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

Deliverable 4.2 Assessing community-level risks of marine biodiversity and habitats in different European regional seas

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Executive summary

Understanding the vulnerabilities of marine life in Europe's regional seas to human pressures is key for B-USEFUL to develop "user-oriented tools and solutions to conserve and protect marine biodiversity" in support of the EU Green Deal and Biodiversity Strategy 2030. The primary aim of work-package 4 (WP4) is to *identify habitats and key species at risk of extinction in sensitive ecosystems* by developing a hierarchical risk-based framework.

Our primary focus is on two key drivers of change: the risks from *climate change* (CC); and those from *fishing pressure* (FP) and associated *physical disturbance* to marine life – two almost ubiquitous pressures in European regional seas. For the epibenthos of the North Sea a comprehensive analysis has been made on how FP and CC could explain changes in biodiversity and vulnerability. For marine benthic habitats, a framework was developed and tested to assess habitat sensitivity to climate change (S_{cc}) and fishing pressure (S_{FP}). Finally for the Mediterranean Sea, an assessment was made on the importance of invasive species as a threat for the local, native biodiversity. The key findings are briefly summarized below.

The trait-based sensitivity assessment in the Mediterranean Sea revealed strong spatial and taxonomic variability where echinoderms and elasmobranchs consistently emerged as most sensitive taxa (especially for FP), while cephalopods showed high resilience. FP hotspots persist in many coastal areas, especially in the Western Mediterranean and Northern Adriatic Sea, remaining at high risk despite reductions in fishing effort. CC impacts are rapidly intensifying, particularly in regions with limited refuge potential. Notably, the Eastern Mediterranean can be considered a hotspot of CC risk. Additionally, functional originality of Western Mediterranean fish was assessed and integrated with different risk metrics, including S_{cc} and S_{FP}. Generally, *K*-strategist fish species (slow-reproducing, long-lived) displayed higher functional originality and risk than *r*-strategists (fast-reproducing, short-lived). The Alboran Sea, Balearic Islands, Sardinia, and Corsica emerged as priority areas for conservation where high originality-risk metrics were found to be prevalent. For the Northeast Atlantic, our analyses reveal region-specific responses of fish communities to fishing and climate. FP has generally declined, particularly in the Celtic Seas while the S_{FP} has increased. S_{CC} displays a north-south gradient, with northern communities more sensitive to warming. This is evident around Iceland and East Greenland, where demersal fish communities' S_{CC} has recently increased, while S_{FP} decreased.

In terms of epibenthos, our results provide evidence for broad-scale shifts in benthic trait composition in the North Sea over the past two decades, including increasing vulnerability scores in previously degraded areas. These changes appear to be partially linked to reduced trawling pressure, though environmental gradients such as temperature and depth continue to play key roles in benthic community structure. The habitats most sensitive to both fishing and climatic stressors are generally those with high ecological value and structural complexity (e.g. biogenic and rocky reefs, seamounts, canyons, and biological aggregations in soft sediments). Abyssal plains, although lower in ecological value, are highly vulnerable to deoxygenation, highlighting an emerging risk. This novel habitat sensitivity assessment stresses the urgent need for habitat-specific management and risk-informed spatial planning to strengthen resilience and prevent irreversible biodiversity loss.

Finally, our risk assessment toward invasive species show that 'Lessepsian migrants', species of Indo-Pacific origin that have entered via the Suez Canal, have rapidly expanded westward within the Mediterranean Sea. Low water temperatures during winter are a constraining factor for the spread of these species, but future sea warming will progressively weaken this natural barrier. Targeted fishing of non-indigenous species could be an effective tool for controlling their populations.

In summary, we have used trait-based approaches to assess the sensitivities, vulnerabilities and risks of marine life to two dominant stressors – climate change and fishing. We have not only done so for marine communities (both fish and epibenthic species) but have also developed a framework to assess marine benthic habitat sensitivities and risks. We have moreover examined the risks from invasives in the Mediterranean Sea, where this is considered a priority. This report has produced a broad range of 'sensitivity maps' and 'risk maps' that can inform what areas are characterised by higher prevalence of sensitive species, and may benefit most from protection; and in what areas species are at highest risk – so-called 'hotspots of risk.' Climate change leads to community shifts and different species that are adapted to those particular changing temperature regimes. A positive message is that recovery from fishing pressure can occur and be achieved by management actions.

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The role of this deliverable

This deliverable (D4.2) is the second of three reports in WP4 of EU project "User-oriented Solutions for Improved Monitoring and Management of Biodiversity and Ecosystem services in vulnerable European Seas" (B-USEFUL) that together comprise "*Risk and vulnerability*". Understanding the sensitivities of Europe's marine species to key pressures – both environmental and human-induced – will support the overarching aim of B-USEFUL to develop tools and solutions to manage marine biodiversity. Furthermore, it will support the EU Green Deal and Biodiversity Strategy 2030. Also on the national level it can support policy-making: like the results will support two aligned policies in the UK: the Marine Environment Plan and UK Biodiversity Strategy. For Icelandic and Greenland waters, B-USEFUL can support the Nordic Biodiversity Framework.

Throughout WP4, the emphasis is on two highly dominating pressures: (1) climate change and (2) fishing pressure (and associated physical seabed disturbance). Anthropogenically accelerated climate change in combination with (over-)exploitation of marine wildlife are seen as key drivers of biodiversity loss – both globally and in Europe's regional seas. Hence, understanding the mechanisms by which climate change and fishing impact alter marine ecosystems, is crucial for biodiversity conservation and sustainable resource management. To this aim, functional approaches, based on species' biological traits, are often used to characterise how vulnerable biological communities are to anthropogenic stressors.

In B-USEFUL WP4, trait-based approaches are used to assess the *sensitivities and vulnerabilities* and of marine communities to the impacts of climate change and fishing pressure (together risks). An important step was the development of two new trait-based sensitivity indicators: (i) sensitivity to climate change (SCC) and (ii) sensitivity to fishing pressure (S_{FP}) presented in D4.1 (Engelhard et al. 2024). The approach is described in a paper published since then (Polo et al. 2025) and allows a 'scoring' of Europe's marine species according to their sensitivities to these two pressures.

In the present, Deliverable 4.2 Report, we scale up from species-level, to assess *community-level* sensitivities and risks to European marine biodiversity. For Europe's major marine regions (Mediterranean, North Sea, North East Atlantic, Iceland and Greenland), we assess:

(1) Spatial patterns and temporal trends in community-level sensitivities or vulnerability of marine life.
(2) Spatial patterns and temporal trends in the two main pressures or 'hazards' – sea temperatures and fishing (trawling) effort.
(3) Spatial patterns and temporal trends in community-level risks – defined as the combination of community-level sensitivities and the level of pressure (warming or fishing). These patterns are subject to in a given time and space.

In combination, these maps allow the identification of 'hotspots' of community-level sensitivities and pressures, and hence also the identification of 'hotspots' of overall risk or vulnerability. For the Mediterranean a risk approach is also developed for the overall ecosystem functions and functionality.

A full chapter in the report is on *habitat sensitivity* (Chapter 8), which introduces a new approach to the assessment of the sensitivity of habitats to climate change and fishing pressure. Twenty-one different benthic habitats (ranging from abyssal plains to seagrass beds to biogenic reefs) are scored for their sensitivity to three main climatic stressors (temperature rise, ocean acidification and reducing oxygen levels) and 5 main fishing gear stressors. The approach has been tested on the Southwest European seas (described here) and is currently being applied in other regional seas.

The final results chapter assesses the risk of a major threat to particularly the Mediterranean Sea: that of invasions by non-indigenous species (NIS), with focus on the infamous ‘Lessepsian’ species (those that have entered the Mediterranean via the Suez Canal). The chapter demonstrates rapid increases in numbers and a steady westward expansion of these NIS, with near-future projections indicating their establishment in westernmost parts within 1-2 decades.

All these approaches are of relevance to the management and conservation of European marine biodiversity risks to climate change and anthropogenic pressures.

This deliverable builds on WP2, by using various catalogues of datasets containing biological traits, as well as of fish species abundances and distributions as informed by survey datasets from the Mediterranean and North-east Atlantic (Spedicato et al. 2024). The use of biological trait-based approaches in WP4 is in close alignment with their use in other WPs of B-USEFUL. See, for example, the report for deliverable 3.1 (Lindegren et al. 2025) for their use to estimate a set of biodiversity indicators (“Essential Biodiversity Variables” or EBVs) to assess European marine life, as part of WP3 “Biodiversity status and cumulative impacts”.

In turn, D4.2 will form the foundation for the upcoming deliverable D4.3 which is aimed at identifying overlap, or potential spatial mismatch, of sensitivity ‘hotspots’ and existing or planned marine protected areas (MPAs). Moreover, it will support WP5 “Forecasting and scenario simulations” as the recent patterns and trends described here, will be used to project species- and community-level risks into the future – the theme of the upcoming deliverable D5.2 “Forecast of species and community-level risks”.

1 General introduction

Europe's marine biodiversity is threatened by a range of pressures such as climate change, fisheries, habitat loss and pollution (Burrows et al. 2011, Poloczanska et al. 2013). To halt the loss of biodiversity requires well-informed science advice and operational decision-support tools, allowing end-users to formulate management plans and evaluate the effectiveness of conservation actions for biodiversity protection, notably with regards to the placement, size and number of marine protected areas (MPAs). This is needed to protect "hotspots" of biodiversity and vulnerable ecosystems, while ensuring their capacity to provide services vital to society and human wellbeing such as food provisioning and climate regulation. The Horizon project B-USEFUL contributes to achieve the ambitious policy goals set out by the EU Green Deal and the Biodiversity Strategy 2030 (as well as two aligned policies in the UK: the Marine Environment Plan and UK Biodiversity Strategy). It does so by developing user-oriented tools and solutions to conserve and protect marine biodiversity, effectively building and improving upon existing European data and governance frameworks.

Work-package 4 (WP4) is aimed at identifying habitats and species at risk of extinction in sensitive ecosystems by developing a hierarchical risk-based framework advancing upon that used by IPCC to assess climate risk (IPCC 2014). To achieve this aim WP4 pursues the following objectives: (1) identify species and/or habitats particularly at risk in different regional European seas (as assessed in Engelhard et al. 2024); (2) assess trends and patterns of community-level risk to inform potential adaptation or mitigation actions (this deliverable); and (3) assess spatial overlap, or potential mismatch, between hotspots of biodiversity, risks, and current marine protected areas.

1.1 Aim of this deliverable

Throughout WP4, the emphasis is on two highly dominating pressures on marine ecosystems: (1) anthropogenic climate change; and (2) fishing pressure (and associated physical seabed disturbance). In combination, these two pressures are widely recognised as primary drivers of biodiversity loss both globally in the world's oceans, and in Europe's regional seas (Burrows et al. 2011, Poloczanska et al. 2013, Kroodsma et al. 2018). In turn, biodiversity loss has major impacts on ocean ecosystem functions and services (Worm et al. 2006), which include supporting and regulating services as well as the provisioning of sustainable seafood (Jennings et al. 2016). A range of studies have demonstrated recent and ongoing impacts of climate change and fishing pressure in European waters, including changes in species composition (Hiddink et al. 2006, 2008, McHugh et al. 2010, Receveur et al. 2024) and in the abundance and distributions of many fish species (Perry et al. 2005, Engelhard et al. 2011, 2014, Azzurro et al. 2019, Baudron et al. 2020), including elasmobranchs (skates and sharks: Sguotti et al. 2016, Fortibuoni et al. 2017, Chatzimentor et al. 2022). These two drivers have also impacted many other forms of marine life (e.g. benthic invertebrates: Greenstreet et al. 2007, Hiddink et al. 2015, Beauchard et al. 2023, cephalopods: van der Kooij et al. 2016, Oesterwind et al. 2022, seabirds: Davies et al. 2013). In many cases, the relative contributions from climate change and fishing have remained poorly known (Rijnsdorp et al. 2009, Gissi et al. 2021). Hence, a better understanding of the risks imposed by these two drivers is important for biodiversity conservation and sustainable resource management (Gissi et al. 2021, IPCC 2022).

In B-USEFUL WP4, biological trait-based approaches are used to assess (i) the *sensitivities* of marine species, habitats, and communities to (ii) the *exposure to the two pressures* posed by climate change and fishing. The combination of *sensitivity* and levels of *exposure to pressure* is then used to assess (iii) the *risks* (or *vulnerabilities*) that marine communities are subject to – as well as the spatial and temporal variations in the levels of sensitivity, pressure or risk (see *Figure 1-1*).

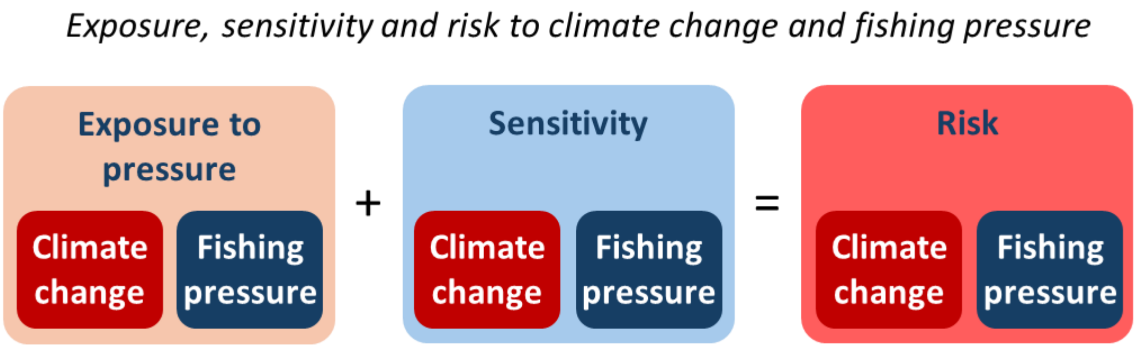

Figure 1-1. Schematic illustrating the approach to assessing exposure, sensitivity and risk to climate change and fishing pressure, as applied in chapters 2, 4, 5 and 6.

As a first step in this process, the initial deliverable of the WP has aimed at assessing which individual *species* are most sensitive to the two stressors (see the recently completed Deliverable 4.1 Report: Engelhard et al. 2024). An important step was the development of two new trait-based sensitivity indicators: (i) *sensitivity to climate change* (SCC) and (ii) *sensitivity to fishing pressure* (S_{FP}). This novel approach has been described in a recently published paper (Polo et al. 2025) and allows a 'scoring' of Europe's marine species according to their sensitivities to these two pressures.

In this deliverable report we build on these developments to assess *community-level* sensitivities, pressure exposures, and risks to European marine biodiversity. We apply the methodology to marine communities in the Mediterranean, the North East Atlantic (including the Greater North Sea, Celtic Seas and Bay of Biscay), Icelandic and Greenlandic waters. For each of these marine regions, we assess:

(1) Spatial patterns and temporal trends in community-level *sensitivities* of marine life;
(2) Spatial patterns and temporal trends in the *exposure* to two main *pressures* – sea temperatures and fishing (trawling) effort;
(3) Spatial patterns and temporal trends in community-level *risks* – based on the combination of community-level sensitivities and the level of pressure (warming or fishing) communities are subject to in a given time and space.

In combination, these maps allow the identification of 'hotspots' of community-level sensitivities and pressure exposures, and hence also the identification of 'hotspots' of risk or vulnerability – of relevance to the management and conservation of European marine biodiversity risks to climate change and anthropogenic pressures.

In **Chapter 2**, the patterns and trends in community-level sensitivities, pressure exposures, and risk are assessed for the Mediterranean Sea. The chapter also includes a regional evaluation of locations where risks may be either higher or lower over longer time-spans. In particular, can 'hotspots' and 'coldspots' of risk be identified, relevant for spatial area management?

In **Chapter 3,** we apply a new methodology within the Mediterranean Sea to assess how climatic and fishing pressures are related to the functional uniqueness, degree of specialisation, and level of endangerment in relation to the trait composition of the communities. Does the functionality of an ecosystem change due to key pressures?

Chapter 4 assesses community-level sensitivities, pressure exposures, and risks for three areas on the Northeast Atlantic Shelf – the OSPAR Regions Greater North Sea, Celtic Seas, and Bay of Biscay and Iberian Coast. In **Chapter 5**, the approach is extended to the highly productive Icelandic waters, and in **Chapter 6**, to (eastern) Greenlandic waters. This implies that in combination, a major portion of Europe's regional seas are covered in the report. It is worth noting that in each of these areas, levels of warming have generally been substantial but also spatially uneven; and there have either been reductions or increases, or redistributions of fishing effort in the various regions (Couce et al. 2020, Kroodsma et al. 2018, Thoya et al. 2021).

In **Chapter 7** we focus on epibenthic organisms in the Greater North Sea, and apply the methodology of Beauchard et al. (2021, 2023). This differs from the methodology of Polo et al. (2025) in that it assesses both *sensitivity* and *recoverability* to fishing (trawling) pressure (trawling disturbance) as separate factors, with these two together forming *vulnerability* (see *Figure 1-2*). In this chapter only the vulnerability and recoverability for fishing pressure are assessed. The sensitivity and recoverability (together vulnerability) for climate change pressure are under development and will be given in deliverable D4.3.

Figure 1-2. Schematic illustrating the approach to assessing sensitivity and recoverability, together comprising vulnerability to fishing pressure, as applied in chapter 7.

Chapter 8 introduces a new approach to the assessment of the sensitivity of habitats to climate change and fishing pressure. Twenty-one different benthic habitats (ranging from abyssal plains to seagrass beds to biogenic reefs) are scored for their sensitivity to three climatic stressors (temperature rise, ocean acidification and reducing oxygen levels) and five main fishing gear stressors (see *Figure 1-3*). The approach is tested on the Southwest European seas and is currently being applied in other regional seas.

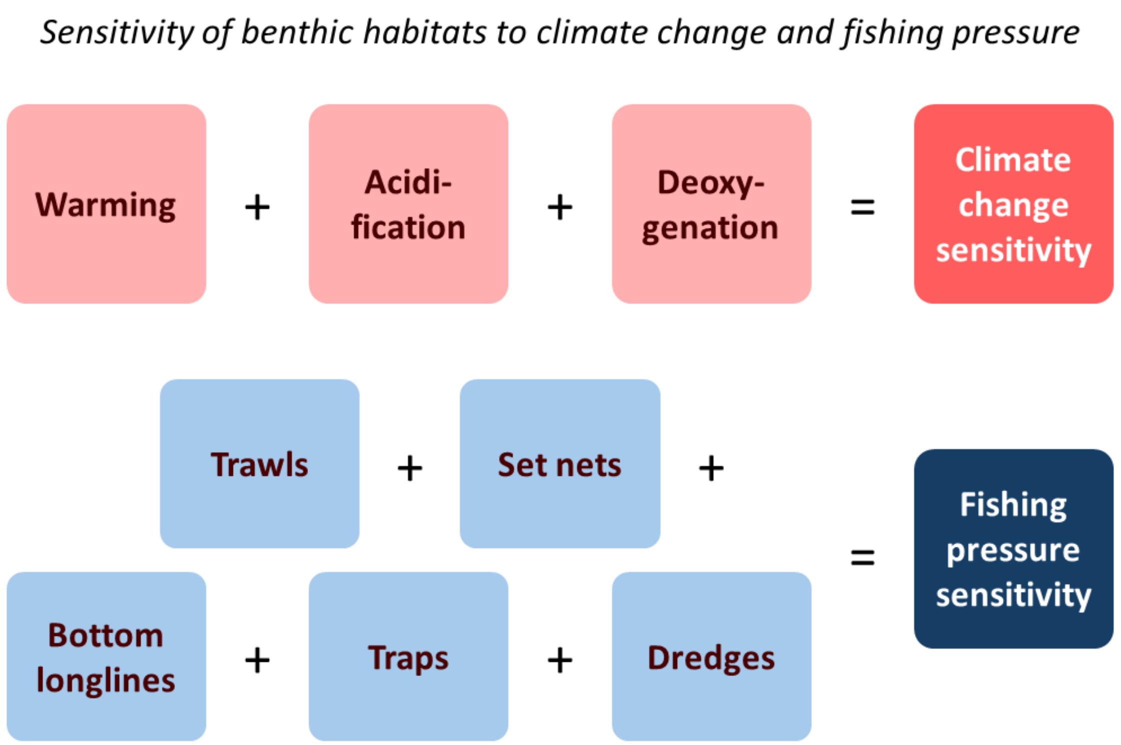

Figure 1-3. Schematic illustrating the approach to assessing sensitivity of benthic habitats to three climate change stressors and five fishing stressors. The combination of stressors make the overarching pressure. This approach is applied in chapter 8.

The Mediterranean Sea harbours over a thousand marine non-indigenous (NIS) species (Zenetos et al. 2022, Galanidi et al. 2023) and has been labelled as “the most heavily invaded marine region in the world” (Azzurro et al. 2022). **Chapter 9** assesses risks posed to the Mediterranean Sea from invasions by NIS, with special focus on so-called ‘Lessepsian’ species (those of Indo-Pacific origin that have entered via the Suez Canal). The chapter demonstrates rapid increases in NIS and a steady westward expansion, that can be linked partially with climate change and fishing; with near-future projections suggesting their establishment in the westernmost Mediterranean parts within 1-2 decades.

The report closes with an overview of the key messages emerging from the chapters, and a consideration of initial management implications and wider perspectives. In turn, this deliverable report is intended to form the foundation for two forthcoming B-USEFUL deliverable reports: on spatial overlap and/or potential mismatch between hotspots of biodiversity, risks, and marine protected areas (Deliverable D4.3 Report); and on future projections on risks and vulnerabilities of European marine life (Deliverable D5.2 Report).

2 Mediterranean Sea

2.1 Introduction

The Mediterranean Sea, while covering only about 0.82% of the global ocean surface and 0.25% of its volume, is considered one of Earth's most complex marine environments (D'Ortenzio & D'Alcalà 2009). This is due to its unique characteristics, such as its geographic position between the temperate climate of Europe and the hot arid climate of North Africa, and its high levels of endemism and species richness (Bianchi et al. 2012). This semi-enclosed sea hosts over 17,000 species, more than 20% of which are endemic (Coll et al. 2015). In recent decades, however, the region has undergone pronounced transformations due to the combined effect of a diversity of pressures, particularly climate change (CC; Mannino et al. 2017, Hidalgo et al. 2018), along with a broad diversity of additional and cumulative anthropogenic impacts, notably fishing pressure (FP). In particular, the Mediterranean Sea is warming at a rate two to three times faster than the global ocean average (Cramer et al. 2018, Marbà et al. 2015). Even small increases in temperature can dramatically affect species growth, survival, and reproduction (Crozier & Hutchings 2014). This can lead to cascading effects, such as changes in abundance (Rubino et al. 2024, Pita et al. 2021), distribution shifts (Azzurro et al. 2019, Sanz-Martín 2024), changing structure and function of marine communities (IPCC 2022, Hidalgo et al. 2022), biodiversity loss (Frid et al. 2023), and productivity decline (Reale et al. 2022). Some of these effects have been exacerbated by recent bioinvasions (Tsirintanis et al. 2022).

CC has become a critical focus of research due to its broad impact on marine ecosystem services, particularly fisheries (Lam et al. 2020). Climate-related stressors add to long-standing anthropogenic pressures such as overfishing, which has significantly shaped the Mediterranean Sea's ecological and economic landscape. Centuries of fishing have led to high levels of exploitation in many parts of the Mediterranean Sea, with most of the current fishing capacity (64%) represented by five countries (Italy, Türkiye, Tunisia, Egypt and Algeria) (FAO 2023). Fisheries landings from the Mediterranean Sea peaked in the mid-1990s, followed by a long-term decline until 2014, with a slight recovery by 2018, with Italy as the top producer (FAO 2023). In spite of recent reductions, a majority of Mediterranean fish stocks continue to be harvested beyond biologically sustainable levels (FAO 2023), with compounding pressures from CC (Cheung 2018, Holsman et al. 2017) that still need to be quantified for the different species and Mediterranean regions (Hidalgo et al. 2022). Consequently, the interplay of stressors along with long-lasting overexploitation of many Mediterranean stocks has posed substantial challenges for the development and enforcement of effective environmental management strategies, given the high priority towards stock recovery.

To assess how biological communities respond to environmental pressures, trait-based functional approaches are increasingly used to evaluate species' sensitivity and vulnerability to multiple stressors (De Juan & Demestre 2012, Polo et al. 2025). By focusing on ecological and life-history characteristics (e.g., trophic level, mobility, lifespan, fecundity), these approaches help predict species' responses and resilience to environmental pressures (Engelhard et al. 2011, Chessman 2013, Pecuchet et al. 2017, Beukhof et al. 2019a, 2019b, Butt et al. 2022).

In this study, a comprehensive trait-based risk assessment for FP and CC was carried out for fish communities across the Mediterranean Sea, covering the northern part of the basin from west to east, for the period 2012–2021. The specific aims were to:

(1) Calculate sensitivities to climate change (S_{CC}) and fishing pressure (S_{FP}) for Mediterranean species belonging to different major taxonomic groups (phyla).
(2) Evaluate spatial patterns and temporal trends in community-level sensitivities to climate change and fishing pressure.
(3) Map the intensity and spatial distribution of these two pressures, generating dedicated exposure layers.
(4) Describe the spatio-temporal dynamics of ecological risk associated with each stressor (i.e. CC and FP risk) and their cumulative effects
(5) Identify persistent hotspots and coldspots of CC risk and FP risk across the basin.

2.2 Methods

The analysis was based on biological data collected through the MEDITS scientific trawl survey, an international monitoring programme coordinated across the Mediterranean Sea (Spedicato et al. 2019). Conducted annually by multiple countries and following a standardised, depth-stratified sampling design (Anonymous 2017), the survey provides harmonised data on demersal species' abundance, biomass, and distribution across 18 Geographical Sub-Areas (GSAs) that comprise the northern Mediterranean Sea (GFCM 2009). Species collected during each haul were taxonomically validated using the World Register of Marine Species (Ahyong et al. 2025), and species density was calculated as the number of individuals per square kilometre (n/km²). To ensure data consistency and analytical robustness, the study focused on the most recent decade of available data (2012–2021) and retained only those species meeting specific spatial and temporal representation thresholds that were based on cumulative richness curves, annual haul coverage, and minimum abundance levels; this resulted in a final dataset including 322 species (Polo et al. 2025, Sáinz-Bariáin et al. 2025). Continuous environmental variables were converted into quantile-based classes to describe each species' central tendency and upper environmental limits. When species-specific trait information was unavailable at the species level, average values at higher taxonomic levels were used. A total of 239 species had complete trait profiles suitable for analysis: 114 fishes, 64 crustaceans, 21 cephalopods, and 40 species belonging to other taxonomic groups (3 commercial, 37 non-commercial; Anonymous 2017). Species-level sensitivity to CC and FP was computed following the trait-based approach described in Engelhard et al. (2024) and Polo et al. (2025). Species-level sensitivity scores were then combined into community-level indices at each sampling station, using species' relative abundance as weights (Escudier et al. 2021).

Twelve traits were used to describe fishing sensitivity (*Table A-1* of Appendix A), while nine traits reflecting ecological and thermal tolerance were used to infer climate sensitivity (*Table A-2*). Environmental affinity and specificity scores were derived for each species by linking occurrence data with sea surface temperature (SST), sea bottom temperature (SBT). The estimated spatial maps describing community-level sensitivity indices (for CC and FP sensitivity) by location were then combined with spatial pressure exposure maps (for CC and FP), as the average of the two components at cell and year level, except if one of them was 0, when the risk was considered 0. This allowed the generation of risk spatial layers for both climate and fishing drivers. FP was reconstructed using the fishing footprint derived from Automatic Identification System (AIS) data provided by Global Fishing Watch (Kroodsma et al. 2018, Thoya et al. 2021), complemented with aggregated effort data from the STECF Fisheries Dependent Information (FDI) data call to correct for temporal bias caused by increased AIS coverage over the course of the time series. Since Albania and Montenegro are not included in the European FDI data call, fishing effort in the eastern part of the Southern Adriatic Sea (GSA 18) is likely underestimated, as the data do not account for the activity of their national fleets. Climate-related pressure exposure was derived from the Copernicus CMEMS reanalysis dataset (Escudier et al. 2021), featuring monthly sea surface temperature estimates at 1/24° resolution (~4–5 km).

Risk scores were modelled across space and time using Generalized Additive Models (GAMs) implemented in the 'mgcv' package in R (Wood 2011, 2017). Separate models were fitted for each pressure, with risk as the response variable and univariate smoothed effects of longitude, latitude, year, depth, and GSA as predictors. We used penalised smoothers and restricted maximum likelihood (REML) estimation, along with a gamma parameter of 1.4 to mitigate overfitting. To identify spatial clusters of temporal persistence of high or low risk, local Gi* statistics (Getis & Ord 1992) were applied to annual prediction grids, using a quantile-based threshold to delineate hotspots and coldspots of risk. The persistence of these spatial patterns over time was then mapped. Finally, a cumulative risk index (R_{cum}) was computed per grid cell and year as the equally weighted mean of the two normalised layers of R_{CC} and R_{FP}, i.e. $R_{cum} = (R_{CC} + R_{FP})/2$.

2.3 Results

2.3.1 Phyla evaluation

The risk analysis across the Mediterranean demersal community revealed important species-specific patterns in sensitivity to FP and CC, reflecting broader variability in ecological and life-history traits. As shown in *Figure 2-1*, the majority of taxa (64%) emerged as having high sensitivity to fishing (defined as $S_{FP} > 0.5$), with a smaller proportion of taxa (36%) having high CC sensitivity (defined as $S_{CC} > 0.5$). Echinoderms, in particular, stand out as one of the most sensitive groups, with 100% of assessed taxa showing high sensitivity to FP and nearly half (47%) also highly sensitive to CC.

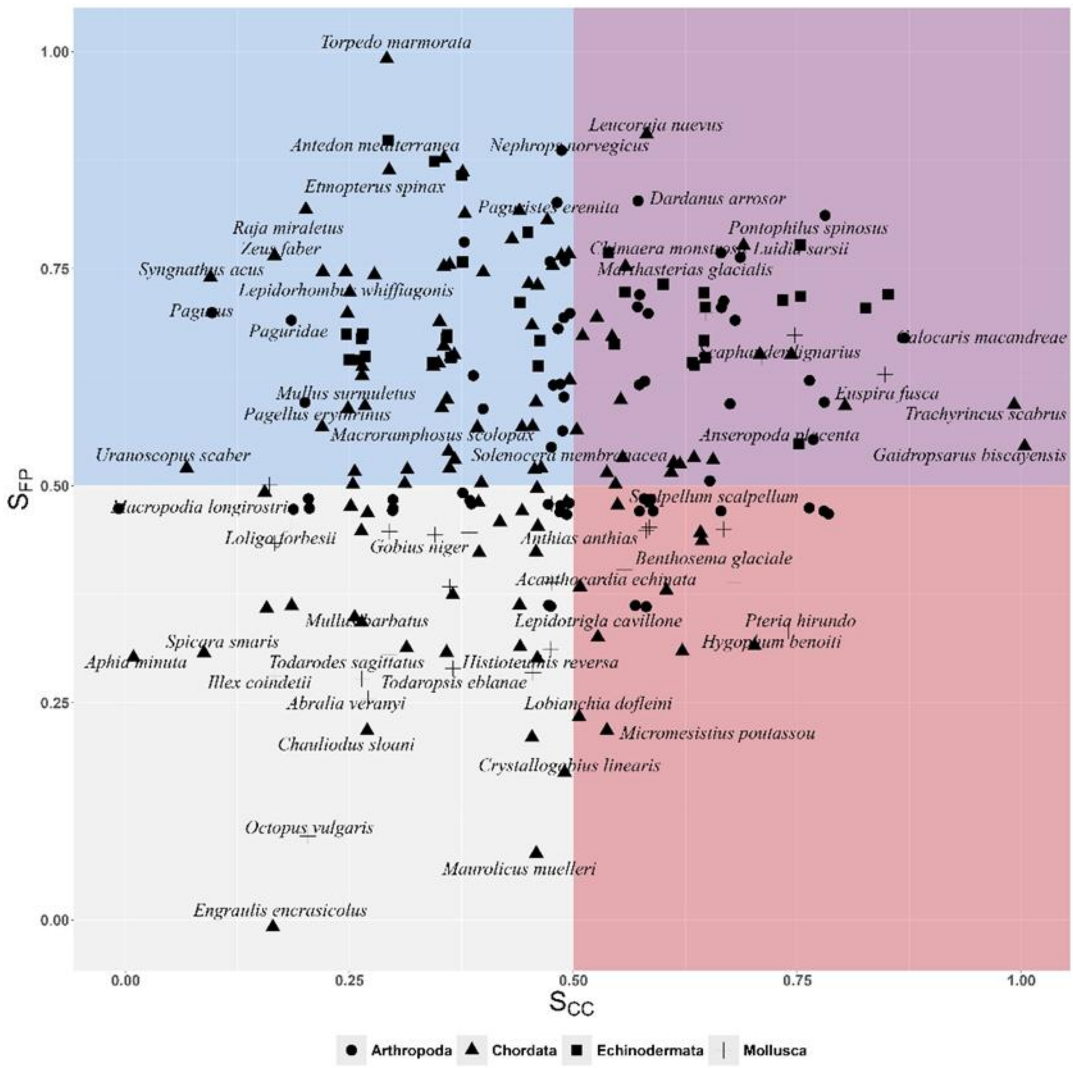

Figure 2-1. Representation of the species-specific position of demersal species from the Mediterranean Sea in the sensitivity space, defined by sensitivity to fishing pressure (S_{FP}) and climate change (S_{CC}). Each point represents a species, plotted according to its estimated sensitivity scores. The background colours indicate four quadrants based on a 0.5 threshold, distinguishing between low and high sensitivity levels. Species are grouped by phylum: Arthropoda (●), Chordata (▲), Echinodermata (■), and Mollusca (+), highlighting taxon-specific patterns of vulnerability.

Among vertebrates, elasmobranchs (e.g., sharks and rays) exhibited uniformly high sensitivity to FP (i.e. 100% with $S_{FP} > 0.5$), but only 8% also showed high (>0.5) sensitivity to CC. Among teleost fishes, a smaller but nevertheless notable majority (63%) showed high (>0.5) sensitivity to FP, with 29% showing high S_{CC}. Arthropods displayed a more balanced sensitivity profile, with 58% of taxa having S_{FP} >0.5 and 45% having S_{CC} >0.5. The Mollusca phylum exhibited more heterogeneous sensitivity levels: only 19% of molluscs ranked highly sensitive to fishing, whereas 37% were highly sensitive to CC. Notably, bivalves and gastropods emerged as more consistently sensitive across both stressors.

2.3.2 Regional evaluation – Sensitivity

The spatial and temporal distributions of community-level sensitivities to CC and FP revealed marked heterogeneity across the Mediterranean.

Climate change sensitivity (S_{CC}) was found to reach its highest levels in several of the deeper strata (*Figure* A-1 of Appendix A), particularly in the Alboran Sea, Strait of Sicily, Aegean Sea, and off Malta. In contrast, low S_{CC} values were observed in the northern Adriatic and Tyrrhenian Seas, particularly in shallower strata. The western Mediterranean Sea tended to have higher S_{CC} than the eastern part. Significant declines in S_{CC} were reported in many areas *Figure A-2* of Appendix A), particularly the Gulf of Lions, Tyrrhenian Sea, and off Sardinia and Malta; these contrasted with increases in S_{CC} in the Northern Adriatic and Aegean Seas (shaded red). These patterns were further confirmed at GSA level (*Table A-3*) with negative trends reported for GSAs 7, 9, 10 and 15 (respectively, Gulf of Lions, Ligurian-Northern Tyrrhenian, Southern-Central Tyrrhenian, and Malta). S_{CC} in the Adriatic Sea remained overall stable over time, with GSA 22 (Aegean Sea) being the only area showing a significant increase in S_{CC}, particularly in its southernmost part.

Fishing pressure sensitivity (S_{FP}) showed a distinct spatial pattern, with higher values in the deeper and southern-central areas of the Mediterranean Sea (*Figure A-3*) and lower values in the northern and coastal areas. Over the period 2012-2021, S_{FP} increased in the Northern Adriatic, Eastern Ionian, and southern Aegean seas (*Figure A-4* of Appendix A), while S_{FP} decreased in the Gulf of Lions, Sardinia, and parts of the Tyrrhenian and Aegean Seas. At GSA level, significant increasing trends (*Table A-3* of Appendix A) were reported for GSAs 17, 20, and 22 (Northern Adriatic, Eastern Ionian, Aegean), while decreasing trends were reported for GSAs 11 and 19 (Sardinia, Western Ionian). These regional dynamics were also visible at subregional scale, where the Adriatic Sea showed an overall increasing trend and the Central Mediterranean a downward trend in S_{FP}.

2.3.3 Regional evaluation – Exposures

The spatial distribution of fishing activity (*Figure A-5*) highlighted persistent fishing hotspots concentrated in different areas, including the Western Mediterranean (particularly along the Spanish coast in Catalan coast, Valencia Channel and North Alboran Sea), the (mainly northern) Adriatic Sea, and parts of the Tyrrhenian Sea and Strait of Sicily, mainly in coastal areas. Temporal patterns revealed a fragmented picture of effort change (*Figure A-6* and *Table A-3* of Appendix A), with notable reductions in effort in the Northern Tyrrhenian (GSA 9), Northern Adriatic (GSA 17) and Aegean Seas (GSA 22). Conversely, effort increased in the Southern Adriatic Sea (GSA 18) and around Cyprus (GSA 25). Importantly, even within GSAs with no significant net trend, localized increases or declines in fishing effort exist, often compensating each other at coarser spatial scales.

The thermal landscape of the Mediterranean Sea revealed a clear west-east gradient in sea surface temperature (SST) with consistently warmer conditions in the south-eastern basin, notably around Cyprus, Crete, and Malta, and cooler in the western and northern sectors (*Figure A-7*). Temporal analyses (*Figure A-8*) confirmed a widespread warming trend over the study period (2012-2021), particularly pronounced in the Central and Eastern Mediterranean, including GSAs 11, 16, 22, and 25 (*Table A-3*A). Western GSAs and areas such as the Northern Adriatic displayed greater interannual variability with weaker or non-significant warming signals.

2.3.4 Regional evaluation – Risks

The distribution of CC and FP risk (R_{CC} and R_{FP}, respectively) within the Mediterranean Sea – derived from the integration of sensitivity (S_{CC} and S_{FP}) and exposure intensity (SST and fishing effort) – was found to show distinct spatial patterns (*Figure A-9*).

On average, higher CC risk was concentrated in the western basin (particularly Alboran Sea, Balearic region) and in southern and eastern areas (including Malta, southern Aegean Sea), especially in the deepest strata. Conversely, lower CC risk values were concentrated in the Northern Adriatic and coastal areas of the northern Aegean and Western Mediterranean Seas, especially in shallower bathymetry. Temporal dynamics further revealed diverging regional trends *Figure A-9*). Increases in CC risk are most evident in the Northern Adriatic and Aegean Seas, while decreases in CC risk are observed locally in areas such as the Gulf of Lions and Southern Tyrrhenian. These trajectories were corroborated by GSA-level analysis (*Table A-3* of Appendix A), which confirmed a pronounced south-eastward spatial risk gradient and identified consistent increasing risk trends in GSAs 20, 22, 23, and 25 (respectively Western Ionian, Aegean, Crete and Cyprus). This highlighted the Eastern Mediterranean as a hotspot of increasing climate risk.

In contrast, FP risk presented spatial patterns distinct from those in CC risk (*Figure A-10*). Higher FP risk values were typically observed in the Western Mediterranean and Adriatic Seas, areas that are both characterised by highly exploited fishing grounds. It should be stressed again that the effort data used here did not include information for the fleets of Albania and Montenegro, likely leading to an underestimation of fishing pressure in coastal areas of the south-western Adriatic Sea.

Temporal trends offered further insight into the spatio-temporal dynamics of FP risk across the Mediterranean (*Figure 2-2*, *Table A-3*). Significant increasing trends in FP risk were evident for the Adriatic Sea (GSAs 17 and 18), Eastern Ionian Sea (GSA 20), and Eastern Mediterranean Sea (GSAs 20, 22, 23 and 25). In addition, at a local scale, significant increasing trends in R_{FP} were also observed (*Figure A-11*) around the Balearic Islands and in the Alboran, Southern Tyrrhenian and Southern Aegean Sea. Overall however, most of the GSAs in the Western and Central Mediterranean Sea exhibited significant decreases in FP risk over the study period.

2.3.5 Regional evaluation – Hotspots and coldspots of risk

The direct interaction of the estimated risks was used to predict the likely cumulative component based on FP and CC risks combined. Several hotspots of persistent high cumulative risk were identified, where both exposure to FP and CC are high (Figure 3); these were in the Alboran Sea, Strait of Sicily, southern Tyrrhenian Sea, and off Crete and Cyprus. By contrast, several areas of persistent low cumulative risk (i.e. risk coldspots) were also identified; these included coastal areas of the Adriatic Sea, the Eastern Ionian Sea, and Aegean Sea.

Temporal trends at the GSA level (*Table A-3*) revealed significant increases in cumulative risk in key areas of the Eastern Mediterranean, notably in GSAs 20, 22, 23, and 25, confirming this subregion as a hotspot of emerging risk, as determined by the combination of the increasing trends observed. The Western and Central Mediterranean Sea are characterized by relatively higher cumulative risk levels in comparison with other areas, for both FP and CC, particularly in their southern parts, where persistent hotspots are concentrated. Nonetheless, both subregions exhibited slight but consistent decreases in cumulative risk over time. In contrast, despite lower temporal persistence of hotspots (*Figure 2-3*) and lower average levels of both

FP and CC risk, the Adriatic Sea displayed a modest yet statistically significant increasing trend in cumulative risk (*Table A-3* of Appendix A).

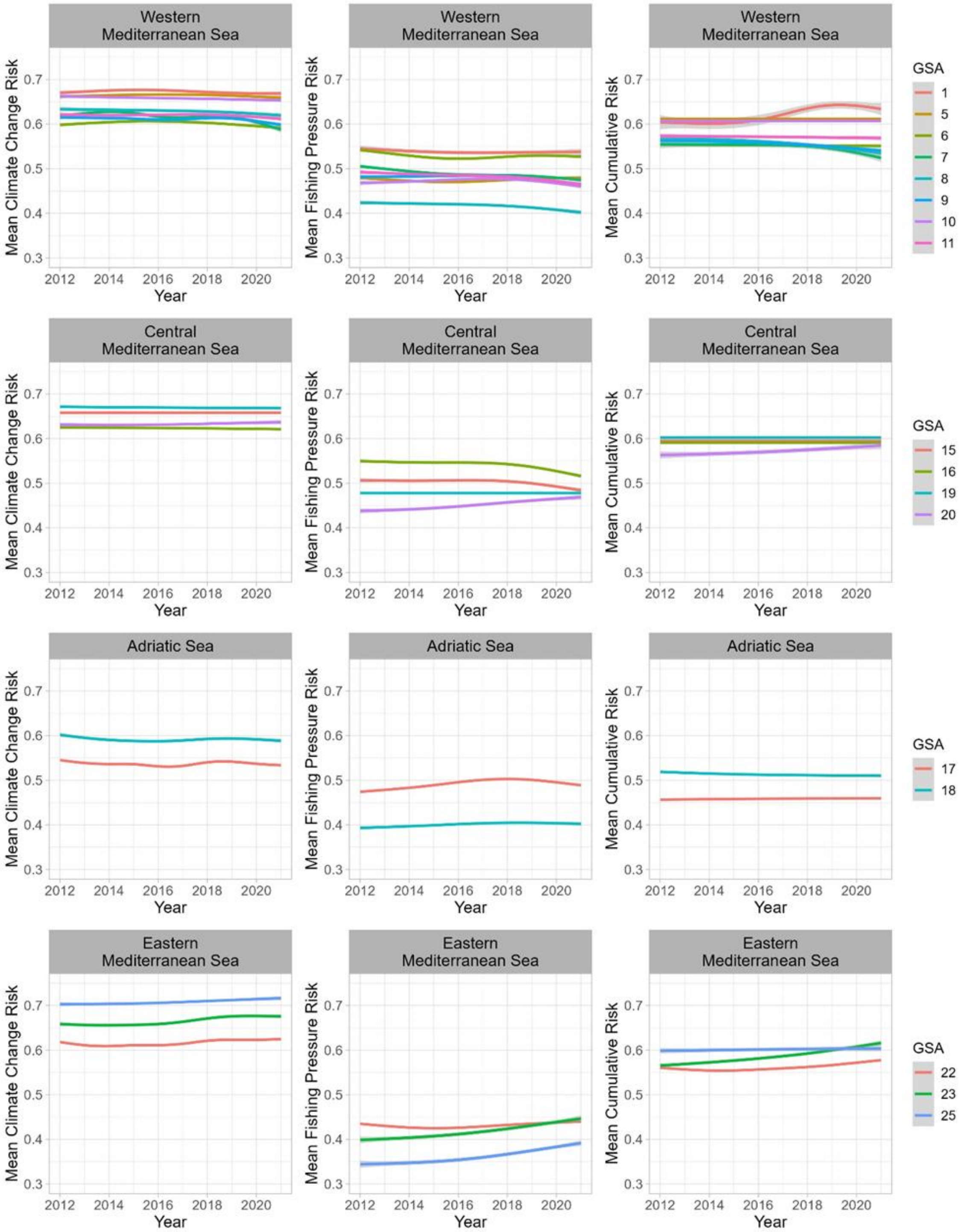

Figure 2-2. Temporal trends of demersal community risk across Mediterranean subregions (2012–2021). Each row shows the average risk values for R_{CC} (left), R_{FP} (center), and R_{cum} (right) in the Western, Central, Adriatic, and Eastern Mediterranean subregions. Lines represent trends for individual GSAs within each subregion, smoothed by means of GAM models.

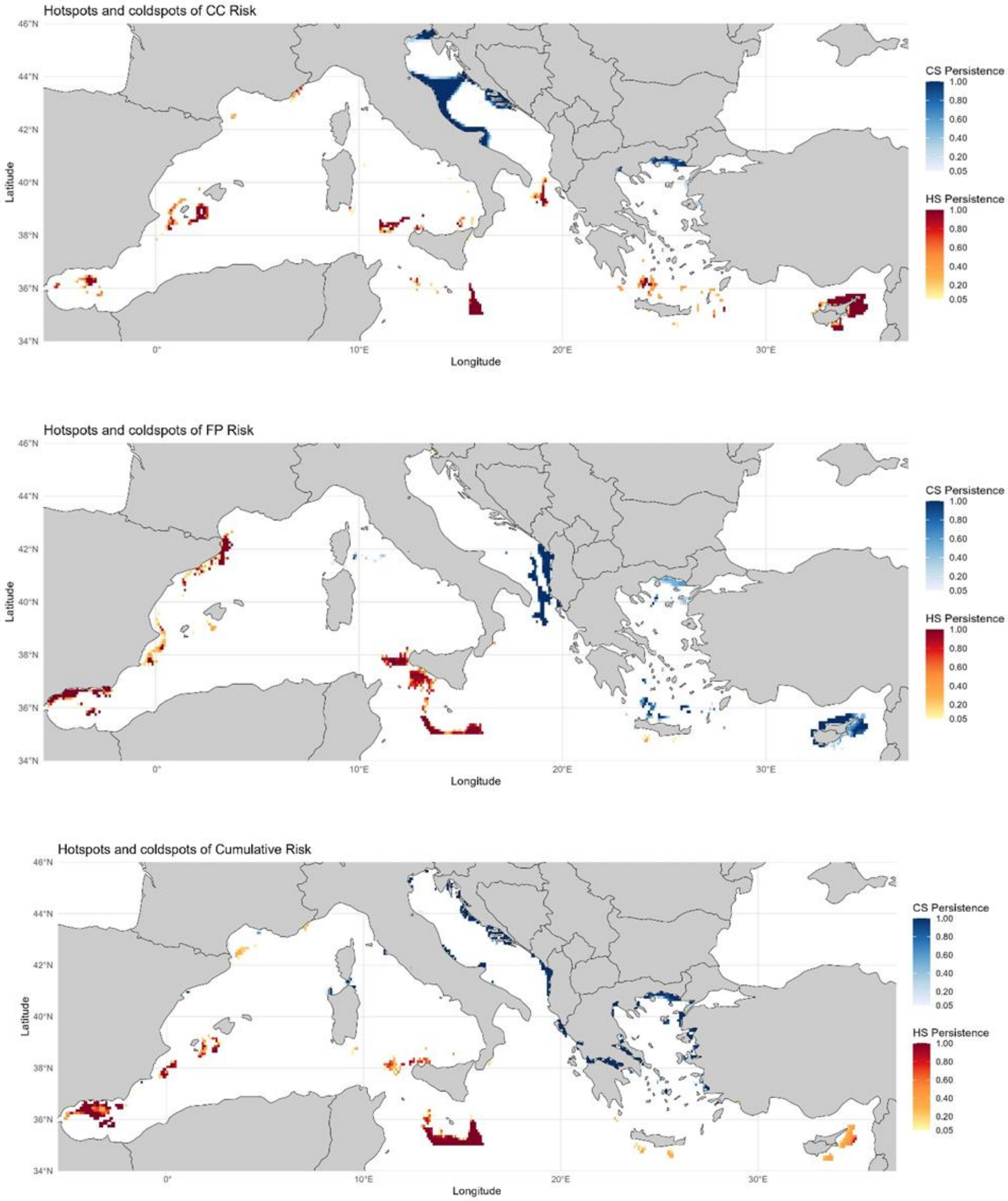

Figure 2-3. Spatial distribution of hotspots (HS, in red) and coldspots (CS, in blue) of risk persistence across the Mediterranean Sea. Each panel shows the location and persistence of high and low persistence areas over time for: (Top) climate change risk (R_{CC}), (Middle) fishing pressure risk (R_{FP}), (Bottom) cumulative risk (R_{cum}).

2.4 Discussion

This cumulative risk analysis of the Mediterranean demersal community revealed distinct species-specific and community-level spatio-temporal patterns in vulnerability to FP and CC, and these were consistent with known spatial heterogeneity of this semi-enclosed Sea. The life history traits considered here allowed to distinguish the echinoderm taxa as the most sensitive, particularly to FP. Indeed, their low mobility, narrow habitat specificity, and slow recovery potential (Alves & Cristina Costa 2009, Engin et al. 2024) highly reduce their adaptive capacity to both anthropogenic and environmental pressures. Vertebrate taxa generally showed different sensitivities to these two drivers: with CC mostly exerting broad, gradual, and systemic impacts, but fishing imposing more acute and immediate pressure, thereby acting as primary driver of decline in many fish population (in line with Gissi et al. 2021). Among the vertebrates, some groups were confirmed to show particularly high sensitivity to FP, notably the elasmobranchs (e.g., sharks and rays: De Juan et al. 2020). Many studies confirm high sensitivity to fishing in elasmobranchs, owing to their longevity, late maturity and low fecundity (Barausse et al. 2014, Giovos et al. 2021). The teleost fishes showed a broad variability in sensitivity to CC and FP.

Among the molluscs, cephalopods showed generally low sensitivity to both FP and CC, likely linked with their short life-cycles (fast growth and reproductive rates) and ecological flexibility of this group (González-Irusta et al. 2018, Polo et al. 2025). This is consistent with recent studies that identified cephalopods as supposed ‘winners’ of CC in the Mediterranean (Veloy et al. 2024) and elsewhere (van der Kooij et al. 2016). By contrast, bivalves and gastropods emerged as generally more sensitive to exposure to both CC and FP, linked with their susceptibility to warming and acidification, as well as to harvesting (Bueno-Pardo et al. 2021).

The study confirmed generally high sensitivity and risk to climate change of marine life in the Mediterranean Sea, where global warming is expected to have severe effects on the survival of natural populations (Gallagher & Albano 2023). The risk is exacerbated by the semi-enclosed nature and mostly east-west orientation of the basin, limiting the potential for latitudinal range shifts; and by the ever increasing socio-economic demands and pressures on the system (Cramer et al. 2018). These geographical limitations may determine the expansion of sensitive species toward deeper strata, allowing to further explain the depth-oriented gradient observed in the spatial distribution of the community-level sensitivity to CC, causing warm-sensitive species to deepen in order to ‘escape’ warming waters (Chaikin et al. 2022, Sanz-Martin et al. 2024) towards colder-water refuges. Within the study area, the Western Mediterranean emerged as a hotspot of vulnerability to CC (Chatzimentor et al. 2023), with a progressive change towards more thermally tolerant communities under ongoing warming, and consequently a decrease of estimated risk level over time (particularly in the Gulf of Lion). In other areas characterised as the last remaining cold refugia in the Mediterranean (e.g., Northern Adriatic and Aegean Seas), an opposite trend of increasing community-level sensitivity was observed, possibly due to the northward migration of thermally sensitive taxa. These spatial patterns directly attributable to CC are mostly determined by either species range expansion or increased abundance, or conversely by spatial contraction and decreased abundance (Poloczanska et al. 2013), or areas characterised by strong winter events and deep-water formation.

CC can affect marine organisms at multiple organisational levels, from cells to organisms to entire ecosystems. These impacts may be direct, by influencing individual physiology such as metabolism and reproduction, or indirectly, by altering interactions with prey, predators, competitors, or parasites (Lord et al. 2017, Millington et al. 2022). As a result, climate effects may lead to changes in metabolic rates, growth, and timing of key life-history events (e.g. breeding), reproductive success, mortality, and species abundance and distribution (Rubino et al. 2024, Pita et al. 2021, Marbà et al. 2015, Coma et al. 2009). Ultimately, these individual- and population-level effects can cascade to influence community structure and overall ecosystem functioning (Pierce et al. 2010). These changes often produce divergent trends that are difficult to explain, as they emerge from antagonistic and synergistic interactions among multiple pressure drivers, along with the evolutionary adaptation of species communities (Harley & Rogers-Bennett 2004).

The findings reported here highlight that species' differential sensitivities are strongly mediated by key life-history traits—such as mobility, reproductive strategy, and habitat specificity—which determine their capacity to withstand or adapt to the cumulative effects of fishing and climate stressors. Also, this variability is evident in the Mediterranean demersal communities. For instance, echinoderms and elasmobranchs consistently exhibit high sensitivity to FP, while molluscs and arthropods display more heterogeneous responses to both drivers. These variabilities arise from complex, species-specific cumulative responses to warming (Burkett et al. 2005) and are further shaped by the combined effects of stressors on key demographic processes. These include the interplay among mortality rates, growth rates, and modifications to population size-structure (Lindmark et al. 2023).

The results reported here clearly provide evidence on how the species and communities' distributions were shaped by the high levels of historical exploitation in the Mediterranean Sea (FAO 2023), since many decades before the onset of available monitoring data. This is reflected in the generally lower FP sensitivity values reported in the shallower and neritic waters, mostly exploited by the commercial fishery in the northern and coastal areas of the Western Mediterranean, Adriatic, and Aegean Seas. The use of bottom-contact fishing gears is known to negatively affect benthic habitats, causing changes to the seabed substrates and disturbing the composition and functioning of benthic communities (Collie et al. 2017, Kaiser et al. 2002). These disturbances often lead to declines in epifaunal biomass and reduced populations of sessile organisms (Polet and Depestele 2010, Tinlin-Mackenzie et al. 2023). This, in turn, favours the selection of short-lived organisms, less vulnerable to fishing-related mortality (Smith et al. 2023, Van Hoey et al. 2023, Zupa et al. 2025). Such organisms typically exhibit great adaptive capacity in frequently disturbed environments and a reduced likelihood of encountering a fishing event within their shorter lifespan (Hiddink et al. 2019, Rijnsdorp et al. 2018). Synergistically, environmental conditions can shape benthic community composition and modulate the impacts of FP. In highly dynamic areas with strong fluctuations in temperature, salinity, hydrodynamics and/or nutrient levels, species may have more plastic traits and life histories, and hence be more resilient to additional stressors; in more stable environments, the species comprising benthic communities tend to be less tolerant and more vulnerable to additional stressors (Dutertre et al. 2013, Jennings & Kaiser 1998). A growing concern exacerbated by CC, is the spread of invasive species, particularly in the Eastern

Mediterranean Sea with increased prevalence of Lessepsian migrants (that have entered via the Suez Canal: Katsanevakis et al. 2020). The expanding presence of these warm-adapted species originating from the Red Sea, may be playing a key role in the CC risk coldspots observed in some coastal areas.

The combined effect of recent reductions in fishing effort in the study area, along with spatio-temporal variations of the FP sensitivity of the marine communities, may explain divergent trends in FP risk across the region. These effort reductions are likely the outcomes of fishery management measures implemented in the study area in recent years (European Union 2019, GFCM 2018b, 2018a, 2019). Overall, a general reduction of the FP risk is evident from our study, particularly in the Western Mediterranean Sea. Here, a synergistic effect between reduced effort and lower community vulnerability suggests possible adaptive transitions towards communities dominated by thermally tolerant taxa (Polo et al. 2025). Conversely, other areas, notably the Adriatic Sea, showed trends of increasing FP risk, largely driven by a rise in the community-level sensitivity. This pattern may be attributable to a direct adaptive response of the community to the fishing effort reduction, which could lead to a proportional increase in sensitive taxa. Additionally, CC may be exerting a strong influence by limiting the northward range shifts of species sensitive to both warming and fishing effort, (Gallagher & Albano 2023) due to the coastline’s limits (Cramer et al. 2018b).

2.5 Conclusions

The different spatio-temporal dynamics here reported underscore the need for a cumulative assessment to inform adaptive management. This joint response further corroborates single-driver patterns and highlights where pressures co-occur to elevate risk. In the Eastern Mediterranean Sea, cumulative risk increased across GSAs, consistently with progressive warming (Shaltout & Omstedt 2014) and rising CC sensitivity; this was particularly the case in the Aegean Sea (Chatzimentor et al. 2023). Rising cumulative risk is in line with limited potential for threatened species at climatic risk to shift their ranges towards less warm regions, due to the semi-enclosed nature of the area (Cramer et al. 2018), and with recent increases in fishing effort, affecting ecosystem structure and functioning in the short term (Dimarchopoulou et al. 2021). Further west in the Mediterranean Sea, potential cumulative-risk hotspots, such as the Alboran Sea, Balearic Islands, and south of Malta, show slightly reducing trends. The Alboran Sea is a transitional area characterised by high turnover and replacement of species between the Atlantic Ocean and Mediterranean Sea (Hidalgo et al. 2022), and by a contemporary decrease in fishing effort; this area showed a recent reduction in both CC and FP risk, possibly reflecting local adaptation or shifts towards less sensitive taxa (Hidalgo et al. 2022, Polo et al. 2025).

The Adriatic Sea exhibited a modest but statistically significant increase in cumulative risk, despite low average levels of FP and CC risk and less persistent risk hotspots. This upward trend is mainly driven by a peak in fishing effort in 2018, followed by a gradual decline likely influenced by the adoption of management measures (GFCM/43/2019/5 2019), afterward confirmed by the commercial fisheries catches reported at Mediterranean level (FAO 2023). A further contributing factor is the rising sensitivity to CC in the northern Adriatic (GSA 17), where cooler waters may act as both the last cold refuge and a potential ecological ‘trap’ for cold-water species as warming continues (Chatzimentor et al. 2023)

This basin-wide, trait-based risk assessment indicates that FP remains the dominant immediate threat, whilst climate change is rapidly intensifying and reshaping spatial risk patterns. Given the simultaneous occurrence and action of both stressors in many locations, rapid and coordinated management interventions are urgently required to support sustainable management, such as depth-inclusive spatial management, basin-wide climate-adaptation measures, and gear/effort limits targeted to sensitive assemblages. These measures are urgent under rapid warming and increasingly frequent and intense marine heatwaves, to prevent further erosion of functional diversity and to secure the ecological and socio-economic ecosystem services on which Mediterranean societies depend.

3 Combining functional originality and risk indicators for western Mediterranean fish

3.1 Introduction

Marine biodiversity is facing unprecedented challenges in the 21st century due to cumulative human impacts, including overfishing, pollution, habitat degradation and climate change. This is highly apparent in the Mediterranean Sea, one of the most ecologically diverse yet heavily impacted marine ecosystems globally (Coll et al. 2010, Micheli et al. 2013). Traditionally, conservation strategies have focused on protecting endangered species or commercially valuable stocks (Batista et al. 2025, Preikshot & Pauly 2005). However, these approaches often overlook a crucial aspect of biodiversity: the specific ecological functions that individual species perform within ecosystems – with some species playing more distinct or 'unique' ecological roles than others (McGill et al. 2006, Morim et al. 2023).

The ecological functions of species are defined by functional traits, which are measurable characteristics of organisms that influence their ecological roles and interactions within an ecosystem. Functional traits can determine how an organism reacts to environmental conditions (e.g., temperature, resource availability) and how it alters the surrounding environment (e.g., nutrient cycling, habitat modification) (Vieira et al. 2006). In turn, the average/summary of the functional traits across the various organisms in a particular ecosystem may determine the nutrient and energy flow through that system (Nock et al. 2016). In this context, the concept of *functional originality* refers to species with distinct functional trait combinations, including those that are unique in their functional role and/or display extreme trait attributes compared to the community they are part of (Griffin et al. 2020, Pimiento et al. 2020, 2023). Despite its importance, functional originality has not received much attention in past biodiversity research and conservation planning. Only a few authors have recently made attempts to design indicators that combine functional originality and endangerment (Griffin et al. 2020, Griffith et al. 2023, Pavoine & Ricotta 2021, 2023, 2024, Pimiento et al. 2020) to integrate functional originality in species-level conservation prioritisation.

This research gap is addressed here for the Western Mediterranean Sea, by identifying the most functionally original fish species based on two metrics: *functional uniqueness* (*FUn*) and *functional specialisation* (*FSp*). In order to identify species-level conservation priorities, we then combined functional originality with four different metrics of species-level risk to calculate four *risk-weighted indicators of functional originality*. These risk metrics included the IUCN Red List status with as in Pimiento et al. (2020), another measure of species rarity (Violle et al. 2017), and the two more measures of sensitivity to fishing pressure and climate change also applied elsewhere in this deliverable report (in line with Engelhard et al. 2024 and Polo et al. 2025). As highlighted previously, fishing pressure and climate change are two of the most prevalent pressures in the Western Mediterranean Sea. The final goal is to improve conservation planning by identifying species that are not only at risk but also play unique and irreplaceable roles in ecosystem functioning; and to identify the areas within the Western Mediterranean Sea where functionally original species and/or communities are typically more prevalent.

3.2 Methods

Data on the presence and abundance of fish species (Chondrichthyes and Teleostei) in the Western Mediterranean Sea were obtained from 12,666 hauls recorded by the Mediterranean International Bottom Trawl Survey (MEDITS) between 1999 and 2021. The data were collected from both continental shelf (10–200 m) and slope zones (200–800 m) and standardised to individual densities per square kilometre (Spedicato et al. 2020). Functional originality was described considering different life-history, distributional, and morphological traits (e.g. body shape or food type; Morim et al. 2023) compiled in the B-USEFUL project (details in deliverable 2.2, Spedicato et al. 2024). Final data selection included 17 functional traits for 176 fish species (*Table B-1* of Appendix B). We analysed continental shelf and slope communities independently, as considerable differences among these have been reported (Farriols et al. 2019, Pennino et al. 2024). The IUCN (International Union for Conservation of Nature) Red list status of each species was included as numeric integers ranging from 0 ("Least Concern") to 4 ("Critically Endangered") and excluding "Data Deficient" species (Pimiento et al. 2020, Griffin et al. 2020). The sensitivity of species to fishing pressure and climate change were estimated based on the trait-based sensitivity scores proposed by Polo et al. 2025. The sensitivity scores were normalised to values ranging from 0 to 1 after dividing the species pool into the shelf and slope communities.

Functional originality was calculated using *FUn* and *FSp*, following Pimiento et al. 2020 and Griffin et al. 2020. *FUn* ranks species according to the distinctiveness of their trait combination in comparison to the studied community and is calculated as the mean minimum distance from the five functionally most similar individuals in the community (Griffin et al. 2020, Violle et al. 2017). In contrast, *FSp* captures functional niche specialisation and measures each species' distance to the centroid of a multidimensional functional space. The original FUSE indicator combines *FUn* and *FSp* with the IUCN Red List categories as a measure of endangerment (Griffin et al. 2020, Pimiento et al. 2020, 2023). We generalised this approach to calculate the four different risk-weighted indicators mentioned above (*Table B-2*): (1) IUCN Red List status (FUSE), (2) taxonomic scarcity (FUSA), (3) sensitivity to fishing pressure ($FUSS_{FP}$), and (4) sensitivity to climate change (FUSSCC). All risk-weighted indicators were rescaled to values between 0 and 1 to facilitate comparability of the results. For each indicator, the highest-ranking species (i.e., most functionally original and rare, endangered, or sensitive species) were defined as those in the highest (10^{th}) decile of each indicator (hereafter referred to as "D10 group"; Griffin et al. 2020). Spatial patterns of functional originality and risk were addressed as: i) the average annual abundance (individuals · km^{-2}) of the species in the D10-groups to identify hotspots in the distribution of these highest scoring species; and ii) as community-weighted averages (i.e., average value obtained by multiplying the indicator value of each species caught by its relative abundance, across all species in the community).

3.3 Results

Functionally original species, i.e., the 10% species with highest *FUn* and *FSp* scores, as well as functionally original and at-risk species, were predominantly Chondrichthyes (cartilaginous fishes including sharks and rays). In total, the D10 groups of *FUn* and *FSp* included 20 and 14 species in the shelf and slope communities, respectively. Species emerging as both functionally unique and highly sensitive to fishing or climate change were common stingray (*Dasyatis pastinaca*), gulper shark (*Centrophorus granulosus*), angular roughshark (*Oxynotus centrina*) and kitefin shark (*Daliatias licha*) – all elasmobranchs.

There was significant variation among the four risk-weighted indicators (*Figure 3-1*). For example, some species ranked high in FUSE (endangerment) but not in $FUSS_{FP}$ (fishing sensitivity), in others the reverse was the case. Notably, several species scoring very high in multiple risk-weighted indicators were not part of the D10 groups of *FUn* and *FSp* (e.g., armless snake eel *Dalophis imberbis* and longnose skate *Dipturus oxyrinchus* in the shelf zone). Eight species were in the D10 groups of risk-weighted indicators in both the shelf and slope communities (conger eel *Conger conger*, thinlip conger *Gnathophis mystax*, european hake *Merluccius merluccius*, blue ling *Molva dypterygia*, Mediterranean starry ray *Raja asterias*, longnose skate *Dipturus oxyrinchus*, marbled electric ray *Torpedo marmorata*, john dory *Zeus faber*: *Figure 3-1*). Only a few species consistently ranked highly across multiple indicators (e.g. dentex *Dentex dentex* and deepwater cusk eel *Benthocometes robustus*: *Figure 3-1*).

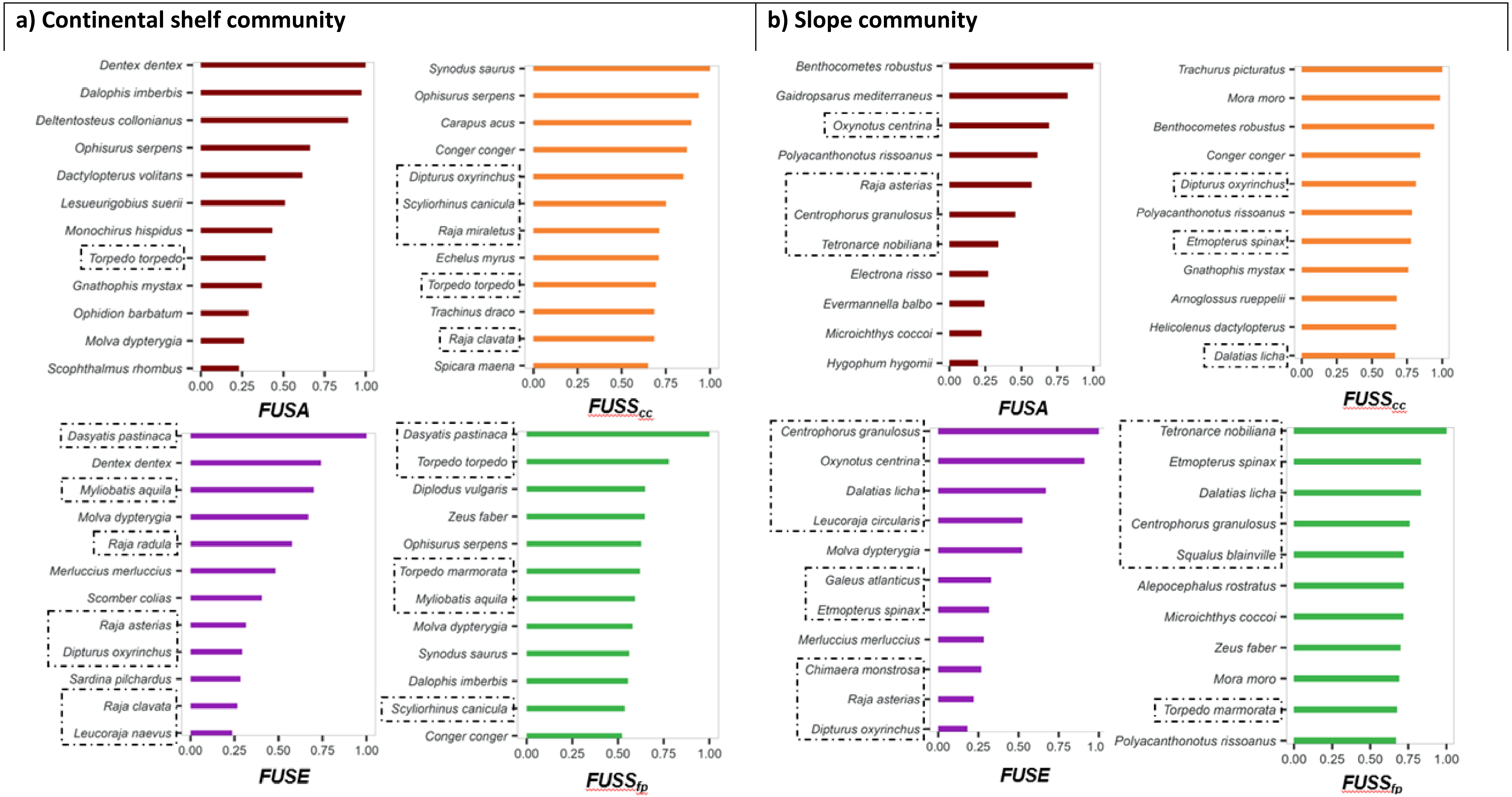

Figure 3-1. Species within the 10th decile (top-10%) in the four risk-weighted indicators of functional originality FUSE (purple), FUSA (red), $FUSS_{FP}$ (green) and $FUSS_{CC}$ (orange) for a) continental shelf and b) slope communities of the Western Mediterranean Sea. Elasmobranch species are framed.

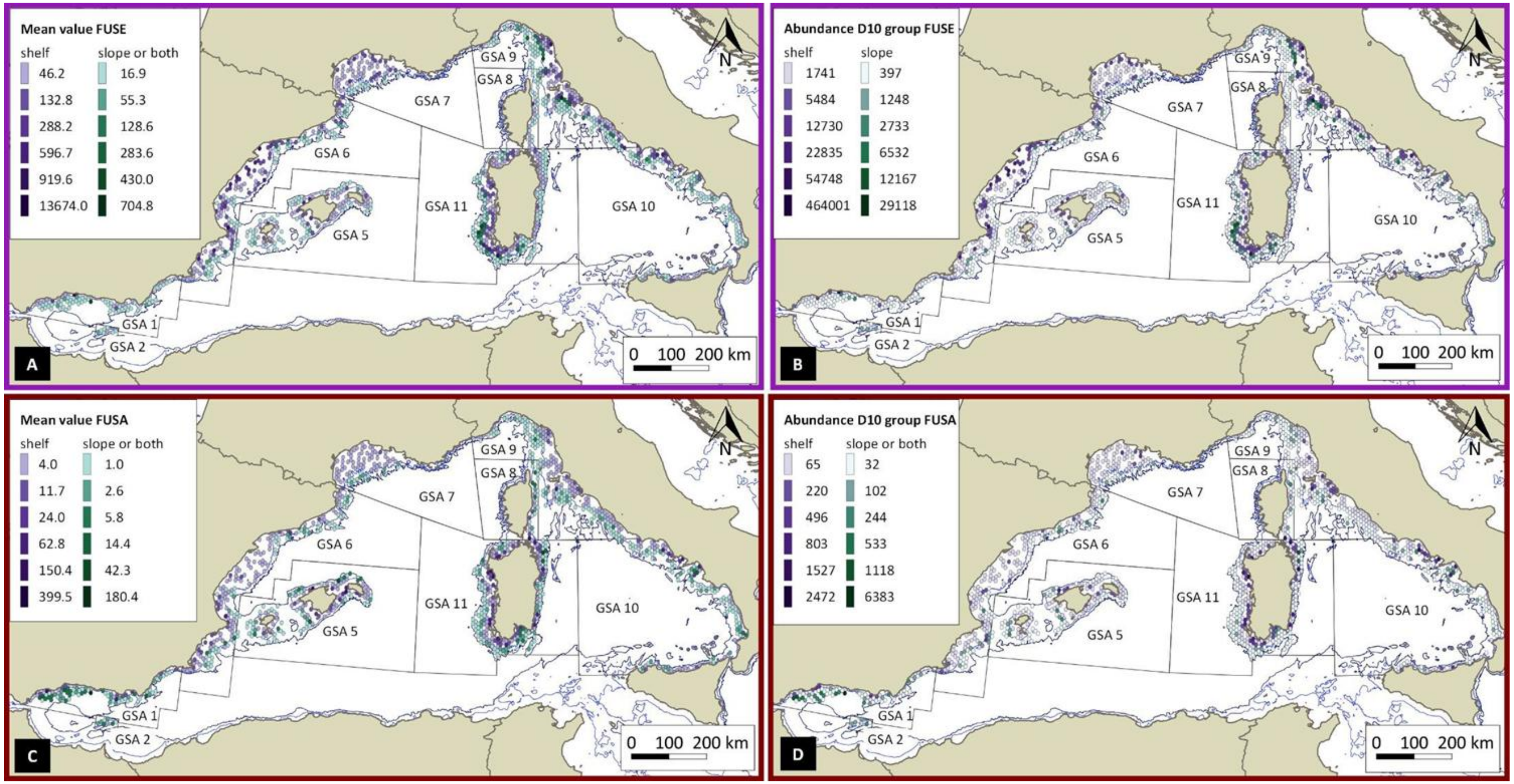

Figure 3-2. Spatial patterns in functional originality and endangerment FUSE (A, B) and functional originality and rarity FUSA (C, D). Visualised as community-weighted annual averages (A, C) and annual average abundance (individuals/km^2) of the 10% highest ranking species (D10 species) (B, D). Black lines denote geographical subareas (GSAs) as designated by the General Fisheries Commission of the Mediterranean (GFCM): GSA 1 (Northern Alboran Sea), GSA 2 (Alboran Island), GSA 5 (Balearic Islands), GSA 6 (Northern Spain), GSA 7 (Gulf of Lion), GSA 8 (Corsica Island), GSA 9 (Ligurian and North Tyrrhenian Sea), GSA 10 (South Tyrrhenian Sea), GSA 11 (Sardinia).

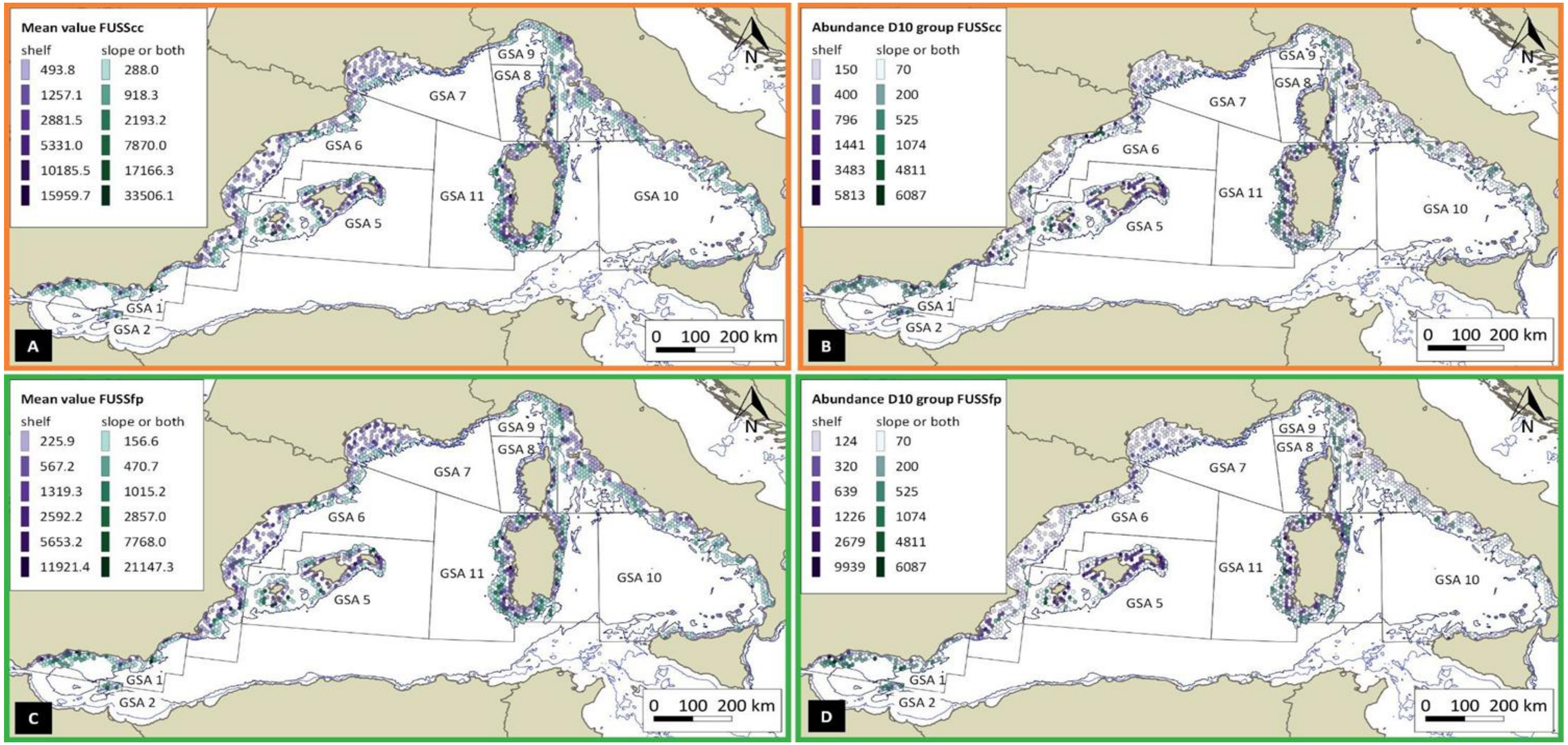

Figure 3-3. Spatial patterns in functional originality and sensitivity to climate change FUSS$_{CC}$ (A, B) and functional originality and sensitivity to fishing pressure FUSS$_{FP}$ (C, D). Visualized as i) community-weighted annual averages (A, C) and ii) annual average abundance (individuals/km^2) of the 10% highest ranking species (D10 species) (B, D). Black lines denote geographical subareas (GSAs) as designated by the General Fisheries Commission of the Mediterranean (GFCM): GSA 1 (Northern Alboran Sea), GSA 2 (Alboran Island), GSA 5 (Balearic Islands), GSA 6 (Northern Spain), GSA 7 (Gulf of Lion), GSA 8 (Corsica Island), GSA 9 (Ligurian and North Tyrrhenian Sea), GSA 10 (South Tyrrhenian Sea), GSA 11 (Sardinia).

Spatial patterns in functional originality varied greatly across the Western Mediterranean, with westernmost regions generally showing higher values. While functional originality indicators often revealed contrasting patterns between species-level and community-level metrics, risk-weighted indicators were more spatially coherent (*Figure 3-2* and *Figure 3-3*). In addition, the spatial patterns in risk-weighted indicators (*FUSE*, *FUSA*, $FUSS_{FP}$, $FUSS_{CC}$) were relatively consistent across community-weighted average vs. D10 abundances (*Figure 3-2* and *Figure 3-3*). Most high-ranking *FUSE* species were found on the shelf of Northern Spain (GSA 6), the shelves and slopes of the Ligurian and North-Tyrrhenian Sea (GSA 9), and in the south-western tip of Sardinia (GSA 11). *FUSA* was highest on the slope in the Western Alboran Sea (GSA 1) and showed local hotspots in the shelves of GSAs 5, 10 and 11. The community means and D10 group abundances of both $FUSS_{CC}$ and $FUSS_{FP}$ were higher in the West, an t in the shelf areas of the Balearic Islands (GSA 5) and on the slope of the Alboran Sea and off Sardinia (GSAs 1 and 11). Additional local hotspots became apparent, especially for *FUSSCC*, for instance in the East of Corsica (GSA 8).

3.4 Discussion and conclusions

This is the first study to assess functional originality in the Western Mediterranean fish community, but it also provides a proof-of-concept for a new, trait-based approach combining functional originality and sensitivity to two key pressures on marine ecosystems – climate change and fishing. This new approach might be a very useful tool for conservation prioritisation at taxonomic, functional and spatial levels. The functional originality of several rare, sensitive and/or endangered species in the Western Mediterranean Sea was highlighted. These include several elasmobranchs (e.g., gulper shark *Centrophorus granulosus*, angular roughskark *Oxynotus centrina*, kitefin shark *Daliatias licha*, common stingray *Dasyatis pastinaca*) and teleosts (e.g. deepsea cusk eel *Benthocometes robustus*, dentex *Dentex dentex*, armless snake eel *Dalophis imberbis*, and the endemic deepwater cardinalfish *Microichthys coccoi*). Many of these species were not only highly functionally original but also exhibited high sensitivity to climate change and fishing pressure, which emphasises their outmost conservation priority. Generally, *K*-strategist fish species (i.e. long-lived, late maturing, with low fecundity), particularly skates and sharks (Chondrichthyes) were most at risk as well as displayed higher functional originality (in line with Pimiento et al. 2020). However, taxonomic class alone was not a reliable predictor of functional value or conservation need. The most functionally original species concentrated in a few localised hotspots; by contrast, the community-weighted originality displayed a more even spatial distribution. This suggests that the most functionally original species tend to have relatively lower abundances or more restricted distribution than species with medium functional originality.

The findings also emphasise limitations when relying solely on IUCN Red List assessments (as used for the FUSE indicator), especially in regions where they can be outdated or missing. The trait-based sensitivity scores to fishing and climate change offer a more dynamic and context-specific alternative that could better inform adaptive management strategies. A substantial number of the 176 species evaluated here displayed a combination of functional originality and high risk according to multiple metrics (i.e., high sensitivity, endangerment, and/or rarity). Importantly, the results also show considerable a sensitivity of functional originality metrics (*FUn*, *FSp*) to the selection and completeness of trait data or spatial cross-scale effects (Flensborg et al. 2025, Sainz-Barain et al. 2025). Changes in trait selection and the spatial scale at which metrics are computed, may produce differences in species originality scores and ranks. Therefore, interpretation of these metrics should be taken with caution considering the context dependency. While this may affect individual rankings of particular species, the results underscore the ecological importance of functional originality and trait-based approaches for marine conservation and spatial planning to preserving ecosystem integrity and resilience.

The overview of different biodiversity and risk aspects (like functionality and sensitivity for particular pressures, etc.), may better help managers and policy makers facing a range of circumstances from large to local spatial scales (Griffin et al. 2020, Pavoine & Ricotta 2024). In addition, fishing pressure is a strong causal factor in the long-term decline of several Mediterranean species and fishing sensitivity is therefore closely related to the IUCN rankings (Engelhard et al. 2024). On the other hand, climate change sensitivity likely approaches changes in spatial distribution and even extinction risk in the Mediterranean Sea due to the local geography that inhibits northward migration to colder waters (Polo et al. 2024, Sanz-Martin et al. 2024). Some prominent candidate areas for spatial conservation priorities were detected as “hotspots”, where high values of the different indicators used reoccurred, most notably the Alboran Sea, the Balearic Islands, Sardinia, and Corsica. These areas likely gather functionally original and at-risk species due to their distinct environmental conditions, including proximity to the Atlantic (Alboran Sea) and lower bottom trawling intensity around the Mediterranean islands compared to the mainland shelves (Quetglas et al. 2012, Russo et al. 2019). In addition, previous results of this deliverable shown these areas are also hotspots of climate change and fishing pressure risk, stressing the urgency for biodiversity conservation.

4 Northeast Atlantic: Greater North Sea, Celtic Seas, Bay of Biscay and Iberian Coast

4.1 Introduction

Climate change and fishing are important pressures on marine life across Europe's Northeast Atlantic waters and adjacent seas, including the area covered in the present section: namely OSPAR Regions II (Greater North Sea), III (Celtic Seas) and IV (Bay of Biscay & Iberian Coast). Within this area characterised by a broad latitudinal temperature gradient, there are also important local differences in the degrees of climatic warming: with some areas regarded as warming 'hotspots' (e.g. southern North Sea: Holt et al. 2012), and others warming far less (e.g. Cantabrian Sea, northwest of Spain: Punzón et al. 2016). Likewise, fishing effort is also rather unevenly distributed; some areas are typically far more frequently being trawled, dredged, or otherwise fished than other areas (e.g. Rijnsdorp et al. 1998, Greenstreet et al. 2007, Lee et al. 2010). There has been a general reduction in fishing effort in the region but not in all areas. For example within the North Sea, the west and south have become less trawled and the north and east more so since the turn of the millennium (Engelhard et al. 2015). Here we ask, how do local and regional differences in the combined threats of climate change and fishing pressure result in spatial and temporal differences in the intensity of these pressures and in sensitivity of fish communities towards these pressures (together forming risks for fish communities)? Can we identify regions of high risks for climate change and fishing pressures?

Across the B-USEFUL project, trait-based approaches are used as a powerful framework for assessing species and community-level sensitivity and vulnerability to multiple pressures (see also the previous deliverable report: Engelhard et al. 2024). In the present section, we assess community-level sensitivity, local pressures and therefrom risks to climate change and fishing pressure in the above-mentioned three OSPAR regions, i.e. the Greater North Sea, Celtic Seas, and Bay of Biscay & Iberian Coast. Specifically, we test the following hypotheses:

(1) Areas with higher fishing pressure will be characterised by a fish community with lower sensitivity to fishing pressure (*fide* Polo et al. 2025), hereafter referred to as S_{FP}.

(2) Areas with a warmer climate will be characterised by a fish community with lower sensitivity to climate change (*fide* Polo et al. 2025), hereafter referred to as S_{CC}.

(3) Those areas where fishing pressure was low or reduced will see high levels or an overall increase in S_{FP}, whereas those areas where fishing pressure increased will see a decrease in S_{FP}.

(4) With ongoing climate change, there will be an overall reduction in S_{CC} in each of the three OSPAR regions; with regions with the greatest warming seeing the greatest decrease in S_{CC}.

To test the above hypotheses, we will (1) assess spatial patterns fishing pressure and S_{FP} and in (2) sea temperatures and S_{CC}; and then assess temporal trends in (3) S_{FP} and (4) S_{CC}.

4.2 Methods

4.2.1 Fishing pressure data

For OSPAR regions Greater North Sea, Celtic Seas, and Bay of Biscay & Iberian Coast, data on fishing pressure were collated based on the data product "OSPAR request on the production of spatial data layers of fishing intensity/pressure" (ICES 2018 and later updates). This includes annual fishing pressure by ICES C-square (0.05° latitude by 0.05° longitude), derived from VMS (Vessel Monitoring Systems) positions of fishing vessels, and quantified as swept area ratio (SAR) at both the seafloor-surface and seafloor-subsurface (in line with Eigaard et al. 2016); here, only surface SAR was included (assuming that subsurface SAR is primarily relevant to benthic organisms). Fishing pressure date were then aggregated from C-square resolution to the resolution of ICES rectangles (0.5° latitude by 1° longitude), in line with the community-level S_{FP} and S_{CC} data. Only the fishing gears likely to impact the seafloor and area just above the seafloor were included: i.e. all types of bottom trawlers, beam trawlers, dredgers, and seiners (excluding purse seiners). It should be noted that consistent, annually and spatially resolved international fishing pressure data for the study area (i.e. with vessel from all countries fishing a given rectangle included) were only available for the period 2009–2020. Within this period, data were incomplete for the southernmost part of the study area (Portuguese coast) for most years, and incomplete for the northwestern Spanish coast for the most recent years. Thus, these data were removed prior to analysis and were not plotted on maps of fishing pressure so as not to misrepresent total fishing pressure along the Iberian coast and northern Spanish coast.

4.2.2 Climate data

Environmental variables were extracted from the model re-analysis products of the NEMO-MEDUSA model (Yool et al. 2013). Annual surface and bottom temperature (°C) were extracted using a nearest neighbour approach for each 0.25° latitude and longitude grid cell over the Northeast Atlantic study area (spatial extent 20°W–15°E, 35°N–70°N, excluding the Mediterranean) over the period 1997-2099 to align with the ecosystem data available. The environmental data were extracted using the nearest neighbour approach to avoid issues with data mismatches across a wide range of latitudes, whereby the limited detail regarding the spatial projections used may represent cells of different total area size when compared to the species distribution data. This method also increases local reliability of climate data per grid cell. For consistency, the WGS84 projection was used for all subsequent data analysis and mapping at an ICES rectangle scale (0.5° latitude by 1° longitude).

4.2.3 Species-level sensitivities

Species abundance data were obtained from WP2 through the FISHGLOB database (Maureaud et al. 2024), a collaborative initiative that compiles standardised fish survey data from scientific bottom trawl surveys across the North Atlantic (and Northeast Pacific). The dataset was cropped to match the spatial extent of our study area. The final dataset included 285 fish species.

Species-level sensitivity to fishing pressure (S_{FP}) scores were calculated using a suite of life-history and ecological traits, as described in B-USEFUL D4.1 report (Engelhard et al. 2024; see also Polo et al. 2025): Parental care, habitat, maximum age, maximum body size, fecundity, offspring size, growth coefficient, trophic level, age at maturity, body shape, feeding mode. Categorical variables were scored between 0 and 1, and continuous variables were rescaled between 0 and 1. Trait scores were summed for each species and rescaled between 0 and 1 to produce a standardised S_{FP} score. Climate change sensitivity (S_{CC}) scores were derived from traits related to thermal tolerance and habitat. These included parental care, habitat type, sea surface temperature (SST) range, sea bottom temperature (SBT) range. Depending on habitat classification, we used either SST or SBT thermal affinity (TP 90), where SST affinity was used in the case of pelagic species, and SBT affinity in the case of demersal or benthic species. As with S_{FP}, trait scores were summed and rescaled to produce standardised S_{CC} scores per species (see Engelhard et al. [2024] for full details of all trait scores by species).

4.2.4 Trends in community-level sensitivities

Community-level sensitivity scores were calculated following the approach of Polo *et al.* (2024). Species-level sensitivity scores were aggregated across hauls within each ICES rectangle in a given year and weighted by the ^{10}log-transformed abundance of each species. Individual species abundances were logged to reduce the influence of dominant, overly abundant taxa and give more weight to rarer species. To assess long-term trends in community-level S_{FP} and S_{CC}, across the study area, three approaches were applied. Firstly, spatiotemporal trends in S_{FP} and S_{CC} across ICES grid cells were assessed using Sen's slope, a non-parametric estimator of trend direction and magnitude over time (Sen 1968, Siegel 1982). This method is particularly robust to outliers and data errors, compared to linear regression (Gocic & Trajkovic 2013). Secondly, generalised additive mixed models (GAMMs) were fitted separately for each of the three OSPAR regions (Greater North Sea, Celtic Seas, and Bay of Biscay & Iberian Coast), with ICES rectangle as a random effect, to capture potential non-linear trends in community-level S_{FP} and S_{CC} at the broader scale. Thirdly, to quantify the overall direction and strength of these trends, linear mixed effects models (LMMs) were fitted per region, with year as main effect and ICES rectangle as a random effect.

4.2.5 Fishing pressure and climate change risk

Weighted community-level sensitivity scores were combined with each exposure (of climate change and fishing pressure) for every ICES grid cell. Fishing effort data (surface SAR) and SST were scaled between 0 and 1 prior to calculating risk. Because fishing effort data were skewed, surface SAR values were ^{10}log-transformed prior to scaling. Fishing pressure risk was then calculated as the mean of the weighted community-level sensitivity score (S_{FP}) and surface SAR for each ICES grid cell per year (following approaches such as those in Payne et al. (2021) and see Cardona et al. (2012) for more information on the overall framework). Similarly, climate change risk was calculated as the mean of the weighted community-level sensitivity score (S_{CC}) and SST for each ICES grid cell per year. Spatiotemporal trends in fishing pressure ($_{FP}$) risk and climate change (CC) risk were assessed using Sen's slope.

4.3 Results

4.3.1 Spatial variation of community-level sensitivity to fishing pressure

Spatial patterns of fishing pressure varied across the Northeast Atlantic over the three time periods (*Figure 4-1*, top row), with a general reduction in pressure observed across several areas, particularly in parts of the Celtic Seas and Bay of Biscay & Iberian Coast (*Figure 4-1*, top right map). Unfortunately, fishing pressure data for the earliest period (prior to 2009) were not available to directly match the community-level S_{FP}. Despite this, the maps of change in S_{FP} (*Figure 4-1*, bottom right map) indicate an increase in sensitivity to fishing in the Celtic Seas and areas of the Bay of Biscay. The map results are consistent with the expectation that reduced fishing pressure in these regions would result in increased sensitivity. The changes in S_{FP} across the Greater North Sea were more varied, with areas of increased sensitivity to fishing in the southwest and declines in S_{FP} in the Northeast.

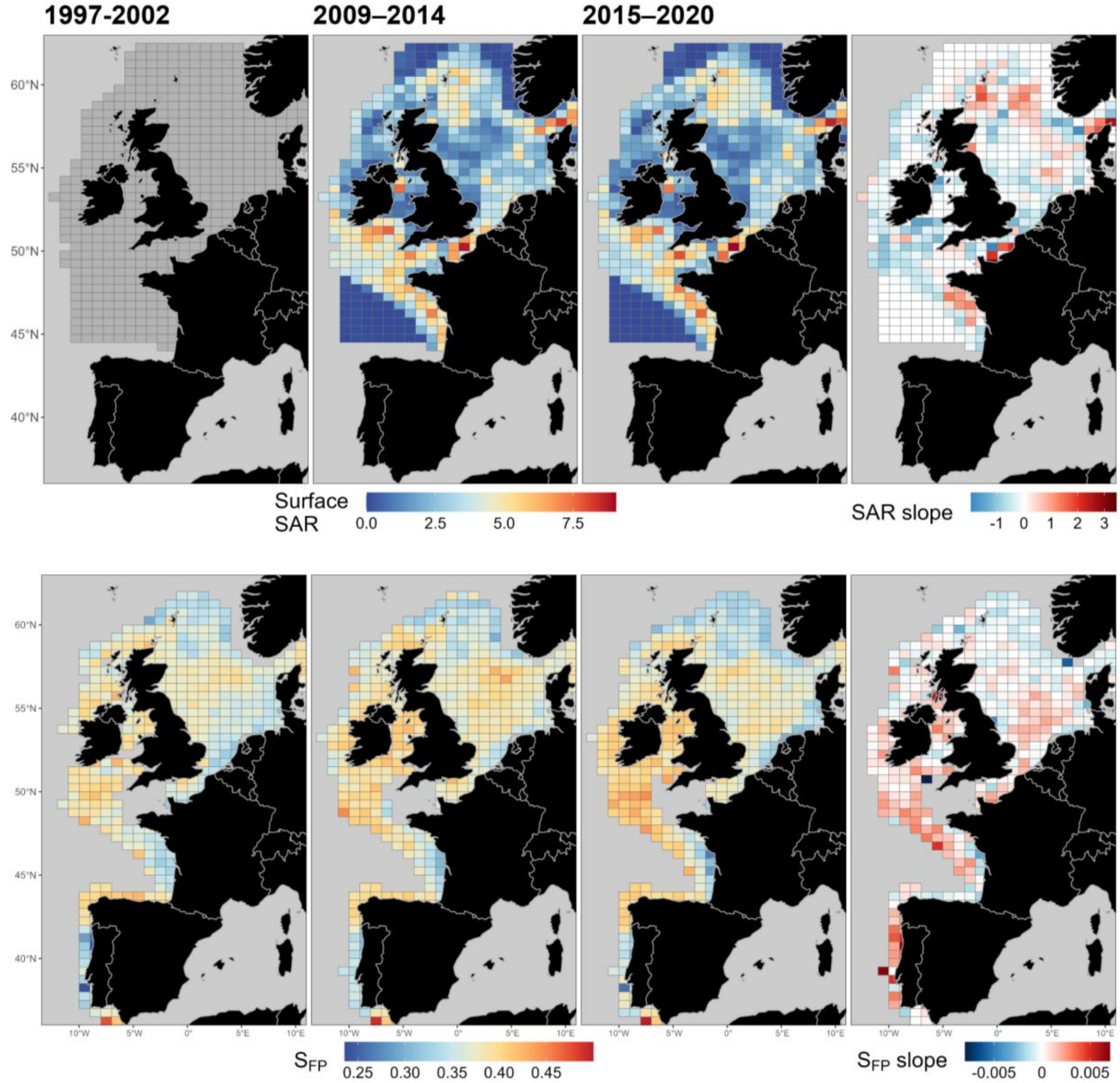

Figure 4-1 Spatial patterns of fishing pressure (surface swept area ratio, SAR; top) and community-level sensitivity to fishing pressure (S_{FP}, bottom) in three periods: 1997-2002, 2009-2014 and 2015-2020. The top row displays surface SAR with values square-root transformed to aid visual interpretation. The rightmost panel in each row illustrates the Sen's slope, representing the direction and magnitude of change (the trend) from 2009 to 2020 for fishing pressure and 1997 to 2020 for S_{FP}. Note that fishing pressure data were not available for the period 1997-2002 to directly match with S_{FP}.

4.3.2 Spatial variation of community-level sensitivity to climate change

There was a clear spatial gradient in community-level sensitivity to climate change (S_{CC}) across the Northeast Atlantic (*Figure 4-2*, left panels). There are more communities that are sensitive to warming in the northern regions, particularly the Greater North Sea and Celtic Seas, while communities in the Bay of Biscay & Iberian Coast have a higher relative abundance of traits less sensitive to warming. In areas experiencing increasing warming, S_{CC} declined over time, consistent with expectations that communities are shifting towards traits associated with lower sensitivity to climate change (*Figure 4-2*, right panel).

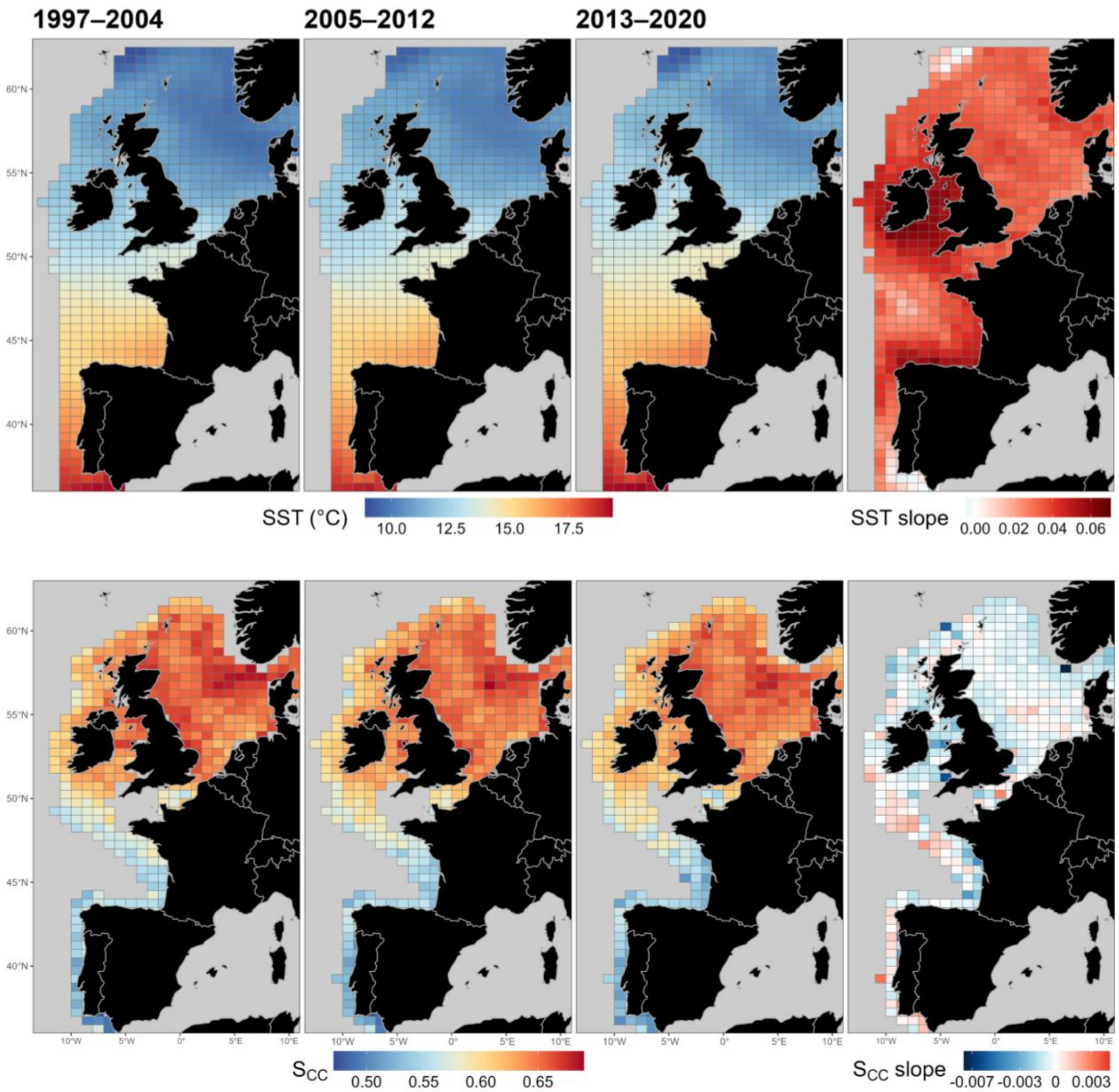

Figure 4-2 Community sensitivity to climate change (S_{CC}) in the periods 1997-2004, 2005-2012 and 2013-2020 (left panel) and spatial variation in the rate of change in S_{CC} (Sen's slope) during 1997-2020 (right panel). A negative trend in S_{CC} (blue) represents a decline in the relative abundance of traits sensitive to climate change (a decrease in sensitive species), while a positive trend (red) indicates the community is becoming more sensitive to climate change (an increase in sensitive species).

4.3.3 Long-term changes in S_{FP}

Community S_{FP} increased over the period 1997-2020 in the Celtic Seas and the Bay of Biscay & Iberian Coast; by contrast over this period no significant change was observed in the Greater North Sea (*Table 4-1*; *Figure 4-3*; *Figure C-2* in Appendix C). The largest increase was observed in the Bay of Biscay & Iberian Coast (annual S_{FP} change = 0.000613 ± 0.000119 year^{-1}), followed closely by the Celtic Seas (annual S_{FP} change = 0.000605 ± 0.000064 year^{-1}).

4.3.4 Long-term changes in S_{CC}

Community-level S_{CC} declined across all OSPAR regions. This decline was greatest in the Celtic Seas (annual S_{CC} change = –0.000525 ± 0.000044 year^{-1}), followed by the Greater North Sea and the Bay of Biscay & Iberian Coast (*Table 4-1*; *Figure 4-3*; *Figure C-2* in Appendix C).

Table 4-1 Annual change in community-level S_{FP} and S_{CC} by region. Results from Linear Mixed-Effects Models (LMMs) with location (ICES rectangle) as random effect.

Variable	Region	Effect Size	Standard Error	*F*	df	*p*-value
S_{FP}	Greater North Sea	0.000058	0.000038	2.33	1, 4516	0.13
	Celtic Seas	0.000605	0.000064	90.33	1, 2229	< 0.001
	Bay of Biscay & Iberian Coast	0.000613	0.000119	26.53	1, 1254	< 0.001
S_{CC}	Greater North Sea	-0.000467	0.000033	203.52	1, 4515	< 0.001
	Celtic Seas	-0.000525	0.000044	139.05	1, 2210	< 0.001
	Bay of Biscay & Iberian Coast	-0.000395	0.000088	20.34	1, 1256	< 0.001

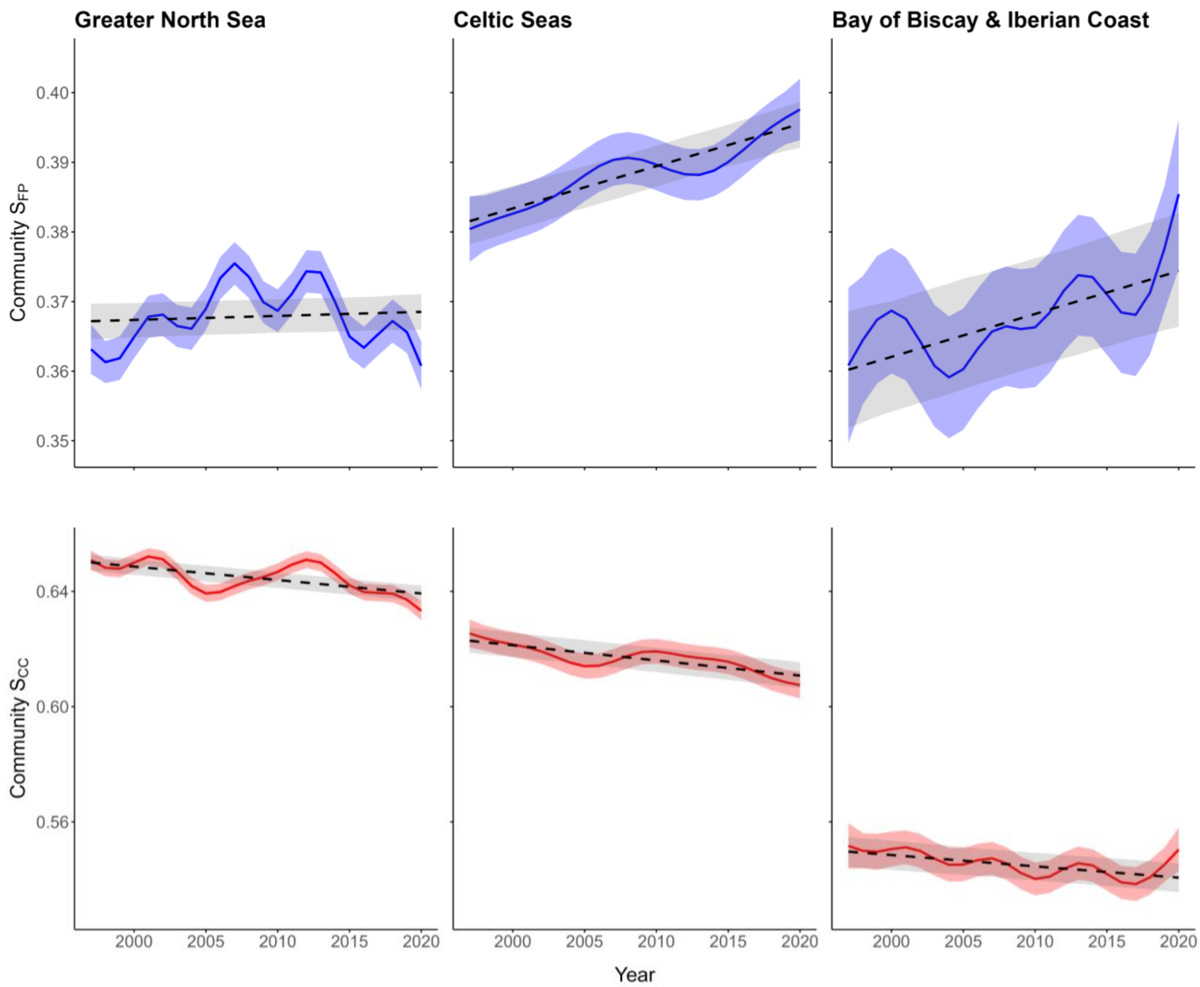

Figure 4-3 Long-term changes in community-level sensitivity to fishing pressure, S_{FP} (top), and to climate change, S_{CC} (bottom), for the Greater North Sea, Celtic Seas, and Bay of Biscay & Iberian Coast. GAMM trends shown as solid blue lines for S_{FP}, as solid red lines for S_{CC} (with 95% CIs lighter shaded). LMM trends for each shown as black dashed lines (with 95% CIs grey shaded).

4.3.5 Risk

FP risk and CC risk values varied in space and time across the Northeast Atlantic. FP risk ranged between 0.13 and 0.68. Higher FP risk was found in southern Celtic Seas, Bay of Biscay and northern French coast (redder colours in left panels in *Figure 4-4*). In contrast, lower FP risk values were found along the east coast of the UK and in central parts of the Celtic Seas. These are areas with both higher community S_{FP} and higher fishing pressures (*Figure 4-1*). Trends in FP risk over time are relatively small in magnitude per year (right panel in *Figure 4-4*), with increases in FP risk most evident in northern and northeastern areas of the Greater North Sea (red colours). Decreases in FP risk are observed in areas along the eastern coast of the UK and across much of the Celtic Seas.

Patterns in CC risk differed considerably from those observed for FP risk. CC risk ranged between 0.38 and 0.75 and followed a consistent south-to-northeast gradient of decline across all time periods (left panel, bottom row in *Figure 4-4*). These patterns mirror the distinct north-south temperature gradient (*Figure 4-2*) and the corresponding gradient in community-level S_{CC}. CC risk is increasing across most of the Northeast Atlantic (red in far-right panel in *Figure 4-4*), with the largest increases occurring in areas that have experienced the greatest warming (*Figure 4-2*).

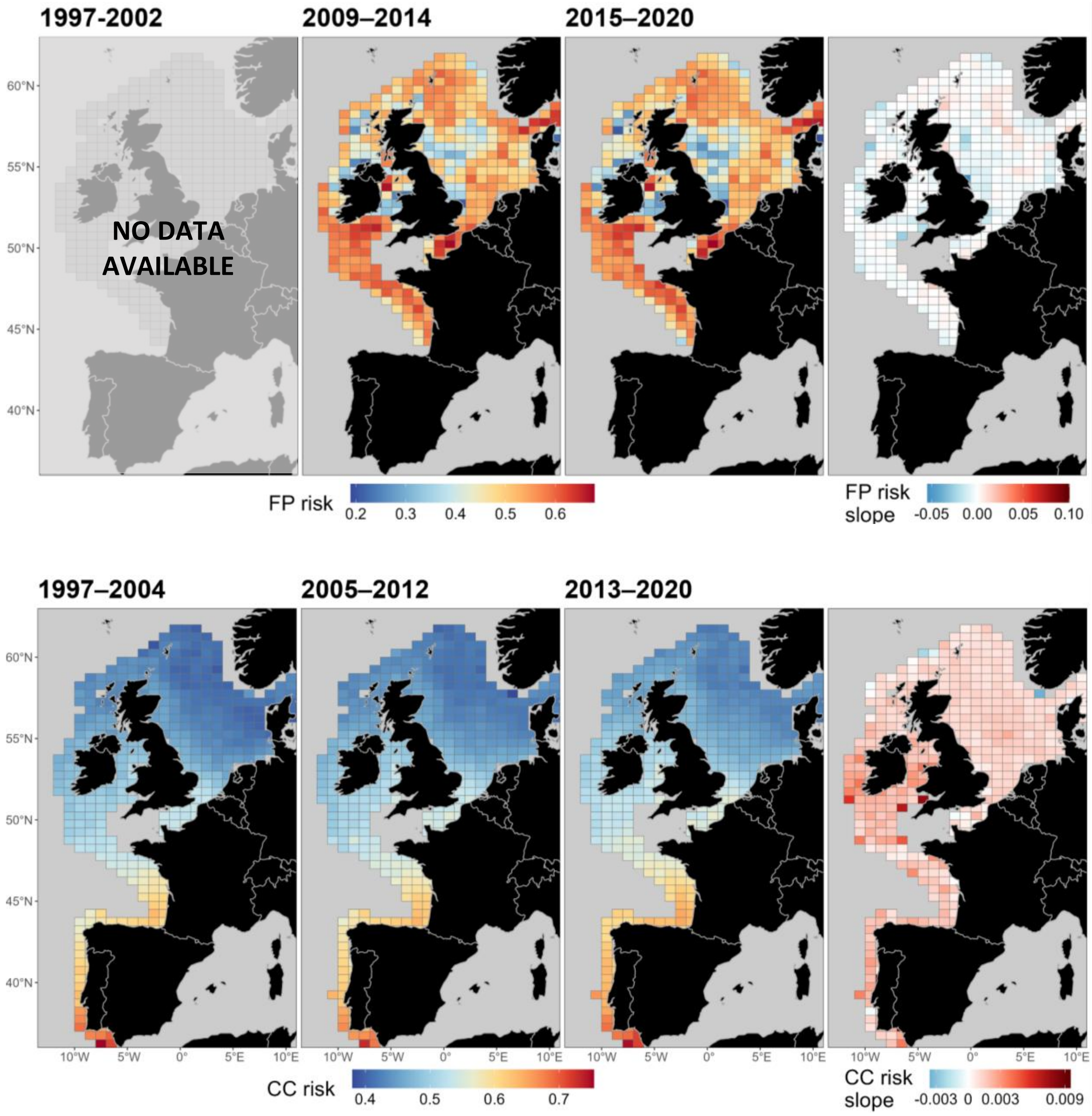

Figure 4-4. Historical fishing pressure (FP) and climate change (CC) risk and the change over time in the Northeast Atlantic. FP and CC risk shown in the periods 2009-2014 and 2015-2020, and the periods 1997-2004, 2005-2012 and 2013-2020 (left panel) for FP risk and CC risk, respectively. The fourth panel shows the spatial variation in the rate of change (Sen's slope) in each risk during 1997-2020 for CC risk and 2009-2020 for FP risk.

4.4 Discussion and conclusions

Using long term data on fish surveys and fishing pressure, this study provides new evidence for long term spatial and temporal patterns in community-level sensitivity to fishing pressure and climate change, and their associated risk, across the Northeast Atlantic. Notably, while fishing pressure has generally declined in many parts of the study region, community-level S_{FP} has generally increased, though this pattern is less pronounced in the North Sea (*Table 4-1*). At the same time, S_{CC} has declined across all OSPAR regions, corroborating the expectations with climate change. Despite the decline in SCC, the climate change risk remains high and has increased across the Northeast Atlantic. These findings suggest that while management efforts may be reducing direct anthropogenic pressures from fishing (Villasante 2010, Cardinale et al. 2013), ecological communities are undergoing complex compositional shifts that may increase their vulnerability to certain other stressors like climate change, nutrient load and pollution.

The observed increase in community-level S_{FP} in the Celtic Seas and Bay of Biscay & Iberian Coast supports expectations that reduced fishing pressure allows for the recovery of species with traits that are more sensitive to exploitation (Johnson et al. 2015; Tinlin-Mackenzie et al. 2023). Disturbances from fishing activities, especially bottom-trawling, can alter the seabed and often lead to declines in benthic habitats and larger-bodied, more sessile organisms, favouring short-lived, opportunistic species that are less vulnerable to fishing-related mortality (Frid & Hall 1999, Rumohr & Kujawski 2000, Polo et al. 2025). Some regions however where S_{FP} is decreasing, are potentially losing fish species most sensitive to fishing, such as elasmobranchs, which suggests possible changes to food web structure and trophic interactions as megafauna decline (Jennings & Kaiser 1998, Dulvy et al. 2004). Elsewhere, the increasing vulnerability of fish communities after reduction of fishing pressures emphasises the importance of not equating reduced fishing effort with reduced ecological risk. The lack of significant change in the Greater North Sea is more surprising considering the decline in fishing effort in recent decades (ICES 2024) and may reflect either a slower trajectory of recovery or variations in localised pressures over time (apparent increase then declining trend since 2010). The spatial analyses show more complex changes in the Greater North Sea where we see a Northwest-Southeast gradient in S_{FP} change. This is in line with expectations from regional fishing effort trends, where (north-)eastern areas have seen increases in trawling pressure, and (south-) western areas decreases, between the 1990s and 2020s (Engelhard et al. 2015, Couce et al. 2020). This mismatch may point to underlying lags in community responses, differences in habitat suitability or the influence of other environmental drivers that modulate community responses to fishing (Doney et al. 2012). This is further reflected in the FP risk results (combination of sensitivity and exposure), which show that fishing-related risk remains spatially heterogeneous and closely tied to local effort levels and decreasing community sensitivities. Overall, the risk to fishing does not change considerably over the period, reflecting areas where communities have responded by shifting to those dominated by species less sensitive to fishing and hence decreasing in risk.

The broad-scale latitudinal gradient in S_{CC}, with higher sensitivity in northern, cooler regions and lower sensitivity in the south, supports expectations that warmer regions are dominated by species with traits less sensitive to warming. The observed decrease in S_{CC} over time across all regions, most pronounced in the Celtic Seas where warming is greatest, is consistent with predictions that communities are adapting to warming by shifting towards higher relative abundances of species with broader thermal tolerances or warmer affinities (Engelhard et al. 2011, Polo et al. 2025). These patterns could be driven by poleward distribution shifts and/or higher productivity of warmer-water species (Perry et al. 2005, Poloczanska et al. 2013, 2016), or by declines in abundance or poleward retractions of cooler-water species (McLean et al. 2021). The observed increase in climate sensitivity and risk further south along the Iberian coast and Bay of Biscay may be driven by the northward expansion of southern, more tropical, species that have shallower thermal gradients and that reside closer to their upper thermal tolerance limits across their range (Trisos et al. 2020). Despite the shift to communities that are less sensitive climate change in areas like the Celtic Seas, these communities are becoming the most at risk from ocean warming because these areas are exposed to the greatest increases in temperature. This suggests that, unlike fishing, which produces more localised ecological risk, climate change is emerging as a widespread escalating driver of vulnerability across the Northeast Atlantic where communities are unlikely to be able to keep pace with the rapid rate of change (Pigot et al. 2023).

Our spatial analyses further show a combined impact of both fishing and climate change pressures, south of Ireland and northwest of France, where we see an increase in community sensitivity to both fishing and climate change. The combination of the sensitivity and exposure showed these areas are increasing in climate change risk more so than fishing pressure risk. This is probably the result of the declining fishing effort in these regions but a greater exposure to increasing temperatures. This dual trend in sensitivity makes this a high-risk area where communities are simultaneously becoming more susceptible to climate stressors and fishing impacts. These results suggest that climate-driven community reassembly is underway, with potential implications for ecosystem functioning and resilience (McLean et al. 2018, Souza et al. 2023).

One limitation was that, unfortunately, this study was lacking longer-term fishing pressure data (prior to 2009) to match to the climate data and community sensitivity information (the latter available from 1997 onwards). Longer-term information on fishing pressure across the study region is needed to support the results presented here and fully contextualise long-term trends. For the North Sea, some longer-term international fishing pressure data sets are available (Greenstreet et al. 2007, Couce et al. 2020, ICES 2022) but this is not the case for the other OSPAR regions assessed here. Additionally, the underrepresentation of fishing effort in the Iberian Coast introduces uncertainty into the regional analyses. Overly conservative approaches by some data managers, particularly in relation to privacy concerns, may restrict fishing effort data accessibility and thereby hinder scientific progress. Despite working over a limited timeframe, especially in terms of detecting climate signals, these findings still highlight shifts in species communities over time in response to multiple stressors.

It is important to note that the observed changes in both S_{FP} and S_{CC} over time are characterised by very small effect sizes (albeit in line with Polo et al. 2025). While statistically significant, these magnitudes suggest that the shifts in community-level sensitivity are subtle and gradual. Such small changes may reflect the limited timeframe at which we conducted our analyses and the inherent inertia in ecological systems, where communities respond slowly to environmental pressures. They may also reflect that on a per-species level S_{FP} and S_{CC} can only vary between 0 and 1, so that variations once aggregated across all species to the community will necessarily be slower (especially in species-rich communities). The GAMM results further illustrate the noise and nonlinear trends within the dataset. This degree of nonlinearity and variation is expected in ecological communities and, together with the relatively short time span of this study, likely contributes most to the magnitudes of the trends. Despite using an abundance-weighted measure for community sensitivity, the patterns we have observed may mask important changes for less abundant, and potentially more vulnerable species. Future work would benefit from focusing these analyses on rarer species or those that are on the OSPAR List of Threatened and/or Declining Species. Nonetheless, even modest shifts in community-level sensitivity can be ecologically meaningful over longer timescales, particularly when compounded by ongoing stressors such as climate change and fishing.

The combined spatial and temporal analyses presented here provide a nuanced insight into how fishing and climate change pressures are reshaping fish communities in the Northeast Atlantic. This study reveals that marine communities are undergoing significant and regionally variable changes in response to these pressures. The contrasting trends in S_{FP} and S_{CC} across regions highlight the dual nature of anthropogenic impacts and highlight the importance of adaptive, region-specific management strategies. While management efforts may be alleviating pressures from fishing, climate change continues to drive directional shifts in community structure. It is worth noting that many warm-water species that are currently increasing in prevalence are also characterised by on average smaller body sizes and faster growth rates than many long-lived cold-water species (Engelhard et al. 2011, Genner et al. 2004, 2010, Martins et al. 2023), so there is an interaction between climate change and fishing. Although the observed changes in community-level S_{FP} and S_{CC} are small in magnitude, their consistency and directionality suggest the early stages of community restructuring – subtle yet persistent shifts that could, over time, reshape the composition, resilience and functioning of Northeast Atlantic ecosystems.

5 Icelandic waters

5.1 Introduction

Iceland is an island nation located in the North Atlantic, and as such it receives the influence from two distinct water masses: the Atlantic and the Arctic/Polar waters (Malmberg & Valdimarsson 2003, Jonsson & Valdimarsson 2005a, Stefánsson 1962). Warm and saline waters are transported on the Icelandic coastal shelf by the Irminger current, which splits from the Gulf Stream and flows westward after encountering the Iceland-Faroe Ridge. The current then continues flowing clockwise around the island, losing strength as it reaches its northern coasts (*Figure 5-1*) (Valdimarsson and Malmberg, 1999). Thus, the hydrographic conditions on the northern portion of the coastal shelf are defined by the mixture of Polar (East Greenlandic current), Arctic (East Icelandic current) and Atlantic waters (*Figure 5-1*), resulting in lower temperature and salinity than in the southwest (Stefansson 1962, Astthorson et al. 2007). This has been linked to the presence of two separate species assemblages: one located predominantly to the south and west of the island and characterized by a greater fraction of Atlantic species, and with a larger fraction of Arctic species in the north and east (Astthorsson et al. 2007, Mecklenburg et al. 2011, Símonarson et al. 2021, Stefansdóttir et al. 2010). However, the transport of the Irminger current along northern Iceland is variable, with stronger years being associated with warmer local seawater temperatures (Malmberg & Valdimarsson, 2003; Jónsson & Valdimarsson, 2005b). Changes in the composition of marine faunal assemblages in response to this variability has been reported in the past (Valdimarsson et al. 2012, Stefansdóttir et al. 2010, Vilhjálmsson 1997), and it is expected to shift towards more southern species during periods of warming (Björnsson & Pálsson 2004; Astthorsson et al. 2007, Sólmundsson et al. 2010).

Being located in this transition zone, marine fish communities around Iceland are likely to undergo changes in species composition due to climate change, and evidence of such changes in co-occurrence with increasing temperatures has already been reported (Campana et al. 2020, Sólmundsson et al. 2010, Stefansdóttir et al. 2010, Valdimarsson et al. 2012). On top of this, high levels of fishing pressure might exacerbate the effects of climate change on local assemblages. In particular, Iceland is one of the most important fishing countries in the world, ranking among the top 20 nations by landings in 2020 (FAO 2018). However so far, mainly stock assessments and only a few other studies have evaluated the impact of fishing in Icelandic waters (Campana et al. 2025, Jaworski et al. 2006, MFRI 2024); to our knowledge, no study exists on the impact of fishing on communities as a whole, and neither in combination with climate change.

The goal of the present study is to use trait-based indices of sensitivity to climate change and fishing – specifically bottom trawling, which is the predominant means of fishing in the area (MFRI, 2024) to investigate whether these two pressures may have caused changes in species composition of bottom-dwelling fish in Icelandic waters. The study focuses on bottom-dwelling fish owing to their generally higher sensitivity to these two stressors, and more limited mobility compared to pelagic fish species (de Juan et al. 2020, Bueno-Pardo et al. 2021, Butt et al. 2022). The specific research questions are:

1. Can recent changes in seawater temperature be related to corresponding changes in community composition, as assessed by species or trait composition?

2. Have sensitivity indicators to climate change and fishing varied in accordance with trends in the intensity of each pressure? Are the two indicators effective in diagnosing changes in community composition owing to anthropogenic impact?
3. Could changes in the intensity of one pressure affect indicator values for the sensitivity to the other pressure, due to possible interactive effects between fishing pressure and climate change?

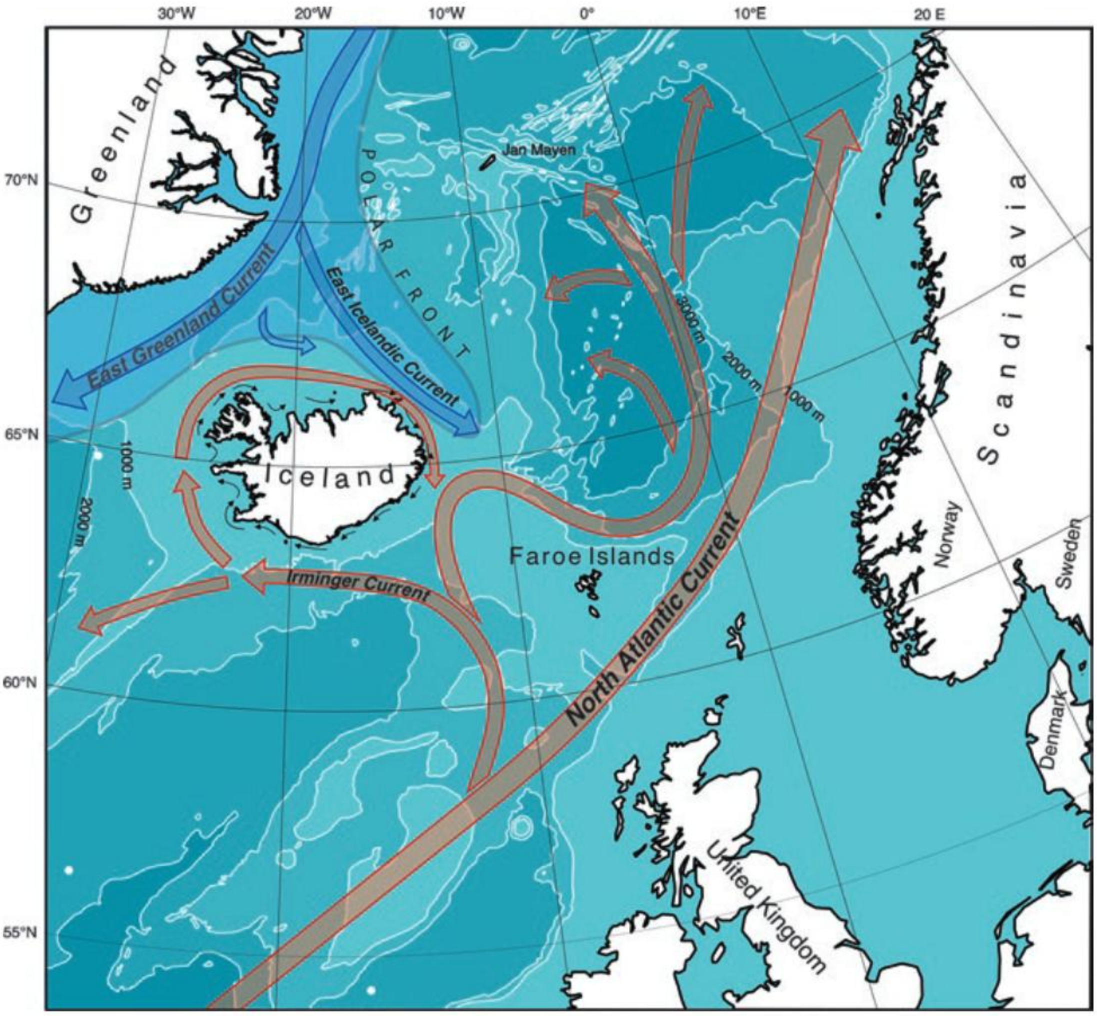

Figure 5-1. The direction of the Atlantic (red) and Arctic/Polar (light and dark blue) water masses around Iceland. From Símonarson et al. 2021.

5.2 Methods

5.2.1 Data collection and calculation of S_{CC} and S_{FP} scores

We collected bottom-trawl survey data including 26,657 samples collected in Icelandic waters during the period 1996–2024, and representing 97 demersal, bathydemersal and benthopelagic marine fish species. All estimated species densities (individuals/km^2) have been log-transformed for the analysis, to reduce potential bias caused by sporadic records of high abundances. Measurements of SST and SBT were obtained from re-analysis data products (Copernicus Marine Service 2025), whereas estimates of fishing intensity from bottom trawling were obtained from fishery log-book data (Fiskistofa 2025). We tested for significant temporal trends in these environmental variables using linear regression.

In order to characterise the species according to their sensitivity to climate change (S_{CC}) and fishing pressure (S_{FP}), 18 traits were selected *a priori* (following Engelhard et al. 2024, Polo et al. 2025). The scores used for this are summarised in *Table D-1* and *Table D-2* of Appendix D. Species' S_{CC} and S_{FP} values were then re-scaled to range between 0 and 1.

To explore temporal trends in species composition depending on climate change, species were grouped into three biogeographical groups referred to here as Arctic, Boreal and Atlantic. Overall trends in proportion of density for each of these groups were modelled with beta regression, after it was confirmed that the data did not include any extreme values (0s and 1s). Further details on the above-described procedures can be found in Appendix D.

After estimating the sensitivity of each species to each of the two pressures, the community-weighted average S_{CC} and S_{FP} per site was calculated by multiplying the sensitivity scores of each species by their density at the site, summing these together, and dividing by the sum of the individual densities of every species found at the site (Polo et al. 2025).

5.2.2 Evaluation of S_{CC} and S_{FP} trends

After the calculation of S_{CC} and S_{FP} values per site, temporal and spatial trends in these indicators were investigated for matching trends in SST, SBT and fishing intensity. Temporal trends were calculated for two regions, the northeast and the southwest of Iceland, using the geographical division based on hydrographical characteristics found in Stefansdóttir et al. (2010).

To aid the interpretation of S_{CC} and S_{FP} trends, and to further explore the relationship between community composition, climate change and fishing intensity, species were grouped in four 'sensitivity groups': species with high sensitivity to both climate change and fishing pressure (S_{CC} and S_{FP} >0.5), species with high sensitivity to climate change but low sensitivity to fishing pressure (S_{CC} >0.5 and S_{FP} <0.5), species with high sensitivity to fishing but low sensitivity to climate change (S_{CC} <0.5 and S_{FP} >0.5), and species with no low sensitivity to both climate change and fishing pressure (S_{CC} and S_{FP} <0.5). Temporal trends of mean and proportional density for each of the sensitivity groups were plotted. To model the overall trends in S_{CC}, S_{FP} and in proportion of density of each one of the biogeographic and sensitivity groups, beta regression was used, after it was confirmed that the data did not include any extreme values (0s and 1s).

Finally, to evaluate the spatial overlap between areas where S_{CC} increased and areas where fishing has been stable or increased, the average change/year in S_{CC} and fishing intensity has been calculated for each one of the 25km hexagonal cells of the grid covering the entirety of the study area.

5.3 Results

The exposure to both pressures – climate change and fishing intensity – has been changing in Icelandic waters throughout the 1996–2024 study period. Overall, temperature increased throughout the water column in both regions (*Figure D-1* of Appendix D), although the northeast warmed at a faster rate than the southwest (*Table **D**-**4***). Temperature showed a relatively steep increase from 1996 until about 2005, and a period of slower increase or even decrease after this time (*Figure D-1*D). On the contrary, fishing effort by bottom trawling has generally decreased during 1996–2024, both in the northeast and in the southwest, where the decrease was faster (*Figure D-2* of Appendix D). Despite an overall decrease in effort, two subperiods of moderate increases in fishing pressure can be recognized, i.e. during 1996-2005 and 2017-2022 (*Figure D-2*).

From the calculation of the species' S_{CC} and S_{FP} scores it is observable that species belonging to the three biogeographical groups were mixed across the 'climate and fishing pressure sensitivity space' (*Figure D-3*). Nevertheless, general patterns in the sensitivity of each of the biogeographical groups can be identified: Arctic species tended to have higher S_{CC} scores (mean 0.595) than Boreal species (mean 0.473) and, in turn, Boreal species tended to have higher S_{CC} scores than Atlantic species (mean 0.402). The average S_{FP} of the Arctic and Boreal groups was similar (means 0.559 and 0.557, respectively), while mean S_{FP} for the Atlantic group was lower (mean 0.443) (*Figure D-3*). Across all 97 species, S_{CC} and S_{FP} were negatively correlated (Pearson's r = -0.24, df = 94, p = 0.017), indicating that species which have high sensitivity to one pressure were likely to have low sensitivity to the other.

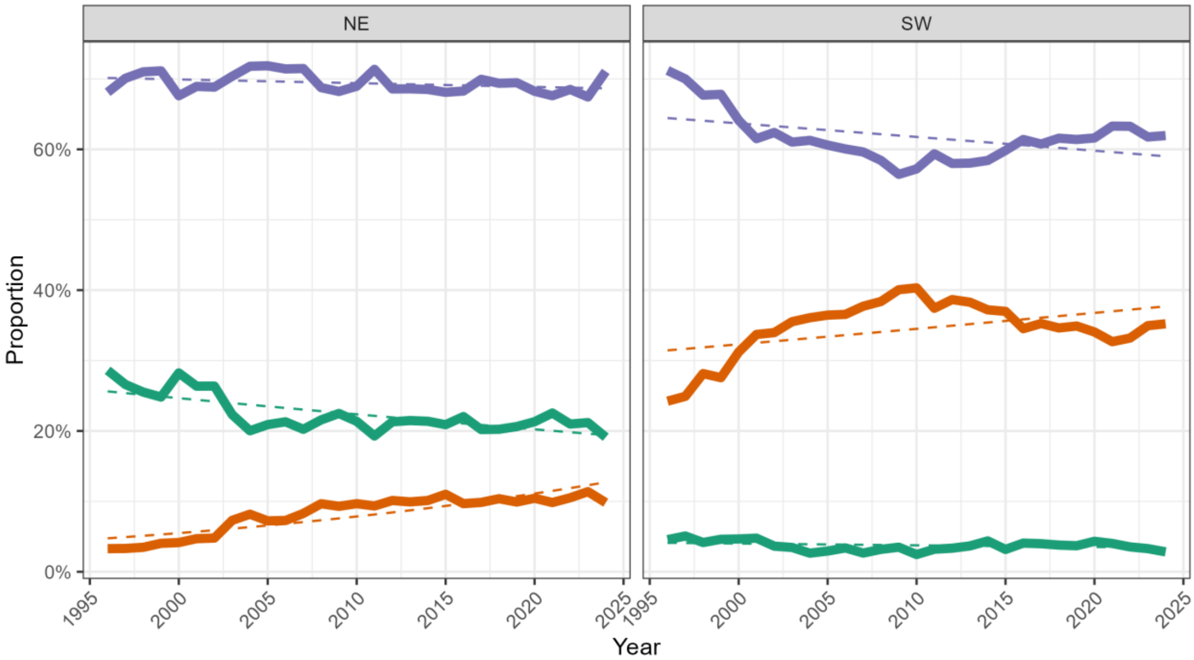

Figure 5-2. Temporal trends in the proportion of log-transformed densities of species classified in the Arctic (green), Boreal (purple) and Atlantic (orange) groups in the northeastern (NE) and southwestern (SW) regions of Iceland. Beta regression lines have been added to aid the visualisation of trends in the proportions of each group.

As expected, the proportion of Atlantic species increased during the study period, while Arctic species decreased, alongside the observed increase in temperature (*Figure 5-2*). S_{CC} had a significant negative correlation with both SST (Pearson's r = -0.52, df = 26456, p = <0.001) and SBT (Pearson's r = -0.29, df = 26456, p = <0.001). In the northeast, S_{CC} increased throughout the study period, regardless of temperature fluctuations; in the southwest, S_{CC} decreased from 1996 to 2005 (matching the period of faster warming), but thereafter increased and plateaued while temperatures fluctuated but stayed high. The overall S_{CC} trend was an increase during the study period in both regions (*Figure 5-3* and *Table 5-1*), concurrently with the observed overall increase in temperature.

No statistically significant correlation between S_{FP} and fishing intensity was found (Pearson's $r = 0.01$, $df = 26653$, $p = 0.12$). S_{FP} generally decreased throughout the study period in both regions, concurrent with the observed decrease in fishing intensity (*Figure 5-3* and *Table 5-1*). The only exception to this trend was the period 2017-2024 when S_{FP} stabilised in the northeast and underwent a slight increase in the southwest.

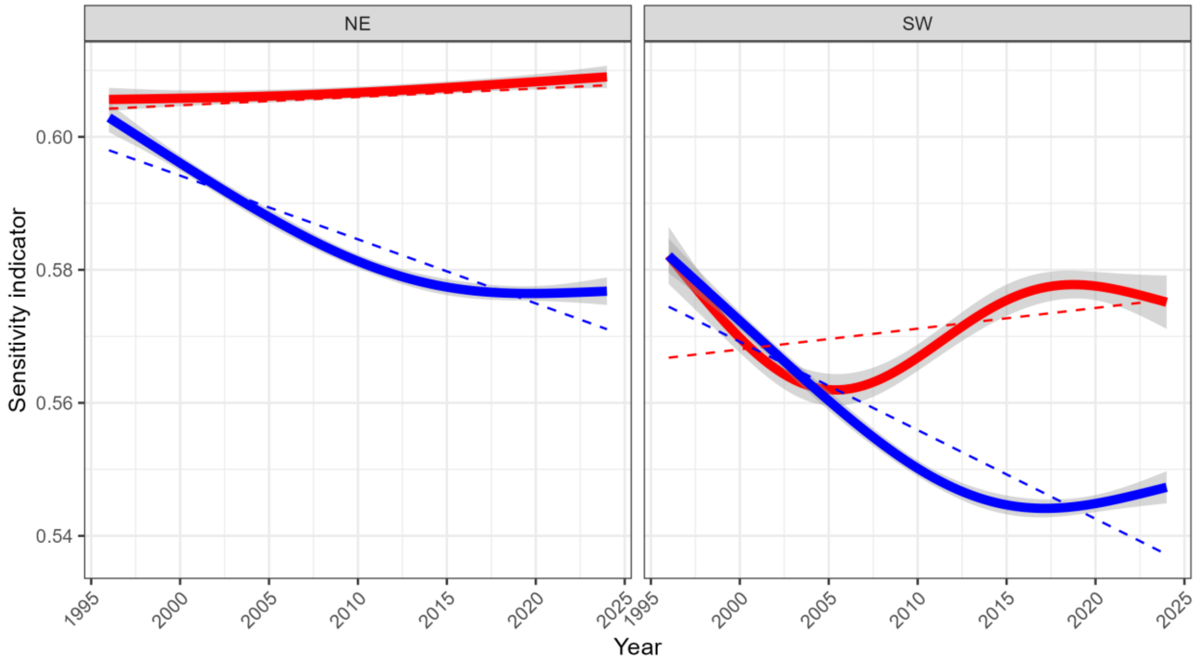

Figure 5-3. Temporal trends in sensitivity to climate change (S_{CC}, red) and in sensitivity to fishing pressure by bottom trawling (S_{FP}, blue) in the northeastern (NE) and in the southwestern (SW) regions of Iceland. The continuous line represents the overall trend for the entire species assemblage modelled with GAMs with the related 95% confidence interval (grey shading), while the dashed line represents the overall trend of each region modelled with beta regression.

There were marked differences in the dynamics of the four sensitivity groups (i.e. species sensitive to either climate change or fishing pressure, or to both pressures, or with low sensitivity to either pressure). In both regions, the proportion of species sensitive to fishing decreased, while that of species sensitive to climate change increased (*Figure 5-4* and *Table D-4*). The proportion of species with low sensitivity to both pressures increased in the northeast and remained stable in the southwest; while the proportion of species with high sensitivity to both pressures was stable in the northeast but decreased in the southwest (*Figure 5-4* and *Table D-4*). When investigating temporal trends for mean density, it becomes apparent that the density of species sensitive to both pressures increased in the southwest, although not as fast as the species sensitive to climate change alone (*Figure 5-4*, *Figure D-4*). Species with low sensitivity to both pressures have been increasing and peaking in 2008-2009, while species with high sensitivity to fishing alone fluctuated in density throughout the years although having a higher density before 2010 (*Figure 5-4*, *Figure D-4*). On the other hand, the northeast has been characterized by a small increase in species with low sensitivity to both pressures, and no significant change in species with high sensitivity to both pressures; while species sensitive to climate change alone increased at the same time of the decrease in species sensitive to fishing (*Figure 5-4*, *Figure D-4*). Trends in overall density (i.e. of the four sensitivity groups combined) differed between the two regions, being stable throughout the study period in the northeast, but increasing in the southwest (*Figure 5-4*, *Figure D-4*).

Table 5-1. Beta regressions describing temporal trends (over 1996–2025) in the proportions of biogeographical groups (based on log-transformed densities), and in community-level sensitivity to climate change (S_{CC}) and fishing pressure (S_{FP}). Each model was developed separately for the northeastern (NE) and the southwestern (SW) region. SE refers to the standard error associated to the model's coefficients. Significant temporal trends (p <0.05) are shown in bold font.

REGRESSION	REGION	SLOPE	SE	Z-VALUE	*P*
Proportion of Arctic species	**NE**	**-0.002**	**4.88×10^{-4}**	**-4.542**	**<0.001**
	SW	-2.43×10^{-4}	2.20×10^{-4}	-1.104	0.270
Proportion of Boreal species	NE	-5.28×10^{-4}	5.40×10^{-4}	-0.978	0.328
	SW	**-0.002**	**5.68×10^{-4}**	**-3.411**	**<0.001**
Proportion of Atlantic species	**NE**	**0.003**	**3.31×10^{-4}**	**8.592**	**<0.001**
	SW	**0.002**	**5.56×10^{-4}**	**4.009**	**<0.001**
S_{CC}	**NE**	**1.26×10^{-4}**	**5.98×10^{-5}**	**2.10**	**0.036**
	SW	**3.12×10^{-4}**	**6.40×10^{-5}**	**4.87**	**<0.001**
S_{FP}	**NE**	**-9.61×10^{-4}**	**4.40×10^{-5}**	**-21.9**	**<0.001**
	SW	**-1.33×10^{-3}**	**4.62×10^{-5}**	**-28.8**	**<0.001**

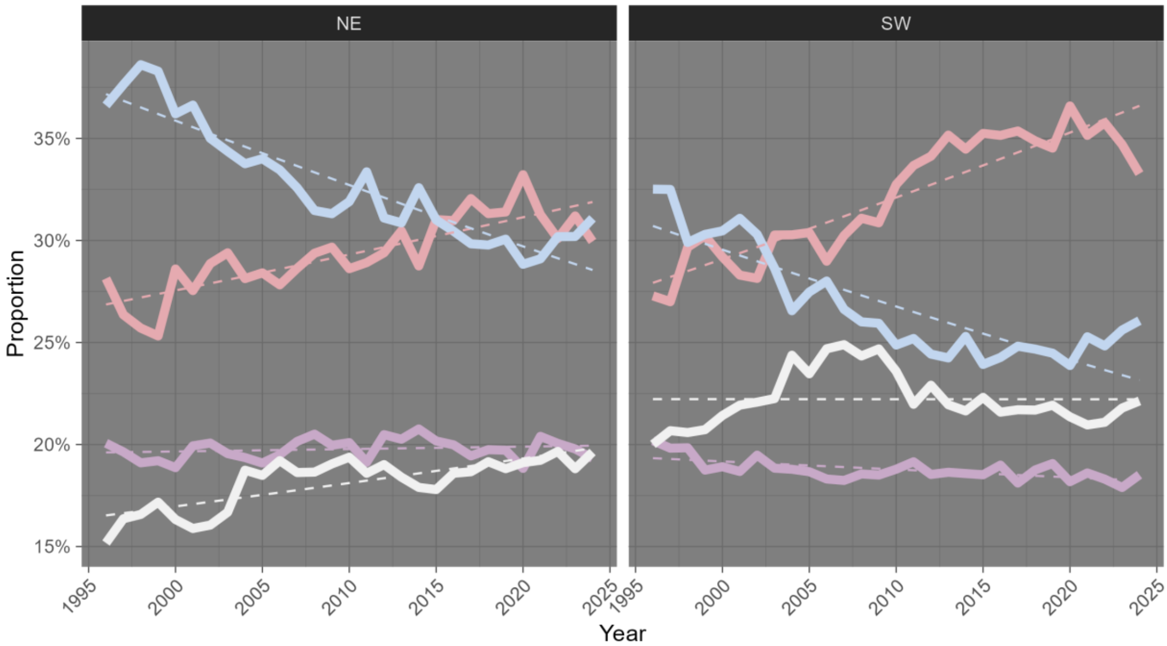

Figure 5-4. Temporal trends in proportions of log-transformed abundance of species with high sensitivity to both climate change and fishing by bottom trawling (light purple), by high sensitivity only to climate change (light red), by high sensitivity only to fishing by bottom trawling (light blue), and by no high sensitivity to both pressures (light grey), for the northeastern (NE) and the southwestern (SW) regions of Iceland. Linear regression lines with their 95% confidence intervals have been added to aid the visualisation of trends in the proportions of each group.

Following this investigation of temporal trends, an examination of spatial trends in S_{CC} showed that this indicator has been on the rise in northern Icelandic waters during 1996–2024, with a cluster of particularly high rates of change around the northwest of Iceland (*Figure D-5*). This area of increase in S_{CC} roughly overlaps with the areas where stable or increasing fishing intensity has been observed throughout the study period (*Figure D-6*), and with areas where SST or SBT has been increasing (*Figure D-7*). On the other hand, S_{FP} has been in decline throughout the study area (*Figure D-8*).

5.4 Discussion and conclusions

For the highly productive seas surrounding Iceland, this study reports a general increase in one of the two considered stressors, seawater temperature, and a decrease in the other one, fishing intensity. Despite these trends, the related indicators did not follow the expectations, with sensitivity to climate change (S_{CC}) showing an overall increase and sensitivity to fishing pressure (S_{FP}) decreasing in value; this was the case in both regions examined – those to the northeast and southwest of Iceland. These changes were found to coincide with a marked decrease in abundance of Arctic species, and increase of Atlantic species, in line with the observed seawater warming. Hence, the study then proceeded with an investigation of the dynamics underlying these trends by using a classification based on 'sensitivity groups'. The key finding is that the proportion of log-transformed densities of species that are sensitive to fishing has decreased significantly in both regions, while the proportion of species sensitive to climate change increased. In the northeast, the total mean density of demersal fish remained stable throughout the study period, due to species sensitive to fishing being substituted by species sensitive to climate change and/or species with low sensitivity to either pressure. In the southwest there was also an increase in mean density of these two groups (especially the group sensitive to climate change) but here the other two groups remained relatively stable in abundance, so that the total mean density of the bottom-dwelling fish community increased.

In the southwest, the observed increase in density of species sensitive to climate change might be explainable by the slower rate of warming observed for both SST and SBT, compared to other areas of the Atlantic (von Schuckmann et al. 2024), and by the increased prevalence of Atlantic species here, as found in our study. New species can easily occupy the warming areas due to the slow development. These three elements indicate that the southwest of Iceland might be constituting a refugium for southern (Atlantic) species that are however sensitive to high temperatures. Such warm-sensitive Atlantic species probably include northern rockling *Ciliata septentrionalis* and lesser sandeel *Ammodytes tobianus*, both characterised by high S_{CC} scores – higher than Boreal species such as wolf-fish *Anarhichas lupus* and thorny skate *Amblyraja radiata*, and Arctic fish species such as seasnail *Liparis liparis* and Arctic skate *Amblyraja hyperborea* (*Figure D-3* of Appendix D). Some 'southern species' were probably already present in the region and increased in abundance, while others may have moved into the region, with poleward distribution shifts linked with climate change (Pinsky et al. 2013, Poloczanska et al. 2013). Indeed, several species newly recorded in Icelandic waters in recent years are speculated to be moving into the region due to warming temperatures (Campana et al. 2020). The limited increase in density of species sensitive to both pressures might instead be due to the relatively high levels of fishing; if this was lower or absent, then this group could have experienced rates of population growth similar to the ones experienced by the group sensitive to climate change. On the other hand, the peak and subsequent drop in density of the group characterised by low sensitivity to both pressures (*Figure 5-4*, *Figure D-4*) is more difficult to explain. The initial rapid rise in abundance (until 2008-2009) might be linked with the faster rate of warming registered during the first decade (*Figure D-1* of Appendix D); factors other than seawater temperature and fishing might instead be behind the following stabilization in numbers. Species-specific environmental preferences (e.g., sea floor topography) (Borland et al. 2021) and biotic interactions (Zobel 1997, Bruno et al. 2003) are some possible explanations to this trend. An in depth analysis looking at species that belong to this group and which density stopped increasing or decreased is likely to be necessary to identify the underlining causes of the group's overall halt in density increase.

In the northeast, stable total abundance combined with a decrease in species sensitive to fishing indicates that exploitation (fishing) might have played an even greater role in defining community composition than in the southwest, equal in importance to temperature. This is despite the relatively low levels of exploitation found in the region, due to the persistence of fishing levels in most of the north of Iceland (*Figure D-6* of Appendix D). This may be explained by differences between the two regions in terms of biogeographical groups within the community: while in the southwest, Arctic species are a minority, in the northeast they constitute the second-most common group (*Figure 5-2*), where they are endemic as this area is included within the Arctic ichthyofaunal region (Mecklenburg et al. 2011). These species are therefore adapted to the cold temperatures that are found in the northeast, which is the region of the two that has been warming at the faster rate. Hence, habitat changes, combined with fishing pressure, might be the main factors explaining the significant decrease in proportion of Arctic species in the region. The Arctic group is the only one of the three where the means of both S_{CC} and S_{FP} were >0.5, which indicates that these species may already be vulnerable at lower levels of exploitation, especially in combination with rising temperatures. On the contrary, fishing pressure combined with warming might explain the rise in density of Atlantic species, which instead have both mean S_{CC} and S_{FP} <0.5. This would account for the increasing proportion of species sensitive to climate change, which are probably favoured by generally low temperatures in the region, and for the significant rise in proportion of species characterized by low sensitivity to both pressures. The relatively stable density of species that have high sensitivity to both pressures may be due to a substitution of individuals belonging to Arctic species with individuals belonging to Atlantic species, the latter moving into the region due to cooler temperatures compared to further south, and low exploitation levels. Where these climate-change sensitive species are probably moving into the region is the northwestern boundary, an area where increases in S_{CC} overlap with sustained or increasing fishing pressure (*Figure D-5* and *Figure D-6*), and where the Irminger Current flows in to bring warmer Atlantic waters (Símonarson et al. 2021).

In conclusion, since the mid-1990s there has been substantial change in the composition of the bottom-dwelling fish species assemblages in the waters surrounding Iceland, with gains in numbers of Atlantic climate-sensitive species and losses in numbers of cold-adapted, fishing-sensitive Arctic species. However, the mechanisms of community reorganisation are different between the northeast and southwest, seemingly due to the different levels in intensity of the two stressors – climate change and fishing pressure – in each region. This study provides evidence that the interpretation of S_{CC} and S_{FP} trends can sometimes be misleading, notably when their changes are not contextualised within the ecological situation of a particular study area. It has also shown that studying changes in community composition in terms of species groupings can greatly help in their understanding – either according to their biogeographical affinities, or according to their relative levels of sensitivity to climate change, fishing pressure, or both. Overall, given the evidence provided here for the presence in these seas characterized by changing temperatures of a facilitation mechanism constituted by fishing mortality and benefitting Atlantic species, a precautionary approach that applies conservation measures such as no-take marine protected areas should be favoured, in order to prevent further changes to the composition of the marine fauna at the detriment of native species. Such areas could be placed in the north-west of Iceland, where the greatest cumulative impact by both pressures – climate change and fishing pressure – can be found.

6 Greenlandic waters

6.1 Introduction

In sub-Arctic and Arctic marine ecosystems, climate change is happening faster than in any other region globally (Hoegh-Guldberg & Bruno 2010). Since the mid-2000s, loss of sea ice and physical changes of sea surface waters have transformed Arctic waters to more closely resemble waters of the North Atlantic. As a result, an increasing Borealisation of Arctic biota is observed in shallow continental shelf seas, meaning that more southerly distributed species invade these high-latitude ecosystems. Along the East Greenland coast, sea ice extent has declined and reached record-lows in the recent two decades, with formerly seasonally ice-covered regions becoming permanently ice-free. The East Greenland ecosystem represents a sub-Arctic transition zone, where the cold East Greenland Current mixes with the temperate Irminger Current and flows southwards following the continental slope (Sutherland & Pickart 2008, *Figure 5-1*). The dominance of the cold East Greenland Current on the shelf and the influence of the warmer Irminger Current along the slope create frontal and transition zones (*Figure 6-1*), where Boreal and Arctic species live (Emblemsvåg et al. 2022). Depending on topography-dependent modification of water bodies, these frontal zones may provide highly productive habitats (Andersen & Born 2002). They are expected to represent a hotspot for the impacts of climate change because species often live close to the boundaries of their thermal affinities here, and so they will respond quickly to changes in the environment (Emblemsvåg et al. 2022).

The waters around Greenland also provide important fishing grounds. The offshore demersal fisheries are characterised by a prevalence of Atlantic cod and redfish in the catches, with significant differences between West and East Greenland (Fock 2008). The dynamics of the West Greenland cod stock reveal that climate may play a major role in changing the ecosystem, concomitant with and yet not distinguishable from fisheries effects (Brander 1996). The population of cod in Greenland is at the edge of the species' distribution range and thus far from environmental optima for cod; the stock is therefore vulnerable to both exploitation and environmental change (Brander 1996).

Historically, cod catches were mainly taken in West Greenland waters, but after 1980 cod catches off East Greenland also increased markedly. However, the cod fisheries collapsed in 1992, after which Greenland's fisheries began to target shrimp (Hamilton et al. 2003). In 2003, signs of cod stock recovery became evident, and the cod fishery reopened in 2006 (Fock 2008).

In the context of these major changes in both climatic drivers and fishing pressure in East Greenlandic waters, the present study examines how local demersal fish communities may have responded in terms of community-level sensitivity to these two pressures using a traits-based approach in which the sensitivity to climate change is assessed (S_{CC}) and to fishing pressure (S_{FP}) (Polo et al. 2025). Specifically, and in line with earlier sections in this report, we ask:

(1) How have average community-level sensitivity to climate change (S_{CC}) and fishing pressure (S_{FP}) of demersal fishes changed in East Greenlandic waters during 1982–2020?

(2) How were the spatial patterns and trends in S_{CC} and S_{FP} in East Greenlandic waters, during two distinct periods – 1982–2003 (prior to the recovery of the depleted cod stock) and 2003–2020 (during the period of recovery of the cod stock)?

(3) Can areas be assigned with higher levels of risk for S_{CC} and/or S_{FP}?

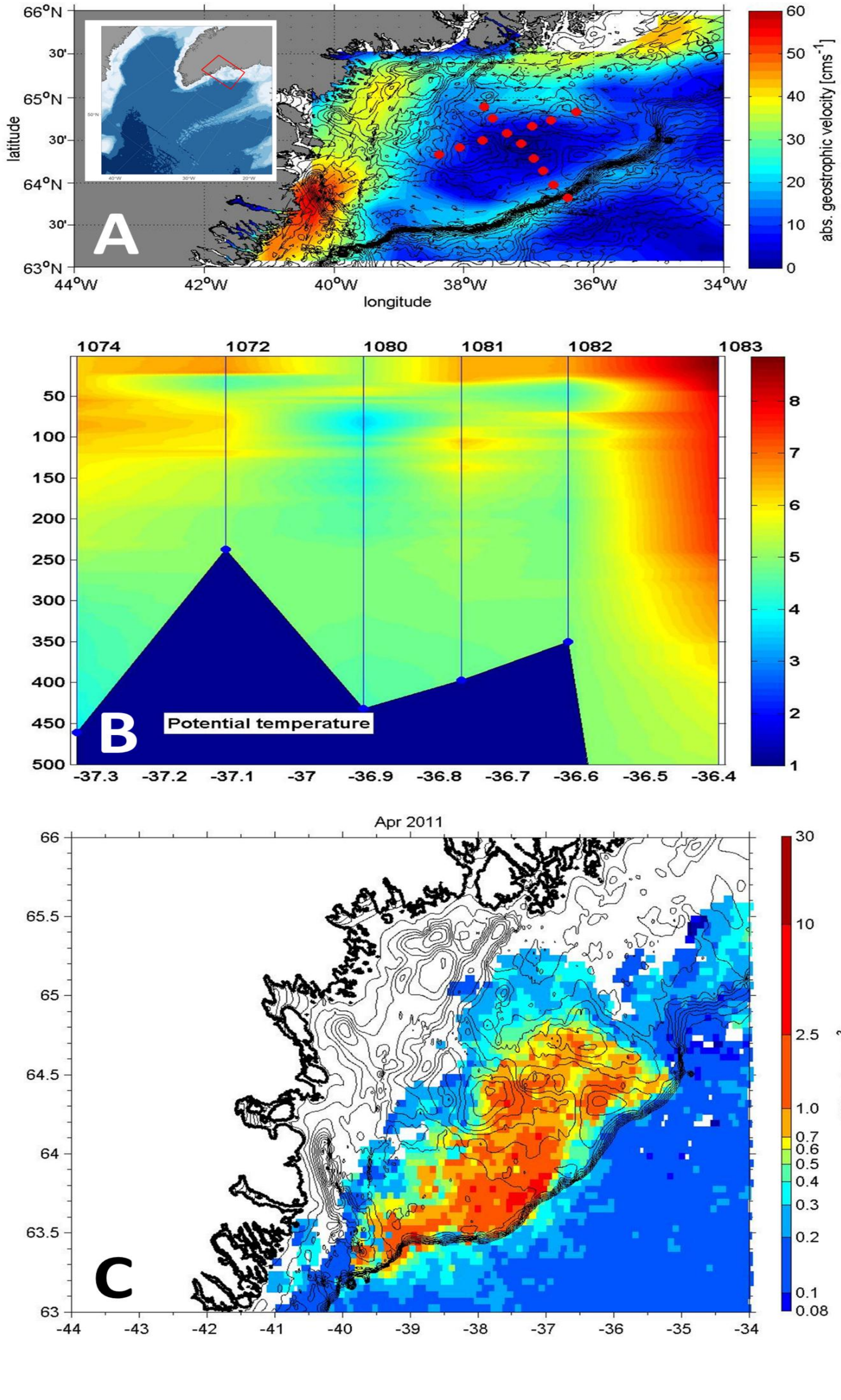

Figure 6-1. Exemplified hydrographic conditions in East Greenlandic waters: (A) Absolute geostrophic current velocities (during October 2012), i.e., water flowing parallel to a pressure gradient, largely driven by topography which in turn is determined by shallow banks, leading water masses to rotate around these. (B) The hydrographic NW-SE cross-section during October 2010 (transect indicated by red dots in A, main axis to the shelf edge). (C) Chlorophyll distribution in April 2011. In (A), the horizontal eddy structure over Kleine Bank is visible by means of calm conditions with low current velocities in the core, paralleled by increased upwelling of cold water in the centre of the eddy and the formation of a cold-water lens at depth of 30-50 m. The upwelling is caused by a cyclonic circulation pattern in the centre of the eddy. The frontal zone towards the Irminger Current is visible in panel B at 36.5°W. Inset with red box in (A) indicates section of East Greenland covered.

6.2 Methods

6.2.1 Reference area and period

The reference area is defined by the main fishery in the area. Recently, based on genetic evidence the cod stock was split into a West Greenland and an East Greenland-Iceland offshore cod stock (ICES 2025a). Accordingly, the focus in this report section is on ICES sub-area 14, i.e., East Greenland. Taking the recovery of the cod stock after 2003, the research period is split into after-2003 and before-2003 (Fock 2008), as well as the entire time series.

6.2.2 Fish assemblage data

Fish assemblage data were obtained from the German Greenland Groundfish Survey (GGS, code G3244). After an initial summer survey in 1981, annual autumn surveys covering the Greenland shelf and continental slope commenced in 1982 (Fock 2008; Fock et al. 2006). The survey covers habitats until 400 m water depth. In East Greenland, shallow habitats (<200 m) mainly consist of banks emerging from the deeper areas, with a prevalence of habitat deeper than 200 m, in contrast to West Greenland.

6.2.3 Fisheries

Catch data must be applied as proxy for fishing effort. From 2000 to 2005, mainly experimental fisheries were carried with catches less than 1000 t per year for Atlantic cod *Gadus morhua*. From 2006 to 2014, catches were limited to about 5000 t per year. Since then, catches have been increasing, with a regional focus on the easternmost part of the Greenland EEZ, the Dohrn Bank adjacent to Icelandic shelf habitats, reaching about 30,000 t per year in 2023 (ICES 2025a).

6.2.4 Climate change and fishing pressure sensitivity

For each species, sensitivity indices for climate change (S_{CC}) and fishing pressure (S_{FP}) were taken from Engelhard et al. (2024) and Polo et al. (2025) and weighted by abundance to calculate community sensitivity by location and by year.

6.3 Results

6.3.1 Long-term trends in community sensitivity indices

Trends of the sensitivity indices for both climate change and fishing pressure revealed three distinct periods in the fisheries time series (*Figure 6-2*). Community-level sensitivity to climate change (S_{CC}) decreased during 1990s, then increased after 2000; the reverse was the case for community-level sensitivity to fishing pressure (S_{FP}). Environmentally, the changes were mainly driven by the drop of sea surface temperature in 1992–1994 and its increase until 2010 (*Figure 6-1*), and in terms of assemblage composition by the abundance dynamics of Atlantic cod (using spawning stock biomass [SSB] as proxy, see *Table 6-1*), and after 2003 also by haddock *Melanogrammus aeglefinus*, saithe *Pollachius virens* and Norway pout *Trisopterus esmarkii*. Accordingly, community-level S_{CC} was relatively low in the break-down era 1992–2003 related with low S_{CC} sensitivities of the deep-water species of wolffish (*Anarhichas* spp.) and redfish (*Sebastes* spp.), however with an increased S_{FP} (*Figure 6-2*).

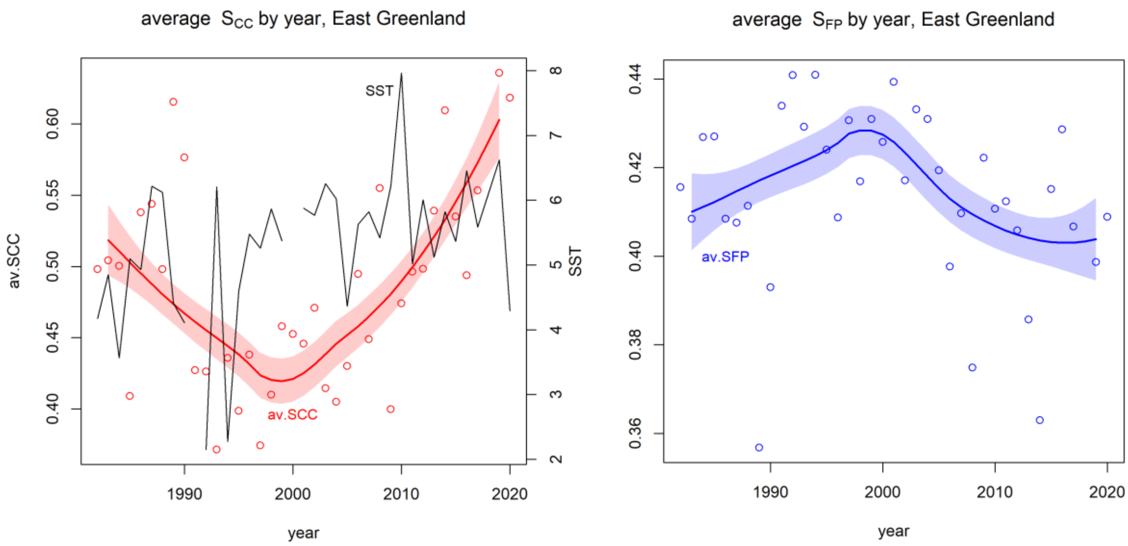

Figure 6-2. Long-term trends in community-level sensitivity indices for climate change (S_{CC}) and fishing pressure (S_{FP}) for the East Greenland demersal fish community over the period 1982–2020. Sea surface temperature (SST) included in left panel.

Table 6-1. Correlations of community-level sensitivity to climate change (S_{CC}) and fishing pressure (S_{FP}) with annual survey observations of sea bottom temperature (SBT) and sea surface temperature (SST) in the months October-November of 1982–2020, and the stock index of Atlantic cod (Cod SSB) and observed cod catch for East Greenland (Catch). Cod SSB and catch obtained from stockassessments.org for the East Greenland stock (significant correlations in bold).

VARIABLE	S_{FP}	S_{CC}	Catch	*in situ* SBT	*in situ* SST
Cod SSB	**-0.53***	**0.61****	**0.68*****	–0.43	–0.13
S_{FP}		**–0.76*****	–0.23	0.01	0.17
S_{CC}			**–0.77*****	–0.14	–0.17
CATCH				**–0.62****	0.08
in situ SBT					–0.14

6.3.2 Spatial distributions of community sensitivity indices

Mapping of the spatial distribution of community-level sensitivity to climate change (*Figure 6-3*) revealed that in the period 1993-2002 low S_{CC} values prevailed along the East Greenland shelf edge, while high S_{CC} values prevailed east of 34°W and on the shallower parts of the shelf. This tendency was strengthened after 2003, with increasing abundance in the bank habitats of the gadoids Atlantic cod, haddock and saithe (each of these having relatively high S_{CC} values).

The low S_{CC} during the period 1993-2002 was mirrored by relatively high sensitivity to fishing pressure S_{FP} (*Figure 6-4*). This was especially the case on the shelf edge from 34°W to 32°W, where redfish were highly abundant during this period. After 2003, with increased abundance of gadoids, S_{FP}-values decreased except for the redfish hotspot.

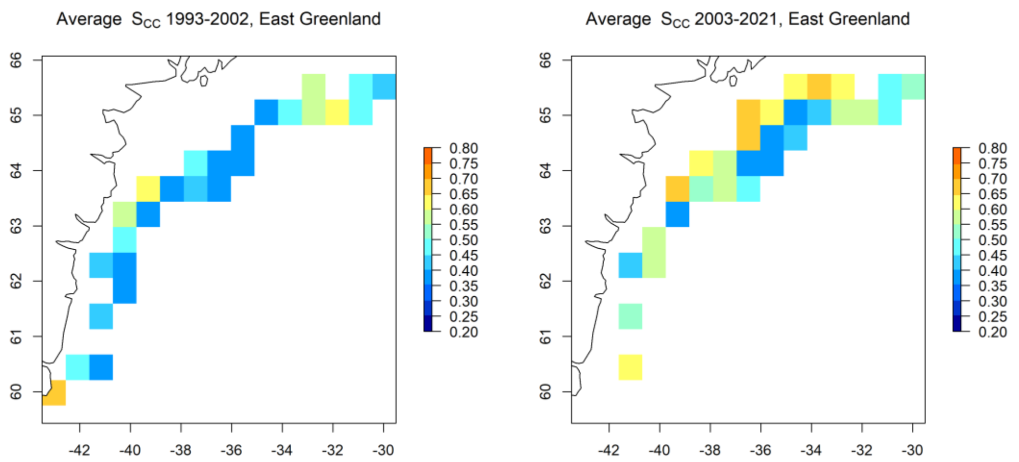

Figure 6-3. Spatial distribution of community sensitivity towards climate change (S_{CC}), East Greenland, for two time periods, prior and post-cod recovery respectively.

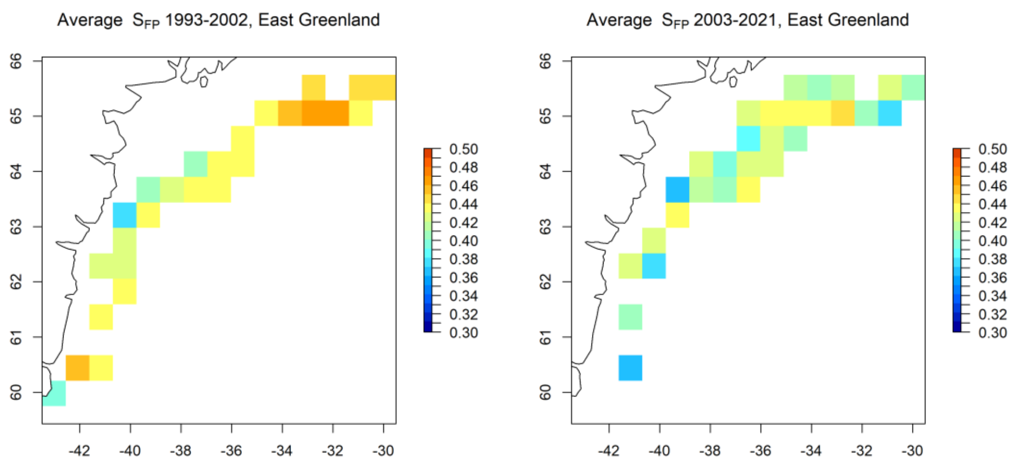

Figure 6-4. Spatial distribution of community sensitivity towards fishing pressure (S_{FP}), East Greenland, for two time periods, prior and post-cod recovery respectively.

6.4 Discussion and conclusions

The results show a clear separation in East Greenlandic community sensitivity dynamics, into three periods within the time series 1982 to 2021 – revealing a high–low–high temporal pattern in S_{CC}, and a low-high-low trend S_{FP}. These changes were largely driven by the decreasing dominance of Atlantic cod and associated Boreal species in the earlier period (1992 to 2003), while the trend reversed thereafter with recovery of the cod stock. This is revealed through significant correlations of the cod index with community S_{FP} and S_{CC} (*Table 6-1*).

Temperature change was the predominant driver of faunal changes in the East Greenland ecosystem (see correlation SBT with S_{CC} in *Table 6-1*). Additional, significant effects of fisheries and of ocean productivity in East Greenland only occurred associated with the climate effect. As such, fisheries and climate were identified as dominant driving forces in the period 1982–1991; productivity (primary production) and climate in the period 1991-2001, notably the significant drop in sea surface temperature (*Figure 6-2*); and climate again after 2001, but now warming (Fock 2008). The warming in the most recent period was associated with a positive phase of both the North Atlantic Oscillation (NAO) and the Atlantic Multidecadal Oscillation (AMO), which led to a displacement of the centre of the NAO (Buch et al. 2003). The preceding, cooling 1991-2001 period had been associated with a positive NAO and negative AMO phase. Accordingly, the warming period before that (before 1991) had been associated with negative NAO as well as negative AMO phases.

The warming trend in East Greenland waters since the beginning of the 21st century led to a steady increase in Boreal species with accordingly high fisheries catches. In West Greenland, the increase in Boreal species was paralleled by decreases in Arctic species such as Arctic shrimp *Pandalus Borealis*. Meanwhile the interplay between warm North Atlantic and cold polar waters in the region provides the source for increased levels of primary production to sustain demersal populations, several of these of high commercial relevance for fisheries.

Elsewhere in Arctic or sub-Arctic waters, similar cases of a 'borealisation' of the fish community have been reported, with Arctic species becoming less abundant (e.g. Beaufort Sea, eastern Alaska Arctic shelf: von Biela et al. 2022). Likewise, our case study for Icelandic waters (see previous section of this report) reported reduced prevalence of Arctic, and increased prevalence of Boreal (and Atlantic) species in the fish community. This contrasts with 'deborealisation' in temperate marine regions, such as the North Sea and Celtic Seas – where Boreal species are decreasing in abundance and warmer-water species are coming in from further south (so-called 'tropicalisation' of the marine fish community: see McLean et al. 2021). Overall, the Icelandic and East Greenlandic case studies confirm a major reorganisation of fish communities in various parts of Europe's regional seas in the North Atlantic, with borealisation, deborealisation, and tropicalisation predominating in different regions.

The interplay of cold- and warm-water currents on the East Greenland shelf determines the distribution of habitats on the shelf in terms of fish populations, which in part depends on atmospheric circulation patterns. Except for localised topography-bound currents, such as those around Kleine Bank (*Figure 6-1*), the environment appears highly dynamic. This was reflected in the non-significant correlations of community indices with measured temperature indices (*Table 6-1*) over the entire investigation period, while significant relationships could be revealed when distinguishing certain periods (Fock 2008). Fisheries in this rough terrain is constrained by the accessible space, which to some degree explains the limited knowledge of inshore habitats in this area, so that the definitions of areas of high risk must remain premature.

7 Sensitivity, recoverability and vulnerability to fishing in North Sea epibenthos

7.1 Introduction

The North Sea is one of the most intensively fished marine regions in the world, with a long history of bottom trawling that has exerted substantial pressure on benthic communities (Emeis et al. 2015; Kenny et al. 2018). Epibenthic organisms—those living on or just above the seabed—are particularly vulnerable to demersal fishing due to their limited mobility, habitat specialisation, and sensitivity to sediment disturbance. Despite growing recognition of their importance for biodiversity and ecosystem functioning, epibenthic taxa remain underrepresented in conservation and monitoring frameworks.

In recent decades, parts of the North Sea have experienced a decline in fishing intensity (Engelhard et al. 2015; ICES 2024a, 2025b), coupled with efforts to manage and mitigate benthic impacts through spatial restrictions, gear innovations, and ecosystem-based management (ICES 2024a; Rijnsdorp et al. 2024). These changes offer an opportunity to assess whether sensitive and functionally important epibenthic taxa are showing signs of recovery or redistribution, and whether current patterns reflect resilience or continued vulnerability.

This chapter aims to:

1. Assess spatial and temporal changes in epibenthic species richness and composition in relation to fishing pressure across the North Sea.
2. Evaluate how community-weighted traits linked to sensitivity, recoverability, and vulnerability to bottom disturbances, respond to spatial gradients and reductions in bottom trawling activity.
3. Identify areas of the North Sea which are at high risk or where recovery of vulnerable taxa may be occurring, and highlight potential implications for benthic ecosystem health and management.

7.2 Methods

7.2.1 Study area

The North Sea is a shallow shelf sea of the northeast Atlantic, bordered by the UK, France, Belgium, the Netherlands, Germany, Denmark, and Norway. Depths range from less than 30 m in southern coastal areas to more than 200 m in the northern part, with seabed habitats shaped by gradients in sediment type, current velocity, and temperature. It is one of the most heavily exploited seas worldwide, with a long history of bottom trawling and other human uses, but also supports diverse benthic and pelagic communities.

7.2.2 Survey Information

This study assessed temporal and spatial changes to epibenthic invertebrate communities in the North Sea by using standardised beam trawl survey (BTS) data collected between 2000 and 2024. Survey coverage ranged between 51°N and 58°N latitude and 3°W to 9°E longitude, focusing on the North Sea and excluding adjacent areas such as the Irish Sea and English Channel. All demersal invertebrate records were extracted from the publicly accessible ICES DATRAS portal (www.datras.ices.dk), comprising samples collected in late summer (Quarter 3) by the Netherlands, Germany, the United Kingdom, and Belgium. Belgian BTS data were excluded for select years (2000–2009, 2010, 2016) due to closed species lists that limited detection of rarer invertebrates. From the total invertebrate catch, 136 epibenthic taxa were identified from the hauls. Data before 2000 were excluded due to differences in methodology.

7.2.3 Biological traits

Trait-based indicators of trawling sensitivity were used to characterise species' response to disturbance. We calculated the response traits to fishing impacts: sensitivity (SE), recoverability (RE), which were added together to obtain vulnerability (VU), following Beauchard et al. (2021). Details on how these traits were calculated can be found in D4.1 (Engelhard et al. 2024). Trait values were re-scaled from 0 to 1 across all species. The values were then weighted by log-transformed abundance per haul to generate spatially and temporally explicit community indices.

7.2.4 Generalised additive models

Environmental covariates associated with each haul location included depth, sediment grain size, orbital current velocity (Wilson et al. 2018), sea surface temperature (Copernicus 1993–2020), and reconstructed trawling effort (Couce et al. 2020). To assess spatial patterns in vulnerability (VU), we used generalized additive models (GAMs) with smooth terms for latitude/longitude, depth, temperature, and fishing effort. Models were fitted separately for the northwest and south/east subregions within the North Sea, and exhibited the following structure:

$$\mathbf{VU} = \beta_0 + f_1(x, y) + f_2(\text{Depth}) + \beta_1 \cdot \text{Gear} + \beta_2 \cdot \text{Sediment\_type} + f_3(\text{Ship}) + f_4(\text{Year}) + f_5(\log(\text{Hours\_trawling})) + f_6(\text{SST})$$

where:

- **VU** is the trait-based community-level vulnerability score per haul.
- $f_1(x, y)$ is a smooth interaction of spatial coordinates (longitude and latitude), modelled using thin-plate splines.
- f_2(Depth) is a smooth effect of depth, modelled using thin-plate regression splines with $k = 3$.
- Gear and Sediment_type are categorical fixed effects with associated coefficients β_1 and β_2.
- f_3(Ship) and f_4(Year) are random effect smoothers for survey vessel and year, respectively.
- f_5(log(Hours_trawling)) models the effect of log-transformed trawling effort.
- f_6(SST) is a smooth term for annual mean sea surface temperature at each haul location.

7.2.5 Multi-variate analysis

Finally, a multivariate co-inertia analysis was conducted to explore correlations between environmental variables and species trait composition using the ade4 package in R (Dray and Dufour 2007). Species data were processed using centred principal component analysis (PCA) on the Hellinger-transformed abundances of epibenthic taxa. Environmental variables which included log-transformed trawling effort, sea surface temperature, year, spatial coordinates, median grain size, depth, and orbital current velocity, were scaled and centred to preserve a relative structure. Co-inertia analysis was then performed to assess the covariance between the species and environmental ordinations, and results were visualized using co-inertia biplots.

7.3 Results

Community-weighted trait scores revealed a clear spatial shift in trait distributions over time (*Figure 7-1*). Elevated sensitivity (SE), recoverability (RE) and vulnerability (VU) scores were initially concentrated in the northwestern North Sea during 2000–2009 and mostly absent from the south and east, but progressively extended into these regions in the following decades (albeit to a lesser extent in the case of RE). By the 2020–2023 period, higher trait scores were more broadly distributed across the study area.

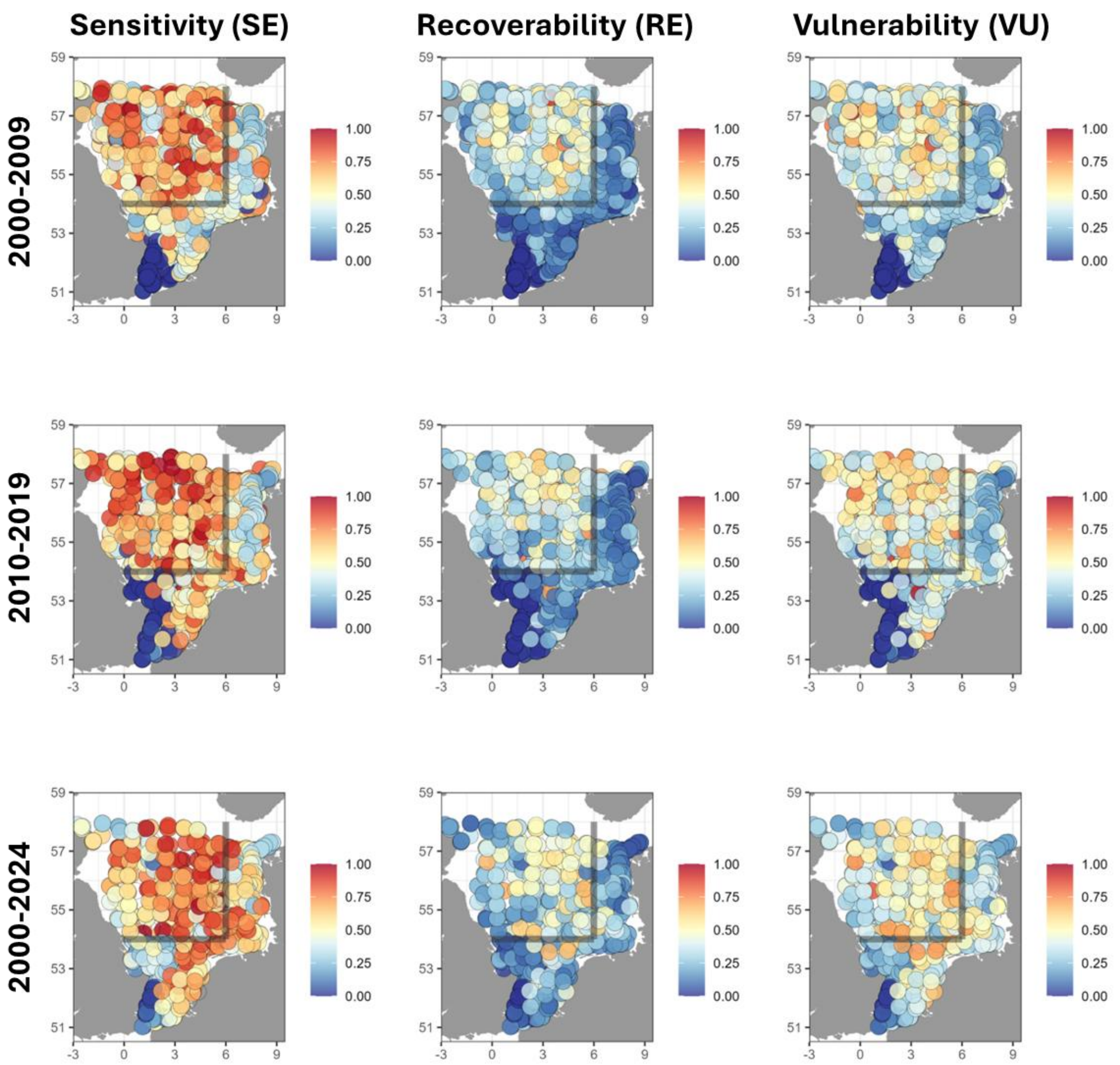

Figure 7-1. Species response traits for vulnerability (VU), sensitivity (SE), and recoverability (RE) traits to demersal fishing activity (trait details described in Beauchard et al. (2021).

Temporal patterns in trait scores, fishing effort, and sea surface temperature differed between the northwestern (north of 54°N, west of 6°E) and southeastern regions of the North Sea (*Figure 7-1* and *Figure 7-2*). In the southeast, all three response traits (SE, RE, and VU) increased after 2015, with sensitivity showing the steepest rise and recoverability displaying a more moderate trend. In contrast, trait scores in the northwest remained relatively stable from 2000 to 2024.

Fishing effort was consistently higher in the southeast and peaked in the mid-1990s, followed by a pronounced decline through to the end of the time series. In the northwest, effort peaked earlier, around 1990, declined until 2010, and then showed a slight upward trend. Sea surface temperature was generally higher in the southeast and increased steadily after 2010. In the northwest, temperatures showed a modest decline after 2005 before rising again after 2013 (*Figure 7-2*).

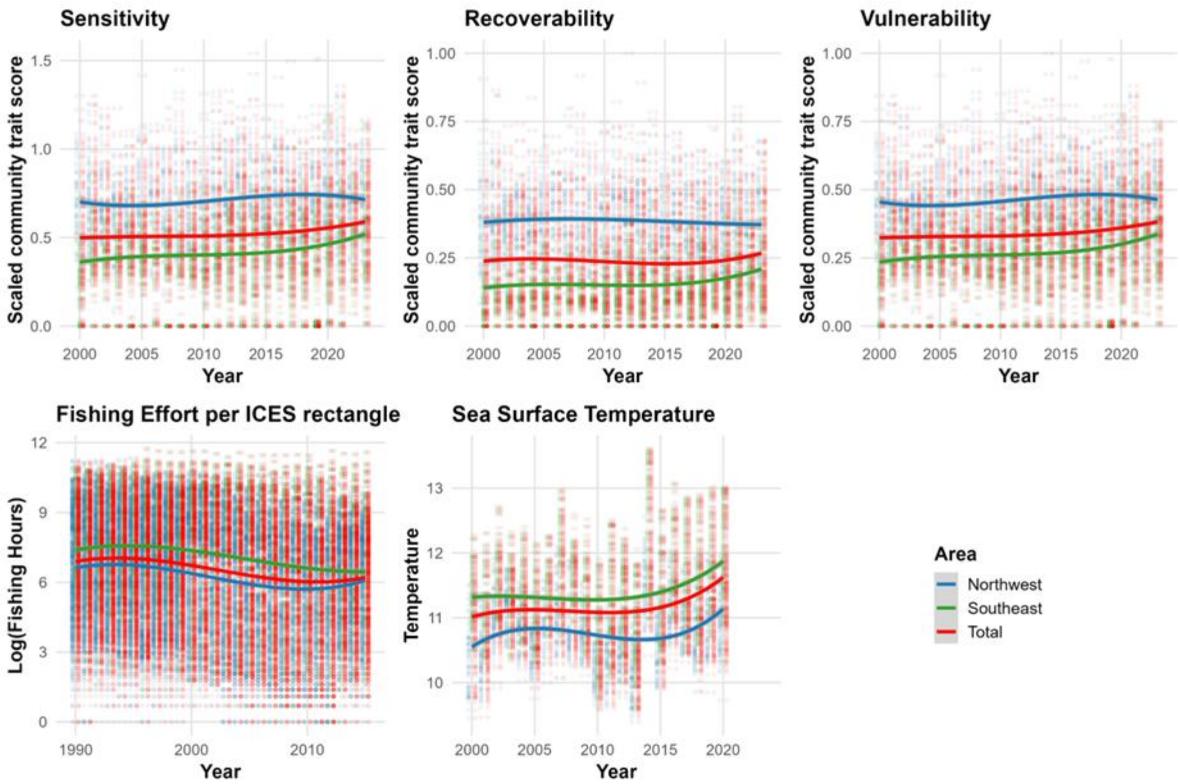

Figure 7-2. Trends in scaled community trait scores for sensitivity, recoverability and vulnerability as well as the trends in fishing effort (log-transformed trawling hours) and sea surface temperature in the northwest vs. the southern/eastern areas of the North Sea.

While these general patterns can be deduced, the underlying data are notably noisy at the annual scale. The spline fits therefore emphasise broad, longer-term trajectories rather than year-to-year fluctuations, which should be interpreted with caution.

Generalised additive models (GAMs) predicting community-weighted vulnerability (VU) trait scores (*Figure 7-3*) explained more deviance in the southeast region (50.7%) than in the northwest (39.1%). Smooth terms for spatial location were highly significant in both regions ($p < 0.001$), indicating strong underlying spatial structure in the data. In the southeast, trawling intensity (*Figure 7-3*, top panels) exhibited a significant negative linear effect on VU scores ($p < 0.001$), whereas no significant relationship was observed in the northwest ($p = 0.212$). Sea surface temperature (*Figure 7-3*, bottom panels) showed a significant U-shaped relationship with vulnerability in both regions ($p < 0.001$), where both relatively low and high SST were associated with high VU but intermediate SST was associated with low VU scores.

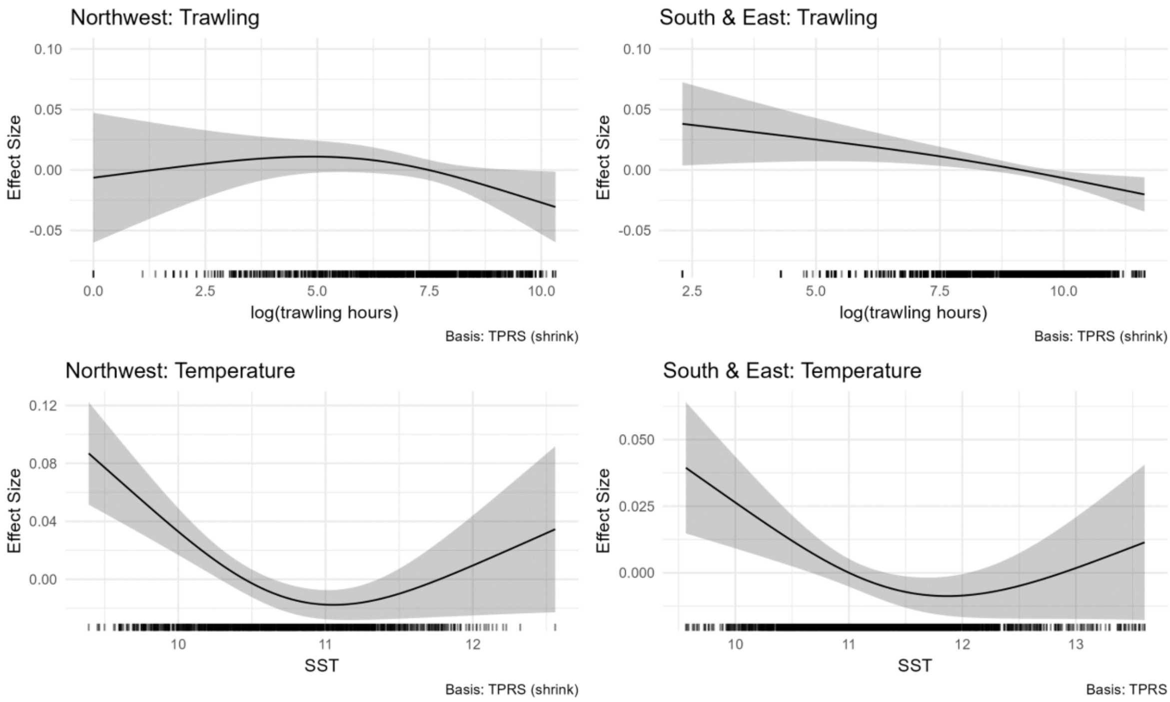

Figure 7-3. Effect of trawling intensity (log-transformed trawling hours) and sea surface temperature on the community weighted vulnerability of epibenthic species in two regions of the North Sea. Panels show smooth terms from GAM models fitted separately for the northwestern (left column) and southern & eastern (right column) North Sea, with shaded regions representing 95% confidence intervals.

The co-inertia analysis showed significant covariation between species and environmental gradients in both the northwestern and southern/eastern areas of the North Sea. This was supported by Monte Carlo tests (p = 0.001, 999 permutations).

In the northwest, the first (horizontal) and second (vertical) axes explained 77.5% and 9.7% of the projected inertia, respectively (*Figure 7-4*). Depth, current velocity and longitude were primarily associated with axis 1, while median grain size (D50), trawling effort and latitude aligned with axis 2. While only a few select species such as the starfish *Astropecten irregularis* and heart urchin *Echinocardium cordatum* were correlated with shallower waters with higher current speeds, several more species were found at greater depths towards the north with low current speeds. Strongly correlated with high trawling effort and temperatures were the cephalopods *Alloteuthis subulata* and *Loligo forbesii* as well as the green sea urchin *Psammechinus miliaris*. Common whelks *Buccinum undatum* showed a strong negative correlation to trawling and were associated with higher latitudes.

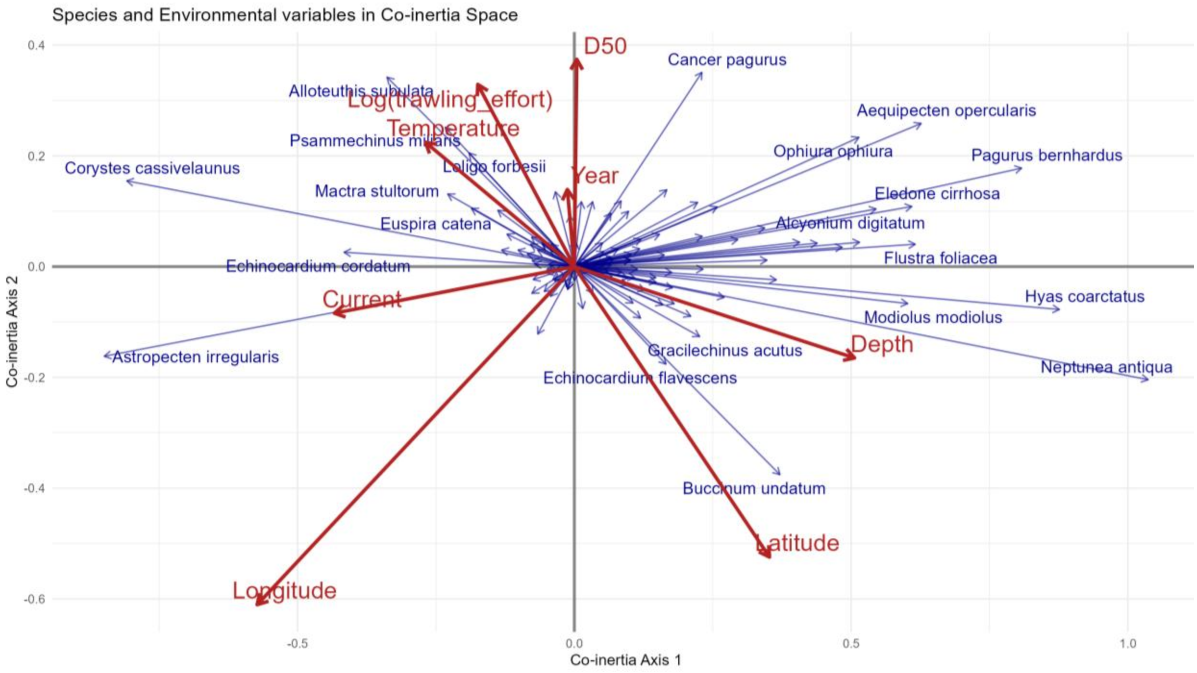

Figure 7-4. Northwestern North Sea: Co-inertia biplot illustrating the joint structure between species composition (blue arrows) and environmental variables (red arrows).

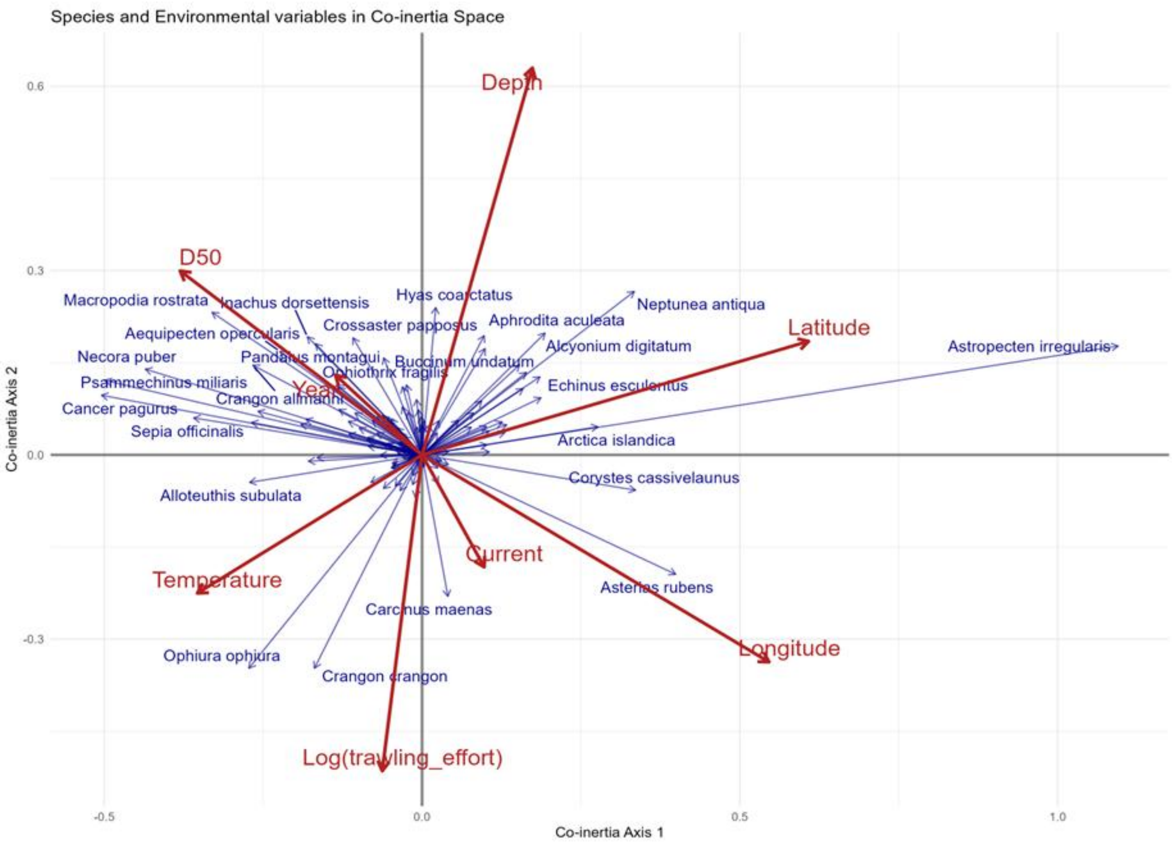

Figure 7-5. Southern & Eastern North Sea: Co-inertia biplot illustrating the joint structure between species composition (blue arrows) and environmental variables (red arrows).

In the southern/eastern region, the first two axes explained 64.4% and 20.0% of the projected inertia (*Figure 7-5*). Axis 1 was associated with grain size (D50), temperature, latitude and longitude, while axis 2 represented strong depth and trawling gradients (Figure 3.5). Species that associated more closely with warmer, shallower areas and higher trawling intensities, included brown shrimp *Crangon crangon*, serpent star *Ophiura ophiura*, and shore crab *Carcinus maenas*. Species that associated with deeper, cooler water in more northerly parts within this part of the North Sea included sand sea star *Astropecten irregularis*, red whelk *Neptunea antiqua*, and ocean quahog *Arctica islandica*.

7.4 Discussion and conclusions

This study provides new insights into long-term spatial and temporal changes in the trait composition of epibenthic invertebrate communities in the North Sea. Community-weighted trait analyses revealed that the distribution of sensitivity (SE), recoverability (RE), and overall vulnerability (VU) scores has shifted markedly over the past 2½ decades. Traits initially concentrated in the northwest of the North Sea have gradually expanded into eastern and southern regions. These spatial redistributions suggest changing ecological conditions and a possible recovery or recolonisation of sensitive taxa in areas that were historically subject to high trawling pressure throughout most of the twentieth century (Callaway et al. 2008).

Trait dynamics were found to visibly diverge between regions. In the southeast North Sea, where historic trawling effort has been higher (Eigaard et al. 2017; Rijnsdorp et al. 2016) and environmental conditions such as temperature are more variable, all three traits, and particularly SE and VU, have shown a consistent increase since 2010. In contrast, the northwest region showed little variation over time, suggesting more stable community composition and less recent change in ecological pressures or response capacity.

Our GAM analyses support the interpretation of regionally distinct dynamics. In the southeast, where fishing effort has declined markedly in recent years (ICES 2024a and 2024b; Couce et al. 2020), we found a significant negative relationship between trawling intensity and VU scores. This suggests lower fishing pressure being associated with an increasing presence of sensitive and vulnerable taxa in the area, consistent with recovery processes observed in other studies (Hiddink et al. 2017; Sciberras et al. 2018; Pitcher et al. 2022). Although this relationship is correlative, the statistical significance of the pattern and the spatial consistency observed in the co-inertia biplots supports the idea that reduced trawling has led to a shift in community composition toward more vulnerable taxa in the southern and eastern North Sea.

Temperature also significantly affected vulnerability scores in both regions, with GAMs revealing U-shaped relationships in both areas potentially reflecting compositional shifts toward both cold- and warm-affinity taxa (Kröncke et al. 2011). However, disentangling the influence of long-term climate trends from short-term variability remains challenging and warrants further investigation.

With the multi-variate co-inertia analysis we were further able to visualise some of the complicated dynamics between environmental gradients and species composition. In the northwest, the species-environment co-structure was primarily aligned with gradients of depth and current velocity, with a more limited set of species associated with shallower, high-energy environments. In contrast, the southeast co-inertia analysis exhibited greater heterogeneity with a broader array of species correlating with gradients in temperature, grain size, and trawling effort. For example, taxa such as brown shrimp *Crangon crangon* and shore crab *Carcinus maenas* were associated with high-intensity trawled areas, while species like ocean quahog *Arctica islandica* and red whelk *Neptunea antiqua* were more common in deeper, cooler, and less frequently trawled northern waters.

The combination of long-term, fisheries-independent survey data with trait-based and multivariate methods represents a major strength of this study. It allows for a more functionally relevant assessment of community change than species richness or biomass alone (Bremner et al. 2003; Beauchard et al. 2021). Still, several limitations should be acknowledged. Changes in taxonomic resolution and identification practices over time may introduce biases in trait composition. Additionally, while VU scores are useful proxies for benthic sensitivity, they do not fully capture the complexity of life histories or species interactions, and the trait datasets themselves are based on best-available expert consensus, which may be incomplete for some taxa.

Assigning areas of high ecological risk is not straightforward. Risk is often conceptualized as the interaction between pressure and vulnerability, yet these components are not independent. Increasing pressures reduces the community weighted vulnerability and vice versa. This dynamic complicates the direct use of vulnerability scores for spatial risk assessments. Nevertheless, community vulnerability can be an important metric to consider when assigning potential MPAs but should be taken into consideration with other criteria such other biodiversity indicators and habitat characteristics. In the Netherlands, potential MPAs were initially assigned based on the biodiversity of benthos, fish, birds and sea mammals and rare habitat characteristics. An area would qualify if it had combinations of several animal groups or very specific habitat characteristics (Lindeboom et al. 2005). A holistic, multi-criteria approach may be essential to ensure that vulnerability metrics are applied meaningfully in spatial management planning.

In summary, our results provide evidence for broad-scale shifts in benthic trait composition in the North Sea over the past two decades, including increasing vulnerability scores in previously degraded areas. These changes appear to be partially linked to reduced trawling pressure, though environmental gradients such as temperature and depth continue to play key roles in benthic community structure. These findings support the utility of trait-based approaches in monitoring benthic recovery and assessing ecosystem resilience. Future research should evaluate whether these shifts in trait composition translate to measurable changes in benthic ecosystem functioning, particularly in relation to bioturbation, nutrient cycling, and habitat provision. For assigning MPAs additional information is required.

8 Sensitivity of benthic habitats

8.1 Introduction

Fishing and climate change are widely recognised as two pervasive pressures on marine ecosystems, driving habitat degradation, biodiversity loss, and fundamental changes in ecosystem functioning (OSPAR QSR 2010; Halpern et al. 2015, IPCC 2023). Overfishing can lead to the collapse of key species populations. It can disrupt trophic interactions, and contribute to the loss and degradation of habitats. Meanwhile, climate change, through ocean warming, acidification, sea level rise and the expansion of oxygen minimum zones, continues to alter habitat conditions and shift species distributions (Doney et al. 2012; Poloczanska et al. 2016). These pressures frequently act in combination, exacerbating the vulnerability of ecologically sensitive habitats. It makes the identification of areas of heightened sensitivity and exposure to stressors fundamental. Spatially explicit assessments and cumulative impact mapping have proven essential tools in this regard, as they can help to define those marine regions where biodiversity and habitats are most at risk (Halpern et al. 2008, Micheli et al. 2013, Piet et al. 2019). This knowledge underpins the need for monitoring strategies that track ecosystem changes over time, and informs the designation of priority areas for protection and conservation. In fact, Marine Protected Areas (MPAs) and other spatial management measures are most effective when they are based on robust ecological data and targeted to those locations where conservation efforts may deliver the greatest benefits in building resilience to ongoing and future pressures (Sala et al. 2021).

Here we developed a systematic framework to assess the sensitivity of marine benthic habitats, along with their associated biological values, to both climate change and fishing pressure. This approach explicitly evaluates sensitivity at the biotope level, incorporating species, community, and habitat-scale responses to each driver of change. Although global-scale cumulative impact model by Halpern et al. (2007) provides broad spatial assessments across major marine ecosystems but does not resolve sensitivity at the biotope scale. In addition, this previous ranking did not explicitly evaluate how stressors affect the biodiversity features and only considered the presence of impacts at different levels of organisation, i.e. whether any functional impact occurs at single or multiple species levels, at single or multiple trophic levels, or at the community level (Halpern et al. 2007). Neither had the distribution of habitats (extension, rarity, fragmentation) or their functional properties been taken into account.

The new framework builds on Stratoudakis et al. (2019), who proposed a new approach for creating representative networks of Marine Protected Areas (MPAs) to aid conservation planning. Their approach prioritised habitats' conservation based on their ecological value. The present work aims to improve that previous assessment by evaluating the expected effects of two major threats to marine environment, fishing and climate change, on habitat structure and functioning. This is achieved by using multiple criteria that represent both biodiversity and habitat changes, with scores assigned through comparisons of habitats for each of the two pressures individually.

In the present framework, 'sensitivity' was defined as the degree to which marine features respond to stressors, which in turn are considered as deviations of environmental conditions beyond the expected range (Zacharias & Gregr 2005). The proposed framework includes the stressors with the greatest potential impact related to climate change and fishing pressures (Halpern et al. 2007, Butt et al. 2022). For climate change, the key stressors considered were rising water temperature, increasing ocean acidity and decreasing dissolved oxygen concentration. For fishing pressure, the key stressors considered were the impacts from bottom-contact fishing gears such as trawls, nets, longlines, traps and dredges. These various stressors are likely to induce different changes on habitats and associated biodiversity.

For the different habitats being assessed, we defined sensitivity scores to each of the above stressors as a function of the vulnerability of the different communities they support, as well as the potential for loss or degradation of the habitat itself (i.e., extension, structural complexity and functional properties). The sensitivity of the communities was defined based on the sensitivity and adaptive capacity of the species that typically characterise the community, in turn based on their species' main life-history traits (Butt et al. 2022). This framework for assessing the sensitivity of habitats based on the sensitivity of the communities they support, and based on habitat features (structural complexity, functioning, extension and distribution), is a first critical step towards integrated biodiversity risk assessments, rather than focused on habitats or species alone. One of the improvements of this framework is that it allows a clearer understanding of the expected changes in habitats and biodiversity they support and of how the different stressors associated to fishing and climate change act differentially across habitats, by ranking them in a comparative way.

In this context, the specific objectives of this chapter were twofold:

(1) Prioritise habitat sensitivities by ranking habitats based on their sensitivity levels in order to identify critical habitats and the main stressors of concern; and

(2) Inform management and conservation, by developing prioritised action items and recommendations to improve habitats' resilience and recovery.

The resulting habitat sensitivity rankings will enable further assessments of habitat vulnerability to each stressor by combining the degree of exposure to the stressor into a comprehensive index (e.g., vulnerability indices for risk mapping), or by combining all stressors together providing an overall vulnerability of each habitat (e.g., cumulative risk maps). As the sensitivity values are independent of the exposure to a stressor, the impacts can then be predicted when the severity or duration of exposure increases/decreases, thereby guiding and prioritising targeted conservation and management actions. For instance, in habitats where sensitivity is highest, minimising or reducing the stressor exposure will lead to more effective conservation outcomes for biodiversity, compared with habitats with lower sensitivity at the same exposure.

8.2 Methods

8.2.1 Framework description

The framework was focused on continental shelf habitats known to occur across different European ecoregions. Habitats were defined based on biotopes, i.e. distinct areas characterised by a unique combination of physical and biological features that create habitats for specific species (see *Table 8-1* for an overview of the habitats considered). These biotopes were delineated based on factors such as substrate type, light availability, structural complexity, and depth, as well as the typical communities they support, in accordance with definitions previously used as the basis to rank the ecological value in a similar approach (Stratoudakis et al. 2019).

Table 8-1. Benthic habitats considered in this sensitivity assessment. See Appendix for detailed information on the typical communities they support and on correspondence with other habitat classifications (EUNIS 2022, MSFD 2017, IUCN 2020, Nature Restoration Law).

Benthic biotopes (RNAMP)	**Definition**
Abyssal plains	The largest group of benthic marine ecosystems, located 3,000–6,000 m deep and covered by thick layers of fine sediment. These areas are food-limited with low biomass but high diversity, mainly composed of meio- and macrofauna. Energy sources derive primarily from fallout of organic particles through the water column.
Aggregations that change physiography in soft sediment	This biotope occurs on cobbles and pebbles on sandy sea bed possibly associated with shallow iceberg ploughmarks, characterised by Axinellid and massive lobose sponges, cup sponges and bryozoan *Reteporella* attached to the cobbles, with squat lobsters sheltering under the cobbles. It is similar to a deeper expression of the shallower biotope “deep sponge communities (circalittoral)".
Biogenic reefs (<200 m)	These are structures formed by living organisms such as corals, molluscs, or polychaetes. Biogenic reefs are crucial for engineering local habitats, providing shelter and substrate for a range of demersal biota in shallower, dynamic waters.
Biogenic reefs (>200 m)	Formed by similar processes as their shallower counterparts, these reefs exist in deeper waters where they provide habitats for specialized communities. They are characterized by slow growth rates and dependency on stable environmental conditions.
Canyons	Submarine canyons serve as geomorphic conduits for resources between continental shelves and ocean basins. These biodiverse habitats feature heterotrophic faunal assemblages influenced by complex hydro-dynamic processes. Canyons are important refuges, nurseries, and spawning areas for various species.
Inner shelf rocky reefs (<50 m)	Rocky reefs found on shallow waters; these reefs are influenced by light availability and wave energy. They host diverse assemblages of macroalgae, sessile invertebrates, and fish, providing critical habitats.
Inner shelf soft sediment (<50 m)	Soft sediments located on the inner shelf, influenced by tidal and wave energy, supporting burrowing fauna and detritivores. These habitats play a significant role in biogeochemical processes and carbon cycling.
Intertidal rocky reefs	Rocky areas exposed during low tide, hosting diverse communities of algae, invertebrates, and fish, adapted to fluctuating environmental conditions.

Intertidal soft sediment (including gravel and cobbles)	Areas with soft sediments, gravel, and cobbles exposed during low tide, supporting burrowing and epifaunal communities.
Macroalgae forests	Forests of macroalgae (e.g., kelp), which provide structural complexity and high primary productivity, supporting diverse marine life.
Maërl	Accumulations of coralline algae that form hard, complex habitats supporting high biodiversity of small invertebrates.
Rocky reefs (50–200 m)	Circalittoral rock in the Atlantic. Mid-depth subtidal habitats characterized by rocky substrates, providing important structural complexity. These reefs support diverse communities of sessile invertebrates and fish, influenced by factors such as light availability and hydrodynamic conditions. Their ecological significance lies in offering shelter, feeding grounds, and breeding habitats within the marine ecosystem
Seagrasses	Beds of marine angiosperms in shallow and sheltered marine environments, providing critical habitats for numerous species and contributing to carbon sequestration.
Seamounts (summit <200 m)	Submarine mountains with summits shallower than 200 m, these areas often host diverse benthic and pelagic communities. They act as biodiversity hotspots and critical stepping stones for species migration
Seamounts (summit 200–1000 m)	These intermediate-depth seamounts provide unique habitats influenced by hydrodynamic conditions, supporting communities adapted to reduced light availability and nutrient influx.
Seamounts (summit >1000 m)	Deep-sea seamounts with summits exceeding 1000 m depth are less biologically productive due to limited energy inputs but are essential for deep-sea organisms adapted to these extreme conditions.
Slope and ramp rocky reefs	Rocky substrates located on continental slopes and ramps, influenced by depth and hydrodynamic forces.
Slope and ramp soft sediment	Sedimentary environments on continental slopes and ramps, supporting burrowing and detritivorous communities.
Soft sediment (50–200 m)	Sedimentary habitats in mid-shelf depths, hosting burrowing organisms and supporting biogeochemical processes.

As stated above, the following three stressors related to climate change were tested: rising water temperature, increasing ocean acidity, and decreasing dissolved oxygen. On the other hand, fishing effects were analysed for each of five main gears impacting the seafloor: trawls, set nets (gill and trammel), bottom longlines, traps, and dredges. To assess the main relevant effects of each stressor, nine criteria organised at the species, community and habitat levels were defined (*Table E-1* in Appendix E). These criteria reflect the primary anticipated changes in habitats, including their extent and distribution, structural complexity, and functional properties. They also address the effects on associated biodiversity, both taxonomic and functional, and on specific species or taxonomic groups that are particularly sensitive to change or that could influence trophic networks or the resilience of the communities. The rationale and importance of each criterion are provided in *Table E-1*. The assessment focused exclusively on native species, excluding potential invasive species, and habitat-forming species were only considered on the criteria directly related with habitat level.

8.2.2 Scoring procedure

For each stressor, the different ecological habitats were ranked using a comparative scoring approach which assessed the main relevant effects that determine the degree of change in biodiversity. The scores were assigned by experts with knowledge of the ecological functioning and characteristic communities of the different habitats or of specific stressors, during a series of dedicated workshops. The experts group consisted of 10 regional specialists in ecology, biology or fisheries, each with expertise in particular species groups (e.g., phytoplankton, zooplankton, macroalgae, sponges, corals, other benthic invertebrates, fish, sensitive species, and species of high conservation concern). The combined expertise of the group covered all habitat types being evaluated. Scoring was done by experts on one ecoregion (Iberian coast). The experts also had wide expertise in other areas, in combination covering all European ecoregions.

The evaluation of each criterion was conducted by stressor, assigning a score to each habitat on a scale from 0 to 4 (0 – absence, 1 – marginal/very low, 2 – medium, 3 – high, 4 – very high sensitivity, NA – not applicable, UK – unknown). The scoring procedure was based on the comparison of expected effects across different habitats within the same stressor and does not imply comparison between stressors. The score was discussed and agreed among all participating experts. At the end of each round, confidence scores were attributed by all participants to each stressor using an indicator with scale varying from 1 (low confidence) to 3 (high confidence).

8.2.3 Data analysis

Sensitivity scores for each habitat under each stressor were estimated by considering all assessed criteria, excluding those marked as NA (not applicable) or UK (unknown). Two different overall sensitivity index estimations were considered to provide complementary perspectives, after testing different options, i.e. precautionary vs. balanced approaches to sensitivity assessment. Both were based on weighted means where habitat, community, and species criteria were assigned weights of 0.5, 0.3, and 0.2, respectively (shaded yellow, blue and green in Table 2, respectively). These weights were agreed upon by the expert group, which considered that sensitivity to a stressor should be amplified if high negative effects occur at the habitat level, since the habitat supports the entire associated biodiversity (both community and species levels). Following the same rationale, a slightly higher weight was given to community-level attributes compared to species-level attributes.

The balanced approach used a straightforward arithmetic weighted mean of the criteria scores; this provides a mean sensitivity score that reflects the proportional influence of each criterion. The precautionary approach used an adjusted exponential weighted mean (using a base-2 exponential transformation); this amplifies higher sensitivity scores disproportionately with greater emphasis on criteria with elevated scores, allowing the identification of those habitats where higher changes are expected, even if only in some criteria.

To easily compare the most and least sensitive habitats as well as differences when comparing both index estimations, sensitivity scores were converted into a ranking score for each stressor. The mean of the confidence scores was also used to assess the confidence in these sensitivity rankings, helping to identify which results are more robust, and which ones may require more cautious interpretation due to higher uncertainty.

8.3 Results and discussion

8.3.1 Sensitivity of benthic habitats to climate change stressors

The sensitivity assessment indicated that climate change stressors impact most marine benthic habitats regardless of depth. A consistent trend revealed that structurally complex habitats of biological origin tend to have high sensitivity across the assessed stressors; such habitats include biogenic reefs, maërl beds, aggregations that change physiography in soft sediments, macroalgae forests, and seagrass meadows. Likewise, habitats with high physical structural complexity (e.g., rocky reefs and seamounts) are highly sensitive (*Table 8-2*). Such complex habitats often rely on sessile or low-mobile species (e.g., gorgonians, corals, sponges, sea anemones and other small invertebrates), some of these adapted to narrow depth ranges. These functional features make them particularly vulnerable to changes in temperature and pH, as they limit the species' ability to escape or adapt to changing environmental conditions since they are strongly associated with the (distribution of the) habitats (Hutchings et al. 2007, Turley et al. 2007, Butt et al. 2022). In contrast, generally lower in sensitivity are soft-sediment habitats, particularly those in intertidal zones and deeper shelf and slope areas (*Table 8-2*). An exception is the abyssal plain habitat, here assessed as highly sensitive to reducing oxygen levels (Table 3). Although soft-sediment habitats support important taxonomic diversity, they are generally less functionally diverse than hard-bottom habitats. Soft-bottom macroinvertebrate communities, which often include species with varying tolerance to environmental stressors, can be categorised into ecological groups along a gradient of sensitivity, from highly sensitive to opportunistic and tolerant species (Borja et al. 2000).

Table 8-2. Final scores for sensitivity indices to climate change stressors for 21 benthic habitats, and the corresponding ranks. Both the balanced approach (weighted mean index) and precautionary approach (adjusted exponential weighted mean index) are presented.

Stressor	Benthic habitats	Sensitivity index		Rank	
		Balanced approach	Precautionary approach	Balanced approach	Precautionary approach
Rising water temperature	Intertidal rocky reefs	1.6	1.9	13	15
	Intertidal soft sediment (including gravel and cobbles)	0.9	1.0	20	20
	Inner shelf rocky reefs (<50 m)	2.1	2.8	8	9
	Inner shelf soft sediment (<50 m)	1.1	1.2	17	17
	Macroalgae forests	3.3	5.4	1	1
	Maërl	2.2	2.7	6	10
	Seagrasses	1.8	1.9	10	14
	Rocky reefs (50-200 m)	1.7	2.5	11	11
	Soft sediment (50-200 m)	0.9	1.1	19	19
	Aggregations that change physiography in soft sediment	2.7	4.0	3	4
	Biogenic reefs (<200 m)	2.7	3.6	5	6
	Biogenic reefs (>200 m)	2.8	4.2	2	3
	Seamounts (summit <200 m)	2.2	3.1	6	8
	Seamounts (summit >1000 m)	1.8	3.3	9	7
	Seamounts (summit 200-1000 m)	1.6	2.5	12	12
	Slope and ramp rocky reefs	1.3	1.8	16	16
	Slope and ramp soft sediment	1.0	1.2	18	17
	Mud volcanoes and cold seeps	2.7	4.4	3	2
	Hydrothermal vents	NA	NA	NA	NA
	Canyons	1.6	2.2	14	13
	Abyssal plains	1.4	3.7	15	5
Increasing ocean acidity (pH)	Intertidal rocky reefs	2.5	4.3	5	4
	Intertidal soft sediment (including gravel and cobbles)	1.9	3.0	13	12
	Inner shelf rocky reefs (<50 m)	2.5	3.9	5	5
	Inner shelf soft sediment (<50 m)	1.8	2.8	14	14
	Macroalgae forests	1.6	1.9	15	16
	Maërl	3.1	4.9	3	3
	Seagrasses	1.4	1.5	18	20
	Rocky reefs (50-200 m)	2.5	3.9	5	5
	Soft sediment (50-200 m)	1.5	1.8	17	17
	Aggregations that change physiography in soft sediment	2.7	3.8	4	7
	Biogenic reefs (<200 m)	3.2	5.3	2	2
	Biogenic reefs (>200 m)	3.3	5.8	1	1
	Seamounts (summit <200 m)	2.4	3.7	8	8
	Seamounts (summit >1000 m)	2.4	3.5	8	9
	Seamounts (summit 200-1000 m)	2.2	3.3	10	10
	Slope and ramp rocky reefs	2.2	3.3	10	10
	Slope and ramp soft sediment	1.6	2.0	16	15
	Mud volcanoes and cold seeps	1.0	1.6	19	18
	Hydrothermal vents	1.0	1.6	19	18
	Canyons	2.2	2.9	12	13
	Abyssal plains	0.8	1.5	21	21
Decreasing dissolved oxygen concentration	Intertidal rocky reefs	0.2	0.6	21	21
	Intertidal soft sediment (including gravel and cobbles)	0.8	0.9	16	16
	Inner shelf rocky reefs (<50 m)	1.1	1.2	13	13
	Inner shelf soft sediment (<50 m)	1.2	1.3	12	12
	Macroalgae forests	0.7	0.9	17	17
	Maërl	0.7	0.9	17	17
	Seagrasses	0.9	1.1	15	15
	Rocky reefs (50-200 m)	1.5	1.8	9	9
	Soft sediment (50-200 m)	1.0	1.1	14	14
	Aggregations that change physiography in soft sediment	1.3	1.4	11	11
	Biogenic reefs (<200 m)	1.7	2.2	3	3
	Biogenic reefs (>200 m)	2.0	3.6	2	2
	Seamounts (summit <200 m)	1.4	1.5	10	10
	Seamounts (summit >1000 m)	1.6	2.0	7	7
	Seamounts (summit 200-1000 m)	1.7	2.2	3	3
	Slope and ramp rocky reefs	1.7	2.2	3	3
	Slope and ramp soft sediment	1.5	1.8	8	8
	Mud volcanoes and cold seeps	0.6	0.8	19	19
	Hydrothermal vents (active)	0.6	0.8	19	19
	Canyons	1.7	2.2	3	3
	Abyssal plains	3.0	3.8	1	1

Among the three climate change stressors considered here, one – reduced dissolved oxygen concentration – tended to be associated with lower sensitivity scores; the other two – rising water temperature and ocean acidification – were consistently linked with higher sensitivity (i.e. a higher number of criteria scored as 3 and 4). This was particularly the case for habitats dominated by calcifying organisms, such as corals, calcareous macroalgae, bivalves, crustaceans, gastropods and echinoderms; and for habitats under stable environmental conditions, therefore composed by species typically less tolerant to physiological stress.

Increasing water temperature (*Table 8-2*, upper section) can significantly influence species distributions, driving range shifts as organisms migrate to deeper waters or higher latitudes where cooler conditions prevail (e.g., Le Luherne et al. 2024). Habitat generalists and species with high dispersal ability and/or wide depth ranges are likely to be better adapted to climate variability than specialists, low-mobility or sessile species, due to their ability to disperse and occupy a greater variety of habitats and environmental conditions (Pinsky et al. 2020). The habitats emerging as most sensitive to warming included macroalgae forests (ranked highest, i.e. 1 in both sensitivity indices), followed by biogenic reefs (both at depths <200 m and >200 m), and mud volcanoes and cold seeps (ranks 2-3 for both sensitivity indices; Table 3). The criteria scores for all these habitats were higher at both the species and community levels. A score of 4 at the habitat level was attributed only to macroalgal forests and biological aggregations such as corals and macroalgae that alter the physiography of soft sediments, since they are highly sensitive to temperature changes (Spalding & Brown 2015, Wernberg et al. 2024). As a result, their extent is likely to decline significantly in the medium to long term. On the other hand, the high sensitivity assessed for mud volcanoes and cold seeps, as well as deep water biogenic reefs (< 200m), was mainly due to the expected loss of both taxonomic and functional biodiversity, rather than habitat changes (criteria scored as 4), related with changes in environmental stability. Given the typical depth of occurrence, these habitats tend to be at more stable environmental conditions and are therefore composed of species with narrow environmental tolerances (e.g., Yasuhara & Danovaro 2016). The particular features of biogenic reefs make them particularly sensitive to temperature change, as even modest warming may have strong effects on the biodiversity they support. Similarly, mud volcanoes and cold seeps, although less diverse than shallower habitats, host species highly dependent on methane fluxes, which are sensitive to temperature variations (Åström et al. 2020), leading to high overall sensitivity despite relatively low taxonomic and functional diversity.

Ocean acidification (*Table 8-2*, middle section), driven by carbon dioxide emissions, implies a decrease in ocean pH and reduces the availability of calcium carbonate to build and maintain organisms' shells and skeletons. Therefore, a decrease is expected in habitats suitable for calcifying species (some of which are habitat-forming), leading to biodiversity loss, population declines and distribution shifts (Hendriks et al. 2010, Hoegh-Guldberg et al. 2017). Indeed, habitats assessed as most sensitive to ocean acidification were those dominated by calcifying species, particularly biogenic reefs (in shallow and deeper locations: ranking 1st and 2nd in terms of sensitivity, respectively). Biogenic reefs had high climate sensitivity scores across the three criteria levels (species, community, and habitat). Next-most sensitive were maërl beds (rank 3), reflecting the structural sensitivity of these systems dominated by calcareous algae.

Ranking 4th and 5th were the habitats formed by aggregations that change physiography in soft sediment, and the various rocky reef habitats (including intertidal and inner shelf rocky reef). All these habitats support high biodiversity of calcifying species, particularly corals, calcareous algae, bivalves, crustaceans and echinoderms (e.g. Knowlton et al. 2010, Chin et al. 2020). Most of these species are sessile or low-mobile, and some show inherently low resilience to environmental change due to their life-cycle features, with functional traits making them particularly vulnerable to ocean acidification (Butt et al. 2022).

Likewise, seamounts and slope rocky reefs also show moderate to high sensitivity as they support many calcifying species, although typically fewer than shallower (<200 m) rocky reefs. Seagrass meadows, macroalgae forests, and soft sediment habitats display low to moderate sensitivity to ocean acidification (ranks 15-17), as their calcifying species are mainly limited to bivalves, crustaceans and gastropods (Pan & Pratolongo 2022).

Habitats assessed as least sensitive to ocean acidification include abyssal plains, mud volcanoes and hydrothermal vents (ranks 18-21); these are typically deep-sea environments with species (mostly arthropods, molluscs and annelids) generally adapted to naturally more acidic (low pH) conditions (e.g., Gollner et al. 2010, Mullineaux 2014). However, for hydrothermal vents species adapted to fluctuating low pH levels, it remains unclear how adults or larvae may respond to any sustained environmental shift such as long-term ocean acidification. Hydrothermal vent species may be particularly sensitive as they often exhibit larval retention and gregarious settlement. PH variations may therefore impair their ability to detect sites suitable for settlement (e.g., Metaxas 2011), a topic requiring further investigation. Additionally, acidification may lead to significant reductions in carbon fluxes in oligotrophic areas, potentially triggering effects cascading through the food web and altering the energy flow for top predators such as fish, seabirds and marine mammals, shifting towards a more detritus-based system (e.g., Ullah et al. 2018). Such potential cascading effects of ocean acidification should also be further evaluated to improve the classification of the "disproportionate changes in specific trophic levels" criterion in such areas.

For the third climate-related stressor – reduced dissolved oxygen concentration (*Table 8-2*, lower section) – the habitats assessed as most sensitive are in deep-sea and canyon environments. Abyssal plains showed the highest low-oxygen sensitivity (rank 1) followed by biogenic reefs, slope and ramp rocky reefs, seamounts at 200–1000 m depth, and canyon habitats (ranks 2-3). These habitats are normally very stable and consequently have species less adapted to cope with environmental fluctuations. This limited adaptive capacity, combined with the already very low oxygen levels of these deep environments, makes these communities particularly vulnerable to further deoxygenation (Levin 2002, Levin & Le Bris 2015). Declining oxygen levels are often associated with water column stratification, reduced ventilation and increased nutrient loading (e.g., Oschlies 2019). Such changes disrupt the balance between oxygen supply and biological demand, and so may lead to widespread physiological stress, habitat degradation, shifts in food web structure, and in severe cases mass mortality events (Breitburg et al. 2018). Vulnerability of these habitats is especially critical given that many resident species are sessile or of low mobility, restricting their ability to relocate in response to local oxygen depletion (e.g., Ross et al. 2020). Deep and poorly ventilated habitats are of particular concern, as limited circulation reduces resilience and increases the likelihood of prolonged hypoxic conditions (Levin 2003, Diaz & Rosenberg 2008). In contrast, the habitats least sensitive to this stressor included intertidal rocky reefs, macroalgae forests and maërl beds, and within the deep sea, non-oxygen dependent habitats such as mud volcanoes and hydrothermal vents (ranks 17-21). Many of these habitats benefit from oxygen-rich surface waters, photosynthesis processes or chemosynthetic adaptations. Finally, soft-sediment habitats were ranked with moderate to low sensitivity: the physiology and behaviour of most species occurring here (even in the slopes and ramps) make them more adapted to oscillating oxygen levels, although there are some sessile or low-mobility species that are more vulnerable to these oscillations (e.g., Levin 2002).

Overall, no significant reductions in habitat extent are expected under the deoxygenation stressor, and only minimal degradation of habitat structural complexity is anticipated, for instance it may slightly impact the vertical complexity of habitats created by some habitat-forming species such as corals (but not expected for sponges). Therefore, monitoring efforts should focus on species and community-level impacts rather than on habitat extent or physical integrity, regardless of depth. This also applies to the assessment of temperature and acidity impacts on habitat extent, except for macroalgae forests, maërl beds, biogenic reefs, aggregations that change physiography in soft sediments, and mud volcanoes and cold seeps habitats, where monitoring changes in extent and fragmentation is particularly important under ongoing climate change.

The group of experts generally assigned higher confidence to the assessment of rising water temperature impacts (mean confidence score and standard deviation 2.1 ± 0.66, out of a range of 1–3; *Table 8-3*) than to the other two climate stressors. Increasing ocean acidification was associated with a more moderate confidence score (mean 1.74 ± 0.65). Both these climate change stressors showed slightly lower confidence levels in criteria related to functional and trophic changes (*Table 8-3*). Decreasing dissolved oxygen concentration was associated with the lowest confidence score (1.33 ± 0.53) across most criteria, except for habitat extension, indicating that further research is needed to better predict potential impacts of deoxygenation, particularly at the species and community levels (*Table 8-3*).

Table 8-3. Mean confidence values (±SD) by criterion and stressor, as assessed by 11 regional experts experienced in benthic habitat assessments

Pressure	**Stressor**	**Overall by stressor**	**Overall by pressure**
Climate change	Rising water temperature	2.1 ± 0.66	1.67 ± 0.69
	Increasing ocean acidity (pH)	1.74 ± 0.65	
	Decreasing dissolved oxygen	1.33 ± 0.53	
Fishing	Trawl (up to 800m depth)	2.56 ± 0.63	2.25 ± 0.70
	Set nets	2.04 ± 0.57	
	Bottom Longlines	2.39 ± 0.62	
	Traps	1.77 ± 0.71	
	Dredges	2.54 ± 0.66	

8.3.2 Sensitivity of benthic habitats to fishing-related stressors

The sensitivity assessment revealed that fishing-related stressors (*Table 8-4*) – where five gear types were assessed separately – have differing levels of impact on habitats. These more selective effects on different habitats contrast with the broad-scale effects of climate change stressors, which were revealed here to influence almost all habitat types (*Table 8-2* and *Table 8-4*). However, it is important to note that although in general each fishing stressor affects fewer habitats than climate change stressors, the physical disturbance caused by bottom-contact gears was identified as the main driver of widespread degradation in benthic habitats across OSPAR regions (OSPAR QSR 2010).

Across all five fishing-related stressors, certain benthic habitats consistently emerged as the most sensitive. This applied particularly to those with high structural complexity and composed by habitat-forming species with ecological fragility, namely biogenic reefs (both < and >200 m), and to habitats with biological aggregations that alter physiography in soft-sediments (ranks 1-2). Seamounts with summits shallower than 200 m, as well as slope and ramp rocky reefs, also tend to exhibit moderate to high sensitivity depending on the gear type. These habitats rank among the top-5 most sensitive to bottom trawls, longlines, traps, and (except for slope and ramp rocky reef habitat) to set nets. These findings are in line with expectations, as the main impacts of fishing are, on top of the removal of organisms, associated with direct physical damage to habitats, particularly for gears with a high degree of contact with the seafloor, which will especially affect sessile and benthic organisms (Thrush & Dayton 2002, Benn et al. 2010, OSPAR QSR 2010, Fabri et al. 2019). These organisms are important components of each of the habitats assessed here as ranking highest in fishing-related sensitivity (Thrush & Dayton 2002, Benn et al. 2010, OSPAR QSR 2010, Fabri et al. 2019). Furthermore, such impacts are especially problematic for habitat-forming species with low recovery capacity (e.g. coral and sponge communities), leading to long-lasting impacts on community structure, species composition, and habitat complexity (Collie et al. 2000, Kaiser et al. 2006, OSPAR QSR 2010, Fabri et al. 2019). In contrast, soft-sediment habitats on the slope and ramp as well as shelf areas, particularly those lacking complex biogenic structures, were assessed as having lower sensitivity to fishing stressors, with exception of bottom trawl and dredging (*Table 8-4*).

Although the scoring approach was not designed to compare intensity of impacts across different stressors (since the evaluations were carried out independently for each set of habitats-stressor), the number of attributes assigned the maximum score (4) can still be indicative to compare between stressors. A high frequency of maximum scores suggests that most criteria across the assessed levels (species, communities, and habitats) are severely affected by the stressor; this was the case for bottom trawling and dredging fisheries, despite their occurrence in a lower overall number of habitats (*Table 8-4*). In accordance, bottom trawling (targeting demersal fish and demersal and epibenthic invertebrates) and dredging (targeting benthic invertebrates) are characterised by low selectivity with low bycatch survival and high physical damage to habitats (OSPAR QSR 2010). This often results in community homogenisation, characterised by an increase in the dominance of benthic scavengers and a few opportunistic/tolerant fish species (e.g. Tillin et al. 2006, Juan et al. 2007, Kaiser & Hiddink 2007, Dimech et al. 2012, Henriques et al. 2014).

Table 8-4. Final scores for sensitivity indices to fishing-related stressors for 21 benthic habitats, and the corresponding ranks. Both the balanced approach (weighted mean index) and precautionary approach (adjusted exponential weighted mean index) are presented.

Stressor	Benthic habitats	Sensitivity index		Rank	
		Balanced approach	Precautionary approach	Balanced approach	Precautionary approach
Bottom trawl	Inner shelf soft sediment (<50 m)	2.6	4.4	9	9
	Soft sediment (50-200 m)	2.7	4.8	4	4
	Aggregations that change physiography in soft sediment	3.4	6.3	1	1
	Biogenic reefs (<200 m)	3.1	5.3	2	2
	Biogenic reefs (>200 m)	3.1	5.3	2	2
	Seamounts (summit <200 m)	2.6	4.7	5	5
	Seamounts (summit 200-1000 m)	2.6	4.7	5	5
	Slope and ramp rocky reefs	2.6	4.7	5	5
	Slope and ramp soft sediment	2.6	4.7	5	5
Set nets	Intertidal soft sediment (including gravel and cobbles)	1.1	1.4	14	14
	Inner shelf rocky reefs (<50 m)	2.2	3.6	7	7
	Inner shelf soft sediment (<50 m)	1.4	2.3	12	11
	Macroalgae forests	2.2	3.3	6	9
	Maërl	1.0	1.2	15	15
	Seagrasses	1.8	2.1	10	13
	Rocky reefs (50-200 m)	2.2	3.6	7	7
	Soft sediment (50-200 m)	1.4	2.3	12	11
	Aggregations that change physiography in soft sediment	2.9	4.8	2	2
	Biogenic reefs (<200 m)	2.9	4.8	2	2
	Biogenic reefs (>200 m)	2.9	5.1	1	1
	Seamounts (summit <200 m)	2.4	4.2	4	4
	Slope and ramp rocky reefs	2.1	3.7	9	6
	Slope and ramp soft sediment	1.5	2.6	11	10
	Canyons	2.3	4.0	5	5
Bottom longlines	Inner shelf rocky reefs (<50 m)	1.8	2.2	9	10
	Inner shelf soft sediment (<50 m)	1.0	1.2	13	12
	Macroalgae forests	1.1	1.2	12	12
	Maërl	0.6	0.8	16	17
	Seagrasses	0.9	1.1	15	15
	Rocky reefs (50-200 m)	1.8	2.2	9	10
	Soft sediment (50-200 m)	1.0	1.2	13	12
	Aggregations that change physiography in soft sediment	2.7	4.3	1	1
	Biogenic reefs (<200 m)	2.3	2.8	2	6
	Biogenic reefs (>200 m)	2.3	2.8	2	6
	Seamounts (summit <200 m)	2.1	3.1	4	4
	Seamounts (summit >1000 m)	1.8	2.6	8	8
	Seamounts (summit 200-1000 m)	2.0	3.2	5	2
	Slope and ramp rocky reefs	2.0	3.2	5	2
	Slope and ramp soft sediment	1.5	2.3	11	9
	Mud volcanoes and cold seeps	0.6	0.9	16	16
	Hydrothermal vents	0.4	0.7	18	18
	Canyons	1.8	2.8	7	5
Traps	Inner shelf rocky reefs (<50 m)	1.6	1.9	2	2
	Inner shelf soft sediment (<50 m)	1.3	1.5	10	11
	Macroalgae forests	1.5	1.6	7	9
	Maërl	0.8	1.1	15	15
	Seagrasses	1.5	1.6	7	9
	Rocky reefs (50-200 m)	1.6	1.9	2	2
	Soft sediment (50-200 m)	1.2	1.3	12	12
	Aggregations that change physiography in soft sediment	2.0	2.7	1	1
	Biogenic reefs (<200 m)	1.6	1.8	2	5
	Biogenic reefs (>200 m)	1.6	1.8	2	5
	Seamounts (summit <200 m)	1.6	1.9	2	2
	Seamounts (summit 200-1000 m)	1.5	1.7	9	7
	Slope and ramp rocky reefs	1.2	1.3	12	12
	Slope and ramp soft sediment	1.2	1.3	12	12
	Canyons	1.3	1.7	10	8
Dredges	Intertidal soft sediment (including gravel and cobbles)	2.2	3.2	4	4
	Inner shelf soft sediment (<50 m)	2.4	4.0	3	3
	Seagrasses	3.5	6.7	1	1
	Aggregations that change physiography in soft sediment	3.3	5.9	2	2

On the other hand, longlines, traps, and set nets are characterised by higher selectivity (*Table 8-4*). The physical damage that these cause to habitats depends largely on habitat structure (i.e. structural complexity and sensitivity to physical disturbance); the degree of gear contact with the seafloor (from high to low: set nets, traps, and longlines); and the extent of the area affected (OSPAR QSR 2010, Fabri et al. 2019). The impacts of set nets (e.g. gillnets and trammel nets) are also highly influenced by mesh size, area, and depth of operation. These gears primarily catch demersal and benthic fish (including elasmobranchs), cephalopods and large crustaceans (OSPAR QSR 2010). Set nets mainly affect soft-bottom habitats and the biological aggregations that alter the physiography of soft sediments (e.g. sponge and coral gardens), but they can also impact seagrass beds, biogenic reefs, and macroalgae forests or sessile organisms on hard-bottom reefs, particularly in coastal areas (OSPAR QSR 2010).

Traps are mainly used to target cephalopods (octopus), crustaceans (e.g. lobsters and crabs), and some fish species. They can be deployed in a variety of habitats, including both soft and hard substrates. While traps generally have a low impact on the seafloor, they can still cause localised abrasion or crushing of benthic and predominantly epibenthic organisms when hauled or dragged (OSPAR QSR 2010). Overall, these patterns explain the high sensitivity of rocky reef habitats down to 200 m depth to the impact of traps, as well as fairly high sensitivity of seamounts (summit <200 m) and canyons to the impact of set nets; although at lower densities than in biological aggregations and biogenic reefs, these habitats usually support corals and sponges, and their damage will significantly reduce vertical complexity (OSPAR QSR 2010, Dias et al. 2020). Longlines, which typically target large predatory bony fish and sometimes pelagic sharks, tend to have a lower impact on the seafloor, but can still result in bycatch and unintentional mortality of non-target sensitive species, including sharks, seabirds and turtles, as well as sensitive habitat-forming species such as corals, sponges and gorgonians (OSPAR QSR 2010).

Among the remaining habitats, photosynthetically active habitats such as macroalgae forests and maërl beds generally show lower sensitivity to set nets, bottom longlines and traps (while trawls and dredges do not target these habitats) (Table 5). In contrast, seagrass beds can be affected notably by dredges, which directly uproot seagrass shoots and rhizomes, leading to immediate loss of plant cover and structure as well as a delay in natural recovery due to break-down of the rhizomes network (which supports regrowth) (OSPAR QSR 2010). Hydrothermal vents and mud volcanoes typically show low sensitivity scores for bottom longlines, the only fishing stressor that may occur (to a low extent) in these remote and deep habitats (Table 5).

Confidence of the expert's group in the assessments was overall higher for fishing-related stressors (2.25 ± 0.70), than for climate change stressors (1.67 ± 0.69; see *Table 8-3*). Mean confidence scores were highest for trawls and dredges (2.56 ± 0.63 and 2.54 ± 0.66, respectively), with high confidence across most criteria, especially in those related to habitat and community levels (*Table 8-3*). Bottom longlines also scored relatively high (2.39 ± 0.62), while traps effects were associated with lower confidence (1.77 ± 0.71), particularly for criteria involving the assessment of effects at species and community levels, suggesting that further research is needed about the impacts of traps on habitats.

8.3.3 Balanced vs precautionary approaches to sensitivity assessment

The comparison between the balanced and precautionary sensitivity index values under climate change and fishing stressors revealed a very stable ranking pattern, with most habitats maintaining nearly the same positions for each stressor (*Table 8-2* and *Table 8-4*). Exceptions, where the ranking of habitats differed markedly, were mainly associated with consistently high scores attributed for the same habitat across multiple criteria. For example, under the rising water temperature stressor, abyssal plains ranked 15th and 5th among habitats under the balanced and precautionary approach respectively, which was primarily due to high sensitivity scores at community and species levels (several scores of 4), given the absence of expected changes at the habitat level (scores of 0). For the same reasons, slope and ramp rocky reefs (for set nets and longlines), as well as canyons, abyssal plains, and deep seamounts (for longlines), changed their sensitivity ranks under the precautionary approach (see Tables 3 and 5 for details). Conversely, the ranks of maërl beds and seagrass meadows slightly lowered under the precautionary approach for climate change stressors. A similar pattern is observed for biogenic reefs, macroalgae forests, and seagrasses under bottom longline and trap stressors (Tables 3 and 5). These habitats generally received low to moderate sensitivity scores across most criteria and lacked high scores (4), which explains their downward shift in ranking under the precautionary approach. Overall, these results highlight increased concern for deep-water habitats if a precautionary approach is to be adopted.

8.4 Synthesis and management recommendations

The ecological values of habitats previously defined in Stratoudakis et al. (2019), combined with the present assessment of benthic habitat sensitivity, together highlight critical conservation and management priorities (*Figure 8-1*). Habitats with high ecological value and structural complexity, such as biogenic reefs, rocky reefs, deep seamounts, canyons and biological aggregations in soft sediments, are of particular concern due to their exposure to both fishing and climate-related stressors, including warming (especially in deep water habitats), acidification and deoxygenation (*Figure 8-1*). Conservation of the ecological value of these habitats would benefit from management measures integrating spatial planning with high protection actions. First, through adequate planning, MPA networks can ensure ecological representativity of these habitats across current and projected climate gradients, while considering connectivity to support species and habitat resilience under shifting environmental conditions (McLeod et al 2009, Stratoudakis et al. 2019). Within these areas, high levels of protection (such as no-take zones or closures to specific fishing activities to which the habitats are sensitive) are expected to enhance ecological conditions. Concurrently, selection of key representative sites where ecological value is high and fishing pressure relatively low, can optimise both conservation impact and socioeconomic feasibility.

In addition, conservation of other habitats especially sensitive to climate change (macroalgae forests, mud volcanoes and cold seeps, and maërl beds) should be precautionary and planned along current and projected climate gradients, wherever possible. Protection of seagrasses and shallow seamounts from fishing impacts is relevant because of their high ecologic value and sensitivity, and could be achieved by establishing no-take zones or closures to specific fishing activities in areas where habitat integrity is already compromised (to promote its recovery) or at risk of degradation (precautionary planning).

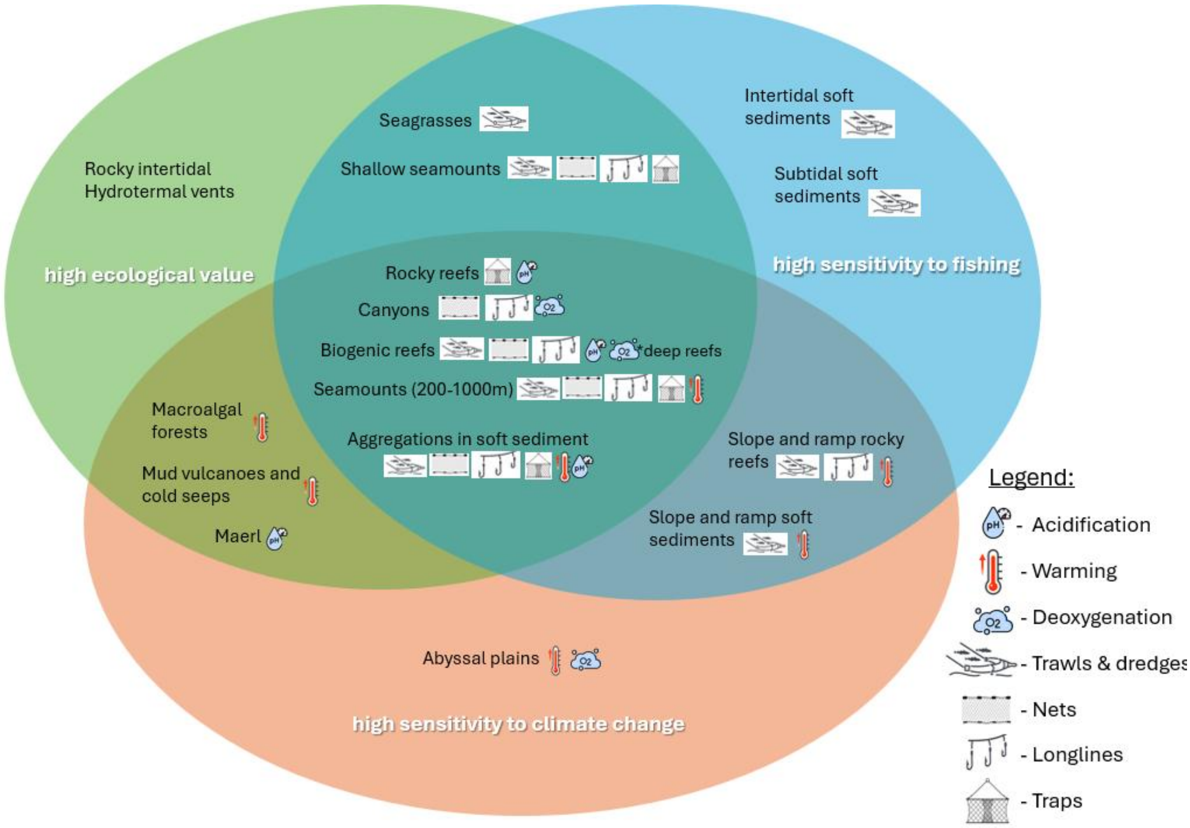

Figure 8-1. Venn diagram illustrating benthic habitats assessed as 'high' in the 'ecological values' assessment of Stratoudakis et al. (2019: green-shaded) and/or in the present study's assessment of habitat sensitivity to fishing-related (blue-shaded) and climate change stressors (orange-shaded). See legend for explanation of symbols related to fishing-related or climate-related stressors.

The high sensitivity of abyssal plains to declining dissolved oxygen concentrations (in extreme cases, hypoxia) and increasing temperature, advises that attention should be given to the increasing threats to deep-sea ecosystems, which depend on stable oxygen conditions to maintain benthic communities (Levin et al. 2009, Vaquer-Sunyer & Duarte 2008). Despite the low ecological value of abyssal plains, the expansion of oceanic hypoxic zones, driven by global warming and eutrophication, is an emerging concern that may severely impact biodiversity and biogeochemical cycles in these deep environments (Diaz & Rosenberg 2008, Breitburg et al. 2018). Therefore, further monitoring efforts must be undertaken to underpin the implementation of mitigating measures if necessary.

It is important to note that most marine benthic habitats are highly sensitive to more than one stressor (*Figure 8-1*). This indicates that future assessments should include multiple stressor interactions, given the cumulative sensitivity, that may amplify or mitigate individual impacts of single stressors (Crain et al. 2008). In addition, both monitoring programmes and conservation measures designed for these habitats should consider the possible cumulative effects of the multiple stressors.

Overall, the outcomes of the present work support the need for habitat-specific management and mitigation strategies, aligned with ecosystem-based approaches as defined in different international commitments (e.g. Marine Strategy Framework Directive, European 30×30 targets, EU Nature Restoration Law). As climate change accelerates, combining ecological sensitivity assessments with spatial data on exposure to pressures will be key to effectively identify both risk and buffer areas. Building on this foundation, there is value in future efforts focusing on the assessment of habitat vulnerability through spatially explicit risk maps that integrate both the sensitivity of habitats and their exposure to stressors. Such risk maps could support the design of targeted monitoring plans by prioritising high-risk areas (i.e. with habitats that are highly sensitive, highly exposed to stressors, or both), allowing early detection of change and more effective management actions. At the same time, identifying low-risk areas that host sensitive habitats (but may have lower exposure to stressors) can help strengthen existing conservation efforts and inform strategic protection measures.

Finally, in the present framework, the scoring approach focused on one stressor at a time, a choice made given the complexity of the assessments and the high number of habitats, criteria and stressors. The different criteria were evaluated based on expected changes on the broad taxonomic and functional structure of the communities typically associated with each habitat. Given that, for example, the rocky reefs habitat shares similar structure in different ecoregions as well as dissimilarities to other habitat types, therefore the overall relative scores among habitats are not expected to change within an ecoregion. As a result, the sensitivity rankings of habitats for each stressor are expected to be applicable for all ecoregions (i.e., compare the different habitats within an ecoregion). However, the obtained sensitivity rankings do not necessarily support direct comparisons between ecoregions (for example, to rank sensitivity gradients across larger spatial scales), because the specific resistance of the species compositions comprising the various taxonomic and functional groups of the communities between ecoregions was not considered.

9 Risks from invasive species in the Mediterranean

9.1 Introduction

The Mediterranean Sea harbours over a thousand non-indigenous marine species (Zenetos et al. 2022; Galanidi et al. 2023). It has thus been appropriately labelled as "the most heavily invaded marine region in the world" (Azzurro et al. 2022). Marine non-indigenous species (hereafter, NIS) arrive in the Mediterranean mainly by shipping (hull fouling, ballast water transmission) or through Port Said via the Suez Canal (Katsanevakis et al. 2013). The latter are frequently called "Lessepsian" migrants or species (Por 1971) and comprise roughly half of the total NIS in the region (Galanidi et al. 2023). A few NIS enter the basin unaided via the Strait of Gibraltar. By and large, this massive migration of species is an unprecedented biotic homogenisation *force* that leads to the tropicalisation or "demediterranisation" of the Mediterranean (Quignard and Tomasini 2000; Bianchi and Morri 2003).

From the total inventory of NIS, about 75% have established populations in the Mediterranean (Zenetos et al. 2022). A subset of these species have become invasive, causing a variety of adverse impacts on native habitats and biodiversity, on economic and social activities, and on human health (Katsanevakis et al. 2014; Galanidi et al. 2018; Bédry et al. 2021). For example, two Lessepsian siganid (rabbitfish) species, the marbled spinefoot *Siganus rivulatus* and the dusky spinefoot *Siganus luridus*, graze intensely on algal forests, leaving behind large areas of bare rock with some occasional patches of crustose barrens (Galanidi et al. 2018), causing significant impacts on natural habitats important for lifecycle maintenance, water purification and climate regulation (carbon storage), as well as displacing the local herbivore *Sarpa salpa* (Katsanevakis et al. 2014; Galanidi et al. 2018). Another invasive Lessepsian, the silver-cheeked toadfish *Lagocephalus sceleratus*, has significant adverse effects on local artisanal fisheries as it depredates on fishing gears, causing damages on catches and the gear itself (Christidis et al. 2024). Additionally, it poses a threat to human health through tetrodotoxin intoxication via its consumption, as well as through physical attacks on swimmers on rare occasions (Ulman et al. 2024).

NIS, and particularly invasive[1] NIS, are an additional threat on top of the effects of climate change and overfishing on the Mediterranean Sea's natural habitats and native species. Especially for Lessepsian migrants (which originate from the Red Sea), sea warming has facilitated an environment with temperature and salinity conditions now more similar to their native habitats than these conditions were before, particularly in the eastern part of the Mediterranean. By contrast, several species native to the Mediterranean Sea suffer from a climate-driven range contraction towards the north and/or in deeper, colder waters, which promotes the further proliferation of NIS in the area (Clark et al. 2020; Albano et al. 2021, Chapter 22). The combined pressures of sea warming and NIS can also dampen the positive effects of fishing effort reductions on the resilience or restoration of native habitats (Corrales et al. 2018). Additionally, fishing pressure reductions through the establishment of Marine

[1] A non-indigenous species is considered invasive if its introduction or spread has been found to threaten or adversely impact upon biodiversity and related ecosystem services (EU Regulation No 1143/2014).

Protected Areas (MPAs) do little or might even assist the spread of NIS since fishing, that may control NIS populations, is prohibited in these areas (Galil 2017; Giakoumi et al. 2019).

Although the rate of introduction of new NIS seems to be slowing down as of late (Galanidi et al. 2023), the successive enlargement of the Suez Canal through time along with the progressive weakening of the natural salinity barriers along the Canal (Bitter Lakes) and around the exit point in Port Said (Nile River floodwater) (Katsanevakis et al. 2013) has amassed a considerable "invasion debt" in the eastern Mediterranean towards the western part of the basin (Galil et al. 2021; Galanidi et al. 2023). Given this fact and the threat that the combined pressures of NIS, sea warming and fishing pressure can pose on native habitats, it is essential to account for the presence of NIS (current *and* future) along the Mediterranean Sea in order to meet the current and planned management targets. In this study we aimed to (1) assess the past, current and near future spread of Lessepsian species in the Mediterranean basin; (2) identify the environmental and anthropogenic variables that influence their spread; and (3) map their current hotspots.

9.2 Methods

We used fish, mollusc and crustacean data from the MEDITS trawl surveys from 1999 to 2021. The mean depth and location of each haul were computed from the associated files (TA). NIS were identified according to the updated 2nd CIESM Atlas of Exotic Species in the Mediterranean (Golani et al. 2021, 2025). The Lessepsian lizardfish species *Saurida undosquamis* was renamed to *Saurida lessepsianus*, as it was most probably misidentified in the original dataset (Russell et al. 2015). We also excluded 16 observations of this species from Geographic Sub-Area (GSA) 15, as it was only observed there in a single year (2016), in multiple hauls and at depth ranges outside the depth niche of the species, hinting to a possible misidentification. From the accepted data, we estimated the total abundance and biomass of each NIS in the Mediterranean by taking into account the MEDITS stratification scheme, as described in the MEDITS Handbook version 9 (Anonymous 2017). The centre of gravity of distribution of the Lessepsian species by year was computed by calculating the mean longitude and latitude of Lessepsian species observations in the dataset.

To estimate the annual spatial extent of Lessepsian species in the Mediterranean we used Generalised Additive Models (GAMs). Many Lessepsian species prefer very shallow waters and steep, rocky substrates (Golani et al. 2021), and thus are not effectively sampled by bottom trawls. Additionally, the MEDITS surveys are not designed to exhaustively sample the shallower strata, but to have adequate coverage of each depth stratum in any particular GSA. To account for this bias, we converted each haul data to presence/absence by assigning 1 to each haul that had *at least one* Lessepsian species present and 0 for the absence of Lessepsian species (*Figure F-1* of Appendix E). Data between 2009–2013 were excluded due to a significant gap for GSAs 20, 22 and 23 that are on the migration path of these species. We then constructed a 'simple spatiotemporal' GAM model using these presence/absence data as the response variable and the haul location, depth and year as explanatory variables.

Since the response variable is binary, the binomial family distribution with the logit function as link was used. For the haul location, the interaction between its coordinates was added as a tensor smooth, and depth and year as smooth terms. For all smoothers, the penalised thin plate regression splines ('ts') were used as basis. Finally, we applied a gamma correction of 1.2 to the model. This model was then used on a 0.1° hexagonal grid, covering all European GSAs and up to 1000 m in depth, to make spatial predictions on the probability of occurrence of *at least one* Lessepsian species, for every year in the period 1999–2021. Additionally, we projected time (i.e., the year) forwards to predict the probability of occurrence for the two upcoming decades (2021 – 2041), in order to gauge the speed and direction of the expansion of Lessepsian migrants throughout the basin.

To test which environmental variables facilitate the spread of Lessepsian species, we used monthly modelled data from the Copernicus CMEMS Mediterranean Sea Physics Reanalysis (Escudier et al. 2021) and the Mediterranean Sea Biochemistry Reanalysis (Teruzzi et al. 2021) products. To test whether fishing had any effect on the presence of Lessepsian species, a trawling fishing pressure index (FPI), scaled from 0 to 1, was calculated according to Kavadas et al. (2015) for the entire Mediterranean and for the same time period (1999 – 2021). The environmental variables tested were sea surface temperature (SST), sea bottom temperature (SBT), surface salinity (SO), bottom salinity (SB), and their anomalies, chlorophyll-a (Chl*a*) concentration (all the above at the month of sampling), summer SST and SBT (July, August, September mean), winter SST and SBT (January, February, March mean) and the winter – summer temperature interactions, and SO's 10th percentile annual values. Using a similar approach as above, we fitted an 'environmental' GAM model with the Lessepsian species' presence/absence as the response variable, and sets of the aforementioned variables as explanatory terms, along with depth and year. The location tensor was excluded from this procedure, since it retained much of the explained deviance on every test, leading to any new variables added in the model not being significant.

Finally, we used the simple spatiotemporal model and the final environmental model to make spatial predictions and map the current (as of 2021) Lessepsian species hotspots, defined as the grid cells with probability of occurrence ≥ 0.5. All figures and analyses were done in R version 4.4.

9.3 Results

From a total of 25,932 hauls in the dataset, 445 unique NIS records were made from 316 hauls. From those 445, 305 were observations belonging to species of Indo-Pacific origin (i.e. Lessepsian) and 140 of Atlantic origin. In total 21 NIS were recorded, and 17 of these are Lessepsian species: the fishes *Champsodon nudivittis* (nakedband gaper), *Etrumeus golanii* (a roundherring), *Fistularia commersonii* (blue-spotted cornetfish), *Lagocephalus lagocephalus, L. sceleratus* and *L. suezensis* (three oceanic pufferfish species), *Pteragogus pelycus* (sideburn wrasse), *Pterois miles* (common lionfish), *Saurida lessepsianus* (a lizardfish), *Siganus luridus* and *S. rivulatus* (dusky and marbled spinefoot), *Sphyraena chrysotaenia* (yellowstripe barracuda), *Stephanolepis diaspros* (reticulated filefish), *Torquigener flavimaculosus* (yellow-spotted puffer), *Upeneus moluccensis* (goldband goatfish) and *Upeneus pori* (Por's goatfish) and the crustacean *Erugosquilla massavensis* (a mantis shrimp). Four of the NIS recorded are of Atlantic origin: the fishes *Psenes pellucidus* (bluefin driftfish), *Solea senegalensis* (Senegalese sole) and *Sphoeroides pachygaster* (blunthead puffer) and the crustacean

Penaeus aztecus (northern brown shrimp). From these species, the oldest and most frequently recorded was the blunthead puffer, *Sphoeroides pachygaster,* which was caught in every year, while the nakedband gaper *Champsodon nudivittis* was the newest recorded species, with one specimen during 2020 (*Figure F-2*). *Sphoeroides pachygaster* had the highest estimated total biomass in the Mediterranean (520354.11 kg), while the most abundant species was the round herring *Etrumeus golanii* (estimated at 6.4×10^7 individuals) (*Figure F-3*).

There was an exponential increase over time in the number of Lessepsian species recorded, as well as in the number of their observations; by contrast for the Atlantic NIS, both remained relatively constant (*Figure 9-1*). Regarding the spatial distribution of NIS along the European Mediterranean Sea, GSA 25 had the highest number of NIS recorded (15 species), followed by GSA 23 (13 species) and GSA 22 (4 species) (*Figure 9-1*). In terms of total estimated NIS abundance and biomass though, GSA 23 surpassed GSA 25 (*Figure F-4*). The calculation of the centre of gravity of Lessepsian migrants in the basin through time yielded mixed results, probably due to the presence of several sampling gaps in the dataset. From 2017 and onwards though, it showed a clear westward and slightly northward shift, from the centre of GSA 25 towards the southeastern part of GSA 22 (*Figure 9-1*).

The simple spatiotemporal model on occurrence probability of Lessepsian NIS explained 77.3% of the total deviance (adj. $R^2 = 0.624$) with very good AUC scores (0.997). Haul location was responsible for most of the explained deviance (75.15%) (indicating the eastern origin and east to west movement of the NIS), followed by depth (14.85%) and year (10%). Year had an almost linear positive effect on the probability of occurrence of Lessepsian NIS (*Figure F-5*). The effect of depth showed that this probability was constrained mostly between 0 and 100 m . From the model's spatial predictions we observed a gradual increase on the probability of occurrence of Lessepsian NIS from the east, along the coasts of Cyprus, towards the west, starting from the northern coasts of Crete and the southern Dodecanese and spreading further northwards and westwards towards the central Aegean Sea and the Ionian Sea, and finally towards the northern Ionian Sea, the western coasts of the northern Aegean Sea, the southern coasts of Sicily, and also in the Gulf of Lions and the northern part of the Gulf of Valencia in the western Mediterranean (*Figure 9-2*).

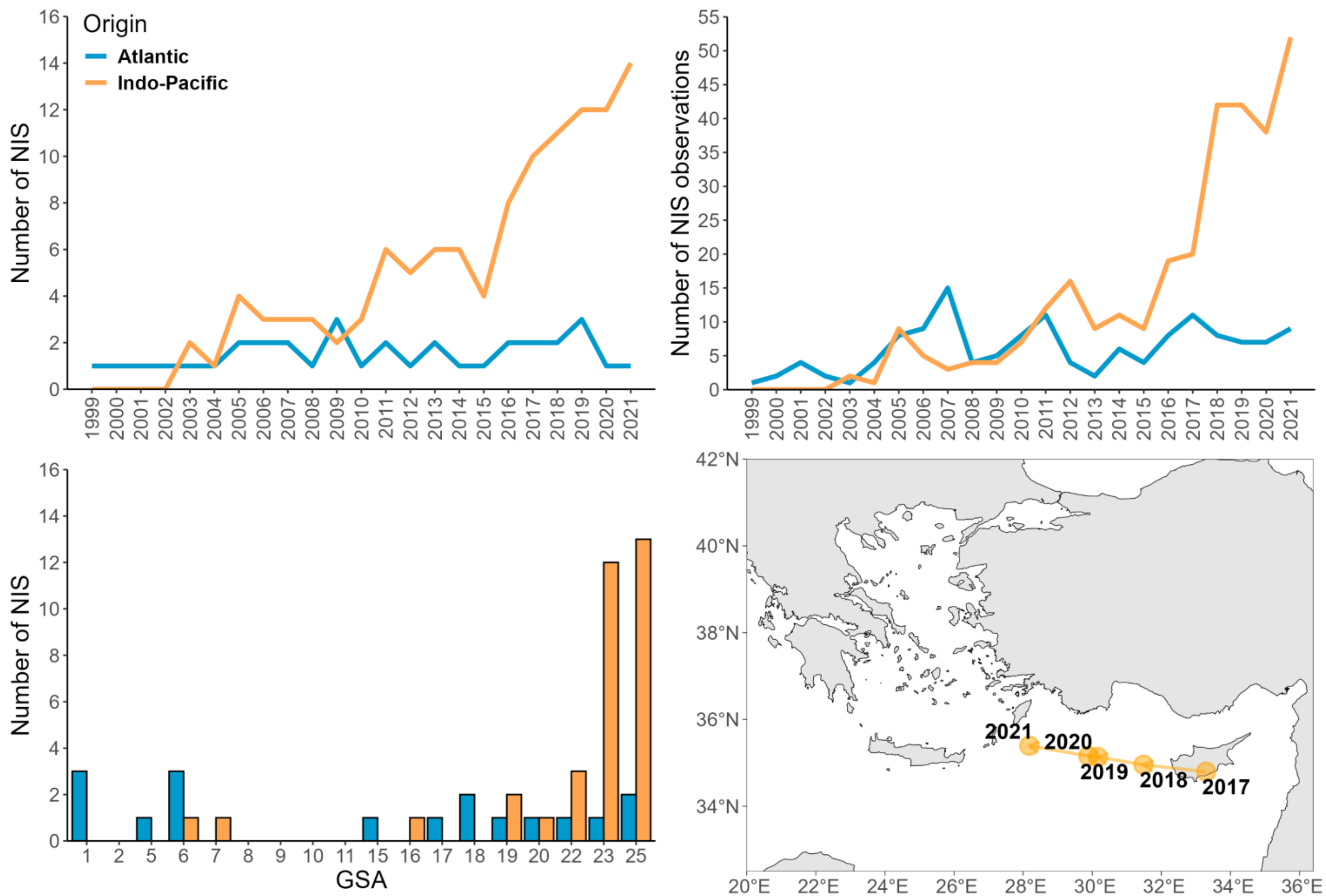

Figure 9-1. Numbers of non-indigenous species (NIS) per year (top left), of total observations of NIS per year (top right), and of NIS per GSA in the MEDITS dataset during 1999–2021. Blue: NIS of Atlantic origin; orange: of Indo-Pacific (Lessepsian) origin. The bottom-right graph shows the centres of gravity of distribution of Lessepsian NIS records during the years 2017–2021.

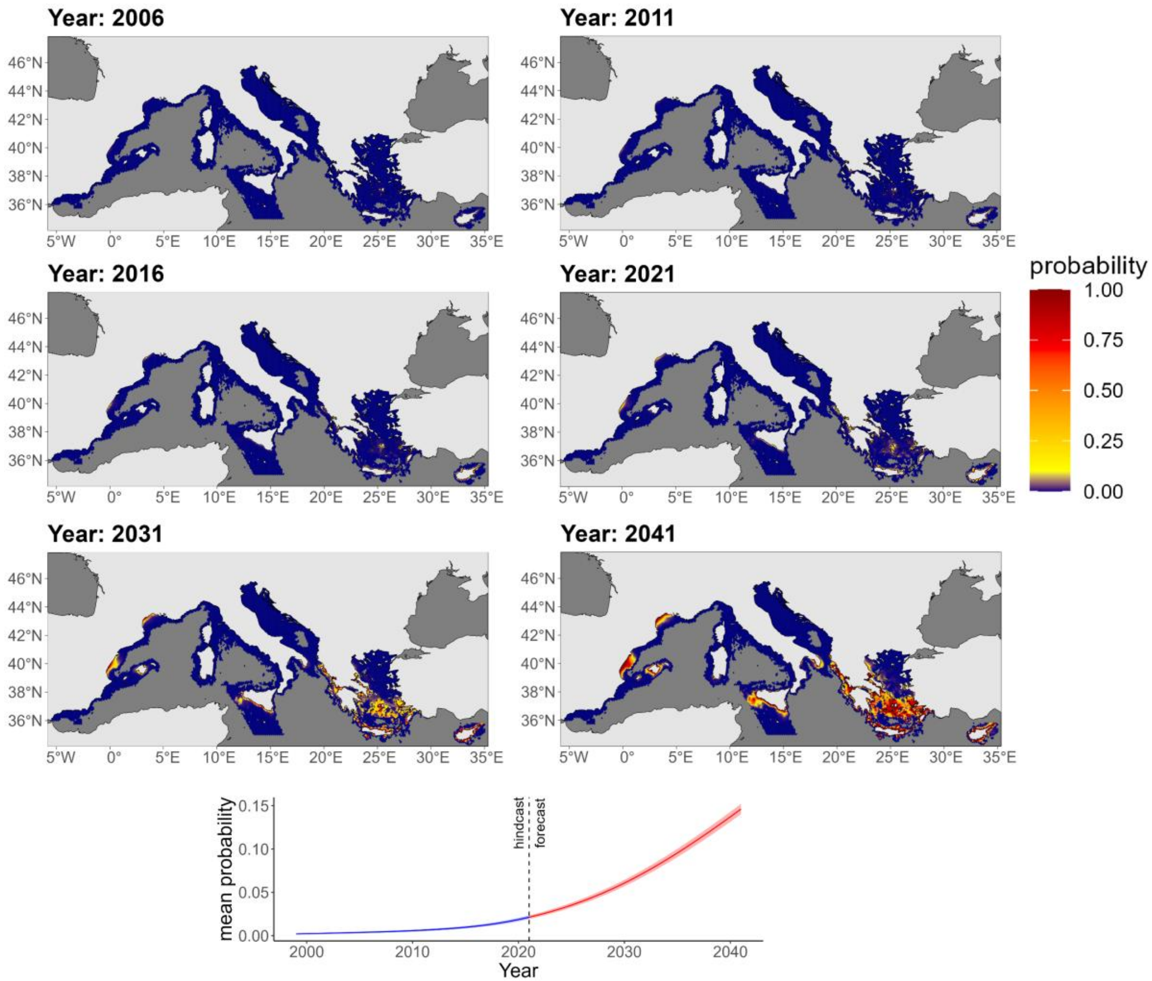

Figure 9-2. Simple spatiotemporal model's spatial predictions for 2006, 2011, 2016 and 2021, and future projections for 2031 and 2041 on the probability of occurrence of Lessepsian NIS. The bottom graph shows the mean probability of occurrence across the entire Mediterranean Sea from 1999 to 2021 (hindcast) and the projections from 2021 to 2041 (forecast).

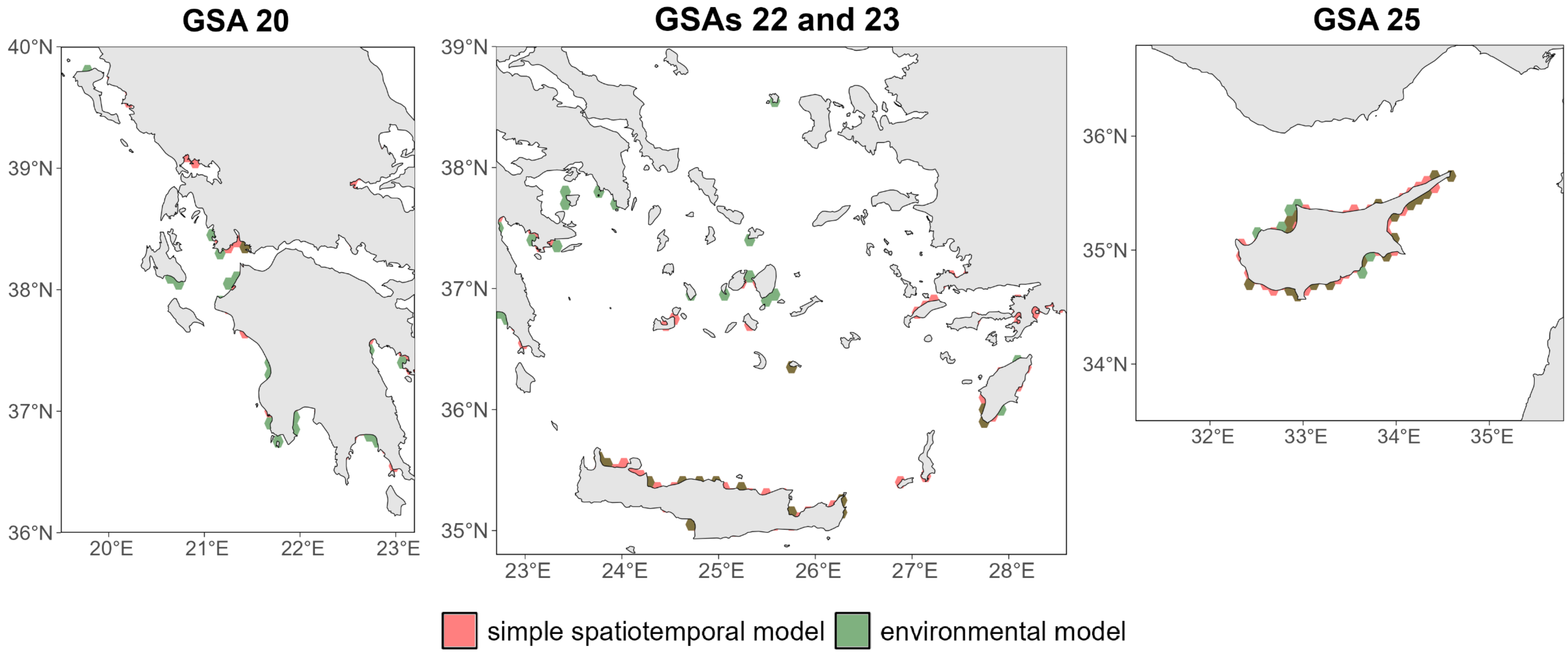

Figure 9-3. Lessepsian species hotspots in the Mediterranean Sea (probability of occurrence ≥ 0.5) as predicted by the two GAM models.

The model's projections for the two upcoming decades (up to 2041) indicate a further northward and westward expansion of Lessepsian migrants, reaching the southern Adriatic Sea and southern coasts of Italy around the Salento peninsula, and the Balearic Islands (*Figure 9-2*). Furthermore, the projections indicate substantial expansion of their range within areas they have already reached, covering almost the entirety of the central and southern Aegean, the coasts of Cyprus, Crete and Sicily, and the eastern coasts along the Ionian Sea by the early 2040s, and also spreading along the shallow waters of the Sicilian Straight and along the shelf of the Gulf of Valencia and Gulf of Lions. Their mean occurrence probability across the entire Mediterranean grid is projected to increase exponentially through time, with no sign of saturation up until at least 2041 (*Figure 9-2*).

From the environmental model trials, the best parsimonious model included year, depth, surface salinity, trawl fishing pressure index (FPI) and the interaction between winter and summer SST (AIC = 433.87). The model explained 74.6% of the total deviance (adj. R^2 = 0.595, AUC = 0.994), most of this explained by the winter–summer SST interaction (41.74%), followed by surface salinity (27.21%), depth (20.09%), FPI (6.12%) and year (4.84%). The strong effect of the winter–summer SST interaction indicated that the occurrence probability of Lessepsian NIS was highest at concurrently high winter and high summer SSTs (*Figure F-6*). In contrast, low winter SSTs were heavily penalised by the model. The effect of surface salinity showed a linear increase of the probability for values above 38; by contrast, salinity values below this threshold were heavily penalised. For fishing pressure (FPI) there was no effect at intermediate values, but for low and high FPI values the probability increased. The effects of year and depth were otherwise the same as in the simple spatiotemporal model.

The current (as of 2021) Lessepsian NIS hotspots in the Mediterranean, as identified by the two GAM models, include almost the entire coastline of Cyprus; much of the north coast of Crete; various locations around the southern and central Aegean Sea (including along the southwest coast of Turkey, the southern Dodecanese Islands, several of the Cyclades Islands, and the Saronic Gulf); many locations around the Peloponnese peninsula; and (in western Greece) the Gulf of Patras and several locations on the Ionian Islands (*Figure 9-3*).

9.4 Discussion and conclusions

Through analysis of long-term survey data in the Mediterranean Sea, this study has demonstrated a substantial expansion of non-indigenous species of Red Sea origin (or from the wider Indo-Pacific). Both the total number of these Lessepsian species and the numbers of observations per species have risen in an accelerating way. Raw data and model results indicate a westward and northward expansion of these NIS in the basin. So far, areas in the Eastern Mediterranean Sea have been most impacted – especially Cyprus, Crete and the Aegean Sea (GSAs 25, 23 and 22, respectively). However, our projections indicate that within two decades, Lessepsian NIS will reach areas across the entire Mediterranean Sea including the westernmost areas. GAM results revealed that the most important variable explaining the occurrence of Lessepsian species was the interaction between winter and summer sea surface temperatures, followed by surface salinity and depth. This is in line with a requirement for sufficiently high temperatures and comparatively higher salinities alike the Red Sea origins of these species, and a preference for shallower waters as expected by the selection mechanism through the shallow Suez Canal (Mavruk & Ansar 2007). Trawl fishing pressure also had a significant, albeit weak effect on Lessepsian species occurrence.

The MEDITS trawl survey dataset contained only 21 NIS, 17 of which were of Indo-Pacific (Lessepsian) origin. This represents only 5.4% of the total Lessepsian fish, crustacean and mollusc species that have ever been recorded in the Mediterranean, according to the updated 2nd CIESM Atlas of Exotic Species (Golani et al. 2021, 2025). This discrepancy confirms what we already expected, i.e. that most Lessepsian species are not effectively captured by bottom trawls, either because they reside in very shallow waters or over hard rock and steeply inclined substrates where bottom trawls cannot fish. Nevertheless, the trawl-surveyed species list includes several notorious fish invaders, notably the lionfish *Pterois miles*, the siganids *Siganus rivulatus* and *Siganus luridus,* the blue-spotted cornetfish *Fistularia commersonii* and silver-cheeked toadfish *Lagocephalus sceleratus*. Almost all of the recorded Lessepsian NIS (barring the oceanic puffer, *Lagocephalus lagocephalus*) have large established populations in areas around the Mediterranean, suggesting that when NIS become well established and relatively abundant, they will start getting captured during the MEDITS trawl surveys.

Our reconstruction of the recent history of expansion of Lessepsian NIS in the Mediterranean through GAM modelling revealed that these species gradually expanded westwards via Cyprus and towards the southeastern Aegean Sea and Crete, then continued spreading westwards and northwards at a faster pace (especially in the last decade) into the central Aegean Sea and along the eastern Ionian coasts, reaching the southeastern edge of the Adriatic and the southern coasts of Sicily (*Figure 9-2*). These results are consistent with other analyses in the Mediterranean (D'Amen and Azzurro 2020; Azzurro et al. 2022), albeit more conservative. Some species like *Fistularia commersonii*, *Lagocephalus sceleratus* and *Etrumeus golanii* are known to have already reached the Western Mediterranean (Azzurro et al. 2022) but have (as of 2021) not yet been captured in the MEDITS surveys carried out there. In fact, so far only two survey hauls in the Western Mediterranean MEDITS database held Lessepsian NIS records: one haul with four individuals of *Siganus luridus* in the Gulf of Valencia (GSA 6) in 2020, and one haul with four individuals of Por's goatfish *Upeneus pori* in the Gulf of Lions (GSA 7) in 2014.

The GAM projections for the near future indicate a continuous westward and northward exponential expansion of Lessepsian NIS in the Mediterranean, with no sign of saturation up until 2041 (*Figure 9-2*). Although this result might seem striking, these range expansion projections are still on the conservative side compared to other studies in the basin (Coro et al. 2018; D'Amen & Azzurro 2020; Loya-Cancino et al. 2023; Mitchell & Almela 2025). This is not unexpected since, as previously mentioned, for a Lessepsian NIS to be caught during a MEDITS survey with some likelihood, it must have an established and fairly large or widespread population; there is a time lag related to this process, i.e. from initial arrival of a species to its establishment (Azzurro et al. 2016).

According to our GAM modelling trials, the strongest environmental driver influencing the spread of Lessepsian migrants was the interaction between winter and summer sea-surface temperature. The higher probability of occurrence when both winter and summer SST were high, suggests that Lessepsian species prefer warm waters all year round (*Figure F-6*). On the other hand, low winter SSTs were heavily penalised in our models; this indicates that

Lessepsian species frequently cannot cope with the cold conditions experienced at least during some winters in parts of the Mediterranean. Indeed, some of these species have fairly high optimal temperatures (e.g. 28.7 ^{o}C for *Pterois* sp. and 27 ^{o}C for *Siganus rivulatus*), and will cease feeding (e.g. at 15.3 ^{o}C for *Pterois* sp. and 14 ^{o}C for *S. rivulatus*) or even perish (e.g. at ~10 ^{o}C for *Pterois* sp.) at low water temperatures (Kimball et al. 2004; Saoud et al. 2008; Barker et al. 2018). Our model results are consistent with other studies in the area, which arrived at similar conclusions (Giakoumi et al. 2019; Clark et al. 2020; Solanou et al. 2023). With climate change, winter warming of the Mediterranean Sea might be one of the most disrupting factors for native communities, threatening ecosystem collapse in exploited communities and facilitating the niche expansion of many non-indigenous species (Giakoumi et al. 2019; Clark et al. 2020; D'Amen & Azzurro 2020).

The second-most influential factor was surface salinity, which showed a threshold value of 38, below which the probability of occurrence of Lessepsian species was heavily penalised. Low salinity has been shown to be a constraining factor for at least *Pterois miles* (Turan 2020; Solanou et al. 2023), but this is also expected to be true for many other Lessepsian NIS. In the Red Sea, where these species originate from, salinity varies from 36.8 in the south to 40.1 in the north (Mezger et al. 2016), but in the Bitter Lakes, along the Suez Canal, salinity can reach up to 49 during summer and down to 44 during winter (Mavruk & Avsar 2007). So, species passing through the Canal must be capable of surviving highly saline waters.

The third influential factor was depth, which showed a positive effect between 0 and 100 m, but was heavily penalised for depths greater than 400 m. This suggests that most Lessepsian migrants prefer shallow waters, which is true for 14 out 17 Lessepsian NIS recorded in the MEDITS dataset. The effect of year being retained in every environmental model trial, along with the very strong effect of haul location in the models, suggested that there is still a significant spatiotemporal effect unexplained by the environmental and anthropogenic variables tested. This hints that Lessepsian NIS are still in the process of spreading to cover every suitable niche along their path of expansion, confirming the so called "invasion debt" the Eastern Mediterranean has amassed towards the western part of the basin (Galil et al. 2021; Azzurro et al. 2022).

Trawling pressure also affected the probability of occurrence of Lessepsian NIS, albeit the effect was weak. Interestingly, the occurrence probability increased when fishing pressure was low, while it was lowest with intermediate levels of fishing. This suggests that fishing might be able to control, at least to some degree, the spread of Lessepsian NIS. Indeed, Giakoumi et al. (2019) found that in eastern Mediterranean MPAs, NIS maintained larger populations than in their neighbouring unprotected areas. In theory, pristine environments are generally considered more resilient to species introductions, but in practice MPAs do not seem to stop the expansion of NIS, and may even facilitate it (Galil 2017; Giakoumi et al. 2019). Lessepsian NIS may therefore complicate effective management of Mediterranean MPAs. Fortunately, we can draw wisdom from the successful management of red lionfish *Pterois volitans* in the Western Atlantic; here, regular targeted removals (by spearfishing, tournaments and fisheries) proved to be an effective tool for controlling this invasive NIS (Ulman et al. 2022). Our results, however, also indicated that high fishing pressure (rather than intermediate levels) may have a positive effect on the occurrence probability of Lessepsian NIS; this suggests that heavily disturbed environments are more prone to invasions (possibly due to the availability of niches left vacant after the depletion of native stocks and large predators by heavy fishing) (Corrales et al. 2018). Accordingly, a recent study found that reducing fishing pressure had a negative impact on alien species but positive effect on several previously exploited and vulnerable species (Corrales et al. 2018). Thus, eliminating overfishing where possible might prove to be beneficial for controlling NIS.

In many parts of the Eastern Mediterranean, Lessepsian species that were established decades ago are now so frequently caught that many fishers consider them part of the native biota (Kleitou et al. 2022). They comprise not only a major part of discards, but also a significant part of commercial catch (Carpentieri et al. 2009; Galil et al. 2021; Kleitou et al. 2022; Papageorgiou and Moutopoulos 2023). Lessepsian NIS in this part of the Mediterranean are considered an inevitability and some authors have called for a shift in management attitude towards a more pragmatic approach of embracing NIS that their positive ecosystem and/or economic benefits outweigh their impacts, promote the sustainable exploitation of others, and the introduction of more radical measures for controlling harmful NIS (Kleitou et al. 2021). Considering the “invasion debt” the Eastern Mediterranean has accumulated through time, the present study suggests that such pragmatic approaches might soon echo throughout the entire Mediterranean.

In conclusion, we showed that the so-called ‘Lessepsian migrants’, species of Indo-Pacific origin entering the Mediterranean Sea through the Suez Canal, have rapidly expanded westwards in the Mediterranean, and will continue to do so in the upcoming two decades, with no signs of slowing down. Winter temperature is the most constraining factor for the spread of Lessepsian NIS, but future sea warming will progressively weaken this natural barrier. Fishing and especially the targeted fishing of NIS could be an effective tool for controlling their populations.

10 General discussion, conclusions and perspectives

10.1 General discussion and conclusions

Using sensitivity and vulnerability in combination with exposure to pressures as a tool, we have been able to assess and map risks for marine communities and biodiversity across Europe's regional seas. Our maps have highlighted clear spatial patterns in areas with high and low risks for marine communities. We have also been able to assess trends over time in changing pressures, community sensitivities/vulnerabilities, and risks.

Assigning areas of high ecological risk is not straightforward. Risk is often conceptualised as the interaction between exposure to pressures and sensitivity/vulnerability, yet these components are not independent. An increase in the exposure to a pressure, or cumulative pressures may reduce the community sensitivity/vulnerability and vice versa. This dynamic complicates the direct use of vulnerability scores for spatial risk assessments. Nevertheless, community vulnerability can be an important metric to consider when assigning potential MPAs but should be taken into consideration together with other criteria, such as other biodiversity indicators and habitats' diversity and integrity.

A key conclusion of this study is that recovery is possible. Increasing fishing pressures result in decreasing vulnerability in marine communities and decreasing species richness. On the other hand, when fishing pressures are decreased, communities are found to respond with increasing species richness and increasing community-level sensitivity/vulnerability. This implies that more sensitive species are present, with the community more closely resembling an 'original' or 'undisturbed' state. This was shown for instance for the North Sea, where reductions in trawling pressure have gone hand in hand with increasing species richness in epibenthos, and more vulnerable species present nowadays then there were some decades ago (Chapter 7). Likewise in the North Sea and Celtic Seas, in areas where fishing pressures were reduced, there was an increase in the abundance or occurrence of species with high sensitivities within fish communities (chapter 4).

For overall fishing pressure, there was no consistent pattern across Europe. In the North Sea, Celtic Seas and Icelandic waters there were generally more areas where fishing pressure was reduced (lower exposure). In the Greenlandic case study, the signal was ambivalent with first rising and next declining fishing pressures. In the Mediterranean Sea there was a patchwork of areas where fishing pressure either increased or decreased. Across Europe the steady and often substantial increases in fishing pressures that characterised the 20th century appeared to have partially reversed or at least not universally continued in the early 21st century (compare our results e.g. with Engelhard (2008) for the North Sea). This might have resulted from a combination of factors, including the European Union's fleet reduction scheme (Villasante 2010), and various local circumstances such as loss of fishing grounds to EU countries following Brexit, closure of areas because of e.g. offshore wind farms, and continually rising fuel prices, resulting in smaller fleet capacity and reduced total fishing effort (Poos et al. 2013, Hamon et al. 2023).

A third key conclusion is that there is a clear north-south gradient in the temperature related pressure. The temperature gradient is shifting northward in line with climate change. Accordingly, biogeographical regions are also shifting northward. Cold adapted communities are replaced with warmer adapted communities. As a result, the signal of sensitivity (and the resulting risk) is less clear because the most sensitive colder-water species may decline or shift northward, but their replacement by more resilient or warm-water species can mask the impact on sensitivity. Since the latter are adapted to warmer temperatures, they still have high sensitivities to CC. They are not surviving the pressure of warm waters but following the temperature increase. These replacing species lead to a normal community distribution on sensitivity to CC with high and low sensitivities.

Temperature changes lead to different communities in time generally following a South to North shift in European waters. However, this signal can be obscured in deeper waters in the Northern Mediterranean where colder water species can seek refuge in deeper water layers (chapter 2). Here distribution shifts are often in a North to South direction.

A wider applicable approach was developed to assess the sensitivity for marine benthic habitats. It emerged that habitats with high ecological value and structural complexity, such as biogenic reefs, rocky reefs, deep seamounts, canyons and biological aggregations in soft sediments, are of particular concern due to their sensitivity to both fishing and climate-related stressors. For each type of habitat, different pressures exhibit different exposures urging for specific management approaches.

For the Mediterranean Sea, an important finding is the substantially increased presence and expansion of non-indigenous species of Red Sea origin (or from the wider Indo-Pacific). Both the total number of these Lessepsian species and the numbers of observations per species have risen in an accelerating way. A significant westward expansion is observed starting from the Suez Canal. Key factors in the colonisation are sufficiently high temperatures especially in wintertime and comparatively higher salinities alike the Red Sea.

A general observation was that the trait-analysis yields patterns on risks which are very useful. However, to truly understand the ecological patterns and drivers, analysis at both the species and community levels is also needed. Acknowledging these limitations, a set of management implications can be derived based on the current study, provided for each basin in the following section.

10.2 Management implications

The essence of B-USEFUL is that it intends to render tools for policy making on marine biodiversity. Therefore we present a concise overview of important take-home messages for biodiversity policy makers and area managers on a basin- as well as Europe-wide level. First we start with some key management advice across areas. Next the management implications per basin are presented.

10.2.1 Key management implications across areas

The combination of climate change and changes in fishing pressure paint a complex pallet in both exposures and the responses of the communities present. This is especially true if major water masses and currents shift in complex patterns in time and space. As a result sensitive, dynamic ecological communities may react capriciously. Continual monitoring and adaptive management are necessary for marine protection and recovery. Both spatial and sectoral measures are necessary to effectively protect high-diversity ecosystems. These dynamic protection measures should stand next to established long-term spatial measures like MPAs (designated based on different considerations like biodiversity indices across phyla).

The trait-based cumulative risk framework provides at different spatial scales sensitivity layers, exposure to pressures layers, and risk layers that turn complex data into clear, mappable priorities, reveal temporal trends, and define actionable thresholds, making the outputs directly usable for adaptive management and spatial planning.

This type of information is of high value to supplement both regular species and community monitoring. It is extremely useful in defining what are the most sensitive species, species groups and habitats, and in what areas these are typically found. This information enables that dedicated management measures can be defined and prioritised.

10.2.2 Mediterranean Sea: community-level risks

What do the actual results imply for the local management of the study area?

- Priority should be given to depth-inclusive spatial management and basin-wide climate-adapted measures, tightening limits and safeguarding cold-water refugia, particularly in areas with the highest climate-change sensitivity.
- Effort and gear controls should be targeted, prioritising the adoption of technological innovation aimed at strengthening gear selectivity/bycatch mitigation, particularly for elasmobranchs and benthic habitats, particularly in areas where S_{FP} and R_{FP} are rising.
- Invasive-species pressures should be addressed by strengthening monitoring, particularly in the Eastern Mediterranean but basin-wide, and by prioritising habitat protections to preserve endemic species and vulnerable native communities.
- Fishing effort-oriented management measures should be differentiated by sub-region or GSA, maintaining effort reductions in areas where risk is declining; applying precautionary effort quotas and habitat protections where both CC/FP risks are increasing.

How functional is the approach in informing and guiding biodiversity policy makers and area managers in their decision making both in the study area and at the European level?

- The trait-based cumulative risk framework provides at different spatial scale sensitivity and risk layers that turn complex data into clear, mappable priorities, reveal temporal trends, and define actionable thresholds, making the outputs directly usable for adaptive management and spatial planning.
- The framework of the analysis produced outputs that can be used directly to support adaptive management decisions and marine spatial planning applying an Ecosystem Based Fishery Management (EBFM) approach.
- Trait-based approaches combined with sensitivity to pressures are more informative than traditional taxonomic and endangerment categories to identify biodiversity hotspots at species and community level from local to regional spatial scales, helping to prioritize areas in spatial conservation management.

What is the most urgent take-home message?

The findings highlight urgent needs for spatially adaptive, climate-smart fisheries management and habitat protection, especially in deeper and eastern zones of the Mediterranean Sea, to safeguard biodiversity and ecosystem services under accelerating environmental change.

10.2.3 Mediterranean: ecosystem functionality risks

What do the actual results imply for the local management of the study area?

- Several areas in the western Mediterranean have been identified for conservation priority based on spatial matching of multiple functional and risk-indicators, most notably the Alboran Sea, the Balearic Islands, Sardinia, and Corsica.

How functional is the approach in informing and guiding biodiversity policy makers and area managers in their decision making both in the study area and at the European level?

- The combination of different risk-indicators with functional approaches provides a broad perspective as well as context-dependent tool for decision-making to prioritize conservation areas.

What is the most urgent take-home message?

Functional originality should be addressed in marine conservation spatial planning to avoid losing species and communities with unique characteristics. Loss of these species in particular might drastically change the ecosystem functioning.

10.2.4 Northeast Atlantic: community-level risks

What do the actual results imply for the local management of the study area?

- Management efforts to reduce fishing pressure are working in some respect, but they do not automatically reduce ecological risk—communities may still be vulnerable due to shifts in species composition. As such, stricter enforcement of fishing restrictions and controls will be necessary to protect Northeast Atlantic fish communities.
- Climate change is emerging as a widespread and escalating driver of ecological risk, even in areas where fishing pressure has declined. Future projections of community-level sensitivity will be needed to ensure spatial management actions (prioritising high-risk hotspots) are effective into the future.
- The Greater North Sea shows complex spatial patterns and slower recovery, indicating the need for localised monitoring and adaptive, area-specific management strategies across the Northeast Atlantic.

How functional is the approach in informing and guiding biodiversity policy makers and area managers in their decision making both in the study area and at the European level?

- The combined spatial and temporal analyses offer nuanced insights into community-level responses, supporting evidence-based, regionally tailored policy decisions. In principle, this framework could be applied to other marine communities (benthic) or even plankton/marine mammals with available trait and abundance data to identify and prioritise hotspots of sensitivities and risks to climate change and fishing across Europe.
- Important to note that these results assess **relative** sensitivity rather than absolute sensitivity (i.e. all species in communities and across study region are assigned score

relative to one another), which is important to remember if comparing to other taxonomic groups.

- Long-term monitoring using community-level sensitivity metrics (S_{FP} and S_{CC}) as indicators provides a valuable tool for tracking ecosystem responses and guiding strategic interventions. Spatial planning actions (MPAs with adequate protected levels and MPA networks) must be future-oriented so as not to protect just a snapshot of biodiversity. Continued monitoring will be required into the future to assess effectiveness of current and/or new MPAs.

What is the most urgent take-home message?

To effectively safeguard Northeast Atlantic fish communities, management must combine stricter fishing controls with climate-adaptive, region-specific strategies that prioritise long-term monitoring and protection of high-risk ecological hotspots.

10.2.5 Icelandic waters: community-level risks

What do the actual results imply for the local management of the study area?

- Major changes are taking place in the composition of marine fish communities in Icelandic waters, both in terms of taxonomic and functional diversity, driven by both climate change and fishing pressure (although the later has generally reduced, but not in all areas).

- Changes are different between the generally warmer waters in the southwest region (influenced by the North Atlantic current) and the much colder waters in northeast region (which receive influx from the Arctic). In the southwest the increase in species sensitive to climate change led to an increase in total abundance. In the northeast increase in species sensitive to climate change appeared to substitute species sensitive to fishing pressure (mostly Arctic species).

- In both regions (SW and NE) a marked decrease in abundance of Arctic species, and increase of Atlantic species was observed. Arctic species are the most sensitive to both climate change and fishing pressures followed by Boreal species and lastly Atlantic species.

How functional is the approach in informing and guiding biodiversity policy makers and area managers in their decision making both in the study area and at the European level?

- In some cases, considering sensitivity to climate change and sensitivity to fishing pressure *in isolation* could lead to misleading conclusions, due to interactive effects between climate change and fishing. This is especially the case if climate-sensitive species are more fishing-resilient, and fishing-sensitive species more climate-resilient.

- In these cases it is necessary to contextualise changes in trait-based indices by either grouping species in 'sensitivity groups' or through other means (e.g., biogeographical groups).

What is the most urgent take-home message?

Additional protection (e.g. through MPAs, MPA networks, restricting fisheries) could be considered for areas where reorganisations are greatest, to protect fishing-sensitive species and especially Arctic species. Also Arctic species need particular attention since they are the most sensitive for both climate change and fishing pressure as compared to both Boreal and Atlantic species. The application of trait-based indices needs to be investigated thoroughly to apply the right conservation measures.

10.2.6 Greenland waters: community-level risks

What do the actual results imply for the local management of the study area?

- The East Greenland shelf is to a large degree inaccessible to fisheries. Hence, based on only fisheries-dependent data, the state of the environment is insufficiently known for the unfished areas. Therefore the definitions of areas of high risk must remain premature.
- The assemblage dynamics on the shelf depend on the interactions of waters of cold Arctic and warmer North-Atlantic origin, which are in turn modified by atmospheric circulation patterns and bottom topography. Impacts on marine assemblages must therefore be expected at regional rather than local scale.
- Given that the fishery for Atlantic cod is the main human activity in the region, management of community sensitivities towards climate change and fishing pressure can both be achieved through an effective management of the cod stock with associated positive impacts on both community sensitivities.

How functional is the approach in informing and guiding biodiversity policy makers and area managers in their decision making both in the study area and at the European level?

- Fisheries is the only significant direct human impact on the East Greenland shelf. The region does not fall under EU jurisdiction, but respective paragraphs could be amended to European Fisheries Partnership Agreements to ensure that a sufficient proportion of the area remains inaccessible to fisheries.

What is the most urgent take-home message?

Due to a significant drop in sea surface temperature in Greenlandic waters in the period after 1990, the time series of community sensitivities to climate change and fishing pressure can be separated into three sections, with the most recent warm period from 2003 to present being characterized by a boreal assemblage dominated by Atlantic cod.

Spatially, the distribution of boreal and Arctic components of the fish assemblage depends on the interaction between warm Atlantic waters and Arctic currents, creating a highly dynamic environment.

Given the vulnerability of Arctic fish communities, spatial management on protection should therefore be flexible and adaptive.

10.2.7 North Sea epibenthos: community-level risks

What do the actual results imply for the local management of the study area?

- North Sea benthic biodiversity is not static but continually shifting in space and time due to the influence of factors like trawling, nutrients, climate change and other environmental variables which are themselves changing through time.
- Monitoring combined with adaptive management is essential to ensure effective protection measures keep pace with ecological changes.
- Trait-based approaches allow us to link biodiversity patterns directly to ecosystem functioning and pressures, offering a useful tool for adaptive spatial planning.
- Sensitive communities are shifting southwards, suggesting that next to static MPAs other spatial protection may be needed to protect emerging biodiversity hotspots.
- A potential option for local management is the integration of regular monitoring with flexible protection strategies to respond to these shifts.

How functional is the approach in informing and guiding biodiversity policy makers and area managers in their decision making both in the study area and at the European level?

- The trait-based risk approach provides spatially explicit, trait-based indicators that directly identify vulnerable habitats and communities.
- This method is easily transferable to other European seas which would be useful for comparison across regions for EU biodiversity targets.

What is the most urgent take-home message?

The findings highlight that sensitive ecological communities are dynamic and continual monitoring and adaptive management is necessary for spatial protection to effectively protect high-diversity benthic ecosystems.

10.2.8 Sensitivity of marine benthic habitats

What do the actual results imply for the local management of the study area?

- **Effective conservation requires habitat-specific information:** To safeguard biodiversity, it is essential to integrate the ecological value, sensitivity and risk assessments into spatial planning. This ensures that habitats that are most sensitive and of highest ecological value are prioritised for protection. Meanwhile stressors and overarching pressures (*Figure 1-3*) should be monitored systematically. Such an approach aligns with international commitments (e.g., MSFD, EU 30x30[2], Nature Restoration Law) and supports resilient, ecosystem-based management under accelerating climate change.

[2] Biodiversity strategy for 2030 - Environment - European Commission, assessed 30-09-2025.

- **Targeted protection of priority habitats:** Tailored management measures should be implemented for habitats of high ecological value and structural complexity (biogenic reefs, rocky reefs, seamounts, seagrasses, canyons and biological aggregations in soft sediments). Such tailored measurements may include no-take zones and restrictions on destructive fishing gears. Additionally, it is needed to ensure an effective representation of these priority habitats within local MPAs and MPA networks.
- **Spatial planning with a focus on connectivity:** Local management should ensure that MPA networks account for ecological connectivity. It is needed to safeguard habitats across environmental gradients and to ensure connectivity among patches of the same habitat type. This will enhance the resilience of habitats and species under changing environmental conditions, especially those highly sensitive to climate change stressors, such as macroalgae forests, mud volcanoes and cold seeps, and maërl beds.
- **Integrated monitoring of multiple stressors:** Most habitats are sensitive to more than one stressor: for example, multiple fishing activities, warming, acidification, deoxygenation. This implies that monitoring programmes should be strengthened to assess cumulative impacts (both stressors and responding ecological components) and enable early detection of ecological changes.
- **Preventive management in emerging risk areas:** Some habitats may have lower ecological value (e.g., abyssal plains) and therefore be overlooked. Still our findings underscore the importance of addressing growing stressors and pressures, such as the expansion of hypoxic zones, through precautionary monitoring and timely mitigation measures

How functional is the approach in informing and guiding biodiversity policy makers and area managers in their decision making both in the study area and at the European level?

- The approach translates complex ecological assessments of habitats into actionable recommendations. It allows the identification of priority habitats, habitats more sensitive to cumulative effects, as well as stressor-specific sensitivities. The approach supports policy makers and managers in designing effective, ecosystem-based conservation strategies for habitats at both regional and European levels. The approach can be applied in any marine region, and can be extended to other pressures not considered here, for example pollution and marine litter.

What is the most urgent take-home message?

Immediate action is needed to safeguard marine habitats, especially those of high ecological value and structural complexity, as well as those habitats highly sensitive to climate change. This can be achieved through targeted habitat-specific protection from fishing and other pressures. It is urgent to implement monitoring programmes that allow the assessment of the state of habitats and their exposure to pressures, in order to assess and prioritise management actions. Dedicated spatial planning on connecting MPAs is needed to ensure climate resilience, connectivity and species exchange.

10.2.9 Risks from invasives in the Mediterranean

What do the actual results imply for the local management of the study area?

- In the Mediterranean Sea, non-indigenous species – especially those of Lessepsian origin (i.e. that have entered from the Red Sea via the Suez Canal) – have substantially increased in recent decades and are rapidly expanding westward. Several of these are invasive, affecting native fish species.
- Invasive species pressures should be addressed by strengthening monitoring, particularly in the Eastern Mediterranean but also basin-wide, and by prioritising habitat protections to preserve endemic species and vulnerable native communities.

How functional is the approach in informing and guiding biodiversity policy makers and area managers in their decision making both in the study area and at the European level?

- The Lessepsian species analysis framework utilises data from standardised scientific trawl surveys that can be annually updated, in order to provide spatial information on the current and future spread of these non-indigenous species.
- The analysis can inform on invasive species 'hotspots', guiding managers and policy makers towards areas with urgent need of specialised mitigation actions, such as targeted removals of harmful species or incentivising fisheries to shift their target species towards these.

What is the most urgent take-home message?

Non-indigenous species of Lessepsian origin are spreading and will continue to spread throughout the Mediterranean. Special action plans, including increased monitoring effort, research on impacts and impact mitigation are needed. The most common alien species should be assessed on a regular basis.

10.3 Perspectives

In the context of marine biodiversity conservation in European regional seas, we have used trait-based approaches to assess the sensitivities, vulnerabilities and risks of marine life to two dominant stressors – climate change and fishing. We have not only done so for marine communities (both fish and epibenthic species) but have also developed a framework to assess marine benthic habitat sensitivities. Moreover, we have examined the risks from invasives in the Mediterranean Sea, where this is considered a priority. This report has produced a broad range of 'sensitivity maps' and 'risk maps' that can inform what areas are characterised by higher prevalence of sensitive species, and may benefit most from protection; and in what areas species are at highest risk – so-called 'hotspots of risk.'

One important, next step is to assess whether areas of high risk are covered by marine protected areas (MPAs): specifically, to what extent are these matched, or are there potential mismatches? This includes taking the types of protection measures into account. An assessment will be made whether the emerging risk areas are under adequate levels of protection. This task is to be addressed in B-USEFUL deliverable D4.3, and will be directly linked to the policy question: based on communities' sensitivities and risks, are there any indications that MPAs may have to be adapted to reduce any potentially encountered high risks?

In future decades, ongoing climate change is projected to lead to further temperature rises in European regional seas; moreover there will be local differences in the degree of warming. Hence the projected climate change pressure will be different toward the middle of the 21st century compared to today. Given the spatio-temporal patterns in community-level sensitivities as described in the present report, we may also expect that the community-level climate risks will be different in future decades compared to the present. Meanwhile, different future scenarios with regards the management of fishing pressure may imply that in future decades, the spatio-temporal patterns in fishing pressure will differ from those of today. This will imply that (combined with communities' sensitivities) the community-level risks from fishing pressure will be different. Building on the present study, we aim to project future patterns in risks from both fishing pressure and climate change, for European marine communities, as B-USEFUL deliverable D5.2 (part of work-package 5 "Forecasting and scenario simulations"). The intention is to project future marine community risks based on sea temperature projections up to 2050, and under scenarios that either assume a 'business-as-usual' scenario with regards trawling pressure, or modest or substantial reductions in trawling pressure.

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A. Appendix: Mediterranean Sea

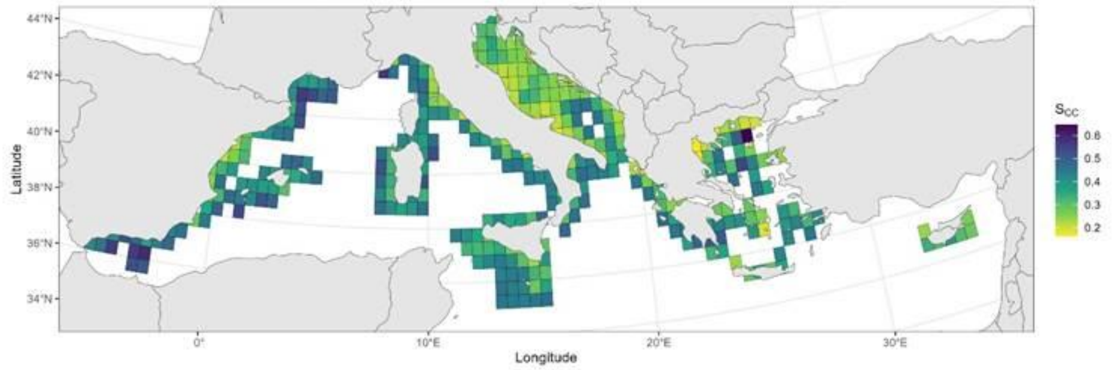

Figure A-1. Spatial variations in community-level sensitivity to climate change (S_{CC}, averaged over 2012-2021) across the Mediterranean study area, estimated over a 0.5° × 0.5° resolution grid.

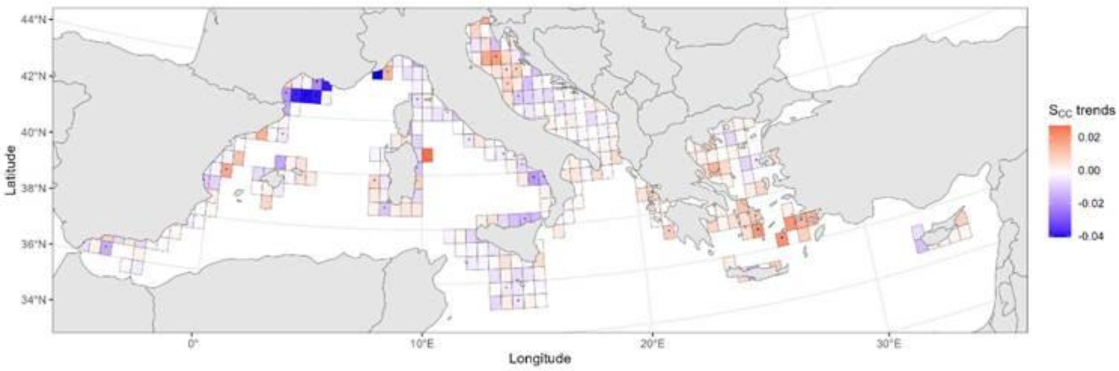

Figure A-2. Spatio-temporal variations in community-level sensitivity to climate change (S_{CC}) across the Mediterranean study area, displayed on a 0.5° x 0.5° resolution grid. Red and violet shading, respectively, indicate increases and decreases in S_{CC} over the period 2012-2021 (see legend). Black dots indicate grid cells where linear correlation analysis revealed statistically significant (Pearson test, $p < 0.05$) trends over time.

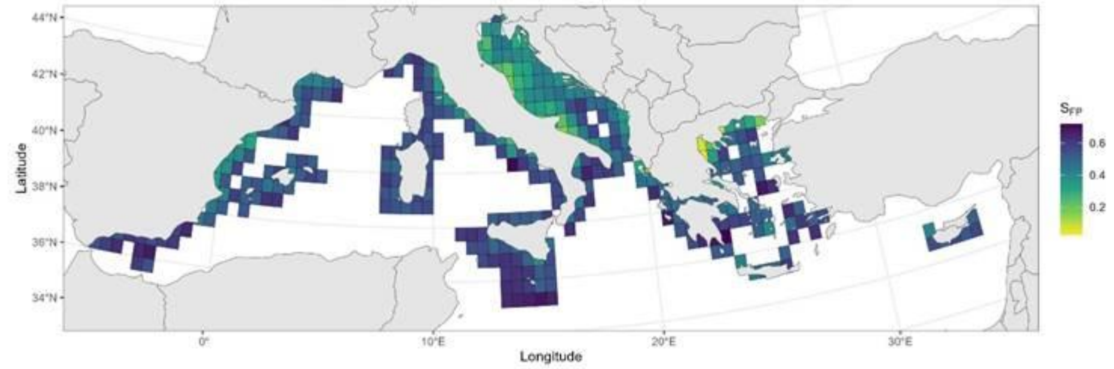

Figure A-3. Spatial variations in community-level sensitivity to fishing pressure (S_{FP}, averaged over 2012-2021) across the Mediterranean study area, estimated over a 0.5° × 0.5° resolution grid.

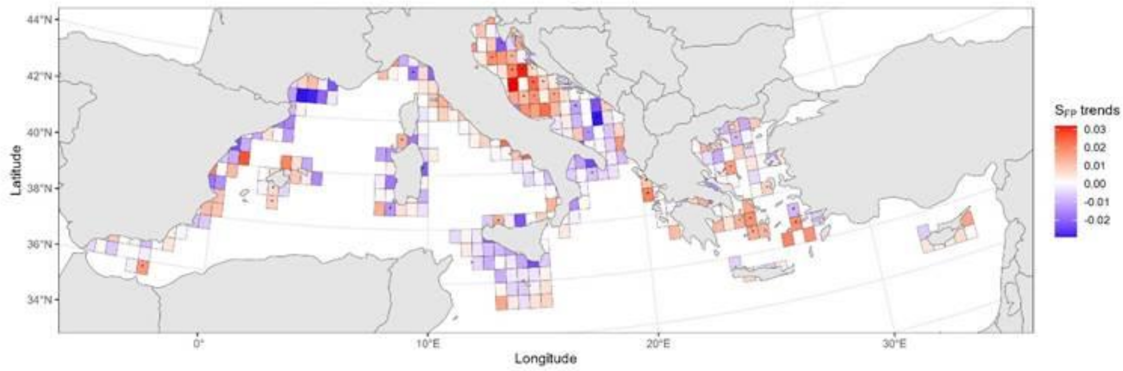

Figure A-4. Spatio-temporal variations in community-level sensitivity to FP (S_{FP}) across the Mediterranean study area, displayed on a 0.5° x 0.5° resolution grid. Red and violet shading, respectively, indicate increases and decreases in S_{CC} over the period 2012-2021 (see legend). Black dots indicate grid cells where the linear correlation analysis revealed statistically significant ($p < 0.05$) trends over time.

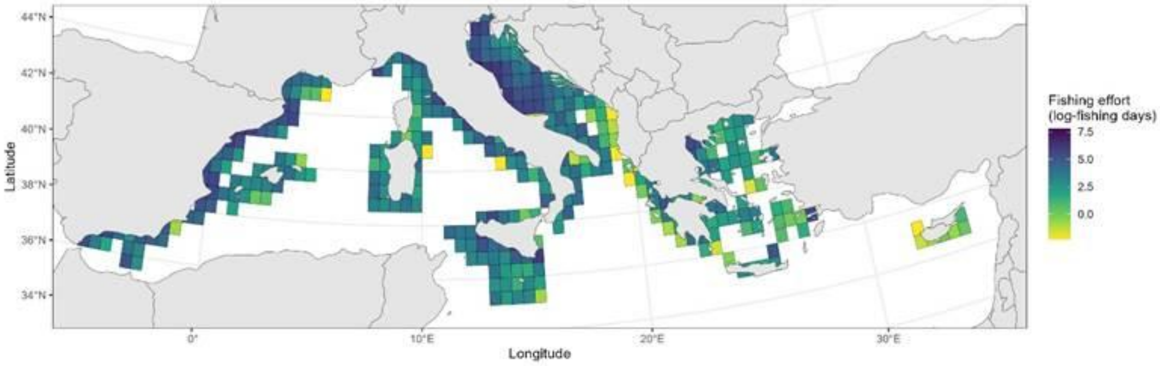

Figure A-5. Spatial distribution of demersal fisheries' fishing effort across the Mediterranean study area, aggregated over a 0.5° × 0.5° resolution grid. Fishing effort is expressed as the natural logarithm (ln) of fishing days.

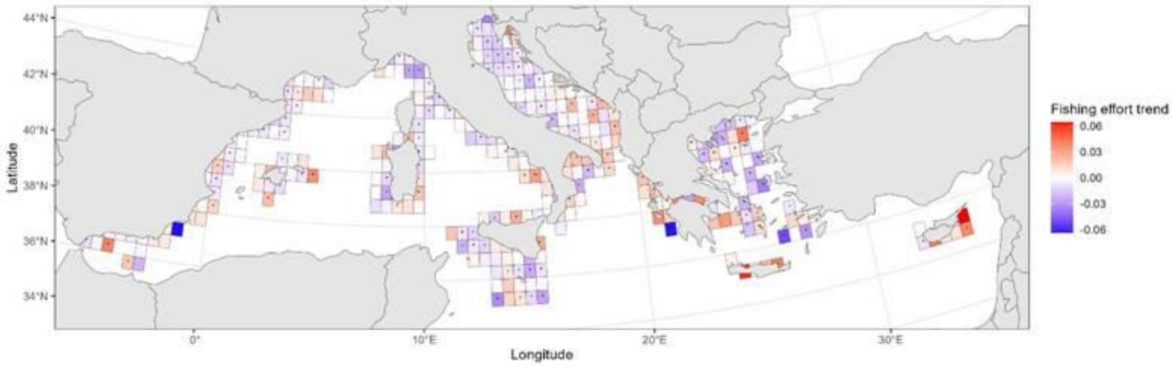

Figure A-6. Spatio-temporal variations in the fishing effort of demersal fisheries across the Mediterranean study area, displayed on a 0.5° x 0.5° resolution grid. Red and violet shading, respectively, indicate increases and decreases in fishing effort over the period 2012-2021 (see legend). Black dots indicate grid cells where the linear correlation analysis revealed statistically significant trends over time.

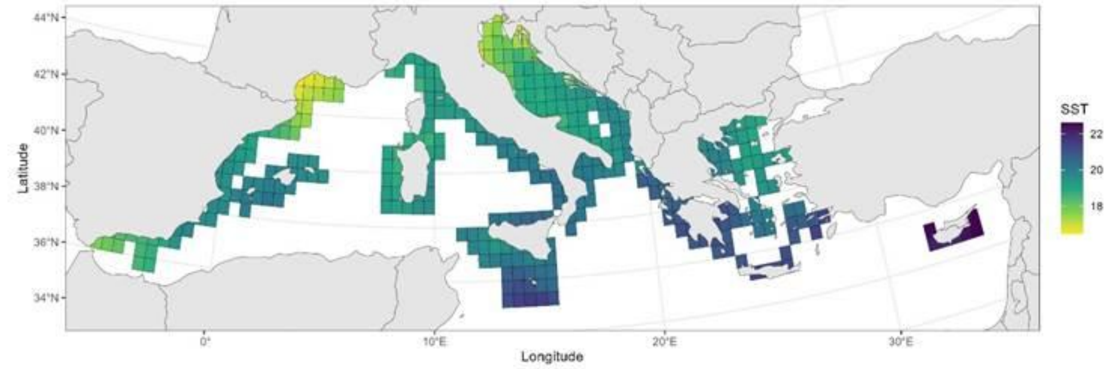

Figure A-7. Spatial variations in average sea surface temperature (SST, averaged over 2012-2021) across the Mediterranean study area, estimated over a 0.5° × 0.5° resolution grid.

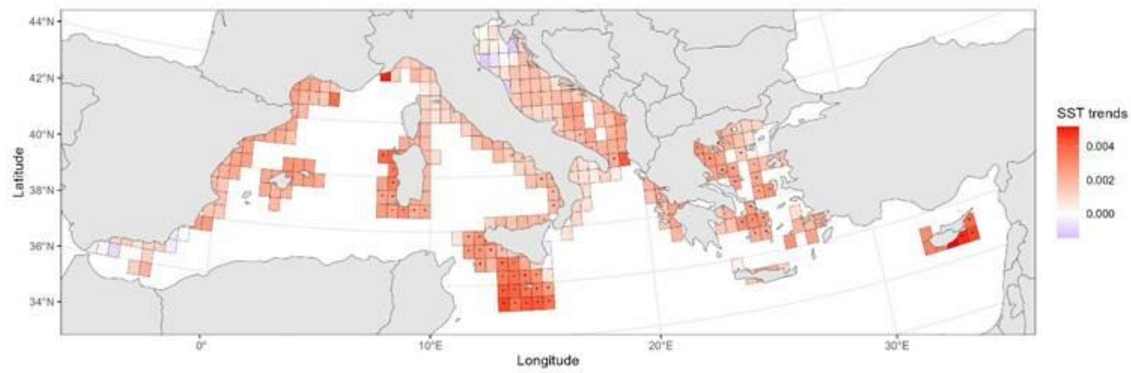

Figure A-8. Spatio-temporal variations in Sea Surface Temperature (SST) across the Mediterranean study area, displayed on a 0.5° x 0.5° resolution grid. Red and violet shading, respectively, indicate increases and decreases in SST over the period 2012-2021 (see legend). Black dots indicate grid cells where the linear correlation analysis revealed statistically significant trends over time.

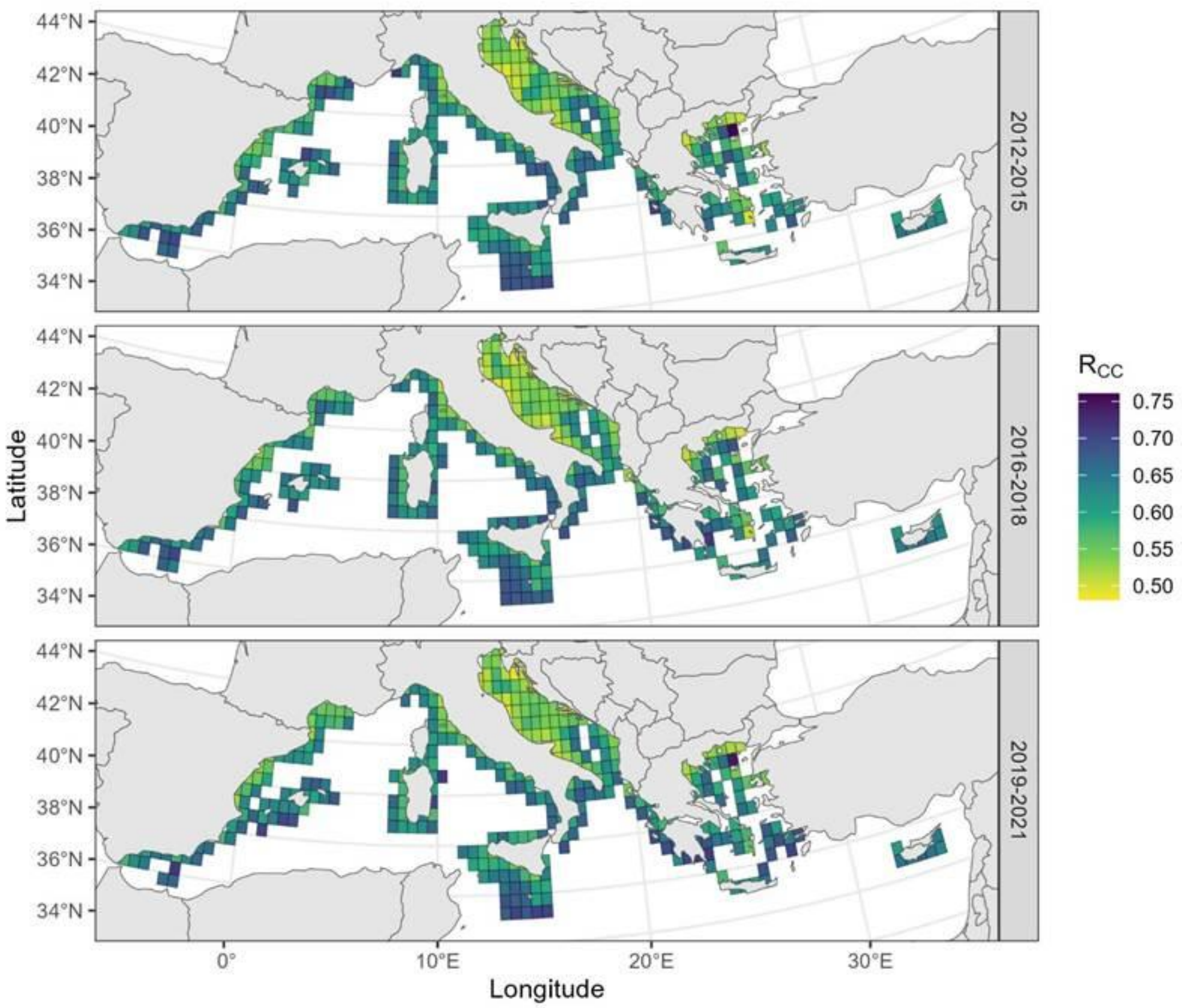

Figure A-9. Spatiotemporal distribution of climate-related risk (R_{CC}) for demersal communities in the Mediterranean Sea. Maps show average R_{CC} values for three time periods: 2012–2015, 2016–2018, and 2019–2021.

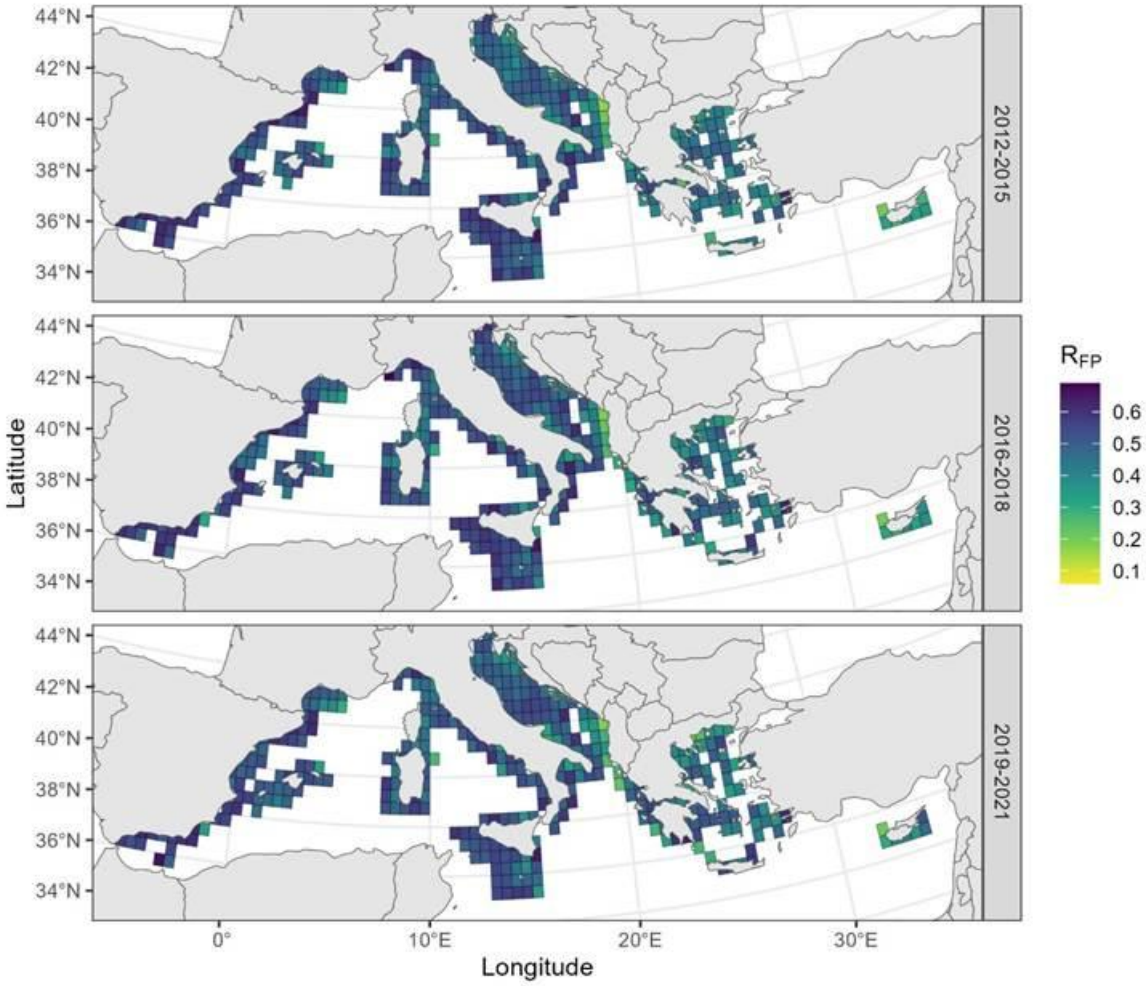

Figure A-10. Spatiotemporal distribution of fishing pressure-related risk (R_{FP}) for demersal communities in the Mediterranean Sea. Maps show average R_{FP} values for three time periods: 2012–2015, 2016–2018, and 2019–2021.

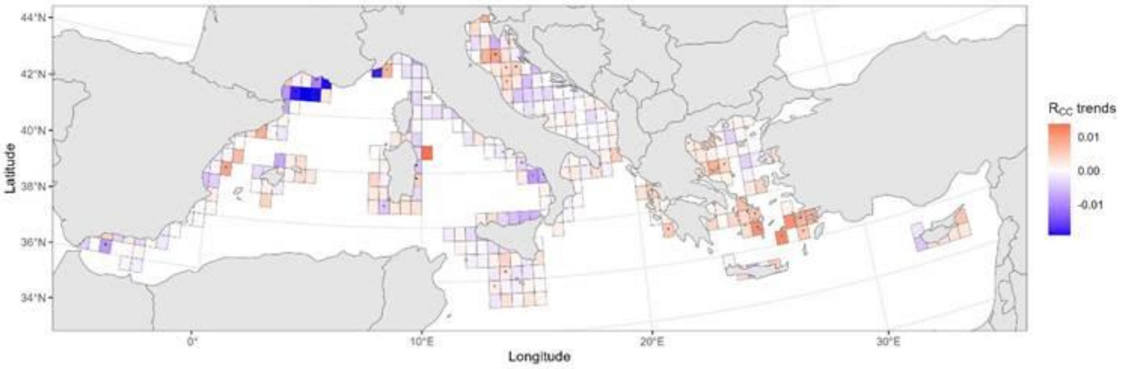

Figure A-11. Map of the temporal trends of risk for climate change (R_{CC}) estimated over the time series at a 0.5°x0.5° grid resolution level. Black dots indicate grid cells where the linear correlation analysis revealed statistically significant trends over time.

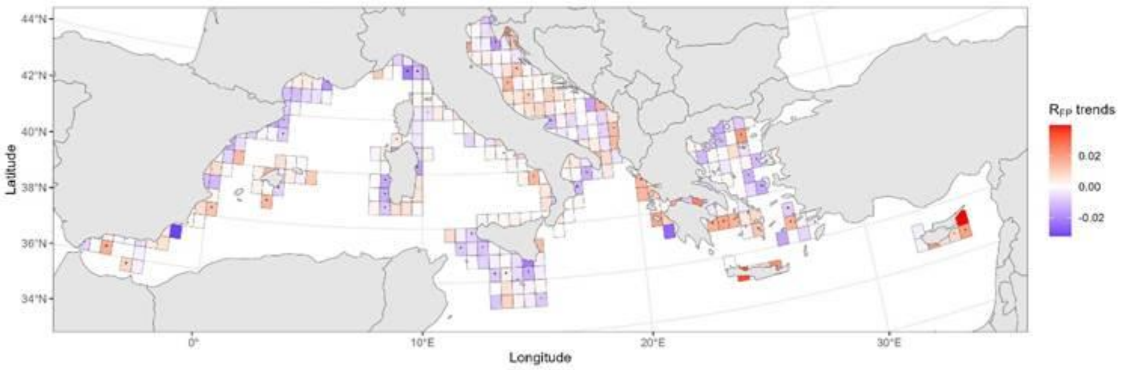

Figure A-12. Map of the temporal trends of risk for fishing pressure (R_{FP}) estimated over the time series at a 0.5°x0.5° grid resolution level. Black dots indicate grid cells where the linear correlation analysis revealed statistically significant trends over time

Table A-1. Thresholds and definition used to characterise the species-specific and ecological preferences and sensitivity to fishing pressure on the base of the biological traits.

Sensitivity to fishing (trawling) pressure	Low sensitivity (Score = 1)	Moderate sensitivity (Score = 2)	High sensitivity (Score = 3)	Very high sensitivity (Score = 4)
Longevity	< 3.4 years	3.4 - 9 years	> 11 years	
Body size	Small < 7 cm	Medium 7 - 35 cm	Large > 35 cm	
Fecundity	> 11310 eggs	11310 - 109492 eggs	< 109492 eggs	
Offspring size	> 1.10 mm	0.79 - 1.10 mm	< 0.79 mm	
Growth coefficient	K > 0.55	0.20 – 0.55	K < 0.20	
Trophic level	< 2.6	2.6 – 3.6	> 3.6	
Age at maturity	< 1.3 years	1.3 – 3 years	> 3 years	
Parental care	Non-guarder planktonic lay, Non-guarder	Non-guarder demersal lay	Guarder brooder (external care)	Guarder bearer (internal care)
Habitat	Pelagic, Bathypelagic	Demersal, Bathydemersal	Benthic, Suprabenthic	
Motility	Swimmer	Burrower, Crawler	Sessile	
Body shape	Fusiform	Eel-like, Elongated, Bullet-like	Flat, Lenticular	Globular, Compressiform, Hook shaped
Feeding mode	Scavenger, Generalist (including piscivorous), Detritivorous	Planktivores	Surface deposit feeders, Benthivores, Suprabenthic feeders	Suspensivores, Suspension feeders

Table A-2. Thresholds and definition used to characterise the species-specific and ecological preferences and sensitivity to climate change (warming) on the base of the biological traits.

Sensitivity to climate change	Low sensitivity (Score = 1)	Moderate sensitivity (Score = 2)	High sensitivity (Score = 3)	Very high sensitivity (Score = 4)
Spawning period	Non-seasonal	Wide spawning season	Narrow spawning season	
Parental care	Guarder-Brooder, Guarder-Bearer	Non-guarder-Planktonic lay	Non-guarder	Non-guarder-Benthic lay
Habitat	Pelagic, Bathypelagic	Demersal, Bathydemersal	Benthic, Suprabenthic	
Surface Temp. affinity	> 19.3°C	18.9 – 19.3°C	≤ 18.9°C	
Surface Temp. specificity (STS)	> 29.4°C	28.9 – 29.4°C	≤ 28.9°C	
Bottom Temp. affinity	> 14.9°C	14.3 – 15.0°C	≤ 14.3°C	
Bottom Temp. specificity (BTS)	> 25.6	22.3 – 27.4°C	≤ 22.7°C	
Mean depth affinity	< 275m	107 – 275m	≤ 107m	
Depth specificity	≤741m	741 - 797m	> 797m	

*Table A-3. Spearman trend test summary of community-level sensitivities, pressure exposure indices and risk levels by GSA and subregion. For each area, ρ (Spearman's trend correlation) and its coded p-value are reported for S_{CC} (climate change sensitivity), S_{FP} (fishing pressure sensitivity), SST (sea surface temperature), FP (fishing effort), R_{CC} (climate change risk), R_{FP} (fishing pressure risk), and R_{cum} (cumulative risk). Significance codes: p-value ≤ 0.001 '***'; 0.001 < p-value ≤ 0.01 '**'; 0.01 < p-value ≤ 0.05 '*'; 0.05 < p-value ≤ 0.1 '.'; no symbol for p-value > 0.1.*

	S_{CC}		S_{FP}		SST		Fishing effort		R_{CC}		R_{FP}		R_{cum}	
Area	**rho**	**p**	**rho**	**p**	**rho**	**p**	**rho**	**p**	**rho**	**p**	**rho**	**p**	**rho**	**p**
GSA 1	-0.533		-0.350		0.383		-0.067		-0.048	*	-0.039	.	-0.206	***
GSA 5	-0.224		0.406		0.539		-0.261		-0.015		0.016		-0.073	***
GSA 6	-0.006		0.006		0.139		-0.164		-0.058	***	-0.060	***	-0.078	***
GSA 7	-0.721	*	-0.418		0.394		0.115		-0.231	***	-0.234	***	-0.267	***
GSA 8	-0.517		-0.417		0.583		-0.383		-0.119	***	-0.226	***	-0.301	***
GSA 9	-0.830	**	0.612	.	0.503		-0.661	*	-0.074	***	-0.110	***	-0.186	***
GSA 10	-0.721	*	0.067		0.503		0.285		-0.082	***	-0.008		-0.148	***
GSA 11	-0.624	.	-0.648	*	0.733	*	-0.345		-0.040	*	-0.152	***	-0.110	***
GSA 15	-0.648	*	-0.212		0.503		-0.697	*	0.009		-0.124	***	-0.108	***
GSA 16	-0.394		-0.297		0.636	.	-0.552		-0.043	*	-0.206	***	-0.166	***
GSA 17	-0.382		0.842	**	0.503		-0.867	**	-0.050	***	0.249	***	0.118	***
GSA 18	-0.224		-0.115		0.212		0.733	*	-0.038	*	0.067	***	-0.028	.
GSA 19	-0.418		-0.697	*	0.200		0.442		-0.034	.	-0.001		-0.081	***
GSA 20	0.771		0.886	*	0.486		0.829	.	0.044	*	0.231	***	0.103	***
GSA 22	0.893	*	0.929	**	0.857	*	-0.964	**	0.097	***	0.091	***	0.116	***
GSA 23	0.257		-0.029		0.486		0.600		0.240	***	0.325	***	0.452	***
GSA 25	0.083		0.317		0.767	*	0.683	.	0.188	***	0.327	***	0.249	***
Adriatic Sea	-0.248		0.709	*	0.248		-0.333		-0.042	***	0.142	***	0.062	***
Central Mediterranean Sea	-0.636	.	-0.733	*	0.758	*	-0.576	.	-0.009		-0.048	***	-0.062	***
Eastern Mediterranean Sea	0.709	*	0.164		0.055		0.345		0.093	***	0.117	***	0.140	***
Western Mediterranean Sea	-0.842	**	-0.224		0.576	.	-0.188		-0.055	***	-0.061	***	-0.096	***

B. Appendix: Functional Originality

Table B-1. Functional traits used in the calculation of functional originality metrics. Trait names are standardised after Morim et al. (2023.)

Trait name	Description	Range or categories
body shape	nominal: the lateral or cross-sectional body shape	"fusiform/normal", "elongated", "eel-like", "flat", "short and/or deep", "compressiform"
caudal fin shape	nominal, the caudal fin shape	"forked", "rounded", "truncated", "lunate", "pointed", or "heterocercal"
aspect ratio of caudal fin	numeric, caudal fin aspect ratio, i.e., squared height divided by the surface area	0.21 to 4.71
body length	numeric, maximum recorded length	3.00 to 300.00 cm
body mass	numeric, weight corresponding to the maximum asymptotic length an individual can reach (parameter in the von Bertalanffy growth equation)	0.75 to 90,527.39 g
reproductive guild and habitat type of settlement	nominal, combines the reproductive guild of fish and the amount of parental care, as well as information on the place of egg deposition or development	"guarder-brooder", "guarder-bearer", "non-guarder unknown" (when egg place of development unknown), "non-guarder planktonic lay", and "non-guarder benthic lay"
food type (categoric)	nominal, diet or feeding mode	"planktivorous", "benthivorous", "piscivorous", or "generalist"
food type (numeric)	numeric, position in the food web (ratio calculated from isotopic signatures)	3.0 to 4.50
life history rate	numeric; speed at which an individual reaches its asymptotic size (parameter k in the von Bertalanffy growth equation)	~ 0.04 to 3.65 [1/year]
natural mortality	numeric; natural mortality, share of the annual population that dies of natural causes	~0.05 to ~6.46 [1/year]
age at maturity	numeric; the age at which half of the population has reached maturity, averaged over sexes	~0.25 to ~36.20 years
fecundity	numeric; the number of eggs or offspring produced by a female per year (if spawning only once) or per batch (if spawning multiple times per year)	3.50 to 60,000,000

offspring size	numeric, egg diameter for teleost fish; length of egg case for skates and rays; body length of a new-born pup for sharks	0.32 to 360.00 mm
habitat	nominal; the (predominant) position of a fish in the water column	"pelagic", "benthic", "benthopelagic", "demersal"
optimal temperature	numeric; average of the common temperature range	4.10 to 24.10 °C
thermal tolerance	numeric; difference between the maximum and minimum temperature at which the species was recorded	0.45 to 20.20 °C
vertical biological zone	nominal; preferred biological zone, based on minimum and maximum recorded depth	"shelf", "slope", or "both"

Table B-2. Mathematical formulation of the functional originality metrics and risk-weighted indicators calculated for each species i. in the functional space of nine Principal Components j. I: IUCN categories, p: relative abundance. S_{CC}: sensitivity to climate change. S_{FP}: sensitivity to fishing pressure. References: [1] Magneville et al. 2022, [2] Violle et al. 2017, [3] Mouillot et al. 2013, [4] Griffin et al. 2020, [5] Pimiento et al. 2020.

Metric	Description	Ref
FUn	Functional Uniqueness. Mean of the distances $D_{i,j}$ between species *i* and its five nearest functional neighbours $k_{1,2,...5}$. $$FUn_i = \frac{1}{5}\sum_{k=1}^{5} D_{i,k}$$	1, 2
FSp	Functional Specialisation. Sum of the Euclidean distances between the coordinates $x_{i,j}$ of a species *i* and the mean coordinate O_j of each of the nine Principal Component $j_{1,2,...,9}$ $$FSp_i = \sqrt{\sum_{j=1}^{9}(x_{ij} - O_j)^2} \text{ with } O_j = \frac{1}{n}\sum_{i=1}^{n} x_{ij}$$	1, 2, 3
FUSE	Functional Uniqueness, Specialisation, and endangerment. *FUn* and *FSp* weighed by the IUCN categories *I*. $$FUSE_i = \log(1 + (FUn_i * I) + \log(1 + (FSp_i * I)$$	1, 4, 5
FUSA	Functional rarity. *FUn* and *FSp* weighed by taxonomic scarcity, calculated as the multiplicative inverse of the relative abundance *p*. $$FUSA_i = \log\left(1 + \left(FUn_i * \frac{1}{p_i}\right) + \log\left(1 + (FSp_i * \frac{1}{p_i}\right)\right.\right.$$	
$FUSS_{CC}$	Functional originality and sensitivity to climate change. *FUn* and *FSp* weighed by the sensitivity to climate change S_{CC}. $$FUSS_{CC,i} = \log(1 + (FUn_i * S_{CC,i}) + \log(1 + (FSp_i * S_{CC,i})$$	
$FUSS_{FP}$	Functional originality and sensitivity to fishing pressure S_{FP}. $$FUSS_{FP,i} = \log(1 + (FUn_i * S_{FP,i}) + \log(1 + (FSp_i * S_{FP,i})$$	

C. Appendix: Northeast Atlantic

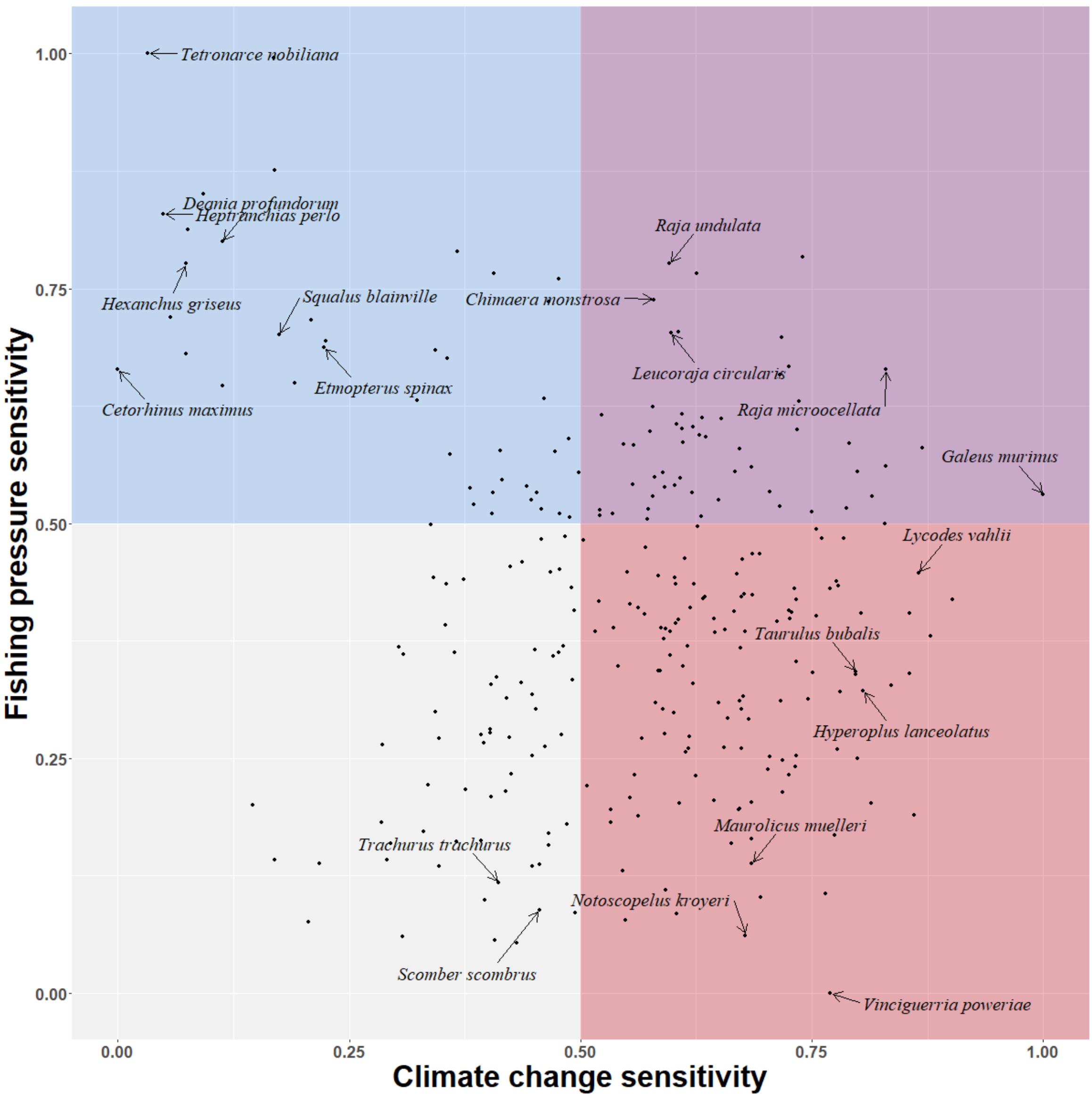

Figure C-1. Species-level sensitivities to fishing pressure and climate change in Northeast Atlantic in a two-dimensional space. Each point corresponds to a species. The background colour of each quadrant reflects combined sensitivity levels: species with low sensitivity to both pressures in white (bottom left); species sensitive to climate change but resistant to fishing in red (bottom right); species sensitive to fishing but resistant to climate change in blue (top left); and species sensitive to both pressures in purple (top right).

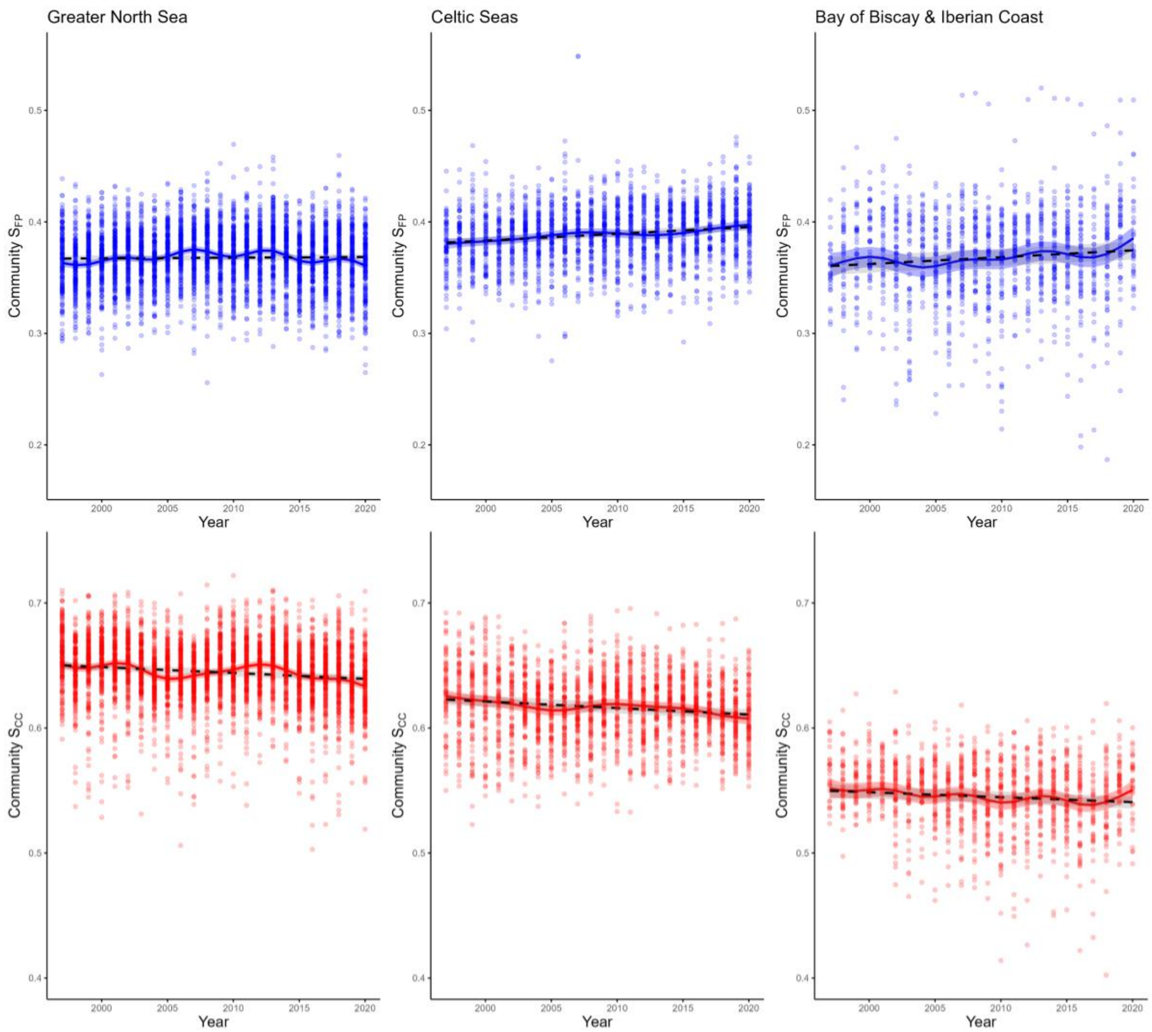

Figure C-2. Long-term changes in community-level sensitivity to fishing pressure, S_{FP} (top), and climate change, S_{CC} (bottom), for the Greater North Sea, Celtic Seas and Bay of Biscay [in the latter, consider excluding Portuguese Coast but this might not be needed if mixed model used]. GAMM trend in blue (with CIs) and LMM trend in red (with CIs), raw data per ICES rectangle shown in blue.

D. Appendix: Icelandic waters

Study area

The data for this study has been collected through bottom trawling as part of the Icelandic Groundfish Survey (SMB) and the Autumn Groundfish Survey (SMH), carried out annually by the Marine and Freshwater Institute of Iceland. The temporal span of the data is from 1996 to 2024, the depth range is 0-1500 metres, while the spatial span is between 62° 12' 50.4" N, 31° 32' 12.6" W and 68° 19' 43.2" N, 9° 36' 49.8" W.

Species selection

For this study, only data concerning species belonging to the classes Actinopterygii, Elasmobranchii, Holocephali, Myxini and Petromyzontida have been used. Rare species with less than 10 occurrence records in time (years) and space (ICES rectangles), and species for which all the selected traits could not be retrieved or estimated were excluded from the analysis (114 species). Pelagic and bathypelagic species were also removed, due to their lower catchability in bottom-trawled gear which can lead to underestimation of their abundance (Walker et al. 2017). The benthopelagic species *Clupea harengus*, *Cyclopterus lumpus* and *Mallotus villosus* were also removed due to possible large geographical variability in abundance given by their mobility. The number of individuals/km^2 was estimated for each species at each site using data on length distribution and fishing gear efficiency estimates from Walker et al. (2017).

Fishing intensity data

Fishing intensity was estimated using data on bottom trawling from logbooks property of the Icelandic Ministry of Fisheries (Fiskistofa 2025). This data was re-elaborated using a methodology similar to the one found in Gerritsen et al. (2013): a nested grid was applied to divide the area into cells containing a roughly equal amount of starting points of the trawling events registered in the logbooks, with the cells being smaller in areas where these points are more clustered; then, the swept area for each of these events was estimated by multiplying the trawling hours by a sailing speed of 4 knots and a breadth of the trawl net opening of 200 m; afterwards, the estimates of swept area calculated of each trawling event belonging to the same cell were summed together, and divided by the area of the cell. This way, for every month in the period 1995 - 2024 a raster is produced, with estimates on how many times the seabed in each cell has been impacted by fishing gear. The final measure of fishing intensity related to each sample used in the study was calculated as the average value for a 20 km radius around each sampling point, for the 12 months preceding the month in which the sample was collected.

Species traits and calculation of species' sensitivity scores

To select the traits used to characterize species in terms of their sensitivity to climate change and fishing pressure, a procedure and rationale similar to the one adopted in Polo et al. (2025) was used. Scores were assigned to trait categories depending on the sensitivity to each of the considered pressures that these conferred to the species. To assign scores, continuous traits were categorised by dividing them into quartiles. A summary of the scores used for the calculation of species' S_{CC} and S_{FP} scores can be found in *Table D-1* and *Table D-2*.

Table D-1. Biological traits and ecological preferences of the considered species that were used to score their sensitivity to climate change (S_{CC}). The last six traits are numerical and were characterized by dividing the continuous variable in quantiles.

Trait	**Score = 1**	**Score = 2**	**Score = 3**
Spawning period (months)	> = 9	3 - 9	< 3
Parental care	Guarder/bearer	Non-guarder	
Habitat	Pelagic/bathypelagic	Benthopelagic	Demersal/bathydemersal
SST affinity (°C)	> 13.5	6 – 13.5	< 6
SST specificity (°C)	> 14	8 – 14	< 8
SBT affinity	> 7	2 – 7	< 2
SBT specificity	> 9	5 – 9	< 5
Depth affinity	< -1013	-1013 – -168	> -168
Depth specificity	> 533	106 – 533	< 106

Table D-2. Biological traits and ecological preferences of the considered species that were used to score their sensitivity to fishing effort by bottom trawling (S_{FP}). The last six traits are numerical and were characterized by dividing the continuous variable in quantiles.

Trait	**Score = 1**	**Score = 2**	**Score = 3**	**Score = 4**
Parental care	Non-guarder	Guarder	Bearer	
Habitat	Pelagic, bathypelagic	Benthopelagic	Demersal, bathydemersal	
Body shape	Fusiform	Elongated, eel-like	Flat	Short, deep, compressiform
Diet	Generalist, piscivorous	planktivorous	Benthivorous	
Trophic level	< 3.5	3.5 - 4	> 4	
Offspring size (mm)	< 1	1 – 4.5	> 4.5	
Age maturity (years)	< 2.4	2.4 – 5.5	> 5.5	
Fecundity	> 110,000	415 – 110,000	< 415	
Growth coefficient (1/yrs)	> 0.3	0.1 – 0.3	< 0.1	
Length max (cm)	< 22	22 – 69	> 69	
Age max (years)	< 7.5	7.5 – 18.5	> 18.5	

Species trait data was gathered from trait databases (Beukhof et al. 2019, Froese and Pauly 2022, Thorson et al. 2017), and supplemented with information from recent literature (Coulon et al. 2023, Emblemsvåg et al. 2020). If trait data was not available for the species, data averaged from the genus or family was used. SST and SBT affinity and sensitivity was obtained through the bioclimatic envelopes developed by AQUAMAPS (Kaschner et al. 2019), while depth affinity and sensitivity of each species was extrapolated using presence records from Ocean Biogeographic Information System database (OBIS 2019) and a bathymetric product from General Bathymetric Chart of the Oceans (GEBCO 2024).

Species classification in biogeographical groups

To aid the interpretation of S_{CC} and S_{FP} trends, species were grouped in categories referred to here as 'biogeographic groups' and defined as Arctic, Boreal and Atlantic. Species were classified in each group following the classification provided by Sólmundsson et al (2025) and following its methodology when specie did not have a biogeographic categorization available. This consisted in calculating region-specific density, using the geographic northeast-southwest division used in Stefansdóttir et al. (2010); then, proportional density within the two subareas was used to classify the species as Arctic (>= 90% of density in the northeastern region), Atlantic (>= 90% of density in the southwestern region), while the rest of the species was classified as Boreal. As the first decade of the study (1996-2005) was a period of relatively fast warming (see *Figure D-1*), it was regarded to be unreliable as a reference; therefore, proportional density was calculated from the entirety of the study period.

Supplementary figures and tables

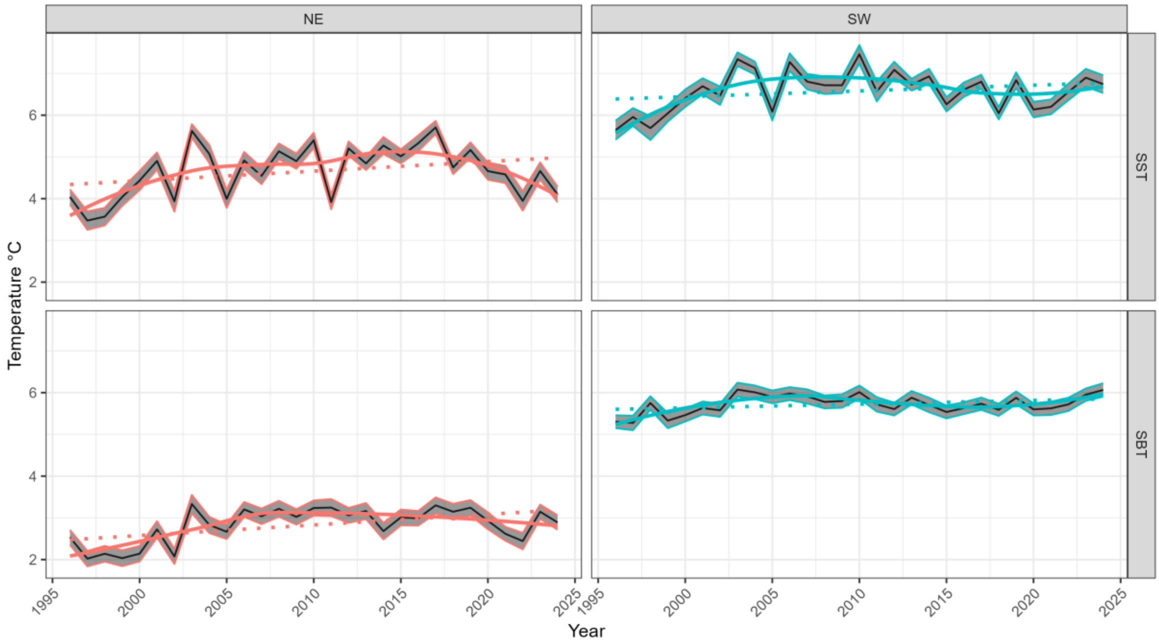

Figure D-1. Temporal trends in temperature for surface seawater temperature (SST) and sea bottom temperature (SBT) in the northeastern (NE) and southwestern (SW) regions of Iceland. The black line represents the yearly average for all the sites, while the shaded grey area represents the 95% confidence interval for the mean. To aid the visualisation of temporal trend, a continuous line using loess regression and a dotted line using linear regression were added.

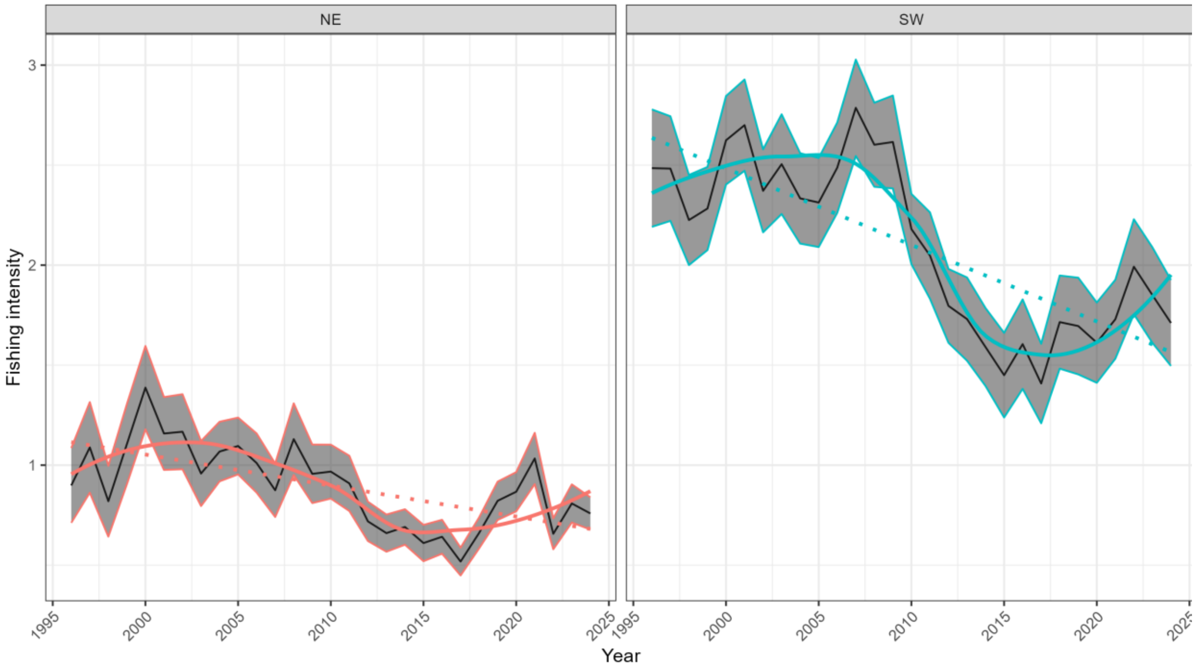

Figure D-2. Temporal trends in fishing intensity (swept area ratio) in the northeastern (NE) and southwestern (SW) regions of Iceland. The black line represents the yearly average for all the sites, while the shaded grey area represents the 95% confidence interval for the mean. To aid the visualisation of temporal trend, a continuous line using loess regression and a dotted line using linear regression were added.

Table D-3. Summary of the results of the linear regressions carried out on the time series sea surface temperature (SST), sea bottom temperature (SBT) and fishing effort. Each model was developed separately for the northeastern (NE) and the southwestern (SW) region. SE refers to the standard error associated to the linear model coefficient. Coefficients with a p <0.05 are highlighted in bold.

Regression	*Region*	*Slope*	*SE*	*p*
SST	**NE**	**0.022**	**0.002**	**$<2.00 \times 10^{-16}$**
	SW	**0.012**	**0.002**	**3.59×10^{-7}**
SBT	**NE**	**0.020**	**0.002**	**$<2.00 \times 10^{-16}$**
	SW	**0.005**	**0.002**	**0.005**
Fishing intensity	**NE**	**-0.016**	**0.002**	**$<2.00 \times 10^{-16}$**
	SW	**-0.039**	**0.003**	**$<2.00 \times 10^{-16}$**

Table D-4. summary of the results of the beta regressions carried out to study temporal trends in the proportion of each one of the 'sensitivity groups' of species. Each model was developed separately for the northeastern (NE) and the southwestern (SW) region. SE refers to the standard error associated to the models' coefficients. Coefficients with a p <0.05 are highlighted in bold.

Regression	Region	Slope	SE	Z-value	*p*
Proportion of species sensitive to both climate change and fishing	NE	1.18×10^{-4}	2.07×10^{-4}	0.5707	0.568
	SW	-3.91×10^{-4}	2.03×10^{-4}	-1.9297	0.054
Proportion of species sensitive to climate change	NE	1.79×10^{-3}	2.36×10^{-4}	7.5975	<0.001
	SW	3.10×10^{-3}	2.41×10^{-4}	12.8643	<0.001
Proportion of species sensitive to fishing	NE	-3.08×10^{-3}	2.42×10^{-4}	-12.6932	<0.001
	SW	-2.70×10^{-3}	2.29×10^{-4}	-11.7724	<0.001
Proportion of species with low sensitivity to both climate change and fishing	NE	1.17×10^{-3}	2.00×10^{-4}	5.8743	<0.001
	SW	-2.82×10^{-6}	2.16×10^{-4}	-0.0131	0.990

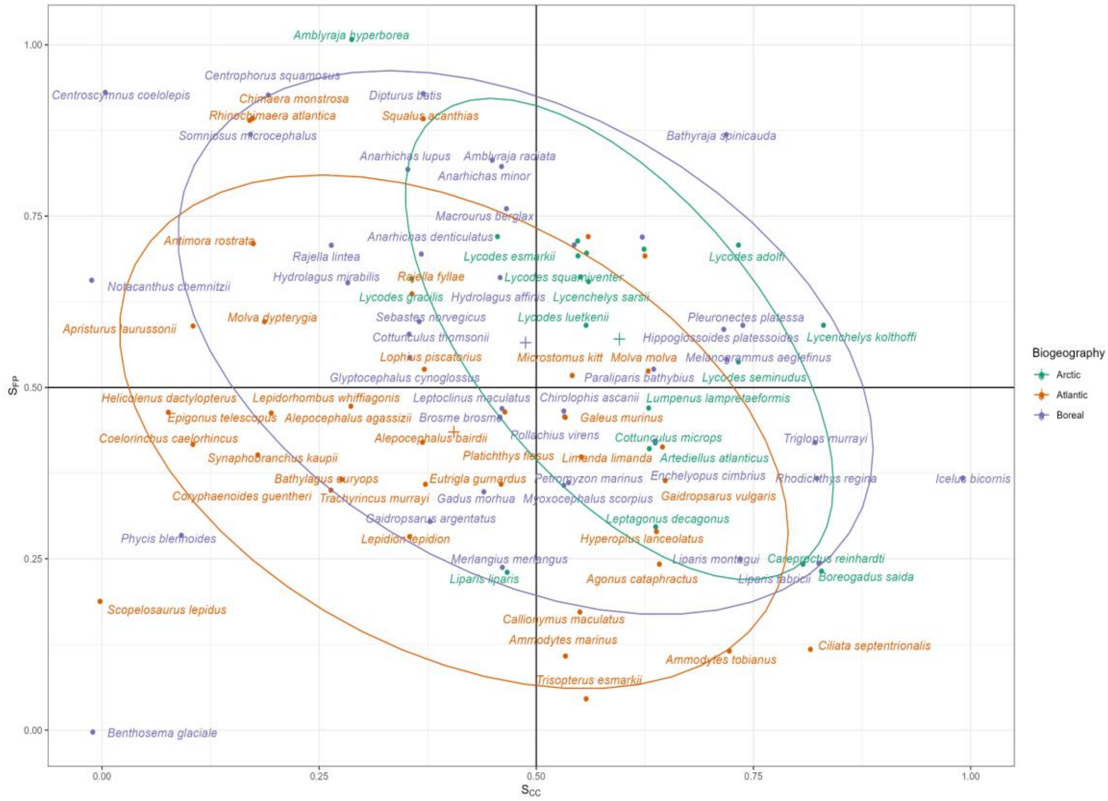

Figure D-3 Species position in the 'sensitivity space'. The x axis represents sensitivity to climate change (S_{CC}) while the y axis represents sensitivity to fishing pressure (S_{FP}). Species are color-coded depending on whether they belong to the Arctic (green), Boreal (purple) or Atlantic (orange) biogeographic group. The cross represents the mean for each group within the space, with the corresponding ellipse representing its 85% confidence region.

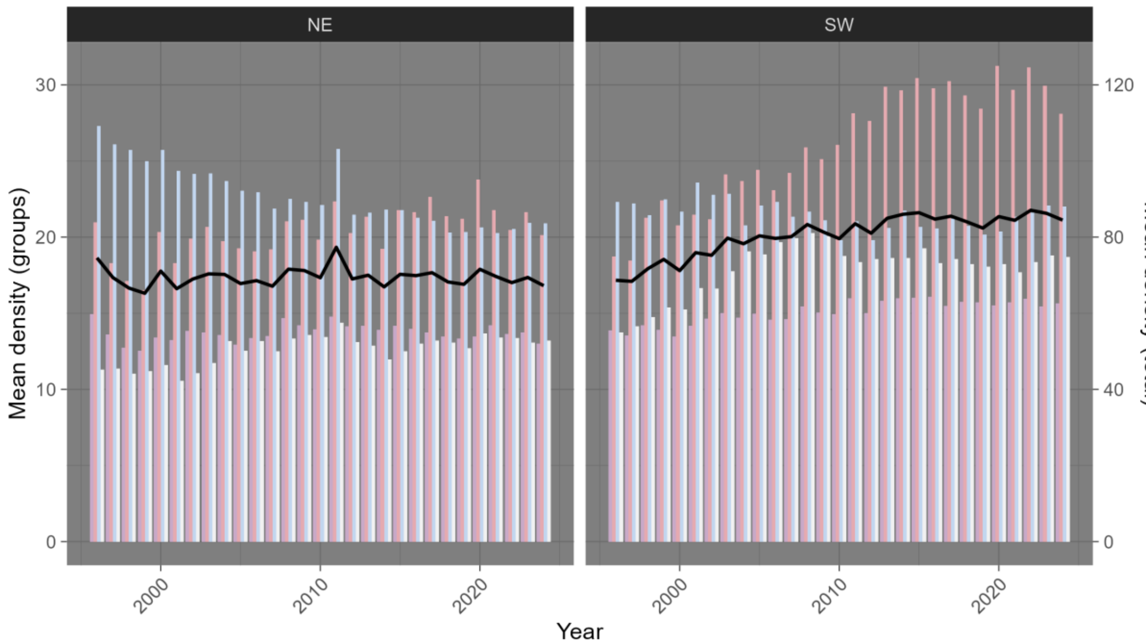

Figure D-4. Yearly mean log-transformed densities for bottom fish species representing four sensitivity groups in northeastern (NE, left) and southwestern (SW, right) regions of Iceland. The sensitivity groups are: fish characterised by high sensitivity (>0.5) to both climate change and fishing pressure (light purple); by high sensitivity only to climate change (light red); by high sensitivity only to fishing pressure (light blue), and by low sensitivity (<0.5) to both pressures (grey). The black line represents the yearly total mean density, and is measured by the y-axis on the right.

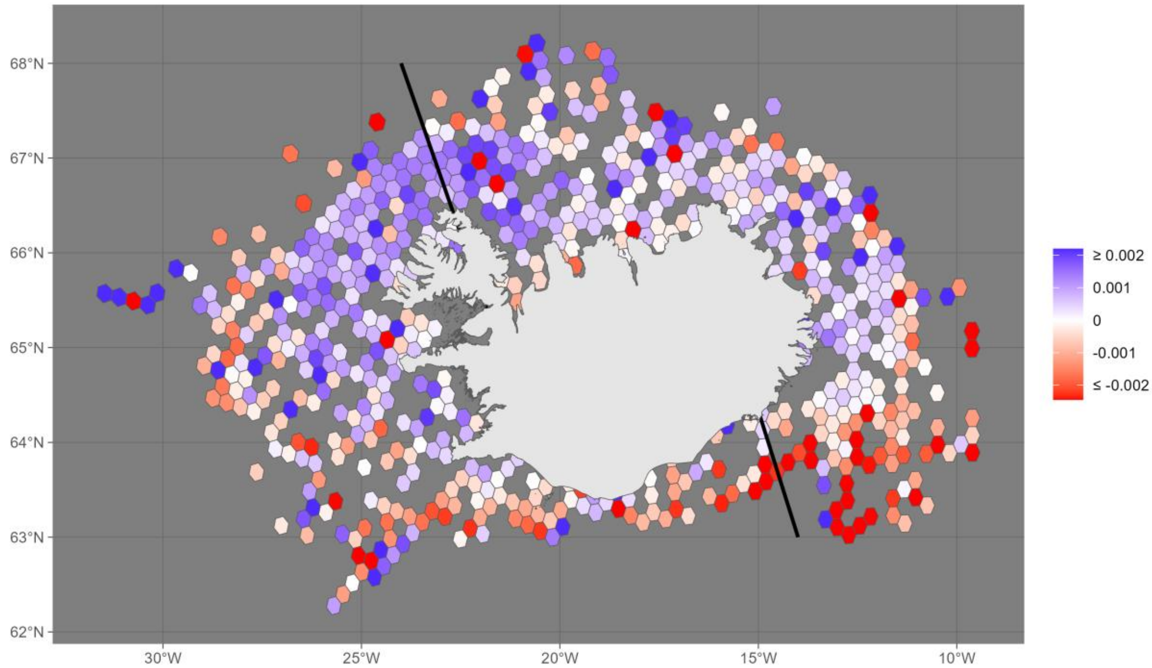

Figure D-5. Yearly change in the sensitivity indicator to climate change (S_{CC}) for the entirety of the study period and area. The black lines represent the division between the northeastern and southwestern region used during this study.

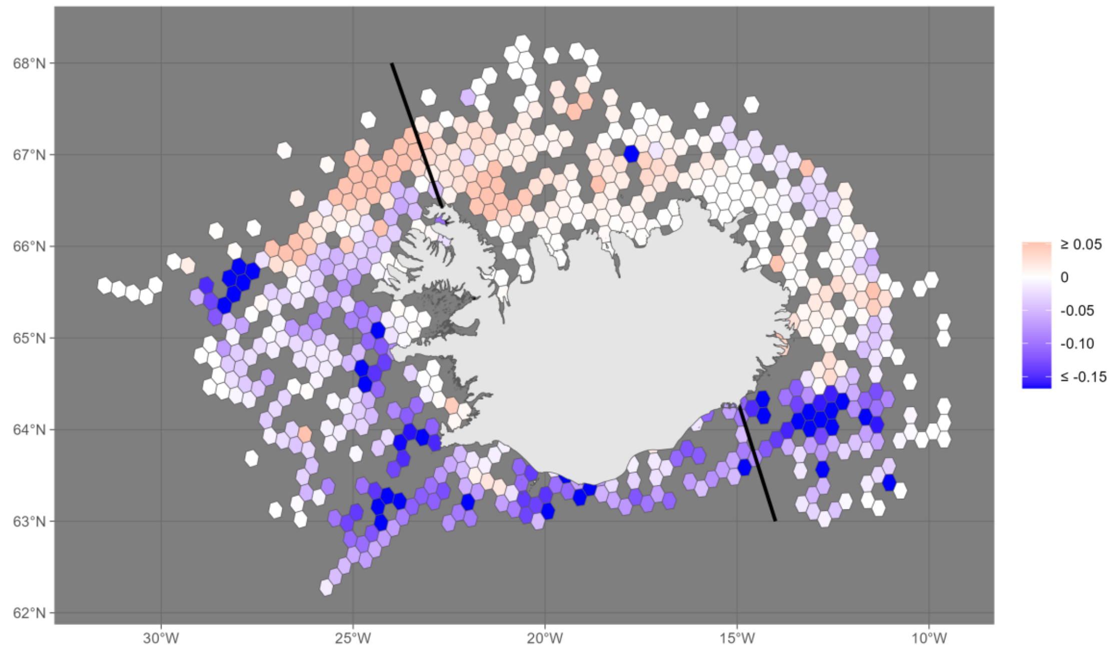

Figure D-6. Yearly change in fishing intensity for the entirety of the study period and area. The black lines represent the division between the northeastern and southwestern region used during this study.

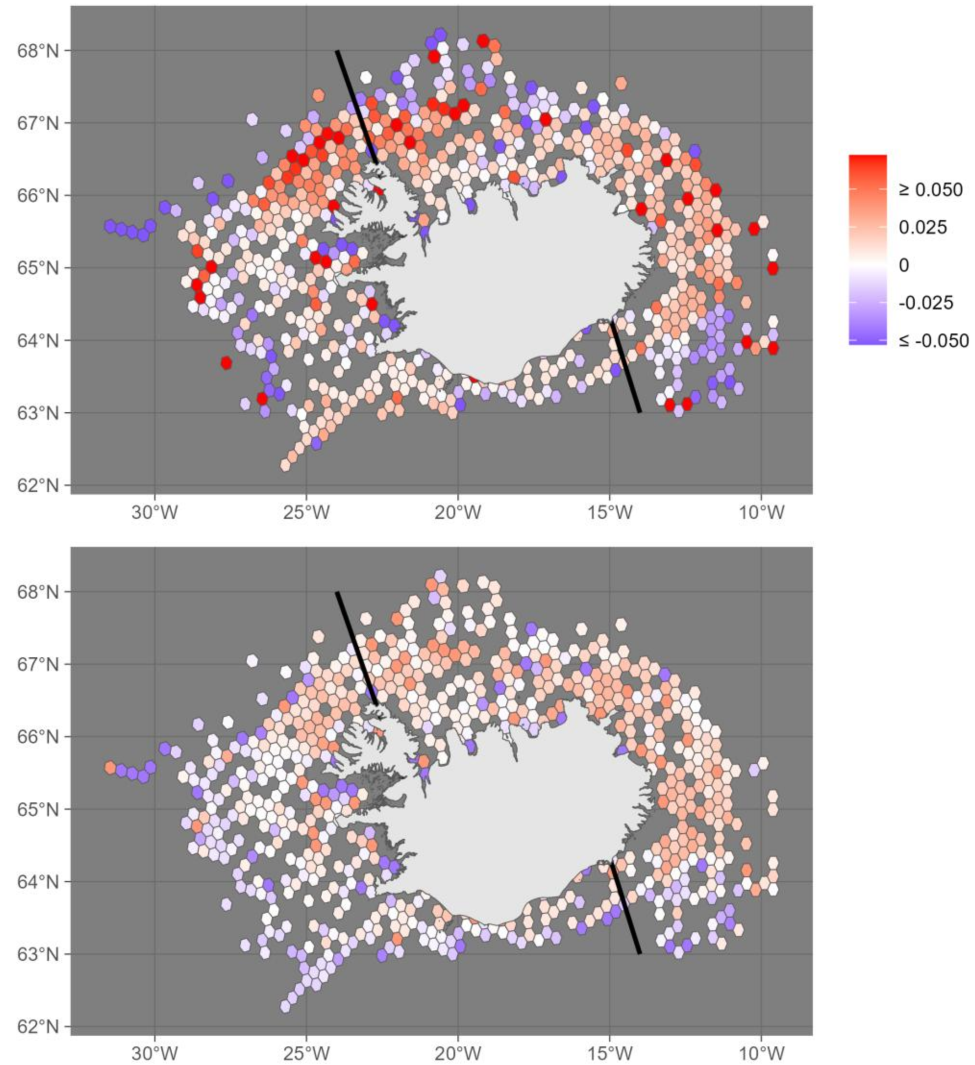

Figure D-7. Change in SST (top) and SBT (bottom) (°C/year) during the study period around Iceland. The black lines represent the division between the northeastern and southwestern region used during this study

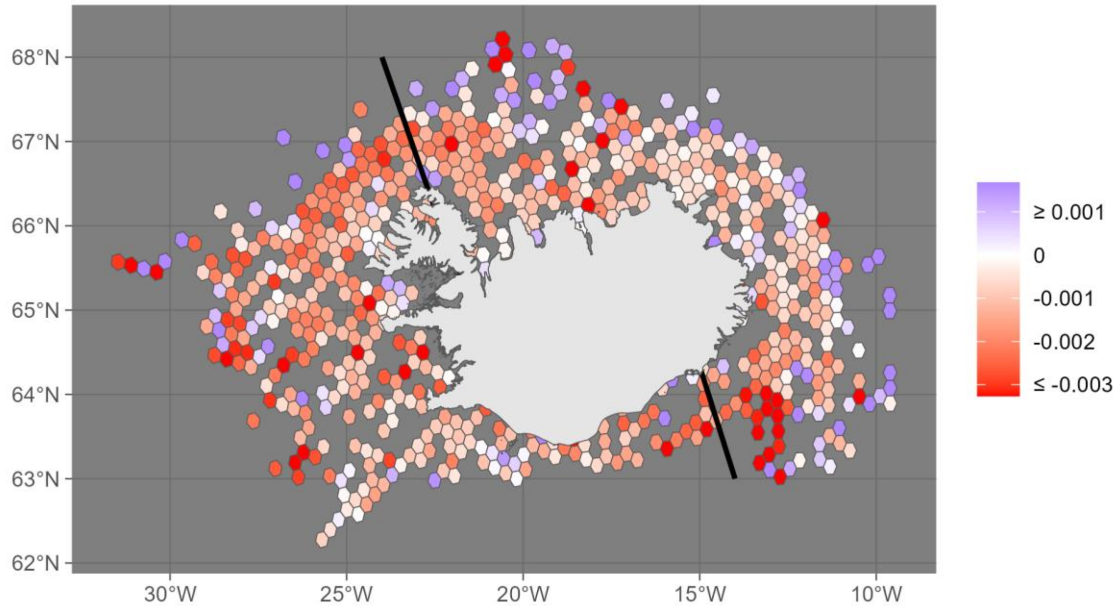

Figure D-8. yearly change in the sensitivity indicator to fishing pressure (S_{FP}) for the entirety of the study period and area. The black lines represent the division between the northeastern and southwestern region used during this study.

E. Appendix: Sensitivity of benthic habitats

Table E-1. Rationale of the different criteria selected to assess habitats' sensitivity and the key questions guiding experts discussions.

	Criterion	Key question	Rationale
Community level	**Loss of taxonomic native biodiversity (diversity and dominance)**	**Will the stressor reduce the taxonomic diversity on the habitats?** (based on the similarity/dissimilarity of native species number and respective abundance)	**Less diverse communities will result in lower habitat resilience.** Habitats with high taxonomic diversity (based on their current species composition) are more resilient to environmental and anthropogenic changes. Communities with lower diversity or an unbalanced species distribution are expected to experience larger shifts in response to disturbances. This assessment focuses solely on the existing species associated with the habitat, excluding new arrivals and not considering habitat-forming species, which are evaluated separately at the species/habitat level.
	Loss of functional native biodiversity (diversity, redundancy and complementarity)	**Will the stressor reduce the functional diversity on the habitats?** (based on the similarity/dissimilarity on native species' functional traits)	**Low functional diversity will result on lower habitat resilience.** Functionally diverse communities, characterised by high richness, redundancy (several species sharing the same traits), and complementarity of functional traits, exhibit greater resilience to anthropogenic and environmental changes. In contrast, communities with greater functional similarity (many species sharing the same traits) are likely to experience larger shifts in response to disturbances. Shifts in species richness and evenness within each habitat can lead to a reduction in functional diversity, complementarity, and redundancy, especially if they preferentially affect specific functional traits. This assessment focuses on functional diversity within the current species composition, excluding habitat-forming species, which are considered at the habitat level.
	Disproportionate changes in specific trophic levels	**Will these taxonomic and functional changes directly affect specific trophic guilds?** (based on structure and function of the conceptual food-web of each habitat; e.g. productivity of key species groups, detritus quantity, top predator diversity, distribution and diversity (abundance/number/biomass) of specific species such as small pelagic fish).	**Significant shifts in specific trophic guilds can trigger changes throughout the entire food web.** These alterations may affect the richness, redundancy, and complementarity of functional roles within the ecosystem, ultimately influencing its stability and resilience. This assessment focuses on the interactions among existing species and their roles within the food web, excluding any newly arrived species.

	Criterion	Key question	Rationale
Species Level	**Decrease in diversity of sessile or low horizontal dispersal species**	**Will the stressor significantly affect species with limited ability to move away?** (based on the diversity of sessile/low horizontal dispersal species associated to each habitat)	**Sessile or low horizontal dispersal species have higher probability to be affected by a stressor.** Species that remain much of their life cycle in the same area (e.g. sessile, sedentary and territorial; low larval dispersal; low mobility) have higher probability to be affected by habitat changes (independently of species' geographical distributions or seasonal/annual migrations).
	Decrease in ecological specialist species and/or species with narrow depth ranges	**Will the species be able to adapt to different environmental conditions/habitats?** (based on the diversity of species with less adaptative capacity associated to each habitat, depending on their depth range and suitable niches; independently of dispersion ability)	**Ecological specialist species (with narrowly defined niches) have higher sensitivity to stressors that drive changes in habitat conditions**. Conversely, species with broader niches generally have lower sensitivity. Species with narrow depth ranges have less capacity to migrate towards deeper, cooler waters.
	Decrease in rare species and/or species with restricted geographic distribution (including endemic)	**Will the stressor significantly affect endemic species, rare species, and those with small ranges of geographical distributions?** (based on the diversity of rate/low range of distribution of the species associated to each habitat)	**Species or populations that occur in a limited geographic area (independently of their ability to move), or rare or endemic species, have higher probability of local extinction**. There is a greater opportunity for favourable habitat (e.g. climate refugia) within larger distributions. Habitat generalist species are more adapted to climate variability and change than specialist species linked with their ability to occupy a greater variety of habitats.
	Reduced abundance of less resilient species or those whose populations are declining	**Does the habitat support a high diversity of less resilient species, sensitive to the stressor assessed?** (based on the relevance of each habitat for a set of less resilient species, both in number and abundance; see manual for species sensitivity vs stressor)	**Species more sensitive to anthropogenic and environmental changes due to their life cycle features** (e.g. low fecundity, slow growth, late maturity, direct and lecithotrophic development) **are also more vulnerable to local extinctions. Changes could be more severe on species whose populations are already declining** (e.g. commercially threatened; not achieving a good environmental status in the scope of MSFD; frequently caught as bycatch) or in an early recovery. This metric should account for both the number and abundance of species with these features, independently of their conservation status.

	Criteria	Key question	Rationale
Habitat level	**Declining spawning areas (ecosystem functioning)**	**In which habitats is the spawning function greater and more sensitive to changes caused by the stressor under evaluation?** (based on the diversity of spawner species sensitive to the pressure being evaluated)	**Impacts on important spawning/nesting habitats for many species** (core areas for species life cycles) **will have larger effects on biodiversity stability**. Different scores should be attributed according to not only habitat relevance for species but also the degree of sensitivity of some species.
	Declining nursery areas (ecosystem functioning)	**In which habitats is the nursery function greater and more sensible to changes caused by the stressor under evaluation?** (based on the diversity of larvae/juveniles of species sensitive to the pressure being evaluated)	**Impacts on important nursery areas for many species** (core areas for species life cycles) **will have larger effects on biodiversity stability.** Different scores should be attributed according to not only habitat relevance for species but also the degree of sensitivity of some species.
	Declining feeding areas (ecosystem functioning)	**In which habitats is the feeding support function greater and more sensible to changes caused by the stressor under evaluation?** (based on the diversity of sensitive species sensitive (to the pressure being evaluated) that aggregate in each type of habitat o feed)	**Impacts on relevant habitats that support feeding grounds for many species** (core areas for species life cycles) **will have larger effects on biodiversity stability**. Different scores should be attributed according with not only habitat relevance for species but also the degree of sensitivity of some species.
	Declining habitat extent	**In which habitats will the stressor cause greater loss on habitat?** (based on the probability of physical loss, critical for fragmented habitats)	**Habitat loss drives biodiversity loss**. Species within less fragmented habitat ranges have greater access to potentially suitable areas (e.g. climate refugia), migration corridors, and larval dispersal. Habitat fragmentation increases the isolation of habitat patches reducing the probability that they can be recolonized following local extinctions.
	Decreasing niche diversity	**In which habitats will the stressor increase niche diversity loss or degradation?** (based on the probability of reduce habitat complexity and habitat forming species)	**Habitats with high structural complexity have lower capacity to recover from physical disturbance** and usually support a higher level of taxonomic and functional diversity. Habitats composed by habitat-forming species are more sensitive to physical damage that reduces their complexity and decrease the number of microhabitats available for species (niches). Vulnerable Marine Ecosystems are less resilient than other habitat-forming species (e.g. corals, sponges, crinoids, gorgonians, sea pens, erect bryozoans, tube-dwelling anemones)

F. Appendix: Risks from invasives in the Mediterranean

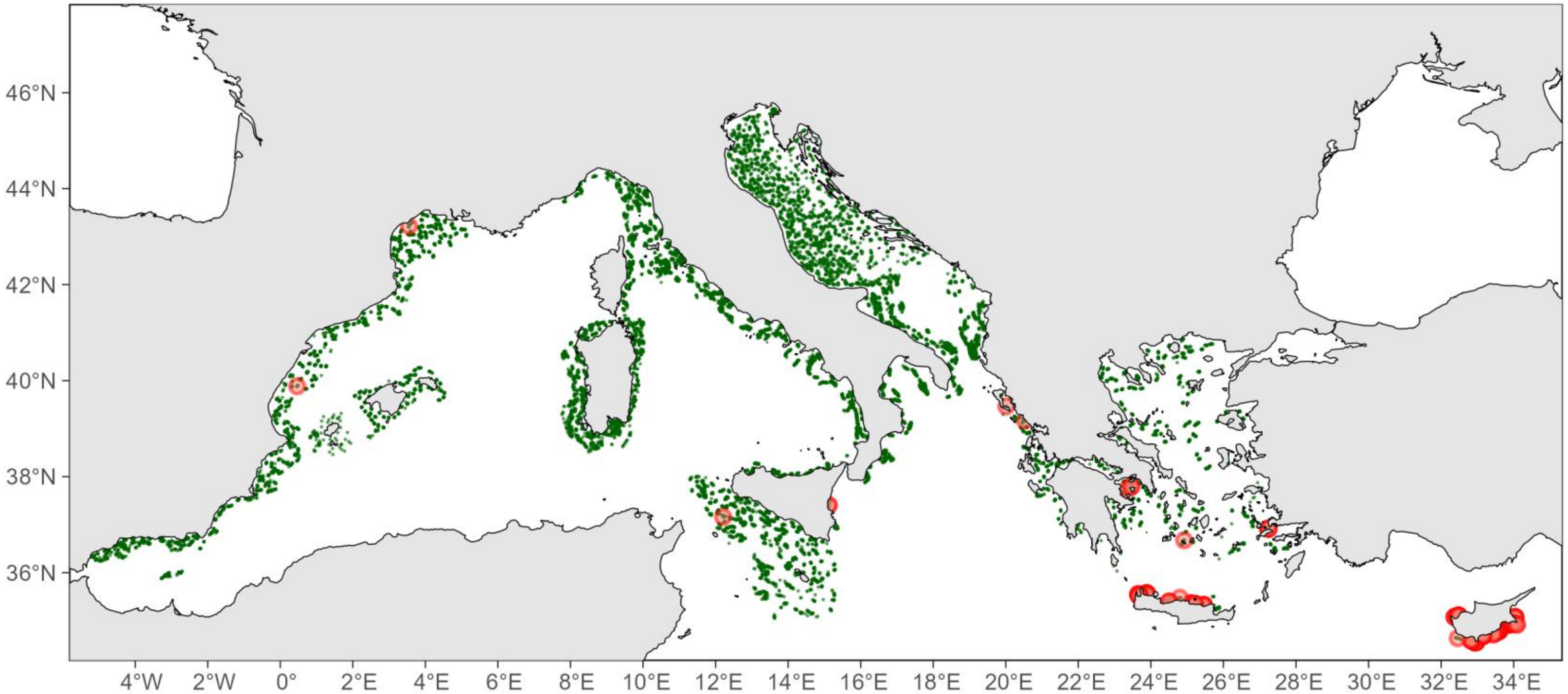

Figure F-1. Location of hauls with at least one Lessepsian NIS record (red circles) along with the location of the rest of hauls (green dots) in the MEDITS dataset between 1999 – 2008, 2014 – 2021.

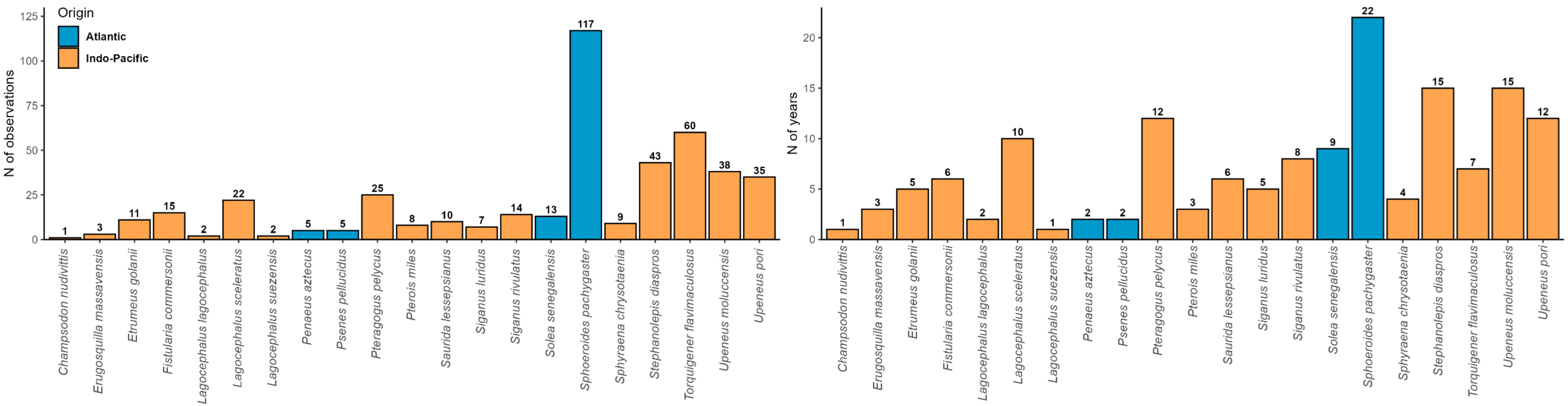

Figure F-2. Number of observations (left) and number of years (right) each NIS appears in the MEDITS dataset between 1999 – 2021.

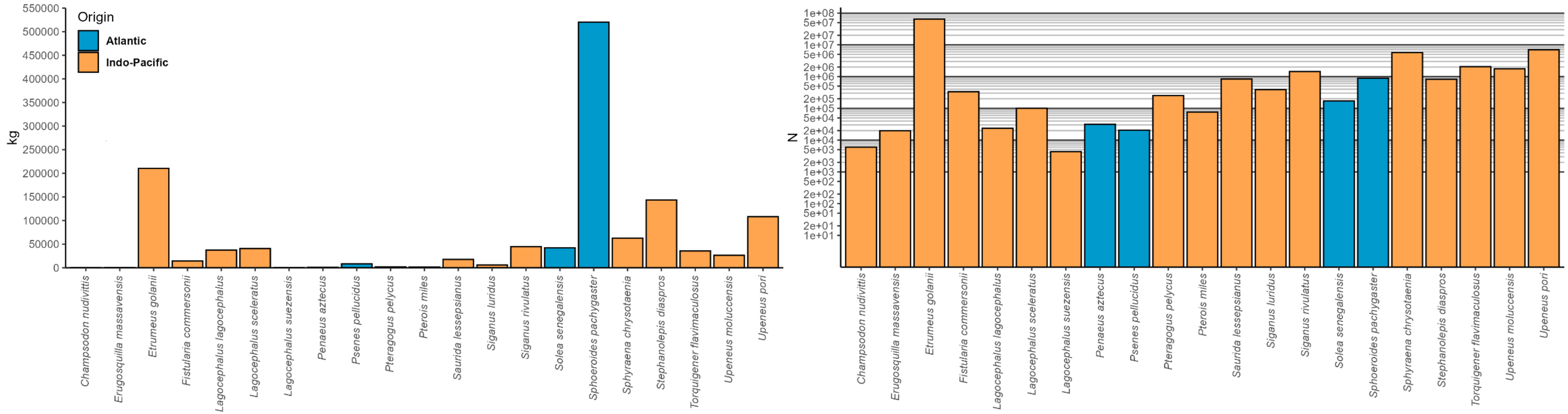

Figure F-3. Estimated total biomass (left) and abundance (right) of each NIS in the entire Mediterranean for the period 1999 – 2021.

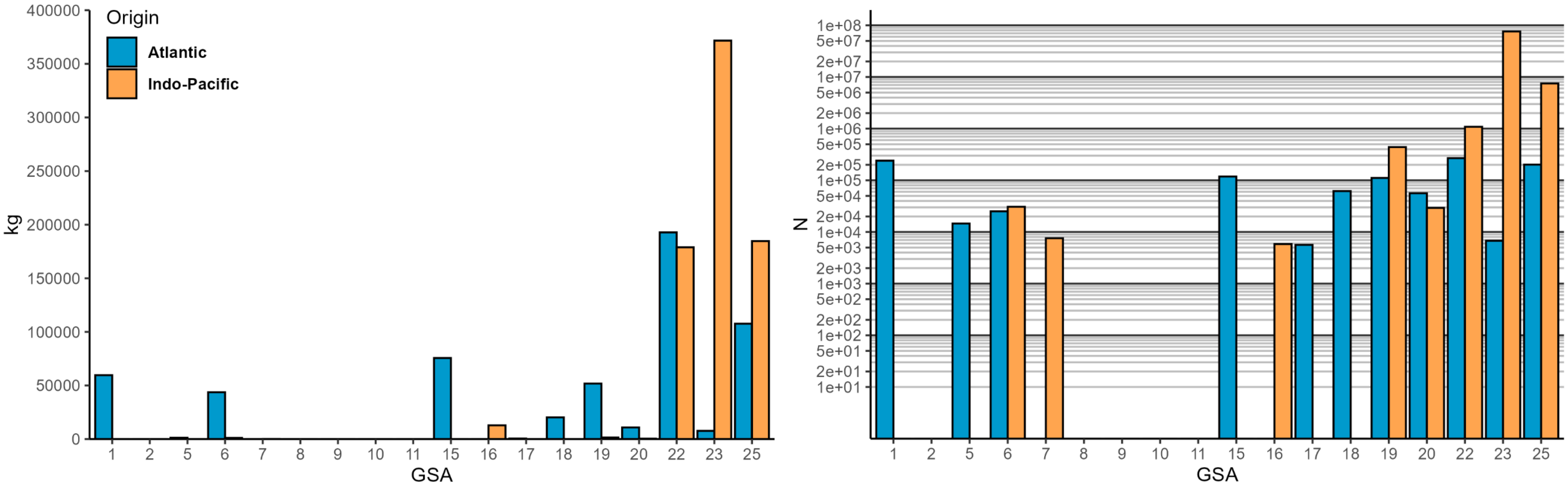

Figure F-4. Estimated total NIS biomass (left) and abundance (right) per GSA for the period 1999 – 2021.

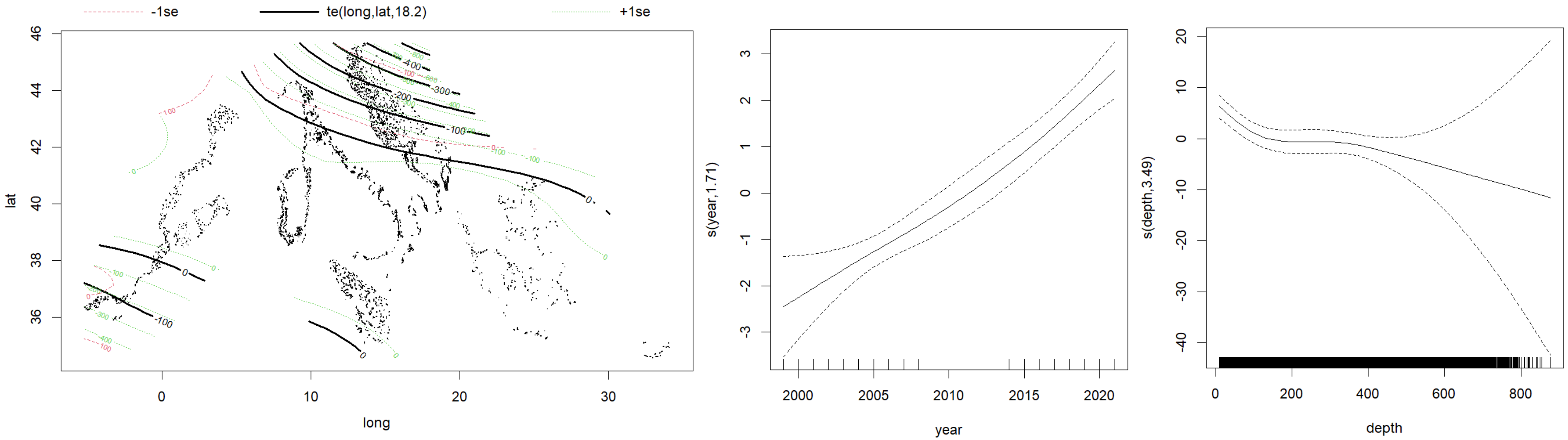

Figure F-5. Simple spatiotemporal model: From left to right, the effects of haul location, year and depth on the probability of occurrence of Lessepsian NIS in the Mediterranean.

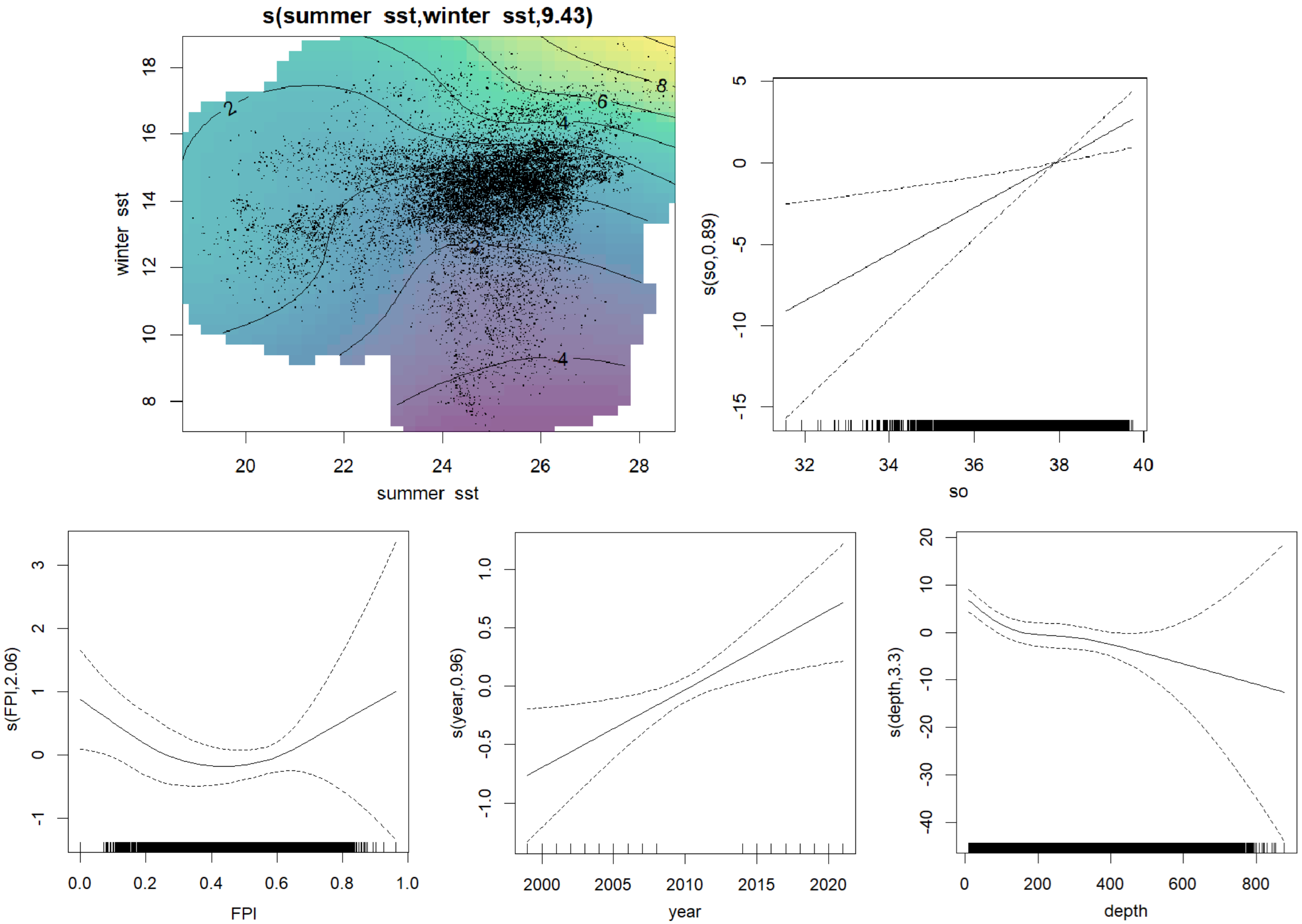

Figure F-6. Final environmental model: The effects of winter – summer SST interaction (top left), surface salinity (SO, top right), trawling fishing pressure (FPI, bottom left), year (bottom middle) and depth (bottom right) on the probability of occurrence of Lessepsian NIS in the Mediterranean.