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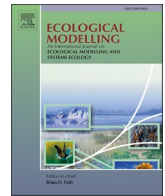
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Habitat suitability modelling for an integrated multi-trophic aquaculture (IMTA) system along Europe's Atlantic coast

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ABSTRACT

As the human population grows, so too does the demand for resources. This demand has led to aquaculture becoming the fastest growing food production sector in the world. Due to environmental concerns associated with finfish aquaculture, Integrated Multi-Trophic Aquaculture (IMTA) has been proposed to minimise any negative impacts, by co-culturing extractive aquaculture species from different trophic levels to remove excess organic and inorganic nutrients, using them for their own growth. This study, in the Atlantic area of Europe, aimed to identify the most suitable locations to establish a new IMTA system for the 3 species *Salmo salar* (Linnaeus, 1758), *Mytilus edulis* (Linnaeus, 1758), and *Laminaria digitata* ((Hudson) JV Lamouroux, 1813). Habitat suitability models were created using spatial jackknifing testing within MaxEnt software and analysed using ArcGIS (ArcMap 10.8.1). All Maxent models were better than random when predicting species distribution, with AUC values of 0.889 (*S. salar*), 0.876 (*M. edulis*) and 0.901 (*L. digitata*), indicating a high level of predictive power. Jackknife testing identified Chlorophyll A (mg m^{-3}) and Salinity (PSS) as the 2 most important variables in the model for each species. Coastal areas of the United Kingdom, Ireland and Northern France were identified as highly suitable, with suitability decreasing in more southern environments. These areas were then assessed based on local vessel density, whether they were within a Marine Protected Area (MPA), and the site accessibility from nearby ports, according to the expected needs of a large-scale aquaculture system. As MaxEnt used wild population data to produce the models, environmental conditions at suitable areas were compared against known *Salmo salar* aquaculture sites in Scotland to further validate the suitability for IMTA purposes. The results of this study, and the identification of optimal conditions for each species, will provide aquaculture businesses with the information required for preliminary site selection, with the goal of further incorporating IMTA systems into the EU market in a sustainable way.

1. Introduction

The global human population is increasing, from reaching 8 billion people in 2022 to an estimated 10.4 billion people by 2100, with the most rapid growth occurring in developing countries (Ezeh et al., 2012; United Nations Department of Economic and Social Affairs, Population Division, 2022). These countries, despite consuming less fish per capita, are more dependant on fish as a dietary source of protein than richer countries (Kent, 1997). This growth has led to an increased demand for resources and, with global wild fish stocks approaching a saturation point for sustainable production, aquaculture has become the fastest growing sector for food production worldwide (Subasinghe et al., 2009; Troell et al., 2014; FAO, 2022a).

Combining aquaculture with modern farming practices has allowed for a high level of production, reaching 122.6 million tonnes in 2020, of which 57.5 million tonnes was from finfish aquaculture (FAO, 2022a). However, these practices can be intensive and have raised concerns regarding nutrient pollution within local ecosystems (Pillay, 2008). Large-scale finfish aquaculture, paired with the high levels of fish feed being added to the system, can cause eutrophication of the local environment due to the nutrient input of uneaten food particles along with both soluble and insoluble waste products produced by the fish. Over time this can result in negative effects for local ecological communities and, eventually, the aquaculture system itself, including lowered immunity and increased mortality (Braaten et al., 1983; Folke and Kautsky, 1992; Naylor et al., 2000). In order to address this issue, Integrated

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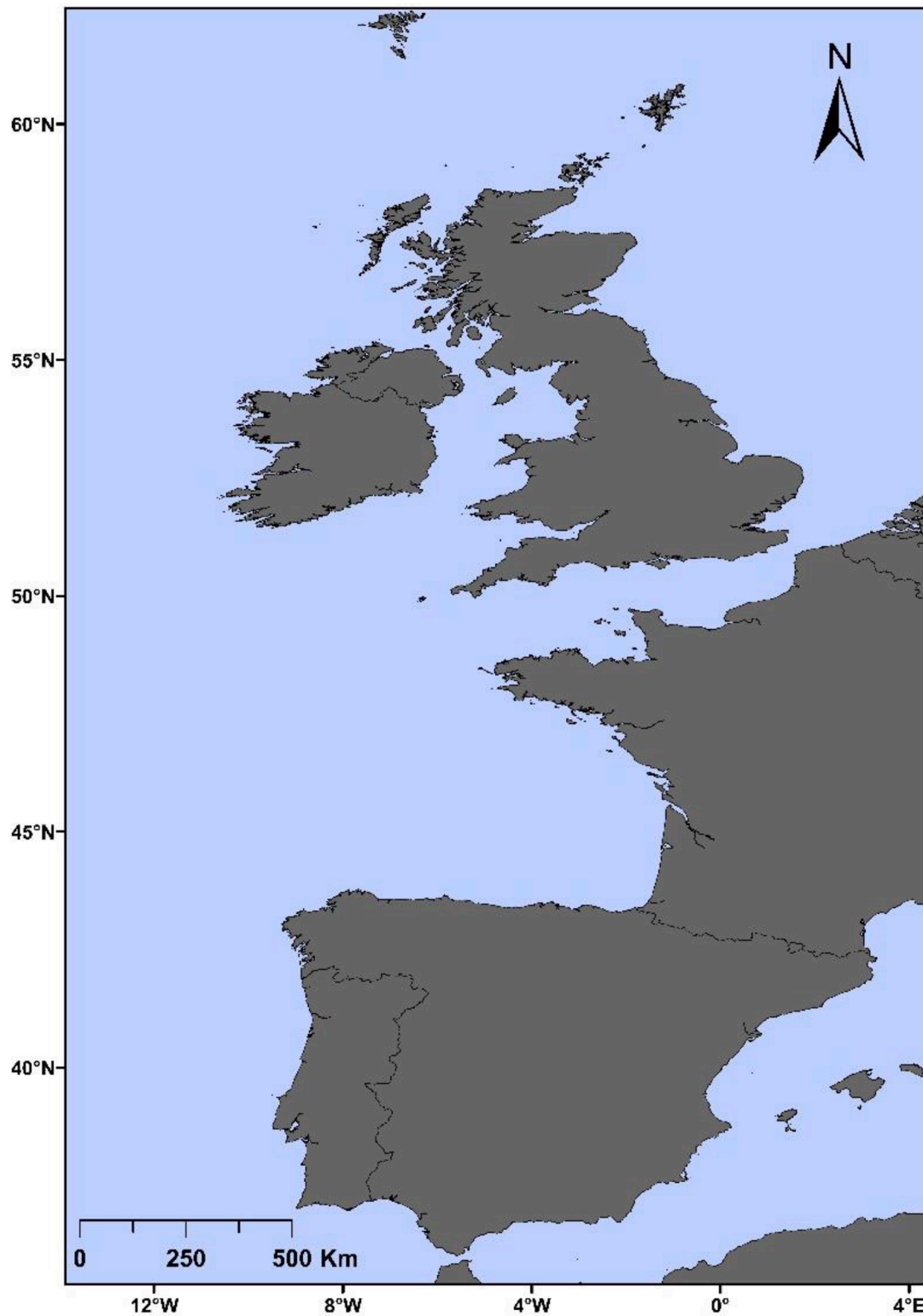


Fig. 1. Area covered by the model, including the INTERREG Atlantic Area without the Canary Islands, Madeira and the Azores, from 36°N to 61°N latitude and 11°W to 2°E longitude.

Multi-Trophic Aquaculture (IMTA) has been proposed as a method to make aquaculture activities more sustainable in the long term (Troell et al., 2009; Khanjani et al., 2022).

IMTA is the practice of farming complementary species from different trophic levels in proximity to each other, allowing waste products from fed species to be recaptured and utilised by organic and inorganic extractive species (Neori et al., 2004; Chopin, 2010). These

systems have proven effective at reducing eutrophication and usually consist of a suspension/deposit feeding species for organic nutrients and a seaweed species for inorganic nutrients (Chopin et al., 2001; Neori et al., 2004; MacDonald et al., 2011). Culturing species within an IMTA system can lead to increased production for the extractive species; significant increases in growth were observed in oysters and mussels when co-cultured with salmon (Gunning et al., 2016), while kelp showed a

22% increase in production when modelled with salmon as part of an IMTA system (Cubillo et al., 2016).

IMTA has been practiced in Asian countries for centuries, with many small systems being found inland at a household scale, combining agriculture and aquaculture (Barrington et al., 2009). Large-scale IMTA systems have been in place for decades, for example in Sanggou Bay, which has practiced IMTA since the late 1980s, using different combinations of species including finfish, bivalves, kelp and abalone (Fang et al., 2016).

Despite the widespread use of IMTA in Asian countries, it is a relatively new concept in Europe, with most IMTA systems only operating at a research or pilot scale (Troell et al., 2009; Alexander and Hughes, 2017; Kleitou et al., 2018). In the interest of improving the uptake of IMTA systems within Europe, this study aims to produce a habitat suitability model for an IMTA system comprising three commercially important species from different trophic levels: Atlantic Salmon *Salmo salar* (Linnaeus), common blue mussel *Mytilus edulis* (Linnaeus), and Oarweed *Laminaria digitata* (Hudson) JV Lamouroux. These genera have been identified as having high potential for use in temperate water IMTA systems due to a combination of established husbandry practices, known ranges, and their effectiveness in biomitigation (Barrington et al., 2009). *M. edulis* and *L. digitata* were selected for use in the IMTA system due to their efficient nutrient assimilation capabilities. In laboratory trials, *M. edulis* has exhibited up to 90% absorption efficiency of salmon (*S. salar*) feed and 86% for salmon faeces, with a 54% absorption of total particulate matter in field trials (Reid et al., 2010). *L. digitata*, meanwhile, has been shown to have an absorption efficiency of approximately 40 $\mu\text{mol nitrate g}^{-1} \text{FW d}^{-1}$, and 1 $\mu\text{mol phosphate g}^{-1} \text{FW d}^{-1}$ (FW = fresh weight) (Gordillo et al., 2002). Additionally, these species contribute significantly to global aquaculture, with *S. salar* making up 4.7% of global finfish production and the Mytilidae family of sea mussels contributing 6.2% of mollusc production (FAO, 2022a). *L. digitata* does not contribute significantly to algae aquaculture, however 96% of algae aquaculture takes place in Asia where *L. digitata* is not natively found, and so this represents an underexploited market in European aquaculture, where a rapid increase in demand is expected in the coming years (Chopin, 2014; Kim et al., 2017).

Species distribution data was collected for *S. salar*, *M. edulis* and *L. digitata* using the European Marine Observation and Data network (EMODnet) database and the Global Biodiversity Information Facility (GBIF) database. Using this data, and environmental data within the European Union's INTERREG Atlantic Area, for the INTEGRATE project, models of habitat suitability were produced using the Maximum Entropy (MaxEnt) modelling approach and input into Geographic Information System (GIS) software (Bella Voak, unpublished). This paper presents the most suitable sites for development of an IMTA system using this species combination within the INTEGRATE project area of Europe's Atlantic coast and provides an example of how to identify optimal locations.

2. Methods

2.1. Study site

Habitat suitability models were built for *S. salar*, *M. edulis* and *L. digitata* within the marine and coastal areas covered by the European Union's INTERREG Atlantic Area, for the INTEGRATE project. This project covers the western European countries bordering the Atlantic Ocean, ranging from the south of Spain to the north of France, including Ireland, the western coast of the United Kingdom and several small islands (Canary Islands, Madeira and the Azores). To avoid the introduction of non-native species these islands were excluded from the model as, of the selected species, only *M. edulis* has confirmed occurrence records at these locations. This study site ranges from 36°N to 61°N latitude and 11°W to 2°E longitude (Fig. 1). It includes the Atlantic Area but is wider in extent as it is a Latitude/Longitude box.

2.2. Data acquisition

The variables used in the model were selected based on a literature search of previous estimates for these species (Mocq et al., 2013; Raybaud et al., 2013; Bergström et al., 2015; Bergström and Lindegarth 2016; Westmeijer et al., 2019). Variables were narrowed down by calculating pairwise correlations and removing variables with a Pearson's $r \geq 0.80$. Models were run using each correlated variable in turn, with the variables that produced more reliable models being retained. This reduces the influence of collinearity, which can lead to over-fitting of the model (Baldwin, 2009; Wei et al., 2018). After filtering, five environmental variables were selected for inclusion in the habitat suitability model: Current Velocity (m s^{-1}), pH, Chlorophyll A (mg m^{-3}), Salinity (PSS), and the mean Sea Surface Temperature (SST, °C). A second model was also created, substituting the mean SST for the maximum SST (°C), in order to identify an upper tolerance limit for each species. The environmental variables used were sourced from BioOracle (Tyberghein et al., 2012; Assis et al., 2018).

Species occurrence records for *S. salar*, *M. edulis* and *L. digitata* were taken from the EMODnet and GBIF databases, which are both provided as presence-only data (EMODnet Biology, 2023; GBIF, 2023a,b,c). The environmental data used is taken as an average value between 2000 and 2014; to accommodate this, the datasets were filtered and all species records from before the year 2000, or with no recorded date, were removed from the dataset. This gave a more accurate representation of the species current distribution and the conditions they occur in. After removing duplicate occurrence records, the final model used a total of 2462 data points (*L. digitata* – 205, *M. edulis* – 753, *S. salar* – 109).

2.3. Data manipulation

Environmental data was collected and manipulated using RStudio (R Core Team, 2021; SI 1). Using RStudio, the geographical coordinate system was set as WGS1984, while the extent for the data was set to encompass the entirety of the INTEGRATE project area as defined in Fig. 1. The specified environmental variables were taken from BioOracle before being resized to match this extent, with all values that fell outside of this area being given an N/A value to exclude them from the dataset. To ensure that all variables had the same pixel resolution, they were resampled to have a resolution of 30 arcseconds. The variables were then re-extended to the study area's extent, to account for the risk of resampling changing their spatial extent. All environmental data were then saved as ascii files for use in MaxEnt and ArcMap respectively. These manipulations were carried out using the 'raster' (Hijmans, 2021), 'rgdal' (Bivand et al., 2021), 'sdmpredictors' (Bosch and Fernandez, 2022) and 'sp' (Pebsma and Bivand, 2005; Bivand et al., 2013) packages.

Species data from 2000 onwards was collated into a single spreadsheet and organised into a 'species, longitude, latitude' format that could be read by both MaxEnt and ArcMap.

2.4. MaxEnt analysis

The five environmental variables were entered into MaxEnt along with the occurrence data for each species. The settings used to create the MaxEnt model are defined in SI 2. The results of the model were evaluated using two methods: the Area Under Curve (AUC) and a jackknife test of variable importance. The AUC (defined as the area under the Receiver Operating Characteristics (ROC) curve) is a threshold-independent method used to assess model performance and is expressed as a value from 0 to 1, with values of 0.5 indicating predictions are no better than random, while values closer to 1 indicate better model fit, although for presence-only data the maximum AUC is always lower than 1 (Fielding and Bell, 1997; Phillips et al., 2006; Townsend Peterson et al., 2007). An initial analysis of variable contributions precedes the jackknife test and determines how heavily the

Table 1Contribution and permutation importance of each variable to the model output for *S. salar*, *M. edulis* and *L. digitata*.

Variable	Species	Contribution (Permutation importance) (%)	Variable	Species	Contribution (Permutation importance) (%)
Mean SST (°C)	<i>S. salar</i>	0 (0)	Chlorophyll A (mg m ⁻³)	<i>S. salar</i>	58 (37.9)
	<i>M. edulis</i>	0.8 (0.7)		<i>M. edulis</i>	98.1 (97.7)
	<i>L. digitata</i>	6.8 (21.6)		<i>L. digitata</i>	89.5 (75.2)
pH	<i>S. salar</i>	4.4 (0)	Salinity (PSS)	<i>S. salar</i>	30.9 (39.8)
	<i>M. edulis</i>	0 (0.1)		<i>M. edulis</i>	0.2 (0.2)
	<i>L. digitata</i>	0 (0.3)		<i>L. digitata</i>	0 (0)
Current Velocity (m s ⁻¹)	<i>S. salar</i>	6.7 (22.3)			
	<i>M. edulis</i>	0.9 (1.3)			
	<i>L. digitata</i>	3.7 (2.9)			

model depends on each variable through their ‘permutation importance’; the values of each variable are randomly permuted and the resulting decrease in training AUC is expressed as a percentage, with larger decreases indicating a more important variable. The jackknife test then assesses variable importance by testing how the inclusion or exclusion of each variable affects the regularized training gain of the final model, with variables that contribute a higher gain being more important for the model result (Phillips, 2017).

2.5. ArcMap analysis

The model outputs produced by MaxEnt were analysed with ArcGIS software (ArcMap 10.8.1) (ESRI, 2020), using the WGS1984 geographic coordinate system. Each map produced in ArcMap used the ‘World Countries’ shapefile (Esri. World Countries., 2021). For each species, the average model output was added to ArcMap and, using the ‘Raster Calculator’ tool within the Spatial Analyst toolbox, the average suitability value at each pixel was calculated for the three species.

2.6. Other factors

To ensure the identified habitats were feasible for an IMTA system, several factors were considered. Firstly, data on Marine Protected Areas (MPAs) (UNEP-WCMC and IUCN, 2022) was overlaid on top of the habitat suitability model, to assess overlap with protected areas. The yearly route density of vessels within Europe in 2022 was added, in order to identify important shipping routes where an IMTA system is more likely to be damaged or cause an obstruction to these vessels (EMODnet Human Activities, 2022). Any sites identified as suitable by the habitat suitability model within shipping lanes were excluded from the final selection, due to the increased risk of damage to the IMTA system caused by a collision. Any suitable areas found within the boundaries of MPAs were also excluded due to the increased difficulty in obtaining an aquaculture license (Brown et al., 2020), and the potential for damaging these areas. The model outputs were examined to determine which areas had the largest amount of >50% suitable habitat and, as a secondary step, the location and size of harbours throughout the

study area was examined, to establish the ease of access for construction and maintenance of the IMTA system (National Geospace Intelligence Agency, 2016). The remaining sites were then assessed based on their location, considering the potential risks associated with an area and the proximity to ports that enable transportation of IMTA products. The MaxEnt models use wild population data to predict suitable habitat conditions to support these species. As *Salmo salar* will be stocked at densities that are not likely to be found in a natural population, it is important to confirm the environmental conditions present are suitable for IMTA. To assess how the predicted suitabilities compare to the conditions required for aquaculture, including engineering aspects, the Current Velocity, Mean SST and Salinity of the sites were compared against known *Salmo salar* aquaculture sites around Scotland (Aquaculture Scotland, 2022). Although not used in the model, Bathymetry (m) and Dissolved Oxygen (ml l⁻¹) data, from MARSPEC (Sbrocco and Barber, 2013) and BioOracle (Tyberghein et al., 2012; Assis et al., 2018) respectively, were also downloaded and compared against these sites. For the purposes of this study, suitable areas were required to have an average depth of at least 20 m.

2.7. Comparison with literature

After using the MaxEnt output to identify the optimal value of each variable for all three species, a literature review was carried out to compare the results of the habitat suitability models against previous research. Comparison against previous research can help determine the reliability of the model, and inform decision making regarding site selection, although not all variables have been studied in relation to each species. Using the model results and information from the literature, tables were produced for direct comparison of these values.

3. Results

3.1. MaxEnt results

For each species, after spatial jackknifing, the AUC value, Omission and feature types were given as: *S. salar* – 0.889, Omission = 0.138,

Table 2Optimal values from the MaxEnt output for each variable in isolation to maximise probability of occurrence for *S. salar*, *M. edulis* and *L. digitata* (SI4). Also includes Max SST values from the secondary model.

Variable	Species	Optimal suitability value	Variable	Species	Optimal suitability value
pH	<i>S. salar</i>	7.8	Chlorophyll A (mg m ⁻³)	<i>S. salar</i>	14 - 32
	<i>M. edulis</i>	8.06		<i>M. edulis</i>	5 - 60
	<i>L. digitata</i>	8.21		<i>L. digitata</i>	4.5
Max SST (°C)	<i>S. salar</i>	23	Salinity (PSS)	<i>S. salar</i>	31.5 – 31.93
	<i>M. edulis</i>	17.28 ⁺		<i>M. edulis</i>	31.8
	<i>L. digitata</i>	14.7		<i>L. digitata</i>	30.42
Current Velocity (m s ⁻¹)	<i>S. salar</i>	0.17 ⁺	Mean SST (°C)	<i>S. salar</i>	11.53
	<i>M. edulis</i>	0.19 – 0.22		<i>M. edulis</i>	12.05 – 12.46
	<i>L. digitata</i>	0.12 - 0.2		<i>L. digitata</i>	7.3* 12.2 – 12.7

* See Discussion for account of why there could be two optimum Mean SSTs.

+ Total suitability decrease is less than 5% from the optimal across the range of measurements for this variable.

Table 3

Optimal values of each variable for *S. salar*, *M. edulis* and *L. digitata* according to a review of literature.

Variable	Species	Optimal value from literature	Source
Current velocity (m s ⁻¹)	<i>S. salar</i>	0.8 Body Lengths s ⁻¹	Solstørm et al., 2015
		0.8 Body Lengths s ⁻¹	Solstørm et al., 2016
		0.3–0.9 Body Lengths s ⁻¹	Hvas et al., 2021
	<i>M. edulis</i>	0.25–0.3 (dependant on substrate type and % mussel cover)	Widdows et al., 1998
		0.2–1.4 (dependant on number of mussels)	Nielsen and Vismann, 2014
	<i>L. digitata</i>	0.05–0.1 0.1–0.22	Edwards and Watson, 2011 Kregting et al., 2015
Salinity (PSS)	<i>S. salar</i>	28–34 33–34	Handeland et al., 1998 FAO, 2022b
		28 30 30–33 (Larvae)	Bergström and Lindegardh, 2016 Riisgård et al., 2012
	<i>M. edulis</i>	20–30 20–55 34–35	Bayne, 1965 Westmeijer et al., 2019 Karsten, 2007
			Raybaud et al., 2013
	<i>L. digitata</i>	16–20 (Juveniles) 13 (Post-Smolt) 12–13 (Post-Smolt)	Jonsson et al., 2001 Handeland et al., 2003
			Reddin et al., 2006
Mean SST (°C)	<i>S. salar</i>	12–17 17 13–18 (Larvae)	Bergström and Lindegardh, 2016 Widdows, 1978 Bayne, 1965
			Westmeijer et al., 2019
	<i>M. edulis</i>	10–15 10 10–15	Bolton and Lüning, 1982 Tom Dieck, 1992
	<i>L. digitata</i>		

Feature Types = Linear and Quadratic; *M. edulis* – 0.876, Omission = 0.089, Feature Types = Hinge, Linear and Quadratic; *L. digitata* – 0.901, Omission = 0.161, Feature Types = Hinge.

The test of variable contribution and permutation importance (Table 1) shows that, based on permutation importance, Chlorophyll A is the most important contributor to the model results for all three species (*S. salar* – 37.9%, *M. edulis* – 97.7%, *L. digitata* – 75.2%), while for each species the variable with the lowest permutation importance was: *S. salar* – pH and Mean SST, both 0%; *M. edulis* – pH, 0.1%; *L. digitata* – Salinity, 0%. The jackknife test (SI 3) indicates that Chlorophyll A had the highest regularised training gain for all three species: *S. salar* – 0.43; *M. edulis* – 0.37; *L. digitata* – 0.74. The variable with the lowest training gain for all three species was Current Velocity: *S. salar* – 0; *M. edulis* – 0.01; *L. digitata* – 0.01. For all species, the variable that decreased the training gain the most when omitted was Chlorophyll A.

3.2. Optimal conditions

Response curves (SI 4) were generated by MaxEnt for each variable in isolation and used to identify the optimal value that maximises the habitat suitability for each species (Table 2). When taken in isolation, the variable that predicted the highest probability of occurrence for each species was Chlorophyll A. When comparing the response curves of variables in isolation against those that also use the other variables, the suitability values are different as the other variables influence the environment. This indicates that, while some variables may be more important in isolation, balancing the optimal conditions for other

variables will have a greater effect on the overall suitability of a habitat. Using the variables that had the largest contribution to the final model can show the sensitivity of these species to environmental changes. The largest contributing variable for *S. salar* was Chlorophyll A, with the habitat suitability being 37% at 0 mg m⁻³, and increasing to 100% from 14 mg m⁻³ to 32 mg m⁻³ before decreasing. Chlorophyll A was the largest contributor for the model of *M. edulis* distribution, rising from 1% at 0 mg m⁻³ to 85% from 5 mg m⁻³ to 60 mg m⁻³. The largest model contributor for *L. digitata* was Chlorophyll A, which has a 0% habitat suitability at 0 mg m⁻³, increasing to 88% suitability at 4.5 mg m⁻³ before decreasing steadily to 37% at 60 mg m⁻³.

The results of the literature search (Table 3) showed that significant research had been conducted on the optimal values of some variables, while others, despite some research, had not identified a specific optimal value and so were not included in the table. The optimal values identified showed similarities to the output of the model (Table 2). Differences were also observed, with the optimal value for current velocity in *M. edulis* distribution lying below the value identified in the literature, although these studies identified that greater numbers of mussels increased their tolerance to high current velocities. Two values were determined for the optimum mean SST for *L. digitata* (7.3 °C and 12.2–12.7 °C). When compared to the literature, the lower value is below the minimum optimal temperature range of 10–15 °C, while the higher value corresponds to the optimal conditions from the literature search.

3.3. Habitat suitability

After averaging the model results for all 3 species, the combined habitat suitability ranged from 4–93.6% suitability. The results indicate there are higher levels of suitable areas around the United Kingdom and Ireland compared to other areas of the INTEGRATE project boundaries (Fig. 2), although areas of >50% suitability can be found as far south as Spain and Portugal. The largest concentration of highly suitable habitats are found along the coast of the United Kingdom and Ireland, with large areas of the Northern and Western coastline of France also having the highest levels of suitability. Habitat suitability tends to decrease as distance from the shore increases, indicating that near-shore IMTA systems may be preferable for use.

To further identify the optimal sites to establish an IMTA system for this species combination, habitats with a suitability score of <50% were excluded from further analysis. Overlaying shipping density and MPA data for France, the United Kingdom and Ireland showed that much of the suitable habitat was no longer available for selection, as these habitats lay within MPA boundaries or were at risk of disruption by passing vessels (Fig. 3). Depth analysis of the remaining habitats allowed for identification of several potential sites, A – D, which represent the locations with the largest areas of suitable habitat and which have comparable conditions to existing *Salmo salar* aquaculture sites around Scotland. Large areas of highly suitable habitat are seen as advantageous, as this allows for flexibility in the precise location of the IMTA system while also providing scope for expansion of the system in the future.

Site A, located on the northwest coast of Ireland, contains ~108 km² of suitable habitat. The closest access to this site is from the very small harbour in the town of Sligo, located ~30 km from this area (Fig. 4).

Site B encompasses suitable areas within Lough Swilly on the north coast of Ireland and areas lying to the east and west of the entrance of the lough. Suitable areas in Lough Swilly are sheltered on all sides by land and the only access to the ocean is from the northern end of the lough. Suitable areas make up ~44 km² while the closest access is from the very small harbour in Rathmullan. Rathmullan harbour is located within Lough Swilly and so is 5–15 km from suitable areas within the lough. It is ~30 km from suitable areas at the mouth of the lough.

Site C is located on the north coast of the Isle of Lewis in Scotland, an exposed area which is subject to the wave action and currents of the

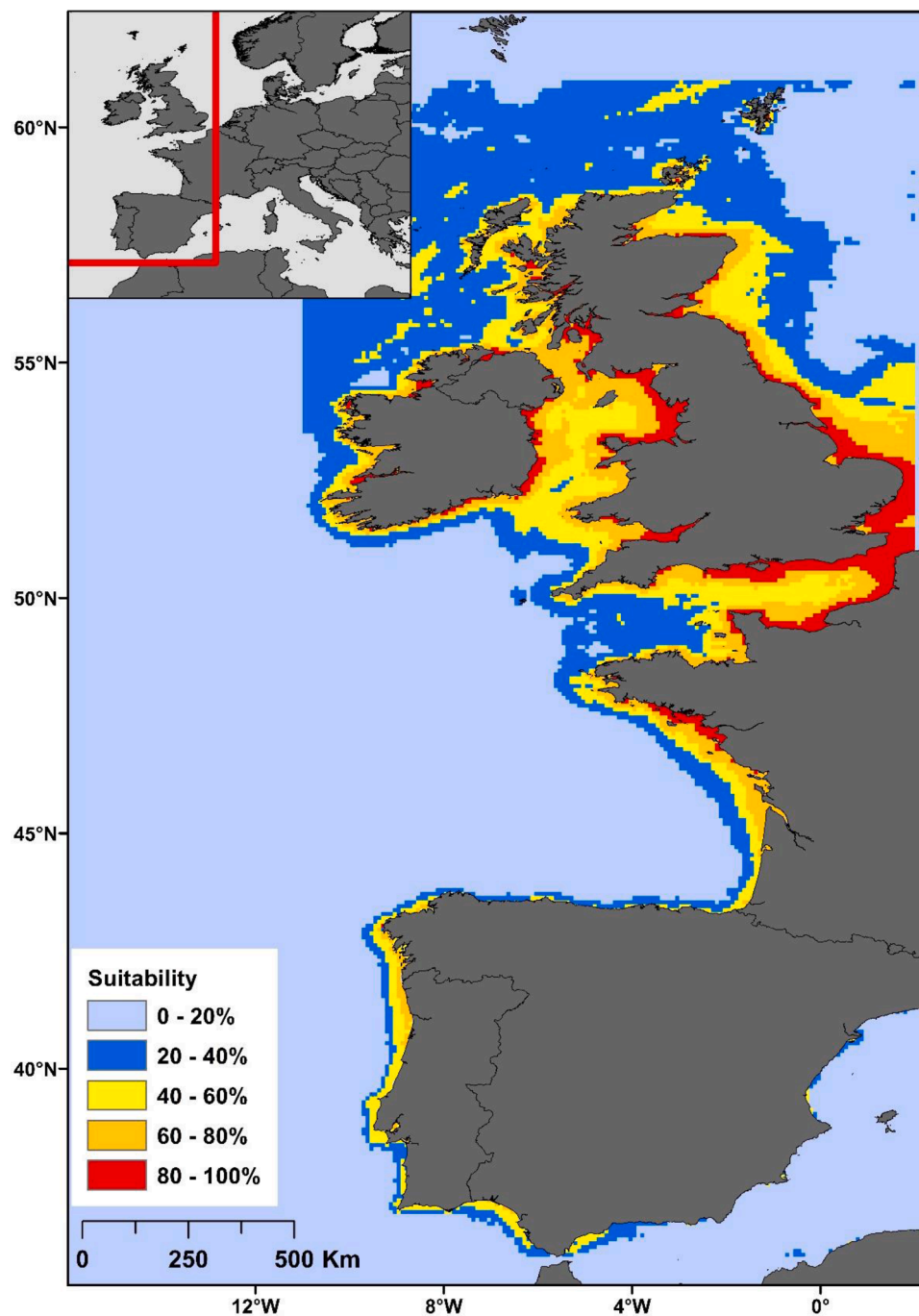


Fig. 2. Output of the habitat suitability model, showing the combined average suitability for *S. salar*, *M. edulis* and *L. digitata* within the INTEGRATE project area.

Atlantic Ocean, meaning that, if selected for use, engineering considerations will be especially important to withstand these conditions. It comprises $\sim 22 \text{ km}^2$ of suitable area along the coastline, with the closest access to this site being from the very small Stornoway harbour on the northeast side of the island. As the suitable area stretches along the coastline, the distance from Stornoway harbour ranges from 60–90 km.

Site D is located on the north coast of Brittany, a peninsula in the northwest of France. The sheltered area surrounding Plage de Keremma (Keremma Beach) is designated as an MPA and so is unavailable for use in this study; however, Site D still contains $\sim 30 \text{ km}^2$ of suitable habitat, with the most suitable areas lying to the east of the MPA. The closest access to Site D is the very small harbour of Port de Roscoff-Bloscon, located $\sim 15 \text{ km}$ from this area.

4. Discussion

MaxEnt was chosen for this study as it can function using presence-only data, can handle small datasets, and has a relatively high level of performance when compared to other modelling approaches (Phillips et al., 2006; Elith et al., 2006; Baldwin, 2009). This approach can model large areas for habitat suitability and it allows for suitable sites to be narrowed down for more detailed consideration, as illustrated by sites A-D in this study. Additional sites could be identified by changing the selection criteria used in this study, for example by including areas that fall within MPA boundaries.

With the results of each model implying a high level of predictive accuracy and, having used the habitat suitability model to determine suitable locations for an IMTA system, consideration must be given to

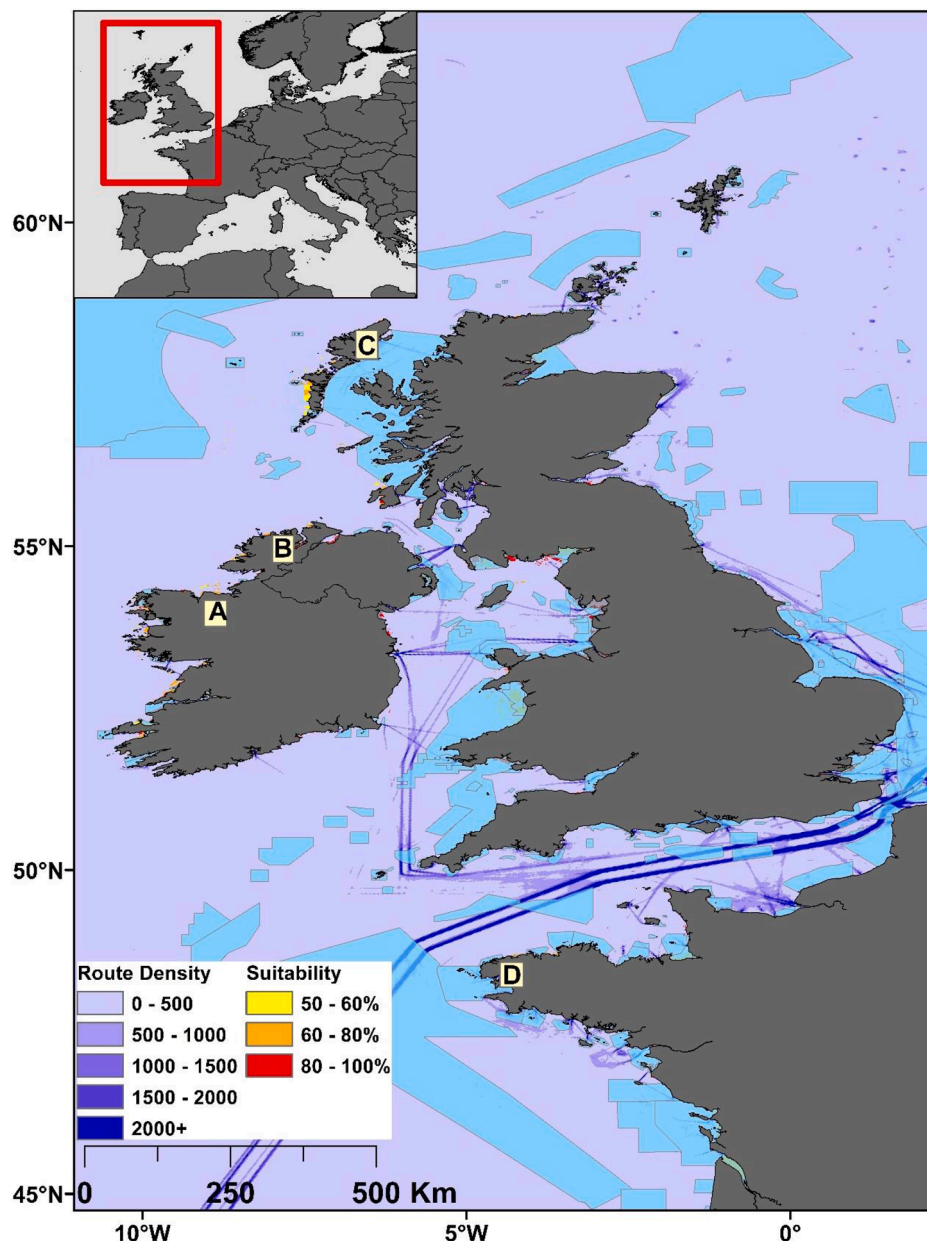


Fig. 3. The location of MPAs (in blue; [UNEP-WCMC & IUCN, 2022](#)) and the route density for vessels within Europe ([EMODnet Human Activities, 2022](#)). Sites A – D represent the areas selected as being most suitable for implementing an IMTA system.

the management and economic viability of each site. By examining Sites A – D, an example of considerations for selecting the optimal site can be outlined. Using current aquaculture site data from the Isles of Skye and Lewis ([Aquaculture Scotland, 2022](#)), and comparing this data to the size of harbours in this area, it can be presumed that harbours classified as ‘Very Small’ are able to meet the demands of operating an aquaculture system, or that distance is not a major point of consideration, as the closest harbour of a larger size is ~100 km from the Isle of Skye.

Site A is located in northwestern Ireland and is exposed to the wave action and currents of the North Atlantic Ocean. Of the four sites, it contains the largest amount of suitable area based on the model criteria (~108 km²), although some of these suitable areas are located >10 km offshore which, due to the challenges associated with offshore IMTA, may impact the feasibility of establishing a system in these areas ([Buck et al., 2018](#)). *M. edulis* and *L. digitata* are found within the area of Site A while *S. salar* has occurrence data in coastal areas to the north and south and the habitat is predicted to be >50% suitable for the species. Sites A

and B are located in the Republic of Ireland which will provide full access to the EU trade market. International transport could be facilitated through Dublin Port, which handles approximately 3.4 million gross tonnes of exports per year ([Dublin Port, 2022](#)).

As shelter from the open ocean acts to reduce wave action, Site B, being almost fully enclosed by land, should have relatively stable conditions in comparison to an exposed site. Although there may be some locally generated wave action within the lough, this shelter from the open ocean should reduce the risk of damage from natural causes to an IMTA system. Freshwater outflow from local rivers within Site B is not considered to be an issue as the salinity within the lough is comparable to the open ocean. Additionally, of the 3 species, *M. edulis* and *L. digitata* are native found within Lough Swilly, and *S. salar*, while not recorded within the lough, are known to travel between the ocean and freshwater environments, with the model predicting >60% suitability for *S. salar* throughout this area. The proximity of Site B to Rathmullan port allows easy access for vessels to perform routine work and maintenance on an

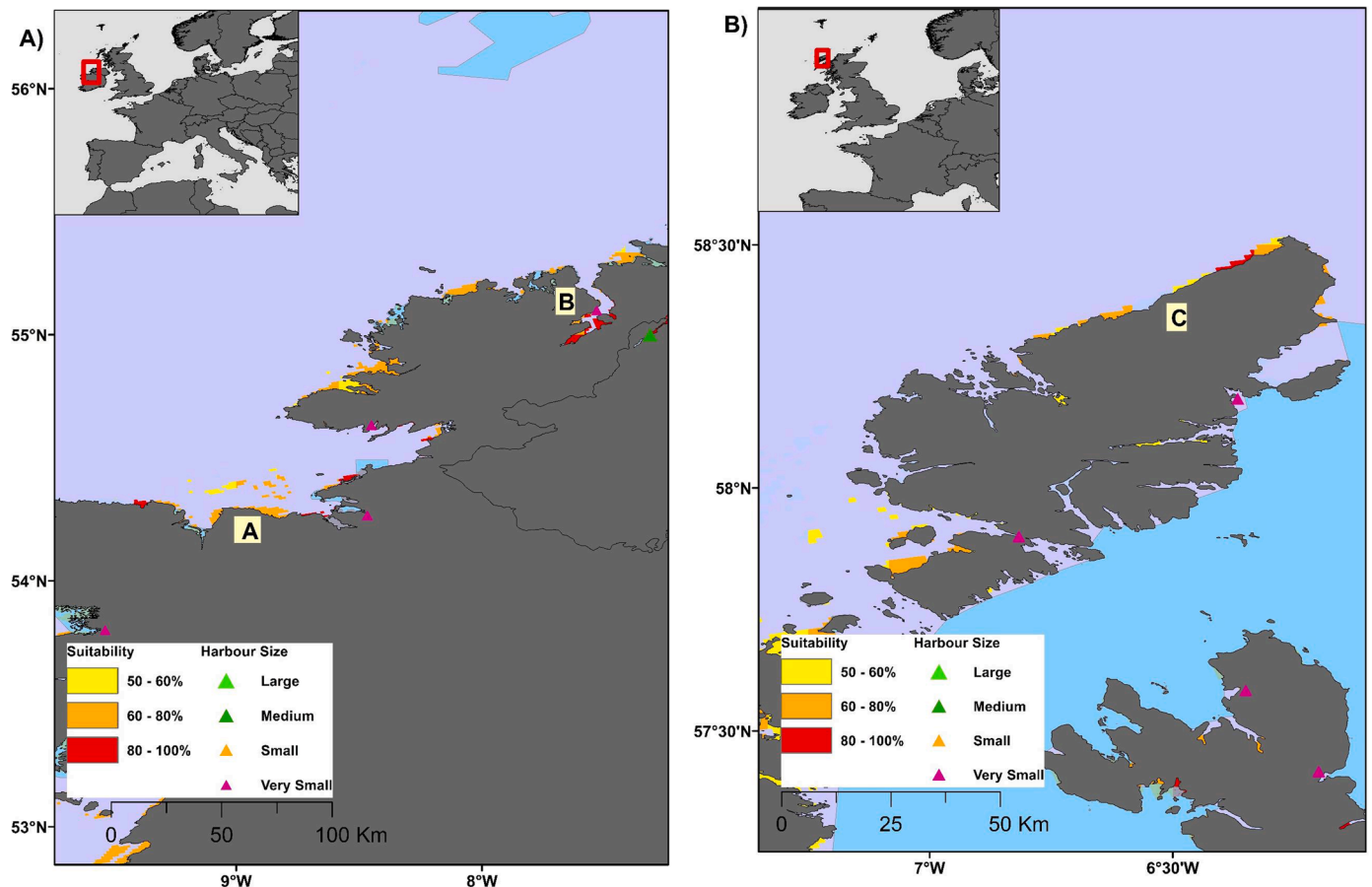


Fig. 4. The size and location of harbours (National Geospace Intelligence Agency, 2016), MPAs (in blue; UNEP-WCMC & IUCN, 2022) throughout the UK and Ireland in relation to the potential sites for an IMTA system. A) Sites A and B in the northwest of Ireland. B) Site C on the northern coast of the Isle of Lewis, Scotland. C) Site D in the northwest of France.

IMTA system, while also providing a transport hub for IMTA products.

Site C, located along the northern coast of the Isle of Lewis, is fully exposed to the conditions of the North Atlantic Ocean. Although the closest harbour is located 60 km away there are currently active marine aquaculture sites along this coast (Aquaculture Scotland, 2022), which shows that aquaculture remains feasible in this location from an operational perspective. However, these active sites are found in the more sheltered areas of the coast south of Site C, indicating that conditions may make aquaculture activities more challenging. All three species have occurrence records in the waters around the Isle of Lewis, further highlighting that these species are suited to the conditions in this area.

Site D is found in the north of Brittany, France in an exposed area at the mouth of the English Channel. If an IMTA site were to be established here then consideration should be given to Plage de Keremma, a beach that is found within this area. Any restrictions put in place as a result of IMTA operations should not restrict public access to this area, as this may negatively impact public support for the project.

The mean SST at Sites A, B and C are approximately 11–12 °C, which is slightly below the optimal temperatures predicted by the model for *M. edulis* and *L. digitata*, while being optimal for *S. salar* (Table 2). Data shows that the mean sea surface temperature in UK coastal waters has risen by between 0.17 to 0.45 °C per decade since 1984, including an average increase of 0.3 °C per decade recorded at Malin Head Coastal Station, Ireland since 1960 (Collins et al., 2020; Cornes et al., 2023). Using these marginally sub-optimal conditions could be seen as a precaution to reduce the effects of future climate change on the IMTA system. Including seaweed within the IMTA system may act to locally reduce some of the effects of climate change, which will benefit the

cultured species as well as the surrounding environment. With the North Sea and UK waters showing a higher rate of ocean acidification than the North Atlantic as a whole, culturing seaweed species can provide benefits by elevating the pH while also oxygenating the water and reducing erosion (Duarte et al., 2017; Williamson et al., 2017).

These results constitute an initial assessment of habitat suitability, however further study should be carried out to ensure any site meets the needs of the aquaculture company. For example, attention must be given to the current direction at a given site, to ensure species are orientated in such a way to maximise their biomitigation ability while reducing the risk of undesirable interactions. Also of concern are the nutrient concentrations in a given area. Although nutrients will be provided from fish food and excretions, it is important to make sure that nutrient provision will not be a limiting factor, by having a suitable level already present in the environment. Prospective aquaculture companies should also seek to identify the optimal location that will have the minimal impact on the surrounding environment, such as by avoiding areas that contain vulnerable species or areas of high biodiversity that are not currently protected.

The predicted suitability of habitats may be limited by the number and selection of environmental variables used when constructing the model, with variables that were not considered having the potential to significantly affect the predicted distributions. Additionally, the environmental variables used in this model were average values taken between 2000–2014, and it is possible that these values are no longer fully representative of the current conditions within the INTEGRATE project area. Local evaluations of individual sites are therefore recommended, to ensure that the current environmental conditions continue to align

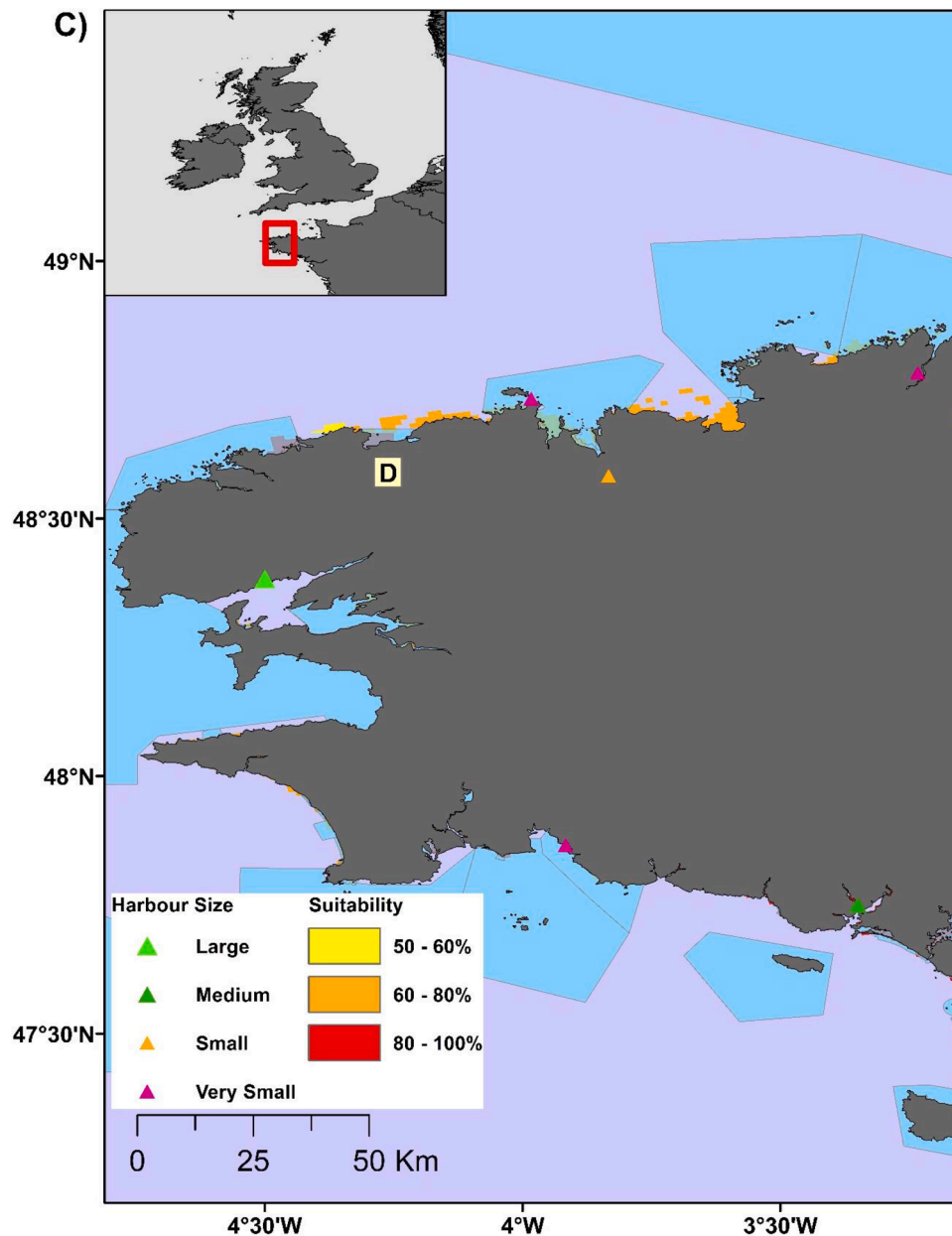


Fig. 4. (continued).

with the optimal values identified within this study.

The 'Maximum training sensitivity plus specificity' (MaxSS) threshold chosen for this model is generally used for presence/absence data, although there is evidence that it is a robust method when considering presence only data (Liu et al., 2013, 2016). Although efforts were made to correct for sampling bias, this model was built using presence only data and so consideration must be given to possible biases associated with this data, where some areas (e.g. near shore locations) will be subject to more sampling than others (e.g. offshore locations), which is known to have a larger effect than on models using presence – absence data (Phillips et al., 2009).

It is worth noting that the habitat suitability model predicts the likelihood of a natural population occurring or being able to survive in a specific area. As this study is identifying sites for an IMTA system, some variables not included in the model (e.g. bathymetry) can be controlled using the equipment associated with these systems, such as longlines and fish cages. Manually selecting the culture depth for each species can minimise potential damage from the surface caused by adverse weather

conditions or boats while also maintaining optimal conditions. If the culture depth allows for access to the surface, this may be of particular importance for *S. salar* for refilling their swim bladders. The inability to refill the swim bladder has been shown to lead to reduced growth, although if this is not feasible then integrating a dome of air into the cage has been shown to be effective in preventing this (Korsøen et al., 2012). When considering each variable in isolation, Chlorophyll A was predicted to be the most important variable for all species when determining habitat suitability. This is important as the optimal levels for *L. digitata* falls outside the optimal range of both *S. salar* and *M. edulis* (SI 4). The lower suitability of *L. digitata* at higher concentrations is possibly due to Chlorophyll A acting as a proxy for phytoplankton concentration, which is known to reduce the photosynthetic capabilities of kelp by increasing light attenuation (Kavanaugh et al., 2009; Thomas et al., 2011), although culturing *L. digitata* on longlines closer to the surface should reduce this effect. *L. digitata* was shown to have 2 optimal values for mean SST (Table 2), which may be indicative of different optimal temperatures between populations or at different stages of the kelp

life-cycle. For example, while the literature search revealed an optimum temperature of 10–15 °C, this optimum has been suggested to be between 5–10 °C during sporogenesis of *L. digitata* (Bartsch et al., 2013). Differences can also be seen in the thermal tolerances of separate populations, with a study of North Sea and Arctic *L. digitata* showing a divergence in the thermal plasticity of the 2 populations when exposed to different temperatures (Martins et al., 2020).

4.1. Conclusion

This habitat suitability model provides insight into the high levels of potential for IMTA systems for this combination of species within the European Union's Atlantic coastline. This study identified optimal values for the selected environmental variables. Some of these values were different to that reported in the literature, suggesting that the optimal values for these variables may require further study to be fully understood. These habitat suitability models should be treated as only a preliminary test of suitability, identifying optimal conditions for natural populations of these species, and it is recommended that local assessments should be performed at any sites identified from the model. Relevant factors affecting final site selection, such as port access, are also introduced and can be used for future models examining different species of interest within the aquaculture sector.

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CRediT authorship contribution statement

Conchúr Hughes: Methodology, Software, Validation, Formal analysis, Investigation, Data curation, Writing – original draft, Visualization, Project administration. **Jonathan W. King:** Conceptualization, Resources, Writing – review & editing, Supervision, Funding acquisition.

Declaration of Competing Interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: Conchur Hughes reports financial support was provided by EU Interreg Atlantic Area. Jonathan W King reports a relationship with EU Interreg Atlantic Area that includes: funding grants.

Data availability

Data will be made available on request.

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Supplementary materials

Supplementary material associated with this article can be found, in the online version, at [doi:10.1016/j.ecolmodel.2023.110459](https://doi.org/10.1016/j.ecolmodel.2023.110459).

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