



Research article

Future cumulative effects on demersal fish in a transforming North Sea pressure landscape



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ABSTRACT

The North Sea is facing a complex pressure landscape driven by a multitude of human activities and environmental drivers. Over the next decades, this landscape is expected to transform substantially due to accelerating changes in key sectors, such as the renewable energy and fisheries sectors, as well as climate change. These changes profoundly affect demersal fish communities through direct alterations to the seabed and modifications to the environmental conditions. Given the complex interactions between these pressures, the net effect remains uncertain. We used a trait-based Bayesian network model combining empirical data with expert knowledge to describe the probabilistic relationships between offshore wind farms (OWFs), fishing, temperature increase, nitrogen concentrations, and demersal fish traits. Specifically, we integrated model data on environmental pressures, survey data on fishing intensity and demersal fish distribution with qualitative information on the effects of OWFs. This approach allowed us to examine how the trait composition of demersal fish communities may change in the future and to develop trait-based indicators for identifying potential areas of concern. We show that the currently designated Natura 2000 areas have limited overlap (<10 %) with the most vulnerable fish communities, which were identified based on selected traits and stressors and were predicted to be predominantly located in the northern part of the study area. These areas are also central to the ambitious expansion plans of OWFs, highlighting the need to understand whether OWFs can partially fulfil an ecosystem enhancement opportunity left unaddressed — a possibility suggested by our network predictions. However, our network also indicated that temperature increases by 2060 will cause substantial, area-wide shifts, while the effects of OWF expansion and potential fisheries spatial redistribution are highly localised, resulting in mild to moderate changes in trait distribution. These findings suggest that climate change will be the key driver of substantial community transformations by 2060.

1. Introduction

The North Sea, a hub of economic activities, is facing a complex pressure landscape driven by a multitude of human activities and environmental drivers (Halpern et al., 2008). This landscape is expected to undergo lasting transformations over the next two decades due to accelerating changes within key sectors. Among those is the renewable energy sector with plans to install 212 GW of offshore wind capacity by 2050 (Gusatu et al., 2021), which will occupy a substantial area of the North Sea. The implementation and operation of offshore wind farms

(OWFs) come along with various pressures, including noise, electromagnetic fields, and hydrological changes (Dannehaim et al., 2020). While some of these pressures exert localised effects, others extend their impact across a broader spatial range. Still, others are facilitated by the network characteristics of these installations (e.g., the invasion of non-native species, Watson et al., 2024). OWF turbines and their scour protection may also transform soft sediment habitats by introducing new three-dimensional hard substrates, which can alter the environment in various ways (Gimpel et al., 2023; Raoux et al., 2019; Slavik et al., 2019; Degraer et al., 2020).

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Bottom trawling was one of the most dominant activities in the North Sea but has steadily declined over the past years due to worsening socio-economic conditions and the decline of target stocks (Stelzenmüller et al., 2024a). Sectoral experts anticipate a further decrease in fishing intensity in the German part of the North Sea driven by the planned installation of OWFs and the expansion of nature conservation areas under the EU Biodiversity Strategy 2030 (Larsner and Barz, 2023; Stelzenmüller et al., 2024b). Excluding fishing inside OWFs can, in turn, have beneficial effects on fish communities by reducing the pressure landscape for target species across the North Sea.

These sectoral changes occur within a broader and spatially variable environmental pressure landscape, characterised by shallow depths and strong seasonal stratification (Ducrotoy et al., 2000). Sea-surface temperatures and wind are the key large-scale physical drivers of the system, influenced by regional factors and by the North Atlantic (Emeis et al., 2015) as well as ongoing global warming trends (Weinert et al., 2016). The coastal areas are also strongly influenced by land-based activities such as agriculture and the land-based industry, particularly through the elevation of nutrient concentration levels (Stelzenmüller et al., 2024b), which in turn can affect primary production, oxygen dynamics and species composition (Camargo and Alonso, 2006). While there has been a considerable reduction in nitrogen concentrations since the 1990s, it is still above environmentally acceptable levels in many parts of the southern North Sea (Voß et al., 2009). Nitrogen can further interact with climate change-related pressures (Radach and Pätsch, 2007), leading to detrimental effects on food-web dynamics. Climate change itself directly affects fisheries target stocks, with projections for the North Sea indicating substantial temperature increases (Mathis et al., 2019; Mathis and Pohlmann, 2014) and latitudinal species shifts (Gordo-Vilaseca et al., 2024). These effects may be especially pronounced in shallow and stratified coastal waters, where salinity levels can strongly vary due to freshwater input from continental rivers (Emeis et al., 2015).

How these various pressures interact and cumulatively reshape the North Sea remains uncertain. Yet, they are expected to significantly impact seabed communities, particularly demersal fish, by directly altering sea floor conditions. Understanding the combined impact is therefore crucial for identifying vulnerable areas and developing effective mitigation strategies. Cumulative effects on the environment are typically assessed by examining their impact on specific species or broad ecosystem components (Halpern et al., 2008; Stelzenmüller et al., 2020). However, it is the traits of a species, rather than its taxonomic identity, that determine its vulnerability to specific pressures. Consequently, evaluating the potential effects of cumulative pressures on community traits offers a more mechanistic and process-oriented approach to understanding these impacts (Butt et al., 2021; O'Hara and Halpern, 2022; Stelzenmüller et al., 2018).

To advance the assessment of future cumulative impacts on demersal fish, we adopted a trait-based Bayesian Belief Network (BN) approach that integrates both quantitative large-scale data and qualitative local information, offering a more comprehensive assessment. This is essential given the limited spatial extent of existing offshore wind farms and the reliance on localised before-and-after or inside-outside assessments. Using this framework, we explore the potential impacts of the planned expansion of OWFs, a subsequent redistribution and further decline in fishing, and an increase in temperature on the demersal fish community in the southern North Sea, while considering the effects of nitrogen concentrations. We examine how the trait composition may change in the future and develop trait-based indicators for identifying potential areas of concern. The network was trained on model and empirical data from the southern North Sea spanning 1985 to 2020, as well as qualitative information from relevant literature. Our integrative approach provides a structured way to explore how future developments of human-related pressures may cumulatively reshape demersal fish communities.

2. Material and methods

2.1. Identifying key vulnerable traits of demersal fish communities

We identified species traits that potentially influence a fish's vulnerability to temperature increases, nutrient enrichment, and pressures from OWFs and benthic trawling. We first identified the life-history characteristics body size (hereafter size), age at sexual maturity (hereafter maturity), and longevity to respond to biological extraction from benthic trawling and temperature changes. Larger species are often disproportionately removed by fishing (Dulvy et al., 2003; Jennings et al., 2001; Reynolds et al., 2005) and are potentially more vulnerable to increasing temperatures because warming will decrease the aerobic capacity and large species are less able to balance oxygen demand and uptake because of their smaller surface area to volume ratio (Baudron et al., 2014; Cheung et al., 2013; Jones and Cheung, 2018). Longevity and maturity are expected to be indirectly impacted as well because they are strongly correlated with size. We also identified the feeding type piscivory to be more vulnerable to habitat disturbances from benthic trawling and nutrient enrichment because of the increased turbidity and the resulting reduction in predation success (Breitburg et al., 2009; Stelzenmüller et al., 2010; Utne-Palm, 2002; Wenger et al., 2017). Given the lack in understanding linkages between OWF-related pressures and species traits (Rehren et al., submitted), we only identified two potential effects from the expansion of OWFs on species with specific traits. We first identified species associated with a complex sea floor structure to potentially benefit from the installations of OWF structures (hereafter, complex-bottom affine) as highlighted by empirical studies (e.g., Glarou et al., 2020; Methratta and Dardick, 2019). Second, from a meta-analysis of studies examining the abundance of fish inside and outside of OWF areas, we assumed that particularly piscivore fish (hereafter piscivory) may benefit from the artificial reef effect (Methratta and Dardick, 2019).

2.2. Data

2.2.1. Community-weighted mean traits

Changes in the community mean of the selected traits were analyzed to better understand potential shifts in the demersal fish community resulting from future changes in the cumulative pressure landscape. For this, we obtained fish abundance data (kg/km^2) from (1) the Demersal Young Fish Survey DYFS, (2) the North Sea International Bottom Trawl Survey NS-IBTS, (3) the Beam Trawl Survey BTS, and (4) the German Autumn Survey in the Exclusive Economic Zone (GASEEZ Survey, Fig. 1). The first three surveys are coordinated by ICES and the data including records on haul length and survey information are available through the ICES DATRAS data portal (<https://www.ices.dk/data/data-portals/Pages/DATRAS.aspx>, accessed June 2024). The GASEEZ survey samples 14 rectangles in the southern, central and northern North Sea and was obtained from the Thünen database.

All gears other than GOV (Grande Ouverture Verticale) trawls were removed from the NS-IBTS survey to assure comparability across hauls. Hauls with no geo-information or catch data were removed from all surveys prior to the analysis. Data on wing spread and towed distance were used to estimate species densities (n/km^2). Missing information on the towed distance was estimated from shoot and haul positions using the function 'distGeo' from the r-package 'geosphere' (version 1.5-18) and all towed distances above 6000 m were considered unrealistic and thus removed. Missing information on the wing spread for beam trawl gears was set equal to beam width. For GOV trawls, missing wing spread was estimated based on a linear regression between wingspread and depth. For the GASEEZ data, the wing spread was set to 23 m for KJN (Kabeljauhopper) gears and 14 m for beam trawls. All double beams have been corrected by doubling the wing spread estimate. Species abundance (n) was aggregated across length class and the species density (n/km^2) per haul was calculated by dividing the total number by the

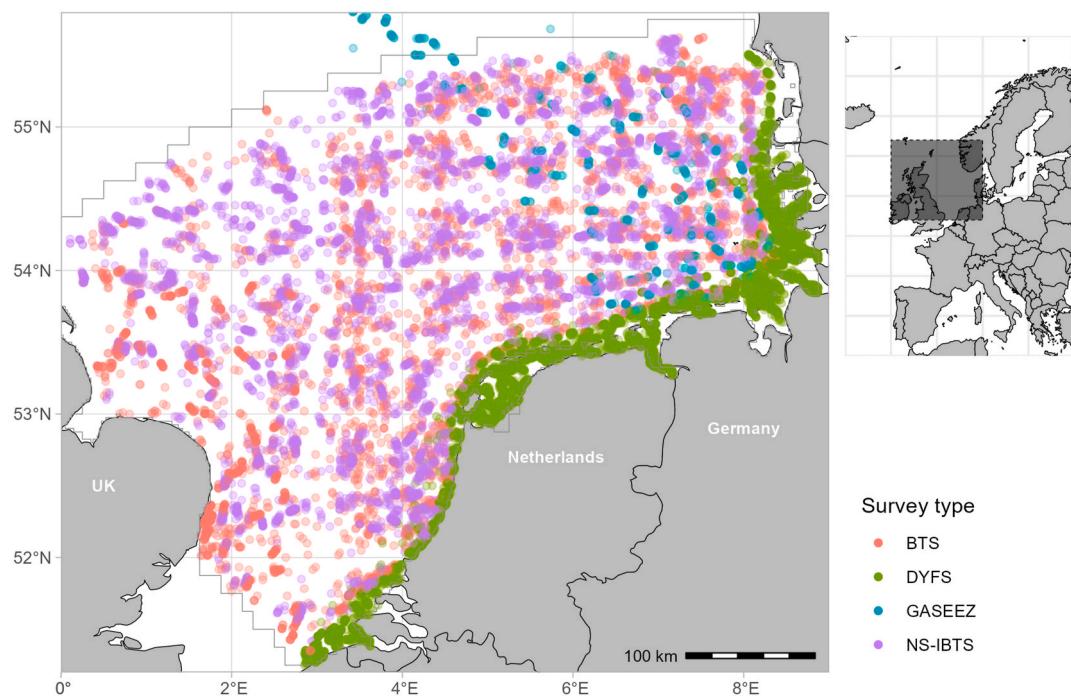


Fig. 1. Study area and sampling points of the scientific surveys between 1985 and 2020 used in the analysis. We used the key fisheries independent demersal surveys bottom trawl survey (BTS), demersal young fish survey (DYFS), German Autumn Trawl Survey in the German exclusive economic zone (GASEEZ), and the North Sea International Bottom Trawl Survey (NS-IBTS).

swept area. We further removed rare species which occurred only in very few hauls ($n \leq 20$). For an estimate of biomass (kg/km^2), we used the length-weight relationship parameters from FishBase (www.fishbase.org, data download at February 08, 2024 via the r-package ‘rfishbase’ Boettiger et al. (2023), using the ‘length-weight’-function), which were further complemented by an internal Thünen-data base (Wilhelms, 2013). We classified 62 species from these surveys as demersal (i.e., demersal, bathydemersal, benthopelagic) following Probst et al. (2021) and the FishBase classification (Froese and Pauly, 2023).

Size, longevity, and age-at-sexual-maturity, were expressed as continuous traits using a mean value per species. The feeding type and habitat preference of the species were assigned values from 0 (none) to 4 (complete) expressing the affinity of a species to a modality (e.g., piscivory, affinity to complex bottom structures) of the trait (i.e., fuzzy coding, Chevenet et al., 1994). We obtained information on mean species size from North Sea fisheries surveys (Wilhelms, 2013), complemented with information from FishBase (Froese and Pauly, 2023). The affinity to complex bottom habitats was taken from the meta-analysis of Methratta and Dardick (2019) and complemented with information from FishBase (Froese and Pauly, 2023).

Information for piscivory, longevity, and age at sexual maturity was obtained from FishBase (Froese and Pauly, 2023), giving more weight to information from the North Sea. A species list with trait information can be found in Appendix A.

Using the species-trait table and a log-transformation of the species biomass (to reduce the skewness in the biomass data), we calculated community-weighted mean traits for each haul by multiplying the trait value by the relative abundance of each species and then aggregating these weighted values across all species.

To obtain a regular grid, the community-weighted mean traits were interpolated on a $0.05^\circ \text{longitude} \times 0.05^\circ \text{latitude}$ spatial grid (hereafter 0.05×0.05 grid) using the inverse distance squared weighted algorithm of the R *gstat* package (Pebesma and Graeler, 2023) and converted back to a data frame using the *rasterToPoints* function from the *raster* package (Hijmans, 2023).

2.2.2. Pressure data

We used the total subsurface swept-area-ratio from ICES (ICES, 2021; <https://doi.org/10.17895/ices.data.8294>) to express the pressures biological extraction and habitat disturbance (i.e., siltation, smothering). Information on the foundations of OWFs has been obtained from 4C Offshore Ltd (<https://www.4coffshore.com/>, last accessed April 2022). We included only those wind parks that have been fully commissioned during the study period (1985–2020). A 500-m buffer zone around the wind park polygons was calculated using the *buffer* function from the *raster* package to account for a potential effect distance and then rasterized on a 0.05×0.05 grid.

High-resolution information (1.5–4 km) on annual averages of bottom maximum temperature and dissolved inorganic nitrogen (proxy for nutrient enrichment) for the periods 1985–1989 and 2004–2012 were obtained from a long-term simulation for the southern North Sea (Xu et al., 2020), which was performed using as key components the hydrodynamic model GETM (Burchard and Bolding, 2002) and the trait-based pelagic ecosystem model MAECS (Kerimoglu et al., 2017; Wirtz, 2019), integrated using the generic coupling frameworks FABM and MOSSCO (Lemmen et al., 2018). All data is available from Wirtz et al. (2024). Maximum bottom temperature and dissolved nitrogen were transformed to raster format on a rectangular raster grid with a resolution of $0.025^\circ \text{longitude} \times 0.025^\circ \text{latitude}$ accounting for an average distance between grid cell centres of 3.262 m. We extracted information on all pressures on each point of our 0.05×0.05 grid using the *extract* function of the *raster* package.

2.3. The Bayesian Belief Network

We constructed a directed acyclic causal Bayesian Belief Network using the software Netica 6.05 Win (CoGFMs64), where each node represented a variable or state corresponding to the selected pressures and demersal fish traits (see section *Identifying vulnerable traits of demersal fish communities*). All nodes except the presence/absence of OWFs were continuous data. Since Netica only handles discrete data, each continuous variable was converted into discrete states (Table 1)

Table 1

Description of variables (nodes) of the Bayesian Belief Network (BN) modelling the effects of cumulative stressors on community traits of demersal fish. Abbreviations: SAR = Subsurface Swept Area Ratio; prop. = proportion.

Node name	Description	States	Unit	Data source
Year		1985–2004	yrs	n.a.
		2004–2013		
		2013–2020		
Pressure nodes				
Maximum bottom temperature	Maximum bottom temperature between 1985 and 2012 obtained from a long-term simulation of the MOSSCO GETM-MAECS model for the southern North Sea. Probabilities for the period 2013–2020 were adjusted using linear regression.	11–14 14–16.2 16.2–24	°C	MOSSCO-GETM-MAECS (Wirtz, 2019)
Benthic trawling	Spatial data layers on fishing intensity/pressure within the OSPAR Maritime Area for 2015–2020. SAR is the cumulative area contacted by a fishing gear within a grid cell over one year (≥ 2 cm penetration depth of the gear components). Probabilities for the period 1985–2013 were adjusted using linear regression.	0–1e–10 1e–10–0.63 0.63–9.9	SAR	(ICES, 2021)
Dissolved inorganic nitrogen	Dissolved inorganic nitrogen between 1985 and 2012 obtained from a long-term simulation of the MOSSCO GETM-MAECS model for the southern North Sea. Probabilities for the period 2013–2020 were adjusted using linear regression.	0.1–5 5–314.6	mmol N/ m ³	MOSSCO-GETM-MAECS (Wirtz, 2019)
Offshore wind farms	Presence/absence of OWF areas obtained from the 4C Offshore Ltd (last accessed April 2022)	0 1		4C Offshore Ltd
Trait nodes				
Community mean size	Interpolated community mean (1985–2020) based on (1) log-transformed species abundance (kg/km^2) from trawl surveys and (2) the trait table (Appendix A) by multiplying the trait value by the relative abundance of each species and aggregating these weighted values across all species.	low (24–55.5) high (55.5–123)	cm	Trawl surveys ICES DATRAS & GASEEZ
Community mean maturity	Interpolated community mean (1985–2020) based on (1) log-transformed species abundance (kg/km^2) from trawl surveys and (2) the trait table (Appendix B) by multiplying the trait value by the relative abundance of each species and aggregating these weighted values across all species.	low (1.04–2.79) high (2.79–5.03)	yrs	Trawl surveys ICES DATRAS & GASEEZ
Community mean longevity	Interpolated community mean (1985–2020) based on (1) log-transformed species abundance (kg/km^2) from trawl surveys and (2) the trait table (Appendix B) by multiplying the trait value by the relative abundance of each species and aggregating these weighted values across all species.	low (2.7–16.3) high (16.3–29.4)	yrs	Trawl surveys ICES DATRAS & GASEEZ
Community mean piscivory	Interpolated community mean (1985–2020) based on (1) log-transformed species abundance (kg/km^2) from trawl surveys and (2) the trait table (Appendix B) by multiplying the trait value by the relative abundance of each species and aggregating these weighted values across all species.	low (0–0.14) high (0.14–0.71)	prop.	Trawl surveys ICES DATRAS & GASEEZ
Community mean complex bottom affinity	Interpolated community mean (1985–2020) based on (1) log-transformed species abundance (kg/km^2) from trawl surveys and (2) the trait table (Appendix B) by multiplying the trait value by the relative abundance of each species and aggregating these weighted values across all species.	low (0–0.23) high (0.23–0.83)	prop.	Trawl surveys ICES DATRAS & GASEEZ
Indicator nodes				
Conservation concern index	Node expressing the probabilities of a community hosting species abundances under conservation concern. Probabilities were based on the proportion of species in the trawl surveys with various combinations of longevity and piscivory states classified as under conservation concern versus not.	low high	n.a.	Calculated
Commercial interest index	Node expressing the probabilities of a community hosting species abundances of commercial interest. Probabilities were based on the proportion of species in the trawl surveys with various combinations of longevity and piscivory states classified as fisheries' target species or not.	low high	n.a.	Calculated
Vulnerability	Node expressing the vulnerability of the demersal fish community to the selected pressures. The node was calculated by multiplying the logarithms of the size, maturity, longevity, and piscivore nodes, based on the assumption that communities with K-strategists (i.e., larger, later maturing, and longer-lived species) and a high abundance of piscivores are more sensitive to the pressures.	0–1.5 1.5–5 8–14.2	n.a.	Calculated

through a binning process, ensuring that each bin contained approximately equal frequencies and thus more robust estimates of probabilities. We limited the number of states to only 2–3 to avoid insufficient observations per category affecting the reliability of probability estimates. We adjusted the binning of the pressure nodes maximum bottom temperature, benthic trawling, and nitrogen to account for potential pressure thresholds. We set the bins of the temperature node based on the temperature preferences of the modelled species obtained from AquaMaps (<https://www.aquamaps.org>), accessed 08/2023). Thresholds were set at the mean and the third quartile of the maximum temperature ranges observed for the modelled species. Information on thresholds for nitrogen and subsurface swept-area-ratio were taken from a recent study on the identification of human and environmental stressor thresholds of seascape fauna composition in the southern North Sea using a Gradient Forest approach (Kraan et al., 2024). The bins of the two nodes were adjusted according to values in these stressor gradients, where significant shifts in the demersal fish community composition occurred. Further, we added a no fishing pressure state (i.e., bin) to the

benthic trawling node to model the effect of fisheries exclusion from future OWFs. While, the available data for nitrogen and maximum bottom temperature span 1985–2012, subsurface swept-area-ratio data span the period 2009–2020. To address this mismatch in periods, we added a year node with three bins (1985–1989, 2004–2012, and 2013–2020) and manually adjusted the probabilities for missing periods using linear regression.

The probabilities of the parent nodes (pressures) and all conditional probabilities of the child nodes (traits) were learned from data, except those related to a zero-fishing state and the presence of OWFs. Since the survey data had insufficient observations for the zero-fishing state, we used linear regression on the probabilities from other states to estimate the conditional probabilities for size, longevity, age at sexual maturity, and piscivory under zero-fishing. The conditional probabilities of piscivory and complex-bottom affinity under the presence of OWFs could likewise not be learned from the data, because the survey data lacked stations within OWF areas. We used the effect sizes of 0.9 and 0.8 from the meta-analysis on studies examining the abundance of fish inside and

outside of OWF areas (Methratta and Dardick, 2019) to adjust the conditional probabilities of the trait nodes piscivory and complex-bottom affinity, respectively. The effect size was converted into an odds ratio and applied to the baseline probabilities estimated by the network under the absence of OWFs.

We used Netica's equation mode to calculate an index representing the vulnerability of the demersal fish community to the selected pressures:

$$\text{Vulnerability} = \log(1 + \text{size}) \times \log(1 + \text{maturity}) \times \log(1 + \text{longevity}) \\ \times \log(1 + \text{piscivorous feeding})$$

The underlying assumption is that communities dominated by species that are larger, mature later, and live longer—along with a high abundance of piscivores, are more susceptible to the selected pressures. The multiplicative approach assumes that these traits interact to shape vulnerability, meaning that communities scoring high across all four traits will have the highest vulnerability scores, while those with lower values will be less affected. We further defined two indices, one expressing the probability of a community to host traditional species of commercial interest (commercial interest index) and one expressing the probability of a community to host species of conservation concern (conservation concern index). Both indices were defined as child nodes of the nodes longevity and feeding strategy. To parameterize the conditional probability tables of the two indicator nodes, we analyzed the survey data to calculate, for each combination of predictor states (low and high longevity, piscivores and non-piscivores), the proportion of species that are of conservation concern (or commercial interest) versus those that are not (Table 1, Appendix B for conditional probability tables).

We tested the network performance by letting the model predict each of the trait nodes separately and comparing the predictions with the observed data using the node-specific error rate and spherical pay-off. The latter measures the overall performance of the network by assessing the balance between correct and incorrect predictions across all nodes (Marcot, 2012). The metric rewards models that maintain high accuracy and minimize the influence of isolated errors. To identify influential variables, areas of uncertainty, and assess the model robustness, we performed a sensitivity analysis for the trait and the indicator nodes. Finally, we compared the spatial predictions of the most probable state of the trait nodes from the model for 1985–2020 with the classified observed data averaged over the same period. To assess the agreement between these two spatial maps of categorical variables, we

calculated Cohen's Kappa using the *caret* package (Kuhn, 2023), which is a statistical measure of inter-rater reliability (Marcot, 2012).

2.4. Future scenarios of cumulative pressures

We used the network to investigate how future changes in implemented OWFs, benthic trawling, and temperature propagate through the network and affect the demersal fish community indicators. In the first scenario (2040OWF), we assumed that the existing development plans for the implementation of OWFs will remain unchanged in the future. All OWF areas were modelled as fisheries exclusion zones. In a second scenario (2040OWF-Redistribution), we assumed that the fisheries would redistribute within a 15 km radius outside of the new OWFs. A third scenario accounted for potential long-term changes in temperature in 2060 (2060-Temperature). While we retained the OWF developments until 2040 and the redistribution approach from the second scenario, we additionally assumed that the long-term fishing effort would decrease by 30 %. This assumption is based on an expert elicitation on the future development of the German North Sea fisheries (Stelzenmüller et al., 2024b). While the development of the German fishery is not representative of the general North Sea fisheries, the scenario can be seen as a worst case in which the future competition for space due to the expansion of OWFs and marine protected areas together with increasing fishing costs and decreasing stocks may result in the loss of fishing opportunities and a general reduction of fishing capacities.

We used all OWF polygons with a full commission date prior to 2041 as provided by the 4C Offshore Ltd data to represent the developments of the sector. Subsurface swept-area-ratio was proportionally redistributed to cells in a 15 km radius of OWFs following the approach from Kruse et al. (2024), assuming that fishers would search for alternative fishing grounds nearby. To forecast the impacts of changes in maximum sea bottom temperature, we adjusted it using sea temperature anomalies between 2004–2012 and 2060–2069 derived from the ensemble mean of statistically downscaled Northwest European Shelf projection under an RCP 8.5 scenario (Mathis et al., 2019).

Predicted values of the indicator nodes for each cell of the regular grid, as provided by the Bayesian Network, were visualized using *ggplot2* (Wickham, 2016).

In addition, we visualized the current network of Natura 2000 areas obtained from EMODnet (<https://emodnet.ec.europa.eu/en/map-week-marine-natura-2000-sites>, last accessed January 2025) to show the overlap between conservation areas and the network indices for the different future scenarios.

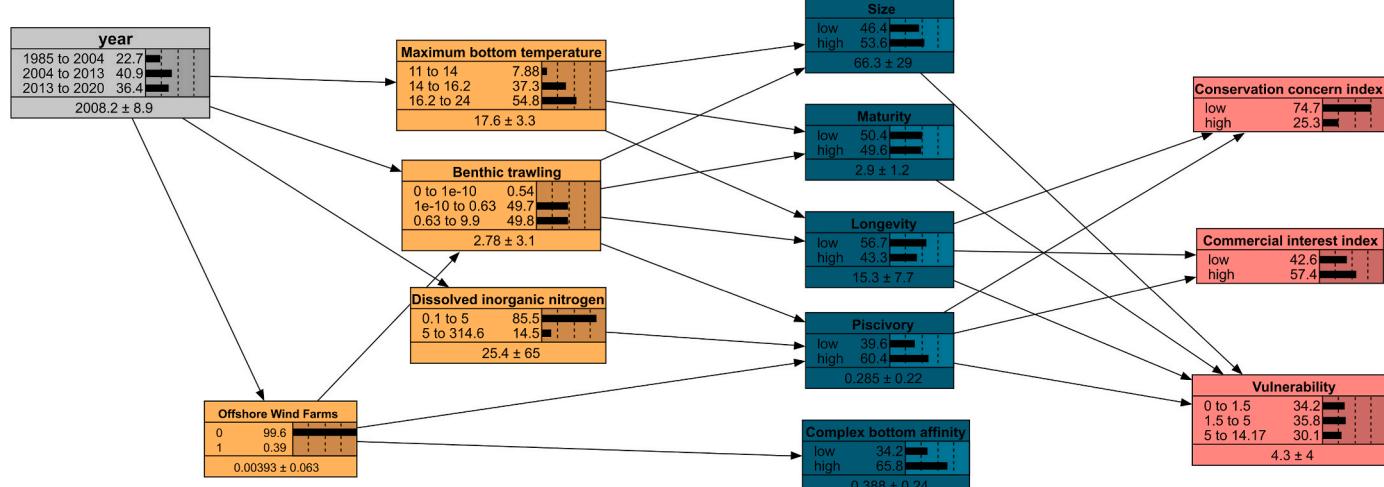


Fig. 2. The Bayesian Belief Network showing the causal structure (arrows) between the selected pressures (orange), traits (blue), and indicators (red). The bars in each node show the probability distribution for the different states, reflecting the likelihood of each state occurring given the network's current conditions and evidence.

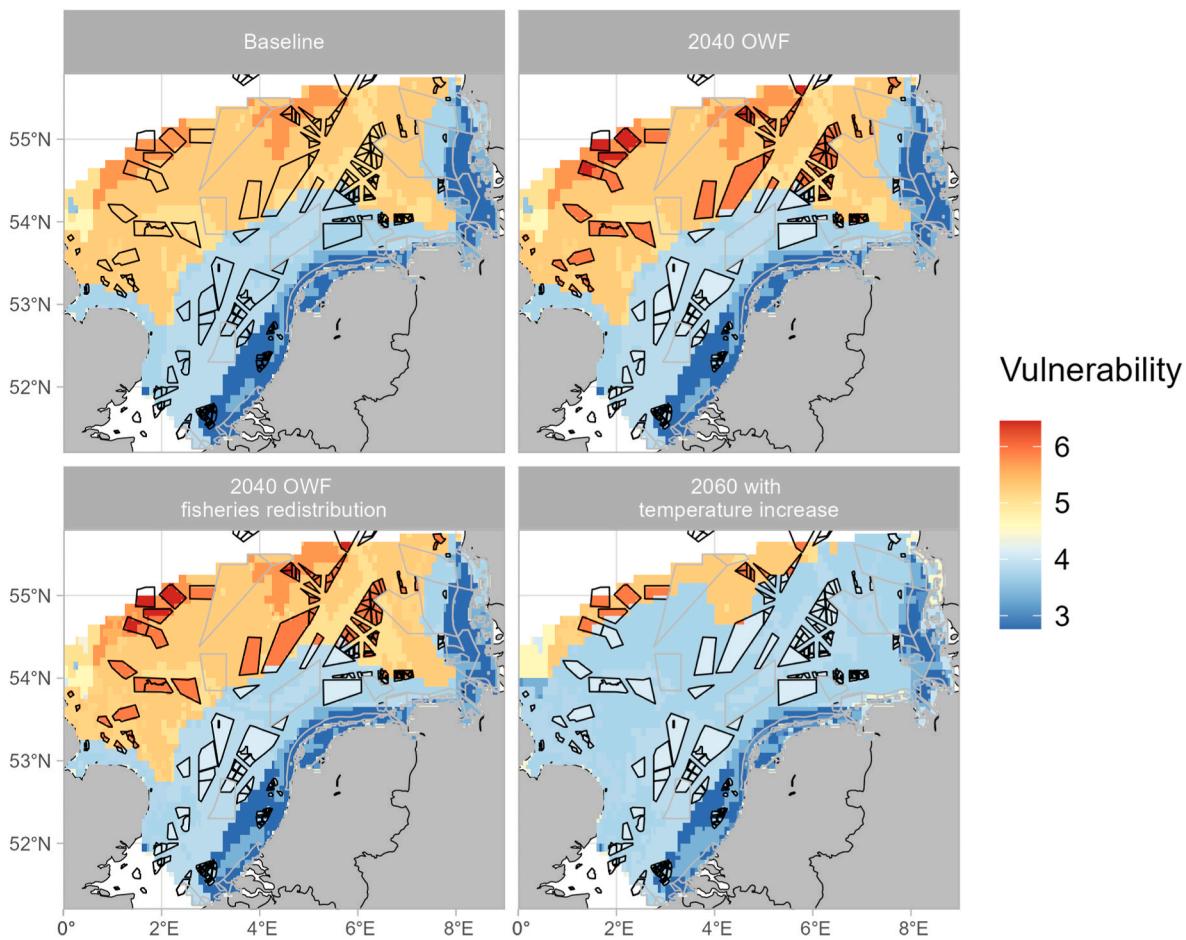


Fig. 3. Spatial distribution of the community vulnerability, based on the combination of vulnerable trait states. The vulnerability of the community to the selected pressures increases from blue to red. This reflects regions most at risk according to the network. Implemented and planned OWF areas are indicated by black lines, and Natura 2000 areas (<https://emodnet.ec.europa.eu/en/map-week-marine-natura-2000-sites>) are shown with grey lines.

3. Results

3.1. Model and model performance

The final network consisted of 13 nodes, with four nodes representing pressures, five trait nodes, and three indicator nodes (Fig. 2). The learned conditional probabilities of the trait nodes reflected the assumed cause-effect relationships well for most pressure-trait relationships. The exception was the effect of benthic trawling on the mean size of the fish community. While benthic trawling was associated with a decrease in the life history strategies, the effect on size was inverted under high temperatures (see Appendix B for the CPTs). Overall, only maximum bottom temperature had a strong effect on the trait nodes due to the correlative strength in the data. The other pressure nodes had only marginal effects on the traits. For piscivory, nitrogen had the strongest impact, followed by benthic trawling and OWF.

The integrated quasi cross-validation of the trait nodes provided relatively good metric values, with an error rate ranging between 29 % and 35 % and a spherical pay-off ranging from 0.74 to 0.77. For size, longevity, and maturity the model predicted the high state (66–74 % true high) and low state (62–70 % true low) equally well. While the model accurately predicted the high state of piscivory and complex bottom affinity with high precision (92–100 % true high), it performed poorly in predicting low states: only 16 % true low for piscivory and 0 % true for complex-habitat affinity.

The predicted maps of the most probable state of longevity and maturity compared with maps of the classified observed data, showed a

moderate agreement (0.47–0.55, Kappa, Appendix C). There was still fair agreement with the model predictions for size and piscivory (0.37–0.38, Kappa), but poor agreement for complex bottom affinity (0, Kappa).

3.2. Impact of future changes in the pressure landscape

The demersal fish community averaged over the training period (Baseline) showed a relatively high vulnerability to the here considered pressures in the northern part of the study area (Fig. 3). This is particularly due to the influence of temperature on late-maturing, large, and long-lived species. The relatively higher mean longevity of the community also predicted a higher probability for species of commercial interest and conservation concern in this area (Figs. 4 and 5). Less than 10 % of Natura 2000 sites overlap with areas of high vulnerability (>5) and high conservation concern (>0.25).

Under the expansion of OWFs (2040OWF), the vulnerability increased inside the OWF areas alongside a community shift towards more piscivory (Fig. 3). Mean longevity increases only inside OWFs in the southern part of the study area, as it is strongly influenced by temperature, accompanied by similar changes in the value of commercial interest inside OWFs. In contrast, the probability of species of conservation concern showed a considerable increase in OWF areas. The fisheries redistribution (2040OWF-Redistribution) had only highly localized effects on maturity and thus almost no effect on any of the indicator nodes (Figs. 3–5).

The predicted temperature increase by 2060, in contrast, had a

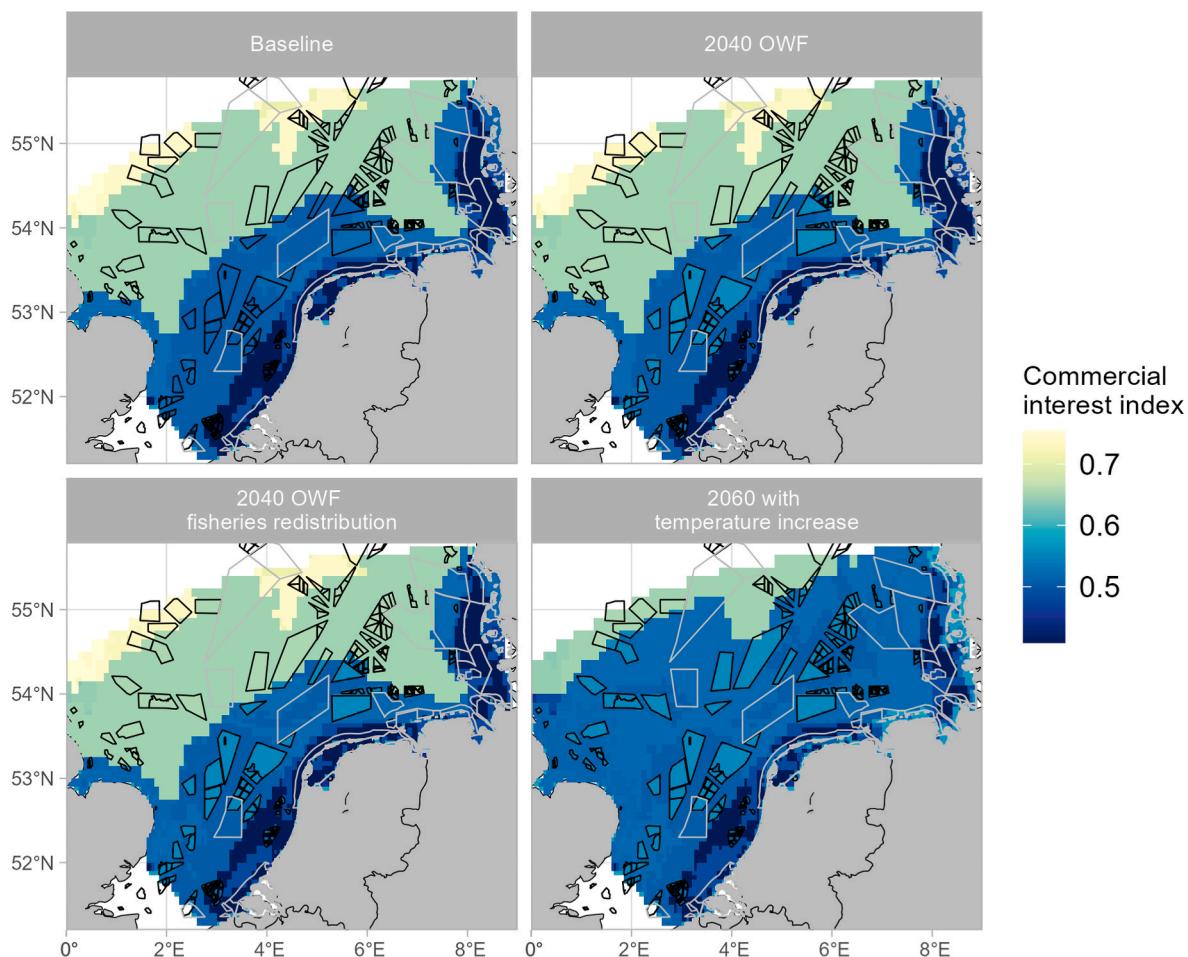


Fig. 4. Spatial distribution of the commercial interest index. The index represents the likelihood of a community hosting species of commercial interest, based on trait state combinations of longevity and piscivory. The node was parameterized by comparing the probabilities of species of commercial interest versus those without commercial interest within each trait combination. Lighter colours indicate areas of potential importance for fisheries as identified by the network. Implemented and planned OWF areas are indicated by black lines, and Natura 2000 areas (<https://emodnet.ec.europa.eu/en/map-week-marine-natura-2000-sites>) are shown with grey lines.

strong impact on the life-history traits and reduced the vulnerability area-wide (Fig. 3). Alongside this change in vulnerability was the decrease of the probability for species of conservation concern and commercial interest (Figs. 4 and 5). But the community vulnerability to cumulative pressures and the conservation concern index remained relatively stable inside OWF areas despite the strong temperature change, given the exclusion of the fisheries.

4. Discussion

We investigated the current and future vulnerabilities of demersal fish communities to key human pressures in the southern North Sea and increasing bottom temperature by combining a trait-based approach with a spatially explicit Bayesian Belief Network. The results of our integrated modelling framework show that the currently designated Natura 2000 areas have limited overlap with the fish communities most vulnerable to the here defined pressures. Furthermore, our findings indicate that the effects of OWF expansion and a potential spatial redistribution of fisheries appear to be limited at local scale and result in low to moderate changes in the spatial distribution of traits. In contrast, predicted temperature increases by 2060 lead to area-wide and substantial distribution shifts.

Our model was based on the effects of benthic trawling and temperature increases on species traits of demersal fish described in Rehren et al. (submitted). The North Sea has been fished intensively for more

than a century (Kerby et al., 2012), leading to a drastic decline of species which are vulnerable to fishing (e.g., elasmobranchs, Bennema and Rijnsdorp, 2015; Fock et al., 2014a; Fock et al., 2014b; Sguotti et al., 2016). Several studies on the changes in mean body size have demonstrated a clear correlation between fishing pressure and the shift towards smaller sizes both in terms of intraspecific and interspecific selection (Dulvy et al., 2003; Jennings et al., 2001; Law, 2000; Monk et al., 2021; Reynolds et al., 2005). Furthermore, empirical evidence indicates a decrease in body size with warming (Baudron et al., 2014; Daufresne et al., 2009; Lavin et al., 2022) and metabolic theory predicts that higher temperatures accelerate metabolic rates, growth, maturation, and mortality (Brown et al., 2004; Portner and Peck, 2010). These expected effects were also reflected in the correlation structure of the data, albeit to a much lesser extent for fishing compared to the increase in temperature. Overall, our modelling results indicated a very low impact of benthic trawling on the here defined traits. In areas with high temperatures ($>16.2^{\circ}\text{C}$), high fishing intensities were even associated with an increase in mean size. However, this is likely a mere association, indicating that coastal fisheries target larger fish. One of the reasons for the low impact of benthic trawling may relate to the fact that fishing and climate change already caused a shift of the trait composition of the demersal fish community (Beukhof et al., 2019; Hofstede et al., 2010; Jennings et al., 1999; Piet and Jennings, 2005). This past shift towards smaller, shorter-lived, faster-growing, and earlier maturing species may not be fully captured by our study period. While we anticipated direct

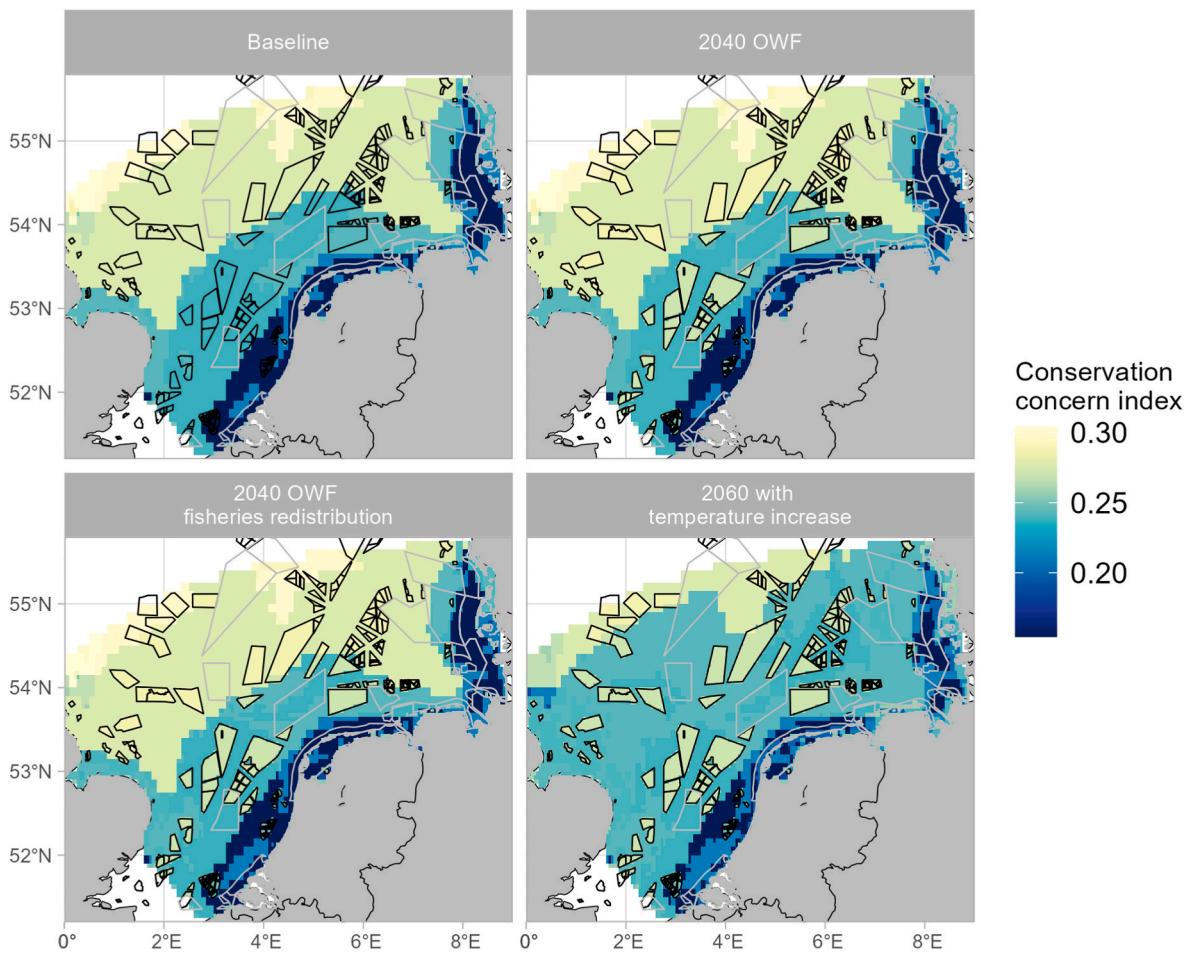


Fig. 5. Spatial distribution of the community conservation index. The index represents the likelihood of a community hosting species of conservation concern, based on trait state combinations of longevity and piscivory. The node was parameterized by comparing the probabilities of species of conservation concern versus those without conservation concern within each trait combination. Lighter colours indicate areas with a higher proportion of species of conservation concern, highlighting regions of potential ecological importance as identified by the network. Implemented and planned OWF areas are indicated by black lines, and Natura 2000 areas (<https://emodnet.ec.europa.eu/en/map-week-marine-natura-2000-sites>) are shown with grey lines.

effects of benthic trawling and temperature on the mean size of the fish community — since fisheries often disproportionately harvest large fish and large fish are less able to manage oxygen demands under warming — the strongest correlation with these pressures was observed for longevity. Longevity has been identified as a key trait to respond to trawling impacts on benthic invertebrates (Tillin et al., 2006) and is used in frameworks to assess the good environmental status of seabed communities (Rijnsdorp et al., 2020). In addition, our model predicted that nutrient enrichment had a higher impact on piscivory compared to benthic trawling and OWFs.

The predictions of the network showed a local increase in K-strategists, piscivory, and complex-bottom affinity by 2040 due to the potential reef effects of OWFs and the exclusion of benthic trawling activities inside the parks. It should be noted, however, that the model tends to overestimate the probability of high levels of piscivory and complex bottom-affinity within the fish community. We found fishing effort redistribution to have only low and highly localised effects on the life-history traits of the demersal fish community, which is partly due to the assumption that fishers tend to stay in the vicinity of their fishing grounds. The effects from benthic trawling and OWFs are strongly overshadowed by the modelled temperature increase, which caused a considerable and area-wide decrease in mean size, longevity, and maturity by 2060 in our network. These findings agree well with previous studies which demonstrated a strong impact of temperature on the mean size of fish communities in the North Sea (Beukhof et al., 2019;

Dulvy et al., 2008; Hofstede et al., 2010). The expansion of OWFs in our network alleviated some of the fishing pressure on the demersal fish community, resulting in areas in the south that still supported a relatively high mean longevity and piscivory in 2060. This resulted in a partial increase in the indices of species of conservation concern and vulnerability, confirming other findings on the role OWFs may play as potential refuge (Probst et al., 2021). Among those species of conservation concern in our data set are the sharks *Galeorhinus galeus* and *Squalus acanthias*, as well as the rays *Amblyraja radiata* and *Raja montagui*. Whether or not these species accumulate around OWFs is unclear, as a general lack of information on OWF impacts on elasmobranchs remains (Gill et al., 2024). In contrast, large piscivores that are associated with complex habitats, such as *Gadus morhua* have been shown to aggregate around OWFs (Bergström et al., 2013; Hal et al., 2017; Lindeboom et al., 2011; Werner et al., 2024; Wilber et al., 2022). While it is still debated whether this aggregation represents a true increase in production or merely a redistribution of biomass, there is growing evidence suggesting new production associated with OWFs (Gimpel et al., 2023; Reubens et al., 2013, 2014).

The fish communities with the highest vulnerability and abundance of species of conservation concern are predicted to be predominantly located in the northern part of the study area. This pattern arises from a community dominated by K-strategists and piscivory, which are generally more susceptible to disturbances (Winemiller and Rose, 1992). Given the model's tendency to overestimate high levels of piscivory, it

may slightly overestimate the spatial extent of areas characterised by high vulnerability. However, since vulnerability is an index derived from multiple traits, this effect may be less pronounced. In contrast, the indices for species of conservation concern and commercial interest only depend on piscivory and longevity. As a result, the model is likely to overestimate the areas with high values for these indices, and they should be interpreted with caution. In addition, large gadoids are found mostly in the northern North Sea, with higher mean sizes and age at first maturity. These areas experience less nutrient discharges, lower fishing pressure and cooler temperatures, and in some of these areas, highly vulnerable communities remain even after strong temperature increases in 2060. At the same time, these areas are central to the ambitious expansion of OWFs and notably, most Natura 2000 areas do not overlap with these vulnerable areas, a finding consistent with previous research examining the mismatch between core areas of demersal species and existing marine protected areas (Probst et al., 2021).

As with most ecological models, a limitation of our network is that it does not represent the full pressure landscape of the southern North Sea. However, the selected human pressures are expected to undergo substantial changes in the future, making them among the most critical factors to examine. While our model focuses on demersal fish, which are not the primary target of Natura 2000 protections, validating the need for additional protection in the identified areas could help strengthen conservation efforts of seafloor functioning. Predicting changes in the North Sea pressure landscape is inherently challenging, as it emerges from a complex social-ecological system and uncertain future developments. To address this issue, our analysis is based on plausible climate scenarios and established political targets. Given the limited understanding of how fisheries respond to spatial restrictions (Stelzenmüller et al., 2024b), we assume that fishers often act based on habit or tradition (Letschert et al., 2025) and that fishing effort will continue to decrease due to increasing spatial competition from other sectors (Stelzenmüller et al., 2024b). Even though the fishing effort scenarios used in our model may be considered conservative, the weak correlation structure between fishing and traits suggests that effort redistribution has only limited effects. Consequently, alternative scenarios within realistic boundaries are unlikely to produce substantially different outcomes in our model. In contrast to those localised effects, the strong area-wide effect of temperature highlights the need to account for climate change when assessing cumulative effects of human pressures (Stelzenmüller et al., 2020) and its relevance for effective climate-smart conservation planning.

The current model focuses on the operational phase of OWFs and incorporates species traits previously linked to positive responses (Hal et al., 2017; Krone et al., 2013; Methratta and Dardick, 2019; Stenberg et al., 2015), allowing us to explore the widely discussed potential benefits under specific conditions. As a result, our network predicts an increase in K-strategists and piscivores – a pattern that persists even under high temperature scenarios and highlights the need to understand whether OWFs can contribute to needed future ecosystem enhancement. However, across their lifecycle OWFs are also associated with negative impacts, including noise effects from pile driving activities (Mooney et al., 2020) or hydrological changes in the vicinity of the parks (Daewel et al., 2022). Quantifying these negative effects, particularly their influence on the trait distribution of demersal fish, remains challenging (Gill et al., 2024). In particular, a more comprehensive understanding of the net effects of OWFs requires the future adaptation of our model to also reflect negative impacts. In turn, such a comprehensive knowledge of the magnitude of OWF impacts requires improved data availability and continued research, including the use of new sampling methods (eDNA, optical, acoustic) to provide a representative overview of the demersal fish community and detect changes in trait composition over time. An orchestrated and harmonised sampling across European OWFs will be key to supporting such advances (ICES, 2025).

5. Conclusions

Recent plans to expand OWFs as part of achieving greenhouse gas neutrality by 2050 (Green Deal, European Commission, 2019), along with major shifts in key sectors such as fisheries and rising sea temperatures due to climate change, are expected to significantly alter the pressure landscape in the southern North Sea. Our trait-based modelling framework incorporates multiple human-induced pressures alongside climate change, enabling the assessment of their combined effects on fish traits. This approach allowed us to examine how spatial patterns of fish community vulnerability may shift under future pressure scenarios in the region. Our findings indicate that rising bottom temperatures will lead to a widespread reduction in K-strategists, whereas the habitat changes caused by OWF developments have more localised effects on the trait distribution. While our model is constrained by the current availability of empirical data on ecological impacts, its integrated and flexible design provides a means to explicitly assess the net effects of OWFs on marine functional diversity. These results support the continued use of trait-based approaches to mechanistically evaluate the cumulative effects of pressures on fish communities. Such integrated methods are particularly valuable in data-limited contexts, where understanding the direction and magnitude of combined human impacts on individual species remains a major challenge. These approaches are needed to anticipate ecological trade-offs and can inform more adaptive conservation and marine spatial planning at appropriate scales by identifying both pressure hotspots and sensitive communities amidst competing demands from biodiversity, energy, and fisheries.

CRediT authorship contribution statement

Jennifer Rehren: Writing – review & editing, Writing – original draft, Visualization, Methodology, Formal analysis, Data curation, Conceptualization. **Maren Kruse:** Writing – review & editing, Methodology, Conceptualization. **W. Nikolaus Probst:** Writing – review & editing, Funding acquisition, Data curation. **Cesc Gordó-Vilaseca:** Writing – review & editing, Conceptualization. **Carsten Lemmen:** Writing – review & editing, Funding acquisition, Data curation. **Shubham Krishna:** Writing – review & editing, Data curation. **Vanessa Stelzenmüller:** Writing – review & editing, Supervision, Resources, Methodology, Funding acquisition, Formal analysis, Data curation, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.jenvman.2025.126727>.

Data availability

Data will be made available on request.

References

Baudron, A.R., Needle, C.L., Rijnsdorp, A.D., Marshall, C.T., 2014. Warming temperatures and smaller body sizes: synchronous changes in growth of north sea fishes. *Glob Chang Biol* 20, 1023–1031. <https://doi.org/10.1111/gcb.12514>.

Bennema, F.P., Rijnsdorp, A.D., 2015. Fish abundance, fisheries, fish trade and consumption in sixteenth-century Netherlands as described by adriaen coenen. *Fish. Res.* 161, 384–399. <https://doi.org/10.1016/j.fishres.2014.09.001>.

Bergström, L., Sundqvist, F., Bergström, U., 2013. Effects of an offshore wind farm on temporal and spatial patterns in the demersal fish community. *Mar. Ecol. Prog. Ser.* 485, 199–210. <https://doi.org/10.3354/meps10344>.

Beukhof, E., Dencker, T.S., Pecuchet, L., Lindegren, M., 2019. Spatio-temporal variation in marine fish trials reveals community-wide responses to environmental change. *Mar. Ecol. Prog. Ser.* 610, 205–222. <https://doi.org/10.3354/meps12826>.

Boettiger, C., Chamberlain, S., Temple Lang, D., Wainwright, P., 2023. Rfishbase: R Interface to Fishbase.

Breitburg, D.L., Hondorp, D.W., Davias, L.A., Diaz, R.J., 2009. Hypoxia, nitrogen, and fisheries: integrating effects across local and global landscapes. *Ann. Rev. Mar. Sci.* 1, 329–349. <https://doi.org/10.1146/annurev.marine.010908.163754>.

Brown, J.H., Gilloly, J.F., Allen, A.P., Savage, V.M., West, G.B., 2004. Toward a metabolic theory of ecology. *Ecology* 85, 1771–1789. <https://doi.org/10.1890/03-9000>.

Burchard, H., Bolding, K., 2002. GETM: a General Estuarine Transport Model; Scientific Documentation. European Commission, Joint Research Centre, Institute for Environment and Sustainability.

Butt, N., Halpern, B.S., O'Hara, C.C., Allcock, A.L., Polidoro, B., Sherman, S., Byrne, M., Birkeland, C., Dwyer, R.G., Frazier, M., Woodworth, B.K., Arango, C.P., Kingsford, M.J., Udyawer, V., Hutchings, P., Scanes, E., McClaren, E.J., Maxwell, S. M., Diaz-Pulido, G., Dugan, E., Simmons, B.A., Wenger, A.S., Linardich, C., Klein, C. J., 2021. A trait-based framework for assessing the vulnerability of marine species to human impacts. *Ecosystems* 13, 17. <https://doi.org/10.1002/ecs2.3919>.

Camargo, J.A., Alonso, A., 2006. Ecological and toxicological effects of inorganic nitrogen pollution in aquatic ecosystems: a global assessment. *Environ. Int.* 32, 831–849. <https://doi.org/10.1016/j.envint.2006.05.002>.

Cheung, W.W.L., Sarmiento, J.L., Dunne, J., Frölicher, T.L., Lam, V.W.Y., Deng Palomares, M.L., Watson, R., Pauly, D., 2013. Shrinking of fishes exacerbates impacts of global ocean changes on marine ecosystems. *Nat. Clim. Change* 3, 254–258. <https://doi.org/10.1038/nclimate1691>.

Chevenet, F., Doledec, S., Chessel, D., 1994. A fuzzy coding approach for the analysis of long-term ecological data. *Freshw. Biol.* 31, 295–309. <https://doi.org/10.1111/j.1365-2427.1994.tb01742.x>.

Daewel, U., Akhtar, N., Christiansen, N., Schrum, C., 2022. Offshore wind farms are projected to impact primary production and bottom water deoxygenation in the north sea. *Commun. Earth Environ.* 3. <https://doi.org/10.1038/s43247-022-00625-0>.

Dannheim, J., Bergstrom, L., Birchenough, S.N.R., Brzana, R., Boon, A.R., Coolen, J.W.P., Dauvin, J.C., De Mesel, I., Dereweduun, J., Gill, A.B., Hutchison, Z.L., Jackson, A.C., Janas, U., Martin, G., Raoux, A., Reubens, J., Rostin, L., Vanaverbeke, J., Wilding, T. A., Wilhelmsen, D., Degraer, S., 2020. Benthic effects of offshore renewables: identification of knowledge gaps and urgently needed research. *ICES J. Mar. Sci.* 77, 1092–1108. <https://doi.org/10.1093/icesjms/fsz018>.

Daufréne, M., Lengfellner, K., Sommer, U., 2009. Global warming benefits the small in aquatic ecosystems. *Proceedings of the National Academy of Sciences of the United States of America* 106, 12788–12793. <https://doi.org/10.1073/pnas.0902080106>.

Degraer, S., Carey, D.A., Coolen, J.W.P., Hutchison, Z.L., Kerckhof, F., Rumes, B., Vanaverbeke, J., 2020. Offshore wind farm artificial reefs affect ecosystem structure and functioning: a synthesis. *Oceanography (Wash. D. C.)* 33, 48–57. <https://doi.org/10.5670/oceanog.2020.405>.

Ducrotoy, J.-P., Elliott, M., de Jonge, V. N., 2000. The north sea. *Mar. Pollut. Bull.* 41 (1–6), 5–23. [https://doi.org/10.1016/S0025-326X\(00\)00099-0](https://doi.org/10.1016/S0025-326X(00)00099-0).

Dulvy, N.K., Rogers, S.I., Jennings, S., Stelzenmüller, V., Dye, S.R., Skjoldal, H.R., 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>.

Dulvy, N.K., Sadovy, Y., Reynolds, J.D., 2003. Extinction vulnerability in marine populations. *Fish Fish.* 4, 25–64. <https://doi.org/10.1046/j.1467-2979.2003.00105.x>.

Emes, K.-C., Beusekom, J. van, Callies, U., Ebinghaus, R., Kannen, A., Kraus, G., Kröncke, I., Lenhart, H., Lorkowski, I., Matthias, V., Möllmann, C., Pätsch, J., Scharfe, M., Thomas, H., Weisse, R., Zorita, E., 2015. The north sea — a shelf sea in the anthropocene. *J. Mar. Syst.* 141, 18–33. <https://doi.org/10.1016/j.jmarsys.2014.03.012>.

European Commission, 2019. A European Green Deal: Striving to Be the First climate-neutral Continent.

Fock, Heino O., Kloppmann, M.H.F., Probst, W.N., 2014a. An early footprint of fisheries: changes for a demersal fish assemblage in the German bight from 1902–1932 to 1991–2009. *J. Sea Res.* 85, 325–335. <https://doi.org/10.1016/j.seares.2013.06.004>.

Fock, H.O., Probst, W.N., Schaber, M., 2014b. Patterns of extirpation. II. The role of connectivity in the decline and recovery of elasmobranch populations in the german bight as inferred from survey data. *Endanger. Species Res.* 25, 209–223. <https://doi.org/10.3354/esr00583>.

Froese, R., Pauly, D., 2023. Fishbase. World wide web electronic publication.

Gill, A.B., Bremner, J., Vanstaen, K., Blake, S., Mynott, F., Lincoln, S., 2024. Limited evidence base for determining impacts (or not) of offshore wind energy developments on commercial fisheries species. *Fish Fish.* 26, 155–170. <https://doi.org/10.1111/faf.12871>.

Gimpel, A., Werner, K.M., Bockelmann, F.D., Haslob, H., Kloppmann, M., Schaber, M., Stelzenmüller, V., 2023. Ecological effects of offshore wind farms on atlantic cod (*gadus morhua*) in the southern north sea. *Science of the total environment* 878. <https://doi.org/10.1016/j.scitotenv.2023.162902>.

Glarou, M., Zrust, M., Svendsen, J., 2020. Using artificial-reef knowledge to enhance the ecological function of offshore wind turbine foundations: implications for fish abundance and diversity. *J. Mar. Sci. Eng.* <https://doi.org/10.3390/JMSE8050332>.

Gordo-Vilaseca, C., Costello, M.J., Coll, M., Juterbock, 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>.

Gusatu, L.F., Menegon, S., Depellegrin, D., Zuidema, C., Faaij, A., Yamu, C., 2021. Spatial and temporal analysis of cumulative environmental effects of offshore wind farms in the north sea basin. *Sci. Rep.* 11, 10125. <https://doi.org/10.1038/s41598-021-89537-1>.

Hal, R. van, Griffioen, A.B., Keeken, O.A. van, 2017. Changes in fish communities on a small spatial scale, an effect of increased habitat complexity by an offshore wind farm. *Mar. Environ. Res.* 126, 26–36. <https://doi.org/10.1016/j.marenres.2017.01.009>.

Halpern, B.S., Walbridge, S., Selkoe, K.A., Kappel, C.V., Michel, F., D'Agrosa, C., Bruno, J.F., Casey, K.S., Ebert, C., Fox, H.E., Fujita, R., Heinemann, D., Lenihan, H.S., Madin, E.M.P., Perry, M.T., Selig, E.R., Spalding, M., Steneck, R., Watson, R., 2008. A global map of human impact on marine ecosystems. *Science* 319, 948–952. <https://doi.org/10.1126/science.1149345>.

Hijmans, R.J., 2023. Raster: Geographic Data Analysis and Modeling.

Hofstede, R. ter, Hiddink, J.G., Rijnsdorp, A.D., 2010. Regional warming changes fish species richness in the eastern north atlantic ocean. *Mar. Ecol. Prog. Ser.* 414, 1–9. <https://doi.org/10.3354/meps08753>.

ICES, 2021. Data for OSPAR request on the production of spatial data layers of fishing intensity/pressure. Data Outputs. <https://doi.org/10.17895/ices.data.8294>.

ICES, 2025. Workshop to scope for harmonized regional monitoring schemes to assess the impact of offshore wind farms on fish, pelagic and benthic communities and ecosystem functions (WKOMO). *ICES Scientific Reports* 7 (73), 57. <https://doi.org/10.17895/ices.pub.29370575>.

Jennings, S., Alvsågå, J., Cotter, A.J.R., Ehrlich, S., Greenstreet, S.P.R., Jarre-Teichmann, A., Mergardt, N., Rijnsdorp, A.D., Smedstad, O., 1999. Fishing effects in northeast atlantic shelf seas: patterns in fishing effort, diversity and community structure. III. International trawling effort in the north sea: an analysis of spatial and temporal trends. *Fish. Res.* 40, 125–134. [https://doi.org/10.1016/S0165-7836\(98\)00208-2](https://doi.org/10.1016/S0165-7836(98)00208-2).

Jennings, S., Greenstreet, S.P.R., Reynolds, J.D., 2001. Structural change in an exploited fish community: a consequence of differential fishing effects on species with contrasting life histories. *J. Anim. Ecol.* 68, 617–627. <https://doi.org/10.1046/j.1365-2656.1999.00312.x>.

Jones, M.C., Cheung, W.W.L., 2018. Using fuzzy logic to determine the vulnerability of marine species to climate change. *Glob Chang Biol* 24, e719–e731. <https://doi.org/10.1111/gcb.13869>.

Kerby, T.K., Cheung, W.W.L., Engelhard, G.H., 2012. The united kingdom's role in north sea demersal fisheries: a hundred year perspective. *Rev. Fish Biol. Fish.* 22, 621–634. <https://doi.org/10.1007/s11160-012-9261-y>.

Kerimoglu, O., Hofmeister, R., Maerz, J., Riethmüller, R., Wirtz, K.W., 2017. The acclimative biogeochemical model of the southern north sea. *Biogeosciences* 14, 4499–4531. <https://doi.org/10.5194/bg-14-4499-2017>.

Kraan, C., Haslob, H., Probst, W.N., Stelzenmüller, V., Rehren, J., Neumann, H., 2024. Thresholds of seascape fauna composition along gradients of human pressures and natural conditions to inform marine spatial planning. *Sci. Total Environ.* 914, 169940. <https://doi.org/10.1016/j.scitotenv.2024.169940>.

Krone, R., Gutow, L., Brey, T., Dannheim, J., Schröder, A., 2013. Mobile demersal megafauna at artificial structures in the german bight - likely effects of offshore wind farm development. *Estuar. Coast Shelf Sci.* 125, 1–9. <https://doi.org/10.1016/j.ecss.2013.03.012>.

Kruse, M., Letschert, J., Cormier, R., Rambo, H., Gee, K., Kannen, A., Schaper, J., Mollmann, C., Stelzenmüller, V., 2024. Operationalizing a fisheries social-ecological system through a bayesian belief network reveals hotspots for its adaptive capacity in the southern north sea. *J. Environ. Manage.* 357, 120685. <https://doi.org/10.1016/j.jenvman.2024.120685>.

Kuhn, M., 2023. Caret: Classification and Regression Training.

Larsner, T., Barz, F., 2023. Küstenfischerei 2045 - erste zielbilder der zukunftswerkstatt. Zeitschrift für Fischerei. <https://doi.org/10.35006/FISCHZEIT.2023.22>.

Lavin, C.P., Gordó-Vilaseca, C., Costello, M.J., Shi, Z., Stephenson, F., Grüss, A., 2022. Warm and cold temperatures limit the maximum body length of teleost fishes across a latitudinal gradient in norwegian waters. *Environ. Biol. Fish.* 105, 1415–1429. <https://doi.org/10.1007/s10641-022-01270-4>.

Law, R., 2000. Fishing, selection, and phenotypic evolution. *ICES (Int. Coun. Explor. Sea) J. Mar. Sci.* 57, 659–668. <https://doi.org/10.1006/jmsc.2000.0731>.

Lemmen, C., Hofmeister, R., Klingbeil, K., Nasrmoaddeli, M.H., Kerimoglu, O., Burchard, H., Kösters, F., Wirtz, K.W., 2018. Modular system for shelves and coasts (MOSSCO v1.0) – a flexible and multi-component framework for coupled coastal ocean ecosystem modelling. *Geosci. Model Dev. (GMD)* 11, 915–935. <https://doi.org/10.5194/gmd-11-915-2018>.

Letschert, J., Müller, B., Dressler, G., Möllmann, C., Stelzenmüller, V., 2025. Simulating fishery dynamics by combining empirical data and behavioral theory. *Ecol. Model.* 501, 111036. <https://doi.org/10.1016/j.ecolmodel.2025.111036>.

Lindeboom, H.J., Kouwenhoven, H.J., Bergman, M.J.N., Bouma, S., Brasseur, S., Daan, R., Fijn, R.C., Haan, D. de, Dirksen, S., Hal, R. van, Lambers, R.H.R., Ter Hofstede, R., Krijgsveld, K.L., Leopold, M., Scheidat, M., 2011. Short-term ecological effects of an offshore wind farm in the dutch coastal zone; a compilation. *Environ. Res. Lett.* 6. <https://doi.org/10.1088/1748-9326/6/3/035101>.

Marcot, B.G., 2012. Metrics for evaluating performance and uncertainty of bayesian network models. *Ecol. Model.* 230, 50–62. <https://doi.org/10.1016/j.ecolmodel.2012.01.013>.

Mathis, M., Elizalde, A., Mikolajewicz, U., 2019. The future regime of atlantic nutrient supply to the northwest european shelf. *J. Mar. Syst.* 189, 98–115. <https://doi.org/10.1016/j.jmarsys.2018.10.002>.

Mathis, M., Pohlmann, T., 2014. Projection of physical conditions in the north sea for the 21st century. *Clim. Res.* 61, 1–17. <https://doi.org/10.3354/cr01232>.

Methratta, E.T., Dardick, W.R., 2019. Meta-analysis of finfish abundance at offshore wind farms. *Reviews in Fisheries Science & Aquaculture* 27, 242–260. <https://doi.org/10.1080/23308249.2019.1584601>.

Monk, C.T., Bekkevold, D., Klefot, T., Pagel, T., Palmer, M., Arlinghaus, R., 2021. The battle between harvest and natural selection creates small and shy fish. *Proc. Natl. Acad. Sci. U. S. A.* 118. <https://doi.org/10.1073/pnas.2009451118>.

Mooney, A., Andersson, M., Stanley, J., 2020. Acoustic impacts of offshore wind energy on fishery resources: an evolving source and varied effects across a wind farm's lifetime. *Oceanography (Wash. D. C.)* 33, 82–95. <https://doi.org/10.5670/oceanog.2020.408>.

O'Hara, C.C., Halpern, B.S., 2022. Anticipating the future of the world's ocean. *Annu. Rev. Environ. Resour.* 47, 291–315. <https://doi.org/10.1146/annurev-environ-120120-053645>.

Pebesma, E., Graeler, B., 2023. *Gstat: Spatial and spatio-temporal Geostatistical Modelling, Prediction and Simulation*.

Piet, G.J., Jennings, S., 2005. Response of potential fish community indicators to fishing. *ICES (Int. Counc. Explor. Sea) J. Mar. Sci.* 62, 214–225. <https://doi.org/10.1016/j.icesjms.2004.09.007>.

Portner, H.O., Peck, M.A., 2010. Climate change effects on fishes and fisheries: towards a cause-and-effect understanding. *J. Fish. Biol.* 77, 1745–1779. <https://doi.org/10.1111/j.1095-8649.2010.02783.x>.

Probst, W.N., Stelzenmüller, V., Rambo, H., Moriarty, M., Greenstreet, S.P.R., 2021. Identifying core areas for mobile species in space and time: a case study of the demersal fish community in the north sea. *Biol. Conserv.* 254, 108946. <https://doi.org/10.1016/j.biocon.2020.108946>.

Radach, G., Pätzsch, J., 2007. *Variability of continental riverine freshwater and nutrient inputs into the North Sea for the years 1977–2000 and its consequences for the assessment of eutrophication*. *Estuar. Coast* 30, 66–81.

Raoux, A., Lassalle, G., Pezy, J.P., Teechio, S., Safi, G., Ernande, B., Mazé, C., Le Loc'h, F., Lequesne, J., Girardin, V., Dauvin, J.C., Niquil, N., 2019. Measuring sensitivity of two OSPAR indicators for a coastal food web model under offshore wind farm construction. *Ecol. Indic.* 96, 728–738. <https://doi.org/10.1016/j.ecolind.2018.07.014>.

Rehren, J., Probst, W.N., Kraan, C., Neumann, H., Krishna, S., Hasenbein, M., Örey, S., Ludwig, K., Wirtz, K.W., Lemmen, C., Gimpel, A., Stelzenmüller, V., submitted. Unravelling cumulative effects of human pressures on demersal fish traits using a driver-pressure-state-impact framework. *Mar. Environ. Res.*

Reubens, J.T., Degraer, S., Vincx, M., 2014. The ecology of benthopelagic fishes at offshore wind farms: a synthesis of 4 years of research. *Hydrobiologia* 727, 121–136. <https://doi.org/10.1007/s10750-013-1793-1>.

Reubens, J.T., Vandendriessche, S., Zenner, A.N., Degraer, S., Vincx, M., 2013. Offshore wind farms as productive sites or ecological traps for gadoid fishes?—impact on growth, condition index and diet composition. *Mar. Environ. Res.* 90, 66–74. <https://doi.org/10.1016/j.marenvres.2013.05.013>.

Reynolds, J.D., Dulvy, N.K., Goodwin, N.B., Hutchings, J.A., 2005. Biology of extinction risk in marine fishes. *Proc. Biol. Sci.* 272, 2337–2344. <https://doi.org/10.1098/rspb.2005.3281>.

Rijnsdorp, A.D., Hiddink, J.G., Denderen, P.D. van, Hintzen, N.T., Eigaard, O.R., Valanko, S., Bastardie, F., Bolam, S.G., Boulcott, P., Egekvist, J., Garcia, C., Hoey, G. van, Jonsson, P., Laffargue, P., Nielsen, J.R., Piet, G.J., Sköld, M., Kooten, T. van, Degraer, S., 2020. Different bottom trawl fisheries have a differential impact on the status of the north sea seafloor habitats. *ICES (Int. Counc. Explor. Sea) J. Mar. Sci.* 77, 1772–1786. <https://doi.org/10.1093/icesjms/fsaa050>.

Sguotti, C., Lynam, C.P., García-Carreras, B., Ellis, J.R., Engelhard, G.H., 2016. Distribution of skates and sharks in the north sea: 112 years of change. *Glob. Change Biol.* 22, 2729–2743. <https://doi.org/10.1111/gcb.13316>.

Slavik, K., Lemmen, C., Zhang, W., Kerimoglu, O., Klingbeil, K., Wirtz, K.W., 2019. The large-scale impact of offshore wind farm structures on pelagic primary productivity in the southern north sea. *Hydrobiologia* 845, 35–53. <https://doi.org/10.1007/s10750-018-3653-5>.

Stelzenmüller, V., Coll, M., Cormier, R., Mazaris, A.D., Pascual, M., Loiseau, C., Claudet, J., Katsanevakis, S., Gissi, E., Evangelopoulos, A., Rumes, B., Degraer, S., Ojaveer, H., Moller, T., Gimenez, J., Piroddi, C., Markantonatou, V., Dimitriadis, C., 2020. Operationalizing risk-based cumulative effect assessments in the marine environment. *Sci. Total Environ.* 724, 138118. <https://doi.org/10.1016/j.scitotenv.2020.138118>.

Stelzenmüller, V., Coll, M., Mazaris, A.D., Giakoumi, S., Katsanevakis, S., Portman, M.E., Degen, R., Mackelworth, P., Gimpel, A., Albano, P.G., Almpanidou, V., Claudet, J., Essl, F., Evangelopoulos, T., Heymans, J.J., Genov, T., Kark, S., Micheli, F., Pennino, M.G., Rilov, G., Rumes, B., Steenbeek, J., Ojaveer, H., 2018. A risk-based approach to cumulative effect assessments for marine management. *Sci. Total Environ.* 612, 1132–1140. <https://doi.org/10.1016/j.scitotenv.2017.08.289>.

Stelzenmüller, V., Ellis, J.R., Rogers, S.I., 2010. Towards a spatially explicit risk assessment for marine management: assessing the vulnerability of fish to aggregate extraction. *Biol. Conserv.* 143, 230–238. <https://doi.org/10.1016/j.biocon.2009.10.007>.

Stelzenmüller, V., Letschert, J., Blanz, B., Blöcker, A.M., Claudet, J., Cormier, R., Gee, K., Held, H., Kannen, A., Kruse, M., Rambo, H., Schaper, J., Sguotti, C., Stollberg, N., Quiroga, E., Möllmann, C., 2024a. Exploring the adaptive capacity of a fisheries social-ecological system to global change. *Ocean Coast Manag.* 258. <https://doi.org/10.1016/j.ocecoaman.2024.107391>.

Stelzenmüller, V., Rehren, J., Örey, S., Lemmen, C., Krishna, S., Hasenbein, M., Püts, M., Probst, W.N., Diekmann, R., Scheffran, J., Bos, O.G., Wirtz, K., 2024b. Framing future trajectories of human activities in the german north sea to inform cumulative effects assessments and marine spatial planning. *J. Environ. Manage.* 349, 119507. <https://doi.org/10.1016/j.jenvman.2023.119507>.

Stenberg, C., Stottrup, J.G., Deurs, M. van, Berg, C.W., Dinesen, G.E., Mosegaard, H., Grome, T.M., Leonhard, S.B., 2015. Long-term effects of an offshore wind farm in the north sea on fish communities. *Mar. Ecol. Prog. Ser.* 528, 257–265. <https://doi.org/10.3354/meps11261>.

Tillin, H.M., Hiddink, J.G., Jennings, S., Kaiser, M.J., 2006. Chronic bottom trawling alters the functional composition of benthic invertebrate communities on a sea-basin scale. *Mar. Ecol. Prog. Ser.* 318, 31–45. <https://doi.org/10.3354/meps318031>.

Utne-Palm, A.C., 2002. Visual feeding of fish in a turbid environment: physical and behavioural aspects. *Mar. Freshw. Behav. Physiol.* 35, 111–128. <https://doi.org/10.1080/10236240290025644>.

Voß, J., Knaack, J., Von weber, M., 2009. *“Okologische Zustandsbewertung der deutschen Übergangs- und Küstengewässer 2009. Ecological Assessment of German Transitional and Coastal Waters*.

Watson, S.C.L., Somerfield, P.J., Lemasson, A.J., Knights, A.M., Edwards-Jones, A., Nunes, J., Pascoe, C., McNeill, C.L., Schratzberger, M., Thompson, M.S.A., Couce, E., Szostek, C.L., Baxter, H., Beaumont, N.J., 2024. The global impact of offshore wind farms on ecosystem services. *Ocean Coast Manag.* 249. <https://doi.org/10.1016/j.ocecoaman.2024.107023>.

Weinert, M., Mathis, M., Kröncke, I., Neumann, H., Pohlmann, T., Reiss, H., 2016. Modelling climate change effects on benthos: distributional shifts in the North Sea from 2001 to 2099. *Estuar. Coast Shelf Sci.* 175, 157–168. <https://doi.org/10.1016/j.ecss.2016.03.024>. ISSN 0272-7714.

Wenger, A.S., Harvey, E., Wilson, S., Rawson, C., Newman, S.J., Clarke, D., Saunders, B. J., Browne, N., Travers, M.J., McIlwain, J.L., Erftemeijer, P.L.A., Hobbs, J.P.A., McLean, D., Depczynski, M., Evans, R.D., 2017. A critical analysis of the direct effects of dredging on fish. *Fish. Fish.* 18, 967–985. <https://doi.org/10.1111/faf.12218>.

Werner, K.M., Haslob, H., Reichel, A.F., Gimpel, A., Stelzenmüller, V., 2024. Offshore wind farm foundations as artificial reefs: the devil is in the detail. *Fish. Res.* 272. <https://doi.org/10.1016/j.fishres.2024.106937>.

Wickham, H., 2016. *ggplot2: Elegant Graphics for Data Analysis*. Springer-Verlag, New York, ISBN 978-3-319-24277-4. <https://ggplot2.tidyverse.org>.

Wilber, D.H., Brown, L., Griffin, M., Decelles, G.R., Carey, D.A., 2022. Demersal fish and invertebrate catches relative to construction and operation of north america's first offshore wind farm. *ICES (Int. Counc. Explor. Sea) J. Mar. Sci.* 79, 1274–1288. <https://doi.org/10.1093/icesjms/fsac051>.

Wilhelms, I., 2013. *Atlas of length-weight relationships of 93 fish and crustacean species from the north sea and the north-east atlantic* Thünen working paper 12 (Report). Johann Heinrich von Thünen-Institut, Braunschweig, pp. 18–23. <https://nbn-resolving.de/urn:nbn:de:gbv:253-201311-dn052688-4>.

Winemiller, K.O., Rose, K.A., 1992. Patterns of life-history diversification in north american fishes: implications for population regulation. *Can. J. Fish. Aquat. Sci.* 49, 2196–2218. <https://doi.org/10.1139/f92-242>.

Wirtz, K.W., 2019. Physics or biology? Persistent chlorophyll accumulation in a shallow coastal sea explained by pathogens and carnivorous grazing. *PLoS One* 14, e0212143. <https://doi.org/10.1371/journal.pone.0212143>.

Wirtz, K.W., Hofmeister, R., Klingbeil, K., Lemmen, C., 2024. MOSSCO Southern North Sea Long-term benthic-pelagic ecosystem simulation 1961–2012. World Data Center for Climate (WDCC) at DKRZ. https://doi.org/10.26050/WDCC/MOSSCO_sim_1961-2012.

Xu, X., Lemmen, C., Wirtz, K.W., 2020. Less nutrients but more phytoplankton: Long-term ecosystem dynamics of the southern north sea. *Front. Mar. Sci.* 7. <https://doi.org/10.3389/fmars.2020.00062>.