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Northern Europe's suitability for offshore European flat oyster (*Ostrea edulis*) habitat restoration: A mechanistic niche modelling approach

Brecht Stechele[1] | Anna Hughes[2] | Steven Degraer[3] | Peter Bossier[1] |
Nancy Nevejan[1]

[1]Laboratory of Aquaculture & Artemia Reference Center, Ghent University, Ghent, Belgium

[2]School of GeoSciences, University of Edinburgh, Edinburgh, UK

[3]Marine Ecology and Management, Operational Directorate Natural Environment, Royal Belgian Institute of Natural Sciences, Brussel, Belgium

Correspondence
Brecht Stechele, Laboratory of Aquaculture & Artemia Reference Center, Ghent University, Coupure Links 653, B-9000, Ghent, Belgium.
Email: brecht.stechele@hotmail.com

Abstract

1. After centuries of overexploitation, European flat oyster (*Ostrea edulis*) habitats are increasingly being protected and large-scale oyster habitat restoration projects have been initiated in the North Sea, the English Channel, the Irish Sea and the north-eastern Atlantic.

2. Understanding the habitat requirements of flat oysters is key in the selection process of restoration sites.

3. In this study, a theoretical niche for all life stages of the flat oyster is determined using a dynamic energy budget model forced with temperature, chlorophyll *a* and salinity in combination with sediment composition. The suitability of Northern Europe's marine environment for flat oysters is evaluated by applying the proposed niche model on a spatial scale and evaluating spatio-temporal variability in life history traits and metabolic characteristics, such as fitness, reproductive output, settlement success and growth.

4. Results show that habitat suitability is limited by low maximum summer temperature and low food availability at higher latitudes and in areas under strong influence of the Atlantic Ocean. Restoration efforts in Ireland and Scotland should be confined to protected and shallow coastal environments. Suitability in the southern North Sea is patchy and mainly depends on seabed substrate. The nearshore areas of the English Channel are highly suitable.

5. The georeferenced dataset shared in this study will be useful for restoration practitioners.

KEYWORDS
dynamic energy budget, European flat oyster, habitat restoration, habitat suitability, niche model, northern Europe, *Ostrea edulis*, species distribution

1 | INTRODUCTION

Oyster reefs are recognized biodiversity hotspots that provide many ecosystem services (Coen et al., 2007; Smyth & Roberts, 2010; Kamermans et al., 2018; Crawford et al., 2019; Hancock & Ermgassen, 2019). Large scale oyster reef protection, restoration and creation projects have been initiated in many locations around the globe (Schulte, Burke & Lipcius, 2009; Gillies et al., 2015; Carranza & Ermgassen, 2020; Pogoda et al., 2020a) to reinstate or support degraded oyster habitats (Beck et al., 2011). Inshore and coastal European flat oyster habitat restoration is well established, but offshore restoration is generally overlooked due to high operational costs and logistical challenges. The rapid expansion of offshore wind in the North Sea and the deployment of hard substrate as scour protection material offer opportunities for large scale flat oyster reef restoration (Smaal et al., 2015; Kamermans et al., 2018; Bennema, Engelhard & Lindeboom, 2020). Understanding the environmental requirements for offshore flat oyster habitat restoration is key in the site selection process, and has been pinpointed as a significant knowledge gap (Pogoda et al., 2017; Pogoda et al., 2019; Pogoda et al., 2020a).

Two types of model are generally used to develop a spatio-temporal representation of species niches, both of which have their advantages and disadvantages. (i) Correlative niche models link species occurrence data to spatial datasets using statistical tools. Correlative niche models define the habitat, i.e. a description of the physical place where an organism actually or potentially lives (Kearney, 2006). These models do not include causal interactions between the environment and the species distribution, and therefore have poor predictive power when applied to new environments (for example, in the case of invasive species) or changing environments (for example, in case of climate change scenarios) (Davis et al., 1998; Dormann, 2007). Correlative niche models can be inconsistent when presence/absence data are scarce. (ii) Mechanistic niche models capture population processes explicitly as functional responses to environmental factors such as resource availability, temperature, salinity or oxygen availability (Kearney et al., 2008; Kearney et al., 2010; Teal et al., 2018). They aim to predict fitness components based on behavioural, morphological and physiological traits (Kearney & Porter, 2009), which again are based on the environmental space deemed suitable. Individual-based models such as the Dynamic Energy Budget (DEB) model (Kooijman, 2010) can be used in mechanical niche models to enable the prediction of survival, reproduction, development and growth, and can provide information on population dynamics (Kearney, 2006; Holt, 2009; Kearney & Porter, 2009). Integrating DEB theory into biogeochemical models provides a framework that enables the evaluation of site suitability for organisms as well as the dynamics of life history events and metabolic traits (Kearney et al., 2008; Thomas et al., 2011; Teal et al., 2018; Palmer et al., 2020). This publication updates the theoretical niche for Northern Europe's population of flat oysters using a mechanical individual-based DEB model and evaluates the suitability of Northern Europe's marine environment for flat oysters.

2 | METHODS

2.1 | Geographical range and spatial data

The research domain for this study encompassed the North Sea, the English Channel, the Irish Sea and part of the north-east Atlantic Ocean, and stretches from 48° to 57°N and −9° to 9°E. This area includes the largest historical offshore flat oyster reefs in northern Europe (Figure 1a), and largely corresponds to the geographical range of the North Atlantic offshore populations (Launey et al., 2002). In the eastern Atlantic, the English Channel and the Irish Sea, coarse sand and muddy sea bed prevails offshore, while rocks and boulders are found nearshore. Apart from the sea bed off eastern England and north-west Denmark, North Sea sediments mainly consist of fine sand and mud, although rocks and boulders do occur sporadically (Figure 1b).

Drivers of the spatial model used in this study included bottom temperature, chlorophyll *a* and salinity and were extracted from the EU Copernicus Marine Service Information database (product id: NWSHELF_MULTIYEAR_PHY_004_009 and NWSHELF_MULTIYEAR_BGC_004_011). Bottom temperature was extracted using the 'sea_water_potential_temperature_at_sea_floor (bottomT)' variable (latitude × longitude × variable). Seawater salinity and chlorophyll *a* were extracted as depth profiles (latitude × longitude × depth × variable). Bottom salinities and bottom chlorophyll *a* concentrations were calculated by extracting the lowest numerical value of the vertical depth profile (personal communication Copernicus Marine Services).

Products were daily 25-hour, de-tided, averages. Extractions were made over a spatial scale of −9° to 9°E and 48° to 57°N from 1 January 2010 to 1 January 2020 at a timestep of 1 day. Horizontal resolution of the datasets is 7 km. European Marine Observation and Data Network (EMODnet) multiscale substrate maps (Folk 5) represent substrate suitability (Emodnet Geology, Kaskela et al., 2019).

The coarse horizontal resolution implies poor data representation for inshore and coastal environments. Inshore areas are defined as areas that are located in fjords, estuaries or coastal lagoons. Inshore waters are typically calm, shallow and are under high influence of the land. Coastal waters directly border the shoreline but are, in contrast to inshore waters, exposed to waves and wind (0–2 km offshore). Nearshore (2–20 km from the shore) and offshore areas (>20 km from the shore) are highly exposed to marine conditions. Cut-off values are set arbitrarily and only apply to this study.

2.2 | Dynamic Energy Budget model

2.2.1 | General

The individual-based model used in this study is underpinned by the DEB theory established by Kooijman (2010). Species-specific parameters describe the important life history traits of the individual (Kooijman, 2010; Lika et al., 2011). Metabolism is defined
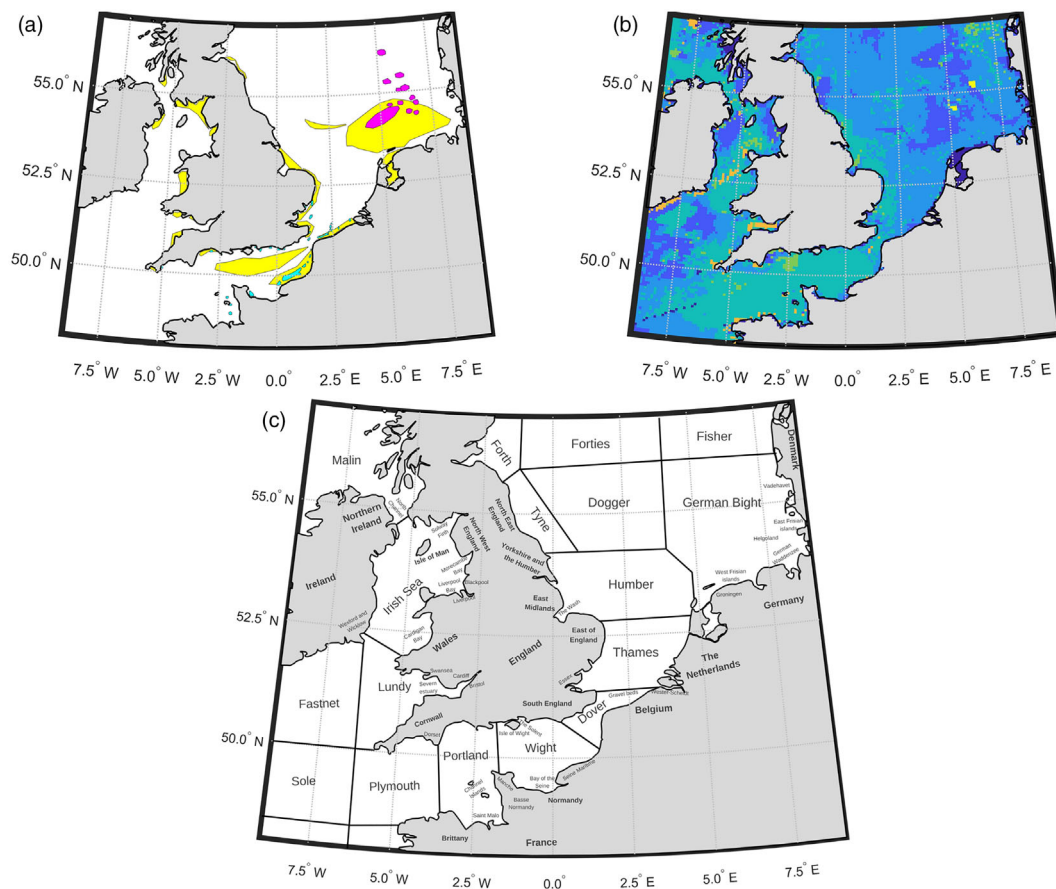
FIGURE 1 (a) Historical distribution of oyster habitats in northern Europe; representation adapted from Olsen's 'Piscatorial Atlas of the North Sea' (1883) (yellow), locations visited by oysterman M. H. Polley (Smaal et al., 2015) (blue) and oyster beds mapped by Gercken & Schmidt (2014) (red) (b) Seabed substrate type; mud (blue), fine sand (light blue), coarse sand (cyan), rocks and boulders (yellow), mixed sediment (green), absence of data (dark blue) (EMODnet Geology, Kaskela et al., 2019).

through four state variables; energy reserve, E (J); body structural volume, V (cm³); the reproduction buffer, E_R (J); and the cumulative investment into development, called maturity, E_H (J) in DEB terminology.

According to Kooijman (2010), an individual's metabolism and energy flows (in joules) are a function of food availability and body temperature. Food availability relates to ingestion ($\dot{p}_X$) and assimilation of energy ($\dot{p}_A$) into the general reserve. Energy is mobilized ($\dot{p}_C$) from the reserve and is used for both somatic (κ) and reproductive ($1-\kappa$) purposes. Energy allocated to somatic growth ($\dot{p}_G$) is used for the construction of functional tissue and overhead costs include the transformation of energy to structure. The functional maintenance ($\dot{p}_S$) flux maintains vital functions and has priority over growth. The remaining fraction $(1-\kappa)\dot{p}_C$ of the mobilized energy is allocated to development ($\dot{p}_R$) (e.g. of the reproductive system, the immune system) if individuals are young and have not reached full maturity ($E_H < E_H^p$). When individuals are fully mature ($E_H = E_H^p$), the flux towards development is diverted toward the reproduction buffer. The reproduction buffer will be transformed into gametes, which will be released during reproduction. There is an additional energy cost for maintaining the state of maturation ($\dot{p}_J$).

The DEB model used in this study was parameterized and validated for the northern European flat oyster population (Stechele et al., 2022), and the DEB formulae and parameters are included as Supporting Information (S1, S2).

2.2.2 | DEB link to environment, validation and simulations

The DEB model used in this study was forced with chlorophyll *a*, temperature and salinity. Chlorophyll levels were linked to food availability using a Holling type II functional response (Kooijman, 2010), with X (µg L⁻¹) the environmental chlorophyll *a* concentration and K_X (µg L⁻¹) the food half saturation constant which indicates the chlorophyll *a* concentration that corresponds to $f_X = 0.5$, with f_X the food availability.

$$f_X = X(X + K_X)^{-1}$$

The effect of salinity on filtration rate is calculated according to Lavaud et al. (2017) and Lavaud et al. (2021), where c_s stands for the

salinity correction factor, S_H is the higher salinity threshold (above which salinity has no observed effect) and S_L is the lower salinity threshold at which filtration stops. Salinity does not influence the maintenance costs of oysters (Hutchinson & Hawkins, 1992; Lavaud et al., 2017).

$$c_S = \begin{cases} 1, & \text{at } S \geq S_H \\ \dfrac{S - S_L}{S_H - S_L}, & \text{at } S_L < S < S_H \\ 0, & \text{at } S \leq S_L \end{cases}$$

The response of ingestion rates to the environment then becomes:

$$\dot{P}_X = f_X \, C_s \, \{p_{Xm}\} \, V^{\frac{2}{3}}$$

with $\{p_{Xm}\}\left(J\,cm^{-2}d^{-1}\right)$ representing the surface specific ingestion rate.

The link between the DEB model and its forcings (temperature, chlorophyll a and salinity) was calibrated using the Add-my-Pet procedure (Lika et al., 2011). The parameters z, K_X, S_L and S_H were optimized by minimizing the loss function in the four-dimensional parameter space using an iterative optimization routine based on the Nelder–Mead simplex algorithm. Optimization is based on the minimization of the weighted squared residuals (mean relative error, MRE) between model and observations (Lika et al., 2011).

During validation, initial state variables of the individual were fixed. V was recalculated from the initial dry weights or shell length. The reproduction buffer was assumed empty ($E_R = 0$). The initial maturity level was assumed to be maximum ($E_H = E_H^p$) and the energy reserve was set at 0.8 of its maximal capacity (this corresponds to a scaled energy density that represents good fitness; $e = 0.8$). See Stechele et al. (2022) for a detailed description of the calibration methodology.

2.3 | Suitability and life history trait simulations

Both the dynamics of life history traits and the metabolism are closely linked to site suitability. Locations determined as suitable should provide an environment that produces fit and reproductive individuals. DEB life traits such as minimum adult fitness, the occurrence of spawning events, the average yearly reproductive output and the age at which individuals mature are indicators of a suitable niche.

The adult fitness and reproductive output were simulated starting from large ($L = 7.5$ cm) and fit ($e = 0.8$) adults (with initial state variables: $\left[E = 2.31\,10^4\,J,\ V = 9\,cm^3, E_H = E_H^p,\ E_R = 200\,J\right]$). Fitness in DEB theory is expressed as the scaled energy reserve ($e = E\,V^{-1}\,E_m^{-1}$), which is calculated using DEB state variables E and V and the DEB compound parameter E_M ($J\ cm^{-3}$). Fitness is expressed in a value between 0 (no energy budget to meet maintenance demands) and 1 (energy reserves are complete) and is an indicator comparable to the condition index. The average reproductive output of one individual,

represented by the number of larvae released during a spawning event $\left(\kappa_R\,E_R\,E_0^{-1}\right)$, with κ_R the reproduction efficiency and E_0 the energy content of an unfertilized egg. Reproduction was triggered by spring temperatures reaching 15 °C (Orton, 1937; Korringa, 1957; Laing, Walker & Areal, 2005; Bromley et al., 2016; McGonigle, Jordan & Geddis, 2016). Second spawning peaks or continuous spawning events were not considered within the scope of this model. The age at which maturity is reached is an indicator of growth rate but also for the timing of first reproduction. Individuals that are mature have a fully developed immune system (Kooijman, 2010) and background mortalities after full maturation are generally low (Walne, 1961). The time required for individuals to reach full maturity (starting from the moment of release) was simulated starting from released larvae ($e = 0.8$, $L = 200$ μm; with initial state variables: $[E = 0.0019\,J,\ V = 2.8\,10^{-6}\,cm^3, E_H = E_H^r, E_R = 0\,J]$).

A Habitat Suitability Index (HSI) was constructed based on life history and metabolic performance. Pixels with minimum adult fitness levels of $e < 0.3$ were considered unsuitable and were given a value of 0. Reproductive output and age at which maturity was reached, were scaled to values between 0 and 1. Fine sand sediments are unsuitable for settlement and were therefore given a value of 0. All other sediment types were considered suitable.

$$HSI = \sqrt[4]{Fitness \cdot Reproduction \cdot Growth \cdot Sediment\,suitability}$$

In the present study, scripts were run using MATLAB version R2019b. All rendered maps are georeferenced and raw output grids are included as Supporting Information (S3).

3 | RESULTS

3.1 | DEB calibration and validation

DEB parameters z, K_X, S_L and S_H were optimized, based on growth curves from the German Bight (dry tissues weight), the Belgian part of the North Sea (shell length) and filtration rates at different salinities collected in the lab (Hutchinson & Hawkins, 1992). These growth curves span three different growth periods (2004, 2007 and 2017–2019), originate from cultivation in inshore, nearshore and offshore conditions, for several size classes (1.1–7.0 cm). The calibration included parameterization of the metabolic responses to food and salinity. The metabolic response to temperature has been already calibrated by Stechele et al. (2022).

The calibration resulted in a good model-to-data fit, expressed in a total MRE of 0.12 (values below 0.2 are acceptable) which indicates a good coupling between the DEB and the 'Atlantic-European Northwest Shelf- Ocean Physics and Biogeochemical' CMEMS datasets (Figure 2).

Estimates of growth at the German Bight (Figure 2a,b) were acceptable, and although spring growth was underestimated, estimations of the final dry weights were good. R^2 values are close to one and indicate sufficient precision of the model.
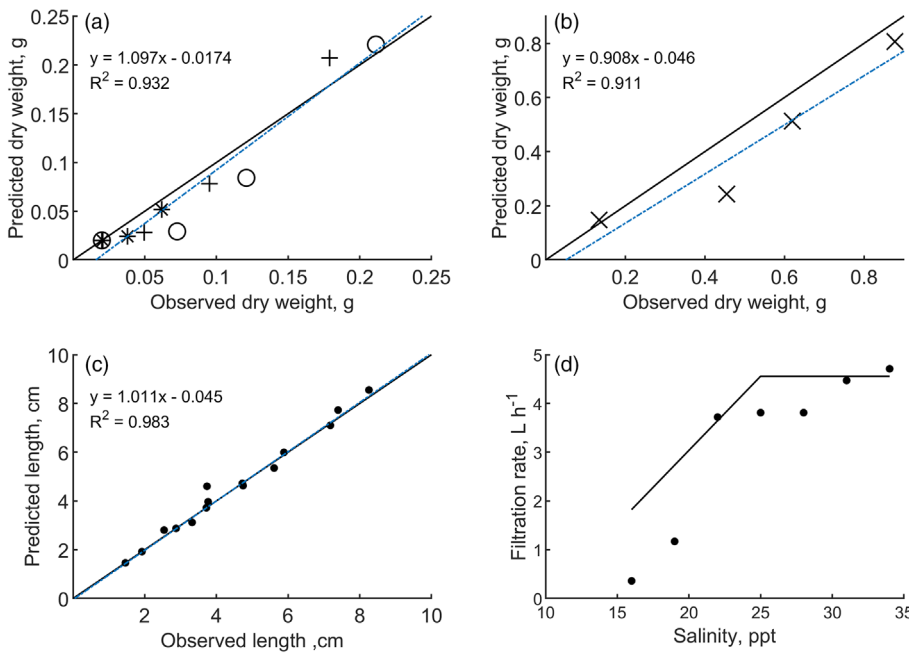
FIGURE 2 Model to data fitting of: (a) Dry weight growth data of juvenile oyster in Butendiek (o), Helgoland (+) and Wursterarm (*), collected in the German Bight (Pogoda, Buck & Hagen, 2011); (b) Dry weight growth data of juvenile oysters in the second year of aquaculture growth at Nordergründe, Germany (Pogoda, Buck & Hagen, 2011). (c) Shell lengths collected from aquaculture growth experiments at Westdiep, Belgium (Delbare, 2019). (d) Filtration rates at different salinities observed during laboratory experiments (Hutchinson & Hawkins, 1992).
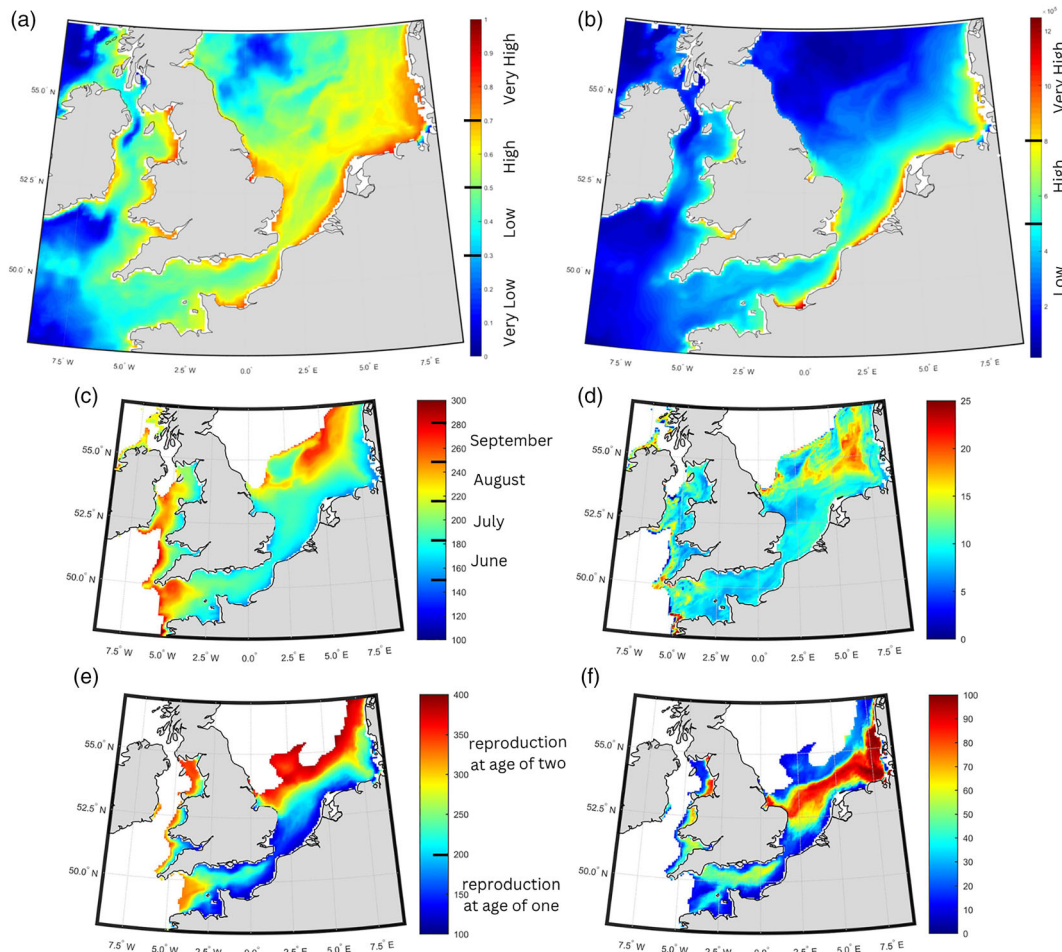

FIGURE 3 (a) Minimum fitness of a European flat oyster adult (7.5 cm). (b) Average yearly reproductive output of an adult oyster (expressed in number of larvae released per adult). Average (c) and standard deviation (d) estimates of the reproduction time based on 15°C temperature threshold (expressed as Julian day of the year). Average (e) and standard deviation (f) of the age at which European flat oyster juveniles reach full maturity (expressed in days since fertilization). All results cover the 10-year period from 2010–2020.

Growth curves collected from different size classes (T8 – adults) in the Belgian part of the North Sea (Figure 2c) were estimated very well. T8, T12 and T20 oysters doubled in size during the first year of growth. T25 oysters grew from 3.72 cm to 5.88 cm and adults from 7.18 cm to 8.25 cm.

The influence of salinity on physiological response was calibrated based on the data of Hutchinson & Hawkins (1992) and the growth data at the Wursterarm location in the German Bight, which is located in the mouth of the River Weser at Bremerhaven and therefore often experiences low salinities (Pogoda, Buck & Hagen, 2011; Stechele et al., 2022). The effect of salinity on the feeding mechanism is captured well. Growth at low salinity (Wursterarm, Germany) was estimated well, but mortalities could not be reproduced with a salinity response defined by $S_L = 10$ ppt and $S_H = 25$ ppt (Pogoda, Buck & Hagen, 2011). The observations of Hutchinson & Hawkins (1992) were generally estimated well (Figure 2d), although the filtration at low salinities was overestimated. Filtration rates at 15 ppt were observed to be close to zero, while our model predicted filtration rates of 2 L h^{-1}.

3.2 | Northern Europe's suitability based on DEB

Distinct environments can be linked to oyster performance and life history traits (Figure 3) leading to a heterogeneous distribution of suitable areas (Figure 4) over the research domain.

3.2.1 | Atlantic

Areas that are heavily influenced by Atlantic waters, including the northern and southern offshore areas of Ireland (Malin, Fastnet and Sole), the offshore areas off Cornwall (UK), Brittany (France) and the northern North Sea regions (Forties, Forth and Tyne), are generally unsuitable (HSI < 0.3) for flat oysters. Atlantic waters in these areas never reach the minimum threshold for spawning and periods of very

low fitness (<0.3) occur due to low food availability. In these marine areas, historical reefs and habitat restoration projects can be present, but are generally located in warmer, nutrient rich, inshore, estuarine, coastal or nearshore areas.

3.2.2 | Irish Sea

The environment in the northern offshore areas of the Irish Sea is unsuitable for flat oyster restoration. The North Channel and offshore areas between Isle of Man and Northern Ireland, are under Atlantic influence and seabed temperatures are too cold for spawning. Northern offshore areas in the Irish Sea are limited in food and fitness in these areas is very low to low (0.3–0.5). Some areas with high (0.5–0.7) to very high HSI (>0.7) do occur in the eastern parts of the Irish Sea, for example off the coast of north-western England and Wales (Solway Firth, Morecambe Bay, the coastal plain of Mersey and Cardigan Bay). The oyster fitness in these nearshore areas is high (0.5–0.7). The reproductive output of fully grown adults is expected to be high (0.5–0.8 million larvae). Reproduction occurs early in summer (during June and July). Flat oyster growth is slow and in the best case, maturity is reached after 250 days making it unlikely that the oysters will spawn during their first year of life. Similar conditions are present in the nearshore areas off the counties of Wicklow and Wexford in the south-western parts of the Irish Sea.

3.2.3 | The English Channel

The offshore western parts of the English Channel (Plymouth and Portland) are heavily influenced by the Atlantic waters and very high HSI for oysters occurs nearshore, around the coast of Dorset (UK), the Channel Islands (UK) and in the Bay of St Malo (France). The eastern parts of the English Channel are indicated by a high HSI offshore and very high HSI nearshore. The minimum fitness of oysters is high to very high throughout the eastern English Channel indicating
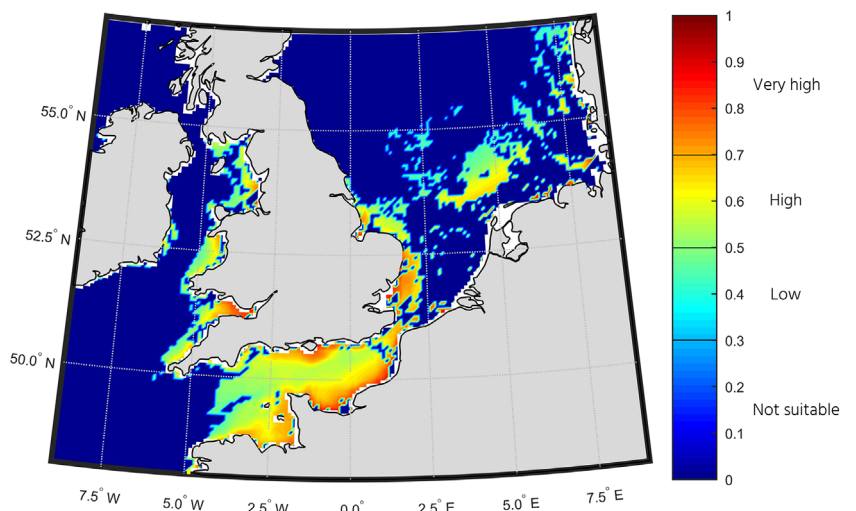

FIGURE 4   Habitat Suitability Index for European flat oyster (*Ostrea edulis*); Suitable locations support locations that support high fitness, growth rate and reproductive output and enable life history events such as spawning and settlement (on suitable substrate).

the absence of starvation periods. Reproductive output is high offshore and very high nearshore (>0.8 million larvae) around the Solent (UK), Manche and Seine Maritime (France). In the nearshore areas of Normandy and South England oysters mature quickly (before day 200) and first reproduction can be expected at the age of 1 year. These areas are likely to support high growth rates.

3.2.4 | North Sea

In the northern offshore parts of the North Sea (Forties) as well as the areas off the coast of north-eastern England and the Yorkshire and the Humber region (UK), suitable niches for flat oysters do not occur offshore or nearshore and restoration efforts as well as historical reefs are located inshore or in coastal areas (Firth of Forth, Dornoch Firth and The Humber). In the Southern Bight of the North Sea (Thames, Dover and Humber), covering the nearshore and offshore areas off the East Midlands, East of England (UK) and the Belgian and Dutch offshore territories, the flat oyster niche is present, and HSI is high to very high. In these areas, oysters have high to very high (>0.7) average fitness levels and reproduction events occur generally in June (Thames and Dover) and July (Humber). Reproductive output is high offshore, and very high nearshore (>0.8 million larvae per spawning event). Low reproduction rates (<0.5 million larvae per spawning event) occur in the north Humber offshore areas. In Thames and Dover, maturity is reached quickly (<200 days) and oysters are expected to reproduce at the age of one. Growth in the Southern Bight is expected to be fast. HSI in the German Bight and the Dogger Bank is high but decreases towards the north (low HIS). Compared to the Southern Bight, spawning events in the Dogger Bank occur later in the summer (July–August) and reproductive output is generally low (<0.5 million larvae per spawning event). Although in general, coastal areas of the German Bight have similar HSI to coastal areas in the Southern Bight (Thames and Dover), the outflow of the Elbe and the Weser rivers creates unsuitable conditions for flat oysters in and around the German Waddenzee.

3.3 | Restoration hotspots

The spatial distribution of suitable niches for flat oysters depends on the spatial variability in metabolic performance (survival, growth, reproduction) and life-history events such as successful spawning and settlement which are linked to substrate suitability. Combining life-history process indicators into one habitat suitability indicator enables the identification of areas suitable for flat oysters, including the presence of hotspots (HSI > 0.7), with very high suitability for flat oysters (Figure 4).

Hotspots occur in coastal or nearshore areas. In and around Ireland, hotspots for flat oysters only occur in the south east on the coasts of Wexford and Wicklow. In England and Wales, some coastal areas can specifically be highlighted as hotspots, such as the coastal areas close to Liverpool and Blackpool, the outer Severn estuary around Bristol, Cardiff and Swansea, the Solent, the Blackwater estuary in Essex and the Wash. On the coast of northern France, hotspots exist in the wider Bay of the Seine and off the coast of Basse Normandie. In Belgium, hotspots exist in the southern Wester-Scheldt estuary, and on the offshore gravel beds. In the Netherlands, hotspots occur off the coast of Groningen. In Germany, hotspots occur around the East Frisian islands, and in and around the area between Helgoland and the West Frisian Islands. In Denmark, hotspots occur off the National Park Vadehavet.

4 | DISCUSSION

4.1 | General

Site suitability studies for flat oyster beds have been performed at national and regional levels and are generally correlative niche models that statistically link environmental conditions to absence/presence data of reefs (Robinson et al., 2017; Kamermans et al., 2018; Bennema, Engelhard & Lindeboom, 2020; Pogoda et al., 2020b; Bergström et al., 2021). Although correlative niche models are useful tools for identifying niches, they are often inconsistent when establishing the niche for endangered species for which presence data are scarce; or unreliable when using historical datasets. The use of historical datasets for correlative niche modelling is potentially problematic for two reasons: (i) historical data are often incorrect, as shown by Bennema, Engelhard & Lindeboom (2020) in the case of flat oysters; and (ii) climate change has altered species distribution in the North Sea (Kröncke et al., 2011), so relating historical presence data to environmental data from contemporary climate conditions will result in the identification of the wrong environmental space deemed suitable for the species (Sillero et al., 2021).

In addition, correlative niche models identify a set of environmental factors linked to species presence data. Which factors to include in the analysis, and the relative importance of these factors differs between studies and sites. van Duren, Kamermans & Kleissen (2022) tested a set of 10 environmental factors, Pogoda et al. (2020b) included six environmental factors while de Mesel et al. (2018) included three environmental factors in their habitat suitability studies.

A complete mechanistic niche model, by contrast, includes all known influences of the environment on the metabolism of the individual and generates traits that are easy to evaluate with regards to suitability. Suitability indicators such as fitness and reproductive output are calculated based on a combination of factors that change over time and space. Therefore, DEB-based mechanistic niche models enable spatio-temporal estimation of the variability of the condition of the individual and therefore can explain, for example, summer or winter mortalities, starvation, or failed reproduction events.

4.2 | Northern Europe's suitability for the flat oyster

The suitability of Northern Europe's marine environment for the flat oyster is limited by various factors. In the north and west of the research area, no flat oysters are expected to occur in offshore and nearshore waters because summer temperatures never reach the spawning threshold of 15°C. Presence data (observations of flat oyster habitats) in northern latitudes (Olsen, 1883; SS, 1889), are limited to shallow inshore and coastal habitats where seawater temperature does exceed the spawning threshold in summer (these environments are not covered by this study). Therefore, suitable locations for flat oysters are limited to coastal and inshore environments in Scotland, Ireland and the eastern coast of England (personal communications, Prof. William Sanderson and Oliver Tully). Where the current study used a threshold of 15°C, various spawning temperature thresholds have been recorded for flat oysters (Mesel et al., 2018). Oysters from the offshore deep water beds in the English Channel and the Helgoland Bank were historically assumed to release spawn at colder temperatures (Korringa, 1957). Unfortunately, these populations that historically thrived in colder waters no longer exist (Thurstan et al., 2013; Bennema, Engelhard & Lindeboom, 2020). Thermo-tolerance and temperature spawning thresholds should be examined when considering translocating flat oysters for restoration. Besides a temperature threshold, several studies recommend the use of temperature-sum (i.e. the accumulated temperature when higher than a threshold temperature, measured in 'degree-days') as a predictor for reproduction timing (Maathuis et al., 2020; Chapman et al., 2021). Nevertheless, temperature-sum is location dependent (Chapman et al., 2021) and non-mechanistic, so can therefore not be used in spatial applications. For example, Maathuis et al. (2020) state that in the Oosterschelde, The Netherlands, a temperature sum of 493–661 degree-days indicates the first larval peak, while in Lake Grevelingen, the first larval peak is expected at a temperature sum of between 313 and 1,100 degree days. Bernard, de Kermoysan & Pouvreau (2011) modified the DEB model to incorporate gonad development in spring and predicted that spawning time is based on a gonado-somatic index as well as a temperature threshold. Including this adaptation to the flat oyster DEB model would optimize estimates of the timing of spawning events.

Unsuitable feeding conditions occur in areas bordering the Atlantic Ocean due to food deprivation. Bottom layers in deeper waters where thermal stratification is strong receive less phytoplankton. Coastal areas that are highly influenced by river runoff are unsuitable for flat oysters as low salinities reduce filtration and ingestion rates. Aside from these factors, suitability is strongly limited by substrate. Flat oyster larvae are able to settle on shell, bedrock, cobble, gravel, boulders, stones or artificial hard substrate (Barry, 1981; Héral & Deslous-Paoli, 1991; Perry & Jackson, 2017). Historically reefs were often present in habitats where hard, muddy or clay sediments prevail (Laing, Walker & Areal, 2005; Perry & Jackson, 2017; Christianen et al., 2018). There are various hypotheses as to why sandy sediments are unsuitable for example:

(ii) increased near-bed flow over smooth, flat sandy bottoms decreases settlement success (Rodriguez-Perez, 2020); or (ii) high bottom sheer stress in combination with sandy sediment results in a mobile sea bed and resuspension of sand, which can cause burial of reefs, or inhibition of feeding (Laing, Walker & Areal, 2005; Kamermans et al., 2018).

4.3 | Completing the theoretical niche

The current study focuses on establishing the theoretical niche of the European flat oyster based on the DEB model. The DEB model successfully links environmental variables to the metabolic performance of individuals. The DEB forcings included in this study were chlorophyll *a*, seawater temperature and salinity. Several other environmental variables such as oxygen, suspended particulate matter, current speed, shear stress and food quality, are known to influence oyster metabolism and including these variables in future iterations will complete the theoretical niche of flat oysters (Bennema, Engelhard & Lindeboom, 2020). However, these variables are not included in this analysis at present because: (i) no scientific observations are currently available to mechanistically link additional variables to the metabolic performance of flat oysters; (ii) management strategies can influence variables such as current speed and shear stress; and (iii) these variables are not expected to influence the metabolism in the geographical range researched in this publication.

The flat oyster's metabolic response to hypoxia has not been studied, but marine bivalves in general can tolerate low oxygen concentrations (Vaquer-Sunyer & Duarte, 2008) (lethal concentration-50 of 1.42 mg O_2 L^{-1} and a lethal time-50 of 412 h), The study area is typically well-oxygenated, and therefore hypoxia is not expected. Limited information is available regarding the tolerance of flat oysters to suspended solids. Presence-absence data (unpublished dataset Historical Ecology working group NORA) suggest that flat oysters are resilient to high concentrations of suspended material. Duchêne, Bernard & Pouvreau (2015) gave an upper limit of 50 mg L^{-1} while Hutchinson & Hawkins (1992) gave a negative correlation between filtration rate and particulate organic matter (algae) concentrations of 5 to 10 mg L^{-1}. Oysters grown in the Dutch part of the North Sea are often exposed to conditions well exceeding 50 mg L^{-1} (Kamermans et al., 2018) but data are too scarce to calibrate and include a particle selection algorithm (Kooijman, 2010) in the proposed DEB model. Current speed can affect filtration rates (Walne, 1961), but more importantly, current speed and related shear stress are factors that can affect settlement success. These factors are variable on a small scale and restoration practices (e.g. deployment of cultch, artificial reefs, scour protection material) and local seabed characteristics (e.g. presence of boulders, rocks, banks) can greatly influence these factors. The resolution of this study is not compatible with the scales at which current speed or shear stress influence the oyster's life cycle and therefore these factors have not been included.

4.4 | Suitability for flat oyster reef formation

The current study evaluates the suitability of northern European waters for flat oysters, indicating which locations have a set of environmental conditions that are potentially suitable for oysters to survive, grow and reproduce. Nevertheless, suitability for an individual is not the same as suitability for populations; and for population numbers to increase, additional environmental conditions will have to be present (e.g. low predation pressure, swarming patterns that support self-recruitment). Since populations exist of individuals, populations will always occur at locations that are suitable for individuals, and reefs should therefore be present at locations indicated as suitable in this study.

Historical and current flat oyster reefs (Olsen, 1883; Lübbert, 1906; Gercken & Schmidt, 2014; Mesel et al., 2018) generally correspond to the hotspots identified in this study (Figure 1a). This can be exemplified using Olsen's historical map (Olsen, 1883), which shows large areas where oyster reefs were historically present. However, according to Olsen, oyster beds were found on sandy substrate (e.g. parts of the Oyster Grounds in Germany and The Netherlands, the Doggerbank, and Belgian coastal areas), which does not correspond with the assumptions related to settlement proposed in this study. Olsen also reports the presence of nearshore oyster reefs off the north east of England and the east of Ireland, which were areas deemed unsuitable (HIS < 0.3) in this study, and Bennema, Engelhard & Lindeboom (2020), have shown that Olsen's historical distribution map cannot be regarded as an unambiguous source and locations of some oyster beds are questionable. A more detailed map of deep-sea reefs in the English Channel frequently visited by oysterman M. H. Polley (Smaal et al., 2015) corresponds with the results of this study, and all historical reefs overlap with hotspots indicated in this study. The oyster beds mapped by Gercken & Schmidt (2014) in the German Bight, largely overlap with the presented hotspots (Figure 4), although some reefs are located on sandy substrate. Also, the current distribution of reefs in the English Channel (Mesel et al., 2018) corresponds fully with the results of this study.

4.5 | Towards a realistic niche model for habitat restoration

To establish models that predict the suitability for flat oyster populations, there is a need to extend the current theoretical niche model towards a realistic niche model by integrating population, dispersal and ecosystem models. Where a theoretical niche model only includes the physical and biological environment, and only estimates suitability on an individual level, realistic niche models also include species interactions (often in the form of competition and predation) and connectivity.

Predation is challenging to quantify in the field (Smaal et al., 2015). Oysters are preyed upon by a variety of species, and often experience high levels of predation from starfish (such as *Asterias rubens*), shore and edible crabs (*Carcinus maenas* and *Cancer pagurus*), and predatory snails such as the sting winkle (*Ocenebra erinacea*) and the common whelk (*Buccinum undatum*) (Smaal et al., 2015; Perry & Jackson, 2017; Mesel et al., 2018). The invasive American oyster drill (*Urosalpinx cinerea*) predates almost exclusively on oyster spat, leading to low levels of survival in young oysters where *U. cinerea* are prevalent (Fey-Hofstede et al., 2010; Perry & Jackson, 2017; Smaal et al., 2017). Young oysters (<3 cm) have thin, weak shells, which are easily penetrated by predators (Gercken & Schmidt, 2014). More work is required to understand and quantify the effect of predation of population dynamics.

Complex interactions leading to interspecific competition are again difficult to quantify but can influence both survival and growth of native oysters (Smaal et al., 2015). Two major types of competition act upon oysters: (i) competition for food; and (ii) competition for settlement area. Other filter feeding organisms compete with oysters for food suspended in the water column. Competitors for settlement space include but are not limited to tube-building polychaetes (*Sabellari*a sp. and *Spirobranchus triqueter*) barnacles (*Balanus crenatus*), anthozoans, ascidians and bryozoans (Mesel et al., 2018). Perhaps the most impactful form of competition is through the introduction of the invasive American slipper limpet (*Crepidula fornicata*) (Helmer et al., 2019; Preston et al., 2020). This species was brought to Europe from North America in the late 1800s through the expansion of commercial aquaculture of the Pacific oyster (*Magallana gigas/ Crassostrea gigas*) and Eastern oysters (*Crassostrea virginica*). Once introduced, *C. fornicata* populations expanded rapidly, and competed with the native oyster for both food and settlement area (Perry & Jackson, 2017). The Pacific oyster itself is also thought to compete with native oysters for food (Zwerschke et al., 2018; Ezgeta-Balić et al., 2020). Some studies, however, suggest that this competition is outweighed by the benefits Pacific oysters bring in increasing stability of the biogenic reef system and providing settlement area, which benefits the native oyster (Christianen et al., 2018).

Connectivity with broodstock is also important to include when determining suitable locations for reef restoration. Broodstock may be naturally occurring reefs or beds, broodstock can also be installed to support restoration projects. In addition, aquaculture sites can also provide larvae to support restoration efforts. Larval connectivity and hence connectivity between adult populations is determined primarily by abiotic factors such as tides, current velocity and trajectory.

When population models that include inter-individual and ecosystem interactions are established, it will become possible to quantify and predict population dynamics. Evaluating location-specific population dynamics will allow accurate site selection and will also enable the evaluation of restoration management strategies in the long term.

5 | CONCLUSION

With increasing interest for flat oyster habitat restoration in northern Europe, the development of site selection tools becomes essential. This coupling of an individual based DEB model with biogeographical datasets provides information on flat oyster fitness, growth potential,

reproductive output and timing of reproduction events on a temporal and spatial scale. Applying this theoretical niche model to northern Europe's offshore and nearshore waters enables the identification of locations that are unsuitable for flat oysters and therefore for flat oyster reef restoration. This model also identifies hotspots where environmental conditions are highly suitable for flat oysters. These hotspots for individuals generally correspond to locations where historical populations were present. The theoretical niche model used in this study can be effectively applied to identify suitable locations outside of the research areas (inshore and coastal areas or areas outside of the geographical range). Further research is required to identify suitable locations for flat oyster populations or flat oyster reef restoration using realistic niche models, which are extensions of theoretical niche models.

AUTHOR CONTRIBUTIONS

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CONFLICT OF INTEREST STATEMENT

The authors declare that there is no conflict of interest.

DATA AVAILABILITY STATEMENT

All data has been submitted as supplementary information.

ORCID

Brecht Stechele https://orcid.org/0000-0001-8450-1133
Nancy Nevejan https://orcid.org/0000-0001-6566-4607

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.