JNCC Report
No. 718

Using an ensemble modelling approach to predict suitable habitat for *Zostera marina* beds, *Modiolus modiolus* beds and *Sabellaria spinulosa* reefs in UK waters

Castle, L., Pinder, J., Lillis, H. & Manca, E.

August 2022

© JNCC, Peterborough 2022

ISSN 0963-8901

JNCC's report series serves as a record of the work undertaken or commissioned by JNCC. The series also helps us to share, and promote the use of, our work and to develop future collaborations.

For further information please contact:
Joint Nature Conservation Committee
Monkstone House
City Road
Peterborough PE1 1JY
https://jncc.gov.uk/
Communications@jncc.gov.uk

This report should be cited as:
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 No. 718,* JNCC, Peterborough, ISSN 0963-8091.
https://hub.jncc.gov.uk/assets/c0b64152-83d5-4164-9a03-794744c9cb82

Acknowledgements:
The authors are grateful to Clara Alvarez Alonso (DAERA), Anna Downie (Cefas), Paul Mayo (Agri Food Biosciences Institute), Karen Robinson (Natural Resources Wales) and Peter Walker (Natural England) for their very valuable comments to this work.

We would like to acknowledge our JNCC colleagues Emma Wright, Becky Trippier and Alun Jones for their technical support with the SDM modelling framework.

Evidence Quality Assurance:
This report is compliant with JNCC's Evidence Quality Assurance Policy
https://jncc.gov.uk/about-jncc/corporate-information/evidence-quality-assurance/

The views and recommendations presented in this report do not necessarily reflect the views and policies of JNCC

Summary

This report describes methods used to pilot the use of JNCC Species Distribution Modelling (SDM) framework to model areas suitable for the establishment of subtidal seagrass beds, *Modiolus modiolus* beds and *Sabellaria spinulosa* reefs in UK waters from environmental variables and records of presence of the habitats. The main driver was this work was the development of two indicators of Good Environmental Status under the UK Marine Strategy namely the "Potential Physical Loss of Habitats' and 'Condition of Biogenic Reefs' indicators. In this report we describe the approach, present, and discuss results and model limitations.

Contents

Summary i
1 Background 1
1.1 Aim 1
1.2 Ecological Review 1
2 Data Preparation 3
2.1 Predictor Variables 3
2.1.1 Sources of Environmental Data 3
2.1.2 Model Extent 3
2.2 Habitat Occurrence Data Selection 12
2.3 Reducing Spatial Autocorrelation 14
2.4 Training and Test Data 15
3 Modelling 16
3.1.1 JNCC SDM Framework 16
3.2 Model Selection 16
3.3 Summarising the Result 16
4 Results 18
5 Discussion 25
5.1 Variable importance 25
5.2 Model Limitations 26
6 Improving the Models 31
7 References 32

1 Background

JNCC is leading on the development of several indicators that will help to assess progress towards achieving Good Environmental Status under the UK Marine Strategy. Some of these indicators require information on the distribution of seabed habitats; however, lack of full-coverage survey data means there are gaps where the habitats have not been observed. Habitat modelling provides a way to predict the suitability of an area of seabed for a habitat and therefore offers to improve our understanding of the distribution of certain habitats.

Two of the indicators in development are referred to as ‘Potential Physical Loss of Habitats’ and ‘Condition of Biogenic Reefs’. Three seabed habitats chosen to test the methods for assessing these indicators are: *Modiolus modiolus* beds (both indicators), *Sabellaria spinulosa* reefs (biogenic reef indicator only) and subtidal *Zostera marina* beds (Potential Physical Loss only).

In 2016 JNCC contracted out work to develop the physical loss indicator method to the University of Hull (Strong 2016), which included modelling the distribution of *Modiolus modiolus* beds and *Zostera marina* beds. At a similar time, the Ecosystem Analysis team at JNCC developed an in-house ‘species distribution modelling (SDM) framework’ (JNCC 2019), for use on terrestrial habitats.

1.1 Aim

The aim of this project is to use the JNCC SDM framework to generate a repeatable, open and consistent method for predicting the distribution of seabed habitats for use in the aforementioned projects. The focus of the initial investigation is on subtidal *Zostera marina* beds, *Modiolus modiolus* beds and *Sabellaria spinulosa* reefs. Users require information on potential natural distribution of the habitats, meaning that data on human-induced pressures are not included as model inputs. Similarly natural pressures (e.g. predation) and biological interactions were not considered in this work.

1.2 Ecological Review

A literature review was conducted to inform the model of the environmental characteristics known to influence the distribution of all habitats, using the following sources:

Zostera marina:

- Strong J.A. (2016)
- The Marine Life Information Network (MarLIN) [see D'Avack *et al*. 2019]
- OSPAR Background document [see Tullrot 2009]
- Brown (2015)
- Bekkby *et al*. (2008)

Modiolus modiolus:

- Strong J.A. (2016)
- The Marine Life Information Network (MarLIN) [see Tyler-Walters 2007]
- OSPAR Background document (Rees 2009)
- Hutchison *et al*. (2016)
- Gormley *et al*. (2013)
- Holt *et al*. (1998)
- Witman (1984)

- Ragnarsson & Burgos (2012)
- Strong *et al*. (2016)
- Lindenbaum *et al*. (2008)
- Sanderson *et al*. (2008)
- Rees *et al*. (2008)
- Kent *et al*. (2017)
- Elsäßer *et al*. (2013)

Sabellaria spinulosa:

- The Marine Life Information Network (MarLIN) [see Jackson & Hiscock 2008]
- Jenkins *et al*. (2018)
- Pearce (2017)
- Lisco *et al*. (2017)
- Gibb *et al*. (2014)

The reviews provided the basis by which environmental data could then be sourced.

2 Data Preparation

2.1 Predictor Variables

2.1.1 Sources of Environmental Data

A suite of environmental variables were selected as model inputs, based on a review of literature on their ability to influence the growth and survivability of each habitat in question (Table 1). Each individual dataset was then projected to ETRS LAEA 1989 and resampled to a common raster grid with a resolution of 300 m before being fed into the model.

2.1.2 Model Extent

Restrictions were applied to the extents of the environmental datasets to ensure data only existed within the depth limits of each habitat.

For *Zostera marina* beds, the model extent was restricted to a depth range between 0 m and 15 m as evidence suggests beds will not occur in deeper waters. Due to limitations in the reliability of K_d*(PAR)* data in shallow environments with high sediment loading, a further restriction was applied to remove the Severn estuary from the *Zostera marina* bed model (Figure 1). The *Modiolus modiolus* beds model extent was restricted to a depth range between 0 m and 242 m based on the deepest observation of *Modiolus modiolus beds* (Figure 2)***.*** The model extent of *Sabellaria spinulosa* reef was restricted between 0 m and 80 m (Figure 3) based on the literature review.

Table 1. A list of predictor variables used as inputs for the predictive modelling.

Predictor Variable	Source	Units	Original Spatial Resolution	Release Date	Data Collection Year	*Zostera marina*	*Modiolus modiolus*	*Sabellaria spinulosa*
Depth to seabed	A combination of the Defra DEM (Defra 2018) One Second mosaic, in the first instance, and EMODnet Bathymetry (Schmitt *et al. 2019)* where the former was not available	Metres (m)	Defra DEM (2018) – 1 arc second EMODnet Bathymetry (2018) – $\frac{1}{16}$ arc minute	Defra DEM – 2018 EMODnet Bathymetry – 2018	Defra DEM – 1956–2018 EMODnet Bathymetry – 1977–2018	✓	✓	✓
Slope of the seabed	Derived from bathymetry data (described above), using TASSE toolbox in ArcGIS based on recommendations by Lecours *et al*. (2017): slope computed using the Horn (1981) method	Degrees (º)	Same as depth to seabed data	Same as depth to seabed data	Same as depth to seabed data	✓	✓	✓
PAR at the seabed	Photosynthetically available radiation (PAR) at the seabed, *I*, calculated from Depth to seabed, *d* (described above), PAR at the sea surface, I_0, and the diffuse attenuation coefficient of PAR in the water column, $K_d(PAR)$, (from [EMODnet Seabed Habitats]) according to the following equation: $I = I_o e^{-d.Kd(PAR)}$	Moles of light per square metre per day (mol·phot·$m^{-2}d^{-1}$)	Surface PAR – 250m K_dPAR – 250 m Depth – same as above	Surface PAR – 2018 K_dPAR – 2018 Depth – same as above	Surface PAR – 2005-2009 K_dPAR – 2005–2009 Depth – same as above	✓	×	×

Predictor Variable	Source	Units	Original Spatial Resolution	Release Date	Data Collection Year	*Zostera marina*	*Modiolus modiolus*	*Sabellaria spinulosa*
Light attenuation coefficient of photo-synthetic active radiation (K_d(PAR))	Average diffuse light attenuation coefficient of photosynthetic active radiation (Kd(PAR)) between 2005-2009, values measured in metres^{-1}. Variable was used a proxy measure of turbidity. Created by the EMODnet Seabed Habitats consortium using data from the European Space Agency MERIS instrument, used in the creation of EUSeaMap 2019.	Per Metre (m^{-1})	250 m	2018	2005–2009	✗	✗	✓
Kinetic energy at the seabed due to waves	EMODnet Seabed Habitats (mean of annual 90th percentile values over six years)	Newtons per Square Metre (N/m^2)	300 m at the coast and 12.5 km elsewhere	2018	2000–2005	✓	✓	✓

Predictor Variable	Source	Units	Original Spatial Resolution	Release Date	Data Collection Year	*Zostera marina*	*Modiolus modiolus*	*Sabellaria spinulosa*
Kinetic energy at the seabed due to currents	EMODnet Seabed Habitats (mean of annual 90th percentile values over six years)	Newtons per Square Metre (N/m^2)	300m 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	✓	✓	✓
Seabed substrate (categorical)	Derived from a combination of the sediment classes (Folk 5) in JNCC's combined EUNIS level 3 map, EUSeaMap 2019, UKSeaMap 2018 and CEFAS sediment modelling outputs (Stephens & Diesing 2015) where the former was not available.	1 – Mud / sandy mud 2 – Sand / muddy sand 3 – Mixed sediment 4 – Coarse sediment 5 – Rock	JNCC Combined Map – variable, high resolution survey data and low-resolution modelled products CEFAS Sediment Model – 500 m	JNCC Combined Map – 2019 CEFAS Sediment Model – 2015	JNCC Combined Map – 2005–2018 CEFAS Sediment Model – See reference for details	✓	✓	✓

Predictor Variable	Source	Units	Original Spatial Resolution	Release Date	Data Collection Year	*Zostera marina*	*Modiolus modiolus*	*Sabellaria spinulosa*
Mean of annual minima temperature at the seabed (over 30-year period)	Derived from the ICES near-bed temperature 30-year climatology dataset (Berx & Hughes 2009).	Degrees Celsius (°C)	300 m	2008	1973–1999	✓	✗	✗
Mean of annual temperature at the seabed (over 30-year period)	Derived from the ICES near-bed temperature 30-year climatology dataset (Berx & Hughes 2009).	Degrees Celsius (°C)	300 m	2008	1973–1999	✗	✗	✓
Absolute maximum of annual temperatures at the seabed (over 30-year period)	Derived from the ICES near-bed temperature 30-year climatology dataset (Berx & Hughes 2009).	Degrees Celsius (°C)	300 m	2008	1973–1999	✗	✓	✗

Predictor Variable	Source	Units	Original Spatial Resolution	Release Date	Data Collection Year	***Zostera marina***	***Modiolus modiolus***	***Sabellaria spinulosa***
Absolute minimum of seasonal salinity	Derived from a National Oceanography Centre (formerly Proudman Oceanographic Laboratory) dataset, the POLCOMS model hindcast from the Atlantic Margin (Holt *et al*. 2012). Used in the production of UKSeaMap 2006 (Connor *et al*. 2006).	Practical Salinity Unit (PSU)	~1 km	2006	1964–2004	✓	✓	✓

Figure 1. Extent of the Zostera marina beds model restricted to a bathymetry 0 m to 15 m depth and excluding the Severn estuary.

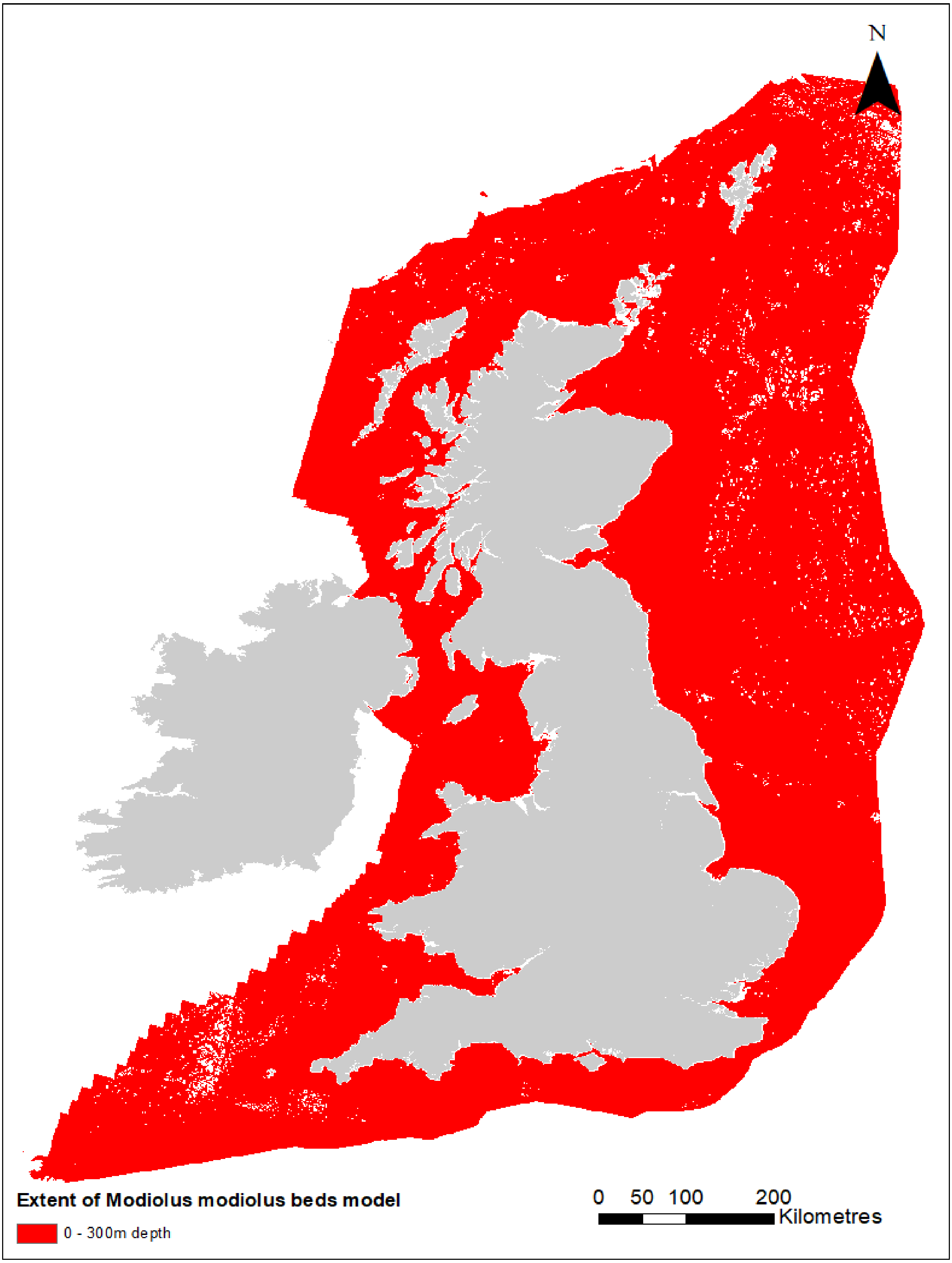

Figure 2. Extent of the Modiolus modiolus beds model restricted to a depth of 0–300 m.

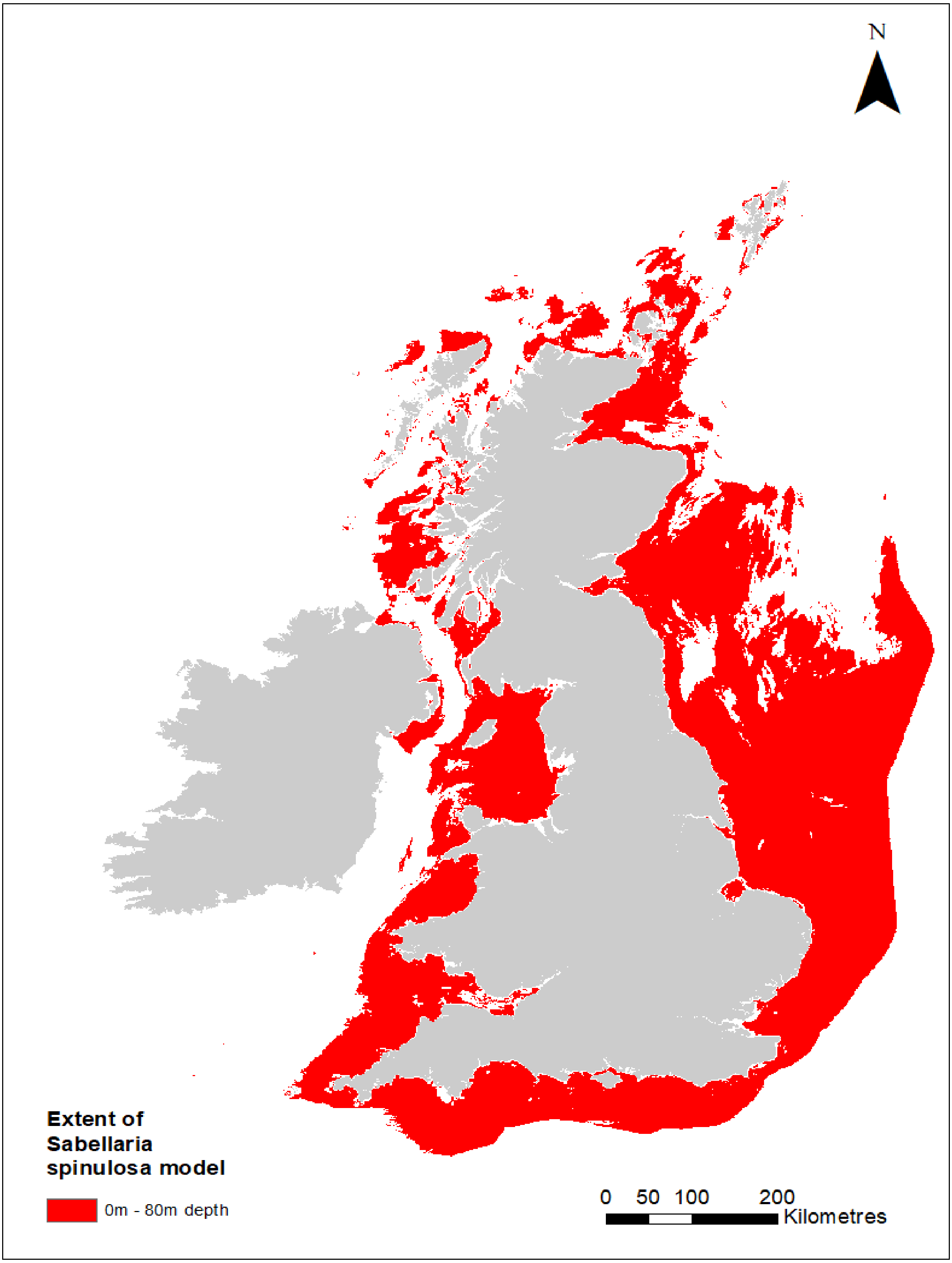

Figure 3. Extent of the Sabellaria spinulosa reefs model restricted to a depth of 0–80 m.

2.2 Habitat Occurrence Data Selection

Habitat suitability models require two types of occurrence data (also known as response data): presence data and absence data. As true absences are particularly scarce in survey data, presence of other habitats was used as a proxy for absences instead; this is referred to as pseudo-absence data.

The chosen sources of occurrence data for the models were the: OSPAR threatened and/or declining habitats database, Natural England Evidence Base database, Marine Recorder database and Annex I Reef database. To ensure the highest confidence in observations, a specific selection method was chosen for each database, the details of which are in Table 2.

Although the distribution of some habitats can vary on a temporal scale, having an additional selection criterion based on observation date would have significantly reduced the number of presence points available to train the model. As such, every observation possible was included in the response dataset.

Although *Zostera marina* can occur in the intertidal zone, the model study areas only include subtidal areas as required for the Potential Physical Loss indicator development.

Table 2. Summary of datasets and selection criteria used for the presence and pseudo-absence response variables.

Source	**Occurrence Type**	***Zostera marina* beds**	***Modiolus modiolus* beds**	***Sabellaria spinulosa* reefs**
OSPAR Threatened and/or declining habitats database 2018	Presence	HabSubType = *Zostera marina* beds HabStatus = Present Certainty = Certain	HabType = *Modiolus modiolus* horse mussel bed HabStatus = Present Certainty = Certain	HabType = *Sabellaria spinulosa* reefs HabStatus = Present Certainty = Certain
OSPAR Threatened and/or declining habitats database 2018	Pseudo-absence	HabType = Maerl beds, *Modiolus modiolus* horse mussel beds, *Sabellaria spinulosa* reefs and sea-pen and burrowing megafauna communities HabStatus = Present Certainty = Certain	HabType = Coral gardens, deep-sea sponge aggregations, Lophelia pertusa reefs, maerl beds, *Sabellaria spinulosa* reefs. sea-pen and burrowing megafauna communities and *Zostera* beds HabStatus = Present Certainty = Certain	HabType = *Modiolus modiolus* horse mussel beds and *Zostera* beds HabStatus = Present Certainty = Certain
Natural England Evidence Base	Presence	×	HAB_TYPE = A5.621, A5.622, A5.623 and A5.624 MCZ_Survey = 2 and 3 MCZ_Source_ID_MR not like “MR” & “JNCC” (filters out Marine Recorder points)	MCZ_Hoci_name = Ross worm (*Sabellaria spinulosa*) reefs MCZ_Survey = 2 and 3 MCZ_Source_ID_MR not like “MR” & “JNCC” (filters out Marine Recorder points)

Source	Occurrence Type	***Zostera marina* beds**	***Modiolus modiolus* beds**	***Sabellaria spinulosa* reefs**
Natural England Evidence Base	Pseudo-absence	×	HAB_TYPE != A5.621, A5.622, A5.623 and A5.624 MCZ_Survey_quality = 2 and 3 MCZ_Source_ID_MR not like "MR" & "JNCC" (filters out Marine Recorder points)	MCZ_Hoci_name != Ross worm (*Sabellaria spinulosa*) reefs MCZ_Survey = 2 and 3 MCZ_Source_ID_MR not like "MR" & "JNCC" (filters out Marine Recorder points)
Marine Recorder Database 2019	Presence	×	EUNIS2007 = A5.621, A5.622, A5.623 and A5.624 Qualifier = Certain match; whole record and Certain match; part record	×
Marine Recorder Database 2019	Pseudo-absence	EUNIS 2007 != A5.51 Qualifier = Certain match; whole record	EUNIS 2007 != A5.621, A5.622, A5.623 and A5.624 Qualifier = Certain match; whole record	EUNIS 2007 != A5.533 Qualifier = Certain match; whole record
Annex I Reefs Database	Presence	×	×	×
Annex I Reefs Database	Pseudo-absence	SubType = Bedrock, bedrock and stony, bedrock and/or stony, biogenic and stony Confidence = High	×	×

2.3 Reducing Spatial Autocorrelation

Due to the nature of surveying, the presence and pseudo-absence observations tended to be clustered so that several data points often occurred within a single 300 m raster grid cell. Reductions were made to both presence and absence data to reduce this clustering within every grid cell within the environmental raster stack.

Observations were passed through a logical statement in R to reduce observations to only one presence or one absence observation per grid square, ensuring a greater degree of independence between observations and, ultimately, ensuring the model did not overestimate the probability of habitat occurrence or absence.

The selection of a single observation was based on whether there were a greater number of presence or pseudo-absence points, in each cell. Due to the significantly greater number of pseudo-absence observations compared to presence observations, a weighting was applied to the pseudo-absences to allow a fair selection between the two observation types. Weighting was calculated by the proportion of total presence observations (*P*) to total pseudo-absence observations (*A*), multiplied by the total number of pseudo-absences within the raster cell (A_n).

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

Once the code identified which observation type (presence or absence) returned the highest total, a random selection was made to extract one point within that category in each cell. Details of how the selection process affected the number of response data for the model are reported in (Table 3).

Table 3. Number of observations per input dataset for the response variables, including the date ranges the biotopes were determined.

Model	Response	Date Range	Number of initial data points	Number of data points after selection process
Zostera marina beds	Presence	1968–2019	11,158	256
Zostera marina beds	Pseudo-Absence	1899–2018	116,454	6,412
Modiolus modiolus beds	Presence	1968–2019	1,097	290
Modiolus modiolus beds	Pseudo-Absence	1954–2019	145,797	22,317
Sabellaria spinulosa reefs	Presence	1978–2019	1,865	568
Sabellaria spinulosa reefs	Pseudo-Absence	1954–2019	35,596	19,905

Before running the models, all the presence and absence points were intersected with the respective model domain to help speed up processing, which subsequently reduces some of the numbers.

2.4 Training and Test Data

For each model run, 25% of the response data were held back for testing the model performance, the remaining 75% were used to train the model.

3 Modelling

3.1 JNCC SDM Framework

To predict habitat suitability, the JNCC Species Distribution Modelling (SDM) Framework (JNCC, 2019) was used. The JNCC SDM is an open-source R package that includes functions for ensemble SDM. The ensemble modelling approach repeatedly runs the model with a random selection of training and test data each time, averaging the predictions from each run to generate a final output.

The SDM package includes several different algorithms for a user to choose, including: Random Forest (RF), Boosted Regression Tree (BRT), Support Vector Machine, General Additive Model (GAM), General Linear Model (GLM) and Maximum Entropy (MaxEnt). The SDM package permits users to select multiple algorithms to execute though the ensemble, subsequently allowing the best performing algorithm to be chosen based on Area Under the Curve (AUC) statistic.

3.2 Model Selection

A combination of advice from the package authors and previous pilot studies utilising the SDM package identified that RF and BRT were typically the best performing models against all other algorithms. A preliminary run of the model was performed for 10 iterations on the *Zostera marina beds* and *Modiolus modiolus* beds models to see which, out of BRT and RF, performed best, based on the average AUC value (Table 4).

Table 4. AUC for 10 iterations of Random Forest and Boosted Regression Tree models. Scores labelled with a * denote the best performing algorithm per run.

Habitat	Model	Run 1	Run 2	Run 3	Run 4	Run 5	Run 6	Run 7	Run 8	Run 9	Run 10	Mean
Zostera m. beds	RF	0.977	0.990*	0.993*	0.988	0.994*	0.988	0.987*	0.992	0.989	0.991*	0.989*
Zostera m. beds	BRT	0.984*	0.989	0.993	0.989*	0.985	0.989*	0.984	0.983	0.991*	0.986*	0.987
Modiolus m. beds	RF	0.987*	0.981*	0.996*	0.998*	0.982*	0.997*	0.984*	0.987*	0.988*	0.997*	0.990*
Modiolus m. beds	BRT	0.957	0.964	0.963	0.971	0.961	0.953	0.941	0.965	0.959	0.975	0.961

In the case of both habitats, the mean AUC over 10 runs was higher in RF than in BRT (AUC_{RF} = 0.989, AUC_{BRT} = 0.987 for *Zostera marina* beds; AUC_{RF} = 0. 9897, AUC_{BRT} = 0. 9607 for *Modiolus modiolus* beds). The predictive outputs generated by the BRT model showed predictive values only to range within 0.3 and 0.6 for both habitats, while the RF model output values gave a wider range between 0.001 and 0.999. With this in mind, and its general ability to handle collinearity between variables and low-prevalence data much better, RF was selected as the final algorithm for the habitat suitability modelling. The model was run for 50 iterations using the “randomForest” package, with each iteration using a random selection of training and test data.

3.3 Summarising the Result

For the Potential Physical Loss indicator, users of the model output need be able to quantify the potential area of habitat loss as a result of human activities in a specified time period. Two approaches were reviewed:

1. Classify the predictive output into ‘suitable’ and ‘unsuitable’ cells. This would allow the calculation of the total area of habitat before and after polygons of human activities are overlain.
2. Do not classify the predictive output. Calculate a total area of ‘suitable’ habitat using the probabilities in the raster output. This is the approach that we chose – see below.

The total potential area of suitable habitat was calculated according to the equation below, where the product of the probability, *P*, and area, *A*, of each cell, *i* was summed over the total number of cells, *N*, in the study area.

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

This approach was suggested by Calabrese *et al*. (2014), who argues that aggregating probabilistic values is more objective than applying ad-hoc thresholds to species distribution model outputs.

4 Results

The AUC scores for all models being above 0.9 denote well-performing models (Table 5), with AUC scores of 1 indicating a perfect model performance (Hanley & McNeil 1982).

The models predicted the total potential area of suitable habitat for *Zostera marina* beds to be 4,194.1 km^2, *Modiolus modiolus* beds at 69,605.7 km^2 and *Sabellaria spinulosa* at 32,199 km^2.

Table 5. Mean ROC AUC values, total calculated area and standard deviation (SD) over all model iterations.

Model	Mean AUC	Total Area of Suitable Habitat	SD	SD% of Total Area of Suitable Habitat
Zostera marina beds	0.941	4,194.1 km^2	± 1,101.5 km^2	26%
Modiolus modiolus beds	0.992	69,605.7 km^2	± 10,967.2 km^2	15%
Sabellaria spinulosa reefs	0.990	32,199 km^2	± 4,579.6 km^2	14%

Plotted mean suitability and standard deviation values (Figures 4 to 9) showed that, across all models, most areas of the model domain exhibited relatively little variability in predictions between model runs. Geographic areas exhibiting the highest standard deviations typically reflect areas of high habitat suitability. Variability, as shown by the standard deviation, can be a useful indicator of the stability and therefore confidence, of the model. However, it is not the full picture; for example, there are large areas predicted to be highly suitable that do not correspond with observations. We might expect the standard deviation to be higher in these areas, but it is quite low.

Figure 4. Mean predictive values of habitat suitability for *Zostera marina* beds across the UK, within the model extent of 0–15 m depth. Insets represent examples of known areas of habitat: Top) Isles of Scilly; Middle) Ryde and Bottom) Isle of Harris / North Uist. Points within the insets illustrate habitat presence points used within the model.

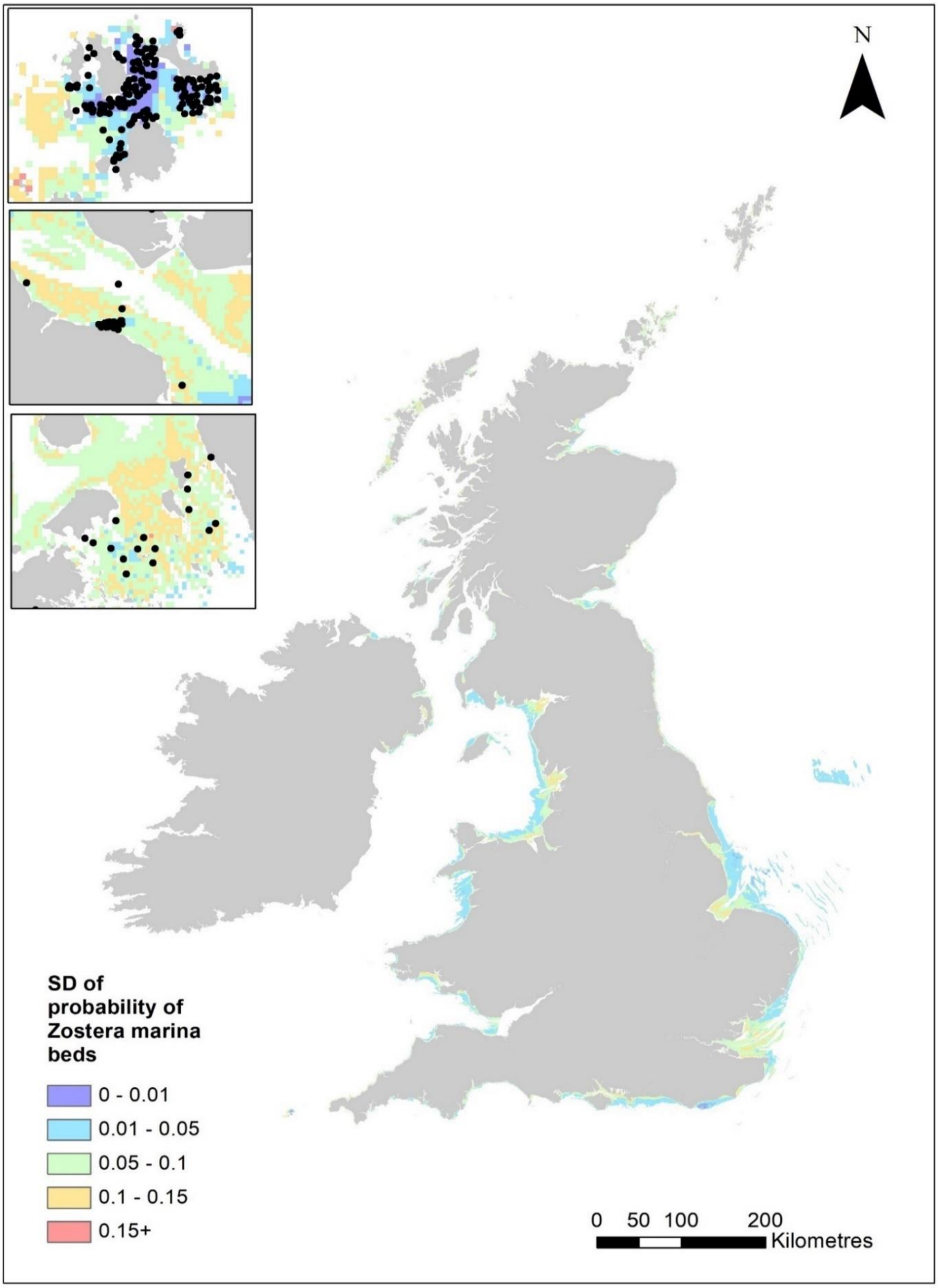

Figure 5. Standard deviation in the predictive values of habitat suitability for *Zostera marina* beds across the UK, within the model extent of 0–15 m depth. Insets represent examples of known areas of habitat: Top) Isles of Scilly; Middle) Ryde and Bottom) Isle of Harris / North Uist. Points within the insets illustrate habitat presence points used within the model. Higher standard deviations denote greater variability in predictive values, which are indicated by orange and red.

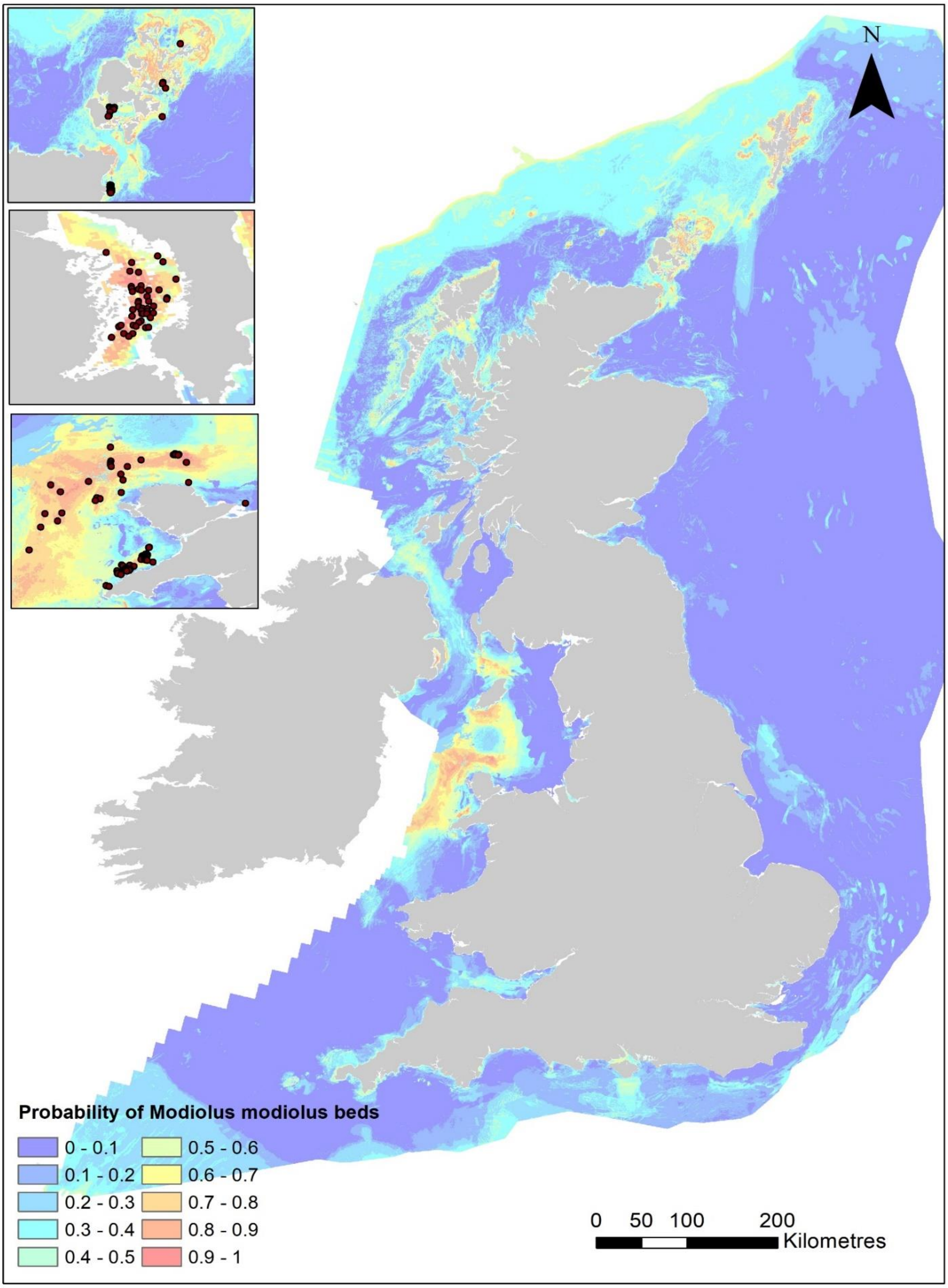

Figure 6. Mean predictive values of habitat suitability for *Modiolus modiolus* beds across the UK, within the model extent of 0–300 m depth. Insets represent examples of known areas of habitat: Top) Orkney & Noss Head, Scotland; Middle) Strangford Lough, Northern Ireland; and Bottom) Anglesey, North Wales. Points within the insets illustrate habitat presence points used within the model.

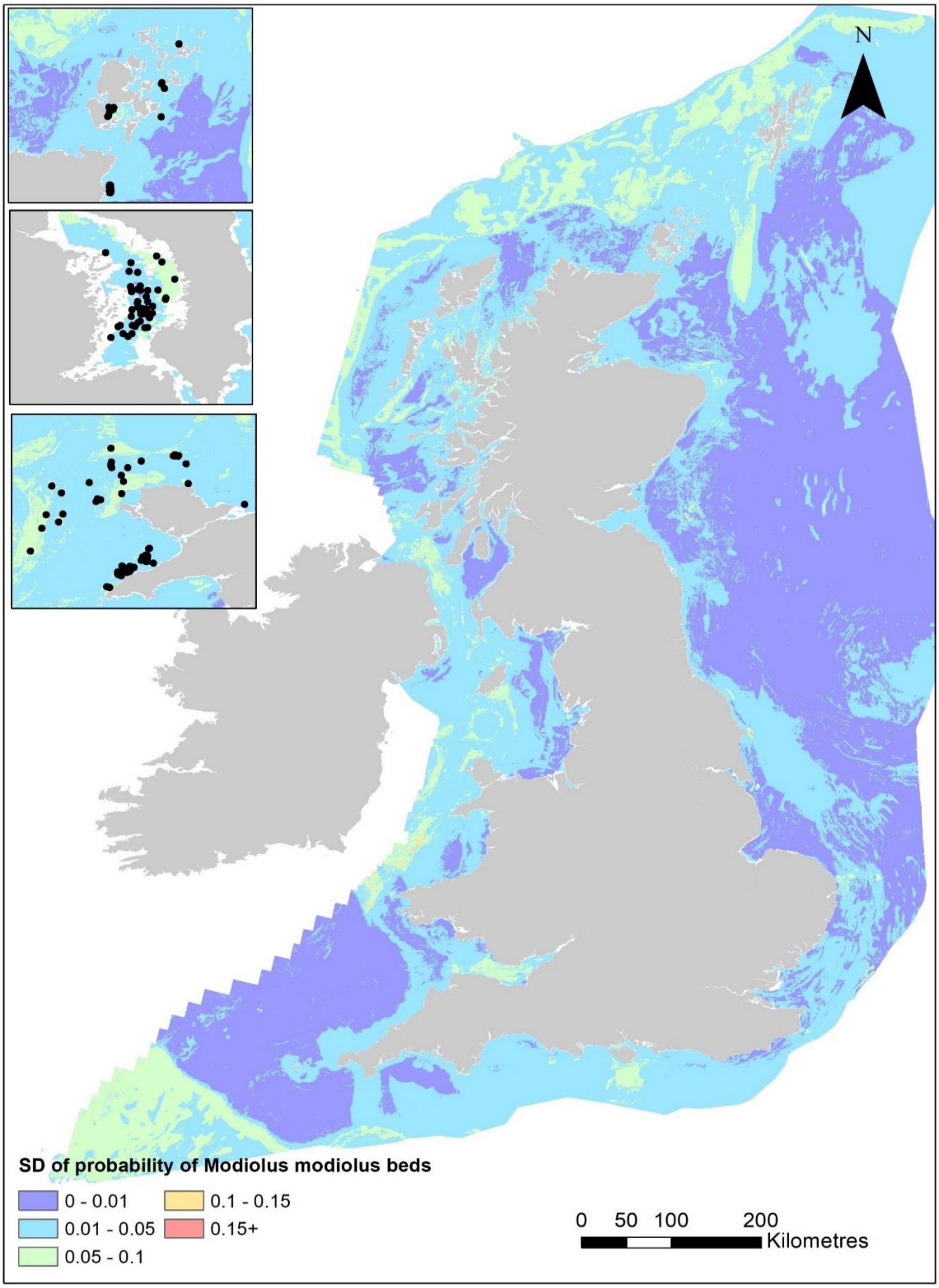

Figure 7. Standard deviation in the predictive values of habitat suitability for *Modiolus modiolus* beds across the UK, within the model extent of 0–300 m depth. Insets represent examples of known areas of habitat: Top) Orkney and Noss Head, Scotland; Middle) Strangford Lough, Northern Ireland; and Bottom) Anglesey, North Wales. Points within the insets illustrate habitat presence points used within the model. Higher standard deviations denote greater variability in predictive values, which are indicated by orange and red.

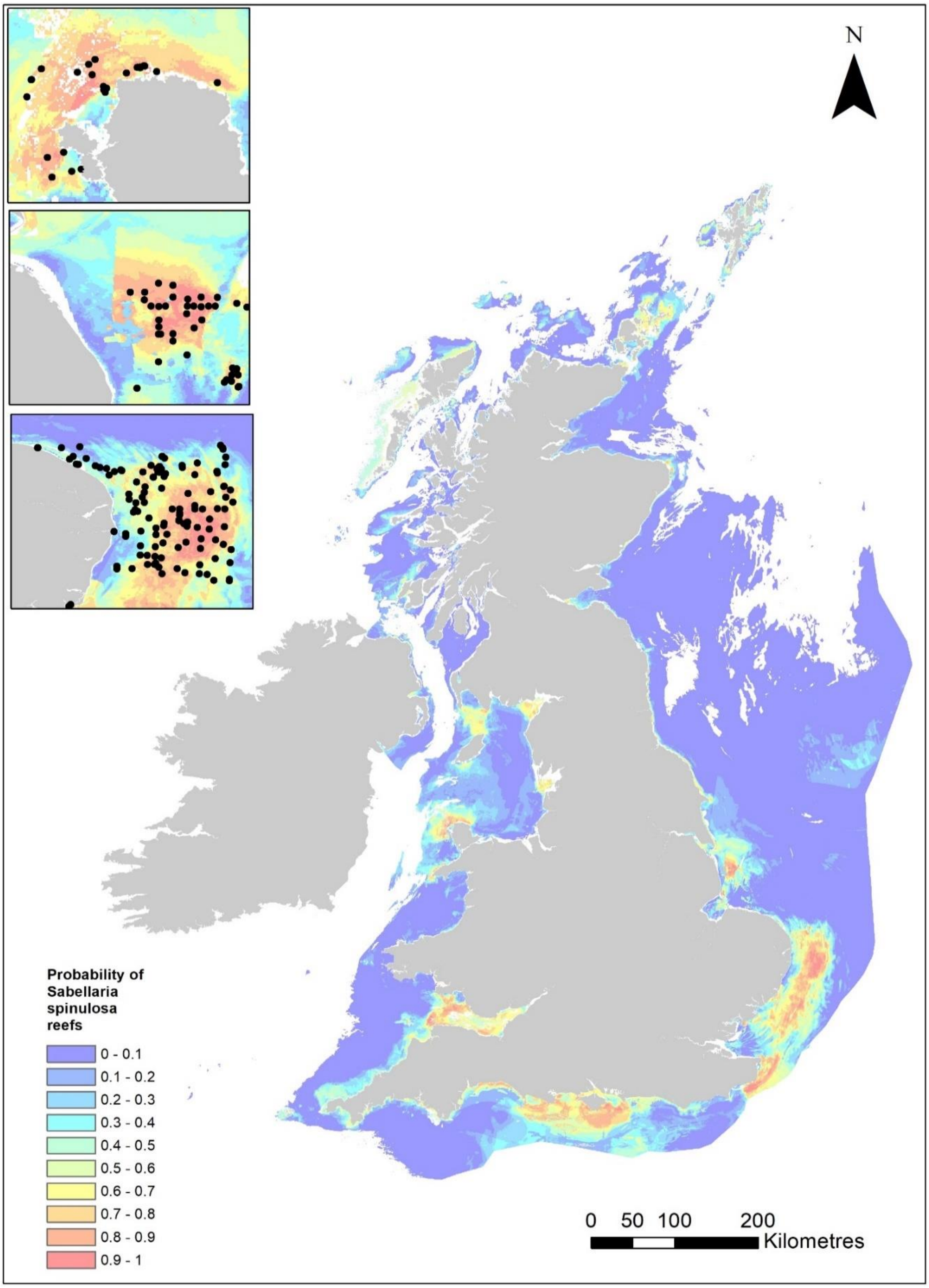

Figure 8. Mean predictive values of habitat suitability for *Sabellaria spinulosa* reefs across the UK, within the model extent of 0–80 m depth. Insets represent examples of known areas of habitat: Top) Anglesey, North Wales; Middle) Lincolnshire coast, England; and Bottom) East of England. Points within the insets illustrate habitat presence points used within the model.

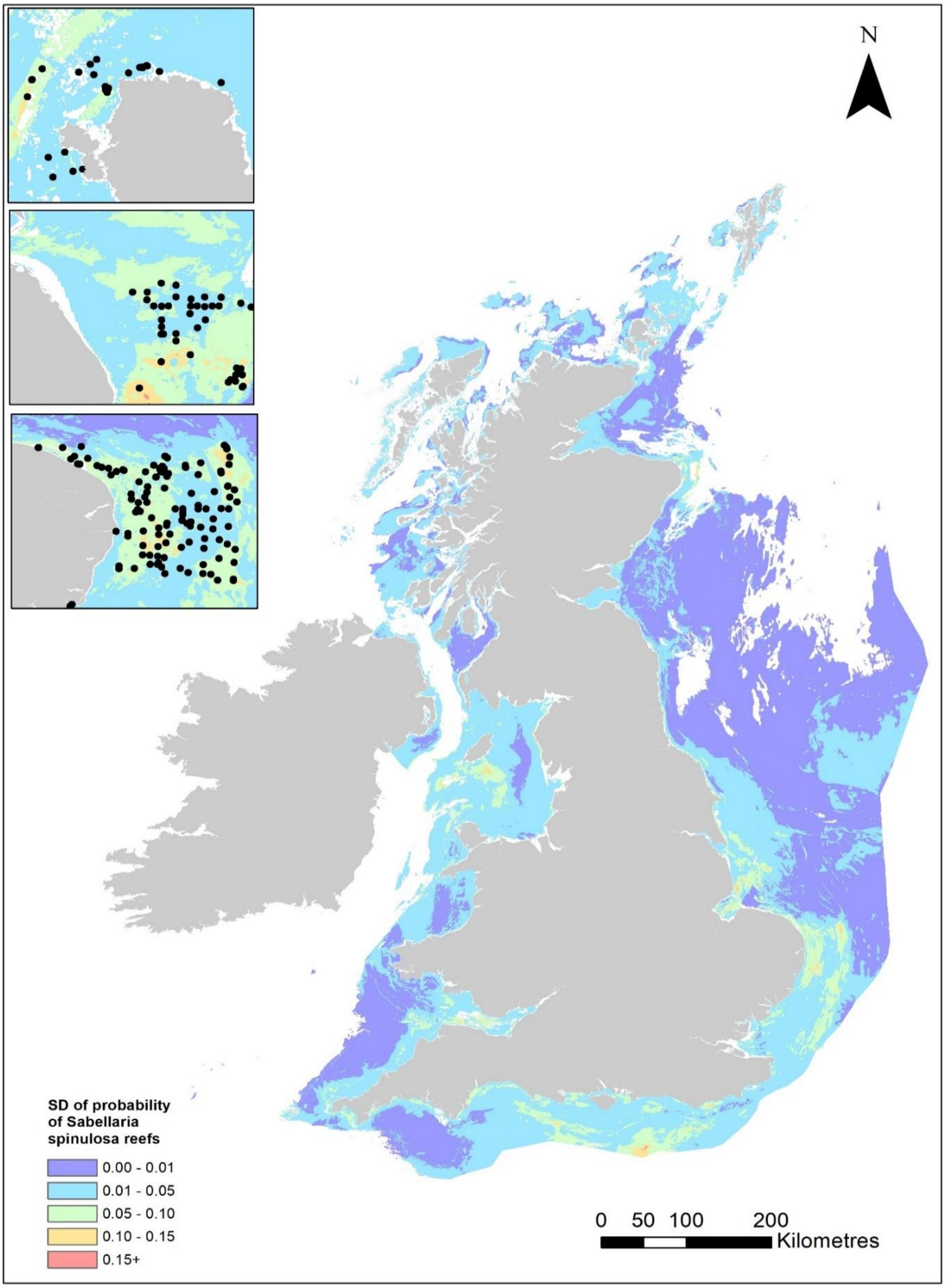

Figure 9. Standard deviation in the predictive values of habitat suitability for *Sabellaria spinulosa* reefs across the UK, within the model extent of 0–80 m depth. Insets represent examples of known areas of habitat: Top) Anglesey, North Wales; Middle) Lincolnshire coast, England; and Bottom) East of England. Points within the insets illustrate habitat presence points used within the model. Higher standard deviations denote greater variability in predictive values, which are indicated by orange and red.

5 Discussion

5.1 Variable importance

The key parameters affecting the suitability of the subtidal *Zostera marina* beds were, in order of importance: depth, PAR at seabed, minimum salinity, mean of annual minima temperature at the seabed and wave energy at the seabed.

Depth and amount of sunlight reaching the seabed (PAR_seabed) are known factors affecting subtidal *Zostera marina* distribution (e.g. Gormley 2014; Bekkby 2008; D'avack 2019). Bottom temperature contributed the most to the model of *Zostera marina* beds at NE Atlantic scale (Gormley *et al*. 2014), indicating that it is a key factor for *Zostera marina* growth. Contrary to what others have found using local wave exposure data (Bekkby *et al*. 2008), wave exposure did not have a high importance value in our model. *et al*This may be due to the coarse resolution of the wave energy dataset used in this work, which may be insufficient to capture small-scale variability, particularly in complex settings. Substrate type was dropped from our model, despite it being cited as a key driver for *Zostera* distribution by various authors (Gormley 2014; D'avack 2019). Further research is required in understanding why this is the case, one hypothesis is that the substrate layer we used as input, classified in five Folk classes, was not suitable for *Zostera* modelling.

Sabellaria reef showed a model response to (in order of importance): current energy at the seabed, light attenuation coefficient, mean salinity at the seabed, mean temperature at the seabed,wave energy at the seabed.

Sabellaria is often found in areas of high-water movement (Gibbs *et al*. 2014; Gomerley 2014) and it requires sand in suspension to build its tubes (Pearce 2017; Gormeley 2014). Therefore, it is understandable that current energy and light attenuation drive the distribution of this habitat as they are proxies for the amount of suspended sediments in the water column. Salinity can affect this habitat's suitability conditions (Gormley 2014) however other authors state that effects of salinity on *Sabellaria* distribution is unclear (Holt *et al*. 1998; Gibbs 2014); *Sabellaria spinulosa* is found mostly in full saline conditions but also in environments with variable salinity (Piearce 2017). Temperature was found to be an important variable in regional-scale OSPAR models, however others describe *S. spinulosa* as tolerant to various ranges of temperature changes.

Sabellaria spinulosa has been recorded on a wide range of substrata and once a colony has been established it is possible for the extent to increase without a requirement for hard substrata or mobile sand (Pearce 2017). Substrate was one of the selected variables in the model, but one of the least important, probably due *Sabellaria* being found in a wide range of substrate types.

Modelled *Modiolus modiolus* beds have shown that useful parameters, in order of importance: minimum salinity at seabed, current energy at seabed, mean temperature at seabed, depth, wave energy at seabed, slope and finally substrate.

The minimum salinity at seabed is an important environmental variable to consider as *M. modiolus* are known to be sensitive to changes in salinity making them dependant on deeper subtidal regions (Halanych *et al*. 2013; Dinesen & Morton 2014). Optimum salinities have been reported to be between 30–35 ppt (Bakhmet *et al*. 2010; Gormley *et al*. 2013; Dinesen & Morton 2014). Current speeds are shown to be the second most important variable to consider when modelling *M. modiolus* distribution. Currents speeds have been suggested to be important factor (Strong *et al*. 2016), however there is disagreement whether *M. modiolus* prefer non-mobile substrates in the absence of excessive currents (Wildish *et al*. 1998) or tidally swept regions where currents can reach 10 cms^{-1} (Wilson *et al.* 2021; Gormley *et al.* 2013). The results of this study have not clarified this disagreement but do support the suggestion that current speeds are an important variable to consider when modelling *M. modiolus* distribution.

5.2 Model Limitations

- In an attempt to predict areas of suitable environmental conditions for these habitats, we have made the following assumptions:
    - Environmental data, which have all been collected from different time periods and different time scales, are representative of current prevailing climactic conditions.
    - The 300 m spatial resolution of the gridded response variables (the environmental data) is high enough to account for the true variability in habitat suitability for each of the three habitats.
- The 300 m resolution of the predictor variables will not capture any small-scale variability in physical conditions, which could impact habitat suitability or patchiness at a much finer scale. Additionally, the resolution makes the number of presence / pseudo-absence points higher per grid cell, making it less likely to get cells with more presence points than pseudo-absence points.
- The strong model performance (AUC > 0.9) is likely due to the low numbers of presence data points used within the model. This raises suspicion that the model performance may be misleading. This will be further investigated in future products.
- Other known environmental datasets that affect the distribution of habitats could not be sourced at the spatial scale required for these models, for example:
    - *Zostera marina* beds: concentration of dissolved inorganic nutrients (e.g. nitrates and phosphates)
    - *Modiolus modiolus* beds: high sedimentation rates result in high mortality rates among *Modiolus modiolus* individuals (Hutchinson *et al*. 2016)
    - *Sabellaria spinulosa* reefs: areas of high turbidity are needed for *Sabellaria spinulosa* settlement (Pearce 2017), with sediment-starved areas potentially resulting in a net erosion of colonies (Davies *et al*. 2009), but given the highly ephemeral nature of *Sabellaria spinulosa* reefs (Hendrick 2008; Hendrick & Foster-Smith 2006; Jenkins *et al*. 2015), there may be additional variables to consider as model inputs.
- The models were unable to make a prediction where there was not complete spatial coverage of all environmental variables (Figures 10–12), particularly in regions with complex coastlines such as northwest Scotland. Other examples of areas include:
    - *Zostera marina* beds:
        - Waterfoot MCZ – absence of depth to seabed data over the southern limits of the MCZ.
        - Narrows of Strangford Lough – absence of wave data, and light inputs used to calculate PAR at the seabed (K_dPAR and surface PAR)
        - Killough Harbour – absence of all variables inshore
        - Dundrum Bay – absence of depth to seabed data
        - Carlingford Lough – absence of depth to seabed data
        - Lough Foyle – absence of depth to seabed data
        - Loch Sween – absence of all variables
        - Firth of Clyde (west coast of Arran) – absence of depth to seabed and wave data, with limited coverage of substrate
        - Loch Ailort – absence of waves and currents data

        - Lyndisfarne National Nature Reserve – absence of depth to seabed, waves and currents data
    - *Modiolus modiolus* beds:
        - North-west Scotland – particularly an issue for modelling *Modiolus modiolus* beds as there are numerous known beds found in sea lochs. The coarse resolution and lack of environmental data made it complicated to model these environments, particularly with the complex coastlines.
    - *Sabellaria spinulosa*:
        - Although mainly subtidal in nature, similar to the *Modiolus modiolus* beds model some areas in Orkney and Shetland were lacking data, as well some inshore estuaries as the Bristol Channel and Thames

Patches of *Modiolus modiolus* bed habitat suitability around the east coast of England (Norfolk coast) appear misleading as beds are not known to occur there. Furthermore, these areas are known distributions of *Sabellaria spinulosa* which require silty, turbid conditions to construct their tubes and reefs (Holt *et al*. 1998), whereas *Modiolus modiolus* are known to suffer from smothering (Hutchison *et al.* 2016). These model outputs are similar to Gormley *et al*. (2013), meaning the model may be focusing more on suitable environmental conditions but does not consider habitat specific factors known to influence *Modiolus modiolus* distribution, such as larval dispersal or connectivity (Millar *et al*. 2019). Some of the environmental data we used was derived from climatologies, for example temperature, salinity and currents. These climatologies do not usually include extreme weather events which are known to have negative effects on habitats (Milllar *et al*. 2019).

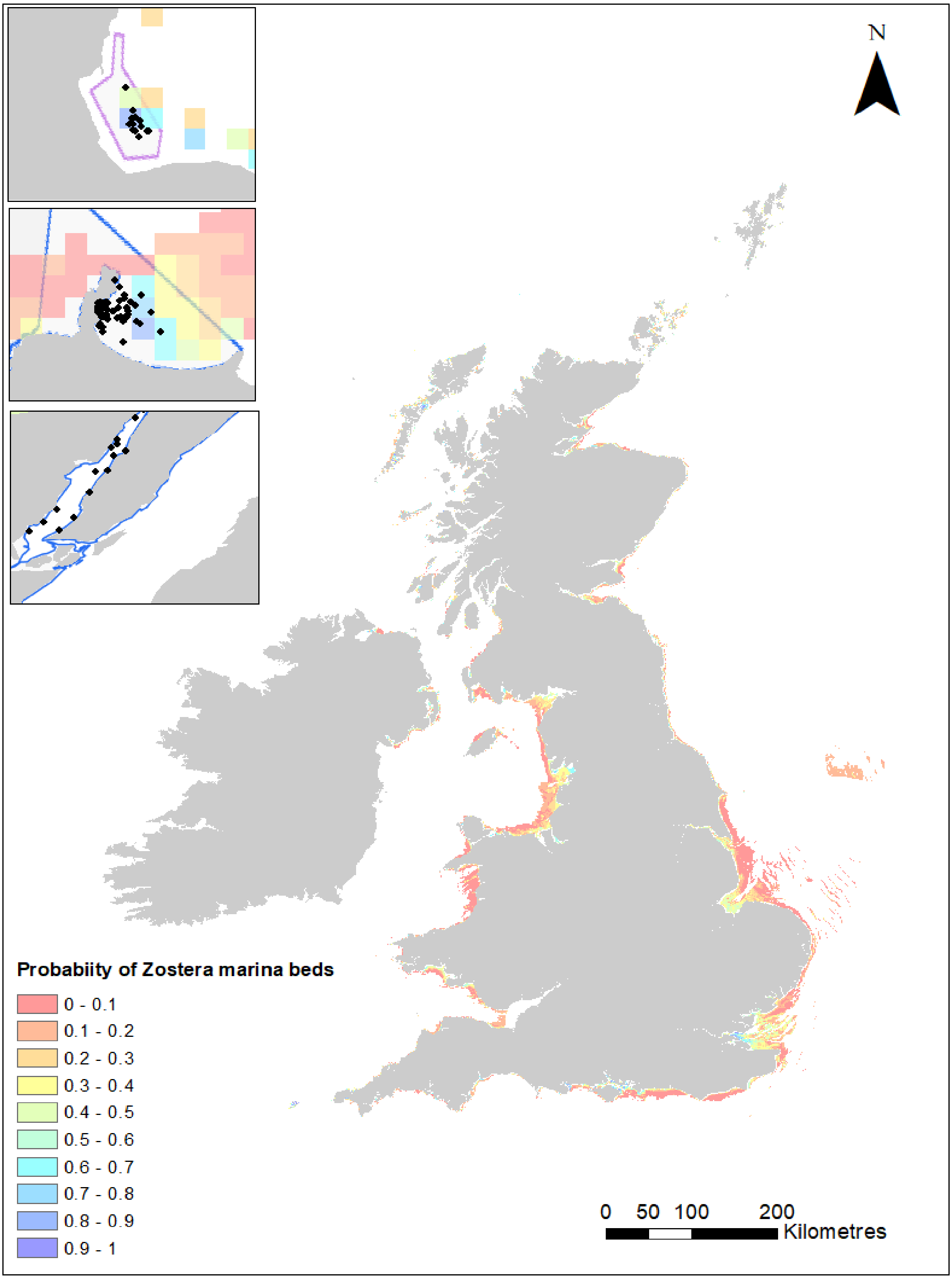

Figure 10. Insets represent examples of known areas of habitat where the model has been unable to sufficiently predict *Zostera marina* suitability: Top) Waterfoot MCZ; Middle) Pen Llŷn a'r Sarnau/ Lleyn Peninsula and the Sarnau and Bottom) Loch Sween. Points within the insets illustrate the full set of habitat presence points prior to applying selection criteria. Main Map: Mean predictive values of habitat suitability for *Zostera marina* beds across the UK, within the model extent of 0–15 m depth.

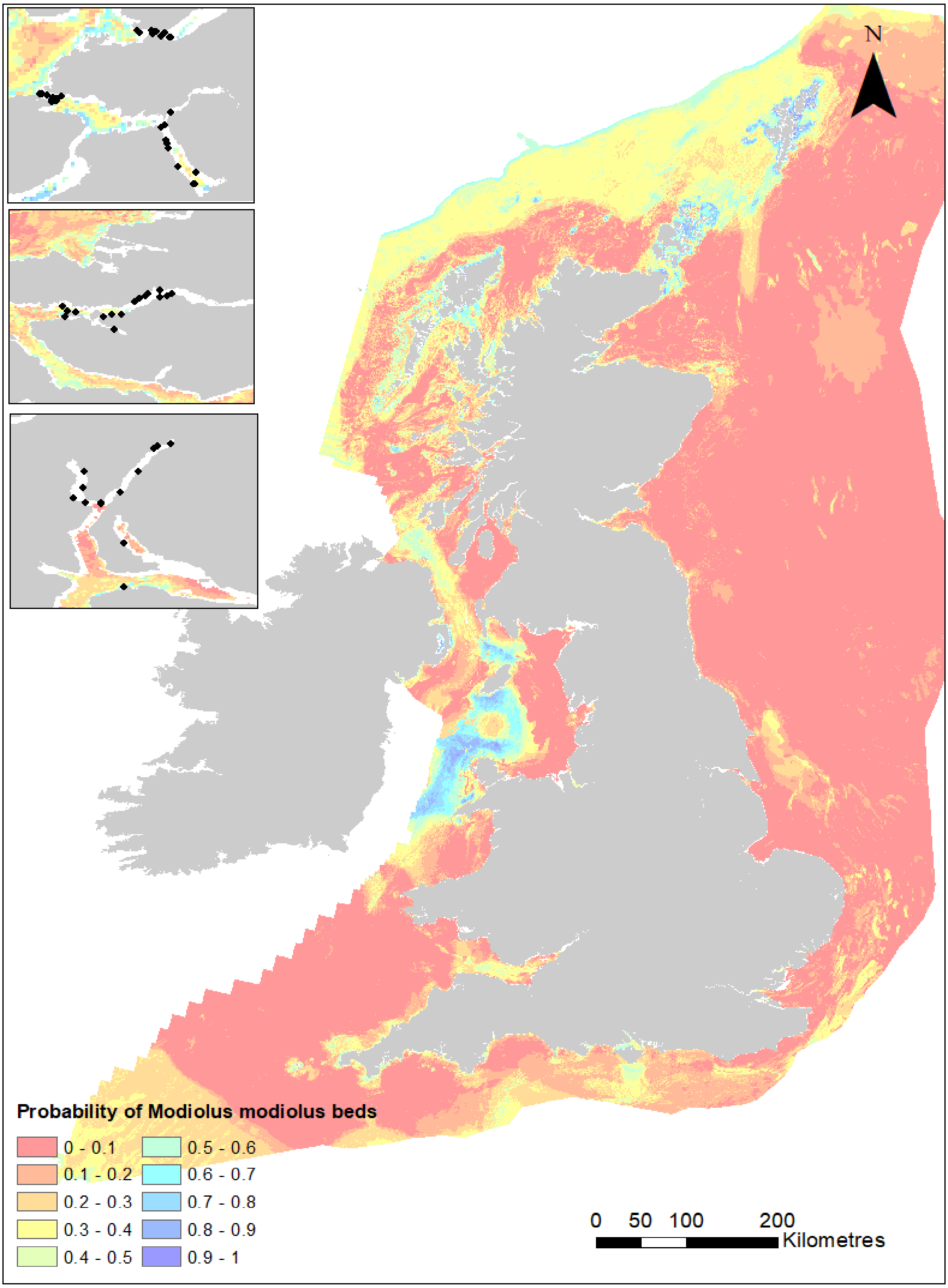

Figure 11. Insets represent examples of known areas of habitat where the model has been unable to sufficiently predict *Modiolus modiolus* suitability due to the lack of environmental data: Top) Inner Sound (Lochs Alsh, Carron & Duich), Scotland; Middle) Loch Sunart, Scotland; and Bottom) Loch Goil & Long, Scotland. Points within the insets illustrate the full set of habitat presence points prior to applying selection criteria. Main Map: Mean predictive values of habitat suitability for *Modiolus modiolus* beds across the UK, within the model extent of 0–300 m depth.

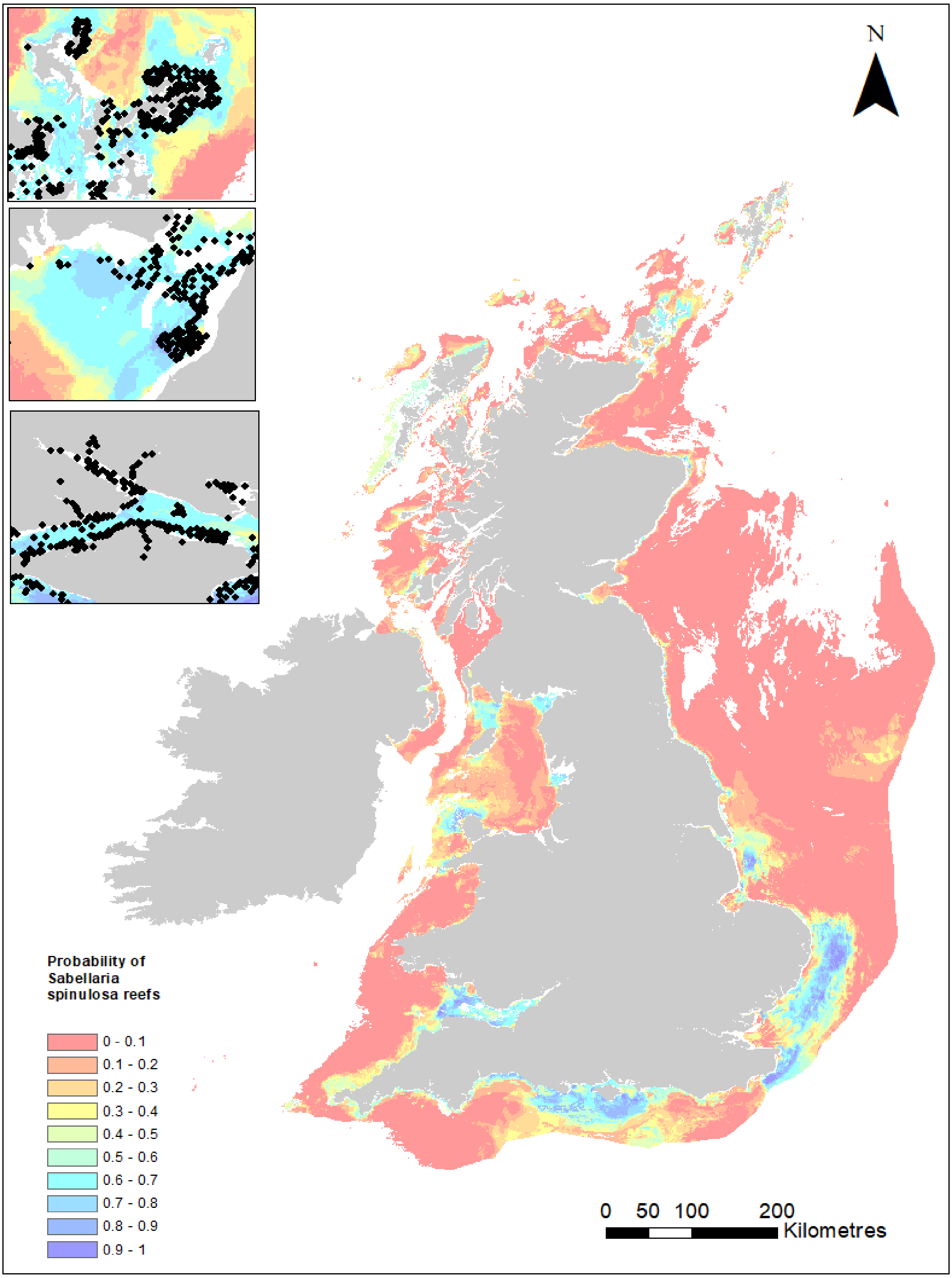

Figure 12. Insets represent examples of predicted high suitability but with no presence data and high pseudo-absence data for the *Sabellaria spinulosa* model: Top) Shetland, Scotland; Middle) Morecambe Bay, England; and Bottom) The Solent, England. Points within the insets illustrate the full set of habitat pseudo-absences. Main map: Mean predictive values of habitat suitability for *Sabellaria spinulosa* reefs across the UK, within the model extent of 0–80 m depth.

6 Improving the Models

- The models only use presence and pseudo-absence points which intersect with all environmental variables, thereby limiting the potential distribution of suitable habitat. This could be improved by sourcing more presence data as the more the model can be trained the accurate the predictive output will be. *Zostera marina.*
- Ideally, the use of true absence data, as opposed to pseudo-absences, is likely to provide a more accurate prediction; however, the existence of such data is very limited. A more careful choice of pseudo-absences and balanced number with presences will be tested in future modelling efforts.
- Trialling the modelling method on a case study with higher resolution environmental raster data would provide informative outputs on local variability of the habitats.
- Increased spatial coverage of environmental variables is needed, particularly for the inshore coastal regions. This could be achieved by either widening the coverage of the inputs themselves or improving the JNCC modelling packages to account for missing environmental data.
- The *Modiolus modiolus* beds model excluded some variables which may limit their presence; for example, Hutchison *et al*. (2016) found that, although surviving for a short-period, adult *Modiolus modiolus* would not be able to emerge from a burial event unless local hydrodynamics assists. Accounting for sedimentation rates, both natural and anthropogenic, would be a valuable input for a future iteration of this model; unfortunately, this data could not be sourced as no UK-wide layer is currently available, however it would be interesting to integrate it on a small sample area if such data exists.
- Similarly, the *Zostera marina* beds model also excluded some environmental variables known to limit their presence. The MarLIN website mentions parameters such as nutrients (phosphate and nitrate) and 'enclosedness' as factors influencing the distribution of *Zostera* beds, however, the data required could not be sourced.
- The framework currently uses a specific R package for Random Forest modelling (Liaw & Wiener 2002), which bases the variable importance on the impurity values, potentially having bias to variables with higher node split points such as continuous or high cardinality variables. Exploring alternative approaches to measure importance metrics, such as conditional permutation (Strobl *et al.* 2008), may help eliminate model bias and additionally account for collinearity amongst predictors.

7 References

Bakhmet, I.N. & Komendantov, A.J. (2012) Effect of salinity change on cardiac activity in Hiatella arctica and *Modiolus modiolus*, in the White Sea. Polar Biology. 35. 143 – 148.

Bekkby, T., Rinde, E., Erikstad, L., Bakkestuen, V., Longva, O., Christensen, O., Isaeus, M. & Isachsen, P. (2008). Spatial probability modelling of eelgrass (*Zostera marina*) distribution on the west coast of Norway. ICES Journal of Marine Science. 65. 1093-1101. 10.1093/icesjms/fsn095. *Available from:* *https://www.researchgate.net/publication/31027725_Spatial_probability_modelling_of_eelgrass_Zostera_marina_distribution_on_the_west_coast_of_Norway*

Berx, B. & Hughes, S. (2009) Climatology of Surface and Near-bed Temperature and Salinity on the North-West European Continental Shelf for 1971–2000 dataset. DOI: 10.7489/1900-1. *Available from: https://ocean.ices.dk/Project/OCNWES/Default.aspx*

Brown, G. (2015) Modelling the potential distribution of *Zostera marina* in Wales. Thesis (MSc), Swansea University. *Available from*: *http://www.projectseagrass.org/Modelling%20distribution%20FINAL%20(002).pdf*

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.

Connor, D.W., Gilliland, P.M., Golding, N, Robinson, P.,Todd, D., & Verling, E. 2006. UKSeaMap: the mapping of seabed and water column features of UK seas. JNCC, Peterborough. http://archive.jncc.gov.uk/PDF/UKSeaMap_2006.pdf

D'Avack, E.A.S., Tyler-Walters, H., Wilding, C. & Garrard, S.M. (2019) [*Zostera (Zostera) marina*] beds on lower shore or infralittoral clean or muddy sand. In Tyler-Walters, H. & Hiscock, K. (eds) Marine Life Information Network: Biology and Sensitivity Key Information Reviews, [on-line]. Plymouth: Marine Biological Association of the United Kingdom. [cited 10-01-2020]. *Available from: https://www.marlin.ac.uk/habitats/detail/257*

Davies, A.J., Last, K.S., Attard, K. & Hendrick, V.J. (2009). Maintaining turbidity and current flow in laboratory aquarium studies, a case study using *Sabellaria spinulosa*. *Journal of Experimental Marine Biology and Ecology*, *370*(1-2), pp.35-40.#

Department for Environment Food and Rural Affairs. (2018) Defra's Marine Digital Elevation Model (DEM) - 1 arc second (north). Metadata and download link. <data accessed 01/10/2019>. Available from: https://data.gov.uk/dataset/ff23520f-ecb2-4a53-890f-ce0cb13b57ac/defra-s-marine-digital-elevation-model-dem-1-arc-second-north

Dinesen, G.E. & Morton, B. (2014) Review of the functional morphology, biology and perturbation impacts on the boreal, habitat-forming horse mussel *Modiolus modiolus* (Bivalvia: Mytilidae: Modiolae). Marine Biology Research. 10(9), 845 – 870.

Elsäßer, B., Fariñas-Franco, J.M., Wilson, C.D., Kregting, L. & Roberts, D. (2013). Identifying optimal sites for natural recovery and restoration of impacted biogenic habitats in a special area of conservation using hydrodynamic and habitat suitability modelling. Journal of Sea Research, 77, 1-21.

Gibb, N., Tillin, H.M., Pearce, B. & Tyler-Walters, H. (2014). Assessing the sensitivity of *Sabellaria spinulosa* to pressures associated with marine activities.

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).

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.

Hendrick, V.J. (2008). *An appraisal of* Sabellaria spinulosa *reefs in relation to their management and conservation* (Doctoral dissertation, University of Newcastle upon Tyne).

Hendrick, V.J. & Foster-Smith, R.L. (2006). *Sabellaria spinulosa* reef: a scoring system for evaluating 'reefiness' in the context of the Habitats Directive. *Journal of the Marine Biological Association of the United Kingdom*, *86*(4), pp.665-677.

Holt, J., Hughes, S., Hopkins, J., Wakelin, S.L. *et. Al*. (2012) Multi-decadal variability and trends in the temperature of the northwest European continental shelf: a model-data synthesis., Progress in Oceanography, 106, 96-117, doi:10.1016/j.pocean.2012.08.001. https://www.bodc.ac.uk/resources/inventories/edmed/report/6020/

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).

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

Halanych, K.M., Thuròczy Vodoti, E., Sundberg, P. & Dahlgren, T.G. (2013). Phylogeography of the horse mussel *Modiolus modiolus.* Journal of the Marine Biological Association of the United Kingdom. 93(7), 1857 – 1869.
https://jncc.gov.uk/our-work/marine-recorder/
https://www.emodnet-seabedhabitats.eu/about/

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).

Jackson, A. & Hiscock, K. 2008. *Sabellaria spinulosa* Ross worm. 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 23-03-2020]. Available from: https://www.marlin.ac.uk/species/detail/1133

Jenkins, C., Eggleton, J., Albrecht, J., Barry, J., Duncan, G., Golding, N. & O'Connor, J. (2015). North Norfolk Sandbanks and Saturn Reef cSAC/SCI management investigation report. JNCC/Cefas Partnership Report, No. 7.

Jenkins, C., Eggleton, J., Barry, J. & O'Connor, J. (2018) Advances in assessing *Sabellaria spinulosa* reefs for ongoing monitoring. Ecol Evol. 8: 7673– 7687. https://doi.org/10.1002/ece3.4292

JNCC. (2019). JNCC SDM Framework: https://github.com/jncc/sdms

JNCC Combined Map: https://jncc.gov.uk/our-work/marine-habitat-data-product-eunis-level-3-combined-map/

Kent, F., Last, K.S., Harries, D.B. & Sanderson, W. (2017). In situ biodeposition measurements on a *Modiolus modiolus* (horse mussel) reef show enhanced sedimentation and provide insights into ecosystem services. Estuarine, Coastal and Shelf Science, 184, pp.151-157.

Kinetic energy at the seabed due to currents: https://www.emodnet-seabedhabitats.eu/access-data/launch-map-viewer/?zoom=5&center=-12.153,56.402&layerIds=43&baseLayerId=-3&activeFilters=

Kinetic energy at the seabed due to waves: https://www.emodnet-seabedhabitats.eu/access-data/launch-map-viewer/?zoom=5&center=-12.153,56.402&layerIds=26&baseLayerId=-3&activeFilters=

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.

Liaw, A. & Wiener, M. (2002). Classification and Regression by randomForest. R News 2(3), 18--22.

Light attenuation coefficient (Kdpar): https://www.emodnet-seabedhabitats.eu/access-data/launch-map-viewer/?zoom=5&center=-7.210,54.124&layerIds=18&baseLayerId=-3&activeFilters=

Lindenbaum, C., Bennell, J.D., Rees, E.I.S., McClean, D., Cook, W., Wheeler, A.J. & Sanderson, W.G. (2008). Small-scale variation within a *Modiolus modiolus* (Mollusca: Bivalvia) reef in the Irish Sea: I. Seabed mapping and reef morphology. Journal of the Marine Biological Association of the United Kingdom, 88(1), pp.133-141.

Lisco, S., Moretti, M., Moretti, V., Cardone, F., Longo, C. & Corriero, G. (2017) Sedimentological features of *Sabellaria spinulosa* bioconstructions. Marine and Petroleum Geology 87: 203–212.

Millar, H., O'Hara Murray, R., Gallego, A., Gormley, K. & Kent, F. (2019). Connectivity of selected Priority Marine Features within and outwith the Scottish MPA network. Scottish Natural Heritage Research Report No. 1048.

OSPAR Threatened and/or declining habitats database (2018): https://www.emodnet-seabedhabitats.eu/access-data/launch-map-viewer/?zoom=3&center=-11.000,51.600&layerIds=801&baseLayerId=-3&activeFilters=

Pearce, B. (2017). *The ecology of Sabellaria spinulosa reefs* (Doctoral dissertation, University of Plymouth).

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

Ragnarsson, S.A. & Burgos, J.M. (2012). Separating the effects of a habitat modifier, *Modiolus modiolus* and substrate properties on the associated megafauna. Journal of Sea Research, 72, pp.55-63.

Rees, E.I.S., Sanderson, W.G., Mackie, A.S.Y. & Holt, R.H.F. (2008). Small-scale variation within a *Modiolus modiolus* (Mollusca: Bivalvia) reef in the Irish Sea. III. Crevice, sediment infauna and epifauna from targeted cores. Journal of the Marine Biological Association of the United Kingdom, 88(1), pp.151-156.

Rees, I. (2009). Background Document for *Modiolus modiolus* beds [on-line] OSPAR Commission. [cited 10-01-2020] Available from: [http://qsr2010.ospar.org/media/assessments/Species/P00425_*Modiolus*.pdf](http://qsr2010.ospar.org/media/assessments/Species/P00425_Modiolus.pdf)

Sanderson, W.G., 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, 88(1), pp.143-149.

Schmitt, T., Dick, S., Spoelstra, G., Benoit, L. & Cyrille, P. (2019). EMODnet Bathymetry a compilation of bathymetric data in the European waters. 10.1109/OCEANSE.2019.8867250. <data access 01/10/2019>. Available from: https://portal.emodnet-bathymetry.eu/?menu=19

Stephens, D. & Diesing, M. (2015). Towards quantitative spatial models of seabed sediment composition. *PLoS One*, *10*(11), p.e0142502.

Strobl, C., Boulesteix, A.L., Kneib, T., Augustin, T. & Zeileis, A. (2008). Conditional variable importance for random forests. *BMC bioinformatics*, *9*(1), p.307.

Strong, J.A. (2016). An evaluation of the Stratified Extrapolation Framework for assessing the irreversible loss of potential habitat for four marine habitats at a regional scale. Defra Project Code: ME5318(B).

Strong, J.A., Service, M. & Moore, H. (2016). Estimating the historical distribution, abundance and ecological contribution of *Modiolus modiolus* in Strangford Lough, Northern Ireland. In Biology and Environment: Proceedings of the Royal Irish Academy (Vol. 116, No. 1, pp. 1-16). Royal Irish Academy.

Tullrot, A. (2009) Background Document for *Zostera* beds, Seagrass Beds [on-line] OSPAR Commission. [cited 10-01-2020] *Available from:* [*http://qsr2010.ospar.org/media/assessments/Species/P00426_Zostera_beds.pdf*](http://qsr2010.ospar.org/media/assessments/Species/P00426_Zostera_beds.pdf)

Tyler-Walters, H. 2007. *Modiolus modiolus* Horse mussel. In Tyler-Walters, H. & Hiscock, K. (eds) Marine Life Information Network: Biology and Sensitivity Key Information Reviews, [on-line]. Plymouth: Marine Biological Association of the United Kingdom. [cited 10-01-2020]. Available from: https://www.marlin.ac.uk/species/detail/1532

Wildish, D.J., Fader, G.B.J., Lawton, P. & MacDonald, A.J. (1998) The acoustic detection and characteristics of sublittoral bivalve reefs in the Bay of Fundy. Continental Shelf Research. 18. 105 – 113.

Wilson, B.R., Brown, C.J., Sameoto, J.A., Lacharité, M., Redden, A.M. & Gazzola, V. (2021) Mapping seafloor habitats in the Bay of Fundy to assess megafaunal assemblages associated with *Modiolus modiolus* beds. Estuarine, Coastal and Shelf Science. 252

Witman, J.D. (1984). Ecology of rocky subtidal communities: the role of *Modiolus modiolus* and the influence of disturbance, competition and mutualism. Doctoral Dissertations. 1438. Available online.