SMMR
Sustainable Management of UK Marine Resources

ReSOW UK
Restoration of Seagrass for Ocean Wealth

Habitat Suitability Modelling Report

C. M. Bertelli and A. E. Becker

December 2024

Swansea University Prifysgol Abertawe

National Oceanography Centre

University of Stirling

Project Seagrass

Contents

Tables

Figures

Introduction

In order to go anywhere near achieving global targets for Net Zero emissions and our ambitions for nature and society, complacency towards our existing natural resources is not enough. Active and targeted restoration is needed to recover what has been lost, but also to enhance environments as a nature-based solution for tackling climate change. Seagrass meadows create a highly efficient and long-term store of carbon in their marine sediments and provide habitat to a wide range of species enhancing biodiversity, and so their restoration allows them to become a key contributor to these solutions.

Habitat suitability modelling (HSM), sometimes used interchangeably with Species Distribution Modelling (SDM), is becoming an increasingly popular tool for determining and predicting species distributions within spatial and temporal timeframes. The general lack of systematic biological survey means it is impossible to be able to account for all individuals of a species all of the time, which makes HSM invaluable in trying to fill these gaps. This tool is used for a number of ecological objectives such as predicting the extent of vulnerable species in relation to changing environmental conditions caused by climate change (Rowden et al., 2017), the distribution and potential spread of invasive species (Wesselmann et al., 2021), and for informing suitable locations for restoration (Burnside et al., 2002). These models predict species distribution at a spatial scale by identifying areas where environmental conditions are conducive to the species in question. To carry out HSM, good quality species presence data is needed as well as the environmental or predictor variables that have been identified as important in determining the distribution of the species.

Around the UK the larger subtidal meadow forming seagrass species *Zostera marina*, was once extensive, but it is now believed that approximately 44% of seagrass has been lost since 1936, and potentially up to 92% is thought to have been lost based on longer term historical records (Green et al., 2021). The implications this has had on marine biodiversity and loss of carbon that was trapped in this habitat in not fully understood. The dramatic loss of *Z. marina* witnessed globally has been attributed to a disease caused by the slime mould *Labyrinthula zosterae*, a pathogen that caused die-offs as a knock-on effect of years of poor water quality causing a reduction of resilience in the seagrass plants (Hughes et al., 2018; Ralph and Short, 2002; Vergeer and den Hartog, 1994). In some areas, improvements to water quality have led to a recovery of seagrass meadows (Bertelli et al., 2018), but in areas where seagrass has significantly declined or has been lost altogether, restoration is a viable route of action to aid recovery. The restoration of seagrass meadows will have a number of ecological benefits as they provide a wide range of ecosystem services such as providing shelter, direct and indirect sources of food, stabilisation of sediments and carbon storage (Nordlund et al., 2016). Using HSM will help to inform the most suitable areas where seagrasses would be able to grow based upon environmental conditions, helping to concentrate restoration efforts which can be costly (Unsworth et al., 2023). HSM, has been extensively used in terrestrial contexts, but is more recently being used for marine habitats. However, seagrasses are one of the least studied groups within the realm of HSM and SDM (Melo-Merino et al., 2020).

Factors affecting seagrass distribution

As primary producers, seagrasses need light to exist, and as marine plants, they have higher minimum light requirements than other marine macrophytes, due to an extensive root and rhizome system that requires more energy to maintain (Hemminga, 1998). Light availability in the form of photosynthetically active radiation (PAR) will determine where seagrasses can exist in the marine environment. Maximum depth limits of seagrasses will vary depending on species but also local conditions affecting water clarity. Turbidity caused by sediment suspension, run-off and nutrient loading causing plankton blooms will affect the amount of light available (Lapointe et al., 1994; Paling et al., 2009). Light will also be attenuated through the water column with depth (Duarte, 1991) and therefore bathymetry is one of the most frequently used parameter used in HSM. Around Europe, *Z. marina* is usually found within a narrow depth range around the coast, typically up to 5-10 m deep depending on water clarity (Davison and Hughes, 1998; Jackson et al., 2013; Krause-Jensen et al., 2003; Nielsen et al., 2002).

Temperature has been found to affect photosynthesis rates of seagrasses (Marsh et al., 1986) and can also have significant influence on life stages, such as flowering and germination (Potouroglou et al., 2014). *Z. marina* tolerates a wide temperature range from -1°C in Arctic regions to 30°C in the subtropics. However, die-backs can occur at the extremes of this range, and the optimal temperature for growth is estimated to be between 15 and 20°C (Zhou et al., 2016). *Z. marina* is also tolerant to a range of salinities and can be found within estuaries as well as fully oceanic conditions, from 18 psu to 40 psu (D'Avack et al., 2019).

Seagrasses are exposed to localised hydrodynamics in the form of waves, tides, wind driven currents and wave driven currents (Koch et al., 2006) and these physical factors have been recognised as important factors in affecting spatial distribution and the minimum depth of colonisation (Stevens and Lacy, 2012). Water movement is important for seagrass growth, but where hydrodynamic energy is too high it can become a limiting factor for seagrass growth (Fonseca and Bell, 1998; Peralta et al., 2002). Morphological changes have been found to be affected by increases in local hydrodynamics (Peralta et al., 2006). Wave energy and wave height also has implications for seed burial and seedling development and is therefore one of the most important environmental variables to consider when choosing restoration sites. Successful seedling establishment has been found to correspond with lowest maximum wave heights in Chesapeake Bay restoration experiments (Marion et al., 2020). Unsurprisingly, *Z. marina* favours bays sheltered from prevailing winds and waves where hydrodynamic energy is not too high allowing the sediment accrual to take place and the deposition of sandy-muddy substrates which can accommodate its extensive root system (Beca-Carretero et al., 2019). Around the UK, *Z. marina* is found within estuaries, bays and coastlines where they are sheltered from prevailing winds and wave exposure.

Methods

Seven case study sites were chosen to represent a gradient in types of coastal topography and conditions in which seagrass meadows are found. These sites were also chosen based upon a range of social interactions with seagrass restoration, from sites where no restoration activity has been undertaken or proposed to a site where active restoration is already taking place. These areas were also known to include existing seagrass meadows to enable HSM to be carried out at the case study site scale. These sites are shown in figure 1.

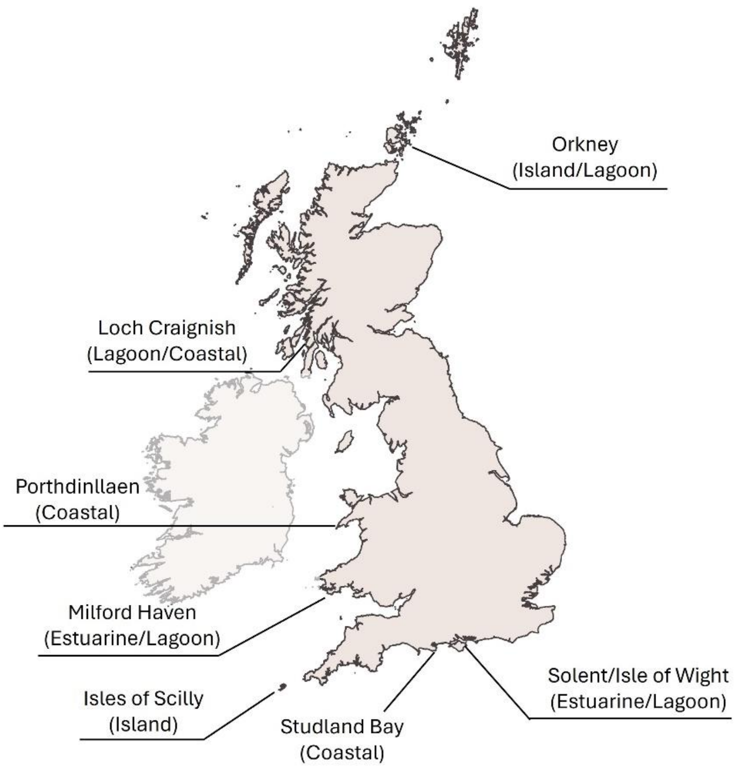


Figure 1 Case study sites around the UK chosen to encompass environmental gradients and locations in which seagrass is found and, in some cases, already being restored.

A previous literature search conducted by the authors (Bertelli et al., 2022) identified the most commonly used environmental variables used for predicting seagrass presence using habitat suitability or species distribution modelling. These included bathymetry, light, salinity, temperature, substrate, wave energy and slope, however these parameters may also be the most readily available. Based upon this, a search for available environmental variables was conducted that were consistent for the whole coast of the UK. The variables chosen are listed in Table 1 with temporal and spatial resolution. Other variables were not included as were not found to be consistent for all shallow UK coast or was not at a low enough resolution (i.e. one pixel of data layer would cover entire case study area). For example, substrate data was incomplete or simply labelled ‘seabed’ or ‘sediment’ so cannot be categorised within the realms of particle size. This was true at the time of data collection for this research.

Table 1 Environmental variables used for HSM, including data source and resolution

Predictor variables	Source	Unit/file type	Spatial resolution	Temporal resolution
Light (PAR) availability at seabed	EMODnet - PAR https://www.emodnet-seabedhabitats.eu/access-data/launch-map-viewer/	Mol.phot.m^{-2}.d^{-1} GeoTiff	~0.3km^2, 1.1 x 0.7 km, 0.003°/10 arc seconds	01 Jan2005 – 31 Dec 2009
Bathymetry	EMODnet Bathymetry and topography http://www.emodnet.eu/emodnet-maps-catalogue	Metres below chart datum Ascii raster (.asc)	~0.115km, 0.001°x 3.75 arc seconds, ~70m x 116m	Downloaded 2022
Temperature	Copernicus Marine Environment Monitoring Service http://marine.copernicus.eu NorthWestShelf_ANALYSIS_FORECAST_PHY_004_013	Ppt NETcdf (.nc)	0.014° × 0.03°, ~1.4km x 3km	2019-present hourly- Daily mean
Salinity	Copernicus Marine Environment Monitoring Service http://marine.copernicus.eu NorthWestShelf_ANALYSIS_FORECAST_PHY_004_013	Ppt NETcdf (.nc)	0.014° × 0.03°, ~1.4km x 3km	2019-present hourly- Daily mean
Wave energy at seabed	EMODnet https://www.emodnet-seabedhabitats.eu/access-data/launch-map-viewer/	N.m^2.s^{-1} GeoTIFF	~0.3km, ~342x195m	29 Feb 2016-30 Mar 2018
Energy at seabed due to currents	EMODnet https://www.emodnet-seabedhabitats.eu/access-data/launch-map-viewer/ Data from EU SeaMap (2016) Energy in the Celtic Sea and North Sea	N.m^2.s^{-1} GeoTIFF	~0.3km, ~342x195m	01 Jan 2001-01 Jan 2010
Slope	Calculated from bathymetry data with GIS software.	GeoTIFF	Varies with input layer.	N/A

The most common methods used for HSM in marine environments are correlative methods including machine-learning and statistical based models (Melo-Merino et al., 2020). A range of methods were chosen to include both regression and machine learning including Generalised Linear Models (GLM), Generalised Additive Models (GAM), Random Forest (RF), Boosted Regression Trees (BRT), Multivariate Adaptive Regression Splines (MARS) and Maximum Entropy (MaxEnt). These methods were chosen based on a previous literature review and subsequent study carried out for small-scale sites around Wales, UK (Bertelli et al., 2022; Bertelli et al., 2023; Guisan et al., 2017; Valle et al., 2013). All HSMs were created using the 'sdm' package (Naimi and Araújo, 2016) in R. This package allows the use of a wide range of the most common modelling algorithms covering parametric, non-parametric, regression and machine-learning methods to be used all at once. The models followed the formula of seagrass presence as a function of the predictor variables (a stack of the environmental variable layers) using the different approaches, repeated ten times per approach. As we only had presence data, the modelling takes a range of 'background' points which are treated as pseudoabsences. This number changed per site dependent upon the number of presence points. The formula used uses a resampling method for data partitioning of the presence point data which is used to test and validate the model using a bootstrapping method in this case which is appropriate for smaller datasets. Predictions of presence are then created for each approach (GLM etc.) and each run (repetition). Finally, all methods were combined within an ensemble model which takes a weighted average of each to give a final output as a raster layer indicating probability of suitability for seagrass presence from 0-1.

Results

The environmental variables used to predict suitability of seagrass presence are displayed with ranges and mean values for each site area in Table 1. Variables were plotted to assess data distribution and those that were significantly skewed were logged before integrating in the HSMs.

Table 2 Ranges and means for each variable at the case study sites to show difference in environmental conditions where seagrass presence was found.

Site		**Current** N.m².s-1	**Waves** N.m².s-1	**PAR** Mol.phot. m-2.d-1	**Slope** degrees	**Bathymetry** m	**Temp. Jan.** °C	**Salinity Aug.** ppt	**Temp. Aug.** °C
Solent	Ave.	115.91	45.93	12.45	2.08	0.82	8.38	33.64	19.00
	Max	1137.58	444.53	25.52	18.44	5.91	8.85	34.28	19.42
	Min	21.30	1.41	0.32	0.38	-8.77	7.87	32.82	18.62
Orkney	Ave.	77.08	9.76	0.58	2.04	-1.38	6.34	34.63	14.20
	Max	2473.24	1166.84	0.97	7.91	12.00	8.16	34.76	15.81
	Min	1.39	0.20	0.00	0.30	-15.00	3.73	34.56	12.82
Milford Haven	Ave.	16.94	55.69	0.13	2.25	-2.73	10.20	33.20	16.45
	Max	113.24	150.41	0.59	13.51	9.71	10.21	33.65	16.46
	Min	3.72	8.22	0.01	0.10	-4.59	9.91	33.17	15.82
Studland	Ave.	29.18	12.19	0.21	0.40	-3.39	9.12	34.42	18.27
	Max	379.74	584.93	0.77	7.79	1.22	9.81	34.74	18.92
	Min	1.28	1.16	0.01	0.03	-13.13	8.71	33.95	17.49
Isles of Scilly	Ave.	47.14	542.94	15.54	3.13	-0.88	10.89	35.05	14.93
	Max	105.06	2625.94	26.89	22.32	2.41	10.93	35.05	15.29
	Min	13.87	53.67	0.00	0.38	-10.22	10.85	35.05	14.44
Craignish	Ave.	2.69	11.31	0.43	3.60	3.30	8.80	34.14	13.60
	Max	54.15	404.63	0.98	15.00	22.43	9.28	34.26	14.64
	Min	0.07	0	0.07	0.02	-1.51	6.59	33.91	13.29
Porthdinllaen	Ave.	89.44	216.05	0.59	89.80	-0.14	8.37	34.24	17.14
	Max	119.40	373.64	0.79	89.99	1.11	8.38	34.24	17.30
	Min	66.46	10.52	0.52	87.92	-2.27	8.30	34.23	17.12
UK, Ireland and Channel Isles	Ave.	37.78	67.32	0.32	4.09	-4.02	9.26	34.20	16.43
	Max	1600.12	1222559.98	0.98	31.20	2	11.28	35.28	20.17
	Min	0.15	0.02	0	0	-17	3.79	30.25	10.28

HSM outputs

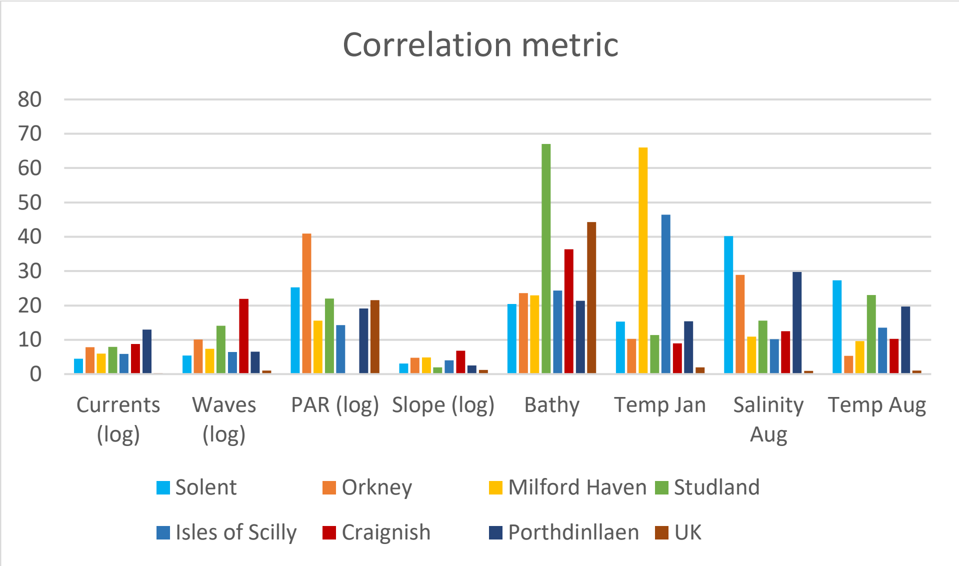
Ensemble models were run successfully for all site areas apart from Craignish where GAM did not converge, likely due to low number of presence data. According to Pearson's correlation (COR), Area Under Curve (AUC) and True Summary Statistic (TSS), all model methods performed well and had an average AUC score > 0.88, COR and TSS >0.7 (see table 3) apart from GAM for Craignish. Also, for Porthdinllaen not all the GAM models converged out of the 10 runs. This is likely due to low spread of presences within the case study area for Porthdinllaen, resulting in little change detectable in environmental conditions throughout the case study site.

*Table 3 Results from the ensemble models per case study location showing the average from10 runs per model method. All variables with logged currents, waves, PAR and slope (except Craignish where waves were not logged due to too many zeros). *GAM did not converge for Craignish and only 20% of times converged for Porthdinllaen.*

Site	Model	AUC	COR	TSS	Deviance
Solent	GLM	0.95	0.82	0.81	0.56
	GAM	0.97	0.94	0.94	1.88
	RF	1	0.97	0.97	0.13
	BRT	0.99	0.93	0.93	0.58
	MARS	0.99	0.92	0.93	0.31
	MaxEnt	0.99	0.93	0.93	0.77
Orkney	GLM	0.92	0.82	0.83	3.65
	GAM	0.92	0.83	0.84	5.06
	RF	0.99	0.89	0.92	0.32
	BRT	0.97	0.84	0.89	0.68
	MARS	0.94	0.84	0.88	3.69
	MaxEnt	0.97	0.82	0.87	0.7
Milford Haven	GLM	0.95	0.8	0.88	0.68
	GAM	0.97	0.9	0.93	1.89
	RF	0.99	0.92	0.96	0.23
	BRT	0.98	0.87	0.92	0.54
	MARS	0.95	0.86	0.89	2.53
	MaxEnt	0.97	0.86	0.92	0.41
Isles of Scilly	GLM	0.88	0.66	0.65	0.87
	GAM	0.95	0.85	0.84	1.11

	RF	0.98	0.9	0.9	0.36
	BRT	0.95	0.81	0.8	0.8
	MARS	0.95	0.82	0.82	0.64
	MaxEnt	0.95	0.81	0.8	0.68
Studland	GLM	0.96	0.82	0.86	0.56
	GAM	0.93	0.82	0.84	4.53
	RF	0.98	0.89	0.93	0.39
	BRT	0.96	0.83	0.85	0.66
	MARS	0.92	0.82	0.83	5.33
	MaxEnt	0.97	0.83	0.87	0.67
Porthdinllaen	GLM	0.96	0.88	0.89	1.75
	GAM*	0.98	0.96	0.96	1
	RF	1	0.96	0.97	0.15
	BRT	0.99	0.91	0.93	0.62
	MARS	0.96	0.91	0.91	2.57
	MaxEnt	0.99	0.92	0.94	0.79
Craignish	GLM	0.71	0.43	0.53	6.14
	GAM	NA	NA	NA	NA
	RF	0.97	0.85	0.92	0.52
	BRT	0.9	0.69	0.73	1.06
	MARS	0.88	0.74	0.8	7.87
	MaxEnt	0.93	0.74	0.86	0.88

Variable importance ensemble models



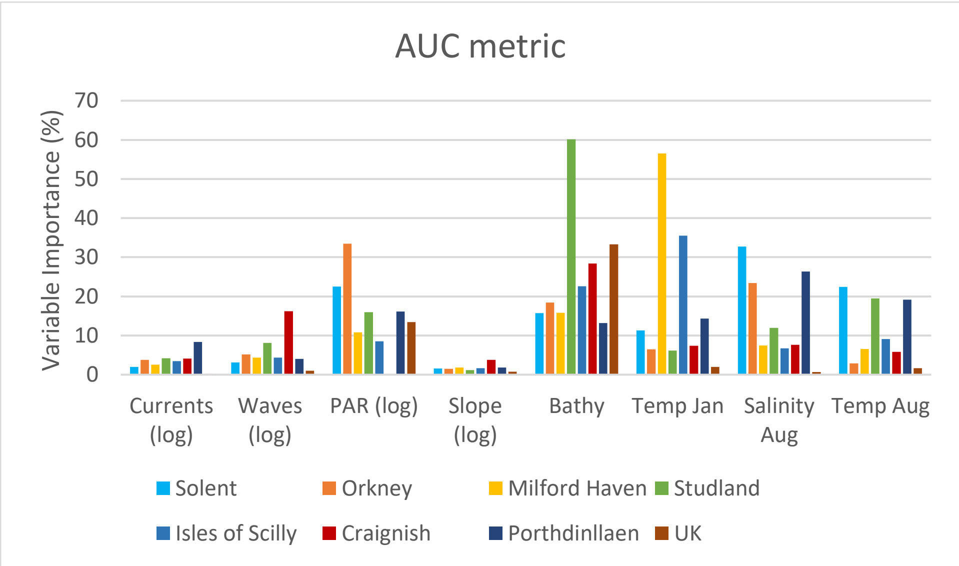


Figure 2 Variable importance from ensemble models based on the correlation metric (top) and AUC metric (bottom) for all case study sites and UK and Ireland model.

Table 4 Variable importance (%) based on Correlation metric and AUC (Area under Curve).

COR	Solent	Orkney	Milford Haven	Studland	Isles of Scilly	Craignish	Porthdinllaen	UK
Currents (log)	4.5	7.8	6	7.9	5.9	8.8	13	0.3
Waves (log)	5.4	10.1	7.4	14.1	6.4	21.9	6.5	1
PAR (log)	25.3	**40.9**	15.6	22	14.3	NA	19.1	21.5
Slope (log)	3.1	4.8	4.9	2	4	6.8	2.5	1.2
Bathy	20.4	23.6	**22.9**	**67**	24.3	**36.4**	21.4	**44.3**
Temp Jan	15.3	10.3	66	11.4	**46.4**	9	15.4	2
Salinity Aug	**40.2**	28.9	10.9	15.6	10.2	12.5	**29.7**	0.9
Temp Aug	27.3	5.3	9.6	23	13.5	10.3	19.7	1

AUC	Solent	Orkney	Milford Haven	Studland	Isles of Scilly	Craignish	Porthdinllaen	UK
Currents (log)	2	3.8	2.6	4.2	3.5	4.1	8.4	0.2
Waves (log)	3.1	5.2	4.4	8.1	4.4	16.2	4	1
PAR (log)	22.5	**33.5**	10.8	16	8.5	NA	16.1	13.4
Slope (log)	1.6	1.5	1.8	1.2	1.7	3.8	1.8	0.8
Bathy	15.7	18.4	15.8	**60.1**	22.6	**28.4**	13.2	**33.3**
Temp Jan	11.3	6.5	**56.5**	6.2	**35.5**	7.4	14.3	2
Salinity Aug	**32.7**	23.4	7.5	12	6.7	7.6	**26.4**	0.7
Temp Aug	22.4	2.9	6.6	19.5	9.1	5.8	19.2	1.7

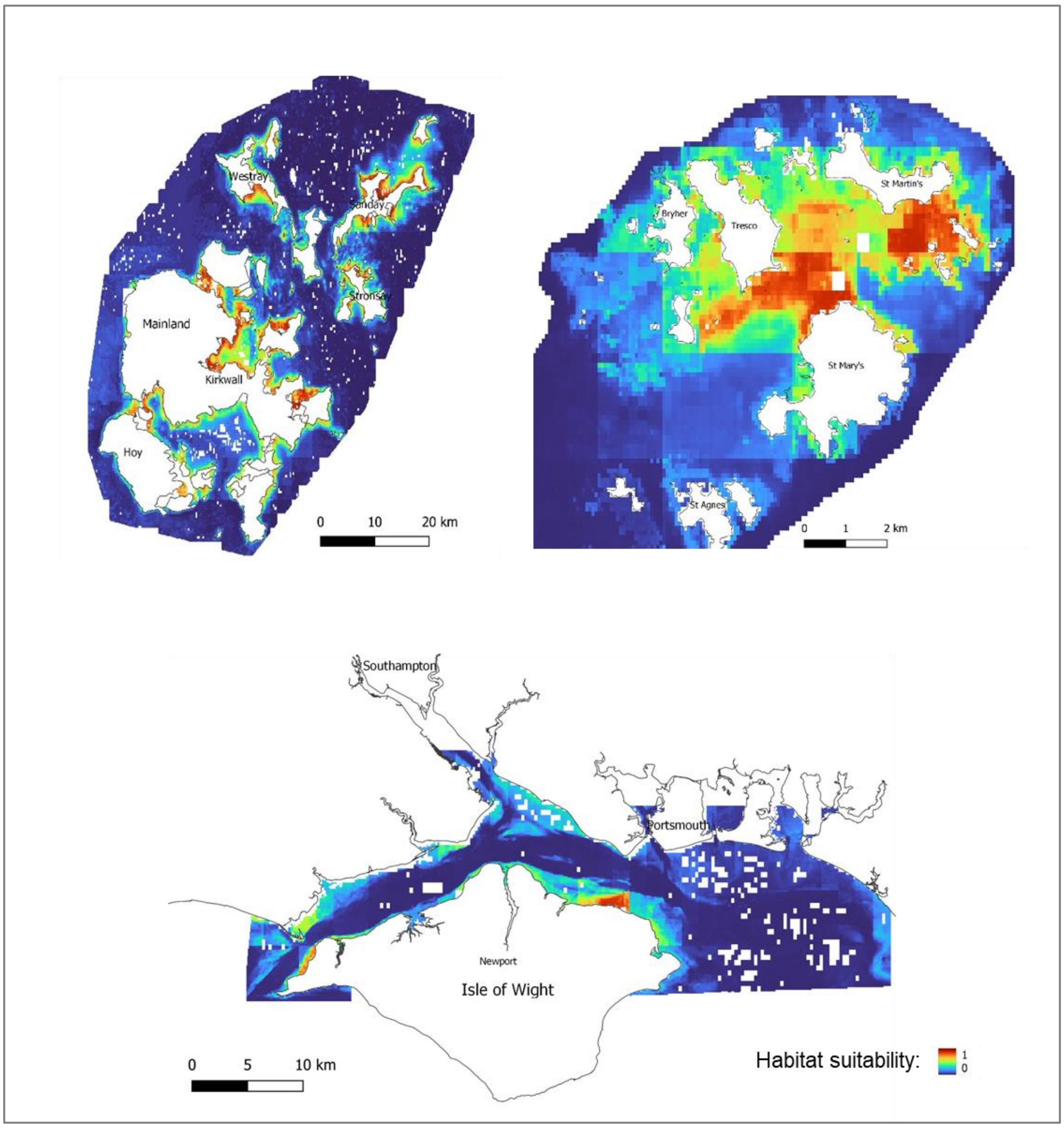


Figure 3 Example results from 3 case study site HSMs, Orkney Isles (top left), Isles of Scilly (top right) and the Solent (bottom). Probability of suitability is from 0-1 displayed as a heat map output.

All results are made available on the ReSOW CEEDS tool which can be found here: https://ceeds.resow.uk/

As is evident from the UK and Ireland HSM, seagrass suitability is heavily overpredicted for the large spatial area. This is likely due to bathymetry being the most important variable in explaining seagrass presence at this scale (Table 4, Fig. 2). The same data, used at a local scale, improves model outputs with much more sensible predictions of suitability despite the same data being used. For example, Figure 4 shows a comparison of results from UK wide broad-scale model and the finer-scale model for the Solent area.

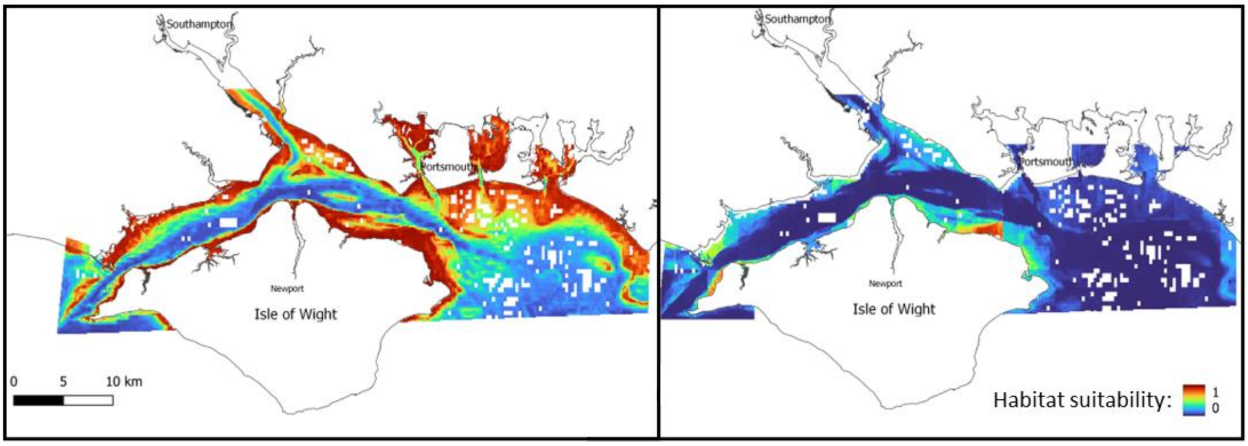


Figure 4 Comparison of ensemble model outputs at the broad-scale (Uk & Ireland, left) and fine-scale (case study area, right) using the Solent as an example.

References

Beca-Carretero, P., Stanschewski, C.S., Julia-Miralles, M., Sanchez-Gallego, A., Stengel, D.B., 2019. Temporal and depth-associated changes in the structure, morphometry and production of near-pristine Zostera marina meadows in western Ireland. Aquat. Bot. 155, 5–17. https://doi.org/10.1016/j.aquabot.2019.02.003

Bertelli, C., Stokes, H., Bull, J., Unsworth, R.K.F., 2022. The use of habitat suitability modelling for seagrass: A review. https://doi.org/10.6084/m9.figshare.20310429.v2

Bertelli, C.M., Bennett, W.G., Karunarathna, H., Reeve, D.E., Unsworth, R.K.F., Bull, J.C., 2023. High-resolution wave data for improving marine habitat suitability models. Front. Mar. Sci. Ocean Obse, 1–14. https://doi.org/10.3389/fmars.2022.1004829

Bertelli, C.M., Bull, J.C., Cullen-Unsworth, L.C., Unsworth, R.K.F., 2021. Unravelling the Spatial and Temporal Plasticity of Eelgrass Meadows. Front. Plant Sci. 12, 1–12. https://doi.org/10.3389/fpls.2021.664523

Bertelli, C.M., Robinson, M.T., Mendzil, A.F., Pratt, L.R., Unsworth, R.K.F., 2018. Finding some seagrass optimism in Wales, the case of Zostera noltii. Mar. Pollut. Bull. 134, 216–222. https://doi.org/10.1016/j.marpolbul.2017.08.018

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

Burnside, N.G., Smith, R.F., Waite, S., 2002. Habitat suitability modelling for calcareous grassland restoration on the South Downs, United Kingdom. J. Environ. Manage. 65, 209–221. https://doi.org/10.1006/jema.2002.0546

Davison, D.M., Hughes, D.J., 1998. Vol.I. Zostera biotopes 1. An overview of dynamic and sensitivity characteristics for conservation management of marine SACs.

Den Hartog, C., 1970. The Sea-grasses of the World, Twwede Ree. ed. North_Holland Publishing company, Amsterdam.

Duarte, C.M., 1991. Seagrass depth limits. Aquat. Bot. 40, 363–377. https://doi.org/10.1016/0304-3770(91)90081-F

Fonseca, M.S., Bell, S.S., 1998. Influence of physical setting on seagrass landscapes. Mar. Ecol. Prog. Ser. 171, 109–121.

Green, A.E., Unsworth, R.K.F., Chadwick, M.A., Jones, P.J.S., 2021. Historical Analysis Exposes Catastrophic Seagrass Loss for the United Kingdom. Front. Plant Sci. 12. https://doi.org/10.3389/fpls.2021.629962

Guisan, A., Thuiller, W., Zimmermann, N.E., 2017. Habitat Suitability and Distribution Models. Cambridge University Press. https://doi.org/10.1017/9781139028271

Heikkinen, R.K., Marmion, M. and Luoto, M., 2012. Does the interpolation accuracy of species distribution models come at the expense of transferability?. *Ecography*, *35*(3), pp.276-288.

Hemminga, M.A., 1998. The root/rhizome system of seagrasses: An asset and a burden. J. Sea Res. 39, 183–196. https://doi.org/10.1016/S1385-1101(98)00004-5

Hughes, R.G., Potouroglou, M., Ziauddin, Z., Nicholls, J.C., 2018. Seagrass wasting disease: Nitrate enrichment and exposure to a herbicide (Diuron) increases susceptibility of Zostera marina to infection. Mar. Pollut. Bull. 134, 94–98. https://doi.org/10.1016/j.marpolbul.2017.08.032

Jackson, E.L., Griffiths, C.A., Durkin, O., 2013. A guide to assessing and managing anthropogenic impact on marine angiosperm habitat - Part 1: Literature review. Natural England Commissioned Reports, Number 111.

Jones, B., Unsworth, R.K.F., 2016. The perilous state of seagrass in the British Isles. R. Soc. Open Sci. 3, 1–14. https://doi.org/10.1098/rsos.150596

Koch, E.W., Sanford, L.P., Chen, S.-N., Shafer, D.J., Smith, J.M., 2006. System-Wide Water Resources Research Program and Submerged Aquatic Vegetation Restoration Research Program (Waves in Seagrass Systems : Review and Technical Recommendations). Eng. Res. Dev. Cent.

Krause-Jensen, D., Pedersen, M.F., Jensen, C., 2003. Regulation of eelgrass (Zostera marina) cover along depth gradients in Danish coastal waters. Estuaries 26, 866–877. https://doi.org/10.1007/BF02803345

Lapointe, B.E., Tomasko, D.A., Matzie, W.R., 1994. Eutrophication and trophic state classification of seagrass communities in the Florida Keys. Bull. Mar. Sci. 54, 696–717.

Marion, S.R., Orth, R.J., Fonseca, M., Malhotra, A., 2020. Seed Burial Alleviates Wave Energy Constraints on Zostera marina (Eelgrass) Seedling Establishment at Restoration-Relevant Scales. Estuaries and Coasts.

Marsh, J. a., Dennison, W.C., Alberte, R.S., 1986. Effects of temperature on photosynthesis and respiration in eelgrass (Zostera marina L.). J. Exp. Mar. Bio. Ecol. 101, 257–267. https://doi.org/10.1016/0022-0981(86)90267-4

Melo-Merino, S.M., Reyes-Bonilla, H., Lira-Noriega, A., 2020. Ecological niche models and species distribution models in marine environments: A literature review and spatial analysis of evidence. Ecol. Modell. 415, 108837. https://doi.org/10.1016/j.ecolmodel.2019.108837

Naimi, B., Araújo, M.B., 2016. Sdm: A reproducible and extensible R platform for species distribution modelling. Ecography (Cop.). 39, 368–375. https://doi.org/10.1111/ecog.01881

Nielsen, S., Sand-Jensen, K., Borum, J., Geertz-Hansen, O., 2002. Depth colonization of eelgrass (Zostera marina) and macroalgae as determined by water transparency in Danish coastal waters. Estuaries and Coasts 25, 1025–1032. https://doi.org/10.1007/bf02691349

Nordlund, L.M., Koch, E.W., Barbier, E.B., Creed, J.C., 2016. Seagrass ecosystem services and their variability across genera and geographical regions. PLoS One 11, 1–23. https://doi.org/10.1371/journal.pone.0163091

Paling, E.I., Fonseca, M., van Katwijk, M.M., van Keulen, M., 2009. Seagrass restoration, in: Coastal Wetlands: An Integrated Ecosystems Approach. pp. 687–713.

Peralta, G., Brun, F.G., Pérez-Lloréns, J.L., Bouma, T.J., 2006. Direct effects of current velocity on the growth, morphometry and architecture of seagrasses: A case study on Zostera noltii. Mar. Ecol. Prog. Ser. 327, 135–142. https://doi.org/10.3354/meps327135

Peralta, G., Pérez-Lloréns, J.L., Hernández, I., Vergara, J.J., 2002. Effects of light availability on growth, architecture and nutrient content of the seagrass Zostera noltii Hornem. J. Exp. Mar. Bio. Ecol. 269, 9–26. https://doi.org/10.1016/S0022-0981(01)00393-8

Peterson A. T. *et al.* 2007. Transferability and model evaluation in ecological niche modeling: a comparison of GARP and Maxent. *Ecography* **30**: 550–560.

Potouroglou, M., Kenyon, E.J., Gall, A., Cook, K.J., Bull, J.C., 2014. The roles of flowering, overwinter survival and sea surface temperature in the long-term population dynamics of Zostera marina around the Isles of Scilly, UK. Mar. Pollut. Bull. 83, 500–7. https://doi.org/10.1016/j.marpolbul.2014.03.035

Ralph, P.J., Short, F.T., 2002. Impact of the wasting disease pathogen, Labyrinthula zosterae, on the photobiology of eelgrass Zostera marina. Mar. Ecol. Prog. Ser. 226, 265–271. https://doi.org/10.3354/meps226265

Rowden, A.A., Anderson, O.F., Georgian, S.E., Bowden, D.A., Clark, M.R., Pallentin, A., Miller, A., 2017. High-resolution habitat suitability models for the conservation and management of vulnerable marine ecosystems on the Louisville Seamount Chain, South Pacific Ocean. Front. Mar. Sci. 4. https://doi.org/10.3389/fmars.2017.00335

Stevens, A.W., Lacy, J.R., 2012. The Influence of Wave Energy and Sediment Transport on Seagrass Distribution. Estuaries and Coasts 35, 92–108. https://doi.org/10.1007/s12237-011-9435-1

Unsworth, R.K.F., Bertelli, C.M., Coals, L., Cullen-Unsworth, L.C., Den Haan, S., Jones, B.J., Rees, S.R., Thomsen, E., Wookey, A. and Walter, B., 2023. Bottlenecks to seed-based seagrass restoration reveal opportunities for improvement. *Global Ecology and Conservation*, p.e02736.

Valle, M., van Katwijk, M.M., de Jong, D.J., Bouma, T.J., Schipper, A.M., Chust, G., Benito, B.M., Garmendia, J.M., Borja, Á., 2013. Comparing the performance of species distribution models of Zostera marina: Implications for conservation. J. Sea Res. 83, 56–64. https://doi.org/10.1016/j.seares.2013.03.002

Vergeer, L.H.T., den Hartog, C., 1994. Omnipresence of Labyrinthulaceae in seagrasses. Aquat. Bot. 48, 1–20. https://doi.org/https://doi.org/10.1016/0304-3770(94)90070-1

Werkowska, Wioletta., Márquez, Ana L., Real, Raimundo and Acevedo, Pelayo. 2017. A practical overview of transferability in species distribution modeling. *Environmental Reviews*. **25**(1): 127-133. https://doi.org/10.1139/er-2016-0045

Wesselmann, M., Chefaoui, R.M., Marbà, N., Serrao, E.A., Duarte, C.M., 2021. Warming Threatens to Propel the Expansion of the Exotic Seagrass Halophila stipulacea. Front. Mar. Sci. 8, 1–14. https://doi.org/10.3389/fmars.2021.759676

Wiens J. A. *et al.* 2009. Niches, models, and climate change: assessing the assumptions and uncertainties. *Proc. Natl Acad. Sci. USA* **106**: 19729–19736.

Zhou, J., Wang, Q., Zhao, W., Yu, D., Guan, S., 2016. Habitat suitability analysis of eelgrass Zostera marina L. in the subtidal zone of Xiaoheishan Island. Chinese J. Oceanol. Limnol. 34, 69–78. https://doi.org/10.1007/s00343-015-4263-y