Marine fish diversity patterns, drivers and underlying processes

Present status and predictions under climate change

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Marine fish diversity patterns, drivers and underlying processes

Present status and predictions under climate change

By

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Summary

Biodiversity is the variety of life forms, from intraspecific gene diversity, to different species, communities and entire ecosystems. The uniqueness of all life forms grants them an intrinsic value. But, biodiversity also contributes to human wellbeing by providing key goods and services that human societies rely on, such as food production and climate regulation. Nonetheless, biodiversity is declining at an unprecedented rate due to anthropogenic pressures such as climate change and overexploitation. Consequently, we are now facing what could be the sixth mass extinction on Earth since life began over 3.5 billion years ago. Anticipating the effects of climate change (and other anthropogenic activities) on natural ecosystems is therefore essential for taking the necessary management and conservation decisions that seek to preserve biodiversity, and thus human well-being. Part of the decisions that need to be taken shall address the suitable placement of Marine Protected Areas (MPAs) that guarantee the adequate management and conservation of “areas of particular importance for biodiversity” in order to reach the objective of protecting 30% of marine areas by 2030.

In this thesis, I use modeling tools to explore the underlying drivers shaping marine fish communities, train models capable of estimating patterns and trends in fish biodiversity, and assess the efficiency of current MPAs in safeguarding this biodiversity.

I begin by studying the underlying drivers of marine fish communities at two different spatial scales, i.e., regional and continental. At the regional scale, I work with the case study of the North Sea, using the survey data from the North Sea International Bottom Trawl Survey to explore the fish community by modelling the responses of 67 species to environmental drivers and fishing pressure. For the continental scale, I compile data from 13 different surveys from the Northeast Atlantic Ocean, modelling the distribution and specific responses of 151 fish species to environmental change. At both spatial scales, temperature and productivity stand out as the main environmental drivers of fish community composition. Moreover, I identify spatially-structured processes that contribute in explaining the community composition. Based on the continental-scale model, I then explore the time horizon at which different facets of marine fish biodiversity can be reliably predicted. The results highlight that, although there are some differences across metrics, the models allow reliable forecasting of fish biodiversity for (at least) 10-20 years ahead, which is a relevant and reasonable timeframe to consider from a management and conservation perspective. Consequently, I use the validated models to predict different biodiversity indices and explore how they are expected to change during the coming decades. The findings highlight that current MPA network is far from the goal of effectively protecting 30% of marina areas, and that the proportion of protected areas with high biodiversity is low in the Northeast Atlantic Ocean. Lastly, I set up a management and conservation scenario (i.e., MPA optimization) where the aim is to protect 30% of the high biodiversity areas while minimizing the impacts on current fisheries (i.e., fishing effort). The findings indicate that current MPA network is protecting a small percentage of high biodiversity areas, due to the small surface covered by MPAs and a mismatch with high biodiversity areas. The MPA optimization scenario shows a high efficiency towards protecting current and future (2030, 2050) biodiversity, with relatively low and very localized imapcts on fishing effort. The findings highlight that there is room for improving current MPA network, and that maximizing their efficiency will be achieved by a more active engagement of stakeholders.

The presented work significantly enhances our understanding of marine ecology by advancing knowledge on community assembly processes. Additionally, it demonstrates the utility of modeling tools in anticipating the effects of climate change and informing management and conservation actions.

Dansk resumé

Biodiversitet er mangfoldigheden af livsformer, fra intraspecifik genetisk diversitet til forskellige arter, artssamfund og hele økosystemer. Denne diversitet har en helt unik iboende værdi i sig selv. Men biodiversitet bidrager også til menneskelig trivsel ved at levere nøglegoder og -tjenester, som mennesker er afhængige af, såsom fødevareproduktion og klimaregulering. Ikke desto mindre aftager biodiversiteten med en hidtil uset hastighed på grund af antropogene presfaktorer såsom klimaændringer og overudnyttelse. Som følge heraf står vi nu over for, hvad der kunne være den sjette masseuddøen på Jorden, siden livet begyndte for over 3,5 milliarder år siden. At forudse virkningerne af klimaændringer (og andre antropogene aktiviteter) på naturlige økosystemer er derfor afgørende for at træffe de nødvendige forvaltnings- og bevarelsesbeslutninger, der sigter mod at bevare biodiversitet og dermed menneskers velbefindende. En del af de beslutninger, der skal træffes, skal adressere den optimale og passende placering af marine beskyttede områder. Dette skal garanterer en tilstrækkelig forvaltning og bevarelse af "områder af særlig betydning for biodiversitet", med henblik på at nå målet om at beskytte 30% af marine områder inden 2030.

I denne afhandling bruger jeg modelleringsværktøjer til at udforske de underliggende faktorer, der former marine fiskeartssamfund og træne modeller, der er i stand til at estimere mønstre og tendenser i fiskebiodiversitet og vurdere effektiviteten af nuværende marine beskyttede områder i at beskytte denne biodiversitet.

Jeg begynder med at studere de underliggende faktorer for marine fiskeartssamfund på to forskellige rumlige skalaer, dvs. regional og kontinental. På regionalt niveau arbejder jeg med et casestudie fra Nordsøen og bruger data fra den internationale bundtrawlsundersøgelse i Nordsøen til at udforske samfundet af fisk ved at modellere responsen fra 67 arter på miljømæssige faktorer og fisketryk. For den kontinentale skala samler jeg data fra 13 forskellige undersøgelser fra det nordøstlige Atlanterhav og modellerer fordelingen og de specifikke reaktioner fra 151 fiskearter på miljøændringer. På begge rumlige skalaer skiller temperatur og produktivitet sig ud som de vigtigste miljømæssige faktorer for sammensætningen af fiskeartssamfund. Desuden identificerer jeg rumligt strukturerede processer, der bidrager til at forklare artsamfundets sammensætning. Baseret på modellen på kontinental skala udforsker jeg derefter, hvornår forskellige aspekter af marine fiskebiodiversitet pålideligt kan forudsiges. Resultaterne fremhæver, at selvom der er visse forskelle på tværs af målemetoder, tillader modellerne pålidelige forudsigelser af fiskebiodiversitet for (mindst) 10-20 år frem i tiden, hvilket er et relevant og rimeligt tidsinterval at overveje fra et forvaltnings- og bevarelsesperspektiv. Som følge heraf bruger jeg de validerede modeller til at forudsige forskellige biodiversitetsindeks og udforske, hvordan de forventes at ændre sig i løbet af de kommende årtier. Resultaterne fremhæver, at det nuværende marine beskyttede områder er langt fra målet om effektivt at beskytte 30% af marine områder, og at andelen af beskyttede områder med høj biodiversitet er lav i det nordøstlige Atlanterhav. Endelig opretter jeg et scenarie for forvaltning og bevarelse (dvs. optimering af marine beskyttede områder), hvor målet er at beskytte 30% af områder med høj biodiversitet, samtidig med at man minimerer påvirkningerne på nuværende fiskeriindsats. Resultaterne indikerer, at de nuværende marine beskyttede områder kun beskytter en lille procentdel af områder med høj biodiversitet, på grund af den lille overflade dækket af marine beskyttede områder og en uoverensstemmelse med områder med høj biodiversitet. Optimeringsscenarioet viser en høj effektivitet med hensyn til at beskytte nuværende og fremtidig (2030, 2050) biodiversitet, med relativt lave og meget lokale påvirkninger på fiskeriindsatsen. Resultaterne fremhæver, at der er plads til forbedring af de nuværende marine beskyttede områder, og at maksimering af deres effektivitet vil blive opnået ved en mere aktiv inddragelse af interessenter.

Det præsenterede arbejde forbedrer væsentligt vores forståelse af marine økosystemer ved at forbedre vores viden om processer for artssamfundsetablering. Derudover demonstrerer det nytten af modelleringsværktøjer til at forudsige virkningerne af klimaændringer og informere forvaltnings- og bevarelsesarbejde.

Preface

This Ph.D. thesis was prepared at the National Institute of Aquatic Resources at the Technical University of Denmark, in fulfilment of the requirements for acquiring a Doctor degree in Philosophy. The research was carried out from April 2021 until April 2024 at the Centre for Ocean Life, a Villum Foundation Centre of Excellence in Kongens Lyngby, Denmark, under the supervision of Martin Lindegren and Benjamin Weigel. Additionally, one external research stay was carried out at the Institute of Marine Sciences (ICM-CSIC) in collaboration with Marta Coll. This Ph.D. was funded by the European Union's Horizon 2020 project "ECOTIP" (ID: 869383). Additional support for conference participation was received from the Otto Mønsted Foundation, ICES-PICES and ASLO.

Kongens Lyngby, 14th April 2024

Marcel Montanyès Solé

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A PhD is a solitary journey, but I have been fortunate to be surrounded by awesome people that has always been there to hear about my problems but especially to have fun. I have to thank Martin again for bringing such a nice group of young researchers together. Louise, Fernanda, Don Fede and Toni, thank you for being great colleagues, having interesting discussions and sharing your knowledge, but especially thanks for being such nice friends. I also want to thank all the people that I had the pleasure to meet at DTU Aqua: Ale, Alexander, Amalia, Anshul, Caroline, Dani, Daniel, Delove, Federica, Kat, Philip, Satish, Sei, Shana, Thanos, Tøger, and Wendel, you make that a grey, rainy and cold day in the office, becomes a day of fun. I want to give a special thanks to my little Danish family, Alfred, Arnau, Mel, Oriol, and Toni. I cannot imagine Denmark without you. You have filled my heart with endless stories of enjoyment, absurdity and good times.

I have been lucky to have an awesome group of followers from the distance. Thanks to all my friends back in Catalunya for always receiving me with open arms and for preserving our friendship, even when I do not show up for months. I want to especially thank my two guardian angels and counselors, Anaïs and Raimon, for always being there. I also feel lucky to have a family that fully supports my career, even though l'àvia Sunsi is still deeply concerned on whether I am going to find a job. Thanks to Greta, Joan, Martina, Bibi, Laia, Arnau M., Maria, Bep, Ton, Lourdes, Arnau S., Sunsi, and especially to tieta Montserrat and Rosa, unconditional supporters.

Monti, wherever you are, I know you would be proud.

List of publications

This PhD thesis is based on the following publications:

I. **Marcel Montanyès**, Benjamin Weigel, and Martin Lindegren. "Community assembly processes and drivers shaping marine fish community structure in the North Sea." Ecography 2023.10 (2023): e06642. https://doi.org/10.1111/ecog.06642

II. **Marcel Montanyès**, Benjamin Weigel, Federico Maioli, Gleb Tikhonov, Pieter Daniël van Denderen, Otso Ovaskainen, and Martin Lindegren "Assessing the forecast horizon for reliably predicting marine biodiversity change" (in preparation)

III. **Marcel Montanyès**, Benjamin Weigel, Pieter Daniël van Denderen, and Martin Lindegren "Marine biodiversity protection can be improved while minimizing effects on other ocean uses" (in preparation)

The following publications represent minor contributions and were not included in the thesis:

I. Louise Catharina Flensborg, **Marcel Montanyès**, Antoni Vivó-Pons, Fernanda Carolina Da Silva, and Martin Lindegren "Scale-dependent stability in marine ecosystem dynamics across European Seas." (in preparation)

II. Warsha Singh, Kristinn Guðnason, **Marcel Montanyès**, and Martin Lindegren "Climate driven regime shift of the Iceland-East Greenland-Jan Mayen capelin distribution" (under review)

III. Francisco Ramírez, Joan Giménez, **Marcel Montanyès**, Jazel Ouled-Cheikh Bonan, Alba Fuster, Laura Julià, Marta Coll, Maria Bas. "Protecting southern areas of ecological importance for marine predators on the move" (in preparation)

IV. Sigrún Huld Jónasdóttir, Gerardo Alonso Bernáldez, **Marcel Montanyès**, Martin Lindegren "Large-scale patterns and drivers of lipid composition in mesopelagic fish communities" (in preparation)

Conference disseminations:

I. Fourth ICES-PICES Early Career Scientist Conference 2022 – **Marcel Montanyès**, Benjamin Weigel, and Martin Lindegren – Oral presentation
II. ASLO Aquatic Sciences Meeting 2023 – **Marcel Montanyès**, Benjamin Weigel, and Martin Lindegren – Oral presentation
III. ASLO Aquatic Sciences Meeting 2023 – Louise Catharina Flensborg, **Marcel Montanyès**, Antoni Vivó-Pons, Fernanda Carolina Da Silva, and Martin Lindegren – Poster presentation

Contents

Chapter 1

1. General introduction

1.1 Marine biodiversity

1.1.1 Current status and threats

We find ourselves in the Anthropocene, a geological epoch marked by human activities modifying the dynamics of Earth's system (Lewis & Maslin, 2015). Therefore, natural habitats and their biodiversity are exposed to a range of anthropogenic pressures such as climate change, habitat destruction, overfishing, pollution and introduction of non-indigenous species (NIS) (Halpern *et al.*, 2015; Maclean & Wilson, 2011; Millennium Ecosystem Assessment, 2005; Worm & Tittensor, 2011). These impacts have both direct and indirect consequences for the natural ecosystems and the goods and services that they provide (IPBES, 2019; Millennium Ecosystem Assessment, 2005; World Economic Forum, 2020).

In marine habitats, anthropogenic impacts are especially relevant in highly populated coastal areas, where coastlines have been modified to accommodate human activities (e.g., harbors, aquaculture farms, oil extraction platforms, submarine electric installations) (Halpern *et al.*, 2015). Wild-caught and farmed seafood contributes a substantial part of the diet to more than three billion people worldwide, being among the main animal protein source especially in developing countries (Troell *et al.*, 2019). The global fisheries production in 2020 added up to 90.3 million tones, 85% of which correspond to marine finfish captures. The percentage of global fish stocks exploited at unsustainable levels has been increasing from 10% in the 1970s to a maximum of 35.4% in 2019 (FAO, 2022). Fisheries can impact marine communities through a selective removal of larger and fast-growing individuals, threatening populations with extinction (such as the collapse of cod stocks in 1992), disrupting marine food webs or by physically damaging the habitat (Dulvy *et al.*, 2003; Halpern *et al.*, 2008; Jennings & Kaiser, 1998; Millennium Ecosystem Assessment, 2005; Pauly, 2006).

Global marine transport has allowed some marine species to overcome natural barriers in the oceans, enabling them to reach and establish in areas otherwise inaccessible. The most frequent introduction pathways of NIS in marine ecosystems are ballast waters, aquarium trade and hitchhiking on marine debris (Bailey, 2015). While the introduction of NIS can have a broad range of effects and implications for the receiving communities (Guy-Haim *et al.*, 2018; Thomsen *et al.*, 2014), there are some well-known cases where the arrival of NIS have caused severe negative impacts, such as the Lionfish (*Pterotis sp.*) in the Caribbean or the blue crab (*Callinectes sapidus*) in the Mediterranean (Clavero *et al.*, 2022; Côté & Smith, 2018). With the intense marine traffic at present, there are high chances of species being transported across seas, which poses a threat to the receiving communities, their diversity and services that they provide (Anton *et al.*, 2019; Seebens *et al.*, 2013).

Pollutants from human activities can reach the oceans through many different pathways: direct discharge, land runoff, ships, atmospheric deposition or deep sea mining (Serra-gonc *et al.*, 2022; Vikas & Dwarakish, 2015). Some of those compounds can be toxic on their own. For instance mercury can bioaccumulate through the trophic chain reaching higher concentrations at top predators, which can then be consumed by humans (Feng *et al.*, 2018). Other compounds may not be toxic on their own, but can lead to eutrophication of marine waters and cause algal blooms that lead to oxygen depletion or even anoxia (Kitsiou & Karydis, 2011). These situations can have direct negative impacts to local communities that can go from avoidance behaviour to low reproduction success (i.e., cod eggs) or even high adult mortality for sessile organisms (Breitburg, 2002; Diaz & Rosenberg, 2014; Wu, 2009).

During the last 50 years, humans have altered natural ecosystems worldwide, while seeking to satisfy their growing demands for food, freshwater, energy and materials. This has resulted in pronounced and irreversible losses of biodiversity (Millennium Ecosystem Assessment, 2005). More specifically, current species extinction rates are at least 10 times higher than the background extinction rate over the last 10 million years (IPBES, 2019; Pimm *et al.*, 2014). Consequently, anthropogenic activities have led to the extinction of at least 680 vertebrate species globally (IPBES, 2019). This is particularly severe in the marine ecosystems, where the

Living Planet Index (i.e., an index indicating the state of world's biological diversity based on vertebrate's population trends) shows that since 1970 the populations of 25% of marine vertebrate species have declined (WWF, 2018). We are therefore now in the midst of a so-called "biodiversity crisis" (Cowie *et al.*, 2022).

The loss of biodiversity (Figure 1.1) is one of the largest threats to humankind in the coming decades (World Economic Forum, 2020), and puts the well-being of future generations at risk, as some of the goods and benefits it provides are essential for our well-being (e.g., food source, medicines, clean water, mental and physical health) (European Commission, 2020; IPBES, 2019; Millennium Ecosystem Assessment, 2005).

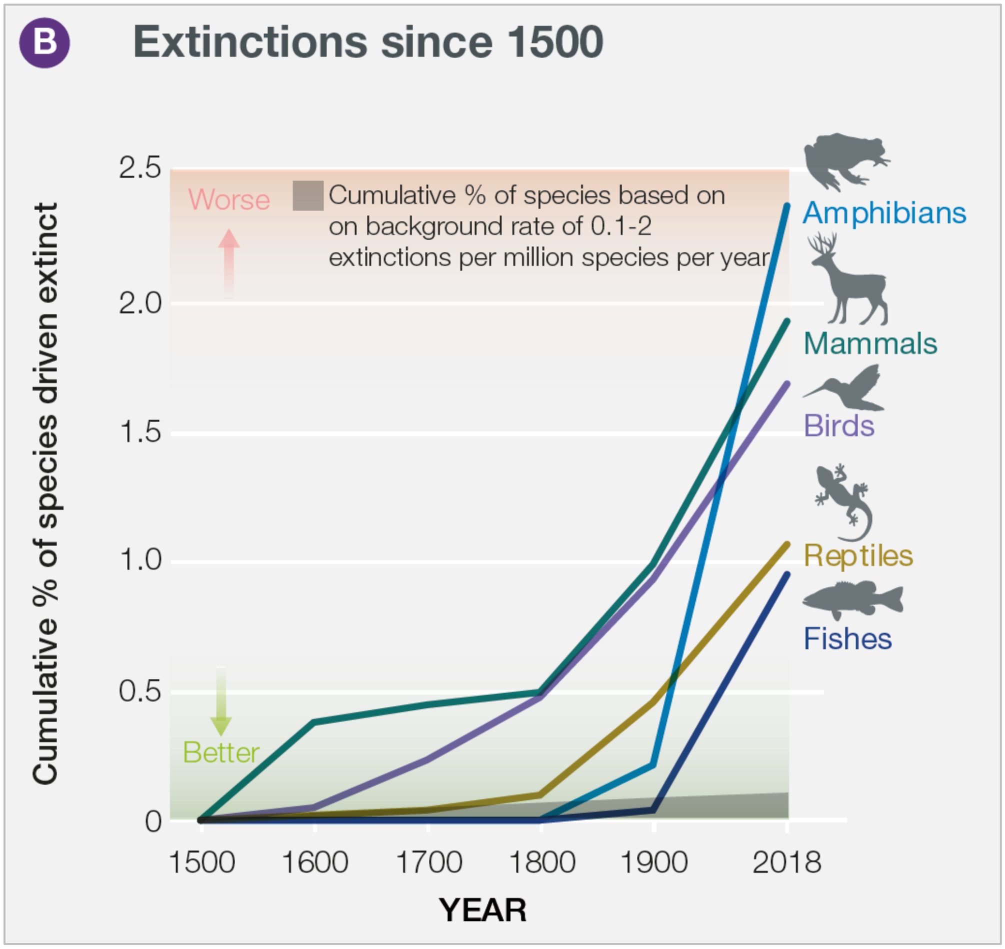

Figure 1.1. Extinction rate of vertebrate groups from 1500 to 2018 assessed by the International Union for Conservation of Nature (IUCN) Red List of Threatened Species (source: IPBES 2019).

1.1.2 Biodiversity history and definitions

Throughout history, humans have been fascinated by the myriad of life forms inhabiting the Earth. In ancient Egypt civilization (3150 BC – 30 BC) various animals were associated with Gods and Goddesses; in ancient Greece, the philosopher Aristotle (384 – 322 BC) dedicated time to the study of animals and plants on Lesbos Island, identifying commonalities and differences among them; and in the Victorian period, Charles Darwin (1809 – 1882) published the theory of evolution after years of studying wildlife and fossils.

The variety of life on Earth, defined by the term biodiversity, spans diverse levels of organization, encompassing genes, species, traits, communities, and entire ecosystems (Rawat & Agarwal, 2015). This manifestation of biological diversity occurs within specific spatio-temporal contexts, reflecting the complexity of a multifaceted concept. Therefore, when addressing biodiversity, we delve into a comprehensive concept that embraces multiple perspectives and dimensions. Traditionally, biodiversity has been quantified by assessing the number and identity of species within an ecosystem. However, contemporary ecology recognizes that each facet of biodiversity holds significance, offering unique perspectives and illuminating diverse ecological processes. The complexity inherent in biodiversity poses challenges in effectively communicating key information, potentially leading to misguided management and conservation efforts. Therefore, establishing a common language for sharing biodiversity knowledge is crucial for managers, researchers and stakeholders in order to optimize resource utilization (Jetz *et al.*, 2019; Pereira *et al.*, 2013).

Biodiversity can supports many different functions in natural ecosystems, which can be related to the storage of organic matter (i.e., productivity), the transfer of material (i.e., herbivory, sinking of death carcass), the stability of ecosystem processes or the resilience towards environmental disturbances (Cardinale *et al.*, 2012). Such functions depend on the species present in the community being able to perform them. Whether certain functions are supported in an ecosystem or not will depend on the identity and ultimately the specific characteristics (i.e., traits) of the species composing it (Waldbusser *et al.*, 2004). Generally, ecosystem function has a positive relationship with biodiversity (Cardinale *et al.*, 2012; Hector & Bagchi, 2007; van der Plas, 2019), since a higher variety of life forms allows for more diverse functions to be fulfilled, until a certain point where increasing biodiversity will have only a minor positive effect on functioning. Nonetheless, richer communities may have higher species trait redundancy, and while this may not increase ecosystem functioning, such redundancy can provide functional resilience (Gladstone-Gallagher *et al.*, 2019; Walker, 1992). This way, ecosystems with high biodiversity will ensure that functions are performed independently of single-species dynamics and will thus be more resilient to disturbances (Schwartz *et al.*, 2000).

Quantifying the value of biodiversity proves challenging, yet its significance is undeniable. Biodiversity has an intrinsic value in the uniqueness of its components. Moreover, humanity reaps numerous goods and services from natural ecosystems, including agricultural materials, food, medicines, or wood, enhances human well-being by supporting outdoor activities such as hiking or diving, and contributes with cultural value (Table 1.1) (Millennium Ecosystem Assessment, 2005; Rawat & Agarwal, 2015). These ecosystem services and goods that humankind benefits from are mostly relying on ecosystem functions sustained by biodiversity, which is thus an important pillar in our lifestyle, although it might not be evident in some cases. The success of one third of our crops depends on pollinators, coastal settlements are protected against extreme weather events by mangroves, and coral reefs contribute to natural hazard management, which is valued with more than US$18 million per square kilometer per year (Convention on Biological Diversity, 2014). The European Commission (2020) recognizes that biodiversity is essential for guaranteeing global food security and facing climate change, and the recent pandemic has evidenced the link between human health and the good status of natural ecosystems. Therefore, it is in the best interest of humankind to adequately preserve, manage and protect biodiversity (Figure 1.2).

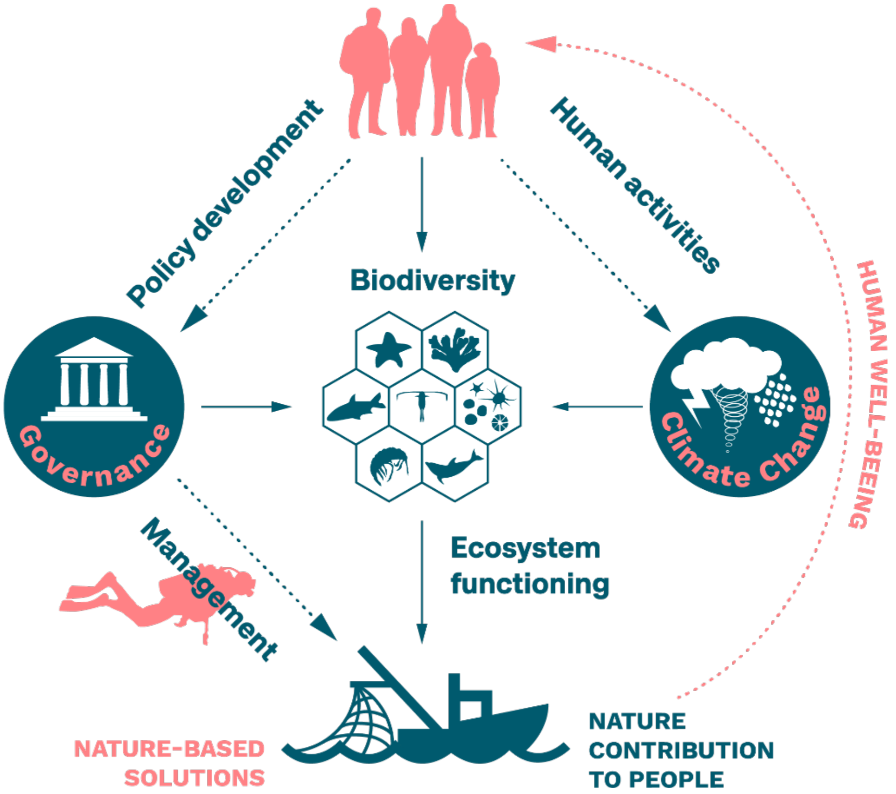

Figure 1.2. Conceptual figure of the socio-ecological context surrounding biodiversity (source: B-USEFUL project).

1.1.1 Essential biodiversity variables

Biodiversity is a multifaceted concept, and the study of its different aspects has generated a myriad of indices to describe it (e.g., Magurran & McGill, 2010). However, having a consistent framework for characterizing biodiversity, better facilitates the monitoring process, and the integration and sharing of data across different habitats, regions, and over time (Navarro *et al.*, 2017). To that end, the Essential Biodiversity Variables (EBV) (Pereira *et al.*, 2013) provide a conceptual framework that aims to clearly identify key biodiversity indicators that can be easily implemented, harmonized and that facilitates communication, among scientist but also with institutions. The EBV comprise six classes of variables that describe different aspects of biodiversity, such as genetic composition, species populations, species traits, community composition, ecosystem structure and ecosystem function (Figure 1.3). These are a set of biological indicators complementary to each other that allow detection and evaluation of patterns, changes, trends and processes in biodiversity (Pereira *et al.*, 2013).

Table 1.1. Global status of provisioning, regulating, and cultural ecosystem services. Status indicates whether the condition of the service globally has been enhanced (↑), degraded (↓) or both (↕, depending on the context) in the recent past (adapted from: Millennium Ecosystem Assessment 2005).

Service	**Sub-category**	**Status**	**Notes**
Provisioning services			
Food	Crops	↑	Substantial production increase
	Livestock	↑	Substantial production increase
	Capture fisheries	↓	declining production due to overharvest
	Aquaculture	↑	substantial production increase
	Wild foods	↓	declining production
Fiber	Timber	↕	forest loss in some regions, growth in others
	Cotton, hemp, silk	↕	declining production of some fibers, growth in others
	Wood fuel	↓	declining production
Genetic resources		↓	lost through extinction and crop genetic resource loss
Biochemicals, natural medicines, pharmaceuticals		↓	lost through extinction, overharvest
Fresh water		↓	unsustainable use for drinking, industry, and irrigation; amount of hydro energy unchanged, but dams increase ability to use that energy
Regulating Services			
Air quality regulation		↓	decline in ability of atmosphere to cleanse itself
Climate regulation	Global	↑	net source of carbon sequestration since mid-century
	Regional and local	↓	preponderance of negative impacts
Water regulation		↕	varies depending on ecosystem change and location
Erosion regulation		↓	increased soil degradation
Water purification and waste treatment		↓	declining water quality
Disease regulation		↕	varies depending on ecosystem change
Pest regulation		↓	natural control degraded through pesticide use

Pollination		↓	apparent global decline in abundance of pollinators
Natural hazard regulation		↓	loss of natural buffers (wetlands, mangroves)
Cultural services			
Spiritual and religious values		↓	rapid decline in sacred groves and species
Aesthetic values		↓	decline in quantity and quality of natural lands
Recreation and tourism		↕	more areas accessible but many degraded

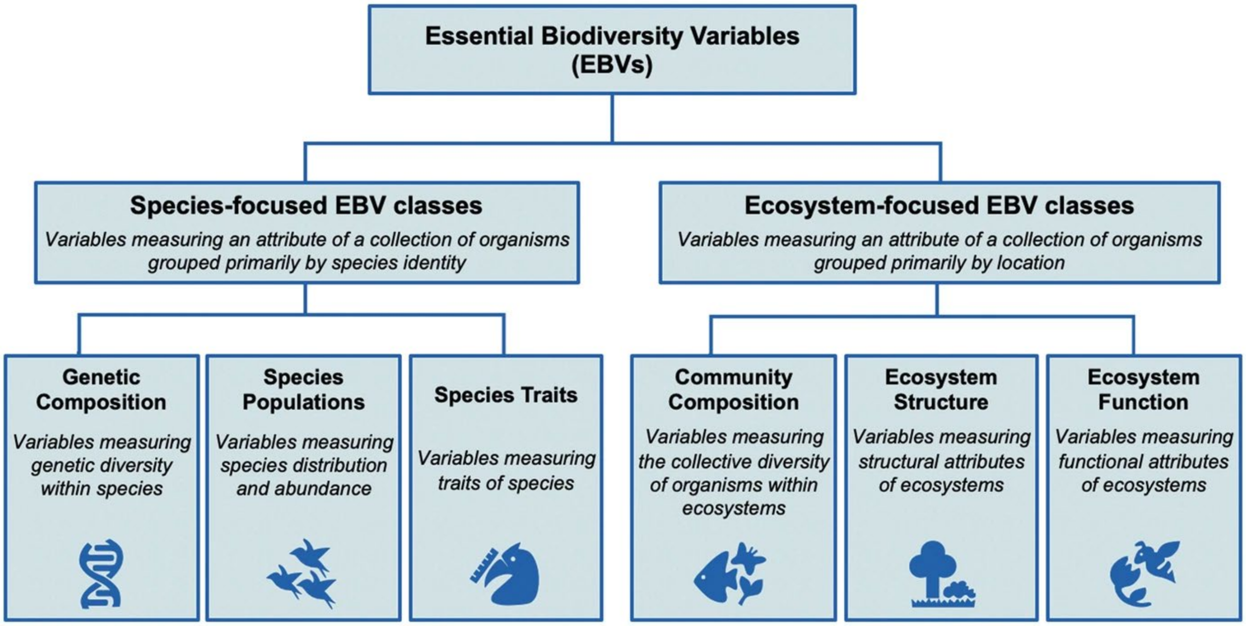

Figure 1.3. Essential Biodiversity Variables and their categories (source: Cavender-Bares, Gamon, and Townsend 2020).

1.1.2 Policy, Management and conservation

The protection of biodiversity should be a global priority, especially since the preservation of biodiversity is essential for guaranteeing global food security. In the European Union (EU), restoration and adequate protection of marine ecosystems has proven beneficial for coastal communities and the EU as a whole, not only from an economic, but also social and health perspective (European Commission, 2020). Nonetheless, the protection and restoration of nature, and the implementation and enforcement of legislation during the last decades have been insufficient to safeguard biodiversity. In this regard, there is a need to join efforts across political boundaries and build a coherent network of protected areas (EEA, 2019; European Commission, 2020).

There are several international and regional directives and initiatives working for the management and conservation of biodiversity and its associated values, such as the Intergovernmental Platform on Biodiversity and Ecosystem Services (IPBES) (Larigauderie & Mooney, 2010), the Sustainable Development Goals of the United Nations Agenda 2030 (United Nations, 2015), or the Convention on Biological Diversity (CBD; Convention on Biological Diversity, 2021). The post-2020 Global Biodiversity Framework (GBF) was adopted during the 15th meeting of the Conference of the Parties (COP 15) by the CBD. It intended to replace the Strategic Plan for Biodiversity (2011-2020) that included the 20 Aichi targets to be achieved by 2020, among which none was fully met. Learning from these failures, the GBF set a pathway to ensure that by 2050 worldwide ecosystems are restored, resilient and adequately protected through a transformation of society's relationship with biodiversity (Convention on Biological Diversity, 2021; European Commission, 2020). To ensure the reduction of threats to biodiversity and that the overall goals are met by 2050, the GBF defines action targets that need to be initiated immediately and completed by year 2030. Target 3 is key, as it sets the objective of protecting 30% from both land and marine areas (Convention on Biological Diversity, 2021):

> ***Target 3.*** *Ensure that at least 30 per cent globally of land areas and of sea areas, especially areas of particular importance for biodiversity and its contributions to people, are conserved through effectively and equitably managed, ecologically representative and well-connected systems of protected areas and other effective area-based conservation measures, and integrated into the wider landscapes and seascapes.*

This highlights that not only 30% of the area shall be protected by 2030, but that (i) such areas must be those of relevant biodiversity, (ii) the conservation actions must be effective, and (iii) there must be a connection among different areas. To achieve Target 3 and the overall objectives set by the GBF by 2050, protected areas are a key tool. A protected area is defined according to Dudley (2008) as a "Clearly defined geographical space, recognized, dedicated and managed, through legal or other effective means, to achieve the long-term conservation of nature with associated ecosystem services and cultural values". Protected areas are an essential tool for the conservation of biodiversity and have direct benefits for humankind: for those living near to those areas, but also for more distant populations. For instance, protected areas provide recreational opportunities, contribute to genetic diversity of wild species, and ensure the well-being of future generations as they will also benefit from the protected goods and services (Dudley, 2008).

Marine Protected Areas (MPAs) allow to manage and protect the functioning of natural marine ecosystems, as well as their resources and values. The establishment of MPAs and the decision on which activities are allowed within them shall be based on the best available knowledge and tools, and with clear aims and objectives. An MPA can take very different meanings, depending on the defined conservation and management objectives: while some MPAs may completely regulate human access and ban exploitation of the natural resources, others may allow the extraction of resources or even be a necessary part of the management (Dudley, 2008).

The current MPA network coverage is low and below the international established targets (O'Leary *et al.*, 2016; Tittensor *et al.*, 2014). Moreover, from the total number of MPAs, few are under high levels of protection (IUCN categories I-III) and therefore, some degree of fishing activities are allowed within those areas (Dudley, 2008; Dudley *et al.*, 2010). Even when fishing is a known key preassure on the marine environment (EEA, 2019), 59% of current European MPAs are commercially trawled. In fact, the trawl intensity is higher (x1.4 times) within MPAs than non-protected areas (Dureuil *et al.*, 2018). The establishment of strictly protected (or no-take) MPAs is typically incompatible with resource extraction (Day *et al.*, 2019) and thus, a source of conflict. This has led in many occasions to the establishment of large MPAs in remote areas where such extractive activates are not taking place, as a mean to avoid conflict and fulfill a coverage objective, i.e., to protect a high percentage of marine areas (Devillers *et al.*, 2015). The effectiveness of such approaches is however dubious, since the biological and ecological components are not a central part of the decision and thus, there is a mismatch between the designated MPAs and areas of high importance for biodiversity (Lindegren *et al*., 2018a; Venter *et al*., 2014, 2018).

The adequate management and enforcement of MPA regulations are a key point in the establishment of MPAs, which otherwise become ineffective. In 2019, 12.4% of the European Union Marine Area was covered by MPAs, but only 1.8% was covered by MPAs with management plans (WWF, 2019), showing a clear need for improvement. Moreover, the enforcement of the regulations within MPAs is essential for meeting conservation and management objectives. A solid and ambitious MPA on paper without a following enforcement can easily become ineffective. Moreover, MPAs with higher levels of regulation enforcement lead to successful results in ecological terms, but also in economic terms for fishermen exploiting the buffer zone surrounding the MPAs (Di Franco *et al.*, 2016).

Furthermore, the complex political architecture involved in the management of European waters can sometimes be a setback for the sustainable management and conservation of biodiversity. For instance, states can fully regulate fishing activities within territorial waters, but beyond that, they can only unillateraly regulate their own fleet. To regulate the activities of third parties, the state needs to engage in multilateral dicusssions with other states, which can go on for several years. This difficults the protection of marine ecosystems and can deter states from implementing MPAs with fishing restrictions, since regulations will apply to the sovereign state, but not to third states until there is a multilateral agreement. One example took place in Portugal, who banned bottom trawl fishing within a large part of its Exclusive Economic Zone and continental shelf to meet its commitment under Birds Habitat Directive and Marine Stragegy Framework Directive. As a consequence, the portuguese fleet was not authorized to bottom trawl in such areas, while other states were (European Court of Auditors, 2020). This kind of situations lead to contexts where commercial fisheries are favoured over conservation of nature (EEA, 2019).

Ultimately, the success of an MPA rests on the engagement of stakeholders and a solid understanding of the key drivers and underlying community assembly process that give rise to biodiversity.

1.1.3 Community assembly processes

The biodiversity patterns from contemporary ecosystems emerge from diverse processes operating across various scales. To effectively manage natural areas and allocate resources for conservation, it is imperative to comprehend the inherent dynamics of these processes and their role in shaping natural communities. Once we are able to disentangle the dynamics of these processes, we can study, understand and anticipate the potential impacts of stressors such as climate change. The community assembly processes framework is one of the main standing ecology theories. The assembly processes theory describes that the communities that we observe in nature are determined by the joint action of a set of filters, which act at different spatio-temporal scales. From a global pool of species, the evolutionary history and the dispersal capabilities of such species will determine a subset that is able to reach a certain region (Cadotte & Tucker, 2017; Keddy, 1992). Then, from the regional pool of species, those that are not adapted to the specific abiotic conditions of the region (i.e., the environment) will be filtered out. Furthermore, biotic interactions will modify the subset of species that have gone through the environmental filter, either excluding species through competitive interactions, or including them through facilitative processes (Bruno *et al.*, 2003; Diamond, 1975; Zobel, 1997). The set of species that has gone through all the filters will comprise the local pool of species and thus the actual assemblage of species that we observe in a specific time and location.

Traditionally, the study of the assembly processes has been centered on the taxonomic identity and diversity of the species forming communities. However, what determines if species can adapt to the local environment, how they interact with other species, and their specific dispersal capabilities are all linked to their functional characteristics, their so-called traits (Figure 1.4). The above-described filters will exclude species that lack certain traits (or their combination) and are therefore poorly adapted to the specific local conditions (Götzenberger *et al.*, 2012; Keddy, 1992; Zobel, 1997). Moreover, this trait perspective enables to find rules that determine community composition and structure between communities with completely different species, enabling to make comparisons and predictions (Keddy, 1992; McGill *et al.*, 2006).

Anthropogenic activities have an impact on the filtering process of the community assembly rules. For instance, climate change is modifying the environmental characteristics of the whole Earth system through e.g., warming, which directly affects the local pool of species as they follow their thermal niche towards higher latitudes or deeper and colder waters (Dulvy *et al.*, 2008; Perry *et al.*, 2005). A second example is the introduction of NIS, which can lead to competitive exclusion of some native species (Clavero *et al.*, 2022; Sparrow, 2008; Thomsen *et al.*, 2014). Lastly, habitat destruction can combine the effects on both environmental and biotic filtering through the modification of the physical conditions of a community such as the habitat complexity. For instance, if the habitat is formed by an organism (e.g., biogenic reefs), its destruction can have severe implications for species interactions if there were some dependencies, but also leaving a bare substrate that can now be colonized by other habitat-forming species (Stachowicz *et al.*, 2007).

A better understanding of the processes and underlying drivers that shape marine communities can improve our knowledge on marine ecosystems and how to better manage and conserve them and their services (Thompson *et al.*, 2022). Species distribution models can be useful tools that, when applied to the extensive datasets available in time and space, can reveal relevant insights on these processes at both single-species and whole-community levels (Brown, 2014; Ovaskainen *et al.*, 2017; Thuiller, 2015). Moreover, the inclusion of traits in modelling exercises can also shed light on trait-environment relationships within communities and may inform about some mechanisms driving community composition and changes. Such modelling tools can produce predictions on how single species, and whole communities, will change under certain climate change scenarios, which can provide important knowledge for management and conservation (Botkin *et al.*, 2010; Franklin, 2023; Urban *et al.*, 2016). This can in fact allow us to anticipate future situations and take the necessary actions for safeguarding healthy ecosystems which can sustain the goods and services that humankind benefits from.

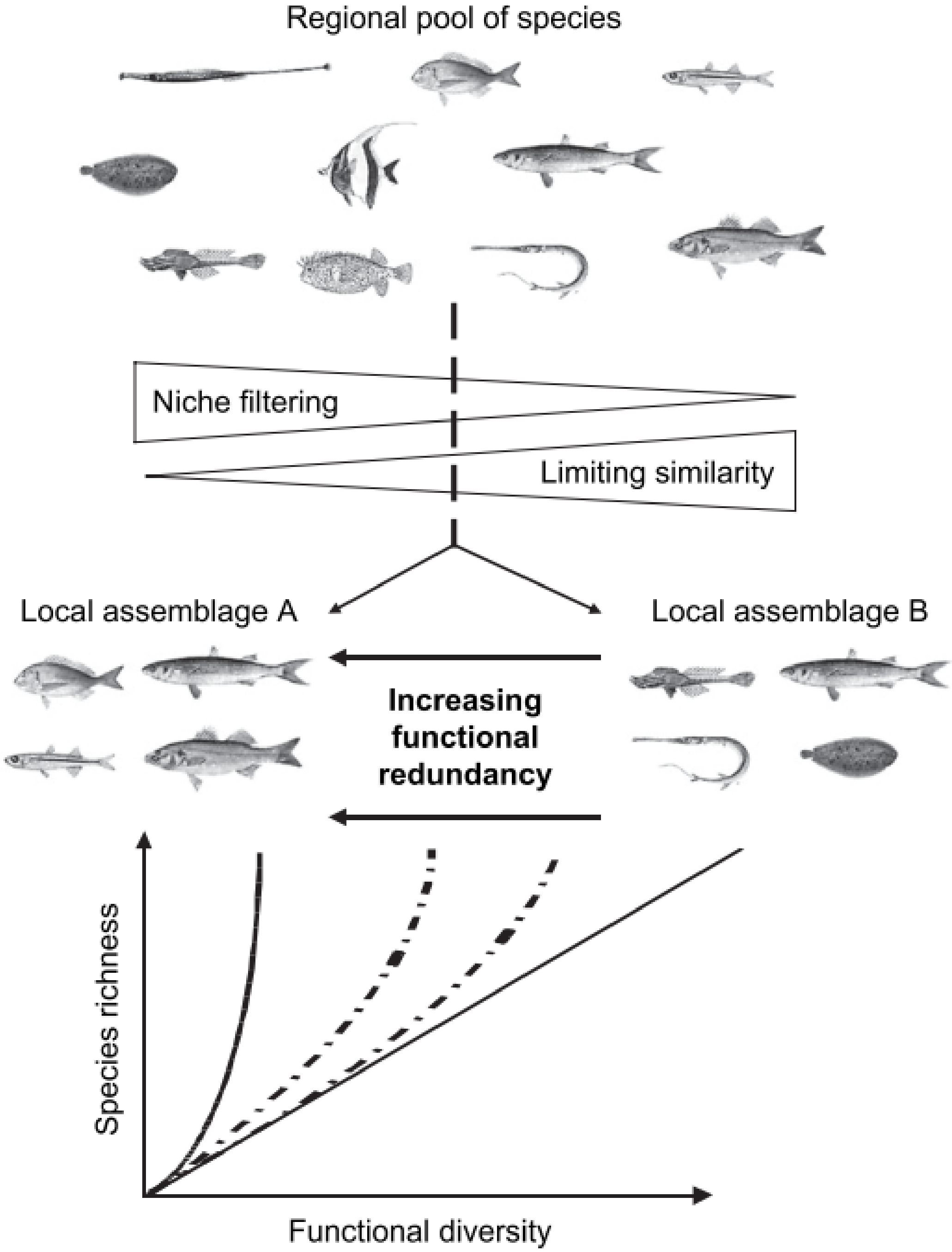

Figure 1.4. Illustration of the community assembly rule concept where species from a regional pool are selected through a niche filtering process and/or limiting similarity process conditioned on their traits. An extreme niche filtering (local assemblage A) will select species with a very specific set of traits and therefore the resulting community will have a high functional redundancy. On the other hand, an extreme limiting similarity filtering (local assemblage B) will lead to species with high trait variation and thus low functional redundancy (source: Mouillot et al., 2007).

1.2 Community modelling

The availability of long-term monitoring data and the accessibility to high-performance computers have made modelling a widely used tool to study the realized niche of species. Statistical models allow us to characterize species niches and to better understand the underlying processes shaping natural communities.

1.2.1 Species distribution models

Species distribution models (SDMs), also known as ecological niche models or habitat models, are a widespread tool used in ecology to understand and estimate the relationship between species occurrence or abundance (or biomass) and environmental conditions, i.e., represent the species realized niche. There are many different methods for performing SDMs (e.g., Generalized Additive Models, Random Forest, Support Vector Machines) each with their advantages and disadvantages (Yates *et al.*, 2018). Moreover, SDMs allow predicting species occurrence or abundance under certain environmental conditions, which can be useful for exploring the outcomes of specific scenarios (e.g., climate change). When the models for making predictions, it is important to test for its predictive power, i.e., how good does the model predict for data that has not been used to fit the model (Charney *et al.*, 2021; Petchey *et al.*, 2015; Yates *et al.*, 2018). A typical approach for that is to perform a k-fold cross-validation (Robert*s et al.*, 2017). For instance, in a 2-fold cross-validation, the available data would be divided into two sets, one for fitting or training the model (training data) and one for testing its predictive performance (testing data). To asses the predictive performance, the fitted model is used to predict e.g., species occurrence under the specific environmental conditions of the testing data, and then such predictions are compared to the true known occurrences. The process is then repeated but the data that was used for training in the first fold is now used for testing and viceversa.

Traditionally, community predictions have been addressed by combining (i.e., stacking) the single-species predictions from SDMs (Grenié *et al.*, 2020). This approach models species individually and thus assumes that they have independent responses to the environment (Guisan & Rahbek, 2011).

1.2.2 Joint species distribution models

A recent development in statistical modelling are the Joint Species Distribution Models (JSDMs), which unlike SDMs consider all species simultaneously and account for the multivariate nature of biological communities. There is a wide variety of JSDM frameworks (e.g., HMSC, BORAL, JDSDM, GJAM, GLLVM, ANN) with different implementation and statistical foundations (Bourhis *et al.*, 2023; Clark *et al.*, 2017b; Hui, 2016; Niku *et al.*, 2019; Ovaskainen & Abrego, 2020; Thorson *et al.*, 2016).

The Hierarchical Modelling of Species Communities (HMSC) is a JSDM framework fitted with Bayesian inference, and conceptually and theoretically rooted on the community assembly processes (Ovaskainen & Abrego, 2020). The framework can incorporate random effects which capture the signal from processes such as biotic filtering, dispersal limitation and environmental filtering not included in the fixed effects, which usually include the environmental predictors. The random effects can be defined by a spatio-temporal structure, aiming to capture processes at a given scale, and are computed through latent variables (similar to a PCA ordination) that can yield a species-to-species residual association matrix. This association matrix reflects co-occurrence patterns of the species within the community that cannot be explained by the environmental niche, i.e., the fixed effects. Consequently, a positive association between two species' occurrence indicates that those species co-occur more often than expected after considering their environmental niche. Whether the underlying process that leads to such pattern is biotic filtering, dispersal limitation or unaccounted environmental filtering in the fixed effects, cannot be disentangled with JSDMs. This is not a shortcoming of JSDMs as such, but rather a result from the type of data used. Nonetheless, the incorporation of such random effects can provide relevant information on potential underlying processes and puts the understanding and knowledge that we have from species niches into perspective (Ovaskainen *et al.*, 2017).

Another interesting feature from HMSC is that it enables including information on species traits. Incorporating traits into the model, not only allows identifying trait-environment relationships, but it actually improves the model performance for some species, typically rare, as it allows information to be shared across species (Norberg *et al.*, 2019; Ovaskainen & Soininen, 2011). In a study comparing the predictive performance of different modelling frameworks (i.e., different stacked SDMs and JSDMs) HMSC was consistently ranked among the best performing, especially when rare species were considered (Norberg *et al.*, 2019). Lastly, HMSC can also incorporate information on species phylogenetic relationship, which accounts for the non-independence of traits among species, i.e. closly related species are likely to share more similar traits than non related species. A strong phylogenetic signal in the model is indicative of a common response towards the environment of closely related species. Hence, following the niche conservatism theory the presence of a phylogenetic signal signifies that there are traits that have not been included in the model that show some relationship with the environment of the studied community. Similar to random effects, the specific traits associated with this signal cannot be disentangled with this method, but finding a phylogenetic signal can highlight the need for further research into trait-environment relationships and generally indicates that closely related species share common responses to the environment, opening avenues for targeted conservation strategies.

1.3 Objectives

The overarching aim of the thesis is to (i) contribute to a better understanding of the underlying processes and drivers that shape the diversity and composition of marine fish communities and, (ii) develop a suite of models capable of forecasting future fish biodiversity, and that can be used for evaluating management actions, including MPA allocation, thereby informing marine conservation efforts and initiatives related to spatial planning. To achieve this overall aims I used HMSC and an extensive collection of high-resoultion survey data on marine fish species occurrences, biomass and traits throughout the Northeast Atlantic in order to answer the following research questions:

- What is the relative importance of the different assembly processes shaping marine fish species and community composition across spatial scales? (Chapters 3-4)
- What are the key environmental drivers determining patterns and trends in species distributions and composition throughout the Northeast Atlantic? (Chapters 3-4)
- To what extent can JSDMs reliably forecast multiple aspects of marine biodiversity (i.e., EBVs) in order to inform decision making with respect to the designation of MPAs? (Chapters 4-5)

Chapter 2

2. Synopsis

2.1 Understanding community assembly

Marine biodiversity is facing a range of anthropogenic pressures, including climate change and overexploitation (Halpern *et al.*, 2015; Maclean & Wilson, 2011; Millennium Ecosystem Assessment, 2005; Worm & Tittensor, 2011). Therefore, there is a need for management and conservation actions based on scientific knowledge to preserve biodiversity and the functions and services it provides to humankind. Consequently, a better understanding of the underlying community assembly processes that shape taxonomic and functional structure and composition of marine communities is needed (Beukhof *et al.*, 2019a; Maclean & Wilson, 2011; McGill *et al.*, 2006; Mouillot *et al.*, 2013; Thompson *et al.*, 2022). In chapter 3 we explore the community assembly processes and drivers shaping marine fish community structure, and the role of species' traits in this context, with a case study in the North Sea.

Here, we model the occurrences of 67 marine fish species with the HMSC framework using a probit link function. The occurrence of species was retrieved from the North Sea International Bottom Trawl Survey (NS-IBTS) from the publicly available scientific monitoring survey DATRAS, hosted by the International Council for the Exploration of the Sea (ICES) (https://datras.ices.dk). We restricted the data to the first and third quarters of the calendar year (i.e., winter and summer, respectively) during the period from 1986 to 2016, for which there is a good sampling coverage of the entire study area and availability of environmental covariates. Furthermore, we selected eleven traits to include in the model, representing species life history, morphology, reproduction and diet collected from available trait data-bases (Beukhof *et al.*, 2019c; Coulon *et al.*, 2023), as well as their phylogeny (Chang *et al.*, 2019). We used environmental data from the model reanalysis products from NEMO-MEDUSA coupled hydro-geochemical model runs (Gurvan *et al.*, 2022; Yool *et al.*, 2013), complemented with seabed substrate composition (EMODnet Geology, 2016) and the combined annual fishing effort of beam and otter trawls (Couce *et al.*, 2020). Lastly, we incorporated two temporal (i.e., year and season) and one spatial random effect (ICES rectangles), which capture assembly processes not explicitly considered by the environmental variables included in the model.

After model training and validation the results show that the environmental (fixed) variables explain on average 35% of the variance in species occurrences, while the random effects explain the remaining 65%. Particularly, the spatial random effect explained 50% of the variance, which suggests that there are spatially-structured processes shaping the community that cannot be solely captured by the environmental variables considered here. On the other hand, temperature accounted on average for 25% of the explained variance, being the environmental covariate with the highest value. This supports previous findings (Beukhof *et al.*, 2019b; Dulvy *et al.*, 2008; Rutterford *et al.*, 2015) and suggests that with ocean warming, species distribution will shift as they track their climate niches (McLean *et al.*, 2021; Pinsky *et al.*, 2013). The fishing effort had a minor direct role in explaining species occurrences, supporting previous studies in the area demonstrating no or weak effects of fishing on contemporary patterns of community structure (Beukhof *et al.*, 2019b; Dencker *et al.*, 2017). In line with these studies, we attribute this to the fact that a very strong pressure would be needed to observe effects on species occurrence, i.e. extirpation, and that these effects are more likely to be observed on the abundances of species or when fishing is first introduced in an unexploited system (Jennings & Kaiser, 1998; Last *et al.*, 2011). Since the North Sea has a long history of fishing (Bennema & Rijnsdorp, 2015) such effects may therefore already have filtered the community. Overall, the traits included in the model explained 12.5% of the variation in species niches. While some trait-environment relationships found in the study were supported by previous studies (e.g., negative relationship between age at maturity with temperature and its seasonality; Beukhof *et al.*, 2019b), some others were not (e.g., negative relationship between temperature and growth), which we attribute to the difference in spatial scale between studies. We also found traits to strongly condition species responses to some environmental variables (i.e., chlorophyll *a* concentration and sediment type) even if these variables explain only little variance of species niches. This highlights that accounting for traits in modelling exercises can contribute to better understand some ecological processes structuring community assembly. Lastly, the high variance attributed to the spatial random effect indicates that there are processes with a strong spatial structure at play, being an important factor for shaping marine fish communities. We argue that biotic interactions are an essential part of such spatial processes, but likely acting in combination with other assembly processes.

Taken together this study enhances the current understanding on the main environmental drivers of community composition in the North Sea and the role of traits in explaining species niches. It further highlights the importance of spatially-structured processes in shaping marine fish communities. In chapter 4 and chapter 5 we expand the spatial scale of the study area to the Northeast Atlantic, seeking to study such process at a much larger scale and with the aim of providing relevant knowledge for management and conservation.

2.2 Assessing the forecast horizon for reliably predicting marine biodiversity change

Climate change, and more especially global warming are causing changes in the composition, distribution and ranges of marine species as they track their thermal niche (Dulvy *et al.*, 2008; Freeman *et al.*, 2018; Pinsky *et al.*, 2013). The rate at which species may be able to track such changes will change from one to other (Perry *et al.*, 2005; Poloczanska *et al.*, 2013), suggesting that changes in community composition will take place, and with that also changes in functioning (Harley *et al.*, 2006). Consequently, understanding and anticipating these changes is essential for guaranteeing adequate management and conservation of “areas of particular importance for biodiversity” (European Commission, 2020). Therefore, we need robust models to forecast future changes in marine biodiversity and composition that can help to inform decision-making, especially with regards to the designation of MPAs. In chapter 4 we model fish communities from the Northeast Atlantic, and perform a thorough cross-validation to study how far ahead are we able to accurately predict multiple aspects of marine fish diversity and composition.

In order to achieve this, fish occurrence and biomass data from 13 scientific bottom trawl surveys across the Northeast Atlantic Ocean were collected, which amounted to 90,029 unique hauls spanning 33 years (1989-2021). All species with a minimum prevalence of 0.1% and available trait data were retained (N = 151), and their biomass was standardized for swept area and gear catchability (van Denderen *et al.*, 2023; Maureaud *et al.*, 2019; Walker *et al.*, 2017). Following the methodology from chapter 3, we fitted the models with 6 traits representing species life history, morphology, reproduction and diet, collected from available trait data-bases (Beukhof *et al.*, 2019c), and environmental variables from the model reanalysis products from NEMO-MEDUSA coupled hydro-geochemical model runs (Gurvan *et al.*, 2022; Yool *et al.*, 2013), together with a season categorical variable to account for seasonality. Due to the prevalence of absences (zeros) in the survey data, we adopted a hurdle model approach and fitted two sets of models: one for species presence-absence using a probit link function and another for the log-transformed biomass conditional on presence with a Gaussian link function. Additionally, we fitted an additional set of models where we also included spatio-temporal random effects (i.e., 574 spatial cells and 33 years). We then evaluated the performance of each set of models and performed a decadal cross-validation where we assessed the model's predictive performance towards taxonomic and functional composition of the community through a suite of different biodiversity metrics, reflectiung both species- and community level EBVs.

All models had a good convergence with the exception of the biomass model including random effects. The occurrence models exhibited an explanatory power of AUC of 0.95 and 0.91, and the biomass models an R^2 of 0.34 and 0.21 for the full and environment whole-period models, respectively. The spatial random effect explained most of the variance when included in the occurrence (77%) and biomass (59%) models. However, when making predictions into the future, the random effects are assumed to remain constant as they cannot be adjusted to climate scenarios. Hence, in cases where they explain the largest proportion of the variance, as in this case, they do not leave much "room" for changing environmental signals to shape the community. Consequently the predicted species distributions and community composition become somewhat static even in the event of large environmental changes. Since the objective here is to study the impact of changing environmental conditions on communities under climate change, and considering that the biomass model with random effects did not reach satisfactory convergence, we proceeded using the models without random effects for making future predictions. This approach sets the sole focus on the environmental filtering species are exposed to, while disregarding the spatially explicit context. The set of models with only fixed effects (i.e., environment), temperature- and productivity-related variables explained most of the variance for both occurrence and biomass. Performing the decadal cross-validation exercise, we found a generally decreasing predictive performance over time, implying that the longer the predictions into the future are made, the more uncertain/inacurate they become. However, within the first 10-20 predicted years the predictive performance was relatively close to the initial explanatory performance. The relatively robust decadal forcast horizon represents a reasonable timeframe for management and conservation objectives that could be assessed or supported by ecological model forecasts. The predictive skill of the models for functional (trait) composition and biodiversity always showed better results than the taxonomic, suggesting that functional aspects of the community are better conserved despite the changes in individual species (Beukhof *et al.*, 2019b). Also, the predictive performance for presence-absence was better than biomass, likely due to an inadequate representation of key processes that regulate the productivity and dynamics of species biomass in the models (van Denderen *et al.*, 2020; Lindegren *et al.*, 2020, 2013) and the fact that binary models, i.e. presence-absence, have less complex nuances than biomass predictions on continuous scales.

The results provide a new understanding on the main underlying drivers of fish community composition at large, relevant for addressing the threats of climate change in marine biodiversity. In particular, we demonstrate the temporal decay in model forcast performance for several biodiversity facets and highlight the temporal scale community model forcasts still perform robustly. Moreover, we provide a robust set of models that can be used to predict taxonomic and functional aspects of biodiversity for exploring and anticipating the effects of climate change in future scenarios. In chapter 5 we use the presented models to predict present and future marine fish biodiversity patterns.

2.3 Marine biodiversity protection can be improved while minimizing effects on other ocean uses

Worldwide biodiversity is threatened by anthropogenic activities such as climate change, and during the recent decades, extinction rates across several taxa have been increasing (Cowie *et al.*, 2022). The loss of biodiversity poses substantial and irreversible consequences for the functioning and services that natural ecosystems provide to humankind (Cardinale *et al.*, 2012), such as food production and climate regulation. Consequently, maintaining biodiversity is key for guaranteeing the structure and functioning of ecosystems as well as human well-being (Cardinale *et al.*, 2012; Loreau, 2000; Stachowicz *et al.*, 2007). In this regard, the Global Biodiversity framwwork has set a target to protect “at least 30 per cent [...] of sea areas, especially areas of particular importance for biodiversity” by 2030, through the establishment of Marine Protected Areas (MPAs) (Convention on Biological Diversity, 2021).

In chapter 5 we aim to (i) describe and compare past and future patterns and trends in multiple taxonomic and functional EBVs; (ii) identify key ”hotspots” of overall high biodiversity and; (iii) evaluate the optimal placement of MPAs achieving 30% protection of biodiversity by ecoregion, while minimizing trade-offs with commercial fishing.

We use the hurdle model from chapter 4 to predict the probability of occurrence and biomass estimates for 151 fish species spanning from 1989 to 2050. To describe and compare past and future patterns in marine fish biodiversity, we computed a suite of six complementary EBVs representing key aspects of biodiversity on the basis of the model predictions (Pereira *et al.*, 2013). We compared the patterns and trends among the biodiversity indicators by performing a PCA using the derived EBVs per location and year (from 2000-2030). Moreover, we computed a Joint Biodiversity Index (JBI) by standardizing and combining the six EBVs, which we used to identify areas of high biodiversity for each of 18 areas defined by their ecoregion and depth. We then simulated a conservation and management scenario (i.e., MPA optimization) where the objective was to protect 30% of the ocean space by prioritizing areas of high biodiversity, while minimizing impacts on fisheries (ICES, 2019). We examined the extent to which high biodiversity areas for each individual EBV overlapped with protected areas within both the existing MPA network (UNEP-WCMC and IUCN 2024), and the optimized MPA. Additionally, we investigated the potential impacts of implementing the optimized MPA scenario on commercial fishing activities.

Our results demonstrate large-scale patterns in overall biodiversity throughout the study area with the northern North Sea, Norwegian coast and southern Iceland showing higher values of the JBI, while the northeast Barents Sea and the Iberian coast show relatively lower indices. The six EBVs underlying the JBI show different spatial patterns and trends, which is also reflected in the PCA. The current MPA network is protecting a small percentage of high biodiversity areas for each of the EBV considered, partially due to the small surface covered by MPAs throughout the study area. Additionally, in most of the ecoregion-depth combinations, the mean JBI value within MPAs is low, and in many is zero due to the lack of implemented MPAs. The outputs from the MPA optimization show a substantial increase on percentage of high biodiversity areas protected for each EBV, which would also remain protected in the future (2020 and 2050). This increase in the protection of EBV with high value is a consequence of increasing the total area covered by MPAs in the optimization scenario, but also reflects that such increase has prioritized areas of high biodiversity. Moreover, the mean JBI value protected by the optimization scenario increases respect to current MPA network, indicating that not only the covered area, but also the value of protected biodiversity can be improved. Lastly, the fishing effort would experience a reduction of 15.51MKw/h or 9% if the optimized MPAs would be fully closed to fishing activities. However, two thirds of such fishing effort are concentrated in the North Sea, one of the most commercially exploited regions, with a long fisheries history (Bennema & Rijnsdorp, 2015; Callaway *et al.*, 2007; Couce *et al.*, 2020). Most of the areas considered would experience very modest reductions amounting to <0.1MKw/h in absolute terms, or <3% of their total fishing effort.

The findings underscore the importance of balancing conservation efforts with economic activities, which requires of active collaboration and dialogue between scientist, managers and stakeholders in order to achieve a sustainable solution. By understanding the trade-offs involved, we can work towards effective marine conservation while supporting human needs and livelihoods.

Chapter 3

3. Community assembly processes and drivers shaping marine fish community structure in the North Sea

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3.1 Abstract

To preserve natural ecosystems and their biodiversity, there is a need to anticipate future ecosystem changes through better understanding of underlying drivers and assembly processes determining community composition. Assembly processes can be understood as a set of filters acting at different spatio-temporal scales that jointly define the structure and composition of communities. Here, we explore the underlying assembly processes shaping marine fish species distribution and composition, using the heavily exploited North Sea. Our aims are to study (i) the relative importance of the different assembly processes shaping marine fish communities, (ii) the key environmental drivers determining species distributions and composition, and to (iii) quantify the role of traits in determining species niches and responses to the environment. Specifically, we fit a Joint Species Distribution Model (JSDM) using 31 years of standardized scientific bottom trawl survey data for 67 fish species. We use a set of environmental variables and species' traits representing morphology, life history, reproduction and diet, while also accounting for phylogenetic relationships of species. Environmental variables, primarily related to temperature, explained over one third of the variance in species occurrence, while spatial effects explained half of the variability across species. This shows that environmental filtering and spatially-structured processes are the main drivers shaping the community assembly. Furthermore, among the total variance of individual species occurrences, 12.5% could be explained by traits, which improve the mechanistic understanding on species responses to environmental change. Hence, model predictions from JSDMs accounting for traits, environmental niches and potential interactions among multiple species can provide relevant simulations and forecasts with the potential to inform spatial management and conservation efforts aiming to preserve biodiversity and its associated services vital for human well-being.

Keywords: community assembly rules, joint species distribution models, traits, marine management, biodiversity

3.2 Introduction

Ecosystems worldwide are exposed to a broad range of natural and anthropogenic pressures, including overexploitation, habitat loss and climate change (Halpern *et al.*, 2015; Maclean & Wilson, 2011; Millennium Ecosystem Assessment, 2005; Worm & Tittensor, 2011). In response to such pressures, notably global warming, many communities have already demonstrated shifts in species distributions and abundances (Freeman *et al.*, 2018; Last *et al.*, 2011; Perry *et al.*, 2005; Pinsky *et al.*, 2013; Poloczanska *et al.*, 2013). Furthermore, the different rates of range shifts between species suggest a pronounced reorganization in community composition, as well as the structure and functioning of ecosystems at large (Poloczanska *et al.*, 2013). In order to take the necessary management and conservation actions that seek to preserve natural ecosystems and their biodiversity, there is a need to anticipate these changes through a better understanding of the underlying drivers and community assembly processes that shape these communities (Beukhof *et al.*, 2019a; Maclean & Wilson, 2011; McGill *et al.*, 2006; Mouillot *et al.*, 2013).

The community assembly rules framework is one of the current standing community ecology theories. The assembly rules or assembly processes can be understood as a set of filters acting at different spatio-temporal scales that jointly define the structure and composition of communities. First, speciation, large-scale migration and dispersal determine the set of species that will be able to reach a particular region based on their evolutionary history and dispersal capabilities (Keddy, 1992). From this set of species, the abiotic environment filters out species that are poorly adapted to the specific conditions of a given area, while biotic interactions further modify this subset through competitive or facilitative interactions (Bruno *et al*., 2003; Diamond, 1975; Zobel, 1997). The set of species that has gone through all these filters will comprise the species pool of any given community. Moreover, these assembly processes are directly determined by species traits, since these filters are excluding species that lack certain traits (or their combinations) (Zobel, 1997). Environmental constraints filter out species with poorly adapted traits to the specific local conditions, while biotic interactions will also be defined by the trait composition of the species (Keddy, 1992; Zobel, 1997). A well-known example considering the role of traits in biotic interactions is in the context of invasion ecology, where non-native species typically have great impacts upon native species with similar traits through competitive exclusion (Mouillot *et al.*, 2013). Besides ecological filters, anthropogenic impacts, such as exploitation, can also have direct effects on communities conditioned on their traits. Notably, commercially important species have shown to shift towards smaller lengths at maturity due to high fishing pressure on large-sized individuals (Dulvy et al, 2004; Genner et al, 2010; Engelhard, Righton and Pinnegar, 2014).

Predictions of species community composition have been widely addressed by combining (i.e., stacking) outputs from single species distribution models (SDMs) (Grenié *et al*., 2020; Norberg *et al*., 2019). However, this approach primarily reflects individual species' habitat suitability (Ferrier & Guisan, 2006), thus not sufficiently describing the underlying community assembly processes that determine the observed communities (Guisan & Rahbek, 2011). Alternatively, joint species distribution models (JSDMs) consider all species simultaneously, thus accounting for the multivariate nature of biological communities (Jetz *et al.*, 2019; Ovaskainen & Soininen, 2011). Moreover, recent advances in JSDM frameworks allow for the inclusion of species' traits, which can reveal key trait-environment relationships and improve model performance, especially of rare species (Norberg *et al.*, 2019). Hence, JSDMs allow seeking for community-level patterns in how species respond to the environment and how those responses are influenced by species traits.

Hierarchical Modeling of Species Communities (HMSC; Ovaskainen & Abrego, 2020; Ovaskainen *et al.*, 2017) is a recent Bayesian JSDMs framework that has been applied to study a variety of natural communities and with different purposes, such as studying biogeographical processes, phenological changes or towards conservation and management (Elo *et al*., 2021; Marjakangas *et al*., 2021; Murillo *et al*., 2020; Odriozola *et al*., 2021; Weigel *et al*., 2021). HMSC is strongly rooted within community ecology theory by linking model setup and outputs to the underlying community assembly rules that define community composition (Ovaskainen & Abrego, 2020). The hierarchical structure of the framework allows to seek for shared patterns across species in how they respond to the environment. This allows improving the performance for many species, especially the rare ones (Norberg *et al.*, 2019; Ovaskainen & Soininen, 2011; Poggiato *et al.*, 2021). Moreover, trait information can be included in HMSC, allowing to relate community-level responses to the environment to traits. This enables included traits to influence species niches. Lastly, phylogenetic relatedness among species can also be included, allowing to evaluate phylogenetic constrains of species response traits (see Ovaskainen *et al.*, 2017).

However, HMSC has not been previously applied to study the drivers and community assembly rules acting on fish communities in large and open marine ecosystems. In this study, we explore the underlying assembly rules shaping marine fish species distribution and composition, using the North Sea as a case study. The North Sea is exposed to a range of human activities and is therefore considered as one the most heavily impacted seas worldwide (Bowler *et al*., 2020; Halpern *et al*., 2008). As a result of such impacts, the area has previously demonstrated substantial declines in individual fish populations (Clausen *et al.*, 2018; Fernandes & Cook, 2013; Lindegren *et al.*, 2018b), as well as large-scale changes in taxonomic and functional diversity (Beukhof *et al*., 2019b; Dencker *et al.*, 2017; Dulvy *et al.*, 2008; Hiddink & ter Hofstede, 2008). The above mentioned impacts, as well as the pronounced spatio-temporal heterogeneity of both environment and fish community makes the North Sea a suitable case study for exploring community assembly processes (Cohen *et al.*, 2017). For that, we pursue the following research questions:

i. What is the relative importance of the different assembly processes shaping marine fish communities?
ii. What are the key environmental drivers determining species distributions and composition?
iii. How large is the role of certain traits in determining species niches and responses to the environment?

3.3 Methods

Community data collection

We collected data from the North Sea International Bottom Trawl Survey (NS-IBTS) from the publicly available scientific monitoring survey DATRAS, hosted by the International Council for the Exploration of the Sea (ICES) (www.datras.ices.dk). The temporal span of the data was restricted to winter and summer surveys (i.e. first and third quarters of the calendar year) for the period 1986-2016, for which there is a good coverage of the entire study area. Spatially, the survey is structured on the basis of the ICES statistical rectangles; these are rectangles of 30’ in latitude by 1º in longitude (approximately 56 by 64 km at the center of the study area) that divide the area between 36°N and 85°30'N and 44°W and 68°30'E into grid cells (Figure 3.1). The ICES statistical rectangles gridding system is a formal spatial structure used in fisheries assessment and marine management advice within ICES. The DATRAS survey identifies catches at species level whenever possible, which we verified and updated with the World Register of Marine Species (WoRMS Editorial Board, 2022) whenever needed. Non-fish taxa were discarded and only organisms identified to species level from the following classes were kept: *Actinopterygii*, *Elasmobranchii*, *Holocephali*, *Myxini* and *Petromyzonti*. The data went through a quality check procedure where we removed invalid hauls and invalid species records, which resulted in presence-absence data for 247 species. Since abundances of pelagic species are generally underestimated, due to their lower catchability in bottom-towed gear (Walker *et al*., 2017), we used presence-absence data only, allowing us to represent the entire fish community, including both pelagic and demersal species. However, we excluded rare species with less than 10 occurrence records in the entire data set (135 species), as well as those species where no trait or phylogenetic information was available (45 species), resulting in a total of 67 species stemming from 17,319 unique hauls across 170 ICES rectangles (Figure 3.1).

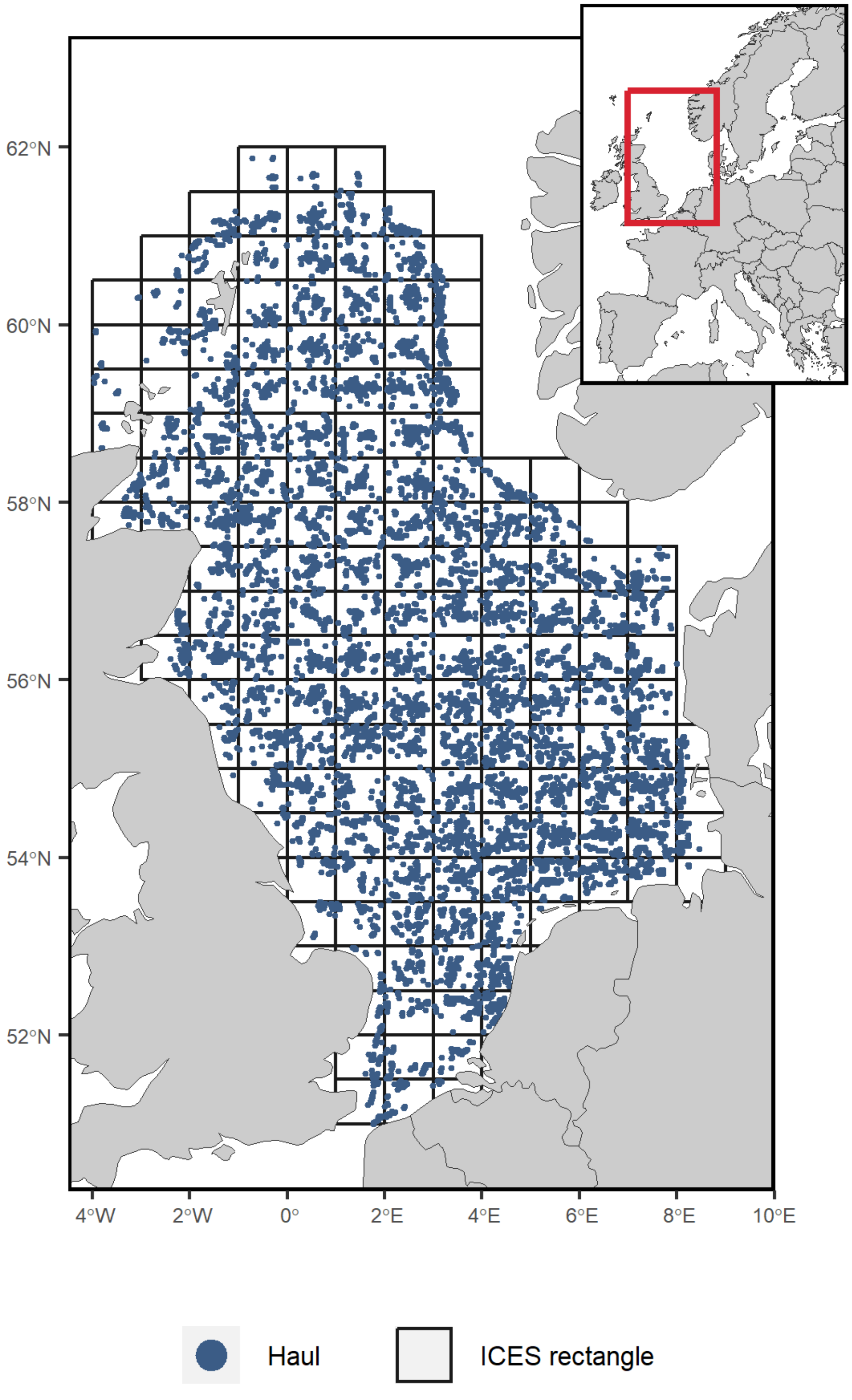

Figure 3.1. Position of all unique hauls of the IBTS surveys performed in the North Sea during the summer and winter seasons between 1986 and 2016. The grid represents the official ICES rectangles included in the study.

Environmental data collection

The availability of in situ environmental data was limited to a few CTD records (i.e., 15% of the hauls) of temperature and salinity. Therefore, in order to ensure a complete and consistent coverage of both physical and environmental covariates across all unique sampling events we used model re-analysis products from the NEMO-MEDUSA coupled hydro-geochemical model runs (Gurvan *et al*., 2022; Yool *et al*., 2013). The available covariates included both surface and bottom temperature (ºC), salinity (PSU), detritus (mmol N per m^3), chlorophyll *a* (mmol N per m^3), dissolved inorganic nitrogen (DIN; mmol N per m^3) and depth. To reflect seasonality in environmental conditions, previously known to affect fish diversity and dynamics (Beukhof *et al.*, 2019a; Dencker *et al.*, 2017; Maureaud *et al.*, 2019) we calculated temperature and salinity seasonality as the standard deviation in each corresponding sampling point and year. We acknowledge that relying on model-derived data may incur potential sources of uncertainty and errors, at least for variables less well-informed by in situ observations or remote sensing, such as sea bottom temperature (SBT). However, given the high correlation ($r = 0.87$; $p < 0.001$) between modelled data and the relatively few available CTD records of SBT measured prior to sampling we consider the risk of introducing errors as marginal. Moreover, seabed substrate composition, reflecting the benthic habitats corresponding to each sampling point was retrieved from EMODnet (European Marine Observation and Data network; www.emodnet-geology.eu; version September 2021) with a maximum spatial resolution of 4 km^2. Finally, to account for potential effects of exploitation, annual fishing effort data (fishing hours) per ICES statistical rectangle for both otter and beam trawlers was extracted (Couce *et al.*, 2020). All the above-mentioned covariates were tested for multi-collinearity and when a correlation >0.7 or <-0.7 was found, the variable which was least correlated with other covariates was kept for the analysis (Supplementary Figure 9.1).

Species traits and phylogeny

We wanted to capture the diversity of traits in the community and quantify their role in determining species niches and responses to the environment. We therefore talk about community cluster traits, i.e., traits that translate taxonomic biodiversity into trait diversity (Streit and Bellwood 2022). We selected eleven traits in order to represent species' morphology, life history, reproduction and diet (Dencke*r et al*., 2017; Supplementary table 9.1). Trait values for each species were collected from available trait data bases (Beukhof *et al.*, 2019c; supplemented with information from recent literature Coulon *et al.*, 2023). Morphology of the species was described as body shape, caudal fin shape and maximum length (cm). Life history was characterized by the age of maturity (years) and the von Bertalanffy growth coefficient K (year^{-1}), while reproduction was represented by spawning type, fecundity (number of eggs) and offspring size (egg diameter in mm). Dietary aspects were captured by diet and trophic level, while the position in the water column was included to represent a pelagic or demersal life style. Finally, we calculated phylogenetic relatedness among species using fishtree R package version 0.3.4. (Chang *et al*., 2019).

Model fitting and diagnostics

To examine the underlying community assembly rules acting on the North Sea fish community we used the HMSC framework (Ovaskainen *et al*., 2017; Tikhonov *et al*., 2020) through the R package 'Hmsc' version 3.0-11 (Ovaskainen & Abrego, 2020; Tikhonov et al, 2021). Similar to other modelling tools, HMSC quantifies the explained variation within the observed communities through included environmental covariates, as well as through random effects, which can account for e.g., patterns arising from spatio-temporal processes. However, HMSC may include random factors that can be linked to species-specific co-occurrence patterns within the unexplained (residual) variation. These random effects are shown through either positive or negative pair-wise species associations reflecting ecological processes that take place in addition to species' responses to the environment (e.g., dispersal limitation, biotic interactions, and random level specific covariates not captured by the fixed effects). Nonetheless, such residual associations are not computed for each pair of species, as the number of parameters to be estimated would quickly escalate with the number of species in the community. Instead, latent variables are used for estimating such parameters, which can be viewed as model-based ordinations (Ovaskainen & Abrego, 2020).

We fitted a presence-absence HMSC model with a probit link function using individual hauls as sampling unit. As linear fixed effects, we included SBT, SBT seasonality, sea bottom salinity (SBS) seasonality, seafloor detritus, surface chlorophyll *a* concentration, surface DIN concentrations, and fishing effort. Since fishing effort was represented by an annual total, we applied a one-year lag, as the possible effects of fishing are expected to be appreciable in the following year's community. Since species usually display optimum ranges in their environmental niches, especially for temperature, we also included a quadratic term for SBT in the model. The environmental covariate and trait matrices are scaled by default by HMSC so that they have zero mean and unit variance over the columns. Such scaling is invisible to the user as the estimated parameters are back-transformed to the original scale when further processed. Finally, we included year and season within year (winter and summer) as temporal unstructured random effects, and the ICES statistical rectangles as spatially explicit random effect. All three random effects were treated independently, and the number of latent variables for each was constrained to a minimum of 1 and a maximum of 5. The model was fitted assuming the default priors described in Supporting Information of Tikhonov *et al.* (2020). Four Markov chain Monte Carlo (MCMC) chains were run, each collecting 250 samples, resulting in 1000 posterior samples. We applied a thinning of 100, resulting in 37,500 iterations per chain of which the first 12,500 were discarded as burn in. MCMC convergence was assessed by examining the potential scale reduction factors (Gelman & Rubin, 1992) of model parameters. MCMC convergence is considered satisfactory if the mean values do not exceed 1.1 (Tikhonov *et al.*, 2020). The model performance was evaluated as explanatory and predictive power (through a 5-fold cross-validation) by means of the area under the receiver operating characteristic curve (AUC), Tjur R^2 and root mean square error (RMSE). AUC is widely used to test SDMs discriminatory ability (i.e., the ability to distinguish between a presence and an absence) by evaluating its sensitivity (true positive rate) and specificity (true negative rate) (Fielding & Bell, 1997).Values of 0.5 suggest no discrimination, 0.7 to 0.8 as acceptable, 0.8 to 0.9 as excellent and >0.9 as outstanding (Mandrekar, 2010). Likewise, Tjur R2 provides a measure of the model's discriminatory ability (Tjur, 2009), while RMSE is a measure of the accuracy (i.e., how close the measurement are to the true value). We conducted all statistical analyses in the R software, version 4.2.1 (R Core Team, 2022).

Assessment of assembly rules, drivers and trait-environment relationships

In order to study the contribution of the different assembly processes determining species distributions and community composition, we examined the variance partitioning of the modelled species niches, i.e. how much of the explained niche variance can be attributed to the included covariates (Ovaskainen *et al*., 2017). We explored species' niches by plotting their responses to the environmental covariates, denoted as '*beta'* parameters in the model, which had statistical support of at least 95% posterior probability. We also examined the joint proportions of variation explained by different sets of covariates, grouped into temperature (temperature -related variables) and productivity variables (chlorophyll *a*, detritus and DIN), also accounting for the joint fractions of explained variation within these groups. HMSC models species environmental niches by incorporating information on how species traits respond to environmental covariates, denoted as '*gamma'* parameters in the model. This allows quantifying how much of the variation in species responses to the environment can be attributed to species traits. Since, traits were found to explain a substantial proportion of species response to surface chlorophyll *a*, we explored the trait relationship with this variable. We used community-weighted means traits to study such relationships, which can be computed with the Hmsc package (Ovaskainen & Abrego, 2020; Tikhonov et al, 2021). Since many traits are phylogenetically conserved (following niche conservationism, i.e. the tendency of species to retain ancestral traits) (Wiens & Graham, 2005), we included the phylogenetic correlation parameter '*rho'* in our model that measures if the residual variation (after accounting for traits) of species responses to the environment is independent or phylogenetically structured. *Rho* ranges between 0 and 1, where

1 would imply fully phylogenetically structured responses of taxa to the environmental covariates, i.e. closely related species respond similarly. Strong phylogenetic signals may therefore point to response traits that have not been specifically accounted for in the model. We thus explored the presence and strength of such phylogenetic signal, looking for signs of missing trait information that can influence species niches.

In addition, we assessed species co-occurrence patterns at the level of the spatial random effect included in the model. These species-specific co-occurrences are based on the covariance structure of the model residuals, after having accounted for the fixed environmental effects. This information highlights pairs of species that co-occur more (or less) frequently than by random, after accounting for their environmental niche HMSC represent these co-occurrences through latent (unobserved) variables, which can be understood as a model-based ordination representing the main axes of variation (Warton et al , 2015; Ovaskainen et al , 2016; Clark et al, 2017). Hence, areas with different site scores (spatial latent factor values) represent different species co-occurrence patterns. However, since our model structure is spatially explicit, the latent factors represent both spatial variation of unobserved co-variates as well as species-to-species variation (Ovaskainen & Abrego, 2020). Here, we assessed the spatial structure of the first three latent factors.

3.4 Results

The MCMC convergence was satisfactory indicated by the mean (and SD) of the potential scale reduction factor being <1.1 for both *beta* and *gamma* parameters, reflecting species responses to the environment and the role of traits, respectively (Supplementary figure 9.2). The effective sample size of the MCMC was close to the number of posterior samples, and we can therefore assume samples not being autocorrelated (Supplementary figure 9.2). The explanatory power of the model had a mean AUC of 0.89, Tjur R^2 of 0.246 and RMSE of 0.199, while the mean predictive power (based on a 5 fold cross validation) was of 0.88, 0.24 and 0.2, respectively (Supplementary Table 9.2). Although there are four exceptions (i.e., *Pholis gunnellus* for AUC, and *Phycis* *blennoides*, *Dicentrarchus labrax* and *Trachinus draco* for Tjur R^2, being the difference of minimal), the explanatory power always outperformed the predicting power, showing no major signs of model overfitting (Supplementary figure 9.3).

Variance partitioning and traits

The variance in species' occurrence explained by the model was attributed to both, the included fixed and random effects that explained on average 35 and 65% of the variance, respectively (Figure 3.2). The spatial random effect was the variable that explained most variability across species, i.e. 50%. Subsequently, the temperature variables (i.e., SBT and SBT seasonality), explained 25% of the variance. Finally, year and productivity explained 12 and 7% of the variance, respectively.

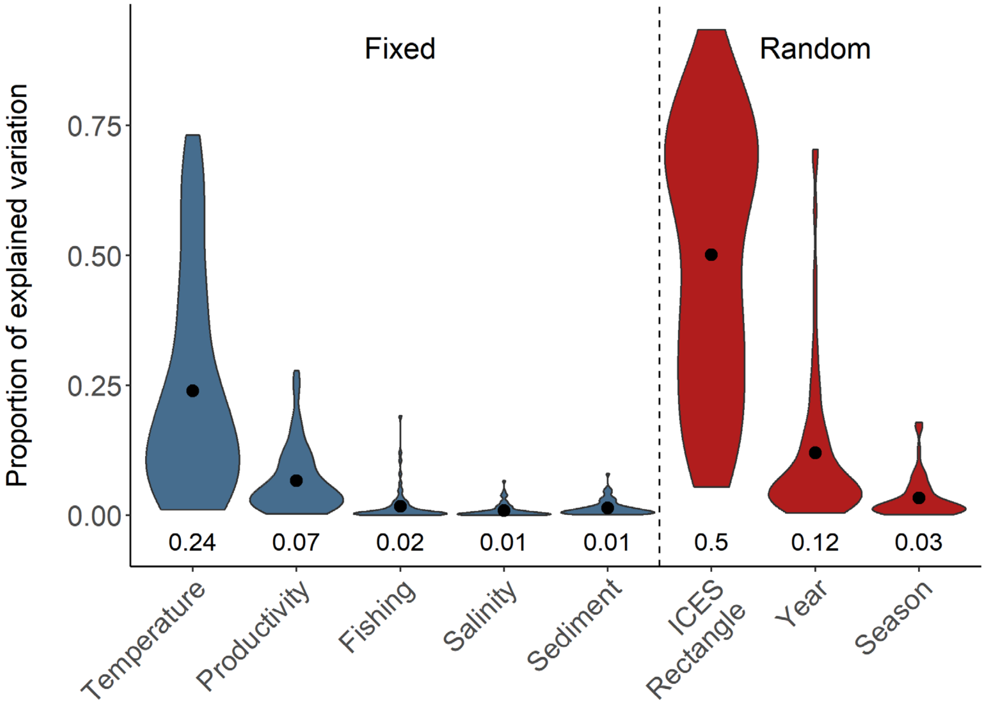

Figure 3.2. The proportion of total variation explained by each group of variables across species. The black dot denotes the mean variance explained by each covariate across the whole fish community, and the actual value is found below each violinplot. The variables belonging to the fixed and random parts of the model are shown on the left and right part of the model, respectively, and separated by a dashed line.

The remaining variables, namely season, sediment SBS seasonality and fishing, each explained ≤5% of the variance in species occurrences. Nonetheless, the contribution of each of each of the variables (both fixed and random) varies across species (Supplementary Figure 9.5). The species responses to the environmental variables were partially explained by the set of traits included in the model. The proportion of species responses to the different environmental variables explained by traits varied from a maximum of 61% for the mixed sediment, to a minimum of 11% for fishing effort (Supplementary Figure 9.4). From the thirteen environmental variables considered (HMSC treats each sediment type as an individual variable), traits explained more than 20% of the response in seven, and between 10-20% in six environmental variables.

Species niches and trait-environment relationships

There is a great diversity of species-specific responses to the set of environmental variables included in the model with a high level of statistical support (posterior probability >0.95), including negative, positive, or non-significant relationships (Figure 3.3; Supplementary Figure 9.6), such as the derived SBT responses of Atlantic cod (*Gadus morhua*), sprat (*Sprattus sprattus*) and European eel (*Anguilla anguilla*). We found that among the total variance of individual species occurrences, 12.5% could be explained by traits. From the included traits, age at maturity, growth coefficient K, maximum length, body shape, caudal fin shape, feeding mode and habitat show a response to at least one of the environmental covariates (Figure 3.4). For example, the growth coefficient K and age at maturity show a negative response to SBT, while age at maturity and maximum length demonstrate a negative or positive response to SBT seasonality, respectively. We found strong support for phylogenetic niche conservatism, with the phylogenetic correlation parameter *rho* being 0.82 (95% credible interval: 0.62-0.89). This indicates that a set of phylogenetically-structured traits, beyond the traits already included in the model, likely influence species niches.

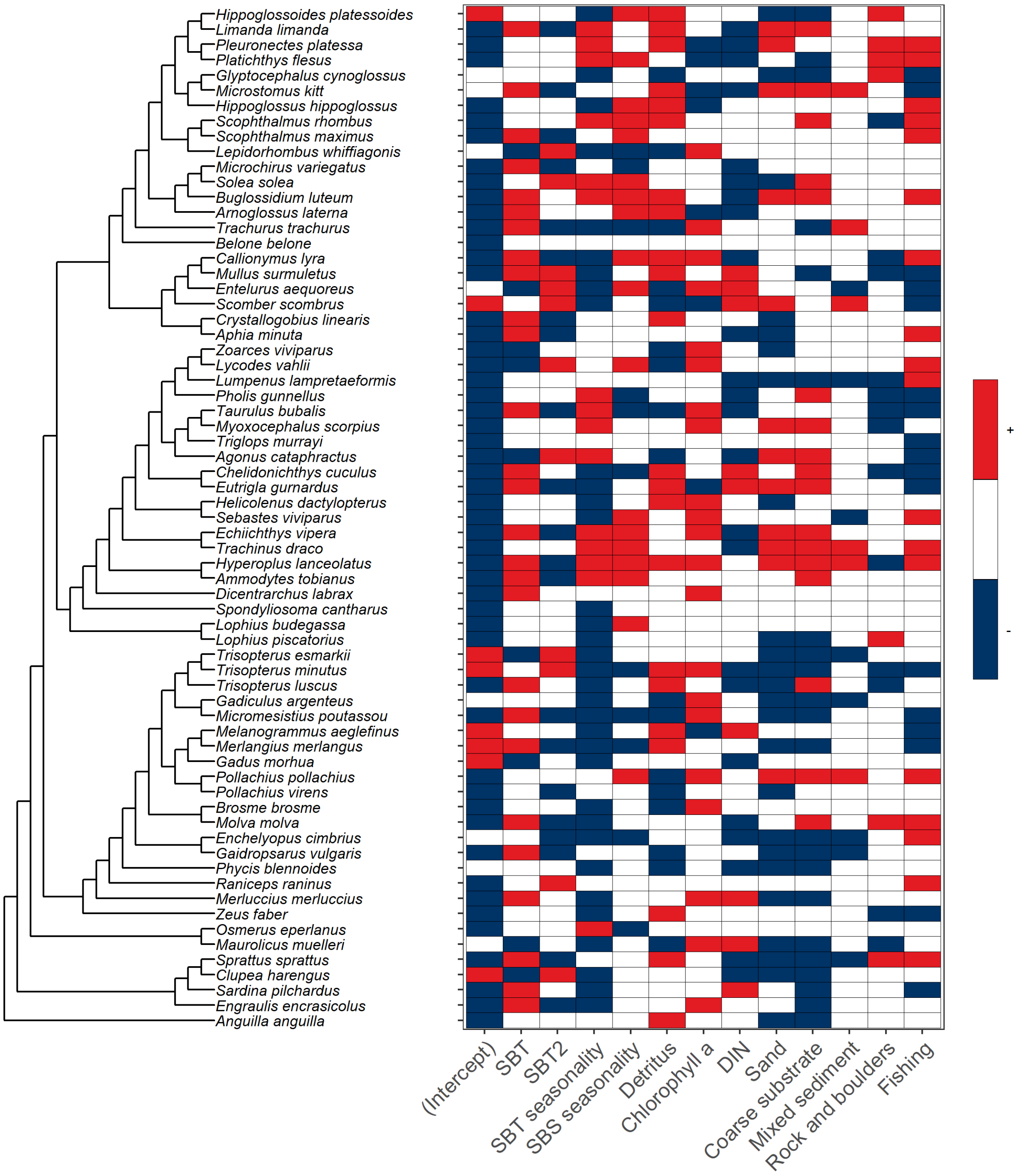

Figure 3.3. Heatmap of estimated beta coefficients indicating positive (red), negative (blue) or no relationships (blank) of species responses to the set of environmental covariates included (with at least a posterior probability of 0.95). Species are sorted vertically according to their phylogenetic relatedness.

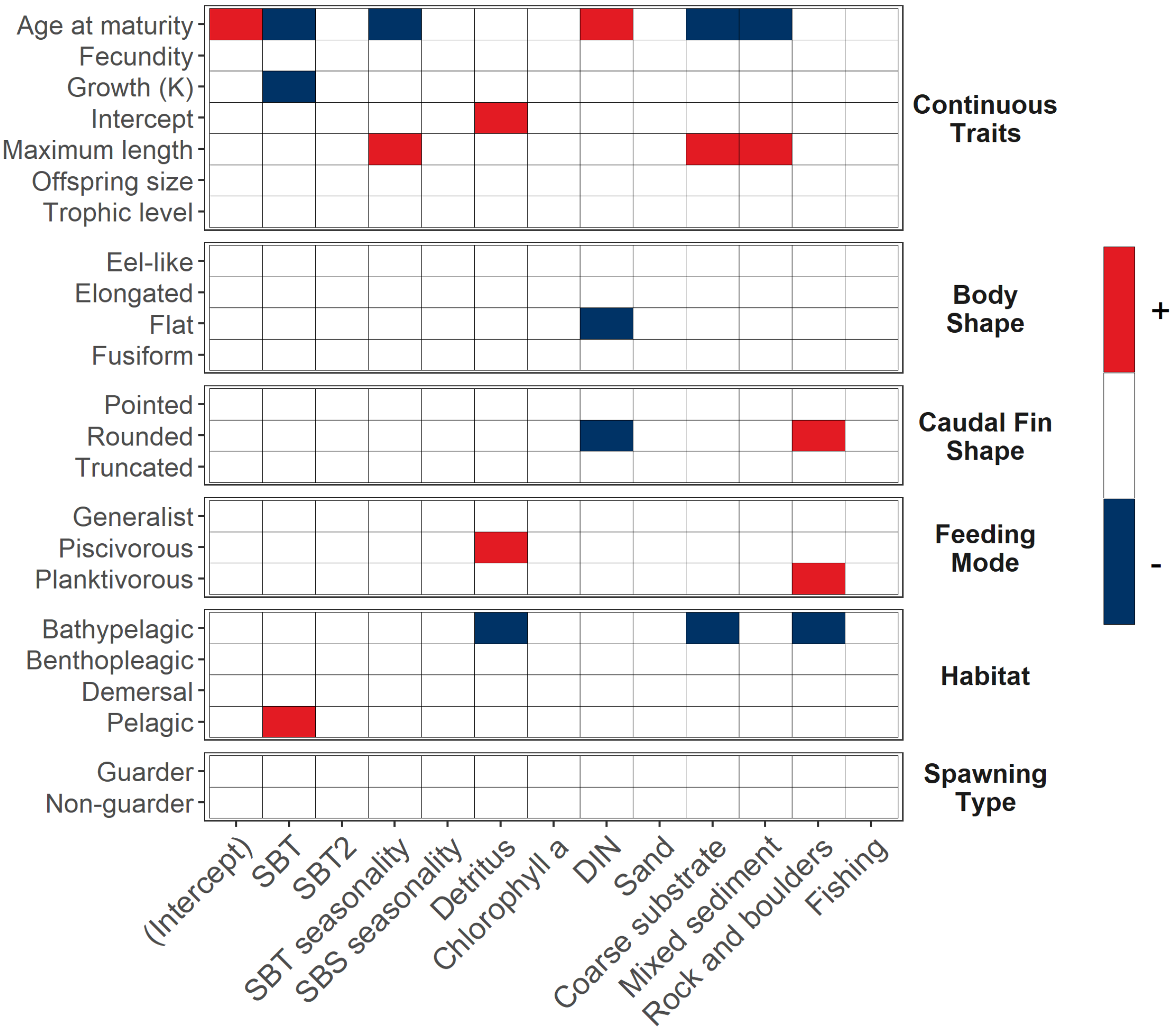

Figure 3.4. Heatmap of estimated gamma coefficients indicating positive (red), negative (blue) or no relationships (blank) of traits to the set of environmental covariates included (with at least a posterior probability of 0.95).

Additionally, we explored the trait relationship with surface chlorophyll *a* concentration, as traits explain a substantial proportion of species response towards this covariate (i.e., 37%; Supplementary Figure 9.4). We found strong relationships between some community-weighted mean traits and chlorophyll *a* concentration (posterior support >0.95; Supplementary Figure 9.7). A positive response to chlorophyll *a* concertation was found for demersal (habitat), eel-like and flat body shapes, pointed and rounded fin shapes, guarder spawners and offspring size. In contrast, negative responses were found for bathypelagic and pelagic (habitat), fusiform, truncate fin, non-guarder spawners, fecundity and trophic level.

Species associations

Since the spatial random factor is the variable that explains most variance of the community composition, we further explored the residual species associations at the included spatial scale (ICES statistical rectangles). After accounting for the fixed effects, representing species responses to the environment conditioned on their traits, we found pronounced residual species co-occurrence patterns with strong statistical supported (posterior support >0.95). These reflect both positive and negative pairwise species associations (Figure 3.5), potentially reflecting biotic interactions, dispersal limitation and/or patterns arising from environmental covariates that have not been included in the model. The first latent factor showed high values in both northern and southern regions of the North Sea, but lower values in the central area, especially towards the western part (Figure 3.6). Low values were also found in the easternmost region, along the German coast. Latent factor 2 shows a more heterogeneous pattern, with alternating high and low values in the north, while towards the center and southern part there is a smoother transition between larger regions characterized by either low, or high values. Lastly, latent factor 3 shows a very clear and smooth latitudinal gradient, from high values in the north to low in the south-west, with the exception of three outlying rectangles in the English Channel that have high values.

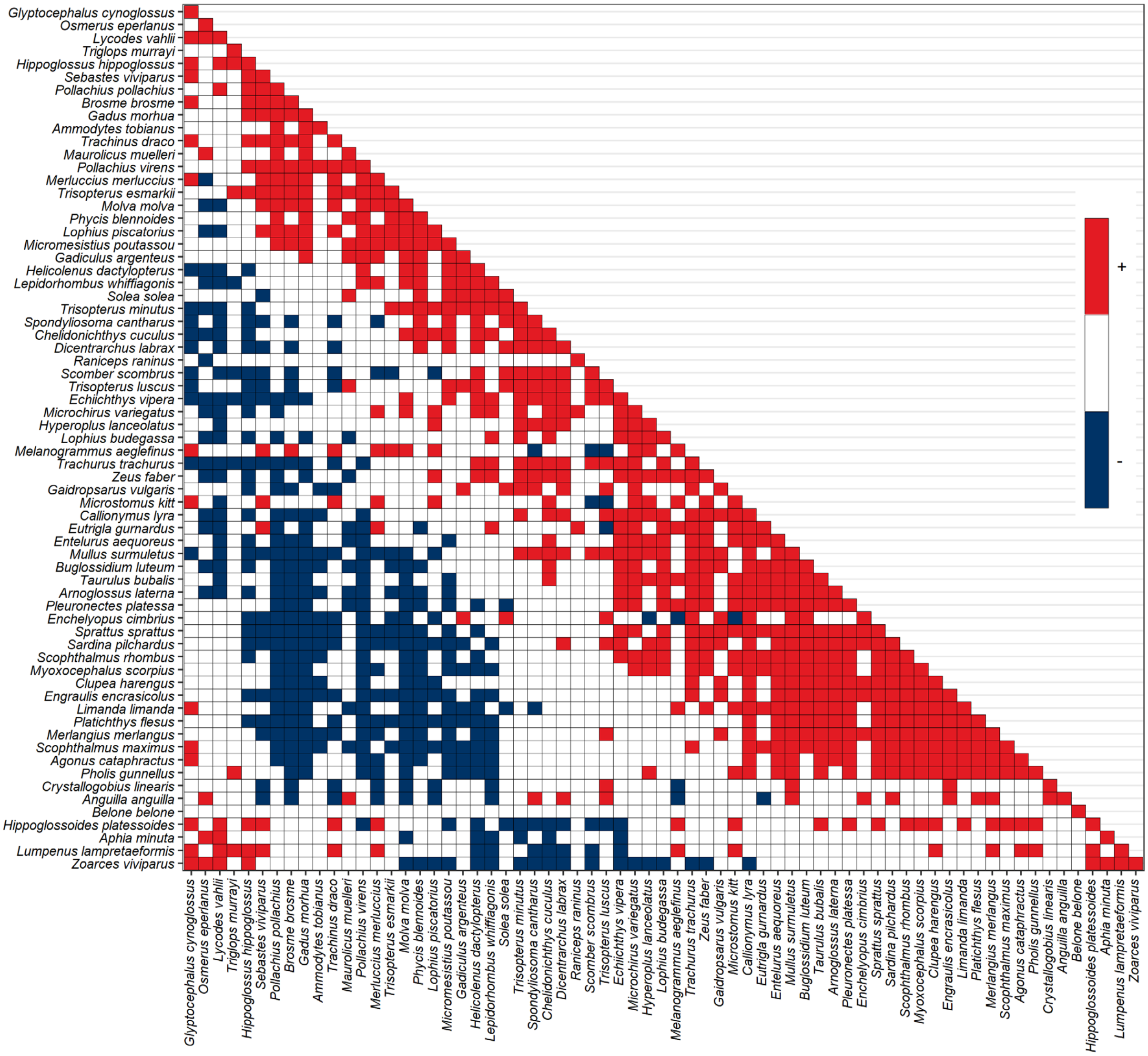

Figure 3.5. Residual species association matrix at the random effect level of ICES statistical rectangle. The red and blue colors show species with positive and negative pair-wise associations (with at least a posterior probability of 0.95), respectively.

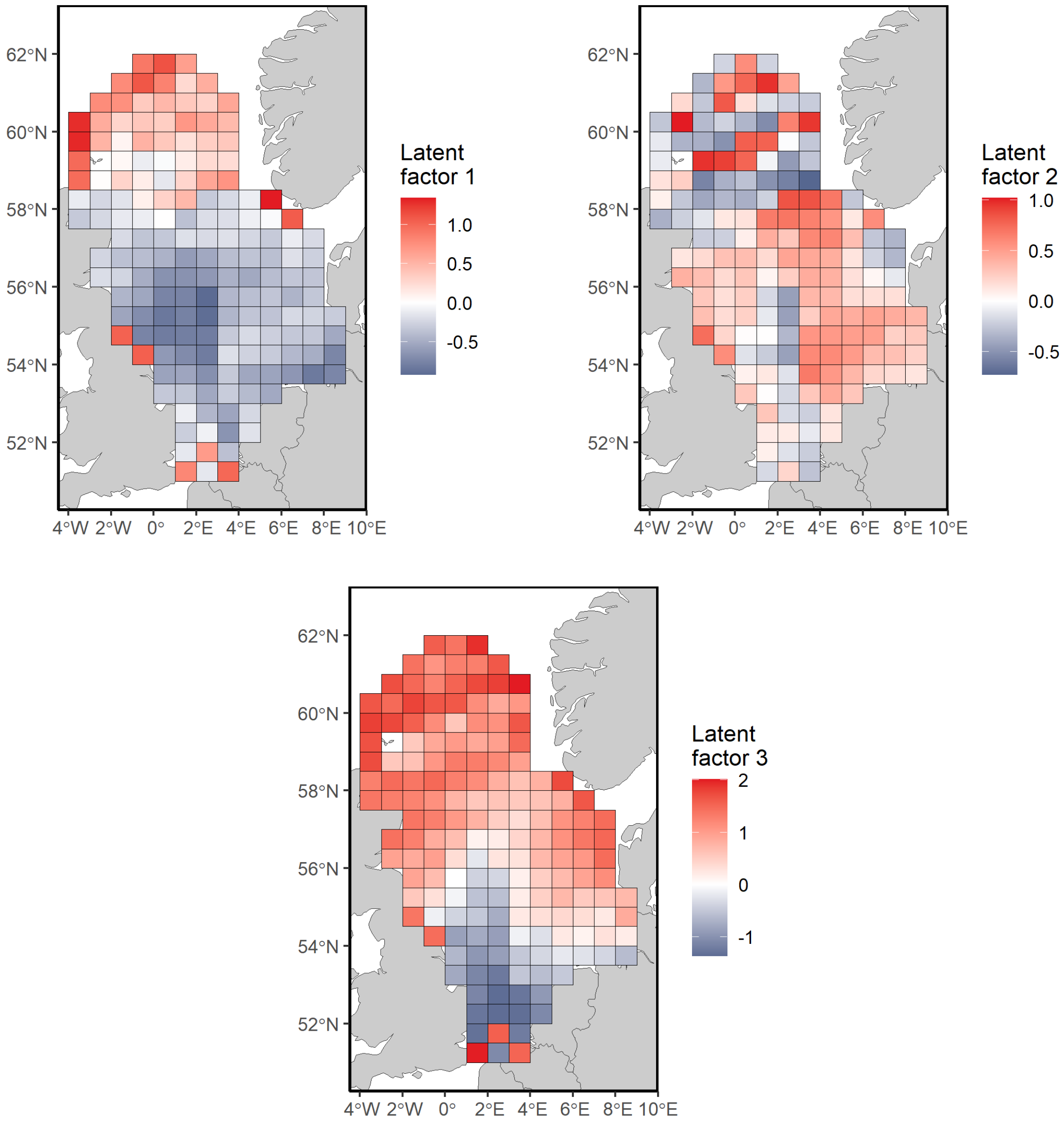

Figure 3.6. Maps of the first three spatial latent factors at the ICES rectangle random level. The latent factors comprise spatially-structured site scores of model residuals, representing unexplained abiotic patterns, dispersal limitation and biotic interactions as species-to-species associations.

3.5 Discussion

Understanding the underlying assembly processes shaping communities is crucial to predict and anticipate future shifts in species distributions and community composition due to climate change (Beukhof *et al.*, 2019a; Maclean & Wilson, 2011; McGill *et al.*, 2006; Mouillot *et al.*, 2013). While recent developments in JSDMs allow modelling multiple species' responses to the environment (Je*tz et al*., 2019), their implementation to understand the responses and range shifts of large, mobile and commercially important marine fish species are scarce (Monaco *et al.*, 2021; Zhang *et al.*, 2022). To overcome this knowledge gap, we used Hiearchical Modelling of Species Communities (HMSC) to investigate the main drivers and assembly process acting on community composition, as well as the contribution of traits on species responses, using the North Sea fish community as a case study.

The variance explained by the fixed effects of the model reflects species responses to the environment, conditioned on their traits, and thus the resulting patterns of community composition arising from environmental filtering. This key assembly process explained about 35% of the observed species' occurrences. However, this is likely a conservative estimate since we cannot discard the possible contribution of additional, yet unaccounted environmental variables, whose effects might be captured in the random part of the model (Ovaskainen *et al*., 2017). Nevertheless, our results suggest that temperature-related covariates such as SBT and SBT seasonality are the main environmental drivers acting on species distribution and community composition, which is in accordance with previous studies on biodiversity indicators in the area (Beukhof *et al.*, 2019b; Burrows *et al.*, 2019; Dulvy *et al.*, 2008; Rutterford *et al.*, 2015). Since temperature is the main environmental driver, the expected warming following the increasing pace of climate change will likely lead to shifts in the community as species track their thermal niche (McLean *et al.*, 2021; Pinsky *et al.*, 2013). This lends support to previous findings demonstrating a northward range shift and deepening of the North Sea fish community in response to warming (Dulvy *et al.*, 2008; Perry *et al.*, 2005).

Although the North Sea is a heavily fished area with a long history of commercial exploitation (Bennema & Rijnsdorp, 2015; Callaway *et al*., 2007; Couce *et al*., 2020), our study shows that fishing intensity had a minor direct role in explaining the current overall species' occurrence patterns. While fishing pressure can have direct long-term effects on individual species distributions and demography (Dulvy *et al.*, 2004; Engelhard *et al.*, 2014; Genner *et al.*, 2010; Last *et al.*, 2011), the effects on overall community composition are more likely visible in species abundances or biomasses, since a very high fishing pressure would be needed to observe local extinction of species (Jennings & Kaiser, 1998)(but see Las*t et al*., 2011). Moreover, the effects of fishing are more likely to be observed when fishing is introduced in an unfished, or moderately exploited system (Jennings & Kaiser, 1998), while the North Sea has been exploited for centuries (Bennema & Rijnsdorp, 2015). Consequently, past changes in species abundances and community composition arising from fishing, notably the historical decline and disappearance of many large and slow growing species, including sharks and rays (Bennema & Rijnsdorp, 2015; Last *et al.*, 2011) may have acted as a primary filtering process on the present communities, even if we cannot attribute a strong overall effect using observations from recent decades. The effect of fishing on species occurrence is highly unlikely, at least on a time scale as the one used here. Therefore, to further investigate the effects of fishing on species occurrence there is a need for studies analyzing longer temporal series (Beukhof *et al.*, 2019a).

The large variety of individual species responses to the environment illustrates the diversity of environmental niches within the fish community. Notable examples include the opposite responses of the key ecologically and commercially exploited species, cod (*G. morhua*) and sprat (*S. sprattus*), whose reproduction and general population dynamics has been shown to be either negatively, or positively related to increasing temperature (e.g., Lindegren & Eero, 2013; MacKenzie *et al.*, 2012; Sguotti *et al.*, 2018; Stige *et al.*, 2006). In order to disentangle this complexity and better understand the underlying mechanisms shaping species niches and community composition at large, embracing a trait-based approach is clearly warranted (Funk *et al*., 2017). In our model, the included traits were able to explain 12.5% of the variation in species niches across the whole community. In particular, we found that age at maturity, growth, maximum length and pelagic fish are responding to temperature. The negative relationships between age at maturity with temperature and temperature seasonality are consistent with trait-environment relationships demonstrated for marine fish across large spatial scales (Beukhof et al. 2019a), while the negative relationship with growth was not supported in these previous studies. Whether due to the smaller spatial extent of our study, or reflecting a region, or ecosystem specific response is unclear and merit further investigation. Nevertheless, our findings highlight the importance of fish life history traits and its reliance on temperature and its seasonality (Beukhof *et al.*, 2019b, 2019a). Furthermore, we found that traits strongly condition the responses of species to other environmental factors, notably sediment type and chlorophyll *a* concentration, even if the importance of these environmental factors explaining the actual species occurrences is rather low. This highlights the relevance of accounting for traits to better characterize species niches and responses to other factors besides temperature, reflecting their potential associations to particular habitats, or areas with different (primary) productivity. The community weighted means for traits associated to the seafloor (demersal habitat, flat or eel-like shape) were found to have a positive response surface chlorophyll *a* concentration. Also, a positive response was found for rounded fin shape, which tends to be associated to species that have small swimming ranges and live in complex habitats (Giammona, 2021). A likely explanation for the above-mentioned positive relationships is the sinking of organic matter, which is higher in more productive areas. This organic matter is a direct energetic input to the benthic habitats, which can thrive better compared to other areas where this energetic input is lower. In contrast, the negative response for pelagic habitat, fusiform body shape, truncate fins and higher trophic levels is likely linked to highly mobile and pelagic species (Webb, 1984). Finally, the presence of a strong phylogenetic signal in our model suggests that there is likely a set of traits shared among phylogenetically similar species of the broader taxon covered that have not been included in the model that might shape species responses to the environment. Hence, the inclusion of such traits would bring in relevant information that could improve our understanding of the underlying processes determining species niches and community composition. Therefore, we stress the need for further trait-based studies identifying key response traits of marine fish and their links to environmental conditions across multiple species and taxon.

After having accounted for the fixed effects, and similar to other HMSC works, the random effects in the model explain a large proportion of the variance (Chiu et al. 2020, Marjakangas et al. 2021, Weigel et al. 2022), especially the spatial random effect (i.e., 50%). This means that there are other spatially-dependent and stochastic processes besides those captured by the environmental drivers that act on species distributions and community composition. The spatial random effect can be explained by the combination of three different, yet not mutually exclusive assembly processes, including: (i) biotic filtering resulting from species interactions; (ii) filtering due to small-scale dispersal limitation; and (iii) filtering caused by environmental variables unaccounted for in the model. Although the environmental variables included in the model are among the primary covariates affecting species distribution and community composition in the North Sea (Cohen et al, 2017), there may still be other unaccounted covariates that contribute to the patterns captured by the spatial random effect. Yet, it is likely that a significant amount of such patterns is derived from biotic interactions and dispersal limitation of the species. The residual species association matrix (derived from the spatial random effect) showed that even after accounting for species niches, there are significant species co-occurrence patterns demonstrating several pairs, or groups of species that co-occur more (or less) often than what would be expected from their environmental niches alone. While we cannot conclude concrete ecological interactions from such kind of co-occurrences (Blanchet *et al*., 2020), they may still provide indications for potential biotic interactions through the positive and negative residual associations (Araújo & Rozenfeld, 2014; Morales-Castilla et al, 2015; Ovaskainen & Abrego, 2020). One potential interaction could be reflected through positive co-occurrence is a facilitation process (D'Amen *et al.*, 2018; Morales-Castilla *et al.*, 2015), where the presence of a species increase the probability of occurrence of another species and vice versa. Another, more common and plausible biotic interaction is a predatory (feeding) interaction, where a given predator is expected to be found in an area relatively close to where their prey can be found. Consequently, a spatial overlap in their occurrences should be expected, at least at a scale of a few km, such as considered in this study. In terms of the documented negative associations, these could reflect competitive exclusion (MacArthur, 1984) where two species with an overlapping environmental niche, but competing for a common resource would have negative co-occurrences. Lastly, the pairwise species associations could be reflecting responses to third party species, i.e., other species within the community that have not been explicitly considered in this study (Popovic *et al.*, 2019). This way, a positive association between two of the modelled species could represent a common response to a third unaccounted species. Taken together, the latent factors of our model reflect underlying community assembly processes shaping species associations, whether these are due to biotic interactions, or the other processes listed above. Interestingly, some of the pronounced spatial structures and patterns of these latent variables partly resembles areas of the North Sea previously suggested as being influenced by limiting similarity (Callaway *et al.*, 2002; Dencker *et al.*, 2017). However, more research is needed to better understand species co-occurrences patterns and the underlying assembly processes explaining the pronounced spatial structuring of the latent variables demonstrated in this study.

3.6 Conclusions

Our modelling study aimed to investigate the relative importance of different community assembly processes and identify drivers shaping the fish community in the North Sea. Using an advanced JSDM (i.e., HMSC) we show that environmental filtering, primarily related to temperature and seasonality, explains a large part of the variance in species distributions and community composition. This supports previous findings that predict important shifts in natural communities with global warming (Freeman *et al*., 2018; Last *et al*., 2011; Perry *et al*., 2005; Pinsky *et al*., 2013; Poloczanska *et al*., 2013) and highlights the need to predict such shifts to anticipate and adapt the necessary conservation and management actions. We also found that there are other assembly processes with a strong spatial structure playing a role in shaping these communities, while at the same time significantly improving model performance. Notably, we argue that biotic factors are likely important in this regard but call for further research to better understand the underlying interactions involved. Finally, we stress the importance of accounting for species traits since their inclusion improves the mechanistic understanding on species responses to environmental change. Hence, model predictions from JSDMs accounting for traits, environmental niches and potential interactions among multiple species can provide relevant simulations and forecasts of species, or community-level responses to various climate and management scenarios deemed relevant by a broad range of stakeholders. This has the potential to inform spatial management and conservation efforts, such as the placement of marine protected areas aiming to preserve biodiversity and its associated services vital for human well-being.

3.7 Acknowledgements

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Chapter 4

4. Assessing the forecast horizon for reliably predicting marine biodiversity change

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4.1 Abstract

Climate change is driving shifts in marine species composition, distribution, and ranges as they adjust to changing thermal conditions. To anticipate these shifts, we require reliable models to forecast future changes in marine biodiversity and composition. In this study, we assess the predictive performance of a Bayesian joint species distribution model (JSDM) framework in representing historical spatio-temporal changes in taxonomic and functional biodiversity using long-term monitoring data on fish community composition and traits across the Northeast Atlantic. We use 90,029 unique hauls from 13 scientific bottom trawl surveys spanning 33 years (1989-2021) to model the occurrence and biomass of 151 fish species. Our results reveal that temperature- and productivity-related variables are the primary environmental drivers of both occurrence and biomass models. While the models demonstrate decreasing predictive performance over time, the performance remains reliable within the first 10-20 predicted years. Notably, the models exhibit better predictive skill for functional (trait) composition compared to taxonomic, and presence-absence compared to biomass, suggesting a stronger conservation of functional aspects of the community and an inadequate representation of key processes regulating species biomass dynamics in the models. Overall, our study provides robust models for predicting taxonomic and functional aspects of biodiversity, facilitating exploration and anticipation of climate change effects in future scenarios.

4.2 Introduction

We are currently experiencing a rapid and accelerating loss of biodiversity worldwide, largely due overexploitation, habitat loss and climate change (Butchart *et al.*, 2010; IPBES, 2019; Lee *et al.*, 2023; Pimm *et al.*, 2014). Global warming has also caused shifts in species distribution, primarily towards higher latitudes, as species follow their thermal niche (Dulvy *et al.*, 2008; Freeman *et al.*, 2018; Pinsky *et al.*, 2013). The rate of extinctions and distributional shifts varies between taxa (Perry *et al.*, 2005; Poloczanska *et al.*, 2013), suggesting that community composition, as well as the structure and functioning of ecosystems may be profoundly altered (Harley *et al.*, 2006). Consequently, understanding the key drivers and underlying assembly processes determining species distribution and composition is essential to anticipate the effects of a changing environment on biodiversity and ecosystem functioning (Harley *et al.*, 2006; McGill *et al.*, 2006; Micheli *et al.*, 2017; Mouillot *et al.*, 2013). Furthermore, more accurate predictions biodiversity changes may allow us to evaluate and devise effective management actions to halt the current loss of biodiversity worldwide (Mace *et al.*, 2005; Pimm *et al.*, 2014). The accomplishment of this ambitious policy goal is regarded to be achievable through an effective and well-connected system of protected areas jointly covering 30% of the land and ocean space (Convention on Biological Diversity, 2021; European Commission, 2020; Hermoso *et al.*, 2022). However, the designation of protected areas, especially towards "areas of particular importance for biodiversity" (European Commission, 2020) needs to be based on a suite of indicators reflecting the multiple facets of biodiversity (Cavender-Bares *et al.*, 2020; Pereira *et al.*, 2013). While the selection of such indicators is facilitated by the recent development of Essential Biodiversity Variables (EBVs) (Navarro *et al.*, 2017; Pereira *et al.*, 2013), robust modelling frameworks to estimate and forecast EBVs is needed in order to inform decision-makers and managers (Jetz *et al.*, 2019).

Recent developments in statistical community models, i.e., joint species distribution models (JSDMs), have shown improved predictive performance compared to traditional methods, especially when modeling rare species (Norberg *et al.*, 2019). However, the degree to which JSDMs are capable of robustly predicting different facets of biodiversity following anticipated environmental changes is still poorly known. In particular, there is no consensus on a the temporal decay in prediction accuracy and which forecast horizon would still provide useful ecological forecasts to inform decision making (Petchey *et al.*, 2015). This is predominantly relevant for the designation and implementation of marine protected areas (MPAs) that typically operates over decadal scales linked to the formal marine spatial planning (MSP) process (Edwards & Evans, 2017; Ehler & Douvere, 2009b).

Here, we performed the first large-scale assessment of a community model forecast horizon to adequately predict multiple biodiversity indicators using a Bayesian JSDM framework (Ovaskainen *et al.*, 2017). More specifically, present a temporal cross validation routine to evaluate the predictive performance of past spatio-temporal changes in taxonomic and functional EBVs, leveraging long-term monitoring data of the Northeast Atlantic fish community composition including species specific traits. Moreover, we explored the environmental drivers shaping marine fish communities in the Northeast Atlantic.

4.3 Methods

Community data

We gathered a comprehensive data set on fish species distribution and biomass from 13 scientific bottom-trawl surveys conducted across the Northeast Atlantic Ocean (Supplementary figure 10.1; Supplementary table 10.1. Bottom trawl surveys included in the study.). The data set encompass 90,029 unique hauls spanning 33 years (1989-2021), thus capturing the active period for most surveys and providing an extensive spatio-temporal coverage of our study area. We focused our analysis solely on fish taxa (i.e., *Elasmobranchii*, *Actinopteri*, *Holocephali*, *Myxini*, *Petromyzonti* and *Teleostei*) identified at the species level and that exhibited a minimum prevalence of 0.1% (i.e., >90 occurrences), resulting in a selection of 151 species. The species names were cross-referenced and updated using the World Register of Marine Species (WoRMS Editorial Board, 2022). For each of the hauls we recorded the presence-absence of species, as well as their biomass standardized for sampling area (km^2) and trawl gear catchability following methodologies detailed in previous studies (van Denderen *et al.*, 2023; Maureaud *et al.*, 2019; Walker *et al.*, 2017).

Trait data

To account for functional (trait) aspects of biodiversity, we selected 6 traits that broadly represent the life history, reproduction, morphology and diet of species (Dencker *et al.*, 2017) following a formal framework developed for other marine organisms (Litchman *et al.*, 2013). Trait information was retrieved from the database created by Beukof and collogues (Beukhof *et al.*, 2019c). The life history of each species was characterized by two parameters: age of maturity (in years) and the von Bertalanffy growth coefficient K (measured in year^{-1}), while the reproductive traits were represented by offspring size, i.e. egg diameter (measured in mm). Morphological characteristics were assessed through maximum length (in cm) and the caudal fin aspect ratio as a proxy for mobility. Lastly, we considered diet by including the trophic level of each species.

Environmental data

To represent the environmental conditions at each unique haul, we retrieved environmental and physical variables from the model re-analysis products of the NEMO-MEDUSA model (Gurvan *et al.*, 2022; Yool *et al.*, 2013). This provided us with surface and bottom details concerning temperature (ºC), salinity (PSU), detritus concentration (mmol N per m^3), chlorophyll *a* concentration (Chl *a*; mmol N per m^3) and dissolved inorganic nitrogen concentration (DIN; mmol N per m^3), as well as depth (m). Additionally, we computed the annual standard deviation for temperature, salinity, and Chl *a* at each location, as a proxy for seasonal variation (Beukhof *et al.*, 2019a; Dencker *et al.*, 2017; Maureaud *et al.*, 2019). Due to the lack of available long-term data on fishing effort throughout the area, the potential effects of commercial fishing were not explicitly accounted for. However, previous large-scale studies on marine fish communities in the area found no, or only weak effects on the species distribution and community trait composition

(Beukhof *et al.*, 2019b; Dencker *et al.*, 2017). After checking for potential collinearity we omitted highly correlated variables (i.e., with Pearson coefficient >0.7; Supplementary figure 10.2). The final set of environmental covariates comprises sea bottom temperature (SBT), SBT seasonality, sea bottom salinity (SBS), SBS seasonality, seafloor detritus, surface DIN, surface Chl *a*, surface Chl *a* seasonality, seafloor Chl *a* seasonality, and depth.

Model fitting

We used the Hierarchical Modelling of Species Communities framework (HMSC; Ovaskainen & Abrego, 2020; Ovaskainen *et al.*, 2017), a Bayesian JSDM firmly rooted in community ecology theory (Ovaskainen & Abrego, 2020). The hierarchical structure enables the identification of shared patterns in species responses to the environment, improving the performance for many species, especially the rare ones (Norberg *et al.*, 2019; Ovaskainen & Soininen, 2011; Poggiato *et al.*, 2021). Additionally, HMSC integrates trait information, allowing for the examination of how traits influence species niches and their community-level responses to the environment. When including phylogenetic information, HMSC also considers underlying phylogenetic constraints of species responses to the environment, while accounting for non-independence of species regarding their traits, i.e. closely related species share more similar traits. In this study, we employed HMSC to model the fish community, treating each unique sample event as a response variable. Given the zero-inflated nature of the data, we adopted a hurdle approach. This involved utilizing one model for presence-absence (probit regression) and another model for biomass conditional on presence (log-linear regression). As fixed effects we incorporated the environmental covariates detailed above, including quadratic terms for sea bottom temperature (SBT) and sea bottom salinity (SBS) to account for potential non-linear species' responses. To account for potential seasonal differences in distribution and biomass (i.e., linked to migrations and spawning) we further included spring/summer and autumn/winter as a fixed factor.

Furthermore, we fitted an additional set of models, incorporating spatial and temporal random effects. We referred to the model set with random effects as 'full models' and those without as 'environment-only models. The full models encompassed spatially (Ovaskainen *et al.*, 2016) and temporally (yearly) structured latent variables. Spatial units were represented by hexagonal cells (N = 574 cells), each covering an area of 7,774 km^2. To determine the relative importance of the environmental covariates we partitioned the explained variation among the fixed and random effects (Ovaskainen & Abrego, 2020; Ovaskainen *et al.*, 2017).

Each model was fitted with four Markov chain Monte Carlo (MCMC) chains taking 250 samples per chain, resulting in 1,000 posterior samples. The thinning applied was specific to each model with the aim of achieving a good model convergence with a reasonable use of computational resources (Supplementary table 10.2. Model fitting specifications.). We assessed MCMC convergence by examining the potential scale reduction factors (PSRFs; Gelman & Rubin, 1992) of model parameters where values <1.1 indicate satisfactory convergence (Tikhonov *et al.*, 2020).

Cross-validation and forecast horizon

We developed an ad-hoc temporal cross-validation routine to assess the predictive performance of our models (Figure 4.1). To achieve this, we partitioned the data into three decades (1989-1999, 2000-2009, 2010-2021) and trained separate models on each decade. In evaluating the explanatory power of these trained models, we employed metrics such as AUC and Tjur R^2 for species presence-absence, R^2 for biomass conditional on presence, and root mean square error (RMSE) for both (Ovaskainen & Abrego, 2020). Subsequently, we tested the models on the remaining decades to assess their out-of-sample predictive performances. For example, if the model was trained on the decade 1989-1999, it was then tested on decades 2000-2009 and 2010-2021. To that end, we constructed three additional decadal models for all species exhibiting a minimum prevalence of 0.1% in each decade, resulting in a selection of 139 fish species. Each decadal model used the same training data as the whole-period models, but was constrained to observations within the respective decade.

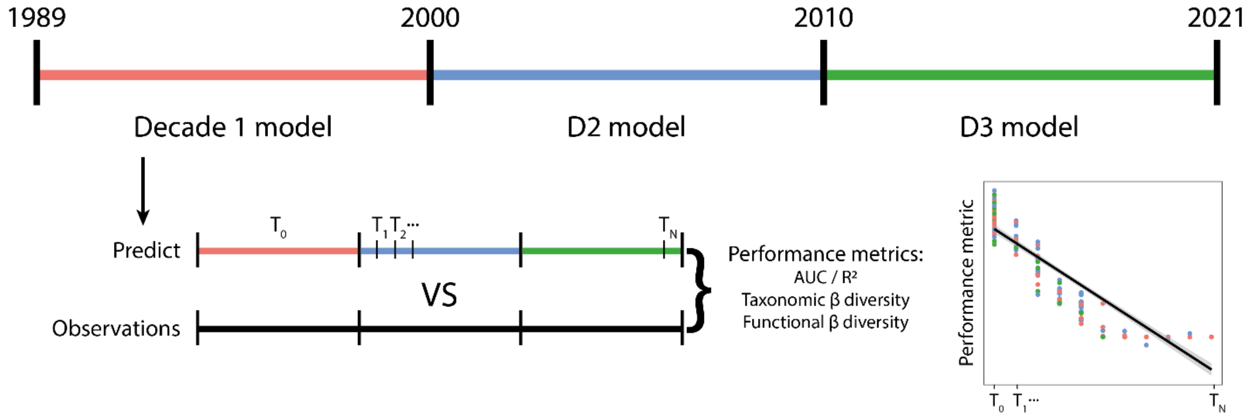

Figure 4.1. Cross-validation routine workflow. In the example, decade 1 model is fitted and then used to predict the communities in all three decades. Then predictions are tested against true observations with different performance metrics, and then the change of performance is assessed through time.

To assess model performance beyond the time period used for training we estimated a suite of metrics targeting various aspects of biodiversity, including both species- and community level EBVs (Jetz *et al.*, 2019; Pereira *et al.*, 2013). Species-level distribution and biomass was represented by the AUC and R^2 of observed vs predicted values, respectively. To assess differences in observed and predicted community composition we used the Whittaker index (Whittaker, 1960) for occurrence and the Bray-Curtis dissimilarity for biomass (Bray & Curtis, 1957). Additionally, we evaluated functional (trait) community composition through functional β-diversity following Magneville et al. (2022). For that, we computed a species distance matrix based on the six traits considered and then calculated a Richness-like ($q = 0$) and a Shannon-like ($q = 1$) metric for occurrence and biomass, respectively. While for the species-level biomass performance we used values from biomass conditional on occurrence, for the community biomass performance we used the outputs from the hurdle model, i.e., combined the occurrence and the biomass conditional on occurrence models. For each of the metrics above we computed the annual mean values per decadal model at increasing temporal distance from the decade used for model training (either past or future). Using the annual means as the response variable and time since training as the explanatory variable (i.e., amounting to a maximum of 21 years), we fitted a linear model for each computed metric and projected the general trends in model performance up to 40 years beyond the training period. For interpretability we transformed all dissimilarity indices to similarity instead, such that values of 1 indicate excellent performance, and 0 poor performance.

Finally, we examined the predictive performance over space by computing each metric per hexagon grid cell and year. The species-level metrics were the RMSE of predicted vs observed occurrences and biomasses, while the community-level metrics reflect the similarity in taxonomic- and functional composition (β-diversity) between predicted and observed values. To assess the forecast horizon, we then computed a linear trend of the derived values and estimated the number of years that it takes for each metric to reach a certain performance threshold since time zero (i.e., the decade at which the model was fitted). In terms of the threshold values used, only the AUC has a predetermined level reflecting excellent (>0.8) or adequate (>0.7) performance (Mandrekar, 2010). For the other metrics we therefore tested the sensitivity of outcomes (i.e., in terms of forecast horizon) across a range of potential thresholds. More specifically, we considered 0.1±0.05 for RMSE based on occurrences and values of 1±0.5 for RMSE based on biomasses (i.e., that are not bounded between 0 and 1). For taxonomic- and functional β diversity we considered values of similarity amounting to 0.5±0.25. All analysis were performed in R version 4.2.1 (R Core Team, 2022) using the following packages: *Hmsc* (Ovaskainen & Abrego, 2020; Rahman *et al.*; Tikhonov *et al.*, 2021), *RANN* (Arya *et al.*, 2019), *vegan* (Oksanen *et al.*, 2022) and *mFD* (Magneville *et al.*, 2022).

4.4 Results and Discussion

The MCMC convergence for the whole-period and decadal models was satisfactory, indicated by the mean of the PSRF being <1.1 (Supplementary figure 10.3; Supplementary figure 10.4), with the exception of the whole period model for biomass (including random effects) that did not show fully satisfactory convergence. In terms of explanatory power, the occurrence models showed high performance overall, indicated by AUC values equal to or exceeding 0.9 for all decadal models (diagonal in Table 4.1), as well as for the whole-period full- (0.95) and environment-only (0.91) models. Conversely, the biomass models show more moderate explanatory power with R^2 values amounting to >0.22 for the decadal models, and 0.34 and 0.21 for the full and environment whole-period models, respectively. The decadal cross-validation routine shows high predictive performance for all occurrence models, indicated by AUC values ranging from 0.86-0.90 for the testing decades not used for model training (off-diagonal in Table 4.1). Conversely, the biomass models demonstrate considerably lower predictive power for decades used for testing with R^2 values ranging from 0.11 to 0.16 (off-diagonal in Table 4.1).

Table 4.1. Decadal models explanatory (diagonal) and predictive (off-diagonal) power for occurrence and biomass environment models. Columns indicate the training decade and rows the testing decade.

Model	Testing decade	Training decade		
		1990	2000	2010
Occurrence (AUC)	1990	0.90	0.87	0.86
	2000	0.88	0.91	0.90
	2010	0.86	0.89	0.91
Biomass (R^2)	1990	0.23	0.13	0.14
	2000	0.13	0.22	0.16
	2010	0.11	0.15	0.22

The variance partitioning for the environment-only models show that temperature- and productivity-associated covariates explain most of the variation in species distributions and biomass (Figure 4.2). For the full models more than half of the variance is instead attributed to the spatial and temporal random effects. This has direct implications for model forecasting since random effects are assumed to remain constant during predictions (Ovaskainen & Abrego, 2020). This means that even in the presence of pronounced past and future environmental changes, model predictions of species distributions will be more static and less suitable to represent species range shifts and changes in overall composition and diversity. Hence, since both MCMC convergence and performance of the environment-only models was equal to, or even better compared to the considerably more complex and computationally demanding random effect models we assessed the predictive performance and forecast horizon exclusively on the basis of the environment-only models.

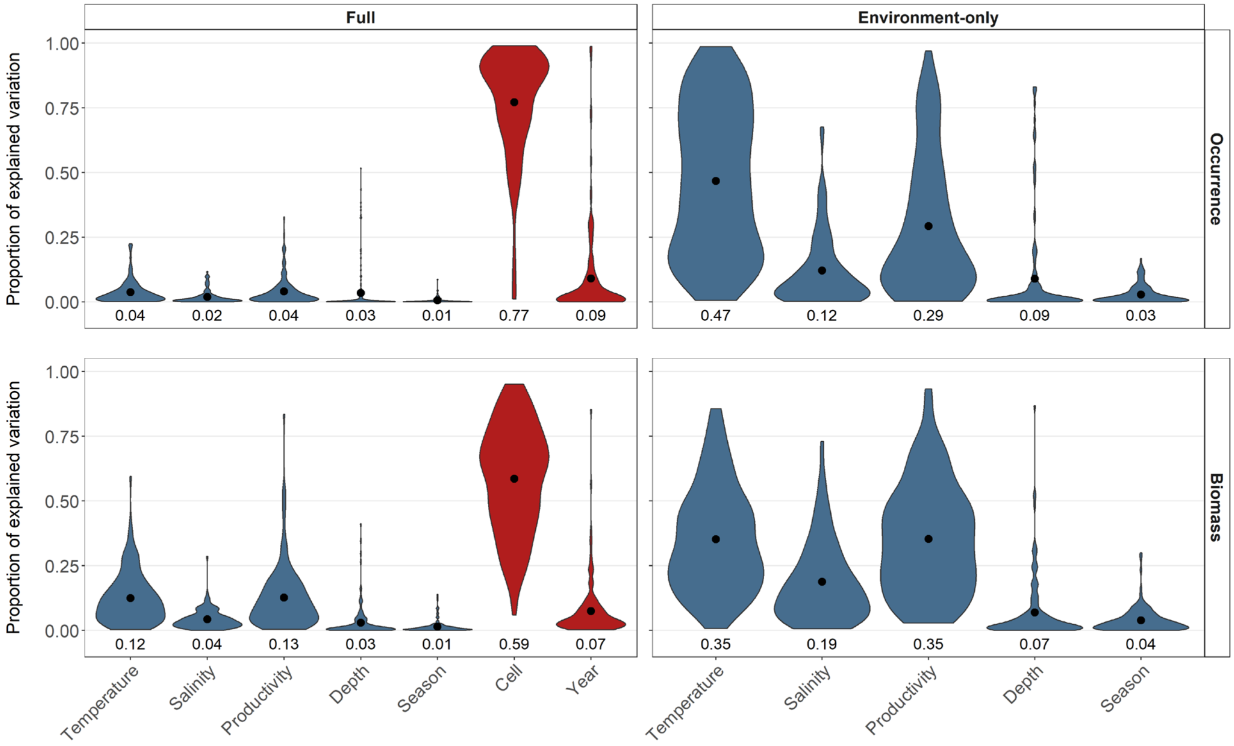

Figure 4.2. Variance partitioning of fixed (blue) and random (red) effects for the full (left) and environment-only models (right) for occurrence (top) and biomass (bottom). The mean value for each violin plot is denoted by a black dot, with values indicated below.

When assessing species responses to environmental variables in the occurrence model, high heterogeneity in the fitted relationships emerged (Figure 4.3). Notably, over 60% of species exhibited a positive linear response to SBT, but a negative response to the quadratic term (SBT2). Similar responses were observed for SBS and its quadratic term. This indicates that a majority of species demonstrate a bell-shaped response to temperature and salinity, albeit with different peak values and spread (Supplementary figure 10.5). This in turn reflects the different environmental niches of marine fish species (i.e., warm- vs cold-water taxa), both in terms of their optimal conditions, but also the width and degree of tolerance, notably to temperature (Magnuson *et al.*, 1979; Pörtner & Farrell, 2008; Stuart-Smith *et al.*, 2017). Among the other environmental covariates, the proportion of species displaying a negative response to SBT seasonality, Chl *a* surface seasonality and depth surpassed those displaying a positive relationship. This indicates that most of the species considered prefer more stable environments with less seasonal changes, which corroborates previous findings on the role of seasonality and depth as primary filtering mechanisms determining fish community structure (Beukhof *et al.*, 2019b; Pecuchet *et al.*, 2017). In terms of the biomass model the proportion of species showing a positive or negative response to the environmental covariates was more balanced. However, a considerably larger number of species demonstrated no significant relationships, as expected from the much weaker explanatory power of the model.

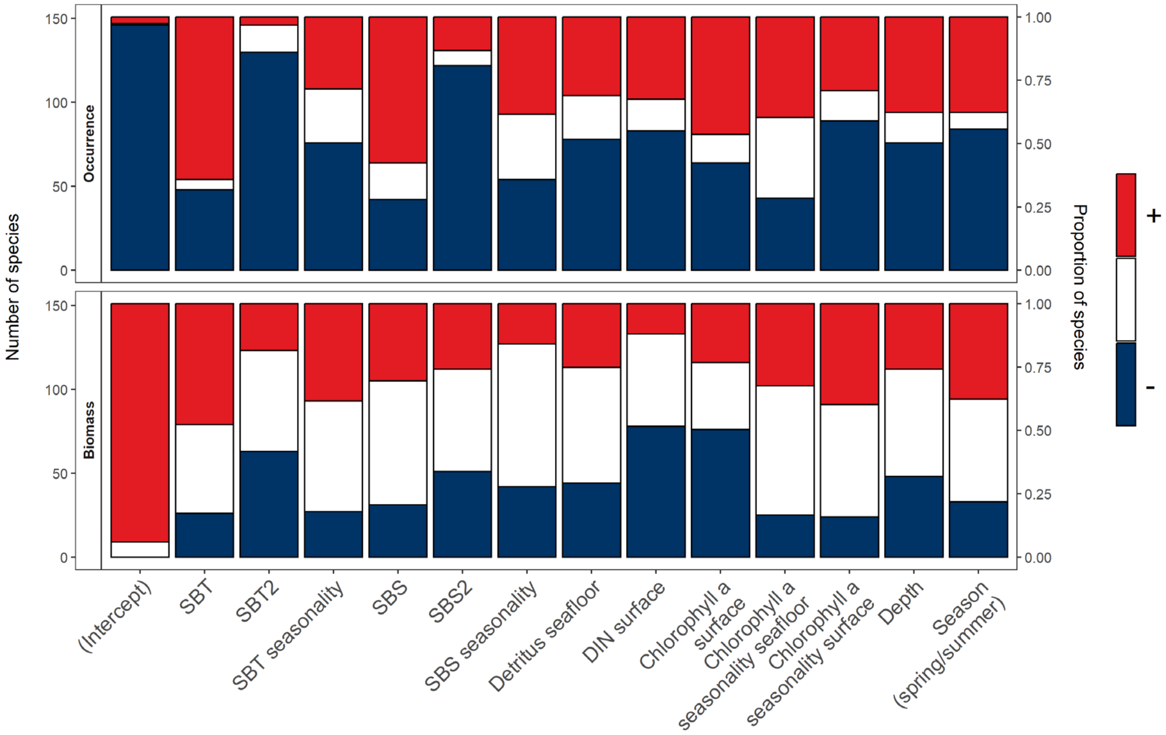

Figure 4.3. Number and proportion of species with positive (red), negative (blue) or no response (white) to each environmental variable, for the occurrence (top) and biomass (bottom) environment-only models.

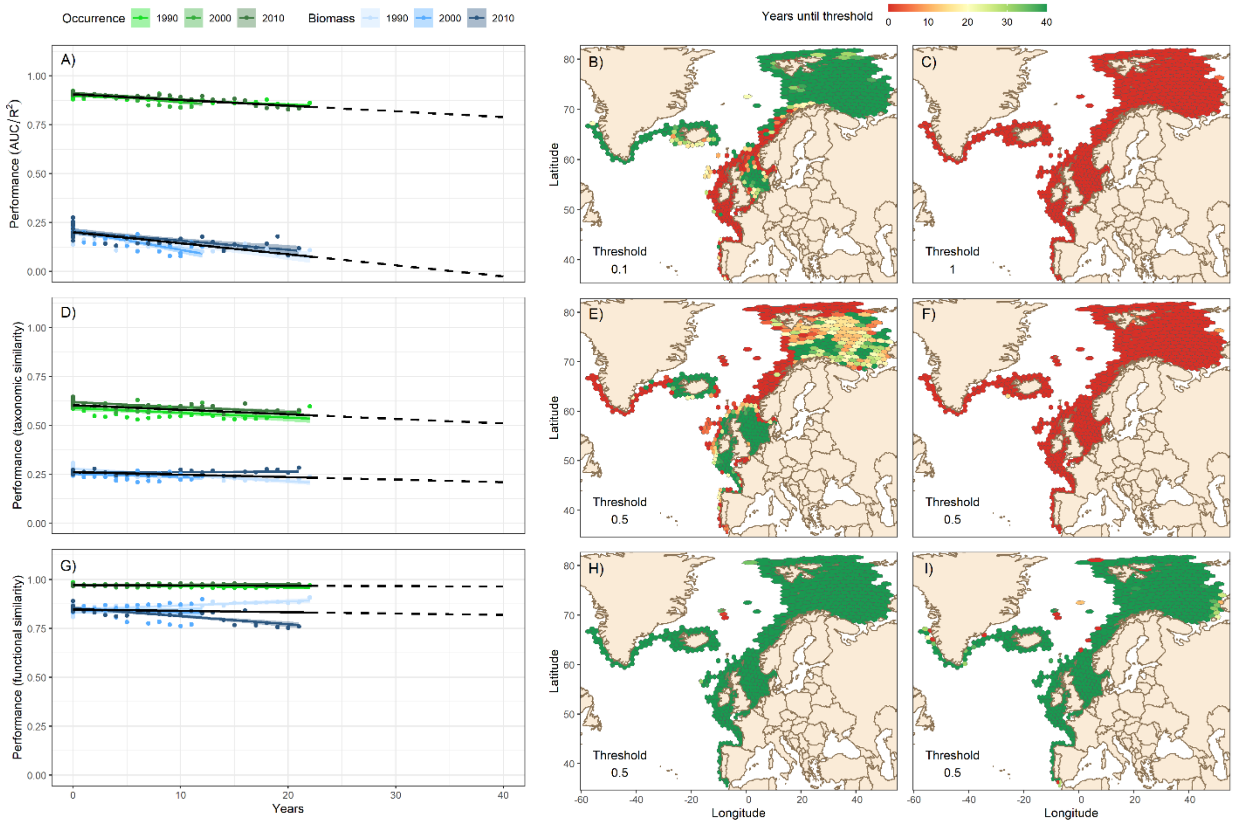

Figure 4.4. Forecast horizons of species- and community-level EBVs based on the cross-validation routine, including predictions of species occurrence and biomass measured by the AUC (occurrence) and R^2 (biomass) (A), as well the taxonomic (D) and functional β diversity (G), reflecting similarity in observed vs predicted community composition. Green and blue colors indicate each fold (decade) of the occurrence and biomass model, respectively while the dashed black lines indicate the predicted linear trend for each metric. The maps show forecast horizons of occurrence- and biomass prediction per grid cell, reflected by the number of years until a certain performance threshold is reached for RMSE (B, C), as well as taxonomic (E, F) and functional community similarity (H, I). Note that panels A and C represent biomass predictions from the biomass conditional model, while panels D, F, G, and I represent predictions from the hurdle model.

In terms of predictive performance over time the models show negative trends in AUC (slope = -0.0029) and R^2 (slope = -0.0056) (Figure 4.4A), indicating declining performance of species occurrence and biomass predictions at increasing time steps beyond the training period. However, the overall performance of the occurrence model remained high (AUC >0.8) throughout the validation period (20 years) and remained acceptable (AUC >0.7) even if extrapolating well beyond this time frame. The overall high performance was reflected also in space where the RMSE of occurrence predictions never exceeded a threshold of 0.1 in half of grid cells (Figure 4.4B). If increasing the threshold to 0.15 most cells show maximum forecast horizons (>40 years) (*Supplementary figure 10.6*), while a decreasing threshold (0.05) yield shorter forecast horizons. In contrast to occurrence predictions, the overall performance of the biomass models show R^2 values <0.25 indicating relatively low explanatory power already at year zero and therefore a weaker forecast horizon. This is also reflected in space where the RMSE of biomass predictions exceeds a threshold of 1 already at time zero in almost all hexagon grid cells (Figure 4.4C). The performance remained at a similar level also when considering a higher or lower threshold value for RMSE (*Supplementary figure 10.6*).

The performance in terms of species composition, assessed by the taxonomic similarity (β diversity), shows intermediate initial values and decreasing trends for both occurrence (slope = -0. 0023) and biomass (slope = -0. 0013) (Figure 4.4D). This indicates a decreasing similarity in the observed vs predicted composition over time, especially if considering species biomass. Furthermore, it highlights that even though the model demonstrates a high overall capability of predicting species distributions (Figure 4.4B), predictions of community composition are sensitive to the performance of individual species (Supplementary table 10.3), especially at finer spatial scales. This is clearly evident from the spatial patterns of similarity between predicted vs observed community composition (Figure 4.4E; Supplementary figure 10.7), where areas on the continental shelves (e.g., Iceland, North Sea, Celtic Sea and Barents Sea) generally demonstrate long forecast horizons (~10 to 30 years), while grid cells situated along the narrow continental shelf slopes (e.g., Portugal, Norway and Greenland) show considerably shorter forecast horizons (~1-5 years). The lower performance predicting community composition in these areas are likely due to more uncertain predictions of species ranges towards the edges of their environmental niches, including both more shallow- or deep-water taxa mixing on the shelf slopes. The community predictions based on the biomass models have a lower performance throughout the area, with forecast horizons at or close to zero years regardless of the thresholds considered (Figure 4.4F; Supplementary figure 10.7). This highlights the complexity in the mechanisms determining species-specific biomass values and suggests that the included environmental drivers may not be able to accurately explain the nuanced and multifaceted nature of these mechanisms, hence making forecasts challenging. In contrast to the predicted species composition, the functional similarity shows high initial values of similarity and non-significant temporal trends for both occurrence (slope = -0.00017) and biomass (slope = -0.00069). This indicates that the trait composition of the communities can be well predicted over multi-decadal time scales, even if the underlying taxonomic composition is variable and uncertain. The higher robustness is also evident when comparing spatial patterns in taxonomic and functional β diversity, where the latter shows long forecast horizons (>20 years) throughout the area regardless of using the 0.5 or 0.75 thresholds for both occurrence and biomass (Figure 4.4H, I; Supplementary figure 10.7).

The general findings from the cross validation routine indicate that the occurrence models have a higher predictive power than the biomass models, which is in accordance with previous modelling studies (e.g., Laaksonen *et al.*, 2020). This implies that future predictions of species- and community-level properties, including EBVs derived from the occurrence model are more reliable and have longer forecast horizons compared to those derived from the biomass model. The poorer predictive performance of the biomass model is primarily due to an inadequate representation of key processes that regulate the productivity and population dynamics of species, including growth, survival and reproduction (van Denderen *et al.*, 2020; Lindegren *et al.*, 2020, 2013). Fortunately, the development of mechanistic trait-based models capable of explicitly addressing these aspects and their inherent trade-offs can be used to generate more robust predictions of fish biomass, at least at the aggregated level of communities or functional groups (Petrik *et al.*, 2020). The cross-validation routine also demonstrates a considerably better skill predicting the functional (trait) composition of communities compared to taxonomic composition. The longer forecast horizon of biodiversity indicators and EBVs based on traits reflects the conserved properties of trait structure in both space and time, despite underlying differences and changes in species identities (Beukhof *et al.*, 2019a).

4.5 Conclusion

Tackling the current biodiversity crisis calls for immediate management actions in order to safeguard "areas of particular importance for biodiversity" (European Commission, 2020). But, the identification and designation of protected areas, including MPAs require modelling frameworks capable of providing useful ecological forecasts of key biodiversity indicators at a scale relevant for decision-makers and managers (Petchey *et al.*, 2015).

Our study shows that JSDMs can provide reasonable forecasts of several species- and community-level EBVs at a relevant timeframe fitting the formal marine spatial planning process (Edwards & Evans, 2017; Ehler & Douvere, 2009b). However, the length of forecast horizons varies in space and between metrics, with continental shelf seas generally providing longer forecast horizons for both taxonomic- and functional (trait) indicators. Consequently, scientists and managers need to account for differences in model performance and uncertainty between multiple EBVs when identifying potential hotspots of biodiversity meriting protection.

4.6 Acknowledgements

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Chapter 5

5. Marine biodiversity protection can be improved while minimizing effects on other ocean uses

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5.1 Abstract

The decline in biodiversity poses significant and irreversible consequences for natural ecosystems, which are crucial for human well-being due to the myriad goods and services they provide. Therefore, it is essential to maintain biodiversity by establishing Marine Protected Areas (MPAs) that aim to ensure the integrity and functionality of ecosystems, thereby safeguarding human well-being. In this study we aim to (i) describe and compare past and future patterns and trends in multiple taxonomic and functional EBVs; (ii) identify key ”hotspots” of overall high biodiversity and; (iii) evaluate the optimal placement of MPAs achieving 30% protection of biodiversity by ecoregion, while minimizing trade-offs with commercial fishing. We use joint species distribution models (JSDM) to predict the fish communities of the Northeast Atlantic continental shelf throughout the period 1989-2050 and calculate six Essential Biodiversity Variables (EBVs). We then identify areas of high biodiversity and set a MPA optimization scenario to maximize the protection of biodiversity, while minimizing the impacts on fisheries. Our results indicate that current MPA network is protecting a small percentage of high biodiversity areas, due to the small surface covered by MPAs and a mismatch with with high biodiversity areas. The MPA optimization shows a high efficienty towards protecting current and future (2030, 2050) biodiversity. The implementation of such scenario would have generally low impacts on fishing effort, i.e., a reduction of 15.51MKw/h (or 9% of the total), which is mostly located in the North Sea (i.e., ~11MKw/h), while being ≤0.1MKw/h in most other areas. While the protection of biodiversity-rich areas is crucial, it requires considering socio-economic activities, such as fisheries. This calls for active collaboration and dialogue between policymakers and stakeholders to achieve a sustainable equilibrium. By understanding the trade-offs involved, we can work towards effective marine conservation while supporting human needs and livelihoods.

5.2 Introduction

Biodiversity worldwide is threatened by anthropogenic activities, including habitat destruction, overexploitation and climate change (Halpern *et al.*, 2008; IPBES, 2019; Millennium Ecosystem Assessment, 2005). Furthermore, global warming is causing rapid changes in species distributions and community composition, as organisms follow their preferred thermal niches (Dulvy *et al.*, 2008; Freeman *et al.*, 2018; Pinsky *et al.*, 2013). The resulting loss and reorganization of biodiversity poses substantial and irreversible consequences for the functioning and services provided by ecosystems (Cardinale *et al.*, 2012), such as food production and climate regulation. Consequently, maintaining biodiversity is critical to ensure the stability and integrity of ecosystems, as well as their contributions to human wellbeing (Cardinale *et al.*, 2012; Loreau, 2000; Stachowicz *et al.*, 2007). In order to reduce threats to biodiversity, the Global Biodiversity Framework (GBF) has set a specific target (i.e., Target 3) to "ensure at least 30% globally of land areas and of sea areas […] are conserved through ecologically representative and well-connected systems of protected areas by 2030" (Convention on Biological Diversity, 2021). The identification of candidate sites meriting protection, especially "areas of particular importance for biodiversity" needs to be based on a suite of indicators reflecting the multiple facets of biodiversity, as highlighted by the Essential Biodiversity Variables (EBVs) framework (Navarro *et al.*, 2017; Pereira *et al.*, 2013). Furthermore, the prioritization and designation of protected areas should not be considered in isolation, but as part of a broader holistic spatial planning process that accounts for other uses of land and ocean space, e.g., infrastructure, agriculture and fishing (European Commission, 2020; European Parliament & Council of the European Union, 2014; Hermoso *et al.*, 2022; Robinson & Culhane, 2020). Finally, the spatial planning process needs to consider climate-driven changes in species distribution and composition to ensure the effectiveness of the protected areas network adequately safeguarding biodiversity both at present and into the future. This requires robust modelling frameworks and decision-support tools capable of estimating, predicting and visualizing multiple EBVs under different scenarios (Jetz *et al.*, 2019), while accounting for trade-offs and synergies with other sectors (Harris *et al.*, 2019; Sarkar *et al.*, 2006).

Among the tools currently used to inform conservation and spatial planning purposes, Species Distribution Models (SDMs) have gained much attention (Elith & Leathwick, 2009; Robinson *et al.*, 2017). However, these are fitted for individual species, while estimates of community-level EBVs (e.g., species richness) are generated by overlaying predictions from multiple species, assuming that they have independents responses to the environment (Grenié *et al.*, 2020; Norberg *et al.*, 2019). This limitation has recently been overcome by training a joint species distribution models (JSDMs) for all the species at once, acknowledging common patterns and covariance of species within communities (Jetz *et al.*, 2019; Ovaskainen *et al.*, 2017). While such JSDMs have shown improved performance, especially for rare species of high conservation value (Norberg *et al.*, 2019), as well as adequate skill forecasting patterns and trends in multiple EBVs (Montanyès *et al.*, in prep), the application of JSDMs in conservation and spatial planning is limited, especially in large and open marine areas. The lack of implementation of such tools hampers our progress towards fulfilling the international and regional policy goals to protect areas of particular importance for biodiversity by 2030 (Convention on Biological Diversity, 2021; European Commission, 2020).

Here we tackle this challenge by performing the first large-scale assessment and model-based optimization of the Marine Protected Area (MPA) network to safeguard current and future hotspots of marine biodiversity throughout European seas while accounting for trade-offs with other ocean uses. More specifically, we use a JSDM trained and cross-validated on high-resolution scientific survey data of marine fish communities and their traits throughout the North-East Atlantic (Montanyès et al., in prep) to: (i) describe and compare past and future patterns and trends in multiple taxonomic and functional EBVs; (ii) identify key ”hotspots” of overall high biodiversity and; (iii) evaluate the optimal placement of MPAs achieving 30% protection of biodiversity by ecoregion, while minimizing trade-offs with commercial fishing.

5.3 Methods

Model setup

We used a hurdle model, developed by Montanyès et al. (in prep), to predict both the occurrence and biomass of 151 fish species. This is a Bayesian JSDM fitted within the Hierarchical Modelling of Species Communities (HMSC) framework (Ovaskainen *et al.*, 2017; Tikhonov *et al.*, 2020). The model was trained on environmental data derived from the NEMO MEDUSA coupled hygro-geochemical model runs (Gurvan *et al.*, 2022; Yool *et al.*, 2013). Consequently, the predictions were informed by the same environmental data from NEMO MEDUSA, providing monthly probability of occurrence and biomass estimates for all 151 species spanning from 1989 to 2050.

Estimation of EBVs

To describe and compare past and future patterns in marine fish biodiversity, we calculated multiple taxonomic and functional biodiversity indicators on the basis of model predictions. We computed a suite of six complementary EBVs representing key aspects of biodiversity (Pereira *et al.*, 2013), including richness, evenness and dispersion. The EBVs were computed for each location and year, and thus aggregated through the months of the year as follows. To reflect the taxonomic richness of communities the total number of species was calculated based on the maximum probability of occurrence of a given species throughout a year, where probabilities equal or higher than 0.5 were considered to represent presence. The same approach was used for computing richness of threatened species, classified as *Vulnerable*, *Endangered* or *Critaically Endangered* (IUCN, 2023). Species lacking classifications were assigned as *Not evaluated*. To account for differences in species evenness we calculated Pielou's evenness using the mean annual estimates of species biomasses in each location. The remaining three EBVs represent functional metrics based on species traits retrieved from publicly available databases (Beukhof *et al.*, 2019c). The selected traits reflect species' morphology (body shape, fin shape, aspect ratio, maximum length), life history (habitat, growth), reproduction (spawning type, offspring size, age at maturity, fecundity) and diet (feeding mode, trophic level) (Dencker *et al.*, 2017; Montanyès *et al.*, 2023). To calculate the functional diversity indices we computed a multidimensional space with a PCoA based on trait-based (Gower) distances (Mouillot *et al.*, 2013). We then used the first 5 PCs (cumulative explained variance of 82%) to compute the functional richness, evenness and dispersion for each year and location. These represent the proportion of functional space filled by the species in the community, the regularity of biomass distribution in the functional space, and the biomass-weighted mean distance to the biomass-weighted mean trait values of the community, respectively (Cornwell *et al.*, 2006; Mouillot *et al.*, 2013). Lastly, we compared the patterns and trends among the biodiversity indicators by performing a PCA using the derived EBVs per location and year (from 2000-2030) as input. All analyses were carried out in R (R Core Team, 2022). Taxonomic EBV were carried with 'vegan' package (Oksanen *et al.*, 2022), and functional EBVs with 'mFD' package (Magneville *et al.*, 2022), while the species conservation classifications were retrieved with the 'rredlis' package (Gearty & Chamberlain, 2023) and complemented with information from the website (IUCN, 2023). The PCA analysis was performed with the 'factoextra' package (Kassambara & Mundt, 2020).

Optimization of the MPA network

After having estimated the EBVs we simulated a conservation and management scenario where the objective was to protect 30% of the ocean space prioritizing areas of high biodiversity. To ensure that the MPA network was ecologically representative throughout the study area and among habitat types, protection was allocated in each of the 9 marine ecoregions considered (Spalding *et al.*, 2007), split into a shallow and deep strata (i.e., above or below median depth). To define candidate areas meriting protection we computed a Joint Biodiversity Index (JBI) by standardizing each of the EBVs between 0 and 1, and thereafter computing the sum of the six indices for each year and location. We then assigned locations as having overall high biodiversity if the JBI exceeded the median value for each ecoregion and depth strata. The median was chosen instead of a more conservative threshold (e.g., 75% quantile) since it allows for more flexibility during spatial optimization of MPAs, while the latter would lead to a deterministic outcome disregarding potential trade-offs with other ocean uses. Hence, to account for such trade-offs the 30% protection was allocated while minimizing impacts on commercial fisheries (i.e., minimizing the fishing effort that would be reduced if the selected areas were completely closed to fisheries). Spatial information on the mean annual fishing effort was extracted from Vessel Monitoring System (VMS) data available from public repositories (Supplementary figure 11.1) (ICES, 2019). Furthermore, information on the current MPA network and the level of protection was extracted from public repositories (UNEP-WCMC & IUCN, 2024; last accessed February 2024) and classified into ‘fully’ or ‘partially’ protected areas according to IUCN category I-III and IV-VI, respectively (Day *et al.*, 2019; Dudley, 2008). Areas not assigned to any of the previous levels, were classified as ‘non-protected’. The final selection of protected areas while including the existing MPAs was then optimized using the ‘prioritizr’ R package (Hanson *et al.*, 2023).

To assess the effectiveness of the MPA optimization in safeguarding biodiversity, we applied a threshold equal to the median value for each individual EBV at three distinct time intervals (e.g., covering the periods 2000-2016, 2030, and 2050). We examined the extent to which these high biodiversity areas for each individual EBV overlapped with protected areas within both the existing MPA network, and the optimized MPA. Additionally, we investigated the potential impacts of implementing the optimized MPA scenario on commercial fishing activities, under the assumption that areas within the MPAs would be closed to fisheries. Therefore, we assessed the absolute (in Million Kw/h) and relative (% of the total) reduction in fishing effort that would occur in each ecoregion and depth stratum, and in the whole study area.

5.4 Results & Discussion

Our results demonstrate large-scale patterns in overall biodiversity throughout the study area with the northern North Sea, Norwegian coast and southern Iceland showing higher values of the JBI, while the northeast Barents Sea and the Iberian coast show relatively lower indices (Figure 5.1A). However, the six EBVs underlying the JBI show very different spatial patterns, with functional evenness and dispersion demonstrating higher spatial homogeneity, while the others are more heterogeneously distributed (Supplementary figure 11.2). The different patterns among EBVs are reflected also in our PCA showing similar positive loadings on PC1 (explaining 43.8% of the total variance) for richness, evenness, functional richness and richness of threatened species, while functional dispersion show high positive loadings on PC2 (19.2% of variance). Functional evenness demonstrates low loadings on both PC axis, indicating a lack of correlation to the other EBVs. In addition to spatial differences in JBI and the underlying EBVs, our model predictions demonstrate different temporal changes throughout the area (Figure 5.1B, Supplementary figure 11.3) with the eastern Barents Sea, northern North Sea, Iceland and Greenland showing increasing trends in the JBI, while the central North Sea, Celtic Sea and Bay of Biscay show declining trends. The different trends reflect underlying changes in species distribution and biomass predictions in response to climate model forecasts, notably the increase in species ranges towards higher latitudes in response to warming (Dulvy *et al.*, 2008; Freeman *et al.*, 2018; Pinsky *et al.*, 2013). Taken together, our results show pronounced spatio-temporal variation within and among EBVs, thus highlighting the difficulty of designating protected areas safeguarding the multiple facets of biodiversity, especially under climate change.

This difficulty is evident from the current MPA network (Figure 5.2A) that is presently capable of protecting only a small fraction of the areas identified as having high biodiversity (i.e., with JBI values larger than the median) for each specific ecoregion-depth combination (Figure 5.1C). The resulting mismatch in protecting each of the EBVs considered (Figure 5.3A) is partially a direct consequence of the small surface currently set aside for MPAs throughout the study area. However, in 12 out of the 18 areas considered the mean JBI inside existing MPAs is below the 50th quantile (Figure 5.4A), indicating an inefficient coverage of high biodiversity areas by current MPAs. If considering only fully-protected areas the mean JBI within MPAs is even lower, with more areas having values of zero (Supplementary figure 11.4). This supports previous findings indicating that the extent and placement of MPAs are insufficient to safeguard multiple aspects of marine biodiversity (Lindegren *et al.*, 2018a; Venter *et al.*, 2014).

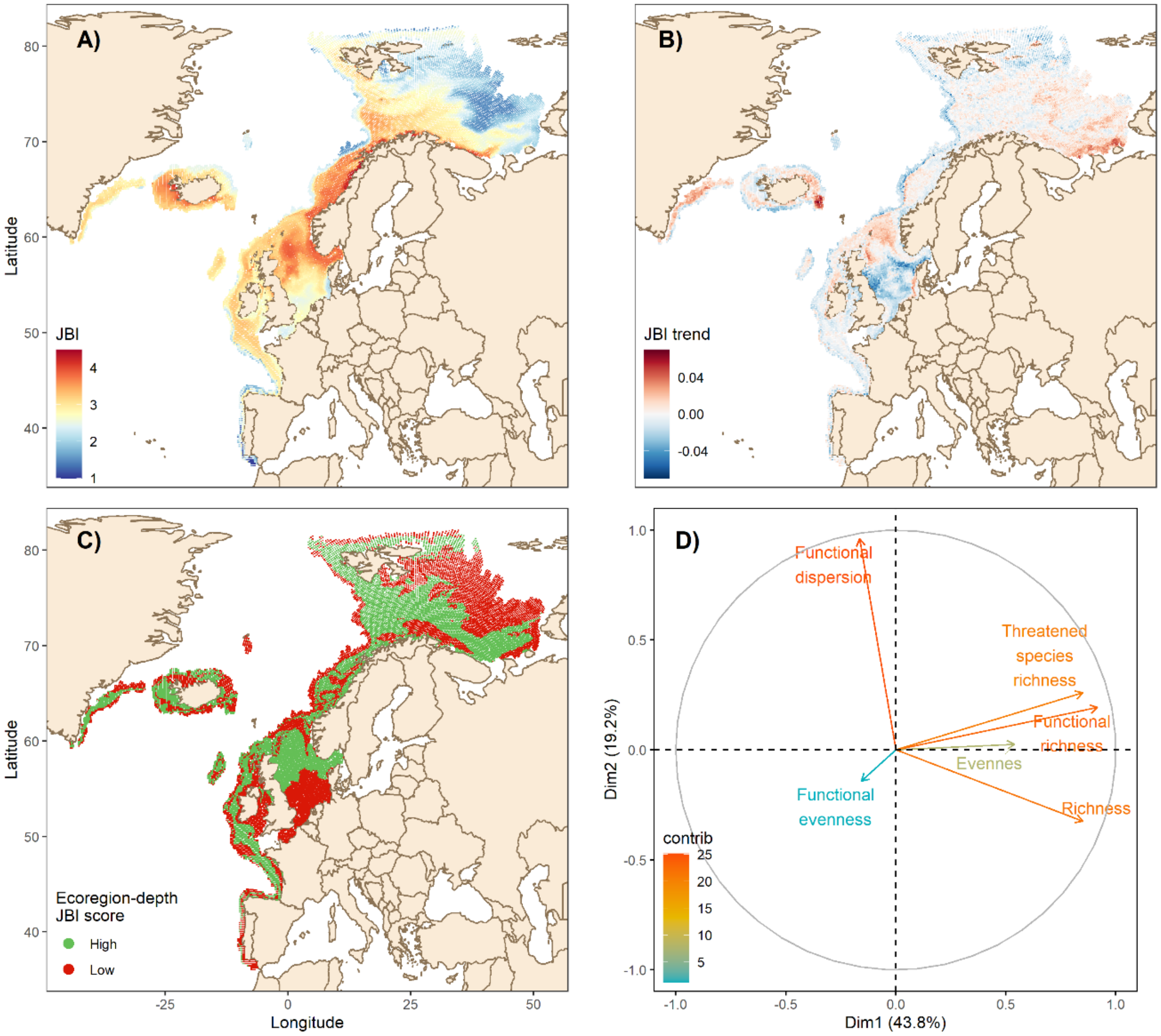

Figure 5.1. Patterns and changes in overall biodiversity given by the mean JBI for the period 2000-2016 (A), as well as the temporal trend in JBI from 2016 to 2030 (B). Locations identified as having high or low biodiversity value for each ecoregion-depth combination (C). Correlations among the underlying EBVs included in the JBI reflected by their associated PCA loadings on the main modes of variation (D).

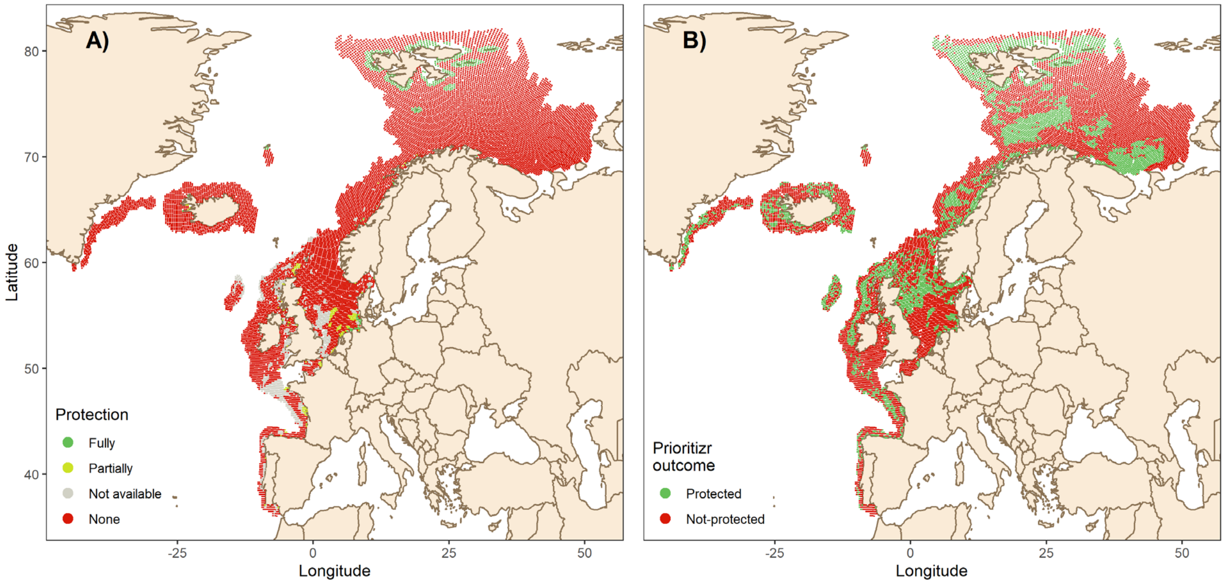

Figure 5.2. Current MPA distribution and protection level (A) and locations selected for protection by model optimization for the period 2000-2016 (B).

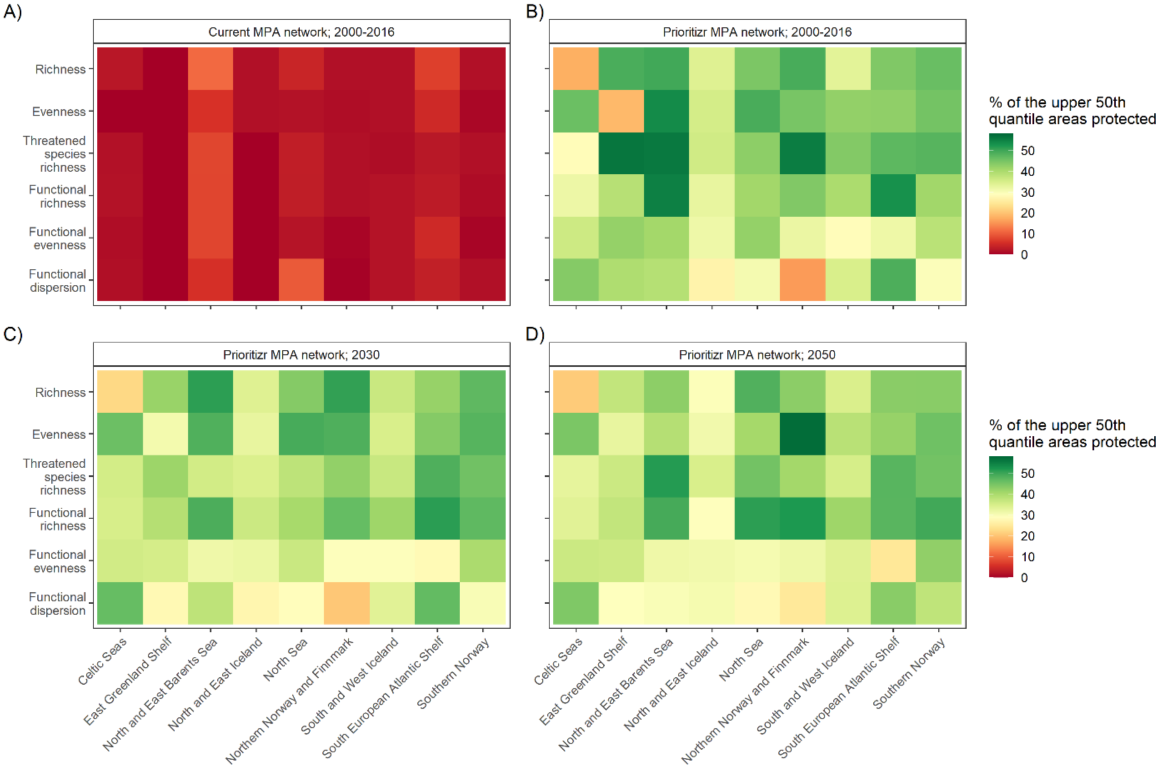

Figure 5.3. Percentage of high biodiversity locations protected within MPAs by EBVs and ecoregion based on the current MPA network (A), and the optimized MPA network given simulated conditions during the time periods 2000 to 2016 (B), 2030 (C) and 2050 (D).

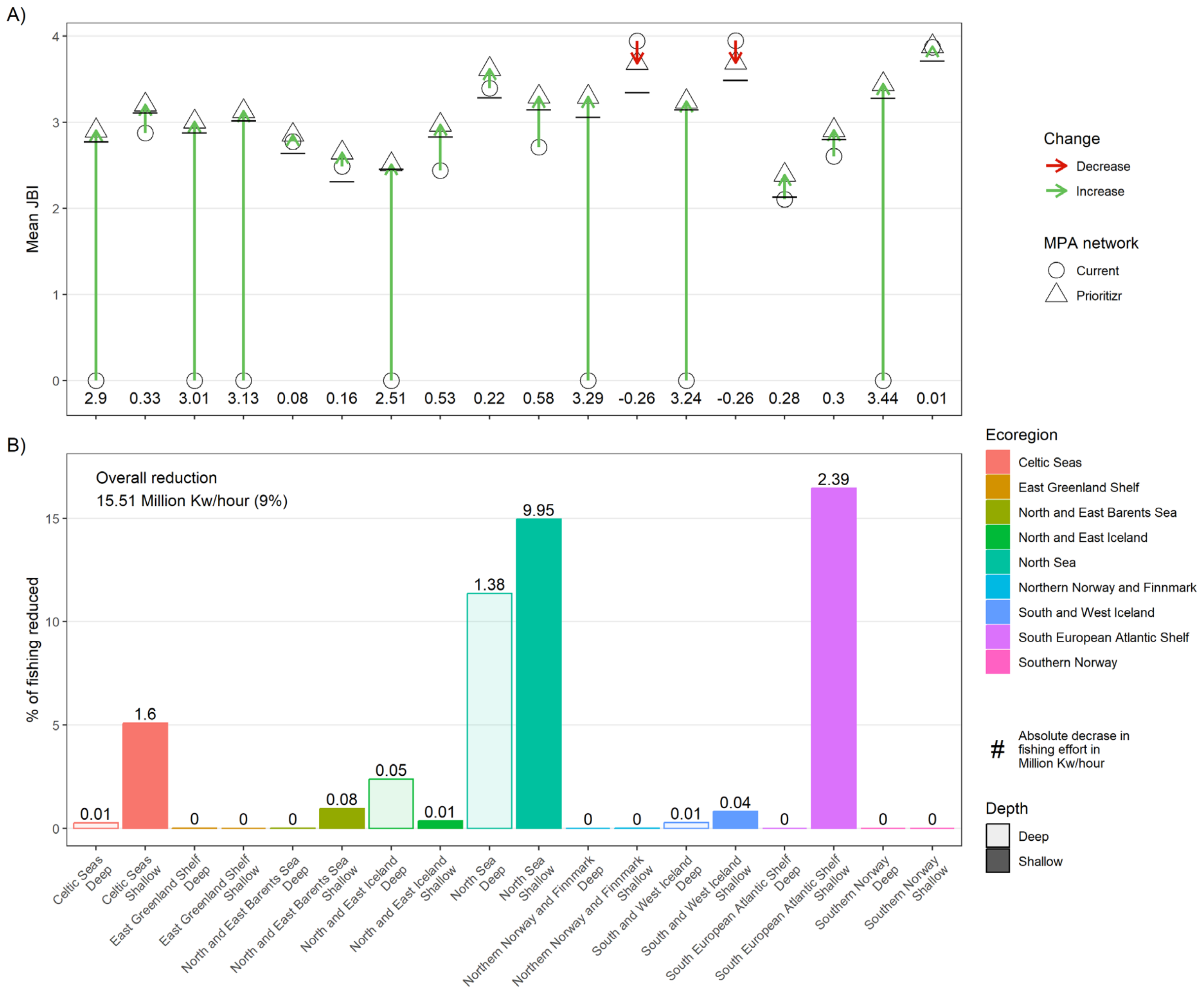

Figure 5.4. (A) Mean 2000-2016 Joint Biodiversity Index (JBI) for each ecoregion and depth within fully or partially protected MPAs considering the current network (open circle) and the suggested by the prioritizr output (open triangle). The arrows indicate the direction of change from current to prioritizr with the value of change at the bottom. Values of zero indicate that there are no MPAs currently implemented. The horizontal lines indicate the 50th quantile of JBI for each Ecoregion and depth. (B) Percent of decrease in the 2012-2016 fishing effort (million Kw/hour) if the MPA network from prioritizr was to be adopted and MPAs were closed to fishing activities, for each ecoregion and depth area. On top of each bar the actual value of decreased fishing effort.

If extending the current protection coverage to reach 30% for each ecoregion-depth combination, the MPA network stemming from our optimization (Figure 5.2B) would lead to a substantial increase in the percentage of high biodiversity areas protected for each EBV (Figure 5.3B). The increase in the protection of EBVs with high values is a consequence of increasing the total area covered by MPAs, but also reflecting that such an expansion of new MPAs prioritizes areas of high biodiversity value. Interestingly, the optimized MPA network demonstrates a high spatial overlap also with future biodiversity hotspots (Figure 5.3C, D), as indicated by the high percentage of high biodiversity areas for each of the EBV that fall within MPAs.

In addition to the larger fraction of high biodiversity areas covered by the optimized MPA network, the mean JBI within MPAs increases in all 18 areas, except for Northern Norway and Southwest Iceland (Figure 5.4A). These two areas possess the highest mean JBI values, indicating that the current MPAs are already located in regions with the highest overall biodiversity values. Consequently, the incorporation of new MPAs into the network leads to a slight reduction in the mean value, since the optimization considers all areas above the median value of JBI equally. Nevertheless, in all cases, the outcomes from our optimized MPA network surpass the 50th quantile threshold, confirming that the recommended MPAs are strategically situated within our designated high biodiversity areas.

Finally, the selection of areas for protection was achieved by prioritizing high biodiversity locations while reducing impacts on commercial fisheries. In some cases, areas of high biodiversity could be set aside without any associated fishing costs, simply because no, or only marginal fishing effort have historically taken place in these areas (Supplementary figure 11.1). However, in heavily fished areas, such as the central North Sea and the northern Celtic Sea, protecting 30% of these areas would entail trade-offs and costs in terms of reduced fishing effort. In fact, among all the considered ecoregions, the North Sea is the area where fisheries would be most impacted (Figure 5.4B). Overall, the reduction of fishing effort would amount to 15.51MKw/h or 9% of the historical fishing effort with two thirds concentrated in the North Sea. However, most of the areas considered would experience very modest reductions amounting to <0.1MKw/h in absolute terms, or <3% in relative terms. While the reductions in fishing effort may incur short-term losses in fishing opportunities and incomes, protecting biodiversity may lead to improved status and productivity of many commercially important species (Chirico *et al.*, 2017; Medoff *et al.*, 2022; Le Port *et al.*, 2017). The higher survival and recruitment inside MPAs may in turn spillover and generate higher landings and revenues in areas beyond MPAs, surpassing the initial costs. Hence, decision regarding MPAs and fishing closures need to consider such long-term net positive effects, while allowing access and a fair share of fishing opportunities, especially to individual fleets or fishermen directly affected by MPAs.

Managers and policy makers have the responsibility to fulfill current conservation targets by deciding on management action serving to safeguard marine biodiversity and its associated values. In order to prioritize conservation efforts, robust modelling tools capable of identifying hotspots of biodiversity, while accounting for trade-offs and synergies with other ocean uses are needed, but largely lacking. Our model-based study illustrates that it is possible to find a compromise between preserving nature and allowing human activities

In conclusion, the findings underscore the importance of balancing conservation efforts with economic activities. This requires active collaboration and dialogue between scientist, managers and stakeholders to achieve a sustainable solution. By understanding the trade-offs involved, we can work towards effective marine conservation while supporting human needs and livelihoods.

5.1 Acknowledgements

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Chapter 6

6. Synthesis

This thesis explores the underlying patterns, processes and drivers shaping marine fish communities in the Northeast Atlantic Ocean through JSDMs. It further evaluates the performance of the fitted JSDMs, and how predictions from such models can inform management and conservation actions. Chapter 6 provides a comprehensive synthesis of the main research findings from chapters 3-5, highlighting their contributions to marine ecology, management, and conservation. Finally, concluding remarks are provided along with suggestions for future research directions.

6.1 Underlying drivers of marine fish communities

Understanding the assembly processes shaping communities is essential for taking informed decisions towards the management and conservation of biological resources (Floury *et al.*, 2021; Yates *et al.*, 2018). Three decades have passed since Keddy (1992) proposed the community assembly framework, and since then the scientific community has made progress towards understanding how species evolutionary history, dispersal capabilities, and their interaction with other species and the environment defines where and when they can be found.

Leveraging on an extensive dataset of scientific bottom-trawl surveys, we apply JSDMs on fish communities at a regional- (North Sea; chapter 3) and continental scale (Northeast Atlantic Ocean; chapter 4) and study the main drivers shaping marine fish communities. Despite the difference in the extent of the study area, in both cases temperature- and productivity-related covariates are the main environmental drivers of the community. Moreover, we found that there are other spatially structured processes that explain a large proportion of the patterns in the community. While the nature of those processes cannot be disentangled with the correlative models used within this thesis, it puts forward relevant knowledge about the spatial structuring of resulting patterns stemming from these processes. Ecological theory would assume that biotic interactions, dispersal limitation and other “hidden” environmental covariates not considered in the study are behind the signal from these spatial components. Nonetheless, one cannot tear apart the contribution of each of those individual processes, nor identify the ultimate drivers behind them. Although it is long known that biotic interactions can have profound implications on species distribution (Connel, 1961), my work accounts for the potential effect of biotic interactions together with other processes in community assembly. The findings from chapter 3 and chapter 4 form the fundament for further research, since a better understanding and separation of such processes would dramatically improve our understanding of community dynamics. Furthermore, in chapter 3 we identify that species traits contribute in explaining a considerable proportion (12.5%) of the responses of species to the environment and reveal the underlying trait-environment relationships within the North Sea fish community leading to this. Such information can be used to study the underlying patterns resulting from the mechanisms driving community assembly, especially with regards to understanding how traits modulate species responses to the environment. Hence, incorporating trait information within HMSC has the potential to reveal important insights of community assembly (Ovaskainen *et al.*, 2017), but it comes with computational challenges to overcome in terms of model complexity, which at times may be at the expense of having to reduce the number of species included in the model. To include a given trait, it must have complete information for all species considered, and since in some instances there is missing trait information for some species this result in either excluding the trait for all species or those species with no trait information. The key is therefore to find a balance to maximize the relevant output from modelling given the limitations of the data used as input. In chapter 3 and chapter 4 we evaluated some of these constraints by fitting models including species and their traits. The inherent reduced number of species in the North Sea, compared to the Northeast Atlantic facilitated that in chapter 3 more traits could be included in the analysis (11 traits) compared to chapter 4 (6 traits). Besides the limitations associated to the trait availability of species, in chapter 4 we also faced computational limitations. The large extent of the data (>90,000 observations for 151 species) made fitting the models not only computationally demanding, but also very time consuming (i.e., several weeks for model training). Hence, reducing the number of traits included in the model is beneficial for limiting model complexity and thus computation time. Therefore, the exploration of assembly processes with modelling tools such as the one used here, usually comes with limitations and consequently decisions to overcome them. In the last years, considerable effort has been made to compile fish traits (Beukhof *et al.*, 2019c), which opens the door to new research possibilities such as the models fitted here. However, our research highlights that there is still work to do in this field towards a more complete list of traits for fish species, which could help to set some of the above-mentioned limitations aside.

An important decision made throughout this thesis was the selection of models without random effects in chapter 4 and chapter 5 (against models with random effects). As described before, when computing predictions with models where random factors take as much variance as those considered here, the signal derived from purly environmental filtering processes becomes blurred and is practically lost, resulting in the model predictions being mainly driven by the random effects that are assumed to remain static in model predicitions. Since the objective of chapter 4 and chapter 5 was to fit models and use them to predict present and future marine fish communities considering climate change, having this random effects that take most of the variance severely constraints the whole purpose. Another constrain is the substatial increase in required computational resources when including random effects, particularly spatially explicit random effects. Lastly, the biomass model from chapter 4 did not fully converge and thus, the results derived from the model will not be fully reliable. As a consequence of these different reasons, we decided to proceed with the models without random effects for the cross-validation (chapter 4) and community predictions (chapter 5).

The reliability of characterizing biodiversity in fringe areas of the study region, such as the southern limit (i.e., the Iberian Peninsula), may be compromised. This is particularly due to the potential expansion or redistribution of species with a more tropical distribution in response to ocean warming. These species are likely to shift northward in the Northern Hemisphere, either expanding their range or altering their distribution towards temperate areas. As these tropical species are not accounted for in the models, potential distributional changes cannot be factored into biodiversity metrics. An alternative approach to calculating biodiversity metrics involves utilizing survey data alongside species accumulation curves (Dencker *et al.*, 2017). These curves depict the increase in the number of species as sampling effort increases, eventually reaching a limiting asymptote as sampling becomes more comprehensive (Gotelli & Colwell, 2011). This data-driven method can rapidly incorporate recent survey data into biodiversity metrics, accounting for newly arriving species. However, it is important to note that this approach lacks the ability to forecast future changes, thus presenting a limitation compared to model-based approaches, especially in terms of informing marine management and conservation.

6.2 Model performance

Modelling tools like SDMs or JSDMs are valuable for predicting species distribution. While all models have a predictive ability, the accuracy of their predictions can vary significantly and is contingent upon the model's performance. Thus, assessing the predictive performance of a model is crucial for interpreting its output adequately. Chapter 4 delves into the predictive performance of JSDMs from a temporal perspective, examining the forecast horizon of fitted models. Evaluating the forecast horizon of models that predict future communities under climate change is pivotal for generating ecologically relevant insights (Franklin, 2023; Petchey *et al.*, 2015; Sequeira *et al.*, 2018).

The findings from chapter 4 underscore that the predictive performance of models differs across types of data (i.e., occurrence and biomass), as well as community and diversity metrics. We conclude that these models can effectively predict various aspects of fish communities and biodiversity within a 10-20 year timeframe. Although performance tends to decrease over time, the values remain relatively close to the initial ones. However, one challenge in assessing the forecast horizon is the lack of established standard metrics and thresholds indicating good performance (Petchey *et al.*, 2015). A notable exception is the AUC, for which established thresholds exist (Mandrekar, 2010). The lack of thresholds complicates the establishment of a solid and fixed time horizon (i.e., number of years into the future) within which the model performs well. Given that model outputs can inform management and conservation efforts (Floury *et al.*, 2021; Yates *et al.*, 2018), it is essential to work towards standardized tools and methods with defined thresholds. This approach would ensure that information is comparable across organisms and contexts and is based on objective and common criteria (Petchey *et al.*, 2015). In situations where established thresholds are lacking, conducting sensitivity tests (as in chapter 4) can offer valuable insights. These tests involve exploring how results might vary with different thresholds. While sensitivity testing may not directly resolve the initial problem, they can provide additional information to contextualize the findings.

One of the primary challenges encountered throughout this thesis, if not the most significant, was the extensive time required by the HMSC framework to fit fully converged models with large datasets and a high number of species, since a large number of MCMC iterations was necessary (Ovaskainen & Abrego, 2020). This prolonged fitting process posed a significant obstacle towards making progress, as some models were taking several weeks to fit. Fortunately, the framework developers recognized this limitation and developed a workflow implementation utilizing High-Performance Computing (HPC), which we were able to leverage on a late stage of the thesis (Rahman *et al.*). However, while this solution dramatically accelerates the fitting process, it also substantially increases the demand for computational resources and, consequently, the associated economic costs. Therefore, achieving a balance between model complexity, fitting time, and resource utilization is key. In this context, exploring alternative JSDM tools with lighter computational requirements may offer some valuable insights into potential trade-offs between computational demands and ecological understanding.

6.3 Marine management and conservation

To effectively manage marine ecosystems, it is crucial to understand the primary factors influencing natural communities and to account for activities such as fishing and other socio-economic activities (Long *et al.*, 2015). Marine Spatial Planning (MSP) represents an ecosystem-based management strategy designed to regulate the utilization of marine areas (e.g., for fisheries, aquaculture, energy production, conservation) in both space and time, with the aim of achieving ecological, economic, and social goals (Douvere, 2008; Ehler & Douvere, 2009a). Given that biological systems transcend political boundaries and that marine activities can often conflict, collaboration among international bodies and stakeholders from various sectors is essential to efficiently implement MSP (Maureaud *et al.*, 2021). Allocating specific areas for activities over space and time requires the consideration of numerous factors and interests, and thereby dialogue among the involved parties (European Commission, 2020; European Parliament & Council of the European Union, 2014; Hermoso *et al.*, 2022; Robinson & Culhane, 2020).

If properly implemented and enforced the establishment of MPAs is an important part of MSP since they guarantee the conservation of “areas of particular importance for biodiversity”, but also the functions, goods and services that it provides to natural ecosystems and humankind (Day *et al.*, 2019; Stolton *et al.*, 2015).

In chapter 5, we study how the expansion of the Europen MPA network could affect fishing activities, since the interests of such activities are a typical point of conflict in MSP. The six EBV used offer a multifaceted view of the main fish biodiversity patterns, reflecting taxonomic and functional aspects of fish communities. Nonetheless, more EBV variables could be included in the analysis in order to bring in other aspects, such as genetic features, populations, nursing areas, rare species or habitats, species resilience towards disturbance, endemisms, or emblematic species (Asaad *et al.*, 2017). While my research contributes relevant insights in the current status and trends of fish biodiversity in the Northeast Atlantic, is important to highlight that this is not an exhaustive representation of the whole spectrum of biodiversity and its values. My work is limited to the study of 151 species from the Northeast Atlantic, and portrays biodiversity patterns at a large spatial scale. Hence, there is room to incorporate more information, some of which might be especially relevant at a regional scale (e.g., populations or rare species). Nonetheless, the information derived from chapter 5 can feed into international initiatives such as the Digital Twin Ocean, that seeks to bring together different types of ocean-based information in order to recreate an accurate digital representation (“twin”) of the oceans. This can thus serve to take informed decisions towards the management and conservation of marine areas based on the best available information and knowledge (Chust *et al.*, 2022; Navarro *et al.*, 2017).

The findings from chapter 5 support previous works highlighting that the current MPA network is not adequately protecting marine biodiversity (Lindegren *et al*., 2018a; Venter *et al*., 2014, 2018). Current MPAs are far from the 30 by 2030 target, since most of the regions are far below the 30% protection objective, or are completely missing those areas with high biodiversity value. Moreover, even if these two essential aspects were fulfilled, such a network does not guarantee an adequate protection of marine biodiversity, since most implemented MPAs do not have management plans, and allow extractive (and destructive) activities known to pose a threat for marine species an habitats (Dureuil *et al.*, 2018; EEA, 2019; WWF, 2019). Therefore, it is essential that the designation of MPAs is not only on paper, and that it forsees an effective management plan with the subsequent enforcement. Since fishing has been identified as a key pressure on the marine environment (EEA, 2019; European Court of Auditors, 2020), the management of MPAs should strongly consider whether allowing fishing, as well as other extractive and destructive activities, is compatible with the conservation objectives. In this regard, chapter 5 shows that closing high biodiversity areas to exploitation would have a generally low impact on fishing effort, with the exception of the North Sea. It should be then a priority to secure those MPAs in areas where there can be an immediate high benefit for biodiversity and a low cost in terms of fisheries. In the case of the highly exploited North Sea (Amoroso *et al.*, 2018; Couce *et al.*, 2020), a longer negotiation considering the interests of the different stakeholders will likely be needed, since closing areas to exploitation would have higher impacts for fisheries compared to the other regions. At the same time it is in the North Sea, where the effects of the closure to fishing have a high potential to show important benefits for biodiversity and ecosystem health.

6.4 Conclusions and future perspectives

In this thesis I applied a novel JSDM to study the main underlying drivers shaping marine fish communities, study the predicting ability of such models, and generate future forecasts to inform management and conservation strategies. The work presented here broadly contributes to a better understanding of marine ecology by improving knowledge on community assembly processes. Moreover, the performed decadal cross-validation shows that the model has varying predictive performance towards different aspects of the communities, and highlights the need of standardized metrics and thresholds for an adequate evaluation. Lastly, this thesis highlights that current conservation and management is not adequately protecting fish biodiversity, which could only be possible to achieve by a more formal marine spatial planning process actively engaging a diverse set of stakeholders and end-users.

With the knowledge gained throughout the process of this thesis I see many different possibilities that could contribute to marine ecology, conservation and management in the future.

First, I find it highly relevant to concentrate efforts on better exploring the random effect part of models such as the presented here, working towards disentangling the nature of the different processes contributing to shape such random effects. Particularly, with a focus on biotic interactions, which could bring some important ecological insights. This could be achieved, for instance, through a post-hoc comparison of the species trait distinctiveness (Vivó-Pons *et al.*, 2023) based on the species association matrix, to assess whether species with negative association are generally functionally similar, or not. While it would still be difficult to prove real species interactions (e.g., competition or predator-prey) on the basis of such associations, this could pose some specific and relevant hypothesis to test in cases where such interactions are better known.

While in this thesis I focus on community aspects of ecology and conservation in this thesis, the generated outputs can also be used to have a more detailed study of specific species of interest (e.g., cod). For instance, exploring species-specific responses to the environment, associations with other species, or possible distributional changes in the future.

Another interesting aspect to explore would be to formally quantify how much the inclusion of traits improves HMSC performance. This could be tested by fitting the same model with an increasing number of traits, and could be done with real data (e.g., chapter 3) or preferably, with simulated data. The outcomes of this kind of exercise could be relevant towards taking a more informed decision on how many traits and species should be included in a model, since more traits will likely restrict the number of species with a complete set of traits.

The models demonstrated superior predictive performance for presence-absence compared to biomass, possibly stemming from an insufficient representation of critical processes governing species biomass productivity and dynamics within the models such as population dynamics (van Denderen *et al.*, 2020; Lindegren *et al.*, 2020, 2013). There are other modelling frameworks with a mechanistic approach that can better characterize such kind of dynamics (e.g., FEISTY; Petrik *et al.*, 2019) and that may provide additional valuable insights to those obtained from HMSC. Exploring methods to integrate the outputs of these diverse frameworks, leveraging their respective strengths, and assessing potential improvements in predictive performance could be an interesting direction for further investigation.

In addition to HMSC, several other frameworks for JSDMs offer alternatives with lighter computational loads. For example, General Linear Latent Variable Models (GLLVMs) (Niku *et al.*, 2019) significantly reduce the time required for model fitting as they do so via maximum likelihood. Another alternative is Artificial Neural Networks (ANN) (Bourhis *et al.*, 2023), which are known for their speed and flexibility. While ANNs are often considered black-box models, recent advancements have been made to enhance understanding of underlying processes (Bourhis *et al.*, 2023). Conducting a formal comparison among these frameworks, and possibly others, could yield valuable insights into potential improvements in predictive performance and help illustrate the trade-offs associated with different modeling approaches.

The management and conservation exercise presented in chapter 5 poses, in my opinion, an interesting learning scenario. But it is, by no means, an exhaustive representation of the complex socio-ecological context in European marine waters. While here, I aimed to keep it at a low level of complexity, this can easily escalate by incorporating more biodiversity variables (resilience, endemisms, populations, β-diversity, regional interests), fragmenting the management areas into smaller units (i.e., habitat types) or by comparing the outputs when defining high biodiversity at different thresholds (other than the median).

Lastly, with the standardized fish data readily available from the Eastern and Western Atlantic, as well as the Eastern Pacific (Maureaud *et al.*, 2024), there is an opportunity to explore and compare the ecological insights derived from modeling these distinct regions. It would be particularly intriguing to investigate and compare potential variations in trait-environment relationships, the influence of environmental covariates, and the manifestation of spatially structured random effects across these areas. Such comparative analyses could offer valuable insights into the ecological dynamics and drivers shaping fish communities in different oceanic regions.

7. Acronyms and Abbreviations

ANN: Artificial Neural Networks

AUC: Area Under the Curve

CBD: Convention on Biological Diversity

Chl *a*: Chlorophyll *a* concentration

CTD: Conductivity, Temperature, and Depth sensor

DIN: Dissolved Inorganic Nitrogen

EBV: Essential Biodiversity Variables

EEA: European Environment Agency

EU: European Union

GBF: Global Biodiversity Framework

GLLVM: General Linear Latent Variable Model

HMSC: Hierarchical Modelling of Species Communities

ICES: International Council for the Exploration of the Sea

IPBES: Intergovernmental Platform on Biodiversity and Ecosystem Services

IUCN: International Union for Conservation of Nature

JSDM: Joint Species Distribution Model

MCMC: Markov Chain Monte Carlo

MPA: Marine Protected Area

MSP: Marine Spatial Planning

NIS: Non-Indigenous Species

PCA: Principal Component Analysis

PSRF: Potential Scale Reduction Factor

PSU: Practical Salinity Unit

RMSE: Root Mean Squared Error

SBS: Sea Bottom Salinity

SBT: Sea Bottom Temperature

SD: Standard Deviation

SDM: Species Distribution Model

8. References

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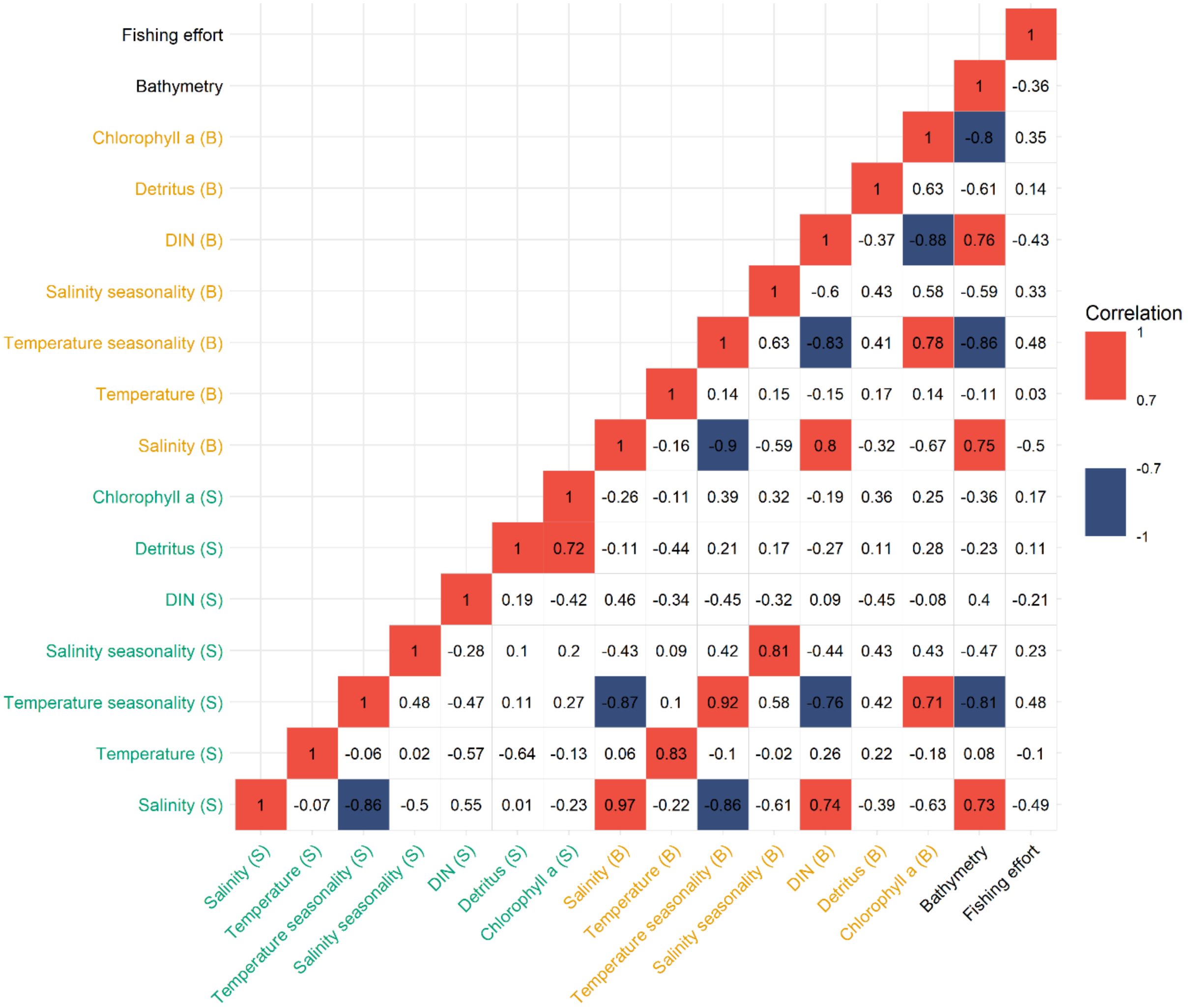
9. Appendix A - Supplementary material to Chapter 3

Supplementary Information to **Community assembly processes and drivers shaping marine fish community structure in the North Sea**

Marcel Montanyès, Benjamin Weigel, Martin Lindegren



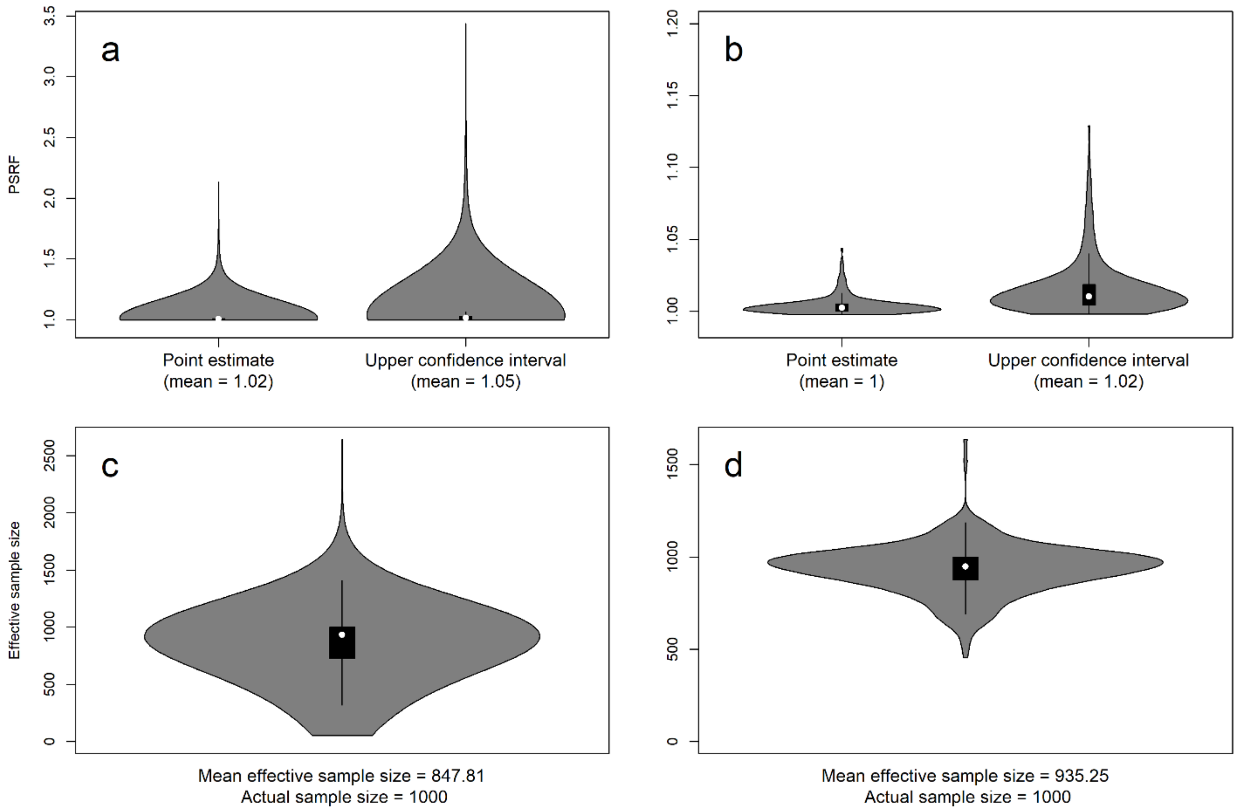
	Salinity (S)	Temperature (S)	Temperature seasonality (S)	Salinity seasonality (S)	DIN (S)	Detritus (S)	Chlorophyll a (S)	Salinity (B)	Temperature (B)	Temperature seasonality (B)	Salinity seasonality (B)	DIN (B)	Detritus (B)	Chlorophyll a (B)	Bathymetry	Fishing effort
Fishing effort																1
Bathymetry															1	-0.36
Chlorophyll a (B)														1	-0.8	0.35
Detritus (B)													1	0.63	-0.61	0.14
DIN (B)												1	-0.37	-0.88	0.76	-0.43
Salinity seasonality (B)											1	-0.6	0.43	0.58	-0.59	0.33
Temperature seasonality (B)										1	0.63	-0.83	0.41	0.78	-0.86	0.48
Temperature (B)									1	0.14	0.15	-0.15	0.17	0.14	-0.11	0.03
Salinity (B)								1	-0.16	-0.9	-0.59	0.8	-0.32	-0.67	0.75	-0.5
Chlorophyll a (S)							1	-0.26	-0.11	0.39	0.32	-0.19	0.36	0.25	-0.36	0.17
Detritus (S)						1	0.72	-0.11	-0.44	0.21	0.17	-0.27	0.11	0.28	-0.23	0.11
DIN (S)					1	0.19	-0.42	0.46	-0.34	-0.45	-0.32	0.09	-0.45	-0.08	0.4	-0.21
Salinity seasonality (S)				1	-0.28	0.1	0.2	-0.43	0.09	0.42	0.81	-0.44	0.43	0.43	-0.47	0.23
Temperature seasonality (S)			1	0.48	-0.47	0.11	0.27	-0.87	0.1	0.92	0.58	-0.76	0.42	0.71	-0.81	0.48
Temperature (S)		1	-0.06	0.02	-0.57	-0.64	-0.13	0.06	0.83	-0.1	-0.02	0.26	0.22	-0.18	0.08	-0.1
Salinity (S)	1	-0.07	-0.86	-0.5	0.55	0.01	-0.23	0.97	-0.22	-0.86	-0.61	0.74	-0.39	-0.63	0.73	-0.49

Supplementary Figure 9.1. Correlation between candidate environmental variables. Positively correlated variables (>0.7) are shown in red; negatively correlated variables (<-0.7) in blue. Variable label colors denote whether the variable is from the sea surface (green), sea bottom (orange) or where this distinction is not applicable (black).

Supplementary table 9.1. Overview of selected traits with included trait-categories, description and ecological relevance.

Trait	**Categories**	**Description**	**Relevance**	**Reference**
Water column position (Habitat)	Bathydemersal Bathypelagic Benthopelagic Demersal Pelagic	Zone of the water column used by the species	Habitat use	Mclean *et al.*, 2019
Body Shape	Compressiform Eel-like Elongated Flat Fusiform	Shape of the body	Related to locomotion and so to prey capture, escape and dispersal capabilities	Giammona, 2021; Neat & Campbell, 2013
Fin shape	Forked Pointed Rounded Truncate	Shape of the caudal fin	Related to locomotion and so to prey capture, escape and dispersal capabilities	Giammona, 2021
Maximum length	Continuous	Maximum reported length	Body size is related the sensitivity to predation, thermal resistance and respiration	Beauchard *et al.*, 2017; Peters, 1983
Growth coefficient (K)	Continuous	Growth coefficient K estimated from the Von Bertalanffy equation	Directly linked to fitness	Kolok, 1999
Age at maturity	Continuous	First age at which the individual is able to reproduce	Maturation at an early age increases demographic resilience in harsh environments. Directly linked to fitness	Beauchard *et al.*, 2017
Spawning type	Bearer Guarder Non-guarder	Type of spawning related to parental care	Offspring survival and recruitment success	Beauchard *et al.*, 2017
Offspring size	Continuous	Diameter if the released eggs, length of the egg case or length of the young (mm)	Directly linked to fitness	Amundsen, 2003

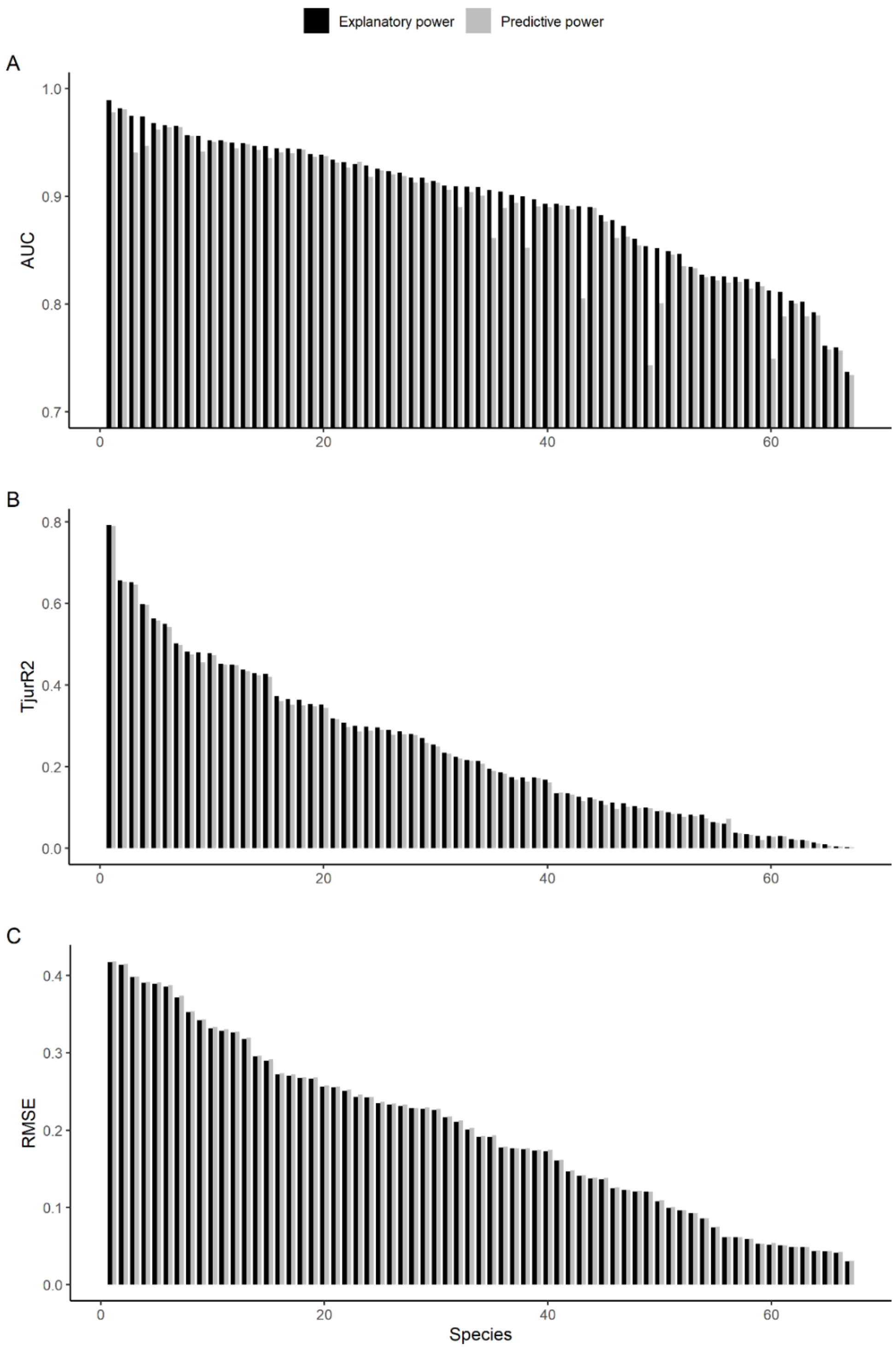
Fecundity	Continuous	Number of offspring per female per batch or per year	Directly linked to fitness, dispersal capabilities	Amundsen, 2003; Beauchard *et al.*, 2017
Feeding mode	Benthivorous	Main food source from stomach contents and biological descriptions of adults	Relates to the preferred food acquisition mode, growth requirements, demographic control and nutrient cycling	Beauchard *et al.*, 2017
	Generalist			
	Piscivorous			
	Planktivorous			
Trophic level	Continuous	Based on the proportion of different prey in stomach; if not available, based on the occurrence of prey	Diet, food web structure	Pasquaud *et al.*, 2010



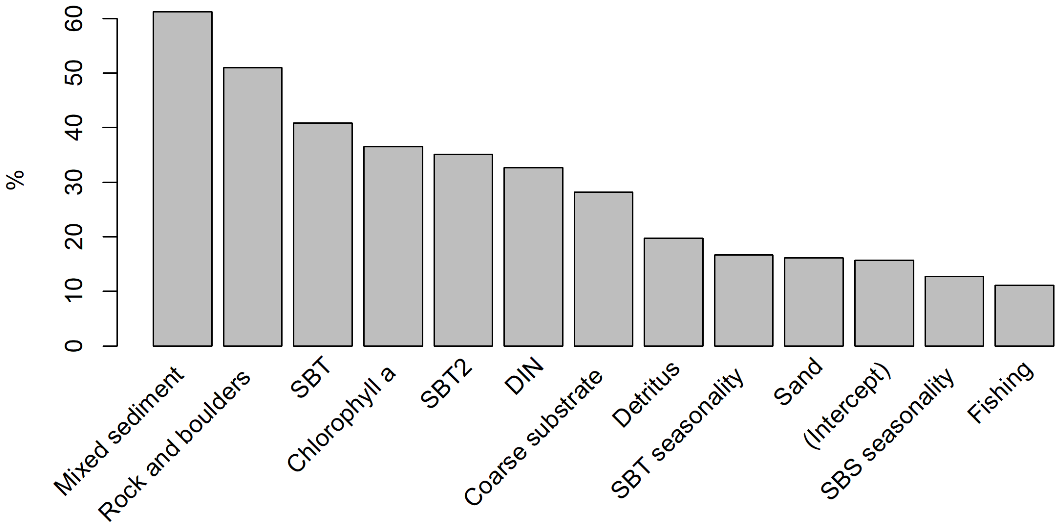
Supplementary figure 9.2. MCMC convergence metrics. Potential scale reduction factor (PSRF) for (a) Beta and (b) Gamma parameters, and effective sample size for (c) Beta and (d) Gamma parameters.

Supplementary Table 9.2. Mean explanatory and predictive powers (from a 5-fold cross-validation) across all modelled species measured as AUC, Tjur R2 and RMSE.

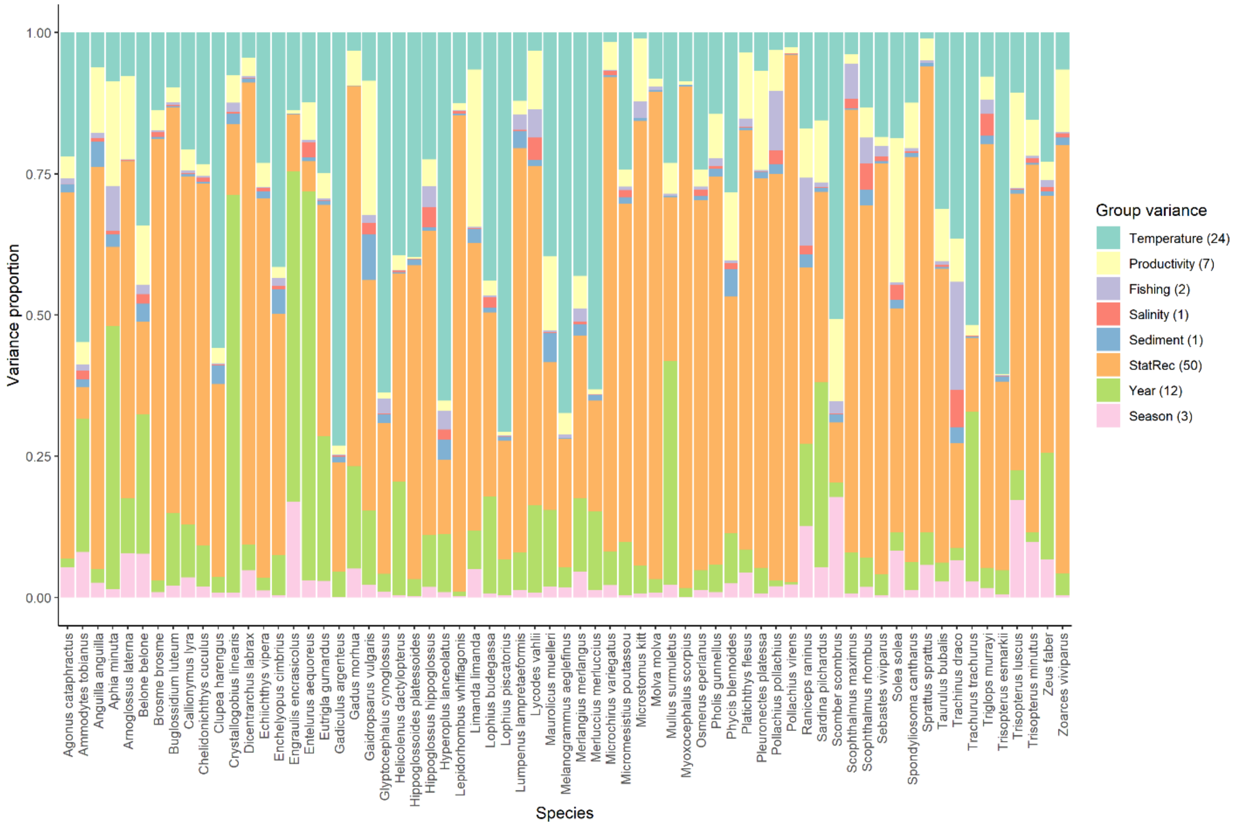
	AUC	**Tjur R^2**	**RMSE**
Explanatory power	0.895	0.246	0.199
Predictive power	0.883	0.240	0.200



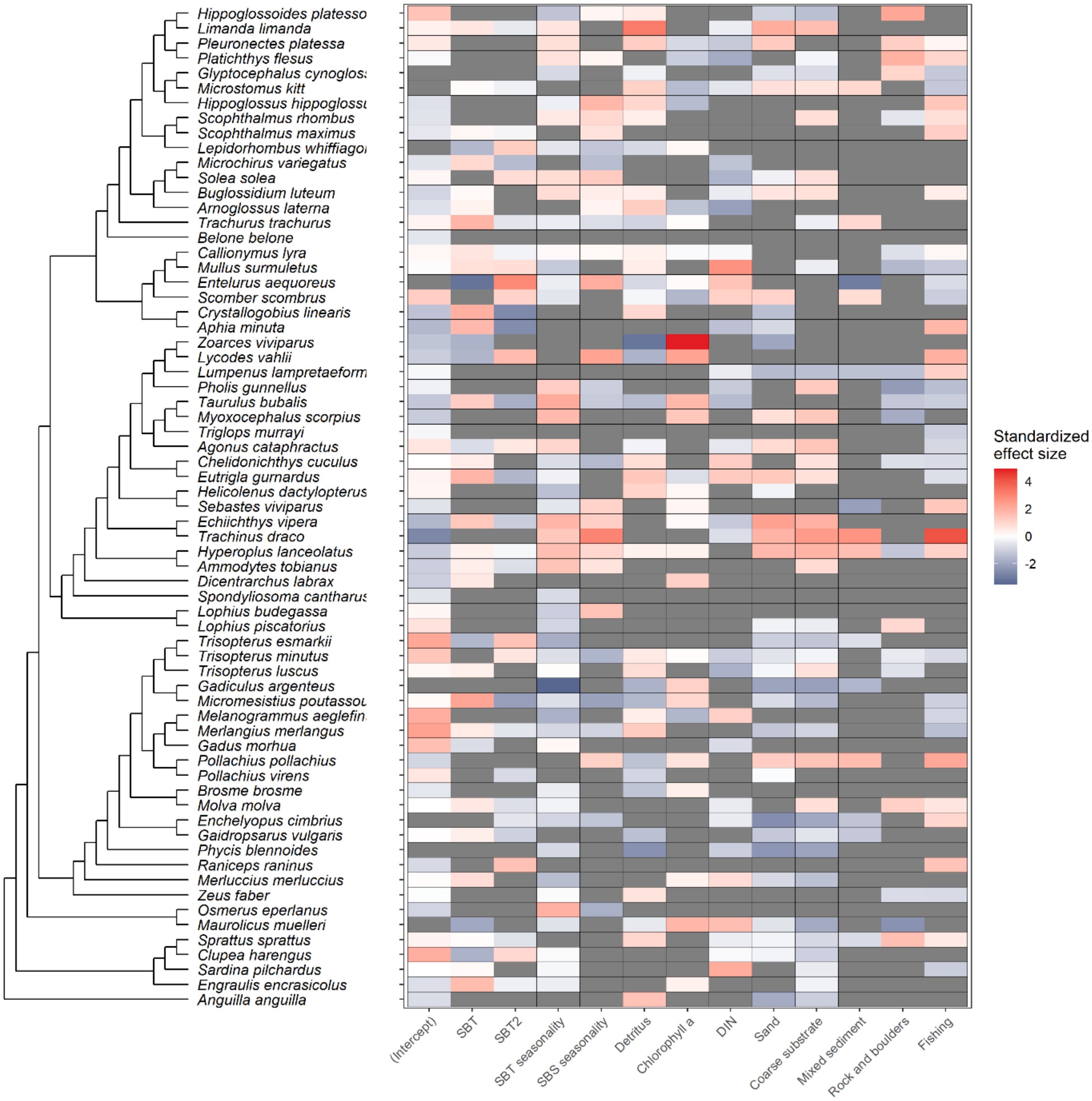
Supplementary figure 9.3. Species' explanatory (black) and predictive (grey) power measured as (A) AUC, (B) Tjur R2 and (C) Root Mean Square Error (RMSE). Predictive power values are derived from a 5-fold cross-validation.



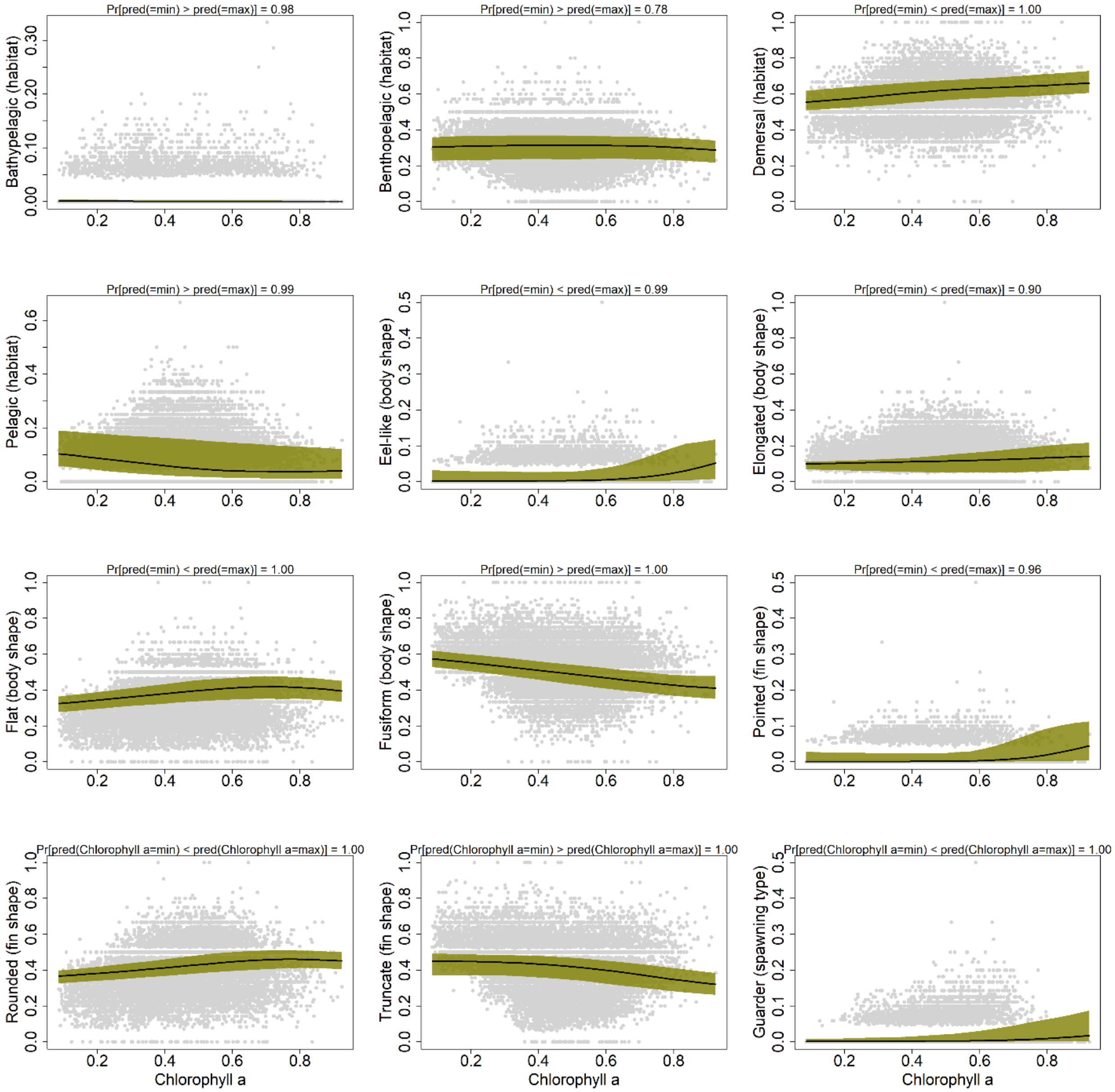
Supplementary Figure 9.4. Proportion of the species response to environmental covariates explained by traits.

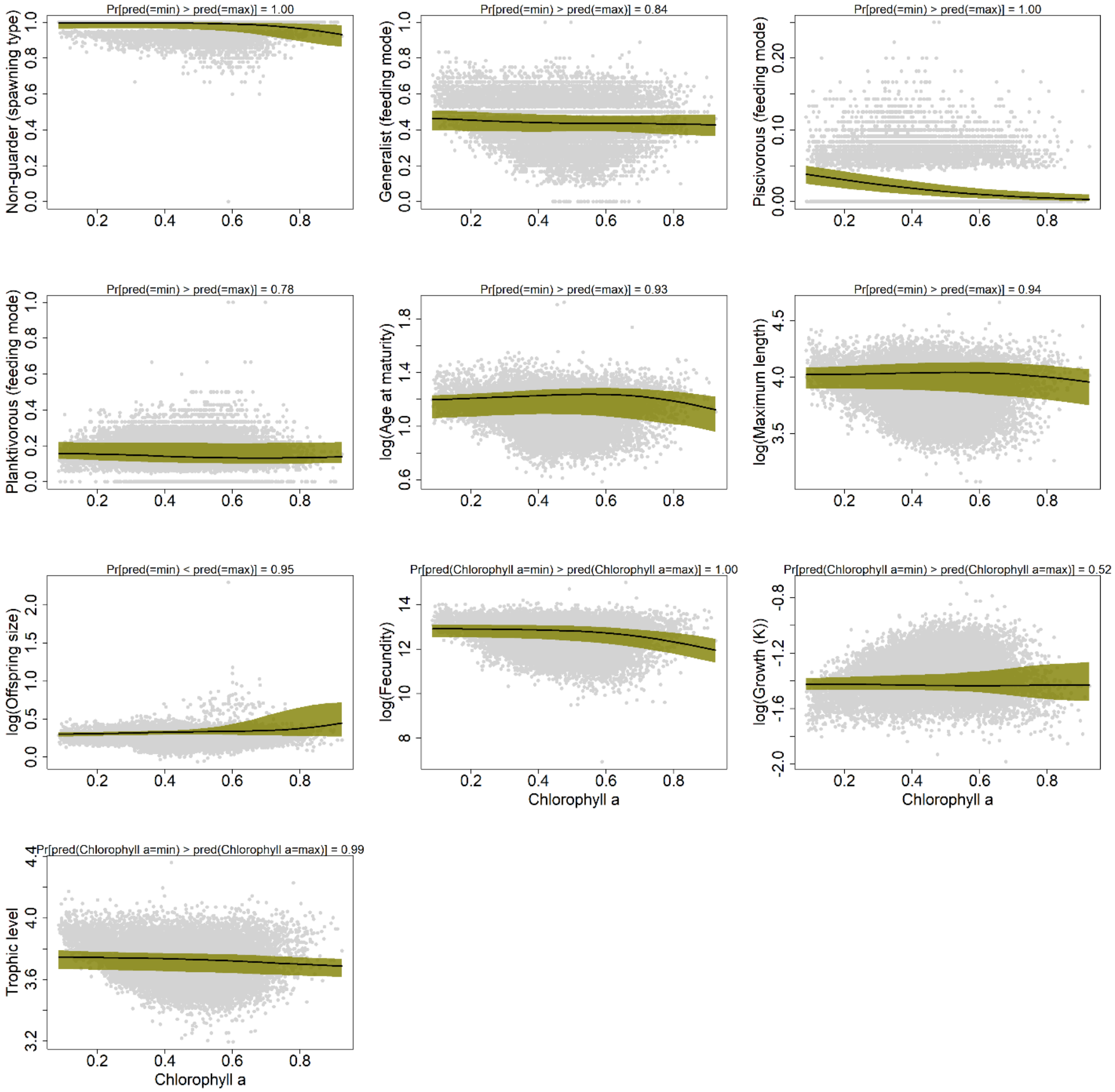


Supplementary Figure 9.5. Variance explained by the fixed and random effects included in the model denoted by different colors. Colors represent the variables (either fixed or random) and the value in brackets next them are the mean variances explained by each.



Supplementary Figure 9.6. Heatmap of the standardized beta coefficients of species responses to the environment. Red color indicates positive coefficient and blue negative coefficient with at least a posterior probability of 0.95. Grey color indicates those relationships with posterior probability <0.95.


Pr[pred(=min) > pred(=max)] = 0.98
Bathypelagic (habitat)
0.00 0.10 0.20 0.30
Pr[pred(=min) > pred(=max)] = 0.78
Benthopelagic (habitat)
Pr[pred(=min) < pred(=max)] = 1.00
Demersal (habitat)
Pr[pred(=min) > pred(=max)] = 0.99
Pelagic (habitat)
Pr[pred(=min) < pred(=max)] = 0.99
Eel-like (body shape)
Pr[pred(=min) < pred(=max)] = 0.90
Elongated (body shape)
Pr[pred(=min) < pred(=max)] = 1.00
Flat (body shape)
Pr[pred(=min) > pred(=max)] = 1.00
Fusiform (body shape)
Pr[pred(=min) < pred(=max)] = 0.96
Pointed (fin shape)
Pr[pred(Chlorophyll a=min) < pred(Chlorophyll a=max)] = 1.00
Rounded (fin shape)
Pr[pred(Chlorophyll a=min) > pred(Chlorophyll a=max)] = 1.00
Truncate (fin shape)
Pr[pred(Chlorophyll a=min) < pred(Chlorophyll a=max)] = 1.00
Guarder (spawning type)
0.2 0.4 0.6 0.8
Chlorophyll a
Chlorophyll a
Chlorophyll a



Supplementary Figure 9.7. Marginal effects of chlorophyll a concentration on ecological traits. On top of each sub-figure panel is the probability (Pr) of the predicted trait values to be either smaller or larger at minimum (min) and maximum (max) concentrations. Shaded areas represent 95% credible intervals. Effects in the manuscript are only reported with probabilities >0.95.

10. Appendix B - Supplementary material to Chapter 4

Supplementary Information to **Assessing the forecast horizon for reliably predicting marine biodiversity change**

Marcel Montanyès, Benjamin Weigel, Federico Maioli, Gleb Tikhonov, Pieter Daniël van Denderen, Otso Ovaskainen, Martin Lindegren

Supplementary table 10.1. Bottom trawl surveys included in the study.

Survey	**Area**	**Years**	**Months**	**Number of Hauls**	**Source**	**Reference**
EVHOE	Bay of Biscay & Celtic Sea	1997 - 2021	Oct.-Dec.	3415	(ICES, 2022)	(ICES, 1997)
FR-CGFS	English channel	1998 - 2021	Sep.-Nov.	911	(ICES, 2022)	(ICES, 2017)
Gre-GFS	Greenland	1989 - 2020	Sep.-Dec	3.121	N/A	(Fock, 2007)
Ice-GFS	Iceland	1989 - 2021	Feb.-Apr.	18.542	N/A	(Sólmundsson *et al.*, 2010)
IE-IGFS	Ireland Shelf Sea	2003 - 2021	Sep.-Dec.	3.037	(ICES, 2022)	(ICES, 2017)
NIGFS	Northern Ireland	2006 - 2021	Feb.-Apr, Oct.-Nov.	1.589	(ICES, 2022)	(ICES, 2017)
NorBTS	Norwegian Sea, Barents Sea and northern North Sea	1989 - 2017	Jan.-Dec.	29.993	(IMR, 2021)	(Mjanger *et al.*, 2006)
NS-IBTS	North Sea	1989 - 2021	Jan.-Mar., Jun.-Sep.	18.959	(ICES, 2022)	(ICES, 2020)

PT-IBTS	Portugal shelf sea	2002 - 2021	Sep.-Nov.	1.100	(ICES, 2022)	(ICES, 2017)
ROCKALL	Rockall plateau	1999 - 2020	Aug.-Sep.	779	(ICES, 2022)	(ICES, 2017)
SP-ARSA	Gulf of Cadiz	1996 - 2020	Feb.-Apr., Oct.-Dec.	1.419	(ICES, 2022)	(ICES, 2017)
SP-NORTH	Cantabrian Sea	1990-2021	Aug.-Nov.	3.433	(ICES, 2022)	(ICES, 2017)
SWC-IBTS	Scotland Shelf Sea	1989 - 2021	Feb.-Apr., Oct.-Dec.	3.731	(ICES, 2022)	(ICES, 2017)
TOTAL				**90.029**		

Sources and references:

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Supplementary table 10.2. Model fitting specifications.

Model type	Data input	Specification	Random factors	Chains	Samples	Thinning
Whole-period	Occurrence	-	Yes	4	250	5.000
Whole-period	Biomass	-	Yes	4	250	5.000
Whole-period	Occurrence	-	No	4	250	10.000
Whole-period	Biomass	-	No	4	250	1.000
Decade	Occurrence	1990	No	4	250	10.000
Decade	Occurrence	2000	No	4	250	10.000
Decade	Occurrence	2010	No	4	250	10.000
Decade	Biomass	1990	No	4	250	100
Decade	Biomass	2000	No	4	250	100
Decade	Biomass	2010	No	4	250	100

Supplementary table 10.3. Individual species explanatory power for the occurrence (AUC) and biomass conditional on presence (R^2) for the whole period environmental models.

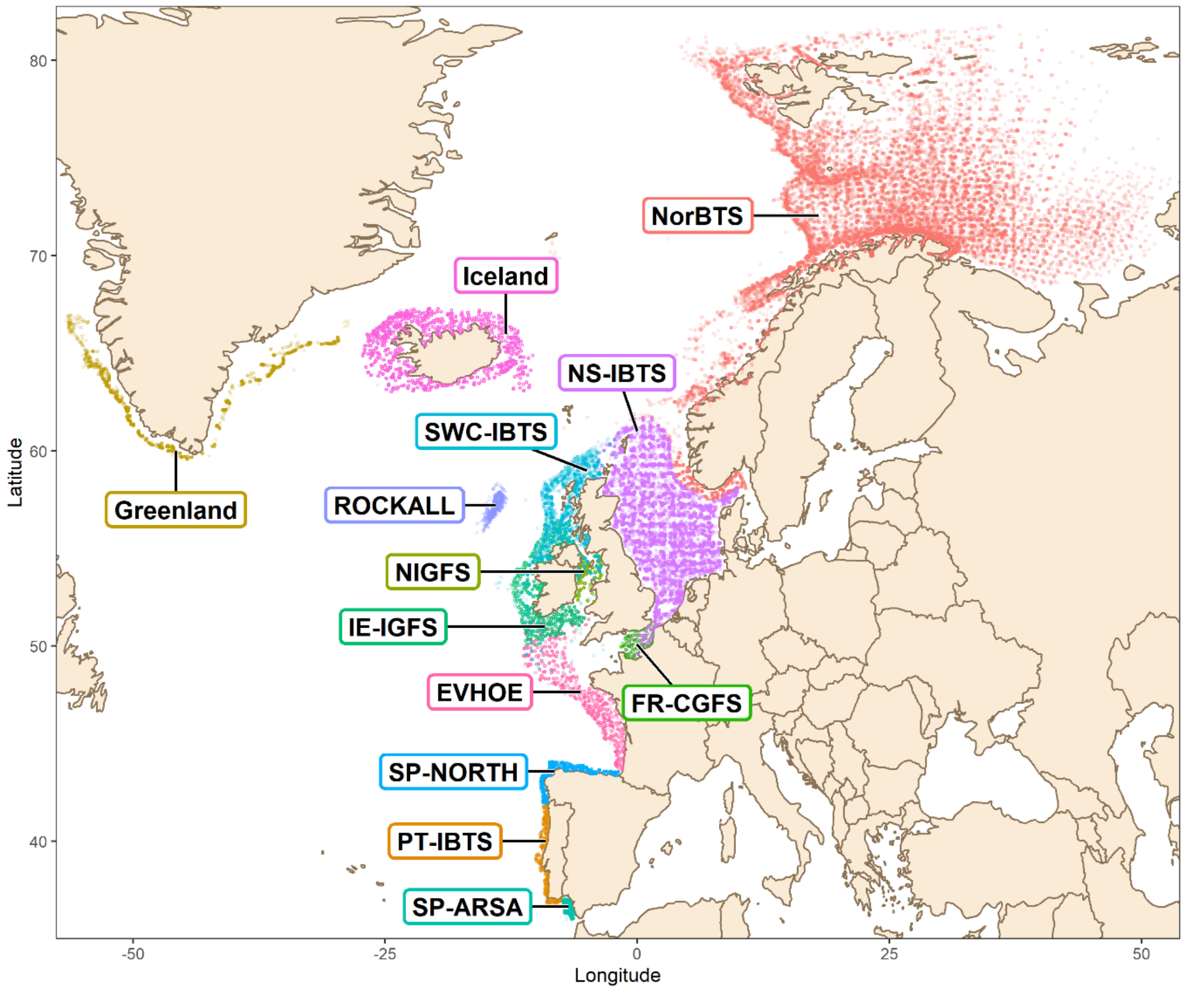
Species	AUC	R^2
Acantholabrus palloni	0,96	0,17
Agonus cataphractus	0,91	0,18
Ammodytes marinus	0,86	0,15
Ammodytes tobianus	0,91	0,05
Anarhichas denticulatus	0,87	0,13
Anarhichas lupus	0,87	0,17
Anarhichas minor	0,87	0,03
Anisarchus medius	0,91	0,14
Aphia minuta	0,90	0,18
Arctogadus glacialis	0,88	0,63
Arctozenus risso	0,91	0,15
Argentina silus	0,88	0,21
Argentina sphyraena	0,86	0,28
Arnoglossus imperialis	0,96	0,15
Arnoglossus laterna	0,90	0,27
Artediellus atlanticus	0,86	0,40
Artediellus uncinatus	0,97	0,16

Aspidophoroides monopterygius	0,98	0,02
Atherina presbyter	0,97	0,32
Bathysolea profundicola	0,99	0,13
Belone belone	0,77	0,18
Benthosema glaciale	0,83	0,43
Blennius ocellaris	0,95	0,21
Boops boops	0,98	0,12
Boreogadus saida	0,93	0,41
Brosme brosme	0,83	0,17
Buglossidium luteum	0,95	0,15
Callionymus lyra	0,90	0,09
Callionymus maculatus	0,89	0,55
Careproctus micropus	0,94	0,42
Careproctus reinhardti	0,88	0,26
Chelidonichthys cuculus	0,92	0,06
Chelidonichthys lastoviza	0,94	0,18
Chelidonichthys lucerna	0,91	0,09
Chelidonichthys obscurus	0,98	0,15
Chimaera monstrosa	0,89	0,10
Ciliata septentrionalis	0,94	0,47
Clupea harengus	0,89	0,15
Coelorinchus caelorhincus	0,96	0,34
Conger conger	0,96	0,21
Coryphaenoides rupestris	0,93	0,15
Crystallogobius linearis	0,91	0,20
Ctenolabrus rupestris	0,90	0,27
Cyclopterus lumpus	0,88	0,22
Deltentosteus quadrimaculatus	0,97	0,07
Dicentrarchus labrax	0,96	0,25
Dicologlossa cuneata	0,98	0,08
Diplodus vulgaris	0,99	0,23
Echiichthys vipera	0,96	0,26
Enchelyopus cimbrius	0,73	0,09
Engraulis encrasicolus	0,90	0,17
Entelurus aequoreus	0,78	0,15
Etmopterus spinax	0,92	0,06
Eumicrotremus spinosus	0,89	0,46
Eutrigla gurnardus	0,92	0,10
Gadiculus argenteus	0,89	0,17
Gadiculus thori	0,94	0,11
Gadus morhua	0,88	0,33
Gaidropsarus argentatus	0,87	0,42

Gaidropsarus macrophthalmus	0,96	0,09
Gaidropsarus vulgaris	0,75	0,18
Galeorhinus galeus	0,93	0,29
Galeus atlanticus	0,99	0,16
Galeus melastomus	0,91	0,12
Gasterosteus aculeatus	0,92	0,05
Glyptocephalus cynoglossus	0,76	0,21
Gymnammodytes semisquamatus	0,88	0,09
Gymnocanthus tricuspis	0,88	0,32
Helicolenus dactylopterus	0,91	0,18
Hexanchus griseus	0,95	0,64
Hippoglossoides platessoides	0,85	0,26
Hippoglossus hippoglossus	0,80	0,23
Hyperoplus immaculatus	0,88	0,07
Hyperoplus lanceolatus	0,94	0,22
Icelus bicornis	0,83	0,61
Labrus mixtus	0,87	0,10
Lampanyctus crocodilus	0,95	0,14
Lepidion eques	0,91	0,25
Lepidopus caudatus	0,98	0,21
Lepidorhombus boscii	0,98	0,41
Lepidorhombus whiffiagonis	0,92	0,17
Lepidotrigla cavillone	0,97	0,17
Leptagonus decagonus	0,91	0,36
Leptoclinus maculatus	0,90	0,33
Lesueurigobius friesii	0,93	0,15
Limanda limanda	0,95	0,39
Liparis bathyarcticus	0,96	0,24
Liparis fabricii	0,92	0,32
Lumpenus lampretaeformis	0,81	0,22
Macrourus berglax	0,94	0,10
Malacocephalus laevis	0,98	0,20
Mallotus villosus	0,88	0,13
Maurolicus muelleri	0,85	0,08
Melanogrammus aeglefinus	0,86	0,13
Merlangius merlangus	0,92	0,26
Merluccius merluccius	0,96	0,18
Microchirus variegatus	0,93	0,10
Micromesistius poutassou	0,86	0,20
Microstomus kitt	0,85	0,12
Molva dypterygia	0,88	0,12
Molva macrophthalma	0,97	0,13

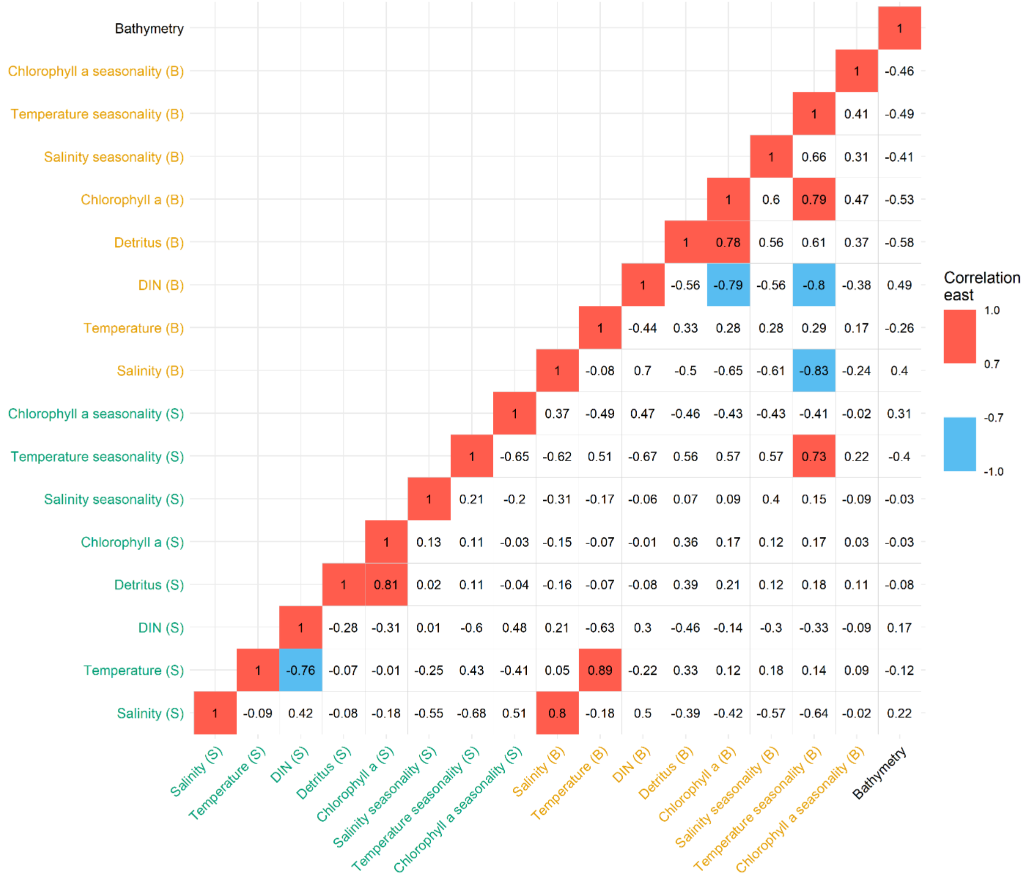
Molva molva	0,82	0,16
Mullus surmuletus	0,90	0,23
Myoxocephalus scorpius	0,89	0,07
Notoscopelus kroyeri	0,98	0,12
Pagellus acarne	0,98	0,08
Pagellus bogaraveo	0,95	0,08
Pagellus erythrinus	0,97	0,16
Paraliparis bathybius	0,93	0,13
Pegusa lascaris	0,92	0,44
Zeugopterus norvegicus	0,81	0,73
Phycis blennoides	0,89	0,16
Platichthys flesus	0,97	0,21
Pleuronectes platessa	0,91	0,11
Pollachius pollachius	0,84	0,12
Pollachius virens	0,80	0,20
Reinhardtius hippoglossoides	0,93	0,34
Sardina pilchardus	0,90	0,21
Scomber colias	0,98	0,06
Scomber japonicus	0,98	0,04
Scomber scombrus	0,90	0,08
Scophthalmus maximus	0,89	0,07
Scophthalmus rhombus	0,90	0,17
Scorpaena loppei	0,97	0,47
Scorpaena notata	0,97	0,17
Scorpaena scrofa	0,97	0,15
Scyliorhinus canicula	0,93	0,12
Scyliorhinus stellaris	0,97	0,47
Sebastes mentella	0,92	0,16
Sebastes norvegicus	0,90	0,24
Sebastes viviparus	0,81	0,24
Serranus cabrilla	0,98	0,09
Solea solea	0,90	0,22
Somniosus microcephalus	0,83	0,11
Spondyliosoma cantharus	0,97	0,25
Sprattus sprattus	0,96	0,24
Squalus acanthias	0,88	0,16
Taurulus bubalis	0,95	0,12
Trachinus draco	0,95	0,13
Trachurus mediterraneus	0,98	0,14
Trachurus picturatus	0,98	0,13
Trachurus trachurus	0,93	0,21
Trigla lyra	0,97	0,10

Triglops murrayi	0,81	0,49
Triglops nybelini	0,96	0,24
Triglops pingelii	0,90	0,21
Trisopterus esmarkii	0,86	0,21
Trisopterus luscus	0,92	0,17
Trisopterus minutus	0,90	0,21
Zeugopterus punctatus	0,90	0,10
Zeus faber	0,93	0,03



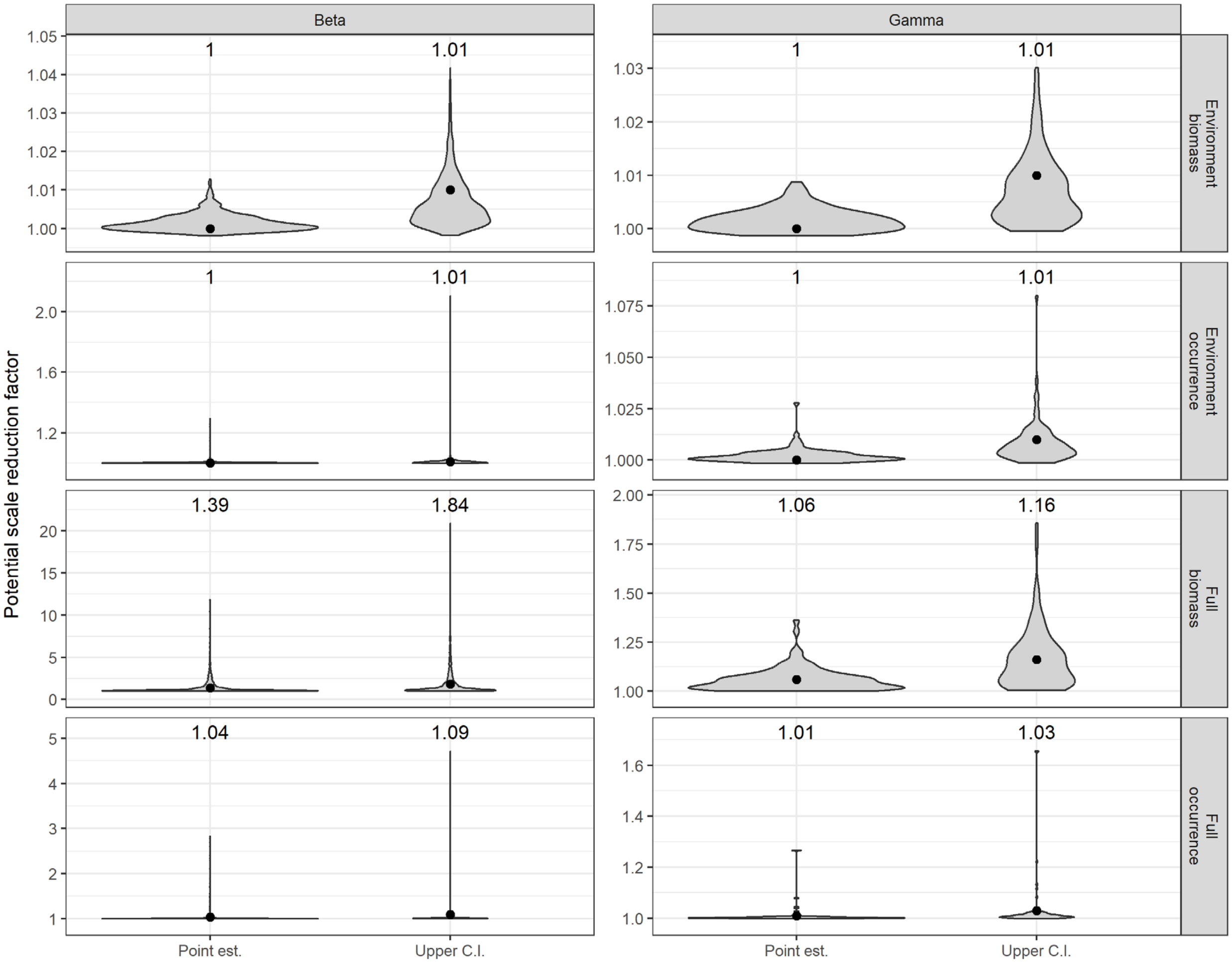
Supplementary figure 10.1. Position of all unique hauls from the different surveys performed in the study area between 1989 and 2021.

To represent the environmental conditions at each unique haul, we retrieved environmental and physical variables from the model re-analysis products from NEMO-MEDUSA coupled hygro-geochemical model runs (Gurvan *et al.*, 2022; Yool *et al.*, 2013). This dataset offers monthly resolution and is based on an irregular spatial grid with a mean resolution of 0.18º, ranging from 0.14º to 0.48º, with only 10 points (0.07% of the data) having distances greater than 0.3º. Aligning each haul with the corresponding environmental data involved a nearest neighbor routine utilizing the R package RANN ver. 2.6.1 (Arya *et al.*, 2019). Our exploration of potential correlations among environmental variables —both surface and bottom—led to the retention of seafloor variables and those less correlated with others when a correlation of ±0.7 was detected (Supplementary figure 10.2).

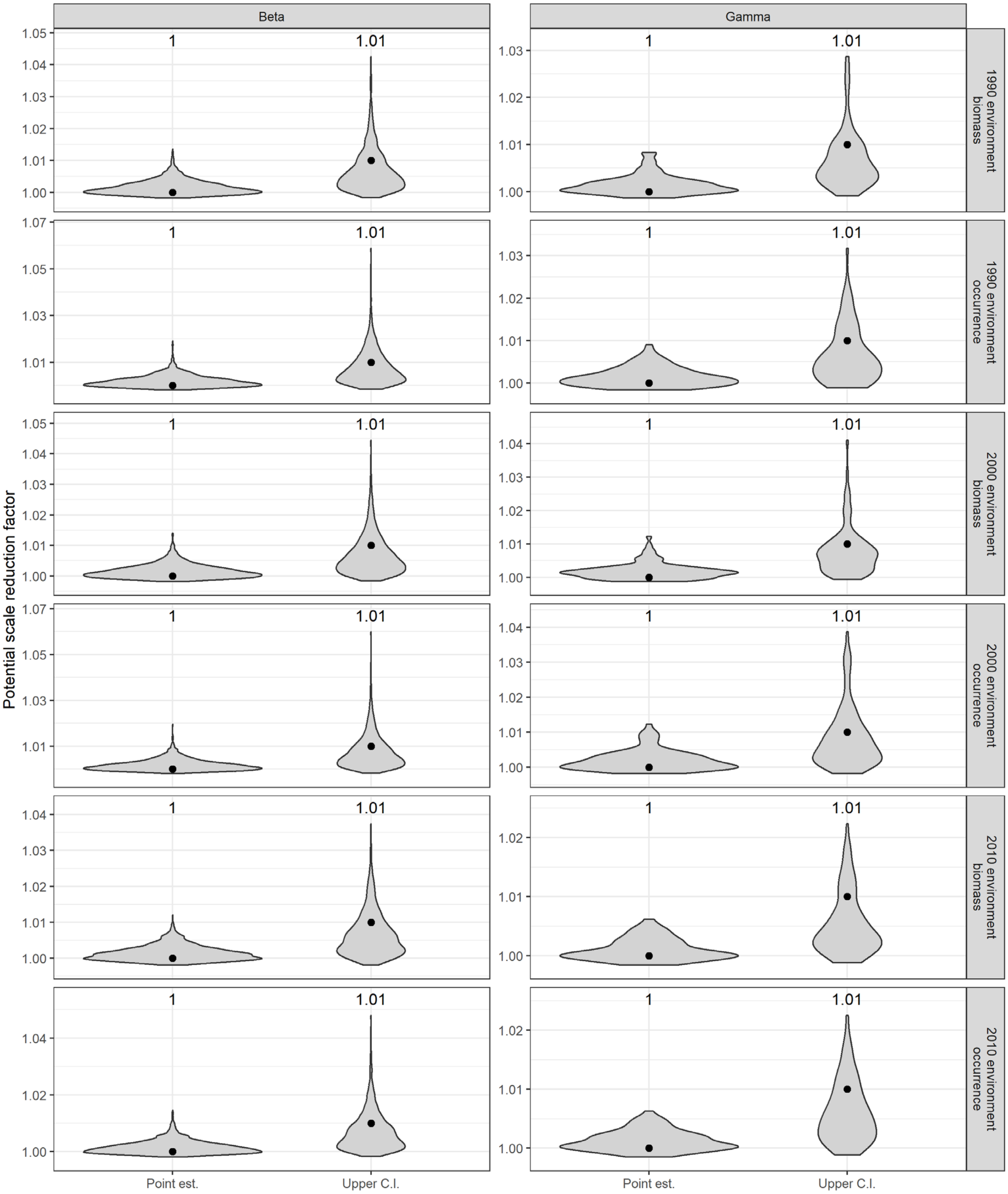


	Salinity (S)	Temperature (S)	DIN (S)	Detritus (S)	Chlorophyll a (S)	Salinity seasonality (S)	Temperature seasonality (S)	Chlorophyll a seasonality (S)	Salinity (B)	Temperature (B)	DIN (B)	Detritus (B)	Chlorophyll a (B)	Salinity seasonality (B)	Temperature seasonality (B)	Chlorophyll a seasonality (B)	Bathymetry
Bathymetry																	1
Chlorophyll a seasonality (B)																1	-0.46
Temperature seasonality (B)															1	0.41	-0.49
Salinity seasonality (B)														1	0.66	0.31	-0.41
Chlorophyll a (B)													1	0.6	0.79	0.47	-0.53
Detritus (B)												1	0.78	0.56	0.61	0.37	-0.58
DIN (B)											1	-0.56	-0.79	-0.56	-0.8	-0.38	0.49
Temperature (B)										1	-0.44	0.33	0.28	0.28	0.29	0.17	-0.26
Salinity (B)									1	-0.08	0.7	-0.5	-0.65	-0.61	-0.83	-0.24	0.4
Chlorophyll a seasonality (S)								1	0.37	-0.49	0.47	-0.46	-0.43	-0.43	-0.41	-0.02	0.31
Temperature seasonality (S)							1	-0.65	-0.62	0.51	-0.67	0.56	0.57	0.57	0.73	0.22	-0.4
Salinity seasonality (S)						1	0.21	-0.2	-0.31	-0.17	-0.06	0.07	0.09	0.4	0.15	-0.09	-0.03
Chlorophyll a (S)					1	0.13	0.11	-0.03	-0.15	-0.07	-0.01	0.36	0.17	0.12	0.17	0.03	-0.03
Detritus (S)				1	0.81	0.02	0.11	-0.04	-0.16	-0.07	-0.08	0.39	0.21	0.12	0.18	0.11	-0.08
DIN (S)			1	-0.28	-0.31	0.01	-0.6	0.48	0.21	-0.63	0.3	-0.46	-0.14	-0.3	-0.33	-0.09	0.17
Temperature (S)		1	-0.76	-0.07	-0.01	-0.25	0.43	-0.41	0.05	0.89	-0.22	0.33	0.12	0.18	0.14	0.09	-0.12
Salinity (S)	1	-0.09	0.42	-0.08	-0.18	-0.55	-0.68	0.51	0.8	-0.18	0.5	-0.39	-0.42	-0.57	-0.64	-0.02	0.22

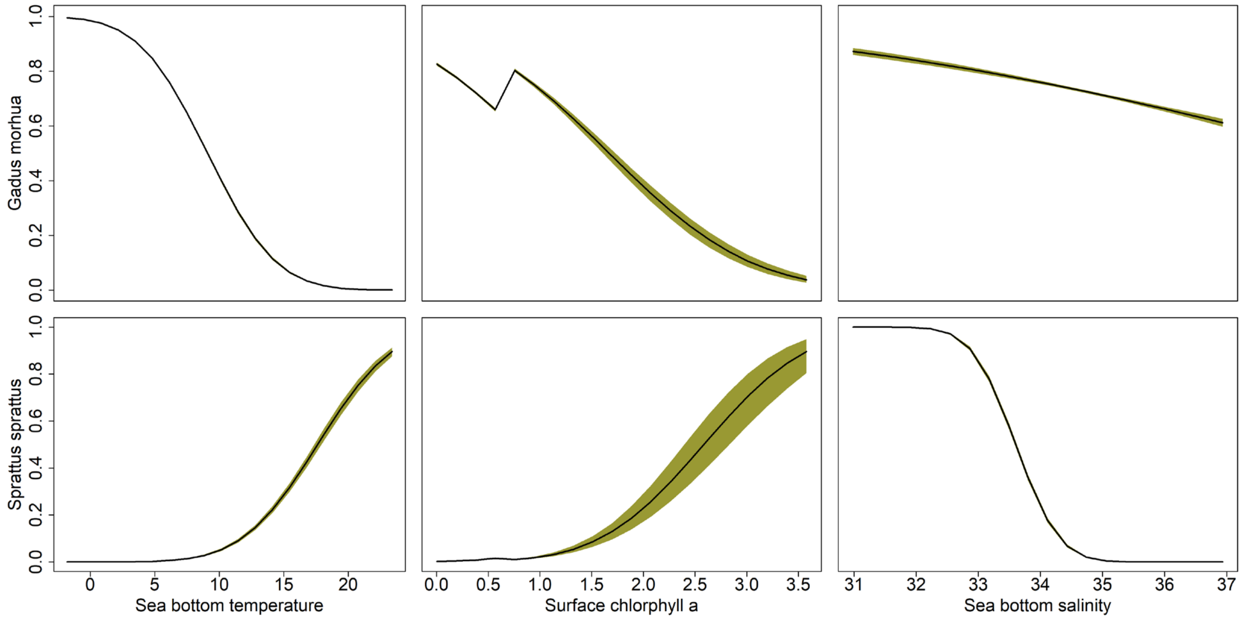
Supplementary figure 10.2. Correlation matrix between candidate environmental variables. Highly positively correlated variables (>0.7) are shown in red; highly negatively correlated variables (<-0.7) in blue. Variable label colors denote whether the variable is from the sea surface (green), sea bottom (orange) or where this distinction is not applicable (black).



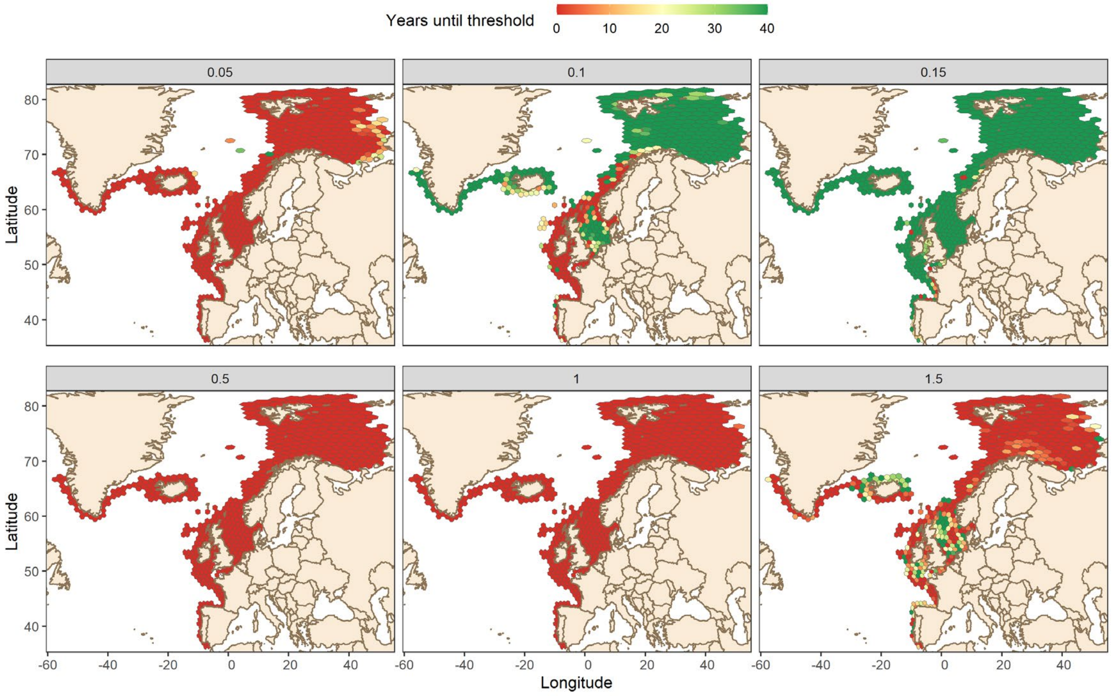
Supplementary figure 10.3. Whole-period models MCMC convergence from the Beta (left column) and Gamma (right column) parameters. Each row shows each model's distribution of the potential scale reduction factor values and its mean (value at the top of each panel) for the point estimate and the upper confidence interval.



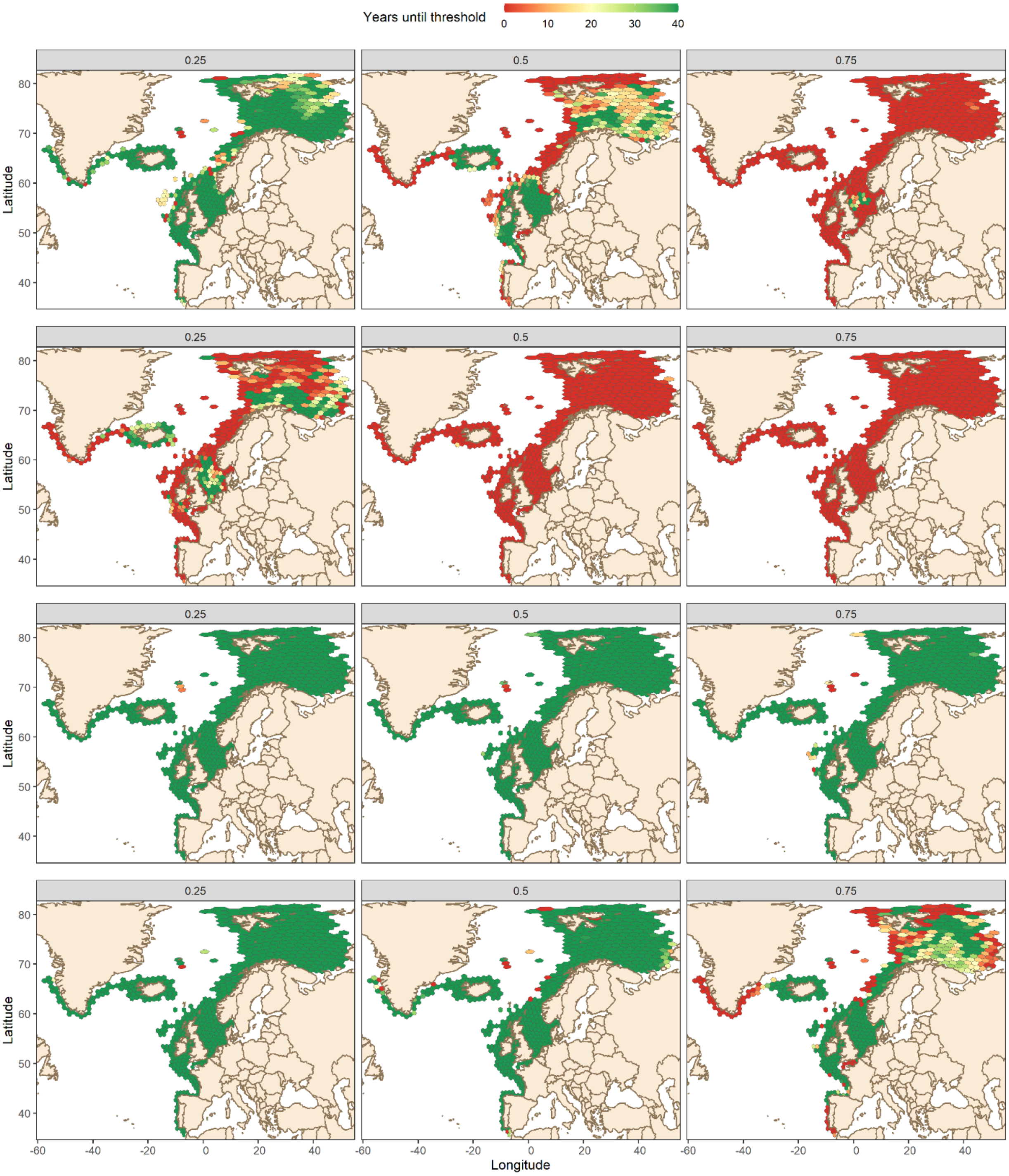
Supplementary figure 10.4. Decade models MCMC convergence from the Beta (left column) and Gamma (right column) parameters. Each row shows each model's distribution of the potential scale reduction factor values and its mean (value at the top of each panel) for the point estimate and the upper confidence interval.



Supplementary figure 10.5. Marginal effects of sea bottom temperature, surface chlorophyll a and sea bottom salinity on the probability of occurrence of cod (Gadus morhua) and sprat (Sprattus sprattus).



Supplementary figure 10.6. Forecast horizons of occurrence- (top) and biomass (bottom) prediction per grid cell, reflected by the number of years until a certain RMSE threshold (indicated at the top of each panel) is reached.

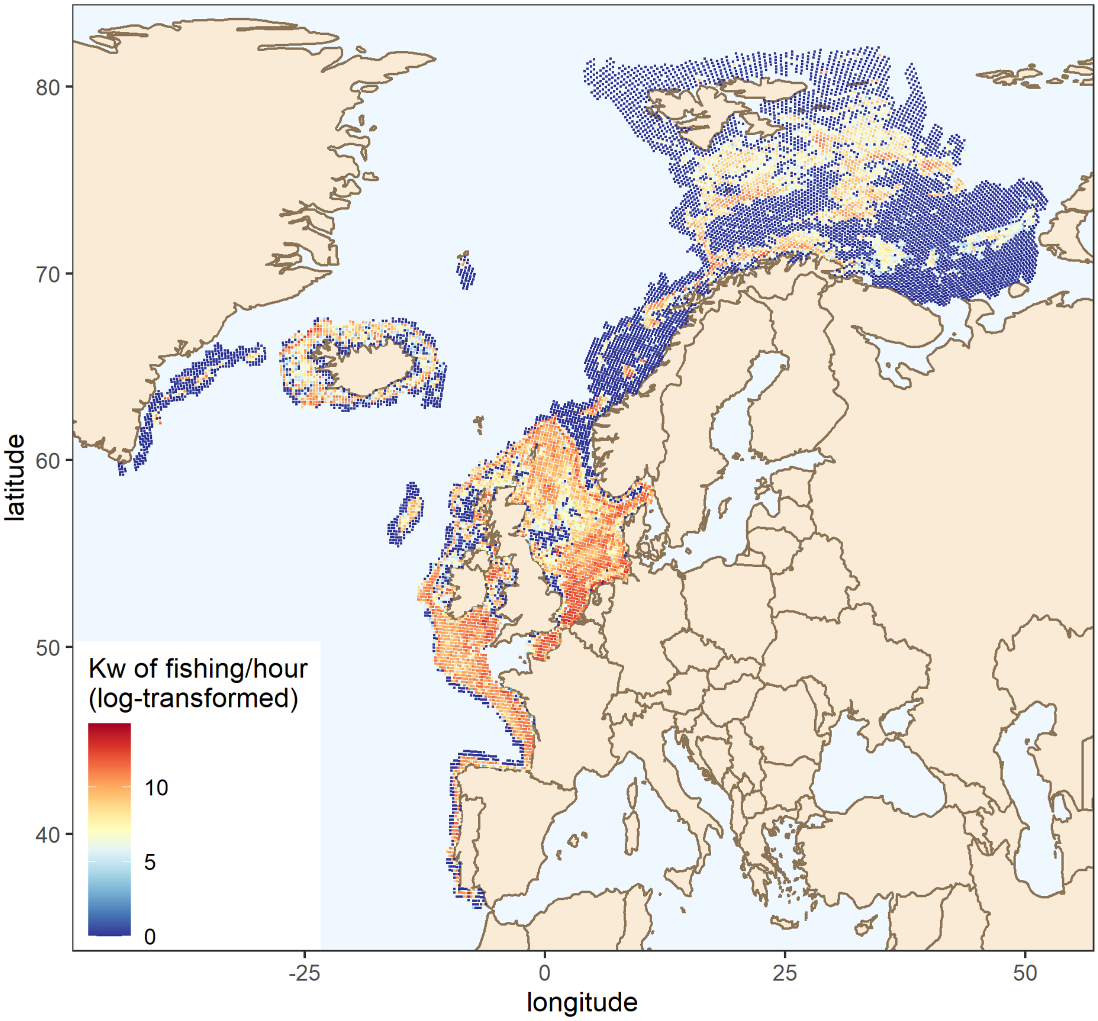


Supplementary figure 10.7. Forecast horizons of community similarity prediction per grid cell, for taxonomic occurrence (first row), taxonomic biomass (second), functional occurrence (third) and functional biomass (forth row), reflected by the number of years until a certain similarity threshold (indicated at the top of each panel) is reached.

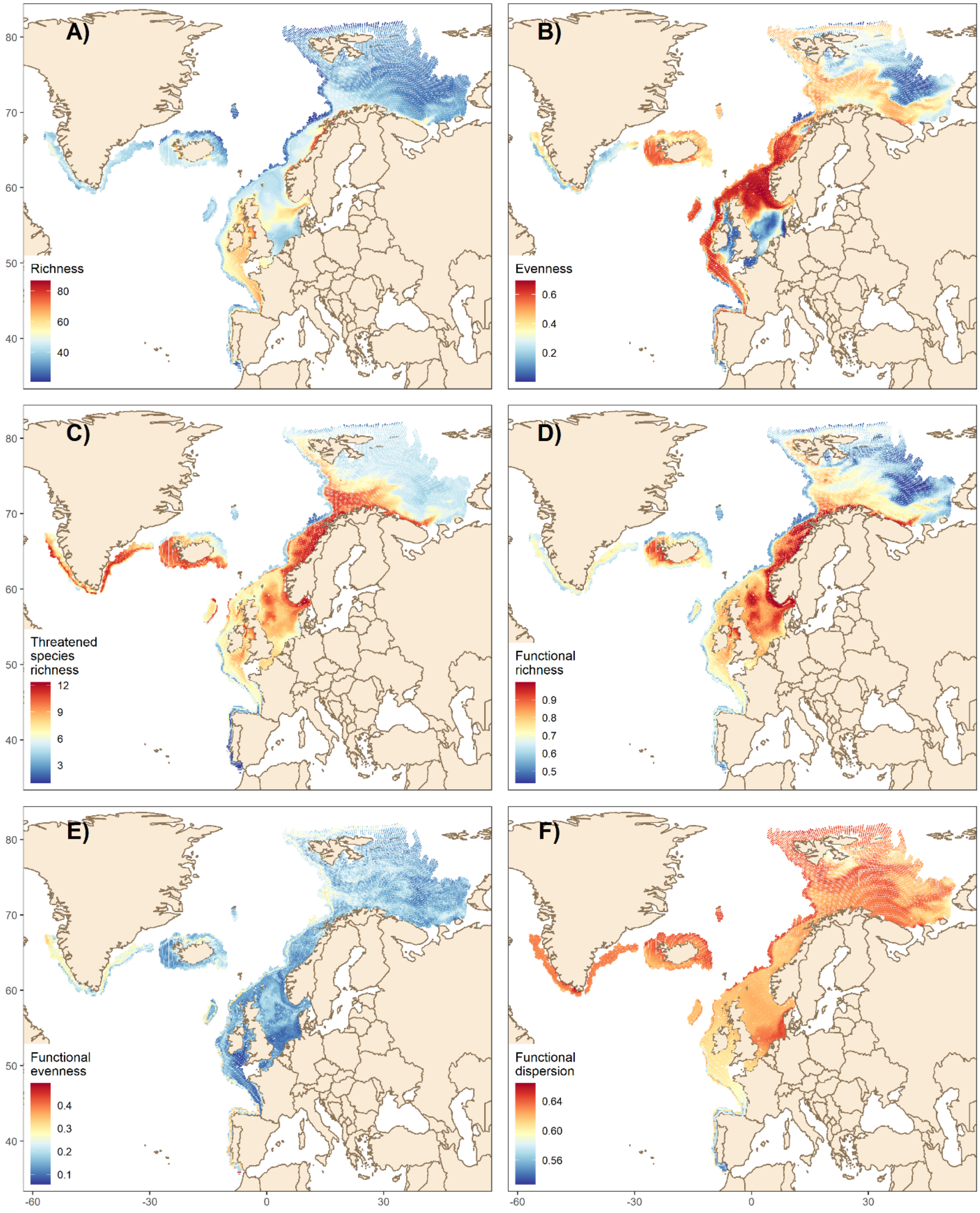
11. Appendix C - Supplementary material to Chapter 5

Supplementary Information to **Marine biodiversity protection can be improved while minimizing effects on other ocean uses**

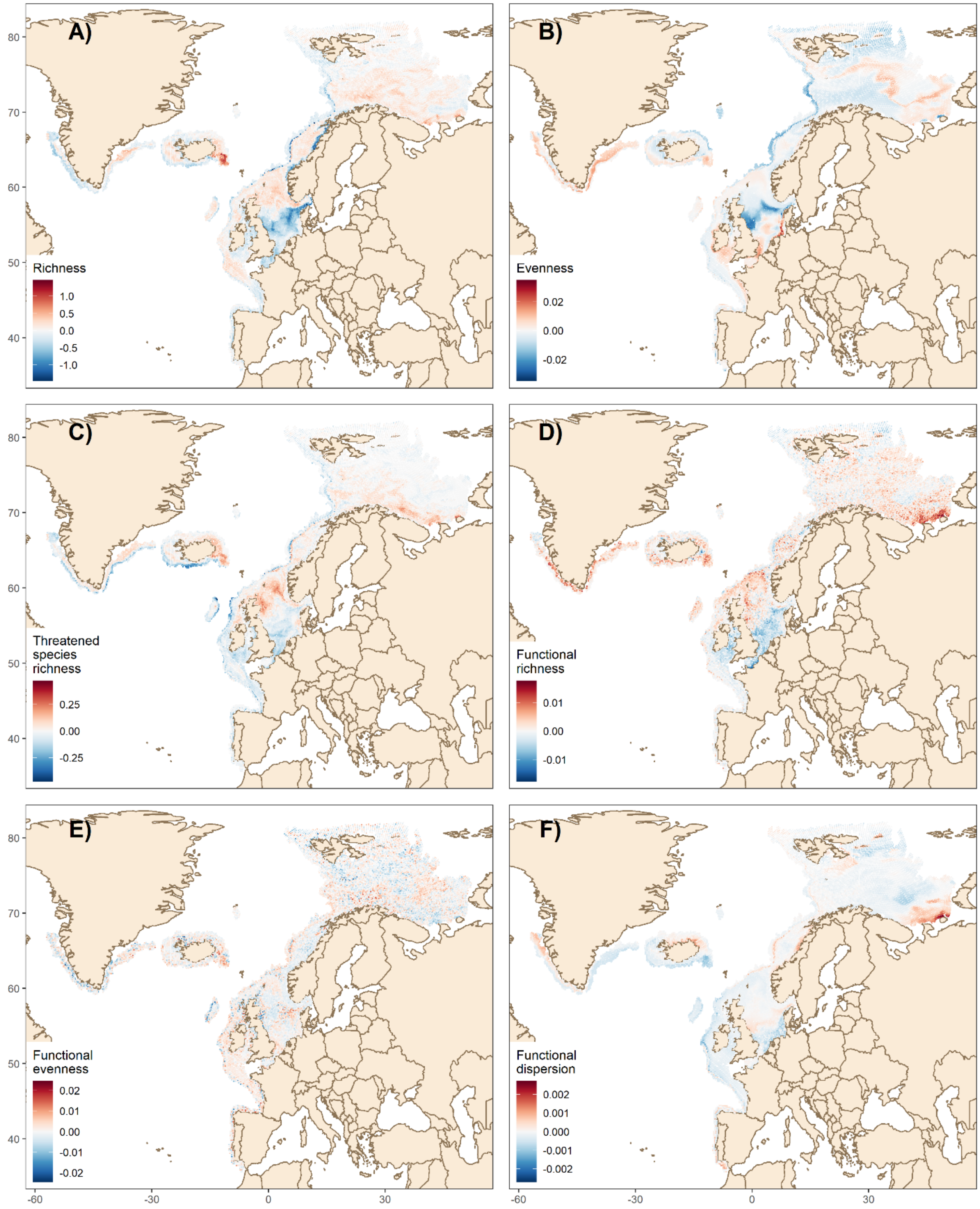
Marcel Montanyès, Pieter Daniël van Denderen, Benjamin Weigel, Martin Lindegren



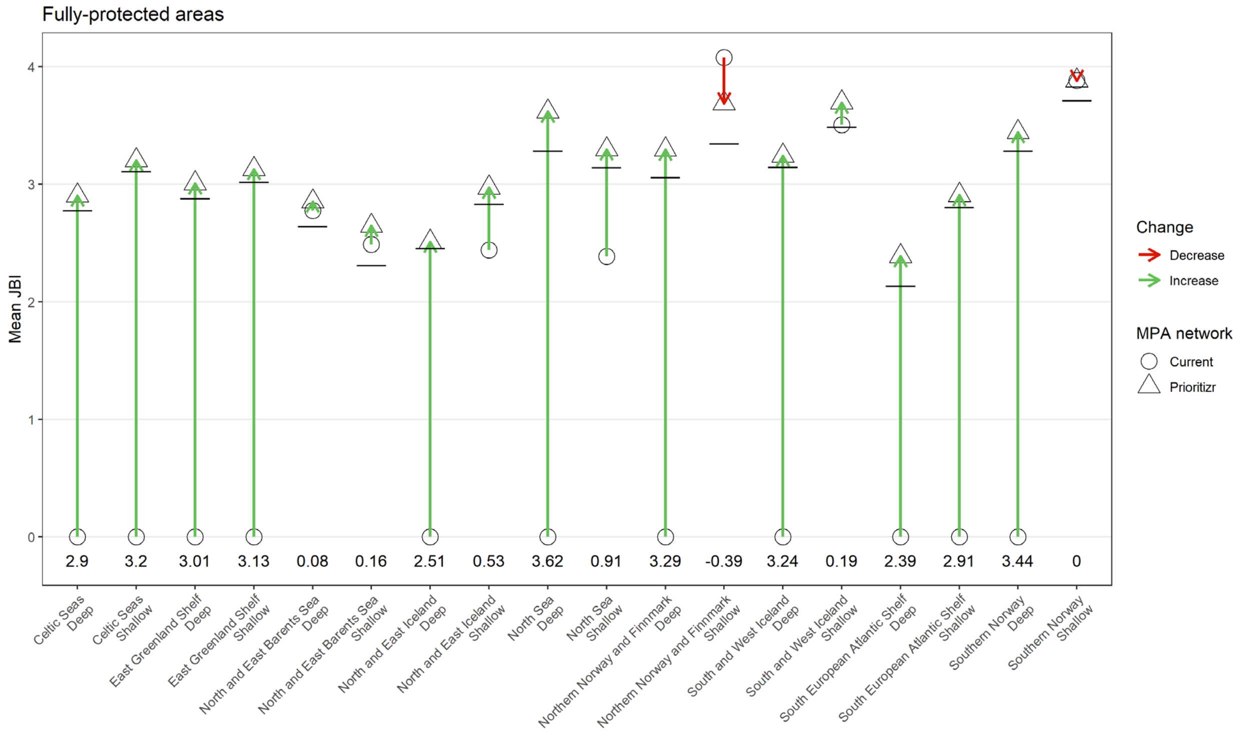
Supplementary figure 11.1. Mean fishing effort from 2012 to 2016.



Supplementary figure 11.2. Essential biodiversity variables patterns for the 2000-2016 period.



Supplementary figure 11.3. Essential biodiversity variables trends throughout the period 2016-2030.



Supplementary figure 11.4. Mean 2000-2016 Joint Biodiversity Index (JBI) for each Ecoregion and depth within fully protected MPAs considering the current network (open circle) and the suggested by the prioritizr output (open triangle). The arrows indicate the direction of change from current to prioritizr with the value of change at the bottom. Values of zero indicate that there are no MPAs implemented. The horizontal lines indicate the 50th quantile of JBI for each Ecoregion and depth.