Modelling potential areas for Seagrass restoration within Plymouth Sound & Estuaries SAC and Solent Maritime SAC as part of the LIFE fund Recreation ReMEDIES project, 2020

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Further information

This report can be downloaded from the Natural England Access to Evidence Catalogue: http://publications.naturalengland.org.uk/ . For information on Natural England publications contact the Natural England Enquiry Service on 0300 060 3900 or e-mail enquiries@naturalengland.org.uk.

LIFE Recreation ReMEDIES

LIFE Recreation ReMEDIES (*LIFE18 NAT/UK/000039*

Reducing and Mitigating Erosion and Disturbance impacts affecting the Seabed.

Foreword

Natural England commission a range of reports from external contractors to provide evidence and advice to assist us in delivering our duties. The views in this report are those of the authors and do not necessarily represent those of Natural England.

Background

LIFE Recreation ReMEDIES is a four-year project that will improve the condition of four marine habitats of European importance. The project will focus on five key Special Areas of Conservation (SACs) in the UK, from Essex in the east to the Isles of Scilly in the west.

The wider ReMEDIES project will demonstrate habitat restoration and management techniques including seagrass restoration and aims to:

- Protect and improve the condition of key intertidal and subtidal habitats in 5 SACs.
- Raise awareness and actively inspire better care of the habitats by key users.
- Monitor, record and evaluate the project to maximise public benefits, conservation impact and repeatability across Europe.

This report summarizes the modelling work conducted to help determine the most appropriate areas for active seagrass restoration, based on environmental variables gathered to investigate correlations with known seagrass beds and predict seabed areas that may be most suited to successful growth & establishment of new seagrass.

Funding

LIFE: LIFE Recreation ReMEDIES (LIFE18 NAT/UK/000039) has received funding from the LIFE Programme which is the European Union's funding instrument for the environment. Funding is awarded to best practice, innovative and demonstration projects that contribute to the objectives of Natura 2000.

Natura 2000: The wider ReMEDIES project includes 5 Special Areas of Conservation that are part of 'Natura 2000' - a network of the very best areas for wildlife across Europe. All SACs have special protection under European & UK laws.

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Amit Malhotra, WEMO engineer at the NOAA Centers for Coastal Ocean Science for providing advice on WEMO software.

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Contents

Executive Summary

This work was undertaken with the aim of developing a novel modelling approach to inform the restoration of *Zostera marina* seagrass habitats within the Plymouth Sound and Estuaries (hereafter Plymouth) and Solent Maritime (hereafter Solent) Special Areas of Conservation (SACs) on the South coast of England.

A Species Distribution Model (SDM) developed by the authors was used to explore the environmental characteristics of locations with existing seagrass beds at each site and used to predict the suitability of other areas for restoration. The eventual aim of the project was to restore an area of *Z. marina* approximately 4 ha in size in each of the SAC's.

The list of environmental characteristics was defined by Natural England as those having shown to be important in other seagrass restoration projects worldwide. They included turbidity, depth, water quality, slope, sediment type, salinity, temperature and wave exposure. The approach utilised existing seagrass presence and absence data provided by Natural England from extensive marine surveys of each estuary. Freely available data on the environmental variables were obtained and combined with outputs from an open source wave exposure model and bathymetry data held under research license by the University of Exeter and used to predict areas suitable for seagrass restoration.

Key findings from the modelling were:

- Overall, the predictions from the model showed good agreement with existing seagrass locations and were biologically sensible despite having a fairly low explanatory power
- Bathymetry had the strongest effect on the distribution of *Z. marina* for the Solent. Depth defines sediment characteristics and light availability, two important factors for successful seagrass colonisation
- A number of variables had moderate effects in the model for Plymouth with relative wave exposure and turbidity being the most ecologically meaningful
- The relationship between probability of seagrass presence and wave energy was complex. For Plymouth, only sheltered sites supported seagrass but in the Solent, moderate to high exposures were tolerated. Relative wave energy values from WEMo were higher overall in the Solent than in Plymouth

The above findings highlight the importance of considering habitat suitability on a site-by-site basis. We discuss and evaluate these findings further in the main sections of the report. In light of these evaluation we recommend 3 areas for each location that would be suitable for restoration. At Plymouth these sites are Cawsands (SX 437 503), Drake Island (SX 469 528) and Jennycliffe Bay (SX 488 528). At The Solent these are Ryde (SZ 608 934), Calshot (SU 486 012) and the North Solent National Nature Reserve (SZ 442 982). These included areas of seabed both within and outside of the SAC's. Each recommendation is accompanied by detail of suitability and potential factors to be aware of. For both the Plymouth Sound and Estuaries and Solent Maritime SACs there a moderately sized ~ 4 ha areas that would have a reasonable chance of success if restoration work were undertaken.

Summary flow chart of steps

Seagrass data Gathering

- Seagrass bed point data records (positives / 'presence' records)
- Sediment grab sample data (negatives / 'absence' records)
- Records of isolated eelgrass / *Zostera marina* were not counted
- Only records in the depth range -10m to +2m were included, to exclude errors and Z. noltii intertidal seagrass beds.

Environmental variable gathering

- Bathymetry
- Slope
- Nitrates
- Phosphates
- Turbidity
- Salinity
- Dissolved oxygen
- Sea surface temperature (max & mean)
- Habitat data (EUNIS polygon data - reclassified into 6 groupings)

WEMo Wave energy modelling

- Using depth and wind speed, the Wave energy within a bay was modelled.
- Outputs were compared to outputs from SWAN spectral wave energy calculations and actual wave energy data at various points in the bay at Plymouth to check consistency. This showed outer bay areas may experience greater wave height and energy than WEMo results suggested, and energy conditions is outer bays should be considered with more caution.

Habitat Suitability modelling

- Data points for seagrass bed habitat from -10m to +2m were used to create a 30m^2 grid of presence / absence to test association with variables
- Variables and model for final model were tested and validated, including interactions between variables
- The final model was clipped to the areas of environmental data (MESS tool) to reduce extrapolation beyond the area of input data.

Selection of recommended Areas in each site

- Final areas described as top 3 sites per area (Plymouth SAC / Solent region) were areas where high probability area was over 4Ha in size. This was due to metananlysis showing that small areas are less successful at restoration & ReMEDIES project anticipated restoration at 4Ha per site
- The results cannot predict optimal areas for thriving seagrass bed - as it was not possible to include % cover as a variable, and the presence of wider defuse pollution or recreational / industrial activity were also not included in the model. Therefore site specific local knowledge also needs to be used in final restoration area selection.
- Smaller areas < 4Ha may also be suitable for restoration, but optimal success of ~40% is mainly achieved if restoration is over 1Ha in area.

Introduction

Two species of seagrass are found in the UK: *Zostera marina* and *Zostera nolii.* Both are associated marine environments and require a sufficient supply of nutrients. *Z. marina* typically forms dense beds in the intertidal and shallow sublittoral zone, most commonly to depths of 7m (though occasionally to 10 m). Below this depth, light inhibits growth, as between 12-37% of surface photosynthetically active radiation is needed to sustain growth (Jackson, Griffiths, & Dunkin, 2013). It is thus likely that in order to survive at greater depths, less turbid conditions are needed. The species typically occurs most commonly on muddy to relatively coarse sediment (occasionally with a mixture of gravel) (Dale, McAllen, & Whelan, 2007). The species is able tolerate temperatures ranging from -1 to 25°C, though optimum conditions for growth appear to be more restricted, ranging from 13 and 24°C (Lee, Park, & Kim, 2007).

As efforts to protect and expand seagrass habitats increase globally, there is now a fairly robust understanding of the key considerations that lead to the highest chances of success. Many of these can be informed by what is already known to influence seagrass health such as environmental parameters that determine light availability like depth and turbidity. However, the dynamic nature of the coastal environments where most seagrass habitats are found adds considerable complexity to restoration and dictates that sites should be considered individually where possible (Fonseca *et al* 2009). Their nature as a foundation species also offers clues as to the importance of self-sustaining feedback in seagrass bed expansion and persistence; larger restoration projects are more robust to the myriad factors that determine their health (Fonseca *et al* 2009). This notwithstanding, global survival rates of seagrass from restoration projects is around 37% with poor site selection, the strong influence of natural environmental perturbations and human stressors being responsible (Fonseca *et al* 1998; Fonseca, 2011; Van Katwijk *et al* 2016).

The most successful projects within these are those that carefully consider site selection (Fonseca *et al* 2009; Van Katwijk *et al* 2016) as the loss of seagrass in the early stages of restoration is reduced (Rezek *et al* 2019). Using existing beds as an indication of restoration suitability is a sensible first step (Jackson *et al*, 2013) but it is important to consider that up to 70% of seagrass extent in northwest Europe was wiped out by the wasting disease *Labyrinthula zosterea* (Fonseca *et al* 2009) and so the current extent of these habitats does not represent the only suitable sites for its growth.

To date, few multivariate analyses of Z*ostera marina* habitat suitability for restoration exist and there is little agreement on the factors that define suitable habitat. Van der Heide *et al* (2009) found that of 26 variables analysed using a logistic regression approach, two (sediment redox potential and light attenuation) explained 77% of variability in coastal *Z. marina* habitats in northern Europe and Scandinavia. To identify suitable habitat for restoration, Kelly *et al* (2001) used a logistic multiple regression approach that featured landscape pattern indices and relative exposure measures to identify suitable habitat for restoration of *Z marina*. Only 7% of the total North Carolina area of 5000 ha was deemed suitable by this approach and to some extent, the authors identify that disentangling the habitat's contribution as a foundation species to the local abiotic conditions from those that control its growth was a challenge. This recognition of the ecological function of seagrass to influence the variables often used in models like this was also highlighted by Valle *et al* (2011) when assessing *Zostera noltii* habitat suitability with modelling.

Here we aim to develop a habitat suitability assessment for seagrass restoration at two sites on the south coast of the UK that are listed as Special Areas of Conservation (SAC's) and contain fragmented beds of *Z. marina.* These sites typify the wide range of conditions that are apparently suitable for Z. marina growth in the UK with notably different exposures and nutrient regimes. Our approach sought to gather variables for all of the factors deemed important for promoting sustained seagrass growth and then modelling which factors were most important at each site individually. From this, we constructed habitat suitability maps for each site that indicate a continuous prediction scale of suitability for restoration.

Methods

Here we use a technique known as species distribution modelling to determine the most appropriate areas for active seagrass restoration. The technique entails identifying locations of occurrence of seagrass species, drawing up a list of potential environmental predictor variables, quantifying their value at locations where seagrasses are present and then fitting statistical models to establish a relationships between probability of occurrence and these environmental variable, in isolation and in combination. The model is then used to infer locations where environmental conditions appear to be suitable seagrass growth.

We gathered a range of environmental variables as predictors of seagrass growth and compared these to known seagrass locations within the SAC's studied. The compilation of environmental variables considered was recommended by NE based primarily on work previously undertaken to gather evidence identifying important biological drivers of seagrass habitats (Jackson, Griffiths, & Dunkin, 2013) (Fonseca, Whitfield, Kelly, & Bell, 2002) (Fonseca, katwijk, Keulen, & Paling, 2009), literature where modelling on seagrass has identified relevant variables for specific study locations (Bekkby, et al., 2008) (Boscutti, et al., 2015) (Detenbeck & Rego, 2015) (Uhrin, Fonseca, & Kenworthy, 2009) (Whitfield, 2002) (Uhrin, Fonseca, & Kenworthy, 2009), and expert knowledge of seagrass beds in the areas of focus. The initial list included nutrients, turbidity, sediment, wind and wave exposure, currents/tides, temperature, salinity, human activity, as possible drivers but slope and distance to mean low water were also later suggested. We include a list of those considered further below and explain the accessibility of each (most of which were freely available). In some cases, we were not able to gather data on a possible predictor of seagrass growth due to a lack of accessibility. These are detailed at thebottom of the below section.

Data Sources Gathered and Their Assessment

Data Provided by Natural England – Presence/Absence data

The priority focus for the modelling was for subtidal beds of *Zostera marina*. Only data identified as seagrass beds, or recorded with a percentage cover > 5% were considered useful as an indicator of seagrass bed habitat. Those beds naturally found with percentage cover less than this are usually on the periphery of the most suitable core habitats, and may be exposed to extreme thresholds of one or more important variables (Jackson, Griffiths, & Dunkin, 2013). Other data with no or very low-density seagrass were treated as 'absence' records. This matches OSPAR criteria for defining seagrass beds and ensures the model doesn't use sparse seagrass, in suboptimal conditions as an indicator for seagrass beds.

Seagrass bed "presence" data were provided from the following sources:

- NE habitat map geodatabase using HOCI and EUNIS codes
- Raw data provided from a range of surveys at sites that included:
    - ER12-185 Plymouth Sound SAC Seagrass Condition Assessment 2012
    - NE Plymouth Seagrass Condition Monitoring July 2018
    - Environment Agency 2018 Plymouth SAC drop down video photo log
    - HIWWT 2012 seagrass survey raw data video analysis
    - Environment Agency 2018 Needles & Solent SAC Subtidal Seagrass Data

Data used as seagrass 'absence' records, were extracted from NE habitat map geodatabase and were selected by using all data within the 'A5' EUNIS classification which represents subtidal sediment data from marine monitoring data and evidence provided by citizen science projects and third parties such as wildlife trusts and data from environmental impact assessments. Additionally, all records with no seagrass or low seagrass density from the above field surveys were treated as "absences". Data were converted from WGS84 to British Nation Grid format of Airy 1830 (EPSG:7001) BNG / OSGB 36 (EPSG:27700) and clipped to Mean Low Water using NE internal MLW data (not publicly available) in ArcGIS. Frequency plots of presence / absence data against bathymetry were then created to inform typical depth.

A significant number of 'presence' records of seagrass appeared to be several metres (up to 5-7m) above 0 in the bathymetry – which corresponds with chart datum / lowest astronomical tide at Newlyn. This was further investigated as *Z. marina* is typically found in 0-5m depth below sea level, but not generally in the upper intertidal. As mean low water is on average approximately 1.3m above chart datum in Plymouth and 1.03m above in Southampton, it would be reasonable to find 'subtidal' *Z. marina* in areas of the lower range of 0-2m above chart datum. It was agreed that seagrass 'presence' points which were found at 2 m or greater above chart datum were likely to be more intertidal including lower fringes of *Zostera noltii* beds.

The spatial position of such points was examined, and many were in upper tributaries / intertidal estuarine mudflat areas. As such, all seagrass points at 2m + or above were removed, and a number of isolated seagrass records erroneously located in deeper areas were also removed with a depth of 10 m (chart datum) used as a cut-off.

After processing the presence and absence points, there were 404 seagrass presence, and 241 seagrass absence points for the Plymouth Sound model (Figure 1); and 1221 presence and 857 Absence points for the Solent Maritime model (Figure 2). Whilst the focus of this project was restoring habitat within the SAC's, presences and absences provided by Natural England were of a greater extent and were included in the modelling process as long as they feel within the estuary area defined by Natural England.

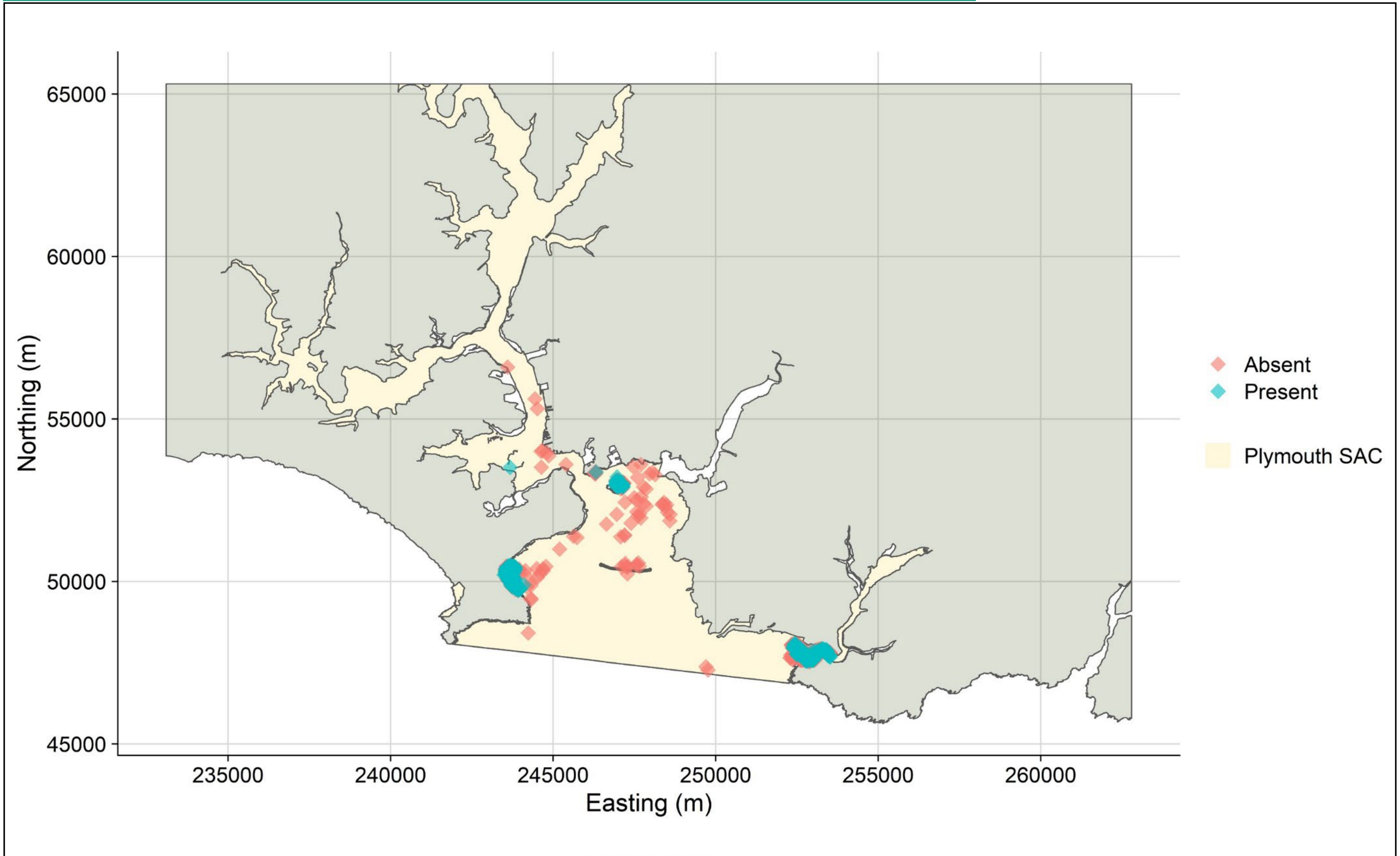


Figure 1: Presence/Absence data used in final model shown within the context of the SAC – Plymouth

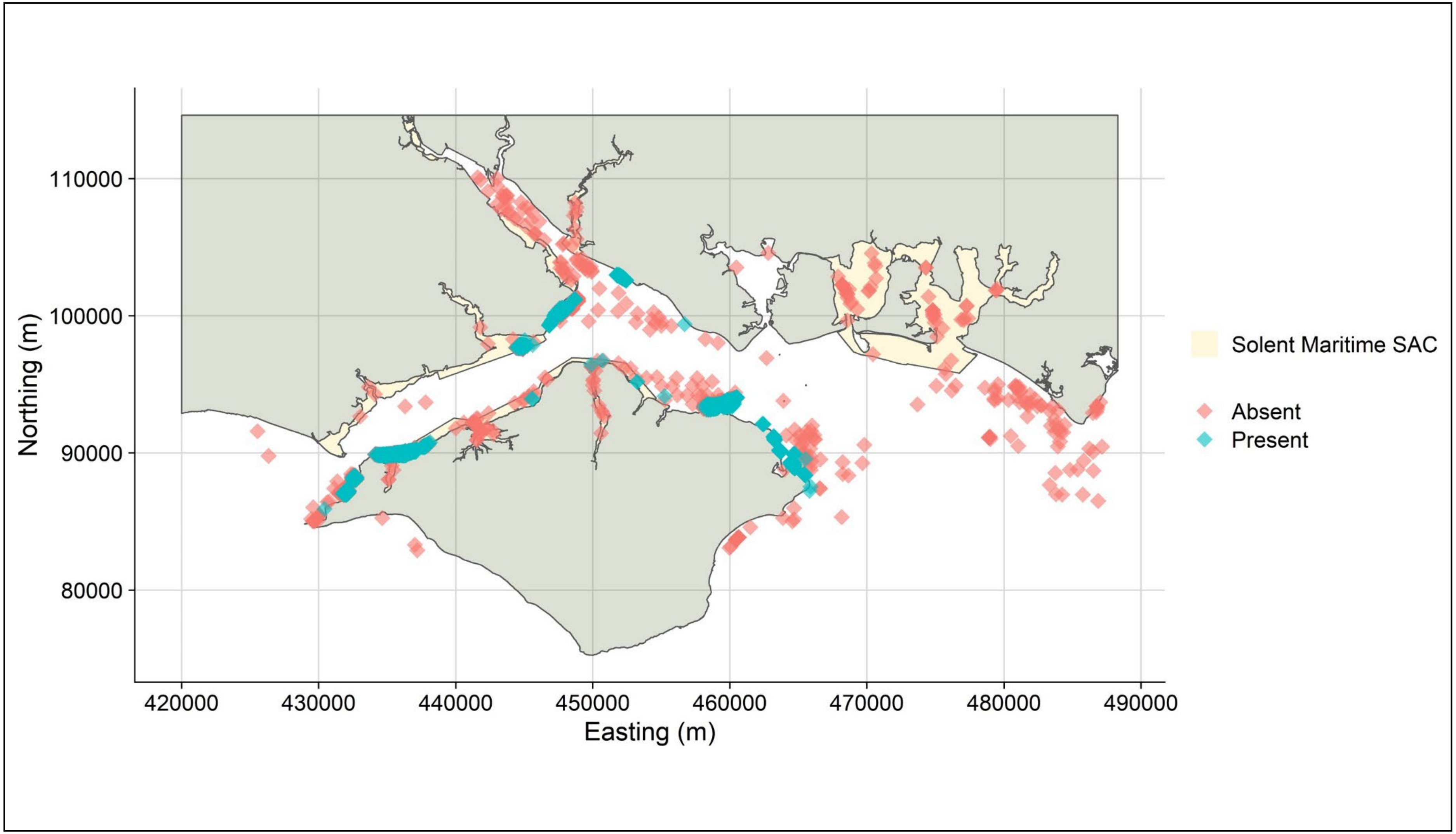


Figure 2: Presence/Absence data used in final model shown within the context of the SAC – Solent.

Bathymetry and slope

An initial assessment of available bathymetry sources was undertaken to find the highest resolution data possible that was freely available. Primarily, this aim was set by NE based where previous tests with WEMo modelling had demonstrated that 25 m gridded bathymetry from echosound surveys offered more useful results than freely available EMODnet bathymetry data at 120 m spatial resolution. In the absence of freely available echosound data for the sites under consideration, Natural England provided the DEFRA Bathymetric Data: One arc sec: England and Wales dataset under licence number Defra012018.001, at a spatial resolution of 1 arc second.

Bathymetry data are natively provided in the WGS84 projection. The data was re-projected to British National Grid projection and resampled back to 30 m spatial resolution. Next, the full extent of the presence/absence data was used to crop the bathymetry data at each site. A coarse 600 m spatial resolution raster was also created from these data, to be used as a template for those variables at coarser spatial resolution. Both the 30 m and 600 m grids form the basis for other predictor variables.

Natural England provided code to calculate slope in R (utilising the raster package) using the 30 m bathymetry dataset.

Nitrate/Phosphorous/Dissolved Oxygen/Salinity

Point data were acquired from https://environment.data.gov.uk/water-quality/view/download/new. The spatial extent of these data is, again, determined by the position of existing sampling stations in the area of study. Plymouth data are included within the 'Devon and Cornwall' region, while the Solent data are within the 'Solent and South Downs' dataset. Data for 2010-2019 was acquired in yearly .csv files, and both compliance and monitoring data was selected. Inverse distance weighting was then used to produce a grid for each variable, based on the 600 m spatial resolution bathymetry raster.

To represent these data, we used measures of the annual mean and coefficient of variation between years. The coefficient of variation (sometimes abbreviated to 'cv') was used instead of standard deviation, as the latter varies strongly with the mean. CV is more appropriate metric for comparison between data that was recorded on scales with an order of magnitude or more difference. A good example of this would be where in one cell, dissolved phosphorous would have a value of less than 1 mg L^{-1} and a salinity value of around 30 psu.

Suspended Particulate Matter (SPM)

Point data was acquired directly from the Environment Agency (EA) by Natural England. Some of this data has previously been used as a proxy for turbidity data in condition assessments but was updated for this project. These data were collected by one of two methods – sub-surface water samples which are analysed in a laboratory, or from a transmissometer attached to a CTD probe deployed off the coastal survey vessel. The results of both methods are converted to SPM in mg L^{-1}. Samples are collected monthly, throughout the year from fixed long-term stations in the waterbody. The spatial extent of this data was limited by the position of existing sampling stations used by EA. As such, data that was contained within the spatial extent of the presence/absence data and that was collected in the years 2010-2019 was selected. Inverse distance weighting was then used to produce a grid, based on the 600 m spatial resolution bathymetry raster. Mean and coefficient of variation were then calculated (as described above).

Sea Surface Temperature (SST)

Gridded SST data was downloaded directly from NOAA servers. The dataset is described here - https://podaac.jpl.nasa.gov/Multi-scale_Ultra-high_Resolution_MUR-SST. Data are provided in netcdf format, and daily measurements were extracted for July, August and September (representing the warmest part of the year) for the years 2010-2019. Maximum and mean values were calculated over this time period and saved as gridded raster outputs. Maximum temperature was chosen to account for the possibility that particularly high temperature deviations would be detrimental to seagrass survival. Data was then resampled, producing a grid based on the 600 m spatial resolution bathymetry raster.

EUNIS Habitat

Habitat data assigned to EUNIS classification was provided by Natural England and assigned to six categories to facilitate modelling, and also represent distinctions in sediment type suitable for seagrass. These categories were agreed following a number of consultations on the resolution required to facilitate modelling, but also adequately represent the fine-scale distinctions in the sediment that may distinguish between subtidal seagrass presences and absences. Under guidance from Natural England, various modifications were made to the data classification process coding to reflect decision making, and deal with troublesome and erroneous points, often resolved through expert knowledge and understanding. This process included a review of literature on this subject, but also used box plots to investigate which EUNIS habitats currently support seagrass presence points taking into account known confidences and errors in the data. With this information, features were grouped into 6 broad habitat categories reflecting habitats which could not support seagrass at all and taking account of key differences between those that could (see supplementary information). Next, for each presence/absence location, the corresponding 30 m grid cell (from bathymetry data) was aligned. Due to the fact 30 m grid squares could potentially contain multiple habitat polygons, the percentage cover of each of the 6 broad habitat categories recorded for each individual grid square. This resulted in six 30 m spatial resolution rasters, with the % cover of each of the 6 broad habitat categories being produced for modelling and mapping purposes.

The 6 groups of EUNIS categories used for the model are listed in the supplementary information section.

Wind and Wave

A review of two wind and wave modelling tools were explored to decide how best to represent wave energy in the model.

Analysis of Representative Wave Energy (RWE)

Natural England recommended the use of the representative wave energy metric in the NOAA wave exposure model (WEMo). Version 4.0 of WEMo which is compatible with ArcGIS 9.3 was downloaded from https://coastalscience.noaa.gov/research/coastal-change/wemo/. An ArcGIS license is required to run the software. Acquiring an older version and complimentary license file for ArcGIS 9.3 is not trivial. Fortunately, a colleague at the University of Exeter was able to assist with acquisition and installation of the legacy software. Once installed, WEMo produced multiple unexplained errors and appeared to be unable to deal with very large datasets. Despite helpful advice from one of the developers, issues with running WEMo remained. Therefore, the original plan for processing RWE values for every point at the centre of every bathymetry cell (30 m spatial resolution) was replaced with a method utilizing a coarser 120 m spatial resolution point dataset. The outputs were therefore RWE values for points spaced 120 m throughout both areas of interest. These output points were then interpolated to a 30 m spatial resolution grid matching the bathymetry data. The inputs to the wave model are described in Table 1:

Table 1. Summary of variables and their attributes used for WEMo modelling

Data	Source	Native Spatial Resolution	Resampled Spatial Resolution	Temporal Extent
Bathymetry	DEFRA Bathymetric Data: One arc sec	30 m	30 m	NA
Wind	ERA5	~30 km	~30 km	2010-2019
Sea Polygon	(created from) OS High Water Line	NA	NA	NA

As part of our contracted role, we assessed the suitability of WEMo to accurately predict wave exposure in the study sites.

WEMo operates as a wave exposure model. For each output location, it calculates the exposure to wave action by measuring the distance over which waves can be generated from all directions. The distance of open water over which a wind blows is termed the fetch and along with the speed of the wind, governs the energy input into ocean waves. As such, a longer fetch generally increases the wave exposure. WEMo also accounts for bathymetry, shallow water will remove energy from the waves and land will block energy. This is also accounted for in the wave exposure. However, WEMo is only accounting for wave energy generated within the computational area. Where a location is exposed to a large fetch, for example the Atlantic Ocean, wave energy can travel into the computational area as ocean swell. WEMo does not account for this.

For this work, the outer area of the Plymouth Sound does have oceanic exposure. As such, it is not feasible to set up the model so that the mean and maximum wave heights will be accurate. However, WEMo also generates relative wave exposure statistics that describe the exposure to waves at each output point relative to others within the domain. By setting a long outer fetch (in this case 15km), the relative exposure to waves will be greatest in those areas where there is an oceanic exposure. As such, this statistic becomes a suitable input to subsequent modelling.

The analysis below highlights that this is an imperfect solution, and there are limitations with WEMo particularly with regards to estimating wave heights. However, the areas with significant exposure to ocean-generated swell are, in the majority of cases, not those where seagrass is found, due to the highly mobile seabed. It is these areas that are least accurate. Conversely, most existing seagrass locations are well-served by WEMo and the relative wave exposure statistics.

Analysis of mean and maximum wave heights at exposed locations

For this analysis, data from a regional computational wave model (Van-Nieuwkoop 2013) that includes the outer reaches of Plymouth sound was compared to WEMo output for the same location. The data were generated using the SWAN spectral wave model SWAN (Booij, 1999). SWAN was run for the larger region and represents processes that generate, dissipate or redistribute wave energy. The model used UK MetOffice global wave model data to represent the incoming wave energy from open ocean generation. This model differs from WEMo as it calculates the energy coming into and out of each grid square every hour, providing a time-series of predicted waves. For this work, data from 2 ½ years between Nov 2009 and May 2012 were used to produce representative mean and maximum wave heights at the entrance to Plymouth sound (50°18'36.0"N 4°09'00.0"W)

Table 2. Comparison between SWAN and WEMo outputs for Plymouth area.

	Mean wave height (m)	Max wave height (m)
SWAN	1.0	6.0
SWAN, nearest	0.4	2.53
WEMo	0.4	0.54

The highest WEMo estimated average wave height in exposed areas was 0.4 m. This is significantly lower than the 1.0 m calculated by SWAN, which is representative of the absence of incoming wave energy in the WEMo calculations. The discrepancy in maximum wave height, where large wave events will be driven almost entirely by winds outside of the WEMo domain, is even greater.

The SWAN model was not set up for nearshore calculations and the computational domain does not extend into the Plymouth Sound. The closest point to shore in this region is 50°19'19.9"N 4°10'31.8"W. Despite continued exposure to the SW, this point is shallower and energy arriving from the SW will be reduced. Here, the average wave height compares favourably with WEMo, whilst the maximum wave height is significantly greater (Table. 2).

The results demonstrate that WEMo-calculated wave heights at exposed locations are not accurate. The model does not account for waves travelling into the computational area. Fetch was set to the maximum sensible limit of 15000 m in WEMo but in exposed areas wave energy can be generated across much greater distances (i.e. the English Channel). The effect is greatest in large wave events. The comparison with a point partially sheltered from the prevailing waves gives some confidence that the WEMo model is accounting for energy for average wave conditions in sheltered areas. However, this work should avoid the use of wave heights generated within WEMo.

The representative wave energy parameters offer a non-dimensional comparative parameter within each WEMo domain. Because wave heights in exposed areas are reduced, the RWE will be smaller than expected and caution must be applied to analysis including these areas. However, for sheltered areas, RWE can be expected to offer a robust parameter for subsequent modelling.

Data Summary

Table 3. Summary for all data sources modelled and other variables created, to be considered in the analysis. ‡Mean and coefficient of variation in these variables were used. See explanation above.

Data	Source	Native Spatial Resolution	Resampled Spatial Resolution	Temporal Extent
Bathymetry	DEFRA Bathymetric Data: One arc sec	30 m	30 m	NA
Slope (calculated from Bathymetry)	DEFRA Bathymetric Data: One arc sec	30 m	30 m	NA

Distance to Mean High Water	OS Boundary Line	NA	30 m	NA
Suspended Particulate Matter (SPM) ‡	Environment Agency	NA / Point	600 m	2010-2019
Nitrate‡	Environment Agency	NA / Point	600 m	2010-2019
Phosphorous‡	Environment Agency	NA / Point	600 m	2010-2019
Dissolved Oxygen‡	Environment Agency	NA / Point	600 m	2010-2019
Salinity‡	Environment Agency	NA / Point	600 m	2010-2019
Sea Surface Temperature (SST)	NOAA	~ 1 km	600 m	2010-2019
EUNIS Habitat	Natural England	NA / Polygon	30 m	NA
WEMo Representative Wave Energy (RWE)	NA	NA/ Point	30 m	2010-2019 (based on wind data)

Summary plots of the how each of the variables are divided between presences and absences can be found in the supplementary outputs section at the end of this report.

Data forms not included in the model

Current

We are not aware of any freely available datasets for current. Therefore *in-situ* measurements would be required to understand how current varies over fine spatial scales within the SACs. This is beyond the scope of this project, which solely utilises data that has already been collected and processed.

Human Activity Levels in Coastal Environments (e.g. recreational water sports, boat usage and moorings)

We had previously proposed that freely available satellite images would be a useful resource for this and that there were potentially some trials we could do with open-source data on recreational water use recorded on activity Apps such as Strava. Due to the complexity of compiling the other variables as well as the presence/absence data however we were unable to include this in our analyses. The existence of moorings near any given site deemed suitable for restoration can be considered prior to commencing planting as a precursory step.

Modelling Approach

We modelled the probability of occurrence of seagrass (as a proxy for suitability for seagrass restoration) using binomial GLMs (Generalized Linear Models) and GLMMs (Generalized Linear Mixed Models) of the presence/absence of seagrass. This is termed a 'Species Distribution Model' (SDM). The output of the SDM identifies the similarity in the measured environmental variables between a given site and the locations where seagrass is currently found.

We originally proposed to use an ensemble of 10 SDM approaches using an R package called Biomod. However, once we collated the environmental data available, it was apparent that the data for many variables were too sparse to interpolate them to a high spatial resolution. This meant some environmental variables were recorded at 30m and some at 600m. Each presence/absence point was given environmental values of the 30m and 600m in which it falls. This is problematic for two reasons. First, adjacent 30m grid-cells will have unique values for 30m resolution variables but identical values for the 600m resolution variables. The 30m data therefore capture variability between grid-cells much more precisely than the 600m data. The unrealistically low (often 0) level of variability between 30m grid-cells for the 600m variables means that the effect of the 600m variables would be measured much less accurately than 30m variables. 600m variables could be found to be important or unimportant spuriously. Second, presence/absence varies strongly between coarse grid-cells because the presences are highly clumped. A coarse grid-cell that contains one presence is likely to also contain many other presences. This clumping would make it appear that the environmental conditions in that grid-cell are more important than they actually are. Thus clumping (a form of spatial autocorrelation) leads to pseudo-replication and inflation of the importance of environmental variables.

Presence/absence was modelled at 30m resolution, with values thinned so a single presence or absence was included per 30m grid-cell, i.e. each 30m grid-cell was only included once. Presence/absence data were trimmed to include only points from between +2 and -10m, to reduce the unevenly high number of absence points from marine monitoring of habitat at deeper depths which could not support *Z. marina*. In the Plymouth area presence/absence data were trimmed to be within the SAC boundary (fig. 18) which contained most of the data provided and the area is unique in conditions. However for the Solent the multiple SAC boundaries don't contain all the areas where seagrass occurs/could occur, and as there was considerable data beyond the boundaries, the remit was extended beyond the boundaries. In the Solent area presence/absence were trimmed to be east of 425000m and north of 82000m (British National Grid Reference, fig. 19). We standardized the environmental variables by subtracting the mean and dividing by the standard deviation before modelling. This is so that the magnitude of the coefficients are comparable (i.e. if coefficient a is twice as large as coefficient b, coefficient a has an effect twice the size of coefficient b). This was also necessary as unstandardized variables can cause GLMMs not to convert. We used a semi-automated approach to select the environmental variables that influence seagrass presence/absence. At each stage (below) models with different combinations of variables were compared using the Akaike Information Criterion adjusted for small sample size if necessary (AICc), where the model with the lowest AICc is considered preferable. This approach identifies the most parsimonious model, i.e. the one that contains all variables that contribute to understanding the distribution of seagrass, while penalising against overly complex models. Thus AICc often retains variables that are not assessed as significant using p-values (Burnham and Anderson, 2002). A ΔAICc threshold of two units was used to select models (a well-used threshold). This means that any combination of variables that did not increase the AICc by more than this, relative to the AICc of the best model in the set of models being compared, was considered equally likely to be as accurate as the best model. At each stage the best subset of models was taken forward.

It was not possible to combine all main and quadratic fixed effects in a single model – these models were too complex to fit. Therefore, automated model selection could not be performed. Instead, we manually investigated the most informative variables for each site using the following steps:

a. **univar**. GLMMs were made of the linear and quadratic effect of each environmental variable with the coarse grid cell random effect included. The AIC was calculated for each model (Estrada *et al* 2015),
b. **multivar1**. The linear terms of the environmental variables from the 'best' univar models were entered into a single multivariate model (excluded variables were reinvestigated in multivar3). 'Best' is defined as having an ΔAIC<50 compared to the best single model.
c. **multivar2**. The AICc of all combinations of variables in multivar1 was calculated and the single best model was retained (Burnham and Anderson, 2002).
d. **multivar2q**. The addition of quadratic terms of all variables in multivar2 was attempted. All quadratic terms of variables in models that are included in the best model subset (ΔAIC<2) were retained. Thus, if a quadratic term of a variable added by itself improved or did not deteriorate the model, it was retained.
e. **multivar3**. The addition of linear effects of all variables not in multivar2q was attempted (even if variables had been excluded previously). All linear terms of models that are included in the best model subset (ΔAIC<2) were retained.
f. **multivar3q**. The addition of quadratic effects of all variables added in multivar3 was attempted. All quadratic terms that were included in the best model subset (ΔAIC<2) were retained.
g. **multivar4**. The AICs of all models constructed in multivar3q were compared. All quadratic terms that were included in the best model subset (ΔAIC<2) were retained (Crawley, 2007).
h. **multivar4i**. Check for interactions between any of the linear terms of the variables retained in multivar4. Interactions measure the effect of one environmental variable on the effect of another environmental variable on seagrass occurrence. Interactions included in the best model subset (ΔAIC<2) were retained (Crawley, 2007).
i. **spatial.** The residuals from the best model subset of the multivar4i model(s) were mapped, and spatial autocorrelation in them calculated. The spatial autocorrelation was then used as an explanatory variable additional to those in the merged model (Crase *et al* 2012).
j. **final.** The best model subset was selected from the merged and spatial models (ΔAIC<2). The variable coefficients for a single final model were calculated as an average of all models in the best model subset, weighted by the sum of the Akaike weights of the models in which the variables appear (Burnham and Anderson, 2002).

For any model applied to this dataset the presence/absence of seagrass will be explained to different degrees by the environmental variables included or the fact that the presences are simply clumped in a few coarse grid-cells. Our approach was to test this at every step, to ensure the most appropriate model was being made. Step a included coarse grid-cell as a random effect by default (results given below). In steps b-j we tested whether including the coarse grid-cell as a random effect was meaningful by (i) comparing the AIC of model(s) with and without the random effect, and (ii) in the mixed model comparing the standard deviation (sd) of the random effect to the estimates of the fixed effects. The random effect was retained if the mixed model had a higher AIC **and** the sd of the random effect was similar or greater than the parameter estimates, **and** the model was identifiable (Zuur *et al* 2009). Mixed models are prone to throwing convergence errors, which indicates that the model is not confident it has found a single best value for each parameter. This can mean that the model is overly complex and poorly fit. Therefore, at each step checks were performed to ask whether non-convergence indicated problems with model fitting. This involved running multiple optimisation algorithms to estimate the fixed effect parameters and standard deviation of the random effect. If the estimates were not identical, this would suggest we consider removing the random effect. If the estimates were near identical, then the random effect was retained. This meant that the best model subset at every stage, including the final stage, could include GLMs and GLMMs.

At each step variance inflation between the linear terms was checked, to ensure that collinearity did not affect results (Burnham and Anderson, 2002). If the variance inflation factor was > 5, terms were removed sequentially in increasing order of partial R^2.

The AUC of the single, final model was calculated using 10-fold cross-validation. The data were randomly split into calibration (70% of data points) and validation (30% of data points) data sets, 10 times. A model containing the variables selected in the final model was fit to the calibration data. The resulting variable coefficients were used to predict the validation data, and the AUC calculated using the auc function of the pROC package.
Two thresholds were calculated to convert probabilities of occurrence into sites suitable and unsuitable for seagrass restoration. The 95% threshold was the probability value that classified 95% of the presence data points as suitable. The sens-spec threshold was the probability value that minimises the difference between sensitivity (the proportion of presence data points that are classified as suitable) and specificity (the proportion of absence data points that are classified as unsuitable).

If possible, (i.e. for GLMs), variable importance in the final model(s) was assessed using the partial R^2 (also called coefficient of partial determination of the variable in all models in the best model subset). This value is the proportion of variation that is explained when the variable is included in the final model once the variance explained by other variables in the final model is accounted for. The formula is:
(deviance explained by the model containing the target variable – deviance explained by model without the target variable) / deviance explained by model without the target variable
In order to map uncertainty we produced rasters of the 95% confidence intervals of the predicted probability of occurrence. It was not always possible to calculate the standard error of the final model (if the model was an average of a GLM and GLMM), and if this occurred we mapped the standard error of the models in the best model subset instead.

We made predictions of the suitability for seagrass restoration using the final averaged model (i.e. the model from step j, above). Model predictions extrapolated into areas where the environmental conditions are outside the range of environmental values used to construct the model (i.e. no-analogue environments) should be treated with extreme caution. Therefore, in order to identify no-analogue location we used the multivariate environmental similarity surface (MESS) tool developed by Elith et al (2010). Negative values indicate areas where at least one variable has a value that is outside the range of environments used in construction. The values in the MESS are influenced by the full distribution of the data used to construct SDMs, so that sites within the environmental range of the construction data, but in relatively unusual environments, will have a smaller value than those in very common environments.

Results

Plymouth Univariate Models

These models contain a single environmental variable each, and a model was constructed for each environmental variable (steps a). Most variables make substantially poorer (i.e. less well fit and less parsimonious) models than the model with bathymetry. Coverage of the EUNIS category “sand” could not be used as there are only eight points where seagrass is present on sand, and none of those points have sea surface temperatures. Mean phosphorous couldn't be used as it only had three values. The negative effect of max sea surface temperature is probably because seagrass is absent from upper estuarine areas that can get very warm in summer.

The standard deviation of the differences between the coarse grid-cells (600m resolution) was 1.5, which is within the range of values of the coefficient estimates in table 4. This means that the variation in seagrass occupancy between coarse grid-cells is similar to the effect of each individual environmental variable. Thus, occupancy varies somewhat between coarse grid-cells and it was appropriate to retain coarse grid-cell ID entering into step b, even if solely to account for pseudoreplication.

Table 4. Results from models that included the main and quadratic effect of the named variables as fixed effects, and coarse grid-cell ID as a random effect in Plymouth (univar). Bathymetry was the variable that performed best in isolation, so all other variables were compared against this. Variables were standardised so coefficients are comparable. Variables in grey-shaded cells were entered into multivariate models.

Variable	Main effect coefficient and significance	Quadratic effect coefficient	AIC
bathy	0.9837	-0.9284	620.5
			ΔAIC of model containing named variable, in comparison to model containing bathymetry.
slope	-0.3076	-0.1055	32.13
sst_max	-0.21	3.8667	35.44
sst_mean	0.2142	-0.0698	45.17
spm_mean	-0.163	0.6105	44.72
spm_cv	1.054	0.6529	44.15
nitr_mean	-2.2975	0.8684	41.35
nitr_cv	-2.0518	-0.0879	37.11
phos_cv	-0.3873	4.045	41.22
sal_mean	-1.1914	-0.7262	43.31
sal_cv	-0.273	0.013	45.09
o2_mean	2.9644	0.951	38.32
o2_cv	-2.799	1.2128	39.31
mhw_dist	-1.5725	-4.3682	1.47
wemo_rwe	-0.4826	0.0102	38.16
eunis_other	-0.4955	0.1228	37.35
eunis_litt	-0.2192	0.0082	43.31
eunis_coar	-1.7563	0.2343	28.81
eunis_mud	-0.0935	-0.0149	43.57
eunis_mix	0.5215	-0.2467	19

Solent univariate models

These models contain a single environmental variable each. Several variables have significant effects in univariate models (Table 5), but also substantially decrease the parsimony of the model compared to the model containing bathymetry (ΔAIC high). The exception is slope, which gives a very similar AICc to that of the bathymetry model Coverage of the EUNIS category “sand” could not be used as there was too little variation in values to be modelled.

The standard deviation of the differences between the coarse grid-cells (600m resolution) was 8.2, which is higher than the range of values of the coefficient estimates in table 5. This means that the variation in seagrass occupancy between coarse grid-cells is greater than the effect of each individual environmental variable. Thus, occupancy varies substantially in coarse grid-cells and coarse grid-cell ID should be retained.

Table 5. Results from models that included the main and quadratic effect of the named variables as fixed effects, and coarse grid-cell ID as a random effect in the Solent (univar). Bathymetry was the variable that performed best in isolation, so all other variables were compared against this. Variables were standardised so coefficients are comparable. Variables in grey-shaded cells were entered into multivariate models.

Variable	**Main effect coefficient and significance**	**Quadratic effect coefficient**	**AIC**
bathy	2.8547	-0.3839	1496.63
			ΔAIC of model containing named variable, in comparison to model containing bathymetry.
slope	-0.7916	0.0182	271.21
sst_max	-0.3832	-0.3161	342.61
sst_mean	0.0808	-0.4948	342.26
spm_mean	0.9785	-0.1848	340.93
spm_cv	-1.0465	-0.4349	337.07
nitr_mean	0.2229	0.114	342.94
nitr_cv	-0.5582	0.0887	341.91
phos_mean	-0.2552	-0.5282	341.83
phos_cv	0.2131	-0.4984	342.1
sal_mean	1.1856	0.1144	337.92
sal_cv	-0.8211	0.1378	341.04
o2_mean	0.169	0.0984	343.48
o2_cv	-0.5164	0.2309	342.52
mhw_dist	-4.9771	0.1057	176.9
wemo_rwe	-2.7193	0.4465	265.36
eunis_other	0.5735	-0.2019	338.86
eunis_litt	4.1677	-1.451	192.29
eunis_coar	0.4503	-0.2126	340.08

eunis_mud	0.9013	-0.8214	223.81
eunis_mix	0.6632	-0.5167	297.85

Responses to environmental variables in Plymouth and Solent are similar in some cases but different in others. In some cases the direction of the relationship differs (see signs of the coefficients). Examples of this are grey-shaded in table 5. On the basis of this, we modelled Plymouth and Solent separately.

Plymouth multivariate model results

Two models were part of the best **spatial** model subset from step i (table S2). Both included the same environmental variables, but one was a GLMM, that included coarse grid-cell as a random effect, and one was a GLM. Both models were equally plausible. Therefore, the **final** spatial model (step j) was the average of these two models. The thresholds used to convert the spatial model's continuous predictions to 'suitable/unsuitable' for restoration were 0.031 (95% threshold) and 0.610 (sens-spec threshold). The AUC of the **final** spatial model was 0.889 (standard deviation = 0.001). Variance inflation in the **final** spatial model was <5 for all variables, indicating multicollinearity was not affecting results.

Adding the spatial autocorrelation of **multivar4i** as an explanatory variable to make the **spatial** model improved the models (only models containing the spatial term were selected in the best model subset). The AUC of spatial and non-spatial models were the same. Including the spatial term decreased substantially the partial R^2 of EUNIS categories calculated with the GLM in the best model subset (table S1 and S2). This is to be expected as habitat is highly aggregated, and so responsible for much of the spatial autocorrelation in the results. The importance of the linear and quadratic terms of mean distance to high water were increased substantially by the inclusion of the spatial term (Table 6).

Model predictions should not be extrapolated into areas where the environmental conditions are outside the range of environmental values used to construct the model (i.e. no-analogue environments). In Plymouth this includes much of the upper estuarine areas and some of the open coast (Figure 5). No-analogue environments in estuaries and along the coastlines were caused by mean turbidity being higher than in model data and coefficient of variation in phosphorous being lower or higher than in model data.

Table 6. Standardised coefficients of all variables retained in the final averaged, spatial model, for Plymouth. Standardised coefficients can be used to compare the relative importance of variables. The quadratic term of the relationship between seagrass and a variable is denoted by ^{2}. To predict suitability they must be used with standardized environmental data. *Note that : indicates an interaction between the two named variables.Note that the coefficients for the spatial models were very small because the numerical values of spatial autocorrelation were very high. This is not problematic, as the units are meaningless.**

Variables	Averaged standardised coefficient final spatial model
(Intercept)	0.069504
Eunis coarse	-0.43795
Eunis mix	0.382102
Eunis mud	0.257808
Mean turbidity	1.740501

Mean turbidity²	0.03573
Mean distance to high water	-2.50452
Mean distance to high water²	-3.02289
Coefficient of variation in phosphorous	-0.30414
Slope	-0.87391
Wemo RWE	-0.54027
Slope : mean turbidity *	-0.77815
Spatial term (mixed GLM)**	2.30E-06
Spatial term (GLM)**	2.14E-06

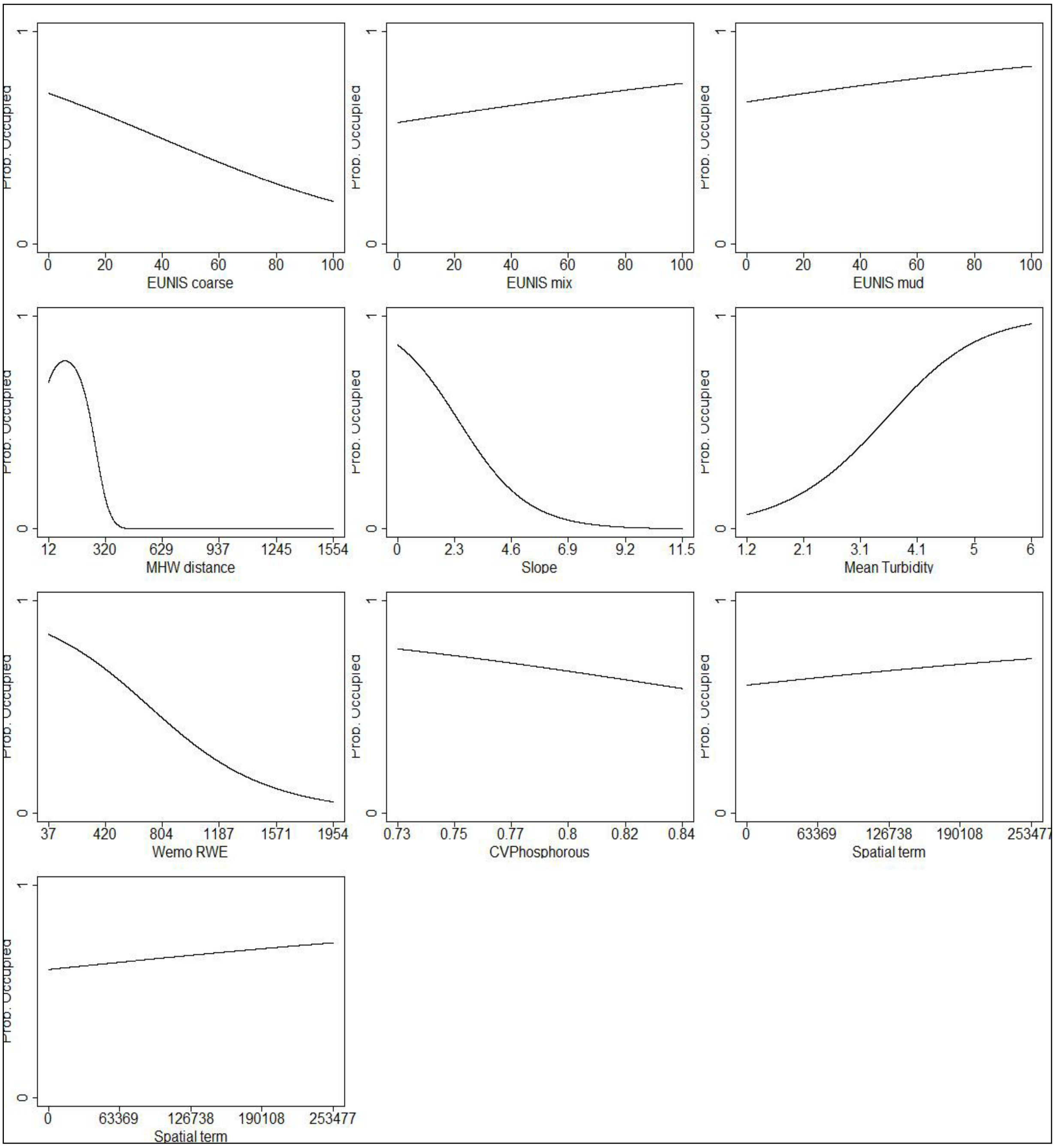


Figure 3. Predicted probability of seagrass occurrence for each explanatory variable in the averaged, spatial model (final) for Plymouth, when all other explanatory variables are held at their means. It is not possible to calculate confidence intervals for an averaged model that combines a mixed and non-mixed model are combined. Therefore, we have given graphs of the two constituent models with confidence intervals in figures S28 and S29.

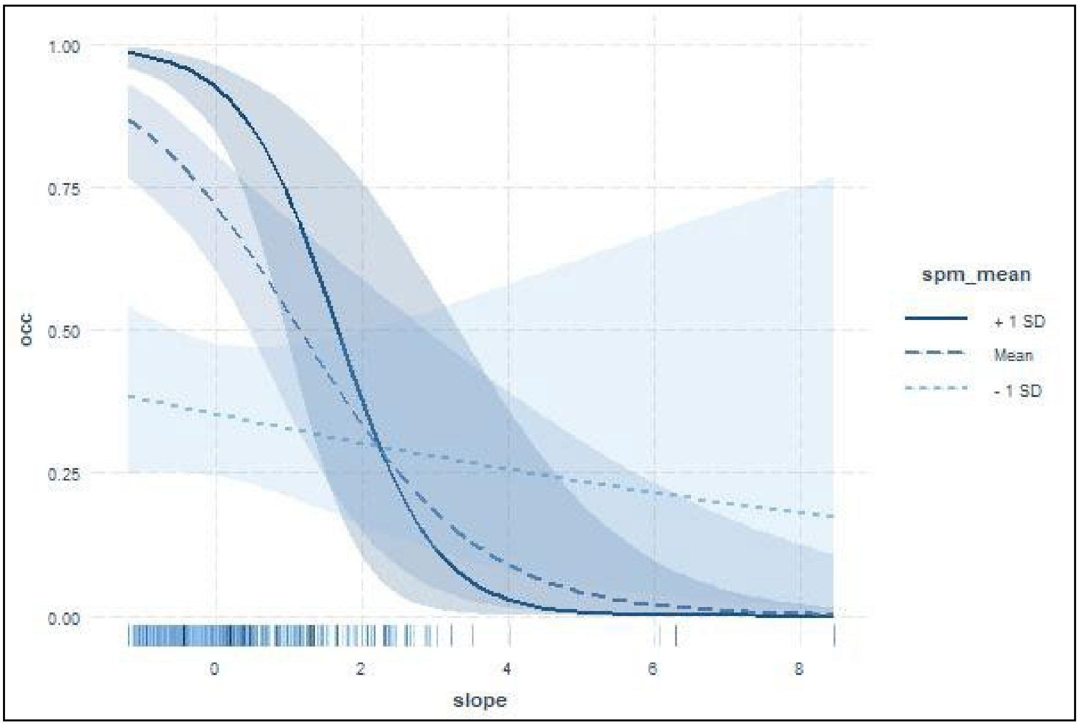


Figure 4. The interaction between slope and mean turbidity in the final spatial model (step j) for Plymouth. This graph is calculated based on the average of the two best models (one which included coarse grid-cell ID as a random effect). Note that the values on the x axis are standardised, not the raw values as in figure 1. The long-dashed line shows the effect of slope when mean turbidity is held at its mean. The solid line shows the effect of slope when mean turbidity is held at 1 standard deviation above the mean. The dotted line shows the effect of slope when mean turbidity is held at 1 standard deviation below the mean. Short blue lines along the x axis indicate the density of data.

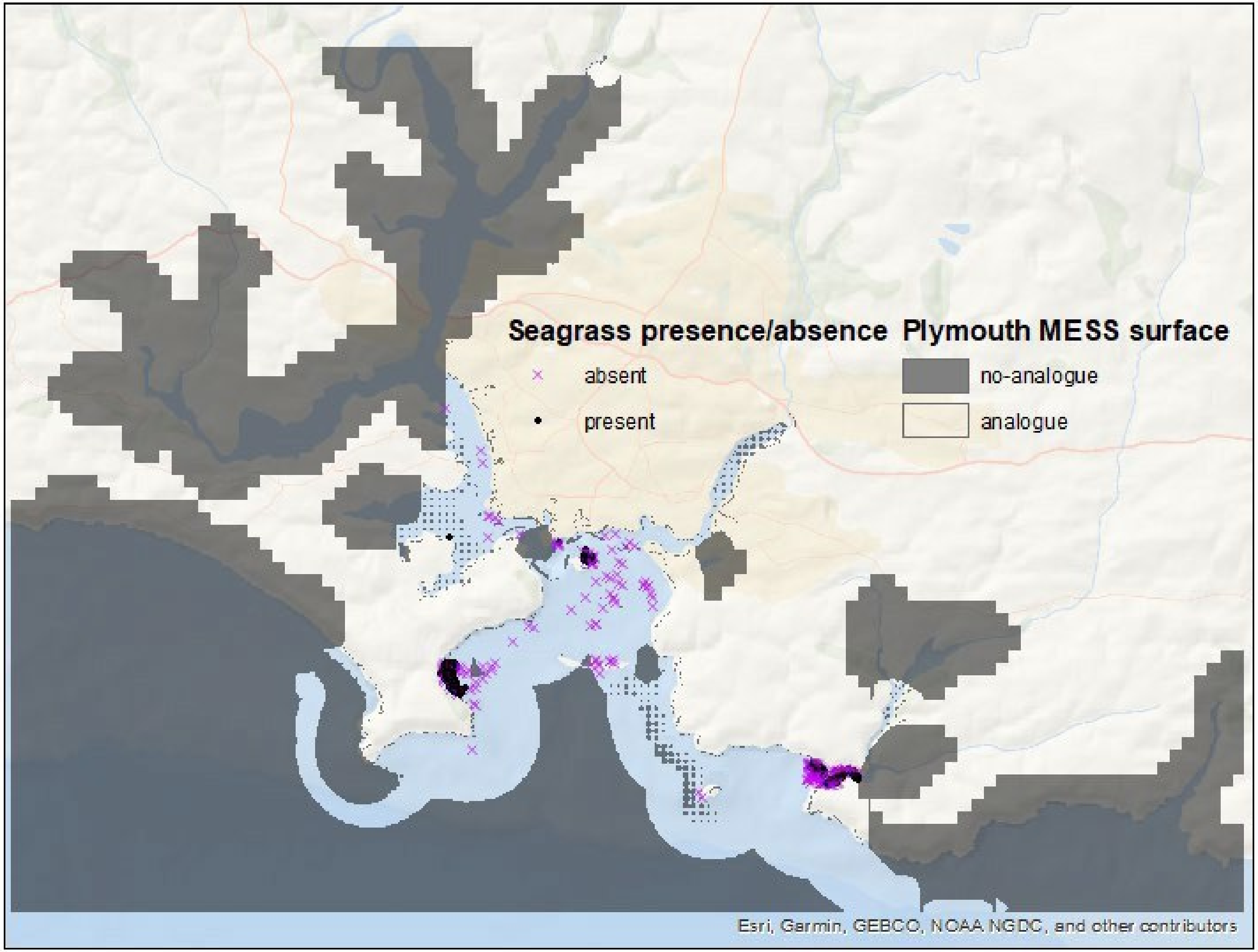


Figure 5. Distribution data used for modelling and MESS surface indicating analogue conditions where predictions of suitability can be made.

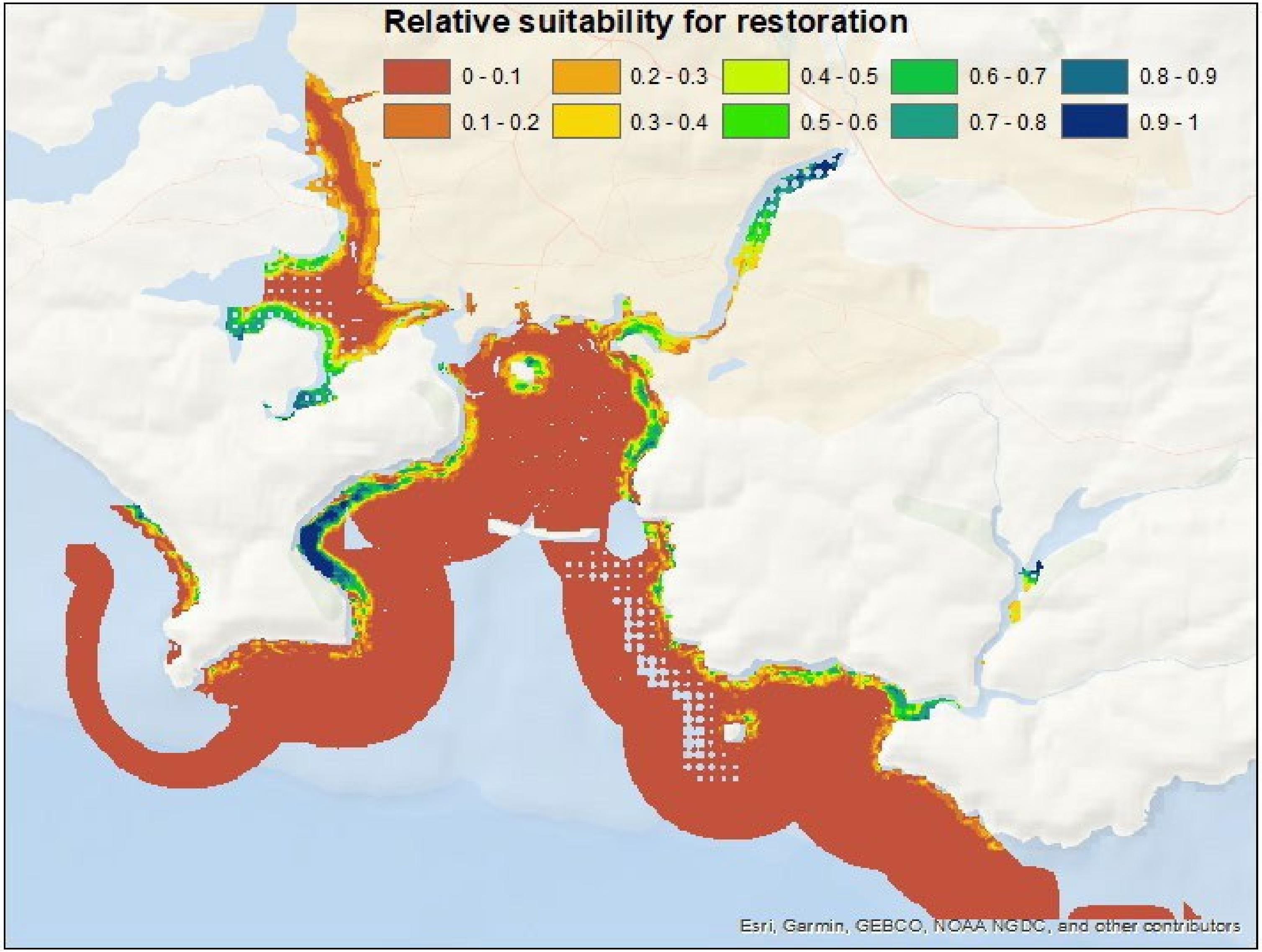


Figure 6. Prediction of suitability based on the averaged final spatial model, trimmed to analogue environmental conditions.

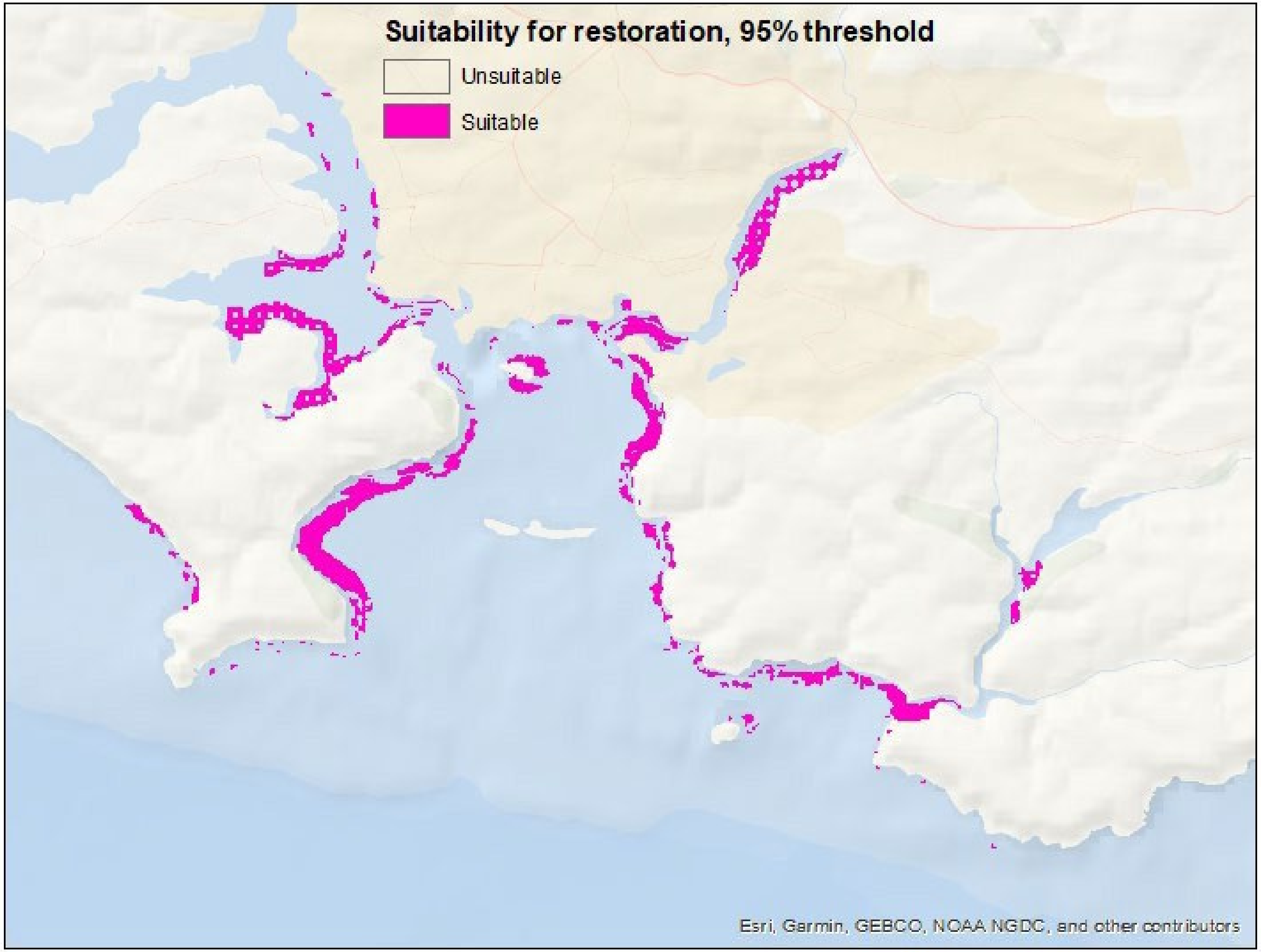


Figure 7. Prediction of suitability based on the averaged final spatial model with 95% threshold imposed, trimmed to analogue environmental conditions.

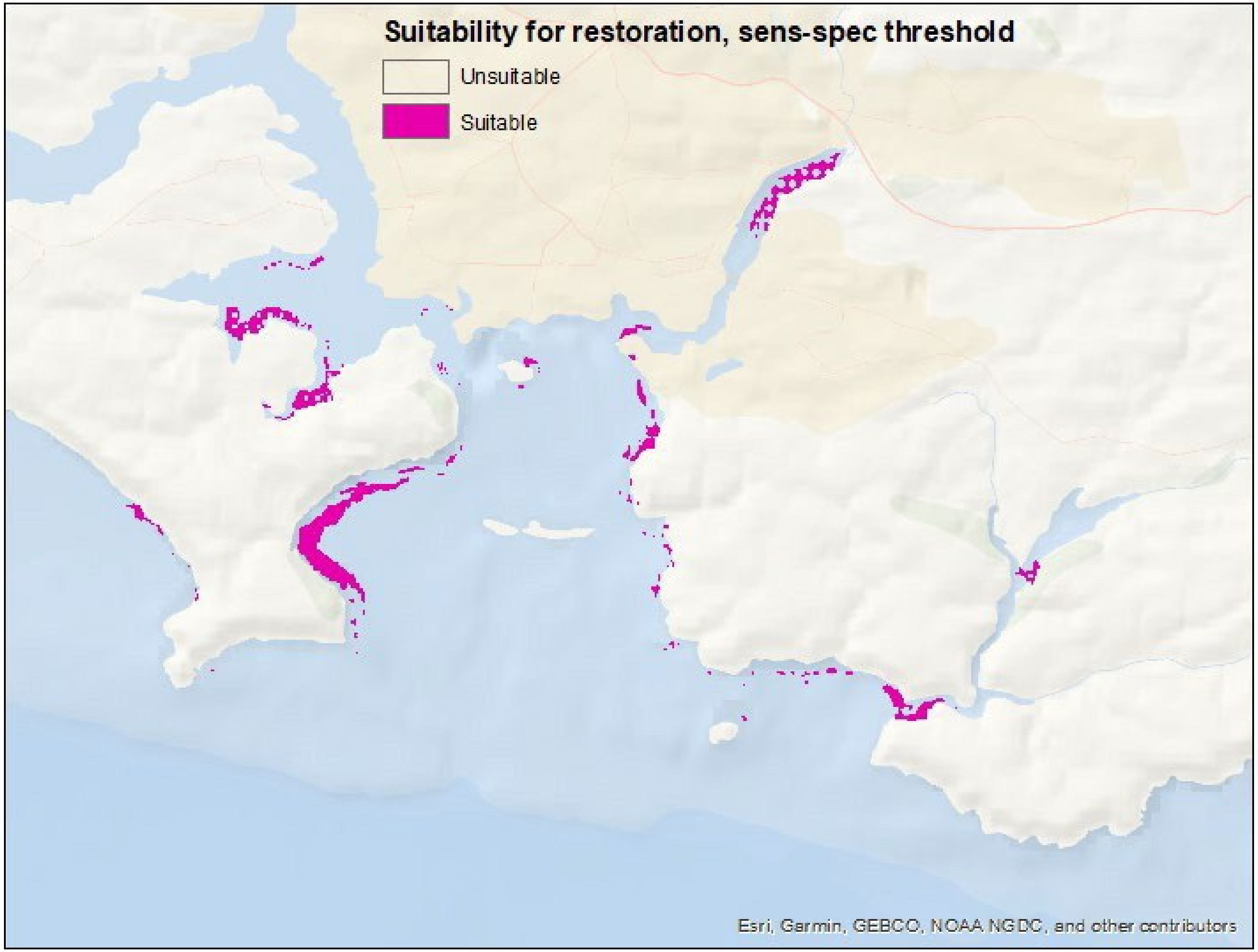


Figure 8. Prediction of suitability based on the averaged final spatial model with sens-spec threshold imposed, trimmed to analogue environmental conditions.

Solent multivariate model results

A single model was selected as the best **final** spatial model. This was a mixed model, which included coarse grid-cell as a random effect (table 7). The thresholds used to convert the spatial model's continuous predictions to 'suitable/unsuitable' for restoration were 0.031 (95% threshold) and 0.190 (sens-spec threshold). Variance inflation levels inflation **final** were <5 for all variables, indicating multicollinearity was not affecting results.

Adding the spatial autocorrelation from **multivar4i** as an explanatory variable to the models in **multivar4i** improved the model ΔAICc=-27. The mean AUC of the **final** spatial model was 0.889 (standard deviation = 0.009). This was slightly greater than that of in **multivar4i** without the spatial covariate, which was 0.867 (standard deviation = 0.012). The most notable change in the estimates of environmental effects caused by including the spatial term was a substantial decrease in the slope of the relationship between seagrass presence/absence and slope (table 7, table S3). This means that in the **final**, spatial model the prevalence of seagrass drops off less dramatically as slope increases, as compared to the non-spatial **multivar4i** model.

Table 7. Standardised coefficients of all variables retained in the final averaged, spatial model, for the Solent. Standardised coefficients can be used to compare the relative importance of variables. The quadratic term of the relationship between seagrass and a variable is denoted by ^{2}. To predict suitability they must be used with standardized environmental data. Note partial R^2 cannot be calculated for variables in a GLMM.

Variables	Averaged standardised coefficient final spatial model
(Intercept)	-0.86541
Bathymetry	2.935188
Bathymetry^2	-0.63116
Eunis littoral	1.106001
Eunis mix	0.646747
Coefficient of variation in nitrate	-0.89386
Slope	-0.02808
Coefficient of variation in turbidity	-1.11953
Coefficient of variation in turbidity^2	-1.07153
Wemo RWE	0.648869
Coefficient of variation in nitrate : slope	-1.14562
Spatial term	0.643334

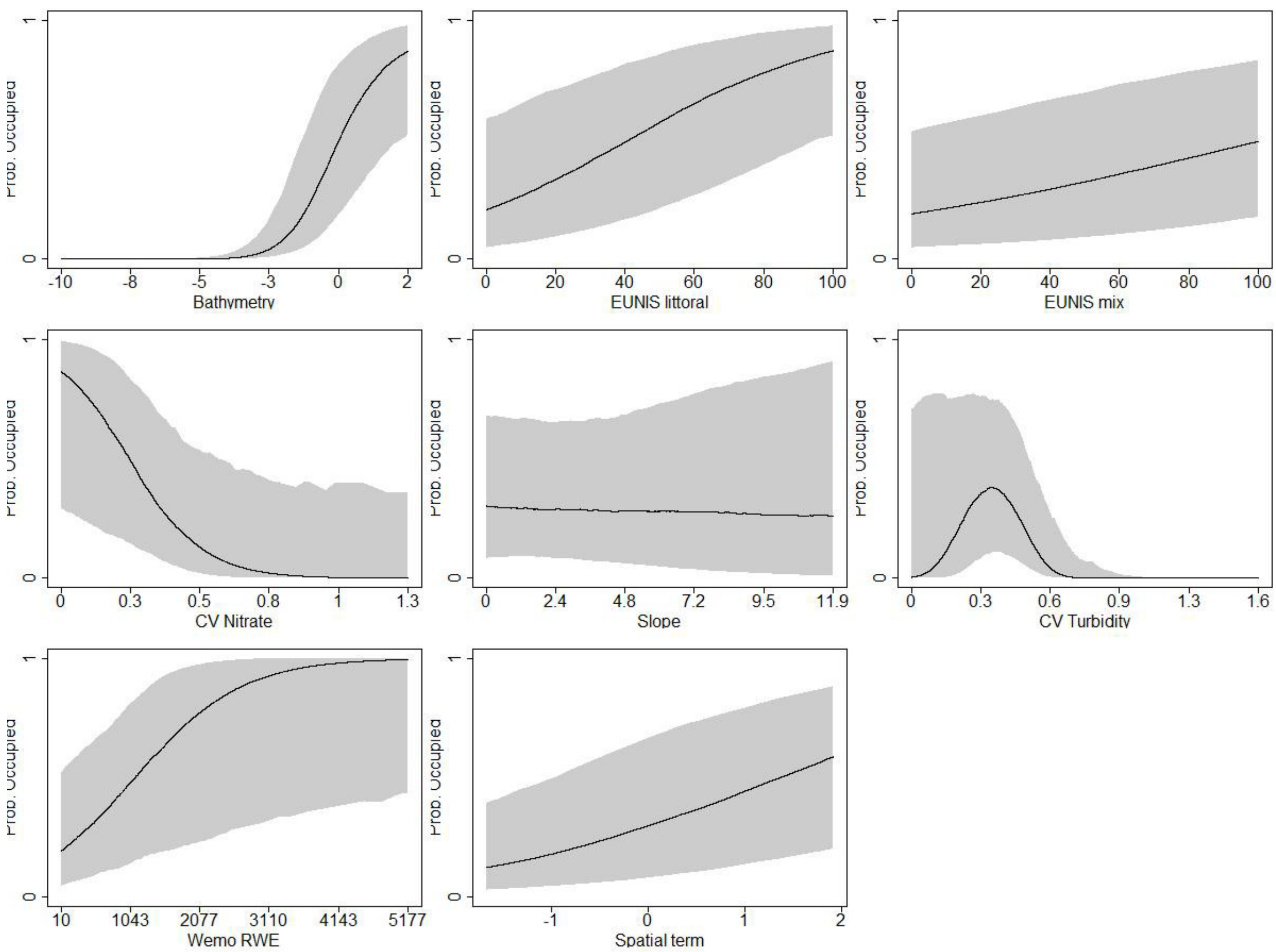


Figure 9. Predicted probability of seagrass occurrence (±95% confidence intervals) for each explanatory variable in the best spatial model for the Solent (final), when all other explanatory variables are held at their means.

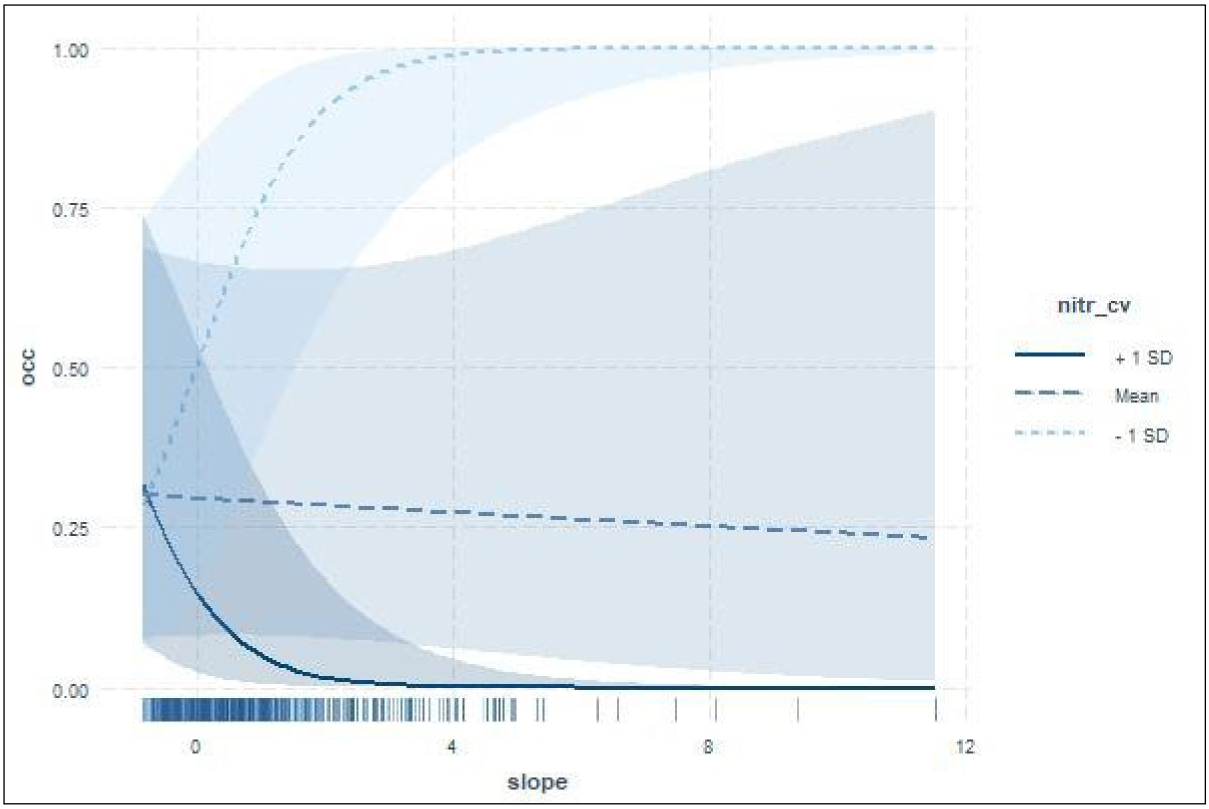


Figure 10. The interaction between slope and coefficient of variation in nitrate in the best spatial model for the Solent (final, step j). Note that the values on the x axis are standardised, not the raw values as in figure 13. The long-dashed line shows the effect of slope when coefficient of variation in nitrate is held at its mean. The solid line shows the effect of slope when coefficient of variation in nitrate is held at 1 standard deviation above the mean. The dotted line shows the effect of slope when coefficient of variation in nitrate is held at 1 standard deviation below the mean. Short blue lines along the x axis indicate the density of data.

Interaction interpretation

Slope has a negative effect on seagrass occurrence by itself (fig. 10), but interacts with coefficient of variation in nitrate so that seagrass is more likely to occupy sloping areas with lower temporal variation in nitrate.

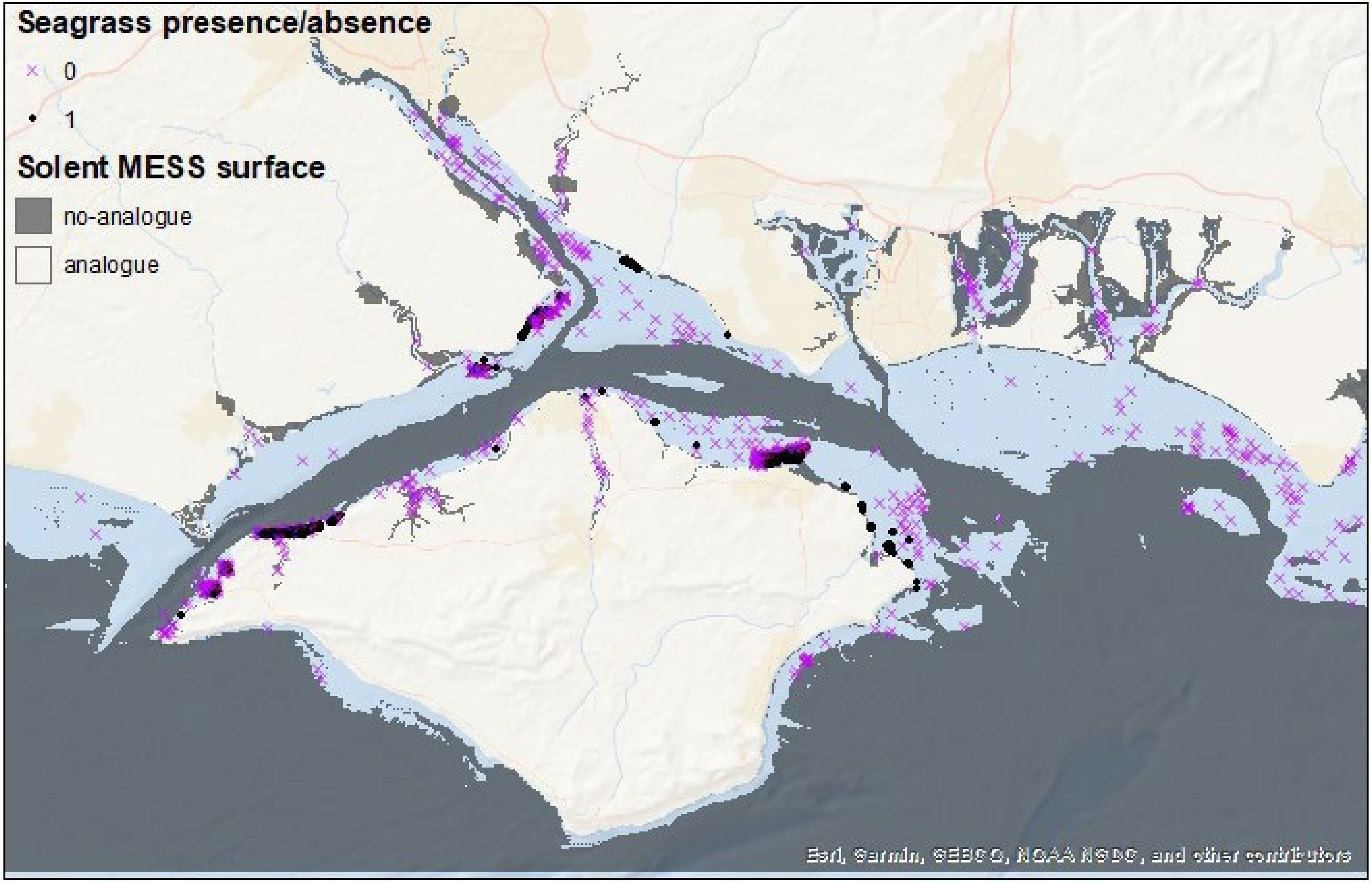


Figure 11. Distribution data used for modelling and MESS surface indicating analogue conditions where predictions of suitability can be made

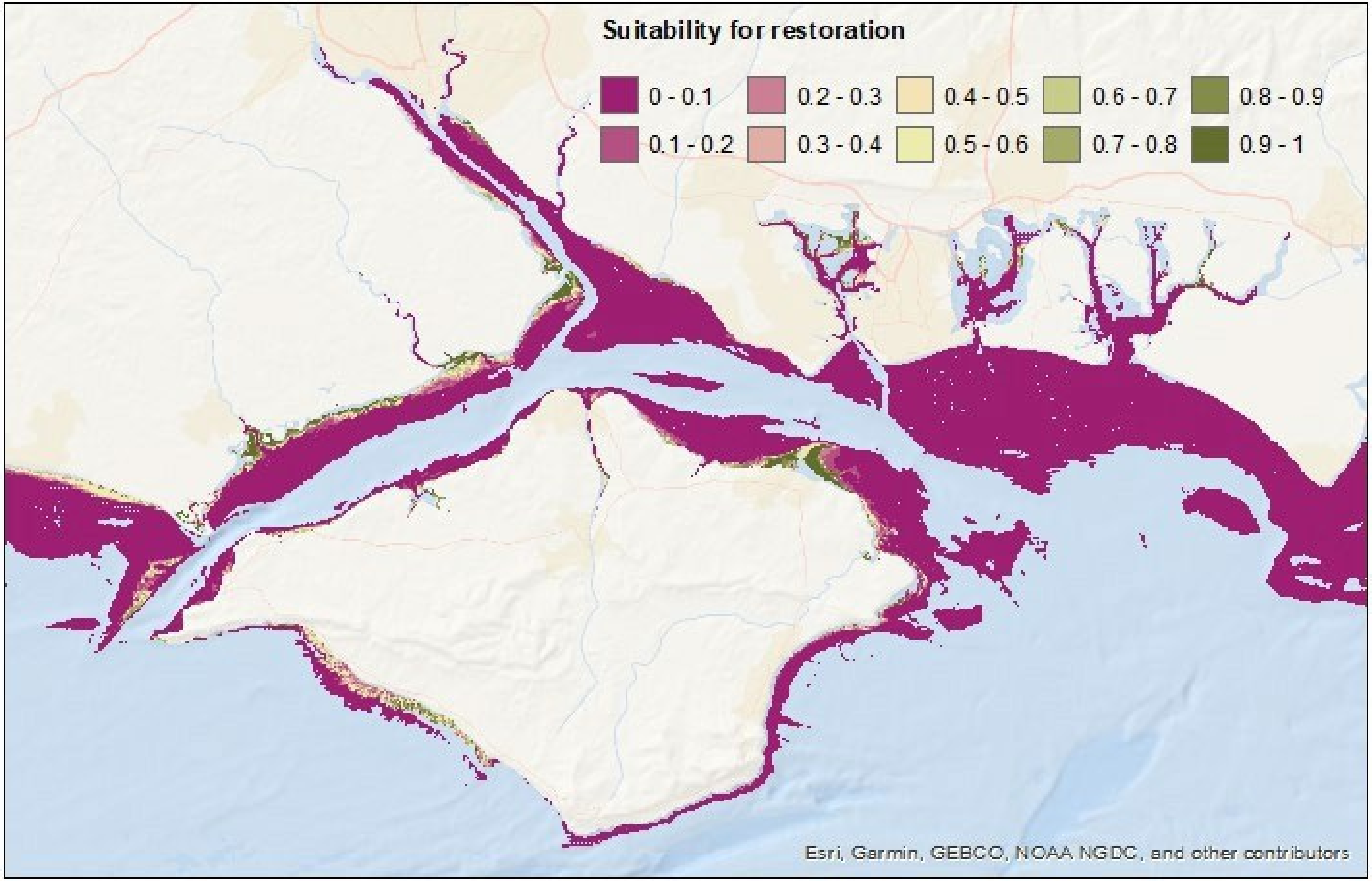


Figure 12. Prediction of relative suitability for restoration based on the final spatial model, trimmed to analogue environmental conditions.

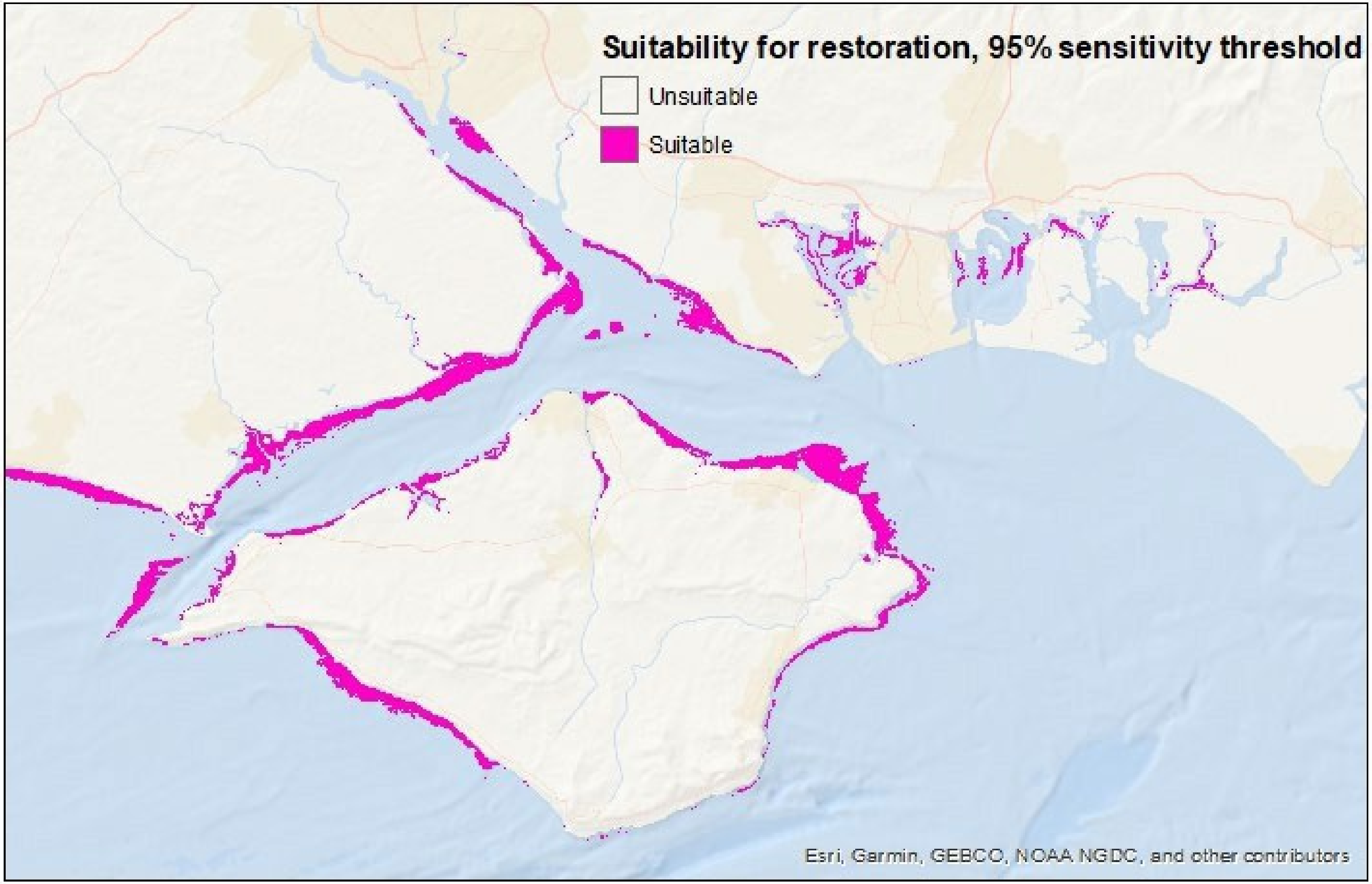


Figure 13. Prediction of relative suitability for restoration based on the final spatial model, trimmed to analogue environmental conditions and with the 95% threshold imposed.

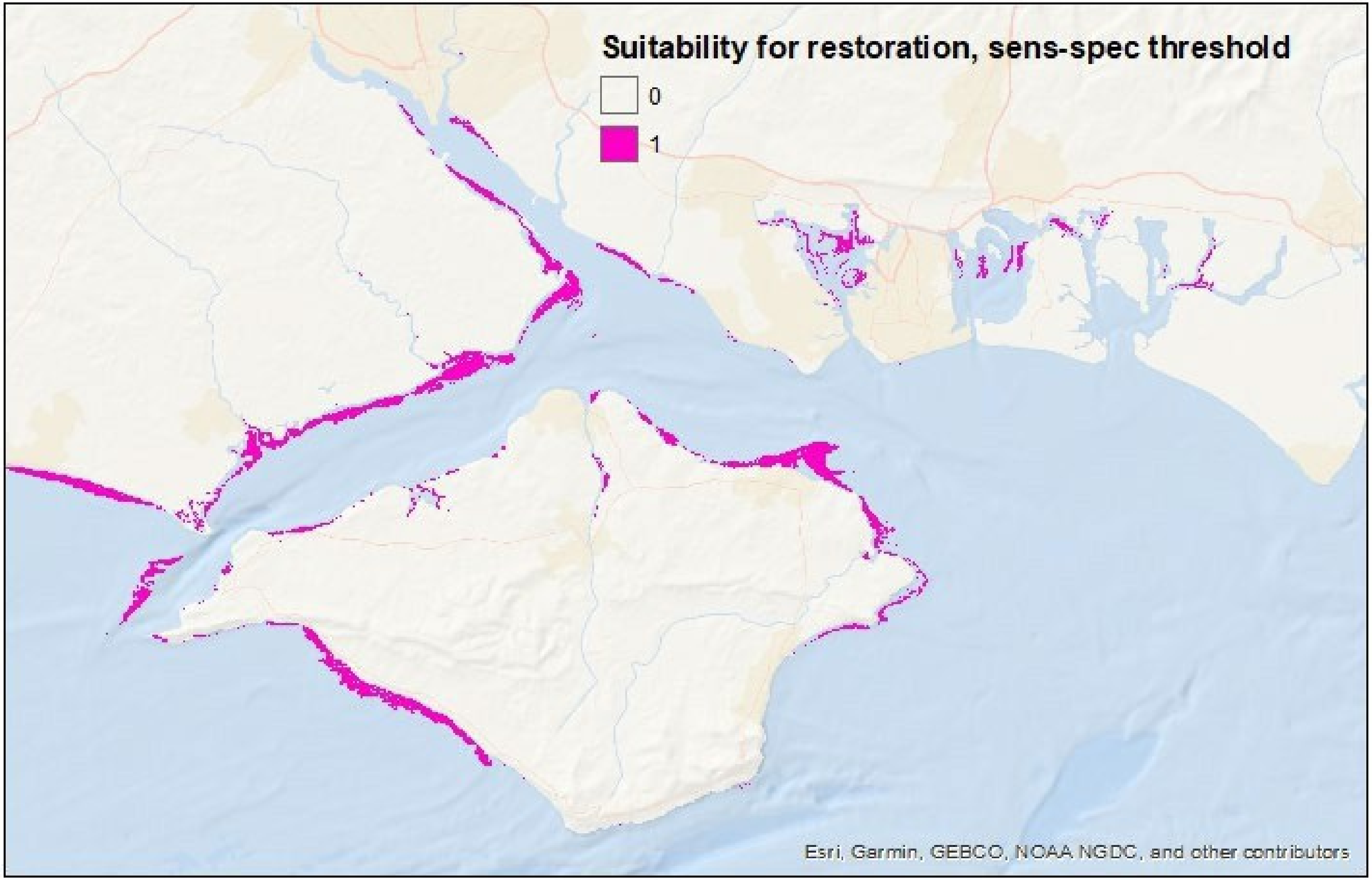


Figure 14. Prediction of relative suitability for restoration based on the final spatial model, trimmed to analogue environmental conditions and with the sens-spec threshold imposed.

Evaluation of Findings

The figures above represent all our initial assessments of the suitability of the modelled seagrass habitats for restoration within the Plymouth and Solent SACs. We advise caution when interpreting suitability in areas where we have low confidence in RWE calculations, i.e. the more exposed areas of Plymouth.

We imposed two thresholds to identify different degrees of 'match' between conditions in any given grid-cell and the conditions in seagrass beds. Thresholds are a trade-off between 'sensitivity' (low thresholds will classify more seagrass presences as suitable for restoration), and 'specificity' (high thresholds will classify more seagrass absences as unsuitable for restoration). The sens-spec thresholds are higher than the 95% thresholds, as the former places more emphasis on specificity. Neither is *a priori* the best approach. In this case, the higher, sens-spec, threshold might be more appropriate. This is because it appears that some seagrass presences are in areas that would appear to have environmental conditions that are similar to the locations where absences have been recorded. In order to include 95% of the presences in the suitable category therefore, this threshold has to take a very low value. This means that the 95% thresholded prediction includes many areas that are likely to be unsuitable for seagrass restoration.

If predictions for the Plymouth and Solent sites are compared, it must be remembered that the absolute values of the continuous predictions are is not important here. The absolute values are influenced by the ratio of presences to absences, and so will vary between Plymouth and the Solent, and are not comparable to any dataset with a different ratio of presences to absences. Instead, it is the relative values of the continuous predictions between grid-cells within either site that should be used to assess suitability for seagrass restoration, and the thresholded predictions.

The SDMs identify quite extensive strips of habitat in which the measured environmental variables appear to be broadly similar to those in the locations where seagrass is currently found. This is because in the data available, seagrass is not currently restricted to a unique set of environmental conditions. This means that there are few strong relationships between seagrass occurrence and environmental variables that are consistent between seagrass beds (even within either of the two sites studied).

To address this in more detail, a model can only ever be as good as the data available. In this case, the challenges of obtaining very strong and consistent relationships between seagrass occurrence and environmental data are illustrated by figures S21, 22, 24 and 25. Seagrass is found in a broad range of many of the environmental variables (when there are no clear peaks in histograms in figs S21 and 24). For most environmental variables, there is little differentiation between the conditions where seagrass is and is not found (when the box plots overlap substantially in figs S22 and 25). Therefore, it does not appear to be the case that complex relationships were missed. Rather, the environmental variables available are not strong predictors of the seagrass presence/absence data available. This is reflected in the modest explanatory power of the SDM results (pseudo R^2 values).

There are two key reasons why there are not strong effects of environment and seagrass presence/absence in this dataset. First, it is likely that environmental variables to which we did not have access affect seagrass distribution, for example recreational boating activity. Second, the rasters of some environmental variables were calculated from a small number of observations scattered across the sites. Because of the sparse data, we could only interpolate these variables to 600m resolution, which is coarse compared to the resolution at which seagrass is likely affected by its environment. Interpolation to any finer resolution would have been highly over-precise, and simply matched variation in the variable used to make the interpolation, e.g. bathymetry. Therefore, the raster values of these variables are calculated with a low degree of precision, and likely accuracy, and are potentially too coarse to reveal strong relationships with seagrass. Furthermore, we would not expect the ranges of the environmental variables modelled to exceed those detrimental for seagrass growth. To use Nitrogen as an example, this nutrient can have a positive effect on seagrass growth to a threshold above which it becomes detrimental for growth and this may be a crucial predictor in other sites. Recent work by Jones *et al* (2018) highlighted that Nitrogen from anthropogenic sources resulted in lower C:N ratios in the seagrass beds studied, but no specific relationship between shoot density or epiphyte biomass. As such, the exact concentration detrimental to *Z. marina* growth in the UK is not clear and may not be surpassed at any site known to support its growth. A number of regions within the Solent Maritime SAC have been identified as problem areas for Nitrogen deposition (Portsmouth and Chichester Harbours for instance) to levels that could result in eutrophication (Painting *et al 2016*). Data available for Nitrogen sourced from the Environment Agency did not highlight these areas in particular as problematic. While these did not include any seagrass presences, they did contain a number of absences with associated Nitrate values which were, proportionately, fairly low. At this time, it is not clear why this discrepancy exists. The explanation of how this would affect the models is given above.

Nonetheless, the environmental relationships obtained are broadly ecologically meaningful. Therefore, in terms of the environmental conditions measured we believe the SDMs have revealed the habitats most similar to areas where seagrass currently occurs in our dataset. For the Solent, the CV of Nitrate had a fairly strong effect on seagrass presence suggesting that tolerance to high levels of seasonal deposition of Nitrogen here is low. At this site however, bathymetry had the strongest effect on the distribution of *Z. marina*. This is logical as depth defines sediment characteristics and light availability, two important factors for successful seagrass colonisation.

Because the data do not suggest small patches of habitat where conditions precisely match those of current seagrass beds, further consideration must be given as to where, within the areas we identify as potentially suitable, restoration should occur. It is likely that environmental variables to which we did not have access affect seagrass distribution, for example recreational boating activity. Such factors could be considered to narrow down the choice of sites. We note that some areas of seabed identified as suitable are intertidal and our confidence in these results specifically is low. In the process of modelling the data, a considerable number of points were identified as being above sea level and differences between chart datum and inclusion of some *Z. noltii* data were identified as the reason for this. We surmise that some of this data may have been retained in the final model but believe this has not had a significant effect on the quality of predictions it generated and suggest that upper estuarine regions should not be targeted for restoration in the section below.

When using these maps to determine sites for seagrass restoration, we recommend selecting areas that have both a high predicted suitability for restoration, and where confidence in suitability is high. The latter can be obtained from the rasters of confidence intervals. Areas where the value of lowest 95% confidence interval or predicted suitability is high are the areas that most closely match the measured environmental conditions in the current seagrass beds. In the case of Plymouth, where a single set of confidence intervals for the averaged, final model could not be calculated, this should be done using the confidence intervals of both the constituent GLM and GLMM.

Here we present an assessment of the variables used to construct the model and consider the model predictions for these two sites and what this could mean at other sites around the UK. To begin, we note that seagrass presence and absence data was compiled from a number of different sources and that not all presence points had an associated density and as such did not meet the criteria described in our methods section. Gathering and harmonizing these sources together and then filtering for presences and absences within a suitable depth range took a substantial proportion of the contract time and thus, the preparation of this data for future projects should not be underestimated.

Overall, the model results are in agreement with what is known about *Z. marina* and its tolerance of a wide range of environmental variables and nutrient regimes. It should be noted that, as stated previously, the existing seagrass locations modelled here represent a small proportion of the areas of seabed suitable for the growth of *Z. marina*. Those beds that remain have survived extensive losses over recent decades from fungal infection and anthropogenic pressures, some of which could not be represented in this report. When these facts are considered, it is not surprising that the explanatory power of the SDM results are fairly modest and that proportionately large areas of seabed fall within the 95% confidence intervals at both sites.

Recommendations for Restoration

For each of the two sites, we can recommend 3 areas of seabed that would be suitable for seagrass restoration, based on modelled habitat suitability. These are presented in order of most suited to least in Table 8, but we understand that other considerations may determine the eventual site chosen. Each location has an associated map, showing the areas identified by the SPM as being most suitable for restoration. It is our recommendation that upper reaches of the estuary should be avoided because a) increased ranges in salinity and temperature will increase stress on young plants and b) shallower depths would exacerbate both these variables and there is an increased risk of desiccation.

Table 8. Summary of our recommendations for sites suitable for *Z. marina* restoration within the Plymouth and Solent estuaries. For each estuary, sites are listed in most to least suitable based on the criteria set out by Natural England and our assessment.

Restoration Site Name	Grid reference (Easting, Northing)	Figure	Within SAC? (Y/N)	Dominant Sediment Type (see list in methods section for details)	Suitability Factors	Potential Issues
Plymouth: Cawsand	SX 4377 5034	15	Y	Mixed and macrophyte dom. sediment and 'Other'. Known to be very fine/fine sand dominant	Adjacent to extensive, existing seagrass bed. Large potential area for restoration (>4ha). Sheltered from prevailing SW winds, access from Cawsand beach	Coastal fringes possibly exposed to breaking waves with S and E winds
Plymouth: Drake Island	SX 4698 5283	16	Y	Mixed and macrophyte dom. sediment and 'Other'	Adequately sheltered from wave action with ease of accessibility from a number of marinas	Small area of highly suitable seabed for restoration (<4 ha)
Plymouth: Jennycliff Bay	SX 4886 5288	17	Y	Sublittoral Mud (a clay/silt/very fine sand mix)	Adequately sheltered from wave action, fairly simple accessibility. Large (~4 ha) area of unfragmented, suitable seabed for restoration	Sedimentation from the Tamar high with associated high turbidity
Solent: Ryde	SZ 6080 9340	18	N	Sublittoral Mud	Adjacent to extensive, existing seagrass bed. Large potential area for restoration (>4ha). Adequately sheltered, potentially low recreational boat traffic for the area	Access via IoW
Solent: North Solent NNR	SZ 4420 9824	19	Y	Mixed and macrophyte dom. sediment	Large (>4 ha) area of suitable seabed for restoration along the coast. Accessed from the mainland	Existing seagrass on habitat modelled as unsuitable with some fragmentation. Most N area of suitability here intertidal
Solent: Calshot	SU 4867 0123	20	N	Mixed and macrophyte dom. sediment and sublittoral sand	A large, suitable, unfragmented area of seabed (>4 ha) borders a small seagrass bed, adjacent to an existing bed. Access from. Access from Calshot beach	The largest seagrass bed lies away from this area and boat traffic could be high

Plymouth Restoration Recommendation Maps

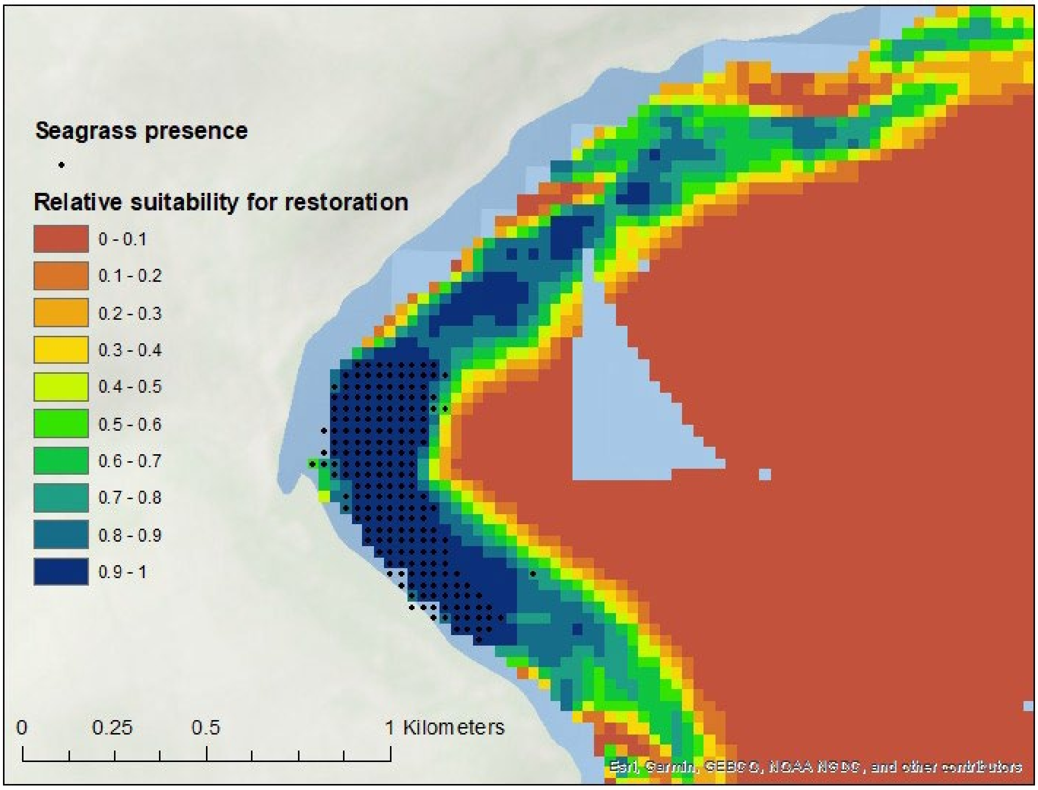


Figure 15. Plymouth: Cawsand site map showing areas suitable for restoration. Grid squares are ~30 m².

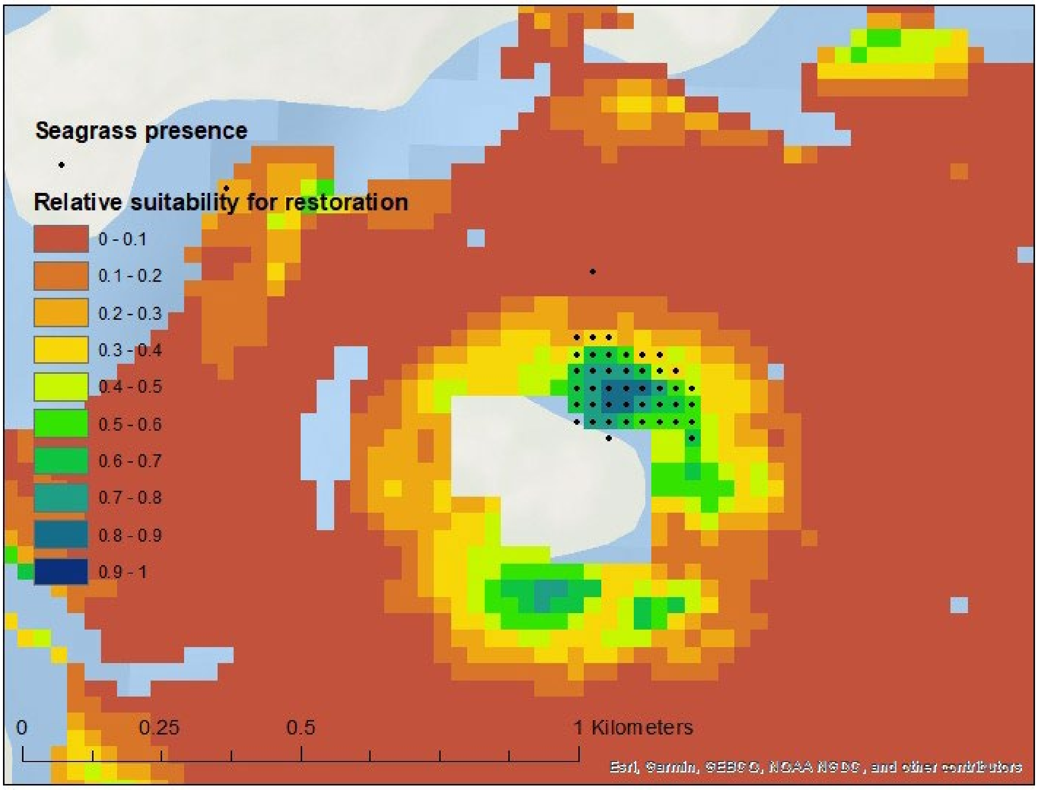


Figure 16. Plymouth: Drake Island site map showing areas suitable for restoration. Grid squares are ~30 m².

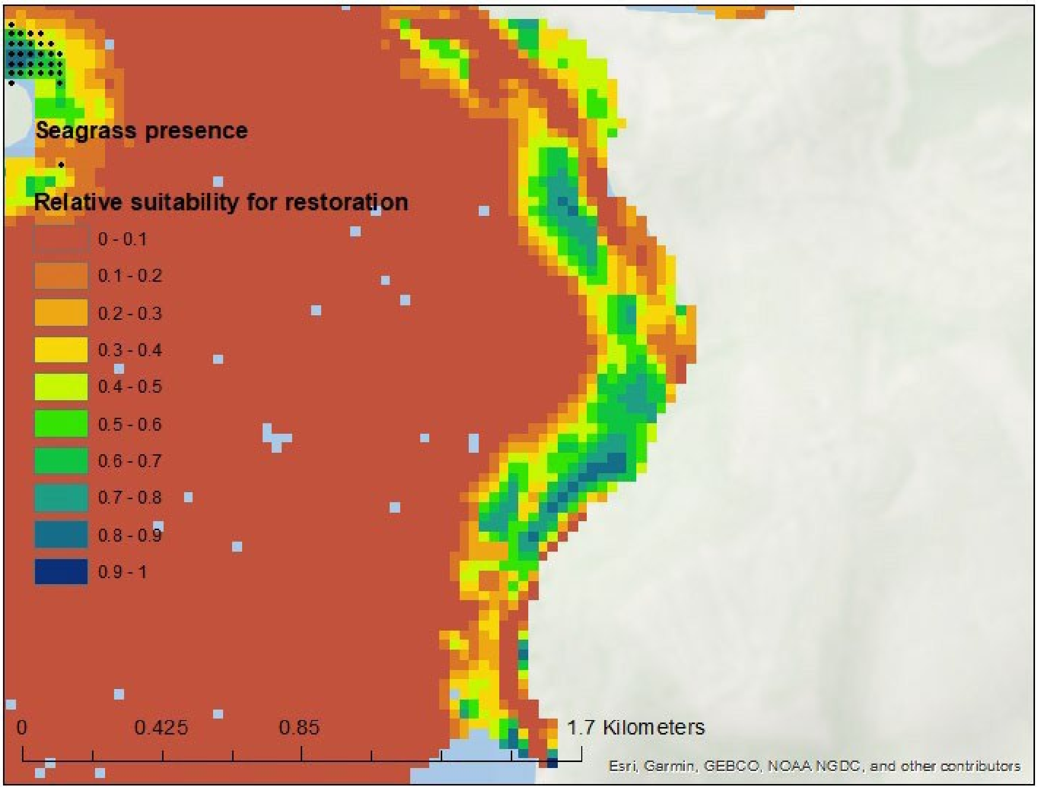


Figure 17. Plymouth: Jennycliff site map showing areas suitable for restoration. Grid squares are ~30 m^2.

Solent Restoration Recommendation Maps

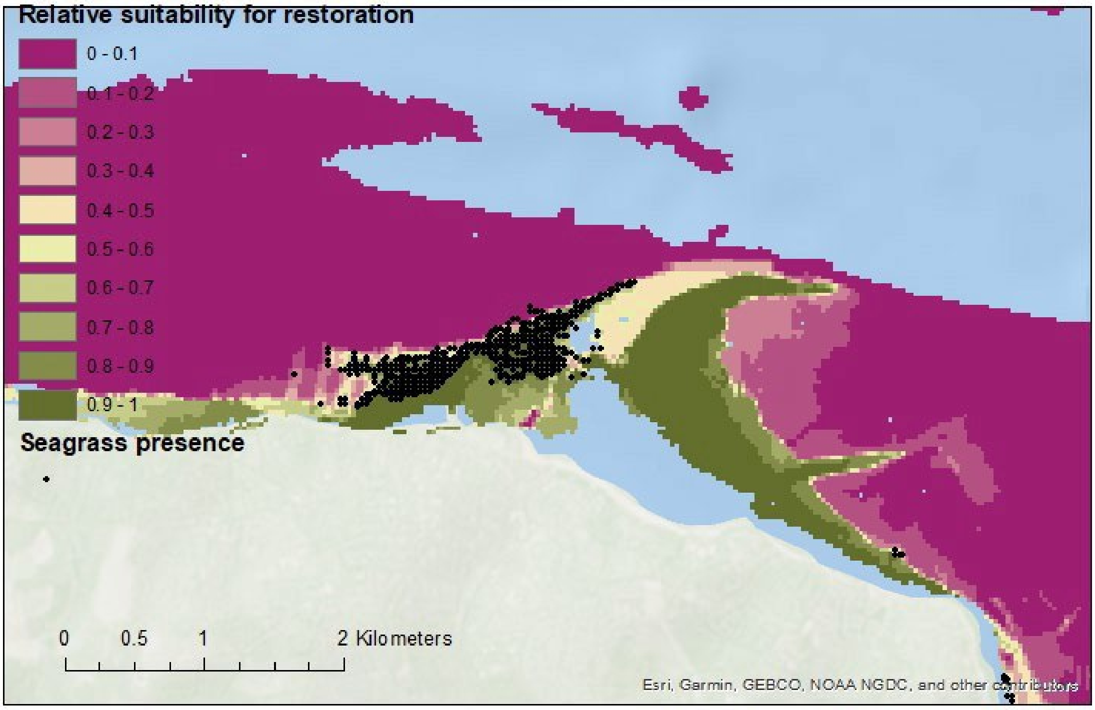


Figure 18. Solent: Ryde site map showing areas suitable for restoration. Grid squares are ~30 m^2.

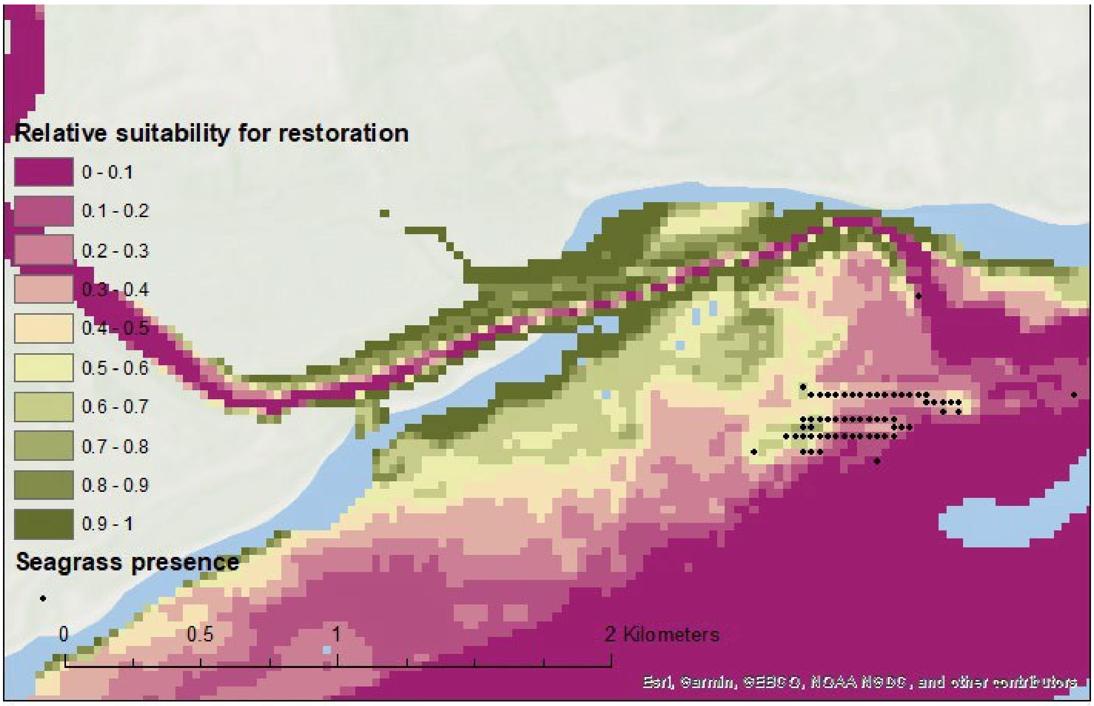


Figure 19. Solent: North Solent National Nature Reserve (NNR) site map showing areas suitable for restoration. Grid squares are ~30 m^2.

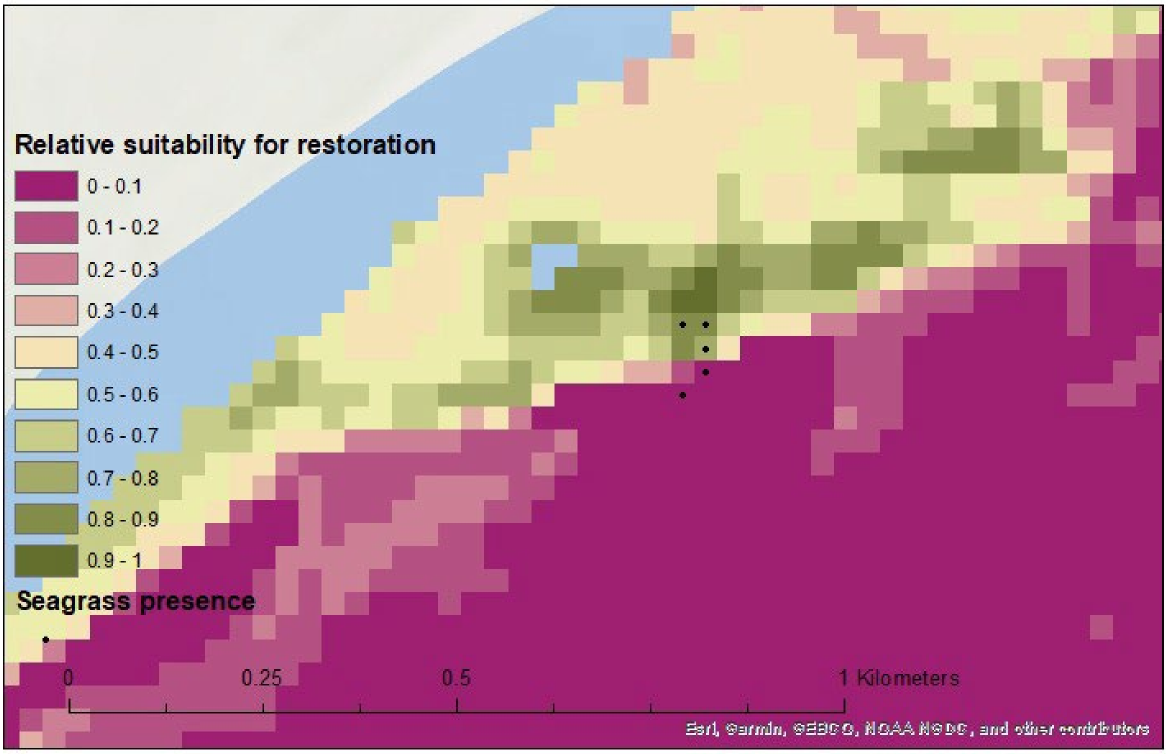


Figure 20: Solent: Calshot site map showing areas suitable for restoration. Grid squares are ~30 m^2. Note that this figure the mean suitability is not shown (as in figs 15-19), but rather the lower 95% estimate of suitability. This is because the mean suitability prediction finds a very large area to be highly suitable for restoration (all of the area categorised as above 0.4 here), but there is low confidence in the suitability for much of this area. The lower 95% estimate illustrates that there are some small patches where we have a high degree of confidence in their suitability (i.e. suitability values are very high in this figure).

Supplementary Information

Environmental Variable Maps

Bathymetry

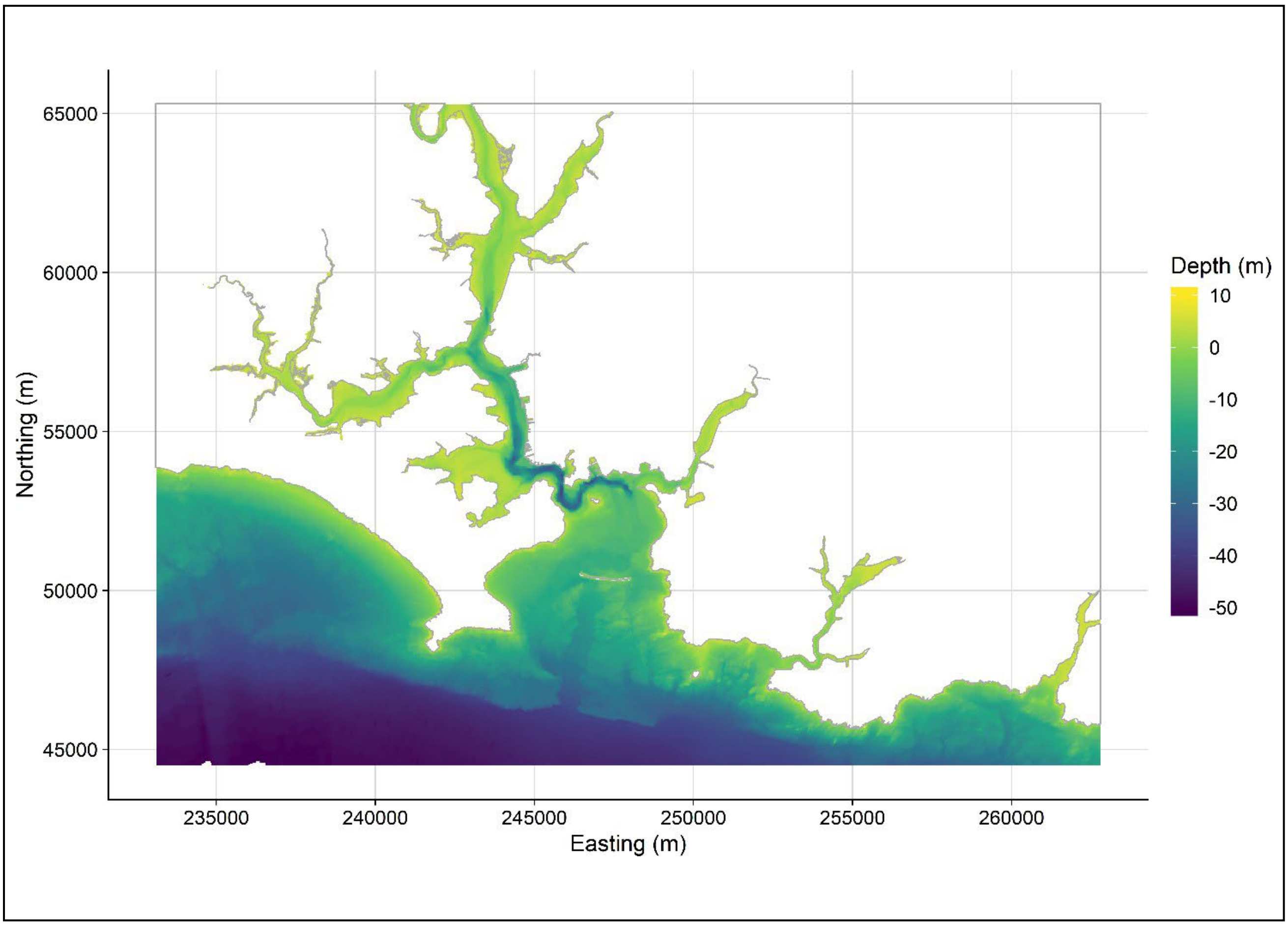


Figure S1: Bathymetry– Plymouth.

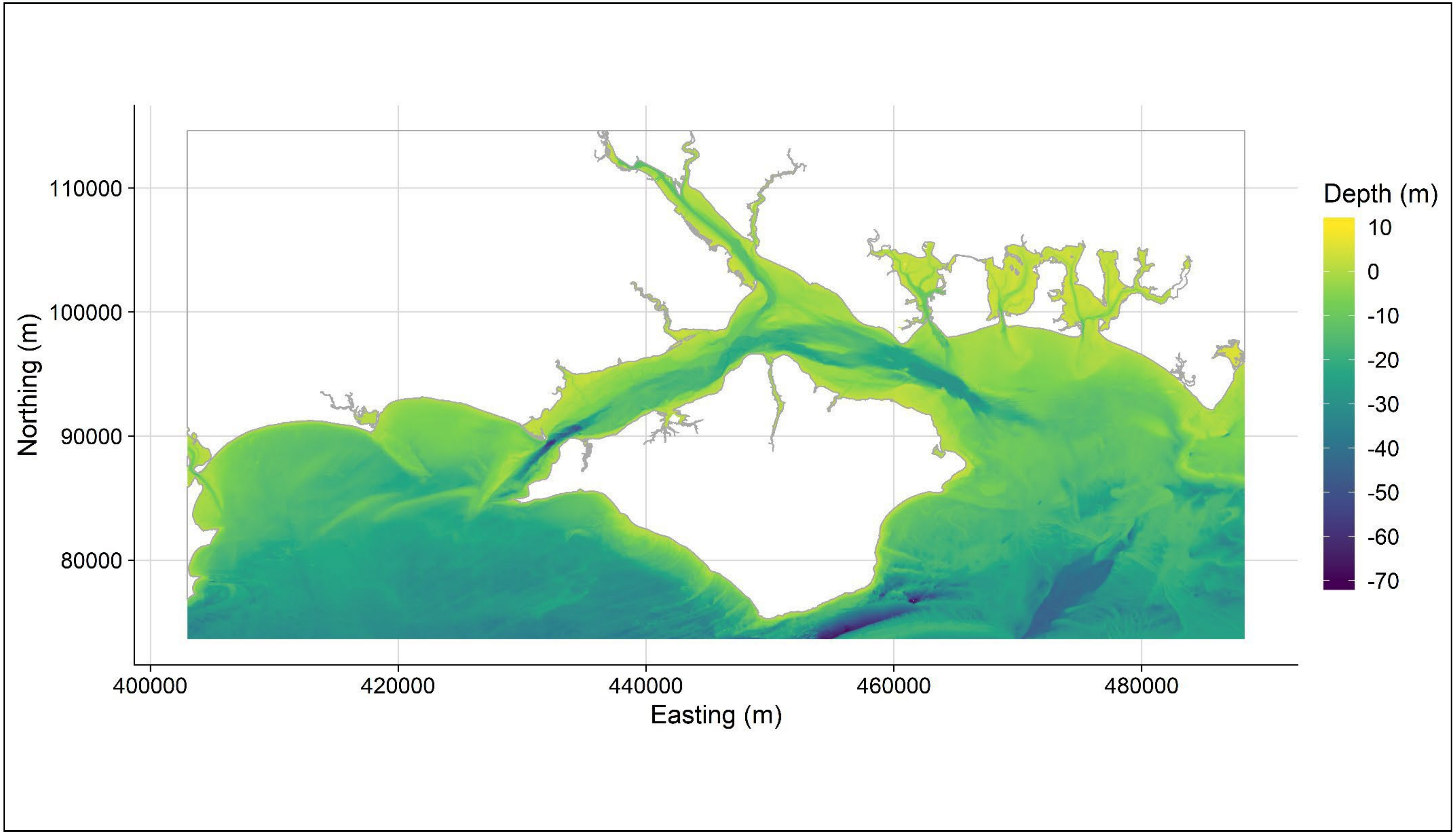


Figure S2: Bathymetry – Solent.

Wave Model Outputs from WEMo

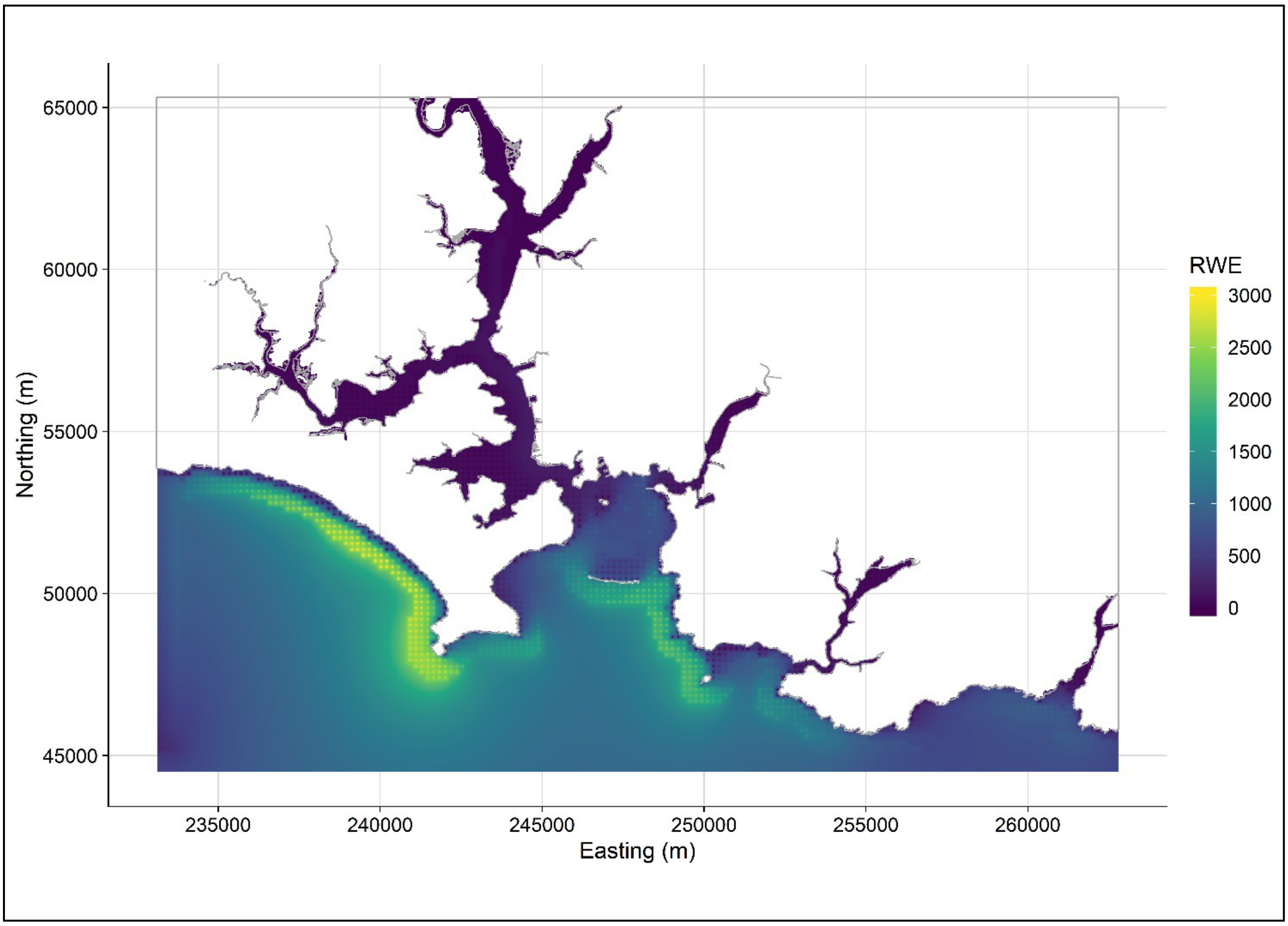


Figure S3: Representative Wave Energy (RWE) values created with WEMO – Plymouth.

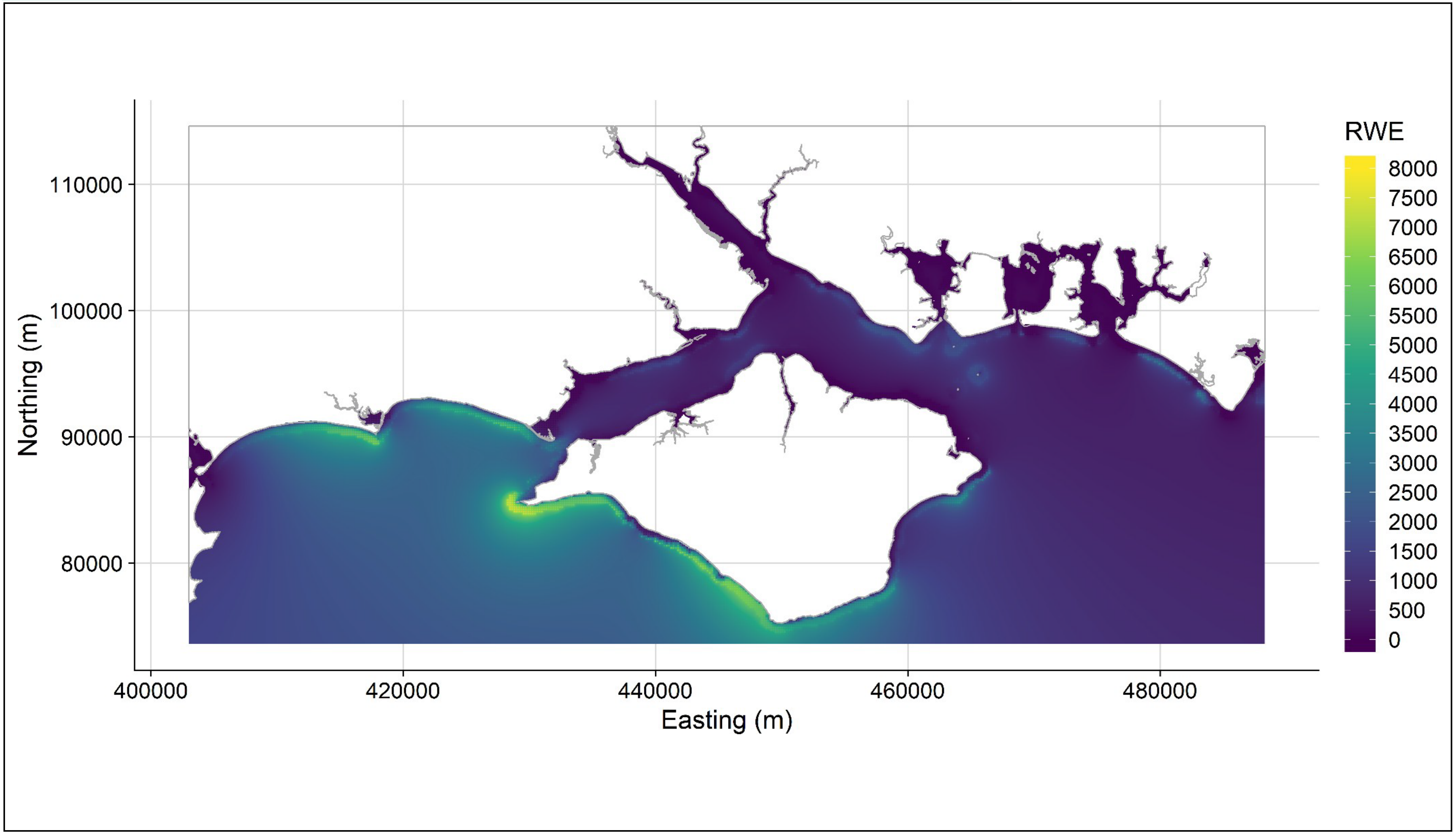


Figure S4: Representative Wave Energy (RWE) values created with WEMO – Solent.

Turbidity (SPM)

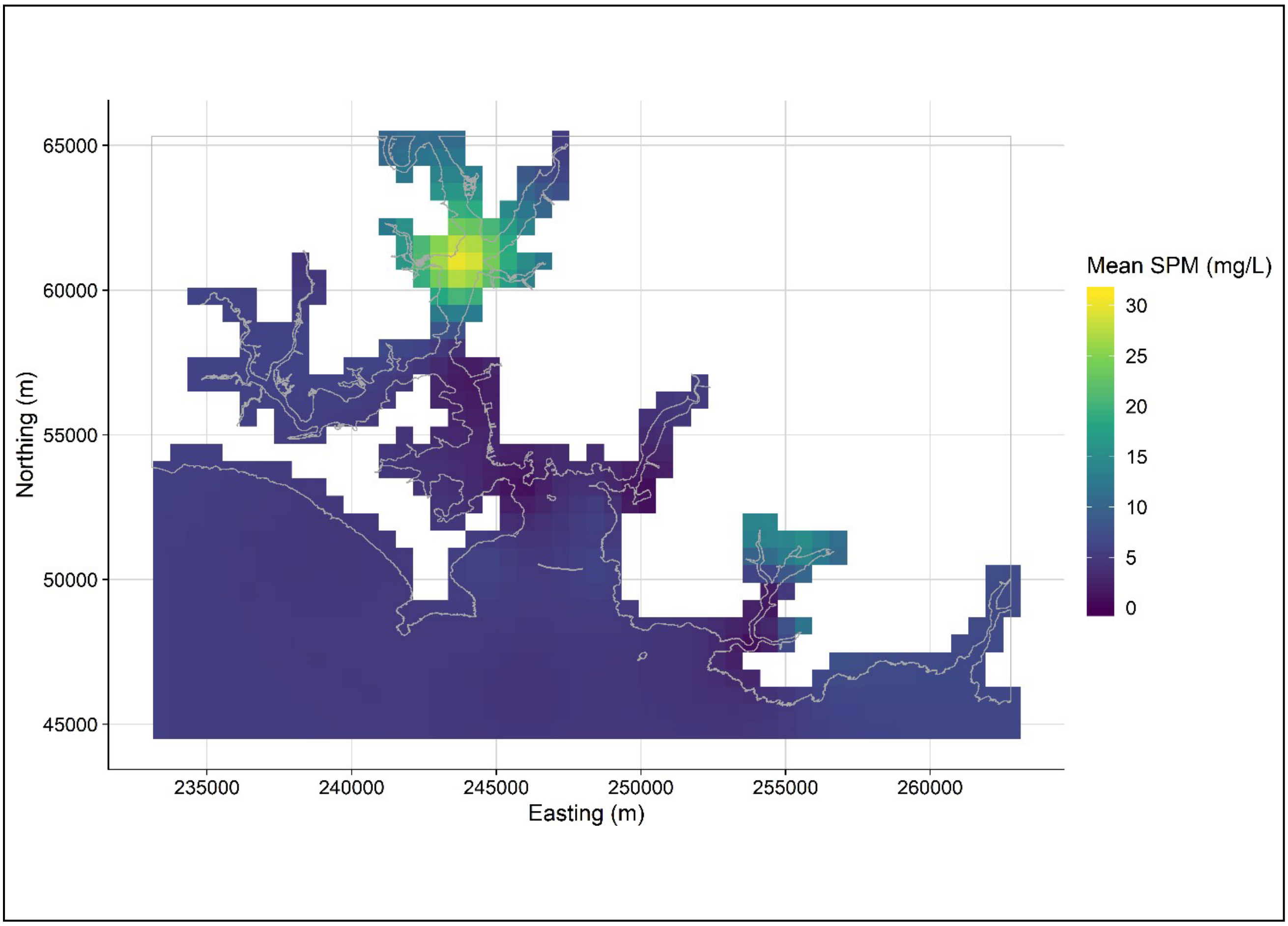


Figure S5: Interpolated mean SPM values – Plymouth (data source: Environment Agency).

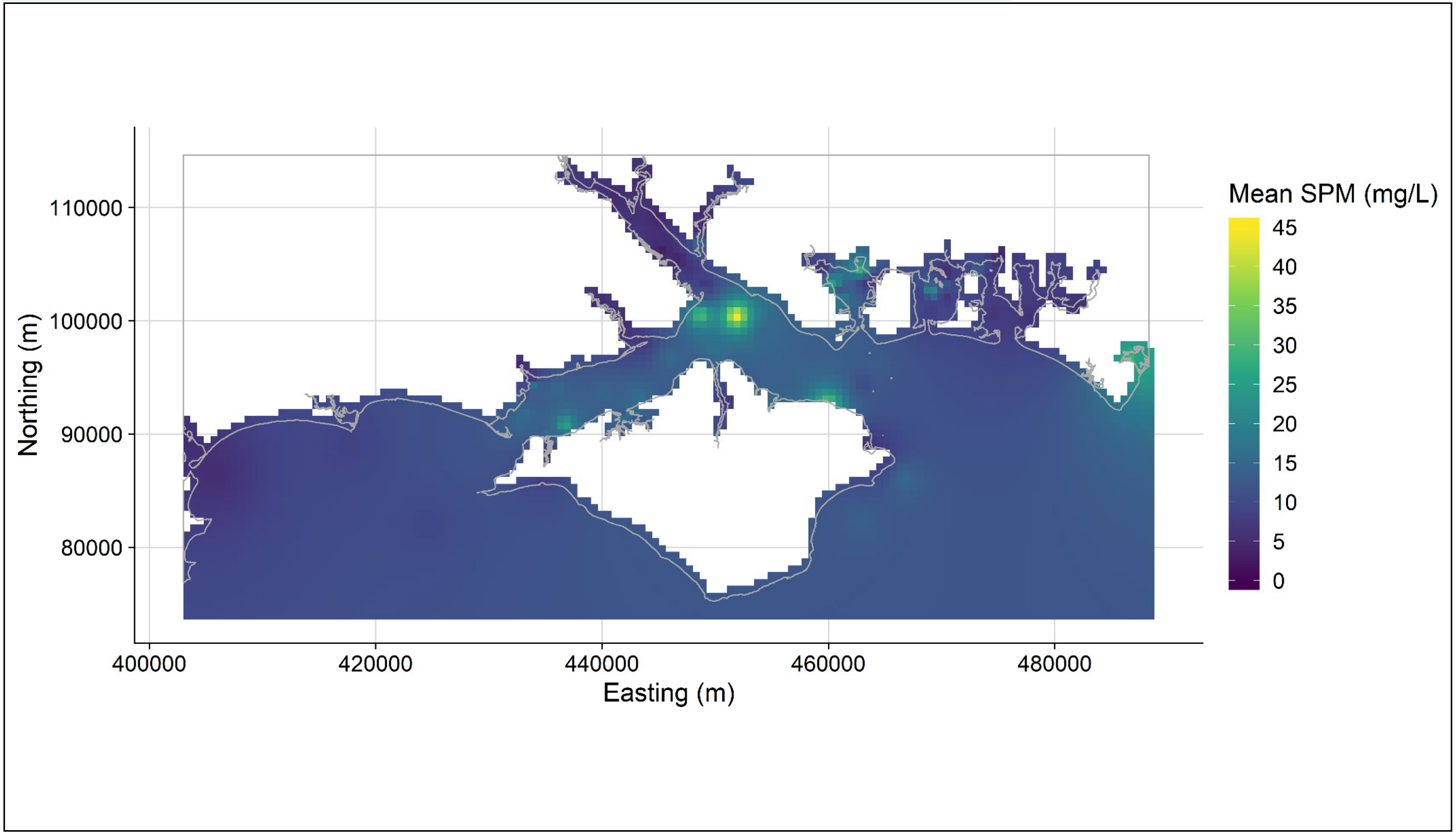


Figure S6: Interpolated mean SPM values – Solent (data source: Environment Agency).

Nitrate

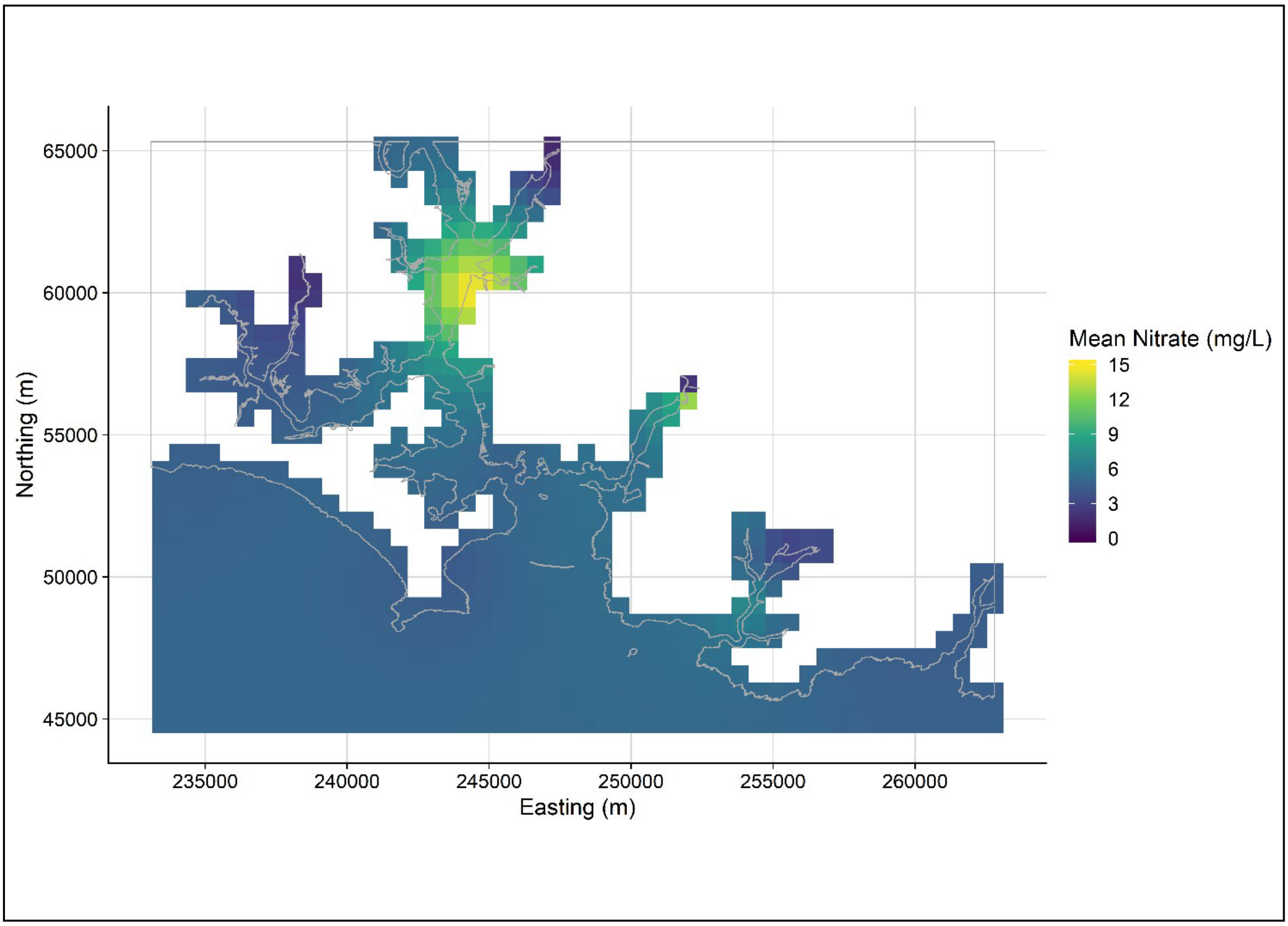


Figure S7: Interpolated mean nitrate values – Plymouth (data source: uses Environment Agency water quality data from the [Water Quality Archive (Beta)](), under the [Open Government Licence]()).

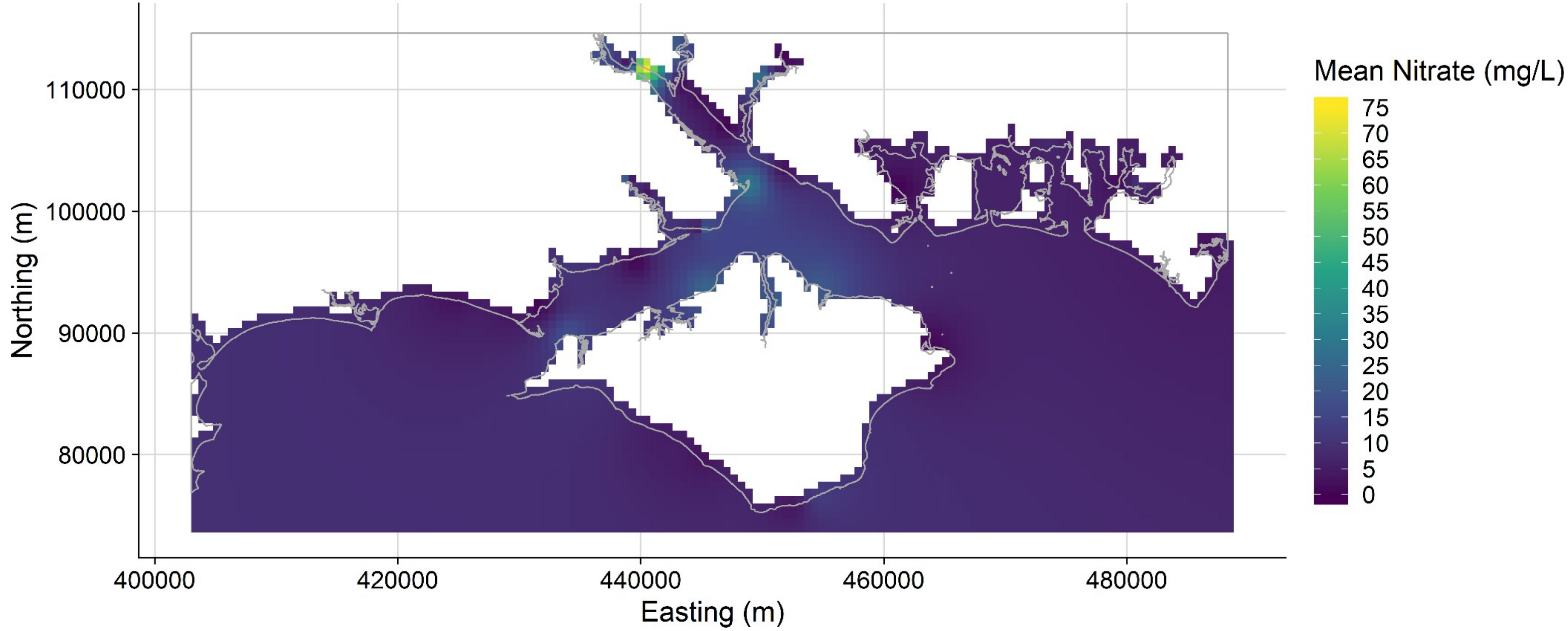


Figure S8: Interpolated mean nitrate values – Solent (data source: uses Environment Agency water quality data from the Water Quality Archive (Beta), under the Open Government Licence).

Phosphorous

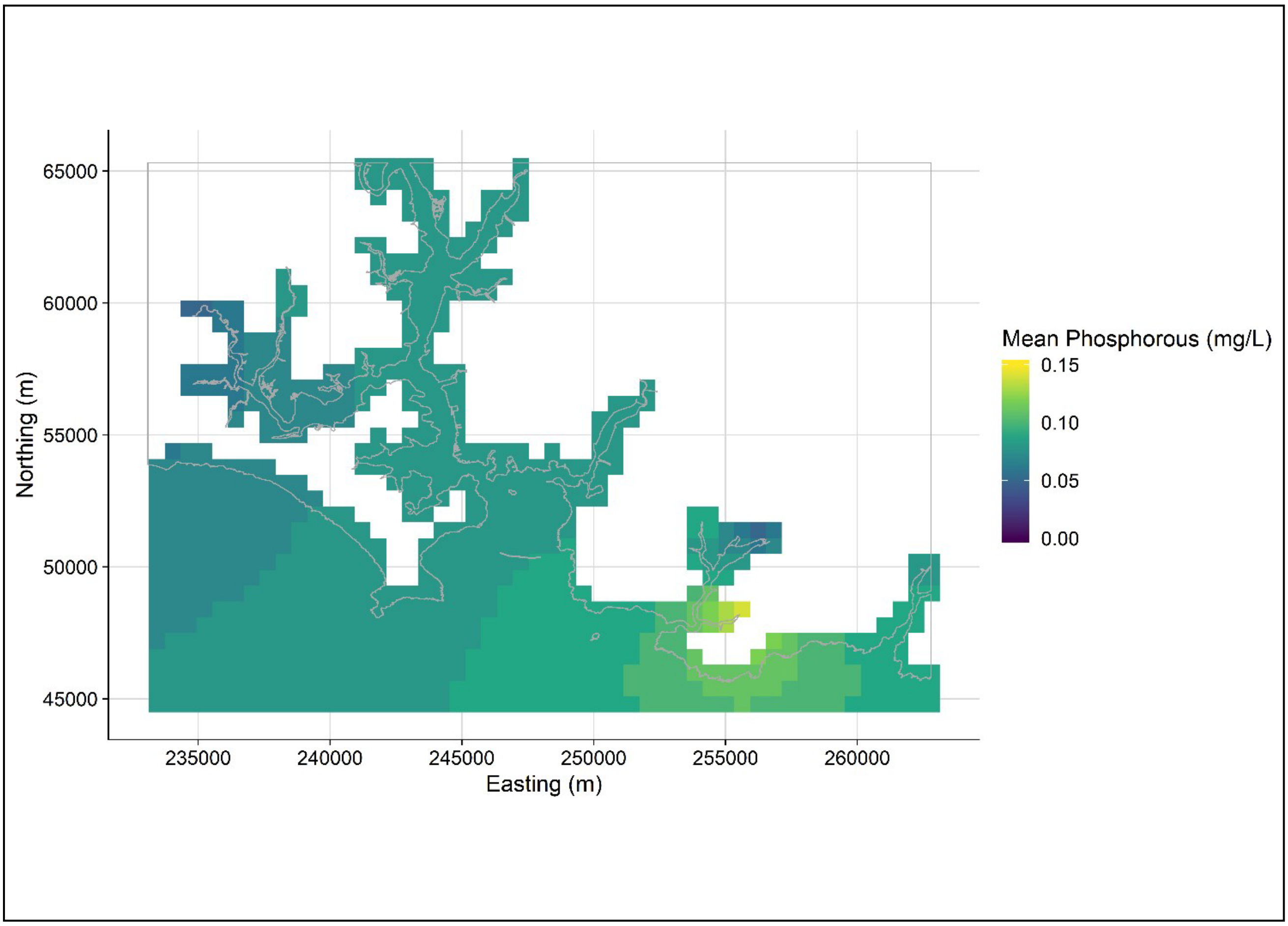


Figure S9: Interpolated mean phosphorous values – Plymouth (data source: uses Environment Agency water quality data from the [Water Quality Archive (Beta)](), under the [Open Government Licence]()).

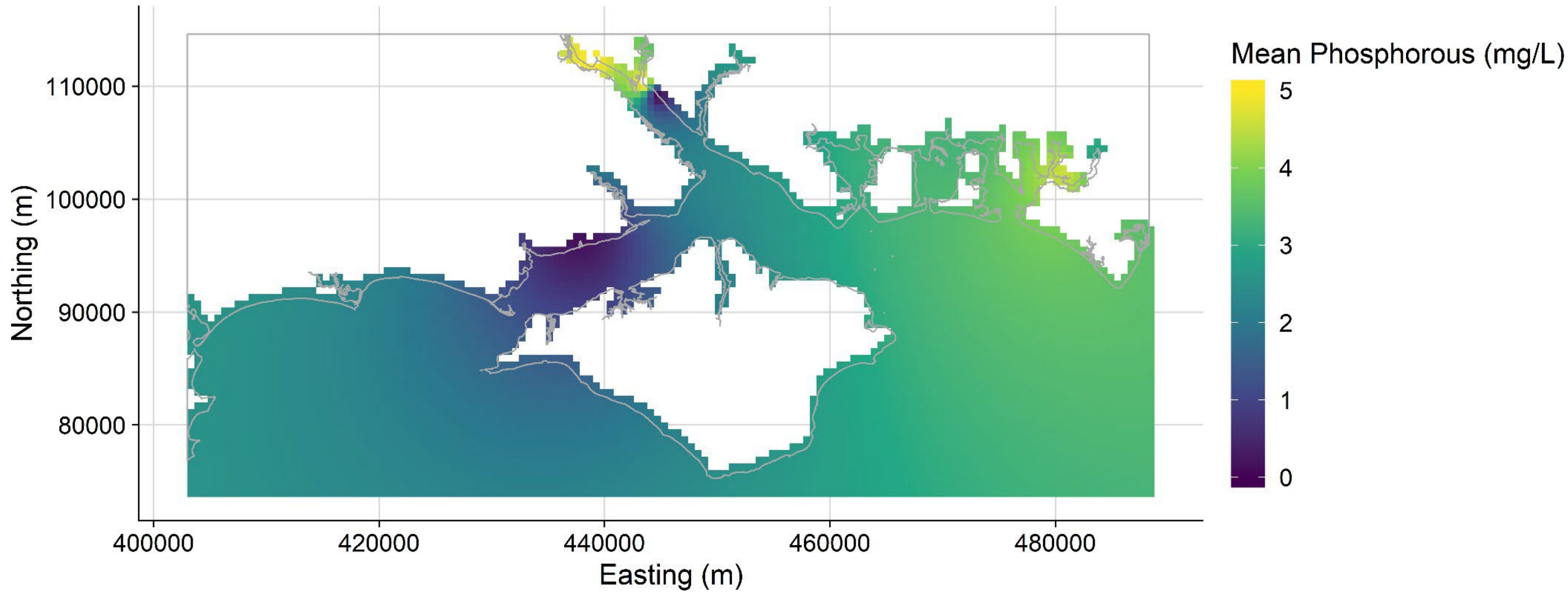


Figure S10: Interpolated mean phosphorous values – Solent (data source: uses Environment Agency water quality data from the [Water Quality Archive (Beta)](), under the [Open Government Licence]()).

Dissolved Oxygen

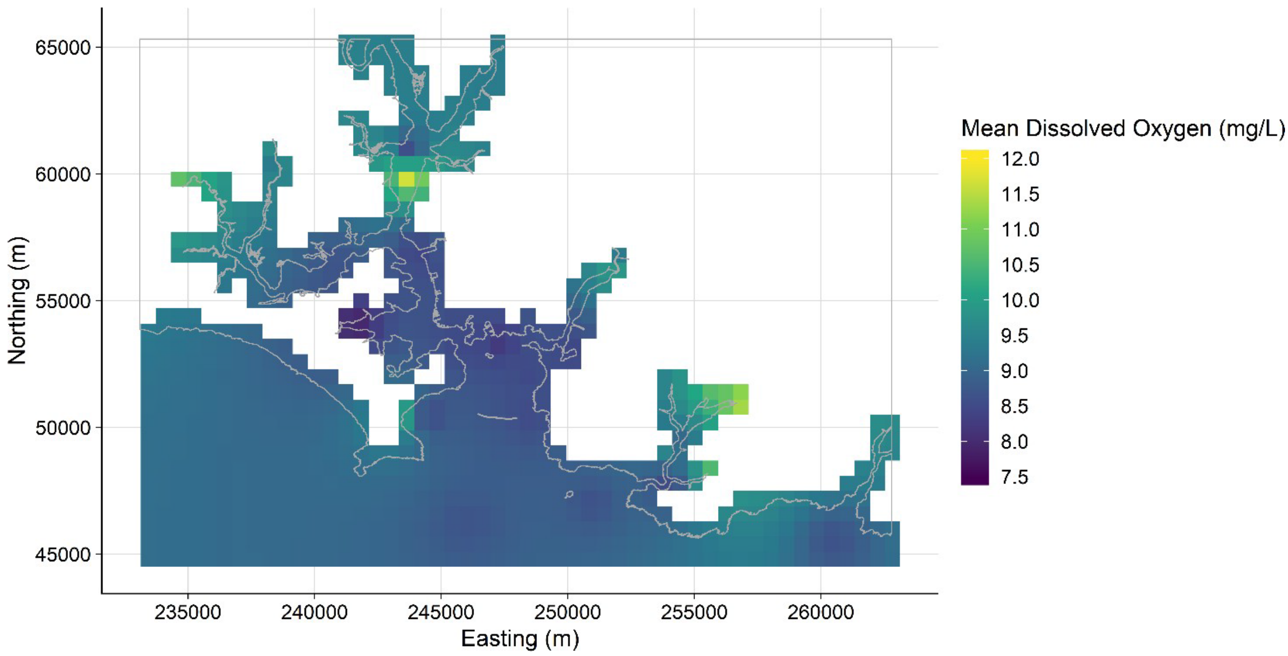


Figure S11: Interpolated mean dissolved oxygen values – Plymouth (data source: uses Environment Agency water quality data from the [Water Quality Archive (Beta)](), under the [Open Government Licence]()).

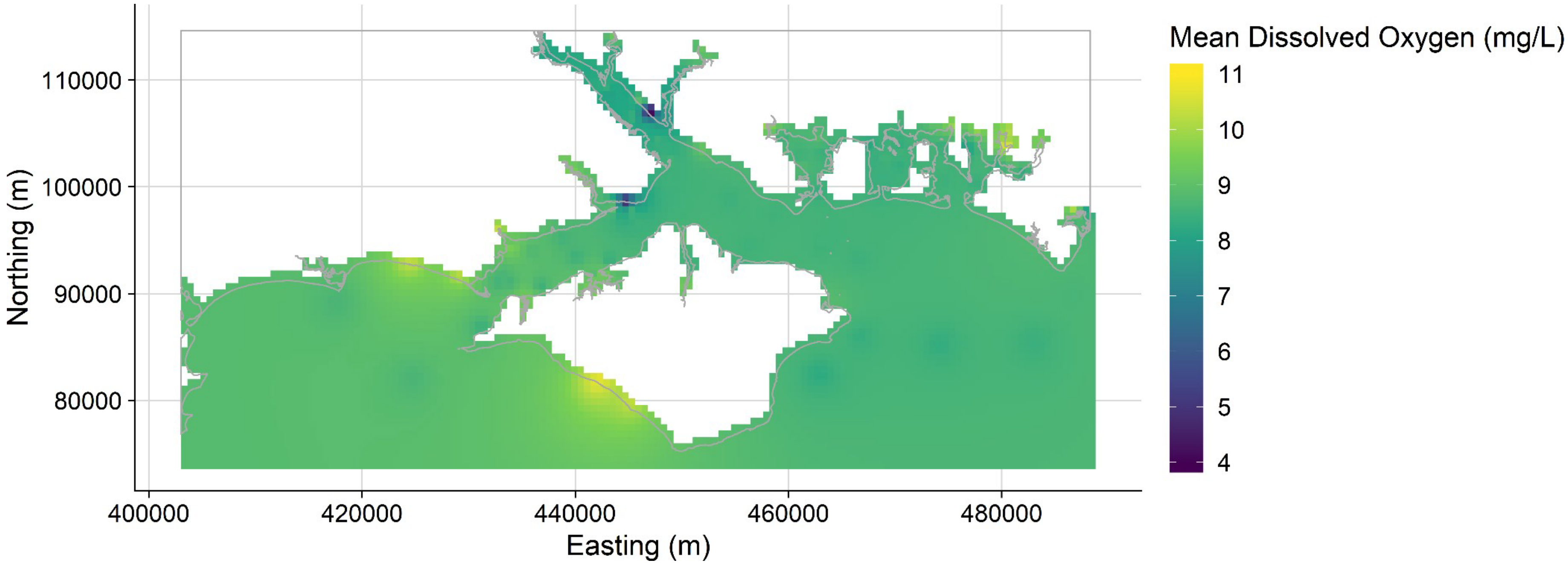


Figure S12: Interpolated mean dissolved oxygen values – Solent (data source: uses Environment Agency water quality data from the [Water Quality Archive (Beta)], under the [Open Government Licence]).

Salinity

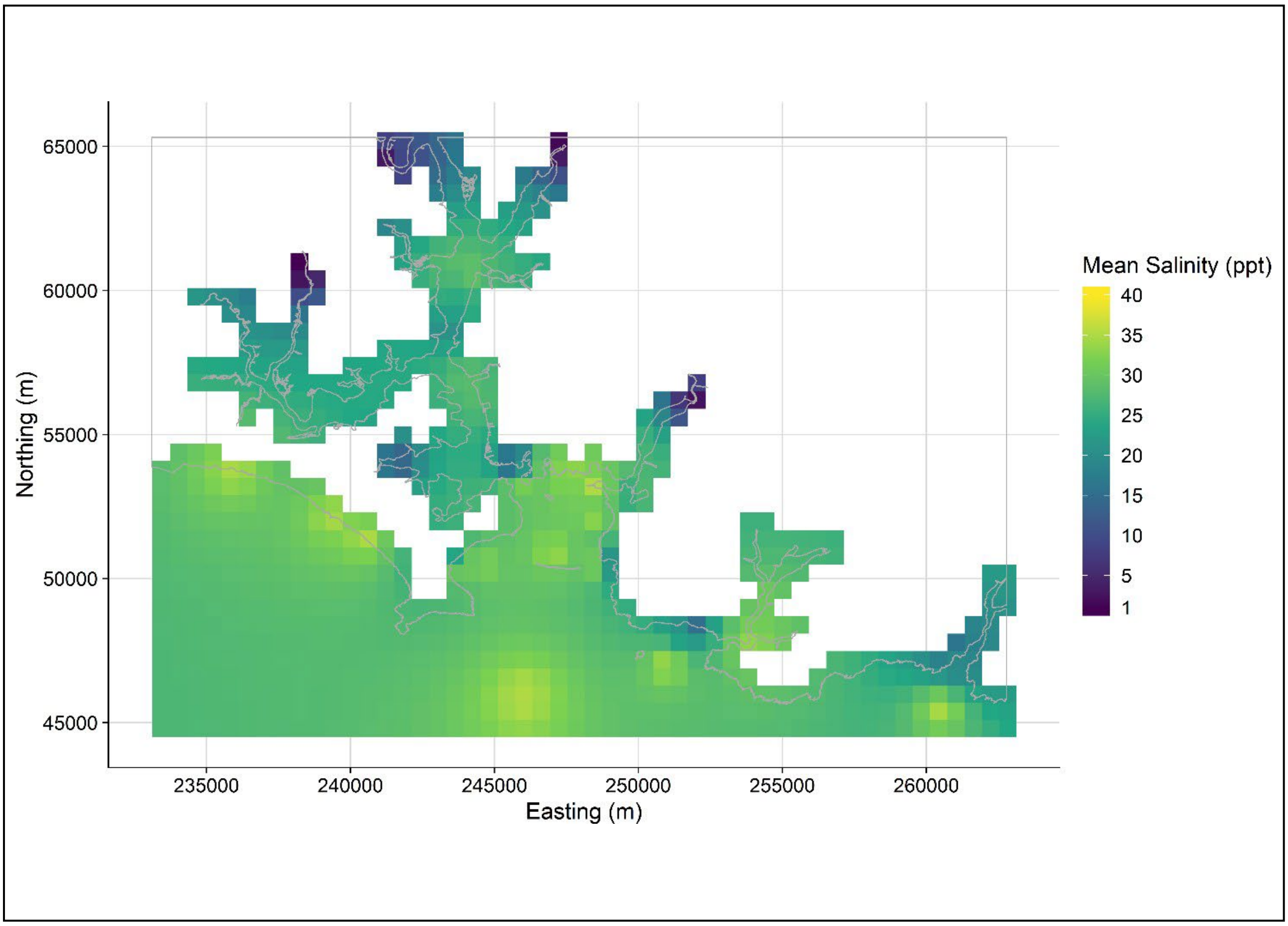


Figure S13: Interpolated mean salinity values – Plymouth (data source: uses Environment Agency water quality data from the [Water Quality Archive (Beta)](), under the [Open Government Licence]()).

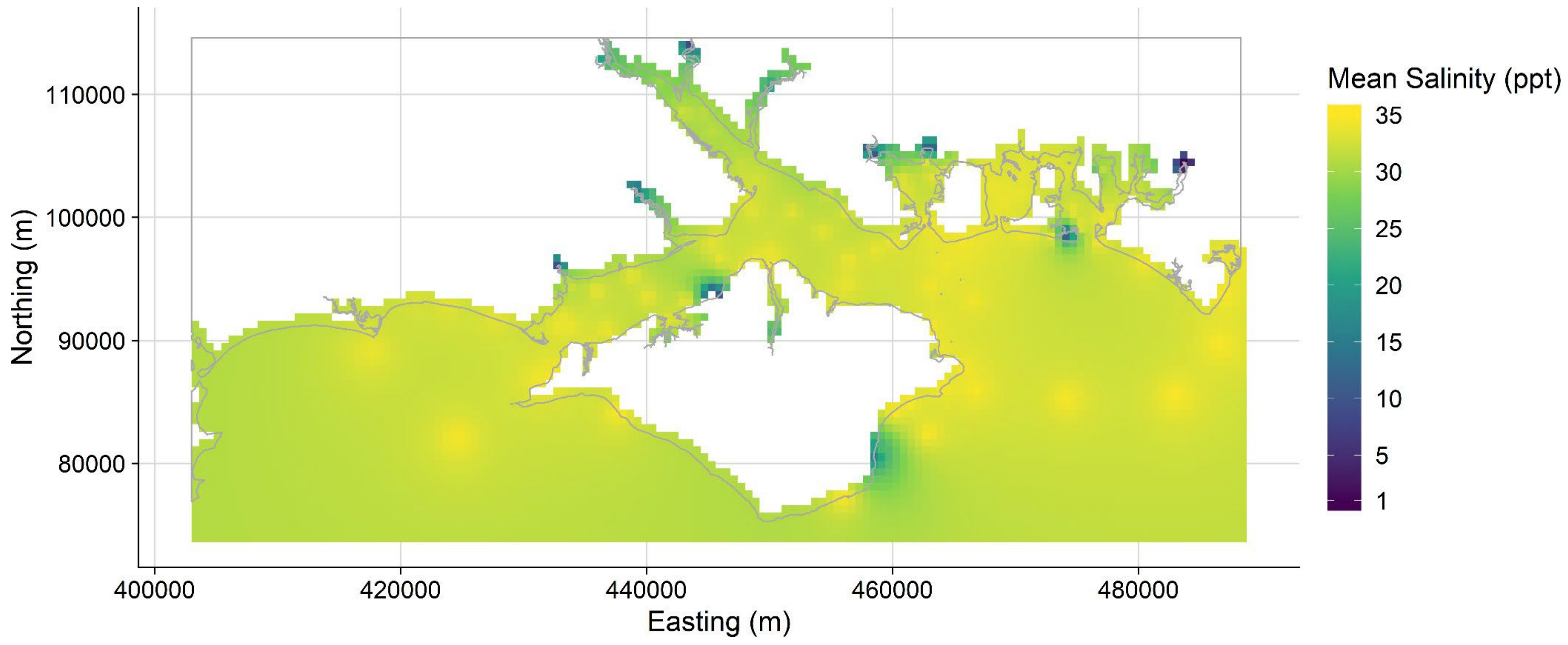


Figure S14: Interpolated mean salinity values – Solent (data source: uses Environment Agency water quality data from the Water Quality Archive (Beta), under the Open Government Licence).

Sea Surface Temperature (SST)

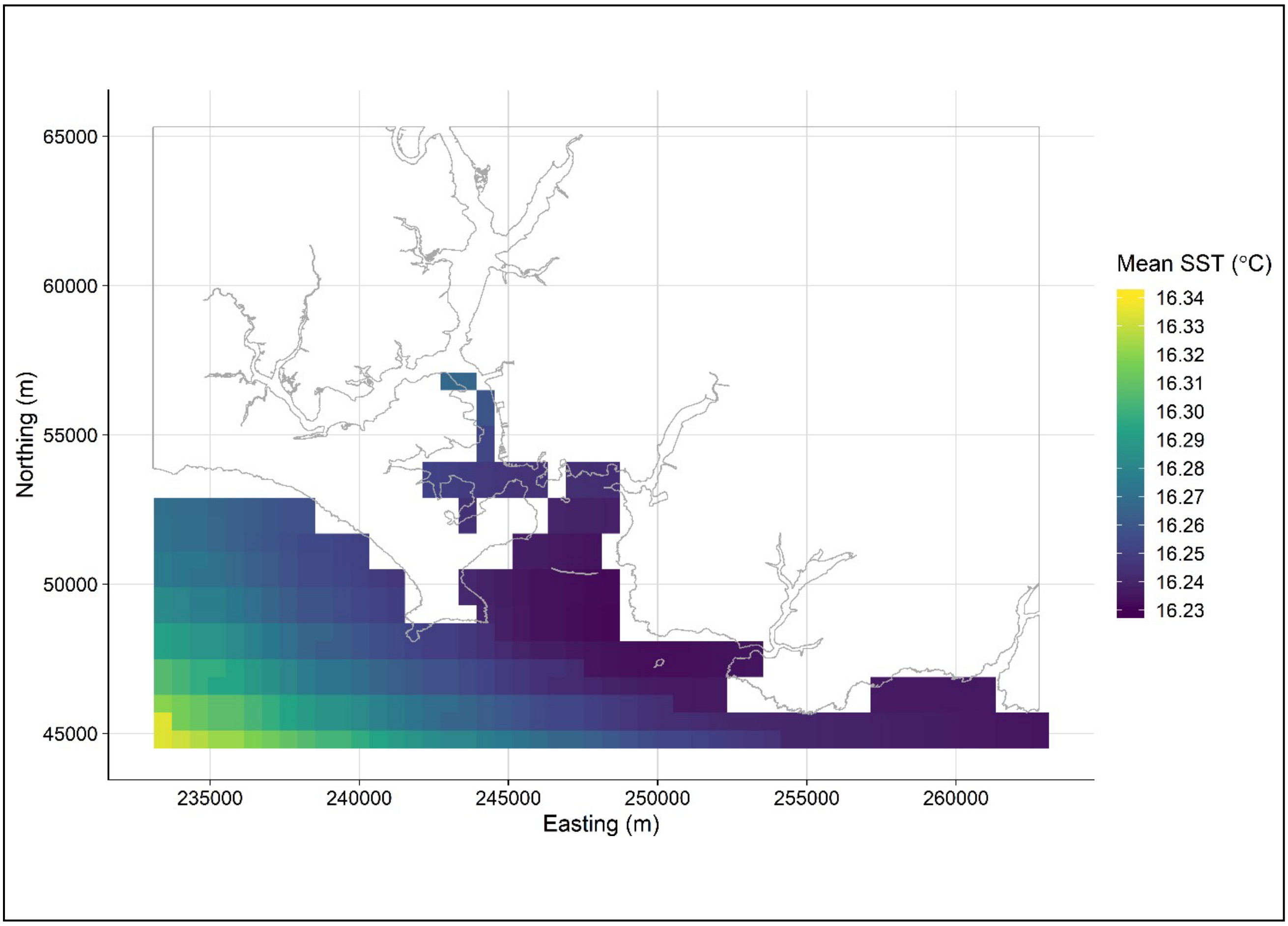


Figure S15: Mean sea surface temperature (SST) - Plymouth (data source: NOAA).

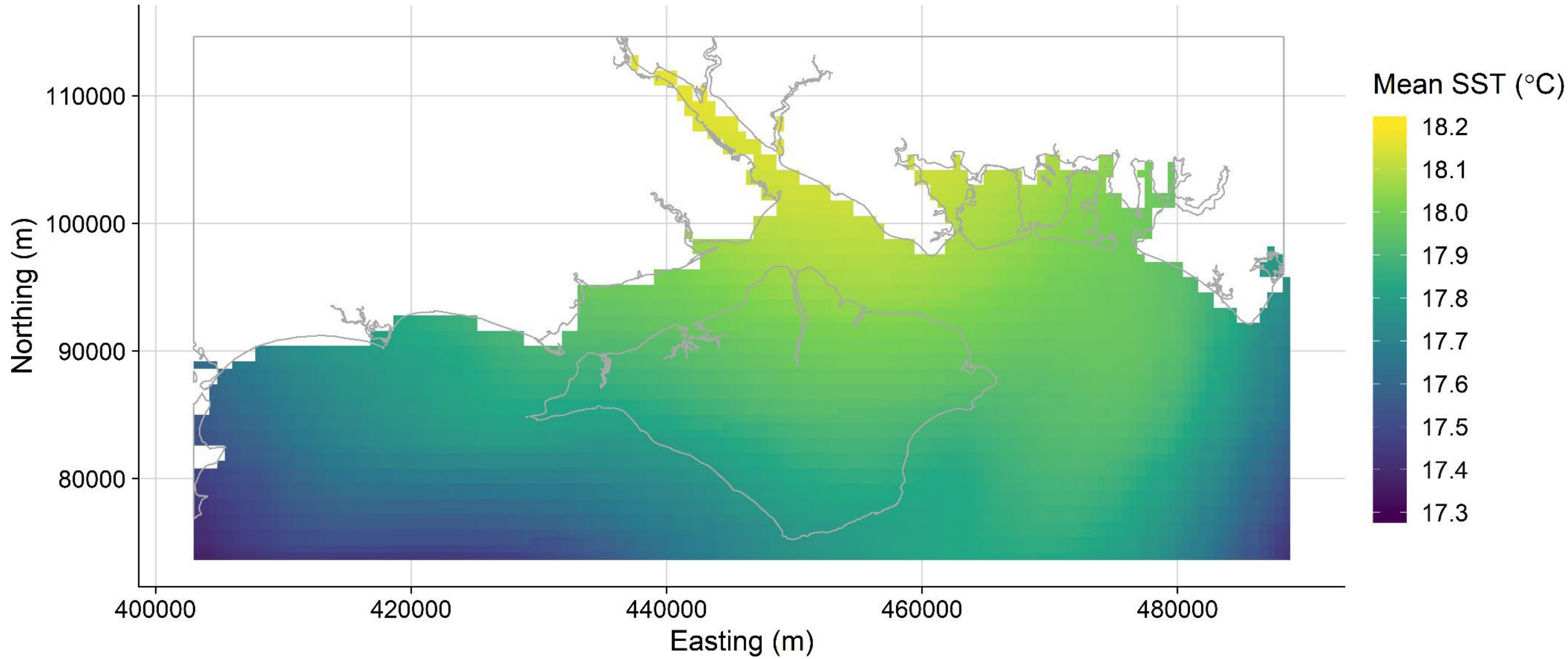


Figure S16: Mean sea surface temperature (SST) - Solent (data source: NOAA).

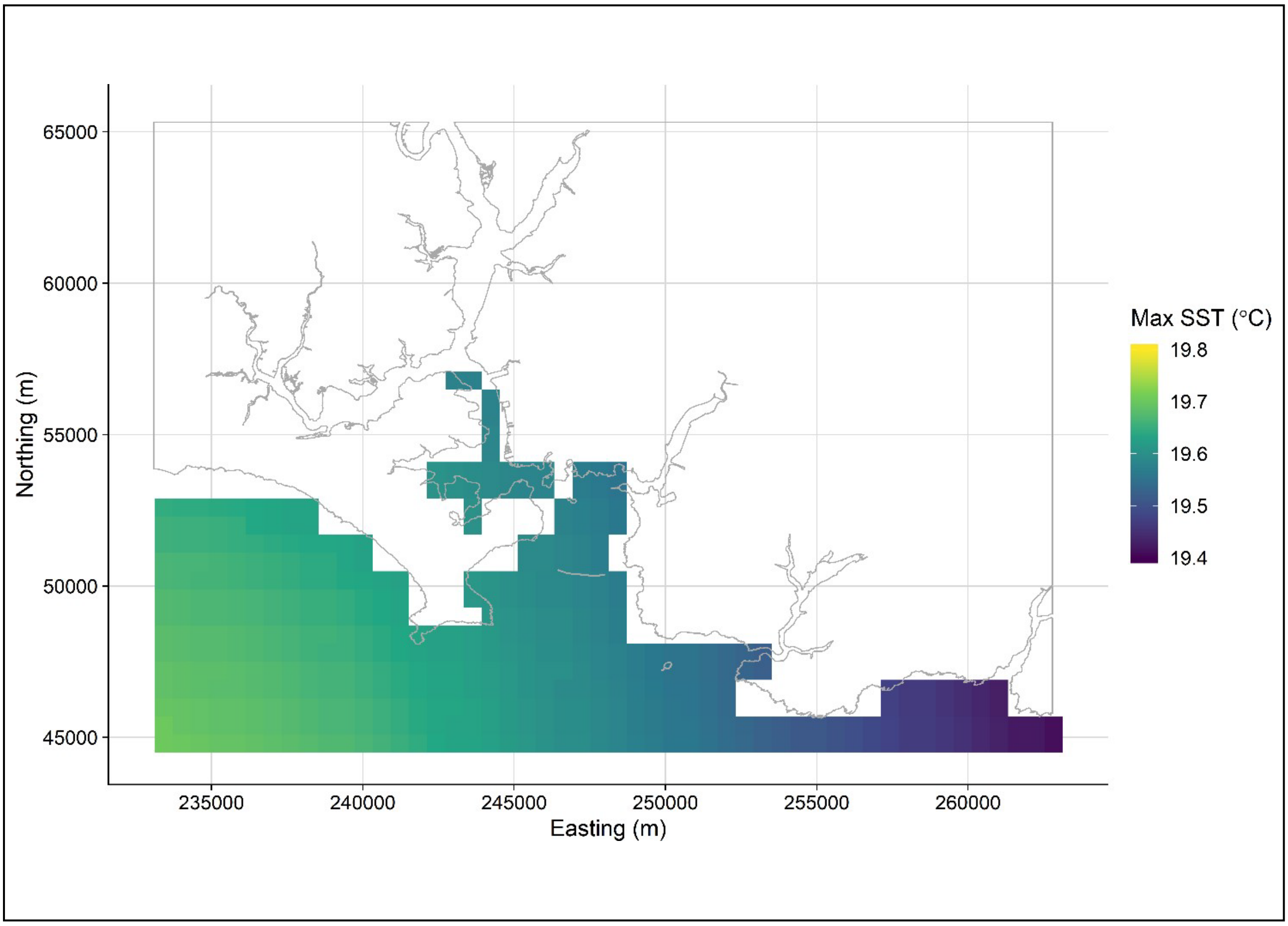


Figure S17: Maximum sea surface temperature (SST) - Plymouth (data source: NOAA).

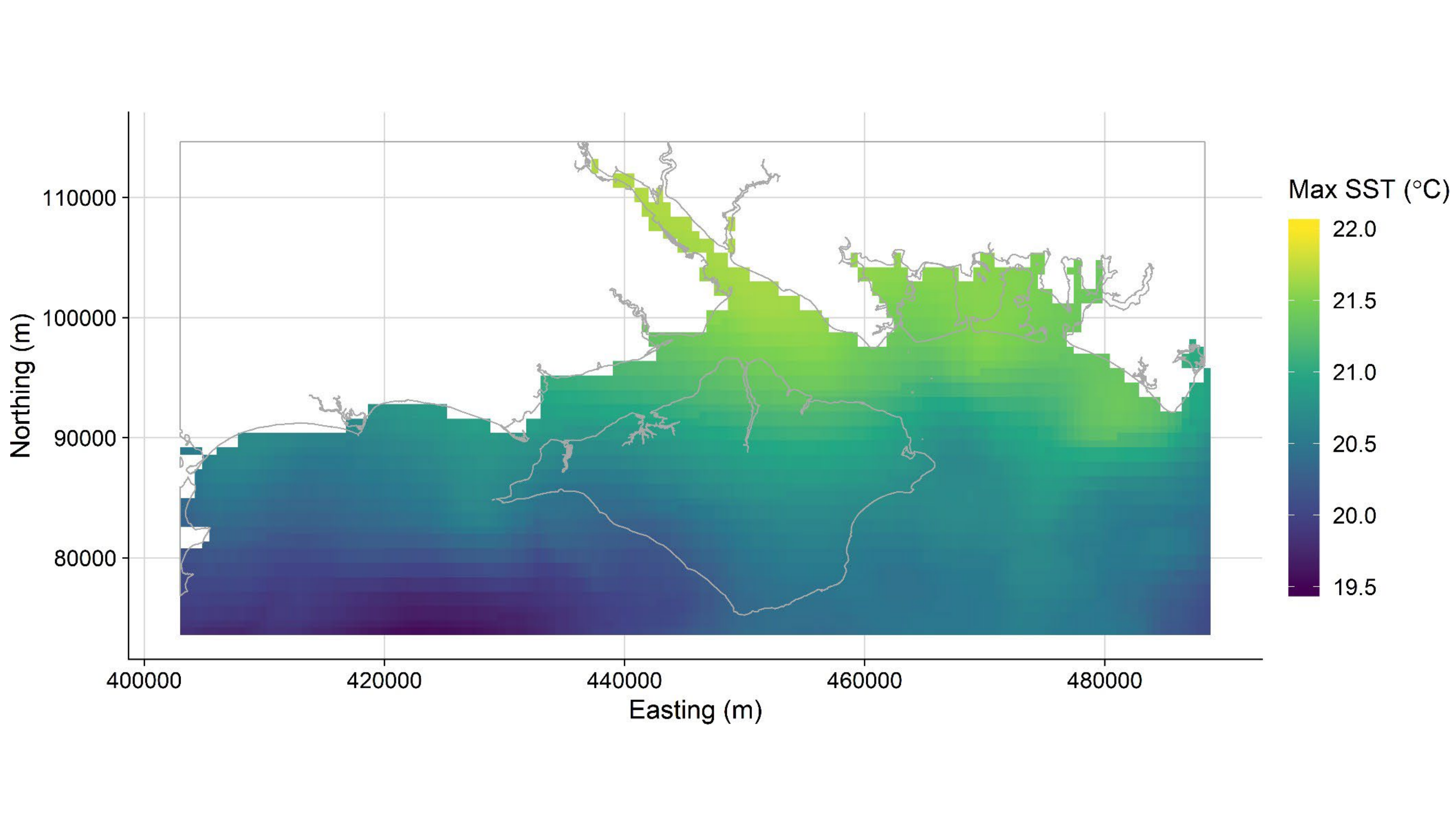


Figure S18: Maximum sea surface temperature (SST) – Solent (data source: NOAA).

EUNIS Habitat

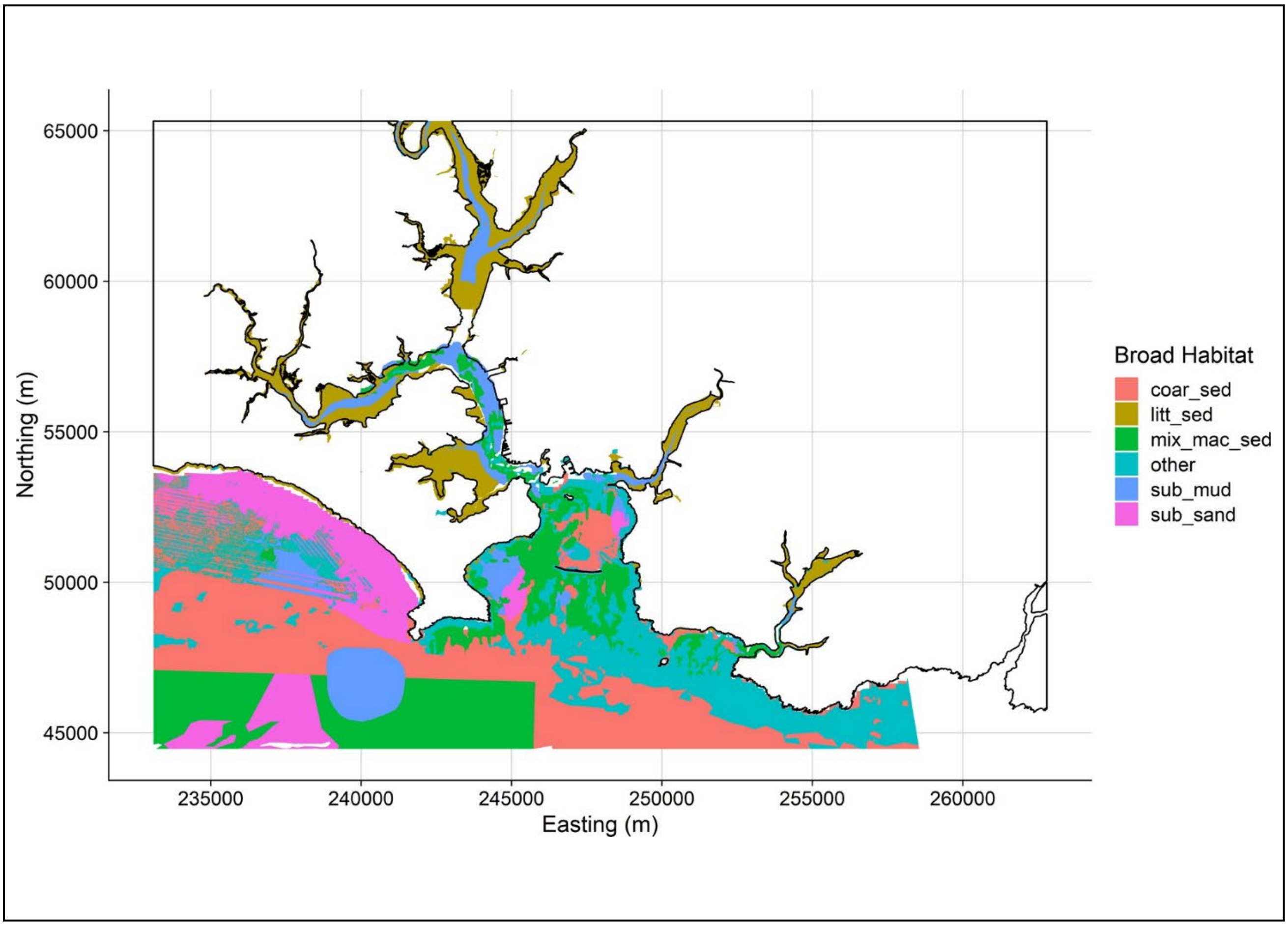


Figure S19: EUNIS seafloor habitat data grouped into 6 broad habitat types – Plymouth.

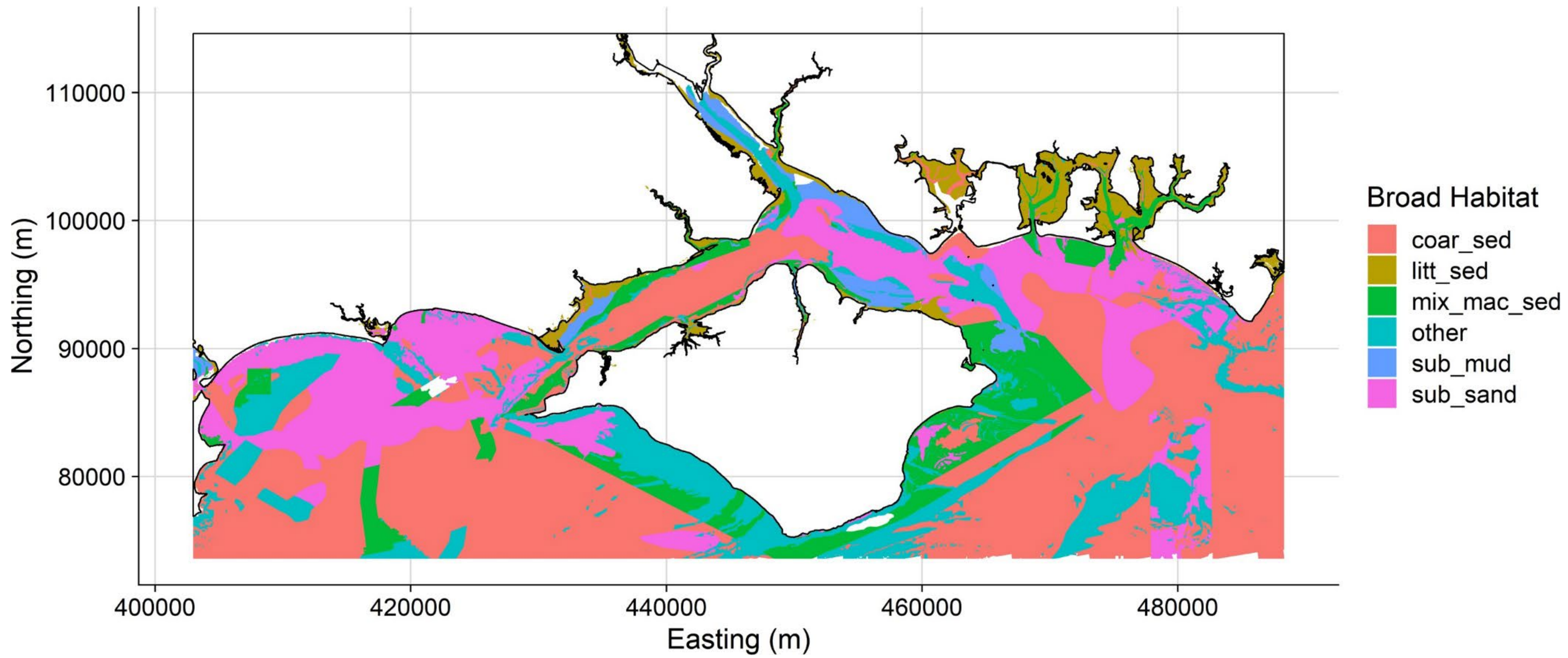
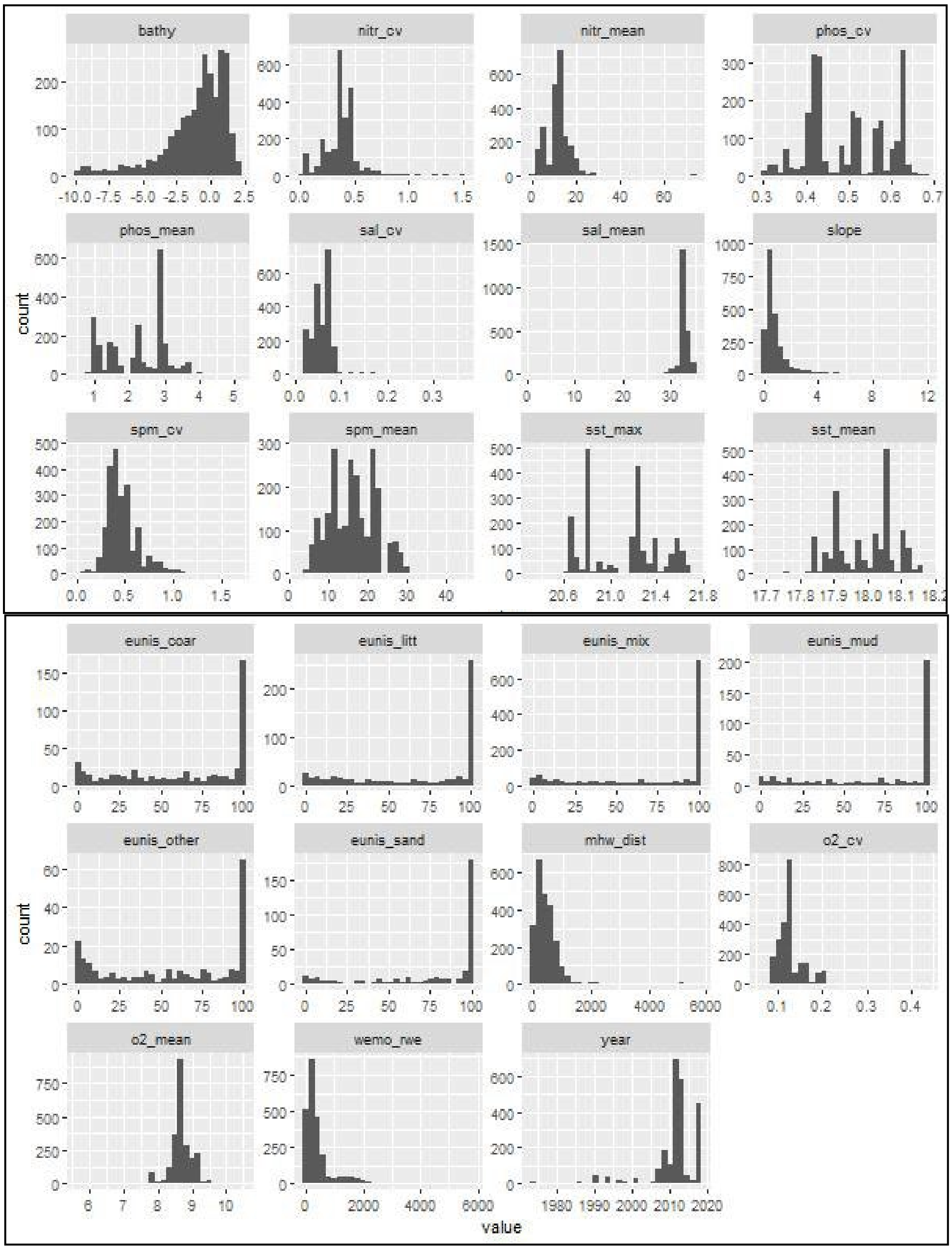


Figure S20: EUNIS seafloor habitat data grouped into 6 broad habitat types – Solent.

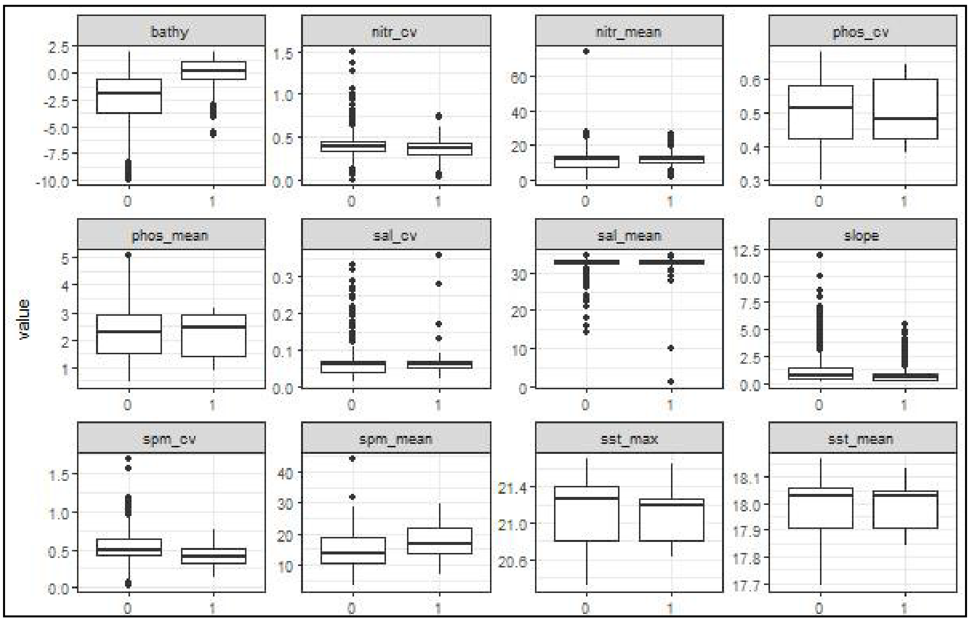
EUNIS classification groupings

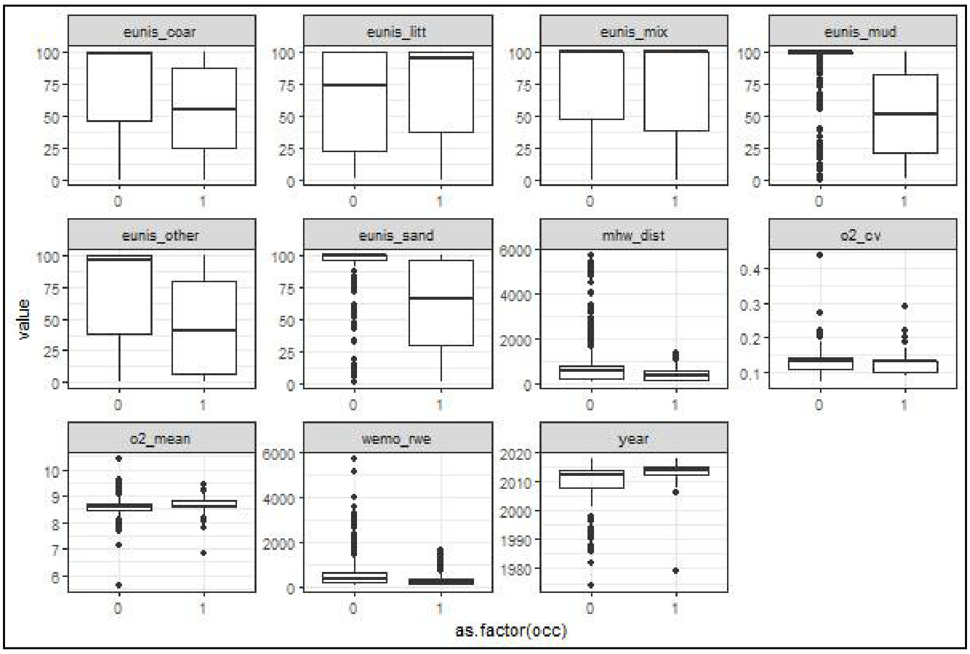
1. OTHER: all rock (A, A1, A3, A4), remaining circa seds. And any other habitats: (All A9.xx, A5.11, A5.15, A5.35, A5.36, A5.37, A5.44, A5.45, A5.6 [all A5.6xx] include any within these at higher EUNIS level A5.441, A5.373 etc)
2. LITT_SED: All A2 Littoral sediments (given that saltmarsh should be excluded from model boundary anyway)
3. COAR_SED: Possible coarse sediment (A5, A5.1, A5.12, A5.13, A5.14, A5.51)
4. SUB_SAND: Probable Sublittoral Sand (all A5.2's)
5. SUB_MUD: Probable Sublittoral mud (A5.3, A5.31, A5.32, A5.33, A5.34) – the rest are circalittoral – so in other.
6. MIX_MAC_SED: Probable mixed & macrophyte-dominate sediment (A5.4, A5.41, A5.42, A5.43 + A5.52, A5.53, A5.54)

Data figures for the variables used within the model for reference for the Solent

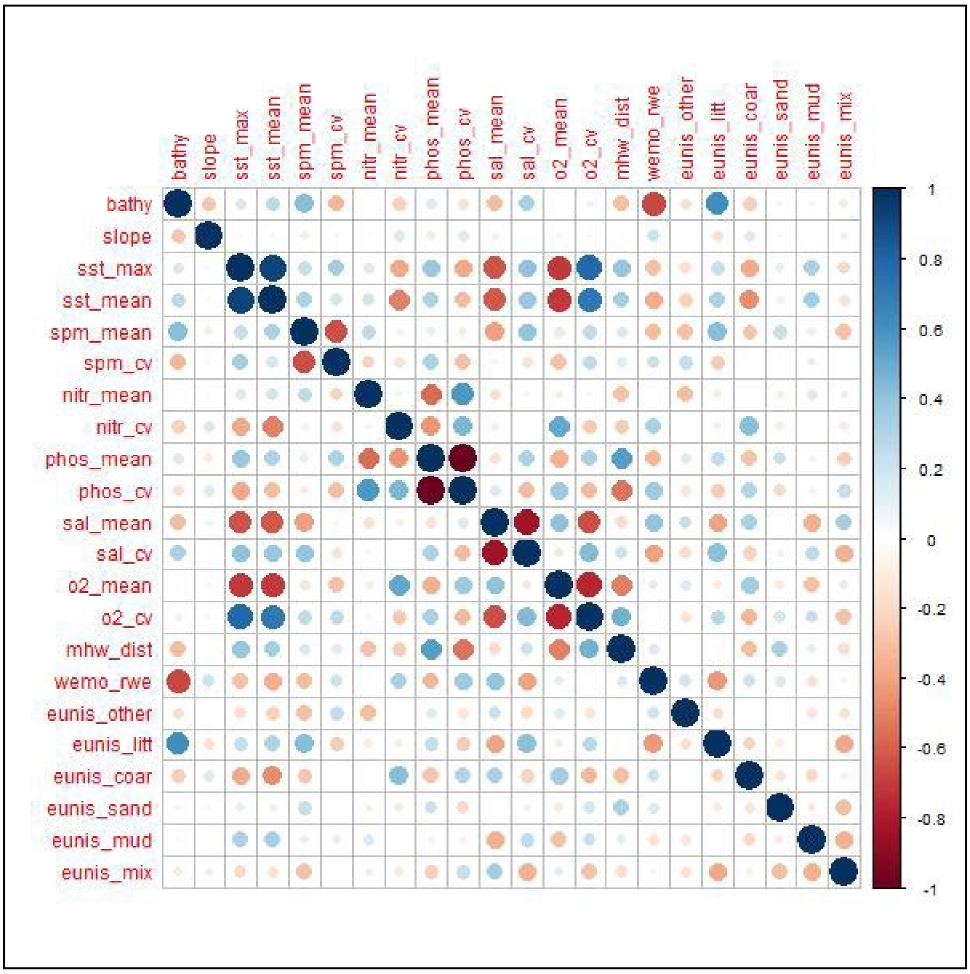


S21: Distributions of variables in Solent area. Note that coefficients of variation are for the different time periods that the measurements were made. We would expect the EUNIS graphs to look like this since most grid-cells fall entirely in one type of habitat.



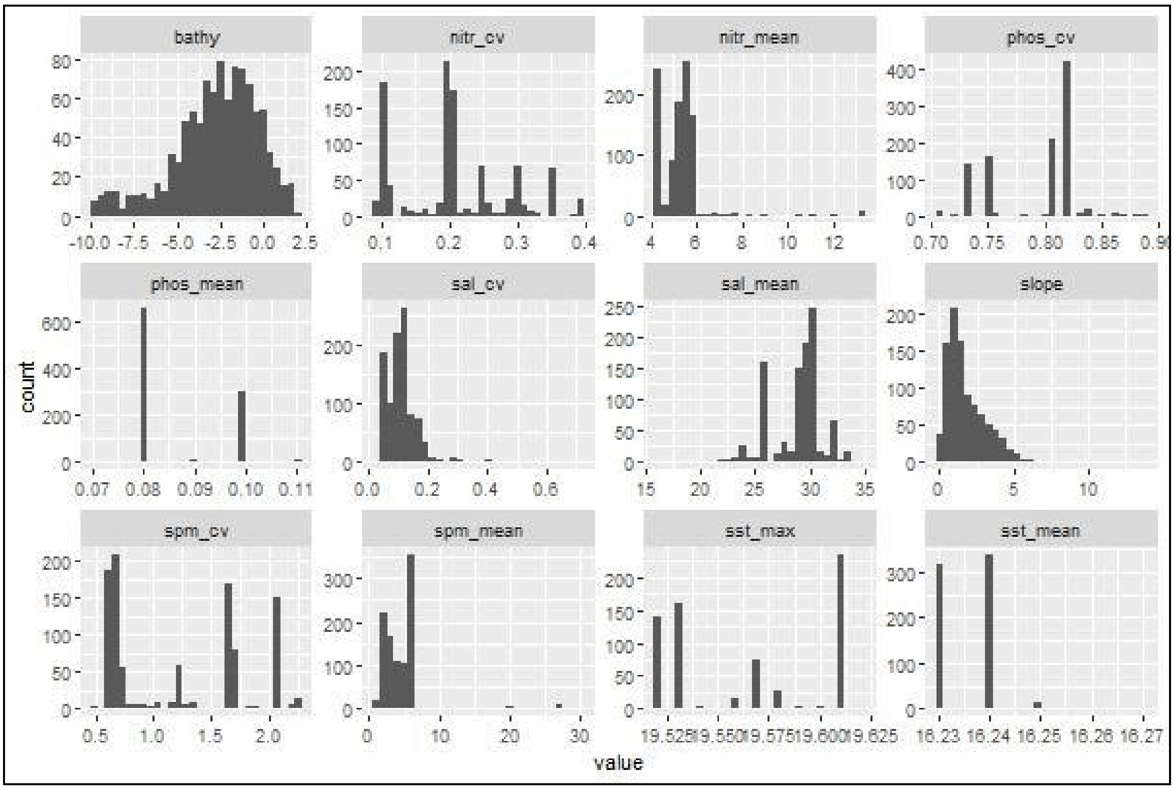


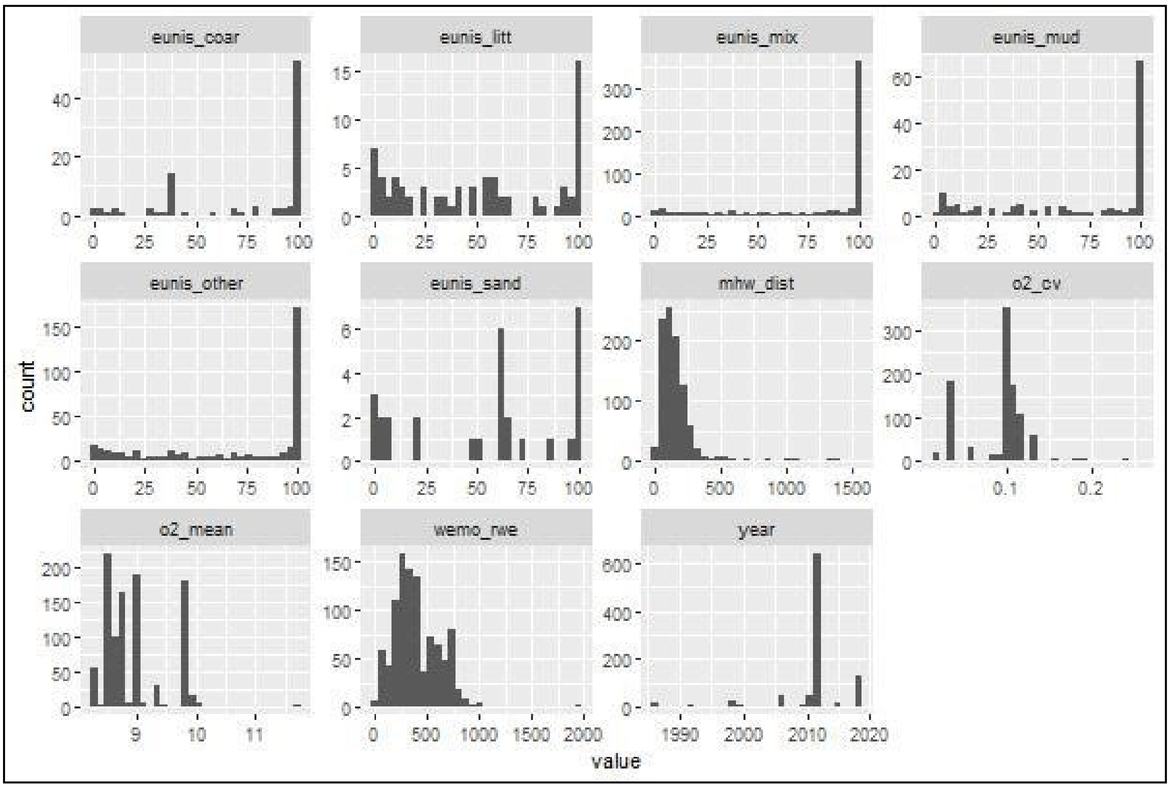
S22: Division of presences and absences between different conditions in Solent area.



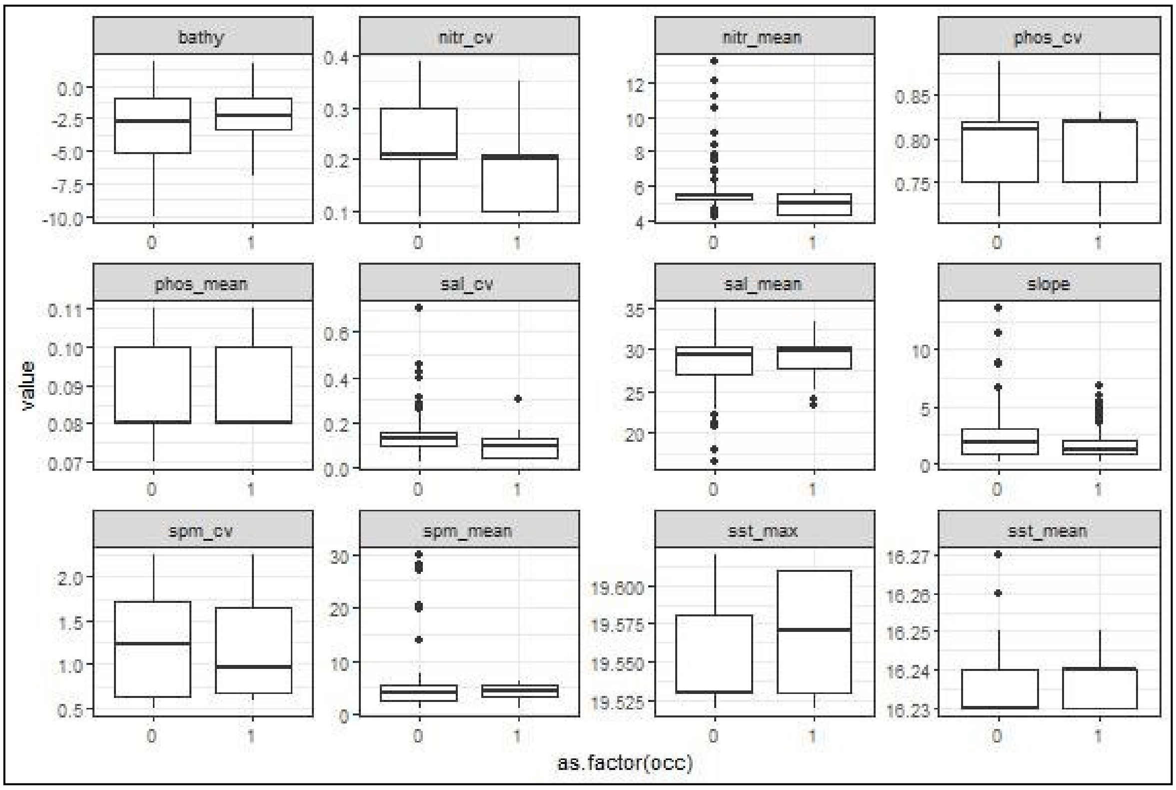
S23: Spearman's correlations between all explanatory variables in the Solent.

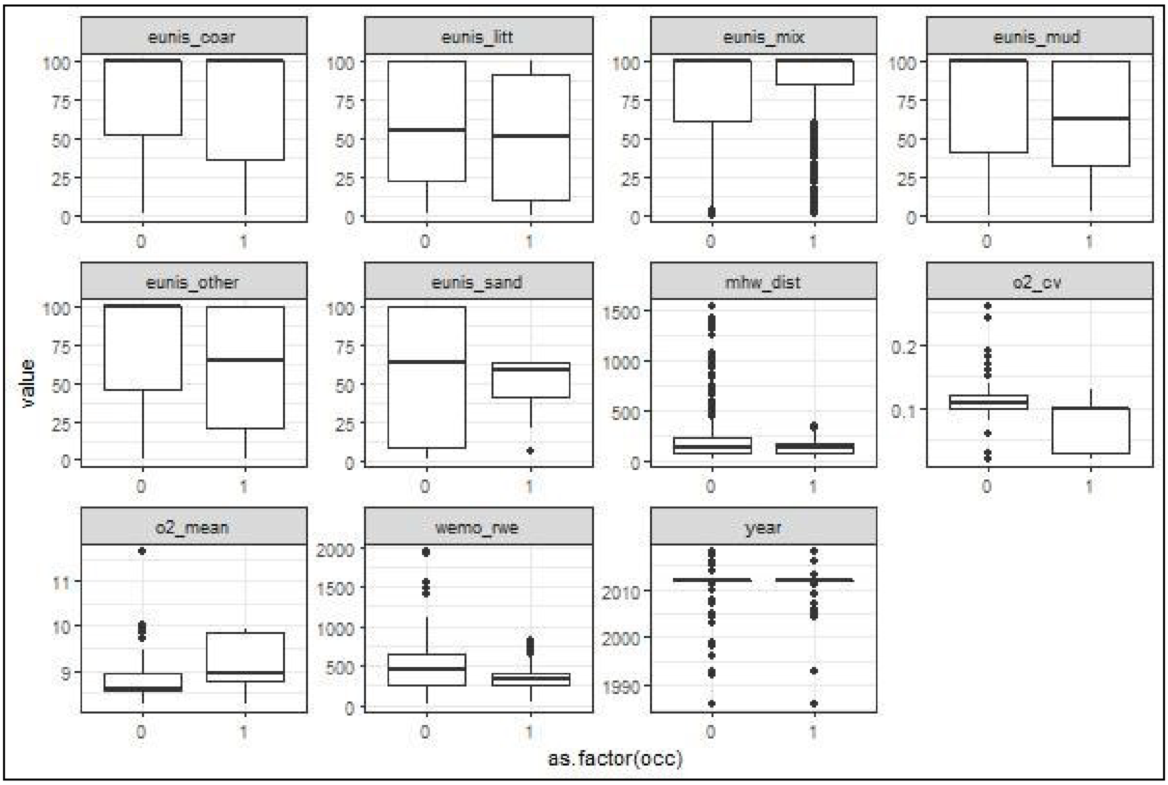
Data figures for the variables used within the model for reference for Plymouth





S24: Distributions of variables in Plymouth area. Note that coefficients of variation are for the different time periods that the measurements were made. We would expect the eunis graphs to look like this since most grid-cells fall entirely in one type of habitat.





S25: Division of presences and absences between different conditions in Plymouth area.

S26: Spearman's correlations between all explanatory variables for Plymouth.

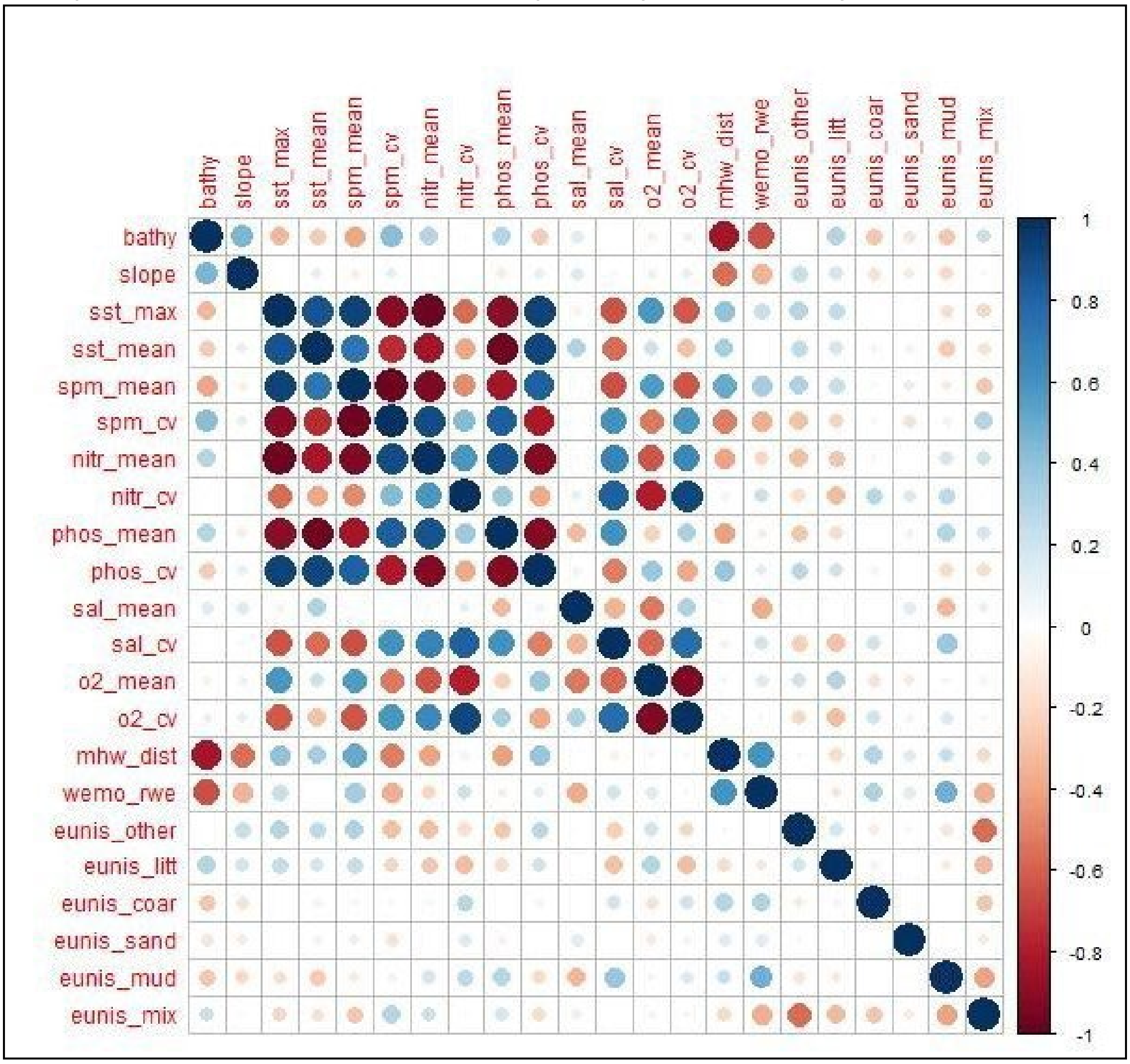


Table S1. Standardised coefficients of all variables retained in the best non-spatial model subset (multivar4i) for Plymouth. Partial R^2 indicates importance of each variable, and can only be calculated for the GLM. The AUC of the averaged non-spatial model was 0.868 (standard deviation=0.011).

Variables	Coefficients GLMM	Coefficients GLM	Partial pseudo R^2 GLM
(Intercept)	0.626789	1.243294	NA
Eunis coarse	-0.55387	-0.60376	0.011
Eunis mix	0.420986	0.427814	0.013
Eunis mud	0.301504	0.266589	0.007
Mean turbidity	2.160587	1.695854	0.074
Mean turbidity^2	0.162328	-0.03882	0
Mean distance to high water	-2.83042	-2.30008	0.037
Mean distance to high water^2	-4.46703	-4.32401	0.051

Coefficient of variation in phosphorous	-0.65993	-0.28371	0.003
Slope	-1.05295	-0.92186	0.036
Wemo RWE	-0.49455	-0.7444	0.03
Slope : mean turbidity	-0.87639	-0.73005	0.034

Table S2. Standardised coefficients of all variables retained in the best spatial model subset, for Plymouth. Partial R^2 indicates importance of each variable, and can only be calculated for the GLM.

Variables	**Coefficients GLMM**	**Coefficients GLM**	**Partial pseudo R^2 spatial GLM**
(Intercept)	-0.09392	0.21615	NA
Eunis coarse	-0.41457	-0.45892	0.007
Eunis mix	0.37002	0.39295	0.012
Eunis mud	0.27730	0.24031	0.006
Mean turbidity	1.94545	1.55658	0.069
Mean turbidity^2	0.04892	0.02390	0
Mean distance to high water	-2.78033	-2.25701	0.035
Mean distance to high water^2	-3.11824	-2.93733	0.021
Coefficient of variation in phosphorous	-0.46350	-0.16114	0.001
Slope	-0.94435	-0.81069	0.024
Wemo RWE	-0.41143	-0.65589	0.021
Slope : mean turbidity	-0.86940	-0.69627	0.031
Spatial term (GLMM)*	0.00000452	NA	
Spatial term (GLM)*	NA	0.00000436	0.016

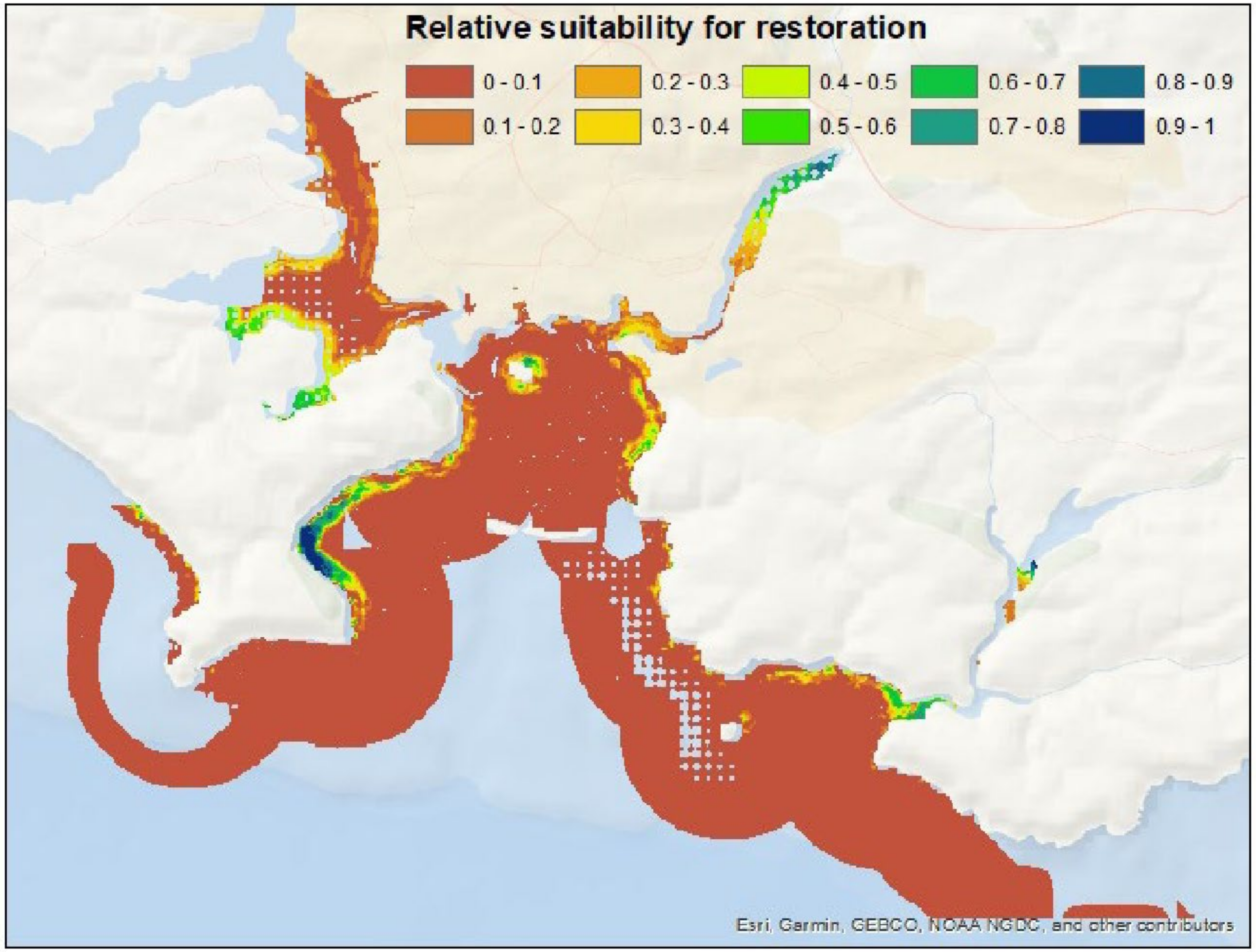


Figure S27: Lowest 95% confidence interval estimate of suitability based on the final spatial GLM for the Plymouth site, trimmed to analogue environmental conditions.

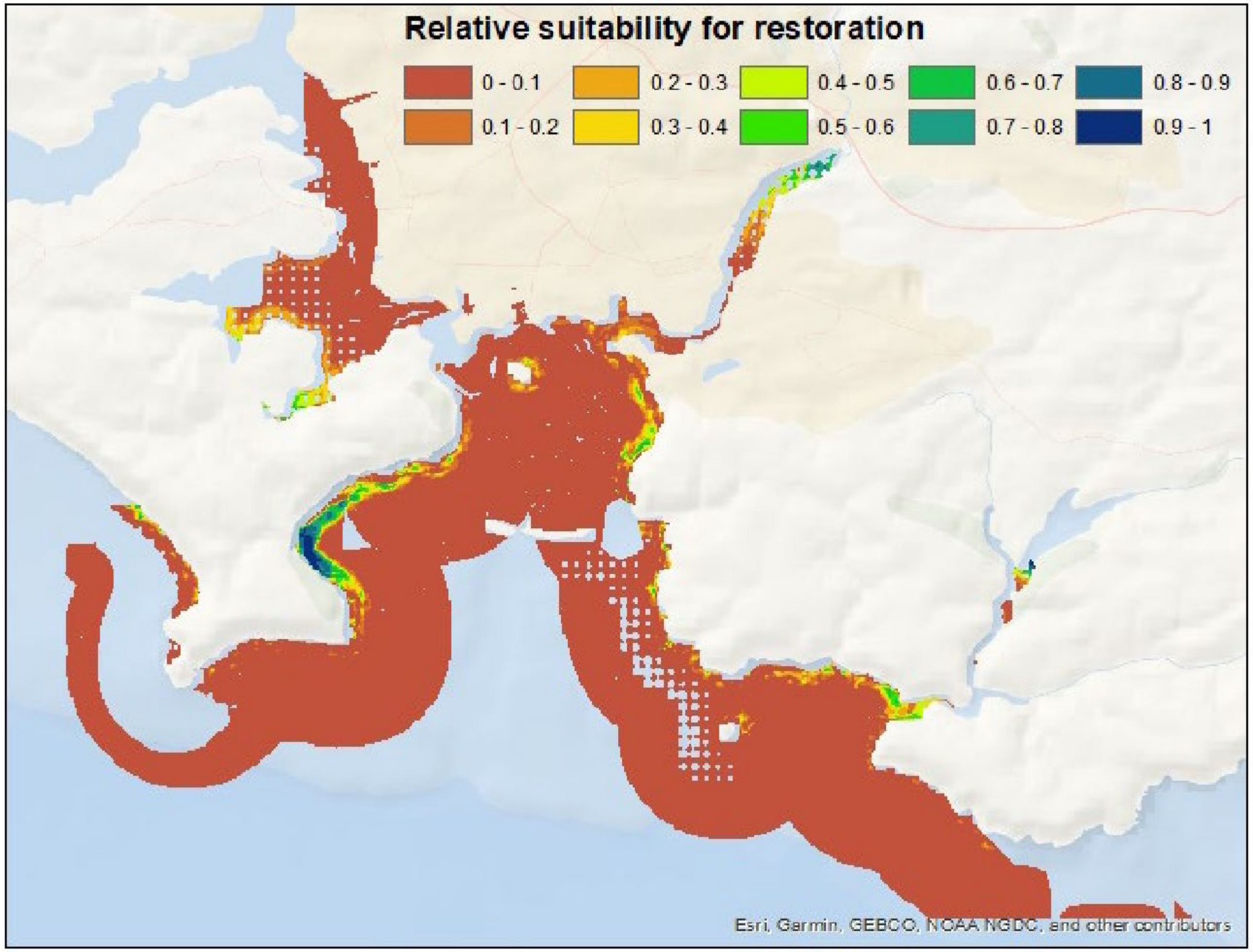


Figure S28: Lowest 95% confidence interval estimate of suitability based on the final spatial GLMM for the Plymouth site, trimmed to analogue environmental conditions.

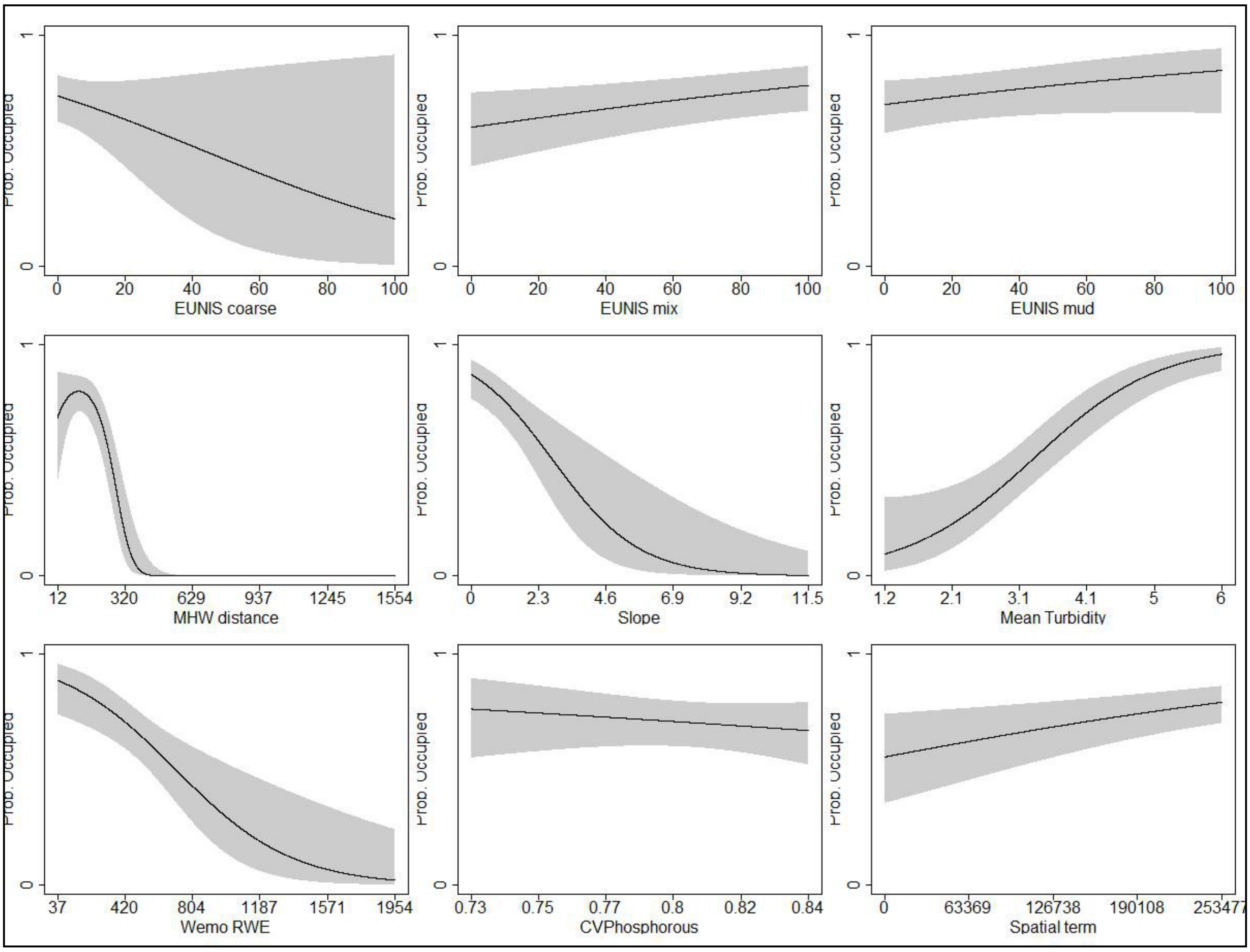


Figure S29: Predicted probability (±95% confidence intervals) of seagrass occurrence for each explanatory variable in the GLM included in the best spatial model subset for Plymouth, when all other explanatory variables are held at their means. Confidence intervals could not be calculated for the final, averaged model as it contains both a GLM and GLMM, therefore we supply the confidence intervals for the two constituent models as supplementary information.

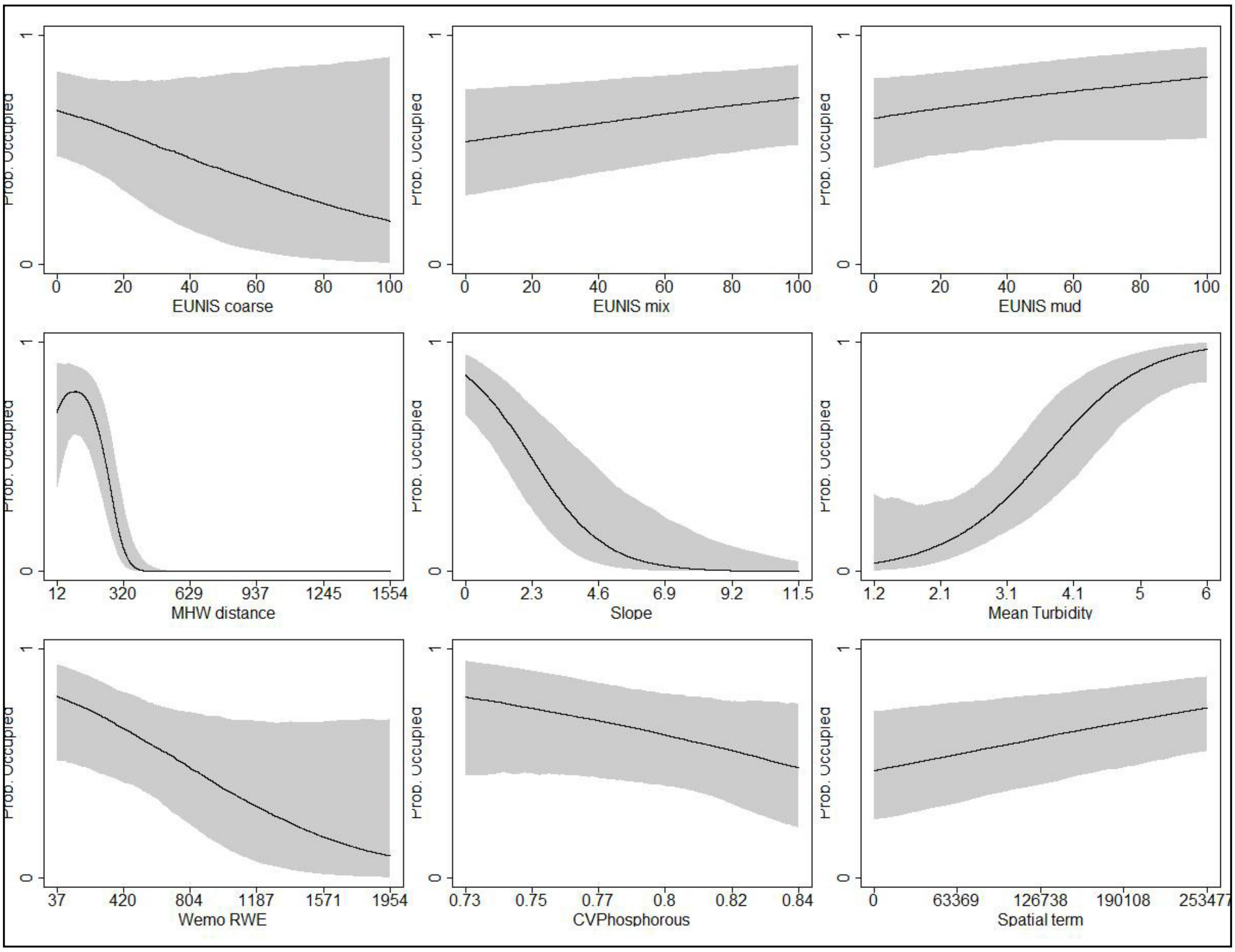


Figure S30: Predicted probability (±95% confidence intervals) of seagrass occurrence for each explanatory variable in the GLMM included in the best spatial model subset for Plymouth, when all other explanatory variables are held at their means. Confidence intervals could not be calculated for the final, averaged model as it contains both a GLM and GLMM, therefore we supply the confidence intervals for the two constituent models as supplementary information.

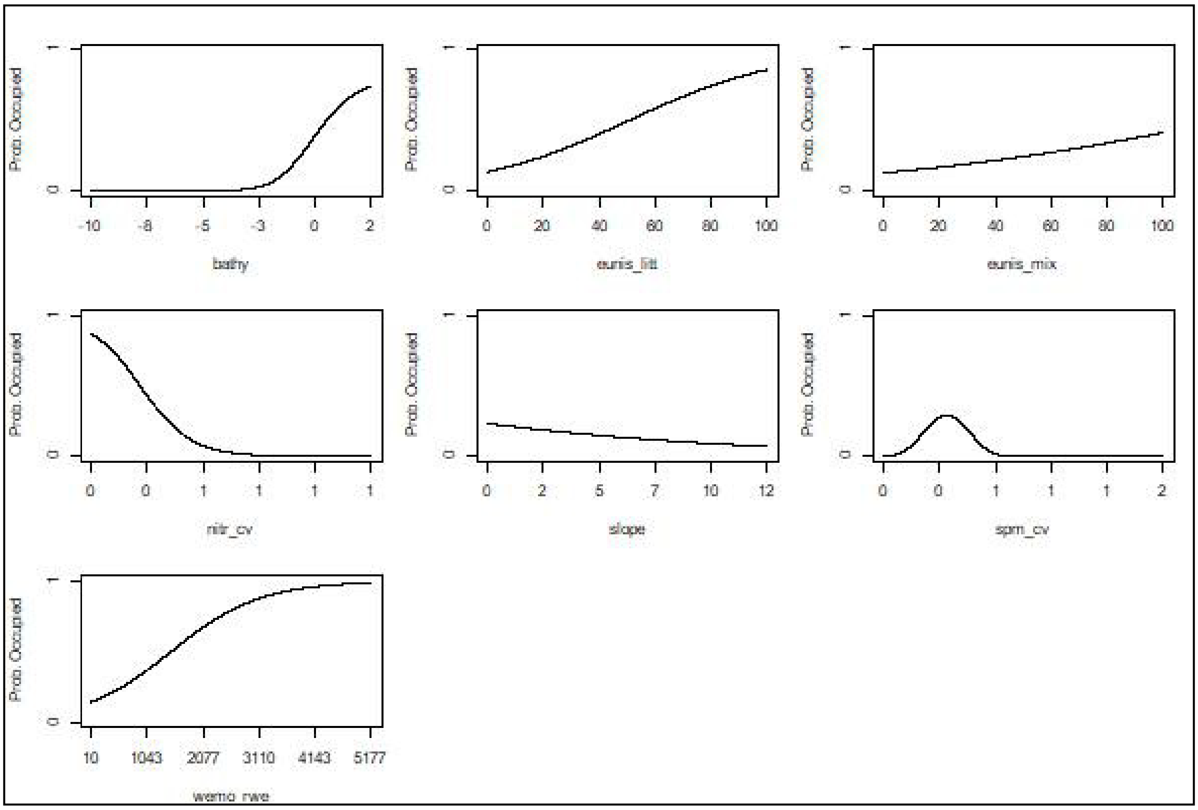


Figure S31: Predicted probability of seagrass occurrence for each explanatory variable in the best non-spatial model for the Solent (multivar4i), when all other explanatory variables are held at their means.

Table S32. Standardised coefficients of all variables that were retained in the best non-spatial model (multivar4i), for the Solent. Note partial R^2 cannot be calculated for variables in a GLMM.

Variables	Coefficients
(Intercept)	-1.28977
Bathymetry	2.86937
Bathymetry^2	-0.82314
Eunis littoral	1.25910
Eunis mix	0.71368
Coefficient of variation in nitrate	-1.06943
Slope	-0.11222
Coefficient of variation in turbidity	-1.40402
Coefficient of variation in turbidity^2	-1.22299
Wemo RWE	0.61368
Coefficient of variation in nitrate : slope	-1.30705

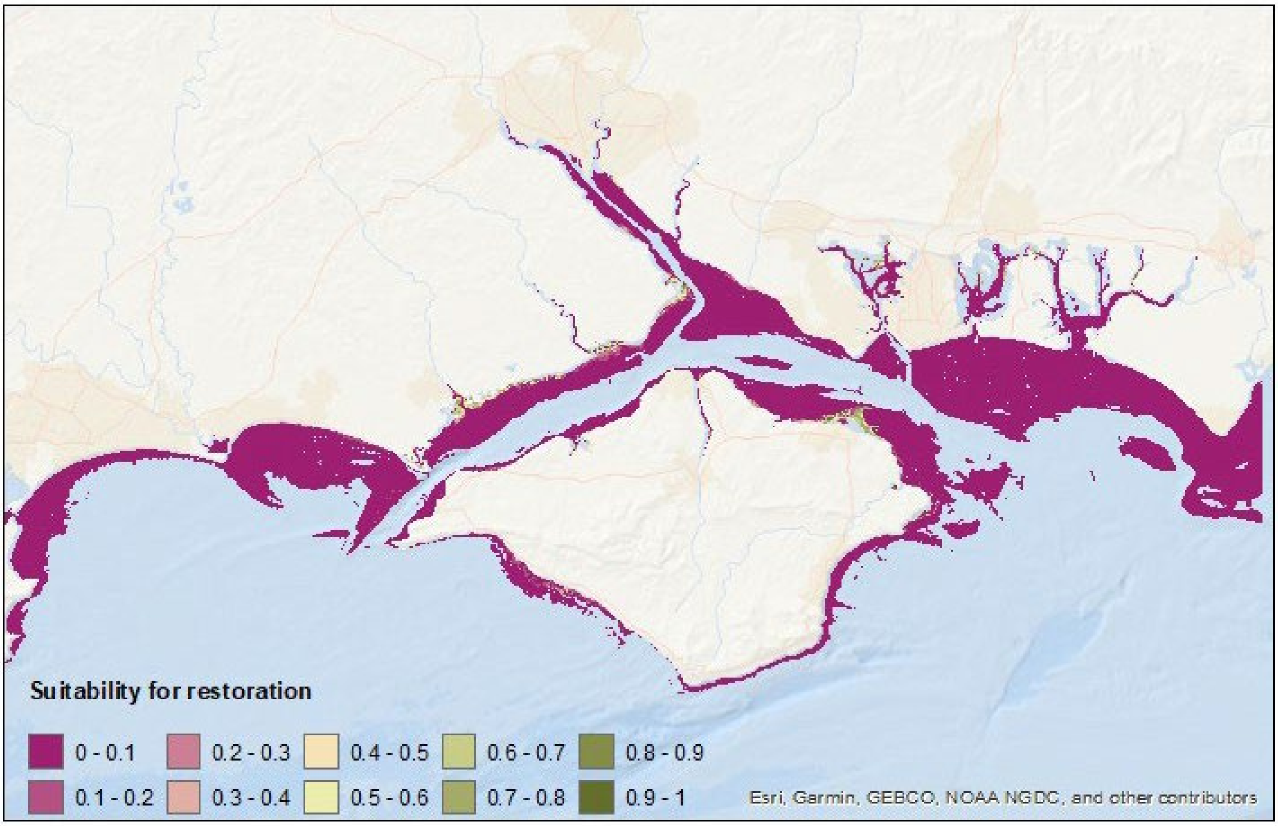


Figure S33: Lowest 95% confidence interval estimate of suitability based on the averaged spatial model for the Solent site, trimmed to analogue environmental conditions.

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