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European Commission

User-oriented Solutions for Improved Monitoring and Management of Biodiversity and Ecosystem services in vulnerable European Seas

Deliverable 3.3 Report on relationships between biodiversity and ecosystem functions and services

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Executive summary

The primary objective of WP3 was to assess and analyse the links between biodiversity, ecosystem functions, and ecosystem services in the European Seas. This was achieved through a combination of conceptual modelling and quantitative analyses.

First, expert input was used to evaluate 996 potential links between 51 socio-ecological variables, including human activities, pressures, biodiversity indicators, and ecosystem services. The resulting conceptual network revealed relationships between group of elements with comparatively high agreement on the direction, such as the relationships between human activities and pressures/drivers, as well as poorly agreed relationships, such as between pressures/drivers and ecosystem structure and functions, that require further investigation. This analysis highlighted critical biodiversity indicators that appears central in the system (i.e. highly linked to the other elements), such as biomass indicators, which may confer robustness to the socio-ecological system, as well as identifying knowledge gaps that point to further research needs.

Building on this foundation, a quantitative analysis focused on the biodiversity-ecosystem function (B-EF) relationship, specifically the link between biodiversity and fish biomass (productivity). Using structural equation modelling (SEM), six case studies conducted across the northern Mediterranean and Northeast Atlantic assessed the consistency of biodiversity-fish biomass relationships across regions and compared the effects of taxonomic versus functional biodiversity indicators. We found that across case-studies, taxonomic evenness consistently add a negative effect on fish biomass whereas taxonomic richness had a consistently positive effect. In general, taxonomic indicators seems as good or better at predicting fish biomass than functional indicators, and biodiversity indicators could explain more of the biomass variability than any environmental indicators. Complementary studies further explored the drivers of fish biomass using varied methods and geographical scales. Temperature and biomass dominance were key determinants of total community biomass in the Barents Sea, while species richness (niche complementarity) played a larger role for non-dominant taxa. Large-scale analyses confirmed that temperature is a dominant driver of fish biomass, with lower biomass observed in warmer regions likely due to reduced trophic efficiency and higher biomass turnover rates, but regional variation in the effects of temperature and primary productivity on biomass are apparent.

Ecosystem multifunctionality was also investigated in the Mediterranean Sea, where spatio-temporal patterns in five functional rates representing major carbon and nutrient flux pathways in fish communities were quantified and mapped. Multifunctionality emerged from complementary species roles, with no single taxon dominating biogeochemical functions. Additionally, studies on community stability revealed that environmental gradients such as salinity, depth, and productivity were key drivers of spatial variation in stability. Biodiversity, particularly species richness and evenness, played a critical role in enhancing community stability. Communities with asynchronous species dynamics (low synchrony) were more stable, but anthropogenic pressures, such as bottom trawling, negatively impacted stability by reducing species evenness.

These findings emphasize the importance of biodiversity, environmental heterogeneity, and functional diversity in maintaining ecosystem functions and services in European Seas. They also highlight the need to assess the effects of anthropogenic pressures and prioritize the conservation of key biodiversity indicators.

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The role of this deliverable

This deliverable (D3.3) is the third of three reports in WP3 that together assess the "*Biodiversity status and cumulative impacts*" of European marine ecoregions. Mapping and understanding the links between biodiversity indicators and ecosystem functions and services, and their relations to key environmental and anthropogenic pressures will support the overarching aim of B-USEFUL to develop "user-oriented tools and solutions to conserve and protect marine biodiversity".

The deliverable is built around two main axes of research:

- Expert-based conceptual modeling of causal relationships between Human Activities, Drivers and Pressures, Ecosystem Structure and Function and Ecosystem Services.
- Quantification of the biodiversity-ecosystem functions relationships, with a focus on explaining spatio-temporal patterns in fish biomass and stability across regions using different methods, such as structural equation models (SEMs) or spatio-temporal models.

We found that biodiversity plays a critical role in shaping ecosystem functions and services, with species richness, evenness, and functional diversity emerging as key drivers of fish biomass and ecosystem stability. Generally, temperature and depth were identified as dominant environmental factors influencing regional and large-scale patterns in fish biomass, while anthropogenic pressures, such as fishing, negatively impacted biomass, although the relationships do not appear universal and regional variations were apparent. Additionally, ecosystem multifunctionality in the Mediterranean Sea highlighted the importance of biodiversity with multifunctionality emerging from complementary species roles, with no single taxon dominating biogeochemical functions. These findings highlight the interconnectedness of biodiversity, environmental gradients, and anthropogenic pressures in shaping ecosystem dynamics.

Integrating expert-based conceptual modeling with quantitative modeling can provide a powerful framework for understanding the links between biodiversity, ecosystem functions, and services in European Seas. This approach not only identifies key biodiversity indicators and environmental drivers of ecosystem functions and services but also highlights the sometimes-hidden impacts of human activities and drivers on the health of the ecosystem. The insights gained from this deliverable can inform targeted conservation strategies and support sustainable marine resource management.

Next steps (T5.3) will analyze future predictions of ecosystem functions and services in the European Sea based on scenarios co-designed with end-users (T1.3). Notably, we will use the expert-based conceptual model built in task T3.3 and presented in this deliverable to perform some qualitative network-based scenarios. This will give insights into potential effects on biodiversity and ecosystem functions and services of, for example removing key variables in the European Seas socio-ecological system, such as human activities or environmental drivers. We will also use a size-based model to quantitively predict and compare fish biomass and potential harvests according to scenarios following varied shared socio-economic pathways.

Participants

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Acronyms and abbreviations

B-EF: Biodiversity – ecosystem functions

BoB: Bay of Biscay

Chla: chlorophyll a concentration

CV: Coefficient of Variation

CWM: Community Weighted Mean

DAPSI(W)R(M): Drivers, Activities, Pressures, State changes, Impacts, (Welfare), and Responses (including Management measures).

EF: Ecosystem functions

EMODnet: European Marine Observation and Data Network

ES: Ecosystem services

FPI: Fishing pressure index

GFW: Global Fishing Watch

GHG: Greenhouse gas emissions

GLMM: Generalised Linear Mixed Model

GSA: GFCM Geographical Sub Area

IBTS: International Bottom Trawl Surveys

ICES: International Council for the Exploration of the Sea

IPBES: The Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services

LFI: Large fish indicator

Medit: Mediterranean Sea

NEA: North-East Atlantic

NPP: Net primary productivity

PE: Portfolio Effect

PP: Primary productivity

SBT: Sea Bottom Temperature

SEM: Structural equation model

SST: Sea Surface Temperature

SSS: Seas Surface Salinity

VIF: Variation Inflation Factor

1. Introduction

Direct resource exploitation, climate change and land/sea use change are recognised as the main direct drivers of biodiversity loss in the world's ocean (IPBES 2019). As human activities keep increasing and diversifying in the ocean, a phenomenon also referred as the blue acceleration (Jouffray et al., 2020), these direct drivers are expected to intensify. Institutions and governance systems play a key role in shaping these interactions (Figure 1-1). The direct drivers of biodiversity changes (i.e. human activities) are themselves caused by indirect drivers that are in turn driven by social values and behaviours (IPBES, 2019, 2024). The root causes of the direct anthropogenic drivers that affect nature are institutions, governance systems, and other indirect drivers. These include the ways societies organize themselves and interact with nature, as well as the resulting influences on other components (IPBES, 2019; 2024). Economic incentives, such as subsidies, and regimes governing property rights and access to resources, can either mitigate or reinforce pressures on ecosystems. For instance, poorly managed fisheries may lead to overexploitation, while well-enforced regulations can promote sustainability. But also, focus on blue growth, as well as lifestyle choices, can increase the demand for marine resources which can have significant impacts on the social and ecological systems (Ehlers, 2016; Leposa, 2020). For example, if changes in consumption patterns would occur, such as an increase in the amount of fish in one's diet, this would lead to a higher demand and thus a higher fish resource exploitation and pressure on the marine ecosystems. But the benefits that human societies obtain from nature, such as seafood and climate regulation, are themselves dependent on healthy and well-functioning ecosystems (Figure 1-1). Indeed, biodiversity loss or changes can have important impacts on ocean ecosystem functions and services (Worm et al., 2006), including supporting and regulating services as well as the provisioning of sustainable seafood (Díaz et al., 2019a).

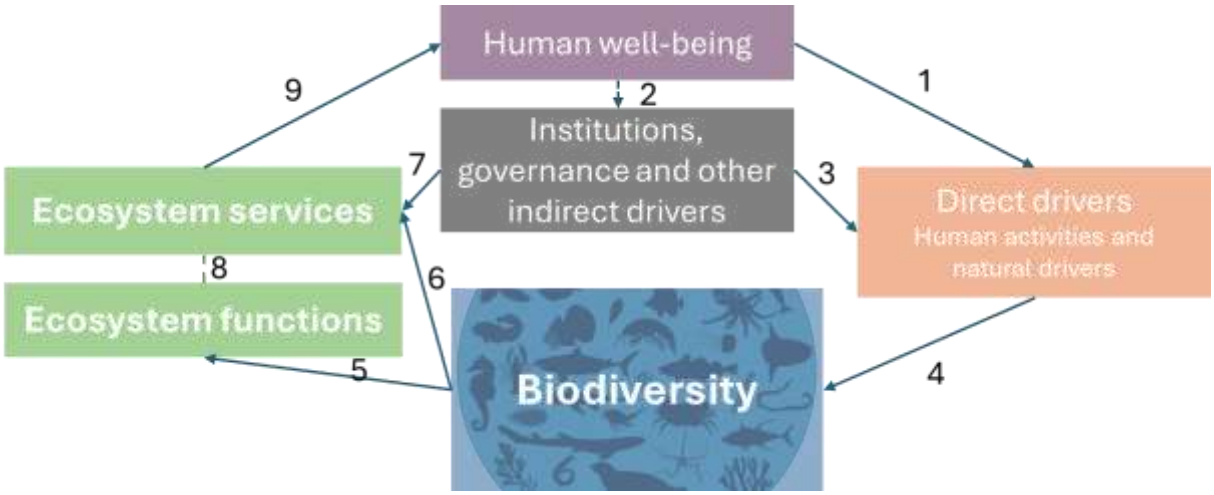


Figure 1-1. A conceptual framework of a marine socio-ecological system, displaying relationships between nature and humans. It links human well-being to governance and human activities and pressures on marine biodiversity and their direct, or indirect effects on multiple ecosystem functions and services. The figure was in part inspired and redrawn from IPBES (2019) conceptual framework of nature-human relationships (Díaz et al., 2015).

Ecosystem functions refer to the natural processes and interactions that maintain ecosystems, such as nutrient cycling, primary production, and habitat provision. In the ocean, for example, coral reefs play a critical role in supporting marine biodiversity (Brandl et al., 2019), while phytoplankton contribute to carbon cycling and oxygen production (Falkowski,

1994). **Ecosystem services** are the supporting, regulating, cultural and provisioning services that human benefit from nature (Millenium ecosystem assessment, 2005). Nature's contributions to people is also a widely used term that encompasses a broader and more inclusive view of the benefits human obtain from natures, including the material, non-material and regulating benefits (IPBES, 2019). Although the term can be criticised due to its utilitarian view of nature, in this deliverable, we will generally use the term ecosystem service. The ocean provides countless and varied benefits to humanity, from food and livelihoods to cultural and recreational value (Figure 1-2). Importantly, most of these benefits, like the provisioning and cultural services, are the result of interactions between nature and societies, i.e. the interaction of human with nature is the needed condition for ecosystem services to arise, emphasizing the interconnectedness of ecological and social systems.

Figure 1-2. Example of some provisioning, regulating and cultural ecosystem services that can be derived from the ocean.

1.1. Biodiversity-Ecosystem functions relationships

The question on whether there exists a relationship between biodiversity and ecosystem functioning, and if so what shape and strength it follows (Figure 1-3), has been a passionate research subject for many decades (Ali, 2023). These potential relations are often referred to in the literature as the "B-EF" relationships and have some extensive theoretical background.

Biodiversity is defined by the Convention on Biological Diversity (CBD) as: "the variability among living organisms from all sources including, inter alia, terrestrial, marine and other aquatic ecosystems and the ecological complexes of which they are part; this includes diversity within species, between species and of ecosystems". Within B-EF research, biodiversity is often described in terms of taxonomic and/or functional richness and abundances variability and equity within communities (e.g. evenness) (Ali, 2023; Loreau et al., 2001; Tilman et al., 2014). Whereas in earlier years of the B-EF research the focus was especially on species richness as the drivers of ecosystem stability and functions, in more recent years, the focus has shifted towards more trait-based diversity measures. Observed

diversity effects of taxonomic richness on ecosystem functions are often interpreted as arising from the positive effect of increasing species on trait diversity (Tilman et al., 2014). Traits might be better than taxonomic measures to explain ecosystem functions as it is hypothesised that it is the species-specific traits and functions in the ecosystem that impact ecosystem functions, e.g. in simpler words more "what are the species doing in the system" rather than "who they are". This is especially important within the niche complementarity hypothesis, which states that diverse functional species within a community will occupy different ecological niches which would lead to more efficient utilization of available resources through niche differentiation and facilitation, and thus increasing ecosystem functioning (Ali, 2023; Loreau et al., 2001).

As stated earlier, ecosystem functions refer to the physical, chemical or biological processes that take place within and sustain the ecosystem. The creation, transformation or recycling of energy and biomass, such as carbon and nutrient fluxes, or biomass productivity, are examples of biological functions of the ecosystem. In B-EF research, biomass is widely used as a metric of ecosystem functioning and as a proxy of productivity (Ali, 2023; Tilman et al., 2014). In this deliverable, we will notably follow this line of research by analyzing the drivers of fish biomass across European seas and using various statistical and modeling methods. We will therefore present and focus on a specific sub-theme of the B-EF theories: the biodiversity-productivity relationship.

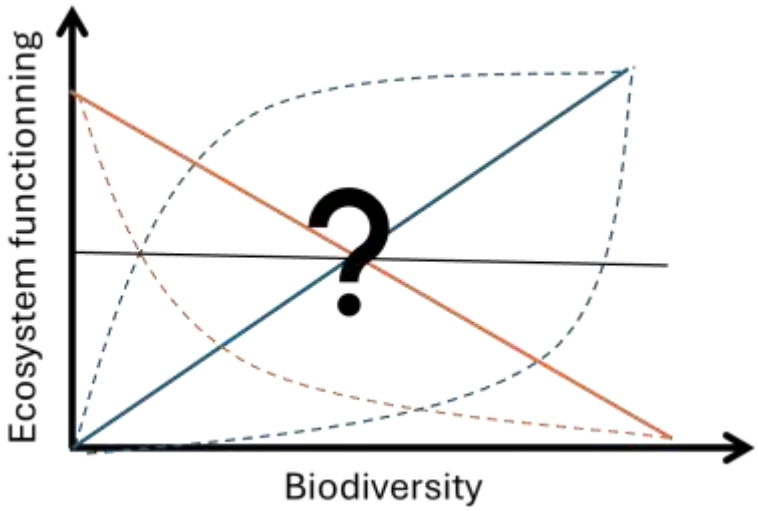


Figure 1-3. The "B-EF" research aims to assess and understand whether a relationship exists between ecosystem functioning and biodiversity. The relationship is hypothesised to follow different directions (e.g. positive or negative) or shapes (e.g. linear or asymptotic) according to different ecological theories.

The biodiversity-productivity theory:

The diversity-productivity hypothesis suggests that biodiversity enhances ecosystem productivity, and therefore that more diverse communities, often in terms of species or functional richness, are generally more efficient at utilizing resources and producing biomass. There exist multiple competing and complementary frameworks using mathematical models that tend to explain why more diverse communities would lead to higher productivity.

Among them is the confounding effect of biodiversity on productivity, which states that just by random, the more species are present in a community, the higher the chances of having a high-productivity species that will drive the biomass higher. This hypothesis is often referred

to as the *sampling or selection probability hypothesis*. For example, (Tilman et al., 1997) provided a foundational theoretical framework for this hypothesis, contrasting two primary models of biodiversity effects on ecosystem function. In their equilibrium competition model, where species compete for a single limiting resource, primary productivity is predicted to increase with species richness due to the likelihood of including highly productive species at higher diversity levels. However, this model also predicts that the most diverse communities would not exceed the productivity of the single best-performing species in monoculture. So, while under this hypothesis higher biodiversity, especially in terms of species richness, would lead to higher productivity, this higher productivity would mainly be due to random chance.

An alternative hypothesis is the *mass-ratio* or *dominance hypothesis* that asserts that the most dominant species and their trait are the driving factor of community productivity (Grime, 1998). Thus, it is expected that it's the dominant species' biomass and not the species richness that drives ecosystem functions. In other words, communities highly dominated by one to few species, so with low biomass evenness, will have higher productivity. Such relationships have been observed widely in natural systems such as in forests where the abundance and traits of the most dominant species, and not taxonomic or trait-based richness, appear to drive forest understorey biomass (Wasof et al., 2018), or in grassland experiments where the dominance of species appears to predict grassland biomass (Zhang et al., 2025). In the marine environment as well, marine fish biomass has been shown to be higher in uneven communities (Eger et al., 2021; Maureaud et al., 2019).

In contrast, niche trade-off models predict that productivity will increase with diversity. Indeed, the *niche complementarity hypothesis* suggests that diverse coexisting species, with variable traits, will follow different ecological niches and therefore would lead to more efficient utilization of available resources in the ecosystem, thereby getting more out of the same pool of resources and therefore increasing ecosystem functioning (Loreau et al., 2001; Tilman et al., 1997). This suggests that certain combinations of species at higher diversity levels can outperform any single more productive species, owing to complementary resource use or facilitation among species (Tilman et al., 2014). Early studies on B-EF relationship using grassland experiments showed notably that plant functional (i.e. trait-based) diversity was an important driver of grassland productivity (Loreau & Hector, 2001; Tilman et al., 1997). Other studies showed the importance of the combination of several plant strategies within a community, such as combination of legumes and c4 grasses, to increase productivity (Fargione et al., 2007). The importance of diverse community composition on ecosystem functions might also be enhanced under stressed or disturbed environment (Ratcliffe et al., 2017), which points to the importance of preserving biodiversity under the current increasing environmental pressures

However, the relationship between biodiversity and productivity is not universal and can follow several of the hypotheses described earlier. It exists complex and varying relationships between biodiversity, ecosystem functioning, and environmental context. Increasingly, studies are attempting to model or assess the various biodiversity-productivity hypothesis in combination rather than isolation. For example, (Loreau & Hector, 2001) theoretical concept integrates multiple ecological hypothesis with the different mechanisms interacting together to shape community biomass (Ali, 2023), such as the dominance effect and the complementarity effect through a dynamic interaction of species traits, species interactions, and environmental factors.

The B-EF relationship in the marine environment has intensified in the last decade, and have notably done so the studies attempting to explain the variation in primary and secondary productivity. Among them, several recent studies analyzed the drivers of fish biomass at regional scale such as in the North Sea (Maureaud et al., 2019), by comparing responses across coastal ecosystems (Mouillot et al., 2025), in seagrass fish communities (Eger et al., 2021) or for global reef fish communities (Yan et al., 2025). Whereas the different studies aims and methods differ, some general conclusion and further research questions can be drawn from them. From these previous studies, we learned that species richness, while important in enhancing biomass in many regions (e.g. Mouillot et al. 2025), usually seems less important than abundance distribution in the communities (Eger et al., 2021; Maureaud et al., 2019; Yan et al., 2025), but these findings appear to vary geographically (Yan et al. 2025; Mouillot et al. 2025). Environmental stressors, and notably temperature might have as strong an effect on fish productivity as diversity indicators (van Denderen et al., 2023; Yan et al., 2025), with biomass usually higher in colder waters due to metabolic constraints on growth in warmer waters (van Denderen et al. 2023; Yan et al. 2025). In addition, other factors might be important in driving fish biomass such as environmental seasonality (Maureaud et al., 2019), sea habitat characteristics and human pressures .

In this deliverable, we aim to address unresolved questions surrounding the drivers of fish biomass and marine ecosystem functions based on the outcomes of the previously mentioned studies. Notably, our research was driven by the following questions:

- How universal is the diversity-biomass relationship? We aimed to assess the relationship between total fish biomass, diversity, and environmental indicators across multiple ecoregions and at various scales, to evaluate the universality of the relationship.
- How are the environment and human pressures impacting or modulating the B-EF relationship? We analyzed jointly the direct effect of biodiversity, and the direct and indirect effects of abiotic variables (e.g. depth, temperature and fishing) on the biomass of fish communities, to assess the contribution of each of these drivers on productivity, and whether biodiversity or other drivers seems to have more effect.
- Is trait-based diversity more important than simpler taxonomic diversity indicators in explaining fish biomass? Whereas the theory tends to postulate that trait composition and diversity is a better explainer of ecosystem productivity and function, there have been some contradictory results in marine literature. As taxonomic diversity is often easier to calculate and interpret, it could be beneficial to use taxonomic instead of functional indicators, if they appeared to be as good in explaining B-EF relationships. This can have important implications for management and communication with end-users.

1.2. Links between biodiversity and ecosystem services

While marine scientific studies on B-EF relationships, particularly biodiversity-productivity dynamics, have grown significantly over the past decades, research on the influence of biodiversity on ecosystem services has comparatively generally lagged behind. This is especially true for studies that quantitatively analyse ecosystem services and their drivers. In contrast, the links between biodiversity and ecosystem services have been more extensively explored through qualitative approaches, often relying on expert-based knowledge (Figure

1-4). Notable examples of such qualitative frameworks include the ecosystem services cascade model (e.g. (Potschin-Young et al., 2018a), the ODEMM (Options for Delivering Ecosystem-Based Marine Management) framework (e.g. (Aarflot et al., 2024), and the DPSIR (Drivers-Pressure-State-Impact-Response) framework (Elliott et al., 2017; Gari et al., 2015). These qualitative models can provide valuable insights into the drivers of ecosystem services (Broszeit et al., 2019).

For instance, (Armoškaitė et al., 2020) introduced an expert-based assessment tool that combines a matrix following the ecosystem services cascade structure with a linkage diagram to visualize the interactions between ecosystem components, functions, and services. This tool was for example applied in Latvian marine waters to assess the relative contribution of selected ecosystem components (e.g. biodiversity) on the supply of ecosystem services, and permitted to highlight the impacts of environmental degradation on ecosystem services.

Similarly, the D(A)PSI(W)R(M) framework, as expanded by Elliott et al. (2017), builds on the simpler DPSIR model by incorporating in addition human Activities, Welfare and Management measures into the framework. It provided a holistic approach to understanding the interactions between human activities, pressures, and their impacts on marine ecosystems and the services they provide. Its nested structure allows for the integration of multiple scales and ecosystems, making it particularly useful for addressing the complexity of marine environmental management. For example, (Bryhn et al., 2020) applied a DAPSIR-based model to Swedish marine waters, using a consensus assessment based on evaluation of available literature and data. The model was used to evaluate the dependencies and impacts of human activities on ecosystem services. This approach could notably demonstrate discrepancies among economic sectors in terms of their reliance on and impact on ecosystem services.

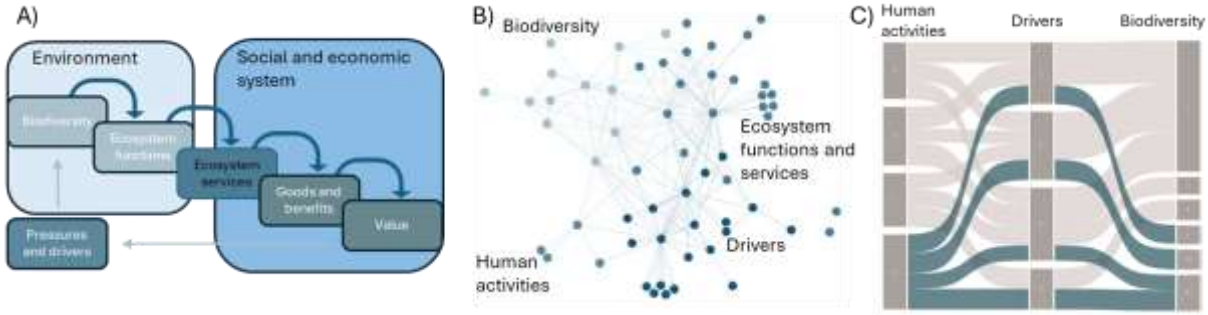


Figure 1-4. Selected examples of different types of conceptual models used to establish links between drivers, biodiversity and ecosystem services. A) Schematic representation of an ecosystem service cascade model (simplified and redrawn from Potschin-Young et al. (2018b). B) a network representing different type of variables (dots) and their relations (lines) to each other. C) a Sankey diagram displaying links among human activities, their associated drivers/pressures and their impact on biodiversity/ecological components, the links are weighted based on the impact risk (i.e. exposure and severity of an interaction), as use for example in ODEMM risk assessment (e.g. Skein et al., 2022).

These conceptual models can be useful tools for environmental management due to their often-simple qualitative structure, and their ability to bridge the gap between ecological science and policymaking. By providing structured frameworks and tools, these models facilitate the integration of ecological, social, and economic dimensions, enabling a more comprehensive understanding of ecosystem services. Their analysis, either qualitative or semi-quantitative, can also help identify trade-offs between different services and support evidence-based decision-making for sustainable resource management (Broszeit et al., 2019). For example, an integrated modelling approach in the Gulf of Cadiz (southern Spain)

demonstrated how anthropogenic pressures and biodiversity loss can affect the delivery of provisioning, regulating, and cultural ecosystem services (Alcorlo et al., 2023).

Each conceptual modelling exercise is tailored to specific research questions; here, we aimed to focus on the specific question "Which are the drivers, and ecosystem functions and services linked to the biodiversity of bentho-demersal communities in the European Seas?". While some variations around this question might have been investigated earlier, this specific question has not. As an exercise in this deliverable, we gathered expert knowledge on the bentho-demersal communities (i.e. invertebrates and fish associated to the sea bottom), their drivers, and their importance in ecosystem processes and services, and used it to build a conceptual model which could act as a robust overview of the associated ecological system.

1.3. This deliverable

The primary aim of WP3 is to **assess and analysed the links between biodiversity and ecosystem functions and services in the European Seas**. First, the potential links within the socio-ecological system of the European Seas were addressed through expert knowledge on the relationship between human activities, pressures, biodiversity and ecosystem function and services. This was done by compiling the judgement of more than 15 experts on marine biodiversity on the potential links between a selected set of 51 variables. For each of a total of 996 potential links, the experts had to evaluate the presence/absence of the link, its direction and strength, and their confidence on each given input. This exercise led to the construction of a conceptual network of the hypothesized links within the European Sea socio-ecological system, with a specific focus on the links between biodiversity indicators and the ecosystem functions and services. The analysis of the network permitted to pinpoint variables and groups of variables whose effects or drivers appears to still be very little known and thus deserve more research attention. In addition, we identified variables that appear central in the network due to their high connectance (i.e. linked with many variables), such as taxonomic-group biomass indicators. Such network analysis can permit to identify key biodiversity indicators that might confer robustness to the system.

The expert-based conceptual network building and analysis was followed by a quantitative analysis of the biodiversity-ecosystem function relationship by focusing on the relationship between biodiversity and fish biomass (i.e. productivity). Knowledge drawn from the expert network was used to establish hypotheses about the potential relationships in this specific fish biomass case-study. We used statistical equation models (SEMs) to assess and quantify the relationships and repeated the same method in 7 case studies (4 in North Mediterranean Sea and 3 in the Northeast Atlantic). The aims of this study was to (i) assess whether the relationships are similar across different regions and (ii) compare the effects of taxonomic vs functional indicators on fish biomass. We found that across case-studies, taxonomic evenness consistently add a negative effect on fish biomass whereas taxonomic richness had a consistently positive effect. In general, taxonomic indicators seems as good or better at predicting fish biomass than functional indicators, and biodiversity indicators could explain more of the biomass variability than any environmental indicators.

Complementary studies to evaluate the drivers of fish biomass in the European Seas were done. A study focusing on the drivers of fish biomass in the Barents Sea showed that temperature and biomass dominance drives total community biomass, irrespective of time-periods or subregions, while niche complementarity, through species richness, becomes more important for explaining the biomass of non-dominant taxa. Two large scale studies focused

on the environmental drivers of fish biomass with one study focusing on the comparison of environmental-biomass relations across regiones, whereas the other focused on whether fish community biomass decline with temperature as expected based on trophic and metabolic theories. In accordance with the other studies, it was found that temperature is a dominant driver of large-scale variation in demersal fish biomass, and that lower biomass in warm regions is due to reduced trophic efficiency and higher turnover rates of biomass. It was also found that biomass peaks at intermediate depths (100–300 m) across all shelf's regions, whereas temperature and primary productivity effects vary between regions.

Whereas B-EF often focus on single ecosystem function (e.g. productivity), it is important to attempt to integrate and analyse functions together to get a more realistic understanding of the system. Ecosystem multi-functions in the Mediterranean Sea were investigated by quantifying and mapping spatio-temporal patterns in five functional rates representing major carbon and nutrient flux pathways and assessing their main drivers. Multifunctionality emerged from complementary species roles as fish' role in biogeochemical functioning was not dominated by specific taxon but instead displayed important functional trade-offs. Fish-mediated biogeochemical multi-functionality was especially high in the western Mediterranean and was positively driven by functional divergence and primary productivity but reduced by depth. Fishing pressure likely played a role in ecosystem multifunctionality by suppressing biogeochemical fluxes.

Finally, two studies investigated spatial and temporal patterns in community stability and how biodiversity affects the systems' stability. Stability was represented as the inverse of the variation in species abundance or biomass. The studies found that community stability displayed large-scale variation, and that environmental gradients, such as salinity, depth, and productivity, were key drivers of spatial variation in fish community stability. Additionally, biodiversity, particularly species richness and evenness, appeared to play an important role in enhancing stability. For example, fish communities with more asynchronous species dynamics (low synchrony) appeared to be more stable. Anthropogenic pressures, such as fishing effort (e.g. bottom trawling), seemed to negatively impact stability through its mediated negative impact on species evenness. The two studies emphasize the importance of biodiversity, environmental heterogeneity, and context-specific factors in shaping community stability.

Based on the findings of this deliverable, we made some recommendation for biodiversity management and current knowledge gaps and uncertainty.

2. Expert modelling of the relationships between biodiversity and ecosystem functions and services.

Lead contributor: Julia Polo (UiT)

In the pursuit of establishing links between biodiversity and ecosystem functions and their associated services, in the context of B-USEFUL task 3.3 we estimated key ecosystem-level indicators and studied their interdependencies through the development of an expert knowledge-based conceptual model (Figure 2-1). A conceptual model would act here as a cognitive network, i.e., a qualitative model of how a system operates, through the depiction of a number of selected components and the relations between them, often shown in the form of a graph (Özesmi & Özesmi, 2004). The methodologies used for its development and the resulting "global conceptual network linking ecosystem services, structure and function, and drivers and pressures of the benthic and demersal marine communities of European seas" are described in this section.

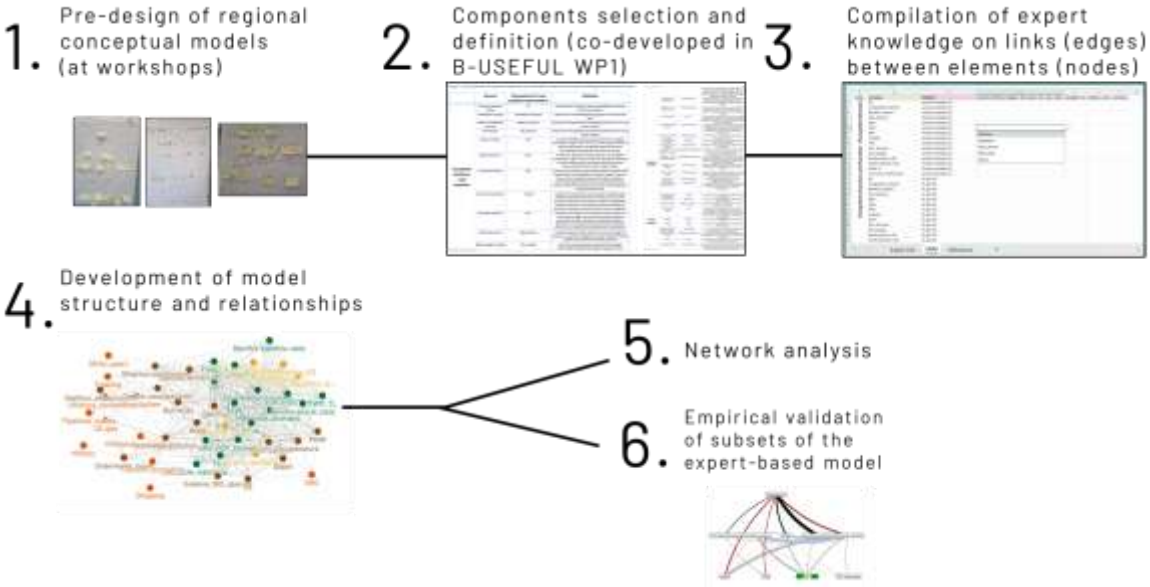


Figure 2-1. Summary of the steps taken to conceptualize the biodiversity-ecosystem function and services network. In step 6, for the empirical validation of the expert-based model, the expert-elicited relationships in the network were validated against field data (for the components for which data was available), in regional Structural Equation Models (SEMs; chapter 3 in this deliverable).

2.1. Compilation of expert knowledge and modelling of the network:

As an introduction to the compilation of expert knowledge on which the conceptual network was to be based, two workshops were held in the 2023 and 2024 (B-USEFUL) project meetings in Palma (Spain) and Lowestoft (UK), respectively.

At the first workshop, the meeting participants, who collectively authored hundreds of papers and technical reports relevant to the subject matter, were invited to group around four regions of study (two for the Mediterranean, western and eastern, and two for the Atlantic, northeastern and southeastern) to design together a simplified conceptual overview of the benthic and demersal ecosystems' functions-services linkages in each region. All conceptual models included at least 2 indicators for functioning, 4 for biodiversity, and the most relevant

drivers and pressures agreed by the participants (Figure 2-2). This first workshop inspired the posterior list of indicators to be used as nodes in the global conceptual network.

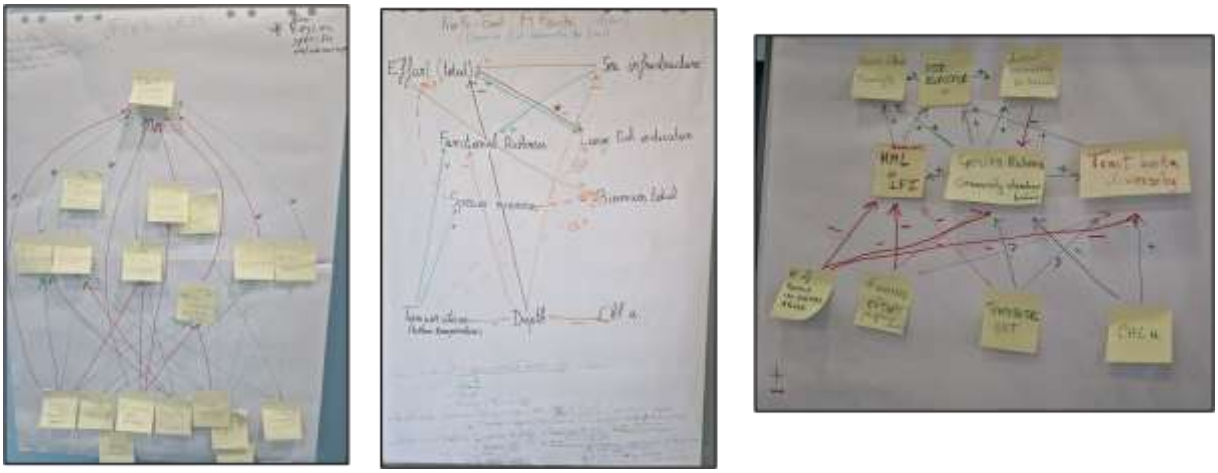


Figure 2-2. Regional conceptual models developed by the experts at a first workshop, held at B-USEFUL's annual 2023 meeting. In this workshop the nodes and relationships of the models were defined in group discussions, differently to the final approach taken to design the global conceptual network, for which experts were asked to work individually, in order to avoid group bias.

At the second workshop, participants of the project annual meeting engaged in a more detailed development of the regional conceptual models (Figure 2-3). For this, divided in 7 groups that corresponded to given ecological/geographical study regions, they selected the components they considered relevant within their study regions, among a set of variables and indicators that had been pre-defined and co-developed with end-users under Task 1.3 (Table 2-1). Then, making use of a virtual board, they represented the direction and magnitude of the links between the components based on their knowledge. To decide on the connections among ecosystem functions, services and drivers in their regions, they engaged in group discussions.

Figure 2-3. Resulting regional networks developed at the second workshop, held at B-USEFUL's annual 2024 meeting. Three groups worked on different aspects of the North-East Atlantic region, focusing on “provisioning of seafood” and “climate regulation” as centres of their network. Two groups worked separately on the Mediterranean Sea ecosystems, with focus on the “provisioning of seafood” as an ecosystem service on the eastern and the western subregions. Another group worked on the North Sea, with focus on the “offshore windfarms”

impacts on the ecosystems. Online attendants to the workshop worked on a conceptual network around the ecosystem service “bioturbation”, as centre of their network.

Both workshops aimed to define the approach for the compilation of expert input that would support the development of the final global network, as well as to train and educate B-USEFUL researchers in this methodology.

After the second workshop was held, experts interested in contributing to the development of the conceptual network were invited individually to formally give their input on a set of 996 potential links between pairs of ecosystem components. They would rate whether there existed a direct causal connection (*link*, from here on) among the component pairs, and if so, which direction it typically takes in European seas. For this, they were given a document with guidelines to follow to register their knowledge (Appendix 1), as well as an annex spreadsheet, containing the actual list of links (Appendix 2). Additional online training sessions were also held. The spreadsheet contained:

- A sheet with the definitions of the ecosystem components/indicators (Table 2-1) and the interpretation of the possible values to be assigned to the “Direction” and “Strength” of the link, and the “Confidence” of the expert on their response (Table 2-2 and Table 2-3).
- A sheet with the list of 996 pairs of components whose links to rate.

Experts who took on the activity were commanded to take a light, low-key approach in the filling of the spreadsheet. They assessed the links’ nature (existence, direction and magnitude) by selecting an option from a drop-down list for each pair of components (see Appendix 2). An emphasis was made to only rate causal direct links (from one element to the other). If they considered there was no causal link among the components, or if there was a link but they considered it not to be direct (i.e., dependant on a third variable or process) experts would choose “None” in the “Direction” column. As for the temporal and spatial scale aspects of the relationships assessed, the experts were encouraged to rate the links between the components at European level, thinking of the relationship between components widely, from Mediterranean to North-East Atlantic (excluding the Baltic Sea due to its very contrasting environmental conditions), and to think rather spatially than temporally.

The expert responses were both blind and mutually independent, so potential group confirmation bias was avoided and therefore responses from all experts were given equal weight for the construction of the conceptual network.

Table 2-1. List of indicators of ecosystem components to be included as nodes in the expert knowledge-based conceptual network.

	Element	Abbreviation	Definition
Ecosystem structure and function	Primary production (ChlA)	PP	concentration of ChlA as proxy for phytoplankton biomass (ChlA concentration)
	Zooplankton biomass	Zooplankton_biomass	total mass of living zooplankton (biomass from survey/CPR data)
	Benthic invertebrate biomass	Benthos_biomass	total mass of living benthic invertebrates (biomass from survey and/or model)
	Fish biomass	Fish_biomass	total mass of living bentho-demersal fish (biomass from survey and/or model)
	Species richness	SRic	number of different species represented in an ecological community or region. Here, we focus on the species richness of the fish and benthic

			invertebrates (bentho-demersal communities) (local species richness form survey)
	Species evenness	SEve	similarity in abundances of each species in an ecological community or region. Here, we focus on the species evenness of the fish and benthic invertebrates (bentho-demersal communities) (Shannon index, Simpson index)
	Functional richness	FRic	number of functionally unique entities based on species traits represented in an ecological community or region. Here, we focus on the functional richness of the fish and benthic invertebrates (bentho-demersal communities) (functional richness: trait-based richness using convex hull area based on species presence-only)
	Functional redundancy	Fredund	overlap in functional traits across species (multiple species sharing the same traits/functions). Here, we focus on the functional redundancy of the fish and benthic invertebrates (bentho-demersal communities) (functional redundancy/ functional uniqueness, presence and/or biomass weighted)
	Functional evenness	FEve	similarity in abundances of functionally unique entities in a community or region. Here, we focus on the functional evenness of the fish and benthic invertebrates (bentho-demersal communities) (functional evenness: trait-based evenness accounting for biomass/abundance distribution)
	Size structure (LFI)	Size_structure	the size distribution within the fish community. (Large-fish indicator = proportion of large fish (usually >40-50cm) biomass relative to the total fish community biomass)
	Bentho-pelagic coupling	BP_coupling	level of connection between the benthic and pelagic communities through the exchange of energy, mass, or nutrients. When the coupling is high, the pelagic biomass level is similar to the benthic biomass level, when it is low, the biomasses are disconnected (i.e., high pelagic biomass but low benthic biomass) (proxys: demersal to pelagic biomass ratio, ratio pelagic biomass/benthic biomass)
	Benthivorous to piscivorous ratio	Benthiv-pisciv_ratio	biomass ratio of benthivorous species versus the biomass of piscivorous species, here, focusing on fish communities. (benthivorous biomass/piscivorous biomass; feeding group biomass).
	Benthivorous to planktivorous ratio	Benthiv-planktiv_ratio	biomass ratio of benthivorous species versus the biomass of planktivorous species, here, focusing on fish communities (benthivorous biomass/planktivorous biomass; feeding group biomass).
	CWM trophic level	CWM_TL	the mean trophic level of the species in a community or region weighted by their biomass. Here, focusing on fish and benthic invertebrate communities (proxy: fish CWM trophic level based on survey and trait dataset)
	Nursery areas, spawning grounds	Life_cycle_maintenance	Essential fish habitats (EFH), critical habitats providing conditions that favour the reproduction and the juvenile stages (after hatching) of certain bentho-demersal species (presence/absence or nursery and/or spawning grounds of commercial fish)
Ecosystem services	Provisionning - seafood landings	seafood_landings_ES	harvest of fish and invertebrates for food (total landings, commercial sps biomass)
	Provisionning - energy oil & gas	oil_gas_ES	extraction of fossil fuels from the marine seabed to provide energy (total oil barrel, gas m3)
	Provisionning - energy windfarm	energy_windfarm_ES	transforming wind into (renewable) energy using offshore wind farms (total kW)
	Regulating - climate regulation (bioturbation)	climate_regulation_bioturbation_ES	disturbance of sediments by benthic invertebrates, helping with nutrient (re)cycling and mitigating GHG emissions. (bioturbation index from benthos survey)
	Regulating - climate regulation (blue carbon)	climate_regulation_bluecarbon_ES	sequestration of carbon in marine life (e.g. benthos, whales) and sediments, mitigating GHG emissions. (proxy: blue carbon estimation based on benthic composition; storage potential based on sediment composition)
	Regulating - waste recycling	waste_recycling_ES	breakdown and filtration of pollutants by marine organisms, maintaining water quality. (proxy: total biomass of filter feeders)
	Cultural - tourism, recreation	tourism_recreation_ES	activities like diving, fishing, and coastal tourism, enhancing coastal well-being and economy (Number of tourists, hotels, recreational licences, income from tourism)
	Cultural - science, education	science_education_ES	research and learning opportunities from the marine ecosystem (research production)

Human activities	Cultural - well being, heritage, spiritual, art	wellbeing_art_ES	providing inspiration, cultural identity, and a sense of connection to marine life and coastal environments (Number of people in coastal areas, existence of specific sea habitats/species)
	Fishing-active bottom dwelling gears	Trawling	commercial harvesting of wild seafood through active bottom trawling gears
	Fishing-other gears	Other_gears	commercial harvesting of wild seafood through pelagic and passive bottom gears
	Offshore aquaculture	Offshore_aquaculture	farming fish and shellfish in marine offshore environments (presence/number of farms)
	Greenhouse gas emissions	GHG	release of gases, such as CO_2, methane, nitrous oxide, and fluorinated gases, into the atmosphere, derived from the burning of fossil fuels, industrial processes, deforestation and intensive agriculture and farming (GHG or Co2 atmospheric concentrations)
	Shipping	Shipping	transportation of goods and passengers by sea (shipping intensity)
	Oil & gas	Oil_gas	exploration and extraction of fossil fuels from seabeds (area with infrastructure)
	Pipelines & cables (incl. Offshore wind farm)	Pipelines_cables	underwater infrastructure for energy, communication, and resource transport (area with infrastructure)
	Offshore renewable energy	Offshore_renewable_energy	generating clean energy from wind, waves, and tides. Here focusing especially on offshore wind farm (presence/number of windfarm)
	Military	Military	naval and defense operations at sea (military operations – but difficult to obtain data, military reserved area)
	Tourism and recreation	Tourism_recreation	activities related to leisure such as boating, diving, recreational fishing, and enjoying the beach and coast (number of hotels, number of leisure boats/harbours, tourist companies)
	Land based activities (Agriculture, forestry, urban and industry)	Land_activities	terrestrial activities contributing runoff and pollution to marine environments
Drivers and pressures (biotic and abiotic)	Sea temperature	Temperature	e.g., SST, SBT, seasonality
	Sea salinity	Salinity	concentration of salt in seawater (SSS, SBS, seasonality)
	Acidification (pH)	Acidification	increase in ocean acidity (decrease in pH)
	Depth	Depth	distance from the ocean surface to the seafloor (seabed depth)
	Wind	Wind	natural movement of air, typically caused by differences in atmospheric pressure
	Oxygen	O2	dissolved oxygen in seawater, crucial for the survival of marine organims. Oxygen enters seawater from the atmosphere and through photosynthesis, and conditions of low dissolved oxygen can lead to hypoxic conditions
	Nutrients (P, N, S)	Nutrients	essential chemical elements and compounds dissolved in seawater, such as nitrogen, phosphorus, and silicates. When imbalanced can lead to harmful blooms
	Type of sediment	Sediment_finetocoarse	the seafloor composition of materials, here, we focus on a gradient from fine grain (sand/mud) to coarse grain (pebbles, rocks) (seabed type Emodnet)
	Extreme events (MHW)	MHW	abnomally high sea temperatures during at least 5 days (MHWs metrics based on SST anomaly: duration, intensity, frequency)
	Seafloor abrasion and habitat loss	Seafloor_abrasion_habital_loss	physical damage to the seabed from human activity (seafloor abrasion from fisheries)
	Siltation/smothering	Siltation_smothering	accumulation of fine sediments on the seafloor
	Invasive and non-indigenous species	Invasive_NIS_species	species that are new to an area, introduced or naturally spreading. (number of recorded new/invasive species)
	Coastal discharges and pollution	Discharge_pollution	entry of contaminants from land-based sources as well as general pollution in the ocean such as plastic (nutrient concentrations nitrate, phosphate, plastic pollution, non-organic bycatch)
	(Selective) Species extraction	Species_extraction	targeted removal of specific species (e.g. through fishing) (total catches)
	Underwater noise	Underwater_noise	sound pollution in the marine environment. It can affect marine ecosystems by disturbing or disorienting aquatic species, particularly those that rely on sound for communication, navigation, and hunting.

	Sediment (carbon) (re)suspension	Carbon_resuspension	release of sediment and stored carbon into the water column

Table 2-2. Interpretation of the possible directions that the links between ecosystem components could take, as given to the experts.

Positive	Element A has a linear positive causal effect on Element B
Negative	Element A has a linear negative causal effect on Element B
Non linear	There is a causal link going from Element A to Element B but the relationship is either U- or Ո-shaped
Not clear	There is a causal link among the elements, but its direction is context dependent or not universal (different responses depending on the species or on the region)
None	There is no causal link among the elements, or it is indirect

Table 2-3. Interpretation of the possible values the experts could assign to the strength of the link and the confidence level on their response.

Strength of link	1	Weak link
	2	Intermediate strength link
	3	Strong link
Confidence level	1	Low confidence in the direction value assigned by the expert
	2	Medium confidence
	3	High confidence

2.2. Analysis of the conceptual network

The compilation of input from 14 experts allowed for the summarization of the information provided in the form of a graphical conceptual network (

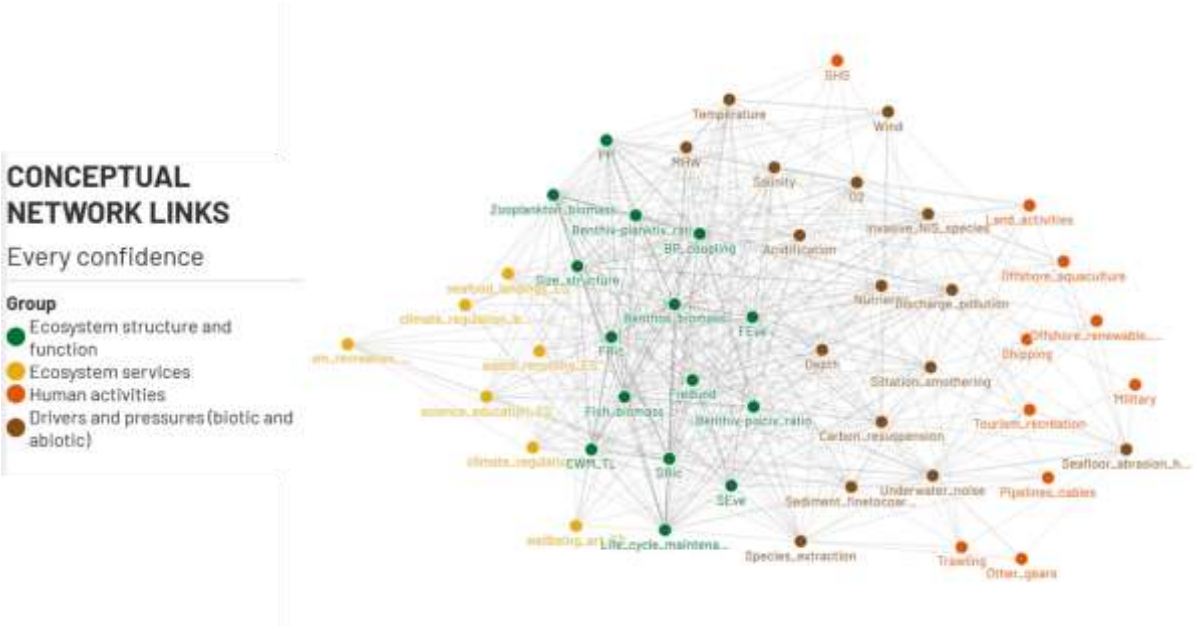


Figure 2-4).

The network has 49 components and 558 links between them. This results on a network connectance of 0.23, which means that 23% of all possible interactions between the components was considered as existing. This is quite high and demonstrates that this marine socio-ecological system is highly connected, and thus changes in one component could have repercussions on many others.

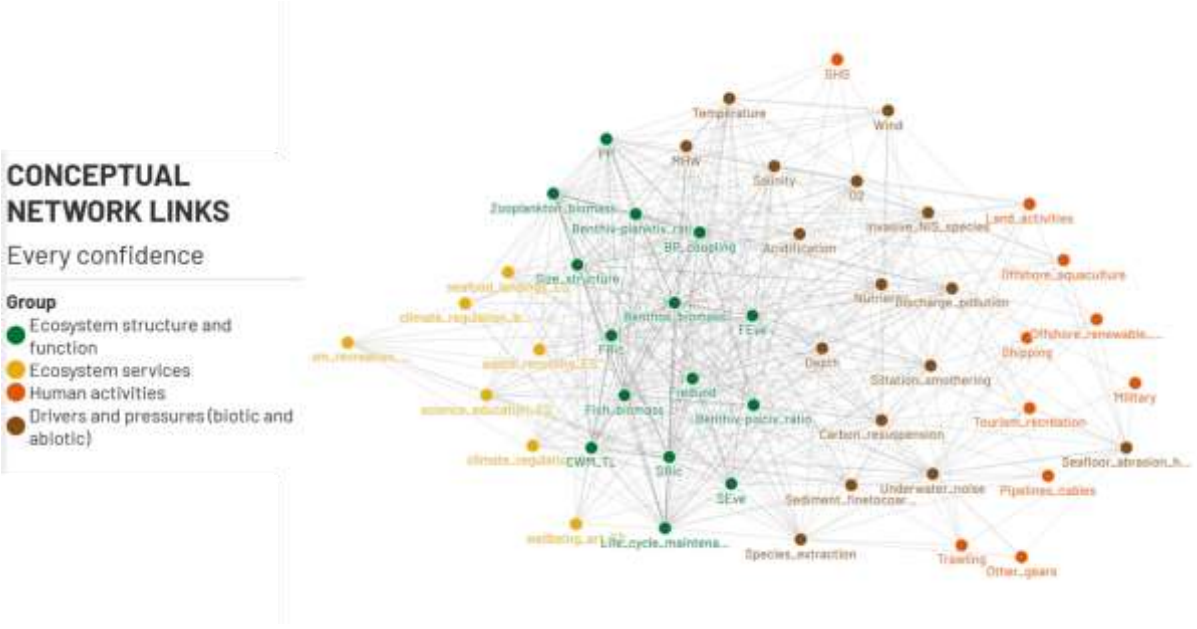


Figure 2-4. A graphical representation of the global conceptual network based on experts' knowledge. In the case of the network represented in this figure, experts' input was not filtered for a high level of confidence. The network is a schematic, out of temporal scale, diagram linking ecosystem functioning and structure, ecosystem services, human activities, drivers and pressures, in European Seas.

Inter-rater agreement:

The conceptual network was analysed for inter-rater agreement. The coherence in ratings across experts, whose background knowledge come from different fields of expertise and marine regions, would indicate that:

(1) there is a common view of the main hazards to, and functioning of, marine ecosystems.

(2) expert elicitation provides a robust basis for the modelling of the human footprint on marine ecosystems (Kallio et al, 2025).

As indices of the inter-rater level of agreement, we explored the following:

- Fleiss' kappa (Gwet, 2021), which measured the level of agreement among the experts beyond what would be expected by chance. Kappa values generally range from -1 to 1, with the following interpretation: <0 less than random chance agreement, 0 - 0.20 slight agreement, 0.21 - 0.40 Fair agreement, 0.41 - 0.60 Moderate agreement, 0.61 - 0.80 strong agreement, 0.81 - 1.00 very strong agreement.
- Kendall's coefficient of concordance (W) (Legendre, 2005), was computed to explore the experts' agreement on the strength of the relationships between ecosystem components.

The calculation of Fleiss kappa also produced a z-score, indicating how many standard deviations away from the mean the Kappa value is under the null hypothesis of "no agreement beyond chance", and a p-value, the probability of observing the data if the null hypothesis of "no agreement beyond chance" was true.

Overall agreement across the 14 experts and 996 links was fair (Table 2-4)., with Fleiss' kappa values of 0.28 for link direction and Kendall's W values of 0.24 for link strength, both highly significant. Agreement on expert confidence was lower (W = 0.23), indicating a great variability in how certain experts felt about their judgments. When simplifying responses to link vs. no-link, agreement increased slightly (kappa = 0.35), still within the fair range.

Table 2-4. Summary of inter-expert agreement across 14 raters and 996 assessed links. Agreement on direction of the link was quantified using Fleiss' kappa, a statistic measuring consistency among multiple raters for categorical judgments. Agreement on link strength and expert confidence was evaluated using Kendall's W, a concordance measure for ordinal ratings. Kappa values indicated for both link direction and the simplified link/no-link classification (in which the 4 possible directions for the links, other than "None", were summarized as "Link", so, existence of link).

AGREEMENT 5 DIRECTION CHOICES				
	Kappa/W:	Z-score	P-value	Agreement
Direction of link	0.28	143	0	Fair
Strength	0.24		2.12e-213	Fair
Confidence	0.23		3.57e-215	High variability
AGREEMENT LINK/NO LINK				
	0.35	106	0	Fair

Exploring the agreement and disagreement of the experts' input, Figure 2-5 and Figure 2-6 illustrate the distribution of expert agreement on the direction of the ecosystem links. For the entire list of 996 links (Figure 2-5), most links show a low consensus, with only a few cases where all or nearly all experts agreed on the direction of the response. When filtering the links to only high-confidence assessments (confidence = 3) (Figure 2-6), the agreement peaked at moderate levels (three to four experts) and declined sharply for complete consensus. Overall, these two figures highlight that while full agreement among experts is rare, confidence-filtered responses tend to cluster around more consistent agreement.

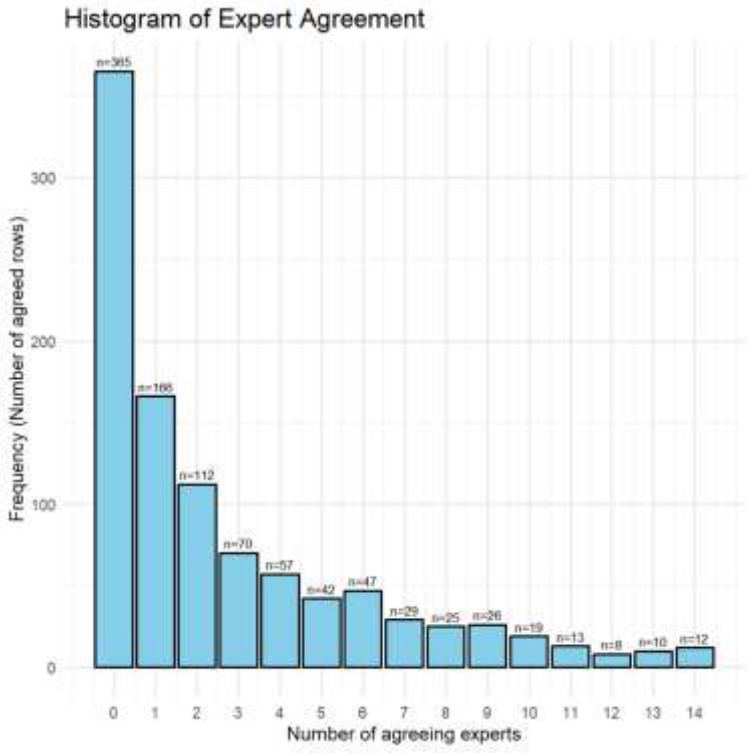


Figure 2-5. Frequency distribution of the experts' agreement on the direction (other than "None") of the links between ecosystem components, drivers and human activities. E.g., for 12 links the 14 experts agreed on the direction of the response; for 10 links there was almost an absolute agreement (13 experts), etc.

When the data was filtered to only keep the rated links with 'high confidence' (confidence = 3), then the Fleiss kappa rose to 0.542, a moderate agreement.

Across link categories, as shown in Table 2-5, expert agreement showed a consistent pattern: agreement on the direction of the links was highest for the category linking Human activities to Pressures/Drivers (Fleiss' kappa = 0.349), indicating a relatively strong consensus on how human actions influence pressures in the system. Agreement on the links' direction was slightly lower for relationships between components of Ecosystem structure and function, and the provisioning of Ecosystem Services (Fleiss' kappa = 0.278), and declined further for interactions within or between Pressures and Ecosystem Structure and Function components. When assessing the strength of the system links the highest concordance appeared for links between Ecosystem structure and function components and the provisioning of Ecosystem Services (Kendall's W = 0.285), followed closely by Human activities – Pressures/Drivers (Kendall's W = 0.255), suggesting experts were more aligned when judging the magnitude of these cross-system relationships. Finally, expert confidence showed the lowest overall

agreement, with Kendall's W values ranging from 0.270 to 0.073, indicating substantial variability in how certain experts felt about their own assessments.

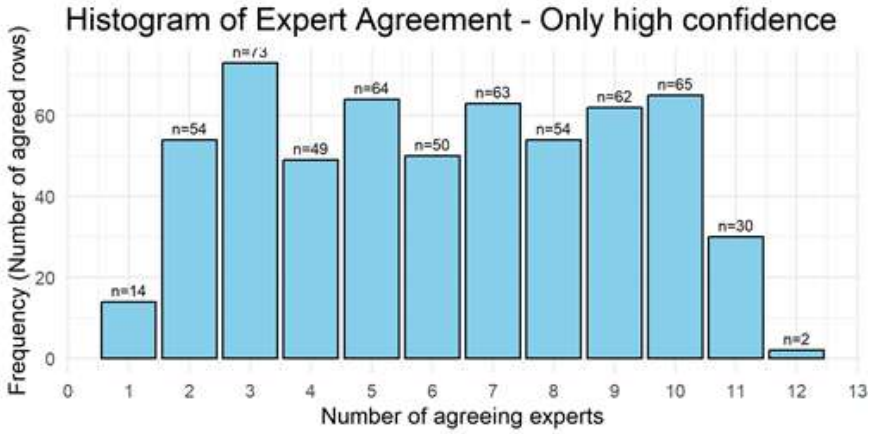


Figure 2-6. Frequency distribution of the experts' agreement, only for the links (between ecosystem components, drivers and human activities) in which the experts showed high confidence (confidence = 3). E.g., for 0 links the 14 experts agreed on the direction of the response; for 2 links there was almost an absolute agreement (13 experts), etc.

Table 2-5. Agreement per group or category of links, from categories with higher agreement (first row) to lower (fifth row). Fleiss kappa was used as a coefficient of the inter-rater (experts) agreement on the direction of the link, given it is well suited for categorical inputs. Kendall's W, well suited for ordinal data, was computed per category of links to explore agreement on the strength of the model's links, as well as the variance of experts' confidence on their responses.

Link category	**Direction of link** (kappa)
Human activities - Pressures/Drivers	0.349
Ecosystem structure and function - Ecosystem Services	0.278
Within Pressures/Drivers	0.249
Pressures/Drivers - Ecosystem structure and function	0.158
Within Ecosystem structure and function	0.087

Link category	**Strength of link** (kendall)
Ecosystem structure and function - Ecosystem Services	0.285
Human activities - Pressures/Drivers	0.255
Pressures/Drivers - Ecosystem structure and function	0.254
Within Ecosystem structure and function	0.170
Within Pressures/Drivers	0.118

Link category	**Expert confidence** (kendall)
Ecosystem structure and function - Ecosystem Services	0.270
Pressures/Drivers - Ecosystem structure and function	0.185
Human activities - Pressures/Drivers	0.098
Within Ecosystem structure and function	0.085
Within Pressures/Drivers	0.073

Table 2-6. The 10 links for which expert input showed a higher variance. PP = Primary productivity.

Links with highest variance in the rating of the direction		
A (cause)	**B (effect)**	**variance**
Temperature	Size structure	2.989011
Zooplankton biomass	Benthivorous-planktivorous ratio	2.989011
Discharge pollution	PP	2.708791
Seafloor abrasion (habitat loss)	Sediment (fine to coarse)	2.686813
Depth	Nutrients	2.571429
Benthos biomass	PP	2.527473
Offshore renewable energy	Underwater noise	2.439560
PP	Bentho-pelagic coupling	2.417582
Salinity	Life cycle maintenance (spawning grounds)	2.417582
Benthivorous-piscivorous ratio	Benthos biomass	2.335165

The 10 links with the highest variance in expert ratings (Table 2-6) reflect relationships for which the assessment of the link's direction was particularly inconsistent. These cases generally involve processes that are complex, context-dependent, or weakly supported by empirical evidence, which could lead experts to diverge in how they interpret causal effects. In the same line of Table 2-5, the high-variance links span interactions between physical drivers (e.g., temperature, salinity, depth) and biological or biogeochemical responses, as well as links involving habitat alteration or trophic structure. As an example of this, the interaction between Temperature (T^e) and Size structure, represented in the Large Fish Indicator (LFI), an indicator of the proportion of large fish biomass relative to the total fish-community biomass (Table 2-9). In this case, 6 out of 14 experts evaluated this relationship as 'negative', implying an increase in sea temperature directly causes a decrease in the relative abundance of large fish in the community. Conversely, 3 out of 14 experts considered this relationship 'not clear', i.e., context-dependent. Table 2-7 shows 10 of the 124 links (including those rated as "None"), for which there was an absolute agreement (14 out of 14 experts).

Table 2-7. An example set of 10 links for which expert input showed no variance, i.e., full agreement. GHG = Greenhouse emissions.

10 links with no variance in the rating of the direction (full agreement)		
A (cause)	**B (effect)**	**Direction agreed upon**
Trawling	Seafloor abrassion (habitat loss)	Positive
Trawling	Carbon resuspension	Positive
Shipping	Underwater noise	Positive
Seafloor abrasion (habitat loss)	Taxonomic richness	Negative
Seafloor abrasion (habitat loss)	Functional richness	Negative
Seafloor abrasion (habitat loss)	Fish biomass	Negative
Taxonomic richness	Tourism and recreation (ES)	Positive
Oil and gas	Underwater noise	Positive
Land activities	Discharge and pollution	Positive
GHG	Temperature	Positive

Table 2-8. An example of the input given by the experts to a specific link, between Temperature (Te) and Size structure.

Link category:	**Element A (cause)**	**Element B (effect)**	**Expert 1**	**Expert 2**	**Expert 3**	**Expert 4**	**Expert 5**	**Expert 6**	**Expert 7**
Pressures/Drivers - Ecosystem structure and function	T^e	Size structure (LFI)	Not clear	Negative	Not clear	Negative	Non-linear	Negative	Negative
			Expert 8	**Expert 9**	**Expert 10**	**Expert 11**	**Expert 12**	**Expert 13**	**Expert 14**
			Positive	Not clear	None	Positive	Negative	Negative	Positive

The ranking of the network components by connectedness degree, betweenness, and closeness (Table 2-9) highlights which components act as the most influential, central, or well-connected nodes within the conceptual network. Across categories, elements such as Land activities, Discharge and pollution, and Benthos biomass consistently emerged in at least one centrality metric, which would indicate certain structural importance in linking different

parts of the system. High-connected elements are those most directly connected to others, while high-betweenness elements function as key intermediaries along shortest paths, and high-closeness elements are efficiently positioned to influence or respond to changes across the network. In the biodiversity domain, Benthos biomass, Fish biomass, and Zooplankton biomass form a tightly connected core, which could be reflecting their relevant role in ecosystem functioning. Within ecosystem services, Seafood landings and Education and science appeared as the most structurally influential, linking ecological processes with human benefits. Together, these metrics aim to reveal the components that play strong roles in shaping the information flow and potential impact propagation within this marine socio-ecological system, but these results should be interpreted with caution. As noted by Crielaard et al. (2023), commonly used centrality metrics can be sensitive to small changes in diagram structure and rest on assumptions that do not fully align with how causal diagrams represent system behaviour. This means they could point to misleading central points and should not be used as definitive guidance for management or policy. Instead, centrality patterns are best treated as exploratory signals that can prompt further investigation rather than firm conclusions.

Table 2-9. Top 3 components within each category with the highest 'connectedness' degree (e.g. number of direct links), highest 'betweenness' (i.e. number of times it is on the shortest path between pairs of elements), and highest 'closeness' (i.e. how well it is connected both directly and indirectly to the other variables, based on the shortest path).

	Degree ("connected")	**Betweenness ("hub")**	**Closeness ("efficient")**
Human activities	Land activities	Renewable energy	Land activities
	Offshore aquaculture	Land activities	Offshore aquaculture
	Renewable energy	Offshore aquaculture	Oil and gas
Drivers and pressures	Discharge, pollution	Discharge, pollution	Depth
	Invasive species	Sediment resuspension	Discharge, pollution
	Depth	Underwater noise	Invasive species
Biodiversity	Benthos biomass	Benthos biomass	Benthos biomass
	Fish biomass	Fish biomass	Zooplankton biomass
	Zooplankton biomass	Functional richness	Primary productivity
Ecosystem services	Seafood landing	Education and science	Education and science
	Education and science	Seafood landing	Seafood landing
	Wellbeing, art	Bioturbation (climate reg.)	Bioturbation (climate reg.)

2.3. Key take-away messages:

- This study contributes to the broader effort to build community-shared conceptual models that unify fragmented ecological perspectives in European Seas. By synthesizing input from 14 experts, the resulting network provides a structured representation of how ecosystem functioning, ecosystem services, human activities, and pressures interact. This aligns with calls in the literature for shared theories and integrative frameworks (Wassmann et al., 2020).

- The network contains 49 components and 558 links, and yields a connectance of 0.23, which is high for a system of this size. This indicates that European demersal ecosystems are tightly intertwined, and that changes in one component can propagate widely through multiple pathways (Levin, 1998). Such connectivity reinforces the need for integrated, cross-sectoral management, rather than isolated, sector-specific approaches.
- Inter-rater agreement was fair for link direction (kappa = 0.28) and link strength (W = 0.24). Agreement increased to moderate (kappa = 0.542) when only high-confidence links were considered.
- Areas of the network with a low confidence and low agreement between experts can help highlight knowledge gaps, or potential areas of needed further study. Here, we found that components within the categories “Within Ecosystem structure and function” and "Within Pressures/drivers” were areas with special low agreement across the experts. This elevated variance indicates substantial uncertainty and heterogeneity in expert judgement for certain relationships, highlighting them as potential priority areas where additional data, clarification of mechanisms, or targeted expert elicitation may be needed.
- The biodiversity elements which appeared to play a central role in the system due to their high linkages were Benthos biomass, Fish biomass, and Zooplankton biomass, over the various diversity metrics explored. This could point at a slight higher difficulty for experts to assess the relevance and inter-connectedness of the more abstract, diversity metrics, over those more tangible indicators of the ecosystem’s structure.
- In Ecology studies, expert elicitation comes in handy when empirical data are incomplete, but its constraints need to be recognized and addressed. Expert judgments can be shaped by knowledge background or regional experience, and some relationships may be simplified, not fully capturing ecological complexity. Agreement among experts reflects a shared perception rather than ecological truth, and conceptual networks themselves are static representations of systems that are constantly changing. For these reasons, conceptual models should be treated as living hypotheses, to be tested, challenged, and refined as new evidence emerges.
- Understanding European Seas robustly requires revisiting entrenched assumptions and moving beyond narrow, sector-based development of marine management actions. Conceptual modelling, in this sense, can help make explicit implicit assumptions , enabling the scientific community to identify which older, confined ideas need revision in light of contemporary ecological understanding and cross-disciplinary evidence.

3. Quantifying the biodiversity-EF/ES relationships

3.1. Assessing the main drivers of fish biomass across regions using SEMs

From the expert-based conceptual network to a "fish biomass" conceptual model

The conceptual networks built out of expert knowledge (ch.2 p18) served as the basis for the quantitative study of the dependencies between biodiversity and marine ecosystems' ecological functioning and service provisioning. To approach the assessment and quantification of such a complex system of causal linkages that includes indirect effects, non-linear relations and non-normal distributions, which is typical in nature, we applied the Structural Equation Modelling (SEM) framework. This is a statistical tool that allows testing multiple hypotheses about various causal relationships simultaneously and provides statistical support on causal paths connecting variables.

We decided to focus on a conceptual model which aims at explaining the main drivers of total fish biomass and their main pathways. Total fish biomass is treated here as a proxy for ecosystem functions and, when retaining the biomass of desirable/commercial fish, is also a proxy for the ecosystem service "seafood production". To build the "total fish biomass" conceptual model, we therefore focused on the subpart of the expert-based conceptual network that was linked to the node "fish biomass", focusing on the indicators related to the categories "main drivers and pressures" and "ecosystem structure and function" (Figure 3-1).

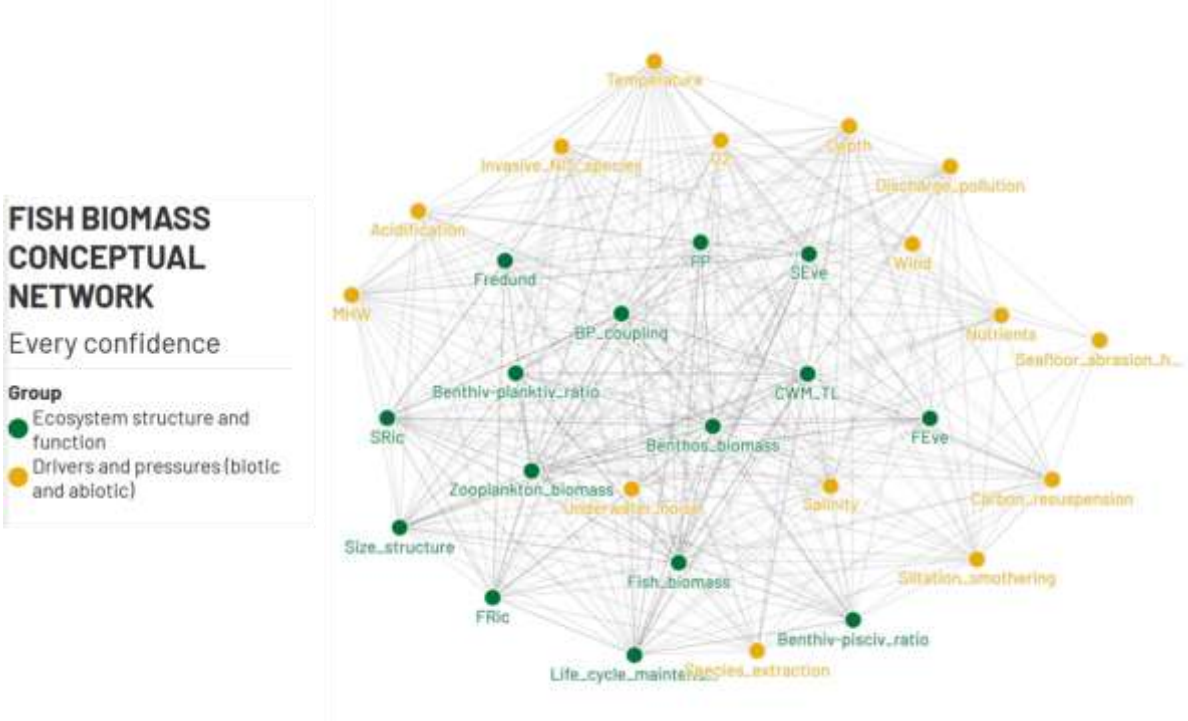


Figure 3-1. Subset of the expert conceptual network with a focus on the ecosystem structure and function and drivers and pressures that are connected to the element "Fish_biomass"

The next step was to simplify the "fish biomass" network to be able to test it across regions using SEMs. To do so, we kept only the variables that we hypothesised to have a clear impact on fish biomass during the current study period and area, as well as pragmatically removed variables that were either hard to measure or for which data was not available.

Defining a common conceptual model to be tested across the different regions.

We defined a simple conceptual model linking fish biomass to key fish community indicators and main environmental drivers to be performed commonly in different ecoregions across the European shelves. In doing so, the **main aim was to test which were the main drivers of fish community biomass and whether the observed relationships between the environment, the biodiversity indicators and ecosystem functions were similar or varying across regions**. SEMs are a useful framework to test such research objective as the strength of the relationships across the variables can be compared across regions based on standardised coefficients. More specifically, we want to answer the questions:

(i) What are the main drivers of fish community biomass in European Seas?
(ii) Are the taxonomic and/or the trait-based indicators best at explaining the variation in the biomass?
(iii) Is there some variation in the diversity-biomass relationships between European regional seas?
(iv) What is the importance of spatial scales in shaping relationships? (single study)

Based on the pre-selection of variables and a-priori hypotheses on the relationship between them, we build a conceptual model based on 3 layers: the environmental layer, the fish community diversity indicators, and the main response variable: fish biomass (Figure 3-2). We hypothesized that the fish community' taxonomic/functional richness, taxonomic/functional evenness and the community weighted mean (CWM) are influencing total fish biomass. Indeed, one of the most hypothesised and tested B-EF relationship is the relation between taxonomic/functional richness and biomass, with the expectation that higher richness leads to higher biomass (Loreau & Hector, 2001; Tilman et al., 1997). In contrast, in some previous studies, biomass evenness has been shown to be an important negative driver of fish biomass, i.e. communities with more dominant species have a higher total biomass (Maureaud et al., 2019). Whereas the size structure in the fish communities is hypothesised to impact fish biomass as larger fish have a higher body weight. In addition, CWM length is also usually highly correlated with the variation in length in the community, as length is a proxy of trophic position in the fish food web (Barnes et al., 2008), we thus expect that a community with high CWM length will have a higher trophic chain length and thus potentially productivity (i.e. fish biomass in the present study). The environmental variables were selected based on previous study in the European Seas that showed they were important drivers of fish community composition (Beukhof, Dencker, Pecuchet, et al., 2019; Maureaud et al., 2019; McKeon et al., 2024; Receveur et al., 2024). They were also important drivers of fish species distribution identified in previous B-Useful studies (see previous B-Useful deliverable D3.1, D3.2). Annual mean sea surface temperature (SST) and bottom temperature (SBT) have been positively linked to taxonomic/functional richness (Dencker et al., 2017; Receveur et al., 2024) and CWM size (Beukhof, Frelat, et al., 2019), and the variability (i.e. seasonality) in SST/SBT has also been shown to influence fish community composition (Beukhof, Dencker, Pecuchet, et al., 2019; Dencker et al., 2017). The variable "Chla" is the annual average concentration of chlorophyll production based on satellite data and is a proxy for primary production. While the impact of primary production on fish communities is likely indirect, as it is not a trophic level directly linked to fish through food web (i.e. very few fish are herbivores), it is a proxy for ecosystem

productivity and used in the absence of more precise data such as zooplankton biomass. Primary productivity is expected to influence total fish biomass through food web cascading effects (Chassot et al., 2010; Friedland et al., 2012), but potentially also community richness and size structure through the enabling of more food resources and ecological niche.

Functional diversity indicators aim to capture the diversity of species' characteristics, rather than focusing solely on their taxonomic identity. By doing so, they provide a deeper understanding of the ecological roles and niches species occupy within an ecosystem (Tilman, 2001). For instance, two flatfish species of similar size and shape may be considered to play a comparable role in the ecosystem. Although functional diversity indicators can be more complex to interpret and communicate to non-ecologists, they are often regarded as the most effective lens for exploring biodiversity-ecosystem functioning relationships. In this study, we choose to retain both taxonomic and functional diversity indicators to assess whether functional diversity better explains total fish biomass compared to taxonomic diversity. Alternatively, if simpler taxonomic indicators perform equally well, they may be prioritized due to their ease of communication and broader accessibility.

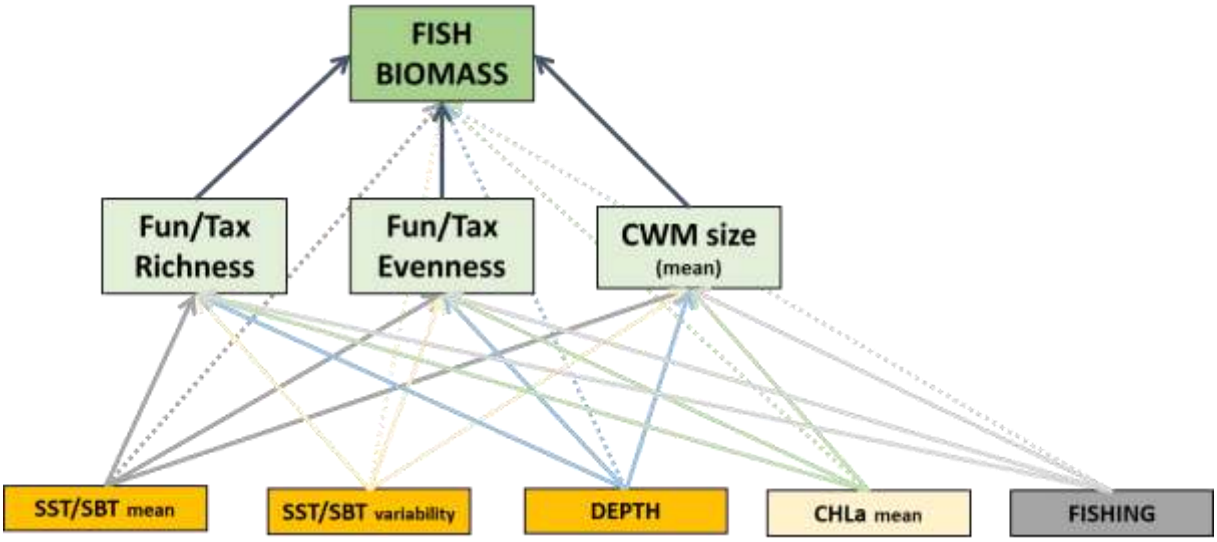


Figure 3-2. Conceptual model of the potential pathways through which biodiversity and environmental and fishing variables might impact total fish biomass. The first layer represents the environment and fishing variables, which can directly affect biodiversity indicators and directly and indirectly (through biodiversity) affect total fish biomass. The second layer is composed of the biodiversity indicators which can directly affect total fish biomass. Fish biomass is the main response variable and focus of the structural equation model analysis.

This simple model was tested across different regions, but, in some regions, some variables were added and/or omitted to better fit the local ecological context and data availability (Table 3-1). More detailed information is available in each case study description.

Table 3-1. Case-studies included in this deliverable for which a structural equation model explaining fish biomass was performed.

Ecoregions	B-EF SEMs case-study included in the deliverable and characteristics
Barents Sea	Common conceptual model explaining fish biomass. Period 2004-2021. Observations at haul levels, with n= 3055. No fishing effort included
North Sea	Common conceptual model explaining fish biomass. Period 1998-2020. Observations at haul levels, with n= 5947. No fishing effort included

Bay of Biscay and Celtic Sea	Common conceptual model explaining fish biomass. Period 1998-2020. Observations at haul levels, with n= 5911. No fishing effort included
Mediterranean Sea -	Common conceptual model explaining fish biomass. Period 1999-2021. Observations at haul levels, with n= 10, 031. Fishing effort from Maina et al. (2026).
North-East Atlantic	Common conceptual model explaining fish biomass. Period 2000-2020. Testing the influence of spatial observation scales on the relationships. Observations at different scales: resolution ~ 95km (n=8), 55km (n=9) and 25km (n=10). Fishing effort from Global Fishing Watch.

3.1.1. Calculating the biodiversity and environmental variables

For the models to be comparable across the different ecoregions, we calculated the diversity and environmental indicators using a common approach. First, we decided that the main response is total fish biomass per haul standardised per swept area (kg/km^2). The diversity indicators are then also calculated at the haul-level and the environment associated with the haul location. Before calculating the diversity indicators, some datasets had to be cleaned (e.g. removing too long/short hauls, hauls deeper than the coastal shelves, removing some gear type, selecting specific months, etc.). Rare species, the ones with less than 1% occurrence during the study period (i.e. occurs in less than 1% of all the hauls each case-study), were also excluded from the analysis. An exception was made for the Mediterranean Sea that decided to include all species as the 1% criteria was eliminating too many species in this species-rich system, whereas it was removing fewer species in the North-East Atlantic.

Three taxonomic diversity indicators (taxonomic richness, taxonomic diversity, and taxonomic evenness), three functional diversity indicators (functional richness, functional evenness, and functional dispersion) and CWM length were calculated (Table 3-2). The taxonomic indicators were calculated using the 'vegan' R-package (Oksanen et al. 2013). Functional diversity indicators were calculated based on a set of nine traits broadly characterizing the functions and ecological role of adult individual of a species. Six traits were continuous: trophic level (the average trophic level of a species diet), offspring size (the size of eggs or live-young), fecundity (the average number of eggs/offspring produced in a year), growth coefficient (K, the growth speed in early years), max length (total maximum body size), max age (the expected maximum age an individual of the species could reach). Three traits were categorical: feeding mode (benthivorous, generalist, piscivorous, planktivorous), body shape (eel-like, elongated, flat, fusiform, short and/or deep), fin shape (forked, pointed, rounded, truncated). The traits were compiled from multiple sources (e.g. (Beukhof, Dencker, Palomares, et al., 2019; Froese & Pauly, 2010) and some of them were inferred for the Mediterranean Sea based on taxonomic relationships and correlations. The functional diversity indicators were calculated using the mFD R-package (Magneville et al., 2022). To calculate the indicators, first, the species' traits matrix was transformed into a dissimilarity matrix using the 'gawdis' function in R (de Bello et al., 2021). This function permit to calculate the dissimilarity between each pair of species based on their traits by balancing the contribution of each trait to the dissimilarity (de Bello et al., 2021). Then, a PCoA was used to estimate a limited number of axes of variation that best describe the traits variability within the species pool and hence build up the trait space. The best number of axes retained was estimated based on how much they contributed to the quality of the functional space and

varied between 3 or 4 across the studies. All weighted-diversity indicators were weighted using the species biomass.

After some preliminary analysis, it became apparent that functional evenness was not the best trait-based indicator to estimate trait evenness in communities. Functional evenness measures the regularity of biomass distributions in the trait space (based on the shortest minimum spanning tree linking all the species in the local pool, (Villéger et al., 2008). Functional evenness appears less sensitive to high unevenness (e.g. one very dominant species) but instead is also influenced by the distribution of "low" biomass species. So, if a community is composed of many species with low biomass and one very dominant species, if the species with low biomass are connected to each other in the trait-based shortest minimum spanning tree, it appears that functional evenness can be very high (example of the community ▽, Figure 3-3B). In contrast, if a community has several species with medium biomass, but that the path between these species in the minimum spanning tree are passing through species with low biomass, the functional evenness becomes low (example of community ○, Figure 3-3A). Therefore, functional evenness does not appear to be the mere "functional" equivalent of taxonomic evenness. Instead, or in complement, functional dispersion appears to have high correlation with taxonomic evenness. In the Barents Sea dataset, for example, taxonomic evenness and functional dispersion were positively correlated (pearson r, 0.77), whereas taxonomic evenness and functional evenness were not correlated (pearson r, -0.01). Therefore, we decided to also include functional dispersion in the trait SEM. As a result, some SEMs case-study added functional dispersion in addition to functional evenness in their analysis.

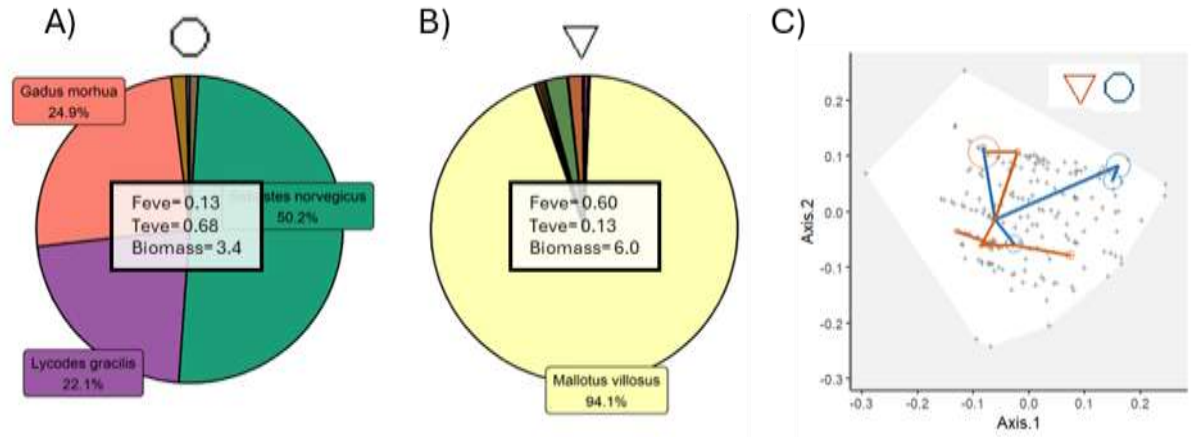


Figure 3-3. Example of two Barents Sea fish communities (haul level) for which the values of functional and taxonomic evenness are highly different. A) A community with high taxonomic evenness (Teve) but low functional evenness (Feve) and B) a community with low Teve but high Feve. Note that the total biomass is log transformed. C) a representation of the calculation of Feve in the trait space for the two community.

Table 3-2. List of the calculated input variables and their definition and calculation method. NA is used when an indicator was not selected in the final conceptual network due to a high variance among expert ratings.

Variable	Definition	Calculation	Expected link to fish biomass based on the expert-based network (majority response)
Fish biomass	Total fish biomass per haul standardised per swept area (kg/km^2)	Sum of all species biomass caught in the haul	*Not relevant*
Taxonomic richness	Number of unique species	Total number of unique taxa per haul	**Positive** (9/14 experts agreed on this direction).
Taxonomic diversity	Account for both species richness and evenness. Increases with both higher species richness and more even distribution of individuals across species	Shannon-Wiener index *H'*, where p_i where is the biomass proportion of a species $_i$ in the community	NA
Taxonomic evenness	Focus on evenness only, where 1 represents complete evenness (all species have equal abundance) and values closer to 0 indicate communities dominated by few species	Pielou's index: *H'/log(tric)*	**Not clear/Positive** (both directions were equally considered in expert ratings.; 5/14).
Functional richness	An indication of the trait-based richness of a community	The volume of the trait space occupied by the species present in the community. Based on presence-only and calculated using a convex Hull.	**Positive** (6/14 experts agreed on this direction).
Functional evenness	How regular is the distribution of species biomass in the trait space.	Calculated based on the minimum spanning tree linking all the species in the community in the functional space and then estimate how evenly the branch lengths are distributed, weighted by species abundances	**Not clear** (6/14 experts agreed on this direction).
Functional dispersion	How spread are the species in the trait space, weighted by their biomass	The average distance of individual species to the centroid of all species in the trait space (i.e. the abundance-weighted mean position of specie) weighted by the species biomass	NA
CWM length	An indication of the size structure in the community based on the average length of an individual in the community	Biomass-weighted mean maximum length of the species in the community	**Positive** (8/14 experts agreed on this direction).

We included environmental variables that were shown to be important drivers of fish community composition in the European Seas. We decided to start with a constrained list of environmental variables to keep the model simple (Table 3-3). The environmental variables SST and SBT were obtained from Copernicus *Global Ocean Physics Reanalysis* data product based on the 0.083 degree and monthly model ("cmems_mod_glo_phy_my_0.083deg_P1M-m"), chlorophyll a concentration was obtained from Global Ocean Colour (cmems_obs-oc_glo_bgc-plankton_my_l4-multi-4km_P1M). For each haul, monthly values of each variable were extracted for the year (i.e. 12 values) preceding the sampling date and integrated over a radius of 2km around the haul. For example, a mean annual SST for a haul sampled in November 2012 is calculated based on the 12-monthly averages from November 2011 to October 2012. Depth was the actual measured depth of the trawl during the survey. Proxy for fishing effort varied across the different studies as no single dataset was considered the best data sources for fishing effort in all the areas. The source of some environmental variables might differ across studies, and if so, this is specified in each study report.

Table 3-3 Environmental variables included in the model, their calculations, and their expected relationships with the different biodiversity and biomass indicators according to the expert-based conceptual network. In parenthesis represent the number of experts that agree on the direction out of 14 experts. NS is used when an indicator was not selected in the final conceptual network due to a high variance among expert ratings (no majority response), NA indicate that the specific relationship was not assessed in the conceptual network.

Variable	Calculation	Expected link to biodiversity based on the expert-based network (majority response)
SST/SBT - mean	One year average of sea surface/bottom temperature, based on monthly values, and calculated the 12 months preceding the sampling time	Fric/Tric: Not clear/Positive (5/6) Feve/Teve: Not clear/NS (6/6) CWM Length: Negative (6) Total biomass: Non-linear (6)
SST/SBT - variability	Seasonality of sea surface/bottom temperature, calculated as the standard deviation of the 12 months values preceding the sampling time	Fric/Tric: NA Feve/Teve: NA CWM Length: NA Total biomass: NA
Depth	Depth of the sample location based on trawl depth	Fric/Tric: Negative/Negative (8/8) Feve/Teve: Not clear/Not clear (6/7) CWM Length: Not clear (5) Total biomass: Negative (8)
Chla - mean	One year average of chlorophyll a concentration, based on monthly values, and calculated the 12 months preceding the sampling time	Fric/Tric: Not clear/NS (5/NA) Feve/Teve: None/None (6/5) CWM Length: None (6) Total biomass: Positive (7)
Chla – variability	Seasonality of chlorophyll a concentration, calculated as the standard deviation of the 12 months values preceding the sampling time	Fric/Tric: NA Feve/Teve: NA CWM Length: NA Total biomass: NA
Fishing pressure	Varying across studies, but a proxy for the fishing intensity in the vicinity of the samples. Can be based on AIS data.	Fric/Tric: Negative/Negative (10/12) Feve/Teve: Negative/Negative (12/13) CWM Length: Negative (12) Total biomass: Negative (12)

3.1.2. General method employed for the "fish biomass" SEM

To evaluate the relationships between biomass as a proxy for seafood provisioning, functional and taxonomic diversity and the set of environmental variables, we fitted a Structural Equation Model (SEM) based on several linear mixed models. The SEM blends process-driven and data-driven approaches, using mechanistic principles to define the model structure and empirical principles to calibrate and refine the model (Lomax, 2004). We used the *piecewise* SEM R package (Lefcheck, 2016). In a *piecewise* SEM, each relationship is tested on its own (e.g., via regression), and the results are combined to evaluate the overall causal structure. Model fit is then assessed by checking whether the set of linked regressions is consistent with the proposed network of relationships.

Different types of models were tested, from simpler to more complex, accounting for spatial and temporal autocorrelation as well as potentially confounding factors (e.g. haul duration, gear). For each sub-model, we first fitted simple linear models, for which the best structure was selected using Akaike Information Criteria (AIC) and the dredge method using the MuMIn R package (Barton et al. 2015). We also tested for multiple collinearities of the explanatory variables based on Pearson correlation and variation inflation factor. Temporal autocorrelation was tested by adding year as a random effect in a linear mixed effect model (lme) using the R-package nlme (Pinheiro et al. 2017). Spatial autocorrelation was tested by adding a correlation structure, we tested four different types of spatial autocorrelation structure (gaussian, spherical, exponential, ratio). In addition, we assessed potential non-linear relationships between the log(biomass) response variables and the predictors by using generalised additive models (gam). When there was clear non-linearity between a driver and biomass, this was accounted for by adding a second term for the predictor variable that reflected the quadratic effect: $(x - \text{mean}(x))^2$ (similar to what was done in Maureaud et al. 2019). This quadratic term was only retained in the final SEM if both the quadratic and non-quadratic term were significant. The variables selected in the "best" final models were chosen based on the dredge method and AIC values, whereas the best structure for the model was selected based on AICs of the different competing model structure (temporal and spatial autocorrelation). The residuals of the "best models" were checked for random distribution, heteroscedasticity and hidden patterns.

Once the "best models" for the biodiversity indicators and the biomass were obtained, they were added to the *sem* R function to estimate and compute the best fitting SEM and obtain the estimated direct and indirect effects of drivers and biodiversity on the total fish biomass. This was done iteratively, as correlations (but not especially causation) between the different biodiversity indicators were added when suggested by the SEM as significant, this was done by adding them as correlated errors (or covariances) between the indicators, and not directly in the models. Doing so accounts for shared unmeasured causes or dependencies between two response variables without assuming a direct causal pathway. We aimed at having final SEMs that had a general good overall model fit, this is indicated by a non-significant p-value ($p>0.05$) of the global test of significance which tests whether any paths are missing from the models. Through this process, the SEM sometimes suggested to add variables into the "best models". These additions were done until we obtained a non-significant p-value for the global test.

3.1.3. Mediterranean Sea

Lead contributor: Fabien Moullec and Bastien Mérigot (UM)

The Mediterranean Sea is one of the world's most distinctive and vulnerable marine socio-ecological systems. Although it represents only about 0.82% of the global ocean surface, it hosts more than 17,000 marine species, with over 20% considered endemic (Coll et al., 2012). This exceptional biodiversity results from the basin's unique biogeographic position between temperate and subtropical climatic regimes, its complex geological history and the strong environmental gradients generated by regional oceanographic circulation (Coll et al., 2010; D'Ortenzio & Ribera d'Alcalà, 2009). The Mediterranean is characterized by marked west-to-east and north-to-south gradients in temperature, salinity and productivity, with generally oligotrophic conditions that become increasingly pronounced toward the eastern basin (Huertas et al., 2012). The coexistence of temperate and subtropical species, combined with highly heterogeneous habitats and oceanographic features, creates a complex seascape supporting diverse fish assemblages and ecosystem functions. At the same time, the Mediterranean Sea is recognized as a hotspot of cumulative anthropogenic pressures and climate change (Cramer et al., 2018; Halpern et al., 2025). The region is warming two to three times faster than the global ocean average, with important consequences for marine biodiversity, species distributions, community structure and ecosystem functioning (Aurelle et al., 2022; Cramer et al., 2018; Hidalgo et al., 2022). Climate-driven changes interact with other major stressors, including intensive fishing, habitat degradation, pollution, biological invasions and emerging diseases. Together, these pressures have contributed to biodiversity loss, changes in fish community composition and declines in ecosystem productivity across several Mediterranean subregions (Azzurro et al., 2019; Bensebaini et al., 2025; Piroddi et al., 2017). Fishing has historically been one of the dominant drivers of ecological change in the Mediterranean (Colloca et al., 2017; Piroddi et al., 2017). Demersal and small pelagic communities support economically and culturally important fisheries, yet many fish stocks remain exploited beyond sustainable levels despite recent management improvements (FAO, 2025). The ecosystem functions provided by Mediterranean fish communities are closely linked to biomass production, trophic regulation, nutrient cycling and energy transfer within marine food webs (Liquete et al., 2016). These functions underpin key ecosystem services, including food provision, fisheries livelihoods, cultural values and regional economic activities associated with coastal communities (Liquete et al., 2016). Given the ecological and socio-economic importance of fish biomass in the Mediterranean Sea, understanding the relationship between biodiversity and ecosystem functioning is particularly relevant for supporting ecosystem-based fisheries management and achieving European policy objectives under the Common Fisheries Policy, the Marine Strategy Framework Directive and the EU Biodiversity Strategy for 2030. This case study aimed to assess how taxonomic diversity, functional diversity and trait composition influence fish biomass across Mediterranean demersal communities, and whether these B-EF relationships vary among Mediterranean subregions.

Materials and Methods

This case study focused on Mediterranean demersal and shelf-associated fish communities, including species-level records of Teleostei and Elasmobranchii. Fish community data were

obtained from the Mediterranean International Trawl Survey (MEDITS), a long-term standardized fishery-independent monitoring programme conducted annually across the Mediterranean Sea (Spedicato et al., 2019). The study encompassed six Geographical Sub-Areas (GSAs 6, 7, 17, 18, 22 and 23) distributed across the northern Mediterranean basin and covered the period 1999-2021 (Figure 1).

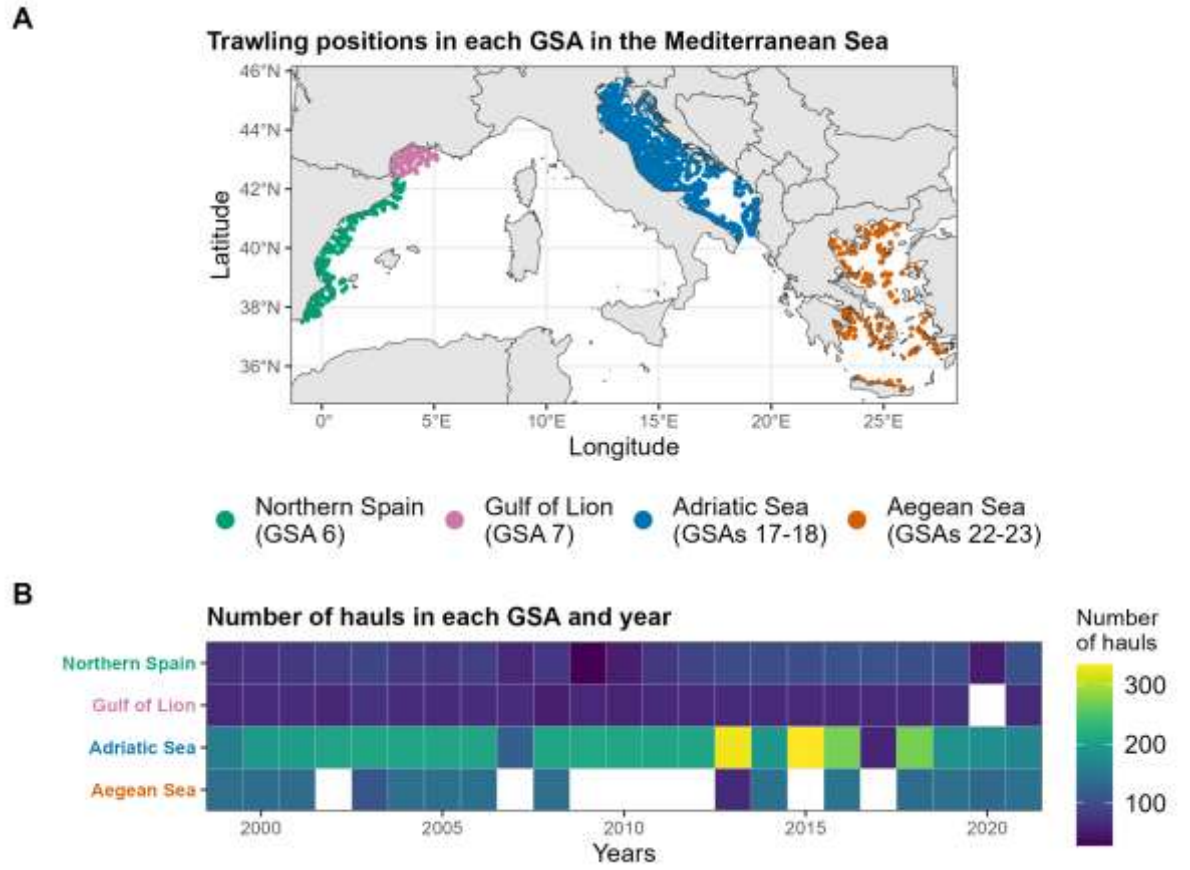


Figure 3-4. Trawling positions in each GSA in the Mediterranean Sea from 1999 to 2021 (A) and number of hauls in each GSA and year (B). The number of hauls is based on the hauls selected for the analysis, which were conducted from May to August (months 5, 6, 7 and 8). No hauls were conducted in GSA 7 in 2020 because the survey was conducted in month 10 (October)

Sampling was carried out using a standardized GOC-73 bottom trawl equipped with a 20 mm stretched-mesh codend, following harmonized MEDITS protocols consistently applied among years and participating countries (Spedicato et al., 2019). Surveys were conducted during late spring-early summer across continental shelf and upper slope habitats ranging from 10 to 800 m depth. Sampling followed a stratified random design based on depth strata (10-50, 51-100, 101-200, 201-500 and 501-800 m). All hauls were performed during daylight at an average towing speed of approximately 3 knots, with a standard duration of 30 minutes on the shelf and 60 minutes on the slope. Gear geometry and trawl performance were continuously monitored using a SCANMAR acoustic system to ensure consistency in swept area estimates and sampling efficiency.

Only hauls with validated gear performance and complete metadata were retained for analyses, resulting in a total of 10,031 hauls. Biomass was standardized as biomass density (kg/km²) using the swept area of each haul. To reduce the influence of extreme values, the

lowest and highest 0.5% of biomass observations were excluded (<15 kg/km² and >5700 kg/km²).

We examined relationships between biodiversity and ecosystem functioning, where fish biomass was used as a proxy for ecosystem functioning and productivity. Biodiversity indicators included both taxonomic and functional components following the common SEM framework developed across case studies. Environmental covariates known to influence fish community structure and biomass were included in the analyses, namely bathymetry (depth), sea surface temperature (SST), bottom temperature (SBT), sea surface salinity (SSS) and chlorophyll-a concentration (chl-a) as a proxy for primary productivity. Environmental data were extracted from Copernicus Marine Service reanalysis products (Cossarini et al., 2021; Escudier et al., 2021), while bathymetry data were obtained from the EMODnet Digital Bathymetry dataset (DTM, 2024).

To account for anthropogenic pressures, two indicators were included: a Fishing Pressure Index (FPI) representing spatial fishing intensity derived from fishing activity and fleet information for bottom trawlers (FPI OTB) and small scale fisheries (FPI SSF) (Kavadas et al., 2015; Maina et al., 2026), and a human gravity index used as a proxy for cumulative coastal human pressures (Cinner et al., 2018). Prior to modelling, multicollinearity among predictors was evaluated using Pearson correlation coefficients and Variance Inflation Factors (VIF) and highly correlated variables were excluded.

SEM was used to quantify direct and indirect relationships between biodiversity, environmental drivers, anthropogenic pressures and fish biomass. In contrast to the common SEM framework applied across all regions, the Mediterranean analysis incorporated interactions between biodiversity indicators and Geographical Sub-Areas (GSAs). This approach allowed the estimation of region-specific biodiversity-ecosystem functioning relationships and enabled assessment of whether the strength and direction of biodiversity effects on fish biomass varied among Mediterranean subregions characterized by contrasting environmental conditions and anthropogenic pressures.

Results and Discussion

The SEM showed a good overall fit to the data. Global model fit assessed using Fisher's C statistic and tests of directed separation indicated no significant missing pathways (Fisher's C = 16.37, df = 22, p = 0.797), suggesting that the hypothesized causal structure adequately captured the main relationships among environmental conditions, anthropogenic pressures, biodiversity components and fish biomass across Mediterranean fish communities (see Table 1 for a complete overview of the sub-models included).

Table 3-4. The selected models explaining the variation in diversity indicators and biomass models. For all the models, after testing multiple models type spatial and temporal autocorrelation structure, an exponential spatial autocorrelation structure and year as random factor was used.

Best models
Tric ~ chla_mean + depth + FPI_OTB + FPI_SSF + gravity + sbt_mean + so_mean + so_sd + sst_mean + sst_sd + GSA

Teve ~ chla_mean + depth + FPI_SSF + gravity + sbt_mean + so_mean + so_sd + sst_mean + sst_sd + GSA
Fric ~ chla_mean + depth + FPI_SSF + gravity + sbt_mean + so_sd + sst_mean + sst_sd + (Tric * GSA)
Feve ~ chla_mean + depth + FPI_SSF + gravity + so_sd + sst_sd + (Teve * GSA)
CWM_length ~ depth + FPI_SSF + gravity + sbt_mean + so_mean + sst_mean + sst_sd + GSA
log_biomass ~ chla_mean + depth + FPI_OTB + FPI_SSF + gravity + sbt_mean + so_mean + so_sd + sst_mean + sst_sd + (Tric + Teve + Fric + Feve + CWM_length) * GSA

The SEM explained a substantial proportion of variance in fish biomass (marginal R^2 = 0.53; conditional R^2 = 0.54), indicating that fixed effects alone captured most of the observed variability in biomass across hauls and regions.

In contrast, explanatory power differed markedly among biodiversity components (Figure 3-5).

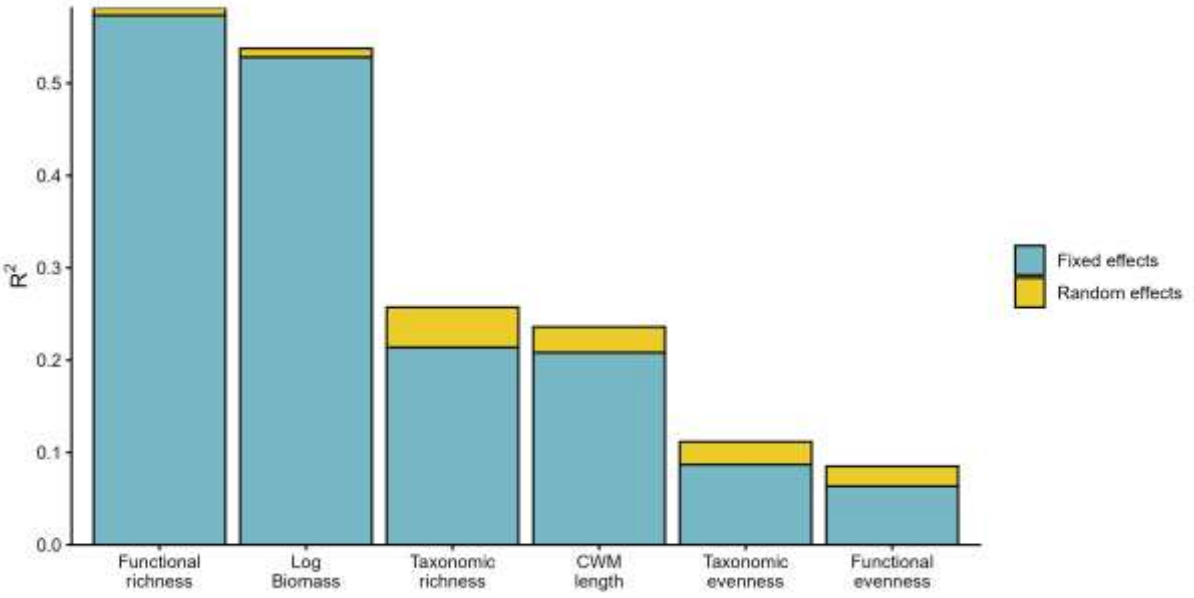


Figure 3-5. Total explained variability (R^2) of the selected models in decreasing order of R^2 in the Mediterranean Sea.

Functional richness was comparatively well explained by the model (marginal R^2 = 0.57), largely reflecting its strong dependence on taxonomic richness and environmental gradients. Taxonomic richness and the community-weighted mean of maximum body length (CWM length) showed moderate explanatory power (marginal R^2 = 0.21 for both variables), whereas taxonomic evenness and functional evenness were only weakly explained by the environmental and anthropogenic predictors included in the model (marginal R^2 = 0.09 and 0.06, respectively). These contrasting explanatory capacities suggest that richness-based biodiversity dimensions are more strongly structured by broad-scale environmental gradients and human pressures than evenness-related metrics. The low explanatory power observed for taxonomic and functional evenness indicates that additional ecological processes not explicitly represented in the SEM, such as species interactions or local habitat complexity,

likely contribute substantially to the organization of community biomass distributions in Mediterranean fish assemblages. Environmental gradients and anthropogenic pressures strongly influenced Mediterranean fish communities and biomass production (Figure 3-6, Figure 3-7). Chlorophyll-a concentration positively affected fish biomass, highlighting the importance of primary productivity in supporting higher trophic levels and reinforcing the bottom-up control of Mediterranean marine food webs (Piroddi et al., 2017).

Temperature-related variables also played an important role in shaping biodiversity and biomass patterns. Sea surface temperature exhibited a direct negative effect on biomass, while bottom temperature positively influenced taxonomic evenness but negatively affected functional richness and average body size. These contrasting responses suggest that warming may promote a more even distribution of species biomass while simultaneously reducing the breadth of ecological strategies and favouring smaller-bodied species (Hattab et al., 2021). Such patterns are consistent with ongoing thermophilization processes documented throughout the Mediterranean Sea, where warming has been associated with shifts toward communities dominated by smaller, warm-affinity species and reduced trophic complexity (Moullec et al., 2019; Sanz-Martín et al., 2024).

Anthropogenic pressures also exerted strong and contrasting effects. Bottom trawling pressure was negatively associated with both taxonomic richness and biomass, confirming the important role of trawl fisheries as a driver of biodiversity erosion and ecosystem degradation in Mediterranean demersal systems (Agnetta et al., 2025). In contrast, the small-scale fisheries index showed positive relationships with biomass and some diversity metrics, particularly taxonomic and functional evenness. This likely reflects the spatial overlap between productive coastal habitats and artisanal fisheries rather than the beneficial ecological effect of fishing itself. Similarly, the human gravity index negatively influenced biomass, functional richness, functional evenness and average body size, supporting previous evidence that cumulative coastal human pressures contribute to the simplification of fish communities and reductions in ecosystem functioning (Bosch et al., 2022; Cinner et al., 2018).

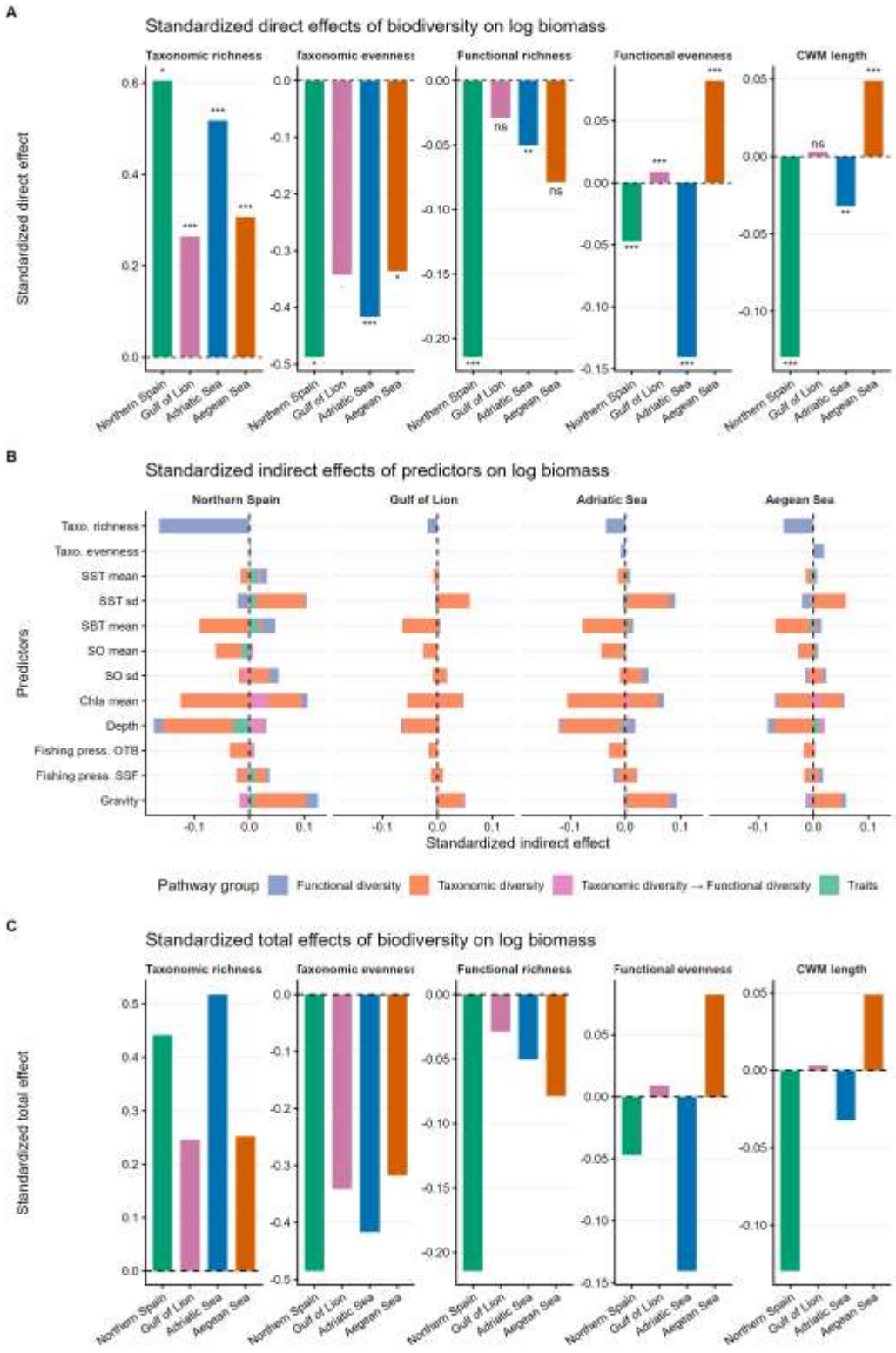


Figure 3-6. Standardized effects of biodiversity on log biomass across GSAs. Panel A shows standardized direct effects of biodiversity components (taxonomic richness, taxonomic evenness, functional richness, functional evenness and CWM length) on log biomass across GSAs. Significance of effects is indicated by stars (* P < 0.05; ** P < 0.01; *** P < 0.001; ns = non-significant). Panel B shows standardized indirect effects of predictors on log biomass across GSAs, decomposed by pathway group: functional diversity (blue), taxonomic diversity (orange), traits (green) and taxonomic diversity → functional diversity (pink). Panel C shows standardized total effects of biodiversity components on log biomass across GSAs. Total effects are the sum of standardized direct effects (from Panel A) and standardized indirect effects (from Panel B) for each predictor and GSA level.

The SEM revealed strong but contrasting relationships between biodiversity dimensions and fish biomass, with clear differences among taxonomic, functional and trait-based indicators (Figure 3-6, Figure 3-7 and Figure 3-8). Taxonomic richness emerged as the strongest positive predictor of biomass across the Mediterranean (standardized effect = 0.52), indicating that species-rich communities generally supported higher fish biomass. This result supports classical biodiversity-ecosystem functioning theory, whereby increased species richness enhances resource use complementarity, trophic diversity and overall ecosystem productivity (Balvanera et al., 2006; Cardinale et al., 2006; Duffy et al., 2017; Gamfeldt et al., 2015). Functional richness, however, showed an overall negative relationship with biomass. The negative association between functional richness and biomass suggests that, in Mediterranean demersal assemblages, high biomass may not necessarily arise from the occupation of a broad functional trait space. Instead, productive communities may be dominated by a limited number of functionally similar and locally adapted species, while broader functional richness may partly reflect the presence of rare or low-biomass species contributing little to standing biomass. This pattern may also indicate that, under strong environmental filtering and fishing pressure, ecosystem functioning relies more heavily on a restricted set of resilient functional strategies than on broad functional complementarity. Functional and taxonomic evenness also exhibited contrasting effects. Taxonomic evenness showed a strong negative relationship with biomass, indicating that highly productive communities were often dominated by a limited subset of abundant species rather than characterized by balanced abundance distributions (Maureaud et al., 2019). Such dominance patterns are common in exploited marine ecosystems where biomass is concentrated in a few highly productive or commercially important taxa (Maureaud et al., 2019). Functional evenness also showed an overall negative effect on biomass, although this relationship varied substantially among regions. Together, these results suggest that ecosystem functioning in Mediterranean fish communities is driven more strongly by species identity, dominance structure and richness than by the equitable distribution of abundances among species or functional traits. The community-weighted mean of maximum body size had a weak but significant negative overall relationship with biomass. This pattern may reflect the long-term effects of fishing pressure in Mediterranean ecosystems, where larger-bodied and late-maturing species have undergone substantial declines, while contemporary biomass is increasingly dominated by smaller-bodied and faster-growing species (Coll et al., 2024; Vasilakopoulos et al., 2014). However, regional interactions revealed that the influence of body size differed among GSAs, highlighting the importance of local ecological and exploitation contexts.

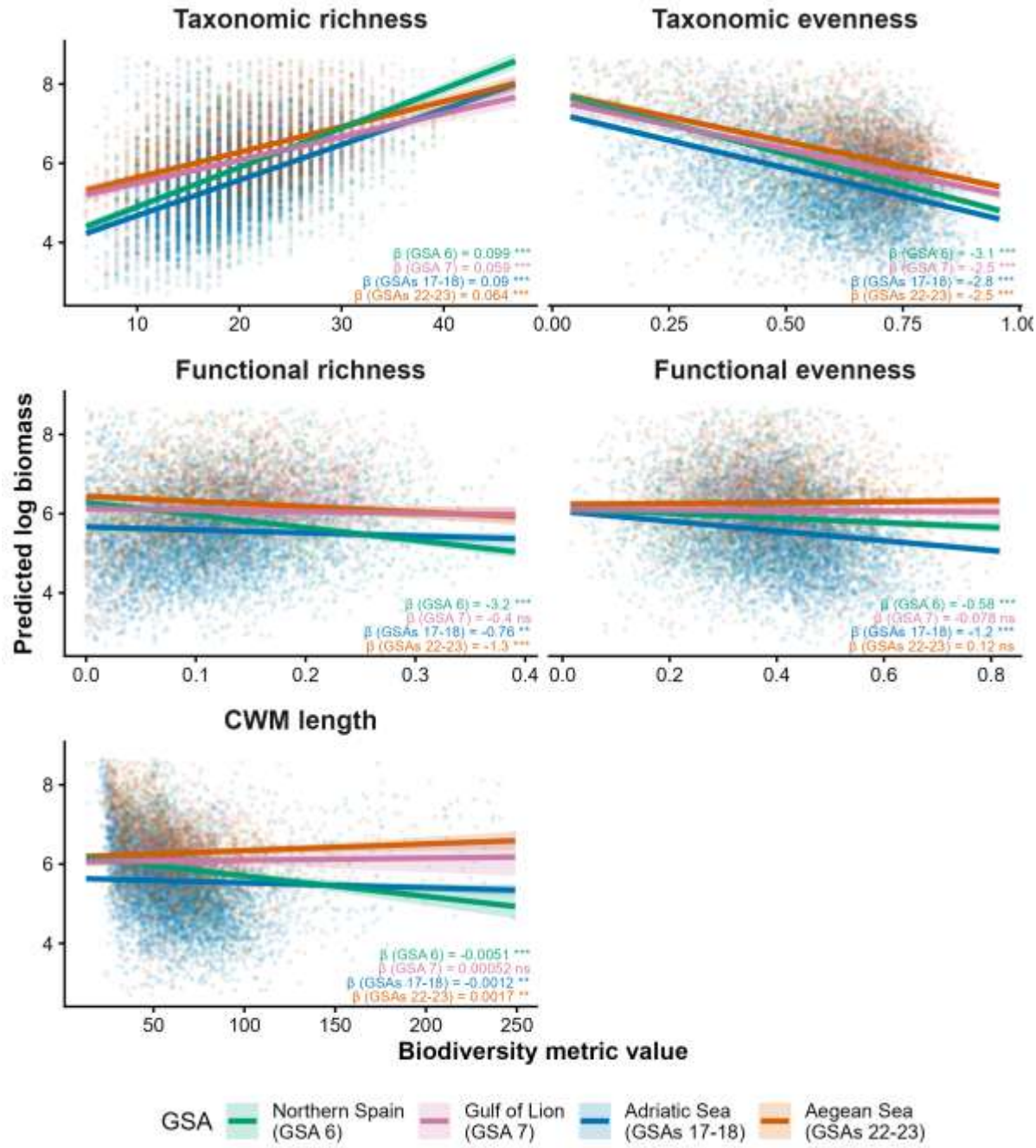


Figure 3-7. Predicted relationships between log biomass and biodiversity metrics across GSAs. Lines represent model predictions from the best-fitting model, with shaded areas indicating 95% confidence intervals. Points represent observed data (with some jitter for visibility). Text annotations indicate the slope (β) and significance level for each GSA and metric.

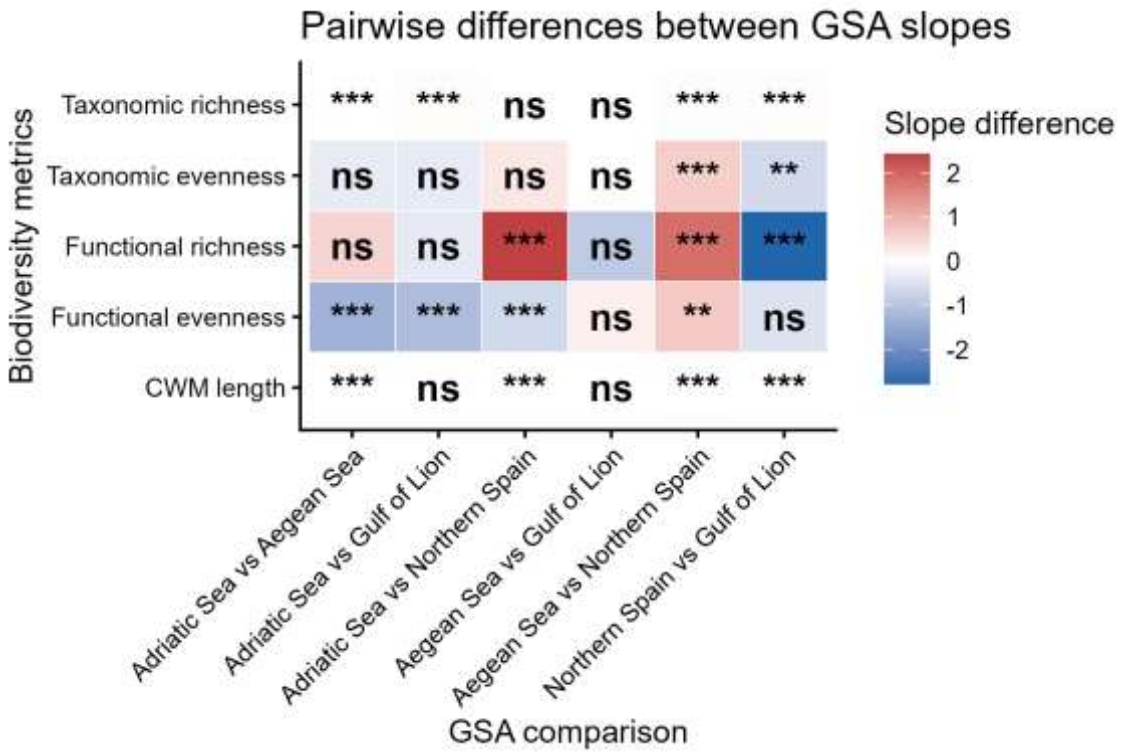


Figure 3-8. Pairwise comparisons of slopes between GSAs for each biodiversity metric. The heatmap shows the estimated slope differences between GSAs for each biodiversity metric, with color indicating the magnitude and direction of the difference (red = higher slope in first GSA, blue = higher slope in second GSA). Stars indicate the significance of the slope difference (* P < 0.05; ** P < 0.01; *** P < 0.001; ns = non-significant). The comparisons are made between the Adriatic Sea, Aegean Sea, Northern Spain and Gulf of Lion.

Incorporating GSA-specific interactions substantially improved the representation of biodiversity-ecosystem functioning relationships across the Mediterranean. Figure 3-6 highlights that indirect effects on biomass differed among pathway groups and regions, revealing marked spatial heterogeneity in the mechanisms linking biodiversity to ecosystem functioning. The positive effect of taxonomic richness on biomass remained significant across all GSAs but varied in magnitude (Figure 3-7 and Figure 3-8). The Northen Spain exhibited a stronger positive richness-biomass relationship relative to the Adriatic reference region, whereas the Aegean Sea and Gulf of Lion showed weaker slopes. These differences likely reflect contrasting productivity regimes, exploitation histories and community structures among Mediterranean subregions (Piroddi et al., 2017, 2020). Regional variability was particularly evident for functional evenness and taxonomic evenness. In the Aegean Sea, functional evenness showed a positive interaction with biomass, contrasting with the overall negative effect observed at the Mediterranean scale. This may indicate that in the comparatively oligotrophic and environmentally constrained eastern Mediterranean, a more balanced distribution of functional traits enhances ecosystem functioning by promoting resource partitioning and stability. Conversely, in the Northern Spain, both taxonomic and functional evenness displayed more negative relationships with biomass, suggesting stronger dominance by a subset of productive species in this heavily exploited and comparatively productive region. Similarly, the effect of functional richness differed among regions. The negative relationship between functional richness and biomass was particularly pronounced in the Northen Spain, whereas no significant regional deviation was detected in the Aegean

Sea or Gulf of Lion. These patterns suggest that the ecological role of functional diversity depends strongly on local environmental filtering and fishing regimes. In highly exploited systems, ecosystem functioning may rely more heavily on a restricted set of resilient functional strategies rather than broad functional complementarity.

A key result of this case study is that taxonomic richness was the most consistent positive biodiversity predictor of biomass, whereas functional diversity metrics showed weaker, or region-specific relationships. This indicates that Mediterranean fish biomass appears generally more strongly linked to species richness and dominance structure than to broad functional trait richness and evenness. More broadly, these results show that biodiversity-ecosystem functioning relationships in Mediterranean demersal communities are highly context dependent and shaped by the interaction between environmental gradients, anthropogenic pressures and regional ecological characteristics (Figure 3-7 and Figure 3-8). While species richness consistently supported higher fish biomass, the effects of functional diversity and community structure varied considerably among Mediterranean subregions. These findings emphasize the importance of incorporating regional ecological contexts when assessing biodiversity-ecosystem functioning relationships and designing ecosystem-based management strategies in Mediterranean marine ecosystems.

Summary and Conclusions

- Among environmental drivers, primary productivity (chlorophyll-a concentration) positively influenced biomass, supporting the importance of bottom-up processes in Mediterranean food webs. In contrast, increasing depth and warmer sea surface temperatures were associated with lower fish biomass, reflecting the oligotrophic nature of deeper and warmer Mediterranean habitats.
- Anthropogenic pressures also played a major role: bottom trawling pressure and cumulative coastal human impacts negatively affected both biodiversity and biomass, confirming the strong influence of fishing and human disturbance on Mediterranean demersal ecosystems.
- Taxonomic diversity indicators were overall more effective than trait-based indicators at explaining variation in fish biomass. Taxonomic richness emerged as the strongest positive predictor of biomass across the Mediterranean Sea, indicating that species-rich assemblages generally support higher ecosystem functioning and productivity. Conversely, several trait-based metrics, including functional richness, functional evenness and community-weighted maximum body size, showed either weak or negative relationships with biomass. This suggests that Mediterranean fish biomass is more strongly linked to species richness and community dominance structure than to broad functional trait dispersion.
- Biodiversity-biomass relationships were not spatially homogeneous across the Mediterranean basin. Significant GSA-specific interactions demonstrated that the strength and even the direction of some biodiversity effects varied among regions. While the positive relationship between taxonomic richness and biomass was generally consistent, its magnitude differed between the Northern Spain, Aegean Sea, Gulf of Lion and Adriatic reference region. Trait-based relationships were even more region dependent, highlighting the importance of local environmental conditions,

exploitation histories and community structure in shaping biodiversity-ecosystem functioning relationships.

- Overall, the results demonstrate that Mediterranean biodiversity-ecosystem functioning relationships are highly context dependent. Species richness consistently supports higher fish biomass, but the role of functional diversity varies according to local ecological and anthropogenic conditions. These findings underline the importance of incorporating regional heterogeneity into ecosystem-based management and conservation strategies in the Mediterranean Sea, particularly under ongoing climate change and cumulative human pressures.

3.1.4. North Sea

Lead contributor: Louise Flensborg (DTU-Aqua) and Laurene Pecuchet (UiT)

The North Sea is a temperate, semi-enclosed shelf sea located between the United Kingdom and continental northwestern Europe. It is characterized by strong environmental gradients in depth, temperature, salinity, and productivity, which create highly heterogeneous habitat conditions across the basin (Couce et al., 2020; Reiss et al., 2010). The region is among the most intensively used marine ecosystems globally, with substantial anthropogenic pressures including commercial fisheries, shipping, offshore energy production, eutrophication, and climate-driven change (Bowler et al., 2020).

Fish communities in the North Sea are diverse and structured by both environmental variability and human impacts. Earlier studies have documented pronounced long-term changes in community composition, including declines in multiple fish stocks and shifts in trophic structure linked to fishing pressure and environmental variability (Alheit et al., 2005; Beaugrand, 2004; Clausen et al., 2018; Fernandes & Cook, 2013; Lindegren et al., 2018). These dynamics highlight strong interactions between climate forcing and exploitation, with consequences for ecosystem stability and resilience (Dickey-Collas et al., 2010; Worm et al., 2009).

The ecosystem supports a highly productive fishery, with key commercial species including Atlantic cod, Atlantic herring, European plaice, Atlantic mackerel, and Haddock, which together contribute substantially to regional biomass extraction and food provision (ICES, 2022, 2024b). In addition to fisheries production, the North Sea provides key ecosystem services such as nutrient cycling, carbon processing, and biodiversity support, while also sustaining important cultural and recreational values (Piet et al., 2024; Selim et al., 2016). Overall, fish community structure and total biomass in the region are jointly shaped by environmental gradients, biological diversity, and intense human pressures (Bowler et al., 2020; Lindegren et al., 2018).

Materials and Methods

The community fish data was obtained from the North Sea International bottom trawl survey (NS-IBTS) conducted each year in quarter 1 and quarter 4 by multiple nations surrounding the North Sea. The survey uses a GOV (Grande Overture Verticale) bottom trawl at a mean towing speed of 3 knots during 30mn, equivalent to a towing distance of ~2.8 km. Here, we focus on the quarter 4 (Oct-Dec) of the survey to be more consistent with the time period of the other

European surveys included in this deliverable which are often in Quarter 3. We restricted the data analysis to the 1998-2020 period to fit the time-series of the Chlorophyll a satellite data. We removed hauls that were extreme, either due to their depth (deeper than 300 m), their biomass (less than 10 kg or more than 400 tons), or their haul duration (outside the 20-40mn range). A total of 5947 hauls were analysed.

We followed the general protocol for the SEM described earlier and used the variables specified in Figure 3-2. We did not use fishing effort data in this case study. Instead of integrating functional and taxonomic indicators into one single analysis we did two separate analyses, one with functional and one with taxonomic indicators and then compared the model fits of the two. This choice was in part motivated due to a high correlation between taxonomic evenness and functional dispersion.

The environmental variables were also highly correlated, we thus had to remove several of them and kept: annual sea bottom temperature (*sbt_mean*), seasonal variation in sea surface temperature (*sst_sd*), log-transformed annual chlorophyll a concentration (*log_chla*) and depth.

Results and Discussion

Total biomass in the hauls appears highly variable even in the same area, but still some spatial patterns emerge, with biomass tending to be higher in the northern North Sea and generally lower in the central North Sea (Figure 3-9 top left). The community weighted maximum length showed a distinct spatial pattern, with higher values in the central North Sea and lower values in the south and north. Taxonomic richness (*tric*) and functional richness (*fric*) displayed similar spatial patterns, with higher values in the northern North Sea (Figure 3-9). A noticeable difference is that taxonomic richness tends to be relatively high in the southern North Sea, near the English Channel, whereas functional richness remains low in this area. Taxonomic evenness and functional dispersion displayed similar patterns with generally higher values in the central North Sea, albeit with large local variations. From these variables, taxonomic richness and functional richness were moderately correlated (Pearson correlation coefficient r of 0.46), and taxonomic evenness and CWM length were moderately to highly correlated with functional dispersion (respectively, r of 0.8 and 0.66).

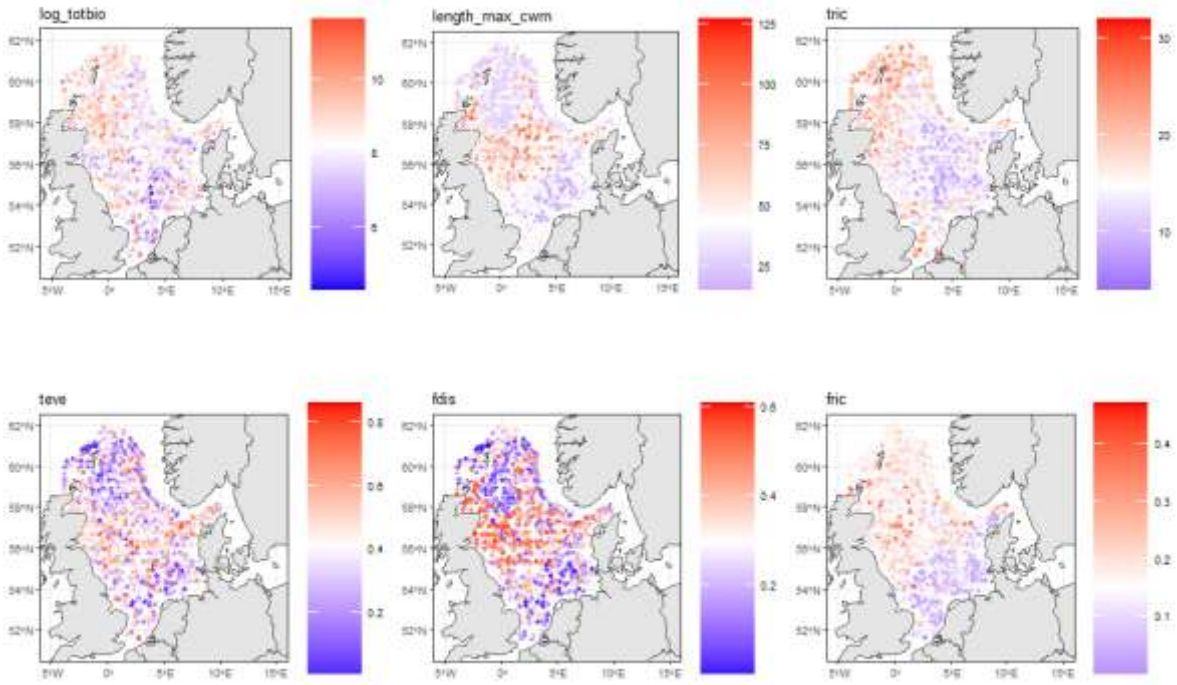


Figure 3-9. Biodiversity indicators and log-transformed total biomass in the North Sea, calculated for each haul.

The environmental variables analyzed displayed similar south-north patterns (Figure 3-10). SBT mean and variability, SST mean, chlorophyll a concentration mean and variability, were all decreasing along a south-north gradient. Mean chlorophyll a concentration also appears to decrease following a coast-offshore gradient. Depth increased from the south to the north, and with higher depth along the coastal slopes in the east. As many environmental variables were highly correlated, we restricted the variables included in the SEM models.

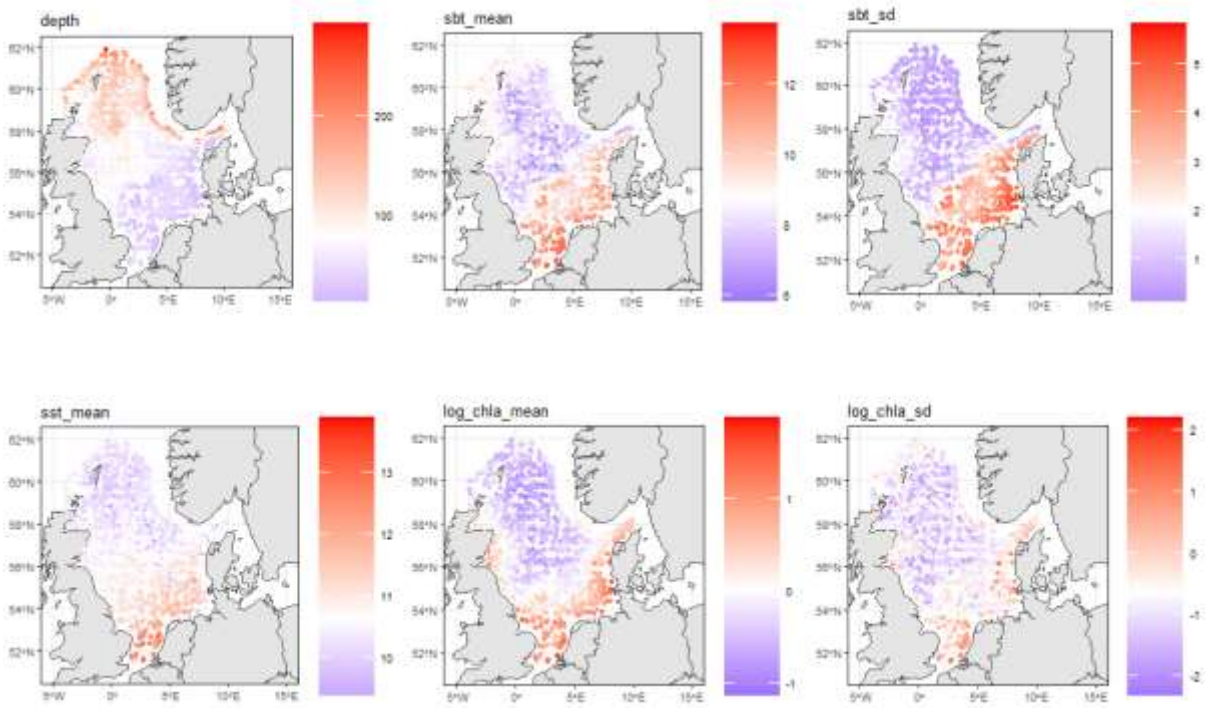


Figure 3-10. Spatial patterns of environmental variables in the North Sea, calculated based on the average values around the haul (4km diameter).

Table 3-5. Best diversity indicators and biomass models. For all the models, after testing multiple models type spatial and temporal autocorrelation structure, a CorGaus spatial autocorrelation and year as random factor was used. Equation in black are common to both taxonomic and trait SEM, in grey for taxonomic SEM, and italics for trait SEM. The fit for the taxonomic SEM (Chi-Squared = 0, P-value = 1 and 0 df) was considered problematic and was due to all variables being included in the biomass model and must therefore be taken with caution. The fit for the trait SEM (Chi-Squared = 2.45, P-value = 0.29 and 2 df; Fisher's C = 5.26, P-value = 0.26 and 4 df) was considered adequate.

Best models
CWM Length ~ SBT*** + SST_var*** + depth*** + log(Chla)***
Tric ~ SBT*** + SST_var*** + depth*** + log(Chla)***
Teve ~ SBT*** + SST_var*** + depth*** + log(Chla)**
Log_biomass ~ teve*** + tric*** + CWM.Length* + SBT*** + SST_var*** + depth*** + log(Chla)**
*Fric ~ SBT*** + SST_var*** + depth*** + log(Chla)*
Feve ~ SST_var + depth*** + log(Chla)*
*Fdis ~ SBT*** + SST_var*** + depth*** + log(Chla)****
*Log_biomass ~ fdis*** + feve*** + fric*** + CWM.Length* + SBT*** + SST_var*** + depth** + log(Chla)***

The selected best models explained the response variable with varying degrees (Figure 3-11), from very low explanatory power for taxonomic evenness ($r^2 < 0.05$) and functional evenness and dispersion ($r^2 \approx 0.1$), to relatively low for the full model total biomass ($r^2 \approx 0.2$), and adequate for taxonomic and functional richness ($r^2 > 0.4$). The generally low explanatory power of some of the diversity indicators and total biomass, as well as the fact that the taxonomic

model retained all explanatory variables (Table 3-5), points out that some variables might be missing in the model. Extra models were performed (not shown) by adding average salinity and fishing pressure, but these didn't improve significantly the models. Dencker et al. (2017) used generalized additive model and a grid cell design to model the drivers of *tric*, *fric*, *teve* and *feve*. They could explain more of the diversity variability (from 36% to 76%), which might be due to the different spatial design, and that they included non-linearities in their model. The explanatory power of the biodiversity models in Maureaud et al. (2019) was very similar with our finding, with taxonomic evenness also very low (5%), whereas it was higher for taxonomic richness (29%) and total biomass (50%). Beukhof et al. (2019b) modelled the spatial pattern of CWM length using a grid cell design, and also found that sea temperature was the main driver, but also that their model explained very little of the total variation (R^2 = 0.02). Notably, depth seems to drive *teve* and *tric* in a non-linear way. Other variables that could be included to improve the model could be other community diversity indicators such as dissimilarity (Maureaud et al. 2019). Another reason for the relatively poor explanatory power could be due to the high noise in the large dataset as we are using "raw" observation (i.e. at the haul level).

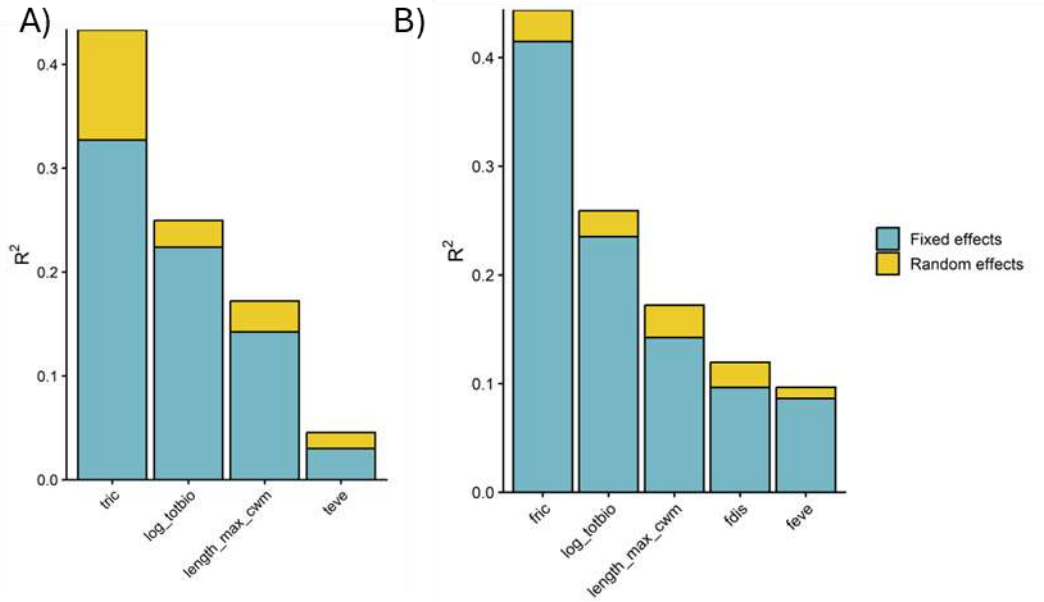


Figure 3-11. Total explained variability of the selected models for the diversity indicators taxonomic evenness (teve), taxonomic richness (tric), functional richness (fric), functional evenness (feve), functional dispersion (fdis), and CWM length (length max_CWM), and the total biomass (log_totbio).

Total fish biomass in the North Sea, as explained by the taxonomic diversity, had a strong negative correlation with taxonomic evenness, and negative relationships with seasonality and averaged sea temperature (Figure 3-12, top panel). This result is in line with Maureaud et al. (2019) who also found, although using somewhat different spatial aggregation and calculation of biodiversity indicators, that North Sea fish biomass was first explained by its negative relation with SST seasonality, followed by a negative effect of taxonomic evenness and averages SST. Here, fish biomass was also positively affected by primary productivity (mean chla) and taxonomic richness. This result contrasts with Maureaud et al. (2019) who found no effect of taxonomic richness on biomass and a weak negative effect of primary productivity. The total effect of environmental variables on total biomass was modified by indirect effect through the diversity indicators. This was notably the case for SST variability which negative effect was reinforced through its indirect effect on taxonomic richness.

Total fish biomass in the North Sea, as explained by the functional diversity, had a strong negative correlation with functional dispersion, followed by a negative contribution of functional evenness (Figure 3-12, lower panel). Seasonality and average sea temperature were also found to negatively impact biomass, and primary productivity and functional richness had a positive effect. The total effect of environmental variables on total biomass is influenced by indirect effect through the functional diversity indicators, but with similar strength in both directions, which render the total effect largely similar than the direct effects.

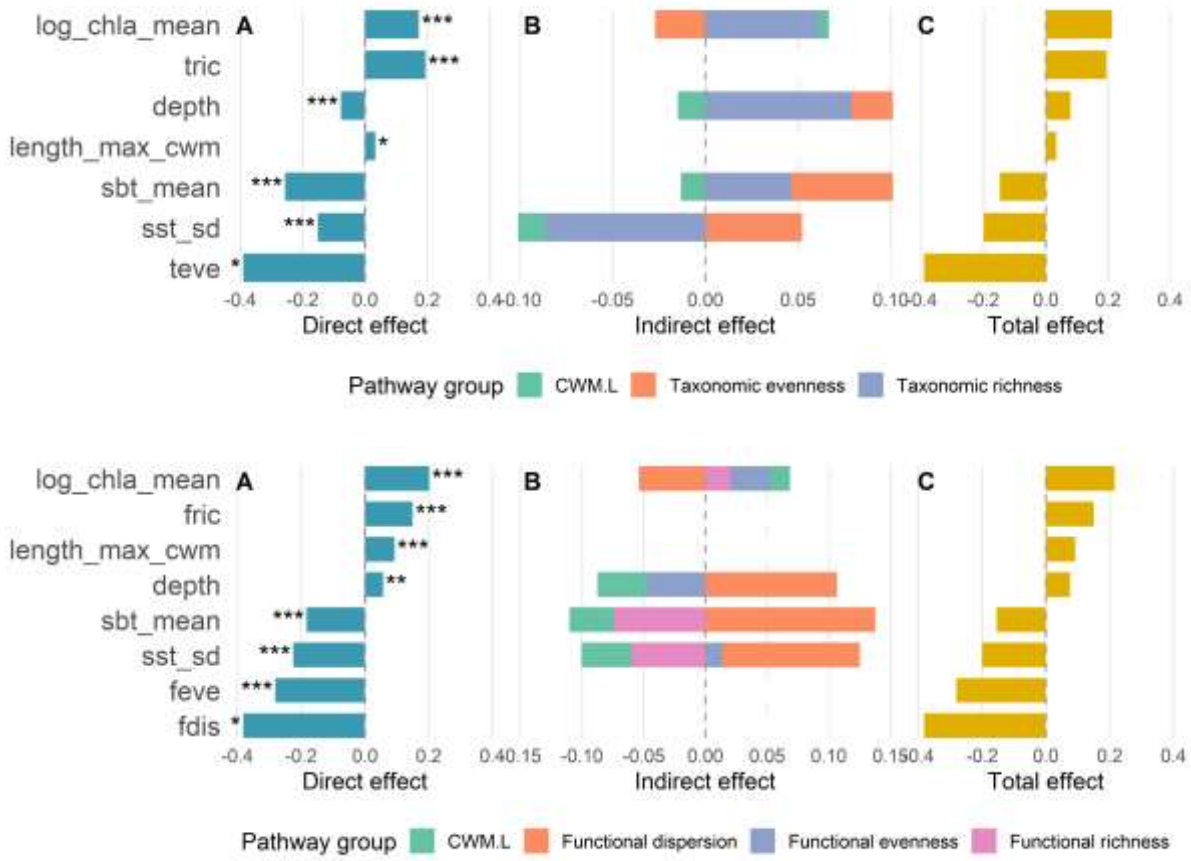


Figure 3-12. Direct, indirect, and total effects of the variables included in the final model explaining the total fish biomass in the North Sea based on the taxonomic indicators (top panel) and functional indicators (lower panel). Indirect effect represents the indirect effects of environmental variables on total fish biomass through their effects on diversity indicators.

Summary and Conclusions

- Fish biomass in the North Sea appears to be negatively impacted by annual means and seasonality in temperature and positively affected by primary production.
- Biodiversity indicators explained a larger part of the variability in fish biomass than any environmental variables.
- Taxonomic evenness negatively impacted fish biomass, and on its own contributed to 40% of the total variance explained in fish biomass.
- Functional dispersion was the strongest and negative drivers of fish biomass (~40% of explained variance), closely followed by functional evenness (~30% of explained

variance). Both functional richness (~15%) and taxonomic richness (~20%) positively impacted fish biomass.

- Results are to be taken with precaution as the biomass models have relatively low explanatory power and thus point out to potentially missing variables.
- There are some signs that both dominance and niche complementarity processes impact on the biomass in the North Sea, with dominance processes being stronger.

3.1.5. Bay of Biscay and south of Celtic Sea

Lead contributor: Julia Polo (UiT and IEO-CSIC) and Marina Sanz (IEO-CSIC)

The Bay of Biscay (BoB) and the Celtic Sea are a temperate region of the northeastern Atlantic Ocean, situated between northwestern France, south of Irland and United Kingdom and north of Spain. The BoB region belongs to the Lusitanian province, and the Celtic Sea belongs to the Northern European Seas, both regions located in the Temperate Northern Atlantic province (Spalding et al., 2007). The BoB has a wide variety of habitats, resulting in high biological richness and diversity within its bentho-demersal communities (Hamel, 2018). These communities are predominantly composed of temperate species, although cold-water taxa are also common, alongside warm-water species. The latter are particularly abundant in the southeastern part of the Bay, where higher summer temperatures favor the presence of species of Mediterranean origin (Hamel, 2018). Overall, biodiversity is generally higher and more variable in coastal areas, whereas communities on the central continental shelf tend to be more stable. This pattern is likely related to the relatively homogeneous geomorphology of continental shelf sediments and the stronger influence of trawling activities in these areas (Serrano et al., 2003). In recent years, benthic and demersal communities in BoB have responded to climate change in several ways. More than 50% of demersal species with temperate biogeographical affinities have shown increases in abundance (Punzón et al., 2016), reflecting a process of meridionalization. In addition, evidence of community tropicalization has been reported in the region, characterized by the increasing occurrence of warm-affinity species originating from southern and/or tropical areas (Bañón et al., 2024; Punzón et al., 2016, 2021). Several important fisheries in the region are already showing responses to oceanographic changes associated with climate change, and further alterations are projected in the future. Key commercial species in the BoB are anchovy, sardine, hake, horse mackerel, anglerfish, and tuna (Punzón et al. 2016).

The Celtic Sea is a highly productive continental shelf system, historically supported substantial demersal fisheries, and since the mid-1990s, management efforts aimed at addressing persistently low biomass and poor recruitment in several stocks have contributed to an overall reduction in fishing pressure (Sturrock et al., 2026). Both regions, the BoB and the Celtic Sea, have experienced significant declines due to overexploitation in several commercially important stocks, in some cases resulting in temporary fishing bans. A notable example is the collapse of the anchovy stock in the BoB in the early 2000s, followed by a fishing ban that ultimately enabled stock recovery (Lazkano et al., 2013).

However, the implementation of specific management regulations in the BoB reduced mortality rates among the main commercial species and promoted the recovery of several stocks (Arroyo et al., 2019; Modica et al., 2014). Consequently, by the end of the 2010s,

benthic and demersal communities in the BoB were considered in a substantially improved ecological state (Fernandes & Cook, 2013; Gascuel, 2016).

In the Celtic Sea, in 2022, only 31% of assessed benthic and demersal stocks with established reference points for fishing pressure were within sustainable limits, indicating that actual fishing mortality still exceeds the level required to achieve maximum sustainable yield. Nowadays a considerable proportion of stocks in the Celtic Sea remain overexploited (Sturrock et al. 2026).

Materials and Methods

Fish communities' data was obtained from the EVHOE («Evaluation Halieutique de l'Ouest Européen») International bottom trawl survey provide observational data on the continental shelves of the Bay of Biscay and the Celtic Sea between 1991-2020 (Laffargue et al., 2025). The surveys operate a standardized bottom trawling gear and are conducted from 15 to 600 m depth, usually in quarter 4 (Oct-Dec), starting at the end of October, consistent with the time period of the other European surveys (Quarter 3) included in this deliverable. Their primary objective is to monitor 22 commercially important fish stocks and 10 cephalopod species in the North-East Atlantic. The dataset also documents regional biodiversity, covering 250 fish taxa, 45 taxa of cephalopods and other commercially important invertebrates, and—since 2008—more than 350 additional taxa of benthic invertebrates (Laffargue et al., 2025). We removed hauls that were extreme, either due to their depth (deeper than 300 m), their biomass (less than 10 kg or more than 400 tons), or their haul duration (outside the 20-40mn range). The analysis was restricted to 1998-2020 to fit with the chlorophyll time-series, a total of 5911 hauls were analysed.

We followed the general protocol for the SEM described earlier and used the variables specified in Figure 3-2. Following previous study cases, we did not use fishing effort data in this case study. Instead of integrating functional and taxonomic indicators into one single analysis, we did two separate analyses, one with functional and one with taxonomic indicators and then compared the model fits of the two. This choice was in part motivated due to a high correlation between taxonomic evenness and functional dispersion.

The environmental variables were also highly correlated, we thus had to remove several of them and kept sea bottom temperature (*sbt_mean*) and standard deviation (*sbt_sd*) , seasonal variation in sea surface temperature (*SST_mean*), log-transformed annual chlorophyll a concentration (*log_chla_mean*) and depth. As previously described, Structural Equation Modelling (SEM) was used to quantify direct and indirect relationships between biodiversity, environmental drivers and fish biomass.

Results and Discussion

Total biomass in the hauls appears to follow a latitudinal gradient with biomass tending to be higher in the southern BoB and generally lower in the central Celtic Sea, despite high variability (Figure 3-13 top left). The community weighted maximum length showed a clear spatial pattern, with higher values in the southern BoB and in deeper areas and lower values in the north and Celtic Sea and shallower zones. Taxonomic richness (tric) and functional richness

(fric) displayed similar spatial patterns, with consistent patterns of higher values in the north BoB and Celtic Sea (Figure 3-13). Functional richness shows lower values despite showing the same pattern. Taxonomic evenness is higher in the Celtic Sea than in south of Bob and functional dispersion displays similar patterns with generally higher values in the Celtic Sea, albeit with large local variations. From these variables, taxonomic richness and functional richness were moderately correlated (Pearson correlation coefficient r of 0.58), and given taxonomic evenness was highly correlated with functional dispersion (r of 0.88), functional dispersion was excluded from further analysis. The same happened with SST and SBT, which had a Pearson correlation coefficient r of 0.65. We kept SBT in further analyses considering its straightforward link to demersal communities.

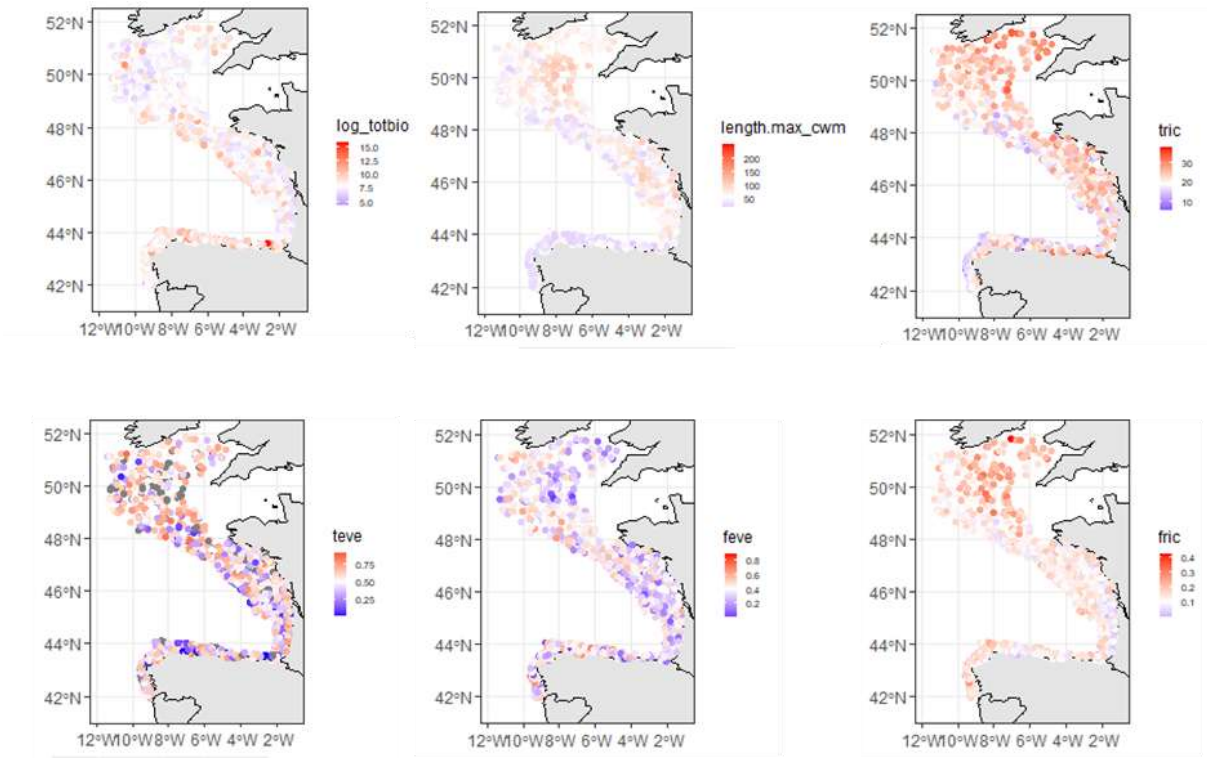


Figure 3-13. Spatial maps of the main biodiversity indicators in the Bay of Biscay and Celtic Sea. Log_totbio = Total fish biomass; length.max_cwm = Community weighted mean maximum body length; tric = Taxonomic richness; teve = taxonomic eveness; feve = functional evennes; fric = functional richness. Grey dots at teve correspond to NAs.

The environmental variables analyzed (*sbtmean, stb_sd and logchla_mean*) displayed similar south-north patterns (Figure 3-14). SBT mean and variability and chlorophyll a concentration mean were all increasing along a north-south gradient, with consistent high values in the French and the northwestern Spain platforms. Mean chlorophyll a concentration also appears to decrease following a coast-offshore gradient. Depth increased from the north to the south, and with higher depth along the coastal Spanish slopes. As many environmental variables were highly correlated, we restricted the variables included in the SEM models.

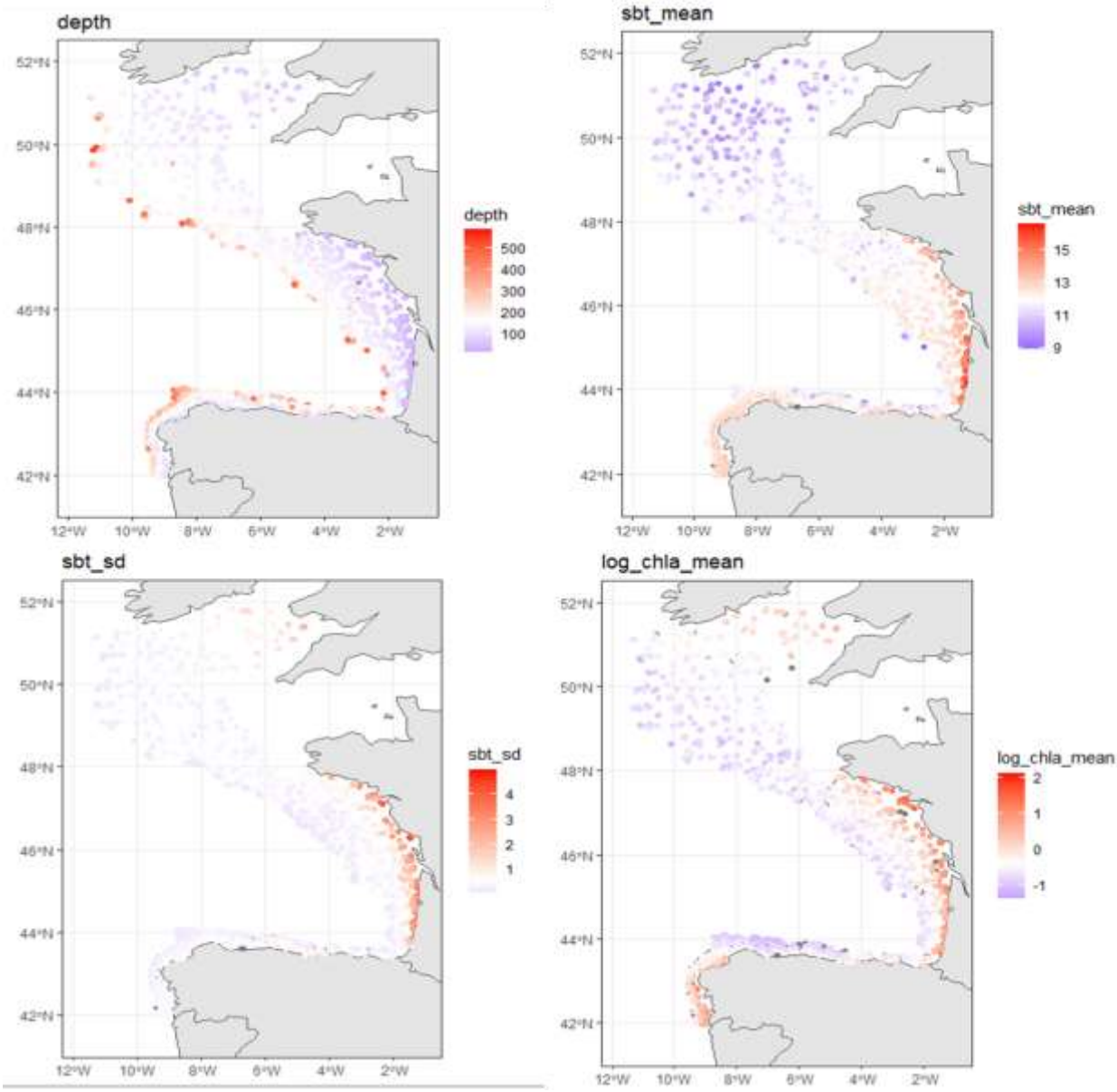


Figure 3-14. Spatial maps of the environmental indicators that were selected in the biomass and biodiversity and taxonomic indicators at the Bay of Biscay and Celtic Sea.

The global goodness-of-fit tests provided mixed results. A significant Chi-squared test (Chi-squared = 1186.709, p-value = 0, df = 12), together with a non-significant Fisher's C test (Fisher's C = 20.726, p-value = 0.189, df = 16), indicate an acceptable fit although not perfectly fitting the data. The low Fisher's p-value highlights that some variability in the data remains unexplained, pointing towards a need for further refinement or inclusion of additional predictors (fishing was not tested in this case study due to a temporal unavailability of fishing data).

In the regional model of the Bay of Biscay, total biomass (log_totbio) seems to be strongly negatively influenced by taxonomic evenness (standardized estimate = -0.57, p-value < 0.001), positively by taxonomic richness (standardized estimate = 0.23, p-value < 0.001), and negatively to the community-weighted length (standardized estimate = -0.25, p-value < 0.001; the bigger the mean size of the community, the smaller the productivity in terms of biomass). Functional richness and evenness had weaker effects on biomass, with functional richness

being non-significant (p-value = 0.253) and functional evenness having a small negative effect (standardized estimate = -0.08, p-value < 0.001). These results suggest that total biomass is primarily driven by taxonomic evenness and richness, as well as the size of the community. The model explained a substantial proportion of the variance in total biomass (Marginal R^2 = 0.50, Conditional R^2 = 0.52) and functional richness (Marginal R^2 = 0.47, Conditional R^2 = 0.50) Figure 3-15. However, the variance explained for functional evenness (Marginal R^2 = 0.02, Conditional R^2 = 0.05) and taxonomic evenness (Marginal R^2 = 0.02, Conditional R^2 = 0.03) was low, indicating that these facets of biodiversity are not well-captured by the current predictors.

Table 3-6. Best diversity indicators and biomass models. For all the models, after testing different model structures with and without spatial and temporal autocorrelation structures, year as random factor was used.

Final models selected for the SEM:	***Spatial autocorrelation structure***
feve ~ tric + teve + fric + sbt_sd + log_chla_mean, random = ~ 1 | year + correlation = corRatio(form = ~ longitude + latitude)	CorGaus
fric ~ tric + sbt_mean + sbt_sd + depth + log_chla_mean, random = ~ 1 | year + correlation = corExp(form = ~ longitude + latitude)	corExp
tric ~ sbt_mean + sbt_sd + depth + log_chla_mean, random = ~ 1 | year + correlation = corSpher(form = ~ longitude + latitude)	corSpher
teve ~ sbt_mean + sbt_sd + depth + log_chla_mean, random = ~ 1 | year + correlation = corExp(form = ~ longitude + latitude)	corExp
length.max_cwm ~ sbt_mean + sbt_sd + depth + log_chla_mean, random = ~ 1 | year + correlation = corExp(form = ~ longitude + latitude)	corExp
log_totbio ~ tric + teve + fric + feve + length.max_cwm + sbt_mean + sbtq + depth + log_chla_mean, random = ~ 1 | year + correlation = corRatio(form = ~ longitude + latitude)	corRatio

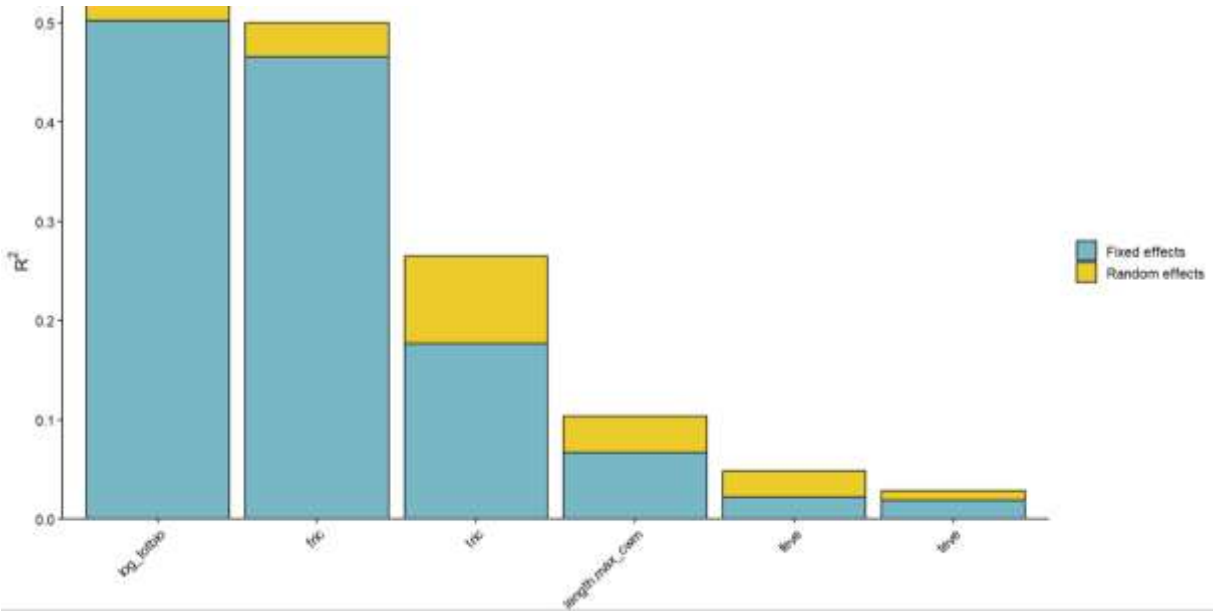


Figure 3-15. Total explained variability (R2) of the selected models in decreasing order of R2 for the total biomass (log_totbio), functional richness (fric), taxonomic richness (tric), CWM length (length max_CWM), functional evenness (feve) and taxonomic evenness (teve) in the Bay of Biscay and Celtic Sea.

The contribution of fixed effects is very strong for all the selected models for the total biomass and the biodiversity and taxonomic indicators, except the taxonomic richness (tric) where the random effect Year has higher contribution (Figure 3-18).

Total biomass and functional richness were comparatively well explained by the model (marginal R^2 = 0.51 and 0.50, respectively), largely reflecting its strong dependence on taxonomic richness and environmental gradients (Figure 3-16). Taxonomic richness showed moderate explanatory power (marginal R^2 = 0.28), whereas the community-weighted mean of maximum body length (CWM length), taxonomic and functional evenness were only weakly explained by the environmental predictors included in the model (marginal R^2 = 0.1, 0.05 and 0.04 respectively, Figure 3-17). These contrasting explanatory capacities suggest that biomass and richness-based biodiversity dimensions are more strongly structured by broad-scale environmental gradients than evenness-related metrics. The low explanatory power observed for community-weighted mean of maximum body length (CWM length), taxonomic and functional evenness indicates that additional ecological processes not explicitly represented in the SEM, such as species interactions or local habitat complexity, likely contribute substantially to the organization of community biomass distributions in Bob and Celtic fish assemblages.

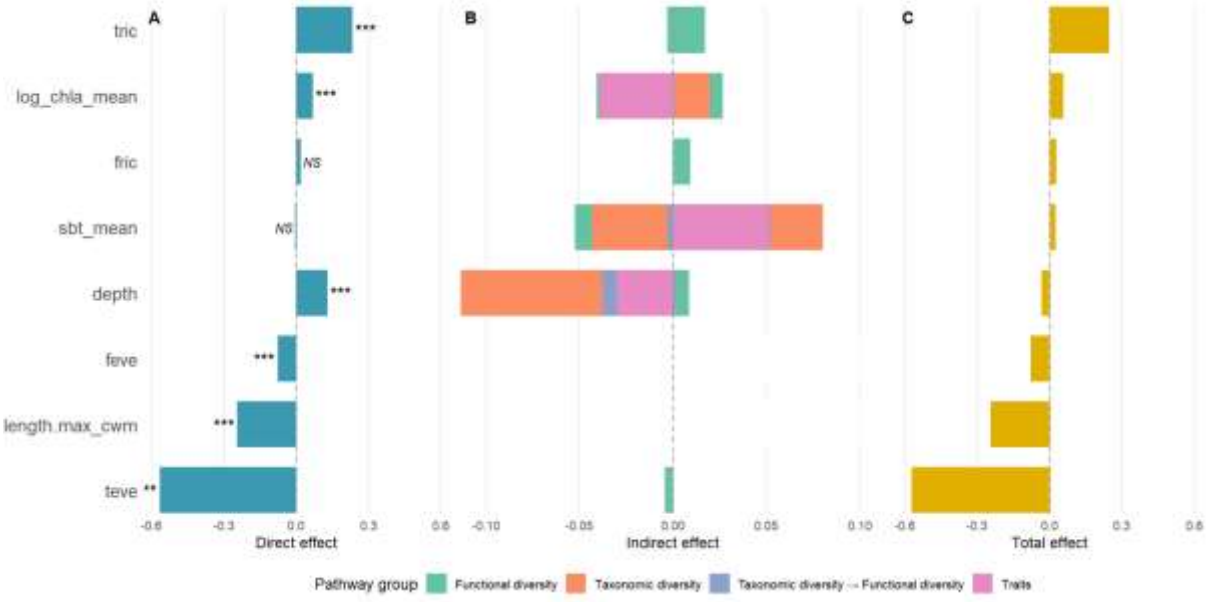


Figure 3-18. Direct, indirect, and total effects of the variables included in the final model explaining the total fish biomass in the Bay of Biscay and Celtic Sea. Indirect effect represents the indirect effects of environmental variables on total fish biomass through their effects on diversity indicators [final model: log_totbio ~ tric + teve + fric + feve + length.max_cwm + sbt_mean + sbtq + depth + log_chla_mean, random = ~ 1 | year + correlation = corRatio(form = ~ longitude + latitude)]

Environmental gradients did not strongly influence Bob and Celtic Sea fish communities and biomass production (Figure 3-19). Depth and chlorophyll *a* have significant direct positive effects on fish biomass, highlighting the importance of bathymetric distributions in fish communities of Bob and Celtic Sea and the PP along the food web (Figure 3-20). In the final model of the total fish biomass in the Bay of Biscay and Celtic Sea, the highest negative direct effect is driven by the taxonomic evenness (teve), followed by the CWM length (length

max_CWM) also negative and the taxonomic richness (tric) through a positive effect (Figure 3-21).

Fish biomass is directly linked to the Functional and taxonomic richness and negatively linked to Functional and taxonomic evenness and CWM length, indicating that richness-based biodiversity dimensions are more strongly structured by broad-scale environmental gradients than evenness-related metrics (Figure 3-22).

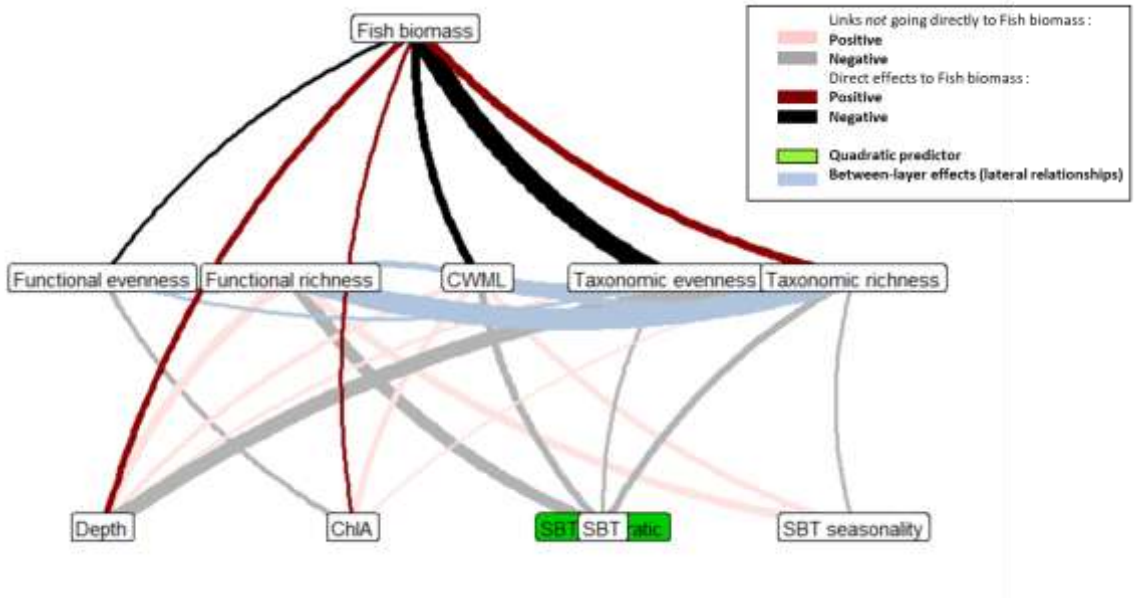


Figure 3-22. Structural equation model structure for fish biomass in the Bay of Biscay, showing its direct and indirect links between environmental variables and different diversity metrics. The green box indicates a significant quadratic effect of SBT as a predictor.

Summary and Conclusions

- Among environmental drivers, primary productivity (chlorophyll-a concentration) and depth positively influenced biomass, supporting the importance of bottom-up processes in Bob and Celtic Sea food webs and the high production of these regions.
- Taxonomic diversity indicators were overall more effective than trait-based indicators at explaining variation in fish biomass.
- Taxonomic evenness showed the strongest negative relationship with biomass, across the Bob and Celtic Sea, indicating that highly productive communities were often dominated by a limited subset of abundant species.
- Taxonomic richness emerged as the second strongest positive predictor of biomass across the Bob and Celtic Sea, indicating that species-rich assemblages generally support higher ecosystem functioning and productivity.

3.1.6. Barents Sea

Lead contributor: Laurene Pecuchet (UiT)

The Barents Sea is a high-latitude marine ecosystem characterized by Atlantic-dominated waters in the south and Arctic-dominated and seasonally ice-covered waters in the north. The fish communities are characterized by a mix of boreal and Arctic fish species. Boreal species are dominating fish communities in the southern Barents Sea, but they are also present in the northern Barents Sea where they make seasonal migrations, they have also expanded their northern distribution due to increased sea temperature in the last decades (Fossheim et al., 2015). The Arctic fish species are especially distributed in the northern Barents Sea. Boreal and Arctic fish species are known to have different traits (Aune et al., 2018; Frainer et al., 2021), with implications for functional diversity (Wiedmann et al., 2014). Functional richness, was shown to be especially high in the central Barents Sea where both boreal and Arctic fish communities co-exist (Wiedmann et al., 2014). Fish communities in the Barents Sea are especially structured by depth, sea bottom and surface temperature and salinity (Aschan et al., 2013; Husson et al., 2020). The Barents Sea harbors a productive fishery industry. The main commercial fish species in the area are boreal gadoid fish such as cod (*Gadus morhua*), haddock (*Melanogrammus aeglefinus*) and saithe (*Pollachius virens*), as well as some invertebrates such as shrimps (*Pandalus borealis*). Other important human activities in the area include oil and gas production and maritime activities (ICES, 2021, 2024a).

Materials and Methods

The community fish data was obtained from a scientific bottom trawl survey conducted each year since 2004 by IMR in August-September in the Norwegian sector of the Barents Sea (Eriksen et al., 2018). The survey uses a Campelen 1800 bottom trawl at a mean towing speed of 3 knots during 15mn, equivalent to a towing distance of ~1.4 km. The mean vertical trawl opening is 25 meters, and the mesh size is 80 millimeters (stretched) in the front and 22 millimeters at the codend, and thus also retaining small fish. A total of 3055 hauls covering the period 2004-2021 were included in the dataset.

Chlorophyll a data was extracted from the GlobColour dataset which uses satellite data; however, it should be noted that this dataset is not ideal for the Barents Sea data has the surface of the ocean is not always adequately visible from satellite due to ice and cloud cover at high latitude. We did not use fishing effort data as no long-term dataset was identified, and available datasets such as GFW have limited temporal coverage and would have reduced greatly the dataset.

We followed the general protocol for the SEM described earlier and used the variables agreed upon. Instead of integrating functional and taxonomic indicators into one single analysis we decided to do two separate analyses, one with functional and one with taxonomic indicators and then compare the model fits of the two. This choice was in part motivated due to a high correlation between taxonomic and functional richness.

Results and Discussion

Total biomass in the hauls appears to be higher in the southern and central Barents Sea and declined in the northern Barens Sea, with quite some variation in the southeastern area (Figure 3-23top left). The mean maximum length in the community is higher in the central Barents Sea and west of Svalbard, whereas it is comparatively lower in the southwestern and northeastern areas. This is consistent with reported length community patterns that show

that fish communities along the polar front in the central Barents Sea, where the Arctic and Atlantic water meets, are generally composed of larger fish species (Bernardo et al., in press). Taxonomic evenness (teve) and functional evenness (feve) displayed different spatial patterns, with teve high in the southern and central Barents Sea whereas feve was higher in the northern Barents Sea (Figure 3-23). It has to be noted though that both had considerable variation within the same area. From these variables, only taxonomic richness and functional richness appears highly correlated (Pearson correlation coefficient r of 0.77). Richness is higher around the coast of Svalbard and northern Norway and in some central areas.

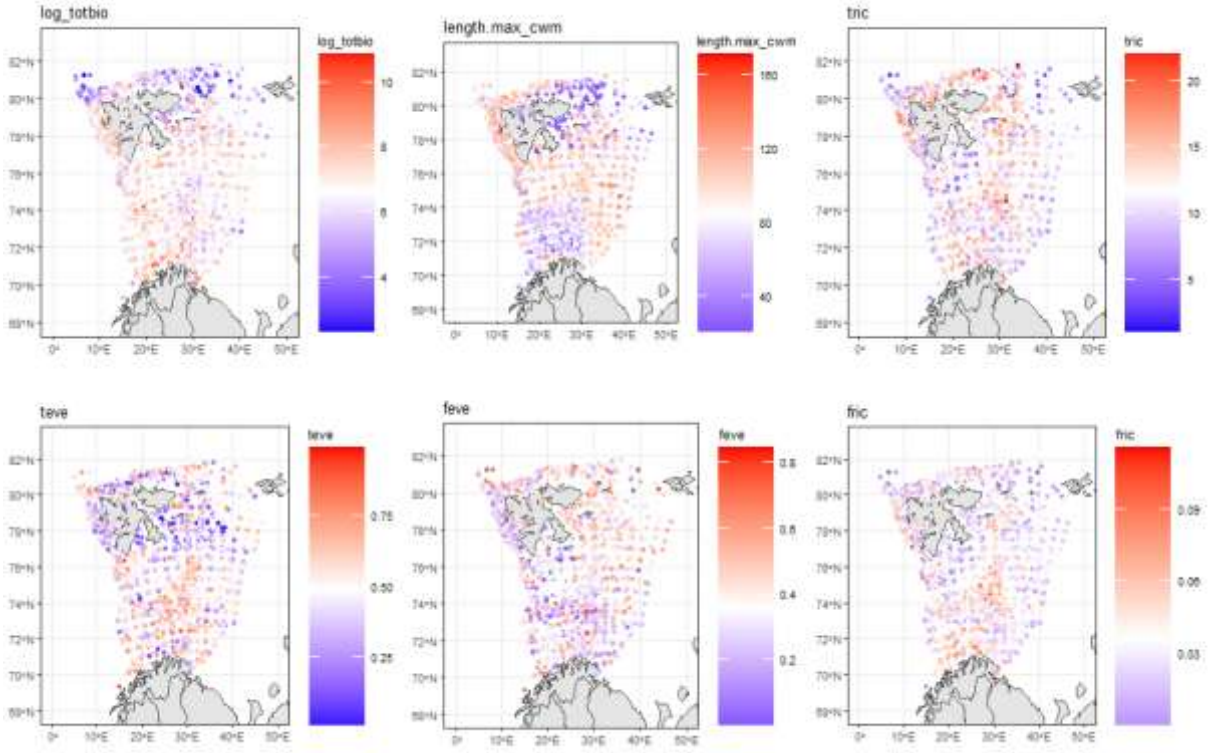


Figure 3-23. Biodiversity indicators and log-transformed total biomass in the Barents Sea, calculated for each haul.

The environmental variables displayed much clearer patterns than the diversity variables. Depth is higher on the slope of the coastal shelves and in some parts of the central Barents Sea (Figure 3-24). Average sea bottom temperature (*sbt_mean*) and sea surface temperature (*sst_mean*) follow a similar pattern, with warmer waters in the southern Barents Sea and along the western coastal shelf. The annual variability in sea bottom temperature (*sbt_sd*) is higher around Svalbard and coastal northern Norway. Average annual chlorophyll concentration (*log_chla_mean*) is especially low in the northern Barents Sea, but it has to be noted that the dataset is imprecise in these high latitude areas. The proportion of the year that is covered by sea ice (*sic_mean*) mirrors the pattern sea surface temperature (*sst_mean*), with the southern Barents Sea being ice-free all year round whereas the northern Barents Sea has varying length of seasonal ice-cover. As this dataset is highly 0-inflated we did not use it in the analysis, and instead included *sst_mean*.

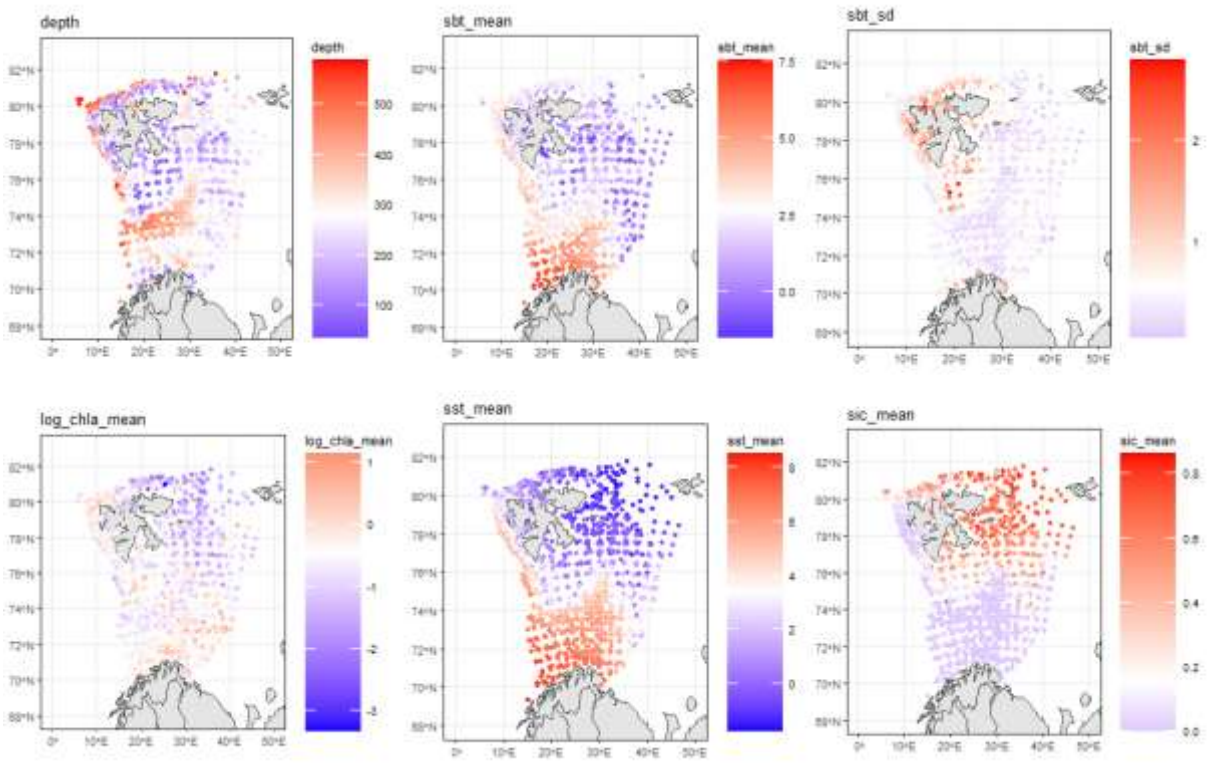


Figure 3-24. Main environmental indicators included in the Barents Sea analysis (not complete), calculated based on the average values around the haul (4km diameter).

In a few cases, and notably for Fdis, variables were added after running the SEM which suggested changes in the model to improve the total SEM fit (Table 3-7). In both cases, the final SEMs were considered to have an adequate fit (Taxonomic SEM p≈0.7; trait SEM p≈0.7).

The selected best models explained the response variable with varying degrees (Figure 3-25), from very low explanatory power for taxonomic richness and functional dispersion ($r^2 < 0.1$) to adequate for the full model total biomass ($r^2 \approx 0.3$). The generally low explanatory power of the diversity indicators points out to missing variables that could be missing in the model, such as salinity or sediment (Husson et al., 2020). Although, in accordance with this study, earlier studies also found that the main drivers of species richness appear to be temperature and depth (Table 3-7, Johannesen et al., 2012). Another reason might be due to the high noise in the data as we are using "raw" observation (i.e. at the haul level), and hence a high variability in the biodiversity values even if the samples are spatially close and thus sharing similar environment.

Total fish biomass in the Barents Sea, as explained by the taxonomic diversity, had a strong negative correlation with taxonomic evenness, followed by a positive relationship with averaged sea surface temperature (*sst_mean*) (Figure 3-26, top panel). It also had a positive relationship with SST seasonality (*sst_sd*) and taxonomic richness, and a negative one with depth. The total effect of environmental variables on total biomass is slightly modified by indirect effect through the diversity indicators, notably some negative indirect effects of SST mean and depth through their positive effect on taxonomic evenness.

Table 3-7. The selected models explaining the variation in diversity indicators and biomass models. For all the models, after testing multiple models type spatial and temporal autocorrelation structure, a gaussian spatial autocorrelation structure and year as random factor was used. Equation in black are common to both taxonomic and trait SEM, in grey for taxonomic SEM, and italics for trait SEM. The fit for the taxonomic SEM (Chi-Squared = 6.32, P-value = 0.70 and 9 df; Fisher's C = 14.04, P-value = 0.73 and 18 df) and trait SEM (Chi-Squared = 5.84, P-value = 0.76 and 9 df; Fisher's C = 13.25, P-value = 0.78 and 18 df) were considered adequate.

Best models
CWM Length ~ sbt*** + sst *** + sst^2 *** + sst_var*** + sbt_var* + depth*
Tric ~ depth*** + sbt *** + log(chla)**
Teve ~ depth*** + sst *** + sst^2** + sst_var* + sbt
Log_biomass ~ teve*** + tric*** + CWM.Length*** + depth*** + sst *** + sst_var*** + log(chla)* + sbt ** + sbt_var
*Fric ~ depth*** + sbt *** + sbt_var** + sst ** + sst^2 * + sst_var*
*Feve ~ sbt_var*** + sst *** + sst^2*** + sst_var**
Fdis ~ sbt_var + log(chla)* + sst^2*** + sst + depth + sbt*
*Log_biomass ~ fdis*** + feve*** + fric*** + CWM.Length*** + depth*** + sst_var*** + sst *** + sst^2+ log(chla)** + sbt*

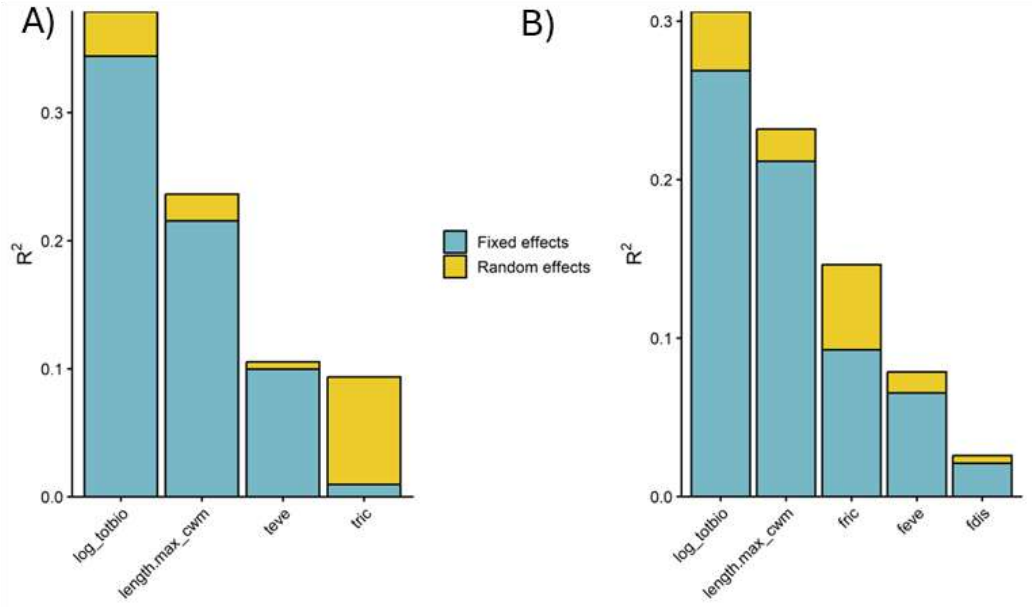


Figure 3-25. Total explained variability of the selected models for the diversity indicators taxonomic evenness (teve), taxonomic richness (tric), functional richness (fric), functional evenness (feve), functional dispersion (fdis), and CWM length (length max_CWM), and the total biomass (log_totbio).

Total fish biomass in the Barents Sea, as explained by the functional diversity, had a strong negative correlation with functional dispersion, albeit at a lower level than the contribution of taxonomic evenness in the taxonomic SEM (Figure 3-26, lower panel). Depth and functional evenness also have a negative effect on total fish biomass, whereas SST mean and variability and functional richness have a positive effect. The total effect of environmental variables on total biomass is influenced by indirect effect through the diversity indicators, but often in both directions, which make the total effect largely similar than the direct effects.

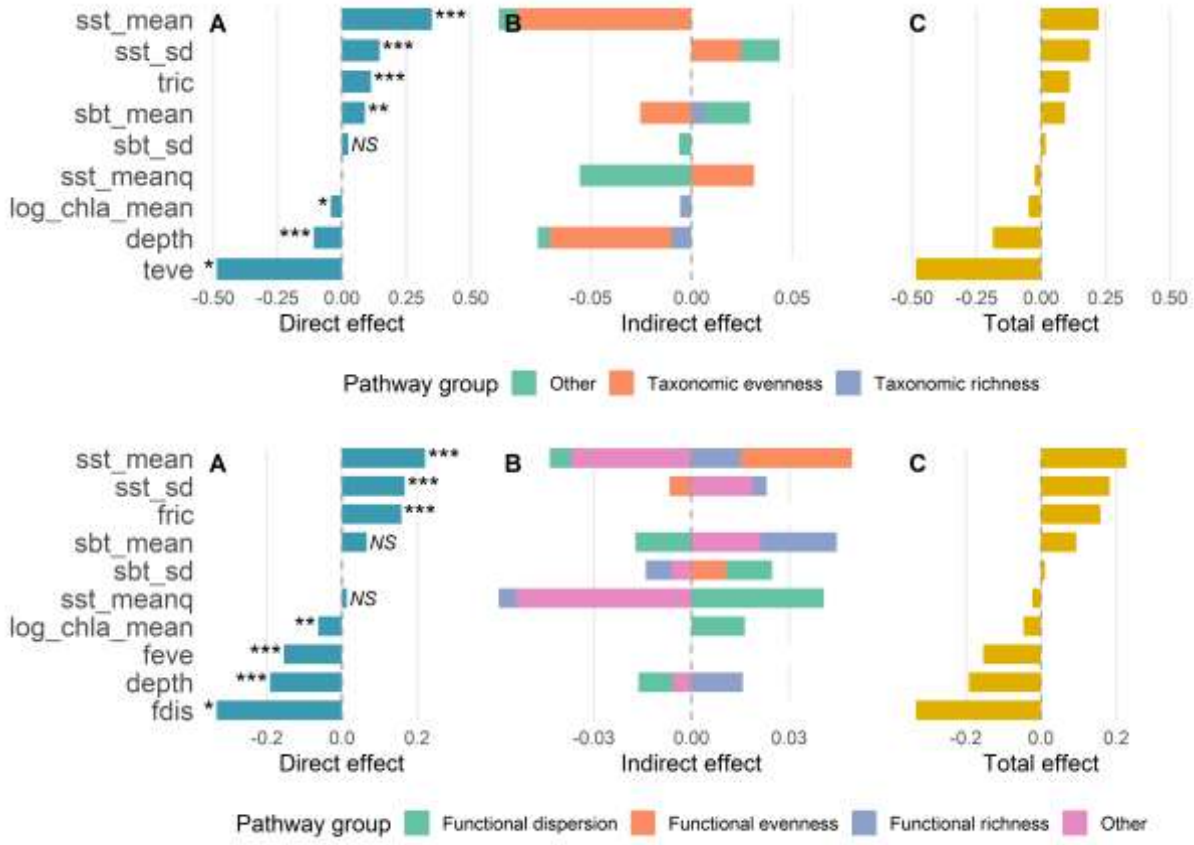


Figure 3-26. Direct, indirect, and total effects of the variables included in the final model explaining the total fish biomass. Indirect effect represents the indirect effects of environmental variables on total fish biomass through their effects on diversity indicators. The pathway group "Other" represents the variable CWM length.

Summary and Conclusions

- Fish biomass in the Barents Sea appears to be positively affected by annual sea surface temperature, and negatively affected by depth.
- Biodiversity indicators explained better the variability in fish biomass than any environmental variables.
- Taxonomic evenness negatively impacted fish biomass, and on its own contributed to 50% of the total variance explained in fish biomass. The biomass model with taxonomic diversity, although including less biodiversity variables than the one with functional diversity (3 vs 4), was better at explaining the variability in biomass.
- Functional dispersion appeared to be the functional equivalent of taxonomic evenness at it was also the strongest and negative drivers of fish biomass, ahead of functional evenness.
- Both functional richness and taxonomic richness positively impacted fish biomass
- There are some signs that both dominance and niche complementarity processes impact on the biomass in the Barents Sea, with dominance processes being stronger.

3.1.7. North-East Atlantic – the effects of scale

Lead contributor: Laurene Pecuchet (UiT)

The fish communities of the Northeast Atlantic have undergone significant changes in recent decades, driven by a combination of anthropogenic and environmental pressures. The Northeast Atlantic is an important historical and current fishing area, with large fish populations such as many small pelagic fish (e.g. mackerel, blue whiting, herring) and large demersal fish species (e.g. hake, haddock, cod, saithe). As one of the most heavily impacted maritime regions globally (Halpern et al., 2012), this area has experienced shifts in species taxonomic and functional composition (e.g. Receveur et al., 2024). These changes are linked to high fishing pressure and warming of sea temperature (Beaugrand, 2004; McQuatters-Gollop et al., 2022). While reductions in fishing fleets and better fishing managements during the 1990s might have alleviated some of the fishing pressures, the legacy of past exploitation and the accelerating impacts of climate change continue to shape community dynamics in this region (Halpern et al., 2012).

Analyses of Northeast Atlantic fish communities reveal how environmental and anthropogenic pressures influence community composition and functional traits. For example, warming temperatures in the North Sea have been linked to reductions in body size for six out of eight fish species, reflecting shifts in optimal trait values under changing environmental conditions (Baudron et al., 2014). In the North Sea, intense fishing has historically led to the prevalence of smaller-bodied species with faster life histories, as larger, slower-growing species were disproportionately targeted and removed from the ecosystem (Jennings et al., 1999).

This case study differs from the previous ones as the main aim is to analyze the impact of the spatial scale of the observations on the strength of the drivers-biomass relationship. More precisely, we aim to assess whether increasing the spatial area of observation (i.e. grid cell) changes which and how much the variables influence total fish biomass.

Materials and Methods

We focus the analysis on the region encompassing the Bay of Biscay, Celtic Sea and North Sea. This corresponds to seven scientific bottom trawl surveys (EVHOE, FR-CGFS, IE-IGFS, NIGFS, NS-IBTS, SP-NORTH, SWC-IBTS). The survey data was obtained from the standardized FISHGLOB dataset (Maureaud et al., 2024). Some surveys are occurring in multiple seasons, we focused the analysis on the most common season, which was quarter 4 for all surveys at the exception of the North Sea for which quarter 3 was kept (due to no survey in quarter 4). We restricted the analysis to the period 2000-2020. We focused on 3 different spatial scales, based on 3 different equal-sized area grid resolutions, with a diameter of approximately: 25km (res 10), 55km (res 9) and 95km (res 8). The grids were built using the dggridR package (Barnes et al.2017). For each of the three grid resolutions, each haul was assigned to a grid cell.

To construct "metacommunities" for each combination of grid resolution and cell, we aggregated fish communities from 10 randomly selected hauls. This was achieved by summing the total biomass of each species encountered across the selected hauls. For each grid cell and resolution, this process was repeated 100 times, resulting in 100 assembled "metacommunities" per grid cell and resolution. Taxonomic and functional diversity indicators were then calculated for each of the generated metacommunities. Environmental variables and fishing pressure data (sourced from Global Fishing Watch) were associated with individual hauls and subsequently averaged based on the random selection of 10 hauls. Finally, for each grid cell and resolution, we computed the mean diversity and environmental variables by

averaging the results across the 100 iterations. This approach ensured a robust estimation of diversity metrics and environmental conditions while accounting for variability in the random selection process.

We then followed the general model selection and SEM framework for the three different spatial resolutions. We computed a single SEM that included together taxonomic and functional diversity, although it should be noted that some variables were slightly correlated, notably functional dispersion and taxonomic evenness (Pearson correlation coefficient r of ≈ 0.65), and taxonomic richness and functional richness (Pearson correlation coefficient r of ≈ 0.55)

Results and Discussion

The general spatial pattern in the selected variables total biomass, taxonomic richness and functional dispersion remain largely unchanged across the three different spatial scales (Figure 3-27). We would have expected to see more local variation in the variables when having more spatially resolved observations (res 10), but this is not apparent here. This might be because, for the three resolutions, the variables are averaged based on 10 hauls which might smooth the observations. Total biomass in the study area was higher in the eastern North Sea (Skaggerak), offshore Bay of Biscay, and the northern North Sea (Figure 3-27). Taxonomic richness was comparatively low in the North Sea and high in the Celtic Sea and Bay of Biscay near the coast. Functional dispersion was high in central and northern North Sea, and comparatively low in the Bay of Biscay (Figure 3-27).

The spatial variation of most biodiversity indicators was poorly explained by the environmental variables, with R^2 between 0.1-0.2 (Figure 3-28). From the biodiversity indicators, only taxonomic richness variation was adequately explained ($R^2 \approx 0.45$). Generally, the explanatory power was similar across the different spatial resolutions, but overall lower for the highest spatial resolution (i.e. local resolution 10). The variation in total biomass was relatively well explained ($R^2 \approx 0.4$).

The total contribution of the environmental and biodiversity variables in explaining total fish biomass displayed both some similarities and differences across the spatial resolutions (Figure 3-29). Functional dispersion was the dominant negative driver of biomass across the three resolutions, but its importance decreased as the resolution increased (i.e. less important at the local scale). Interestingly, as the resolution increased towards more local scale, taxonomic evenness became more important (also with negative effect) whereas it was non-significant at the lowest spatial resolution. It might point out that at large scale it is the trait of the dominant species that impact biomass (in accordance with the *dominance* hypothesis) whereas at a more local scale whether a species' biomass is very high becomes as important as the trait dominance.

Another interesting finding is that fishing pressure had a negative but very weak effect on total biomass at the local scale, whereas its negative effect increases at lower spatial resolution (Figure 3-29). This finding is in accordance with a study from (McKeon et al., 2024) who found that the effect of fishing on fish community composition becomes increasingly apparent as the spatial scale of the observation increases. They argued that this might be because many fish are moving and thus also experiencing fishing effort at larger scale.

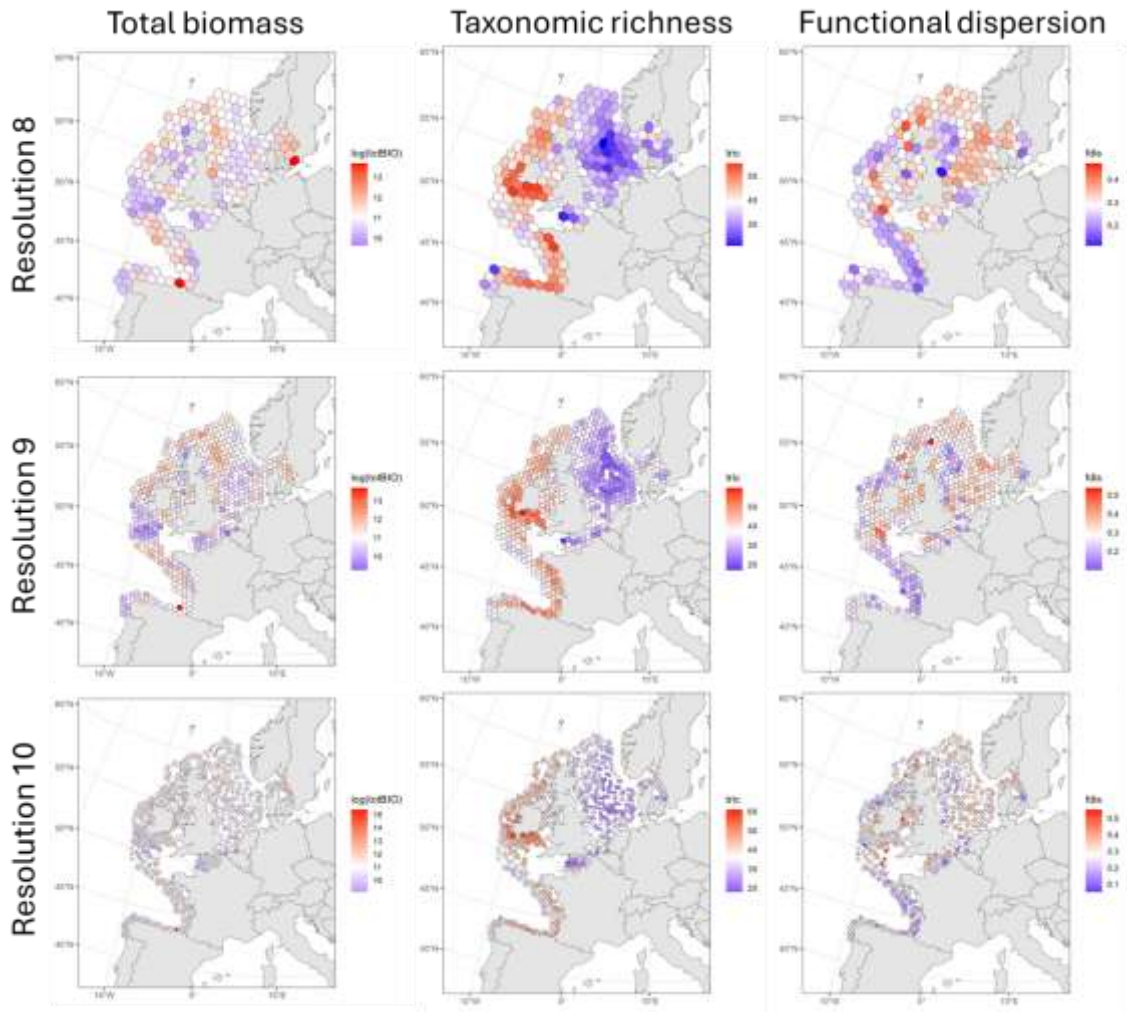


Figure 3-27. Biodiversity indicators (taxonomic richness and functional dispersion) and log-transformed total biomass in the North-East Atlantic across three different spatial resolutions, from larger resolution (res 8) to more local resolution (res 10). The indicators were calculated as the average indicators based on 100 randomly assembled communities from 10 hauls.

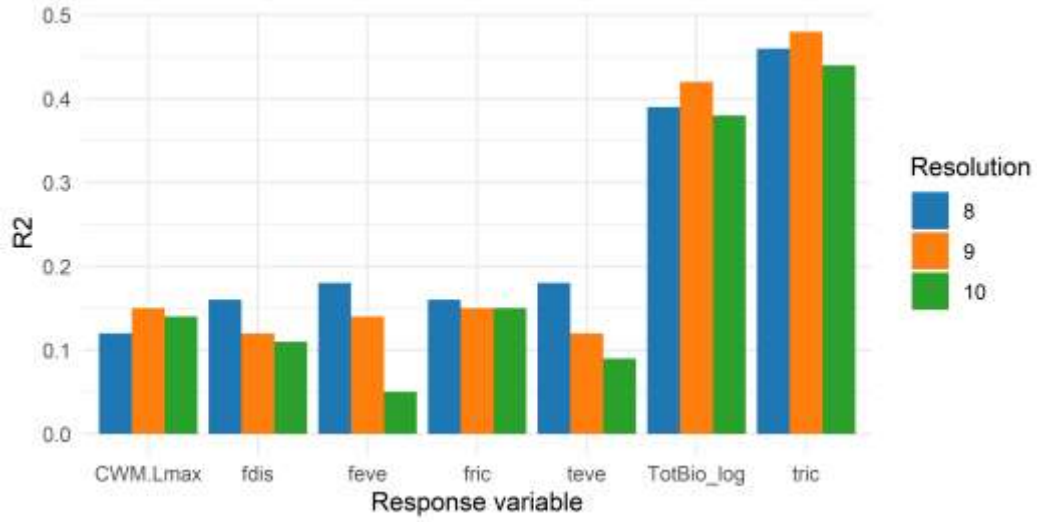


Figure 3-28. Total explained variability of the selected models for the diversity indicators and total biomass based on the different spatial resolution and ranked from least to most variability explained: CWM length (CWM.Lmax), functional dispersion (fdis), functional evenness (feve), functional richness (fric), taxonomic evenness (teve), the total biomass (TotBio_log) and taxonomic richness (tric).

Taxonomic richness had a clear positive effect on total fish biomass and explained on average 30% of the variance explained. On the other hand, functional richness was not retained (i.e. non-significant) in any of the final biomass models. Although the two indicators are correlated, it is interesting that taxonomic richness is a better predictor of fish biomass, as this is somewhat opposite to the expectation that it should be more the richness of the type of species (i.e. species traits) than their number per se that impact ecosystem functions and productivity (Loreau & Hector, 2001; Tilman et al., 1997). CWM length was also not retained in the final Here, it appears that a combination of functional and taxonomic indicator (functional dispersion and taxonomic richness) is best at explaining the biomass variation.

The biodiversity indicators explained the largest part of the explained variation in biomass, whereas environmental and fishing pressure variables explained comparatively little. Average sea surface temperature and depth were the environmental variables that comparatively affected the most biomass with a negative (≈15%) and positive (≈15%) effect, respectively (Figure 3-29).

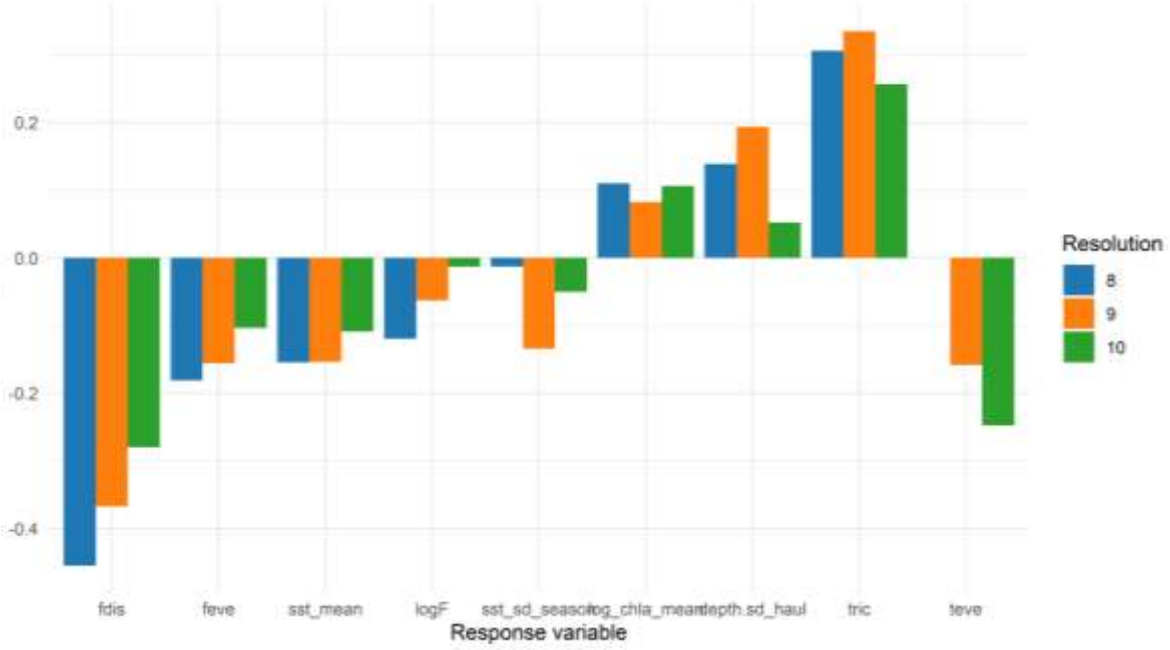


Figure 3-29. Total contribution of the variables included in the final best model explaining the total fish biomass based on the different spatial resolution. CWM length (CWM.Lmax), functional dispersion (fdis), functional evenness (feve), taxonomic evenness (teve), the total biomass (TotBio_log) and taxonomic richness (tric), averaged sea surface temperature (sst_mean), seasonality in sea surface temperature (sst_sd), total fishing effort of demersal gears (logF), averaged chlorophyll concentration (log_chla_mean), and depth variability (depth.sd_haul).

Summary and Conclusions

- Biodiversity indicators explained better the variability in fish biomass than any environmental variables.
- Functional dispersion and taxonomic evenness negatively impacted fish biomass. Functional dispersion had especially a strong effect at large spatial scale, and on its own contributed to 45% of the total variance explained in fish biomass, whereas taxonomic evenness had no effect on biomass at the large scale but an important effect on the local scale (≈25%).

- Taxonomic richness positively impacted fish biomass at all spatial resolutions, whereas functional richness was not retained in the final biomass models.
- A mix of taxonomic and trait-based indicators seem the best at explaining total fish biomass.
- There are some signs that both dominance and niche complementarity processes impact on the biomass in the Northeast Atlantic, with dominance processes being stronger
- The spatial scale at which the community is defined as an impact on which variable is retained in the biomass model and best explains its variability, but overall, no drastic changes are apparent, and the direction of impact remains across the different spatial scales. Sensitivity analysis such as this one are therefore useful to test the robustness of the SEM results.

3.2. Linking community diversity and environmental drivers to total fish biomass in the Barents Sea

Lead contributor: Filippomaria Cassarino (UiT)

Fishes are the most abundant and diverse vertebrates on Earth and remain a vital food source for humanity (Bar-On et al., 2018; Costello et al., 2020; FAO, 2024; Mora et al., 2011). However, unsustainable fishing has caused widespread declines in fish biomass (Durant et al., 2024; Tremblay-Boyer et al., 2011; Watson & Tidd, 2018), while global warming is emerging as another major driver of change (Díaz et al., 2019b). Rising temperatures can affect fish biomass by increasing metabolic demands and decreasing energy transfer efficiency in food webs (Eddy et al., 2021; Gillooly et al., 2001). Arctic areas have been warming nearly four times faster than the global average (Rantanen et al., 2022). Consequent changes in high-latitude fish community biomass have been predicted, but they have not yet been observed (Bryndum-Buchholz et al., 2019; van Denderen et al., 2023). What has been noted is instead the borealization of Arctic communities - the alteration of high-latitude biodiversity linked to the inflow of boreal species and their traits into Arctic assemblages (Husson et al., 2024).

Biodiversity can shape ecosystem process through dominance and richness-related mechanisms, often outweighing the effects of environmental factors (Duffy et al., 2017; Loreau et al., 2001). Since diversity also depends on the environment, studies have attempted to define the relationships shared by biomass, diversity, and environmental factors at once (Danet et al., 2021; Duffy et al., 2016; Maureaud et al., 2019; Woods et al., 2020). This has helped to discern the role of different effects of diversity and the environment on fish community biomass.

To our knowledge, no study has yet jointly defined the links between fish biomass, diversity, and environmental factors in a high-latitude system, where clarifying the biomass-diversity relationship seems a necessary step to fully grasp the potential effects of warming. Here, we examine these links in the Barents Sea, a polar sea located at the interface between the boreal and Arctic regions, featuring rapid warming and community borealization (Fossheim et al., 2015; Gerland et al., 2023). The aim is to identify the main drivers of fish community biomass, discern the role of different facets of fish diversity, and investigate the presence of diversity-

mediated environmental effects. By doing so, this study improves our understanding of the ongoing ecological change and its consequences for ecosystems and humanity alike.

3.2.1. Material and Methods

Study area

The Barents Sea is a shelf sea found between the Norwegian and Russian exclusive economic zones (EEZs). The basin features warm Atlantic water flowing in from the southwest and cold Arctic water from the north and east (Loeng, 1991). The temperature gradient is followed by a biogeographical one, ranging from boreal to Arctic communities (Fossheim et al., 2015). Boreal communities are dominated by larger and more abundant taxa, resulting in high total biomasses, while Arctic ones harbour fewer and generally smaller species (Bernardo et al., 2024; Johannesen et al., 2017; Kortsch et al., 2015). In recent decades, the Barents Sea has experienced pronounced changes in its physical and biological features, with increasing temperatures, decreasing sea-ice, and northward species migrations (Fossheim et al., 2015; Frainer et al., 2017; Gerland et al., 2023; Ingvaldsen et al., 2021). Since the early 2000s, three different warming phases have been identified: an initial colder period (2005–2011), followed by a very warm period (2012–2016), and finally a cooler period (2017–2022) (Eriksen et al., 2025). The area has also long been a major fishing ground, with demersal species usually dominating landings (ICES, 2024a; Nakken, 1998).

Community data

Data on Barents Sea fish communities was obtained from the Barents Sea Ecosystem Survey (Eriksen et al., 2018; Michalsen et al., 2013), which is conducted annually between August and September by Norway and Russia. Sampling followed a fixed grid of stations ~65 km apart, with each country surveying its EEZ while jointly covering a central area of international waters. Fish communities were sampled using a Campelen 1800 bottom trawl equipped with 22 mm cod-end mesh, towed for ~15 minutes at ~3 knots, resulting in a ~1.4 km towing distance. Only the Norwegian share of the data is currently accessible, so this study could only focus on the western half of the Barents Sea. Data was sourced from the FISHGLOB_data dataset (Maureaud et al., 2019) and filtered to focus on shelf communities by excluding hauls deeper than 500 m. To reduce biases from sampling duration, only hauls between 10-20 minutes were retained. The resulting community dataset comprised 106 taxa from 3452 hauls, distributed between 2004–2022, spanning 70–82°N and 8–47°E (~1 million km²).

Taxon-specific abundance was expressed as individuals and biomass per unit area (km²), and total fish biomass as the summed mass of all taxa per unit area. Diversity was measured through richness and evenness metrics to discern the respective roles of complementarity and dominance in shaping fish community biomass (Hillebrand et al., 2008; Loreau et al., 2001). Each of the two diversity dimensions was measured both at the taxonomic and functional level. Taxonomic richness (Tric) was computed as the number of species per haul. Taxonomic evenness (Teve) was instead derived from the equation $E = \log(2D)/\log(S)$, where S is the number of species and 2D is the Hill's number equivalent to Simpson's diversity (Hill, 1973; Jost, 2010). Functional diversity was summarized using functional trait information from Beukhof et al. (2019) to construct a multidimensional trait space to compute richness and evenness metrics. Trait data was explored following Palacio et al. (2022) resulting in the

selection of 9 traits: 3 categorical (feeding mode, body shape, fin shape) and 6 continuous (trophic level, offspring size, fecundity, growth coefficient, maximum length, age at maturity). Then, the data transformations outlined in Mammola et al. (2024) were carried out to enable the inclusion of categorical traits and reduce trait space dimensionality. Lastly, the functional diversity of each haul was modelled in the trait space using probabilistic hypervolumes (Blonder et al., 2014, 2018; Mammola et al., 2021; Mammola & Cardoso, 2020). Two diversity measure were extracted for each haul: functional richness (Fric), the total volume of the hypervolume, and functional evenness (Feve), the overlap between the observed hypervolume and a second, imaginary one where traits and abundances are evenly distributed within their possible range.

Environmental variables

Data on mean monthly sea surface temperature (SST), sea bottom temperature (SBT), sea ice concentration (SIC), and chlorophyll a concentration (Chla) spanning from 2003 to 2022 was compiled from the E.U. Copernicus Marine Service (Global Ocean Physics Reanalysis, https://doi.org/10.48670/moi-00021; Global Ocean Colour, https://doi.org/10.48670/moi-00281). Fishing effort data was instead obtained from GFW (Kroodsma et al., 2018) as monthly sums of trawling hours from 2012 (earliest available year) to 2022. For SIC, SST, SBT, and Chla, the mean and standard deviation values of a year before sampling were computed to capture mean conditions and seasonality (e.g. SBT mean and SBT SD), while fishing effort was converted to the sum of trawling hours of a year before sampling to approach its cumulative impact. The values of the processed environmental layers were extracted at each haul location in space and time using an 8km resolution, which was selected considering the original data resolution and the motility of fish.

Statistical analysis

All relationships were modelled using spatiotemporal generalised linear mixed models to account for spatial and temporal dependencies. Biomass was modelled as a response to environmental variables and diversity, fitting a general model excluding fishing to use the entire available time series of community data, and a shorter time-series to quantify the potential effect of fishing. Additionally, the generality of the relationships found by the general model was assessed by fitting models on data subsets reflecting three different climate periods (as classified by Eriksen et al., 2025) and biogeographical areas. The latter distinction was defined using the quantiles of SBT mean, with the upper 25% of observations classified as boreal and the lower 25% as Arctic. To evaluate sensitivity to dominant species, the ten most abundant ones were sequentially removed from total biomass, fitting a partial biomass model for each new response. A general model and one including fishing were also fitted for all diversity metrics including only environmental predictors.

Prior to modelling, data was investigated following Zuur et al. (2010). Skewed covariates were log-transformed, and all predictors standardised (mean = 0, sd = 1). Collinearity was assessed using Pearson's r and VIF, ensuring the detection of potentially weak ecological signals by adopting conservative values of $r \geq |0.65|$ and $VIF \geq 2$ to drop variables (Zuur et al., 2010). Models were fitted using the sdmTMB package, which enables to efficiently compute complex spatial effects using Gaussian Markov random fields (Anderson et al., 2022). The spatial structure of the data was simplified with a custom triangular mesh, which was built with a

minimum allowed distance between vertices of ~60km, approaching the one between stations. Model selection focused only on random effects to better compare fixed effects across models, assess weakly supported effects, and reduce computation. Each model was fitted with spatial random fields (time-stable spatial correlation), spatiotemporal random fields (time-varying spatial correlation), and spatial and spatiotemporal random fields assuming anisotropy (directionally dependent spatial correlation). Spatiotemporal random fields were estimated both as independent and identically distributed (iid, independent between years) and stationary first-order autoregressive (ar1, dependent between years). The best random structure was selected based on the lowest Akaike information criterion (AIC), considering two models different in quality when showing a ΔAIC > 2. The 95% confidence intervals (CI) of the fixed effects' coefficients were employed to identify effects that significantly differed from 0. Model assumptions were validated using the DHARMa package (Hartig, 2017) following Zuur & Ieno (2016).

3.2.2. Results and discussion

Variables

Total biomass was dominated by few species, with Atlantic cod (*Gadus morhua*) accounting for 31% of total biomass and the first ten species for 90% (Figure 3-30). Data exploration prior to modelling identified several correlated pairs of covariates, which were largely maintained within data subsets. Three exclusions allowed to remove almost all excessive correlations: SST mean was dropped in favour of SBT mean, given the focus on bottom communities, while SIC SD and log chla SD were dropped in favour of their mean counterparts, which are more easily interpretable. This resulted in a shared pool of environmental variables for all models: log fishing effort, Teve, Tric, Feve, Fric, SBT mean, SIC mean, SBT SD, SST SD, log chla mean, and depth. The only exception was the climate period model for 2017-2022, where SIC mean was removed due to a VIF of 2.3.

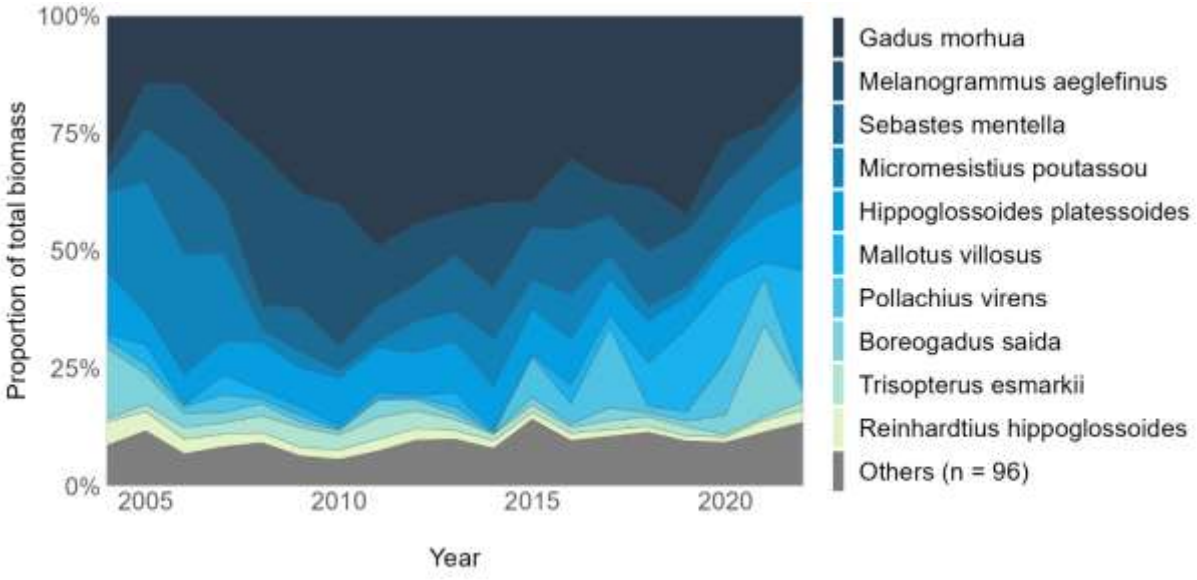


Figure 3-30. Proportion of biomass shared by the ten most dominant species, from the most abundant (top) to the least abundant (bottom), compared to the cumulative biomass of all other 96 species.

Biomass models

All biomass models were fitted with a lognormal distribution. Spatiotemporal random field with ar1 correlation structure were always selected as the best random component, usually with isotropic spatial correlation. Model validation did not reveal patterns indicating the violation of model assumptions.

The general biomass model (Figure 3-31, black) identifies Teve as the main driver of total fish biomass along with SBT mean (slopes of -0.32 and 0.33, respectively). Tric displays instead a minor positive effect (slope = 0.05), while functional diversity metrics have similar but overall weaker effects compared to their taxonomic counterparts (slope of Feve = 0.16; slope of Fric = 0.07). This contradicts the notion that function diversity is better suited to approach ecosystem processes (Petchey & Gaston, 2006; Tilman, 2001). However, this result likely stems from some methodological shortfall, possibly concerning the availability and choice of traits, which can greatly influence resulting metrics (Legras et al., 2020; Ohlert et al., 2024). Notably, evenness metrics display stable dominant effects across biogeographical areas (Figure 3-31– B) and climate periods (Figure 3-31– C), while richness metrics shows a more variable yet always secondary effect. Similar effects of Teve and Tric have also been observed for fish communities at lower latitudes of the Northeast Atlantic (Maureaud et al., 2019), indicating that at various spatial scales over a large area (from the Bay of Biscay to the northern Barents Sea), evenness is a leading driver of total biomass while richness plays a minor role, if any. However, the partial biomass models (Figure 3-31– D) reveal that this hierarchy is sensitive to the inclusion of the most dominant species, because when they are progressively removed, the effect of Teve gradually decreases while the one of Tric rapidly increases. Richness and evenness respectively relate to two distinct mechanisms by which diversity can affect community biomass: niche complementarity and the mass ratio hypothesis. Niche complementarity describes how increasing species and traits can broaden the resources a community is able to exploit, leading to higher biomass (Danet et al., 2021; Duffy et al., 2017; Loreau et al., 2001). The mass ratio hypothesis predicts instead that ecosystem processes are mainly driven by the traits of abundant species, so they are mostly a result of dominance (Grime, 1998; Lisner et al., 2023; Maureaud et al., 2019). In this case, total biomass is mainly determined by dominant species and functions, indicating the prevalence of the mass-ratio hypothesis, while niche complementarity appears to be the main driver of the biomass attributed to the “rare” species assemblage in the community. For total biomass, complementarity effects are likely diluted by some level of independence displayed by the most dominant species. Given the strong relationships shared by total biomass and Teve and “rare” biomass and Tric, changes in diversity patterns are likely to ultimately influence biomass.

The general model also finds SBT mean as the leading positive driver of total biomass. This effect is largely maintained through the climate periods (Figure 3-31– C), but it is lost in boreal areas (Figure 3-31– B). Contrary to Teve and Tric, the effect of SBT mean is largely maintained when removing the most dominant species, hinting at a community-wide benefit in terms of biomass. Generally, higher temperature can result in lower fish biomass due to increasing metabolic costs (van Denderen et al., 2023). However, the Barents Sea lays at the interface with the Arctic, where communities harbour fewer, smaller, and less abundant species, resulting in lower biomasses at lower temperatures (Johannesen et al., 2012). Indeed, the positive effect of SBT mean disappears when excluding the communities found in colder waters (boreal model; Figure 3-31-B), and it has been found to be negative at lower latitudes

of the Northeast Atlantic (Maureaud et al., 2019). In Arctic areas, SBT mean maintains instead a positive effect (Arctic model, Figure 3-31-B), likely reflecting both the borealization process and the current positive effect of temperature on Arctic species (Eriksen et al., 2025; Husson et al., 2024). Consequently, warming may directly support biomass increases in colder areas. However, this relationship may be transitory, given the expected eventual decrease of Arctic fish biomass under increased warming (Gordó-Vilaseca et al., 2024).

The model including fishing effort (Figure 3-31-A) supports a positive effect of this driver on total fish biomass. Fisheries are a major driver of fish biomass by removing it directly (Tremblay-Boyer et al., 2011). This typically translates into a negative relationship between them (Durant et al., 2024). Hence, the positive relationship found here does not describe an effect of fishing on biomass, but rather the opposite, where fishing activities target biomass-rich areas.

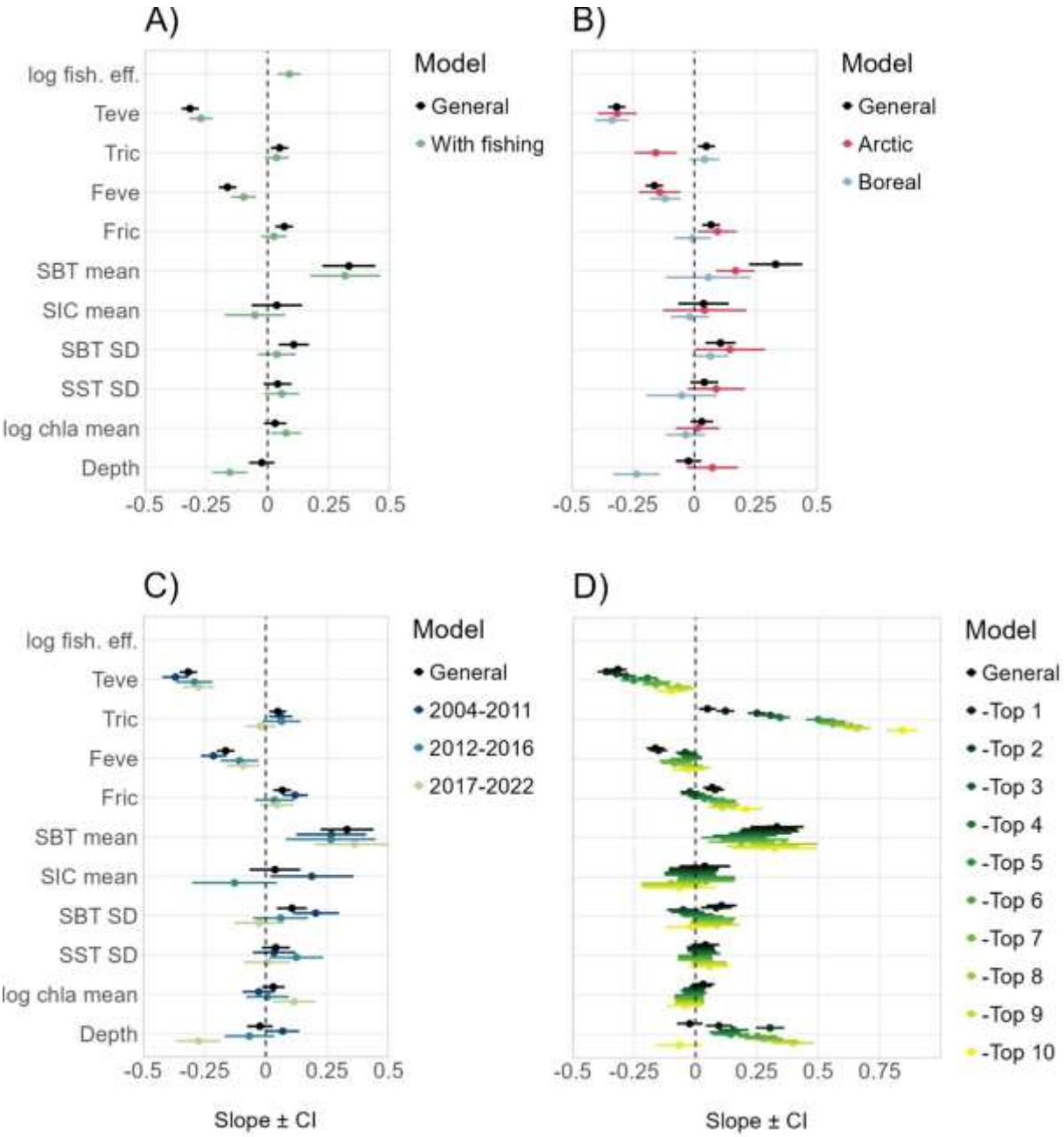


Figure 3-31. Slopes and 95% confidence intervals of the biomass models. Plots compare the general model (black) to the model including fishing (A), the Arctic and Boreal models (B), the climate period models (C), and models where the 10 most abundant species are progressively removed (D).

Diversity models

All diversity models were fitted with a Gaussian distribution. Spatiotemporal random fields with an ar1 correlation structure and isotropy were always supported as the favoured random component. Model validation did not reveal patterns indicating the violation of model assumptions.

The general models identify few relationships with a confidence interval not including 0 (Figure 3-32-A). The strongest one is found between Tric and SBT mean (slope: 0.26). Teve instead shows a weaker negative relationship with SIC mean (slope: -0.09). Fric also shows a positive relationship with SBT mean, but to a lower extent (slope: 0.13), while Feve relates to

SBT SD (slope: -0.09). The positive effect of SBT mean on the number of species and functions supports previous interpretations of diversity distributions and warming effects (Frainer et al., 2017, 2021; Gordó-Vilaseca et al., 2023). Rising temperatures may increase richness, resulting in a positive indirect effect on biomass, especially of non-dominant taxa. Retreating sea ice may instead have a weak negative effect on biomass through Teve.

The models including fishing show no support for an effect of fishing effort on any diversity metric (Figure 3-32-B). Yet, in the Barents Sea, fishing has been involved in commercial species declines and collapses (Hjermann et al., 2004; Nakken, 1998; Olsen et al., 2010). The inability of the present study to detect the expected negative effect of fishing on both biomass and diversity may be attributed to the steady presence of trawling in the Barents Sea for almost 100 years (Nakken, 1998). Communities exposed to stable pressures can undergo a progressive loss of their most sensitive components and appear as more resilient, with fewer fluctuations in structure and function (Polo et al., 2025). Another explanation may lay in the need for a specific time lag or spatial resolution to detect any fishing signal (McKeon et al., 2024).

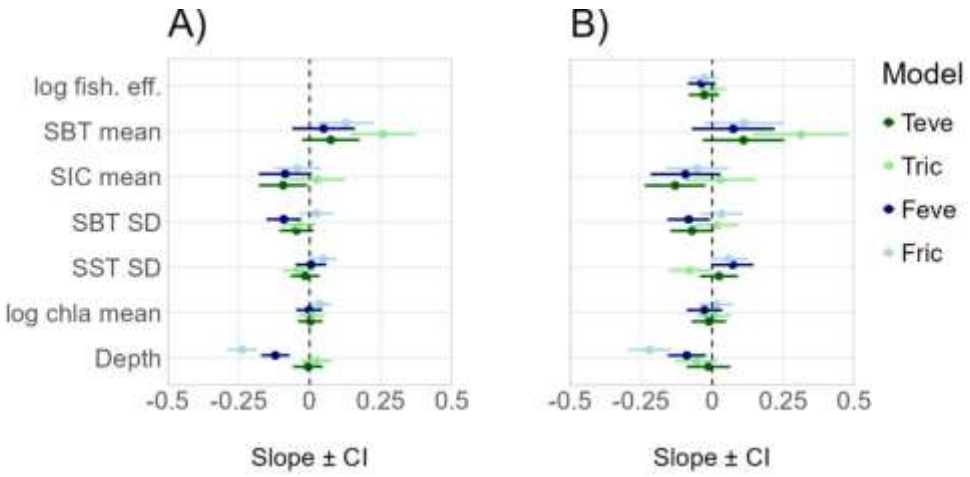


Figure 3-32. Slopes and respective 95% confidence intervals of the general diversity models (A) and the diversity models including fishing (B)

3.2.3. Summary and conclusion

- Barents Sea fish biomass mainly depends on temperature and diversity-mediated processes
- Dominance drives total community biomass, while niche complementarity mainly shapes the cumulative biomass of non-dominant taxa.
- Warming likely leads to an increase in biomass also indirectly through diversity
- No negative effects from fishing were found, possibly due to prolonged exploitation or inappropriate spatial and temporal scales
- Management should expect important shift in fish community biomass in association to warming

3.3. Drivers and stressors of demersal fish biomass across the North Atlantic and Northeast Pacific

Lead contributor: Federico Maioli (DTU-Aqua)

Marine ecosystems are changing due to climate variability and human activities, affecting biodiversity and ecosystem functioning. Fish biomass is a key link to ecosystem services such as food provision, but the processes shaping its large-scale distribution are still not well resolved. Most existing studies focus on population-level dynamics or rely on spatially aggregated data, limiting inference on how community-level biomass patterns emerge across environmental gradients (e.g., van Denderen et al., 2023). In particular, the relative roles of baseline ecological drivers (e.g., depth, temperature, productivity) versus stressors (e.g., fishing, climate variability) remain difficult to disentangle.

Here, we analyze demersal fish biomass across the North Atlantic and Northeast Pacific, which together account for approximately 15% of global fisheries catch (Watson, 2017). Using high-resolution bottom-trawl survey data linked to environmental and anthropogenic variables, we assess how biodiversity-related biomass patterns relate to ecosystem functioning across large spatial scales.

Specifically, we address two questions:

(i) Can ecological drivers and stressors be detected as significant influences on fish biomass using high-resolution spatiotemporal models?

(ii) Do these effects differ between regions?

3.3.1. Materials and Methods

Spatiotemporal extent of the analysis

Our analysis focuses on the continental shelf seas of the Northeast Pacific, Northeast Atlantic and West Atlantic (Figure 3-33). Although fish biomass data span several decades, we limited our study to the period from 1997 to 2020 (up to 2019 for the Northeast Pacific) to align with the availability of environmental covariates and ensure consistency in survey standardization.

Fish data

Demersal fish biomass data were obtained from FISHGLOB (Maureaud et al., 2024), a comprehensive collection of scientific bottom-trawl surveys spanning pronounced latitudinal gradients (Figure 3-33).

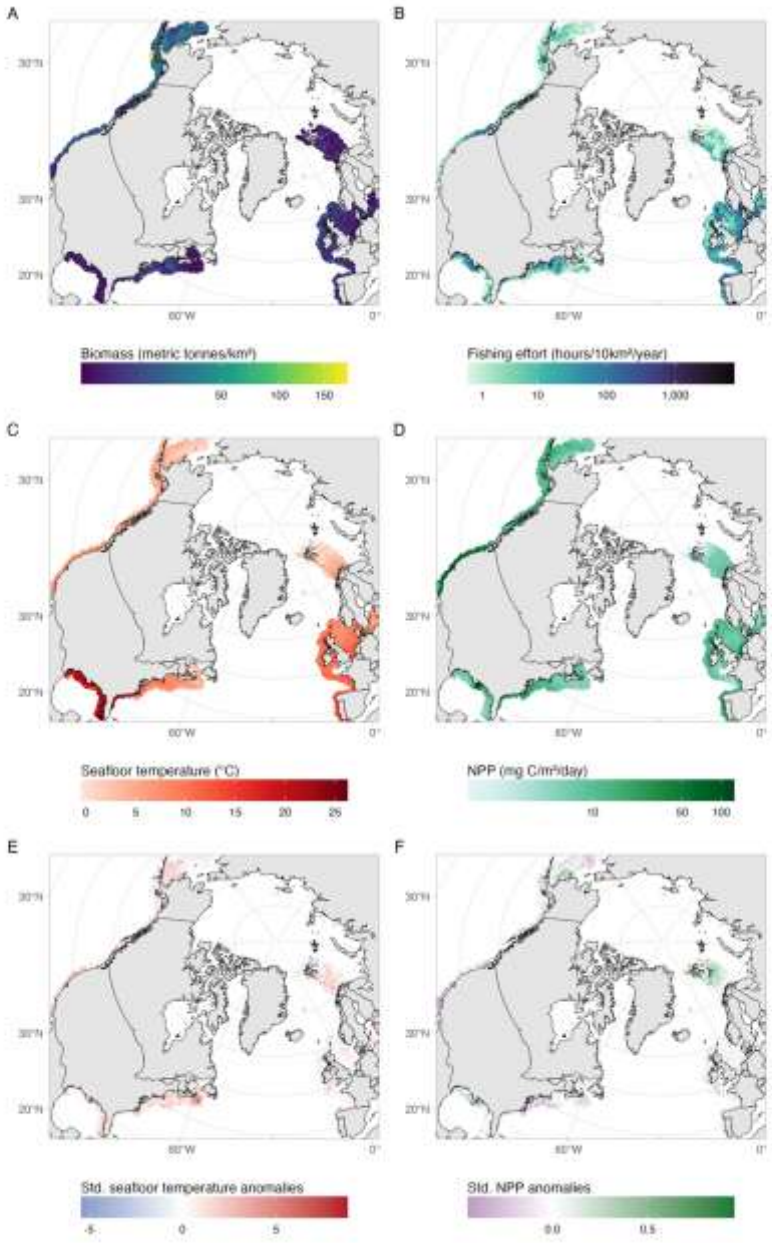


Figure 3-33. Study regions and variables in 2015. Legends in panels B and D use transformed scales to enhance spatial contrast.

Environmental drivers and stressors data

Environmental data were obtained from the E.U. Copernicus Marine Service Information. Monthly sea water potential temperature at sea floor data, with a horizontal resolution of 0.083° × 0.083°. These data were sourced from the Global Ocean Physics Reanalysis available at https://doi.org/10.48670/moi-00021.

Monthly net primary production (NPP) data at a 0.25° × 0.25° resolution were obtained from the Global Ocean Biogeochemistry Hindcast dataset (https://doi.org/10.48670/moi-00019). Additionally, higher-resolution NPP data (4 km) were sourced from the Copernicus-GlobColour Global Ocean Colour dataset (Bio-Geo-Chemical, L4, monthly and interpolated), based on satellite observations from 1997 to the present (https://doi.org/10.48670/moi-00281).

Fishing effort data were obtained from GFW. These data are derived from the positions of vessels equipped with automatic identification system (AIS) transponders, with up to ~96,000 active each year globally. Vessel identification is conducted using a combination of machine learning models, vessel registry databases, and expert manual review. Fishing effort is measured in hours, calculated by assigning each AIS position the time elapsed since the vessel's previous AIS position. A neural network-based fishing detection model determines whether the vessel was engaged in fishing activity at each recorded position. Monthly fishing effort data are aggregated into grid cells of 0.01° latitude × longitude. Since GFW data do not distinguish between pelagic and bottom trawling, we used a global fishing effort dataset (Rousseau et al., 2022) to estimate the proportion of bottom-to-pelagic trawling per EEZ and adjusted the fishing effort per cell by multiplying effort by this proportion.

To characterize large-scale environmental conditions and anthropogenic pressures influencing fish biomass, we aggregated seafloor temperature, net primary productivity (NPP), and fishing effort data at broader spatial and temporal scales than their native resolutions. Specifically, we resampled sea temperature and NPP to a spatial resolution of 0.5° × 0.5°, averaging values over the period 2000–2010. This time window captures long-term environmental variability and is centered within the overall time span of the biomass observations.

Similarly, we quantified fishing pressure by resampling global fishing effort data to a resolution of 0.5° × 0.5° aiming to smooth the high spatial heterogeneity. Fishing effort was normalized to hours per 10 km² by adjusting for cell area and averaged over the period 2016–2024 to reflect the improved reliability and coverage of AIS-based vessel tracking data in recent years.

To capture local-scale environmental stressors, we quantified anomalies in seafloor temperature and net primary production (NPP). For seafloor temperature, we calculated standardized anomalies by expressing seasonal deviations—defined as the difference between the observed temperature in a given season and the long-term seasonal average (2000–2010)—relative to the standard deviation of intraseasonal variability during the same baseline period (Williams et al., 2007). This approach identifies periods when bottom temperature conditions depart substantially from expected seasonal norms, thereby representing potential thermal stress for demersal fish communities.

We applied a similar approach to NPP, though limited to the summer season (Q3), as this period is most representative of peak biological productivity. To align trawl timing with ecologically relevant productivity signals we used the Q3 NPP value from the same year for biomass observation collected in Q3 or Q4, and the Q3 value from the previous year for observations outside these quarters. This ensures that the anomaly reflects productivity available to fuel food web prior to or during the survey period.

Anomalies were computed at the native resolutions of 0.083° × 0.083° for seafloor temperature and 4 km for NPP. These anomalies thus provide a measure of ecological stressors capturing short term departures from background conditions that may influence fish biomass distribution.

Statistical modelling

To evaluate the effects of environmental and anthropogenic drivers on fish biomass, we employed spatiotemporal generalized linear mixed models (GLMMs) using the Stochastic Partial Differential Equation (SPDE) approach (Lindgren et al., 2011). We tested 16 candidate model structures per region, varying key covariates and their forms (Table 3-8). Model selection was based on the Akaike information criterion (AIC), with the most parsimonious model chosen for each region. When multiple models were within 10 AIC units, we selected the final model by evaluating the realism of covariate responses and associated uncertainties.

Table 3-8. Overview of the fitted generalized linear mixed models (GLMMs) with different specifications of depth (raw or log-transformed), primary productivity (log(NPP) or using a breakpoint function breakpt()), and the inclusion or exclusion of bottom temperature and NPP anomalies. It also indicates whether a first-order interaction between depth and bottom temperature is included. Fishing effort, seafloor temperature, and the random effects (Year, Survey, Month) are always included and therefore not reported. The 'Region' column indicates the region in which a model was selected as the best-fitting GLMM.

Model	Depth Variable	Productivity Term	Seafloor Temp Anomaly	NPP Anomaly	Seafloor Temp × Depth Interaction	Region
logdepth_pp_anomaly	log(Depth)	log(NPP)	Yes	Yes	No	
logdepth_breakpt_anomaly	log(Depth)	breakpt(log(NPP))	Yes	Yes	No	
logdepth_pp_noanomaly	log(Depth)	log(NPP)	No	No	No	
logdepth_breakpt_noanomaly	log(Depth)	breakpt(log(NPP))	No	No	No	
depth_pp_anomaly	Depth	log(NPP)	Yes	Yes	No	
depth_breakpt_anomaly	Depth	breakpt(log(NPP))	Yes	Yes	No	
depth_pp_noanomaly	Depth	log(NPP)	No	No	No	
depth_breakpt_noanomaly	Depth	breakpt(log(NPP))	No	No	No	
logdepth_interact_pp_anomaly	log(Depth)	log(NPP)	Yes	Yes	Yes	East Pacific
logdepth_interact_breakpt_anomaly	log(Depth)	breakpt(log(NPP))	Yes	Yes	Yes	NE Atlantic
logdepth_interact_pp_noanomaly	log(Depth)	log(NPP)	No	No	Yes	
logdepth_interact_breakpt_noanomaly	log(Depth)	breakpt(log(NPP))	No	No	Yes	
depth_interact_pp_anomaly	Depth	log(NPP)	Yes	Yes	Yes	West Atlantic
depth_interact_breakpt_anomaly	Depth	breakpt(log(NPP))	Yes	Yes	Yes	
temp_depth_interact_pp_noanomaly	Depth	log(NPP)	No	No	Yes	
depth_interact_breakpt_noanomaly	Depth	breakpt(log(NPP))	No	No	Yes	

All models included seafloor temperature, depth, net primary production (NPP), and fishing effort as fixed effects, alongside random intercepts for year, survey, and month (except in the East Pacific, where month was excluded due to data structure).

Depth was always included as a second-degree polynomial, either in its original or log-transformed form, to account for potential nonlinear and scale-dependent relationships. NPP was modeled linearly or using a breakpoint function to capture potential nonlinear threshold effects (Table 1). A breakpoint function consists of two pieces. For values of x less than b_1, the function grows linearly with a slope of b_0, meaning that the output increases proportionally with x. Once x reaches b_1 or higher, the function stops increasing and stays constant at the value $b_1 \cdot b_0$. In other words, b_0 controls how steeply the function rises before the threshold, and $b_1 \cdot b_0$ is the level it flattens out to after the threshold. There are no restrictions on the values of b_0 or b_1, allowing the model to flexibly capture both gradual and abrupt threshold-like responses in NPP.

We further tested the inclusion of quarterly seafloor temperature anomalies and Q3 NPP anomalies to account for deviations from long-term seasonal trends. Additionally, we incorporated a first-order interaction between temperature and depth in a subset of models to examine whether thermal effects varied with depth. Fishing effort was included as a linear term in all models. Prior to analysis, all covariates were normalized by subtracting their mean and dividing by their standard deviation.

This approach enabled a structured comparison of alternative ecological hypotheses while accounting for spatial structure via a spatial random field and, when applicable, a spatially varying coefficient for seafloor temperature and NPP anomalies.

All the models can generically be written as:

$$y_{s,t} \sim N(\mu_{s,t}, \sigma^2)$$

$$\mu_{s,t} = X_{s,t}^{main} * \beta + \alpha_g + X_{s,t}^{svc} * \zeta_s + \omega_s$$

Where:

- $y_{s,t}$ is the response variable (fish biomass) at location s and time t
- $\mu_{s,t}$ is the expected value (mean)
- $X_{s,t}^{main}$ are the main fixed effects
- β is the vector of fixed-effect coefficients
- α_g is a group-level random intercept $\left(\alpha_g \sim N(0, \sigma_\alpha^2)\right)$
- $X_{s,t}^{svc} * \zeta_s$ are spatially varying coefficients $\left(\zeta_s \sim MVN(0, \Sigma_\zeta)\right)$
- ω_s is the spatial random field $\left(\omega_s \sim MVN(0, \Sigma_\omega)\right)$

For instance, the model "depth_pp_noanomaly" in Table 1 corresponds to the following fitted GLMM:

$$log(\text{Biomass}) = \beta_0 + \beta_2\,\text{Depth} + \beta_3\,\text{Depth}^2 + \beta_4 log(NPP) + \beta_5 Seafloor\ temperature + \beta_6 Fishing + \alpha_{Year} + \alpha_{Survey} + \alpha_{Month} + \omega_s$$

We fit the models using R Statistical Software (R Core Team, 2021) version 4.3.3 using the package sdmTMB (Anderson et al., 2024) version 0.6.0.9004. We evaluated model convergence by confirming that the Hessian matrix was positive definite, and the maximum absolute log-likelihood gradient with respect to fixed effects was < 0.001.

3.3.2. Results and Discussion

Fish biomass across all regions was structured by depth, temperature, and primary production (NPP), with additional variation associated with fishing effort and environmental anomalies.

Depth showed the most consistent relationship with biomass. Although model selection differed, favoring log-transformed depth in the East Pacific and Northeast Atlantic and raw depth in the West Atlantic (Figure 3-34), both formulations produced similar patterns. Biomass peaked at intermediate depths (~100–300 m) across all regions (Figure 3-35), consistent with a depth range where environmental conditions and resource availability support higher biomass.

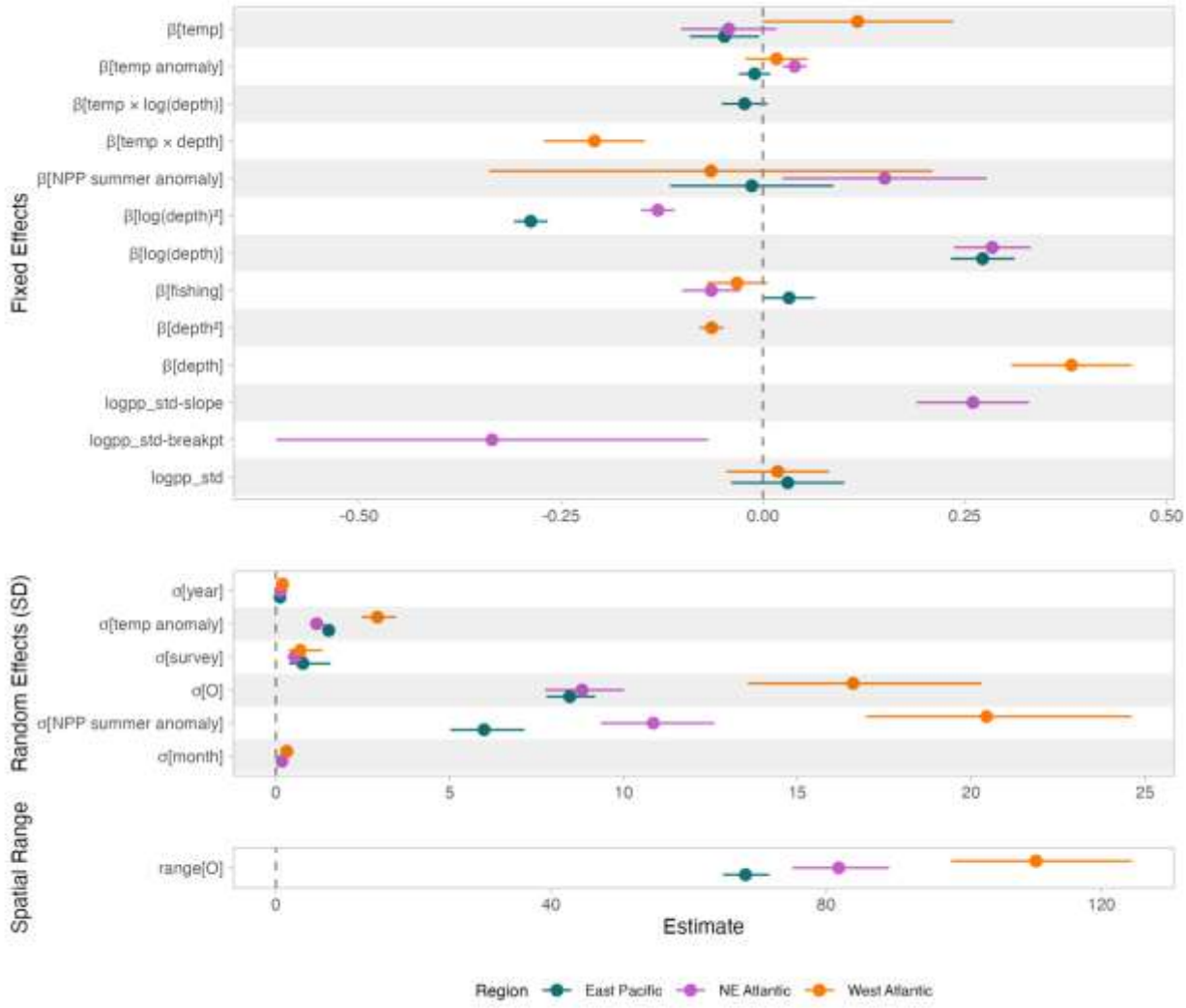


Figure 3-34. Estimated parameters from the best-fitting models fitted to demersal fish biomass across regions. Points represent mean estimates, with horizontal lines indicating 95% confidence intervals. The range parameter is expressed in km, while all other parameters are presented as standardized effect sizes.

The effect of seafloor temperature varied among regions and depended on depth. Temperature was positively associated with biomass in the West Atlantic and negatively associated in the East Pacific and Northeast Atlantic, although uncertainty was high in the latter (Figure 3-34). Interaction terms between temperature and depth were retained in two regions, indicating non-uniform effects along the bathymetric gradient. In the West Atlantic, temperature effects were positive in shallow waters and negative at greater depths, whereas in the East Pacific negative effects intensified with depth (Figure 3-35). These patterns are not consistent with a single directional response to warming and instead point to depth-mediated responses that vary across systems.

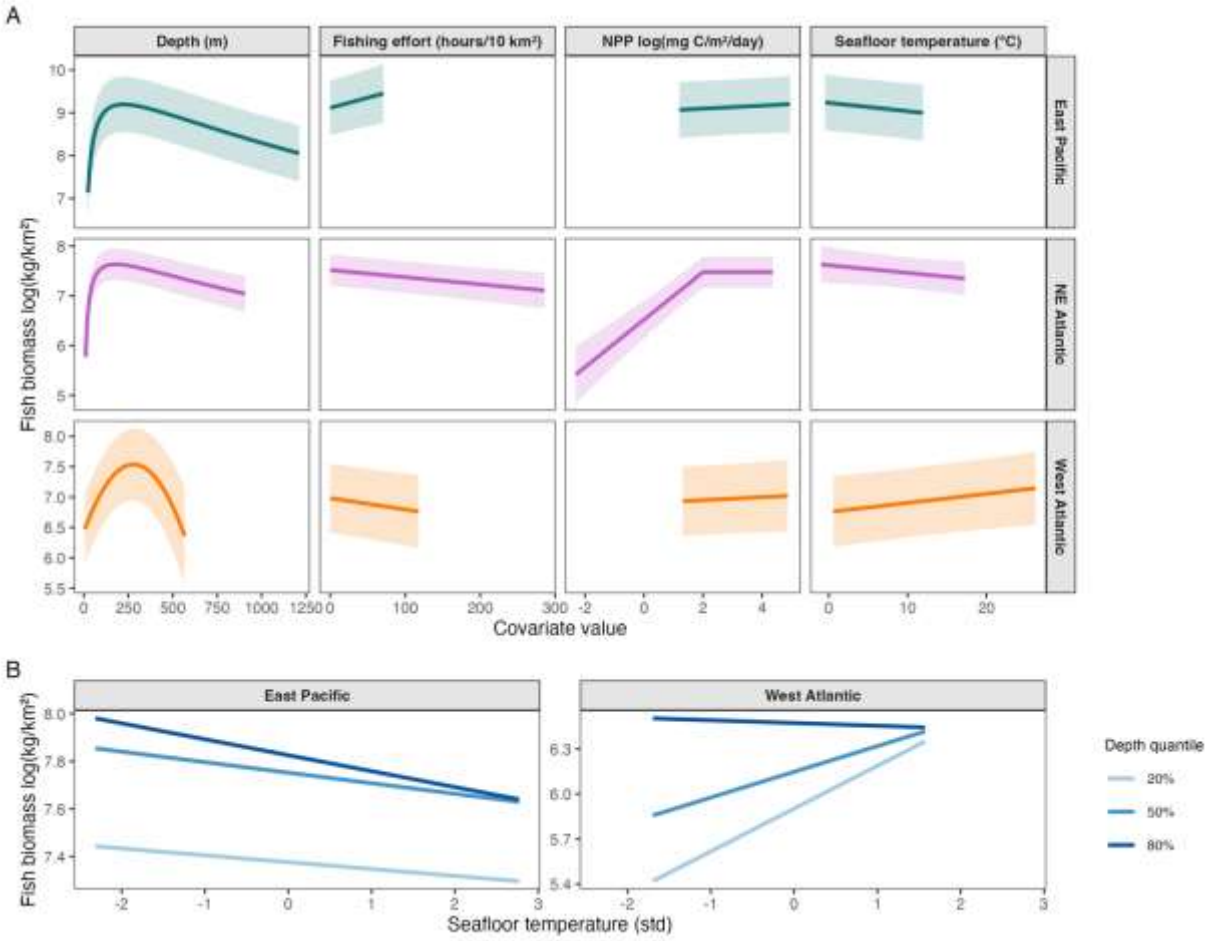


Figure 3-35. Effects of covariates on demersal fish biomass, as estimated by spatiotemporal models. (A) Partial effects across regions. (B) Interaction effects between depth and seafloor temperature. Lines indicate mean predictions; shaded ribbons represent 80% confidence intervals.

Responses to NPP were generally positive but weak. In the Northeast Atlantic and East Pacific, nonlinear relationships were supported, with biomass increasing at low NPP and plateauing at higher values. Due to uncertainty in the East Pacific threshold, a linear formulation was retained with comparable support (within 10 AIC units). In the Northeast Atlantic, the threshold occurred at relatively low productivity (~7 mgC/m³/day), with a steep increase below this level (Figure 3-35), suggesting stronger biomass limitation at low productivity. In contrast, NPP effects in the West Atlantic and East Pacific were weak and uncertain (Figure 3-35), consistent with already productive shelf systems where NPP may not be a primary limiting factor.

Fishing effort showed region-specific associations with biomass. Negative relationships in the Northeast Atlantic and, to a lesser extent, the West Atlantic align with patterns expected under sustained exploitation. The positive association observed in the East Pacific (Figure 3-34) likely reflects spatial concentration of effort in areas of higher biomass rather than a direct positive effect of fishing.

Environmental anomalies in temperature and NPP were retained in all models. While average effects were small, spatially varying coefficients revealed pronounced regional responses. Positive associations between temperature anomalies and biomass were observed in the

Bering Sea, southern Baltic Sea, and Northeast U.S. Shelf (Figure 3-36), alongside positive responses to summer NPP anomalies in the Bering Sea and Northeast U.S. Shelf. In contrast, negative associations were identified in the eastern Gulf of Mexico and on the Scotian Shelf, where deviations from baseline conditions coincided with reduced biomass. These patterns indicate that short-term environmental variability contributes to spatially heterogeneous responses that are not captured by mean conditions alone.

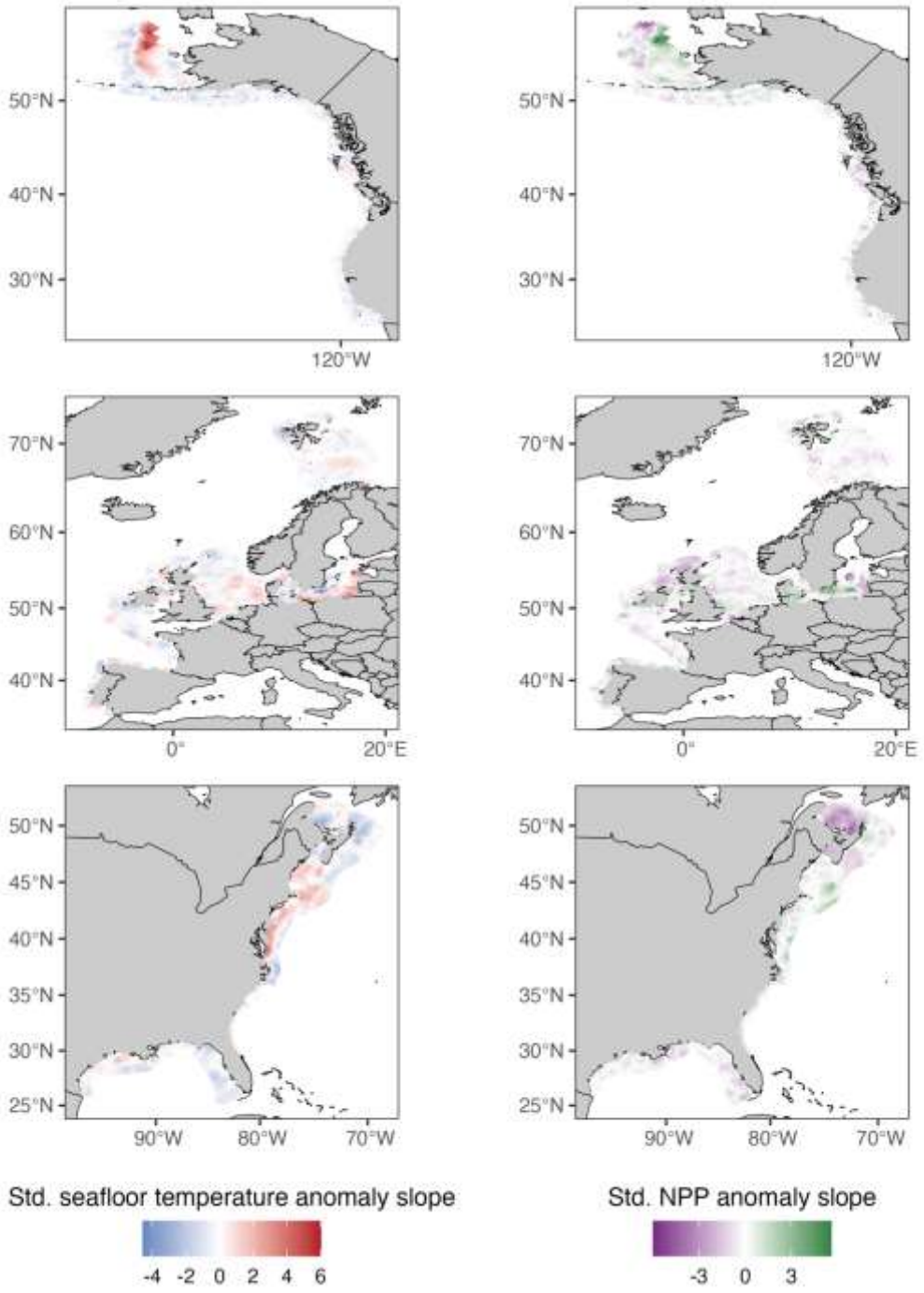


Figure 3-36. Standardized spatially varying random slopes by region. Left: slope of seafloor temperature anomalies. Right: slope of net primary production (NPP) anomalies. All fields are standardized (mean = 0, SD = 1) to enhance visual comparability across regions.

The spatial random field accounted for the largest share of variance across all regions, exceeding survey, interannual, and seasonal components. This highlights the importance of spatially structured processes not explicitly included in the models, such as habitat heterogeneity or species interactions. The spatial correlation range was similar across regions (70–130 km), suggesting a consistent scale of biomass organization across continental shelf systems.

3.3.3. Summary and Conclusions

- Fish biomass is mainly driven by depth, temperature, and productivity.
- Biomass peaks at intermediate depths (100–300 m) across all regions.
- Temperature and productivity effects vary between regions.
- Fishing and environmental anomalies modify biomass patterns, but not consistently.
- Spatial structure explains a large share of variation, indicating missing drivers.
- Management: Effects of fishing and climate are region-specific, so uniform management approaches are unlikely to work.

3.4. Demersal fish biomass declines with temperature across productive shelf seas

Lead contributor: Daniel van Denderen (DTU-Aqua)

Marine fish community biomass is shaped by environmental conditions, resource productivity, trophic interactions and human pressures. This study examined how these drivers influence demersal fish community biomass across 21 productive continental shelf regions in the North Atlantic and Northeast Pacific. Specifically, we assessed responses of demersal fish biomass to spatial and temporal variation in temperature by analysing large-scale patterns in community biomass. The overarching objective was to test the hypothesis that fish community biomass declines with increasing temperature, driven by higher metabolic turnover rates and temperature-induced reductions in trophic transfer efficiency. Specifically, the research aimed to:

- Quantify the cross-regional relationships among temperature, primary production, fishing pressure, and demersal fish biomass.
- Determine whether temperature mediates the link between net primary production (NPP) and demersal fish biomass.
- Evaluate whether recent warming (1980–2015) has resulted in detectable biomass changes within regions.

3.4.1. Materials and Methods

Study Areas and Environmental Context

The study covered 21 continental shelf regions spanning the North Atlantic and Northeast Pacific, encompassing broad gradients in temperature and fishing pressure. These marine shelf systems are characterized by high primary production and support diverse demersal fish assemblages, comprising both teleosts and elasmobranch species. Ambient temperatures

varied substantially among regions, allowing investigation of temperature–biomass relationships at a macroecological scale.

Taxa and Variables Analysed

We compiled high-resolution bottom trawl survey data of fish biomass containing 166,000 unique tows and corrected biomass for differences in sampling area and trawl gear catchability. We examined whether relationships between net primary production and demersal fish community biomass are mediated by temperature, food-web structure and the level of fishing exploitation, as well as the choice of spatial scale of the analysis.

The analysis focused on demersal fish communities, including all species consistently sampled in bottom trawl surveys. The response variable was total biomass in tonnes per km^2. Variables examined included: bottom temperature, net primary production, zooplankton production, detrital flux to the seafloor, community weighted trophic level, and fishing exploitation levels (estimated as catch/biomass).

Analytical Approach

The analysis proceeded in two steps:

1. Cross-regional analysis: Relationships between demersal fish biomass, temperature, productivity, fishing pressure, and food-web structure were quantified using a structural equation model that allowed testing whether temperature mediates the NPP–biomass relationship. In addition, a trophodynamic model incorporating temperature-dependent trophic efficiency was evaluated as an explanatory mechanism.
2. Temporal (within-region) analysis: Time-series models assessed whether biomass within each region changed with temperature over the 35-year study period. The goal was to determine whether recent temperature changes produced detectable in-situ biomass changes.

3.4.2. Results and Discussion

Cross-regional biomass patterns

Demersal fish biomass varied 40-fold among regions. Biomass was consistently highest in colder shelf seas and in regions experiencing low fishing exploitation, such as the Northeast Pacific regions (Figure 3-37).

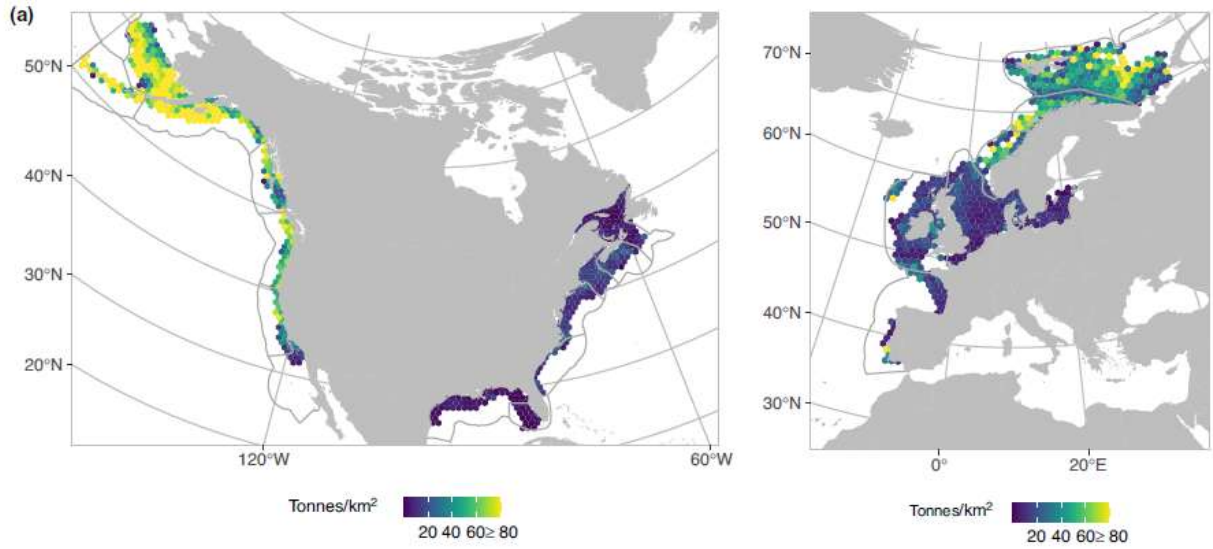


Figure 3-37. Map of mean demersal fish biomass per grid cell (6000 km2) in 1990–2015.

Temperature and fishing exploitation emerged as the primary drivers of the cross-regional differences in fish community biomass (Figure 3-38 and Figure 3-39). NPP mediated zooplankton production, which was positively associated with biomass. The effect of zooplankton production on biomass was relatively small. This weak effect is likely since all studied shelf systems have moderate to high productivity and productivity varies less than a factor 4. It is thus expected that prey production could become more important for predicting changes in demersal fish biomass along a broader productivity gradient (e.g. from shelf to open ocean).

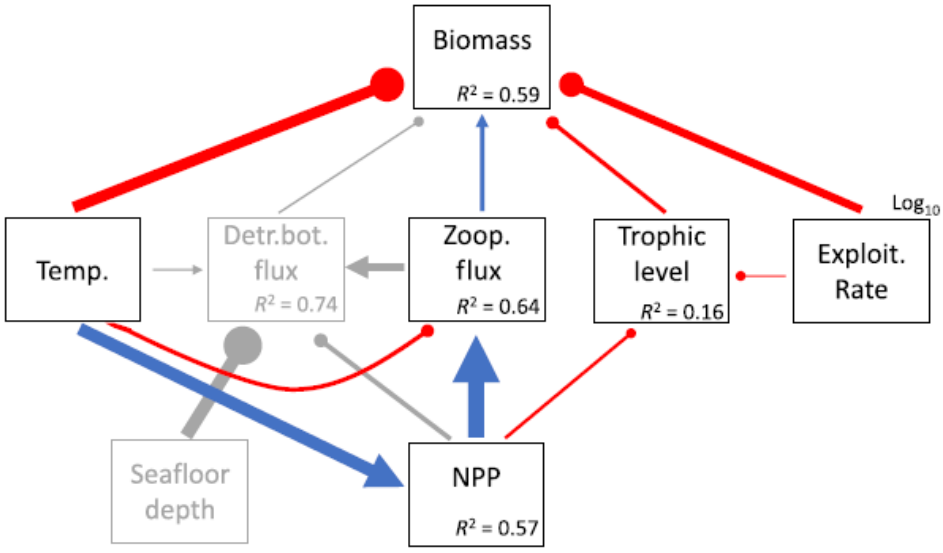


Figure 3-38. Final structural equation model with the direct and indirect effects of predictors on demersal fish biomass. The colour and thickness of the arrows shows the sign (blue arrow = positive, red oval = negative). The coefficient of determination (R2) is indicated for each response variable. The grey predictor variables and pathways are not included in the final SEM as they were not important for explaining fish biomass.

Average trophic level had a weak effect on biomass, suggesting that communities with larger abundance of predators, corrected for temperature and NPP, have less total community biomass due to loss of energy each trophic transfer (Figure 3-38 and Figure 3-39).

A trophodynamic model incorporating temperature-dependent trophic efficiency best captured the observed biomass distributions, supporting the idea that metabolic costs increasingly limit biomass at higher temperatures.

Temporal Trends Within Regions

Despite clear spatial effects, we found no evidence that recent warming (1980–2015) caused detectable biomass declines within individual marine regions. Temperature and fisheries catch fluctuate in time and fish populations may have lagged responses to both. We expect that the observed variations in temperature were too small to reveal a signal on total community biomass.

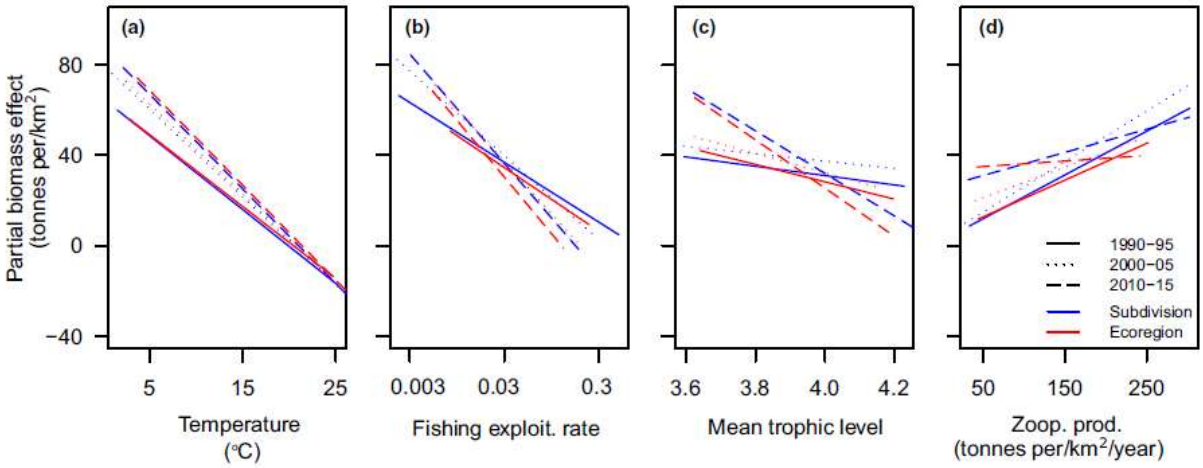


Figure 3-39. Partial effect of temperature (a), exploitation rate (b), mean trophic level (c) and zooplankton production (d) on demersal fish biomass as estimated from the SEM (Figure 2). The plots show the change in demersal fish biomass along the range of each predictor while keeping the other variables fixed at their mean values. The lines represent different spatial scales and time periods.

3.4.3. Summary and Conclusions

- Biomass varies 40-fold across regions, reflecting combined influences of temperature, prey productivity, and fishing pressure.
- Temperature is a dominant driver of large-scale variation in demersal fish biomass in shelf ecosystem with warm regions supporting substantially less biomass due to reduced trophic efficiency and higher turnover rates of biomass.
- No significant temperature-driven biomass trends were detected within regions (1980–2015), likely since the observed variations in temperature were too small to reveal a signal.
- Fisheries and ecosystem management should account for expected long-term biomass declines under continued warming. Our empirical findings can serve as an independent dataset to validate historic biomass estimates of process-based ecosystem models to improve projections of biomass change in the future.

3.5. Synthesis on the drivers of fish biomass in European Seas

In this chapter, we investigated the main drivers of fish biomass across ecoregions and scales using both similar methodology (e.g. SEMs) as well as other methods and design (e.g. large scale, GLMMs). Below, we synthesise the results of the different studies (Table 3-9) based on the questions we aimed to answer.

Table 3-9 Summary of the overall effect of the different biodiversity indicators and environmental variables on total fish biomass across the various case study. The top 8 case-study are based on similar method and framework, whereas the bottom 3 studies use different design and methods. The colours blue and red represent positive and negative relationships with biomass, respectively, whereas the colour shade represent how strong the relationship was (semi-qualitative based on the total effects of the variable). NS means the variable did not clearly impact fish biomass, shaded areas means that the variable was not included in the analysis. N= North, E= East, NEA= North-East Atlantic, Atl= Atlantic, Pac= Pacific, Medit= Mediterranean Sea, SEM = Structural equation model, GLMMs = generalized linear mixed models, SSF=small-scale fisheries, OTB=bottom trawlers.

Case study	Tric	Fric	Teve	Fdis	Feve	CWM.L	SST	SBT	SST.sd	SBT.sd	Depth	Chla	Fishing
North Sea SEM													
Celtic and BoB SEM										NS			
Barents Sea SEM						NS							
Medit-SEM N.Med Spain													NS (SSF +) (OTB -)
Medit-SEM Gulf of Lion		NS			NS	NS							
Medit-SEM Adriatic Sea													
Medit-SEM Aegan Sea					NS								
NEA SEM		NS				NS					NS		
Barents Sea GLMMs													
N.Atl and NE.Pac SEM								in NEA			∩		in NEA
N.Atl and NE.Pac GLMMs											NS		

(i) What are the main drivers of fish community biomass in European Seas?

Across the studies, we analyzed multiple type of drivers on fish biomass, including environmental variables, fishing effort and biodiversity indicators. Summarizing the main effect and direction of the different drivers on fish biomass across these various studies can give a robust understanding of the main drivers (Table 3-9). First, in the SEM studies that integrated both biodiversity and abiotic variables as explanatory variables of the fish biomass, it appears that biodiversity indicators had a strongest total effect on fish biomass than the environment or fishing (Table 3-9). From the biodiversity indicators, there is an agreement across the different case-studies that taxonomic evenness has a negative impact on fish biomass, whereas taxonomic richness has a positive impact. Functional evenness has generally a negative impact, but less clear, and taxonomic evenness has a contrasting impact between the north-east Atlantic and north Mediterranean case-studies (although this might be due to different methods used between the two areas). CWM length has no clear directional effect on fish biomass, and when it has it is comparatively weaker. From this cross-

studies comparison, we can thus conclude that: **evenness has a negative impact on fish biomass whereas richness has a positive impact**. This result reflects the interplay between dominance and complementarity mechanisms in biodiversity-ecosystem productivity relationships. While increased species richness enhances resource use complementarity and overall productivity (Loreau & Hector, 2001; Tilman et al., 1997), dominance effects, as indicated by the negative relationship with evenness, suggest that biomass is often concentrated in a few highly productive species (Maureaud et al., 2019). These dominant species likely drive ecosystem productivity in exploited systems, where community composition is shaped by selective pressures favoring commercially valuable or ecologically efficient taxa.

The environmental variables and fishing effort were not consistently assessed across all studies, but some patterns do emerge from the comparisons (Table 3-9). Primary productivity, included in all studies, is positively linked to fish biomass in all case studies but one, and although often with a low effect. Primary productivity most likely have an indirect effect on fish biomass (van Denderen et al., 2023), and influence total fish biomass through food web cascading effects (Chassot et al., 2010; Friedland et al., 2012). The weak negative effect found in the Barents Sea is probably due to primary productivity being highly seasonal in this high-latitude ecosystem, making annual average less relevant, as well as problematic measure of satellite-based chlorophyll a data due to ice and cloud cover in the area. Depth had a negative effect on fish biomass in most case-study but was weakly positive in the North Sea and hump-shaped at large spatial scale (Northeast Atlantic). The differences in direction across the case-studies might be due to the depth range included in each case-studies, with depth potentially peaking at intermediate depths but being lower at shallow or very deep areas, which for most coastal shelves included in the SEM comparative case-studies, as the very shallow areas were excluded might result to the observed negative relationship. Sea bottom temperature had contrasting effects across the different case-studies, it had a weak positive effect in the north Mediterranean, Barents Sea, Celtic Sea and Bay of Biscay case-studies, whereas it had a negative effect on biomass in the North Sea and at large scale (e.g. North-east Atlantic). Warmer temperatures accelerate physiological rates, such as consumption and metabolism, leading to higher biomass turnover rates (Brown et al., 2004), due to that colder environments are hypothesized to support higher fish community biomass due to lower turnover rates and more efficient energy transfer (van Denderen et al. 2023). Seasonality in temperature, when included in the studies, generally appears to have a negative effect on fish biomass, apart from the Barents Sea where it had a negative impact. Fishing shows contrasting effects on fish biomass across the study, at large spatial scale (e.g. Northeast Atlantic and Mediterranean Sea) it has a weak negative effect on fish biomass, whereas it had weak negative effects at more regional scales (e.g. Barents Sea), or based on different metrics (small scale fisheries in Mediterranean Sea). Fishing impact on fish communities and biomass might be more apparent at larger observational scales than local scales (e.g. McKeon et al. 2024), and at local scales positive relationship might be arising from an effect of “attraction” of fishing vessels to productive fishing grounds rather than causal relationship. We can thus conclude that: **primary productivity was a weak but positive effect, whereas depth has a generally weak negative impact on fish biomass** (if shallow/coastal areas are excluded)**. Sea surface and bottom temperature effects are region-specific.**

(ii) Are the taxonomic or the trait-based indicators best at explaining the variation in the biomass?

In the comparative SEM studies, taxonomic richness consistently had a stronger (positive) effect on biomass than functional richness, at the exception of the Barents Sea (Table 3-9). This result is surprising, as based on ecological theory, we would expect that it is more the trait richness that impact ecosystem functions, and thus productivity rather than taxonomic richness . This can point out to methodological problems, such as the functional richness calculation not adequately representing the richness in terms of traits due to e.g. the selection of traits. But, it can also point out that high trait diversity does not necessarily lead to high biomass but that instead species-rich communities, simply through the sampling effect, will be likely to be composed of productive species. Similarly, taxonomic evenness had a stronger negative relationship with fish biomass than functional evenness across all case study. This signals that it is not especially the trait characteristic of the dominant species, but whether there is a dominant species in the community, that impact fish biomass. However, when using functional dispersion instead of functional evenness, strong negative relationship with fish biomass were also apparent, pointing out that functional evenness is maybe not the optimal "trait-based" indicator that would be equivalent to taxonomic evenness. This also highlights a common problem with functional indicators compare to taxonomic indicator: their calculation and interpretation is often not straightforward. In conclusion, **functional diversity indicators do not appear to be better than taxonomic indicators at predicting fish biomass**, here we found rather the opposite, **there is actually indications that taxonomic indicators are better at predicting fish biomass**.

(iii) Is there some variation in the diversity-biomass relationships between European regional seas?

Taxonomic richness and taxonomic evenness relationship with biomass were consistent across the different case-studies (Table 3-9). This was also the case for functional dispersion and functional evenness, at the exception of some non-significant relationship. For functional richness, opposite direction was observed for the Mediterranean and Atlantic case-studies, but this might be due to differing methodology. In the Mediterranean Sea case study, it was discussed that the role of functional diversity appeared to vary according to local ecological and anthropogenic conditions. In contrast, the relationship between the environment and the biomass displayed more variation. This highlights that the environmental context of the study region (e.g. tropical vs boreal) has an impact on the environment-biomass relationship, but that the effect of community composition is similar across the regions. In conclusion, **there is important variation between the environment-biomass relationships, but rather consistency in the diversity-biomass relationships**.

(iv) What is the importance of spatial scales in shaping relationships?

The effect of spatial scales can be assessed through the North-East Atlantic SEM case-study (where the fish community was assembled based on three different spatial scales), but also by comparing the regional case-study results to the large-scale results (North Atlantic and Pacific studies). First, based on the NEA SEM, we found that the direction of the relationship between the indicators and biomass didn't change with scale, but that the strength of the effect did. Second, when increasing the scale of the observation, it appears that the relationship might change due to more variability in the ecosystems included in the analysis (e.g. addition of warm/cold ecosystems). We conclude that **the spatial scale at which the**

ecological communities are define, as well as the spatial extent of the study, will have an impact on the observed indicator-biomass relationship, and that exploratory and/or sensitivity analysis should be done to assess the robustness of observed relationships.

4. Spatio-temporal patterns and drivers of ecosystem functions and services

4.1. Two decades of fish community change reshape biogeochemical functioning in the Mediterranean Sea

Lead contributor: Jérémy Carlot (IEO-CSIC)

Understanding how biodiversity change influences ecosystem functioning remains a central challenge in ecology, particularly under accelerating global pressures. In marine systems, fish communities play a pivotal role in carbon (C), nitrogen (N), and phosphorus (P) cycling through growth, metabolism, feeding, and excretion, yet the basin-scale functional consequences of shifting fish assemblages remain largely unresolved (see Schiettekatte et al., 2020). These uncertainties are especially critical in the Mediterranean Sea, a region undergoing rapid warming, long-term fishing exploitation, and strong productivity gradients, making it a natural laboratory to explore the links between biodiversity change and biogeochemical processes.

Despite the recognised importance of animals in mediating elemental fluxes, most large-scale biogeochemical assessments still focus on microbes, phytoplankton, and abiotic processes (Allgeier et al., 2016). As global change reshapes fish communities through redistribution, compositional turnover, and altered trait structures, the degree to which these reorganisations buffer, enhance, or erode ecosystem functioning remains poorly quantified (Schiettekatte et al., 2022). Recent research suggests that functional traits—such as body size, growth rate, metabolic demand, and trophic strategy—determine species-specific contributions to elemental cycling, and that changes in community trait composition may offset or exacerbate functioning losses caused by declining taxa or shifting biomass distributions (Mouillot et al., 2011).

4.1.1. Objective and research questions

This case study evaluates how two decades of fish community change in the Mediterranean Sea influence key biogeochemical functions across the C, N, and P cycles. Specifically, we (1) quantify five functional rates representing major carbon and nutrient flux pathways, (2) map spatial patterns and temporal trends in functioning across the basin, and (3) identify the environmental and anthropogenic drivers associated with changes in ecosystem multifunctionality. We ask:

- Do shifts in Mediterranean fish communities lead to functional losses, maintenance, or gains?
- How do functional traits and functional divergence structure spatial and temporal patterns of ecosystem functioning?
- Which environmental and human pressures most strongly modulate changes in multifunctionality?

4.1.2. Materials and Methods

Study area and fish community data

We analysed 23 years of standardised biomass data (1999–2021) from the MEDITS bottom-trawl survey program, which samples continental shelf and upper-slope habitats (50–800 m depth) across the European Mediterranean using harmonised gear and protocols (Spedicato et al., 2019). The compilation included 25,863 stations, 402 fish species, and 18 Geographical Sub-Areas (GSAs). Biomass was standardised to swept area and expressed as g m^{-2} d^{-1}.

Estimating functional rates through the FishFlux framework

We used the *FishFlux* (Schiettekatte et al., 2020) Bayesian metabolic–stoichiometric model to estimate five ecosystem functions capturing major biogeochemical fluxes: 1) Carbon production; 2) Nitrogen excretion; 3) Phosphorus excretion; 4) Carbon ingestion through planktivory; and 5) Carbon ingestion through benthivory. Six parameter classes fed into the model: metabolic, growth, morphological, trophic, survey-specific, and constants. Species traits (*e.g.,* asymptotic length, growth parameters, trophic level, diet composition, fin morphology) were assembled primarily from FishBase (Froese and Pauly, 2025), complemented by literature values for metabolic rates (Schiettekatte et al., 2022; Vanni et al., 2017). Missing data were imputed phylogenetically. Metabolic parameters were derived from Bayesian power-law fits between metabolic rate and body mass, accounting for temperature via activation-energy scaling. Excretion rates used consistent N and P turnover constants from previous FishFlux studies. Dietary stoichiometry and assimilation efficiencies were assigned from literature sources, and elemental body composition was predicted as Bayesian functions of trophic level. Because survey data provide total biomass but not full-size distributions, individuals of each species–station combination were assumed to share average mass. While this reduces fine-scale individual variation, community-level functional patterns are dominated by biomass and species identity. Functional rates were scaled from individual to species, station, and regional levels. Planktivory and benthivory were estimated via species assignments to trophic guilds, partitioning generalist diets proportionally.

Functional traits, functional entities, and functional divergence

Each species was characterised using five functional traits representing ecological strategy: maximum length, lifespan, vertical habitat, diet, and thermal preference. These traits were combined to form 144 functional entities, representing unique multidimensional trait combinations (Maire et al., 2015). A Gower-distance matrix capturing pairwise functional dissimilarity was ordinated using PCoA; a 3-dimensional functional space was selected based on optimal space quality.

Functional divergence (F_{Div}) was quantified as a biomass-weighted measure of how species are distributed within trait space. High F_{Div} indicates dominance by species with extreme trait

combinations, reflecting functional complementarity; low F_{Div} reflects clustering near the centre of trait space (Mouillot et al., 2011; Villéger et al., 2008).

Environmental and anthropogenic drivers

We extracted bottom temperature anomalies and surface chlorophyll-a from Copernicus reanalyses (Mediterranean Sea Physics Reanalysis; Teruzzi et al., 2021) and used a multi-criteria Fishing Pressure Index (FPI) integrating trawling, purse-seining, and small-scale fisheries (Kavadas et al., 2015). Depth was included as an abiotic structuring variable.

Temporal trends and modelling ecosystem multifunctionality

Stations sampled for ≥10 years (n = 20,416) were aggregated to hexagonal spatial units. For each hexagon, linear regressions quantified temporal trends for each functional variable. A Bayesian GLMM evaluated the probability that multifunctionality increased over time as a function of temperature anomaly, depth, chlorophyll-a, fishing pressure, and functional divergence, with GSA as a random effect. A Bernoulli response represented increasing (1) or decreasing (0) multifunctionality. Posterior distributions and conditional effects were used to quantify the direction and strength of each predictor.

4.1.3. Results and Discussion

Functional trade-offs across taxa

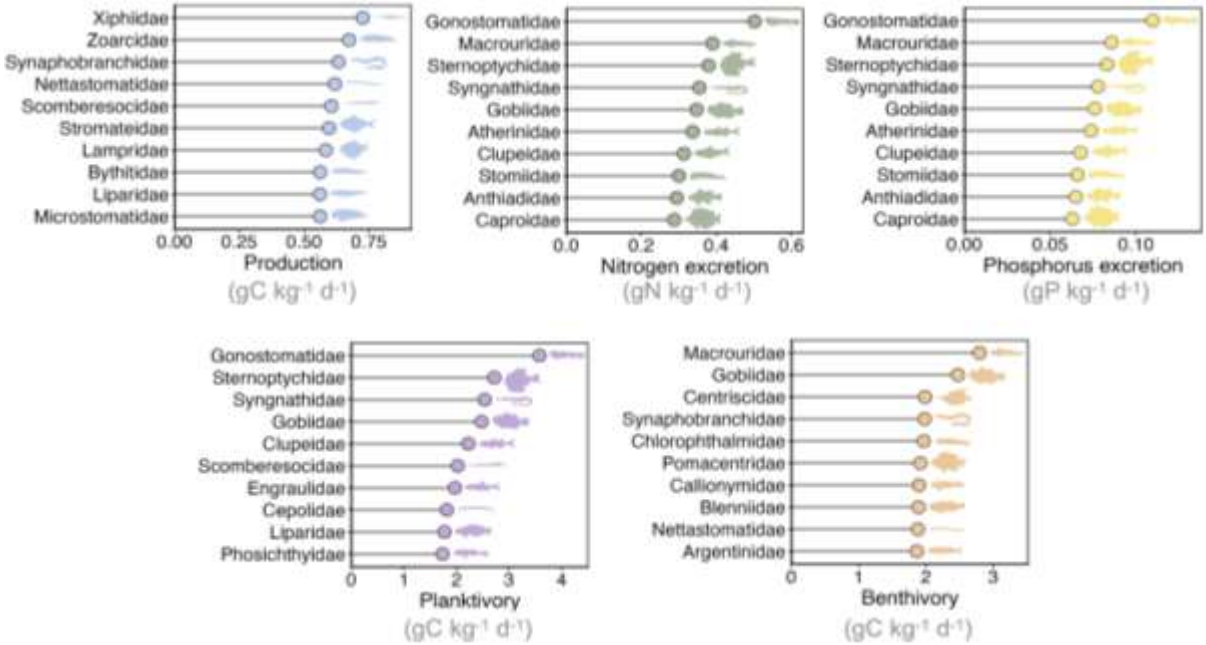


Figure 4-1. Relative contributions of fish families to five key ecosystem functions, expressed as maximum mass-specific rates (per kg of fish). For each function, the ten families with the highest contributions are shown. Functions include carbon production through somatic growth (blue), nitrogen excretion (green), phosphorus excretion (yellow), carbon ingestion through planktivory (purple), and carbon ingestion through benthivory (orange). Values represent family-level maxima across all species.

Across all processes, no fish family maximised all functions simultaneously, demonstrating strong functional trade-offs and indicating that ecosystem functioning emerges from community-level complementarity rather than dominance by a few taxa (Figure 4-1). Families such as *Gonostomatidae* ranked highly for nutrient excretion and planktivory, while large-bodied or fast-growing families dominated carbon production. Benthivory was largely driven by demersal taxa. This mosaic of specialists illustrates that maintaining high ecosystem functioning requires retaining species with contrasting ecological strategies.

Spatial heterogeneity in ecosystem functioning

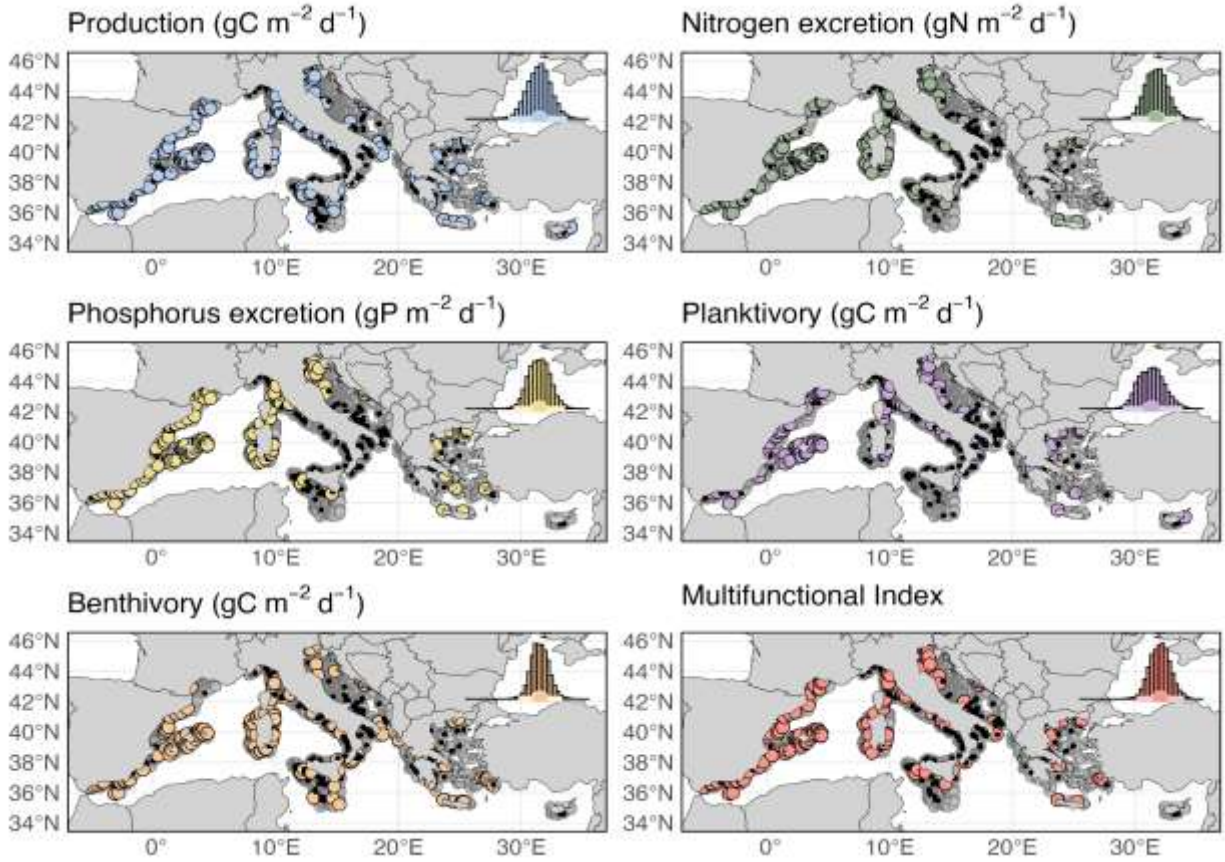


Figure 4-2. Spatial distribution of hotspots and coldspots of five key ecosystem functions in the Mediterranean Sea. Colored points represent hotspots (upper 5% of all station values), black points represent coldspots (lower 5%), and grey points represent intermediate values. Each point corresponds to a single sampling station. The inset (upper right) shows the lognormal distribution of biomass values across all stations in the dataset.

Functional rates varied across several orders of magnitude, producing distinct hotspots and coldspots for each function (Figure 4-2). Hotspots were most common in the western Mediterranean, linked to higher productivity, biomass, and more functionally diverse communities. Coldspots were common in deeper or oligotrophic regions. Importantly, hotspot locations rarely overlapped across functions, confirming that ecosystem multifunctionality rarely peaks in single locations. The multifunctionality index mirrored this spatial pattern: high values occurred where complementary functional roles coexist, rather than where any single function was maximised.

Temporal trajectories of ecosystem functioning

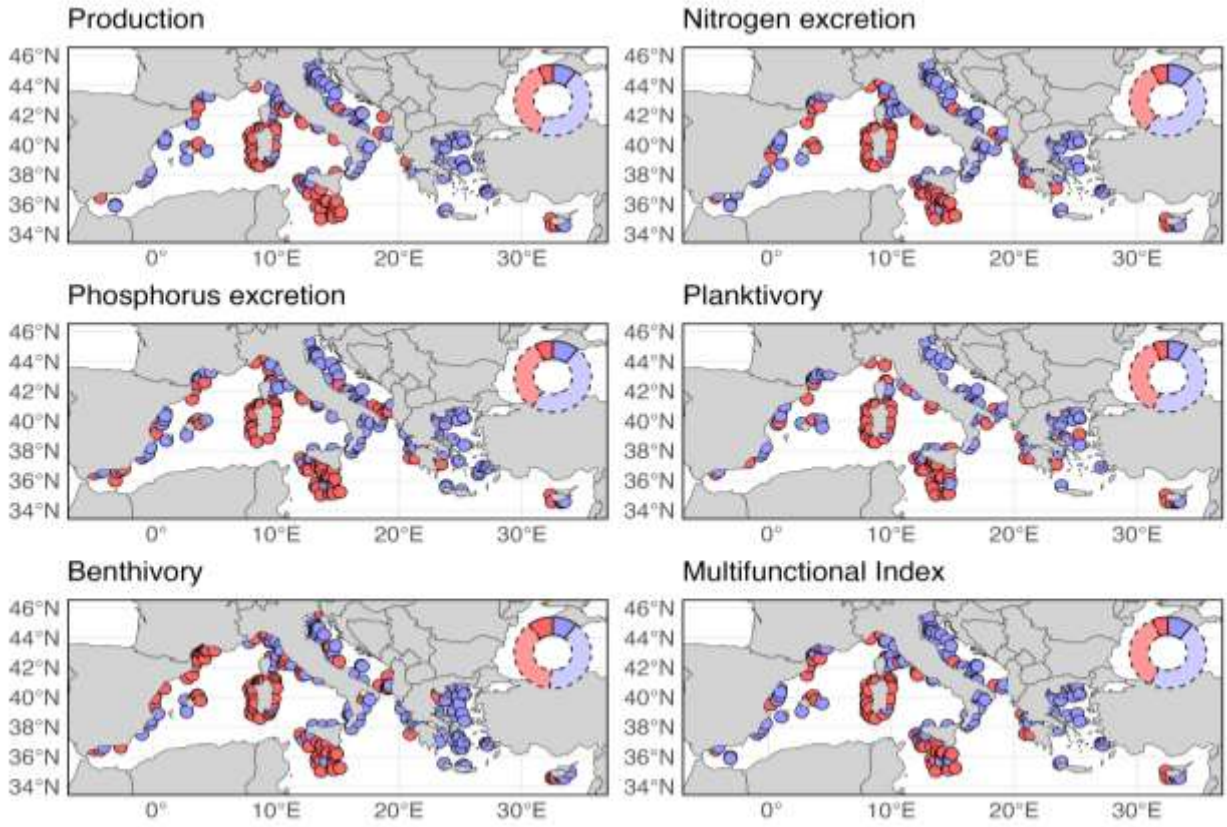


Figure 4-3. Temporal trends in ecosystem functions, including (carbon production via somatic growth; nitrogen and phosphorus excretion; and carbon ingestion through planktivory and benthivory) and in the multifunctionality index. Blue points denote significant positive trends, whereas red points denote significant negative trends. Doughnut plots (upper right of each panel) summarize the proportional distribution of trends across the full dataset, with dashed outlines indicating non-significant trends and solid outlines indicating significant trends.

Temporal trends revealed regionally coherent but spatially heterogeneous trajectories (Figure 4-3). The Adriatic and Aegean Seas exhibited predominantly increasing trends across functions, whereas Sicily and Sardinia showed more consistent declines. Yet, only ~15–21% of time series showed statistically significant trends, emphasising strong interannual variability driven by environmental fluctuations. Basin-wide, positive trends modestly outweighed negative ones for all functions, suggesting a slight net increase in fish-mediated biogeochemical functioning over the 23-year period.

Drivers of multifunctionality change

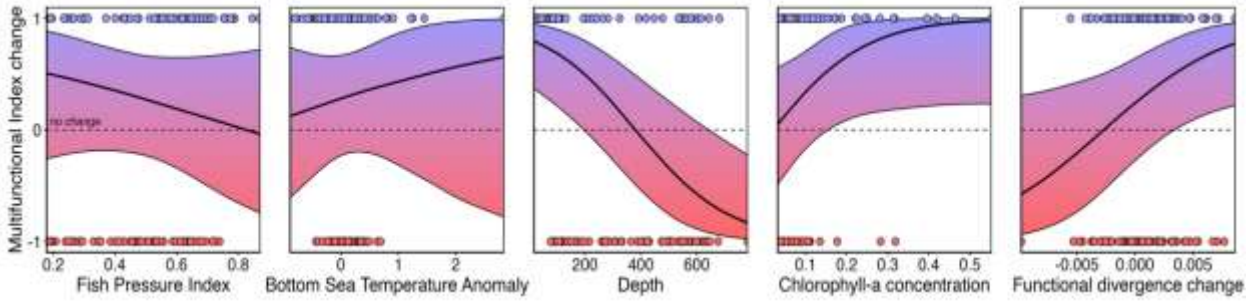


Figure 4-4. Effect of drivers on the probability of increasing (blue), or decreasing (red) temporal trends in multifunctionality. The dashed line at y = 0 represents equal probability of increasing and decreasing trends under the binomial model. Shaded ribbons show the 5th–95th credible intervals from the Bayesian model.

Our Bayesian model identified four key patterns: 1) Chlorophyll-a increased the probability of multifunctionality gains, highlighting strong coupling between primary production and fish-mediated carbon and nutrient fluxes; 2) Functional divergence (F_{Div}) positively predicted functional increases, supporting theory that high functional complementarity enhances multifunctionality (Figure 4-4). Communities dominated by species with extreme trait combinations were more likely to sustain or enhance functioning despite community turnover (Figure 4-4); 3) Depth negatively influenced multifunctionality, reflecting declining biomass and a shift toward taxa with limited contributions to benthic and pelagic nutrient pathways; and 4) Fishing pressure (FPI) and temperature anomalies showed weaker, more uncertain effects, but their directional tendencies were consistent with expectations: higher fishing pressure suppressed multifunctionality, while warming (via metabolic acceleration) slightly favoured increases.

4.1.4. Summary and Conclusions

- Fish-mediated biogeochemical functioning in the Mediterranean is shaped by strong functional trade-offs, with no taxon dominating all ecosystem processes; multifunctionality emerges from complementary species roles.
- Spatial patterns reveal pronounced heterogeneity, with multifunctionality hotspots concentrated in the western Mediterranean where biomass, productivity, and functional divergence are higher.
- Functional divergence and primary productivity are the strongest predictors of multifunctionality increases, whereas depth reduces functioning and fishing pressure likely suppresses biogeochemical fluxes.

4.2. Biodiversity and stability of Northeast Atlantic fish communities across scales

Lead contributor: Louise Flensborg (DTU-Aqua)

The functional diversity of communities is argued to provide important resilience and stability of ecosystems to withstand and buffer against changes (Holling, 1973; Peterson et al., 1998; Tilman et al., 2014). While experimental and theoretical studies on functional diversity support a positive relationship with the overall stability of the system (Naeem & Li, 1997; Tilman et al., 2006; Yachi & Loreau, 1999), the role and relative importance of different aspects of functional diversity and resilience remains unclear in natural ecosystems. This limitation is especially true in ecosystems with complex trophic interactions, variable environmental conditions and vast spatiotemporal scales, such as our oceans. Long-term data can help bridge this knowledge gap and uncover the complex effect of biotic and abiotic drivers and relationships with community stability and resilience (Magurran et al., 2010; Symstad et al., 2003). Furthermore, testing and comparing these relationships against predicted theory may yield important insight into the driving mechanisms of resilience and stability in ecosystems. In that regard, structural equation modelling (SEM) can provide a statistical tool to investigate potential diversity-stability relationships (Eschenbrenner & Thébault, 2023), including both direct and indirect links with the environment (Streiner, 2006). In this study, we use SEM and long-term monitoring data on demersal (bottom-living) fish communities across European shelf Seas to empirically investigate the presence and relative importance of direct and indirect relationships between multiple resilience indicators, environmental conditions and community stability.

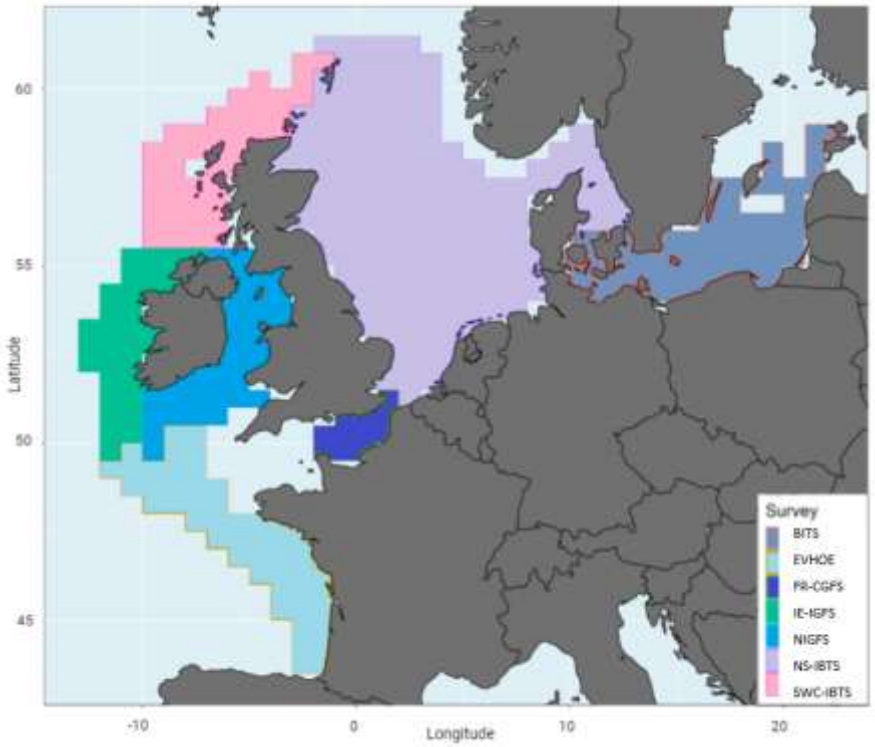


Figure 4-5. A map of the study area, including the position of the surveys (See table S2 for detailed descriptions of the surveys).

4.2.1. Material and Method

Survey and trait data

We compiled data of demersal fish species abundances using available scientific bottom-trawl survey including a total of 11.427 unique hauls and 279 species throughout the study area (Figure 4-5). All abundances were standardized for swept area accounting for the duration of the haul, the speed of the vessel and the opening of the gear (Maureaud et al., 2019). After these standardizations, all hauls were assigned to a corresponding grid cell of 1° longitude by 0.5° latitude grid cells, reflecting the standard spatial subunits considered by ICES. We estimated the inverse of the coefficient of variation in total biomass for all grid cells across years (calculated as CV = σ/μ, μ being the mean biomass over the time period considered and σ the standard deviation). Invariance was estimated as 1/CV and will throughout the text be referred to as stability. This proxy for stability, has been widely used as a reliable estimator of temporal stability in natural ecosystems (Eschenbrenner & Thébault, 2023). In addition to the community data, we extracted available information on 8 traits representing different morphological, physiological and behavioral aspects of fish ecology. The trait information was used to assign each species into functional groups sharing a similar set of traits. The functional grouping was achieved through hierarchical clustering of the provided traits for all species included in the analysis following the approach by Flensborg et al. (2023) based on Gower distances using the FD function in the "dbFD" package (Gower, 1971; Villéger et al., 2008).

Environmental data and fishing activity

We collected environmental data from the NEMO-MEDUSA coupled hydro-geochemical model (Yool et al., 2013). This was done to ensure complete and consistent coverage across all unique sampled hauls across all included covariates. More specifically, we extracted the following environmental data: bottom temperature (ºC), salinity (PSU), chlorophyll a (mmol N per m3) and detritus (mmol N per m3). We furthermore estimated seasonality as the difference between summer and winter bottom temperature, reflecting the stability of the thermal environment. Depth information was obtained from the individual surveys. We furthermore included the mean fishing effort per ICES rectangle for both otter and beam trawlers based on available records from 2012-2018. The fishing effort was estimated as a swept area ratio – the area of a grid cell that is trawled each year divided by the total grid cell size.

Indicators of stability and resilience

We calculated various resilience indicators reflecting the functional attributes of fish communities, including functional group richness, redundancy, evenness and asynchrony (Flensborg et al., 2023). Functional group richness (henceforward referred to as richness) was estimated as the mean number of functional groups present per grid cell, while the functional group redundancy (henceforward referred to as redundancy) was estimated as the mean number of species present per functional group. The functional group evenness (henceforward referred to as evenness) was represented by the mean of Shannon diversity index per functional group, while the functional group response diversity (henceforward referred to as asynchrony) was represented by the mean degree of asynchrony in species abundance fluctuations within functional groups. To estimate the metrics, we used the R packages "vegan" and "synchrony" (Loreau & de Mazancourt, 2008). All indicators were estimated for each grid cell and represented as the mean based on 100 random bootstraps of

hauls with a sample size given by Species Accumulation Curves (SACs) in order to account for differences in sampling effort.

Structural equation modelling

We used SEM to investigate the effect and relative importance of links between the resilience indicators, environmental variables and stability, while accounting for both direct and indirect pathways. We performed the analysis using R and the package "piecewiseSEM" (Lefcheck, 2016) by fitting five models with linear generalized least squares gls regression to explain stability, richness, redundancy, evenness and asynchrony (Table S5). Afterwards, we selected the best covariance structure for each model to account for spatial autocorrelation. Lastly, we selected the most parsimonious model using the "dredge" function in the "MuMln" R package (Barton, 2012). We compared the relative importance of each variable on stability by estimating both the direct and indirect effects, the latter only for environmental variables. Indirect effects on stability were estimated by multiplying the standardized path coefficients from any environmental variable by the path coefficient of any resilience indicator that showed a significant link with stability.

4.2.2. Results

The spatial patterns of resilience indicators show pronounced heterogeneity across the study area for functional group richness, redundancy, evenness and asynchrony (Figure 4-6). Similarly, stability represented by invariance, showed pronounced variability with generally high values (high stability) in the southern and eastern Baltic Sea and central North Sea and low values (low stability) in the rest of the region. The individual spatial patterns of each indicator are largely confirmed by a PCA analysis (Figure 4-6e) where functional redundancy and evenness both load positively on PC1, while the indicator of asynchrony are highly correlated with PC2. Since the PC axes are orthogonal to one another, this shows that the indicators are representing different and complementary aspects of resilience.

The resilience indicators and environmental variables in the final SEM explained a reasonably high degree of the observed variation in stability throughout the area (r^2 = 49%). The SEM identified several significant interactions between resilience indicators and stability (Figure 4-7). More specifically, we found a significant positive effect between asynchrony and stability, but a negative effect between functional redundancy and stability. The SEM further indicated there was no significant relationship between richness or evenness on stability. Finally, a significant positive effect between fishing intensity and functional redundancy was found. In terms of overall importance, the resilience indicators had a weak effect on stability compared to the environmental variables (Figure 4-8). More specifically, salinity, depth, and chlorophyll a had particularly strong effects on stability (Figure 4-8b), whereas fishing and temperature were found to have smaller and solely indirect effects.

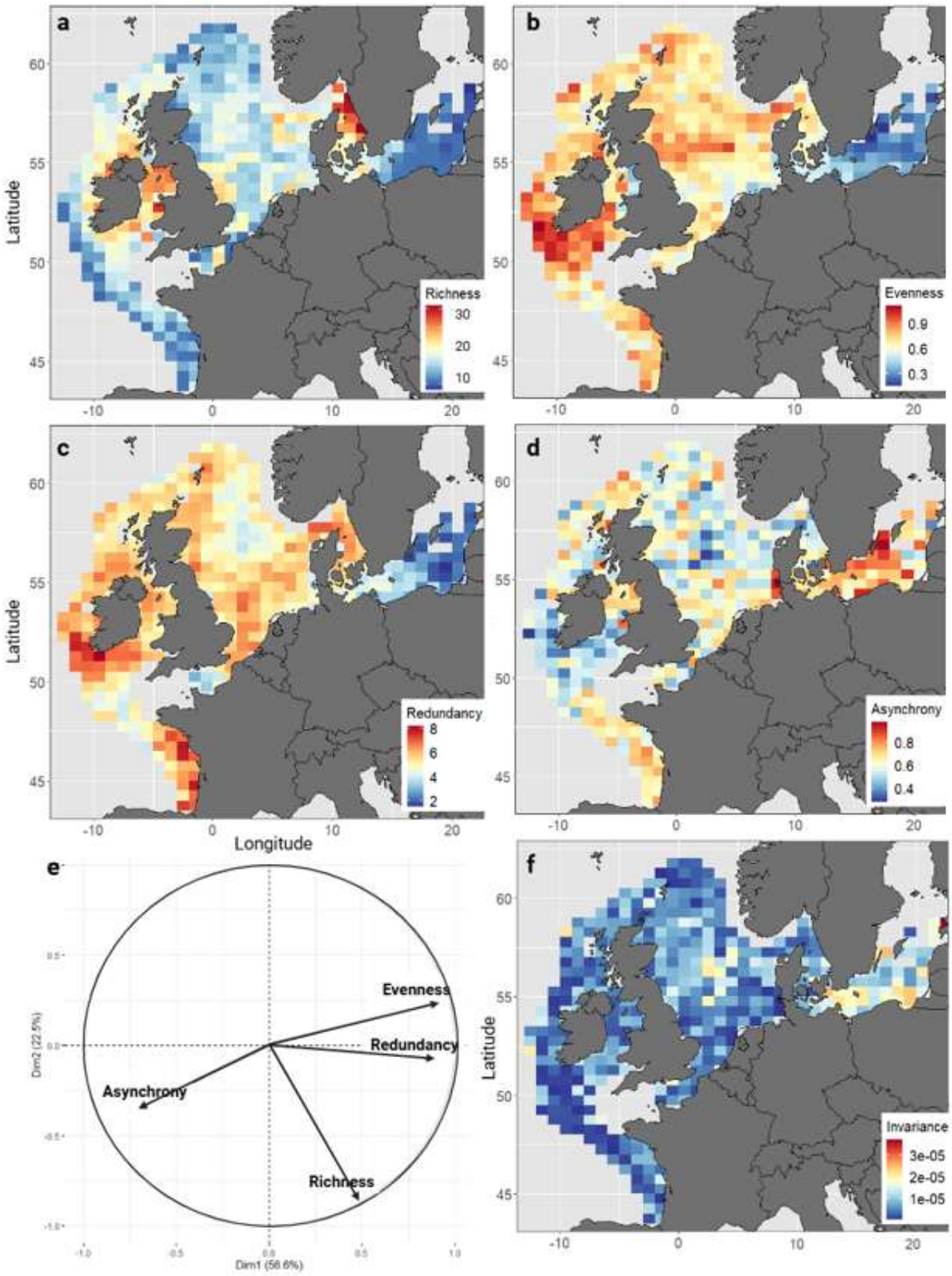


Figure 4-6. Spatial patterns of demersal fish community resilience indicators and stability across the Northwest European seas. All indicators are calculated with the mean standardized number of species representing 50% of the estimated asymptotic richness per grid cell a) Functional species richness, b) functional redundancy, c) functional evenness (i.e. Simpson's evenness calculated with species abundances), d) functional response diversity (i.e. asynchrony calculated with species abundances), e) Principle component analysis (PCA) of resilience indicators in the study area, f) fish community biomass stability reported as invariance.

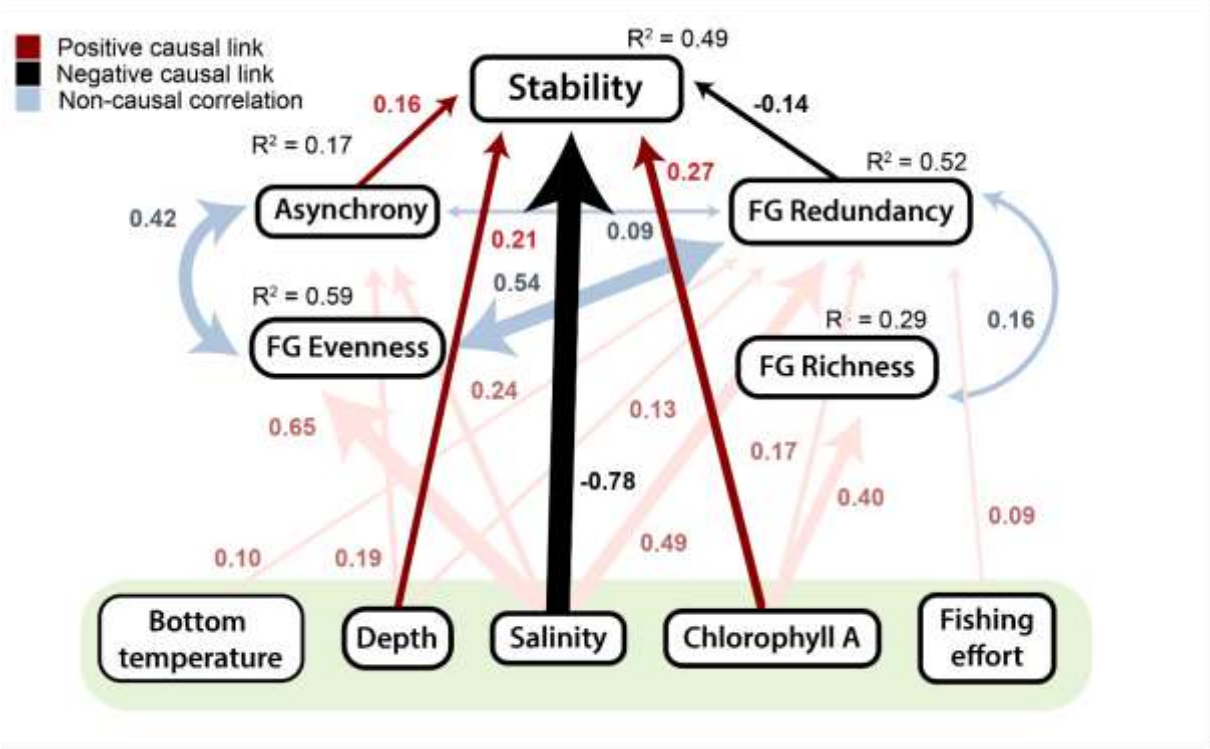


Figure 4-7. The final SEM including significant links between metrics of biodiversity (resilience indicators), community stability (invariance), fishing and environmental variables. Red and black lines indicate positive and negative relationships, respectively, while the thickness of the lines indicate the relative strength of the effects. Transparent arrows represent links (correlations) between metrics.

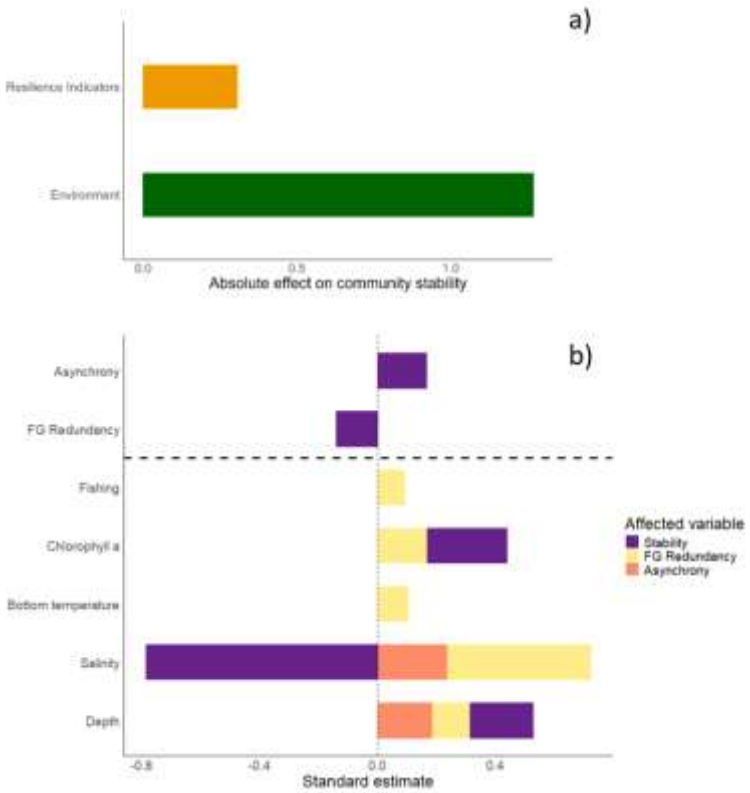


Figure 4-8. Standardized direct effects of all environmental variables and resilience indicators on stability (A), as well as the individual direct effects of the environment on both resilience indicators and stability.

4.2.3. Discussion

We identified potential relationships between stability, resilience indicators and environmental conditions using observational data on demersal fish communities covering European Shelf seas. Our results demonstrate that environmental factors play an important role in explaining large-scale patterns and differences in community stability across the study area. This finding aligns with previous research indicating that stability at broader spatial scale is more strongly influenced by environmental drivers, whereas at smaller spatial scales internal community dynamics tend to have a greater impact (Leibold et al., 2004; Mouillot et al., 2007; Wang & Loreau, 2016). A strong environmental driver identified in our study is bottom salinity, which had a direct negative effect on stability, i.e. higher stability in areas with low salinity. This effect is likely driven by the reported higher stability in the southern and eastern parts of the Baltic Sea combined with the pronounced natural gradient and difference in salinity between the brackish Baltic Sea and the other regional seas. In addition to salinity, we found that depth has both a strong direct and indirect positive effect on stability, channelled through redundancy and asynchrony. This finding is in line with previous studies showing that demersal fish communities at greater depths are primarily composed of larger, long-lived and slow growing species (Beukhof et al., 2019; Pecuchet et al., 2017).

While temperature is a fundamental driver of many key ecological processes and vital rates of organisms (Gillooly et al., 2005; Savage et al., 2004), as well as a strong determinant of global species richness patterns (Hillebrand, 2004; Tittensor et al., 2010), we found a significant positive effect of bottom temperature only on redundancy, indicating a higher number of species per functional group at higher temperatures. This outcome corroborates previous studies on marine fish communities in the area documenting positive effects of temperature on species richness (Dencker et al., 2017; Maureaud et al., 2019). However, higher temperatures did not lead to a significant increase in the number of functional groups (i.e., functional group richness), indicating that the overall trait composition is retained across a range of temperatures. Furthermore, the SEM did not show a significant relationship between temperature and stability, indicating that higher mean temperatures do not seem to confer a direct stabilizing effect on community biomass. Despite the well-documented consequences of fishing on stock health and productivity, we only found a significant and positive direct link between fishing intensity and redundancy. This observed positive effect of fishing on redundancy should be treated with caution since it may simply result from a spatial co-occurrence between areas of high overall fishing pressure and redundancy (such as the heavily fished southern North Sea The absence, or weakness of links to fishing may either result from data limitations, or alternatively be due to historical effects of fishing occurring well before the study period which may mask the effects of fishing (Pinnegar & Engelhard, 2008; Soga & Gaston, 2018).

As evident from above it is clear that community stability depends not only on external forcing through the environment, but on the internal properties, including the number and composition of species, their functional characteristics and the complexity of their population dynamics and interactions (Loreau & de Mazancourt, 2013; McCann, 2000). However, among the key resilience indicators included in our study, we only found a direct positive effect on stability from asynchrony. This finding supports previous studies demonstrating asynchrony in species fluctuations as an important driver of overall community stability (Craven et al., 2018; Lindegren et al., 2016; Schnabel et al., 2021). Although we found no direct link with the number of functional groups, the positive effect of redundancy on asynchrony may indicate

that functional groups containing more species have a higher likelihood of displaying asynchronous dynamics, or at least uncorrelated abundance fluctuations, that both serve to increase stability through compensatory dynamics or statistical averaging, respectively (Yachi & Loreau, 1999). Furthermore, we found that higher asynchrony is also associated with higher evenness, suggesting that communities characterized by more even abundances may indirectly serve to increase stability, simply because the overall community biomass will be less variable, or sensitive to the fluctuations in one or a few dominant species. Taken together this supports a "portfolio effect" (Anderson et al., 2013) contributing to overall stability.

4.2.4. Summary and conclusions

- Our study highlights a complex network of direct and indirect pathways influencing fish community stability, with substantial spatial variation in resilience indicators and stability.
- Key environmental gradients, such as salinity, depth, and productivity, were identified as primary drivers of resilience and stability at broad spatial scales.
- The observed relationships and underlying mechanisms may not be universally applicable across different ecosystem types or spatio-temporal scales, underscoring the need for further research into context and scale-dependence.
- These findings can guide targeted management and conservation actions, such as biodiversity protection and restoration, tailored to local or regional environmental contexts to enhance ecosystem resilience and stability.

4.3. Diversity and stability relationships across marine fish communities facing contrasting environmental and anthropogenic pressures

Lead contributor: Manuel Hidalgo and Jaime Otero (IEO-CSIC), Martin Lindegren (DTU-Aqua)

Stability is an emergent property of complex adaptive systems encompassing multiple components, including temporal variability, resistance, resilience, persistence and robustness (Donohue et al., 2013). Due to its essential role in determining the responses of ecosystems to natural or anthropogenic stressors, stability has received long-standing attention within ecology (Donohue et al., 2016; Ives & Carpenter, 2007). However, understanding the drivers and mechanisms responsible for providing stability, and whether they vary across ecosystems subjected to different species composition and environmental conditions, remains a considerable challenge (Donohue et al., 2013; Thibaut & Connolly, 2013).

Theoretical, experimental and observational studies have historically focused on how ecosystem characteristics, mainly the number of species, but also food-web structure or the strength of species interactions, affect stability (e.g. Arnoldi et al., 2019; Loreau & de Mazancourt, 2008; Tilman et al., 2006). The results of this cumulative research have revealed that increasing diversity in terms of species richness has a dual effect on stability: it stabilizes total community biomass while, at the same time, it destabilizes individual species abundances by increasing the variability of species' responses to environmental fluctuations (de Mazancourt et al., 2013; Roscher et al., 2011). These effects make the overall community

abundance of highly species-rich communities less sensitive to temporal fluctuations in the environment and to anthropogenic impacts (Donohue et al., 2016; Thibaut & Connolly, 2013).

Typically, studies dealing with stability use the temporal stability metric of an aggregate ecosystem property, that is, the invariability, measured as the inverse of the coefficient of variation through time. However, several other metrics have been proposed to quantify ecological stability (e.g. Bell et al., 2014; Lindegren et al., 2016; Yachi & Loreau, 1999). Among them, the portfolio effect (PE) has recently gained much popularity (Loreau et al., 2021). Introduced more than two decades ago (Doak et al., 1998; Tilman, 1999), PE denotes how independent fluctuations at the population level decrease variability at the community level (Schindler et al., 2010; Tilman et al., 1998; Vasseur & Gaedke, 2007). Several interacting community properties have been identified to contribute to PE largely representing the multidimensional attributes of ecological stability and the complementary mechanisms that determine it (e.g. Donohue et al., 2016; Downing et al., 2014; Hillebrand et al., 2018). Among them, synchrony in species fluctuations (i.e., reflecting the degree of common sensitivities of species within a community to external drivers; Loreau & de Mazancourt, 2008, 2013) and evenness (i.e., the distribution of abundances among species) have been denoted as two of the main structural properties jointly affecting PE (Thibaut & Connolly, 2013).

Although numerous human pressures and environmental drivers can directly or indirectly influence the effect(s) of biodiversity on ecosystem processes and stability (Donohue et al., 2016), empirical evidence at large macroecological scales is scarce and mainly originate from terrestrial studies (Craven et al., 2018; García-Palacios et al., 2018; Morin et al., 2014). Here, we used scientific bottom trawl surveys data from 54 marine ecosystems covering sub-Arctic to sub-tropical waters in the North Atlantic Ocean and the Mediterranean Sea to evaluate how biodiversity, in terms of richness and evenness, community structure, and environmental and anthropogenic factors affect community stability. To do that, we analyzed, at the ecosystem scale, the direct and indirect effects of the community properties, environmental conditions and anthropogenic pressures on stability measured through two PE metrics, which either ignores or accounts for the mean temporal abundance and variance of the species within communities (i.e., Taylor's power law) (Anderson et al., 2013).

4.3.1. Material and methods

Biological data

We compiled scientific bottom trawl survey data from 54 continental shelf ecosystems across the North Atlantic Ocean and the Mediterranean Sea spanning from 1980 to 2015, for which an updated source data and surveys characteristics can be found in Maureaud et al. (2024, 2021). These surveys cover wide latitudinal and environmental gradients, ranging from sub-tropical waters in West Africa and the Gulf of Mexico to sub-Arctic seas in Greenland and Iceland (Figure 4-9), and have been broadly assigned to five large biogeographic regions: sub-Arctic, West Atlantic, East Atlantic, Canary Current Upwelling, and Mediterranean Sea. As the primary focus of this study is on demersal (bottom-living) fish communities on continental shelves, we only selected hauls sampled between 20 to 200 m depth. For each community, annual time series of fish species abundances were obtained from standardized catches per swept area (number of individuals km^{-2}) for each haul. Species not primarily associated with continental shelves and for which abundances are biased due to low catchability in bottom-trawling gears (e.g., littoral, pelagic and mesopelagic species) were excluded. However,

demersal species that are part of this habitat were retained even if they appeared in very low abundances or just in specific years. The final dataset resulted in a total of 419 unique species included in the analyses. For all fish species three life-history traits providing complementary information in terms of survival, reproduction and feeding were selected (Beukhof, Dencker, Palomares, et al., 2019; Pecuchet et al., 2017). These life-history traits were somatic growth rate (K parameter from the Von Bertalanffy growth equation), length at 50% maturity, and trophic level. Traits information was extracted from FishBase (Froese & Pauly, 2025), published reviews (Beukhof, Dencker, Palomares, et al., 2019; Tsikliras & Stergiou, 2015) available studies (Pecuchet et al., 2017).

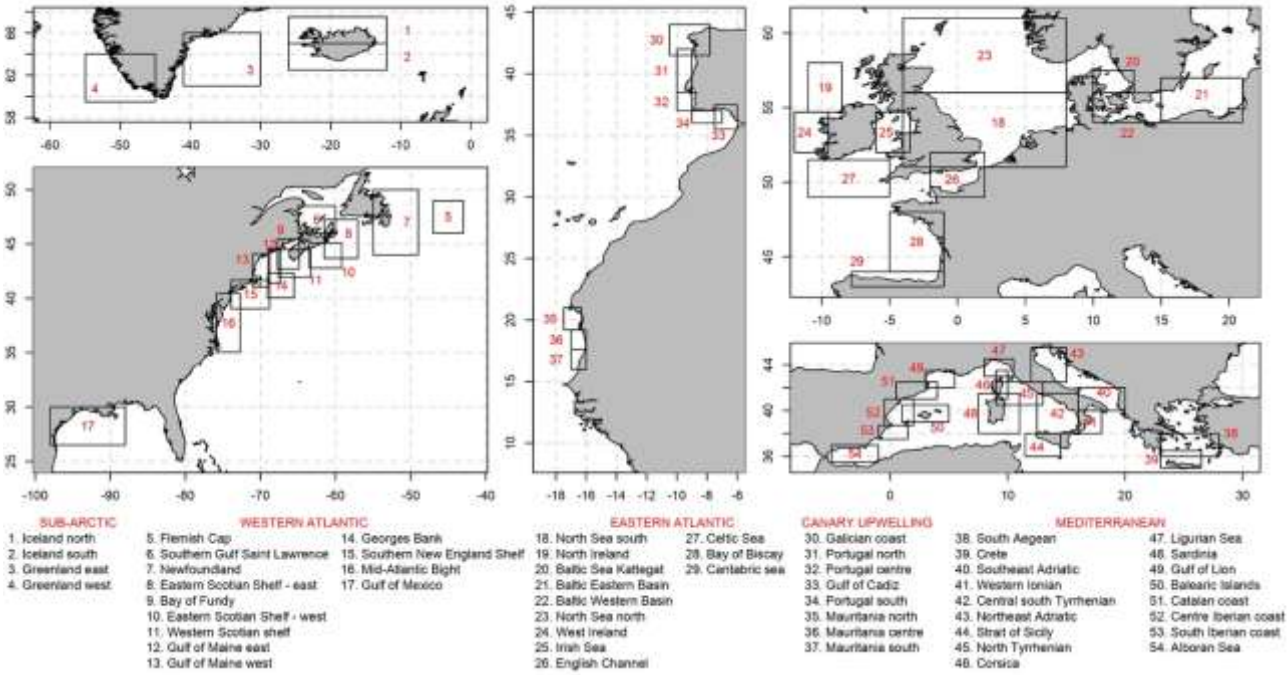


Figure 4-9. Location of the 54 systems from which information on scientific bottom trawl surveys were obtained. Systems are presented in five large biogeographical regions: Sub-Arctic, West Atlantic, East Atlantic, Canary Current Upwelling and Mediterranean Sea. Rectangles represent the area used to calculate indicators for the environmental conditions, anthropogenic impacts and bathymetry. Further information is provided in Table S1.

Environmental and anthropogenic pressures data

Environmental variables describing oceanographic conditions in each area were obtained from different sources. Chlorophyll-*a* concentration (Chl *a*), acting as a proxy for primary production, was obtained from the Global Colour Project (http://www.globcolour.info). We downloaded monthly Chl *a* data at a grid resolution of 100 km^2 from the MODIS AQUA sensor and AV model from January 2003 to December 2015 (Maritorena et al., 2010). Furthermore, Sea Surface Temperature (SST) was obtained from the NOAA Earth System Research Laboratory (http://www.esrl.noaa.gov/psd/). We used the monthly Optimum interpolation SSTv2 product available at 1º grid resolution from a combination of satellite and *in situ* measurements from January 1982 to December 2015 (Reynolds et al., 2002). Additionally, sea bottom temperature (SBT) was obtained from the World Ocean Atlas 2013 at 1º grid resolution (https://www.ncei.noaa.gov/products/world-ocean-atlas). In order to account for a representative range of potential drivers of community structure and dynamics, we

computed both the mean value and variability of the environmental variables as indicators of spatiotemporal heterogeneity. Chl *a* variability was estimated as the spatial coefficient of variation (CV) of the mean spatial pattern calculated over time, while the mean seasonal range temperature-related variables were calculated as the difference between mean summer and mean winter values. The mean estimates can generally be associated with large-scale impacts over the whole system, whereas the range and CVs serve to represent processes and mechanisms operating over finer spatial scales (Wedding et al., 2011). Finally, sampling depth was also used as a potential driver, where the mean and CV of all sampling stations within each community and year were calculated, and subsequently averaged over the entire time series as an indication of the potential influence of both the bathymetric mean and heterogeneity in a given community.

In order to have representative indicators of potential human impacts in each ecosystem, available estimates, matching with the period of the study, of bottom trawling impact and of cumulative impacts of several other human activities were obtained from Halpern et al. (2008). Bottom trawling impact (Trawl) was estimated as the tons of catch using demersal gear types and standardized by the net primary production, while the total anthropogenic impact (TAI) was calculated by normalized additive combinations considering 17 anthropogenic drivers in all ecosystems (see further details in Halpern et al., 2008). Using this spatial database, mean values and CVs were calculated across the different grid cells within each of the systems examined.

Community metrics

Each community was characterized using the following metrics calculated per year from the standardized species abundances by year matrices, and afterwards averaged over time: total abundance, calculated as the sum of individual species' abundance; richness (S), calculated as the number of species; Shannon diversity (H), calculated as $-\Sigma p_j \cdot \ln(p_j)$ with p_j representing the proportion of the entire community made up of species j; and evenness (J), calculated as H/ln(S). Furthermore, for each system, we used the life-history traits information to calculate community-weighed trait composition. Community weighted-mean (CWMs) traits were calculated as the average trait value weighted by the species abundances averaged across the whole sampling period of each survey. This was done for the three traits, growth rate (CWM_K), length at maturity (CWM_{L50}) and trophic level (CWM_{TL}), which characterize key life-history strategies along the 'fast vs. slow' life-history continuum (Beukhof et al., 2019a).

Communities were also characterized by their synchrony in species fluctuations. Synchrony is a community property strongly associated with stability (Anderson et al. 2013; Thibaut & Connolly, 2013) and provides information on the degree of common sensitivities of the species within a community to fluctuations in external drivers (e.g., environment, human activities). Thus, stabilization through asynchronous dynamics requires the existence of differential responses of different species in a community to the fluctuations of the external drivers (Loreau & de Mazancourt, 2013). To estimate synchrony, we followed the approach developed by Loreau & de Mazancourt (2008):

[illegible]

where the superscript *c* designates community-level quantities, the superscript *s* designates species-level quantities, *n* is the number of species in the community and *v* denotes variances and covariances. Thus, $v_n^s(i,i)$ is the variance (over time) of the abundance of species *i*; $v_n^s(i,j)$ is the temporal covariance of the abundances of species *i* and *j*; and v_n^c is the variance

of the total community abundance for a community with *n* species. The denominator is the variance of a hypothetical community with the same species-level variances but in the presence of perfect covariance. Synchrony varies from zero to one when abundance fluctuations are perfectly asynchronous or synchronous across species, respectively.

Finally, for each community we further calculated the Taylor's power law z-value, that is, we estimated z as the slope of a linear regression of the *i* species' mean temporal log abundance (μ) and variance (σ^2) as follows:

$$\log(\sigma^2_i) = \beta_0 + z \log(\mu_i) + \varepsilon_i \quad [2]$$

where β_0 is the intercept and ε_i is the residual error.

Portfolio effect metrics

We assessed the performance of two stability metrics proposed by Anderson et al. (2013) and defined as the average coefficient of variation portfolio effect (hereafter CVPE) and the mean-variance portfolio effect (hereafter MVPE). On the one hand, the CVPE was computed as the ratio of the mean temporal coefficient of variation (CV) of the species abundances to the CV of the total abundance of the community. On the other hand, we calculated the MVPE taking advantage of the Taylor's power law outlined above, which is known to vary across communities. By using that model, already applied in recent studies at the community level (Flensborg et al., 2023; Lázaro et al., 2022), we extrapolated the mean-variance relationship to the observed total community mean abundance to obtain the predicted variance value that we would expect if the portfolio was composed of a homogeneous community in terms of mean-variance relationship. The MVPE was then calculated as the ratio of the observed variance in the total community abundance and the predicted variance (Anderson et al., 2013). Traditional calculations of stability, as the inverse of the coefficient of variation or the CVPE, assume that the z-value of the mean-variance scaling equals two. However, previous studies have shown that z usually tends to be less than two due to demographic stochasticity or competitive interactions (Loreau, 2010). Thus, it is preferable to account for the observed mean-variance scaling relationship when quantifying metapopulation or community portfolio effects that we have done following the methods proposed by Anderson et al. (2013). Confidence intervals for both PE metrics were obtained by recalculating the PE using the 95% confidence intervals on the predicted community variance.

Statistical analyses

The community level metrics based on standardized abundance were analyzed sequentially in accordance with the specific objectives outlined in the study. We investigated the contribution of intrinsic community properties and external drivers (i.e., environment and anthropogenic forcing) either via direct or indirect effects on both PE metrics. To do that, we fitted structural equation models (SEM) for which we established *a priori* the hypotheses on the causal links based on Anderson et al. (2013) and Thibaut & Connolly (2013) frameworks. More specifically, we hypothesized that PEs could be explained directly by the community metrics and the environmental and human stressors. In turn, the community properties would also be response variables potentially explained by the environment and anthropogenic impacts representing indirect effects. During the model fitting process, non-significant links related to the environment and the human pressures were removed. Before fitting the SEMs, Trawl, Chl

α and the range of SBT were log-transformed and all variables were standardized to 0 mean and 1 standard deviation. Model adequacy was assessed based on a χ^2 goodness-of-fit test.

4.3.2. Results

Portfolio effects

Across the studied communities, the mean of the z-value of the Taylor's power law was 1.98 (± 0.13 sd) ranging from 1.71 to 2.24, and with significant deviations from 2 in numerous ecosystems (Figure 4-10A). Regarding the estimated PE metrics, these varied between methods due to the mean-variance scaling. While the MVPE ranged from 0.54 to 3.14 with a mean value of 1.59 (Figure 2B), the CVPE ranged from 0.75 to 4.89 with a mean value of 1.97 (Figure 4-10C). No clear geographical pattern was observed across the large macroecological area investigated with the exception of the Mediterranean Sea, which showed a slight decreasing pattern in the CVPE from east to west (Figure 4-10C).

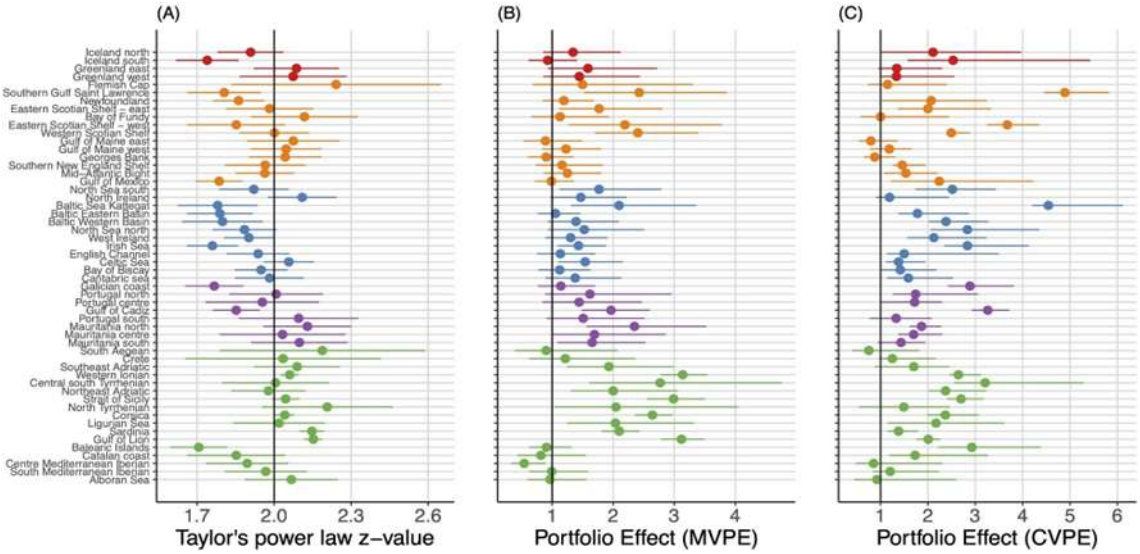


Figure 4-10. Values and 95% CI for (A) Taylor's power law z-value, (B) mean-variance portfolio effect, and (C) average CV portfolio effect across the 54 demersal fish communities. Communities are grouped into five large biogeographical regions: Sub-Arctic, West Atlantic, East Atlantic, Canary Current Upwelling, and Mediterranean Sea (Figure 1). Within each biogeographical region systems were sorted according to the mean latitude, except in the Mediterranean Sea in which systems were organized according to their mean longitude from east to west. Color coding: Arctic (red), Western Atlantic (orange), Eastern Atlantic (blue), Upwelling (purple) and Mediterranean (green).

The SEM fitted to the MVPE (Figure 4-11A) showed that the model was adequate (χ^2 = 23.7, df = 32, p-value = 0.86) and explained a moderate to large proportion of the variability in MVPE (63%), z-value (34%), synchrony (37%), evenness (43%) and richness (33%). Two factors affected MVPE directly, with a more stabilizing MVPE with increasing z and, especially, when species' abundance was more asynchronous (Figure 4-11B). Regarding biodiversity, richness favoured an increase in MVPE through its negative effects on the z-value (Figure 4-11A) and on synchrony (Figure 4-11A). On the other hand, the indirect effect of evenness was stronger (Figure 4-11B) and also mediated by its positive and negative relationship with the z-value and synchrony, respectively. Most of the environmental parameters had a stabilizing indirect effect (Figure 4-11B) highlighting the bathymetric heterogeneity through its positive association with biodiversity. The exception was the range of SBT, which had a negative effect

(Figure 4-11B) mediated by its positive relationship with synchrony and evenness (Figure 4-11A). The productivity of the ecosystem did not seem to have important net effects on stability (Figure 4-11B); however, Chl *a* concentration was a key parameter for synchrony and biodiversity with more productive regions having less rich and more uneven and asynchronous assemblages (Figure 4-11B). With respect to the anthropogenic pressures, both bottom trawling and TAI had a negative effect on evenness and synchrony (Figure 4-11A), resulting in negative and positive net effects of trawling and TAI on MVPE.

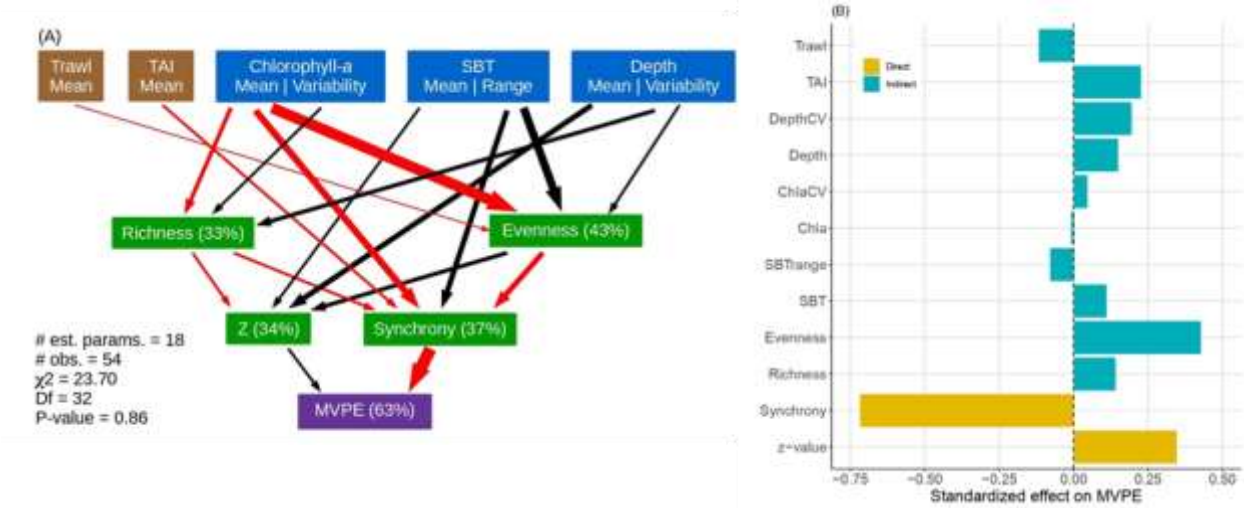


Figure 4-11. (A) Results from the structural equation model (SEM) fitted to the MVPE. Black and red arrows represent positive and negative causal links, respectively. The thickness of the arrows varies depending on the strength of the relationship. Variables were coloured according to their nature: purple for the PE, green for community metrics, blue for environmental variables and brown for the anthropogenic stressors. The percentage of variance explained by the endogenous factors on each structural component, and MVPE, is also indicated. (B) Standardized direct and indirect effects of all intrinsic structural properties and external drivers on MVPE. The indirect effects for a given variable were computed by multiplying the standardized coefficients along each path, and then summing over all paths connecting that variable and the MVPE.

4.3.3. Discussion

Two metrics of the portfolio effect were used here as measures of stability. We found that the estimation of a portfolio effect that assumes that the slope of the mean temporal abundance and variance relationship equals two (i.e. CVPE), results in an overestimation of the stabilizing effect of the species diversity compared to a homogeneous community. Additionally, the direct effect of biodiversity on stability only becomes significant when the mean-variance scaling is not considered in the calculations. In other words, ignoring that the Taylor's power law z-value differs from two leads to more stabilizing PE at the community level, which is in close agreement with the theoretical and empirical work done by Anderson et al. (2013) for other terrestrial and aquatic meta-populations. In consequence, the main difference between metrics is how they depend on the z-value. As such, our SEM approach showed that while the CVPE related negatively to z, the MVPE was positively affected. This implies that for stability calculations in terms of temporal variability (i.e. CVPE metric), an increased z-value means that all species are more variable but also more deviated from the theoretical value z = 2, triggering a destabilizing effect at the community level (Anderson et al., 2013). Less variable species in terms of z-value occurred in shallower though cooler waters suggesting that this metric of community structure further captures the effects of environmental variability across large scales as already shown for regional seas (Cobain et al., 2019). Importantly, the number of species and the distribution of their abundance related negatively and positively to the z-value

as observed by Anderson et al. (2013), meaning that richness and evenness would exert indirect positive effects on PE; however, the importance of biodiversity varied with the portfolio metric considered.

Multiple theoretical and empirical studies have shown that greater biodiversity increases stability (e.g. Tilman et al., 2014) with a higher number of species typically reducing the variability in ecosystem processes in different realms (e.g. Loreau et al., 2021) and across scales (Liang et al., 2022). Furthermore, some of this research also highlights the dual effect of species richness on stability, stabilizing total community abundance while, at the same time, destabilizing individual species abundances by increasing the species variability (de Mazancourt et al., 2013; Roscher et al., 2011), as species-specific dynamics is a major driver of stability beyond species interactions (Meng et al., 2025). This is consistent with our results. The SEM for CVPE showed the direct negative effect of richness on stability, while the indirect positive effect mediated by the z-value is the one persisting when the stability metric accounted for the z-value (i.e., MVPE). Besides richness, our findings also support the theoretical expectation that evenness has an important dual indirect effect on increasing stability (Thibaut & Connolly, 2013). While low dominance increases the variability of the species in terms of z-value, more even communities promote asynchronous fluctuations meaning that greater dominance reduces the stability of demersal communities (Y. Yan et al., 2021). Nonetheless, synchrony was the factor that had the largest effect on the PEs, implying that fish communities with more asynchronous species would have greater stability as also observed in grasslands (Craven et al., 2018), plant (Valencia et al., 2020), or tree (Schnabel et al., 2021) communities. Therefore, greater synchrony would be more common in communities with low evenness (i.e., high dominance), whose dominant species would also display greater fluctuation variability.

In terms of the environmental drivers, most effects were found to be indirect through the community properties. The variability in sampling depth positively affected the PEs through effects mediated by biodiversity, suggesting that a fish community that occurs in a habitat with more variable depths or variable habitats across depths may promote a higher capacity to buffer external impacts and, in turn, enhance stability through its positive effects on richness and evenness. Chlorophyll *a* concentration was an important factor affecting community properties, with more productive ecosystems leading to communities with a lower number of species, as observed for reef fishes (Duffy et al., 2016). Also, communities with higher dominance tended to occur in ecosystems with higher primary production (Maureaud et al., 2019), but also with more asynchronous fluctuating dynamics. Nonetheless, the net effect of primary producers on stability was negligible when accounting for the mean-variance scaling. The extent of the range of bottom temperature causes net negative effects on stability mediated by both evenness and synchrony. This is likely because high seasonal changes in bottom temperature would expose fish communities to a more seasonally predictable environment. In turn, this would lead to more common fluctuating responses of the dominant species to the environmental variability (Winemiller & Rose, 1992). By contrast, the positive link between mean bottom temperature and z-value could be related to the species composition, as bottom temperature scaled positively with communities with a higher contribution of fast-growing species (Beukhof et al., 2019) which tend to display more variable fluctuations. Nonetheless, the environmental effects mediated by the mean-variance scaling, such as mean bottom temperature and depth, showed contrasting effects on both PE metrics due to the differing effect of z-value on the PEs.

We detected effects of anthropogenic pressures on evenness and synchrony. First, the cumulative anthropogenic impact (TAI) had a strong negative effect on synchrony with more intense human activities leading to more asynchronous communities. Since human activities often lead to a fragmentation of habitats, species and communities (Halpern et al., 2015; Hughes et al., 2005), a consequence of such cumulative anthropogenic forcing would be that ecosystems become more spatially heterogeneous and, thus, more dependent on and exposed to ecological processes and drivers at small spatial scales, resulting in larger diversity of species responses to persistent and dynamic environmental variability that ultimately have a net positive effect on PE. Second, we observed that systems subjected to more bottom trawling impact were characterized by more uneven communities, which could be attributed to the preference of the fisheries for areas where a few dominant species are targeted (Maureaud et al., 2019).

4.3.4. Summary and conclusions

- Richness and evenness favored stability in terms of the portfolio effect of the demersal communities, though stability was more sensitive to changes in species dominance when the mean-variance scaling of the species was considered (MVPE). By contrast, richness gained importance in the case of using the average of the coefficient of variation of the species (CVPE). Hence, accounting for the Taylor's power law z-value when calculating stability metrics was fundamental.
- Apart from biodiversity, synchrony was the main property contributing to stability irrespective of the PE metric used, with more asynchronous communities showing higher stability as observed in numerous aquatic or terrestrial ecosystems.
- The environmental variability mostly affected stability indirectly through effects channeled by the community properties, though their importance was minor with exception of the bathymetric heterogeneity which clearly enhanced stability.
- Finally, anthropogenic disturbances increased stability mediated by synchrony, though more trawling decreased the portfolio effect through its negative effect on evenness.

5. Synthesis and discussion

Linking biodiversity to ecosystem functions (EF) and ecosystem services (ES)

The conceptual model developed in this work provides an integrated view of how biodiversity, ecosystem functions, and ecosystem services interact within European marine ecosystems (2 p18). By combining expert knowledge with quantitative network analysis, the models helped identify ecological components and environmental drivers most influential in shaping system behaviour, particularly benthos, fish, and zooplankton biomass, which consistently emerged as central. as well as areas of high uncertainty. At the same time, areas of low agreement among experts, especially within internal ecosystem function and structure, and among the pressures acting on them, highlighted where understanding remains uncertain or highly context dependent. Together, these results point at the strong interdependence between biodiversity, and the functions and services ecosystems provide, while also showing where current knowledge is incomplete.

Some biodiversity elements were identified as key drivers across multiple EF and ES. Functional divergence, for example, was crucial for ecosystem multifunctionality in the Mediterranean Sea (4.1 p96), while evenness was found to play a significant role in stabilizing fish communities and enhancing seafood provisioning at large scale (3.3 p80, 4.2 p72). However, the links between biodiversity and EF and ES were not universal across all functions or services and case studies. For example, while functional divergence supported multifunctionality (4.1 p96), species dominance (low evenness) was more closely linked to higher fish biomass in some European sea regions (3.1 p32). Although the different studies included here are using a variety of methods and testing different predictors (e.g. functional divergence vs functional dispersion, SST vs SBT), which challenge the comparison and the generalization of the most important drivers of EF and ES. More generally, observed differences between the biodiversity-EF/ES relationships points to the need to consider regional-specific biodiversity elements relevant to each EF or ES.

Based on the conceptual network (2 p18), it appeared that the relationships between biodiversity and ecosystem functions and services were relatively satisfactorily agreed upon. Yet, future research on linking biodiversity to EF and ES could focus on underexplored links, which can be indirect links in the network that indirectly influence the relationship with ES and EF. For instance, the links within ecosystem structure and functions (i.e. biodiversity), as well as the links with their drivers, which had overall the lowest expert agreements. This might also be due to these relationships being more likely to be region-specific, pointing out for the need to study them across different spatial and temporal scales and extent. Additionally, incorporating anthropogenic pressures and environmental variability into biodiversity-EF/ES models could provide a more nuanced understanding of these relationships, for example as investigated by both Fu et al. (2015) and Selim et al. (2016). These studies illustrate how path analysis and similar modeling approaches can help quantify the relative direct and indirect effects of fishing pressure and environmental conditions on ecosystem services.

Tools such as the conceptual models developed here can serve not only to synthesize existing knowledge but also to identify where further scientific evidence or re-evaluation of assumptions is needed to support robust ecosystem management. This was notably seen when confronting the expected relationship between biodiversity and biomass based on expert knowledge to empirical quantitative analysis of the relationships. There, we found that

for several relationships, like between evenness and biomass, the expected knowledge-based relationship didn't hold when confronted with data.

What drives fish biomass?

The SEM studies presented here consistently identify biodiversity as a critical driver of fish biomass (2.1 p32). Taxonomic and functional indicators, such as species richness, functional richness, and evenness, were shown to influence biomass across various ecosystems. Notably, taxonomic evenness and functional dispersion emerged as strong negative drivers, suggesting that dominance is a key-process shaping fish biomass. These findings support the dominance/mass-ratio hypothesis, where a few dominant species with specific traits drive ecosystem productivity (Grime, 1998; Lisner et al., 2023; Loreau et al., 2001). However, evidence of niche complementarity is also present, with taxonomic and/or functional richness positively impacting fish biomass in all the studies, although to a lower extent than unevenness. Additionally, the Barents Sea GLMMs study (3.2 p72), which did several sensitivity analyses, pointed out that richness becomes more and more important at explaining the biomass of the non-dominant (i.e. rare) species in the communities. This is an important finding, as rare species can have an exacerbated role in ecosystem function (Mouillot et al. 2013), beyond the single biomass production ecosystem function studied here. Rare species can also have substantial impacts on ecosystem services through both direct and indirect contributions, notably through species interactions (Dee et al. 2019). This points out that richness, either in terms of species or functions, does not have a trivial role on EFs, and should thus be monitored closely and conservation effort should also focus on richness.

Environmental drivers also played a significant role in shaping fish biomass. Temperature, depth, and primary productivity were consistently identified as key factors. For example, biomass was higher in colder regions (3.3 p80), likely due to reduced metabolic costs and higher trophic efficiency, while intermediate depths (100–300 m) supported the highest biomass levels across regions (3.2 p72). Primary productivity, as a proxy for food availability, positively influenced biomass, although its effects varied across ecosystems. Whereas key drivers of biomass, the SEM studies also showed that biodiversity metrics might be better predictors of biomass than any environmental variables (2.1 p32).

Both the dominance and the complementarity processes were supported by the results to be shaping fish biomass in the North-East Atlantic. This suggests that management strategies should keep on strengthening the current management of key fish populations, which are overwhelmingly corresponding to the main commercial species, as these contribute disproportionately to biomass while also protecting taxonomic and functional diversity. This also supports the need to go from single-species fisheries management towards ecosystem-based fisheries management, that considers not only the more productive species but also biodiversity. Conservation through tools such as MPAs could also help safeguards biodiversity, among which rare species, to enhance ecosystem resilience, functions and services (Marcos et al. 2021; Villasante et al. 2023). In addition, addressing root causes of ecosystem degradation, by mitigating environmental stressors such as warming and habitat loss and alleviating human pressures on the marine ecosystems through better marine spatial planning and rethinking of the blue economy, such as post-growth, will be key for maintaining fish biomass and associated ecosystem services (Hadjimichael, 2018).

What drives fish community stability and resilience?

Fish community stability and resilience are essential for sustaining ecosystem services, such as seafood provisioning, under changing environmental conditions. The studies in this deliverable identified key drivers of stability, including biodiversity indicators like species richness and evenness, as well as environmental factors such as salinity, depth, and productivity (4.2 p102 and 4.3 p108). Environmental gradients, such as salinity and depth, were found to strongly influence stability at broad spatial scales. For example, stability was higher in areas with low salinity and greater depth, likely due to the presence of long-lived, slow-growing species that contribute to community resilience (4.2 p102). Anthropogenic pressures, such as fishing, negatively impacted stability by reducing species evenness and increasing dominance, highlighting the need for sustainable management practices. High species richness and asynchrony in species dynamics were consistently associated with greater stability, supporting the portfolio effect hypothesis (4.3 p108). Communities with asynchronous species fluctuations were better able to buffer environmental variability, showing the importance of maintaining diverse communities.

These findings support the importance of biodiversity conservation to enhance community stability and resilience. As stated earlier, this highlights the need to, among others, focus on reducing anthropogenic pressures and protecting key species and functional groups to maintain ecosystem stability and resilience. MPAs can potentially be a useful tool in preserving temporal stability of fish species diversity (Pettersen et al. 2022). Additionally, understanding of the drivers on stability is still little known and calls for more research (Donohue et al. 2016), in line with the studies included in this deliverable. A greater incorporation of stability metrics into ecosystem-based management approaches can help ensure the long-term sustainability of marine resources.

Next steps in biodiversity and ecosystem (multi-)functions and services

Understanding and predicting the links between biodiversity, ecosystem functions, and ecosystem services remain a significant challenge due to the complexity of these relationships. While this deliverable provides valuable insights into individual EF and ES, and notably the drivers of fish biomass and ecosystem stability, future research should aim to integrate multiple EF and ES into their analyses to account for potential trade-offs and synergies. For example, the drivers of fish biomass may differ from those of carbon sequestration, and enhancing one service may come at the expense of another. The inevitable trade-offs between ecosystem services also points to the need for prioritization of ecosystem services through stakeholders' management (Custodio et al. 2022). In addition, quantitative multi-functionality or -services frameworks, as investigated in 4.1 (p96), which consider multiple EF simultaneously, offer a promising approach to addressing these challenges (Byrnes et al. 2014).

Future research should also focus on establishing stronger empirical links between biodiversity and ES, particularly for under investigated services such as climate regulation and waste recycling, or emerging ones such as renewable energy. Offshore wind farms were shown to have both positive and negative impacts on biodiversity and ecosystem services, depending on the construction and operational phases (Watson et al. 2024), for instance construction activities predominantly caused negative effects on fish and bird populations, but the study also highlighted significant knowledge gaps of potential ES impacts from offshore wind farms.

The next steps in this project will involve predicting EF and ES in European Seas under future scenarios, incorporating both biodiversity and environmental drivers. These predictions will provide valuable insights into the potential impacts of climate change and anthropogenic pressures on marine ecosystems and can help inform adaptive management strategies.

By advancing our understanding of biodiversity-EF/ES relationships and integrating these insights into decision-making, we can develop more effective conservation and management strategies to protect marine ecosystems and the benefits that they provide to us and the future generations to come.

Appendices

The *Appendices* linked to this report comprise annex material regarding the development of the Global Conceptual Network of the Ecosystem Services associated to Bentho-demersal Fish and Invertebrate Diversity across European Seas. Appendix 1: the guidelines shared with experts to provide their input. Appendix 2: the spreadsheet containing the list of links for experts to fill and the definitions of the system components.

APPENDIX 1: GUIDELINES FOR EXPERT INPUT ON ECOSYSTEM SERVICE NETWORK.

Scope of the task:

CONCEPTUAL NETWORK OF THE ECOSYSTEM SERVICES ASSOCIATED TO BENTHO-DEMERSAL FISH AND INVERTEBRATE DIVERSITY ACROSS EUROPEAN SEAS

Dear colleagues, we invite you to help us develop this network (that will feed into a B-USEFUL deliverable and derived studies and publications) by filling out the links between ecosystem elements in the attached spreadsheet.

The spreadsheet contains a list that looks like this:

Element A (cause)	Element B (effect)	Direction of the link	Strength of link	Confidence	Comments
…	…	…	…	…	…
…	…	…	…	…	…

We are interested in your thoughts on how elements under column "Element A" interact with elements in column "Element B", and how the nature of their relationship is, based on your knowledge and experience studying marine ecosystems. If you think there is a **direct causal link** (from A to B) you would specify in the column "Direction of the link" whether you think this link is linear and positive, linear and negative, non-linear or context dependent. If you think **there is no causal link among the elements, or if there is a link but it is probably not direct** (it depends on a third variable or process) you would go for "None" in the "Direction" column.

The task may seem quite detailed, but we encourage you to take a low-key approach, focusing on initial impressions rather than overthinking each link.

Suggested Approach:

- **Daily Target**: Aim for ~50 links/day.
- **Scale**: think at links between the elements at European level, so from Mediterranean to NE Atlantic (excluding the Baltic!), and think rather spatially than temporally. Sometimes, the temporal aspect might be much clearer to you, if so and you thought temporally when filling the link make a note in the "Comments" column.

Uncertainty and optional research: When you are not sure at all of the existence or direction of a link, consider the possibility of it not being clearly positive or negative (Not_clear), or them not being **directly**

causally linked (None). You may suggest supporting info, but do avoid extensive literature searches or the task will become too time-consuming.

Examples and how will your inputs be interpreted:

To get started, you would consider, for example:

> *Is there a direct causal relationship between Temperature and Primary Production? (e.g., does higher temperature cause higher primary production?).*

These are four possible combinations of how you could rate the direction, strength, and confidence of the link between ecosystem variables, as well as how we will interpret them:

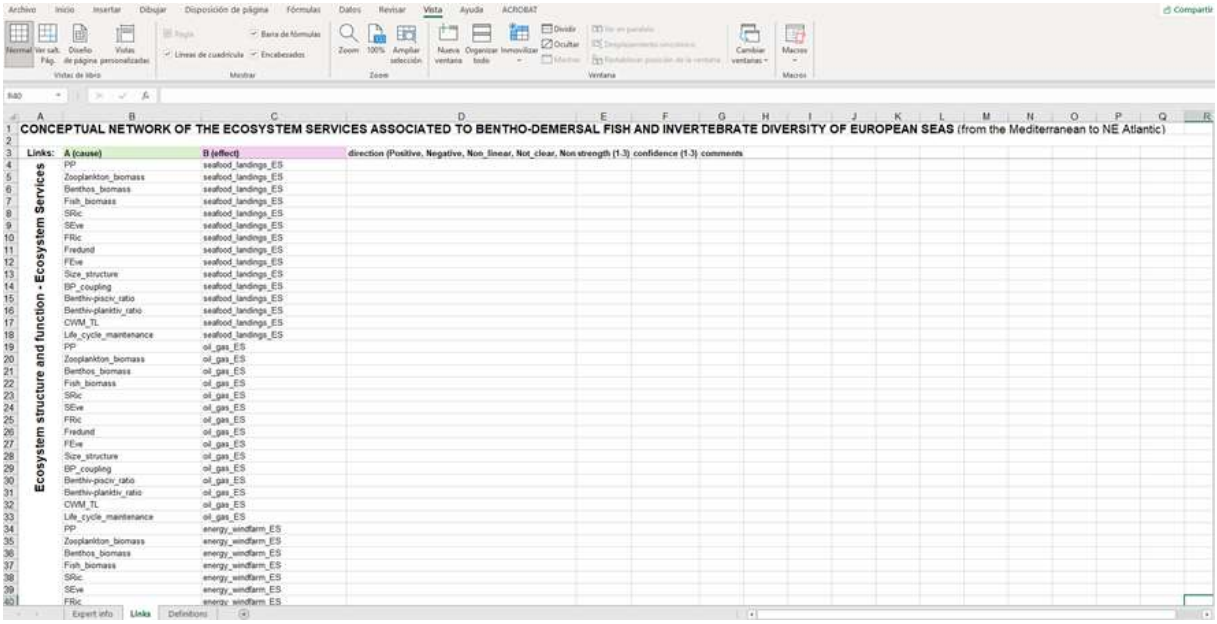
Element A (cause)	Element B (effect)	Direction of the link	Strength of link	Confidence
Temperature	PP	*Positive*	*3*	*1*
		Not_clear	*1*	*2*
		Non_linear	*3*	*1*
		None		*3*

- Primary production strongly increases with T°. You have low confidence in this.
- Either the causal link between T° and Primary production is at some scales positive and some other negative, or there are cases in which its modality changes (non-stationarity, for example, if depending on the region the response shifts from linear to non-linear). Your confidence level for this is moderate.
- Primary production is strongly influenced by T°, in a non-linear manner. You have low confidence in this.
- You are certain that there is not a causal (and/or) direct link between PP and T°

  * In the case of a "None", you can leave the "Strength" blank or set any value.

Thank you so much for participating in this collective effort!

APPENDIX 2: Spreadsheet for the collection of expert input.



CONCEPTUAL NETWORK OF THE ECOSYSTEM SERVICES ASSOCIATED TO BENTHO-DEMERSAL FISH AND INVERTEBRATE DIVERSITY OF EUROPEAN SEAS (from the Mediterranean to NE Atlantic)

Links:	A (cause)	B (effect)	direction (Positive, Negative, Non_linear, Not_clear, Non strength (1-3) confidence (1-3) comments
Ecosystem structure and function - Ecosystem Services	PP	seafood_landings_ES	
	Zooplankton_biomass	seafood_landings_ES	
	Benthos_biomass	seafood_landings_ES	
	Fish_biomass	seafood_landings_ES	
	SRic	seafood_landings_ES	
	SEve	seafood_landings_ES	
	FRic	seafood_landings_ES	
	Fredund	seafood_landings_ES	
	FEve	seafood_landings_ES	
	Size_structure	seafood_landings_ES	
	BP_coupling	seafood_landings_ES	
	Benthiv-pisciv_ratio	seafood_landings_ES	
	Benthiv-planktiv_ratio	seafood_landings_ES	
	CWM_TL	seafood_landings_ES	
	Life_cycle_maintenance	seafood_landings_ES	
	PP	oil_gas_ES	
	Zooplankton_biomass	oil_gas_ES	
	Benthos_biomass	oil_gas_ES	
	Fish_biomass	oil_gas_ES	
	SRic	oil_gas_ES	
	SEve	oil_gas_ES	
	FRic	oil_gas_ES	
	Fredund	oil_gas_ES	
	FEve	oil_gas_ES	
	Size_structure	oil_gas_ES	
	BP_coupling	oil_gas_ES	
	Benthiv-pisciv_ratio	oil_gas_ES	
	Benthiv-planktiv_ratio	oil_gas_ES	
	CWM_TL	oil_gas_ES	
	Life_cycle_maintenance	oil_gas_ES	
	PP	energy_windfarm_ES	
	Zooplankton_biomass	energy_windfarm_ES	
	Benthos_biomass	energy_windfarm_ES	
	Fish_biomass	energy_windfarm_ES	
	SRic	energy_windfarm_ES	
	SEve	energy_windfarm_ES	
	FRic	energy_windfarm_ES	

References

Aarflot, J. M., Bjørdal, V. R., Dunlop, K. M., Espinasse, M., Husson, B., Lindstrøm, U., Keulder-Stenevik, F., Ono, K., Siwertsson, A., & Skern-Mauritzen, M. (2024). Ecosystem risk from human use of ocean space and resources: A case study from the Norwegian coast. Ocean & Coastal Management, 256, 107299. https://doi.org/10.1016/j.ocecoaman.2024.107299

Agnetta, D., Vascotto, I., Panzeri, D., Celić, I., Solidoro, C., Fortibuoni, T., Raicevich, S., & Libralato, S. (2025). Bottom trawling and environmental variables drive the biodiversity of mediterranean demersal assemblages. Scientific Reports, 15(1), 27188. https://doi.org/10.1038/s41598-025-12258-2

Alcorlo, P., García-Tiscar, S., Vidal-Abarca, M. R., Suárez-Alonso, M. L., & Santos-Martín, F. (2023). Unravelling Complex Interaction among Coastal Management and Marine Biodiversity: A Case Study in Southern Spain. Sustainability, 15(8), 6544. https://doi.org/10.3390/su15086544

Alheit, J., Möllmann, C., Dutz, J., Kornilovs, G., Loewe, P., Mohrholz, V., & Wasmund, N. (2005). Synchronous ecological regime shifts in the central Baltic and the North Sea in the late 1980s. ICES Journal of Marine Science, 62(7), 1205–1215. https://doi.org/10.1016/j.icesjms.2005.04.024

Ali, A. (2023). Biodiversity–ecosystem functioning research: Brief history, major trends and perspectives. Biological Conservation, 285, 110210. https://doi.org/10.1016/j.biocon.2023.110210

Allgeier, J. E., Valdivia, A., Cox, C., & Layman, C. A. (2016). Fishing down nutrients on coral reefs. Nature Communications, 7(1), 12461. https://doi.org/10.1038/ncomms12461

Anderson, S. C., Cooper, A. B., & Dulvy, N. K. (2013). Ecological prophets: Quantifying metapopulation portfolio effects. Methods in Ecology and Evolution, 4(10), 971–981. https://doi.org/10.1111/2041-210X.12093

Anderson, S. C., Ward, E. J., English, P. A., Barnett, L. A. K., & Thorson, J. T. (2022). sdmTMB: An R Package for Fast, Flexible, and User-Friendly Generalized Linear Mixed Effects Models with Spatial and Spatiotemporal Random Fields. Ecology. https://doi.org/10.1101/2022.03.24.485545

Anderson, S. C., Ward, E. J., English, P. A., Barnett, L. A. K., & Thorson, J. T. (2024). sdmTMB: An R Package for Fast, Flexible, and User-Friendly Generalized Linear Mixed Effects Models with Spatial and Spatiotemporal Random Fields (p. 2022.03.24.485545). bioRxiv. https://doi.org/10.1101/2022.03.24.485545

Armoškaitė, A., Puriņa, I., Aigars, J., Strāķe, S., Pakalniete, K., Frederiksen, P., Schrøder, L., & Hansen, H. S. (2020). Establishing the links between marine ecosystem components, functions and services: An ecosystem service assessment tool. Ocean & Coastal Management, 193, 105229. https://doi.org/10.1016/j.ocecoaman.2020.105229

Arnoldi, J.-F., Loreau, M., & Haegeman, B. (2019). The inherent multidimensionality of temporal variability: How common and rare species shape stability patterns. Ecology Letters, 22(10), 1557–1567. https://doi.org/10.1111/ele.13345

Arroyo, N.-L., Safi, G., Vouriot, P., López-López, L., Niquil, N., Le Loc'h, F., Hattab, T., & Preciado, I. (2019). Towards coherent GES assessments at sub-regional level: Signs of fisheries expansion processes in the Bay of Biscay using an OSPAR food web indicator, the mean trophic level. ICES Journal of Marine Science, 76(6), 1543–1553. https://doi.org/10.1093/icesjms/fsz023

Aschan, M., Fossheim, M., Greenacre, M., & Primicerio, R. (2013). Change in Fish Community Structure in the Barents Sea. PLOS ONE, 8(4), e62748. https://doi.org/10.1371/journal.pone.0062748

Aune, M., Aschan, M. M., Greenacre, M., Dolgov, A. V., Fossheim, M., & Primicerio, R. (2018). Functional roles and redundancy of demersal Barents Sea fish: Ecological implications of environmental change. PLOS ONE, 13(11), e0207451. https://doi.org/10.1371/journal.pone.0207451

Aurelle, D., Thomas, S., Albert, C., Bally, M., Bondeau, A., Boudouresque, C.-F., Cahill, A. E., Carlotti, F., Chenuil, A., Cramer, W., Davi, H., De Jode, A., Ereskovsky, A., Farnet, A.-M., Fernandez, C., Gauquelin, T., Mirleau, P., Monnet, A.-C., Prévosto, B., … Fady, B. (2022). Biodiversity, climate change, and adaptation in the Mediterranean. Ecosphere, 13(4), e3915. https://doi.org/10.1002/ecs2.3915

Azzurro, E., Sbragaglia, V., Cerri, J., Bariche, M., Bolognini, L., Ben Souissi, J., Busoni, G., Coco, S., Chryssanthi, A., Fanelli, E., Ghanem, R., Garrabou, J., Gianni, F., Grati, F., Kolitari, J., Letterio, G., Lipej, L., Mazzoldi, C., Milone, N., … Moschella, P. (2019). Climate change, biological invasions, and the shifting distribution of Mediterranean fishes:

A large-scale survey based on local ecological knowledge. Global Change Biology, 25(8), 2779–2792. https://doi.org/10.1111/gcb.14670

Balvanera, P., Pfisterer, A. B., Buchmann, N., He, J.-S., Nakashizuka, T., Raffaelli, D., & Schmid, B. (2006). Quantifying the evidence for biodiversity effects on ecosystem functioning and services. Ecology Letters, 9(10), 1146–1156. https://doi.org/10.1111/j.1461-0248.2006.00963.x

Bañón, R., Pardo, P. C., Álvarez-Salgado, X. A., de Carlos, A., Arronte, J. C., & Piedracoba, S. (2024). Tropicalization of fish fauna of Galician coastal waters, in the NW Iberian upwelling system. Regional Studies in Marine Science, 70, 103369. https://doi.org/10.1016/j.rsma.2024.103369

Barnes, C., Bethea, D. M., Brodeur, R. D., Spitz, J., Ridoux, V., Pusineri, C., Chase, B. C., Hunsicker, M. E., Juanes, F., Kellermann, A., Lancaster, J., Ménard, F., Bard, F.-X., Munk, P., Pinnegar, J. K., Scharf, F. S., Rountree, R. A., Stergiou, K. I., Sassa, C., … Jennings, S. (2008). Predator and Prey Body Sizes in Marine Food Webs. Ecology, 89(3), 881–881. https://doi.org/10.1890/07-1551.1

Barnes, R., Sahr, K., Evenden, G., Johnson, A., & Warmerdam, F. (2017). dggridR: discrete global grids for R. *R package version 0.1*, *12*, 963.

Bar-On, Y. M., Phillips, R., & Milo, R. (2018). The biomass distribution on Earth. Proceedings of the National Academy of Sciences, 115(25), 6506–6511. https://doi.org/10.1073/pnas.1711842115

Barton, K. (2012). MuMIn: Multi-model inference. R package version 1.7.2. Http://CRAN.R-Project.Org/package=MuMIn. https://cir.nii.ac.jp/crid/1571417126341064832

Baudron, A. R., Needle, C. L., Rijnsdorp, A. D., & Tara Marshall, C. (2014). Warming temperatures and smaller body sizes: Synchronous changes in growth of North Sea fishes. Global Change Biology, 20(4), 1023–1031. https://doi.org/10.1111/gcb.12514

Beaugrand, G. (2004). The North Sea regime shift: Evidence, causes, mechanisms and consequences. Progress in Oceanography, Regime Shifts in the Ocean. Reconciling Observations and Theory, 60(2), 245–262. https://doi.org/10.1016/j.pocean.2004.02.018

Bell, R. J., Fogarty, M. J., & Collie, J. S. (2014). Stability in marine fish communities. Marine Ecology Progress Series, 504, 221–239. https://doi.org/10.3354/meps10730

Bensebaini, C. M., Certain, G., Gourguet, S., Thébaud, O., Hattab, T., Billet, N., Jadaud, A., & Fromentin, J.-M. (2025). Identifying statistical interaction networks in marine communities using multivariate time series analysis: An application in the Gulf of Lions. Fisheries Research, 281, 107177. https://doi.org/10.1016/j.fishres.2024.107177

Bernardo, C. P., Pecuchet, L., Husson, B., Morais, D. K., Polo, J., Santos, J., & Primicerio, R. (in press). Rapid climate change impacts spatial patterns of fish size-structure in a subarctic ecosystem.

Bernardo, C. P., Pecuchet, L., Santos, J., Dolgov, A. V., Fossheim, M., Husson, B., & Primicerio, R. (2024). Warming changes the life history composition of marine fish communities at high latitudes. Marine Ecology Progress Series, 732, 119–133. https://doi.org/10.3354/meps14537

Beukhof, E., Dencker, T. S., Palomares, M. L. D., & Maureaud, A. A. (2019). A trait collection of marine fish species from North Atlantic and Northeast Pacific continental shelf seas [Data set]. PANGAEA. https://doi.org/10.1594/PANGAEA.900866

Beukhof, E., Dencker, T. S., Pecuchet, L., & Lindegren, M. (2019). Spatio-temporal variation in marine fish traits reveals community-wide responses to environmental change. Marine Ecology Progress Series, 610, 205–222. https://doi.org/10.3354/meps12826

Beukhof, E., Frelat, R., Pecuchet, L., Maureaud, A. A., Dencker, T. S., Sólmundsson, J., Punzón, A., Primicerio, R., Hidalgo, M., Möllmann, C., & Lindegren, M. (2019). Marine fish traits follow fast-slow continuum across oceans. Scientific Reports, 9(1), 17878. https://doi.org/10.1038/s41598-019-53998-2

Blonder, B., Lamanna, C., Violle, C., & Enquist, B. J. (2014). The n-dimensional hypervolume. Global Ecology and Biogeography, 23(5), 595–609. https://doi.org/10.1111/geb.12146

Blonder, B., Morrow, C. B., Maitner, B., Harris, D. J., Lamanna, C., Violle, C., Enquist, B. J., & Kerkhoff, A. J. (2018). New approaches for delineating n-dimensional hypervolumes. Methods in Ecology and Evolution, 9(2), 305–319. https://doi.org/10.1111/2041-210X.12865

Bosch, N. E., Monk, J., Goetze, J., Wilson, S., Babcock, R. C., Barrett, N., Clough, J., Currey-Randall, L. M., Fairclough, D. V., Fisher, R., Gibbons, B. A., Harasti, D., Harvey, E. S., Heupel, M. R., Hicks, J. L., Holmes, T. H., Huveneers, C., Ierodiaconou, D., Jordan, A., … Langlois, T. J. (2022). Effects of human footprint and biophysical factors on the body-size structure of fished marine species. Conservation Biology, 36(2), e13807. https://doi.org/10.1111/cobi.13807

Bowler, D. E., Bjorkman, A. D., Dornelas, M., Myers-Smith, I. H., Navarro, L. M., Niamir, A., Supp, S. R., Waldock, C., Winter, M., Vellend, M., Blowes, S. A., Böhning-Gaese, K., Bruelheide, H., Elahi, R., Antão, L. H., Hines, J., Isbell, F., Jones, H. P., Magurran, A. E., … Bates, A. E. (2020). Mapping human pressures on biodiversity across the planet uncovers anthropogenic threat complexes. People and Nature, 2(2), 380–394. https://doi.org/10.1002/pan3.10071

Brandl, S. J., Rasher, D. B., Côté, I. M., Casey, J. M., Darling, E. S., Lefcheck, J. S., & Duffy, J. E. (2019). Coral reef ecosystem functioning: Eight core processes and the role of biodiversity. Frontiers in Ecology and the Environment, 17(8), 445–454. https://doi.org/10.1002/fee.2088

Broszeit, S., Beaumont, N. J., Hooper, T. L., Somerfield, P. J., & Austen, M. C. (2019). Developing conceptual models that link multiple ecosystem services to ecological research to aid management and policy, the UK marine example. Marine Pollution Bulletin, 141, 236–243. https://doi.org/10.1016/j.marpolbul.2019.02.051

Brown, J. H., Gillooly, J. F., Allen, A. P., Savage, V. M., & West, G. B. (2004). Toward a Metabolic Theory of Ecology. Ecology, 85(7), 1771–1789. https://doi.org/10.1890/03-9000

Bryhn, A., Kraufvelin, P., Bergström, U., Vretborn, M., & Bergström, L. (2020). A Model for Disentangling Dependencies and Impacts among Human Activities and Marine Ecosystem Services. Environmental Management, 65(5), 575–586. https://doi.org/10.1007/s00267-020-01260-1

Bryndum-Buchholz, A., Tittensor, D. P., Blanchard, J. L., Cheung, W. W. L., Coll, M., Galbraith, E. D., Jennings, S., Maury, O., & Lotze, H. K. (2019). Twenty-first-century climate change impacts on marine animal biomass and ecosystem structure across ocean basins. Global Change Biology, 25(2), 459–472. https://doi.org/10.1111/gcb.14512

Byrnes, J. E., Gamfeldt, L., Isbell, F., Lefcheck, J. S., Griffin, J. N., Hector, A., ... & Emmett Duffy, J. (2014). Investigating the relationship between biodiversity and ecosystem multifunctionality: challenges and solutions. Methods in Ecology and Evolution, 5(2), 111-124.

Cardinale, B. J., Srivastava, D. S., Emmett Duffy, J., Wright, J. P., Downing, A. L., Sankaran, M., & Jouseau, C. (2006). Effects of biodiversity on the functioning of trophic groups and ecosystems. Nature, 443(7114), 989–992. https://doi.org/10.1038/nature05202

Chassot, E., Bonhommeau, S., Dulvy, N. K., Mélin, F., Watson, R., Gascuel, D., & Le Pape, O. (2010). Global marine primary production constrains fisheries catches. Ecology Letters, 13(4), 495–505. https://doi.org/10.1111/j.1461-0248.2010.01443.x

Cinner, J. E., Maire, E., Huchery, C., MacNeil, M. A., Graham, N. A. J., Mora, C., McClanahan, T. R., Barnes, M. L., Kittinger, J. N., Hicks, C. C., D'Agata, S., Hoey, A. S., Gurney, G. G., Feary, D. A., Williams, I. D., Kulbicki, M., Vigliola, L., Wantiez, L., Edgar, G. J., … Mouillot, D. (2018). Gravity of human impacts mediates coral reef conservation gains. Proceedings of the National Academy of Sciences, 115(27), E6116–E6125. https://doi.org/10.1073/pnas.1708001115

Clausen, L. W., Rindorf, A., van Deurs, M., Dickey-Collas, M., & Hintzen, N. T. (2018). Shifts in North Sea forage fish productivity and potential fisheries yield. Journal of Applied Ecology, 55(3), 1092–1101. https://doi.org/10.1111/1365-2664.13038

Cobain, M. R. D., Brede, M., & Trueman, C. N. (2019). Taylor's power law captures the effects of environmental variability on community structure: An example from fishes in the North Sea. Journal of Animal Ecology, 88(2), 290–301. https://doi.org/10.1111/1365-2656.12923

Coll, M., Bellido, J. M., Pennino, M. G., Albo-Puigserver, M., Báez, J. C., Christensen, V., Corrales, X., Fernández-Corredor, E., Giménez, J., Julià, L., Lloret-Lloret, E., Macias, D., Ouled-Cheikh, J., Ramírez, F., Sbragaglia, V., & Steenbeek, J. (2024). Retrospective analysis of the pelagic ecosystem of the Western Mediterranean Sea: Drivers, changes and effects. Science of The Total Environment, 907, 167790. https://doi.org/10.1016/j.scitotenv.2023.167790

Coll, M., Piroddi, C., Albouy, C., Ben Rais Lasram, F., Cheung, W. W. L., Christensen, V., Karpouzi, V. S., Guilhaumon, F., Mouillot, D., Paleczny, M., Palomares, M. L., Steenbeek, J., Trujillo, P., Watson, R., & Pauly, D. (2012). The Mediterranean Sea under siege: Spatial overlap between marine biodiversity, cumulative threats and marine reserves. Global Ecology and Biogeography, 21(4), 465–480. https://doi.org/10.1111/j.1466-8238.2011.00697.x

Coll, M., Piroddi, C., Steenbeek, J., Kaschner, K., Lasram, F. B. R., Aguzzi, J., Ballesteros, E., Bianchi, C. N., Corbera, J., Dailianis, T., Danovaro, R., Estrada, M., Froglia, C., Galil, B. S., Gasol, J. M., Gertwagen, R., Gil, J., Guilhaumon, F., Kesner-Reyes, K., … Voultsiadou, E. (2010). The Biodiversity of the Mediterranean Sea: Estimates, Patterns, and Threats. PLOS ONE, 5(8), e11842. https://doi.org/10.1371/journal.pone.0011842

Colloca, F., Scarcella, G., & Libralato, S. (2017). Recent Trends and Impacts of Fisheries Exploitation on Mediterranean Stocks and Ecosystems. Frontiers in Marine Science, 4. https://doi.org/10.3389/fmars.2017.00244

Cossarini, G., Feudale, L., Teruzzi, A., Bolzon, G., Coidessa, G., Solidoro, C., Di Biagio, V., Amadio, C., Lazzari, P., Brosich, A., & Salon, S. (2021). High-Resolution Reanalysis of the Mediterranean Sea Biogeochemistry (1999–2019). Frontiers in Marine Science, 8. https://doi.org/10.3389/fmars.2021.741486

Costello, C., Cao, L., Gelcich, S., Cisneros-Mata, M. Á., Free, C. M., Froehlich, H. E., Golden, C. D., Ishimura, G., Maier, J., Macadam-Somer, I., Mangin, T., Melnychuk, M. C., Miyahara, M., de Moor, C. L., Naylor, R., Nøstbakken, L., Ojea, E., O'Reilly, E., Parma, A. M., … Lubchenco, J. (2020). The future of food from the sea. Nature, 588(7836), 95–100. https://doi.org/10.1038/s41586-020-2616-y

Couce, E., Schratzberger, M., & Engelhard, G. H. (2020). Reconstructing three decades of total international trawling effort in the North Sea. Earth System Science Data, 12(1), 373–386. https://doi.org/10.5194/essd-12-373-2020

Cramer, W., Guiot, J., Fader, M., Garrabou, J., Gattuso, J.-P., Iglesias, A., Lange, M. A., Lionello, P., Llasat, M. C., Paz, S., Peñuelas, J., Snoussi, M., Toreti, A., Tsimplis, M. N., & Xoplaki, E. (2018). Climate change and interconnected risks to sustainable development in the Mediterranean. Nature Climate Change, 8(11), 972–980. https://doi.org/10.1038/s41558-018-0299-2

Craven, D., Eisenhauer, N., Pearse, W. D., Hautier, Y., Isbell, F., Roscher, C., Bahn, M., Beierkuhnlein, C., Bönisch, G., Buchmann, N., Byun, C., Catford, J. A., Cerabolini, B. E. L., Cornelissen, J. H. C., Craine, J. M., De Luca, E., Ebeling, A., Griffin, J. N., Hector, A., … Manning, P. (2018). Multiple facets of biodiversity drive the diversity–stability relationship. Nature Ecology & Evolution, 2(10), 1579–1587. https://doi.org/10.1038/s41559-018-0647-7

Crielaard, L., Quax, R., Sawyer, A. D., Vasconcelos, V. V., Nicolaou, M., Stronks, K., & Sloot, P. M. (2023). Using network analysis to identify leverage points based on causal loop diagrams leads to false inference. Scientific reports, 13(1), 21046.

Custodio, M., Moulaert, I., Asselman, J., Van der Biest, K., van de Pol, L., Drouillon, M., ... & Everaert, G. (2022). Prioritizing ecosystem services for marine management through stakeholder engagement. Ocean & Coastal Management, 225, 106228.

Danet, A., Mouchet, M., Bonnaffé, W., Thébault, E., & Fontaine, C. (2021). Species richness and food-web structure jointly drive community biomass and its temporal stability in fish communities. Ecology Letters, 24(11), 2364–2377. https://doi.org/10.1111/ele.13857

de Bello, F., Botta-Dukát, Z., Lepš, J., & Fibich, P. (2021). Towards a more balanced combination of multiple traits when computing functional differences between species. Methods in Ecology and Evolution, 12(3), 443–448. https://doi.org/10.1111/2041-210X.13537

de Mazancourt, C., Isbell, F., Larocque, A., Berendse, F., De Luca, E., Grace, J. B., Haegeman, B., Wayne Polley, H., Roscher, C., Schmid, B., Tilman, D., van Ruijven, J., Weigelt, A., Wilsey, B. J., & Loreau, M. (2013). Predicting ecosystem stability from community composition and biodiversity. Ecology Letters, 16(5), 617–625. https://doi.org/10.1111/ele.12088

Dee, L. E., Cowles, J., Isbell, F., Pau, S., Gaines, S. D., & Reich, P. B. (2019). When do ecosystem services depend on rare species?. Trends in ecology & evolution, 34(8), 746-758.

Dencker, T. S., Pecuchet, L., Beukhof, E., Richardson, K., Payne, M. R., & Lindegren, M. (2017). Temporal and spatial differences between taxonomic and trait biodiversity in a large marine ecosystem: Causes and consequences. PLOS ONE, 12(12), e0189731. https://doi.org/10.1371/journal.pone.0189731

Díaz, S., Demissew, S., Carabias, J., Joly, C., Lonsdale, M., Ash, N., Larigauderie, A., Adhikari, J. R., Arico, S., Báldi, A., Bartuska, A., Baste, I. A., Bilgin, A., Brondizio, E., Chan, K. M., Figueroa, V. E., Duraiappah, A., Fischer, M., Hill, R., … Zlatanova, D. (2015). The IPBES Conceptual Framework—Connecting nature and people. Current Opinion in Environmental Sustainability, Open Issue, 14, 1–16. https://doi.org/10.1016/j.cosust.2014.11.002

Díaz, S., Settele, J., Brondízio, E. S., Ngo, H. T., Agard, J., Arneth, A., Balvanera, P., Brauman, K. A., Butchart, S. H. M., Chan, K. M. A., Garibaldi, L. A., Ichii, K., Liu, J., Subramanian, S. M., Midgley, G. F., Miloslavich, P., Molnár, Z., Obura, D., Pfaff, A., … Zayas, C. N. (2019a). Pervasive human-driven decline of life on Earth points to the need for transformative change. Science, 366(6471), eaax3100. https://doi.org/10.1126/science.aax3100

Díaz, S., Settele, J., Brondízio, E. S., Ngo, H. T., Agard, J., Arneth, A., Balvanera, P., Brauman, K. A., Butchart, S. H. M., Chan, K. M. A., Garibaldi, L. A., Ichii, K., Liu, J., Subramanian, S. M., Midgley, G. F., Miloslavich, P., Molnár, Z., Obura, D., Pfaff, A., … Zayas, C. N. (2019b). Pervasive human-driven decline of life on Earth points to the need for transformative change. Science, 366(6471), eaax3100. https://doi.org/10.1126/science.aax3100

Dickey-Collas, M., Nash, R. D. M., Brunel, T., van Damme, C. J. G., Marshall, C. T., Payne, M. R., Corten, A., Geffen, A. J., Peck, M. A., Hatfield, E. M. C., Hintzen, N. T., Enberg, K., Kell, L. T., & Simmonds, E. J. (2010). Lessons learned from stock collapse and recovery of North Sea herring: A review. ICES Journal of Marine Science, 67(9), 1875–1886. https://doi.org/10.1093/icesjms/fsq033

DTM (2024). EMODnet Digital Bathymetry. EMODnet Bathymetry Consortium https://doi.org/10.12770/cf51df64-56f9-4a99-b1aa-36b8d7b743a1.

Doak, D. F., Bigger, D., Harding, E. K., Marvier, M. A., O, 'Malley R. E., & Thomson, D. (1998). The Statistical Inevitability of Stability-Diversity Relationships in Community Ecology. The American Naturalist, 151(3), 264–276. https://doi.org/10.1086/286117

Donohue, I., Hillebrand, H., Montoya, J. M., Petchey, O. L., Pimm, S. L., Fowler, M. S., Healy, K., Jackson, A. L., Lurgi, M., McClean, D., O'Connor, N. E., O'Gorman, E. J., & Yang, Q. (2016). Navigating the complexity of ecological stability. Ecology Letters, 19(9), 1172–1185. https://doi.org/10.1111/ele.12648

Donohue, I., Petchey, O. L., Montoya, J. M., Jackson, A. L., McNally, L., Viana, M., Healy, K., Lurgi, M., O'Connor, N. E., & Emmerson, M. C. (2013). On the dimensionality of ecological stability. Ecology Letters, 16(4), 421–429. https://doi.org/10.1111/ele.12086

D'Ortenzio, F., & Ribera d'Alcalà, M. (2009). On the trophic regimes of the Mediterranean Sea: A satellite analysis. Biogeosciences, 6(2), 139–148. https://doi.org/10.5194/bg-6-139-2009

Downing, A. L., Brown, B. L., & Leibold, M. A. (2014). Multiple diversity–stability mechanisms enhance population and community stability in aquatic food webs. Ecology, 95(1), 173–184. https://doi.org/10.1890/12-1406.1

Duffy, J. E., Godwin, C. M., & Cardinale, B. J. (2017). Biodiversity effects in the wild are common and as strong as key drivers of productivity. Nature, 549(7671), 261–264. https://doi.org/10.1038/nature23886

Duffy, J. E., Lefcheck, J. S., Stuart-Smith, R. D., Navarrete, S. A., & Edgar, G. J. (2016). Biodiversity enhances reef fish biomass and resistance to climate change. Proceedings of the National Academy of Sciences, 113(22), 6230–6235. https://doi.org/10.1073/pnas.1524465113

Durant, J. M., Holt, R. E., & Langangen, Ø. (2024). Large biomass reduction effect on the relative role of climate, fishing, and recruitment on fish population dynamics. Scientific Reports, 14(1), 8995. https://doi.org/10.1038/s41598-024-59569-4

Eddy, T. D., Bernhardt, J. R., Blanchard, J. L., Cheung, W. W. L., Colléter, M., du Pontavice, H., Fulton, E. A., Gascuel, D., Kearney, K. A., Petrik, C. M., Roy, T., Rykaczewski, R. R., Selden, R., Stock, C. A., Wabnitz, C. C. C., & Watson, R. A. (2021). Energy Flow Through Marine Ecosystems: Confronting Transfer Efficiency. Trends in Ecology & Evolution, 36(1), 76–86. https://doi.org/10.1016/j.tree.2020.09.006

Eger, A. M., Best, R. J., & Baum, J. K. (2021). Dominance determines fish community biomass in a temperate seagrass ecosystem. Ecology and Evolution, 11(15), 10489–10501. https://doi.org/10.1002/ece3.7854

Ehlers, P. (2016). Blue growth and ocean governance—How to balance the use and the protection of the seas. WMU Journal of Maritime Affairs, 15(2), 187–203. https://doi.org/10.1007/s13437-016-0104-x

Elliott, M., Burdon, D., Atkins, J. P., Borja, A., Cormier, R., de Jonge, V. N., & Turner, R. K. (2017). "And DPSIR begat DAPSI(W)R(M)!"—A unifying framework for marine environmental management. Marine Pollution Bulletin, 118(1), 27–40. https://doi.org/10.1016/j.marpolbul.2017.03.049

Eriksen, E., Gjøsæter, H., Prozorkevich, D., Shamray, E., Dolgov, A., Skern-Mauritzen, M., Stiansen, J. E., Kovalev, Yu., & Sunnanå, K. (2018). From single species surveys towards monitoring of the Barents Sea ecosystem. Progress in Oceanography, Multidisciplinary Integrated Surveys, 166, 4–14. https://doi.org/10.1016/j.pocean.2017.09.007

Eriksen, E., Husson, B., Skaret, G., Ingvaldsen, R. B., Dalpadado, P., Johannesen, E., Jørgensen, L. L., Bogstad, B., Dolgov, A. V., Prozorkevich, D. V., Prokhorova, T. A., Russkikh, A. A., Strelkova, N. A., Trofimov, A. G., Prokopchuk, I. P., & Filin, A. A. (2025). The living Barents Sea response to peak-warming and subsequent cooling. Scientific Reports, 15(1), 13008. https://doi.org/10.1038/s41598-025-96964-x

Eschenbrenner, J., & Thébault, É. (2023). Diversity, food web structure and the temporal stability of total plant and animal biomasses. Oikos, 2023(2), e08769. https://doi.org/10.1111/oik.08769

Escudier, R., Clementi, E., Cipollone, A., Pistoia, J., Drudi, M., Grandi, A., Lyubartsev, V., Lecci, R., Aydogdu, A., Delrosso, D., Omar, M., Masina, S., Coppini, G., & Pinardi, N. (2021). A High Resolution Reanalysis for the Mediterranean Sea [Ressource électronique]. Frontiers in Earth Science. https://doi.org/10.3389/feart.2021.702285

Falkowski, P. G. (1994). The role of phytoplankton photosynthesis in global biogeochemical cycles. Photosynthesis Research, 39(3), 235–258. https://doi.org/10.1007/BF00014586

FAO. (2024). The State of World Fisheries and Aquaculture 2024. Blue Transformation in action. FAO. https://doi.org/10.4060/cd0683en

Fargione, J., Tilman, D., Dybzinski, R., Lambers, J. H. R., Clark, C., Harpole, W. S., Knops, J. M. H., Reich, P. B., & Loreau, M. (2007). From selection to complementarity: Shifts in the causes of biodiversity–productivity relationships in a long-term biodiversity experiment. Proceedings of the Royal Society B: Biological Sciences, 274(1611), 871–876. https://doi.org/10.1098/rspb.2006.0351

Fernandes, P. G., & Cook, R. M. (2013). Reversal of Fish Stock Decline in the Northeast Atlantic. Current Biology, 23(15), 1432–1437. https://doi.org/10.1016/j.cub.2013.06.016

Flensborg, L. C., Bravo, D. N., & Lindegren, M. (2023). An indicator-based approach for assessing marine ecosystem resilience. ICES Journal of Marine Science, 80(5), 1487–1499. https://doi.org/10.1093/icesjms/fsad077

Fossheim, M., Primicerio, R., Johannesen, E., Ingvaldsen, R. B., Aschan, M. M., & Dolgov, A. V. (2015). Recent warming leads to a rapid borealization of fish communities in the Arctic. Nature Climate Change, 5(7), 673–677. https://doi.org/10.1038/nclimate2647

Frainer, A., Primicerio, R., Dolgov, A., Fossheim, M., Johannesen, E., Lind, S., & Aschan, M. (2021). Increased functional diversity warns of ecological transition in the Arctic. Proceedings of the Royal Society B: Biological Sciences, 288(1948), rspb.2021.0054, 20210054. https://doi.org/10.1098/rspb.2021.0054

Frainer, A., Primicerio, R., Kortsch, S., Aune, M., Dolgov, A. V., Fossheim, M., & Aschan, M. M. (2017). Climate-driven changes in functional biogeography of Arctic marine fish communities. Proceedings of the National Academy of Sciences of the United States of America, 114(46), 12202–12207. https://doi.org/10.1073/pnas.1706080114

Friedland, K. D., Stock, C., Drinkwater, K. F., Link, J. S., Leaf, R. T., Shank, B. V., Rose, J. M., Pilskaln, C. H., & Fogarty, M. J. (2012). Pathways between Primary Production and Fisheries Yields of Large Marine Ecosystems. PLOS ONE, 7(1), e28945. https://doi.org/10.1371/journal.pone.0028945

Froese, R., & Pauly, D. (2025). *FishBase*. https://www.fishbase.org

Fu, C., Large, S., Knight, B., Richardson, A. J., Bundy, A., Reygondeau, G., ... & Shin, Y. J. (2015). Relationships among fisheries exploitation, environmental conditions, and ecological indicators across a series of marine ecosystems. Journal of Marine Systems, 148, 101-111.

Gamfeldt, L., Lefcheck, J. S., Byrnes, J. E. K., Cardinale, B. J., Duffy, J. E., & Griffin, J. N. (2015). Marine biodiversity and ecosystem functioning: What's known and what's next? Oikos, 124(3), 252–265. https://doi.org/10.1111/oik.01549

García-Palacios, P., Gross, N., Gaitán, J., & Maestre, F. T. (2018). Climate mediates the biodiversity–ecosystem stability relationship globally. Proceedings of the National Academy of Sciences, 115(33), 8400–8405. https://doi.org/10.1073/pnas.1800425115

Gari, S. R., Newton, A., & Icely, J. D. (2015). A review of the application and evolution of the DPSIR framework with an emphasis on coastal social-ecological systems. Ocean & Coastal Management, 103, 63–77. https://doi.org/10.1016/j.ocecoaman.2014.11.013

Gerland, S., Ingvaldsen, R. B., Reigstad, M., Sundfjord, A., Bogstad, B., Chierici, M., Hop, H., Renaud, P. E., Smedsrud, L. H., Stige, L. C., Årthun, M., Berge, J., Bluhm, B. A., Borgå, K., Bratbak, G., Divine, D. V., Eldevik, T., Eriksen, E., Fer, I., … Wassmann, P. (2023). Still Arctic?—The changing Barents Sea. Elementa: Science of the Anthropocene, 11(1), 00088. https://doi.org/10.1525/elementa.2022.00088

Gascuel, Didier. 2016. «L'évaluation et la gestion des stocks de poissons». *Institut Océanographique-Fondation Albert 1er de Monaco, Paris*.

Gillooly, J. F., Allen, A. P., West, G. B., & Brown, J. H. (2005). The rate of DNA evolution: Effects of body size and temperature on the molecular clock. Proceedings of the National Academy of Sciences, 102(1), 140–145. https://doi.org/10.1073/pnas.0407735101

Gillooly, J. F., Brown, J. H., West, G. B., Savage, V. M., & Charnov, E. L. (2001). Effects of Size and Temperature on Metabolic Rate. Science, 293(5538), 2248–2251. https://doi.org/10.1126/science.1061967

Gordó-Vilaseca, C., Costello, M. J., Coll, M., Jüterbock, A., Reiss, H., & Stephenson, F. (2024). Future trends of marine fish biomass distributions from the North Sea to the Barents Sea. Nature Communications, 15(1), 5637. https://doi.org/10.1038/s41467-024-49911-9

Gordó-Vilaseca, C., Stephenson, F., Coll, M., Lavin, C., & Costello, M. J. (2023). Three decades of increasing fish biodiversity across the northeast Atlantic and the Arctic Ocean. Proceedings of the National Academy of Sciences, 120(4), e2120869120. https://doi.org/10.1073/pnas.2120869120

Gower, J. C. (1971). A General Coefficient of Similarity and Some of Its Properties. Biometrics, 27(4), 857–871. https://doi.org/10.2307/2528823

Grime, J. P. (1998). Benefits of plant diversity to ecosystems: Immediate, filter and founder effects. Journal of Ecology, 86(6), 902–910. https://doi.org/10.1046/j.1365-2745.1998.00306.x

Gwet, K. L. (2021). Large-Sample Variance of Fleiss Generalized Kappa. Educational and Psychological Measurement, 81(4), 781–790. https://doi.org/10.1177/0013164420973080

Hadjimichael, M. (2018). A call for a blue degrowth: unravelling the European Union's fisheries and maritime policies. Marine Policy, 94, 158-164.

Halpern, B. S., Frazier, M., O'Hara, C. C., Vargas-Fonseca, O. A., & Lombard, A. T. (2025). Cumulative impacts to global marine ecosystems projected to more than double by mid-century. Science, 389(6766), 1216–1219. https://doi.org/10.1126/science.adv2906

Halpern, B. S., Frazier, M., Potapenko, J., Casey, K. S., Koenig, K., Longo, C., Lowndes, J. S., Rockwood, R. C., Selig, E. R., Selkoe, K. A., & Walbridge, S. (2015). Spatial and temporal changes in cumulative human impacts on the world's ocean. Nature Communications, 6(1), 7615. https://doi.org/10.1038/ncomms8615

Halpern, B. S., Longo, C., Hardy, D., McLeod, K. L., Samhouri, J. F., Katona, S. K., Kleisner, K., Lester, S. E., O'Leary, J., Ranelletti, M., Rosenberg, A. A., Scarborough, C., Selig, E. R., Best, B. D., Brumbaugh, D. R., Chapin, F. S., Crowder, L. B., Daly, K. L., Doney, S. C., … Zeller, D. (2012). An index to assess the health and benefits of the global ocean. Nature, 488(7413), 615–620. https://doi.org/10.1038/nature11397

Halpern, B. S., Walbridge, S., Selkoe, K. A., Kappel, C. V., Micheli, F., D'Agrosa, C., Bruno, J. F., Casey, K. S., Ebert, C., Fox, H. E., Fujita, R., Heinemann, D., Lenihan, H. S., Madin, E. M. P., Perry, M. T., Selig, E. R., Spalding, M., Steneck, R., & Watson, R. (2008). A Global Map of Human Impact on Marine Ecosystems. Science, 319(5865), 948–952. https://doi.org/10.1126/science.1149345

Hamel, J.-F. (2018). World Seas: An Environmental Evaluation: Volume I: Europe, The Americas and West Africa. Academic Press.

Hartig, F., & Hartig, M. F. (2017). Package 'dharma'. *R package*, *531*(532), 435.

Hattab, T., Gucu, A., Ventero, A., Felice, A. D., Machias, A., Saraux, C., et al. (2021). Temperature strongly correlates with regional patterns of body size variation in Mediterranean small pelagic fish species. Mediterr. Mar. Sci. 22, 800–811. doi: 10.12681/mms.26525

Hidalgo, M., Vasilakopoulos, P., García-Ruiz, C., Esteban, A., López-López, L., & García-Gorriz, E. (2022). Resilience dynamics and productivity-driven shifts in the marine communities of the Western Mediterranean Sea. Journal of Animal Ecology, 91(2), 470–483. https://doi.org/10.1111/1365-2656.13648

Hill, M. O. (1973). Diversity and Evenness: A Unifying Notation and Its Consequences. Ecology, 54(2), 427–432. https://doi.org/10.2307/1934352

Hillebrand, H. (2004). On the Generality of the Latitudinal Diversity Gradient | The American Naturalist: Vol 163, No 2. The American Naturalist. https://www.journals.uchicago.edu/doi/10.1086/381004

Hillebrand, H., Bennett, D. M., & Cadotte, M. W. (2008). Consequences of Dominance: A Review of Evenness Effects on Local and Regional Ecosystem Processes. Ecology, 89(6), 1510–1520. https://doi.org/10.1890/07-1053.1

Hillebrand, H., Langenheder, S., Lebret, K., Lindström, E., Östman, Ö., & Striebel, M. (2018). Decomposing multiple dimensions of stability in global change experiments. Ecology Letters, 21(1), 21–30. https://doi.org/10.1111/ele.12867

Hjermann, D. Ø., Ottersen, G., & Stenseth, N. Chr. (2004). Competition among fishermen and fish causes the collapse of Barents Sea capelin. Proceedings of the National Academy of Sciences, 101(32), 11679–11684. https://doi.org/10.1073/pnas.0402904101

Holling, C. S. (1973). Resilience and stability of ecological systems. Annual Review of Ecology and Systematics, 4:1–23.

Huertas, I. E., Ríos, A. F., García-Lafuente, J., Navarro, G., Makaoui, A., Sánchez-Román, A., Rodriguez-Galvez, S., Orbi, A., Ruíz, J., & Pérez, F. F. (2012). Atlantic forcing of the Mediterranean oligotrophy. Global Biogeochemical Cycles, 26(2). https://doi.org/10.1029/2011GB004167

Hughes, T. P., Bellwood, D. R., Folke, C., Steneck, R. S., & Wilson, J. (2005). New paradigms for supporting the resilience of marine ecosystems. Trends in Ecology & Evolution, 20(7), 380–386. https://doi.org/10.1016/j.tree.2005.03.022

Husson, B., Bluhm, B. A., Cyr, F., Danielson, S. L., Eriksen, E., Fossheim, M., Geoffroy, M., Hopcroft, R. R., Ingvaldsen, R. B., Jørgensen, L. L., Lovejoy, C., Meire, L., Mueter, F., Primicerio, R., & Winding, M. (2024). Borealization impacts shelf ecosystems across the Arctic. Frontiers in Environmental Science, 12, 1481420. https://doi.org/10.3389/fenvs.2024.1481420

Husson, B., Certain, G., Filin, A., & Planque, B. (2020). Suitable habitats of fish species in the Barents Sea. Fisheries Oceanography, 29(6), 526–540. https://doi.org/10.1111/fog.12493

ICES. (2021). Barents Sea Ecoregion – Ecosystem overview [Report]. ICES Advice: Ecosystem Overviews. https://doi.org/10.17895/ices.advice.9438

ICES. (2022). Greater North Sea ecoregion – fisheries overview [Report]. ICES Advice: Fisheries Overviews. https://doi.org/10.17895/ices.advice.21641360.v1

ICES. (2024a). Barents Sea ecoregion – fisheries overview (p. 7818567 Bytes). ICES Advice: Fisheries Overviews. https://doi.org/10.17895/ICES.ADVICE.21640814

ICES. (2024b). Greater North Sea Ecoregion—Fisheries Overview [Report]. ICES Advice: Fisheries Overviews. https://doi.org/10.17895/ices.advice.27879879.v2

Ingvaldsen, R. B., Assmann, K. M., Primicerio, R., Fossheim, M., Polyakov, I. V., & Dolgov, A. V. (2021). Physical manifestations and ecological implications of Arctic Atlantification. Nature Reviews Earth & Environment, 2(12), 874–889. https://doi.org/10.1038/s43017-021-00228-x

IPBES. (2019). Summary for policymakers of the global assessment report on biodiversity and ecosystem services of the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services. S. Díaz, J. Settele, E. S. Brondízio E.S., H. T. Ngo, M. Guèze, J. Agard, A. Arneth, P. Balvanera, K. A. Brauman, S. H. M. Butchart, K. M. A. Chan, L. A. Garibaldi, K. Ichii, J. Liu, S. M. Subramanian, G. F. Midgley, P. Miloslavich, Z. Molnár, D. Obura, A. Pfaff,

S. Polasky, A. Purvis, J. Razzaque, B. Reyers, R. Roy Chowdhury, Y. J. Shin, I. J. Visseren-Hamakers, K. J. Willis, and C. N. Zayas (eds.). IPBES secretariat, Bonn, Germany. 56 pages.

IPBES. (2024). Thematic Assessment Report on the Underlying Causes of Biodiversity Loss and the Determinants of Transformative Change and Options for Achieving the 2050 Vision for Biodiversity of the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services (Transformative Change Assessment). O'Brien, K., Garibaldi, L., and Agrawal, A. (eds.). IPBES secretariat, Bonn, Germany.

Ives, A. R., & Carpenter, S. R. (2007). Stability and Diversity of Ecosystems. Science, 317(5834), 58–62. https://doi.org/10.1126/science.1133258

Jennings, S., Greenstreet, Simon. P. R., & Reynolds, John. D. (1999). Structural change in an exploited fish community: A consequence of differential fishing effects on species with contrasting life histories. Journal of Animal Ecology, 68(3), 617–627. https://doi.org/10.1046/j.1365-2656.1999.00312.x

Johannesen, E., Høines, Å. S., Dolgov, A. V., & Fossheim, M. (2012). Demersal Fish Assemblages and Spatial Diversity Patterns in the Arctic-Atlantic Transition Zone in the Barents Sea. PLOS ONE, 7(4), e34924. https://doi.org/10.1371/journal.pone.0034924

Johannesen, E., Jørgensen, L. L., Fossheim, M., Primicerio, R., Greenacre, M., Ljubin, P. A., Dolgov, A. V., Ingvaldsen, R. B., Anisimova, N. A., & Manushin, I. E. (2017). Large-scale patterns in community structure of benthos and fish in the Barents Sea. Polar Biology, 40(2), 237–246. https://doi.org/10.1007/s00300-016-1946-6

Jost, L. (2010). The Relation between Evenness and Diversity. Diversity, 2(2), 207–232. https://doi.org/10.3390/d2020207

Jouffray, J.-B., Blasiak, R., Norström, A. V., Österblom, H., & Nyström, M. (2020). The Blue Acceleration: The Trajectory of Human Expansion into the Ocean. One Earth, 2(1), 43–54. https://doi.org/10.1016/j.oneear.2019.12.016

Kallio, N., Andersen, J. H., Carstensen, J., Gissi, E., Halpern, B. S., Hammar, L., ... & Korpinen, S. (2025). Challenges in expert ratings of marine habitat and species sensitivity to anthropogenic pressures. Scientific Reports, 15(1), 12546.

Kavadas, S., Maina, I., Damalas, D., Dokos, I., Pantazi, M., & Vassilopoulou, V. (2015). Multi-Criteria Decision Analysis as a tool to extract fishing footprints and estimate fishing pressure: Application to small scale coastal fisheries and implications for management in the context of the Maritime Spatial Planning Directive. Mediterranean Marine Science, 16(2), 294–304. https://doi.org/10.12681/mms.1087

Kortsch, S., Primicerio, R., Fossheim, M., Dolgov, A. V., & Aschan, M. (2015). Climate change alters the structure of arctic marine food webs due to poleward shifts of boreal generalists. Proceedings of the Royal Society B: Biological Sciences, 282(1814), 20151546. https://doi.org/10.1098/rspb.2015.1546

Kroodsma, D. A., Mayorga, J., Hochberg, T., Miller, N. A., Boerder, K., Ferretti, F., Wilson, A., Bergman, B., White, T. D., Block, B. A., Woods, P., Sullivan, B., Costello, C., & Worm, B. (2018). Tracking the global footprint of fisheries. Science, 359(6378), 904–908. https://doi.org/10.1126/science.aao5646

Laffargue, P., Delaunay, D., Badts, V., Berthele, O., Cornou, A. S., & Garren, F. (2025). EVHOE Bottom Trawl Survey catch data: Long term benthic community dataset for fish and invertebrates on the continental shelves of the Bay of Biscay and the Celtic Sea [Data set]. SEANOE. https://doi.org/10.17882/80041

Lázaro, A., Gómez-Martínez, C., González-Estévez, M. A., & Hidalgo, M. (2022). Portfolio effect and asynchrony as drivers of stability in plant–pollinator communities along a gradient of landscape heterogeneity. Ecography, 2022(3), e06112. https://doi.org/10.1111/ecog.06112

Lazkano, I., Nøstbakken, L., & Prellezo, R. (2013). Past and Future Management of a Collapsed Fishery: The Bay of Biscay Anchovy. Natural Resource Modeling, 26(3), 281–304. https://doi.org/10.1111/j.1939-7445.2012.00138.x

Lefcheck, J. S. (2016). piecewiseSEM: Piecewise structural equation modelling in r for ecology, evolution, and systematics. Methods in Ecology and Evolution, 7(5), 573–579. https://doi.org/10.1111/2041-210X.12512

Legendre, P. (2005). Species associations: The Kendall coefficient of concordance revisited. Journal of Agricultural, Biological, and Environmental Statistics, 10(2), 226–245. https://doi.org/10.1198/108571105X46642

Legras, G., Loiseau, N., Gaertner, J.-C., Poggiale, J.-C., & Gaertner-Mazouni, N. (2020). Assessing functional diversity: The influence of the number of the functional traits. Theoretical Ecology, 13(1), 117–126. https://doi.org/10.1007/s12080-019-00433-x

Leibold, M. A., Holyoak, M., Mouquet, N., Amarasekare, P., Chase, J. M., Hoopes, M. F., Holt, R. D., Shurin, J. B., Law, R., Tilman, D., Loreau, M., & Gonzalez, A. (2004). The metacommunity concept: A framework for multi-scale community ecology. Ecology Letters, 7(7), 601–613. https://doi.org/10.1111/j.1461-0248.2004.00608.x

Leposa, N. (2020). Problematic blue growth: A thematic synthesis of social sustainability problems related to growth in the marine and coastal tourism. Sustainability Science, 15(4), 1233–1244. https://doi.org/10.1007/s11625-020-00796-9

Levin, S. A. (1998). Ecosystems and the Biosphere as Complex Adaptive Systems. Ecosystems, 1(5), 431–436. https://doi.org/10.1007/s100219900037

Liang, M., Baiser, B., Hallett, L. M., Hautier, Y., Jiang, L., Loreau, M., Record, S., Sokol, E. R., Zarnetske, P. L., & Wang, S. (2022). Consistent stabilizing effects of plant diversity across spatial scales and climatic gradients. Nature Ecology & Evolution, 6(11), 1669–1675. https://doi.org/10.1038/s41559-022-01868-y

Lindegren, M., Checkley, D. M., Jr, Ohman, M. D., Koslow, J. A., & Goericke, R. (2016). Resilience and stability of a pelagic marine ecosystem. Proceedings of the Royal Society B: Biological Sciences, 283(1822), 20151931. https://doi.org/10.1098/rspb.2015.1931

Lindegren, M., Van Deurs, M., MacKenzie, B. R., Worsoe Clausen, L., Christensen, A., & Rindorf, A. (2018). Productivity and recovery of forage fish under climate change and fishing: North Sea sandeel as a case study. Fisheries Oceanography, 27(3), 212–221. https://doi.org/10.1111/fog.12246

Lindgren, F., Rue, H., & Lindström, J. (2011). An Explicit Link between Gaussian Fields and Gaussian Markov Random Fields: The Stochastic Partial Differential Equation Approach. Journal of the Royal Statistical Society Series B: Statistical Methodology, 73(4), 423–498. https://doi.org/10.1111/j.1467-9868.2011.00777.x

Liquete, C., Piroddi, C., Macías, D., Druon, J.-N., & Zulian, G. (2016). Ecosystem services sustainability in the Mediterranean Sea: Assessment of status and trends using multiple modelling approaches. Scientific Reports, 6(1), 34162. https://doi.org/10.1038/srep34162

Lisner, A., Konečná, M., Blažek, P., & Lepš, J. (2023). Community biomass is driven by dominants and their characteristics – The insight from a field biodiversity experiment with realistic species loss scenario. Journal of Ecology, 111(1), 240–250. https://doi.org/10.1111/1365-2745.14029

Loeng, H. (1991). Features of the physical oceanographic conditions of the Barents Sea. Polar Research, 10(1), Article 1. https://doi.org/10.3402/polar.v10i1.6723

Lomax, R. G. (2004). *A beginner's guide to structural equation modeling*. psychology press.

Loreau, M., Barbier, M., Filotas, E., Gravel, D., Isbell, F., Miller, S. J., Montoya, J. M., Wang, S., Aussenac, R., Germain, R., Thompson, P. L., Gonzalez, A., & Dee, L. E. (2021). Biodiversity as insurance: From concept to measurement and application. Biological Reviews, 96(5), 2333–2354. https://doi.org/10.1111/brv.12756

Loreau, M. (2010). From populations to ecosystems: Theoretical foundations for a new ecological synthesis. Princeton University Press.

Loreau, M., & de Mazancourt, C. (2008). Species Synchrony and Its Drivers: Neutral and Nonneutral Community Dynamics in Fluctuating Environments. The American Naturalist, 172(2), E48–E66. https://doi.org/10.1086/589746

Loreau, M., & de Mazancourt, C. (2013). Biodiversity and ecosystem stability: A synthesis of underlying mechanisms. Ecology Letters, 16(s1), 106–115. https://doi.org/10.1111/ele.12073

Loreau, M., & Hector, A. (2001). Partitioning selection and complementarity in biodiversity experiments. Nature, 412(6842), 72–76. https://doi.org/10.1038/35083573

Loreau, M., Naeem, S., Inchausti, P., Bengtsson, J., Grime, J. P., Hector, A., Hooper, D. U., Huston, M. A., Raffaelli, D., Schmid, B., Tilman, D., & Wardle, D. A. (2001). Biodiversity and Ecosystem Functioning: Current Knowledge and Future Challenges. Science, 294(5543), 804–808. https://doi.org/10.1126/science.1064088

Magneville, C., Loiseau, N., Albouy, C., Casajus, N., Claverie, T., Escalas, A., Leprieur, F., Maire, E., Mouillot, D., & Villéger, S. (2022). mFD: An R package to compute and illustrate the multiple facets of functional diversity. Ecography, 2022(1). https://doi.org/10.1111/ecog.05904

Magurran, A. E., Baillie, S. R., Buckland, S. T., Dick, J. M., Elston, D. A., Scott, E. M., Smith, R. I., Somerfield, P. J., & Watt, A. D. (2010). Long-term datasets in biodiversity research and monitoring: Assessing change in ecological communities through time. Trends in Ecology & Evolution, 25(10), 574–582. https://doi.org/10.1016/j.tree.2010.06.016

Maina, I., Politikos, D., & Kavadas, S. (2026). tools4MCDA: An R-Package to estimate spatial fishing effort, weight and value of landings using multi-criteria decision analysis. Ecological Modelling, 516, 111541. https://doi.org/10.1016/j.ecolmodel.2026.111541

Maire, E., Grenouillet, G., Brosse, S., & Villéger, S. (2015). How many dimensions are needed to accurately assess functional diversity? A pragmatic approach for assessing the quality of functional spaces. Global Ecology and Biogeography, 24(6), 728–740. https://doi.org/10.1111/geb.12299

Mammola, S., & Cardoso, P. (2020). Functional diversity metrics using kernel density n-dimensional hypervolumes. Methods in Ecology and Evolution, 11(8), 986–995. https://doi.org/10.1111/2041-210x.13424

Mammola, S., Carmona, C. P., Guillerme, T., & Cardoso, P. (2021). Concepts and applications in functional diversity. Functional Ecology, 35(9), 1869–1885. https://doi.org/10.1111/1365-2435.13882

Mammola, S., Graco-Roza, C., Ballarin, F., Hesselberg, T., Isaia, M., Lunghi, E., Mouron, S., Pavlek, M., Tolve, M., & Cardoso, P. (2024). Functional convergence underground? The scale-dependency of community assembly processes in European cave spiders. Global Ecology and Biogeography, 33(6), e13840. https://doi.org/10.1111/geb.13840

Marcos, C., Diaz, D., Fietz, K., Forcada, A., Ford, A., García-Charton, J. A., ... & Pérez-Ruzafa, A. (2021). Reviewing the ecosystem services, societal goods, and benefits of marine protected areas. Frontiers in Marine Science, 8, 613819.

Maritorena, S., d'Andon, O. H. F., Mangin, A., & Siegel, D. A. (2010). Merged satellite ocean color data products using a bio-optical model: Characteristics, benefits and issues. Remote Sensing of Environment, 114(8), 1791–1804. https://doi.org/10.1016/j.rse.2010.04.002

Maureaud, A. A., Frelat, R., Pécuchet, L., Shackell, N., Mérigot, B., Pinsky, M. L., Amador, K., Anderson, S. C., Arkhipkin, A., Auber, A., Barri, I., Bell, R. J., Belmaker, J., Beukhof, E., Camara, M. L., Guevara-Carrasco, R., Choi, J., Christensen, H. T., Conner, J., … T. Thorson, J. (2021). Are we ready to track climate-driven shifts in marine species across international boundaries? - A global survey of scientific bottom trawl data. Global Change Biology, 27(2), 220–236. https://doi.org/10.1111/gcb.15404

Maureaud, A. A., Palacios-Abrantes, J., Kitchel, Z., Mannocci, L., Pinsky, M. L., Fredston, A., Beukhof, E., Forrest, D. L., Frelat, R., Palomares, M. L. D., Pecuchet, L., Thorson, J. T., Van Denderen, P. D., & Mérigot, B. (2024). FISHGLOB_data: An integrated dataset of fish biodiversity sampled with scientific bottom-trawl surveys. Scientific Data, 11(1), 24. https://doi.org/10.1038/s41597-023-02866-w

Maureaud, A., Hodapp, D., Van Denderen, P. D., Hillebrand, H., Gislason, H., Spaanheden Dencker, T., Beukhof, E., & Lindegren, M. (2019). Biodiversity–ecosystem functioning relationships in fish communities: Biomass is related to evenness and the environment, not to species richness. Proceedings of the Royal Society B: Biological Sciences, 286(1906), 20191189. https://doi.org/10.1098/rspb.2019.1189

Maureaud, A., Hodapp, D., van Denderen, P. D., Hillebrand, H., Gislason, H., Spaanheden Dencker, T., Beukhof, E., & Lindegren, M. (2019). Biodiversity–ecosystem functioning relationships in fish communities: Biomass is related to evenness and the environment, not to species richness. Proceedings of the Royal Society B: Biological Sciences, 286(1906), 20191189. https://doi.org/10.1098/rspb.2019.1189

McCann, K. S. (2000). The diversity–stability debate. Nature, 405(6783), 228–233. https://doi.org/10.1038/35012234

McKeon, C. M., Buckley, Y. M., Moriarty, M., Lundy, M., & Kelly, R. (2024). Increased signal of fishing pressure on community life-history traits at larger spatial scales. Global Ecology and Biogeography, 33(5), e13815. https://doi.org/10.1111/geb.13815

McQuatters-Gollop, A., Guérin, L., Arroyo, N. L., Aubert, A., Artigas, L. F., Bedford, J., Corcoran, E., Dierschke, V., Elliott, S. A. M., Geelhoed, S. C. V., Gilles, A., González-Irusta, J. M., Haelters, J., Johansen, M., Le Loc'h, F., Lynam, C. P., Niquil, N., Meakins, B., Mitchell, I., … Vina-Herbon, C. (2022). Assessing the state of marine biodiversity in the Northeast Atlantic. Ecological Indicators, 141, 109148. https://doi.org/10.1016/j.ecolind.2022.109148

Meng, B., Luo, M., Loreau, M., Hong, P., Craven, D., Eisenhauer, N., Isbell, F., Liang, M., Reuman, D., Wilsey, B., van Ruijven, J., Zhao, L., & Wang, S. (2025). Stabilizing effects of biodiversity arise from species-specific dynamics rather than interspecific interactions in grasslands. Nature Ecology & Evolution, 9(10), 1837–1847. https://doi.org/10.1038/s41559-025-02787-4

Michalsen, K., Dalpadado, P., Eriksen, E., Gjøsæter, H., Ingvaldsen, R. B., Johannesen, E., Jørgensen, L. L., Knutsen, T., Prozorkevich, D., & Skern-Mauritzen, M. (2013). Marine living resources of the Barents Sea – Ecosystem understanding and monitoring in a climate change perspective. Marine Biology Research, 9(9), 932–947. https://doi.org/10.1080/17451000.2013.775459

Millenium ecosystem assessment. (2005). Ecosystems and human well-being: Wetlands and water. World resources institute.

Modica, L., Velasco, F., Preciado, I., Soto, M., & Greenstreet, S. P. R. (2014). Development of the large fish indicator and associated target for a Northeast Atlantic fish community. ICES Journal of Marine Science, 71(9), 2403–2415. https://doi.org/10.1093/icesjms/fsu101

Mora, C., Tittensor, D. P., Adl, S., Simpson, A. G. B., & Worm, B. (2011). How Many Species Are There on Earth and in the Ocean? PLOS Biology, 9(8), e1001127. https://doi.org/10.1371/journal.pbio.1001127

Morin, X., Fahse, L., de Mazancourt, C., Scherer-Lorenzen, M., & Bugmann, H. (2014). Temporal stability in forest productivity increases with tree diversity due to asynchrony in species dynamics. Ecology Letters, 17(12), 1526–1535. https://doi.org/10.1111/ele.12357

Mouillot, D., Bellwood, D. R., Baraloto, C., Chave, J., Galzin, R., Harmelin-Vivien, M., ... & Thuiller, W. (2013). Rare species support vulnerable functions in high-diversity ecosystems. PLoS biology, 11(5), e1001569.

Mouillot, D., de Juan, S., Trégarot, E., Villéger, S., Casal, G., Cornet, C. C., Maréchal, J.-P., Maynou, F., Meesters, E., Simide, R., van der Geest, M., & Juhel, J.-B. (2025). Biodiversity mediates the effects of socio-environmental factors on coastal fish biomass: A structural equation modeling approach in three ecoregions. Marine Environmental Research, 210, 107351. https://doi.org/10.1016/j.marenvres.2025.107351

Mouillot, D., Dumay, O., & Tomasini, J. A. (2007). Limiting similarity, niche filtering and functional diversity in coastal lagoon fish communities. Estuarine, Coastal and Shelf Science, 71(3), 443–456. https://doi.org/10.1016/j.ecss.2006.08.022

Mouillot, D., Villéger, S., Scherer-Lorenzen, M., & Mason, N. W. H. (2011). Functional Structure of Biological Communities Predicts Ecosystem Multifunctionality. PLOS ONE, 6(3), e17476. https://doi.org/10.1371/journal.pone.0017476

Moullec, F., Barrier, N., Drira, S., Guilhaumon, F., Marsaleix, P., Somot, S., Ulses, C., Velez, L., & Shin, Y.-J. (2019). An End-to-End Model Reveals Losers and Winners in a Warming Mediterranean Sea. Frontiers in Marine Science, 6. https://doi.org/10.3389/fmars.2019.00345

Naeem, S., & Li, S. (1997). Biodiversity enhances ecosystem reliability. Nature, 390(6659), 507–509. https://doi.org/10.1038/37348

Nakken, O. (1998). Past, present and future exploitation and management of marine resources in the Barents Sea and adjacent areas. Fisheries Research, 37(1–3), 23–35. https://doi.org/10.1016/S0165-7836(98)00124-6

Ohlert, T., Kimmel, K., Avolio, M., Chang, C., Forrestel, E., Gerstner, B. P., Hobbie, S. E., Reich, P., Whitney, K. D., & Komatsu, K. (2024). The impact of trait number and correlation on functional diversity metrics in real-world ecosystems. PLOS ONE, 19(9), e0306342. https://doi.org/10.1371/journal.pone.0306342

Olsen, E., Aanes, S., Mehl, S., Holst, J. C., Gjøsæter, H., & Aglen, A. (2010). Cod, haddock, saithe, herring, and capelin in the Barents Sea and adjacent waters: A review of the biological value of the area. ICES Journal of Marine Science, 67(1), 87–101. https://doi.org/10.1093/icesjms/fsp229

Oksanen, J., Kindt, R., Legendre, P., O'Hara, B., Stevens, M. H. H., Oksanen, M. J., & Suggests, M. A. S. S. (2007). The vegan package. *Community ecology package*, *10*(631-637), 719.

Özesmi, U., & Özesmi, S. L. (2004). Ecological models based on people's knowledge: A multi-step fuzzy cognitive mapping approach. Ecological Modelling, 176(1–2), 43–64. https://doi.org/10.1016/j.ecolmodel.2003.10.027

Palacio, F. X., Callaghan, C. T., Cardoso, P., Hudgins, E. J., Jarzyna, M. A., Ottaviani, G., Riva, F., Graco-Roza, C., Shirey, V., & Mammola, S. (2022). A protocol for reproducible functional diversity analyses. Ecography, 2022(11), e06287. https://doi.org/10.1111/ecog.06287

Pecuchet, L., Lindegren, M., Hidalgo, M., Delgado, M., Esteban, A., Fock, H. O., Gil de Sola, L., Punzón, A., Sólmundsson, J., & Payne, M. R. (2017). From traits to life-history strategies: Deconstructing fish community composition across European seas. Global Ecology and Biogeography, 26(7), 812–822. https://doi.org/10.1111/geb.12587

Petchey, O. L., & Gaston, K. J. (2006). Functional diversity: Back to basics and looking forward. Ecology Letters, 9(6), 741–758. https://doi.org/10.1111/j.1461-0248.2006.00924.x

Peterson, G., Allen, C. R., & Holling, C. S. (1998). Ecological Resilience, Biodiversity, and Scale. Ecosystems, 1(1), 6–18. https://doi.org/10.1007/s100219900002

Pettersen, A. K., Marzinelli, E. M., Steinberg, P. D., & Coleman, M. A. (2022). Impact of marine protected areas on temporal stability of fish species diversity. Conservation Biology, 36(2), e13815.

Piet, G., Bentley, J., Jongbloed, R., Grundlehner, A., Tamis, J., & de Vries, P. (2024). A cumulative impact assessment on the marine capacity to supply ecosystem services. Science of The Total Environment, 948, 174149. https://doi.org/10.1016/j.scitotenv.2024.174149

Pinheiro, J., Bates, D., DebRoy, S., Sarkar, D., Heisterkamp, S., Van Willigen, B., & Maintainer, R. (2017). Package 'nlme'. *Linear and nonlinear mixed effects models, version*, *3*(1), 274.

Pinnegar, J. K., & Engelhard, G. H. (2008). The 'shifting baseline' phenomenon: A global perspective. Reviews in Fish Biology and Fisheries, 18(1), 1–16. https://doi.org/10.1007/s11160-007-9058-6

Piroddi, C., Coll, M., Liquete, C., Macias, D., Greer, K., Buszowski, J., Steenbeek, J., Danovaro, R., & Christensen, V. (2017). Historical changes of the Mediterranean Sea ecosystem: Modelling the role and impact of primary productivity and fisheries changes over time. Scientific Reports, 7(1), 44491. https://doi.org/10.1038/srep44491

Piroddi, C., Colloca, F., & Tsikliras, A. C. (2020). The living marine resources in the Mediterranean Sea Large Marine Ecosystem. Environmental Development, Large Marine Ecosystems of Africa: Assessment, Sustainability, and Management, 36, 100555. https://doi.org/10.1016/j.envdev.2020.100555

Polo, J., López-López, L., Engelhard, G. H., Punzón, A., Hidalgo, M., Rutterford, L. A., Bariáin, M. S., González-Irusta, J. M., Esteban, A., García, E., Vivas, M., & Pecuchet, L. (2025). Trait-Based Indicators of Marine Communities' Sensitivity to Climate Change and Fishing. Diversity and Distributions, 31(1), e13959. https://doi.org/10.1111/ddi.13959

Potschin-Young, M., Haines-Young, R., Görg, C., Heink, U., Jax, K., & Schleyer, C. (2018a). Understanding the role of conceptual frameworks: Reading the ecosystem service cascade. Ecosystem Services, SI: Synthesizing OpenNESS, 29, 428–440. https://doi.org/10.1016/j.ecoser.2017.05.015

Potschin-Young, M., Haines-Young, R., Görg, C., Heink, U., Jax, K., & Schleyer, C. (2018b). Understanding the role of conceptual frameworks: Reading the ecosystem service cascade. Ecosystem Services, SI: Synthesizing OpenNESS, 29, 428–440. https://doi.org/10.1016/j.ecoser.2017.05.015

Punzón, A., López-López, L., González-Irusta, J. M., Preciado, I., Hidalgo, M., Serrano, A., Tel, E., Somavilla, R., Polo, J., Blanco, M., Ruiz-Pico, S., Fernández-Zapico, O., Velasco, F., & Massuti, E. (2021). Tracking the effect of temperature in marine demersal fish communities. Ecological Indicators, 121, 107142. https://doi.org/10.1016/j.ecolind.2020.107142

Punzón, A., Serrano, A., Sánchez, F., Velasco, F., Preciado, I., González-Irusta, J. M., & López-López, L. (2016). Response of a temperate demersal fish community to global warming. Journal of Marine Systems, 161, 1–10. https://doi.org/10.1016/j.jmarsys.2016.05.001

R Core Team. (2021). R: a language and environment for statistical computing [Manual]. R Foundation for Statistical Computing. https://www.R-project.org/

Rantanen, M., Karpechko, A. Y., Lipponen, A., Nordling, K., Hyvärinen, O., Ruosteenoja, K., Vihma, T., & Laaksonen, A. (2022). The Arctic has warmed nearly four times faster than the globe since 1979. Communications Earth & Environment, 3(1), 168. https://doi.org/10.1038/s43247-022-00498-3

Ratcliffe, S., Wirth, C., Jucker, T., van der Plas, F., Scherer-Lorenzen, M., Verheyen, K., Allan, E., Benavides, R., Bruelheide, H., Ohse, B., Paquette, A., Ampoorter, E., Bastias, C. C., Bauhus, J., Bonal, D., Bouriaud, O., Bussotti, F., Carnol, M., Castagneyrol, B., … Baeten, L. (2017). Biodiversity and ecosystem functioning relations in European forests depend on environmental context. Ecology Letters, 20(11), 1414–1426. https://doi.org/10.1111/ele.12849

Receveur, A., Leprieur, F., Ellingsen, K. E., Keith, D., Kleisner, K. M., McLean, M., Mérigot, B., Mills, K. E., Mouillot, D., Rufino, M., Trindade-Santos, I., Van Hoey, G., Albouy, C., & Auber, A. (2024). Long-term changes in taxonomic and functional composition of European marine fish communities. Ecography, 2024(9), e07234. https://doi.org/10.1111/ecog.07234

Reiss, H., Degraer, S., Duineveld, G. C. A., Kröncke, I., Aldridge, J., Craeymeersch, J. A., Eggleton, J. D., Hillewaert, H., Lavaleye, M. S. S., Moll, A., Pohlmann, T., Rachor, E., Robertson, M., Vanden Berghe, E., van Hoey, G., & Rees, H. L. (2010). Spatial patterns of infauna, epifauna, and demersal fish communities in the North Sea. ICES Journal of Marine Science, 67(2), 278–293. https://doi.org/10.1093/icesjms/fsp253

Reynolds, R. W., Rayner, N. A., Smith, T. M., Stokes, D. C., & Wang, W. (2002). An Improved In Situ and Satellite SST Analysis for Climate. https://journals.ametsoc.org/view/journals/clim/15/13/1520-0442_2002_015_1609_aiisas_2.0.co_2.xml

Roscher, C., Weigelt, A., Proulx, R., Marquard, E., Schumacher, J., Weisser, W. W., & Schmid, B. (2011). Identifying population- and community-level mechanisms of diversity–stability relationships in experimental grasslands. Journal of Ecology, 99(6), 1460–1469. https://doi.org/10.1111/j.1365-2745.2011.01875.x

Rousseau, Y., Blanchard, J., Novaglio, C., Kirsty, P., Tittensor, D., Watson, R., & Ye, Y. (2022). Global Fishing Effort [Data set]. Institute for Marine and Antarctic Studies. https://doi.org/10.25959/MNGY-0Q43

Sanz-Martín, M., Hidalgo, M., Puerta, P., Molinos, J. G., Zamanillo, M., Brito-Morales, I., González-Irusta, J. M., Esteban, A., Punzón, A., García-Rodríguez, E., Vivas, M., & López-López, L. (2024). Climate velocity drives unexpected southward patterns of species shifts in the Western Mediterranean Sea. Ecological Indicators, 160, 111741. https://doi.org/10.1016/j.ecolind.2024.111741

Savage, V. M., Gillooly, J. F., Brown, J. H., West, G. B., Charnov, E. L., & null, null. (2004). Effects of Body Size and Temperature on Population Growth. The American Naturalist, 163(3), 429–441. https://doi.org/10.1086/381872

Schiettekatte, N. M. D., Barneche, D. R., Villéger, S., Allgeier, J. E., Burkepile, D. E., Brandl, S. J., Casey, J. M., Mercière, A., Munsterman, K. S., Morat, F., & Parravicini, V. (2020). Nutrient limitation, bioenergetics and stoichiometry: A new model to predict elemental fluxes mediated by fishes. Functional Ecology, 34(9), 1857–1869. https://doi.org/10.1111/1365-2435.13618

Schiettekatte, N. M. D., Brandl, S. J., Casey, J. M., Graham, N. A. J., Barneche, D. R., Burkepile, D. E., Allgeier, J. E., Arias-Gonzaléz, J. E., Edgar, G. J., Ferreira, C. E. L., Floeter, S. R., Friedlander, A. M., Green, A. L., Kulbicki, M., Letourneur, Y., Luiz, O. J., Mercière, A., Morat, F., Munsterman, K. S., … Parravicini, V. (2022). Biological trade-offs underpin coral reef ecosystem functioning. Nature Ecology & Evolution, 6(6), 701–708. https://doi.org/10.1038/s41559-022-01710-5

Schindler, D. E., Hilborn, R., Chasco, B., Boatright, C. P., Quinn, T. P., Rogers, L. A., & Webster, M. S. (2010). Population diversity and the portfolio effect in an exploited species. Nature, 465(7298), 609–612. https://doi.org/10.1038/nature09060

Schnabel, F., Liu, X., Kunz, M., Barry, K. E., Bongers, F. J., Bruelheide, H., Fichtner, A., Härdtle, W., Li, S., Pfaff, C.-T., Schmid, B., Schwarz, J. A., Tang, Z., Yang, B., Bauhus, J., von Oheimb, G., Ma, K., & Wirth, C. (2021). Species richness stabilizes productivity via asynchrony and drought-tolerance diversity in a large-scale tree biodiversity experiment. Science Advances, 7(51), eabk1643. https://doi.org/10.1126/sciadv.abk1643

Selim, S. A., Blanchard, J. L., Bedford, J., & Webb, T. J. (2016). Direct and indirect effects of climate and fishing on changes in coastal ecosystem services: A historical perspective from the North Sea. Regional Environmental Change, 16(2), 341–351. https://doi.org/10.1007/s10113-014-0635-7

Serrano, A., Velasco, F., Olaso, I., & Sánchez, F. (2003). Macrobenthic crustaceans in the diet of demersal fish in the Bay of Biscay in relation to abundance in the environment. Sarsia, 88(1), 36–48. https://doi.org/10.1080/00364820308469

Skein, L., Sink, K. J., Majiedt, P. A., van der Bank, M. G., Smit, K. P., & Shannon, L. J. (2022). Scoping an integrated ecosystem assessment for South Africa. Frontiers in Marine Science, 9. https://doi.org/10.3389/fmars.2022.975328

Soga, M., & Gaston, K. J. (2018). Shifting baseline syndrome: Causes, consequences, and implications. Frontiers in Ecology and the Environment, 16(4), 222–230. https://doi.org/10.1002/fee.1794

Spalding, M. D., Fox, H. E., Allen, G. R., Davidson, N., Ferdaña, Z. A., Finlayson, M., Halpern, B. S., Jorge, M. A., Lombana, A., Lourie, S. A., Martin, K. D., McManus, E., Molnar, J., Recchia, C. A., & Robertson, J. (2007). Marine Ecoregions of the World: A Bioregionalization of Coastal and Shelf Areas. BioScience, 57(7), 573–583. https://doi.org/10.1641/B570707

Spedicato, M. T., Massutí, E., Mérigot, B., Tserpes, G., Jadaud, A., and Relini, G. (2019). The MEDITS trawl survey specifications in an ecosystem approach to fishery management. *Sci. Mar.* 83, 9–20. doi: 10.3989/scimar.04915.11X

Streiner, D. L. (2006). Building a Better Model: An Introduction to Structural Equation Modelling. The Canadian Journal of Psychiatry, 51(5), 317–324. https://doi.org/10.1177/070674370605100507

Sturrock, C., Minto, C., Poole, R., Reid, D., Vaughan, L., & Brophy, D. (2026). Disentangling the effects of climate, population dynamics, and fishing on the body size of key commercially important species in the Celtic Sea Ecoregion. ICES Journal of Marine Science, 83(3), fsag038. https://doi.org/10.1093/icesjms/fsag038

Symstad, A. J., Chapin, F. S., Wall, D. H., Gross, K. L., Huenneke, L. F., Mittelbach, G. G., Peters, D. P. C., & Tilman, D. (2003). Long-Term and Large-Scale Perspectives on the Relationship between Biodiversity and Ecosystem Functioning. BioScience, 53(1), 89–98. https://doi.org/10.1641/0006-3568(2003)053%5B0089:LTALSP%5D2.0.CO;2

Teruzzi, A., Bolzon, G., Feudale, L., & Cossarini, G. (2021). Deep chlorophyll maximum and nutricline in the Mediterranean Sea: Emerging properties from a multi-platform assimilated biogeochemical model experiment. Biogeosciences, 18(23), 6147–6166. https://doi.org/10.5194/bg-18-6147-2021

Thibaut, L. M., & Connolly, S. R. (2013). Understanding diversity–stability relationships: Towards a unified model of portfolio effects. Ecology Letters, 16(2), 140–150. https://doi.org/10.1111/ele.12019

Tilman, D. (1999). The Ecological Consequences of Changes in Biodiversity: A Search for General Principles. Ecology, 80(5), 1455–1474. https://doi.org/10.1890/0012-9658(1999)080%5B1455:TECOCI%5D2.0.CO;2

Tilman, D. (2001). Functional Diversity. In Encyclopedia of Biodiversity (pp. 587–596). Elsevier Inc. https://doi.org/10.1016/B978-0-12-384719-5.00061-7

Tilman, D., Isbell, F., & Cowles, J. M. (2014). Biodiversity and Ecosystem Functioning. Annual Review of Ecology, Evolution, and Systematics, 45(Volume 45, 2014), 471–493. https://doi.org/10.1146/annurev-ecolsys-120213-091917

Tilman, D., Knops, J., Wedin, D., Reich, P., Ritchie, M., & Siemann, E. (1997). The Influence of Functional Diversity and Composition on Ecosystem Processes. Science, 277(5330), 1300–1302. https://doi.org/10.1126/science.277.5330.1300

Tilman, D., Lehman, C. L., & Bristow, C. E. (1998). Diversity-Stability Relationships: Statistical Inevitability or Ecological Consequence? The American Naturalist, 151(3), 277–282. https://doi.org/10.1086/286118

Tilman, D., Reich, P. B., & Knops, J. M. H. (2006). Biodiversity and ecosystem stability in a decade-long grassland experiment. Nature, 441(7093), 629–632. https://doi.org/10.1038/nature04742

Tittensor, D. P., Mora, C., Jetz, W., Lotze, H. K., Ricard, D., Berghe, E. V., & Worm, B. (2010). Global patterns and predictors of marine biodiversity across taxa. Nature, 466(7310), 1098–1101. https://doi.org/10.1038/nature09329

Tremblay-Boyer, L., Gascuel, D., Watson, R., Christensen, V., & Pauly, D. (2011). Modelling the effects of fishing on the biomass of the world's oceans from 1950 to 2006. Marine Ecology Progress Series, 442, 169–185. https://doi.org/10.3354/meps09375

Tsikliras, A. C., & Stergiou, K. I. (2015). Age at maturity of Mediterranean marine fishes. Mediterranean Marine Science, 5–20. https://doi.org/10.12681/mms.659

Valencia, E., de Bello, F., Galland, T., Adler, P. B., Lepš, J., E-Vojtkó, A., van Klink, R., Carmona, C. P., Danihelka, J., Dengler, J., Eldridge, D. J., Estiarte, M., García-González, R., Garnier, E., Gómez-García, D., Harrison, S. P., Herben, T., Ibáñez, R., Jentsch, A., … Götzenberger, L. (2020). Synchrony matters more than species richness in plant community stability at a global scale. Proceedings of the National Academy of Sciences, 117(39), 24345–24351. https://doi.org/10.1073/pnas.1920405117

van Denderen, D., Maureaud, A. A., Andersen, K. H., Gaichas, S., Lindegren, M., Petrik, C. M., Stock, C. A., & Collie, J. (2023). Demersal fish biomass declines with temperature across productive shelf seas. Global Ecology and Biogeography, 32(10), 1846–1857. https://doi.org/10.1111/geb.13732

Vanni, M. J., McIntyre, P. B., Allen, D., Arnott, D. L., Benstead, J. P., Berg, D. J., Brabrand, Å., Brosse, S., Bukaveckas, P. A., Caliman, A., Capps, K. A., Carneiro, L. S., Chadwick, N. E., Christian, A. D., Clarke, A., Conroy, J. D., Cross, W. F., Culver, D. A., Dalton, C. M., … Zimmer, K. D. (2017). A global database of nitrogen and phosphorus excretion rates of aquatic animals. Ecology, 98(5), 1475–1475. https://doi.org/10.1002/ecy.1792

Vasilakopoulos, P., Maravelias, C. D., & Tserpes, G. (2014). The Alarming Decline of Mediterranean Fish Stocks. Current Biology, 24(14), 1643–1648. https://doi.org/10.1016/j.cub.2014.05.070

Vasseur, D. A., & Gaedke, U. (2007). Spectral Analysis Unmasks Synchronous and Compensatory Dynamics in Plankton Communities. Ecology, 88(8), 2058–2071. https://doi.org/10.1890/06-1899.1

Villasante, S., Ainsworth, G. B., Pita, P., Belgrano, A., Bennett, N., & Sumaila, U. R. (2023). The role of marine protected areas (MPAs) in providing ecosystem services to improve ocean and human health. In Oceans and human health (pp. 23-37). Academic Press.

Villéger, S., Mason, N. W. H., & Mouillot, D. (2008). New Multidimensional Functional Diversity Indices for a Multifaceted Framework in Functional Ecology. Ecology, 89(8), 2290–2301. https://doi.org/10.1890/07-1206.1

Wang, S., & Loreau, M. (2016). Biodiversity and ecosystem stability across scales in metacommunities. Ecology Letters, 19(5), 510–518. https://doi.org/10.1111/ele.12582

Wasof, S., Lenoir, J., Hattab, T., Jamoneau, A., Gallet-Moron, E., Ampoorter, E., Saguez, R., Bennsadek, L., Bertrand, R., Valdès, A., Verheyen, K., & Decocq, G. (2018). Dominance of individual plant species is more important than diversity in explaining plant biomass in the forest understorey. Journal of Vegetation Science, 29(3), 521–531. https://doi.org/10.1111/jvs.12624

Wassmann, P., Carmack, E. C., Bluhm, B. A., Duarte, C. M., Berge, J., Brown, K., Grebmeier, M., Holding, J., Kosobokova, K., Kwok, R., Matrai, l., Agusti, S., Babin, M., Bhatt, U., Eicken, H., Polyakov, I., Rysgaard, S. & Huntington, H. P. (2020). Towards a unifying pan-arctic perspective: A conceptual modelling toolkit. *Progress in Oceanography*, *189*, 102455.

Watson, R. A. (2017). A database of global marine commercial, small-scale, illegal and unreported fisheries catch 1950–2014. Scientific Data, 4(1), 170039. https://doi.org/10.1038/sdata.2017.39

Watson, R. A., & Tidd, A. (2018). Mapping nearly a century and a half of global marine fishing: 1869–2015. Marine Policy, 93, 171–177. https://doi.org/10.1016/j.marpol.2018.04.023

Watson, S. C., Somerfield, P. J., Lemasson, A. J., Knights, A. M., Edwards-Jones, A., Nunes, J., ... & Beaumont, N. J. (2024). The global impact of offshore wind farms on ecosystem services. Ocean & Coastal Management, 249, 107023.

Wedding, L. M., Lepczyk, C. A., Pittman, S. J., Friedlander, A. M., & Jorgensen, S. (2011). Quantifying seascape structure: Extending terrestrial spatial pattern metrics to the marine realm. Marine Ecology Progress Series, 427, 219–232. https://doi.org/10.3354/meps09119

Wiedmann, M., Aschan, M., Certain, G., Dolgov, A., Greenacre, M., Johannesen, E., Planque, B., & Primicerio, R. (2014). Functional diversity of the Barents Sea fish community. Marine Ecology Progress Series, 495, 205–218. https://doi.org/10.3354/meps10558

Williams, J. W., Jackson, S. T., & Kutzbach, J. E. (2007). Projected distributions of novel and disappearing climates by 2100 AD. Proceedings of the National Academy of Sciences, 104(14), 5738–5742. https://doi.org/10.1073/pnas.0606292104

Winemiller, K. O., & Rose, K. A. (1992). Patterns of Life-History Diversification in North American Fishes: Implications for Population Regulation. Canadian Journal of Fisheries and Aquatic Sciences, 49(10), 2196–2218. https://doi.org/10.1139/f92-242

Woods, T., Comte, L., Tedesco, P. A., & Giam, X. (2020). Testing the diversity–biomass relationship in riverine fish communities. Global Ecology and Biogeography, 29(10), 1743–1757. https://doi.org/10.1111/geb.13147

Worm, B., Barbier, E. B., Beaumont, N., Duffy, J. E., Folke, C., Halpern, B. S., Jackson, J. B. C., Lotze, H. K., Micheli, F., Palumbi, S. R., Sala, E., Selkoe, K. A., Stachowicz, J. J., & Watson, R. (2006). Impacts of Biodiversity Loss on Ocean Ecosystem Services. Science, 314(5800), 787–790. https://doi.org/10.1126/science.1132294

Worm, B., Hilborn, R., Baum, J. K., Branch, T. A., Collie, J. S., Costello, C., Fogarty, M. J., Fulton, E. A., Hutchings, J. A., Jennings, S., Jensen, O. P., Lotze, H. K., Mace, P. M., McClanahan, T. R., Minto, C., Palumbi, S. R., Parma, A. M., Ricard, D., Rosenberg, A. A., … Zeller, D. (2009). Rebuilding Global Fisheries. Science, 325(5940), 578–585. https://doi.org/10.1126/science.1173146

Yachi, S., & Loreau, M. (1999). Biodiversity and ecosystem productivity in a fluctuating environment: The insurance hypothesis. Proceedings of the National Academy of Sciences, 96(4), 1463–1468. https://doi.org/10.1073/pnas.96.4.1463

Yan, H. F., Morais, R. A., & Bellwood, D. R. (2025). Species abundances surpass richness effects in the biodiversity-ecosystem function relationship across marine fishes. Nature Communications, 16(1), 7789. https://doi.org/10.1038/s41467-025-63210-x

Yan, Y., Connolly, J., Liang, M., Jiang, L., & Wang, S. (2021). Mechanistic links between biodiversity effects on ecosystem functioning and stability in a multi-site grassland experiment. Journal of Ecology, 109(9), 3370–3378. https://doi.org/10.1111/1365-2745.13725

Yool, A., Popova, E. E., & Anderson, T. R. (2013). MEDUSA-2.0: An intermediate complexity biogeochemical model of the marine carbon cycle for climate change and ocean acidification studies. Geoscientific Model Development, 6(5), 1767–1811. https://doi.org/10.5194/gmd-6-1767-2013

Zhang, P., Seabloom, E. W., Foo, J., MacDougall, A. S., Harpole, W. S., Adler, P. B., Hautier, Y., Eisenhauer, N., Spohn, M., Bakker, J. D., Lekberg, Y., Young, A. L., Carbutt, C., Risch, A. C., Peri, P. L., Smith, N. G., Stevens, C. J., Prober, S. M., Knops, J. M. H., … Borer, E. T. (2025). Dominant species predict plant richness and biomass in global grasslands. Nature Ecology & Evolution, 9(6), 924–936. https://doi.org/10.1038/s41559-025-02701-y

Zuur, A. F., & Ieno, E. N. (2016). A protocol for conducting and presenting results of regression-type analyses. Methods in Ecology and Evolution, 7(6), 636–645. https://doi.org/10.1111/2041-210X.12577

Zuur, A. F., Ieno, E. N., & Elphick, C. S. (2010). A protocol for data exploration to avoid common statistical problems: Data exploration. Methods in Ecology and Evolution, 1(1), 3–14. https://doi.org/10.1111/j.2041-210X.2009.00001.x