Seagrass habitat suitability model for Redang Marine Park using multibeam echosounder data: Testing different spatial resolutions and analysis window sizes

Muhammad Abdul Hakim Muhamad¹, Rozaimi Che Hasan¹ *, Najhan Md Said², Jillian Lean-Sim Ooi³

¹ Razak Faculty of Technology and Informatics, Universiti Teknologi Malaysia, Kuala Lumpur, Malaysia, ² National Hydrographic Centre, Pulai Indah, Selangor, Malaysia, ³ Department of Geography, Faculty of Arts and Social Sciences, Universiti Malaya, Kuala Lumpur, Malaysia

* rozaimi.kl@utm.my

Abstract

Integrating Multibeam Echosounder (MBES) data (bathymetry and backscatter) and underwater video technology allows scientists to study marine habitats. However, use of such data in modeling suitable seagrass habitats in Malaysian coastal waters is still limited. This study tested multiple spatial resolutions (1 and 50 m) and analysis window sizes (3 × 3, 9 × 9, and 21 × 21 cells) probably suitable for seagrass-habitat relationships in Redang Marine Park, Terengganu, Malaysia. A maximum entropy algorithm was applied, using 12 bathymetric and backscatter predictors to develop a total of 6 seagrass habitat suitability models.

The results indicated that both fine and coarse spatial resolution datasets could produce models with high accuracy (>90%). However, the models derived from the coarser resolution dataset displayed inconsistent habitat suitability maps for different analysis window sizes. In contrast, habitat models derived from the fine resolution dataset exhibited similar habitat distribution patterns for three different analysis window sizes. Bathymetry was found to be the most influential predictor in all the models. The backscatter predictors, such as angular range analysis inversion parameters (characterization and grain size), gray-level co-occurrence texture predictors, and backscatter intensity levels, were more important for coarse resolution models. Areas of highest habitat suitability for seagrass were predicted to be in shallower (<20 m) waters and scattered between fringing reefs (east to south). Some fragmented, highly suitable habitats were also identified in the shallower (<20 m) areas in the northwest of the prediction models and scattered between fringing reefs. This study highlighted the importance of investigating the suitable spatial resolution and analysis window size of predictors from MBES for modeling suitable seagrass habitats. The findings provide important insight on the use of remote acoustic sonar data to study and map seagrass distribution in Malaysia coastal water.
Introduction

Seagrass ecosystems provide many critical ecological functions that support the well-being and livelihoods of local communities [1, 2]. Seagrass ecosystems provide food for many marine species [3, 4] and serve as nursery grounds for fishes [5, 6]. They are also known for their capacity to produce and export organic carbon, regulate carbon dioxide through photosynthesis, absorb and recycle nutrients, stabilize sediment, reduce coastal erosion [7–9], and reduce pathogens and disease prevalence in neighboring coral reefs [9]. Seagrass occurs in tropical and temperate waters and is generally found in coastal subtidal and intertidal areas [10]. In Malaysia, seagrass is distributed into four primary regions on the west and east coast of Peninsular Malaysia and Sabah and Sarawak in East Malaysia [11–15]. The coast of Peninsular Malaysia is relatively broad, and ecological conditions vary on the east and west coasts. Seagrasses are usually found in calm lagoons on the west coast, sheltered from the open sea behind the tidal sand ridges. On the east coast, they are found on offshore islands (e.g., Sibu Island, Tinggi Island, and Redang Island) with fringing corals and colonize the outer coastal area between the coral and semi-open seas. On the west coast, seagrass can be found in open sea coastal waters. In Sabah, patches of seagrass beds are found extensively along the west coast (e.g., Bak-Bak, Tanjung Mengayau, Sepangar Bay, and Gaya Island), south-eastern coast, and offshore islands (e.g., Sipadan, Maganting, Tabawan, and Bohey Dulang). In Sarawak, seagrasses are normally scattered near river estuaries (e.g., Bintulu River, Punang–Sri Lawas River estuary). Furthermore, seagrass also inhabits deep subtidal areas and intertidal sandy, rocky shores on Kuala Similajau, Bintulu, Sarawak.

Seagrass ecosystems are susceptible to both natural and anthropogenic threats [16, 17]. Malaysian seagrass ecosystems continually face serious threats from natural causes (e.g., erosion, flooding, surface water temperature, and turbidity) and human activities (e.g., dynamite fishing, sand mining, dredging, settlement, and construction) that cause significant degradation and possible habitat loss [17, 18]. The Sungai Pulai estuary in Johor is a threat that has arisen because of the development of coastal zones and islands. The development involves sand mining, filling, and land reclamation, which have immediately and substantially affected the marine environment and its resources. Land reclamation has led to heavy loads of suspended sediments, which often deposit a layer of silt that are several centimeters deep over the seagrass and benthic communities [18]. The seagrass at Gaya Island in Sabah declined because of heavy loads of suspended sediments, which reduced the sub-surface light intensity. Human activities involve dynamite fishing and construction, which are directly responsible for suspended sediments and water turbidity in coastal waters and seagrass habitat decline [19]. Furthermore, the seagrass at Pengkalan Nangka in Kelantan, Paka in Terengganu, and Punang-Sari Lawas in Sarawak degraded in term of occurrences because of human activities such as sand mining, heavy loads of suspended sediments, heavy rains, and floods. Due to this reason, efforts to systematically manage and map seagrass habitat in Malaysia is needed to map and monitor the seagrass ecosystems.

In the last few decades, scientists have been using underwater acoustic survey technologies to establish the relationship between geomorphological characteristics and benthic communities [20–25]. Multibeam echosounders (MBES), which are able to perform full-coverage mapping with a high spatial resolution dataset, have been used for the development of marine habitat suitability maps for fishes [26, 27], corals [28–32], starfishes, and crinoids [31], seagrass [33], and kelp [34]. Bathymetry maps and backscatter mosaics are the two primary products from MBES that can be used as surrogates for mapping patterns and processes on the seafloor (e.g., seafloor morphology and sediment composition) that influence the distribution of marine habitats. Bathymetry provides information on seafloor depth and multiple measures of
seafloor complexity through terrain analysis [35]. The applications of bathymetry data, together with a wide range of physical predictors (e.g., aspect, slope, and rugosity) in mapping habitat distribution, have been demonstrated in previous studies [26, 31, 35–38], revealing the relationship between the acoustic measurements of seabed types and benthic habitats [39–41]. Backscatter data can provide information on different substrates by referring to different intensity levels [42]. These data have been used to identify the substratum type of seafloor in many habitat suitability predictions [31, 43].

Various modeling methods using bathymetry, backscatter, and their secondary derivatives (constructed from bathymetry or backscatter) for habitat suitability model (HSM) have been used previously [44–46]. These techniques have differed widely, in terms of the implemented algorithms and input data features. Combining these techniques with in-situ data to characterize the physical and biological datasets makes it possible to produce accurate HSMs [47]. Habitat suitability modeling is a widely used technique for predicting the spatial distribution of species and has been implemented in benthic-related studies [44, 48–50]. Habitat suitability modeling generally quantifies the relationship between occurrence data and predictors to explore the spatial distribution of a species and the response curve in relation to environmental factors [51–54].

The selection of a suitable spatial resolution dataset is important in marine environments [55–57]. High spatial resolution data will produce maps with detailed information, which is useful for detailed marine spatial management and planning [55]. In contrast, a low spatial resolution dataset might be used in a biogeographic study that involved measurement and monitoring patterns of species richness across broad spatial extents [58], such as influencing the accuracy of the HSM and management effectiveness in the marine environment [59]. Previous studies [50, 60] have conducted HSMs using several spatial resolutions by utilizing predictors extracted from various types of data sources. Spatial resolution was found to influence the correlation among predictors, model performance, suitability of predictors to predict habitat, and the spatial pattern of habitat suitability. Investigations of a suitable spatial resolution in habitat suitability studies are still limited; however, choosing the appropriate spatial resolution is expected to result in more meaningful habitat models [61].

Predicted habitats may also theoretically react to predictors for different analysis window sizes [27, 62]. However, there is limited understanding of the optimal window size for interpreting the relationship between species and habitat [63]. Associated predictors (e.g., bathymetric and backscatter predictors) are normally computed for specific analysis window sizes [44, 64]. Predictors are extracted from the primary data (e.g., bathymetry map and backscatter mosaic) using focal or neighborhood cell analysis. The derivation of predictors from the primary data at particular sizes of analysis windows (e.g., 3 × 3 or 9 × 9 cells) may not be sufficient to reflect the processes of interest [65, 66]. Furthermore, to our knowledge, no specific study has examined the effect of these window sizes on seagrass HSM. Thus, a detailed study is needed to investigate the proper analysis window size for seagrass HSMs. Adopting a multi-scale approach to mapping seagrass habitats should ensure the capture of relevant scale-dependent predictors of ecological patterns and processes [67].

The primary objective of this study was to demonstrate the effect of different spatial resolutions and analysis window sizes on the production of seagrass habitat suitability maps. First, we collected and processed the bathymetry and backscatter datasets from the MBES. Second, we constructed the secondary predictors from bathymetry and backscatter using several analysis window sizes (3 × 3, 9 × 9, and 21 × 21 cells) and different spatial resolutions (1 and 50 m). Finally, we compared the performance of various habitat suitability models built using maximum entropy (MaxEnt) and identified the contributions of each variable to the prediction of seagrass habitat.
Materials and methods

Study area

The Redang archipelago is located in the South China Sea off the east coast of Peninsular Malaysia, in the state of Terengganu. It is located approximately 24 nautical miles off Terengganu’s coastline (Fig 1). Since 1993, the Department of Marine Park (now the Marine Park and Resource Management Division, Department of Fisheries Malaysia, Ministry of Agriculture and Food Industry) was responsible for protecting the offshore islands and their surrounding coastal waters. In the same year under the Fisheries (Prohibited Areas) Regulations 1983 (Fisheries Act, 1963), the Redang archipelago was initially designated as a Fisheries Prohibited Area. With the establishment of the Marine Park Malaysia Order 1994 (Fisheries Act in 1995), the Redang archipelago was designated as a marine park, known as Redang Marine Park (RMP). The boundary of the RMP extends from the coastline (i.e., lowest sea level) up to two nautical miles and was established by the Marine Park and Resource Management Division [68]. This archipelago comprises Redang as the main island, together with eight small islands. The smaller islands are Pinang, Lima, Ekor Tebu, Kerengga Kecil, Kerengga Besar, Paku Besar, Paku Kecil, and Ling. Among these islands, Redang, Pinang, Lima, and Ekor Tebu have been established as part of the RMP.

![Study Area Map](https://doi.org/10.1371/journal.pone.0257761.g001)

Fig 1. Location of the study area. Study areas are marked with a red dashed polygon which extends two nautical miles from the shoreline of Pulau Redang and other small islands.

https://doi.org/10.1371/journal.pone.0257761.g001
The objective of marine parks is to provide protection to marine resources and habitats. Simultaneously, the marine park serves as a management tool to encourage sustainability in the marine ecosystem to ensure that marine resources are utilized sustainably [69]. Marine parks have been recognized to comprise at least one of these three main marine ecosystems: coral reefs, mangroves, or seagrass. RMP comprises two marine ecosystems: coral reefs [70] and seagrass [71]. Three seagrass species were recorded around the RMP from 13 species that were distributed over the broad areas of Peninsular Malaysia, including *Halophila decipiens*, *H. minor*, and *Halodule pinifolia* [71]. Most of these species can be found at Chagar Hutang, Redang River estuary, Pasir Panjang, and Teluk Dalam (Fig 1) and are generally distributed in subtidal areas. The species depth ranged from 2.5 to 24 m [71] and mainly occurred on the sedimentary substrate composed of silt and sand [71]. Equally important, Redang Island is known as a turtle nesting area [72, 73], and the *H. decipiens* meadows in the coastal area serve as feeding grounds for turtles [71].

Data acquisition and processing

**MBES survey.** A Multibeam Echosounder (MBES) survey was carried out at two nautical miles from Redang Island and within the Redang archipelago (Fig 1) from April 6 to 24, 2019. The MBES dataset (e.g., bathymetry and backscatter) was acquired using a port-side mount Kongsberg EM2040C MBES system. Data logging, real-time quality assurance, display, and navigation were performed using Kongsberg Maritime’s acoustic data acquisition software, Seafloor Information System (SIS). The MBES operated at a frequency of 300 kHz, with different ping rates and pulse lengths that were automatically adjusted to the water depth in a high-density equidistant mode (400 beams per ping). Sound velocity profiles were collected using a sound velocity profiler once a day using a Valeport Monitor Sound Velocity Profiler. Tides were collected using a TideMaster Portable Tide Gauge at regular intervals of 10 min during MBES survey. The vessel’s position was acquired by a differential global positioning system (DGPS) mode using GPS/GLONASS corrections received by radio from the Fugro Marine Star satellite positioning service. A precise motion sensor system was used to measure the vessel motion data (e.g., heave, pitch, roll, yaw, and heading), which were recorded and set aside for data processing.

**Ground-truth survey.** Ground-truth data were recorded using a GoPro Hero 4 high-definition camera mounted on a stainless-steel frame. This frame was then dropped from the water surface to the seafloor, and the depth of each observation was ≤30 m. Within the MBES surveyed area, a cluster sampling technique was used in this study, where the targeted seagrass habitat locations were carefully chosen to capture all seagrass distributions based on a previous study [71]. The recorded video data were used to obtain video and photographic evidence of the occurrence of seagrass at each drop point. Surface positioning information was achieved using the AtlasLink H10 Smart Antenna. The position accuracy was improved by the DGPS method, which received the Atlas GNSS global correction service (accuracy of ± 50 cm). The expected error range for the true underwater position of each drop was estimated within a MBES pixel. Each recorded video data was analyzed and classified according to seagrass occurrence. All presence-only seagrass occurrence data were randomly selected for model training (75%) and model testing (25%).

**Bathymetry data processing.** The raw MBES bathymetry data were processed using CARIS HIPS & SIPS version 10.4 following these steps: a) filtering of the position information using DGPS data, b) filtering of the motion information using attitude data (e.g., heading, heave, pitch, roll), c) depth correction using tidal observation data, and sound speed correction using sound velocity profiler data, d) data cleaning to remove uncertain data, and e) processed
Bathymetry data were gridded at several spatial resolutions, including 1 and 50 m (WGS 1984, UTM Zone 48 N) (Fig 2). The 1m dataset was used to test the effect of the high-resolution MBES dataset on the performance and prediction distribution of seagrass HSM. At the same time, 50m data was used to see the results of a low spatial resolution MBES dataset which is suited for regional studies (i.e., larger areas).

**Backscatter data processing.** The raw MBES backscatter data were processed using Fledermaus Geocoder Toolbox (FMGT) 7.4.4. The backscatter beam average data type was used as a backscatter data source, and all beams (400 beams) were used (starting and cut-off beam angles of 0˚ and 90˚, respectively). The beam average was used to produce a backscatter mosaic image owing to some artifacts observed when processing the “beam time-series” data types. This was mostly due to the automatic mode used during MBES data acquisition (i.e., the pulse length is automatically adjusted according to the current water depth). The processing parameters remained closer to the FMGT default settings to maintain continuity between the surveys of the backscatter mosaics at the potential detriment of the subjective nature of each mosaic. Finally, the processed backscatter data were gridded to produce a backscatter mosaic at two spatial resolutions: 1 and 50 m (WGS1984, UTM Zone 48 N) (Fig 3). Two types of backscatter mosaics were used for this study: backscatter intensity presented in decibel (dB) values and backscatter intensity scaled to 8-bit grayscale values. The backscatter mosaic in dB values was
the original intensity derived in FMGT while scaled intensity was used in the texture analysis. Apart from the mosaic, the prediction of sediment types and properties was also extracted using the angular range analysis (ARA) method in FMGT [74]. The mean grain size (phi) and sediment characterization were the two main outputs extracted from ARA processing and were used for this study. Each ARA parameter was exported to the raster format for further analysis.

**Bathymetric predictors.** A suite of bathymetric derivatives was obtained from the bathymetry maps to further describe the local variability within the MBES bathymetry data and delineate the topographic features [35, 59]. A set of four bathymetric predictors derived from bathymetry data were collected by the MBES survey using Geomorphometry for Ecology tool (Raster) in TASSE Toolbox v.1.1 [75]. The bathymetric predictors were derived using different surface analysis methods for extracting the geomorphological characteristics, such as slope, curvature [43], eastness, and northness [35, 38, 76, 77] (Table 1).

**Backscatter predictors.** Backscatter predictors (a continuous variable) characterize the acoustic reflectivity of the seafloor and are valuable surrogates for substratum features [27]. To further describe the local variability within the MBES backscatter data and delineate the seafloor substrate features, a suite of backscatter textural properties was produced from the backscatter mosaic (8-bit grayscale) using Haralick gray-level co-occurrence matrices (GLCMs) [24, 78]. The GLCM predictors were correlation, entropy, and homogeneity (Table 1).

---

**Fig 3. Backscatter mosaic of Redang archipelago.** Backscatter mosaic of the study areas. Red and blue dots represent the presence and absence of seagrass occurrence, respectively.

https://doi.org/10.1371/journal.pone.0257761.g003
Derivation of predictors at different analysis window sizes. The effect of analysis window size in bathymetric and backscatter predictors on the model predictions was tested by deriving all predictors at several analysis window sizes. This was completed using the focal statistics (mean) analysis function in ArcMap. Focal statistics (mean) analysis identified the average value of a variable within a specified window size centered on a given cell and positioned these data to the corresponding cell location. Three different window sizes (3×3, 9×9, and 21×21 cells) were used to mimic a range of analysis window sizes at which the topography (bathymetric predictors) and substratum (backscatter predictors) features might affect the distribution of seagrass (Table 1).

Correlation analysis of predictors. Correlations between the entire set of candidate predictors were initially reduced by excluding highly correlated predictors, based on the Pearson product-moment correlation coefficient [82]. The removal of high correlated predictors has been shown to be useful for habitat suitability model development in marine environment [31, 83]. Predictors with low correlations to other predictors which occurred in unique clusters were prioritized to avoid omitting information that was not already provided by other predictors and to avoid including only high-performing variables that provided similar information. Predictors with value correlation coefficients >0.5 were considered to have high correlation [84]. For each model prediction, individual predictor performance was tested using an iterative ‘leave-one-out’ procedure (the best predictor was retained when the value correlation coefficients were <0.5). Predictors with value correlation coefficients of >0.5 were eliminated from the model development, and only low correlation predictors were used for further analysis.

Habitat suitability modeling. Habitat suitability modeling was carried out using maximum entropy (MaxEnt) species distribution modeling in MaxEnt software v3.4.1 [85]. MaxEnt used presence-only species occurrence data to estimate the probability of occurrence of a species that was used to distinguish between suitable and unsuitable areas [86]. MaxEnt has been found to be amongst the consistent methods with high accuracies for presence-only

### Table 1. Multiple analysis window sizes of bathymetric and backscatter predictors for seafloor morphology and sediment properties used in this study.

| Predictors                              | Description                                                                 | Analysis window size (cell) | Software                   |
|-----------------------------------------|-----------------------------------------------------------------------------|------------------------------|-----------------------------|
| Bathymetry                              | Measures the depth (negative elevation) of the seafloor surface [79]         | 3×3, 9×9, 21×21              | Focal Statistics (ArcGIS 10.5) |
| Slope                                   | Rate of maximum change in depth from each cell of a surface raster in degree unit [80] | 3×3, 9×9, 21×21              | TASSE Toolbox v.1.1          |
| Eastness                                | Measures the seafloor surface direction for the east and west directions    | 3×3, 9×9, 21×21              | TASSE Toolbox v.1.1          |
| Northness                               | Measures the seafloor surface direction for the north and south directions  | 3×3, 9×9, 21×21              | TASSE Toolbox v.1.1          |
| Curvature                               | Calculates the curvature of a raster surface [81]                           | 3×3, 9×9, 21×21              | TASSE Toolbox v.1.1          |
| Backscatter Mosaic in decibels (dB)     | Represents the acoustic intensity scattered by the seafloor [42]             | 3×3, 9×9, 21×21              | Focal Statistics (ArcGIS 10.5) |
| Backscatter Mosaic 8-bit greyscale      | Backscatter Mosaic was reduced into greyscale raster (0–255 units)          | 3×3, 9×9, 21×21              | Focal Statistics (ArcGIS 10.5) |
| Homogeneity, Entropy, and Correlation   | GLCM texture features predictors [78]                                      | 3×3, 9×9, 21×21              | ENVI                        |
| Phi and Characterization                | ARA-parameters for acoustic seafloor characterization [74]                  |                               | FMGT                        |

https://doi.org/10.1371/journal.pone.0257761.t001
modelling in several marine studies [26, 87–95]. MaxEnt determined the probability distribution of the maximum entropy (i.e., the most dispersed or the closest to the uniform), and then constrained the distribution by utilizing a series of environmental predictors with a variety of values identified by the landscape at the locations where the species was known to occur [85]. MaxEnt is based on the premise that the unknown distribution of probabilities should have maximum entropy but is restricted by the niche’s environmental characteristics. MaxEnt controlled overfitting and variable selection using a regularization that smoothed out the distribution models, with a penalized maximum likelihood model that balances the model with the complexity of the model [49, 96]. MaxEnt was run using all seagrass occurrence data and selected MBES predictors. All models were using default settings in MaxEnt software, which were previously found to achieve excellent model performance [96–99]. For all models, auto features were used, which allows automatic limiting of feature types according to the amount of ground-truth data (i.e., seagrass presence data). The interaction between MBES predictors is automatically allowed to improve model performance. [96, 98, 99]. Twenty replicates and bootstrap procedures were used to obtain a firm model. Each replicate used randomly selected presence-only seagrass occurrence data for training data and test data (75% and 25% of the data, respectively) [98]. The output format portrayed in the logistic habitat suitability index ranged from the lowest "0" as low suitability for seagrass habitat to the highest "1" as high suitability for seagrass habitat.

In this study, the models that were trained with six different sets of predictors derived from MBES bathymetry and backscatter data were as follows:

a. Model1_3—Uncorrelated predictors gridded at 1 m and derived using 3 × 3 analysis window size.
b. Model1_9—Uncorrelated predictors gridded at 1 m and derived using 9 × 9 analysis window size.
c. Model1_21—Uncorrelated predictors gridded at 1 m and derived using 21 × 21 of analysis window size.
d. Model50_3—Uncorrelated predictors gridded at 50 m and derived using 3 × 3 analysis window size.
e. Model50_9—Uncorrelated predictors gridded at 50 m and derived using 9 × 9 analysis window size.
f. Model50_21—Uncorrelated predictors gridded at 50 m and derived using 21 × 21 of analysis window size.

Assessment of model performance. Receiver operating characteristic (ROC) curves were constructed, and the area under the curve (AUC) was used to compare the performance of the models [100]. The AUC is a test statistic that uses the presence and absence records to assess predictive model performance across the threshold ranges. This study utilized the Phillips approach [85] which applied randomly chosen pseudo-absences to ROC AUC rather than observed absences. The AUC was calculated based on the specificity and sensitivity of the predictive model. The specificity and sensitivity indicated the success rate for classifying suitable or less suitable seagrass habitats, respectively. The built-in function of the MaxEnt program produced mean AUC values of twenty replicates. AUC values >0.9 were indicated as excellent, 0.8–0.9 as very well, 0.7–0.8 as satisfactory and <0.7 represented poor discriminative ability [101, 102].
**Results**

**Variable selection**

This study found a weak correlation ($<0.5$) among several predictors derived from bathymetry data but not among those from backscatter data. The number and type of predictors with weak correlations varied between the models (Table 2). For Model1_3 and Model1_9, a weak correlation was found among bathymetry, slope, eastness, northness, and GLCM entropy with other predictors (S1 and S2 Figs). For Model1_21, only four predictors derived from bathymetry data such as slope, eastness, and northness were found to be uncorrelated predictors, among others (S3 Fig). For Model50_3, bathymetry, slope, and eastness derived from bathymetry data were found to be uncorrelated predictors, and GLCM correlation, GLCM entropy, and ARA characterization derived from backscatter data were found as uncorrelated predictors (S4 Fig). For Model50_9, low correlated predictors were found among bathymetry, slope, eastness, and northness derived from bathymetry data, and ARA characterization derived from backscatter data (S5 Fig). Bathymetry, slope, eastness, northness, and backscatter mosaic were observed as low correlation predictors in decibels (dB) for Model50_21 (S6 Fig).

**Seagrass presence from ground-truth**

From the ground-truth dataset, 61 video drops were collected from the survey area. From all points, only nine points (red dots) were identified as having seagrass occurrences (Fig 2), while the remaining 52 drop points (blue dots) were absent data. Seagrass presence data were primarily found in the shallow water area with water depths ranging from 5.7 to 18.3 m (Fig 2). These areas displayed backscatter intensity levels between -14.1 and 22.0 dB (Fig 3).

**Model performance**

The mean AUC values for the training dataset were 98% (1 m) and 96% (50 m), while the AUC values for the test dataset were 96% (1 m) and 94% (50 m) (Table 3). Model performance measured by mean training AUC and mean test AUC was generally excellent for training and test models. The AUC values indicated that training and test models showed a similar pattern of seagrass habitat suitability. In other words, the mean training and test AUC values of the high-resolution model were generally close to the results obtained by the low-resolution models.

**Variable importance**

The study found that bathymetry was the most influential variable for all models, with the contribution value percentages for each model varying from 85.3% to 95.9% (Fig 4).
contributions of the other predictors were low and varied according to the model. Apart from bathymetry, the slope was listed in all the models. For backscatter predictors such as GLCM textures, GLCM entropy was the highest among the GLCM textures (4.3% in Model1_3). ARA characterization was the second-highest in Model50_3 and the third-highest contribution in

![Image: Relative contributions of the bathymetric and backscatter predictors by MaxEnt models.]

These predictors were used to build the seagrass habitat suitability models.

Fig 4. Relative contributions of the bathymetric and backscatter predictors by MaxEnt models. These predictors were used to build the seagrass habitat suitability models.

https://doi.org/10.1371/journal.pone.0257761.g004

Table 3. Training and test AUC values (mean) for both models and measured model performance for the high-resolution (1 m) and low-resolution model (50 m).

| Model    | Training Mean AUC (%) | Test Mean AUC (%) |
|----------|-----------------------|-------------------|
| Model1_3 | 98                    | 93                |
| Model1_9 | 98                    | 93                |
| Model1_21| 98                    | 97                |
| Model50_3| 99                    | 95                |
| Model50_9| 99                    | 98                |
| Model50_21| 99                  | 98                |

Training and test AUC values (mean) described the model performance during model development and validation.

https://doi.org/10.1371/journal.pone.0257761.t003
Model50_9; however, it did not contribute to other models. Interestingly, the backscatter mosaic (8-bit grayscale) was only important in one model (Model50_21).

**Prediction models**

Generally, the prediction models (i.e., Models1_3, 1_9, 1_21, 50_3, and 50_9) gave similar results in predicting a suitable habitat for seagrass (Fig 5A–5E). Meanwhile, Model F showed significant spatial pattern differences in predicting the highest habitat suitability for seagrass (Fig 5F). Overall, the prediction models identified that seagrass habitats are broadly scattered across the shallow waters of the Redang archipelago. Areas of seagrass habitat were predicted to be in shallower (<20 m) waters and scattered between fringing reefs (east-south) (Fig 5).

Some fragmented, seagrass habitats were also predicted throughout the shallow areas in the northwest of the prediction models and were scattered between fringing reefs (Fig 5). All models showed that seagrass was absent in deep water (>20 m).

The effects of various spatial resolutions and analysis window sizes on the prediction models are illustrated in Fig 6. The models highlighted that the spatial pattern from all prediction models showed that the shallow area along the coastline primarily showed "high suitability for seagrass habitats", except for the entrance to the Redang estuary (Site A). From the three small sites (sites A–northern area of Pinang Island, B–Cina Terjun cape, and C–Ekor Tebu Island), it can be seen that Models1_3, 1_9, and 1_21, showed a similar pattern of seagrass habitat suitability but were completely different from Models50_3, 50_9, and 50_21. This indicated that although all the prediction models were excellent (>90% accuracy), the habitat distribution did not necessarily agree with each other.

**Discussion**

**Main findings**

This study was among the first to explore the integration of high-resolution acoustic data, presence occurrence data, and the HSM to produce a seagrass habitat suitability map for RMP located within Malaysia's coastal areas. Based on the produced HSMs, from 182.55 km² of the total study area, 0.15–0.25 km² were predicted as the most suitable habitat (suitability >0.8).

Previous seagrass habitat investigations in the RMP area relied more on direct sampling methods, where no full coverage map was available [103]. In other marine parks in Malaysia, the probability estimation of seagrass occurrences has been produced through the extrapolation of the sparse point dataset at Tinggi Island [104]. The primary advantage of using acoustic data compared to conventional data (i.e., in-situ) is the ability of the former to obtain high-resolution spatial seafloor data, thus providing a more detailed representation of the habitat distributions. Although this technique was not entirely successful in revealing the seagrass at the species level (i.e., using the ground sampling technique), using acoustic data can produce a rapid and broad-scale seagrass habitat suitability map within the RMP for quick decision-making that does not require species-level accuracy. Habitat suitability map is also useful in directing further ground-truth surveys and pre-planning in other areas as well. Furthermore, this study focused on predicting the spatial distribution of seagrass habitat in the RMP as a function of the measured and modeled bathymetry and backscatter predictors of the area. This study demonstrated that the seagrass habitat was not randomly distributed, with depth being the most important variable for determining the most suitable habitats for seagrass. These results are supported by a previous study, which showed that the shallow subtidal zones in the inner bays (i.e., sheltered coastal waters) are dominated by fine sand [71]. However, this study appears to contradict with a previous study, where seagrass occurrence at Chagar Hutang occurred at <15 m in this study and 24 m in the previous study [71]. The presence of seagrass
Fig 5. Model predictions on the suitability of the seagrass habitat across the MBES surveyed area. These models were produced using predictors derived from three analysis window sizes (n = 3, 9, and 21) and gridded at 1 m and 50 m; (A) 1 m (n = 3), (B) 1 m (n = 9), (C) 1 m (n = 21), (D) 50 m (n = 3), (E) 50 m (n = 9), and (F) 50 m (n = 21). The suitability index ranges from 1 (high suitability) to 0 (low suitability).

https://doi.org/10.1371/journal.pone.0257761.g005
Fig 6. Model predictions of the suitability of seagrass habitat zoomed into three sites within the east-south area. Site A–northern area of Pulau Pinang; Site B–Cina Terjun cape; Site C–Pulau Ekor Tebu. The suitability index ranges from 1 (high suitability) to 0 (low suitability), while for spatial resolution and scale, (A) 1 m (n = 3), (B) 1 m (n = 9), (C) 1 m (n = 21), (D) 50 m (n = 3), (E) 50 m (n = 9), (F) 50 m (n = 21), respectively.

https://doi.org/10.1371/journal.pone.0257761.g006
at different depths may be due to the vertical datum issue. The depth of seagrass suitability models was relatively reduced by vertical datum (i.e., Lowest Astronomical Tide). Meanwhile, in the previous study, the depth of seagrass locality points was relatively reduced by unknown vertical datum, which might be different from the present study. The results obtained in this study demonstrate that the seagrass habitat suitability maps are valuable in predicting seagrass habitats across the entire RMP.

**Predictor contribution**

Among all predictors, bathymetry was the main contributor for all models. The results of this study were consistent with those of several previous studies that showed depth as an essential environmental parameter that limited seagrass habitats [71, 105, 106]. For example, seagrass habitats are known to colonize specific seafloor features in shallow water areas (< 24 m) and in the subtidal zone [11, 71]. Similarly, seagrass is a common species that inhabits shallow water over a range of depths and calm water that is sheltered from monsoonal effects [107]. Several studies have highlighted the importance of depth in the identification of seagrass habitat distributions [72, 106, 108]. Depth is a proxy variable for light attenuation [106] and temperature stress [109], and is directly significant to seagrass habitat distribution. Generally, the availability of sufficient light to support photosynthesis in seagrass depends on water depth [110]. Temperature also plays a critical role in controlling the growth rate of seagrass. Seagrass photosynthesis rates peak at an optimum temperature, and when it exceeds the optimum temperature, the photosynthesis efficiency declines rapidly [109, 111, 112]. Although no high-resolution temperature model from MBES is available, integrating the temperature derived from satellite imagery [113–117] for regional seagrass habitat suitability modeling might improve our understanding of the effect of climate change on seagrass distributions in the future.

Backscatter data, commonly used for the discrimination of seabed types and benthic communities, has been shown to improve HSMs [26]. While the use of bathymetric predictors to describe seabed characteristics is common in habitat suitability mapping using HSM, more proximal and functionally relevant predictors (e.g., backscatter predictors) are highly desirable for geological purposes. The present study revealed that adding backscatter predictors along with bathymetric predictors positively impacted model performance. The results from this study also supported that the analysis of the texture properties and angular backscatter intensity analysis (i.e., ARA) was more important than the backscatter mosaic itself. This was because most of the models used predictors from different analysis window sizes, which were almost similar to how GLCM predictors were constructed. Previous studies have shown that this signal-based method can differentiate between sediment classes using backscatter at different incidence angles. However, the contribution of these predictors was less important than that of bathymetry because the seagrass habitats are mainly occur where the sediment consists of fine sand that did not differ much in the study area (as predicted from the ARA technique). These results suggest that the contribution of backscatter predictors derived from different analysis methods could effectively capture the variation in sediment characteristics and should be integrated into the predictive modeling technique of marine species.

**Spatial resolution and analysis window size**

Similar to terrestrial habitat mapping, identifying the 'most suitable' or 'best' analysis window sizes and resolutions to study marine habitat associations and habitat selection has not been performed [56]. Due to complex interactions between the physical characteristics of the seafloor, marine habitats have been considered difficult for predictive modeling [118] and to be mapped [119, 120]. This study showed that different analysis window sizes (e.g., 3, 9, and 21
cells) and resolutions (e.g., 1 and 50 m) had impacts on model performances and variable contributions. First, the contributions of most of the backscatter predictors could only be seen in the models with coarser spatial resolutions and less in the fine resolution models. One possible explanation is that the sediment type for seagrass with a higher suitability index was mostly sandy sediment that did not change significantly in these areas (as observed in Fig 6A–6C). Hence, the predictors from ARA (mean grain size and characterization types) were most likely similar and did not play an important role in predictive models A, B, and C (fine resolution), except for GLCM entropy and correlations. However, many of the contributions of backscatter predictors existed at coarser resolutions (Model50_3, 50_9, and 50_21), such as ARA characterization, GLCM (entropy and correlations), and backscatter intensity levels. This shows that the sediment type properties predicted from backscatter data were better observed at a coarser spatial resolution in this area. This suggests that backscatter data are useful for constructing predictive habitat models of marine species where complex sediment types are observed in a particular area. Second, although models with a coarser spatial resolution dataset achieved high accuracy, the spatial distribution pattern from these habitat suitability maps was not consistent (i.e., especially areas with high suitability indexes for sites A, B, and C in Fig 6). For Model50_3, it produced many small patches (Fig 6D) in which the habitat suitability values were not consistent with the adjacent areas; this problem was not observed in analysis window sizes of 9 × 9 (Fig 6E) and 21 × 21 (Fig 6F). However, the spatial distributions of seagrass suitability between these two analysis window size settings were completely different, as observed at sites B and C (Fig 6E and 6F). In other words, the effect of different analysis window sizes at coarser resolutions was more dominant than that of the fine resolution dataset. This highlights that the use of a high spatial resolution dataset is important for producing consistent predictive maps in the marine environment. In some studies, coarser analysis window sizes and spatial resolution models have been shown to underrepresent the area of suitable habitat because the finer scale habitat features that drive the species distributions were not captured by the coarser data [121, 122] or vice versa [56]. Thus, a modeling approach using different analysis window sizes [123, 124] and spatial resolutions may be considered an essential strategy in habitat suitability modeling [56, 125]. These findings can assist the future use of MBES techniques in similar environments using the specific analysis window size and for seagrass habitat suitability mapping.

**Limitations and recommendations**

This study has several limitations. First, this study only used one-time sampling integrated with bathymetric and backscatter predictors to produce seagrass HSM. Due to the seagrass life cycle and threats to seagrass, interval or continuous sampling is needed to produce a temporal (i.e., dynamic) seagrass HSM [126–129]. It is important to examine the distribution of seagrass habitats with a different biology and ecology of seagrass species [128–131]. Thus, further study is needed to produce dynamic HSM models based on the temporal cycle of seagrass habitat. The current study only considered a specified analysis window size for each model. Previous studies found that different analysis window sizes may affect the distribution of benthic communities on the seafloor [31]. Furthermore, different multi-scale methods for calculating terrain information using an analysis distance approach are generally successful in identifying distinct seabed terrain features and making mapping results more transferable and interpretable [124]. These approaches may outperform single analysis window size method for modeling seagrass habitat suitability. While this study only focuses on correlation coefficient analysis between predictors, spatial correlation analysis [132–134] might improve the selection of the most important predictors. In addition, the present study area extends deeper than the
maximum depth of seagrass presence observations in which depth has been identified (i.e., bathymetric map) as the dominant predictor. Thus, further study is needed to investigate the effect when the study area extends deeper than the maximum depth of seagrass presence observations. The current study only attempted to predict seagrass habitat at RMP, a coastal area of Redang, which is an offshore island with fringing corals. In this study area, the seagrass habitat is only found in subtidal areas, 2.5 to 24 m depth, and silt-sand area [71]. Further studies are also required to predict seagrass habitats that are distributed in different coastal zones (e.g., intertidal, sub-tidal, and lagoon) and substrate compositions (e.g., sandy-mud, fine sand, and muddy sand) [11, 71] along the coastal area of Peninsular Malaysia (e.g., west and east coast) and East Malaysia (e.g., Sabah and Sarawak). Furthermore, the current study only focused on acoustic data captured using a swath mapping system, while seagrass distributions are also dependent on other physical parameters [135] such as light availability [136], temperature [137, 138], and waves [3, 71, 139–141]. Combinations of these parameters will influence the prediction of spatial patterns of seagrass habitats in marine environments [139, 142]. In terms of spatial data coverage, MBES dataset gaps existed in shallow areas (<5 m depth) due to navigation safety and time restrictions considerations when using survey vessels as the MBES platform. Thus, satellite imagery, hyperspectral imagery, unmanned aerial vehicles, and airborne bathymetric lidar can be alternatives for producing seagrass HSMs that occur in these shallow areas [33, 143–145]. The current study only developed seagrass HSMs by using a maximum entropy modeling technique. Although this technique showed promising results [93, 94, 146], there are modeling techniques such as ecological-niche factor analysis [27], random forest, boosted regression tree, and generalized additive model [31] which are reported to perform well. Thus, future study is required to develop seagrass HSM by using several modeling techniques. Comparison of different modelling techniques with similar datasets can provide insight into different HSM performances or combine multiple methods into a single ‘best’ model, such as an ensemble forecasting approach to species distribution [147]. Current study only used the ROC AUC to assess the accuracy model where different validation measures can be used to assess the model performance, such as sensitivity and specificity, and the true skill statistic (TSS) for measuring the efficiency of species distribution models [100, 148].

Conclusion
The present study has shown the applicability and usefulness of integrating an acoustic dataset from MBES, species occurrence data, and HSM techniques that could be used for seagrass habitat modeling at RMP. As high spatial resolution data were used, a detailed suitability map was produced where the information of the most suitable habitat for seagrass could be identified. With different spatial resolution data tested in this study, the results from the fine resolution dataset produced consistent suitability maps as compared to the coarser resolution dataset, although similar accuracies were observed. This study also concluded that the depth from bathymetry was the most influential predictor, regardless of the analysis window size and spatial resolution. In addition, a comparison of the spatial distribution of predicted seagrass habitat built using various spatial resolutions and analysis window sizes used in this study, may offer insight into the impacts of local-scale variation of seagrass habitat. Finally, the findings of the present study provide useful information for marine spatial planning for seagrass habitat and RMP management in Malaysian coastal waters using MBES data. This detailed seascapes information is needed for designing field efforts to identify seagrass habitat localities and assessment of the distribution of seagrass habitat under protection and conservation management strategies at RMP.
Supporting information

S1 Fig. Pearson’s correlation coefficients between predictors on all presence occurrence data (n = 9) for Model A (spatial resolution = 1m & analysis window size = 3). Correlations ≥ 0.5 were emphasised. (TIF)

S2 Fig. Pearson’s correlation coefficients between predictors on all presence occurrence data (n = 9) for Model B (spatial resolution = 1m & analysis window size = 9). Correlations ≥ 0.5 were emphasised. (TIF)

S3 Fig. Pearson’s correlation coefficients between predictors on all presence occurrence data (n = 9) for Model C (spatial resolution = 1m & analysis window size = 21). Correlations ≥ 0.5 were emphasised. (TIF)

S4 Fig. Pearson’s correlation coefficients between predictors on all presence occurrence data (n = 9) for Model D (spatial resolution = 50m & analysis window size = 3). Correlations ≥ 0.5 were emphasised. (TIF)

S5 Fig. Pearson’s correlation coefficients between predictors on all presence occurrence data (n = 9) for Model E (spatial resolution = 50m & analysis window size = 9). Correlations ≥ 0.5 were emphasised. (TIF)

S6 Fig. Pearson’s correlation coefficients between predictors on all presence occurrence data (n = 9) for Model F (spatial resolution = 50m & analysis window size = 21). Correlations ≥ 0.5 were emphasised. (TIF)

S7 Fig. Receiver operating characteristic curves (ROC) was built and the area under the curve (AUC) for Model A. Mean training AUC value is 0.98 were indicated as excellent discriminative ability. (TIFF)

S8 Fig. Receiver operating characteristic curves (ROC) was built and the area under the curve (AUC) for Model B. Mean training AUC value is 0.98 were indicated as excellent discriminative ability. (TIFF)

S9 Fig. Receiver operating characteristic curves (ROC) was built and the area under the curve (AUC) for Model C. Mean training AUC value is 0.98 were indicated as excellent discriminative ability. (TIFF)

S10 Fig. Receiver operating characteristic curves (ROC) was built and the area under the curve (AUC) for Model D. Mean training AUC value is 0.99 were indicated as excellent discriminative ability. (TIFF)

S11 Fig. Receiver operating characteristic curves (ROC) was built and the area under the curve (AUC) for Model E. Mean training AUC value is 0.99 were indicated as excellent
discriminative ability.

S12 Fig. Receiver operating characteristic curves (ROC) was built and the area under the curve (AUC) for Model F. Mean training AUC value is 0.99 were indicated as excellent discriminative ability.

Acknowledgments
The authors would like to thank the National Hydrographic Centre (NHC), Royal Malaysian Navy for the acoustic data collection. Special thanks to the team partners from the Department of Fisheries Malaysia (DoF) and the Institute of Oceanography and Environment (INOS), Universiti Malaysia Terengganu. We are also grateful for the reviews, comments, and suggestions from three reviewers for improving our manuscript.

Author Contributions
Conceptualization: Muhammad Abdul Hakim Muhamad, Rozaimi Che Hasan, Jillian Lean-Sim Ooi.
Formal analysis: Muhammad Abdul Hakim Muhamad.
Methodology: Muhammad Abdul Hakim Muhamad, Rozaimi Che Hasan, Najhan Md Said, Jillian Lean-Sim Ooi.
Resources: Rozaimi Che Hasan, Najhan Md Said.
Software: Najhan Md Said.
Supervision: Rozaimi Che Hasan, Najhan Md Said.
Visualization: Muhammad Abdul Hakim Muhamad.
Writing – original draft: Muhammad Abdul Hakim Muhamad, Rozaimi Che Hasan.
Writing – review & editing: Rozaimi Che Hasan, Najhan Md Said, Jillian Lean-Sim Ooi.

References
1. Cullen-Unsworth LC, Nordlund LM, Paddock J, Baker S, McKenzie LJ, Unsworth RK. Seagrass meadows globally as a coupled social–ecological system: Implications for human wellbeing. Marine Pollution Bulletin. 2014; 83(2):387–97. https://doi.org/10.1016/j.marpolbul.2013.06.001 PMID: 23800460
2. Nordlund LM, Koch EW, Barbier EB, Creed JC. Seagrass ecosystem services and their variability across genera and geographical regions. PLoS One. 2016; 11(10).
3. Hossain MS, Bujang JS, Zakaria MH, Hashim M. Marine and human habitat mapping for the Coral Triangle Initiative region of Sabah using Landsat and Google Earth imagery. Marine Policy. 2016; 72:176–91. https://doi.org/10.1016/j.marpol.2016.07.003.
4. François R, Thibaud M, Michel LN, Gilles L. Seagrass organic matter transfer in Posidonia oceanica macrophytodetritus accumulations. Estuarine, Coastal and Shelf Science. 2018; 212:73–9.
5. Criales MM, Cherubin LM, Browder JA. Modeling larval transport and settlement of pink shrimp in South Florida: dynamics of behavior and tides. Marine and Coastal Fisheries. 2015; 7(1):148–76.
6. Criales MM, Robblee MB, Browder JA, Cardenas H, Jackson TL. Field observations on selective tidal-stream transport for postlarval and juvenile pink shrimp in Florida Bay. Journal of Crustacean Biology. 2011; 31(1):26–33.
7. Oreska MP, McGlathery KJ, Porter JH. Seagrass blue carbon spatial patterns at the meadow-scale. PloS one. 2017; 12(4).
8. Gumusay MU, Bakirman T, Tuney Kizilkaya I, Aykut NO. A review of seagrass detection, mapping and monitoring applications using acoustic systems. European Journal of Remote Sensing. 2019; 52(1):1–29. https://doi.org/10.1080/22797254.2018.1544838

9. Lamb J, Van de Water J, Bourne D, Altier C, Hein M, Fiorenza E, et al. Seagrass ecosystems reduce exposure to bacterial pathogens of humans, fishes, and invertebrates. Science. 2017; 355:731. https://doi.org/10.1126/science.aal1956 PMID: 28209895

10. Short F, Carruthers T, Dennison W, Waycott M. Global seagrass distribution and diversity: a bioregional model. Journal of Experimental Marine Biology and Ecology. 2007; 350(1–2):3–20.

11. Bujang JS, Zakaria M, Arshad AB. Distribution and significance of seagrass ecosystems in Malaysia. Aquatic Ecosystem Health & Management. 2006; 9:203–14. https://doi.org/10.1080/14634980600705576

12. Bujang JS, Zakaria MH, Kanamoto Z, Mohd Pauzi A. Seagrass communities of the Straits of Malacca. Japar Sidik B, Arshad A, Tan SG, Daud SK Jambari HA and Sugiyama S (eds), Aquatic resources and environmental studies of the Straits of Malacca: Current research and reviews. 2001:81–98.

13. Bujang JS, Arshad A, Law A. Inventory for seagrass beds in Malaysia. UNEP: EAS-35: Malaysia Inventory of Watersheds, Coastal Wetlands, Seagrasses and Coral Reefs Department of Environment, Ministry of Science, Technology and Environment KL Malaysia. 1995:48–79.

14. Bujang JS. The marine angiosperms, seagrass2012.

15. Bujang JS, Zakaria MH, Arshad A, Lam SL, Ogawa H. Flowers and sexes in Malaysian seagrasses. Coastal Marine Science. 2006; 30(1):184–8.

16. Waycott M, Duarte CM, Carruthers TJ, Orth RJ, Dennison WC, Olyarnik S, et al. Accelerating loss of seagrasses across the globe threatens coastal ecosystems. Proceedings of the national academy of sciences. 2009; 106(30):12377–81. https://doi.org/10.1073/pnas.0905620106 PMID: 19587236

17. Short FT, Polidoro B, Livingstone SR, Carpenter KE, Bandeira S, Bujang JS, et al. Extinction risk assessment of the world’s seagrass species. Biological Conservation. 2011; 144(7):1961–71.

18. Bujang JS, Zakaria MH, Short F. Seagrasses in Malaysia: Issues and Challenges Ahead. 2016. p. 1–9.

19. Freeman AS, Short FT, Isnain I, Razak FA, Coles RG. Seagrass on the edge: Land-use practices threaten coastal seagrass communities in Sabah, Malaysia. Biological Conservation. 2008; 141(12):2993–3005. https://doi.org/10.1016/j.biocon.2008.09.018.

20. Schimel A, Beaudoin J, Parnum I, Le Bas T, Schmidt V, Keith G, et al. Multibeam sonar backscatter processing. Marine Geophysical Research. 2018; 39. https://doi.org/10.1007/s11001-018-9341-z

21. Janowski L, Trzcinska K, Tegowski J, Kruss A, Rucinska-Zjadacz M, Pocwiardowski P. Nearshore benthic habitat mapping based on multi-frequency, multibeam echosounder data using a combined object-based approach: a case study from the rowy site in the Southern Baltic Sea. Remote Sensing. 2018; 10(12):2993–3005. https://doi.org/10.1007/s11001-018-9341-z

22. Brown CJ, Blondel P. Developments in the application of multibeam sonar backscatter for seafloor habitat mapping. Applied Acoustics. 2009; 70(10):1242–7. https://doi.org/10.1016/j.apacoust.2008.08.004.

23. Li D, Tang C, Xia C, Zhang H. Acoustic mapping and classification of benthic habitat using unsupervised learning in artificial reef water. Estuarine, Coastal and Shelf Science. 2017; 185:11–21. https://doi.org/10.1016/j.ecss.2016.12.001.

24. Che Hasan R, Ierodiaconou D, Laurenson L, Schimel A. Integrating multibeam backscatter angular response, mosaic and bathymetry data for benthic habitat mapping. PLoS One. 2014; 9(5):e97339–e. https://doi.org/10.1371/journal.pone.0097339 PMID: 24824155.

25. Che Hasan R, Rattray A, Monk J, Laurenson L. Applications of multibeam echo sounder data and video observations for biological monitoring on the south east Australian continental shelf 2011.

26. Monk J, Ierodiaconou D, Versace V, Bellgrove A, Harvey E, Rattray A, et al. Habitat suitability for marine fishes using presence-only modelling and multibeam sonar. Marine Ecology Progress Series. 2010; 420:157–74. https://doi.org/10.3354/meps08858

27. Monk J, Ierodiaconou D, Bellgrove A, Harvey E, Laurenson L. Remotely sensed hydroacoustics and observation data for predicting fish habitat suitability. Continental Shelf Research. 2011; 31(2, Supplement):S17–S27. https://doi.org/10.1016/j.csr.2010.02.012.

28. Rengstorff AM, Mohn C, Brown C, Wisz MS, Grehan AJ. Predicting the distribution of deep-sea vulnerable marine ecosystems using high-resolution data: Considerations and novel approaches. Deep Sea Research Part I: Oceanographic Research Papers. 2014; 93:72–82. https://doi.org/10.1016/j.dsr.2014.07.007.
29. Rengstorf AM, Grehan A, Yesson C, Brown C. Towards high-resolution habitat suitability modeling of vulnerable marine ecosystems in the deep-sea: resolving terrain attribute dependencies. Marine Geodesy. 2012; 35(4):343–61.

30. Ross R, Howell K. Use of predictive habitat modeling to assess the distribution and extent of the current protection of ‘listed’ deep-sea habitats. Diversity and Distributions. 2012; 19. https://doi.org/10.1111/di.12010

31. Rowden AA, Anderson OF, Georgian SE, Bowden DA, Clark MR, Pallentin A, et al. High-Resolution Habitat Suitability Models for the Conservation and Management of Vulnerable Marine Ecosystems on the Louisville Seamount Chain, South Pacific Ocean. Frontiers in Marine Science. 2017; 4(335). https://doi.org/10.3389/fmars.2017.00335

32. Miyamoto M, Kyota M, Murase H, Nakamura T, Hayashihara T. Effects of Bathymetric Grid-Cell Sizes on Habitat Suitability Analysis of Cold-water Gorgonian Corals on Seamounts. Marine Geodesy. 2017; 40(4):205–23. https://doi.org/10.1080/01490419.2017.1315543

33. Bakirman T, Gumusay MU. A novel GIS-MCD A-based spatial habitat suitability model for Posidonia oceanica in the Mediterranean. Environmental Monitoring and Assessment. 2020; 192(4):231. https://doi.org/10.1007/s10661-020-8198-1 PMID: 32166406

34. Bajjouk T, Rochette S, Laurans M, Ehrhold A, Hamdi A, Le Niliot P. Multi-approach mapping to help spatial planning and management of the kelp species L. digitata and L. hyperborea: Case study of the Molène Archipelago, Brittany. Journal of Sea Research. 2015; 100:2–21. https://doi.org/10.1016/j.seares.2015.04.004.

35. Wilson MF, O’Connell B, Brown C, Guinan JC, Grehan AJ. Multiscale terrain analysis of multibeam bathymetry data for habitat mapping on the continental slope. Marine Geodesy. 2007; 30(1–2):3–35.

36. Haggarty D, Yamanaka K. Evaluating Rockfish Conservation Areas in southern British Columbia, Canada using a Random Forest model of rocky reef habitat. Estuarine, Coastal and Shelf Science. 2018; 208:191–204. https://doi.org/10.1016/j.ecss.2018.05.011

37. Boswarva K, Butters A, Fox CJ, Howe JA, Narayanaswamy B. Improving marine habitat mapping using high-resolution acoustic data; a predictive habitat map for the Firth of Lorn, Scotland. Continental Shelf Research. 2018; 168:39–47. https://doi.org/10.1016/j.csr.2018.09.005.

38. Anderson OF, Guinotte JM, Rowden AA, Tracey DM, Mackay KA, Clark MR. Habitat suitability models for predicting the occurrence of vulnerable marine ecosystems in the seas around New Zealand. Deep Sea Research Part I: Oceanographic Research Papers. 2016; 115:265–92. https://doi.org/10.1016/j.dsr.2016.07.006.

39. Rzhanov Y, Cutter GR, Mayer LA, editors. Seafloor segmentation based on bathymetric measurements from multibeam echosounder data. Seventh International Symposium on Signal Processing and Its Applications, 2003 Proceedings; 2003: IEEE.

40. Holmes KW, Van Niel KP, Radford B, Kendrick GA, Grove SL. Modelling distribution of marine benthos from hydroacoustics and underwater video. Continental Shelf Research. 2008; 28(14):1800–10.

41. Markert E, Holler P, Kröncke I, Bartholomä A. Benthic habitat mapping of sorted bedforms using hydroacoustic and ground-truthing methods in a coastal area of the German Bight/North Sea. Estuarine, Coastal and Shelf Science. 2013; 129:94–104.

42. Le Bas T, Huenne V. Acquisition and processing of backscatter data for habitat mapping–comparison of multibeam and sidescan systems. Applied Acoustics. 2009; 70(10):1248–57.

43. Ribó M, Macdonald H, Watson SJ, Hillman JR, Thrush SF, et al. Predicting habitat suitability of filter-feeder communities in a shallow marine environment, New Zealand. Marine Environmental Research. 2021; 163:105218. https://doi.org/10.1016/j.marenvres.2020.105218 PMID: 3385975

44. Porskamp P, Rattray A, Young M, Ierodiaconou D. Multiscale and Hierarchical Classification for Benthic Habitat Mapping. Geosciences. 2018; 8(4). https://doi.org/10.3390/geosciences8040137 PMID: 30147946

45. Viaia C, Lamouret M, Abadie A. Seafloor classification using a multibeam echo sounder: A new rugos-ity index coupled with a pixel-based process to map Mediterranean marine habitats. Applied Acoustics. 2021; 179:108067. https://doi.org/10.1016/j.apacoust.2021.108067.

46. Cui X, Liu H, Fan M, Ai B, Ma D, Yang F. Seafloor habitat mapping using multibeam bathymetric and backscatter intensity multi-features SVM classification framework. Applied Acoustics. 2021; 174:107728. https://doi.org/10.1016/j.apacoust.2020.107728.

47. Lauria V, Cristina M, Attrill MJ, Fiorentino F, Garofalo G. Predictive habitat suitability models to aid conservation of elasmobranch diversity in the central Mediterranean Sea. Scientific Reports. 2015; 5 (1):13245. https://doi.org/10.1038/srep13245 PMID: 26272502
48. Reiss H, Cunze S, König K, Neumann H, Kröncke I. Species distribution modelling of marine benthos: a North Sea case study. Marine Ecology Progress Series. 2011; 442:71–86.

49. Robinson L, Elith J, Hobday A, Pearson R, Kendall B, Possingham H, et al. Pushing the limits in marine species distribution modelling: Lessons from the land present challenges and opportunities. Global Ecology and Biogeography. 2011; 20:789–802. https://doi.org/10.2307/41239474

50. Kinlan BP, Poti M, Drohan AF, Packer DB, Dorfman DS, Nizinski MS. Predictive modeling of suitable habitat for deep-sea corals offshore the Northeast United States. Deep Sea Research Part I: Oceanographic Research Papers. 2020; 158:103229. https://doi.org/10.1016/j.dsr.2020.103229.

51. Amir M, Turkesh M, Jafari R, Jetschke G. Bioclimatic variables from precipitation and temperature records vs. remote sensing-based bioclimatic variables: Which side can perform better in species distribution modeling? Ecological Informatics. 2020; 57:101060. https://doi.org/10.1016/j.ecoinf.2020.101060.

52. Franklin J. Mapping species distributions: spatial inference and prediction: Cambridge University Press; 2010.

53. Droz B, Amoux R, Bohnenstengel T, Laesser J, Spaar P, Ayé R, et al. Moderately urbanized areas as a conservation opportunity for an endangered songbird. Landscape and Urban Planning. 2019; 181:1–9.

54. Coll M, Pennino MG, Steenbeek J, Sole J, Bellido JM. Predicting marine species distributions: Complementarity of food-web and Bayesian hierarchical modelling approaches. Ecological Modelling. 2019; 405:86–101. https://doi.org/10.1016/j.ecolmodel.2019.05.005

55. Brown CJ, Smith SJ, Lawton P, Anderson JT. Benthic habitat mapping: A review of progress towards improved understanding of the spatial ecology of the seafloor using acoustic techniques. Estuarine, Coastal and Shelf Science. 2011; 92(3):502–20.

56. Lecours V, Devillers R, Schneider D, Lucieer V, Brown C, Edinger E. Spatial scale and geographic context in benthic habitat mapping: Review and future directions. Marine Ecology Progress Series. 2015; 535:259–84. https://doi.org/10.3354/meps11378

57. Lecours V, Devillers R, Simms AE, Lucieer VL, Brown CJ. Towards a framework for terrain attribute selection in environmental studies. Environmental modelling & software. 2017; 89:19–30.

58. Chiarucci A, Scheiner S. Old and new challenges in using species diversity for assessing biodiversity. Philosophical transactions of the Royal Society of London Series B, Biological sciences. 2011; 366:2426–37. https://doi.org/10.1098/rstb.2011.0065 PMID: 21768157

59. Ross LK, Ross RE, Stewart HA, Howell KL. The influence of data resolution on predicted distribution and estimates of extent of current protection of three ‘listed’ deep-sea habitats. PloS one. 2015; 10 (10). https://doi.org/10.1371/journal.pone.0140061 PMID: 26496639

60. Nezer O, Bar-David S, Gueta T, Carmel Y. High-resolution species-distribution model based on systematic sampling and indirect observations. Biodiversity and Conservation. 2017; 26(2):421–37. https://doi.org/10.1007/s10531-016-1251-2

61. Olivero J, Toxopeus A, Skidmore A, Real R. Testing the efficacy of downscaling in species distribution modelling: A comparison between MaxEnt and Favourability Function models. Animal Biodiversity and Conservation. 2016; 39:99–114. https://doi.org/10.3280/abc.2016.39.0099

62. Freemark KE, Merriam HG. Importance of area and habitat heterogeneity to bird assemblages in temperate forest fragments. Biological Conservation. 1986; 36(2):115–41. https://doi.org/10.1016/0006-3207(86)90002-9.

63. Wiens JA. Spatial scaling in ecology. Functional ecology. 1989; 3(4):385–97.

64. Ierodiaconou D, Schimel ACG, Kennedy D, Monk J, Gaylard G, Young M, et al. Combining pixel and object based image analysis of ultra-high resolution multibeam bathymetry and backscatter for habitat mapping in shallow marine waters. Marine Geophysical Research. 2018; 39(1):271–88. https://doi.org/10.1007/s11001-017-9338-2

65. Gambi C, Danovaro R. A multiple-scale analysis of metazoan meiofaunal distribution in the deep Mediterranean Sea. Deep Sea Research Part I: Oceanographic Research Papers. 2006; 53(7):1117–34.

66. Bradtter U, Kunin WE, Allrington JD, Thom TJ, Benton TG. Identifying appropriate spatial scales of predictors in species distribution models with the random forest algorithm. Methods in Ecology and Evolution. 2013; 4(2):167–74.

67. Fakiris E, Blondel P, Papatheodorou G, Christodoulou D, Dimas X, Georgiou N, et al. Multi-Frequency, Multi-Sonar Mapping of Shallow Habitats—Efficacy and Management Implications in the National Marine Park of Zakynthos, Greece. Remote Sensing, 2019. https://doi.org/10.3390/rs11040461

68. Ghazali AF, Jamil NR. Population and Trend Analysis for Green Turtle (Chelonid a mydas) and Hawksbill Turtle (Eretmochelys imbricata) in Marine Park Centre Redang, Terengganu and Marine Park Centre Rusukan Besar, Labuan, Malaysia. Pertanika Journal of Science & Technology. 2019; 27(3).
69. Rawi SB. The Use of Choice Modelling in Assessing Tourists Destinations: A Case Study of Redang Marine Park (RMP) Malaysia [PhD Thesis]. Newcastle: Newcastle University; 2012.

70. Department of Marine Parks M. Annual Report 2011; 11/09/2012 Report No.

71. Zakaria MH, Bujang JS, Razak F. Occurrence and Morphological Description of Seagrasses from Pulau Redang, Terengganu, Malaysia. Jurnal Teknologi. 2003; 38. https://doi.org/10.1113/j.t.v38.491

72. Chan EH. A report on the first 16 years of a long-term marine turtle conservation project in Malaysia. Asian Journal of Conservation Biology. 2013; 2:129–35.

73. Stewart TA, Booth DT, Rusli MU. Influence of sand grain size and nest microenvironment on incubation success, hatching morphology and locomotion performance of green turtles (Chelonia mydas) at the Chagar Hutang Turtle Sanctuary, Redang Island, Malaysia. Australian Journal of Zoology. 2018; 66(6):356–68. https://doi.org/10.1071/ZO19025.

74. Fonseca L, Mayer L. Remote estimation of surficial seafloor properties through the application Angular Range Analysis to multibeam sonar data. Marine Geophysical Researches. 2007; 28(2):119–26. https://doi.org/10.1007/s11001-007-9019-4

75. Lecours V. TASSE (Terrain Attribute Selection for Spatial Ecology) Toolbox v. 1.12017.

76. Dolan M. Calculation of slope angle from bathymetry data using GIS—effects of computation algorithms, data resolution and analysis scale. NGU Report. 2012.

77. Monk J, Versace V, Bellgrove A, Harvey E, Rattray A, Laurensen L, et al. Habitat suitability for marine fishes using presence-only modelling and multibeam sonar. Marine Ecology Progress Series. 2010; 420:157–74. https://doi.org/10.3354/meps08858.

78. Haralick RM, Shanmugam K, Dinstein IH. Textural features for image classification. IEEE Transactions on systems, man, and cybernetics. 1973;6(6):610–21.

79. Jena B, Kurian PJ, Swain D, Tyagi A, Ravindra R. Prediction of bathymetry from satellite altimeter based gravity in the Arabian Sea: Mapping of two unnamed deep seamounts. International Journal of Applied Earth Observation and Geoinformation. 2012; 16:1–4. https://doi.org/10.1016/j.jag.2011.11.008.

80. Burrough PA, McDonnell R, McDonnell RA, Lloyd CD. Principles of geographical information systems: Oxford university press; 2015.

81. Walbridge S, Slocum N, Pobuda M, Wright JD. Unified Geomorphological Analysis Workflows with Benthic Terrain Modeler. Geosciences. 2018; 8(3). https://doi.org/10.3390/geosciences8030094

82. Gaida TC, Snellen M, van Dijk TAGP, Simons DG. Geostatistical modelling of multibeam backscatter for full-coverage seabed sediment maps. Hydrobiologia. 2019; 845(1):55–79. https://doi.org/10.1007/s10750-018-3751-4

83. Trzcinska K, Janowski L, Nowak J, Rucinska-Zjadacz M, Kruss A, von Deimling JS, et al. Spectral features of dual-frequency multibeam echosounder data for benthic habitat mapping. Marine Geology. 2020; 427:106239. https://doi.org/10.1016/j.margeo.2020.106239.

84. Merow C, Smith MJ, Silander JA Jr. A practical guide to MaxEnt for modeling species’ distributions: what it does, and why inputs and settings matter. Ecography. 2013; 36(10):1058–69.

85. Linklater M, Ingleton T, Kinsela M, Morris B, Allen K, Sutherland M, et al., editors. Techniques for Classifying Seabed Morphology and Composition on a Subtropical-Temperate Continental Shelf 2019.

86. Giusti M, Bo M, Angiolillo M, Cannas R, Cau A, Follesa MC, et al. Habitat preference of Virmiella flagellum (Alcyonacea: Ellisiellidae) in relation to bathymetric variables in southeastern Sardinian waters. Continental Shelf Research. 2017; 138:41–50. https://doi.org/10.1016/j.csr.2017.03.004.

87. Anderson OF, Guinotte JM, Rowden AA, Clark MR, Mormede S, Davies AJ, et al. Field validation of habitat suitability models for vulnerable marine ecosystems in the South Pacific Ocean: Implications for the use of broad-scale models in fisheries management. Ocean & Coastal Management. 2016; 120:110–26. https://doi.org/10.1016/j.ocecoaman.2015.11.025.

88. Howell K-L, Piechaud N, Downie A-L, Kenny A. The distribution of deep-sea sponge aggregations in the North Atlantic and implications for their effective spatial management. Deep Sea Research Part I: Oceanographic Research Papers. 2016; 115:309–20. https://doi.org/10.1016/j.dsr.2016.07.005.
92. Miller RJ, Juska C, Hocevar J. Submarine canyons as coral and sponge habitat on the eastern Bering Sea slope. Global Ecology and Conservation. 2015; 4:85–94. https://doi.org/10.1016/j.gecco.2015.05.009.

93. Elith J, H. Graham C, P. Anderson R, Dudık M, Ferrier S, Guisan A, et al. Novel methods improve prediction of species’ distributions from occurrence data. Ecography. 2006; 29(2):129–51. https://doi.org/10.1111/j.0906-7590.2006.04596.x.

94. Bittner RE, Roesler EL, Barnes MA. Using species distribution models to guide seagrass management. Estuarine, Coastal and Shelf Science. 2020; 240:106790. https://doi.org/10.1016/j.ecss.2020.106790.

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

96. Phillips SJ, Dudık M. Modeling of species distributions with Maxent: new extensions and a comprehensive evaluation. Ecography. 2008; 31(2):161–75. https://doi.org/10.1111/j.0906-7590.2008.5203.x.

97. Halvorsen R. A strict maximum likelihood explanation of MaxEnt, and some implications for distribution modelling. Sommefeltia. 2013; 36:1–132. https://doi.org/10.2478/v10208-011-0016-2.

98. Wang B, Xu Y, Ran J. Predicting suitable habitat of the Chinese monal (Lophophorus huyssi) using ecological niche modeling in the Qionglai Mountains, China. PeerJ. 2017; 5:e3477. https://doi.org/10.7717/peerj.3477 PMID: 28695066.

99. Blondel P, Gómez Sichí O. Textural analyses of multibeam sonar imagery from Stanton Banks, Northern Ireland continental shelf. Applied Acoustics. 2009; 70(10):1288–97. https://doi.org/10.1016/j.apacoust.2008.07.015.

100. Fielding AH, Bell JF. A review of methods for the assessment of prediction errors in conservation presence/absence models. Environmental Conservation. 1997; 24(1):38–49. Epub 2002/05/10. https://doi.org/10.1017/S0376892997000088.

101. Swets JA. Measuring the accuracy of diagnostic systems. Science. 1988; 240(4857):1285–93. https://doi.org/10.1126/science.3287615 PMID: 3287615.

102. Hosmer DW Jr, Lemeshow S, Sturdivant RX. Applied logistic regression. John Wiley & Sons; 2013.

103. Zakaria MH, Bujang JS. Occurrence and Distribution of Seagrasses in Waters of Perhentian Island Archipelago, Malaysia. Journal of Fisheries and Aquatic Science. 2013; 8:441–51. https://doi.org/10.7717/peerj.3477 PMID: 28695066.

104. Ooi JLS, Van Niel KP, Kendrick GA, Holmes KW. Spatial Structure of Seagrass Suggests That Size-Dependent Plant Traits Have a Strong Influence on the Distribution and Maintenance of Tropical Multi-species Meadows. PLOS ONE. 2014; 9(1):e86782. https://doi.org/10.1371/journal.pone.0086782 PMID: 24497978.

105. Duarte CM. Seagrass depth limits. Aquatic botany. 1991; 40(4):363–77.

106. Aoki LR, McGlathery KJ, Wiberg PL, Al-Haj A. Depth Affects Seagrass Restoration Success and Resilience to Marine Heat Wave Disturbance. Estuaries and Coasts. 2020; 43(2):316–28. https://doi.org/10.1007/s12237-019-00685-0.

107. Ooi JLS, Kendrick GA, Van Niel KP, Affendi YA. Knowledge gaps in tropical Southeast Asian seagrass systems. Estuarine, Coastal and Shelf Science. 2011; 92(1):118–31. https://doi.org/10.1016/j.ecss.2010.12.021.

108. Micallef A, Le Bas TP, Huvenne VA, Blondel P, Hühnerbach V, Deidun A. A multi-method approach for benthic habitat mapping of shallow coastal areas with high-resolution multibeam data. Continental Shelf Research. 2012; 39:14–26.

109. Lee K-S, Park SR, Kim YK. Effects of irradiance, temperature, and nutrients on growth dynamics of seagrasses: a review. Journal of Experimental Marine Biology and Ecology. 2007; 350(1–2):144–75.

110. Ralph P, Durako MJ, Enríquez S, Collier C, Doblin M. Impact of light limitation on seagrasses. Journal of Experimental Marine Biology and Ecology. 2007; 350(1–2):176–93.

111. Collier CJ, Uthicke S, Waycott M. Thermal tolerance of two seagrass species at contrasting light levels: implications for future distribution in the Great Barrier Reef. Limnology and Oceanography. 2011; 56(6):2200–10.

112. Bulthuis DA. Effects of temperature on photosynthesis and growth of seagrasses. Aquatic Botany. 1987; 27(1):27–40.

113. Phinn SR, Kovacs EM, Roelfsema CM, Canto RF, Collier CJ, McKenzie LJ. Assessing the potential for satellite image monitoring of seagrass thermal dynamics: for inter- and shallow sub-tidal seagrasses in the inshore Great Barrier Reef World Heritage Area, Australia. International Journal of Digital Earth. 2018; 11(8):803–24. https://doi.org/10.1080/17538947.2017.1359343.
114. Esaias WE, Abbott MR, Barton I, Brown OB, Campbell JW, Carder KL, et al. An overview of MODIS capabilities for ocean science observations. IEEE Transactions on Geoscience and Remote Sensing. 1998; 36(4):1250–65.

115. Carlson DF, Yarbro LA, Scolaro S, Poniatowski M, McGee-Absten V, Carlson PR. Sea surface temperatures and seagrass mortality in Florida Bay: Spatial and temporal patterns discerned from MODIS and AVHRR data. Remote Sensing of Environment. 2018; 208:171–88. https://doi.org/10.1016/j.rse.2018.02.014.

116. Daud M, Pin T, Handayani T, editors. The spatial pattern of seagrass distribution and the relation with salinity, sea surface temperature, and suspended materials in Banten Bay. IOP Conference Series: Earth and Environmental Science; 2019: IOP Publishing.

117. Dekker A, Brando V, Anstee J, Fyfe S, Malthus T, Karpouzli E. Remote sensing of seagrass ecosystems: use of spaceborne and airborne sensors. Seagrasses: Biology, Ecology and Conservation: Springer; 2007. p. 347–59.

118. Professor J, Franklin J. Mapping Species Distributions: Spatial Inference and Prediction. Mapping Species Distributions: Spatial Inference and Prediction. 2010; 1. https://doi.org/10.1017/CBO9780511810602

119. Zajac RN. Challenges in marine, soft-sediment benthoscape ecology. Landscape Ecology. 2008; 23(1):7–18. https://doi.org/10.1007/s10980-007-9140-4

120. Rigby P, Pizarro O, Williams SB. Toward adaptive benthic habitat mapping using gaussian process classification. Journal of Field Robotics. 2010; 27(6):741–58. https://doi.org/10.1002/rob.20372.

121. Seo C, Thorne JH, Hannah L, Thuiller W. Scale effects in species distribution models: implications for conservation planning under climate change. Biology Letters. 2009; 5(1):39–43. https://doi.org/10.1098/rsbl.2008.0476 PMID: 18986960

122. Vierod ADT, Guinotte JM, Davies AJ. Predicting the distribution of vulnerable marine ecosystems in the deep sea using presence-background models. Deep Sea Research Part II: Topical Studies in Oceanography. 2014; 99:6–18. https://doi.org/10.1016/j.dsr2.2013.06.010.

123. Lecours V, Devillers R, Lucieer VL, Brown CJ. Artefacts in marine digital terrain models: A multiscale analysis of their impact on the derivation of terrain attributes. IEEE Transactions on Geoscience and Remote Sensing. 2017; 55(9):5391–406.

124. Misiuk B, Lecours V, Dolan MFJ, Robert K. Evaluating the Suitability of Multi-Scale Terrain Attribute Calculation Approaches for Seabed Mapping Applications. Marine Geodesy. 2021; 44(4):327–85. https://doi.org/10.1080/01490419.2021.1925789

125. Wu XB, Smeins FE. Multiple-scale habitat modeling approach for rare plant conservation. Landscape and Urban Planning. 2000; 51(1):11–28. https://doi.org/10.1016/S0169-2046(00)00095-5.

126. Santos Rolando O, Lirman D. Using habitat suitability models to predict changes in seagrass distribution caused by water management practices1. Canadian Journal of Fisheries and Aquatic Sciences. 2012; 69:1380–8. https://doi.org/10.1139/f2012-018

127. Grech A, Coles RG. An ecosystem-scale predictive model of coastal seagrass distribution. Aquatic Conservation: Marine and Freshwater Ecosystems. 2010; 20(4):437–44. https://doi.org/10.1002/aqc.1107.

128. Shafer D, Swannack T, Saltus S, Kaldy J, Davis A, Saltus C. Development and validation of a habitat suitability model for the non-indigenous seagrass Zostera japonica in North America. Management of Biological Invasions. 2016; 7:141–55. https://doi.org/10.3391/mbi.2016.7.2.02

129. Hastings R, Cummins V, Holloway P. Assessing the Impact of Physical and Anthropogenic Environmental Factors in Determining the Habitat Suitability of Seagrass Ecosystems. Sustainability. 2020; 12(20):8302. https://doi.org/10.3390/su12208302

130. Duarte CM, Larkum AW, Orth RJ. Seagrasses: biology, ecology and conservation: Springer; 2006.

131. Alonso Aller E, Eklof JS, Gullstroem M, Kloiber U, Linderholm HW, Nordlund LM. Temporal variability of a protected multispecific tropical seagrass meadow in response to environmental change. Environmental Monitoring and Assessment. 2019; 191(12):774. https://doi.org/10.1007/s10661-019-7977-z PMID: 31773384

132. Duque-Lazo J, van Gils H, Groen TA, Navarro-Cerrillo RM. Transferability of species distribution models: The case of Phytophthora cinnamomi in Southwest Spain and Southwest Australia. Ecological Modelling. 2016; 320:62–70. https://doi.org/10.1016/j.ecolmodel.2015.09.019.

133. Sillero N, Barbosa AM. Common mistakes in ecological niche models. International Journal of Geographical Information Science. 2021; 35(2):213–26. https://doi.org/10.1080/13658816.2020.1798968

134. Naimi B, Skidmore AK, Groen TA, Hamm NA. Spatial autocorrelation in predictors reduces the impact of positional uncertainty in occurrence data on species distribution modelling. Journal of Biogeography. 2011; 38(8):1497–509.
135. Stankovic M, Kaewsrirkhaw R, Rattanachat E, Prathep A. Modeling of suitable habitat for small-scale seagrass restoration in tropical ecosystems. Estuarine, Coastal and Shelf Science. 2019; 231:106465. https://doi.org/10.1016/j.ecss.2019.106465.

136. Collier C, Waycott M, McKenzie L. Light thresholds derived from seagrass loss in the coastal zone of the northern Great Barrier Reef, Australia. Ecological Indicators. 2012; 23:211–9.

137. Kemp WM, Boynton WR, Adolf JE, Boesch DF, Boicourt WC, Brush G, et al. Eutrophication of Chesapeake Bay: historical trends and ecological interactions. Marine Ecology Progress Series. 2005; 303:1–29.

138. Cullen-Unsworth L, Unsworth R. Seagrass meadows, ecosystem services, and sustainability. Environment: Science and policy for sustainable development. 2013; 55(3):14–28.

139. Short FT, Coles RG. Global seagrass research methods: Elsevier; 2001.

140. Bekkby T, Rinde E, Erikstad L, Bakkestuen V, Longva O, Christensen O, et al. Spatial probability modelling of eelgrass (Zostera marina) distribution on the west coast of Norway. ICES Journal of Marine Science. 2008; 65(7):1093–101. https://doi.org/10.1093/icesjmfsn095

141. Downie A-L, von Numers M, Bostrom C. Influence of model selection on the predicted distribution of the seagrass Zostera marina. Estuarine, Coastal and Shelf Science. 2013; 121–122:8–19. https://doi.org/10.1016/j.ecss.2012.12.020.

142. Townsend M, Thrush SF, Lohrer AM, Hewitt JE, Lundquist CJ, Carbin M, et al. Overcoming the challenges of data scarcity in mapping marine ecosystem service potential. Ecosystem Services. 2014; 8:44–55.

143. Pan Z, Glennie C, Fernandez-Diaz JC, Starek M. Comparison of bathymetry and seagrass mapping with hyperspectral imagery and airborne bathymetric lidar in a shallow estuarine environment. International Journal of Remote Sensing. 2016; 37(3):516–36. https://doi.org/10.1080/01431161.2015.1131869

144. Nahirnick N, Reshitnyk L, Campbell M, Hessin‡ Lewis M, Costa M, Yakimishyn J, et al. Mapping with confidence: delineating seagrass habitats using Unoccupied Aerial Systems (UAS). Remote Sensing in Ecology and Conservation. 2019; 5:121–35.

145. Duffy JP, Pratt L, Anderson K, Land PE, Shutter JD. Spatial assessment of intertidal seagrass meadows using optical imaging systems and a lightweight drone. Estuarine, Coastal and Shelf Science. 2018; 200:169–80. https://doi.org/10.1016/j.ecss.2017.11.001.

146. Eilith J, Leathwick JR. Species Distribution Models: Ecological Explanation and Prediction Across Space and Time. Annual Review of Ecology, Evolution, and Systematics. 2009; 40(1):677–97. https://doi.org/10.1146/annurev.ecolsys.110308.120159

147. Thuiller W, Lafourcade B, Engler R, Araújo MB. BIOMOD—a platform for ensemble forecasting of species distributions. Ecography. 2009; 32(3):369–73. https://doi.org/10.1111/j.1600-0587.2008.05742.x.

148. Liu C, White M, Newell G. Measuring and comparing the accuracy of species distribution models with presence–absence data. Ecography. 2011; 34(2):232–43. https://doi.org/10.1111/j.1600-0587.2010.06354.x.