

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

Deliverable 5.2 Projected risks and vulnerabilities of species and communities in European regional seas

Georg H. Engelhard, Stratos Batziakas, Antonella Consiglio, Elizabeth R. Gillie, Francesco Golin, Sofia Henriques, Manuel Hidalgo, Ingibjörg G. Jónsdóttir, Martin Lindegren, Bastien Mérigot, Fabien Moullec, Laurene Pecuchet, Panagiota Peristeraki, Louise A. Rutterford, Maria Teresa Spedicato, Michael Taylor, George Tserpes, Walter Zupa & Marcel J.C. Rozemeijer



Deliverable Title: Projected risks and vulnerabilities of species and communities in European regional seas

Work package: 5 – Forecasting and scenario simulations

Deliverable no: D5.2

Lead beneficiary: Centre for Environment, Fisheries & Aquaculture Science (Cefas)

Lead responsible for the report: Georg H. Engelhard (Cefas)
georg.engelhard@cefas.gov.uk

Submission date: 30th June 2026

Dissemination Level: PU

PU: Public

PP: Restricted to other programme participants (including the Commission Services)

RE: Restricted to a group specified by the consortium (including the Commission Services)

CO: Confidential, only for partners of the consortium (including the Commission Services)



Version History

HISTORY OF CHANGES		
Version	Date	Changes
1	10/05/2026	Report structure and core text by Georg Engelhard, Laurene Pecuchet and Marcel Rozemeijer (GE, LP, MR)
2	31/05/2026	Individual chapter contributions by various co-authors
3	15/06/2026	Final concept submitted for final review by project leader Martin Lindegren (ML)
4	22/06/2026	Review by project leader ML finished
5	24/06/2026	Final version GE, LP and MR for sign-off by ML
6	30/06/2026	Final version updated and submitted by project leader ML



Contributors

Georg H. Engelhard, Centre for Environment, Fisheries and Aquaculture Science (Cefas), Pakefield Road, Lowestoft NR33 OHT, UK; and University of East Anglia (UEA), Norwich, NR4 7TJ, UK

Stratos Batziakas, Hellenic Centre for Marine Research (HCMR), Institute of Marine Biological Resources and Inland Waters, Thalassokosmos, 71500 Heraklion, Greece

Antonella Consiglio, Fondazione COISPA ETS, Via dei Trulli 18-20, 70126 Bari, Italy

Elizabeth R. Gillie, Centre for Environment, Fisheries and Aquaculture Science (Cefas), Pakefield Road, Lowestoft NR33 OHT, UK

Francesco Golin, Marine and Freshwater Institute of Iceland, Fornubúðum 5, 220 Hafnarfjörður, Iceland

Sofia Henriques, Instituto Português do Mar e da Atmosfera (IPMA), Avenida Alfredo Magalhães Ramalho 6, 1495-165 Algés, Portugal; and Universidade de Lisboa, Campo Grande, 1749-016, Lisbon, Portugal

Manuel Hidalgo, Centro Oceanográfico de Baleares, Instituto Español de Oceanografía (IEO-CSIC), Palma de Mallorca, Spain

Ingibjörg G. Jónsdóttir, Marine and Freshwater Institute of Iceland, Fornubúðum 5, 220 Hafnarfjörður, Iceland

Martin Lindegren, National Institute of Aquatic Resources, Technical University of Denmark, Kemitorvet Bygning 202 2800 Kgs. Lyngby, Denmark

Bastien Mérigot, Marine Biodiversity, Exploitation and Conservation (MARBEC), University of Montpellier, Sète, France

Fabien Moulec, Marine Biodiversity, Exploitation and Conservation (MARBEC), University of Montpellier, Montpellier, France

Laurene Pecuchet, Norwegian College of Fishery Science, The Arctic University of Norway (UiT), Tromsø, Norway

Panagiota Peristeraki, Hellenic Centre for Marine Research (HCMR), Institute of Marine Biological Resources and Inland Waters, Thalassokosmos, 71500 Heraklion, Greece

Louise A. Rutterford, Centre for Environment, Fisheries and Aquaculture Science (Cefas), Pakefield Road, Lowestoft NR33 OHT, UK

Maria Teresa Spedicato, Fondazione COISPA ETS, via dei Trulli 18-20, 70126 Bari, Italy

Michael Taylor, Centre for Environment, Fisheries and Aquaculture Science (Cefas), Pakefield Road, Lowestoft NR33 OHT, UK

George Tserpes, Hellenic Centre for Marine Research (HCMR), Institute of Marine Biological Resources and Inland Waters, Thalassokosmos, 71500 Heraklion, Greece

Walter Zupa, Fondazione COISPA ETS, via dei Trulli 18-20, 70126 Bari, Italy

Marcel J.C. Rozemeijer, Wageningen Marine Research, Haringkade 1, 1976 CP IJmuiden, The Netherlands



Executive summary

This deliverable report is part of Horizon project B-USEFUL, which aims at developing “*user-oriented tools and solutions to conserve and protect marine biodiversity*” in support of the EU Green Deal, Biodiversity Strategy 2030, and national biodiversity policies. Within B-USEFUL, the specific objective of the present deliverable (D5.2) is to *project changes in species- and community-level risks and vulnerabilities* in European regional seas. It looks especially at the risks posed by two key pressures on marine communities: climate change and fishing. With a particular emphasis on near-future decades up to mid-century, this deliverable aims to:

- (1) Project future sensitivities and risks to demersal fish and macroinvertebrate communities in the Mediterranean Sea;
- (2) Project future sensitivities and risks to demersal fish communities in the Northeast Atlantic (Greater North Sea, Celtic Seas and Bay of Biscay);
- (3) Project future distribution changes and risks to demersal fish communities and conservation priority areas in Icelandic waters; and
- (4) Project future risks posed by non-indigenous species in the Eastern Mediterranean Sea, including potential impacts on juvenile nursery areas of foodfish species.

To address these aims, trait-based approaches were used to estimate communities’ sensitivities and risk (developed in WP4 “Risk and vulnerability”). These were combined with spatial forecasting, based on recent survey and environmental data combined with future environmental data, assuming the high-emissions climate scenario RCP8.5 (in line with the overall WP5 “Forecasting and scenario simulations”).

Across case studies, an important finding was that risk is not projected to increase uniformly, but to remain especially concentrated in identifiable, persistent hotspots, while intensifying in some areas but also decreasing locally, with gradual redistributions of risk in space:

- In the Mediterranean Sea, both climate change risk (R_{CC}) and fishing pressure risk (R_{FP}) to demersal communities are projected to increase toward 2050, but in spatially coherent areas rather than across the whole basin. Persistent climate risk hotspots are projected around the Aegean Sea, Cyprus, and Strait of Sicily, while fishing risk hotspots remain linked with current fishing grounds such as the Spanish coast, Gulf of Lion, Ligurian Sea, Sardinian Channel, Strait of Sicily, Malta, and parts of the Adriatic.
- In the Greater North Sea, Celtic Seas and Bay of Biscay, climate risk hotspots are projected to be spatially stable, concentrated in southern, western and shelf regions of the Celtic Seas and Bay of Biscay, and to persist or expand slightly through time. In contrast, fishing pressure risk is projected to be more spatially variable and fragmented, with hotspots mainly in the northern North Sea and parts of the Celtic Seas. Areas where climate and fishing risks overlap (e.g., southern Celtic Seas) represent potential zones of compounded vulnerability.
- Icelandic waters show strong evidence of “borealisation:” projected biomass changes indicate a decline in Arctic-affiliated species, especially on the continental slope, and increases in southern/Atlantic-affiliated species. Biomass levels of commercial



species, at-risk species (based on IUCN criteria), species sensitive to climate change, and those sensitive to fishing pressure, are projected to increase in areas where these are already high, particularly on the southern slope and around the Reykjanes Ridge.

- In the Central and Eastern Mediterranean, future warming is projected to make conditions increasingly suitable for non-indigenous species (NIS) including invasive Lessepsian species (i.e. those that originally entered via the Suez Canal). By 2050, the probability of catching at least one Lessepsian species is projected to become high as far north as the southern Adriatic Sea and as far west as western Sicily. Areas around Cyprus, Crete, the southern Aegean and eastern Ionian Sea and southern Sicily may approach near-certain occurrence. This greatly increases likely interaction with marine protected areas, fishery-restricted areas, and nursery grounds of native fish species.

Importantly, all results presented should be interpreted with caution and as screening-level forecasts only, rather than as exact predictions of most likely future states. Further limitations include the use of only one climate scenario (RCP8.5, high-emissions scenario), noting that future projections have considerable uncertainty; and that future fishing effort distribution was mostly held constant because robust future spatial scenarios were unavailable. We also acknowledge various region-specific uncertainties. Even so, the framework is considered robust enough to identify where future risk from climate change and/or fishing pressure to the species groups being considered may be most likely to persist, intensify, or shift.

This is expected to add significantly to the overall evidence base to support policy and management advice around the protection of marine biodiversity and the sustainable use of living resources in European regional seas.



The role of this deliverable

This deliverable (D5.2) is the second of three reports in WP5 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 “*Forecasting and scenario simulations*”.

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. This work supports international policies including the EU Green Deal, the Biodiversity Strategy 2030 and Marine Strategy Framework Directive (MSFD). It also supports national policies: within the UK, it is relevant for the Marine Environment Plan and UK Biodiversity Strategy; and for Icelandic waters, the work supports the Nordic Biodiversity Framework.

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 life are seen as key drivers of biodiversity loss, both globally and in Europe’s regional seas. These drivers operate through multiple ecological mechanisms including trophic restructuring, habitat degradation, shifts in species distributions and loss of functional diversity (IPCC 2022; IPBES 2019). Hence, understanding the mechanisms by which climate change and fishing pressure impact marine ecosystems is crucial for biodiversity conservation and sustainable resource management.

In B-USEFUL WP4 functional approaches based on species’ biological traits are used. Firstly, we assessed the *sensitivities and vulnerabilities of marine species* to the impacts of climate change and fishing pressure (Deliverable D4.1, Engelhard et al. 2024). This was done through the development of two new trait-based sensitivity indicators: (i) *sensitivity to climate change* (S_{CC}) 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.

The second step has been to scale up from species-level, to assess *community-level* sensitivities and risks to European marine biodiversity (Deliverable D4.2, Rozemeijer et al. 2025). Community-level sensitivity is estimated based on the weighted average sensitivities across all species that comprise a local marine community; this allows establishing where local ‘community-level sensitivity hotspots’ exist, as well as assessing changes in community-level sensitivity over time. Sensitivities, in combination with spatio-temporal variations in the *exposure to pressures* (either climate change or fishing pressure, or both) allow the estimation of community-level *risks* (to either pressure, or both). Thus, in addition to ‘sensitivity hotspots’, also ‘risk hotspots’ have been estimated for European marine life as part of D4.2 (Rozemeijer et al. 2025). This has been done for Europe’s major marine regions (Mediterranean, North Sea, North East Atlantic, Icelandic and Greenlandic waters). As part of D4.2, we have moreover assessed the risks posed by a major threat to the Mediterranean Sea: that of non-indigenous species (NIS), with focus on the so-called ‘Lessepsian’ species (those that have entered the Mediterranean via the Suez Canal).



This report also builds on the third deliverable of WP4, D4.3, which has identified important biodiversity ‘hotspots’ in European regional seas, and then assessed to what extent hotspots either are or are not appropriately protected – either through marine protected areas (MPAs, which is preferred) or through fishery-restricted areas (FRAs). There has been a particular emphasis on discussing where there are clear ‘mismatches’ between biodiversity, sensitivity or risk hotspots and protection or conservation measures, and provide policy recommendations.

The report is part of WP5, which builds on WP3 and WP4, and is aimed at forecasting and future scenario simulations up to mid-21st century. To achieve this, WP5 aims at achieving three objectives achieved with associated deliverable reports: (D5.1) performing seasonal-to-decadal forecast of species distributions and biodiversity indicators; (D5.2) projecting changes in species and/or habitats’ risk and vulnerabilities, and (D5.3) forecasting changes in ecosystem functions and services. It is the second of these three deliverables that is described in the present report. Specifically, the present deliverable takes WP4 into the near-future and aims at assessing the projected risks and vulnerabilities of European marine life during the 2030s and 2040s up to 2050. Specifically, it aims to:

- (1) Project future sensitivities and risks to demersal fish and macroinvertebrate communities in the Mediterranean Sea;
- (2) Project future sensitivities and risks to demersal fish communities in the Northeast Atlantic (Greater North Sea, Celtic Seas and Bay of Biscay);
- (3) Project future distribution changes and risks to demersal fish communities and conservation priority areas in Icelandic waters;
- (4) Project future risks posed by non-native species in the Eastern Mediterranean Sea.



Contents

Version History	3
Contributors	4
Executive summary.....	5
The role of this deliverable	7
Contents	9
1 General introduction	10
2 Mediterranean Sea.....	12
3 Northeast Atlantic: Greater North Sea, Celtic Seas and Bay of Biscay	30
4 Icelandic waters	48
5 Projected risks from invasive species in the Mediterranean	56
6 General discussion and management implications	66
7 References	76
A. Appendix: Mediterranean Sea	90
B. Appendix: Northeast Atlantic	97
C. Appendix: Icelandic waters.....	104
D. Appendix: Projected risks from invasive species in the Mediterranean	105



1 General introduction

Europe's marine biodiversity faces multiple pressures arising from climate change, fisheries, habitat loss and pollution (Burrows et al. 2011; Poloczanska et al. 2013; Hidalgo et al. 2022). Halting biodiversity loss requires robust scientific advice to guide management plans and assess conservation measures, especially the design and placement of marine protected areas (MPAs), fisheries restricted areas (FRAs) and Other Effective Area-based Conservation Measures (OECMs). Decision-support tools are required to help safeguard 'biodiversity hotspots' and vulnerable ecosystems, while safeguarding key ecosystem services, such as food provisioning and climate regulation. The Horizon project B-USEFUL develops user-oriented decision-support tools to help conserve marine biodiversity, building on existing European data and governance frameworks. In doing so, it contributes to the policy goals of the [European Green Deal](#) and [EU Biodiversity Strategy 2030](#), as well as to the [Marine Strategy Framework Directive \(MSFD\)](#). It also contributes to aligned national policies, including the UK's [National Biodiversity Strategy and Action Plan \(NBSAP\)](#), and for Icelandic waters, the [Nordic Biodiversity Framework](#).

Two dominant pressures on marine ecosystems include (1) climate change and (2) fishing pressure (and associated physical seabed disturbance). Climate change, together with the (over-)exploitation of marine life, is seen as a key driver of biodiversity loss globally and in Europe's regional seas. These drivers operate through multiple ecological mechanisms, including trophic restructuring, habitat degradation, shifts in species distributions, and loss of functional diversity (IPCC 2022; IPBES 2019). Understanding how climate change and fishing pressure affect marine ecosystems is therefore crucial for biodiversity conservation and sustainable resource management – and a central theme with the B-USEFUL project.

Within B-USEFUL, two WPs have aimed at assessing recent and current changes in marine biodiversity in European regional seas. The aims of WP3 are to assess the status, trends, and cumulative impacts of pressures acting on multiple biodiversity indicators and establish their links to ecosystem functions and services (Lindegren et al. 2025; Pecuchet et al. 2026). The aims of WP4 are to assess the key risks and vulnerabilities to marine life (Engelhard et al. 2024; Rozemeijer et al. 2025; Engelhard et al. 2026). This report forms part of WP5, which builds on WP3 and WP4, but is aimed at forecasting and future scenario simulations – looking ahead towards the near-future decades, up to mid-21st century. To achieve this aim, WP5 pursues the following objectives achieved through three deliverable reports: (D5.1) to perform seasonal-to-decadal forecast of species distributions and biodiversity indicators; (D5.2) to project changes in species and/or habitats' risk and vulnerabilities, and (D5.3) to forecast changes in ecosystem functions and services. It is the second of these three deliverables that is described in the present report.

We have previously shown in WP4 that functional approaches based on species' biological traits can be used to assess the sensitivities and vulnerabilities of marine species to climate change and fishing pressure (D4.1, Engelhard et al. 2024). An important step was the development of two new trait-based sensitivity indicators: (1) *sensitivity to climate change* (S_{CC}) and (2) *sensitivity to fishing pressure* (S_{FP}), presented in D4.1 (Engelhard et al. 2024). The



approach is described in a subsequent paper (Polo et al. 2025) and allows Europe's marine species to be scored according to their sensitivities to these two pressures.

We then scaled up from the species level to assess *community-level* sensitivities and risks to European marine biodiversity (D4.2, Rozemeijer et al. 2025). Community-level sensitivity is estimated as the weighted average sensitivity across the species comprising a local marine community; this identifies local 'community-level sensitivity hotspots' and assesses changes in community-level sensitivity over time. Sensitivities, combined with spatio-temporal variation in *exposure to pressures* (climate change, fishing pressure, or both), allow estimation of community-level *risks* (to either pressure, or both). Thus, in addition to 'sensitivity hotspots', we also estimated 'risk hotspots' for European marine life as part of D4.2 (Rozemeijer et al. 2025). This was done for Europe's major marine regions (Mediterranean, North Sea, Northeast Atlantic, Icelandic and Greenlandic waters). As part of D4.2, we moreover assessed the risks posed by a major threat to the Mediterranean Sea: non-indigenous species (NIS), with a focus on the so-called 'Lessepsian' species (those that have entered the Mediterranean via the Suez Canal).

Thirdly, as part of WP4, we identified important biodiversity 'hotspots' in European regional seas (4.3, Engelhard et al. 2026) and assessed whether they are appropriately protected through marine protected areas (MPAs) or fishery-restricted areas (FRAs). Particular emphasis was placed on discussing clear 'mismatches' between biodiversity, sensitivity or risk hotspots and protection or conservation measures, and on providing policy recommendations.

The present deliverable takes WP4 into the near future and assesses the projected risks and vulnerabilities of European marine life during the 2030s and 2040s, up to mid-century. Specifically, it aims to:

- (1) Project future sensitivities and risks to demersal fish and macroinvertebrate communities in the Mediterranean Sea (Chapter 2);
- (2) Project future sensitivities and risks to demersal fish communities in the Northeast Atlantic (Greater North Sea, Celtic Seas and Bay of Biscay: Chapter 3);
- (3) Project future sensitivities and risks in demersal fish communities in Icelandic Waters, and identify conservation priority areas (Chapter 4);
- (4) Project future risks posed by non-native species in the Eastern Mediterranean Sea (Chapter 5).

The report closes with Chapter 6, providing an overview of the key messages emerging from the preceding chapters, a consideration of management implications specific to each case study region, and the broader-scale implications relevant beyond each region.



2 Mediterranean Sea

2.1 Introduction

The Mediterranean Sea represents a highly complex and dynamic semi-enclosed basin characterised by strong environmental gradients, high biodiversity, and a large proportion of endemic species (Bianchi et al. 2012, Bianchi & Morri 2000, Coll et al. 2013). This ecological uniqueness is increasingly threatened by multiple and interacting anthropogenic stressors (Coll et al. 2013, Tsirintanis et al. 2022), particularly climate change (Cramer et al. 2018, Marbà et al. 2016), which is acting at a rate exceeding the global average (Lionello & Scarascia 2018), and fishing pressure (Marguin et al. 2025). These drivers have substantially altered marine ecosystem structure, functioning, and productivity (Hidalgo et al. 2018, Mannino et al. 2017, Marbà et al. 2016). Consequently, important ecological responses have become evident, including shifts in species distributions (Azzurro et al. 2019, Sanz-Martín et al. 2024), changes in abundance and functions of marine communities (Hidalgo et al. 2022, Pita et al. 2021, Rubino et al. 2024), productivity decline (Reale et al. 2022), and biodiversity loss (Frid et al. 2023). The overexploited situation of many stocks has been reversed in the recent years, though there are cases with harvesting beyond sustainable levels despite management measures (FAO 2025). As a consequence, marine ecosystems are currently shaped by the cumulative and interactive effects of climate-driven and anthropogenic pressures, with important implications for biodiversity conservation and fisheries sustainability. The Mediterranean is also shaped by strong regional contrasts. Western, Central, Eastern, and Adriatic subregions differ in their thermal regimes, bathymetry, productivity, biogeographical composition, and fishing history (D'Ortenzio et al., 2009; Colloca et al., 2017; Kubin et al., 2023). These contrasts are important because community sensitivity to climate change and fishing pressure is not expected to change uniformly across the basin. Areas that are already warm, quite heavily exploited, or dominated by species with vulnerable life history traits may become increasingly exposed to cumulative risks. Conversely, some northern or deeper areas may become more important as potential refugia or as zones of community reorganisation (Cramer et al., 2018; Chaikin et al., 2022).

Trait-based functional approaches are particularly useful in this context because they allow to assess the vulnerability of communities through the biological characteristics of the species, and to examine species sensitivity, exposure, and risk to multiple pressures (De Juan & Demestre 2012, Polo et al. 2025, Rozemeijer et al. 2025). These approaches make use of ecological and life-history traits such as trophic position, mobility, longevity, and fecundity, which allow to provide useful insights into species' responses and their capacity to withstand environmental disturbances (Hiddink et al. 2026, Zupa et al. 2025, Beukhof et al. 2019, Butt et al. 2022, Pecuchet et al. 2018). By combining species level sensitivity scores with community composition data, it is possible to estimate community level sensitivity to climate change (S_{CC}), and sensitivity to fishing pressure (S_{FP}). These indicators provide a basis for projecting how the risk profile of Mediterranean demersal assemblages may evolve under future warming. In this context, understanding not only the current impacts of these pressures but also future projections of species sensitivity and risk is becoming increasingly



essential for effective conservation and management strategies, as required by the Convention on Biological Diversity (2021).

To address these challenges, scenario-based approaches have become central tools for exploring plausible future projections of climate and anthropogenic pressures. Climate scenarios, such as Representative Concentration Pathways (RCPs), enable the assessment of potential ecosystem responses under different emission trajectories, supporting the analysis of impacts, vulnerabilities, and adaptation strategies (van Ruijven et al. 2013, Völz & Hinkel 2023). By explicitly accounting for uncertainty, scenario planning provides a framework to inform decision-making and develop robust management strategies in the face of ongoing environmental change (Lawrence et al. 2021, Oriol et al. 2024). In particular, the use of high-emission scenarios (i.e. RCP8.5) enables exploring upper-bound ecological responses and the identification of the potential worst-case scenario for marine communities in the Mediterranean Sea.

Understanding how marine communities respond to these combined pressures requires analytical frameworks that integrate spatial, temporal, and environmental complexity. In this study, a unified forecasting workflow was developed to disentangle and project the effects of climate change and fishing pressure across Mediterranean demersal assemblages, for near-to medium-future decades up to 2050. We project future sensitivity and risk patterns for Mediterranean demersal fish and macroinvertebrate communities under a high-emission climate scenario. The analysis combines spatio-temporal modelling, environmental projections, exposure layers, hotspot detection, and centre of gravity analyses. It aims to identify not only where future risk may be highest, but also where risk hotspots may persist, intensify, or shift across Mediterranean subregions. The specific aims are:

1. To project future community-level sensitivity to climate change under a high-emission scenario (RCP8.5) and fishing pressure across the Mediterranean Sea up to 2050, using a spatio-temporal Beta Generalised Additive Modelling (GAM) framework;
2. To estimate climate change risk, R_{CC} , and fishing pressure risk, R_{FP} , by combining projected sensitivity with exposure to thermal conditions and fishing pressure;
3. To identify persistent hotspots and areas of rapid change in projected risk, through predictive mapping and rate of change metrics;
4. To assess whether the spatial centre of gravity of risk is expected to shift through time at basin and subregional scales, by analysing shifts in the Centre of Gravity (COG) of R_{CC} and R_{FP} ;
5. To provide an integrated and reproducible forecasting framework capable of supporting ecosystem-based fisheries management, marine spatial planning, and biodiversity conservation across future environmental change scenarios.

2.2 Methods

The community-level risk to climate change, R_{CC} , and to fishing pressure, R_{FP} , assessment was conducted across the Mediterranean Sea using a spatially explicit annual prediction grid, spanning the period 2012-2050. The workflow integrated environmental predictors,



statistical forecasting modelling, extrapolation diagnostics, uncertainty estimation, hotspot analysis, and spatial analysis of centres of gravity (COG) to evaluate both the magnitude and spatial dynamics of R_{CC} and R_{FP} . The analysis was conducted considering two different spatial scales: the whole Mediterranean Sea and the sub-regional level, dividing the area into Western, Central, Eastern Mediterranean, and Adriatic Sea.

The first step of the analysis aimed to estimate community-level sensitivity to climate change, S_{CC} , and fishing pressure, S_{FP} , following the approach adopted in Deliverable 4.2 of this project (Rozemeijer et al. 2025). Specifically, scientific trawl survey data from the MEDITS survey (Bertrand et al., 2002 Spedicato et al., 2019, European Commission, 2026) were used to derive trait-based, species-specific sensitivity estimates. These estimates were then combined with species abundance data at haul level to calculate community-weighted mean sensitivity indices (Polo et al. 2025).

The sensitivity indices were then incorporated into a modelling framework based on Generalised Additive Models (GAMs), fitted with a Beta regression family and a logit link, to account for the bounded distribution of the indices between 0 and 1. This ensured that all predictions remained within biologically interpretable bounds. Environmental predictors included in the tested models accounted for annual sea surface temperature (SST), annual sea bottom temperature (SBT), and their corresponding anomalies assessed using the hindcast period (2012-2021) as reference. Spatial variation was accounted including the depth of each haul included in the analysis, and the interaction between the longitude and latitude variables. Environmental variables were derived from Copernicus Climate Change Service (2020), bias corrected (Kuehn 2023) according to the hindcast reanalysis product from Copernicus (Escudier et al. 2020). Environmental predictors were selected to capture the expected climate-mediated reassembly of demersal communities, which may alter their trait composition and therefore their community-level sensitivity to both climate change and fishing pressure. Therefore, future changes in temperature, bottom thermal conditions, and thermal anomalies were considered relevant predictors not only for S_{CC} , but also for S_{FP} , as they may indirectly affect fishing sensitivity through climate-mediated community reassembly.

Conversely, fishing effort was not used as a primary predictor of future S_{FP} because fishing-pressure hotspots showed high spatial persistence during the reference period, with temporal variation mainly affecting hotspot intensity rather than producing major shifts in their spatial configuration, as reported in Deliverable 4.2 (Rozemeijer et al. 2025). Accordingly, fishing effort was retained as the exposure component in the subsequent estimation of R_{FP} , while environmental predictors were used to model changes in the community-level sensitivity component.

Several candidate GAM formulations of increasing complexity were tested and compared on the basis of AIC (Akaike et al. 1974), explained deviance, and adjusted R^2 before selecting the final calibrated models, which better described the complexity of sensitivity given by the environmental variations in the training dataset. Candidate models included combinations of spatial smooths, bathymetric effects, climatic anomalies, and tensor-product interactions describing nonlinear relationships among environmental predictors and spatial structure.



Models' evaluation and selection finally included the analysis of residual diagnostics, basis dimension, with a correlation threshold set at 0.6, and hierarchical deviance partitioning analyses.

First, a rolling one-step-ahead validation was performed. For each test year, the model was calibrated using all observations from the preceding years and then used to predict the following independent year. Predictive performance was assessed by comparing observed and predicted values for each test year using root mean squared error (RMSE) and observed-predicted R^2 .

Second, a sliding window validation was applied by fitting the models on sequential 5-year calibration windows across the 2012-2021 historical time series. For each calibration window, predictions were generated for all years with available observations, and annual predictive performance was quantified using RMSE and R^2 . The performance metrics were then related to the temporal distance between each predicted year and the corresponding calibration window, allowing the expected stability of the fitted relationships and the degradation of forecasting performance to be extrapolated up to 10 years beyond the calibration period.

Model predictions of the selected fitted model were generated annually for all grid cells using the final calibrated model.

Predictions were obtained, including associated standard errors and 95% confidence intervals. For each annual prediction, the predicted climate sensitivity value and its lower and upper 95% confidence limits were generated, and the width of the confidence interval was used as a measure of uncertainty. Annual S_{CC} and S_{FP} projections were subsequently aggregated into three temporal windows, which included the baseline: 2012-2021; near future projection years: 2026-2030; and long-term future 2046-2050. Within each period, mean predicted sensitivity and uncertainty metrics were calculated for every grid cell.

To evaluate the robustness of future projections and identify potential extrapolation issues, all future environmental conditions were compared against the range observed in the model training dataset. Binary out-of-range indicators were computed for each predictor variable. For each year, we calculated the percentage of cells exhibiting at least one of the out-of-range predictors, the corresponding mean number, and the maximum extrapolation level. Then, spatial extrapolation maps were produced for selected future years to identify regions potentially affected by novel environmental conditions. To quantify temporal changes relative to the baseline period, spatial delta maps were baselined to visualise changes in predicted S_{CC} and S_{FP} across future periods.

R_{CC} and R_{FP} were estimated by combining sensitivity with exposure: thermal exposure (SST) for R_{CC} , and fishing effort exposure for R_{FP} . Fishing pressure was represented by demersal fishing effort reported for the study area by DCF Fisheries Dependent Information (FDI), spatially disaggregated using a fishing footprint derived from Global Fishing Watch (GFW). For future R_{FP} projections, fishing effort exposure was fixed to the mean spatial configuration observed during the last three years of the reference period, as no spatially explicit and management-consistent future fishing effort scenarios were available at the resolution required by the analysis. First, SST exposure was normalised to a 0-1 scale using the global



minimum and maximum SST values across all years and cells; also, the log-transformed fishing effort values were normalised to a 0-1 scale across all years and cells. Then, the final scores for both risks were computed as the arithmetic mean of normalised exposure and predicted sensitivity. This approach produced a spatially explicit composite risk indicator combining exposure and predicted sensitivity.

To evaluate temporal trends in both risks, the annual rate of change in risks was estimated for each grid cell using a linear regression of R_{CC} and R_{FP} over the year, and maps were produced to identify areas undergoing the most rapid changes in climate-related vulnerability. The resulting slope coefficients were interpreted as spatial rates of risk change and mapped to identify areas experiencing the most rapid increases or decreases in climate-related community vulnerability. Regional differences in R_{CC} were statistically evaluated among periods and subregions using Kruskal-Wallis tests to assess overall differences among periods, followed by pairwise Wilcoxon tests for post-hoc comparisons. Spatial clustering of R_{CC} and R_{FP} was assessed using the Getis-Ord G_i^* statistic (Getis & Ord 1992). Local G_i^* statistics were then calculated at grid cell level for each year to identify statistically significant hotspots of elevated R_{CC} and R_{FP} at the 95% confidence level. Hotspot persistence was subsequently estimated as the proportion of years within each temporal period during which a cell was classified as a hotspot, and then maps were generated.

Finally, the spatial centres of gravity (COG) for R_{CC} and R_{FP} were estimated annually for the entire Mediterranean Sea and at the sub-region levels, to identify regional redistributions of vulnerability across the Mediterranean basin. Potential shifts in the COG over time were assessed using the Mann-Kendall test for trend analysis. The rate of spatial displacement was quantified using Sen's slope estimator, expressed in degrees latitude or longitude shifted per year ($^\circ \text{ year}^{-1}$). COG coordinates were calculated as weighted spatial means using R_{CC} and R_{FP} values as weights.

2.3 Results

2.3.1 Model Performance and Structuring

The final GAM structures for S_{CC} and S_{FP} were defined following exploratory analyses of covariate relationships using a Pearson pairwise correlation matrix (*Figure A-1*), together with model diagnostics and performance evaluation. No strong collinearity was detected among predictors, as all pairwise correlations remained below the value 0.6. No major convergence issues were detected during the fitting of the S_{CC} and S_{FP} GAM models. Goodness-of-fit metrics progressively improved from simpler formulations to more flexible model structures, incorporating nonlinear smoothers and tensor-product interactions.

The formulas and the fitting parameters of the final selected models for both S_{CC} and S_{FP} are reported in *Table 2-1*. Both models showed a good predictive performance and explained a substantial proportion of variability in sensitivity patterns across the Mediterranean Sea. Specifically, the S_{CC} achieved a robust fit, explaining 68% of the deviance with an adjusted R^2 of around 0.67. Similarly, the S_{FP} model demonstrated strong structuring explained 60.4% of

the deviance ($R^2 = 0.58$). The inclusion of nonlinear smooths and tensor-product interactions improved model performance, indicating that demersal community sensitivity was structured by complex spatial, bathymetric and thermal gradients.

Table 2-1. Performances of S_{CC} and S_{FP} models, indicating AIC (Akaike Information Criterion), R^2 (adjusted coefficient of determination), and explained deviance percentage of the final selected GAM models. Model formulation included spatial smoothers (s), tensor-product smoothers describing nonlinear interactions (te), and interactions (ti).

Model	Predictors	AIC	R^2	Explained Deviance
S_{CC}	$S_{CC} \sim s(lon,lat) + te(depth,SBT) + ti(SSTa,SBTa) + ti(lon,lat,SBT,d = c(2,1))$	-29630.59	0.67	68.0%
S_{FP}	$S_{FP} \sim s(lon,lat) + s(depth) + ti(SSTa,SBTa) + ti(lon,lat,SBT)$	-18470	0.58	60.4%

Model diagnostics indicated good agreement between observed and fitted values for both S_{CC} and S_{FP} models. Residual distributions (*Figure A-2*) were generally centred around zero, and the model diagnostics supported the adequacy of the selected GAM formulations for both models.

Partial-effect smoothers (*Figure A-3* and *Figure A-4*) confirmed that strong spatial and environmental structuring characterised both models across the Mediterranean Sea. For S_{CC} , the two-dimensional spatial smoother revealed a marked geographical heterogeneity, while the interactions among the variables indicated nonlinear responses across bathymetric and thermal gradients, as well as interaction between thermal anomalies that generated complex, non-additive responses. These spatial variations demonstrated the existence of region-specific thermal sensitivity patterns. A similar pattern emerged for S_{FP} : nonlinear effects associated with depth contributed substantially to the spatial organization, reinforcing that both S_{CC} and S_{FP} are governed by complex interactions among spatial configuration, bathymetry, and thermal environmental gradients, rather than single predictors acting independently.

2.3.2 Variance partitioning and model validation

Variance partitioning analyses (*Figure A-5*) highlighted that the spatial structure was the dominant factor driving both S_{CC} and S_{FP} (contributing approximately 40% to 50% of explained deviance, respectively). Beyond this large-scale pattern, the predictive power of both models relied heavily on non-additive environmental interactions. Specifically, the depth-temperature and spatially varying temperature interactions were consistent among the most crucial components. These interaction effects significantly contributed to model performance, while standalone thermal anomalies played only a marginal role (<5%) in explaining the total variability.



To further evaluate the temporal robustness of the modelling framework, rolling one-step-ahead cross-validation and sliding temporal-window validation procedures were implemented for the models.

The rolling validation, in which each model was iteratively calibrated using all years preceding a given test year and then used to predict that independent annual period, indicated stable predictive performance over time, with higher accuracy for S_{CC} than S_{FP} (Figure A-6; Table 2-2). For the S_{CC} model, RMSE showed only moderate variation, ranging from 0.068 to 0.080, with a high correlation between observed and predicted values (0.78), supporting good temporal generalization. The S_{FP} model showed lower, but still consistent, predictive skill, with RMSE values between 0.106 and 0.128, and a correlation of 0.69.

Table 2-2. Rolling temporal cross-validation performance for S_{CC} and S_{FP} GAM models. Reported metrics included the mean root mean square error (RMSE) and the Pearson correlation coefficient between observed and predicted sensitivity values.

Model	Rolling validation years	Mean RMSE	Correlation
S_{CC}	2017-2021	0.07	0.78
S_{FP}	2017-2021	0.11	0.69

The sliding 5-year window validation, Figure A-6, provided no evidence of a systematic degradation in predictive performance for S_{CC} as the temporal distance from the calibration window increased. The nonlinear model fitted to R^2 showed no significant temporal decay, and RMSE also remained statistically stable, with no significant relationship with temporal distance, $p = 0.122$. This indicates that S_{CC} predictive performance did not show a detectable deterioration across the validation horizon. For S_{FP} (Figure A-7), R^2 similarly showed no significant temporal decay. RMSE displayed only a small increase with temporal distance, with weak statistical support, $p = 0.0489$, suggesting at most a limited increase in prediction error. Overall, the sliding-window validation indicated that model performance was largely stable through time, with no significant degradation in R^2 for either S_{CC} or S_{FP} and no significant RMSE increase for S_{CC} , being suitable for exploring future climate-related changes in the sensitivity across the Mediterranean Sea.

Extrapolation-risk analyses indicated generally low out-of-range risk for both S_{CC} and S_{FP} models projections, although with a clear increase in future periods, mainly driven by thermal anomaly variables (**Error! Reference source not found.** and **Error! Reference source not found.**). For S_{CC} , anomaly-related extrapolation increased from 0.03% in the baseline to 0.44% in 2026–2030 and 13.51% in 2046–2050, while depth–bottom temperature and space–bottom temperature extrapolation remained low, around 0.52–0.57% and 0.03–0.08%, respectively. A similar pattern was observed for S_{FP} , with anomaly-related extrapolation increasing from 0.03% in the baseline to 0.46% in 2026–2030 and 13.85% in 2046–2050, whereas depth-related extrapolation remained stable at about 0.51% and space–bottom temperature extrapolation remained negligible.



2.3.3 Sensitivity and Risk estimates for CC and FP

Predicted sensitivity for the period 2012-2050 was evaluated for both CC and FP across the Mediterranean Sea. For S_{CC} , predictions revealed a strong spatial structuring, with a projected increase in S_{CC} in the Aegean Sea (top row in *Figure 2-1*). For S_{FP} , projections indicated higher sensitivity scores in the southern part of the basin and in the Aegean Sea (top row in *Figure 2-2*). It is important to note that the associated confidence intervals were relatively narrow (bottom rows in *Figure 2-1* and *Figure 2-2*).

Delta analyses (*Figure A-10*) highlighted non-uniform changes in both S_{CC} and S_{FP} , with localised increases dominating basin-wide patterns and only limited areas of stability or decrease in sensitivity (either S_{CC} or S_{FP}).

Risk indices, i.e., R_{CC} and R_{FP} , were derived for climate change and fishing pressure by combining sensitivity with standardised exposure to both drivers: SST for climate change and FDI fishing effort combined with AIS Global Fishing Watch data for fishing pressure. Both R_{CC} and R_{FP} were predicted to consistently increase across future periods examined in each subregion of the study area (*Figure 2-3*). Moreover, significant shifts in risk distribution were predicted between current and future periods. This was further confirmed by boxplot analyses (*Figure A-11* and *Figure A-12*), indicating an increasing exposure-weighted vulnerability over time.

Hotspot detection (using Getis-Ord G_i^* statistics) identified persistent areas of elevated risk for R_{CC} and R_{FP} (*Figure 2-3*), with increasing hotspot persistence over time in coming decades. For R_{CC} , persistent hotspots were particularly identified in the southern part of the Strait of Sicily, around Cyprus, and in the Aegean Sea. For R_{FP} , persistent hotspots were especially identified in the western Mediterranean Sea off the Spanish coast, in the Gulf of Lion, Ligurian Sea, Sardinian Channel, the Strait of Sicily, Malta, and localised areas in the Adriatic Sea, corresponding to the most intensively exploited fishing grounds. Additionally, risk delta analyses (*Figure A-13*) revealed a widespread intensification of both R_{CC} and R_{FP} across most of the basin, with the strongest increases occurring in the same regions where hotspot persistence was highest, confirming a spatial convergence between emerging risk areas and stable high-risk zones.

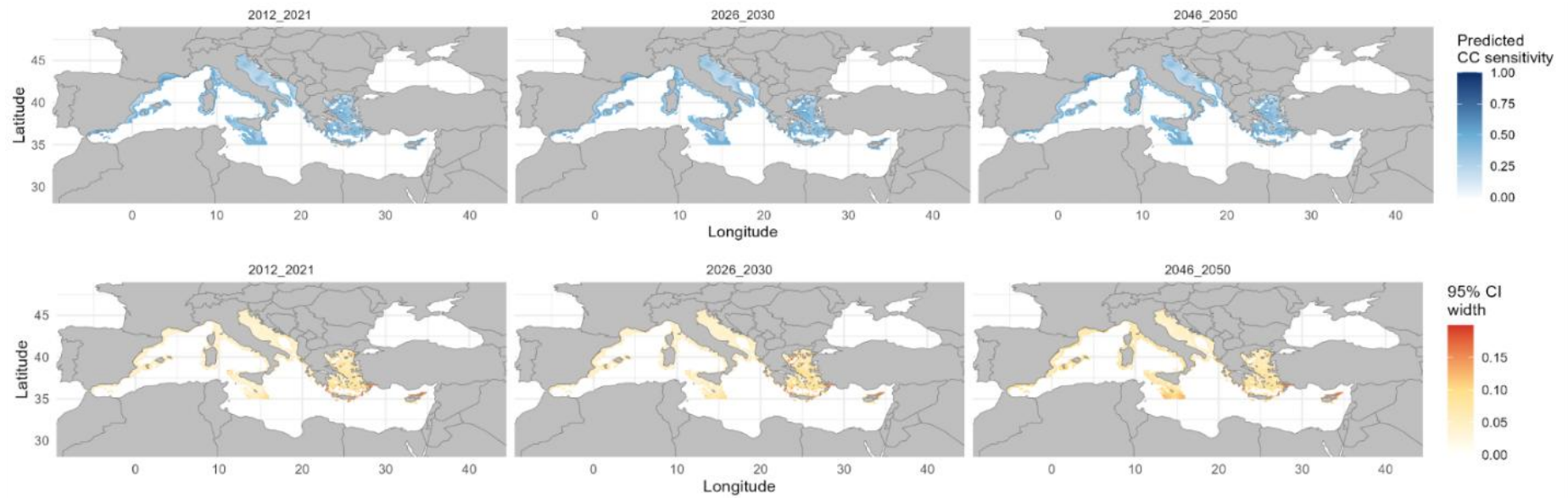


Figure 2-1. Top row: Spatial projections of S_{cc} across the Mediterranean Sea over the three periods: 2012-2021, 2026-2030, 2046-2050, with darker blue shading indicating higher CC sensitivity. Bottom row: the associated prediction uncertainty expressed as confidence interval width, with darker orange shading indicating higher uncertainty in S_{cc} predictions.

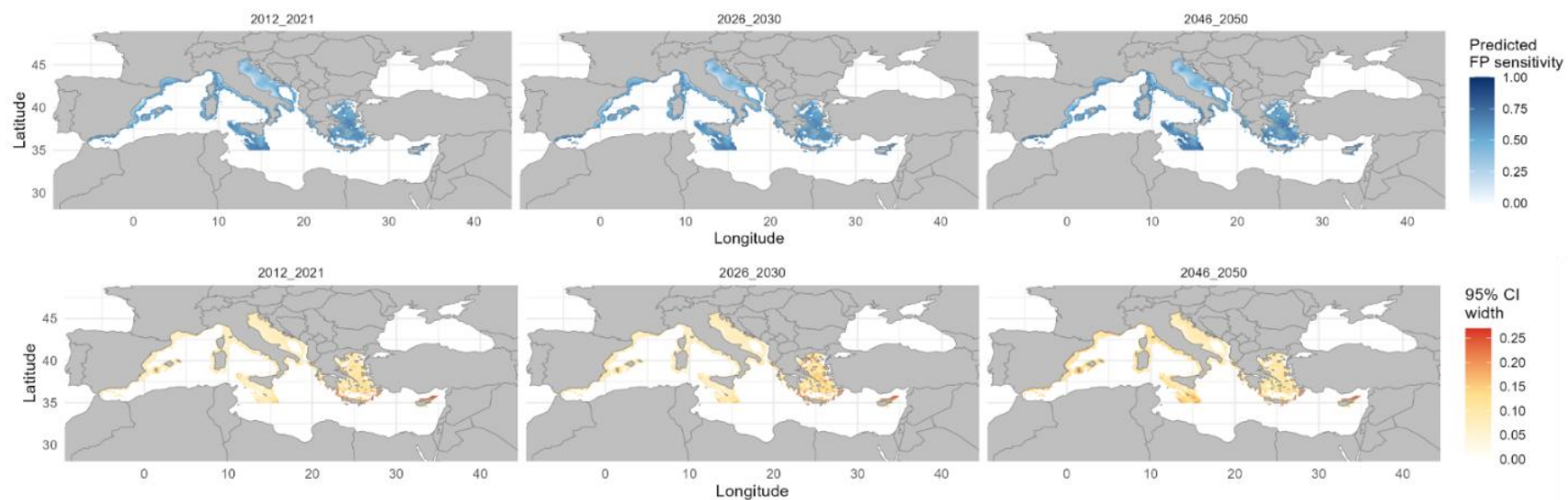


Figure 2-2. Top row: Spatial projections of S_{FP} across the Mediterranean Sea over the three periods: 2012-2021, 2026-2030, 2046-2050, with darker blue shading indicating higher FP sensitivity. Bottom row: the associated prediction uncertainty expressed as confidence interval width, with darker orange shading indicating higher uncertainty in S_{FP} predictions.

Rcc

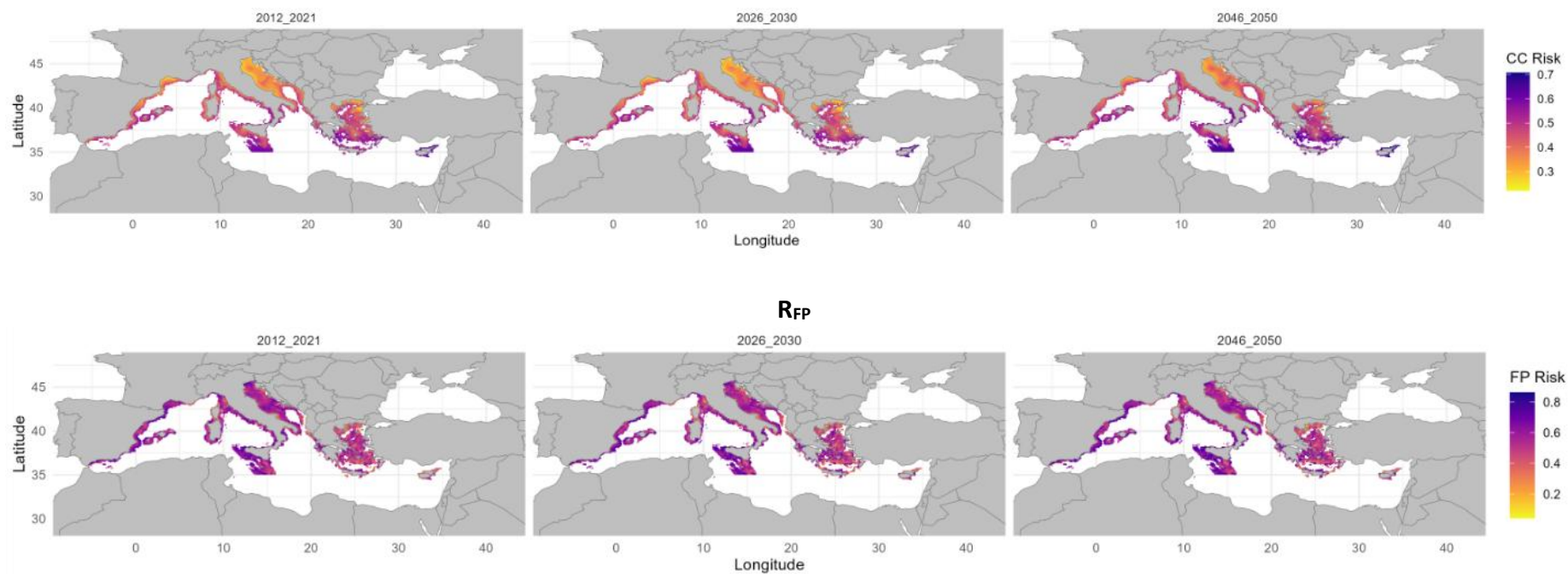


Figure 2-3. Spatial distribution of R_{CC} (upper panels) and R_{FP} (lower panels) across the Mediterranean Sea in the three periods: 2012-2021, 2026-2030, 2046-2050.

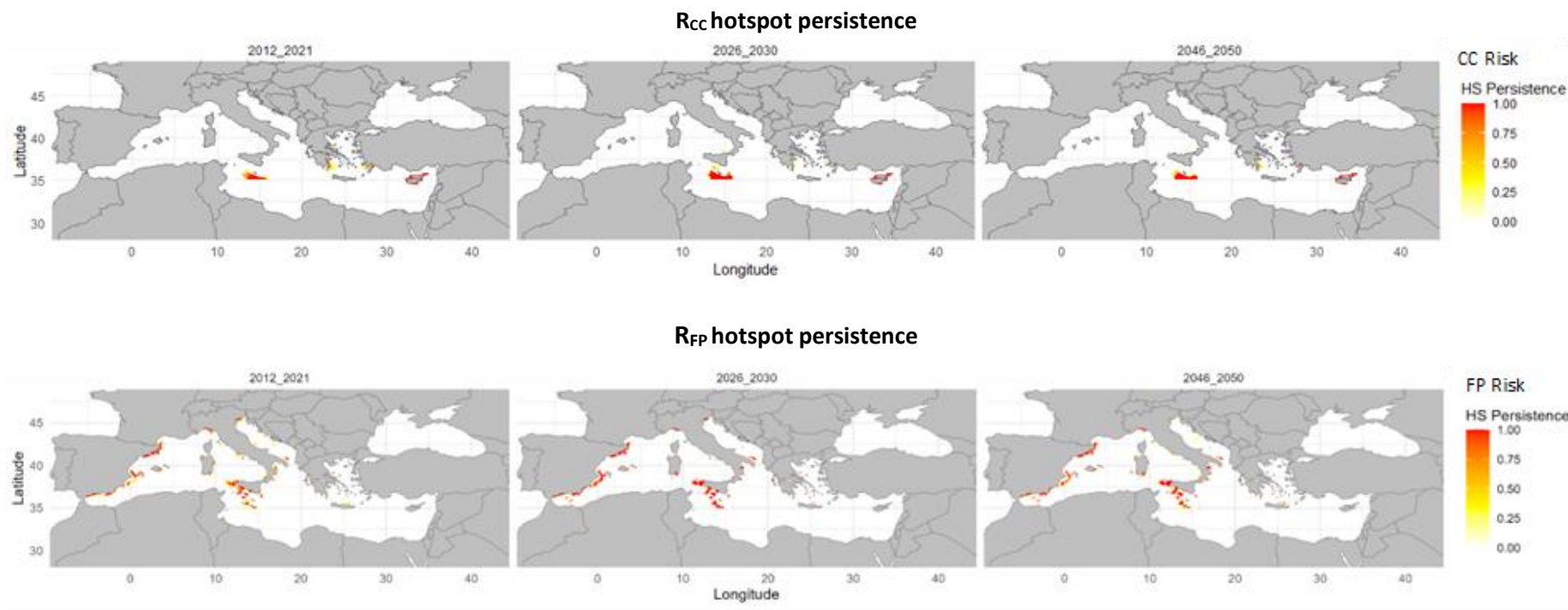


Figure 2-4. Hotspot persistence for R_{CC} (upper panel) and R_{FP} (lower panel) across the Mediterranean Sea in three periods: 2012-2021, 2026-2030, 2046-2050.

Spatial analyses on projected annual rates of change in R_{CC} and R_{FP} are shown in *Figure* . This revealed relatively moderate but spatially coherent rates of change in risk, mostly characterised by slight increases by up to +0.003 per year for R_{CC} , and ranging from -0.01 to $+0.01$ per year for R_{FP} (i.e. both local increases and decreases in R_{FP}). This indicates a slightly higher temporal variability and faster redistribution dynamics for R_{CC} compared with R_{FP} .

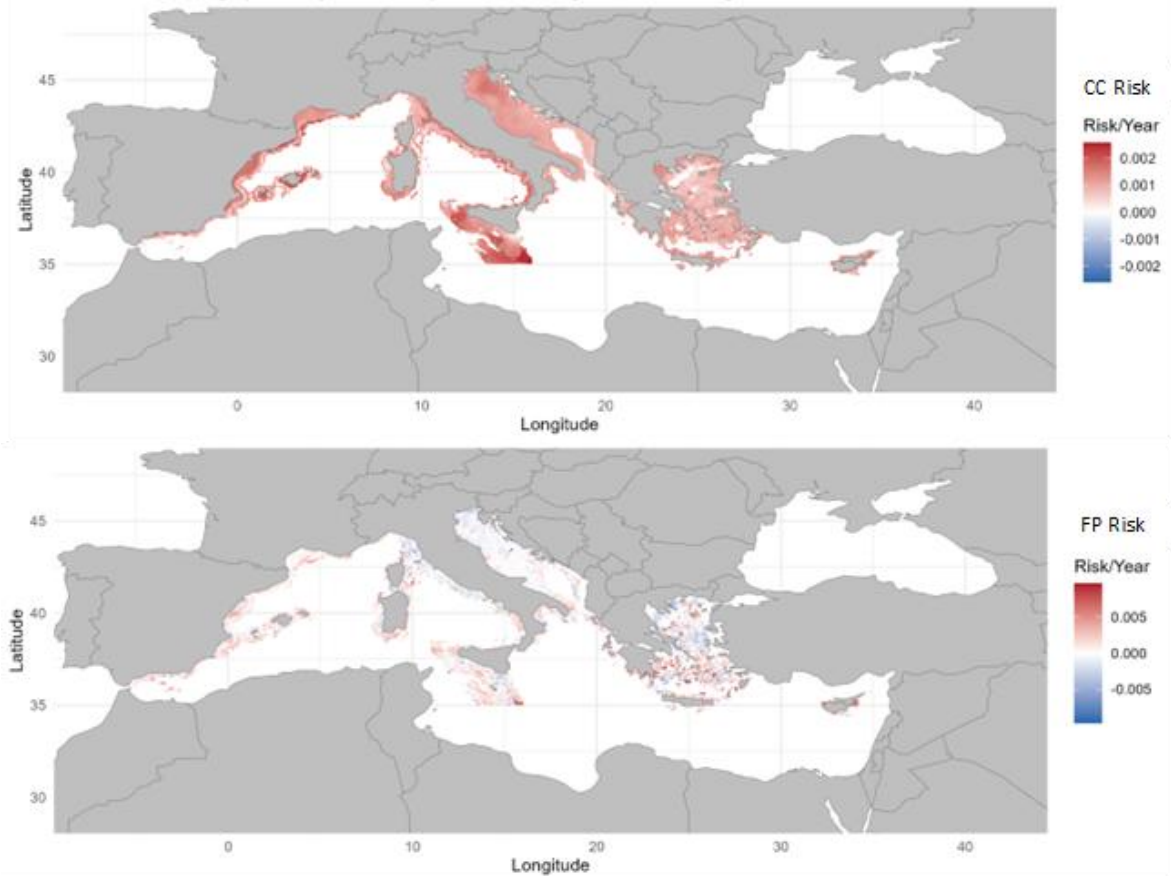


Figure 2-5. Spatial patterns in rates of change in R_{CC} (upper panel) and R_{FP} (lower panel) across the Mediterranean Sea between 2012 and 2050.

2.3.4 Spatio-temporal variations of risk centre of gravity

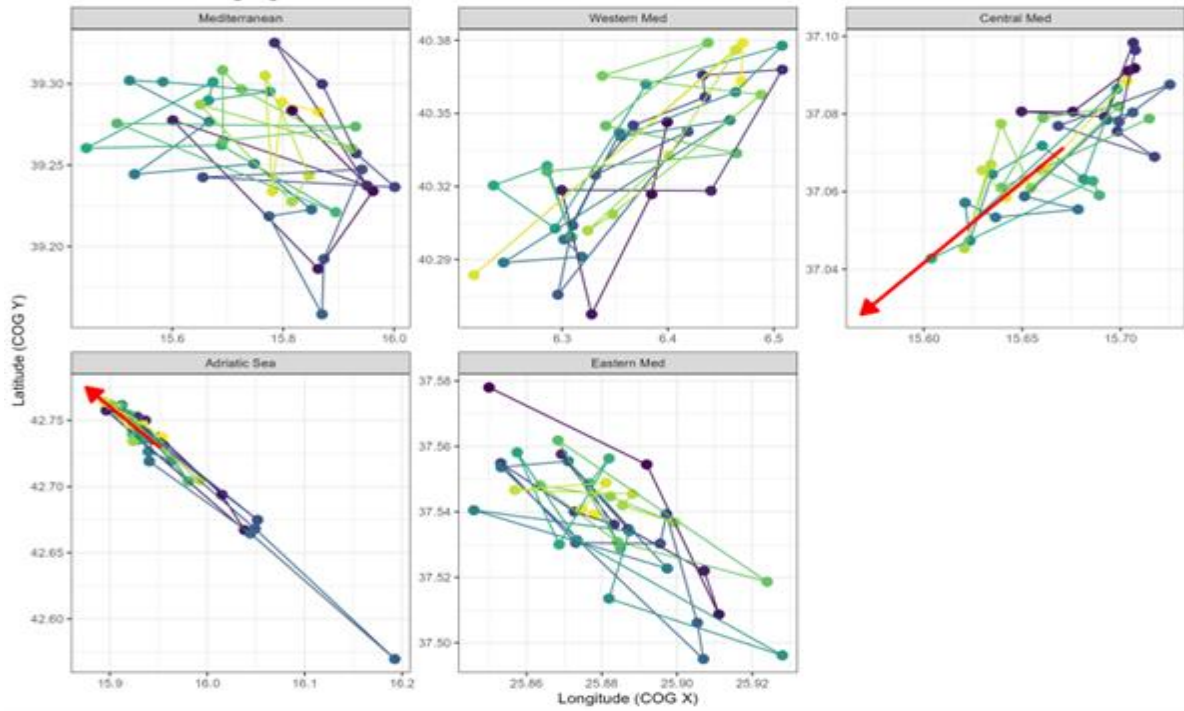
Finally, risk centre of gravity (COG) analyses (*Figure 2-6*) revealed a coherent spatial redistribution of both R_{CC} and R_{FP} , with a gradual basin-scale displacement of the risk centroid through time and directional shifts varying within sub-regions.

For R_{CC} , COG exhibited relatively limited displacement over time at the Mediterranean-wide level (*Figure 2-6*, top panel), suggesting moderate redistribution at this scale. At the sub-regional scale, however, clearer directional trends emerged in two of the four sub-basins (the Central Mediterranean and the Adriatic Sea), where significant trends were detected (indicated by red arrows in *Figure 2-6*). In the Central Mediterranean, the south-westward displacement of the COG suggests that R_{CC} is progressively increasing in the southern and western sectors of the sub-basin. This shift appears to be largely driven by the marked rate of change observed in the Strait of Sicily (around Malta, *Figure A-11*), where climate-related risk is expected to increase more rapidly. This increase likely reflects the combined effect of rising thermal exposure (SST) and high sensitivity of the local demersal community. In the Adriatic Sea, by contrast, the projected increase in community sensitivity over the study period, particularly in the north-western part of the basin, suggests a possible restructuring of the assemblage, with a progressive increase in more climate-sensitive taxa towards the north.

R_{FP} COG trends (*Figure 2-6*) showed clearer progressive and statistically significant directional changes than R_{CC} , both at basin and sub-regional scales. At the Mediterranean scale, absolute spatial displacement remained relatively limited but was nevertheless significant in mostly southward direction. This pattern occurred associated with greater predicted changes in the sensitivity component in the southern Mediterranean, where temperature-related variation was more pronounced. At the sub-regional scale, the Western Mediterranean showed a significant south-westward displacement, consistent with the R_{CC} COG results. The Central Mediterranean displayed year-to-year fluctuations around a relatively compact spatial cluster, but with a significant overall displacement towards the south. The Adriatic Sea and Eastern Mediterranean exhibited significant south-eastward shifts, indicating that R_{FP} -weighted COG changes were spatially coherent and tended to follow areas where projected temperature-driven sensitivity changes were more marked.

Overall, the GAM framework showed a strong explanatory and predictive performance for both S_{CC} and S_{FP} , capturing complex nonlinear interactions among spatial, bathymetric, and thermal drivers. Projections indicate a consistent increase in both climate- and fishing-related sensitivities and risks across the Mediterranean Sea in the long-period projections, with persistent hotspot regions clear spatial redistribution patterns. These findings highlight a progressively intensifying and spatially structured risk landscape, supporting the need for targeted, region-specific management actions under future environmental and anthropogenic threats.

Change in R_{CC} centre of gravity (COG)



Change in R_{FP} centre of gravity (COG)

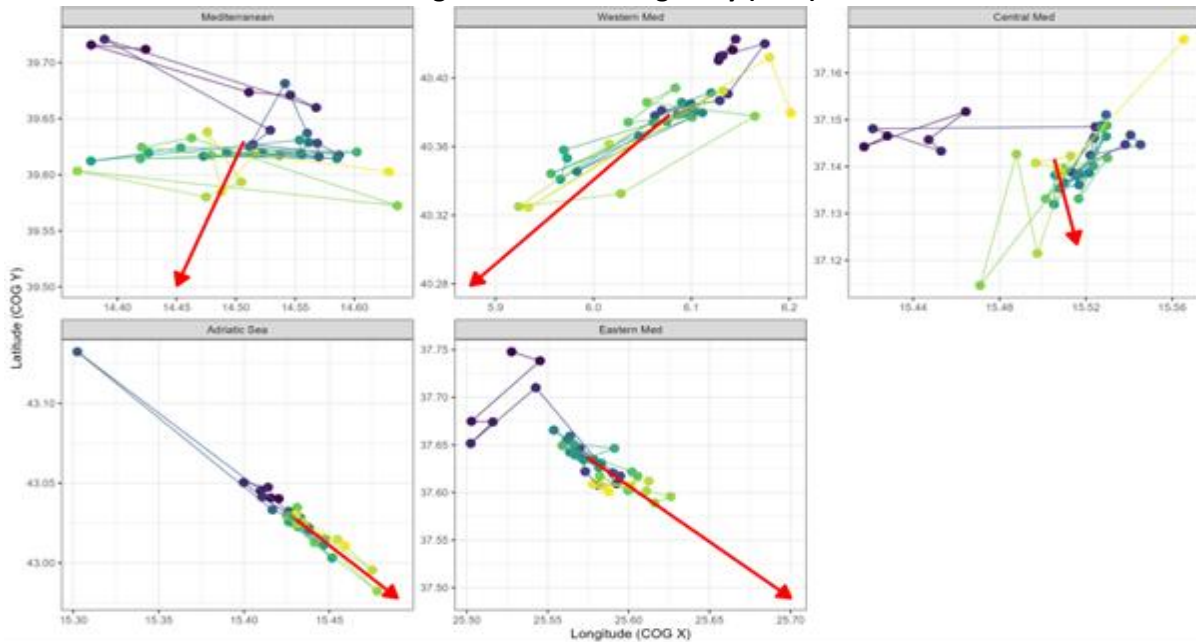


Figure 2-6. Temporal trajectories of annual centres of gravity (COG) for R_{CC} and R_{FP} across the Mediterranean Sea and in four sub-regions between 2012 and 2050, illustrating the spatial redistribution and directional displacement of projected risk patterns over time. Red arrows indicate the direction and magnitude of statistically significant trends in the COG of R_{CC} and R_{FP} within each region, based on Sen's slope estimates ($p < 0.05$, Mann-Kendall test). Arrow direction reflects the dominant shift in latitude and longitude, and arrow length is scaled to the rate of change over time.

2.4 Discussion and conclusions

This study provides a scenario-based projection of climate- and fishing-related sensitivity and risk for the Mediterranean demersal communities under a high-emission climate scenario. Building on the hindcast assessment developed in previous analyses (Roze-meijer et al. 2025), the present work extends the evaluation from baseline conditions to future projections, allowing to assess whether previously identified spatial risk structures are likely to persist, intensify, or shift through time. By integrating trait-based sensitivity indices with spatio-temporal GAM projections, hotspot persistence analyses, and COG dynamics, the results revealed a risk landscape with persistent and localised risk hotspots. Projected changes were generally moderate in magnitude, yet spatially coherent, with persistent hotspot regions, localised increases in sensitivity and risk, and gradual redistributions in the areas of higher risk across the basin. More precisely, R_{CC} and R_{FP} are not expected to increase uniformly across the basin, but rather to intensify in spatially coherent areas where sensitive communities coincide with high environmental or fishing exposure (*Figure 2-3*). Persistent R_{CC} hotspots were identified in the Aegean Sea, Cyprus and the in the Strait of Sicily, while R_{FP} hotspots remained closely associated with historically important fishing grounds, including parts of the western Mediterranean, Gulf of Lion, Ligurian Sea, Strait of Sicily and localised Adriatic areas.

The projected spatial structuring of S_{CC} and S_{FP} across the Mediterranean Sea is consistent with previous evidence suggesting that climate change and fishing pressure affect demersal communities unevenly across the Mediterranean Sea (Ramirez et al., 2018; Aragão et al., 2022; Hidalgo et al. 2022; Agnetta et al., 2025). Importantly, the broad spatial stability of future patterns should not be interpreted as an ecological stasis (Rubenstein et al. 2023, Lawlor et al. 2024); rather, it suggests that future risk remains anchored to persistent biogeographical, bathymetric, and environmental gradients and processes (Danovaro et al. 2009). Local dynamics may arise from changes in the relative abundance (hence contribution) of sensitive versus resilient taxa, as well as from increasing thermal exposure, particularly in the southern sectors of the basin. Furthermore, the semi-enclosed nature of the Mediterranean and its predominantly east-west orientation constrain latitudinal range shifts and may therefore force warm-sensitive taxa to redistribute toward deeper and northern habitats in response to increasing temperatures (Cramer et al. 2018). Such climate-mediated reorganisation processes may contribute to the projected increase of climate-sensitive assemblages in some northern sectors, including in the Aegean and Adriatic Seas, and are consistent with previous evidence of species migration to colder-water refugia under ongoing warming (Chaikin et al. 2022, Sanz-Martín et al. 2024).

The higher projected values of sensitivity to fishing pressure in the southern Mediterranean and Aegean Sea should therefore be interpreted with caution. Because future fishing pressure was kept constant in the projections, the predicted patterns do not necessarily indicate an intensification of fishing impacts, nor do they provide direct evidence of fishing-driven selection. Rather, they suggest that community-level sensitivity to a fixed fishing-pressure layer may vary under changing climatic conditions (Polo et al. 2025). In these areas, increasing temperature and thermal anomalies may modulate the relative contribution of taxa with different ecological and life-history traits, thereby altering community-level estimates of sensitivity to fishing pressure. This interpretation is broadly consistent with the trait-based



framework used to derive S_{FP} , in which community-level sensitivity can change when taxa with different vulnerability traits contribute differently to assemblage composition. However, since the present analysis was conducted at the community level, it cannot directly identify the species responsible for these projected changes. The observed increase in S_{FP} in parts of the southern basin should therefore be regarded as an indication of possible climate-mediated modulation of fishing sensitivity, rather than as direct evidence of a specific taxonomic replacement process. In this context, communities in relatively stable environments may be less resilient to additional stressors, whereas highly dynamic systems may favour species with greater ecological plasticity and adaptive capacity (Dutertre et al. 2013, Jennings & Kaiser 1998).

In the present framework, future S_{FP} changes are not driven by projected increases in fishing effort, but by changes in community sensitivity under future environmental conditions. This suggests that warming, in terms of bottom-temperature changes and thermal anomalies, may favour assemblages with trait combinations that are more sensitive to fishing pressure. As a result, R_{FP} may increase even under a constant fishing-exposure footprint, not because fishing pressure is projected to intensify, but because climate-driven changes in community composition can increase the sensitivity component of risk in areas already exposed to fishing. This mechanism is particularly relevant because it indicates that climate change may not only increase climate-related risk directly but may also reinforce the ecological consequences of fishing by increasing the vulnerability of communities already exposed to fishing pressure. Such climate-driven restructuring processes may further alter trophic interactions, ecosystem functioning, and recovery capacity, particularly in heavily exploited regions where multiple stressors converge in space, potentially amplifying ecological vulnerability and reducing ecosystem resilience under continued environmental change (Ramírez et al., 2018).

More broadly, these projected sensitivity patterns support the hypothesis that future Mediterranean demersal assemblages will undergo progressive spatial reorganisation under the combined effects of climate and anthropogenic pressures (Albouy et al. 2013, Ouled-Cheikh et al. 2022, Quattrocchi et al. 2026). Species responses to the drivers are also strongly correlated to life-history traits such as mobility, reproductive strategy, habitat specificity, and recovery potential, which influence their adaptive capacity and vulnerability to cumulative stressors (Burkett et al. 2005, Lindmark et al. 2023). Therefore, the changes in S_{CC} and S_{FP} likely reflect the emergence of localised ecological transitions and community restructuring processes that may intensify over time under continued environmental change, rather than as evidence of basin-wide regime shifts within Mediterranean demersal communities (Kamberi et al. 2025).

Both R_{CC} and R_{FP} increased consistently over time, with persistent risk hotspots concentrated in ecologically sensitive and more exploited regions, such as the western Mediterranean, the Adriatic, and the Aegean Seas. The persistence of these risk hotspots likely reflects the combined influence of increasing environmental exposure and the high sensitivity of local demersal communities. It also suggests that multiple stressors may increasingly overlap within the same subregions, potentially reducing ecosystem resilience and recovery capacity under continued warming. Similar patterns of spatial congruence among anthropogenic and climate-related pressures have previously been identified across the Mediterranean Sea (Ramírez et



al. 2018), supporting the hypothesis that cumulative stressors may amplify ecological vulnerability and constrain the adaptive capacity of demersal assemblages.

The COG analyses further support this interpretation by showing that projected changes are expressed as gradual shifts in the relative spatial weight of sensitivity and risk within an otherwise persistent basin-scale structure. The limited magnitude of annual changes should therefore not be interpreted as evidence of negligible ecological change. Rather, this pattern may be consistent with delayed or gradual community responses to environmental change, particularly in demersal assemblages whose spatial organisation is strongly constrained by persistent bathymetric, habitat, and biogeographical gradients (Gage 2002; Danovaro et al. 2009; Essl et al. 2015a, 2015b; Dulvy et al. 2008). The slow rate of projected change does not weaken the ecological signal, but suggests that community sensitivity and risk may be undergoing gradual, cumulative reorganisation within an apparently stable spatial structure. In particular, the south-westward displacement of the risk centroid observed in the Central Mediterranean, especially around the south-eastern part of the Strait of Sicily, suggests a progressive intensification of climate-related vulnerability in areas experiencing increasing thermal exposure, which may explain the localised acceleration in R_{CC} observed in the annual rate-of-change and delta analyses. The temporal consistency of these shifts indicates that even small year-to-year changes may accumulate into detectable spatial trends over multi-decadal time scales, reinforcing the interpretation of a coherent adjustment of demersal community vulnerability to changing climate conditions over time (Pinsky et al. 2013).

Overall, from a management perspective, these findings support the need for adaptive and region tailored measures. In persistent high-risk areas, priority should be given to reducing cumulative pressure, improving fisheries selectivity, limiting seabed disturbance, and strengthening the effectiveness of spatial protection. In areas where risk is projected to shift or intensify, specific monitoring should be designed to detect early changes in community composition, trait structure, and risk indicators. Because many countries share the Mediterranean Sea, these actions will require coordination at basin and subregional scales, especially in transboundary areas such as the Strait of Sicily, the Adriatic, and the Aegean Seas.

In conclusion, the present study demonstrates that climate change and fishing pressure are expected to progressively intensify and spatially reorganise ecological risk by mid-century for Mediterranean demersal communities under future warming scenarios. The combined use of trait-based sensitivity indices with spatio-temporal GAM projections, hotspot persistence, and COG analyses provide a useful framework for identifying priority areas for future specific management actions. The results revealed a risk landscape characterised by strong spatial structuring and a gradual redistribution over time. Although projected changes are generally moderate in magnitude, their spatial coherence and persistence indicate that the stressors overlap in ecologically vulnerable areas, potentially reducing ecosystem resilience and adaptive capacity. These findings emphasise the need to move from static conservation planning towards adaptive risk-based management that can account for both persistent vulnerabilities and gradual climate-driven redistribution of demersal communities to mitigate the future impacts of climatic and anthropogenic pressures on Mediterranean demersal ecosystems.

3 Northeast Atlantic: Greater North Sea, Celtic Seas and Bay of Biscay

3.1 Introduction

Marine ecosystems across the Northeast Atlantic are subject to increasing pressure from multiple anthropogenic drivers, with commercial fishing and climate change among the most pervasive (Halpern et al. 2008, Holt et al. 2012, Punzón et al. 2016). Long-term warming trends and associated environmental changes are already reshaping species distributions and community composition (Thompson et al. 2023, Carroll et al. 2024), while fishing pressure continues to influence population structure, size composition and habitat condition across the region and globally (Pinnegar et al. 2002, Shephard et al. 2012, Johnson et al. 2015). Together, these pressures often interact and reshape communities and are affecting the capacity of marine systems to sustain biodiversity and support ecosystem services such as food provision (Poloczanska et al. 2013, Link & Watson 2019, du Pontavice et al. 2020). These pressures are recognised as major drivers of biodiversity change, with important implications for the resilience of marine ecosystems and the sustainability of ecosystem services, especially as these trends intensify into the future.

Understanding how marine communities respond to these pressures requires approaches that capture both intrinsic ecological vulnerability and external exposure. While previous work focused primarily on retrospective analyses and recent historical conditions (Deliverables D4.1, D4.2 and D4.2), there is a growing need to move beyond retrospective analyses towards forward-looking assessments that consider how these patterns may evolve under future environmental change. In the Northeast Atlantic, projected increases in sea temperature, combined with ongoing fishing pressure, are expected to further alter community composition and potentially increase vulnerability in some regions, while other areas may experience shifts in sensitivity as species distributions change (Fernandes et al. 2020; Thompson et al. 2023; Townhill et al. 2023). Understanding how these changes will translate into shifts in community-level sensitivity is essential for anticipating future risks and supporting adaptive management strategies.

To address this gap, this section identifies future community-level sensitivity and risk to climate change (CC) and fishing pressure (FP) for bottom-dwelling fish (see also the previous deliverable reports: Engelhard et al. 2024, Rozemeijer et al. 2025). It then identifies hotspots of high risk to climate change and fishing across the Greater North Sea, Celtic Seas and Bay of Biscay. We aim:

- (1) To project future sensitivities and risks of demersal fish and macroinvertebrate communities in the Greater North Sea, Celtic Seas and Bay of Biscay (henceforth Northeast Atlantic) under a high-emission scenario (RCP8.5) using a spatiotemporal Beta Generalised Additive Modelling (GAM) framework;
- (2) To assess the spatial and temporal dynamics of climate- and fishing-driven risk through predictive mapping, hotspot persistence and rate of change metrics;



- (3) To identify potential spatial redistributions of sensitive and high-risk areas by analysing shifts in the Centre of Gravity (COG) of climate change risk (R_{CC}) and fishing pressure risk (R_{FP}) across Northeast Atlantic subregions.

By quantifying the potential future impacts of climate change and fishing on community sensitivity and risk, the analysis provides an integrated and reproducible forecasting framework capable of supporting ecosystem-based fisheries management and biodiversity conservation across future environmental change scenarios. The work provides a screening level assessment of areas where fish communities may be most vulnerable under future climate change and fishing scenarios.

3.2 Methods

This section builds on the community-level sensitivity for bottom-oriented fish and risk layers developed in the preceding reports (Rozemeijer et al. 2025; Engelhard et al. 2026). The analysis here focused on the Northeast Atlantic, covering the Greater North Sea, Celtic Seas and Bay of Biscay (OSPAR regions II, III and IV). The Iberian Coast was excluded from region IV due to the lack of accurate fishing pressure data and to ensure consistency between modelling approaches for each pressure (climate change and fishing pressure). Henceforth, all mentions of region IV refer to the Bay of Biscay only. All analyses and data were conducted and aggregated to a regular ICES rectangle grid (0.5 degrees of latitude by 1 degree of longitude). Here, we briefly summarise the previously used data and methods, and outline additional methods specific to this report.

3.2.1 Fishing pressure and environmental data

We used the same fishing pressure data from the International Council for the Exploration of the Sea (ICES) “OSPAR request” spatial fishing-intensity product (ICES 2018 and updates). We used the same environmental data as the previous reports from NEMO-MEDUSA reanalysis (Yool et al. 2013), providing annual sea surface and bottom temperatures on a 0.25° grid across the Northeast Atlantic (20°W–15°E, 35°N–70°N). These were available to match our species data from 1997–2020. Annual SST and SBT data from 2020 to 2050 for each ICES rectangle were additionally downloaded for the analysis on future community sensitivity and risk to climate change. Annual anomalies for SST and SBT were calculated at the grid-cell level by subtracting the long-term mean for each cell from the annual value, thereby isolating interannual variability from spatial gradients.

3.2.2 Species and community data

Community composition data and species-level sensitivities (used to calculate community sensitivities) were derived from the FISHGLOB database as before and aggregated to the ICES grid and annual time steps (1997–2020). Full trait definitions, scoring protocols and methods are in D4.1 (Engelhard et al. 2024), D4.2 (Rozemeijer et al. 2025) and D4.3 (Engelhard et al. 2026). Community-level sensitivity scores were calculated following Polo et al. (2025). Species-level sensitivity scores were aggregated across hauls within each ICES rectangle in a given year and weighted by $^{10}\log$ -transformed abundance of each species. Species



abundances were logged to reduce the influence of overly abundant taxa and give more weight to rarer species. More detailed methods can be found in D4.2 (Rozemeijer et al. 2025).

3.2.3 Modelling community-level sensitivities

Community-level sensitivity to climate change (S_{CC}) and fishing pressure (S_{FP}) was modelled using beta Generalised Additive Models (GAMs) with a logit link, appropriate for response variables bounded between 0 and 1. The response variable was the weighted community sensitivity value, with models being run for sensitivity to climate change and fishing pressure separately. A suite of 11 candidate GAMs was constructed to explore alternative representations of the relationships between sensitivity and environmental predictors. Models included combinations of spatial smooths (longitude, latitude), depth, SST and SBT (annual absolute values and anomalies), and interaction terms (tensor product smooths; te and ti) capturing non-linear interactions between environmental variables and spatial structure. All models were fitted using the *mgcv* package with restricted maximum likelihood (REML) estimation. Prior to modelling, multicollinearity among predictors was assessed (**Error! Reference source not found.**). SST and SBT anomalies were strongly correlated ($r > 0.7$) and were therefore not included simultaneously within the same model.

Model performance was compared across all candidate models using Akaike Information Criterion (AIC), alongside adjusted R^2 and deviance explained. The model with the lowest AIC was selected as the final model used for projections. Model diagnostics included: concurvity assessment to evaluate redundancy among smooth terms; checks of the adequacy of smoothing parameters via k-index tests; and inspection of residuals and fitted values. Variance partitioning was conducted using hierarchical partitioning to quantify the relative contributions of each variable to model deviance explained.

Predictive performance was assessed using two complementary validation approaches. First, we used rolling one-step-ahead validation, where models were trained on data up to year t and used to predict year $t + 1$, iteratively across the time series. This approach evaluates short-term predictive skill under realistic forecasting conditions. Second, we used sliding 5-year window evaluation, where models were trained on five-year windows and tested on out-of-window years. This method allows evaluation of predictive performance as a function of temporal extrapolation distance. Model skill was quantified using root mean squared error (RMSE), mean absolute error (MAE), bias, correlation and R^2 between observed and predicted values. In addition, performance decay with increasing temporal extrapolation was modelled using both log-linear and nonlinear decay functions, providing an estimate of forecast reliability over extended time horizons.

3.2.4 Projecting community-level sensitivities

The selected GAM was applied to a predictive grid of environmental variables (SST, SBT, anomalies and depth) spanning 1997-2050. Predictions of community-level sensitivity were generated annually and subsequently aggregated into three periods: reference period (2016-2020), near future (2026-2030) and mid-century (2046-2050). This allowed assessment of temporal changes in spatial patterns of community sensitivity.

3.2.5 Fishing pressure and climate change risk

Community-level risk was calculated by combining projected sensitivity with exposure layers, following the framework established in previous deliverables. Climate change risk was derived from the absolute values of SST rather than the temperature anomalies (from the NEMO-MEDUSA model scenario RCP8.5). Since we do not have reliable and accurate predictions of future fishing effort, fishing risk was derived from current fishing pressure as the exposure layer. Risks were calculated as the mean of the projected community-sensitivity score and the SST (for R_{CC}) or surface SAR (for R_{FP}) for each ICES grid cell per year. To evaluate temporal trends in climate and fishing-related risk across the Northeast Atlantic, the annual rate of change in both RCC and RFP was calculated for each grid cells using linear regression. The resulting regression slopes represented the annual rate of change in risk and were mapped to identify areas experiencing the greatest increases or decreases in risk over time. Differences in risk among study periods and OSPAR region were assessed using Kruskal-Wallis tests, with pairwise Wilcoxon signed-rank tests conducted as post-hoc comparisons where significant differences were detected.

3.2.6 Hotspots of risk

Hotspots of high and low risk were identified using spatial clustering approaches consistent with previous analyses (*e.g.*, Getis-Ord G_i^* ; see D4.3 (Engelhard et al. 2026)). This method identifies statistically significant spatial clustering of high and low values of risk (fishing pressure and climate change separately). For each grid cell the Getis–Ord G_i^* statistic compares the sum of risk values in the cell’s local neighbourhood (cell plus neighbours) to the overall study-area distribution, producing a standardised z-score and p-value that indicate clustering strength and significance. Positive significant z-scores indicate hotspots (clusters of high values), while negative significant z-scores indicate coldspots (clusters of low values); the magnitude reflects clustering intensity. We identified robust high-risk clusters by classifying $\geq 95\%$ hotspots as cells with G_i^* z-score > 0 and $p \leq 0.05$ (two-sided), and did not further categorise lower-confidence hotspots or coldspots for mapping. To assess temporal stability, hotspot persistence was quantified across time periods, highlighting areas where high or low risk consistently occurs. This enabled identification of priority regions where communities will potentially be persistently exposed to high combined risk from climate change and fishing pressure in future.

3.2.7 Centres of gravity analysis

To examine large-scale spatial redistributions of risk across the Northeast Atlantic, annual centres of gravity (COGs) for R_{CC} and R_{FP} were calculated for the study region and its subregions (OSPAR regions). COG coordinates were derived as weighted spatial means, using RCC and RFP values as weights. Temporal trends in COG location were assessed using the Mann-Kendall trend test, while the rate of spatial displacement was estimated using Sen’s slope estimator and expressed as degrees of latitude or longitude shifted per year.

3.3 Results

3.3.1 Model performance and structuring

Generally, models performed very well, but S_{CC} models outperformed S_{FP} models (Table 3-1). The S_{CC} model had strong predictive ability, explaining a higher proportion of deviance (88%) and higher R^2 (0.89) compared to the S_{FP} model (52% deviance explained, $R^2 = 0.49$). Based on these metrics, the S_{CC} model was considered highly robust for projection, while the S_{FP} model, although weaker, was retained as the best-performing formulation for representing fishing sensitivity. Both final models incorporated spatial structure, depth and interactions with climate. Spatial variables were the most important of the variables for predicting both S_{CC} and S_{FP} , more so than environmental variables alone (**Error! Reference source not found.**). Spatial variables accounted for >60% of explained deviance in S_{CC} models and >70% of explained deviance in S_{FP} models (**Error! Reference source not found.**).

Table 3-1. Final S_{CC} and S_{FP} models selected and their performance, indicating n (sample size), AIC (Akaike Information Criterion), R^2 (adjusted coefficient of determination), and explained deviance percentage of the final selected Generalised Additive Models (GAMs). Model formulation included spatial smoothers (s), tensor-product smoothers describing nonlinear interactions (te), and interactions (ti). CC = climate change, FP = fishing pressure.

Model	Predictors	n	AIC	R^2	Explained Deviance
CC	$s(lon,lat)+s(SSTa)+s(depth)+ti(lon,lat,SBT)+ti(depth,SBT)$	7605	-25253	0.89	88%
FP	$s(lon,lat)+te(depth,SBT)+ti(lon,lat,SBT)$	7605	-9282	0.49	52%

Model diagnostics indicated good agreement between observed and fitted values for both the CC and FP models, supporting the adequacy of the selected GAM formulations. Partial-effect smoothers demonstrated strong spatial and environmental structuring in both models, with clear evidence of non-linear and non-additive relationships among predictors (Figure B-3 and Figure B-4). For the CC model, the two-dimensional spatial smoother revealed pronounced geographical heterogeneity, with depth exerting a strong non-linear influence and thermal variables contributing more subtle effects. Interaction terms highlighted complex responses across spatial, bathymetric, and thermal gradients, indicating that CC risk is shaped by combined environmental drivers rather than single variables. A similar overall pattern was observed for the fishing pressure model, with strong spatial structuring and significant non-linear interactions, particularly involving depth and bottom temperature. However, the fishing pressure model exhibited more spatially irregular and patchy response patterns, suggesting a stronger influence of localised processes. Overall, both models indicated that risk patterns are governed by complex interactions between spatial location, bathymetry, and thermal conditions, rather than independent effects of individual predictors.

3.3.2 Model validation

To evaluate the temporal robustness of the S_{CC} and S_{FP} sensitivity models, a rolling one-step-ahead cross-validation approach was applied, whereby the model was sequentially trained on all available data up to a given year and used to predict the subsequent year. Across all validation iterations (2014–2020), model performance remained consistently high for both S_{CC} and S_{FP} , indicating strong temporal transferability. Predictive accuracy showed relatively limited variation between years, with RMSE values ranging from 0.037 to 0.053 and mean absolute error (MAE) ranging from 0.028 to 0.042 in CC models (*Table 3-2*). For FP models, RMSE values ranged between 0.126 to 0.136 and MAE ranging from 0.096 to 0.103 (*Table 3-2*). Model fit remained strong throughout the validation period, more so for the S_{CC} than S_{FP} model, with correlations between observed and predicted values consistently high (0.93–0.95), corresponding to R^2 values between 0.87 and 0.91. These results demonstrate that the models are able to reliably reproduce interannual variability in community-level climate sensitivity.

A slight decline in predictive performance was observed in later test years for both S_{CC} and S_{FP} models, with marginal increases in RMSE and positive bias values, indicating a tendency towards mild overprediction in more recent periods. However, these changes were modest, and overall performance remained robust. The consistency in correlation and error metrics across all validation years suggests that the model effectively captures the underlying relationships between environmental predictors and community sensitivity, supporting its application for future projections.

Across all sliding 5-year validation windows, model performance remained consistently high, with mean RMSE of approximately 0.05 and MAE of approximately 0.038. The model maintained strong agreement between observed and predicted values (mean correlation ≈ 0.93 ; $R^2 \approx 0.87$), indicating good predictive skill even when extrapolating beyond the training period.

Table 3-2. Mean cross-validation statistics from rolling one-step-ahead approach for final models predicting community sensitivities to climate change and fishing pressure. Performance metrics include RMSE (root mean square error), MAE (mean absolute error), bias (mean difference between observed and predicted values), correlation (Pearson correlation coefficient between observed and predicted values) and R^2 values (proportion of variance in observations explained by model predictions).

Model	Rolling validation years	RMSE	MAE	Bias	Correlation	R^2 observed: predicted
S_{CC}	2013-2020	0.05	0.04	0.02	0.94	0.89
S_{FP}	2013-2020	0.13	0.10	0.01	0.64	0.41

3.3.3 Sensitivity and risk estimates for CC and FP

Predicted sensitivity for the period 2016-2050 was evaluated for both CC and FP across the Northeast Atlantic. For S_{CC} , predictions revealed a clear spatial gradient in community-sensitivity to warming across the north of the study region, particularly the Greater North Sea and Celtic Seas, while communities in the Bay of Biscay have a higher relative abundance of traits less sensitive to warming (*Figure 3-1*). These trends reflect the actual data for present-day S_{CC} , shown in D4.2 (Rozemeijer et al. 2025). Generally, the change in predicted S_{CC} is small and mostly declines in future across most of the study region in relation to present-day (*Figure B-7*). The width of confidence intervals arounds the S_{CC} predictions remains small, and only a few grid cells have lower confidence (bottom row, *Figure 3-1*).

For S_{FP} , present-day predictions generally follow the actual values in D4.2 (Rozemeijer et al. 2025), with specific areas in the central Greater North Sea and Celtic Seas as areas of high community-level sensitivity to fishing pressure. Sensitivity to fishing pressure increases across most of the study region over time, which is particularly pronounced in the southern Celtic Seas (red grid cells in *Figure 3-2* and see absolute change in *Figure B-7*). Once again, it is important to note that the associated confidence intervals were relatively narrow (bottom row, *Figure 3-2*).

The calculated risk associated with climate change was spatially widespread across the study area in all time periods, with consistently higher risk in the western, southwestern and some southern shelf regions, and lower risk across much of the central and northern North Sea (top row, *Figure 3-3*). The overall general pattern in future periods remained broadly similar to the baseline. By mid-century however, risk increases slightly and becomes more extensive in some western and central areas, suggesting that climate-driven risk is likely to remain spatially persistent and increase modestly over time. R_{CC} increases across most of the Northeast Atlantic region (top row, *Figure 3-4*) with larger increases occurring between present and mid-century compared to present versus near future.

The calculated risk associated with fishing pressure showed a different spatial pattern, with higher risk more concentrated across the northern North Sea and around the shelf edges, and comparatively lower risk in parts of the southern and central regions. This distribution remained broadly consistent between the baseline (2016–2020) and near-future (2026–2030) periods, indicating persistence in the main areas of fishing-related risk. By mid-century (2046–2050), the overall pattern remained similar, although some areas showed slight reductions in intensity and increased spatial heterogeneity. These changes are more noticeable in *Figure 3-4* and *Figure B-9* whereby changes in time vary spatially, with the largest increases in R_{FP} occurring in the southern Celtic Seas.

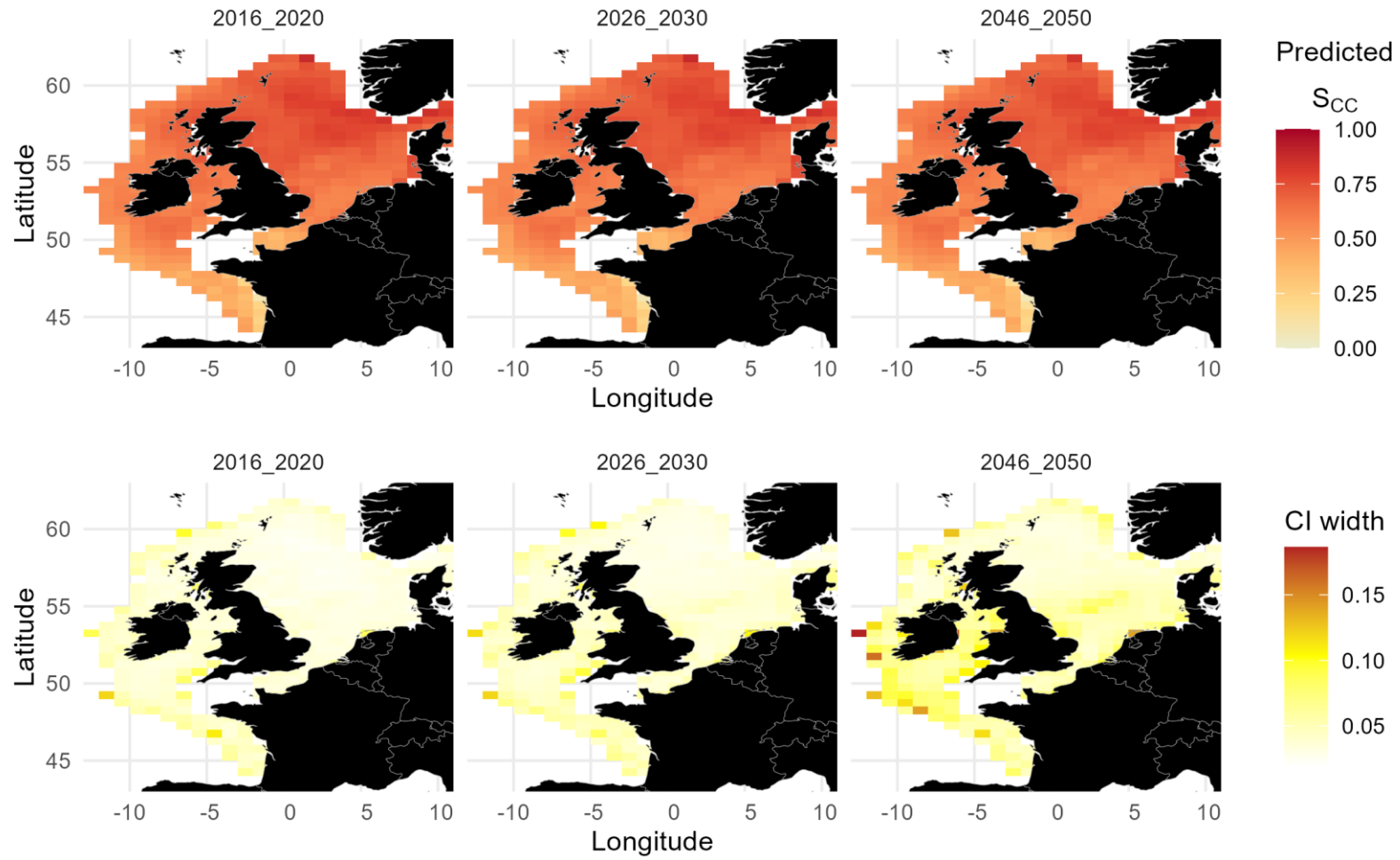


Figure 3-1. Projected community-level sensitivity to climate change (S_{cc}) for current, near-future and mid-century using beta GAMs (top panel). Associated confidence intervals are shown in the bottom panel. See Figure B-7 in the Appendix for maps of absolute change between reference period and future periods.

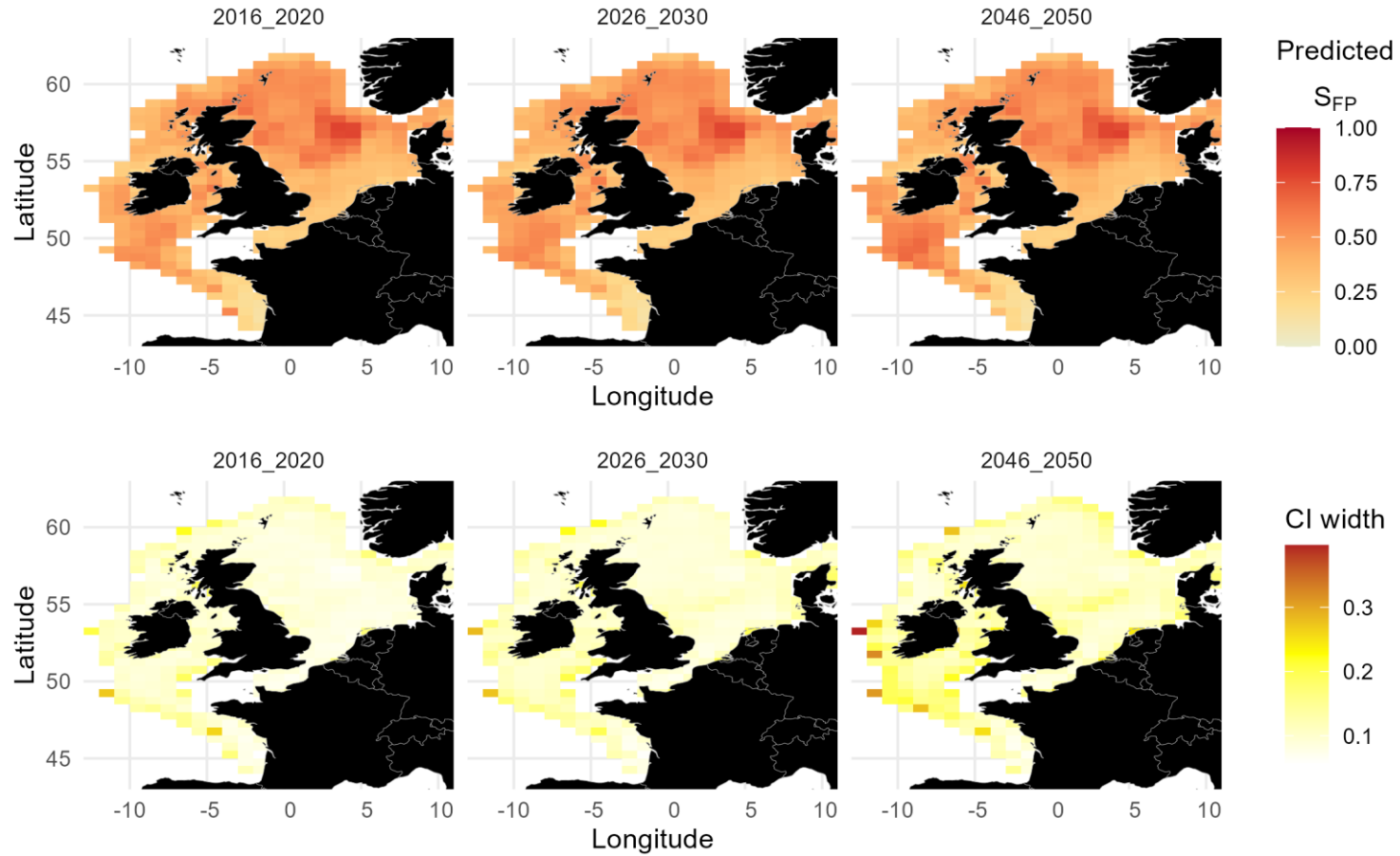


Figure 3-2. Projected community-level sensitivity to fishing pressure (S_{FP}) for current (reference period), near-future and mid-century using beta GAMs (top panel). Associated confidence intervals are shown in the bottom panel. See Figure B-7 in the Appendix for maps of absolute change between reference period and future periods.

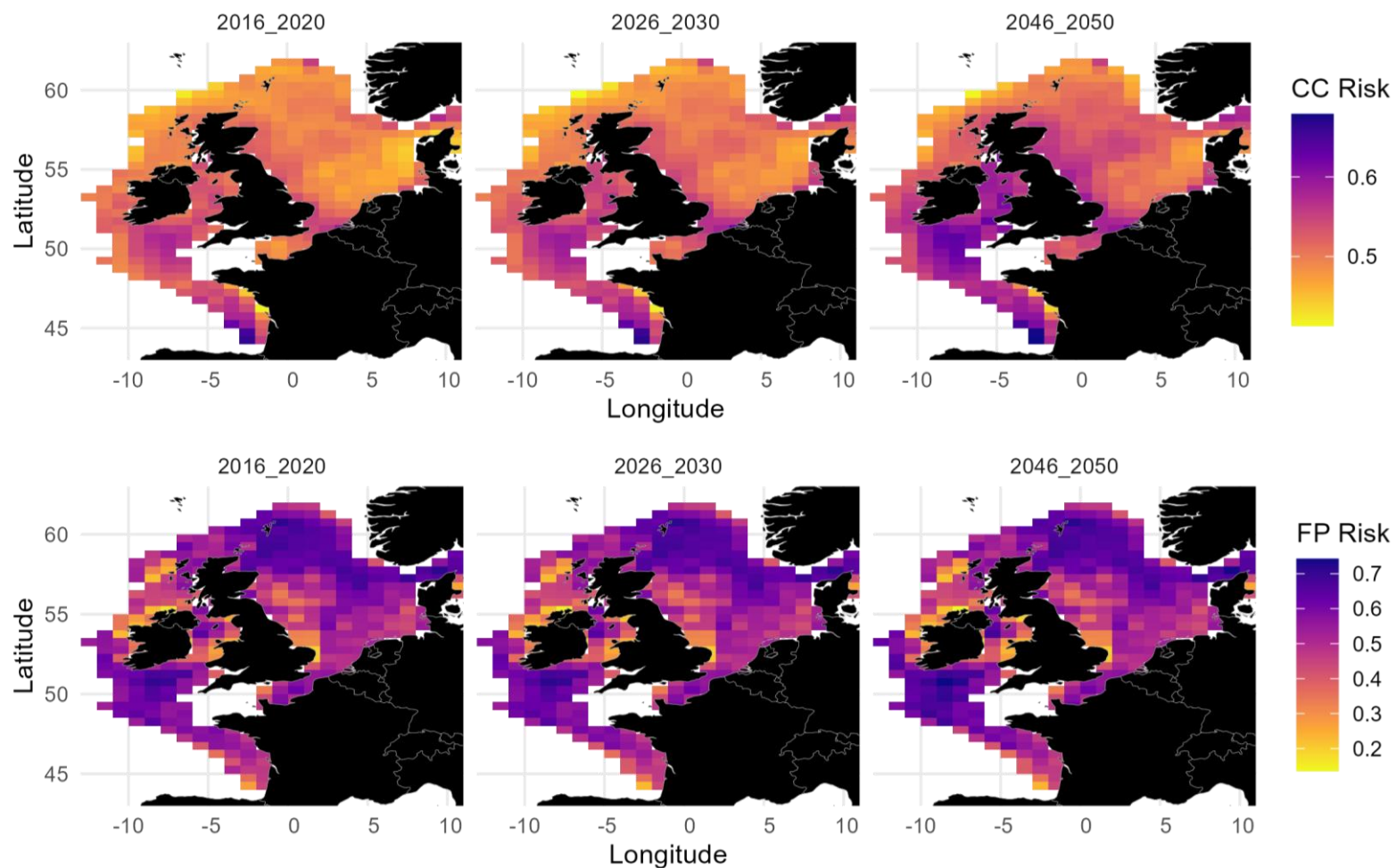


Figure 3-3. Community-level risk to climate change (CC) and fishing pressure (FP) for current (reference period), near-future (2026-2030) and mid-century (2046-2050). Risk was calculated by combining the projected community-level sensitivities to CC with normalised SST exposure.

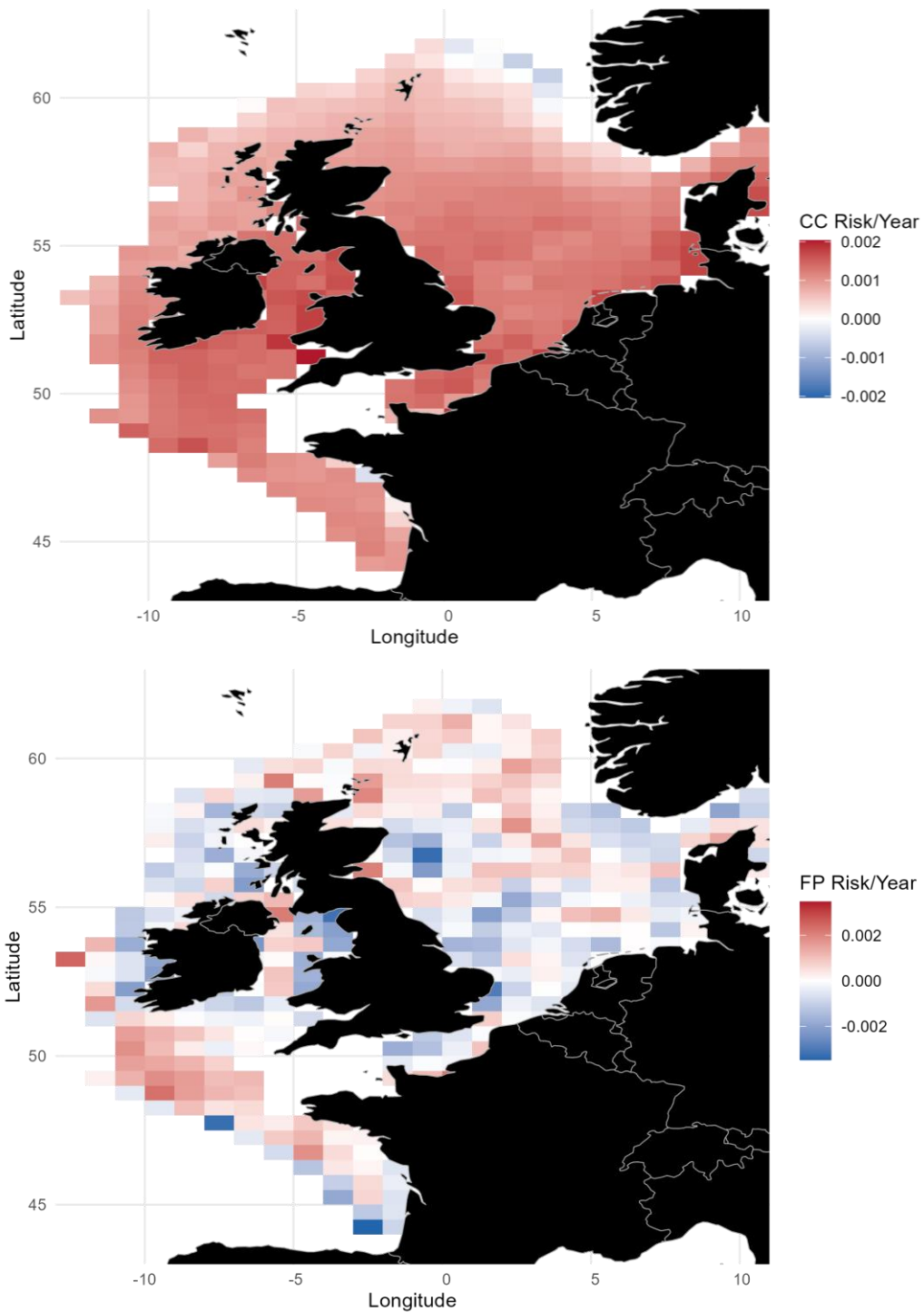


Figure 3-4. Annual rate of change (linear slope from 1997 to 2050) in climate change (CC) risk (upper) and fishing pressure (FP) risk (lower). The slope was calculated using a simple linear model. Red shows an increase in risk, blue shows a decrease in risk.



3.3.4 Hotspots of future community-level risk to CC and FP

Hotspots of elevated R_{CC} in the baseline period (1997-2020), based on the predicted risk scores and Getis–Ord $G_i^* \geq 95\%$ threshold, are concentrated in a band extending across the southern North Sea, eastern English Channel, and parts of the Celtic Sea, with the highest intensity areas occurring in more southerly and coastal regions in the Bay of Biscay (red areas in *Figure 3-*). This overall pattern persists into the near future, with hotspots remaining spatially coherent and largely unchanged in extent, although there is a slight intensification and consolidation of high-risk cells in the central-southern shelf areas. By mid-century, the core hotspot regions continue to persist, indicating strong temporal stability in the location of highest risk, but with a modest expansion and increased persistence in some areas, particularly along the western and southwestern margins of the study region. In contrast, northern areas consistently exhibit lower risk levels across all time periods, with only limited emergence of hotspots (near the southern coast of Norway).

The R_{FP} hotspots occurred in a different spatial and temporal patterns compared to the R_{CC} hotspots (*Figure 3-*). During the historical period (2008-2020), elevated R_{FP} is concentrated primarily in northern areas of the study region, particularly across the northern North Sea and areas of west Norway and Scotland. There were additional R_{FP} hotspots in the southern Celtic Seas, which overlap with hotspots of R_{CC} . In the near future, the northern hotspots persist but show some contraction and redistribution, with high-risk areas becoming more fragmented and slightly reduced in spatial extent. The cluster in the Celtic Seas remains, with more grid cells within the cluster becoming more persistent over time. By mid-century, the spatial footprint of R_{FP} becomes further reduced and patchier overall, with only isolated high-risk cells remaining in the northern North Sea. The hotspots in the Celtic Seas become more persistent, covering a larger area with high risk to fishing pressure.

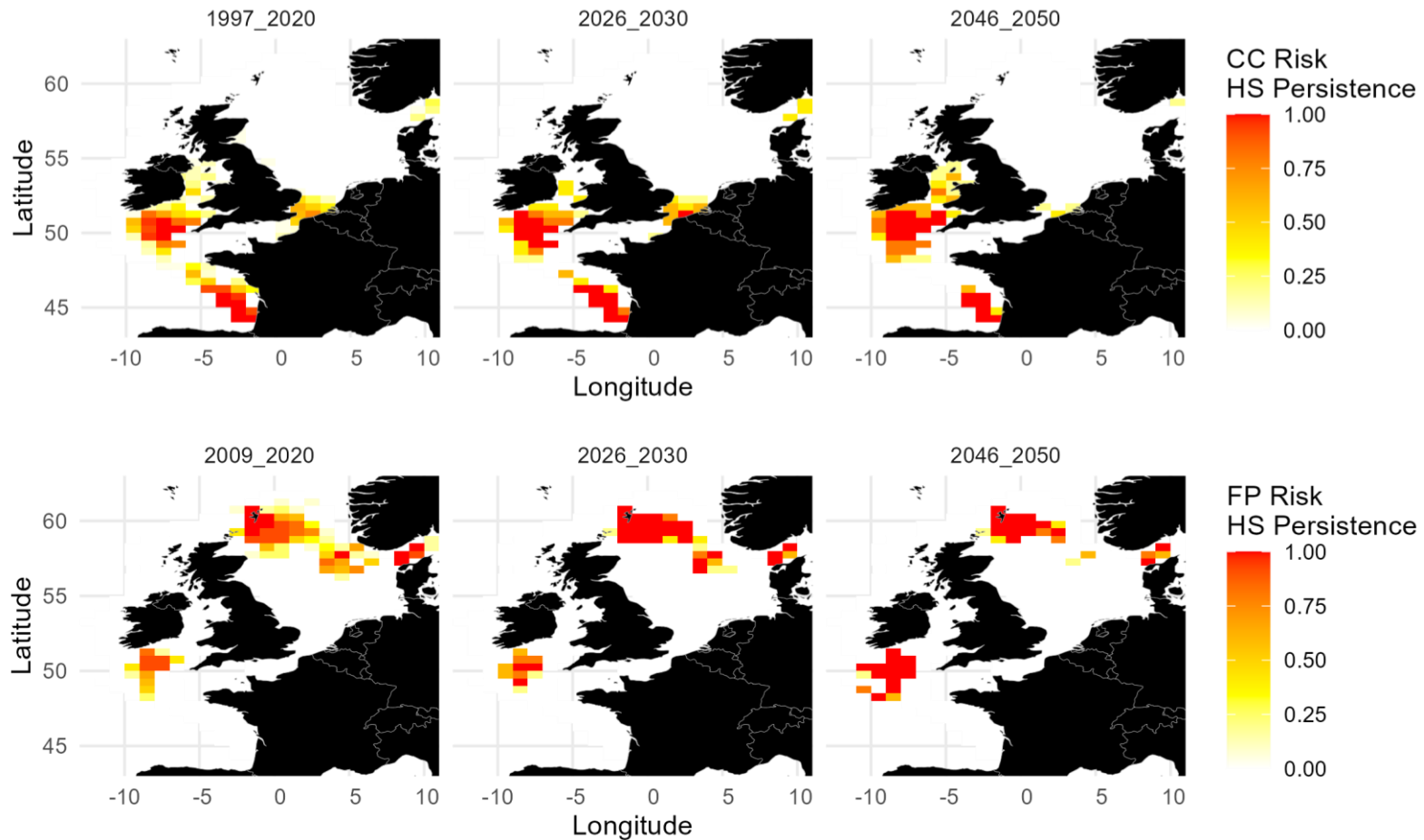


Figure 3-5. Hotspots (HS) of community-level risk to climate change (CC, upper panel) and fishing pressure (FP, lower panel) and their persistence over time for current, near-future and mid-century. Hotspots of highest persistence are shown in red, less persistent in yellow. Current periods (1997-2020 and 2009-2020) reflect the available data for climate and fishing pressure.

3.3.5 Spatiotemporal variations of risk centre of gravity (COG)

R_{CC} exhibited distinct spatial shifts among the Northeast Atlantic regions (**Error! Reference source not found.**). In the Greater North Sea, the centre of gravity shifted significantly southward (Sen's slope, latitude coefficient = $-0.00174^\circ \text{ year}^{-1}$; Mann-Kendall, $p < 0.001$) and eastward (longitude coefficient = $0.00130^\circ \text{ year}^{-1}$, $p = 0.003$). The Celtic Seas also showed a significant southward ($-0.00090^\circ \text{ year}^{-1}$, $p = 0.014$) and eastward ($0.00038^\circ \text{ year}^{-1}$, $p = 0.018$) displacement, although the magnitude of these shifts was smaller than in the Greater North Sea. In contrast, the Bay of Biscay displayed no significant latitudinal trend ($0.00018^\circ \text{ year}^{-1}$, $p = 0.069$), but the centre of gravity shifted significantly westward ($-0.00083^\circ \text{ year}^{-1}$, $p < 0.001$).

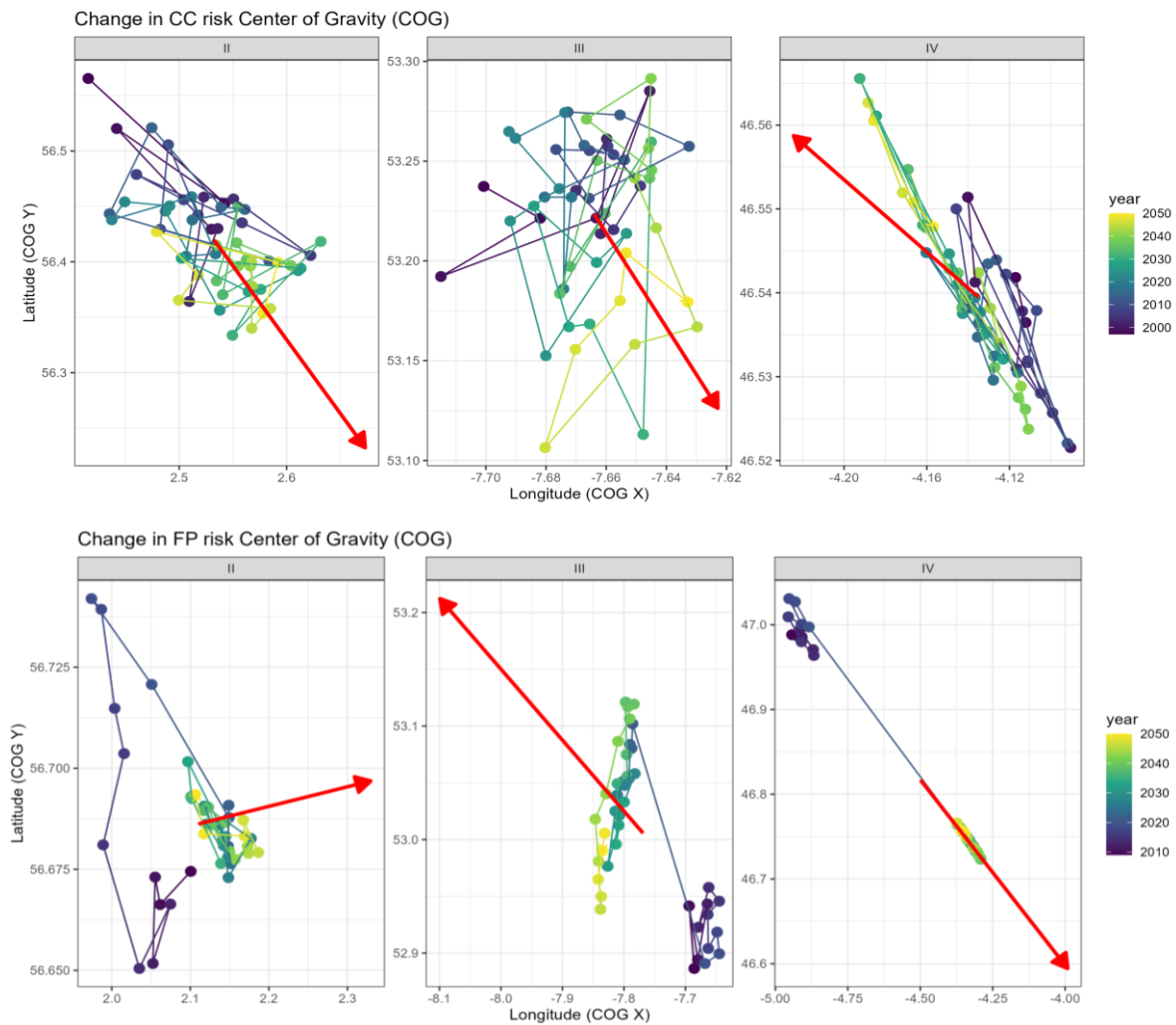


Figure 3-6 Temporal trajectories of annual centres of gravity (COG) for R_{CC} and R_{FP} across the Northeast Atlantic and in three OSPAR regions between 1997-2050 for CC and 2009-2050 for FP, illustrating the spatial redistribution and directional displacement of projected risk patterns over time. Region II = Greater North Sea, region III = Celtic Seas, and region IV = Bay of Biscay (not including Iberian Coast). Red arrows indicate the direction and magnitude of statistically significant trends in the COG of R_{CC} and R_{FP} within each region, based on Sen's slope estimates ($p < 0.05$, Mann-Kendall test). Arrow direction reflects the dominant shift in latitude and longitude, and arrow length is scaled to the rate of change over time.



The spatial distribution of centres of gravity of fishing pressure risk showed contrasting patterns among the Northeast Atlantic regions (**Error! Reference source not found.**). In the Greater North Sea, no significant latitudinal shift was detected (Sen's slope = $0.00013^{\circ} \text{ year}^{-1}$; Mann-Kendall, $p = 0.410$), although the centre of gravity moved significantly eastward ($0.00261^{\circ} \text{ year}^{-1}$, $p < 0.001$). The Celtic Seas exhibited a significant northward shift ($0.00246^{\circ} \text{ year}^{-1}$, $p = 0.022$) coupled with a significant westward shift ($-0.00393^{\circ} \text{ year}^{-1}$, $p < 0.001$). In the Bay of Biscay, the COG shifted significantly southward ($-0.00265^{\circ} \text{ year}^{-1}$, $p = 0.003$) and eastward ($0.00605^{\circ} \text{ year}^{-1}$, $p = 0.001$). Overall, the spatial redistribution of R_{FP} differed markedly from that of R_{CC} , with no common directional trend across regions. Instead, each region exhibited distinct patterns of displacement, in contrast to the more consistent south-eastward shifts observed for R_{CC} in the Greater North Sea and Celtic Seas.

3.4 Discussion and conclusions

This study provides new evidence for potential spatial and temporal patterns in community-level sensitivity to climate change and fishing pressure, and their associated risk, across the Northeast Atlantic into the future. The S_{CC} model performed strongly and suggested that projected sensitivity to climate change declines slightly in many areas, through time, in line with decreased prevalence of warm-sensitive and increased prevalence of warm-resistant species. Changes in S_{FP} are much more spatially heterogeneous but this notably increases in the Celtic Seas and Bay of Biscay. Notably, we find that climate change is likely to become the more spatially persistent and temporally consistent source of community-level risk across the Northeast Atlantic, whereas fishing-related risk is more locally variable and less spatially coherent through time. R_{CC} increases across most of the region and remains spatially persistent, with hotspots concentrated in in southern, western and shelf-associated areas and becoming slightly more extensive by mid-century. By contrast, R_{FP} is more spatially heterogeneous, with hotspots concentrated further north and becoming more fragmented through time, although persistent and increasing areas of risk remain in parts of the Celtic Seas. Centres of gravity analysis further showed that climate and fishing risks redistribute differently through space, with R_{CC} exhibiting more regionally consistent directional shifts than R_{FP} .

Our model projecting community-level sensitivity to climate change explained a very high proportion of deviance and showed strong temporal transferability, suggesting that community sensitivity to climate change is structured by broad, repeatable environmental gradients that are well captured by location, depth and thermal conditions. This agrees with regional studies showing that sea temperature is a primary driver of fish community structure across Northeast Atlantic shelf seas (Rutterford et al. 2022), with depth and spatial variables as additionally important drivers (Tittensor et al. 2010; Eme et al. 2022), and that future warming is expected to reorganise assemblages over large spatial scales (Jones & Cheung 2015; Thompson et al. 2023). By contrast, the community-sensitivity to fishing model was acceptable but weaker, which likely reflects the fact that fishing sensitivity is shaped not only by environment and community composition, but also by more localised and less easily



modelled processes which we could not consider in this study, including historical exploitation, stock-specific management, habitat-specific gear interactions and the patchiness of fishing footprints. Hence, the predicted increases in community-level sensitivity are much more heterogeneous in space.

We found that the risk from climate change increased from present day until mid-century. Community-level sensitivity to climate change is projected to decline in future, so the increased risk from climate change reflects more the increased exposure from increasing sea-surface temperatures. The decreasing sensitivity to climate change is consistent with expectations that communities are adapting to warming by increasing in relative abundance of species with broader thermal tolerances (Polo et al. 2025). These patterns may be related to poleward distribution shifts and/or changes in community structure as a result of changing temperatures (Magurran et al. 2015; McLean et al. 2019). Previous studies have shown that regional and local-scale biodiversity patterns were driven by increased productive energy, especially the benthic-pelagic trophic link (Eme et al. 2022). Diversity changes were driven by an increasing abundance and diversity of small pelagic species, which then positively impacted the abundance of demersal species. Our results may be explained by this phenomenon as smaller, faster-growing species with higher thermal preferences are likely to benefit from climate warming and hence community sensitivity to climate change would decrease (McLean et al. 2019). However, a decline in the sensitivity index does not imply ecological relief: it may instead indicate ongoing restructuring, trait replacement and redistribution of ecosystem function, while the exposure component of risk continues to rise under continued warming.

A more complex pattern emerged for fishing sensitivity and risk. Patterns in R_{FP} largely reflect the underlying contemporary fishing exposure layer and therefore remain partly anchored to the present-day spatial footprint of fishing pressure. This helps explain why R_{FP} hotspots broadly resemble current risk patterns from earlier deliverables, D4.2 and D4.3 (Rozemeijer et al. 2025; Engelhard et al. 2026), and why future change is more modest and spatially uneven than for R_{CC} . At the same time, projected increases in community sensitivity to fishing pressure, particularly in parts of the southern Celtic Seas, suggest that future community composition in some areas may increasingly favour combinations of traits associated with greater vulnerability to fishing. This is not entirely straightforward, because warm-affinity species moving into shelf systems are often smaller-bodied and faster-growing (Cheung et al. 2009; Pereira et al. 2010; Sailley et al. 2025), traits that are commonly associated with greater recovery potential after fishing mortality (Cheung et al. 2007; Rijnsdorp et al. 2009). For that reason, the increase in community-level fishing sensitivity is unlikely to be explained simply by the arrival of individually more fishing-vulnerable species. A more plausible interpretation is that climate-driven redistribution, the movement of commercially important species, and shifts in relative abundance are together reweighting the community so that less resilient components contribute more strongly to the overall sensitivity metric (Rijnsdorp et al. 2009; Hermant et al. 2010; Le Luherne et al. 2024). In other words, the projected increase in S_{FP} may reflect an emergent change in community balance, rather than a simple one-to-one trait response of the species moving in. This interpretation is consistent with studies showing that



distributional responses in the Celtic–Biscay shelf are shaped by combined effects of climate, abundance dynamics and fishing pressure (Le Luherne et al. 2024), and that community responses are often localised, species-specific and mediated by fisheries management history (Engelhard et al. 2014; Le Luherne et al. 2024). Ultimately, community recoveries from long-term fishing are likely incomplete and potentially constrained in the longer term by climate change.

The hotspot analysis is particularly informative from a management perspective. Climate-change risk hotspots were more consistently located in southern and central shelf regions and showed strong persistence through time. The persistence and gradual intensification and expansion in these regions by mid-century, aligns with well-documented gradients in ocean warming, stratification, and biogeochemical change across the Northeast Atlantic, where shallower, more dynamic shelf areas tend to experience stronger and more ecologically significant climate signals (Schmidt et al. 2020; Holt et al. 2022; Dong et al. 2025). The fact that these hotspots remain spatially coherent through the near future and mid-century suggests that they are not transient artefacts of interannual variability but likely represent recurrently vulnerable areas that warrant sustained monitoring and climate-adaptive management.

The centre-of-gravity analysis adds an important nuance. The southward and eastward displacement of R_{CC} in the Greater North Sea and Celtic Seas does not necessarily contradict the broader literature on poleward species shifts. Rather, it highlights that the analysis concerns the spatial centre of risk, not the centre of species distributions. In many Northeast Atlantic studies, individual taxa shift northward or into deeper waters in response to warming (Perry et al. 2005; Engelhard et al. 2014; Gordó-Vilaseca et al. 2024), but these responses are far from uniform, and some species or communities show south-eastward, north-westward or depth-related redistributions depending on local conditions, abundance dynamics and fishing history (Rubenstein et al. 2023; Le Luherne et al. 2024). A south-eastward shift in the centre of climate risk may therefore arise if the highest combined values of warming exposure and community sensitivity increasingly concentrate in southern/eastern shelf areas, even while some taxa themselves shift poleward. Put differently, the geography of risk can move differently from the geography of species occurrence, because risk is a composite metric shaped by both exposure and sensitivity.

Taken together, these results suggest that climate change is likely to represent a more pervasive and increasingly dominant source of ecosystem risk, while fishing pressure, although still significant, may become more localised and potentially more manageable through targeted interventions. From a management perspective, this suggests that climate adaptation needs to be integrated more explicitly into ecosystem-based fisheries management and biodiversity conservation (Robinson et al. 2025; Fuchs et al. 2026), with persistent R_{CC} hotspots treated as priority areas for monitoring, resilience-building and potentially adaptive spatial management (Barnett & Baskett 2015). The differing spatial signatures also imply that areas of overlapping high risk may shift over time, with important implications for marine spatial planning and ecosystem-based management. In particular, regions where high climate risk coincides with persistent fishing pressure (southern Celtic



Seas) may represent priority areas for adaptive management, whereas areas dominated by climate risk alone may require longer-term resilience-based strategies (Horta e Costa et al. 2025). Overall, the findings reinforce the importance of considering both persistent environmental drivers and dynamic anthropogenic pressures when assessing future ecosystem risk and identifying management priorities.

Finally, the study should be viewed as a screening-level forecasting exercise rather than a definitive prediction of future ecosystem states. The use of a high-emission scenario (RCP8.5), the absence of dynamic future fishing effort, and the dominance of spatial terms in the models all indicate that some projected patterns are emergent empirical relationships that likely integrate unmeasured processes such as habitat differences, species interactions, historical exploitation and biogeographic legacy. Nevertheless, the strong validation results, especially for S_{CC} , show that the framework has substantial predictive value for identifying broad patterns of future sensitivity and risk. In that sense, the main contribution of the analysis is not to predict exact future community states, but to identify where risk is most likely to persist, intensify or redistribute, thereby providing a useful evidence base for forward-looking marine management in a changing Northeast Atlantic.

Ultimately, this work contributes to the development of decision-support tools for marine spatial planning and biodiversity conservation. By identifying areas of persistently high or emerging risk, the approach can inform the prioritisation of management actions, including the design and adaptation of MPAs and other spatial measures. In doing so, it helps address the broader challenge of ensuring that conservation strategies remain effective under dynamic environmental conditions driven by climate change and human activities.

4 Icelandic waters

4.1 Introduction

Iceland is an island nation located in the North Atlantic, and as such receives the influence from two distinct water masses: the Atlantic, and the Arctic/Polar waters (Stefánsson 1962, Malmberg & Valdimarsson 2003, Jónsson & Valdimarsson 2005). Warm, saline waters are transported on the Icelandic coastal shelf by the Irminger current coming from the south, which splits from the Gulf Stream and, after encountering the Iceland-Faroe Ridge, flows westward. This current then continues flowing clockwise around the island, losing strength as it reaches its northern coasts (*Figure*) (Valdimarsson & Malmberg 1999). This current then continues flowing clockwise around the island, losing strength as it reaches its northern coasts (Valdimarsson & Malmberg 1999). Thus, hydrographic conditions on the northern portion of the coastal shelf are defined by a mixture of Polar (East Greenlandic Current), Arctic (East Icelandic Current) and Atlantic waters (*Figure*), resulting in lower temperature and salinity than in the south west (Stefánsson 1962, Astthorsson et al. 2007).

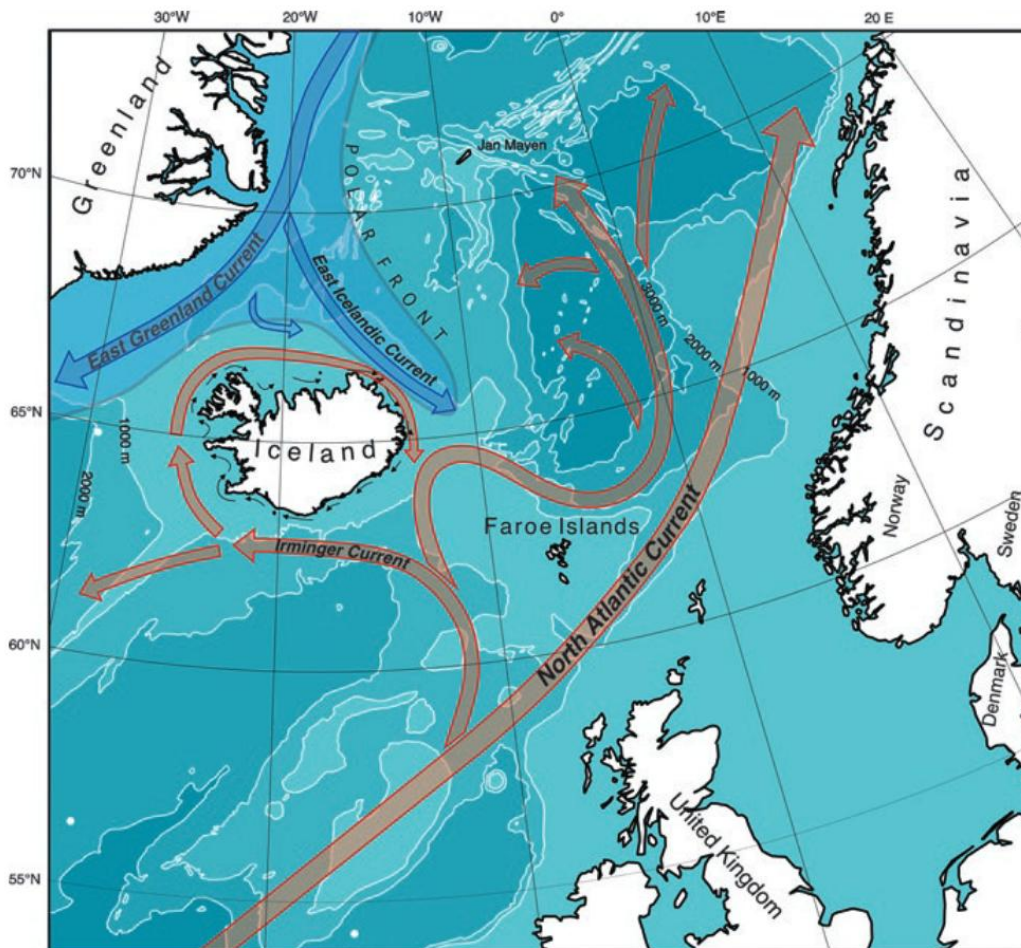


Figure 4-1. The direction of the Atlantic (red) and Arctic/Polar (light and dark blue) water masses around Iceland. From Símonarson et al. (2021).

This heterogeneity in predominant water masses has been linked to the presence of two separate species assemblages: one located mostly to the south and west of Iceland, characterised by a majority of Atlantic species, and one in the north and east, with a majority



of Arctic species (Astthorsson et al. 2007, Stefánsdóttir et al. 2010, Mecklenburg et al. 2011, Símonarson et al. 2021). Notably, transport of the Irminger current along northern Iceland is variable, with years of stronger inflow associated with warmer local water temperatures (Malmberg & Valdimarsson 2003, Jónsson & Valdimarsson 2005). Changes in the composition of marine faunal assemblages in response to this variability have been reported in the past (Vilhjálmsón 1997, Stefánsdóttir et al. 2010, Valdimarsson et al. 2012, Sólmundsson et al. 2025), with shifts towards more southern species expected during periods of warming (Björnsson & Pálsson 2004, Astthorsson et al. 2007, Sólmundsson et al. 2025).

Such community changes might become more frequent and range expansions more persistent as global temperatures warm due to climate change. The arctic and sub-arctic have been warming at a fast rate, with the former having warmed almost four times faster than the global average since 1979 (Rantanen et al. 2022). This has been associated with widespread shifts in the composition of demersal fish communities around Iceland (Campana et al. 2020, Valtýsson & Jónsson 2018, Sólmundsson et al. 2025), off southeastern Greenland (Emblemsvåg et al. 2022) and in the northern Barents Sea (Frainer et al. 2021). Warming-induced shifts in species composition are expected to carry on into the future as well. For example, Gordó-Vilaseca et al. (2024) projected high extinction risk for Arctic demersal fish in the Barents Sea towards the end of the century, if no climate refugia will be available. This increased extinction risk was projected to be accompanied by an expansion in the range of southern temperate species. Similar scenarios could occur in Iceland, due to the warm Atlantic water transport around the island.

The aim of this work is to investigate how Icelandic groundfish species distribution patterns are likely to change with climate change in near-future decades up to mid-century. To accomplish this, we estimated the present and future density of biomass of five categories of marine species also previously analysed in B-USEFUL report D4.3 – Arctic species, commercial species, IUCN Red List species, species with high sensitivity to climate change, and species with high sensitivity to fishing pressure (Engelhard et al. 2026). All these species groups are particularly relevant for marine spatial planning, owing to their sensitivity to anthropogenic pressures and/or economic importance. Furthermore, we investigated whether the locations of areas of high importance for the conservation of groundfish diversity are likely to change substantially from their current position to the future.

4.2 Methods

We used a hurdle model, developed by Golin et al. (in review), to predict both the occurrence and the biomass of 79 demersal and bathydemersal fish species for the period 2015-2050 and a $0.083^\circ \times 0.083^\circ$ ($0^\circ 5' \times 0^\circ 5'$) resolution of longitude and latitude. The model consisted of a joint species distribution model (JSDM) fitted within the hierarchical modelling of species communities framework (HMSC) (Ovaskainen et al. 2017, Tikhonov et al. 2020). To develop predictions of species distribution, the model used environmental data derived from the NEMO-MEDUSA coupled hydro-geochemical model runs (Yool et al. 2011, Madec et al. 2024). As the focus of this study was on the effect of environmental variability on the composition of groundfish communities we did not include spatial or temporal random effects when



developing the predictions. More information on model setup, parametrisation and diagnostics is given in B-USEFUL report D3.1 (Lindegren et al. 2025).

From these predictions we obtained estimates of biomass (kg/km^2) for the period 2015-2024 (average biomass, representing the baseline) and for the years 2030, 2040, and 2050. We thus compared recent and expected distributions in biomass of Arctic species, commercial species, at-risk species, species sensitive to climate change, and species sensitive to fishing pressure. To define commercially important and at-risk species we used the information available in the Fisheries Overview by the Marine and Freshwater Research Institute of Iceland (MFRI 2024) and the Red List of Threatened Species of the International Union for Conservation of Nature (IUCN, information accessed through the R package 'rredlist') (Gearty & Chamberlain 2025). To define species sensitive to climate change and fishing we availed of the information collected and outlined in Rozemeijer et al. (2025), while species with Arctic affiliation were identified using the information available in both Rozemeijer et al. (2025) and Sólmundsson et al. (2025). More information on the classification of groundfish species in these five categories is available in Engelhard et al. (2026).

To investigate expected future changes in the distribution of priority areas for the conservation of groundfish communities, we compared priority areas identified in 2015-2024 with projected priority areas in 2030, 2040, and 2050. We used the software Zonation 5 (Moilanen et al. 2022) to outline such areas of high priority ranking. Zonation selects priority areas by iterative ranking and by removing the raster grid cells that can be lost with the smallest aggregate loss of marine biodiversity (Virtanen et al. 2018). Weights can be associated to the species distribution rasters to influence the prioritisation algorithm and specify which features to favour in the prioritisation (Virtanen et al. 2018, Moilanen et al. 2024). The rasters used in the prioritisation all belong to the five categories of groundfish species that have been outlined above. The same five categories, with subdivisions based on species-specific depth preferences, were also the target of prioritisation as outlined in B-USEFUL report D4.3 (Engelhard et al. 2026). The weights and prioritisation settings used in this analysis are the same as those used for the previous report's analysis. Because of this, we refer to that report for additional details on the prioritisation process.

4.3 Results

The five categories of groundfish species (Arctic species, commercially important species, at-risk species, species sensitive to climate change, and species sensitive to fishing pressure) differed markedly in their biomass distribution patterns. This was the case both for their distributions in the recent past (*Figure 4-2*, left-most maps, *Figure 4-3*) and as projected for the future in 2030, 2040 and 2050 (*Figure 4-2*, middle maps). From 2015 to 2050, modest changes in biomass are projected for each of the five categories (*Figure 4-2*, right-most maps).

Arctic species were found – and are projected to be found – in higher densities on the slopes surrounding the Icelandic shelf (both the northern and southern sections: *Figure 4-2*, top row), with commercially important species showing highest biomass levels on the coastal shelf itself (*Figure 4-2*, second row). At-risk (IUCN Red List) species were, and are projected to be, mostly present in both the northern and in the southern sections of the coastal slope, especially in

the deeper part of its southern section, on either side of the Reykjanes Ridge (Figure 4-2, third row). Similar patterns were found for species sensitive to climate change and species sensitive to fishing pressure (Figure 4-2, bottom two rows). High levels of biomass on the southern slopes for at-risk species, species sensitive to climate change and species sensitive to fishing pressure corresponded to high estimated population density for roundnose grenadier *Coryphaenoides rupestris*. Out of the five categories of groundfish species, only the Arctic species are projected to decrease in biomass density on the Icelandic continental slope (Figure 4-2, top row). All other categories are expected to undergo an increase in biomass density, with the seabed surrounding the Reykjanes ridge in the south being the area where the highest increase in the biomass of at-risk species, species sensitive to climate change and species sensitive to fishing effort is expected (Figure 4-2).

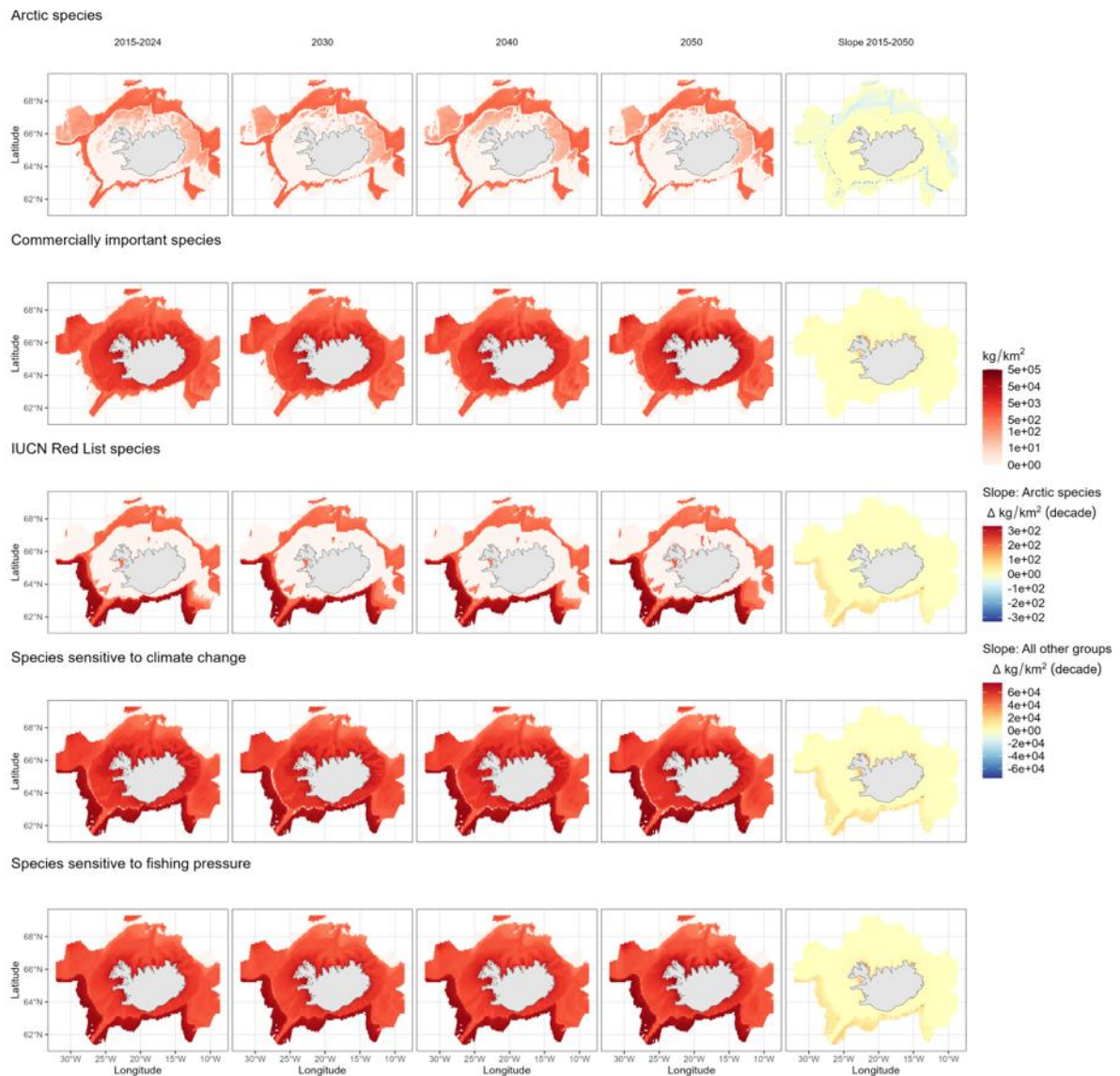


Figure 4-2. Estimated biomass levels in five groundfish species categories, in recent years (2015-2024, left-most maps) and projected for the future (2030, 3040 and 2050); the right-most maps show the projected change in biomass (from 2015 to 2050) for each of the five categories. Note that the legend for decadal change in biomass for Arctic species is separate from the legend for decadal change of all the other groups, to highlight the changes in biomass of that relatively rare group.

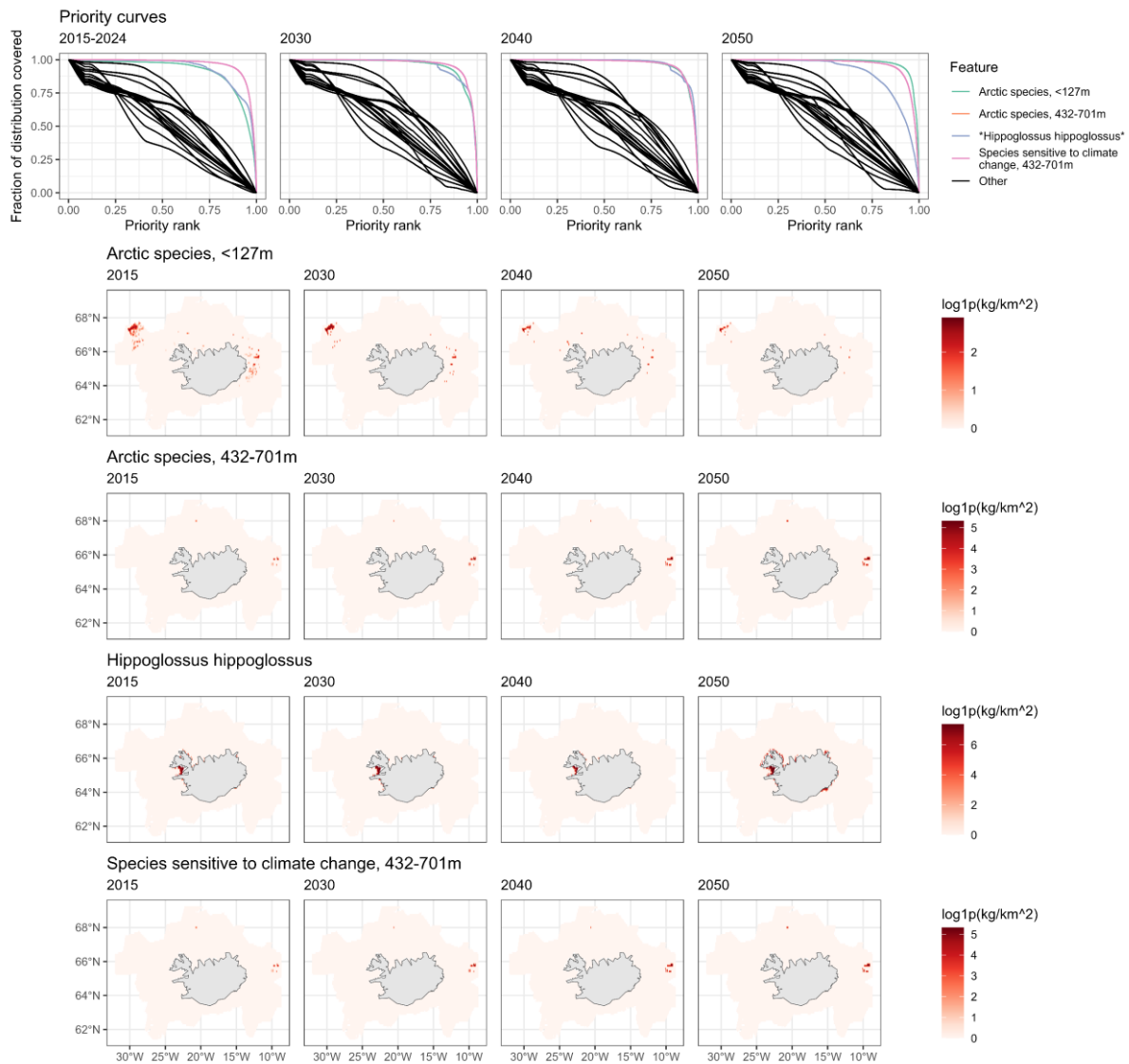


Figure 4-3. Detailing how the different categories contribute to the final prioritisation.

Priority areas for the conservation of groundfish communities are shown in Figure 4-4. For the baseline period 2015-2024, high-priority areas were identified mainly on the Icelandic coastal shelf, and on the southern section of the continental slope of Iceland (shaded light-yellow in Figure 4-4 A). In future decades, patterns in priority ranking are projected to undergo large changes (Figure 4-4 Figure B-E). Areas expected to *increase* in priority score, include the Iceland-Faroe Ridge, as well as several sections of the northern Icelandic coastal shelf and slope. On the other hand, areas expected to *decrease* in priority ranking, include the Greenlandic coastal shelf, as well as the southern section of the Icelandic coastal slope and the easternmost section of the Icelandic coastal shelf (Figure 4-4 B-E).

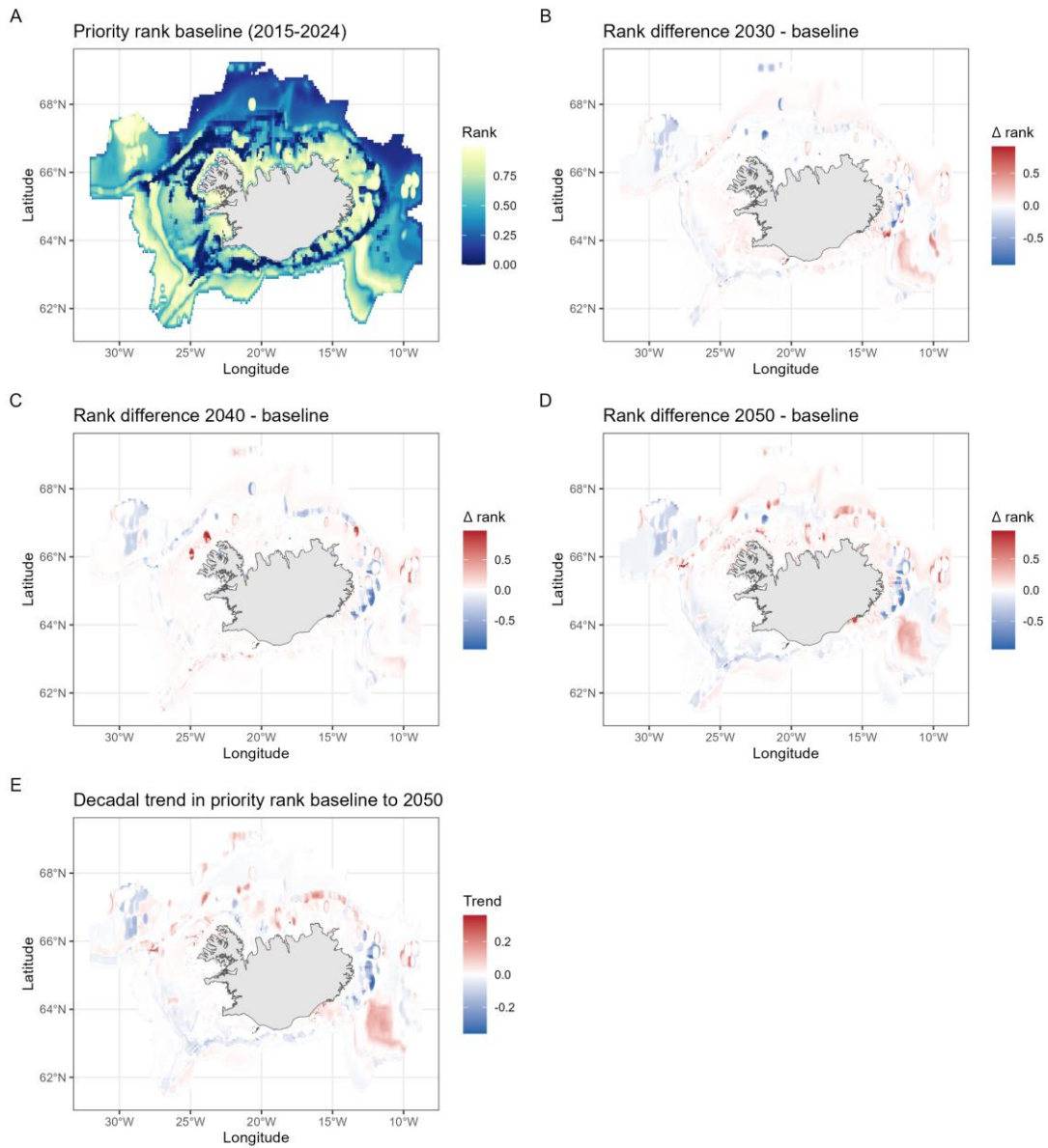


Figure 4-4. Priority rank for the conservation of Icelandic groundfish communities during the baseline 2015-2024 (A), with light-yellow indicating highest-priority areas; and the change in rank from the baseline to 2030 (B), 2040 (C), and 2050 (D). The decadal trend in priority ranking is reported in (E).

4.4 Discussion and conclusions

This study investigated projected future changes in the distribution of biomass for five categories of groundfish species around Iceland: Arctic species, commercially important species, at-risk species, species sensitive to climate change and species sensitive to fishing pressure. The results show that the overall biomass levels of at-risk species, species sensitive to climate change and species sensitive to fishing are expected to increase in the same locations where biomass is currently at its highest levels, i.e. the continental slope surrounding the Reykjanes Ridge, in the southwest of the study area. This increase is mostly attributable to the projected increase in biomass of the roundnose grenadier *Coryphaenoides rupestris*.



This species has been categorised as Endangered (Cook et al. 2015) as well as being both sensitive to climate change and fishing pressure (Rozemeijer et al. 2025). The present-day biomass distribution and projected increase of this single species are closely linked to the current biomass distribution and projected increases for these three categories as well, of which this species forms an important component. Roundnose grenadier is an Atlantic species (Sólmundsson et al. 2025), which means that an increase in seawater temperatures is likely to cause a biomass increase of this species around Iceland. Moreover, it is also a bathydemersal species, accordingly, a warming trend is also expected for the bathyal zone in the Icelandic seas. On the other hand, Arctic species are expected to decrease in biomass, especially where these are currently mainly found: the continental slope of Iceland. These findings are in line with the observed borealisation of continental slope communities in co-occurrence with increasing temperatures as reported for nearby eastern Greenland (Emblemsvåg et al. 2020, 2022). It is likely that a similar process to the one observed in this neighbouring region is occurring in the Icelandic seas as well, and that the next decades will see an increase in the biomass of groundfish species with southern affiliation.

In turn, these projected changes in groundfish community composition have implications for the distribution of areas of high priority for conservation of groundfish. Expected trends in priority ranking are quite large for some areas, reaching an absolute value of 0.2-0.3 per decade while the total possible range in priority ranking is 0-1. These large changes in priority ranking are expected also in areas for which no large trends in biomass for the five categories of species are projected. For example, none of the five categories are projected to undergo a great increase or decrease in biomass on the Iceland-Faroe ridge, in the southeast of the study area. However, the priority ranking of this area is expected to increase by ~ 0.5 by 2050. While this would seem incongruous, the explanation is probably found in how Zonation 5 works: as areas of high biomass in all (or most) of the five categories are the most favoured by the prioritisation algorithm, a decrease in biomass for some (or all) categories in certain parts of the study area mean that the algorithm will reward the areas where biomass of all categories has been maintained. These areas might effectively constitute climate refugia that can provide protection from global environmental changes (Roberts et al. 2017, Beyer et al. 2018).

Special attention needs to be given to the Arctic species. The approach of assigning priority areas uses the sum of the rankings for 5 categories (Arctic species, commercially important species, at-risk species, species sensitive to climate change, and species sensitive to fishing pressure). *Figure 4-2* shows 4 categories generally increasing and only one (Arctic species) decreasing. As a result of summing the importance of Arctic species is not acknowledged in the prioritisation process in many regions. *Figure 4-2* also shows important decreases in Arctic species especially on the slopes; dedicated measures seem therefore necessary for this category. Some climatic refugia for Arctic species might be found in the northern part of the study area, in the sites highlighted by an increase in the priority ranking. Protection of such sites can contribute to the resilience of Icelandic groundfish species sensitive to environmental changes and can thus safeguard the resilience of ecosystem functioning to climate change.

This phenomenon also shows that the developments of each category in time and space should be analysed at their own merits as well.



It is acknowledged that the baseline (2015-2024) predictions of biomass for these five categories of groundfish species are different from those presented in report D4.3 for comparable time periods (Engelhard et al. 2026). This is probably due to several factors. First, the predictions of biomass distribution presented here were developed using an environmental data product different from that used for report D4.3. The present analysis used NEMO-MEDUSA data, while the D4.3 analysis used Copernicus data products (Copernicus Marine Service 2025a, 2025b). NEMO-MEDUSA was chosen here over Copernicus, as the latter could not provide future estimates of environmental covariates. Second, contrary to the predictions developed for D4.3, the newer predictions were not developed using information on spatial and temporal random effects. The lack of random effects in developing the species distribution predictions eliminates the bond between species and specific locations and years, effectively allowing for a much larger degree of freedom in the spatiotemporal distribution of occurrence probability and biomass of the 79 groundfish species. A possible sensitivity analysis would be to re-develop the predictions of species distribution from NEMO-MEDUSA data but with the inclusion of the spatial and temporal random effects, and then to repeat the same steps of this analysis to compare those results with the ones shown here.



5 Projected risks from invasive species in the Mediterranean

5.1 Introduction

Biological invasions are severe disruptors of marine ecosystems, comparable in magnitude to overexploitation, habitat destruction, and pollution (Edelist et al., 2013). Climate change is a major driver of marine bio-invasions, reshaping communities worldwide and leading to the rapid homogenisation of marine assemblages across multiple regions (Molinos et al. 2015, Angeles-Gonzalez et al. 2026). Among all regions, the Mediterranean stands out as the most invaded sea by a significant margin, with over a thousand marine non-indigenous species (NIS) recorded to date (Azzurro et al. 2022, Zenetos et al. 2022, Galanidi et al. 2023). Alien species enter the Mediterranean through natural (or anthropogenically assisted) dispersal from the Gibraltar Strait, through Port Said via the Suez Canal, through ship fouling or ballast waters, via aquarium releases, or via aquaculture escapes (Katsanevakis et al. 2013). The species that enter the basin through the Suez Canal are frequently referred to as “Lessepsian” species/migrants, commemorating the French diplomat’s role, Ferdinand de Lesseps, in the construction of the Canal (Por 1971).

Climate change is expected to further facilitate the spread of Lessepsian species by weakening thermal barriers and creating increasingly favourable conditions across the Mediterranean Sea. This process is already transforming native communities in parts of the Eastern Mediterranean, where invasive herbivores, predators and toxic species have affected biodiversity, habitats, ecosystem functioning, fisheries and human health (Katsanevakis et al. 2014; Galanidi et al. 2018; Bédry et al. 2021). Sea warming, through the progressive weakening of climatic barriers, has assisted the spread of the Lessepsians around the Mediterranean (Azzurro and D’Amen 2022, Azzurro et al. 2022, D’Amen et al. 2022). Moreover, through the cause of climate-driven range contractions of native species, sea warming has also weakened the biotic barriers on the Lessepsian expansion (Clark et al. 2020, Albano et al. 2021). To date, these NIS have proliferated as far west as Gibraltar and as far north as the Gulf of Trieste in the Adriatic (Azzurro 2023). The rate of spread of some of these species has been staggering, approaching 1000-1500 km per year in the case of the blue-spotted cornetfish *Fistularia commersonii*, which was able to colonise almost the entire basin in seven years from its first confirmed sighting in the Mediterranean (Azzurro et al. 2013). As warming continues, the expansion front of NIS is likely to move further northward and westward, increasing the probability of interactions with marine protected areas, fisheries restricted areas and juvenile fish nursery grounds.

These interactions are particularly important for conservation planning. Marine protected areas (MPAs) can help reduce human pressures and support ecosystem resilience, but they may also provide refuge for invasive populations if no specific control measures are implemented. The establishment of the Lessepsian NIS has led to a variety of negative interactions with MPAs as well as with habitats critical for early life-stages of key foodfish species. Invasive herbivorous fish have caused intensive deforestations along several locations of the eastern and central Mediterranean Sea, with abrupt impacts and a multitude of negative cascading effects (Katsanevakis et al. 2018, Giakoumi et al. 2019, Dimitriadis et al. 2021, 2024). Invasive predatory species can also cause local native species extirpations, if their populations are left unmanaged (Galanidi et al. 2018). Climate change is expected to



exacerbate these interactions as MPA susceptibility to invasions increases basin-wide (D'Amen and Azzurro 2020). In addition, MPAs and fisheries-restricted areas may serve as safe harbours or unintended major feeding grounds for harmful NIS, assisting in the establishment of large NIS populations and their propagation further into the basin (Galil 2017, Giakoumi et al. 2019, Kleitou et al. 2024). This ultimately complicates biodiversity conservation efforts in the area, as the potentially beneficial effects of fishing effort reductions, which are already projected to diminish due to future sea warming (Corrales et al. 2018), must be coupled by NIS-specific management actions lest their populations increase massively (Kleitou et al. 2024).

The present study builds on our previous work (Rozemeijer et al. 2025, Engelhard et al. 2026, Hidalgo et al. 2026). It projects the future occurrence probability of Lessepsian species under a high emission climate scenario and assesses how alternative fishing pressure scenarios may influence their expansion. It also examines projected changes in juvenile fish diversity and the persistence of nursery grounds in the Central and Eastern Mediterranean. The specific objectives are:

1. To project the potential future expansion of Lessepsian NIS in the Central and Eastern Mediterranean up to 2050.
2. To assess how future warming and alternative fishing effort scenarios may affect their occurrence probability.
3. To evaluate projected changes in juvenile fish diversity and nursery ground locations, in relation to projected NIS hotspots.

We then discuss management implications for marine protected areas, fisheries-restricted areas and sensitive nursery habitats.

5.2 Methods

Benthic nekton data (fishes, molluscs, crustaceans) from the Mediterranean International Trawl Surveys (MEDITS) from 1999 to 2021 were used to construct Lessepsian NIS presence/absence generalised additive models (GAMs), as detailed in Chapter 9 of Deliverable 4.2 (Rozemeijer et al. 2025). As covariates we used monthly averaged environmental variables from the Copernicus Marine Environment Monitoring Service (CMEMS) Mediterranean Sea Physics (Escudier et al. 2021) and Biochemistry (Teruzzi et al. 2021) Reanalysis products, as well as annual fishing pressure indices calculated through the Multi-Criterion Decision Analysis (MCDA) tool developed during RDBFIS-II (Kavadas et al. 2015, 2025). The MEDITS dataset, up to 2021, is only sparsely populated by a small minority of the introduced Lessepsian species in the Mediterranean, therefore we aggregated their occurrences at haul level and considered hauls with at least one Lessepsian NIS as a presence, and hauls without any Lessepsian NIS as an absence. Two models were made, a) a simple spatiotemporal model, with haul coordinates, depth and year as predictors; and b) an environmental model, with the winter – summer sea surface temperature interaction, surface salinity, depth, trawling fishing pressure index and year as predictors (Rozemeijer et al. 2025).

We then used RCP8.5 (high-emissions climate change scenario) bias-corrected environmental modelled data (POLCOMS/NEMO-ERSEM) (Kay et al. 2020) to make future projections on the



Lessepsian NIS occurrence probability, up to 2050. Because two different environmental covariate datasets were used, we applied a bias correction to the projected data to match their mean with the historical data baseline (Kuehn 2023). For fishing effort, three scenarios were considered, a) a “baseline” scenario, where fishing effort was assumed to stay constant at 2021 levels, b) a “reduced” fishing effort scenario, where a 15% universal decrease in effort was assumed, and c) an “increased” fishing effort scenario, with a 15% universal increase in effort. Subsequently, we calculated the NIS occurrence probability in the Central-Eastern Mediterranean, from 2000, and for every five years, up to 2050 (except for 2045 due to data unavailability). The spatial predictions were made on a 0.1° square grid (same as the resolution of the environmental data) and up to 1000 m in depth. To compare the effect of fishing effort on the projected occurrence of Lessepsian NIS, we calculated the probability difference between the “reduced” and the “increased” fishing effort scenarios from the “baseline” scenario.

In addition, we explored possible future shifts in the locations of fish nursery grounds as well as changes in the juvenile fish alpha diversity, for the same fishing effort scenarios under RCP8.5. We used Hierarchical Models for Species Communities (HMSC) (Ovaskainen & Abrego 2020) to model 60 juvenile and 44 adult life stages of 61 unique species in the Central-Eastern Mediterranean, as described in Chapter 5 of Deliverable 3.2 (Hidalgo et al. 2026). We then ran the spatial hindcasts and forecasts using the same grid resolution and datasets as above, with the exception of fishing pressure, which was the sum of trawling, purse seine and small-scale fisheries indices, rescaled back to [0, 1] range. These predictions were then used to calculate the juvenile fish Shannon diversity (H), species richness (R) and Pielou’s evenness (J’) indices. Mann-Kendall trend tests were used to find monotonically significant trends per grid cell and for every index (Mann, 1945). Finally, to identify the fish nursery grounds in the area, we first normalised the juvenile life stages’ abundances to unit variance, by dividing each value with the annual standard deviation of each species, and then summarised the normalised abundances into a single juvenile abundance index (Hidalgo et al. 2026). This index was then used to find local areas of spatial dependence by calculating the Getis-Ord G_i^* statistic for each year. The analysis was run on Queen’s contiguity spatially weighted neighbours for 20000 simulations, to ensure consistency. Hotspots (grid cells with $G_i^* > 0$) were identified at two significance levels ($p \leq 0.05$ and $p \leq 0.01$).

All analyses were done in R (v. 4.5 to 4.6). The R packages ‘mgcv’ (v. 1.9-4) and ‘Hmsc’ (v. 3.3-7) were used to run the GAM and the HMSC model predictions, respectively. Alpha diversity indices were calculated with the help of the R package ‘vegan’ (v. 2.7-3). Mann-Kendall trend tests were conducted through the ‘Kendall’ R package (v. 2.2.2), and the Getis-Ord G_i^* statistic was calculated with the help of the ‘sfdep’ R package (v. 0.2.5).

5.3 Results

According to the simple spatiotemporal GAM projections, Lessepsian NIS will continue to proliferate further north and west from locations where they already established a permanent presence (

Figure 5-1). By 2050, projections indicate that the probability of catching a Lessepsian species will be significant as far north as the southern Adriatic and the northwestern Aegean Sea, and as far west as western Sicily. Additionally, in areas such as Cyprus, Crete, southern Aegean, eastern Ionian and the southern coasts of Sicily, the occurrence probability is projected to approach unity by 2050, suggesting the establishment of permanent and large populations of, probably multiple, Lessepsian species in these areas.

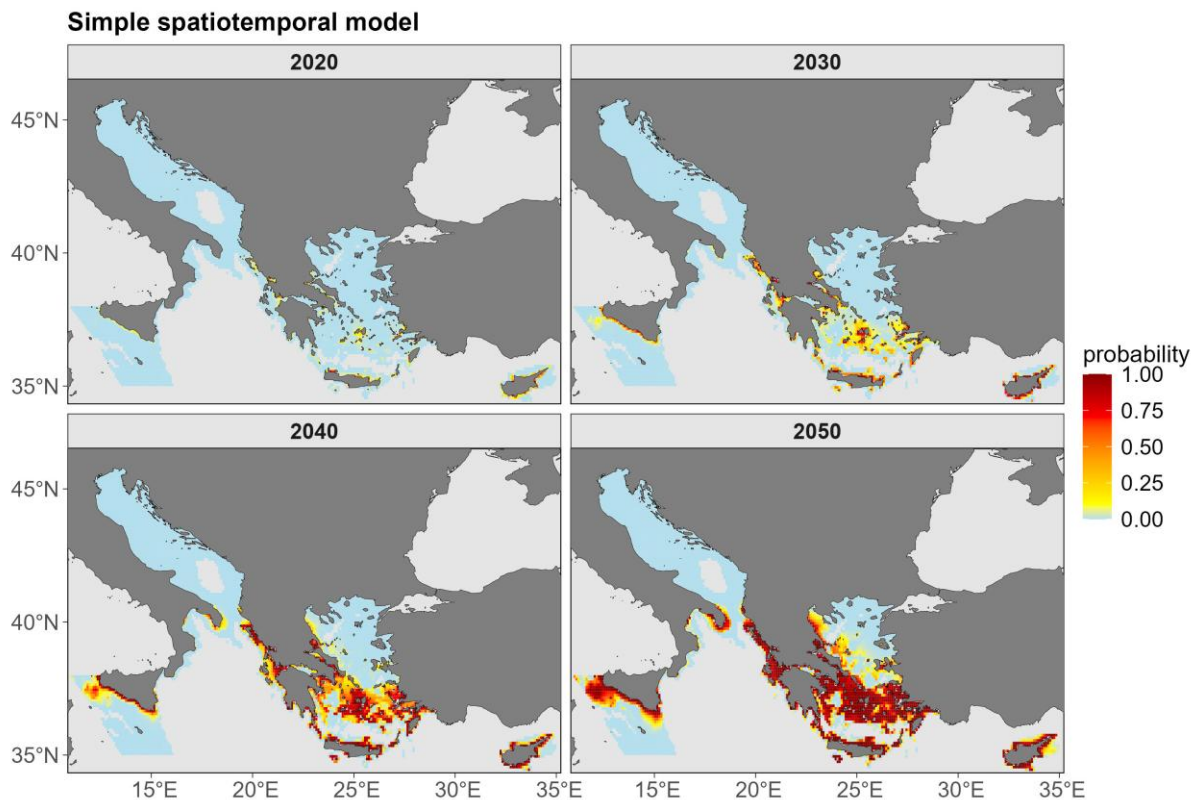


Figure 5-1. Projected Lessepsian NIS occurrence probability in the Central-Eastern Mediterranean based on simple spatiotemporal GAM, under the “baseline” (constant) fishing effort scenario, for 2030, 2040 and 2050, compared to the 2020 extent. This figure denotes the rate of spread of these NIS towards the western and northern part of the basin (i.e. the speed of the migration).

The environmental GAM model, which was influenced predominantly by temperature and salinity variations, and to a much lesser degree by year (Rozemeijer et al. 2025), indicated that future climatic conditions will become more favourable for the Lessepsians, facilitating their spread. Their occurrence probabilities modelled for 2020, and projected for 2030, 2040 and 2050 (assuming no change in fishing effort since 2020), are shown in (*Figure 5-2*).

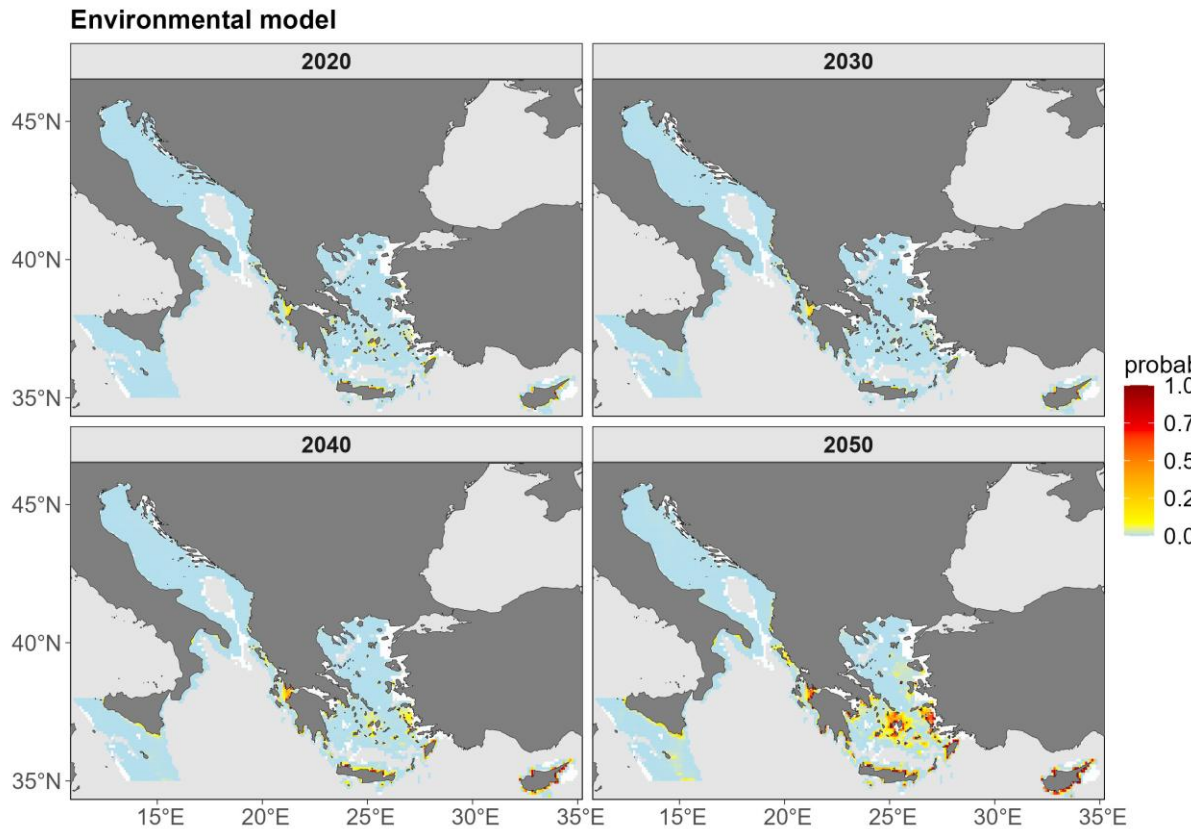


Figure 5-2. Projected Lessepsian NIS occurrence probability in the Central-Eastern Mediterranean of the environmental GAM, under the “baseline” (constant) fishing effort scenario, for 2030, 2040 and 2050, compared to the 2020 extent. This figure denotes mainly the effects the climatic variables (sea surface temperature and salinity) have on the occurrence probability of Lessepsian migrants.

Projected occurrence probabilities under two scenarios assuming either increased or decreased future fishing effort, tested through the environmental GAM, are shown in *Figure 5-3*. These indicated that reducing trawling fishing pressure by 15% is projected to mildly reduce the occurrence probability of Lessepsian NIS by 2050, with increasing fishing pressure by the same amount having the opposite effect (*Figure 5-3*).

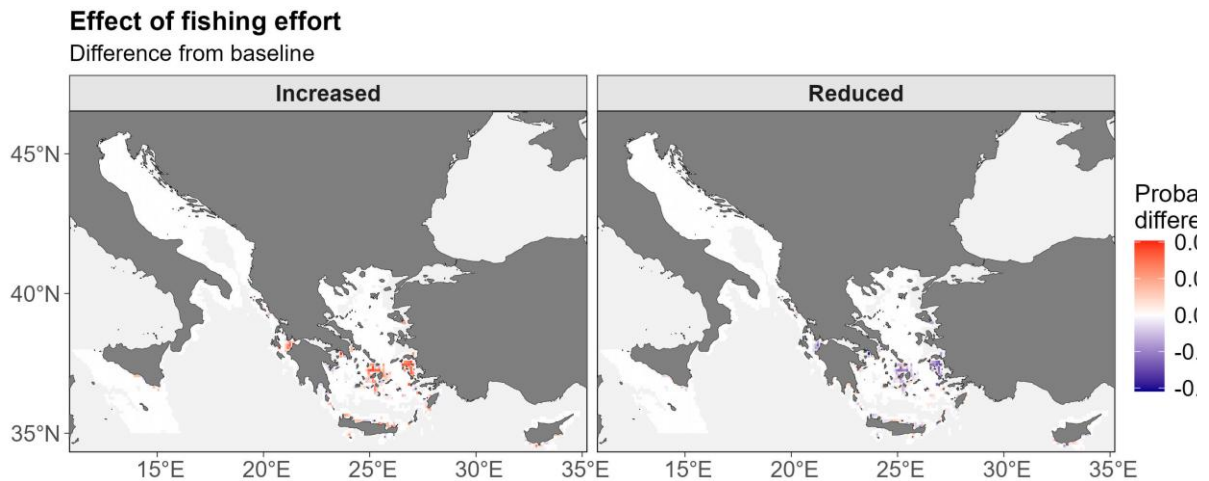


Figure 5-3. Effect of a 15% increase (left) or reduction (right) in fishing effort on the occurrence probability of Lessepsian NIS on the year 2050, according to the environmental GAM projections. The effect is expressed as the probability difference from the “baseline” (constant) fishing effort scenario.

Juvenile fish alpha diversity is projected to show fluctuations over time in all indices, with few grid cells showing monotonically significant trends by 2050; nevertheless, several consistent patterns emerged. Up to 2050, notable drops in juvenile fish Shannon diversity (H) and Pielou’s evenness (J') are projected along the southeastern Adriatic coasts, in the northern Adriatic west of Istria, at several locations along the slope waters and southern coasts of Sicily, with sporadic drops in the southern Aegean and central-eastern Ionian Seas (*Figure D-1* and *Figure D-2*). Conversely, notable increases in juvenile fish diversity and evenness are projected in intermediate and deep waters of the northern Aegean Sea and at various locations around Cyprus (*Figure D-1* and *Figure D-2*). Concerning species richness (R) in juvenile fish, no patterns remained monotonically significant by 2050. Regardless, the central Adriatic Sea, Crete, and southeastern Aegean Sea (between the islands Samos and Kos) are projected to suffer a net loss in species richness (*Figure D-3*).

According to projections, a 15% reduction in fishing pressure will have a predominantly positive effect on juvenile fish alpha diversity across all three indices (*Figure D-4*). In contrast, a 15% increase in fishing pressure will result in losses in diversity and evenness in the northern, western and southeastern Adriatic, in the south Sicilian coasts, in the eastern Ionian, in the northern Aegean and in the southern coasts of Cyprus (*Figure D-5*). Interestingly, this increase will have a positive effect on species richness compared to the “baseline” (constant) fishing pressure scenario (*Figure D-5*).

Finally, the locations of fish nursery grounds in the Central-Eastern Mediterranean are projected to remain largely constant between the present and 2050 (*Figure 5-4*: with red zones indicating juvenile fish hotspots). Projections for 2030, 2040 and 2050 fluctuate slightly on the significance level of the hotspots; however, the general area demarcations are projected to remain remarkably stable.

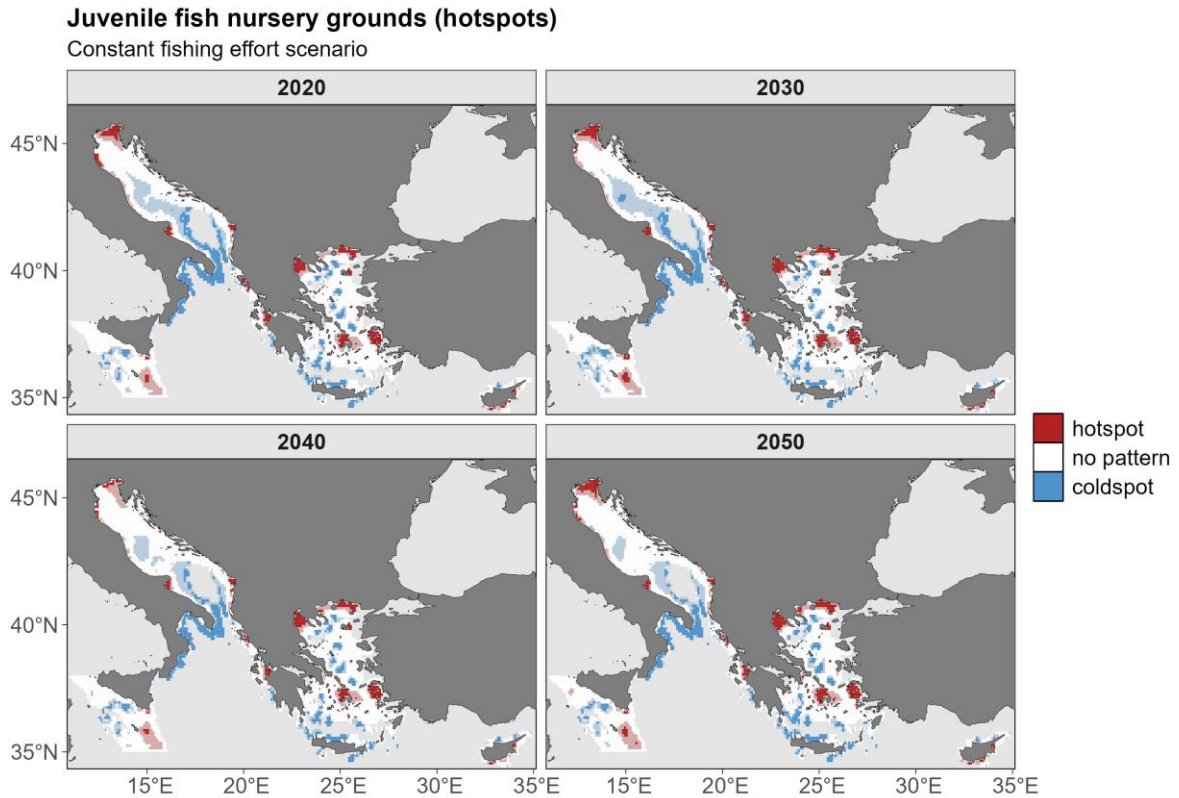


Figure 5-4. Juvenile fish nursery grounds (hotspots) and coldspots in the Central-Eastern Mediterranean for 2020 (hindcast), 2030, 2040 and 2050 (forecasts). Darker colours denote significance at $\alpha = 0.01$ and lighter colours at $\alpha = 0.05$.

5.4 Discussion and conclusions

The so-called Lessepsian migrants have become a common sight in the Eastern Mediterranean Sea (Azzurro & D'Amen M 2022; Azzurro 2023), as corroborated in our previous work showing that active NIS hotspots now reach as far north as Corfu Island (Ionian Sea) and as far west as Sicily (Engelhard et al. 2026). This new study, projecting into near-future decades, indicates that Lessepsian NIS will continue expanding rapidly northwards especially into the Adriatic, and westwards establishing a strong presence in the shelf waters along the Strait of Sicily. Future climatic conditions (namely, sea surface temperature and salinity) are projected to favour this expansion. Unavoidably, this will increase NIS interactions with fish nursery grounds, which are projected to remain mostly where they presently are in the Central-Eastern Mediterranean, up until 2050. Furthermore, losses in juvenile fish alpha diversity are projected for areas including the southeastern Adriatic coasts, coasts of Sicily, eastern Ionian and southern Aegean Seas, and Crete; these losses might get exacerbated due to NIS impacts. Fishing pressure reductions may alleviate this, as a 15% reduction in fishing effort is predicted to result in a drop in the Lessepsian NIS occurrence probability and a net gain in juvenile fish alpha diversity.

Our Lessepsian NIS models are subject to some limitations that should be addressed. The simple spatiotemporal GAM was initially made for the purpose of using a data-poor dataset



to map the occurrence probability of these NIS in the Mediterranean from 1999 to 2021, by putting constraints on their distribution through the inclusion of haul location and depth as a penalised tensor and smoother respectively, and using year as the main forcing driver to simulate an ongoing process. Therefore, this model did not put any environmental constraints on the Lessepsians' occurrence probabilities, other than depth (which is static), and cannot inform how future climatic conditions will shape their distributions around the basin. This model is more useful to gauge the speed and direction of the Lessepsian expansion, i.e. *where* and *when* these NIS will be present in the basin, assuming the absence of potent environmental barriers. Furthermore, because we were forced to aggregate the Lessepsians under a single binary variable due to data density constraints, the modelled occurrence probability loses its informative value once it saturates in an area. In other words, the model informs that a Lessepsian NIS observation will be *guaranteed* in that area, but gives no information on *which species*, *how abundant* or *how damaging* they will be.

On the other hand, the environmental GAM incorporates variables such as surface temperature, salinity, and trawling pressure. Consequently, it can help determine whether environmental and/or anthropogenic barriers or drivers are influencing the expansion of Lessepsian species. This model though, does not include an explicitly spatial factor that can inform better on the direction of the expansion, and the year effect is much less influential by comparison, making it less informative regarding the speed of the expansion. Instead, the environmental GAM projections are more useful for observing *how climate change* will benefit the Lessepsians, by making conditions more favourable for these species around the basin, and for testing the *effect of fishing effort reductions or increases* on their probability of occurrence. Finally, neither of our models include biotic interactions, which can be important (Mellin et al. 2016) but are largely unknown for most of the Lessepsian species in the Mediterranean. It is expected that, as time passes and Lessepsian NIS continue to proliferate across the Mediterranean, they will also be sampled more frequently during the MEDITS surveys, increasing data density and allowing for the construction of better, more sophisticated models that can inform on both species' abundances and their vector of expansion, as well as allowing species-specific analyses.

Despite these, arguably, severe limitations, we are fairly confident that the rate of the expansion the simple spatiotemporal model predicts is realistic and in line with other, previously published models (Coro et al. 2018; D'Amen & Azzurro 2020; Loya-Cancino et al. 2023; Mitchell & Almela 2025), albeit on the conservative side due to the low catchability of these NIS in trawls. Occurrence records for harmful Lessepsian NIS such as the silver-cheeked toadfish *Lagocephalus sceleratus*, the blue-spotted cornetfish *Fistularia commersonii* and the common lionfish *Pterois miles*, show that these NIS have already expanded across the entire Mediterranean (Ulman et al. 2021, Azzurro et al. 2022, Azzurro 2023, Bottacini et al. 2024, Iveša et al. 2025). It is expected that impacts of these NIS will start to materialise in the Adriatic and western Mediterranean Sea sooner rather than later. We can also be fairly confident that future climatic conditions are bound to favour the Lessepsians, mostly through the weakening of the low water temperature barrier that several locations around the Mediterranean currently still exhibit during winter. There is now extensive evidence of climate change benefiting invasive and thermophilic species, not only in the Mediterranean, but globally (Molinos et al. 2015, Clark et al. 2020, D'Amen & Azzurro 2020, Albano et al. 2021, Angeles-



Gonzalez et al. 2026). Sea warming is expected to lead to rapid large-scale biotic homogenisations across the globe, severely compromising conservation schemes built on assumptions that are becoming progressively irrelevant under the future biodiversity landscape (Molinos et al. 2015, D'Amen & Azzurro 2020, Engelhard et al. 2026).

One of the most important aspects of marine biodiversity conservation efforts will be the protection of fish nursery grounds across the Central-Eastern Mediterranean. Thankfully, according to our models, the nursery ground locations will persist largely unchanged in the sub-basin, making spatial prioritisation easier. The spread of the Lessepsians will certainly create complications towards this goal. As shown here and in our previous work (Engelhard et al. 2026), these sensitive habitats have already been compromised by the presence of NIS in Cyprus, the southern Aegean and eastern Ionian Seas. Serious NIS impacts on these habitats have already been reported in these areas (Katsanevakis et al. 2018, Giakoumi et al. 2019, Dimitriadis et al. 2021, 2024). According to our model results, the expansion of the Lessepsian migrants is projected to reach the southern Adriatic, the northern Aegean and the south Sicilian nursery grounds within the few coming decades. The go-to solution for the management of such habitats has been assigning them under some level of protection status, prohibiting certain or all human activities in the area. Indeed, there is merit for such approaches since our analyses showed that mild reductions in the overall fishing effort can have positive effects in both juvenile fish alpha diversity and in reducing the occurrence probability of NIS, in agreement with previous studies in the Mediterranean (Corrales et al. 2018, Clark et al. 2020). However, overall reductions in fishing effort are conceptually and substantively quite different from localised fisheries closures. Total prohibitions of fishing activity may lead to the opposite of the desired effect, potentially increasing the presence and the abundance of NIS inside protected areas (Galil 2017, Giakoumi et al. 2019, Kleitou et al. 2024). Therefore, fisheries closures should be always coupled by specific NIS management plans that include targeted removals of harmful NIS, public engagement and, ultimately, the economic exploitation of these species (Kleitou et al. 2021, 2024, Ulman et al. 2022).

In conclusion, the projections indicate that the Lessepsian migrants, marine species of Indo-Pacific origin that include several invasive species, are likely to continue expanding northward and westward across the Mediterranean during the coming decades. By 2050, these non-indigenous species are projected to establish a strong presence in the southern Adriatic and across the shelf area south of Sicily, while remaining highly prevalent in the Eastern Mediterranean, including Cyprus, Crete, the southern Aegean and the eastern Ionian Sea. Future sea warming is expected to facilitate this expansion by making climatic conditions increasingly suitable for thermophilic invaders. The projected spread of Lessepsian species is particularly concerning because juvenile fish nursery grounds are expected to remain relatively stable in space. This stability is useful for spatial prioritisation, but it also means that nursery habitats may become increasingly exposed to invasive species as the invasion front progresses. Areas such as the southern Adriatic, south Sicily, the eastern Ionian, the southern Aegean and Crete should therefore be treated as priority zones for monitoring and adaptive management. The fishing pressure scenarios suggest that moderate reductions in fishing effort may contribute to lower occurrence probability of Lessepsian species and may benefit juvenile fish diversity. However, broad reductions in fishing effort should not be confused with local fisheries closures. In invaded areas, closures without active invasive species management



may unintentionally favour the build-up of invasive populations inside protected areas. Consequently, spatial protection in the Mediterranean should be coupled with specific management plans for non-indigenous species, including early detection, targeted removals, public engagement, fisher involvement and the development of selective fishing practices where appropriate. Overall, the management of Lessepsian species should become an explicit component of Mediterranean conservation planning. Marine protected areas and nursery grounds cannot be managed only by reducing conventional human pressures. They must also account for the changing biogeographical context produced by climate warming and biological invasions. This requires adaptive, site-specific and species-specific strategies that combine biodiversity protection with active control of harmful invasive populations.



6 General discussion and management implications

6.1 Brief synopsis of key findings

This deliverable provides a forward looking assessment of projected risks and vulnerabilities of marine species and communities across selected European regional seas. Building on the trait-based sensitivity and risk framework developed in WP4, the analyses presented here move from retrospective assessment towards scenario-based projections for the coming decades up to mid-century. An innovative methodology was applied to map hotspots of biodiversity, marine communities' sensitivity, vulnerability, and risk to fishing pressure and climate change across Europe's regional seas. Across the Mediterranean Sea, Northeast Atlantic and Icelandic waters, the results show that future ecological risk will be shaped by both the persistence of current vulnerability patterns and the gradual spatial redistribution of species, communities, sensitivities and pressures under future climate change. Overall, this means that mid- and long-term conservation planning and fisheries management at basin- and area-specific scales should not rely only on present-day hotspot maps, but should consider projections, their uncertainties, and regular monitoring.

6.2 Strengths and weaknesses

The main strength of this deliverable is the integration of trait-based sensitivity indices with spatially explicit environmental projections, exposure layers and hotspot analyses. This allows risk to be assessed not only as a function of external pressures (also referred to as 'hazard'), but also as a function of the biological characteristics of the communities exposed to that pressure (i.e. sensitivity). The framework is therefore useful for identifying areas where ecological vulnerability or risk may persist or intensify in the future.

A further strength is that the spatially explicit maps describing projected risks and sensitivities are useful for evaluating the designation and management of MPAs. In our previous deliverable report (D4.3) we already showed that sensitivity or risk hotspots may shift over space and time as a result of climate-driven range shifts of species, thereby both informing and complicating evaluation and decision-making (Engelhard et al. 2026). The maps on projected risk hotspots may provide additional information to support the inherently complex decisions around MPAs, FRAs and OECMs, which require a balancing of stakeholder, management, and conservation interests.

One limitation is that our maps on projected biodiversity hotspots describe sensitivities and risks to two (arguably highly dominating) key pressures only – climate change and fishing (Polo et al. 2025). However, other important drivers are also impacting marine life; these include pollution, marine traffic, oil and gas extraction, aggregate dredging, offshore windfarms, recreational activities, and further pressures (Kenny et al. 2009, 2018; Tiano & Rozemeijer in Lindegren et al. 2025, Piet et al., 2023). As also highlighted previously (Engelhard et al. 2026), a possible extension of this research would be to include sensitivity and risk maps to these other anthropogenic pressures (e.g. dredging, Piet et al. 2023), and so obtain more integrated maps of the risks to marine biodiversity. Ideally, such an extension would incorporate future projections of these other important pressures on marine life – some of which might increase,



others decrease in the future, partly depending on future climate change, fisheries multi-annual management plans and socio-political scenarios (Pinnegar et al. 2021).

An important limitation is also that future projections depend on the quality and resolution of the available environmental and biological data. There is considerable uncertainty in future climate projections; these should be seen as ‘possible futures’, not as definitive predictions of most likely trajectories (Pinnegar et al. 2021). Moreover, the only climate variable included here was temperature, while other environmental changes such as salinity, ocean currents, wind speed and storms are also likely to impact marine species and communities. It should also be acknowledged that the model’s sliding window validation approach was limited in the total duration over which the ability of the GAM to project could be calibrated. As existing models indicate declining model ability when tested into the future (Rutterford et al. 2015), we have lower confidence in the model projections beyond 5 years and increasingly to 2050.

Several other limitations should be acknowledged. First, fishing effort scenarios remain difficult to define consistently across regions, and in several analyses fishing exposure had to be held constant or simplified. Second, the communities explored here are primarily the surveyed demersal species of the case study areas, which do not include a wide range of taxonomic and trait-based diversity, including seabirds, marine mammals, phyto- and zooplankton, and infauna. Third, important habitats and communities were not included in the analysis, such rocky grounds, sites very close to the coast, or deep-sea areas. Fourth, projections of community sensitivity do not fully account for biotic interactions, behavioural adaptation, evolutionary responses, or unexpected ecological thresholds. Fifth, the taxonomic focus differs among regions. All these considerations mean that the results should be interpreted as regional case studies rather than a fully harmonised pan-European assessment.

Despite these limitations, the analyses provide a useful screening-level framework for identifying future risk and sensitivity patterns and management priorities. They have defined more or less persistent risk hotspot areas over time, which may be seen as ‘no-regret’ areas regarding targeted management action. The resulting sensitivity and risk maps should not be seen as definitive predictions or concrete forecasts of future ecosystem states, but rather be part of the evidence to support decisions, guide management and further targeted analyses.

6.3 Management implications per basin

At the core of B-USEFUL is the intention to provide tools for policy making on marine biodiversity. The following section provides a range of take-home messages for biodiversity policy makers and area managers, emerging from this report’s focus on future projections of sensitivity and risk hotspots for marine biodiversity. First, we highlight key messages and management implications at the basin or area level; next, the implications beyond basins or areas are presented, valid more widely across European regional seas and beyond.

6.3.1 Mediterranean Sea

What are the key findings?

- The Mediterranean Sea case study has projected how climate change- and fishing-related sensitivity (S_{CC} , S_{FP}) and risk (R_{CC} , R_{FP}) may evolve for Mediterranean demersal



communities under a high-emission scenario (RCP8.5). Overall, the results suggest that previously identified spatial patterns of risk are likely to persist, with moderate changes at the basin scale but local intensification in specific hotspot areas.

- Although projected shifts in risks are generally moderate, risk is expected to increase in several priority areas. The locations of major hotspots remains relatively stable compared with current patterns, suggesting persistence rather than a complete spatial reorganisation of risk.
- Projected climate change risk, R_{CC} , to the Mediterranean's demersal communities highlights persistent hotspots, particularly around Cyprus, in the southern Aegean Sea, and in the south of Strait of Sicily. These areas combine high thermal exposure with demersal communities that are sensitive to climate driven change.
- Projected fishing pressure risk, R_{FP} , remains associated with historically exploited fishing grounds, including areas off the Iberian coasts, the Gulf of Lion, the Sardinian Channel, the Strait of Sicily, and localised parts of the Adriatic and Western Ionian Seas.

At basin level: To improve protection, what policy recommendations are emerging from this case study?

- **Adaptive spatial management** is recommended in projected risk hotspots if these are persistent, intensifying, or emerging, especially if currently only **partially** covered by effective protection such as MPAs, FRAs or OECMs. These recommendations should be interpreted alongside wider ecological evidence, monitoring data and existing management frameworks.
- At basin level, existing MPAs, FRAs and spatial management measures should be maintained and strengthened where they already overlap with projected risk hotspots, or extended as well as new measures would also be required where persistent or emerging hotspots remain outside effective protection.
- This study indicates that priority areas regarding projected R_{CC} (including south of Cyprus, Aegean Sea, south of the Strait of Sicily) are important because they combine high thermal exposure with sensitive demersal communities, which suggests increasing ecological vulnerability under continued warming. **Response measures** could include strengthening protection in existing high-risk areas, limiting impactful demersal gears where risk and fishing pressure overlap, and strengthening management in areas already identified as persistent hotspots.
- The study has also highlighted priority areas regarding projected R_{FP} (areas off the Iberian coasts, the of Gulf of Lion, south of Sardinian Channel, southern Strait of Sicily, localised parts of the Adriatic Sea and western Ionian seas). In these areas, risk to demersal communities may increase because of the combined climate-driven effect on the community and consequent reorganisation that may increase sensitivity to fishing pressure even if fishing effort remains constant. **No-regret measures** may include managing fishing pressure more precautionarily in climatically exposed subregions, especially where high fishing effort already coincides with rising ecological sensitivity. This may be achieved through improving selectivity, reducing seabed disturbance, protecting structurally important habitats, and continue in targeting effort reductions in grounds where persistent R_{FP} hotspots are already evident.



- Projected shifts in risk centres of gravity indicate that Mediterranean management cannot remain static. Given the uncertainties associated with projections, ecosystem responses and future pressure trajectories, an **adaptive management** approach is needed, supported by regular monitoring. Our approach can aid in evaluating the developments alongside other projections exploring ecosystem risk. A basin-level monitoring framework should be used to update hotspot maps regularly and to detect changes in community composition, sensitivity, exposure and risk. The tracking of risk hotspots could be readily achieved as both could be calculated from routine MEDITS survey data, combined with traits data by species. These indicators, as early-warning signals, would allow management to respond to emerging hotspots before they become long-term areas of high vulnerability.

At the European level: what broad-scale recommendations are emerging from this case study, relevant to biodiversity protection across European basins?

- The effectiveness of protection of marine biodiversity in European regional seas depends on whether management measures reduce the pressures that drive ecological risk. For fishing-related risk, this means that spatial measures (e.g. MPAs, FRAs and other spatio-temporal measures) must guarantee effective regulation of fishing activities. For climate-related risk, protection should be combined with broader actions that enhance resilience, reduce local stressors and maintain ecological connectivity.
- Marine management should explicitly consider the interaction between climate change and fishing pressure. The Mediterranean projections suggest that warming may alter community composition in ways that increase sensitivity to fishing pressure. This means that fisheries management should also take into account possible effects of climate adaptation.
- Adaptive management should become a core principle of European marine conservation. This would account for the combination of (1) persistent hotspots (offering the potential for no-regret measures); (2) shifting hotspots, urging for adaptive management; and (3) a lack of overlap between MPAs and risk hotspots (Rozemeijer et al., 2025, Engelhard et al., 2026). Current boundaries of protected areas in the mid- and long term may be insufficient when risk hotspots shift over time. Regular monitoring, scenario-based projections and periodic reassessment of spatial and management measures are needed to ensure that conservation networks remain aligned with ecological vulnerability.

6.3.2 Northeast Atlantic (Greater North Sea, Celtic Seas and Bay of Biscay)

What are the key findings?

- In the Northeast Atlantic case study area, climate change risk is projected to increase across most of the region into the future, despite slight declines in community-level climate sensitivity. This indicates that rising exposure (warming) is the main driver of increasing risk and outpaces communities' rates of change in climate sensitivity.
- Community-level sensitivity to fishing pressure is projected to increase in the Celtic Seas and Bay of Biscay, despite the model's assumption of constant fishing exposure.



This suggests community restructuring and changing trait composition, rather than increased fishing effort, play a role in increased S_{FP} .

- Climate risk hotspots are projected to be spatially stable, concentrated in southern, western and shelf regions of the Celtic Seas and Bay of Biscay, and persist or expand slightly through time. In contrast, fishing pressure risk is more spatially variable and fragmented, with hotspots mainly in the northern North Sea and parts of the Celtic Seas.
- Areas where climate and fishing risks overlap (e.g., southern Celtic Seas) represent potential zones of compounded vulnerability.

At basin level: To improve protection, what policy recommendations are emerging from this case study?

- It is recommended to prioritise persistent climate-risk hotspots (southern, western and shelf regions) for long-term monitoring, protection and adaptive management, as these are likely recurrent areas of vulnerability.
- Climate change should be explicitly integrated into ecosystem-based fisheries management (EBFM), recognising that warming is increasingly becoming a primary driver of ecosystem risk. The implementation of adaptive spatial management measures (e.g. dynamic MPAs or flexible closures) would allow responding to shifting risk patterns and species distributions.
- Management efforts should focus on areas of overlapping climate risk and fishing risk (e.g. Celtic Seas), where communities may face compounded pressures. Where evidence supports it, enhanced habitat connectivity and protection in high-risk areas is recommended, allowing species redistribution and adaptation.
- It may need to be recognised that community change may be unavoidable in some areas. Therefore, management may need to shift from strict preservation towards adaptive strategies. This might potentially include supporting transitions to new community states.

At the European level: what broad-scale recommendations are emerging from this case study, relevant to biodiversity protection across European basins?

- At the European level, climate change needs to be embedded as a central pillar of marine biodiversity policy (e.g., European Green Deal, EU Biodiversity Strategy 2030, MSFD), not just as a secondary consideration.
- There is a need to transition from static conservation approaches to adaptive, forward-looking strategies. This would account for dynamic species distributions, changes in community structure and shifting risk patterns. MPA networks and spatial measures need to be climate-resilient, with consideration of connectivity, shifting habitats and future conditions.
- Strengthening integration between fisheries management and biodiversity conservation policy would be beneficial. This would ensure that policies address both combined and interacting pressures rather than treating these separately.
- Cross-border coordination in marine spatial planning is encouraged, reflecting that climate-driven species redistribution and risk patterns occur at large spatial scales beyond national jurisdictions.



- The development of pan-European risk mapping and forecasting frameworks to would help identify future vulnerability hotspots across basins. Over-reliance on single-model outputs should be avoided – instead, multi-model, multi-scenario approaches are needed to build confidence and consensus in projections. All outputs like this should be seen as screening-level, decision-support evidence, rather than definitive predictions, to guide iterative policy development and adaptive management.

6.3.3 Icelandic waters

What are the key findings?

- In Icelandic waters in future decades up to mid-century, projections in groundfish biomass patterns differ strongly among species groups. Arctic species, which are concentrated on the continental slopes, are projected to decline. Relatively stable or increasing biomass levels are projected for commercially important species, at-risk fish species (classed as Endangered by IUCN), climate-sensitive species, and fishing-sensitive species. Increase are especially protected, especially around the Reykjanes Ridge (south-west of Iceland) where the warming waters arrive.
- This case study indicates an ongoing, climate-driven reorganisation of Icelandic groundfish communities (with likely borealisation) and decreases in Arctic species and implications for future marine spatial planning and protection.
- The methodology of using five species categories aids in obtaining an overview of the general patterns. Still, it is also urged to carefully analyse the development for the individual category as well. Essential information can be retrieved from that analysis as well (as was shown for the Arctic species category).

At basin level: To improve protection, what policy recommendations are emerging from this case study?

- Projected changes in groundfish community composition have implications for the distribution of areas of high priority for conservation of groundfish around Iceland. These are expected to shift by 2050, with increasing importance of the Iceland–Faroe Ridge and parts of northern Iceland, and decreasing priority in parts of the southern slope, eastern shelf and Greenlandic shelf. Adopting dynamic, climate-informed conservation planning is recommended, rather than relying only on static protected areas, because priority areas for groundfish conservation are projected to shift by 2050.
- Safeguarding potential climate refugia and vulnerable deep-slope habitats is recommended, particularly those supporting Arctic species and species sensitive to climate change and fishing pressure, to maintain biodiversity resilience under ongoing warming.

At the European level: what broad-scale recommendations are emerging from this case study, relevant to biodiversity protection across European basins?

- The Icelandic case study re-emphasises that at the European level, marine conservation policy should become more climate-adaptive and dynamic, recognising that sensitivity and risk hotspots, and priority areas for conservation, may shift

substantially over coming decades rather than remain spatially fixed. This is in close agreement with the Europe-wide implications arising from the Mediterranean case study.

- Marine protected area design and broader marine spatial planning should incorporate projected species redistribution and climate refugia, especially in northern and sub-Arctic seas where warming-driven borealisation is already reshaping ecosystems.

6.3.4 Mediterranean non-native species

What are the key findings?

- Lessepsian non-indigenous species (NIS) are projected to continue to rapidly expand westward and northward in the near future.
- By 2050, Lessepsian NIS will have established a strong presence as far west as the entire shelf area south of Sicily and as far north as the southern Adriatic coasts.
- Sea warming is projected to further facilitate their spread; however, fishing effort reductions on native species might slightly curtail it. Reduced fishing effort is expected to leave the original communities less disturbed with less open niches to occupy.
- The locations of fish nursery grounds are projected to remain mostly unchanged by 2050. With an increasing coverage by NIS, fish nursery grounds are anticipated to be increasingly influenced.

At basin level: To improve protection, what policy recommendations are emerging from this case study?

- NIS-specific management plans should be developed and implemented in MPAs across the Mediterranean, focusing on active population management (e.g. selective fisheries) in areas where NIS are already present and on early detection and mitigation in areas where they are expected to arrive in the future.
- NIS-specific management plans should also cover sensitive habitats such as nursery grounds, including those relevant to key foodfish species, or any areas deemed necessary to achieve conservation targets and mitigate the ecological impacts of invasive NIS.
- As also previously argued, engaging stakeholders and the public to incentivise the sustainable exploitation of NIS will be crucial. Investing in the development of highly selective fishing gears could support this goal, while simultaneously minimising the ecological footprint of fisheries. In this context, targeted NIS fisheries can be a useful tool within an integrated management strategy.

At the European level: what broad-scale recommendations are emerging from this case study, relevant to biodiversity protection across European basins?

- Climate change is expected to lead to rapid biotic homogenisations world-wide on native ecosystems and potentially leading to range contractions or area shifts of indigenous species. In addition, increasing NIS pressure will add additional pressure on these developments. Therefore Europe-wide and beyond, adopting NIS-specific management plans focused on early detection, mitigation and where possible removal will be beneficial. Large-scale biodiversity changes should be monitored, and existing



management plans and policies should be reassessed if deemed inadequate for achieving conservation targets in the context of NIS.

- Research on the biology, biotic interactions, and impacts of harmful or potentially harmful NIS is essential, as these factors remain largely unknown for most species in both their native and invasive ranges. Such research and species-specific ecological knowledge are strongly encouraged to enable the development of effective species-specific NIS management plans.

6.4 Generalised management implications at the European level

This work provides evidence towards the outcome of supporting thriving future marine communities and protecting 30% of the marine environment in European regional seas by 2030, including species sensitive to climate change and fishing pressure, whilst also enabling continued valuable exploitation and development of the marine environment. At the European level, important broad-scale recommendations emerge from each of the above case studies. This section synthesises these recommendations in a general perspective valid for biodiversity protection across all basins.

- We have an informative methodology allowing projections of biodiversity, sensitivity and risk into the future, so far applied to several important groups of species. Building on this, it is advised to apply this methodology to all relevant species groups across sea basins.
- Protection should be evaluated in terms of ecological effectiveness, not only spatial coverage. The achievement of area-based targets such as 30×30 will be insufficient if protected areas do not overlap with vulnerable communities or if permitted activities continue to generate the pressures that drive risk.
- The study has shown that biodiversity, risk or sensitivity hotspots can shift over time, which is challenging to accommodate through marine spatial planning and regulations that are rigid – understandably so given the high stakes and governmental complexity. Appropriate and regular monitoring and risk assessment will generate management warning signals that could indicate potential shifts in vulnerability. Such information could underpin decisions on additional spatial-temporal management measures (e.g. temporary area closures) to hotspots in need of protection.
- Management should prioritise areas along two lines. The first line is to protect areas that appear persistent risk hotspots through time; here the projections and modelling results appear to have a certain robustness. This could justify no-regret measures on protecting and assigning functional MPAs. The second line is to protect areas where multiple pressures overlap. In the Mediterranean, this includes regions where warming, fishing pressure and biological invasions interact. In the Northeast Atlantic, this includes areas where climate exposure and fishing risk coincide. In Icelandic waters, this includes areas where Arctic species and other vulnerable groundfish categories are likely to experience climate-driven redistribution.
- Across all basins, there is a need for strengthened monitoring to support system understanding and informed decision-making. Better monitoring of the present state will support enhanced projections of future ecosystem states.



- Targeted (additional) monitoring could also support adaptive management, required given the substantial changes projected. Monitoring should be designed to detect changes in community composition, trait structure, biomass distribution, juvenile and spawning habitats, invasive species occurrence and the effectiveness of management actions. In addition, because projections into the future have high uncertainties, targeted monitoring is needed to continuously reassess projections and potential impacts, to be able to adapt when and where urgencies shift in time and space.
- Non-indigenous species require adaptive management, not only in the Eastern Mediterranean but Europe-wide. Drawing from successful management examples, these plans should contain monitoring of their populations and regular targeted removals of harmful NIS, especially where these are entering MPAs, and/or where these may impact negatively on nursery areas of native species.
- As marine basins are typically shared between countries, it is advisable to strengthen European collaboration in both monitoring and management. Transboundary cooperation will support the achievement of (inter)national targets, including the 30×30 target, through effective biodiversity conservation measures.
- At the European level and beyond, no-regret advice includes minimising climate change pressure through mitigation (i.e. reducing greenhouse gas emissions), to reduce exposure and therefore risk to sensitive marine communities. This would likely not only reduce climate pressure on communities but potentially also offer greater capacity for species to build resilience and adapt.

6.5 Perspectives

This deliverable demonstrates the value of combining trait-based indicators, climate projections, exposure layers and spatial analyses to anticipate future biodiversity risks. The approach can support decision-making by identifying areas of persistent vulnerability, emerging risk and potential spatial mismatch between ecological priorities and management measures. Ideally such an approach is developed for economic users and socioeconomic interests as well.

The work has largely built on B-USEFUL deliverable D4.2 (Rozemeijer et al. 2025), which mapped present-day biodiversity and risk hotspots for a broad range of marine communities across surveyed areas of European regional seas – but it has extended the analyses by projecting risks into the future up to 2050. Previous work by B-USEFUL also assessed to what extent present-day biodiversity and risk hotspots are sufficiently protected through Europe’s MPA network, or are lacking adequate protection levels (D4.3, Engelhard et al. 2026). A possible extension of the present deliverable could be an evaluation to what extent the current MPA network might be appropriate and effective in protecting future hotspots. This could be achieved by combining information on MPAs and other protected or regulated areas (such as FRAs and OECMs) with the projected sensitivity and risk hotspots as described in this deliverable report. Importantly, there is a need to explore additional evidence sources to corroborate the projections to add confidence and consensus to support decisions that take account of future risks.



The use of additional climate models, ensemble members and scenarios (as these become available) would enable greater understanding of the uncertainty around projections, not only for future conditions but also on how these may influence biological responses. Inclusion of additional environmental variables, influenced by climate, that impact marine species is needed. The use of several community sensitivity modelling approaches would offer indications of confidence and consensus (or lack thereof) between approaches to support decision making.

Looking ahead towards a more thorough reassessment, we recommend that the approach is extended to assess the hotspots of biodiversity, sensitivity, and risks for the many other marine taxonomic groups of the seas of Europe. This would need to consider additional and/or cumulative pressures beyond fishing and temperature affecting marine communities. A temporal analysis should be included in that approach to assess for any shifts in space and time of both hotspots and the pressures. It should also integrate more detailed fishing scenarios, socio-economic constraints, habitat data, biotic interactions and uncertainty analyses. For the Mediterranean Sea in particular, attention should be given to the combined effects of warming, fishing pressure and non-indigenous species expansion, as these pressures are likely to interact strongly in shaping future biodiversity outcomes.

The biggest challenge is in its application. Across earlier studies (e.g. Claudet et al. 2020; Conners et al. 2022; Aminian-Biquet et al. 2024) and recent deliverable reports (Rozemeijer et al., 2025, Engelhard et al., 2026, this report) it was noted that current MPAs may not provide sufficient protection to various taxonomic or ecologically sensitive groups, due to spatial mismatches with biodiversity hotspots and/or insufficient pressure reduction. How to proceed with adaptive management in such a densely regulated environment with many high value activities? An important starting point is to include the engagement of human stakeholders and a consideration of their interests. Calculating ecological exposure layers for different (climate) impact scenarios and combining these with economic exposure and impact layers will yield insights in zones of conflicting economic and ecological considerations. A possible approach would include mapping biodiversity or risk hotspots, sites of overlap and non-overlap with human activities, and defining potential no-regret measures. In combination, this would allow for a more holistic assessment, integrating the needs and services to human society with the requirements and risks to marine life when assessing how to optimise spatio-temporal management measures in European waters.

Overall, the findings support a shift towards adaptive, risk-based and spatially explicit biodiversity management. European marine conservation strategies should be designed taking into account the present-day biodiversity patterns, but also looking beyond and projecting into the future, to remain effective under the changing ecological conditions expected in the coming decades.

7 References

- Agnetta D, Vascotto I, Panzeri D, Celić I, Solidoro C, Fortibuoni T, Raicevich S, Libralato S (2025) Bottom trawling and environmental variables drive the biodiversity of Mediterranean demersal assemblages. *Sci. Rep.* 15: 27188. <https://doi.org/10.1038/s41598-025-12258-2>
- Akaike H (1974) A new look at the statistical model identification. *IEEE Trans. Autom. Contr.* 19: 716–723. <https://doi.org/10.1109/TAC.1974.1100705>
- Albano PG, Steger J, Bošnjak M, Dunne B, Guifarro Z, Turapova E, Hua Q, Kaufman DS, Rilov G, Zuschin M (2021) Native biodiversity collapse in the eastern Mediterranean. *Proc. R. Soc. B* 288: 20202469. <https://doi.org/10.1098/rspb.2020.2469>
- Albouy C, Guilhaumon F, Leprieur F, Lasram FBR, Somot S, Aznar R, Velez L, Le Loc’h F, Mouillot D (2013) Projected climate change and the changing biogeography of coastal Mediterranean fishes. *J. Biogeogr.* 40: 534–547. <https://doi.org/10.1111/jbi.12013>
- Aminian-Biquet J, Gorjanc S, Sletten J, Vincent T, Laznya A, Vaidianu N, Claudet J, Young J, Horta e Costa B (2024) Over 80% of the European Union’s marine protected area only marginally regulates human activities. *One Earth* 7: 1614–1629. <https://doi.org/10.1016/j.oneear.2024.07.010>
- Angeles-Gonzalez LE, Villalobos-Guerrero TF, Delgadillo-Nuño MA, Torrejón-Magallanes J, Escamilla-Aké A, Díaz F, Rosas C (2026) Thermal niches and climate change reshape marine invasion risk worldwide. *Mar. Environ. Res.* 217: 107919. <https://doi.org/10.1016/j.marenvres.2026.107919>
- Aragão GM, López-López L, Punzón A, Guijarro E, Esteban A, García E, González-Irusta JM, Polo J, Vivas M, Hidalgo M (2022) The importance of regional differences in vulnerability to climate change for demersal fisheries. *ICES J. Mar. Sci.* 79: 506–518. <https://doi.org/10.1093/icesjms/fsab134>
- Astthorsson OS, Gislason A, Jonsson S (2007) Climate variability and the Icelandic marine ecosystem. *Deep-Sea Res. II* 54: 2456–2477. <https://doi.org/10.1016/j.dsr2.2007.07.030>
- Azzurro E (2023) ORMEF. <http://www.ormef.eu>
- Azzurro E, D’Amen M (2022) Climate change paves the way for a new inter-ocean fish interchange. *Front. Ecol. Environ.* 20: 558–563. <https://doi.org/10.1002/fee.2459>
- Azzurro E, Sbragaglia V, Cerri J, Bariche M, Bolognini L, Ben Souissi J, Busoni G, Coco S, Chryssanthi A, Fanelli E, Ghanem R, Garrabou J, Gianni F, Grati F, Kolitari J, Guglielmo L, Lipej L, Mazzoldi C, Milone N, et al. (2019) Climate change, biological invasions, and the shifting distribution of Mediterranean fishes: A large-scale survey based on local ecological knowledge. *Glob. Change Biol.* 25: 2779–2792. <https://doi.org/10.1111/gcb.14670>
- Azzurro E, Smeraldo S, D’Amen M (2022) Spatio-temporal dynamics of exotic fish species in the Mediterranean Sea: Over a century of invasion reconstructed. *Glob. Change Biol.* 28: 6268–6279. <https://doi.org/10.1111/gcb.16362>
- Azzurro E, Soto S, Garofalo G, et al. (2013) *Fistularia commersonii* in the Mediterranean Sea: Invasion history and distribution modeling based on presence-only records. *Biol. Invasions* 15: 977–990. <https://doi.org/10.1007/s10530-012-0344-4>
- Barnett LAK, Baskett ML (2015) Marine reserves can enhance ecological resilience. *Ecology Letters* 18: 1301–1310. <https://doi.org/10.1111/ele.12524>



- Bédry R, de Haro L, Bentur Y, Senechal N, Galil BS (2021) Toxicological risks on the human health of populations living around the Mediterranean Sea linked to the invasion of non-indigenous marine species from the Red Sea: A review. *Toxicon* 191: 69–82. <https://doi.org/10.1016/j.toxicon.2020.12.012>
- Bertrand JA, De Sola LG, Papaconstantinou C, Relini G, Souplet A (2002) The general specifications of the MEDITS surveys. *Sci. Mar.* 66 S2: 9-17. <https://doi.org/10.3989/scimar.2002.66s2>
- Beukhof E, Dencker TS, Palomares MLD, Maureaud A (2019) A trait collection of marine fish species from North Atlantic and Northeast Pacific continental shelf seas. *PANGAEA*. <https://doi.org/10.1594/PANGAEA.900866>
- Beyer HL, Kennedy EV, Beger M, Chen CA, Cinner JE, Darling ES, Eakin CM, Gates RD, Heron SF, Knowlton N, Obura DO, Palumbi SR, Possingham HP, Puotinen M, Runting RK, Skirving WJ, Spalding M, Wilson KA, Wood S, Veron JE, Hoegh-Guldberg O (2018) Risk-sensitive planning for conserving coral reefs under rapid climate change. *Conserv. Lett.* 11: e12587. <https://doi.org/10.1111/conl.12587>
- Bianchi CN, Morri C (2000) Marine biodiversity of the Mediterranean Sea: Situation, problems and prospects for future research. *Mar. Pollut. Bull.* 40: 367–376. [https://doi.org/10.1016/S0025-326X\(00\)00027-8](https://doi.org/10.1016/S0025-326X(00)00027-8)
- Bianchi CN, Morri C, Chiantore M, Montefalcone M, Parravicini V, Rovere A (2012) Mediterranean Sea biodiversity between the legacy from the past and a future of change. In: Stambler N (ed) *Life in the Mediterranean Sea: A Look at Habitat Changes*. Nova Sci. Publ. <https://www.researchgate.net/publication/242397422>
- Björnsson H, Pálsson ÓK (2004) Distribution patterns and dynamics of fish stocks under recent climate change in Icelandic waters. *ICES CM* 2004/K30: 1-29.
- Bottacini D, Pollux BJA, Nijland R, Jansen PA, Naguib M, Kotrschal A (2024) Lionfish (*Pterois miles*) in the Mediterranean Sea: A review of the available knowledge with an update on the invasion front. *NeoBiota* 92: 233–257. <https://doi.org/10.3897/neobiota.92.110442>
- Burkett VR, Wilcox DA, Stottlemeyer R, Barrow W, Fagre D, Baron J, Price J, Nielsen JL, Allen CD, Peterson DL, Ruggerone G, Doyle T (2005) Nonlinear dynamics in ecosystem response to climatic change: Case studies and policy implications. *Ecol. Complex.* 2: 357–394. <https://doi.org/10.1016/J.ECOCOM.2005.04.010>
- Burrows MT, Schoeman DS, Buckley LB, Moore P, Poloczanska ES, Brander KM, Brown C, Bruno JF, Duarte CM, Halpern BS, Holding J, Kappel CV, Kiessling W, O'Connor MI, Pandolfi JM, Parmesan C, Schwing FB, Sydeman WJ, Richardson AJ (2011) The pace of shifting climate in marine and terrestrial ecosystems. *Science* 334: 652–655. <https://doi.org/10.1126/science.1210288>
- Butt N, Halpern BS, O'Hara CC, Allcock AL, Polidoro B, Sherman S, Byrne M, Birkeland C, Dwyer RG, Frazier M, Woodworth BK, Arango CP, Kingsford MJ, Udyawer V, Hutchings P, Scanes E, McClaren EJ, Maxwell SM, Diaz-Pulido G, et al. (2022) A trait-based framework for assessing the vulnerability of marine species to human impacts. *Ecosphere* 13: e3919. <https://doi.org/10.1002/ecs2.3919>
- Campana SE, Stefánsdóttir RB, Jakobsdóttir K, Sólmundsson J (2020) Shifting fish distributions in warming sub-Arctic oceans. *Sci. Rep.* 10: 16448. <https://doi.org/10.1038/s41598-020-73444-y>
- Carroll G, Abrahms B, Brodie S, Cimino MA (2024) Spatial match–mismatch between predators and prey under climate change. *Nature Ecol. Evol.* 8: 1593–1601. <https://doi.org/10.1038/s41559-024-02454-0>



- Chaikin S, Dubiner S, Belmaker J (2022) Cold-water species deepen to escape warm water temperatures. *Glob. Ecol. Biogeogr.* 31: 75–88. <https://doi.org/10.1111/GEB.13414>
- Cheung WWL (2018) The future of fishes and fisheries in the changing oceans. *J. Fish Biol.* 92: 790–803. <https://doi.org/10.1111/JFB.13558>
- Cheung WWL, Lam VWY, Sarmiento JL, Kearney K, Watson R, Pauly D (2009) Projecting global marine biodiversity impacts under climate change scenarios. *Fish Fish.* 10: 235–251. <https://doi.org/10.1111/j.1467-2979.2008.00315.x>
- Cheung WWL, Watson R, Morato T, Pitcher T, Pauly D (2007) Intrinsic vulnerability in the global fish catch. *Mar. Ecol. Prog. Ser.* 333: 1–12. <https://doi.org/10.3354/meps>
- Clark NJ, Kerry JT, Fraser CI (2020) Rapid winter warming could disrupt coastal marine fish community structure. *Nat. Clim. Change* 10: 862–867. <https://doi.org/10.1038/s41558-020-0838-5>
- Claudet J, Loiseau C, Sostres M, Zupan M (2020) Underprotected marine protected areas in a global biodiversity hotspot. *One Earth* 2: 380–384. <https://doi.org/10.1016/j.oneear.2020.03.008>
- Coll M, Navarro J, Palomera I (2013) Ecological role, fishing impact, and management options for the recovery of a Mediterranean endemic skate by means of food web models. *Biol. Conserv.* 157: 108–120. <https://doi.org/10.1016/J.BIOCON.2012.06.029>
- Collie J, Hiddink JG, van Kooten T, Rijnsdorp AD, Kaiser MJ, Jennings S, Hilborn R (2017) Indirect effects of bottom fishing on the productivity of marine fish. *Fish Fish.* 18: 619–637. <https://doi.org/10.1111/FAF.12193>
- Conners MG, Sisson NB, Agamboue PD, Atkinson PW, Baylis AMM, Benson SR, Block BA, Bograd SJ, Bordino P, Bowen WD, Brickle P, Bruno IM, González Carman V, Champagne CD, Crocker DE, Costa DP, Dawson TM, Deguchi T, Dewar H, Doherty PD, Eguchi T, Formia A, Godley BJ, Graham RT, Gredzens C, Hart KM, Hawkes LA, Henderson S, Henry RW, Hückstädt LA, Irvine LM, Kienle SS, Kuhn CE, Lidgard D, Loredó SA, Mate BR, Metcalfe K, Nzegoue J, Kouerey Oliwina CK, Orben RA, Ozaki K, Parnell R, Pike EP, Robinson PW, Rosenbaum HC, Sato F, Shaffer SA, Shaver DJ, Simmons SE, Smith BJ, Sounguet G-P, Suryan RM, Thompson DR, Tierney M, Tilley D, Young HS, Warwick-Evans V, Weise MJ, Wells RS, Wilkinson BP, Witt MJ, Maxwell SM (2022) Mismatches in scale between highly mobile marine megafauna and marine protected areas. *Front Mar Sci* 9: 89710. <https://doi.org/10.3389/fmars.2022.897104>
- Convention on Biological Diversity. (2021). First Draft of the Post-2020 Global Biodiversity Framework. CBD/WG2020/3/3. 2021, pp. 1–12.
- Cook R, Fernandes P, Florin A, Lorange P, Nedreaas K (2015) *Coryphaenoides rupestris* (Europe assessment). International Union for Conservation of Nature (IUCN).
- Copernicus Climate Change Service, Climate Data Store, (2020): Marine biogeochemistry data for the Northwest European Shelf and Mediterranean Sea from 2006 up to 2100 derived from climate projections. Copernicus Climate Change Service (C3S) Climate Data Store (CDS). <https://doi.org/10.24381/cds.dcc9295c>
- Copernicus Marine Service (2025a) Global Ocean Biogeochemistry Hindcast.
- Copernicus Marine Service (2025b) Global Ocean Physics Reanalysis.
- Coro G, Vilas LG, Magliozzi C, Ellenbroek A, Scarponi P, Pagano P (2018) Forecasting the ongoing invasion of *Lagocephalus sceleratus* in the Mediterranean Sea. *Ecol. Model.* 371: 37–49. <https://doi.org/10.1016/j.ecolmodel.2018.01.007>



- Corrales X, Coll M, Ofir E, Heymans JJ, Steenbeek J, Goren M, Edelist D, Gal G (2018) Future scenarios of marine resources and ecosystem conditions in the Eastern Mediterranean under the impacts of fishing, alien species and sea warming. *Sci. Rep.* 8: 14284. <https://doi.org/10.1038/s41598-018-32666-x>
- Cramer W, Guiot J, Fader M, Garrabou J, Gattuso J-P, Iglesias A, Lange MA, Lionello P, Llasat MC, Paz S, et al. (2018) Climate change and interconnected risks to sustainable development in the Mediterranean. *Nat. Clim. Change* 8: 972–980. <https://doi.org/10.1038/s41558-018-0299-2>
- D'Amen M, Azzurro E (2020) Lessepsian fish invasion in Mediterranean marine protected areas: A risk assessment under climate change scenarios. *ICES J. Mar. Sci.* 77: 388–397. <https://doi.org/10.1093/icesjms/fsz207>
- D'Amen M, Smeraldo S, Di Franco A, Azzurro E (2022) The spread of Lessepsian fish does not track native temperature conditions. *ICES J. Mar. Sci.* 79: 1864–1873. <https://doi.org/10.1093/icesjms/fsac121>
- Danovaro R, Canals M, Gambi C, Heussner S, Lampadariou N, Vanreusel A (2009) Exploring benthic biodiversity patterns and hotspots on European margin slopes. *Oceanography* 22: 16–25. <https://doi.org/10.5670/oceanog.2009.02>
- De Juan S, Demestre M (2012) A trawl disturbance indicator to quantify large scale fishing impact on benthic ecosystems. *Ecol. Indic.* 18: 183–190. <https://doi.org/10.1016/J.ECOLIND.2011.11.020>
- Dimitriadis C, Fournari-Konstantinidou I, Sourbès L, Koutsoubas D, Katsanevakis S (2021) Long-term interactions of native and invasive species in a marine protected area suggest complex cascading effects challenging conservation outcomes. *Diversity* 13: 71. <https://doi.org/10.3390/d13020071>
- Dimitriadis C, Marampouti C, Calò A, et al. (2024) Evaluating the long-term effectiveness of a Mediterranean marine protected area to tackle the effects of invasive and range-expanding herbivorous fish on rocky reefs. *Mar. Environ. Res.* 193: 106293. <https://doi.org/10.1016/j.marenvres.2023.106293>
- Dong B, Aksenov Y, Colfescu I, Harvey B, Hirschi J, Josey S, Lu H, Mecking J, Oltmanns M, Osprey S, Robson J, Rynders S, Shaffrey L, Sinha B, Sutton R, Weisheimer A (2025) Key drivers of large scale changes in North Atlantic atmospheric and oceanic circulations and their predictability. *Clim. Dyn.* 63: 113. <https://doi.org/10.1007/s00382-025-07591-1>
- du Pontavice H, Gascuel D, Reygondeau G, Maureaud A, Cheung WWL (2020) Climate change undermines the global functioning of marine food webs. *Global Change Biol.* 26: 1306–1318. <https://doi.org/10.1111/gcb.14944>
- Dulvy NK, Rogers SI, Jennings S, Stelzenmüller V, Dye SR, Skjoldal HR (2008) Climate change and deepening of the North Sea fish assemblage: A biotic indicator of warming seas. *J. Appl. Ecol.* 45: 1029–1039. <https://doi.org/10.1111/j.1365-2664.2008.01488.x>
- Dutertre M, Hamon D, Chevalier C, Ehrhold A (2013) The use of the relationships between environmental factors and benthic macrofaunal distribution in the establishment of a baseline for coastal management. *ICES J. Mar. Sci.* 70: 294–308. <https://doi.org/10.1093/icesjms/fss170>
- Edelist D, Rilov G, Golani D, Carlton JT, Spanier E (2013) Restructuring the sea: Profound shifts in the world's most invaded marine ecosystem. *Divers. Distrib.* 19: 69–77. <https://doi.org/10.1111/ddi.12002>



- Emblemsvåg M, Núñez-Riboni I, HT C, Nogueira A, Gundersen A, Primicerio R (2020) Increasing temperatures, diversity loss and reorganization of deep-sea fish communities east of Greenland. *Mar. Ecol. Prog. Ser.* 654: 127–141. <https://doi.org/10.3354/meps13495>
- Emblemsvåg M, Pecuchet L, Velle LG, Nogueira A, Primicerio R (2022) Recent warming causes functional borealization and diversity loss in deep fish communities east of Greenland. *Divers. Distrib.* 28: 2071–2083. <https://doi.org/10.1111/ddi.13604>
- Eme D, Rufino MM, Trenkel VM, Vermard Y, Laffargue P, Petitgas P, Pellissier L, Albouy C (2022) Contrasted spatio-temporal changes in the demersal fish assemblages and the dominance of the environment vs fishing pressure, in the Bay of Biscay and Celtic Sea. *Prog. Oceanogr.* 204: 102788. <https://doi.org/10.1016/j.pocean.2022.102788>
- Engelhard GH, Bartilotti C, Batziakas S, Chiarini M, Consiglio A, Fock H, Gillie ER, Golin F, Gran A, Henriques S, Hidalgo M, Jonsdottir IG, Lindegren M, Martins A, Mériçot B, Mouillec F, Moura T, Oliveira PB, Pecuchet L, Peristeraki N, Polo J, Puerta P, Rutterford LA, Spedicato MT, Tiano J, Vasconcelos R, Zupa W, Rozemeijer MJC (2026) B-USEFUL. Match/mismatch between European marine protected areas and ‘hotspots’ of sensitivity or risk from climate change and fishing. Technical University of Denmark. <https://b-useful.eu/library/deliverables/>
- Engelhard GH, Polo J, Pecuchet L, Tiano T, Henriquez S, Lindegren M, Mouillec F, Rozemeijer M, Rutterford L (2024) B-USEFUL. Report on species and/or habitats particularly at risk in different European regional seas. Technical University of Denmark. <https://b-useful.eu/library/deliverables/>
- Engelhard GH, Righton DA, Pinnegar JK (2014) Climate change and fishing: a century of shifting distribution in North Sea cod. *Global Change Biol.* 20: 2473–2483. <https://doi.org/10.1111/gcb.12513>
- Escudier R, Clementi E, Cipollone A, Pistoia J, Drudi M, Grandi A, Lyubartsev V, Lecci R, Aydogdu A, Delrosso D (2021) A high-resolution reanalysis for the Mediterranean Sea. *Front. Earth Sci.* 9: 702285. <https://doi.org/10.3389/feart.2021.702285>
- Escudier, R., Clementi, E., Omar, M., Cipollone, A., Pistoia, J., Aydogdu, A., Drudi, M., Grandi, A., Lyubartsev, V., Lecci, R., Cretí, S., Masina, S., Coppini, G., & Pinardi, N. (2020). Mediterranean Sea Physical Reanalysis (CMEMS MED-Currents) (Version 1) [Data set]. Copernicus Monitoring Environment Marine Service (CMEMS). https://doi.org/10.25423/CMCC/MEDSEA_MULTIYEAR_PHY_006_004_E3R1
- Essl F, Dullinger S, Rabitsch W, Hulme PE, Pyšek P, Wilson JRU, Richardson DM (2015) Delayed biodiversity change: No time to waste. *Trends Ecol. Evol.* 30: 375–378. <https://doi.org/10.1016/j.tree.2015.05.002>
- Essl F, Dullinger S, Rabitsch W, Hulme PE, Pyšek P, Wilson JRU, Richardson DM (2015) Historical legacies accumulate to shape future biodiversity in an era of rapid global change. *Divers. Distrib.* 21: 534–547. <https://doi.org/10.1111/ddi.12312>
- European Commission, Joint Research Centre (2026): 2024 – EU Mediterranean and Black Sea Fisheries Independent Survey Data up to 2023. [Dataset] doi: 10.2905/JRC.6Q57KS8; 10.2905/f25092c4-3f0f-449f-ba60-5fbfe385defc PID: <http://data.europa.eu/89h/f25092c4-3f0f-449f-ba60-5fbfe385defc>
- FAO. (2023). The State of Mediterranean and Black Sea Fisheries 2023. The State of Mediterranean and Black Sea Fisheries 2023. <https://doi.org/10.4060/CC8888EN>



- Fernandes JA, Rutterford L, Simpson SD, Butenschön M, Frölicher TL, Yool A, Cheung WWL, Grant A (2020) Can we project changes in fish abundance and distribution in response to climate? *Global Change Biol.* 26: 3891–3905. <https://doi.org/10.1111/gcb.15081>
- Frainer A, Primicerio R, Dolgov A, Fossheim M, Johannesen E, Lind S, Aschan M (2021) Increased functional diversity warns of ecological transition in the Arctic. *Proc. R. Soc. B* 288: 20210054. <https://doi.org/10.1098/rspb.2021.0054>
- Frid O, Malamud S, Di Franco A, Guidetti P, Azzurro E, Claudet J, Micheli F, Yahel R, Sala E, Belmaker J (2023) Marine protected areas' positive effect on fish biomass persists across the steep climatic gradient of the Mediterranean Sea. *J. Appl. Ecol.* 60: 638–649. <https://doi.org/10.1111/1365-2664.14352>
- Fuchs G, Stelljes N, Kroos F, Scherer C, Lønborg C, Bauer B, Cambra E, Gissi E, Cortez Gallegos GE, Peck MA (2026) Towards climate-ready marine protected areas: challenges and strategic pathways. *npj Ocean Sustain.* 5: 15. <https://doi.org/10.1038/s44183-026-00184-3>
- Galanidi M, Aissi M, Ali M, Bakalem A, Bariche M, Bartolo AG, et al. (2023) Validated inventories of non-indigenous species (NIS) for the Mediterranean Sea as tools for regional policy and patterns of NIS spread. *Diversity* 15: 962. <https://doi.org/10.3390/d15090962>
- Galanidi M, Zenetos A, Bacher S (2018) Assessing the socio-economic impacts of priority marine invasive fishes in the Mediterranean with the newly proposed SEICAT methodology. *Mediterr. Mar. Sci.* 19: 107–123. <https://doi.org/10.12681/mms.15940>
- Galil BS (2017) Eyes wide shut. In: Goriup PD (Ed.), *Management of Marine Protected Areas* (Chap. 10). Wiley. <https://doi.org/10.1002/9781119075806.ch10>
- García Molinos J, Halpern BS, Schoeman DS, et al. (2016) Climate velocity and the future global redistribution of marine biodiversity. *Nat. Clim. Change* 6: 83–88. <https://doi.org/10.1038/nclimate2769>
- Gearty W, Chamberlain S (2025) Rredlist: IUCN Red List Client.
- Getis A, Ord JK (1992) The analysis of spatial association by use of distance statistics. *Geogr. Anal.* 24: 189–206. <https://doi.org/10.1111/j.1538-4632.1992.tb00261.x>
- Giakoumi S, Pey A, Di Franco A, Francour P, Kizilkaya Z, Arda Y, Raybaud V, Guidetti P (2019) Exploring the relationships between marine protected areas and invasive fish in the world's most invaded sea. *Ecol. Appl.* 29: e01809. <https://doi.org/10.1002/eap.1809>
- González-Andrés C, Guijarro B, Ramirez-Romero E, Massuti E (2025) Long term predictions on the population dynamics of two contrasting demersal fishing resources in the western Mediterranean. *Front. Mar. Sci.* 12: 1587297. <https://doi.org/10.3389/fmars.2025.1587297>
- Gordó-Vilaseca C, Costello MJ, Coll M, Jüterbock A, Reiss H, Stephenson F (2024) Future trends of marine fish biomass distributions from the North Sea to the Barents Sea. *Nat. Commun.* 15: 5637. <https://doi.org/10.1038/s41467-024-49911-9>
- Halpern BS, Walbridge S, Selkoe KA, Kappel CV, Micheli F, D'Agrosa C, Bruno JF, Casey KS, Ebert C, Fox HE, Fujita R, Heinemann D, Lenihan HS, Madin EMP, Perry MT, Selig ER, Spalding M, Steneck R, Watson R (2008) A global map of human impact on marine ecosystems. *Science* 319: 948–952. <https://doi.org/10.1126/science.1149345>
- Hermant M, Lobry J, Bonhommeau S, Poulard J-C, Le Pape O (2010) Impact of warming on abundance and occurrence of flatfish populations in the Bay of Biscay (France). *J. Sea Res.* 64: 45–53. <https://doi.org/10.1016/j.seares.2009.07.001>



- Hidalgo M, Barrier N, Batziakas S, Billy M, Blum S, Chaves C, Consiglio A, Cooper K, Couce E, Engelhard G, Fock HO, Gran A, Greig L, Hélaouët P, Henriques S, Kaninas A, Kavadas S, Maire E, Martins A, Mérigot B, Montanyes M, Moullec F, Maioli F, Moura T, Palomares MLD, Peck MA, Peristeraki P, Pecuchet L, Pinnegar JK, Puerta P, Rozemeijer M, Silva F, Sole M, Sguotti C, Spedicato MT, Thompson M, Tiano J, Tserpes G, van Denderen D, Vasconcelos R, Velez L, Vivó-Pons A, Zupa W, Lindegren M (2026) B-USEFUL. Report on biodiversity status, state-pressure relationships and cumulative impacts across European waters. Technical University of Denmark. <https://b-useful.eu/library/deliverables>
- Hidalgo M, Bartolino V, Coll M, Hunsicker ME, Travers-Trolet M, Browman HI (2022) 'Adaptation science' is needed to inform the sustainable management of the world's oceans in the face of climate change. ICES J. Mar. Sci. 79: 457–462. <https://doi.org/10.1093/icesjms/fsac014>
- Hidalgo M, El-Haweet AE, Tsikliras AC, Tirasin EM, Fortibuoni T, Ronchi F, Lauria V, Ben Abdallah O, Arneri E, Ceriola L, Milone N, Lelli S, Hernández P, Bernal M, Vasconcellos M (2022) Risks and adaptation options for the Mediterranean fisheries in the face of multiple climate change drivers and impacts. ICES J. Mar. Sci. 79: 2473–2488. <https://doi.org/10.1093/icesjms/fsac185>
- Hidalgo M., Mihneva V., Vasconcellos M., & Bernal M. (2018). Impacts of climate change on fisheries and aquaculture Synthesis of current knowledge, adaptation and mitigation options.
- Hidalgo, M., Barrier, N., Batziakas, S., Billy, M., Blum, S., Chaves, C., et al. (2026). Biodiversity status and drivers of fish juvenile life-stages in the Central-Eastern Mediterranean Sea. In *B-USEFUL: Report on biodiversity status, state-pressure relationships and cumulative impacts across European waters*. Technical University of Denmark. <https://b-useful.eu/library/deliverables>
- Hiddink JG, Valanko S, Batts L, Beukhof ED, Blomqvist M, Bolam S, Calero B, Casini M, Delgado M, Depestele J, Desmidt J, Di Bona G, Di Lorenzo B, Dinesen GE, D'Onghia G, Egekvist J, Fanelli E, Farriols MT, Franceschini G, ... van Denderen PD (2026) Assessment of bottom trawl impacts on the status of seabed communities in European seas. Fish Fish. 27: 285–299. <https://doi.org/10.1111/faf.70054>
- Holsman K, Samhuri J, Cook G, Hazen E, Olsen E, Dillard M, Kasperski S, Gaichas S, Kelble CR, Fogarty M, Andrews K (2017) An ecosystem-based approach to marine risk assessment. Ecosyst. Health Sustain. 3: e1256. <https://doi.org/10.1002/ehs2.1256>
- Holt J, Harle J, Wakelin S, Jardine J, Hopkins J (2022) Why is seasonal density stratification in shelf seas expected to increase under future climate change? Geophys. Res. Lett. 49: e2022GL100448. <https://doi.org/10.1029/2022GL100448>
- Holt J, Hughes S, Hopkins J, Wakelin SL, Penny Holliday N, Dye S, González-Pola C, Hjøllø SS, Mork KA, Nolan G, Proctor R, Read J, Shammon T, Sherwin T, Smyth T, Tattersall G, Ward B, Wiltshire KH (2012) Multi-decadal variability and trends in the temperature of the northwest European continental shelf: A model-data synthesis. Prog. Oceanogr. 106: 96–117. <https://doi.org/10.1016/j.pocean.2012.08.001>
- Horta e Costa B, de Benito-Abelló C, Pike E, Turnbull J, MacCarthy J, Harasta N, Fragkopoulou E, Roessger J, Sullivan-Stack J, Grorud-Colvert K, Gill D, Morgan L, Gonçalves EJ, Zupan M, Gonçalves JMS, Claudet J (2025) Marine protected areas stage of establishment and level of protection are good predictors of their conservation outcomes. Cell Rep. Sustain. 2: 100345. <https://doi.org/10.1016/j.crsus.2025.100345>
- IPBES (2019) Global assessment report on biodiversity and ecosystem services of the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services. [Brondizio



- ES, Settele J, Díaz S, Ngo HT (eds)] IPBES Secretariat, Bonn, Germany. 1148 pages.
<https://doi.org/10.5281/zenodo.3831673>
- IPCC (2022) Summary for Policymakers [Pörtner H-O, Roberts DC, Poloczanska ES, Mintenbeck K, Tignor M, Alegría A, Craig M, Langsdorf S, Löschke S, Möller V, Okem A (eds)]. In: Climate Change 2022: Impacts, Adaptation, and Vulnerability. Contribution of Working Group II to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change [Pörtner H-O, Roberts DC, Tignor M, Poloczanska ES, Mintenbeck K, Alegría A, Craig M, Langsdorf S, Löschke S, Möller V, Okem A, Rama B (eds)]. Cambridge University Press, Cambridge, UK and New York, NY, USA, pp. 3-33. <https://doi.org/10.1017/9781009325844.001>
- Iveša N, Buršić M, Dulčić J (2025) Northernmost Mediterranean record of the silver-cheeked toadfish, *Lagocephalus sceleratus* (Actinopterygii, Tetraodontiformes, Tetraodontidae). Acta Ichthyol. Piscat. 55: 77–81. <https://doi.org/10.3897/aiep.55.146945>
- Jennings, S., & Kaiser, M. J. (1998). The effects of fishing on marine ecosystems. In Advances in marine biology (Vol. 34, pp. 201–352). Elsevier.
- Johnson AF, Gorelli G, Gorelli G, Hiddink JG, Hinz H (2015) Effects of bottom trawling on fish foraging and feeding. Proc. R. Soc. B 282: 20142336. <https://doi.org/10.1098/rspb.2014.2336>
- Jones MC, Cheung WWL (2015) Multi-model ensemble projections of climate change effects on global marine biodiversity. ICES J. Mar. Sci. 72: 741–752. <https://doi.org/10.1093/icesjms/fsu172>
- Jónsson S, Valdimarsson H (2005) 4. Recent developments in oceanographic research in Icelandic waters. In: Developments in Quaternary Sciences. Caseldine C, Russell A, Harðardóttir J, Knudsen Ó (eds) Elsevier, pp. 79–92. [https://doi.org/10.1016/S1571-0866\(05\)80006-5](https://doi.org/10.1016/S1571-0866(05)80006-5)
- Kaiser MJ, Collie JS, Hall SJ, Jennings S, Poiner IR (2002) Modification of marine habitats by trawling activities: prognosis and solutions. Fish Fish. 3: 114–136. <https://doi.org/10.1046/J.1467-2979.2002.00079.X>
- Kamberi E, Hala E, Kule M, Möllmann C (2025) Evidence of climate-driven regime shifts in Adriatic Sea fisheries. Sci. Mar. 89: e108. <https://doi.org/10.3989/scimar.05566.108>
- Katsanevakis S, Belchior C, Zenetos A, Cardoso AC (2013) Invading European seas: Assessing pathways of introduction of marine aliens. Ocean Coast. Manage. 76: 64–74. <https://doi.org/10.1016/j.ocecoaman.2013.02.024>
- Katsanevakis S, Wallentinus I, Zenetos A, Leppäkoski E, Cinar M, Oztürk B, Grabowski M, Golani D, Cardoso AC (2014) Impacts of invasive alien marine species on ecosystem services and biodiversity: A pan-European review. Aquat. Invasions 9: 391–423. <https://doi.org/10.3391/ai.2014.9.4.01>
- Katsanevakis, S., Rilov, G., & Edelist, D. (2018). Impacts of marine invasive alien species on European fisheries and aquaculture—Plague or boon? In *Engaging Marine Scientists and Fishers to Share Knowledge and Perceptions—Early Lessons* (pp. 125–132). CIESM Publishers.
- Kavadas S, Maina I, Damalas D, Dokos I, Pantazi M, Vassilopoulou V (2015) Multi-criteria decision analysis as a tool to extract fishing footprints and estimate fishing pressure: Application to small-scale coastal fisheries and implications for management in the context of the Maritime Spatial Planning Directive. Mediterr. Mar. Sci. 16: 294–304. <https://doi.org/10.12681/mms.1087>
- Kavadas, S., Chamodrakas, I., Bitetto, I., Zupa, W., Maina, I., Ligas, A., et al. (2025). *Final report of the RDBFIS: Hosting, maintenance and further development of the regional database for the*



- Mediterranean and the Black Sea*. Publications Office of the European Union.
<https://doi.org/10.2926/5619525>
- Kay, S. (2020). *Marine biogeochemistry data for the Northwest European Shelf and Mediterranean Sea from 2006 up to 2100 derived from climate projections* [Data set]. Copernicus Climate Change Service Climate Data Store. <https://doi.org/10.24381/cds.dcc9295c>
- Kenny AJ, Jenkins C, Wood D, Bolam SG, Mitchell P, Scougal C, Judd A (2018) Assessing cumulative human activities, pressures, and impacts on North Sea benthic habitats using a biological traits approach. *ICES J. Mar. Sci.* 75: 1080–1092. <https://doi.org/10.1093/icesjms/fsx205>
- Kenny AJ, Skjoldal HR, Engelhard GH, Kershaw PJ, Reid JB (2009) An integrated approach for assessing the relative significance of human pressures and environmental forcing on the status of Large Marine Ecosystems. *Prog. Oceanogr.* 81: 132–148.
<https://doi.org/10.1016/j.pocean.2009.04.007>
- Kleitou P, Crocetta F, Giakoumi S, Giovos I, Hall-Spencer JM, Kalogirou S, Kletou D, Moutopoulos DK, Rees S (2021) Fishery reforms for the management of non-indigenous species. *J. Environ. Manage.* 280: 111690. <https://doi.org/10.1016/j.jenvman.2020.111690>
- Kleitou P, Rees SE, Kletou D, Harris HE, Cai LL, Green S, Hadjioannou L, Savva I, Giovos I, Jimenez C, et al. (2024) Marine protected areas can increase the abundance of invasive lionfish (*Pterois miles*). *Conserv. Sci. Pract.* 6: e13147. <https://doi.org/10.1111/csp2.13147>
- Kuehn, B. (2023). *Tutorial—Ways to bias correct climate projections* [Software]. Figshare.
<https://doi.org/10.6084/m9.figshare.23514618.v1>
- Lam VWY, Allison EH, Bell JD, Blythe J, Cheung WWL, Frölicher TL, Gasalla MA, Sumaila UR (2020) Climate change, tropical fisheries and prospects for sustainable development. *Nat. Rev. Earth Environ.* 1: 440–454. <https://doi.org/10.1038/s43017-020-0071-9>
- Lawlor JA, Comte L, Grenouillet G, Lenoir J, Baecher JA, Bandara RMWJ, Bertrand R, Chen I-C, Diamond SE, Lancaster LT, Moore N, Muriene J, Oliveira BF, Pecl GT, Pinsky ML, Rolland J, Rubenstein M, Scheffers BR, Thompson LM, van Amerom B, Villalobos F, Weiskopf SR, Sunday J (2024) Mechanisms, detection and impacts of species redistributions under climate change. *Nat. Rev. Earth Environ.* 5: 351–368. <https://doi.org/10.1038/s43017-024-00527-z>
- Lawrence DJ, Runyon AN, Gross JE, Schuurman GW, Miller BW (2021) Divergent, plausible, and relevant climate futures for near- and long-term resource planning. *Clim. Change* 167: 38.
<https://doi.org/10.1007/S10584-021-03169-Y>
- Lawrence DJ, Runyon AN, Gross JE, Schuurman GW, Miller BW (2021) Divergent, plausible, and relevant climate futures for near- and long-term resource planning. *Clim. Change* 167: 38.
<https://doi.org/10.1007/s10584-021-03169-y>
- Le Luherne E, Pawlowski L, Robert M (2024) Northeast Atlantic species distribution shifts over the last two decades. *Global Change Biol.* 30: e17383. <https://doi.org/10.1111/gcb.17383>
- Lindmark M, Karlsson M, Gårdmark A (2023) Larger but younger fish when growth outpaces mortality in heated ecosystem. *eLife* 12. <https://doi.org/10.7554/elife.82996>
- Link JS, Watson RA (2019) Global ecosystem overfishing: Clear delineation within real limits to production. *Sci. Adv.* 5: eaav0474. <https://doi.org/10.1126/sciadv.aav0474>
- Lionello P, Scarascia L (2018) The relation between climate change in the Mediterranean region and global warming. *Reg. Environ. Change* 18: 1481–1493. <https://doi.org/10.1007/S10113-018-1290-1>



- Loya-Cancino KF, Ángeles-González LE, Yañez-Arenas C, Ibarra-Cerdeña CN, Velázquez-Abunader I, Aguilar-Perera A, Vidal-Martínez VM (2023) Predictions of current and potential global invasion risk in populations of lionfish (*Pterois volitans* and *Pterois miles*) under climate change scenarios. *Mar. Biol.* 170: 27. <https://doi.org/10.1007/s00227-023-04174-8>
- Madec G, Bell M, Benshila R, Blaker A, Boudrallé-Badie R, Bricaud C, Bruciaferri D, Carneiro D, Castrillo M, Calvert D, Chanut J, Clementi E, Coward A, Lavergne C de, Dobricic S, Epicoco I, Éthé C, Fiedler E, Ford D, Furner R, Ganderton J, Graham T, Harle J, Hutchinson K, Iovino D, King R, Lea D, Levy C, Lovato T, Maisonnave E, Mak J, Sanchez JMC, Martin M, Martin N, Martins D, Masson S, Mathiot P, Mele F, Mocavero S, Moulin A, Müller S, Nurser G, Oddo P, Paronuzzi S, Paul J, Peltier M, Person R, Rousset C, Rynders S, Samson G, Schroeder D, Storkey D, Storto A, Téchené S, Vancoppenolle M, Wilson C (2024) NEMO Ocean Engine Reference Manual.
- Magurran AE, Dornelas M, Moyes F, Gotelli NJ, McGill B (2015) Rapid biotic homogenization of marine fish assemblages. *Nat. Commun.* 6: 8405. <https://doi.org/10.1038/ncomms9405>
- Malmberg SA, Valdimarsson H (2003) Hydrographic conditions in Icelandic waters, 1990–2000. In: *Hydrographical Variability in the ICES Area, 1990–1999*. ICES Ma. Sci. Symp. 219: 50–60. <https://doi.org/10.17895/ices.pub.19271738>
- Mann HB (1945) Nonparametric tests against trend. *Econometrica* 13: 245–259. <https://doi.org/10.2307/1907187>
- Mannino AM, Balistreri P, Deidun A (2017) The marine biodiversity of the Mediterranean Sea in a changing climate: The impact of biological invasions. In *Mediterranean Identities – Environment, Society, Culture*. InTech. <https://doi.org/10.5772/intechopen.69214>
- Marbà N, Jordà G, Agustí S and Duarte CM (2016) Evidences of impacts of climate change on Mediterranean biota. *Front. Mar. Sci.* 3: 3. <https://doi.org/10.3389/fmars.2016.00003>
- Marguin A, Bussotti S, Guidetti P, Rossi F (2025) A systematic review of fishing impacts on the trophic level of fish populations and assemblages in the Mediterranean Sea. *Front. Mar. Sci.* 12: 1489965. <https://doi.org/10.3389/fmars.2025.1489965>
- McLean M, Mouillot D, Lindegren M, Villéger S, Engelhard G, Murgier J, Auber A (2019) Fish communities diverge in species but converge in traits over three decades of warming. *Global Change Biol.* 25: 3972–3984. <https://doi.org/10.1111/gcb.14785>
- McLean MJ, Auber A, Graham NAJ, Dulvy NK, Mouillot D (2019) Functional reorganization of marine fish nurseries under climate warming. *Glob. Change Biol.* 25: 660–674. <https://doi.org/10.1111/gcb.14501>
- Mecklenburg CW, Møller PR, Steinke D (2011) Biodiversity of arctic marine fishes: taxonomy and zoogeography. *Mar. Biodiv.* 41: 109–140. <https://doi.org/10.1007/s12526-010-0070-z>
- Mitchell E, Dominguez Almela V (2025) Modelling the rise of invasive lionfish in the Mediterranean. *Mar. Biol.* 172: 18. <https://doi.org/10.1007/s00227-024-04580-6>
- Moilanen A, Kohonen I, Lehtinen P, Kivistö I, Jalkanen J, Virtanen EA, Kujala H (2024) Zonation 5 v2.0; User manual. <https://zonationteam.github.io/Zonation5/publications.html>
- Moilanen A, Lehtinen P, Kohonen I, Jalkanen J, Virtanen EA, Kujala H (2022) Novel methods for spatial prioritization with applications in conservation, land use planning and ecological impact avoidance. *Methods Ecol. Evol.* 13: 1062–1072. <https://doi.org/10.1111/2041-210X.13819>



- Oriol LE, Jorns J, Channell K, Rood RB (2024) Scenario planning for climate adaptation and management: A high-level synthesis and standardization of methodology. *Front. Clim.* 6: 1415070. <https://doi.org/10.3389/fclim.2024.1415070>
- Ouled-Cheikh J, Coll M, Cardona L, Steenbeek J, Ramírez F (2022) Fisheries-enhanced pressure on Mediterranean regions and pelagic species already impacted by climate change. *Elementa* 10: 00028. <https://doi.org/10.1525/elementa.2022.00028>
- Ovaskainen O, Tikhonov G, Norberg A, Guillaume Blanchet F, Duan L, Dunson D, Roslin T, Abrego N (2017) How to make more out of community data? A conceptual framework and its implementation as models and software. *Ecol. Lett.* 20: 561–576. <https://doi.org/10.1111/ele.12757>
- Ovaskainen, O., & Abrego, N. (2020). *Joint species distribution modelling: With applications in R*. Cambridge University Press. <https://doi.org/10.1017/9781108591720>
- Papantoniou G, Sgardeli V, Vassilopoulou V and Tsagarakis K (2025) Investigating the potential impacts and interactive effects of climate warming and multi-gear fishing on the Eastern Ionian Sea ecosystem using EwE and ecological indicators. *Front. Mar. Sci.* 12: 1621603. <https://doi.org/10.3389/fmars.2025.1621603>
- Piet GJ, Grundlehner A, Jongbloed R, Tamis J, de Vries P (2023) SCAIRM: A spatial cumulative assessment of impact risk for management. *Ecol. Indic.* 157: 111157. <https://doi.org/10.1016/j.ecolind.2023.111157>
- Pinnegar JK, Hamon KG, Kreiss CM, Tabeau A, Rybicki S, Papathanasopoulou E, Engelhard GH, Eddy TD, Peck MA (2021) Future socio-political scenarios for aquatic resources in Europe: a common framework based on Shared-Socioeconomic-Pathways (SSPs). *Front. Mar. Sci.* 7: 568219. <https://doi.org/10.3389/fmars.2020.568219>
- Pinsky ML, Worm B, Fogarty MJ, Sarmiento JL, Levin SA (2013) Marine taxa track local climate velocities. *Science* 341: 1239–1242. <https://doi.org/10.1126/science.1239352>
- Pita I, Mouillot D, Moullec F, Shin YJ (2021) Contrasted patterns in climate change risk for Mediterranean fisheries. *Glob. Change Biol.* 27: 5920–5933. <https://doi.org/10.1111/gcb.15814>
- Polo J, López-López L, Engelhard GH, Punzón A, Hidalgo M, Rutterford LA, Bariáin MS, González-Irusta JM, Esteban A, García E, Vivas M, Pecuchet L (2025) Trait-based indicators of marine communities' sensitivity to climate change and fishing. *Divers. Distrib.* 1: e13959. <https://doi.org/10.1111/ddi.13959>
- Poloczanska ES, Brown CJ, Sydeman WJ, Kiessling W, Schoeman DS, Moore PJ, Brander K, Bruno JF, Buckley LB, Burrows MT, Duarte CM, Halpern BS, Holding J, Kappel CV, O'Connor MI, Pandolfi JM, Parmesan C, Schwing F, Thompson SA, Richardson AJ (2013) Global imprint of climate change on marine life. *Nat. Clim. Change* 3: 919–925. <https://doi.org/10.1038/nclimate1958>
- Por, F. D. (1971). One hundred years of Suez Canal—A century of Lessepsian migration: Retrospect and viewpoints. *Systematic Biology*, 20, 138–159. <https://doi.org/10.2307/2412054>
- Quattrocchi F, Bono G, Cattano C, Fiorentino F, Lauria V, Calò A, Milazzo M, Garofalo G (2026) Warming-driven biotic differentiation of demersal fish across depths in the central Mediterranean Sea. *Mar. Environ. Res.* 213: 107627. <https://doi.org/10.1016/j.marenvres.2025.107627>
- Ragheb E (2024) A view on climate change and its impact on the Mediterranean fisheries. *Blue Econ.* J. 2: 5. <https://doi.org/10.57241/2805-2994.1020>



- Ramírez F, Coll M, Navarro J, Bustamante J, Green AJ (2018) Spatial congruence between multiple stressors in the Mediterranean Sea may reduce its resilience to climate impacts. *Sci. Rep.* 8: 14871. <https://doi.org/10.1038/s41598-018-33237-w>
- Rantanen M, Karpechko AY, Lipponen A, Nordling K, Hyvärinen O, Ruosteenoja K, Vihma T, Laaksonen A (2022) The Arctic has warmed nearly four times faster than the globe since 1979. *Commun. Earth Environ.* 3: 168. <https://doi.org/10.1038/s43247-022-00498-3>
- Reale M, Cossarini G, Lazzari P, Lovato T, Bolzon G, Masina S, Solidoro C, Salon S (2022) Acidification, deoxygenation, and nutrient and biomass declines in a warming Mediterranean Sea. *Biogeosciences* 19: 4035–4065. <https://bg.copernicus.org/articles/19/4035/2022/>
- Rijnsdorp AD, Bolam SG, Garcia C, Hiddink JG, Hintzen NT, van Denderen PD, van Kooten T (2018) Estimating sensitivity of seabed habitats to disturbance by bottom trawling based on the longevity of benthic fauna. *Ecol. Appl.* 28: 1302–1312. <https://doi.org/10.1002/EAP.1731>
- Rijnsdorp AD, Peck MA, Engelhard GH, Möllmann C, Pinnegar JK (2009) Resolving the effect of climate change on fish populations. *ICES. J. Mar. Sci.* 66: 1570–1583. <https://doi.org/10.1093/icesjms/fsp056>
- Roberts CM, O’Leary BC, McCauley DJ, Cury PM, Duarte CM, Lubchenco J, Pauly D, Sáenz-Arroyo A, Sumaila UR, Wilson RW, Worm B, Castilla JC (2017) Marine reserves can mitigate and promote adaptation to climate change. *Proc. Natl. Acad. Sci. U.S.A.* 114: 6167–6175. <https://doi.org/10.1073/pnas.1701262114>
- Robinson C, Sabine C, Isensee K (2025) Providing solutions to mitigate, adapt, and build resilience to the effects of climate change. *ICES. J. Mar. Sci.* 82: fsae170. <https://doi.org/10.1093/icesjms/fsae170>
- Rozemeijer MJC, Bartilotti C, Batziakas S, Blum S, Consiglio A, Fock H, Gillie ER, Golin F, Henriques S, Hidalgo M, Jonsdottir IG, Lindegren M, Lobo Arteaga J, Merigot B, Moullec F, Moura T, Pecuchet L, Peristeraki N, Polo J, Puerta P, Rutterford LA, Spedicato MT, Tiano J, Vasconcelos R, Zupa W, Engelhard GH (2025) B-USEFUL. Assessing community-level risks of marine biodiversity and habitats in different European regional seas. Technical University of Denmark. <https://b-useful.eu/library/deliverables/>
- Rubenstein MA, Weiskopf SR, Bertrand R, Carter SL, Comte L, Eaton MJ, Johnson CG, Lenoir J, Lynch AJ, Miller BW, Morelli TL, Rodriguez MA, Terando A, Thompson LM (2023) Climate change and the global redistribution of biodiversity: Substantial variation in empirical support for expected range shifts. *Environ. Evid.* 12: 7. <https://doi.org/10.1186/s13750-023-00296-0>
- Rubino C, Adelfio G, Abbruzzo A, Bosch-Belmar M, Di Lorenzo M, Fiorentino F, Gancitano V, Colloca F, Milisenda G (2024) Exploring the effects of temperature on demersal fish communities in the Central Mediterranean Sea using INLA-SPDE modeling approach. *Environ. Ecol. Stat.* 31: 629–647. <https://doi.org/10.1007/s10651-024-00609-7>
- Rutterford LA, Simpson SD, Bogstad B, Devine JA, Genner MJ (2023) Sea temperature is the primary driver of recent and predicted fish community structure across Northeast Atlantic shelf seas. *Global Change Biol.* 29: 2510–2521. <https://doi.org/10.1111/gcb.16633>
- Rutterford LA, Simpson SD, Jennings S, Johnson MP, Blanchard JL, Schön P-J, Sims DW, Tinker J, Genner MJ (2015) Future fish distributions constrained by depth in warming seas. *Nat. Clim. Change* 5: 569–573. <https://doi.org/10.1038/nclimate2607>
- Sailley SF, Catalan IA, Batsleer J, Bossier S, Damalas D, Hansen C, Huret M, Engelhard G, Hamon K, Kay S, Maynou F, Nielsen JR, Ospina-Álvarez A, Pinnegar J, Poos JJ, Sgardeli V, Peck MA (2025)



- Multiple models of European marine fish stocks: Regional winners and losers in a future climate. *Global Change Biol.* 31: e70149. <https://doi.org/10.1111/gcb.70149>
- Sanz-Martín M, Hidalgo M, Puerta P, Molinos JG, Zamanillo M, Brito-Morales I, González-Irusta JM, Esteban A, Punzón A, García-Rodríguez E, Vivas M, López-López L (2024) Climate velocity drives unexpected southward patterns of species shifts in the Western Mediterranean Sea. *Ecol. Indic.* 160: 111741. <https://doi.org/10.1016/j.ecolind.2024.111741>
- Schmidt K, Birchill AJ, Atkinson A, Brewin RJW, Clark JR, Hickman AE, Johns DG, Lohan MC, Milne A, Pardo S, Polimene L, Smyth TJ, Tarran GA, Widdicombe CE, Woodward EMS, Ussher SJ (2020) Increasing picocyanobacteria success in shelf waters contributes to long-term food web degradation. *Global Change Biol.* 26: 5574–5587. <https://doi.org/10.1111/gcb.15161>
- Shephard S, Fung T, Houle JE, Farnsworth KD, Reid DG, Rossberg AG (2012) Size-selective fishing drives species composition in the Celtic Sea. *ICES. J. Mar. Sci.* 69: 223–234. <https://doi.org/10.1093/icesjms/fsr200>
- Simonarson LA, Eiríksson J, Knudsen KL (2021) The marine realm around Iceland: A review of biological research. In: Pacific - Atlantic Mollusc Migration: Pliocene Inter-Ocean Gateway Archives on Tjörnes, North Iceland. Eiríksson J, Simonarson LA (eds) Springer International Publishing, Cham, pp. 13–35. https://doi.org/10.1007/978-3-030-59663-7_2
- Sólmundsson J, Sigurðsson ÓÁ, Jónsdóttir IG, Jónsson S (2025) How different life-history strategies respond to changing environments: A multi-decadal study of groundfish communities. *Sci. Rep.* 15: 20441. <https://doi.org/10.1038/s41598-025-02204-7>
- Spedicato MT, Massutí E, Mérigot B, Tserpes G, Jadaud A, Relini G (2019) The MEDITS trawl survey specifications in an ecosystem approach to fishery management. *Sci. Mar.* 83 S1: 9–20. <https://doi.org/10.3989/scimar.04915.11X>
- Stefánsdóttir L, Sólmundsson J, Marteinsdóttir G, Kristinsson K, Jonasson JP (2010) Groundfish species diversity and assemblage structure in Icelandic waters during recent years of warming. *Fish. Oceanogr.* 19: 42–62. <https://doi.org/10.1111/j.1365-2419.2009.00527.x>
- Teruzzi, A., Di Biagio, V., Feudale, L., Bolzon, G., Lazzari, P., Salon, S., Coidessa, G., & Cossarini, G. (2021). *Mediterranean Sea biogeochemical reanalysis (CMEMS MED-Biogeochemistry, MedBFM3 system) (Version 1)* [Data set]. Copernicus Marine Environment Monitoring Service. <https://doi.org/10.48670/mds-00374>
- Thompson MSA, Couce E, Schratzberger M, Lynam CP (2023) Climate change affects the distribution of diversity across marine food webs. *Global Change Biol.* 29: 6606–6619. <https://doi.org/10.1111/gcb.16881>
- Tikhonov G, Opedal ØH, Abrego N, Lehikoinen A, De Jonge MMJ, Oksanen J, Ovaskainen O (2020) Joint species distribution modelling with the R-package HMSC. *Methods Ecol. Evol.* 11: 442–447. <https://doi.org/10.1111/2041-210X.13345>
- Tittensor DP, Mora C, Jetz W, Lotze HK, Ricard D, Berghe EV, Worm B (2010) Global patterns and predictors of marine biodiversity across taxa. *Nature* 466: 1098–1101. <https://doi.org/10.1038/nature09329>
- Townhill BL, Couce E, Tinker J, Kay S, Pinnegar JK (2023) Climate change projections of commercial fish distribution and suitable habitat around north western Europe. *Fish Fish.* 24: 848–862. <https://doi.org/10.1111/faf.12773>



- Tsirintanis K, Azzurro E, Crocetta F, Dimiza M, Froglija C, Gerovasileiou V, Langeneck J, Mancinelli G, Rosso A, Stern N, Triantaphyllou M, Tsiamis K, Turon X, Verlaque M, Zenetos A, Katsanevakis S (2022) Bioinvasion impacts on biodiversity, ecosystem services, and human health in the Mediterranean Sea. *Aquat. Invasions* 17: 308-352. <https://doi.org/10.3391/ai.2022.17.3.01>
- Ulman A, Ali FZ, Harris HE, Adel M, Mabruk SAAA, Bariche M, Candelmo AC, Chapman JK, Çiçek BA, Clements KR, et al. (2022) Lessons from the Western Atlantic lionfish invasion to inform management in the Mediterranean. *Front. Mar. Sci.* 9: 865162. <https://doi.org/10.3389/fmars.2022.865162>
- Ulman A, Yildiz T, Demirel N, Canak O, Yemişken E, Pauly D (2021) The biology and ecology of the invasive silver-cheeked toadfish (*Lagocephalus sceleratus*), with emphasis on the Eastern Mediterranean. *NeoBiota* 68: 145–175. <https://doi.org/10.3897/neobiota.68.71767>
- Valdimarsson H, Astthorsson OS, Palsson J (2012) Hydrographic variability in Icelandic waters during recent decades and related changes in distribution of some fish species. *ICES J. Mar. Sci.* 69: 816–825. <https://doi.org/10.1093/icesjms/fss027>
- Valdimarsson H, Malmberg S-A (1999) Near-surface circulation in Icelandic waters derived from satellite tracked drifters. *Rit Fiskideildar* 16: 23-39.
- Valtýsson HP, Jónsson S (2018) Impacts of a changing climate on Icelandic marine stocks. In: Mueter FJ, Baker MR, Dressel SC, Hollowed AB (eds) *Impacts of a Changing Environment on the Dynamics of High-latitude Fish and Fisheries*. Alaska Sea Grant, University of Alaska Fairbanks. <https://doi.org/10.4027/icedhlff.2018.01>
- van Ruijven BJ, Levy MA, Agrawal A, Biermann F, Birkmann J, Carter TR, Ebi KL, Garschagen M, Jones B, Jones R, Kemp-Benedict E, Kok M, Kok K, Lemos MC, Lucas PL, Orlove B, Pachauri S, Parris TM, Patwardhan A, ... Schweizer VJ (2013) Enhancing the relevance of Shared Socioeconomic Pathways for climate change impacts, adaptation and vulnerability research. *Clim. Change* 122: 481–494. <https://doi.org/10.1007/s10584-013-0931-0>
- Vilhjálmsón H (1997) Climatic variations and some examples of their effects on the marine ecology of Icelandic and Greenland waters, in particular during the present century. *Marine and Freshwater Research Institute of Iceland. Rit Fiskideildar* 15: 1-63.
- Virtanen EA, Viitasalo M, Lappalainen J, Moilanen A (2018) Evaluation, gap analysis, and potential expansion of the Finnish marine protected area network. *Front. Mar. Sci.* 5: 402. <https://doi.org/10.3389/fmars.2018.00402>
- Völz V, Hinkel J (2023) Climate learning scenarios for adaptation decision analyses: Review and classification. *Clim. Risk Manag.* 40: 100512. <https://doi.org/10.1016/j.crm.2023.100512>
- Yool A, Popova EE, Anderson TR (2011) Medusa-1.0: a new intermediate complexity plankton ecosystem model for the global domain. *Geosci. Model Dev.* 4: 381–417. <https://doi.org/10.5194/gmd-4-381-2011>
- Zenetos A, Albano PG, López Garcia E, Stern N, Tsiamis K, Galanidi M (2022) Established non-indigenous species increased by 40% in 11 years in the Mediterranean Sea. *Mediterr. Mar. Sci.* 23: 196–212. <https://doi.org/10.12681/mms.29106>
- Zupa W, Carbonara P, Bitetto I, Casini M, Maiorano P, D’Onghia G, Isajlovic I, Spedicato MT, Van Hoey G, Rindorf A (2025) Relative benthic status guides sustainable trawl management in the Adriatic-Ionian Seas. *ICES J. Mar. Sci.* 82: 148. <https://doi.org/10.1093/ICESJMS/FSAF148>

A. Appendix: Mediterranean Sea

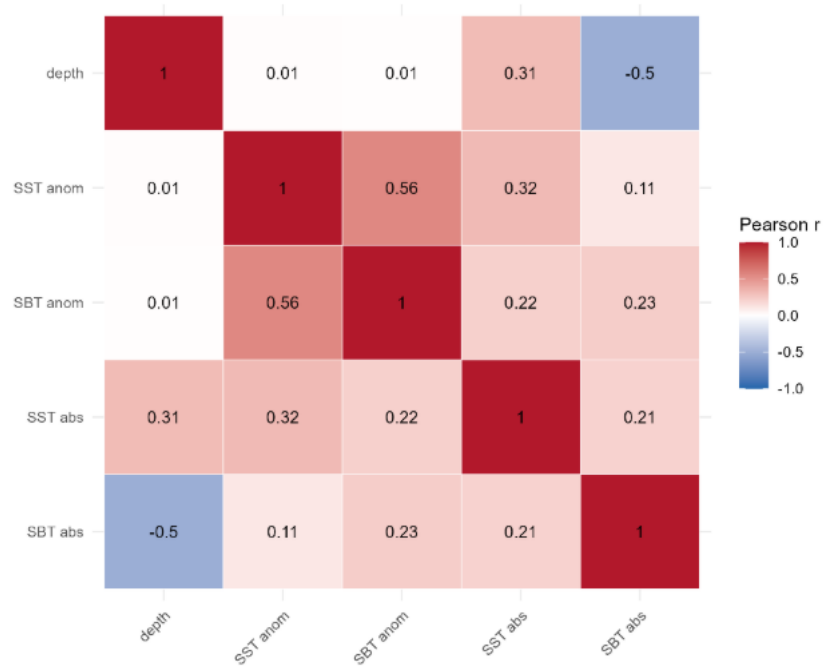


Figure A-1. Pairwise Pearson correlation matrix of the environmental predictors included in the GAM modelling framework.

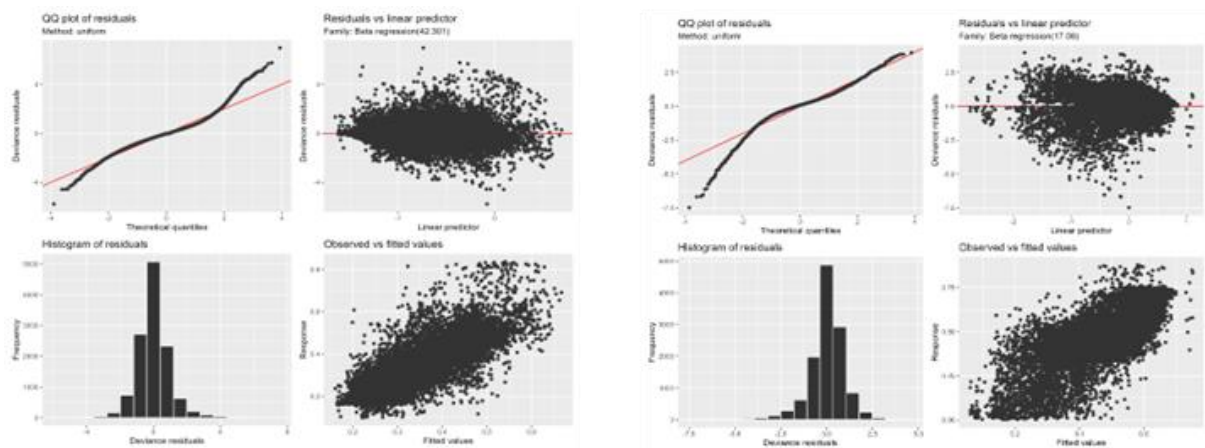


Figure A-2. Residual inspection of the S_{CC} (left panel) and S_{FP} (right panel) GAM models, including residual distributions, fitted-versus-observed relationships, and QQ-plots.

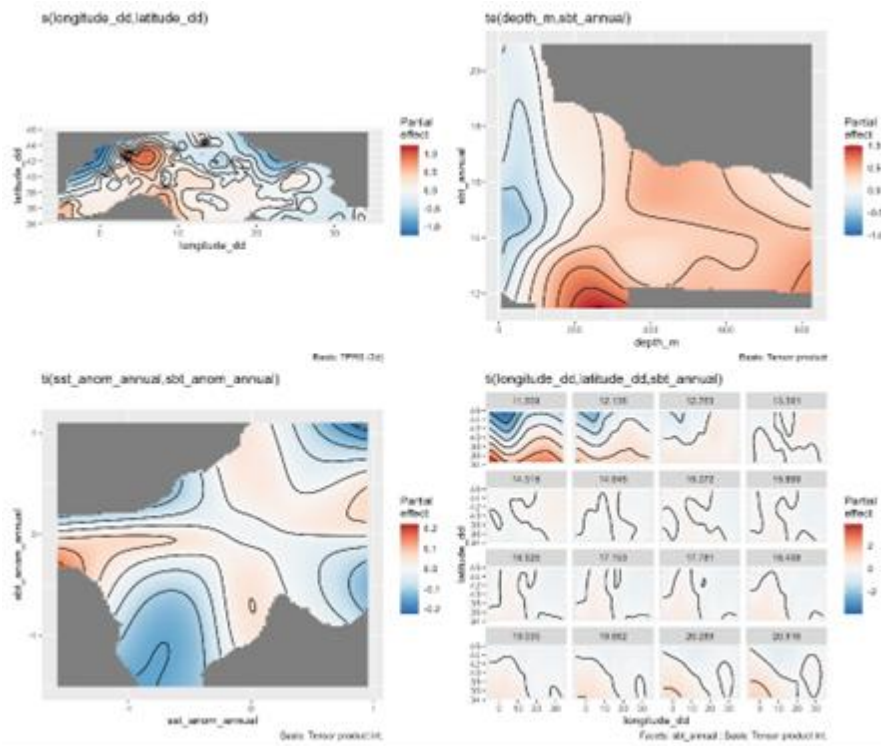


Figure A-3. Partial-effect smoothers of the S_{CC} GAM, illustrating the nonlinear effects of spatial, bathymetric, and thermal predictors included in the final model formulation.

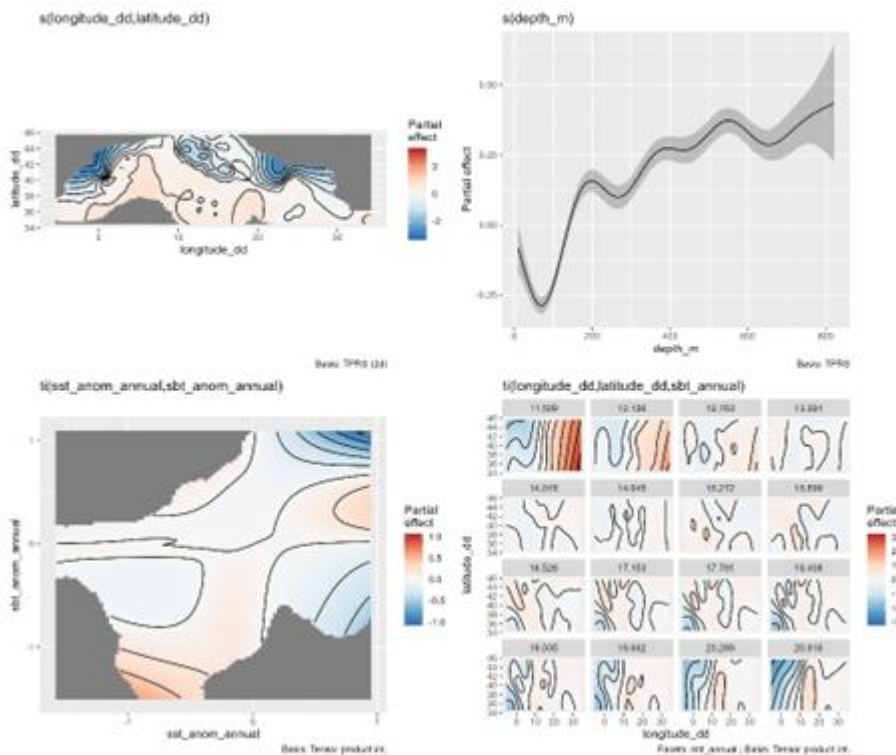


Figure A-4. Partial-effect smoothers of the S_{FP} GAM, illustrating the nonlinear effects of spatial, bathymetric, and thermal predictors included in the final model formulation.

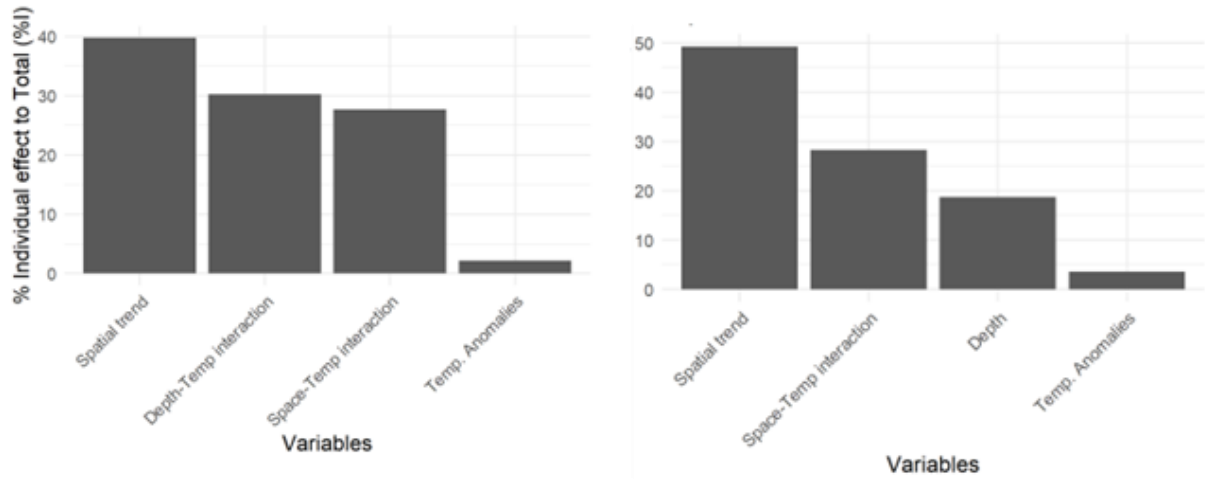


Figure A-5. Variance partitioning of S_{CC} (left panel), and S_{FP} (right panel) GAM models, showing the relative contribution of predictor groups to the total explained deviance.

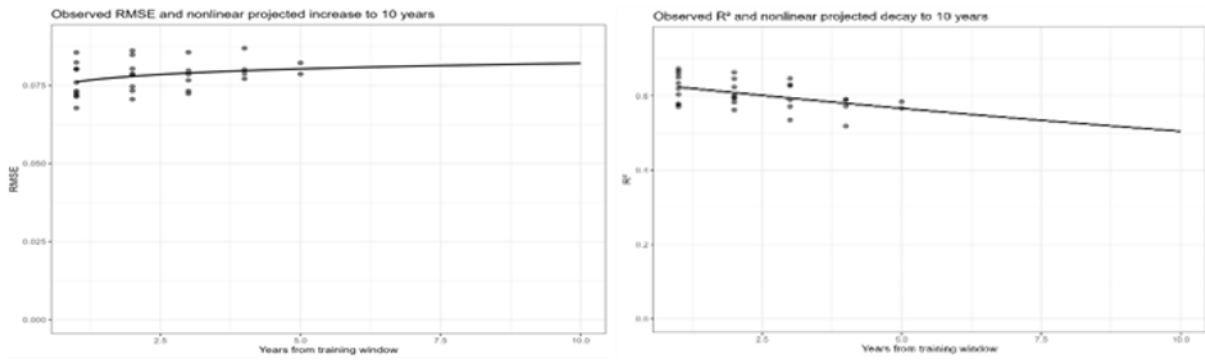


Figure A-6. Sliding-window temporal validation of the S_{CC} model. Left panel: observed RMSE values and projected nonlinear variation up to 10 years beyond the calibration period. Right panel: R^2 and projected nonlinear variation up to 10 years beyond the calibration period.

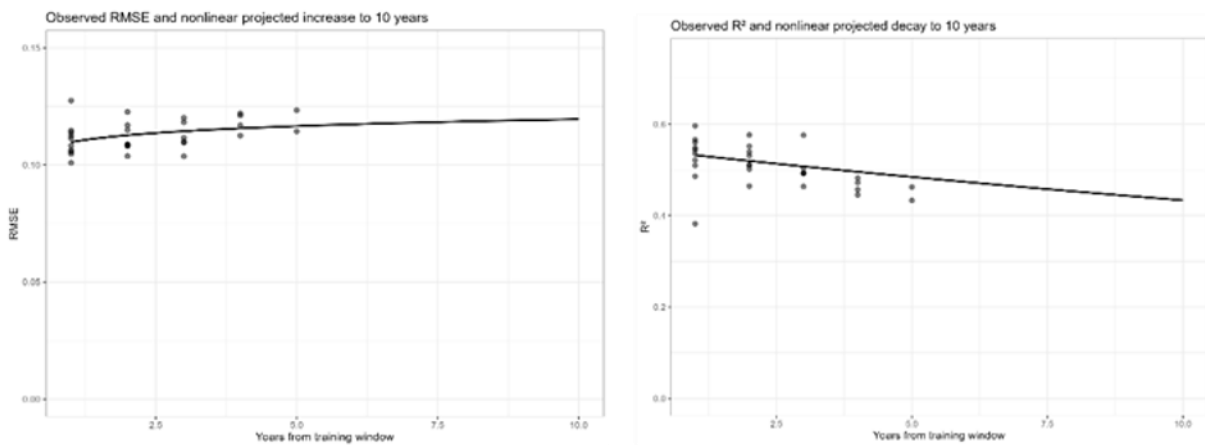


Figure A-7. Sliding-window temporal validation of the S_{FP} model. Left panel: observed RMSE values and projected nonlinear variation up to 10 years beyond the calibration period. Right panel: R^2 and projected nonlinear variation up to 10 years beyond the calibration period.

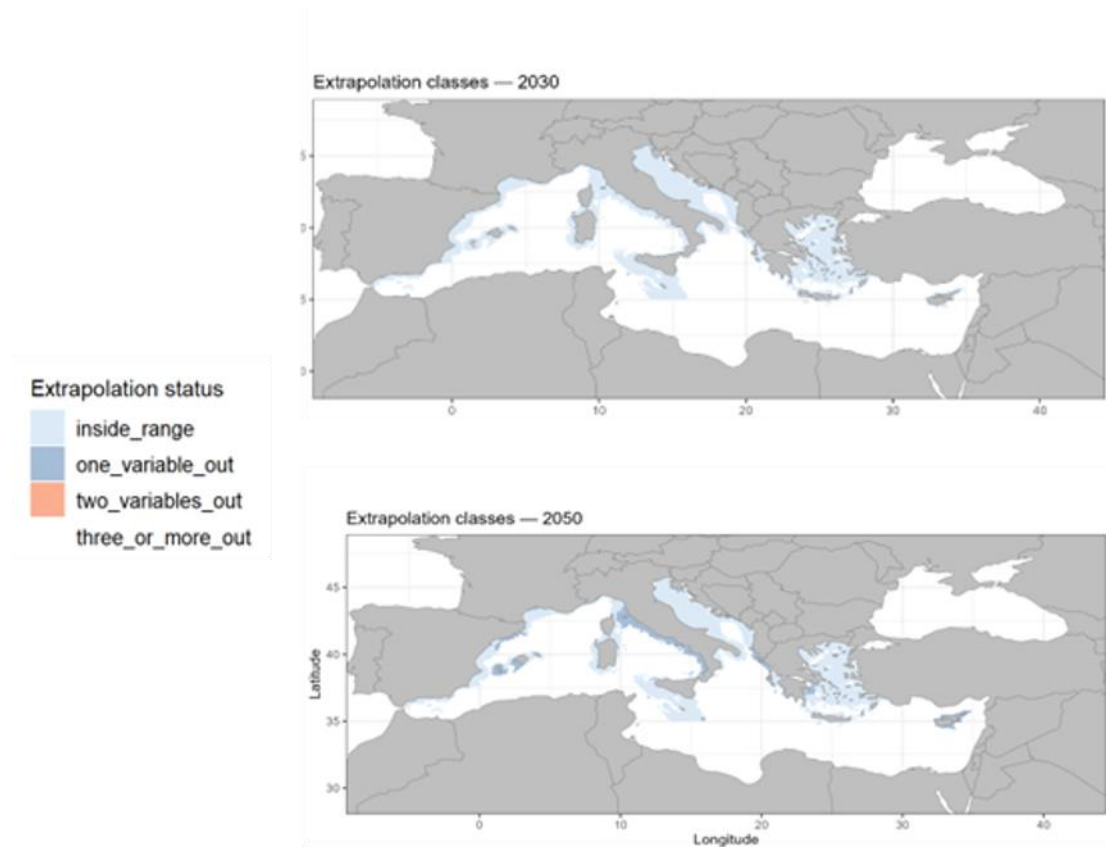


Figure A-8. Spatial extrapolation-risk maps for the S_{cc} model for selected future periods (2030 and 2050), showing the proportion of environmental predictors exceeding the calibration range of the fitted GAM.

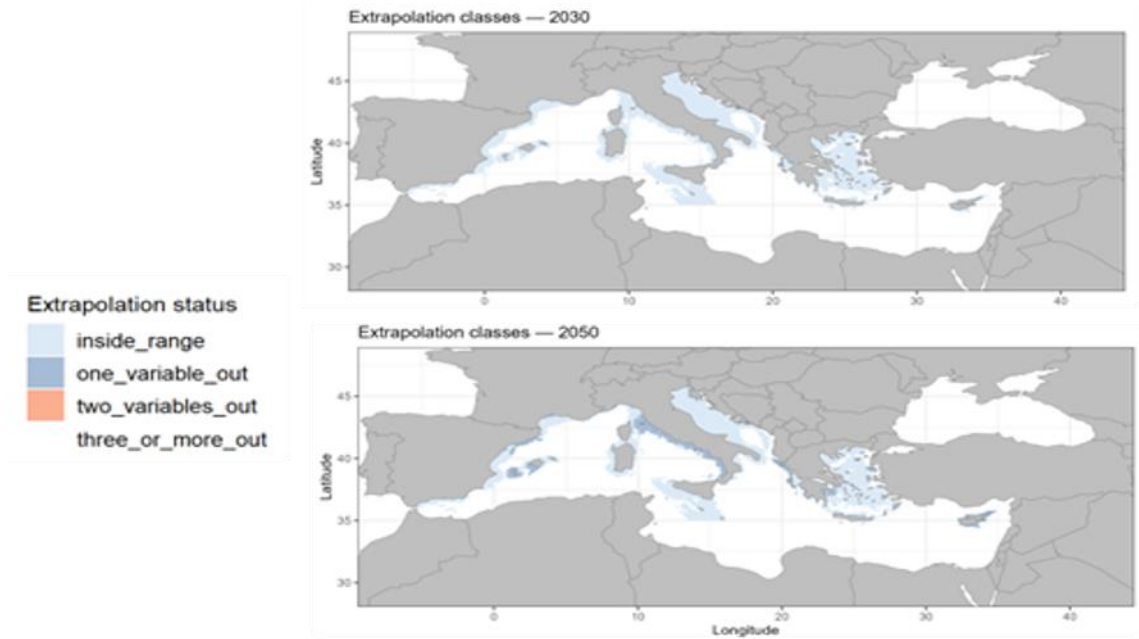


Figure A-9. Spatial extrapolation-risk maps for the S_{FP} model for selected future periods (2030 and 2050), showing the proportion of environmental predictors exceeding the calibration range of the fitted GAM.

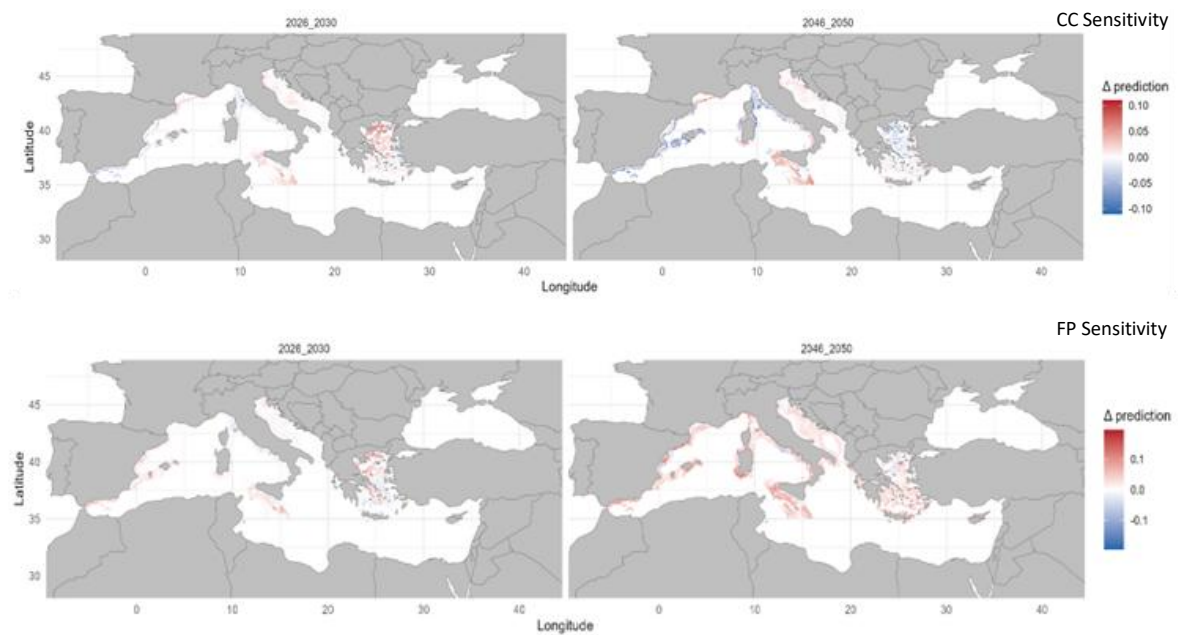


Figure A-10. Delta predictions for the future periods relative to the baseline period (2012–2021) of S_{CC} (upper panel) and S_{FP} (lower panel), illustrating the magnitude and spatial distribution of projected changes.

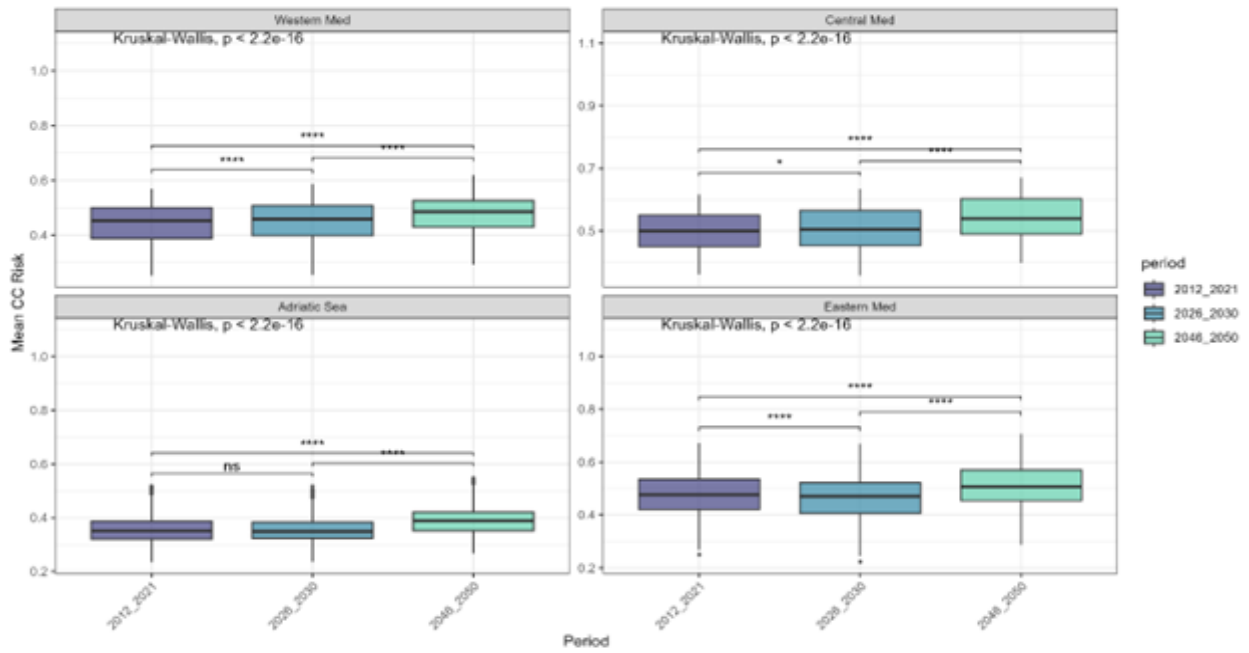


Figure A-11. Boxplots of the distribution of R_{CC} predictions across temporal periods and Mediterranean subregions, illustrating regional differences and temporal shifts in projected exposure-weighted vulnerability. The statistical analyses were based on the Kruskal-Wallis test, followed by pairwise Wilcoxon rank-sum comparison.

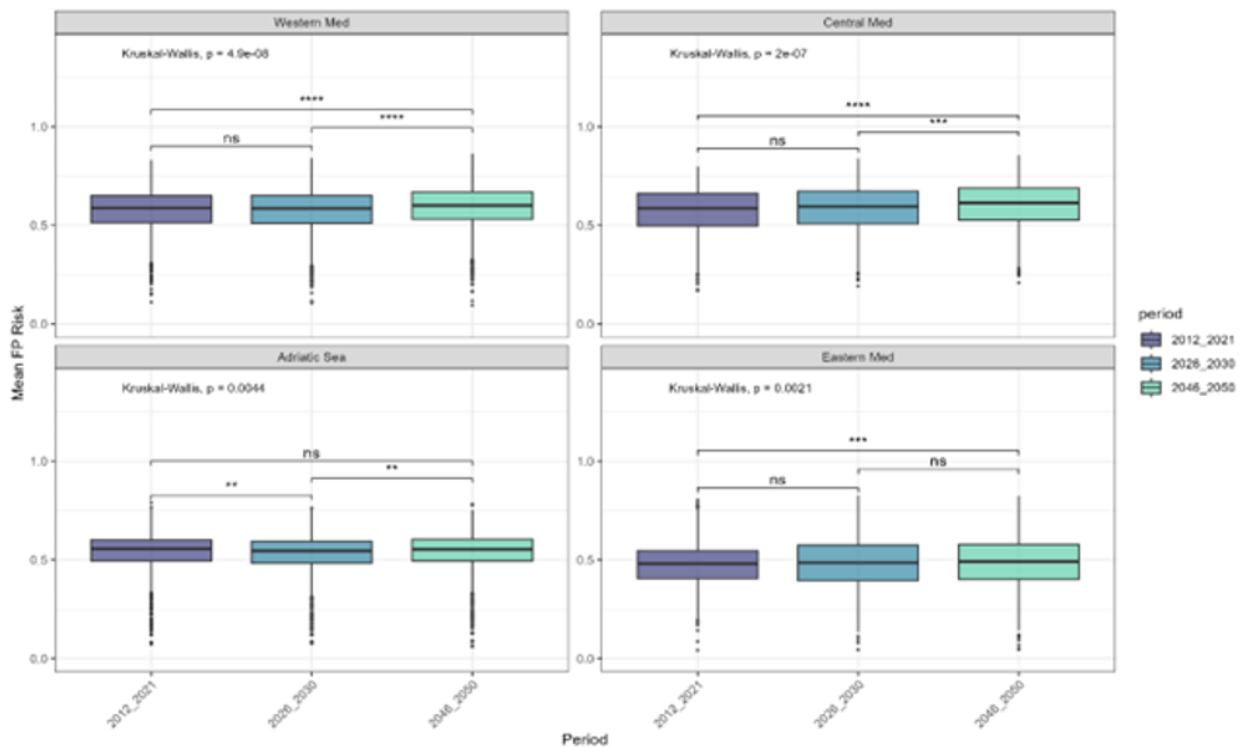


Figure A-12. Boxplots of the distribution of R_{FP} predictions across temporal periods and Mediterranean subregions, illustrating regional differences and temporal shifts in projected exposure-weighted vulnerability. The statistical analyses were based on the Kruskal-Wallis test, followed by pairwise Wilcoxon rank-sum comparison.

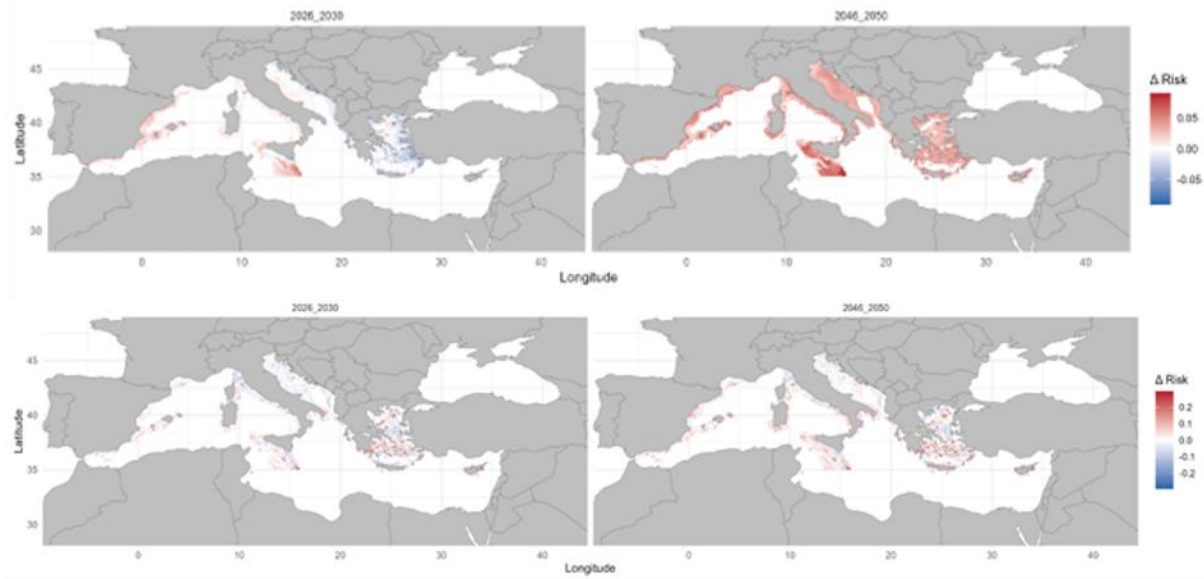


Figure A-13. Delta projections of R_{CC} (upper panel) and R_{FP} (lower panel) for future periods relative to the baseline period (2012–2021), highlighting spatial patterns of projected risk intensification (red) and decline (blue) across the Mediterranean Sea.

B. Appendix: Northeast Atlantic

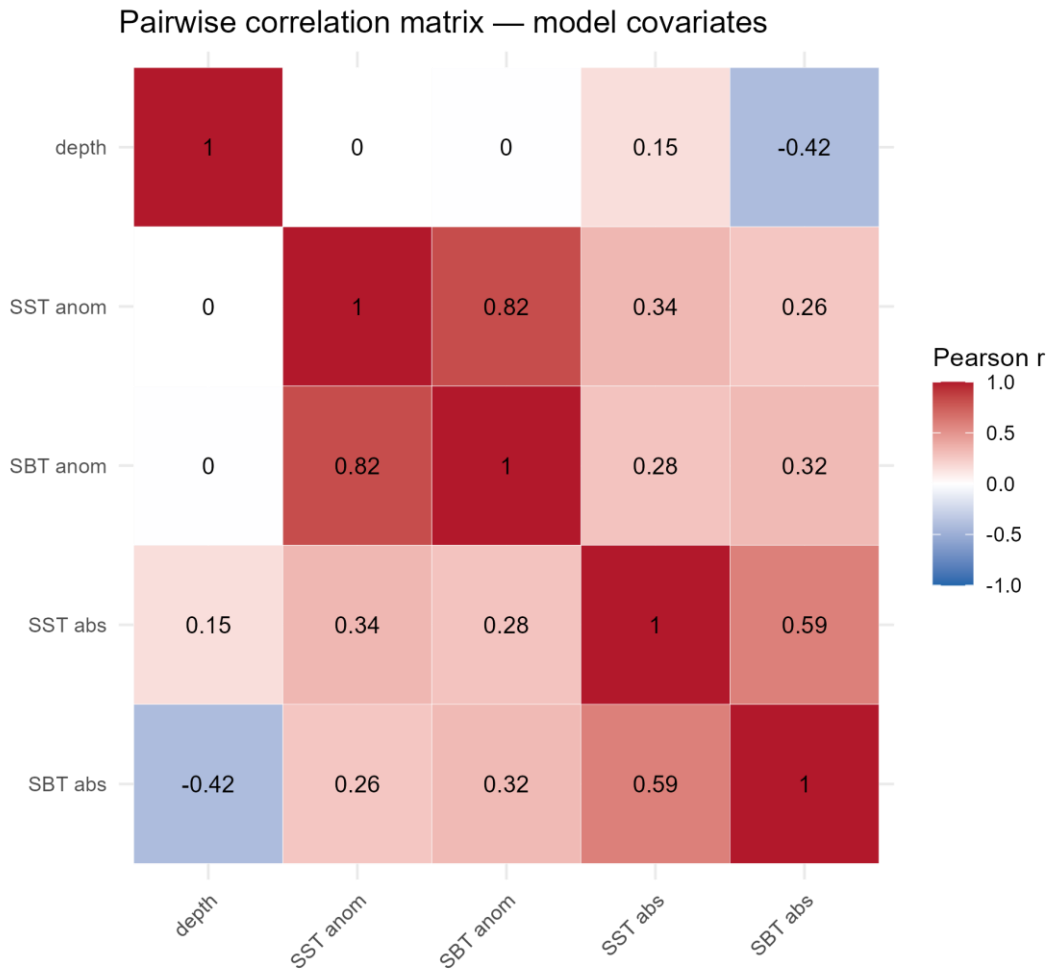


Figure B-1. Correlation matrix of environmental variables considered for inclusion in the GAM modelling framework. Those pairs of variables with $r > 0.7$ were not included in the same models.

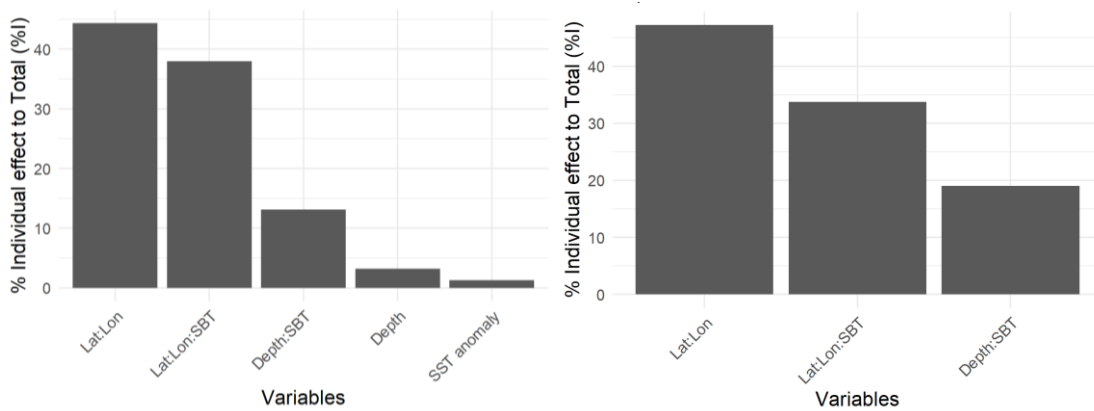


Figure B-2. Variance partitioning plots showing the relative contribution of each predictor to the total explained deviance in the GAM models for predicting community-level sensitivity to climate change (left) and fishing pressure (right).

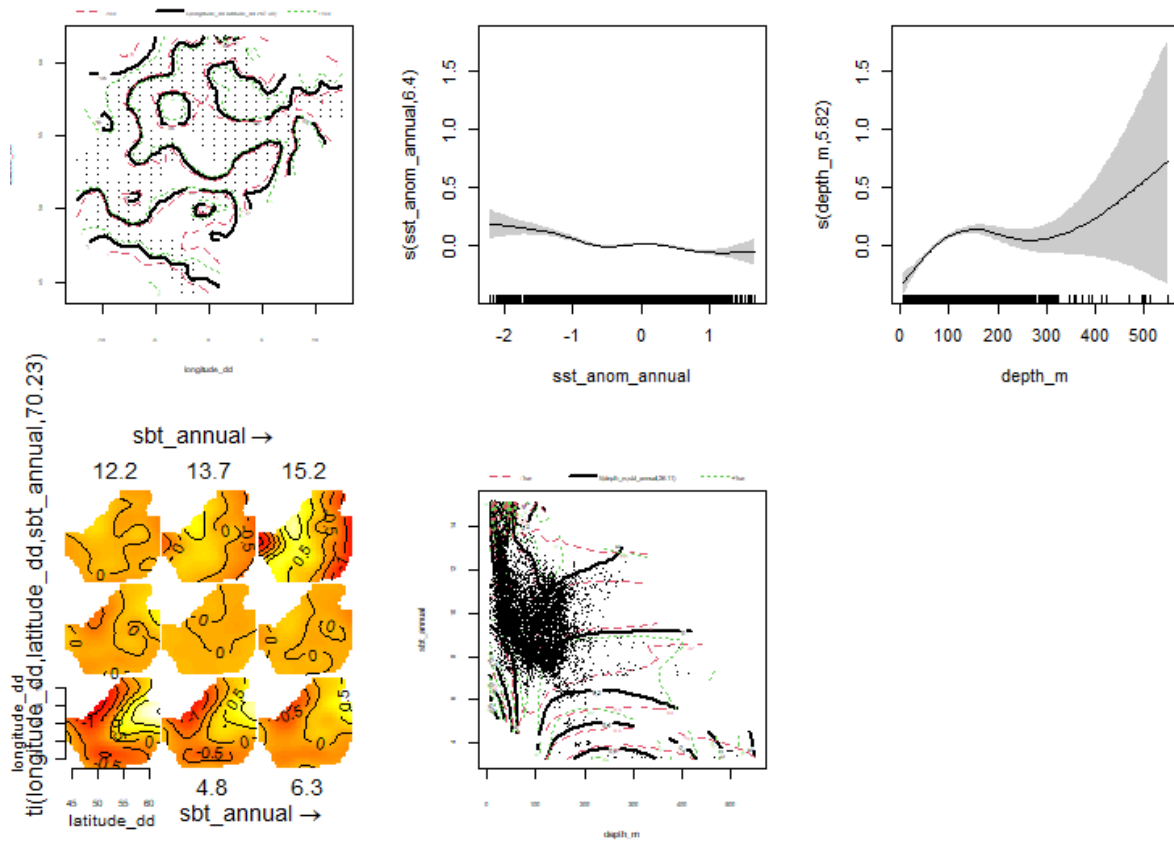


Figure B-3. Partial effect smoothers for the GAM models that predict community-level sensitivity to climate change.

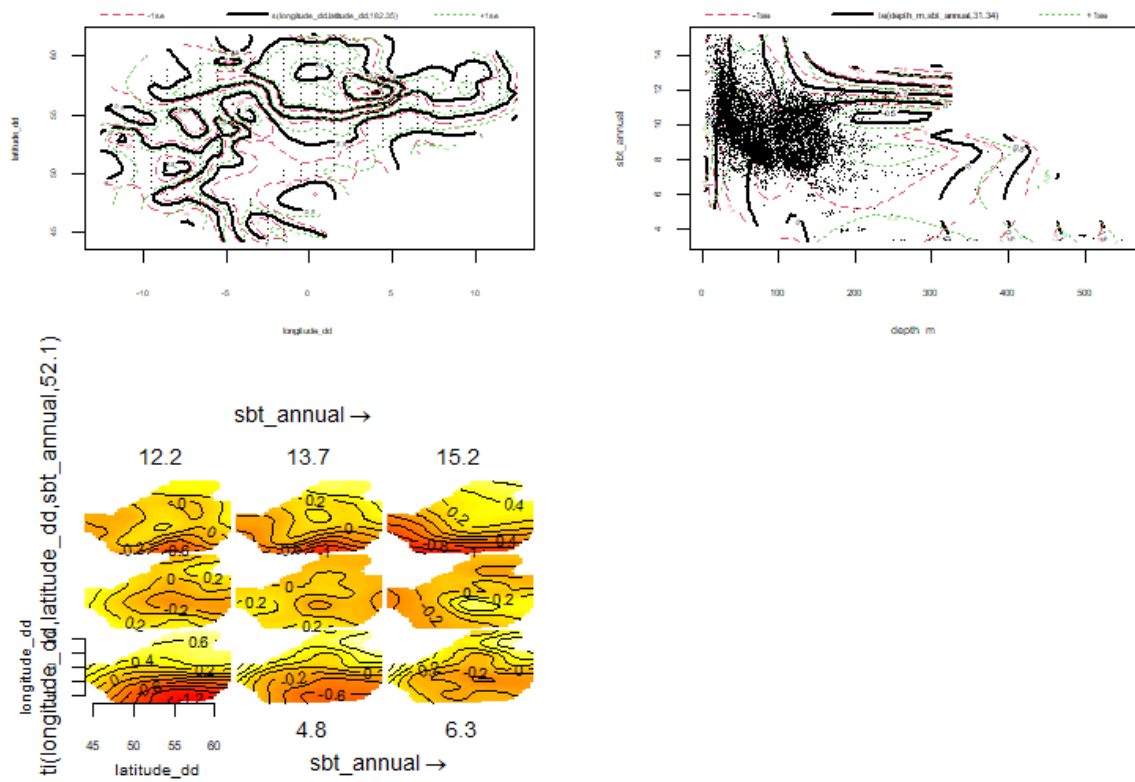


Figure B-4. Partial effect smoothers for the GAM models that predict community-level sensitivity to fishing pressure.

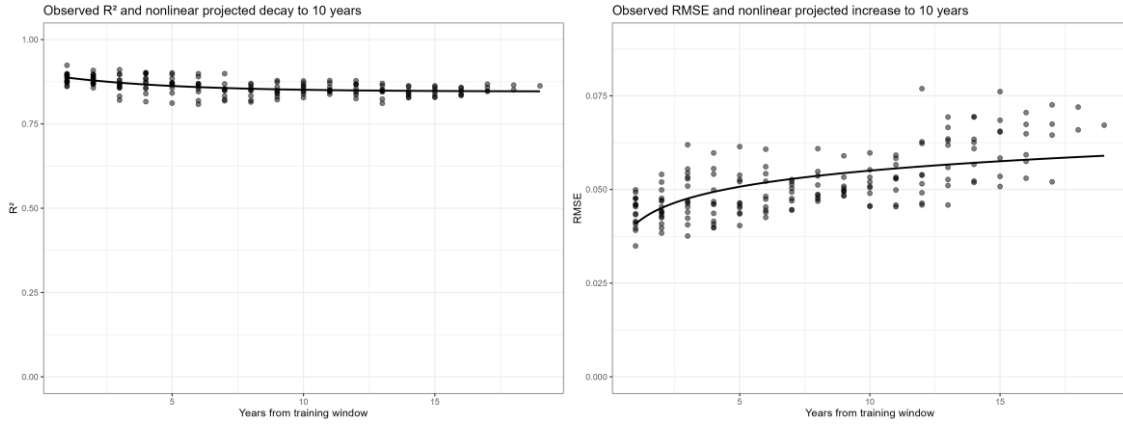


Figure B-5. Results from sliding-window validation analysis for predicted community-level sensitivity to climate change. Left panel shows the observed R^2 and projected nonlinear variation up to 19 years beyond the calibration period. The right panel shows the RMSE values and projected nonlinear variation up to 19 years beyond the calibration period.

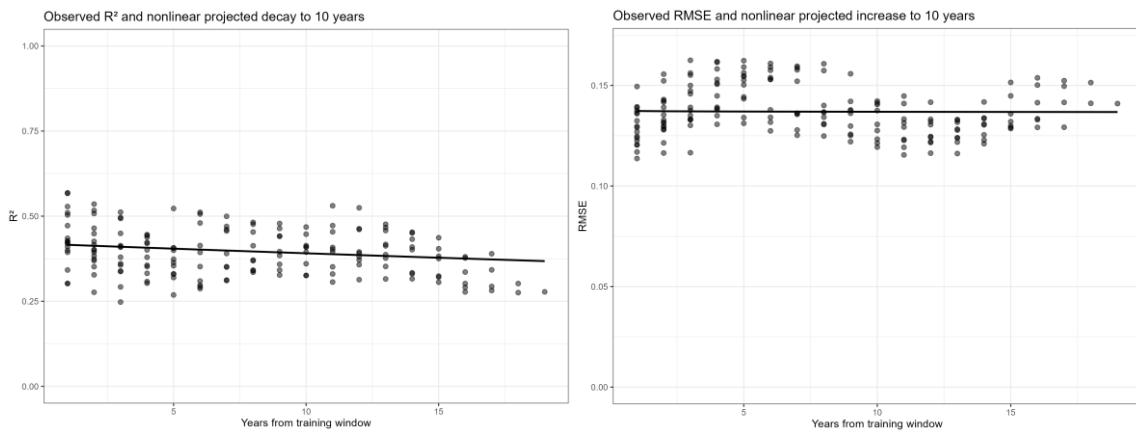


Figure B-1. Results from sliding-window validation analysis for predicted community-level sensitivity to fishing pressure. Left panel shows the observed R^2 and projected nonlinear variation up to 19 years beyond the calibration period. The right panel shows the RMSE values and projected nonlinear variation up to 19 years beyond the calibration period.

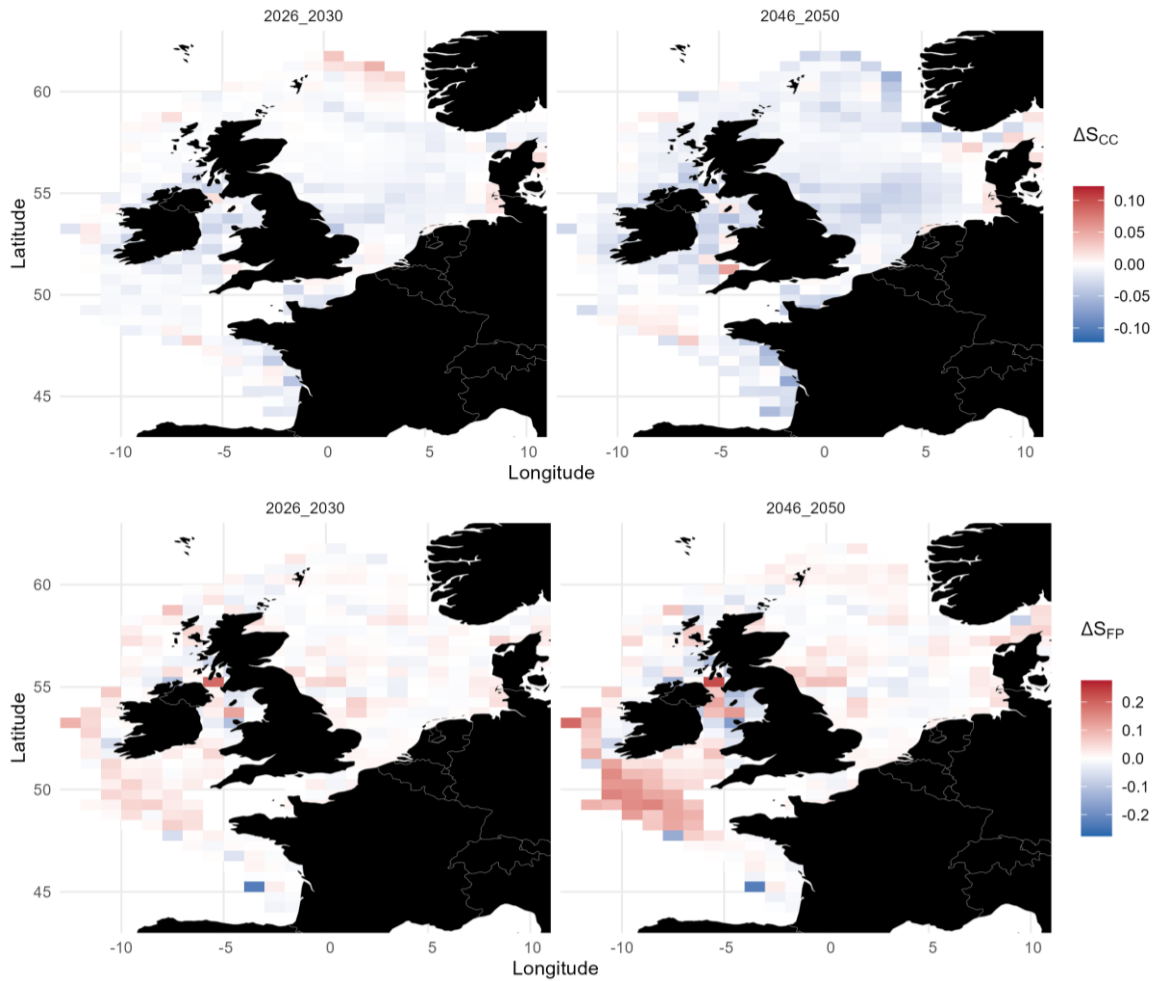


Figure B-6. Absolute change in predicted community-level sensitivity to climate change (CC; upper panel) and fishing pressure (FP; lower panel) between the reference period (2016-2020) and near-future (left panel) and mid-century (right panel). Increases in sensitivity are shown in red, decreases in sensitivity are shown in blue.

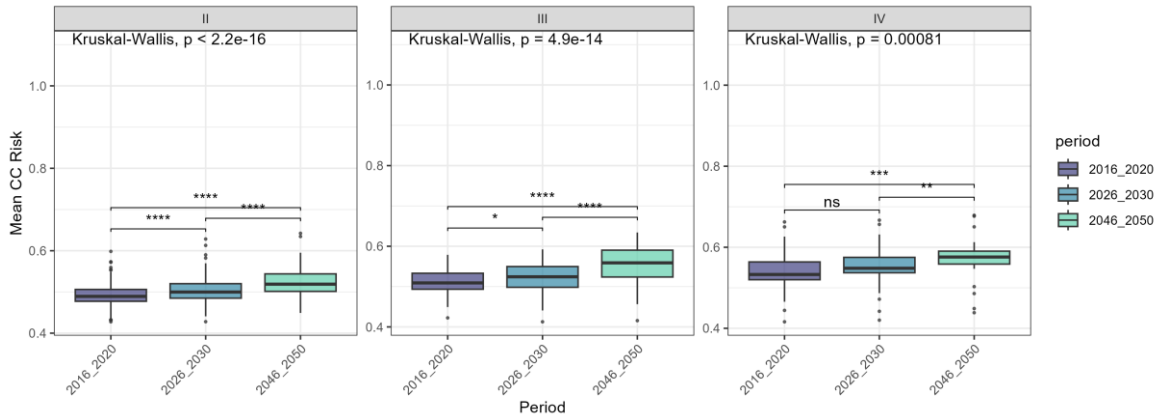


Figure B-7. Boxplots of the distribution of R_{CC} predictions across three OSPAR regions in the Northeast Atlantic and temporal periods, illustrating spatio-temporal shifts in projected exposure-weighted vulnerability. Region II = Greater North Sea, Region III = Celtic Seas, and Region IV = Bay of Biscay (not including Iberian Coast). The statistical analyses were based on the Kruskal-Wallis test, followed by pairwise Wilcoxon rank-sum comparison.

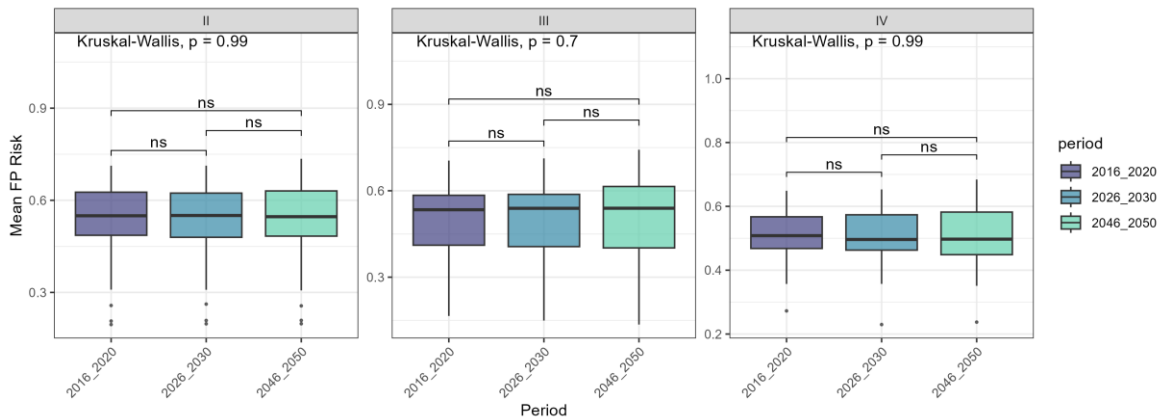


Figure B-8. Boxplots of the distribution of R_{FP} predictions across three OSPAR regions in the Northeast Atlantic and temporal periods, illustrating spatio-temporal shifts in projected exposure-weighted vulnerability. Region II = Greater North Sea, Region III = Celtic Seas, and Region IV = Bay of Biscay (not including Iberian Coast). The statistical analyses were based on the Kruskal-Wallis test, followed by pairwise Wilcoxon rank-sum comparison.

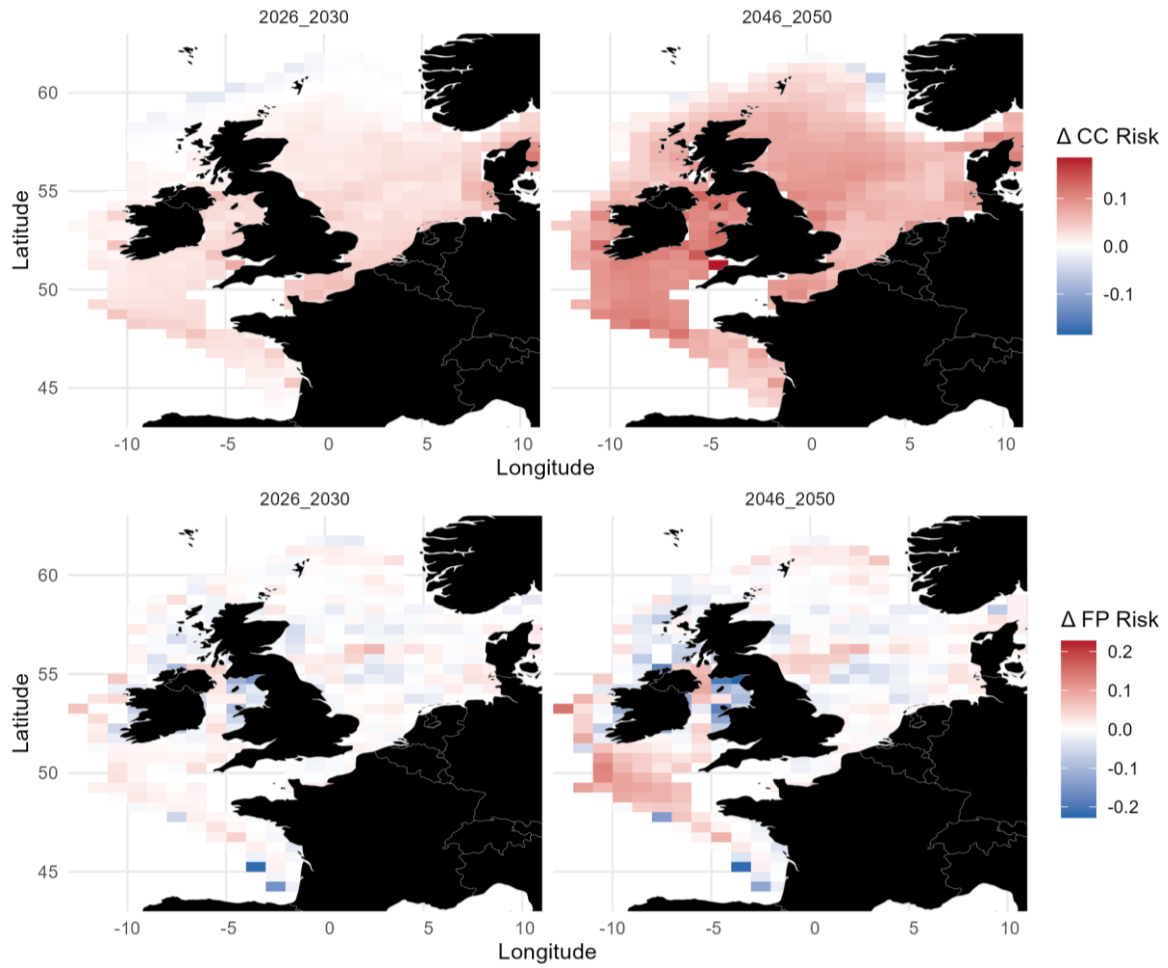


Figure B-9. Proportional change in climate change (CC) risk and fishing pressure (FP) risk in near future (2026-2030) and mid-century (2046-2050) compared to reference period (2016-2020). Increases in risk are shown in red, while decreases are shown in blue.

C. Appendix: Icelandic waters

Table C-1. Weights associated with each feature during the prioritisation.

Group	Group's weight	Feature	Individual weight	Effective weight
Arctic species	26.00	$D_{\text{aff}} < 127\text{m}$	30	9.750
		$127 \leq D_{\text{aff}} < 216$	20	6.500
		$217 \leq D_{\text{aff}} < 431$	10	3.250
		$432 \leq D_{\text{aff}} < 701$	10	3.250
		$D_{\text{aff}} \geq 701$	10	3.250
Species sensitive to climate change	13.50	$D_{\text{aff}} < 127\text{m}$	30	5.063
		$127 \leq D_{\text{aff}} < 216$	20	3.375
		$217 \leq D_{\text{aff}} < 431$	10	1.688
		$432 \leq D_{\text{aff}} < 701$	10	1.688
		$D_{\text{aff}} \geq 701$	10	1.688
Species sensitive to fishing pressure	38.50	$D_{\text{aff}} < 127\text{m}$	30	14.438
		$127 \leq D_{\text{aff}} < 216$	20	9.625
		$217 \leq D_{\text{aff}} < 431$	10	4.813
		$432 \leq D_{\text{aff}} < 701$	10	4.813
		$D_{\text{aff}} \geq 701$	10	4.813
Commercial species	7.25	<i>Anarhichas lupus</i>	1.3	0.094
		<i>Brosme brosme</i>	0.2	0.015
		<i>Gadus morhua</i>	63.2	4.582
		<i>Lophius piscatorius</i>	0.2	0.015
		<i>Melanogrammus aeglefinus</i>	13	0.943
		<i>Microstomus kitt</i>	0.5	0.036
		<i>Molva molva</i>	1.1	0.080
		<i>Pleuronectes platessa</i>	1.9	0.138
		<i>Pollachius virens</i>	8.6	0.624
		<i>Sebastes norvegicus</i>	10	0.725
At-risk species (Endangered)	19.75	<i>Anarhichas denticulatus</i>	4	2.926
		<i>Anarhichas minor</i>	1	0.731
		<i>Centrophorus squamosus</i>	4	2.926
		<i>Chimaera monstrosa</i>	1	0.731
		<i>Coryphaenoides rupestris</i>	4	2.926
		<i>Hippoglossus hippoglossus</i>	2	1.463
		<i>Molva dypterygia</i>	2	1.463
		<i>Reinhardtius hippoglossoides</i>	1	0.731
		<i>Sebastes mentella</i>	4	2.926
		<i>Squalus acanthias</i>	4	2.926
Marine pressures	-5.00	Bottom trawling intensity	1	-5.000
Total:	100.00		Total:	100.000

D. Appendix: Projected risks from invasive species in the Mediterranean

Shannon diversity

Difference from year of reference (2020)

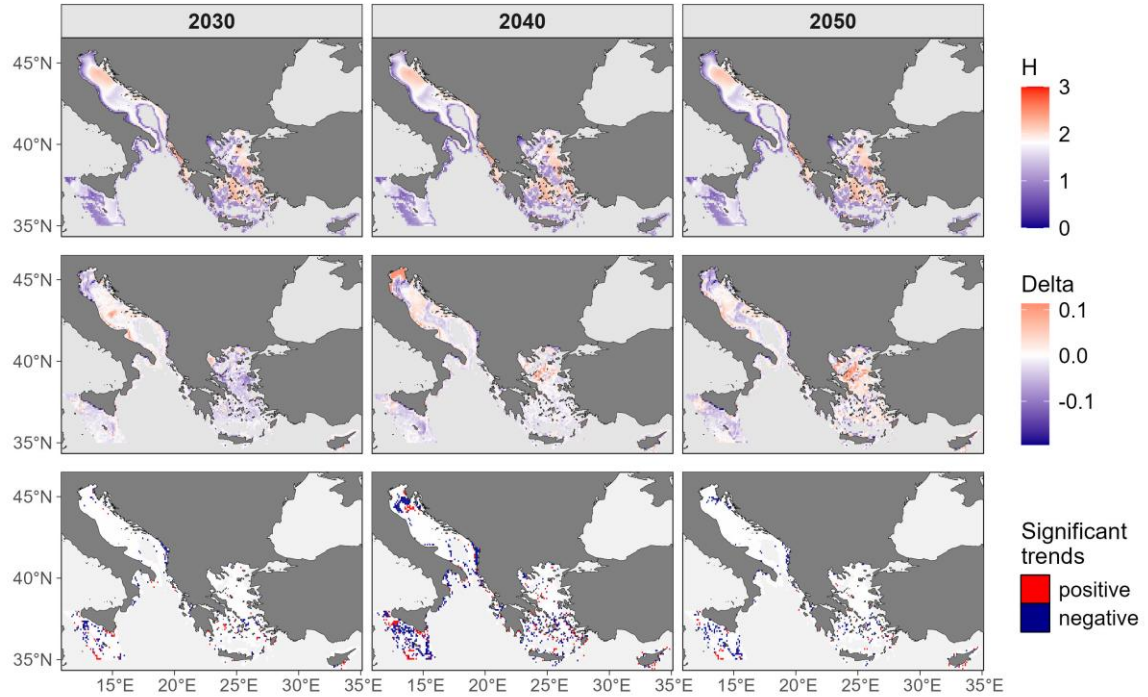


Figure D-1. Juvenile fish Shannon diversity projections in the Central-Eastern Mediterranean for the years 2030, 2040 and 2050. The top row shows the value of the index, the middle row the relative change (delta) from the year of reference (2020) and the bottom row the Mann-Kendall significant trends.

Pielou's evenness

Difference from year of reference (2020)

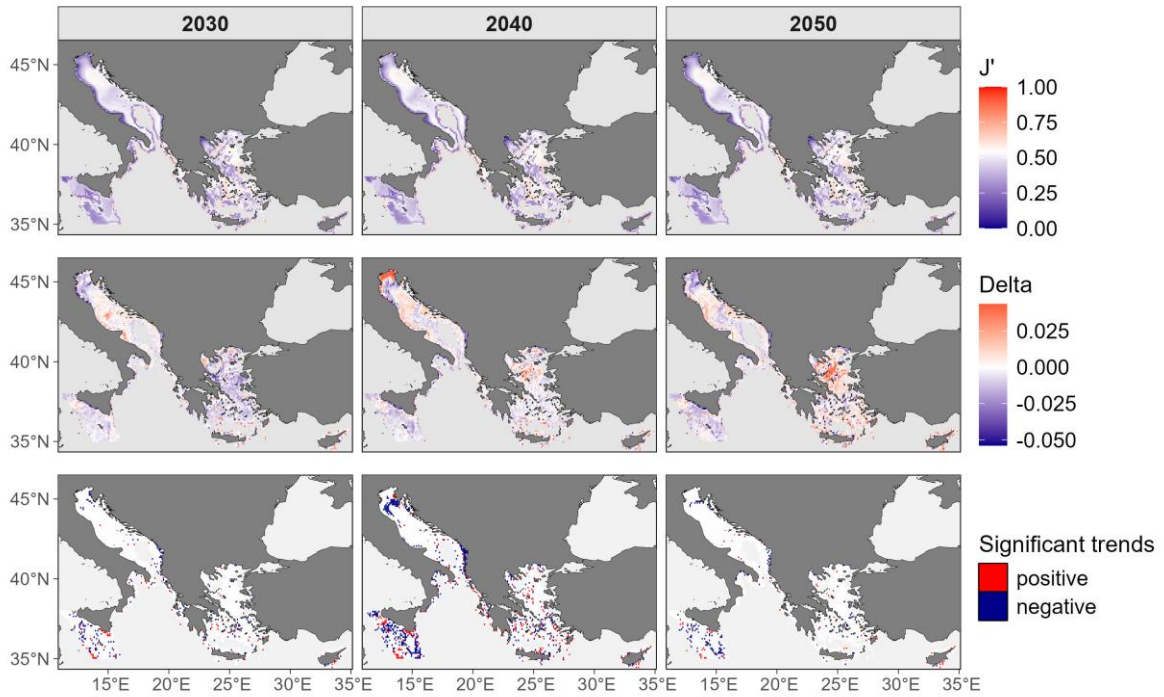


Figure D-2. Juvenile fish Pielou's evenness projections in the Central-Eastern Mediterranean for the years 2030, 2040 and 2050. The top row shows the value of the index, the middle row the relative change (delta) from the year of reference (2020) and the bottom row the Mann-Kendall significant trends.

Species richness

Difference from year of reference (2020)

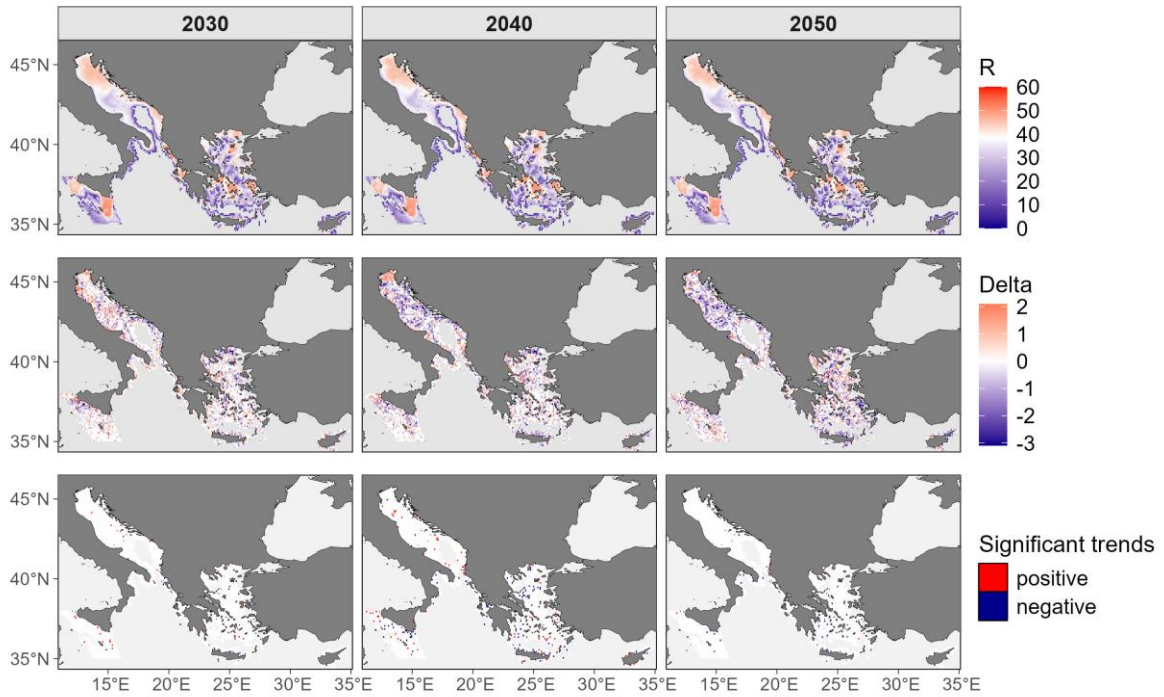


Figure D-3. Juvenile fish species richness projections in the Central-Eastern Mediterranean for the years 2030, 2040 and 2050. The top row shows the value of the index, the middle row the relative change (delta) from the year of reference (2020) and the bottom row the Mann-Kendall significant trends.

Reduced fishing effort scenario

Difference from baseline

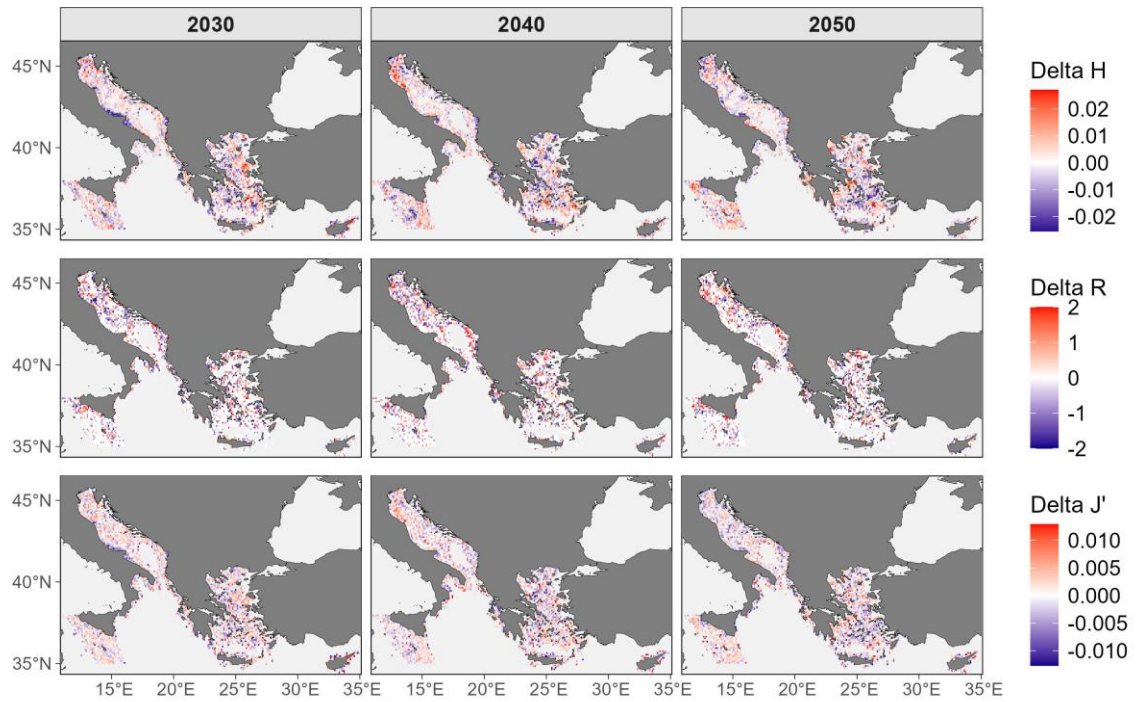


Figure D-4. Effect of a 15% reduction in fishing effort in juvenile fish alpha diversity projections in the Central-Eastern Mediterranean for the years 2030, 2040 and 2050. The effect is expressed as the relative difference between the “reduced” and the “baseline” (constant) fishing effort scenario. Top row (H): Shannon diversity, middle row (R): species richness, bottom row (J’): Pielou’s evenness.

Increased fishing effort scenario
Difference from baseline

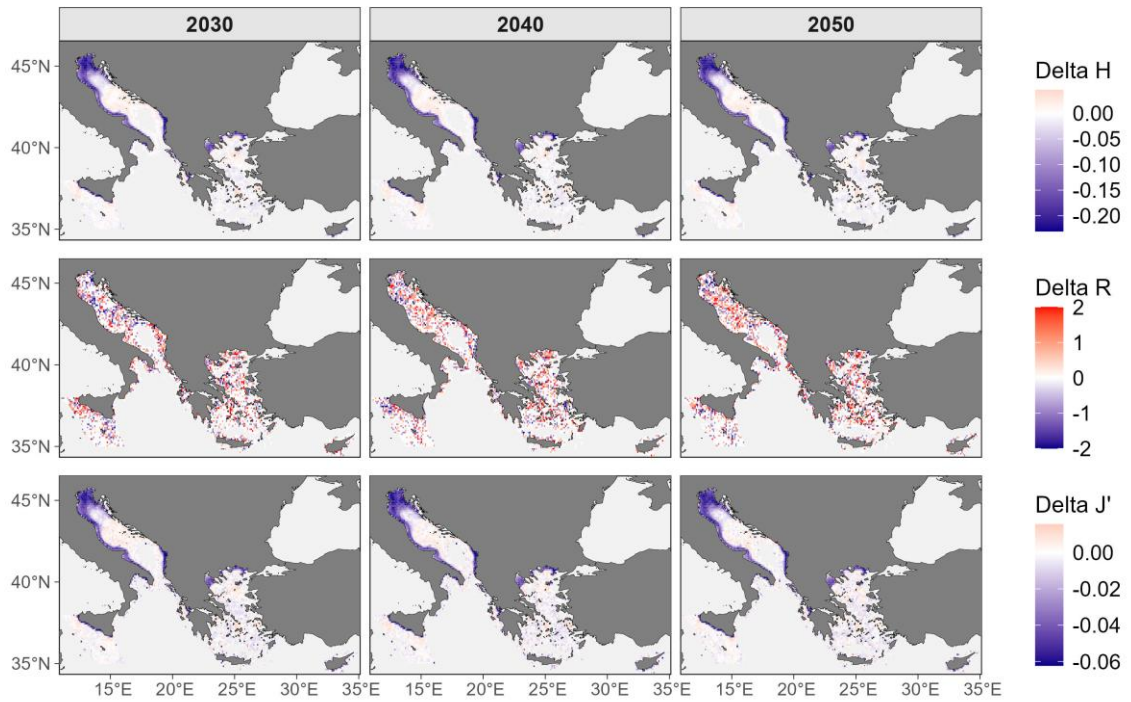


Figure D-5. Effect of a 15% increase in fishing effort in juvenile fish alpha diversity projections in the Central-Eastern Mediterranean for the years 2030, 2040 and 2050. The effect is expressed as the relative difference between the “increased” and the “baseline” (constant) fishing effort scenario. Top row (H): Shannon diversity, middle row (R): species richness, bottom row (J’): Pielou’s evenness.