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Mapping habitat suitability of subtidal mussels *Mytilus edulis* in the Dutch western Wadden Sea

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ABSTRACT

Understanding environmental predictor variables of species occurrence may contribute to conservation management. In this paper we test the use of a spatial binomial model, estimated with the combined INLA-SPDE method, to relate the probability of occurrence of the mussel *Mytilus edulis* in the subtidal part of the western Dutch Wadden Sea in the period 1992–2022, to a range of environmental and human-impact related variables. Salinity and orbital velocity appeared to be the most important driving variables, and maximum probability of occurrence was predicted at intermediate salinity levels around 22 PSU and low orbital velocity. Mussel occurrence was also lower in the shipping lanes that are regularly dredged. One of the hypotheses is that at lower salinity physiological stress occurs, but that at higher salinity levels predation limits the occurrence. The spatial structure of the unexplained variation is described by a Gaussian field, but it remained unclear what the type of underlying explanatory mechanisms could have been that some areas had much lower probability of occurrence than expected on the basis of environmental conditions. Further understanding of these observed patterns, for example by including temporal dynamics or experimentally testing settlement limitations, could benefit future decision making for conservation management.

1. Introduction

Knowledge of the relationship between the spatial distribution of a species and environmental predictor variables can contribute to species conservation or restoration (Guisan et al., 2013). It can, for example, be used in the delineation of no-take zones for commercial species (Guisan et al., 2013). In estuaries and coastal zones, important commercial species such as mussels and oysters have shown a worldwide decline in abundance (Lotze et al., 2006). An important question is to what extent human impacts, for example due to bottom disturbance by fisheries, affect the distribution and abundance of these bivalve species. Better understanding of the influence of human activities versus natural environmental factors (e.g. salinity or sediment type) in a spatial context may provide a basis of governmental policy measures to better protect or possibly restore bivalve beds. While an earlier study has already produced a mussel habitat suitability map for the intertidal areas of the Dutch Wadden Sea (Brinkman et al., 2002), this has so far not been done for the subtidal areas. In this study we specifically focus on the subtidal blue mussel *Mytilus edulis* in the Western Wadden Sea, which is an important species with high biomass (Dekker, 1989), and for which a long-term data set of presence–absence (from 1992 onwards) is available.

Statistical species distribution models (SDMs) can be used to unravel the importance of natural environmental variables and human-related disturbances in determining the abundance and spatial distribution of species. SDMs have been widely applied in ecology to provide species distribution maps, also called habitat suitability maps (Guisan and Thuiller, 2005; Guisan et al., 2013). In species distribution modelling, as in many other fields of statistical modelling, two different approaches can be distinguished. The first approach uses formal statistical data models, such as for example a Generalized Linear Model (GLM) or Generalized Additive Model (GAM), which should not only enable prediction, but also provides information on how the response variable is exactly linked to the predictor variables. The second approach

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relies on black box type algorithms, often called machine-learning techniques, merely aiming for prediction (Breiman, 2001). Examples of such algorithms are Random Forest models (RF) or Boosted Regression Trees (BRT). A disadvantage of these techniques is the difficulty to understand how the predictions are actually made. Various authors have used both approaches, generally arriving at the conclusion that in terms of prediction performance none of the two approaches is overall superior to the other (Segurado and Araújo, 2004; Elith and Graham, 2009; Marmion et al., 2009; Syphard and Franklin, 2009; Huang et al., 2011; Oppel et al., 2012; Fernandes et al., 2018; Stock et al., 2018; Mohammadi et al., 2019; Luan et al., 2024). Although Huang et al. (2011) observed that 'overall machine-learning models achieved the best prediction performance', Fernandes et al. (2018) noted that models fitted by GAM/GLM had a higher accuracy and lower variance than BRT/RF, while other authors got mixed results. For example, Stock et al. (2018) observed that the best performing method differed among the response variables, but also that the machine learning models overfitted their data. Luan et al. (2024) concluded that GLM slightly outperformed GAM and RF overall, while RF showed more robust spatial extrapolations in many cases.

Species data are most likely spatially auto-correlated, which means that neighbouring locations are more likely to be similar than sites far apart, even when corrected for environmental differences. Since incorporating spatial auto-correlation in machine-learning methods is still in development (Jemeljanova et al., 2024; Koldasbayeva et al., 2024), and because we are also interested in interpreting the precise role of the predictor variables, we have chosen to walk the first avenue and focus on an explicit statistical data model including a term that accounts for spatial autocorrelation.

In the present case, presence–absence data are available for a number of sample stations, and the relationship with environmental variables can be described by means of a Generalized Linear Model (GLM) with a binomial link and a linear predictor providing a unimodal relationship with one or more environmental variables. The model can subsequently be used to predict presence–absence in the entire area of interest if environmental information is available. Initially spatial auto-correlation was ignored when fitting SDMs, but this may lead to biased estimates and inflated error rates (Dormann et al., 2007). The spatial structure can be modelled by a continuous Gaussian field, where it usually is assumed that the covariance of the error terms at any two locations is a function of the distance between the two locations. Both the environmental variables and the spatial random field will account for part of the overall variation and mapping the contribution of the environmental variables and the spatial random field to the predictor will shed light on their relative importance and may lead to further hypotheses on underlying processes.

Even more challenging than the case with only presence–absence data, is when abundance data, usually containing a lot of zero values, are also available. In a previous research program we developed and implemented a general procedure for mapping species abundance when the data consists of zero-inflated (i.e. containing a lot of zero values) and spatially correlated counts (Lyashevska et al., 2016a,b). A spatial zero-inflated Poisson mixture model was used to relate species counts to environmental covariates. The model contains two-processes: a Bernoulli process and a Poisson process. The first process focuses on species prevalence, which means that only the probability that the species is present or absent is considered. The second process focuses on intensity, conditional on the first process predicting presence. Intensity is a statistical term and can here be interpreted as the species density. Roughly speaking the model predicts two types of zeros: the species will not be present at a specific site (Bernoulli zero) or the species can be present (Bernoulli one) but is just absent by coincidence (Poisson zero). The covariance of the error terms at any two locations was modelled as a function of the distance between the two locations. The model was used to make predictions for sites where no species and only environmental data were available. Unfortunately, the method is rather computer intensive and computation time was about 72 h on a 8-cores x86-64 platform, a powerful personal computer. Furthermore, the method is not easy to use for a non-specialist.

In the last decade the recently developed Integrated Nested Laplace Approximation algorithm combined with the Stochastic Partial Differential Equation approach (INLA-SPDE) to estimate and predict the spatial field (a Gaussian Markov Random Field (GMRF) based on a Mátern correlation function), has shown to be a practical alternative to the method described above (Lindgren, 2012; Lindgren and Rue, 2015). The method is based on a Bayesian approach and not on a frequentist approach as our previous study was. It only provides an approximation to the optimal solution, but in practice the results are very similar to exact methods that are much more computer-intensive. The method is very flexible and is able to deal with zero-inflated and spatially autocorrelated data. Another advantage is that a well-documented package in the open source R-environment (which is nowadays more or less the standard computing program in statistical ecology and used by most quantitative ecologists and statisticians, see https://www.r-inla.org/) is available, with additionally easily accessible tutorials, see e.g. Blangiardo and Cameletti (2015), Zuur et al. (2017), Moraga (2019) and Gómez-Rubio (2020) or various websites (e.g. https://punama.github.io/BDI_INLA/). In ecology, agriculture and forestry studies, the INLA-SPDE approach is increasingly used to describe spatially auto-correlated species abundance data in relation to the environment (Sadykova et al., 2017; Lezama-Ochoa et al., 2020; Engel et al., 2022; Fichera et al., 2023; Morera-Pujol et al., 2023).

This study aims to determine which natural environmental variables play the most important role in determining mussel presence, assess whether human-related disturbance add further explanatory power, and map and interpret the spatial field of unexplained error. Out of a range of abiotic environmental variables, including salinity, bottom depth, hydrodynamic variables and sediment characteristics, the best fitting model will be selected using the INLA-SPDE approach. Two human-related disturbances, that is shrimp fisheries intensity and dredging, will be added to the selected model. The results will be discussed in light of their potential contribution to optimize possible management policy options aimed at increasing mussel presence in the subtidal Wadden Sea.

2. Methods

2.1. Study area

The Wadden Sea is located in the south-eastern coastal zone of the North Sea and consists of saltmarshes, intertidal flats, shallow subtidal flats, drainage gullies and deeper inlets and channels. It is the largest barrier-island tidal system in the world outside the tropical zone (Wolff, 1983). Our study area contains most of the subtidal zone of the western Dutch Wadden Sea, that is the area ranging from the Marsdiep tidal channel in the west, between Texel and Den Helder, to the tidal divide between the island of Terschelling and the Frisian coast (Fig. 1). Tidal amplitude in the study area is approximately 1.5 m, and sediment composition, which is strongly affected by currents and wind-driven waves, ranges from coarse-grained sands close to the inlets and in the tidal gullies to fine mud in the shallow areas close to the mainland and tidal divides (Van Straaten and Kuenen, 1958; Oost, 1995). Salinity is mainly affected by fresh water discharges from the IJsselmeer. The study area has a surface area of 1262 km^2.

2.2. Mussel abundance data

Long-term (1992–2022) density data of sublittoral mussels are available for a fixed grid of approximately 500 × 500 m within the study area. The grid contains 3195 points that are located in the subtidal, which is here defined as the area that is immersed for more than 95% of the time according the InterTides model (Rappoldt et al.,

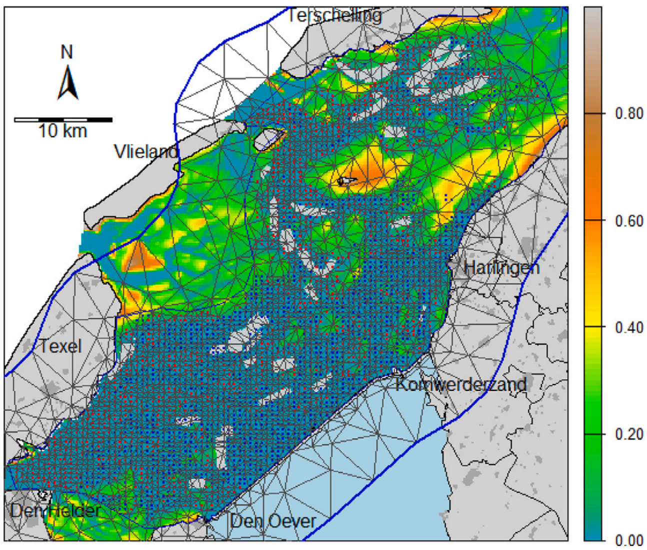

Fig. 1. Sampling points plotted on a map of the western Wadden Sea indicating the fraction of the total time not immersed (scale at the right), plus the non-convex hull mesh used in the INLA-SPDE analysis. Visited points are indicated by blue dots. Red dots show the non-visited grid points. Thick blue line shows the border of the non-convex hull mesh, thin blue line the border of the study area. Commercial plots are shown in grey. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

2020), and for which all environmental data are available. Commercial mussel plots are excluded from the grid. Each year sampling occurs in the period March–April. In the core area where mussel occurrence is almost certain (based on historical distribution patterns), all grid points are sampled. Outside this area sampling effort is reduced. The area where no mussels are expected is covered with an even lower sampling density. The expected occurrence of mussels outside the core area is based on a combination of data from the previous year and ad hoc sampling in the preceding autumn. Each autumn, newly formed mussel beds are located in the period August–September, aided by information from fishermen, fisheries inspectors, satellite images (for the shallower parts) and historical occurrences. Mussel presence is established through sampling with a mussel dredge with a width of 1.9 m towed along a distance of approximately 100–200 m. The contours of the newly-formed beds are roughly estimated based on multiple dredge tracks and expert judgment. In the present study non-sampled points are assumed to contain no mussels. On average 539 grid points (range 347–824) are sampled annually.

Sampling in spring is done using two devices. Sampling points at water depths below 10 m are sampled with a commercial suction dredge that was modified specifically for the sampling of mussels and other macro-benthic fauna. At water depths over 10 m, a specially-constructed towed dredge is used. Both devices consist of a cage (5 mm mesh) that is towed along the seafloor, with a knife that cuts to a depth of 7 cm into the sediment. The suction dredge has a 10-cm wide opening and is towed along the sea floor with the suction tube. The sample is flushed directly onto the deck through the ship's suction and flushing system. The towed dredge has a 20-cm wide opening and is towed along the sea floor using a steel cable. The sample is collected in the cage and emptied on deck after hauling the device. The total area sampled is dependent on the towing distance, which is measured using either a counting wheel (towed dredge) or by demarcating the beginning and end of the track using DGPS (suction dredge). The towing distance is approximately 150 m, resulting in a sampled surface area of about 15–30 m^2. Dredge tracks pass the intended position of the sampling station within a distance of 25 m. On deck, mussels (and other species) are sorted and counted.

Table 1
Environmental predictor variables.

Variable	Unit
Annual average salinity at high tide	PSU
Salinity variability	–
Water depth	m
Maximum current velocity	m/s
Orbital velocity of waves	m/s
Maximum bottom shear stress due to currents	Pa
Sediment silt content	%
Sediment median grain size	μm

The present study is restricted to a spatial analysis, working with averages over time. Such an approach is simpler and easier to perform than a spatio-temporal approach, working with a series of annual data. Such spatio-temporal approach would also require the availability of annual data for all environmental variables, which is not the case. Mussel data are summarized as the number of years (out of 31 years within the period 1992–2022) that mussels are present at each grid point.

2.3. Environmental data

Environmental spatial data that are available and may affect mussel distribution and abundance are bathymetry (bottom depth), annual average salinity at high tide, salinity variability, maximum current velocity, maximum bottom shear stress due to currents, orbital velocity of waves in a representative period, sediment silt content, and finally sediment median grain size (Table 1). Depth data, in m relative to 'Normaal Amsterdams Peil' (NAP), were derived from a bathymetric grid at a resolution of 20 by 20 m throughout the Dutch Wadden Sea. This bathymetry was largely based on LIDAR soundings for the intertidal and interpolated single-beam echo soundings for the subtidal performed by Rijkswaterstaat in the period 2006–2012. For more details, see Elias and Wang (2013) and Meijer et al. (2023).

The average salinity (PSU), salinity variability (coefficient of variation) and hydrodynamic environmental parameters (current velocity, shear stress, and orbital velocity) are obtained by hydrodynamic numerical model simulations. For salinity, flow velocities and bed shear stresses the Dutch Wadden Sea Model (DWSM) in the Delft3D Flexible Mesh software is used (Van Weerdenburg and Zijl, 2019). As this model does not simulate waves, an operational wave-forecasting model of the Dutch coast in SWAN (Simulating WAves Nearshore) is used to obtain orbital flow velocities from. Although we provide a few details below, we refer to Van Weerdenburg (2021) for a detailed description of the numerical model simulations.

The domain of the DWSM model runs from IJmuiden to the German Wadden Sea and includes the Dutch Wadden Sea, the Ems-Dollard estuary and a wide strip of the North Sea along the Dutch Wadden Islands. Current velocities (m/s) and bed shear stresses (Pa) are determined from a 2D version of the model with approximately 100 m × 100 m horizontal resolution in the area of interest. Salinity is determined using a 3D version of the model with 10 vertical layers and approximately 200 m × 200 m horizontal resolution in the area of interest. The DWSM model is validated against measured time-series of water level variations, flow velocities and salinity at observations points in both the Wadden Sea and the North Sea.

For the present study, flow velocities and bed shear stresses due to currents are simulated for the two spring-neap tidal periods from June 23rd to July 22nd, 2017. The tidal conditions during these spring-neap periods are representative for the tidal variations in the period 2013–2017. The salinity is determined based on a 3D simulation for 2017, such that seasonal variations are included in both the time-averaged values and the variation.

Orbital velocities (m/s) are determined using an operational wave-forecasting model of the Dutch coast in SWAN. The horizontal resolution of this model in the Wadden Sea is approximately 300 m. The wave model is forced by meteorological conditions from the KNMI HARMONIE model and is calibrated and validated against observed wave parameters. The simulated results for March 2020 were found to be representative for year-averaged wave conditions.

The sediments of the subtidal Dutch Wadden Sea were sampled in 2019, during the subtidal sampling campaign of project 'Waddenmozaïek' (Franken et al., 2026). Samples were taken on a 1000 m grid and on randomly located stations within the grid to improve the fine-scale accuracy of spatial interpolations (Bijleveld et al., 2012). Sampling took place between February and May. Sediment samples were taken with a small core with a diameter of 33 mm from the larger box-core samples to a depth of 4 cm. In the laboratory, the samples were freeze-dried, homogenized, and weighed. Grain size distributions were measured with a particle size analyser which uses laser diffraction and Polarization Intensity Differential Scattering technology. It measures grain sizes from 0.04 to 2000 μm in 126 size classes. Samples were not treated with hydrogen chloride and hydrogen peroxide to remove calcium and organic material. For further details concerning sediment analysis we refer to Bijleveld et al. (2012) and Compton et al. (2013). The grain size distributions is summarized by the median grain size (μm) and the silt content (%). Silt content is defined as the percentage of the volume of the particles between 0.04 and 63.00 μm of all particles. Both median grain size and silt content were interpolated using ordinary kriging to obtain sediment maps that cover the research area (Franken et al., 2026)

2.4. Human impact data

Shrimp fisheries intensity data are derived from Vessel Monitoring System (VMS) records in combination with vessel logbook information for the period 2016–2022. Usage of VMS is obligatory for all shrimpers. Fishing intensity (average total area that is fished annually within each grid cell of 200 m by 200 m expressed as a fraction of the grid cell area) is based on combining VMS and logbook data using the methods described in Hintzen et al. (2010, 2012), using the R package 'vmstools'. The 'cubic Hermite spline' interpolation method is used with an interpolation parameter value $f_m = 0.05$. Details of the procedure can be found in Glorius (2023). The highly skewed data were transformed into a categorical variables, with three classes: no fishing, low intensity fishing (lower than the median of all non-zero data) and high intensity fishing (above the median).

A map of the areas within the shipping lanes that are regularly dredged was provided by Rijkswaterstaat.

2.5. Statistical methods

The response variable Y_i is the number of years (out of a total of $N = 31$ years in the period 1992–2022) in which mussels were present at site i. A binomial distribution with a logit link to a linear predictor is assumed. The linear predictor is a quadratic function of one or more covariates, including all second-order interaction terms, plus a Gaussian field. That is when, for example, two covariates x_1 and x_2 are present the model is given by

$$Y_i \sim \mathrm{Bin}(p(s_i), N) \tag{1}$$

where $p(s_i)$ is the probability that mussels are present in a specific year at site i. The logit function links the probabilities to a linear predictor

$$\mathrm{logit}(p(s_i)) = \beta_0 + \beta_1 x_1 + \beta_2 x_1^2 + \beta_3 x_2 + \beta_4 x_2^2 + \beta_5 x_1 x_2 + \psi(s_i) \tag{2}$$

where the βs are parameters of the deterministic part of the model and $\psi(s_i)$ represents the Gaussian field and is given by

$$\psi(s_i) \sim N(0, \Sigma) \tag{3}$$

The covariance matrix Σ is determined by a Mátern correlation function, and the Gaussian field is approximated by a Gaussian Markov Random Field.

All environmental data were first aggregated on a spatial raster of 200 m by 200 m, and subsequently projected on the grid points. Various of the environmental variates were highly correlated (e.g. depth and orbital velocity) and because the use of highly correlated variables as independent variables in a statistical model will lead to undesired estimation problems, an a-priori selection of variables is required. The choice which variables to include was made on basis of a Principal Component Analysis, examining the dimensionality of the environmental data set, aided by calculating variance inflation factors (VIFs) and by graphical inspection of all bivariate correlations. We have chosen not to use the principal components (or eigenvectors) themselves as predictors (as has, for example, been done by Le Rest et al. (2013)), because of the cumbersome interpretation of the model coefficients.

As advocated by Lindgren (2012) and Lindgren and Rue (2015), the Integrated Nested Laplace Approximation algorithm combined with the Stochastic Partial Differential Equation approach (INLA-SPDE) is applied to estimate model parameters, including those for the spatial Gaussian field based on a Mátern correlation function, and to make predictions. The spatial field is approximated by a Gaussian Markov Random Field (GMRF). We used the R_INLA package and basically followed the procedure described in detail by among others Blangiardo and Cameletti (2015), analysing Swiss rainfall data (see also https://inla.r-inla-download.org/r-inla.org/case-studies/Blangiardo-et-al-2012/Report-version-Oct-2012.pdf).

A mesh, which is required in the INLA-SPDE approach, was created within a non-convex hull around the 1598 grid points that were used for estimation, which is 50% of all sites. The remaining 1597 sites were used for validation (Fig. 1). The largest allowable edge length of a triangle within the mesh was set to 10 km. The constructed mesh contained 2066 vertices. For all possible combinations of the a-priori selected environmental covariates, parameters were estimated using the INLA-SPDE approach and final model selection was based on the Watanabe-Akaike Information Criterion (WAIC), using the predictions and observations on the 1598 selected sampling points. As not much was known about the parameter values beforehand, diffusive priors were used. Fitted values were graphically compared with observed values using the validation points. Predictions on the mesh vertices were projected on a 200 m grid for map making.

Next, human-impact related categorical variables, i.e. shrimp fisheries intensity (three categories: no fishing, low intensity, high intensity) and dredging (two categories: dredged and not dredged), were added to the selected environmental model to see whether model fit could be improved. Additionally, Gaussian field predictions of the environmental model were visually related to the human impact variables by means of box-and-whisker plots.

All analyses were performed using the program R (R Core Team, 2024). The package 'INLA' was downloaded from https://www.r-inla.org/ and the additional packages 'fmesher', 'raster', 'sf', 'stars', and 'terra' were downloaded from the CRAN website https://cran.r-project.org/. Scripts are available in the Zenodo repository, DOI 10.5281/zenodo.16628410.

3. Results

3.1. Selection of environmental variables

The eight physical environmental variables (water depth, annual average salinity at high tide, salinity variability, maximum current velocity, maximum bottom shear stress due to currents, orbital velocity of waves in a representative period, sediment silt content, and sediment median grain size) show strong linear correlations, as reflected by a principal components analysis in which the first three components already account for 90% of the total variance. A biplot

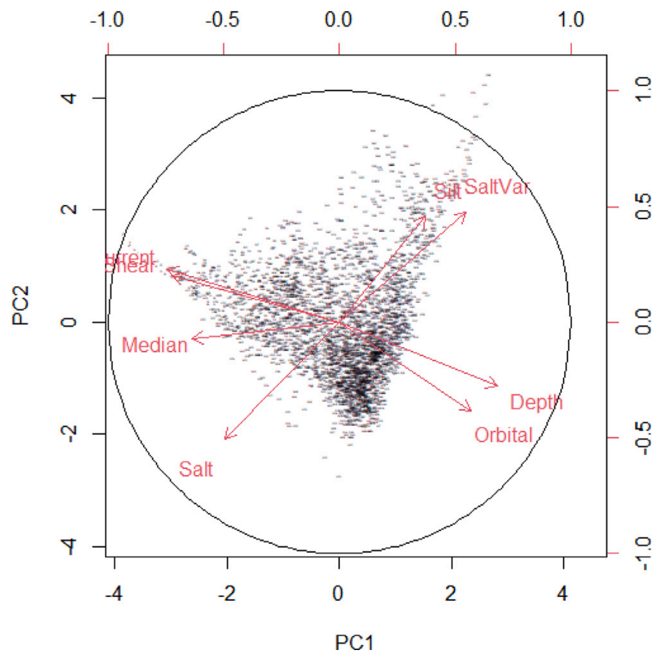

Fig. 2. A principal components analysis biplot based on eight physical environmental variables (bottom depth, annual average salinity at high tide, salinity variability, maximum current velocity, maximum bed shear stress due to currents, orbital velocity of waves, sediment silt content, and sediment median grain size). The first component explained 58% of the overall variation, the second one 20%; $n = 3195$.

visualizes the correlation structure and indicates strong (positive or negative) correlation among depth and the hydrodynamic variables (current velocity, shear stress, orbital velocity), and between salinity and salinity variability (Fig. 2). Median grain size and silt content are less correlated. Bivariate plots (see Supplementary Material, Figs. 1 and 2) and Variance Inflation Factors (VIFs) confirm these observations. A non-spatial generalized linear model with only linear terms for all eight variables showed a maximum VIF of 14.7, but after sequentially deleting the variables salinity variability, water depth and current velocity, the maximum VIF was reduced to 3.2. Next, a forward model selection procedure was applied to assist in a further variable selection. Non-spatial generalized linear models of increasing complexity were fitted to relate the binomial variable mussel frequency of occurrence to one or more of five selected variables (salinity, the two hydrodynamic variables shear stress and orbital velocity, and the two sediment variables silt content and median grain size). The linear predictor contained all quadratic terms. From these five variables median grain size contributes least in the explained deviance (see Supplementary Material, Fig. 4), and was excluded from further spatial INLA-SPDE analyses.

3.2. Fitting the INLA-SPDE model

INLA-SPDE analyses showed that the model that included salinity and orbital velocity had the lowest WAIC (Table 2). Adding a third environmental variable only increased the WAIC. Validation revealed a relatively good fit between the average observed value and the predicted values (Fig. 3), but also showed that at the scale of the individual sampling units there is still quite some variation left. The residual mean squared error (RMSE) equalled 2.79. The fitted quadratic response curve shows a unimodal relationship with salinity and a merely decreasing relationship with orbital velocity, with a maximum predicted value at intermediate salinity levels of about 22 PSU and at low orbital velocities (Fig. 4). The model with salinity and orbital velocity, but without the spatial field revealed a much poorer fit (WAIC = 11 231). The Mátern correlation function revealed a range, which is the distance at which the correlation has diminished to 0.1, of 3.3 km with a 95% credible interval that goes from 2.73 to 3.91 km (see Supplementary Material, Fig. 5). Adding the variable dredging to the environmental INLA-SPDE model slightly decreased the WAIC.

Table 2
WAIC of the various spatial models, using the predictions and observations in the 1598 selected points. Best fitting models in bold. Environmental variables are 1 Salinity, 2 Silt content, 3 Orbital velocity, and 4 Shear Stress. Human-impact variables are 5 Shrimp fisheries, and 6 Dredging. All possible combinations of one, two or three environmental variables are examined, but human-impact variables are only added to the best fitting environmental model.

Model	ModelWAIC
0	4663
1	4558
2	4599
3	4436
4	4663
1+2	4536
1+3	**4364**
1+4	4510
2+3	4407
2+4	4518
3+4	4431
1+2+3	4364
1+2+4	4491
1+3+4	4372
2+3+4	4398
1+3+5	4373
1+3+6	**4357**

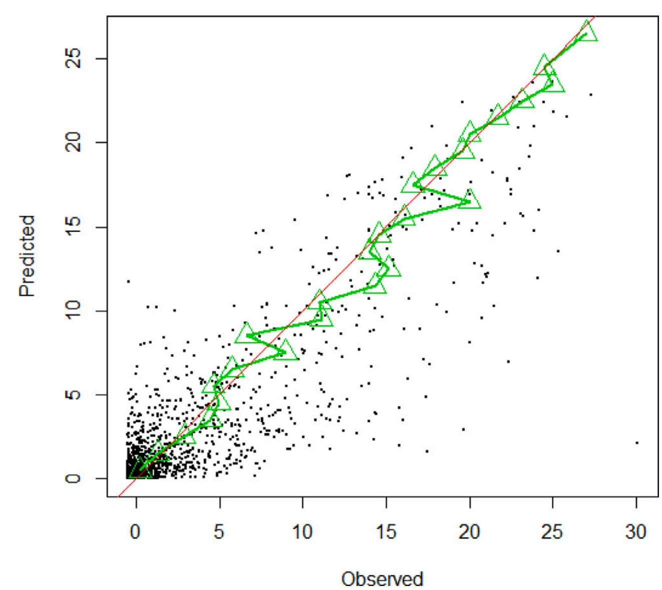

Fig. 3. Predicted versus observed values of the frequency of mussel occurrence in number of years out of 31 years. The prediction is obtained by multiplying the predicted probability by the number of years. The green triangles show the average observed value for each single unit-class of predicted values. Some jitter has been added to the observed frequency to prevent overlap of points.

3.3. Mapping

The predicted effects of the covariates (Fig. 5) (in terms of their overall contribution to the linear predictor) showed a larger variability (standard deviation of the projections on the 200 m grid equalled 3.37) than the variability (standard deviation of 1.27) of the Gaussian field values (Fig. 6), meaning that most of the variability explained by the

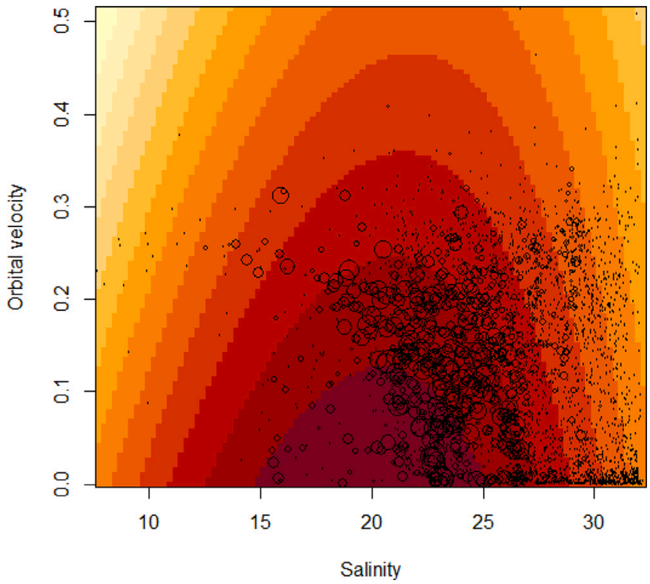

Fig. 4. The quadratic response curve of the selected INLA-SPDE model (with environmental variables salinity and orbital velocity) relating the sum of all covariate terms in the linear predictor (thus ignoring the Gaussian field) to average salinity at high tide (PSU) and orbital velocity (m/s). Red indicates a high value of these summed linear predictor terms, pointing to a high probability of occurrence, whereas yellow indicates a relatively low value. Data are shown by dots that are proportional in size to the frequency of occurrence. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

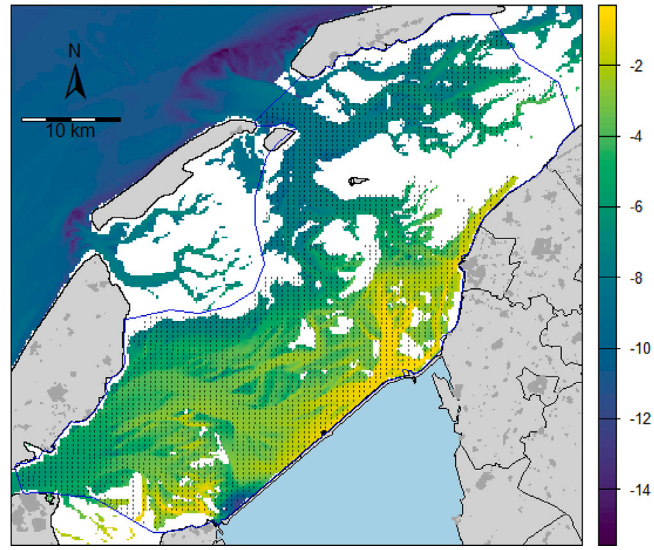

Fig. 5. Map of the sum of all linear predictor terms (scale on the right) related to the two covariates salinity and orbital velocity of the selected INLA-SPDE model, thus ignoring the Gaussian field.

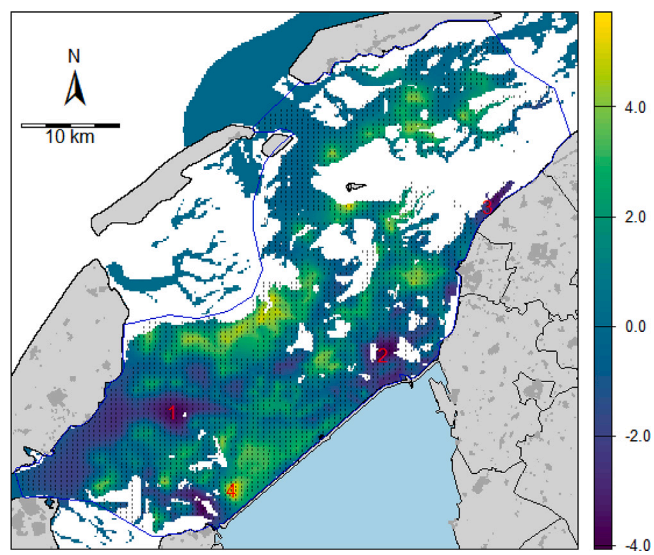

Fig. 6. Map of the Gaussian Markov Random Field term (scale on the right) within the linear predictor of the selected INLA-SPDE model. Areas 1 (Bollen), 2 (off Kornwerderzand), 3 (Kimstergat), and 4 (off Afsluitdijk) are mentioned in the text.

linear predictor can be attributed to the covariates. A visual comparison of these two separate maps with the map of the combined effect of the covariates and the random field in terms of the predicted probability of occurrence (Fig. 7) showed that the low frequency of occurrence of mussels near the Frisian islands, but also very close to the fresh water outlet of the Afsluitdijk at Den Oever, can mainly be understood from the unimodal relationship with salinity and orbital velocity. The Gaussian field (Fig. 6) shows the spatial 'unexplained' variation and reveals that, for example, the relatively low predicted probability in the Kimstergat, east of Harlingen, in the area close to Kornwerderzand and in the Bollen area (represented by the light-brownish coloured areas in Fig. 6) cannot be explained by the two covariates that were included in the best fitting model. Neither can the relatively high probability close to the Afsluitdijk completely be understood from the effect of the environmental covariates. Yet, a link between the Gaussian field and the human-impact variables (shrimp fisheries intensity and dredging) was absent or weak (Fig. 8), and adding the variable dredging to the INLA-SPDE model only slightly decreased the WAIC (Table 2).

4. Discussion

The probability of subtidal mussel occurrence was most strongly related to salinity and orbital velocity, with maximum probability at intermediate salinity levels of around 22 PSU and orbital velocities lower than approximately 0.3 m/s. Whereas the lower probability at low salinity values might be the result of a direct physiological stress effect, the lower probability at higher salinity levels is likely an indirect effect of starfish predation. Adults of the predatory starfish *Asterias rubens* from the North Sea cannot tolerate salinity levels below 23 PSU (Binton, 1961). They are therefore more sensitive to low salinity levels than the mussel, for which juveniles and adults showed no decrease in survivorship at salinity levels between 20 and 25 PSU (Qiu et al., 2002). At such intermediate salinity between 20 and 25 PSU predation pressure on mussels is probably reduced (Agüera et al., 2015). Salinity is directly affected by man-induced fresh-water discharge from the IJsselmeer, the main source of fresh water entering the western Wadden Sea (van Aken, 2008). It is expected that climate change may effect future discharge regime with possible consequences for mussel abundance. Our statistical analysis was not able to provide any indication of an effect of bottom disturbance related to intensity of shrimp fisheries, but adding dredging (and distribution of dredged material) slightly improved the model fit, suggesting that dredging is detrimental to mussel occurrence. We did not explore the impact of mussel seed fishing, which, not surprisingly, mainly takes place in areas with a high probability of mussel occurrence. The expected positive relation between mussel fisheries and mussel occurrence would not yield much insight and a much more detailed experimental approach (with randomly chosen areas temporarily or permanently closed for fisheries) is required to shed light on the possible impact of mussel fisheries.

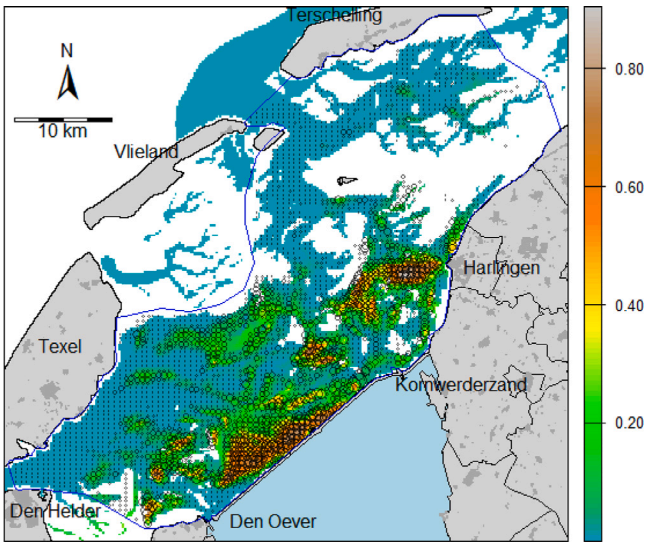

Fig. 7. Map of the predicted probability of occurrence of mussels (scale on the right) based on the selected INLA-SPDE model (effect of covariates plus Gaussian field). Observed frequencies are proportional to the surface area of the dots.

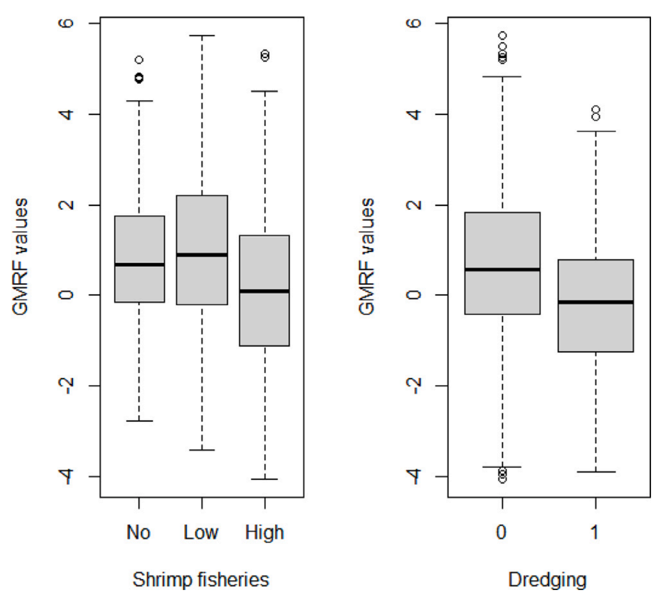

Fig. 8. Box-and-whisker plot of the Gaussian Markov Random Field values versus (left panel) the three classes of shrimp fisheries intensity (no, low, and high), and (right panel) the two classes of dredging (no 0 or yes 1).

Of course, our analysis is basically a correlation study, and generally human impact studies, whether about mussel fisheries, shrimp fisheries or dredging, will strongly benefit from manipulative experiments, with replicated randomized plots, a wide spatial coverage of the study area, and sufficient power.

The large difference between the WAIC values of the model with and without the Gaussian field (and both with the covariates salinity and orbital velocity included) indicates that the spatial model should be preferred. The map of the GMRF showed that several areas had much lower linear predictor values than predicted solely on the basis of the covariates, whereas for other areas the opposite is true. It is not easy to hypothesize on possible underlying mechanisms that could explain the GMRF. Why, for example, is the probability of occurrence in areas 1, 2 and 3 (Fig. 6) much lower than expected based on the predicted effects of the covariates? It could be that high levels of fresh-water discharge over short time periods at Kornwerderzand, which hardly affects annual mean salinity but is detrimental for mussels, may be a cause. Using three classes of shrimp fishing intensity, we found no indication that this factor influenced the probability of mussel occurrence in these areas. Paradinas et al. (2023) noticed that in ecology, the residual spatial pattern most likely accommodates for complex and multi-scaled systems, which makes the biological interpretation very difficult. They also mentioned that the residual spatial pattern improves the predictive capacity of the model at locations that are within the sampled area, and the main advantage of adding an explicit spatial term probably lies more in more accurate prediction than in interpretation.

Without further understanding of the low occurrence of mussels in the areas with low GMRF values, it seems premature to actively try to increase mussel occurrence there. It seems more promising to first experimentally test factors contributing to mussel settlement and survival to gain a more mechanistic understanding of these patterns, or to explore whether more sophisticated ways of describing the environmental predictor variables may increase the explanatory power of the covariates. This study used, for example, annual average salinity at high tide for a single year, which was considered to be representative for the entire 31-years period, but it might be that, for example, the duration of exceeding a specific salinity level during specific months calculated for each year separately provides a better description of the salinity effect. A full spatio-temporal data analysis may indeed be considered, in which temporal variables (variable discharges and resulting variability in salinity over the years, changing sediment composition, fishing intensity, etc.) can be included. Ignoring interannual environmental variability in a dynamic system like the Wadden Sea undoubtedly introduces uncertainty. It remains, however, to be seen whether such data can be made available by detailed hydrodynamic modelling on the basis of available data. Besides, fitting statistical SDMs rely on the assumption that the species is in equilibrium with the environment (Elith et al., 2010). The mussel *Mytilus edulis* is known to show an erratic recruitment pattern over time, with occasionally a very good recruitment year interspersed with years of low recruitment (Beukema et al., 2010; van der Meer et al., 2019). Hence, our choice of considering the overall occurrence over a very long period of time (31 years) seems more in line with the equilibrium assumption than trying to apply a statistical SDM for predicting annual occurrences.

Apart from shedding light on which environmental variables are most strongly related to species occurrence, SDMs based on statistical data models are also used for predicting species occurrence not only at locations that are within the sampled area, but also at locations elsewhere. When the model is applied in a new (projection) area that has overlapping ranges of the environmental variables with the original (training) area that was used for model fitting, a prediction is often called interpolation (Rousseau and Betts, 2022), and only when ranges do not overlap one talks about extrapolation. This distinction is, however, problematic. In multidimensional environmental space, two sets of sampling points (think, for example, of intertwined banana-shaped point clouds) from two different areas may have exactly the same range for each separate variable, but exhibit no overlap at all. Hence, a more promising approach is to quantify the minimal environmental distance between each new projection point and all original training points, e.g. by the Mahalanobis distance (Velazco et al., 2023). One can then explore, for example by fitting the model for only a part of the area for which data are available (see e.g. Luan et al. (2024)), the relation between this distance and the reliability of the prediction. The reliability will furthermore very much depend upon whether the applied environmental variables are directly and causally or only indirectly and correlative related to species occurrence (Elith et al., 2010). In the latter case the correlation may easily break down in new areas. Our study used only abiotic environmental variables, and the link with mussel occurrence is partly indirect (recall the remarks on high salinity and the presence of predating starfish). Unfortunately no accurate spatial information on food availability (microalgae) or predators was available. Finally, the reliability of the prediction will depend on the magnitude of the unexplained and possibly spatially correlated variation. One major advantage of the approach applied in this paper is that the spatially correlated, but unexplained variation is explicitly quantified and visualized by means of the Gaussian field (GMRF). The relatively large contribution of the GMRF to the final prediction implies that extrapolation of the model to other areas for which environmental data are available, such as for example the eastern Wadden Sea, will have limited value, even when the environmental variables are very similar to those of the study (training) area. To obtain accurate predictions on probability of mussel occurrence in these areas, it is therefore recommended to extend the sampling campaign to that region.

CRediT authorship contribution statement

Jaap van der Meer: Writing – original draft, Formal analysis, Conceptualization. **Oscar Franken:** Data curation, Investigation, Writing – review & editing. **Sander Glorius:** Data curation, Investigation, Writing – review & editing. **Tjisse van der Heide:** Data curation, Investigation, Writing – review & editing. **Karin Troost:** Data curation, Investigation, Writing – review & editing. **Roy van Weerdenburg:** Data curation, Investigation, Writing – review & editing.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary material related to this article can be found online at https://doi.org/10.1016/j.ecoinf.2025.103458.

Data availability

Data and code will be posted on ZENODO repository after acceptance

Mapping habitat suitability of subtidal mussels Mytilus edulis in the Dutch western Wadden Sea (Original data) (Zenodo)

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