

WORKING GROUP ON BIODIVERSITY SCIENCE (WGBIODIV)

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i Executive summary

Working Group on Biodiversity Science (WGBIODIV) aims to develop the scientific understanding of processes supporting marine biodiversity and provide evidence of change in biodiversity patterns through space and time.

The group progressed work in relation to three objectives: (1) testing an indicator that captures the response of benthic communities to fishing pressure and exploring its effectiveness in both the North Sea and Bay of Biscay; (2) investigating predator and prey interactions structuring trophic guilds and ecosystems; (3) examining the efficacy of spatial management measures as means of maintaining marine biodiversity.

WGBIODIV's benthic indicator work demonstrated that a suite of biological traits related to *sensitivity* to, and *recoverability* from trawling were functionally independent for trawled communities of endo-benthos in the North Sea and epibenthos from the Bay of Biscay. Biological traits can be used to understand the changing status of benthic communities over short and long time scales (relative to the species life-span). Benthic diversity also changes spatially and the spatial scale is important to consider in relation to conservation and management. For example, biodiversity 'hotspots' differ in location and environmental conditions depending on whether α -, β - or γ -diversity is studied. Both the environment and anthropogenic influences can stress benthic communities and we demonstrate that cumulative effects can exceed thresholds, leading to structural change in ecosystems. To capture change in trophic guilds, we developed an indicator, based on ICES year of the stomach and Cefas DAPSTOM records that can aggregate predators by commonality in their diets. Combined ICES coordinated surveys, spatial change in feeding guild biomass can be monitored over time and inform on change in food web function and impacts by fisheries and environmental change. Multi-species food web modelling demonstrated that fish stocks within feeding guilds become at risk of depletion as primary production of phytoplankton diminishes, with planktivores most sensitive to this risk and piscivores least sensitive. Where risks to benthic communities, mobile species and food web function exist, spatial protection from trawling and other pressures may be appropriate. We show that currently there is little overlap between the core areas of sensitive demersal fish and the Natura 2000 network of MPAs, since these were typically designated to protect habitats, seabirds and marine mammals, and even less overlap between core areas of these species and offshore windfarms. Nevertheless, further fisheries management within MPAs could provide rewards for some species in some areas: e.g. for lump sucker, cod, brill and spurdog in the Skagerrak/Kattegat and for thornback ray and tope off the southeast coast off England.

Future work aims to: develop a multidimensional perspective of biodiversity change (e.g. trait and taxonomic diversity in their alpha, beta and gamma forms); identify thresholds responses of biota and ecosystem structure to highlight areas where marine biodiversity is at risk; further examine the efficacy of spatial exclusions to protect biodiversity and support ecosystem services.

ii Expert group information

Expert group name	Working Group on Biodiversity Science (WGBIODIV)
Expert group cycle	Multiannual
Year cycle started	2019
Reporting year in cycle	3/3
Chair(s)	Andrea Belgrano, Sweden
	Christopher Lynam, UK
Meeting venue(s) and dates	4–8 February 2019, ICES HQ, Copenhagen, Denmark (13 participants)
	11–12 February 2020, Barcelona, Spain (18 participants)
	8–12 February 2021, Online meeting (18 participants)

1 Benthic communities and impacts of fishing (ToR A)

Developing a trait-based indicator to assess vulnerability of benthic communities to trawling-induced disturbance

Introduction

Many studies assessing the status of benthic communities focus on taxonomic approaches, i.e. the identities of organisms sampled. These studies do not generally take into account differences in life history characteristics that may affect organism responses to, and capacity of populations to recover from, changing environments. Depletion and recovery rates following physical disturbance are estimated for the whole benthic community in generic habitats (Kaiser *et al.*, 2006; Sciberras *et al.*, 2018) which may not be representative for the specific aspects of the benthic community occurring in a local habitat. Consequently, the use of trait information to infer the vulnerability of species to disturbance by proxy is increasingly being explored as a complementary approach (Beauchard *et al.*, 2017).

Tyler-Walters *et al.* (2009) introduced the concepts of species' "intolerance" and "recoverability", subsequently developed further by Bolam *et al.* (2014) as "instantaneous sensitivity" and "long-term sensitivity" to trawling disturbance. Here, we expand such approaches, using the term "sensitivity" to indicate the extent to which a species is likely to be affected by the passage of a trawl, and "recoverability" to indicate the capacity of a population to recover from the disturbance and the timescale over which recovery will occur. The generic relevance of using functional traits in such a framework was confirmed in a study on the vulnerability of demersal fish assemblages to trawling, where the combination of catchability and resistance represented sensitivity while resilience represented recoverability (de Juan *et al.*, 2020).

Currently, there is a tendency to focus on a single trait, i.e. longevity, to explain the response of the benthic community composition to trawling intensity (Rijnsdorp *et al.*, 2020). This, however, only covers (part of) the recovery aspect and ignores the depletion aspect entirely. As part of a more comprehensive and generic approach, we use biological traits representing the instantaneous effect of the passage of a trawl, i.e. sensitivity, and traits representing recoverability in the longer term. We applied these to endo-benthos from the Dutch sector of the North Sea and epibenthos from the Bay of Biscay. We hypothesize that:

H1: Traits reflecting the sensitivity and recovery of a benthic community to trawling are independent and provide complementary information on the community's vulnerability.

H2: Combined traits are more responsive to trawling than single traits.

For testing H1, we defined a series of benthic community traits that account for sensitivity and recoverability, and analysed the relationships between these traits. We tested H2 by analysing the relationships between survey data weighted by those traits, and data on trawling intensity. Importantly, in doing this, we corrected for the potentially confounding effects of environmental variation on these relationships. Although this work is intended to provide information to support development of a generic indicator based on the functional duality of sensitivity versus recovery, we propose a specific version adapted to areas with long histories of fishing exploitation.

Materials and Methods

Traits to be considered

Scientific consensus exists on the mechanisms underlying the response of benthic communities to physical disturbance (hereafter “trawling”) on the sea floor (ICES, 2017a; Pitcher *et al.*, 2016; Rijnsdorp *et al.*, 2018). Organisms densities can decline following the passage of a trawl, as a result of death or removal of the affected fauna (i.e. depletion). Recovery may take place after this initial effect, potentially until the community returns to its untrawled state. Whether this full recovery occurs or, if not, what alternative equilibrium the community may reach, depends on the magnitude and frequency of trawling, as well as the recovery potential of the community. If trawling is sufficiently frequent, communities may not have time to recover entirely between trawling events, leading to longer term shifts in community composition with increased dominance of less sensitive species and lower densities or extirpation of the more vulnerable species.

This mechanistic understanding is not, however, reflected in a simple trade-off between recoverability and vulnerability. For some level of disturbance, a species with a high intrinsic rate of natural increase will have both a higher potential to recover to pre-disturbance densities and a lower vulnerability to disturbance. In general, this intrinsic rate of increase results from a combination of growth and reproductive traits that favour population expansion.

Other traits that are not directly related to population growth are also relevant to sensitivity and recovery. For example, a trait related to sensitivity such as an armoured body may provide some defence from the immediate physical effects of a trawl, but only if the trawl makes contact with an individual directly. In addition to processes within the trawl’s footprint, such as growth of surviving fauna, recovery may also be influenced by traits reflecting larger-scale factors such as an organism’s ability to recruit and recolonise, or to actively migrate into, the trawled area.

Species with low recovery potential may not be sensitive to disturbance, for example slow growing species which are deep burrowers (Bergman *et al.*, 2000). Conversely, species with high recoverability may be sensitive if disturbance exceeds a frequency at which they are depleted. Thus, different biological traits from adult, juvenile and larval stages determine population vulnerability to trawling. Some traits are relevant to the instantaneous effect of the passage of a trawl (*sensitivity*), while entirely different traits may represent the capacity of organisms and their populations to recover from trawling (*recoverability*).

Sensitivity. Some species are fragile and easily damaged, while others are more robust. A buried organism is less likely to be exposed to trawling than an epibenthic one, with a greater chance of survival as its burrowing depth increases. Direct exposure to trawling can be mitigated by body size. Smaller species are generally less sensitive than larger-bodied taxa as the former can escape through the net more easily if captured (Bolam *et al.*, 2014). The sensitivity component (SE) of a benthic assemblage can therefore be expected to be a function of standardised body fragility (FR), burrowing depth (BD) and body length (BL). In most previous and similar works, composite indicators were built by adding trait scores. Generally, multiplicative aggregation is preferable due to (possibly irrelevant) compensatory effects of additive aggregation (Gan *et al.*, 2017). With this in mind, SE is here defined as:

$$SE = FR \times BD \times BL$$

Recoverability. Mobile species are likely to recolonise a trawled area by migrating more quickly than less mobile species, so recoverability is likely to be a function of motility (MO). Recoverability also depends on recruitment from larval settlement and subsequent growth to the adult stage. Late-maturing, slow-growing or poorly-recruiting species will all have low recoverability (MacDonald *et al.*, 1996). Life span (LS), as used in the “longevity approach” of Rijnsdorp *et al.*

(2018), and age at maturity (AM) are traits of critical importance. Some species require a long time to achieve minimal reproductive success, including those with the naturally high juvenile mortality that is often driven by stochastic environmental conditions (Kingsvader *et al.*, 2016). LS is expected to respond negatively to trawling intensity in habitats dominated by species that live for years or even decades, as are often encountered in rarely disturbed benthic habitats (e.g. coral reefs). However, in areas where the seafloor has been intensively trawled for more than a century, such as the European continental shelves, the density of long-lived organisms may be too low to detect significant trawling effects. In such areas, and especially under high trawling frequencies, AM expresses a more relevant critical aspect of the life cycle, namely the chance of experiencing at least one reproduction before being killed by a trawl, especially if reproductive life span (RLS = LS – AM), for the same AM, is reduced compared to truly long-lived species. In general, AM is correlated with LS (Charnov, 1993), and AM may account for a potential LS-effect. However, this relationship is not perfect when considering several phyla or limited spatial biogeographic extent. AM / RLS emphasises the critical time necessary to reach maturity and achieve reproductive success over a shorter RLS. For the same AM, very long-lived species, assumed to be largely depleted in intensively trawled areas, perform less successfully. However, the AM / RLS ratio, as defined, can take the same value for species with different AM and RLS, so a species maturing at 1 year of age and dying after 2 years is attributed the same value as another species maturing at 2 years and dying after 4 years. To counteract this, the ratio can be multiplied by AM to introduce an appropriate penalty for RLS in long-lived species with late AM. We call the resultant term relative maturity (RM); with 1 added to RLS to deal with cases where LS = AM (semelparity, in which case then RLS = 0), both measured in years:

$$RM = \frac{AM}{RLS + 1} \times AM$$

These age-related aspects are of paramount importance in life history strategies of organisms (Charnov, 1993), but some independent traits relevant to reproduction and offspring may be complementary. In the marine benthos, offspring can be released by parents at different developmental stages, depending on the species, with different chances of survival before settling as juveniles. For example, broadcasted eggs in the water column are more vulnerable to planktotrophy than brooded larvae, and both are more vulnerable than juveniles released as miniature adults after internal incubation (Giangrande *et al.*, 1994; Pechenik, 1999). Large eggs have a shorter critical pelagic phase, because of faster development, than smaller ones (Giangrande, 1997; Giangrande *et al.*, 1994). The potential for recovery of the benthic community (RE) will therefore be a function of motility (MO), offspring type (OT) and offspring size (OS) as well as RM. Generally, OS is negatively correlated to fecundity due to the constraints of energetic allocation (Kingsvader *et al.*, 2016), whereas OT can be independent of fecundity (e.g. many bivalves broadcast millions of eggs, and some crabs brood millions of larvae). Hence, RE includes many relevant aspects of species' life histories, and is here defined as:

$$RE = RM \times MO \times OT \times OS$$

Vulnerability. Finally, we defined vulnerability by combining SE and RE by addition and multiplication (SE + RE and SE × RE). Although we preferred multiplicative aggregation within the SE and RE components, both additive and multiplicative variants of the combined components were calculated to compare their distributions and associated variations.

We tested H1 on the fauna from two case studies for which we compiled the described traits from the literature (next sections). Then, we compared SE and RE trait relationships in order to assess their degree of complementarity. As part of H2 testing, for each case study, the taxa × traits

matrix (including individual traits, trait combinations, SE, RE and vulnerability) was combined with survey data in order to test the relationships between organism density-weighted traits and trawling intensity.

Benthic data

The responsiveness to trawling intensity of individual traits, and SE and RE components separately and in different (additive and multiplicative) combinations, were tested using benthic data from two contrasting case studies, representing different components of the marine benthos sampled using different methods (Figure 1).

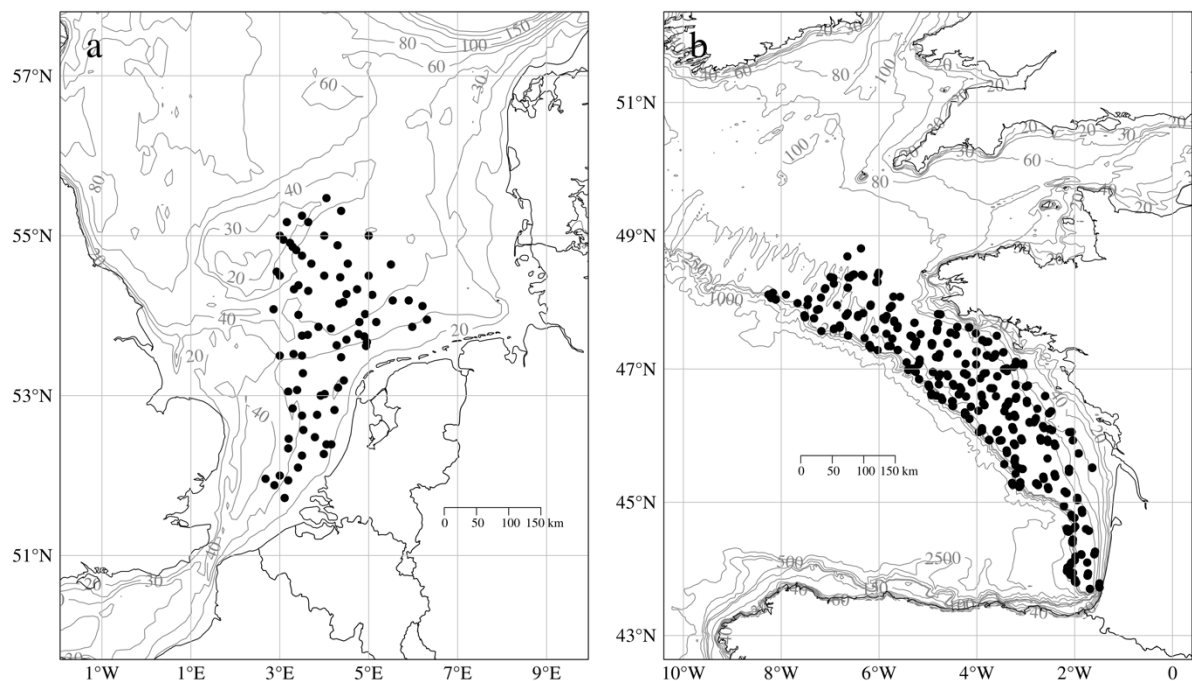


Figure 1. Case studies: a) Dutch Exclusive Economic Zone (EEZ); b) Bay of Biscay. Black dots, sampling stations. Grey lines, isobaths displaying depths in meters.

Dutch EEZ

The Dutch EEZ ranges from 51.62°N to 55.47°N. Seventy-nine stations (Figure 1a), excluding coastal stations heavily impacted by shrimp trawling, were sampled annually from 1995 to 2010, and then in 2012 and 2015. Sediment was sampled with a box corer; detailed information on the sampling procedure is provided in Daan and Mulder (2009). The resultant dataset consists of biomass (ash free dry weight) and number of individual organisms. Associated abiotic variables were particulate organic matter and carbon (measured from field samples), means of monthly median bottom current speed and bottom wave energy (Deltares Institute, Delft, The Netherlands), depth (EMODnet Bathymetry, 2018) and primary productivity (Baretta *et al.*, 1995).

Bay of Biscay

The study area ranges between 48.8 °N in the north and the northern margin of Gulf de Cap Breton in the south (43.7 °N), and a total of 523 stations (Figure 1b) were considered (65 stations

on average each year). The selected stations mainly cover the soft bottom habitats of the continental shelf (50 to 200 m), including some stations on the upper slope (200 to 735 m). In the French Groundfish Survey in the Celtic Sea and Bay of Biscay (Mahe and Laffargue, 1987), a 36/47 GOV trawl (Grande Ouverture Verticale) is used, with a 20 mm mesh cod-end liner, to sample benthic assemblages. Each haul lasts for approximately 30 minutes. We use a dataset on epibenthic macroinvertebrates (wet biomass and number of individuals) covering the period from 2009 to 2016. We also selected data deeper than 50 m to reduce the bias due to incomplete effort data for fishing vessels smaller than 12 m long that mainly operate in the shallower areas. Associated abiotic variables include mean annual bottom temperature, mean bottom salinity and the bottom current speed, obtained from the outputs of the MARS 3D model (Lazure and Dumas, 2008), sediment characteristics derived from discrete sediment categories (Bouysse, 1985; Shom, 2014), and depth recorded during the surveys (Mahe and Laffargue, 1987).

Trawling intensity

This study covers the period 2010–2015 for the Dutch EEZ, and the period 2009–2016 for the Bay of Biscay. Fishing effort was quantified as the sum of the area covered by a fishing gear over one year divided by a 0.05×0.05 degree grid cell. This swept area ratio (SAR) was considered for the year preceding the sampling date in both case studies. In the North Sea study area, trawling intensity was computed according to van Denderen *et al.* (2015). For the Bay of Biscay, we utilized the surface abrasion dataset computed from the ICES (ICES, 2017b) and the publicly-available OSPAR database (OSPAR, 2017a).

Trait data

Trait data was collected and compiled for all taxa in both datasets, mostly at the genus and species level. Trait information was mostly obtained from peer-reviewed articles, with additional books and grey literature (theses, reports). Trait information for the Bay of Biscay was complemented using the MERP trait explorer (https://www.marine-ecosystems.org.uk/Trait_Explorer). Most traits had ordinal modalities. These were ranked according to their responsiveness to trawling in such a way that all responses to trawling were expected to be negative. Traits, their modalities and scores are shown in Table 1.

Table 1. Traits and their modalities. Scores express the relative degree of responsiveness of each trait to physical disturbance.

Trait	Modality	Raw score	Standardized score	Trait	Modality	Raw score	Standardized score
Fragility	Robust	1	0.00	Life span (years)	<1	1	0.00
	Intermediate	2	0.50		1-3	2	0.33
	Fragile	3	1.00		3-10	3	0.67
Burrowing depth (cm)	>15	1	0.00		>10	4	1.00
	5-15	2	0.33	Motility	Crawler-Swimmer	1	0.00
	0-5	3	0.67		Crawler	2	0.33
	0	4	1.00		Tubicolous	3	0.67
Body length (cm)	<1	1	0.00		Sessile	4	1.00
	1-3	2	0.25	Offspring type	Juvenile	1	0.00
	3-10	3	0.50		Larva	2	0.50
	10-20	4	0.75		Egg	3	1.00
	>20	5	1.00	Offspring size (µm)	>1500	1	0.00
Age at maturity (years)	<1	1	0.00		500-1500	2	0.33
	1-3	2	0.50		100-500	3	0.67
	>3	3	1.00		<100	4	1.00

Six different types of organism densities were incorporated into stations \times taxa matrices: biomass m^{-2} , number of individuals m^{-2} and number of taxa m^{-2} as absolute values and also as relative values calculated by dividing absolute values by sample totals. Several types of faunal data provide different kinds of research opportunities depending on fundamental or conservation aspects. Absolute densities generally reflect faunal responses along gradients of production, and not necessarily specific functional aspects independent of production. For instance, the use of relative densities is relevant to conservation purposes when functional aspects are given priority over total abundance. Thus a habitat may be considered vulnerable if it is dominated by vulnerable taxa whatever their total abundance.

Data analyses

To test H1, we investigated the relationships among trait distributions in the SE and RE components across taxa, using centred Principal Component Analysis (PCA) of the species \times standardized traits matrices from the two case studies. The use of traits independently of field data ensured equal weights for vulnerable and resilient or resistant taxa in order to reflect an ideal non-disturbed pattern.

To test H2, for each case study traits were combined with survey data by aggregating organism densities per station and per trait to generate sampling-stations \times response variables matrices (using community weighted mean, CWM; Kleyer *et al.*, 2012). Prior to calculating CWM, all individual and combined traits within SE and RE were computed in each taxa \times standardized traits matrix, generating 26 response variables, as well as the SE + RE and SE \times RE variables.

Then, in order to compare the relative effects of abiotic variables and trawling intensity on the CWM traits, we decomposed the variance of each response variable, accounting for the effects of environmental variables and trawling intensity using variation partitioning (Legendre and Legendre, 2012). In general, benthic communities are not randomly distributed, and environmental conditions that may benefit or exclude some species may also benefit fishing. As a consequence, a significant indicator response to trawling can be a spurious effect if an environmental variable is also correlated with the response and is the true explanation of the variation. Therefore, response variation to trawling intensity was analysed by partial regression, after removing the variance of environmental variables common to response and trawling intensity variables in order to capture the pure trawling effect. Variation partitioning proceeds linearly and variables were therefore \ln -transformed prior to analysis. Figure 2 summarises our analytical approach.

Analyses were done with R 4.0.3 (R Core Team, 2020); PCA with the package “ade4” (Chessel *et al.*, 2004), and variation partitioning with the package “vegan” (Oksanen *et al.*, 2010).

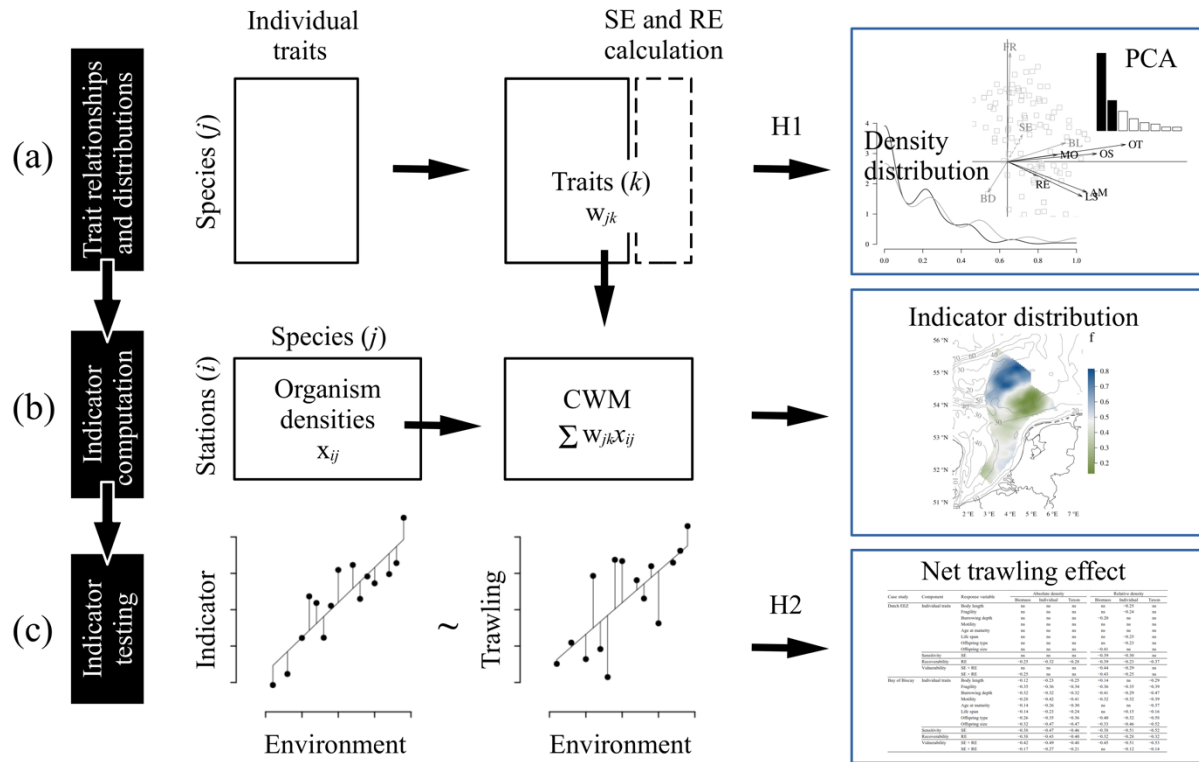


Figure 2. Summary of data analyses. a) Sensitivity (SE) and recoverability (RE) components are calculated from the species \times individual traits matrix; then PCA and distribution analyses are used to test H1. b) Trait data are combined with organism densities from survey data through community weighted means (CWM), enabling representations of SE and RE spatial distributions. c) CWM indicator data are then related to observed trawling intensity through variation partitioning; the net trawling influence is derived by the correlation of the residuals from the regressions of indicator and trawling variables on abiotic descriptors, assessing hypothesis H2.

Results

Trait relationships

PCA ordinations (Figure 3) display the relationships between traits for each of the two faunas. In both case studies, all recoverability traits positively covaried along the first axis. Adult traits (life span and age at maturity) diverged together from the combination of offspring traits (type and size), motility keeping an intermediate position. In contrast, sensitivity traits, more expressed along the second axis, were less covariant. Except for body length, traits were more covariant within than between sensitivity and recovery components. Sensitivity and recoverability components were globally independent as displayed by their orthogonality (Dutch EEZ, $r = 0.02$, $p = 0.768$; Bay of Biscay, $r = 0.13$, $p = 0.102$; overall, $r = 0.08$, $p = 0.140$). Both variables, projected as passive elements, showed similar norms (vector length), indicating that they contributed similarly to biological variations between taxa. This functional independence between sensitivity and recoverability suggests that both components could provide complementary information about short- and longer-term responses to trawling. As such, our first hypothesis was supported.

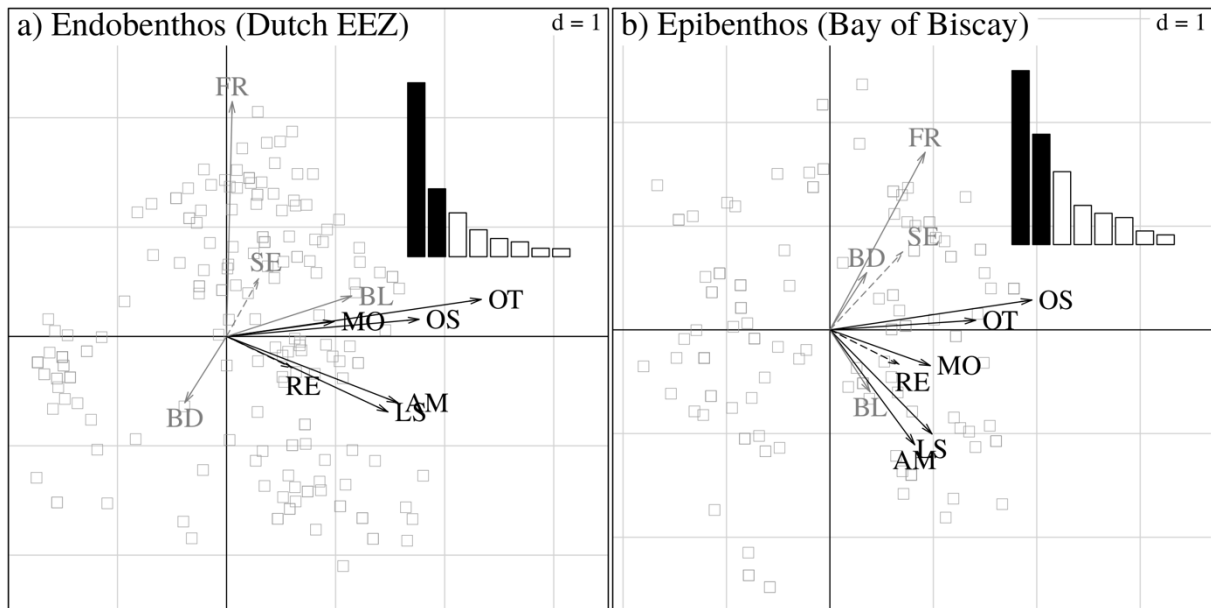


Figure 3. Principal Component Analysis of biological trait covariances from taxa \times standardised traits matrices. Bar diagrams, eigenvalues (black, axes 1 and 2). Grey arrows, traits of the sensitivity component (SE). Black arrows, traits of the recovery component (RE). Dashed arrows, SE and RE components projected as passive elements. Grey squares, taxa. “d” indicates the grid scale. AM, age at maturity; BD, burrowing depth; BL, body length; FR, fragility; LS, life span; MO, motility; OS, offspring size; OT, offspring type.

Trawling intensity and confounding effects with environmental variables

Trawling intensity (swept area ratio, SAR) was similarly distributed in both case study areas, with low values dominating (Figure 4a and 4b). The range of SAR values, however, was significantly wider for the Bay of Biscay (25 % of SAR values above 4.6) than for the Dutch EEZ (maximal SAR = 4.7). In the Dutch EEZ, trawling intensity was strongly predicted by abiotic variables (trawling intensity regressed on abiotic variables, $R^2 = 0.78$). Consequently, increasing trawling intensity was inexorably accompanied by an increase in confounded effects of trawling intensity and environmental characteristics (Table 3). This hampered the detection of true trawling effects on response variables following variation partitioning (Figure 4c). A similar trend, although detected (trawling *vs.* environment, $R^2 = 0.14$), was less pronounced in the Bay of Biscay (Figure 4d).

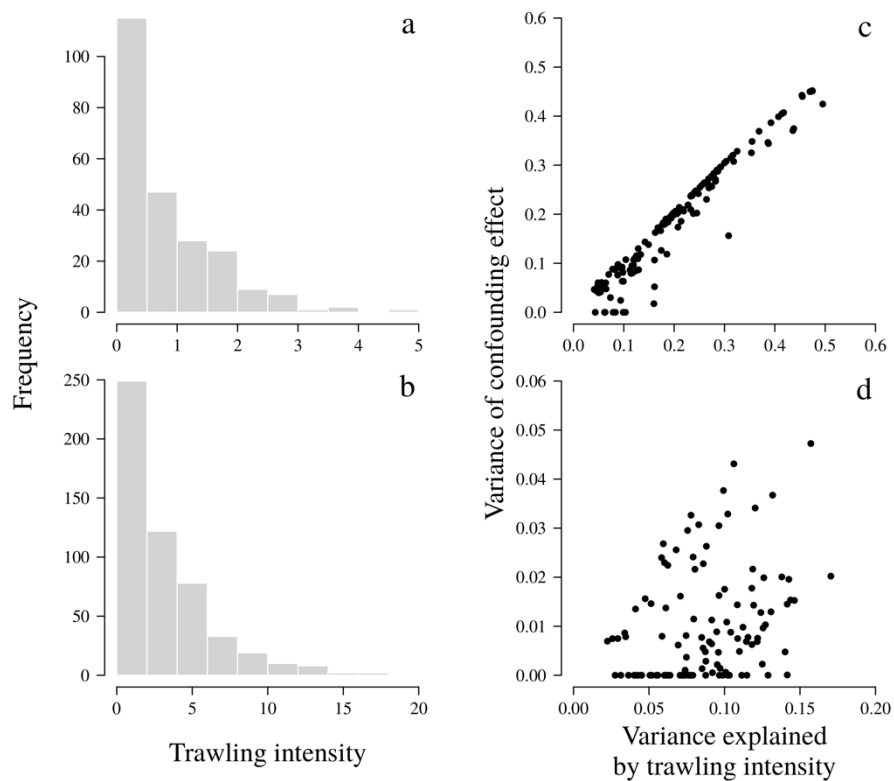


Figure 4. Left, frequency distributions of trawling intensities expressed as swept area ratio for the Dutch EEZ (a) and the Bay of Biscay (b). Right, variance of response variables (individual traits and combinations of traits) concurrently explained by abiotic variables and trawling intensity plotted against variance explained by raw trawling intensity only (respectively c and d). Each dot refers to a response variable (individual trait or combination of traits) for which the conditional trawling effect was significant; see Table 3 and 4.

Trait responses to trawling

Generally, trait combinations were more responsive to trawling intensity than individual traits (Table 2, higher partial correlations). As expected, when significant, all traits responded negatively to trawling, except offspring type and size, especially in the Bay of Biscay. Table 3 and 4 display complementary results for different sub-combinations of traits within SE and RE components, including confounding effects.

Table 2. Trait responses to trawling intensity. Values are partial r , Pearson's r -correlation coefficient between trait and trawling intensity after controlling for the effect of abiotic variables (partial regression). "ns" for not significant ($p \geq 0.05$).

Case study	Component	Response variable	Absolute density			Relative density		
			Biomass	Individual	Taxon	Biomass	Individual	Taxon
Dutch EEZ	Individual traits	Body length	ns	ns	ns	ns	-0.25	ns
		Fragility	ns	ns	ns	ns	-0.24	ns
		Burrowing depth	ns	ns	ns	-0.20	ns	ns
		Motility	ns	ns	ns	ns	ns	ns
		Age at maturity	ns	ns	ns	ns	ns	ns
		Life span	ns	ns	ns	ns	-0.25	ns
		Offspring type	ns	ns	ns	ns	-0.23	ns
		Offspring size	ns	ns	ns	-0.41	ns	ns
	Sensitivity	SE	ns	ns	ns	-0.39	-0.30	ns
	Recoverability	RE	-0.25	-0.32	-0.28	-0.39	-0.23	-0.37
	Vulnerability	SE + RE	ns	ns	ns	-0.44	-0.29	ns
		SE \times RE	-0.25	ns	ns	-0.43	-0.25	ns
Bay of Biscay	Individual traits	Body length	-0.21	-0.22	-0.24	ns	ns	-0.35
		Fragility	-0.34	-0.28	-0.29	-0.24	-0.28	-0.32
		Burrowing depth	-0.30	-0.24	-0.25	-0.24	-0.20	-0.30
		Motility	-0.32	-0.34	-0.35	-0.25	-0.29	-0.31
		Age at maturity	-0.22	-0.23	-0.25	ns	-0.09	-0.31
		Life span	-0.23	-0.20	-0.21	ns	ns	-0.14
		Offspring type	-0.30	-0.28	-0.29	-0.33	-0.27	-0.42
		Offspring size	-0.35	-0.38	-0.39	-0.29	-0.38	-0.41
	Sensitivity	SE	-0.36	-0.38	-0.39	-0.29	-0.42	-0.42
	Recoverability	RE	-0.39	-0.36	-0.35	-0.26	-0.28	-0.26
	Vulnerability	SE + RE	-0.41	-0.40	-0.41	-0.36	-0.45	-0.43
		SE \times RE	-0.29	-0.32	-0.27	-0.20	-0.22	-0.21

In the Dutch EEZ, relative biomass was the most responsive density to trawling. Overall, individual trait responses were mostly insignificant, except offspring size based on relative biomass. Trait responses were strongly obscured by confounding effects of abiotic variables, masking the effect of trawling intensity (Figure 4c), with limited amounts of explained variance left when controlling for the effect of the environment. In general, SE was less responsive than RE, in spite of smaller confounding effects (Table 3, average adjusted $R^2 = 0.12$ for SE against 0.33 for RE). Vulnerability based on the additive combination of SE and RE for relative biomass responded most strongly (Figure 5a-c).

In the Bay of Biscay, the three types of densities (and their relative counterparts) responded similarly, with higher partial correlations for relative individual and taxon densities. In addition to smaller confounding effects, explained variances were often higher than in the Dutch EEZ (Table 3 and 4). Vulnerability, as the strongest response, was also obtained with the additive combination of SE and RE. The additive combination of SE and RE, as well as the two components separately showed similar spatial patterns notwithstanding the type of densities.

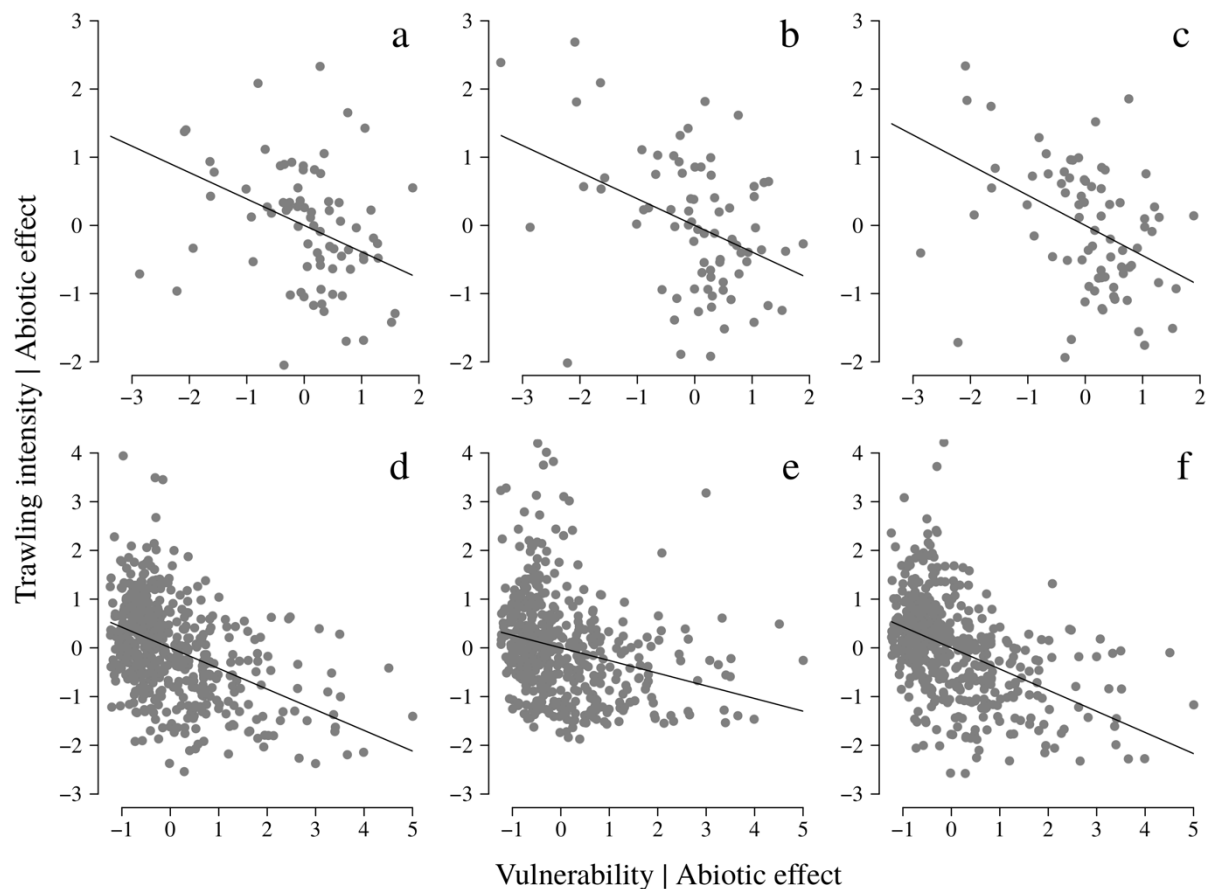


Figure 5. Strongest indicator responses obtained for each case study. a-c) Dutch EEZ, relative biomass density. d-f) Bay of Biscay, relative number of taxa. Variables are standardised residuals from regression on abiotic variables (symbol “|”, partial regression). Vulnerability = Sensitivity + Recoverability.

Discussion

Responsiveness of benthic community traits to trawling

The observed response of benthic community traits to trawling was consistent with our expectations. Our results clearly advocate for the use of multiple traits rather than a single trait. While recent studies proposed life span as the single trait determining the benthic community response (e.g. the “longevity approach”; Hiddink *et al.*, 2019; Rijnsdorp *et al.*, 2020), this (1) assumes that the single trait adequately represents the recoverability component (RE) and (2) ignores the sensitivity component (SE). Out of twelve tests (six densities in each case study), life span was found significant only five times compared to RE, which was always significant. This supports the contention that densities of long-lived species may lose their indicator potential beyond a certain level of trawling intensity, whereas the alternative relative maturity (RM) may indicate fishing effects, even at high and prolonged trawling intensities.

In the Dutch EEZ, the lower SE responsiveness may have been due to a much higher proportion of buried species compared to purely epibenthic ones. Only 13 taxa with a high (> median) SE score (7 % of the total) were epibenthic, against 35 taxa (18 %) of deep burrowers (> 5 cm). By contrast, 68 taxa with high SE scores (40 %) in the Bay of Biscay were epibenthic and none were deep burrowers, probably explaining the regular SE responsiveness there. Significant responses from SE in the Dutch EEZ, only observed for relative biomass and individual densities, may have been due to dominant epibenthic or shallow dwelling taxa with high SE scores. In intensively

trawled areas, burrowing depth seems to be a driving characteristic of vulnerability, as suggested by the large functional independence of burrowing depth from RE traits and in accordance with the supported hypothesis H1. A larger proportion of the epibenthos from the Bay of Biscay, with various degrees of recoverability, was more exposed to trawling gears than the endobenthos in the Dutch EEZ, supporting the regular responsiveness of both SE and RE components.

Confounding effects

The strong confounding environmental effects encountered in the Dutch EEZ were probably responsible for the absence of significant responses for many variables, as explained variances were of similar magnitudes. Consequently, removing the confounding effect from the total effect left only small amounts of variance in the benthic community traits to be explained by trawling intensity. In the Dutch EEZ, trawling intensity increases from the deeper water in the north to the shallow water in the south, as does primary productivity (correlated to trawling intensity, $r = 0.66$, $p < 0.001$), so that it is difficult to appraise the true trawling effect on what is effectively a correlated gradient. The response of benthic communities could therefore be the result of an increase in trawling intensity, a change in habitat, or both. This was also observed for species richness by Duineveld *et al.* (1992). In our study, this is demonstrated by the generally high level of variance in abiotic variables. Besides, opposing directions of change in trawling intensity and a given indicator could mask the effects of trawling disturbance buffered by environmental suitability (i.e. compensating depletion). As observed in the Dutch EEZ, the use of relative densities may, to some extent, mitigate the confounding effect of production gradients by emphasizing the functional nature of communities more compared to analyses based on species richness or total organism density (Beauchard *et al.*, 2017).

Few benthic studies have explicitly taken confounding effects into account (Cyrielle *et al.*, 2020; Hinz *et al.*, 2009; Lindegarth *et al.*, 2000; Reiss *et al.*, 2009). To our knowledge, no work describing composite trait indicator development has considered this potential issue concerning statistical validation. Many studies were carried out along gradients of commercial fishing intensity, several of which are probably correlated with environmental dynamics. The conclusions drawn from such studies should be considered with caution. Variation in fishing intensity often follows variation in fish abundance and habitat suitability, both of which are driven by variation in the environment (Pommer *et al.*, 2016).

Developing a trait-based vulnerability indicator

Here, we present a generic approach that can be used to develop a trait-based indicator to assess the vulnerability of benthic communities to fishing-induced physical disturbance. This approach is based on two processes derived from a mechanistic understanding of trawling effects on the benthic community, i.e. sensitivity and recoverability, and well-grounded in benthic ecological theories. We chose to offer a generic approach so that it can be adjusted to fit specific contexts in terms of data availability and knowledge of the benthic fauna. The proposed approach is flexible in terms of trait selection to express both SE and RE processes, which can then be combined in an indicator that is responsive with an appropriate level of conservatism. As trait scores take the value 0 in species that are not vulnerable, null scores of combined variables are likely to increase with more traits, leading to a larger number of species that do not contribute to the community score. This ensures that non-null scores arise from vulnerable species which are not resistant and with limited resilience. In areas where benthic communities are extremely impoverished, it may be necessary to limit the number of traits considered, in order to minimise the number of null scores. However, in the case of correlated traits such as in the RE component, the number of null scores of combined variables is limited as vulnerable species have high scores for most of the

traits. By contrast, the use of the SE component may be more conservative for the detection of trawling effects, given the strong independence of SE traits.

Further work, using data collected under controlled conditions, is recommended before deciding on a definitive version of an indicator combining both SE and RE components. Indeed, there may not be a single “best” vulnerability indicator but a range of similar ones that are tailored to the benthic community being sampled and the overall local conditions. For example, in the case of a benthic community not impacted by trawling previously, the species composition would be characterised by a large spread of SE and RE scores due to higher proportions of vulnerable species. When trawling commences, the relative contributions of SE and RE components to the decreasing vulnerability indicator is expected to change over time, i.e. first dominated by the SE and later on by RE component. After the initial trawl pass, it can reasonably be assumed that the first individuals/species will be those with higher SE scores (e.g. sea pens). Then, under continued and frequent trawling that does not allow recovery, only species with sufficient resilience relative to trawling intensity will survive continued trawling, while the SE score remains low. Once fishing ceases, indicator response is determined, chronologically, firstly by the SE component, followed by the RE component dominated initially by high relative maturity (RM) scores and later by life span. After implementation of a marine protected area, for example, the indicator responsiveness is determined in the short term by SE and in the long term by RE. In our case study areas, both of which involved trawled communities, SE responses may be considerably smaller than what might have been expected under pristine, or at least less degraded, circumstances. As such, both SE and RE need to be included in a benthic vulnerability indicator that is expected to perform well in very different circumstances.

Conclusions

Based on a theoretically-sound mechanistic understanding of trawling effects on the benthic community, this study advocates the use of multiple biological traits for assessing the status of the seabed habitats specifically in relation to trawling-induced physical disturbance. We emphasise the complementarity of SE and RE components, their relative importance depending on the context and how this may vary over different time scales. In this study, their independence is a major finding, implying that vulnerability cannot be fully understood using only a single trait or several ones that only reflect the intrinsic rate of natural increase. Our results show that an assessment of the status of seabed habitats, and how these are affected by physical disturbance, requires the full consideration of the benthic community, including both endo- and epibenthic components, each needing different sampling techniques.

This study provides a generic approach for the development of a benthic community vulnerability indicator which can be adapted to specific contexts. Depending on the availability of data from monitoring programs, such as type of fauna sampled (endo- or epibenthos), faunal data recorded (numbers, biomass) and traits were distinguished, an indicator can be created that is likely to perform well even in areas with a long history of exploitation.

Table 3. Complete output of variation partitioning for the Dutch EEZ. Symbols: “|”, conditional effect; “∩”, confounding effect between environmental variables and trawling intensity (intersection). AM, age at maturity; BD, burrowing depth; BL, body length; FR, fragility; LS, life span; MO, motility; OS, offspring size; OT, offspring type; RE, recoverability; SE, sensitivity. Partial *r* indicates the Pearson’s *r*-correlation coefficient between the response variable and trawling intensity when controlling for the effect of abiotic variables; it also indicates the sign of variation of the relationship.

Density	Component	Response variable	Abiotic	Trawling	Abio. + Trawl.	Abio. Trawl.	Abio. ∩ Trawl.	Trawl. Abio.	Partial <i>r</i>
Absolute biomass	Individual traits	BL	0.38	0.05	0.38	0.32	0.06	ns	ns
		FR	0.40	ns	0.40	0.38	0.02	ns	ns
		BD	0.25	0.06	0.24	0.19	0.06	ns	ns
		MO	0.37	0.07	0.36	0.29	0.08	ns	ns
		AM	0.32	ns	0.31	0.30	0.02	ns	ns
		LS	0.30	ns	0.30	0.27	0.04	ns	ns
		OT	0.34	0.04	0.34	0.30	0.05	ns	ns
		OS	0.27	0.10	0.28	0.19	0.08	ns	ns
	Sensitivity	BL×FR	0.36	0.05	0.35	0.30	0.05	ns	ns
		BL×BD	0.25	0.09	0.24	0.16	0.09	ns	ns
		FR×BD	0.28	0.05	0.29	0.24	0.04	ns	ns
		SE	0.26	0.10	0.27	0.18	0.09	ns	ns
	Recoverability	MO×OT	0.29	0.08	0.28	0.20	0.09	ns	ns
		MO×OS	0.25	0.13	0.26	0.13	0.12	ns	ns
		OT×OS	0.26	0.09	0.27	0.19	0.08	ns	ns
		MO×OT×OS	0.24	0.12	0.25	0.13	0.11	ns	ns
		RM	0.26	0.05	0.27	0.22	0.04	ns	ns
		RM×MO	0.25	0.06	0.26	0.20	0.05	ns	ns
		RM×OT	0.23	0.05	0.25	0.19	0.04	ns	ns
		RM×OS	0.19	0.12	0.23	0.11	0.08	0.04	−0.24
		RM×MO×OT	0.23	0.06	0.25	0.18	0.05	ns	ns
		RM×MO×OS	0.19	0.13	0.23	0.10	0.09	0.04	−0.26
		RM×OT×OS	0.19	0.11	0.22	0.11	0.08	0.04	−0.24
		RE	0.19	0.13	0.23	0.10	0.09	0.04	−0.25
	Vulnerability	SE+RE	0.26	0.12	0.28	0.16	0.10	ns	ns
		SE×RE	0.23	0.24	0.26	ns	0.20	0.04	−0.25
Absolute number of individuals	Individual traits	BL	0.75	0.19	0.75	0.55	0.20	ns	ns
		FR	0.67	0.20	0.66	0.46	0.20	ns	ns
		BD	0.61	0.20	0.61	0.41	0.20	ns	ns
		MO	0.71	0.24	0.70	0.46	0.24	ns	ns
		AM	0.75	0.27	0.75	0.48	0.28	ns	ns
		LS	0.69	0.29	0.68	0.39	0.30	ns	ns
		OT	0.68	0.23	0.67	0.44	0.24	ns	ns
		OS	0.66	0.24	0.65	0.41	0.25	ns	ns
	Sensitivity	BL×FR	0.74	0.19	0.74	0.55	0.19	ns	ns
		BL×BD	0.74	0.20	0.74	0.53	0.21	ns	ns
		FR×BD	0.66	0.19	0.66	0.47	0.19	ns	ns
		SE	0.73	0.18	0.73	0.54	0.19	ns	ns
	Recoverability	MO×OT	0.70	0.26	0.70	0.44	0.26	ns	ns
		MO×OS	0.71	0.27	0.70	0.43	0.28	ns	ns
		OT×OS	0.69	0.26	0.68	0.42	0.26	ns	ns
		MO×OT×OS	0.71	0.29	0.71	0.42	0.29	ns	ns
		RM	0.77	0.24	0.77	0.53	0.24	ns	ns
		RM×MO	0.76	0.39	0.76	0.37	0.39	ns	ns
		RM×OT	0.76	0.24	0.75	0.51	0.25	ns	ns
		RM×OS	0.80	0.31	0.80	0.48	0.32	ns	ns
		RM×MO×OT	0.75	0.41	0.75	0.35	0.40	ns	ns
		RM×MO×OS	0.76	0.47	0.78	0.31	0.45	0.02	−0.31
		RM×OT×OS	0.80	0.31	0.79	0.48	0.32	ns	ns
		RE	0.75	0.47	0.77	0.30	0.45	0.02	−0.32
	Vulnerability	SE+RE	0.79	0.29	0.79	0.50	0.29	ns	ns
		SE×RE	0.81	0.35	0.82	0.47	0.35	ns	ns

Table 3. Continued.

Density	Component	Response variable	Abiotic	Trawling	Abio. + Trawl.	Abio. Trawl.	Abio. \cap Trawl.	Trawl. Abio.	Partial r
Absolute number of taxa	Individual traits	BL	0.71	0.20	0.71	0.50	0.21	ns	ns
		FR	0.66	0.21	0.65	0.44	0.21	ns	ns
		BD	0.61	0.19	0.61	0.42	0.18	ns	ns
		MO	0.73	0.28	0.73	0.45	0.28	ns	ns
		AM	0.65	0.28	0.65	0.37	0.28	ns	ns
		LS	0.64	0.28	0.64	0.35	0.29	ns	ns
		OT	0.68	0.24	0.67	0.44	0.24	ns	ns
		OS	0.66	0.26	0.66	0.40	0.26	ns	ns
	Sensitivity	BL \times FR	0.70	0.18	0.70	0.52	0.18	ns	ns
		BL \times BD	0.68	0.18	0.68	0.51	0.18	ns	ns
		FR \times BD	0.63	0.17	0.63	0.46	0.17	ns	ns
		SE	0.66	0.13	0.66	0.53	0.13	ns	ns
	Recoverability	MO \times OT	0.73	0.29	0.73	0.44	0.30	ns	ns
		MO \times OS	0.74	0.32	0.73	0.42	0.32	ns	ns
		OT \times OS	0.69	0.27	0.69	0.42	0.27	ns	ns
		MO \times OT \times OS	0.74	0.33	0.73	0.41	0.33	ns	ns
		RM	0.64	0.23	0.64	0.41	0.24	ns	ns
		RM \times MO	0.66	0.41	0.67	0.26	0.40	ns	ns
		RM \times OT	0.63	0.23	0.62	0.39	0.24	ns	ns
		RM \times OS	0.68	0.30	0.67	0.37	0.31	ns	ns
		RM \times MO \times OT	0.65	0.42	0.66	0.24	0.41	ns	ns
		RM \times MO \times OS	0.66	0.47	0.68	0.20	0.45	0.02	-0.28
		RM \times OT \times OS	0.67	0.30	0.67	0.37	0.30	ns	ns
		RE	0.65	0.47	0.67	0.20	0.45	0.02	-0.28
	Vulnerability	SE+RE	0.72	0.25	0.71	0.46	0.25	ns	ns
		SE \times RE	0.74	0.37	0.74	0.37	0.37	ns	ns
Relative biomass	Individual traits	BL	0.10	0.05	ns	ns	0.06	ns	ns
		FR	0.36	ns	0.36	0.37	0.00	ns	ns
		BD	0.34	ns	0.37	0.34	0.00	0.03	-0.20
		MO	0.55	0.14	0.55	0.41	0.14	ns	ns
		AM	0.10	ns	0.13	0.14	0.00	ns	ns
		LS	0.19	ns	0.22	0.23	0.00	ns	ns
		OT	0.31	ns	0.34	0.35	0.00	ns	ns
		OS	0.32	0.06	0.42	0.36	0.00	0.11	-0.41
	Sensitivity	BL \times FR	0.24	0.10	0.24	0.15	0.09	ns	ns
		BL \times BD	0.25	0.07	0.30	0.22	0.03	0.04	-0.27
		FR \times BD	0.28	0.06	0.37	0.30	0.00	0.08	-0.36
		SE	0.21	0.16	0.32	0.16	0.05	0.11	-0.39
	Recoverability	MO \times OT	0.38	0.13	0.39	0.26	0.12	ns	ns
		MO \times OS	0.32	0.19	0.39	0.20	0.12	0.07	-0.33
		OT \times OS	0.32	0.04	0.40	0.36	0.00	0.08	-0.37
		MO \times OT \times OS	0.31	0.16	0.36	0.20	0.11	0.05	-0.30
		RM	0.12	ns	0.18	0.17	0.00	0.06	-0.28
		RM \times MO	0.19	ns	0.24	0.21	0.00	0.06	-0.29
		RM \times OT	0.15	ns	0.21	0.20	0.00	0.06	-0.29
		RM \times OS	0.12	0.08	0.25	0.17	0.00	0.13	-0.40
		RM \times MO \times OT	0.20	ns	0.26	0.23	0.00	0.06	-0.30
		RM \times MO \times OS	0.16	0.10	0.29	0.18	0.00	0.12	-0.40
		RM \times OT \times OS	0.13	0.08	0.25	0.17	0.00	0.12	-0.39
		RE	0.17	0.10	0.28	0.18	0.00	0.12	-0.39
	Vulnerability	SE+RE	0.23	0.16	0.37	0.21	0.02	0.14	-0.44
		SE \times RE	0.14	0.31	0.29	ns	0.16	0.15	-0.43

Table 3. Continued.

Density	Component	Response variable	Abiotic	Trawling	Abio. + Trawl.	Abio. Trawl.	Abio. \cap Trawl.	Trawl. Abio.	Partial r
Relative number of individuals	Individual traits	BL	0.30	0.10	0.33	0.23	0.06	0.04	-0.25
		FR	0.22	0.10	0.26	0.16	0.06	0.03	-0.24
		BD	0.46	0.06	0.46	0.40	0.06	ns	ns
		MO	0.50	0.05	0.50	0.44	0.05	ns	ns
		AM	0.60	0.16	0.60	0.44	0.16	ns	ns
		LS	0.40	0.21	0.43	0.21	0.19	0.03	-0.25
		OT	0.32	0.11	0.35	0.24	0.09	0.03	-0.23
		OS	0.36	0.12	0.37	0.25	0.11	ns	ns
	Sensitivity	BL \times FR	0.33	0.17	0.37	0.20	0.13	0.05	-0.29
		BL \times BD	0.49	0.21	0.53	0.32	0.17	0.03	-0.28
		FR \times BD	0.38	0.22	0.39	0.17	0.21	ns	ns
		SE	0.45	0.25	0.49	0.25	0.20	0.04	-0.30
	Recoverability	MO \times OT	0.44	0.06	0.44	0.38	0.06	ns	ns
		MO \times OS	0.40	0.05	0.40	0.36	0.04	ns	ns
		OT \times OS	0.43	0.13	0.45	0.32	0.11	ns	ns
		MO \times OT \times OS	0.39	0.05	0.39	0.34	0.05	ns	ns
		RM	0.60	0.19	0.61	0.41	0.19	ns	ns
		RM \times MO	0.68	0.27	0.68	0.42	0.26	ns	ns
		RM \times OT	0.58	0.21	0.59	0.38	0.20	ns	ns
		RM \times OS	0.60	0.23	0.61	0.38	0.22	ns	ns
		RM \times MO \times OT	0.66	0.28	0.67	0.39	0.27	ns	ns
		RM \times MO \times OS	0.64	0.28	0.65	0.37	0.27	ns	ns
		RM \times OT \times OS	0.60	0.23	0.61	0.38	0.22	ns	ns
		RE	0.64	0.28	0.65	0.37	0.27	0.02	-0.23
	Vulnerability	SE+RE	0.52	0.26	0.55	0.29	0.23	0.03	-0.29
		SE \times RE	0.50	0.23	0.53	0.29	0.21	0.02	-0.25
Relative number of taxa	Individual traits	BL	0.53	ns	0.53	0.50	0.03	ns	ns
		FR	0.34	ns	0.34	0.34	0.00	ns	ns
		BD	ns	ns	ns	ns	0.01	ns	ns
		MO	0.66	0.21	0.67	0.46	0.20	ns	ns
		AM	0.48	0.19	0.47	0.28	0.19	ns	ns
		LS	0.45	0.25	0.46	0.21	0.24	ns	ns
		OT	0.51	0.10	0.51	0.41	0.11	ns	ns
		OS	0.42	0.17	0.42	0.25	0.17	ns	ns
	Sensitivity	BL \times FR	0.48	ns	0.47	0.47	0.01	ns	ns
		BL \times BD	0.63	ns	0.63	0.60	0.03	ns	ns
		FR \times BD	0.26	ns	0.25	0.26	0.00	ns	ns
		SE	0.51	ns	0.51	0.51	0.00	ns	ns
	Recoverability	MO \times OT	0.60	0.22	0.61	0.39	0.21	ns	ns
		MO \times OS	0.60	0.27	0.61	0.34	0.25	ns	ns
		OT \times OS	0.53	0.18	0.53	0.35	0.18	ns	ns
		MO \times OT \times OS	0.58	0.27	0.60	0.33	0.26	0.02	-0.24
		RM	0.35	0.09	0.34	0.25	0.10	ns	ns
		RM \times MO	0.53	0.39	0.57	0.18	0.35	0.04	-0.31
		RM \times OT	0.27	0.08	0.26	0.19	0.09	ns	ns
		RM \times OS	0.37	0.18	0.37	0.19	0.18	ns	ns
		RM \times MO \times OT	0.49	0.39	0.53	0.15	0.34	0.04	-0.31
		RM \times MO \times OS	0.48	0.44	0.55	0.11	0.37	0.06	-0.37
		RM \times OT \times OS	0.35	0.17	0.34	0.17	0.17	ns	ns
		RE	0.47	0.44	0.54	0.10	0.37	0.07	-0.37
	Vulnerability	SE+RE	0.63	0.15	0.65	0.50	0.14	ns	ns
		SE \times RE	0.66	0.32	0.67	0.35	0.31	ns	ns

Table 4. Complete output of variation partitioning for the Bay of Biscay. Symbols: “|”, conditional effect; “∩”, confounding effect between environmental variables and trawling intensity (intersection). AM, age at maturity; BD, burrowing depth; BL, body length; FR, fragility; LS, life span; MO, motility; OS, offspring size; OT, offspring type; RE, recoverability; SE, sensitivity. Partial r indicates the Pearson’s r -correlation coefficient between the response variable and trawling intensity when controlling for the effect of abiotic variables; it also indicates the sign of variation of the relationship.

Density	Component	Response variable	Abiotic	Trawling	Abio. + Trawl.	Abio. Trawl.	Abio. ∩ Trawl.	Trawl. Abio.	Partial r
Absolute biomass	Individual traits	BL	0.01	0.03	0.06	0.03	ns	0.04	-0.21
		FR	0.02	0.08	0.10	0.02	0.01	0.08	-0.34
		BD	0.03	0.07	0.11	0.03	ns	0.07	-0.30
		MO	0.03	0.08	0.12	0.04	ns	0.08	-0.32
		AM	0.03	0.04	0.08	0.04	ns	0.05	-0.22
		LS	0.03	0.04	0.08	0.04	ns	0.05	-0.23
		OT	0.03	0.07	0.10	0.03	ns	0.07	-0.30
		OS	0.05	0.09	0.14	0.05	0.01	0.08	-0.35
	Sensitivity	BL×FR	0.02	0.09	0.10	0.01	0.01	0.09	-0.36
		BL×BD	0.03	0.09	0.11	0.02	ns	0.08	-0.34
		FR×BD	0.03	0.09	0.12	0.02	0.01	0.08	-0.35
		SE	0.03	0.09	0.11	0.02	0.01	0.09	-0.36
	Recoverability	MO×OT	0.07	0.11	0.17	0.06	0.01	0.10	-0.38
		MO×OS	0.09	0.10	0.18	0.08	0.01	0.09	-0.38
		OT×OS	0.07	0.11	0.16	0.05	0.01	0.09	-0.40
		MO×OT×OS	0.10	0.12	0.20	0.09	0.02	0.10	-0.41
		RM	0.06	0.03	0.10	0.07	ns	0.04	-0.19
		RM×MO	0.07	0.05	0.13	0.08	ns	0.06	-0.26
		RM×OT	0.09	0.07	0.16	0.09	ns	0.07	-0.30
		RM×OS	0.13	0.07	0.20	0.13	0.01	0.06	-0.31
		RM×MO×OT	0.11	0.09	0.19	0.11	0.01	0.08	-0.35
		RM×MO×OS	0.15	0.07	0.22	0.15	0.01	0.07	-0.33
		RM×OT×OS	0.15	0.10	0.23	0.13	0.02	0.08	-0.38
		RE	0.17	0.10	0.25	0.15	0.02	0.08	-0.39
	Vulnerability	SE×RE	0.08	0.12	0.18	0.06	0.01	0.11	-0.41
		SE×RE	0.04	0.06	0.09	0.03	0.01	0.05	-0.29
Absolute number of individuals	Individual traits	BL	ns	0.05	0.07	0.02	ns	0.06	-0.22
		FR	ns	0.08	0.08	ns	ns	0.08	-0.28
		BD	0.02	0.06	0.09	0.03	ns	0.07	-0.24
		MO	ns	0.10	0.11	0.01	ns	0.10	-0.34
		AM	0.06	0.05	0.12	0.07	ns	0.06	-0.23
		LS	0.03	0.04	0.08	0.04	ns	0.05	-0.20
		OT	0.02	0.07	0.10	0.02	ns	0.08	-0.28
		OS	0.03	0.12	0.14	0.02	0.01	0.11	-0.38
	Sensitivity	BL×FR	ns	0.11	0.12	ns	ns	0.11	-0.35
		BL×BD	ns	0.10	0.10	ns	ns	0.10	-0.32
		FR×BD	ns	0.10	0.10	ns	ns	0.10	-0.32
		SE	ns	0.13	0.13	ns	ns	0.12	-0.38
	Recoverability	MO×OT	0.02	0.12	0.14	0.02	0.01	0.11	-0.38
		MO×OS	0.03	0.12	0.14	0.02	0.01	0.11	-0.37
		OT×OS	0.04	0.14	0.17	0.03	0.01	0.13	-0.43
		MO×OT×OS	0.04	0.13	0.16	0.02	0.01	0.12	-0.41
		RM	0.15	0.04	0.20	0.16	ns	0.05	-0.21
		RM×MO	0.06	0.07	0.14	0.07	ns	0.08	-0.28
		RM×OT	0.14	0.10	0.23	0.13	ns	0.09	-0.32
		RM×OS	0.12	0.11	0.23	0.11	0.01	0.10	-0.36
		RM×MO×OT	0.07	0.09	0.16	0.07	ns	0.09	-0.33
		RM×MO×OS	0.09	0.09	0.18	0.09	ns	0.08	-0.32
		RM×OT×OS	0.14	0.14	0.26	0.12	0.02	0.12	-0.41
		RE	0.10	0.10	0.19	0.09	0.01	0.10	-0.36
	Vulnerability	SE×RE	0.02	0.14	0.15	0.01	ns	0.14	-0.40
		SE×RE	0.02	0.06	0.08	0.02	ns	0.07	-0.32

Table 4. Continued.

Density	Component	Response variable	Abiotic	Trawling	Abio. + Trawl.	Abio. Trawl.	Abio. \cap Trawl.	Trawl. Abio.	Partial r
Absolute number of taxa	Individual traits	BL	ns	0.06	0.08	0.03	ns	0.07	-0.24
		FR	ns	0.08	0.08	ns	ns	0.08	-0.29
		BD	0.03	0.06	0.10	0.04	ns	0.06	-0.25
		MO	ns	0.10	0.11	ns	ns	0.10	-0.35
		AM	0.05	0.06	0.12	0.06	ns	0.07	-0.25
		LS	0.03	0.04	0.09	0.04	ns	0.06	-0.21
		OT	0.02	0.08	0.11	0.03	ns	0.08	-0.29
		OS	0.03	0.13	0.15	0.02	0.01	0.12	-0.39
	Sensitivity	BL \times FR	ns	0.11	0.12	ns	ns	0.12	-0.36
		BL \times BD	ns	0.10	0.11	0.01	ns	0.11	-0.33
		FR \times BD	ns	0.10	0.10	ns	ns	0.10	-0.33
		SE	ns	0.13	0.13	ns	ns	0.13	-0.39
	Recoverability	MO \times OT	0.01	0.12	0.12	ns	0.01	0.11	-0.38
		MO \times OS	0.02	0.11	0.12	0.01	0.01	0.11	-0.38
		OT \times OS	0.04	0.14	0.17	0.03	0.02	0.13	-0.42
		MO \times OT \times OS	0.02	0.13	0.14	ns	0.01	0.12	-0.40
		RM	0.12	0.06	0.19	0.13	ns	0.07	-0.26
		RM \times MO	0.04	0.07	0.12	0.04	ns	0.08	-0.30
		RM \times OT	0.11	0.11	0.22	0.11	ns	0.11	-0.35
		RM \times OS	0.11	0.12	0.22	0.09	0.01	0.11	-0.38
		RM \times MO \times OT	0.04	0.09	0.13	0.04	ns	0.09	-0.33
		RM \times MO \times OS	0.06	0.09	0.15	0.06	ns	0.08	-0.33
		RM \times OT \times OS	0.11	0.14	0.24	0.09	0.02	0.12	-0.41
	Vulnerability	RE	0.06	0.10	0.15	0.06	ns	0.09	-0.35
		SE+RE	ns	0.14	0.15	0.01	ns	0.14	-0.41
		SE \times RE	0.02	0.05	0.09	0.03	ns	0.06	-0.27
Relative biomass	Individual traits	BL	0.10	ns	0.10	0.10	ns	ns	ns
		FR	0.06	0.06	0.10	0.04	0.02	0.04	-0.24
		BD	0.08	0.06	0.11	0.05	0.03	0.03	-0.24
		MO	0.07	0.05	0.11	0.06	0.01	0.04	-0.25
		AM	0.10	ns	0.10	0.10	ns	ns	ns
		LS	0.23	ns	0.23	0.23	ns	ns	ns
		OT	0.16	0.10	0.22	0.12	0.04	0.06	-0.33
		OS	0.10	0.08	0.14	0.07	0.03	0.05	-0.29
	Sensitivity	BL \times FR	0.04	0.08	0.10	0.02	0.02	0.06	-0.28
		BL \times BD	0.07	0.10	0.13	0.03	0.03	0.07	-0.32
		FR \times BD	0.07	0.07	0.11	0.05	0.03	0.04	-0.26
		SE	0.05	0.09	0.11	0.03	0.02	0.06	-0.29
	Recoverability	MO \times OT	0.12	0.08	0.17	0.09	0.03	0.05	-0.32
		MO \times OS	0.09	0.06	0.13	0.07	0.02	0.03	-0.26
		OT \times OS	0.14	0.11	0.20	0.10	0.04	0.06	-0.34
		MO \times OT \times OS	0.12	0.08	0.16	0.09	0.03	0.05	-0.30
		RM	0.09	ns	0.09	0.09	ns	ns	ns
		RM \times MO	0.07	ns	0.07	0.07	ns	ns	-0.10
		RM \times OT	0.16	0.03	0.18	0.15	0.01	0.02	-0.21
		RM \times OS	0.16	0.02	0.17	0.15	0.01	0.02	-0.19
		RM \times MO \times OT	0.11	0.03	0.14	0.10	0.01	0.03	-0.23
		RM \times MO \times OS	0.13	0.03	0.15	0.12	0.01	0.02	-0.20
	Vulnerability	RM \times OT \times OS	0.18	0.06	0.22	0.16	0.02	0.04	-0.30
		RE	0.14	0.05	0.17	0.13	0.02	0.03	-0.26
		SE+RE	0.11	0.12	0.20	0.08	0.03	0.09	-0.36
		SE \times RE	0.03	0.04	0.06	0.02	0.01	0.03	-0.20

Table 4. Continued.

Density	Component	Response variable	Abiotic	Trawling	Abio. + Trawl.	Abio. Trawl.	Abio. \cap Trawl.	Trawl. Abio.	Partial r
Relative number of individuals	Individual traits	BL	0.14	ns	0.14	0.14	ns	0.01	ns
		FR	0.04	0.08	0.11	0.03	0.01	0.07	-0.28
		BD	0.11	0.03	0.13	0.10	0.01	0.03	-0.20
		MO	0.08	0.07	0.14	0.07	0.02	0.05	-0.29
		AM	0.07	ns	0.08	0.08	ns	ns	-0.09
		LS	0.09	ns	0.09	0.09	ns	ns	ns
		OT	0.13	0.06	0.17	0.11	0.01	0.05	-0.27
		OS	0.15	0.13	0.24	0.11	0.04	0.10	-0.38
	Sensitivity	BL \times FR	0.05	0.15	0.18	0.04	0.02	0.13	-0.39
		BL \times BD	0.13	0.13	0.24	0.11	0.02	0.11	-0.37
		FR \times BD	0.04	0.12	0.13	0.02	0.02	0.10	-0.35
		SE	0.04	0.17	0.19	0.02	0.02	0.15	-0.42
	Recoverability	MO \times OT	0.08	0.09	0.14	0.05	0.03	0.06	-0.31
		MO \times OS	0.06	0.08	0.11	0.03	0.02	0.06	-0.30
		OT \times OS	0.18	0.16	0.29	0.13	0.05	0.11	-0.41
		MO \times OT \times OS	0.08	0.10	0.14	0.05	0.03	0.07	-0.32
		RM	0.13	ns	0.13	0.13	ns	ns	ns
		RM \times MO	ns	0.02	0.03	ns	ns	0.02	-0.17
		RM \times OT	0.17	0.07	0.22	0.16	0.01	0.05	-0.30
		RM \times OS	0.14	0.09	0.21	0.12	0.02	0.07	-0.34
		RM \times MO \times OT	0.02	0.05	0.06	0.02	0.01	0.04	-0.24
		RM \times MO \times OS	0.04	0.05	0.08	0.04	0.01	0.04	-0.24
		RM \times OT \times OS	0.18	0.13	0.27	0.14	0.04	0.09	-0.40
	Vulnerability	RE	0.05	0.06	0.10	0.04	0.01	0.05	-0.28
		SE+RE	0.04	0.20	0.20	0.01	0.03	0.17	-0.45
	Relative number of taxa	SE \times RE	0.02	0.05	0.07	0.02	ns	0.05	-0.22
	Individual traits	BL	0.12	0.10	0.22	0.12	0.01	0.09	-0.35
		FR	0.06	0.11	0.15	0.04	0.02	0.08	-0.32
		BD	0.11	0.11	0.18	0.07	0.04	0.07	-0.30
		MO	0.09	0.10	0.15	0.05	0.03	0.06	-0.31
		AM	0.09	0.09	0.15	0.06	0.03	0.06	-0.31
		LS	0.06	0.02	0.06	0.05	0.01	0.01	-0.14
		OT	0.16	0.18	0.27	0.09	0.06	0.12	-0.42
		OS	0.15	0.17	0.26	0.09	0.06	0.11	-0.41
	Sensitivity	BL \times FR	0.07	0.16	0.21	0.05	0.02	0.14	-0.40
		BL \times BD	0.12	0.20	0.27	0.07	0.04	0.15	-0.44
		FR \times BD	0.06	0.14	0.17	0.03	0.03	0.11	-0.37
		SE	0.06	0.18	0.21	0.03	0.03	0.15	-0.42
	Recoverability	MO \times OT	0.08	0.10	0.15	0.04	0.04	0.07	-0.33
		MO \times OS	0.07	0.10	0.13	0.03	0.03	0.06	-0.31
		OT \times OS	0.17	0.19	0.29	0.10	0.06	0.12	-0.44
		MO \times OT \times OS	0.07	0.11	0.14	0.04	0.04	0.07	-0.33
		RM	0.14	0.04	0.17	0.13	0.01	0.03	-0.21
		RM \times MO	0.03	0.04	0.06	0.02	0.01	0.03	-0.20
		RM \times OT	0.15	0.12	0.24	0.12	0.04	0.08	-0.36
		RM \times OS	0.13	0.12	0.22	0.10	0.04	0.09	-0.36
		RM \times MO \times OT	0.05	0.06	0.09	0.03	0.01	0.04	-0.24
		RM \times MO \times OS	0.06	0.05	0.10	0.04	0.01	0.04	-0.24
		RM \times OT \times OS	0.15	0.15	0.25	0.10	0.05	0.10	-0.40
	Vulnerability	RE	0.06	0.07	0.11	0.04	0.02	0.05	-0.26
		SE+RE	0.07	0.19	0.23	0.04	0.03	0.16	-0.43
	Relative number of taxa	SE \times RE	0.03	0.05	0.08	0.03	ns	0.05	-0.21

Making sense of biodiversity ‘hotspots’

Thompson *et al.* (2021) assessed whether local and large-scale biodiversity ‘hotspots’ were consistent with one-another using two UK marine benthic datasets (Figure 6). They assessed γ -diversity (regional richness) with diversity partitioned between α (local richness) and β (dissimilarity), and found hotspots were largely inconsistent across these metrics with each relating uniquely to gradients of environmental change (Figures 7–8). A key conclusion being that biodiversity has multidimensional properties such that areas of high biodiversity can appear inconsistent across different metrics. However, through the joint use of α -, β - and γ -diversity and in understanding how they relate to one-another, differences between them provide information about the scale of biotic response which can direct conservation and management to the appropriate scale for intervention (Figures 9–10).

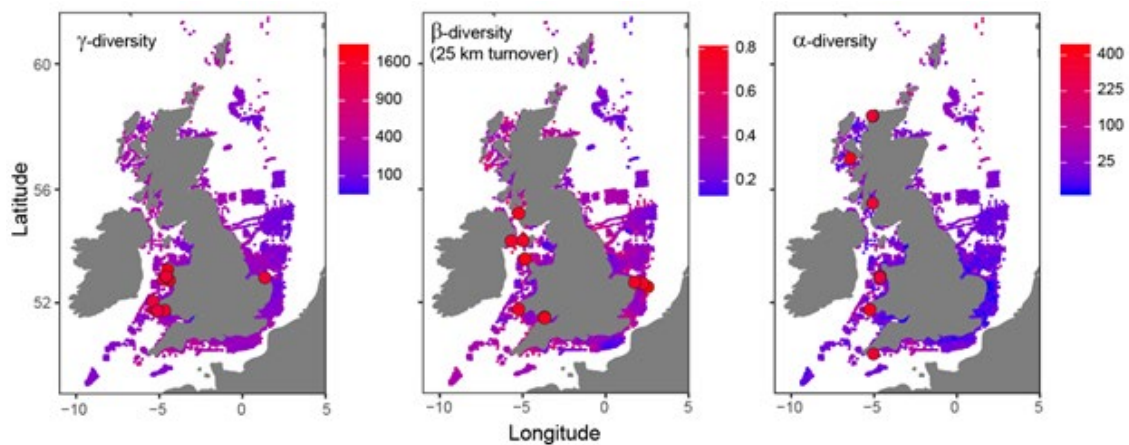


Figure 6. The top ten marine benthic ‘hotspots’ (large points) plotted over spatial estimates of γ -, β - and α -diversity across the UK EEZ using the combined dataset. Values are based on means where multiple temporal observations exist.

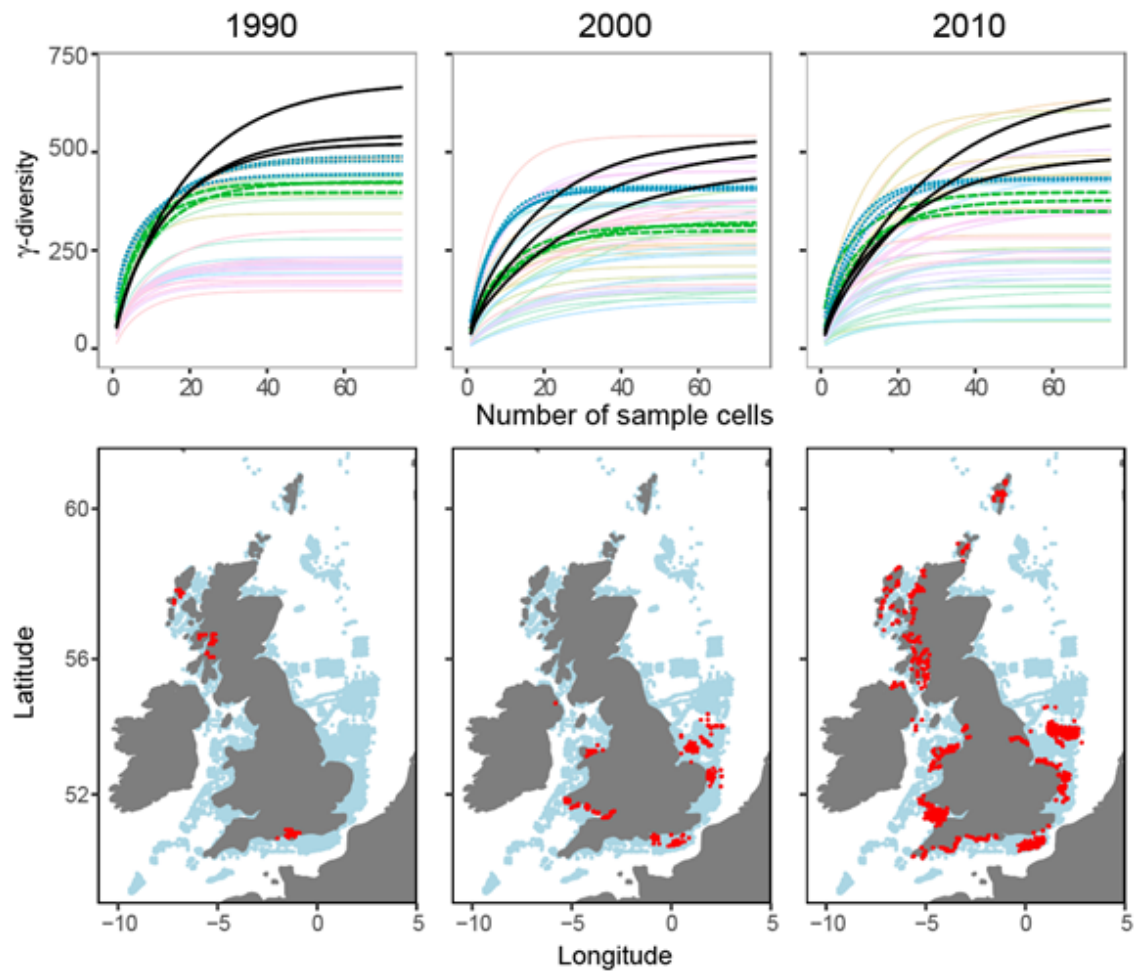


Figure 7. Top panels: rarefaction of marine benthic assemblages used to estimate γ -diversity for years 1990, 2000 and 2010. Crossing curves demonstrate that the sites rank-order based on richness is not conserved as the number of sample-cells (i.e. spatial units) increases, and this feature is consistent over time ($n = 50$ cells were randomly selected in 2000 and 2010 where there were data for > 50). We highlight areas which may have relatively low to intermediate species richness based on a low number of sample-cells (black lines) compared with other areas (e.g. blue dotted and green dashed lines) but, because of higher dissimilarity between local assemblages, tend to have some of the highest species richness values at larger scales. Based on these results, we would draw contrasting conclusions about which area was most diverse depending on whether we looked at 1, 20 and 60 sites within a region. Bottom panels: maps show differences in spatial data distribution between respective years (red = data collected in that year, blue = all data).

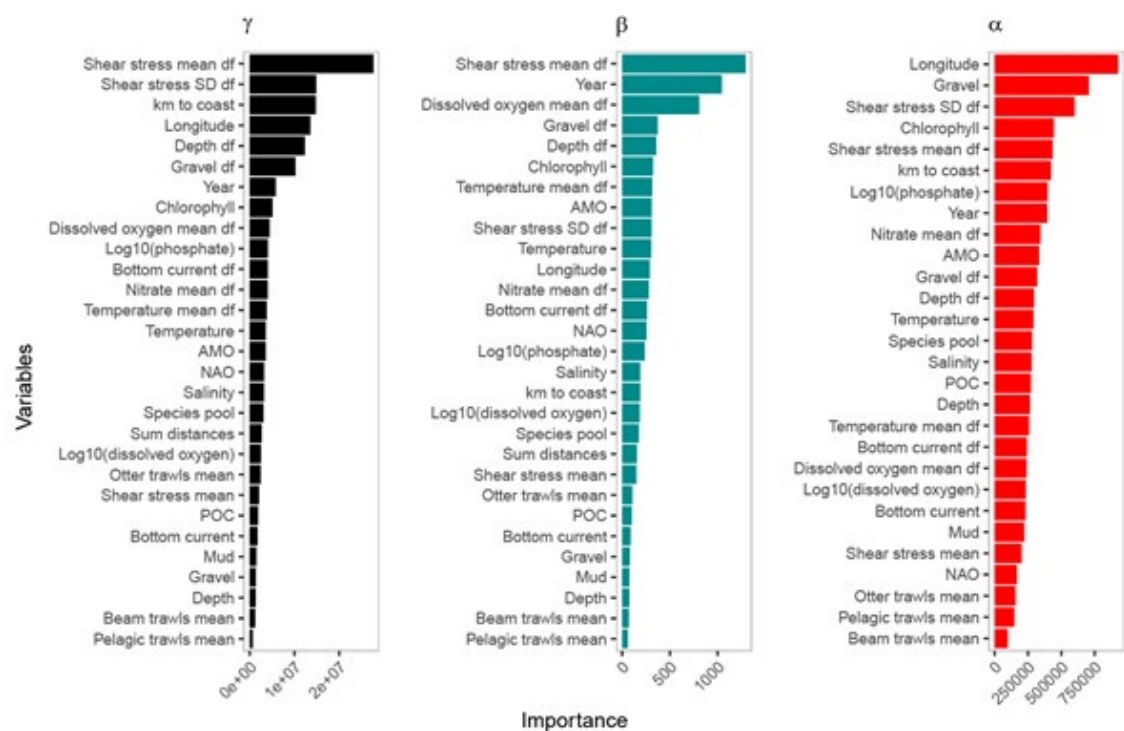


Figure 8. Variable importance based on node impurity ordered along the y-axis from most important (top) to least important (bottom) following random forest analysis on the combined data. The suffix “df” represents a variable’s heterogeneity based on mean pairwise differences across selected sample-cells within a 25 km radius.

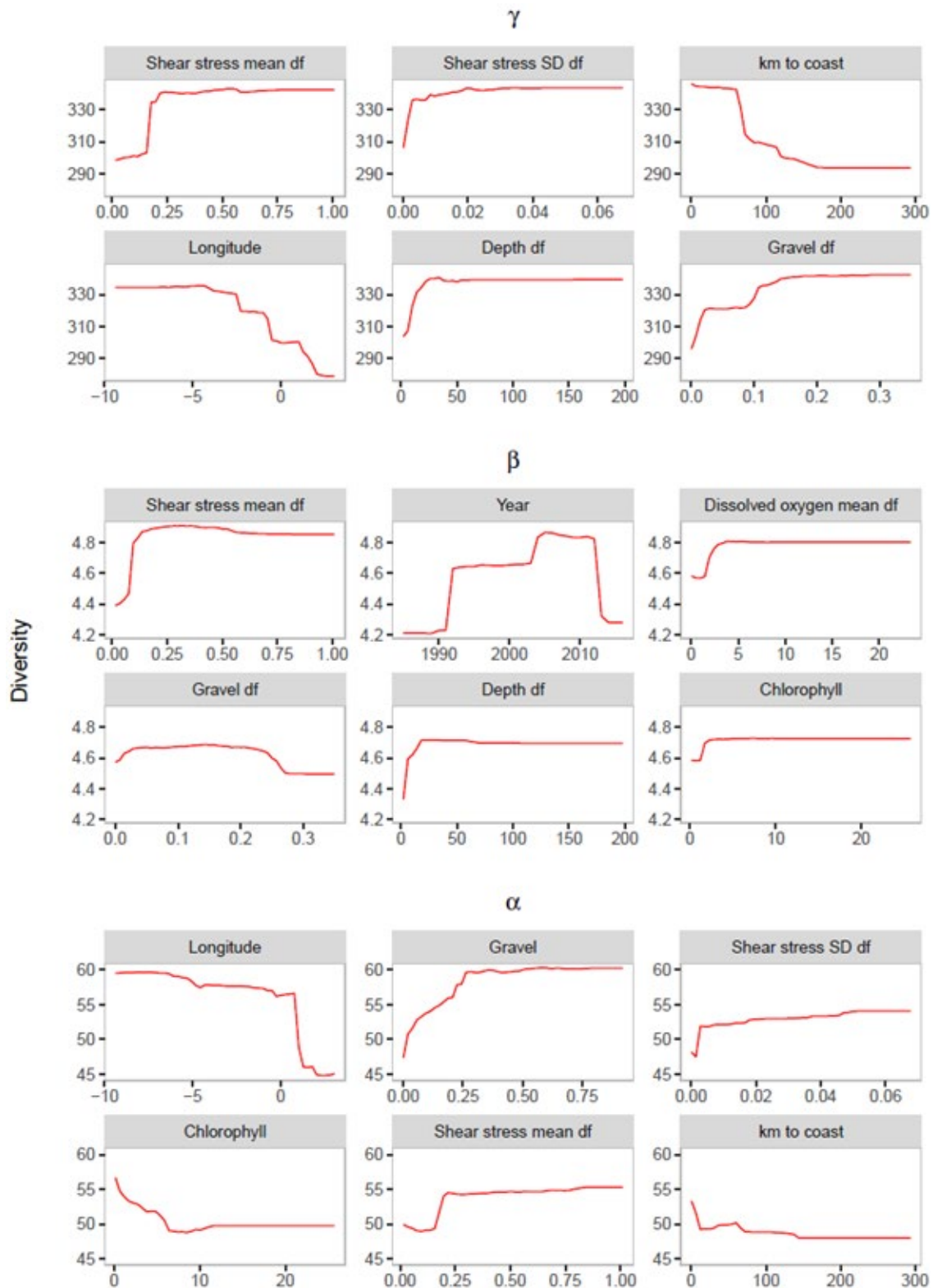


Figure 9. Partial dependence plots showing model predictions (red line) of γ -, β - and α -diversity (y-axis) using the combined dataset in response to the six most important covariates (x-axis) as determined by node impurity (Figure 8), while keeping other variables fixed at their average values. The suffix “df” represents a variable’s heterogeneity based on mean pairwise differences across selected sample-cells within a 25 km radius.

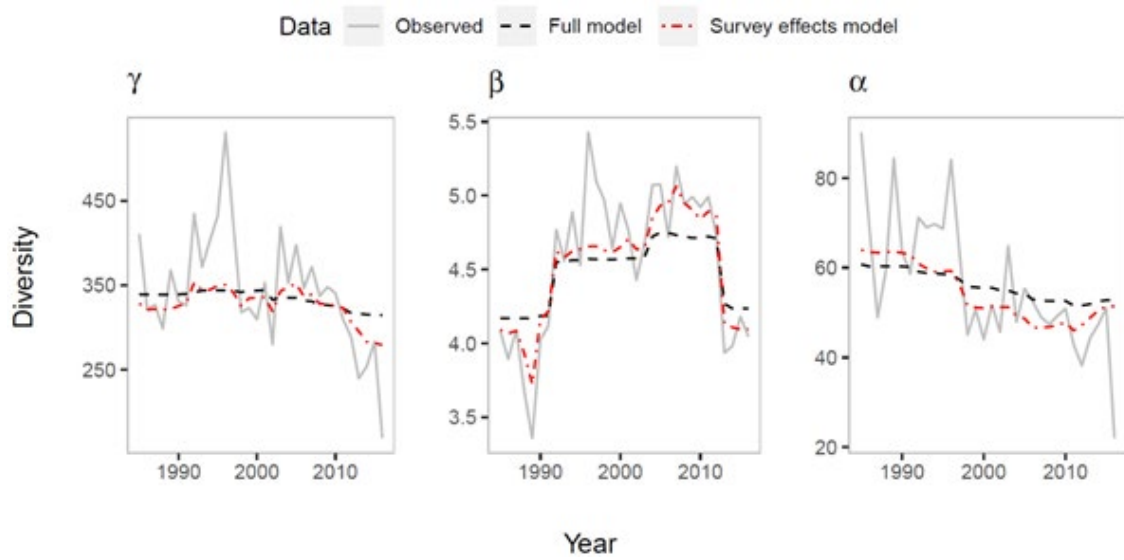


Figure 10. Observed vs partial dependence plots for full model and survey effects model estimates of temporal diversity. Change was partly captured by our environmental and survey covariates, revealed by the more limited change related to 'Year' in the full models, followed by the survey effects models, with most variation in our observed values.

Threshold responses

Couce *et al.* 2020, using a dataset for the North Sea covering a 21-year period, assessed the threshold responses of marine benthos along gradients of both natural and anthropogenic change (Figures 11–12). Their findings showed that shear stress resulted as the most important predictor of changes in benthic community composition, and associated cumulative changes in sea bottom temperature and bottom trawling activities, can result in larger responses providing communities response thresholds that can be used as potential early-warning signals that may lead spatially to structural and functioning changes within ecosystems (Figure 13).

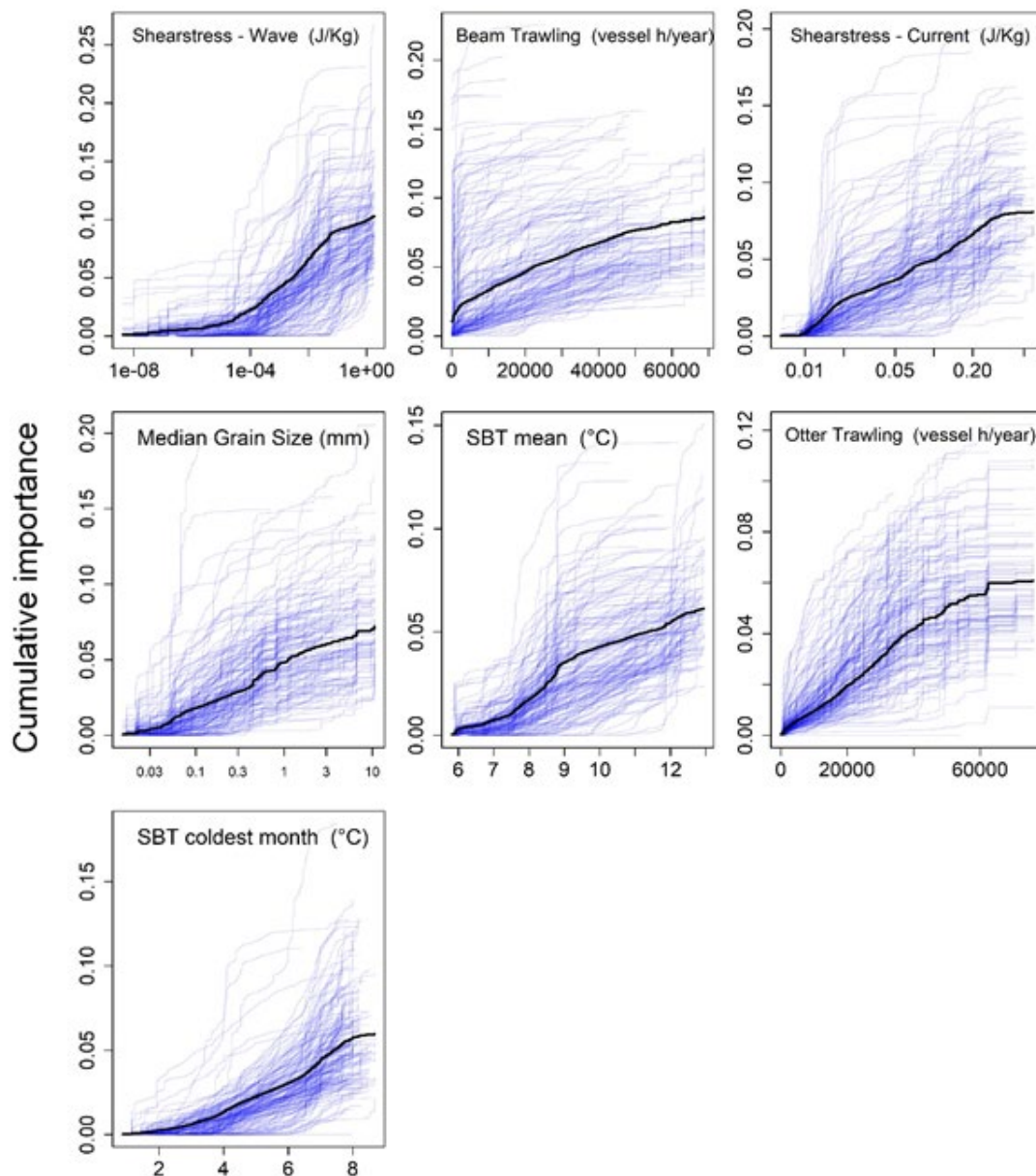


Figure 11. Compositional change along each environmental gradient for all infauna genera. Each blue line denotes a genus while the thicker black line denotes the average (e.g., the overall pattern of genus compositional change along the gradient). The y-axes have been normalised so that the maximum corresponds to the relative variable importance. Individual plots are arranged (left to right) from the most to the least important predictor.

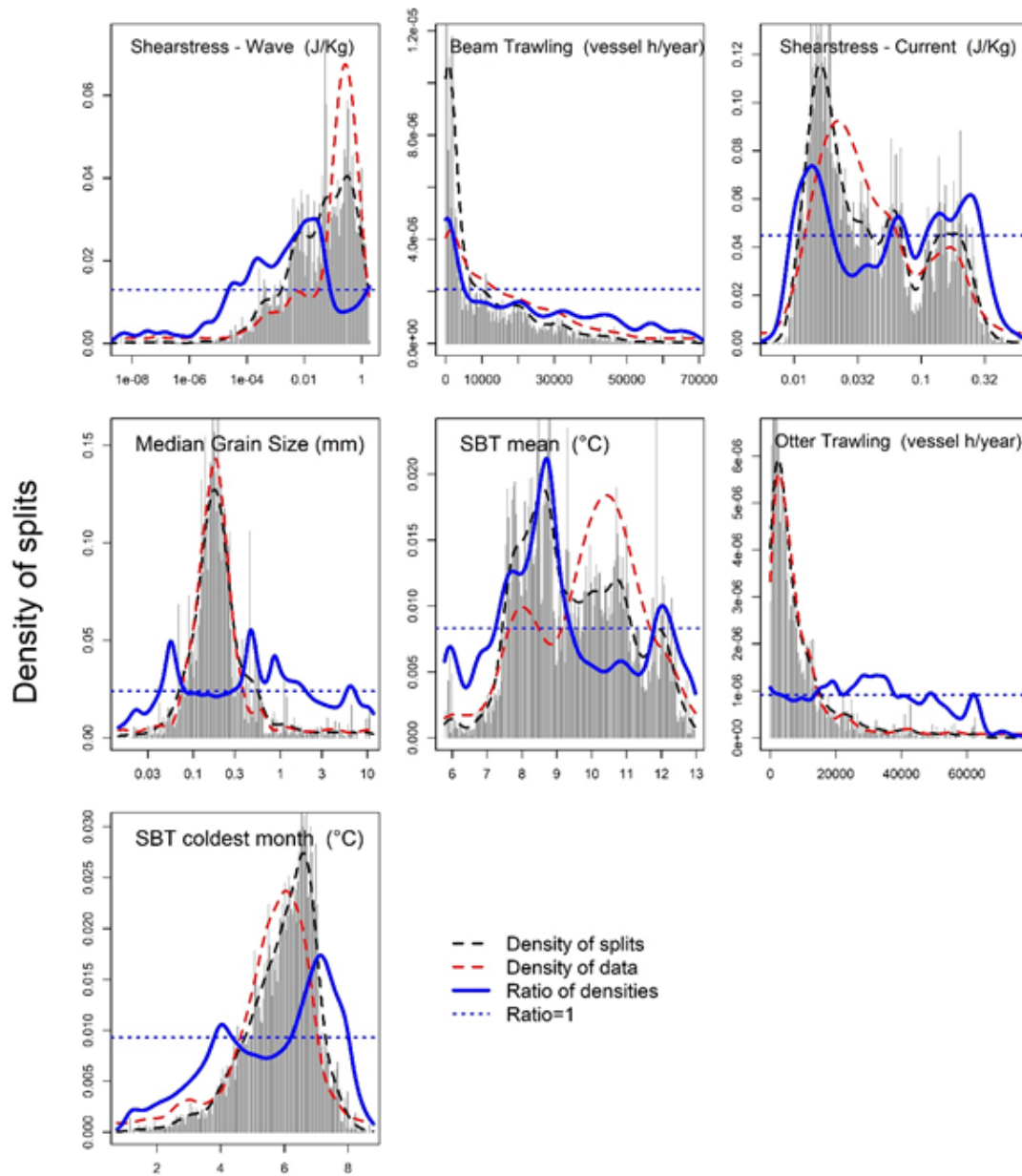


Figure 12. Frequency histograms of gradient values at which splits occur in the regression trees for all infauna genera, showing where along environmental gradients important compositional changes are taking place. Black lines are the kernel density of the histograms, red lines show the (normalised) distribution of the data along the environmental gradients, and blue lines indicate the ratio between splits and data (ratio between black and red lines). Thus ratios >1 (above the dotted line) indicate conditions of relatively greater change in genus composition (i.e. community thresholds). Individual plots are arranged (left to right) from the most to the least important predictor.

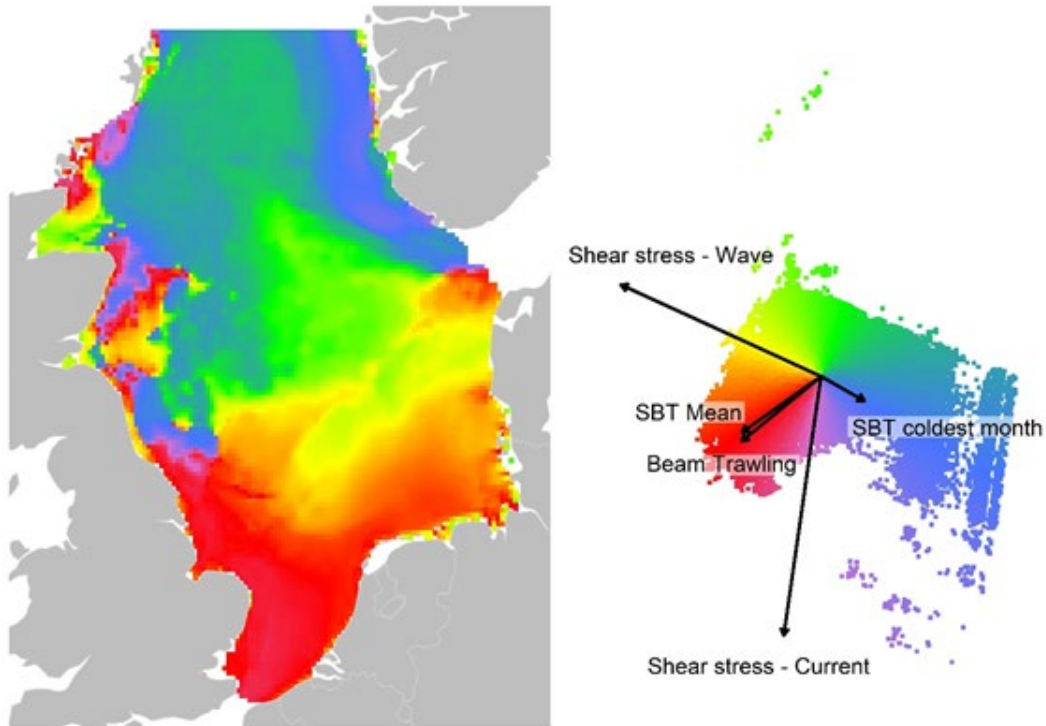


Figure 13. Changes of infauna community composition predicted by the Gradient Forest analysis for the environmental and trawling pressure data for the year 2000. These changes have been mapped over the first two dimensions of a biologically transformed environmental space that accounts for their respective influence in dictating compositional patterns (together capturing 80% of the explained variance). The colour key shows the environmental variables driving those compositional changes (longer arrows denote stronger influences; arrows for median grain size and other trawling are not shown because their contribution is less significant).

2 Food web functioning (ToR B)

Feeding guild food web indicator

Thompson *et al.* 2020 propose a food web indicator which has been explicitly called for to inform policy via food web status assessment as part of the European Union's Marine Strategy Framework Directive and the indicator toolkit supporting The Convention for the Protection of the Marine Environment of the North-East Atlantic (the 'OSPAR Convention'). Using a newly compiled dataset of trophic interactions from across the northeast Atlantic shelf seas, they grouped predators into 'feeding guilds' based on their diets. They then assessed change in feeding guilds across the North Sea between 1985–2016 (Figure 14) in response to resource availability, temperature, fishing, and the biomass of other guilds (Figures 15–16).

Guild biomasses were largely consistent through time at the North Sea-level and spatially aggregated at the regional level with change relating to changes in resource availability, temperature, fishing, and the biomass of other guilds. This suggests that fish biomass was partitioned across broad feeding and environmental niches, and changes over time were governed partly by guild carrying capacities, but also by a combination of covariates with contrasting patterns of change. Management of the North Sea ecosystem could therefore be adaptive and focused towards specific guilds and pressures in a given area.

This work is continuing to develop, extending the study area and guild responses of Thompson *et al.* 2020. We characterised groundfish survey data for the northeast Atlantic shelf seas (Figure 17) from 1997–2016 (i.e. where long-term, comparable processed survey data exist). We also investigate change in guild biomass in relation to novel response variables such as guild size-structure and measures of diversity. Here, we use a relatively simple set of guilds (i.e. we take a higher split in the classification tree), and these can be described as planktivores (combining both Generalist planktivore and Zooplanktivore), benthivores (Coastal benthivore, Generalist benthivore and Specialist benthivore) and demerso-piscivores (Piscivore and Zoobenthivore). We did this so that we could elegantly capture a broad set of ecosystem components while also explore a complex suite of responses. This has provided a large-scale baseline of guild structure and revealed clear regions of temporal change related to environmental characteristics and anthropogenic pressure gradients.

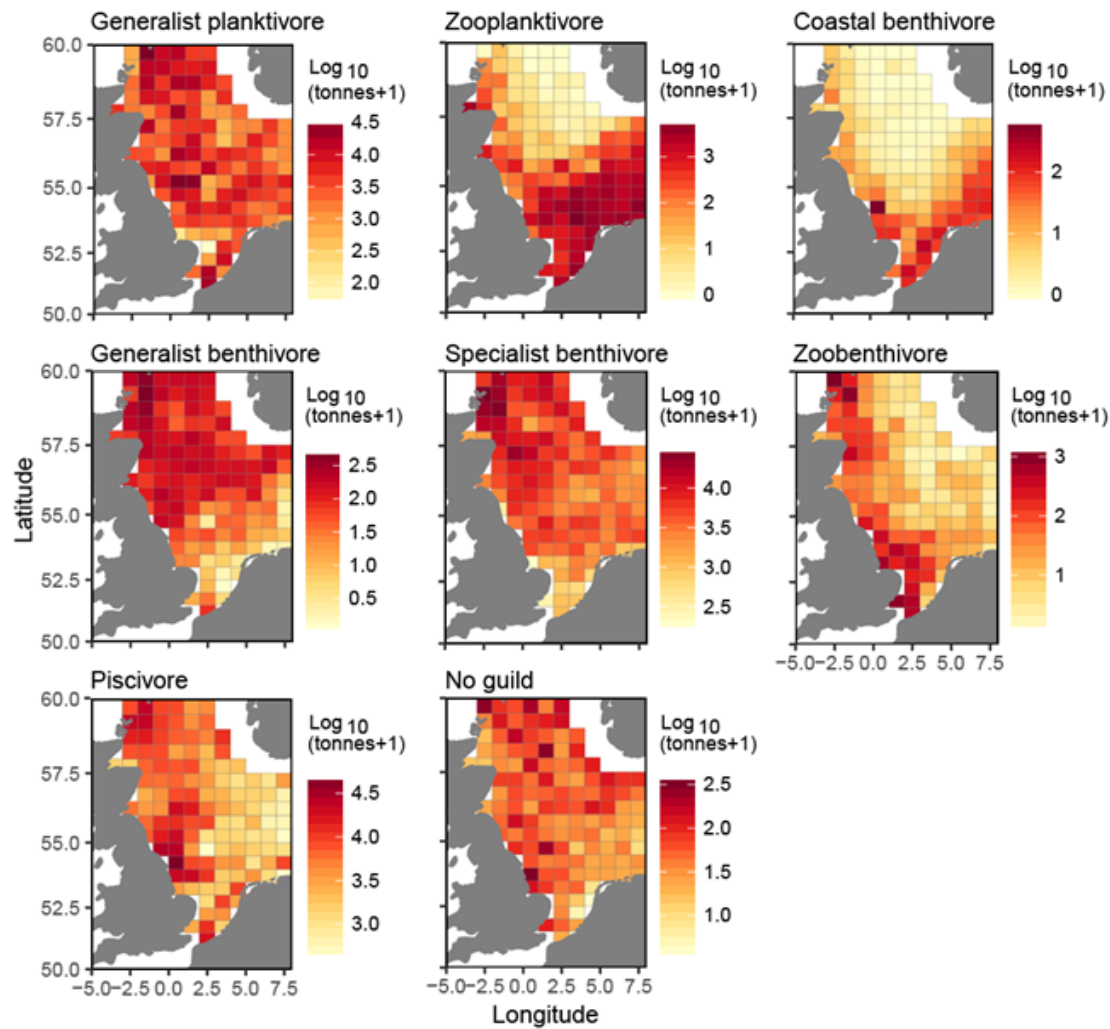


Figure 14. Mean feeding guild biomass distribution between 1985 and 2014 across ICES statistical rectangles in the North Sea.

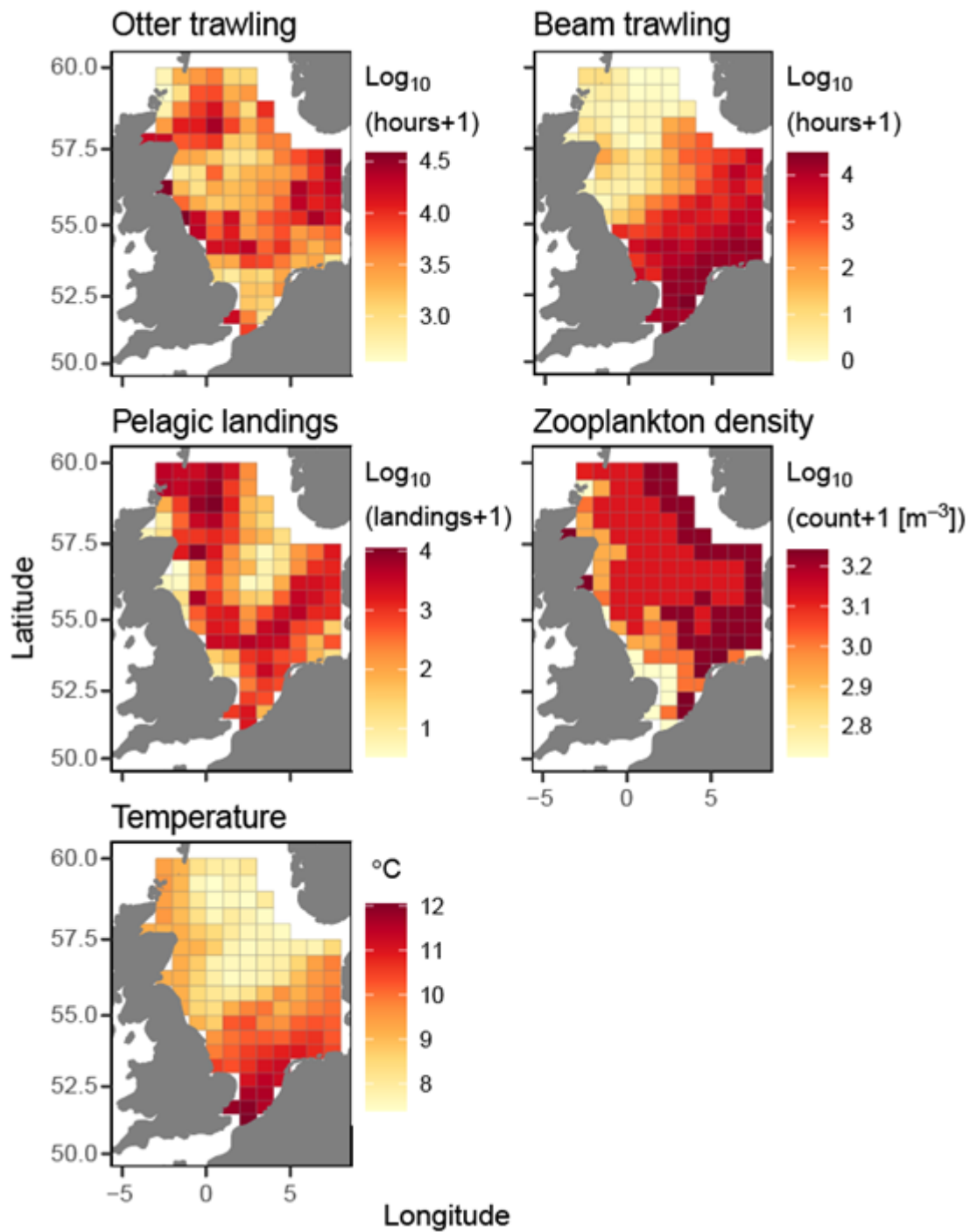


Figure 15. Mean covariate distributions between 1985 and 2014 across ICES statistical rectangles in the North Sea. Zooplankton density per m3 has been calculated for hydraulic zones following Capuzzo *et al.*, (2017).

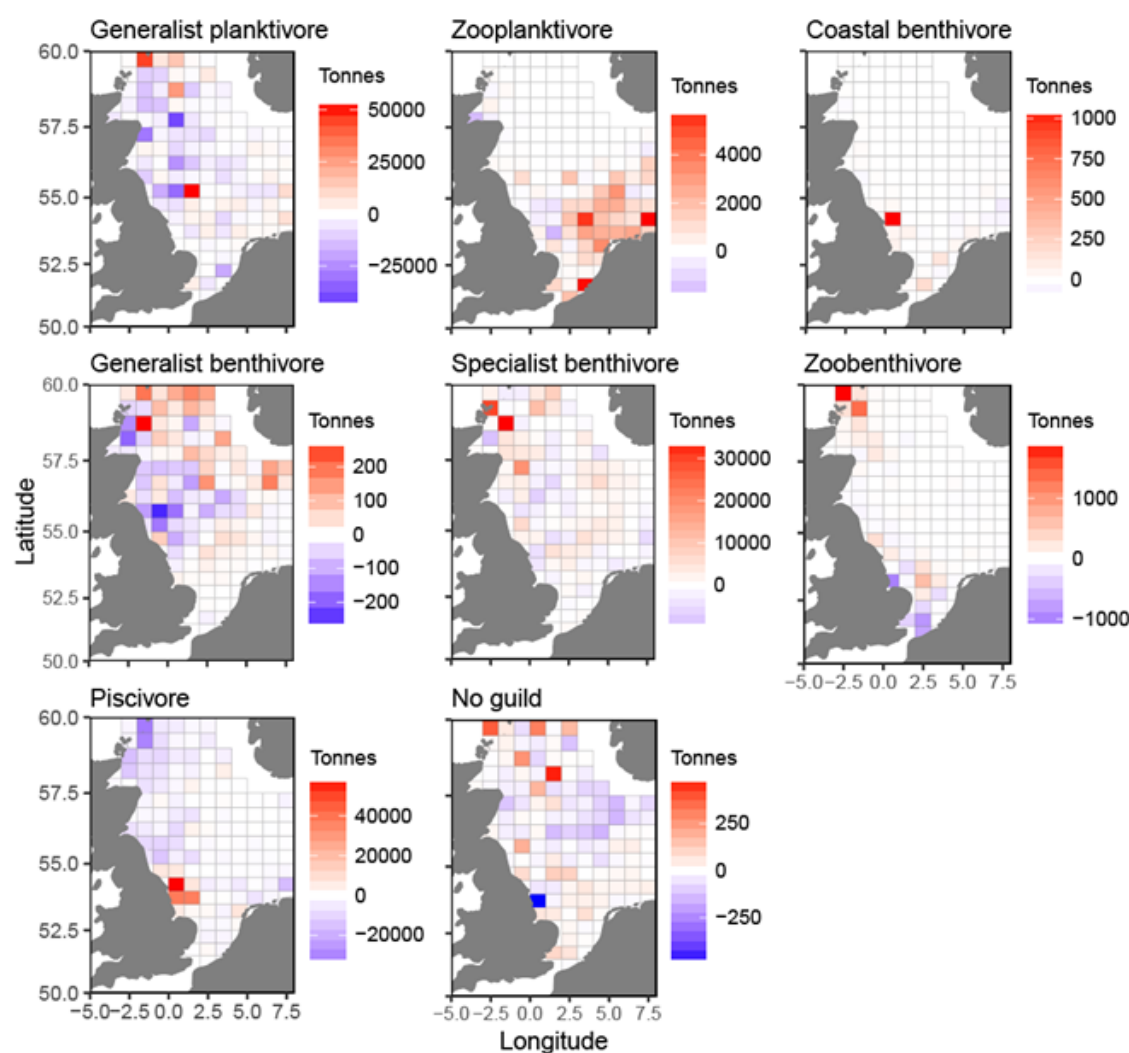


Figure 16. Feeding guild biomass change over time between 1985 to 1999 and 2000 to 2014 across ICES statistical rectangles in the North Sea.

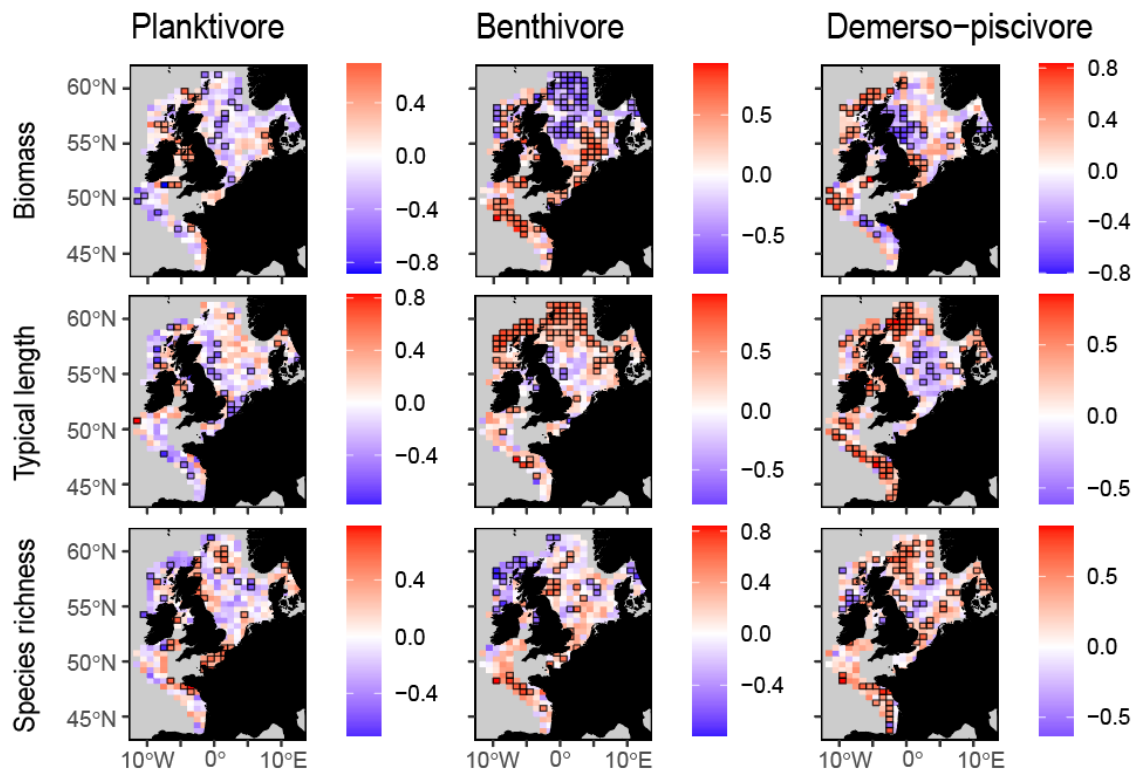


Figure 17. Temporal change in feeding guild responses per ICES statistical rectangle between 1997–2016 based on GOV quarter 1 and 4 survey data. Increases in indicators are shown by red cells (Pearson's correlation values between 0 and +1) and declines in blue cells (correlation values between 0 and -1). ICES statistical rectangles where the temporal change (correlation) is significant are highlighted with black borders.

Primary production impacts on foodwebs and fisheries

Declines in primary production (PP) of phytoplankton, as a result climate change, have been hypothesized to cause a bottom-up cascade of events in marine food webs ultimately altering the biomass of fish stocks and the commercial fisheries that they support. Change in primary production has been highlighted by OSPAR (2017b) as a key variable required to understand food web processes and declines in PP in the North Sea have been linked to declines in the biomass of copepods and recruitment of commercial fish stocks (Capuzzo *et al.* 2018). OSPAR demonstrated that structural change within pelagic habitats has occurred in the northeast Atlantic, but the impact of this change on higher trophic levels has proven unclear. Developing our understanding of the potential consequences of climate change through impacts of primary production can greatly advance our management of fisheries within the Ecosystem Approach to Management, particularly when modelling studies are considered routinely as part of the management and assessment cycle (Lynam *et al.* 2016). We extend a fisheries multi-species model Thorpe *et al.* (2015, 2017) to investigate how primary production changes might cascade in the North Sea ecosystem, at differing levels of trophic organisation. The extended model (Lynam and Thorpe *in prep*) includes a total of 28 finfish stocks (additionally including seabass, spurdog, hake, ling, megrim, thornback ray, turbot; Table 5) and *Nephrops* in the form of 9 functional units. The model was also re-formulated to allow for food-dependent growth, as stock growth trajectories depend upon the available food. If food is abundant, fish grow in accord with the von Bertalanffy relation. If there is less food, but enough for maintenance, fish grow in proportion to the amount of food that is surplus to maintenance requirements (which will be at a slower rate). If there is insufficient food to support maintenance, the fish do not grow at all and starvation occurs at a rate proportional to the food deficit.

Model simulations were run to contrast two fishing scenarios (no fishing from 2020 or stocks fished at F_{MSY}) and primary production (PP) ranging from zero to 2.5 times the baseline. The PP baseline represents the final estimates from Capuzzo *et al.* 2018. On this scale, change in PP consistent with the Intergovernmental Panel on Climate Change's Representative Concentration Pathways (RCPs) were determined through an analysis of long term projections obtained from the U.S. National Oceanic and Atmospheric Administration's Climate Change Web portal <https://www.esrl.noaa.gov/psd/ipcc/ocn/>. The RCP4.5 'medium scenario' equates to a decline to 74% of the baseline by the 2090s, while the RCP8.5 'high scenario' equates to a decline to 64% of the baseline by the 2090s.

Model data on the biomass of each species by length class were averaged over the final decade of the simulation (2090–2099) and these data used to calculate the unexploited biomass (B_0) of each stock following a recovery from fishing and two reference points based on a percentage of the unexploited biomass: $B_{Lim} = 0.20 B_0$ and $B_{Collapse} = 0.10 B_0$. The lower reference point $B_{Collapse}$ permits relatively severe stock depletion leading to elevated risk of collapse of stocks Thorpe *et al.* (2017, 2019). The higher reference point, B_{Lim} , was set at 20% of B_0 as this is considered equal to $0.5 B_{MSY}$ and below this point stocks are likely to suffer reduced recruitment. This interpretation of B_{Lim} is the Harvest Strategy Policy target implemented for all fisheries managed by the Australian Commonwealth government since 2008 (Smith *et al.* 2009). Within each model simulation, the percentage of stocks at risk was calculated and change in food web structure and function was captured through change in guild biomass. Guilds considered are the seven feeding guilds described by Thompson *et al.* (2020) supplemented with an 8th group composed solely of functional units of *Nephrops*. While the majority of the 29 species considered here fall into the Piscivore guild (Table 5), only two taxa (sprat and small herring) were representative of the Zooplanktivore guild and of these only one (sprat) were included in the indicators following the implementation of the lower cut off of 15 cm (Thorpe *et al.*, 2015). A simple classification of three guilds was also considered based on a higher split in the classification tree of Thompson *et al.* (2020) and including *Nephrops* within the benthivore guild.

Table 5. Fish and elasmobranch species within the multi-species model and guild classifications used in the analysis.

Scientific name	Model species (and size split)	Optimal Guild Classification	Simple Classification
<i>Limanda limanda</i>	Dab	Specialist benthivore	Benthivore
<i>Dicentrarchus labrax</i>	Bass	Coastal benthivore	Benthivore
<i>Melanogrammus aeglefinus</i>	Haddock	Specialist benthivore	Benthivore
<i>Microstomus kitt</i>	Lemon Sole	Generalist benthivore	Benthivore
<i>Hippoglossoides platessoides</i>	Long Rough Dab ≥ 32 cm	Generalist benthivore	Benthivore
<i>Pleuronectes platessa</i>	Plaice	Specialist benthivore	Benthivore
<i>Solea solea</i>	Sole ≥ 19 cm	Specialist benthivore	Benthivore
<i>Solea solea</i>	Sole < 19 cm	Coastal benthivore	Benthivore
<i>Glyptocephalus cynoglossus</i>	Witch	Generalist benthivore	Benthivore
<i>Nephrops</i>	<i>Nephrops</i>	<i>Nephrops</i>	Benthivore
<i>Gadus morhua</i>	Cod	Piscivore	Demerso-piscivore
<i>Leucoraja naevus</i>	Cuckoo Ray	Zoobenthivore	Demerso-piscivore
<i>Squalus acanthias</i>	Spurdog	Piscivore	Demerso-piscivore
<i>Eutrigla gurnardus</i>	Gurnard	Piscivore	Demerso-piscivore
<i>Merluccius merluccius</i>	Hake	Piscivore	Demerso-piscivore
<i>Trachurus trachurus</i>	Horse Mackerel ≥ 19 cm	Piscivore	Demerso-piscivore
<i>Molva molva</i>	Ling	Piscivore	Demerso-piscivore
<i>Lepidorhombus whiffiagonis</i>	Megrim	Piscivore	Demerso-piscivore
<i>Lophius piscatorius</i>	Monkfish	Piscivore	Demerso-piscivore
<i>Hippoglossoides platessoides</i>	Long Rough Dab < 32 cm	Piscivore	Demerso-piscivore
<i>Pollachius virens</i>	Saithe ≥ 31 cm	Piscivore	Demerso-piscivore
<i>Amblyraja radiata</i>	Starry Ray	Piscivore	Demerso-piscivore
<i>Raja clavata</i>	Thornback Ray	Zoobenthivore	Demerso-piscivore
<i>Scophthalmus maximus</i>	Turbot	Piscivore	Demerso-piscivore
<i>Merlangius merlangus</i>	Whiting	Piscivore	Demerso-piscivore
<i>Trisopterus minutus</i>	Poor Cod	Zoobenthivore	Demerso-piscivore
<i>Ammodytidae</i>	Sandeel	Generalist planktivore	Planktivore
<i>Clupea harengus</i>	Herring < 13 cm	Zooplanktivore	Planktivore
<i>Clupea harengus</i>	Herring ≥ 13 cm	Generalist planktivore	Planktivore
<i>Trachurus trachurus</i>	Horse Mackerel < 19 cm	Generalist planktivore	Planktivore
<i>Scomber scombrus</i>	Mackerel	Generalist planktivore	Planktivore
<i>Trisopterus esmarkii</i>	Norway Pout	Generalist planktivore	Planktivore
<i>Pollachius virens</i>	Saithe < 31 cm	Generalist planktivore	Planktivore
<i>Sprattus sprattus</i>	Sprat	Zooplanktivore	Planktivore

Results

Of the scenarios considered, the forecasted long-term total SSB of stocks in the 2090s, is greatest under the high PP values, and is lowest under the RCP 8.5 (high emissions forecast). Over the range of PP modelled, the relationship between PP and SSB of each group appeared linear. However, as PP approaches zero this relationship is likely to become highly variable as stocks collapse. Indeed, the risk of depletion ($SSB < B_{Lim}$) of stocks fished at F_{MSY} becomes unacceptable

overall (>5% of stocks at risk of depletion) as PP declines 13% from current level. A severe risk to stock collapse is considered unacceptable only at 29% of 1980s PP levels i.e. half of current PP and below the expected levels in the 2090s even in the high emissions scenario, suggesting that stocks fished at F_{MSY} are not at risk of collapse even under the additional stress associated with climate change through this pathway. At the current level of PP (Figure 18) the total risk of depletion when fished at F_{MSY} levels is acceptable (<5% of stocks at risk), suggesting that the MSY targets are precautionary for the prevailing environmental conditions. The climate change impacts on PP alone (through either RCP4.5 or 8.5) are not enough to lead to a high risk of stock collapse alone.

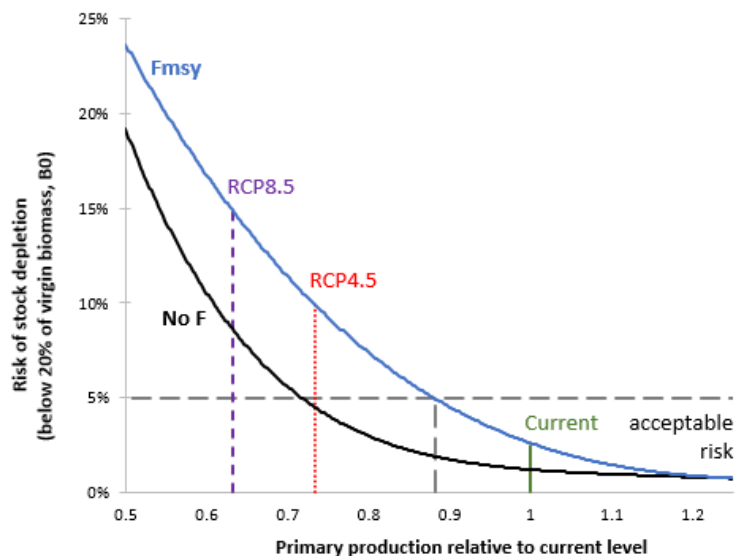


Figure 18. Risk of depletion of stocks below B_{Lim} in the long term (by 2090s) as a function of primary production for the whole community of 37 stocks when fished at F_{MSY} or not fished. Overall, 5% of stocks at risk is considered an acceptable level (dashed horizontal black line).

When fished at F_{MSY} , the biomass of feeding guilds generally declines as PP declines. The exception is the Zoobenthivore and *Nephrops* guilds that also benefit as their predators are depleted (peaking under current PP or the RCP8.5 respectively). The biggest depletion in biomass, as a result of decreases in modelled PP, occurs for the planktivores (including the two guilds with diets that are highly planktonic: Generalist planktivore and Zooplanktivore) that are dominated by pelagic fish. Indeed, these plankton feeding guilds are the first to be at risk of depletion (>5% of stocks within the guild with $SSB < B_{Lim}$) and in the long-term forecast will be at risk even at current PP levels (Figure 19). Stocks within guilds of Specialist Benthivores, such as plaice *Pleuronectes platessa* and sole *Solea solea* and Coastal Benthivores, such as seabass *Dicentrarchus labrax*, become at risk when the overall community reaches an unacceptable level of risk (a loss of 13% of current PP). In contrast, the model suggests that *Nephrops*, the Generalist Benthivore (including Lemon sole *Microstomus kitt*), Zoobenthivore (e.g. poor cod *Trisopterus minutus*) and Piscivore (e.g. cod *Gadus morhua* and hake *Merluccius merluccius*) guilds are more resilient to a decrease in PP than the community overall.

Conclusion

If a 13% decrease in PP below current levels occurred, then the current MSY targets would no longer be acceptable for the community overall (across all stocks and guilds). As a result, planktivorous pelagic fish would be expected to decline and ecosystem function would become more dependent of benthic functioning. To address any additional risk of stock depletion due to ecosystem overfishing, PP and guild indicators should be monitored and F_{MSY} targets for commercial fisheries should be revised when the prevailing environmental conditions change.

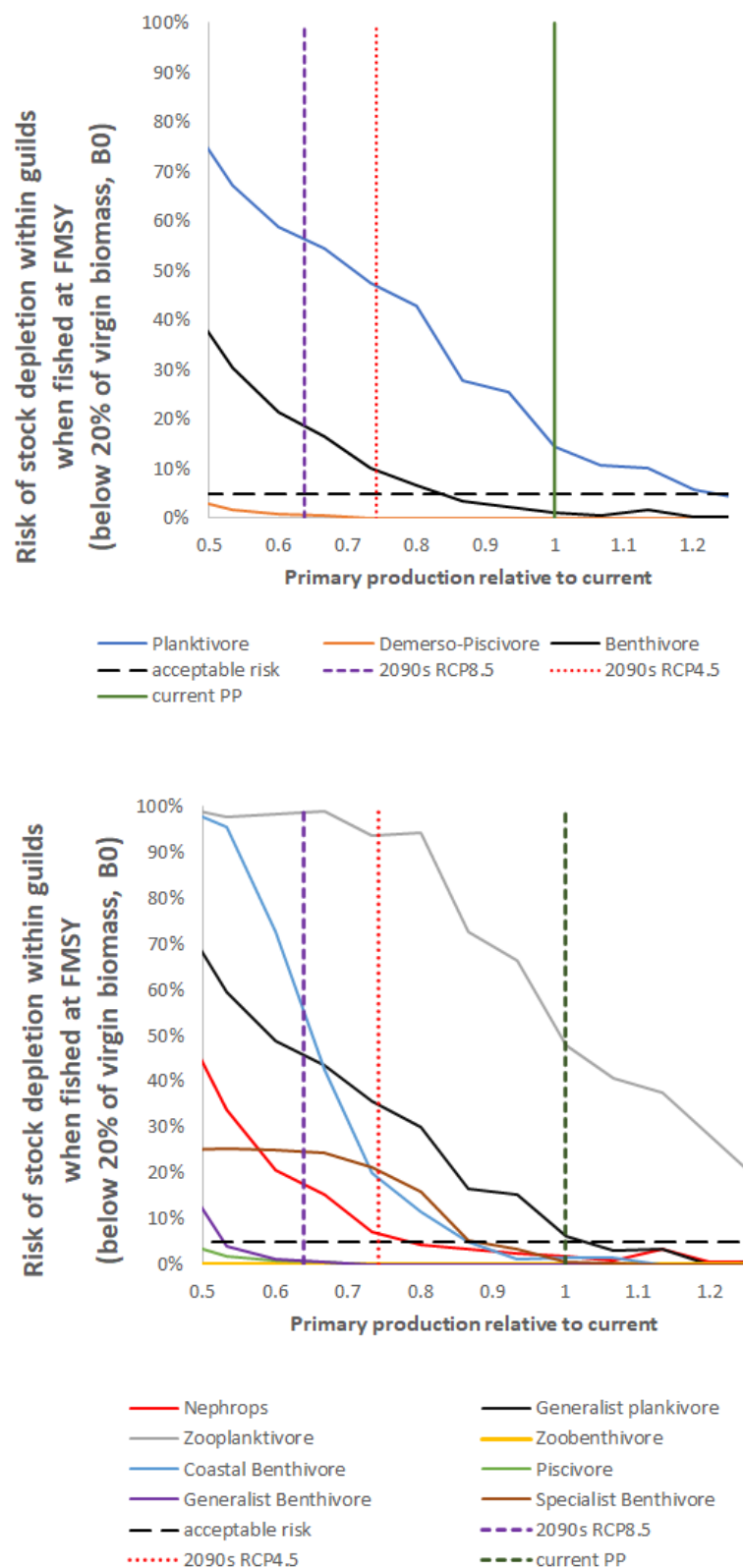


Figure 19. LeMans modelled risk of depletion of stocks within feeding guilds in the long term (by 2090s); (i.e. stocks below 20% of virgin biomass that are likely recruitment impaired) as a function of primary production for the whole community of 37 stocks when fished at F_{MSY} . Overall, 5% of stocks at risk within guilds is considered an acceptable level (dashed horizontal black line).

3 Biodiversity and spatial management (ToR C)

Database on spatial protections and management measures

Introduction

There are a number of country-level and international obligations and ambitions to designate Marine Protected Areas (MPAs). Among the most notable for Europe, are the requirements to designate a network of Sites of Community Importance (SCIs) under the EU Habitats (92/43/EEC) and Bird Directives (2009/147/EC) known as the Natura 2000 network. This network spans both terrestrial and marine environments protecting species and habitats of conservation interest. Beyond the Natura 2000 network, there are also requirements to establish protected area networks under the Convention on Biological Diversity and via OSPARs Biodiversity and Ecosystem Strategy for the North East Atlantic. Countries may also designate sites to meet local and regional conservation needs.

Although the specific objectives behind these designations may differ, their common goal is to contribute to the conservation of the species and habitats they protect. In most cases, this requires some level of management and monitoring to ensure the designations are effective. Assessing the effectiveness of protected areas in relation to meeting conservation obligations on regional scales is key, but often hampered by data accessibility. Owing to its prominence as the single biggest pressure on benthic marine habitats and species, information on the management of fishing activities is particularly important, but also particularly fragmented.

While several online resources exist collating spatial and descriptive information on MPAs, to the authors best knowledge there is no single database covering the European marine region which brings together up to date information on the protected features of sites, management measures and site boundaries in a useable format for spatial analyses. Work was therefore undertaken under this TOR to develop a working spatial database of all MPAs in this region, linking site boundaries with information on the habitats and species they are designated to protect, and work is in progress to add fisheries management boundaries and measures to this database.

Materials & methods

Spatial and descriptive data for European MPAs (Figures 20–21) were collated from a number of sources, namely:

- The Natura 2000 access database (NATURA: downloaded 18/01/21 from <https://www.eea.europa.eu>)
- The National Designated Areas database (CDDA: downloaded 18/01/21 from <https://www.eea.europa.eu>)
- The World Database on Protected Areas (WDPA: downloaded 18/01/21 from <https://www.unep-wcmc.org>)

Datasets were first filtered to remove terrestrial sites based on whether or not the site was designated for marine features; sites with no marine features were removed. The NATURA dataset was taken as a template as this database allowed for cross referencing of sites with their protected features and contained the most useable information. Data was then standardised across the three datasets before the datasets were merged. Duplicates were identified and removed based

on site name, designation type and protected features, and sites falling outside the European marine areas were also removed. The CDDA and the WDPA datasets contained no information on protected features; the final step is to add this information manually from the [European Nature Information System](#).

Information on fisheries measures is still being compiled but so far data has been gathered from the following sources:

- NMPi
- AIFCA
- MMO
- Regulation xx
- Regulation xx

The MPA locations can then be filtered to demonstrate where restrictions are currently in place.

Downloadable spatial files for fishing measures are not always publicly available – in these cases, requests have been sent to relevant authorities or spatial files have been created from scratch using coordinate data given in the associated fishing regulations.

Results & discussion

Considerable progress has been made with the database. Spatial data for the European seas region have been cleaned and processed. This dataset currently holds spatial data for 3478 MPAs with information on feature and designation type and metadata added for ~95% of these sites (Figures 20–21). There are some gaps in the Mediterranean area but efforts are ongoing to complete this dataset.

For the Greater North Sea dataset, all feature and designation type data and metadata have been added for the 529 MPAs falling in this region. Further, a dataset containing over 70 spatial restrictions for fishing within these MPAs, with linked detail on the restriction types, has been created (see Figure 22) which will be integrated with the Greater North Sea dataset once completed.

Work is ongoing to complete and bring these datasets together and to improve usability for spatial analyses. It is intended that this database will then be updated on a rolling basis to support the work of WGBIODIV.

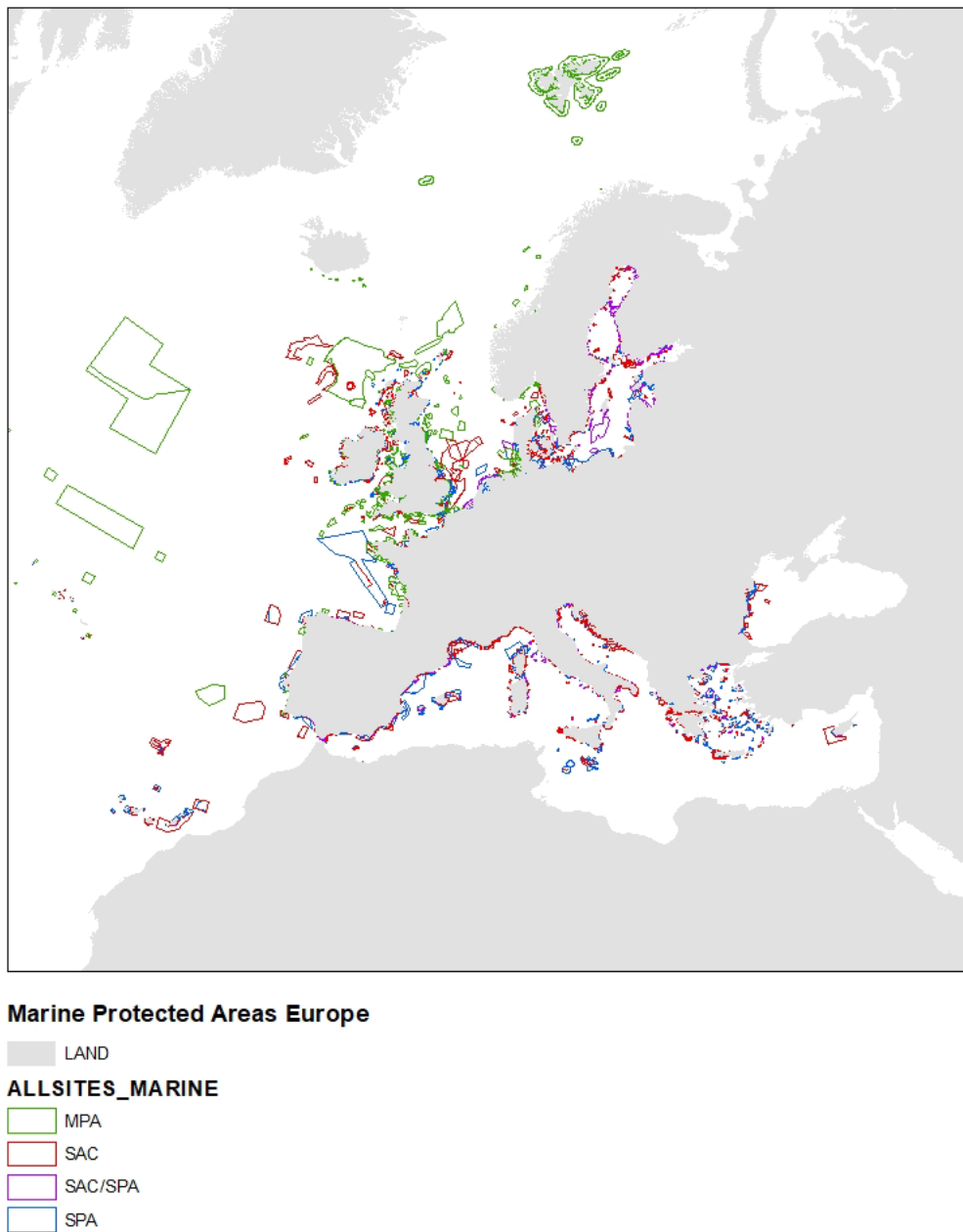


Figure 20. Spatial dataset for all MPAs in the wider European seas area. This dataset currently contains 3478 MPAs with linked feature information, designation type and metadata for ~95% of sites. This dataset is not yet complete as there are gaps in the national designations for the Mediterranean region. SAC= Special areas of Conservation according to the Habitats Directive, SPA= Special Protected Areas according to the Birds Directive, MPA = other marine protected areas.

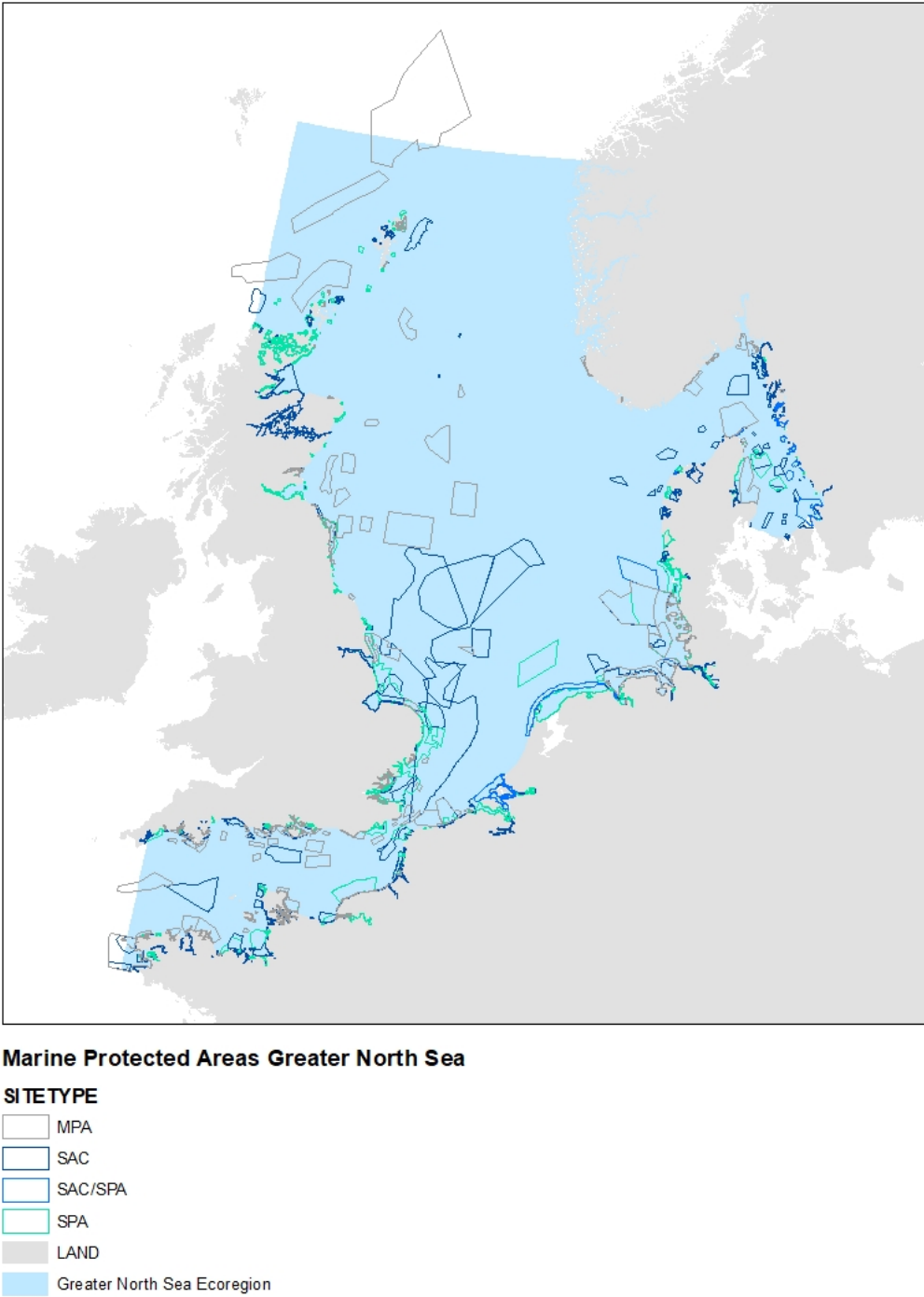


Figure 21. Spatial dataset of MPAs in the Greater North Sea region. This spatial dataset contains feature information, designation type and other metadata for 529 MPAs in this ecoregion. Abbreviations as in Figure 20.

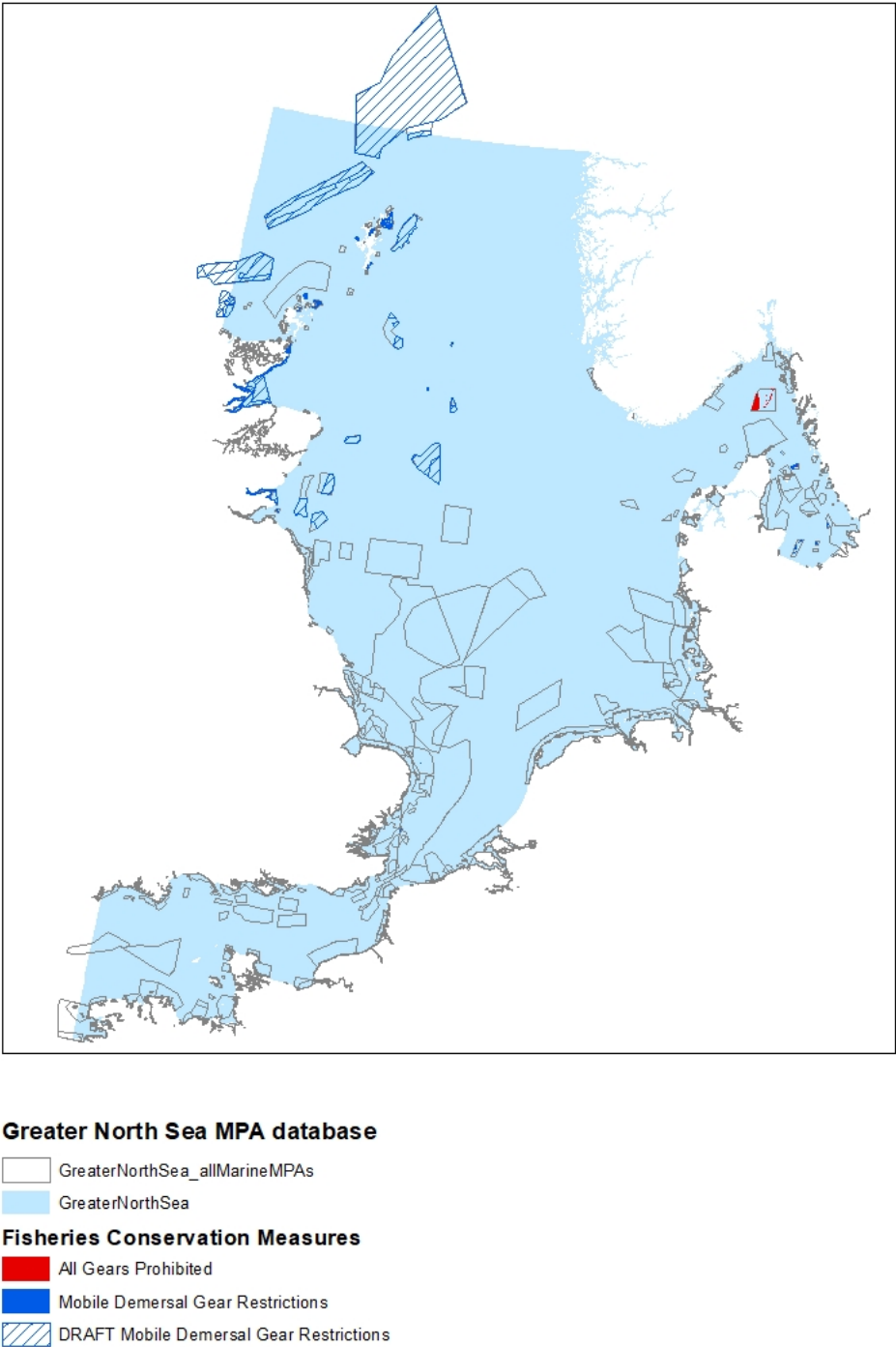


Figure 22. Current spatial dataset of fishing restriction for the Greater North Sea. This dataset holds spatial data and restriction descriptors for 72 fishing restriction zones in this region.

North Sea case study on overlap between offshore windfarms and core areas of fish distributions

Introduction

The management of marine sectors in the North Sea has undergone profound change since the implementation of marine spatial planning (MSP), which has instigated the spatial structuring of marine human activities such as shipping, offshore-renewables, nature conservation and fishing (Ehler and Douvere, 2009; Katsanevakis *et al.*, 2011; Frazão Santos *et al.*, 2019). Today, marine spatial plans for zoning marine uses and conservation in space and time exist in each country bordering the North Sea. The effort for MSP has gained impetus by the ratification of the EU Marine Spatial Planning Directive 2014/89/EU.

Among the most prominent and innovative spatial features that are associated with national marine spatial plans are the designation of sites for the implementation of marine protected areas (MPA); (Pedersen *et al.*, 2009; EEA, 2015) and the development of offshore renewables (Berkenhagen *et al.*, 2010; Stelzenmüller *et al.*, 2020); (Figure 23). The majority of MPAs within the North Sea are implemented via the EU Habitats (92/43/EEC) and Bird Directives (2009/147/EC), known as Natura 2000 network, other MPAs are devised under the regime of the Oslo-Paris convention (OSPAR).

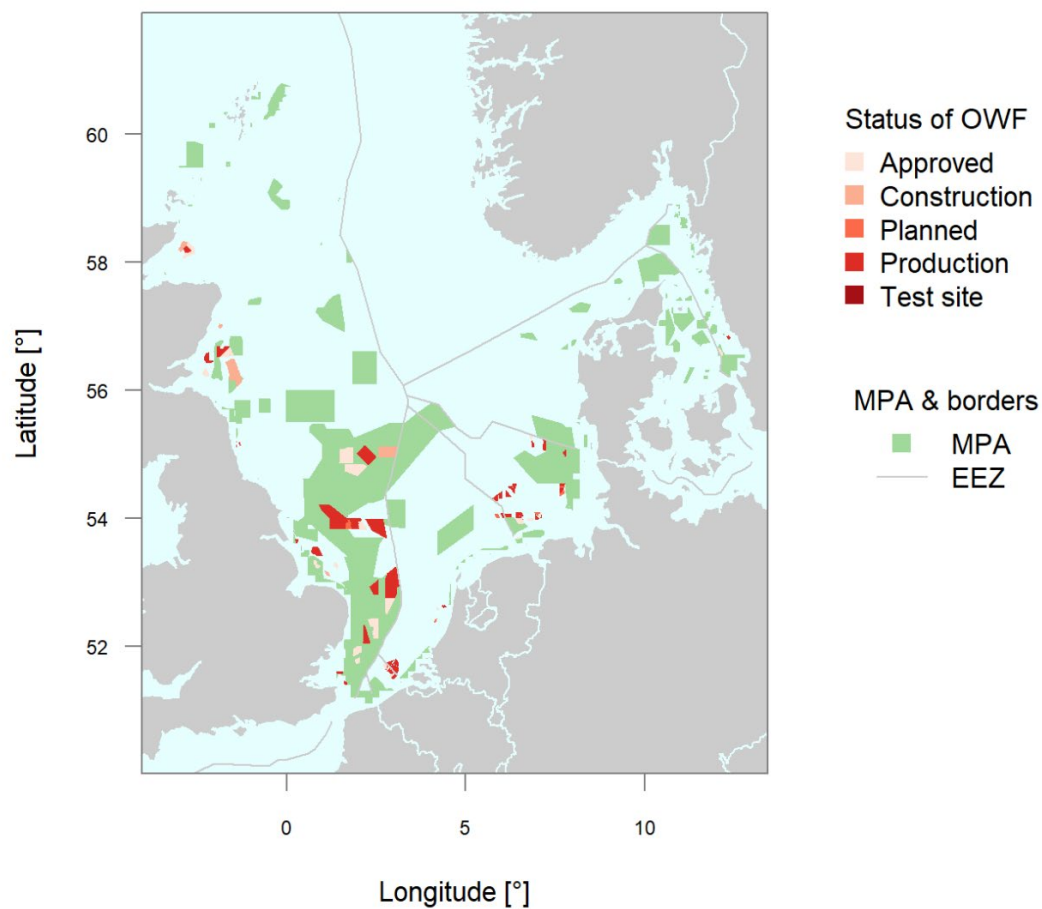


Figure 23. Location of marine protected areas (MPA) and offshore windfarms (OWF) in the North Sea based on the WGBIODIV MPA database and EMODNet human activities database (<https://www.emodnet-humanactivities.eu>, downloaded on 09.02.2021). OWF are colour coded by their status, where production is referring to OWF in operation. EEZ = Exclusive economic zone.

The MPAs of the Natura 2000 network are designated to protect seabirds, benthic habitats and marine mammals and a small number of fish – predominantly diadromous and estuarine species. Consequently, many marine Natura 2000 sites were located to protect these ecosystem components without considering the conservation of most marine fish.

Probst *et al.* (2021) revealed that the neglect of marine fish species by the Habitats Directive is mirrored in the weak overlap between MPAs and species' consistently preferred areas of presence (consistent core areas, CCA). The study points out that alternative spatial features such as offshore windfarms could be designated as protected sites to serve as stepping-stones for the conservation or re-establishment of sensitive demersal fish species (Fock, 2014; Fock *et al.*, 2014b). Here the overlap between the consistent core areas of nine endangered or threatened demersal fish species as outlined in Probst *et al.* (2021) and offshore windfarms is analysed in a pilot study. The analysis by Probst *et al.* (2021) was extended to include updated data on MPAs in the North Sea, building on the MPA database developed by WGBIODIV.

Materials & methods

Locations of CCA were extracted from Probst *et al.* (2021) for nine species that have been listed as endangered or threatened by OSPAR or IUCN. These species were lump sucker *Cyclopterus lumpus*, tope *Galeorhinus galeus*, cod *Gadus morhua*, Atlantic halibut *Hippoglossus hippoglossus*, thornback ray *Raja clavata*, spotted ray *Raja montagui*, turbot *Scophthalmus maximus*, brill *Scophthalmus rhombus* and spurdog *Squalus acanthias*.

A shapefile of MPA were generated from the WGBIODIV MPA database (see above). A shapefile of OWF, including areas approved for development and sites that are planned, in construction or in production, were extracted from the EMODNet-Human-Activities database on 09.02.2021.

The projection of all shapefiles was transformed to WGS84 (EPSG:4326). Shapefiles were overlaid to determine the relative overlap between CCA and MPA and/or OWFs in winter, summer and both seasons. Because some OWFs are located within designated MPAs, the contribution of MPAs and OWFs only were analysed by clipping the MPA-shapefile with the OWF-shapefile and vice a versa to obtain overlaps with CCAs.

Results & discussion

The overlap analysis between CCAs, MPAs and OWFs indicates that for all species the overlap between CCAs and MPAs is higher than between CCAs and OWFs (Figure 24). This demonstrates that MPAs still hold the majority of potential conservation benefit when considering the nine species of conservation concern. The OWFs that are currently planned, designated or in operation may only provide a minor contribution to the spatial protection of these species. However, the CCAs of thornback ray in winter and tope in summer show some overlap ($\leq 5\%$) with OWFs, suggesting that some of them indeed do have the potential to serve as stepping stones for the re-establishment of elasmobranch species in subregions of the North Sea, where species have become scarce or extirpated (Fock, 2014; Fock *et al.*, 2014a; Fock *et al.*, 2014b).

Stelzenmüller *et al.* (2020) indicate that more OWFs are planned after 2025 than are currently contained within the EMODNet Human-Activities database. Hence this analysis may not reflect the full conservation potential of OWFs in the North Sea

The coverage of CCAs by MPAs has increased when compared to the study by Probst *et al.* (2021). For example, the overlap of CCAs of thornback ray and MPAs has increased from less than 30 % to at least 60 % in any season. This is due to the fact that Probst *et al.* (2021) only considered the Natura 2000 MPA network, but not did not include additional national designations. These additional MPAs, of which many are located in the northern North Sea, might hold substantial potential for the conservation of demersal fish species of conservation concern.

The analysis presented here can only indicate the potential for conservation of the designated MPAs, as no management measures to restrict fishing are in place in many of the MPAs (Dureuil *et al.*, 2018). The collation of these planned management measures within the WGBIODIV MPA database will yield more detailed understanding on the conservation potential of the MPA network for demersal fish.

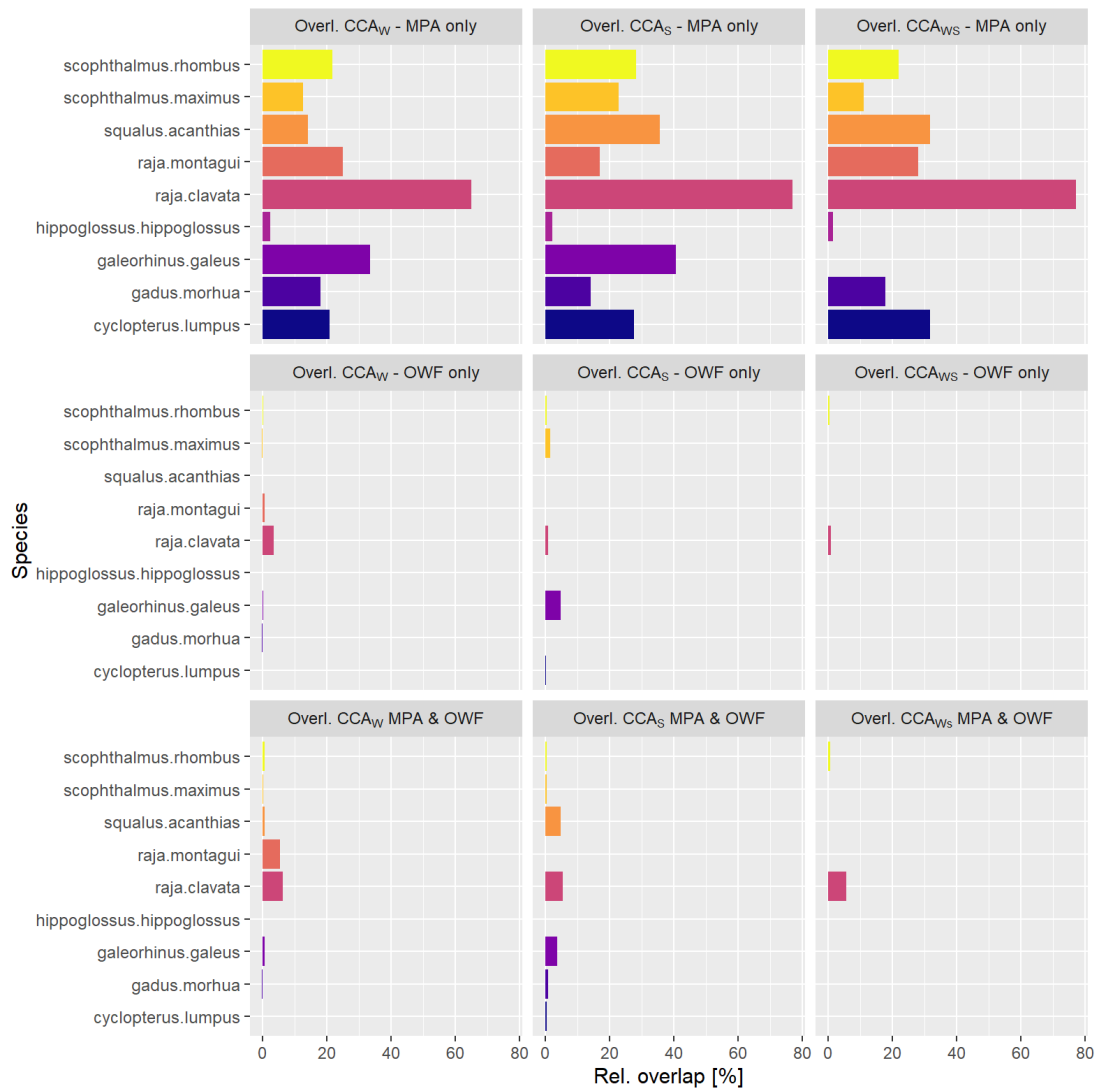
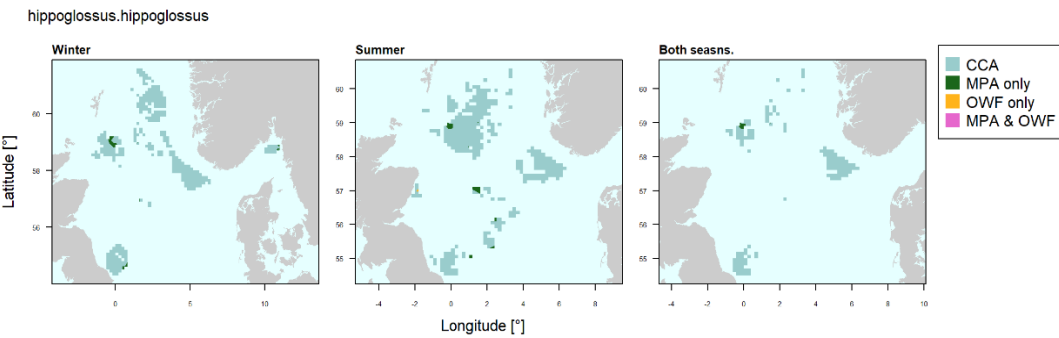
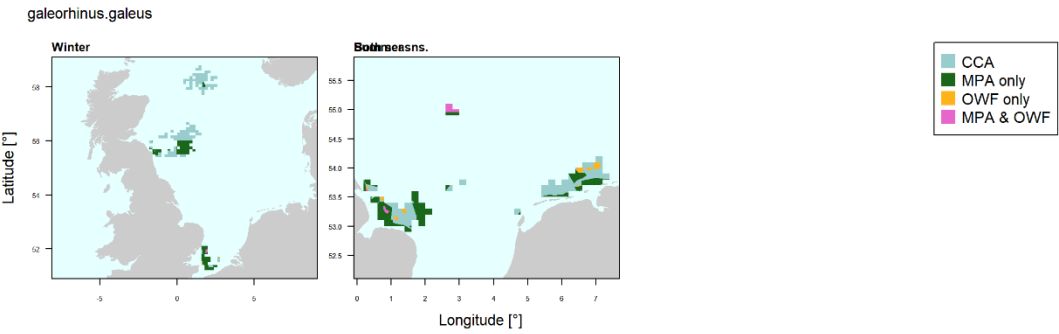
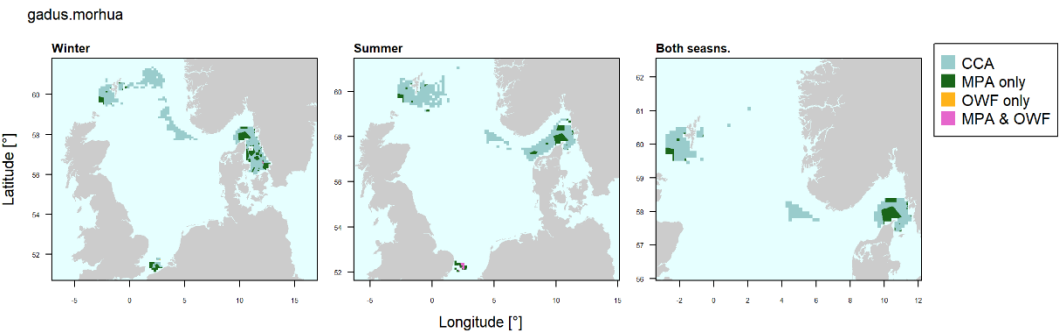
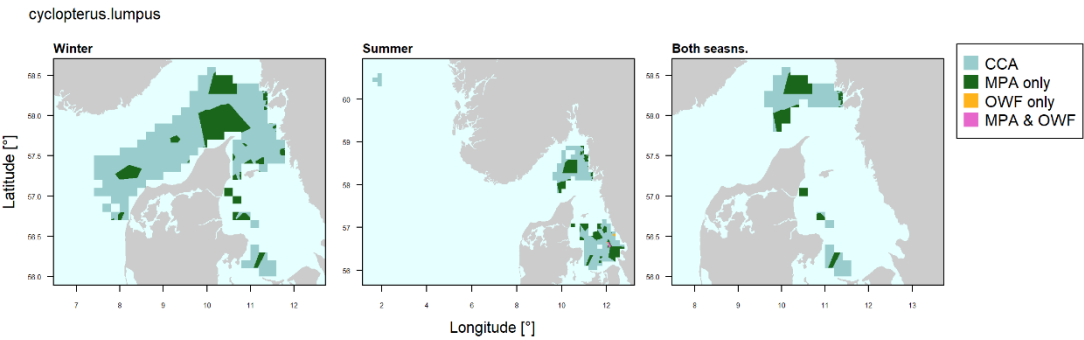
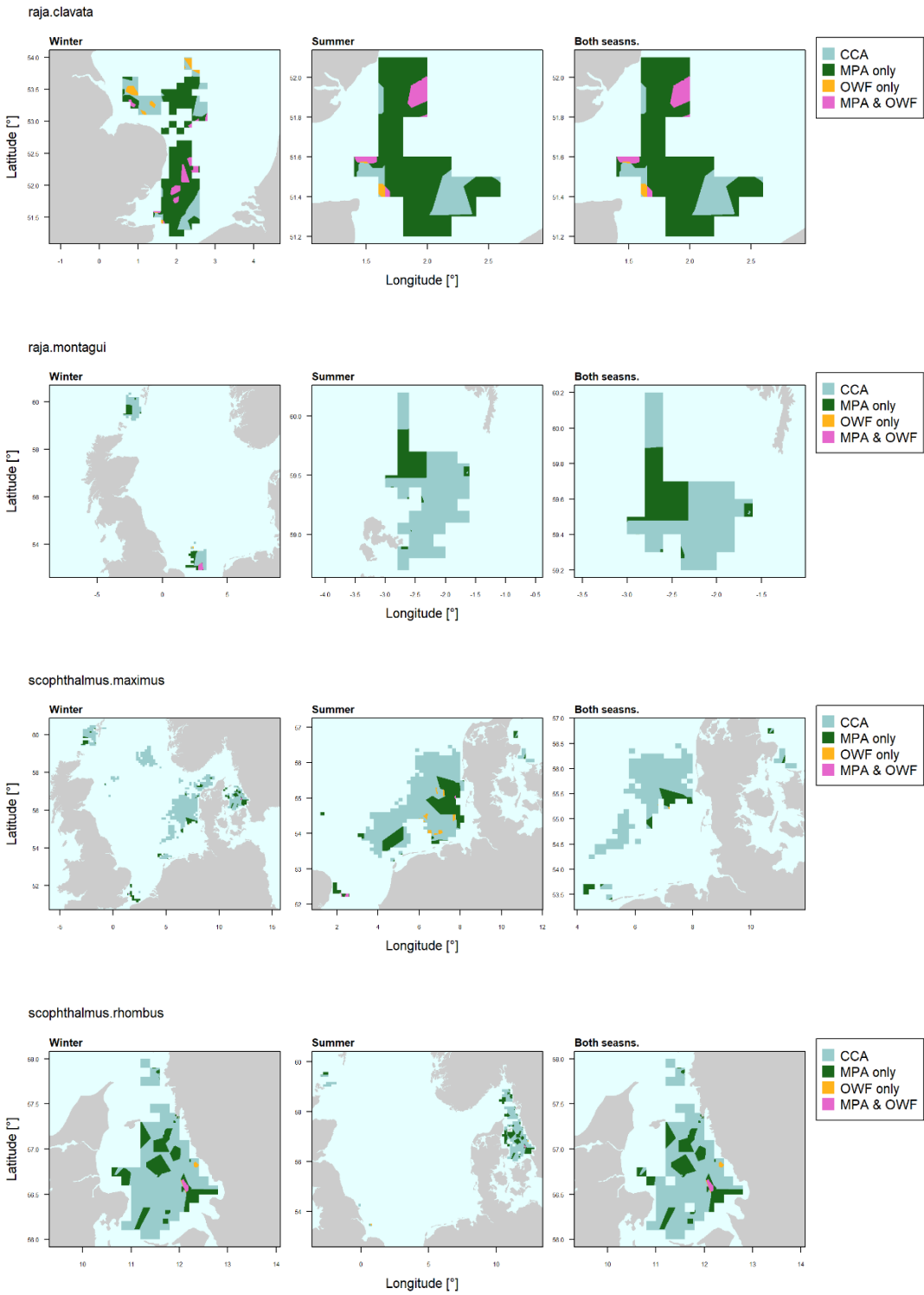


Figure 24. Relative overlap between consistent core areas (CCA) in winter (W), summer (S) or both seasons (WS) and areas which are covered by marine protected areas (MPA) only, offshore windfarms (OWF) only or both (MPA & OWF).

Also, rules for fishing within and around OWFs differ between countries (Schupp *et al.*, 2021). In Germany, fishing within OWF is not permitted for safety reasons, whereas in the UK fishing in OWFs after the construction phase may still be allowed.

The maps of overlap of each single species in each season (Figure 25) show that areas of CCA-MPA and CCA-OWF overlap are found in the Skagerrak/Kattegat (for lump sucker, cod, brill and spurdog) and southeast coast off England (for thornback ray and tope). Again, these maps indicate that MPAs have higher overlap with CCAs than OWFs and hence fisheries management measures within MPAs are likely to offer greater protection to sensitive demersal fish species than areas of increased protection around OWFs.





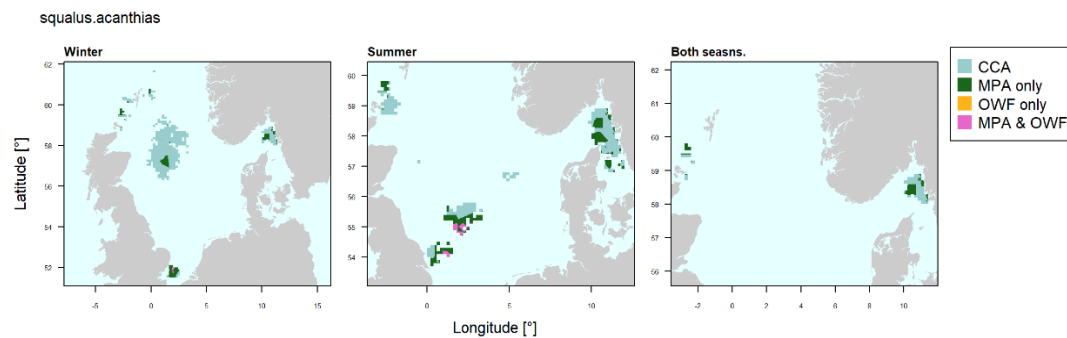


Figure 25. Maps of spatial overlap between consistent core areas (CCA), marine protected areas (MPA) and offshore windfarms (OWF) in winter (left panels), summer (middle panels) and both seasons (right panels).

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Annex 1: List of participants

WGBIODIV 2021 meeting

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WGBIODIV 2020 meeting

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WGBIODIV 2019 meeting

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Annex 2: Resolutions

The **Working Group on Biodiversity Science** (WGBIODIV), chaired by Christopher Lynam, UK, and Andrea Belgrano, Sweden, will work on ToRs and generate deliverables as listed in the Table below.

	MEETING DATES	VENUE	REPORTING DETAILS	COMMENTS (CHANGE IN CHAIR, ETC.)
Year 2019	4–8 February	Copenhagen, Denmark		
Year 2020	10–14 February	Barcelona, Spain		
Year 2021	8–12 February	Online meeting	Final report by 1 April to SCICOM	

ToR descriptors

TO R	DESCRIPTION	BACKGROUND	SCIENCE PLAN CODES	DURATION	EXPECTED DELIVERABLES
a	Test the benthic response indicator: Capacity to support formal assessment and management advice Use the indicator to explore its effectiveness in different disturbance/environmental change scenarios Explore the utility of the indicator in a broader geographical context	In the previous three-year term WGBIODIV concluded that indicators to assess biodiversity are not working due to the lack a theoretical foundation. WGBIODIV addressed this problem by designing a trait-based sensitivity indicator of benthic communities. For example, establishment of pressure-state relationships, validation of indicator calculations and evaluation against the WGBIODIV indicator quality criteria is still pending. Indicator testing is the logical next step following the successful completion of the previous ToR.	2.1; 2.2; 6.1	3 years	A tested and operational indicator of community response to ecosystem change will be delivered through WG report. Potential production of a peer review paper.
b	Investigate mechanisms linking trophic guilds under contrasting levels of pressure and/or primary production in case study areas: Using diet/trait information, and both predator and prey abundance to estimate potential impact on prey due to consumption by predators. Contrast risk due to natural mortality	Understanding of pressure-state relationships are fundamental to indicator assessments. However, as pressure is removed through management and ecosystems begin to recover, the nature and/or strength of previously defined pressure-state relationships may change. Climate change effects may further modify or mask the effects of anthropogenic pressures.	2.2; 2.3; 2.5	3 years	Identify whether recovery of ecosystem components (e.g. predatory fish) can lead to depletion of prey groups such that natural processes dominate change. Delivered through WG report. Potential production of a peer review paper.

	(consumption) with risk due to fishing pressure Project change in risk for prey groups due to increase in predator abundance or shifts in community composition as predator communities recover Clearly define roles of top down control and bottom up limitation at different trophic levels	This ToR will investigate responsiveness of indicators to pressure in regional seas where demersal fishing pressure has been reduced and temperature has increased.			
c	Examine the efficacy of spatial management measures as means of conserving, protecting and promoting marine biodiversity	The implementation of the management plans for the Natura 2000-sites is under way and will have substantial impacts on human activities, namely by spatial measures such as (partial) fisheries closures and marine reserves. However, the Habitat Directive addresses only a limited range of taxa i.e. excluding the majority of epibenthic species and marine fish. WGBIODIV considers that is important to know, how much the current MPA networks will contribute to the protection of these taxa.	6.1; 6.3; 6.4	3 years	Production of maps of biodiversity in selected marine regions to inform on occurrence of biodiversity and to guide spatial management for its conservation.

Summary of the Work Plan

Year 1	Develop assessment targets for benthic response indicator; provide first analysis on trophic guilds and linkages to pressures; develop method to create and overlay single-species distributions.
Year 2	Final evaluation of benthic response indicator; progress analysis of trophic guilds vs. anthropogenic pressures; create maps of biodiversity hotspots.
Year 3	Finalise and evaluate work on trophic guild and hotspots.

Supporting information

Priority	The current activities of this group will lead ICES into issues related to the integrated ecosystem assessments and the implementation of the ecosystem approach to marine management. Consequently, these activities are considered to have a very high priority.
Resource requirements	The research programmes which provide the main input to this group are already underway, and resources are already committed. The additional resource lies in the commitment of scientist from different member states to participate in the group.
Participants	Participation in WGBIODIV has slightly increased due to the outreach strategy of hosting meeting in Spain and Italy, thereby attracting scientist from host countries and Mediterranean area.
Secretariat facilities	None
Financial	No financial implications.

Linkages to ACOM and groups under ACOM	There is a linkage to ACOM/SCICOM steering group Integrated Ecosystem assessments (IEA). The results of WGBIODIV are important to WGECO and may be of relevance for WGINOSE and WGIAB.
Linkages to other committees or groups	The outcomes of WGBIODV will be important to the ICES high priority work area 'Marine Strategy Framework Directive (MSFD)'.
Linkages to other organizations	OSPAR, HELCOM, European Commission