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The development of Habitat Suitability Models to predict the presence of potentially suitable habitat for subtidal *Zostera marina* beds and *Modiolus modiolus* reefs in UK waters

Adam Smith, Jenny Booth, Laura Pettit, Ashley Cordingley and Cristina Vina-Herbon

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For further information please contact:
JNCC, Quay House, 2 East Station Road, Fletton Quays, Peterborough PE2 8YY.
https://jncc.gov.uk/

Communications@jncc.gov.uk

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Summary

The following report describes the methods to develop Habitat Suitability Models for the presence of potentially suitable habitat for subtidal *Zostera marina* beds and *Modiolus modiolus* reefs in UK waters using a collection of environmental variables known to influence the extent and distribution of each habitat, and presence and pseudo-absence records of habitat to test and validate the models. The modelling approach can be considered useful as an evidence product to help inform policy, for example the UK Marine Strategy. The report details the methods, outputs and limitations of the models.

Contents

1. Background

Benthic habitats are vital for the health of marine ecosystems, and when productive, sufficiently extensive and ecologically coherent, can provide essential ecological processes. *Modiolus modiolus* (commonly known as horse mussel) reefs, and *Zostera marina* (commonly known as eelgrass) beds, are two benthic biogenic habitats that provide essential ecosystem services, representing nursery grounds, refuges, and food sources for a wide variety of species (Heck *et al.* 1997; Zieman & Wetzel 1990; Duarte & Chiscano 1999; Sanderson *et al.* 2008; McDevitt-Irwin *et al*. 2016; Nordland *et al.* 2016; Kent *et al.* 2016, 2017).

Modiolus modiolus are a north Atlantic species of bivalve molluscs found subtidally around the British Isles that can aggregate into extensive reefs where conditions are suitable, for example off the north and northwest coasts (Tyler-Walters 2007). *Modiolus modiolus* reefs are created by the dense accumulation of individuals found on a range of substrata ranging from cobbles to sand (OSPAR 2008).

Zostera marina, which is a type of seagrass, is a marine angiosperm found in sublittoral and infralittoral zones. *Zostera marina* is distributed patchily throughout the UK, primarily off the coasts of south and south-west England, Wales, Orkney, the Shetland Islands, and Scotland (d'Avack *et al.* 2022). *Zostera marina* forms dense "beds" defined as where plant densities account for at least 5% cover of the seabed, though usually more than 30% cover (OSPAR 2009).

Modiolus modiolus reefs and *Zostera marina* beds are fragile and sensitive to a range of permanent and transient anthropogenic activities (Magorrian & Service 1998; Tyler-Walters 2007; Cook *et al.* 2013; Jones & Unsworth 2016; Elliott *et al.* 2017; d'Avack *et al.* 2022), including trawling (Holt *et al.*1998; De la Torriente *et al.* 2022), aggregate extraction and aquaculture (Holt *et al.* 1998). The direct impacts of anthropogenic activities represent the biggest threat to *Modiolus modiolus* reefs (OSPAR 2008) and *Zostera marina* beds (Elliott *et al.* 2017). These habitats are particularly sensitive to activities that cause physical change of habitat, suspension of sediments, smothering, and abrasion (d'Avack *et al.* 2022; Tyler-Walters 2007). Persistent damage can potentially cause irreversible habitat loss if the substrate, morphology or topography is permanently altered, thus causing physical loss of habitat. Physical loss of habitat frequently leads to habitat fragmentation. For *Modiolus modiolus* and *Zostera marina*, this can severely impact larval and seedling dispersal, and the presence of sources and sinks with consequences on successful recruitment, and the ability of a population to persist (Kendrick *et al.* 2016; Mackenzie *et al*. 2022).

Data on location and extent of biogenic habitats are limited and the full-scale and frequent mapping of habitats across the UK for regional scale assessments required by policy drivers such as the UK Marine Strategy is not feasible. Therefore, there is a paucity of data on the extent and distribution of horse mussel reefs and eelgrass beds. Habitat suitability models (HSMs) are widely used in place of *in-situ* habitat data as a proxy for habitat distribution (Gormley *et al*. 2013; Strong *et al*. 2018). If a habitat is lost or its distribution changes, this has consequences on associated natural capital and ecosystem services.

The environmental variables that influence presence and extent of *Modiolus modiolus* reefs and *Zostera marina* beds have been well studied (Tyler-Walters 2007; Gormley *et al.* 2013; d'Avack *et al.* 2022; Bertelli *et al.* 2022), and Castle *et al.* (2022) produced HSMs to predict the distribution of these habitats. However, as new methods and data become available, updated models that incorporate more recent biological and environmental data are required to more accurately predict extent and distribution and to assist in the management of these habitats.

1.1. Aims and objectives

This report provides updated HSMs for *Modiolus modiolus* reefs and *Zostera marina* beds in subtidal UK waters, hereafter referred to as *Modiolus modiolus* HSM and *Zostera marina* HSM. By refining the previous HSMs produced by Castle *et al.* (2022) and using the most recent datasets for biological presence and pseudo-absence data, the models presented herein can be used to estimate the extent and location of these important habitats, protected under international and national legislation and conventions**.**

2. Data Preparation

2.1. Environmental predictor variables

Habitat-specific environmental variables that influence the growth and survival of *Modiolus modiolus* reefs and *Zostera marina* beds were used to predict the extent and location of suitable habitat. These predictor variables were selected based on the literature review performed by Castle *et al.* (2022) (Table 1). Environmental data were sourced as raster layers in tagged image file format (tif) from respective databases and clipped to the UK Exclusive Economic Zone (EEZ) using the “extract raster by mask” tool in ArcGIS v10.1 (ESRI 2012). Each environmental layer raster was projected to Lambert azimuthal equal-area (LAEA) European Terrestrial Reference System (ETRS)-extended 1989 European Petroleum Survey Group (EPSG): 3035 and resampled to a common raster grid with a resolution of 300 m prior to input into the model.

All environmental layers except for the “depth to seabed” and “slope” layers were input directly into the model. The “depth to seabed” layer was created by sourcing the higher resolution Department for Environment, Food and Rural Affairs (Defra) Digital Elevation Model (DEM; Defra, 2020) which was supplemented with the European Marine Observation and Data network (EMODnet) Digital Bathymetry Digital Terrain Model (DTM) (2022) where the former was not available. The two raster layers were merged using the tool “Mosaic to New Raster (Data Management)” in ArcGIS v10.1 (ESRI 2012). The resultant raster was resampled to a resolution of 300 m by 300 m using the “Resample” tool in ArcGIS v10.1. The “slope” layer was derived directly from the “depth to seabed” layer created above using the Terrain Attribute Selection for Spatial Ecology (TASSE) v1.1 toolbox (Lecours *et al.* 2017) in ArcGIS, using the Horn (1981) method.

Following the methodology in Castle *et al.* (2022), bathymetry layers were restricted to specific depths for each habitat. Based on the occurrence of *Zostera marina* beds within the presence dataset, depth in the HSM was restricted to 0 – 15 m (d’Avack, *et al.* 2022). For the *Modiolus modiolus* HSM, depth was restricted to 0 – 248 m, based on the occurrence of reefs and the deepest sample observed within the available presence dataset. Following Castle *et al.* (2022), the model was also restricted to remove the Severn Estuary, which is an area of high sediment loading, meaning that Modiolus reefs are unlikely to occur due to their sensitivity to smothering.

The HSMs were used to predict the probability of suitable habitat only for those 300 m^2 grid cells where environmental values were available from each environmental predictor variable layer. In the absence of one or more layers, a prediction on the probability of suitable habitat was not made. Whilst the coverage of both models was limited by data paucity to some extent, the *Zostera marina* HSM extent was further limited to 5 km from the coastline to match the wave fetch layer (Burrows 2020). The Burrows (2020) wave fetch layer was introduced to reduce the probability of predicted suitable habitat for *Zostera marina* beds in high energy environments. Thus, preventing shallow offshore areas unsuitable for *Zostera marina* (such as Dogger Bank) being represented in the model at low probability, which would inflate the area of predicted suitable habitat.

The sources of environmental predictor variables used in both models are shown in Table 1.

Table 1: List of predictor variables used for modelling. The most recent available data were used where possible.

Predictor variable	Source	Units	Original Spatial Resolution	Release Date	Data Collection Year	*Modiolus modiolus* HSM	*Zostera marina* HSM
Depth to seabed	Defra's Marine Digital Elevation Model (DEM' Defra 2020), supplemented with EMODnet Digital Bathymetry DTM (2022) where the former was not available.	Metres (m)	Defra Marine DEM: 1 arc second EMODnet Digital Bathymetry DTM: 1/16 arc minute	Defra Marine DEM: 2020 EMODnet Digital Bathymetry DTM: 2022	Defra Marine DEM: 1851–2020 EMODnet Bathymetry: 1815–2022	Yes	Yes
Slope of the seabed	Derived from the "Depth to the seabed" layer (above), using the Terrain Attribute Selection for Spatial Ecology (TASSE) toolbox in ArcGIS as recommended in Lecours *et al.* (2017). Calculated by using the Horn (1981) method.	Degrees (°)	Same as "Depth to seabed" layer	Same as "Depth to seabed" layer	Same as "Depth to seabed" layer	Yes	No

Predictor variable	**Source**	**Units**	**Original Spatial Resolution**	**Release Date**	**Data Collection Year**	***Modiolus modiolus* HSM**	***Zostera marina* HSM**
Kinetic energy at the seabed due to waves	EMODnet Seabed Habitats (mean of annual 90th percentile values over six years). EMODnet (2019).	Newtons per Square Metre (N/m^2)	North Sea and Celtic Seas inshore (< 6 km from the coast) 100 to 300 m. North Sea and Celtic Seas inshore (> 6 km from the coast) 12.5 km.	2023	2000–2005	Yes	Yes
Kinetic energy at the seabed due to currents	EMODnet Seabed Habitats (mean of annual 90th percentile values over six years). EMODnet (2015).	Newtons per Square Metre (N/m^2)	300 m at the coast and combination of 1.8 km in the North and Celtic Sea and 10 km in the North East Atlantic	2018	2000–2005	Yes	Yes

Predictor variable	**Source**	**Units**	**Original Spatial Resolution**	**Release Date**	**Data Collection Year**	***Modiolus modiolus* HSM**	***Zostera marina* HSM**
Seabed substrate (categorical)	EMODnet Seabed Habitats Biogenic substrate in Europe, used in EUSeaMap (2023).	1 Mud/ sandy mud, 2 Sand/ muddy sand, 3 Mixed sediment, 4 Coarse sediment, 5 Rock, 6 Biogenic substrate	N/A - vector	2023	1991–2023	Yes	Yes
Mean of annual minima temperature at the seabed	Bio-ORACLE Minimum temperature derived from the mean depth of benthic layers. Assis *et al*. (2017).	Degrees Celsius (°C)	0.08°	2017	2000–2014	No	Yes
Maximum temperature at the seabed	Bio-ORACLE Maximum temperature derived from the mean depth of benthic layers. Assis *et al*. (2017).	Degrees Celsius (°C)	0.08	2017	2000–2014	Yes	No
Minimum salinity	Bio-ORACLE Minimum salinity derived from the mean depth of benthic layers. Assis *et al*. (2017).	Practical Salinity Unit (PSU)	0.08	2017	2000–2014	Yes	Yes

Predictor variable	**Source**	**Units**	**Original Spatial Resolution**	**Release Date**	**Data Collection Year**	***Modiolus modiolus* HSM**	***Zostera marina* HSM**
Wave fetch	Wave fetch GIS layers for the UK and Ireland at 200 m scale (Burrows 2020)	Log_{10} cells	200 m	2020	Modelled	No	Yes

To reduce overfitting of the HSMs, the correlation between the different environmental predictor variables was plotted; in the event of high correlation between layers, where the correlation was greater than 0.8, one of the correlated layers would be removed (Warton 2022). The initial run of the *Zostera marina* model contained photosynthetic active radiation (PAR) at the seabed as a predictor variable (PAR at the seabed, EMODnet 2018), however this was found to be highly correlated with “depth to seabed”. The high positive correlation was explained by the fact that PAR at the seabed was derived from light at the surface and adjusted for depth using EMODnet Digital Bathymetry DTM (EMODnet 2022), one of the layers used to create the “depth to seabed” layer. Therefore, PAR at the seabed was removed and depth retained in the model for the following reasons:

- The resolution of the bathymetry layer was higher, allowing the resulting model to better fit the coastline.
- PAR has high intra-annual variability, being affected by storms, run-off, algal blooms among others, whereas depth is consistent.

2.1.1. Model extent

All layers used as environmental predictor variables for each habitat were processed so that the extent and resolution matched. All environmental layers were cropped and resampled to the “depth to seabed layer” using the "raster” package (Hijmans 2023). Environmental layers were then combined into a raster stack for processing.

2.2. Habitat occurrence response variables

To improve the accuracy of habitat prediction in HSMs, habitat presence data can be supplemented with absence data. Due to the paucity of true absence information from survey data, samples indicating the presence of habitats not known to co-exist with the habitat modelled (Table 2) were used as a proxy for the absence of the respective habitats, hereafter termed pseudo-absence data (a common practice in HSMs; Chefaoui *et al.* 2016; Castle *et al.* 2022; Charbonnel *et al.* 2023). The combinations of presence and pseudo-absence data are referred to as response variables.

The following parameters were taken into consideration prior to running the model:

- Presence / pseudo-absence data were not restricted by date – since temporal variability is inherent in all biological datasets, this maximised the data available from these under sampled habitats to train and test the HSM.
- Only habitat records were used for presence / pseudo-absence data - species data were excluded from the model; this provided the best estimate of the distribution and extent of habitats.
- Point rather than polygon data were used to denote occurrence type - to ensure the highest accuracy of environmental conditions required to support the prediction of suitable habitat. The model only accepts biological response variables in point format, polygon data would therefore have to be converted into point data at a specific density per polygon, potentially introducing bias into the model, and affecting the weighting of presence against pseudo-absence. Additionally, effective duplicate removal of the data would be unfeasible.
- Only subtidal habitat records were used - *Zostera marina* beds occur in both intertidal and subtidal regions, but only subtidal habitats were considered.
- Taxonomic status – *Zostera angustifolia* records were considered as taxonomic synonyms of *Zostera marina* (d'Avack 2022; Guiry & Guiry 2023).

2.2.1. Sources of habitat occurrence data

The following datasets were chosen as sources of presence and pseudo-absence data: OSPAR threatened and/or declining habitats database (OSPAR 2022), Natural England Marine Evidence Base (Natural England 2021), Small Isles Marine Protected Area (MPA) survey (Greathead *et al.* 2023), Annex I Reef database (Duncan *et al.* 2022) and the Marine Recorder database (JNCC 2022). For each database, a specific selection method was used to obtain high confidence occurrence (see Table 2 for further details).

To avoid pseudo-replication, and introducing bias into the weighting of the model, duplicate data points were removed from all datasets for both presence and pseudo-absence data.

Table 2: Summary of datasets and selection criteria used for the presence and pseudo-absence response variables. Please see footnotes for explanation of habitats and codes. FOCI = Features of Conservation Importance, HOCI = Habitat of Conservation Importance (NE & JNCC 2010).

Habitat	Source	Habitats indicating presence	Habitats indicating pseudo-absence
Zostera marina beds	Annex I Reefs Database 2022	N/A	All Annex I Reef habitats.
	Marine Recorder August 2022	EUNIS 2007 habitat code: A5.5331 [1]	All EUNIS 2007 habitat codes excluding: A5.533 [2] A5.5331 [1]
	OSPAR Threatened and/or declining habitats database 2022	OSPAR T&D habitat: *Zostera marina* beds	All OSPAR T&D habitat types excluding: Carbonate mounds Intertidal mudflats Intertidal *Mytilus edulis* beds on mixed and sandy sediments Littoral chalk communities, Maerl beds Seamounts *Zostera* beds
Modiolus modiolus reefs	Natural England Evidence Base 2021	FOCI name: Horse mussel (*Modiolus modiolus*) beds	All FOCI codes excluding HOCI 9 [3] AND All FOCI names excluding those containing “modiolus” AND All Marine Habitat Classification for Britain and Ireland habitats and excluding: LR [4] LS [5]

Modiolus modiolus reefs	Marine Recorder August 2022	EUNIS 2007 habitat codes: A5.621 [6] A5.622 [7] A5.623 [8] A5.624 [9]	All EUNIS 2007 habitat codes excluding A5.621 [6] A5.622 [7] A5.623 [8] A5.624 [9]
	Small Isles MPA survey	Community code abbreviations: MXMS [10] MXM [11] MXMA [12] MXMP [13]	All community code abbreviations excluding: MXMS [10] MXM [11] MXMA [12] MXMP [13]
	OSPAR Threatened and/or declining habitats database 2022	OSPAR T&D habitat: *Modiolus modiolus* horse mussel bed	All OSPAR T&D habitat types excluding: Carbonate mounds Intertidal mudflats Intertidal *Mytilus edulis* beds on mixed and sandy sediments Littoral chalk communities Seamounts *Modiolus modiolus* horse mussel beds *Ostrea edulis* beds Oceanic ridges with hydrothermal vents/fields

1 - A5.5331 = *Zostera marina*/ *angustifolia* beds on lower shore or infralittoral clean or muddy sand.

2 - A5.33 = *Zostera* beds in full salinity infralittoral sediments.

3 – HOCI 9 = Horse mussel (*Modiolus modiolus*) reefs.

4 – LR = Littoral rock (and other hard substrata).

5 – LS = Littoral sediment.

6 - A5.621 = *Modiolus modiolus* beds with hydroids and red seaweeds on tide-swept circalittoral mixed substrata.

7 - A5.622 = *Modiolus modiolus* beds on open coast circalittoral mixed sediment.

8 - A5.623 = *Modiolus modiolus* beds with fine hydroids and large solitary ascidians on very sheltered circalittoral mixed substrata.

9 - A5.624 = *Modiolus modiolus* beds with *Chlamys varia*, sponges, hydroids and bryozoans on slightly tide-swept very sheltered circalittoral mixed substrata.

10 – MXMS = Mixed sediment and cobbles, occasional boulders with few burrows and Faunal Turf with *Arachnanthus sarsi* and *Modiolus modiolus.*

11 – MXM = Mixed sediment and cobbles, occasional boulders with few burrows and Faunal Turf and *Modiolus modiolus.*

12 – MXMA = Mixed sediment and cobbles, occasional boulders with few burrows and Faunal Turf with *Modiolus modiolus* and *Atrina fragilis.*

13 – MXMP = Mixed sediment and cobbles, occasional boulders with few burrows and Faunal Turf and *Modiolus modiolus* with *Pachycerianthus multiplicatus.*

Prior to producing the HSMs, all presence and pseudo-absence data were intersected with the extent of the respective models to expedite processing efforts, which subsequently reduced numbers of available habitat records.

2.3. Reducing spatial autocorrelation

To maximise efficiency of data collection, sampling is often conducted in relatively small areas, such as MPAs, or as part of environmental assessments for industrial purposes in a specified location. As such, samples of both presence and pseudo-absence observations were frequently found to be clustered together within raster grid cells.

To reduce the effect of the clustered data points, both observation types were reduced to a single random observation of presence or pseudo-absence per grid cell (by assigning unique cell IDs to samples) using the programming language R (R Core Team 2019) in R Studio (RStudio Team 2022) and the “raster” package (Hijmans 2023). The reduction in observation data ensures a greater degree of independence between observations, reducing the effects of spatial autocorrelation, and improving the accuracy of the model by not over-predicting the probability of habitat presence or absence. The selection of occurrence was determined by which observation type had the greater number of records per grid cell. However, as the number of records of pseudo-absence were greater than the number of presence records, pseudo-absence records were weighted to balance the selection of points between the two observation types. Weighted pseudo-absence was calculated using the following equation:

Equation 1: The calculation of weighted pseudo-absences per grid cell.

$$Weighted\ pseudo\text{-}absences = \left(\frac{\sum P}{\sum A}\right) A_n$$

Where the ratio between the total number of presence observations (P) and the total number of pseudo-absence observations (A) is multiplied by the number of pseudo-absence observations within the raster cell (An).

One point was randomly selected from the observation type with the highest value (i.e. number of presence records or value of weighted absence). In the event of a cell with equal values of presence to weighted absence, the observation type was marked as present. The number of records used as biological response data for the HSMs is shown in Table 3.

Table 3: Number of observations used to produce the HSM, per input dataset for the response variables, and after the selection process used to reduce the effect of spatial clustering. The date range of the biological response records used in the HSM are also shown.

Model	Response	Date Range	Number of initial data points	Number of data points used to produce HSM after selection process
Zostera marina	Presence	1976 – 2023	4,730	886
Zostera marina	Pseudo-Absence	1962 – 2023	157,200	29,618
Modiolus modiolus	Presence	1966 – 2021	1,471	473
Modiolus modiolus	Pseudo-Absence	1962 – 2023	175,818	29,440

2.4. Training and test data

In model development, response data are used to both train and test the model. For each run of the HSMs, a random selection of 75% of the response data were used to train the model, and the remaining 25% used to test the model.

3. Modelling

3.1. Random Forest Modelling Approach

The JNCC Species Distribution Modelling (SDM) Framework (an open-source R package; JNCC (2023): https://github.com/jncc/sdms) was used to produce HSMs for *Modiolus modiolus* reefs and *Zostera marina* beds. As an ensemble modelling approach, the JNCC SDM Framework includes Boosted Regression Tree, Support Vector Machine, General Additive Model, General Linear Model, Maximum Entropy, and Random Forest (RF) algorithms. However, only the RF algorithm was used in the production of HSMs based on expert opinion from the package authors and previous pilot studies (Castle *et al*. 2022) that identified it as the best performing model. A bootstrap aggregation approach was used, which takes the average probability of occurrence of habitat from a user-defined number of model runs, as the output. For this assessment, the number of iterations (runs) of each HSM was set to 50 to avoid model overfitting, ensure model stability and accuracy, whilst reducing uncertainty, 50 runs were also recommended by the package authors.

The output of the RF algorithm creates a prediction across the extent of the raster stack of environmental predictor variables. As a result, probability is calculated regardless of whether the habitats assessed are present in-situ or not. Although the probability of suitable habitat may be high, it does not necessarily represent realised (occupied) habitat. Additionally, the model is limited to the specific environmental variables that are used as predictor variables to describe the occurrence of each habitat. Other biological and environmental factors which might limit extent, such as disease, competition, storm events, and anthropogenic activities are not accounted for when predicting habitat suitability.

The receiver operating characteristic (ROC) curve shows the performance of the model, plotting the false positive rate against the true positive rate. The area under the plotted ROC curve (AUC) is used to evaluate model performance (from 0 to 1). An AUC score of 0 indicates that the model has performed poorly (100% of predictions are wrong), an AUC score of 1 indicates that the model has performed extremely well (Hanley & McNeil 1982). The AUC scores for all 50 runs of the *Modiolus modiolus* HSM were between 0.914 and 0.972, with a mean of 0.949, denoting that the model performed well. For the *Zostera marina* HSM the AUC scores were between 0.877 and 0.961, with a mean of 0.924, similarly denoting good model performance.

3.2. Environmental variable importance

Alongside the HSM, the JNCC SDM framework outputs environmental variables used to predict habitat distribution ranked in order of importance, based on the mean increase in node purity (IncNode purity). A higher mean IncNode purity indicates the higher importance of the variable in predicting probability of occurrence, allowing the comparison of variables within the model (note there is no maximum value).

The variable identified as the most important to predict the presence suitable habitat for *Modiolus modiolus* reefs in this study was maximum temperature at the seabed, followed closely by seabed substrate and minimum salinity (Table 4).

Table 4: Importance of all environmental variables in the *Modiolus modiolius* HSM produced for this assessment.

Rank	Environmental Variable	Mean IncNode Purity
1	Maximum temperature at the seabed	23.81
2	Seabed substrate	22.06
3	Minimum salinity	20.72
4	Kinetic energy at the seabed due to currents	18.18
5	Kinetic energy at the seabed due to waves	17.23
6	Depth to seabed	12.37
7	Slope of the seabed	8.66

The variable identified as the most important to predict the presence of *Zostera marina* beds in this study was wave fetch, followed by depth to seabed and minimum temperature at the seabed (Table 5).

Table 5: Importance of all environmental variables in the *Zostera marina* HSM produced for this assessment.

Rank	Environmental Variable	Mean IncNode Purity
1	Wave fetch	18.17
2	Depth to seabed	15.73
3	Minimum temperature at the seabed	10.58
4	Minimum salinity	7.64
5	Current energy at the seabed	6.48
6	Wave energy at the seabed	6.18
7	Seabed substrate	3.18

3.3. Habitat suitability model processing

3.3.1. Raster to vector

HSMs produced by the JNCC SDM package were output in raster format, where the value for each grid cell indicated the probability of occurrence of the associated habitat. To provide statistics such as the area of predicted suitable habitat, model outputs were imported into R version 3.6.1 (R Core Team 2019) using the “raster” package (Hijmans 2023) and converted to vector format using the “rasterToPolygon” function.

3.3.2. Area calculation

Following conversion to vector format, the HSMs were intersected with the UK Marine Strategy layer and the area of each polygon was calculated. Area was calculated using the “st_area” function from the “sf” package (Pebesma 2018, 2023). This area was then multiplied by the associated probability of the habitat occurrence, and divided by one million, to obtain the area of predicted habitat per polygon in km^2. To obtain the total area of habitat predicted by each HSM, the area of suitable habitat per polygon was summed for the entire extent of the HSM. This approach to predict the area of suitable habitat, followed the methodology used by Castle *et al*. (2022) and suggested by Calabrese *et al*. (2014), and was adopted to prevent applying ad-hoc thresholds based on the probability of presence for HSMs. This calculation of predicted suitable habitat area may be summarised by the following equation:

Equation 2: Method of calculating the total potential area of suitable habitat per HSM.

$$Total\,potential\,area\,of\,suitable\,habitat = \sum_{i=0}^{N} A_i P_i$$

Where the area (A) was multiplied by the probability (P) for each polygon (i) and summed over all polygons (N) in the HSM.

4. Results

The AUC values produced by the JNCC SDM framework for both *Modiolus modiolus* and *Zostera marina* HSMs were both above 0.9 (Table 6), denoting well performing models (Hanley & McNeil 1982).

The total area of predicted suitable habitat for *Modiolus modiolus* reefs was 67,327 km^2 and for *Zostera marina* beds was 2,596 km^2. Standard deviation as a percentage of total area of predicted suitable habitat was calculated as 31% for *Modiolus modiolus* reefs and 27% for *Zostera marina* beds (Table 6).

Table 6: Mean AUC, area of predicted suitable habitat, and standard deviation over all model iterations and percentage of standard deviation of total area of predicted suitable habitat for both *Modiolus modiolus* reefs and *Zostera marina* beds.

Model	Mean AUC	Total Area of Predicted Suitable Habitat	Standard Deviation	Standard Deviation of Total Area of Predicted Suitable Habitat
Modiolus modiolus	0.949	67,327 km^2	21,016 km^2	31.22%
Zostera marina	0.932	2,596 km^2	697 km^2	26.86%

4.1. *Modiolus modiolus*

The JNCC SDM package used the random forest algorithm to predict the probability of suitable habitat for *Modiolus modiolus* reefs across the UKMS region (Figure 1). Of the 67,327 km^2 of *Modiolus modiolus* reefs, areas identified to have high habitat suitability included the Western Channel and Celtic Sea; the Irish Sea; Strangford Lough; the waters around Northern Ireland and the Firth of Clyde; and the Small Isles and Orkney (Figure 2).

The modelling approach presented in this report has reduced the prediction of potentially erroneous suitable habitat presence in some locations, for example the model does not predict the erroneous presence of habitat suitable for *Modiolus modiolus* reefs off the coast of Norfolk identified in previous studies (Figure 1; Gormley *et al*. 2013; Castle *et al*. 2022). *Modiolus modiolus* reefs are not known to occur in this area, likely due to smothering from turbid and silty conditions, which is known to cause absence of reefs (Hutchinson *et al*. 2016). Additionally, the model also predicts presence of *Modiolus modiolus* reefs in the Bristol Channel (Figure 1) (outside of the Severn Estuary); although this differs from previous HSMs (Gormley *et al*. 2013; Castle *et al*. 2022), other publications have highlighted that dense aggregations of juvenile *Modiolus modiolus* occur in the Bristol Channel, which are not thought to survive to adulthood (Fletcher *et al*. 2012).

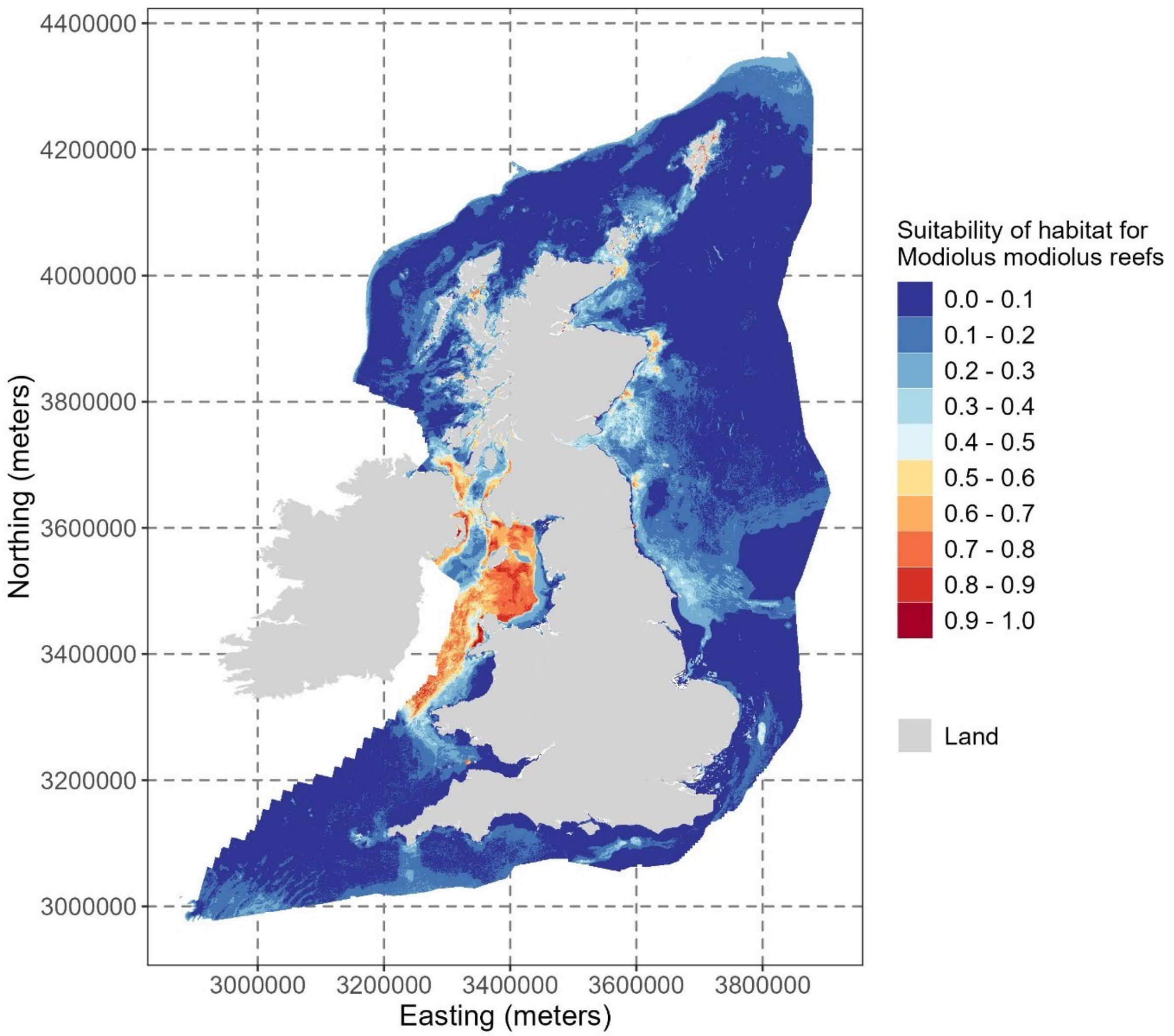

Figure 1. Mean predictive values of habitat suitability for *Modiolus modiolus* reefs across the UK within the model extent of 0 - 248 m depth. © JNCC 2024, Map projection: EPSG 3035, Not to be used for navigation.

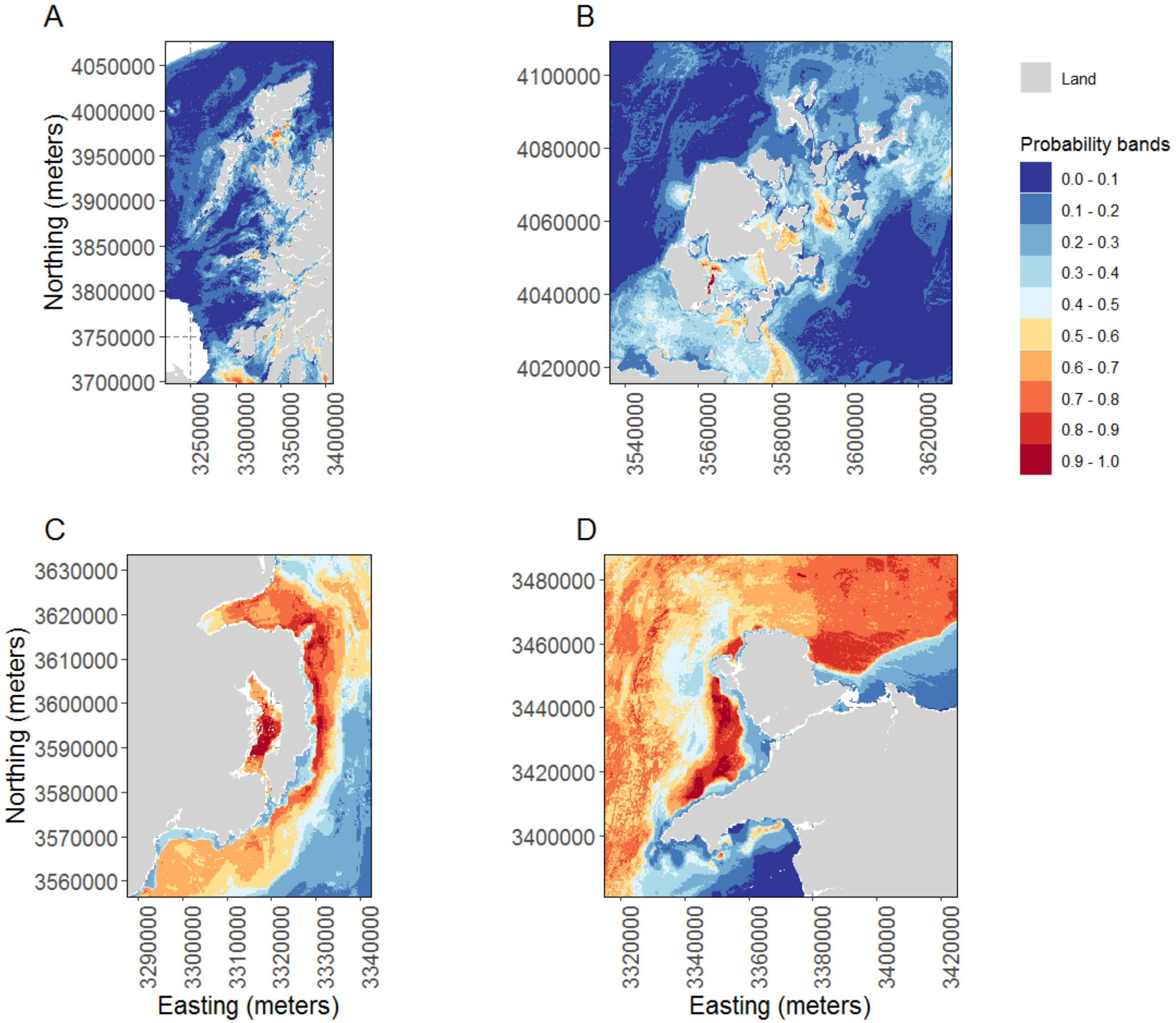

Figure 2: Mean predictive values of habitat suitability for *Modiolus modiolus* reefs for A – the Hebrides; B – Orkney; C – Strangford Lough; and D – North Wales / Anglesey. © JNCC 2024, Map projection: EPSG 3035, Not to be used for navigation.

The standard deviation for *Modiolus modiolus* reefs accounted for 21,016 km^2 of predicted suitable habitat across UK waters. Variability was largely confined to areas of high probability of suitable habitat for *Modiolus modiolus* reefs, such as the Irish Sea and Scottish Islands (Figure 3). Interestingly, small patches of higher standard deviation were observed off the coast of Norfolk, where the mean probability for suitable habitat for *Modiolus modiolus* reefs was low.

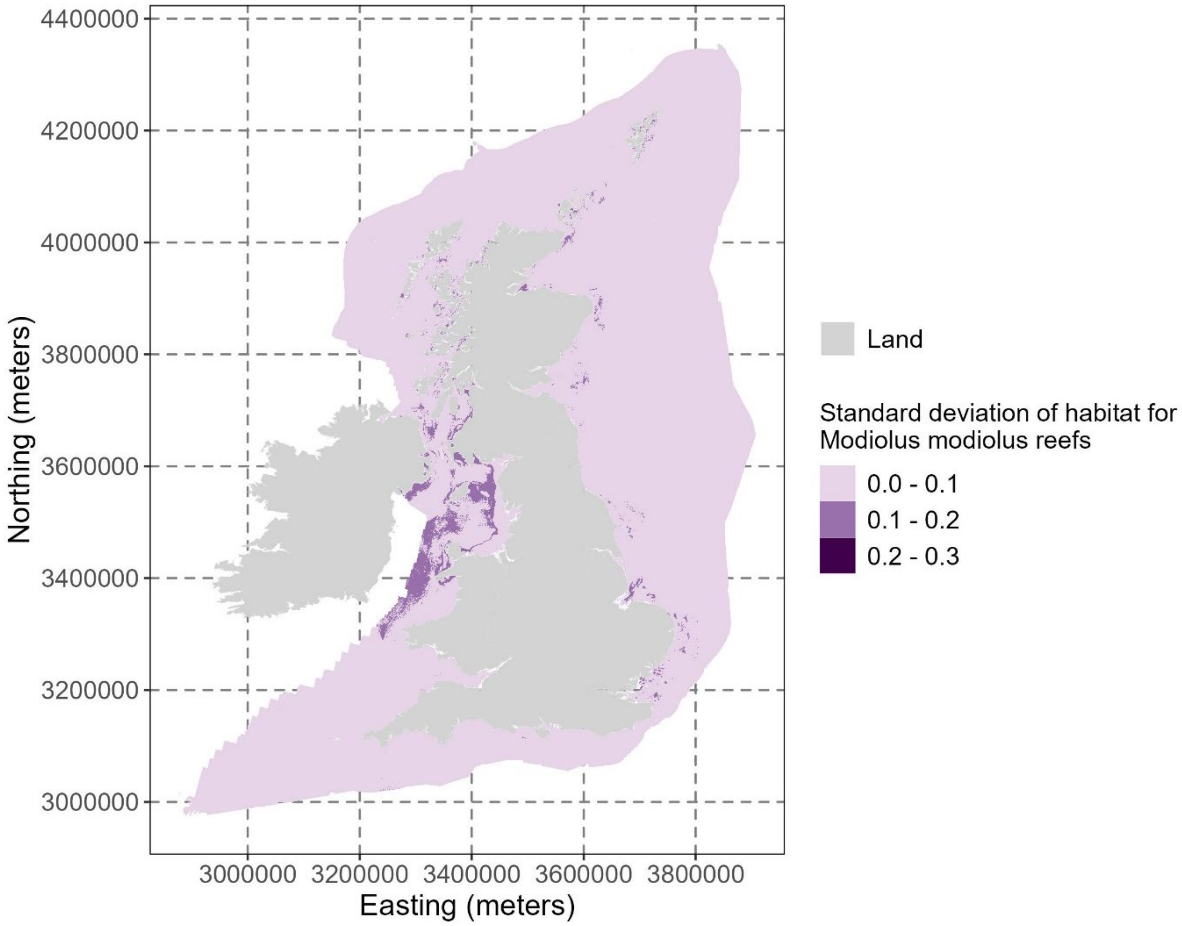

Figure 3: Standard deviation in the predictive values of probability of habitat suitability for *Modiolus modiolus* reefs across the UK, within the model extent of 0 - 248 m depth. © JNCC 2024, Map projection: EPSG 3035, Not to be used for navigation.

4.2. *Zostera marina*

The JNCC SDM package used the RF algorithm to predict the probability of suitable habitat for *Zostera marina* beds within UK waters (Figure 4). Of the 2,596 km^2 predicted suitable habitat for *Zostera marina* beds, areas identified to have high probability were the Llŷn Peninsula, Portsmouth, the Isles of Scilly and Islay (Figure 5). Strangford Lough, Loch Ryan, the Hebrides, Orkney, Luce Bay, Moray Firth and Dornoch Firth, also had high probability of suitable habitat for *Zostera marina* beds.

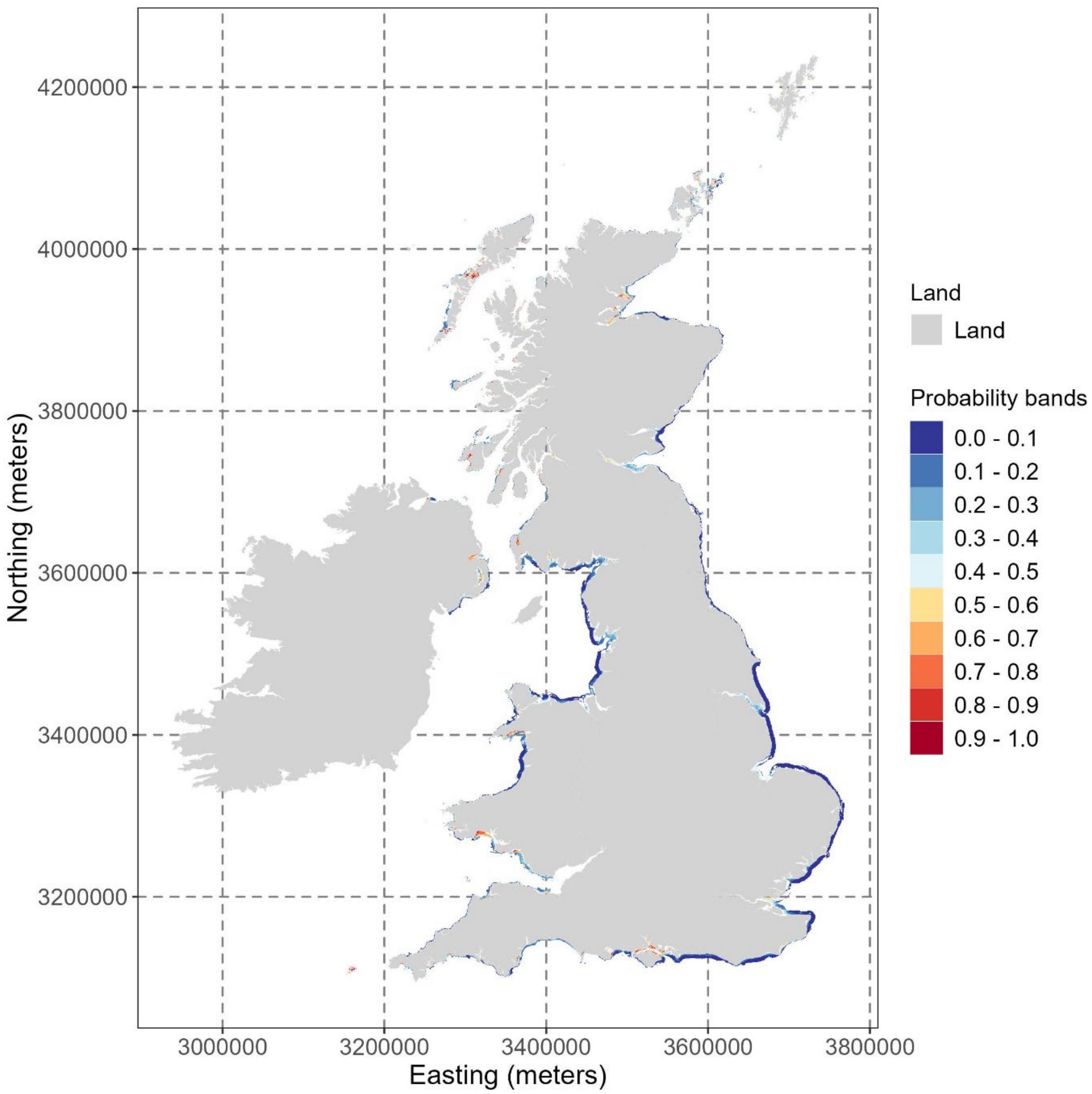

Figure 4: Mean predictive values of habitat suitability for *Zostera marina* beds across the UK within the model extent of 0 - 15 m depth. © JNCC 2024, Map projection: EPSG 3035, Not to be used for navigation.

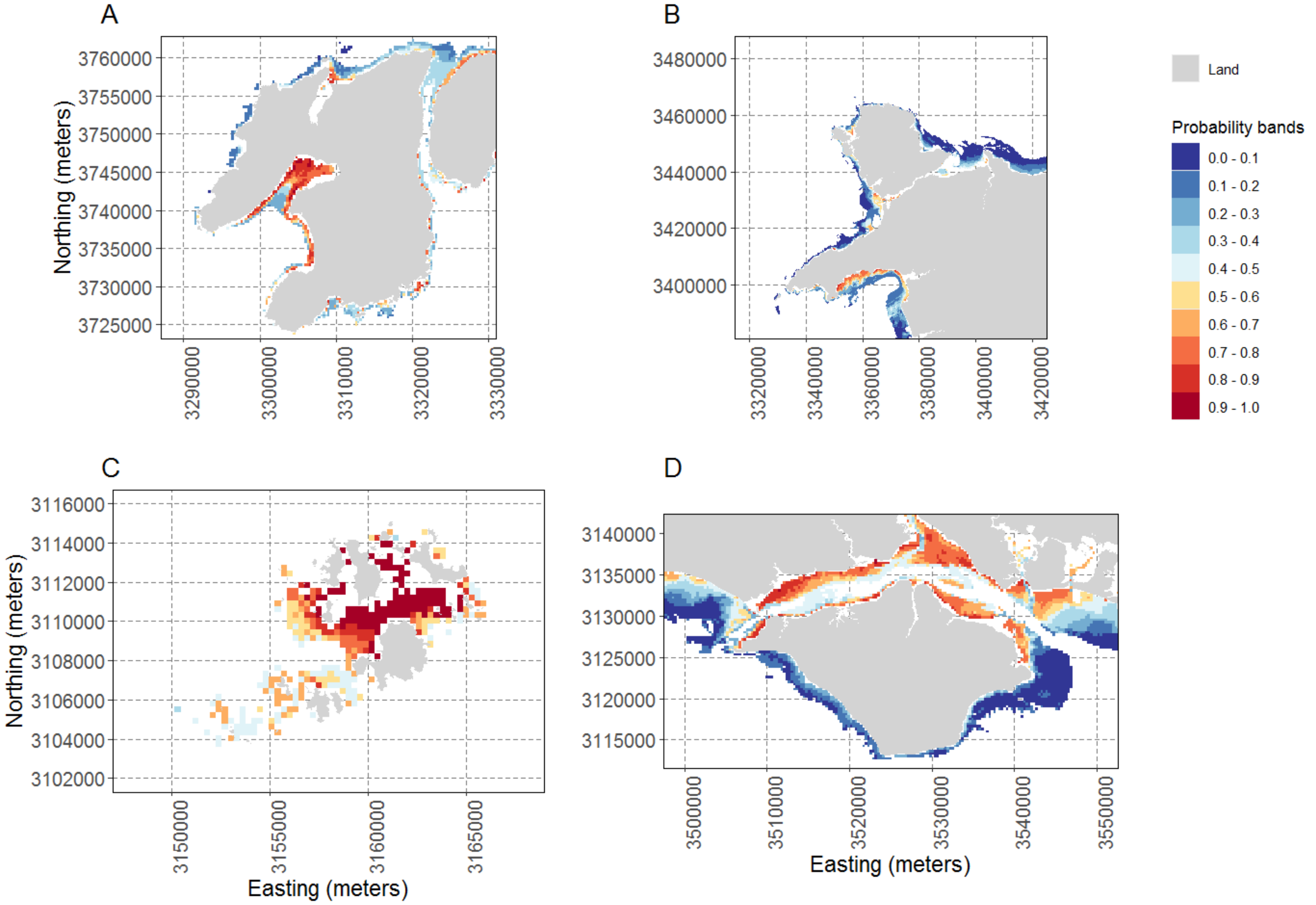

Figure 5: Mean predictive values of habitat suitability for *Zostera marina* beds for A – Islay; B – Anglesey and the Llŷn Peninsula; C – the Isles of Scilly; and D – Portsmouth and the Isle of Wight. © JNCC 2024, Map projection: EPSG 3035, Not to be used for navigation.

The standard deviation for *Zostera marina* beds accounted for 697 km^2 of predicted suitable habitat across UK waters. Variability was largely confined to areas of high probability of suitable habitat for *Zostera marina* beds. However, there were some exemptions to this general pattern, for example areas such as the Solway Firth and the Humber exhibited low probability of suitable habitat for *Zostera marina* but relatively high standard deviation (Figure 6).

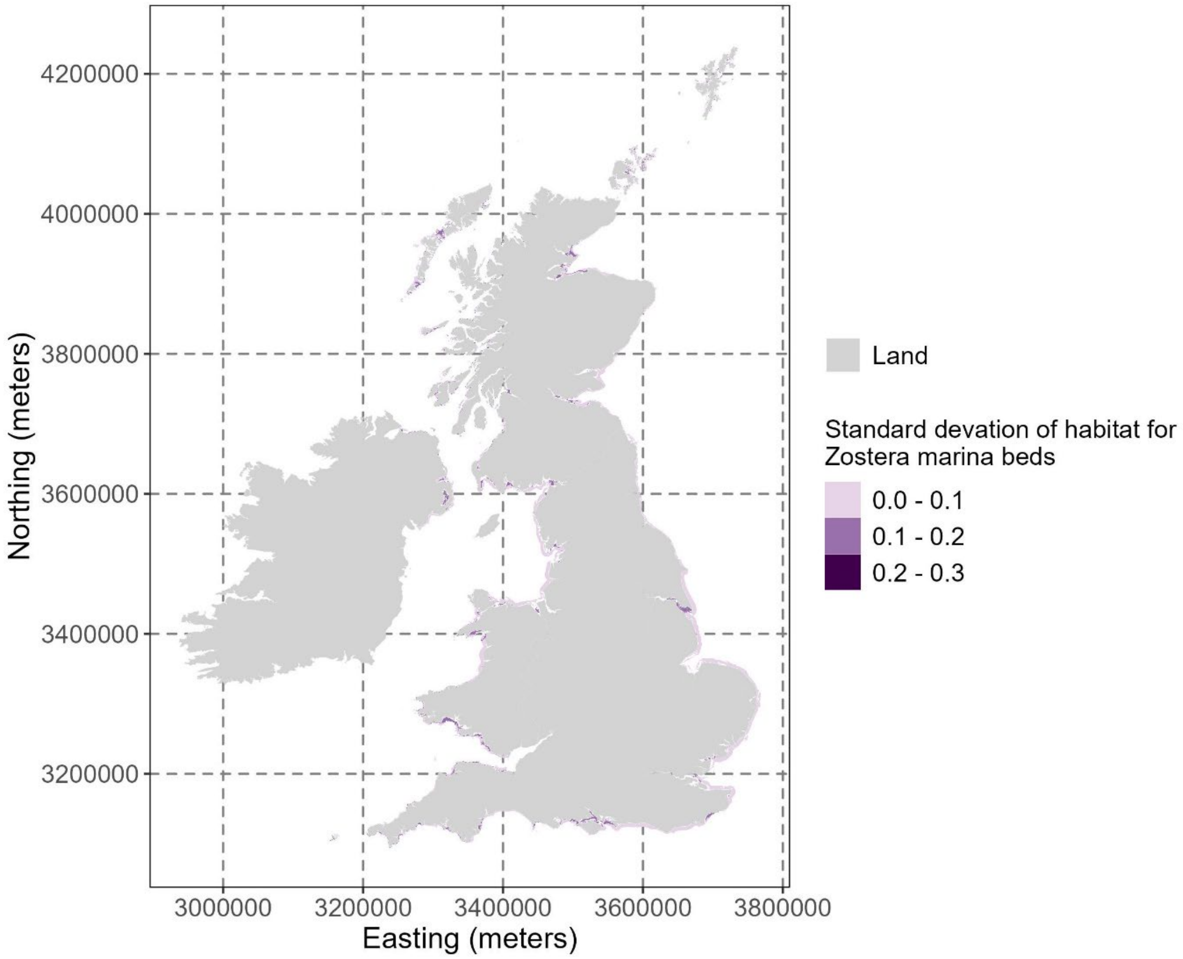

Figure 6: Standard deviation in the predictive values of probability of habitat suitability for *Zostera marina beds* across the UK, within the model extent of 0 - 15 m depth. © JNCC 2024, Map projection: EPSG 3035, Not to be used for navigation.

5. Discussion

5.1. Environmental variable importance

Environmental data on some factors known to influence assessed habitat distribution and persistence were either unavailable or unsuitable to be incorporated into the current model. Future work to assess the availability and applicability of data on additional environmental variables that influence habitat distribution would assist in improving model accuracy.

The importance of environmental variables in predicting areas of suitable habitat for both *Modiolus modiolus* reefs and *Zostera marina* beds (Table 4 and Table 5) indicates the environmental conditions that are most crucial for those habitats to be able to persist.

5.1.1. Modiolus modiolus

Modiolus modiolus are tolerant to a broad range of environmental conditions (Lesser & Kruse 2004). However, in our model the environmental variables that were the most important in predicting areas of suitable habitat for *Modiolus modiolus* reefs were maximum temperature at the seabed, seabed substrate and minimum salinity. Low salinity has been shown to reduce the survival of *Modiolus modiolus* (Gainey 1994; Zhan *et al*. 2018) and whilst dense aggregations have been observed in low salinity environments, these are often juveniles which do not survive to adulthood (Bayne 1976). *Modiolus modiolus* reefs have a lower thermal limit than other aggregating mussel species (Bayne 1976) and are thought to be susceptible to increasing seawater temperatures which could reduce survival, impair reproductive output and impact fitness of larvae (Hiscock *et al*. 2004). The importance of the seabed substrate may be explained by *Modiolus modiolus* requiring a hard substratum for initial attachment, despite being associated with a wide variety of substrates (Anwar *et al*. 1990). There are other environmental predictor layers that could improve the predication of potentially suitable habitat for *Modiolus modiolus*, for example, reefs are known to be impacted by burial events (Hutchison et al. 2016), however there is currently no UK-wide layer available for sedimentation rates.

5.1.2. Zostera marina

Zostera marina is known to be impacted by the availability of light, therefore it seems appropriate that depth to the seabed, impacting the amount of photosynthetically active radiation reaching the seabed, was one of the most important variables in predicting areas of suitable habitat (Erftemeijer & Lewis 2006). Wave fetch was also an important variable because *Zostera marina* beds are unlikely to settle and thrive in areas with higher wave fetch due to not being able to physically remain attached to the sediment. Nutrient limitation, particularly of nitrates and phosphates, is also known to impact the growth of *Zostera marina* (Leoni *et al*. 2007). Considering the dynamic availabilities in concentrations of these nutrients, a UK-wide nutrient dataset would be a valuable addition to the *Zostera marina* HSM.

Importantly, the HSMs presented here predict habitat suitability based on known presence and pseudo-absence, including historical records of where these habitats have occurred previously but may not occur now due to environmental changes or changes in anthropogenic pressures. While the modelled environmental conditions may be suitable for these two biogenic habitats to occur, additional variables may affect their actual presence or absence.

5.2. Biological and environmental data considerations

5.2.1. Data availability

The availability of habitat occurrence response data for *Modiolus modiolus* reefs and *Zostera marina* beds was limited. For instance, only 1,471 presence records for *Modiolus modiolus* reefs and 4,730 presence records for *Zostera marina* beds were initially collated, which were reduced to 473 and 886 respectively after the selection process to determine presence / pseudo-absence per grid cell (Table 3).

Additionally, the paucity of true absence of habitat records meant that pseudo-absence data had to be used in place of absence data. The use of pseudo-absence data is common in HSMs, and the best available habitat occurrence datasets for the UK were used for this occurrence type. However, the use of true absence data would mitigate the risk of classifying habitats as pseudo-absence that have understudied relationships with those modelled in this report and would also improve confidence in the models.

Future work, firstly, could look at increasing survey efforts for the modelled habitats across the UK, including both presence and true absence, which could be incorporated into the HSMs to provide more evidence of habitat occurrence and environmental range. Secondly, when incorporating habitat occurrence response variables into future HSMs, exploration of alternative methods to balance the number of presence and pseudo-absence records to ensure that the model better predicts where the habitat is present rather than where it is absent should be considered.

The HSMs presented in this report do not account for the impacts of climate change on predicted habitat suitability. Although temperature at the seafloor is included as an environmental predictor variable in both HSMs, future HSMs could incorporate environmental variables directly linked to climate change to improve their predictive power. *Zostera marina*, for example, is sensitive to elevated temperatures (Shields *et al.* 2018; Scalpone *et al.* 2020; Sawall *et al.* 2021), sedimentation (Mills & Fonseca 2003), light stress (Wong *et al.* 2021), and storm events (d'Avack *et al.* 2022), all of which are likely to increase in frequency due to climate change. The inclusion of environmental predictor variable layers related to climate change pressures may ensure that impacts that have already occurred as a result of changing climate are incorporated into the prediction of suitable habitat for both *Modiolus modiolus* reefs and *Zostera marina* beds, improving the predictive power of the models.

Additionally, the current extent and distribution of presence and pseudo-absence points that feed into the HSM as predictor variables may also not be representative of preferred environmental conditions. Anthropogenic activities and resultant pressures and responses may already have impacted the range of the habitat for both *Modiolus modiolus* reefs and *Zostera marina* beds and thus the environmental conditions present may already be sub-optimal for their presence.

5.2.2. Temporal resolution

Historical presence and pseudo-absence records were used in the production of HSMs for both *Modiolus modiolus* reefs and *Zostera marina* beds to maximise the available data to feed into the models. Since the predictor variables (environmental data) were sourced from the most recent and up to date data sources, the environmental data assigned to historical presence or pseudo-absence records may not be representative of the environmental conditions at the time of sampling. This is of particular importance when considering the effects of climate change and anthropogenic activities. This may affect the range of environmental conditions ultimately used for predicting areas of suitable habitat for *Modiolus*

modiolus reefs and *Zostera marina* beds, resulting in a shift in distribution of most suitable predicted habitat. Further iterations of the HSMs could consider only using temporally aligned biological and environmental variables, although this would drastically reduce the available biological records unless more extensive surveying efforts were undertaken.

5.2.3. Spatial resolution

The production of HSMs for predicted suitable habitat for *Modiolus modiolus* reefs and *Zostera marina* beds used biological and environmental variables at different spatial resolutions. Biological data was available as point records, whereas environmental data layers were resampled to a 300 m^2 grid from their original resolution (Table 1). As a result, the environmental conditions assigned to presence and pseudo-absence records may not be representative of the conditions where the sample was taken. In future, finer resolution environmental layers may be sourced to reduce the disparity in spatial resolution, however the inclusion of such layers may be limited by computer processing power. The use of a higher resolution environmental raster for a specific case study area with intricate coastlines such as the Hebrides or Orkney, if available, may provide useful information on the effect of this type of variability on the HSM output.

Additionally, detail on the fine-scale resolution, and therefore distribution, of presence and pseudo-absence records was reduced when the location of points was aggregated up to the 300 m^2 grid cell. Presence and pseudo-absence data were further simplified by calculating the proportion of presence to weighted pseudo-absence records per grid cell, thereby categorising the whole cell by one occurrence type. In future, finer resolution grid cells obtained from the environmental variables may mitigate the reduction in resolution of the biological sample points, though this may be restricted by computer processing power.

5.2.4. Connectivity dynamics

The current HSMs do not capture the dynamics of sources and sinks, in terms of patterns of larval dispersal and genetic connectivity for *Modiolus modiolus* and propagule dispersal for *Zostera marina*. Although the HSMs predict areas of potentially suitable habitat in terms of environmental conditions, a population may not be able to persist in that location if connectivity and self-recruitment are limited.

Current evidence suggests medium to high genetic connectivity between modiolus beds in the UK, with the exception of east coast modiolus beds (Mackenzie *et al.* 2018, 2022). This genetic connectivity provides some buffer to extent loss; however, it may reduce adaptive capacity due to low genetic variation (Mackenzie *et al.* 2022). To provide the highest resilience potential, both identifying and conserving source and sink populations is key. Certainly, population dynamics need to be examined on a location-by-location basis.

6. Improving the models

6.1. Incorporation of ground-truth habitat maps

The data paucity in relation to the distribution and extent of *Modiolus modiolus* reefs and *Zostera marina* beds necessitates the use of HSMs to fill these data gaps. To refine the models, where available, the observed distributions (mapping of realised habitat) could be incorporated to improve the accuracy and confidence in the extent and distribution of both habitats in UK waters. The creation of this combined habitat map could be achieved in a similar way to the EUNIS Combined Map (Matear *et al.* 2019), which utilises habitat maps derived from direct survey efforts, supplemented by modelled broad-scale habitat data in locations where survey derived habitat information is unavailable. In the UK, some designated sites, such as the Small Isles Nature Conservation Marine Protected Area, Strangford Lough Special Area of Conservation (SAC), and Isles of Scilly Complex SAC are designated for the protection of *Modiolus modiolus* reefs and/or *Zostera marina* beds, and further survey work within sites designated for the protection of these features would help to supplement this effort.

6.2. Spatial blocking

Due to the targeted nature of surveying the marine environment, habitat occurrence records were often in proximity to each other, potentially increasing the risk of autocorrelation within the model. The model may therefore perform artificially better in cells near sample data, but poorer in cells further away. The implementation of spatial blocking to address autocorrelation may improve the predictive accuracy of the HSM and is considered best practice when partitioning data because it improves the spatial independence of the training and test data (Valavi *et al.* 2019). The use of spatial blocking may help to improve the predictive performance of the HSMs in this report leading to more accurate predictions of extent and distribution.

7. Conclusions

This report details the methodology used to refine the HSMs for two biogenic benthic habitats, *Modiolus modiolus* reefs and *Zostera marina* beds, using current environmental predictor and biological response variable data. These HSMs are available in raster and vector format and aim to fill acknowledged data gaps in the estimation of the distribution and extent of these modelled habitats.

Areas of high suitability of habitat for *Modiolus modiolus* reefs were identified from the models around the Western Channel, Celtic Sea, the Irish Sea, Strangford Lough, the waters around Northern Ireland, the Firth of Clyde, the Small Isles and Orkney. The probability of suitable habitat for the presence of *Zostera marina* was highest in the Llŷn Peninsula, Portsmouth, the Isles of Scilly and Islay.

Future iterations of the HSMs could be refined by incorporating other environmental variables known to impact the settlement, survival and persistence of these habitats, such as the impacts of climate change, as well as incorporating ground-truthed habitat maps, and other modelling improvements.

These HSMs can be used to provide an estimation of current and future potentially suitable habitat for Marine Spatial Planning, assessment of suitable sites for restoration, management of anthropogenic activities and designation of protected areas.

References

Anwar, N.A., Richardson, C.A. & Seed, R. 1990. Age determination, growth rate and population structure of the horse mussel *Modiolus modiolus*. *Journal of the Marine Biological Association of the United Kingdom* 70:441–57.

Assis, J., Tyberghein, L., Bosh, S., Verbruggen, H., Serrão, E.A. & De Clerck, O. (2017). Bio-ORACLE v2.0: Extending marine data layers for bioclimatic modelling. *Global Ecology and Biogeography*. DOI: 10.1111/geb.12693

d'Avack, E.A.S., Tyler-Walters, H., Wilding, C.M. & Garrard, S.L. 2022. *Zostera* (*Zostera*) *marina* beds on lower shore or infralittoral clean or muddy sand. In Tyler-Walters H. and Hiscock K. (eds) Marine Life Information Network: Biology and Sensitivity Key Information Reviews, [on-line]. Plymouth: Marine Biological Association of the United Kingdom. [cited 18-07-2023]. Available from: https://www.marlin.ac.uk/habitat/detail/257

Bayne, B.L. (Ed.). (1976). Marine mussels: their ecology and physiology.

Bertelli, C.M., Stokes, H.J., Bull, J.C. & Unsworth R.K.F. 2022. The use of habitat suitability modelling for seagrass: A review. Front. Mar. Sci. 9:997831. https://doi.org/10.3389/fmars.2022.997831

Burrows, M. 2020. Wave fetch GIS layers for the UK and Ireland at 200m scale. figshare. Dataset. https://doi.org/10.6084/m9.figshare.12029682.v1

Calabrese, J.M., Certain, G., Kraan, C. & Dormann, C.F. 2014. Stacking species distribution models and adjusting bias by linking them to macroecological models. *Global Ecology and Biogeography*, 23, 99–112.

Castle, L., Pinder, J., Lillis, H. & Manca, E. 2022. Using an ensemble modelling approach to predict suitable habitat for *Zostera marina* beds, *Modiolus modiolus* beds and *Sabellaria spinulosa* reefs in UK waters. *JNCC Report 718*, JNCC, Peterborough, ISSN 0963-8091. https://hub.jncc.gov.uk/assets/c0b64152-83d5-4164-9a03-794744c9cb82

Charbonnel, A., Lambert, P., Lassalle, G., Quinton, E., Guisan, A., Mas, L., Paquignon, G., Lecomte, M. & Acolas, M., 2023. Developing species distribution models for critically endangered species using participatory data: The European sturgeon marine habitat suitability. *Estuarine, Coastal and Shelf Science*, 280.

Chefaoui, R.M., Assis, J., Duarte, C.M. & Serrão, E.A. 2016. Large-Scale Prediction of Seagrass Distribution Integrating Landscape Metrics and Environmental Factors: The Case of *Cymodocea nodosa* (Mediterranean–Atlantic). *Estuaries and Coasts*, 39, 123–137.

Cook, R., Fariñas-Franco, J.M., Gell, F.R., Holt, R.H.F., Holt, T., Lindenbaum, C., Porter, J.S., Seed, R., Skates, L.R., Stringell, T.B. & Sanderson, W.G. 2013. The Substantial First Impact of Bottom Fishing on Rare Biodiversity Hotspots: A Dilemma for Evidence-Based Conservation. *PLoS ONE* 8(8): e69904. https://doi.org/10.1371/journal.pone.0069904

De la Torriente Diez, A., González-Irusta, J.M., Serrano, A., Aguilar, R., Sánchez, F., Blanco, M. & Punzón, A. 2022. Spatial assessment of benthic habitats vulnerability to bottom fishing in a Mediterranean seamount, *Marine Policy*, Volume 135. https://doi.org/10.1016/j.marpol.2021.104850.

Department for Environment Food and Rural Affairs. (2020) Defra's Marine Digital Elevation Model (DEM) - 1 arc second.

Duarte, C.M. & Chiscano, C.L. 1999. Seagrass biomass and production: a reassessment. *Aquat Bot*. 65:159–174.

Duncan, G., Pinder, J., Lillis, H. & Allen, H. (2022). Method for creating version 8 of the UK Composite Map of Annex I Reefs. Joint Nature Conservation Committee, Peterborough.

Elliott, M., Burdon, D., Atkins, J.P., Borja, A., Cormier, R., De Jonge, V.N. & Turner, R.K. 2017. “And DPSIR begat DAPSI(W)R(M)!” – A unifying framework for marine environmental management. *Marine Pollution Bulletin* 118: 27–40.

EMODnet. 2015. Kinetic energy at the seabed due to currents in the Atlantic. Available from: https://emodnet.ec.europa.eu/geoviewer/

EMODnet. 2018. Light (PAR) at the seabed - Europe-wide. Available from: https://emodnet.ec.europa.eu/geoviewer/

EMODnet. 2019. Kinetic energy at the seabed due to waves - Celtic, North Sea (mean of annual 90th percentile). Available from: https://emodnet.ec.europa.eu/geoviewer/

EMODnet. 2022. EMODnet Digital Bathymetry (DTM 2022). Available from: https://emodnet.ec.europa.eu/geoviewer/

Erftemeijer, P.L. & Lewis III, R.R.R. 2006. Environmental impacts of dredging on seagrasses: a review. *Marine Pollution Bulletin*, *52*(12), pp.1553-1572. https://doi.org/10.1016/j.marpolbul.2006.09.006

ESRI. 2012. ArcGIS Release 10.1. Redlands, CA.

Fletcher, S., Saunders, J., Herbert, R., Roberts, C. & Dawson, K. 2012. Description of the ecosystem services provided by broad-scale habitats and features of conservation importance that are likely to be protected by Marine Protected Areas in the Marine Conservation Zone Project area. Natural England Commissioned Reports, Number 088.

Gainey, L.F. 1994. Volume regulation in three species of marine mussels. *Journal of Experimental Marine Biology and Ecology* 181:201–11. 10.1016/0022-0981(94)90128-7

Gormley, K.S., Porter, J.S., Bell, M.C., Hull, A.D. & Sanderson, W.G. 2013. Predictive habitat modelling as a tool to assess the change in distribution and extent of an OSPAR priority habitat under an increased ocean temperature scenario: consequences for marine protected area networks and management. *PLoS ONE*, 8(7), e68263.

Gormley, K., Mackenzie, C., Robins, P., Coscia, I., Cassidy, A., James, J., Hull, A., Piertney, S., Sanderson, W. & Porter, J. 2015. Connectivity and Dispersal Patterns of Protected Biogenic Reefs: Implications for the Conservation of *Modiolus modiolus* (L.) in the Irish Sea. *PLoS ONE* 10(12): e0143337. doi:10.1371/journal.pone.0143337.

Greathead, C., Boschen-Rose, R.E., Langton, R., Clarke, J., Wright, P.J. & Boulcott, P. 2023. Priority marine feature surveys within the Small Isles MPA and surrounding waters. Main Report. *Scottish Marine and Freshwater Science* Vol 14 No 1, 52p.

Guiry, M.D. & Guiry, G.M. 2023. AlgaeBase. World-wide electronic publication, National University of Ireland, Galway (taxonomic information republished from AlgaeBase with permission of M.D. Guiry). *Zostera angustifolia* (Hornemann) Reichenbach, 1845. Accessed through: World Register of Marine Species at: https://www.marinespecies.org/aphia.php?p=taxdetails&id=182740

Hanley, J.A. & McNeil, B.J. 1982. The meaning and use of the area under a receiver operating characteristic (ROC) curve. *Radiology*, 143(1), pp.29-36.

Heck, K., Nadeau, D. & Thomas, R. 1997. The Nursery Role of Seagrass Beds. Gulf of Mexico Science 15 (1). Retrieved from https://aquila.usm.edu/goms/vol15/iss1/8

Hijmans, R. (2023). _raster: Geographic Data Analysis and Modeling. R package version 3.6-20, https://CRAN.R-project.org/package=raster

Hiscock, K., Southward, A., Tittley, I. & Hawkins, S. 2004. Effects of changing temperature on benthic marine life in Britain and Ireland. *Aquatic Conservation: Marine and Freshwater Ecosystems* 14:333–62. 10.1002/aqc.628

Holt, T.J., Rees, E.I., Hawkins, S.J. & Seed, R. 1998. Biogenic reefs (Volume IX). An overview of dynamic and sensitivity characteristics for conservation management of marine SACs. Scottish Association for Marine Science (UK Marine SACs Project), 174 pp.

Horn, B.K.P. 1981. Hill shading and the reflectance map. Proceedings of the IEEE 69(1), 14– 47.

Hutchison, Z.L., Hendrick, V.J., Burrows, M.T., Wilson, B. & Last, K.S. 2016. Buried alive: the behavioural response of the mussels, *Modiolus modiolus* and *Mytilus edulis* to sudden burial by sediment. *PloS ONE*, 11(3).

JNCC. 2022. Data derived from UK Marine Recorder (All) snapshot (v20220804), available from https://jncc.gov.uk/our-work/marine-recorder/ - downloaded on 24/04/2023. Data licenses, access and use limitations as described per survey as contained within the database.

Jones, B. & Unsworth, R. 2016. The perilous state of seagrass in the British Isles. *R. Soc. Open sci.* 3: 150596. http://dx.doi.org/10.1098/rsos.150596

JNCC Species Distribution Modelling (SDM) Framework (an open-source R package; JNCC, 2023; https://github.com/jncc/sdms)

Kendrick, G.A., Orth, R.J., Statton, J., Hovey, R., Montoya, L.R., Lowe, R.J., Krauss, S.L. & Sinclair, E.A. (2016). Demographic and genetic connectivity: the role and consequences of reproduction, dispersal and recruitment in seagrasses. *Biological Reviews*. 92, 2, 921-938.

Kent, F.E., Gray, M.J., Last, K.S. & Sanderson, W.G. 2016. Horse mussel reef ecosystem services: evidence for a whelk nursery habitat supporting a shellfishery. *Int. J. Biodivers. Sci. Ecosyst. Serv. Manag*. 12, 172–180.

Kent, F.E., Last, K.S., Harries, D.B. & Sanderson, W.G. 2017. In situ biodeposition measurements on a *Modiolus modiolus* (horse mussel) reef provide insights into ecosystem services. *Estuar. Coast. Shelf*. 84, 151–157.

Lecours, V., Devillers, R., Simms, A.E., Lucieer, V.L. & Brown, C.J. 2017. Towards a framework for terrain attribute selection in environmental studies. *Environmental modelling & software*, 89, pp.19-30.

Leoni, V., Vela, A., Pasqualini, V., Pergent-Martini, C. & Pergent, G. 2007. Effects of experimental reduction of light and nutrient enrichments (N and P) on seagrasses: a review. *Aquatic Conservation: Marine and Freshwater Ecosystem*, 18, 2, 202-220.

Lesser, M.P. & Kruse, V.A. 2004. Seasonal temperature compensation in the horse mussel *Modiolus modiolus*: metabolic enzymes, oxidative stress and het shock proteins. *Comp. Biochem. Physiol.* 137A: 495-504.

Mackenzie, C.L., Kent, F.E., Baxter, J.M., Gormley, K.S., Cassidy, A.J., Sanderson, W.G. & Porter, J.S. (2022). Genetic connectivity and diversity of a protected, habitat-forming species: evidence demonstrating the need for wider environmental protection and integration of the marine protected area network. *Frontiers in Marine Science*, *9*, 772259.

Magorrian, B.H. & Service, M. 1998. Analysis of underwater visual data to identify the impact of physical disturbance on horse mussel (*Modiolus modiolus*) beds. *Marine Pollution Bulletin*, 36: 354-359.

Matear, L., Pinder, J. & Lillis, H. 2019. Method for updating the UK full-coverage EUNIS level 3 seabed habitat map integrating fine- and broad-scale maps. https://hub.jncc.gov.uk/assets/538e8eaa-83cc-40cf-bc5a-ef599a716b79

McDevitt-Irwin, J., Iacarella, J. & Baum, J. 2016. Reassessing the nursery role of seagrass habitats from temperate to tropical regions: A meta-analysis. *Marine Ecology Progress Series*. 557. 10.3354/meps11848.

Mills, K.E. & Fonseca, M.S. 2003. Mortality and productivity of eelgrass Zostera marina under conditions of experimental burial with two sediment types. *Marine Ecology Progress Series*, 255, pp.127-134.

Natural England. 2021. Marine Habitats and Species Open Data (England), version June 2021. Available at: https://naturalengland-defra.opendata.arcgis.com/maps/25867d305dc545509e4d87420e296e12/about (Accessed 09/12/2021).

Natural England & JNCC. (2010). The Marine Conservation Zone Project: Ecological Network Guidance. Sheffield and Peterborough, UK. Available here: https://data.jncc.gov.uk/data/94f961af-0bfc-4787-92d7-0c3bcf0fd083/MCZ-Ecological-Network-Guidance-2010.pdf

Nordlund, L.M., Koch, E.W., Barbier, E.B. & Creed, J.C. 2016. Seagrass ecosystem services and their variability across genera and geographical regions. *PLoS ONE*, 11, e0163091.

OSPAR Commission. 2008. Case Reports for the OSPAR List of Threatened and/or Declining Species and Habitats, 239-242, https://www.ospar.org/site/assets/files/44271/horse_mussel_beds.pdf

OSPAR. 2009. Background document for *Zostera* beds, Seagrass beds. Biodiversity Series. OSPAR Commission. http://www.ospar.org/documents?d=7190

OSPAR. 2022. OSPAR Threatened and/or declining habitats database. Accessed 18/05/2023. Available from: https://emodnet.ec.europa.eu/geoviewer/

Pebesma, E. 2018. Simple Features for R: Standardized Support for Spatial Vector Data. *The R Journal* 10 (1), 439-446, https://doi.org/10.32614/RJ-2018-009

Pebesma, E. & Bivand, R. 2023. Spatial Data Science: With Applications in R (1st ed.). Chapman and Hall/CRC. https://doi.org/10.1201/9780429459016

R Core Team. 2019. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL https://www.R-project.org/

RStudio Team. 2022. RStudio: Integrated Development Environment for R. RStudio, PBC, Boston, MA URL: http://www.rstudio.com/

Sanderson, W., Holt, R.H.F., Kay, L., Ramsay, K., Perrins, J., McMath, A.J. & Rees, E.I.S. 2008. Small-scale variation within a *Modiolus modiolus* (Mollusca: Bivalvia) reef in the Irish Sea. II. Epifauna recorded by divers and cameras', *Journal of the Marine Biological Association of the United Kingdom*, vol. 88, no. 1, pp. 143-149. https://doi.org/10.1017/S0025315408000040

Sawall, Y., Ito, M. & Pansch, C. 2021. Chronically elevated sea surface temperatures revealed high susceptibility of the eelgrass *Zostera marina* to winter and spring warming. *Limnol Oceanogr*, 66: 4112-4124. https://doi.org/10.1002/lno.11947

Scalpone, C.R., Jarvis, J.C., Vasslides, J.M., Testa, J.M. & Ganju, N.K. 2020. Simulated estuary-wide response of seagrass (*Zostera marina*) to future scenarios of temperature and sea level. *Frontiers in Marine Science*, 7, p.539946.

Shields, E.C., Moore, K.A. & Parrish D.B. 2018. Adaptations by *Zostera marina* Dominated Seagrass Meadows. *Response to Water Quality and Climate Forcing Diversity* 10, no. 4: 125. https://doi.org/10.3390/d10040125

Strong, J., Vina-Herbon, C., Doria, L., Carter, A., Edwards, D., Lillis, H., Parry, M., Robson, L., Singleton, G., Young, M., Mackie, T., Boulcott, P. & Robison, K. 2018. Potential physical loss of predicted seafloor habitats. UK Marine Online Assessment Tool, available at: https://moat.cefas.co.uk/biodiversity-food-webs-and-marine-protected-areas/benthic-habitats/physical-loss/

Tyler-Walters, H. 2007. *Modiolus modiolus* Horse mussel. In Tyler-Walters H. Marine Life Information Network: Biology and Sensitivity Key Information Reviews, [on-line]. Plymouth: Marine Biological Association of the United Kingdom. [cited 24-08-2023]. Available from: https://www.marlin.ac.uk/species/detail/1532

Valavi, R., Elith, J., Lahoz-Monfort, J.J. & Guillera-Arroita, G. 2019. Block CV: An r package for generating spatially or environmentally separated folds for k-fold cross-validation of species distribution models. *Methods in Ecology and Evolution*, 10(2), 225–232.

Warton, D.I. (2022). Eco-stats: Data analysis in ecology." *Cham, Switzerland: Springer Nature Switzerland AG*

Wong, M.C., Vercaemer, B.M. & Griffiths, G. 2021. Response and Recovery of Eelgrass (*Zostera marina*) to Chronic and Episodic Light Disturbance. *Estuaries and Coasts* 44, 312–324 (2021). https://doi.org/10.1007/s12237-020-00803-3

Zhan, Y., Yang, M., Cui, D., Li, J., Sun, J., Ning, J., Hao, Z., Zhang, W. & Chang Y. 2018. Combined effects of temperature and salinity on growth, survival, gill morphology, and antioxidant capabilities in the horse mussel *Modiolus modiolus*. *Invertebrate Survival Journal* 15, 83-93.

Zieman, J.C. & Wetzel, R.G. 1990. Productivity in seagrasses: Methods and rates. In Phillips, R.C. & McRoy, C.P. (editors). Handbook of seagrass biology: An ecosystem perspective. New York: Garland STPM Press; pp 87–116.