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# Mapping marine benthic biological traits to facilitate future sustainable development

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## Abstract

Escalating societal demands placed on the seabed mean there has never been such a pressing need to align our understanding of the relationship between the physical impact of anthropogenic activities (e.g., installation of wind turbines, demersal fishing) and the structure and function of the seabed assemblages. However, spatial differences in benthic assemblages based on empirical data are currently not adequately incorporated into decision-making processes regarding future licensable activities or wider marine spatial planning frameworks. This study demonstrates that, through harnessing a Big Data approach, large-scale, continuous coverage maps revealing differences in biological traits expressions of benthic assemblages can be produced. We present independent maps based on a suite of response traits (depicting differences in responses to natural or anthropogenically induced change) and effects traits (reflecting different functional potential), although maps derived using single traits or combinations of a range of traits are possible. Models predicting variations in response traits expression provide greater confidence than those predicting effects traits. We discuss how such maps may be used to assist in the decision-making process for the licensing of anthropogenic activities and as part of marine spatial planning approaches. The confidence in such maps to reflect spatial variations in marine benthic trait expression may, in the future, inherently be improved through (1) the inclusion of more empirical macrofaunal assemblage field data; (2) an improved knowledge of marine benthic taxa trait expression; and (3) a greater understanding of the traits responsible for determining a taxon's response to an anthropogenic pressure and a taxon's functional potential.

KEYWORDS
anthropogenic pressure, biological traits, marine benthos, sustainable management

## INTRODUCTION

Most marine ecosystems have, at all spatial scales, been altered by human activities (Halpern et al., 2008, 2015). Indeed, as much as 41% of the World's oceans have been subject to multiple anthropogenic perturbations (Halpern et al., 2008), with coastal and shelf seas being particularly susceptible due to their proximity to the World's largest

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cities (Crain et al., 2008; Houde et al., 2014). The role that the marine environment plays in supporting important ecosystem processes and in stemming further impacts associated with climate change is becoming increasingly understood (Ruckelshaus et al., 2013). Sedimentary benthic ecosystems, in particular, play an integral role in some important ecosystem services (Rife, 2018) but their capacity to effectively perform this is directly and indirectly altered by physical disturbances (Epstein et al., 2022; Tiano et al., 2019).

In 2019, the UK Government passed an act (The Climate Change Act 2008 [2050 Target Amendment] Order 2019; http://www.legislation.gov.uk/uksi/2019/1056/contents/made) that set out a framework to reduce net emissions of greenhouse gases by 100% relative to 1990 levels by 2050, making the UK a "net zero" emitter. An increased reliance on offshore wind energy is expected to help meet this and, in conjunction with the increasing demands placed by the other sectors (e.g., demersal fishing, aggregate extraction), represents an unprecedented demand for seabed space within UK waters. This situation is relevant to other European countries (Korpinen et al., 2021) and is likely to be reflected globally over the coming decades. The current (and future) areas of seabed harboring wind farm arrays occur in the vicinity of, and in some areas overlap with, other activities which each exert their own direct and/or indirect impacts on the seabed (Goodsir et al., 2015; Palanques et al., 2014). The combined and cumulative effects resulting from the current increase in human activities, and the demands and pressures on marine resources resulting from multiple industrial sectors, increases the risks of inducing long-term and possibly permanent changes in marine ecosystem functions (Dannheim et al., 2020; Houde et al., 2014; Nogues et al., 2021). As such, there is a growing need to manage the demands of this diverse array of activities in a sustainable manner to ensure that the role the marine sedimentary environment plays in supporting important ecosystem services is safeguarded (Stelzenmüller et al., 2018).

Different areas of the seabed respond differently to, and show varying temporal trajectories in, recovery from anthropogenic pressure (Korpinen et al., 2021; Rijnsdorp et al., 2018; van Denderen et al., 2015). Currently, physical-based maps of the seabed (Davies et al., 2004; Goodsir et al., 2015; Korpinen et al., 2021) are heavily relied upon for initial assessments regarding potentially suitable areas for licensing various anthropogenic activities. While such maps undoubtedly provide an important perspective regarding the potential areas of, for example, Annex I habitats designated under the EU Habitats Directive, it has become increasingly evident that the capacity of physical-based maps to predict the actual type of seabed assemblage or assemblages that are likely to be present (Cooper et al., 2019) and, therefore, potentially impacted, is limited. Assessments based on ecological features over the large spatial scales needed to effectively manage the suite of interacting pressures implicitly require the availability and suitable interpretation of vast amounts of empirical biological data. The development of reliable biological-based seabed maps covering large spatial scales has, until recently, been hindered by both data access limitations and a lack of suitable IT infrastructure (hardware/software; Stelzenmüller et al., 2015). However, Cooper and Barry (2017) demonstrated that a comprehensive macrofaunal dataset (OneBenthic https://rconnect.cefas.co.uk/onebenthic_portal/) compiled through the integration of empirical data acquired from seabed sampling efforts by both governmental and nongovernmental (e.g., marine aggregates, offshore wind, oil, and gas) sectors could be used to create a robust biological baseline assessment for UK shelf waters. In a management context, the availability of such maps (Cooper et al., 2019; O'Brien et al., 2022) is appealing, as differences in the component taxa between different assemblages will undoubtedly manifest through differences in sensitivity to, and functional responses from, anthropogenic pressures.

Recovery rates following disturbance and ecological functional potential of seabed assemblages have recently been proxied using biological traits approaches (BTA; Beauchard et al., 2021; Bolam et al., 2021; Bolam & Eggleton, 2014; Martins & Barros, 2022). Although the relevant traits vary between differing scales of ecological organization (Gladstone-Gallagher et al., 2019), the responses of organisms to changes in their environment (whether these are natural or anthropogenically imposed) are ultimately governed by their inherent traits expressions. Furthermore, a principle that is well routed in ecological theory (Statzner et al., 2001), BTA centered on a series of life history, morphological and behavioral characteristics of the species present may serve as a surrogate for ecological functioning (Doledec & Statzner, 1994; McGovern et al., 2020; Verberk et al., 2015). This is especially insightful given the absence of empirical data directly measuring benthic functioning (Degen et al., 2018). BTA has been successfully applied to assess the ecological implications of a suite of anthropogenic activities such as demersal trawling (Tillin et al., 2006; van Denderen et al., 2015), aggregate extraction (Cooper et al., 2008), estuarine restoration (Veríssimo et al., 2012) and fish farming (Papageorgiou et al., 2009). Studies have incorporated both "response traits" (those that affect a taxon's capacity to withstand or respond to a change in the physical environment) and "effects traits" (those that influence ecosystem properties; Lavorel & Garnier, 2002; Petchey et al., 2009; Suding et al., 2008), although few have undertaken independent assessments of these two groups to evaluate the causes of change and the potential

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functional significance respectively (Beauchard et al., 2017; Bolam et al., 2016, 2021; Mensens et al., 2017).

In this paper, we demonstrate that empirical macrofaunal abundance data obtained using a Big Data approach can be used to identify categories representing groups of typically co-occurring traits. We model their distribution through their relationships with environmental conditions to produce continuous maps of the distribution of the trait-based categories for large spatial scales (UK shelf and across the North Sea) relevant to management decisions. We produce two categorical, trait-based maps: one based on biological response traits to delineate regions that show similar potential to respond to physical disturbance; and a second map based on a suite of biological effects traits to outline seabed areas that show comparable areas of ecological functional potential. We discuss how these, and future iterations of such maps, may facilitate decisions regarding the licensing of anthropogenic activities by ensuring that such pressures may be directed toward regions of greatest recovery potential and/or away from functionally unique or functionally important habitats. Moreover, as our maps describe the inherent behavioral and functional characteristics of benthic assemblages across large areas, they may assist in cross-sectoral decisions as part of national marine spatial planning approaches.

# METHODS

## The database

The empirical macrofaunal data used in this study are contained in the OneBenthic database (https://rconnect.cefas.co.uk/onebenthic_portal/). OneBenthic brings together publicly available disparate benthic datasets (macrofaunal abundance/biomass and sediment particle size) in a cloud-based PostgreSQL database. The resulting dataset (as accessed on 20 May 2022) includes information from 46,882 grab and core samples (from 834 surveys) collected over a 50-year timeframe (1976–2019). The spatial extent of the dataset spans UK shelf waters and also encompasses regions of other northeast Atlantic countries such as France, Belgium, The Netherlands, Germany, Denmark, and Norway.

The OneBenthic database incorporates taxonomic information from the World Register of Marine Species (WoRMS, see https://www.marinespecies.org/), allowing data to be outputted using standardized nomenclature. WoRMS data are accessed via the R package *worms*, with each taxon uniquely identified by the aphiaID field.

From the available dataset of 46,882 samples, we selected a subset of 31,838 for which the data were considered comparable (i.e., sampled using a 0.1 $m^2$ grab or core and processed using a 1 mm sieve) and were sampled outside all seabed boundaries licensed for anthropogenic pressures (e.g., dredging/extraction, disposal, renewables). Colonial taxa were included and given a value of 1. A fourth-root transformation was then applied to the raw abundance data to downweigh the influence of highly abundant taxa.

To address spatial autocorrelation in the data, and in keeping with the approach adopted by Cooper et al. (2019), samples closer than 50 m were removed from the dataset, reducing the overall number to 18,348.

## Biological traits

In total, 10 biological traits were selected to describe the life history, morphological and behavioral characteristics of the macrofauna (Table 1). There is currently no accepted methodology for selecting the most appropriate traits for a given study and the final selection is often heavily guided by the limited biological information available for benthic invertebrate taxa (Bremner, 2008; Costello et al., 2015; de Juan et al., 2022). The 10 traits (Table 1) represent those most commonly adopted (Bremner, 2008; Degen et al., 2018; McLaverty et al., 2021) and for which biological information is relatively well established for marine benthic invertebrates (de Juan et al., 2022).

The selected traits represent a combination of both response traits and effects traits (sensu Díaz & Cabido, 2001; Lavorel & Garnier, 2002; Petchey et al., 2009; see Table 1) based on the classification by Bolam et al. (2016, 2021). We acknowledge that, while this trait categorization is both conceptually and ecologically important (Beauchard et al., 2017) and has previously been adopted to derive benthic functional groups (Lundquist et al., 2018), it nevertheless polarizes traits into one category or another when, in reality, most traits represent both groups to varying degrees. As macrofaunal responses are likely to be pressure dependent, the response traits selected here represent those that are theoretically likely to affect a taxon's ability to respond to (i.e., to withstand/tolerate and/or recover from) a natural or anthropogenic change in the environment (Table 1). That is, we have not selected traits pertinent to a specific environmental change or anthropogenic pressure. Meanwhile, as the traits that govern a taxon's functional potential will depend on the function in question (de Juan et al., 2022; Martins & Barros, 2022), we consider the five effects traits used here to relate varyingly to a suite of functions. Each trait was subdivided into multiple "categories" chosen to encompass the range of possible attributes of all the taxa (Clare et al., 2022a; Table 1).

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**TABLE 1** The 10 traits and the corresponding trait categories used in the present study.

| Trait group | Trait | Category | Description (and relevance for response traits and/or effects traits) |
|---|---|---|---|
| Response traits | Morphology | Soft<br>Tunic<br>Exoskeleton<br>Crustose<br>Cushion<br>Stalked | External characteristics of the taxon. Different morphologies vary in their relative susceptibility to damage from physical pressure (e.g., demersal fishing).<br>Soft-bodied organisms are generally vulnerable to direct physical disturbance, and stalked taxa are also generally fragile. A tunic or exoskeleton will provide some protection, while cushioned and crustose living forms are often able to withstand direct physical disturbance. The sensitivity to some disturbances, such as increased suspended solids, tends, however, to be taxonomically specific as opposed to trait dependent. |
| | Egg development location | Asexual<br>Pelagic<br>Benthic<br>Brood | Species can reproduce asexually (fragmentation, budding) or by releasing eggs into the water column (pelagic), or onto/into the bed, either free or maintained by mucous (benthic), or eggs are maintained by an adult for protection, either within a parental tube or within the body cavity (brood).<br>These different mechanisms vary in their potential susceptibility to damage from physical pressures. The egg development mechanism also affects a species' recolonization potential as, for example, pelagic egg producers have a greater potential recolonization range. |
| | Living habit | Tube<br>Burrow<br>Free-living<br>Crevice<br>Epi/endo zoic/phytic<br>Attached | Species may inhabit tubes (lined with sand, mucus, or calcium carbonate), live within a permanent or temporary burrow, or are not limited to any restrictive structure at any time (free-living). Species may be cryptic (crevice), predominantly found inhabiting tubes made by biogenic species or algal holdfasts (epi/endo zoic/phytic), live on other organisms, or are attached to larger substrata.<br>This trait indicates the potential for the adult stage to be exposed to physical disturbance. Epiphytes and attached organisms are directly exposed to any imposed change in the environment, while burrowers and/or tube-dwellers, for example, may either be buffered from or able to locally evade an acute disturbance. |
| | Sediment position | Surface<br>0–5 cm<br>5–10 cm<br>>10 cm | Typical living position in the sediment profile.<br>Species will generally need to re-establish their vertical sediment position following a physical disturbance to undertake their biological processes (e.g., feeding). Deeper-dwelling taxa are less likely to be affected by pressures such as demersal fishing and, potentially, sediment overburden than surface dwellers. |

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**TABLE 1** (Continued)

| Trait group | Trait | Category | Description (and relevance for response traits and/or effects traits) |
|---|---|---|---|
| | Mobility | Sessile<br>Crawl/creep/climb<br>Burrowers<br>Swim | Species in which the adults have no, or very limited, mobility (sessile) have some, but generally limited, movement along the sediment surface (crawl, creep, climb), in faunal species where adults are capable of active movement within the sediment (burrowers), or where adults actively swim in the water column.<br>Mobility is intrinsically related to disturbance avoidance and/or subsequent return post disturbance. Faster moving species (particularly swimmers) are more likely to evade local physical pressure, while those capable of movement within the sediment may regain sediment position following burial by a sediment overburden (Bolam, 2011). Mobility also affects the ability for adult recolonization of disturbed areas. |
| Effects traits | Body size | <10<br>10–20<br>21–100<br>101–200<br>201–500<br>>500 | Maximum size of an individual (in millimeters). Has implications for the movement of organic matter within the benthic system as large organisms hold organic matter (low turnover) within the system relative to small-bodied species (high turnover) (Pearson & Rosenberg, 1978). Often referred to as a "master trait" (Martini et al., 2020), size influences most of the ecological, physiological, and behavioral functions of organisms due to metabolic laws. |
| | Longevity | <1<br>1–3<br>3–10<br>>10 | The maximum lifespan of the adult stage (years). A trait that has been shown to act as a response trait, longevity also strongly relates to function through its direct role in thermodynamics and, therefore, energy flows through ecological systems. Longevity is intrinsically linked with energy metabolism rates (Speakman, 2005) and reflects the relative investment of energy into somatic growth as opposed to reproductive growth. |
| | Larval development location | Planktotrophic<br>Lecithotrophic<br>Benthic (direct) | Indicates the potential for dispersal of the larval stage prior to settlement from direct (no larval stage), lecithotrophic (larvae with yolk sac, pelagic for short periods) to planktotrophic (larvae feed and grow in a water column).<br>This trait is heavily associated with the export of carbon and energy (under the form of offspring) out of the system (i.e., source/sink concept) and represents a critical factor in the effect of the community on ecosystem stability (e.g., temporal variation, resilience sensu Webster et al., 1974). |
| | Feeding mode | Suspension<br>Surface deposit | The removal of particulate food taken from the water column (suspension feeding), active |

(Continues)

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**TABLE 1** (Continued)

| Trait group | Trait | Category | Description (and relevance for response traits and/or effects traits) |
|---|---|---|---|
| | | Subsurface deposit<br>Scavenger/opportunist<br>Predator | removal of detrital material from the sediment surface (surface deposit), removal of detrital material from within the sediment matrix (subsurface) and feeding upon dead animals (scavenger/opportunist) or actively predating upon living animals (predation).<br>Feeding mode has important implications for the transfer of carbon between the sediment and water and within the sediment matrix. Feeding mode also has important repercussions for many biogeochemical processes (Rosenberg, 1995). |
| | Bioturbation mode | Diffusive mixing<br>Surface deposition<br>Upward conveyor<br>Downward conveyor<br>None | Describes the ability of the organism to rework sediments. This can be either upward (e.g., maldanid worms), downward (e.g., oweniid worms), onto the sediment (surface deposition) or diffusive mixing of the sedimentary matrix (e.g., glycerid worms).<br>Bioturbation mode has important implications for sediment–water exchange and sediment biogeochemical properties (Mermillod-Blondin & Rosenberg, 2006). |

*Note*: Traits are categorized according to response and effects traits according to Bolam et al. (2016).

Trait information was obtained from Cefas' macrofaunal trait data repository (Clare et al., 2022a, 2022b) collected over many years from a variety of sources; principally from published journal papers and books, and websites of various scientific institutions (e.g., http://marlin.ac.uk/biotic/). While it was possible to access reliable information for many taxa from these sources regarding certain traits (e.g., larval development location), published information describing other traits (e.g., longevity) was not available for large proportions of the taxa. In such cases, the category entries for the most closely related taxa were used as a basis for entering missing information essentially using the best professional judgment method adopted by comparable studies (e.g., Bolam & Eggleton, 2014; de Juan et al., 2022; Tyler-Walters et al., 2009).

A fuzzy coding approach (Chevenet et al., 1994) was adopted for assigning taxa to trait categories as many taxa display multifaceted behavior depending upon, for example, prevailing environmental conditions and local resource availability. Fuzzy coding allows taxa to exhibit multiple trait categories for the same trait, thus avoiding the obligate assignment of a taxon to a single category which can lead to inaccurate characterization of biological or ecological profiles (Usseglio-Polatera et al., 2000). To classify a taxon according to its affinity for more than one category, each category was given a score between 0 and 3, where 0 conveys that the taxon has no affinity for that category, 1 or 2 express partial affinity and three indicates total and exclusive affinity for that category (Bolam & Eggleton, 2014). When all taxa had been coded for the species by trait matrix, the codes were converted to proportions for each taxon so that the total for each trait = 1.

## Inclusion of biological traits into the OneBenthic database

All 4340 taxa (as accepted by WoRMS) in the database required associated traits information for this study. To ensure this, several iterative steps were conducted. First, traits were not assigned to taxa (199 in total) not typically included in benthic macrofaunal analyses (e.g., fish, insects, algae eggs). Second, 143 taxon entries considered too high a taxonomic level for meaningful trait description (e.g., "animalia," "mollusca," entries at the phylum level) were removed. Of the remaining 3998 taxa, 1000 were not identified within Cefas' biological traits repository (Clare et al., 2022a), principally since many taxa within OneBenthic are at the species level, while the trait information of Clare et al. (2022a) is based on the genus level or above. This issue was addressed by assigning, where possible, taxa to traits based on the traits of the most closely related taxa, mostly

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using the existing traits information for genera within the same family (de Juan et al., 2022). This left 723 taxa with no matching trait information. A taxon list is based on sampling, so many stations across a large spatial extent will inherently contain several taxa that are rare and, by inference, contribute relatively little to trait expression. Thus, for the remaining taxa for which traits information was not available, those that were present in less than 0.1% of the samples and, where sampled, attained a mean abundance of less than 10 per sample, were excluded. Traits information for the remaining taxa was acquired based on, as previously described, traits information from as closely related taxa as possible, although the relatively taxonomically isolated nature of these remaining taxa meant that, often, higher taxonomic levels had to be used for traits information and in these cases, the trait category scores were very fuzzy coded for some traits.

## Outputting the data matrices

Once all the (a) taxon abundance by station data, and (b) the taxon by fuzzy coded traits information was finalized within the database, a SQL query was used to create a station-by-traits matrix. This matrix comprised the proportion of each trait category of each station based on the fourth-root transformed abundance of each taxon and its traits. In essence, it represents the merger of the two table matrices (i.e., [a] and [b]).

Two station-by-traits matrices were produced in this way:

1. A station-by-“response traits” matrix. Based on the five biological response traits (Table 1), this matrix forms the basis of analyses to create the map of potential responses of benthic assemblages to physical disturbance or anthropogenic pressure.
2. A station-by-“effects traits” matrix. Based on the five biological effects traits (Table 1), this matrix forms the basis of the analyses to create the map of potential benthic function.

## Clustering

An elbow plot (Thorndike, 1953) was used to identify an appropriate number of cluster groups. Elbow plots are helpful when determining how many principal components (PCs) are needed to capture the majority of the variation in the data by visualizing the standard deviation of each PC. Where the “elbow” appears is usually the threshold for identifying the majority of the variation, although the location of the elbow can often be subjective. Clustering was performed in R using a k-means approach (base R function “kmeans”) with the MacQueen algorithm (MacQueen, 1967). This clustering method works by choosing the cluster solution that minimizes the within-cluster sum of squares, summed over all variables and clusters. A k-means clustering approach was specifically chosen due to (1) its utility for analyzing large datasets (hierarchical clustering approaches would not work with a dataset of this size), and (2) the ability to, in future, match new sample data to existing cluster groups. To establish the relationship (i.e., similarity/dissimilarity) between the different trait cluster groups, the absolute distances between each of the cluster centers across all variables were computed (R function “dist”). The resulting dissimilarity matrix was then used to generate a dendrogram based on group average hierarchical clustering (R function “hclust”).

## Environmental variables

Various raster predictor layers for environmental variables affecting marine macrofaunal species and assemblages (Appendix S1: Figure S1) were sourced for use in modeling. These layers came from Bio-ORACLE (https://www.bio-oracle.org/; Assis et al., 2018; Tyberghein et al., 2012), and Mitchell, Aldridge, and Diesing (2019); Mitchell, Aldridge, and Deising (2019). With the exception of water depth, which was sourced via the R library “sdmpredictors,” all Bio-ORACLE layers (Temperature, Salinity, Current velocity, Nitrate, Phosphate, Silicate, Dissolved molecular oxygen, Iron, Chlorophyll, Phytoplankton, Primary productivity, Light at bottom) were obtained using the Download Manager with the following options: Period = Present; Depth of layers = Benthic layers; Format of files(s) = Tiff Raster file (.tif); Bio-ORACLE version = 2.2; Layers to download = All (Mean).

Available layers from Mitchell, Aldridge, and Diesing (2019); Mitchell, Aldridge, and Deising (2019) included data products (percent Mud, percent Sand, and percent Gravel; https://doi.org/10.14466/CefasDataHub.63), and associated predictor variables (Suspend inorganic particulate matter, Peak wave orbital velocity; https://doi.org/10.14466/CefasDataHub.62). Two additional environmental layers representing seafloor topography were derived from the Bio-ORACLE bathymetry layer (water depth) using SAGA GIS tools for QGIS (v. 3.2; Conrad et al., 2015): a variable combining topographic slope length and steepness (gradient over the length, the LS-Factor), and the relative location along the entire length of a discrete slope ranging from 0 to 1 from the bottom to the top of the slope (Relative Slope Position [RPS], Böhner & Selige, 2006). The LS-Factor is used to predict

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erosion potential in the terrestrial environment (Desmet & Govers, 1996) and can analogously be applied in the marine context to reflect the potential stability of sediment deposits and hence the likelihood of exposed hard substrata. The RPS can again be interpreted to represent different current conditions nearer the bottom or top of the slope. Raster layers from Bio-ORACLE were cropped and resampled so that the spatial extent and pixel resolution matched those from Mitchell, Aldridge, and Diesing (2019); Mitchell, Aldridge, and Deising (2019).

## Modeling

Full coverage macrofaunal response and effects trait cluster maps were produced using Random Forest, an ensemble modeling method where a large number of decision trees (typically 500–1000) are built using random subsets of the samples and predictor variables in the input data (Breiman, 2001; Cutler et al., 2007). Classification trees are used for response variables consisting of discrete factor classes, such as the functional assemblage cluster groups and spatial predictions can be made either as class-specific probabilities, derived from the proportion of component trees predicting the class, or as the class with a majority vote. Random Forest was selected because of its suitability for predicting factor-type response variables and its ability to account for the multiple interactions and nonlinear relationships between the response and predictor variables (Rodriguez-Galiano et al., 2012). The models were built in R (v.4.0.2, R Development Core Team, 2020), using the "randomForest" implementation of Random Forests in the *randomForest* package (Liaw & Wiener, 2001). The models were run on the default settings using 1000 trees.

Preliminary single models using all environmental variables were run first to select the best variables and remove variables with high covariance. Variables were dropped from the models based on redundancy (high correlation with another variable), or poorly defined relationship with the response variable. With respect to correlations in variables, the variable regarded as least likely to express a mechanistic link with traits was removed. Covariance between environmental variables was investigated using values extracted from the predictor rasters at the grab sample locations taken forward for analysis. Correlation analysis (Appendix S1: Figure S2) and hierarchical clustering of Euclidean distance plotted as a dendrogram (Appendix S1: Figure S3) were used as two different ways to represent covariance and allow the main predictor variables to be identified. Although Random Forest models are not sensitive to covariance effects, models with fewer predictor variables are simpler and easier to interpret. Furthermore, the way variable importance statistics for the models are calculated also makes them more accurate in models with fewer variables compared with those that include highly correlated predictor variables (which are interchangeable in the component trees and hence can mask the importance of other variables).

Cross-validation via repeated subsampling was performed to evaluate the robustness of the model estimate and predictions for data subsetting. This also allowed additional information to be extracted from the model outputs to create maps of confidence in the predicted distribution (Mitchell et al., 2018). The cross-validation was done on 10 split sample datasets with 75% of the data used to train and 25% to test models, randomly sampled within the levels of the response variable to maintain the class balance. The final model output was plotted as the cluster class with the majority vote of all 10 model runs. Three confidence layers were also produced consisting of: (1) the frequency of the most common class, (2) the average probability of the most common class and (3) combined confidence computed by multiplying the previous two. Model performance was assessed using multiple commonly used accuracy statistics calculated from a confusion matrix. Sensitivity, specificity, and balanced accuracy (BA) were calculated both for individual classes and for the model overall. Thus, the final maps from the model presented consist of (a) the predicted distribution of each trait assemblage cluster class (derived from a majority vote of 10 model runs each indicating the most likely class) and (b) a confidence map layer (high values represent high confidence) calculated by multiplying the frequency of the most common class by its average probability over the 10 model runs.

The R script used to execute the analyses in this paper can be found at https://doi.org/10.14466/CefasDataHub.137.

# RESULTS

## Biological response traits

The k-means clustering of the response traits data produced six discernible cluster groups (Appendix S1: Figure S4). Performance statistics for the distribution model (Table 2) indicate a moderately well performing model with an overall BA score of 0.72. The model does, however, tend to underpredict the distribution of the less common cluster classes (clusters 5 and 6), while showing preference toward the more common classes observed in the grab dataset. Clusters 2 and 4 had the highest rate of

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correct prediction at 0.76 (±0.01) and 0.78 (±0.01) BA, respectively. Suspended Matter was notably the most influential predictor variable in the model, followed by wave velocity, light, and salinity (Appendix S1: Figure S5).

The relative similarity between the six clusters varied: cluster 2 was the most dissimilar, clusters 3 and 4 (and cluster 1 to a lesser extent) displayed a greater similarity as did clusters 5 and 6 (Figure 1). Some traits over several of the response trait categories were ubiquitously present in low proportions and thus showed little or no differentiation between cluster groups (Figure 2). These included "tunic," "crustose" and "cushion" (morphology); "crevice" (living habit); and ">10 cm" (sediment position). Meanwhile, some trait categories were proportionally dominant in all assemblages and the varying proportions of these largely contributed to cluster group delineations. That is, cluster groups were principally differentiated by the relative dominance of "soft" versus "exoskeleton" (morphology), "pelagic" versus "brooding" (egg development mode), "surface" versus "0–5 cm" (sediment position) and "sessile" versus "burrower" (mobility). "Living habit" shows the most variability over all of the included traits across cluster groups. The cluster groups may thus be described by which of these trait categories displayed elevated compositions within their macrofaunal assemblages. Cluster 2, the most discretely different cluster, represents assemblages in which sessile (mobility; 59.4%), surface-dwelling (sediment position; 69.2%) and egg brooding (egg development mode; 48.6%) traits are

**TABLE 2** Validation results (mean ± SD over 10 split sample runs) for the response traits Random Forest model.

| Group | *N* | Sensitivity | Specificity | Balanced accuracy |
|---|---|---|---|---|
| Cluster 1 | 1071 | 0.55 ± 0.02 | 0.82 ± 0.01 | 0.69 ± 0.01 |
| Cluster 2 | 767 | 0.6 ± 0.01 | 0.91 ± 0.01 | 0.76 ± 0.01 |
| Cluster 3 | 919 | 0.5 ± 0.02 | 0.89 ± 0 | 0.69 ± 0.01 |
| Cluster 4 | 993 | 0.68 ± 0.01 | 0.87 ± 0 | 0.78 ± 0.01 |
| Cluster 5 | 281 | 0.25 ± 0.02 | 0.97 ± 0 | 0.61 ± 0.01 |
| Cluster 6 | 424 | 0.31 ± 0.02 | 0.95 ± 0 | 0.63 ± 0.01 |
| Model | 13,375 | 0.53 ± 0.01 | 0.91 ± 0 | 0.72 ± 0 |

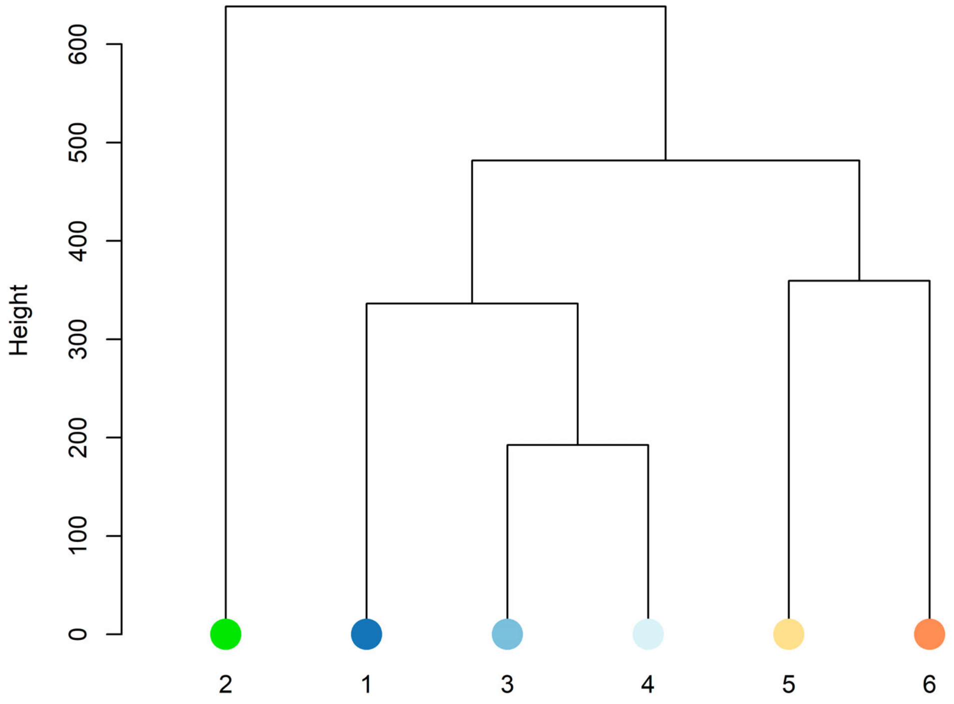

**FIGURE 1** Dendrogram showing the relative similarities of the six trait clusters formed following the classification of the five response traits. Colors have been selected to reflect the relative similarities in cluster groups to ease the interpretation of subsequent result outputs.

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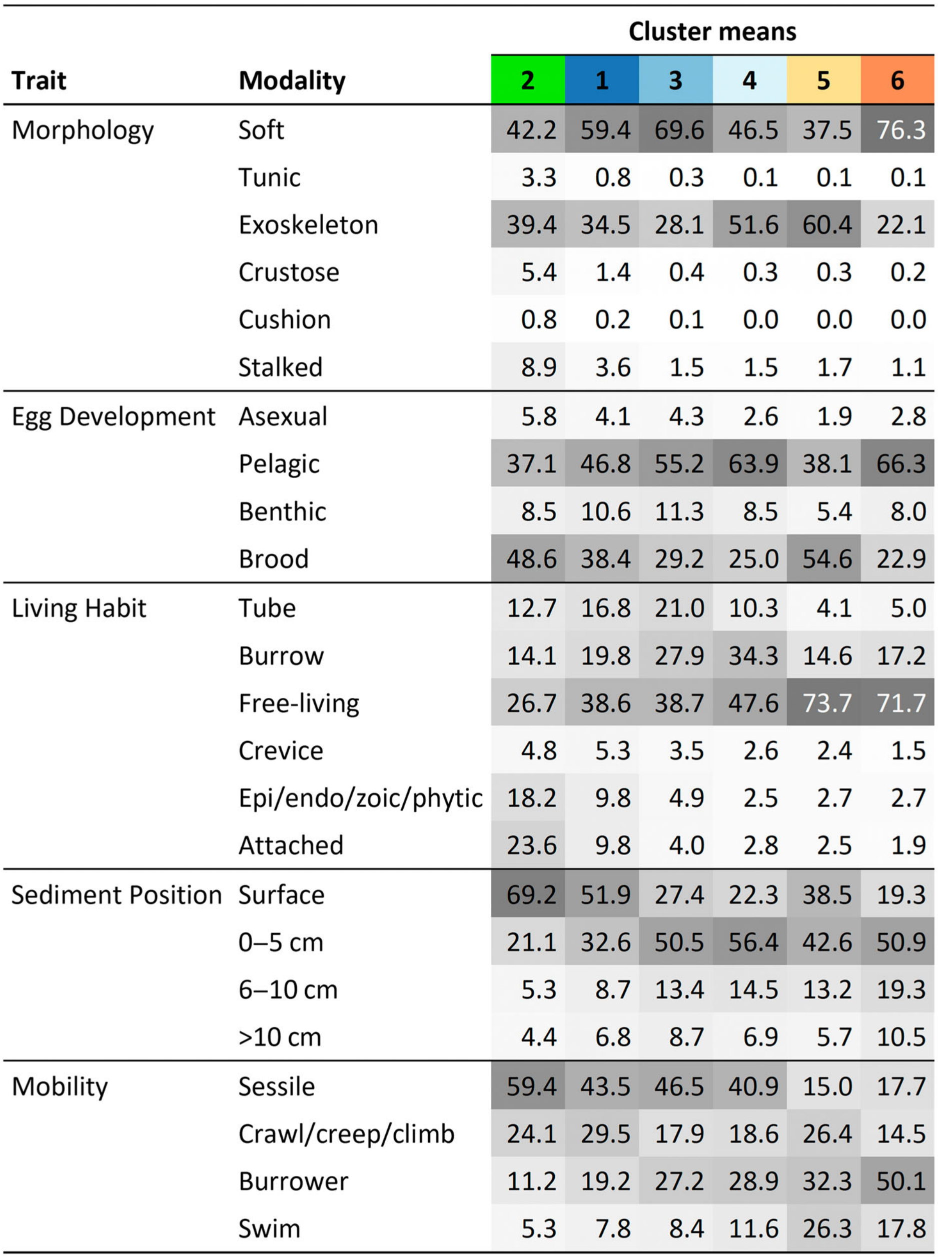

| | | Cluster means | | | | | |
|---|---|---|---|---|---|---|---|
| **Trait** | **Modality** | **2** | **1** | **3** | **4** | **5** | **6** |
| Morphology | Soft | 42.2 | 59.4 | 69.6 | 46.5 | 37.5 | 76.3 |
| | Tunic | 3.3 | 0.8 | 0.3 | 0.1 | 0.1 | 0.1 |
| | Exoskeleton | 39.4 | 34.5 | 28.1 | 51.6 | 60.4 | 22.1 |
| | Crustose | 5.4 | 1.4 | 0.4 | 0.3 | 0.3 | 0.2 |
| | Cushion | 0.8 | 0.2 | 0.1 | 0.0 | 0.0 | 0.0 |
| | Stalked | 8.9 | 3.6 | 1.5 | 1.5 | 1.7 | 1.1 |
| Egg Development | Asexual | 5.8 | 4.1 | 4.3 | 2.6 | 1.9 | 2.8 |
| | Pelagic | 37.1 | 46.8 | 55.2 | 63.9 | 38.1 | 66.3 |
| | Benthic | 8.5 | 10.6 | 11.3 | 8.5 | 5.4 | 8.0 |
| | Brood | 48.6 | 38.4 | 29.2 | 25.0 | 54.6 | 22.9 |
| Living Habit | Tube | 12.7 | 16.8 | 21.0 | 10.3 | 4.1 | 5.0 |
| | Burrow | 14.1 | 19.8 | 27.9 | 34.3 | 14.6 | 17.2 |
| | Free-living | 26.7 | 38.6 | 38.7 | 47.6 | 73.7 | 71.7 |
| | Crevice | 4.8 | 5.3 | 3.5 | 2.6 | 2.4 | 1.5 |
| | Epi/endo/zoic/phytic | 18.2 | 9.8 | 4.9 | 2.5 | 2.7 | 2.7 |
| | Attached | 23.6 | 9.8 | 4.0 | 2.8 | 2.5 | 1.9 |
| Sediment Position | Surface | 69.2 | 51.9 | 27.4 | 22.3 | 38.5 | 19.3 |
| | 0–5 cm | 21.1 | 32.6 | 50.5 | 56.4 | 42.6 | 50.9 |
| | 6–10 cm | 5.3 | 8.7 | 13.4 | 14.5 | 13.2 | 19.3 |
| | >10 cm | 4.4 | 6.8 | 8.7 | 6.9 | 5.7 | 10.5 |
| Mobility | Sessile | 59.4 | 43.5 | 46.5 | 40.9 | 15.0 | 17.7 |
| | Crawl/creep/climb | 24.1 | 29.5 | 17.9 | 18.6 | 26.4 | 14.5 |
| | Burrower | 11.2 | 19.2 | 27.2 | 28.9 | 32.3 | 50.1 |
| | Swim | 5.3 | 7.8 | 8.4 | 11.6 | 26.3 | 17.8 |

**FIGURE 2** Relative compositional dominance (i.e., proportional biomass distribution across traits) of the biological response trait categories in determining the six response traits cluster groups. The mean percent composition of each trait within the macrofaunal assemblages in each cluster is presented and shading is proportional to the values from 0% (no shading) to 100% (full shading). Cluster groups are colored and ordered to match the dendrogram (Figure 1) to ease interpretation.

comparatively dominant (Figure 2). These assemblages generally dominate large shelf regions of the mid and western English Channel and can also be observed in inshore regions of the east coast of England, along the Celtic Sea and in isolated areas in the southern North Sea and eastern English Channel (Figure 3a). Clusters 3 and 4, which shared many of their dominant response traits and describe the assemblages found across a significant majority of the study region (Figure 3a), are typically characterized by relatively higher numerical proportions of soft-bodied (morphology; 69.6% and 46.5%; clusters 3 and 4 respectively), pelagic egg-producing (egg development mode; 55.2% and 63.9%) and 0–5 cm sediment depth-dwelling (sediment position; 50.5% and 56.4%) organisms. Assemblages of cluster 1, which occupy much of the English Channel, the southwest coast of England and the Celtic Sea, showed some of the trait dominants as those of clusters 3 and 4, while sharing the elevated proportions of the surface-dwelling trait (51.9%) associated with cluster 2. What delineates cluster 1 from

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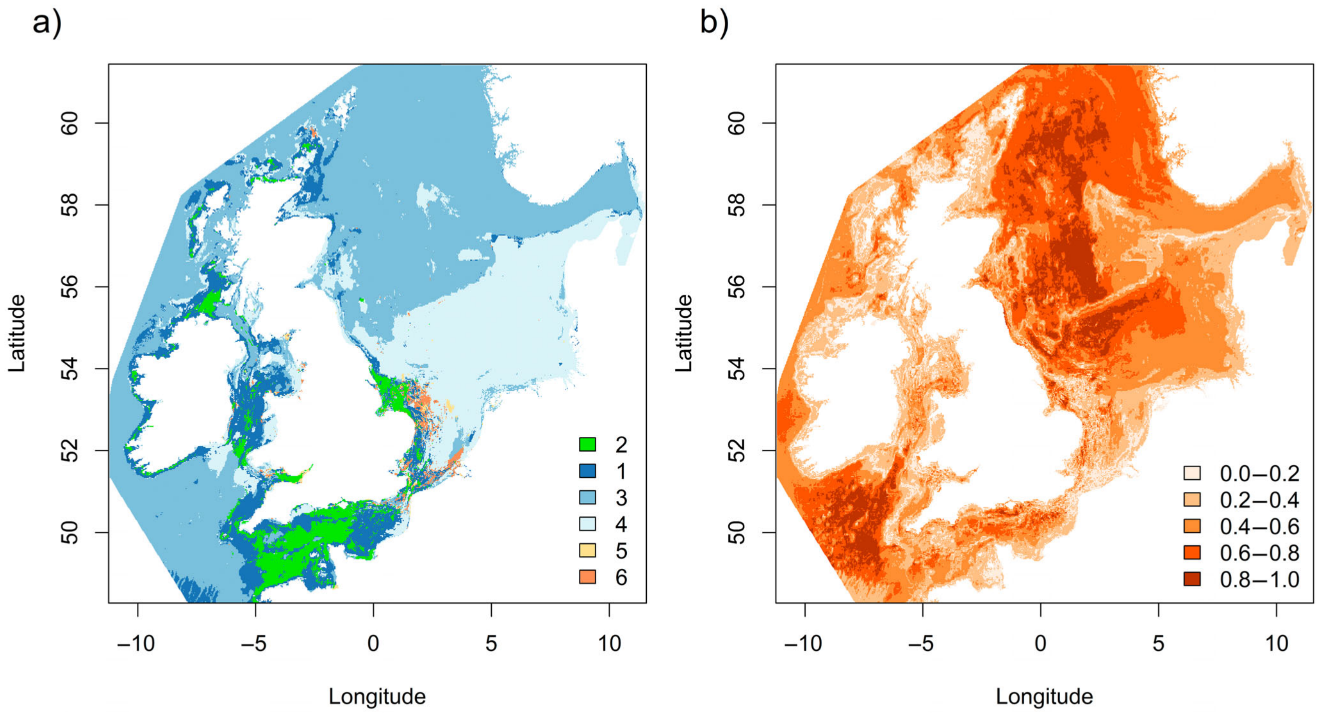

**FIGURE 3** (a, b) Classification map showing the spatial locations of the six cluster groups formed based on the five macrofaunal biological response traits (a). To aid interpretation, clusters are colored and ordered in the legend to match those presented in Figures 1 and 2. Confidence map showing the relative confidence in the model in predicting the traits cluster groups (b).

clusters 3 and 4 is its greater trait expression of surface-dwelling organisms (51.9%) and less (32.6%) expression of subsurface (0–5 cm; sediment position) traits. Meanwhile, clusters 5 and 6 shared common traits such as relatively high proportions of free-living (living habit; 73.7% and 71.7%; clusters 5 and 6 respectively) individuals but possessed traits which characterize them from other clusters such as cluster 5; "exoskeleton" (morphology; 60.3%) and "egg brooding" (egg development mode; 54.5%): cluster 6; "soft-bodied" (morphology; 76.3%) and "pelagic egg brooding" (egg development mode; 66.3%; Figure 2). Assemblages of these two clusters occupy relatively small extents of the study region, being restricted to the southern North Sea and isolated areas in the Bristol Channel, the Celtic Sea, off the North coast of Scotland and off the southern Norwegian shelf (Figure 3a).

The confidence in the map to predict assemblage clusters based on response trait composition indicates that the model has high confidence for large areas of the study area (Figure 3b). The highest model confidence regions generally represent the more offshore, deeper areas generally coincidental with response trait cluster groups 3 and 4. The model has a lower confidence in the more inshore regions where clusters 1, 2, 5, and 6 are predicted. This observation is likely to result from the clusters in the inshore areas generally being less governed by environmental variables used in the model and/or due to higher spatial heterogeneity in the environment in inshore regions relative to further offshore, resulting in relatively insufficient observational (traits) data in these classes.

## Biological effects traits

Clustering based on the five biological effects traits data resulted in, akin to that based on response traits, six evident cluster groups (Appendix S1: Figure S6). Performance statistics for the effects traits distribution model (Table 3) indicated a similar performance to the response traits model with an overall BA score of 0.73. Clusters 1, 2, and 5 have the highest rate of correct prediction at 0.74, 0.71, and 0.75 BA, respectively. Again, the distribution of the less common cluster classes, 3, 4, and especially 6, is underpredicted in favor of the more common classes, the latter having the lowest sensitivity score at 0.19. Suspended matter was again the most influential predictor variable explaining the effects traits variability, followed by depth, sediment gravel content and salinity (Appendix S1: Figure S7). Clusters 2, 4, and 5 shared the greatest similarity, forming the closest subgroup, with clusters 1, 3, and 6 showing increasing dissimilarity from this subgroup (Figure 4).

Several effects trait categories numerically represented minor proportions (<10% of total abundance; Figure 5) of

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**TABLE 3** Validation results (mean ± SD over 10 split sample runs) for the effects traits Random Forest model.

| Group | *N* | Sensitivity | Specificity | Balanced accuracy |
|---|---|---|---|---|
| Cluster 1 | 902 | 0.6 ± 0.02 | 0.89 ± 0 | 0.74 ± 0.01 |
| Cluster 2 | 1521 | 0.66 ± 0.01 | 0.76 ± 0.01 | 0.71 ± 0 |
| Cluster 3 | 275 | 0.28 ± 0.03 | 0.97 ± 0 | 0.62 ± 0.01 |
| Cluster 4 | 560 | 0.29 ± 0.02 | 0.93 ± 0.01 | 0.61 ± 0.01 |
| Cluster 5 | 1043 | 0.63 ± 0.01 | 0.88 ± 0 | 0.75 ± 0.01 |
| Cluster 6 | 154 | 0.19 ± 0.03 | 0.98 ± 0 | 0.59 ± 0.01 |
| Model | 13,375 | 0.55 ± 0 | 0.91 ± 0 | 0.73 ± 0 |

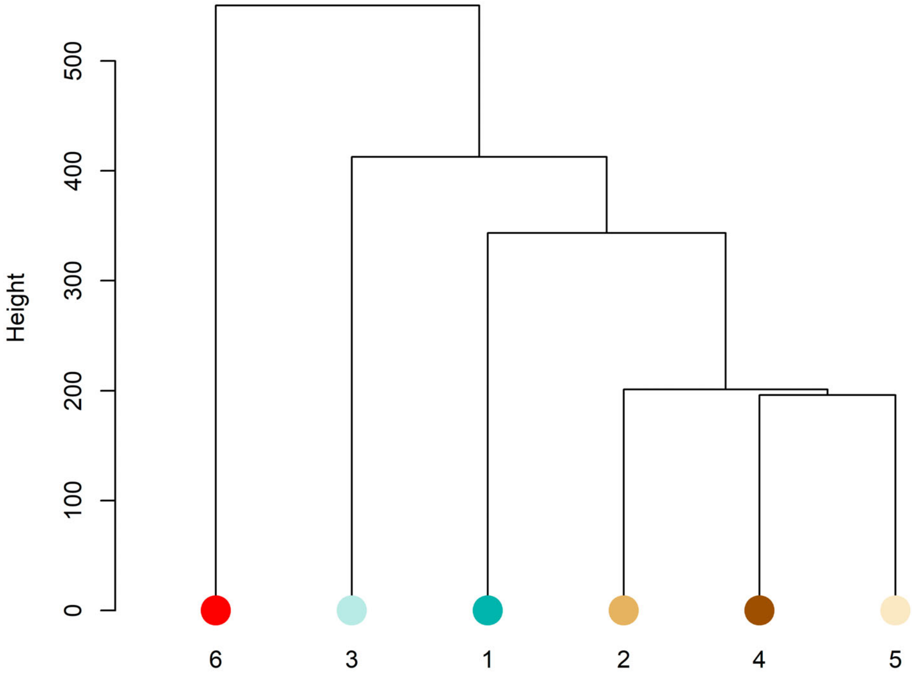

**FIGURE 4** Dendrogram showing the relative similarities of the six trait clusters formed following the classification of the five effects traits. Colors have been selected to reflect the relative similarities in cluster groups to ease interpretation of subsequent result outputs.

the assemblages across the whole survey region. These include the two largest maximum size classes "200–500 mm" and ">500 mm" (maximum body size); the longest longevity category ">10 years" (longevity); "parasite" (feeding mode) and both "upward conveyor" and "downward conveyor" (bioturbation mode). Differences in clusters 1–6 are governed principally by changes in the relative proportions of the remaining trait categories.

Clusters 2, 4, and 5 represent a group of assemblages that share many common traits. These three assemblage types (especially cluster 2) occupy most of the seabed across the study region with cluster 5 dominating the southern North Sea (Figure 6a). The commonality of these three clusters is principally due to the absence of any single trait category displaying an evident increase in relative proportion, while all possessed high proportions of "21–100 mm" (maximum body size); "1–3 years" and "3–10 years" (longevity); a dominance of "planktotrophic larval development" (larval development mode); a range of feeding modes and high proportions of "diffusive mixing" and "surface deposition" (bioturbation mode; Figure 5).

Cluster 6, which is the most distinct group, occupies a very small area of seabed, restricted to small regions of the Celtic Sea and southern North Sea (Figure 6a), and displays a notable dominance of "3–10 years" (longevity; 71.1%); "planktotrophic larval development" (larval development mode; 74.9%) and "diffuse mixing" (bioturbation mode; 76.7%; Figure 5). This cluster group is also distinct in displaying elevated proportions of both "scavenger" (25.1%) and "predator" (29.3%) feeding modes relative to the other clusters.

Cluster 3, found in the southern North Sea and in the mid North Sea toward the southern shelf of Norway, is

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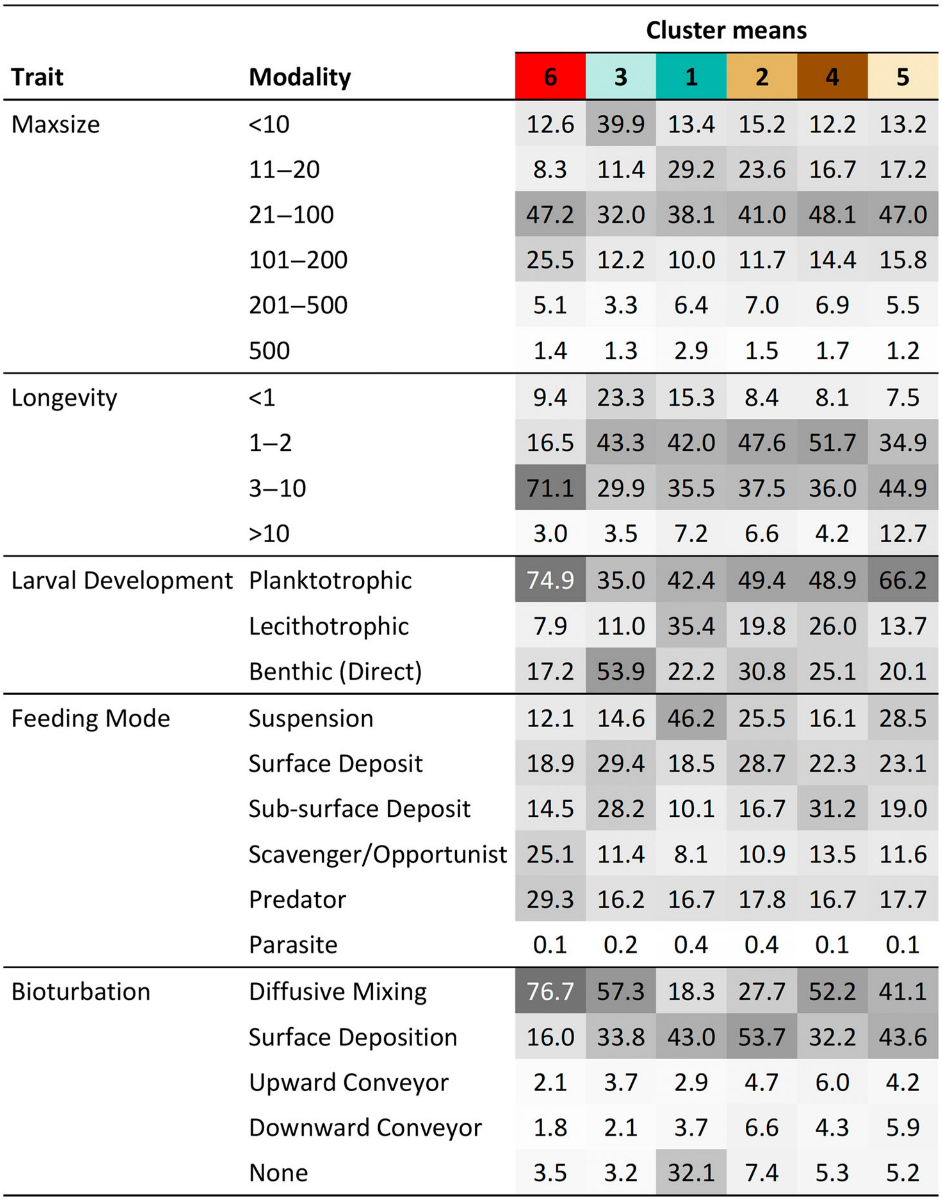

| Trait | Modality | Cluster means 6 | 3 | 1 | 2 | 4 | 5 |
|---|---|---|---|---|---|---|---|
| Maxsize | <10 | 12.6 | 39.9 | 13.4 | 15.2 | 12.2 | 13.2 |
| | 11–20 | 8.3 | 11.4 | 29.2 | 23.6 | 16.7 | 17.2 |
| | 21–100 | 47.2 | 32.0 | 38.1 | 41.0 | 48.1 | 47.0 |
| | 101–200 | 25.5 | 12.2 | 10.0 | 11.7 | 14.4 | 15.8 |
| | 201–500 | 5.1 | 3.3 | 6.4 | 7.0 | 6.9 | 5.5 |
| | 500 | 1.4 | 1.3 | 2.9 | 1.5 | 1.7 | 1.2 |
| Longevity | <1 | 9.4 | 23.3 | 15.3 | 8.4 | 8.1 | 7.5 |
| | 1–2 | 16.5 | 43.3 | 42.0 | 47.6 | 51.7 | 34.9 |
| | 3–10 | 71.1 | 29.9 | 35.5 | 37.5 | 36.0 | 44.9 |
| | >10 | 3.0 | 3.5 | 7.2 | 6.6 | 4.2 | 12.7 |
| Larval Development | Planktotrophic | 74.9 | 35.0 | 42.4 | 49.4 | 48.9 | 66.2 |
| | Lecithotrophic | 7.9 | 11.0 | 35.4 | 19.8 | 26.0 | 13.7 |
| | Benthic (Direct) | 17.2 | 53.9 | 22.2 | 30.8 | 25.1 | 20.1 |
| Feeding Mode | Suspension | 12.1 | 14.6 | 46.2 | 25.5 | 16.1 | 28.5 |
| | Surface Deposit | 18.9 | 29.4 | 18.5 | 28.7 | 22.3 | 23.1 |
| | Sub-surface Deposit | 14.5 | 28.2 | 10.1 | 16.7 | 31.2 | 19.0 |
| | Scavenger/Opportunist | 25.1 | 11.4 | 8.1 | 10.9 | 13.5 | 11.6 |
| | Predator | 29.3 | 16.2 | 16.7 | 17.8 | 16.7 | 17.7 |
| | Parasite | 0.1 | 0.2 | 0.4 | 0.4 | 0.1 | 0.1 |
| Bioturbation | Diffusive Mixing | 76.7 | 57.3 | 18.3 | 27.7 | 52.2 | 41.1 |
| | Surface Deposition | 16.0 | 33.8 | 43.0 | 53.7 | 32.2 | 43.6 |
| | Upward Conveyor | 2.1 | 3.7 | 2.9 | 4.7 | 6.0 | 4.2 |
| | Downward Conveyor | 1.8 | 2.1 | 3.7 | 6.6 | 4.3 | 5.9 |
| | None | 3.5 | 3.2 | 32.1 | 7.4 | 5.3 | 5.2 |

**FIGURE 5** Relative compositional dominance (i.e., proportional biomass distribution across traits) of the biological effects trait categories in determining the six effect traits cluster groups. The percent composition of each trait within the macrofaunal assemblages in each cluster is presented and shading is proportional to the values from 0% (no shading) to 100% (full shading). Cluster groups are colored and ordered to match the dendrogram (Figure 4) to ease interpretation.

identified by an increased numerical proportion of the smallest size trait category "<10 mm" (maximum body size; 39.9%), the shortest longevity class "<1 year" (longevity; 23.3%), "benthic larval development" (larval development mode; 53.9%) and, in common with cluster 6, a notable representation of "diffusive mixing" (bioturbation mode; 57.3%).

The remaining cluster, cluster 1, which is found in the mid North Sea, inshore regions of the east coast of England, the southwest approaches and the central Irish Sea, is characterized by a notable increase in the proportion (32.1%) of "nonbioturbators" (bioturbation mode) (with a reduced proportion [18.3%] of "diffusive mixers"), "suspension feeders" (feeding mode; 46.2%) and "lecithotrophic larval developers" (larval development mode; 35.4%).

The confidence in the model for the clusters based on effects traits appears lower than that for the model governed by response traits. The higher confidence classes (0.6–0.8 and 0.8–1.0) are more-or-less restricted to the northern North Sea (represented by effects traits cluster group 2) and the lowest two confidence classes dominate much of the remaining regions of the study area (Figure 6b). Thus, interpretation and utilization of the

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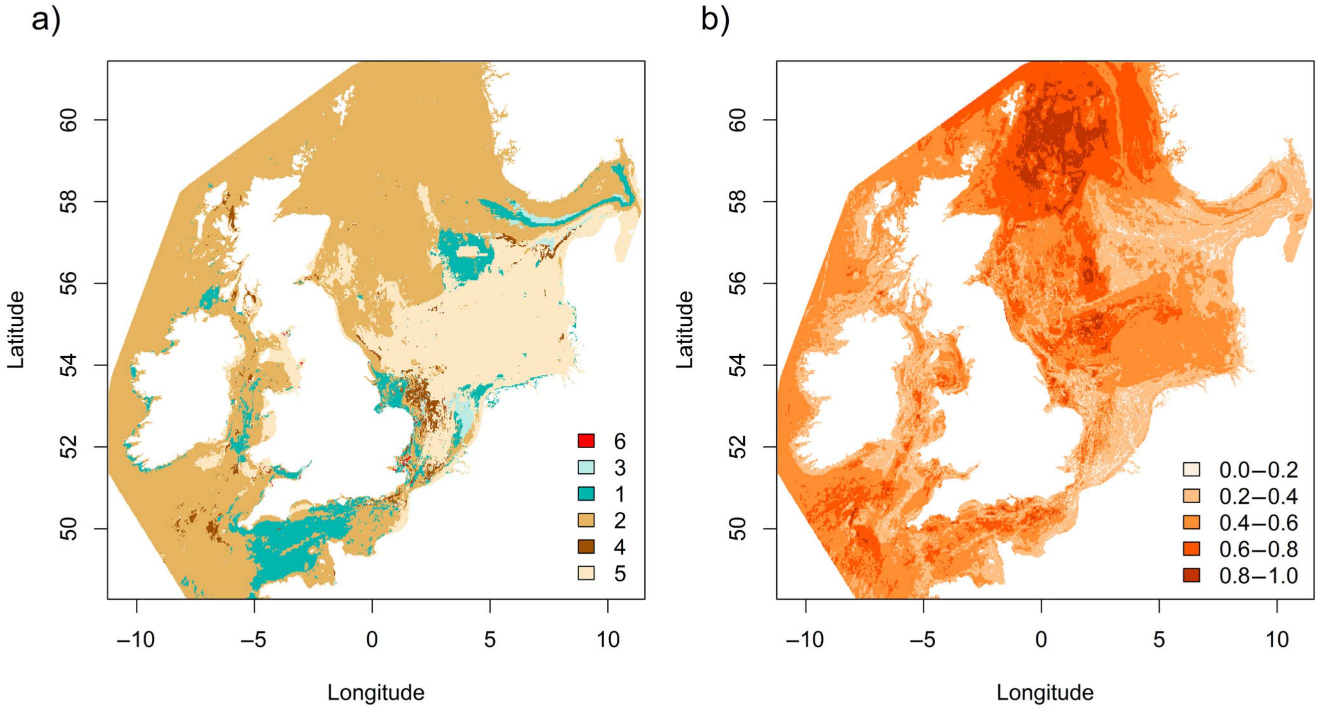

**FIGURE 6** (a, b) Classification map showing the spatial locations of the six cluster groups formed based on the five macrofaunal biological effects traits (a). Clusters are colored and ordered in the legend to match those presented in Figures 4 and 5. Confidence map showing the relative confidence in the model in predicting the traits cluster groups (b).

cluster map, and the clusters delineated for regions where the confidence is low, must be undertaken with caution. This relatively low prediction confidence for effects traits compared with response traits is, perhaps, not unexpected given it is response trait expressions that govern a taxon's relationship with its environment.

## DISCUSSION

The assemblages living in or on the seabed play a fundamental role in defining functions that drive important ecosystem processes which ultimately underpin the goods and services upon which we depend (Culhane et al., 2018; Snelgrove et al., 2014). Meanwhile, escalating societal demands placed on the seabed means that there is an urgent need to align our understanding of the effects of anthropogenic pressures (e.g., installation of wind turbines, demersal fishing, sediment disposal, and extraction) on both the structure and function of the seabed assemblages (Foley et al., 2017; Korpinen et al., 2021; Stelzenmüller et al., 2018). This tenet is central to an ecosystem-based approach to management (EBM; Katsanevakisa et al., 2011; Long et al., 2015) which is increasingly enshrined within relevant policy to ensure that the demands placed on the seabed are sustainably managed. Implicitly, implementation of an EBM requires an understanding of where pressures are most likely to result in the most significant functional impacts and factoring this information into licensing decisions. To date, management of seabed resources and predictions of which areas are most ecologically suitable for anthropogenic pressures are principally founded on broad-scale maps of physical habitat (Galparsoro et al., 2014; Quemmerais-Amice et al., 2020) as empirical benthic biological data limitations have historically hindered a more biological-based grounding (Cooper et al., 2019). Maps offer great potential for linking decision-making with science as they are an effective means of communication (Wright, 2016), and those that represent the actual or predicted spatial distribution of organisms and ecological features offer the best available spatial decision-support tools (Lecours, 2015; Levin et al., 2014). However, available broad spatial scale maps generally provide limited information about the occurrence of individual organisms (Harris & Baker, 2012). Our trait-based maps, based on a Big Data approach, provide a framework to support licensing decisions by highlighting areas where the likely tolerance of benthic assemblages to a particular disturbance is likely to be highest and regions where the potential ecological function should be safeguarded.

The benthic assemblages across the large spatial scale of our study region exhibit distinct clusters based on both sets of response and effects traits. Centered on a collective suite of response and effects "primary" traits, the

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observed cluster group regions might be regarded as representing different types of "secondary traits" according to the terminology posed by Costello et al. (2015). Secondary traits have previously been used to approximate functional potential, for example, bioturbation based on mobility, burrowing, and biomass (Queirós et al., 2013) and dispersal potential based on motility and the environment (Angert et al., 2011). Some of our response trait categories (e.g., "cushion" and "tunic" [morphology], "crevice" [living habit], ">10 cm" [sediment depth]) and effects trait categories (e.g., "200–500 mm" and ">500 mm" [maximum size], ">10 years" [longevity], "parasite" [feeding mode], "upward conveyor" and "downward conveyor" [bioturbation mode]) categories show low proportional expressions across the whole region. Meanwhile, other trait categories generally show ubiquitously high proportional expression in assemblages regardless of physical setting (e.g., response traits: "soft" [morphology], "pelagic egg development" [egg development mode]; effects traits: "21–100 mm" [maximum size], "3–10 years" [longevity], "planktotrophic larval development" [larval development mode]). However, other traits expressed significantly varying proportions and it is the influence of these key trait categories that is likely to portray differences in the relative sensitivities to pressures and to different functional potentials across the study region.

The use of trait information to infer the vulnerability of species to disturbance by proxy is increasingly being explored (Beauchard et al., 2017; Bolam et al., 2016; Gladstone-Gallagher et al., 2019; Gonzalez-Irusta et al., 2018). Trait-based vulnerability assessments can provide improved information for species-level conservation, which is often the scale at which managers operate (Butt et al., 2022). Combined with professional judgment (Bolam et al., 2016; Foveau et al., 2017) the coupling between traits and sensitivity to pressure has previously been addressed through informed but theoretical preconceptions about which trait categories are likely to impart sensitivity or tolerance and/or influence recoverability (Beauchard et al., 2021; Gonzalez-Irusta et al., 2018; Hinz et al., 2021) together with those informed from in situ observations. For example, traits such as "scavenger" (feeding mode), "surface-dwelling" (sediment position) and "short-lived" (longevity) have been observed to be associated with taxa associated with relatively highly fished regions (McLaverty et al., 2021; van Denderen et al., 2015), with "long-lived" and "suspension feeding" traits conferring higher sensitivity or lower tolerance to chronic trawling. Van Denderen et al. (2019) found that low salinity regions of the Baltic were more dominated by short-lived organisms, which are more resilient to bottom trawling and hypoxia. Bolam et al. (2016), meanwhile, observed that soft-bodied, exoskeleton, 6–10 cm deep-dwelling and burrowing traits were proportionally more dominant in assemblages exposed to regular dredged material disposal off the northeast coast of England. The loss of such species-specific traits associated with these disturbances has important ecosystem function implications (Thrush & Dayton, 2002). Based on such empirical observational studies, ranking or scoring the relevant trait categories allows the relative sensitivity and/or the recoverability of different assemblages to be formulated (Hinz et al., 2021). This approach has been adopted to ascertain relative differences in the sensitivity of benthic assemblages to demersal trawling (Bolam & Eggleton, 2014; Foveau et al., 2017; Gonzalez-Irusta et al., 2018) and across a suite of different pressures (Butt et al., 2022; Kenny et al., 2017).

The present study derived a map showing regions, which vary with respect to, principally, certain response traits such as morphology, egg development mode, living habit, sediment position, and mobility. Coupling the trait categories with specific pressures allows our response trait cluster map to serve as a proxy pressure-specific sensitivity map. For example, based on the findings of Bolam et al. (2016), the relatively higher proportions of soft-bodied, deep-dwelling burrowers of assemblage cluster 6 which are found in the southern North Sea (especially off the coast of The Netherlands) and in small regions of the Bristol Channel and the Irish Sea, potentially display greater tolerance to the disturbance associated with routine dredged material disposal. Similarly, the elevated expression of free-living, swimming, and exoskeleton traits of cluster 5 theoretically implies that these assemblages, which are located in certain parts of the southern North Sea, are more tolerant to chronic trawling. Applying this concept, Foveau et al. (2017) compared the map created following response traits rankings for the English Channel ICES region with that of trawling pressure to produce a map of risk/sensitivity of benthic habitats and communities to trawling damage. However, we suggest that further refinement is needed in the use of such maps for direct utility as sensitivity maps. First, it is well acknowledged that sensitivity to pressure will undoubtedly be governed by specific trait categories depending on the nature of the pressure (Hewitt et al., 2018; Kenny et al., 2017) and thus the traits used within numerical approaches should be carefully selected based on the specific pressure being targeted. Second, while Baird and van den Brink (2007) and Beauchard et al. (2021) support our philosophy that a multiple biological traits basis is preferable over single trait approaches for assessing the status of seabed habitats specifically in relation to disturbance, de Juan et al. (2022) warned that the response of a species to pressure depends on a certain combination of traits, some of which may be interacting with each other,

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and these interactions are not random. The interaction between traits does not always emerge from the outcome of the traits approaches. Using trawling as an example, they propose that, in general, species living on the surface of the seabed are highly likely to be exposed to the physical impact of the gear; however, if these species at the same time are of small size, mobile, and have a highly resistant shell, they may survive physical contact. Finally, it is important to either delineate from the outset those traits which play an important role in determining a species' initial sensitivity to pressure from those that convey its ability to recolonize following the disturbance (Bolam & Eggleton, 2014; Gladstone-Gallagher et al., 2019), although the integration of both provides complementary information to bridge the gap between impact assessment and status assessments (Beauchard et al., 2021).

It is widely understood that benthic macrofaunal organisms are major providers of ecosystem functioning in marine habitats (Lam-Gordillo et al., 2021; Villnäs et al., 2019). They modify soft-sediment habitats through biological processes such as ingestion, digestion, excretion, and bioturbation, which facilitates microbial recycling of nutrients, detoxification of pollutants, and organic matter remineralization (Snelgrove et al., 2014; Wyness et al., 2021). In transferring energy across trophic levels, benthic macrofauna also connects benthic and pelagic ecosystems (Kristensen et al., 2014; Murillo et al., 2020). The mechanistic links between species and function are intrinsically governed by the traits the species express (Naeem & Wright, 2003), or more specifically, their effects traits (Hooper et al., 2005). Improving our understanding of effects traits, therefore, better informs us of the links between community structure, ecosystem function and ecosystem service provision (Martini et al., 2020). Effects traits and their interactions determine the functioning and stability of communities and ecosystems (Loreau et al., 2001) and thus represent valuable surrogate variables for ecosystem function (de Juan et al., 2015). Our effect traits-based map, portraying the spatial patterns exhibited by the six assemblage types based on the five effects traits adopted here, identifies regions that possess (dis)similar functional potential: functional differences being dictated by those effects traits that show different levels of expression between cluster assemblages. For example, the assemblages of the most distinct cluster, cluster 6, which is found in very small, isolated regions of the Celtic Sea and the southern North Sea, have a greater expression of longer lived (3–10 years) taxa, a feeding mode of scavengers and predators and a diffusive mixing bioturbation mode. Such assemblages are, based on current theoretical understanding, likely to have different roles in trophic energy transfer and carbon capture and remineralization than those of cluster group 1 where nonbioturbators and suspension feeders occupy much higher numerical proportions (Bremner et al., 2005; de Juan et al., 2022; Hinz et al., 2021). The relatively small spatial extents represented by cluster 6 would imply that anthropogenic activities in such seabed areas should be carefully considered to safeguard their potentially functionally unique characteristics. The linking of specific traits categories with ecological function in marine benthos is still in its relative infancy (Lam-Gordillo et al., 2021), although it is very much the focus of current laboratory-based and in situ experimental approaches (Gogina et al., 2018; O'Meara et al., 2020; Wrede et al., 2019). The different effects traits cluster regions identified here may be used to assist such effects traits-function mechanistic links. Functional properties, either under in situ or laboratory mesocosm experiments, of core samples taken from each of the cluster regions may assist in ground-truthing our cluster groups. The clustering and modeling approach adopted here, and indeed future comparable approaches, should keep abreast of the outcomes of future developments and future iterations should be aligned to ensure that the maps are based on the traits which have been established to have strong links with specific functions (Beauchard et al., 2017; Bremner, 2008; de Juan et al., 2022).

The layers produced here, and subsequent layers based on other potential permutations of different traits (or sets of traits), should be used alongside other metrics and/or approaches that form the basis for current decisions regarding the suitability of regions of the marine environment for licensing human activities. For example, in the UK the current statutory process involves consideration of the presence and spatial extent of designated habitats (e.g., Annex I Habitats) relative to the footprint of the application. While these statutory policy-based considerations will undoubtedly continue to be central to the decision-making process, we propose that layers such as those presented here should be used to augment and/or assist (i.e., not replace) the existing process and provide additional insights regarding the ecological attributes of the potentially affected assemblages. Undoubtedly, the information contained in the types of layers provided here represents an increased understanding of ecological features for the large areas of seabed currently outside designated boundaries where this type of evidence base is otherwise comparatively limited. Furthermore, these layers allow the potentially affected seabed assemblages to be placed into a wider spatial context than hitherto by, as we have demonstrated here, identifying localized areas where benthic assemblages potentially possess functionally unique roles. We do not believe the current decision-making frameworks allow for such context dependency.

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In Europe, the EU Marine Strategy Framework Directive (MSFD) has adopted spatial assessments (European Commission, 2017) that place increased demands for up-to-date spatial data which cannot be achieved using traditional monitoring by Member States but must rely on model-based outputs that require more data-rich approaches and spatial data (Korpinen et al., 2021). As raster layers, our continuous maps can be superimposed with various current or planned licensed areas for pressures which directly impact the seabed (Goodsir et al., 2015). This would allow areas of greatest potential risk to be highlighted, that is, those in which pressures correlate with regions of highest sensitivity to that disturbance (and thus based on a suite of pressure-specific relevant traits) and/or areas of greatest or unique functional potential. This is analogous to the approach conducted by Quemmerais-Amice et al. (2020) for the coast of France, albeit seabed sensitivity was based on a habitat (EUNIS) approach as opposed to one based on a suite of traits. Refining the response traits to those that have been empirically shown to influence benthic ecological responses (Hewitt et al., 2018), as we have tentatively done here but for a generic physical pressure, should improve one of the key uncertainties in risk assessments (Halpern & Fujita, 2013; Korpinen & Andersen, 2016). The layers may assist in understanding the relationships between current marine protected areas and seabed function and potentially identify functionally important regions of seabed not yet offered protection. Finally, since the maps convey differences in relative sensitivity and potential ecological functioning, they may also form an important basis for broadscale assessments under marine spatial planning approaches which inherently require the integration of cross-sectoral interests.

Here we have produced 100% spatial cover maps based on five response and five effects traits. While one may argue over the theoretical basis for classifying functional traits into these two distinct classes, it is of course possible to select individual or smaller subsets of traits to produce different maps. We support the notion of Beauchard et al. (2021) and Baird and van den Brink (2007) of the limitations of estimating sensitivity based on single traits; long-term stability is likely to manifest through the combination of a species' instantaneous (i.e., acute response) and long-term (chronic response) sensitivity (sensu Bolam & Eggleton, 2014) and that different traits contribute to each of these in turn. It is also theoretically likely that the most suitable proxies for the ecological function will result from a combination of a suite of traits as opposed to a single trait (Villnäs et al., 2018). In view of this, we have developed the numerical architecture to easily output continuous maps based on an unrestricted permutation of any number of traits, classified into response or effects traits, to allow for any such unclassified approaches.

While the macrofaunal data used within this study were away from known licensed anthropogenic activities (offshore exploration, renewables, sediment extraction, sediment disposal), we have not accounted for the effect of demersal fishing (trawling) activities on benthic assemblages. Although its intensity and spatial and temporal footprint vary, demersal trawling is widespread across our study region (Foden et al., 2011; Lee et al., 2010). This pressure has been widely shown to affect both the taxonomic and traits composition of macrofaunal assemblages, particularly in more naturally benign habitats such as deep, muddy regions. Changes in how this pressure is estimated during the timeframe of the compilation of the sampled benthic data, together with spatial scaling mismatches between the scales at which it is modeled with that of a grab sample, were deciding factors to not include fishing pressure into our modeling in this study.

We have clearly identified that confidence in our current ability to predict trait expressions across this large study area varies from region to region. Our models reveal that differences in the sensitivity/tolerance to physical changes or pressure (i.e., response traits map) are currently more predictable than differences in functional potential (effects traits map). This might have been an expected outcome since environmental variables were used to model both sets of traits and it is only response traits which are theoretically linked to such driving variables. Interestingly, the environmental variable "suspended matter" was the most influential variable in the modeling of both trait types (Appendix S1: Figures S5 and S7). Future improvements in traits expression maps would, undoubtedly, benefit from the further collection and/or collation of historic benthic empirical data, especially in those areas identified where the model performs less well, and improved physical environmental predictor layers such as those depicting seabed sediment granulometry (Mitchell et al., 2018). Furthermore, as the observational species abundance data used here were exclusively acquired through grab and core samples, the modeled layers assume that the whole study region consists of sediments that can be sampled using these devices. It is well understood that there are seabed regions within our spatial extent which comprise coarser areas of the seabed (e.g., gravel, cobble and rock; Irving, 2009; Jackson-Bué et al., 2022) which the current sediment predictor layer models do not identify (see Mitchell, Aldridge, & Deising, 2019). To address this issue, coarse habitat areas should be clipped from the spatial raster layers during subsequent iterations of our numerical modeling. Alternatively, if the traits expressions of benthic assemblages associated with coarser habitats could be established, then these regions could be included in future models to create maps that more

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realistically reflect traits associated with the wider range in seabed physical habitats.

## AUTHOR CONTRIBUTIONS

Stefan G. Bolam and Keith Cooper conceived the idea for the paper, designed the methodology and collated the relevant data. Stefan G. Bolam managed the traits data for the taxa within OneBenthic. Keith Cooper undertook all the clustering and initial numerical modeling. Anna-Leena Downie performed the final modeling, including the generation of associated confidence maps. Stefan G. Bolam led the writing of the manuscript and all authors gave final approval for publication.

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## CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

## DATA AVAILABILITY STATEMENT

Trait expression data and novel code (Bolam et al., 2023) are available in the Cefas repository: https://doi.org/10.14466/CefasDataHub.137. Small numbers of individual datasets used in this study are owned by third parties and are not automatically publicly available and have therefore been withheld from our Cefas repository; these datasets and the organizations that own the data are summarized in Appendix S1: Table S1. Raster data are available in the Cefas repository from Mitchell, Aldridge, and Diesing (2019) at https://doi.org/10.14466/CefasDataHub.63 and Bio-Oracle (https://www.bio-oracle.org/); detailed instructions to query the Bio-Oracle data are provided in our *Methods* section.

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## SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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