected at the beginning and end of each sampling, hourly, and at each sighting. Whenever a cetacean (or group) is sighted, observers identify the species (or the lowest possible taxon); the number of individuals; the animal´s reaction to the presence of the ship (approach, avoid, or indifferent); and, using the compass and scale of the binoculars, the distance, displacement and angle of the animal(s) in relation to the ship. During a sighting, while observers are collecting the data, the sampling effort is interrupted. Due to the occasional difficulty in correctly counting the number of individuals in the sighted group, the minimum and maximum number of animals is registered, as well as the best estimate (based on the perception of the observers on board). Along with the vessel routes, geographic positions of other megafauna sightings (e.g. turtles, sharks, moonfish) are also collected. All routes and data collection are recorded in the tablet with integrated GPS.

For the present work, we used the geographic position of cetacean occurrences collected within CETUS, between 2012 and 2020. Data collected on-board the cargo ships started in 2012, while monitoring from navy vessels started in 2017 (Table 1).

Table 1. Areas covered by the CETUS Project, for cetacean monitoring purposes, on-board cargo ships (C) and navy vessels (N), between 2012 and 2020.

	Mainland		Archipelagos			
	Iberia	NW Africa	Azores	Madeira	Canaries	Cape Verde
2012	C			C		
2013	C			C		
2014	C		C	C		
2015	C	C	C	C	C	C
2016	C	C	C	C	C	C

2017	C / N	C	C / N	C	C	C
2018	C		C	C		
2019	C / N		C / N	C / N		
2020	N		N			

The surveyed routes covered an extensive area of the Eastern North Atlantic, from the Mainland Portugal to the Northwestern Africa, and the Macaronesia archipelagos (Azores, Madeira, Canaries and Cape Verde). The position of the sightings was considered as the GPS position of the vessel at the time of the sighting (therefore, distance and angle of the sightings was not computed). Each sighting corresponded to an individual or group of individuals of the same species / taxon. Since species from the genus *Globicephala* are indistinguishable at-sea, the sightings identified as *Globicephala* sp. were compiled as being identified to the species level. For the comparative analysis of dedicated and opportunistically collected data, two datasets were analysed: dedicated sightings collected during survey effort; and opportunistic sightings collected during interrupted survey effort (i.e., due to weather conditions or no access to the observation standouts) (Figure 7).

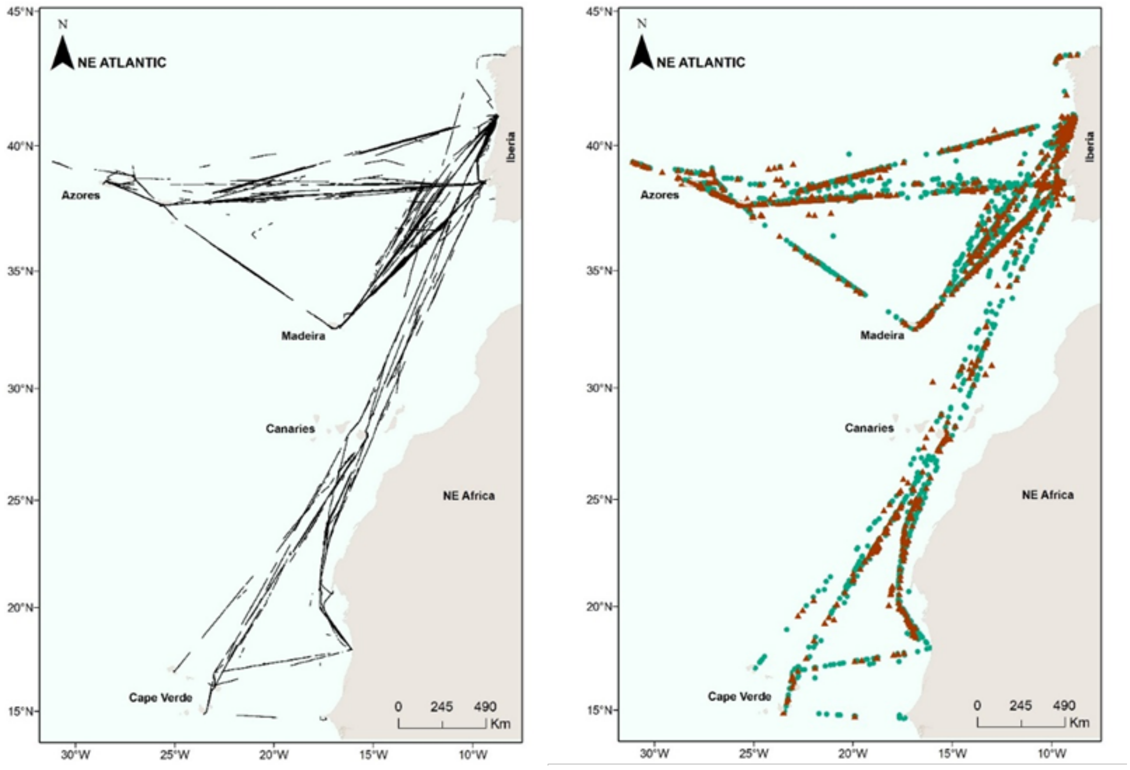


Figure 7. CETUS Project data used for the present work, collected between 2012 and 2020. Left: Survey effort for cetacean monitoring. Right: Cetacean occurrence records with the dataset of the dedicated data in green circles and the dataset of opportunistically collected data in red triangles.

Habitat Data

Geographic (latitude and longitude) and topographic variables (depth, slope, distance to coast, and distance to seamounts) were extracted to the position of the sightings, for a comparative analysis between habitat range assessed with the dedicated and opportunistic datasets. Seabed topographic features are related with upwelling systems, turbulence and aggregation of prey species, and consequently highly influence cetacean distribution (Correia et al. 2021). Geographical variables were obtained from the GPS data recorded during the at-sea surveys. Bathymetry was extracted to the study area from GEBCO, at a resolution of 30-arc second. Seabed slope was derived from bathymetry data. For distance to seamounts, we delimited topographic features classified as seamounts, banks, hills, ridges, and rises, in GEBCO. We used contour lines created every 50 m and defined a polygon from the outermost closed contour line around the geographic location of the top of the features. Then, we calculated the distance from the base of the seamounts and from the coastline (distance to coast) to the sightings. Both slope and distances were computed using ArcGIS 10.7, as well as the extraction of habitat data to the sighting positions.

Data Analysis

For the two datasets (dedicated and opportunistic), a spatial-temporal analysis was conducted on the cetacean occurrence data. For a more in-depth analysis, we then selected four species i) representing toothed and baleen cetaceans, ii) differing in terms of occurrence frequency and abundance in the area, and iii) with different degrees of difficulty to detect and identify them:

- ✓ *Delphinus delphis* (Common dolphin): the most frequently sighted species, easily detected and identified;
- ✓ *Ziphius cavirostris* (Cuvier’s beaked whale): less frequent in the area, difficult to detect and identify;
- ✓ *Physeter macrocephalus* (Sperm whale): frequent in the area, often difficult to detect but easy to identify;
- ✓ *Balaenoptera acutorostrata* (Minke whale): less frequent in the area, often easy to detect but difficult to identify.

While for dedicated data, survey effort can be used to calibrate the variation in the number of sightings, no calibration measure was available for opportunistic data. Since the aim of the present work was to perform a comparative analysis between the two datasets, a measure of prevalence for each target species, and dataset, was computed i) per monitoring year to assess inter-annual variation, and ii) spatially, on a grid of 30 km resolution, to assess distribution. Prevalence was calculated as follows:

(Number of sightings of target species / Number of total cetacean sightings) X 100

To study habitat range, boxplots were constructed by species and dataset, for each variable. The results obtained with the two datasets (dedicated and opportunistic) were statistically compared through a Mann-Whitney-Wilcoxon test, with a significance level set to 0.05.

The spatial analysis was conducted in the ArcGIS 10.7 and the statistical tests under the R Software.

2.1.3 Results and Conclusions

Effort and Cetacean Occurrence

The inter-annual variations of number of sightings and number of reported species followed a similar trend between the dedicated and opportunistic datasets (Figure 8).

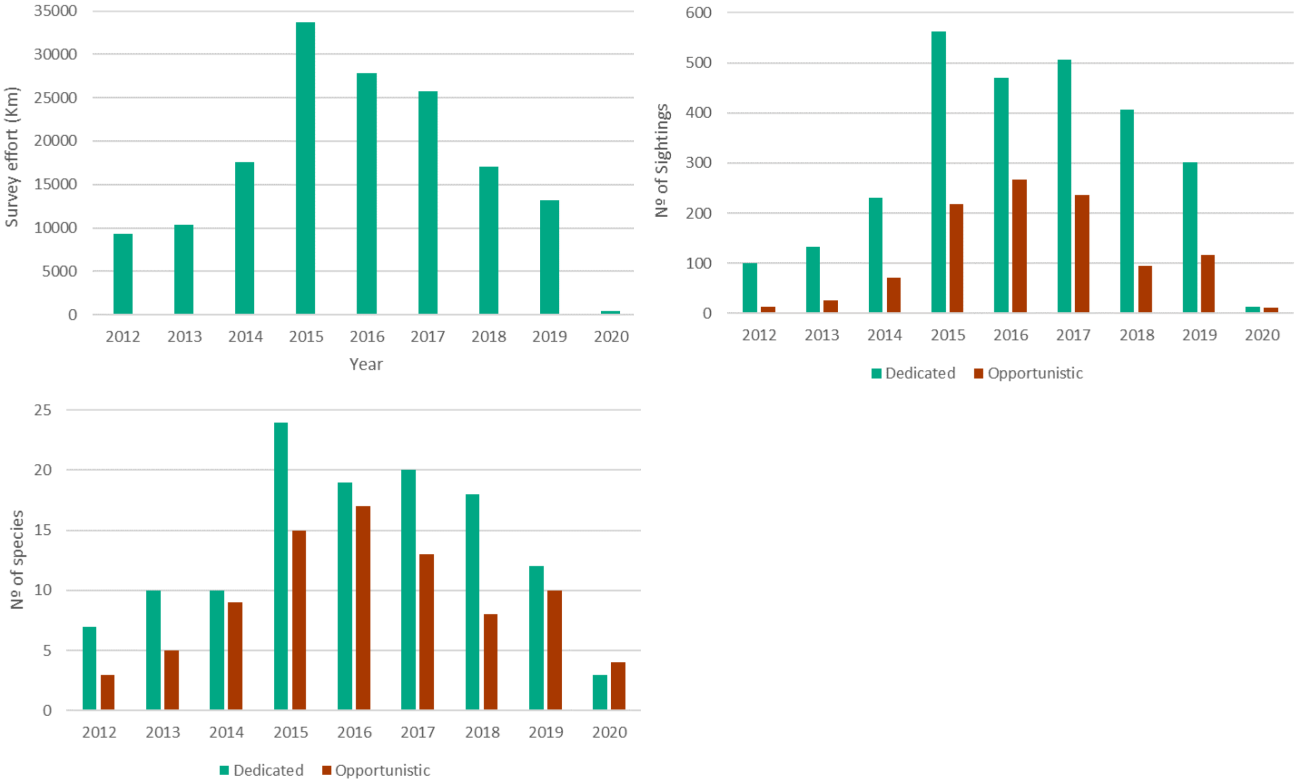
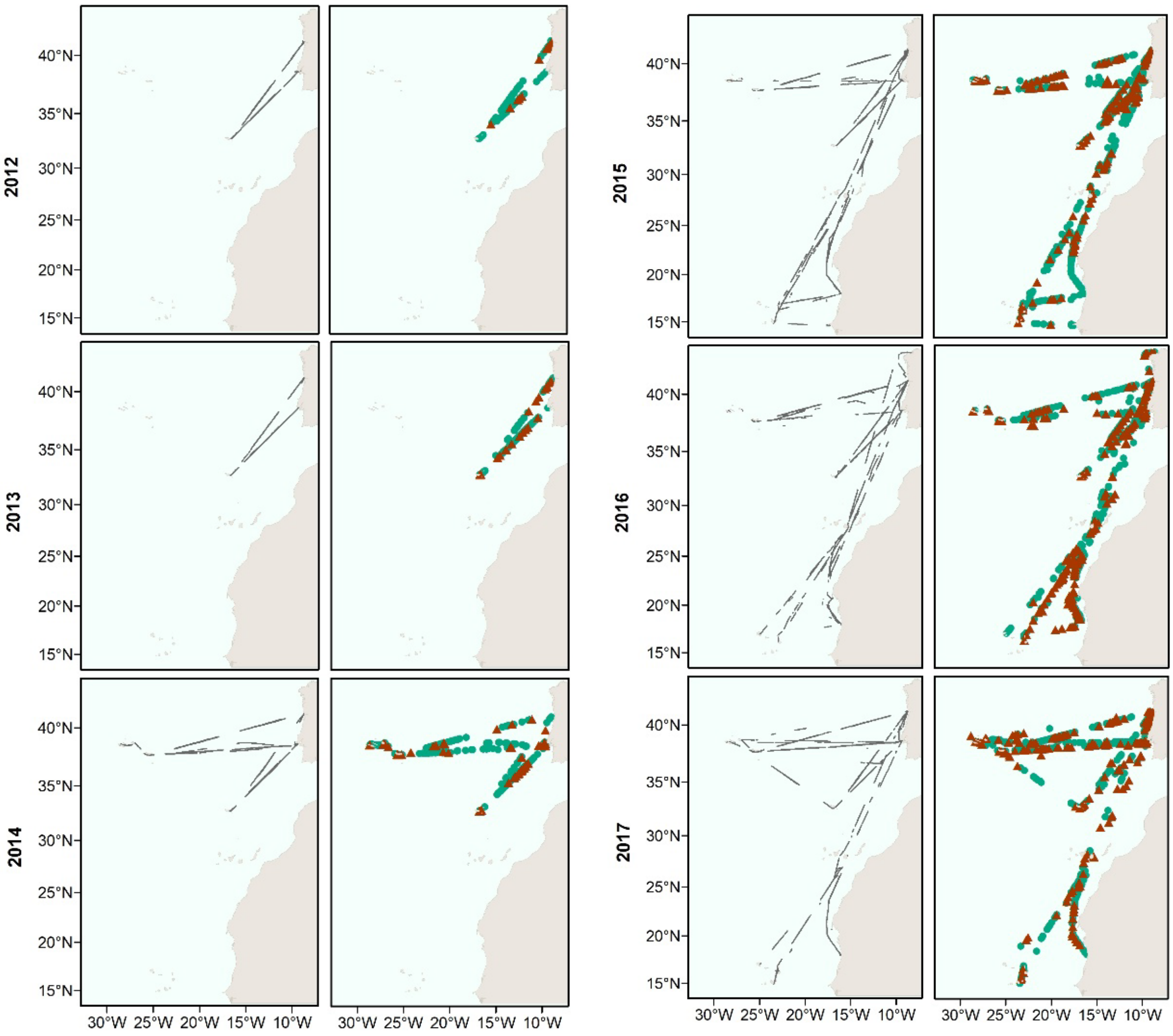


Figure 8. Inter-annual variation of survey effort, dedicated and opportunististically collected cetacean sightings, and number of cetacean species reported with dedicated and opportunistic data, from CETUS Project, between 2012 and 2020.

Overall, the years of 2015, 2016, and 2017, had more survey effort, sightings, and species reported, due to an increased number of campaigns and monitored area (Figure 9).


2012
2013
2014
2015
2016
2017
40°N
35°N
30°N
25°N
20°N
15°N
30°W 25°W 20°W 15°W 10°W

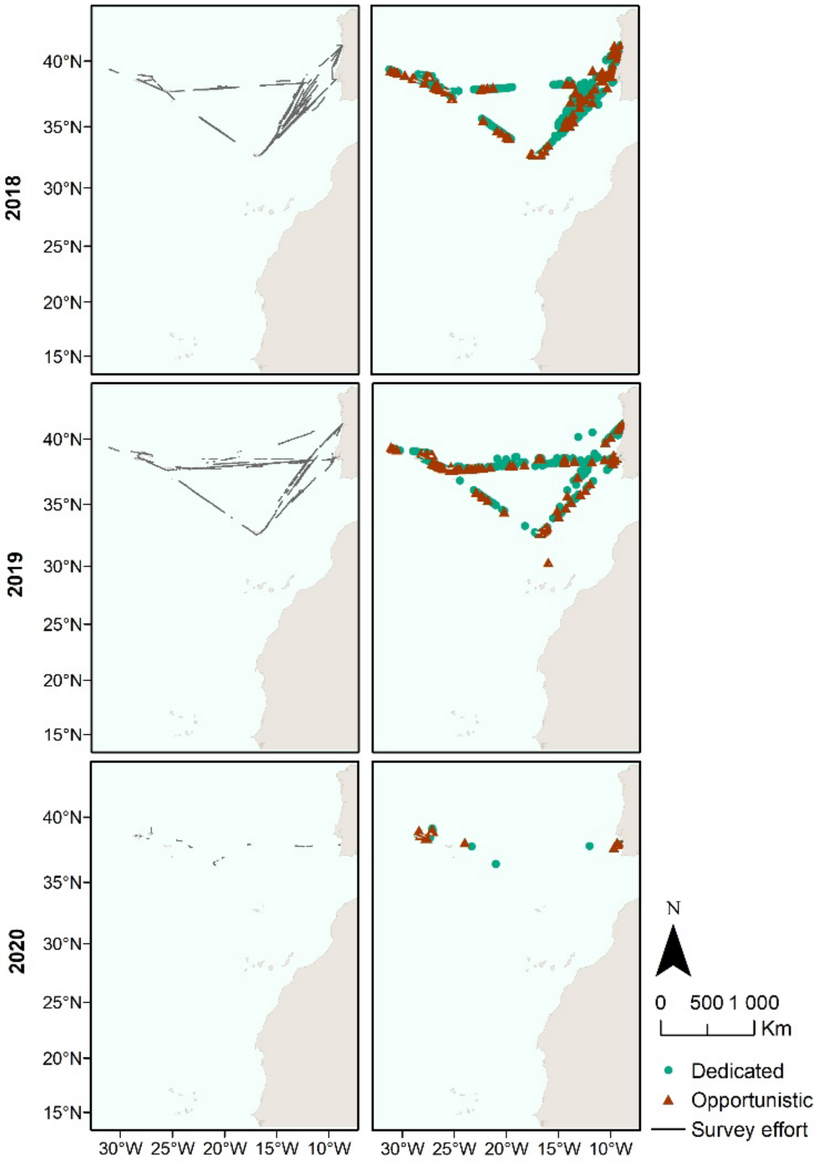


Figure 9. Inter-annual spatial distribution of survey effort and sightings from the dedicated and opportunistic datasets, obtained from the CETUS Project surveys, undertaken between 2012 and 2020.

In total, 3785 sightings were collected, distributed between 2727 dedicated sightings and 1058 sightings collected opportunistically. A high diversity of species was registered, summing up to 27 species. All species were present in both the dedicated and opportunistic surveys, with the exception of 5 less frequent species that had no data in opportunistic surveys (Northern bottlenose whale, Fraser’s dolphin, Blainville’s beaked whale, Spinner dolphin, Rough-toothed dolphin) (Table 2).

Table 2. Number of dedicated and opportunistically collected sightings, by species, obtained from CETUS Project, between 2012 and 2020.

Species	Common name	Dedicated	Opportunistic	Total
Balaenoptera acutorostrata	Minke whale	78	17	95
Balaenoptera borealis	Sei whale	4	1	5
Balaenoptera edeni	Bryde´s whale	4	2	6

Balaenoptera musculus	Blue whale	2	1	3
Balaenoptera physalus	Fin whale	29	9	38
Cetacea	Non-identified cetacean	281	151	432
Delphinidae	Dolphins	733	282	1015
Delphinus delphis	Common dolphin	341	148	489
Globicephala sp.	Pilot whale	54	17	71
Grampus griseus	Risso´s dolphin	11	4	15
Hyperoodon ampullatus	Northern bottlenose whale	6	0	6
Kogia sp.	Pygmy/Dwarf Sperm whale	7	1	8
Lagenodelphis hosei	Fraser's dolphin	1	0	1
Lagenorhynchus albirostris	White-beaked dolphin	3	1	4
Megaptera novaeangliae	Humpback whale	8	1	9
Mesoplodon densirostris	Blainville's beaked whale	8	0	8
Mesoplodon europaeus	Gervais's beaked whale	3	1	4
Mysticeti	Baleen whale	263	111	374
Orcinus orca	Killer whale	5	3	8
Peponocephala electra	Melon headed whale	2	2	4
Phocoena phocoena	Harbour porpoise	7	2	9
Physeter macrocephalus	Sperm whale	135	44	179
Pseudorca crassidens	False killer whale	9	5	14
Stenella attenuata	Pantropical spotted dolphin	4	3	7
Stenella clymene	Clymene dolphin	14	3	17
Stenella coeruleoalba	Striped dolphin	142	46	188
Stenella frontalis	Atlantic spotted dolphin	238	94	332
Stenella longirostris	Spinner dolphin	6	0	6
Steno bredanensis	Rough-toothed dolphin	4	0	4
Tursiops truncatus	Bottlenose dolphin	118	57	175
Ziphiidae	Beaked whale	143	34	177
Ziphius cavirostris	Cuvier´s beaked whale	64	18	82
Total		2727	1058	3785

Cetacean Diversity

The cetacean community composition was similar between the two datasets (dedicated VS opportunistic), considering the 10 most frequently sighted taxa and species, only differing in the least frequently sighted out of the 10 (for the taxa, variation between Minke whale and Cuvier’s beaked whale; for the species, variation between Clymene dolphin and Melon headed whale) (Figure 10).

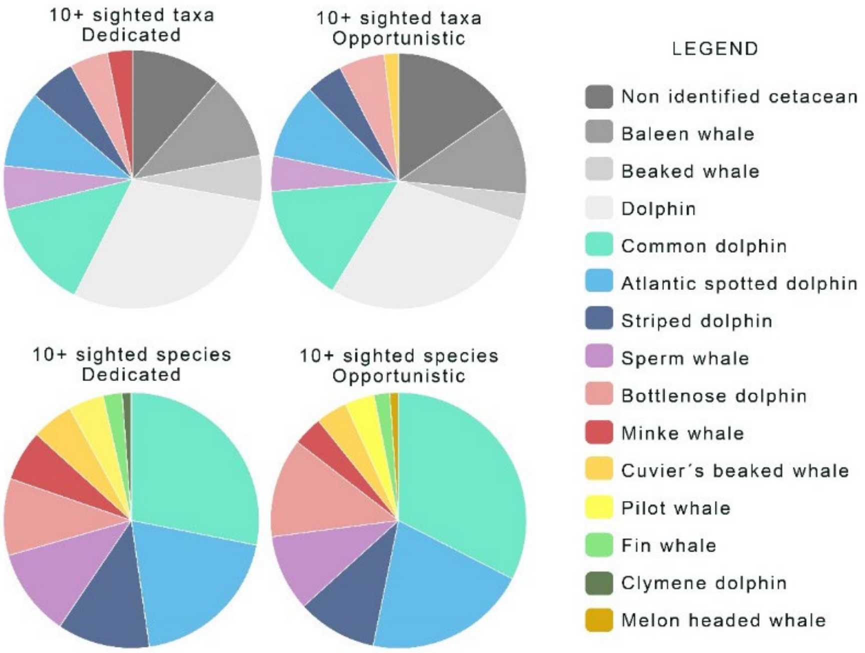


Figure 10. Cetacean community composition as assessed from the datasets of dedicated and opportunistic data, obtained from the CETUS Project, between 2012 and 2020. The 10 most sighted taxa (upper panel) and the 10 most sighted species (bottom panel) were considered.

Prevalence

The more frequently sighted the species is, the more similar are the prevalence distribution patterns of the target cetacean species between dedicated and opportunistic datasets. While for common dolphin, prevalence assessed with the opportunistic data is representative (i.e., very similar to patterns assessed with the dedicated dataset), for Cuvier's beaked whale, the opportunistic data results in a substantially different prevalence map. For sperm whales, prevalence maps obtained with dedicated and opportunistic data are still very similar, especially for the areas with higher prevalence . On the other hand, for Minke whale, only a few areas of high prevalence are common and equally represented on both maps. In all cases, opportunistic data provides information on the species occurrence (often with high prevalence) in areas where no dedicated data exists (Figure 11).

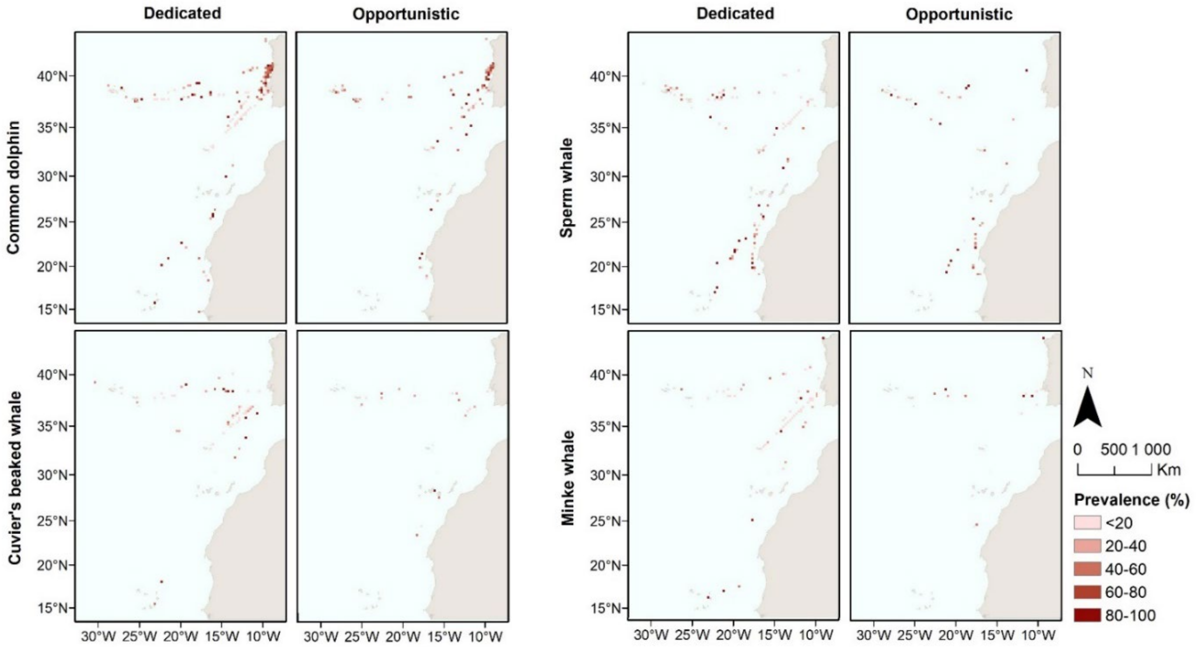
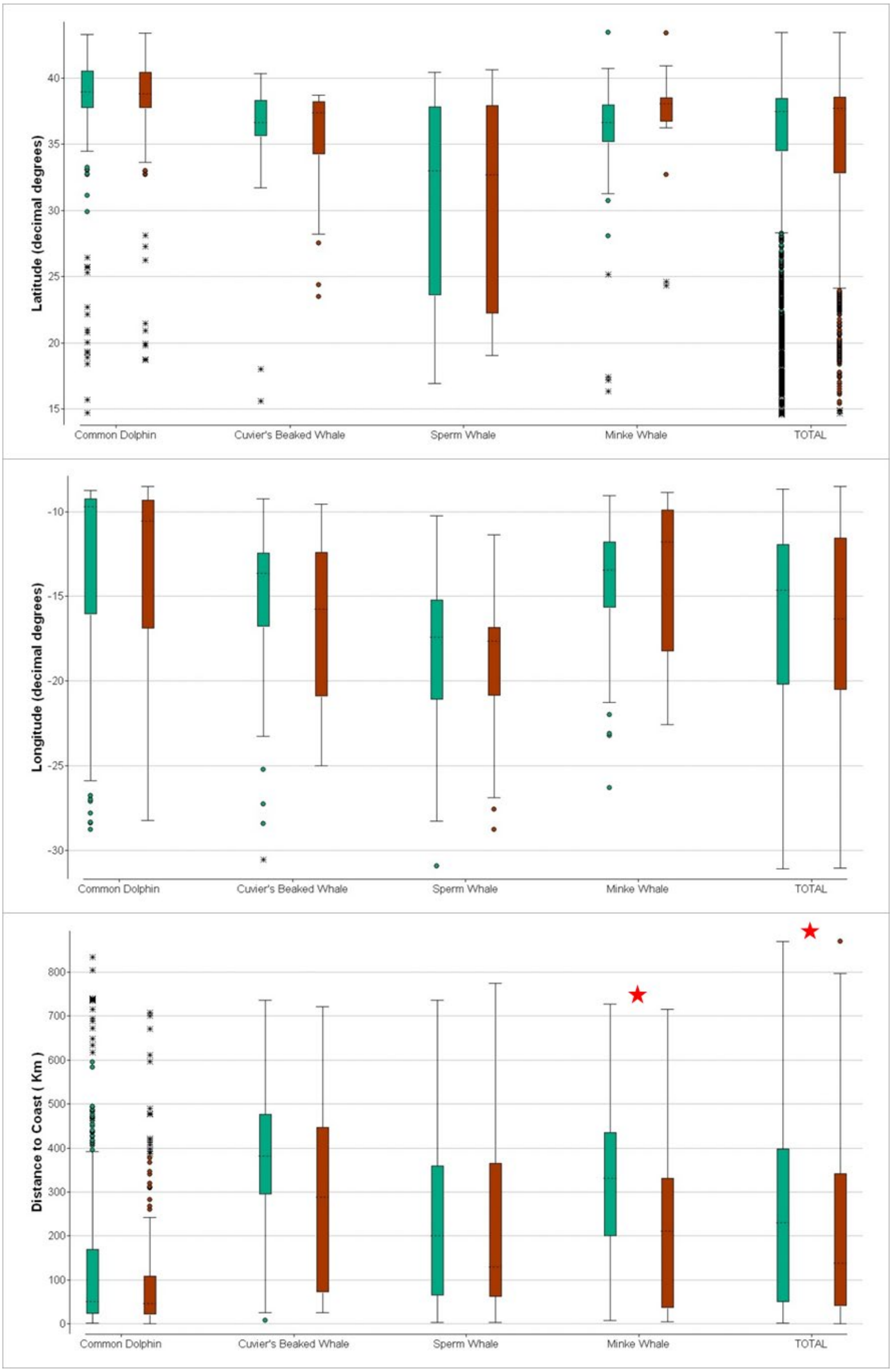


Figure 11. Prevalence of target species within the cetacean community, in the Eastern North Atlantic, across the area covered by the CETUS Project, as assessed with the datasets of dedicated and opportunistic cetacean occurrence data. Grid with 30 km resolution.

Habitat Range

For geographic variables (latitude and longitude), habitat range was similar between dedicated and opportunistic datasets, for the target species and for the total of cetacean sightings. Still considering the total cetacean community, opportunistic data provided significantly different results for the remaining habitat variables (occurrences closer to the coast, further from the seamounts, in shallower waters, and higher slopes). For Common dolphins, no significant differences were found between the two datasets. With opportunistic data, when comparing the results obtained with the dedicated dataset, Sperm and Minke whales appeared further from the seamounts, with the later species closer to the coast; and Cuvier’s beaked whales occurred in shallower waters, in higher slope areas (Figure 12).


Latitude (decimal degrees)
40
35
30
25
20
15
Common Dolphin
Cuvier's Beaked Whale
Sperm Whale
Minke Whale
TOTAL
Longitude (decimal degrees)
-10
-15
-20
-25
-30
Common Dolphin
Cuvier's Beaked Whale
Sperm Whale
Minke Whale
TOTAL
Distance to Coast (Km)
800
700
600
500
400
300
200
100
0
Common Dolphin
Cuvier's Beaked Whale
Sperm Whale
Minke Whale
TOTAL

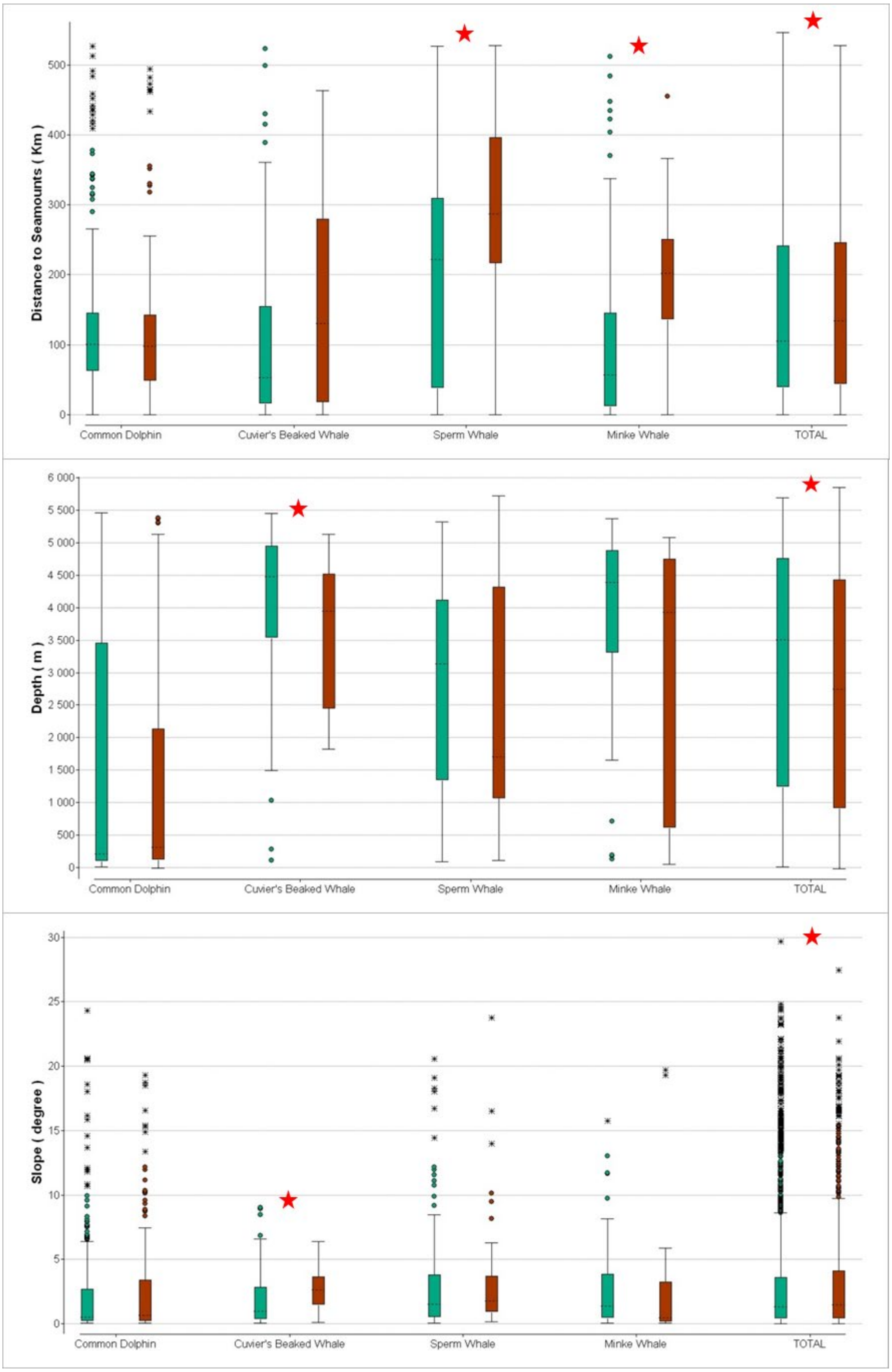


Figure 12. Habitat range assessed with dedicated and opportunistic datasets of cetacean occurrence data, for target species and in total. Where statistically significant differences ($p < 0.05$) exist between the two datasets, these are marked with a red star

Results from the statistical tests (Mann-Whitney Wilcoxon, α = 0.05), comparing between the dedicated and opportunistic datasets for the species habitat range, are presented below (Table 3).

Table 3. Statistical tests to assess differences between the habitat range of target cetacean species, and in total, assessed with dedicated and opportunistic datasets. Statistically significant results (p > 0.05) are presented in a darker colour.

Mann-Whitney-Wilcoxon test					
	TOTAL	Common Dolphin	Cuvier´s Beaked Whale	Sperm Whale	Minke Whale
Latitude	W = 1420464, p-value = 0.464	W = 26724, p-value = 0.300	W = 560 p-value = 0.862	W = 3294 p-value = 0.279	W = 468 p-value = 0.059
Longitude	W = 1493693 p-value = 0.090	W = 27473 p-value = 0.119	W = 662 p-value = 0.338	W = 3479 p-value = 0.088	W = 564 p-value = 0.339
Distance to coast	**W = 1603114 p-value < 0.001**	W = 26927, p-value = 0.238	W = 726, p-value = 0.094	W = 3156, p-value = 0.534	**W = 891, p-value = 0.027**
Distance to Seamounts	**W = 1362706 p-value = 0.008**	W = 26722, p-value = 0.3001	W = 485.5 p-value = 0.3132	**W = 2162 p-value = 0.007**	**W = 345.5 p-value = 0.002**
Depth	**W = 1598813, p-value < 0.001**	W = 24069, p-value = 0.417	**W = 791 p-value = 0.016**	W = 3432.5, p-value = 0.122	W = 849.5 p-value = 0.071
Slope	**W = 1370670 p-value = 0.017**	W = 23255 p-value = 0.168	**W = 372 p-value = 0.023**	W = 2623.5 p-value = 0.246	W = 771 p-value = 0.297

CONCLUSIONS

Although opportunistically collected data on cetacean occurrence yields a smaller dataset and it often lacks associated information usually available with dedicated records (e.g., survey effort), both types of data provide similar results in terms of trends in total sightings, number of species recorded, and cetacean community composition (at least, for the most frequently sighted taxa / species). At the species level, the more frequent the species is in the area (i.e., the higher the number of available sightings and opportunistic records), the more representative are the prevalence distribution patterns obtained with opportunistic data (i.e., closer to results obtained with dedicated data). For frequently sighted species with a sufficient amount of data, opportunistic datasets also provide representative results in terms of habitat range. This is rarely the case for most of the habitat variables when the entire cetacean community and less frequently observed species are considered. Nevertheless, whenever possible, opportunistic and dedicated datasets should be used together, as there is often a substantial amount of opportunistic data where no survey effort was undertaken.

2.2 The use of opportunistic data to validate species distribution predictions in delineating conservation priority areas

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2.2.1 Context and case study

To improve our understanding on the location and extent of marine megafauna critical habitats, few studies have tried to spatially delineate foraging grounds using distribution models (e.g., loggerhead turtles at Republic of Cape Verde and surrounding regions at eastern Atlantic, Pikesley et al. 2015; loggerhead turtles at Kimberley region of northern Australia, Thums et al. 2017). Yet, the outputs of these models, which rely on statistical links between occurrence data and environmental information, are susceptible to a degree of uncertainty and might not always be able to capture the underlying ecological complexity of species behavior (Elith and Leathwick 2009). Therefore, integrating independent data from different sampling sources to validate the predictions from species distribution models (Pinto et al. 2016), could serve as an effective way to assess the accuracy of the delineated habitat ranges, but any such framework has not been applied yet on sea turtle studies targeting foraging sites.

The Mediterranean Sea represents a discrete conservation unit (Rees et al. 2016), with loggerheads having distinct demographic and morphological characteristics (Wallace et al. 2010), being characterized by certain climatic niche and potential adaptations to local conditions (Almpanidou et al. 2017) and exhibiting different level of resilience to risk (Wallace et al. 2011). Studies on the distribution of foraging adult turtles across the Mediterranean Sea have primarily been conducted on local scales through various approaches (e.g., satellite tracked animals in Tyrrhenian sea, Italy; Luschi et al. 2018, stranding individuals in Fethiye-Göcek, Turkey; Başkale et al. 2018) or at broader extent through the analysis of telemetry post-nesting data derived from individuals using certain nesting sites (e.g., Schofield et al. 2010; Zbinden et al. 2008). Still, limited efforts to systematically integrate information at a basin scale have been carried out (e.g., rough indication of the distribution based on literature synthesis, Casale et al. 2018; baseline modeled representation of foraging grounds merging data for both adults and juveniles, Mazor et al. 2016). Focusing on adult foraging animals, we applied a series of distribution models combined with a field-based validation procedure to generate a map of foraging habitats distributed across the Mediterranean Sea. To advance our understanding on the additive impact of overlapping threats reported at the foraging sites, we estimated the integrated risk caused by fisheries (longline, trawling, fixed net and purse seine) and marine litter accumulation. Our methodological framework, which combined modeling techniques, field data and a risk assessment framework, allowed us to spatially delineate key foraging areas and hotspots of threats, offering some critical information on sites where conservation actions and mitigation efforts should be prioritized.

2.2.2 Methodology

To ensure that we could build our spatial analysis upon precise and standardized information on foraging habitat use in the Mediterranean, we decided to focus on locations of foraging animals obtained through satellite telemetry data. These data have been obtained based on the same principles and technological characteristics, and even though they might be subjected to potential biases (e.g., tagging location, sample size, data gaps and processing), they are critical for improving the knowledge of broad-scale habitat use (O'Toole et al. 2021). We initially searched Google Scholar using the terms "sea turtles" or "marine turtles", "satellite telemetry" and "Mediterranean". In the search, we included scientific papers and grey literature (conference proceedings, theses and reports). Since 1982, a total of 1300 sources of reference for satellite tracked sea turtles in the Mediterranean were identified (by July 2020) and reviewed.

Validating foraging map based on independent data Species distribution models are more likely able to identify and highlight suitable areas in the vicinity of the input data (Elith and Leathwick 2009). Still, a challenge for these models is the ability to accurately determine the extent of these areas and predict suitable sites distant from input data. Here, in an attempt to validate the overall model performance by means other than the statistical tests, we assessed prediction capacity of the models, by using additional, unpublished information. To gather this information, we focused on four (4) regions where published information on satellite telemetry studies was rather limited or even absent. For these areas we collected and used alternative types of data that justify the use of foraging habitats by adults.

Sea turtles at Spanish coasts and the Balearic Islands

Records of 513 loggerhead sea turtles have been collected based on stranding or incidental bycatch across the coasts of mainland Spain and the Balearic Islands from 2012 to 2019. The curved carapace length (CCL) of these individuals ranges from 16.0 to 99.5cm (Figure 13). To determine the adult sea turtles, we used the threshold of 75cm, resulting in nineteen sea turtles with CCL larger than 75cm. From these individuals, five have been collected based on incidental bycatch and reported as alive and thus, included in the current study.

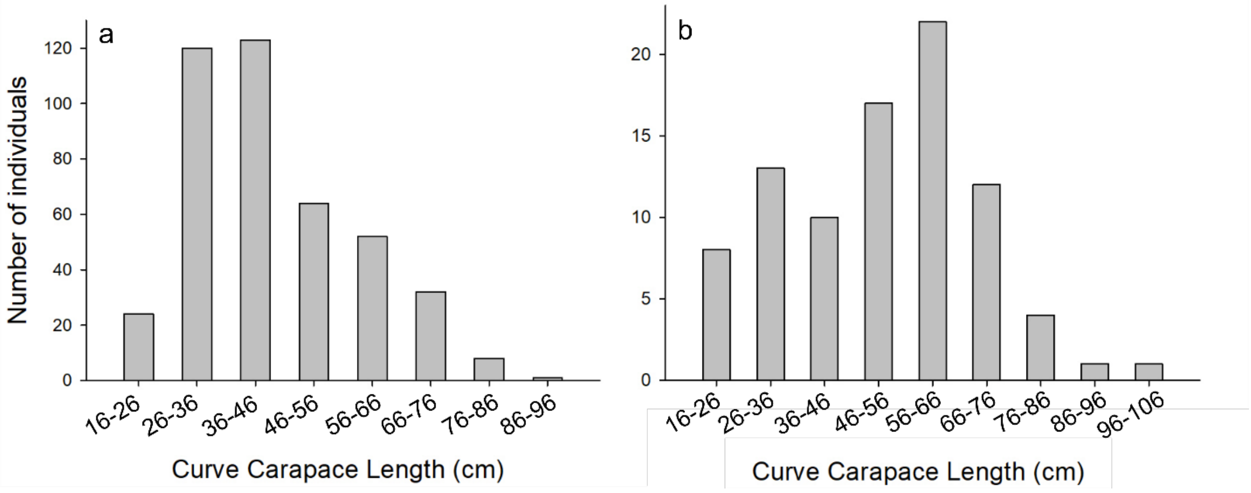

Figure 13. The distribution of the size, expressed as Curve Carapace Length (CCL in cm), of the individuals of loggerhead sea turtles that have been recorded at a) mainland Spain and b) at Balearic Islands. Five sea turtles were considered as adults (i.e., CCL>75cm) and reported based on incidental bycatch.

Sea turtles at French coasts

The French Mediterranean waters including Corsica and continental coasts are frequented by five species of sea turtles of which Caretta caretta is the most abundant. Data on loggerhead occurrence and size derived from fisheries by-catch data and at-sea observations regularly recorded in the database of the French network Réseau Tortues Marines de Méditerranée Française, RTMMF, since 1905. In addition, stranding data, which have not been used in the current study, are collected, along with biological information as digestive contents from dead individuals, proving that loggerhead adults come mainly from June to August for feeding in the Gulf of Lions abundantly supplied with nutrients by the waters of the Rhône and Hérault rivers. The analysis of digestive contents of loggerheads necropsied by the French network RTMMF allowed to identify remains of 11 taxa of preys using visual determination and additional 8 taxa through eDNA metabarcoding.

Sea turtles at Northeastern Aegean Sea

From January 2017 to July 2019, sea turtles’ presence has been recorded in the Northeastern Aegean Sea, around Samos Island, based on different methods. Data at sea were recorded by Archipelagos researchers through boat-based surveys, focusing on dolphins, and snorkel visual survey, focusing on coastal biodiversity and habitat assessment. Sightings occurred all around the island of Samos within 500 meters from the coast. Morphometric measurements of the individuals sighted at sea were estimated by the researchers with all sea turtles considered to be adults. Alive individuals were recorded during summer and spring.

Sea turtles at Southern Aegean/Mediterranean coasts of Turkey

Occurrence data on sea turtles for the Southern Aegean/Mediterranean coasts of Turkey were based on projects implemented by the Sea Turtle Research, Rescue and Rehabilitation Center DEKAMER, from 2011 to 2017. The six adult turtles used in the current study, were caught during breeding/nesting activities, equipped with satellite transmitters and monitored for 87 to 721 days, including foraging activities as residents in the area. The first two transmitters of the considered individuals were placed during the 35th International Sea Turtle Symposium held in 2015 in Dalaman, Turkey, (http://www.seaturtle.org/tracking/index.shtml?project_id=1092&dyn=1588255196). The rest of the studied animals were monitored by DEKAMER (i.e., Dalyan, Fethi, Bodrum Karya, Osman; http://www.seaturtle.org/tracking/index.shtml?project_id=674). The curve carapace length of the considered sea turtles was 68 to 75 cm. These tracking data are subjected to specific copyright protocols, they have not yet been published or made available to the public, offering us the opportunity to consider some novel information on habitat use in the Southern Aegean Sea, Eastern Mediterranean.

The four regions distributed at Western, Central and Eastern Mediterranean: Spanish coasts and Balearic Islands, French coasts, Northeastern Aegean Sea (around Samos Island in Greece) and Southern Aegean/ Mediterranean coasts of Turkey, are shown in Figure 14.

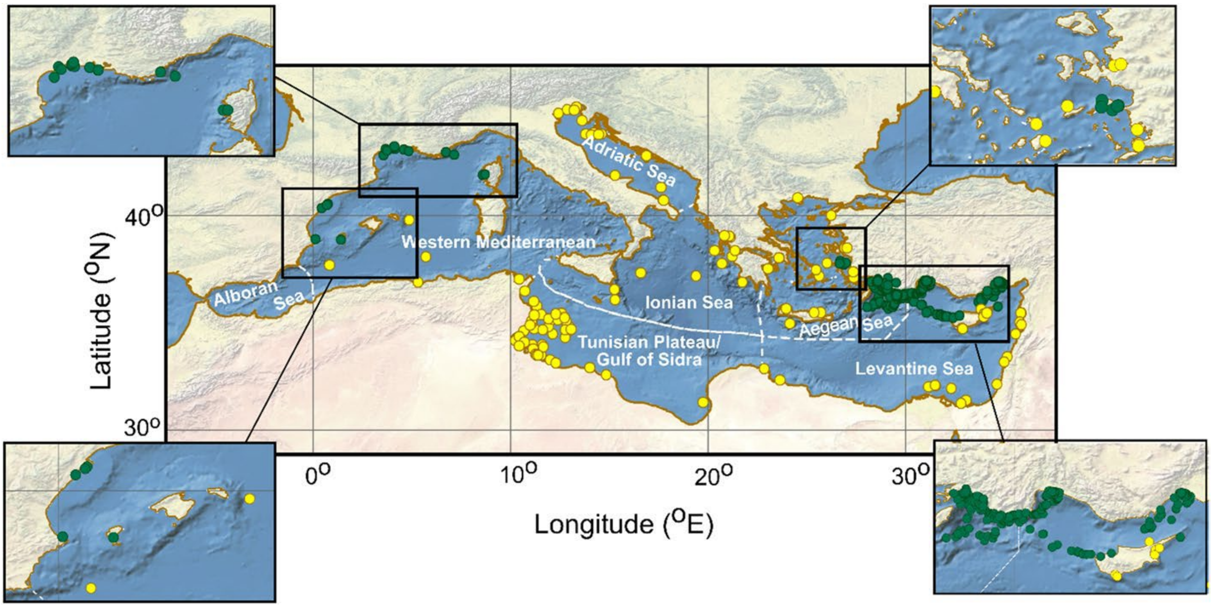

Figure 14. Locations (yellow points) that represent foraging adult loggerhead sea turtles, Caretta caretta, across the Mediterranean Sea, derived from the available published satellite tracked data, and used as input to the models that developed for delineating the distribution of foraging grounds under current climatic conditions (1991–2020). Green points represent locations of foraging adult loggerheads, derived from additional, unpublished sources, that were used to validate the developed distribution map. Marine ecoregions (sensu Spalding et al. 2007) comprising the Mediterranean Sea are delineated by white dashed lines

Data were gathered based on different methods, e.g., on boat observations, bycatch incidents, tracked turtles. No stranded individuals were used in the analyses. In cases that it was not clear whether sea turtles were adults or not, we considered as adults those with curve carapace length larger than 75 cm. In total, we were able to use geographic locations for: (a) five adult individuals at the Spanish coasts and the Balearic Islands reported from incidental bycatch over the period from 2012 to 2019, (b) 15 adults detected along French coasts from 1988 to 2017 by the French network of observers on Mediterranean sea turtles (Réseau Tortues Marines de Méditerranée Française—RTMMF), (c) five individuals reported though boat surveys around Samos Island in Greece, Northeastern Aegean Sea, from 2017 to 2019, and (d) occurrence data from six animals at the Southern Aegean/Mediterranean coasts of Turkey collected from 2011 to 2017 with satellite devices deployed by the Sea Turtle Research, Rescue and Rehabilitation Center (DEKAMER). For each one of these datasets we determined the extent of core areas of habitat use by applying a kernel density estimate (KDE) approach. To estimate the optimized bandwidth (i.e., search radius distance), we used the least square cross validation method. A 0.083° × 0.083° cell size was applied for the KDE analysis, to ensure agreement with the resolution of the environmental data used (see “Environmental variables” section). The volume of the KDE distribution was determined at 50%, which has been applied for the same purpose by similar studies (e.g., Snape et al. 2016). The analysis was performed, using the adehabitatHR package (Calenge 2006) in R. To examine the ability of the model to accurately predict the locations of foraging habitats at areas where no published tracking data were available but for which our field data justified their importance, we intersected the outlined polygons, representative of habitat use for each region, with the developed distribution map of foraging grounds. Next, we estimated the proportion of foraging area that was enclosed within their boundaries.

2.2.3 Results and Conclusions

We found that about 15% of the Mediterranean basin encompasses conditions which were predicted to be suitable for hosting foraging grounds of adult loggerhead sea turtles. The developed ensemble model was considered to exhibit a very good predictive capacity in generating a distribution map of foraging grounds based on the considered metrics (i.e., AUC = 0.93, TSS = 0.81), with all distinct modeling algorithms identifying the areas of high suitability with some differentiations at local scales (Figure 15). The foraging grounds were mainly hosted within the neritic zone (about 10% of the Mediterranean basin, Figure 16), with most of the suitable sites located at the Central and Eastern Mediterranean. The Adriatic Sea and the Tunisian Plateau, at the Central Mediterranean, hosted the largest proportion of foraging area throughout the basin (22% and 31.1% of the total foraging area, respectively).

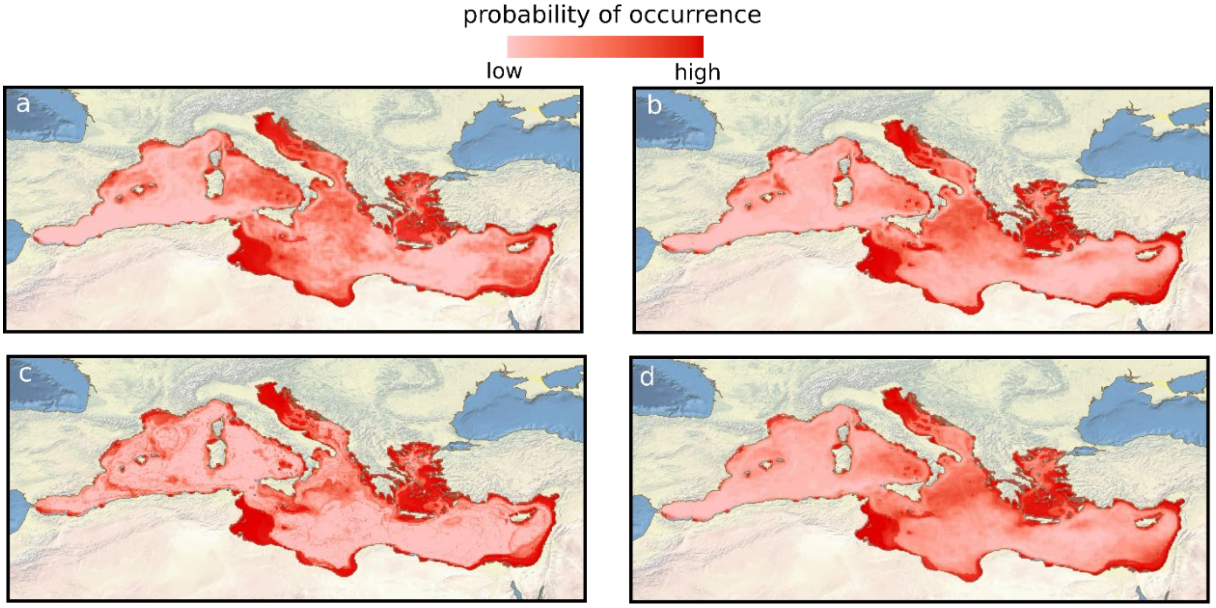

Figure 15. The distribution patterns of foraging areas for adult loggerhead sea turtles across the Mediterranean region, based on the different modelling algorithms: a) Generalized Linear Models, b) Generalized Additive Models, c) Random Forest and d) Multivariate Adaptive Regression Spline.

The Levantine Sea (15.40% of the total area) and parts of the Aegean Sea (17.19% of the total area) were listed among the areas of the Eastern Mediterranean covered by critical foraging grounds for loggerhead turtles, with lower coverages detected at the Ionian Sea (4.91% of the total foraging area). In the Western Mediterranean, foraging grounds were mainly identified along the French and Spanish coasts (8.84% of the total foraging area), with Alboran Sea hosting a very small proportion (0.62% of the total foraging area). The oceanic part of the foraging grounds was found to cover 5.79% of the Mediterranean Sea (~ 144,750 km2), with these sites being located mainly at the central and eastern parts of the basin, adjacent to the neritic habitat.

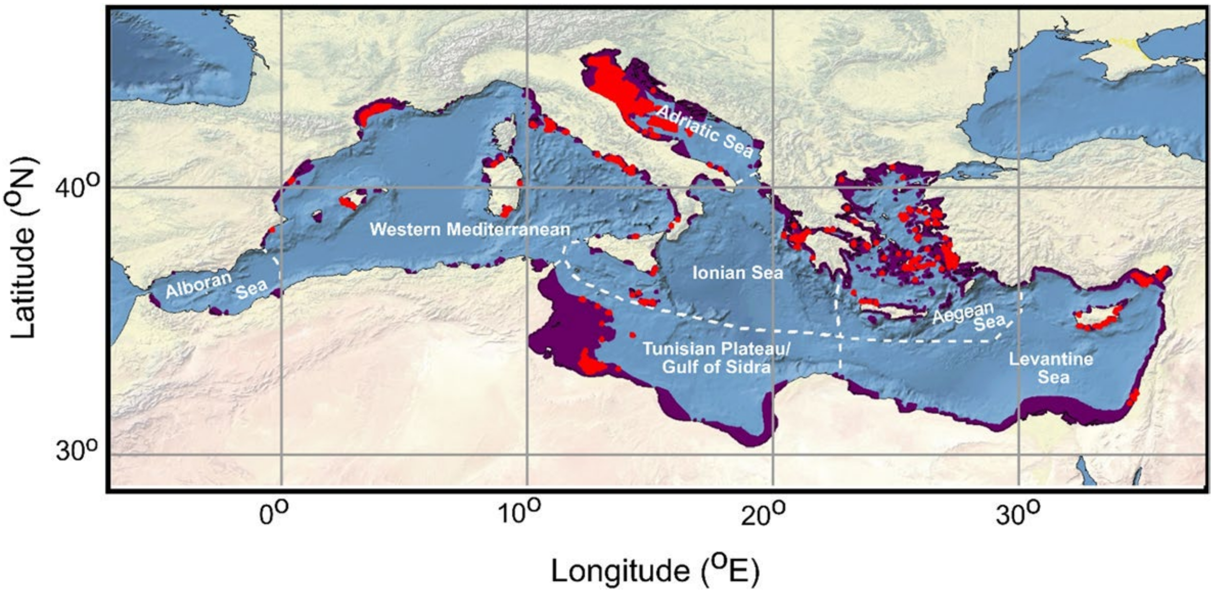

Figure 16. The distribution of neritic foraging grounds (purple polygons) of adult loggerhead sea turtles, Caretta caretta across the Mediterranean Sea and hotspots of high/very high cumulative risk (red polygons) within the boundaries of the foraging areas, derived from different human-related threats (longlines, trawlers, fixed nets and purse seines fisheries, marine litter accumulation). Marine ecoregions (sensu Spalding et al. 2007) comprising the Mediterranean Sea are delineated by white dashed lines

For several of the sites that were identified as potential foraging grounds, there are no published evidence to support their existence; still, when comparing the foraging map derived from the ensemble model with the core areas of habitat use generated by field data, it was revealed that the predicted suitable sites indeed represented areas inhabited by adult loggerheads. The core polygon of habitat use in the Southern Aegean/Mediterranean coasts of Turkey were found to encompass within its boundaries a large portion (86.3%) of the foraging grounds derived from the model while the corresponding area in the Northeastern Aegean Sea entirely enclosed foraging grounds. An important proportion of the outlined foraging habitat was also detected within the core area of use at the French and the Spanish coasts (75% and 78.6%, respectively).

CONCLUSIONS

The approach developed here, by applying modeling techniques and validating their outputs with independent field data, allowed us to obtain a better view on the key foraging sites for adult loggerheads across the Mediterranean. Assessing the exposure of these habitats to the combined risk of different human-related threats, we provided spatially explicit information for determining hotspots of particular conservation concern. Conservationists and practitioners could build upon this knowledge to determine site-specific needs and direct targeted and effective management and monitoring efforts.

Our findings provided a comprehensive overview on the distribution of foraging grounds for adult loggerheads sea turtles in the Mediterranean Sea, highlighting the relative importance of neritic areas at the central (Adriatic, Ionian Sea and the Tunisian Plateau) and the eastern (Aegean and Levantine Sea) part of the Mediterranean Sea, including previously recognized sites known to be frequented by adult loggerheads (Haywood et al. 2020; Luschi and Casale 2014; Schofield et al. 2013; Zbinden et al. 2008). In addition, our analysis revealed important foraging areas at the western part of the basin. Even though there is a scarcity of satellite telemetry data for adult loggerheads in the Western Mediterranean (only few adults satellite tracked in the Central and Eastern Mediterranean have been detected to forage in the western part of basin; Haywood et al. 2020; Schofield et al. 2013), evidence suggest that animals inhabit these areas but probably at relatively lower abundance (e.g., French coasts; Darmon et al. 2017). The presence of foraging adults at this region was also supported by our field data, emphasizing the necessity to safeguard these habitats which might represent potentially valuable areas for the viability of the Mediterranean loggerhead population.

2.3 Modelling species detectability using bycatch data

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2.3.1 Context and case study

Unintended catch of non-target species ("bycatch") has long been identified as one of the most common anthropogenic threat causing at-sea mortality and driving population declines of several protected, endangered, and threatened species (PETs) (Read et al. 2006; Oliver et al. 2015; Dias et al. 2019). Fisheries-related bycatch mortality has become a major conservation concern specially for long-lived and highly migratory species causing several ecological effects, either directly reducing species populations or indirectly changing dynamics of oceans systems (Lewison et al. 2014; McCauley et al. 2015). On one hand, an increase in adult mortality of longlived species (i.e. those with slow growth, late maturation, and low fecundity) could cause a population decline over short timescale (i.e. decades; Campioni et al. 2020), while, on the other, highly mobile species perform wide-ranging movements frequently encountering multiple fisheries, and often aggregatingin high biological production areas (Schoombie et al. 2018; Yurkowski et al. 2019) coinciding with high fishing activity zones (Zhou et al. 2019).

Artisanal fisheries, which compose a large majority of the world's fleets (Pauly 2006), tend to operate in regions featuring high productivity, and overlapping with megafauna high-use areas. While the overall ecological impact of artisanal fishing might have similar effects to those of industrial fishing (Peckham et al. 2007; Alfaro-Shigueto et al. 2010), artisanal fisheries are generally understudied and often unregulated, creating a knowledge gap representing a major challenge to sustainable fisheries management and the conservation of PETs (Fabio et al. 2016).

Spatio-temporal abundance patterns of great shearwater were obtained by developing spatial abundance models, which integrates information of different ecosystem components collected during integrated ecosystem surveys.

2.3.2 Methodology

Data acquisition

Seabird at-sea observations, biomass estimates of pelagic prey species, and physical data were gathered during the JUVENA oceanographic surveys over the period 2013–2019. JUVENA surveys take place yearly during September covering offshore and shelf-slope areas of the BoB with the aim of acoustically assessing the biomass of the European anchovy (*Engraulis encrasicolus)* and other small pelagic fishes (Boyra et al. 2013). The sampling strategy is based on parallel transects arranged perpendicular to the coast, regularly spaced at 15 nautical miles (nmi). Data were collected by two research vessels simultaneously covering the area potentially occupied by the European anchovy.

Seabird data

Great shearwaters at-sea observations were collected by two observers following visual line-transect protocols (Buckland et al. 2001) along acoustic transects when the R/V was navigating at constant heading and speed during daytime. For each species sighting, observers recorded detection distance, and the angle with respect to the track line based on an angle meter. At the beginning of each observation period (leg), observers recorded the environmental conditions that could affect sightings (i.e. Beaufort Sea state, swell height, and direction, wind speed and direction, cloud coverage, visibility, sun glare, and an overall subjective assessment of detection conditions of the sightings). Observation effort was georeferenced every minute with the vessel's GPS (García-Barón et al. 2019).

Environmental and prey data

Three different types of variables were considered: prey, physical, and physiographic variables. Biomass of juvenile and adult European anchovy (hereafter, ANEJ and ANEA, respectively) and European pilchardus (Sardina pilchardus; hereafter, PIL) were selected as prey variables in accordance with previous spatial abundance studies of great shearwater performed in the area (Louzao et al. 2019). Spatial biomass patterns of ANEJ, ANEA, and PIL at different depths were obtained based on trawl-acoustic methodologies (Simmonds and MacLennan 2005). Original biomass values of ANEJ, ANEA, and PIL were laid over a grid of 0.1◦ spatial resolution and totaled for each cell. Finally, small pelagic fish biomass estimations were obtained using a combination of universal kriging and an automatic variogram fitting procedure using the Rpackage automap (Stelzenmüller et al. 2005 & 2009; Louzao et al. 2019). Six physical variables were used to model seabird's spatial density, surface temperature (TEM; ◦C) and its spatial gradient (TEMg), salinity (SAL; psu), geostrophic velocity (GVel; ms−1), the depth of maximum temperature gradient (DTG; m), and the maximum temperature gradient (MTG; ◦Cm−1). Spatial fields of physical variables were solved from vertical depth profiles (from surface to a depth of 200 m) of TEM and SAL obtained during CTD casts. Further methodological details about prey and physical variables can be found in supplementary material. Data spatial resolution and correlation scales used for the interpolation allowed to solve the main mesoscale features in the area, including eddies and frontal areas.

Additionally, four physiographic variables were selected: bathymetry (BAT; m) and its spatial gradient (BATg; dimensionless), closest distance to the coastline (DistCO; km), and closest distance to the shelf-break (measured as the distance to the 200 m isobath; DistSB; km). The four physiographic variables were directly obtained or calculated at the spatial scale of the standard grid from ETOPO1 (Amante and Eakins 2009). Louzao et al. (2019) demonstrated that the 3D environment of the great shearwater in the BoB was better explained by the shallowest physical and trophic conditions. Consequently, prey variables represented the sum of their biomass from 5 to 15m depth and the physical variables TEM, SAL, and GVel were described by the shallowest depth available, that is, 10m depth. The remaining physical variables (DTG, MTG, and TEMg) and the physiographic variables were not modified by any vertical criteria.

Artisanal tuna fisheries data

Information on artisanal tuna fishing activity during the 2013–2019 period was obtained from the VMS and logbooks data provided by the Spanish General Secretary of Fisheries. Whilst the VMS data provide information on the identity, position, speed, and heading of the vessels (European Commission 2011), the logbooks report the fishing gear used and the effort at an aggregated spatial scale. Thus, these data enable the analyses of the spatial and temporal distribution of disaggregated fishing activity to distinguish between metiers and fishing and non-fishing effort (Bastardie et al. 2010). Finally, data on great shearwater bycatch events were obtained from an observer monitoring programme implemented by AZTI since 2016 and 2017 in LHP and LTL, respectively, to monitor discards and interaction with PETs during the fishing season.

Density surface modelling - Species detectability based on environmental conditions

Species detectability was modelled using Conventional and Multiple-Covariate Distance Sampling (CDS and MCDS; Buckland et al. 2001; Marques and Buckland 2004), the latter allowing to consider the effect of the environmental conditions during the observation effort. Detection functions were estimated pooling great shearwater sightings from the period 2013–2019 (Figure 17). Only sightings with a Beaufort Sea-state ≤5, wave height ≤2m, and overall medium and good visibility conditions were used to fit the detection functions (García-Barón et al. 2019). Perpendicular distances were truncated to exclude sightings beyond 600m (around 5% of the individuals detected at the longest distances; Buckland et al. 2001), and sightings of individuals attracted to the ship or associated with human activities (individuals following the R/V or scavenging on fishing discards) were excluded from further analyses to avoid density overestimation (Authier et al. 2018). Covariates considered in MCDS were only those descriptors related to the effort (Astarloa et al. 2021), including beaufort sea-state, swell height categorized, cloud coverage, visibility, overall detection conditions, and year.

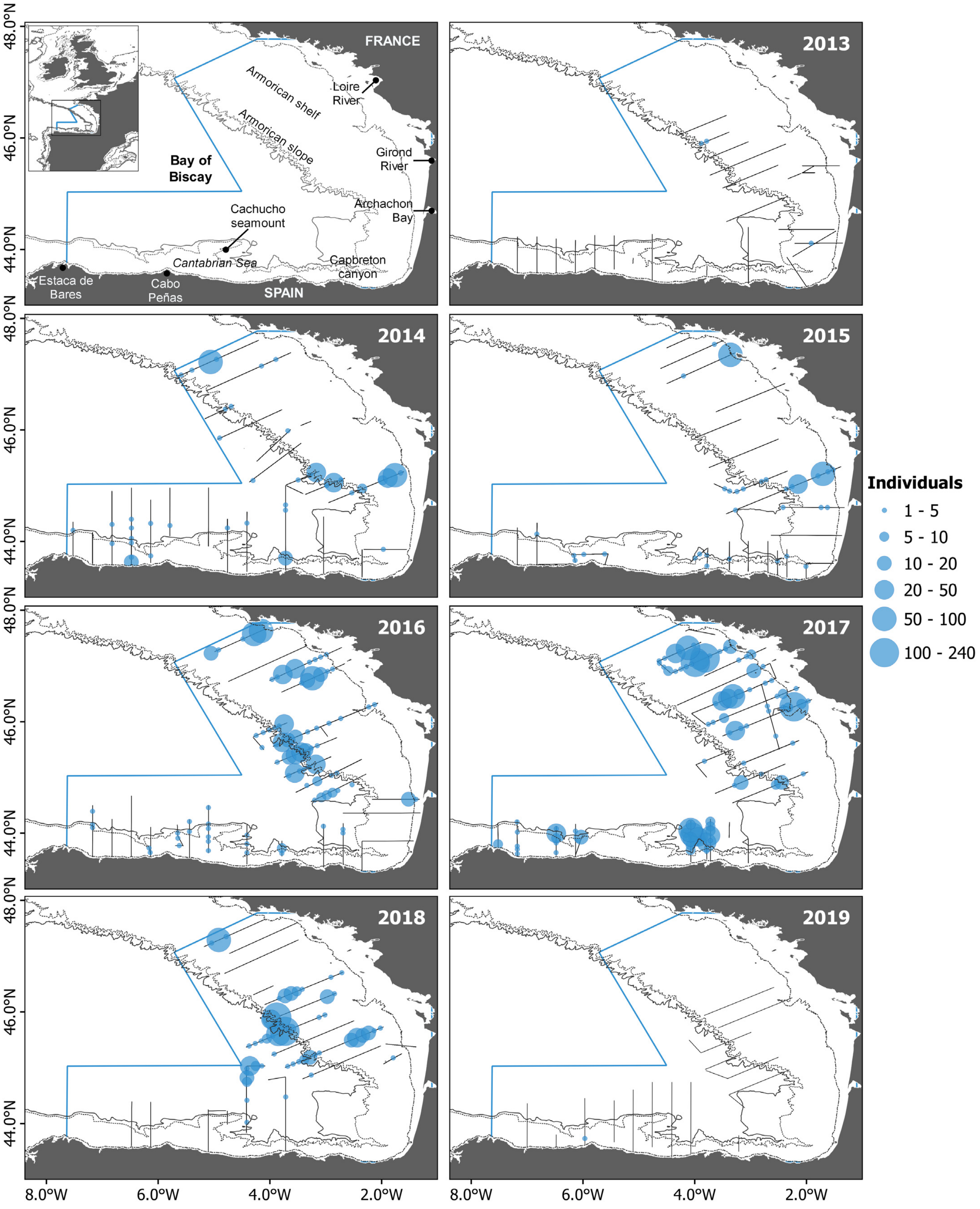


Figure 17: Maps showing the study area (blue polygon), the line-transect sampling and the great shearwater sightings by year during JUVENA surveys (2013–2019). Bathymetry contours indicate the 50m isobath and the edge of the continental shelf. Geographical references mentioned in the text are shown in the first map.

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 Cramer–von Mises goodness-of-fit tests (Thomas et al. 2010) using the Rpackage mrds (Laake et al. 2015). The final detection function was selected based on parsimony (similar explicative power but fewer parameters; Arnold 2010), when the two best detection functions did not show a difference in AIC >2 (i.e. AIC <2). The effective strip half-width (ESW) was calculated as the perpendicular distance in which the missing detections at smaller distances were equal to the recorded detections at bigger distances. In the case of the MCDS detection functions, the ESW was calculated for each level of the covariate.

Model fitting

Surveyed legs were subdivided into 10 km segments with homogeneous sighting conditions to limit the variability of the environmental characteristics within segments (García-Barón et al. 2020). To fit the models on the best quality data, segments with a Beaufort Sea-state ≤5, wave height ≤2m, and overall medium to good visibility conditions were used for further analysis. For every segment, we summed up the group size of the sightings and the centroid of each segment was used to assign the environmental data to the segments. Density surface models (DSMs) were fitted using generalized additive models (GAMs) to identify the most important environmental covariates explaining great shearwater density patterns. After checking for alternative distribution families (e.g. Tweedie, zero-inflated Poisson), we selected a negative binomial distribution, and a log-link function to account for overdispersion. Flexible smoothing splines were constrained to a maximum of two degrees of freedom (k = 3) to avoid over-fitting of the data, and a maximum number of four covariates were used to avoid over complexifying the models (Lambert et al. 2017). The effective sampled area of each segment calculated as the length of the segment multiplied by twice the ESW was included as an offset. Prior to modelling and to avoid co-linearity, we calculated the pairwise Spearman-rank correlation coefficients (r) and did not include correlated variables (e.g. with r ≥ |0.5|; Dormann et al. 2013). Thus, we selected the non-correlated predictors by selecting the variable yielding the lowest AIC value corrected for small sample sizes (AICc) from univariate models of the two predictors. GAMs were implemented following the Information theoretic approach using the dredge function of the R-package MuMIn (Barton 2016). We evaluated all the possible models by assessing their relative support compared with the others based on the AICc and the Akaike weight (ωi; normalized relative likelihoods that model i is the best model) (Burnham and Anderson 2002). Models were ranked based on their AICc and, if no clear best model was identified (ωi > 0.95), a model averaging approach was used (Burnham and Anderson 2002). Model averaging was performed using a 95% confidence set of models where the cumulative sum of ωi was ≥ 0.95, starting with the model with the highest ωi (Johnson and Omland 2004). This 95% confidence set of models was used to obtain averaged coefficients and variance estimator. The relative importance of the explanatory variables was calculated as the sum of the ωi of the models in which the covariate was included and the response plots were constructed based on averaged coefficient of the 95% confidence set. Finally, selected models included within the 95% confidence set were used to predict the spatial density of great shearwater for every September. The density estimates presented here were uncorrected for any detection bias.

VMS and logbook data processing

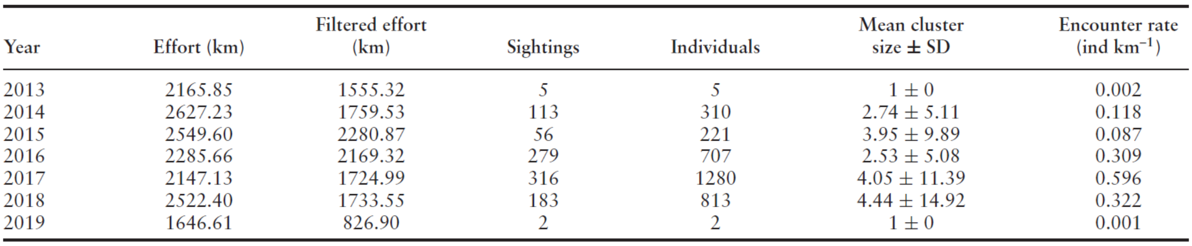
VMS and logbook data were first cleaned removing (i) records with invalid positions (e.g. records located on land or in ports), (ii) records associated with high speeds (>20 knots) and heading outside compass range, (iii) records duplicated or pseudoduplicated (<5min) records, and (iv) records when arrival date occurs before departure date. Second, VMS and logbook data were linked removing unlinked records using the R-package vmstools (Hintzen et al. 2021). Third, the artisanal tuna fishery was identified as those trips where >80% of the catches were tuna species according with the logbook data. Then, the corresponding metier was assigned based on the SpanishNational Fleet Census modalities. However, no vessels are registered as LHP or LTL since the same vessel changes the gear through the different fishing seasons and the census only registers one main fishing gear. Thus, those vessels with >80% of the catches being tuna species and registered on the Spanish National Fleet Census under the purse seiners modality were identified as LHP and the rest of the vessels registered in other modalities as LTL. Fourth, we used a vessel speed range to discriminate between fishing and non-fishing activity. Thus, all the records with speeds included within the range of 6–7 knots for LTL and of 0–3 knots for LHP were considered fishing effort (Fernandes et al. 2019). The fishing effort in hours obtained for each metier, month, and year were overlaid over a regular grid of 0.1 × 0.1◦ to obtain the same spatial resolution as great shearwater spatial density predictions. Finally, we explored the fishing effort performed by a metier during the time-series 2013–2019 to select those months when the effort was higher.

2.3.3 Results and Conclusions

Spatio-temporal patterns of seabird abundance

A total of 15,944 km was surveyed during the period 2013–2019 of which 12,050 surveyed km remained after filtering for weather conditions. A global number of 954 sightings of great shearwaters were recorded with a total of 3338 individuals observed (Table 4). Then, detection functions were developed based on 954 great shearwater sightings. The hazard-rate function with no adjustment terms, including year and swell height categorized as covariates, was selected as the best-fitting detection function based on parsimony grounds from which the corresponding ESW was 193.44±75 m.

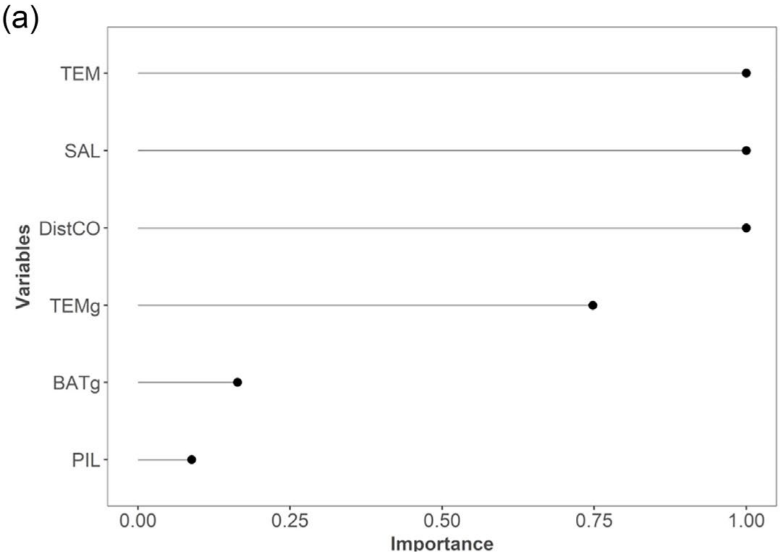
Table 4. Effort, filtered effort (i.e. Beaufort Sea-state ≤5, wave height ≤2m, and medium to good general conditions), number of sightings, number of individuals, mean group size of the sightings ± standard deviation, and encounter rate of great shearwaters during JUVENA surveys.



Year	Effort (km)	Filtered effort (km)	Sightings	Individuals	Mean cluster size ± SD	Encounter rate (ind km^{-1})
2013	2165.85	1555.32	5	5	1 ± 0	0.002
2014	2627.23	1759.53	113	310	2.74 ± 5.11	0.118
2015	2549.60	2280.87	56	221	3.95 ± 9.89	0.087
2016	2285.66	2169.32	279	707	2.53 ± 5.08	0.309
2017	2147.13	1724.99	316	1280	4.05 ± 11.39	0.596
2018	2522.40	1733.55	183	813	4.44 ± 14.92	0.322
2019	1646.61	826.90	2	2	1 ± 0	0.001

A total of 1306 segments of which 308 included 3338 individuals from 954 sightings were used to fit DSMs. Among highly correlated variables, BAT and DistSB were the least explanatory variables (r ≥|0.5| and higher AICc in univariate models) and they were removed. The number of models combined to achieve the 95% confidence set was 3 out of a total of 385 for which the explained deviances ranged between 14.7 and 15.2%. The main variables driving the spatial abundance patterns of the species were DistCO, SAL, TEM, and TEMg (Figure 18), whilst BATg and PIL were the least important variables within the 95% confidence set. ANEJ, ANEA, DTG, MTG, and GVel were not included in any of the models within the 95% confidence set. Densities of great shearwater increased as DistCO increase, with maximum values at ~125km from the coast, whilst warmer TEM influenced the abundance negatively driving the higher abundances over the northern French continental shelf. Seabird densities also showed a quadratic relationship with SAL, indicating a preference for medium to high values (>35 psu) and a preference for lower values of TEMg, inducing higher densities far from the coast.

(a)



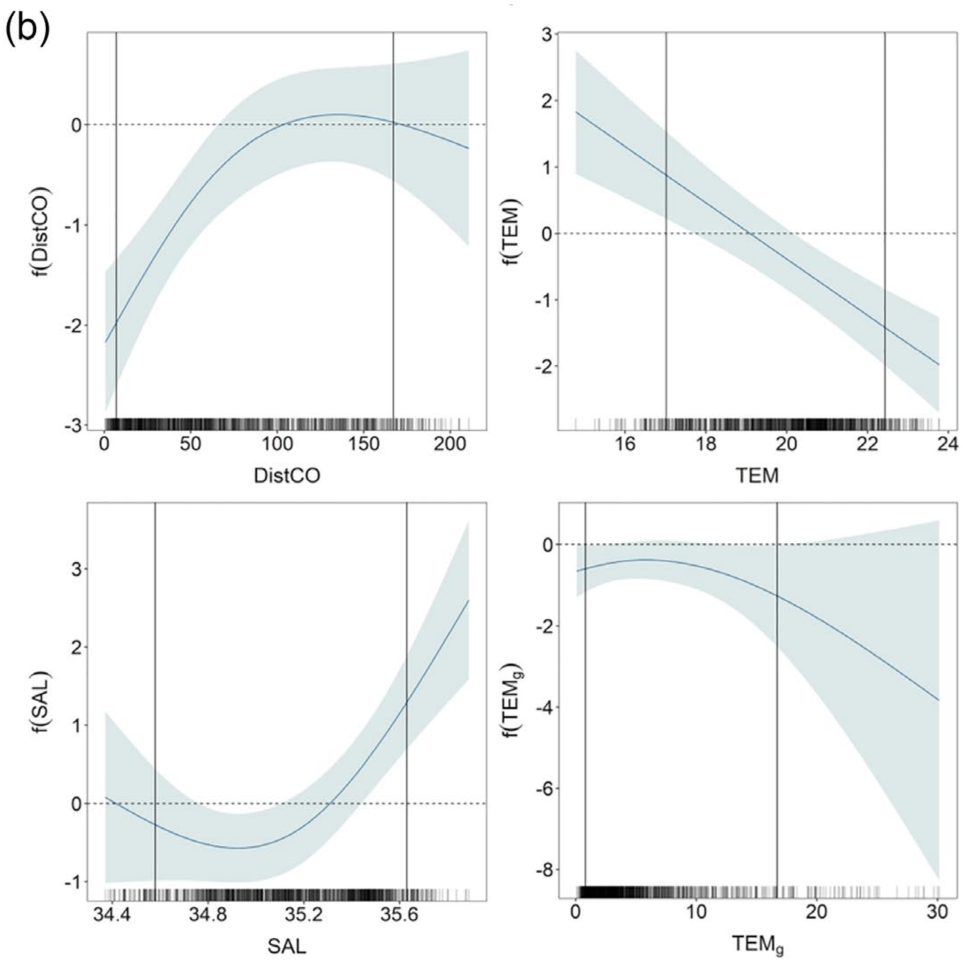


Figure 18. Main environmental variables driving great shearwater abundance patterns characterized by means of (a) relative variable importance and (b) smoothed fits of the main covariates where the x-axis shows the predictor variable values, the y-axis represents the centred smooth term contribution to the model on the scale of the linear predictor and the two vertical black lines indicate the 5 and 95% quantiles interval. Interpretation of relationships outside this range should be avoided, since the smooth splines may not be reliable. Blue shaded area indicates approximate 95% confidence bounds. TEM: temperature; SAL: salinity; DistCO: closest distance to the coastline; TEMg: sea surface temperature gradient; BATg: depth spatial gradient; and PIL: biomass of European pilchard.

Although the highest density areas showed a high inter-annual variability (Figure 19), the area over the Armorican slope supported the highest densities most of the years (but not 2015). Furthermore, the southern sector of the BoB also showed high densities, mainly located over the Cachucho and the area between Estaca de Bares and Cabo Peñas. Less dense areas were located over the southern French and eastern Spanish continental shelves (Figure 19).

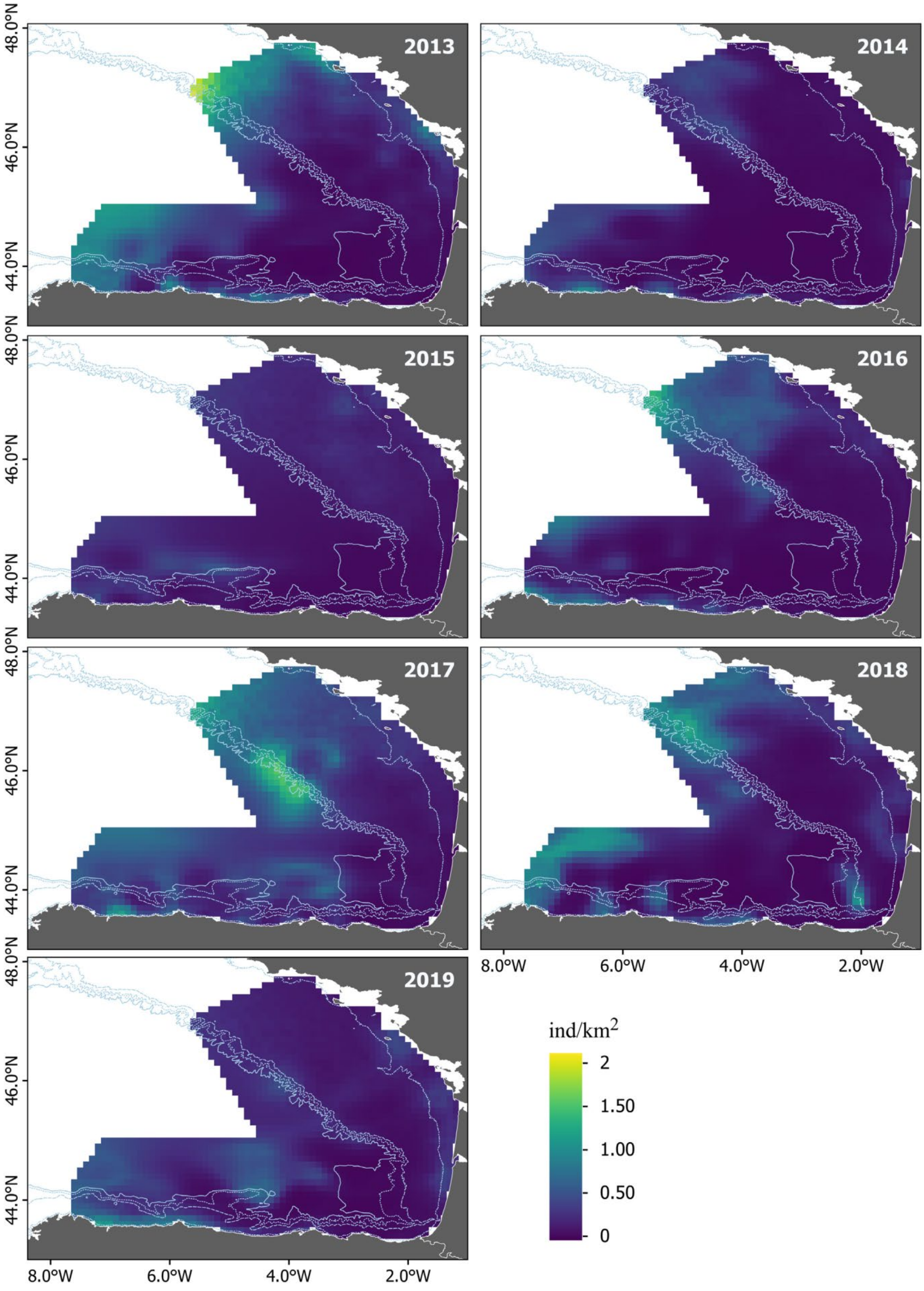


Figure 19. Great shearwater spatial density predictions in the Bay of Biscay during September (2013–2019) surveys. Bathymetry contours indicate the 50m isobath and the edge of the continental shelf.

CONCLUSIONS

The spatial density of great shearwaters was mainly driven by the distance to the coast, highlighting offshore waters as the preferred habitat for the species. In accordance with Pettex et al. (2017) and Louzao et al. (2019), the northern Armorican slope in French waters and offshore waters of the Spanish sector supported the highest densities of the species. Along the shelf edge (e.g. Armorican slope), tides generate internalwaves that propagate both on- and off-shelf (Pairaud et al. 2010), which seems to be responsible for significant mixing and nutrient upwelling at the shelf-break, where they have their maximum intensity, and thus their greatest impact on primary production (Lavín et al. 2006). Consequently, these areas aggregate small prey species (Scott et al. 2010) being highly relevant for top predator species (García-Barón et al. 2019; Pettex et al. 2017). In addition, the results showed high densities of great shearwater over the western Cantabrian coastal area. This great shearwater aggregation may be explained by the easterly winds favouring both the arrival of great shearwaters from their breeding areas (northwest Atlantic) to the BoB (Louzao et al. 2015) and a coastal upwelling along the Cantabrian coast, stronger in the western area during spring–summer (Alvarez et al. 2010). The latter enhances the aggregation of large biomass of small pelagic fish (Astarloa et al. 2019), representing a potential feeding ground for great shearwaters.

Fishing activity performed by the Spanish artisanal tuna fishery was mainly located over the outer French (Armorican slope) and Spanish continental shelfs and adjacent waters, the Cantabrian Sea, and offshore waters of the BoB. Although the effort showed little inter annual variability over the study period, during 2014 the fishing activity drastically declined. That year, the albacore tuna shifted north-westward, driving the fleet outside the study area in search of more productive fishing grounds (Chust et al. 2019).

3. Assessing ocean warming impacts

3.1 Projected shifts in sea turtles foraging habitats and identification of critical sites for conservation

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3.1.1 Context and case study

The identification of important areas of charismatic marine megafauna is a primary and essential step to enhance our conservation capacity (Hays et al. 2019). At the present time, even though the ability to map the current distribution of species could greatly buttress management initiatives, additional challenges on the spatial delineation of such areas arise when considering the potential impacts of CC (Gissi et al. 2019). Habitat-shifts and/or important habitat loss have been widely documented for marine megafauna, such as for whales (Learmonth et al. 2006), shark species (Birkmanis et al. 2020) and sea turtles (Willis-Norton et al. 2015). Yet, several uncertainties still exist on where and how CC could affect such highly migratory species at the different areas they inhabit during their life cycle (Albouy et al. 2020; Payne et al. 2016). Thus, the delineation of important areas under climate change scenarios outlines a key research and conservation priority for current and future species' protection.

Having a complex life cycle and a highly migratory behavior, sea turtles use various and often distinct habitats for breeding, development and foraging (Bolten et al. 2003). Foraging habitats are critical for population persistence, in order for individuals to restore their energy reserves, enhance population growth and facilitate successful breeding migrations. Yet, the identification of important foraging habitats for different life cycle stages of the species remains unclear. Sea turtles embrace a range of foraging strategies and their diet includes a variety of prey resources. Along with that, they could be subjected to passive dispersal likely to direct even individuals that were born at the same site to different foraging grounds (Hays et al. 2010). Yet, mature animals that breed at a given rookery could use distinct and very distant foraging sites (Schofield et al. 2013).

Few efforts have been made on the delineation of important areas for sea turtles within the marine realm, e.g., in the Arabian region (Pilcher et al. 2014) and the Caribbean for hawksbill sea turtles (Nivière et al. 2018) and the Indian Ocean for green sea turtles (Hays et al. 2014). However, these studies have been conducted at a small spatial scale, covering limited areas in comparison to regional management units (i.e., spatially defined areas which host populations of sea turtles with distinct genetic, demographic and behavioral characteristics), which have been proposed as a valuable scheme for prioritizing the conservation and management of sea turtles (Wallace et al. 2010). In the Mediterranean, previous studies have undertaken valuable efforts to delineate crucial foraging habitats for sea turtles, providing a general overview based on literature synthesis (e.g., (Margaritoulis et al. 2003; Hawkes et al. 2009)) or focusing on distinct foraging grounds (e.g., through genetic analyses, (Clusa et al. 2014)). While there is consensus that climate change could alter the distribution of sea turtles (Poloczanska et al. 2009; Hawkes et al. 2009), studies to assess whether and how climate change projections will alter the distribution of potential foraging habitats at a broad scale are rather limited (Payne et al. 2016), but see (Patel et al. 2016; Maffucci et al. 2016) challenging the effectiveness of current conservation measures.

Here, we aimed to spatially delineate important foraging habitats for loggerhead sea turtles (*Caretta caretta*) in the Mediterranean basin. The Mediterranean loggerheads are subjected to multiple human-related threats at sea with the need for their protection being highlighted (Rees and Margaritoulis 2013). We compiled a digital database of all existing published data of foraging individuals based on satellite telemetry conducted across the Mediterranean Sea. Based on this information, we developed climatic niche models to predict the distribution of foraging grounds for juvenile and adult life stages under current conditions and make projections based on future conditions. Our approach, recognizing life-cycle specific and climatically stable habitats of sea turtles, could offer a new understanding on spatial configuration of the species' habitats and useful insights for future conservation planning that takes under consideration the impacts of climate change.

3.1.2 Methodology

To determine important foraging areas for loggerhead sea turtles in the Mediterranean, the applied methodology included three key steps: i) collection and digitization of satellite tracked data on the location of juvenile and adult foraging loggerhead sea turtles to compile a digital database on regional information, ii) extraction of sea surface temperature (SST) data and construction of bioclimatic variables and iii) development of climatic niche models for the different life stages.

Species data

To collect presence data of juvenile loggerhead sea turtles in the Mediterranean, we conducted a literature review in relevant scientific papers and grey literature (e.g., technical reports, conference proceedings, book chapters), using the search engine of Google Scholar. The search strategy included the terms: ("marine turtle*" OR "sea turtle*") AND "Mediterranean" AND ("subadult*" OR "juvenile*" OR "immature*"). A total of 248 sources of reference for juvenile satellite tracked sea turtles were identified (by July 2020) and reviewed. We included in the analysis only sources that matched the following criteria: i) the geographical extent of the data provided by the sources should be enclosed within the Mediterranean Sea, ii) data should have been obtained through satellite telemetry (as a more accurate and precise form of spatial occurrence information; (Hijmans et al. 2011), iii) spatial information should be provided in the form of a map or coordinates and iv) sea turtles that were caught should have been alive and healthy so as to maximize the possibility that they actually used the area for foraging and minimize the possibility of them got carried away passively due to wounding. In the case of a source that did not clearly mention the tracked individuals as juveniles, we used a threshold value based on the reported curved carapace length (CCL), for the selection of presence data. Individuals with a CCL equal or less than 66.5 cm were defined as juveniles, representing the minimum of the range of means of the size of loggerhead sea turtles found nesting in the Mediterranean (Casale et al. 2018). The size of individuals varied from 26cm to 66.5 cm CCL. Individuals above 40 cm CCL are considered as subadults, being able to swim much more independently of sea currents (Casale et al.

2018). However, due to unclear distinctions and complexity among different life stages, we included individuals both above and below 40cm CCL so as to avoid setting arbitrary thresholds. Therefore, the search ended up in 10 source papers [list of papers; Supp. Methods], including data for 51 juvenile loggerhead sea turtles.

The collected tracks of juvenile sea turtles were georeferenced and digitized using ArcGIS 10.1 (E.S.R.I., 2011). As a first step, the whole track line was digitized. Next, to convert the line to presence points, the digitized route was overlaid with a grid of cell size 0.0625° x 0.0625 ° (approximately 7km x 7km), so as to be consistent with the resolution of climatic data (see section 2.2). If the tracked line passed by a cell of the grid, then a presence point was assigned to the centroid of this cell. Thus, we resulted in 3105 presence points for juvenile sea turtles.

In the case of adult loggerhead sea turtles, we used presence points derived from 126 foraging individuals, based on satellite tracked data, extracted by a literature review following similar procedure and rules as for the juveniles. A total of 1300 sources of reference for satellite tracked sea turtles in the Mediterranean were identified and reviewed. The extracted locations of foraging adult loggerheads were georeferenced and digitized. For data on post- or pre-nesting migration, the end or start point of the route that each tracked individual had followed to reach the foraging area was considered as a presence point. When many satellite telemetry points were given for a tracked animal that exhibited foraging behavior, we determined as presence the centroid of the 50% data distribution isopleth derived from kernel density estimations. When a certain point was indicated as the location of a foraging turtle, this information was extracted.

Climatic data

When conducting the present work, the FutureMARES climatic projections were not yet available (but see chapter 3.2), so climatic data on SST for the Mediterranean region were obtained from the Centro Euro-Mediterraneo sui Cambiamenti Climatici (CMCC) (Cavicchia et al. 2015). The dataset contained historical and projected mean daily SST data covering the Mediterranean Sea for the period from 1950 to 2100, at a 0.0625° spatial resolution. These climatic projections were used because FutureMares projections were not . To define present climatic conditions, we used SST data for the period of 1991 – 2020. For future climatic conditions, we used SST data, covering the period of 2051 – 2080, based on projections of the Fifth Assessment Report of the Intergovernmental Panel on Climate Change and the RCP 8.5 emission scenario, which was used as a worst-case scenario to assess the risk of climate change.

As for juveniles, SST during the whole year was used for the construction of the predictor variables, as their activity in foraging areas is year-round (Bolten et al. 2003; Hawkes et al. 2009). On the contrary, adults use foraging areas during all year, except for their reproduction and post- and pre-migration phase (Rees and Margaritoulis 2013). So, to define the most representative foraging period, we used SST data from September (i.e., after the completion of the nesting season) to March (i.e., before the beginning of pre-nesting migration).

Based on SST data, we constructed bioclimatic variables (sensu (Hijmans et al. 2011)) so as for climate data to have an ecological meaning for sea turtles, whose viability and activities are linked to temperature (Davenport 1997; Mrosovsky 1980). Bioclimatic variables were constructed in R studio (version 4.0.0), using ncdf4 (Etten and Hijmans 2012), raster (Pierce 2019) and dismo packages

(Chambault et al. 2021). We used the nine bioclimatic variables relevant to temperature: Mean annual temperature, Mean diurnal range, Isothermality, Temperature seasonality, Max temperature of warmest month, Min temperature of coldest month, Temperature annual range, Mean temperature of warmest quarter and Mean temperature of coldest quarter. Previous studies that used climatic niche models for assessing sea turtle distribution have utilized a number of bioclimatic variables providing no suggestion on an explicit use of specific ones (Chambault et al. 2021; Pikesley et al. 2015). Therefore, here we applied a principal component analysis (PCA) to produce a number of new predictors that allowed to capture the grand majority of the variance of the bioclimatic variables (Martorano et al. 2019). The RStoolbox package (Benjamin et al. 2019) was used to conduct the PCA. The first three axes of the PCA (accounting for 99.4% of data variability) were chosen for our analysis and used as predictor variables in the models.

Climatic niche models

To determine the important foraging areas for juvenile and adult loggerhead sea turtles, we developed a series of climatic niche models, based on the sdm package in R (Naimi and Araujo 2016). For ensuring the best predictability, we applied an ensemble modelling approach, combining different algorithms, so as to take into consideration simple as well as complicated models in the final output of climatic suitability (Le Heron 2006). This way, overfitting of a model was avoided and the ability of the model to be transferred in time and space was enhanced (New and Araujo 2006). The combination of algorithms could also counterbalance the uncertainty of the selection of a single model (Hao et al. 2019). Therefore, the combination of algorithms used herein consisted of: Generalized Linear Models (GLM), Generalized Additive Models (GAM), machine-learning Random Forest (RF) and Multivariate Adaptive Regression Spline (MARS).

Since reliable data on the true absence of the species were unavailable, the cells of no presence records served to extract potential pseudoabsences. Pseudoabsences were randomly selected with a standard distance (buffer) away from the presence data. Applying alternative distances (3, 5, 8 and 10 cells away from presence data), we observed that, as distance increased, the performance of the models increased, reaching a plateau for a distance of 8 cells. Therefore, a buffer of 8 cells was used as the threshold above which pseudoabsences were sampled. A total of 3105 pseudoabsences was selected for juveniles, as an equal number of presence and absence points is suggested for large number of datasets (Barbet-Massin et al. 2012). A set of 1000 pseudoabsences was selected for adults, as suggested for low prevalence datasets (Barbet-Massin et al. 2012). Ten random sets of pseudoabsences were sampled for the two life stages, so as to avoid sampling bias.

To assess the predictive accuracy of the models, a ten-fold cross-validation was applied. For the evaluation of the models, we used the Area Under the Curve (AUC; (Fielding and Bell 1997) and the True Skill Statistics (TSS; (Allouche et al. 2006)). The final model was produced as the mean value of probabilities given by all cross-validated models and ten random sets. It should be noted that the final ensemble models exhibited a very good predictive accuracy for juveniles and adults, based on both metrics (AUC equal to 0.91 for juveniles and 0.82 for adults; TSS equal to 0.75 for juveniles and 0.62 for adults).

The conversion of the final model outputs that represented continuous distributions to binary, indicative of a presence-absence distribution, was based on the threshold of maximization of TSS, a method frequently used and suggested by the literature (Comte 2013; Liu et al. 2016). We estimated changes between present and future distributions relying on differences in number of cells of presence for each raster. Presence in neritic and oceanic grounds was estimated by the 200m isobath adapted from the General Bathymetric Chart of the Oceans - GEBCO_2014, version 20150318, (https://www.gebco.net/data_and_products/gridded_bathymetry_data/). It is known that in many cases foraging grounds are frequented by both juvenile and adult loggerhead sea turtles, especially when subadults start approaching neritic grounds for feeding (Clusa et al. 2016). In order to find possible common foraging grounds, we identified overlapping surfaces between juvenile and adult potential distributions in the Mediterranean Sea. Precisely, we overlapped the rasters of adult and juvenile present and future potential distributions, in the environment of ArcGIS 10.1.

By using the projections on climatically suitable habitats generated under present and future climate, we spatially delineated the important foraging areas in the region. The important foraging areas were defined herein as the sites which could host climatically suitable foraging grounds for both juveniles and adults under both current and future conditions.

3.1.3 Results and Conclusions

Determine foraging areas under current conditions

Our analysis revealed that the distribution of foraging areas for juvenile loggerheads was broad, covering more than half of the Mediterranean Sea (56% of the entire basin). These sites covered mostly the central and western part of the basin. The large majority (73%) of climatically suitable foraging habitats for juveniles were found in oceanic waters and, apart from central and western Mediterranean, they were also detected to cover an extended area of the Ionian and the Aegean Sea (Figure 20a). The foraging areas of adult loggerheads were spatially more confined, covering 16% of the entire basin and were mainly distributed at the eastern and central part of the Mediterranean Sea. More than half (57%) of these areas were located within the neritic zone (Figure 20b).

About 6.7% of the Mediterranean basin hosts habitats which were predicted as suitable for both juveniles and adults. Most of them (67%) were identified in the neritic zone, mainly in the central Mediterranean. Along with sites located in the Tunisian plateau and the northwestern Adriatic Sea, neritic areas suitable for both life stages were identified also in the west coasts of Turkey and the northern Aegean Sea (eastern Mediterranean) and in the Spanish and French coasts (western Mediterranean). The remaining one third (33%) of common foraging grounds were found in the oceanic zone, mainly at the Tyrrhenian sea and the area close to Sicily (central Mediterranean).

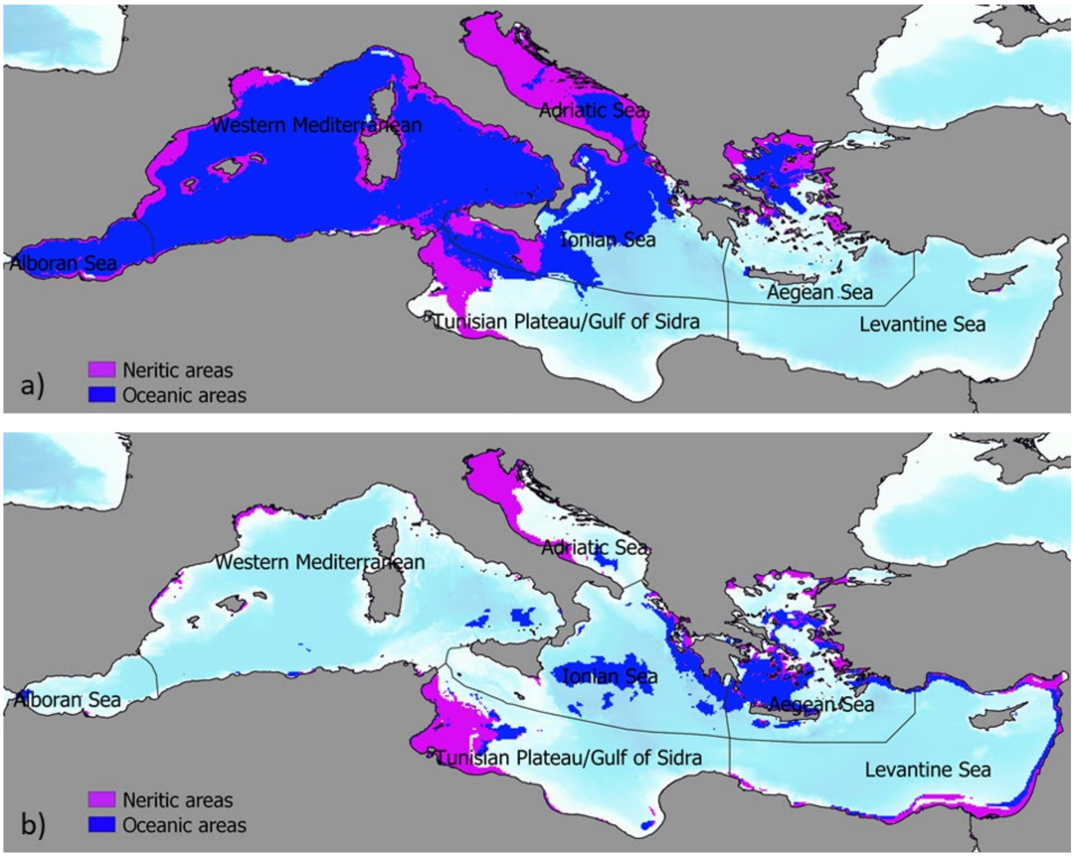

Figure 20. The distribution of foraging grounds of (a) juvenile and (b) adult loggerhead sea turtles, Caretta caretta, under present (1991-2020) climatic conditions across the Mediterranean Sea. Neritic grounds are colored in purple, while oceanic ones are colored in dark green. Marine ecoregions (sensu [54]) comprising the Mediterranean Sea are delineated by black dashed lines.

Assessing foraging areas under future conditions

Our models predicted a redistribution of juvenile foraging grounds, both at the neritic and oceanic zone, with the overall cover remaining rather stable (Figure 21a). By 2080, it is probable that some new suitable habitats, covering in total 5% of the Mediterranean will be created in the Aegean, the Ionian Sea (eastern Mediterranean) and the gulf of Gabes (central Mediterranean). These gains would counterbalance the loss of sites identified as suitable under current conditions mainly in the Tunisian plateau and the area near Sicily (central Mediterranean) (loss of 6% of the Mediterranean coverage).

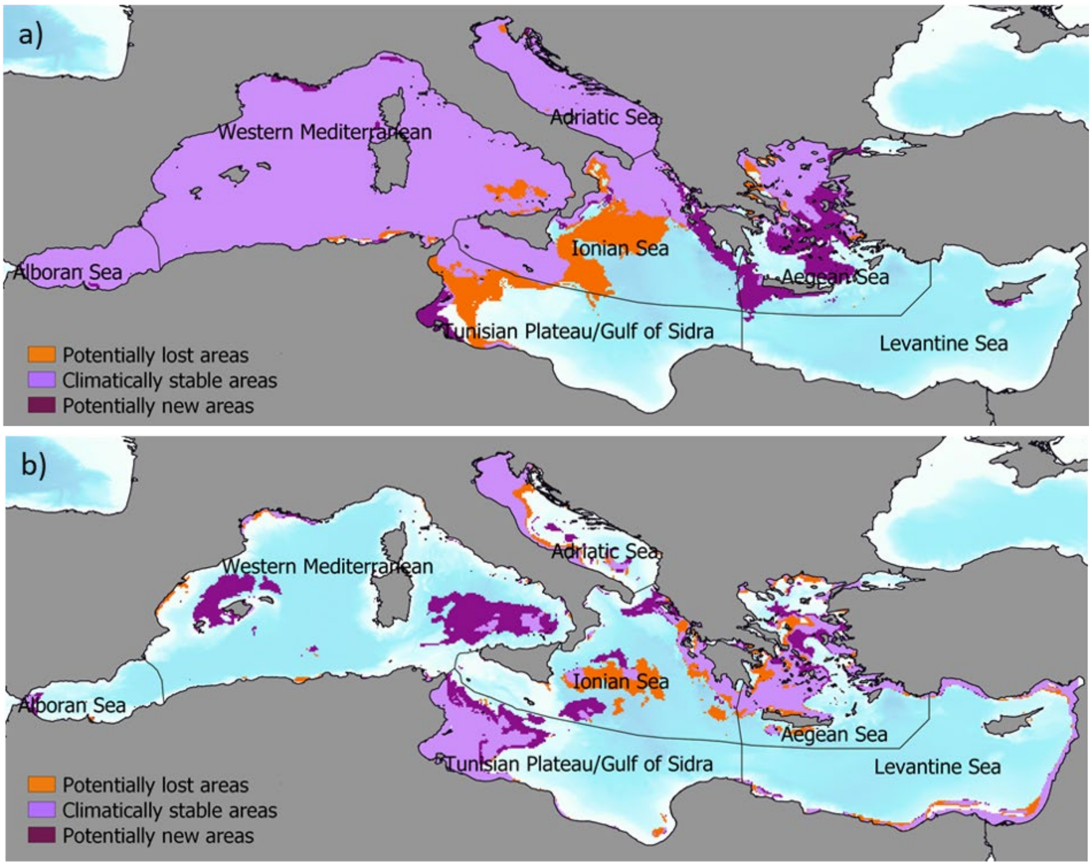

Figure 21. The distribution of foraging grounds of (a) juvenile and (b) adult loggerhead sea turtles, Caretta caretta, under present (1991-2020) and future climatic conditions (2051-2080) across the Mediterranean Sea. Areas that will persist on supporting foraging both in the present and future conditions are delineated in pink color, while new potential foraging areas are in green. Present areas that might no longer support foraging in the future are colored in dark red. Marine ecoregions (sensu [54]) comprising the Mediterranean Sea are delineated by black dashed lines.

The future climate is likely to favor the expansion of foraging grounds suitable for adult loggerheads. The foraging grounds were projected to increase from 16% to 19% of the cover of the entire Mediterranean basin. Actually, this increase was the result of a notable redistribution of sites located throughout the basin. While a large portion of the projected suitable habitats would remain stable (covering 11.8% of the Mediterranean), potential new suitable sites, covering an additional surface of 6.8% of the Mediterranean, would projected to emerge in the future (Figure 21b). Some of these suitable areas were projected to be hosted in regions with limited previous cover such as the Balearic Islands while others were predicted to be expanded such as suitable areas in the Tyrrhenian Sea (Figure 21b). Our analysis further revealed a likely shift in the distribution of foraging habitats towards the western Mediterranean Sea. Still, approximately one fourth of the current foraging sites may no longer support suitable conditions in the future; particularly critical oceanic sites currently found in the central Mediterranean and the southern Ionian Sea might experience contractions.

Overall, the coverage of future neritic suitable sites will remain stable throughout the whole basin (Figure 21b). On the other hand, oceanic areas that are suitable for adults and predicted to currently cover 7% of the Mediterranean are likely to increase their coverage up to 10% of the total marine surface of the Mediterranean, with such changes being more notable at the western part of the basin.

As for the foraging areas that could host both adults and juveniles, their cover is likely to increase in the future from 7% to 11% of the Mediterranean basin. The new areas were predicted to be located in the western (Balearic Islands, Tyrrhenian Sea) and the eastern Mediterranean (Ionian and Aegean Seas). The increase was mainly driven by a projected expansion of oceanic sites located in the western Mediterranean (i.e., in the Balearic Islands and the Tyrrhenian Sea) and in the eastern part (i.e., in the Ionian and the Aegean Seas). Yet, neritic areas in the Tunisian plateau and the Spanish coasts would lose their current climatic suitability for hosting both life stages in the future.

Overall, important areas, where both juveniles and adults are predicted to co-occur under both current and future conditions, were identified to be distributed sparsely throughout the basin. These areas cover 3% of the surface of the Mediterranean Sea. They were mainly located in the neritic zone, at a coverage of 77%. Our analyses highlighted that the northwestern Adriatic Sea (central Mediterranean) hosts an extensive important foraging area. Likewise, smaller important sites were identified in the coasts of the Aegean and the Ionian Sea (eastern Mediterranean), the coasts of the Tunisian shelf (central Mediterranean), the gulf of Lions in France and the Tyrrhenian sea (western Mediterranean).

CONCLUSIONS

Whereas suitable habitats for juveniles seem to be hosted mainly at the central and western Mediterranean, on the contrary, suitable areas for adults were found to be mostly distributed across the central and eastern part of the basin. An encouraging finding of our study was the projected increase in the suitable surface for foraging sites of adults and the relative stability of suitable surface for foraging for juveniles. A projected redistribution of the foraging grounds for adults towards the western Mediterranean is likely to trigger a shift of common foraging areas currently located mainly at the neritic zone of the central and eastern Mediterranean, supporting suitable climatic conditions for both life stages. Despite the general pattern of contractions and expansions of the foraging space, there are important foraging areas for both life stages projected to maintain their climatic suitability. Our analyses add a missing dimension to conservation efforts, related to the basin-wide distribution of important areas, offering novel insights towards incorporating climate change into conservation planning.

Under future climate change scenarios, our findings suggest that the overall cover of suitable areas for juveniles will remain stable, along with a redistribution of foraging habitats that could take place over large areas. While these findings imply that species are likely to gain new suitable space in the future, the actual use of these areas remains uncertain. Furthermore, for adult loggerheads, our findings revealed new foraging areas at the western Mediterranean in the future, suggesting that a shift of the distribution for adult loggerheads might be facilitative, as alternative sources to the main foraging ground will continue to be suitable. Occurrences of adult loggerheads at the oceanic zone around the Balearic Islands and the Tyrrhenian sea have been already recorded but probably at lower abundances (Carreras et al. 2004; Luschi et al. 2018). Still, adult sea turtles forage on a certain depth range, as they use their lungs to attain close to neutral buoyancy (Hays et al. 2004), and usually use areas of low depth range, frequently no more than 25m deep (Hochscheid et al. 1999). Thus, we caution that some of the sites which have been identified here as potential new foraging grounds i.e., oceanic areas in the Tyrrhenian Sea, in the Balearic Islands and the Aegean and Ionian Sea, might not be ideal in terms of bathymetry. Under this context, it is likely that improved foraging conditions at these regions might support only occasionally foraging activities in the future. The highly mobile nature of this species could help them avoid unfavorable climatic conditions and search for more suitable habitats (Luschi et al. 2003). Still, the degree of the fidelity to certain foraging areas that loggerheads exhibit could also affect any adaptive responses (Casale et al. 2012), even though evidence supports that sea turtles could show flexibility and relocate to new foraging sites when conditions become harsh (Shimada et al. 2020). In addition, it may be easier for next-generation adults to tend to new suitable areas and maintain fidelity to those sites. Considering that the passive dispersal of post-hatchlings influences the subsequent selection of foraging sites, new climatically suitable areas arising with climate change and changes in oceanic circulation might lead to new colonizations by future generations (Hays et al. 2010).

Use of new areas will also depend on several parameters that we may be unaware of and, thus, should enrich our knowledge. For example, prey availability is a major biotic factor determining the actual use of a potential climatically suitable area, due to its critical influence in the reproductive success, because of the dependence on food resources for vitellogenesis and subsequent migration and nesting events (Patel et al. 2016). Loggerheads in the Mediterranean feed on benthic organisms associated with seagrass beds (Patel et al. 2016). So, it is unknown whether new climatically suitable areas will sustain prey availability for the individuals and how climate-induced rising temperatures would affect seagrass meadows and other species that represent loggerheads' prey (Patel et al. 2015). But even if such range shifts take place, they could lead to excessive competition between individuals in the area over food and space (Poloczanska et al. 2009). In any case, potential shifts in distribution towards the western Mediterranean for adults and eastern Mediterranean for juveniles might pose additional challenges in the current management plans and marine spatial planning by reducing the efficacy of current conservation regulations in marine protected areas.

3.2 Assessing 3D climatically suitable foraging areas of loggerhead sea turtles under climate change

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3.2.1 Context and case study

Under the context of the three-dimensionality of the marine space, important areas of marine species thriving at various depths gain an additional spatial dimension, that of bathymetry. Many species of marine megafauna move among different habitats of differentiated depth (Schaber et al. 2022; Derville et al. 2020), as well as species distinct life stages might inhabit and forage in habitats of different bathymetry, as do benthic fish with a pelagic larva phase (Leis and McCormick 2002). Thus, species exposure to climate change risk gets even more complicated, as assessment of risk should consider for the differentiated spatial arrangement of life stages and the three-dimensional habitats used by species. As human activities are gradually extended to deeper seas, incorporating depth in conservation planning gives us the opportunity to identify marine areas hosting climatic and biodiversity stability with vertical coherence (Brito-Morales et al. 2022; Doxa et al. 2022). In order to assess and quantify the risk of species to climate change, it is important to identify species exposure to warming seas inside their distribution range (Foden et al. 2019), and especially, in areas identified as important for species lifecycle and persistence, such as common foraging grounds or nursery areas. Considering species' depth range could also provide us with a more accurate picture of their risk under climate change, as not all marine species will be exposed only in sea surface warming (Chatzimentor et al. 2023).

Sea turtles make use of habitats along a bathymetric gradient during a single day but also during different life stages of their lifecycle. Having a complex life cycle, they use various and distinct habitats for breeding, development and foraging, which span across neritic as well as oceanic areas (Bolten et al. 2003). Adults usually forage on benthic macroinvertebrates living on the seafloor, as well as on pelagic prey found in the water column, and emerge very often on the sea surface to breathe. Before reaching maturity, juvenile sea turtles usually forage in the water column of oceanic waters (Bolten et al. 2003). Both life stages are expected to be impacted by sea warming, which might cause a shift in their distribution range, alter their patterns of phenology, increase their foraging activity and indirectly affect them by degrading their habitats and feeding prey (Poloczanska et al. 2009). Particularly for the Mediterranean Sea, potential impacts have been modelled for sea surface warming scenarios (Chatzimentor et al. 2021), however attention should be also be drawn to understanding and projecting changes to their deep water habitats. As benthic habitats in the Mediterranean are jeopardized by increasing human pressures (Fanelli et al. 2021) and as sea turtles take advantage of deep waters in order to feed, it is important to identify hotspots of potential foraging which might be vertically cohesive.

In the current study, we aim to identify important marine areas for sea turtles in the Mediterranean across various depths and in face of the threat of climate change. In order to delineate three-dimensional important foraging grounds of sea turtles in the Mediterranean Sea, we identify climatically suitable areas of loggerhead sea turtles for distinct marine depth layers. We apply a modelling framework built on existing published data of foraging individuals in the Mediterranean Sea in order to explore climatically suitable marine habitats under current conditions, focusing on two different life stages of loggerheads, i.e., juvenile and adult. We further investigate the potential shifts of these sites due to climate change. We aim to identify vertically connected suitable marine areas for foraging individuals in the Mediterranean Sea, in order to fully represent the foraging behavior of adult and juvenile sea turtles which is depth-concise. Examining their potential impacts under climate change could unravel areas of great climatic stability, where conservation actions could be directed to. Our approach, recognizing life-cycle specific, depth-related and climatically stable habitats of sea turtles, could offer an advanced and more holistic understanding over the spatial delineation of the species' habitats and useful insights for future conservation planning that takes under consideration the impacts of climate change.

3.2.2 Methodology

To determine important foraging areas in various bathymetric layers for loggerhead sea turtles in the Mediterranean, we applied the methodology developed by Chatzimentor et al. (2021), which included three key steps: (i) collection and digitization of satellite tracked data on the location of juvenile and adult foraging loggerhead sea turtles to compile a digital database, (ii) extraction of sea temperature data at 5m, 25m depth and sea bottom, (iii) construction of bioclimatic variables based on these temperature data and (iv) development of climatic niche models for the different life stages. Adult sea turtles are capable of foraging in the whole water column but only reach the seabed when found in the neritic zone, so we projected their distribution for 5m, 25m depth and neritic bottom waters (<=200m depth) (Casale et al. 2018). Juvenile sea turtles are also capable of foraging in the whole water column (Casale et al. 2018). Individuals mainly feed on gelatinous zooplankton in oceanic habitats (water depths > 200 m), while when recruiting to neritic habitats (depths < 200 m) they switch to a diet of benthic invertebrates such as molluscs and crustaceans (Hatase et al. 2007). So, we included 5m and 25m depth sea temperature layers, but restricted bottom temperature layer to 200m of depth.

Species data

Species data were adapted from the publication of Chatzimentor et al. (2021) and they represented satellite tracked sea turtles found in the Mediterranean Sea, both in the juvenile life stage (51 individuals) and the adult life stage (126 individuals), for which spatial information in the form of a map or provided geographical coordinated were available. In the case of data on post- or pre-nesting migration of adults, the end or start point of the route, that each tracked individual had followed to reach the foraging area, was considered as a presence point. When many satellite telemetry points were given for a tracked animal that exhibited foraging behaviour, we determined as presence the centroid of the 50% data distribution isopleth derived from kernel density estimations. When a certain point was indicated as the location of a foraging turtle, this information was extracted.

Climatic Data

Climatic data on sea temperature for the Mediterranean region were obtained based on the FutureMARES projections. The dataset contained historical and projected monthly temperature values annually averaged data covering the Mediterranean Sea for the period from 1993 to 2100, at a 0.083°

spatial resolution. To define present climatic conditions, we used SST data for the period of 1993–2022. For future climatic conditions, we used SST data, covering the period of 2051–2080, based on projections of the Fifth Assessment Report of the Intergovernmental Panel on Climate Change and the SSP5-8.5 scenario, which was used as a worst-case scenario to assess the risk of climate change.

As for juveniles, sea temperature during the whole year was used for the construction of the predictor variables, as their activity in foraging areas is year-round (Bolten et al. 2003; Hawkes et al. 2009). On the contrary, adults use foraging areas during all year, except for their reproduction and post- and pre-migration phase (Rees and Margaritoulis 2013). So, to define the most representative foraging period, we used sea temperature data from September (i.e., after the completion of the nesting season) to March (i.e., before the beginning of pre-nesting migration).

Based on sea temperature data, we constructed bioclimatic variables (sensu Hijmans et al. 2011) so as for climate data to have an ecological meaning for sea turtles, whose viability and activities are linked to temperature (Davenport 1997; Mrosovsky 1980). Bioclimatic variables were constructed in R studio (version 4.0.0), using ncdf4 (Etten and Hijmans 2012), raster (Pierce 2019) and dismo packages (Chambault et al. 2021). We used the nine bioclimatic variables relevant to temperature: Mean annual temperature, Mean diurnal range, Isothermality, Temperature seasonality, Max temperature of warmest month, Min temperature of coldest month, Temperature annual range, Mean temperature of warmest quarter and Mean temperature of coldest quarter. Previous studies that used climatic niche models for assessing sea turtle distribution have utilized a number of bioclimatic variables providing no suggestion on an explicit use of specific ones (Pikesley et al. 2015). Therefore, here we applied a principal component analysis (PCA) to produce a number of new predictors that allowed to capture the grand majority of the variance of the bioclimatic variables (Martorano et al. 2019). The RStoolbox package (Benjamin et al. 2019) was used to conduct the PCA. The first two axes of the PCA (accounting for greater than 99% of data variability) were chosen for our analysis and used as predictor variables in the models.

Climatic niche models

To determine the important foraging areas for juvenile and adult loggerhead sea turtles, we developed a series of climatic niche models, based on the sdm package (Naimi and Araujo 2016). For ensuring the best predictability, we applied an ensemble modelling approach, combining different algorithms, so as to take into consideration simple as well as complicated models in the final output of climatic suitability (Heron 2006). This way, overfitting of a model is avoided and the ability of the model to be transferred in time and space is enhanced (New and Araujo 2006). The combination of algorithms also counterbalanced the uncertainty of the selection of a single model (Hao et al. 2019). Therefore, the combination of algorithms used herein consisted of: Generalized Linear Models, Generalized Additive Models, machine-learning Random Forest and Multivariate Adaptive Regression Spline.

Since reliable data on the true absence of the species were unavailable, the cells of no presence records served to extract potential pseudoabsences. Pseudoabsences were randomly selected with a standard distance (buffer) away from the presence data. A buffer of 8 cells was used as the threshold above which pseudoabsences were sampled. A total of 3105 pseudoabsences was selected for juveniles, as an equal number of presence and absence points is suggested for large number of datasets (Barbet-Massin et al. 2012). A set of 1000 pseudoabsences was selected for adults, as suggested for low prevalence datasets (Barbet-Massin et al. 2012). Ten random sets of pseudoabsences were sampled for the two life stages, so as to avoid sampling bias.

To assess the predictive accuracy of the models, a ten-fold cross-validation was applied. For the evaluation of the models, we used the Area Under the Curve (AUC; (Fielding and Bell 1997) and the True Skill Statistics (TSS; (Allouche et al. 2006)). The final model was produced as the mean value of probabilities given by all cross-validated models and ten random sets. It should be noted that the final ensemble models exhibited a good predictive accuracy for juveniles and adults, based on both metrics (Table 7).

Table 5. Evaluation metrics of the models predicting the potential distribution of juveniles and adult loggerheads in waters of 5m, 25m and neritic bottom depth. AUC and TSS indices were calculated as the mean value of ten models.

	AUC	**TSS**
Juveniles (5m)	0.88	0.66
Juveniles (25m)	0.89	0.7
Juveniles (bottom)	0.72	0.53
Adults (5m)	0.77	0.57
Adults (25m)	0.78	0.57
Adults (bottom)	0.91	0.79

The conversion of the final model outputs that represented continuous distributions to binary, indicative of a presence-absence distribution, was based on the threshold of maximization of TSS, a method frequently used and suggested by the literature (Comte 2013; Liu et al. 2016).

We estimated changes between present and future distributions relying on differences in number of cells of presence for each raster. Presence in neritic and oceanic grounds was estimated by the 200 m isobath adapted from the General Bathymetric Chart of the Oceans-GEBCO_2014, version 20,150,318, (https://www.gebco.net/data_and_products/gridded_bathymetry_data/). It is known that in many cases foraging grounds are frequented by both juvenile and adult loggerhead sea turtles, especially when subadults start approaching neritic grounds for feeding (Clusa et al. 2016). In order to find possible common foraging grounds, we identified overlapping surfaces between juvenile and adult potential distributions in the Mediterranean Sea. Precisely, we overlapped the rasters of adult and juvenile present and future potential distributions for 5m, 25m and bottom neritic waters, in the environment of ArcGIS 10.1 (E.S.R.I. 2011). In order to identify key areas hosting suitability in all the water column for adults and juveniles (3D areas), we estimated overlapping predicted suitable surfaces among the three depth layers (5m, 25m, neritic bottom waters) for each life stage (juveniles, adults).

3.2.3 Results and Conclusions

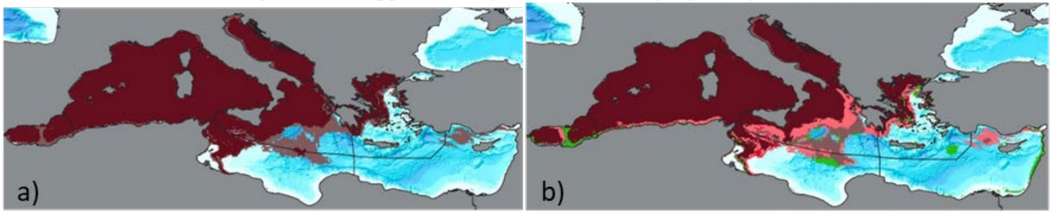
Delineating lifecycle-specific and depth-concise foraging areas under current conditions

Our analysis revealed that the distribution of foraging areas for juvenile loggerheads was broad, covering more than half of the Mediterranean Sea for surface waters (59% of the Mediterranean basin) and deeper waters up to 25m depth (56% of the basin). Suitable habitats reaching on the seabed of the neritic zone expand over a cover of 25% of the Mediterranean basin. Climatically favorable sites covered mostly the central and western part of the basin. The large majority (75%) of climatically suitable foraging habitats for juveniles were found in oceanic waters for both 5m and 25m depth levels and, apart from central and western Mediterranean, they were also detected to cover an extended area in the Ionian and the Aegean Sea.

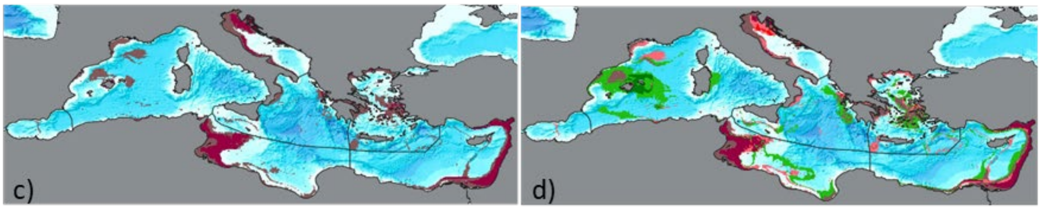
Climatically suitable areas for juveniles in 5m and 25m deep waters overlap covering a 53% of the Mediterranean basin (75% of the areas are found in oceanic waters), with most areas being concentrated in the western Mediterranean, Adriatic Sea, central Mediterranean and Aegean Sea (Figure 36a, 36b). Areas lost and gained are found in range edges of the predicted distribution and more specifically in the southeast edges.

Our models predicted not significant changes for the distribution of the juvenile foraging grounds, both at the neritic and oceanic zone, with the overall cover remaining rather stable, for both waters of 5m (57%) and 25m depth (52%) (Figure 36b). Most areas still were predicted to be hosted outside the neritic zone (75% of the Mediterranean basin for waters of 5m depth and 73% for waters of 25m depth). By 2080, it is probable that some new suitable habitats, covering in total 1% of the Mediterranean will be created in the Aegean Sea and the Levantine Sea (eastern Mediterranean). These gains would counterbalance the loss of sites identified as suitable under current conditions mainly in the Tunisian plateau and the area below Sicily (central Mediterranean) (loss of 3% of the Mediterranean coverage). Deeper waters (bottom 200m) are predicted to gain an overall habitat suitability cover of 15% of the Mediterranean Sea, with key sites located in the Adriatic Sea, in the majority of the Aegean and Ionian Sea (east Mediterranean), the coasts of north Africa (Libya, Egypt) as well as in the coasts of the Balearic Islands and Spain and coasts of the Tyrrhenian Sea.

Potential present distribution of juveniles loggerheads (5m and 25m depth) and predicted climate-induced changes



Potential present distribution of adults loggerheads (5m and 25m) and predicted climate-induced changes



Potential present and future distribution of adults and juvenile loggerheads for both 5m and 25m

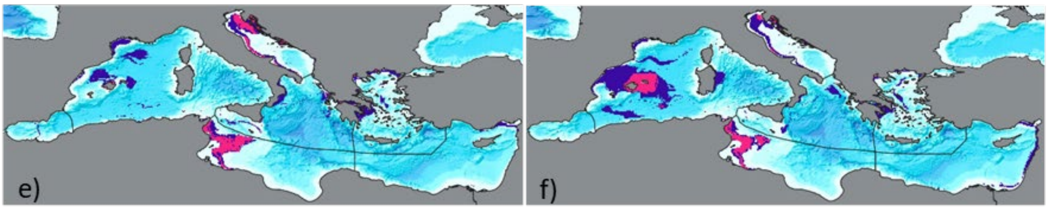


Figure 22. Predictions on the potential climatic suitability of (a) juvenile and (c) loggerheads in waters of 5m and 25m depth for the present conditions and predicted changes under future scenario of climate change (b, d). With dark red color are climatically suitable areas in only one depth layer. Potential common foraging grounds of adults and juveniles overlapping in 5m and 25m depth under current climatic conditions (e), and future climatic conditions (f). With pink color are climatically suitable marine areas which overlap for both 5m and 25m of depth, for both juveniles and adults, while with blue color are climatically suitable marine areas of one lifecycle stage for 5m and 25m depth overlapping with climatically suitable marine areas of the other lifecycle stage found in only one depth layer.

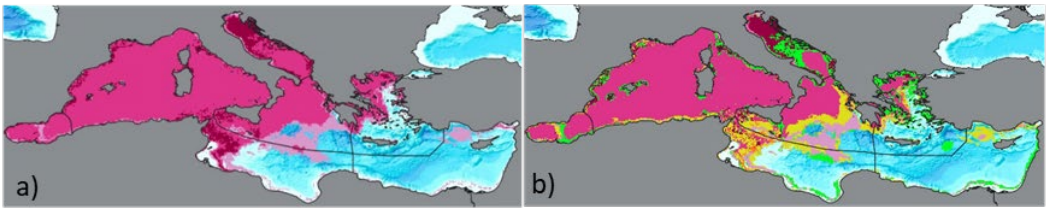
The foraging areas of adult loggerheads were spatially more confined, covering 11% of the entire basin and were mainly distributed at the eastern and central part of the Mediterranean Sea, both for waters of 5m and 25m depth (10% of the Mediterranean Sea). More than half of these areas were located within the neritic zone (66% of the Mediterranean basin for waters of 5m depth, 56% for 25m depth). Potential foraging areas for adult loggerheads largely covered the bottom waters of neritic zone, covering a 13% of the Mediterranean Sea. Climatically suitable areas for adults in 5m and 25m deep waters overlap covering a 5% of the Mediterranean basin, for which 72% of it is predicted to be found in neritic waters. More specifically, they are hosted particularly in the Tunisian plateau, the North Adriatic Sea, the Levantine waters and sparse areas in the Aegean and Ionian Sea (Figure 36c, 36d). These areas remain stable in total cover in the future,

The future climate is likely to favor the expansion of foraging grounds suitable for adult loggerheads, which were found to increase in cover from 11% to 15% of the entire Mediterranean basin (11% for waters of 25m depth and stability at 13% for bottom neritic waters). Half of the climatically suitable areas belong to the neritic waters, with 47% of the predicted distribution belonging to neritic zone for waters of 5m depth and 42% of the predicted distribution for waters of 25 m depth. Actually, this increase was the result of a notable redistribution of sites located throughout the basin. While a large portion of the projected suitable habitats would remain stable (covering 8% of the Mediterranean), potential new suitable sites, covering an additional surface of 7% of the Mediterranean (5% for 25 m, 1% for neritic bottom waters), would probably emerge in the future. Some of these suitable areas were projected to be hosted in regions with limited previous cover such as the Balearic Islands (both for waters of 5m and 25m depth), while others were predicted to be expanded such as suitable areas in the Levantine Sea. Bottom climatic suitability is predicted to remain rather stable, with limited contraction of areas in the central Adriatic Sea. Climatically suitable areas for adults in less deep waters (5m and 25m depth) remain stable in total cover in the future.

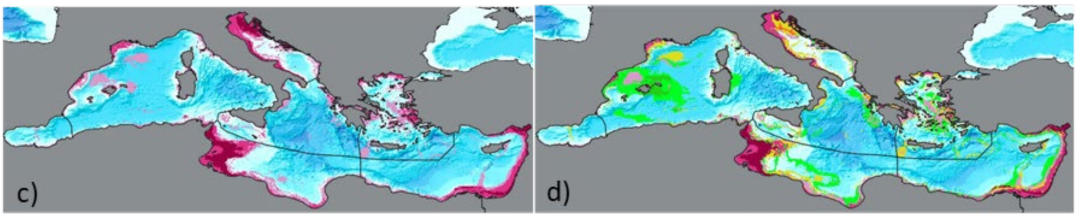
3D climatically suitable areas were considered as those areas where climatic suitability was identified in all three depth layers i.e. overlap in 5m, 25m depth and the neritic bottom waters. 3D climatically suitable areas for juveniles occurred in 5% of the Mediterranean basin, mostly in the Tunisian plateau, the Adriatic Sea and the eastern coasts of Spain and France (Figure 37a). For adults, 3D climatically suitable areas covered a 3% of the Mediterranean basin and were mostly found at the Tunisian plateau and the north Adriatic Sea (Figure 37c).

3D climatically suitable areas for juveniles in the future were projected to increase their total cover from 5% to 9% of the basin, as suitability is predicted to increase near already existing suitable 3D habitats. Suitability loss and gain at the 3D space is predicted to be minimum (<0.1%). Loss is predicted to occur mostly in the south central and eastern borders of the predicted distribution and gain is predicted to occur in already existing 3D areas and new areas of singly bathymetry revealed for the northern coasts of central-eastern Africa and Levantine (Figure 37b).

Under future scenarios, 3D areas are predicted to remain stable covering a 3% of the basin. Losses and gains at the 3D space were predicted to be minimum (<0.1% of the Mediterranean basin). Loss in suitability is predicted to occur for the eastern coasts of Turkey in the Aegean Sea, as well as the eastern coasts of the Ionian Sea, near an important foraging spot of sea turtles, the Amvrakikos bay. Cells with 3D changes are predicted to occur also in the North Adriatic Sea, and suitability is predicted to increase for the areas around Balearic Islands (Figures 37d).



Potential present suitable 3D areas of juveniles loggerheads (5m,25m,bottom) and predicted climate-induced changes



Potential present suitable 3D areas of adult loggerheads (5m,25m,bottom) and predicted climate-induced changes

Figure 23. Predictions on the potential climatic suitable areas of (a) juvenile and (c) loggerheads in 5m, 25m and neritic bottom waters under present conditions, and predicted changes under future scenario of climate change (b, d).

Depth-concise foraging areas for both lifecycle stages and climate-related changes

Climatically suitable areas where foraging areas of both adults and juveniles overlap for5m and 25m deep waters cover 2% of the Mediterranean Sea, most of which are hosted in the neritic zone (64% of their distribution) and are concentrated in the core areas of the Tunisian plateau and the coasts of the north Adriatic Sea (Figure 36e, 36f). Under future scenarios, the overall cover is predicted to remain stable. Climatically suitable areas of adults in 5m and 25m depth overlapping with only suitable areas for juveniles found in only one depth layer and the opposite, span over 5% of the Mediterranean Sea, with overlapping suitable habitats being found all over the Mediterranean Sea, at the western Mediterranean (Gulf of Lions, Balearic Islands), the central Mediterranean (Tunisian plateau and Adriatic Sea) and eastern Mediterranean (coasts of the eastern Ionian Sea, Aegean Sea and south-eastern Turkey). Under future scenarios, their overlapping suitable areas are predicted to increase in cover from 5% to 8%, with areas being largely concentrated in the Balearic Islands and scattered areas in the Aegean Sea, while losses are predicted to be in the Tunisian plateau and Ionian Sea.

Climatically suitable and depth-concise marine areas for both lifecycle stages span across the Mediterranean Sea, with key spots being identified in the western Mediterranean (Gulf of Lions, east coasts of Spain), in the central Mediterranean (Tunisian plateau, northern Adriatic Sea, eastern Ionian coasts) and eastern Mediterranean (Aegean coasts and coasts of the northern and southern Levantine Sea) (Figure 38a). Under the future scenario of climate change, climatic suitability of these depth-concise marine areas is predicted to expand in current locations, particularly evident for the waters of the Balearic Islands and the Aegean coasts (Figure 38b). West-ward increase of suitability mainly derives from the adults' distribution shift (Figure 37d), and eastern-ward increase of suitability mainly from the juveniles' distribution shift (Figure 37b).

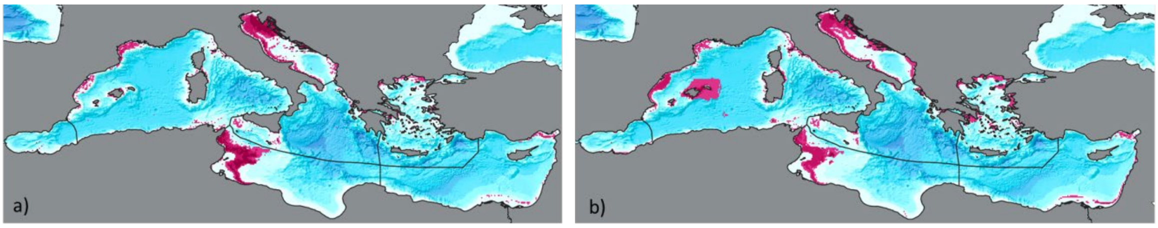


Figure 24. Predictions on the potential climatic suitable areas of juvenile and adult loggerheads in 5m, 25m and neritic bottom waters under present conditions (a), and future conditions (b). These areas represent climatically suitable marine areas of one lifecycle stage for the three-depth layers overlapping with climatically suitable marine areas of the other lifecycle stage found in at least one depth layer.

CONCLUSIONS

The North Adriatic Sea and the Tunisian plateau in the central Mediterranean Sea, as well as the coasts of Balearic Islands and the Gulf of Lions in the west Mediterranean Sea were revealed as important foraging areas for both life stages of loggerhead sea turtles in all depth layers in the Mediterranean Sea. However, the important foraging hotspot of the North Adriatic Sea might bear a significant loss of its climatic suitability for adults foraging there, under the climate change scenario, which if coupled with other anthropogenic activities like bycatch, might have important impacts on the local populations. For adults, a westward shift in climatically suitable areas is predicted, which is also supported by a growing number of observations of sparse nesting activities in western areas. Still, there are some areas predicted to gain climatic suitability in the eastern and central Mediterranean, like in the eastern Ionian, in the Levantine Sea and the central and eastern north Africa, where major rookeries exist. The 3D approach reveals suitability gains in the deeper waters for the eastern basin, not previously apparent for the surface layer. However, deeper layers of 25m depth in the northern areas of the basin (north Aegean, north Adriatic, Gulf of Lions) follow a similar pattern predicted to lose suitability for adults. Our analysis predicted a potential loss of climatic suitability of their southeast range edges, a pattern which is compliant with climate change related shifts in abundance and might provoke reduction in the abundance of juveniles in these areas. However, for juveniles, predicted suitability losses are fewer than gains, with a significant suitability gain in the Adriatic Sea, expected to become an important 3D climatically suitable area in the future.

3.3 Megafauna and prey species interactions - Seabirds and cetaceans' projections in the Bay of Biscay

Contributors: Xabier Corrales, Isabel García Baron, Amaia Astarloa, Jose A. Fernandes-Salvador

3.3.1 Context and case study

Seabirds and cetaceans have been long considered good ecological indicators, as they face numerous impacts and respond to different ecosystem changes while moving across their vast distributional ranges (Piatt and Sydeman 2007, Hazen et al. 2019). They are in addition protected under different international agreements, such as the Bird Directive 2009/147/EC and the Habitat Directive 92/43/EEC (e.g., bottlenose dolphin *Tursiops truncatus,* fin whale *Balaenoptera physalus,* Cory's shearwater *Calonectris diomedea*), which aim to promote and maintain biological diversity through the conservation of natural habitats and biodiversity in the European Union territory. But despite the conservation efforts, many cetacean species are still intentionally killed or indirectly impacted by commercial fisheries (e.g, common dolphin *Delphinus delphis*), while seabirds are yet one of the most threatened groups with some critically endangered species (e.g., Balearic shearwater *Puffinus mauretanicu*s) (Croxall, Butchart et al. 2012*,* Allen 2014*,* Dias, Martin et al. 2019*)*. For this reason, these species are often called PETs (Protected, Endangered and Threatened species), which usually includes large charismatics species, such as marine mammals, seabirds and turtles. These groups are used for the WP6 ecosystem services and decision support systems. Ecosystem services valuation of seabirds and cetaceans is performed at the groups level, not the species level.

A variety of marine mammal species are present in the Bay of Biscay. The seabird community is of relevance during certain periods of the year through an important migratory flyway and more than 700 species of fishes have been reported. The migration of marine megafauna (i.e., cetacean, seabirds and large pelagic fishes) is highly influenced by early stages of pelagic fishes, such as the European anchovy Engraulis encrasicolus (García-Barón et al. 2019a, Louzao et al. 2019b, Lezama-Ochoa et al. 2010). Regarding biotic interactions between marine megafauna and pelagic prey, schooling in prey (e.g., anchovy–sardine), local enhancement/facilitation in predators (e.g., Cory's shearwater–fin whale), and predation between predator–prey species (e.g., northern gannet–horse mackerel) have been characterised by positive associations, while predator avoidance behaviour (e.g., striped dolphin–blue whiting) has been characterised by negative associations (Astarloa et al. 2019). Mammals are vulnerable to fishing bycatch, vessel collision, and pollution-related threats, whilst seabirds are particularly sensitive to oil spills, fishing bycatch and marine litter (García-Barón et al. 2019b).

3.3.2 Methodology

The Ecopath with Ecosim model for the Bay of Biscay (BoB) encompasses the area from Brest (Brittany, France) to Cabo de Finisterre (Galicia, Spain), including the continental shelf and upper slope, between

0 and 1000 m isobaths (Figure 27). The model covers an area of 120.433 km^2 and includes the ICES divisions 8abc (Figure 27). Ecological and fishery features of the area were used to establish the bathymetric and latitudinal limits.

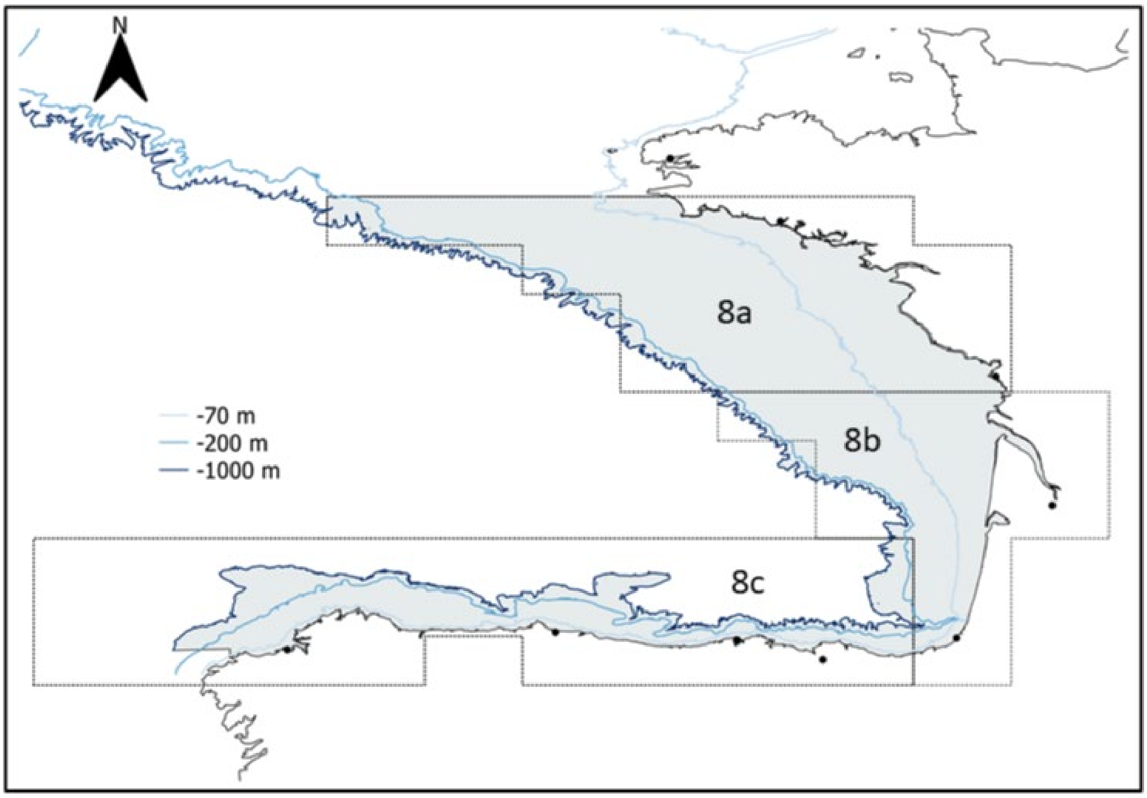


Figure 25. The Bay of Biscay (ICES 8a,b,c,d), showing the modelled area and depth contours.

The model includes 52 main commercial fish species and functional groups (Figure 24), ranging from primary producers to top predators. Hake was split into two age groups (i.e., multi-stanza groups) (large hake, i.e., ≥ 27 cm of total length and small hake < 27 cm) attending fisheries and ecological reasons (Velasco and Olaso 1998, Mahe, Amara et al. 2007). Vulnerable species such as seabirds and marine mammals were grouped in four functional groups according to their ecological role: (1) diving and pursuit divers seabirds, (2) surface feeders seabirds, (3) baleen whales, which mainly feed on zooplanktonic organisms, and (4) toothed cetaceans and pinnipeds, which mainly feed on pelagic fishes and squids.

The model comprises 13 fishing fleets from Spain and France: Spanish demersal trawl, Basque demersal trawl, Spanish purse seine, Spanish coastal fishery, Spanish offshore fishery, French demersal trawl, French pelagic trawl, French Nephrops trawl, French purse seine, French coastal fishery, French offshore fishery, Spanish recreational fishery, and French recreational fishery (Figure 28). For an extensive description of the BoB Ecopath model, species composition of the functional groups and its input data see Corrales et al. (2022).

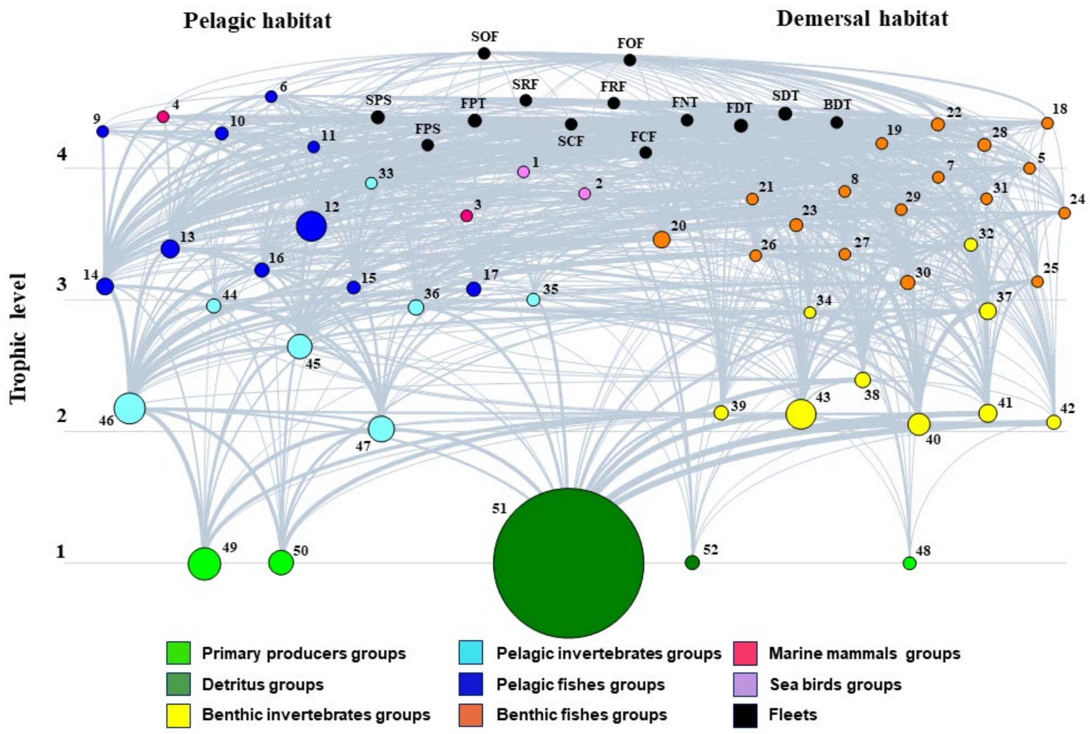


Figure 26. Flow diagram of the Bay of Biscay ecosystem representing the period 2000-2003. Fleets: SDT = Spanish demersal trawl; BDT = Basque demersal trawl; SPS = Spanish purse seine; SCF = Spanish coastal fishery; SOF = Spanish offshore fishery; FDT = French demersal trawl; FNT = French Nephrops trawl; FPS = French purse seine; FCF = French coastal fishery; FOF = French offshore fishery; SRF = Spanish recreational fishery; FRF = French recreational fishery. Numbers identify the functional groups in the model. Circle size is proportional to the biomass of the functional group. Connecting lines thickness is proportional to the magnitude of the flows.

The environmental response functions that link the species or functional groups dynamics with the environmental drivers were obtained using shape-constrained generalized additive models (SC-GAMs) (Citores et al. 2020), except for albacore, for which data from AQUAMAPS (Kaschner et al. 2019) (www.aquamaps.com) was used. SC-GAMs build species distribution models under the ecological niche theory framework (Soberón and Nakamura 2009) where response curves are unimodal and concave with respect to environmental gradients (Citores, et al. 2020). Data for the presence of the species came from OBIS (https://obis.org/) and GBIF (https://www.gbif.org/es/).

The temporal dynamic module Ecosim (Corrales et al. In preparation) was used to evaluate the effect of plausible future scenarios for major stressors in the area (Table 5) (Amate 2022). All scenarios were run for 80 years, from 2019 to 2099.

Table 6. List of the FutureMARES scenarios simulated and the combinations between fishing and climate change conditions.

Scenario (Scn.)	Name	Fishing	Climate
1	Global sustainability	0.8 * MSY	RCP 4.5
2	World markets	0.8 * MSY	RCP8.5
3	National enterprise	1 * MSY	RCP8.5

To assess the impact of climate change, future SST, SBT and PP from the ensemble projections of CMIP6 data on the Bay of Biscay through the FutureMARES project (https://www.futuremares.eu/) were used (Figure 29).

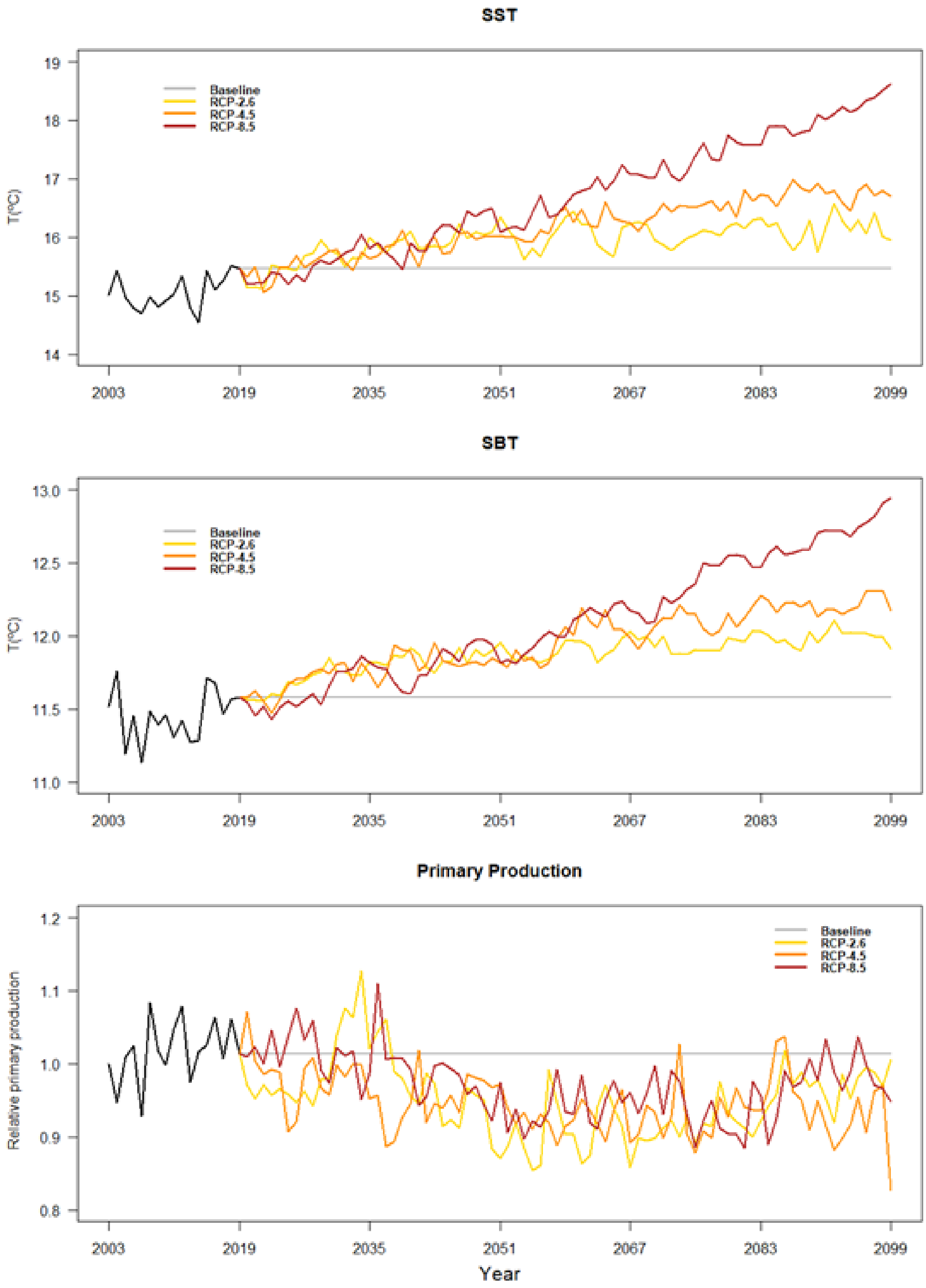


Figure 27. Historical (black line) and projections of each variable under the three IPCC climate change scenarios for the Bay of Biscay. SST: sea-surface temperature; SBT: sea-bottom temperature. Primary production values are represented by their relative value compared to the value of 2003. Values are annual averages downscaled at the study area. Source: Amate 2022.

In the FutureMARES project there are three main scenarios (Table 5): Global Sustainability, National Enterprise and World Markets. These scenarios were used to analyse future trajectories of functional groups of PETS vulnerable species or functional groups, such as the ones included in functional groups called (1) diving and pursuit divers seabirds (FG1), (2) surface feeders seabirds (FG2), (3) baleen whales (FG3), and (4) toothed cetaceans (FG4). Three alternative scenarios of fishing were evaluated (Table 5): (1) fishing at the advised F_{MSY} for the functional groups with available stock assessment; (2) 20% decrease in the F_{MSY}; and (3) 20% increase in the F_{MSY}. The 20% decrease and increase in the F_{MSY} were based on Hansenet al. (2019), which defined scenarios considering socio-political aspects.

3.3.3 Results and Conclusions

Future biomass of functional groups of PETS predicted by the model were presented in Figure 30. Biomass of diving and persuit divers seabirds, surface feeder's seabirds and toothed cetaceans increased in all the scenarios, especially in the National Enterprise scenario. The increase of the abundance for these functional groups in the three scenarios could be attributed to a reduced fishing mortality on these functional groups in the period prior to the scenario (2018-2019) and the increased availability of preys through the simulation (i.e., forage fishes and discards). In fact, the abundance of forage fishes (i.e., the anchovy, sardine, mackerel, horse mackerel, other planktivorous fishes, mesopelagic fishes and blue whiting) increased through the simulated period, mainly due to the increase in the biomass of anchovy. The largest abundance of forage fishes was predicted in the National Enterprise scenario, mainly due to lower abundance of its main predators (i.e., albacore, bluefin tuna and hake) due to higher fishing impacts, which could explain the higher abundance of other predators (i.e., seabirds and dolphins). The higher fishing mortalities in the National Enterprise scenario also caused a higher abundance of discards. The abundance of baleen whales decreased in the Global Sustainability scenario while increased in the National Enterprise and Global Markets scenarios. This could be related to lower abundance of its main prey (i.e., macrozooplankton), which is mainly affected by the dynamics in the lower part of the food web (i.e., zooplankton and phytoplankton groups).

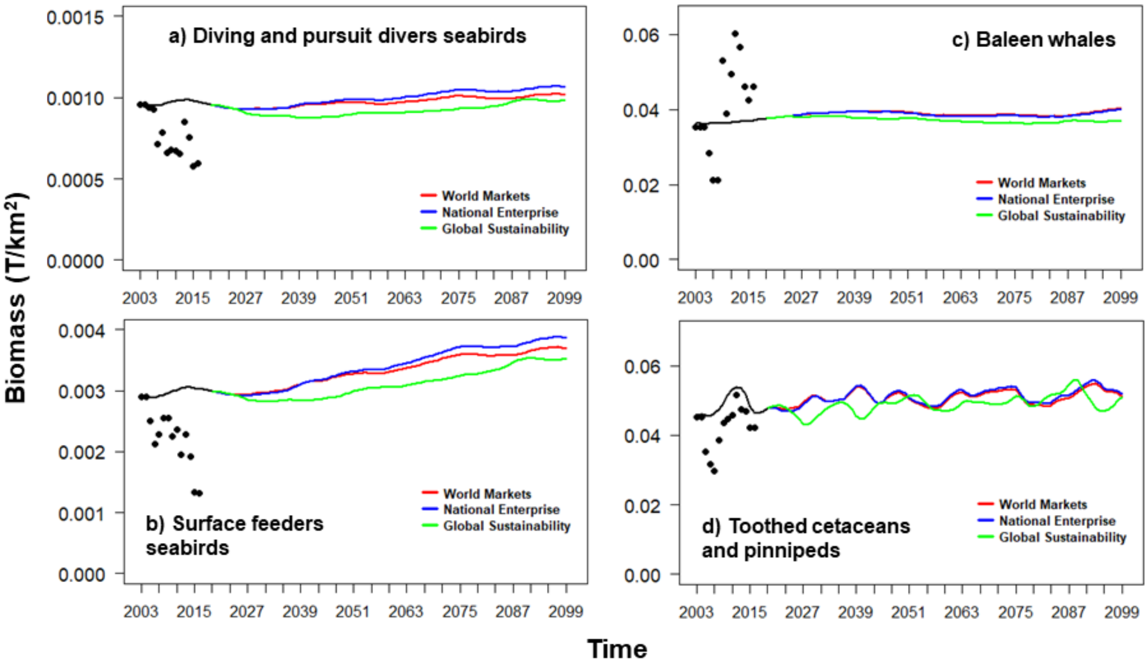


Figure 28. Comparison between the predicted (solid lines) and observed (dots) time series of biomass (t·km-2), and projections for (a) diving and pursuit divers seabirds, (b) surface feeders seabirds, (c) baleen whales, and (d) toothed cetaceans under different future scenarios of combined stress by climate change and fishing for the Bay of Biscay (BoB) ecosystem model for the period 2003–2099. Black line represents historical model predictions and coloured lines represent different scenarios.

CONCLUSIONS

Large changes or differences among the scenarios for these species were not projected by the ecosystem model. However, the model considers them as large functional groups without a deep understanding or depiction of their ecophysiology and the biological mechanisms that impact their populations. This limited work implies a positive message about the potential resilience to CC of these species. Future work should focus on studying individual species from a more mechanistic point of view.

3.4 Projected declining trends of Puffinus mauretanicus in the Bay of Biscay

Contributors: Asier Anabitarte, Amaia Astarloa, Maite Louzao, Maite Erauskin-Extramiana, Isabel García Baron, Jose A. Fernandes-Salvador

3.4.1 Context and case study

The Balearic Shearwater, *Puffinus mauretanicus* is the most threatened European seabird, and it is currently listed as Critically Endangered on the IUNC Red List due to its restricted breeding range and small and declining population size (BirdLife International 2018). It breeds solely on the Balearic Islands (Louzao et al. 2012) and spends the non-breeding period (from May to October) along the northeast Atlantic Ocean in relatively shallow and coastal waters (Guilford et al. 2012; Lambert et al. 2017). In the Bay of Biscay, the distribution of Balearic shearwaters has been related to an oceanographic thermal front, characterized by cold (16-18ºC) surface water mases and to the occurrence of fish prey, particularly pilchard *Sardinus pilchardus* and anchovy *Engraulis encrasicolus* (Yésou 2003; Lambert et al. 2017). In addition to the inter-annual variability of populations of prey fish, such as the small clupeids other factors such as long-term climate change may influence the at-sea distribution of this species. Indeed, the increase in annual surface temperature that could have triggered the rapid northward expansion of the Balearic shearwater in sea regions around the British Isles through a trophic cascade, involving plankton and fish prey (Luczak et al. 2011).

3.4.2 Methodology

Since Balearic shearwater is mainly present in the Bay of Biscay during between May-October, sightings were obtained from the JUVENA survey (2013-2019), a multidisciplinary survey that samples plankton, fish, megafauna and physical oceanography and marine litter every September (Boyra et al. 2013; Louzao et al. 2019). Seabird's sightings were recorded by experienced observers that followed line-transect methodology (Buckland et al. 2001) and were fitted by means of a detection function that allowed to consider the effect of the environmental conditions during the observation effort (more details in García-Barón et al. 2022).

To obtain the distribution and abundance patterns of the species, generalized additive models (GAMs) were fitted from the previous detection function analyses. After checking for alternative distribution families (e.g. Tweedie, zero-inflated Poisson), we selected a negative binomial distribution, and a log-link function to account for overdispersion. Degrees of smoothness were limited to fit unimodal response curves and restricted to three (Bruge et al. 2016) to avoid overfitting (Burnham and Anderson 2002). As explanatory variables static (e.g., depth) and dynamic (e.g., temperature) variables were used. To avoid model complexity, a maximum number of four covariates was selected (Lambert et al. 2017). Before modeling and to avoid collinearity, all variables were standardized to have a mean of zero and a standard deviation of one (Zuur et al. 2007) and subsequently analysed by means of

Spearman's rank correlation coefficient to identify highly correlated (|r| ≥ .5) pairwise predictors (Dormann et al. 2007). The most plausible model was selected based on the lowest AIC (Guisan and Zimmermann 2000). When models differed in 2 units of AIC (ΔAIC < 2), they were considered statistically equivalent and the one with a smaller number of variables was chosen following the parsimony principle (Arnold 2010). Once the most plausible models were defined, densities were predicted per year over the standard grid (latitudinal range: 43– 48°N; longitudinal range: 1– 10°W, 0.08° spatial resolution).

In the FutureMARES project there are three main scenarios (Table 6): Global Sustainability, National Enterprise and World Markets. These scenarios were used to analyse future trajectories of this species in its main distribution area in French (ICES area 8a,b) and Spanish (ICES area 8c) coast (Figure 31). Since two of the scenarios use the same RCP 8.5, here the RCP 2.6 was also considered on request of local stakeholders.

Table 7. List of the FutureMARES scenarios simulated and the combinations between fishing and climate change conditions.

Scenario (Scn.)	Name	Climate
1	Global sustainability	RCP 4.5
2	World markets	RCP 8.5
3	National enterprise	RCP 8.5
4		RCP 2.6

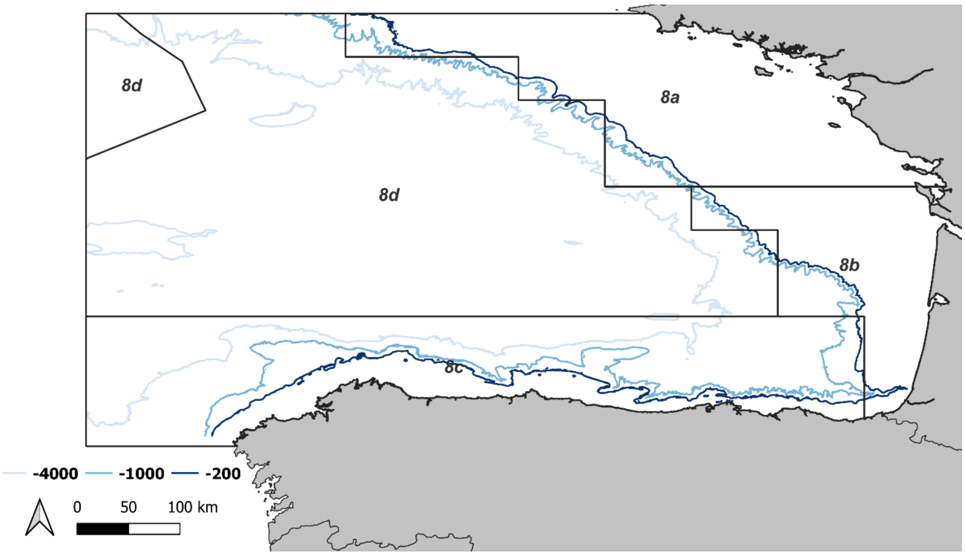


Figure 29. The Bay of Biscay (ICES 8a,b,c,d), showing the modelled area and depth contours.

3.4.3 Results and Discussion

The selected model included depth, distance to the coast, distance to the shelf break and chlorophyll-a concentration. The functional relationship with these variables showed that the density of Balearic shearwater decreases as depth and distance to coast increase, and distance to the shelf break decreased. The relationship with Chl-a was positive, indicating a preference for waters rich in chlorophyll (Figure 32).

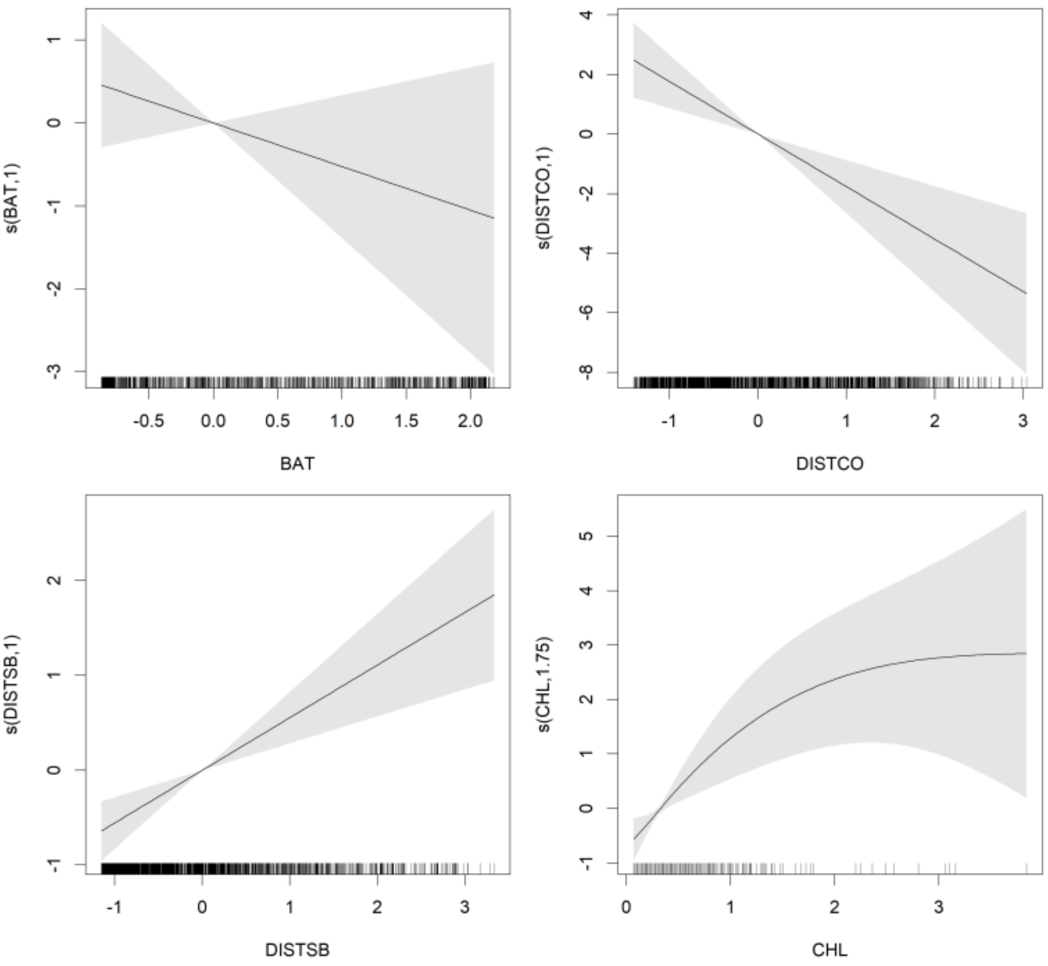


Figure 30. Functional relationship between Balearic shearwater density and the main explanatory variables: a) depth, b) distance to coast, c) distance to shelf break and d) chlorophyll.

Spatially, this resulted in a very shallow and costal distribution, restricted to northern French waters that showed very little variation across the study period (2013-2019) time (Figure 33).

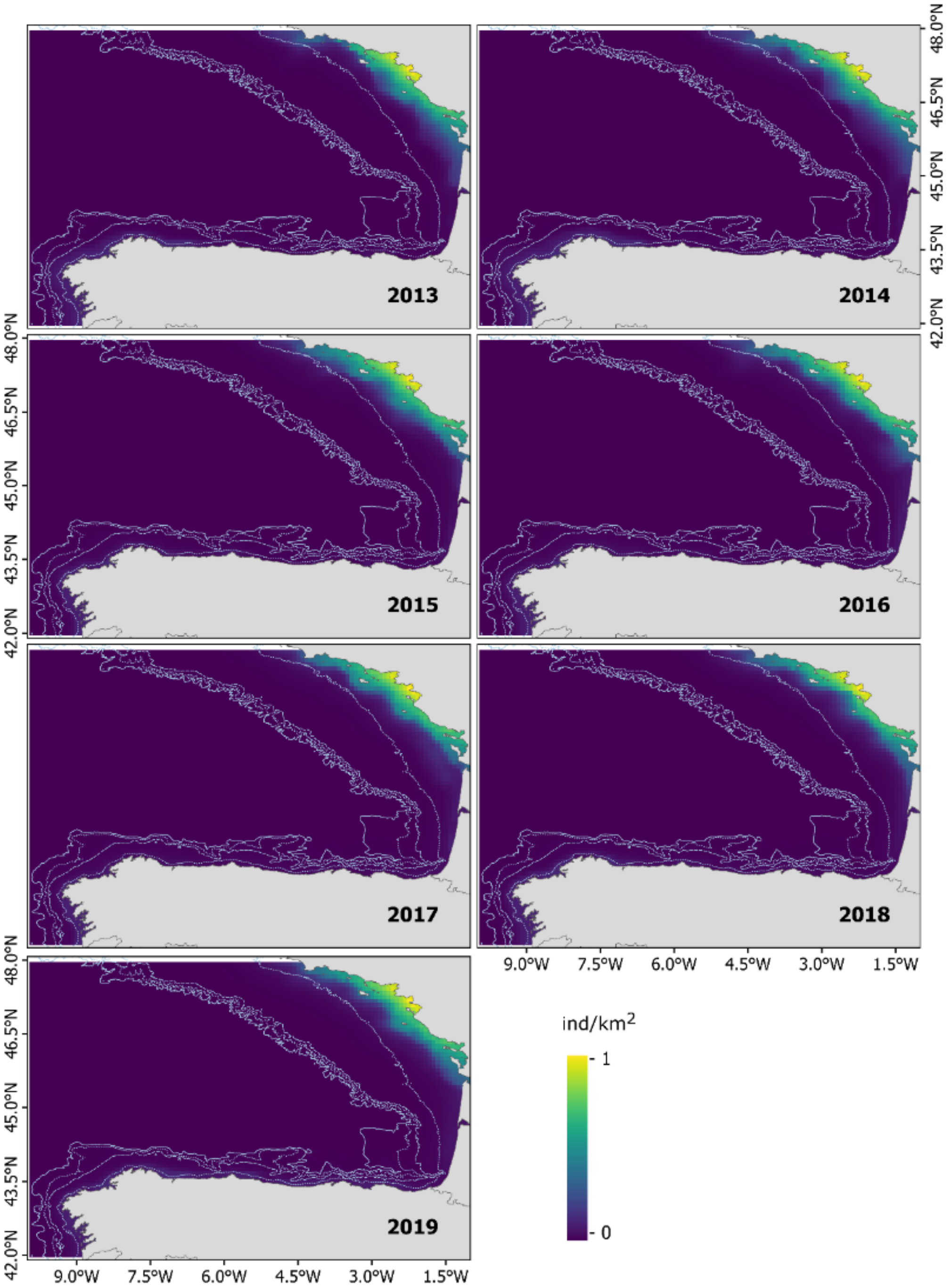


Figure 31. Relative density predictions of Balearic shearwater in the Bay of Biscay for 2013-2019 period.

The static and dynamic explanatory variables influencing the density patterns of Balearic shearwaters have been previously identified as main drivers of its spatiotemporal distribution. During the non-breeding season in the BoB, the Balearic shearwater prefers those variables linked to land or shelf-break (Astarloa et al. 2021) occupying coastal waters (Authier et al. 2018). In addition, Astarloa et al. (2021) found a strong preference of Balearic shearwaters for small-medium sardine *Sardina pilchardus*, sprat *Sprattus sprattus*, mackerel *Scomber scombrus* and anchovy *Engraulis encrasicolus* (adult and juvenile) distributed along the northwestern Atlantic French coast, i.e. from the Gironde estuary (~45º) to Belle-Ille (~47º). Similar habitat preference has been found as well during the breeding period in the western Mediterranean (Louzao et al. 2006; Louzao et al. 2012; Arcos et al. 2012).

Future projections

To assess the impact of climate change, and given that Chl was the only dynamic variable found in the distribution model, future chl-*a* from the ensemble projections of CMIP6 data on the Bay of Biscay through the FutureMARES project (https://www.futuremares.eu/) were used (Figure 34).

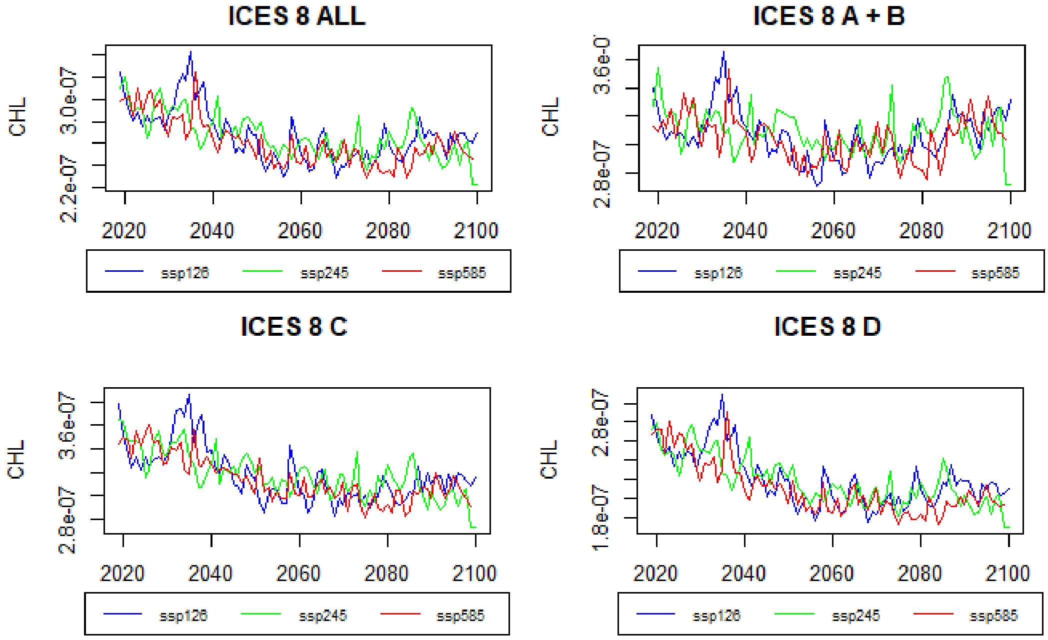


Figure 32. Projected chl-a for ICES area 8 and its subareas under three scenarios.

Future density of the Balearic shearwater *Puffinus mauretanicus* predicted by the model were presented in Figure 35. The model predicts a decreasing trend until the end of 2070s, with a potential recovery by the end of century, particularly in the subareas a and b. Subarea d would be the subarea most benefited from a reduction of emissions. The Basque coast and north of Spain in general (subarea c) shows a less positive recovery and it is aligned with previous assessments of negative assessments for the species. Previous forecasts in the literature are more pessimistic with high probability of extinction (Genovart et al. 2016).

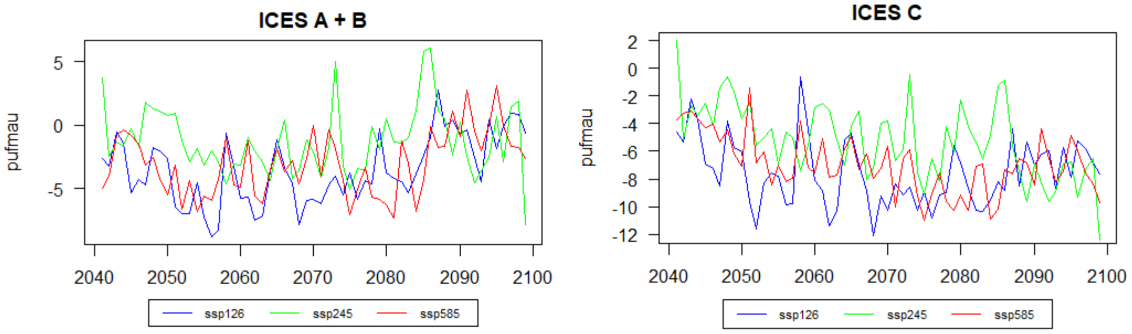


Figure 33. Projected abundance of Puffinus mauretanicus in the Bay of Biscay (ICES area 8 and subareas).

The projected declining trend of Balearic shearwater densities estimated by the changes in chlorophyll values are partially in agreement with the estimated global population decline. For example, Genovart et al. (2016) predicted a time to extinction of 61 years (95% CI: 55–69) for the Balearic shearwaters with adult survival being much lower than expected (0809, SE: 0013) for a long-lived seabird and largely influenced by bycatch, which accounted for a minimum of 0455 (SE: 0230) of total mortality (Genovart et al. 2016). Therefore, the projected increase of the at-sea densities in the BoB would not follow the same pattern as population trajectories. These could be related to the fact that causes of non-natural mortality are not considered in the projected density estimations. However, provided future at-sea densities still follow a similar trend within the following 60 years, which corresponds to the time window before the species is predicted to become extinct (Genovart et al. 2016).

CONCLUSIONS

This work confirms previous forecast of decreasing trends of species abundance under climate change. Although potential species extinction by 2060s has been suggested under previous projections, the present work is a bit more optimistic suggesting a potential recovery if the species survives beyond mid-century. However, the present work considers only one environmental factor as predictor and does not consider additional human pressures faced by the species.

3.5 Assessing the influence of oceanographic currents in migration movement of loggerhead sea turtles

Contributors: Panagiotis Petsas, Marianna Tzivanopoulou, Aggeliki Doxa, Sevrine F. Sailley, Antonios D. Mazaris

3.5.1 Context and case study

With numerous organisms performing repeated, directional, and persistent movements, migration is one of the most impressive phenomena in nature. Seasonal migration offers the chance for animals to find suitable environmental conditions, utilize alternative food sources and visit appropriate habitats for foraging and breeding (Dingle and Drake 2007; Louzao et al. 2015; Nathan 2008). As migration assists animals to cover their biological needs and to avoid adverse conditions, it contributes to their persistence (Alerstam and Bäckman 2018; Dingle and Drake 2007). Still, traveling to reach a suitable area often results in high energy demands (Hays and Scott 2013). Thus, species have to choose paths that minimize their energetic costs and their exposure to environmental pressures to achieve efficient migrations (Hein et al. 2012). However, whether species follow optimal migration paths is largely unknown and represents a major scientific challenge, particularly when developing effective conservation measures.

The optimal migration paths depend on species traits, as well as the environment's opposition (e.g. unsuitable habitat, high human activity) to species movement (Adriaensen et al. 2003; Halpern et al. 2019). Given that climatic features largely determine seascape opposition to movement between two patches (e.g., sea temperature, (Almpanidou et al. 2019); sea surface winds, (González-Solís et al. 2009; Liechti and Bruderer 1998)), climate change could alter current optimal routes, constraining alternative migratory corridors or even favor previously unsuitable routes (Robinson et al. 2009). Altered climate could either raise thermal barriers, leading to biophysical changes that might constrain species physiological limits, or lead to spatiotemporal shifts in environmental parameters (e.g., sea currents) that could facilitate or hinder movements.

Sea currents are among the most influential oceanographic features that largely determine the flow of energy and material in the marine environment (Gaspar et al. 2006; Kumagai et al. 2018). They can greatly affect connectivity (i.e., the extent to which landscape/seascape facilitates or impedes species movement among habitat patches; (Taylor et al. 1993)), as they provide directionality. From an ecological perspective, currents often promote dispersal and colonization (Treml et al. 2008); and affect food chain by concentrating prey in specific areas (Foster and Vincent 2004; Luschi and Casale 2014). Nevertheless, their degree of influence may vary among species, since animals can move with the current direction to reduce energetic cost, or move against it, requiring higher energetic demands (Caldwell and Gergel 2013).

Sea turtles are an ideal species to explore the role of sea currents in migratory movement and further detect whether a projected spatially explicit dynamic environment could favor or hinder existing traveling routes in the future. They are migratory species, traveling periodically between distinct breeding and foraging areas, covering thousands of kilometers (Hays and Scott 2013). Sea currents are shown to affect sea turtles' nesting distributions and hatchlings' migration (Putman et al. 2010), as they have a profound role in their movements (Boyle et al. 2009). Yet, the extent to which sea currents might influence adult sea turtles' movements is more controversial. Although an influence of sea currents on movement of adults has been reported (Bentivegna et al. 2007), more recent studies reported the opposite results (Hays et al. 2014; Hays et al. 2010). The effect of sea currents on movement has also been reported to differ among sea turtle species (Mestre et al. 2014). Since most of the previous studies focus only on a limited number of individuals, it would be interesting to assemble a larger amount of observed migration tracks, to explore whether and to what extent sea turtles follow an optimal migration route that minimizes their exposure to sea currents.

Here, we spatially delineate optimal routes, in form of paths and corridors that minimize exposure to sea currents, between four pairs of breeding and foraging areas of loggerhead sea turtles (*Caretta caretta*) in the Mediterranean Sea and compare them with real migration routes. The study was performed for two different 20-year periods, reflecting present (2000-2019) and projected future (2040-2059) conditions. We built upon the algorithms of least-cost path (Adriaensen et al. 2003) and randomized shortest path (Saerens et al. 2009), evaluating sea current opposition towards which the individual moves at any given point of the seascape. We compared the projected optimal outputs with a total of 39 real migration tracks, extracted from tracking studies, inspecting whether the optimal corridors overlap with the observed corridors. As the energetic cost is a major determinant of the sea turtle's movement, we compared the energy amount required between the observed tracks and their corresponding optimal paths. Finally, we assessed the spatial overlap of the optimal corridors over the two time periods, to evaluate if they are expected to persist over time under climate change.

3.5.2 Methodology

The applied methodology included several key steps: (i) we extracted all available satellite telemetry data from studies on loggerhead sea turtles in the Mediterranean Sea using Google Scholar, (ii) we extracted surface sea current data at the finest available resolution (1/8◦ degrees), (iii) we modeled and projected optimal migration paths and corridors, using the least-cost path (LCP) and the randomized shortest path (RSP) algorithms, (iv) we compared the observed and optimal routes among the three time intervals and (v) we estimated the energetic cost of migration, based on the Dynamic Energy Budget (DEB) theory. The conceptual diagram of the methods used is shown in Figure 22.

Data on migratory corridors of sea turtles

All available satellite telemetry data, between 1991 and 2020, on loggerhead sea turtles in the Mediterranean Sea were extracted from the existing literature. Overall, 39 migration tracks of female individuals' travels were identified in a total of four (4) pairs of breeding – foraging areas: (i) Alagadi (Cyprus) – Gabes (Tunisia), (ii) Crete (Greece) – Gabes, (iii) Zakynthos (Greece) - Adriatic Sea and (iv) Zakynthos - Gabes.

Climatic data - Sea current data

We extracted surface sea current data from CNRM-CM5 model derived by the MEDCORDEX (medcordex.eu) in a resolution of 1/8 degrees for both historical sea current projections and future projections based on the scenario of RCP 8.5. We considered three time periods: (i) historical data from 2000 to 2019 for the dates between July 20th to August 31st, when sea turtle post nesting migrations commonly occur in the region (Schofield et al. 2013; Zbinden et al. 2011), (ii) future projections, spanned from 2040 to 2059, considering the same dates as previously and (iii) future projections, for the same period (i.e. 2040 to 2059) but considering dates between June 10th and July 22nd, to account for a potential shift in migration onset due to climate change. Sea current direction and the overall sea current velocity was estimated for the three time periods, based on the mean horizontal and vertical sea current velocity values from all days and years.

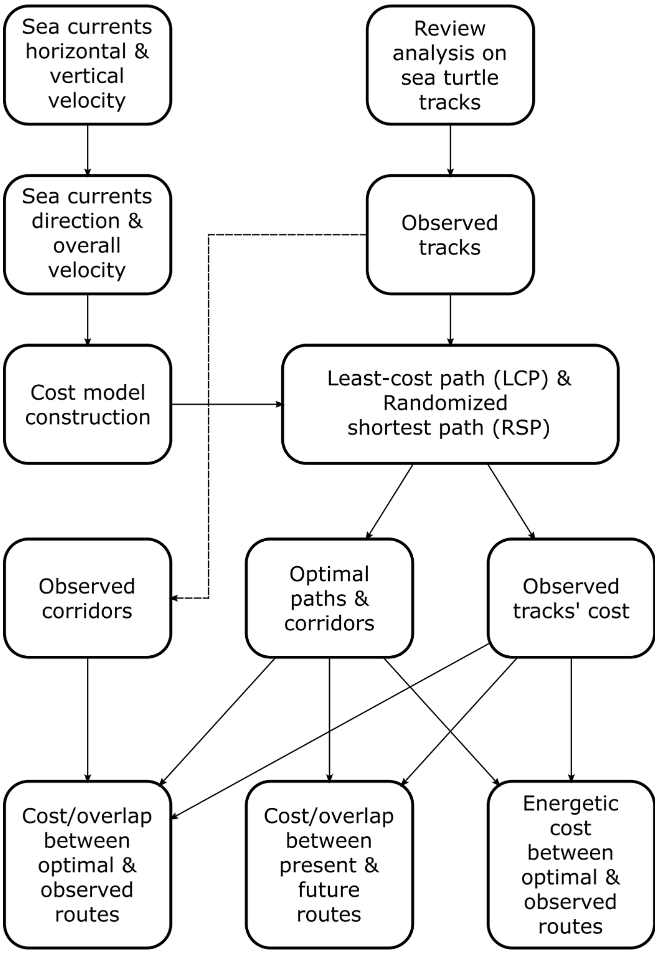


Figure 34. The conceptual diagram presenting the methods used.

Modeling seascape opposition to movement

We used the least-cost path (LCP) (Adriaensen et al. 2003) and the randomized shortest path (RSP) (Saerens et al. 2009) algorithms to project optimal migration paths and corridors from breeding to foraging areas respectively. Both LCP and RSP evaluate the transition between two points based on the seascape opposition to movement on the costs of multiple transitions between neighboring cells.

The cumulative cost of the path quantifies the effort required to perform the movement. RSP provides a map that evaluates each cell of the seascape with the probability that an individual pass through it.

The transition cost for movement between two neighboring cells was calculated based on sea current's direction, as well as the direction of movement between neighboring cells (Figure 23).

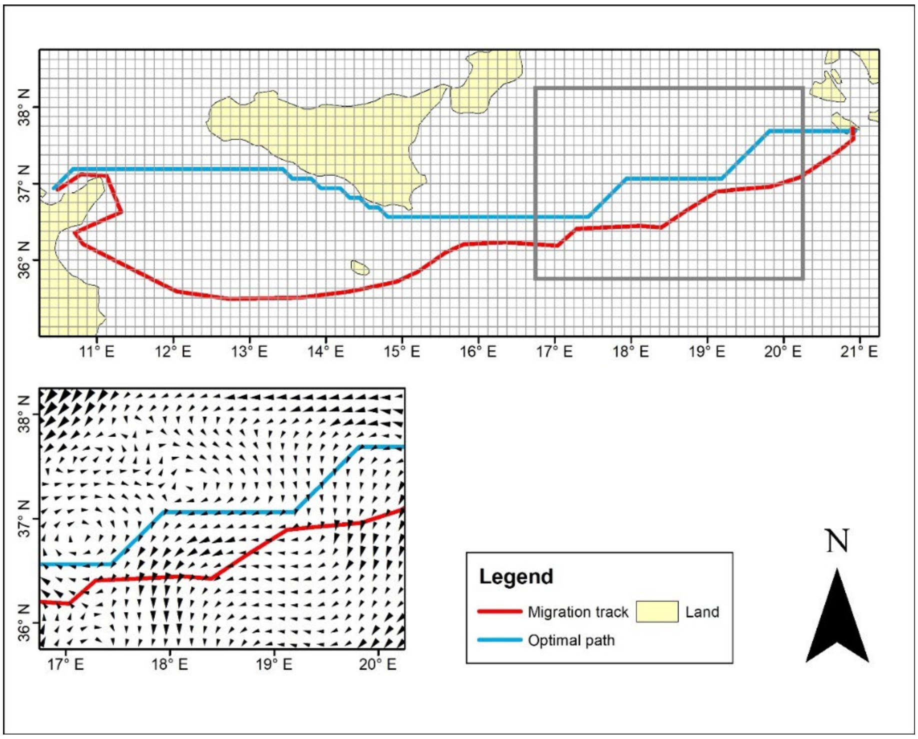


Figure 35. Comparison of an observed track (red), initiated from the nesting sites in Zakynthos, towards the breeding areas in Gabes, with its corresponding least-cost path (blue), between the same start and end points. The lower panel highlights how these routes follow the sea currents (black arrows showing sea current direction, with size analogous to its velocity).

Identification of projected optimal paths and corridors

In order to quantify the energy required for the turtles to traverse between breeding and foraging areas, by accounting for sea currents' opposition to movement, we also computed the cumulative cost of the observed migration tracks for all time intervals, by adjusting them in the cell grid of the study area. To compare the projected migration corridors from RSP with the corridors formed by the observed migration tracks, we considered four ensemble models, one per pair of breeding – foraging areas, by computing the mean probability values of the RSP that correspond to this pair's tracks. The observed corridors, as delineated by the migration tracks, were created by generating one kernel density map per pair of breeding – foraging areas. This procedure was performed in ArcMap v10.7, with the search radius for these kernel density maps being extracted by the Silverman's rule of thumb (Harpole et al. 2014). In regard to the parameter values, we selected k=4 and θ=0.3, and conducted a sensitivity analysis on these parameters on the models' outputs.

Comparison of projected paths and corridors with observed migration tracks

Furthermore, we used Spearman correlation analyses between the time intervals for each attribute of the migration tracks (i.e., cumulative cost and length), optimal paths (i.e., cumulative cost), and corridors (cell-wise probability values), to examine whether they share similar properties among the different climatic conditions

To assess the extent to which the migration corridors between foraging and breeding areas were similar between the different time intervals, we used the Jaccard index of similarity. This index ranges from 0 to 1, with values close to 1 indicating high proportions of cells identified as corridors by both time intervals.

Data analysis of digitized tracks was conducted in ArcMap v10.7 (ESRI). The connectivity models and the statistical analyses were conducted in R v4.0.3, using “raster”, “ncdf4”, “gdistance” and “tidyverse” packages.

Migration energetic cost

To provide an estimate on the energy amount that could be saved if the optimal path was preferred over the observed one, we applied a mechanistic context that allowed us to transfer difference of travel days into reproductive output. The key context of our models relay on the assumption that a day less spent at sea could be used for the production of more eggs. Assuming that individuals cover 50 km/day on average (Hays et al. 2014), we estimated the travel days of each observed migration route. Using the cost ratio of observed migration tracks and their corresponding optimal path, we estimated the travel days of the corresponding optimal paths derived by LCP algorithm. The difference of travel days between observed tracks and optimal paths indicate the travel days that could be saved if the optimal path would have been chosen. To transfer the gain of these days into a potential difference in egg production we had to estimate first the amount of energy that would be required to ensure the key metabolic processes.

We calculated the minimum energetic cost spent per day, based on the Dynamic Energy Budget (DEB) theory (Kooijman and Kooijman 2010). Since loggerheads do not feed while migrating from foraging to breeding grounds, individuals use their reserves to cover basic metabolism and produce their eggs (Hays et al. 2014). We considered an average turtle with a straight carapace length (SCL) of 78.5 cm (Margaritoulis et al. 2003), which corresponds to a structural length (L) of 29.045 cm ($L = SCL*\partial M$ with $\partial M = 0.3744$) (Marn et al. 2017), with L being a measure of the turtle size used in DEB models that reflects the size and thus, the energetic demand of an individual. Based on Marn et al. (2017), we considered a daily metabolic cost of structure maintenance equal to 13.25 J/cm3. Considering that the energetic value of an egg being on average 209,640 J (Marn et al. 2017), we estimated a minimum number of eggs that could be produced per day. Next, we summed the number of eggs that could be saved if a number of days would be saved once the optimal path is chosen.

To further provide an alternative estimation of the actual number of eggs that could be produced, we applied the approach of Hays et al. (2014b), where spent energy is translated in days away from foraging grounds. We estimated that one day of travelling corresponds to the production of 7.33 eggs per day, by considering that the mean clutch size is 110 eggs (Hays and Scott 2013) and is produced within 15 days (Hays et al. 2014b).

3.5.3 Results and Conclusions

Our analysis revealed a significant, positive relationship between the cumulative cost of the observed migration tracks and the cumulative cost of their corresponding optimal paths ($r_s = 0.86, p < 0.05$). However, the observed migration tracks were found to have on average 1.25 times (±0.15) the cost of their corresponding optimal path. Overall, we observed medium to low correlations between the observed and the projected migration corridors i.e. Crete-Gabes case ($r_s = 0.43, p < 0.05$), Zakynthos-Gabes case ($r_s = 0.42, p < 0.05$) and Zakynthos-Adriatic Sea case ($r_s = 0.30, p < 0.05$). For the case of Alagadi-Gabes route, that the most notable difference was detected in the direction of observed and projected corridors, the association reached even a negative sign ($r_s = -0.18, p < 0.05$) (Figure 24).

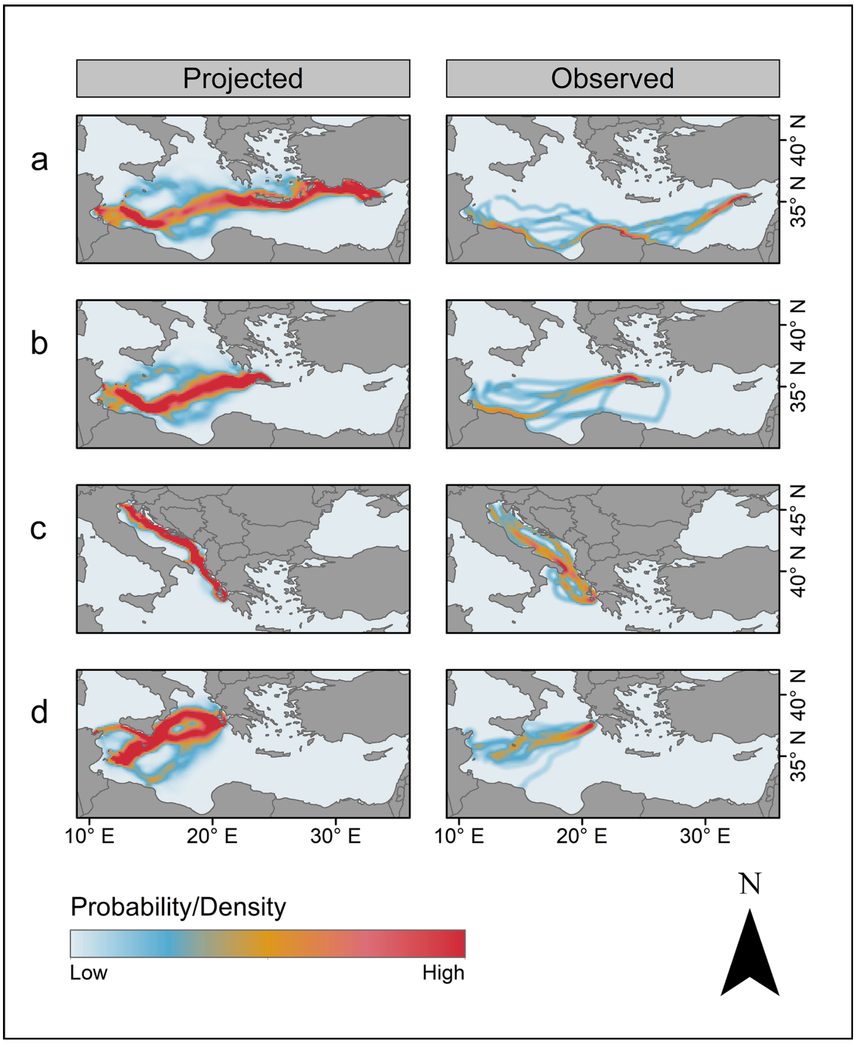


Figure 36. Comparison of optimal corridors, derived from randomized shortest path (RSP) algorithm with kernel density map derived from the observed tracks. Each row corresponds to a pair of foraging –breeding areas, being a) Alagadi (Cyprus) to Gabes (Tunisia), b) Crete (Greece) to Gabes c) Zakynthos (Greece) to the Adriatic Sea and d) Zakynthos to Gabes. Cell values

indicate probability that an individual traversing between the areas passes through it (left panels), and number of detected observed tracks within the cell's proximity (right panels).

The optimal paths exported by LCP had a positive degree of association among the time intervals ($r_s > 0.99$, $p < 0.05$ for both cumulative cost and length, for each pair of time intervals). Similarly, positive correlations were found for the cumulative cost of migration tracks, as well as the probability values of RSP maps between the three time intervals ($r_s > 0.98$, $p < 0.05$). The Jaccard index of similarity provided values over 0.70, indicating that corridors among the time intervals were relatively similar in terms of their spatial extent. The main differences were detected on sub-corridors that emerge in the proximity of the main corridors (Figure 25). As an example, a visual inspection on the projected migration corridors for Alagadi – Gabes and Crete – Gabes indicated that in the projected future movement through the coastal area of Libya and Tunisia will be more profound (Figure 25a&b), while corridors projected under a potential phenological shift would more likely take place through southern coast of Italy. The corridor that connected Zakynthos nesting sites to the Adriatic Sea foraging sites was projected to be rather narrower under a potential earlier onset of migration (Figure 25c). In addition, for the migration corridors between Zakynthos and Gabes, we observed that a small sub-route from the coast of southern Sicily had lower probability to be selected, if a phenological shift is observed in the future (Figure 25d).

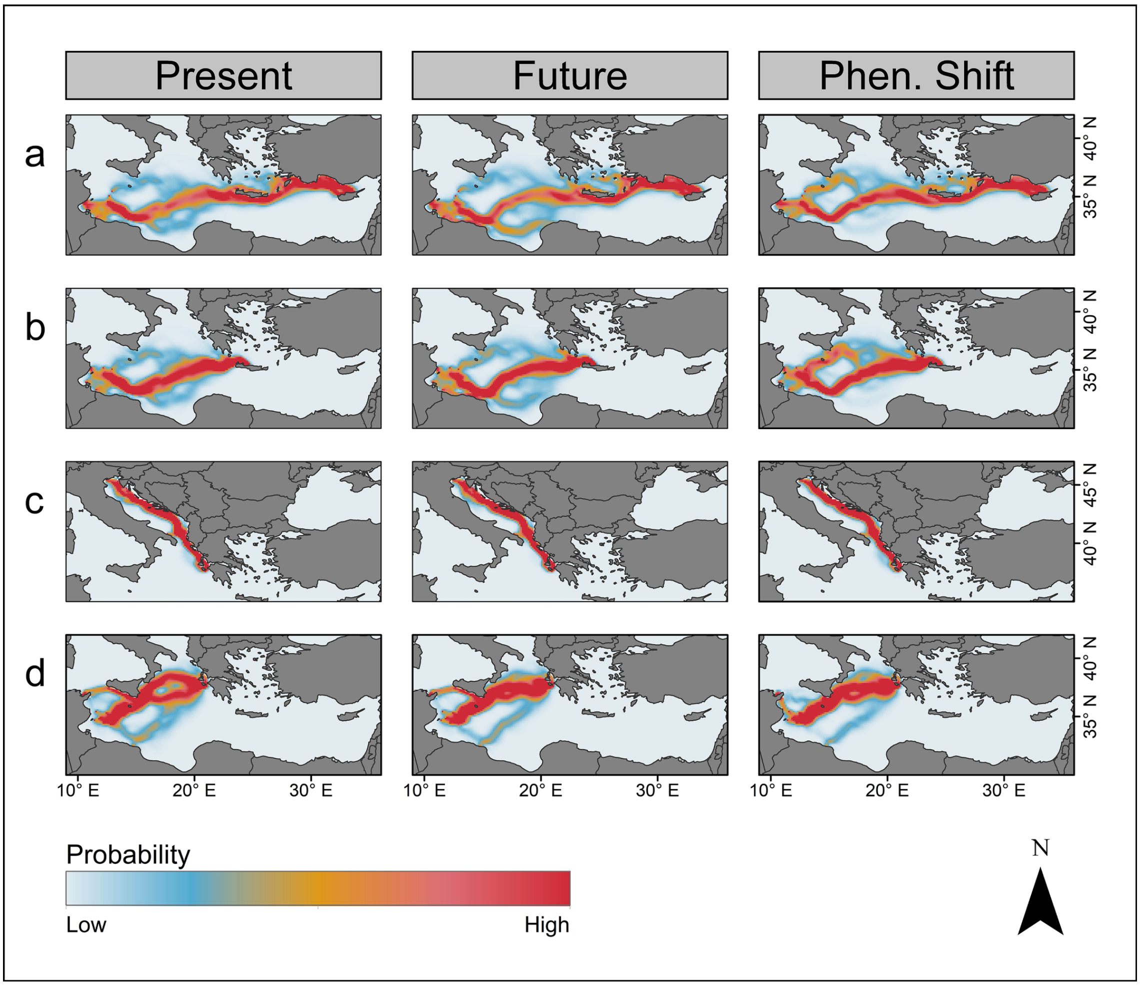


Figure 37. Optimal corridors derived from randomized shortest path (RSP) algorithm for three different climatic conditions. Each row corresponds to a pair of foraging –breeding areas, being a) Alagadi (Cyprus) to Gabes (Tunisia), b) Crete (Greece) to

Gabes c) Zakynthos (Greece) to the Adriatic Sea and d) Zakynthos to Gabes. Cell values indicate probability that an individual traversing between the areas passes through it.

Theoretical considerations on energetic costs

Following the optimal path between breeding and foraging areas could save on average 4.87 days (Figure 26). Using the DEB theory, we estimated that loggerheads daily metabolism would be equal to 324,660.9 J. This means that for each day that a turtle is migrating, there is a minimum energetic loss that corresponds to 1.55 eggs per day, indicating that on average, the optimal path could result turtles to save the energy for 7.55 (±6.99) eggs. Considering that this energy comes out of existing reserves it means that for each additional day spent migrating there should be additional time needed to be spent at the foraging ground rebuilding that reserve before any energy is allocated to reproduction. This is a conservative estimate as it only considers the basic metabolism and does not account for any of the added cost of swimming against currents, change in metabolism based on sea temperature or any other factors that will increase the energetic cost. Our alternative approximation on the exact number of eggs that could be produced under the shorter, optimal path, showed that the energy saved could be translated in a mean number of 35.74 eggs (±34.02).

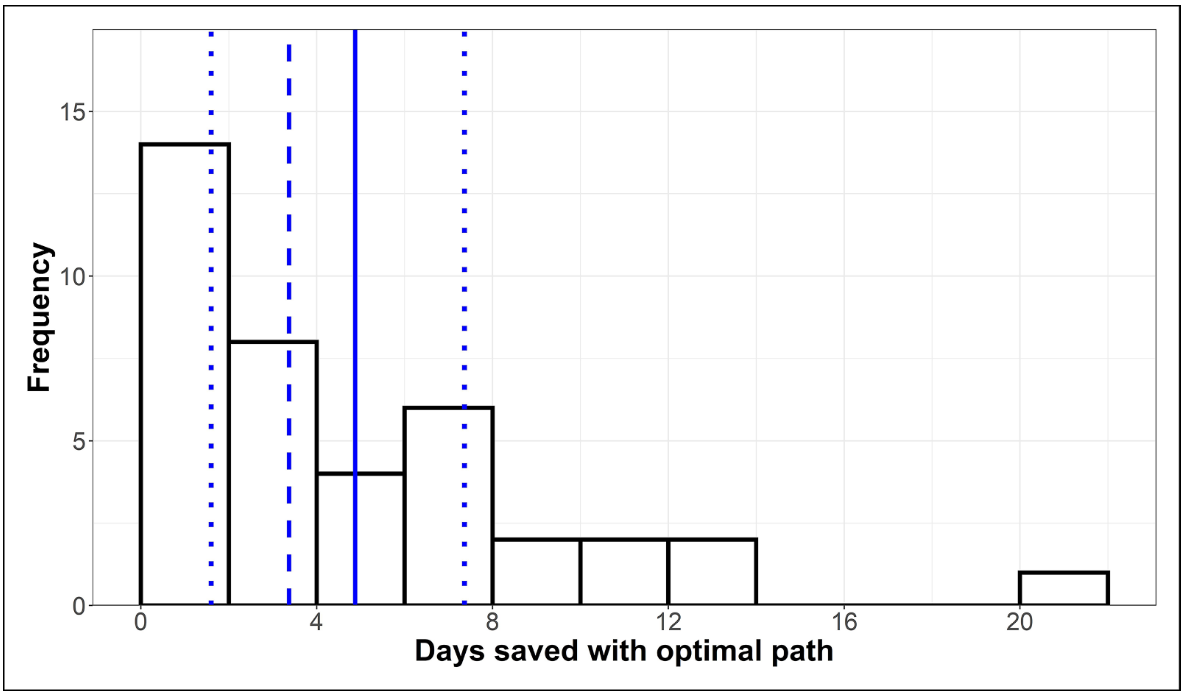


Figure 38. Number of days saved if an individual would follow the optimal path instead of its tracked movement. The solid line indicates the mean value, the dashed line indicates the median value, while the dotted lines indicate 25th and 75th percentiles.

CONCLUSIONS

Our results indicate that loggerheads do not explicitly take advantage of ocean currents to facilitate long-distance migrations and reduce energetic demands, and that the effect of climate change on sea currents is not expected to alter contemporary migration routes of loggerhead sea turtles. The contemporary and future migration routes are characterized by similar energetic demands and together with their strong spatial overlap suggest that climate change is expected to minimally alter the species migration routes in the future. The approach presented here could be applied to different spatial scales and marine taxa, allowing possible mechanisms between sea currents (or other environmental characteristics) and species movements to be elucidated. Incorporating connectivity assessments, such as this work, to conservation planning approaches is crucial for future conservation design under climate change.

Our study demonstrated a cost mismatch between the observed tracks and their corresponding optimal paths. Other marine species also travel independent of sea currents. For instance, whale sharks travel against sea currents, counter-balancing energetic costs with regular foraging (Sleeman et al. 2010), while humpback whales exhibit highly directional movement in open sea, constantly adjusting displacement caused by sea currents and bathymetry (Horton et al. 2011). The preference for coastal areas over open sea could be explained by the potential for opportunistic feeding while travelling (Cheng 2000; Godley et al. 2002). However, while this might occur for green turtles (Cheng 2000), loggerhead turtles also feed in the open sea (Foley et al. 2013). Both empirical evidence and models show that climate change alters the migratory routes of marine species (Anderson et al. 2013; Robinson et al. 2009). Yet, our analysis showed that optimal corridors based on present sea current data were similar to future ones, even when considering a potential phenological shift due to climate change. The only notable differences were identified in sub-corridors, which had different climatic conditions in each time interval. The cumulative cost of both optimal paths and observed tracks minimally differed among the three time intervals. While the exact location of optimal paths might change over time due to climate change, suitable oceanographic conditions could probably be found within the surroundings.

Nevertheless, climate change could affect the location of nesting areas, as climatic conditions strongly affect hatchling success and sex ratios (Fuentes et al. 2011; Pike 2013; Turkozan et al. 2021), regulating population viability (Mazaris et al. 2005). Furthermore, certain climatic factors, such as marine heatwaves, could constrain food availability at contemporary foraging grounds (Konsta et al. 2022), forcing them to shift to alternative, suitable, foraging locations. Such changes to foraging and breeding areas would, in turn, alter the migratory routes between them. In addition, climate change could affect migrating turtles through other facets, such as increased warming (Almpanidou et al. 2019), hindering their movement, which would significantly impact the energetics of the migration and, by extension, the reproductive effort of turtles (Hays et al. 2002).

3.6 New mechanistic model for Megafauna and prey species interactions

Contributors: Sevrine F. Sailley, Ana M Queirós

3.6.1 Context and case study

The above studies deal with specific aspects of the life of megafauna species, that is their preferred habitat, migration route and/or prey capture. To do this they use statistical methods such as species distribution models (SDM) that allow for a fast extrapolation from the data. If one wants to resolve population dynamics, energetics and how these would be impacted by CC, one needs to go the route of more mechanistical models where the relationships are derived from data not driven by them through the use of statistical methods. This allows for the application of the model to broader area and experiment with more simultaneous changes, and to combinations of environmental conditions not observed at present, as projected for the future ocean, where many ocean variables exceed current observed ranges (i.e. climate signal; Kearney and Porter 2009; Silber et al. 2017; Bindoff et al. 2019). This type of model is not yet available for megafauna. This is due to the complexity of life stages, high mobility, and sometimes elusiveness of the species which make it difficult to get the right parameterisation for a mechanistic model. For proper management and NBS, having as much information as possible on the possible impacts of climate change on charismatic species is key. To this end, as core aim of this task has been to develop mechanistic models for two widespread species of high conservation value to Europe, *Caretta caretta*, the loggerhead turtle, in the Mediterranean Sea, and *Tursiops truncatus*, the bottlenose dolphin, in the Northeast Atlantic. These developmentse serve as stepping stones for the model structure developed in FutureMARES, and showcase a transportable, easily adaptable model that can be applied to any species in the future provided relevant data and information are available.

3.6.2 Methodology

Required outputs and model structure

To be useful for management decisions and NBS as well as significant for exploring scenarios we decided the model needed to output several different metrics:

a. Individual distribution, preferred habitat
b. Population structure (e.g. age cohort, sub-population) and number of individuals in any sub-structure for the population. For example, for the turtle the model identifies turtle by their nesting site, whether there are juvenile or adults, and their age.
c. Individual state (e.g. size, age, reproductive status, etc.)

The needed information helps direct the model as we can then select the best approach for the final model by nesting the different necessary required part to become a functioning whole. We identified a number of models that fill the requirement:

a. Species Distribution Models (SDM) - distribution
b. Population model (PM) - population dynamics
c. Dynamic Energy Budget (DEB) models – energetics and reproductive effort

In addition, we need outputs from a biogeochemical model to provide information from the environment to determine which habitat are suitable and what are the conditions there that could affect the growth, reproduction and survival of the species of interest. These came from FutureMARES WP2.

Beyond the choice of models, we have to take into account how they would interact with each other. That is the flow of information within and between the model parts. At the core, the DEB is a model for resolving the energetics of individual organisms and work on a scale of days, with no inherent spatial resolution. The Pop model uses individuals as a metric for the population growth and mortality with the spatio-temporal scale varying on the model and its application. Finally, SDMs generally resolve species distribution on an annual basis at the population level for whichever spatial scale is investigated.

This means we need to carefully mesh each approach to obtain a coherent whole. Using agent-based model we can create super individuals (SI) that correspond to specific sub-populations, the SI allows for merging the information between the DEB and PM. Finally, the SDM provides us with location of the animals and allows us to extract environmental conditions from the biogeochemical models to feed to the relevant section of the DEB and PM (see Figure 39 for model structure).

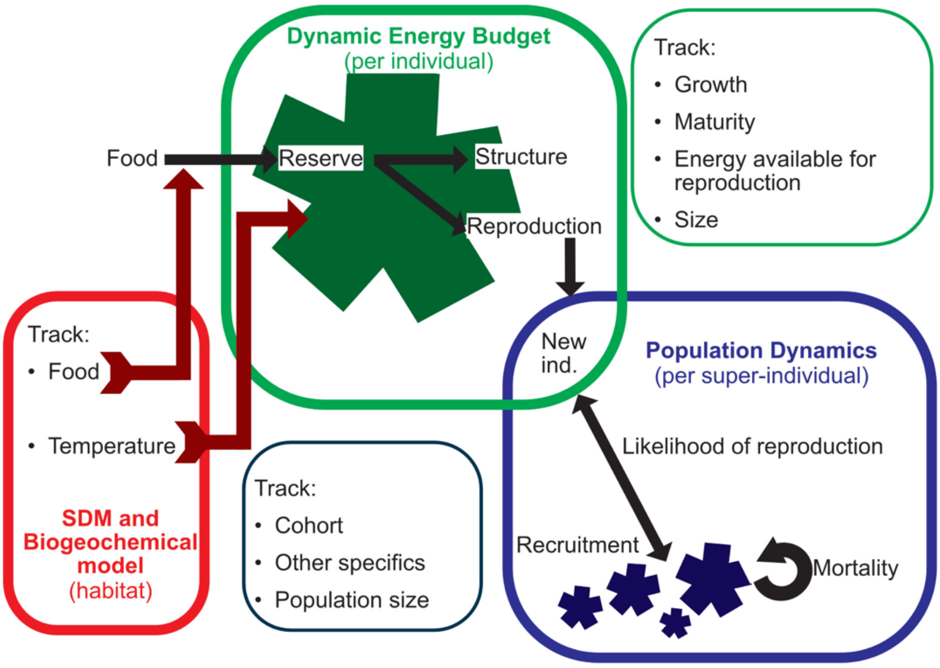


Figure 39. Schematic of the mechanistic model structure showing the three model components (SDM, DEB and Pop) and their interaction at specific stages. The square star shape represents a generic organisms rather than a specific one, highlighting whether the model is at the individual or at the super individual/sub-population scale.

The SDM reads the environmental variables from the biogeochemical model and derives where the organisms are more likely to be found. From there the temperature and productivity in the area are extracted from the biogeochemical model to provide variables to the DEB model. The primary productivity is processed to be the available food available for the growth of the organisms while the temperature will impact the various metabolic processes (respiration, growth, maintenance of the organisms) and how much is available for reproduction once all the base metabolic needs have been taken care of. From there the DEB model determines whether reproduction is possible and how many new individuals can be expected, that is, for the case of the sea turtles, how many eggs will be layed per individual, or for the dolphins' case, how many females have a reproductive event. The number of new individuals is then passed to the Pop model to become a new cohort. The population model will look at recruitment of the new individuals and apply age specific mortality to each cohort individually (e.g. in the case of the turtle there is a high mortality of the juveniles).

Data

To build the models we need a number of different source of data to parametrise, initiate and validate the model. These fall in broad categories:

- Distribution data (e.g. sightings, telemetry); from literature and OBIS (https://obis.org/).
- Species specific data like nesting sites for *C. caretta*; from literature and the State of the Sorld Sea turtle (https://seamap.env.duke.edu/swot)
- Rates of population dynamics (e.g. mortality rate, recruitment rate, frequency of reproduction, …); from literature
- Rates for the DEB model; from literature and associated DEB model parameter repository "Add my Pet" (https://www.bio.vu.nl/thb/deb/deblab/add_my_pet/)

The table below (Table 8) indicates the sources for the models and data used here. Note that all data come in different format and resolve different spatio-temporal scales. This means that similarly to the meshing of the model the data need to be curated and formatted to be used in the models.

Table 8: Table showing the source for the data and model information for the two target megafauna species

	Turtle	Dolphin
DEB	Marn et al. 2017a & 2017b Stubbs et al. 2020 Add my Pet Koijmaan et al. 2005	Add my Pet Koijmaan et al. 2005
Pop model	Mazaris et al. 2006	Not yet sourced
SDM	Chatzimentor et al. 2021 (section 3.5)	Waggit et al. 2020
Distribution data	Chatzimentor et al. 2021 (section 3.1) OBIS	OBIS
Nesting sites	SWOT	N/A
Biogeochemical model	WP2	WP2

3.6.3 Results and Conclusions

Model status and preliminary results

Model, parameter values and data have been source for all aspects of the *C. carretta* model and only a few elements are missing for the *T. truncatus* model (see Table 8). The implementation of the DEB and Pop models using the super-individuals approach was successful and made it possible to track cohorts by nesting sites, number of eggs laid by individuals or cohort (see Figure 40 for the number of eggs produced by a specific cohort over the years as well as the number of individuals in said cohort), and extract population statistics on a year-to-year basis such as distribution of size and age (see Figure

41, which shows the population structure with number of individuals per cohort). This provides in-depth information in the dynamics of the population, but also individual and cohort health.

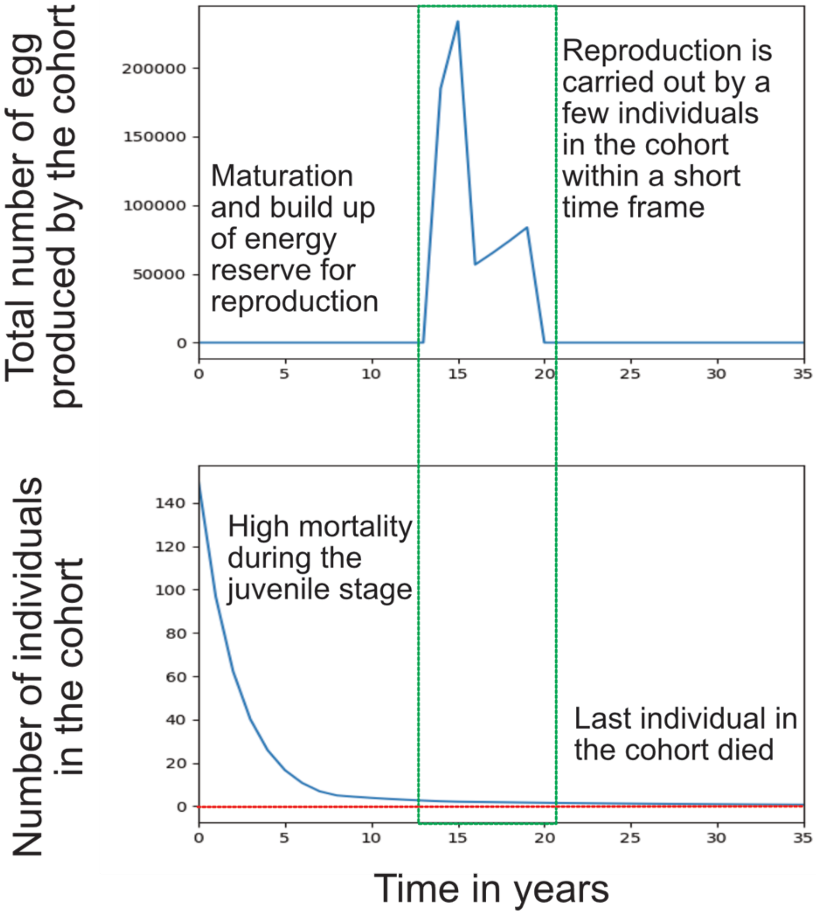


Figure 40. Example outputs from the DEB and Pop model. The top graph shows the egg production for one cohort as the years passed and the individuals within it mature. The bottom graph shows the size of the cohort, from the initial recruit to the last individual. The green box shows the reproductive output for this cohort, and how many individuals actually make it to this period. The various text highlight different phases for the cohort dynamics.

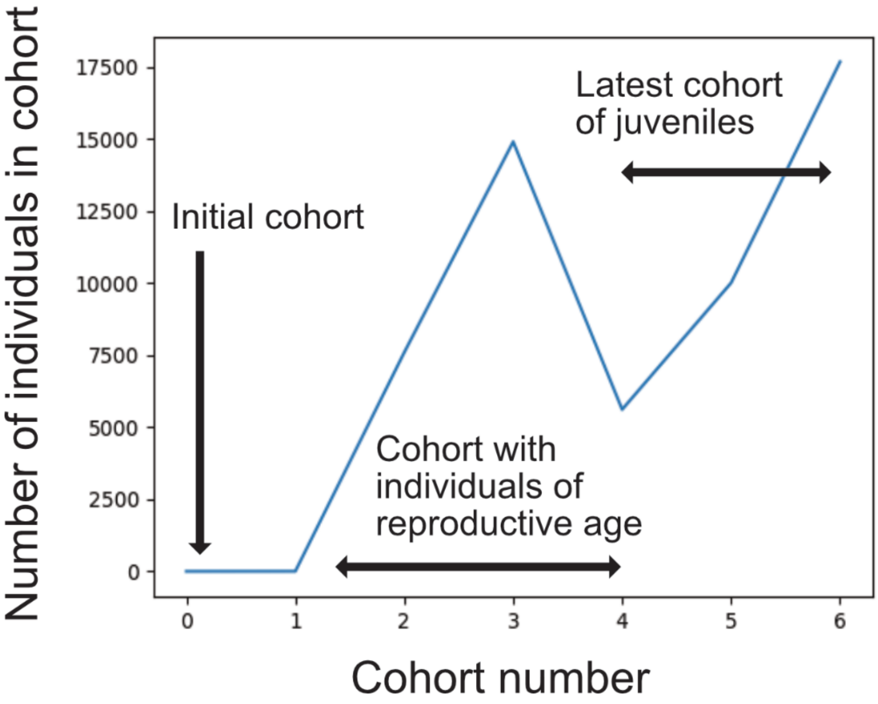


Figure 41. Example of outputs looking at population statistics. In this case, the number of individuals per cohort after the model was run for a 20 years period. The initial cohort is long extinct and we see the current cohorts of reproductive age as well as the cohorts of reproductive age.

The integration of the information from the habitat model as well as using those to extract relevant environmental information from WP2 proved to take more time both in ensuring data coherence and data flow between the different model elements. And cannot yet be presented. Once this is resolved the models will be run on a climatology of early 21st century conditions for 100years to create a mature population. The information from this that will then be used to start the climate change projections runs.

Conclusion

The results presented above highlight the great potential of this type of model for assessing population dynamic response to CC, once the environmental conditions and habitat can be factored in it will add another dimension to the model looking at distribution of the species and impact of changes in the environmental conditions they habit (e.g. temperature and productivity change) as well as any change in spatial distribution (e.g. smaller habitat, displacement of population).

This also highlight that the higher complexity of the mechanistic models despite being more driven by processes makes them a complicated and hard to develop tool with statistical models being a faster approach to solve specific questions. To this end these models were also developped in a way that makes them portable to over regions (provided data are avaialble) but also in theory the modelling framework is flexible enough to allow for its adaptation to other marine megafauna whether they have specific nesting site on land or at sea like sea turtles (e.g. penguins, seals) or spend their entire lifetime at sea like dolphins (e.g. whales, sharks). The results presented here are a great illustration of the technological advancement in the mechanistic modelling of megafuana species distributions that FutureMARES is delivering.

4. Conclusions

The work undertaken within Task 4.2 and presented in this deliverable highlighted important aspects that will empower future surveys of CC impacts on marine megafauna, while highlighting potential conservation and/or modelling challenges and perspectives.

The compilation of extensive distribution and movement datasets resulted in validation of monitoring technics for the survey of marine megafauna:

- Opportunistically collected data, such as sightings of cetacean species from ships, can be a valuable supplementary source of information, adequately complementing systematic monitoring protocols. Although more scarce and less detailed than dedicated records, both types of data provided similar results in terms of abundance trends, number of species recorded, and resulted to similar cetacean community compositions, at least for the most frequently sighted taxa / species. For frequently recorded species, opportunistic datasets also provided representative results in terms of habitat range. However, oppurtunistic data can be rather limited regarding habitat variables and less frequent species. Given the acknowledged challenges to adequately and systematically monitor cetacean species, opportunistic and dedicated datasets should be used together, whenever possible, as there is often a substantial amount of opportunistic data where no survey effort was undertaken.
- Applying different modeling techniques and validating their outputs with independent field data, allowed to obtain a better view on the key foraging sites for adult loggerheads across the Mediterranean. Assessing the exposure of these habitats to the combined risk of different human-related threats, provided spatially explicit information for determining hotspots of particular conservation concern.

The compilation of extensive distribution and movement datasets resulted in the developement and optimization of widely used statistical distribution models:

- Future projections for loggerhead sea turtles showed that several important foraging areas for both juveniles and adults are expected to maintain their climatic suitability in the future. However, foraging areas that are now located at the central and eastern Mediterranean are projected to shift towards the western Mediterranean. Given the species fidelity to both nesting and foraging areas, this raises concerns about the species adaptive response and a possible shift of the distribution for adult loggerheads towards the west.
- These findings, based on SST projections and species distribution modelling, were also confirmed when using depth specific climatic data, as resulted from the FutureMARES project for the Mediterranean Sea at three depth levels (5m, 25m and bottom temperatures). Important foraging areas in all depth layers and for both life stages of loggerhead sea turtles were mainly revealed in the central (North Adriatic Sea, Tunisian plateau) and west Mediterranean Sea (Balearic Islands, Gulf of Lions). For adults, a westward shift in climatically suitable areas was predicted, while for juveniles, important 3D climatically suitable foraging areas were projected to occur in the Adriatic Sea. However, an overall potential loss of climatic suitability was predicted for the edges of the southeast range of habitats, a pattern which agrees with climate change related shifts in abundance and might cause a reduction in the abundance of juveniles in these areas.

- Alarming projections were presented for the Balearic shearwater, predicting decreasing trends of species abundance under future climate change. However, contrarily to previous studies suggesting a potential species extinction by 2060s, the current projections suggest a potential recovery of the species by the end of century, if the mid-century extinction risk is prevented. Although relatively optimistic, this analysis considered only one environmental factor for future predictions, while it neglected additional human pressures faced by the species, which may synergistically increase the species extinction risk to climate change.
- The spatial density of great shearwaters was revealed to be mainly driven by the distance to the coast, highlighting offshore waters as the preferred habitat for the species. Along the shelf edge, tides generate internal waves that propagate both on- and off-shelf, which seemed to be responsible for significant mixing and nutrient upwelling at the shelf-break. Consequently, these areas aggregate small prey species being highly relevant for top predator species. Great shearwater aggregations were also linked to favorable wind direction, facilitating the arrival of great shearwaters from their breeding areas. Potential feeding grounds for great shearwaters were also revealed in cases of coastal upwelling, enhancing the aggregation of large biomass of small pelagic fish.

Ecosystem based modelling was developed and used to investigate possible links between marine megafauna and prey distributions:

- The ecosystem model did not project large changes or differences among the CC scenarios for seabird and cetacean species, implying a positive message about the potential resilience to climate change for these species. However, large functional groups were considered as the model input, without deep understanding of the different eco-physiological and other biological mechanisms. Future work should focus on studying individual species from a more mechanistic point of view.

Novel mechanistic distribution models were developed for marine mammals and sea turtles, based on the DBEM framework, shedding light on species energetic demands and population dynamic responses to climate change:

- Regarding the influence of climate change on sea currents and the putative effects on sea turtles' migration movements, the analyses revealed that loggerheads do not explicitly take advantage of ocean currents to facilitate long distance migrations and reduce energetic demands. The contemporary and future migration routes were projected to have similar energetic demands. Their strong spatial overlap, even when considering a potential phenological shift due to climate change, suggested that climate change is expected to minimally alter the species migration routes in the future. Nevertheless, climate change could affect the location of nesting areas and certain climatic factors, such as marine heatwaves, could constrain food availability at contemporary foraging grounds, forcing sea turtles to shift to alternative, suitable, foraging locations. Such changes to foraging and breeding areas would, in turn, alter the migratory routes between them. The approach presented here could be applied to different spatial scales and marine taxa, allowing possible mechanisms between sea currents (or other environmental characteristics) and species movements to be elucidated. Incorporating connectivity assessments, such as this work, to conservation planning approaches is crucial for future conservation design under climate change.

- Novel modelling approaches allowing to properly integrate process-based information is highlighted by assessing population dynamic responses to climate change for cetaceans and sea turtles' species. While statistical models remain the tools available to meet this task, higher complexity mechanistic models provide novel insights which could help curtail the current limited skill of statistical based models for species distributions.

5. Indexes

5.1 Index of Figures

5.2 Index of Tables

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