

**Assessing habitat suitability of marine fish in the face of climate change –
Implications for conservation and management**

“ Documento Definitivo ”

Doutoramento em Biologia e Ecologia das Alterações Globais
Especialidade de Biologia e Ecologia Marinha

Friederike Peiffer

Tese orientada por:

Professora Doutora Susanne E. Tanner

Professor Doutor Emanuel J. Gonçalves

Doutor Gonçalo J. F. Silva

Documento especialmente elaborado para a obtenção do grau de doutor

UNIVERSIDADE DE LISBOA
FACULDADE DE CIÊNCIAS



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ABSTRACT

Climate change and other anthropogenic stressors are threatening the biodiversity and integrity of ecosystems worldwide. One of the most common consequences of climate change is the poleward shift in species distribution. However, not all ecosystems and geographic regions are equally affected. Species traits play a key role in determining their sensitivity to environmental change. Species Distribution Modelling (SDM) has been widely used as a tool to inform conservation and spatial planning, as well as to predict the impacts of climate change on species distributions. This thesis aimed to understand how the traits of marine fish species influence species–habitat relationships and the response to climate change, and to link these findings to conservation and fisheries management. This was achieved by combining multi-scale and multi-level SDM approaches. The model outcomes revealed differential responses to climate change across species with varying life-history strategies (i.e. opportunistic, periodic, and equilibrium) and dispersal abilities. Predicted range contractions of primarily equilibrium species, in contrast to consistent habitat gains for opportunistic species, support the theory of trait-based responses to climate change and demonstrate the relevance of this framework for ecosystem-based management. Furthermore, modelling range shifts for sedentary species with passive dispersal (seahorse) highlighted the role of oceanographic connectivity and intrinsic dispersal mechanisms in climate-driven range shifts. Besides, the practical application of SDM at the regional scale identified hotspot areas for the conservation of seahorses along the Iberian coast and limitations in the coverage of the current MPA network. The systematic comparison of modelling approaches provided further evidence of the importance of aligning modelling choices with species ecological requirements and the environmental variability of the study area. Overall, this thesis provided critical insights into the use of SDM, advanced the knowledge on trait–environment relationships and highlighted the need for adapting management measures to species’ ecology and climate change.

KEYWORDS

Trait-based ecology, Biogeography, Species Distribution Modelling, Dispersal, Life-history

RESUMO

As alterações climáticas e outras pressões antropogénicas estão a ameaçar a biodiversidade e a integridade dos ecossistemas globalmente. A mudança na distribuição das espécies em direção aos polos é uma das consequências mais comuns das alterações climáticas. Contudo, nem todos os ecossistemas e regiões são igualmente afetados, e as características das espécies desempenham um papel fundamental na sua sensibilidade às alterações. A modelação da distribuição de espécies (SDM) tem sido amplamente utilizada para informar a conservação, o planeamento espacial e prever os impactos das alterações climáticas. Esta tese teve como objetivo compreender como as características das espécies de peixes marinhos e as alterações climáticas influenciam as relações entre espécies e habitats, articulando estes resultados com medidas de conservação e gestão das pescas. Para tal, foram combinadas abordagens multi-escala e multinível de modelação de adequabilidade de habitat. Os resultados revelaram respostas diferenciadas às alterações climáticas entre espécies com diferentes estratégias de história de vida (i.e., oportunista, periódica e de equilíbrio) e capacidades de dispersão. As contrações do habitat previstas para espécies do grupo equilíbrio, juntamente com os ganhos consistentes para espécies oportunistas, demonstraram o papel fundamental das características da história de vida nas respostas às alterações climáticas e a sua relevância para a gestão baseada nos ecossistemas. A modelação de espécies sedentárias com dispersão passiva (cavalos-marinhos) em diferentes cenários climáticos destacou ainda o papel da conectividade oceanográfica e dos mecanismos intrínsecos de dispersão nas mudanças da distribuição. A aplicação prática de SDMs em escalas regionais permitiu identificar ‘hotspots’ de conservação para cavalos-marinhos na costa ibérica, evidenciando também limitações na cobertura da atual rede de AMP. No geral, esta tese forneceu informação relevante sobre a utilização de SDMs, avançou o conhecimento sobre as relações espécie-ambiente e destacou a necessidade de adaptar as medidas de gestão à ecologia das espécies e às alterações climáticas.

PALAVRAS-CHAVE

Biogeografia, Modelação da Distribuição de Espécies, Dispersão, História de vida, Mares europeus

RESUMO ALARGADO

As pressões antropogénicas sobre os ecossistemas marinhos estão a aumentar em todo o mundo, tendo causado a sua degradação e promovido a diminuição local de espécies. Prevê-se que as alterações climáticas afectem os organismos marinhos com efeitos em cascata na dinâmica dos ecossistemas. As espécies marinhas acompanham as alterações mais rapidamente do que as espécies terrestres, sendo a mudança da distribuição das espécies em direção aos polos uma das consequências das alterações climáticas mais comuns e bem documentadas. As alterações de habitat adequado induzidas pelo clima podem afetar negativamente o ecossistema, alterando a estrutura funcional através de alterações na teia trófica e em outras interações bióticas. Além disso, podem ter consequências para as comunidades pesqueiras e para a gestão das pescas. Nem todos os organismos seguem a mesma tendência nas alterações à sua distribuição; em vez disso, a distribuição é influenciada por uma combinação de fatores abióticos locais e regionais (por exemplo, clima, geomorfologia), características intrínsecas (capacidades de dispersão), interações bióticas (por exemplo, disponibilidade de alimento, biomassa de predadores) e influências antropogénicas. Os Modelos de Distribuição de Espécies (Species Distribution Modelling (SDM)/Modelos de Adequação de Habitat (Habitat Suitability Modelling (HSM)) são utilizados como a principal ferramenta para prever a adequabilidade do habitat e as alterações na distribuição das espécies. Os modelos correlacionam os dados das espécies (presença, presença/ausência) com as variáveis ambientais para identificar as condições ambientais adequadas para uma espécie ao longo do espaço e do tempo. Devido à sua ampla aplicabilidade, os SDMs/HSMs tornaram-se uma ferramenta valiosa para apoiar o planeamento da gestão dos recursos e da conservação.

O principal objetivo desta tese foi compreender como as relações espécie-habitat são influenciadas por características específicas e alterações climáticas, e avaliar as implicações para as medidas de conservação e gestão das pescas. Para tal, recorreu-se à combinação de abordagens multi-escala e multinível de modelação de adequabilidade de habitat. A tese foi organizada em seis capítulos, compostos pela introdução geral (Capítulo 1), quatro artigos científicos (Capítulos 2 a 5) e uma discussão final (Capítulo 6).

O primeiro capítulo apresenta uma visão geral do tema da tese, com foco nos impactos das alterações climáticas e de outras pressões antropogénicas no meio marinho, bem como no papel das características da história de vida das espécies. Além disso, apresenta a Modelação de Distribuição de Espécies como uma ferramenta para avaliar as alterações provocadas pelo clima e a sua aplicação na conservação e gestão das pescas.

No capítulo 2, foi utilizada uma abordagem de planeamento espacial regional para avaliar a sobreposição dos habitats principais de espécies sensíveis, sedentárias e com baixa capacidade de dispersão com as Áreas Marinhas Protegidas (AMP) existentes numa área de estudo de pequena escala e alta resolução (Península Ibérica). Como espécies modelo, as duas espécies de cavalo-marinho (*H. hippocampus* e *H. guttulatus*) foram selecionadas com base na sua vulnerabilidade intrínseca às alterações do habitat (por exemplo, baixa mobilidade, baixo recrutamento, pequeno tamanho populacional), e nos esforços recentes para proteger as suas populações e habitats (por exemplo, Resolução 95/2020 da IUCN, CITES, OSPAR, Decreto-Lei Português 38/2021 e Decreto Real Espanhol 139/2011). Os resultados identificaram lacunas na sua proteção e áreas prioritárias para implementar medidas de conservação. No geral, este capítulo mostra como os SDM podem ajudar a direcionar as medidas de conservação, avaliando se as estratégias de gestão espacial existentes são adequadas, dadas as distribuições atuais das espécies.

No Capítulo 3, as distribuições das mesmas espécies de cavalos-marinhos foram modeladas numa escala mais ampla para avaliar os impactos das alterações climáticas na distribuição global das espécies. Foi utilizada uma nova abordagem de planeamento espacial mecanístico para incorporar a conectividade oceanográfica e o potencial intrínseco de dispersão nos resultados das previsões futuras para as duas espécies que dependem da dispersão passiva. Os resultados destacam que o planeamento espacial deve considerar a capacidade de dispersão para prever as alterações na distribuição das espécies e orientar o estabelecimento de redes de AMPs resilientes.

No Capítulo 4, estabeleceu-se uma abordagem ao nível da comunidade, examinando como espécies de peixes com diferentes histórias de vida e características ecológicas respondem às alterações climáticas, e como estas respostas influenciam a estrutura funcional da comunidade. Esta abordagem revelou padrões específicos dos grupos nas alterações e contrações da distribuição adequada das espécies que podem ter implicações importantes para o funcionamento do ecossistema. Agrupar espécies por estratégias de história de vida, ou outras características relevantes, para avaliar respostas diferenciadas às alterações climáticas é uma ferramenta poderosa, aplicável a diversos grupos taxonómicos e ecossistemas. Além disso, pode fornecer recomendações práticas para o planeamento espacial marinho adaptativo e gestão baseada em ecossistemas no contexto de alterações ambientais dinâmicas.

No Capítulo 5, foi utilizada uma abordagem de modelação sistemática para comparar os efeitos de diferentes escolhas de modelação, comuns na aplicação a espécies de peixes com distintos requisitos ecológicos, de modo a formular recomendações gerais para uma utilização mais

adequada de modelos da distribuição de espécies na conservação e gestão dos recursos. O estudo destacou a importância da seleção cuidadosa da extensão espacial e da resolução temporal do treino do modelo, dado que estas escolhas influenciam significativamente as previsões específicas da espécie e a identificação de áreas “hotspot”. O treino de modelos com extensões e resoluções alinhadas com os requisitos ecológicos das espécies melhora a precisão, enquanto as escolhas inadequadas de modelos podem levar à sobrestimação ou subestimação de habitats adequados.

O Capítulo 6 apresenta uma discussão geral dos resultados obtidos e das perspectivas futuras de investigação, destacando o contributo deste trabalho com novos conhecimentos relevantes sobre a utilização da modelação da adequabilidade de habitats em múltiplas espécies com características variadas e em múltiplas escalas. Os resultados apresentados enfatizam a necessidade de uma gestão dinâmica adaptada às alterações climáticas e a importância de modelar as futuras alterações na estrutura funcional dos ecossistemas.

PALAVRAS-CHAVE

Biogeografia, Modelação da Distribuição de Espécies, Dispersão, História de vida, Mares europeus

DECLARATION

According to paragraph 2a) of Article 26 of the Regulation of the Post-graduate Studies of the University of Lisbon (Diário da República No 175 de 2020, 2a série de 8 de setembro de 2020), this thesis is composed of a compilation of scientific papers published in collaboration with other co-authors. The articles correspond to Chapters 2 to 5, of which Friederike Peiffer is the leading author and was responsible for the conceptualisation, methodology, formal analysis, investigation, data curation, visualisation, and manuscript writing of all the papers. The four papers have been published or submitted to international peer-reviewed journals (Q1):

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Chapter 5

Peiffer, F.; Lima, A.R.A.; Henriques, S.; Silva, G.J.F.; Tanner, S.E.

Multi-scale assessment of marine species distributions: effects of spatial extent and temporal resolution across contrasting ecological niches.

Submitted to: *Ecological Modelling*

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LIST OF ABBREVIATIONS AND ACRONYMS

AA	Archetypal Analysis
ANNs	Artificial Neural Networks
AUC	Area Under the ROC Curve
BI	Boyce Index
Biomod2	Ensemble Platform for Species Distribution Modelling
Bio-ORACLE	Marine environmental layers for ecological modelling
BM	Biophysical Model
BOB	Bay of Biscay & Iberian Coast
BS	Baltic Sea
CBS	Celtic-Biscay Shelf
CITES	Bern Convention on International Trade in Endangered Species of Wild Fauna and Flora
CS	Celtic Sea
CTA	Classification Tree Analysis
EBFM	Ecosystem-Based Fisheries Management
EFH	Essential Fish Habitat
ENMs	Ecological Niche Models
ESDM	Ensemble Species Distribution Modelling
ESU	Evolutionarily Significant Unit
FAO	Food and Agriculture Organization
FDA	Flexible Discriminant Analysis
FishGlob	Analysis of data from scientific bottom trawl surveys
GAMs	Generalised Additive Models
GBIF	Global Biodiversity Information Facility
GBM	Generalized Boosting Model
GIS	Geographic Information Systems
GLMs	Generalised Linear Models
HS	Habitat Suitability
HSMs	Habitat Suitability Models
IBI	Iberia–Biscay–Irish
IBTS	International Bottom Trawl Survey

ICES	International Council for the Exploration of the Sea.
IUCN	International Union for Conservation of Nature
KAPPA	Cohen's kappa coefficient
LME	Large Marine Ecosystems
MARS	Multiple Adaptive Regression Splines
Marxan	Tool for decision-making in conservation planning
Maxent	Maximum Entropy
MPA	Marine protected area
MSP	Marine Spatial Planning
Natura 2000	Network of protected areas in Europe
NS	North Sea
NWS	European Northwest Shelf
OBIS	Ocean Biodiversity Information System
OSPAR	Convention for the protection of marine environment of the Northeast Atlantic
PCA	Principal Component Analysis
PD	Propagule Duration
QGIS	Geographic Information System platform
RCP	Representative Concentration Pathways
RF	Random Forest
ROC	Receiver Operating Characteristic curve
RSS	Residual Sum of Squares
SBTS	Scientific bottom-trawl surveys
SDM	Species Distribution Modelling
SDMs	Species Distribution Models
SRE	Surface Response Envelope
SSP	Shared Socio-Economic Pathways
TSS	True Skill Statistics

CHAPTER 1

GENERAL INTRODUCTION

THESIS OBJECTIVES

THESIS OUTLINE

General Introduction

Climate change and other anthropogenic impacts on the marine environment

Anthropogenic pressures are increasing worldwide, leading to habitat and biodiversity loss (Barnosky et al., 2011; O’Hara et al., 2019). Consequently, species extinction rates are increasing, nearly causing a sixth mass extinction in Earth’s history (Penn & Deutsch, 2022). The main threats to marine ecosystems include overexploitation, destructive fishing practices, coastal development, pollution, invasive species, and climate change (Halpern et al., 2007; Korpinen et al., 2021; Pilotto et al., 2020). Climate change affects species ecology and physiology, with cascading effects on ecosystem structure and dynamics (Pecl et al., 2017; Pilotto et al., 2020; Poloczanska et al., 2013; Wernberg et al., 2016). If the world continues with “business as usual” concerning greenhouse gas emissions, 80% of threatened and commercially valuable species in European Seas are projected to be at risk due to future novel climate conditions, especially those located in enclosed and semi-enclosed seas (Predragovic et al., 2024). Ocean warming pushes coastal marine organisms beyond their thermal limits, thus disrupting vital physiological processes (Pörtner, 2010; Stuart-Smith et al., 2015). Besides, marine organisms at their higher thermal limits are more prone to have low resilience to additional climate-related stressors (e.g., ocean acidification and deoxygenation) (Lima, Booms, et al., 2024; Lima, Lopes, et al., 2024; Pörtner et al., 2005), and other stressors (e.g., overfishing, reduced water quality, invasive species, habitat depletion) (Wernberg et al., 2011). Species may cope with climate change by tracking suitable habitats, leading to the redistribution or range shifts of their habitats (Chen et al., 2011; Lawlor et al., 2024; Perry et al., 2005; Poloczanska et al., 2013, 2016). Marine species tend to track changes even six times faster than terrestrial species (Lenoir et al., 2020), closely following the isotherms, since changes in marine distributions are primarily driven by changes in sea temperature (Alheit et al., 2012; Fernandes & Fallon, 2020; Le Luherne et al., 2024; Rutterford et al., 2023). Some observations also hint at the potential effects of changing oxygen, salinity, productivity, wave climate, and/or ocean acidification on the distribution of marine species (Poloczanska et al., 2016; Sampaio et al., 2021). For instance, oxygen availability has been shown to influence the distribution of fish species over small spatial and temporal scales, predominantly in regions with oxygen minimum zones (Coffey et al., 2017; Gutiérrez-Bravo et al., 2024).

Climate change impacts are not uniformly distributed across the species’ native ranges, and predictions may vary depending on the method, taxonomic group, and spatial and temporal

scales. Yet, a poleward shift of species distribution is one of the most common and well-documented consequences of global climate change on land and in the sea (Hastings et al., 2020; Hickling et al., 2006). In the case of marine species, in addition to shifting northward, species were further observed migrating to deeper waters (Dulvy et al., 2008; Le Luherne et al., 2024; Perry et al., 2005; Poloczanska et al., 2016). However, thermal niches are often limited by seasonality at higher latitudes (Hastings et al., 2020; Stuart-Smith et al., 2017). Besides, not all taxa follow the same trend of shifting toward higher latitudes and depths (Rubenstein et al., 2023). Instead, realised distributions are shaped by a combination of local and regional environmental processes (e.g., oceanographic connectivity), biological interactions (e.g., predator-prey interactions, competition), ecological requirements (e.g., habitat types), and anthropogenic influences (e.g., fishing pressure) (Roberts et al., 2020; Rubenstein et al., 2023). Climate-driven range shifts can have similar negative impacts as invasive species on the ecosystem functioning and human well-being (Sorte & Williams, 2010). For instance, changes in distributions can result in alterations of predator-prey interactions and other biotic interactions, with implications for the entire food web (Albouy et al., 2014; Cormon et al., 2016; Hattab et al., 2016; Pecl et al., 2017; Pecuchet et al., 2020; Skaret et al., 2015). Changes in species' distribution can also alter the connectivity between essential fish habitats of their life stages (Britten et al., 2016). Besides, for commercially important species, redistribution can have profound effects on fishing communities and economies (Baudron et al., 2020; Cruz et al., 2024; Hollowed et al., 2013; Roessig et al., 2004).

Relation of species traits and vulnerability to anthropogenic stressors

Not all ecosystems and geographic regions are equally affected by anthropogenic threats (Halpern et al., 2007; Vasconcelos et al., 2017). The vulnerability of marine species is determined by a combination of their life history traits (e.g., body size, trophic level and fecundity) and spatial traits (e.g., preferred habitat types) (Butt et al., 2022; de Juan et al., 2020; Pearson et al., 2014). The most vulnerable species to human pressures are typically long-lived, slowly reproducing species occupying high trophic levels (Coulon et al., 2023; Mérillet et al., 2021; Polo et al., 2025; Walls & Dulvy, 2021). Smaller sedentary species, such as seahorses and corals, are threatened by habitat degradation due to their limited ability to escape threats actively (Caldwell & Vincent, 2012; Hoegh-Guldberg et al., 2007). The extent to which species' traits predict vulnerability and range shifts in responses to climate change remains under discussion (Angert et al., 2011; MacLean & Beissinger, 2017; Rincón-Díaz et al., 2024). Traits that are found to influence the sensitivity of species to climate change are habitat breadth, thermal niche

width, biogeographic affinity, range size and boundaries (MacLean & Beissinger, 2017; Pearson et al., 2014; Walls & Dulvy, 2021). Species near their upper or lower thermal limits and those with restricted spatial ranges are more prone to shift their distribution with climate change (Campana et al., 2020). Furthermore, life history traits such as trophic level, body size, and dispersal ability could determine range shifts of fish species (Rincón-Díaz et al., 2024). Pelagic species are more likely to closely follow suitable habitat conditions, while demersal species are more likely to be limited by physical constraints such as depth and substrate (Rijnsdorp et al., 2009; Roberts et al., 2020; Rutterford et al., 2015). Larger-bodied species often have slower population growth rates and longer generation times, which may reduce their capacity to adapt to warming through rapid demographic response (Angert et al., 2011; Pearson et al., 2014; Perry et al., 2005). Supporting this, it was found that large-bodied endemic species tend to be the most vulnerable species to climate change (Jones & Cheung, 2018). In contrast, species with faster life cycles and smaller body sizes react strongly and quickly to climate change because of their potential for rapid population growth (Le Luherne et al., 2024; Lima et al., 2022; Perry et al., 2005; Rose, 2005). However, not all regions are equally affected by climate change, e.g., some regions warm faster than others (von Schuckmann et al., 2024). Attention should be paid to these regional variations since it has been found that rapidly warming regions are experiencing an increase of r-strategy fish species, while slower warming regions show a rise in k-strategy species (Receveur et al., 2024).

The role of dispersal and oceanographic connectivity

The potential of species to reach new suitable habitats is mainly determined by the species' dispersal ability and recruitment success (Angert et al., 2011). Colonisation of new suitable areas can only occur if sufficient nearby populations within the phylogeographic region are maintained, and connectivity between viable populations can be established (Boehm et al., 2013; Scales, 2010; Teske et al., 2007). The connectivity between populations can be facilitated via active movement (e.g., in mobile species with wide home ranges) or passive dispersal (e.g., drifting as gametes, larval stages, or free-living juveniles) (Cowen & Sponaugle, 2009). Species with small home ranges rely on passive dispersal for long-distance range expansions (Boehm et al., 2013), with passive dispersal outcomes shaped by the interaction between ocean current patterns and a species' intrinsic dispersal potential (Trembl et al., 2012). Thus, oceanographic connectivity plays a crucial role in the geographic distribution of species and can have a profound impact on marine species distribution under climate change (García Molinos et al., 2017; Gouvêa et al., 2023). A special form of passive dispersal is rafting, where juveniles or adults

are found drifting attached to rafts over long distances (Fraser et al., 2011; Luzzatto et al., 2013; Nikula et al., 2013; Thiel & Gutow, 2005; Vandendriessche et al., 2006). Sporadic colonisation events via rafting of a small number of individuals can result in the establishment of new populations (Teske et al., 2005) but may be insufficient for sustaining genetic connectivity (Boehm et al., 2013; Silva et al., 2017). Habitat preferences can also play a role in the dispersal capabilities; for instance, species with a preference for shallow coastal habitats show restricted colonisation of new suitable habitats (Lourie et al., 2005). This also indicates that habitat patchiness can result in limited dispersal and closed populations (Pinsky et al., 2012). Furthermore, larval dispersion is often restricted by retention mechanisms to maximise local recruitment (Cowen et al., 2000; Cowen & Sponaugle, 2009). For instance, tidal vertical migrations ensured the retention of larvae in sheltered inshore habitats (e.g., estuaries, lagoons) (Borges et al., 2007).

Species Distribution Modelling

One of the widely used tools to predict suitable habitat and distribution shifts is Species Distribution Modelling (SDM). Species Distribution Models (SDMs), Ecological Niche Models (ENMs), and Habitat Suitability Models (HSMs) all describe models that associate species data (presence, presence/absence, and/or abundance) with environmental variables to identify suitable environmental conditions for a species (Guisan & Zimmermann, 2000). Based on this knowledge, models can predict the spatial distribution of suitable habitats for unknown locations and for the future (Pearson, 2010). The central premise of this approach is that the observed distribution of a species accurately reflects its environmental requirements (Pearson, 2010). Therefore, it is of utmost importance that the input data of the models (species' occurrence records and environmental variables) are spatially and temporally representative enough to inform on the realised species-habitat relationship (Čengić et al., 2020; Commander et al., 2022). The spatial scale of the input data has two decisive components: extent and resolution. Extent refers to the size of the region over which the model is run, whilst resolution refers to the size of grid cells (Fournier et al., 2017). Typically, datasets covering large extents have coarse data resolution, whereas those with small extents tend to have finer resolutions (Pearson, 2010). Equally, the temporal resolution (i.e., monthly, seasonal, annual, or decadal data) plays a role in describing the species-habitat relationship and depends on data availability and the scale of underlying processes (Mannocci et al., 2017; Pennino et al., 2019). Geo-referenced species occurrence data can be compiled from various sources, each with its advantages, limitations, and biases (Arenas-Castro et al., 2022; Bosso et al., 2024; La Marca et al., 2019; Pennino et al., 2016). For instance, large national or international surveys span a broader extent

(e.g., International Bottom Trawl Survey (IBTS)) (Maureaud et al., 2024) but often have coarser spatiotemporal resolutions than species-dedicated field surveys. Furthermore, citizen science records and fishers' knowledge are low-effort and cost-effective data collections, but they can be prone to sampling bias due to accessibility of sampling locations or species identification errors (Aylesworth et al., 2017; Bosso et al., 2024; Bradter et al., 2018; Noviello et al., 2021; Theobald et al., 2015; Tiago et al., 2017). Platforms that combine extensive data from all kinds of sources, such as the Global Biodiversity Information Facility (GBIF) and Ocean Biodiversity Information System (OBIS), are frequently used in SDMs (Hodapp et al., 2023). However, caution is needed since the data often lack quality control and standardisation, as well as contain coordinate uncertainties, records of dead species, and records of captured species that require consideration. Overall, most sources do not provide reliable information on true absences; therefore, pseudo-absences need to be generated following best-practice guides (Barbet-Massin et al., 2012). Environmental variables tend to describe primarily the abiotic environment and should be chosen based on their relevance in determining species-habitat relationships (Bucklin et al., 2015; Guisan & Thuiller, 2005). Information on climatic conditions is made available nowadays through advances in remote sensing and geographic information systems (GIS), as well as enhanced processing, computing, and storing capacities (Melo-Merino et al., 2020). In addition, global climate models have been used to generate scenarios of future climates (e.g., Bio-ORACLE) (Assis et al., 2024). Predicted future climate scenarios can be used to estimate the potential impacts of climate change on biodiversity (Maltby et al., 2020; Martins et al., 2021; Predragovic et al., 2024). However, depending on the purpose of the study, the available spatial extent and resolution will determine the quality of the model outcomes (Goh et al., 2024; Karp et al., 2025; Klaassen et al., 2025; Mannocci et al., 2017; Núñez-Riboni et al., 2021). Several modelling algorithms are available to classify the probability of species' presence (and absence) as a function of a set of environmental variables (Melo-Merino et al., 2020). Some methods use statistical approaches (e.g., Generalised Linear Models (GLMs) and Generalised Additive Models (GAMs)), whilst other approaches are based on machine-learning techniques (e.g., maximum entropy (Maxent) and artificial neural networks (ANNs)) (Melo-Merino et al., 2020). To validate the ability of the model to predict independent data, a set of species occurrence records is used as independent test data for cross-validation, whose performance is usually evaluated by the Receiver Operating Characteristic (ROC) curve, the True Skill Statistics (TSS) and the Kappa statistic (KAPPA) (Melo-Merino et al., 2020). Since each algorithm has its assumptions and limitations, Ensemble Species Distribution Modelling (ESDM) has been increasingly used, which averages the outputs of all model algorithms to reduce the respective

limitations of single algorithms (Araújo & New, 2007). The modelling results in continuous relative habitat suitability scores, or so-called probability of occurrence, per grid cell over the study area, with values ranging from zero (lowest suitability) to one (highest suitability) (Guisan & Zimmermann, 2000). Afterwards, the output maps with the continuous values can be converted into binary maps (presence (1)/ absence (0)) by setting a threshold value, above which the species is predicted as being present (i.e. suitable habitat) (Jiménez-Valverde & Lobo, 2007). Species Distribution Modelling has become a valuable tool for informing management and conservation planning for the present and future (Abecasis et al., 2014; Karp et al., 2025; Porfirio et al., 2014). It has been commonly used to a) guide field surveys and fill the gaps around known occurrences (Fois et al., 2018), b) project potential impacts of climate change (Maltby et al., 2020; Martins et al., 2021), c) predict species' invasion (Ahmad et al., 2019) d) identify essential habitats and support conservation prioritisation and reserve selection (Faure-Beaulieu et al., 2023), e) compare palaeodistributions and phylogeography (Forester et al., 2013), and f) guide reintroduction of endangered species (Malone et al., 2018). Here, it is important to note that modelling choices (e.g., temporal and spatial scales of input data) can significantly influence model outcomes, resulting in differential recommendations for conservation or management (Karp et al., 2025; Klaassen et al., 2025).

Conservation and Management

Marine Protected Areas (MPAs), especially those with a high level of protection, have been recognised as one of the most important tools to mitigate the impact of anthropogenic stressors and to manage marine resources sustainably (Edgar et al., 2014; Grorud-Colvert et al., 2021; Palumbi, 2002). The global 30x30 target agreed upon under the Convention on Biological Diversity (Target 3, Kunming-Montreal Global Biodiversity Framework) implies that 30% of the ocean should be effectively conserved and managed by 2030. To date, there is concern about the effectiveness of MPAs when they are not implemented or sufficiently managed (Grorud-Colvert et al., 2021), since those areas provide little or no additional protection compared to outside areas (Horta e Costa et al., 2019). For instance, according to the MPA Guide, the network of MPAs throughout Europe provides only minimal protection (Aminian-Biquet et al., 2024). Furthermore, the Natura 2000 sites were often found to be ineffective for the protection of marine fish and mammals, still allowing measures known to affect these species in this region (e.g., bottom trawling and dredging) (Fortuna et al., 2018; Guidetti et al., 2019; Trochet & Schmeller, 2013). The spatial assessment of species distribution can guide the adequate design and management of MPAs and provide a better understanding of the true potential of MPAs

and MPA networks in effectively protecting marine species (Abecasis et al., 2014; O'Hara et al., 2019). Often charismatic species, also referred to as flagship species, are used as a tool to raise awareness and engage stakeholders to protect their habitats and constituent species (Zacharias & Roff, 2001). To date, management plans and policies at local, national, regional, and international levels are not prepared to address the geographic shifts in marine species expected to occur due to climate change in the coming decade (Araújo et al., 2011; Pinsky et al., 2018). Marine spatial planning must effectively integrate climate change (Frazão Santos et al., 2020). The knowledge of the future distribution of threatened and commercial species is essential as a basis for making decisions on adaptive management and climate change mitigation strategies (Gormley et al., 2015; Whitney et al., 2023). Thus, it is vital to identify climate refugia and establish a network of fully protected MPAs that can provide resilience and sufficient gene flow between populations and serve as corridors for range shifts (Ashcroft, 2010; Planes et al., 2009; Warren et al., 2013; Wilson et al., 2020). Furthermore, climate change and the redistribution of commercial fish species are challenging fisheries management and fishing communities (Baudron et al., 2020; Cruz et al., 2024; Hollowed et al., 2013; Rogers et al., 2019). For instance, spatiotemporal mismatches between species' regional abundances and catch quota allocations can lead to political and socio-economic challenges (Fernandes & Fallon, 2020; Gullesstad et al., 2020). Tracking changes in the species distribution using high-resolution modelling helps to address these challenges (Azevedo & Silva, 2020). Another critical aspect in fisheries management is the reduction of bycatch and discards, which can be addressed by closely tracking species distribution and implementing dynamic fishing closures (Hazen et al., 2018; Hobday et al., 2010; Pons et al., 2022; Stock et al., 2020). Ecosystem-based fisheries management emerges as a valuable tool to manage resources sustainably and at the same time preserve biodiversity and ecosystem functioning (Cisneros-Montemayor et al., 2020; Link et al., 2011; Tommasi et al., 2021). In this context, integrating functional traits within existing fisheries analysis can improve estimates of community dynamics (Barnett et al., 2019). Furthermore, identifying essential fish habitats to protect the connectivity between life stages supports sustainable ecosystem-based fisheries management (Moore et al., 2016).

Study region and taxa

The study region encompasses the continental shelf areas of the Northeast Atlantic and adjacent seas: the North Sea, Mediterranean Sea, Black Sea, and Baltic Sea. The area includes the trailing edge of the distribution of boreal species, as well as the leading edge of the distribution of subtropical and temperate species (Baudron et al., 2020). The North Sea is one of the most

productive areas in the world, due to its strong benthic-pelagic coupling between communities (Walday & Kroglund, 2008). The Baltic Sea is the largest brackish water system in the world, inhabited by freshwater, brackish water, and marine species, all at their limit of distribution (Walday & Kroglund, 2008). The Mediterranean Sea is one of the areas in the world with the highest species richness and endemism (Zenetos et al., 2008). The Black Sea has a generally lower diversity, and deep organisms are largely absent due to anoxic zones in deeper layers (Zaitsev et al., 2008). Fishing has a high socio-economic importance in the region, resulting in high fishing pressure (Eme et al., 2022; Korpinen et al., 2021; ter Hofstede and Rijnsdorp, 2011). In general, the study area is highly impacted by human activities, with the main threats being non-sustainable fishing practices (bottom trawling, bycatch), pollution (eutrophication, marine transport, contaminants), invasive species, and habitat loss (Korpinen et al., 2021). On top of that, nearly the entire Northeastern Atlantic and adjacent seas are affected by an increase in sea surface temperature, with about 43% of the area warming at a rate two times faster than the global average warming rate, i.e. in the Mediterranean Sea, North Sea, Baltic Sea, and Black Sea (von Schuckmann et al., 2024). Besides, the Norwegian Sea, North Sea, and Celtic-Biscay Shelf belong to the Large Marine Ecosystems (LME) classified within a “superfast” warming category (above 0.21 °C per decade) (Kessler et al., 2022). On the other hand, the Iberia–Biscay–Irish (IBI) and the European Northwest Shelf (NWS) seas are characterised by milder warming rates (von Schuckmann et al., 2024). At the same time, marine heatwave events are increasing in frequency, intensity, and duration throughout the Northeast Atlantic and adjacent seas (von Schuckmann et al., 2024). However, systems with regular upwelling events, like in the Iberian coast, can mitigate the impacts of increasing temperatures and marine heatwaves, and could serve as a climate refugia (Lourenço et al., 2016; Varela et al., 2021).

The first part of the thesis focuses on sedentary species, characterised by low dispersal and strong habitat association, with two seahorses, *Hippocampus hippocampus* (Linnaeus, 1758) and *Hippocampus guttulatus* Cuvier, 1829. The species have distinct life-history traits (e.g., limited dispersal, small home ranges, and complex reproduction strategies (i.e., low fecundity, seasonal breeding, and mate fidelity) (Foster & Vincent, 2004), which makes them more sensitive to human impacts and the risk of local extinction (Pollom et al., 2021). Furthermore, seahorses are important flagship species (Shokri et al., 2009; Zacharias and Roff, 2001); therefore, the implementation of adequate conservation strategies would resonate with other species and ecosystems of conservation concern (IUCN World Conservation Congress, 2020). Both species are listed as Data Deficient in the IUCN Red List for the Atlantic and as Near Threatened for

the Mediterranean (Pollom, 2017; Woodall, 2017), and are protected by the Bern Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES), the IUCN resolution WCC-2020-Res-095, and the OSPAR List of threatened and/or declining species and habitats (OSPAR Commission, 2013a, 2013b). The two species have a wide geographic range extending across most of Europe and North Africa (Lourie et al., 2016). However, their ecological distribution is heterogeneous, and population densities fluctuate from rare individual sightings to locally abundant aggregations (Pierri et al., 2022; Woodall et al., 2018). Thus, recent population declines reported across Europe have raised concern about the conservation of these species (Caldwell and Vincent, 2012; Correia, 2022; Lazic et al., 2018; Pierri et al., 2021; Vivas et al., 2024).

The second part of the thesis focuses on mobile, widely distributed Northeast Atlantic species as model species, including Atlantic, Boreal, and Lusitanian species. The selected species were mostly demersal species and some pelagic species that are regularly caught in scientific bottom-trawl surveys (SBTS) (Maureaud et al., 2024). Those species have experienced changes in their distribution over the last decades in the form of shifts in suitable habitat areas and density-dependent use of these areas (Baudron et al., 2020; Le Luherne et al., 2024). To perform trait-based analyses, the 21 selected species represented three life-history strategies, 7 for each group: opportunistic (small, short-lived, low-trophic, high fecundity), periodic (medium-long lifespan, high trophic level, high fecundity) and equilibrium (large, long-lived, high-trophic, low fecundity) (Pecuchet et al., 2017).

Thesis objectives

The main aim of the thesis was to assess current and future habitat suitability under different climate change scenarios for marine fish species with varying life-history traits and ecological requirements to inform conservation planning and fisheries management strategies. To this end, diverse modelling approaches with multiple spatiotemporal scales and ecological levels were used across the different chapters of the thesis to align with the specific objective of each study. The specific objectives were to a) evaluate the effectiveness of regional spatial planning in aligning core seahorse habitats with Marine Protected Area (MPA) coverage at the population level, b) to predict future seahorse distributions at broader scales by integrating ensemble species distribution models with biophysical connectivity, explicitly accounting for low dispersal potential and oceanographic dynamics, c) to assess the impacts of climate change on multiple species and communities using trait-based models across extensive ecosystem scales, including

the Northeast Atlantic, and d) to quantify how different modelling choices, applied across varying spatial extents and temporal resolutions, influence predictions for species with diverse ecological requirements. The results from the four chapters provide a basis for generalising findings across spatial and temporal scales, as well as across different levels of biological organisation. Overall, the combined insights of these multi-scale and multi-level analyses offer a comprehensive understanding of how species traits shape species-habitat relationships, and how these, in turn, influence the effects of climate change on the species distributions. By assessing both species-specific (population-level) responses, using seahorses as a model, and broader community-level responses across multiple scales, our modelling approaches can be successfully applied to a broader array of marine fishes and habitats. Such an integrated understanding can inform adaptive management strategies and marine spatial planning, emphasising the need for dynamic conservation measures that can keep pace with rapidly changing environmental conditions.

Thesis outline

The thesis was organised into six chapters composed of the general introduction (Chapter 1); four scientific articles published or submitted to peer-reviewed international journals (Chapters 2 to 5), and a final discussion (Chapter 6), which synthesises the main outcomes and outlines future research directions. Outlined below are the summaries of the specific objectives, methods, and results of each of the four papers presented in the thesis.

In chapter 2, a regional spatial planning approach aimed to assess how much of the core habitat of two sedentary species is protected by current Marine Protected Areas (MPAs) in a small-scale, high-resolution study area (Iberian Peninsula). The two seahorse species (*Hippocampus hippocampus* and *Hippocampus guttulatus*) were selected as model species based on recent efforts to protect their populations and habitats (e.g., IUCN Resolution 95/2020, CITES, OSPAR, Portuguese Decree Law 38/2021, and Spanish Royal Decree 139/2011) and their vulnerability to habitat changes (e.g., low mobility, low recruitment, small population size). The results identified gaps in their protection and priority areas for conservation measures. Overall, this chapter provided a practical conservation perspective by evaluating whether existing spatial management strategies are adequate given the current species distribution.

In Chapter 3, the same seahorse species were used as model species, however, the study region was expanded to the entire distribution range of the species to assess the impacts of climate change on the species' distribution. Furthermore, a novel mechanistic spatial planning approach

was used to incorporate oceanographic connectivity and intrinsic dispersal potential in the outcomes of future predictions for the two species that rely on passive dispersal. The results highlight that spatial planning should consider dispersal abilities to predict species range changes and guide the establishment of resilient MPA networks.

In Chapter 4, a trait-based approach builds on the previous framework by scaling up to the community level, examining how different life-history strategy groups of ecologically and economically important fish respond to climate change and how these responses shape the community's functional structure. This approach revealed group-specific patterns of range shifts and contractions that could have significant implications for ecosystem functioning. Grouping species by life-history strategies (or any other relevant traits) to assess differential responses to climate change is a powerful tool that can be applied across various taxonomic groups and ecosystems to provide actionable recommendations for adaptive marine spatial planning and ecosystem-based management in the context of dynamic environmental change.

In Chapter 5, a systematic modelling approach compares the effects on model outcomes using common modelling choices for fish species with different ecological requirements to make general recommendations for using species distribution modelling in conservation and management. The study underscored the importance of careful selection of model training extent and temporal resolution, as these choices significantly influence species-specific predictions and hotspot identification. Training models with extents and resolutions aligned with species' ecological requirements improves accuracy, while inappropriate model choices can lead to over- or underestimation of suitable habitats.

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CHAPTER 2

CHAPTER 2: Habitat suitability of two flagship species, *Hippocampus hippocampus* and *Hippocampus guttulatus*, in the Atlantic coast of the Iberian Peninsula - implications for conservation

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Habitat suitability of two flagship species, *Hippocampus hippocampus* and *Hippocampus guttulatus*, in the Atlantic coast of the Iberian Peninsula - implications for conservation

Abstract

Anthropogenic pressures on marine ecosystems are increasing worldwide, causing loss of biodiversity and ecosystem functioning, and driving species towards risk of extinction. To protect vulnerable species and habitats, Marine Protected Areas (MPAs) are increasingly established worldwide as conservation measures. Seahorses act as flagship species for coastal ecosystem conservation due to their charismatic appearance and high vulnerability to habitat degradation. Here, the habitat suitability of the two European seahorse species, *Hippocampus hippocampus* and *Hippocampus guttulatus*, was assessed along the western Iberian Peninsula, using an ensemble species distribution modelling approach. Furthermore, the coverage of their core habitat (relative habitat suitability (HS) ≥ 0.5) with MPAs was estimated. The results show that the main drivers for habitat suitability were distance to the coast, aspect of the sea floor, tidal amplitude, and temperature. However, the importance differed between the two species. The suitable habitat of *H. hippocampus* extended to higher distances to the coast, while *H. guttulatus* were mostly restricted to areas in the vicinity of the coast and facing away from the open sea (i.e., the westerly aspect of the seafloor). Furthermore, temperature contributes more to the variation in habitat suitability in *H. hippocampus* than in *H. guttulatus*. The areas with the highest habitat suitability are estuarine or inlet waters and sheltered coasts in northwestern Spain, central and southern Portugal. Both species' core habitats are covered by about 19–20 % with implemented protected areas in Portugal. In comparison, there is less coverage for both species in Spain, with 12% for *H. guttulatus* and 6% for *H. hippocampus*. Besides, full protection zones cover less than 0.5 % of the core habitat, while the rest of the protected areas provide only moderate to low restrictions and do not specifically address the protection of seahorses in their management plans. The results provide useful information on the distribution and the different habitat preferences of the two species, indications for further monitoring of populations, and recommendations for efficient spatial conservation areas that can protect the species and other associated vulnerable species and habitats.

Keywords

European seahorses, Habitat suitability, Spatial conservation, Marine protected areas, Ensemble species distribution modelling, Flagship species

Introduction

Anthropogenic pressures on marine ecosystems worldwide are increasing and have caused extensive degradation of marine habitats and promoted local species depletion (Barnosky et al., 2011; Dulvy et al., 2021; O'Hara et al., 2019). Overexploitation and destructive fishing practices, coastal development and pollution, the introduction of invasive species, and climate change are threatening the biodiversity and integrity of coastal ecosystems worldwide (Halpern et al., 2007; Pilotto et al., 2020). However, not all ecosystems and latitudes are equally affected by those threats (Halpern et al., 2007; Stratoudakis et al., 2019). For instance, it was found that in higher latitudes, more vulnerable species are associated with estuarine habitats that have high connectivity with the marine ecosystem (Vasconcelos et al., 2017). Consequently, the vulnerability of marine species to human impacts is not only determined by their life history traits but also by spatial traits such as home ranges and preferred habitats (Butt et al., 2022; de Juan et al., 2020; Pearson et al., 2014).

To protect vulnerable species and habitats, in line with global targets agreed upon under the Convention on Biological Diversity, Marine Protected Areas (MPAs) are increasingly established worldwide to mitigate the impact of anthropogenic stressors and to sustainably manage marine resources (Edgar et al., 2014; Gaines et al., 2010; Grorud-Colvert et al., 2021; Palumbi, 2002). Spatial assessment of habitat suitability for marine species at risk inside and outside an area of protection can provide a better understanding of the true potential of MPAs and MPA networks in effectively protecting marine species and the need for future conservation measures (Abecasis et al., 2014; O'Hara et al., 2019). Often charismatic species, also referred to as flagship species, are used as a tool to raise awareness and engage stakeholders to protect their habitats and constituent species (Zacharias & Roff, 2001). Recently, the International Union for Conservation of Nature (IUCN) resolution 95/2020 encouraged the use of iconic Syngnathides as flagship species to promote the protection and restoration of transitional and coastal habitats important for Syngnathides species while urging governments to enforce regulations on fisheries, area-based management, and habitat protection (IUCN World Conservation Congress, 2020).

Seahorses belong to the Syngnathidae family and are considered particularly sensitive to human pressures, due to their low dispersal, small home ranges and complex reproduction strategies (i.e., low fecundity, seasonal breeding and mate fidelity) (Foster & Vincent, 2004). Particularly,

habitat degradation and fragmentation caused by coastal development, aquaculture, dredging activities and destructive fishing practices (e.g., bottom trawling), pose a threat to seahorse populations (Caldwell & Vincent, 2012b; Curtis et al., 2007; Guimarães et al., 2011; Pollom et al., 2021). Furthermore, marine traffic can harm seahorses through anchoring, noise pollution and a decrease in the water quality (Palma et al., 2019). Although seahorses are known to be sedentary, they can adapt to progressive habitat changes by moving to more suitable areas or occupying alternative habitats, like artificial structures (e.g., trash, mooring lines, lost fishing gear) (Correia et al., 2018; Correia, Koldewey, et al., 2015; Masonjones et al., 2010). Nevertheless, forced dispersal through habitat destruction might fragment local populations and directly impact reproductive success (Caldwell & Vincent, 2012a). Another threat to seahorses is the use of non-selective fishing gear, which can promote accidental bycatch (Curtis et al., 2007; Vasconcelos et al., 2019). In some locations, seahorses are also targeted by illegal fishing for the Chinese medicine market and ornamental trade (Correia, 2021; Foster et al., 2016; Pierri et al., 2021). Other than that, the impact of climate change could be manifold in the future, either indirectly by changes in the hydrodynamics and morphology of the habitat due to increasing storms and sea level rise, or directly by increasing water temperatures resulting in physiological impairments (Aurélio et al., 2013; Costa et al., 2023). However, the intensity of the impact of the various factors is likely to vary depending on the seahorse species and location.

This study focuses on two sympatric European seahorses, the short-snouted seahorse (*Hippocampus hippocampus* Linnaeus 1758) and the long-snouted seahorse (*Hippocampus guttulatus* Cuvier 1829). Both species are listed as Data Deficient in the IUCN Red List for the Atlantic and as Near threatened for the Mediterranean (Pollom, 2017; Woodall, 2017). Efforts have been made to increase the protection of these species, such as the inclusion in Appendix II of the Bern Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES) and the IUCN resolution WCC-2020-Res-095, as well as the inclusion of these species on the OSPAR List of threatened and/or declining species and habitats (OSPAR Commission, 2013a, 2013b) and the protection by law in Portugal (Decree Law 38/2021) and Spain (Royal Decree 139/2011). The two species have a wide geographic range extending across most of Europe and northern Africa, including the Atlantic Ocean, Mediterranean Sea, and Black Sea (Lourie et al., 2016). However, their ecological distribution is not continuous, and population densities fluctuate from rare to locally abundant across the species' range (Pierri et al., 2022; Woodall et al., 2018). Our research effort was focused on the Atlantic coast of the Iberian Pen-

insula based on previous knowledge of the genetic population structure and special habitat preferences of the two seahorses in this location (Pierri et al., 2022; Woodall et al., 2011; Woodall et al., 2015). Furthermore, the Iberian Atlantic coast is important for conservation since it is a recognised transition zone between warm-water species and cold-water species, thus highly susceptible to range changes due to climate change (Pinho et al., 2016; Tuya et al., 2012). Additionally, it was considered to host the largest European seahorse population in the world, which suffered from drastic declines of 70%- 90% of the population (Caldwell & Vincent, 2012b; Curtis & Vincent, 2006). However, besides dedicated studies in the Ria Formosa lagoon, only a few studies focused on seahorses within the study area (e.g., Planas et al., 2021). The information is limited to seahorse occurrences in grey literature, or as part of marine faunal assemblage assessments (Guerreiro et al., 2021; Leitão et al., 2007; Pombo & Rebelo, 2002; Serrano Gordo & Nogueira Cabral, 2001; Valladares et al., 2014). Nonetheless, population declines reported in the Ria Formosa and other places in Europe have raised concern about the conservation of the species (Caldwell & Vincent, 2012b; Correia, 2021; Lazic et al., 2018; Pierri et al., 2021).

In this context, this study aims to assess and predict the habitat suitability of the seahorse species *H. hippocampus* and *H. guttulatus* to improve efficient spatial conservation. The specific objectives were to use Ensemble Species Distribution Modelling to 1) identify the most important variables governing the species' habitat suitability, 2) to predict the core habitats (i.e., relative habitat suitability ≥ 0.5), and 3) to assess whether MPAs cover core habitats.

Materials and Methods

Study area

The study area of the model lies inside the temperate Large Marine Ecosystem (LME) “Iberian Coastal” which extends along the western coast of the Iberian Peninsula (-12.6°W, -5.1°W, 34.38°N, 45°N) (Fig. 2.1). LMEs represent multi-country, ecosystem-based management units that are characterized by their unique undersea topography, current and water mass structure, marine productivity, and food chain interactions (Sherman, 2001). The study area includes important estuarine waters and salty lagoon areas such as the Rias Baixas in northern Spain, and the main estuaries and coastal lagoons in Portugal (Vasconcelos et al., 2017). Due to limited genetic connectivity between ecoregions and strong population structure across the geographic range in the case of seahorses (Pierri et al., 2022; Woodall et al., 2011; Woodall et al., 2015),

the research was focused on this study area to increase resolution and targeted conservation efforts. The western coast of the Iberian Peninsula is the northern zone of the Canary Upwelling System, one of the four major coastal upwelling regions in the world (Patti et al., 2008), resulting in high primary productivity (which occurs mainly during the spring-summer season) and biodiversity (Alvarez et al., 2008; Herrera et al., 2008). In this region, the swell predominantly comes from the west, i.e., the open Atlantic Ocean, thus the coastlines facing the west are the most exposed to strong waves and currents, particularly in winter (Hernández-Urcera et al., 2021; Planas, 2022). The seabed varies between sandy bottom and hard substrates on the coast, and muddy to fine sand substrates in the estuaries and coastal lagoons (Vasquez et al., 2021).

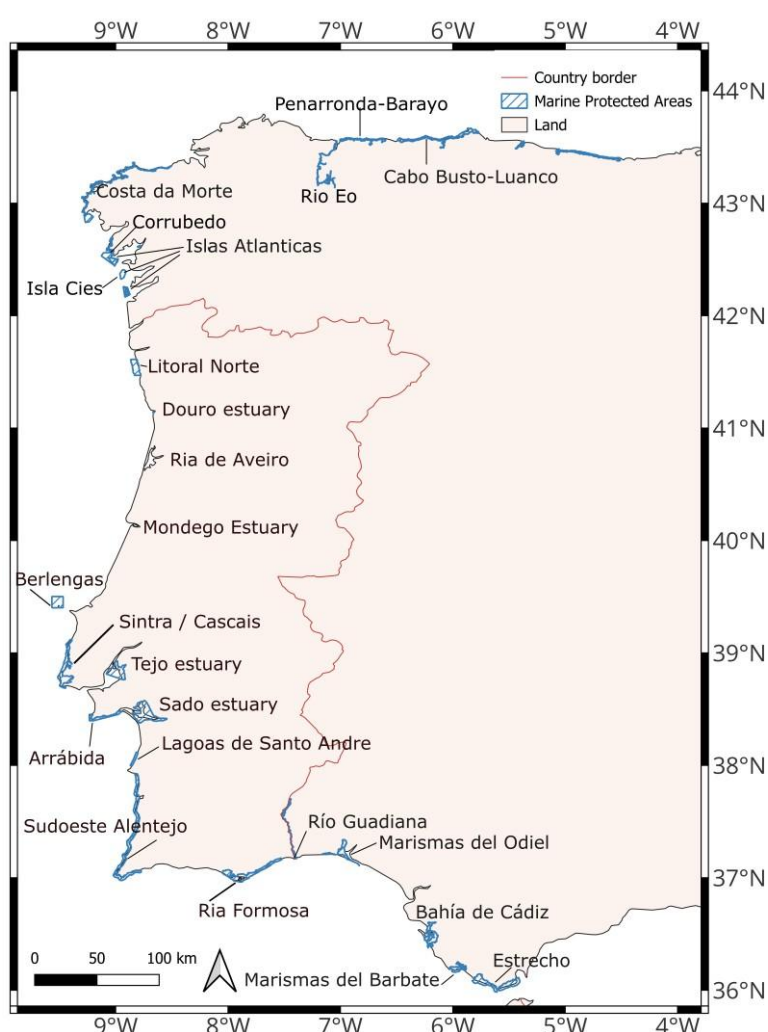


Figure 2.1. Study area including the outlines of the designated and implemented Marine Protected Areas in blue.

Species data

As seahorse are cryptic and rare species, geo-referenced occurrence data of the seahorse species are scarce. Therefore, data were compiled from a variety of sources, including several databases

and scientific surveys from projects of various institutes, which included dedicated surveys as well as opportunistic sightings in various environments (Appendix 1, Table A1.1). Additionally, an independent citizen science survey was conducted between July and September 2022 among dive centres in the study area. It was a call to report seahorse sightings with date, location, habitat, and photos whenever available. Duplicated data in date and location among different databases and spatial points located on land or outside the known range were excluded from the datasets. The final dataset included a total of 155 occurrence points for *H. hippocampus* and 115 points for *H. guttulatus* for the time range between the years 1990 and 2022 (Appendix 1, Fig. A1.1), which conformed to the minimum required number for robust predictions (Liu et al., 2019; Wisz et al., 2008). While there might be a sample bias that could decrease prediction performance, it was decided that occurrence points were not filtered to increase sample size, since sample size and the choice of modelling method are more important than spatial bias (Gaul et al., 2020).

Environmental predictors

A total of 18 biotic, climate, and geophysical variables, which were available and assumed to be relevant, were tested to define the present-day habitat suitability of the two seahorse species (Appendix 1, Table A1.2). Data of the variables was downloaded from different web sources (Appendix 1, Table A1.2) and transformed into raster layers with a common spatial resolution of 0.0083° (about 1 km) and cropped to the extent of the study area by using the resample function in the raster package in R software 4.2.3 (Maintainer & Hesterberg, 2015; R Core Team, 2023). To increase coverage along the coast, raster layers were interpolated in the spatial analysis tool QGIS using the process tool ‘GDA’ and the function ‘Fill no data’. The function fills raster cells with no data values by interpolation from nearby cells, using inverse distance weighting. In this study, phytoplankton biomass, which supports planktonic crustaceans, which are the primary food source of seahorses, was used as a proxy for food availability (Gurkan et al., 2011). Furthermore, the constant supply of prey to the sessile seahorses is facilitated by the exchange of water determined by the average maximum tidal amplitude (Cereja et al., 2021; Lopes & Dias, 2014; Silva & Duck, 2001). Exposure to waves and currents was represented by current velocity and the east-west aspect of the seafloor. The east-west aspect of the seafloor is the horizontal orientation of the seafloor and gives information on which direction the seafloor is facing. The reasoning behind including this variable is that in the study region, the west-facing coastline is the most exposed to waves and currents. Furthermore, a raster of substrate types was created by rasterising the EUSeaMap (2021) (Vasquez et al., 2021). In the process of

rasterising, the occurring substrate types were assigned category numbers ranging from 1 (small grain size) to 9 (big grain size) according to the hierarchy of the Folk 7 classification system (Kaskela et al., 2019) (Appendix 1, Table A1.3). In this region, the substrate layer does not include biological habitats, such as seagrass and seaweed, since no consistent data layers were available. The correlation among all layers was tested by Pearson's correlation matrix, and to avoid multicollinearity, only layers with a correlation below 0.7 were included in the same set of environmental predictors (Dormann et al., 2013). Since there was a correlation between ecologically relevant variables (e.g., temperature, salinity, and depth), it was necessary to run several models with different sets of environmental variables (Čengić et al., 2020). The relative contribution of each variable in determining the habitat suitability for *Hippocampus* spp. was calculated in three permutations with the function 'get_variables_importance' in the Biomod2 package (Thuiller, 2024). On a scale from 0 to 1, the higher the value, the more influence the variable has on the ensemble model. Additionally, response curves were computed, which showed the variability of habitat suitability relative to each explanatory variable, while the other variables were fixed as constant (Elith et al., 2005). The final model setup for assessing the habitat suitability of *H. hippocampus* and *H. guttulatus* was decided based on evaluation metrics, variable importance, response curves, and the predictive performance of the models.

Model selection, calibration, and evaluation

To predict the present-day habitat suitability of the two Iberian seahorses *Hippocampus* spp., occurrence data were modelled as a function of topographic, biological, and oceanographic variables, using an ensemble modelling approach in the Biomod2 package (Thuiller, 2024) in R (version 4.2.1). Ensemble modelling combines predictive outputs from several different algorithms into a unique ensemble model to achieve a more robust predictive performance (Araújo & New, 2007). The model algorithms used to build the ensemble model included the Generalized Linear Model (GLM), Generalized Additive Model (GAM), Artificial Neural Network (ANN), Flexible Discriminant Analysis (FDA), Generalized Boosting Model (GBM), Maximum Entropy (MAXENT), Random Forest (RF), Classification Tree Analysis (CTA), Surface Response Envelope (SRE) and Multiple Adaptive Regression Splines (MARS). Since there were no true absence points available, pseudo-absences had to be generated randomly using the same number of pseudo-absences as available presences and with equal weighted sums of presence and absence (Barbet-Massin et al., 2012; Liu et al., 2019; Thuiller, 2024). This framework provides reliable predictions for rare species' distribution with a low number of presence points and pseudo-absences (Breiner et al., 2015; Hernández-Urcera et al., 2021;

Liu et al., 2019). For model validation, the presence and pseudo-absence data were partitioned randomly into 80% for calibration and 20% for testing in each model run (Guisan & Zimmermann, 2000). Two metrics were used to evaluate the predictive performance of the algorithms: the True Skill Statistic (TSS) (Allouche et al., 2006) and the Area Under the receiver-operating characteristic Curve (AUC or ROC; Fielding & Bell, 1997). Predictive performance of algorithms is considered good ($AUC \geq 0.9$; $TSS \geq 0.6$), moderate ($0.7 \leq AUC \leq 0.9$; $0.2 \leq TSS \leq 0.6$), or poor ($AUC \leq 0.7$; $TSS \leq 0.2$) (Landis & Koch, 1977; Pearce & Ferrier, 2000), but only algorithms with a TSS of ≥ 0.7 were combined to run the Ensemble Models. The evaluation metric TSS was chosen as the primary criterion for selecting models for ensemble forecasting, as this metric is more closely related to the accuracy of predictions and has a higher variability among models (Allouche et al., 2006). The predictive performance of the model was also assessed by checking the plausibility of the fitted species-environment relationship by evaluating the variable importance and visual inspection of response curves. The ensemble forecast provides the prediction as an estimated species probability of occurrence translated into relative habitat suitability (HS) of each grid cell, where 0 represents the lowest suitability and 1 indicates the greatest suitability. Relative suitability above 0.25 indicates a suitable habitat. Core habitat is defined as cells having an $HS \geq 0.5$, which is considered moderate to high suitability. Hotspots were defined as areas with suitability higher than 0.75 (Ahmad et al., 2019; Garzon et al., 2020).

Coverage with existing protected areas

To assess the coverage of the core habitats by MPAs, the overlap of the surface area of the core habitat ($HS \geq 0.5$) with protected areas of different designation types and the actual habitat suitability within each MPA was calculated with the vector overlap and zonal statistics tool in QGIS. The list of MPAs and their designation types was sourced from the Protected Planet database for Portugal and Spain (Protected Planet, 2023). To further assess the effectiveness of protection, information on dredging activities and levels of fishing protection were extracted from Protected Seas Navigator (ProtectedSeas, 2023), Marine Protection Atlas (Marine Conservation Institute, 2023) and the European Marine Observation and Data Network (EMODnet) (European Commission, 2023). Unimplemented MPAs and protected areas that do not serve the protection of the seahorse species, such as the NATURA 2000 sites under the Birds Directive and RAMSAR wetland sites, were excluded from the analysis to avoid a false sense of protection (Horta e Costa et al., 2019; Trochet & Schmeller, 2013). Additionally, the coverage

of the core habitat with zones of full protection / no-take zones (Prof Luiz Saldanha Marine Park) and designated seahorse refuge areas (Ria Formosa) was calculated.

Results

Model performance

The ensemble models for *H. guttulatus* and *H. hippocampus* achieved an AUC of 1.00 and a TSS of 0.98, respectively (Appendix 1, Fig. A1.2). The scores indicate that the model predicted the distribution of both species with high accuracy (Pearce & Ferrier, 2000). The predictive accuracy of the individual algorithms used in the ensemble model was good but varied between algorithms, with RF, MAXENT and MARS performing the best (Appendix 1, Fig. A1.3). However, all models reached the threshold to be included in the Ensemble Model (Appendix 1, Fig. A1.3).

Importance of predictors

The final run of the *H. guttulatus* and *H. hippocampus* ensemble models included seven out of the eighteen variables tested: distance to coast, temperature, east-west aspect, current velocity, phytoplankton, substrate, and tidal amplitude (Appendix 1, Table A1.4). The most significant predictors out of the tested predictors in the model governing the habitat suitability of *H. guttulatus* were the distance to the coast and the east-west aspect of the seafloor (Fig. 2.2a). In contrast, the most significant variables governing the distribution of *H. hippocampus* were distance to coast and temperature (Fig. 2.2b). The rest of the variables made relatively low contributions, but the model did not improve when excluding the variables (Fig. 2.2a, b).

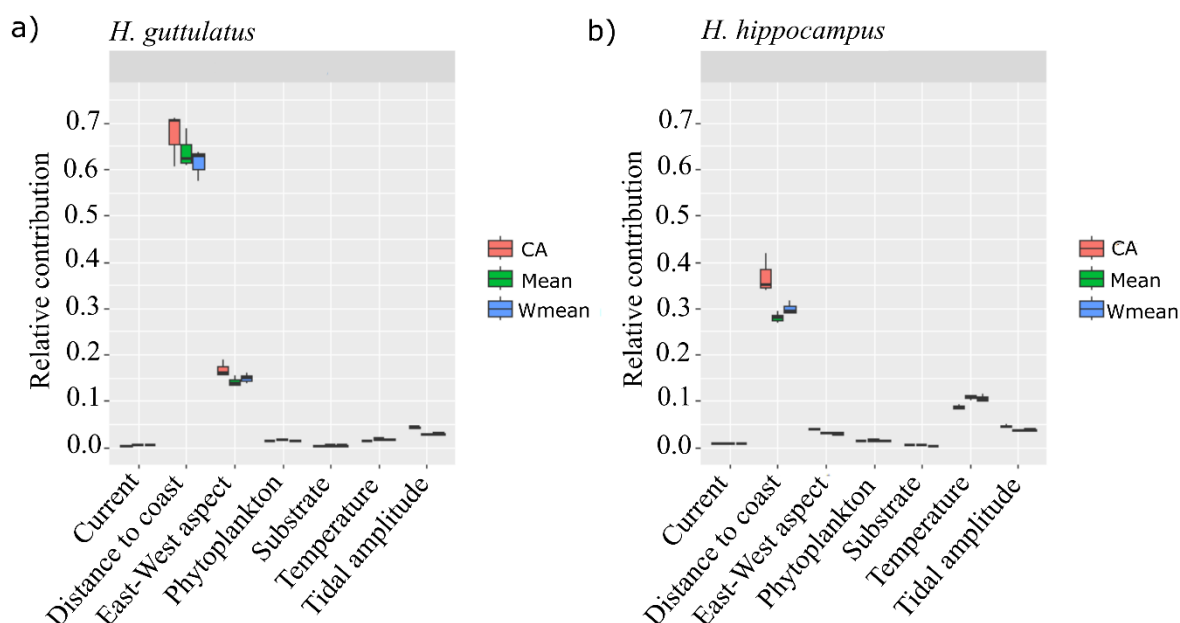


Figure 2.2. Relative contribution of the seven predictors in the habitat suitability derived from the Ensemble Model of a) *H. guttulatus* and b) *H. hippocampus* based on the Ensemble models' community averaging (ca), mean (mean) and weighted mean (wmean).

The response curves (Fig. 2.3) showed that the habitat suitability decreases with distance to the coast, with an optimum of less than 5 km for *H. guttulatus* and less than 10 km for *H. hippocampus*. The orientation of the seafloor towards the west decreases the habitat suitability of *H. guttulatus* more than of *H. hippocampus*, while for *H. hippocampus* the habitat suitability also decreases slightly with increasing aspect (i.e., orientation) towards the east. Habitat suitability first increases with increasing mean temperature for both species but decreases again after 17.5°C for *H. guttulatus* and after 18.5°C for *H. hippocampus*. In the case of phytoplankton, the habitat suitability for both species increases with increasing phytoplankton biomass and stays high throughout the whole range. Tidal amplitude does not have a significant effect on the habitat suitability of *H. hippocampus*, but decreases for *H. guttulatus* after 0.5 m. In the case of current velocity, for both species, habitat suitability is high up to 0.2 m/s and then decreases, with a steeper decrease for *H. guttulatus*. Concerning substrates, the type of substrate does not affect the habitat suitability for *H. hippocampus*. Still, for *H. guttulatus*, it is highest in sandy and muddy substrates and decreases with coarse sediment and hard substrata.

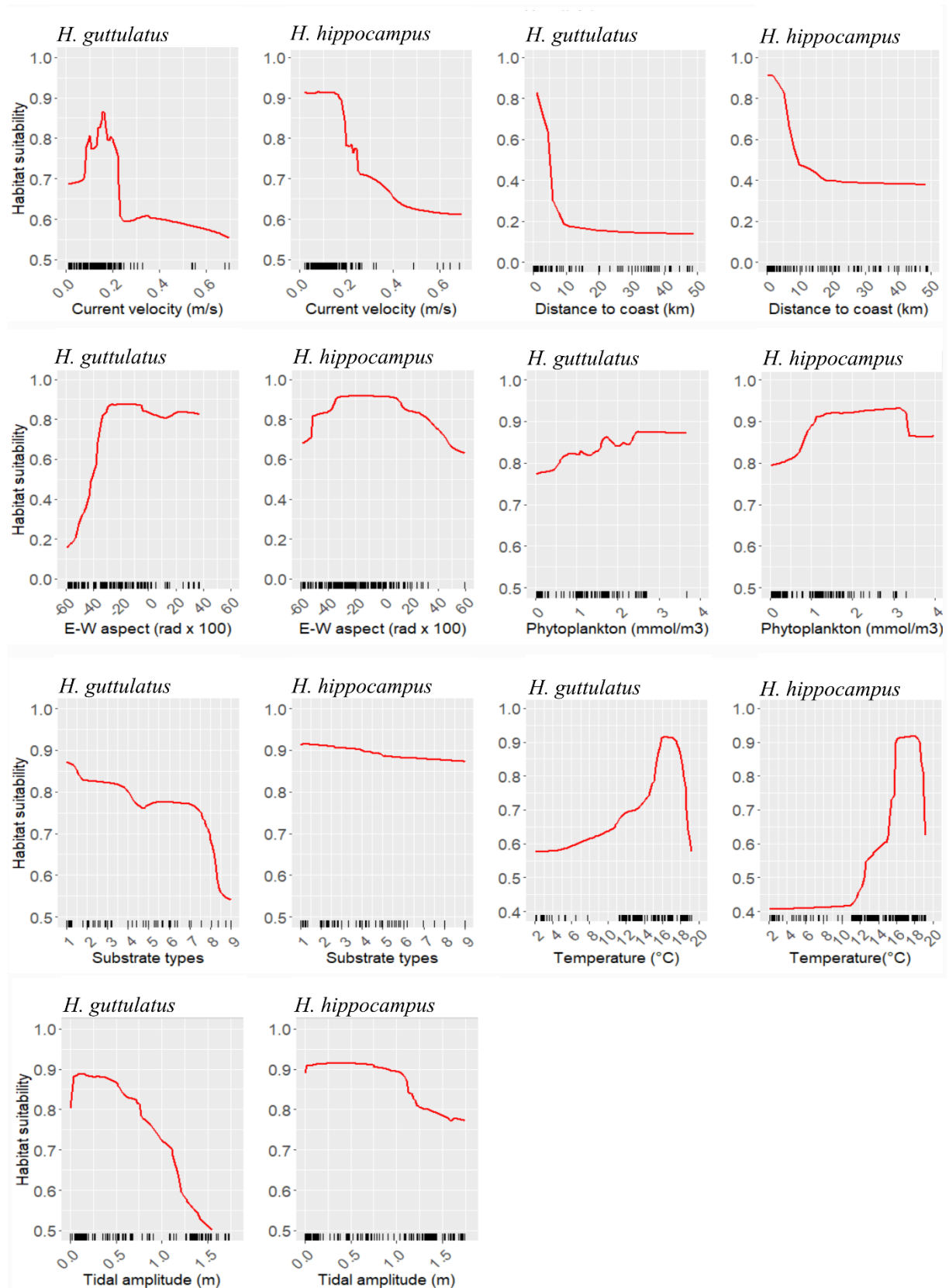


Figure 2.3. Response curves of the ensemble mean of each variable for both species when the median is used as a fixed constant for the remaining variables.

Predictive maps of habitat suitability

The predictive maps of the final ensemble models revealed that presently, the hotspots (habitat suitability ≥ 0.75) of *H. hippocampus* and *H. guttulatus* are concentrated in the estuarine and coastal lagoon waters of central and south Portugal, and for *H. guttulatus* also in the northwestern Spain (Fig. 2.4). Furthermore, the habitat suitability is generally lower for *H. hippocampus* than for *H. guttulatus* in northern Spain. Additionally, sheltered and shallow coastal areas such as Arrábida and the south coast of Portugal (Algarve) showed higher habitat suitability for both species (habitat suitability ≥ 0.5). In the south of Spain, the habitat suitability is highest (habitat suitability ≥ 0.5) in the estuaries of the Rio Tinto and Guadiana, and around Barbate. Additionally, the core habitat (habitat suitability ≥ 0.5) of *H. hippocampus* also stretches along the coast of Sintra/Cascais, Berlengas, Costa Vicentina, and the Bay of Cadiz.

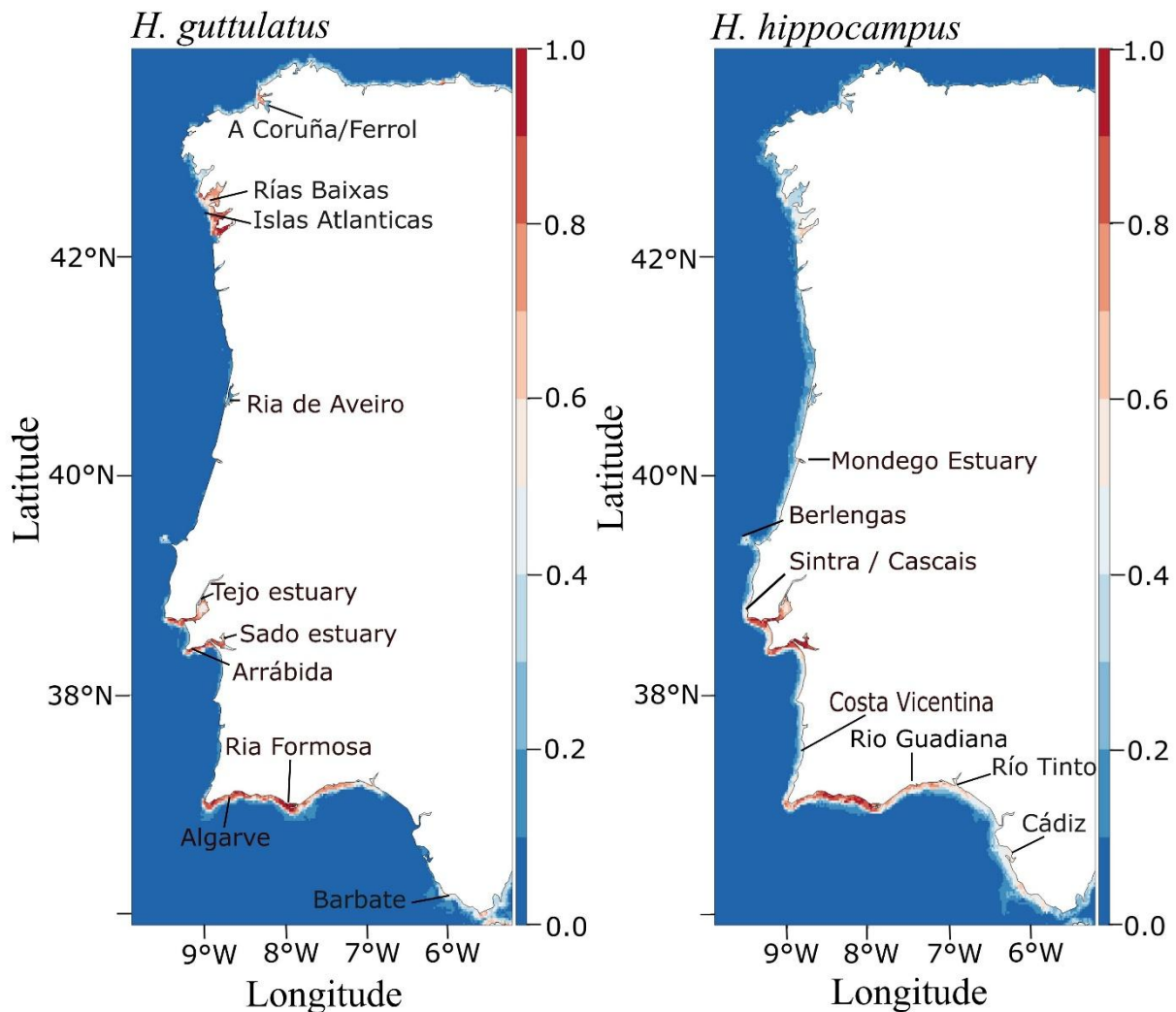


Figure 2.4. Current habitat suitability of *H. guttulatus* and *H. hippocampus* based on the Ensemble Species Distribution Model with the variables distance to coast, temperature, east-west aspect of the seafloor, current velocity, phytoplankton, substrate, and tidal amplitude.

MPA coverage

Both species' core habitat is covered by about 19-20% with implemented protected areas in Portugal. In comparison, there is less coverage for both species in Spain with 12% for *H. guttulatus* and 6% for *H. hippocampus*. All implemented areas (i.e., operational with concomitant management in place that aims to ensure compliance and enforcement) are considered as “low” protected (i.e., areas that afford some protection but allow moderate to extensive extraction and associated impacts) (Marine Conservation Institute, 2023). Zones of full protection cover less than 0.5% of the core habitat. In Portugal, the protected areas with the highest mean, maximum and majority of habitat suitability for both species were Arrábida (Nature Park /OSPAR), Sudoeste Alentejano e Costa Vicentina (Nature Park/OSPAR), Ria Formosa (Nature Park) and the Sado estuary (Nature Reserve) (Appendix 1, Figs. A 1.4, A1.5, A1.6). In Spain, the protected areas with the highest mean, maximum and majority of habitat suitability were Marítimo-Terrestre de las Islas Atlánticas de Galicia and Rio Guadiana (Natura 2000) for *H. guttulatus* and Rio Guadiana and Cabo Busto-Luanco (Natura 2000) for *H. hippocampus* (Appendix 1, Figs. A1.7, A1.8, A1.9). According to the ProtectedSeas Navigator, the most restrictive areas in terms of fishing and coastal development are Berlengas, Sado estuary, Sudoeste Alentejano and Ria Formosa in Portugal and Bahía de Cádiz, Estrecho, Marismas del Barbate and Marítimo-Terrestre de las Islas Atlánticas de Galicia in Spain (ProtectedSeas, 2023).

Discussion

This is the first study to assess the degree of protection of the data-deficient flagship species, *H. hippocampus* and *H. guttulatus*, through the estimation of habitat suitability and the overlap between MPAs and species' core habitat, across the Atlantic Coast of the Iberian Peninsula. The results indicate that the protection of the two species is low considering that the species are vulnerable to noise caused by ship traffic (Palma et al., 2019) and to destructive fishing practices (Correia, 2021), and the coverage with full protection/no-take areas was less than 0.5%, while all other implemented areas allow moderate to extensive extraction and associated impacts (Marine Conservation Institute, 2023). Furthermore, our findings revealed new insights into the differences in habitat preferences between the two *Hippocampus* species and provided reliable information for spatial conservation due to its high resolution and assessment of protected area coverage. The extent and resolution of the model considered the population structure of the species, which was decisive in identifying special habitat characteristics and the core habitat in the Iberian Atlantic population. Due to their cryptic nature and rarity, the collection

of a large sample size of occurrence points without sample bias is difficult to achieve which poses a challenge to modelling their habitat suitability. The sample sizes of our models were relatively small, however considering the nature of the species and the extent of the study, the sample size was large enough and sufficiently representative of the species since occurrence data was collected from various sources (Bosso et al., 2024; Camins et al., 2024; Wisz et al., 2008; Zhang & Vincent, 2017, 2018). Furthermore, pseudo-absences had to be commuted; thus, the ultimate strength of the model may be affected. However, previous studies confirmed that SDMs based on small sample sizes and using pseudo-absences can provide useful predictions (Patrão et al., 2015; Pearson et al., 2007; Stirling et al., 2016).

Importance of environmental drivers

Our results show that the distribution of both *H. hippocampus* and *H. guttulatus* are mostly influenced by a few environmental factors, and the relative importance of these factors in determining habitat suitability varies between species. For instance, distance to the nearest coast was the most important predictor for both species, but the relative importance was higher for *H. guttulatus* than for *H. hippocampus*. Furthermore, the second most important predictor for *H. guttulatus* was the east-west aspect of the seafloor, while for *H. hippocampus* it was temperature. The decrease in habitat suitability with increasing aspect of the seafloor towards the west is more pronounced in *H. guttulatus*, which indicates that *H. guttulatus* prefers habitats that face away from exposure to waves and currents. These findings are supported by field observations which found *H. guttulatus* more associated with confined water habitats, while *H. hippocampus*, has been found more frequently in marine shelf areas and habitats with comparably higher current velocities (Caldwell & Vincent, 2012b; Pierri et al., 2022; L. Woodall et al., 2018). In places where *H. guttulatus* and *H. hippocampus* occur in sympatry, *H. hippocampus* tends to have lower population densities than *H. guttulatus* (L. Woodall et al., 2018), suggesting that the species require different habitat conditions to thrive according to the co-occurrence theory of species (Sfenthourakis et al., 2006). Furthermore, an increased density of *H. guttulatus* and artificial habitat negatively correlated with the activity of *H. hippocampus* (Spatafora et al., 2023). Temperature was a more important predictor for the habitat suitability of *H. hippocampus* than for *H. guttulatus*, which suggests that predicted temperature changes could affect the habitat suitability of *H. hippocampus* more strongly. So far, it is known that the distribution of Syngnathidae species is expected to continue shifting poleward with progressing climate change (Monteiro et al., 2023). Furthermore, temperatures above 24°C cause physiological

stress in *H. guttulatus* (Costa et al., 2023). In the field, temperatures above 17°C were negatively correlated with the abundance of *H. guttulatus* (Correia et al., 2018), which confirms the result of the response curve. The response of *H. hippocampus* is less known; however, the resident extent of *H. hippocampus* reaches further south (Woodall, 2017), and its temperature range is wider than that for *H. guttulatus* (Froese, 2020). The maximum tidal amplitude, which is decisive for the exchange of sediment and food particles between the estuary and the ocean (Cereja et al., 2021; Lopes & Dias, 2014; Silva & Duck, 2001), contributed a fair amount to the habitat suitability. Higher tidal amplitudes generally correspond to stronger tidal currents, which bring food but can also cause seahorses to become dislodged from their preferred habitat. These two causalities are reflected in the response curves of the species, which show an increase in habitat suitability up to a certain point and then a decrease with increasing tidal amplitude, which is more pronounced in *H. guttulatus*, which prefers habitats with less current. Dredging navigation channels, coastal development and rising sea levels influence the tidal amplitude and may lead to an increase in the tidal current or an increase in sedimentation, which can make the seahorse habitat unsuitable (Woodall et al., 2011; Woodall et al., 2015). The substrate type was a less decisive predictor, although the response curve showed a decrease towards a hard substrate for *H. guttulatus*. Here, it needs to be considered that the substrate type alone does not provide information on the holdfast availability. Particularly for *H. guttulatus*, positive correlations between the population densities and natural complex holdfast availability have been observed (Correia, Caldwell, et al., 2015). Thus, the result is not surprising since *in situ* studies showed that both seahorse species occupy all sediment types (L. Woodall et al., 2018), and hard substrate with less vegetation is most often found at exposed sites (Hernández-Urcera et al., 2021). However, seahorses rely on holdfast availability to grasp with their tail, which can range from low complexity (e.g., shells, sponges, tunicates, tube-dwelling polychaetes (*Sabella* sp.) to complex macrophyte communities (Correia et al., 2018; Curtis & Vincent, 2005; Foster & Vincent, 2004). Across the native range with several interspecific differences, seagrasses were the most used holdfasts of both species (Pierri et al., 2022). We tested the importance of seagrass by including proximity to seagrass as a predictor in one of the model set-ups, which showed high importance (Appendix 1, Fig. A1.10). However, proximity to seagrass is highly correlated with distance to the coast and thus proximity to other algae and invertebrate communities, as well as a higher density of artificial structures. It has been shown that whenever seagrass is not present or has disappeared over time, both species use other objects as holdfasts, including intentionally placed artificial structures or simply trash, i.e., in the form of ropes, abandoned traps and nets (Correia et al., 2015; Woodall et al., 2018).

Predictive habitat suitability maps

Both seahorse species have a wide geographic range that extends across most of Europe, including the Atlantic Ocean, Mediterranean Sea, and Black Sea (Pierri et al., 2022), however, *H. hippocampus* is resident in the north of Africa (Woodall, 2017), while the Iberian region is the southernmost limit of the resident extent of *H. guttulatus* on the Atlantic Coast (R. Pollom, 2017). Our study showed that northern Iberia provides a higher habitat suitability for *H. guttulatus* than for *H. hippocampus*, while southern Spain seems to be more suitable for *H. hippocampus*. The western Iberian coast is interlinked with a diversity of shallow ecosystems, from coastal habitats to lagoons and estuaries, which are influenced by complex hydrodynamic factors such as tidal ranges and upwelling events (Relvas et al., 2007). According to literature, in the eastern Atlantic Ocean, both species are mainly present in confined areas (lagoons, estuaries, or semi-enclosed bays), while in other seas both species are most frequently found in marine shelf areas (Pierri et al., 2022). This difference in habitat use is also reflected in our models since the predictive maps showed higher habitat suitability in both species on the Iberian coast for wide estuarine waters, which also provide suitable habitat for a high diversity of other fish, birds, and invertebrate species. For instance, the Rias Baixas and Tagus estuary are confirmed Key Biodiversity Areas of international significance (KBAs) (Key Biodiversity Areas, 2023). In northern Portugal, the habitat suitability was low, and the occurrence of live seahorses in the wild could not be confirmed either by scientific surveys or citizen science. However, while recent scientific surveys in Ria de Aveiro did not find seahorses, there were several recent sightings of washed-up *H. hippocampus* in the Ria Aveiro lagoon (iNaturalist, 2024); Nuno Monteiro personal communication 2023) and an older sighting from literature (Pombo & Rebelo, 2002). Nevertheless, in the Mondego estuary, *H. hippocampus* observations in scientific surveys have become more frequent over the last decade (Guerreiro et al., 2021; Martinho et al., 2015), which could be related to the observed increase in the abundance of marine fish in higher latitudes due to climate change (Hastings et al., 2020), thus, it should be monitored and taken into consideration when planning conservation measures.

Implications for conservation

The coverage of the core habitat of *H. guttulatus* and *H. hippocampus* with protected areas was estimated to be between 6% and 20%, with higher protection in Portugal than in Spain. These numbers are lower than recently reported for seahorse populations in Italy (Bosso et al., 2024). Furthermore, there is concern about the effectiveness of MPAs when they are not properly implemented or do not have strict protection measures in place (Grorud-Colvert et al., 2021; Horta

e Costa et al., 2016; Roessger et al., 2022), such as is the case for most of the protected areas in Portugal and Spain (Marine Conservation Institute, 2023). These areas provide little or no additional protection compared to outside areas (Horta e Costa et al., 2019). Only in a few of the protected areas are management plans implemented, and both bottom trawling and dredging are restricted or prohibited (e.g., Arrábida, Berlengas, Sado estuary, Sudoeste Alentejo and the Ria Formosa), which can serve as important refuges for seahorses. Natura 2000 sites were found to be less effective for marine fish and mammal species (Fortuna et al., 2018; Guidetti et al., 2019; Trochet & Schmeller, 2013), allowing the main threats known to affect these species in this region (i.e., fishery bycatch, bottom trawling, and dredging). In line with this, studies confirming the effectiveness of MPAs in protecting seahorses are still lacking, while some studies show either no effect or a potentially negative impact due to increased predator abundance (Harasti et al., 2014; Martin-Smith & Vincent, 2005; Yasué et al., 2012). Seahorses face multiple threats that can also originate from outside the MPAs and are often more affected by habitat degradation than direct exploitation (Martin-Smith & Vincent, 2005). That is why careful planning when designing an MPA and proper management are important to avoid negative impacts on seahorse populations by accounting for increased predator abundance (Harasti et al., 2014), key habitat requirements (Zhang & Vincent, 2018), and adaptations to climate change (Monteiro et al., 2023). Nonetheless, predictive maps of habitat suitability are a useful tool to inform on management and conservation of seahorses (Bosso et al., 2024; Zhang & Vincent, 2018). In our case, the extent and resolution of the predictive maps were appropriate in indicating specific locations for further research and highlighting areas where more conservation efforts need to be invested. As both *H. guttulatus* and *H. hippocampus* are currently classified as Data Deficient at the global scale and as Near Threatened for the Mediterranean region (Pollom, 2017; Woodall, 2017), population presences and trends are unknown in many locations; therefore, conservation measures should include monitoring activities. Based on the maps, recommended regions for further research and population assessment are, from north to south, the coast between Ribadeo and Cabo Pena, Ria da Coruña and Ferrol, Cascais/Sintra, Sudoeste Alentejo, and the region of Cadiz, Barbate and Estrecho (Tarifa). Furthermore, regions recommended for increased protection are the Tagus and Mondego estuaries and the south coast of Portugal (Algarve) between the protected areas of Sudoeste Alentejo and Ria Formosa. Furthermore, it is recommended to do more research on the potential presence of populations around Porto, Berlengas, Ria Aveiro and Lagoa de Óbidos where seahorses have been sighted historically or otherwise irregularly in bycatch or washed up on the shore (Almeida et al., 2018; Pombo &

Rebelo, 2002). Besides, bycatch data and interviews with fishermen can also be important initial indications for the presence/absence of the two species (Aylesworth et al., 2017). Another important aspect to consider is the difference in their habitat suitability since *H. hippocampus* has a wider spatial habitat suitability and occurs further away from shore, while *H. guttulatus*' habitat suitability is more concentrated in less exposed inshore areas such as estuaries and coastal lagoons. It has been shown in previous studies that *H. guttulatus* benefits more than *H. hippocampus* from habitat restoration or enhancement of habitat complexity through artificial structures, as well as the protection from indirect effects of destructive bottom-touching fishing gears on benthic habitats (Correia, Koldewey, et al., 2015; Curtis et al., 2007; Spatafora et al., 2023). *H. hippocampus*, on the other hand, is more often directly affected by fishing practices as accidental bycatch with different fishing métiers in coastal shallow sandy areas (Almeida et al., 2018; Cabral et al., 2003; Vasconcelos et al., 2019). Thus, an increase in conservation efforts in inner-shelf soft-sediment, low-complexity habitats, and outside of MPAs would not only be beneficial to *H. hippocampus* but also to other endangered demersal species such as *Rostroraja alba* and *Raja undulata* (Sousa et al., 2018; Stratoudakis et al., 2019). The best conservation measure for both species is to create fully protected areas with a total ban on destructive fishing practices, dredging and boat activities, covering areas of both high and low-complexity habitats and with appropriate extents for both species. Furthermore, as charismatic fish, seahorses can function as flagship species to engage the public and policymakers (Zacharias & Roff, 2001), who can serve as active conservation agents by denouncing illegal fishing activities and promoting the reduction of pollution in the local communities.

Conclusions

To conclude, the final predictive maps reflect well the habitat suitability of the two species and can be used as a tool to inform where to invest more research and conservation efforts. For instance, our findings highlight a lack of spatial protection of the Iberian population and the importance of conserving highly vulnerable habitats such as estuaries and coastal lagoons as well as inner-shelf soft sediment habitats. The mere designation of protected areas is not sufficient for seahorse protection; instead, in the future, it is recommended to involve stakeholders in decision-making and implement specific measures such as the prohibition of fishing and dredging in essential fish habitats, the restoration of habitats (e.g., seagrass meadows), and monitoring of the existing populations. Furthermore, the results suggested that there are differ-

ences in habitat preferences of the two species, thus a potential niche partitioning in the congeneric species, which must be considered when monitoring and discussing protective measures and assessing the conservation status of the two species, since the conservation measures can affect the two species differently.

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CHAPTER 3

CHAPTER 3: Projected climate change and limited dispersal potential threaten the seahorse species *Hippocampus hippocampus* and *Hippocampus guttulatus*

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Projected climate change and limited dispersal potential threaten the seahorse species *Hippocampus hippocampus* and *Hippocampus guttulatus*

Abstract

Climate change is predicted to drive species redistribution, altering the composition of marine communities and affecting ecosystem functioning. There is increasing evidence that fish distributions follow a trend of poleward expansion, while realised niches often decrease in range size. This study aimed to assess the influence of oceanographic connectivity and intrinsic dispersal mechanisms on changes in suitable habitats of the European seahorses (*Hippocampus hippocampus* and *Hippocampus guttulatus*) from the present (2010-2020) until the end of the century (2090-2100). Habitat suitability was assessed using Ensemble Species Distribution Modelling under two Shared Socio-Economic Pathways (SSP2 and SSP5) coupled with biophysical modelling to estimate oceanographic connectivity. The results show that intrinsic dispersal mechanisms and oceanographic connectivity limit the northward range expansion, while predicted habitat loss remained constant in all dispersal scenarios, with the highest habitat loss forecasted in the Mediterranean and northern Africa. Consequently, considering restricted dispersal, *H. guttulatus* was projected to experience a negative range change (or habitat contraction [-45% (SSP5)] as opposed to an expansion with unlimited dispersal (standard model) [+6% (SSP5)]. On the other hand, for *H. hippocampus*, a more limited range expansion [+8% (SSP5)] was forecasted compared to the standard model [+17% (SSP5)]. In addition, the lower emission scenario (SSP2) resulted in half of the habitat losses, while maintaining climate refugia for *H. guttulatus* populations in the north Mediterranean, Iberian Atlantic Coast, and Black Sea. This study highlights the importance of considering dispersal abilities when assessing climate change impacts on marine species distribution.

Keywords

European seahorses; Species Distribution Modelling; Habitat loss; Climate refugia; Connectivity; Conservation

Introduction

Climate change is predicted to have profound impacts on marine organisms and trigger cascading effects on ecosystems (Parmesan, 2006; Pecl et al., 2017; Pilotto et al., 2020; Wernberg et al., 2016). While projections vary depending on the species, spatial and temporal extent, most indicate significant biodiversity losses, raising concerns that, under worst-case scenarios, climate change could lead to a sixth mass extinction in Earth's history (Bellard et al., 2012; Penn & Deutsch, 2022). Ocean warming can push coastal marine organisms beyond their thermal limits, disrupting vital physiological and ecological processes (Pörtner, 2010; Roessig et al., 2004; R. Stuart-Smith et al., 2015). At their higher thermal limits, marine organisms are less resilient to additional climate-related stressors, such as ocean acidification and deoxygenation (Lima, Booms, et al., 2024; Lima, Lopes, et al., 2024; Munday et al., 2009; Pörtner et al., 2005) and non-climate stressors (e.g., overharvesting, reduced water quality, introduced species, habitat depletion) (Sinopoli et al., 2019; Wernberg et al., 2011). Species may cope with climate change by tracking suitable habitats, leading to shifts in their geographic ranges (Anker-Nilssen et al., 2008; Chen et al., 2011; Lawlor et al., 2024). There is increasing evidence that fish distributions follow a consistent trend of a poleward movement in fish distribution, although the availability of thermal niches at higher latitudes is often limited by seasonal variability (Hastings et al., 2020; Le Luherne et al., 2024; Stuart-Smith et al., 2017). However, range shifts may vary according to the species' geographic range size, thermal niche width, and life-history traits (e.g., dispersal capacity) (Assis et al., 2017; Lima et al., 2022). Climate-induced range shifts can have negative impacts on ecosystem functioning and human well-being (Pecl et al., 2017), like those caused by introduced species (Sorte & Williams, 2010). Furthermore, range shifts tend to occur faster in marine than terrestrial environments (Sorte & Williams, 2010). These interrelations underline the importance of predictive forecasts of species redistributions for biodiversity conservation and management (Porfirio et al., 2014).

There is an increasing concern about the impact of climate change on seahorses, which belong to the Syngnathidae family and the genus *Hippocampus* and are characterised by their elongated bodies, prehensile tails and unique reproductive behaviour (i.e., males carry and give birth to the offspring) (Lourie et al., 2016). Seahorses are indicator species of their habitat status and important flagship species for conservation (Shokri et al., 2009). Experiments have shown that warming induces substantial changes in metabolic rates, growth, feeding, and activity levels, with more pronounced effects in juvenile than in adult seahorses (Aurélio et al., 2013; Costa et

al., 2023; Faleiro et al., 2015). In the wild, the combined effects of warming, oxygen depletion, and acidification, as well as changes in hydrodynamics induced by increasing storms and sea level rise, may affect seahorses in unpredictable ways (Pearce & Selley, 2024). Recent studies have discovered that thermal anomalies influence seahorse migratory behaviour along the Western Atlantic coast (Freret-Meurer et al., 2022) and that gradual warming causes the West African seahorse, *Hippocampus algiricus*, to expand its habitat northward to the Canary Islands (Otero-Ferrer et al., 2015). Although seahorses can adapt to unfavourable conditions by moving to more suitable areas, this may fragment local populations and impact reproductive success (Caldwell & Vincent, 2012a; Correia et al., 2015). In addition, seahorses naturally have low density and low dispersal ability (Teske et al., 2007), which increases the risk of local extinction (Pollom et al., 2021; Shaffer, 1981). Adult seahorses have small home ranges (Foster & Vincent, 2004) and are therefore largely reliant on passive dispersal mechanisms for long-distance movement. This occurs primarily during the juvenile pelagic stage (Foster & Vincent, 2004; Luzzatto et al., 2013; Vandendriessche et al., 2005; Wong & Teh, 2017) or via rafting (juveniles or adults), while attached to seaweed, seagrass, or marine debris (Boehm et al., 2013; Li et al., 2021; Teske et al., 2007). The extent and duration of passive dispersal are shaped by the interaction between oceanographic patterns and a species' intrinsic dispersal potential (Tremblay et al., 2012). Oceanographic connectivity thus plays a key role in determining species distributions and can significantly influence climate-driven range shifts (García-Molinos et al., 2017). However, our understanding of how oceanographic connectivity and the dispersal capabilities of seahorses affect their potential to track suitable habitats in the face of climate change remains limited.

Here, we focused on two native European seahorses, *Hippocampus hippocampus* (Linnaeus, 1758) and *Hippocampus guttulatus* (Cuvier, 1829). Their geographic range stretches from the UK to Northern Africa (Lourie et al., 2016), exhibiting heterogeneous distribution and population densities that vary from rare sightings to locally established dense populations (Bosso et al., 2024; Peiffer et al., 2024; Pierri et al., 2022b; Woodall et al., 2018). According to the IUCN Red List, the two species are listed as Data Deficient in the Atlantic and Near Threatened in the Mediterranean (Pollom, 2017; Woodall, 2017). Recent population declines reported across Europe have raised concerns regarding their conservation (Caldwell & Vincent, 2012b; Correia, 2022; Lazic et al., 2018; Pierri et al., 2021). Thus, this study aimed to assess changes in the extent of suitable habitat for *H. guttulatus* and *H. hippocampus* until the end of this century by combining Ensemble Species Distribution Modelling with biophysical

modelling as an estimate of connectivity. More specifically, the following key questions were investigated: (1) To what extent do patterns of habitat expansion and contraction differ between species, regions, and Shared Socioeconomic Pathway scenarios (SSP2 and SSP5)? and (2) How does the integration of ocean connectivity and intrinsic dispersal potential into ESDM influence projection outcomes compared to the standard model? This framework will be pivotal to understanding the effects of dispersal on species-specific redistribution driven by climate change.

Materials and Methods

Study area

The study areas encompassed the native geographic ranges of both species, whose distribution ranges extend from the UK to the Black Sea for *H. guttulatus* and from the UK to Guinea for *H. hippocampus*, including the Mediterranean Sea (Lourie et al., 2016). The extent of the study area was expanded to allow the projection of habitats due to predicted range expansions [*H. guttulatus*: (12.1°W, 29.5°N, 45.1°E, 73.15°N); *H. hippocampus*: (37.4°W, 8.75°N, 44.65°E, 76.25°N)]. Although sympatric, these species show differences in micro-habitat preference and macro-habitat distribution (Correia et al., 2018; Curtis et al., 2007; Woodall et al., 2018): *H. guttulatus* is mainly found in confined waters, while *H. hippocampus* is found not only in confined, but also in marine shelf waters (Pierri et al., 2022b).

Species distribution data

Occurrence data of the two European *Hippocampus* species were compiled from various sources, including open-source databases, scientific surveys, and citizen science surveys (Appendix 2, Table A2.1). Duplicated data among different databases and spatial points on land, outside the known range, or with low coordinate accuracy were excluded from the datasets. Occurrence data on seahorses are limited (Pierri et al., 2022b); therefore, we prioritised data quantity over spatial data thinning given the importance of the number of occurrence points (Gaul et al., 2020). The final dataset consisted of 780 occurrence points for *H. hippocampus* and 571 points for *H. guttulatus*, spanning from the years 2000 to 2022 (Appendix 2, Figs A 2.1, A 2.2) and allowing robust predictive performances (Liu et al., 2019; Wisz et al., 2008).

Environmental data

To extract the current and future environmental conditions for the two species, environmental raster layers were downloaded from Bio-Oracle (V 3.0) under the “present” (2010-2020) and for future climate scenarios (2090-2100) according to two distinct SSP scenarios (SSP2 and SSP5) (Assis et al., 2024). The raster files have a spatial resolution of 0.05° and a decadal temporal resolution from the present day to the end of the 21st century (2000–2100). Raster layers were interpolated using inverse distance weighting with the “GDA” tool in QGIS to slightly extend the grid cells along coastal zones and estuarine habitats. Subsequently, the “fill no data” function was applied to replace missing values and ensure better coverage along the coastline. The variables were chosen based on their relevance to seahorses’ habitat and survival requirements (i.e., bathymetry, temperature, salinity, oxygen, primary productivity, and current velocity) or on whether they could become relevant in the future (i.e., pH) (Correia et al., 2018; Faleiro et al., 2015; Foster & Vincent, 2004; Peiffer et al., 2024; Zhang & Vincent, 2018). Owing to the demersal and mostly shallow distribution of seahorses (Pierri et al., 2022b), we used environmental data at the minimum depth. Additionally, variables included in the models were selected based on their availability across both present-day and future scenarios (Appendix 2, Table A2.2). The Pearson correlation analysis was used to avoid using variables with a high correlation coefficient ($r > 0.7$) in the same model to improve the model performance (Ahmad et al., 2019).

Modelling approach

The Ensemble Species Distribution Modelling (ESDM) approach was used to identify suitable habitats in the present (2010-2020) and future (2090-2100). The models were trained using present-day climate conditions and projected onto future climate conditions under two different SSP scenarios: the “fossil-fuelled development” or highest emission scenario (SSP5) and the “Middle of the Road” scenario (SSP2) (Lee & Romero, 2023). The ESDM approach was applied using the Biomod2 package in R (Thuiller, 2024) to combine the outcomes of individual models of nine algorithms (Generalized Linear Models (GLM), Generalized Additive Models (GAM), Generalized Boosted Models (GBM), Classification Tree Analysis (CTA), Flexible Discriminant Analysis (FDA), Artificial Neural Networks (ANN), Maximum Entropy (MAXENT), Random Forest (RF), Surface Response Envelope (SRE)). An equivalent number of pseudo-absences was randomly generated to match the number of presence points (Barbet-Massin et al., 2012). The models were built using 80% of the data to train the model and 20% of the data for the evaluation of the model performance, and each model was generated three

times. The accuracy of the model predictions was evaluated using two evaluation metrics: the Area Under the Curve (AUC) of Receiver Operating Characteristics (ROC) and the True Skills Statistics (TSS) (Allouche et al., 2006). Model algorithms that produced a TSS score of 0.7 or higher were included in the final ensemble model.

Variable importance

The variable's importance in predicting habitat suitability was calculated in three permutations with the function 'get_variables_importance' in the Biomod2 package (Thuiller, 2024). Hereby, the importance of each variable was estimated by calculating the Pearson correlation between the original prediction and the predictions generated with the shuffled variable, while keeping the other variables constant (Thuiller, 2024). The importance score was then computed as one minus the correlation score, resulting in a scale from 0 to 1, whereby a greater value indicates a higher influence of the variable on the model prediction (Elith et al., 2005). After multiple assessments of variable importance across different sets of uncorrelated variables, eight variables were selected for inclusion in the models: bathymetry, distance to the nearest coast, temperature, salinity, pH, dissolved oxygen, primary productivity, and current velocity (Appendix 2, Table A2.3).

Species range change

The predictive maps from the ESDM were reclassified into binary presence-absence maps based on habitat suitability, using a threshold that maximised the sum of sensitivity (i.e., true positive rate) and specificity (i.e., true negative rate), as determined by the TSS (Jiménez-Valverde & Lobo, 2007; Liu et al., 2013). Thus, grid cells classified as 'presence' were interpreted as suitable habitat. To measure the gains, losses, and range change under future climatic conditions, we used the function 'BIOMOD_RangeSize' implemented in 'biomod2' (Thuiller, 2024). This function calculates the number of grid cells representing habitat loss, stability, and gain, as well as their corresponding relative proportions (%) by comparing present and future binary projections from ESDMs (Thuiller, 2024). The changes were estimated considering the geographic native range and the population structure of the two species individually (Woodall et al., 2011, 2015). Accordingly, *H. hippocampus* range change predictions were subdivided into UK/Bay of Biscay, Mediterranean Sea, Iberia, and West Africa (Woodall et al., 2011), while for *H. guttulatus*, the predictions were subdivided into the UK/Bay of Biscay, Iberia, Mediterranean Sea, and Black Sea (Woodall et al., 2015).

Connectivity

The influence of oceanographic connectivity and intrinsic dispersal mechanisms on potential range expansions under climate change was quantified by coupling the ensemble models with coastalNet, a biophysical model (BM) that simulates the influence of oceanographic currents and propagule durations (PD) on the connectivity of passively dispersed species (Assis et al., 2025). The coastalNet model has been validated against independent population genetics and demographic data (Abecasis et al., 2024; Assis et al., 2015; Gouvêa et al., 2023; Klein et al., 2016; Tavares et al., 2023). The model employs a forward-in-time Lagrangian simulation of passive dispersal, assimilating daily ocean current direction and intensity data from the Global Ocean Physics Reanalysis (EU Copernicus Marine Service product, ~9.2 km spatial resolution (Copernicus Marine Service, 2024)). This reanalysis product integrates satellite and in-situ observations and is forced by the ERA-Interim and ERA5 atmospheric reanalyses. The Lagrangian simulation used an Uber H3 grid system (Uber Technologies Inc., 2024) to define equal-area (~9.85 km resolution) source and sink hexagon sites. From these sites, particles were released daily over 21 years (2000-2020), totalling 7,670 particles per site and 12,617,150 particles overall. Particles were transported by ocean velocity fields for maximum durations of 14 and 100 days (see Dispersal Mechanisms below), and their positions were tracked hourly until reaching a sink site. Of the total particles released, 11,565,758 and 12,408,059 performed pairwise connectivity events for the 14-day and 100-day PDs, respectively. Connectivity matrices were generated by calculating pairwise connectivity, defined as the total number of particles exchanged between sites *i* and *j*, divided by the number of particles released from site *i*. Multigenerational dispersal estimates, accounting for cumulative stepping-stone connectivity pathways, were derived using a graph-theoretical approach. In this approach, graph nodes represented the sites, and edges represented the corresponding pairwise oceanographic connectivity. The Dijkstra algorithm was applied to find the shortest path between each pair of sites by minimising the sum of log-transformed distances. Multigenerational dispersal estimates were calculated by multiplying the probabilities along each shortest path (Assis et al., 2025). The binary maps from the standard ESDM were used to define target source and sink sites by linking the coordinates of raster grid cells classified as suitable habitat (value = 1) to the corresponding Hexagon IDs. After running the biophysical model, the Hexagon IDs were converted back into the spatial grid format of the original species distribution model. In this binary grid, successfully connected sites were assigned a value of 1 to indicate that a suitable habitat can be reached via passive dispersal. As mentioned above, the propagule duration (PD) during the connectivity event was determined by the species' dispersal mechanisms (Assis et

al., 2025). The two main dispersal scenarios for seahorses were assessed: The first scenario is the pelagic drifting dispersal after juvenile seahorses are released from the brood pouch, which lasts about 14 days until their tails are developed enough to start the grasping behaviour (Novelli et al., 2017; Otero-Ferrer et al., 2010). The second scenario is a passive dispersal via rafting as adults or juveniles when seahorses are attached to algae, seaweed, seagrass, or marine debris (Boehm et al., 2013; Luzzatto et al., 2013; Teske et al., 2007). The duration of this type of dispersal can vary depending on environmental conditions, raft type, food supply, the biological traits of the rafter, and ecological interactions (Vandendriessche et al., 2006; Vandendriessche, Messiaen, et al., 2007; Vandendriessche, Vincx, et al., 2007). However, with increasing travel time, organisms experience bottlenecks, and on average, most organisms stay up to 100 days on the raft (Thiel & Gutow, 2005). Therefore, we also ran one scenario with 100 days as an estimate for rafting time, hence PD time. The resulting binary maps of the dispersal models were used to calculate gains, losses and stability of suitable habitat in the same way as for the standard models. The standard ESDMs represented unrestricted dispersal, meaning that the seahorses can reach long-distance sites if sporadic long-distance dispersal events are not impaired by environmental conditions (Li et al., 2021; Otero-Ferrer et al., 2017; Teske et al., 2007).

Results

Evaluation of model metrics and the relative importance of environmental variables

The final ESDMs showed high predictive performance with both evaluation estimates, AUC and TSS, higher than 0.9 for both species (Appendix 2, Fig. A2.3). The most significant variables governing the habitat suitability of *H. guttulatus* and *H. hippocampus* were temperature, distance to the coast, and bathymetry (Fig. 3.1). However, distance to the coast was more important for the habitat suitability of *H. guttulatus* than for *H. hippocampus*. The relative importance of the other variables in contributing to the model's performance was below 0.1; however, the stepwise exclusion of the variables did not improve the evaluation score of the model, hence the variables were retained.

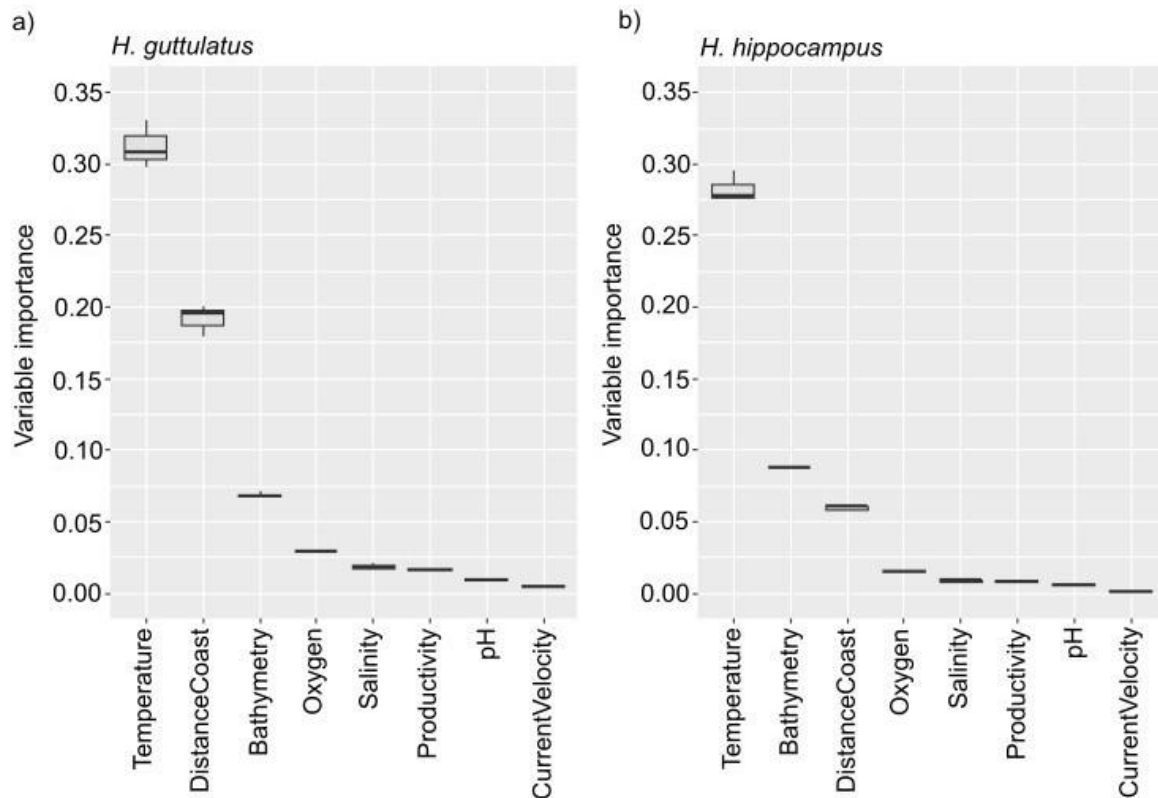


Figure 3.1. Variable importance derived from the Ensemble Species Distribution Models of a) *H. guttulatus* and b) *H. hippocampus* ranked from the highest to the lowest relative importance.

Present-day habitat suitability

The seahorse *H. guttulatus* favours sheltered coasts spanning from the Netherlands to Portugal, encompassing the southern shores of the UK and Ireland, the Western Mediterranean, and the northern Black Sea (Fig. 3.2a). In contrast, the *H. hippocampus* seahorse demonstrates a preference for the North Sea, the Bay of Biscay, the southern Mediterranean, the African Atlantic, Macaronesia, and the Canary Islands, while largely not present in the eastern Mediterranean and the Black Sea (Fig. 3.2b).

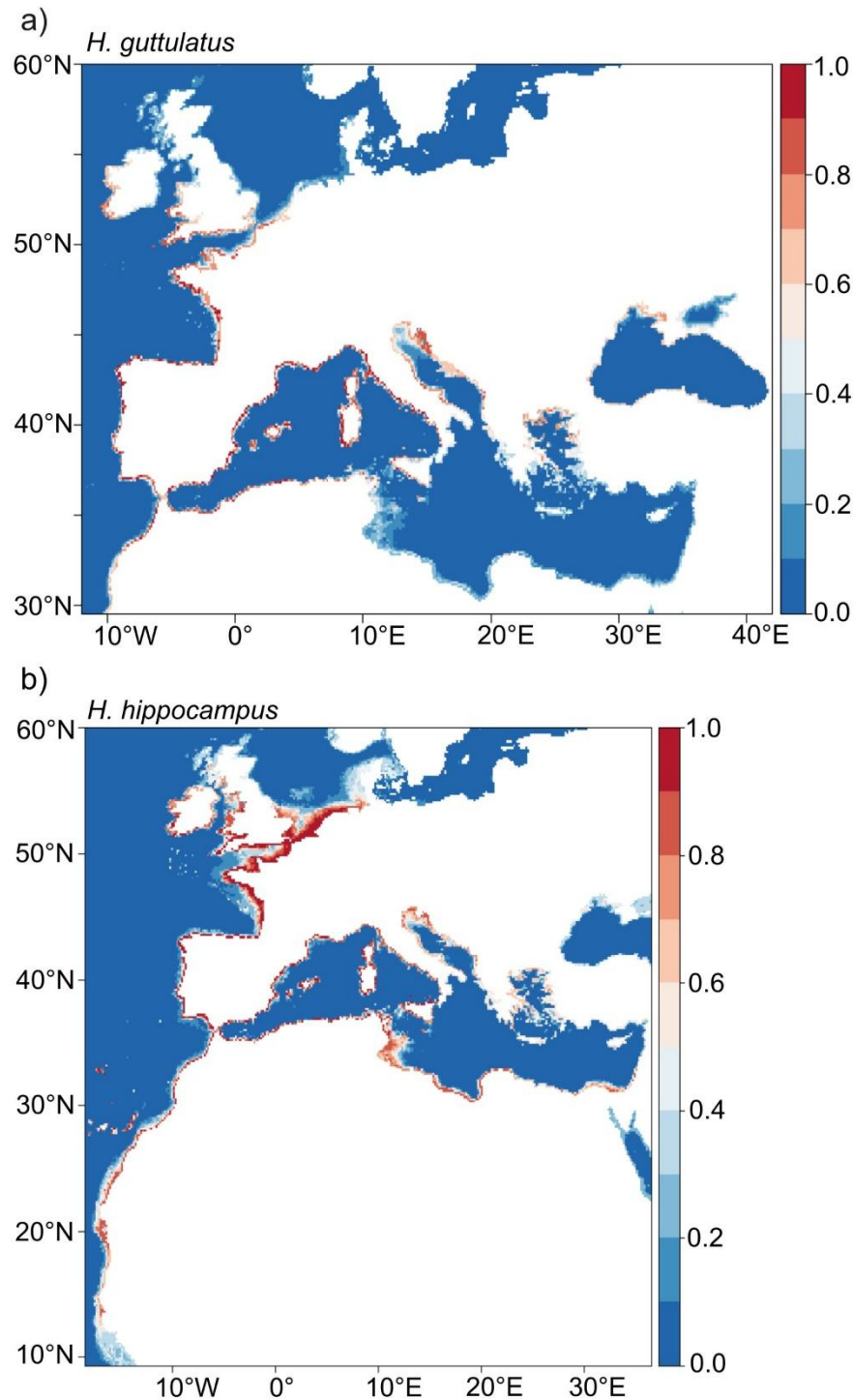


Figure 3.2. Present-day habitat suitability maps of a) *Hippocampus guttulatus* and b) *Hippocampus hippocampus*.

Connectivity influences on the distribution of seahorses

The predictions indicated that *H. hippocampus* and *H. guttulatus* will undergo significant range shifts under future climatic conditions, which differ by region, climate scenario, and dispersal

mechanism (Figs. 3.3, 3.4, Appendix 2, Figs. A2.8, A2.9). Our integrative connectivity approach projected habitat suitability losses of ~34% under SSP2 and ~54% under SSP5 for *H. guttulatus* by the end of the century (Appendix 2, Fig. A2.4). For *H. hippocampus*, habitat suitability losses are generally lower, with projections showing losses of ~13% under SSP2 and ~26% under SSP5 (Appendix 2, Fig. A2.5). On the other hand, habitat suitability gain is higher for *H. hippocampus* even for the most restricted dispersal [22% (SSP2); 34% (SSP5)] than for *H. guttulatus* [7.5% (SSP2); 8.5% (SSP5)] (Appendix 2, Figs. A2.6, A2.7). The difference between shorter pelagic drifting dispersal (D14) and longer passive dispersal via rafting (D100) was negligible (<1%) for *H. guttulatus* (Appendix 2, Fig. A2.6.). In contrast, for *H. hippocampus*, the gain of suitable habitat differed by 2% under SPP2 and 4 % under SSP5 between dispersal scenarios (Appendix 2, Fig. A2.7). Notably, oceanic connectivity and dispersal abilities limit the northward expansion of suitable habitats compared with unlimited dispersal (i.e., the standard models) (Figs. 3.3, 3.4, Appendix 2, Figs. A2.6, A2.7). Overall, the native distribution range was projected to experience overall contractions of suitable habitat for *H. guttulatus* (nearly -45% under both dispersal scenarios) and expansions for *H. hippocampus* [+8% (D14 pelagic scenario) and +12% (D100 rafting scenario)] under SSP5 (Appendix 2, Figs. A2.8, A2.9). For both species, distribution range contractions were predicted in the Mediterranean, Iberia, and Africa, whereas expansions were predicted in the North Sea and the UK/ Bay of Biscay (Figs. 3.3, 3.4, Appendix 2, Figs. A2.8, A2.9). However, some of the present-day suitable areas were projected to remain suitable under future climate conditions, primarily the North Sea, the Bay of Biscay, and the northern parts of the Iberian Atlantic coast (Figs. 3.3, 3.4). The Mediterranean Sea exhibited the most severe loss of suitable habitats under SSP5, with 80% for *H. guttulatus* and 50% for *H. hippocampus* (Appendix 2, Figs. A2.4, A2.5). In contrast, merely half of the suitability losses were observed under the lower emission scenario (SSP2) (Appendix 2, Figs. A2.4, A2.5, A2.10, A2.11). Severe habitat losses were also projected for the Black Sea and Iberian populations of *H. guttulatus* under SSP5 (Fig. 3.3; Appendix 2, Figs. A2.4, A2.10). Furthermore, losses of suitable habitats are predicted to occur for West African populations of *H. hippocampus* (Figs. 3.3, 3.4; Appendix 2, Figs. A2.5, A2.11).

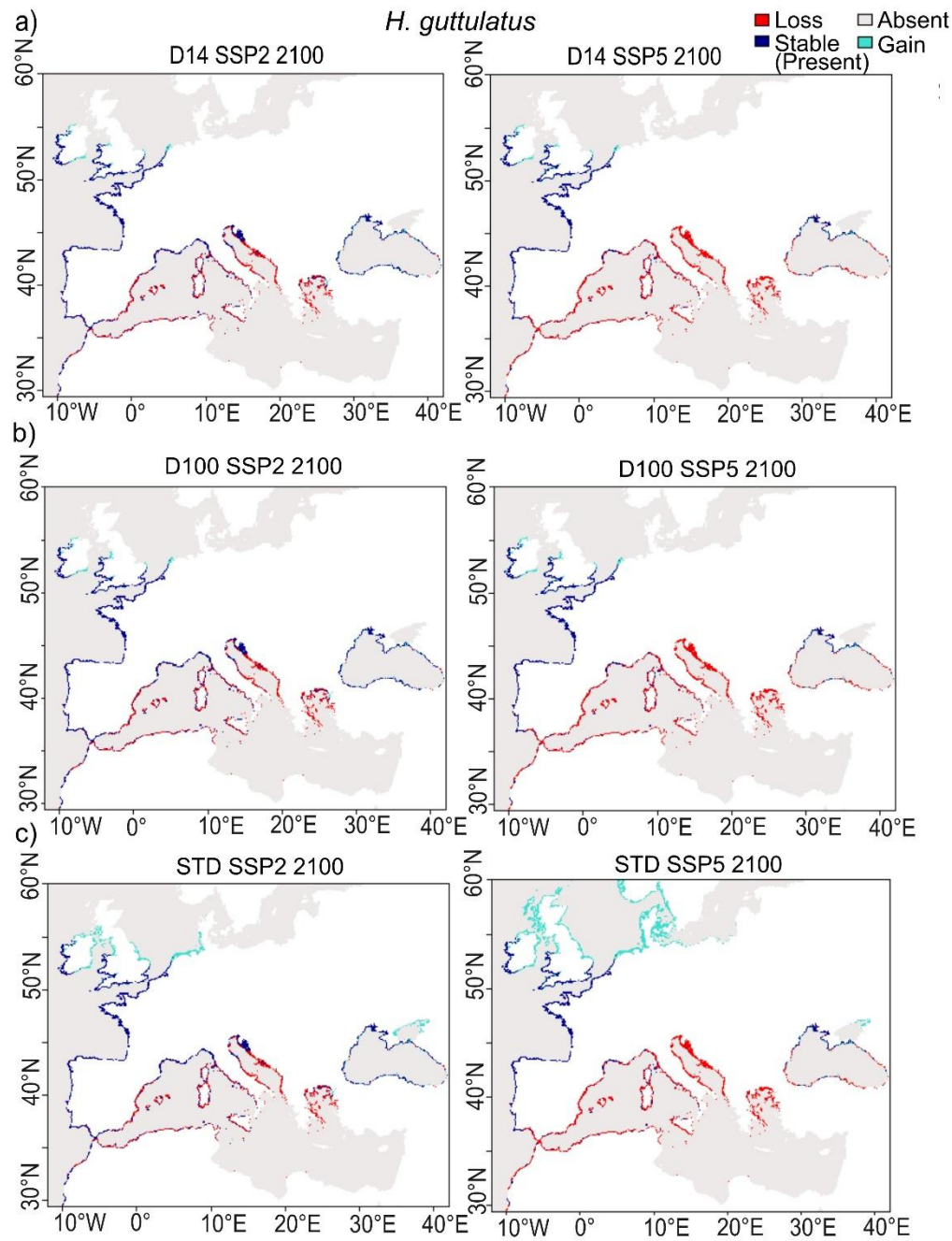


Figure 3.3. Predicted gains (turquoise), losses (red), and stability (blue) of suitable habitat of *Hippocampus guttulatus* for a) 14 days of pelagic drifting dispersal (“D14”) b) 100 days of passive dispersal via rafting (“D100”) and c) unlimited dispersal (“STD” - standard model) for SSP2 and SSP5 future climate scenarios until the year 2100. Grey represents the area where species were predicted to be absent in the present and future, while blue represents the area where species were predicted to be present in the present and future.

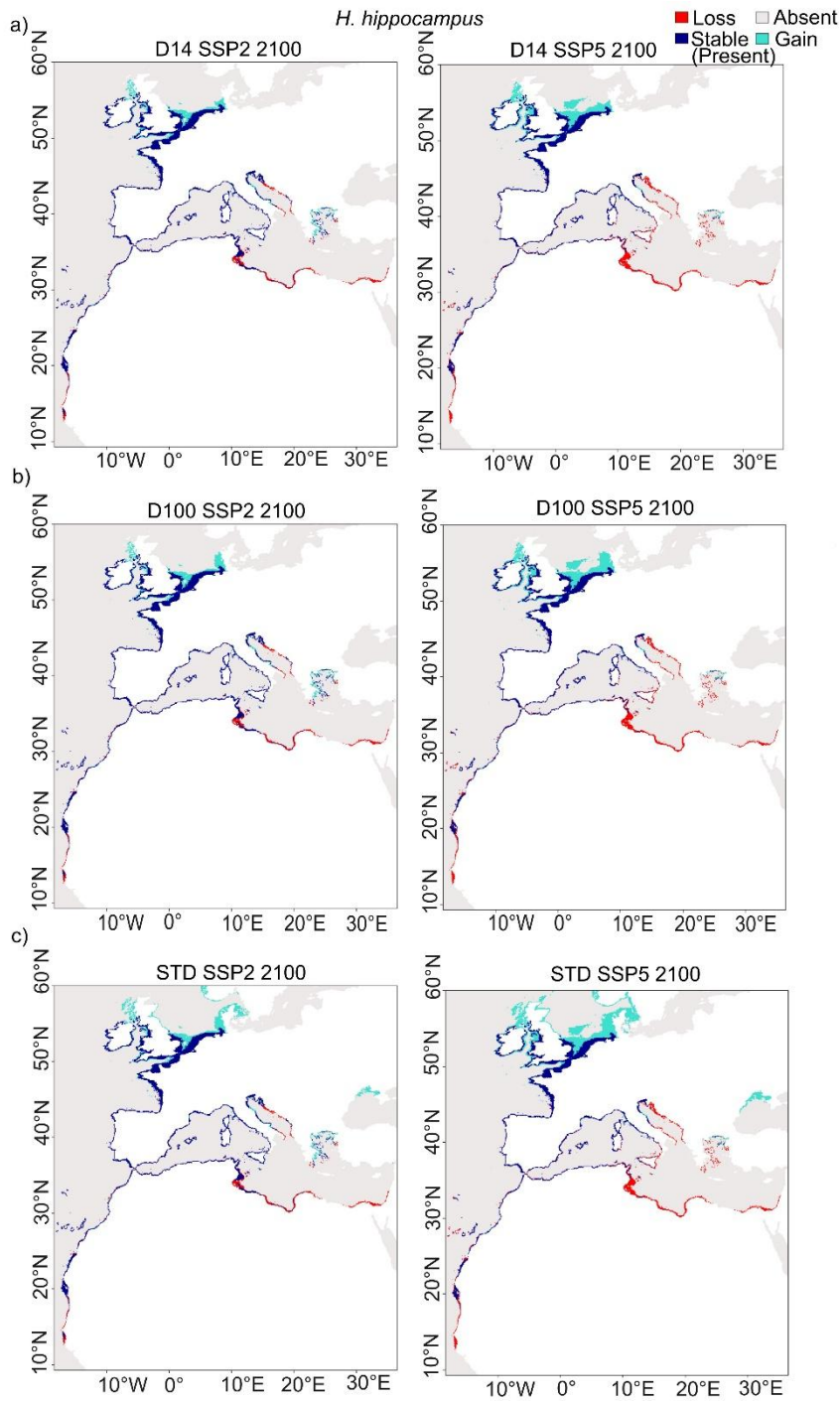


Figure 3.4. Predicted gains (turquoise), losses (red), and stability (blue) of suitable habitat of *Hippocampus hippocampus* for a) 14 days of pelagic drifting dispersal (“D14”) b) 100 days of passive dispersal via rafting (“D100”) and c) unlimited dispersal (“STD” - standard model) for SSP2 and SSP5 future climate scenarios until the year 2100. Grey represents the area where species were predicted to be absent in the present and future, while blue represents the area where species were predicted to be present in the present and future.

Discussion

Our integrated assessment of *H. guttulatus* and *H. hippocampus* distributions under two climate change scenarios raised concerns about the future sustainability of the populations in the Mediterranean, North Africa, and southwestern Iberia. The projected northward expansion and anticipated range contractions across the southern regions, coupled with the stable habitat suitability in the Celtic-Bay of Biscay area, are aligned with existing projections on the effects of climate change along European coasts (Monteiro et al., 2023; Philippart et al., 2011). Although the poleward shift is one of the most documented consequences of climate change on species distribution (Hastings et al., 2020; Hickling et al., 2006), our integrated projections inform that the dispersal mechanisms influenced by ocean currents emerge as a crucial limiting factor to range expansions, especially under the “business as usual” SPP5-8.5 scenario.

The variable importance analysis shows that temperature plays a key role in the present-day species’ distribution, raising concerns about the suitability of habitats under an expected warmer ocean (Garcia-Soto et al., 2021). Indeed, our projections showed that the species will experience significant habitat losses under future conditions. However, the impact of climate change is not uniformly distributed across the native ranges of the species. Therefore, the outcomes were further divided into sub-regions aligned to previously identified population units (Woodall et al., 2011, 2015). The most affected regions in terms of habitat loss were the Mediterranean and northern Africa, where declining trends of both species were identified in the IUCN Red List assessment (Pollom, 2016b, 2016a). Our results further show that in the Mediterranean, where *H. hippocampus* and *H. guttulatus* currently coexist, the loss of suitable habitats in the future is likely to be higher for *H. guttulatus* than for *H. hippocampus*. Among others, it was predicted that *H. guttulatus* populations in Mar Menor and Mar Piccolo will suffer from a substantial loss of suitable habitat due to climate change in the future. Seahorse density declines are often associated with illegal fishing or habitat quality depletion, caused by destructive fishing activities, dredging and pollution, whose impact has caused declines of up to 90% in populations (Correia, 2022; Harasti, 2016; Pierri et al., 2021; Vivas et al., 2024). Nonetheless, negative correlations between *H. guttulatus* densities and temperature were detected in the Ria Formosa lagoon (Correia et al., 2018) and the Mar Piccolo of Taranto (Pierri et al., 2021). Furthermore, the reasons behind some of the declines of seahorse populations across the Mediterranean Sea remain uncertain. For instance, seahorses once reported in Stagnone di Marsala (Sicily), up until about 20 years ago, have now completely disappeared from the area (Pierri et

al., 2022a). In the case of *H. hippocampus*, critical habitat losses are projected along the southern coastline of the Mediterranean, the coasts of Mauretania, Senegal, the Gambia, Guinea, and, to a lesser extent, the Canary Islands. Apart from climate change, West African populations of *H. hippocampus* and *H. algiricus* are threatened by illegal capture and trade for the Asian market (Cisneros-Montemayor et al., 2016; Foster et al., 2016). Based on genetic analysis, these populations of *H. hippocampus* are separated from those inhabiting the Mediterranean, Atlantic European coasts, and Macaronesia (Woodall et al., 2011). *H. hippocampus* used to be the only seahorse species reported in the Canary Islands (López et al., 2010; Lourie et al., 2016); however, recently, *H. algiricus* has been recorded at Gran Canaria, evidencing a northward expansion and a potential risk of hybridisation with *H. hippocampus* (Otero-Ferrer et al., 2015). Another case of interspecific interaction or hybridisation could occur in the Azores between the native *H. hippocampus* and the lined seahorse *H. erectus*, which likely reached the Azores via rafting (Woodall et al., 2011). According to the model results, the Iberian coast will remain stable and lose less than 10% of its suitable habitat under almost all scenarios because it is an upwelling centre that works as a refuge against warming sea temperatures (Lourenço et al., 2016). However, under the high emission scenario (SSP5), suitable habitats for *H. guttulatus* may decrease drastically (-30%) until the end of the century. This prompt decrease might be due to its preference for coastal lagoons and estuaries in this region (Pierri et al., 2022b), which tend to heat faster (Rodrigues et al., 2021). The contraction mostly affects the southern Portuguese and Spanish coasts, which harbour one of the largest populations of seahorses in Europe (Correia, 2022). Thus, in the high-emission scenario, the Iberian region would lose the potential to become a climate refuge and corridor for the movement of the Mediterranean population, should range shifts occur. In addition, a 40% decrease under the high-emission scenario was projected for *H. guttulatus* in the Black Sea. In contrast, under the low-emission scenario, the decrease may be smaller (3%). The habitat loss in this region can be attributed to its shallowness and the high stratification of the Black Sea, which results in rapid temperature increases and subsequent declines in oxygen levels (Capet et al., 2016; Korotaev et al., 2024; Sakalli et al., 2018). In the Mediterranean, the coastline of southern France and the northern Adriatic can hold suitable habitats and serve as refugia for *H. guttulatus* under lower emission scenarios, such as those recently detected by Monteiro et al. (2023). On the other hand, the species is likely to disappear under the higher emission scenarios. The Thau Lagoon, in southern France, hosts one of the largest populations of *H. guttulatus*, which is considered an Evolutionarily Significant Unit (ESU) only found in Mediterranean lagoons (Riquet et al., 2019). This finding hints at the limited dispersal potential of this species in the region. If those regions become increasingly

unsuitable, *H. guttulatus* will face limited opportunities for dispersal, significantly increasing the risk of substantial population declines. In the case of *H. hippocampus*, a lower emission scenario can halve the losses in the Mediterranean, especially in the Adriatic and Aegean Seas, where the presence of *H. hippocampus* is higher than that of *H. guttulatus* (Correia et al., 2020).

Several future climate projections predict the emergence of suitable habitats for Northeast Atlantic fish extending toward the North Pole (Monteiro et al., 2023; Philippart et al., 2011). Our models indicate that under restricted dispersal, *H. hippocampus* could gain up to 34% in suitable habitat by the end of the century, whereas gains for *H. guttulatus* remain below 9%. For both species, most of these shifts are concentrated in the northernmost parts of their native ranges (UK and Central North Sea). Under unlimited dispersal, gains in suitable habitats are substantially greater, reaching nearly 48% for *H. hippocampus* and 58% for *H. guttulatus*, and extending further north and toward Norway. Both approaches align with recent findings documenting an increasing presence of species with southern biogeographic affinities in the North Sea (Beare et al., 2004; Hiddink & ter Hofstede, 2008). However, the contrasting results between dispersal scenarios highlight the importance of including dispersal into species distribution models, as it allows for a more mechanistic understanding of the constraints species face when shifting their ranges. While models assuming unlimited dispersal predict broad northward expansions, integrating dispersal limitations may reveal more realistic, spatially constrained outcomes. To date, the two seahorse species have been reported along the coasts of Belgium (Vandendriessche et al., 2005), the Netherlands (Nijssen et al., 1974), the south-western coasts of the UK and Ireland, and the English Channel (Garrick-Maidment & Newman, 2011). Between 2001 and 2007, the first records of *H. hippocampus* in the Central North Sea (Dogger Bank) were recorded in the summer (Pinnegar et al., 2008). In 2023, dead individuals of *H. hippocampus* and *H. guttulatus* were recorded in Denmark (iNaturalist, 2024), while in the same year, a seahorse was found alive in southern Sweden, which was assumed to be an *H. hippocampus* (<https://www.gu.se/en/news/first-discovery-of-a-seahorse-in-sweden>). However, it remains questionable whether these findings point to viable seahorse populations or if they were isolated arrivals of drifted specimens. Moreover, it remains unclear if the reported increase in the occurrence of *H. hippocampus* in the North Sea is a result of ocean warming or changes in the Gulf Stream (Stebbing et al., 2002) or due to increased awareness and sampling efforts (Garrick-Maidment & Newman, 2011).

Seahorses have small home ranges (Foster & Vincent, 2004); thus, their potential for range expansions largely depends on passive dispersal, which is shaped by oceanographic connectivity (Boehm et al., 2013). There is a gap in knowledge about the extent to which pelagic juveniles contribute to the long-distance dispersal of seahorses; however, juveniles have been occasionally found drifting freely or attached to rafts (Luzzatto et al., 2013; Vandendriessche et al., 2005) whereas molecular evidences show that adults and subadults can raft for long distances hooked onto clumps of mobile macroalgae or debris (Teske et al., 2007). Thus, passive dispersal via rafting of a small number of individuals could lead to the foundation of new populations and could be a means of range expansion over longer distances (Boehm et al., 2013; Teske et al., 2007). Sporadic dispersal events could also explain the connection between the populations of *H. hippocampus* from Madeira, the Azores, and the Canary Islands (Otero-Ferrer et al., 2017). However, in some cases, sporadic dispersal may be limited by barriers or be insufficient to sustain genetic connectivity (Boehm et al., 2013; Teske et al., 2007). In this study, incorporating both dispersal and ocean connectivity limited the expansion of the distribution range, resulting in an overall loss of suitable habitat range for *H. guttulatus*. Habitat preferences for shallow coastal habitats may influence dispersal capabilities and restrict colonisation of new habitats, as was found for two seahorses in Southeast Asia (Lourie et al., 2005). Comparably, the preference of *H. guttulatus* for shallow inshore waters and coastal lagoons (Peiffer et al., 2024; Pierri et al., 2022b) might explain the reduced dispersal potential compared to *H. hippocampus*, which has been captured on offshore sandbanks and in deeper waters (Garrick-Maidment & Newman, 2011; Pinnegar et al., 2008). Sheltered bay habitats are often disjoint, resulting in limited dispersal and population mixing, which is particularly concerning for *H. guttulatus* (Woodall et al., 2015). Species with restricted dispersal ability tend to form isolated populations, which limits the potential of connectivity between populations and can hinder the colonisation of new suitable areas (Lourie et al., 2005). Furthermore, pelagic juveniles of sedentary coastal fish (rocky reefs and estuaries) use a retention mechanism to maximise local recruitment close to the sheltered inshore habitats (Borges et al., 2007). Based on this knowledge of larval ecology in sedentary coastal fish species and their traits (i.e. parental care, number of offspring, low swimming ability, growth rate, and habitat specificity), seahorses are expected to show similar patterns. For instance, juveniles of *H. guttulatus* in the Ria Aveiro (Portugal) and of *H. patagonicus* in San Antonio Bay (Patagonia) were collected at the surface during high tides, and near the bottom during ebb tides, which suggests that juveniles undergo vertical migrations to be retained in estuaries and lagoons (Luzzatto et al., 2013; Pires, 2010). This retention mechanism limits the pelagic dispersal of juveniles and might explain why *H. guttulatus* (and to some

extent *H. hippocampus*) are mainly found in enclosed bays in the Atlantic (Pierri et al., 2022b). However, due to the coarse resolution of the climate projections, our models fail to capture near-shore processes. Therefore, finer-scale nearshore climate models are urged to improve model outcomes and to confirm this theory.

According to the IUCN assessment, the resident extent of *H. hippocampus* does not encompass the Black Sea (Woodall, 2017; Woodall et al., 2011); however, some studies have reported the capture of *H. hippocampus* in the Eastern Black Sea (Başusta et al., 2014; Taylan et al., 2020; Uncumusaoğlu et al., 2012). Historically, the presence of *H. hippocampus* was reported in the Romanian Black Sea waters; however, in recent works, only *H. guttulatus* has been reported (Nenciu et al., 2018). Our predictive models with unlimited dispersal suggest increased habitat suitability for *H. hippocampus* in the northern Black Sea, whereas the model with restricted dispersal showed no response. Possibly, *H. hippocampus* has entered the Black Sea via passive dispersal on many occasions; however, it struggles to maintain a viable population, possibly due to the Bosphorus Strait, which can act as a barrier to dispersal (Debes et al., 2008; Durand et al., 2013). This uncertainty about the *H. hippocampus* population in the Black Sea highlights a knowledge gap in the dispersal of this species.

The cumulative impacts of multiple stressors and high uncertainty in how the species will respond challenge the accurate assessment of climate change risk and the development of conservation planning (Pearce & Selley, 2024). Marine protected area networks can mitigate the adverse effects of climate change and promote the stability of fish communities (Benedetti-Cecchi et al., 2024). However, the current MPA network throughout Europe provides minimal protection, e.g., allowing destructive fishing practices, dredging and anchoring (Aminian-Biquet et al., 2024; Assis et al., 2021; Bosso et al., 2024; Monteiro et al., 2023; Peiffer et al., 2024). For seahorses, marine protected areas are not always beneficial, as they can lead to increased predator biomass (Harasti et al., 2014), while other threats, such as pollution, persist outside the MPA and continue to impact habitat quality (Yasué et al., 2012). Thus, addressing local stressors (e.g., pollution, anchoring), restoring habitat or creating artificial habitat (Correia et al., 2013; Simpson et al., 2020), and limiting non-selective and illegal fishing practices in the area (Curtis et al., 2007) can be relevant protection measures. In the face of climate-induced range shifts, it is crucial to increase protection measures in climate refugia and establish a network of protected sites to enhance resilience and maintain gene flow between seahorse populations (Ashcroft, 2010; Planes et al., 2009; Warren et al., 2013; Wilson et al., 2020). Additional measures, such as translocating individuals or introducing captive-bred individuals to suitable

habitat areas, could enhance conservation efforts if other main threats have been resolved and habitat requirements have been fulfilled (Caldwell & Vincent, 2012a; Harasti et al., 2022). Seahorses are an important umbrella and flagship species; thus, implementing adequate conservation strategies would certainly resonate with other species and ecosystems of conservation concern (Pollom et al., 2021).

Conclusions

In conclusion, our study revealed that seahorse populations tend to be displaced from south to north following a global trend, implying the reduction of suitable habitat in their southern range border and the potential colonisation of new territories in the north. On the other hand, it was found that the northward expansion can be limited by dispersal ability and oceanographic connectivity, resulting in overall range contractions for *H. guttulatus* and limited range expansions for *H. hippocampus*. Despite that, both species are likely to experience losses in suitable habitat along their southernmost distribution range. Nevertheless, the model is relatively optimistic regarding dispersal mechanisms, as it assumes annual dispersal and that individuals reaching a certain point can disperse again in the following year. This underscores the need for further investigation on dispersal mechanisms and connectivity in different life stages to propose more robust measures related to spatial planning for seahorse conservation. Special attention should be paid to climate refugia for isolated *H. guttulatus* populations in the Mediterranean (Thau Lagoon, Mar Menor) and the Black Sea. Regular monitoring of populations, identification of dispersal mechanisms, and efforts to mitigate stressors in target areas, including those pointed out as potential climate refugia, will be crucial to alleviate the impacts of climate change on seahorses.

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CHAPTER 4

CHAPTER 4: Life-history traits drive key patterns of species distribution shifts in response to climate change

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Abstract

A major consequence of climate change is the poleward shift in species distributions, which has profound implications for the functional community structure and the dynamics of ecosystem food webs. In this study, we assessed the effects of climate change on habitat suitability for three fish life-history strategy groups (equilibrium, opportunistic, and periodic). To do so, we used occurrence data from the FishGlob dataset, which contains standardised and quality-filtered data from the ICES International Bottom Trawl Survey. Ensemble Species Distribution Modelling for the present (2000-2020) and the Future (2090-2100) under the SSP5 scenario was used to predict changes in habitat suitability based on key environmental variables, including bottom temperature, salinity, productivity, and dissolved oxygen. Our results partially align with the widely observed trend that climate-induced habitat changes drive species to shift their distributions northward and into deeper waters. However, contrary to expectations, significant range contractions were identified in the southern part of the North Sea, Celtic Sea, and Irish Sea. Notably, species predicted to experience range contractions were characterised by larger body sizes and higher trophic levels (equilibrium and periodic groups). In contrast, species with smaller body sizes and faster life cycles (opportunistic group) were consistently projected to gain habitat under future scenarios. This mismatch in response was predicted to lead to regional losses in functional richness, which could disrupt the ecosystem's functional structure and alter the dynamics of the food web. Thus, our results underscore the importance of incorporating trait-based responses into marine fish conservation and management strategies.

Keywords

Species Distribution Modelling, biogeography, functional composition, Northeast Atlantic fish, FishGlob, trait-based approach

Introduction

There is growing concern that the effects of climate change could significantly impact marine biodiversity, leading to another mass extinction (Penn & Deutsch, 2022). If the world continues with “business as usual” concerning greenhouse gas emissions, 9% of the ocean is projected to contain ecosystems in which at least 50% of constituent species are at high climate risk (Butt et al., 2022). In the European seas, 80% of threatened and commercially important species are projected to be at risk due to future novel climate conditions, especially species found in enclosed and semi-enclosed seas (Predragovic et al., 2024). A key consequence of climate change is the redistribution of species driven by environmental changes in their habitats (Perry et al., 2005a; Poloczanska et al., 2016; Rutterford et al., 2023), with marine species tracking temperature changes even faster than terrestrial species (Lenoir et al., 2020). Over recent decades, demersal fish species in the Northeast Atlantic have experienced changes in their distribution in the form of shifts in suitable habitat areas and density-dependent use of these areas (Baudron et al., 2020; Le Luherne et al., 2024a). An overall northward shift has been observed, with a more frequent contraction of areas occupied by species with northern biogeographic affinities, e.g., Boreal species, and an expansion of areas occupied by species with southern biogeographic affinities, e.g., Lusitanian and subtropical species (Anker-Nilssen et al., 2008; Brander et al., 2003; Hiddink & ter Hofstede, 2008; Punzón et al., 2016; ter Hofstede et al., 2010; ter Hofstede & Rijnsdorp, 2011). In addition to shifting northward, species have also been observed migrating to deeper waters, where they find suitable and more stable temperatures and habitat (Dulvy et al., 2008a; Le Luherne et al., 2024a). On the other hand, contractions of species distribution in the trailing edge might lead to local population depletion or extinction (Pinsky et al., 2020) and can impair the species' ability to adapt to future environmental changes through the loss of genetic diversity (Layton et al., 2024).

However, not all species follow the same trend of expected range shift (Rubenstein et al., 2023). Instead, the species' biogeographical distribution largely depends on the interaction of species' physiological and behavioural traits with the environment (McLean, Mouillot, & Auber, 2018; Pinsky et al., 2020; Violle et al., 2014). The species trait-environment relationship is shaped by the interaction of abiotic environmental conditions (e.g., temperature, salinity, habitat complexity), biotic interactions (e.g., competition), and the species' functional traits (McGill et al., 2006; Violle et al., 2007). Functional traits related to growth, reproduction, and survival (e.g., body size, lifespan, fecundity, offspring size, trophic level, dispersal ability) respond most strongly

to the environment and determine the species' ability to persist and colonise habitats (Costello et al., 2015; Estrada et al., 2016; Luiz et al., 2012; Violle et al., 2007). One well-studied example of species trait-environment relationship is the correlation between body size and temperature, which underlies Bergmann's rule for endotherms and the temperature-size rule commonly observed in ectotherms (Angilletta et al., 2003). Concurrently, it was found that fish with smaller bodies are more prevalent in warmer waters, while fish with larger body sizes are more prevalent in cooler waters (Beukhof, Frelat et al., 2019; Henriques et al., 2017), due to size-dependent metabolisms and selection from competition and predation (Edeline et al., 2013; Ohlberger, 2013). For instance, water at higher temperatures has lower oxygen concentrations, which favour smaller species that have a physiological advantage due to shorter oxygen diffusion paths and lower energy requirements (Edeline et al., 2013; Ohlberger, 2013). Body size is a key trait related to metabolism, mobility, and trophic interactions and is associated with several other life-history and ecological traits (Costello et al., 2015; Luiz et al., 2012). For instance, large-sized species tend to have periodic or equilibrium life-history strategies (i.e., low fecundity, long lifespan, high trophic level). In contrast, small-sized species tend to be associated with an opportunistic strategy (i.e., high fecundity, short lifespan, low trophic level) (Pecuchet et al., 2017). Accordingly, species with an opportunistic strategy were found to prevail in environments with elevated temperature and strong seasonality, while the equilibrium strategy prevails in environments with lower and more stable temperatures (Beukhof, Dencker, et al., 2019; Beukhof, Frelat, et al., 2019; González-Bergonzoni et al., 2012; Henriques et al., 2017; Kulbicki et al., 2015). Consequently, environmental variables that most strongly drive the biogeographic pattern of fish community structure are sea temperature, followed by depth, salinity, and seasonality, while oxygen and productivity are usually correlated with temperature, but can have a significant impact at local scales (Beukhof, Dencker, et al., 2019; Henriques et al., 2017; Pecuchet et al., 2017; Receveur et al., 2024; Rutterford et al., 2023).

These findings suggest that environmental conditions drive functional trait composition more consistently and more rapidly than taxonomic diversity (Coulon et al., 2024; Henriques et al., 2017; McLean, Mouillot, & Auber, 2018; McLean et al., 2019), which means that the spatio-temporal distribution of organisms and their functional role in ecosystems depend on their traits rather than on their taxonomic affiliation (Kjørboe et al., 2018). Life-history traits, such as body size, lifespan, and reproductive traits, play a key role in the sensitivity of species to climate change (Boyce et al., 2022; Butt et al., 2022). In the face of climate change, environmental filters act on the community's trait composition, which might result in assemblages with similar

trait composition that are adapted for the new environmental conditions, despite hosting distinct species pools (McLean et al., 2019, 2021). Even though large-bodied species are expected to have high dispersal ability due to their mobility as well as their broad environmental tolerance (Luiz et al., 2012), most studies have shown that species with shifting distributions often have smaller body sizes and faster life cycles than non-shifting species (Perry et al., 2005a; Rose, 2005). Thus, increasing water temperatures seem to favour smaller, faster-growing, short-lived, and lower trophic level fish species (Bernardo et al., 2024; Beukhof, Dencker, et al., 2019; Receveur et al., 2024). The life-history characteristics allow them to respond quickly to environmental changes due to short generation times, fast population turnover, and high dispersal rates (Beukhof, Dencker, et al., 2019; Estrada et al., 2016; McLean, Mouillot, & Auber, 2018; Pecuchet et al., 2017). Thus, rapid warming can lead to considerable spatial restructuring in the trait composition of fish communities. For example, following a warming period in the late 1990s, such changes were observed in the English Channel and southern North Sea, where the northwards shift of small, faster-growing, shorter-living pelagic species feeding at low trophic levels led to an inversion in functional structure between the two ecosystems (McLean, Mouillot, & Auber, 2018). Accordingly, the mean body size of the fish community of the southern North Sea was found to have decreased during a warming period (ter Hofstede & Rijnsdorp, 2011). This suggests that ocean warming-induced responses in traits such as average body size may be more consistent at the community level than at the individual level (Audzijonyte et al., 2020), due to shifts in species distribution and abundances, which in turn alter competitive and predatory interactions (Cheung et al., 2012; Ohlberger, 2013). These causalities support the argument that future species range shifts driven by climate change could lead to a severe decline in the functional diversity of fish assemblages and an increase in the functional similarity among assemblages (Buisson et al., 2013; McLean et al., 2019). Changes in the functional composition of communities have significant implications on ecosystem functioning by affecting food web structure, biotic interactions, nutrient cycling, and benthic-pelagic coupling (Amelot et al., 2023; Casini et al., 2012; McCann et al., 2005; Pecuchet et al., 2020; Vergés et al., 2014).

To date, regional and international policies lack the ability to effectively address climate-induced species range shifts in adaptive management and conservation planning (Baudron et al., 2020; Gormley et al., 2015; Whitney et al., 2023). For instance, the redistribution of commercial fish resulted in a mismatch between quota shares and regional abundance within management areas (Fernandes & Fallon, 2020). Linking species' life-history traits to their responses to climate change is a valuable method for scaling up individual impacts to the community level,

bridging knowledge on biodiversity with ecosystem functioning and services (McGill et al., 2006; Strong et al., 2015; Violle et al., 2014). Thus, to improve our understanding of fish community composition responses to climate change in the Northeast Atlantic, we used a trait-based approach to assess the impact of climate scenarios on the future distribution of suitable habitats according to species life-history traits. Using data compiled through a standardised spatial and temporal sampling framework, we modelled the suitable habitat of representative species of three life-history strategy groups, equilibrium, opportunistic, and periodic, under the SSP5 climate scenario, projecting changes for the end of the 21st century. The information on changes in each group was then combined to provide a more integrative view of how the functional composition of the fish community might change in the future. The findings can provide critical insights for designing effective management and conservation strategies aimed at addressing future challenges and mitigating potential conflicts over resource and habitat use.

Materials and Methods

Study area

The present study covers the continental shelf of the Atlantic ICES ecoregions: Norwegian Sea, Baltic Sea, Greater North Sea, Celtic Seas, Bay of Biscay, and the Iberian Coast. These areas harbour diverse geomorphological and environmental characteristics. In the north, the Norwegian Sea is influenced by both warm, saline Atlantic waters and cold Arctic waters, and features a narrow shelf surrounded by deep basins and deep fjords with cold, nutrient-rich waters (ICES, 2022). In contrast, the Baltic Sea is a shallow, semi-enclosed basin with strong salinity gradients and hypoxic zones (ICES, 2024a). The Greater North Sea is a broad, shallow shelf strongly influenced by tidal events and water exchange with the Baltic and Atlantic Seas (ICES, 2024c). At the same time, the Celtic Seas mainly consists of the continental shelf area ($< 200\text{m}$) and adjacent slopes, which are highly influenced by the ocean currents of the Atlantic Ocean (ICES, 2024b). The Bay of Biscay and the Iberian Coast cover shallow shelf seas and adjacent deeper Atlantic waters and are characterised by seasonal wind-driven upwelling and high productivity with considerable variation across the region (ICES, 2024b). Overall, the study area hosts temperate species (e.g., hake), the southern distribution of sub-boreal species (e.g., cod), and the northern distribution of subtropical species (e.g., Atlantic horse mackerel) (Baudron et al., 2020). Furthermore, it is an important fishing ground and is highly affected by human activities (Froese et al., 2021; Korpinen et al., 2021).

Collection of traits

Six key traits essential for species performance in its ecosystem (i.e., feeding, survival, and reproduction) were selected: maximum length, lifespan, trophic level, fecundity, offspring size, and parental care (Winemiller, 2005; Winemiller et al., 2015). The trait values were extracted from the literature (Beukhof, Dencker, et al., 2019; Pecuchet et al., 2017) and supplemented with values from FishBase using the “rfishbase” R package (Boettiger et al., 2024). Maximum length refers to the maximum total length recorded for a species, while lifespan is the maximum age a species can reach. Trophic level indicates a species' position in the food chain, with marine fish ranging from 2 for herbivores and detritivores to 4.5 for apex predators. Fecundity refers to the average number of offspring a mature female can produce each year. Offspring size is the typical size of the offspring released into the environment, whether as eggs for oviparous species or larvae/juveniles for ovoviviparous species. Parental care reflects the extent of parental investment in offspring survival. This trait was converted from categorical to continuous values using the approach outlined by Pecuchet et al. (2017), with categories ranging from (1) pelagic egg, (2) benthic egg, (3) hidden brood, (4) guarded brood, to (5) bearer.

Analysis of life-history strategies

The species included in this study were selected from the FishGlob dataset containing 448 species for the European seas (Maureaud et al., 2024), which were further filtered by depth (above 200 m) and by years (2000-2020), resulting in 337 remaining species. Of the 337 species, 202 had complete data for all six traits and were included in an Archetypal Analysis (AA). Although this selection represents only half of the species recorded in the surveys, it consists of the most frequently observed species. The AA was used to characterise the selected marine fish species into three distinct life-history strategy groups (opportunistic, periodic, and equilibrium), following procedures described in Pecuchet et al. (2017). In the analysis, extreme values represent archetypes, which form the corners of the convex hull volume encompassing the trait space (Mørup & Hansen, 2012). Since traits were measured on different scales, the values of fecundity, offspring size, body size, and lifespan were normalised before input to AA by a log10 transformation, and all six traits were standardised (i.e., to a mean of 0 and a variance of 1) to ensure equal weights in the AA. The AA was performed for a fixed number of strategies ($k = 10$), and the residual sum of squares (RSS) was calculated for 10 iterations for each k using the 'archetypes' package in R. The best number of strategies was found using the 'elbow criterion', which means visually identifying the point where the RSS drops significantly. Furthermore, a principal component analysis (PCA) was performed on the six traits to compute a biplot that

visualises the position of the archetypes and the species in the trait space. Each grid cell contains a sum of the proportion of each archetype, hence the corresponding life-history strategy (Pecuchet et al., 2017).

Species occurrence data for Species Distribution Modelling

Species occurrence points were extracted from the FishGlob dataset (Maureaud et al., 2024). FishGlob is a comprehensive dataset that combines publicly available bottom trawl surveys, sampling demersal communities across the subtropical to polar marine continental shelves and slopes of North America and Europe. It includes data on 2,170 fish taxa and 216,548 hauls collected between 1963 and 2021. The advantage of using this dataset is that it is standardised and pre-processed by including only hauls sampled with otter-trawl gears to ensure uniform catchability and detectability (Maureaud et al., 2024). Furthermore, surveys in the dataset are already quality filtered (e.g., different gear types or missing geolocation data were excluded) (Maureaud et al., 2024). The dataset was extended with data from the continental shelf of the Norwegian Sea provided by the Norwegian Institute of Marine Research and follows the same quality filtering criteria as above. Some regions and depths were sampled more frequently than others; therefore, to reduce sampling bias and standardise occurrence points, we filtered the dataset to surveys conducted in depths above 200m between the years 2000 and 2020 during autumn, since surveys were conducted regularly in this season throughout the study area. In the few sites where autumn data were not available (i.e., for the survey NS-IBTS and Norway), data from the winter were used.

Environmental predictors

Six environmental variables that are known to influence the biogeography and distribution of marine fish species were selected for inclusion in the modelling analysis (Costello et al., 2015). Temperature, salinity, oxygen, and productivity at maximum depth, between 2000 and 2020, were extracted as monthly means from the Global Ocean Physics Reanalysis of Copernicus at 0.083° resolution and averaged to an annual mean to be compatible with future projections. Environmental values were obtained for each data point (presences and pseudo-absences) at the corresponding spatial position and year for inclusion in the model. The static predictor bathymetry was downloaded from Bio-ORACLE at 0.05° resolution (Assis et al., 2024), and the distance to the nearest coast was retrieved from Ocean Colour Web (NASA Earth Data) at 0.01° resolution. All environmental layers were rescaled to the same resolution (0.05°). The final data

matrix included coordinates, dates, and values for the six variables. For future projections, temperature, salinity, oxygen, and productivity at maximum depth were downloaded from BioOracle as decadal means (2090-2100) under the SSP5 scenario at 0.05° resolution (approximately 5.5 km at the equator) (Assis et al., 2024). The variables were assessed for correlation using Pearson's correlation coefficient (r), and variables were excluded from the model if $r > 0.7$.

Modelling Approach

The Ensemble Species Distribution Modelling (ESDM) approach within the 'biomod2' package (version 4.2–2 in R) was used to predict species distribution and habitat use (Araújo & New, 2007; Thuiller, 2024). The ESDM approach aims to combine and average out multiple Species Distribution Models (SDMs), each of which has constraints and biases (Araújo & New, 2007). In our study, SDMs were generated using nine algorithms (Generalized Linear Models (GLM), Generalized Additive Models (GAM), Generalized Boosted Models (GBM), Classification Tree Analysis (CTA), Flexible Discriminant Analysis (FDA), Artificial Neural Networks (ANN), Maximum Entropy (MAXENT), Random Forest (RF), Surface Response Envelope (SRE)). The predictive performance of each SDM model was evaluated using Receiver Operating Characteristic (ROC) and True Skill Statistics (TSS), with values ranging from 0 to 1. Scores above 0.5 indicate better-than-random performance, while scores below 0.5 suggest chance-level predictions (Allouche et al., 2006). Only models with the evaluation metric TSS greater than the threshold of 0.7 were combined and averaged to create an ensemble prediction. Ensemble model predictions were used to provide a visual output of relative habitat suitability, where values range from 0, meaning lowest suitability, to 1, meaning highest suitability in the modelled cell. To project the present suitability, the temporally explicit predictors (sea temperature, salinity, oxygen, and productivity) were averaged over the study period (2000-2020) and paired with static predictors. The future predictions were projected on raster layers with decadal means (2090-2100). Predictive maps were converted into presence-absence maps using a TSS-optimised threshold for each species. To account for data limitations, binary maps were restricted to areas with less than 200m depth before calculating habitat loss, gain, and range changes. The binary maps were summed using the mosaic command in R to determine the spatial variation in the number of species within each of the life history strategy groups. Additionally, maps showing differences in the numbers of species between the present and future were computed. The importance of the variables in determining habitat suitability was calculated with the function 'get_variables_importance' in the Biomod2 package (Thuiller, 2024). Predictions were made by altering only one target variable at a time, while keeping all other

variables constant at their median values. The relevance of each variable was estimated by calculating the difference between the original prediction and the prediction made with the permuted variable, divided by one minus the correlation score. On a scale from 0 to 1, a higher value indicates a greater influence of the variable on the ensemble model (Elith et al., 2005).

Functional richness

Functional richness represents the volume of functional space occupied by the community and was estimated by calculating the convex hull volume using the FD package in R. (Laliberté, 2024; Villéger et al., 2008). To calculate functional richness for each grid cell for the present and future, the presence-absence data of the ESDM were combined with the species-by-trait matrix of the AA. Thereby, changes in the presence and absence of the species due to climate change are reflected in the functional richness values.

Results

Life-history strategy groups

The results of the AA showed that the optimal number of archetypes (k) was three, and the position of the archetypes and the species in the traits space was visualised using a principal component analysis (PCA) biplot performed on the six traits (Appendix 3, Fig. A3.1). Each extreme point (archetype) represents a unique combination of trait characteristics that correspond to the equilibrium, opportunistic, and periodic life-history strategies (Pecuchet et al., 2017). Each point (species) in the trait space is represented by proportions of the three archetypes based on the proximity of the point to each archetype. The opportunistic strategy group includes species that are small, have short lifespans, occupy low trophic levels, and exhibit high fecundity. The periodic strategy group consists of species with medium to long lifespans and body sizes, higher trophic levels, and high fecundity but low parental care and offspring size. The equilibrium strategy group is characterised by species with large body sizes, long lifespans, and high trophic levels, but typically have low fecundity, produce large offspring, and provide substantial parental care. Based on the results, seven species per life-history strategy group were chosen for modelling taking into account their number of occurrence points (minimum of 450 points), balanced spatial representativity along the distribution area (significant extent inside study area; balanced number of species with northern affinity and with southern affinity), and depth range (mostly occurring above 200m) (Table 4.1).

Table 4.1. Fish species selected for each of the three life-history strategy groups, with main characteristics of the biogeographic and physical habitat requirements sourced from the “rfishbase” R package (Boettiger et al., 2024). The number of occurrence points that were used in the SDMs is also listed.

Species	Biogeographic affinity	Vertical position	Depth range (m)	Distribution Range	Temp. range (°C)	Occurrence points (N)
Opportunistic Species						
<i>Ammodytes tobianus</i>	Boreal	demersal	1-96	72°N - 36°N, 23°W - 42°E	7.3 - 13.5	580
<i>Callionymus lyra</i>	Lusitanian	demersal	5-430	66°N - 16°N, 42°W - 42°E	11.7 - 19.5	10147
<i>Engraulis encrasicolus</i>	Lusitanian	pelagic	0-400	62°N - 37°S, 18°W - 42°E	7.1 - 18.0	4464
<i>Mullus surmuletus</i>	Lusitanian	demersal	5-409	62°N - 14°N, 19°W - 42°E	7.0 - 16.1	3706
<i>Pagellus acarne</i>	Lusitanian	benthopelagic	0-500	58°N - 12°N, 26°W - 36°E	12.0 - 18.4	924
<i>Sardina pilchardus</i>	Lusitanian	pelagic	10-100	68°N - 14°N, 32°W - 43°E	7.1 - 17.3	2554
<i>Sprattus sprattus</i>	Atlantic	pelagic	10-150	69°N - 30°N, 11°W - 42°E	4.3 - 15.3	10296
Periodic Species						
<i>Conger conger</i>	Lusitanian	demersal	0-1171	68°N - 12°N, 32°W - 42°E	4.4 - 14.4	3665
<i>Dicentrarchus labrax</i>	Lusitanian	demersal	10-100	72°N - 11°N, 19°W - 42°E	7.3 - 19.5	1266
<i>Gadus morhua</i>	Boreal	benthopelagic	0-600	83°N - 35°N, 76°W - 86°E	0.5 - 10.3	15547
<i>Merlangius merlangus</i>	Lusitanian	benthopelagic	10-200	72°N - 35°N, 27°W - 42°E	7.0 - 11.9	16163
<i>Merluccius merluccius</i>	Lusitanian	demersal	30-1075	76°N - 18°N, 30°W - 42°E	7.9 - 15.4	10549
<i>Trisopterus luscus</i>	Lusitanian	benthopelagic	30-100	62°N - 25°N, 19°W - 16°E	7.1 - 12.8	2920
<i>Zeus faber</i>	Lusitanian	benthopelagic	5-400	75°N - 49°S, 17°W - 177°E	6.7 - 23.7	5993
Equilibrium Species						
<i>Galeorhinus galeus</i>	Atlantic	benthopelagic	0-1100	70°N - 58°S, 111°E - 37°E	6.7 - 23.2	486
<i>Leucoraja naevus</i>	Atlantic	demersal	12-900	63°N - 15°N, 18°W - 36°E	7.2 - 16.7	3400
<i>Raja brachyura</i>	Atlantic	demersal	10-380	60°N - 22°N, 18°W - 24°E	7.1 - 16.2	532
<i>Raja clavata</i>	Atlantic	demersal	5-1020	70°N - 38°S, 25°W - 50°E	7.1 - 15.8	3776
<i>Raja montagui</i>	Atlantic	demersal	8-530	61°N - 16°N, 18°W - 25°E	7.0 - 16.0	2713
<i>Scyliorhinus canicula</i>	Atlantic	demersal	10-780	63°N - 3°N, 32°W - 37°E	7.2 - 16.2	10509
<i>Squalus acanthias</i>	Atlantic	benthopelagic	0-1460	78°N - 57°S, 82°W - 171°W	4.2 - 18.7	2446

Variable importance

Variable importance varied among species within life-history strategy groups. On average, bathymetry showed the highest importance for the opportunistic group, while temperature was the most influential for the periodic and equilibrium groups (Fig. 4.1). Notably, periodic species showed the highest variability in the variable importance of bathymetry and temperature. Other variables had low importance, though there were some group- and species-specific differences. Distance to the coast was slightly more important for species in the equilibrium and periodic groups. Outliers were found for distance to the coast, which was more important for *Raja brachyura* and *Pagellus acarne* than for other species in their respective groups (Appendix 3, Fig. A3.2). Oxygen was more important for *Galeorhinus galeus* and *Sardina pilchardus* (Appendix 3, Fig. A3.2). The importance of bathymetry was higher than average for *Squalus acanthias* and *Sprattus sprattus*, but low for *P. acarne*. Temperature was of lower-than-average importance for *S. sprattus*, while salinity and productivity had unusually high importance for *Ammodytes tobianus* (Appendix 3, Fig. A3.2).

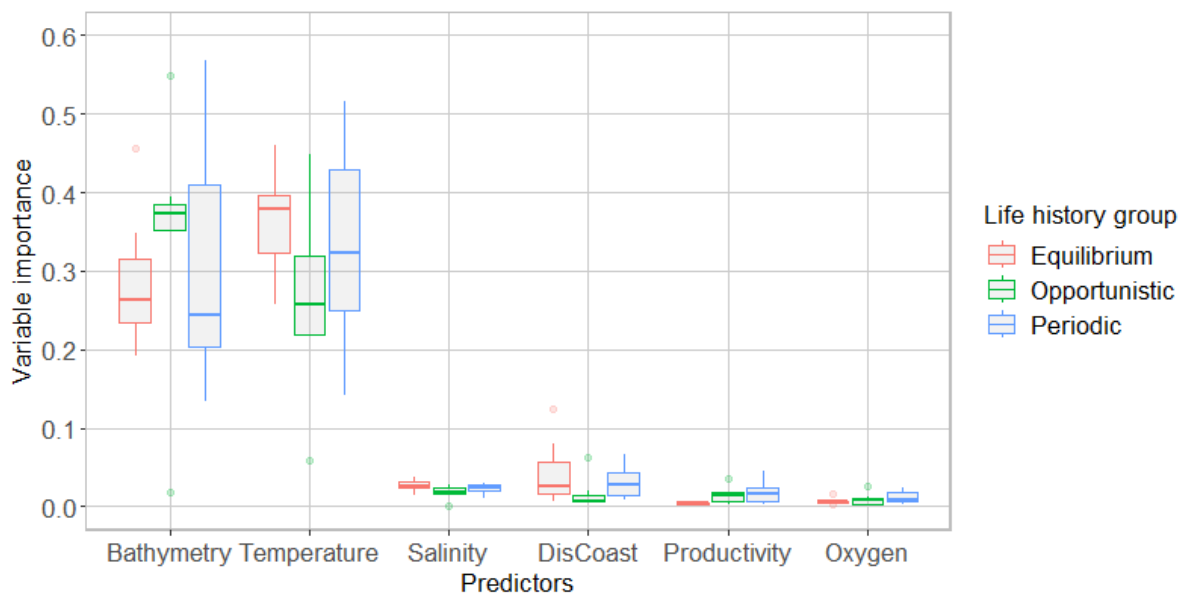


Figure 4.1. Variation in the variable importance of the environmental predictors for each of the three life-history strategy groups.

Habitat loss, gain, and range change

On average, losses were significantly higher in the equilibrium group compared to the other two groups (Fig. 4.2; Appendix 3, Fig. A3.3). While there were no significant differences in gains or range changes between all groups, the range change in the equilibrium group was significantly lower than in the opportunistic group (Appendix 3, Fig. A3.3). The periodic group showed high variability, while the equilibrium and opportunistic groups presented some outliers

(Fig. 4.2). Outlier in the opportunistic groups were *P. acarne* with a higher-than-average gain and range change, while *S. sprattus* presented lower-than-average values for both. On the other hand, in the equilibrium group, losses were higher than average for *Raja montagui* and *S. sprattus* (Appendix 3, Fig. A 3.7).

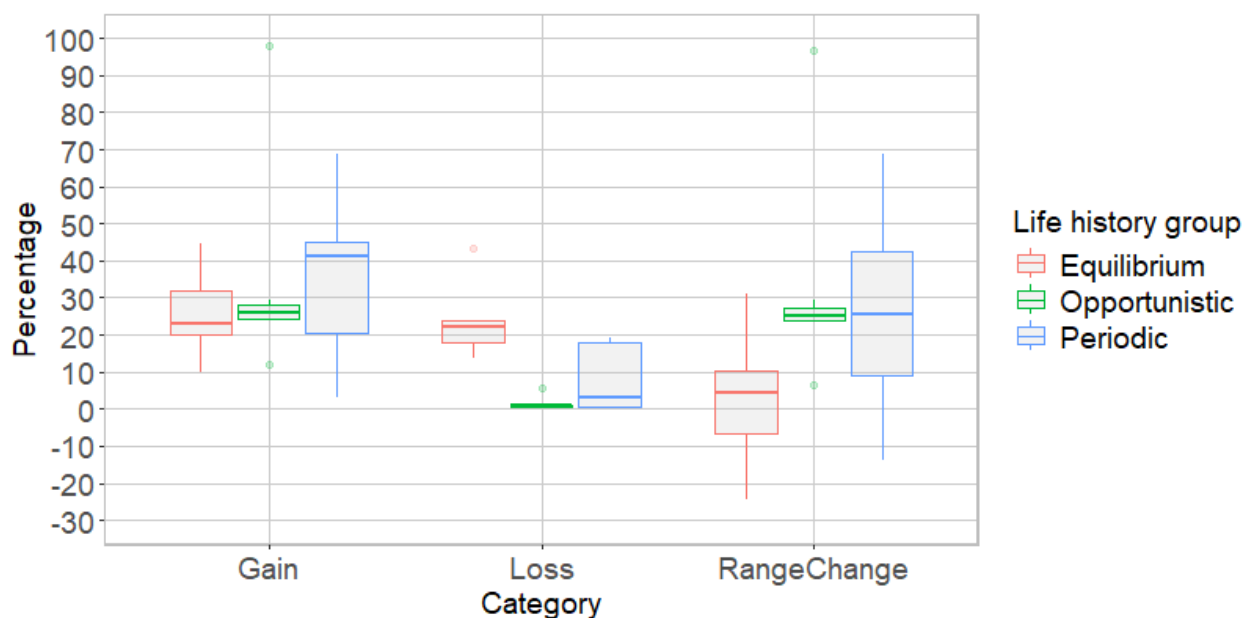


Figure 4.2. Percentage of gains, losses, and range change of habitat suitability for the three life-history strategy groups, between the current (2000-2020) and future projection (2090-2100).

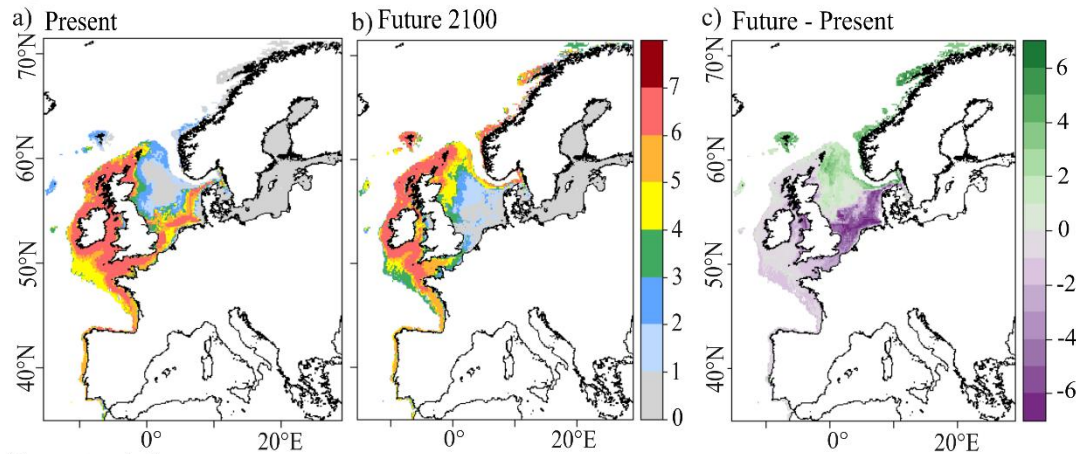
Changes in life-history strategy group distributions

The highest number of the selected species belonging to the equilibrium group was found in the southern North Sea, English Channel, Celtic Sea, and Irish Sea, particularly in coastal areas in the present (Fig. 4.3). When comparing current and future habitat suitability, the highest predicted losses in terms of the number of species in the equilibrium group were predicted along the southern North Sea and the Irish Sea (Fig. 4.3), with significant losses also expected in the western Celtic-Biscay Shelf Sea, the Northern Iberian Coast, and the English Channel. Species' gains were predicted to occur in the northern North Sea, the Norwegian Sea, and around the Faroe Islands (Fig. 4.3). The species within this life-history strategy group showed similar patterns in gains and losses with some exceptions (Appendix 3, Fig. A3.4). For instance, the spiny dogfish, *S. acanthias*, was predicted to lose most of its habitat in the western Celtic Sea, the Bay of Biscay, and along the northern Iberian coast, resulting in an overall negative range change for this species (Appendix 3, Figs. A3.4, A3.7). Furthermore, *R. montagui* and *R. brachyura* were not predicted to extend their habitat towards the deeper Central North Sea (Appendix 3, Fig. A3.4). The species with the highest loss and range change in this group was found to be

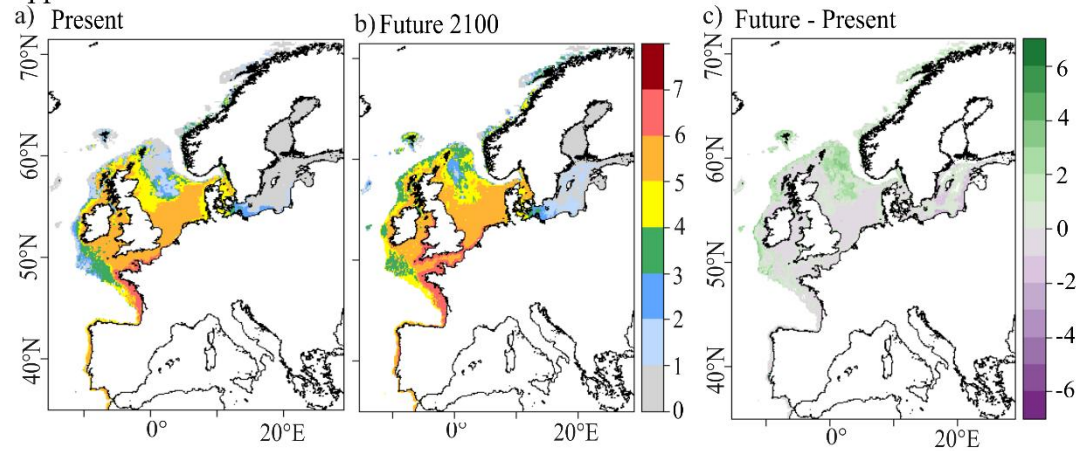
R. montagui, which also shows contractions along the Iberian coast (Appendix 3, Figs. A3.4, A3.7). The selected species of the opportunistic group were predicted to be widespread across the study area, with the highest number on the eastern Celtic-Biscay shelf in the present (Fig. 4.3). Looking at the difference in the number of species in the opportunistic group between present and future showed mostly stable ranges in the North Sea and the Celtic-Biscay Shelf (Fig. 4.3). The highest losses in the number of species were expected in the shallow areas of the Baltic Sea. In contrast, the highest gain was projected to occur further north and in deeper waters (Central North Sea, Norwegian Sea, and western Celtic-Biscay Shelf) (Fig. 4.3). The loss of species in the Baltic Sea was attributed to the loss of *S. sprattus* and *Engraulis encrasicolus* in the southern Baltic, while *E. encrasicolus* was predicted to gain more habitat in the central and northern part of the Baltic (Appendix 3, Fig. A3.5).

In the periodic group, most of the selected species were concentrated along the southern and western coasts of the UK and eastern Ireland in the present (Fig. 4.3). The changes in the number of species in the periodic group were characterised by the loss of species in the shallow areas of the Baltic, along the coast of the southern North Sea, and the mid-shelf of the Celtic Sea (Fig. 4.3). The main gain in species was predicted in the northern North Sea and the Norwegian Sea (Appendix 3, Fig. A3.6). However, the species-specific responses varied in this group (Appendix 3, Fig. A3.7). Species projected to experience habitat loss in the future included *Gadus morhua*, *Trisopterus luscus*, and *Zeus faber*; however, the location of losses varied among species (Appendix 3, Fig. A3.7). In many cases, habitat gains for one species coincide with losses for another, resulting in a limited change in the number of species. For instance, *T. luscus* and *Dicentrarchus labrax* extended their suitable habitat to the western Celtic-Biscay shelf, where *G. morhua* experienced habitat loss (Appendix 3, Fig. A3.6). On the other hand, *T. luscus* lost habitat in areas where *Merluccius merluccius* and *Conger conger* gained suitable habitat (i.e., the Central North Sea, the Irish Sea, the English Channel, and the southern North Sea) (Appendix 3, Fig. A3.6).

Equilibrium



Opportunistic



Periodic

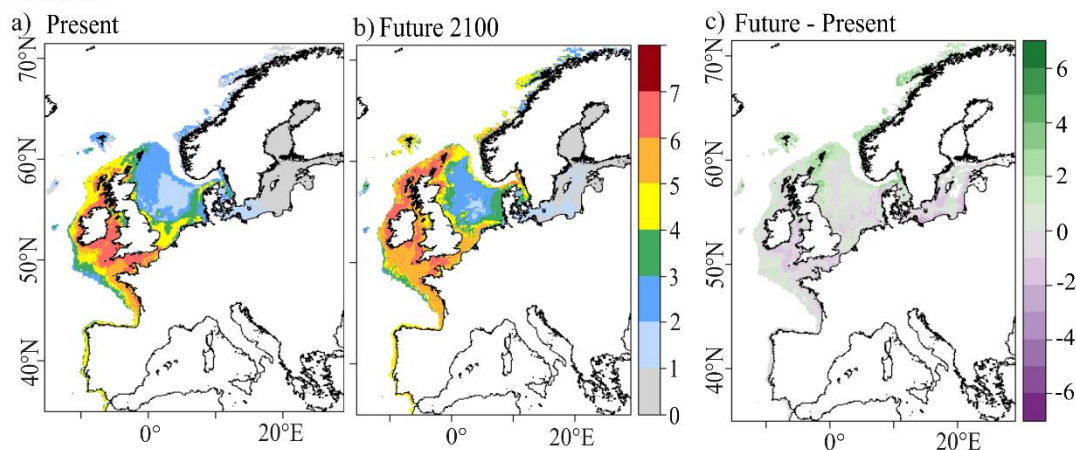


Figure 4.3. Number of species present within each of the three life-history strategy groups (equilibrium, opportunistic, and periodic) in a) the present (2000-2020), b) the future (2090-2100), and c) the difference between the present and future.

Changes in functional richness

Changes in the distribution of the selected species of the life-history strategy groups resulted in changes in functional richness across the study area with the highest losses in the southern North Sea, the English Channel, and the Irish Sea and highest gains along the Norwegian Sea, the northeastern North Sea and the outer continental shelf edge of the Atlantic (Fig. 4.4).

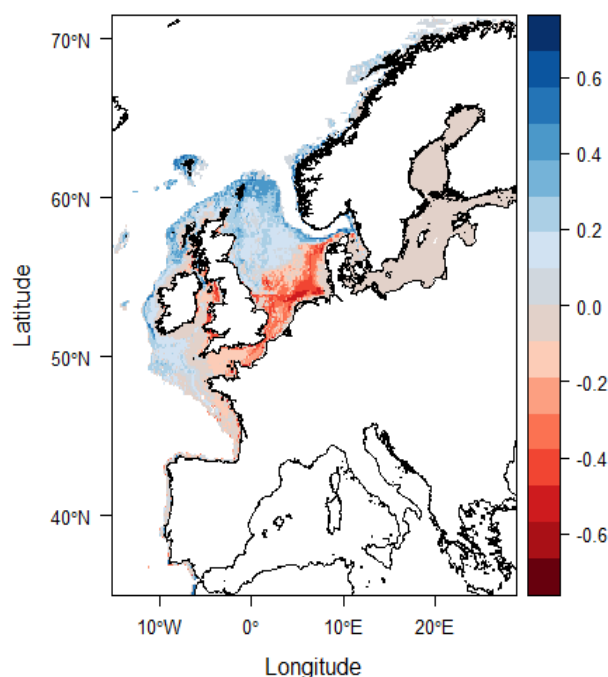


Figure 4.4. Difference in functional richness between the present and the future (future – present) for all species combined.

Discussion

Our results showed a northward and deepening shift of the Lusitanian and Atlantic species within shelf areas, consistent with previous studies (Dulvy et al., 2008b; Le Luherne et al., 2024b; Martins et al., 2021; Perry et al., 2005b; Poloczanska et al., 2016). However, the projections also showed significant range contractions in the southern North Sea, Celtic, and Irish Seas. Notably, the species with predicted range contractions were species of large body size and high trophic level (equilibrium and periodic groups). In contrast, species with small body sizes and a fast life cycle (opportunistic group) were projected to consistently gain habitat in the future. These differential responses among life-history strategy groups can lead to altered species interactions and changes in trophic dynamics and are predicted to result in regional changes in functional richness, which could have substantial consequences for ecosystem functioning and services (Pinsky et al., 2020). By using the novel approach of linking species' functional traits to their spatial dynamics, our results provide predictive insight into which functional groups are likely to expand, decline, or shift, if the trends observed could be found in species sharing common traits (Barnett et al., 2019; Coulon et al., 2023). The choice of species data and environmental data limited the projections of our models to species susceptible to certain

fishing gear (i.e., otter trawl) in habitats above 200 m, largely excluding the deep-sea fish community, some bigger pelagic species, and rare species. Besides, additional factors could influence the ability of the species to persist and colonise new suitable habitats, such as dispersal ability and genetic adaptations (Layton et al., 2024). Furthermore, the impact of climate change on the distribution of larval and juvenile stages might vary from that of adults, resulting in reduced connectivity in essential fish habitats (Lima, Garrido, et al., 2022). Nonetheless, our study highlights the critical role of life-history strategy in driving future range shifts and, consequently, reshaping community structure within ecosystems. Thus, this approach enhances our ability to anticipate community responses to global change.

Responses in life-history strategy group distributions and functional richness

Our study predicted range contractions predominantly for species with large body sizes, high trophic levels, and slow reproduction (equilibrium group). In contrast, species of small body sizes, low trophic levels, and a fast life cycle (opportunistic group) were predicted to experience range expansions. Most of the opportunistic species (e.g., *S. pilchardus*, *E. encrasilous*, *S. sprattus*) were predicted to follow the commonly reported trend of northward expansion of suitable habitat in the North Sea and along the Norwegian coast and a westward shift towards deeper waters in the Celtic Sea and the Bay of Biscay (Le Luherne et al., 2024; Lima, Baltazar-Soares, et al., 2022). Generally, species with smaller body sizes and faster life cycles can respond quickly to changing environmental conditions because of their high dispersal and rapid population growth (Beukhof, Dencker, et al., 2019; Beukhof, Frelat, et al., 2019; Pecuchet et al., 2017) and thus are more likely to expand into new regions under climate change. In contrast, large species that are long-lived with slow reproduction and high trophic level tend to be the most vulnerable species to anthropogenic stressors, including climate change (Bender et al., 2013; Butt et al., 2022; Olden et al., 2007; Walls & Dulvy, 2021). Species' vulnerability to a stressor is defined as a function of its sensitivity (the degree to which it is affected by a stressor) and adaptive capacity (ability to adapt to or recover from a stressor) (Butt et al., 2022). In case of climate change, the negative temperature-size relationship increases the sensitivity of large species to rising temperatures, while reproductive traits (e.g., longer lifespan, slow population turnover) reduce the adaptive capacity of the species (Coulon et al., 2024; Gonzalez-Suarez et al., 2013; Jones & Cheung, 2018). Species of the periodic group showed varying responses to climate change, which are likely due to the biogeographic affinities of the species. Species with southern biogeographic affinities (*Mullus surmuletus* and *D. labrax*) showed increases in suitable habitat, while boreal species (e.g., *G. morhua*) experienced substantial decreases in suitable

habitat (Maltby et al., 2020; Townhill et al., 2023). These predictions align with the observations that the number of warm-water species (Lusitanian species) has increased in the North Sea, Celtic Seas, and the English Channel (Brander et al., 2003; Le Marchand et al., 2020). However, other traits and factors than biogeographic affinity can influence the range shift of fish species, such as water column habitat, population size, range size, and dispersal ability (MacLean & Beissinger, 2017; Pearson et al., 2014; Rincón-Díaz et al., 2024). However, in this study, the latter traits were less relevant or comparable, as all selected species had broad distribution ranges, large population sizes, and moderate to high dispersal abilities.

Over the last 30 years, the North Sea fish community has diverged in species composition but converged in trait composition, with an increasing prevalence of pelagic, smaller, and faster-growing species (McLean et al., 2019; McLean, Mouillot, Lindegren, et al., 2018). Concurrently, the mean body size of the community decreased in the southern North Sea during times of warming, independent of fishing pressure (ter Hofstede & Rijnsdorp, 2011). Furthermore, within the elasmobranch community, the northeastward shifts and/or to deeper waters in the Northeast Atlantic led to a change in the trait composition, namely a decrease in mean trophic level and fecundity, and an increase in size at maturity (Coulon et al., 2024). These observed trends in the reorganisation of life-history strategy groups are predicted to prevail or exacerbate according to our findings, resulting in regional loss of functional richness. Range shifts are known to alter the functional structure and diversity of communities, with changes occurring unevenly across space and potentially resulting in functional losses at the local scale (Barbet-Massin & Jetz, 2015). Maintaining functional diversity is crucial for sustaining ecosystem health and enhancing ecosystem resilience to environmental change (Biggs et al., 2020; Carturan et al., 2022). The disproportional loss of multiple species within a trait group can significantly affect the functional redundancy of the community, which could disrupt the basic ecological structure and the ecological stability/resilience of the community (Biggs et al., 2020; Guillemot et al., 2011). Our projections showed that mostly long-lived species with high trophic levels experienced suitable habitat loss in the southern North Sea. Such a shift can alter feeding interactions (Pecuchet et al., 2020) and can trigger cascading effects that change and destabilise the food web structure (McCann et al., 2005; Myers & Worm, 2003; Pecuchet et al., 2020; Pimiento et al., 2020; Rooney et al., 2006; Selden et al., 2018), and ultimately affect top-down controlled ecological processes, leading to changes in nutrient transfer and productivity (Estes et al., 2016). Furthermore, the distribution shifting of gadoid species has been found to affect biotic interactions; for instance, the recent expansion of hake into the North Sea increased competition with saithe (Cormon et al., 2016). Furthermore, the northward expansion of mackerel

has led to increased predation on herring larvae, which is an important food source in the Norwegian Sea (Skaret et al., 2015). On the other hand, cod stocks are declining due to limited spatial overlap with their prey fish (sprat and herring), which have moved northward (Eero et al., 2020). In contrast, sprat has benefited from warming temperatures and the release of predators (Rijnsdorp et al., 2009). However, with increased temperatures and reduced sea ice in the northern Baltic Sea (Meier et al., 2022), both species are predicted to extend their range northwards. Trophic interactions have the potential to alter the progression of both range expansions and contractions (Bates et al., 2017). At the same time, the redistribution of species alters predator-prey relationships (Buba et al., 2022; Casini et al., 2012). Furthermore, simulated extinction scenarios predict marked declines in functional richness of marine megafauna, especially sharks (Pimiento et al., 2020, 2023), while a substantial proportion of threatened species are functionally distinct and thus may play unique roles in ecosystem functioning (Coulon et al., 2023). In summary, understanding the consequences of species range shifts on biogeographic patterns of functional trait combinations is crucial for assessing the broader implications of climate-driven community changes on ecosystem functioning and services (Gilson et al., 2021).

Regional differences

Most of the literature found temperature as the primary driver of recent and predicted changes in the fish community across the Northeast Atlantic shelf seas (Alheit et al., 2012; Le Luherne et al., 2024a; Rutterford et al., 2023). In our study, the habitat suitability of all three life-history strategy groups was mainly determined by temperature and bathymetry, while the other variables had lower importance. In general, species whose habitat suitability was primarily determined by temperature were predicted to increase their suitable habitat more than species whose habitats are mainly determined by depth, aligning with observed shifts in the last decades (Roberts et al., 2020). Dissolved oxygen did not show a high importance in determining the habitat suitability of the selected species over the extent of our study area. However, some studies showed that oxygen availability can influence the distribution of fish species over small spatial and temporal scales (Coffey et al., 2017; Gutiérrez-Bravo et al., 2024; Meyer-Gutbrod et al., 2021). Persistent oxygen minimum zones in Kattegat and the Baltic Sea, due to high eutrophication and strong stratification, are known to affect the spawning success of Atlantic Cod (*Gadus morhua*) and potentially hinder a deepening distribution shift (Breitburg, 2002; Breitburg et al., 2018). These zones are comparably small and localised compared to the overall distribution area; this might be why our SDMs still show overall low importance of oxygen.

The regions identified as experiencing the most significant predicted habitat loss (i.e., the Celtic and Irish Seas, the southern North Sea, and the Baltic Sea) are also warming at twice the global average rate (von Schuckmann et al., 2024) and have been classified as “superfast” warming Large Marine Ecosystems (Kessler et al., 2022). Our results concur with the observation that rapidly warming regions are experiencing an increase of r-strategy fish species, while more slowly warming regions show an increase of K-strategy species (Receveur et al., 2024). The equilibrium species, *S. canicula*, *S. acanthias*, *Leucoraja naevus*, *R. brachyura*, and *R. montagui*, are currently at the upper limit of their thermal niche (i.e., cold-temperate and temperate species), which means it is expected that their habitat suitability decreases when temperature increases (Coulon et al., 2024). Recent shifts of suitable habitats of these species north-eastwards and/or to deeper waters were detected (Coulon et al., 2024; Sguotti et al., 2016; Townhill et al., 2023). Furthermore, the declining trend of *G. galeus*, *L. naevus*, and *S. acanthias* in the southern North Sea, the English Channel, and the Irish Sea in the last decade coincides with recent warming (Coulon et al., 2024; Sguotti et al., 2016), and the decrease of habitat suitability for *R. clavata* and *S. canicula* along the German, Dutch, and Belgian coasts (Coulon et al., 2024) supports our predictions of habitat loss. Instead, the occurrence of the cold-water species *L. naevus* and *S. acanthias* has increased along the northern continental shelf and the Norwegian Deep in the last decades, which suggests a shift to deeper waters in the future (Coulon et al., 2024; Dulvy et al., 2008a; Perry et al., 2005a; Sguotti et al., 2016), as predicted by our models. It suggests that the two species associated with deeper waters could use the continental slope as a climate change refugium (Ashcroft, 2010). However, declining oxygen, food, and shelter limitations in deeper waters could limit the availability of suitable habitats in the future (Breitburg et al., 2018). For shallow coastal species, the capacity to remain in cooler waters by changing their depth distribution has been largely exhausted in the shallow North Sea (Dulvy et al., 2008a; Rutterford et al., 2015) due to other habitat requirements such as substrate and proximity to estuaries (Martin et al., 2012; Sguotti et al., 2016). Accordingly, elasmobranch species with shallow distributions are more vulnerable to extinction risks (Walls & Dulvy, 2021). Besides, contrary to the general pattern of habitat expansion for Lusitanian species (Perry et al., 2005a), our models also predicted major habitat contractions for the warm water species *T. luscus* and *Z. faber* in the southern North Sea, English Channel, and Irish Sea, comparable to the patterns of the equilibrium species.

In the Bay of Biscay, the northward shift of pelagic species and the westward shifts of benthic and demersal species could result in species loss in the coastal areas and/or a high species dis-

placement with the arrival of species with warm-water affinity (Le Marchand et al., 2020). Accordingly, our study predicted an increase in suitable habitat for gadoid species associated with warm water (*M. merluccius*, *Merlangius merlangus*) and a decrease in cold-water gadoid species (*G. morhua*) in the North and Celtic Seas (Brander et al., 2003; Maltby et al., 2020; Townhill et al., 2023). These shifting patterns match observations of the last decades that find that Lusitanian species in the Celtic Biscay Shelf move northwards and/or westward and experience distribution range expansion, while boreal species move mainly eastward and experience distribution range contractions (Baudron et al., 2020; Le Marchand et al., 2020; Le Luherne et al., 2024a; Perry et al., 2005a; Poloczanska et al., 2016; Punzón et al., 2016). On the other hand, the Iberia–Biscay–Irish (IBI) and the European Northwest Shelf (NWS) seas are characterised by milder warming rates (von Schuckmann et al., 2024), which reflects in our predictions of mostly stable habitat suitability in this region and makes the region's optimal climate refugia (Lourenço et al., 2016). Accordingly, some of the Lusitanian species (e.g., *S. sprattus*, *M. merlangius*, *D. labrax*) were predicted to experience southward range expansions attributed to a shift to deeper waters and/or the use of upwelling regions as refugia along the Iberian coast. Overall, the results show high spatial variations in the response to climate change across the life-history strategy trait groups and considerable structural changes in the fish communities.

Conclusions

Trait-based approaches are increasingly used to evaluate how marine ecosystems respond to environmental stressors like climate change, pollution, and fishing (Degen et al., 2018; Hinz et al., 2021). Our study underscores the value of trait-based approaches by analysing range shifts in relation to life-history fish trait groups and identifying life-history strategy groups that are more susceptible to climate-driven habitat alterations. Thus, the study shows that understanding global dynamics of species distribution based on traits in a biogeographic context aids future management of community function and ecosystem services. The role of species traits in maintaining ecosystem functioning and stability has been neglected by current conservation measures (Vasconcelos et al., 2017). However, it has been increasingly recognised that assessing multiple dimensions of diversity is pivotal in conservation planning to ensure that priorities are ecologically comprehensive (Brum et al., 2017). Functional diversity is often found to be more sensitive to disturbances and more ecologically relevant than taxonomic diversity; thus, integrating information on species diversity with ecological function is essential for an-

ticipating ecological shifts and informing adaptive conservation and ecosystem-based management strategies in a rapidly changing world (Coleman et al., 2015; Stuart-Smith et al., 2013). Furthermore, using functional traits to detect population and community dynamics in response to fishing and environmental drivers can serve as an ecological basis to ecosystem-based fisheries management (EBFM), informing on ecosystem integrity and resilience (Barnett et al., 2019). Our findings on regional differences in the response of different trait groups helped to identify regions highly susceptible to loss of habitat suitability, such as the southern North Sea, the English Channel, and the Irish Sea. At the same time, these areas are essential fishing grounds (Eme et al., 2022; Jennings et al., 1999), which further increases the vulnerability of the equilibrium species (e.g., *R. clavata*, *S. canicula*, *S. acanthias*) and periodic species (e.g., *G. morhua*, *Z. faber*, *T. luscus*) in these regions. Trait-based insights help to flag these species for more cautious monitoring and management that minimise long-term impacts on vulnerable species or functional groups. Thus, in areas that will experience significant losses of suitable habitat, it is relevant to reduce the cumulative effects of stressors and protect essential fish habitats of affected species (e.g., spawning and nursery areas, foraging grounds, migration pathways) by establishing Marine Protected Areas (MPAs), or implementing other complementary or alternative measures (e.g. seasonal spatiotemporal fishing closures or dynamic bycatch avoidance (Hazen et al., 2018; Karp et al., 2025)). At the same time, areas where no or little losses of habitat suitability are predicted, such as the Iberian coast and the European Northwest Shelf (NWS), could serve as climate refugia (Angeles-Gonzalez et al., 2024; Lourenço et al., 2016). Besides, projections of the opportunistic and periodic groups suggest future changes in the availability and catchability of important commercial species, which can cause a mismatch between regional abundance and allocated quota (Fernandes & Fallon, 2020), which can lead to high economic losses and unnecessary discards (Cruz et al., 2024; Roessig et al., 2004). The changing fish distributions challenge the effective management of European fisheries (Baudron et al., 2020); thus, it is crucial to understand the spatiotemporal changes in distribution patterns of fish communities to enable adaptive fisheries management in the context of climate change. The approach of our study is relevant and applicable outside of the Northeast Atlantic and could be advanced in future research by adding species abundances and biotic interactions (e.g., competition and predation) into the models.

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CHAPTER 5: Multi-scale assessment of marine species distributions: effects of spatial extent and temporal resolution across contrasting ecological niches

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Multi-scale assessment of marine species distributions: effects of spatial extent and temporal resolution across contrasting ecological niches

Abstract

A fundamental aspect of ecology is understanding how species are distributed across space and time. Species distribution models (SDMs) are widely used as a tool to characterise species-habitat relationships and to guide a broad range of marine spatial management decisions. Selecting the appropriate spatiotemporal scale of the environmental and occurrence data is of utmost importance for the model's performance. This study used Ensemble Species Distribution Modelling to assess how three spatial extents (total, regional, local) and two temporal resolutions (annual vs. decadal means) influence model performance, variable importance, and spatial projections of three species with contrasting life histories and ecological niches (*Engraulis encrasicolus*, *Merluccius merluccius*, *Scyliorhinus canicula*). The results showed that variable importance varied among species, temporal approach, and spatial extent: temperature dominated at broader scales, whereas other predictors gained relevance at finer scales for *S. canicula* and *E. encrasicolus*. The evaluation metrics and spatial predictions revealed that equilibrium species dependent on persistent habitat features (*S. canicula*) were better modelled with a decadal-trained model at a broader scale. On the other hand, the distribution of the opportunistic species, *E. encrasicolus*, was better captured with yearly trained models at the regional extent, reflecting their sensitivity to short-term environmental change. For the periodic species, *M. merluccius*, whose habitat suitability was mainly governed by temperature, the best model performance was achieved at broader extents, regardless of the temporal approach. Overall, the considerable variation in spatial predictions suggests that careful consideration is required when interpreting model transferability across scales. Furthermore, the results highlight that the appropriate spatiotemporal scale in species distribution modelling should be guided by species' ecology, environmental variability, and the study objective.

Keywords

Species Distribution Modelling, Life-history strategies, Scale-dependencies, Environmental variability, Spatial predictions, Northeast Atlantic

Introduction

A fundamental aspect of ecology is understanding how species are distributed across space and time, particularly in relation to their physical environment and changing habitat conditions. Species distribution models (SDMs) are a widely used approach to predict species distributions and characterise species-habitat relationships by analysing correlative relations between species occurrence and environmental conditions (Elith & Leathwick, 2009; Guisan & Thuiller, 2005; Melo-Merino et al., 2020). The fitted species-environment relationship is used to determine habitat suitability and predict distributions in unsampled areas or under future environmental conditions (Pecl et al., 2017; Pinsky, Selden, et al., 2020). This knowledge is crucial to support management and conservation decision-making (Zurell et al., 2022, 2023). Field surveys to collect data on species occurrence and abundance are typically costly, time-consuming, and labour-intensive, resulting in limited data coverage across the desired spatial and temporal scales (Pennino et al., 2016). SDMs produce maps of habitat suitability that highlight areas where species are most likely to occur, thus enabling the optimisation of survey efforts (Oyafuso et al., 2021; Zwolinski et al., 2011). Furthermore, the modelling of spatial and temporal patterns in the occurrence or abundance of commercial species can provide valuable information for fish stock structure and support delineation of stock units for assessment purposes (Lindegren et al., 2022). Furthermore, assessing species-habitat associations can serve as a foundation to identify essential fish habitats for spawning, breeding, feeding or migration (Bellido et al., 2008; Elliott et al., 2024; Moore et al., 2016; Valavanis et al., 2008). Thus, SDMs can inform strategic spatial planning of protected areas and fishery closure zones, whether dynamic or static, to conserve biodiversity, reduce bycatch and promote sustainable stock management (Gormley et al., 2015; McGowan et al., 2013; Porfirio et al., 2014; Smith et al., 2021). These are all crucial elements for sustainable and effective ecosystem-based management (Karp et al., 2025; Tommasi et al., 2021). Additionally, SDMs are commonly used to predict species distributions in the future and resulting changes in biodiversity indicators (Pinsky et al., 2018; Pinsky, Rogers, et al., 2020; Pinsky, Selden, et al., 2020; Poloczanska et al., 2016). To sum up, SDMs can provide a robust ecological basis to guide a broad range of marine spatial management decisions, from survey optimisation to fisheries stock assessment, spatial fisheries management, and designation of protected areas, as well as understanding the impacts of climate change (Karp et al., 2025; Klaassen et al., 2025).

Species' responses to the environment are scale-dependent, since different biological and physical mechanisms drive variability at different spatial and temporal scales (Karp et al., 2025). At

broad spatial extents, species distributions are primarily dictated by abiotic factors, particularly climate and oceanographic features, while biotic factors related to habitat and prey become more important at a smaller scale (King et al., 2021). Thus, selecting the appropriate spatiotemporal scale of environmental and occurrence data is of utmost importance for the outcome of the models, requiring careful consideration from both ecological and management perspectives (Commander et al., 2022; Fernandez et al., 2017; Mannocci et al., 2017; Melo-Merino et al., 2020; Núñez-Riboni et al., 2021). The decision on the spatial scale is crucial for management because it influences which data is included in the assessment and over which spatial domain the resulting management advice will be relevant (Seo et al., 2008). In the case of SDMs, the spatial extent strongly determines the inferred species-environment and thus the predicted distribution patterns (Amaro et al., 2023; Commander et al., 2022). This underscores the need for caution when selecting environmental data for planning future protected areas, because inadequate choices can lead to unsuitable size and location decisions (Seo et al., 2008). Furthermore, temporal scales, ranging from near real-time to seasonal, yearly, and decadal forecasts, play a decisive role when considering static versus dynamic spatial management (El-Gabbas et al., 2021; Hobday et al., 2010, 2016; Pons et al., 2022). The role of the temporal resolution, specifically, how well species occurrence data align with environmental conditions over time, has received less attention in the context of species distribution modelling. Some studies have shown that for SDMs to accurately capture the dynamics of species-environment relationships and improve predictive accuracy, model training must be informed by the environmental gradients, across both space and time, observed at the moment of species occurrence sampling (dynamic SDMs) (El-Gabbas et al., 2021; Fernandez et al., 2017; Milanese et al., 2020; Pennino et al., 2019). While the choice of temporal resolution is often constrained by data availability, especially in the marine environment, where data collection is time- and resource-intensive and associated with high operational costs, it should be guided by the underlying ecological question and the spatial extent of the study area (Mannocci et al., 2017). Aligning temporal resolution with ecological relevance is essential to ensure meaningful and robust model outcomes. Overall, Marine Spatial Planning (MSP) requires information on species' distributions across multiple spatial and temporal scales, depending on the purpose of application (Karp et al., 2025; Klaassen et al., 2025; Núñez-Riboni et al., 2021). To date, most studies have applied spatial and temporal resolutions or extents without critically evaluating how these choices influence model performance, projected spatial patterns and the ecological relevance of the outcomes. This is particularly concerning when models are used to inform management or conservation actions in spatially and temporally dynamic environments. To the best of our knowledge, few

studies have systematically evaluated SDMs in terms of how species-environment relationships and spatial predictions vary across multiple spatial and temporal scales in the marine environment (Goh et al., 2024; Núñez-Riboni et al., 2021; Pennino et al., 2019). Notably, none of them compared modelling at different spatial extents and examined the interaction between spatial extent and temporal resolution. To address this knowledge gap, a multi-level assessment of marine species distribution was conducted using Ensemble Species Distribution Modelling to investigate how varying spatial extents and temporal resolution impact model performance and outcomes, considering species with different ecological niches and requirements. More precisely, evaluation metrics and spatial projections were compared to assess differences in model performances, spatial patterns of hotspot habitats and the importance of environmental drivers. The analysis was performed for three species with different life history strategies (*Engraulis encrasicolus*, *Merluccius merluccius*, *Scylliorhinus canicula*), across three spatial extents (total extent, regional and local) and two temporal resolutions for model training (annual mean vs. 10-year mean). The findings are discussed in the context of the best practices for modelling species-habitat relationships across different ecological niches, to inform decision-making in fisheries and conservation management.

Materials and Methods

Study area

The study area lies within the Northeast Atlantic and was analyzed at three spatial extents: Total extent which combines three ICES Ecoregions (i.e. Greater North Sea, Celtic Seas, Bay of Biscay & Iberian Coast); three regional extents, each corresponding to one of these ICES ecoregions; and a local extent, represented by the Irish Sea ICES statistical area. The total extent encompasses the main shared distribution range in the Northeast Atlantic of the model species in this study, according to ‘Fishbase’ (Froese & Pauly, 2025). The regional extents are based on ICES ecoregions, which are geographical units used to provide regional advice on monitoring programs and ecosystem-based management (ICES, 2023). The local extent is based on a single ICES statistical area, a geographical unit within FAO Major Fishing Area 27, used for fish statistics, such as catch per unit effort (CPUE) and stock estimates (ICES, 2005). The ICES statistical area was chosen because its spatial extent enabled the incorporation of a broader range of environmental variables with low collinearity.

Species data and sampling of pseudo-absence points

The three selected species represent different life-history strategy groups (Pecuchet et al., 2017): *Engraulis encrasicolus* represents the opportunistic group characterized by small size, low trophic level, short life span but high fecundity and fast reproduction suited to highly variable environments, fast population turnover, and strongly influenced by short-term environmental fluctuations; *Merluccius merluccius* represents the periodic group characterized by medium to large size, medium to long life span, high trophic level, high fecundity and fast reproduction, adapted to seasonal environments, reproduction often tied to environmental cycles, and slower population growth; *Scyliorhinus canicula* represents the equilibrium group characterized by large size, long life span, high trophic level, low fecundity, slow reproduction and high parental care, adapted to stable environments and lower population resilience to rapid disturbance. Occurrence records of these species were extracted from FishGlob, which is a combined dataset of bottom trawl surveys across North America and Europe (Maureaud et al., 2024). Surveys within the dataset are already quality filtered for precise geolocation, date, taxonomic identification, taxa abundance and/or weight, haul duration and/or swept area, and gear type (otter-trawl gears) (Maureaud et al., 2024). However, some regions and depths were sampled more frequently than others; therefore, to reduce sampling bias, the dataset was filtered for surveys conducted between 2000 and 2020, above 200m depth, during autumn or winter, when autumn data were unavailable (e.g., for the survey NS-IBTS), to reduce sampling bias, since surveys were conducted regularly in these seasons throughout the study area. Presence points outside the study extent and duplicated records were removed. To decrease the likelihood of spatial autocorrelation, only one presence point per grid cell was kept (Hijmans, 2025). Additionally, presence points were spatially thinned using the `thin()` function in the `spThin` package in R by selecting only points that are at a minimum distance of 1° (1 degree $\approx$ 111 km at the equator) from each other (Aiello-Lammens et al., 2019). Pseudo-absences were randomly generated to match the same number of presences (Barbet-Massin et al., 2012; Liu et al., 2019; Thuiller, 2024), following the same spatial filtering procedures as for presence points. Furthermore, pseudoabsences were sampled outside a 10 km buffer zone around each presence point (Iturbide et al., 2015; VanDerWal et al., 2009). This approach creates wider effective buffer zones when presence points are clustered closely together, thereby reducing the likelihood of sampling pseudo-absences within the species' realised niche. Presence and pseudo-absence points were initially filtered within the total extent (or combined ecoregions) and subsequently adjusted to the regional (or individual ecoregions) and local (or statistical area) extents to maintain the same

points across different spatial scales, thereby enabling reliable comparisons over the same environmental gradients.

Environmental data selection and temporal data preparation

Environmental variables (i.e. distance to the nearest coast, bathymetry, primary productivity, oxygen, salinity, and sea temperature), which are known to influence the distribution of marine fish species (Bender et al., 2013; Beukhof et al., 2019; Henriques et al., 2017), were assessed for collinearity before inclusion in the model. The variables were cropped and masked to produce raster stacks for each spatial extent, which were subsequently assessed for correlation across extents using Pearson's correlation coefficient (r). Temperature was prioritised as a key variable to be maintained in the model due to its importance in marine fish distributions (Rutherford et al., 2023), excluding those with correlations higher than 0.7 either with temperature or among themselves. The final set of variables included temperature, salinity, oxygen, and distance to the coast since they were not strongly correlated at any of the spatial extents. Sea temperature, salinity, and oxygen at maximum depth were extracted as monthly means from the Global Ocean Physics Reanalysis of Copernicus (Copernicus Marine Service, 2024), and averaged over two temporal resolutions: (1) the yearly approach consists of annual means from the years 2000 to 2020, and (2) the decadal approach consists of annual means averaged over 10 years (2000 - 2010 and 2010 - 2020, respectively). The distance to the nearest coast was considered a static predictor and was retrieved from Ocean Colour Web (NASA Earth Data) at 0.01° resolution. All environmental layers were rescaled to the same resolution of 0.05° . Presence and pseudo-absence points were split into separate datasets for each year from 2000 to 2020, and into two 10-year datasets (i.e. 2000–2010 and 2010–2020). Annual and decadal averaged environmental variables were extracted for each point to build year- and decade-specific datasets used to train the yearly and decadal models, respectively.

The modelling approach

An Ensemble Species Distribution Modelling (ESDM) approach using the 'biomod2' package (version 4.2–2 in R) was applied to the generated yearly- and decadal-specific datasets to forecast present-day habitat suitability within the different spatial extents and for each species (Araújo & New, 2007; Thuiller, 2024). For each scenario, six individual models were generated by each of the following algorithms, covering regression-based, tree-based, and machine-learning-based presence-only modelling approaches: Generalised Additive Models (GAM), Classi-

fication Tree Analysis (CTA), Maximum Entropy (MAXENT), Random Forest (RF), and Multivariate Adaptive Regression Splines (MARS). The predictive performance of each SDM model was evaluated using Receiver Operating Characteristic (ROC) and True Skill Statistics (TSS), with values ranging from 0 to 1. Scores above 0.5 indicate better-than-random performance, while scores below 0.5 suggest chance-level predictions (Allouche et al., 2006). Thus, only models with ROC values greater than 0.7 were retained. Each selected model trained under finer temporal resolution was projected individually onto the environmental raster stacks averaged over the entire 20-year period to generate the spatial predictions of habitat suitability. The final ensemble models were created by averaging these individual spatial predictions, combining the strengths of multiple algorithms to reduce uncertainty and improve predictive accuracy (Araújo & New, 2007). These ensemble models considered three fish species, two temporal training approaches (i.e. yearly and decadal) and five spatial scales (i.e. total extent, three regional extents, and local extent), resulting in a total of 30 ESDMs. Each grid cell in the resulting maps has a suitability value ranging from 0 (unsuitable habitat) to 1 (highest suitability).

Evaluation of models and the importance of environmental variables

For model evaluation, presence and pseudo-absence data were randomly divided into 80% for training and 20% for testing (Guisan & Zimmermann, 2000). The cross-validation was repeated six times. Two metrics were used to evaluate the calibration and validation of the models for each algorithm, respectively: the True Skill Statistic (TSS) (Allouche et al., 2006) and the Area Under the Receiver-Operating Characteristic Curve (AUC or ROC) (Fielding & Bell, 1997). Predictive performance was considered good ($AUC \geq 0.9$; $TSS \geq 0.6$), moderate ($0.7 \leq AUC < 0.9$; $0.2 \leq TSS < 0.6$), or poor ($AUC < 0.7$; $TSS < 0.2$) (Pearce & Ferrier, 2000). Here, we evaluated whether the model performance of the yearly or decadal models significantly differed at different spatial extents. More precisely, it was tested whether evaluation metrics (i.e. ROC and TSS) differ as a function of the interaction between metric types (i.e. calibration vs. validation) and temporal training approaches (i.e. yearly vs. decadal). To compare distinct model performance, separate factorial generalised linear models (GLMs), using a Gaussian error distribution and an identity link function, were run for each species and spatial extent. Furthermore, for each model projection, the continuous Boyce Index (BI) was calculated to evaluate models' performance based on presence-only data. This index compares the predicted habitat suitability at known presence locations to the suitability values across a background using a moving window approach (Boyce et al., 2002; Hirzel et al., 2006). Thereby, it measures the extent to which the model predicts higher suitability values at observed presences than in the

overall background. The BI ranges from -1 to +1, where values close to +1 indicate a high concentration of presences in areas predicted as highly suitable (i.e. good model performance), values near 0 indicate random performance, and values below 0 suggest that the model predicts lower suitability in areas where presences occur, indicating counterproductive predictions (Boyce et al., 2002; Hirzel et al., 2006). For each species, we assessed whether BI values calculated for each spatial extent significantly outperformed or underperformed under both yearly- and decadal-trained projections. We also used factorial GLMs to test differences in BI as a function of the interaction between spatial extents and temporal training approaches. To isolate species-specific responses, separate models were run for each species to evaluate these effects independently. Additionally, for each species, the number of poorly performing projections (i.e., $BI < 0.5$) and the variability in BI values across spatial extents and temporal approaches were further explored using boxplots. Finally, the importance of the variables in determining habitat suitability was calculated with the function ‘get_variables_importance’ in the biomod2 package (Thuiller, 2024). Predictions were made by altering only one variable at a time, while keeping all other variables constant at their median values. The relevance of each variable was estimated by calculating the difference between the original prediction and the prediction made with the permuted variable, divided by one minus the correlation score. On a scale from 0 to 1, a higher value indicates a greater influence of the variable on the ensemble model (Elith et al., 2005). Here, we tested whether variable importance differed significantly between yearly- and decadal-trained models within specific spatial and ecological contexts using single-factor GLMs. To capture spatial scale-dependent effects and species-specific ecological differences, separate models were run for each spatial extent and species to evaluate these effects independently.

Hotspot analysis

Predictive maps were converted into binary maps by setting a fixed threshold of 0.6, above which habitats were classified as hotspots, representing areas of moderate to high suitability (Ahmad et al., 2019). Here, a spatial comparison is provided to understand how temporal and spatial model training choices affect hotspot delineation, with implications for conservation prioritisation and management decisions. Spatial agreement and divergence in hotspot projections were evaluated based on two issues often found in the literature: (1) the effect of spatial extent, by comparing yearly and decadal hotspot projections generated directly within smaller regional or local extents against those obtained by cropping the total extent model projections to the same smaller extents; and (2) the influence of temporal resolution, by comparing hotspot

projections derived from models trained on yearly versus decadal environmental data. For each species, hotspot maps were compared by calculating the difference between the binary maps of the temporal approaches (yearly vs. decadal) and the spatial approaches (regional model vs. total extent model) by subtracting twice the decadal model values from the yearly model values, and twice the cropped full extent model values from the regional model values. This yielded a spatial classification of each grid cell with values ranging from -2 to 1: '-2' indicates hotspot grids predicted only by the decadal approach or by the cropped full extent; '-1' indicates agreement between approaches on hotspot grids; '0' indicates grids classified as non-hotspot in both approaches; '1' indicates hotspot grids predicted only by the yearly approach or by the regional approach). Furthermore, we quantified the proportion of presence and pseudo-absence points located within hotspot grids to evaluate further consistency between models trained at different temporal resolutions and spatial extents.

Results

Evaluation of model performance using ROC and TSS

Overall, metric type (calibration vs. validation) was the primary factor explaining variability in ROC and TSS across regions. The temporal training approach had a significant effect only in the North Sea, specifically influencing TSS for *M. merluccius*, and both ROC and TSS for *S. canicula*. For the remaining spatial extents, the temporal approach does not have a significant effect (Appendix 4, Fig. A4.1). For *M. merluccius*, yearly trained models showed underperformance (i.e., calibration > validation, $p < 0.01$) for ROC in the Bay of Biscay & Iberian Coast and Celtic Seas, and for TSS across all extents except the total extent ($p > 0.05$). Under decadal training, underperformance was observed for ROC and TSS in the Irish Sea, Bay of Biscay and Iberian Coast. For *E. encrasicolus*, yearly trained models underperformed in the Irish Sea and North Sea for ROC, and in the total extent, Irish Sea, and North Sea for TSS ($p < 0.01$). Under decadal training, underperformance occurred in the Irish Sea and Celtic Seas. For *S. canicula*, yearly training led to underperformance in the Irish Sea, Bay of Biscay & Iberian Coast, and North Sea for both metrics ($p < 0.01$). With decadal training, underperformance was limited to the Irish Sea, Bay of Biscay and Iberian Coast. More aligned calibration and validation values were found for the Total extent, except for the yearly approach of *E. encrasicolus*. When focusing exclusively on validation metrics to determine which training approach better generalises to new data, we found that, in the North Sea, models for *M. merluccius* and *S. canicula*

consistently achieved significantly higher TSS and ROC validation scores under decadal training. In contrast, for the other extents, the choice of temporal training approach was less critical (Appendix 4, Fig. A4.1).

Evaluation of model performance using the Boyce Index

For *M. merluccius* and *E. encrasicolus*, projection performance was significantly influenced by spatial extent, while the temporal approach had no significant effect (Fig. 5.1). For *M. merluccius*, averaged BI values were highest in the Celtic Seas, regardless of training approach, and significantly outperformed those in the North Sea under yearly training (Fig. 5.1). In the case of *E. encrasicolus*, the lowest average BI values were observed in the Irish Sea under both training approaches (Fig. 5.1). In contrast, for *S. canicula*, projection performance was significantly influenced by the interaction between spatial extent and training approach (Fig. 5.1). Decadal-trained models yielded higher BI values than yearly trained models in the total extent, with performance levels comparable to those observed in the Celtic Seas, regardless of training resolution (Fig. 5.1). Furthermore, although BI variability across spatial extents differs among species, the number of poor projections ($BI < 0.5$) is similar between temporal training approaches (Appendix 4, Fig. A4.2). However, in some cases, the number of poor projections between approaches differed by more than two (Appendix 4, Fig. A4.2). For *M. merluccius* in the Irish Sea, decadal training produced poorer projections (6) than yearly training (1), whereas in the North Sea, the opposite was observed; yearly training yielded poorer projections (6) than decadal training (3). For *S. canicula* in the Irish Sea, decadal training also led to poorer projections (6) compared to yearly training (4). In contrast, in the total extent and the Bay of Biscay and Iberian Coast, yearly training resulted in more poor projections (4 and 8) than decadal training (0 and 5) (Appendix 4, Fig. A4.2).

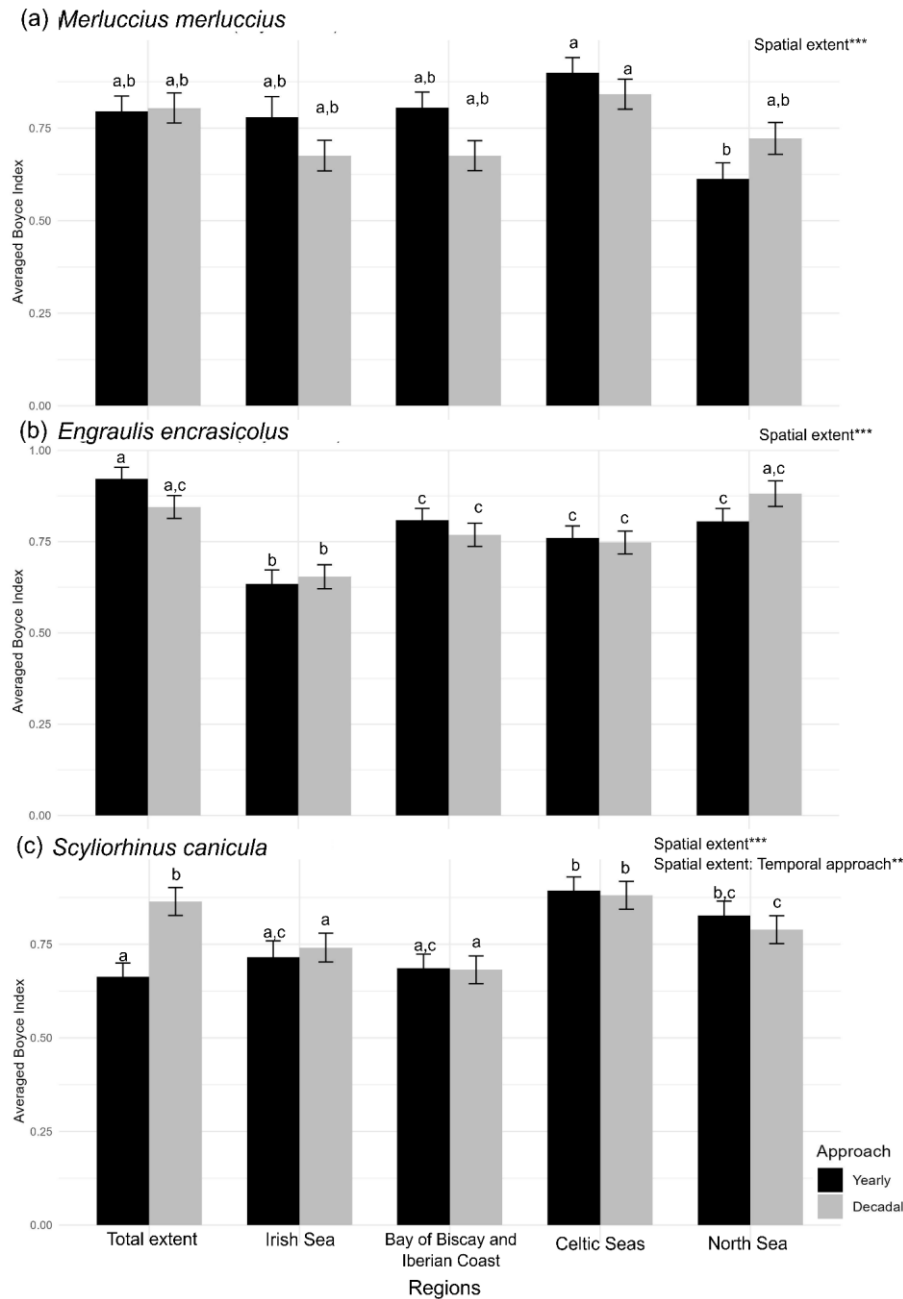


Figure 5.1. Evaluation of projection performance across spatial extents and temporal training approaches (black – yearly approach; grey - decadal approach) based on the Boyce Index for a) *Merluccius merluccius*, b) *Engraulis encrasicolus* and c) *Scyliorhinus canicula*. Error bars indicate standard errors. Different lowercase letters indicate statistically significant differences between spatial extents and temporal approach for each species using GLM (Boyce index values ~ spatial extent * temporal training approach).

Variation in variable importance between temporal approaches and spatial extents

Most variability in variable importance is significantly influenced by the temporal training approaches ($p < 0.05$), except for the Bay of Biscay and Iberian Coast for distance to coast for *M. merluccius*, and dissolved oxygen for *E. encrasicolus* and *S. canicula*, respectively (Fig. 5.2). The variable distance to the coast was more important in the yearly than in the decadal approach, except for *E. encrasicolus* in the Bay of Biscay & Iberian Coast and Celtic Seas (Fig. 5.2). In

contrast, “oxygen” and “salinity” tended to be more important in the decadal approach, except for specific cases: oxygen was more important in the yearly approach for *E. encrasicolus* and *S. canicula* in the Irish Sea, and salinity was more important in the yearly approach for *S. canicula* in the North Sea (Fig. 5.2). Regarding general trends, variable importance also varied across spatial extents. Temperature consistently emerged as the most important predictor for *M. merluccius* across all extents (Fig. 5.2). However, for *E. encrasicolus* and *S. canicula*, the ranking of predictors shifted between extents. For example, distance to coast was the top predictor for both species in the Irish Sea, and for *E. encrasicolus* in the Celtic Seas. In contrast, salinity was most important for *E. encrasicolus* in the North Sea (Fig. 5.2b, c). Across the larger extents (i.e. total extent and Bay of Biscay & Iberian Coast), temperature was consistently the most influential variable for all species.

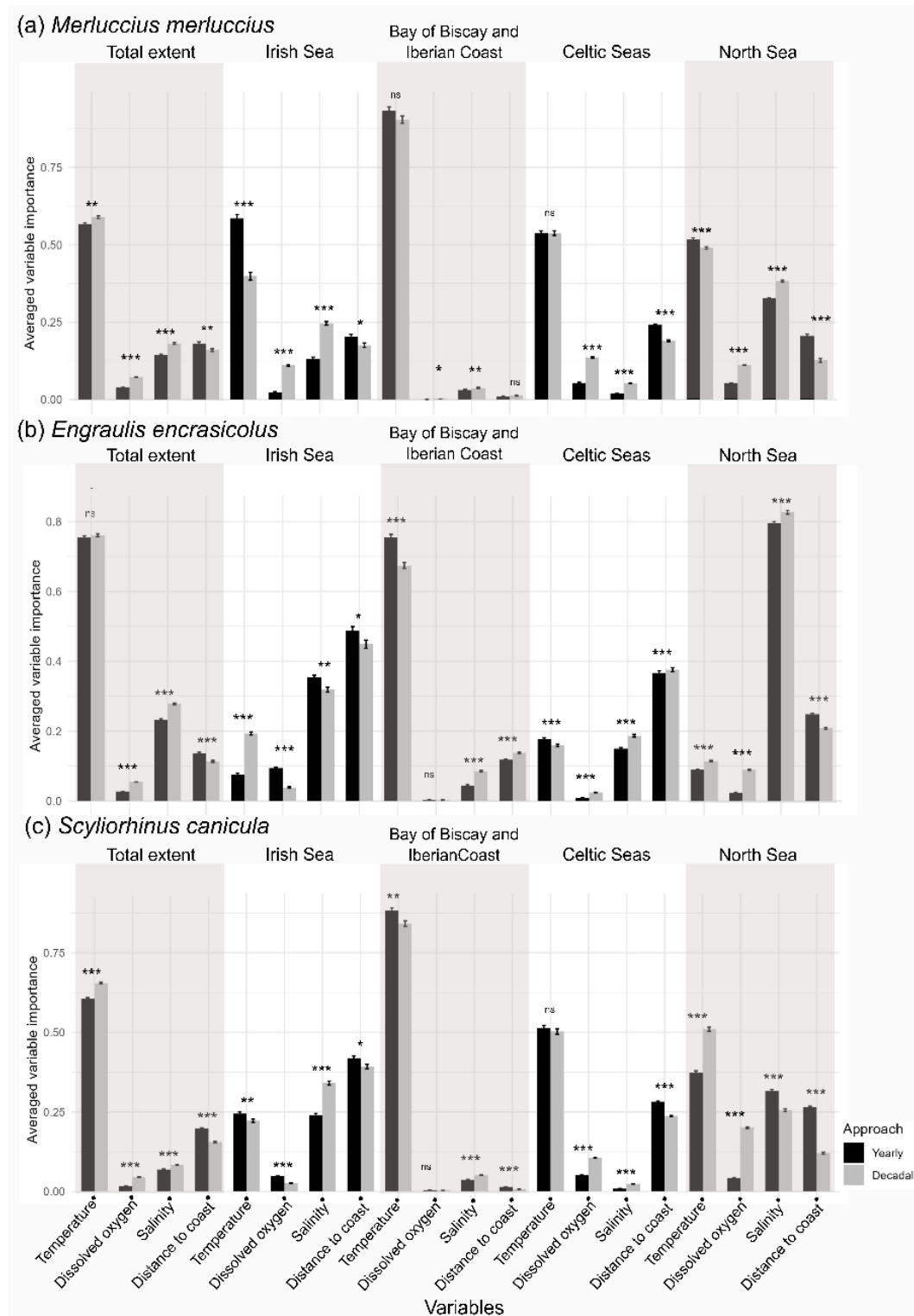


Figure 5.2. Variability in variable importance between yearly- and decadal-trained ensemble models within different spatial extents for a) *Merluccius merluccius*, b) *Engraulis encrasicolus* and c) *Scyliorhinus canicula*. Error bars indicate standard errors. Asterisks denote statistical differences between yearly and decadal approaches using GLM (variable importance values ~ temporal training approach; ***p < 0.001; **p < 0.01; *p < 0.05).

Spatial variation in hotspots between yearly- and decadal-trained models

The maps of spatial variation in hotspots show that the temporal approach influences the delineation of the hotspots (Fig. 5.3). The local extent (Irish Sea) showed the highest differences

between temporal approaches for all three species, with the yearly approach consistently predicting more hotspot area (Fig. 5.3). For *M. merluccius* and *S. canicula*, none of the temporal approaches show a significantly higher percentage of hotspot area at the Total extent; however, the location of the hotspot area varies at the range edges. The same pattern applies for *M. merluccius* in the Celtic Sea and *S. canicula* in the North Sea. For *M. merluccius* in the North Sea, the yearly approach predicted more hotspots in the Northeastern part of the extent. For *E. encrasicolus*, the yearly approach predicted more hotspot areas in all regional extents (Celtic Seas, North Sea, Bay of Biscay and Iberian Coast), while in the total extent, the yearly approach captured less hotspot area, especially on the western coast of Ireland. For *S. canicula*, less hotspot area was detected by the yearly approach in the southern part of the Celtic Seas. The yearly approach captured fewer true presences inside hotspots in the Total extent, Celtic Sea and North Sea for all species while capturing more false positives, especially in the Irish Sea (Appendix 4, Table A4.1). In the Bay of Biscay and the Iberian coast, detection of true presences and pseudo-absences within hotspots is similar between approaches (Appendix 4, Table A4.1). The least true presences were captured by the yearly approach for *M. merluccius* in the North Sea, for *E. encrasicolus* in the Total extent and for *S. canicula* in the Celtic Seas (Appendix 4, Table A4.1).

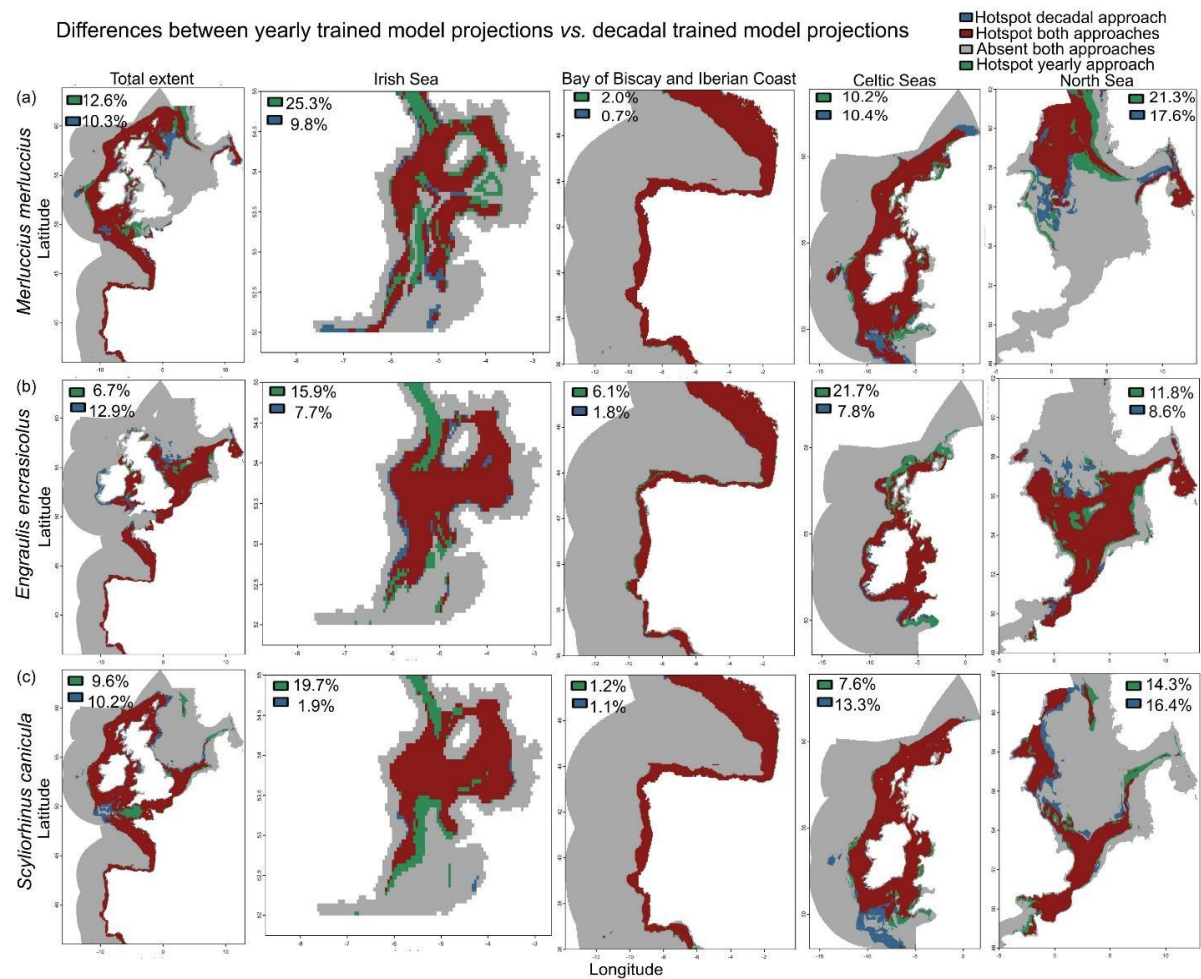


Figure 5.3. Spatial congruence and divergence in predicted hotspot habitats between yearly- and decadal-trained models across different spatial extents for a) *Merluccius merluccius*, b) *Engraulis encrasicolus* and c) *Scyllorhynchus canicula*. Red indicates habitat classified as a hotspot by both modelling approaches (hotspot agreement); blue indicates hotspot grid cells predicted only by the decadal training approach; green indicates hotspot grid cells predicted only by the yearly training approach; and grey indicates areas outside the suitability threshold for hotspots in both temporal training approaches. The percentage values in each panel indicate the extent gained under each of the modelling approaches in relation to the maintained hotspot agreement.

Spatial variation in hotspots between regional and cropped total extent projections

The maps of hotspots show that there were some substantial differences between the local/regional trained models and the cropped Total extent model. For the Bay of Biscay of the Iberian coast, the difference between the regionally trained models and the cropped total extent models was very low for all species and temporal approaches. For *M. merluccius*, the locally trained models in the Irish Sea generated a larger extent of hotspot area compared to the cropped approach. In contrast, for *E. encrasicolus* and *S. canicula*, the cropped approach predicted almost 50% more hotspot area (Fig. 5.4). In the Celtic Seas, the regionally trained models generated up to 60% more hotspot area compared to the cropped approach for *E. encrasicolus*, while for the other two species, the cropped approach generated more hotspot area, especially in the South (Fig. 5.4). In the North Sea, the regionally trained models predicted more hotspots for all species

than the cropped Total extent models (Fig. 5.4). The relations of the percentages of hotspot and the spatial variations were similar for both the yearly and decadal approaches, except for *E. encrasicolus* in the North Sea and Bay of Biscay and Iberian coast, where relations between percentages were switched. The local/regional trained projections capture more or the same true presences than the cropped models for most species and extents. However, the cropped models projected more true presences for the Irish Sea extent for the species *E. encrasicolus* and *S. canicula* and the Celtic Seas for *S. canicula* (Appendix 4, Table A4.2). For *M. merluccius*, only with the yearly trained models, the locally trained models captured more true presences in the Irish Sea. On the other hand, a high percentage of false positives (30%) was detected for the Irish Sea for *E. encrasicolus* and *S. canicula* for cropped full extent models (Appendix 4, Table A4.2). The highest difference between the spatial approaches was found for *E. encrasicolus* in the Celtic Sea, with yearly trained regional models capturing 28% more true presences, while capturing only 8% more false positives than the cropped total extent model (Appendix 4, Table A4.2). The highest difference in the number of false positives was detected for *S. canicula* for the decadal trained models in the local extent (Irish Sea), with the cropped approach capturing 36% more pseudo-absences in the hotspot area while also capturing 20% more true presences.

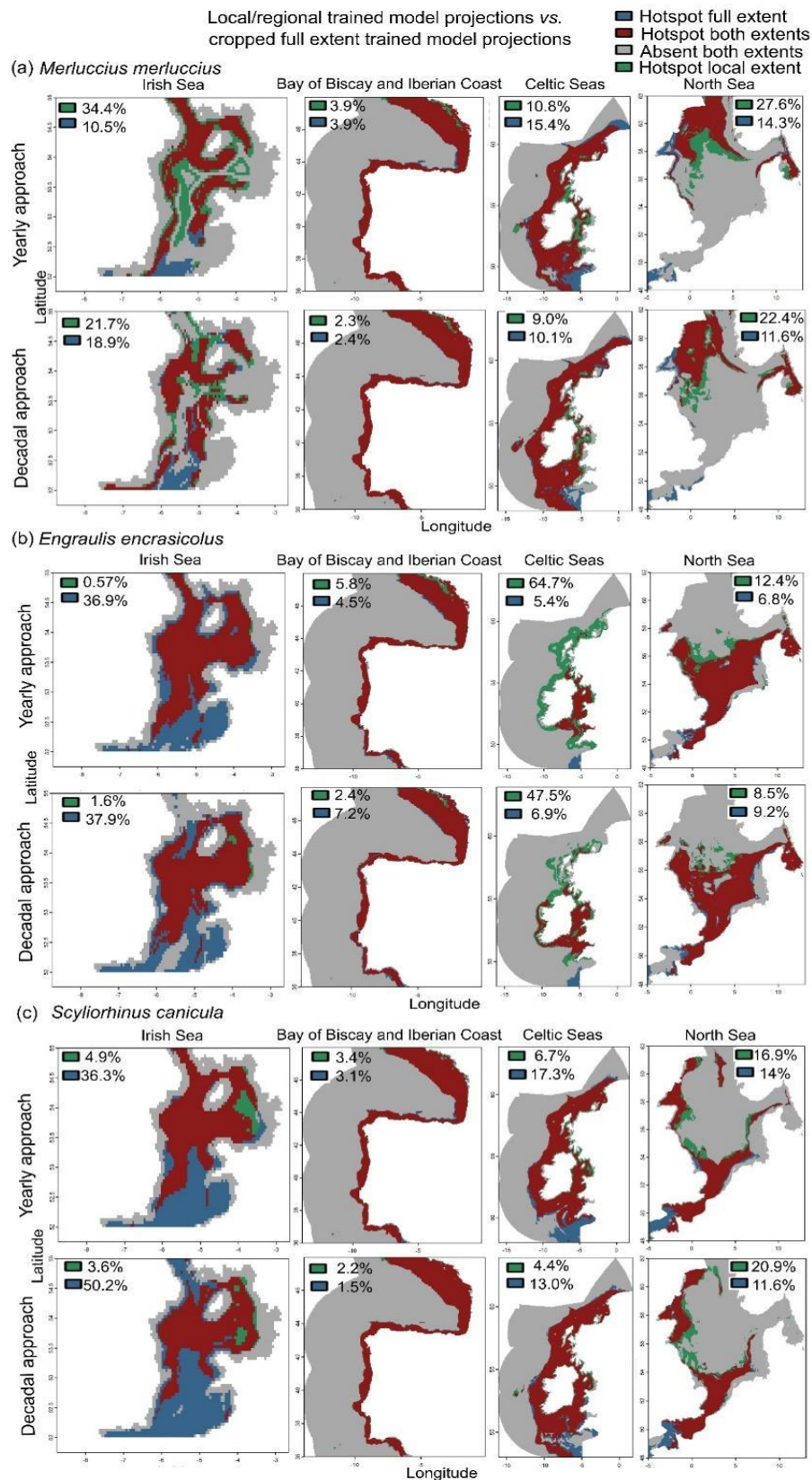


Figure 5.4. Spatial congruence and divergence in predicted hotspot habitats between local/regional trained models and cropped Total extent trained models for a) *Merluccius merluccius*, b) *Engraulis encrasicolus* and c) *Scyliorhinus canicula*. Red indicates habitat classified as a hotspot by both modelling approaches (hotspot agreement); blue indicates hotspot grid cells predicted only by the cropped total extent model; green indicates hotspot grid cells predicted only by the local/regional trained models; and grey indicates areas outside the suitability threshold for hotspots in the different spatial extents used for models. The percentage values in each panel indicate the extent gained under each of the modelling approaches in relation to the maintained hotspot agreement.

Discussion

This study shows that both temporal resolution (annual vs. decadal) and spatial extent (total, regional, and local extent) influence the performance of species distribution models (SDMs) across marine species with distinct life-history traits. The significant variation in spatial predictions depending on the approaches implies that caution in model choices is needed when SDMs are used in spatial planning. Furthermore, the different model outcomes for species with varying life histories and ecological niches highlighted the importance of carefully selecting spatial extent and temporal resolution according to study objective, species' ecological requirements, and environmental variability within the study region. This study did not address the aspect of spatial scale in terms of grid cell size; however, it has been shown to be influential in the model performances (Núñez-Riboni et al., 2021).

Variable importance and spatial–temporal interactions

In our study, the order and magnitude of variable importance varied across models depending on the spatial extent and species, which conforms with other studies addressing varying spatial and temporal resolution (Goh et al., 2024; Mannocci et al., 2017; Núñez-Riboni et al., 2021; Pennino et al., 2019). Sea temperature was the primary predictor at the larger extents with the highest temperature gradients (total extent and Bay of Biscay & Iberian Coast), whereas distance to coast and other predictors increased in importance in regional and local extents. For *M. merluccius*, temperature emerged as the dominant predictor across all extents. In contrast, the importance of distance to coast and salinity surpassed temperature in the smallest extent (Irish Sea) for both *S. canicula* and *E. encrasicolus*, and in the North Sea for *E. encrasicolus*, reflecting these species' reliance on coastal habitat and response to local environmental variability. These results are consistent with biogeographic patterns of fish biodiversity and their underlying drivers. Sea temperature is widely recognised as the primary predictor of structuring distributions of fish biodiversity at global scales (Briggs & Bowen, 2012; Tittensor et al., 2010), while local habitat features (e.g., substrate types, distance to the coast or key habitats, food availability) and historical processes (e.g., speciation, dispersal limitations, connectivity) contribute more strongly at regional levels (Bender et al., 2013; Henriques et al., 2017; Hillebrand & Blenckner, 2002).

Comparison of temporal approaches within each extent revealed consistent ranking patterns; however, the magnitudes of variable importance differed significantly for all variables and ex-

tents. Dynamic predictors (temperature, oxygen, salinity) showed a higher importance in decadal than in yearly models at the total extent, aligning with evidence that species–environment associations are better modelled at coarser temporal scales across large extents for mobile species (Goh et al., 2024; Mannocci et al., 2017). Furthermore, oxygen and salinity had higher importance in decadal models at the regional scale (BOB and CS), likely due to interannual variability in these regions (Mannocci et al., 2017), caused by upwelling and seasonal stratification (von Schuckmann et al., 2024). At the same time, the static predictor distance to coast gained importance in the yearly approach across all taxa and regions, except for BOB and CS for *E. encrasicolus*. This contradicts the hypothesis that associations with large-scale, persistent oceanographic features are best modelled using coarser temporal resolutions (Mannocci et al., 2017). Furthermore, at a smaller spatial scale, the importance of oxygen and salinity was higher in the yearly model for *E. encrasicolus* and *S. canicula*, presumably better capturing fine-scale ephemeral processes (Mannocci et al., 2017). These results highlight the importance of selecting appropriate predictors for species distribution models (SDMs) depending on the temporal and spatial context and the species’ ecology, to improve predictive accuracy and ecological realism.

Aligning spatial extent with species traits and ecological niche

Although algorithms are designed to propose the best solution of model outcomes, common model choices (e.g., selection of predictors and their interactions, spatial and temporal resolutions of the data, as well as sampling of pseudo-absences) have profound effects on model outcomes (Commander et al., 2022; Goh et al., 2024; Melo-Merino et al., 2020; Núñez-Riboni et al., 2021).

According to TSS and ROC evaluation metrics, the models of all extents performed moderately to well, with better scores and lower risk of overfitting at larger extents (e.g., total extent, Bay of Biscay and Iberian coast, Celtic Seas), while the highest risks of overfitting was detected at the local extent (IS) for all species. When modelling at small spatial extents, sampling of pseudo-absences is often constrained to fall in grid cells closer to presences (Liu et al., 2019; Stokland et al., 2011). This reduces the environmental contrast between suitable and unsuitable habitats, thereby weakening the model’s ability to discriminate between presence and absence when applied to unknown data (model validation) (Liu et al., 2019; Stokland et al., 2011). Looking at the hotspot analysis, results emphasise that projections derived from models trained at broader spatial extents and subsequently cropped to smaller areas differ from models trained

directly within smaller extents. For instance, total extent models captured broader habitat patterns with a higher risk of overestimation (false positives) when cropped into smaller areas, particularly in heterogeneous environments. The discrepancies between modelling at larger versus modelling at smaller extents have also been found in studies in terrestrial environments (Fallgatter et al., 2025; Jarnevich et al., 2022; Jones et al., 2010), which suggests that careful consideration is required when interpreting the transferability of spatial predictions across extents. In this study, the limitation of transferability was most evident in the Irish Sea, where cropped full-extent models produced high false-positive rates (~30%) for both *E. encrasicolus* and *S. canicula*. Given their use of shallow coastal habitats, *S. canicula* and *E. encrasicolus* are better represented by regional or local-scale models, where other key habitat drivers (e.g., distance to coast, salinity, oxygen) gain in importance. For instance, for the Celtic Sea, regional extent models for *E. encrasicolus* with the yearly approach captured 28% more true presences and only 8% more false positives than the cropped total extent model, highlighting the benefit of scale-matching for mobile species in dynamic coastal zones. On the other hand, *M. merluccius*, whose habitat suitability is mainly governed by temperature, can yield the best model performance at broader spatial scales according to the hotspot analysis and evaluation metrics. Restricting the spatial extent to areas near the edge of the species' distribution may limit the capture of environmental gradients defining suitable and unsuitable habitats for some species, resulting in niche truncation (Anselmetto et al., 2025; Chevalier et al., 2022). Similarly, using a model that is not accurately specified in terms of predictors and spatiotemporal fields leads to bias in mean distribution, particularly when species depend on highly variable predictors that are better captured at finer scales (Commander et al., 2022). Thus, modelling at multiple scales is recommended to capture both fine-scale species-habitat relationships (e.g., food availability, proximity to essential habitats) and broad-scale processes (e.g., environmental gradients, connectivity, oceanographic processes) (Fournier et al., 2017). Overlapping areas across models with different extents, as seen in hotspot agreements in this study, could be a good indication of important areas for conservation or management decisions.

Temporal resolution and environmental variability

The temporal scale and resolution of predictor variables can significantly influence the predictive outcome of SDMs, and therefore, should be carefully considered from both ecological and statistical perspectives (Fernandez et al., 2017; Mannocci et al., 2017; Núñez-Riboni et al., 2021; Scales et al., 2017). Selecting appropriate temporal resolutions in environmental predictors is critical, since marine species interact with dynamic oceanographic processes that vary at

different timescales (Pennino et al., 2019). In our study, the TSS and ROC evaluation metrics indicated that decadal models significantly outperformed yearly models for *M. merluccius* and *S. canicula* in the North Sea. At the same time, in other regions, the temporal resolution had no significant effect. In the Celtic Sea, decadal models showed a higher risk of overfitting than yearly models for *E. encrasicolus*, whereas the opposite was true for *M. merluccius*. Yearly models also exhibited greater overfitting risk in the North Sea and across the total extent for *E. encrasicolus*. Other studies also found that higher temporal resolution resulted in decreased model performance in terms of evaluation metrics (Núñez-Riboni et al., 2021; Pennino et al., 2019). According to the Boyce Index, there was no significant difference in the performance between models trained with yearly or decadal means, except for *S. canicula*. In this case, the decadal approach in the total extent resulted in a significantly higher Boyce index, which means that predictions closely match observed presences. This concurs with the hypothesis that long-lived species' distributions are primarily driven by long-term averaged environmental conditions (Goh et al., 2024), while medium and short-lived species are sensitive to immediate environmental conditions (Mannocci et al., 2017). However, despite the lack of clear advantages of selecting a temporal training approach in most cases, some projections within the ensemble models performed worse according to the Boyce index. This suggests that model selection based solely on ROC may be insufficient and that incorporating Boyce Index or multiple metrics could improve the reliability of ensemble SDMs (Bracho-Estévez et al., 2024).

Previous studies showed that model prediction performance improves when aggregated environmental data are used, whereas time-specific data better represent the relationship between species and their habitats (Pennino et al., 2019). Thus, when studies are aimed at understanding the relationship between species and habitat characteristics, a time-specific data approach is most appropriate (Pennino et al., 2019). Consistent with this, our hotspot analysis indicates that yearly models captured more environmental variability and suitable habitat along the trailing edges of the species' niches. However, these models are also more sensitive to short-term environmental fluctuations, resulting in higher numbers of false positives (overestimations), particularly at the local extent (IS), which is a fast-warming region (von Schuckmann et al., 2024). In contrast, decadal models offered more conservative and stable predictions, making them more suitable for long-term trend analysis and species less affected by interannual environmental variability (e.g., *S. canicula*). However, the decadal approach may underestimate habitat shifts associated with environmental changes that have already emerged in recent decades. However, the decadal approach may miss habitat shifts due to changes in the environmental conditions over the last two decades (Le Luherne et al., 2024).

In summary, the results suggest that at a broad scale (total extent), both temporal approaches show similar performances, except for *S. canicula*, whose distribution is better described with a coarser temporal resolution (decadal approach) due to its association with persistent habitat features (e.g., distance to coast) (Mannocci et al., 2017). At medium scale (regional extent), the distribution of short-lived species such as *E. encrasicolus* is better outlined by yearly trained models, as these species are well-adapted to colonise and live in more dynamic and unstable environments with frequent short-term changes in environmental conditions. Controversially, yearly trained models tend to estimate more suitable habitats at the smallest scale (Irish Sea) for all species. The results reinforce that the ecological context, species life-history, study area extent and environmental characteristics should guide the choice of temporal resolution.

Recommendations for fisheries and conservation management

Species distribution models are often used to inform decisions on fisheries and conservation management across multiple spatial and temporal scales (Karp et al., 2025). The application of SDMs ranges from survey design and optimisation, fisheries stock assessments, designating Essential Fish Habitat (EFH), spatial management decisions, and understanding the impacts of climate variability (Karp et al., 2025). The management approaches could be static (e.g., seasonal fishery closure, MPAs) or dynamic, using near-real-time seasonal data to guide spatio-temporal locations of fishing to avoid bycatch or reduce risk of interaction with protected species (Hobday et al., 2010; Redfern et al., 2013). Thus, the appropriate temporal and spatial aggregations for environmental predictor data need to be carefully selected for modelling species distributions (Pennino et al., 2019). Thereby, the spatial extent defines the unit of assessment over which the management advice will be relevant, while the temporal resolution decides if dynamic short-term or stable long-term conditions are captured (Karp et al., 2025). In line with these findings, our study suggests that the choice of spatial and temporal resolution should align with the objective of the study, species ecology (e.g. life-history, mobility, habitat affinity, water column position) and area of interest (linked to species distribution or management unit). Considering the study objective, short-term, local, and dynamic management (e.g., monitoring, seasonal closures, regional MPA design) benefits from yearly trained, regional models, which offer finer resolution and responsiveness to dynamic changes (Karp et al., 2025). Long-term distribution trends (e.g., climate-driven range shifts) and large-scale planning (European network of MPAs, EU-wide stock assessments) are better served by decadal models at broader extents, which offer more stable trend predictions (Karp et al., 2025). Concerning species ecology, we found that the distribution of the opportunistic species, *E. encrasicolus*, was better

captured with yearly trained models at the regional extent, reflecting their sensitivity to short-term environmental change. According to this, opportunistic species could better be managed with local, and dynamic management. For the periodic species, *M. merluccius*, the distribution was better reflected at a broader scale, thus transboundary management of stocks might be essential to account for a broader distribution and changes in long-term temperature trends. Equilibrium species, like *S. canicula*, were better modelled with a decadal-trained model at a broader scale which means long-term trends in the environment are decisive on the larger scale. However, persistent habitat features were increasing in importance on a smaller scale, which shows their dependence on coastal habitat features, which could be important nursery grounds or feeding grounds. Thus, identifying and protecting those essential habitats would be a good management measure for those species. At the same time, the simultaneously modelling of fishing activities and target species on a regional scale could avoid unintentional bycatch.

Conclusions

Our results underscore that careful selection of model training extent and temporal resolution is crucial, as these choices significantly influence species-specific predictions and hotspot identification. For instance, some areas showed stable suitability across both temporal and spatial approaches, indicating potential priority areas for management. Training models at spatial scales aligned with species' ecology improves accuracy, while inappropriate model choices can lead to over- or underestimation of suitable habitats across regions. Overall, there is no generalizable best approach that can be applied universally to any species or region, both for modelling species distributions and outcome application (management and conservation). Instead, model configuration should be guided by the species' ecology, the study's spatial and temporal context, and the intended management application. Using a single modelling framework across species and contexts risks misrepresentation. To ensure that models' performances are robust and predictions are ecologically relevant, it is recommended to consider testing multiple temporal and spatial scales, especially in variable environments or when key drivers are scale sensitive.

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CHAPTER 6

GENERAL DISCUSSION

FUTURE PERSPECTIVES

General Discussion

Species distribution modelling assesses species-environment relationships that can be used to predict future distribution patterns or distributions in unsampled areas (Elith & Leathwick, 2009; Guisan & Thuiller, 2005). The thesis aimed to provide new insights for adaptive management that better aligns conservation and fisheries management efforts with the realities of a changing marine environment. Specifically, the studies examined the application of SDMs to identify priority areas of conservation (Chapter 2) and to assess the impacts of climate change on species distributions (Chapters 3 and 4). Furthermore, the consequences of different modelling choices on the predictive outcomes were explored (Chapter 5). By doing so, this work advanced our current understanding of species-specific habitat relationships and provides evidence of the important role of life-history traits in shaping species' responses to climate change.

Modelling species–habitat relationships and the impacts of climate change on range shifts of species with varying life-history strategies and ecological requirements

One of the main impacts of climate change is the shift in species distribution driven by changes in environmental conditions (Hastings et al., 2020; Pecl et al., 2017; Poloczanska et al., 2016). Marine species track isotherms six times faster than terrestrial species (Lenoir et al., 2020), leading to mostly poleward shifts of an average of 72 km per decade across the oceans (Poloczanska et al., 2013, 2016). Accordingly, sea temperature has been identified as the main driver for shifts in the community structure across the Northeast Atlantic (Rutterford et al., 2023). Besides, a deepening shift of about 3.6 m per decade in demersal fish assemblages was observed in the North Sea (Dulvy et al., 2008). In this thesis, climate change impacts on species distribution were investigated across marine species with varying ecological and life-history traits by predicting changes of habitat suitability until the end of the century of a) seahorses with small-scale habitat specificities, low dispersal and small population size (Chapters 2 and 3) and b) representatives of three life-history strategy groups; equilibrium, opportunistic, and periodic (Chapter 4). Among environmental predictors included in the models, temperature, depth, and/or distance to the coast had the highest importance in predicting habitat suitability for all species, consistent with identified drivers of biogeographic patterns of fish biodiversity (Bender et al., 2013; Henriques et al., 2017; Tittensor et al., 2010).

The model predictions of Chapter 3 and 4 partially correspond with the trend of poleward shifts and/or east- and westward shifts into deeper waters (Perry et al. 2005; Dulvy et al. 2008; Rutterford et al. 2023; Le Luherne et al. 2024). On the other hand, a global multi-species study found that the core habitat will decline for almost half of all marine species by 2100 under the “business as usual” scenario, with the Equator being mostly affected (Hodapp et al., 2023). Our findings revealed that spatial patterns of core habitat gains and losses were driven by species' ecological traits, with some species experiencing up to 40% (*R. montagui*) to 50% habitat loss (*H. guttulatus*). For instance, in Chapter 4, significant range contractions were predicted in the southern part of the North Sea, eastern Celtic Sea, and Irish Sea, which are regions warming at a faster rate than the rest of the Northeast Atlantic (Kessler et al., 2022; von Schuckmann et al., 2024). Species predicted to experience range contractions were characterised by larger body sizes and higher trophic levels (equilibrium and periodic group). In contrast, species with smaller body sizes and rapid life cycles (opportunistic group) were consistently projected to gain habitat, following the expected northward trend. These findings contradict observations in the English Channel in the late 1990s, where warmer sea temperatures due to Atlantic Multidecadal Oscillation were associated with a decrease in abundance of opportunistic species and an increase in equilibrium species (McLean et al., 2018). Nonetheless, both findings reinforce that the response to climate change is influenced by life-history traits and suggest a rapid response of opportunistic species to changes in the environment. Furthermore, our results concur with the observation that rapidly warming regions are experiencing an increase of r-strategy fish species, while more slowly warming regions show an increase of k-strategy species (Receveur et al., 2024).

More importantly, the varying response of trait groups, as predicted in Chapter 4, could significantly alter the functional structure of the ecosystem. Changes in the functional organisation of fish communities can have major consequences for ecosystem functioning by affecting the food web structure, biotic interactions, nutrient cycling, and benthic-pelagic coupling (Amelot et al., 2023; Casini et al., 2012; McCann et al., 2005; Pecuchet et al., 2020; Vergés et al., 2014). For instance, the predicted loss of nearly all equilibrium species in the North Sea could reduce the top-down control and destabilise coupled food webs (McCann et al., 2005), and the redistribution of opportunistic and periodic species could lead to increased competition for food sources (Amelot et al., 2023). Further, our findings also suggest that fish communities converge in traits, increasing functional evenness instead of diversity (McLean, Mouillot, et al., 2019).

Besides the six main life history traits examined in Chapter 4, other traits could play an important role in the vulnerability of species to distribution shifts (Butt et al., 2022; Estrada et al., 2016; McLean, Auber, et al., 2019; Pacifici et al., 2017; Polo et al., 2025). For instance, oceanographic connectivity and intrinsic dispersal potential played a key role in the outcomes of future distributions of species that rely on passive dispersal, such as *H. hippocampus* and *H. guttulatus* (Chapter 3). These processes limited the northward range expansion, resulting in significant reductions in habitat gain. Limited expansion was more pronounced in *H. guttulatus* than in *H. hippocampus*, presumably due to their different habitat use and population structure. The preference of *H. guttulatus* for mainly shallow inshore waters and coastal lagoons (Pierri et al., 2022) likely restricts their potential for colonisation of new habitats through closed populations (Cowen et al., 2000; Cowen & Sponaugle, 2009; Lourie et al., 2005). Overall, the habitat suitability maps produced for the different species (Chapters 3 and 4) allowed identifying critical areas of habitat loss and, at the same time, areas that could serve as climate refugia (e.g., the Iberian Coast, Northern Mediterranean, and Black Sea). If these areas could be connected through a network of effectively managed protected areas, it would surely not only benefit the seahorses in maintaining their population connectivity (Assis et al., 2021; Lourenço et al., 2016; Rassweiler et al., 2020; Sundblad et al., 2011). This highlights the importance of incorporating spatial variability into conservation planning and fisheries management. Besides, findings in Chapter 3 show that it is crucial to strive to curb emissions in the coming years, as doing so could halve projected losses and maintain climate refugia for seahorses.

Choices of input data in Species Distribution Modelling

Collecting occurrence data in the marine environment is challenging due to limited accessibility and the high operational cost of surveys (Pennino et al., 2016). Data from fishery-independent surveys (e.g., International Bottom Trawl Survey (IBTS)), which were used in Chapter 4, provide standardised and quality-controlled data homogeneously distributed over a wide spatial area (Maureaud et al., 2024; Pennino et al., 2016). However, gear selectivity limits the detection of certain species and coverage of some habitats (e.g., rocky reefs) (Maureaud et al., 2021). In contrast, biodiversity repositories such as GBIF and OBIS compile records from multiple sources, which can fill gaps, especially for non-commercial or rare species like seahorses (Chapters 2 and 3), where data quantity might be more decisive (Gaul et al., 2020). Furthermore, the citizen science survey used for Chapters 2 and 3 has been proven to be efficient and cost-effective in detecting more locations for seahorse (Appendix 5), as also shown in other studies (Bosso et al., 2024; Zhang & Vincent, 2018). However, non-standardised sampling may suffer

from issues such as spatial bias, uncertain identifications, and variable data quality, which influences model results (Feldman et al., 2021). Ultimately, the choice of the occurrence data source is generally a trade-off between quality and quantity, which varies with species and study area.

Modelling in the marine environment is challenge by various oceanographic processes, which cause environmental variability across three dimensions (space, depth and time), ranging from short-term local fluctuations (e.g., tides, currents) to long-term broad scale shifts (e.g., El Niño-Southern Oscillation (ENSO) and the North Atlantic Oscillation (NAO)) (Kroeker et al., 2020). Building SDMs that produce robust and ecologically meaningful predictions requires that all environmental variables are available at matching spatial and temporal scales and are not correlated (Melo-Merino et al., 2020). Many oceanographic variables are often unavailable at fine spatial and temporal resolutions or have been interpolated (El-Gabbas et al., 2021; Fernandez et al., 2017). The lack of spatially explicit information on specific habitat requirements (e.g. holdfast availability for seahorse (Correia et al., 2018; Pierri et al., 2022; Woodall et al., 2018)) may be overcome by using correlated variables (Chapters 2 and 3). In these studies, distance to the coast represented proximity to seagrass, macroalgal communities and artificial habitats. Furthermore, the importance of environmental variables may differ among spatial and temporal extents (Chapter 5). In Chapters 2 and 3, substrate type was tested as a predictor, since it was deemed important in other studies on seahorses (Woodall et al. 2018). However, its importance in the models was negligible, which could be attributed to the spatial scale of the study or to the downscaling of the original sampling resolution of the variable to that of the study (Mourguiart et al., 2024; Núñez-Riboni et al., 2021). Overall, the selection of environmental predictors needs to be adapted to the objective and scale of the study. For instance, in Chapter 2, the habitat suitability of the seahorses was modelled for a smaller extent, with a higher spatial resolution and including more variables specific to the spatial extent (i.e. the aspect of the seafloor, tidal amplitude). This approach allowed us to identify the main habitat preferences of seahorses in this region (i.e., shallow protected habitats in estuarine or lagoon environments) and to precisely pinpoint the hotspot areas to guide conservation efforts and scientific surveys. Besides, it showed the importance of the availability of environmental data at finer spatial resolution and homogeneously distributed across the study area.

As shown by Chapter 5 and confirmed by other studies, the size of the model extent significantly affects the predicted suitable area and role of the variables (Acevedo et al., 2012; Amaro

et al., 2023; Fallgatter et al., 2025). Thus, predictions on a larger spatial extent cannot necessarily be transferred accurately to smaller spatial extents, as shown in Chapter 5. However, the modelling at smaller extents risks a potential niche truncation, since the model misses the environmental variability of the entire realised niche (Jarnevich et al., 2022). However, often SDMs with broader scale overestimate suitable habitat (Fallgatter et al., 2025; Jones et al., 2010). Findings from Chapter 5 show that choices on spatial extents and temporal resolution not only influence the model's performance but also the predictive map outcomes, resulting in varying extents of suitable habitat. This can have major implications for guiding conservation (e.g., delineation of protected areas) and fisheries management (e.g., decision on stock unit). It is common practice to correlate occurrence data with long-term averages (decades) of dynamic covariates (e.g., temperature), which disregards the temporal aspect of the occurrence data and the inherent variability of the environmental covariates, rendering rather static species-environment relationships (Milanesi et al., 2020). Using coarse climatological data in habitat models for marine predators can misrepresent environmental preferences, especially in dynamic oceans where animals rely on real-time conditions (Scales et al., 2017). In line with this, a study found that species-habitat relationships of medium-lived species are better described with finer temporal resolution due to their sensitivity to seasonal environmental conditions (Pennino et al., 2019). In contrast, studies with long-lived marine mammals indicated that their distributions are better predicted by long-term temporal means and coarse spatial scales (Goh et al., 2024). Furthermore, a review on temporal resolution in SDMs concluded that the optimal temporal resolution should match the ecological question and ecosystem variability (Mannocci et al., 2017). In Chapter 4, dynamic environmental data were spatiotemporally matched to species occurrence data by correlating occurrences with yearly means instead of decadal means (Milanesi et al., 2020), acknowledging that environmental conditions and species distributions are not static over decades (Foster et al., 2022; Le Luherne et al., 2024). On the other hand, coarser temporal resolutions smooth out short-term variability and may be sufficient at broad scales or when interannual variability is weak (Mannocci et al., 2017). Furthermore, it was found that the species' responses to environmental dynamics depend on its movement behaviours (Andrew & Fox, 2020). Following this rationale, the use of a coarse temporal resolution in Chapters 2 and 3 was suitable since the species are sedentary and in Chapter 3, the focus was to model the broad habitat suitability of a species across its native range.

To sum up, the model outcomes of the four studies advance our knowledge on the role of species' life history traits and ecological requirements (sedentary vs. mobile), as well as the role of temporal and spatial context in Species Distribution Modelling. These aspects are of utmost

importance to guide the application of SDMs for future marine resource management, as recently pointed out by two review studies (Karp et al., 2025; Klaassen et al., 2025).

Implications for conservation and management

The knowledge of the spatial distribution of species, habitats, and ecological communities is the basis for marine spatial planning and effective ocean management (Pinsky, Rogers, et al., 2020). Species Distribution Modelling is used as a tool for various applications, ranging from survey design optimisation, fisheries stock assessment, designation of essential fish habitat, marine spatial planning, dynamic ocean management, and climate change impacts (Klaassen et al., 2025). In this thesis, we explored how the static protection of habitats in the form of marine protected areas benefit the conservation of two sedentary species (Chapter 2), how climate change impacts challenge conservation measures (Chapter 3), how to improve ecosystem-based (e.g., fisheries) management (Chapter 4), and how different choices regarding temporal and spatial scales influence model outcomes and thus the information these may provide to support spatial management of species with varying ecological requirements (Chapter 5).

The predictive maps, produced in Chapter 2, provided useful information on the distribution and the different habitat preferences of the two European seahorse species, *Hippocampus hippocampus* and *Hippocampus guttulatus* and allowed identifying priority areas for scientific surveys and conservation efforts. The results show that the calculated percentage of species' suitable habitat overlap with protected areas is often optimistic. The gap between the percentage of area protected by implemented protected areas (20%) and fully protected (<1%) area in Chapter 2 highlights the importance of understanding what is effectively protected with designation of the respective MPA (Grorud-Colvert et al., 2021; Pike et al., 2024; Sullivan-Stack et al., 2024). In the case of the seahorses, it was concluded that increased protection measures suited to seahorses are needed, instead of relying on designated non-enforced MPAs. For this case, the designation of a community-led protected area by involving stakeholders in decision-making was recommended (Guimarães et al., 2023). Furthermore, the importance of eliminating specific threats to seahorses (e.g., destructive fishing, dredging, pollution) and the restoration of habitat was highlighted. In the frame of the project CavALMar, the results of Chapter 2 were delivered to the Portuguese Institute for Nature Conservation and Forests (ICNF) in August 2024, which resulted in the funding of further monitoring projects Cavalos-de-Tróia and CavalSado (2025), where, among other partners, ICNF play a central role. Furthermore, the information was integrated into the "Plano Nacional de Acção para a Conservação dos Cavalos-marinhos" that was

also delivered to ICNF in the beginning of the year. Besides, the results of Chapter 2 were disseminated to the public via several newspaper and magazine articles (Appendix 5).

Multi-species SDMs have shown that about half of marine species will shift distributions under climate change (Hollowed et al., 2013; Pecl et al., 2017; Pinsky, Selden, et al., 2020; Poloczanska et al., 2016), which poses new challenges and risks for conservation and fisheries management as well as the communities that depend on marine resources (Pinsky, Rogers, et al., 2020). SDMs are considered a critical tool for exploring contemporary and future regional and global changes in marine biodiversity (Jones & Cheung, 2018). SDMs in Chapters 3 and 4 provide insights into how species distributions with different ecological requirements and life-history traits will change under various future climate scenarios. The outputs from these projections identified species and areas of particular risk to habitat loss and also identified climatic refuge areas. This information is crucial to adapt current conservation measures to climate-driven changes. For instance, a global assessment showed that marine reserves can reduce climate-driven fish biomass losses, but their effectiveness depends strongly on placement, size, and accounting for shifting species ranges (Palacios-Abrantes et al. 2023). Other studies showed that many species will lose suitable habitat inside MPAs, which means that static protection may not safeguard species in the future (Liu et al., 2024; Weinert et al., 2021). These findings highlight the risk of ignoring climate distribution shifts and underscore the value of climate-informed measures (e.g., climate-resilient MPA networks), facilitated through spatial planning tools such as SDMs and Marxan (Blair et al., 2022; Palacios-Abrantes et al., 2023; Whitney et al., 2023). As the results of Chapter 4 show, not all species react the same way to changes in their habitat, which can lead, for instance, to changes in the composition of multispecies fisheries (O. R. Liu et al., 2023). The spatiotemporal mismatch of species distribution and quota allocation can lead to high amounts of discard on the one hand and loss of income on the other (Fernandes & Fallon, 2020). According to findings in Chapter 4, opportunistic fish track environmental changes faster than equilibrium species and are often important commercial species (Fernandes et al., 2020; Siple et al., 2021). Furthermore, small pelagic fish can be well modelled with fine temporal resolution according to Chapter 5. Thus, dynamic ocean planning would be a recommended tool to manage populations of commercial opportunistic species as ocean conditions change (Andrew & Fox, 2020). The simultaneous modelling of multiple species could inform on spatiotemporal overlap between non-target and target species (Hobday et al., 2010; Maxwell et al., 2015; Pons et al., 2022). Ecosystem-based fisheries management aims to make conservation and fisheries-related decisions considering the whole ecosystem and by including

stakeholders. This demands knowledge on ecosystem and biodiversity indicators (e.g., richness, evenness, diversity) as well as functional structure and food web dynamics. In this context, a trait-based approach was used in Chapter 4 to model species distributions of several species from different life-history strategy groups to infer changes in functional richness and diversity under climate change. Our results predicted differences between gains and losses of species of different trait groups which could have substantial implications for the food web structure. Building up on this, the trait-based approach could be enhanced by modelling whole communities, e.g., through joint-species distribution modelling, and including biotic interactions, e.g., through the Spatially Explicit Species Assemblage Modelling (SESAM) framework. Further, focusing on different life-stages these approaches could identify essential fish habitats (e.g., spawning, nursery) for the species.

Overall, this thesis provides critical insights into single and multi-species distribution modelling and its application in conservation and management. It highlights the importance of accounting for species ecology, environmental dynamics, and the study objectives when designing a species distribution model.

Future perspectives

The outcomes of this thesis emphasise knowledge gaps and further research needs concerning the use of habitat suitability models in predicting impacts of climate change on marine fish communities and in informing conservation and fisheries management measures. Underlying the high variability of response observed among species with varying ecological traits, the integration of trait information into future studies linked with Species Distribution Modelling and Ecosystem-based management is essential. To better understand the implications of climate-driven range shifts, multi-species models are needed that can provide information on biotic interactions, e.g., changes in the food web structure or competition (Coll et al., 2019; Poggiato et al., 2025). Another critical challenge identified by this thesis is the knowledge gap on population connectivity and how it influences the response of species to environmental changes. In this context, the connectivity between Essential Fish Habitats also plays an important role; therefore, there is a need for modelling suitable habitats for all life stages (Zhang et al., 2023). Apart from that, the thesis showed that the quality and quantity of species and environmental data at appropriate scales are of utmost importance for the performance of the model. Thus, standardised monitoring activities across multiple species and habitats need to be optimised and integrated into transboundary management plans (Maureaud et al., 2021), potentially supported

by emerging monitoring tools such as eDNA and acoustic monitoring (Rees et al., 2014). Besides, currently under discussion is the integration of genetic information into Species Distribution Modelling frameworks to account for the adaptive potential of species (Layton et al., 2024). For instance, this could improve decision-making on fish stocks by considering variations in response to climate change within a population (Baltazar-Soares et al., 2023) or might identify population units at risk of climate change for species with limited population connectivity, such as seahorses. Ultimately, this thesis highlights the need for management strategies that are flexible and responsive to ongoing environmental changes and consider the species' ecological requirements and role in the ecosystem.

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APPENDICES

APPENDIX 1 - Supplementary material of Chapter 2

APPENDIX 2 - Supplementary material of Chapter 3

APPENDIX 3 - Supplementary material of Chapter 4

APPENDIX 4 - Supplementary material of Chapter 5

APPENDIX 5 - Public outreach and other achievements

APPENDIX 1 - Supplementary Material of Chapter 2

Table A 1.1. Databases for the collection of occurrence points

Name	Source
Ocean Biodiversity Information System (OBIS)	www.obis.org
Global Biodiversity Information Facility (GBIF)	www.gbif.org
Biodiversity4all, iNaturalist, iSeahorse ^{*1}	www.inaturalist.org ; www.biodiversity4all.org
International Council for the Exploration of the Sea (ICES)	www.ices.dk/data/data-portals/Pages/DATRAS.aspx
Coastal Monitoring Network (COASTNET)	https://coastnet.pt/
Project: Inforbiomares	https://arrabidaparquemarinho.ualg.pt/en/
Project: CavALMar	(Silva et al., 2023)

^{*1} Biodiversity4all, iNaturalist and iSeahorse have obscured coordinates by default, sightings could only be used in the model when the owner allowed access to the original coordinates.

^{*2} Gonçalo Silva, Mariana Coxey & Miguel Correia, 2023. “CavALMar - Avaliação populacional das espécies de cavalos-marinhos na frente ribeirinha do concelho de Almada”, Relatório técnico final, 82 pp., Almada, Portugal.

Table A 1.2. Selected variables that were tested in different combinations in the Ensemble Species Distribution Model for both species. High correlations ($pc > 0.7$) were found between depth, salinity, and temperature, as well as between chlorophyll a, phytoplankton, primary productivity, and kinetic wave energy and between slope and rugosity.

Categories	Variables	Units	Original Resolution	Source
Topographic	Bathymetry	m	0.0083°	General Bathymetric Chart of the Oceans (GEBCO)
	Rugosity		0.0083°	Derived from bathymetry
	Slope	degree	0.0083°	Derived from bathymetry
Geographic	Distance to nearest coast	Km	0.01 °	https://ocean-color.gsfc.nasa.gov/docs/distfromcoast/
Physical-Chemical	Temperature at minimum depth	°C (mean)	0.083°	BIO ORACLE ^{*1}
	Salinity at minimum depth	PSS (mean)	0.083°	BIO ORACLE
	Dissolved oxygen at minimum depth	mol.m-3 (mean)	0.083°	BIO ORACLE
	Chlorophyll a at minimum depth	mg.m-3 (mean)	0.083°	BIO ORACLE
	Light at bottom at minimum depth		0.083°	BIO ORACLE
Biological	Primary productivity at minimum depth	g.m-3.day-1 (mean)	0.083°	BIO ORACLE

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	Phytoplankton at minimum depth	umol.m-3 (mean)	0.083°	BIO ORACLE
Hydrodynamic	Current velocity at minimum depth	m/s (mean)	0.083°	BIO ORACLE
	Kinetic energy due to waves on the seabed		0.04°	EMODNET (https://emodnet.cc.europa.eu/geoviewer/)
	East-west aspect of seafloor	radians x 100	0.083°	GMED (https://gmed.auckland.ac.nz/layersd.html)
	North-south aspect of seafloor	radians x 100	0.083°	GMED
	Avg. of maximum tidal amplitude	m	0.25° x 0.25°	GMED
Habitat	Substrate	Substrate types (s. Table 3)	250 m = 0.0025°	EUSeaMap*2
	Seagrass proximity	Distance (m) to <i>Zostera marina</i> , <i>Z. nolti</i> , <i>Cymodocea nodosa</i>	0.0083°	OBIS, GBIF

*1(Assis et al., 2018; Tyberghein et al., 2012)

*2(Vasquez et al., 2021)

Table A 1.3. Substrate types used in the substrate layer from the EUSeaMap (Vasquez et al., 2021) and sorted by the Folk 7 classification from small (category 1) to big grain sizes (category 9) (Kaskela et al., 2019). The substrate types ‘seabed’ and ‘coarse & mixed sediment’ are not part of the Folk 7 sediment triangle and had to be added as separate categories. The substrate type ‘seabed’ can be ‘fine mud, sandy mud, or muddy sand’, which is not distinguished in the EUSeaMap (Vasquez et al., 2021).

Category	Substrate type
1	Seabed
2	Sand
3	Muddy sand
4	Sandy mud
5	Fine Mud
6	Mixed Sediment
7	Coarse & Mixed Sediment
8	Coarse substrate
9	Rock or hard substrata

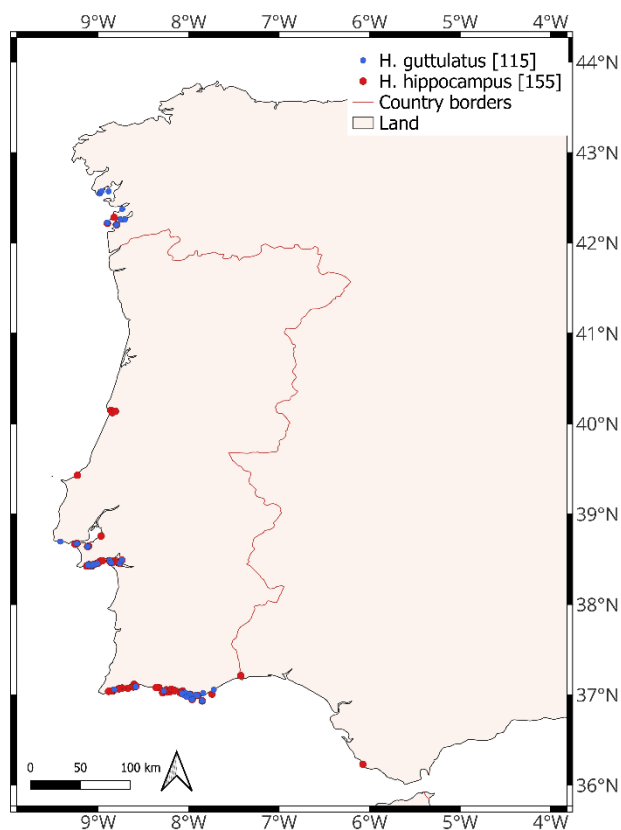


Figure A 1.1. Occurrence points of *H. hippocampus* and *H. guttulatus* from the years 1990-2022 used in the Ensemble Model as presence data.

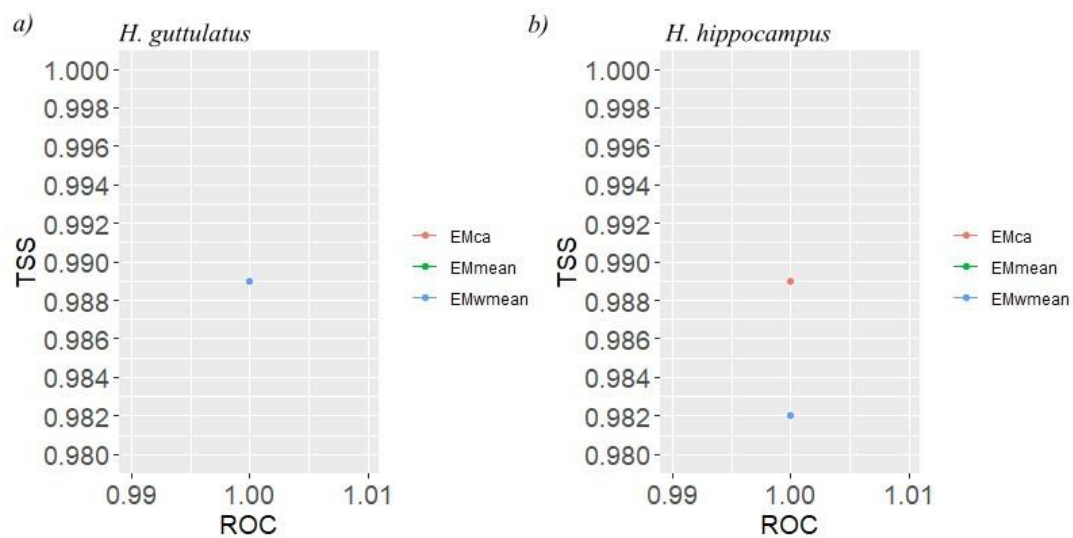


Figure A 1.2. Scores of Evaluation metrics (TSS, AUC (ROC)) for community averaging (EMca), mean (EMmean), and weighted mean (EMwmean) of the Ensemble Model of *H. guttulatus* and *H. hippocampus*.

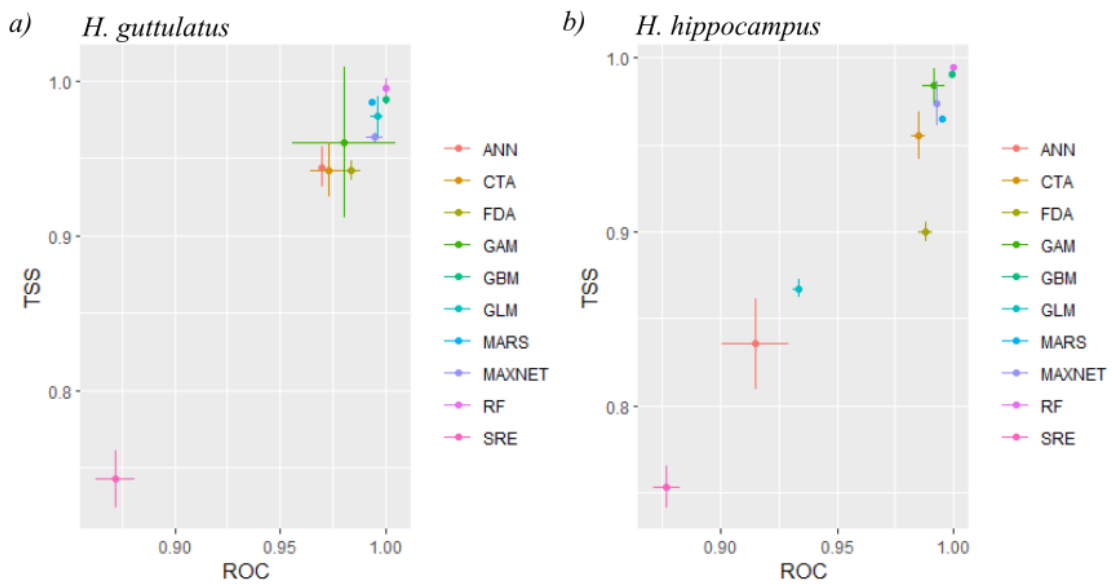


Figure A 1.3. Scores of Evaluation metrics (TSS, AUC (ROC)) for the different algorithms of the Ensemble Model of a) *H. guttulatus* and b) *H. hippocampus*.

Table A 1.4. Environmental predictors used in the final model set-up.

Categories	Variables	Units	Original Resolution	Source
Geographic	Distance to the nearest coast	km	0.01 °	https://ocean-color.gsfc.nasa.gov/docs/distfromcoast/
Physical-Chemical	Temperature at minimum depth	°C	0.083°	BIO ORACLE
Biological	Phytoplankton at minimum depth	mol.m-3	0.083°	BIO ORACLE
Hydrodynamic	Current velocity at the minimum depth	m/s	0.083°	BIO ORACLE
	East-west aspect of the sea-floor	radians x 100	0.083°	GMED
	Avg. of maximum tidal amplitude		0.25° x 0.25°	GMED
Habitat	Substrate	Substrate types (s. Table 3)	250 m = 0.0025°	EUSeaMap

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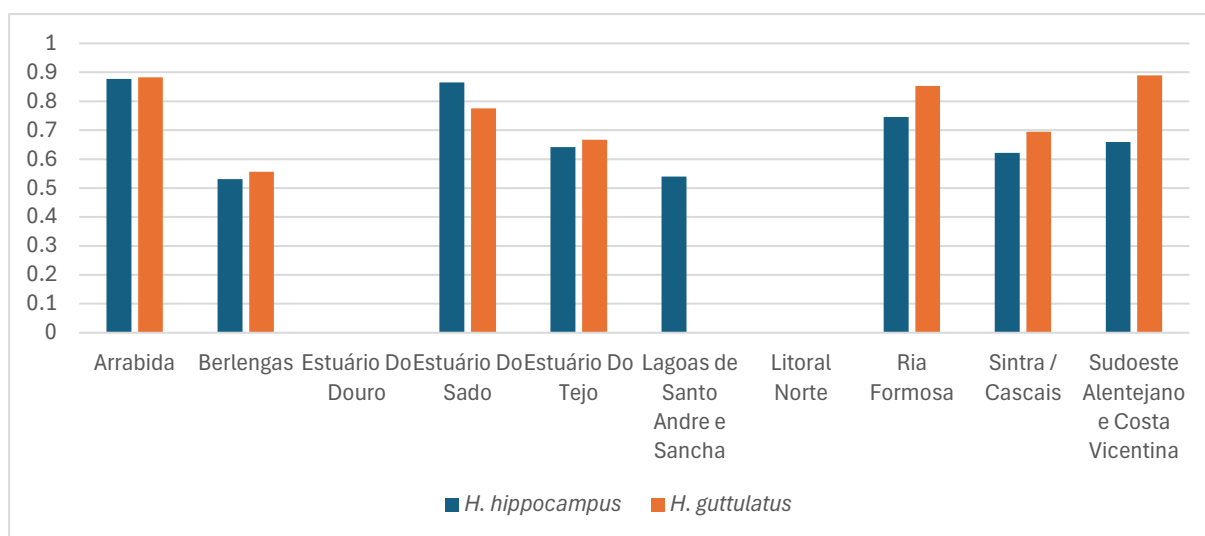


Figure A 1.4. Mean habitat suitability inside protected areas in Portugal.

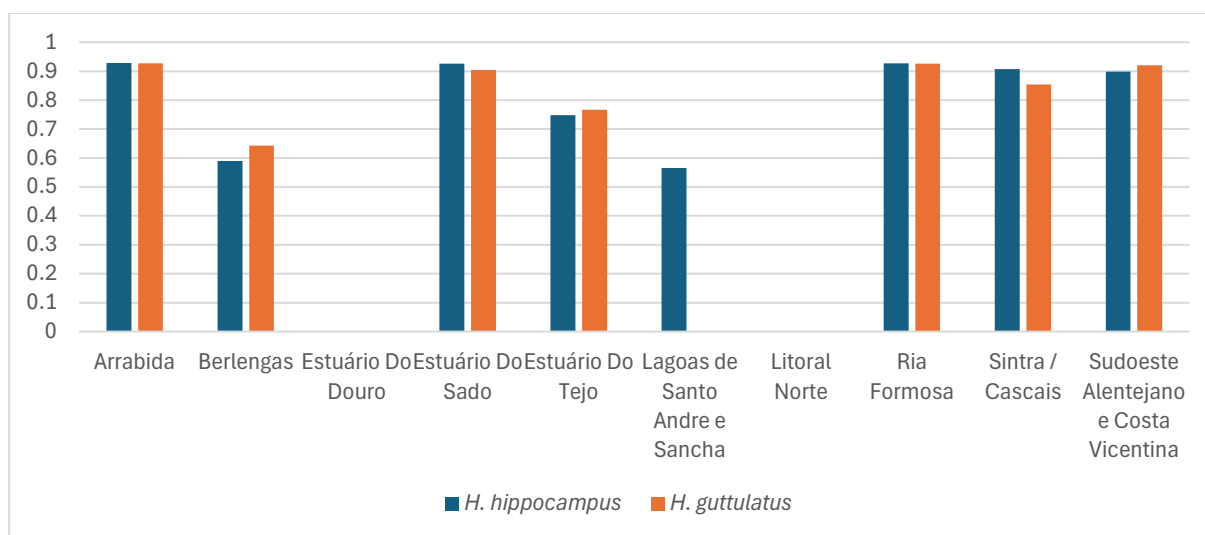


Figure A 1.5. Maximum habitat suitability inside protected areas in Portugal.

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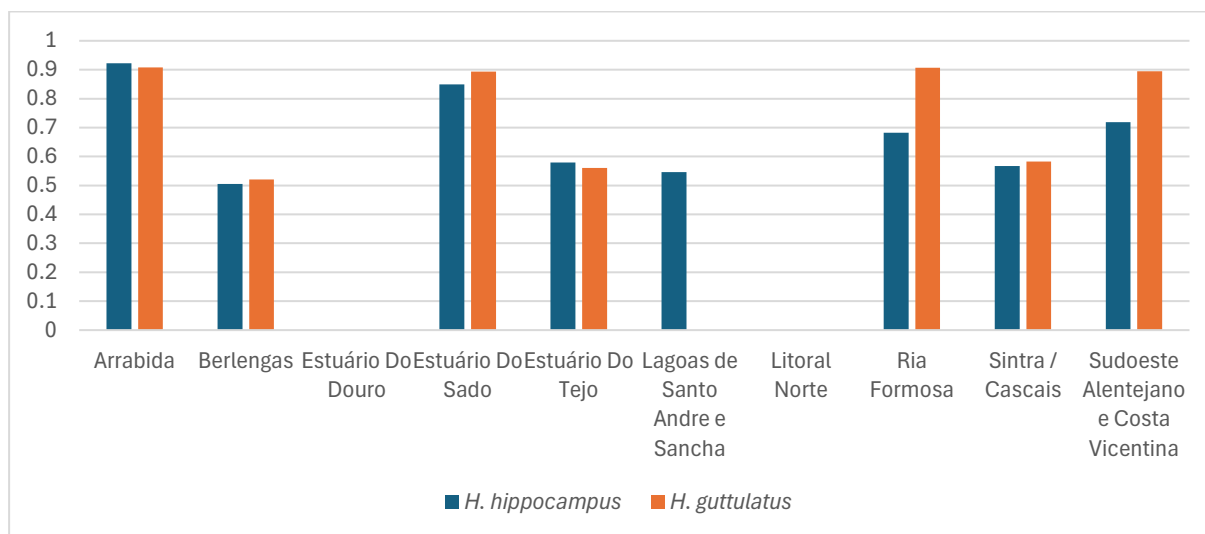


Figure A 1.6. Majority of habitat suitability inside protected areas in Portugal.

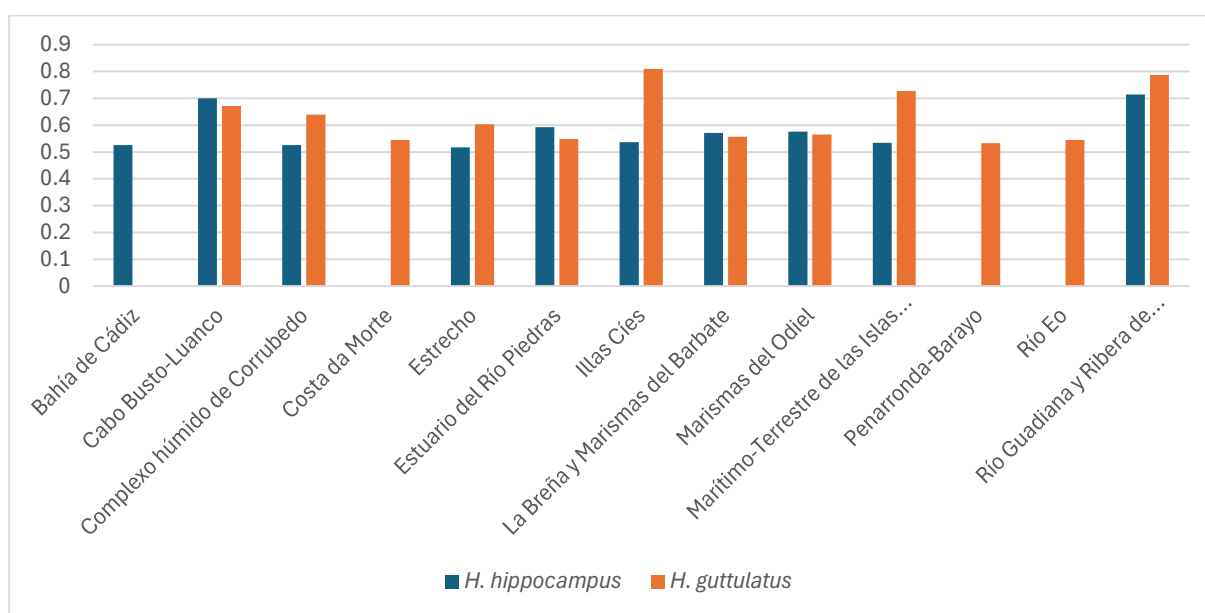


Figure A 1.7. Mean habitat suitability inside protected areas in Spain.

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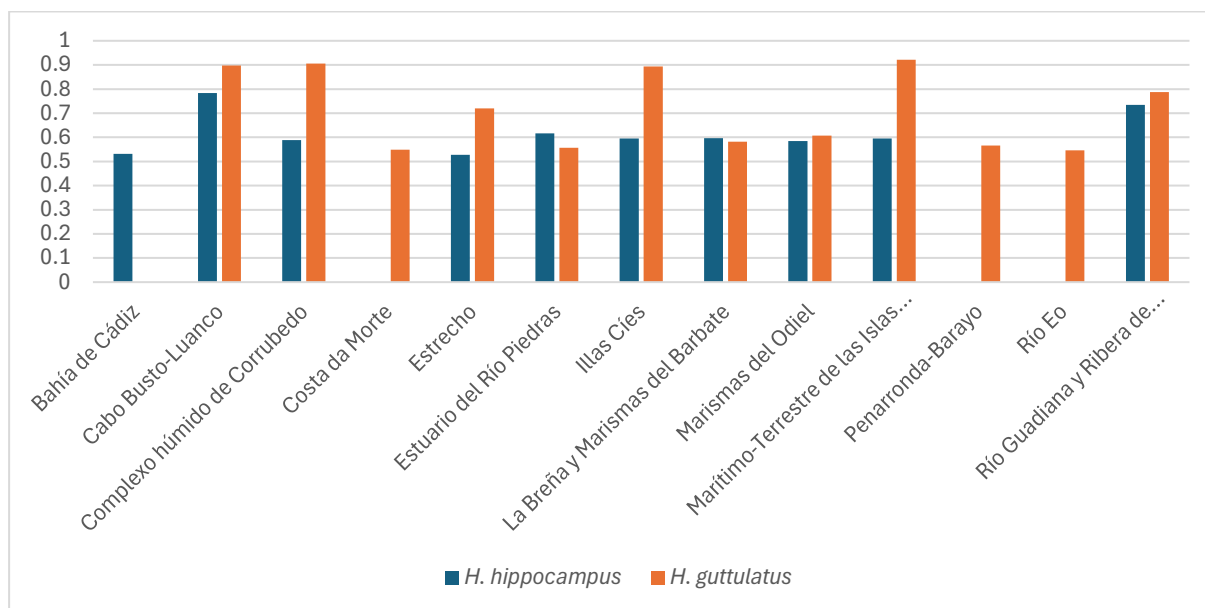


Figure A 1.8. Maximum habitat suitability inside protected areas in Spain.

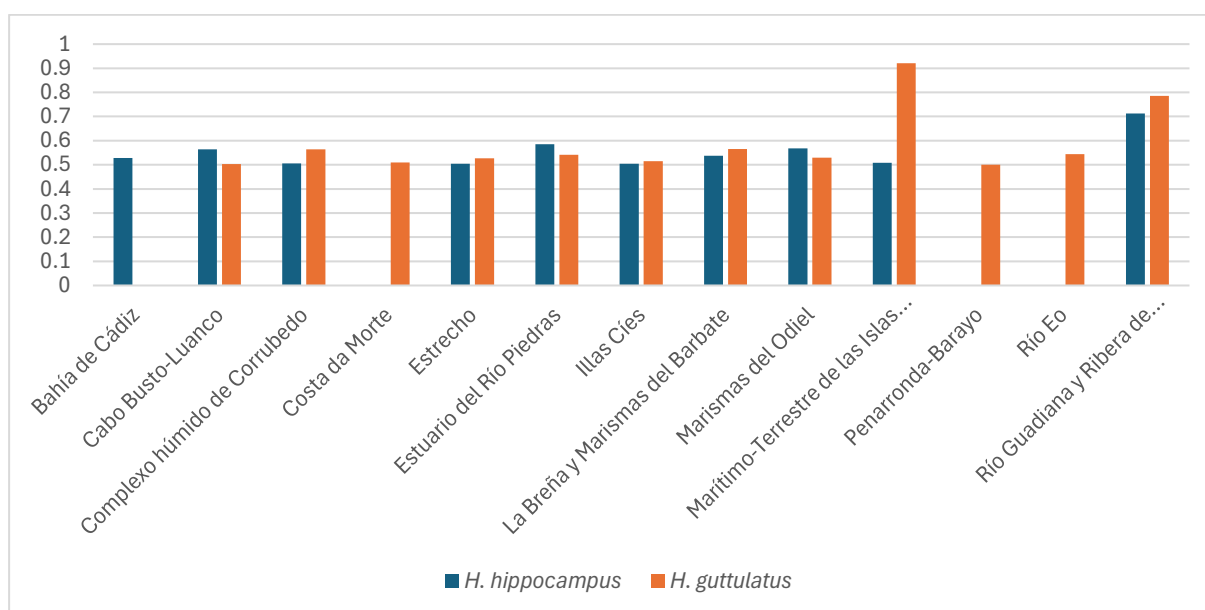


Figure A 1.9. Majority of habitat suitability inside protected areas in Spain.

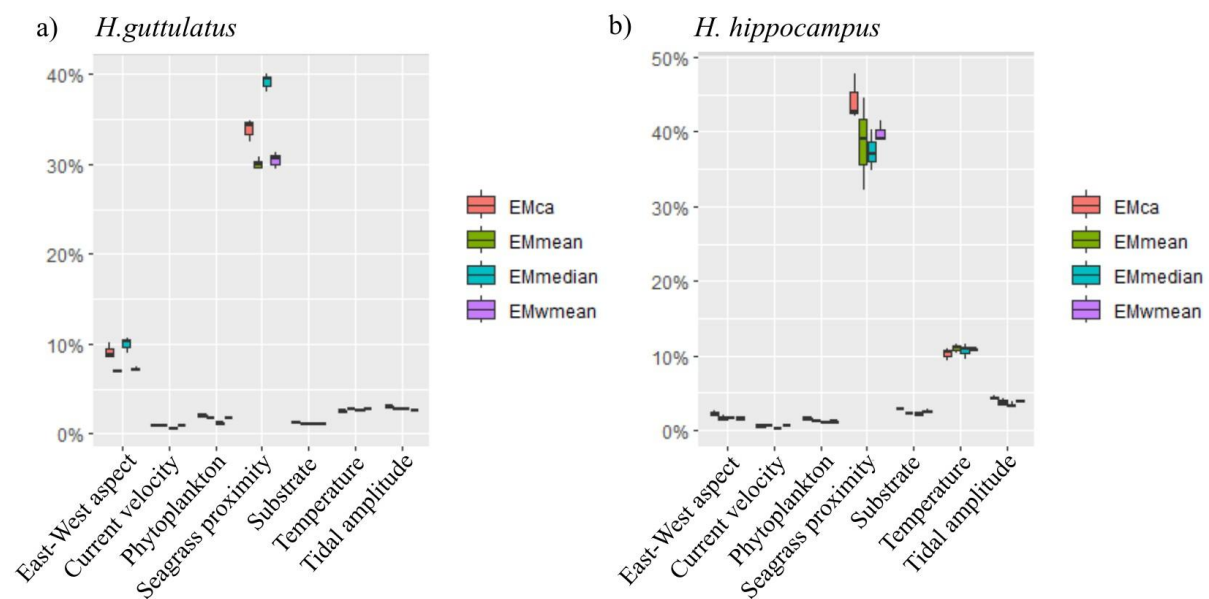


Figure A 1.10. Variable importance of the Ensemble models of a) *H. guttulatus* and b) *H. hippocampus* including the variable seagrass proximity instead of distance to the coast.

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APPENDIX 2 - Supplementary Material of Chapter 3

Table A 2.1. Databases for the collection of occurrence points.

Name	Source
Ocean Biodiversity Information System (OBIS)	www.obis.org
Global Biodiversity Information Facility (GBIF)	www.gbif.org
Biodiversity4all, iNaturalist, iSeahorse ^{*1}	www.inaturalist.org ; www.biodiversity4all.org
International Council for the Exploration of the Sea (ICES)	www.ices.dk/data/data-ports/Pages/DATRAS.aspx
Coastal Monitoring Network (COASTNET)	https://coastnet.pt/
Project: Inforbiomares	https://arrabidaparquemarinho.ualg.pt/en/
Project: CavALMar	(Silva et al., 2023)

^{*1} Biodiversity4all, iNaturalist and iSeahorse have obscured coordinates by default; sightings could only be used in the model when the owner allowed access to the original coordinates.

^{*2} Gonçalo Silva, Mariana Coxey & Miguel Correia, 2023. “CavALMar - Avaliação populacional das espécies de cavalos-marinhos na frente ribeirinha do concelho de Almada”, Relatório técnico final, 82 pp., Almada, Portugal.

Table A 2.2. Selected variables that were tested in different combinations in the Ensemble Species Distribution Model for both species.

Variables	Units	Original Resolution	Source
Distance to the nearest coast	km	0.01°	NASA ^{*1}
Bathymetry (min, mean, max)	m	0.05°	BIO ORACLE ^{*2}
Terrain ruggedness index	-	0.05°	BIO ORACLE*
Topographic slope	-	0.05°	BIO ORACLE*
Topographic aspect	-	0.05°	BIO ORACLE*
Topographic position index	-	0.05°	BIO ORACLE*
Temperature at minimum depth (min, mean, max)	°C	0.05°	BIO ORACLE*
Salinity at minimum depth (min, mean, max)	-	0.05°	BIO ORACLE*
Dissolved oxygen at minimum depth (min, mean, max)	mmol. m-3	0.05°	BIO ORACLE*
Chlorophyll at minimum depth (min, mean, max)	mmol. m-3	0.05°	BIO ORACLE*
Primary productivity at minimum depth (min, mean, max)	mmol. m-3	0.05°	BIO ORACLE*
Sea water velocity at minimum depth (min, mean, max)	m.s-1	0.05°	BIO ORACLE*
Nitrate	mmol. m-3	0.05°	BIO ORACLE*
Phosphate	mmol. m-3	0.05°	BIO ORACLE*
Silicate	mmol. m-3	0.05°	BIO ORACLE*
Iron	mmol. m-3	0.05°	BIO ORACLE*
pH	-	0.05°	BIO ORACLE*

^{*1}<https://oceancolor.gsfc.nasa.gov/docs/distfromcoast>

^{*2}(Assis et al., 2024)

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Table A 2.3. Environmental predictors used in the final model set-up.

Variables	Units
Distance to the nearest coast	Km
Bathymetry (at minimum depth)	M
Temperature at minimum depth (mean)	°C
Salinity at minimum depth (mean)	-
Primary productivity at minimum depth (mean)	mol.m-3
Sea water velocity at the minimum depth (mean)	m/s
pH at minimum depth (mean)	-
Dissolved oxygen at minimum depth (mean)	mol.m-3

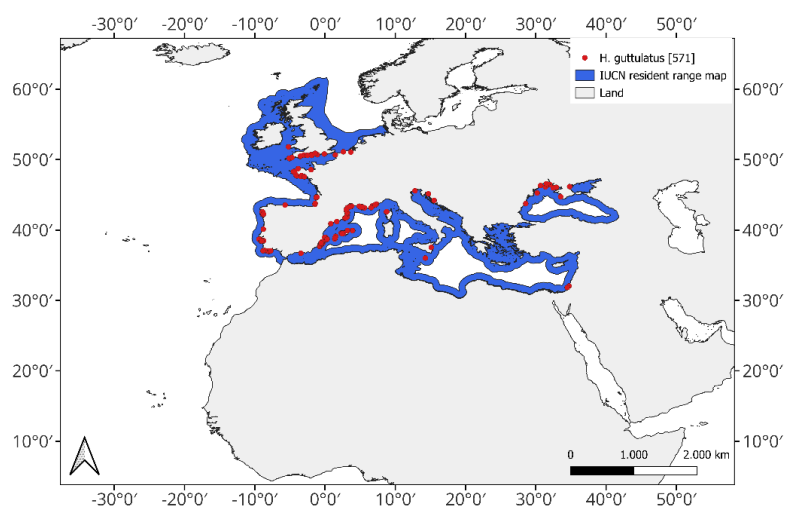


Figure A 2.1. Occurrence points of *H. guttulatus* from the years 2000-2022 used in the Ensemble Model as presence data and the IUCN resident range map as a polygon vector layer (Pollom, 2017a).

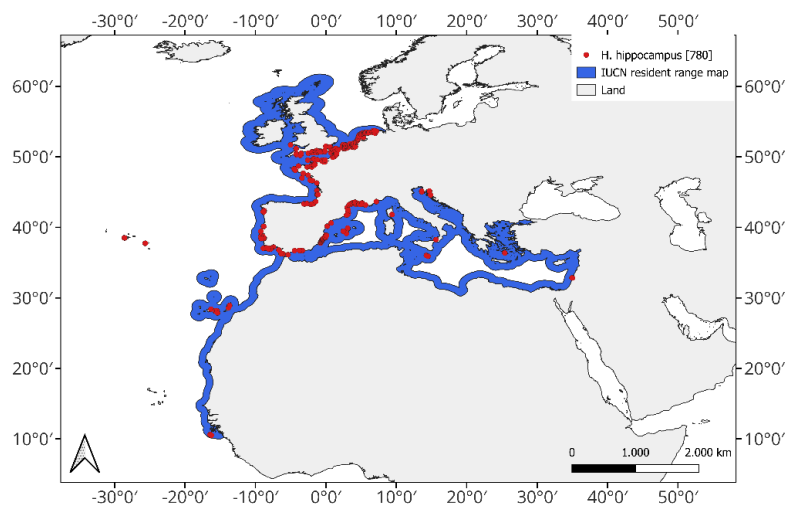


Figure A 2.2. Occurrence points of *H. hippocampus* from the years 2000-2022 used in the Ensemble Model as presence data and the IUCN resident range map as a polygon vector layer (Woodall, 2017a).

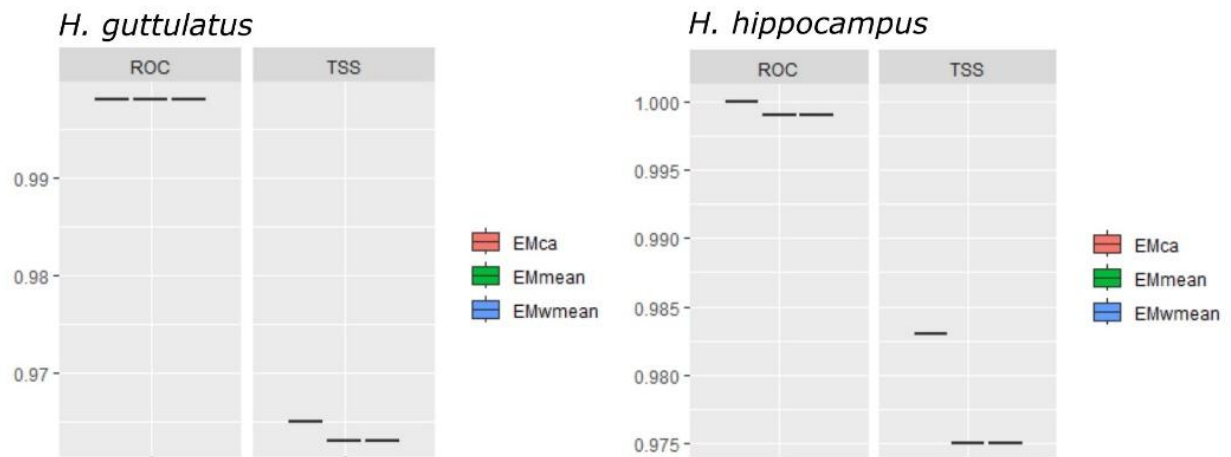


Figure A 2.3. Evaluation metrics of the Ensemble models for *Hippocampus guttulatus* and *H. hippocampus*. EMca = Ensemble model community average; EMmean = Ensemble model mean; EMwmean = Ensemble model weighted mean.

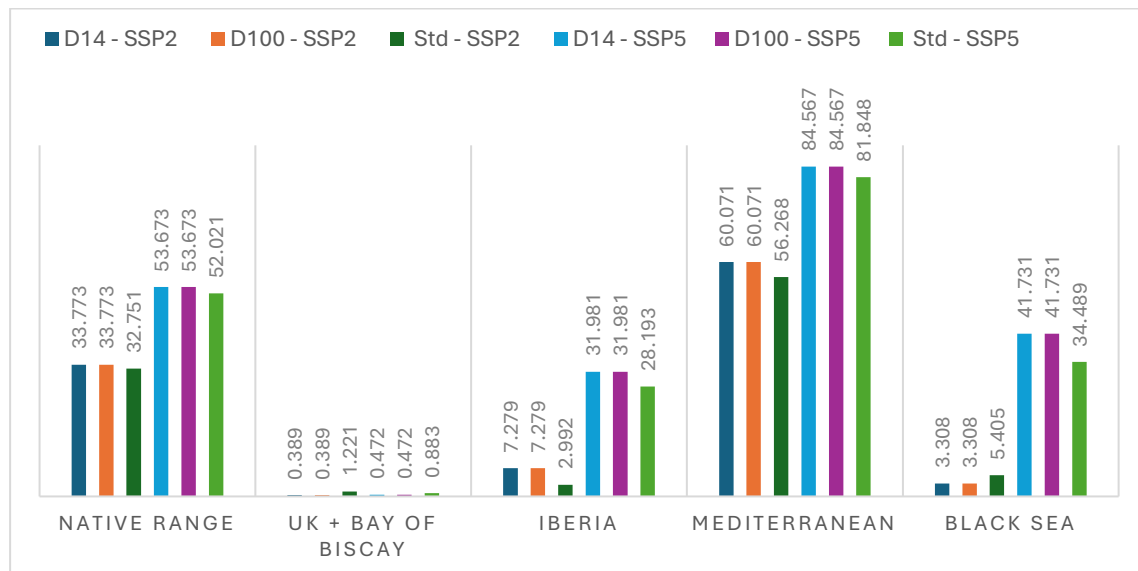


Figure A 2.4. Percentage of loss in suitable habitat for *H. guttulatus* calculated as the proportion of grid cells predicted as present in the present-day but absent in future projections, based on binary maps. The areas are divided by population units (“Native range”, “UK + Bay of Biscay”, “Iberia”, “Mediterranean”, “Black Sea”) under two future climate scenarios (SSP2 and SSP5) for unlimited dispersal according to the standard model (“Std”) and for restricted dispersal due to connectivity for 14 Days (“D14”, “D100”).

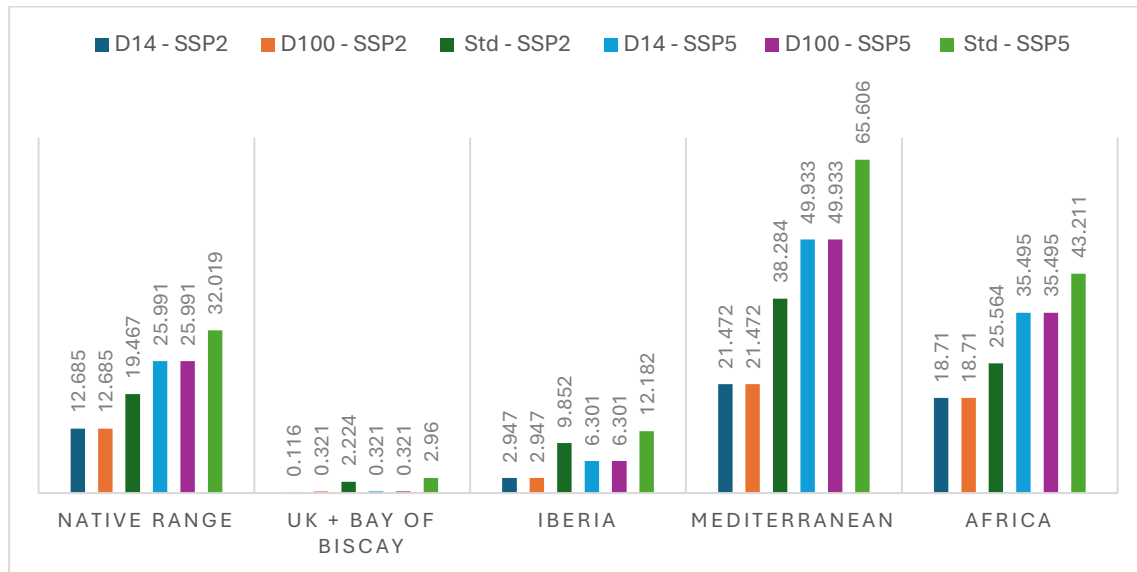


Figure A 2.5. Percentage of loss in suitable habitat for *H. hippocampus* calculated as the proportion of grid cells predicted as present in the present-day but absent in future projections, based on binary maps. The areas are divided by population units (“Native range”, “UK + Bay of Biscay”, “Iberia”, “Mediterranean”, “Black Sea”) under two future climate scenarios (SSP2 and SSP5) for unlimited dispersal according to the standard model (“Std”) and for restricted dispersal due to connectivity for 14 Days and 100 Days (“D14”, “D100”).

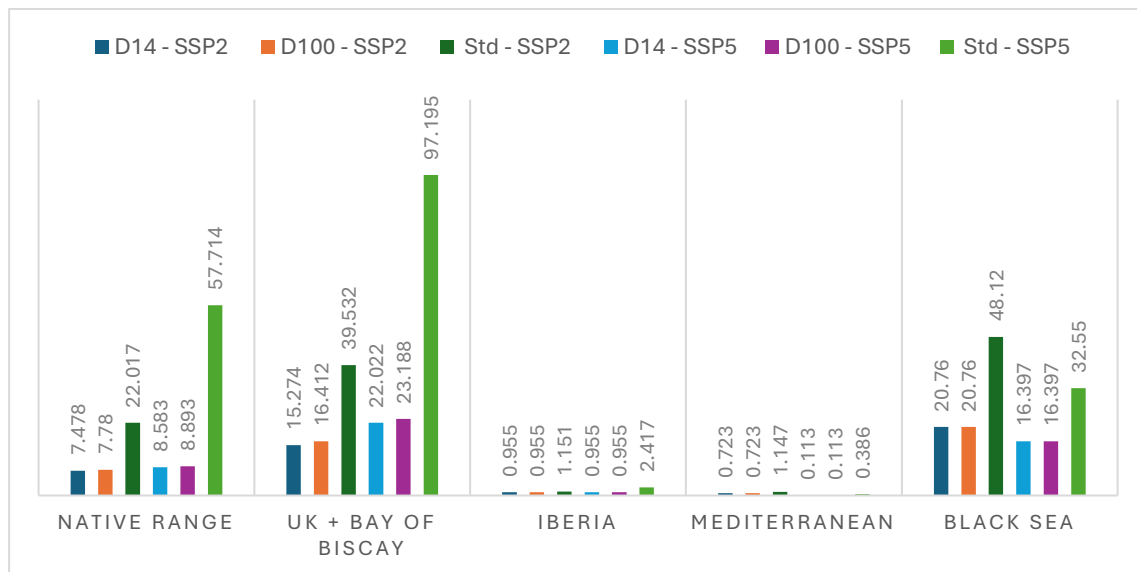


Figure A 2.6. Percentage of gain in suitable habitat for *H. guttulatus* calculated as the proportion of grid cells absent in the present but predicted as suitable in future projections, based on TSS-selected binary maps. The areas are divided by population units (“Native range”, “UK + Bay of Biscay”, “Iberia”, “Mediterranean”, “Black Sea”) under two future climate scenarios (SSP2 and SSP5) for unlimited dispersal according to the standard model (“Std”) and for restricted dispersal due to connectivity for 14 Days and 100 Days (“D14”, “D100”).

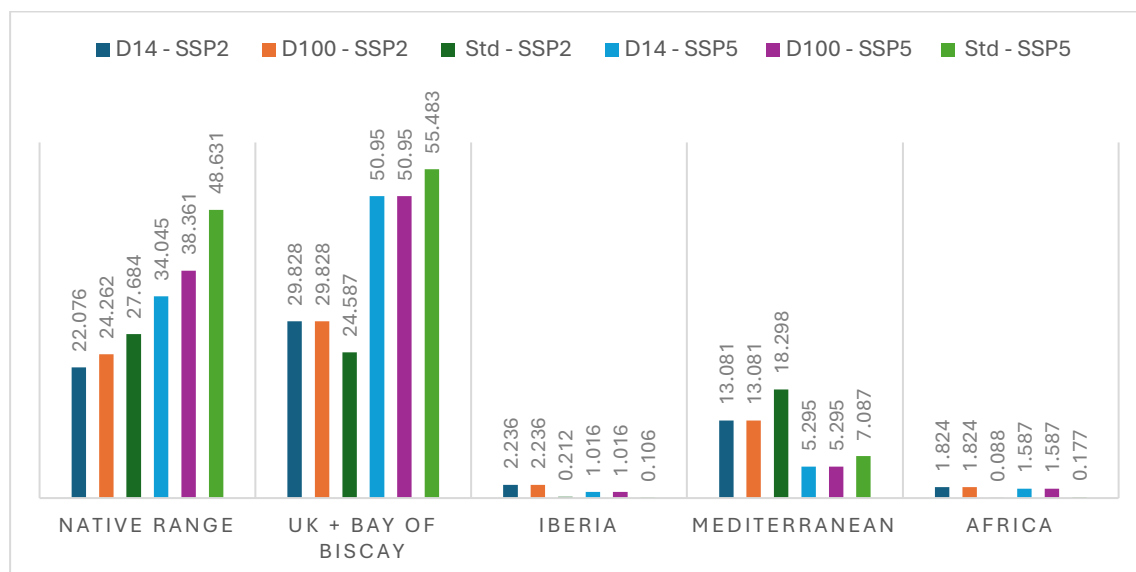


Figure A 2.7. Percentage of gain in suitable habitat for *H. hippocampus* calculated as the proportion of grid cells absent in the present but predicted as suitable in future projections, based on binary maps. The areas are divided by population units (“Native range”, “UK + Bay of Biscay”, “Iberia”, “Mediterranean”, “Black Sea”) under two future climate scenarios (SSP2 and SSP5) for unlimited dispersal according to the standard model (“Std”) and for restricted dispersal due to connectivity for 14 Days and 100 Days (“D14”, “D100”).

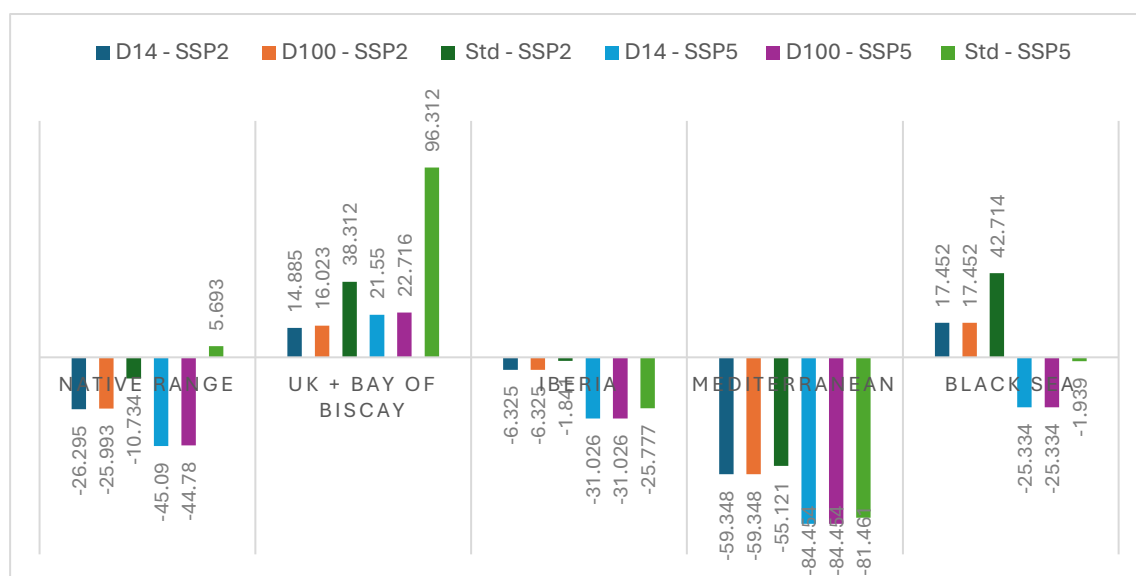


Figure A 2.8. Expansions (+%) and contractions (-%) in the distribution range of *H. guttulatus* expressed as overall change in suitable habitat area. The areas are divided by population units (“Native range”, “UK + Bay of Biscay”, “Iberia”, “Mediterranean”, “Black Sea”) under two future climate scenarios (SSP2 and SSP5) for unlimited dispersal according to the standard model (“Std”) and for restricted dispersal due to connectivity for 14 Days and 100 Days (“D14”, “D100”).

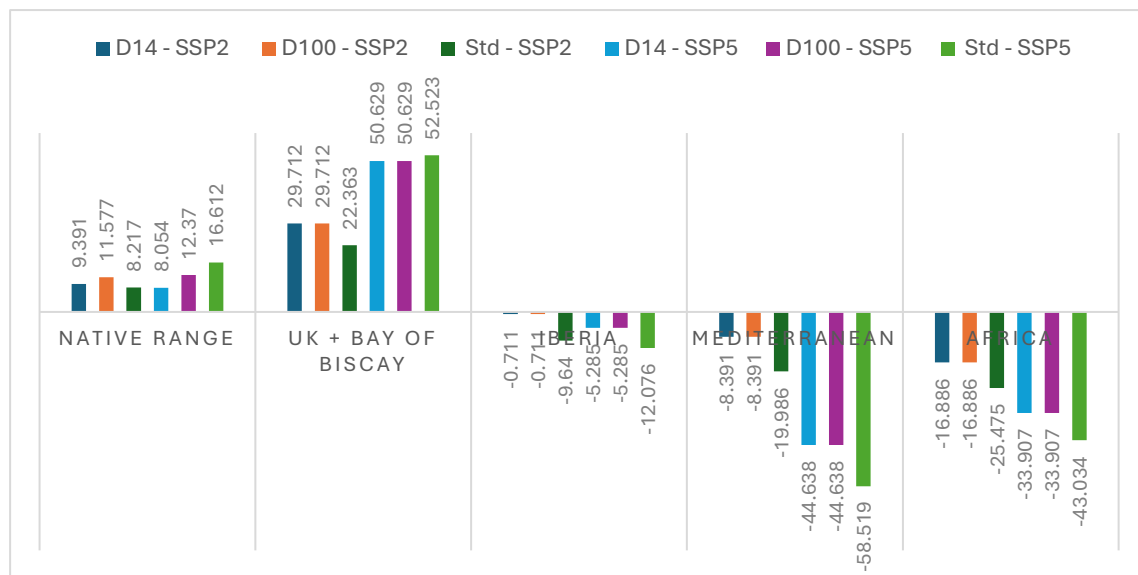


Figure A 2.9. Expansions (+%) and contractions (-%) in the distribution range of *H. hippocampus* expressed as overall change in suitable habitat area. The areas are divided by population units (“Native range”, “UK + Bay of Biscay”, “Iberia”, “Mediterranean”, “Black Sea”) under two future climate scenarios (SSP2 and SSP5) for unlimited dispersal according to the standard model (“Std”) and for restricted dispersal due to connectivity for 14 Days and 100 Days (“D14”, “D100”).

References

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- Woodall, (2017). *Hippocampus hippocampus*. *The IUCN Red List of Threatened Species 2017: e.T10069A67618259*. <https://www.iucnredlist.org/species/10069/67618259>

APPENDIX 3 - Supplementary Material of Chapter 4

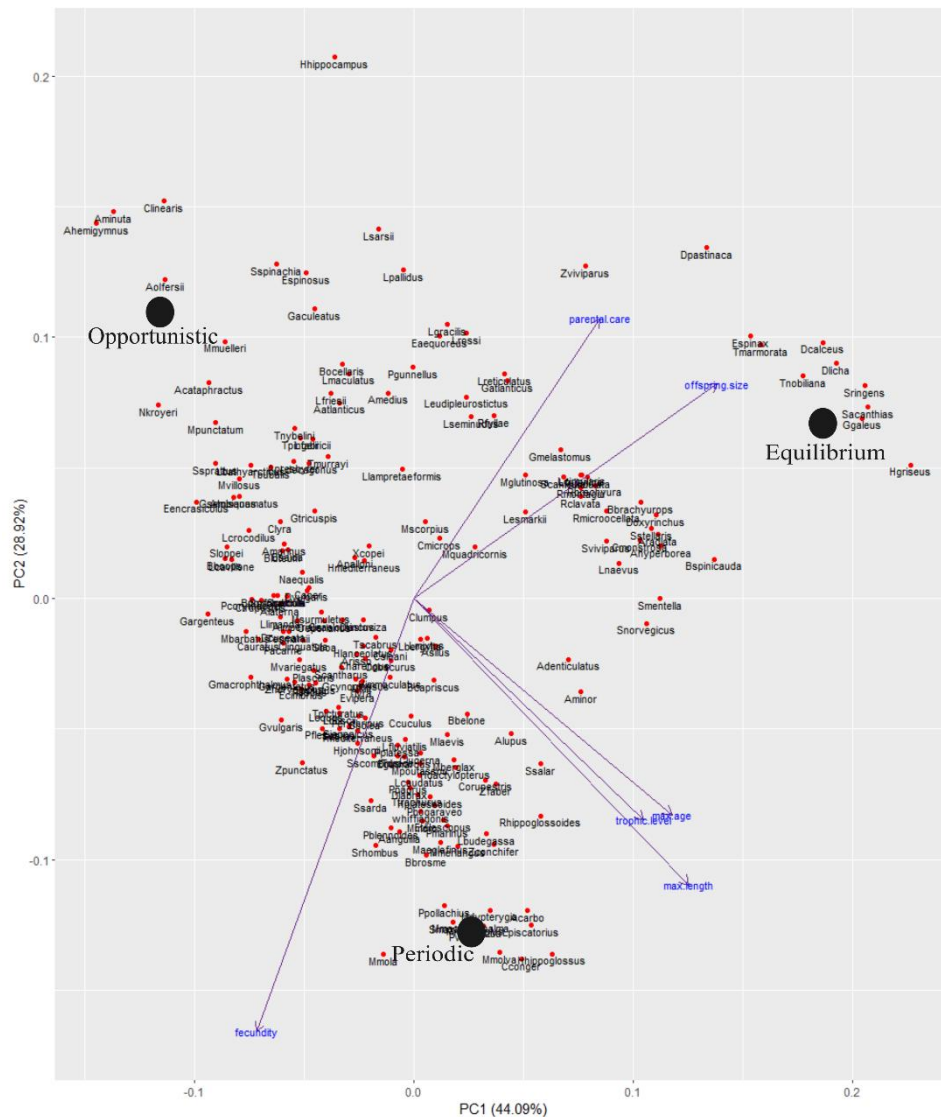
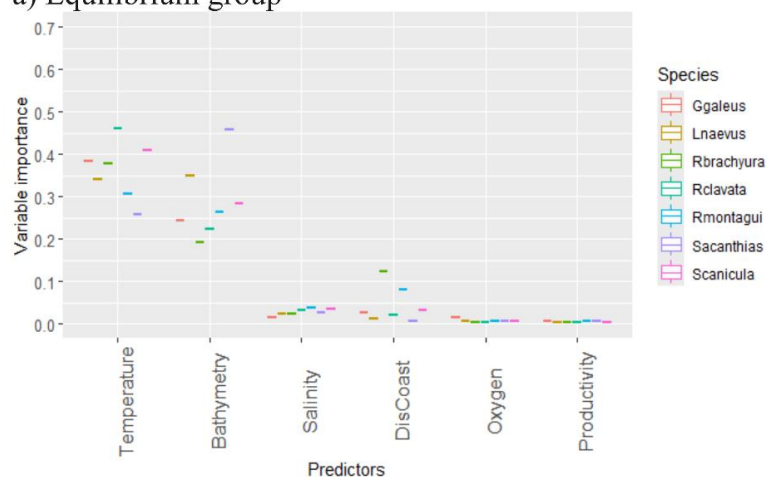


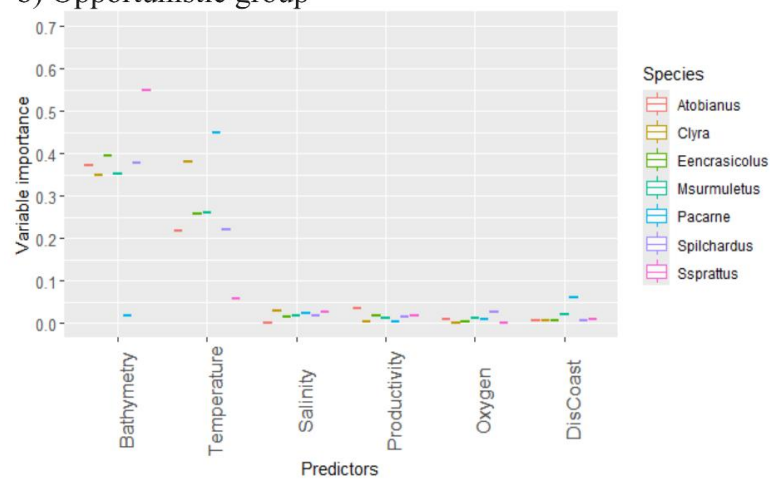
Figure A 3.1 Plot of the first and second principal components (PC1 and PC2) based on a principal component analysis (PCA) on the six selected traits. The three extreme points (archetypes) that encompass the trait-space are represented by black dots, corresponding to the equilibrium, opportunistic and archetypic strategies, respectively.

APPENDICES

a) Equilibrium group



b) Opportunistic group



c) Periodic group

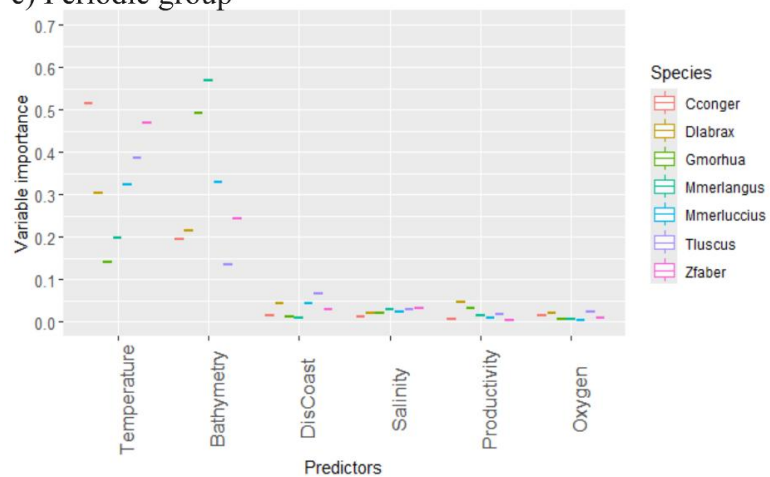


Figure A 3.2. Variable importance of the predictors used in the SDMs for each species separately divided by the three life-history strategy groups.

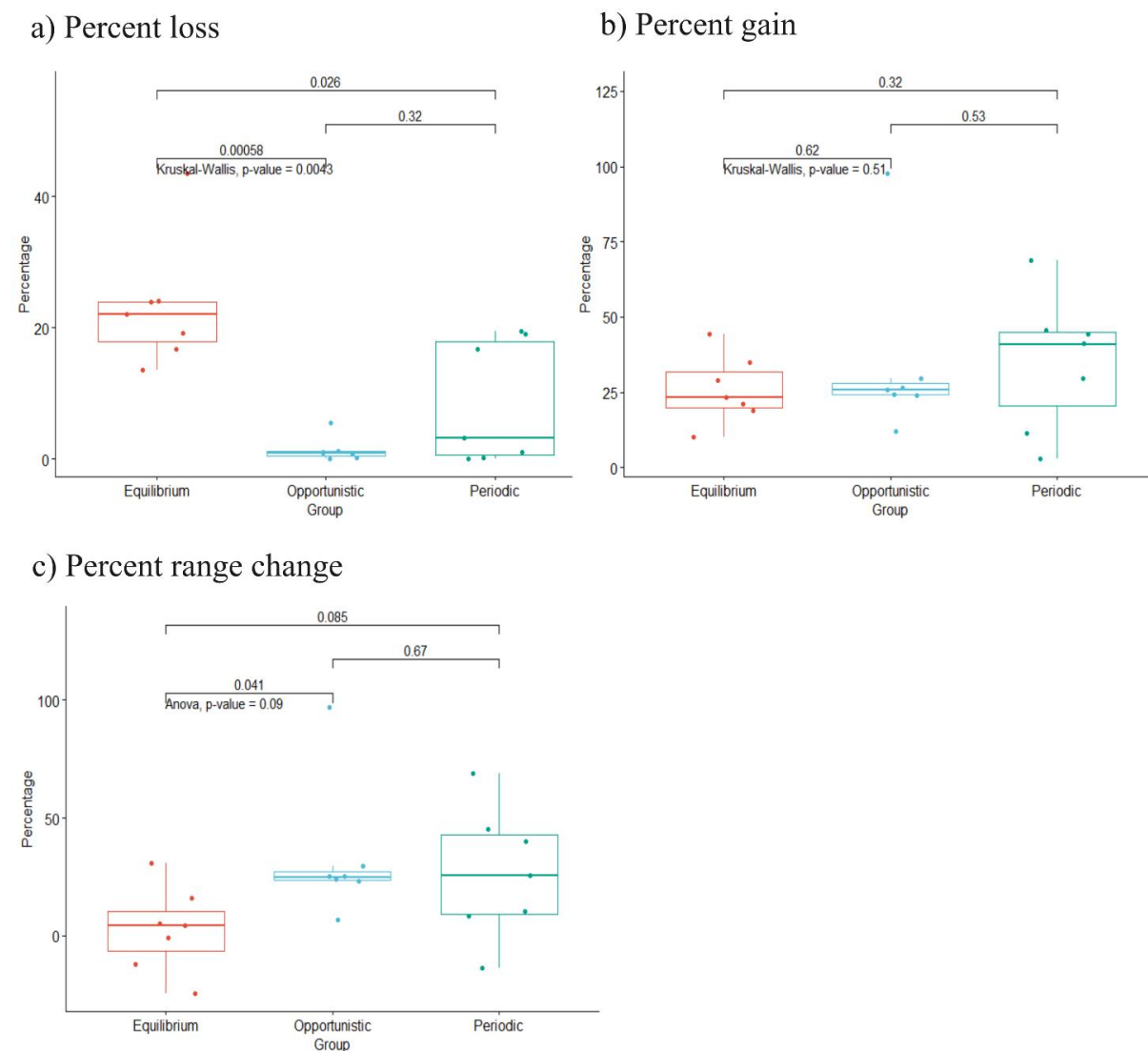


Figure A 3.3. Statistical differences between groups for percentage of gain, losses, and range change. Data distribution was checked by the Shapiro test. The data on loss and gain were not normally distributed. Statistical differences in these factors were determined with a non-parametric test (Kruskal-Wallis test and Wilcox test) while the factor percent range change was tested with an ANOVA and a t-test.

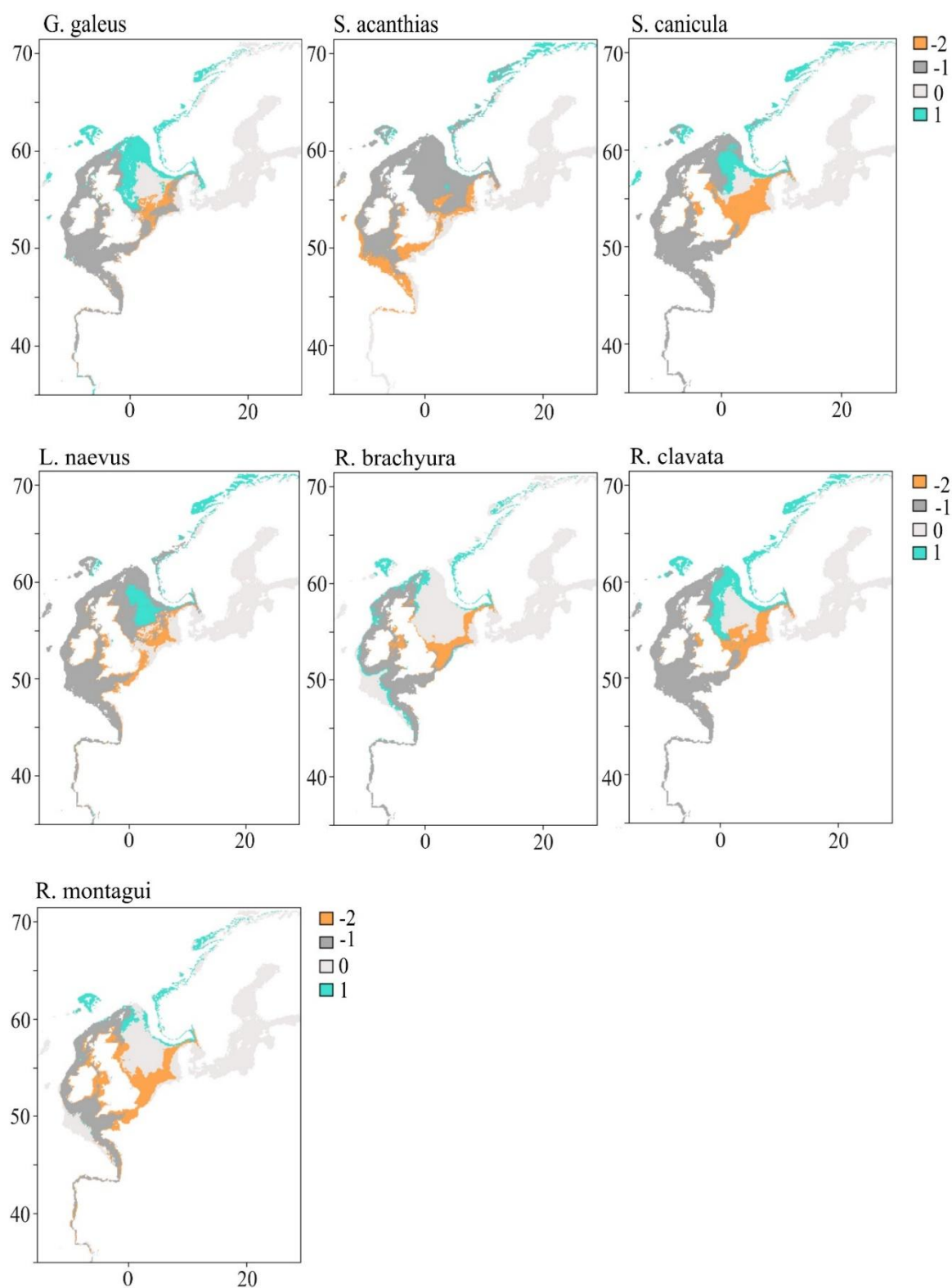


Figure A 3.4. Differences in habitat between present (2000-2020) and future (2090-2100). Maps of losses (-2), gains (1) of habitat; and stable absent (0) and stable present (1) habitat for each species in the Equilibrium group.

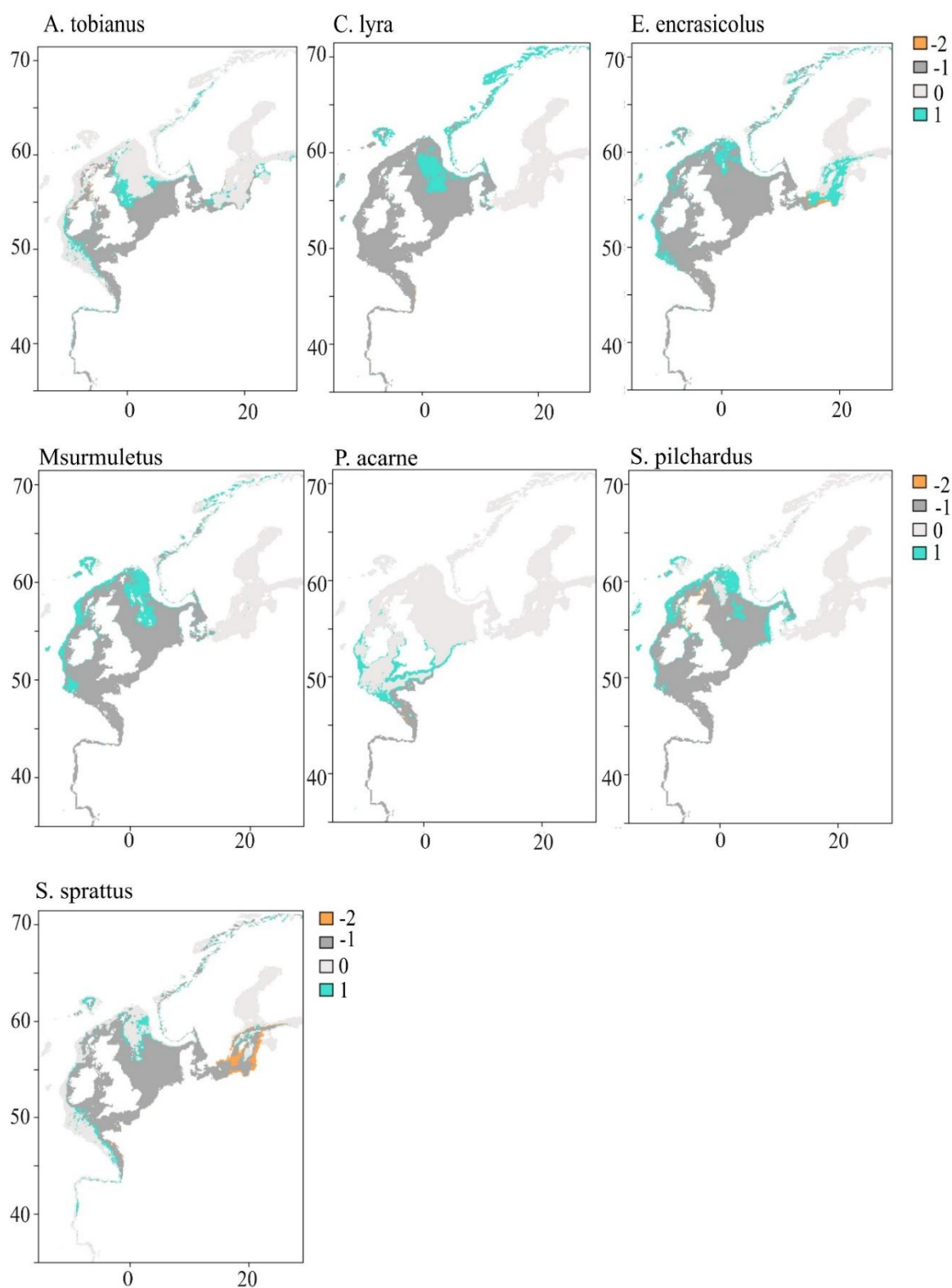


Figure A 3.5. Differences in habitat between present (2000-2020) and future (2090-2100). Maps of losses (-2), gains (1) of habitat; and stable absent (0) and stable present (1) habitat for each species in the Opportunistic group.

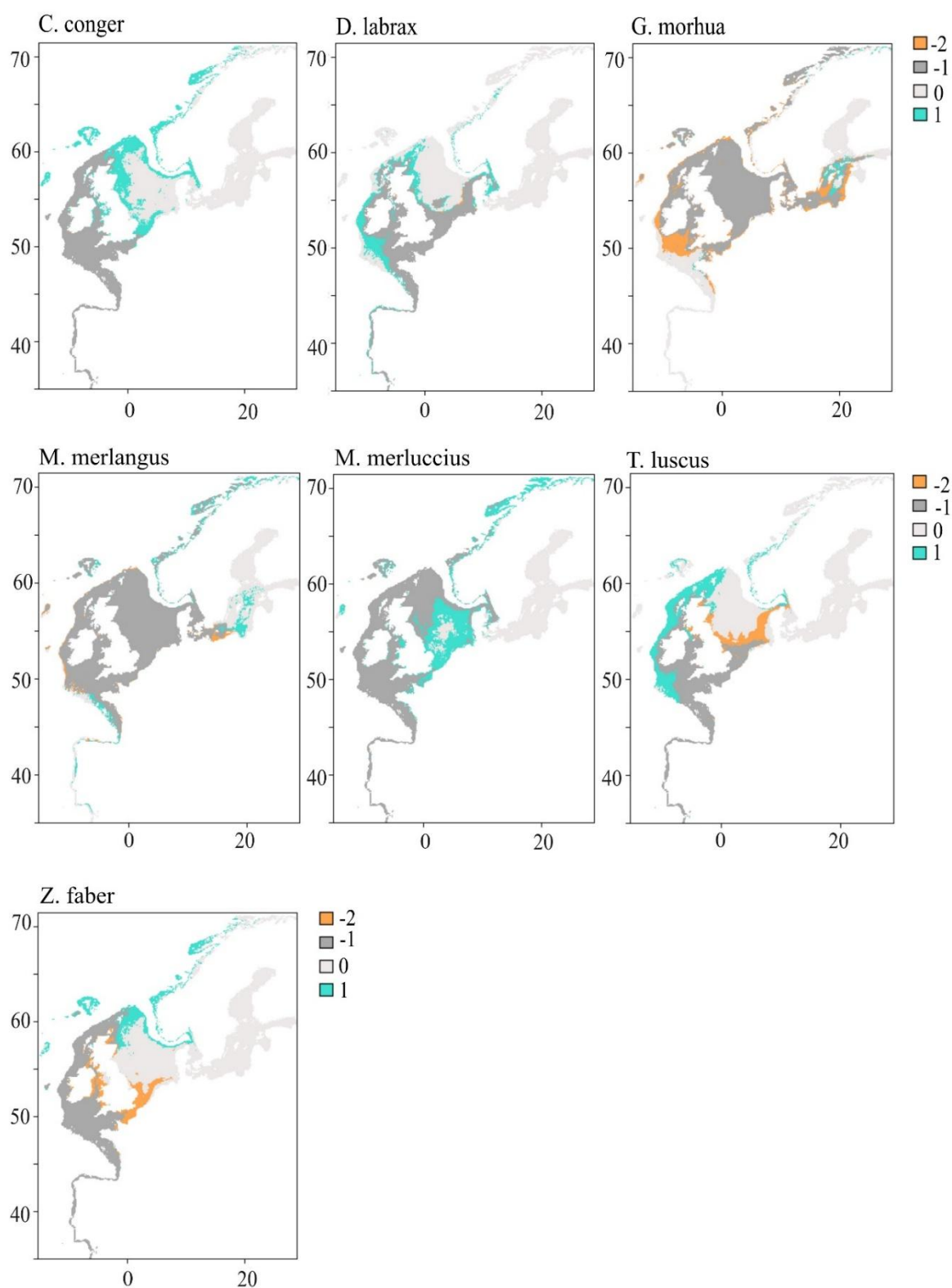
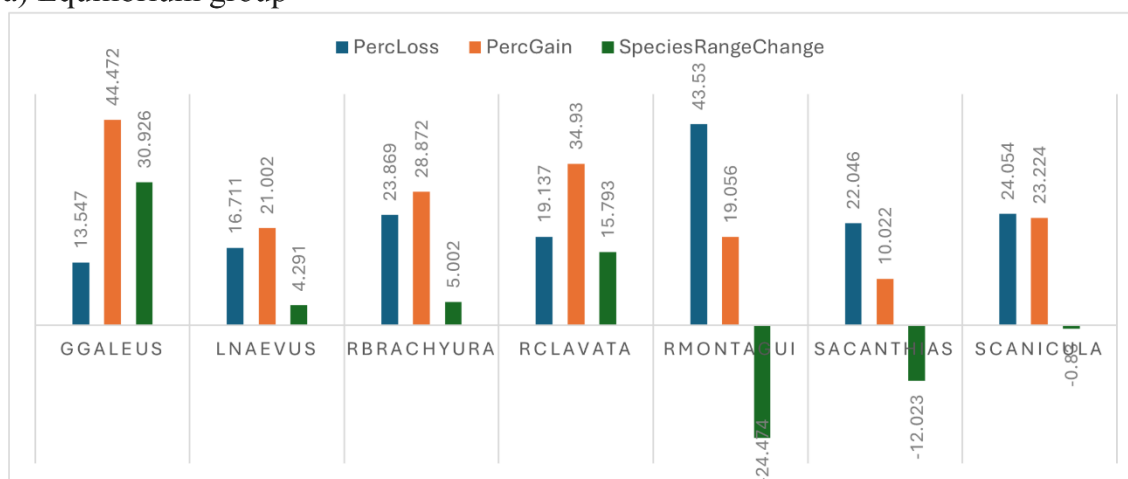
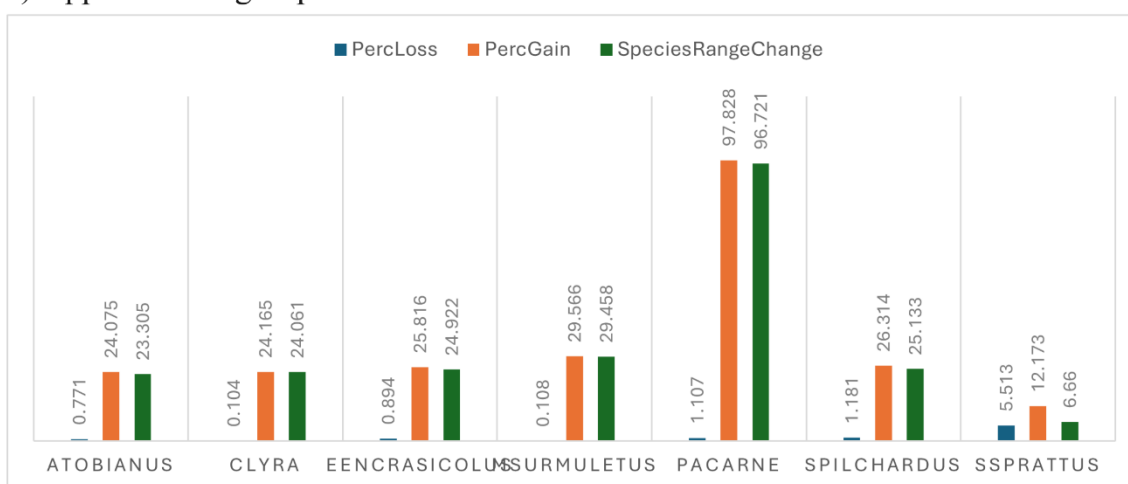


Figure A 3.6. Differences in habitat between present (2000-2020) and future (2090-2100). Maps of losses (-2), gains (1) of habitat; and stable absent (0) and stable present (1) habitat for each species in the Periodic group.

a) Equilibrium group



b) Opportunistic group



c) Periodic group

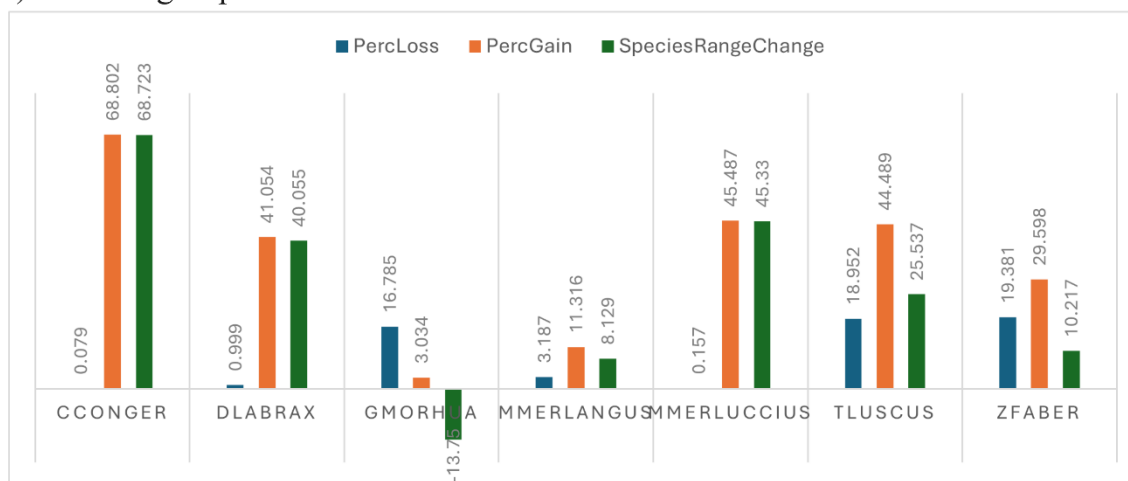


Figure A 3.7. Percentage of gain, loss, and range change of habitat for each species in the respective life-history strategy group

APPENDIX 4 - Supplementary Material of Chapter 5

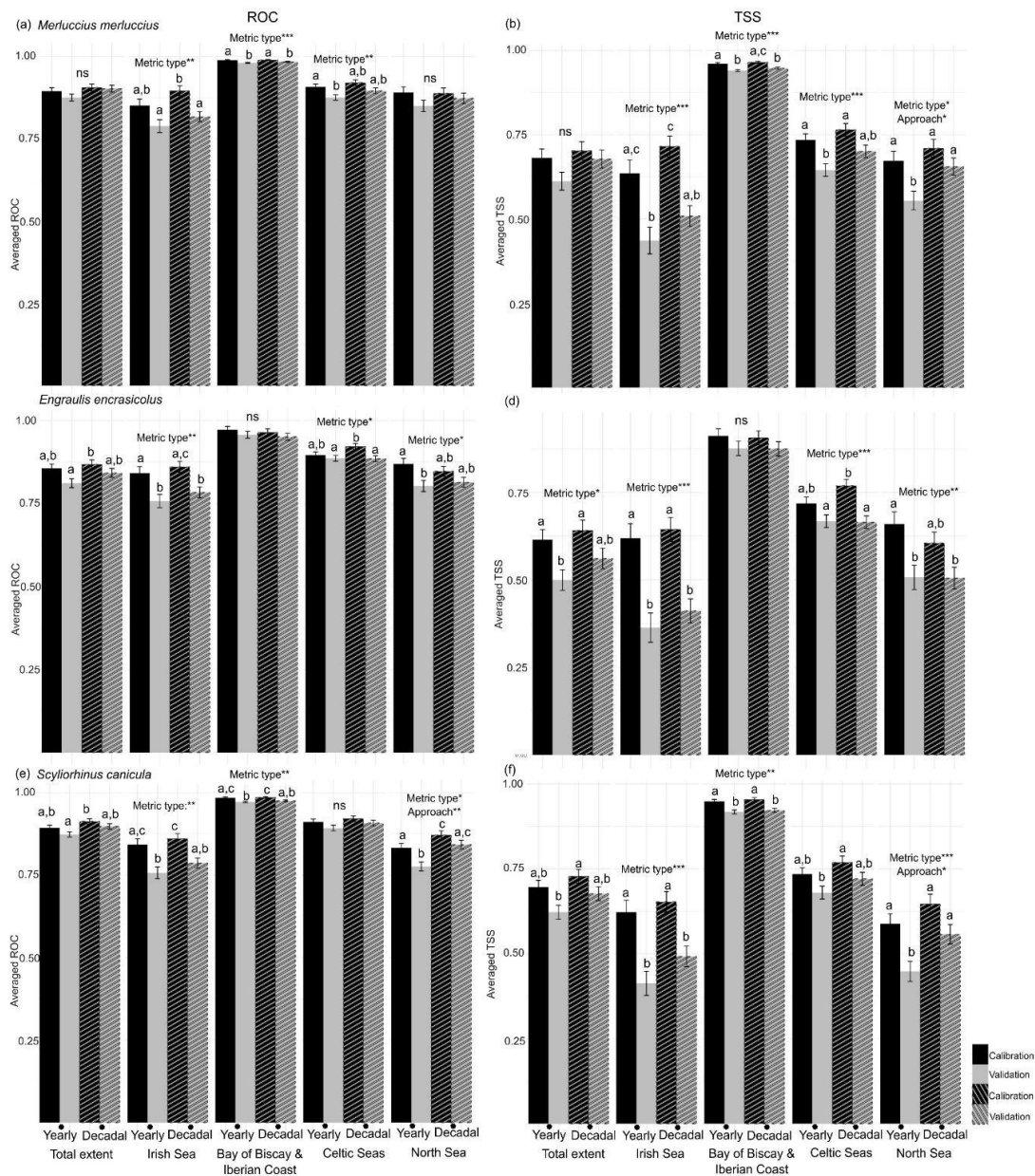


Figure A 4.1. Yearly and decadal-trained model performances based on ROC and TSS evaluation metrics compared as a function of the interaction between metric types (i.e. calibration vs. validation) and temporal training approaches (i.e. yearly vs. decadal) within different spatial extents for a, b) *Merluccius merluccius*, c, d) *Engraulis encrasicolus* and e, f) *Scyliorhinus canicula*. GLM: metric values ~ metric type * temporal training approach. Error bars indicate standard errors. Different lowercase letters indicate statistically significant differences between metric type and temporal training approaches for each species.

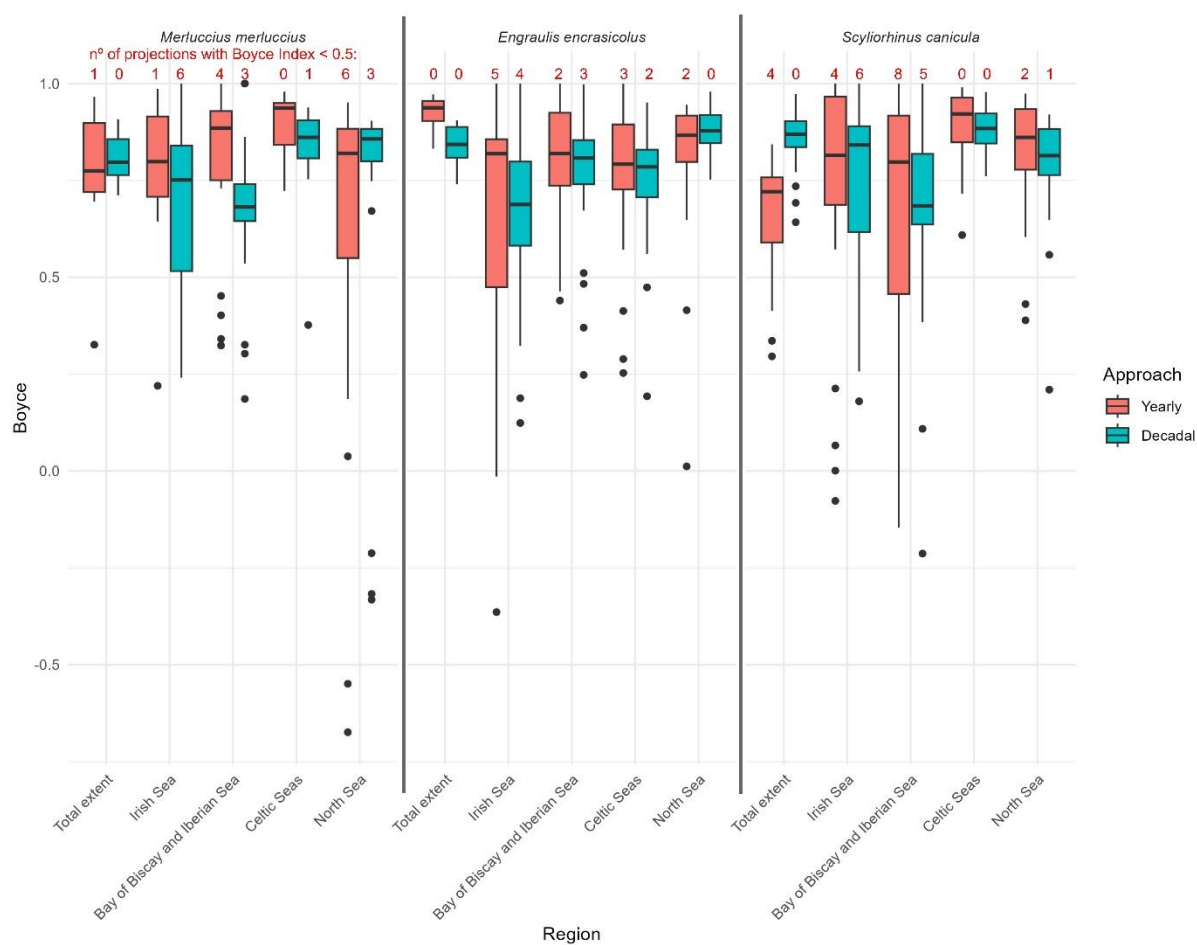


Figure A 4.2. Boxplot showing the variability in Boyce Index values across spatial extents and temporal training approaches for *Merluccius merluccius*, *Engraulis encrasicolus* and *Scyliorhinus canicula*. The number of poorly performing projections (i.e., BI < 0.5), often appearing as outliers, is depicted in red numbers on top of the bars.

APPENDICES

Table A 4.1. Variation in proportion of presence points (true positives) and pseudo-absence points (false positives) predicted within hotspot areas between yearly vs. decadal trained models at different extents for each species (*Merluccius merluccius*, *Engraulis encrasicolus* and *Scyliorhinus canicula*).

Species	Region	Proportion of presences within hotspots			Proportion of pseudo-absences within hotspots		
		Yearly	Decadal	Difference	Yearly	Decadal	Difference
<i>Merluccius merluccius</i>	Total extent	83.27	92.06	-8.79	14.45	10.46	3.99
	Irish Sea	80.81	80.81	0.00	24.71	11.77	12.94
	Bay of Biscay & Iberian	99.91	99.72	0.18	3.66	3.09	0.56
	Celtic Seas	90.10	95.36	-5.26	19.29	16.03	3.26
	North Sea	75.97	89.49	-13.52	14.82	8.37	6.45
<i>Engraulis encrasicolus</i>	Total extent	76.57	85.75	-9.19	19.75	15.76	3.99
	Irish Sea	78.40	83.20	-4.80	28.21	17.09	11.11
	Bay of Biscay & Iberian	98.50	99.36	-0.86	6.93	4.76	2.17
	Celtic Seas	83.44	86.36	-2.92	15.46	9.87	5.59
	North Sea	77.72	84.17	-6.45	23.31	17.58	5.73
<i>Scyliorhinus canicula</i>	Total extent	83.16	89.40	-6.25	17.68	14.84	2.84
	Irish Sea	79.00	75.50	3.50	20.23	13.30	6.94
	Bay of Biscay & Iberian	99.67	99.78	-0.11	4.49	3.82	0.67
	Celtic Seas	85.65	94.87	-9.22	14.68	14.09	0.59
	North Sea	68.84	77.49	-8.65	13.83	10.81	3.02

Table A 4.2. Variation in the proportion of presence points (true positives) and pseudo-absence points (false positives) predicted within hotspots between local/regional trained models and cropped Total extent trained models for each of the temporal approaches for the three species *Merluccius merluccius*, *Engraulis encrasicolus*, and *Scyliorhinus canicula*.

Species	Region	Proportion of presence points within hotspots						Proportion of pseudo-absence points within hotspots					
		Yearly projections			Decadal projections			Yearly projections			Decadal projections		
		Regional	Cropped	Difference	Regional	Cropped	Difference	Regional	Cropped	Difference	Regional	Cropped	Difference
<i>Merluccius merluccius</i>	Irish Sea	80.81	66.67	14.14	80.81	83.84	-3.03	24.71	22.35	2.35	11.77	14.12	-2.35
	Bay of Biscay & Iberia	99.91	98.71	1.20	99.72	99.54	0.19	3.66	4.03	-0.38	3.09	3.47	-0.38
	Celtic Seas	90.10	88.12	1.98	95.36	95.15	0.20	19.29	22.69	-3.40	16.03	17.42	-1.39
	North Sea	75.97	61.67	14.30	89.49	80.55	8.95	14.82	13.00	1.82	8.37	7.56	0.81
	Irish Sea	78.40	92.80	-14.40	83.20	99.20	-16.00	28.21	61.54	-33.33	17.09	41.88	-24.79
<i>Engraulis encrasicolus</i>	Bay of Biscay & Iberia	98.50	98.28	0.22	99.36	98.93	0.43	6.93	7.79	-0.87	4.76	7.79	-3.03
	Celtic Seas	83.44	54.87	28.57	86.36	71.43	14.94	15.46	6.58	8.88	9.87	4.93	4.93
	North Sea	77.72	72.47	5.25	84.17	83.20	0.98	23.31	23.39	-0.08	17.58	18.84	-1.26
	Irish Sea	79.00	88.00	-9.00	75.50	95.50	-20.00	20.23	47.98	-27.75	13.30	50.29	-36.99
	Bay of Biscay & Iberia	99.67	99.33	0.33	99.78	99.67	0.11	4.49	4.60	-0.11	3.82	3.59	0.23
<i>Scyliorhinus canicula</i>	Celtic Seas	85.65	87.32	-1.67	94.87	96.31	-1.44	14.68	21.05	-6.38	14.09	18.36	-4.27
	North Sea	68.84	62.05	6.79	77.49	68.56	8.93	13.83	18.31	-4.48	10.81	12.76	-1.95

APPENDIX 5 - Public outreach and other achievements

Projects and Expeditions

I was part of the scientific field research team of the project “CavALMar - Avaliação populacional das espécies de cavalos-marinhos na frente ribeirinha do concelho de Almada” (Silva et al. 2023). I reviewed the IUCN status assessment of *Hippocampus hippocampus* and *Hippocampus guttulatus* for the “Livro Vermelho dos Peixes Marinhos de Portugal”, and I reviewed an article on seahorses in the Black Sea for the journal *Marine Biodiversity*. Furthermore, I co-led the Baited Remote Underwater Video (BRUV) surveys for the benthic environment on the expedition “Expedição Oceano Azul - Cascais | Mafra | Sintra” (Cabral et al., 2023). The results of this survey, among others, were used as baseline information for the potential designation and implementation of a community-based MPA; however, discussions are still in the process.

Oral Presentations

Peiffer, F., Lima, A. R. A., Henriques, S., Pardal, M. A., Martinho, F., Gonçalves, J.M.S., Gonçalves, Correia, M. & Silva, G. J. F. (2023, November 22–25). Identifying habitat suitability of two flagship species, *Hippocampus hippocampus* and *Hippocampus guttulatus*, for conservation benefits [Oral presentation]. 22º Encontro Nacional de Ecologia, Universidade do Algarve, Faro, Portugal. <https://www.speco.pt/22ene/22ene-resumos>

Peiffer, F., Lima, A. R. A., Henriques, S., Pardal, M. A., Martinho, F., Gonçalves, J.M.S., Gonçalves, E. J., Assis, J., Correia, M. & Silva, G. J. F. (2024, October 13–18). Current and future habitat suitability of two European flagship species, *Hippocampus hippocampus* and *Hippocampus guttulatus* - implications for conservation [Oral presentation]. 7th International Marine Conservation Congress (IMCC7), Cape Town, South Africa. <https://scbmarineprogram.org/meetings-imcc7/>

APPENDICES

Table A 5.1. Table of articles that report on the results of the article in Chapter 2.

SIC Notícias	https://sicnoticias.pt/mundo/2024-06-04-areas-marinhas-protegidas-na-peninsula-iberica-nao-sao-suficientes-para-proteger-cavalos-marinhos-b0a873ff
Postal	https://postal.pt/sociedade/investigadores-alertam-para-insuficiente-protecao-dos-cavalos-marinhos-em-portugal-e-espanha/
Greensavers	https://greensavers.sapo.pt/areas-marinhas-protegidas-em-portugal-e-espanha-nao-sao-suficientes-para-proteger-os-cavalos-marinhos/
Público	https://www.publico.pt/2024/06/04/azul/noticia/proteccao-cavalosmarinhos-portugal-insuficiente-alertam-investigadores-2092863
Notícias ao Minuto	https://www.noticiasao minuto.com/pais/2574173/investigadores-alertam-para-insuficiente-protecao-dos-cavalos-marinhos
RTP Online	https://www.rtp.pt/noticias/pais/investigadores-alertam-para-insuficiente-protecao-dos-cavalos-marinhos_n1576750
Renascença	https://rr.sapo.pt/noticia/pais/2024/06/04/investigadores-alertam-para-insuficiente-protecao-dos-cavalos-marinhos/381095/
Wilder	https://www.wilder.pt/historias/investigadores-alertam-areas-marinhas-protegidas-precisam-de-fazer-mais-para-proteger-cavalos-marinhos
Portal Ambiente Online	https://www.ambienteonline.pt/noticias/areas-marinhas-protegidas-na-peninsula-iberica-nao-sao-suficientes-para-proteger-os-cavalos-marinhos
Sul Informação ENG	https://www.sulinformacao.pt/en/2024/06/investigadores-alertam-para-insuficiente-protecao-dos-cavalos-marinhos/
Sul Informação PT	https://www.sulinformacao.pt/2024/06/investigadores-alertam-para-insuficiente-protecao-dos-cavalos-marinhos/
Estrategizando	https://estrategizando.pt/noticia/areas-marinhas-protegidas-em-portugal-e-espanha-nao-sao-suficientes-para-proteger-os-cavalos-marinhos-J100pKrEHq000
Health News	https://healthnews.pt/2024/06/04/investigadores-alertam-para-insuficiente-protecao-dos-cavalos-marinhos/
Barlavento	https://www.barlavento.pt/ambiente/investigadores-alertam-para-insuficiente-protecao-dos-cavalos-marinhos

ATTENTION!

Já viu um **cavalo-marinho** e/ou uma **marinha** na natureza em Portugal continental ou no noroeste da Espanha?



Foto: (c) Emanuel Gonçalves

Participe da nossa pesquisa para ajudar a identificar áreas prioritárias para conservação, com avistamentos entre o ano 2000 e 30.09.22! A pesquisa pode ser preenchida repetidamente! Quem fizer mais contribuições ganha um prémio!

Escaneie o QR Code ou contata: Friederike,
Aluna de doutoramento no
Universidade de Lisboa e MARE-ISPA:
f.peiffer@alunos.fc.ul.pt




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Figure A 5.1. Poster of the citizen science survey which was sent to dive centres across Portugal and Spain. There also exists a Spanish and English version.

Results of the citizen science survey of seahorse/pipefish sightings

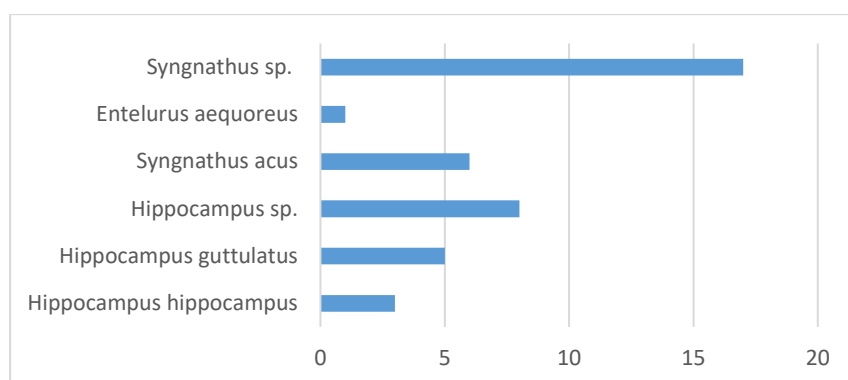


Figure A 5.2. Number of recorded sightings per species (Total N= 40).

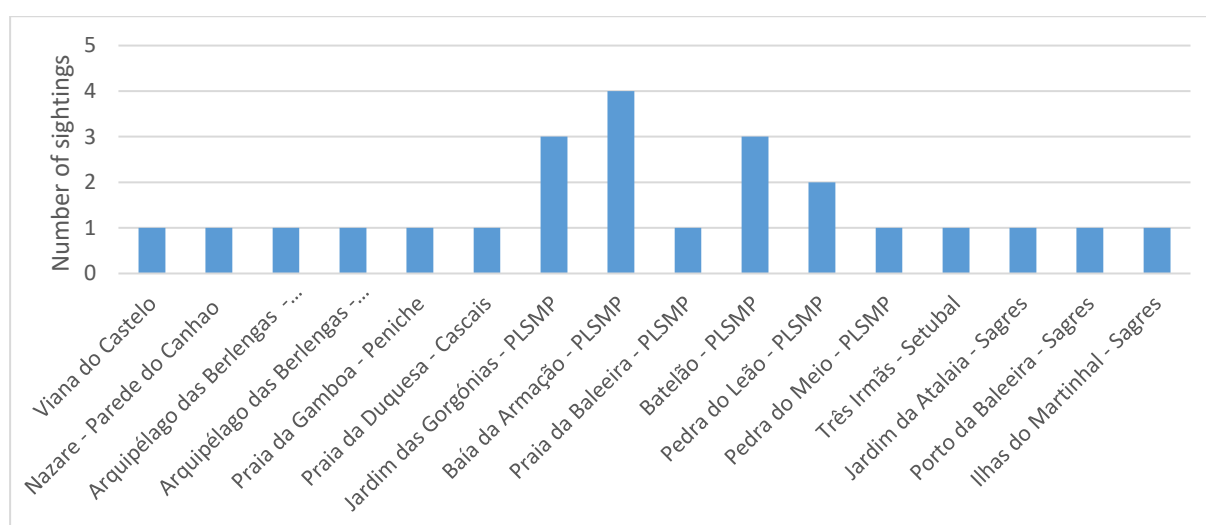


Figure A 5.3. Number of recorded sightings per location for pipefish.

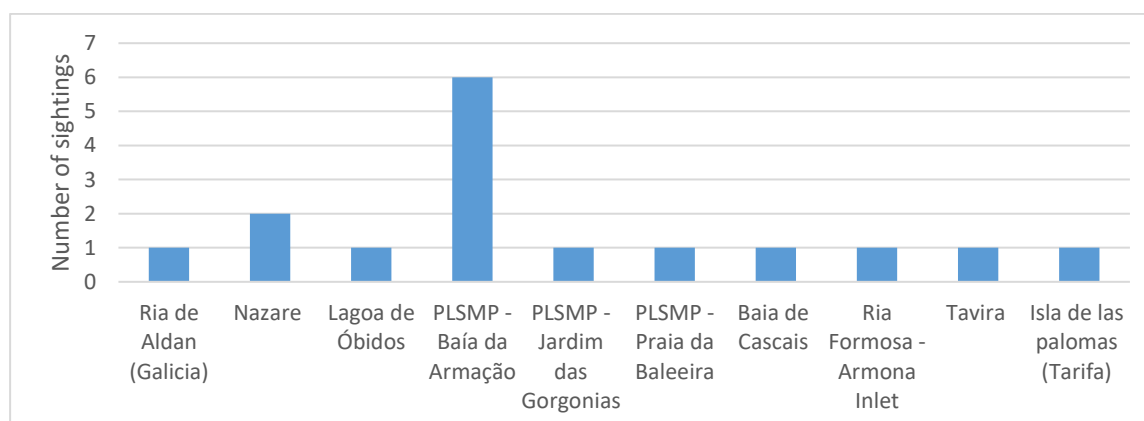


Figure A 5.4. Number of recorded sightings per location for seahorses.

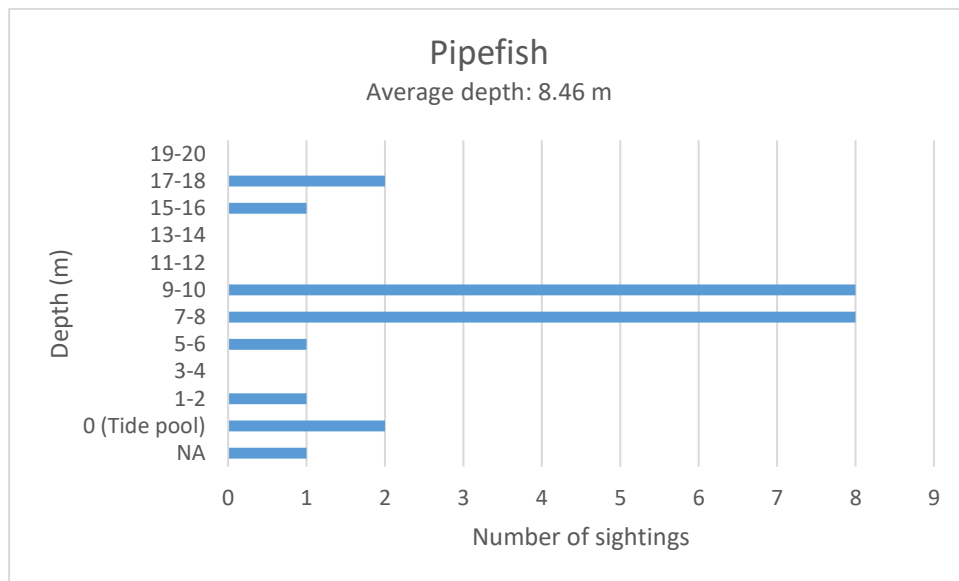


Figure A 5.5 Number of sightings of pipefish recorded for different depth (m) intervals.

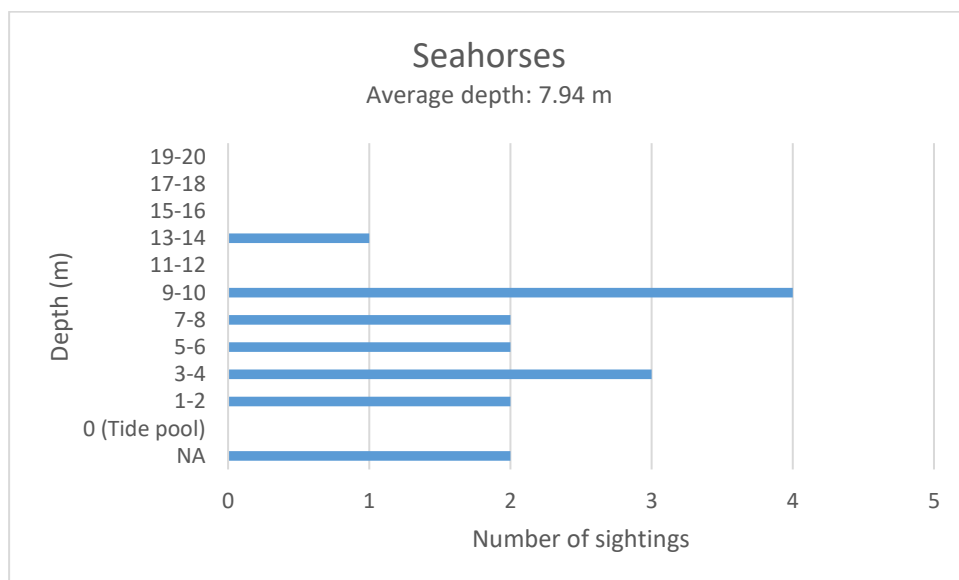


Figure A 5.6. Number of sightings of seahorses recorded for different depth (m) intervals.

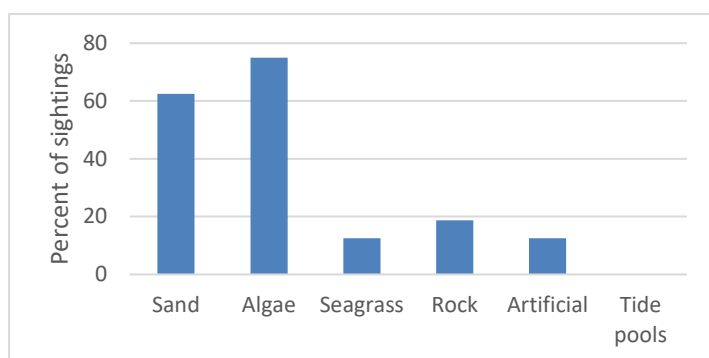


Figure A 5.7. Percentage of sites at which each habitat type was present according to the observer of the citizen science survey.

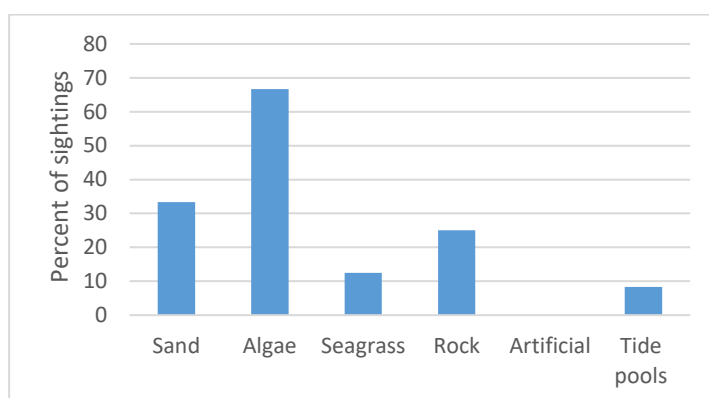


Figure A 5.8. Percentage of sites at which each habitat type was present according to the observer of the citizen science survey.

References

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- Silva, G., Coxey, M., & Correia, M. (2023). CavALMar - Avaliação populacional das espécies de cavalos-marinhos na frente ribeirinha do concelho de Almada. *Relatório Técnico Final*, 1–88.