



Thresholds of seascape fauna composition along gradients of human pressures and natural conditions to inform marine spatial planning

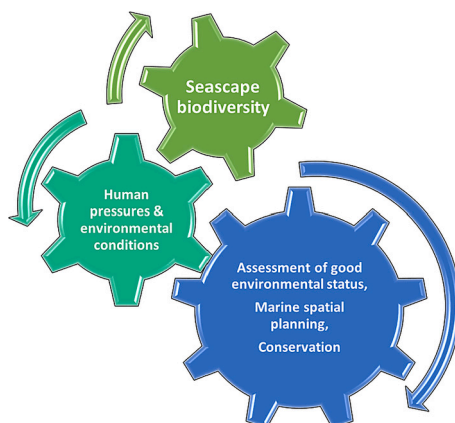
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HIGHLIGHTS

- Marine biodiversity is impacted by human activities and environmental conditions
- Using community data enables a holistic approach to identify critical human pressures and environmental conditions
- Defining thresholds of human pressures and environmental conditions informs management and conservation measures
- Spatial planning requires an integrated assessment framework covering multiple species

GRAPHICAL ABSTRACT



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ABSTRACT

Knowledge about the cumulative impacts of anthropogenic activities and environmental conditions on marine ecosystems is incomplete and details are lacking. Compositional community changes can occur along gradients, and community data can be used to assess the state of community resilience against combined impacts of variables representing human pressures and environmental conditions. Here we use a machine learning approach, i. e., Gradient Forest, to identify explanatory variable thresholds and select relevant epibenthic fauna and demersal fish species, which can be used to inform an integrated management of multiple human pressures and conservation planning in the southern North Sea. We show that a broad selection of anthropogenic and environmental variables, such as natural disturbance of the seafloor and euphotic depth, determined community composition thresholds of 67 epibenthic fauna and 39 demersal fish species along environmental conditions and human pressure gradients in the southern North Sea between 2010 and 2020. This has the potential to inform resilience assessments under the Marine Strategy Framework Directive to promote and retain a good environmental status of marine ecosystems.

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1. Introduction

In the marine domain, many areas are exposed to increasing cumulative anthropogenic impacts, such as fisheries and climate change (e.g., Halpern et al., 2015; Duarte et al., 2020), which often interact with varying environmental conditions, such as sediment features, topography, freshwater input and bottom shear stress (e.g., Couce et al., 2020). Knowledge about the key human-driven pressures or environmental conditions that have the most impact on the marine ecosystem state is critical to inform marine spatial planning (MSP) and biodiversity conservation efforts (Halpern et al., 2015; Couce et al., 2020; Stelzenmüller et al., 2020; Gissi et al., 2021). Preferably, such management and conservation efforts go beyond a single-species-single-pressure approach, since co-occurring species respond differently to the same pressures, potentially resulting in community-level thresholds or tipping points at other levels than assumed or predicted for single species (Rilov et al., 2019). Indeed, mitigation success, expressed as recovery rates of marine ecological structure, functions, resilience, and ecosystem services (Duarte et al., 2020), requires an ecosystem approach that acknowledges such complexity.

A well-known framework aiming for the implementation of an ecosystem approach to environmental protection and nature conservation is the European Marine Strategy Framework Directive (MSFD), in which achieving or maintaining a 'good environmental status (GES)' is a central premise (e.g., Borja et al., 2013). In theory, when this status is realized, human activities shall cause no significant adverse effects to marine ecosystems. As yet, the understanding of which community features represent good environmental status and how they are affected by cumulative anthropogenic pressures and environmental conditions is often incomplete and subject to ongoing research and development (see HELCOM HOLAS III and OSPAR Quality Status Report 2023 for reference). We have yet to understand where along different gradients of human pressures or environmental conditions major changes in community composition occur (Couce et al., 2020), or how many and which species should be included in ecosystem assessments to inform on system resilience and tipping points (Borja et al., 2010, 2013).

Here we address these gaps and use a machine learning approach to explore thresholds of human pressures and environmental conditions and select relevant epibenthic fauna and demersal fish species to inform management and conservation efforts in the southern North Sea. The southern North Sea is a past and a present global hotspot for research, MSP, and co-occurring cumulative impacts on the marine ecosystem (Emeis et al., 2015; Halpern et al., 2015; Stenseth et al., 2020; Moullec et al., 2021; Solaun et al., 2021). Moreover, this area will remain the centre of future offshore renewable developments, consequently, there exists a large potential for conflict between human activities and maintaining or achieving a GES in a system with high rates of natural disturbances (Stelzenmüller et al., 2022).

To date, few approaches exist to perform community modelling along variable gradients, i.e., constrained canonical analysis (CCA), generalized dissimilarity modelling (GDM) and Gradient Forest (GF; see Pitcher et al., 2012 for a comparison of methods). We use the latter, which extend random forest models (Breiman, 2001) for single species to multispecies responses to variable gradients (Ellis et al., 2012; Pitcher et al., 2012). GF models fit an ensemble of regression or classification trees for predicting the distribution of organisms as a function of explanatory variables (Ellis et al., 2012; Pitcher et al., 2012). As sentinels for capturing biotic changes, we use epibenthic fauna and demersal fish communities. Epibenthos consists of rather stationary and long-lived species. They are important for nutrient cycling, ecosystem functioning (e.g., by providing habitat structure, such as biogenic reefs), and as a food source for higher trophic levels (e.g., Birchenough et al., 2015). Additionally, epibenthic species are sensitive to human impacts such as demersal fishing, making them a good indicator for seabed habitats vulnerable to anthropogenic impacts. Some demersal fish species have a large commercial value, they are of key importance in international

marine policies and conservation measures, and their distribution is strongly linked to anthropogenic pressures and environmental conditions (Ehrich et al., 2009; Neumann et al., 2013; Sell and Kröncke, 2013; Probst et al., 2021).

The specific aims of this study are (1) to identify distinct epibenthos and demersal fish communities in the southern North Sea and (2) to determine the dominant variables associated with these distinct communities. Moreover, we (3) examine the composition of the identified communities to identify potential indicator species, and, finally, (4) quantify variable threshold levels at which changes in community composition occur.

2. Methods

2.1. Biotic data

We used epibenthic fauna data from the international offshore beam-trawl surveys (BTS; ICES, 2021), downloaded from the ICES open-access database of trawl surveys (DATRAS; <https://www.ices.dk/data/data-portals/Pages/DATRAS.aspx>). We limited these to Dutch data only (1075 trawls in total, 73–114 trawls annually) since these matched our area of interest, i.e., the southern North Sea, covering the years 2010–2020 (Fig. 1). Data comprised standardized (per 30 min. trawl) epibenthos biomass of 167 operational taxonomic units (called species hereafter) caught with an 8 m beam-trawl. This species definition accommodates the existence of species complexes, in which specimen are not identifiable to species level.

Demersal fish data, encompassing the southern North Sea as well, were compiled from the DYFS (Demersal Young Fish Survey; e.g., Tulp et al., 2016), BTS, IBTS (North Sea International Bottom-Trawl Survey), and GASEEZ (German Autumn Survey Exclusive Economic Zone) monitoring programs (e.g., Neumann et al., 2013). DYFS, BTS and IBTS data are available at DATRAS; GASEEZ data were extracted from the Thünen-database. Between 2010 and 2020, 4213 trawls (274–543 trawls annually) have been conducted (Fig. 1) with eight types of standardized trawling gears (dominated by 8 m beam-trawl and GOV), recording the biomass (kg/km^2) of 70 demersal fish taxa identified to species-level. Trawl duration was 30 min with a tow speed of 4–5.5 knots (ICES, 2021).

Prior to modelling, biomass was $\log(x + \min(x, x > 0))$ -transformed. All species were included in the analysis, since species with no predictive power ($R^2 < 0$) are omitted automatically from the combined estimate of species turnover.

2.2. Explanatory variables

We selected 21 commonly used anthropogenic and environmental variables for their likely role in structuring epibenthic and demersal fish communities (e.g., Neumann et al., 2017; Couce et al., 2020; Weinert et al., 2021). Each was downloaded from an open-access portal, cropped to the extent of the study area (WGS84; Latitude ranges from 0.5 to 8.5 degrees, Longitude ranges from 51 to 57 degrees), rasterized ('raster' package [Hijmans, 2020] in R [R Core Team, 2021]) to 0.05×0.05 degrees, and overlaid with sampling points to extract values. Extensive meta-data, describing each modelled and interpolated variable, are available from their sources cited below (see Supplementary material SM Table 1). Moreover, predictions were limited to the 'training area' to avoid problems with model transferability (see Yates et al., 2018; Meyer and Pebesma, 2021).

Collinearity between variables was checked, but we decided to exclude none a priori due to correlations generally being <0.7 (see Dormann et al., 2013). Furthermore, random forests have been demonstrated to be rather insensitive to collinearity of predictor variables (Breiman, 2001).

2.3. Gradient Forest

To model gradients of explanatory variables and changes in epibenthic fauna and demersal fish community composition, we used GF (Ellis et al., 2012; Pitcher et al., 2012; available online at: <http://gradientforest.r-forge.r-project.org/>). GF is an extension of random forest modelling (Breiman, 2001; Prasad et al., 2006) to the community level, which fits an ensemble of regression tree models between individual species biomass and explanatory variables. From these, GF accumulates standardized measures of species changes along explanatory variable gradients for each species and uses them to assess compositional change for each explanatory variable (Ellis et al., 2012; Leaper et al., 2011; Pitcher et al., 2012). Contrary to random forest, this enables us to determine if changes in community composition occur along explanatory variable gradients and if these changes are continuous or occur at thresholds (Pitcher et al., 2012; Large et al., 2015; Couce et al., 2020).

We ran GF in R (R Core Team, 2021), using the packages ‘extendedForest’ (version 1.6.1; Liaw and Wiener, 2002) and ‘gradientForest’ (version 0.1_18; Ellis et al., 2012). We used a forest of 1000 bootstrapped trees for each species, where each tree was fitted to a random subsample (~2/3 by default) of observations. Each split was selected from a random subset out of 21 explanatory variables. The predictive performance for each species (R^2) was assessed with cross-validation using the remaining (~1/3) observations. To account for correlation between explanatory variables, we used a conditional approach (see Strobl et al., 2008; Smith et al., 2011) with standard settings to determine explanatory variable importance (Ellis et al., 2012; Pitcher et al., 2012). Species composition gradients were weighted by species importance (R^2) and explanatory variable importance, where explanatory variable importance was estimated by the degradation of performance when randomly permuting each predictor (Ellis et al., 2012; Pitcher et al., 2012). We assumed that spatial autocorrelation was neglectable, due to the large distances between sampling points (see, e.g., Kraan et al., 2010; Pitcher et al., 2012).

Finally, we employed the standard transformation of explanatory

variables using the cumulative importance curves for each explanatory variable (Ellis et al., 2012; Pitcher et al., 2012), which resulted in a prediction space of turnover in community composition for each explanatory variable. Then, we predicted epibenthic fauna and demersal fish community compositions across 19,200 new locations at a 0.05×0.05 degree grid resolution. Finally, we used a Principal Component Analysis (PCA), function PRCOMP in R, to reduce the dimension of 21 explanatory variables to the first three principal components for plotting (Thomson et al., 2014). Pitcher et al. (2020) provides an extensive GF tutorial in R.

3. Results

We fitted GF models separately to biomass information of 167 epibenthic species, 70 demersal fish species, and a broad selection of anthropogenic and environmental variables (see Supplementary material SM Table 1) to determine community composition thresholds along explanatory variable gradients in the southern North Sea. In total, 67 epibenthic species and 39 demersal fish species were associated with the selected explanatory variables ($R^2 > 0$). For epibenthos, we captured on average 25 % (range: 0.9 % for *Thia scutellata* - 82 % for *Astropecten irregularis*) of the variation in species distributions (Supplementary material SM Fig. 1). For demersal fish, we captured on average 29 % (range: 0.8 % for *Lophius budegassa* - 72 % for *Hippoglossoides platessoides*) of the variation in species distributions (Supplementary material SM Fig. 1).

All 21 selected explanatory variables contributed to predicting epibenthos and demersal fish distributions (Fig. 2). When ranking these explanatory variables in order of their contribution, the ten most important ones for epibenthos were euphotic depth (*eupd*), bottom phosphate concentration (*bpbo*), both range (*rmsst*) and mean sea surface temperature (*msst*), bottom oxygen concentration (*boxy*), temperature of the seabed (*tbed*), distance to land (*ldis*), tidal range (*tide*), primary production (*pp*), and depth (*depth*). Amongst others, median grain size (*mgs*), mud content (*mud*) and man-made constructions, such

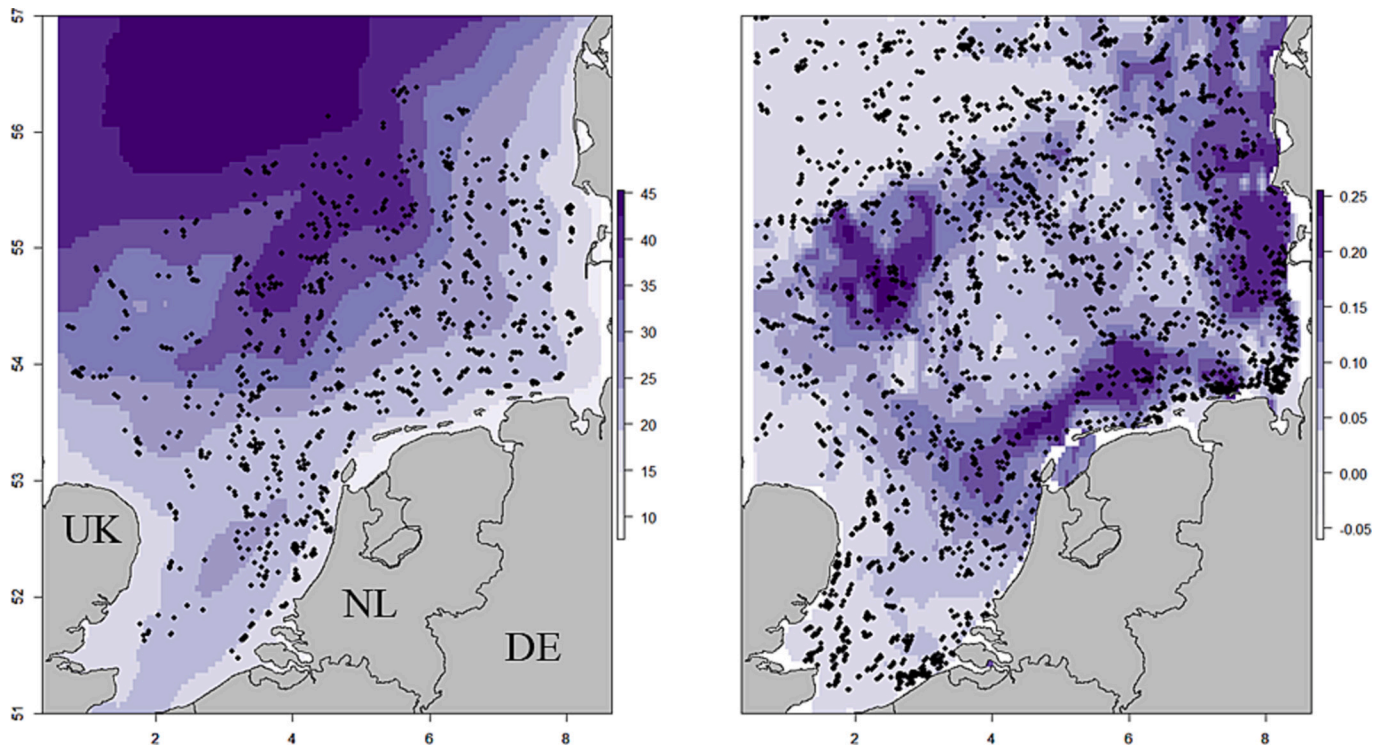


Fig. 1. The geographical distribution of epibenthos (left) and demersal fish (right) sampling stations (dots) in the southern North Sea. Purple colors indicate “Euphotic depth (m)” (left) and “Variation in natural seafloor disturbance rate (%)” (right), the most important explanatory variables identified by GF for each community.

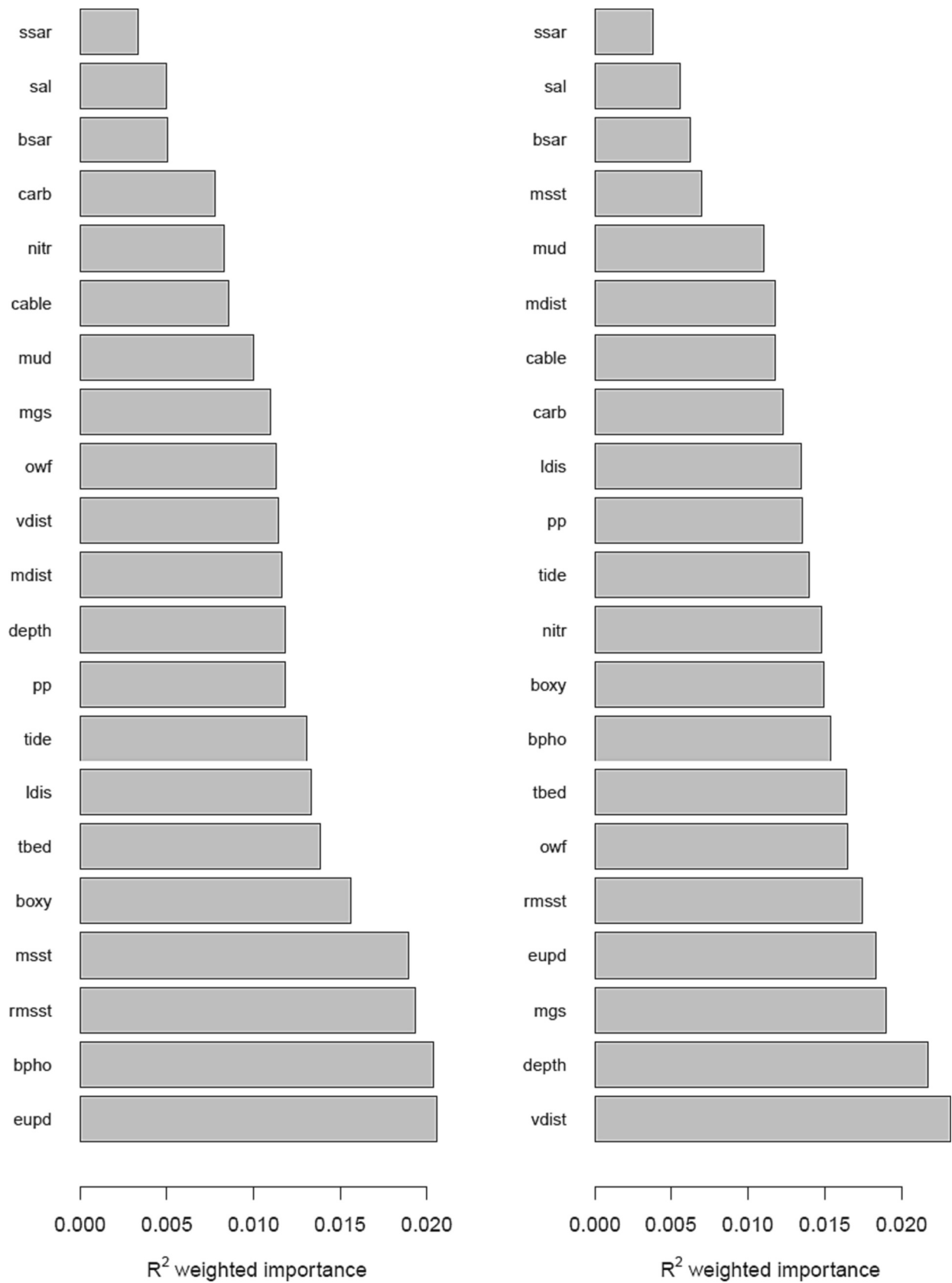


Fig. 2. Overall conditional explanatory variable importance for predicting epibenthos (left) and demersal fish (right) distributions. See text for the abbreviation of the most important explanatory variables and Supplementary material SM Table 1 for the remaining ones.

as distance to power lines (*cable*) and offshore wind farms (*owf*), ranked somewhere mid-field. Mean surface swept-area-ratio (*ssar*), an indicator of bottom-touching fishing pressure, ranked least important (Fig. 2). For demersal fish, the ten highest-ranking explanatory variables consisted of natural variation in bottom disturbance (*vdist*), depth, median grain size, euphotic depth, range of mean sea surface temperature, seabed temperature, distance to offshore wind farms, bottom phosphate concentration, bottom oxygen concentration, and nitrate concentration at the seabed (*nitrr*). Amongst others, mud content, distance to cables and distance to land (*ldis*) ranked mid-field. Mean surface swept-area ratio ranked as least important (Fig. 2).

We identified thresholds of epibenthic fauna and demersal fish distributions, so pinpointing where community changes are occurring, by frequency histograms of split importance (Fig. 3; Supplementary material SM Fig. 2). Each of the explanatory variables had a unique role in changing epibenthic fauna and demersal fish community composition (Fig. 3; Supplementary material SM Fig. 2). For epibenthos, for example, along the euphotic depth gradient, thresholds occurred around 20 m and around 30–42 m. Along the range of sea surface mean temperature gradient, thresholds occurred at a range of 8–11.5 °C and around 16 °C, whereas along the tidal range gradient a threshold occurred at a tidal range of about >1.5 m. For demersal fish, for example, along the natural variation in bottom disturbance gradient, a threshold occurred around

10 %. Along the depth gradient, a threshold occurred at a depth range of 40–90 m, whereas along the median grain size gradient a threshold occurred at phi-values of 0–2 (coarse sand, 1–2 mm grain size) and 3.5–4 (very fine sand, 62.5–125 µm grain size) (Fig. 3; Supplementary material SM Fig. 2).

A predictive map can show epibenthic fauna and demersal fish community changes in geographical space, based on the most important explanatory variables associated with that change (Fig. 4; see Pitcher et al., 2012). For example, epibenthic community changes in the southern part of our study area were mainly related to temperature (*msst* and *tbed*), whereas bottom phosphate concentration and euphotic depth was related to changes in the north. For demersal fish, seabed temperature was related to community changes in the southern part and along the coasts of our study area. In central regions, natural variation in seafloor disturbance and depth were important variables related to demersal fish community changes.

Individual species have a different sensitivity to individual explanatory variables (Supplementary material SM Table 2). Species that show a strong response to an explanatory variable might qualify as ‘indicator’ species for that explanatory variable in the MSFD framework. For example, the distribution of the Norway lobster *Nephrops norvegicus* was strongly related to increasing mud content (*mgs* and *mud*) (Supplementary material SM Table 2). The sand sea star (*Astropecten irregularis*) was

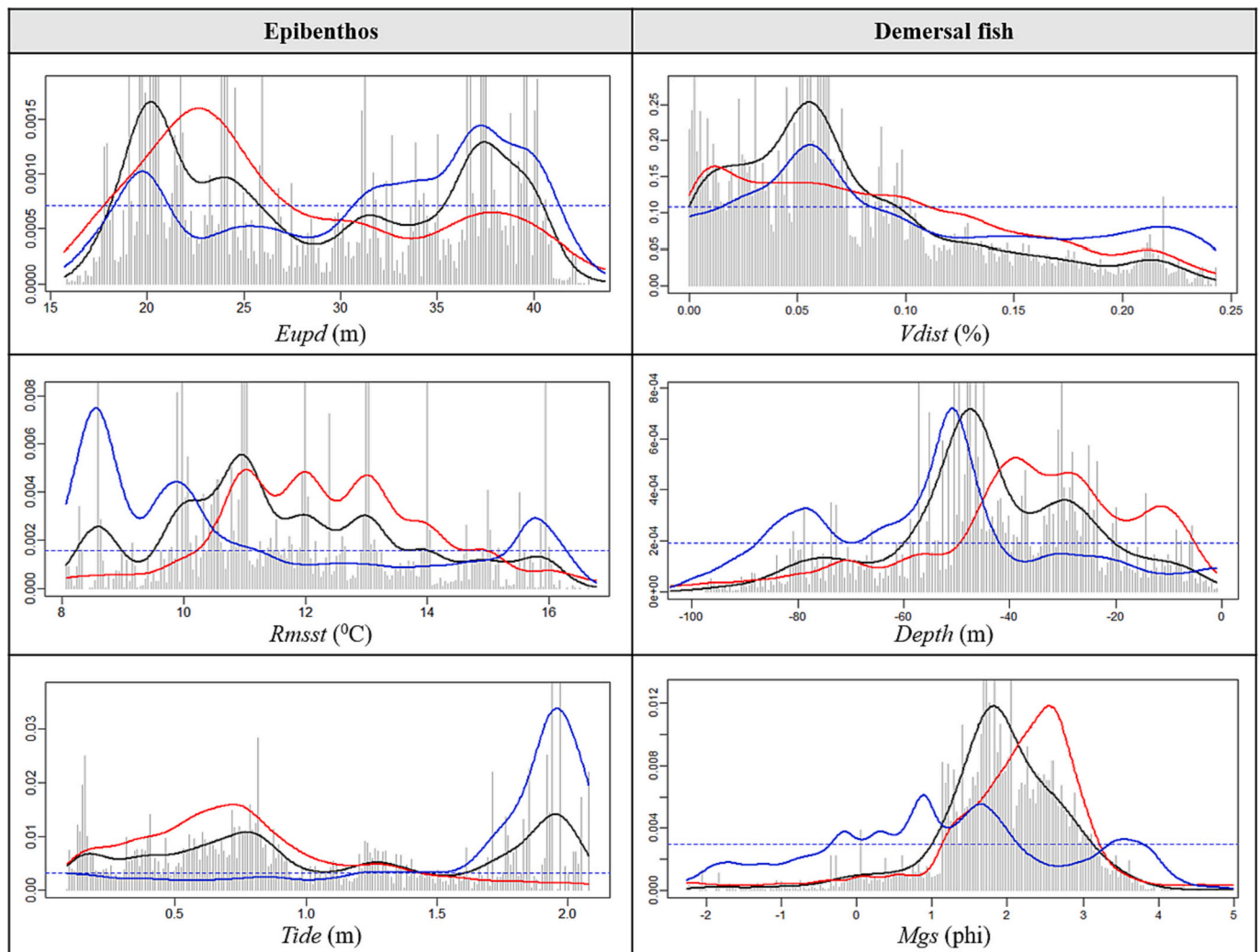


Fig. 3. Frequency histograms of splits location and importance (spikes) on gradient values for three important explanatory variables, showing compositional changes in epibenthic fauna and demersal fish community. Black lines show the kernel density of the histograms, red lines show the normalized distribution of the data along explanatory variable gradients, and the blue line represents the split density standardized by the density of the data. Ratios >1 (above dotted line) indicate a relatively greater change in epibenthos and demersal fish species composition (Supplementary material SM Fig. 2 shows all explanatory variables).

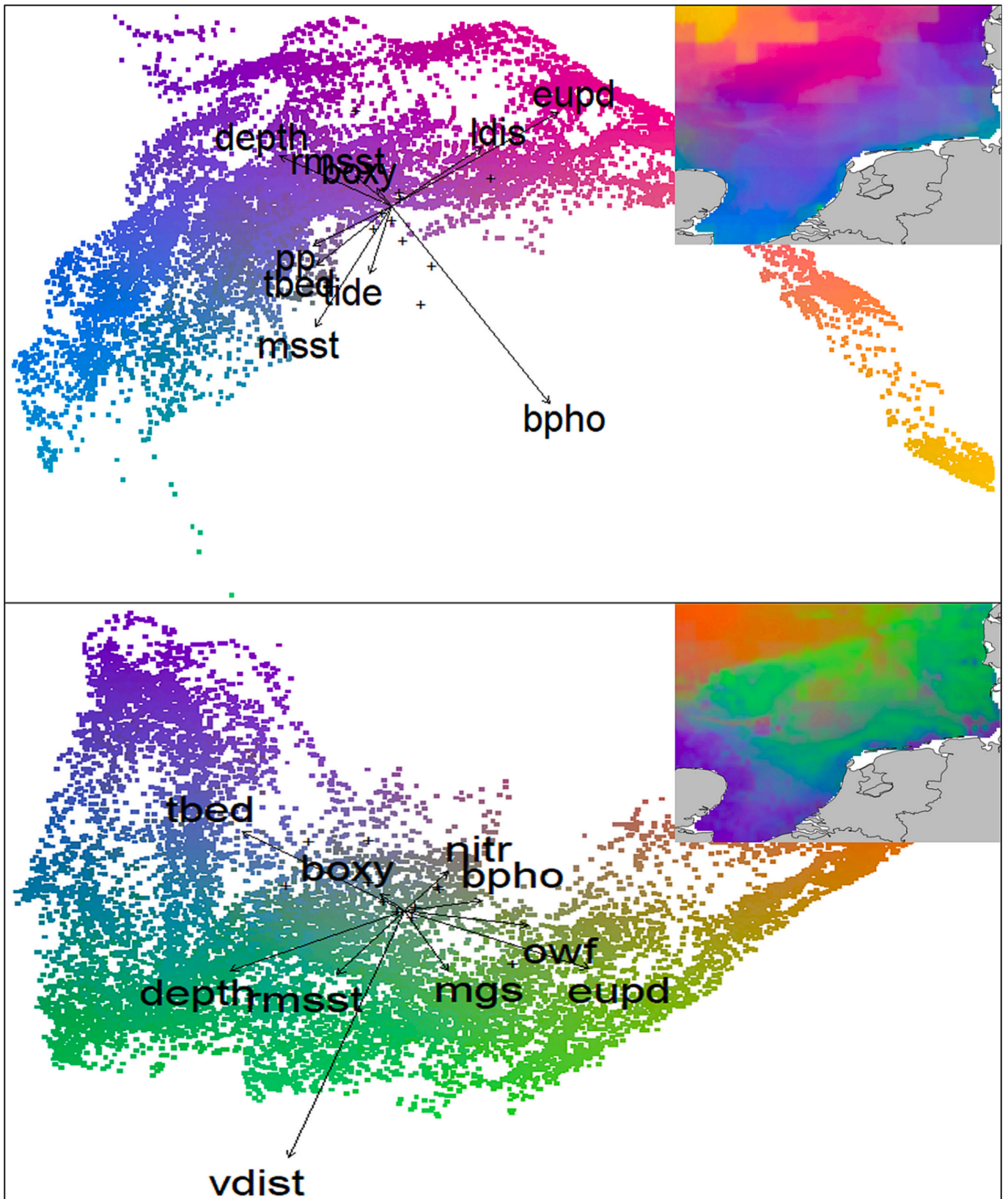


Fig. 4. Changes of epibenthic fauna (top) and demersal fish (bottom) community composition predicted by GF for the ten most important explanatory variables (inset). We mapped these changes over the first two dimensions of a biologically transformed explanatory variable space that accounts for their respective influence in dictating compositional patterns (PC1 and PC2 capture 72 % (epibenthos) and 78 % (demersal fish) of the variation respectively). The color key shows the explanatory variables most associated with those compositional changes, where arrows indicate the direction and magnitude of explanatory variables.

strongly related to phosphate-enriched sediments, whereas the common whelk (*Buccinum undatum*) was related to increasing mean sea surface water temperatures (Supplementary material SM Table 2). The distribution of the grey gurnard *Eutrigla gurnardus* was strongly associated with light penetration into the water (Supplementary material SM Table 2). American plaice (*Hippoglossoides platessoides*) was related to increasing variation in natural disturbance of the seafloor, as well as shallow depths (Supplementary material SM Table 2).

4. Discussion

We used Gradient Forest (Ellis et al., 2012; Pitcher et al., 2012) to determine where compositional changes of epifauna and fish communities occur in the southern North Sea along gradients of anthropogenic pressures and environmental conditions. We found that a broad selection of anthropogenic and environmental variables determined community composition, and identified the explanatory variable levels at which changes in community composition occurred. Moreover, we assessed which species were associated with these human pressures and environmental conditions at this large scale, and therefore might be candidate-indicators for management or monitoring measures. For example, Norway lobster could serve as indicator for muddy habitats. Consequently, our results can aid in informing GES assessments under MSFD to promote adequate conservation measures.

Marine management and conservation efforts require and have access to ever-increasing data-volumes, increasingly complex technical approaches, and increasing amounts of detail to be able to address cumulative impacts of human pressures and environmental conditions on marine ecosystems at relevant resolution (e.g., Solaun et al., 2021). A major challenge in assessing GES, or most other MSP success indicators that require biodiversity monitoring, is accommodating climate change effects, since such effects result in shifting baselines (Dayton et al., 1998; Kenny et al., 2009; Elliott et al., 2015). Key signals of climate change are changes in the temperature regime, which leads to species redistribution or (local) extinctions (Weinert et al., 2021) and consequently to changes in community structure. Indeed, our GF analysis showed that explanatory variables related to temperature generally were important for predicting epibenthos and demersal fish distributions. Particularly in the south of the southern North Sea (English Channel) and along the coasts, sea surface temperature was important in dictating composition patterns. Along the coast, due to their shallow depths, temperature change has a large impact on benthos and demersal fish biodiversity, most likely related to loss of suitable habitat and demographic changes resulting in recruitment and spawning failure (e.g., Andresen et al., 2013). This corroborates previous studies (Hinz et al., 2011; Neumann and Kröncke, 2011; Rombouts et al., 2012; Weinert et al., 2016), suggesting that continued warming enables species to move northward due to increased suitable habitat ('Lusitanian' species, such as Anchovy *Engraulis encrasicolus*). On the other hand, species may recede northwards due to increasingly unsuitable habitat ('Boreal' species, such as Atlantic cod *Gadus morhua*) (see Jiming, 1982; Dulvy et al., 2008).

In offshore areas in the north of the southern North Sea, euphotic depth, natural variation in bottom disturbance (Wilson et al., 2018), depth, and distance to land are structuring epibenthos and demersal fish distributions. These are all elements from the overarching factor mixing and ultimately stratification (Emeis et al., 2015). Whereas coastal habitats have a mixed water column throughout the year, summer stratification increases offshore and results in lower seasonal temperature variation than in the coastal areas. In addition, coastal water masses are diluted by freshwater run-off from rivers and salinity increases at decreasing nutrient concentrations offshore (Becker et al., 1992). Climate change leads to more stable stratification with increasing stratification seen in the North of our study area (cf. Emeis et al., 2015), and changes therein determine epibenthos and demersal fish community composition.

Man-made constructions, such as power cables and offshore wind farms, were explanatory variables of intermediate importance. Perhaps this illustrates that their impact on epibenthos and demersal fish communities was not captured at the appropriate spatial scale in our approach, since samples from within an offshore windfarm are rarely available due to restricted access (Stelzenmüller et al., 2022). This suggests the need for an improved research-agenda with a focus on local impacts of man-made constructions on epibenthos and demersal fish fauna, since these represent a rapidly expanding industry in the North Sea with a large conflict potential with other marine resource users (Letschert et al., 2021; Schupp et al., 2021; Stelzenmüller et al., 2022).

Contrary to Couce et al. (2020), the impact of bottom trawling was of limited importance in driving community patterns in the period under consideration. Perhaps this demonstrates how scale-dependent and prone to overestimation demersal fisheries-impact assessments can be (see Amoroso et al., 2018), in which we focused on a much higher spatially resolved and therefore more conservative fishing impact. Another potential reason for this discrepancy might be our large number of important stressors included in the analysis compared to Couce et al. (2020). This allowed an increasingly detailed joint consideration of varying habitat features and fisheries impact (van der Reijden et al., 2018; Hintzen et al., 2021), enabling suitable benthic fauna and demersal fish habitats to remain relatively unimpacted, rather than generalizing and lumping across habitats. Consequently, our results reflect that in the southern North Sea there is a long tradition of bottom-trawling fisheries since the early 1900s (e.g., Frid et al., 2000; Fock, 2008), and many major epibenthos and demersal fish community changes have already occurred. The current epibenthic fauna and demersal fish communities likely are composed of species resilient to a certain degree of chronic bottom-touching fishing impact. In addition, estimating SAR-values relies on processing and modelling VMS-data (Hintzen et al., 2012). During this process, a number of assumptions are made, such as vessel fishing speed, interpolating fishing tracks, and spatial resolution, which all influence estimated SAR-values (Amoroso et al., 2018). Consequently, there are ongoing discussions about the need to increase ping-rates to improve high-resolution assessments of fishing impacts on the sea bottom (Lambert et al., 2012). Moreover, fishing, epibenthic fauna, and demersal fish data are based on trawled gears, which therefore excludes certain rock and boulder areas that damage such gears (Neumann et al., 2013).

Various attempts have been made to select representative species that can serve as indicator-species, for example, under the MSFD D1 (biological diversity) indicator development requirements. Here, Sarrazin et al. (2021) created a list of North Sea fish species based on an approach that combines species distributions, life-history-traits and conservation measures, retaining sensitive and threatened species. Although there is overlap in potential indicator species, our approach to assign species as indicator is purely data-driven and focused on species associated with the human pressures and environmental conditions we included in the analysis. Therefore, our emphasis is geared towards human impacts and environmental changes in the ecosystem, rather than maintaining biodiversity. Ultimately, a combination of both approaches would be critical to advance the assessment of ecosystem features listed in the MSFD, in which GF informs on the constraints explanatory variables impose on species communities and where changes in their occurrence occurs, whereas current MSFD indicators are used to track single flagship species within these communities.

5. Conclusions

Fundamental gaps remain about quantifying cumulative impacts on marine ecosystems (Halpern et al., 2019), which hampers targeted mitigation efforts and MPA development. In a worst-case scenario, under such changing conditions, species might shift distributions and occur outside MPAs, as shown for demersal fish (Probst et al., 2021). Our work offers an important way forward and demonstrates that multiple

human and natural variables are associated with epibenthos and demersal fish community composition, although the magnitude differs greatly between single species and different faunas. Some species are rather structured by biotic interactions (Dormann et al., 2018; Kraan et al., 2020), or explanatory variables we failed to include, whereas others are strongly driven by environmental and human variables and could serve as indicator species for monitoring. For example, the common whelk (*Buccinum undatum*) could serve as indicator for increasing mean sea surface water temperatures. The grand challenge for MSP is now to integrate sustainable co-use solutions of limited marine areas by fisheries, offshore renewables (e.g., wind farms; Letschert et al., 2021), shipping, and recreation, as well as the increasing impact of climate change.

CRedit authorship contribution statement

Casper Kraan: Conceptualization, Formal analysis, Funding acquisition, Methodology, Software, Supervision, Validation, Writing – original draft, Writing – review & editing. **Holger Haslob:** Data curation, Validation, Writing – original draft, Writing – review & editing. **Wolfgang N. Probst:** Data curation, Funding acquisition, Writing – review & editing. **Vanessa Stelzenmüller:** Conceptualization, Funding acquisition, Writing – review & editing. **Jennifer Rehren:** Data curation, Validation, Writing – review & editing. **Hermann Neumann:** Conceptualization, Data curation, Formal analysis, Funding acquisition, Writing – original draft, Writing – review & editing.

Declaration of competing interest

All authors confirm there are no known conflicts of interest associated with this publication and funding by BMBF did not influence the outcome.

Data availability

All data were obtained from open-access sources, and cited in the main text

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.scitotenv.2024.169940>.

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