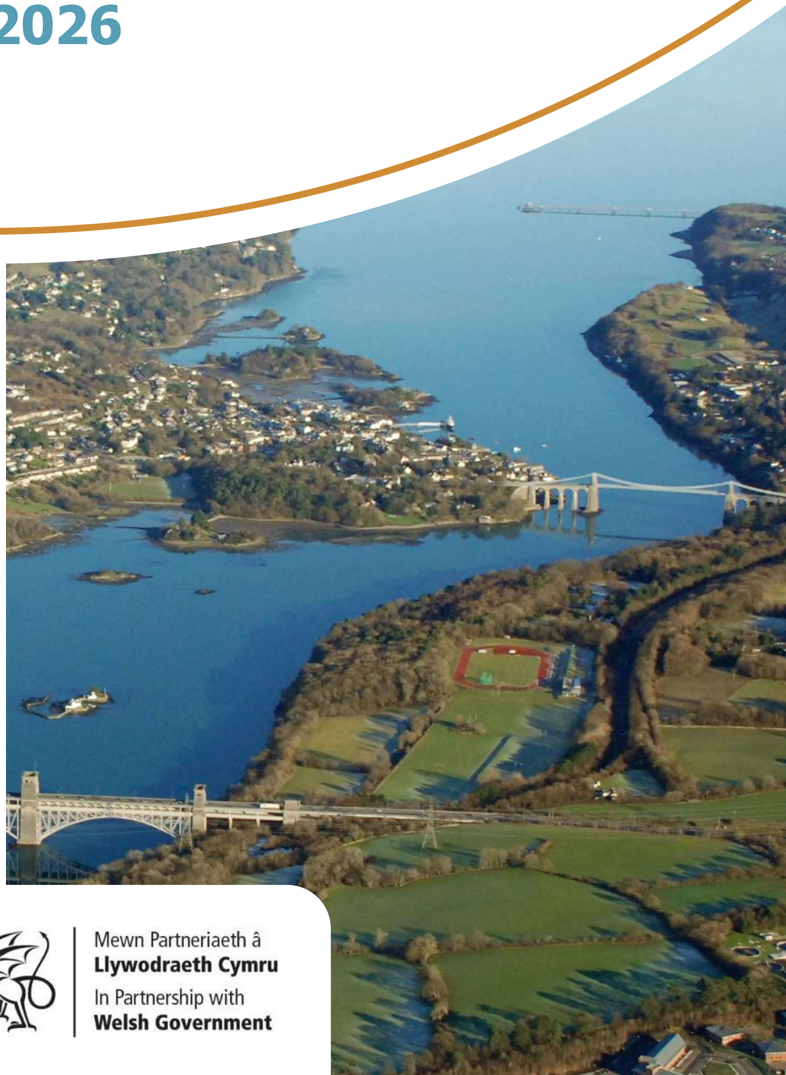
Zostera noltei Habitat Suitability Modelling in North Wales

May 2026



Cronfa Treftadaeth Heritage Fund

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In Partnership with Welsh Government

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Crynodeb Gweithredol

Mae'r astudiaeth hon yn datblygu model addasrwydd cynefinoedd (HSM) cydraniad uchel ar gyfer morwellt rhynglanw *Zostera noltei* ar hyd arfordir Gogledd Cymru i hybu cadwraeth a chynllunio gwaith adfer. Mae *Z. noltei* yn beiriannydd ecosystem pwysig sy'n creu cynefin meithrin, sy'n sefydlogi gwaddodion, ac yn gwella gwydnwch arfordirol, ond mae ei ddosbarthiad yn cael ei gyfyngu gan ffactorau amgylcheddol fel dyfnder y dŵr, hydrodynameg, halwynedd, math o waddodion, a gloywder y dŵr.

Cafodd data mynychder gan Cyfoeth Naturiol Cymru eu cyfuno â naw rhagfynegydd amgylcheddol, gan gynnwys bathymetreg, straen croesrym y gwely, halwynedd, tymheredd, cyfanswm y mater mewn daliant (TSM), cyfansoddiad gwaddodion, buanedd y cerrynt, llethr, a phellter i'r lan, i gyd wedi'u cyfuno ar grid cydraniad 30 m. I leihau bias gofodol, cafodd cofnodion presenoldeb eu chwynnu i 95 o achosion annibynnol. Roedd fframwaith modelu ensemble yn cael ei weithredu yn R gan ddefnyddio'r sdm pecyn R a oedd yn integreiddio chwe thechneg modelu: Modelau Llinol Cyffredinol, Modelau Atodol Cyffredinol, Sbleiniau Atchwel Addasol Amlamrywedd, Hapgoedwig, Coed Atchwel Cyfnerthedig, ac Entropi Uchaf.

Roedd y model yn rhagweld crynodiad o gynefin addas dros ben mewn amgylcheddau bas, cysgodol arfordirol ac aberol, gyda thri phrif leoliad ym Môn, Llŷn, ac Aber Afon Conwy. Dyfnder dŵr oedd y rhagfynegydd trechol, ac yna straen croesrym y gwely a halwynedd, gyda TSM yn cyfrannu fawr ddim at berfformiad y model er ei fod yn lleihau'n sylweddol nifer y cofnodion presenoldeb defnyddiadwy. Roedd y cynefin addas a ragwelwyd yn gysylltiedig â dŵr bas iawn, ynni hydrodynamig isel i gymedrol, ac amodau gwaddodol sefydlog.

Roedd data a gasglwyd o setiau data presennol yn canolbwyntio ar Afon Menai ac Ardal Cadwraeth Arbennig Bae Conwy, lle cafodd ardaloedd addas a ragfynegwyd eu troshaenu â setiau data sy'n disgrifio gwelyau morwellt presennol, ardaloedd morol gwarchodedig, pysgodfeydd cregyn, seilwaith mordwyol, cychod hwylio hamdden, ac asedau hanesyddol. Mae'r asesiad hwn yn dilysu'r rhagfynegiadau model graddfa fanwl ac yn nodi rhai ardaloedd lle gall gwaith adfer gael ei gyfyngu gan weithgarwch pobl neu ofynion rheoliadol.

Mae'r astudiaeth yn argymell arolygon o safleoedd penodol i ddilysu amodau amgylcheddol, i asesu pwysau amgylcheddol ac anthropogenig, ac i gadarnhau'r potensial ar gyfer adfer tymor hir. Dylid rhoi blaenoriaeth i safleoedd gerllaw gwelyau morwellt presennol i hybu ailgoloneiddio naturiol a chysylltedd genetig. Dylai gwaith yn y dyfodol ymgorffori rhagfynegiadau newid yn yr hinsawdd, ymgysylltiad â nodweddion lleol, ac asesu cyfyngiadau gweithredol a rheoliadol. Mae'r astudiaeth yn rhoi sylfaen dystiolaeth gynnar fel rhan o'r prosiect *Cysylltu Conwy* i asesu'r potensial am adferiad ar raddfa morlun yn y dyfodol o fewn ac yng nghyffiniau Afon Menai ac Ardal Cadwraeth Arbennig Bae Conwy.

Executive Summary

This study develops a high-resolution habitat suitability model (HSM) for the intertidal seagrass *Zostera noltei* along the North Wales coastline to support conservation and restoration planning. *Z. noltei* is an important ecosystem engineer that provides nursery habitat, stabilises sediments, and enhances coastal resilience, but its distribution is constrained by environmental factors such as water depth, hydrodynamics, salinity, sediment type, and water clarity.

Occurrence data from Natural Resources Wales were combined with nine environmental predictors, including bathymetry, bed shear stress, salinity, temperature, total suspended matter (TSM), sediment composition, current speed, slope, and distance to shore, all harmonised onto a 30 m resolution grid. To reduce spatial bias, presence records were thinned to 95 independent occurrences. An ensemble modelling framework implemented in R using the R package sdm integrated six modelling techniques: Generalised Linear Models, Generalised Additive Models, Multivariate Adaptive Regression Splines, Random Forest, Boosted Regression Trees, and Maximum Entropy.

The model predicted that highly suitable habitat is concentrated in shallow, sheltered coastal and estuarine environments, with three principal hotspots around Anglesey, the Llŷn Peninsula, and the Conwy Estuary. Water depth was the dominant predictor, followed by bed shear stress and salinity, while TSM contributed little to model performance despite substantially reducing the number of usable presence records.

Predicted suitable habitat was associated with very shallow water, low to moderate hydrodynamic energy, and stable sediment conditions.

Initial ground-truthing of existing datasets focused on the Menai Strait and Conwy Bay Special Area of Conservation, where predicted suitable areas were overlaid with datasets describing existing seagrass beds, marine protected areas, shellfisheries, navigational infrastructure, recreational boating, and historic assets. This assessment validated the fine-scale model predictions and identified some areas where restoration may be constrained by human activities or regulatory requirements.

The study recommends site-specific surveys to verify environmental conditions, assess environmental and anthropogenic pressures, and confirm long-term restoration potential. Priority should be given to sites near existing seagrass beds to maximise natural recolonisation and genetic connectivity. Future work should incorporate climate change projections, local actor engagement, and assessment of operational and regulatory constraints. This study provides an early evidence base as part of the *Connecting Conwy* project to assess the future potential for seascape-scale recovery within and around the Menai Strait and Conwy Bay Special Area of Conservation.

Introduction

Overview

Successful ecological restoration requires a robust understanding of the relationship between species distribution and the spatial variability of environmental conditions. In coastal ecosystems, this is particularly important for habitat-forming species such as seagrasses, whose occurrence is strongly controlled by physical and biogeochemical factors including light availability, hydrodynamics, sediment characteristics, and water quality.

Habitat Suitability Models (HSMs), also referred to as Species Distribution Models (SDMs), provide a quantitative framework to describe and predict species–environment relationships. These models estimate the probability of species occurrence across a defined region based on environmental predictors, and are increasingly used to inform conservation planning and site selection for restoration. By identifying areas that meet the ecological requirements of a target species, HSMs can improve the likelihood of restoration success while reducing associated costs and uncertainties.

For seagrass ecosystems, and particularly for *Zostera marina*, previous studies have demonstrated the value of high-resolution habitat suitability modelling in identifying ecologically suitable restoration sites and understanding spatial patterns of distribution (e.g. Bertelli et al., 2021; Bertelli et al., 2022). Similar modelling approaches have been applied to *Zostera noltei*, a key intertidal seagrass species across European coasts. However, these studies have highlighted important limitations, notably the restricted availability of high-resolution environmental data, which can constrain both the spatial extent and predictive accuracy of habitat suitability models (e.g. Grigg et al., 2025).

In this context, the present study aims to develop a high-resolution habitat suitability model for *Zostera noltei* along the North Wales coastline providing spatially explicit insights to support restoration and management efforts.

Dwarf eelgrass, *Zostera noltei*

Zostera noltei is an intertidal seagrass adapted to highly variable coastal and estuarine environments. It tolerates a wide range of conditions, including regular emersion, desiccation, and fluctuating salinity (typically 18–30 psu), allowing it to occur from upper intertidal zones to shallow subtidal areas.

The species can withstand low to moderately strong currents but is sensitive to increased wave exposure, which may cause sediment erosion and plant loss. Moderate currents can be beneficial in turbid environments by reducing suspended sediments and improving light availability. Unlike Zostera marina, *Z. noltei* shows high tolerance to both low and high light conditions, supporting its presence in both exposed and turbid habitats.

Z. noltei also exhibits broad temperature tolerance (approximately 5–30 °C) and is relatively resilient to moderate environmental fluctuations. However, it remains sensitive to nutrient and organic enrichment, which can reduce water clarity and limit growth. Climate change may have mixed effects, with increased storminess posing risks through physical disturbance, while other factors such as milder winters may be beneficial.

Study area

This study examines the coastal waters of North Wales, within the eastern Irish Sea, extending from northern Cardigan Bay to Liverpool Bay (approximately 52.2°N–53.6°N, 5.2°W–2.5°W). The area is characterised by pronounced spatial heterogeneity, with physical conditions varying over relatively short distances.

Regional hydrodynamics are primarily driven by tidal forcing, which generates strong currents and maintains a well-mixed water column throughout the year. The tidal regime is macrotidal, with ranges exceeding 8 m in places. The strongest currents occur near exposed headlands with steep bathymetric gradients, particularly around northwest Anglesey, where velocities can exceed 3 m s^{-1}. In contrast, much of the nearshore zone is relatively shallow, with depths generally less than 10 m within 1 km of the coastline.

Extensive intertidal areas are a key feature of the region, especially toward Liverpool Bay, where large mudflat and sandflat systems are exposed during low tide. Offshore, conditions differ markedly: to the east of Anglesey, water depths exceed 100 m and hydrodynamic conditions are comparatively less energetic. This combination of energetic headlands, sheltered embayments, and transitional coastal zones creates a wide range of hydrodynamic environments. These variations strongly influence sediment distribution, resulting in a mosaic of seabed types ranging from fine-grained depositional sediments to coarser, mobile substrates.

The North Wales coastline is also subject to significant anthropogenic pressure. Activities include commercial and recreational navigation, supported by major port infrastructure such as Holyhead, as well as fisheries, tourism, and coastal defence developments. In addition, offshore renewable energy installations have expanded in recent years. These combined pressures have contributed to habitat alteration and degradation, particularly affecting vegetated coastal ecosystems. While the area is subject to many pressures, many protections levels have been set in place in effort to protect its marine ecosystem with 8 Special Protection Areas (SPAs) including Traeth Lafan SPA; 8 Special Areas of Conservation (SACs) including Pen Llŷn a'r Sarnau SAC, and 41 Sites of Special Scientific Interest (SSSIs) including Y Foryd SSSI and Aber Mawddach SSSI. Consequently, the region provides a relevant and representative setting for assessing habitat suitability and restoration potential for the seagrass *Zostera noltei*.

Method

Data acquisition

Seagrass presence and environmental variables were harmonised onto a common high-resolution grid covering the study domain (52.55°N–53.65°N, 5.2°W–2.5°W). The grid resolution was set to 1/2000° in longitude and 1/4000° in latitude (approximately 30 m), allowing fine-scale spatial variability to be retained. This resolution was selected to adequately capture the complex coastal morphology of North Wales, where rapid changes in bathymetry and seabed substrate occur, particularly in nearshore areas that would be insufficiently resolved using coarser grids. All datasets were interpolated onto this grid using linear interpolation.

Environmental data

Environmental data were compiled from multiple sources to maximise spatial resolution and were subsequently harmonised onto a common 30 m resolution grid for the North Wales study area using interpolation (see Figure 1).

Bathymetry (or water depth relative to mean sea level) was obtained from the R50 model grid described by Ward et al. (2023), which provides <50 m horizontal resolution in near-shore areas. This dataset integrates the 2018 EMODnet Digital Terrain Model (~115 m resolution, www.emodnet-bathymetry.eu) with high-resolution multibeam data (2–4 m) from the UK Hydrographic Office ADMIRALTY Marine Data Portal (www.admiralty.co.uk). Bathymetric slope and distance to the nearest shore were derived from this dataset after resampling to the 30 m grid. Slope calculated over a 60 m baseline (sl_{60}) was computed in degrees as:

$$sl_{60} = \operatorname{atan}\left(\sqrt{(dz/dx)^2 + (dz/dy)^2}\right) * 180/\pi.$$

For each grid cell, the Euclidian distance to all shore grid cell was computed, and the minimum value was retained as the distance to the nearest shore.

Tidal velocities and tidally-driven maximum bed shear stress were obtained from Ward et al. (2023), based on a TELEMAC-2D hydrodynamic model on an unstructured mesh (R50 grid). Tidal velocities were quantified using mean depth-averaged values and represent an average over a 28-day tidal cycle. The tidally induced maximum bed shear stress (bss_t) was estimated from peak tidal velocities as:

$$bss_t = \rho\, uv_f$$

where ρ =1025 kg/m^3 is the sea water density and uv_f is the friction velocity.

Wave-driven bed shear stress (bss_w) was estimated using winter monthly mean significant wave height (H_s) and period (T) from Neill (2024), based on a nested SWAN model configuration covering a lower resolution North Atlantic setup and a high resolution (1/120 x 1/202°) Irish Sea model for the period 2014-2020. The wave induced bed shear stress (bss_w) was calculated as:

$$bss_w = \frac{1}{2}\rho\, f_w {U_b}^2$$

where $f_w = 0.02$ is the wave friction factor and U_b is the near-bed orbital velocity amplitude. U_b was estimated using the empirical formulation of Soulsby (1997):

$$U_b = \frac{H_s}{2}\left(\frac{g}{h}\right)^{1/2} \exp\left[-\left(4.41\frac{h}{\sqrt{gT}}\right)^{2.45}\right]$$

Where $g = 9.81$ m/s^2 is the gravitational acceleration and h is the water depth. The exponential term accounts for finite-depth attenuation, with coefficients derived from empirical fits to linear wave theory.

To account for nonlinear interactions between waves and tidal currents, the combined wave–current bed shear stress (bss_{wc}) was estimated following the parametrisation of Soulsby (1997), which provides a direction-averaged approximation of the original model of Grant and Madsen (1979):

$$bss_{wt} = bss_t \sqrt{1 + 1.2\frac{bss_w}{bss_t} + \left(\frac{bss_w}{bss_t}\right)^2}$$

Bottom temperature and salinity were extracted from the Copernicus Marine Service North-West Shelf Ocean Physics Analysis and Forecast product (https://data.marine.copernicus.eu/product/NWSHELF_ANALYSISFORECAST_PHY_004_013/description, DOI: 10.48670/moi-00054), which provides ~1/36° resolution. Monthly mean for 2023–2024 were used to derive annual minimum values prior to interpolation onto the 30 m grid.

Monthly satellite-derived mean total suspended matter (TSM) data were obtained from the EMODnet Physics database (https://erddap.emodnet-physics.eu/erddap/griddap/TSM_NORTHSEA.html) as a Level-3 gridded product with an approximate spatial resolution of 0.00314°. Monthly data from March 2011 to February 2012 were averaged to derive annual mean TSM conditions. However, the dataset does not fully cover nearshore areas, resulting in some data gaps close to the coastline.

Seabed sediment data were compiled from Smeaton et a l. (2021, Supplementary Materials https://www.frontiersin.org/articles/10.3389/feart.2021.593324/full#supplementary-material; Table 1.xlsx). The dataset aggregates habitat surveys, the European Nature Information System (EUNIS), and additional records from the UK Hydrographic Office and the British Geological Survey. Sediments were classified using a modified Folk classification scheme (Folk, 1954; Kaskela et al., 2019), which categorises seabed material into 16 classes based on proportions of mud (<63 µm), sand (63–2000 µm), and gravel (>2000 µm) with additional categories indicating shell presence. The mean spacing between sediment samples is ~270 m across the study area, decreasing to ~110 m within 100 m of the coastline. Point observations were interpolated onto the 30 m grid using nearest-neighbour interpolation to produce categorical substrate maps. Percentage of gravels was derived from these classifications; however, the discrete nature of the Folk16 scheme (five classes of percentage of gravels) results in spatial discontinuities. To improve suitability for habitat modelling, percentage of gravels were refined by assuming higher gravel fraction in sandy sediments relative to muddy sediments.

Seagrass presence

Spatial distribution data for *Zostera noltei* were obtained from Natural Resource Wales, which compiles biodiversity records for habitats of principal importance for the conservation and enhancement of biodiversity in Wales, including seagrass beds. The dataset is available via the DataMap Wales platform (https://datamap.gov.wales/layergroups/inspire-nrw:MarineBAPOSPARHabitats) and includes both points and polygons records describing the location and spatial extent of marine habitats. These data were used to generate a seagrass presence mask on the 30 m resolution North Wales grid. Grid cells containing at least one seagrass observation point or intersecting a mapped polygon were classified as presence. After processing and standardisation, 2,470 presence records were identified on the 30 m resolution North Wales grid.

Table 1. Data sources used to derive environmental variables across the North Wales study area.

Environmental variable	**Resolution**	**Data source**
Water depth	50 m	Model grid from Ward et al. (2023)
Bed shear stress	50 m	Ward et al. 2023
Salinity (annual minimum)	~1/36°	Copernicus Marine Service North-West Shelf Ocean Physics Analysis and Forecast product
Temperature (annual minimum)	~1/36°	Copernicus Marine Service North-West Shelf Ocean Physics Analysis and Forecast product
Total suspended matter (mean)	0.00314°	EMODnet Physics database
Sediment type	Mean resolution 270 m (110 m close to the shore)	Smeaton et al. (2021, Supplementary Materials)
Average water flow speed at seabed	50 m	Ward et al. 2023
Slope	50 m	Ward et al. (2023) model grid
Distance from closest shore	30 m	Ward et al. (2023) model grid

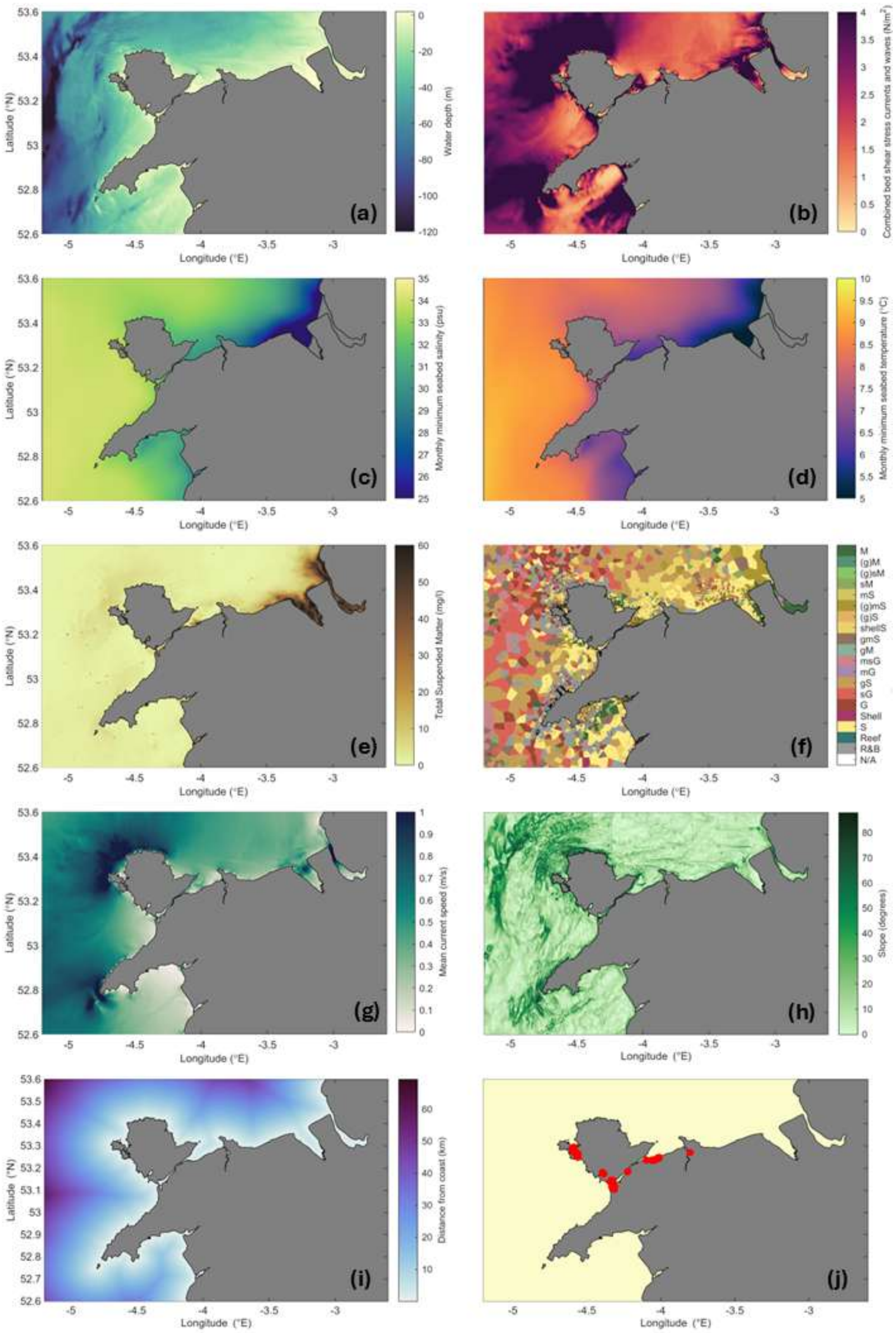

Figure 1. Spatial distribution of environmental variables and Zostera noltei presence across the North Wales study area. Panels show: (a) bathymetry, (b) bed shear stress, (c) minimum seabed salinity, (d) minimum seabed temperature, (e) total suspended matter, (f) sediment composition, (g) mean current speed, (h) seabed slope, (i) distance from the coast, and (j) seagrass presence (red dots).

Habitat Suitability Model

Two sets of habitat suitability models (HSMs) were generated: one including all environmental predictors listed in Table 1: Data sources used to derive environmental variables across the North Wales study area (Table 1) and another excluding the total suspended matter (TSM) predictor. The inclusion of TSM reduced the number of available *Zostera noltei* presence records from 2,470 to 1,667 because the satellite-derived TSM dataset did not fully extend to nearshore areas. As a result, occurrences located closest to the shoreline were excluded, introducing a potential distance-to-shore bias in the spatial distribution of presence records (see Figure 2). The two HSM configurations were subsequently compared to evaluate the influence of the TSM predictor on model performance and habitat suitability predictions.

Habitat suitability modelling was performed using an ensemble modelling framework following the Bertelli et al. (2021) method used for Z. *marina*. All environmental variables were uploaded into R as raster files and *Z. noltei* presence cells as spatial data frames. An ensemble modelling strategy was implemented using the sdm R package (Naimi and Araújo 2016), which enables the integration of multiple statistical and machine learning algorithms within a unified framework. Six commonly used modelling techniques in ecological modelling were applied: Generalised Linear Models (GLM; McCullagh and Nelder (1989)), Support Vector Machines (SVM; Corted and Vapnik (1995)), Multivariate Adaptive Regression Splines (MARS; Friedman (1991)), Random Forest (RF; Breiman (2001)), Boosted Regression Trees (BRT; Friedman (2001)), and Maximum Entropy (MaxEnt; Phillips et al. (2006)). Model fitting was based on the relationship between seagrass occurrence and a set of environmental predictors, expressed as spatially explicit covariates.

From the presence mask built on the 30 m resolution North Wales grid, not all 2470 occurrence were used as presence points for the HSM. Most presence records were spatially clustered, with observations concentrated in a limited number of areas, resulting in spatial autocorrelation among records. To account for environmental similarity between nearby points and to prevent inflated model performance, a spatial thinning approach was applied to reduce clustering. All occurrences were then ranked according to spatial isolation, and a greedy filtering procedure was applied. Only presence records separated by at least 150 m (five grid cells) from other retained records were selected. This approach reduces over-representation of densely sampled areas while preserving overall spatial coverage and reducing bias introduced by clustered polygon observations. Using this method, the dataset was reduced to 123 presence records of *Zostera noltei*, of which 94 overlapped with the TSM environmental dataset), as the spatial coverage of the TSM product does not extend fully to the shoreline.

As true absence data were unavailable, pseudo-absence (background) points were generated within the study area using a 10:1 ratio relative to presence points. Following preliminary testing, this ratio provided the best balance between discrimination, calibration, and statistical stability. To avoid artificially inflating model performance through the inclusion of environmentally unrealistic offshore habitats, pseudo-absence points were randomly generated within a 2 km buffer surrounding the 2,470 *Z. noltei* presence records identified on the 30 m resolution North Wales grid. Restricting background sampling to environmentally accessible coastal areas reduced environmental divergence between presence and background data, thereby improving model reliability and ecological interpretability.

Model performance was evaluated using a resampling approach in which the occurrence dataset was repeatedly partitioned into training and testing subsets through two runs of both bootstrapping and k-fold cross-validation. Cross-validation (k = 3) was used to assess predictive performance on independent data subsets, while bootstrapping was applied to quantify model stability and uncertainty associated with sampling variability. For each algorithm, multiple model runs were conducted, generating spatial predictions of probability of occurrence expressed as continuous probabilities ranging from 0 (unsuitable) to 1 (highly suitable).

Finally, predictions from all modelling techniques and repetitions were combined using a weighted averaging approach based on TSS statistics to produce an ensemble map of occurrence probability. This ensemble approach reduces uncertainty associated with individual models and has been shown to improve predictive robustness by integrating the complementary strengths of different modelling techniques (e.g. Araújo and New (2007); Marmion et al. (2009)).

Suitability maps were then derived by applying a threshold to convert continuous probabilities of occurrence into a binary habitat classification (suitable/unsuitable). The threshold was determined using the maximum sensitivity plus specificity criterion, which identifies the value that optimally balances the errors due to missing true habitat (false negatives) and overpredicting habitat (false positives). For the ensemble model, the final threshold was defined as the mean of the thresholds obtained from each model replication. In addition, suitability outputs were further refined by classifying continuous probability values into four ordinal categories—"low," "moderate," "good," and "excellent"—using the 25th, 50th, and 75th percentiles as breakpoints.

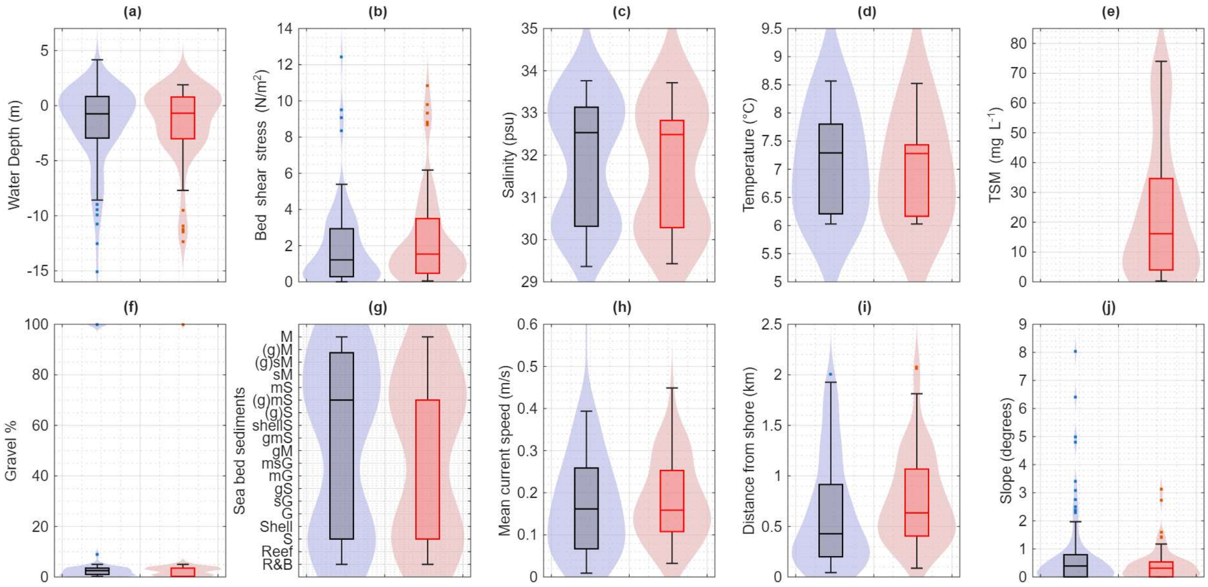

Figure 2. Distribution of environmental variables for presence data, comparing datasets with and without the TSM mask (red and blue, respectively). For each dataset, the shaded area shows a violin plot with an overlaid boxplot.

Results

Predictor selection

The removal of correlated variables is recommended during predictor selection to improve parameter estimation in species distribution models (e.g. Guisan et al., 2017).

Multicollinearity among the nine environmental predictors was assessed using the variance inflation factor (VIF). Results indicated that bottom temperature was strongly correlated with several other variables. To reduce collinearity in the habitat suitability model (HSM), temperature was excluded from the set of predictors, resulting in VIF values below 4 for all remaining variables.

Habitat suitability model performance

The ensemble habitat suitability model predicted that highly suitable habitat for *Z. noltei* is primarily restricted to shallow nearshore environments along the North Wales coastline (Figure 3; see Figures 11-22 in Appendix for more detailed maps). High probabilities of occurrence were concentrated within sheltered embayments, estuarine margins, and intertidal coastal zones, whereas offshore areas exhibited low habitat suitability, reflecting the strong influence of shallow water depth on habitat distribution. Areas such as the River Dee (Figure 18), Liverpool Bay (Figure 19) and Barmouth Bay (Figure 9) showed comparatively lower suitability, likely associated with elevated TSM concentrations (Figure 1e). Similarly, regions characterised by high bed shear stress were predicted to be less suitable for *Z. noltei*, including the western and northern coasts of the Llŷn Peninsula (Figure 11), the shoreline adjacent to the Morfa Dyffryn dunes (Figure 3d) and exposed coastal sections west and north of Anglesey that lack protection from small embayments (Figure 13 and Figure 14).

Three major hotspots of predicted habitat suitability were identified:

1. Figure 3b: around Anglesey, particularly along sheltered coastal margins near around Caernarfon and Malltraeth Bay (Figure 12), Holy Island (Figure 13), the north coast of Anglesey (Figure 14) and around Red Wharf Bay and Lavan Sands (Figure 15).
2. Figure 3c: within the Conwy Bay estuarine (Figure 16) and in a few embayment systems of the Llandudno peninsula (Figure 17).
3. Figure 3d: Along the south side of the Llŷn Peninsula in sheltered embayments (Figure 11) and the estuarine region of Tremadog Bay (Figure 10).

Both habitat suitability modelling frameworks demonstrated good to excellent predictive performance across all modelling algorithms (Table 2 & 3), with consistently high AUC values (>0.80) and moderate to high TSS values (>0.53), indicating strong discrimination between suitable and unsuitable habitats. Across both model configurations, machine-learning approaches outperformed simpler statistical methods, with RF consistently achieving the highest predictive performance (AUC = 0.91; TSS = 0.69–0.71; COR = 0.54–0.56; deviance = 0.38–0.39). BRT, MaxEnt, and MARS also performed well, demonstrating strong discriminatory ability and relatively high classification accuracy. In contrast, GLM and SVM showed comparatively lower performance, suggesting reduced capacity to capture complex non-linear relationships between environmental predictors and species occurrence.

The inclusion of TSM slightly improved overall model performance for several algorithms, particularly GLM, BRT, and MARS. For example, GLM performance increased from AUC = 0.80 to 0.85 and from TSS = 0.53 to 0.63, while BRT improved from AUC = 0.88 to 0.90 and from TSS = 0.66 to 0.69. These improvements suggest that TSM contributed ecologically relevant information that enhanced the models' ability to explain spatial variation in habitat suitability. RF performance remained consistently high across both model configurations, indicating strong robustness to predictor selection and suggesting that the environmental signal underlying habitat suitability was well captured regardless of the inclusion of TSM.

Correlation coefficients (COR) were moderate overall, which is commonly observed in ecological modelling using presence–absence data, given the inherent sampling noise and the typically complex, non-linear relationships between species occurrence and environmental predictors. The highest COR values were obtained for RF and BRT, indicating comparatively stronger agreement between observed and predicted suitability values for these models. Deviance values were generally low to moderate, particularly for RF and BRT, suggesting a relatively good model fit and limited unexplained variation. In contrast, MaxEnt consistently showed slightly higher deviance values despite strong AUC and TSS scores, indicating that while the model performed well in discriminating suitable from unsuitable habitat, its predicted suitability values were comparatively less well calibrated.

Uncertainty in ensemble predictions was assessed using both confidence intervals (CI) and coefficients of variation (CV) across model runs (Figures 4 and 5, respectively). Confidence intervals were generally low throughout the study area, ranging from approximately 0.04 to 0.23, indicating relatively consistent predictions among model replicates (Figures 4). The lowest uncertainty was observed in offshore zones where predicted habitat suitability was minimal, whereas slightly higher uncertainty occurred in nearshore areas associated with higher predicted suitability. Analysis of the influence of the upper and lower confidence interval bounds on habitat suitability showed that areas classified as having excellent suitability remained largely unaffected, while regions of good suitability were only slightly reduced (Figure 6). In contrast, areas classified as moderate to low suitability were substantially reduced or excluded when the lower confidence interval bound was applied to the probability of occurrence, this is particularly visible at Holy Island. The coefficient of variation showed the lowest values within the core suitable habitat areas, indicating strong agreement among model predictions in these regions (Figures 5). Higher CV values were primarily concentrated around the margins of suitable habitats, likely reflecting greater model disagreement regarding the spatial extent of transitional or marginal environments.

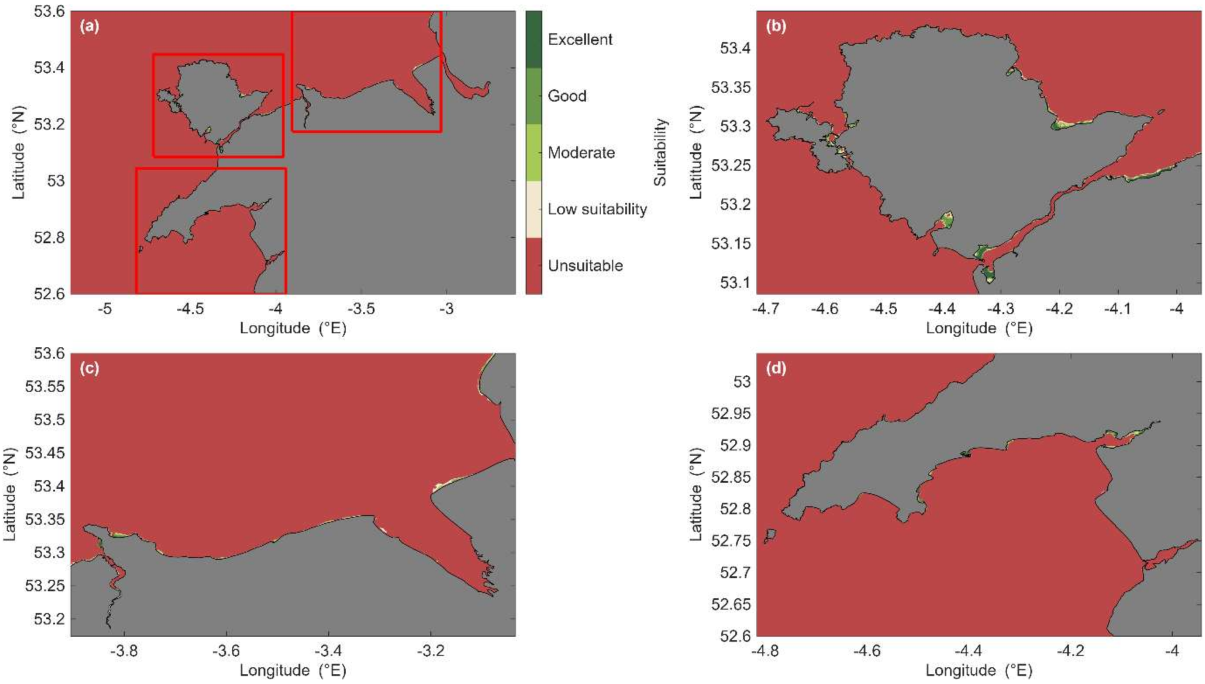

Figure 3. Predicted suitability of seagrass habitat from the ensemble model using the threshold optimisation method, with habitat categorised as unsuitable and 4 class of suitable habitats "low", "moderate", "good" and "excellent": (a) North Wales study area, (b) zoomed view of Anglesey, (c) Llŷn Peninsula and Cardigan Bay, and (d) coastline from Colwyn Bay to Liverpool Bay.

Table 2. Model performance metrics, including mean AUC (Area Under the Curve), COR (correlation coefficient), TSS (True Skill Statistic), and deviance, which represents the amount of variation remaining after model fitting.

Methods	AUC	COR	TSS	Deviance
GLM	0.8	0.29	0.53	0.51
SVM	0.84	0.29	0.58	0.55
MARS	0.87	0.43	0.64	0.46
RF	0.91	0.56	0.69	0.38
BRT	0.88	0.48	0.66	0.47
MaxEnt	0.89	0.46	0.66	0.65

Table 3. Model performance metrics, including mean AUC (Area Under the Curve), COR (correlation coefficient), TSS (True Skill Statistic), and deviance, which represents the amount of variation remaining after model fitting for the model considering TSM.

Methods	AUC	COR	TSS	Deviance
GLM	0.85	0.36	0.63	0.47
SVM	0.84	0.35	0.58	0.52
MARS	0.87	0.44	0.67	0.58
RF	0.91	0.54	0.71	0.39
BRT	0.9	0.51	0.69	0.45
MaxEnt	0.89	0.47	0.67	0.62

Figure 4. 95% significance confidence intervals from the ensemble modelling

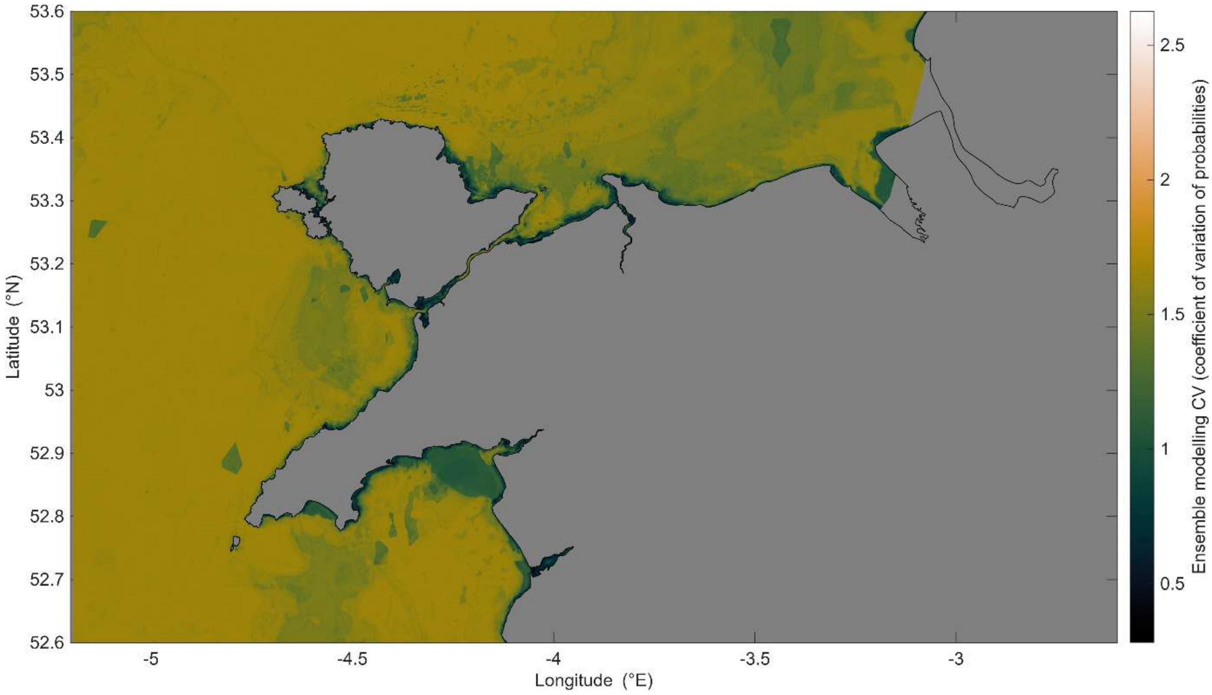

Figure 5. Coefficient of variation of predicted probabilities from the ensemble model, showing the level of agreement among the six modelling approaches included in the ensemble.

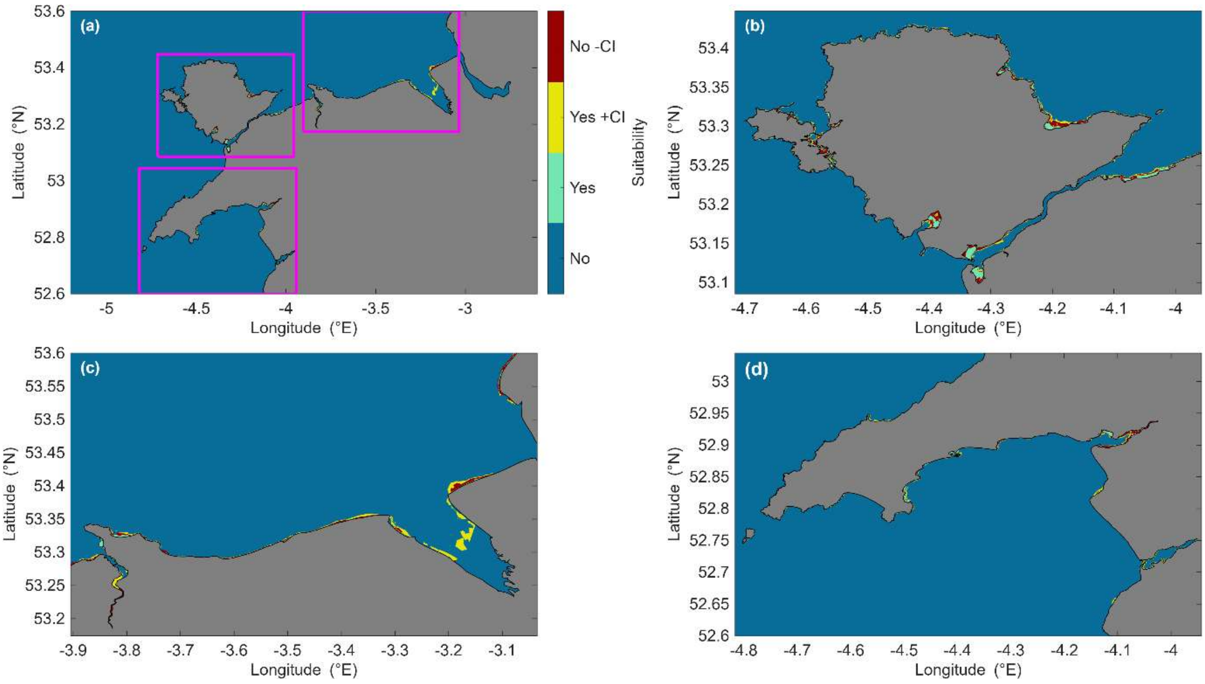

Figure 6. Predicted suitability of seagrass habitat using the threshold optimisation method, including the influence of ensemble model (without TSM) confidence intervals. Suitable habitats (all four classes of suitability combined together) are shown in green, non-suitable habitats in blue, areas that become suitable when using the upper confidence interval bound in yellow, and areas that become non-suitable when using the lower confidence interval bound in red. The four panels show: (a) North Wales study area, (b) zoomed view of Anglesey, (c) Llŷn Peninsula and Cardigan Bay, and (d) coastline from Colwyn Bay to Liverpool Bay.

Relative contribution of environmental variables

The relative contribution analysis identified bed shear stress as the dominant predictor of habitat suitability across both model configurations. In the model excluding TSM, bed shear stress contributed 60.4% and 37.7% based on the correlation metric and AUC, respectively, highlighting the importance of hydrodynamic conditions in structuring *Z. noltei* habitat suitability. Following the inclusion of TSM, the contribution of bed shear stress decreased to 48.0% and 26.6%, respectively.

A similar reduction was observed for average seabed water flow speed, with contributions declining from 14.8% and 14.1% to 8.7% and 7.5% (correlation metric and AUC, respectively). Salinity maintained a consistent moderate influence across both model configurations, but also showed a decrease in relative importance, from 10.1%

and 9.8% to 6.4% and 6.2%. These reductions suggest shared explanatory information among predictors and indicate that TSM captured part of the environmental variability previously explained by hydrodynamic variables.

In contrast, the relative importance of water depth increased from 12.1% and 10.5% to 18.2% and 12.6% following the inclusion of TSM. However, this increase is likely influenced by limitations in resolving presence records located closest to the shoreline, potentially reducing the representation of nearshore habitat conditions and causing shallow areas to not be considered as suitable in the TSM-based model. A comparable interpretation may apply to seabed slope, whose contribution decreased slightly from 10.2% and 9.5% to 7.8% and 5.7% (correlation metric and AUC, respectively), as the steepest slopes also occur predominantly near the shoreline.

TSM itself contributed modestly (2.7%) but improved overall model performance, suggesting that it may interact with other environmental drivers rather than acting as an independent limiting factor. TSM altered the relative importance of several environmental predictors, particularly reducing the contribution of bed shear stress while increasing that of water depth. This supports previous studies suggesting that light availability and turbidity-related processes are important secondary controls on *Z. noltei* distribution and productivity. Sediment characteristics and distance to shore showed relatively low contributions overall, indicating a limited influence at the spatial resolution considered.

Table 4. Summary of the relative contribution of the environmental variables to the model.

Environmental variable	Correlation metric (%) (without TSM)	AUC (%) (without TSM)	Correlation metric (%) (with TSM)	AUC (%) (with TSM)
Water depth	12.1	10.5	18.2	12.6
Bed shear stress	60.4	37.7	48	26.6
Salinity	10.1	9.8	6.4	6.2
Suspended matter concentration	-	-	2.7	2.7
Sediment type	1.7	2.6	3.8	2.4
Gravel %	1.3	1.8	1.1	0.6
Average water flow speed at seabed	14.8	14.1	8.7	7.5
Seabed slope	10.2	9.5	7.8	5.7
Distance to shore	1.3	2.3	1.2	1.8

Discussion

Environmental variability of suitable areas

The ensemble habitat suitability models helped to quantify a relatively constrained environmental niche for *Z. noltei* in the North Wales study site, with suitable habitats generally occurring in shallow, sheltered coastal environments characterised by low hydrodynamic energy and fine to mixed sediments (Figure 7; Table 5). Across both ensemble configurations, suitable areas were typically associated with shallow water depths between approximately −4 and 7 m, low bed shear stress (0-3 N m^{-2}), gentle seabed slopes (0-2 degrees), and close proximity to the shoreline (0-1 km). Suitable habitats also occurred under a large range of monthly mean seabed salinity conditions (18-34 psu) and relatively cool monthly minimum seabed temperatures (4.7–8.7 °C). Sediment distributions indicated a preference for mud, gravelly muddy sand, sand, reef, and rock-and-boulder substrates, while gravel content remained consistently low (<5%). The inclusion of total suspended matter (TSM) in the model slightly broadened the environmental envelope for several variables, particularly salinity and current speed, while also identifying suitable habitats within a moderate TSM range of approximately 17–50 mg L^{-1}. Compared with the model excluding TSM, the TSM-inclusive model predicted suitability in areas with slightly higher current velocities, greater distances from shore, and lower seabed slopes, suggesting that suspended sediment dynamics may partially mediate the influence of hydrodynamic exposure on *Z. noltei* distribution.

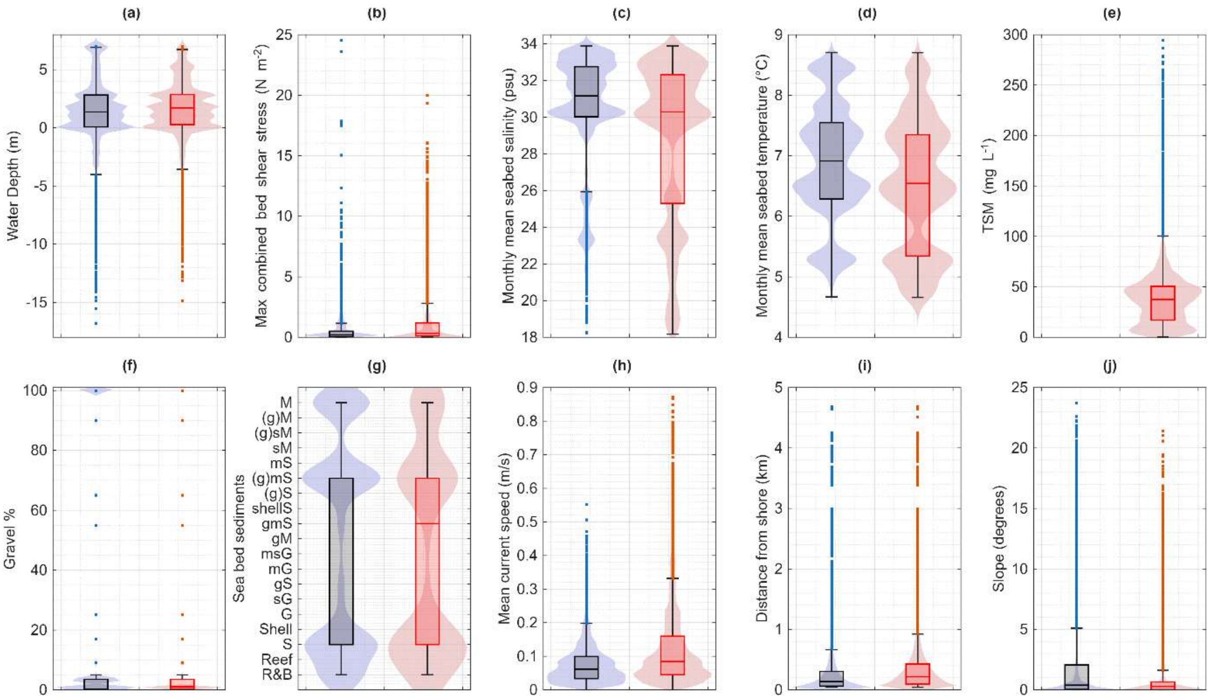

Figure 7. Distribution of environmental variables within suitable habitat areas (including all four suitability classes) for the ensemble models without TSM (blue) and with TSM (red). Violin plots illustrate the density distribution of each environmental variable, while embedded box plots show the median and interquartile range (25th and 75th percentiles). Points located beyond the whiskers represent outliers. The environmental variables presented are: (a) water depth, (b) bed shear stress, (c) minimum seabed salinity, (d) minimum seabed temperature, (e) total suspended matter (TSM), (f) gravel percentage, (g) sediment type, (h) mean current speed, (i) distance from shore, and (j) seabed slope.

Table 5. Summary of lower and upper quartiles of environmental factors determining Zostera noltei habitat suitability.

Environmental factors	Suitable range (no TSM)	Suitable range (with TSM)
Water depth (m)	[-4, 6.9]	[-3.6, 6.1]
Bed shear stress (N/m²)	[10^{-18}, 1.15]	[10^{-5}, 2.8]
Salinity (psu)	[25.9, 33.9]	[18.2, 33.9]
Temperature (°C)	[4.7 8.7]	[4.7 8.7]
TSM (mg/L)	-	[17, 50]
Gravel %	[0.2, 5]	[0.2, 5]
Sed bed sediments (Folk16 classification)	M (mud), (g)mS (gravelly muddy sand), S (sand), Reef, R&B (Rocks & boulder)	M (mud), (g)mS (gravelly muddy sand), S (sand), Reef, R&B (Rocks & boulder)
Mean currents speed (m/s)	[10^{-5}, 0.2]	[10^{-4}, 0.3]
Distance from shore (km)	[0.04, 0.7]	[0.4, 0.9]
Slope (degrees)	[0.03, 2.1]	[0.01, 0.6]

Comparison with other *Z. noltei* HSM studies

Other habitat suitability modelling (HSM) studies for *Zostera noltei* have identified broadly similar environmental controls, although the relative importance of predictors varies among regions. Previous studies conducted in the Thames Estuary, UK (Grigg et al., 2025), and the Basque Country, Spain (Valle et al., 2011) provide useful comparisons with the present study. In the Thames Estuary, Grigg et al. (2025) identified distance from shore as the most important predictor of *Z. noltei* suitability (39.2%), whereas bed shear stress contributed relatively little to the model. These differences likely reflect regional environmental contrasts. The Thames Estuary is comparatively sheltered from wave exposure and characterised by gentler coastal morphology and bathymetry than the more exposed and topographically complex North Wales coastline. Grigg et al. (2025) also found suspended matter concentration to be more influential (12.9%) than in the present study, likely because the Thames Estuary is generally more turbid than the North Wales coast, thereby imposing stronger constraints on *Z. noltei* development. Despite differences in the relative importance of environmental drivers, the environmental ranges associated with suitable habitats were broadly consistent between studies. Whereas Grigg et al. (2025) did not investigate sediment characteristics, Valle et al. (2011) focused primarily on sediment-related variables. In their study, sediment grain size was identified as the dominant predictor of *Z. noltei* distribution (70%), followed by intertidal height (33%). Gravel percentage was also much more influential than in the present study (12%), possibly reflecting differences in spatial scale, sediment dataset resolution or geomorphology between study areas. In the present study, hydrodynamic variables may also indirectly capture part of the sedimentary variability, thereby reducing the apparent independent contribution of sediment descriptors. Valle et al. (2011) further reported a preference for fine sandy sediments with a mean gravel content of 0.81%, together with a relatively narrow elevation range associated with tidal submersion. These findings are consistent with the environmental preferences identified in the present study.

Limitations and recommendations

Overall, the habitat suitability models demonstrated good predictive performance. High predictive accuracy was achieved across both simpler statistical approaches and more flexible machine-learning algorithms, suggesting that model performance was driven by strong and consistent relationships between *Z. noltei* occurrence and environmental conditions. Ensemble predictions were spatially coherent and ecologically realistic, with suitable habitats primarily restricted to shallow, sheltered coastal environments known to support *Z. noltei*. Uncertainty analyses based on confidence intervals and coefficients of variation indicated relatively low variability within core suitable habitats, demonstrating good consistency among model replicates. In addition, multicollinearity among predictors was reduced prior to modelling through variance inflation factor (VIF)-based variable selection, thereby limiting the risk of spurious relationships. Spatial autocorrelation among occurrence records was also minimised through spatial thinning procedures.

As discussed in the results, interpretation of the TSM-based model should be undertaken cautiously because the satellite-derived TSM dataset did not fully extend into shallow nearshore areas. As a result, some occurrence records located close to the shoreline were excluded from model calibration, potentially biasing the environmental representation of nearshore habitats and reducing the contribution of shoreline-related variables. Similar limitations associated with environmental data availability and high spatial resolution have also been acknowledged in previous *Z. noltei* habitat suitability studies (Grigg et al. 2025).

Additionally, the sediment dataset used in the present study may not fully capture the sedimentary characteristics relevant to *Z. noltei* distribution. The only available sediment information was based on the Folk16 classification scheme, which categorises seabed sediments into 16 classes according to the relative proportions of mud, sand, and gravel. Although this classification provides a useful general description of sediment composition, it remains relatively coarse in spatial and thematic resolution and only indirectly represents sediment grain size. Previous work by Valle et al. (2011) demonstrated that sediment grain size was one of the most important predictors of *Z. noltei* suitability in the Basque Country. This suggests that access to a higher-resolution sediment grain-size dataset for North Wales could substantially improve future habitat suitability modelling. If such a dataset is not currently available, the development of a dedicated regional sediment grain-size map would represent an important priority for future research.

Another limitation identified in the present HSM study was that suitability threshold values decreased with increasing numbers of background samples, reflecting greater environmental overlap between occurrence and pseudo-absence locations. This pattern was partly related to the realistic coastal background sampling strategy, which used randomly generated pseudo-absence points within a 2 km buffer surrounding *Z. noltei* occurrences. Although this approach improved ecological realism and reduced the likelihood of sampling environmentally unrealistic absences, it also reduced artificial environmental separation between presences and pseudo-absences, resulting in more conservative estimates of suitable habitat. Conversely, using too few pseudo-absence points (e.g., numbers similar to the occurrence dataset) may inadequately represent the available environmental space and produce unstable model thresholds, including high variability in specificity between model runs. Increasing the number of pseudo-absence points generally stabilised model performance; however, it also made specificity easier to maximise because many additional low-suitability background cells were included. As a consequence, model optimisation tended to favour lower suitability thresholds in order to maintain sensitivity.

Sensitivity analyses indicated that, for the scale of this study, using 1,000 pseudo-absence points within the realistic coastal background provided the best compromise between ecological realism and model stability, while also reducing variance among model runs. Furthermore, to avoid over-interpreting binary suitable/unsuitable predictions based on a single threshold value, habitat suitability was classified into four categories ("low", "moderate", "good", and "excellent"), which provided a more ecologically meaningful representation of habitat suitability gradients. Another potential way to address threshold sensitivity would be to expand the study area and incorporate additional occurrence records. Although further *Z. noltei* observations are available from southern Wales, these data were not included in the present study because high-resolution environmental datasets were not consistently available beyond the North Wales region.

Restoration potential and future work

The two habitat suitability model (HSM) configurations, with and without the inclusion of total suspended matter (TSM), produced broadly similar spatial patterns of suitable habitat for *Zostera noltei*. The ensemble model excluding TSM identified approximately 1,422,060 m^2 of suitable habitat (including all four suitability classes), whereas the model incorporating TSM identified 1,348,140 m^2. The approximately 5% reduction in suitable habitat area in the TSM-based model was primarily related to the reduced spatial extent available for modelling, caused by the lower nearshore coverage of the satellite-derived TSM dataset. Consequently, the TSM-based model tended to increase suitability scores in areas already identified as highly suitable by the non-TSM model, reflecting the smaller overall area classified as suitable (Figures 8–19 in the Appendix).

The modelling results identified several highly suitable areas for *Z. noltei* restoration or future colonisation. The most suitable sites included Tremadog Bay (Figure 10), several embayments along the southern Llŷn Peninsula near Abersoch and Pwllheli (Figure 11), Cemaes Bay and Dulas Bay on the northern coast of Anglesey (Figure 14), Red Wharf Bay (Figure 15), and the northeastern part of Conwy Sands together with Llandudno Bay (Figure 16). In addition, Caernarfon and Malltraeth (Figure 12), the Inland Sea near Holy Island (Figure 13), and the Lavan Sands (Figure 15) also exhibited high suitability scores, although *Z. noltei* presence records already exist at these locations.

These identified sites represent important targets for future restoration and conservation planning. Future research should assess how projected sea-level rise and associated coastal changes may affect the long-term suitability of these habitats. In particular, identifying sites that are less vulnerable to sea-level rise could help prioritise areas with the greatest potential for long-term restoration success and habitat persistence.

Ground-truthing

Initial ground-truthing using existing data was undertaken to verify the outputs of the habitat suitability model and to assess whether areas predicted to be highly suitable for restoration of dwraf eelgrass, *Zostera noltei*, exhibited site conditions consistent with successful seagrass establishment and long-term persistence. The purpose of this process was to inform validation of fine-scale model predictions.

The habitat suitability model output extends from northern Cardigan Bay to Liverpool Bay, but this initial ground-truthing exercise focused on the Menai Strait and Conwy Bay SAC.

Results

Collation of existing datasets

A comprehensive assessment using available data layers considered any activities that may affect restoration success. The presence of marine assets such as submarine cables and pipelines was assessed to avoid conflicts with infrastructure. Existing nature conservation designations was considered, which may provide both opportunities and regulatory constraints. Fishing regulations were reviewed to determine existing protections (ie. inshore fisheries legislation).

Datalayers were unavailable for some recreational activities which could have a potentially significant impact on restoration success, anchoring, mooring, and launching. Royal Yachting Association (RYA) UK Coastal Atlas of Recreational Boating dataset utilises Automatic Identification System (AIS) data to indicate the intensity of boating activity in coastal waters around the UK. Figure 8 provides an indication of boating activity within the Menai Strait and Conwy Bay SAC, with higher intensity recorded within navigational channels and surrounding harbours, marinas and ports.

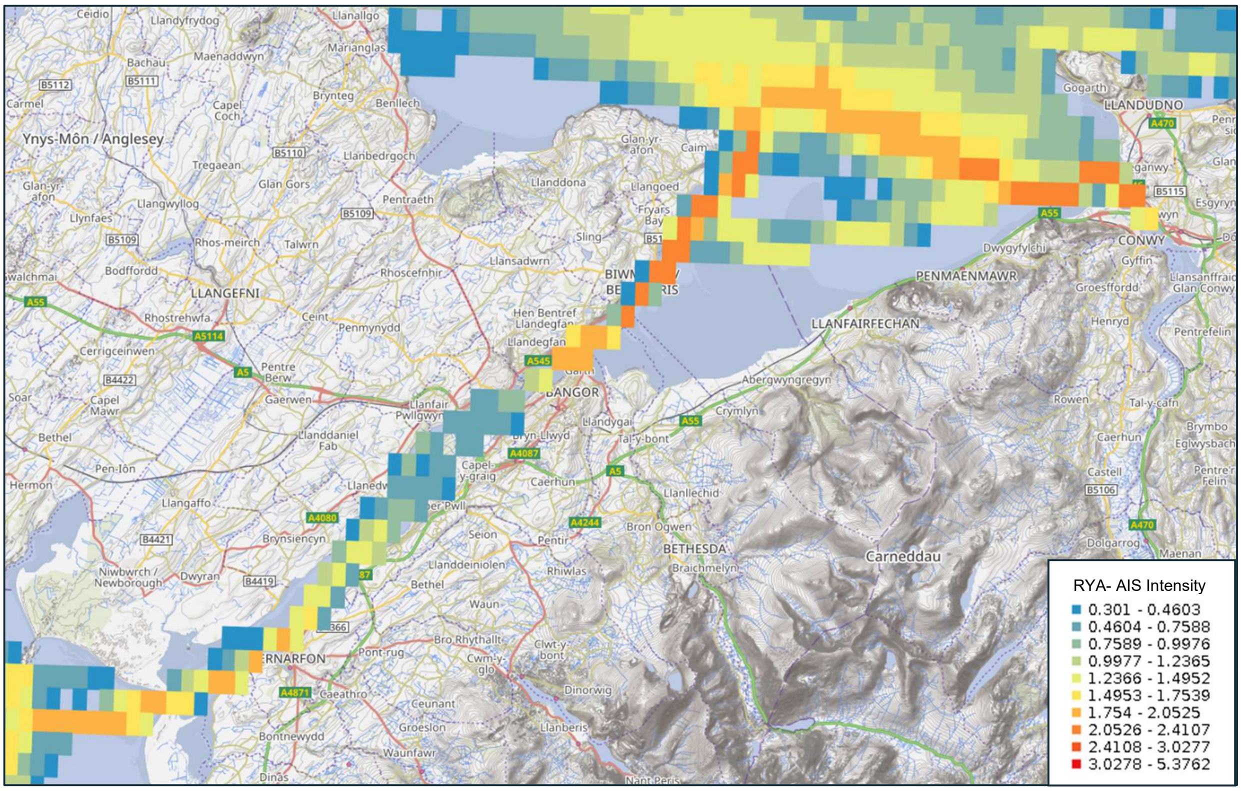

Figure 8. Map to indicate the intensity of boating activity in the Menai Strait and Conwy Bay SAC from the Royal Yachting Association (RYA) UK Coastal Atlas of Recreational Boating dataset which utilises Automatic Identification System (AIS) data. Published data in August 2019. © Data reproduced under licence from the Royal Yachting Association. Sourced from DataMap Wales.

The dwarf eelgrass restoration potential map (Figure 3), where a suitability threshold of 0.43 was applied, a parameter generated by the model (Figure 6) was overlaid with existing datalayers sourced from DataMap Wales. Factors including significant activities (navigational dredging, ports and harbours), fishing regulations (several and regulating orders), existing nature conservation designations (MPAs) and historical and maritime assets (designated wrecks and scheduled monuments) were assessed within this region (Figure 9). Existing *Zostera noltei* spatial extent and location data was also overlaid as a marine habitat of "Principal Importance" under Section 7 and are regarded as "threatened or declining" under OSPAR in Wales.

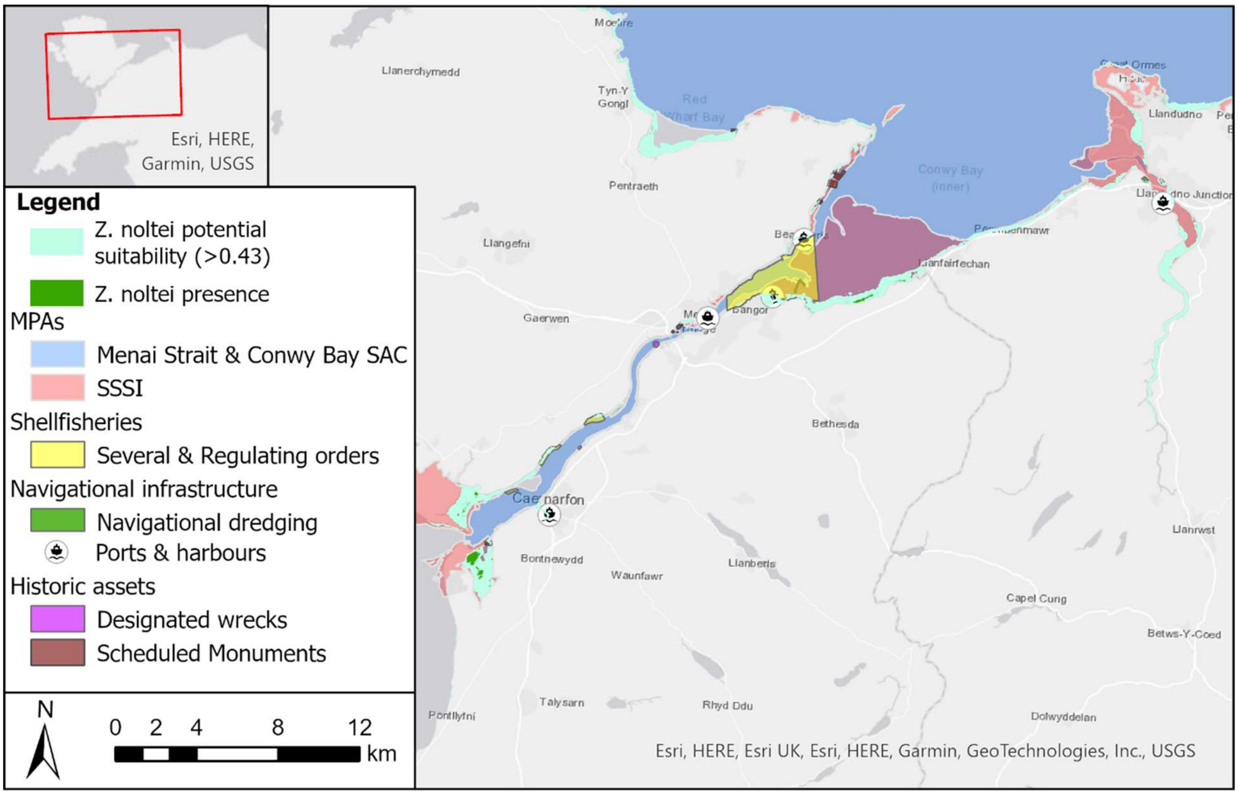

Figure 9. Map of the dwarf eelgrass potential suitability (>0.43 threshold) areas (light blue) within the Menai Strait and Conwy Bay SAC overlaid with datalayers for Z. noltei presence, MPAs, shellfisheries, navigational infrastructure, historic assets. Contains Natural Resources Wales information © Natural Resources Wales and Database Right. All rights Reserved. Contains Ordnance Survey Data. Ordnance Survey Licence number AC0000849444. Crown Copyright and Database Right. Derived in part from data provided under licence by the British Geological Survey © NERC

Recommendations

Site-specific characterisation and ground-truthing surveys should be designed to validate habitat suitability model outputs for *Zostera noltei* (dwarf eelgrass) and to identify the most suitable locations for conservation management and potential restoration. Certain areas predicted as potentially suitable for *Z. noltei*, support existing seagrass (such as Y Foryd, Traeth Lafan, Treath Melynog). Sites close to established beds may have a greater likelihood of natural recolonisation and are generally more favourable for restoration because of natural propagule supply, genetic connectivity, and potential donor material availability. However there are further criteria that need to be considered (Gamble et al., 2021). It is important to confirm whether areas predicted by the HSM supported dwarf eelgrass historically but are now unoccupied (Green et al., 2021). However Welsh estuaries have experienced major alterations including land reclamation, embankment construction, and channel rerouting altering sediment dynamics, water quality and habitats present (Unsworth et al., 2026). Restoration efforts should not aim to return to a historical state or baseline, but focus on building ecosystem resilience, biodiversity and wellbeing of coastal communities.

Survey sites should be selected through a process of elimination, considering logistical and environmental constraints. Site-specific surveys would confirm the presence of the environmental conditions necessary for successful recolonisation or restoration and identify any pressures that would limit long-term establishment and persistence. This process should combine model outputs, historical records, local knowledge, site-specific environmental data, and practical project considerations.

Understanding environment and pressures

Incorporating field-based observations improves confidence in the final site selection. For example, water depth, slope, salinity, temperature, and total suspended matter were factors considered in the HSM but the data was derived from satellite imagery. Existing environmental conditions should be assessed to determine whether they meet the habitat requirements for dwarf eelgrass. Existing monitoring of presence and extent of seagrass in the Menai Strait and Conwy Bay SAC is conducted by NRW under the Water Framework Directive (WFD), Habitats Directive, Environment (Wales) Act 2016 Section 7 and by researchers at Bangor University. Current monitoring frequency and expanse leaves large gaps in our overall knowledge of seagrass extent and health in Wales (Butterworth et al., In Review).

Information on key parameters including turbidity and total suspended solids (TSS) is needed to assess the extent to which suspended sediments reduce light penetration. Sustained adequate light availability (Photosynthetically Active Radiation) is one of the most important determinants of seagrass survival. Water depth and elevation relative to tidal datums to define inundation frequency. Water quality also needs to be assessed for factors including salinity, temperature, nutrient concentrations, and contaminants. Site-specific water quality testing is needed in addition to existing monitoring under the

Water Frameworks Directive (Figure 10). Predominant sediment type and properties need to be characterised. Benthic communities need to be assessed as bioturbators can either enhance sediment oxygenation or destabilise the seabed, depending on their abundance and behaviour. Wave exposure, and tidal current speeds can be recorded using loggers to understand if hydrodynamic conditions are appropriate.

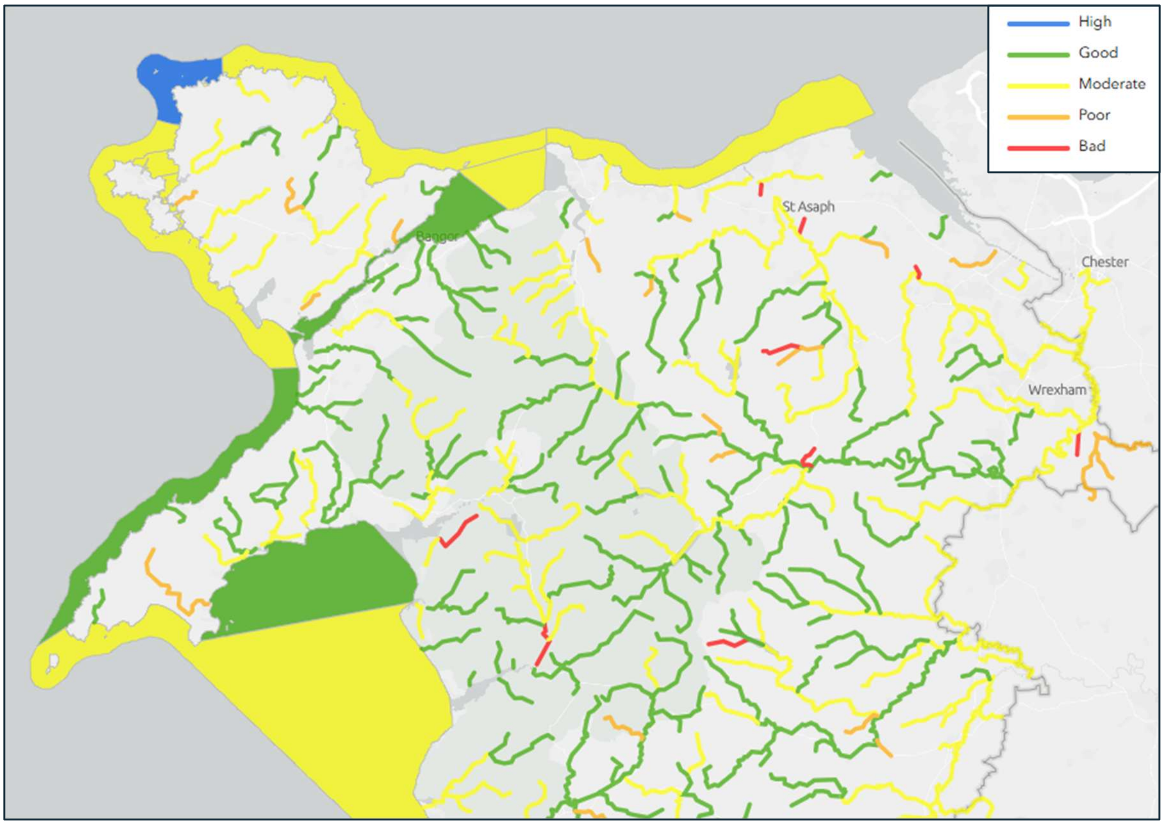

Figure 10. Water Watch Wales map provides information about each individual waterbody from Water Framework Directive (WFD) Regulations Cycle 3 Classification (Interim 2024) Rivers, Waterbodies and Coastal Water graded from high (blue) to bad (red) condition.

Areas within the protected site network, especially where *Z. noltei* is a protected feature (such as Traeth Lafan SSSI) can provide some level of protection. Restoration within a protected site may also cause logistical challenges (site access, disturbance to important wading birds etc.) and activities may also require additional consents. These sites are still affected by environmental and anthropogenic pressures.

Local knowledge is often invaluable for understanding the intensity and seasonality of current and historical disturbance from anthropogenic pressures, especially where accessible data is limited. Proximity to ports and harbours can be a constraint (increased maritime traffic) but more information is needed about anchoring, moorings, launching and vehicle access which can damage seagrass. NRW carried out surveys in 2019 identifying areas of Welsh seabed potentially vulnerable to anchoring, mooring and launching. There were no priority locations of seagrass that are potentially impacted within the Menai Strait and Conwy Bay SAC but it was reported that seagrass comes into very close proximity to a launching site is at Y Foryd (Grant, 2021). Further investigations would be needed to verify the level of activity taking place and any evidence that the habitat is being impacted by the recreational boating activities. Protective measures can be put in place (such as eco-moorings, awareness signage, voluntary no-anchoring site) where disturbance poses a risk.

Important shellfisheries, historical assets and areas near navigational/ maintenance dredging areas should be avoided. Inshore vessel monitoring systems (iVMS) are installed on fishing vessels and transmit information to the fisheries authority, Welsh Government. However, a spatial layer of the iVMS data collected is currently not available to better understand fishing activity in the area. Information is needed on the location and intensity of bait digging. NRW investigated bait digging at 12 sites in Wales and recorded the greatest total area of digging was 33.5 ha on Y Foryd (Perrins et al., 2020). Surveys were conducted at spring low water in winter which posed challenges (short daylight, poor weather conditions). More bait digging activity is also likely during summer months if bait is collected for the visitor market (Perrins et al., 2020). Further investigations during summer months are needed to understand the level of bait digging taking place and any evidence that the *Z. noltei* is being impacted.

Ecological risks, such as wasting disease caused by the protist called *Labyrinthula zosterae* needs to be considered. Although populations of *Z. noltei* do not suffer losses to the same extent as *Z. marina* as the disease is less likely in low salinities (Bockelmann et al., 2012). Seagrass is also an important food source for grazing wildfowl. Brent geese primarily fed on *Zostera* in their wintering grounds in Britain, Ireland and continental Europe before flying north to breed in the Arctic (Ganter, 2000). Healthy seagrass meadows can regenerate fully until the following season, however overgrazing can cause long-term reductions in seagrass biomass or coverage (Kollers et al., 2017).

Short-term climate change implications could be incorporated into restoration planning to identify priority sites with greater abiotic stability for improving the resilience and success of future marine restoration initiatives. Predicted changes in sustained light levels due to increased turbidity, sea-level rise, increased storminess and wave exposure, heat stress and shifts in salinity regimes may affect the stability and persistence of restored seagrass beds over time. Marine heatwaves contributed to the failure of a large-scale intertidal *Z. marina* restoration effort in Noth Wales where over 1.1 million seeds had been sown (Thomas et al., 2026; Unsworth et al., 2026). However, long-term scenarios should not deter restoration trials taking place as provide key lessons learnt for future restoration efforts.

The long-term dynamics of *Z. noltei* and the species resilience and survival to these increasing pressures is unknown. Intertidal *Z. noltei* extent has increased in recent years in parts of Wales including within the Pembrokeshire Marine SAC, particularly in Angle Bay, with possible new patches discovered (Moore et al., 2021; Jackson-Bué et al., 2025; West et al., 2025) Certain *Z. noltei* populations have been reported to be robust to high disturbance, turbidity and nutrient enhancement (Bertelli et al., 2018). Management of waterways appears to have a positive impact on *Z. noltei* extent, although existing long-term trends are limited and show variability (Bertelli et al., 2018).

Consultation and collaborative working

Early and sustained engagement with regulators, harbour authorities, fisheries representatives, conservation organisations, recreational users and other interested parties is strongly recommended to identify constraints and build support and to codesign restoration activities. Any restoration needs to be operational, place-based, and co-designed with local actors and communities, as seen in existing restoration projects for *Z. marina* in North Wales (Project Seagrass, Seagrass Ocean Rescue).

Land ownership and seabed rights should be confirmed at an early stage. In most cases, the seabed is owned by The Crown Estate, although local exceptions may apply. This is also a key consideration for accessing to the shoreline and transporting equipment for monitoring.

Following ground-truthing and consultation, sites can be ranked according to their overall suitability and the specific drivers of the project. Ranking criteria may include environmental suitability, ecological risk, likelihood of long-term persistence, logistical feasibility, local support, and regulatory complexity.

This process enables restoration practitioners and collaborators to identify the most suitable locations for active and/or passive restoration initiatives and to prioritise sites with the greatest probability of ecological and operational success.

Conclusion

This study developed a high-resolution ensemble habitat suitability model for *Z. noltei* along the North Wales coastline using a combination of statistical and machine-learning approaches integrated within an ensemble modelling framework. The results demonstrated that in this region habitat suitability for *Z. noltei* is primarily controlled by hydrodynamic conditions, particularly bed shear stress, together with shallow water depth and sheltered nearshore environments. Suitable habitats were consistently associated with intertidal embayments, estuarine margins, and low-energy coastal zones characterised by low to moderate current velocities and gentle seabed slopes.

The inclusion of total suspended matter (TSM) slightly improved overall model performance and modified the relative contribution of several environmental predictors, suggesting that turbidity-related processes interact with hydrodynamic controls on *Z. noltei* distribution. However, limitations in the spatial coverage of the satellite-derived TSM dataset reduced the representation of shallow nearshore habitats and introduced potential biases in shoreline-related predictors. Despite this limitation, both model configurations produced broadly similar spatial patterns of habitat suitability, indicating that the dominant environmental controls on *Z. noltei* distribution were consistently captured.

Several areas of high restoration potential were identified, particularly around Tremadog Bay, sheltered embayments along the southern Llŷn Peninsula, northern Anglesey, Red

Wharf Bay, Conwy Sands, and Llandudno Bay. These locations provide important targets for future restoration and conservation planning and may support natural expansion or assisted recovery of *Z. noltei* meadows.

Overall, this study demonstrates the value of combining high-resolution environmental datasets with ensemble habitat suitability modelling to support coastal ecosystem management. The modelling framework developed here provides a transferable approach for identifying suitable seagrass restoration sites in dynamic coastal environments. Future work should focus on improving nearshore environmental datasets, particularly sediment grain-size and total suspended sediment concentration products, while also assessing the long-term influence of climate change and sea-level rise on habitat suitability and restoration success.

References

Araújo, M.B. and New, M., 2007. Ensemble forecasting of species distributions. *Trends in ecology & evolution*, *22*(1), pp.42-47.

Bertelli, C.M., Bennett, W., Bull, J.C., Karunarathna, H., Reeve, D.E. and Unsworth, R.K., 2021. Habitat Suitability modelling for informing Zostera marina restoration in Wales.

Bertelli, C.M., Robinson, M.T., Mendzil, A.F., Pratt, L.R. and Unsworth, R.K., 2018. Finding some seagrass optimism in Wales, the case of Zostera noltii. *Marine pollution bulletin*, *134*, pp.216-222.

Bertelli, C.M., Stokes, H.J., Bull, J.C. and Unsworth, R.K., 2022. The use of habitat suitability modelling for seagrass: A review. *Frontiers in Marine Science*, *9*, p.997831.

Bockelmann, A.C., Beining, K. and Reusch, T.B., 2012. Widespread occurrence of endophytic Labyrinthula spp. in northern European eelgrass Zostera marina beds. *Marine Ecology Progress Series*, *445*, pp.109-116.

Breiman, L., 2001. Random forests. *Machine learning*, *45*(1), pp.5-32.

Butterworth, E., Rice, D., and Fox, E. (In Review). *Monitoring: Review of Seagrass Health Monitoring*. Natur am Byth! Marine Conservation Society.

Cortes, C. and Vapnik, V., 1995. Support-vector networks. *Machine learning*, *20*(3), pp.273-297.

Folk, R.L., 1954. The distinction between grain size and mineral composition in sedimentary-rock nomenclature. *The Journal of Geology*, *62*(4), pp.344-359.

Friedman, J.H., 2001. Greedy function approximation: a gradient boosting machine. *Annals of statistics*, pp.1189-1232.

Friedman, J.H., 1991. Multivariate adaptive regression splines. *The annals of statistics*, *19*(1), pp.1-67.

Gamble C., Debney, A., Glover, A., Bertelli, C., Green, B., Hendy, I., Lilley, R., Nuuttila, H., Potouroglou, M., Ragazzola, F., Unsworth, R. and Preston, J., (eds) 2021. *Seagrass Restoration Handbook*. Zoological Society of London, UK., London, UK.

Ganter, B., 2000. Seagrass *Zostera* spp. as food for brent geese *Branta bernicla*: an overview. *Helgoland Marine Research*, 54, pp. 63–70.

Grant, L., 2021. *Identifying areas of Welsh seabed potentially vulnerable to anchoring, mooring and launching*. NRW Evidence Report No: 556, 65pp, Natural Resources Wales, Bangor

Grant, W.D. and Madsen, O.S., 1979. Combined wave and current interaction with a rough bottom. *Journal of Geophysical Research: Oceans*, *84*(C4), pp.1797-1808.

Green, A.E., Unsworth, R.K., Chadwick, M.A. and Jones, P.J., 2021. Historical analysis exposes catastrophic seagrass loss for the United Kingdom. *Frontiers in plant science*, *12*, p.629962.

Grigg, M., Cucknell, A., Marten, K., Cox, T. and Yesson, C., 2025. Habitat suitability modelling for restoration of intertidal seagrass, Zostera noltei: A case study from the Greater Thames Estuary, UK. *Estuarine, Coastal and Shelf Science*, *312*, p.109039.

Guisan, A., Thuiller, W. and Zimmermann, N.E., 2017. *Habitat suitability and distribution models: with applications in R*. Cambridge University Press.

Jackson-Bué, M., Wynter, E., Cuthbertson, S. and Hatton-Ellis., M. 2025. *Condition Assessments for the Designated Features of Ardal Cadwraeth Arbennig Sir Benfro Forol / Pembrokeshire Marine Special Area of Conservation.* NRW Evidence Report No. 909, 359pp, Natural Resources Wales, Cardiff

Kaskela, A.M., Kotilainen, A.T., Alanen, U., Cooper, R., Green, S., Guinan, J., van Heteren, S., Kihlman, S., Van Lancker, V., Stevenson, A. and EMODnet Geology Partners, 2019. Picking up the pieces—harmonising and collating seabed substrate data for European maritime areas. *Geosciences*, *9*(2), p.84.

Kollars, N.M., Henry, A.K., Whalen, M.A., Boyer, K.E., Cusson, M., Eklöf, J.S., Hereu, C.M., Jorgensen, P., Kiriakopolos, S.L., Reynolds, P.L. and Tomas, F., 2017. Meta-analysis of reciprocal linkages between temperate seagrasses and waterfowl with implications for conservation. *Frontiers in plant science*, *8*, p.2119.

Marmion, M., Parviainen, M., Luoto, M., Heikkinen, R.K. and Thuiller, W., 2009. Evaluation of consensus methods in predictive species distribution modelling. *Diversity and distributions*, *15*(1), pp.59-69.

McCullagh, P. and Nelder, J.A., 1989. Generalized Linear Models. 2nd Edition, Chapman and Hall, London.

Moore, J, Bunker, F. St P.D, Mercer, T., Howson, C.H. and Brazier, D.P. 2021. Wales intertidal SAC feature assessment summary 2004-2017. NRW Evidence Report No 063, 43pp, Natural Resources Wales, Bangor.

Naimi, B. and Araújo, M.B., 2016. sdm: a reproducible and extensible R platform for species distribution modelling. *Ecography*, *39*(4), pp.368-375.

Neill, S.P., 2024. Wave resource characterization and co-location with offshore wind in the Irish Sea. *Renewable Energy*, *222*, p.119902.

Perrins, J., Lush, M., Taylor, T., Holt, R. and Bunker, F., 2020. *Investigating the location and intensity of bait digging in Wales.* NRW Evidence Report Series No: 449, 190pp, NRW, Bangor.

Phillips, S.J., Anderson, R.P. and Schapire, R.E., 2006. Maximum entropy modeling of species geographic distributions. *Ecological modelling*, *190*(3-4), pp.231-259.

Smeaton, C., Hunt, C.A., Turrell, W.R. and Austin, W.E.N., 2021. *Marine sedimentary carbon stocks of the United Kingdom's exclusive economic zone. Frontiers in Earth Science, 9, 50* [online]

Soulsby, R., 1997. Dynamics of marine sands.

Thomas, O.R.R., Patterson, B.M.M., Rowland, C., Berthou, S., Worsfold, M., Yates, E., Keen, C., Den Haan, S. and Unsworth, R., 2026. MARINE HEAT WAVES ENDANGER THE REBUILDING OF MARINE LIFE. *Environmental Research Letters*.

Unsworth, R.K., Bullimore, B., Cullen-Unsworth, L.C. and Jones, B.L., 2026, January. 300 Years of Degradation in Wales Estuaries and Coasts. In *Natural Resources Forum*. Oxford, UK: Blackwell Publishing Ltd.

Unsworth, R.K., Comey, I. and Jones, B.L., 2026. Seagrass Meadows as a Foundational Concept for One Health. *BioScience*, p.biaf208.

Valle, M., Borja, Á., Chust, G., Galparsoro, I. and Garmendia, J.M., 2011. Modelling suitable estuarine habitats for Zostera noltii, using ecological niche factor analysis and bathymetric LiDAR. *Estuarine, Coastal and Shelf Science*, *94*(2), pp.144-154.

Ward, S.L., Robins, P.E., Owen, A., Demmer, J. and Jenkins, S.R., 2023. The importance of resolving nearshore currents in coastal dispersal models. *Ocean Modelling*, *183*, p.102181.

West, V.A., Upson, M. and Frost, N.J., 2025. *Impacts of bait collection on Welsh Marine Protected Areas.* NRW Evidence Report No: 862, 359pp, Natural Resources Wales, Cardiff.

Appendix

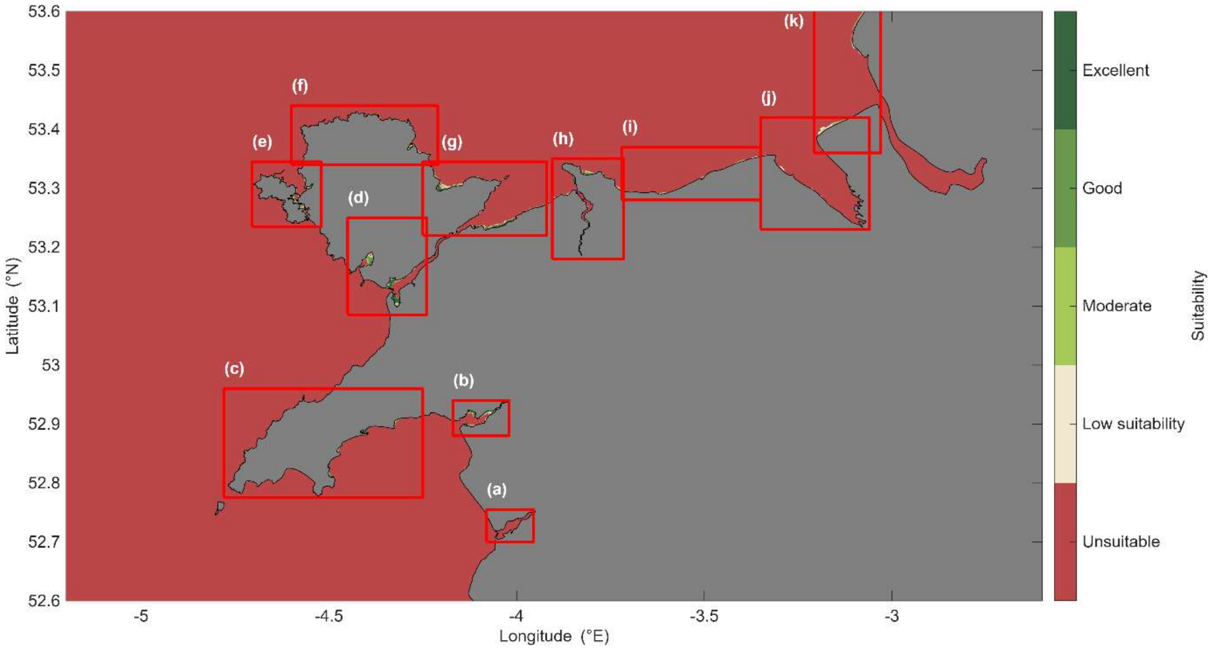

Figure 11. Predicted seagrass habitat suitability derived from the ensemble model (without TSM) using the threshold optimisation approach. Habitat suitability was classified into five categories: unsuitable, low, moderate, good, and excellent suitability. Eleven key areas were identified: (a) Barmouth Bay, (b) Tremadog Bay, (c) Llŷn Peninsula, (d) Caernarfon and Malltraeth Bay, (e) Holy Island, (f) North Anglesey, (g) Red Wharf Bay and Lavan Sands, (h) Conwy Bay, (i) Colwyn Bay, (j) River Dee, and (k) Liverpool Bay.

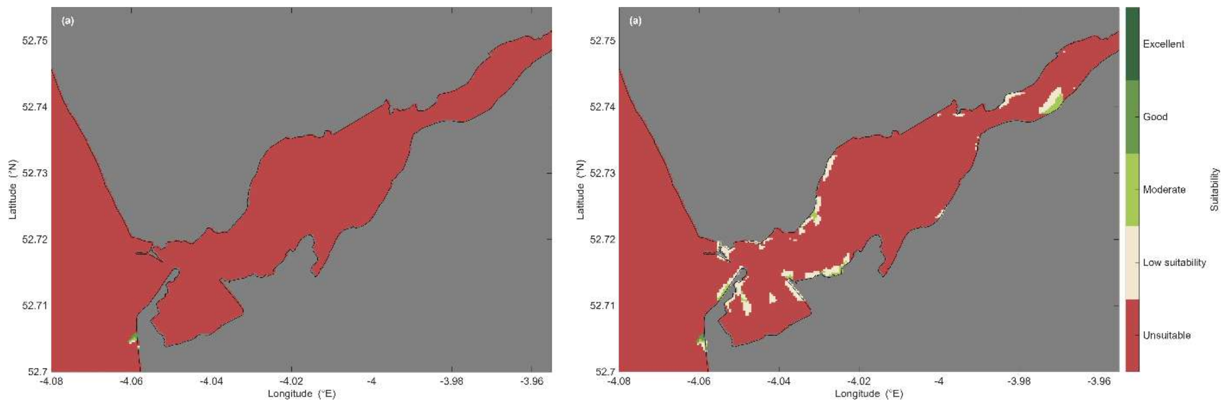

Figure 12: For Barmouth Bay, predicted seagrass habitat suitability derived from the ensmble model (without TSM on left panel and with TSM on right panel) using the threshold optimisation approach.

Habitat suitability was classified into five categories: unsuitable, low, moderate, good, and excellent suitability.

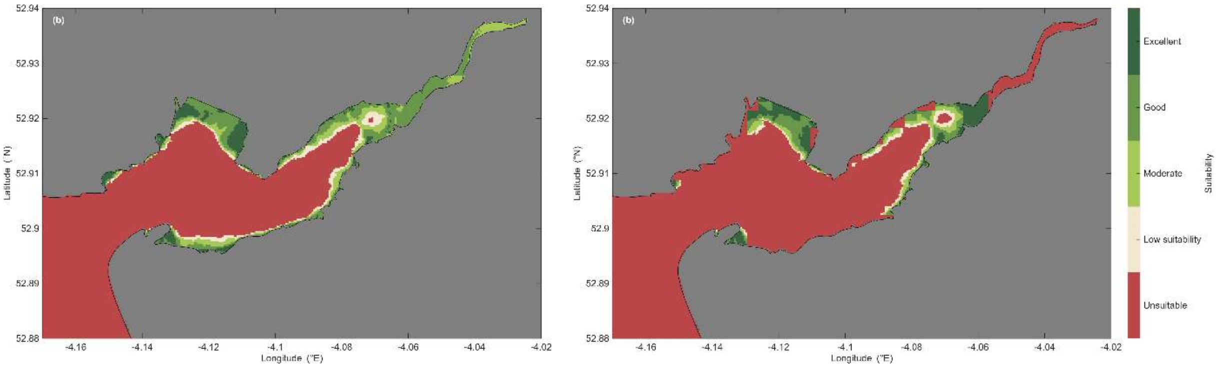

Figure 13: For Tremadog Bay, predicted seagrass habitat suitability derived from the ensemble model (without TSM on left panel and with TSM on right panel) using the threshold optimisation approach. Habitat suitability was classified into five categories: unsuitable, low, moderate, good, and excellent suitability.

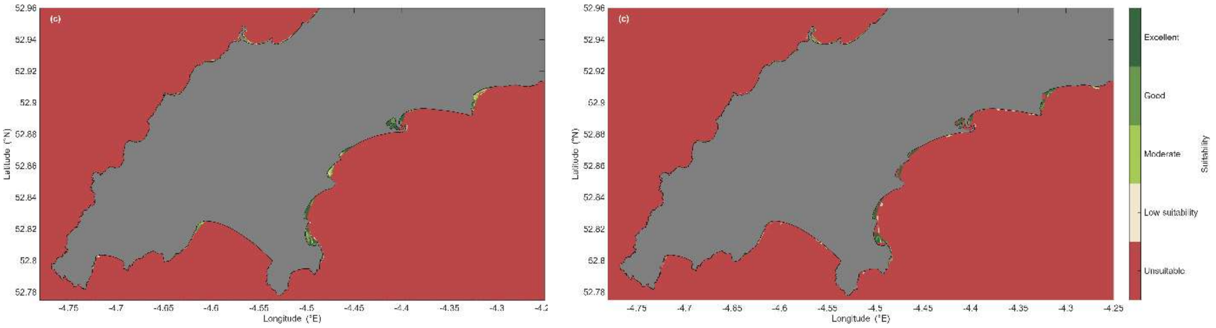

Figure 14: For the Llŷn Peninsula, predicted seagrass habitat suitability derived from the ensemble model (without TSM on left panel and with TSM on right panel) using the threshold optimisation approach. Habitat suitability was classified into five categories: unsuitable, low, moderate, good, and excellent suitability.

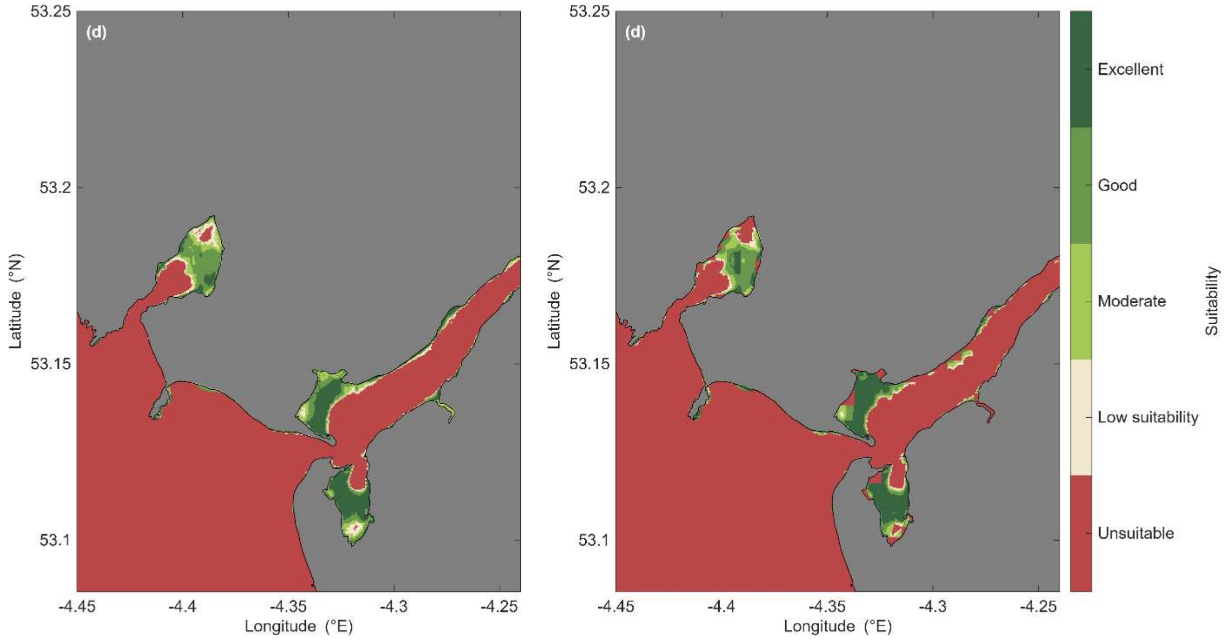

Figure 15: For Caernarfon and Malltraeth Bay, predicted seagrass habitat suitability derived from the ensemble model (without TSM on left panel and with TSM on right panel) using the threshold optimisation approach. Habitat suitability was classified into five categories: unsuitable, low, moderate, good, and excellent suitability.

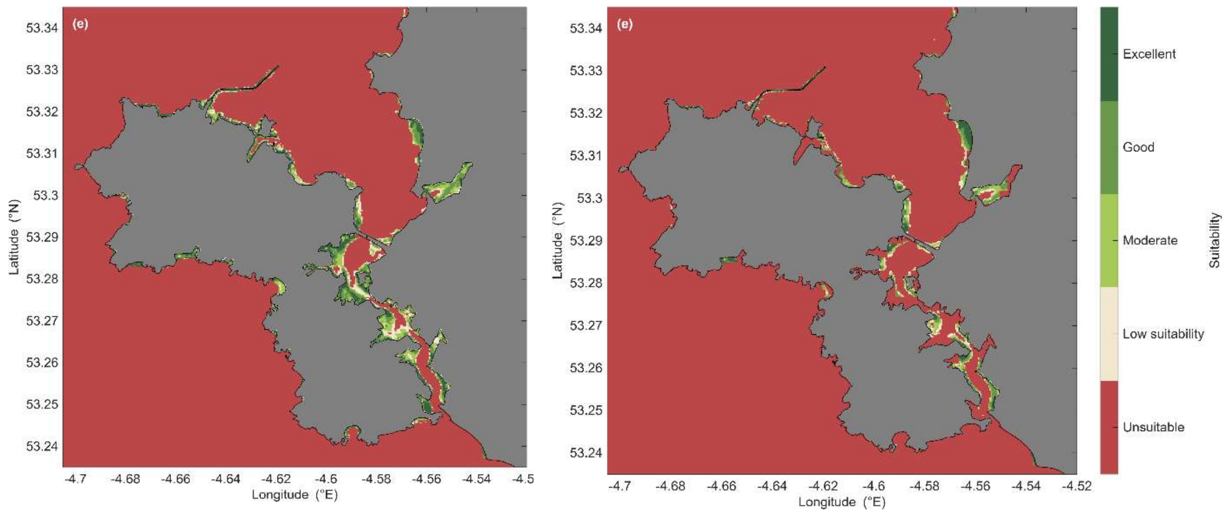

Figure 16: For Holy Island, predicted seagrass habitat suitability derived from the ensemble model (without TSM on left panel and with TSM on right panel) using the threshold optimisation approach. Habitat suitability was classified into five categories: unsuitable, low, moderate, good, and excellent suitability.

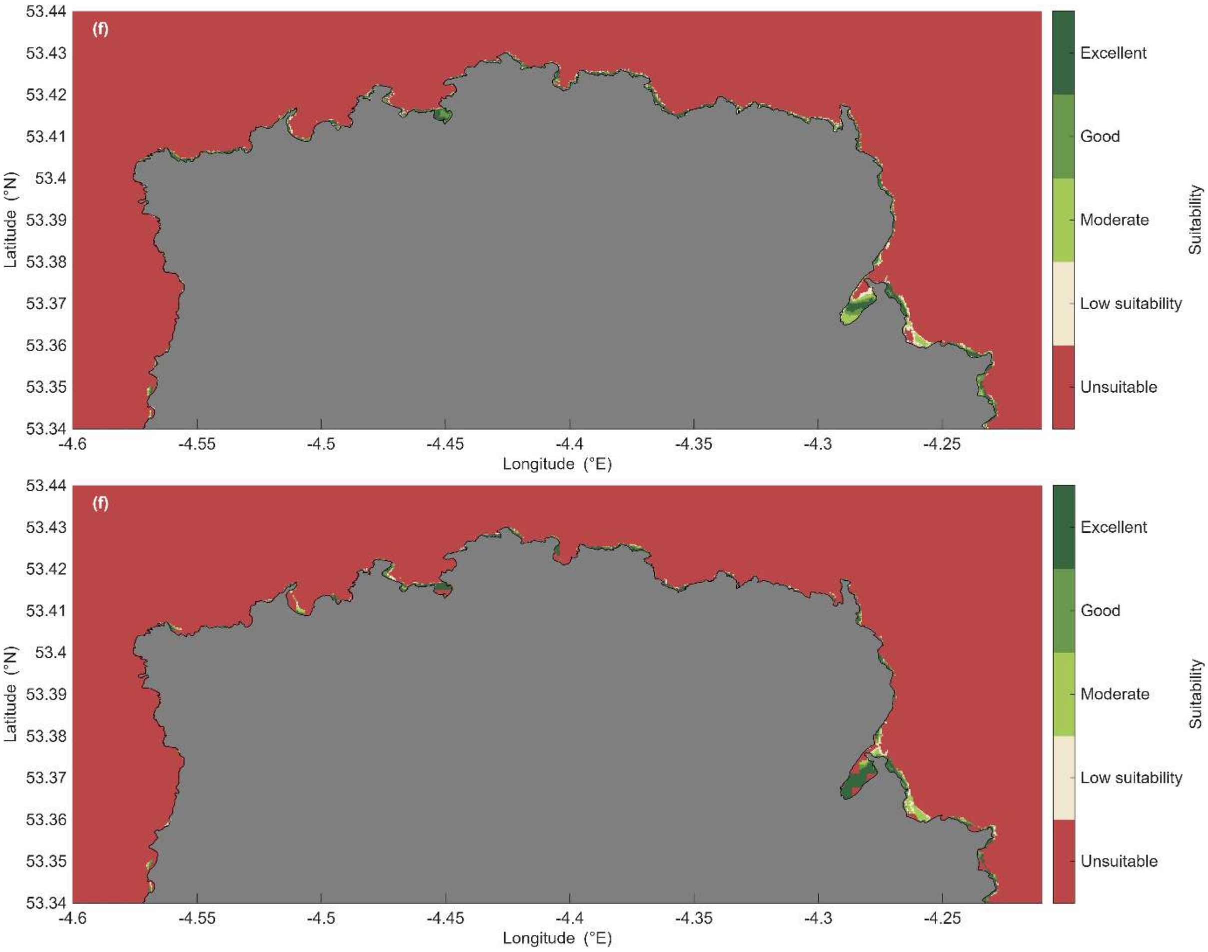

Figure 17: For North Anglesey, predicted seagrass habitat suitability derived from the ensemble model (without TSM on upper panel and with TSM on bottom panel) using the threshold optimisation approach. Habitat suitability was classified into five categories: unsuitable, low, moderate, good, and excellent suitability.

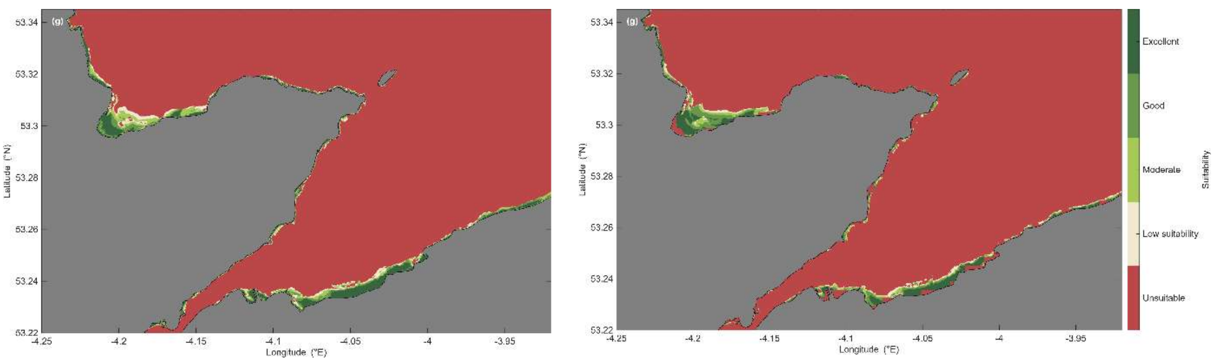

Figure 18: For Red Wharf Bay and Lavan Sands, predicted seagrass habitat suitability derived from the ensemble model (without TSM on left panel and with TSM on right panel) using the threshold optimisation approach. Habitat suitability was classified into five categories: unsuitable, low, moderate, good, and excellent suitability.

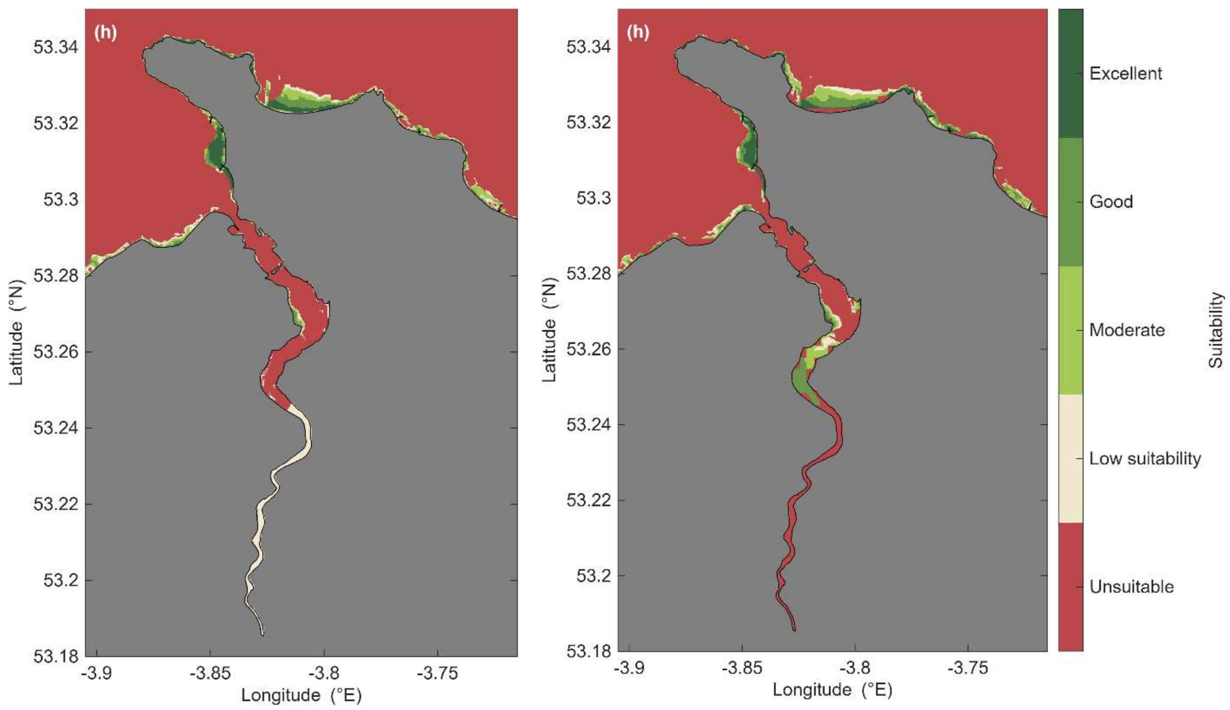

Figure 19: For Conwy Bay, predicted seagrass habitat suitability derived from the ensemble model (without TSM on left panel and with TSM on right panel) using the threshold optimisation approach. Habitat suitability was classified into five categories: unsuitable, low, moderate, good, and excellent suitability.

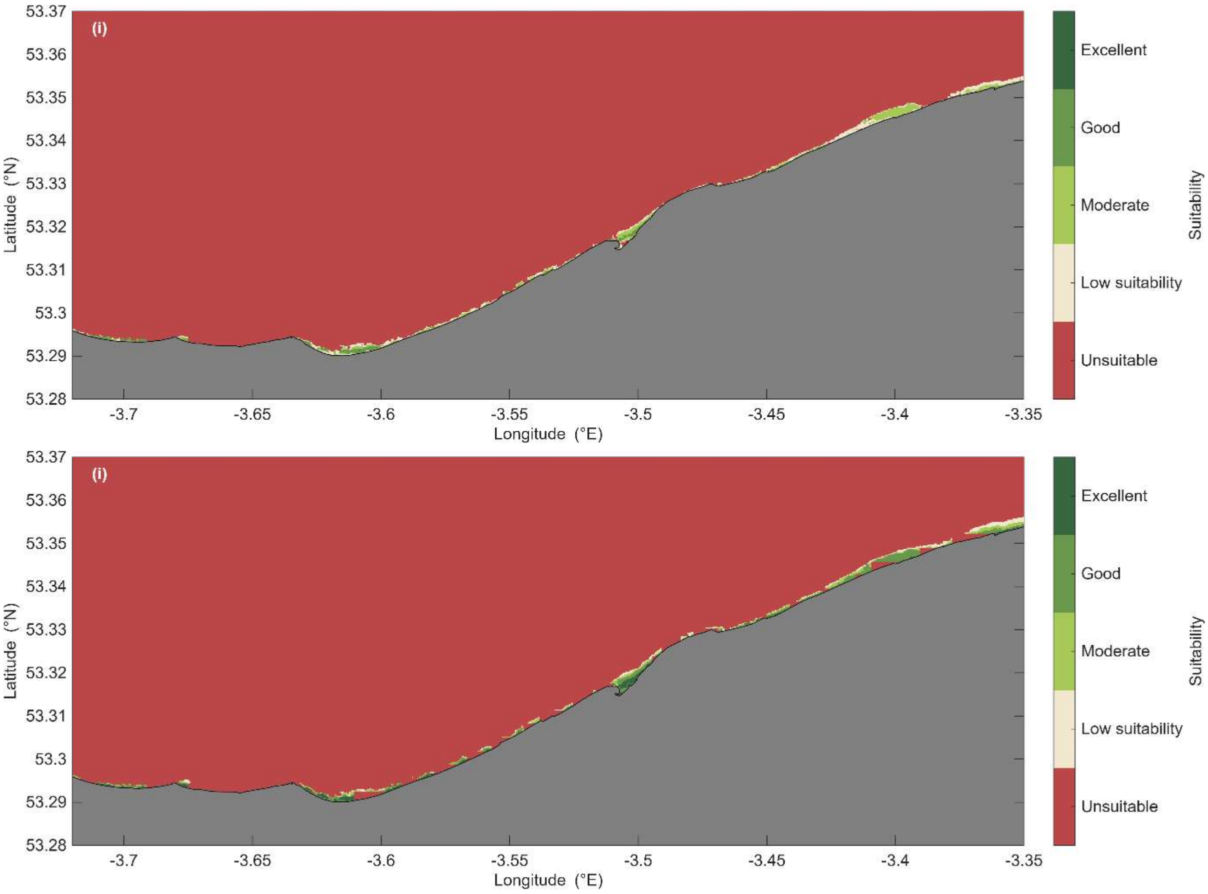

Figure 20: For Colwyn Bay, predicted seagrass habitat suitability derived from the ensemble model (without TSM on upper panel and with TSM on bottom panel) using the threshold optimisation approach. Habitat suitability was classified into five categories: unsuitable, low, moderate, good, and excellent suitability.

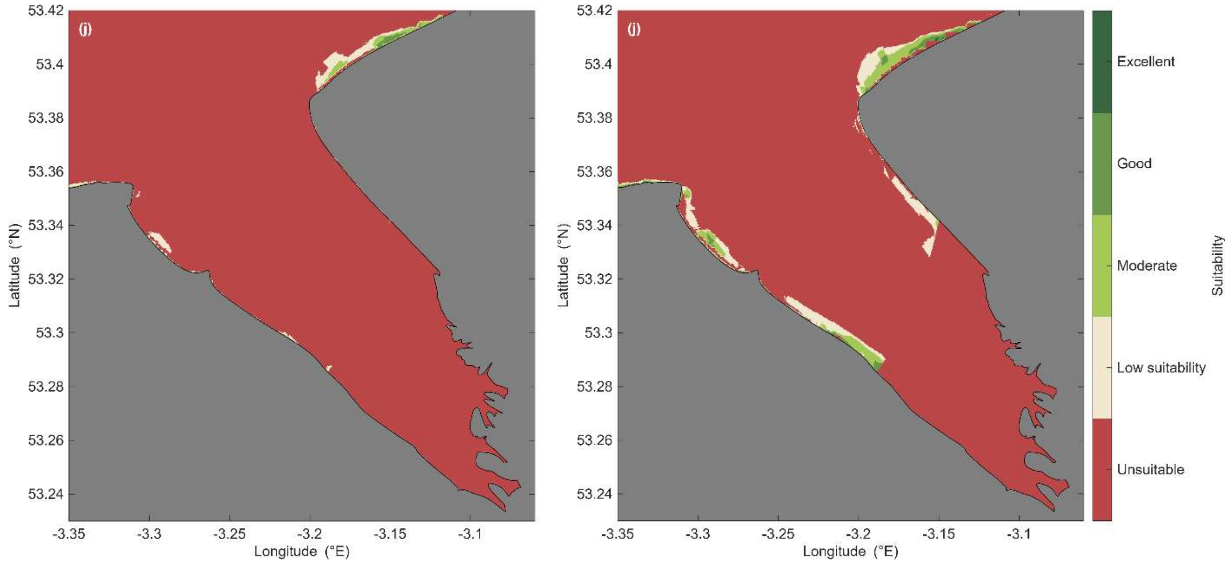

Figure 21: For the River Dee, predicted seagrass habitat suitability derived from the ensemble model (without TSM on left panel and with TSM on right panel) using the threshold optimisation approach. Habitat suitability was classified into five categories: unsuitable, low, moderate, good, and excellent suitability.

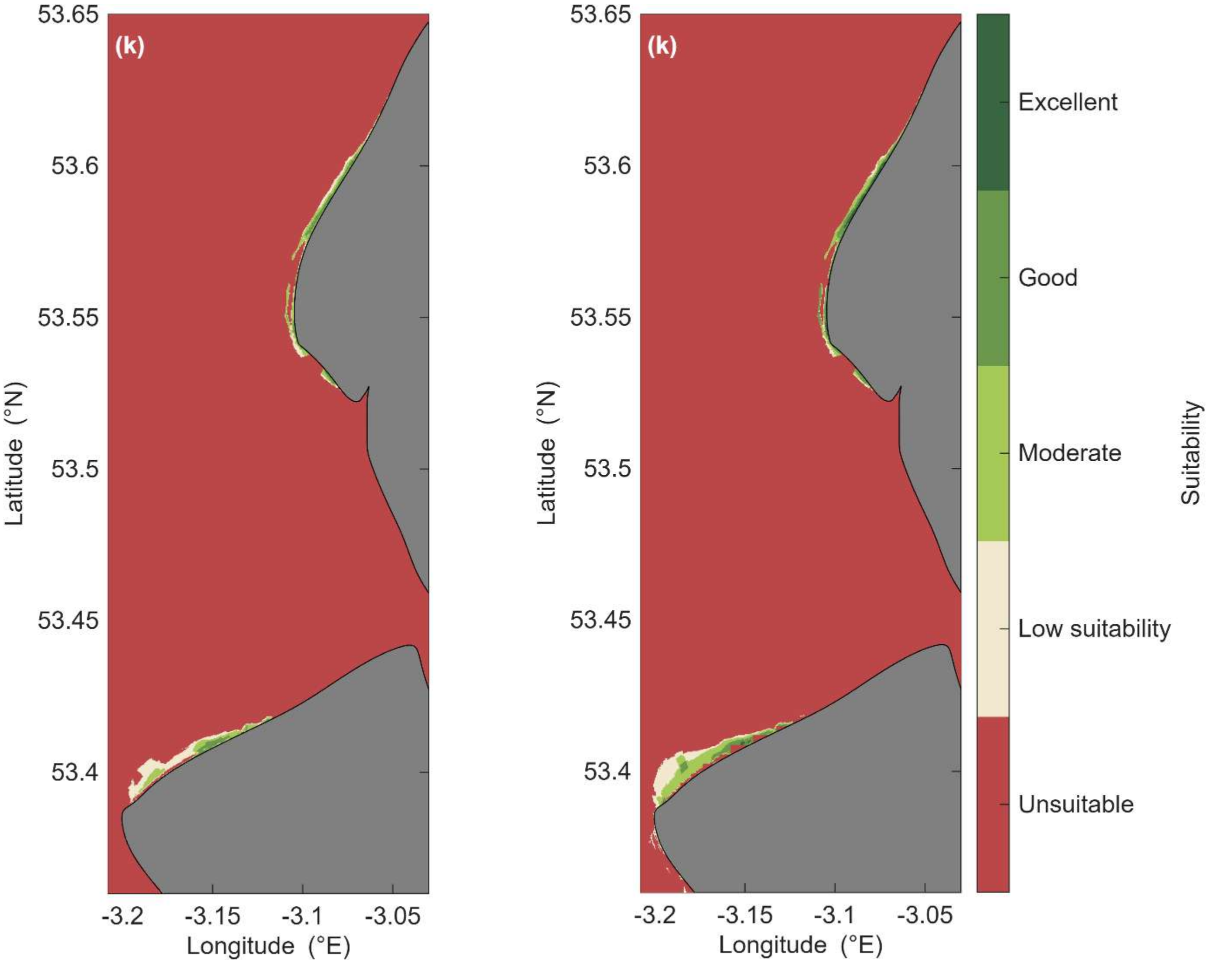

Figure 22: For Liverpool Bay, predicted seagrass habitat suitability derived from the ensemble model (without TSM on left panel and with TSM on right panel) using the threshold optimisation approach. Habitat suitability was classified into five categories: unsuitable, low, moderate, good, and excellent suitability.