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The Application of Habitat Suitability Modelling to Mapping VME Distribution in the Deep Sea to Inform Spatial Management

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THE APPLICATION OF HABITAT SUITABILITY MODELLING TO MAPPING VME DISTRIBUTION IN THE DEEP SEA TO INFORM SPATIAL MANAGEMENT

by

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AUTHOR'S DECLARATION

At no time during the registration for the degree of Research Masters (ResM) has the author been registered for any other University award without the prior agreement of the Doctoral College Quality Sub-Committee. Work submitted for this research degree at the University of Plymouth has not formed part of any other degree either at the University of Plymouth or at another establishment. This degree was funded and in collaboration with the Marine Institute (Galway) in which they provided biological (SeaRover) data.

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ABSTRACT

THE APPLICATION OF HABITAT SUITABILITY MODELLING TO MAPPING VME DISTRIBUTION IN THE DEEP SEA TO INFORM SPATIAL MANAGEMENT

Kyran Patrick Graves

As the development of new technologies continues, so do industrial activities. As a result, such industries can extract natural resources and use the marine environment at deeper and deeper depths, for example, fisheries, oil and gas, submarine cabling, and – the latest emergence – deep-sea mining. Despite these developments, the majority of the deep ocean, including national waters and the High Seas, remains unmapped. The absence of data across large swathes of the deep sea means that conducting adequate environmental impact assessments when new activities are proposed is difficult, and what data is available is often sparse. Predictive habitat models are tools that can be used in a deep-sea context to help address the lack of observational data, by creating full coverage maps of the predicted distribution of a species or habitat.

This thesis reviews predictive habitat models and how these models are currently used in deep-sea settings. Additionally, this thesis aims to utilise habitat suitability models – a type of predictive habitat model – to predict the distribution of seven Vulnerable Marine Ecosystems (VMEs) across the UK and Irish national waters, and evaluate their performance. The model outputs are used to demonstrate how they can be used to inform spatial management, such as assessing the effectiveness of existing marine protection measures and identifying areas where VMEs are at high risk from deep-sea bottom fisheries. The evaluation of model performance suggest that habitat suitability models used are effective at predicting the presence of VMEs and that; generally, combining modelling methods (ensembling) improves the model's ability to successfully predict

occurrences. The assessment of model outputs concerning existing conservation measures suggests that the 800 m ban on bottom-fishing is a highly successful conservation measure for the seven VME modelled, whilst also identifying that the network of marine protected areas is considerably less effective. The study also identifies two example areas of the Irish continental slope where suitable habitat for several VMEs is high but coincides with historically intense bottom-fishing activities that have since ceased, and therefore recommends these areas for habitat-recovery monitoring. Lastly, this thesis discusses the potential uses of spatial transfers in addressing the regional disparities in available distribution data, as well as the challenges around the acceptability of PHMs in formal advice to marine conservation managers and policymakers.

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GLOSSARY OF TERMS

AAN	Artificial Neural Network
ABNJ	Area Beyond National Jurisdiction
AcaArb	*Acanella arbuscula* Assemblages
AUC	Area Under the Receiver-Operated Characteristic Curve
BBPI	Broad Bathymetric Position Index
BIOCLIM	Bioclimatic Envelope Model
BODC	British Oceanographic Data Centre
BRT	Boosted Regression Trees
BurAne	Burrowing Anemone Fields
CART	Classification and Regression Trees
CTA	Classification Tree Analysis
CWC	Cold-water Coral
EC	European Commission
ECS	Extended Continental Shelf
EEZ	Exclusive Economic Zone
EMODnet	European Marine Observation and Data Network
EU	European Union
EUNIS	European Union Nature Information System
FAO	Food and Agricultural Organisation
FBPI	Fine Bathymetric Position Index
FDA	Flexible Discriminant Analysis
GAM	Generalised Additive Model
GBM	Generalised Boosted Model
GEBCO	General Bathymetric Chart of the Oceans

GLM	Generalised Linear Model
GUI	Graphical User Interface
HSM	Habitat Suitability Model
ICES	International Council of the Exploration of the Sea
JNCC	Joint Nature Conservation Committee
MARS	Multivariate Adaptive Regression Splines
MaxEnt	Maximum Entropy
MCZ	Marine Conservation Zone
MicCor	Mixed Cold-Water Coral Community (Coral Garden)
MPA	Marine Protected Area
MSFD	Marine Strategy Framework Directive
MSP	Marine Spatial Planning
NCMPA	Nature Conservation Marine Protected Area
NEAFC	North-East Atlantic Fisheries Commission
PCC	Percent Correctly Classified
PHM	Predictive Habitat Model
RF	Random Forest
RFMO	Regional Fisheries Management Organisation
ROV	Remotely Operated Underwater Vehicle
SAC	Special Area of Conservation
SDM	Species Distribution Model
SolRee	*Solenosmilia variabilis* Reef
SolScl	Solitary Scleractinian Fields
SpnMeg	Sea pens and Burrowing Megafauna
SRE	Surface Range Envelop (or BIOCLIM)
SVN	Support Vector Machine

SyrFra	*Syringammina fragilissima* Fields
TSS	True Skill Statistic
UN	United Nations
UNGA	United Nations General Assembly
VME	Vulnerable Marine Ecosystem
VMS	Vessel Monitoring System
WGDEC	Working Group on Deep-water Ecology

Chapter 1: Review of Predictive Habitat Modelling Methods and Applications to the Deep Sea Environment

1.1 Introduction

Species distribution models and habitat suitability models are powerful tools in biogeography and ecology because of their increasing ability to make accurate spatial predictions of distribution. As a result, their applications continue to evolve and range from spatial planning to epidemiology. This review (1) identifies the best performing methods of building models, (2) how they are currently applied to the deep-sea environment, with a particular focus on marine spatial planning and conservation efforts, (3) as well as identifying gaps in this area of deep-sea research and potential opportunities to address them.

1.2 What are Species Distribution and Habitat Suitability Models?

Species distribution models (SDMs) and habitat suitability models (HSMs) – also known as predictive habitat models (PHMs) – have their roots in ecological niche theory. A species' ecological niche was originally described by Grinnell (1917) as the distinct set of ecological parameters suitable for a species to exist. This concept was later developed with distinctions drawn between a species (1) fundamental niche, a strict set of environmental conditions under which a species can exist, and (2) realised niche, the part of the fundamental niche in which a species actually occupies after accounting for intra- and inter-specific ecological interactions and processes, e.g. competition, which is smaller than the fundamental niche (Hutchinson, 1957). This led to the conception of the BAM-diagram (Soberón et al., 2017) by which a species range can be defined by three factors: (B) biotic interactions, the (A) abiotic environmental conditions and the species ability to (M) move into a suitable area, whether that be by active swimming or passive dispersal (Figure 1.1).

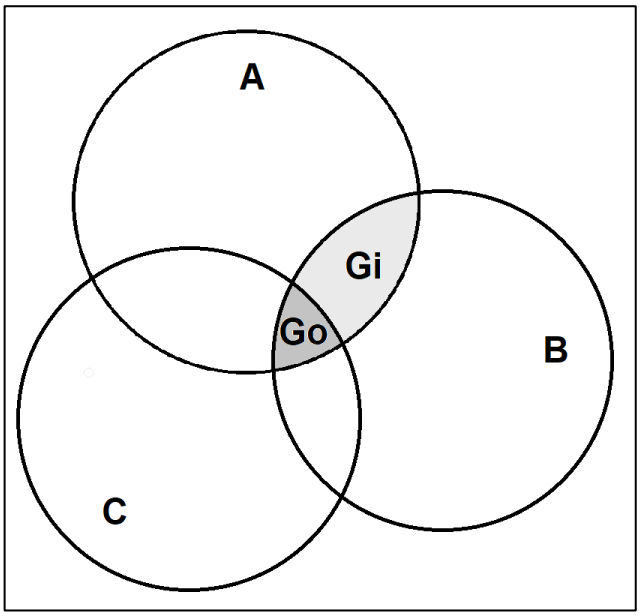

Figure 1.1. BAM diagram redrawn from Soberón et al. (2017) depicting the interplay between (B) biotic factors, (A) abiotic factors and (M) capacity of movement in determining a species fundamental (Gi) and realised niche (Go).

What BAM factors are incorporated in the modelling process largely depends on the model type, which can be described as:

1. Correlative – calculate estimates of species requirements from known geographical species occurrence data and environmental variables.
2. Mechanistic – which incorporate physiological data and biophysics principles.
3. Process-orientated – which incorporate dynamic processes such as dispersal and species interactions.

As recent literature reviews have highlighted, correlative model methods are the most widely implemented (Melo-Merino et al., 2020) and are the focus of this review.

1.2.1 Modelling Methods

Correlative SDMs can be built using presence-only, presence-background, presence-absence and abundance/density species datasets with methodologies split into three main groups: profile, machine-learning, and regression-based models. The different types of model input data play a large part in determining the type of modelling framework that

can be used. Presence-only models require no absent data and therefore are usable in most circumstances as they only require occurrence data. Presence-background point models still only require occurrence data but also require background points. Background points are used to characterise the environment, including areas where a target species occur, but do not inform models in any way about known species distribution – presence nor absence – and therefore predict relative suitability. Background points can be random, sampled regularly or targeted to tackle known biases within a dataset (Guillera-Arroita et al. 2014). Other modelling methods do allow for the incorporation of absence data, where available, which allows such models to distinguish between areas of presence and absence, not just the suitability of a given area based on known occurrences.

The most simple of SDM algorithms is bioclimatic envelope modelling (BIOCLIM). BIOCLIM is a presence-only approach to SDMs that calculates bounding boxes around minimum and maximum values of environmental variables where a species occurs. Although its simplicity makes results easy to interpret, BIOCLIM is prone to overfitting with limited ability to address this (ie, clipping envelopes by standard deviations) which leads to over-predictions.

Common regression-based methods are generalised linear models (GLMs) and generalised additive models (GAMs), as well as the less common multivariate adaptive regression splines (MARS). GLMs are commonly binomial, linear, logistic or Poisson regression, enabling the modelling of presence-absence and count/density species data (McCullagh and Nelder, 1989). GLMs are capable of modelling simple non-linear (e.g. polynomial) species-environmental relationships and interactions between explanatory variables. GAMs are a non-parametric extension of GLMs that use smoothing functions (Hastie and Tibshirani, 1986). This allows GAMs to fit more complex, multi-modal species-environmental relationships making them more powerful than GLMs, but require more computational power. However, both GAMs and GLMs require a robust model

selection process to identify and remove non-significant and correlated explanatory variables.

Widely used machine-learning modelling methods include maximum entropy (MaxEnt), classification and regression trees (CART), boosted regression trees (BRT), and random forest (RF). MaxEnt, the most popular SDM method (Li and Wang, 2013), is a presence-background point modelling method so is useful when true-absences are not available. MaxEnt predicts the suitability of an area by calculating the largest spread (maximum entropy) of presences in geographical space in relation to the background environmental data points (Phillips et al., 2004). MaxEnt accommodates six different feature types, which allows different response curves to be fitted: linear, product, quadratic, hinge, threshold and categorical. Overfitting can be avoided by utilising the regularisation parameters and when carefully calibrated, MaxEnt can show good predictive performance (Duan et al., 2014). CARTs is a method of supervised machine-learning that uses a single decision tree and is grown by the recursive binary splitting of the dataset into increasingly smaller, homogenous groups until a classification is made (Breiman et al., 1984). Despite being easy to interpret, CARTs can be unstable, have poor predictive accuracy and require "pruning" (reduction of splits) to avoid overfitting (Ying, 2019). As a result, more complex decision tree-based models have been developed – BRT and RF. Both BRT and RF, unlike CARTs, build multiple decision trees on subsets of data, which are then ensembled using majority voting rules that in turn improve model accuracy. The difference between BRT and RF is the methods of ensemble. RF uses a "bagging" method in which the subsampled data being used to train every tree has an equal probability of being re-selected in another sub-sample in a subsequent tree (Breiman, 2001). BRT uses a "boosting" method in which weights subset data by their performance in a previous decision tree, meaning poorly fitted data is more likely to be re-selected (Friedman et al., 2000; Schapire, 2003), such as outliers. As a result of its weighted nature, subsequent

trees try to continually improve model accuracy. The ensemble approach of BRT and RF results in accurate models that can work on large datasets and are robust to outliers. However, these methods are computationally demanding and both require true-absence data.

1.2.2 Model Ensembles

There is no "silver bullet" SDM algorithm which consistently outperforms all others (Qiao et al., 2015). As a result, the modelling community is moving towards an ensemble-modelling approach. Ensemble models are where multiple SDM outputs are combined through different statistical means to increase model accuracies and decrease uncertainty. The most commonly used approach of an ensemble in SDMs is by the weighted averages of individual models. Predictions can be weighted by various metrics, such as the area under the receiver-operated characteristic curve (AUC) for presence-absence models (Oppel et al., 2012; Valle et al., 2013; Anderson et al., 2016; Georgian et al., 2019), or correlation between predicted and observed (R^2) values for abundance models (Rowden et al., 2017). These methodologies work by weighting predictions in favour of better performing models. Where individual models show similar performance, and therefore similar weightings, ensemble approaches still improve model accuracy and reduce model uncertainty (Rowden et al., 2017). This is critical for end-users, such as conservation managers, if they are to have confidence in SDM outputs and integrate them into the decision making process.

The move towards ensemble SDMs has seen the development of two R packages – 'SSDM' and 'biomod2' (Table 1.1) – focused on ensemble modelling. Each package is designed to make ensemble modelling as accessible as possible, in particular 'SSDM', which can run entirely as a GUI. Each package is capable of ensembling multiple model

algorithms through many different methods, as well as evaluating and visualising model outputs. Both packages are also capable of running model-forecasting (transfers).

Table 1.1. Ensemble SDM packages available in R Studio, the algorithms they implement and methods of ensemble available.

Package	Algorithms	Ensemble Methods	Reference
SSDM	GAM, GLM, MARS, CTA, GBM, MaxEnt, AAN, RF, SVM	Simple average, Weighted average (metrics can be user-defined).	(Schmitt et al., 2017)
biomod2	GAM, GLM, MARS, CTA, GBM, MaxEnt, AAN, RF, SRE, FDA.	Mean or median of probability, Confidence intervals, Weighted mean, Committee averaging.	(Thuiller et al., 2009)

1.3 The Application of PHMs to the Deep-Sea Environment

The fitting of a HSM helps to identify important environmental drivers of a species or biotope, as well as predict their distribution and extents. In the deep sea, this is a particularly powerful tool where, for the most part, there are still wide knowledge gaps around the most basic ecological questions: Where do they occur, and what drivers those distributions? The implementation of HSMs has helped to conceptualise typical niches that some deep-sea species and community assemblages occupy. For example, SDMs have helped identify different drivers of the reef-forming cold-water coral species *Desmophyllum pertusum* (previous known as *Lophelia pertusa*) such as temperature, substrate type, local hydrodynamics and topographical features at varying scales (Ross and Howell, 2013; Georgian et al., 2014; Rengstorf et al., 2014; Ross et al., 2015).

PHMs have the powerful ability to take point observations and make full coverage predictions of species and habitat distributions. The ability to map and sample all parts of the seafloor with current technology is logistically challenging and financially unrealistic at regional scales, let alone at a basin-wide scale. Creating these full coverage maps from

existing data is relatively inexpensive, yet provide a baseline of data in the deep sea. These maps can be utilised in several ways, from simply identifying areas for scientific exploration and data collection, to informing marine spatial planning and conservation efforts.

Biological maps of the seafloor are important tools when managing human activity in the deep sea and as a result, PHMs have started to feed into the conservation of deep-sea fisheries and vulnerable marine ecosystems (VMEs). In deep-sea fisheries, PHMs have helped to identify key areas of suitable habitat for commercial important deep-sea fishes, as well as assess the extent of suitable habitat and the effectiveness of existing conservation measures. Parra et al. (2017) identified that despite the extensive expanse of the Azores EEZ, the suitability of eight commercially important species is very patchy and is restricted to seamount slopes and summits, offshore banks and island slopes. Further assessments of these distributions show that despite current bottom trawling restrictions protecting the majority of suitable areas for all species (89%+), all predicted suitable areas have some level of exploitation from other methods, such as bottom longlines. Rowden et al. (2017) predicted the suitable habitat of three deep-sea snapper species across the EEZ of 32 Island Nations in the Western Central Pacific. These PHMs highlighted the need for a more collaborative approach in managing these fish stocks across administrative boundaries and provided a baseline of data to aid the establishment of a long-term monitoring project.

Similarly, PHMs have been used to make assessments about the distribution and extent of VMEs, as well as the effectiveness of conservation measures. These have typically taken the form of,

1. Highlighting areas predicted as hotspots of density and biodiversity (Gonzalez-Mirelis and Buhl-Mortensen, 2015; Rowden et al., 2017; Burgos et al., 2020) and

those at risk to potential human activity such as mining (Ramiro-Sánchez et al., 2019).

2. Assessing the extent of predicted habitat covered by marine protected area (MPA) networks within National EEZs and areas beyond national jurisdictions (ABNJ) (Ross et al., 2015; Howell et al., 2016a).
3. Identifying species or biotopes more sensitive to disturbance, such as trawling (Lauria et al., 2017).

Despite an ever-progressing implementation of PHMs in the deep sea, the number of habitats successfully modelled and mapped remain limited to a select group of taxa, namely: Reef-building coral such as *Lophelia pertusa* (Ross et al., 2015; De Clippele et al., 2017) and *Solenosmilia variabilis* (Rowden et al., 2017), aggregating sponges such as *Pheronema carpenteri* (Ross et al., 2015), *Poliopogon amadou* (Ramiro-Sánchez et al., 2019), Ostur (Howell et al., 2016a) and to an even lesser extent, sea pen fields (Lauria et al., 2017). This is due to an overall lack of presence, absence or abundance data as a result of the historic under-sampling of the deep-sea when compared to shallow water and terrestrial settings. However, where extensive seabed mapping projects exist, successful attempts of modelling and mapping a broad range of deep-sea biotopes have been achieved. Buhl-Mortensen et al. (2020) created full coverage maps of predicted suitable habitats for 27 different biotopes, 10 of which were characterised by VME indicator species. This was achieved by the collection of a vast amount of seabed and environment data (752 sampling stations), coordinated through the long-term Norwegian seabed mapping program, MAREANO. These biotopes comprise a wide range, including: basket star aggregations, Iceland scallop aggregations, *Psolus* (holothurian) and cauliflower corals, tube anemones, *Reteporella* bryozoans, a number of aggregating sea pen species, as well as the typically modelled aggregating sponges. This research highlights the power of effective long-term sampling programs to generate vast amounts of data across

multiple disciplines, and the informative tools and products that can be produced for the purpose marine spatial planning when such data is available.

1.4 Concluding Remarks

After reviewing the literature, there is a clear body of evidence suggesting that robust, accurate PHMs can be achieved through careful data preparation, pre-selection of variables and ensemble modelling methods. When carefully communicated, the end products of HSMs, such as full coverage biotope maps, can be used as legitimate tools in marine spatial planning and integrated into policymaking. The provision to include predictions of VME is already built into some existing policy frameworks – e.g. The European Commission in legislative Acts (Regulation (EU) 2016/2336) refer to where "VMEs are known to occur, or are likely to occur" when discussing measures aiming to minimise the impact of fishing activities and encounters with deep-water VMEs.

There are also clear gaps in research surrounding the implementation of PHMs in the deep-sea, all borne out of a lack of biological and environmental data, such as high-resolution bathymetric data. To overcome these challenges of the under-sampling of the deep-sea, investment in long-term seabed mapping and monitoring programs (ie, MAREANO), as well as coordinated and collaborative efforts between nations to collect biological and bathymetric data is required. The UN Decade of Ocean Science (Howell et al., 2020b, 2020a) and the Nippon Foundation-GEBCO Seabed 2030 Project are two opportunities that set the foundations for the vast acquisition of biological and bathymetric data over the next 10 years. The increase in the availability of biological occurrence data should allow for the broadening of different habitats that can be successfully mapped and modelled using PHMs.

Chapter 2: Mapping the Distribution of Vulnerable Marine Ecosystems across the UK and Ireland

2.1 Introduction

2.1.1 Marine Habitat Classification: UK, Ireland and wider NE Atlantic

Successful Marine Spatial Planning (MSP) is underpinned by an understanding of the distribution of the species and habitats in the area of interest, i.e. maps, whether that be at a highly localised, regional or basin-wide scale. This has posed the problem, particularly in the instance of habitats, of defining and classifying biological assemblages into feasibly map-able units. This has resulted in the development of marine habitat classification systems, primarily taking a hierarchical approach. Historically, fine-scale marine habitat classifications have focused on coastal regions, negating deep-sea habitat in national waters and across the area beyond national jurisdiction (ABNJ). However, more recently, fine-scale deep-sea habitat classifications have been devised.

Across Europe, the primary regional classification system that has been developed is the European Union Nature Information System (EUNIS) habitat classification. The aim of this was to provide a hierarchal reference system of common habitats across Europe and provide a mechanism for newly collected habitat data to be consistently analysed, assigned and reported in a standardised manner. Despite having a marine section, the original EUNIS habitat classification carried flaws, particularly for biological communities below 200 m as discussed by Howell (2010), having largely been based upon the Marine Habitat Classification for Britain and Ireland (Connor et al., 2004), the JNCC Classification – a collaborative effort between experts and the Joint Nature Conservation Committee (JNCC). The JNCC Classification was later revised in 2015 with the addition of the deep sea section (Parry et al., 2015) which was a significant development. The updated deep sea section, based largely upon Howell (2010), consists of five renewed levels,

- Level 1, Environment – Inferred from the distance from the high water mark. Either marine, coastal or terrestrial.
- Level 2, Biological Zone – A combination of vertical biological zonation and biogeographic region, based upon water mass properties, e.g. depth, salinity, temperature, etc.
- Level 3, Substratum – Type of substratum is taken from EUNIS level 3, with the addition of biogenic substratum, i.e. cold-water coral reef.
- Level 4, Broad Community (Biotope complex) – Based on the taxa present.
- Level 5, Biological Community (Biotope) – Species-specific assemblages.

This differs from the original EUNIS habitat classification because it incorporates biogeographic regions and vertical zones, whilst removing topographical features. This new classification also translated directly into existing listed EUNIS habitats, and broadly into existing Marine Strategy Framework Directive (MSFD) habitats. Since its publication, the JNCC Classification with updated deep sea section has been incorporated into revised versions of the EUNIS habitat classification; a system now used by deep sea researchers, managers, advisory bodies and Governments across Europe, and a model system globally.

2.1.2 Vulnerable Marine Ecosystems

Many of the Level 4 and 5 habitats within the JNCC Classification can also be classified as Vulnerable Marine Ecosystems (VMEs). Conceptually, VMEs emerged following discussions in 2006 amongst the United Nations General Assembly (UNGA), Resolution 61/105, to be used in the context of fisheries management (UNGA, 2006). VMEs are defined as groups of species, biological communities or habitats that are physically and/or functionally vulnerable to significant adverse impacts from fishing activity. Consequently, the UN's Food and Agricultural Organization (FAO) have since developed

the VME concept and embedded it within deep-sea fisheries management across ABNJ. The FAO, through the International Guidelines for the Management of Deep-Sea Fisheries in the High Seas (FAO, 2009), has defined a list of characteristics that are used as criteria to aid the identification of VMEs. Those criteria are (1) uniqueness or rarity, (2) functional significance of the habitat, (3) fragility, (4) life-history traits of component species that make recovery difficult and (5) structural complexity. As a result, regional fisheries management organisations (RFMOs) have defined their regional-specific lists of VME Habitats and indicators for integration within their regional management plans. The North-East Atlantic Fisheries Commission (NEAFC), an RFMO, following advice from the International Council of the Exploration of the Sea (ICES), have devised a list of VME Habitats distributed across the NE Atlantic, and a list of VME indicator taxa. This list of VME Habitats occurring across the NE Atlantic also directly translate into level 4 biotope complexes or level 5 biotopes defined and described under the JNCC Marine Habitat Classification.

2.1.3 Marine Conservation Legislation Applicable to the UK and Ireland

UNGA Resolution 61/105 (UNGA, 2006) and Regulation European Union (EU) 2016/2336 (European Commission, 2016) require RFMOs, and EU member states including Ireland, and also the UK to prevent significant adverse impacts on VMEs from deep-sea bottom-fishing activity where VMEs occur or are *likely* to occur. In addition, the EU Habitat Directive (92/43/EEC; European Commission, 1992) requires EU Member states and the UK to designate special areas of conservation to protect listed habitats and species, contributing to the EU-wide protected area network (Natura 2000) and achieving "favourable conservation status". Included within this legislation are numerous deep-sea habitats and species. The UK also has its domestic legislation that affords potential protection to deep-sea habitats and species – the UK Marine and Coastal Access Act, 2009 (DEFRA, 2009) – and enables the designation of Marine Conservation

Zones. This legislation also provides the statutory instruments required to fulfil the UK's obligations as signatories of the Convention on Biological Diversity (UN, 1992) and the OSPAR Convention (OSPAR, 1998).

In Ireland, there is currently very limited domestic legislation relating to marine conservation; with the Wildlife Acts providing no protection beyond 12 nautical miles. As a result, the only statutory instruments available to Irish policymakers for establishing deep-sea marine protected areas (MPAs) comes from the EU Habitats Directive and the OSPAR Convention. In their report to the Irish Government, the Marine Protected Area Advisory Group state "habitats and species that are not listed in the EU Directives, but which may be locally, nationally or internationally important, cannot currently be afforded the necessary protection" (Marine Protected Area Advisory Group, 2020). To address such issues, the Irish Government have since announced that, in due course, they will publish an MPA Regime, a Marine Spatial Plan and the accompanying Marine Planning and Development Management Bill. Claiming this will provide the necessary legislation to expand Ireland's MPA network to 30% of its entire EEZ by 2030.

2.1.4 Deep-Sea Habitat Mapping: UK and Ireland

As a result of the obligations under the legislation set out in the previous section, and in combination with a clear, deep sea habitat classification system, momentum has shifted to mapping deep sea VME across the UK and Ireland. Despite this area being one of the areas most understood and sampled globally (Menegotto and Rangel, 2018), there is still a lack of distribution data. Predictive habitat models (PHMs) are a tool that can provide full coverage of spatial data in the absence of observations. Across the UK and Ireland, two approaches have been used in mapping VME distributions using PHMs; the first models the distribution of the species that are indicative of the wider habitat, e.g. VME indicators, the second models the distribution of the habitat or specific assemblages of

species e.g. the VME. In the first instance, models have been limited to the reef-building scleractinian species *Desmophyllum pertusum*, *Solenosmilia variabilis* and *Madrepora oculata* (Robert et al., 2015; De Clippele et al., 2017; Pearman et al., 2020), and aggregating seapen species *Funiculina quadrangularis*, *Virgularia mirabilis* and *Pennatula phosphorea* (Greathead et al., 2014). Models of habitat distribution across the UK and Ireland have encompassed *D. pertusum* reef, *Pheronema carpenteri* aggregations, Stylasterids and lobose sponges, Xenophyophore fields, and the species-specific *Syringammina fragilissima* (xenophyophore) aggregations (Rengstorf et al., 2013; Ross and Howell, 2013; Piechaud et al., 2014; Ross et al., 2015; Howell et al., 2016a). Where both approaches have been used across the UK and Ireland, results suggest that predicted habitat distribution is a highly restricted subset of predicted species distribution, and, where possible, mapping efforts should focus on habitat rather than species at fine (<100 m) scales (Howell et al., 2011).

2.1.5 Aims

Building on preliminary models assessing the extent and distribution of *D. pertusum* reef and *P. carpenteri* in the UK and Irish waters (Ross et al., 2015; Howell et al., in review), this study will extend mapping efforts to more habitats by using existing datasets to 1) model the extent of selected VME across the UK and Irish waters using an ensemble approach, 2) evaluate the resulting models, and 3) demonstrate the potential use of those model outputs in informing spatial management of the study area.

2.2 Methods

2.2.1 Study Area

The study area considers a partial extent of the UK and the entire extent of the Irish extended continental shelf claim areas (Figure 2.1). This area encompasses topographical

features such as the continental shelf, continental slope, canyon networks, and seamounts. (Figure 2.1).

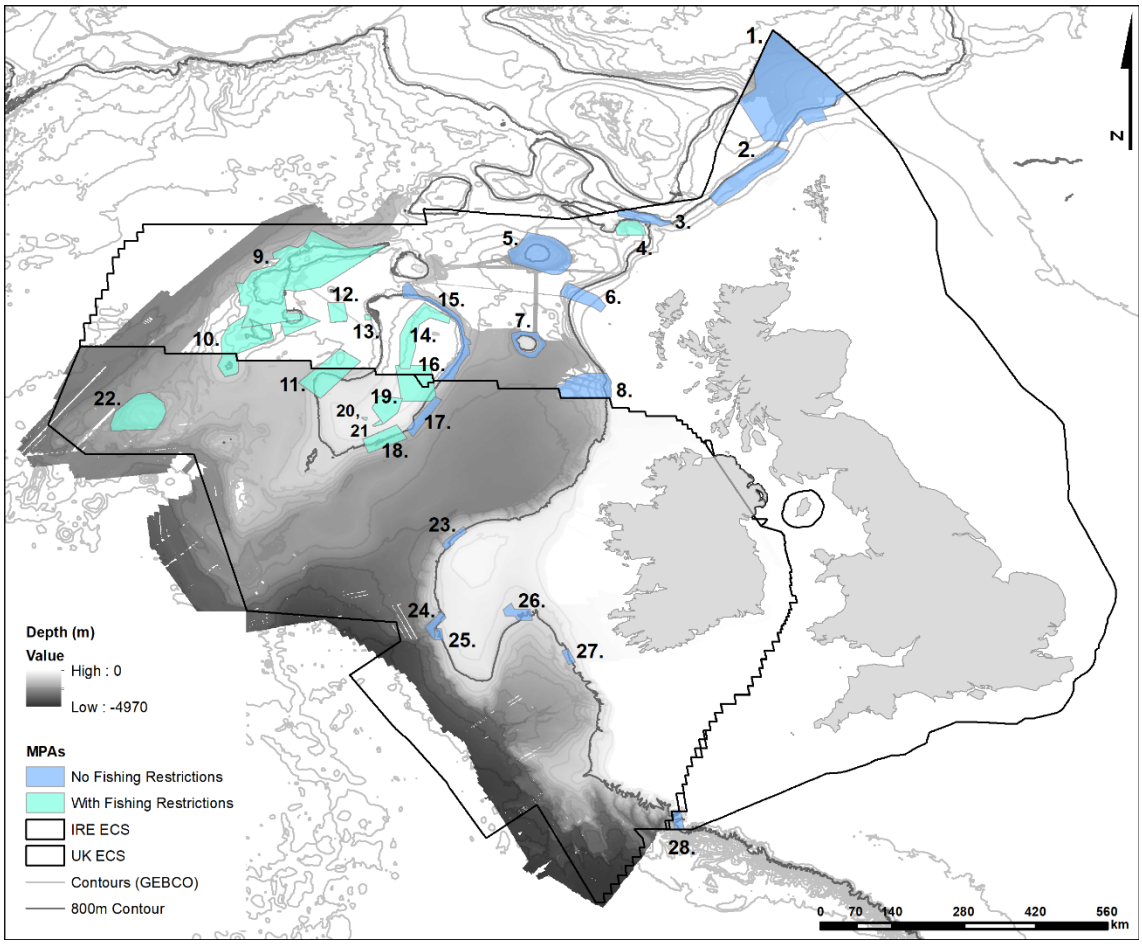

Figure 2.1. The study area including the model's extent (indicated by shaded bathymetry), 800 m trawl-ban (800 m contour) and MPA network. The following MPAs are found within the study area: 1. North-East Faroe-Shetland Channel, 2. Faroe-Shetland Sponge Belt, 3. Wyvile Thompson Ridge, 4. Darwin Mounds, 5. Rosemary Bank Seamount, 6. Geikie Slide and Hebridean Slope, 7. Anton Dohrn Seamount, 8. The Barra Fan and Hebrides Terrace Seamount, 9. Hatton Bank, 10. Hatton Bank 2, 11. West Rockall, 12. Hatton-Rockall Basin, 13. Hatton-Rockall Basin Area 1, 14. North-West Rockall Bank, 15. East Rockall Bank, 16. Haddock Box, 17. South East Rockall Bank, 18. Logachev Mounds, 19. South West Rockall, 20. South West Rockall Bank Area 1, 21. South West Rockall Bank Area 2, 22. Edora Bank, 23. North-West Porcupine Bank, 24. Porcupine Bank Canyon, 25. South-West Porcupine Bank, 26. Hovland Mound Province, 27. Belgica Mound Province, 28. The Canyons. Bathymetric contours are provided by GEBCO, starting at 250 m then every 250 m until 2000 m, then every 500 m from therein. ECS = Extended continental shelf.

Within the study area, several types of MPA are designated; Special Areas of Conservations (SACs), Marine Conservation Zones (MCZs), Nature Conservation MPAs (NCMPAs), and North-East Atlantic Fisheries Commission (NEAFC) bottom trawl

closures – all with different (or no) management measures in place. Many of these MPAs also contribute to the wider OSPAR MPA network. In addition to the MPA network, Part 5, Chapter 7 of the European Union's Common Fisheries Policy and Aquaculture Statutory Instrument (2019, No. 753) state that *"no fishing authorisation shall be issued for the purpose of fishing with bottom trawls at a depth below 800 metres"* throughout the EU and UK EEZ, and therefore applies to the study area. Additionally, the statutory instrument also implements restrictions on fishing between 400-800 m where VMEs occur or are likely to occur. These measures aim to minimise the effects of fishing activities on VMEs.

2.2.2 Environmental Data

Available high-resolution bathymetry data (≤ 200 x 200m grid cell size) from across the study area were collated (see Appendix 1 for sources). Any bathymetry of a resolution finer than 200 m was resampled by cubic convolution to 200 x 200 m resolution using the 'Resample' tool in ArcMap (version 10.7). All bathymetric data were then re-projected from their original projection into Goode Homolosine Ocean (equal-area) and finally merged into one continuous bathymetry raster in ArcMap. Using the Benthic Terrain Modeller 3.0 (Walbridge et al., 2018) add-on application in ArcMap, the following bathymetry-derived variables were calculated at 200x200m resolution: broad-scale bathymetric position index (BBPI), fine-scale bathymetric position index (FBPI), terrain ruggedness (rugosity), slope, curvature (slope of slope), profile curvature and planar curvature. These bathymetrically derived variables have been used widely in previous deep-sea modelling studies – such as Ross & Howell 2013, Ross et al. 2015, Rooper et al. 2017 and Ramiro-Sánchez et al. 2019 – and have produced good results.

Bathymetric position index (BPI) is an indicator of the height of the seabed at a given point compared to the surrounding area and is calculated using a neighbourhood analysis.

A value between -1 and 1 is returned; positive values indicate that a point is higher than its surroundings (e.g. a hill), negative values indicate that a point is lower than its surroundings (e.g. a valley), and a value near zero indicates flat seabed. In this study, BPI was calculated at two different spatial scales to capture bathymetric features of different scales. Inner and outer radiuses (cells) used to calculate BBPI and FBPI were 1/10 and 1/3 respectively. 1/10 was selected to identify broader-scale (2km) seabed features such as canyons, with 1/3 selected to identify finer-scale (<1km) features such as gullies. Rugosity is the ratio of seabed surface area to planar area – or, seabed complexity / 'ruggedness' – where the higher the rugosity value, the more complex the seabed surface. The slope is the seabed angle in degrees, and curvature is calculated as the 'slope of slope'. Profile and planar curvature determine the shape of the sloping seabed; positive values indicate a convex slope, whilst negative values indicate a concave slope. Planar curvature is calculated on the y-axis, whilst profile curvature is calculated on the x and y-axis.

Generalised Additive Models (GAMs) were used to build a bottom temperature layer using in-situ CTD data from ROV and drop camera transects, as well as archived CTD casts from the British Oceanographic Data Centre (BODC) database. GAMs were implemented in R (R Core Team 2020) using the 'mcgv' package with depth, latitude, and longitude used as explanatory variables. A detailed description is given in Appendix 2.

2.2.3 VME Data

Presence-pseudo-absence VME data were obtained by collating historical video transect data from multiple research cruises that has already been classified into biotope / biotope complex types following the deep-sea section of the JNCC Classification (Parry et al.,

2015; Table 2.1). In total, there were 373 transects of varying lengths, from 100m to 3.1 km (Figure 2.2).

Table 2.1. Video transects data sources by year, data collection type, regions sampled and cruise reference.

Dataset	Year of Collection	Data Collection	Areas Covered	Reference
FRS/JNCC/UoP	2005	Drop Frame & Sledge Camera Systems	Rockall Bank, Continental Slope	(Narayanaswamy et al., 2006; Howell et al., 2009)
SEA7 (Partial)	2005	Drop Frame	Rockall Bank	Howell et al., 2009
SEA7-SAC	2006	Drop Frame	Hatton Bank, Rosemary Bank, Wyville Thomson Ridge, Faroe Shetland Channel, Polygonal Faults	(Howell et al., 2007)
MESH	2007	Drop Frame	South West Canyons	(Davies et al., 2008)
JNCC AD-ER	2009	Towed Camera	Anton Dohrn Seamount, Rockall Bank	(Stewart et al., 2009)
JC60	2011	ROV	Darwin Mounds, Polygonal Faults, Rockall Bank	(Howell et al., 2014)
DeepMap (CE15011)	2015	ROV	Porcupine Seabight, Hatton-Rockall Basin	(Howell et al., 2015)
DeepLinks (JC136)	2016	ROV	Rockall Bank, George Bligh Bank, Anton Dohrn Seamount, Wyville-Thomson Ridge, Rosemary Bank	Howell et al. (2016)
SeaRover (RH17001 RH18002 CE19015)	2017 2018 2019	ROV	Porcupine Bank, Rockall Bank, Porcupine Seabight, Goban Spur, Southwest Approaches	(O'Sullivan et al., 2017, 2018, 2019)

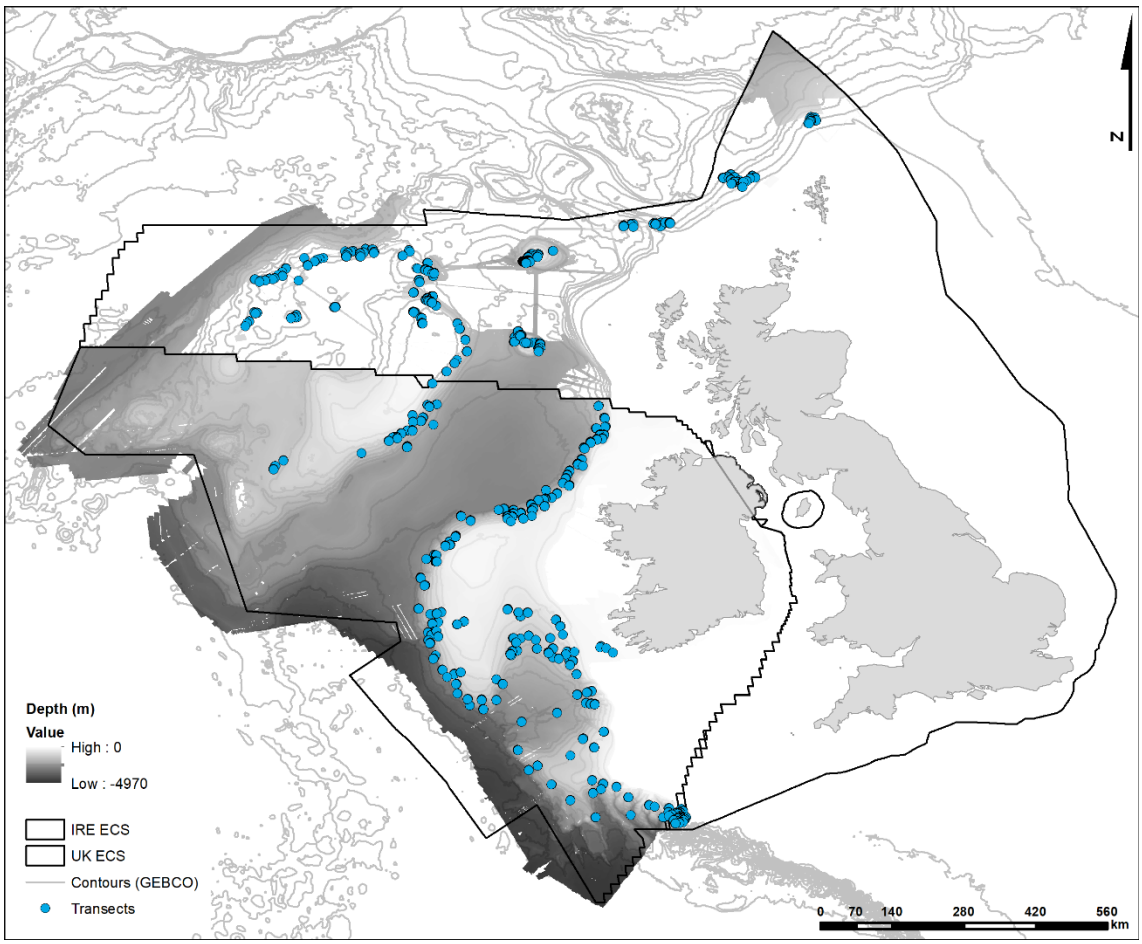

Figure 2.2. Distribution of transects (blue) across the study area.

Classification of image-based data into biotopes / biotope complex was achieved in two ways. For datasets up to and including 2009 quantitative analysis of image 'samples' followed by multivariate analysis were used to define deep-sea biotopes that were later incorporated into the Parry et al. (2015) (see Howell et al., 2010), these analyses were used to inform classification of the corresponding video datasets from which image samples were taken. For all subsequent datasets, expert opinion only was used to classify video datasets based on biotope / biotope complex definitions provided in Parry et al. (2015). For all video data, transects were reviewed at least twice and conducted by stopping and starting to ensure that all biotopes and boundaries between were captured and logged. Four annotators undertook this classification exercise. The presence of any biotope / biotope complex was confirmed by at least two experts and designated when the

extent satisfied the OSPAR minimum biotope area threshold (25 m^2). For quality assurance, 5% of all transects were independently analysed by another experienced researcher following inter-observer agreement standards used in published evidence (MacLeod et al., 2010).

From the video analysis, seven of the 34 biotopes / biotope complexes identified during analysis were determined as vulnerable marine ecosystems (VMEs) with sufficient data to model their distribution – these VMEs were selected for use in this study (Figure 2.3). The presence-pseudo-absence datasets generated through video analysis were plotted in ArcMap as USBL-derived camera position points for each of the selected VMEs. Each VME dataset was then reduced to one-point-per-cell, where each point's value was either 0 (pseudo-absence) or 1 (presence) for each 200 x 200 m cell (Table 2.2). Absences were considered 'pseudo-absences' because of uncertainty and therefore unable to be considered 'true-absences'. Absences are not 'true absences' because only a small proportion of each 200 x 200 m cell has been sampled (e.g. ROV transect) – not each entire cell. Therefore, it cannot be said with complete certainty that each 200 x 200 m cell is truly absent of a given biotope.

In ArcMap, environmental data were extracted for each presence-pseudo-absence point for each VME dataset. Thus, creating seven final presence- pseudo-absence datasets with corresponding environmental variables for statistical analysis.

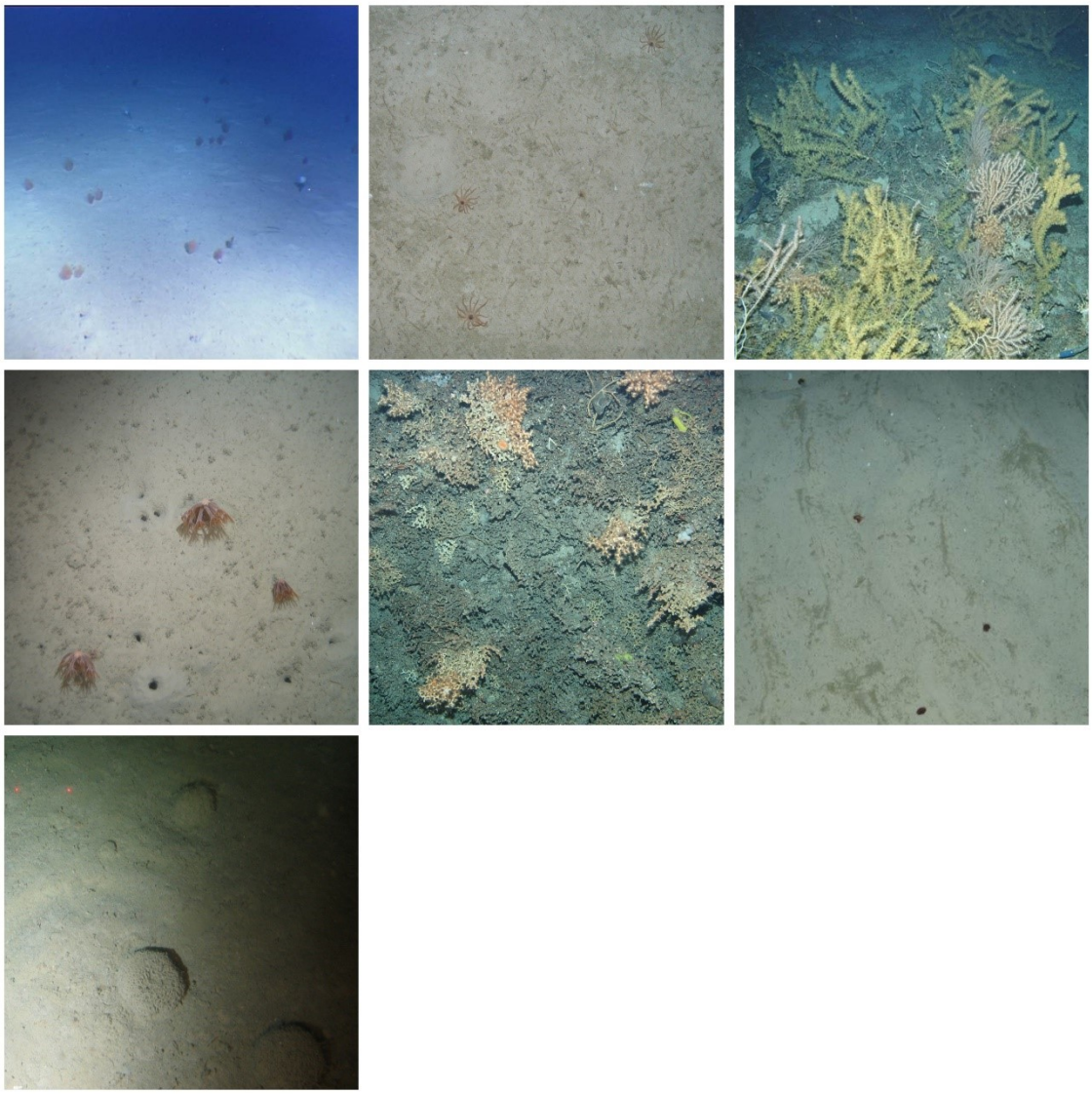

Figure 2.3. Representative images obtained from transect data of the VMEs selected for modelling, including Acanella arbuscula assemblages (top left), burrowing anemone fields (top center), mixed cold-water coral community (top right), Seapens and burrowing megafauna (middle left), Solenosmilia variabilis reef (middle center), solitary sclearactinian fields (middle right), and Syringammina fragilissima fields (bottom left).

Table 2.2. The number of presence and pseudo-absence one-point-per-cell points per VME at 200 x 200 m resolution. The total number of points in each dataset was 3,036.

VME	Classification Code	Classification Level	Presence Points	Absence Points
Acanella arbuscula assemblage	AcaArb	5	30	3,006
Burrowing anemone fields	BurAne	4	70	2,966
Mixed cold-water coral community (Coral Garden)	MixCor	4	251	2,785
Sea pens and burrowing megafauna	SpnMeg	4	94	2,942
Solenosmilia variabilis reef	SolRee	5	80	2,956
Solitary Scleractinian fields	SolScl	4	58	2,978
Syringammina fragilissima fields	SyrFra	5	251	2,785

2.2.4 Pre-Selection of Variables and Model Tuning

Pearson's correlation coefficients were calculated between environmental variables using the "cor()" function in the core "stats" package in R, v4.1.0 (R Core Team, 2021) to identify highly correlated variables (≥ ±0.7). Of these highly correlated pairs, the correlate dropped was determined during the pre-selection process for each of the chosen modelling frameworks, as detailed below.

2.2.4.1 MaxEnt

One modelling framework selected for use in this study was the Maximum Entropy (MaxEnt) machine-learning approach (Phillips et al., 2006). MaxEnt, described in Chapter One, was used because of its robust predictive accuracy with small samples sizes (Melo-Merino et al., 2020). In addition, MaxEnt was selected because of its presence-only approach, making MaxEnt more resistant to the effect of false absences caused by

anthropogenic activity (Elith et al., 2011). Variables were selected for each MaxEnt model based upon variable importance, and jackknife and AUC scores; where jackknifing calculates the individual contribution of response variables to the overall model (termed 'gain'), and where AUC (Area Under [the Receiver Operating Characteristic] Curve) is a measure of a model's ability to correctly classify. Firstly, a MaxEnt model was fit using all the environmental variables. Using the model gain scores – both 'without variable' and 'with only variable' scores – the worst-performing correlates were identified and removed from any subsequent MaxEnt analysis. Another MaxEnt model was then built with the remaining variables, and the next poorest performing variable was identified and removed based on jackknife scores. This process continued in a stepwise fashion until the most parsimonious model was reached, with overall model performance inferred from the AUC scores. The final model was then tuned by systematically trialling different model settings. This included feature classes (hinge, linear, product, and quadratic). In all instances linear, product, and quadratic features were applied across all models, with the addition of hinge features for SpnMeg. Various regularisation parameters were also systematically trialled, varying from 0.1 – 5.0. This process of variable selection and model tuning were undertaken for each of the VME in R, using the 'SDMtune' package (Vignali et al., 2020).

2.2.4.2 Random Forest

Random Forest (Breiman, 2001), described in Chapter One, was selected as the second modelling method because of its powerful performance, and ability to fit complex relationships between the response and environmental variables (Valle et al., 2013). Feature selection for Random Forest was carried out by implementing the Boruta algorithm in R with the 'Boruta' package (Kursa and Rudnicki, 2010). The Boruta algorithm helps to identify the most relevant and important variables in a dataset (Kursa and Rudnicki, 2010). Firstly, a Boruta algorithm was fitted with all response variables.

From these results, any variables deemed as unimportant were immediately discarded, along with the least important correlate in any pair of correlated variables. In a similar approach to MaxEnt variable selection, a new Boruta algorithm was fitted with the remaining variables; the least important variable was identified, removed from the analysis, and a new Boruta algorithm fitted. This continued in a stepwise approach until the most parsimonious model was detected, with overall model performance evaluated after each iteration using the out-of-bag (OOB) estimate of error rate. Once the final list of variables had been selected, a Random Forest model was fit and tuned using the 'tuneRF' function from the 'randomForest' package (Liaw and Wiener, 2002) in R. This process of tuning determined the optimal mtry value (number of variables randomly sampled as candidates at each split) concerning the OOB estimate of error.

2.2.5 Modelling

Once the variables for each modelling method and VME had been determined, habitat suitability models were constructed using the 'biomod2' package (Thuiller et al., 2009) in R. The 'biomod2' package is designed for ecologists to run individual habitat suitability modelling algorithms, and ensemble them together.

The model parameters applied to each algorithm and VME were those selected in the previous model-tuning step. For Random Forest models, the number of trees grown (ntree) for each model was set to 500. For MaxEnt models, *randomly* selected 'background points' were not used. Instead, using the 'samples-with-data approach', the locations of pseudo-absence points for each VME were used as 'background points'. Although not a common approach, this has been used in previous studies (Ross et al. 2015, Howell et al. *In-Press*) as it allows some control over the biases in sampling locations and thus improves model predictive performance. This methodology of implementing MaxEnt has been proved to be robust when tested with independent

validation datasets by Howell et al. (*In-press*) who tested four published deep-sea SDMs (Ross & Howell 2013, Ross et al. 2015). One criticism of this approach is that background points may not accurately characterise the available environmental conditions and that the environmental envelope encompassed by the background points may not also encompass the environmental envelope encompassed by presence points. Simple plots of VME presence-pseudo-absence against environmental variables indicated that the background points did characterise the environmental conditions of both presence points and the wider study area. This is likely because of the large amount of pseudo-absence data available (~2,800-3,000 points) across a vast area. An example of these plots for SolScl is provided in Appendix 3.

The 'full' MaxEnt and Random Forest model for each VME was then used to make spatial predictions across the study area at 200 x 200 m resolution and masked for novel climates.

2.2.6 Model Evaluation

To evaluate model performance, an additional 10 models for each algorithm were run. For each evaluation model run, the VME presence-absence datasets were partitioned into training (70%) and test (30%) datasets. The train-test datasets were compiled manually, rather than using the automatic evaluation run feature in 'biomod2'. This ensured that the prevalence (% of presence points in the dataset) in each train-test dataset remained > ±1% of that in the full presence-absence dataset for each VME. Additionally, spatial autocorrelation could be accounted for, avoiding a scenario where a transect would be split into training and testing points, leading to a within-transect testing point validating the same transect (Ross et al., 2015).

For each VME, 22 models were run in total: One MaxEnt and one Random Forest built with their full presence-absence dataset (full independent models), and 10 evaluation

MaxEnt and 10 evaluation Random Forest models built with the 70/30 split training-test datasets.

All models were evaluated using threshold-independent and -dependent techniques in R using the 'PresenceAbsence' (Freeman and Moisen, 2008) and 'biomod2' package. The presence.absence.accuracy() function from the 'PresenceAbsence' package was used to calculate model AUC scores (threshold-independent), as well as sensitivity, specificity, percent correctly classified (PCC) across three different thresholding methods. The three thresholding methods used were,

1. 'Sens=Spec' where the threshold selected yields equal sensitivity and specificity scores.
2. 'MaxSens=Spec' where the threshold applied maximises the sensitivity and specificity scores, minimising the mean of error rate.
3. 'MinROCdist' minimises the distance between the ROC (Receiver Operating Characteristic) plot and the upper left corner of the unit square.

Both threshold-independent and -dependent metrics were calculated across all models, including the 10 evaluation models, for each VME, allowing a mean and standard deviation to be calculated. When choosing the final threshold to create binary maps of predicted habitat distribution, all performance metrics were considered. However, because the primary purpose of these maps is to identify the areas of the seafloor where these VMEs *occur*, the effect of thresholding methods on sensitivity scores was given considerable consideration.

Additionally, the true skill statistic (TSS) was calculated for each model within 'biomod2' using the get_evaluations() function, where TSS = the true positive rate + the true negative rate – 1. This is a common metric used across modelling studies (Rooper et al. 2018, Ramiro-Sánchez et al. 2019) because it is independent of prevalence and therefore

favoured over some other metrics, such as Kappa (Allouche et al. 2006). TSS scores for each model were used to weight models when ensembling by performance.

2.2.7 Model Ensemble and Ensemble Evaluation

For each VME, the full independent models (MaxEnt and Random Forest) were ensembled by the weighted sum of probabilities; probabilities were weighted by the TSS scores calculated in 'biomod2' during the evaluation stage. The 10 train-test runs were also ensembled for evaluation. All ensembled model outputs were evaluated using the same methods and metrics as used to evaluate the independent MaxEnt and Random Forest models in the previous step.

The full ensemble models for each biotope were then used to make spatial predictions across the study area at 200 x 200 m resolution and masked for novel climates. When choosing the final threshold method to create the binary habitat suitability maps, the same considerations were also given when thresholding the independent maps.

2.2.8 Analysis of Model Outputs in the Context of Marine Spatial Planning

A series of analyses were conducted across the final binary model predictions. For each VME, the predicted area (km^2) of suitable habitat for the following were calculated.

1. Within UK and IRE extended shelf claim areas.
2. Within the 2020 MPA network and a breakdown per nation.
3. Below the 800m trawl ban and a breakdown per nation.

This was calculated by masking the binary prediction rasters using the raster package (Hijmans, 2021) in R with the relevant shapefiles, i.e. extended shelf claim areas, MPA network and 800 m contour. The number of 200 x 200 m cells of predicted presence within the target areas were then calculated and converted into km^2.

In addition, an assessment of the extent of predicted suitable habitat potentially impacted by fishing and oil and gas activities was made.

Bottom fishing intensity (surface) data was obtained from the OSPAR Commission for the years 2009-2016. These layers were combined in ArcMap to create a raster of fishing footprint and the total of hours trawled throughout 2009-2016 (Figure 2.4). The native resolution of the fishing intensity data was 0.05 ° (60 °N) which was re-gridded as a 200 x 200 m resolution to align with the model predictions. The area of predicted suitable habitat falling within the fishing footprint was calculated in R. To assess the impact of the EU's 800m bottom trawling ban (2016/2336), introduced in 2016, the area and percentage of predicted suitable habitat within the fishing footprint below 800m was calculated. In addition, the percentage of predicted suitable habitat falling below 800m whether previously fished or not was calculated. Finally, areas of the seafloor below 800m where high levels of trawling activity coincided with predicted habitat suitability were identified as potential regions to monitor recovery from bottom trawling activity.

For oil and gas activities the area of predicted suitable habitat that fell within areas currently licenced for oil and gas exploration were quantified. Up-to-date oil and gas licence shapefile polygons were obtained from EMODnet. Binary predictions were masked with these polygons to calculate the area (km^2) of each VME within licenced blocks.

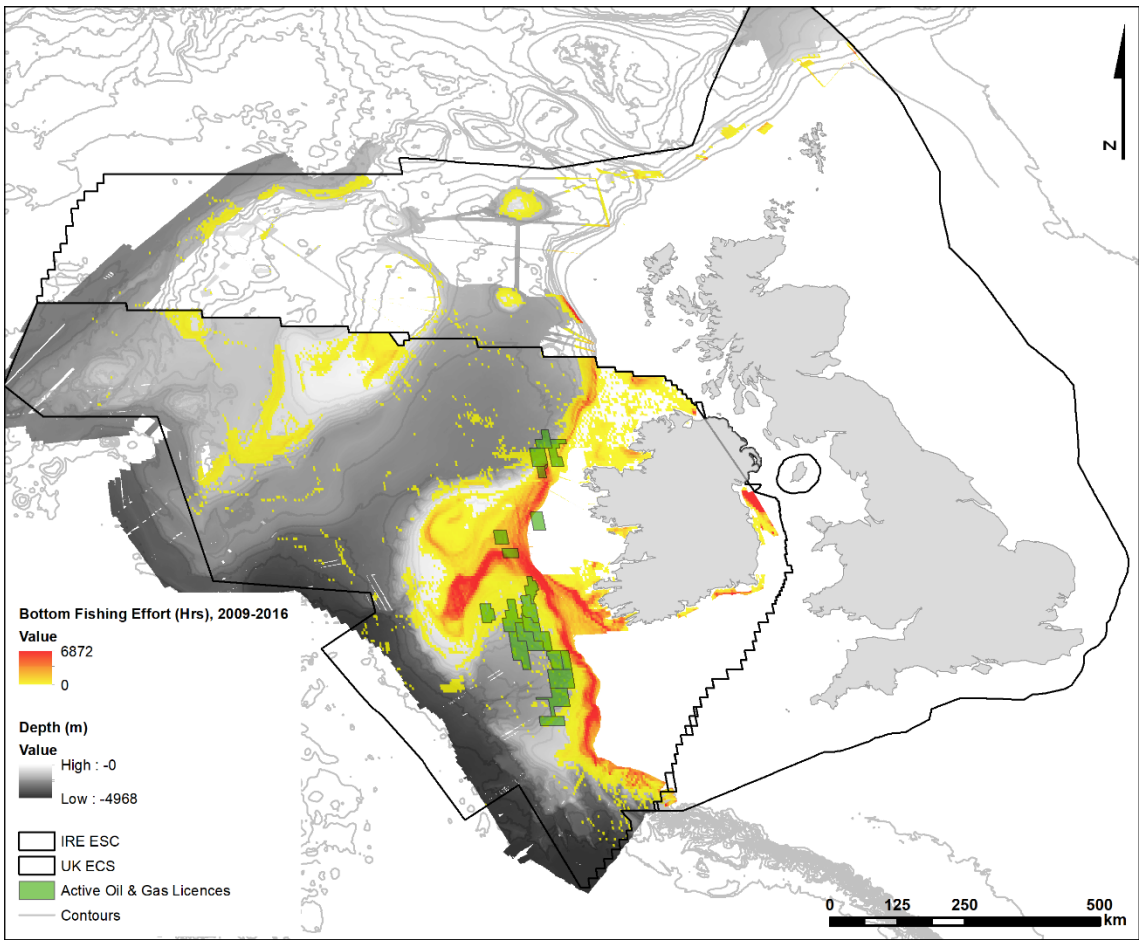

Figure 2.4. Historical bottom fishing footprint (2009 - 2016) and intensity (hours), and active oil and gas licences (green) falling within masked model extents. ECS = Extended continental shelf.

2.3 Results

2.3.1 Pre-Selection of Variables and Model Tuning

Pearsons Correlation

Pearson's correlation coefficient results suggest that within the presence-absence VME dataset, curvature and FBPI, curvature and profile curvature, and curvature and plan curvature are highly correlated (-0.7 < or > 0.7). Which correlate to remove in each correlated pair was determined during the variable selection (next step) for MaxEnt and Random Forest models.

2.3.2 Variable Selection and Model Tuning

Variables selected for MaxEnt and Random Forest models were the same across both modelling frameworks for each VME (Table 2.3); bathymetry, BBPI and temperature were the only variables to be selected across all VME. The Jackknife plots for each final VME model are in Appendix 4. The Boruta plots and OOB estimate of error rate for each final VME model are in Appendix 5.

Table 2.3. Final variable lists and model algorithm parameters selected for each VME; where "mtry" is the number of variables randomly sampled as candidates at each split, and "RP" is "regularisation parameter". Variables included in the models are indicted by Y = yes, N= no.

VME	Variables									Random Forest	MaxEnt
	Bathymetry	BBPI	Curvature	FBPI	Plan Curvature	Profile Curvature	Rugosity	Slope	Temp	mtry	RP
AcaArb	Y	Y	N	N	N	N	Y	Y	Y	4	0.10
BurAne	Y	Y	N	Y	N	N	Y	Y	Y	4	0.50
MixCor	Y	Y	N	N	N	N	Y	Y	Y	2	1.00
SpnMeg	Y	Y	N	Y	N	N	Y	N	Y	5	0.75
SolRee	Y	Y	N	Y	N	N	Y	N	Y	4	0.10
SolScl	Y	Y	N	N	Y	Y	N	Y	Y	4	1.00
SyrFra	Y	Y	N	N	N	N	Y	Y	Y	4	1.00

2.3.3 Model Evaluation – Independent MaxEnt and Random Forest Models

According to the average AUC scores, Random Forest training models across all variables were deemed 'excellent' (0.9-1.0) (Table 2.4). When cross-validated using the test datasets, performance across all metrics dropped for all VME. The best performing Random Forest model was SyrFra – the only VME model to maintain an average

‘excellent’ AUC score (0.9). SolRee, SolScl and SpnMeg AUC test scores dropped to ‘good’ (0.8-0.9), whilst the AUC test scores for AcaArb, BurAne, and MixCor dropped to ‘fair’ (0.7-0.8). The average AUC scores for two MaxEnt training models, SpnMeg and SolScl, were deemed ‘excellent’ (0.9-1.0), and the remaining nine were ‘good’ (0.8-0.9). When cross-validated with the testing datasets, the performance of all MaxEnt VME models was reduced. Average test AUC scores deemed BurAne, MixCor, SolRee, SolScl and SyrFra as ‘good’ (0.8-0.9), whilst AcaArb and SpnMeg were deemed ‘fair’ (0.7-0.8).

Although the full and training Random Forest models consistently perform considerably better than MaxEnt models, when tested through cross-validation, the difference in performance between both methods becomes much narrower. In some instances (BurAne, MixCor and SolScl), MaxEnt models perform better than Random Forest models once tested through cross-validation. This suggests that the Random Forest algorithm has overfitted to the training datasets, whilst MaxEnt is more generalised; thus reinforcing the decision to ensemble these two methods together. Results across all metrics are in Appendix 6.

Table 2.4. Results of full, training and testing models by VME the evaluation metrics sensitivity (sens), specificity (spec) and area under the curve (AUC). The threshold methods selected for each model are denoted as MaxSS (MaxSens=Spec), SS (Sens=Spec) and MinROCd (MinROCdist).

VME	Model	Full			Train (Average)			Test (Average)			Thresholding Method
		Sens	Spec	AUC	Sens	Spec	AUC	Sens	Spec	AUC	
AcaArb	RF	1.00	1.00	1.00	1.00	1.00	1.00	0.56	0.86	0.74	MaxSS
	MaxEnt	1.00	0.64	0.88	0.97	0.68	0.89	0.96	0.62	0.73	MaxSS
	Ensemble	1.00	1.00	1.00	1.00	0.96	0.99	0.95	0.59	0.73	MaxSS
BurAne	RF	1.00	1.00	1.00	1.00	1.00	1.00	0.71	0.85	0.77	MaxSS
	MaxEnt	0.88	0.71	0.88	0.87	0.73	0.88	0.93	0.71	0.84	MaxSS
	Ensemble	1.00	0.99	1.00	0.98	0.93	0.99	0.94	0.74	0.85	MaxSS
MixCor	RF	1.00	1.00	1.00	1.00	1.00	1.00	0.80	0.65	0.77	MaxSS
	MaxEnt	0.72	0.72	0.81	0.73	0.73	0.80	0.72	0.72	0.80	SS
	Ensemble	0.99	0.99	1.00	0.97	0.92	0.99	0.87	0.66	0.81	MaxSS
SpnMeg	RF	1.00	1.00	1.00	1.00	1.00	1.00	0.77	0.91	0.85	MaxSS
	MaxEnt	0.83	0.92	0.94	0.88	0.89	0.94	0.59	0.87	0.77	MaxSS
	Ensemble	1.00	0.96	1.00	0.99	0.97	0.99	0.77	0.87	0.85	MaxSS
SolRee	RF	1.00	1.00	1.00	1.00	1.00	1.00	0.87	0.73	0.86	MaxSS
	MaxEnt	0.83	0.77	0.87	0.84	0.77	0.87	0.82	0.73	0.82	MinROCd
	Ensemble	1.00	0.98	1.00	0.98	0.98	1.00	0.87	0.74	0.86	MinROCd
SolScl	RF	1.00	1.00	1.00	1.00	1.00	1.00	0.77	0.90	0.86	MaxSS
	MaxEnt	0.83	0.89	0.91	0.84	0.88	0.91	0.95	0.85	0.89	MaxSS
	Ensemble	1.00	0.98	1.00	0.97	0.95	0.99	0.95	0.87	0.92	MaxSS
SyrFra	RF	1.00	1.00	1.00	1.00	1.00	1.00	0.91	0.79	0.90	MaxSS
	MaxEnt	0.88	0.69	0.85	0.81	0.74	0.84	0.85	0.79	0.89	MinROCd
	Ensemble	1.00	0.99	1.00	0.96	0.96	0.98	0.96	0.71	0.80	MaxSS

2.3.4 Variable Importance – Independent MaxEnt and Random Forest Models

Common important variables across each of the VME models are depth (bathymetry), temperature, slope and BBPI. Depth will most likely be the most important as it is most often a proxy for other processes or drivers, e.g. water mass structure, silicate concentration, internal wave activity, etc. The temperature will also consistently be important as it is critical for sustaining life and determining a species' niche, whilst also being a directly relevant variable (not a proxy). Common important variables were not only found across VME but also, generally, between MaxEnt and Random Forest models. This confirms that during the pre-selection of variables, both MaxEnt and Random Forest were consistently identifying the most appropriate and important variables. Bar charts of variable importance are available in Appendix 7.

2.3.5 Model Evaluation – Ensemble Models

In general, the weighted ensemble models were weighted towards Random Forest models because of their better performing TSS scores (Appendix 6). The MaxEnt spatial predictions of areas of predicted presence are more extensive when compared to Random Forest, owing to the nature of MaxEnt to over generalise and Random Forest to overfit. As a result, the final ensemble model spatial predictions provide a middle ground between the two. Maps of spatial predictions for ensemble models are found in Appendix 8.

When Random Forest and MaxEnt training models were ensembled together, averaged AUC scores across all biotopes were deemed 'excellent' (0.9-1.0), scoring either 0.99 or 1.00. The averaged AUC test scores after ensemble showed a reduction in performance across all biotopes, with one model (SolScl) deemed as 'excellent' (0.92), five models (BurAne, MixCor, SpnMeg, SolRee and SyrFra) deemed 'good' (0.8-0.9), and one (AcaArb) model was deemed 'fair' (0.7-0.8). Despite the decrease in performance three biotope ensemble model average test AUC results were better than both Random Forest

and MaxEnt scores (BurAne, MixCor, SolScl), two ensemble models (SpnMeg and SolRee) where they were equal with one method but better than the other, and two ensemble models (AcaArb and SyrFra) where they were equal with one method or worse.

However, even in instances such as SyrFra, where according to averaged AUC scores the ensemble model performance is worst, the ensemble model is far more successful at predicting presences than both the Random Forest and MaxEnt models; where the sensitivity scores for the ensemble, Random Forest and MaxEnt models are 0.96, 0.91 and 0.85 respectively. Three of the seven ensemble models displayed better sensitivity scores than both Random Forest and MaxEnt models, three of the seven ensembles were equal to one and better than another modelling method, with only one ensemble model (AcaArb) having worse sensitivity scores than both the Random Forest and MaxEnt models. The drop in average ensemble AUC test scores reflects a drop in specificity scores which are greater than the improved sensitivity scores.

2.3.6 VME Analysis

2.3.6.1 Marine Protected Areas

The assessment of predicted VME distribution related to the MPA network suggests that the effectiveness of the network is mixed, offering VMEs varying levels of inclusion within the network. In declining order, the VME with the greatest percentage of predicted presence falling within the network is BurAne (27.40%), MixCor (26.25%), SyrFra (15.68%), SolRee (15.27%), SpnMeg (14.36%), AcaArb (5.72%), and SolScl (2.74%). When broken down further into the UK and Irish MPA network, the UK MPA network covers a greater area of predicted suitable habitat when compared to the Irish MPA network (Table 2.5).

Table 2.5. The area (km^2) of predicted suitable area for each VME by the entire model extent and by nation, with a percentage breakdown of how much of each area falls within designated marine protected areas (MPAs).

VME	Total Model Extent		UK		Ireland	
	Area	%MPA	Area	%MPA	Area	%MPA
AcaArb	2,135	5.72%	77	78.41%	2,058	3.01%
BurAne	9,990	27.40%	1,496	83.48%	8,494	17.53%
MixCor	3,258	26.25%	723	77.72%	2,534	11.55%
SpnMeg	18,004	14.36%	4,350	33.72%	13,651	8.19%
SolRee	26,902	15.27%	4,184	60.63	22,718	6.91%
SolScl	4,577	2.74%	261	29.65%	4,316	1.11%
SyrFra	34,141	15.68%	5,557	60.20%	28,583	7.02%

2.3.6.2 Fishing Impacts

Across all HSMs, there is overlap between areas of suitable habitat and the historical (2009 – 2016) fishing footprint (Table 2.6). The VME with the greatest overlap between the total area predicted as suitable habitat and the historical fishing footprint is MixCor (55.46%). Three VMEs (BurAne, MixCor and SolRee) have 50-60% overlap, three VMEs (AcaArb, SolScl and SyrFra) have 40-50% overlap, with the final VME, SpnMeg, having only 17.81% overlap. Based on these predictions, a considerably smaller percentage area of suitable SpnMeg habitat is likely to have been subjected to historical (2009-2016) bottom fishing activity compared to other VME (Table 2.6).

The effectiveness of the 800m bottom-fishing ban with respect to historical fishing activity overlapping predicted suitable habitat is varied (Table 2.6). Of the areas of predicted suitable AcaArb, SolRee, SolScl and SyrFra habitat that overlaps with historic bottom fishing activity, 100% of those areas are now closed to bottom fishing practices as a result of the 800m ban, and 97.12% and 83.59% for MixCor and SpnMeg respectively. However, in the case of BurAne, only 29.41% of these overlapping areas fall below 800 m. This leaves 70.59% of the area predicted as suitable BurAne habitat

that coincides with historical bottom fishing still vulnerable to bottom fishing activities, e.g. trawling; a good example of this is found on Rosemary Bank seamount (Figure 2.5).

Considering those areas of VME habitat that occur below 800m and are protected from bottom trawling, regardless of previous fishing effort, 100% of predicted suitable habitat for AcaArb, SolRee, SolScl and SyrFra are protected by the 800m bottom trawling ban. MixCor receive 97.91% protection and SpnMeg 97.19%. However, only 21.75% of BurAne area is protected from bottom trawling activities.

Table 2.6. The breakdown of the percentage of the total area of suitable habitat falling below 800 m and therefore protected by the bottom trawl fishing ban. Additionally, the percentage of the total area of suitable habitat falls within the historical (2009-2016) fishing footprint. A further breakdown indicates the percentage of suitable habitat falling within the historical fishing footprint fall above and below the 800 m contour.

VME	Areas of predicted suitable habitat impacted by bottom trawl fishing activities	%	% of Total Area of Suitable Habitat >800m
AcaArb	All model domain	48.71	100.00
	Above 800m	0.00	
	Below 800m	100.00	
BurAne	All model domain	50.35	21.75
	Above 800m	70.59	
	Below 800m	29.41	
MixCor	All model domain	55.46	97.91
	Above 800m	2.88	
	Below 800m	97.12	
SpnMeg	All model domain	17.81	97.19
	Above 800m	16.41	
	Below 800m	83.59	
SolRee	All model domain	55.27	100.00
	Above 800m	0.00	
	Below 800m	100.00	
SolScl	All model domain	45.58	100.00
	Above 800m	0.00	
	Below 800m	100.00	
SyrFra	All model domain	49.68	100.00
	Above 800m	0.00	
	Below 800m	100.00	

Two examples of areas of the seafloor below 800m that could be useful in monitoring potential VME recovery from fishing activities are identified along the continental slope (Figure 2.6). Here, areas of suitable habitats for AcaArb, BurAne, MixCor and SolRee are predicted within areas of previous bottom fishing activity. In some instances (Figure 2.6b), suitable MixCor habitat is predicted in areas that were previously intensely fished, with a peak of 2,082 hours of bottom fishing occurring in one cell between 2009-2016.

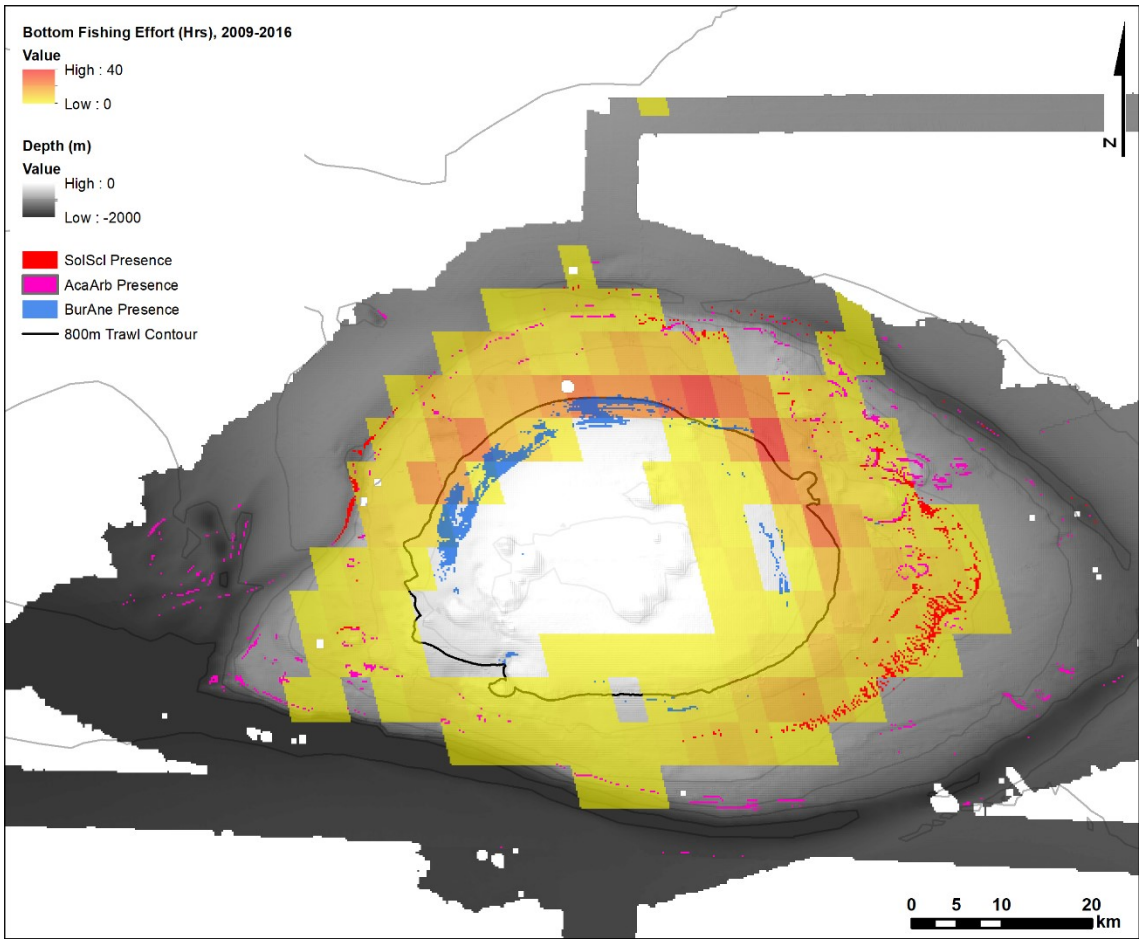

Figure 2.5. Historical bottom-fishing intensity (2009-2016) across Rosemary Bank Seamount, overlaid with areas where suitable SolScl (red), AcaArb (pink) and BurAne (blue) habitat is predicted as present, in relation to the 800 m bottom-contacting fishing ban (bold black 800 m contour)

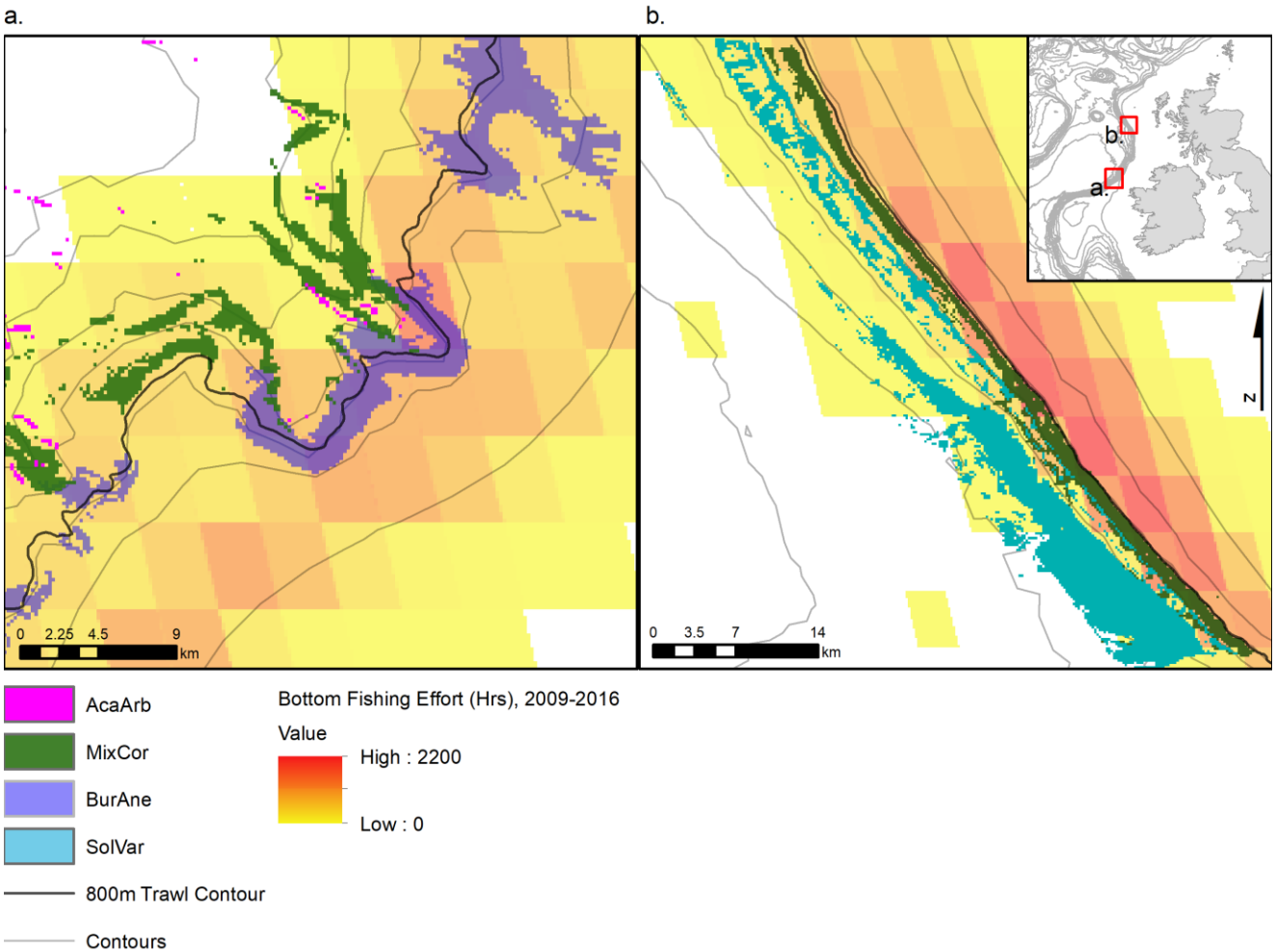

Figure 2.6. Two example areas of the seabed were identified as potential monitoring sites. Map insert depicts example locations along the continental slope. Historical fishing intensity (2009-2016) is overlaid with areas where suitable AcaArb (pink), MixCor (dark green), BurAne (purple) and SolRee (teal) habitat is predicted as present.

2.3.6.3 Oil and Gas Licensed Area

Analysis of areas of VME within active oil and gas licenced blocks show that for the majority of VME, less than 10% of the area of predicted suitable habitat is impacted; BurAne 2.61%, MixCor 5.19%, SpnMeg 8.18%, SyrFra 9.98%, except for AcaArb 11.97%, SolRee 10.40% and SolScl 17.41%.

2.4 Discussion

2.4.1 Model Outputs

The maps of habitat suitability show that across the study area, all seven VME may be widely distributed. The results suggest that important drivers of suitable AcaArb habitat are depth, temperature and slope – particularly, shallow sloping, where sediment is likely to be softer. AcaArb habitat is predicted on the upper canyon networks of the Irish Continental Slope, particularly in the Porcupine Seabight and south of Goban Spur. Additionally, AcaArb is also associated with the shallower-sloping flanks of Anton Dohrn Seamount (ADS), Rosemary Bank and pinnacles across Fangorn Bank.

BurAne has the shallowest distribution, 300-1000 m, of all the VMEs modelled in this study. Areas of suitable habitat include the summit of Rockall Bank, Rosemary Bank, and the heads on canyon networks along the Irish continental slope. Random Forest and MaxEnt models identified BBPI as an important predictor variable, with BurAne occupying regions of low, negative BBPI values – synonymous with the shallower sloping tops of canyons networks.

MixCor, or 'Coral Garden', as with other VME modelled here is a biotope complex and therefore represents numerous biotopes (assemblages of animals) composed of different taxa with different depth distributions. As a result, depth (bathymetry) was a poorer predictor variable than compared to other VME models, with temperature and slope

deemed the most important. This is likely to be a result of the large depth band over which MixCor occurs in this study area (400-2,500 m), reflecting the nature of the biotope complex. Predicted suitable MixCor habitat are associated with steep sloping features (10-30°) with large positive and negative BBPI values, denoting canyons, pinnacles, and banks. These features are associated with increased current speeds because of elevation or the channelling of currents through canyons, which deep-sea coral are known to occur within proximity of (van der Kaaden et al., 2021).

SpnMeg is also a biotope complex composed of many different biotopes (assemblages of animals). Through the pre-selection of variables, it was clear that at least two biotopes occurred in this dataset with two distinct depth distributions; this is also evident in the spatial predictions. A distinctly shallower band of suitable SpnMeg is often found to overlap with suitable BurAne habitat predictions, such as south of the Wyville-Thompson Ridge and across canyon heads along the continental slope. This is largely expected given that the two share a similar niche – low rugosity, shallow sloping, muddy/soft substrate – and seapens and burrowing anemone species are observed together (Davies et al., 2008). The deeper of the two distinct distributions share a similar topographical niche, but instead occupies the base of shallower sloping features such as the flanks of ADS and Rosemary Bank, canyons along the Irish continental slope and the PSB.

Important predictor variables of suitable SolRee habitat in this study were depth and temperature. SolRee niche is characterised by steep sloping, rugose terrain such as canyons, seamount flanks, banks and pinnacles. Predictions of suitable SolRee habitat have some considerable overlap with MixCor predictions. The topographical niche identified in this study for SolRee is similar to that of *Desmophyllum pertusum* reef (formally *Lophelia pertusa*) in these regions as identified by other HSMs (Ross et al., 2015). The distinguishable difference in the niche between both of these cold-water coral reefs is depth distribution, with *Solenosmilia variabilis* reef distributed much deeper (800-

1,700 m) than *Desmophyllum pertusum* reef (500-1200 m) in this region. Although the SolRee HSMs performed well even after cross-validation, some spatial predictions are questionable. For example, there is a large area of suitable habitat predicted across Goban Spur. Although this region is at the correct depth and temperature range for SolRee to occur, Goban Spur is a largely flat area, characterised by fauna typical of soft sedimented areas, e.g. *Pheronema carpenteri* (Hughes and Gage, 2004). Therefore, this is likely an inaccurate spatial prediction, likely a result of missing variables that would have better-characterised regions such as Goban Spur as unsuitable.

Spatial predictions of suitable SolScl habitat are fairly restricted to the PSB and Goban Spur, with some small predictions on Rockall Bank and along the Irish continental slope, north of Porcupine Bank. The variable deemed the most important was depth by a considerable margin. This suggests that the distribution of SolScl may not be topographically-driven but instead by other depth-dependent processes or features, e.g. oceanographic, chemical or biological, which depth is acting as a proxy for.

SyrFra has the greatest predicted extent of suitable habitat of all the VME modelled in this study. The results of these models suggest that SyrVar has a large depth (800-2,200 m) and temperature (3.0-8.5 °C) distribution, as well as a wide topographical niche – shallower sloping and lower rugosity, reflective of the soft sediment requirements of *Syringammina fragilissima*.

2.4.2 Model Performance

RF v MaxEnt v Ensemble Models

When comparing models fitted to training data (70%), RF consistently outperformed MaxEnt models. However, once tested with the remaining 30% of the data, according to sensitivity scores, performance between the two methods became much closer, with no method showing consistently better performance over the other. The significant drop in

Random Forest performance once tested is reflective of its tendency to overfit training datasets. However, the overfitting tendency of Random Forest means this algorithm is more capable of fitting more complex relationships in the data. For example, although the performance of both Random Forest and MaxEnt models dropped when SpnMeg training models were tested, Random Forest and ensemble models performed significantly better – 0.18 higher sensitivity score – than MaxEnt models. This is a result of Random Forest's ability to better discriminate the two different seapen biotopes depth distributions in the dataset, despite hinge features being used in the MaxEnt model.

Ensemble models consistently performed on par with the best performing single modelling method, or better. This is consistent with other deep-sea HSM studies, confirming that ensembling modelling methods can improve performance. However, it is worth noting that all evaluation through this study was carried out using internal cross-validation methods. To best assess these models, their performance should be evaluated by instead validating model predictions using an independent dataset of an unsampled area. However, because presence-absence data is sparse in the deep-sea, there have been few published examples of independently validated HSMs (Anderson et al., 2016; Howell et al., in review; Rooper et al., 2016, 2018).

2.4.3 HSMs as Tools for Conservation Managers and in Marine Spatial Planning

This study provides simplistic examples of how HSM outputs could be useful tools for conservation managers, including assessing the effectiveness of MPAs and other management measures; identifying areas where VMEs have been potentially adversely affected by bottom-fishing activity for investigation and monitoring and recovery; and identifying potential risks from future licensable activities.

The effectiveness of the MPA network across the study area in protecting modelled VME is variable. For some VME, protection is relatively poor; for AcaArb, less than 3% of predicted suitable habitat falls within MPA designations, and less than 7% for SolScl. This compares to MixCor and BurAne with over 25% of predicted suitable habitat falling within MPAs. When broken down into national designations, the UK MPA network contains a higher percentage of the suitable habitat for each VME when compared to Ireland. However, it is worth noting that for each VME modelled, the model extent and predicted distribution in Ireland are far greater than in the UK. More specifically, much of the multibeam bathymetry available for the UK is within MPAs, with large areas of multibeam bathymetry unavailable outside of the MPAs, compared to Ireland which has near-complete multibeam coverage (Appendix 9). This will undoubtedly see an artificial increase in the percentage area of suitable habitat falling within the UK MPA network compared to Irelands. Nonetheless, Ireland has fewer offshore deep-sea MPAs designated (13 of 29) compared to the UK (18 of 29), with three spanning across both UK and Irish ECSs.

There are various types of MPA designated across the study area, with differing MPA-specific management measures, including 13 North-East Atlantic Fisheries Commission (NEAFC) closures designated across Rockall-Hatton Bank (Figure 2.1). These closures prohibit bottom-fishing activities thereby protecting VME from trawling damage, disturbance and removal. Beyond the NEAFC closures, only one other management measurement is designated in the study area – across the Darwin Mounds where vessels are prohibited from using any bottom trawl (EC Regulation No. 602/2004). Beyond those areas, the remaining 15 MPAs have no existing management measures or restrictions in place. As a result, the majority of MPAs across the study area have no direct protection measures or restrictions for the direct protection of VME – often termed ‘paper parks’.

However, blanket EU and NEAFC-wide fisheries restrictions provide a greater extent of protection than the MPA network.

Analysis of suitable VME habitat in this study suggests that the 800 m ban on bottom-contacting mobile gear is the single most effective conservation measure enacted across the study area, with 6 out of 7 predicted suitable VME habitats receiving greater than 97% protection. There is also considerable overlap between the 800 m ban and MPAs with no specific area-based management measures or restrictions, as all MPAs partially or entirely exceed 800 m (Figure 2.1). Therefore, the widespread blanket ban provides VMEs within MPAs and beyond with a high degree of protection from bottom-contacting fishing, despite the lack of MPA-specific regulations in most instances.

In the instance of AcaArb, SolRee, SolScl and SyrFra, the ban on bottom-trawling below 800m has protected 100% of the predicted suitable habitat for each VME that has been historically (2009-2016) fished. The conservation measure has also been successful relative to suitable MixCor and SpnMeg habitats. However, it is far less successful at protecting the shallower distributed BurAne because these measures are fundamentally depth-limited, thus failing to protect shallower VMEs. If changes were to be made to improve these measures, either the 800 m bottom-fishing ban should be expanded to assist the conservation of the shallower VME, or specific area-based restrictions could be considered in prediction 'hotspots', similar to NEAFC closures.

This study identified two areas of predicted suitable VME habitat within the historical fishing footprint that were previously fished. In the case of BurAne, the model outputs suggest (Figure 2.6a) suggest suitable habitat is present across the 800 m depth contour, in a region of previous intense bottom-fishing activity. As a result, this region may provide an opportunity for monitoring suitable BurAne habitat, amongst others, in areas where fishing is now prohibited (below 800 m) and compared to where bottom fishing is

still prohibited (above 800 m). Additionally, this area should be subjected to further research given that, under the EU Common Fisheries Policy, fishing activity should be restricted between 400-800 m where VMEs occur or are *likely* to occur. It may be necessary to designate an MPA or an area-based fishing restriction in this region.

However, some limitations must be acknowledged when overlaying the predictions of suitable habitats with the fishing intensity data. Data obtained and mapped through the Vessel Monitoring Systems (VMS) are at a lower resolution than the model outputs, meaning careful interpretation of results is required. For example, habitats with the highest percentage overlap with fishing activity are surprisingly MixCor and SolRee, both of which occur on steeply sloping, hard substrates that are effectively un-trawl-able. It is likely that in these scenarios, bottom-fishing activity is occurring in soft sediment areas adjacent to MixCor or SolRee, and that these areas result in good consistent catches.

Finally, analysis of model outputs suggests overlap between areas where oil and gas licences have been permitted and areas of suitable VME habitat. Although the licences granted across the study area are in the 'exploration' phase, should licences be re-issued for "exploitation", the necessary precautions should be made to ensure no adverse effects are had against any potential VMEs.

Chapter 3: Wider Discussion and Conclusion

By building upon previous research (Ross et al., 2015; Howell et al., in review), chapter 2 has expanded the number of maps of predicted deep-sea VME distribution available in this region and resolution. Previous models have been limited in the habitats modelled, namely *D. pertusum* reef, *P. carpenteri* aggregations and Xenophyophore fields. This study extends this to new habitats; *Acanella arbuscula* assemblages, Burrowing anemone fields, coral gardens, seapens and burrowing megafauna, *Solenosmilia variabilis* reef, solitary scleractinian fields, and *Syringammina fragilissima* fields. Expanding the number of habitat distribution maps is an important step, particularly in the context of marine spatial planning and conservation.

Additionally, chapter 2 successfully tests the resultant models through cross-validation. The process of evaluation has proven that MaxEnt and Random Forest methods can produce accurate predictions of deep-sea habitat occurrence. Furthermore, this study evidences how combining the outputs of individual modelling methods to create an ensemble can increase model accuracy. This adds to the existing evidence that where appropriate, this additional step should be taken to improve performance, thus instilling more confidence in the model outputs.

Finally, chapter 2 demonstrated how HSMs can be used to inform marine spatial planning and conservation efforts. Specifically, how model outputs can be used to assess the effectiveness of current conservation measures. In this instance, model outputs suggest that the current MPA network across the study area does protect VMEs. However, the effectiveness of the MPA network varies considerably between VMEs, with some receiving considerably more protection (e.g. BurAne) than others (e.g. SolScl). The disparity between the level of protection is also seen between nations, with the UK's MPA network providing far more protection across all VMEs when compared to Ireland. The analysis afforded by these model outputs, however, suggest that blanket depth-based fishing regulations are far greater at providing *realised* protective measures for the

modelled VME in this study compared to the MPA network. In many instances, 100% of the area predicted as suitable for VME habitats was protected. Additionally, this analysis has quantified the reduction in the fishing footprint that overlaps suitable habitat as a result of the 800 m bottom-fishing ban, as well as identified candidate areas for monitoring habitat recovery.

3.1 The Use of Model Transfers

One aspect of PHMs not utilised in chapter 2 is model transfers but can have impactful applications in a deep-sea context. Model transfers are the extrapolation of a model to outside the domain in which it was fitted and has many applications. There are three types of SDM transfer (Werkowska et al., 2017),

1. Spatial transfer – fitting a model in one geographical location and extrapolating the predictions into another novel location.
2. Changes in spatial resolution – where the resolution (e.g. cell size) of the novel location is different (finer or coarser) to which the model was trained.
3. Temporal transfer – a trained model is transferred to another period. This can be forecasting, such as future climate scenarios, or hindcasting, such as creating ecological scenarios for the testing of evolutionary hypothesises.

The transferring of SDMs has been implemented to achieve many different research objectives (Table 3.1).

Table 3.1. Examples of how model transfers can be applied to answer several different research questions.

Research Objective	**Transfer Type**	**Examples**
Predicting change in species distribution or habitat suitability under future climate change scenarios.	Temporal	(Allyn et al., 2020) (Simon-Nutbrown et al., 2020) (Zhang et al., 2019)
Evolutionary history and historical distributions	Temporal	(Pelletier et al., 2015)
Predict potential invasions of non-native species and their potential distributions.	Spatial and Temporal	(Lyons et al., 2020) (Goldsmit et al., 2020) (Battini et al., 2019) (Barbet-Massin et al., 2018)
To provide information about data deficient areas.	Spatial	(Scharf and Fernández, 2018)

So far, there have been few applications of model transfers in a deep-sea scenario, all of which have been limited to temporal transfers. Temporal transfers in the deep sea have been limited to forecasting the changes in the suitable habitat of deep-sea species under future climate change scenarios (Basher and Costello, 2016; Morato et al., 2020; Beazley et al., 2021). Morato et al. (2020) used PHMs to assess future losses and gains in suitable habitats in the North Atlantic across different cold-water coral (CWC) species and commercially important deep-sea fishes. When compared to HSMs built from a present-day climatic scenario, under a future high emissions scenario (2081-2100) suitable habitat across all CWC species decreases (28-100%), with a shift in suitable habitat between 2.0-9.9º towards higher latitudes in deep-sea fishes. Only two fish species (*Helicolenus dactylopterus* and *Sebastes mentella*) saw a net gain in suitable habitat, with all other species retracting. In these instances, HSMs identify limited refugia under future scenarios and some species, such *Paragorgia arborea*, as having almost no refugia. These types of assessments, made possible by temporal model transfers, are critical in highlighting those species most sensitive to warming in the deep-ocean and where conservation efforts should focus.

However, there are currently no published examples of spatial transfers within the deep-sea environment, despite their potential useful applications. The spatial transfer of models could help provide baseline data for regions where data is currently lacking; a PHM could be fitted using data from a relatively 'data-rich' region and transferred to 'data-poor' regions. Following the study detailed in the previous chapter, a good next step could be to transfer the HSMs – where appropriate – to data-poor regions. For example, from a simple review of OBIS data, *Solenosmilia variabilis* is distributed across the entire Atlantic Ocean. A good follow-on study would be to collate appropriate environmental data (same variables and resolution) across the Central and South Atlantic Ocean, allowing a transfer of the NE Atlantic *SolRee* model to the Central and South Atlantic. Across the Atlantic, there is a large disparity in distribution information for deep-sea species and habitats, with the North being relatively data-rich when compared to the Central and South (Howell et al., 2020b). This lack of available data across nations EEZs and ABNJ makes effective management of the deep sea across these basins challenging. By transferring models from data-rich regions, complete coverage maps of predicted distribution could be obtained which would be of great value, providing a baseline of data for a relatively low cost. These maps could then be used to better target research resources and survey time; provide data to conduct preliminary assessments of existing conservation measures; identify areas of suitable habitat at high risk from adverse effects from anthropogenic activity, and for potential monitoring.

However, the current lack of published transfers is likely due to limited occurrence data not only in reference systems (where the model is trained) but also within target systems (area of transfer) to provide independent validations of predictions. Even where models have not been transferred, very few published deep-sea HSMs have been independently validated (Rooper et al., 2016, 2017) and have instead relied upon internal validation techniques such as cross-validation. This predicament again roots back to the lack of

species occurrence data to begin with – eloquently summarised by Yates et al (2018): "*This leads to a catch-22, where the absence of knowledge encourages the search for transferable models but also impedes their evaluation*". However, by having preliminary maps, future surveys could be planned using such maps and collect data that could subsequently ground-truth the model transfers.

It is likely to take several years or decades to fully address the current uneven sampling effort of the deep-ocean across the globe and with current technology, impossible to sample all areas of the seabed. As a result, the spatial transfers of deep-sea PHMs have to start being implemented to produce baseline data, and "fill the gaps" between seabed sampling sites.

3.2 PHMs in Formal Marine Spatial Planning Advice

UNGA Resolution 61/105 and Regulation EU 2016/2336 require Regional Fisheries Management Organisations (RFMOs) and EU Member States to prevent significant adverse impacts on VMEs from deep-sea bottom-fishing activity where VMEs occur or are *likely* to occur. The incorporation of the term 'likely' is an important inclusion within these legally binding agreements for two reasons, (1) the vast majority of the deep sea is un-sampled and (2) often areas that are sampled have limited data. On the latter point, advisory bodies have consequently developed multi-criteria assessment (MCA) methods to extract the most possible information from limited data. For example, the ICES Working Group on Deep-water Ecology (WGDEC) have developed VME weighting algorithms to determine the *likelihood* ('High', 'Medium' or 'Low') that records of VME indicators represent a VME Habitat. As a result of the addition of "*likely* to occur" within the UNGA Resolution and EU Regulations, WGDEC have been able to use mapped outputs from the VME weighted algorithms, alongside VME Habitat records, in ICES advice to NEAFC and the European Commission (EC) on the distribution of VMEs.

Moreover, these outputs have been subsequently used to support VME-based closure recommendations in NEAFC regulated areas, including within the UK and Ireland extended continental shelf. However, sufficient VME indicator data is required for this approach, data which can be sparse and therefore spatially limiting where advice can be given.

The addition of 'likely' also provides the opportunity to utilise the likelihood and prediction outputs from PHMs and overcomes the spatial constrictions of MCA approaches by providing complete coverage maps. Given this, the UN General Assembly has explicitly recognised that predictive models have identified "areas where VMEs … are likely to occur" and have been used in "the adoption of conservation and management measures to prevent significant adverse impacts on such ecosystems, including the closure of areas to bottom fishing" (UNGA, 2016). Despite this, across the study area and the wider NE Atlantic, outputs of PHMs have not been incorporated into formal advice given to NEAFC and the EC; in 2019, ICES WGDEC noted this (ICES, 2019). Since then, a series of workshops have been convened to discuss how PHM outputs could be incorporated into advice-giving processes. The reason for this delay is the many outstanding challenges and issues surrounding the application of PHMs in advice-giving. These must be addressed to instil the confidence of managers in the model outputs before they can be used as tools or evidence in advice.

The challenges and issues can be split broadly into three areas (ICES, 2021). All three attribute to the 'value' a given map of predicted habitat suitability has, or conversely, the constraints a model places on its potential applications, i.e. advice to managers.

1. Model response variables – The value of a model based on indicator taxa density or biomass would be of greater value to managers than a presence-absence model, as this would more likely indicate areas of VME Habitat. However, a presence-absence

model of VME Habitat would also be of value, with biomass and density-based being greater again.

2. Spatial extent and model resolution – There is often a trade-off in models between spatial extent and model resolution because of the underlying environmental variables. At high resolutions, model extents are often limited to relatively small, localised patches of bathymetry. Although lacking in extent, high-resolution models would attain a greater level of detail and information, forming better advice in the case of area-based management. Basin-scale models are usually limited to coarse resolutions in the order of kilometres as they are often built upon coarse GEBCO bathymetry. Therefore, these maps could not be used to form advice on area-based decisions, as the resolution is not at a high enough resolution. However, these maps still have value – they could be used to highlight general areas of likely distribution that should be investigated at a higher resolution should new licensable practices be proposed or amended in the region.
3. Map Quality – A definable threshold of model performance must be decided upon to objectively benchmark models. Not only must the absolute performance scores be considered, but also the methodological approach that is taken. The gold standard would be for models to be validated with an independent dataset, but as previously discussed, this has been achievable in very few deep-sea scenarios. Therefore, the next best alternatives must be agreed to ensure model outputs are both statistically and ecologically sound.

From these broad areas, transparent and unambiguous criteria can be devised to benchmark and score PHMs for their suitability in giving advice in an objective and scientifically robust manner. Work amongst ICES experts and managers is ongoing to define such criteria (ICES, 2021) to tackle issues of acceptability, and eventually bring

PHMs into official ICES advice to RFMOs, the EU, OSPAR Commission and national governments.

3.3 Conclusion

The study in chapter 2 successfully developed new maps of VME habitat suitability across the UK and Ireland, extending the existing mapping efforts in this region into VMEs not previously mapped. The development of these models has also provided further evidence of the importance of ensemble modelling techniques, reinstating the need for a general movement in the modelling community to this modelling approach. Furthermore, this research concludes that the spatial transfer of PHMs should be utilised to tackle the regional disparities in distribution data availability (chapter 3), illustrating how this work could be done in a follow-up study using the models developed in chapter 2. Additionally, the study outlined in chapter 2 illustrates multiple ways in which PHMs can be utilised in marine spatial planning and conservation scenarios. Whilst also recognising the issues surrounding the acceptability of PHMs in formal advice, and the ongoing work to address this.

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APPENDICES

Appendix 1 – Bathymetry sources

Table A1.1 Bathymetry data sources listed by data set, reference, location, native cell size (before resampling) and the projection of the native source file.

Data set	Reference	Location	Native cell size	Projection of source file
BAS	Howell et al., 2006	Rosemary Bank	100m	ED 1950 UTM (29N)
CD118 UNCLOS	MacLachlan et al., 2008	Hatton	100m	WGS84 UTM (27N)
CD174	Wallis et al., 2005	Rockall Trough surrounding Anton Dohrn Seamount	0.001°	WGS84
CD91 LOIS	McCartney et al., 1995	Barra Fan	0.0025°	WGS84
IFREMER	Not available	Hebrides Terrace/Donegal Fan	0.0025°	WGS84
Irish National Seabed Survey	http://www.infomar.ie/	Whole Irish deep-water area	111m	WGS84
JC60	Huvenne et al., 2011	Darwin Mounds, Hatton Rockall Basin, Rockall Bank	10-50m	WGS84 UTM (28N or 29N)
JC136	Howell et al., 2016	Rockall Bank, Anton Dohrn Seamount, Hebrides Continental Shelf, Rosemary Bank, Rockall Trough, Wyville-Thomson Ridge	0.5-100m	WGS84 UTM (28N or 29N)
MESH	Stewart and Davies 2007	SW Approaches, Explorer and Dangaard Canyons	25m	UTM (29N)

NISS	Not available	Rockall Bank approx. Haddock Box	0.000225°	WGS84
SEA7_KJ2005	Jacobs, 2005	Anton Dohrn Seamount, Rockall Bank, George Bligh Bank, Hatton Bank, Hatton-Rockall Basin, Rockall Trough, Rosemary Bank	0.0025°	WGS84
SEA-SAC2006	Jacobs & Howell, 2007 Stewart & Davies, 2007	Rosemary Bank, Hatton Bank, George Bligh Bank, Wyville Thomson Ridge	25m	UTM (27N, 28N, 29N, 30N)

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Appendix 2 – Bottom temperature model

Generalised additive models (GAMs) were implemented in R (R Core Team, 2021) to create a bottom temperature raster grid for the study area. The GAMs was built using temperature data obtained from ROV and drop-frame CTD probes, with additional archived CTD casts obtained from the British Oceanographic Data Centre (Table S1.1). The geographic extent of the model covers two distinct water masses; North Atlantic and Arctic bottom water. These two water mass structures are separated by the Wyville Thomson Ridge (WTR) at the northern end of the Rockall Trough basin, with the two water masses interacting and mixing periodically over the WTR. The decision was made to create models based on their water mass structure and oceanography, so the following three models were created for bottom temperature: (1) the WTR, (2) North and (3) South of the WTR.

The bottom temperature was modelled in a previous project across the WTR (Stashchuk et al., 2011) and 200 x 200 m resolution, so this model was used for this region. For the North and South of the WTR, a series of bottom temperature GAMs were constructed using the "*gam"* function from the "mgcv" package (Wood, 2011) in R. This series of models, in turn, trialled different combinations of variables (depth, latitude, longitude) and parameters (knots). Model performance was evaluated by assessing the GCV score, deviance explained (%) and the accuracy of temperature predictions. The best performing GAM for the North and South were selected (Table S1.2) and used to predict onto the bathymetry raster, gridded at 200 x 200m. The North, South and WTR bottom temperature models were then merged, creating a final bottom temperature raster grid of a 200 x 200 m resolution.

Table A2.1 Summary of temperature data used to build bottom temperature generalised additive models.

Model	Dataset	Number of Temperature Points	Type
South of WTR	2009/03-JNCC	38,727	Drop-frame CTD probe
	Canyons	852	ROV CTD probe
	Deep Links (JC136)	968,208	ROV CTD probe
	DeepMap (Eurofleets2)	135,385	ROV CTD probe
	SEA/SAC Survey 2007	275,156	ROV CTD probe
	JC060	31,083	ROV CTD probe
	SeaRovers 2017 (CE17009)	1,412,129	ROV CTD probe
	Data archived via BODC, provided by the following institutes: National Oceanography Centre Southampton, Scottish Association for Marine Science, University of Liverpool Department of Earth Sciences, Institute of Oceanographic Sciences Wormley Laboratory, University of Southampton Department of Oceanography, Fisheries Research Services Aberdeen Marine Laboratory, University of Hamburg Department of Chemistry, Institute of Oceanographic Sciences Deacon Laboratory, University of Bremen, Center for Marine Environmental Sciences, Royal Netherlands Institute for Sea Research, Leibniz Institute for Baltic Sea Research.	37,815 points from 107 casts	CTD cast
	SEA/SAC Survey 2007	38,251	ROV CTD probe

North of WTR	Data archived via BODC, provided by the following institutes: Institute of Marine Research Norway, Fisheries Research Services Aberdeen Marine Laboratory.	6,888 points from 62 casts	CTD cast

Table A2.2 Final selected generalised additive models.

Model	Formula	p-value	GCV Score	Deviance Explained (%)
South of WTR	temp ~ s(depth, k=8) + s(lat, k=3) + s(long, k=4)	< 0.001	0.22624	91.90
North of WTR	temp ~ s(depth, k=8)	< 0.001	1.0196	94.20

Appendix 3 – SolScl Scatterplots

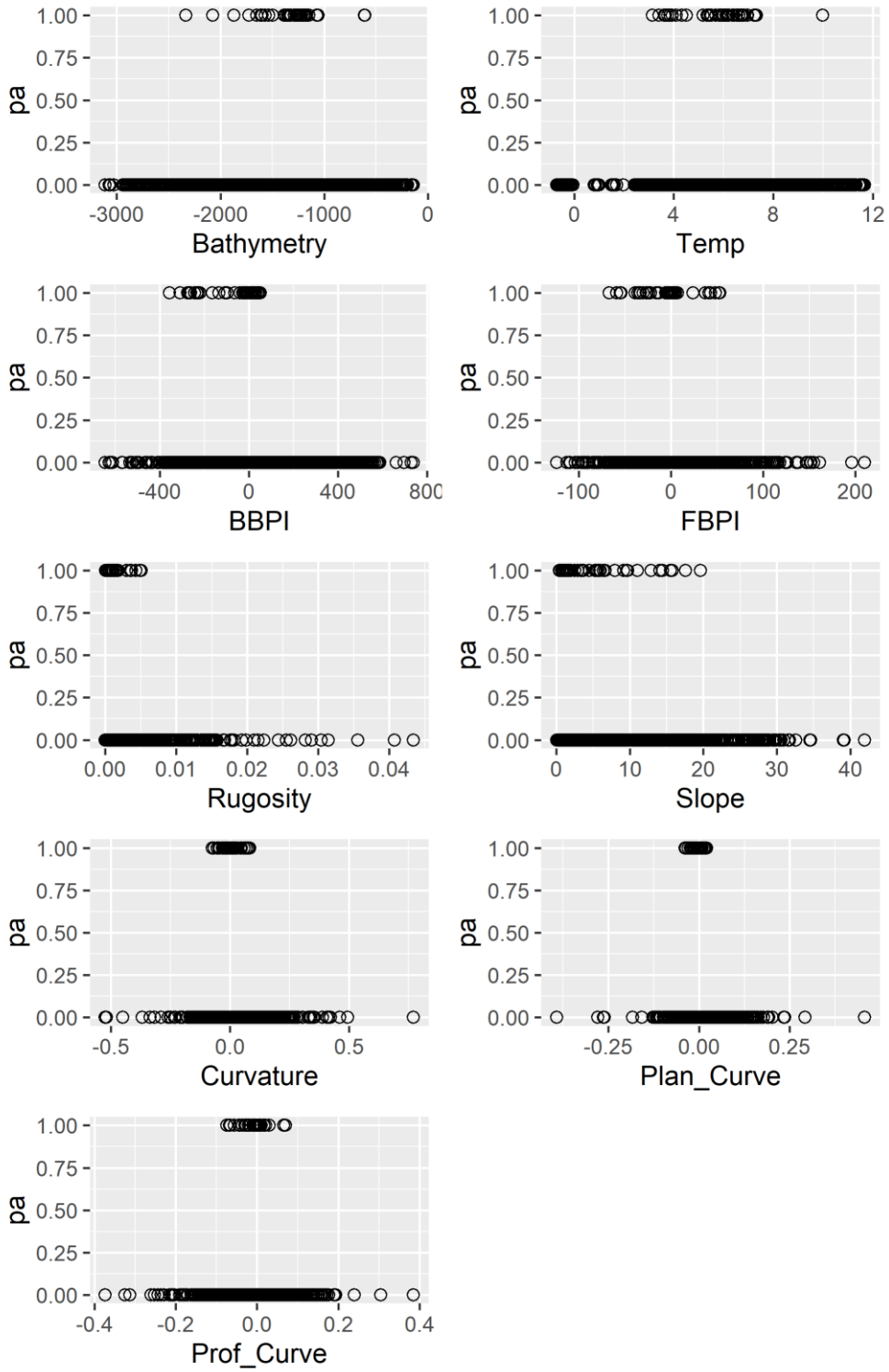


Figure A3.1 Scatter graphs of SolScl presence-absence (PA) against environmental variables.

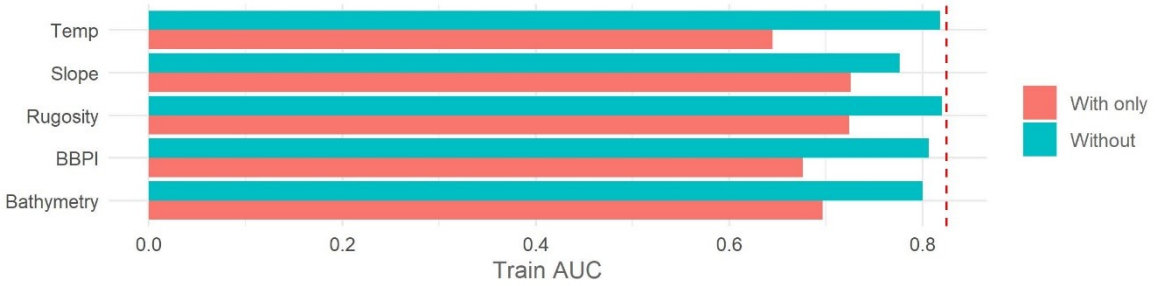
Appendix 4 – MaxEnt Jackknife Plots

Jackknife plots for the final MaxEnt model selected for each biotope.

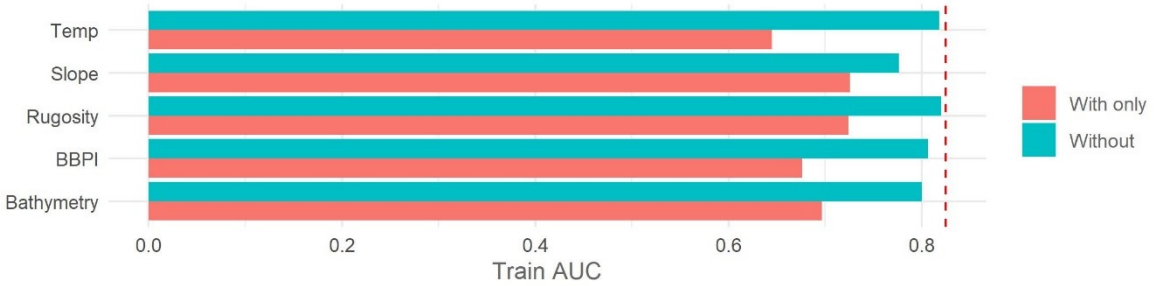
A4.1. AcaArb

A4.2. BurAne

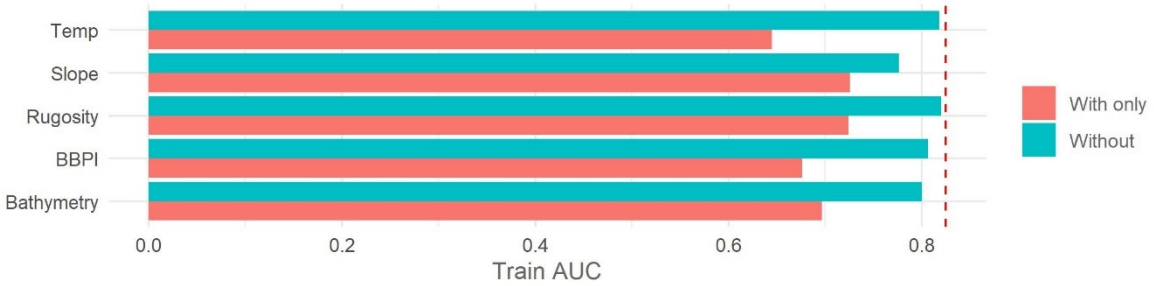
A4.3. MixCor



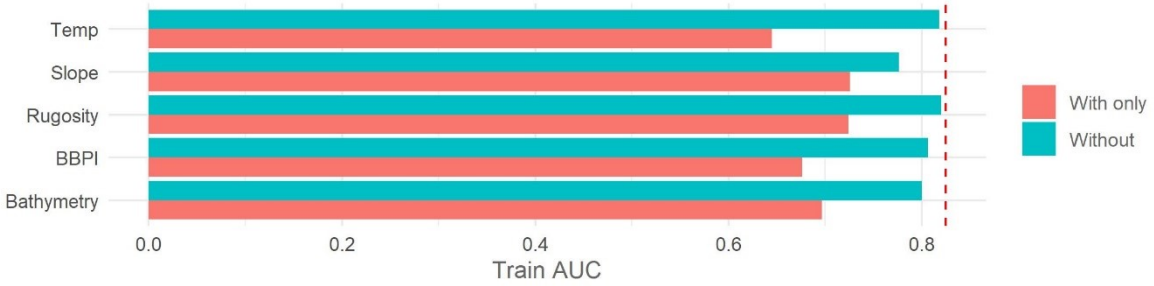
A4.4. SpnMeg



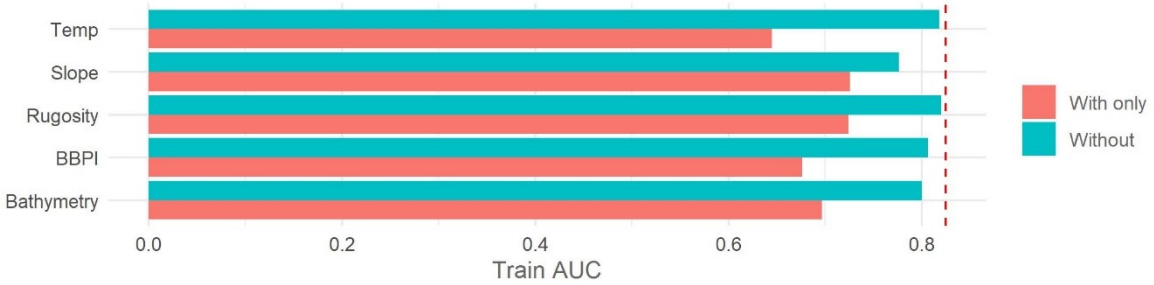
A4.5. SolRee



A4.6. SolScl



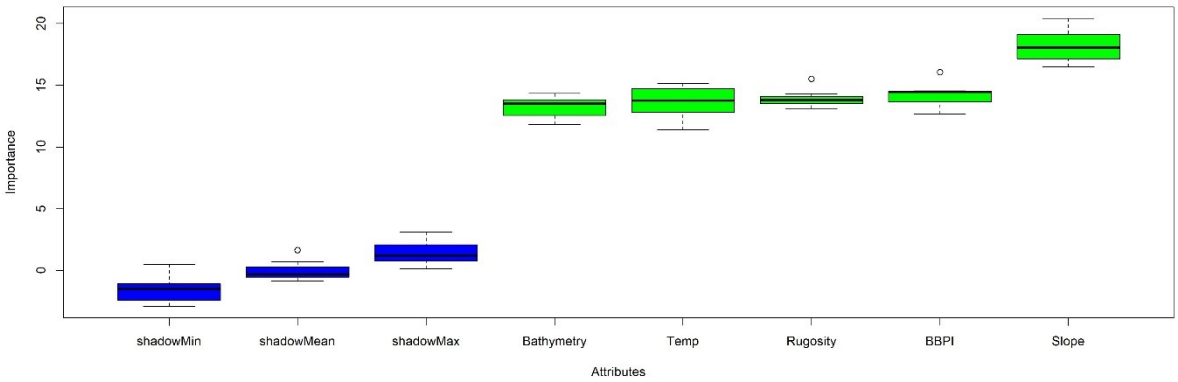
A4.7. SyrFra



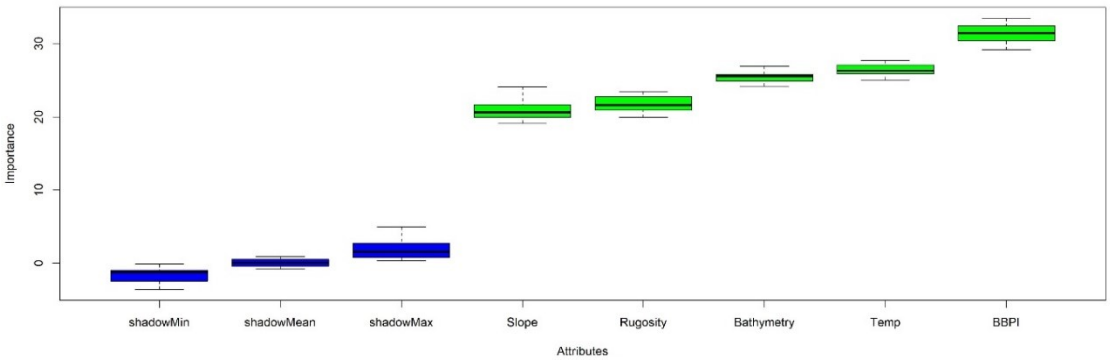
Appendix 5 – Random Forest Boruta Plots

Boruta plots and out-of-bag (OOB) estimate of error for the final Random Forest model selected for each biotope.

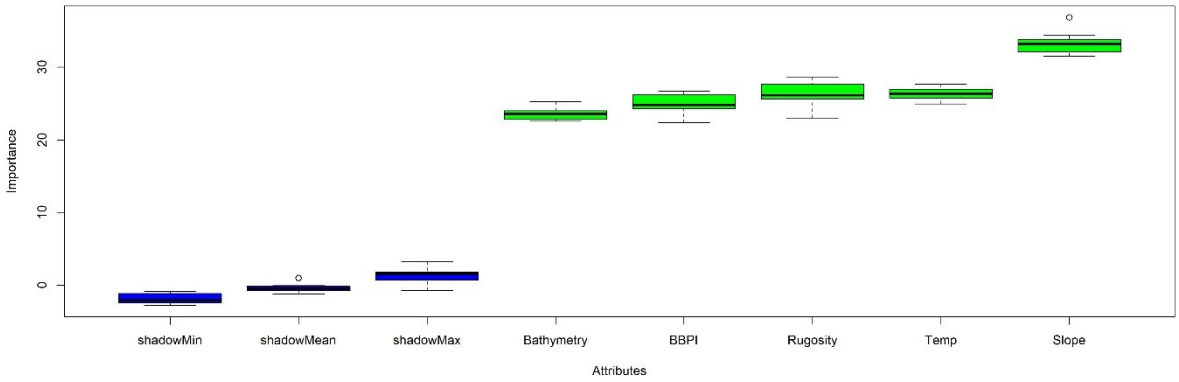
A5.1. AcaArb



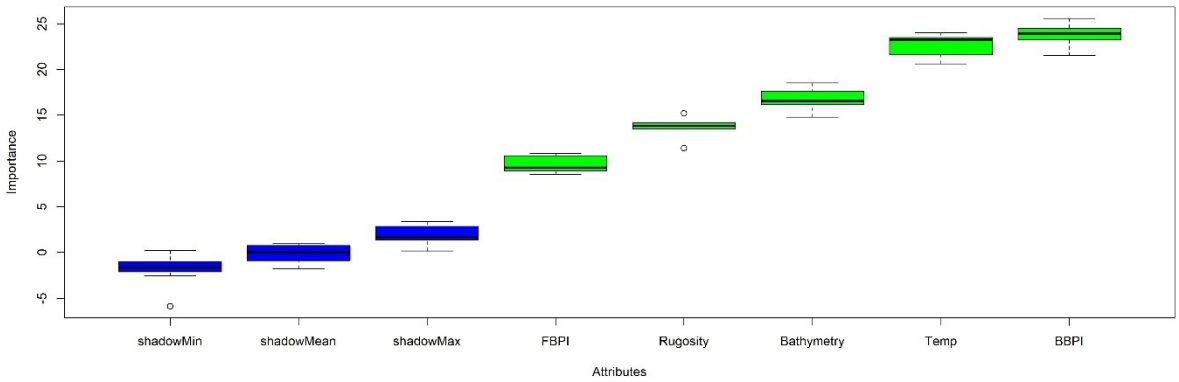
A5.2. BurAne



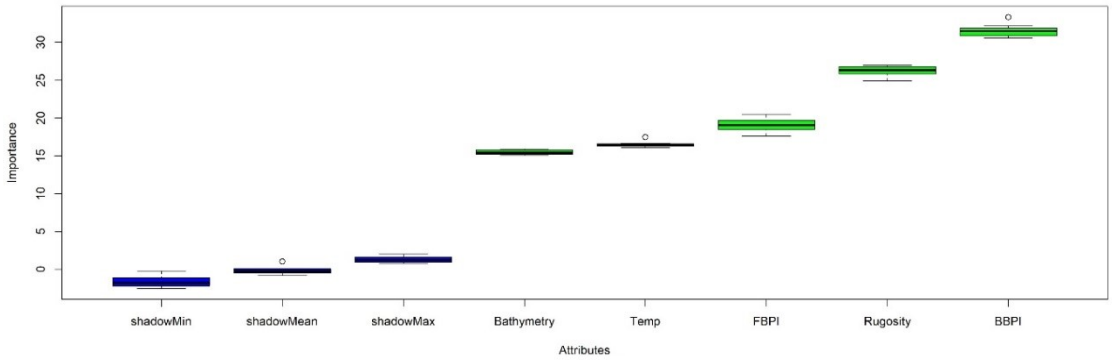
A5.3. CorRee



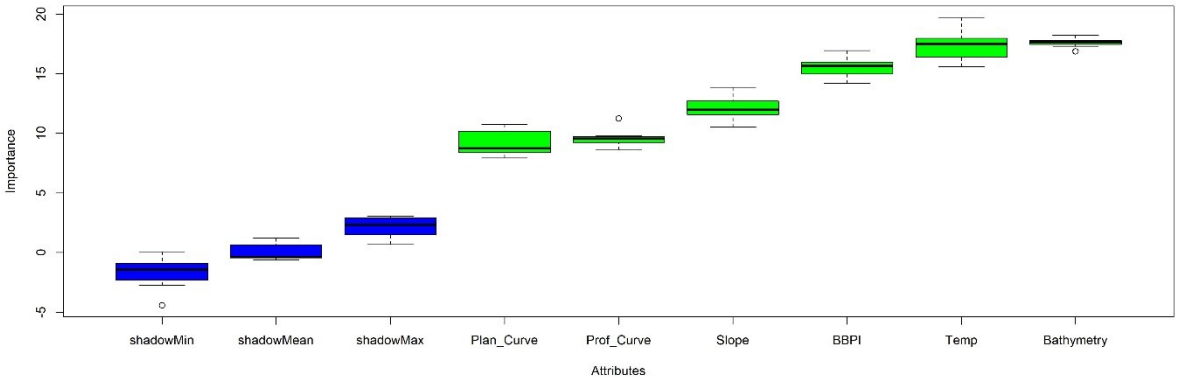
A5.4 SpnMeg



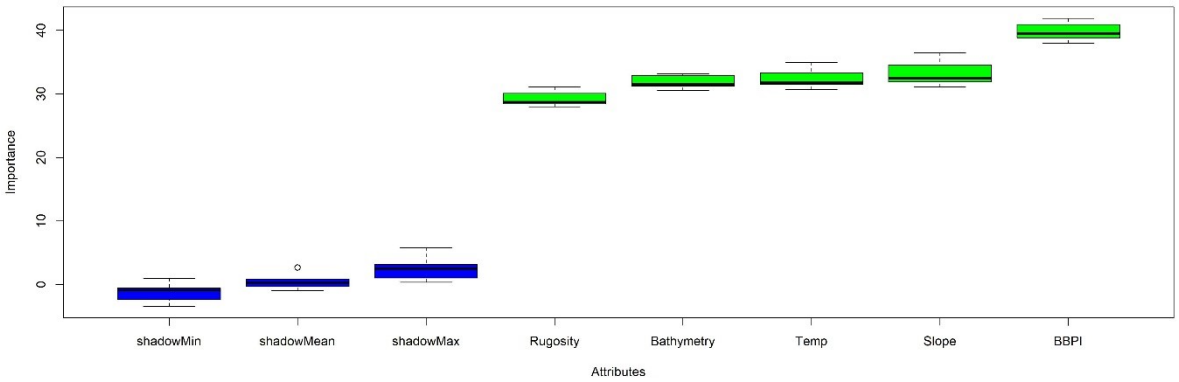
A5.5 SolRee



A5.6 SolScl



A5.7 SyrFra



Appendix 6 – Model Results

Table A6.1. Break down of biotope model results by modelling method and thresholding metric.

Biotope	Model	Metric	Random Forest			MaxEnt			Ensemble		
			SS	MaxSS	MinROCd	SS	MaxSS	MinROCd	SS	MaxSS	MinROCd
AcaArb	Full	Threshold	0.39	0.39	0.39	0.28	0.17	0.25	0.38	0.38	0.38
		PCC	1.00	1.00	1.00	0.76	0.64	0.73	1.00	1.00	1.00
		Sens	1.00	1.00	1.00	0.77	1.00	0.83	1.00	1.00	1.00
		Spec	1.00	1.00	1.00	0.76	0.64	0.73	1.00	1.00	1.00
		Kappa	1.00	1.00	1.00	0.04	0.03	0.04	0.97	0.97	0.97
		AUC	1.00	1.00	1.00	0.88	0.88	0.88	1.00	1.00	1.00
	Train	PCC	1.00	1.00	1.00	0.78	0.68	0.78	0.97	0.96	0.97
		Sens	1.00	1.00	1.00	0.77	0.97	0.82	0.97	1.00	0.98
		Spec	1.00	1.00	1.00	0.78	0.68	0.78	0.97	0.96	0.97
		Kappa	1.00	1.00	1.00	0.05	0.05	0.07	0.57	0.55	0.60
		AUC	1.00	1.00	1.00	0.89	0.89	0.89	0.99	0.99	0.99
	Test	PCC	0.83	0.86	0.86	0.66	0.62	0.66	0.66	0.59	0.66
		Sens	0.51	0.56	0.56	0.63	0.96	0.89	0.63	0.95	0.84
		Spec	0.83	0.86	0.86	0.66	0.62	0.66	0.66	0.59	0.65
		Kappa	0.02	0.03	0.03	0.02	0.03	0.03	0.02	0.02	0.03
		AUC	0.74	0.74	0.74	0.73	0.73	0.73	0.73	0.73	0.73
BurAne	Full	Threshold	0.33	0.33	0.33	0.32	0.26	0.26	0.32	0.32	0.32
		PCC	1.00	1.00	1.00	0.75	0.71	0.71	0.99	0.99	0.99
		Sens	1.00	1.00	1.00	0.75	0.88	0.88	1.00	1.00	1.00

		Spec	1.00	1.00	1.00	0.75	0.71	0.71	0.99	0.99	0.99
		Kappa	1.00	1.00	1.00	0.08	0.08	0.08	0.84	0.84	0.84
		AUC	1.00	1.00	1.00	0.88	0.88	0.88	1.00	1.00	1.00
	Train	PCC	1.00	1.00	1.00	0.77	0.73	0.75	0.94	0.93	0.94
		Sens	1.00	1.00	1.00	0.76	0.87	0.84	0.94	0.98	0.96
		Spec	1.00	1.00	1.00	0.77	0.73	0.75	0.94	0.93	0.94
		Kappa	1.00	1.00	1.00	0.10	0.11	0.11	0.50	0.47	0.50
		AUC	1.00	1.00	1.00	0.88	0.88	0.88	0.99	0.99	0.99
	Test	PCC	0.75	0.85	0.82	0.72	0.72	0.76	0.74	0.74	0.75
		Sens	0.70	0.71	0.71	0.72	0.93	0.88	0.74	0.94	0.92
		Spec	0.75	0.85	0.82	0.72	0.71	0.76	0.75	0.74	0.74
		Kappa	0.08	0.17	0.12	0.05	0.10	0.11	0.07	0.10	0.10
		AUC	0.77	0.77	0.77	0.84	0.84	0.84	0.85	0.85	0.85
MixCor	**Full**	Threshold	0.38	0.36	0.36	0.33	0.38	0.34	0.38	0.38	0.38
		PCC	1.00	1.00	1.00	0.72	0.78	0.74	0.99	0.99	0.99
		Sens	1.00	1.00	1.00	0.72	0.67	0.71	0.99	0.99	0.99
		Spec	1.00	1.00	1.00	0.72	0.79	0.74	0.99	0.99	0.99
		Kappa	0.98	0.98	0.98	0.19	0.24	0.20	0.94	0.94	0.94
		AUC	1.00	1.00	1.00	0.81	0.81	0.81	1.00	1.00	1.00
	Train	PCC	1.00	1.00	1.00	0.73	0.69	0.74	0.94	0.92	0.93
		Sens	1.00	1.00	1.00	0.73	0.79	0.73	0.94	0.97	0.95
		Spec	1.00	1.00	1.00	0.73	0.68	0.74	0.94	0.92	0.93
		Kappa	0.98	0.98	0.98	0.20	0.19	0.21	0.67	0.63	0.65
		AUC	1.00	1.00	1.00	0.80	0.80	0.80	0.99	0.99	0.99
	Test	PCC	0.71	0.66	0.70	0.72	0.71	0.75	0.74	0.68	0.74
		Sens	0.70	0.80	0.74	0.72	0.80	0.73	0.74	0.87	0.77
		Spec	0.71	0.65	0.70	0.72	0.70	0.75	0.74	0.66	0.73

		Kappa	0.17	0.17	0.18	0.20	0.25	0.23	0.22	0.22	0.23
		AUC	0.77	0.77	0.77	0.80	0.80	0.80	0.81	0.81	0.81
SpnMeg	**Full**	Threshold	0.36	0.36	0.36	0.27	0.44	0.44	0.29	0.27	0.36
		PCC	1.00	1.00	1.00	0.83	0.92	0.92	0.97	0.96	0.99
		Sens	1.00	1.00	1.00	0.83	0.83	0.83	0.96	1.00	0.96
		Spec	1.00	1.00	1.00	0.83	0.92	0.92	0.97	0.96	0.99
		Kappa	0.99	0.99	0.99	0.12	0.25	0.25	0.48	0.46	0.76
		AUC	1.00	1.00	1.00	0.94	0.94	0.94	1.00	1.00	1.00
	Train	PCC	1.00	1.00	1.00	0.87	0.89	0.89	0.98	0.97	0.98
		Sens	1.00	1.00	1.00	0.86	0.88	0.88	0.98	0.99	0.98
		Spec	1.00	1.00	1.00	0.87	0.89	0.89	0.98	0.97	0.98
		Kappa	0.97	0.97	0.97	0.19	0.23	0.22	0.70	0.66	0.70
		AUC	1.00	1.00	1.00	0.94	0.94	0.94	0.99	0.99	0.99
	Test	PCC	0.88	0.90	0.90	0.65	0.87	0.85	0.80	0.87	0.84
		Sens	0.77	0.77	0.77	0.58	0.59	0.57	0.74	0.77	0.80
		Spec	0.88	0.91	0.91	0.65	0.87	0.86	0.80	0.87	0.84
		Kappa	0.21	0.22	0.22	0.06	0.13	0.11	0.15	0.15	0.15
		AUC	0.85	0.85	0.85	0.77	0.77	0.77	0.85	0.85	0.85
SolRee	**Full**	Threshold	0.36	0.36	0.36	0.40	0.32	0.37	0.38	0.36	0.36
		PCC	1.00	1.00	1.00	0.79	0.74	0.77	0.99	0.98	0.98
		Sens	1.00	1.00	1.00	0.79	0.87	0.83	0.99	1.00	1.00
		Spec	1.00	1.00	1.00	0.79	0.73	0.77	0.99	0.98	0.98
		Kappa	0.98	0.98	0.98	0.30	0.26	0.28	0.92	0.91	0.91
		AUC	1.00	1.00	1.00	0.87	0.87	0.87	1.00	1.00	1.00
	Train	PCC	1.00	1.00	1.00	0.79	0.72	0.77	0.97	0.97	0.98
		Sens	1.00	1.00	1.00	0.79	0.91	0.84	0.97	0.98	0.98
		Spec	1.00	1.00	1.00	0.79	0.71	0.77	0.97	0.97	0.98

		Kappa	0.98	0.98	0.98	0.30	0.26	0.29	0.85	0.85	0.86
		AUC	1.00	1.00	1.00	0.87	0.87	0.87	1.00	1.00	1.00
	Test	PCC	0.77	0.74	0.77	0.74	0.67	0.74	0.76	0.71	0.75
		Sens	0.77	0.87	0.81	0.74	0.92	0.82	0.76	0.94	0.87
		Spec	0.77	0.73	0.77	0.74	0.65	0.73	0.76	0.69	0.74
		Kappa	0.26	0.26	0.28	0.22	0.21	0.24	0.24	0.24	0.28
		AUC	0.86	0.86	0.86	0.82	0.82	0.82	0.86	0.86	0.86
SolScl	**Full**	Threshold	0.37	0.37	0.37	0.49	0.54	0.54	0.31	0.30	0.33
		PCC	1.00	1.00	1.00	0.85	0.88	0.88	0.98	0.98	0.99
		Sens	1.00	1.00	1.00	0.84	0.83	0.83	0.98	1.00	0.98
		Spec	1.00	1.00	1.00	0.85	0.89	0.89	0.98	0.98	0.99
		Kappa	1.00	1.00	1.00	0.15	0.19	0.19	0.68	0.60	0.78
		AUC	1.00	1.00	1.00	0.91	0.91	0.91	1.00	1.00	1.00
	Train	PCC	1.00	1.00	1.00	0.84	0.88	0.88	0.95	0.95	0.95
		Sens	1.00	1.00	1.00	0.84	0.84	0.84	0.95	0.97	0.97
		Spec	1.00	1.00	1.00	0.84	0.88	0.88	0.95	0.95	0.95
		Kappa	1.00	1.00	1.00	0.15	0.21	0.21	0.46	0.51	0.49
		AUC	1.00	1.00	1.00	0.91	0.91	0.91	0.99	0.99	0.99
	Test	PCC	0.83	0.90	0.85	0.86	0.85	0.86	0.88	0.87	0.88
		Sens	0.77	0.77	0.78	0.87	0.95	0.94	0.88	0.95	0.94
		Spec	0.83	0.90	0.85	0.86	0.85	0.86	0.88	0.87	0.88
		Kappa	0.22	0.31	0.25	0.13	0.14	0.14	0.26	0.26	0.27
		AUC	0.86	0.86	0.86	0.89	0.89	0.89	0.92	0.92	0.92
SyrFra	**Full**	Threshold	0.38	0.37	0.37	0.41	0.28	0.32	0.41	0.39	0.41
		PCC	1.00	1.00	1.00	0.76	0.69	0.71	1.00	0.99	1.00
		Sens	1.00	1.00	1.00	0.76	0.95	0.88	1.00	1.00	1.00
		Spec	1.00	1.00	1.00	0.76	0.66	0.69	0.99	0.99	0.99

		Kappa	0.98	0.98	0.98	0.24	0.23	0.23	0.97	0.96	0.97
		AUC	1.00	1.00	1.00	0.85	0.85	0.85	1.00	1.00	1.00
	Train	PCC	1.00	1.00	1.00	0.76	0.68	0.74	0.95	0.96	0.96
		Sens	1.00	1.00	1.00	0.76	0.91	0.81	0.95	0.96	0.96
		Spec	1.00	1.00	1.00	0.76	0.66	0.74	0.95	0.96	0.96
		Kappa	0.97	0.97	0.98	0.25	0.22	0.25	0.58	0.59	0.59
		AUC	1.00	1.00	1.00	0.84	0.84	0.84	0.98	0.98	0.98
	Test	PCC	0.83	0.80	0.82	0.79	0.76	0.79	0.73	0.71	0.73
		Sens	0.83	0.91	0.87	0.79	0.91	0.85	0.74	0.96	0.90
		Spec	0.83	0.79	0.82	0.79	0.75	0.79	0.73	0.71	0.73
		Kappa	0.34	0.31	0.34	0.28	0.29	0.31	0.13	0.14	0.14
		AUC	0.90	0.90	0.90	0.89	0.89	0.89	0.80	0.80	0.80

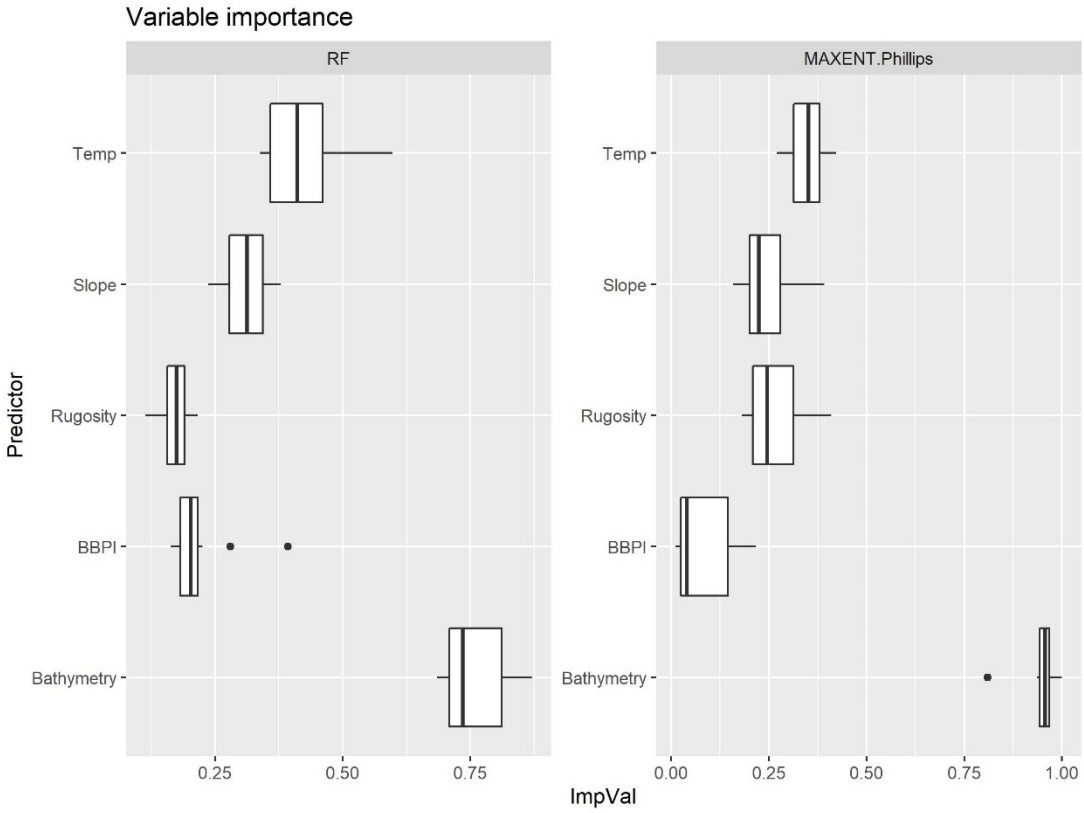
A6.2. Break down of biotope model results by modelling method and thresholding metric.

Biotope	Model	TSS	Threshold	Sensitivity	Specificity
AcaArb	RF	1.00	0.39	100.00	100.00
	MaxEnt	0.64	0.17	100.00	63.54
BurAne	RF	1.00	0.33	100.00	100.00
	MaxEnt	0.59	0.24	91.18	67.42
MixCor	RF	1.00	0.36	100.00	99.64
	MaxEnt	0.47	0.39	66.95	79.65
SpnMeg	RF	1.00	0.36	100.00	99.64
	MaxEnt	0.47	0.39	66.95	79.65
SolRee	RF	1.00	0.35	100.00	99.61
	MaxEnt	0.60	0.32	86.75	73.37
SolScl	RF	1.00	0.37	100.00	100.00
	MaxEnt	0.71	0.54	82.76	88.38
SyrFra	RF	1.00	0.36	100.00	99.57
	MaxEnt	0.61	0.28	94.78	66.55

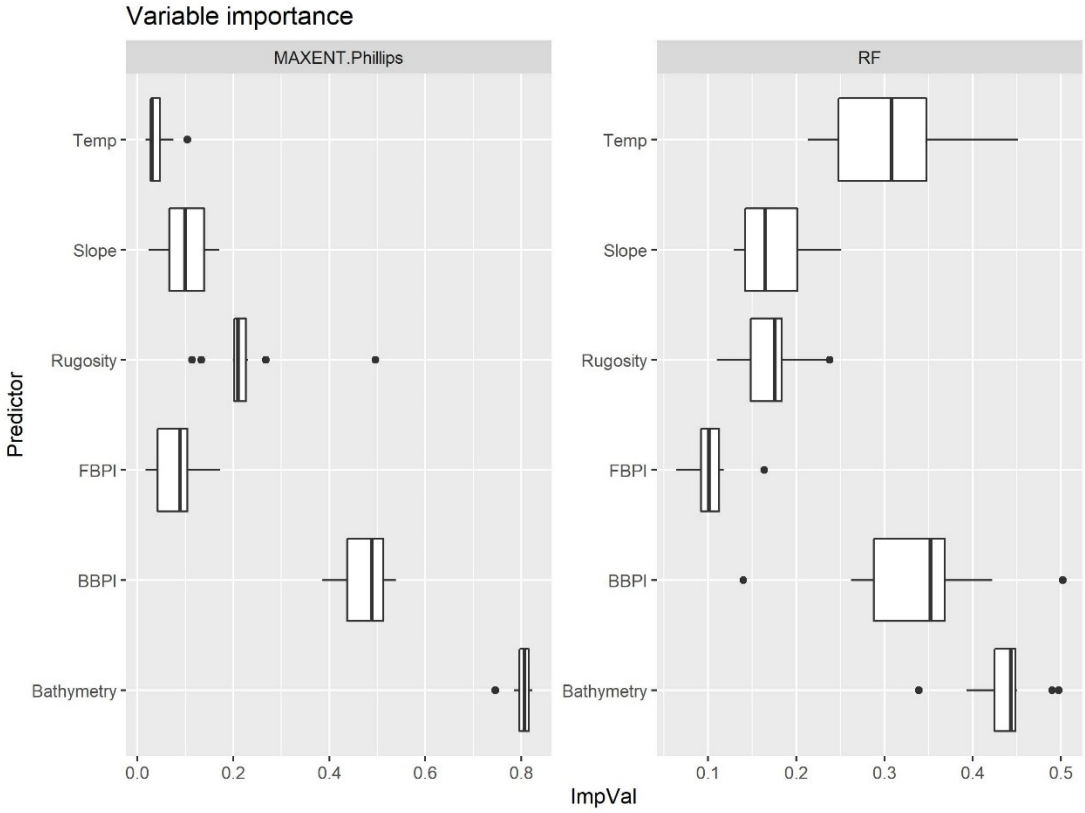
Appendix 7 – Variable Importance

Plots of predictor variable importance for each modelling method, for each VME.

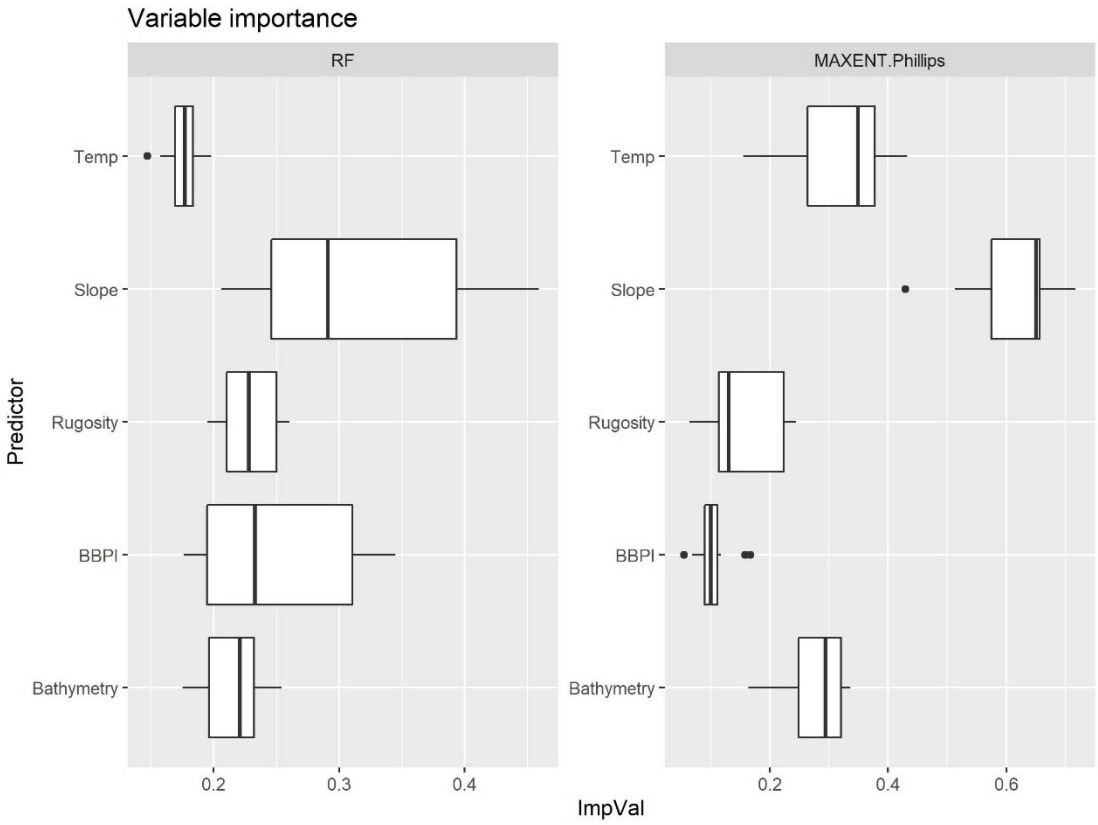
A7.1. AcaArb



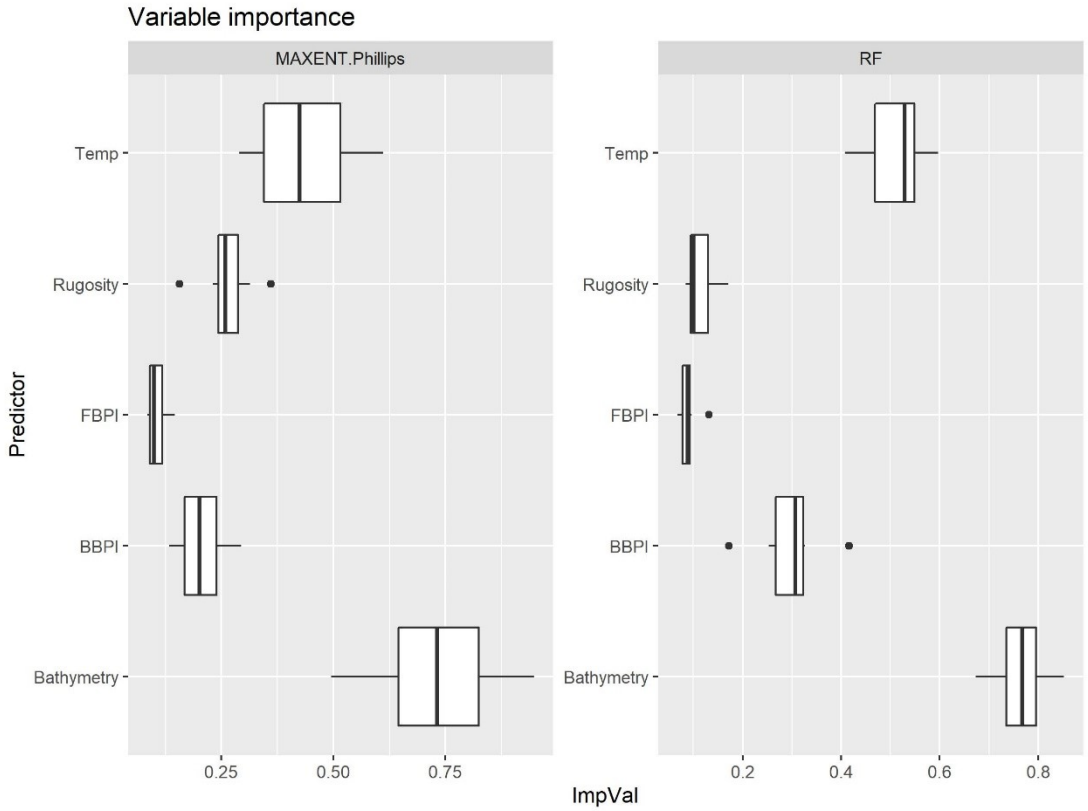
A7.2. BurAne



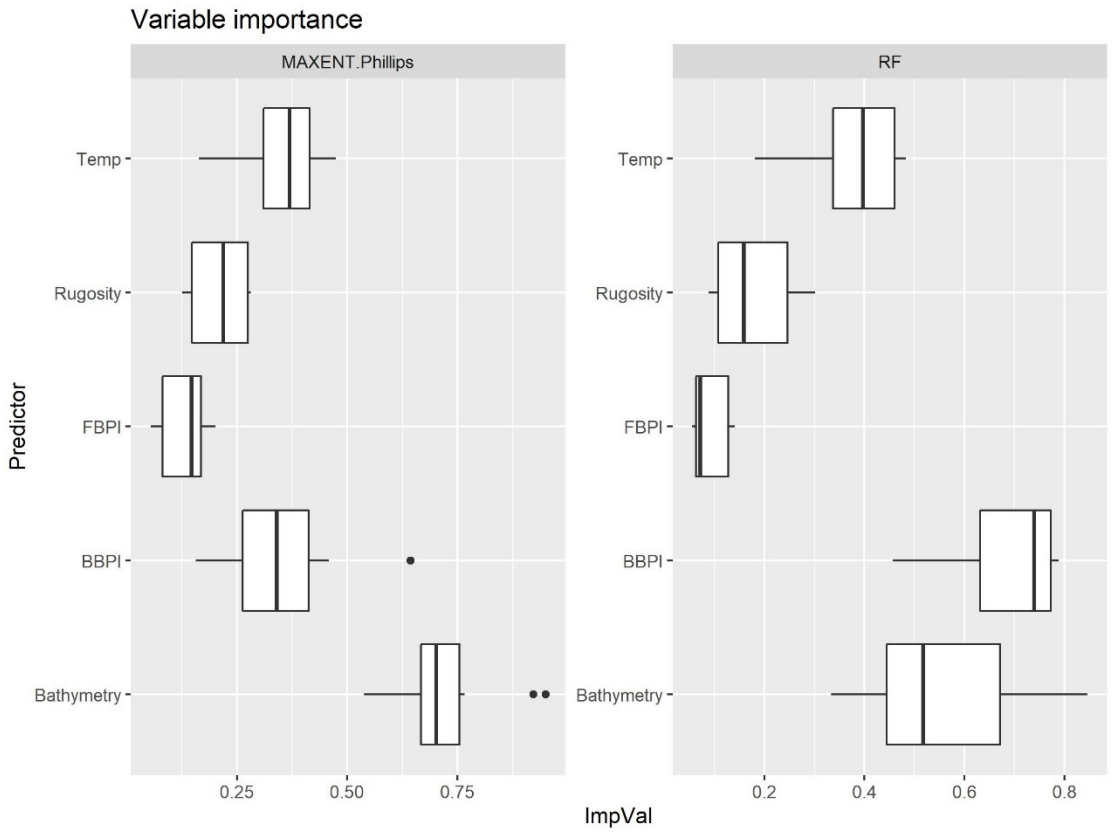
A7.3. MixCor



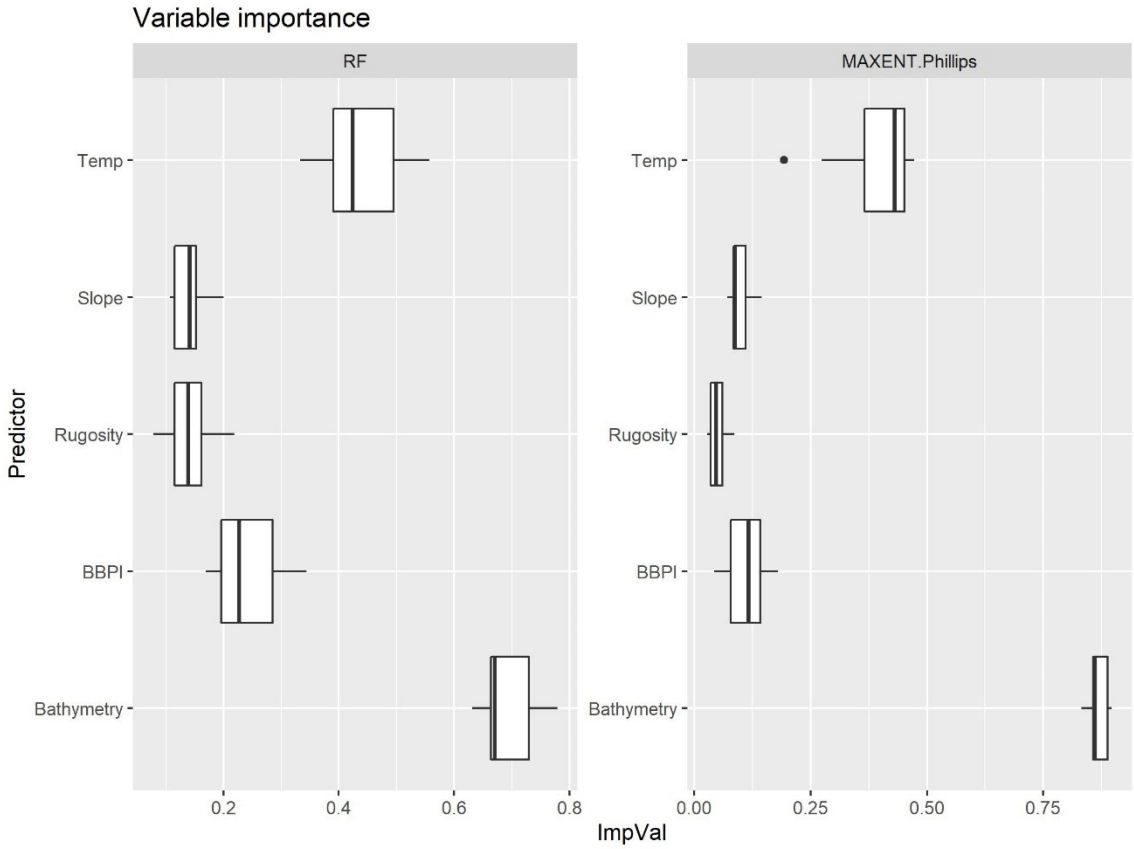
A7.4. SpnMeg



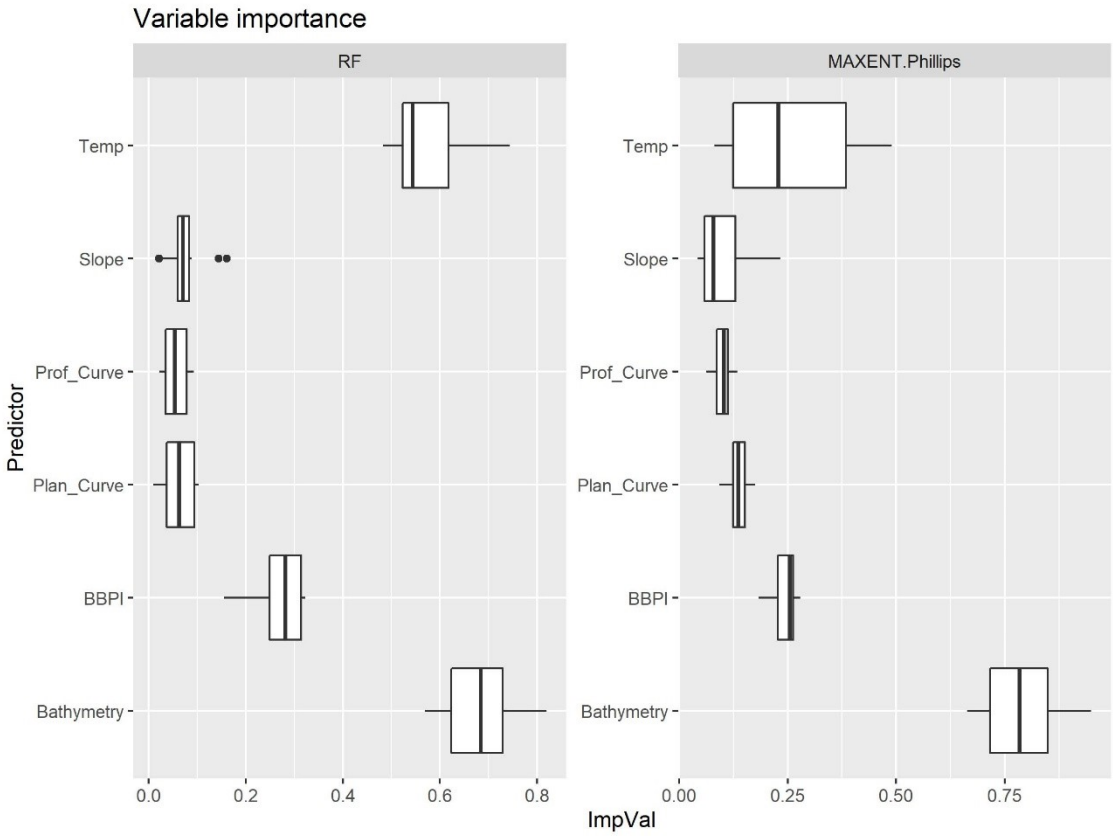
A7.5. SolRee



A7.6. SolScl

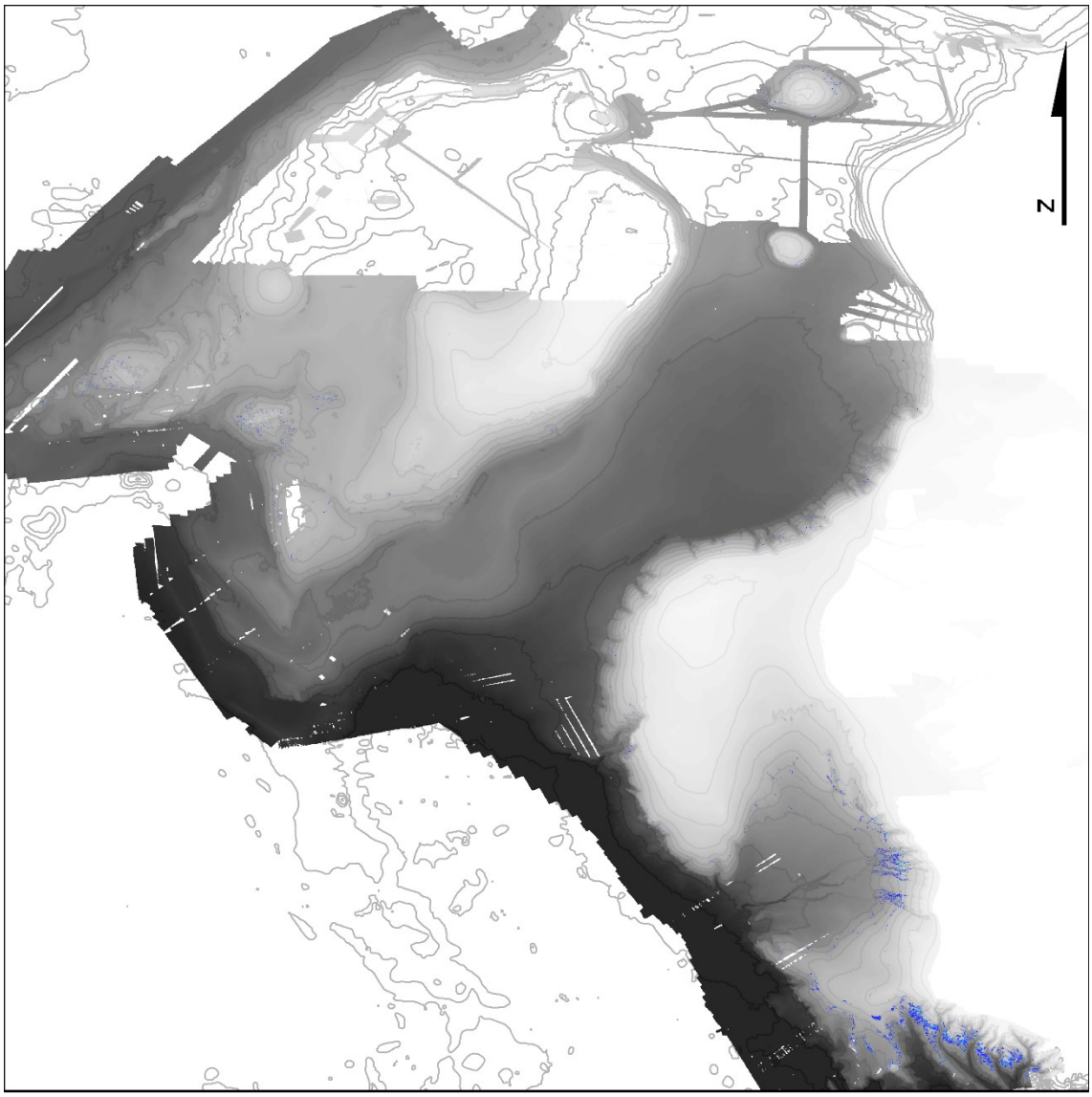


A7.7. SyrFra



Appendix 8 – Spatial Predictions of VME Distribution

The continuous predictions of ensemble models for each VME above the final threshold selected, overlaid on bathymetry data. BIOMOD creates predictions on a 0-1000 scale; consider this as a classical probability (0-1) multiplied by 1000.



Probability of AcaArb Suitable Habitat

Value

High : 846

Low : 380

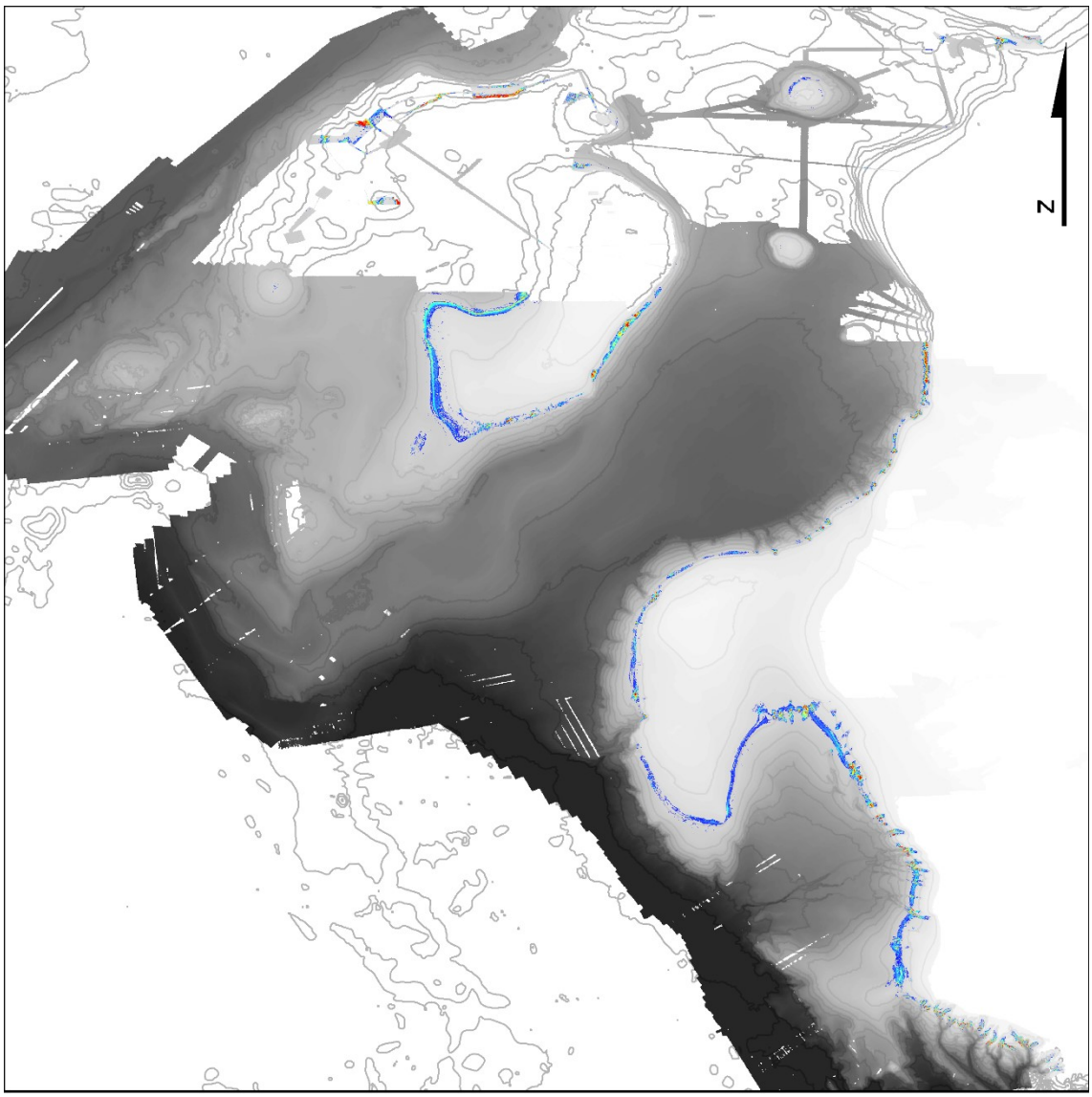
Depth & Model Extent

Value

High : 0

Low : -4000

Contours (GEBCO)



Probability of BurAne Suitable Habitat

Value

High : 958

Low : 320

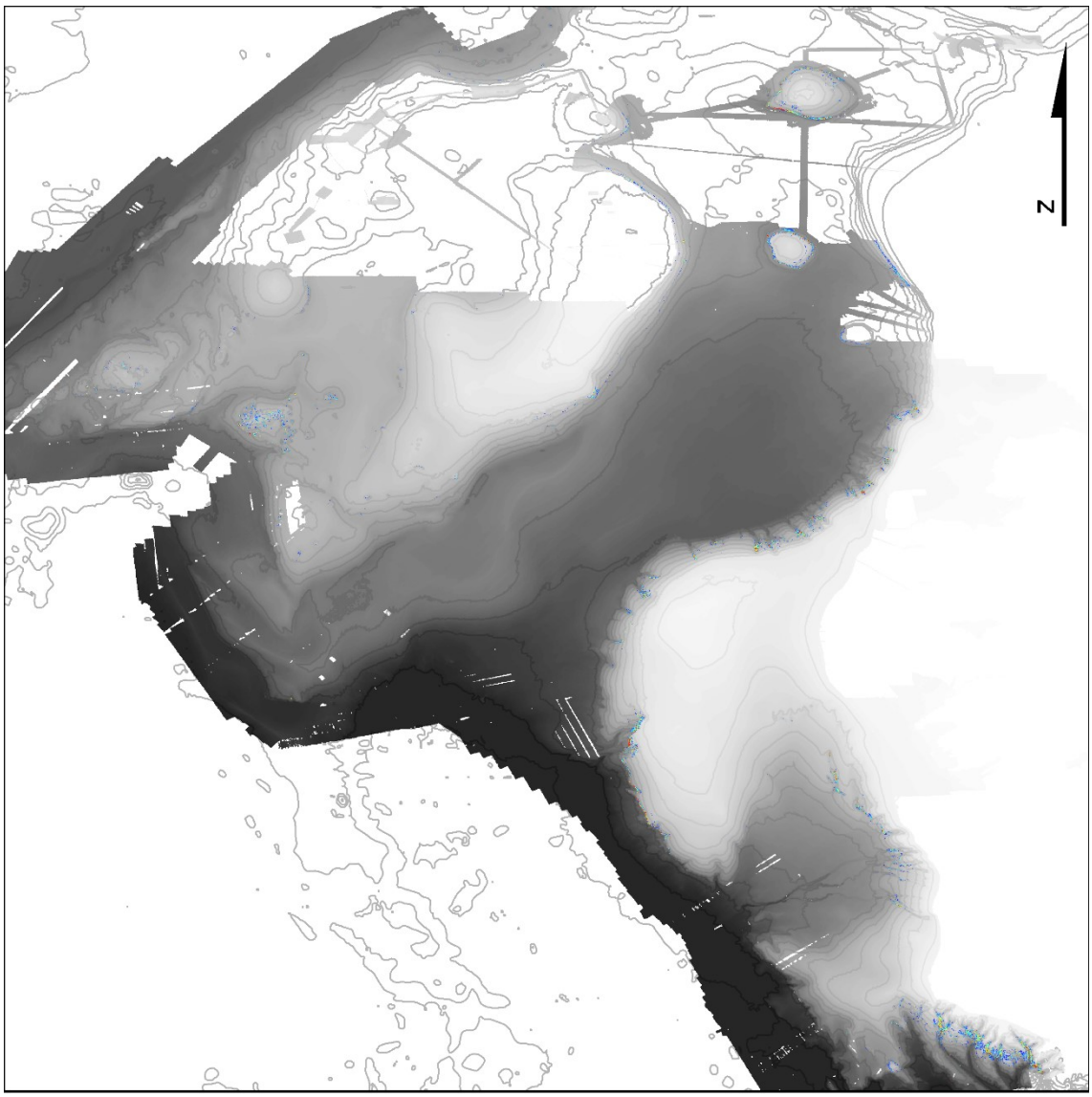
Depth & Model Extent

Value

High : 0

Low : -4000

Contours (GEBCO)



Probability of MixCor Suitable Habitat

Value

High : 988

Low : 380

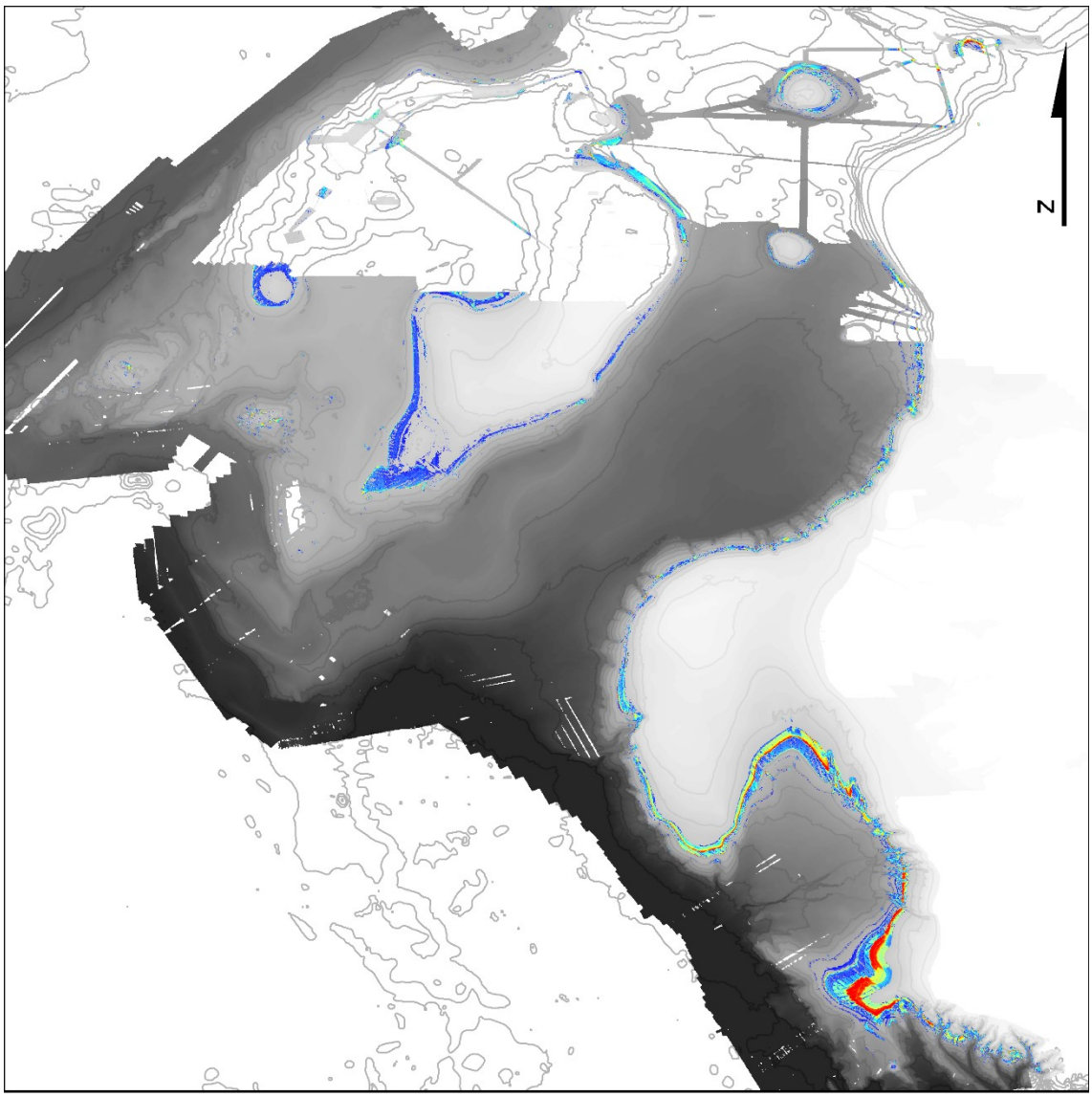
Depth & Model Extent

Value

High : 0

Low : -4000

Contours (GEBCO)



Probability of SolRee Suitable Habitat

Value

High : 946

Low : 360

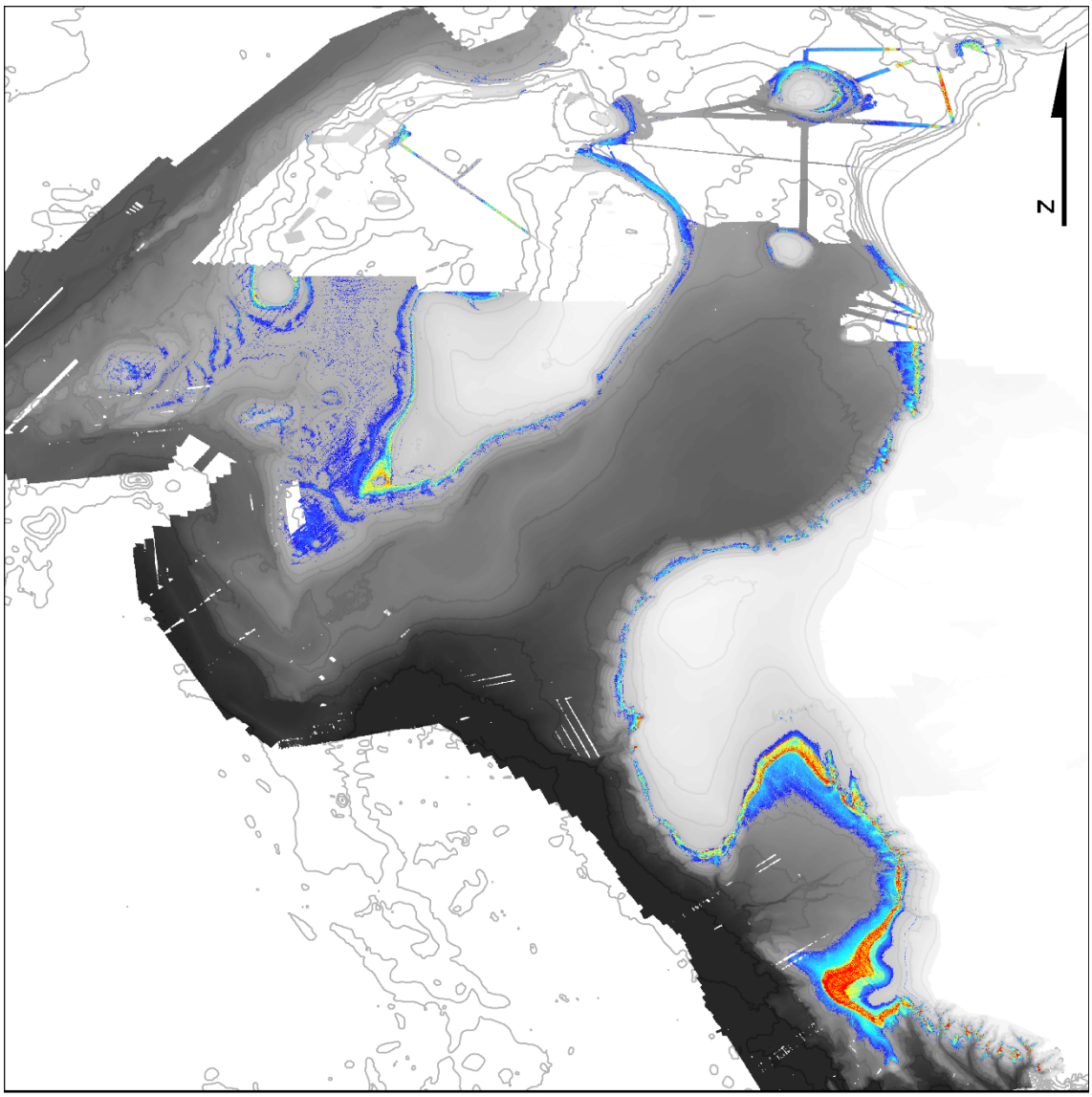
Depth & Model Extent

Value

High : 0

Low : -4000

Contours (GEBCO)



Probability of SolScl Suitable Habitat

Value

High : 963

Low : 300

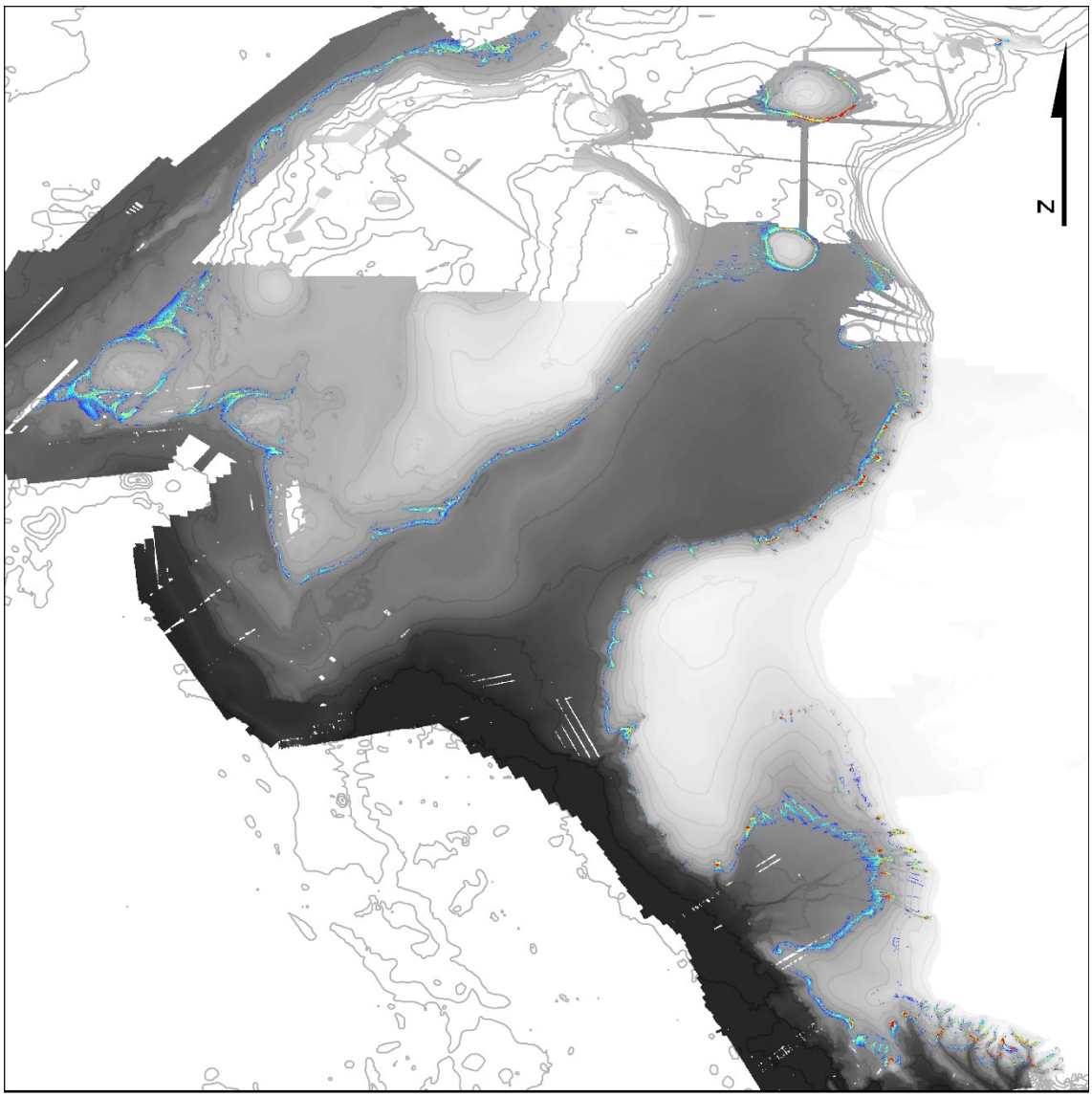
Depth & Model Extent

Value

High : 0

Low : -4000

Contours (GEBCO)



Probability of SpnMeg Suitable Habitat

Value

High : 920

Low : 270

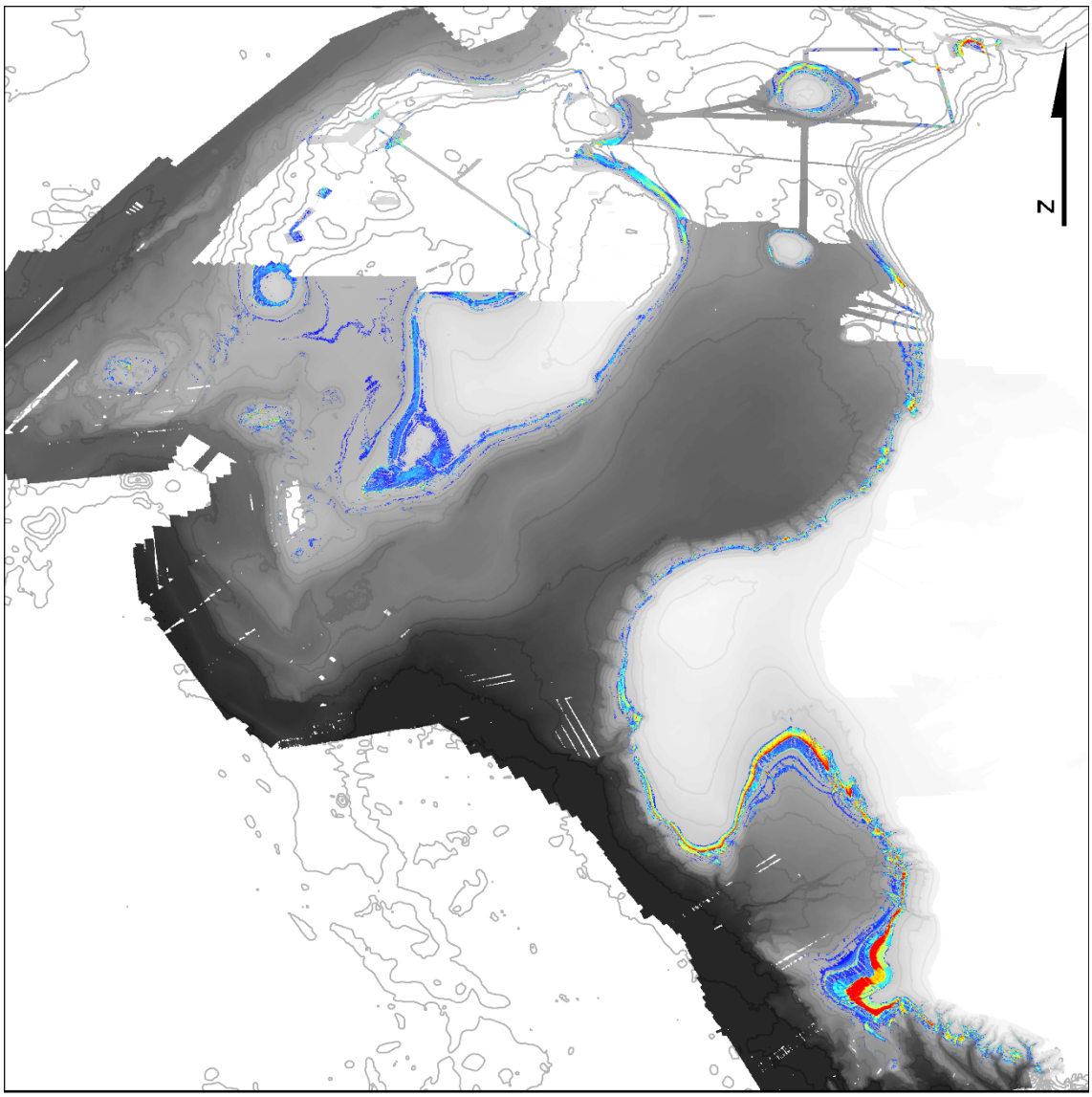
Depth & Model Extent

Value

High : 0

Low : -4000

Contours (GEBCO)



Probability of SyrFra Suitable Habitat

Value

High : 960

Low : 390

Depth & Model Extent

Value

High : 0

Low : -4000

Contours (GEBCO)

Appendix 9 – Extent of Multibeam Bathymetry

Table A9.1. The area of multibeam bathymetry (km^2) available for each nation and by national marine protected area (MPA) network.

Nation	ECS (km^2)	MPA (km^2)	% of National Bathymetry within MPAs
UK	106,990	37,407	34.96%
IRE	574,080	22,615	3.94%